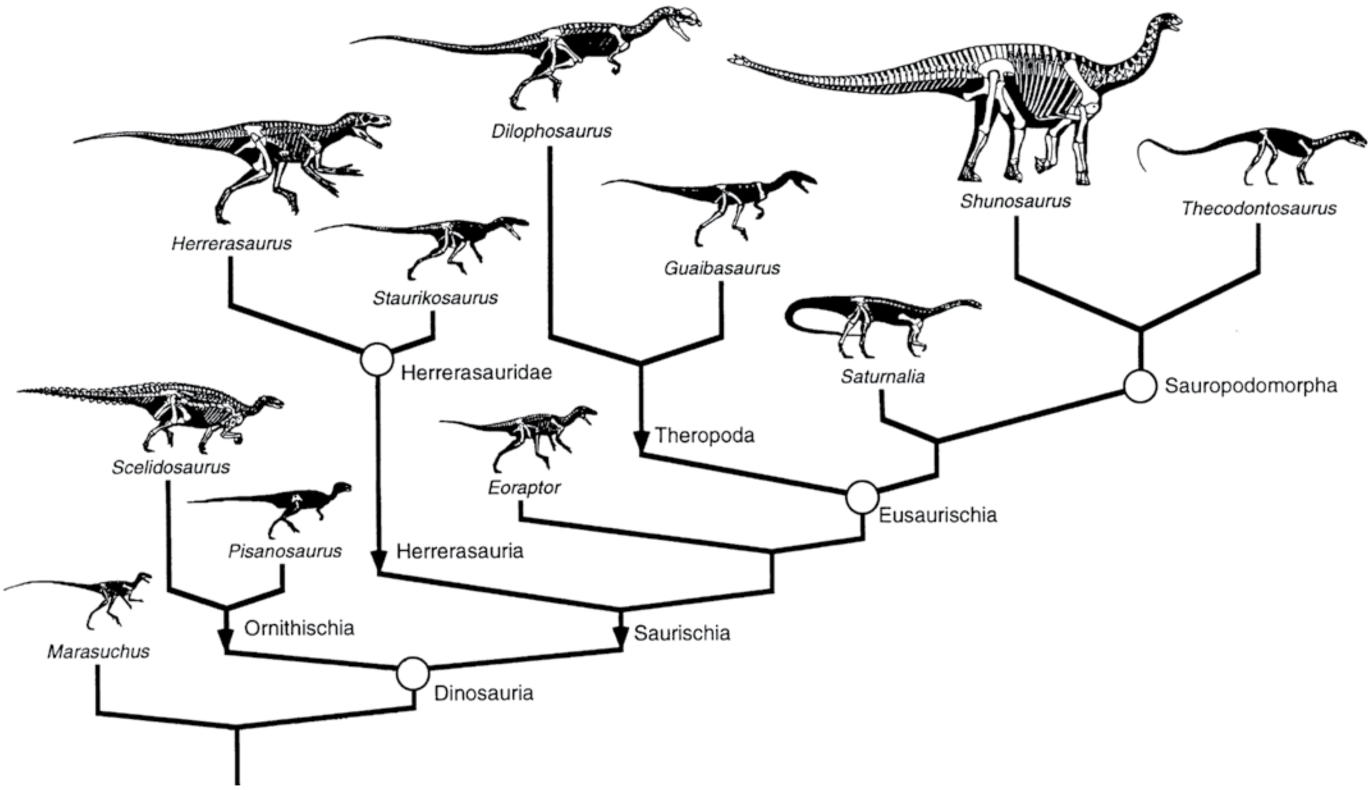


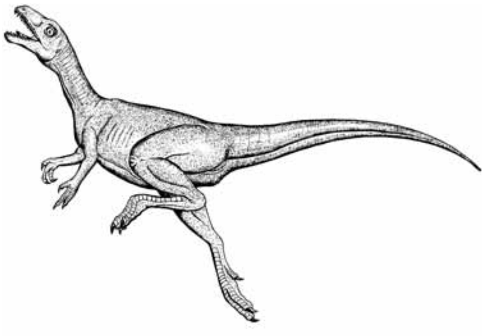
18.1. Cladogram showing suggested relationships of the basal dinosaurs.

Courtesy of Max Langer.

Origin and Early Evolution of Dinosaurs

18

Michael J. Benton



The dinosaurs arose in the Triassic, and probably during the Early to Middle Triassic. They entered a world far different from the typical Age of Dinosaurs scenes, a world in which the dominant herbivores were synapsids (dicynodonts and chiniquodontids) and rhynchosaurs, and carnivores were cynodonts and basal archosaurs of various kinds, previously called thecodontians (see Chapter 17, this volume). Into this world came the dinosaurs, initially small bipedal carnivores. They rose to dominance at some point during the second half of the Triassic. Certainly, by the end of the Triassic Period, dinosaurs were abundant and reasonably diverse, and all the major lineages had emerged and diversified.

Since 1980, paleontologists' views have changed dramatically, and new specimens and new methods have revolutionized our understanding of the origin of the dinosaurs. Most important has been the widespread use of cladistics as the key tool in disentangling the tree of life (see Chapter 11, this volume). Second, new, high-precision methods of dating the rocks give a much firmer timescale of events. There are still debates, however, about the relative importance of different groups of land vertebrates through the Triassic and the kinds of ecological processes that might have been involved in the rise and initial expansion of the clade Dinosauria.

Three key topics will be explored here: phylogeny (defining what is a dinosaur, spurious early records, the first dinosaurs), geology (dating the rocks), and models (how evolutionary radiations happen).

Definition of the Dinosauria

Richard Owen assumed in 1842 that his new group, the Dinosauria, was a real group, a monophyletic group, or a clade, in modern parlance (see Chapter 2, this volume). In other words, he assumed that the Dinosauria had a single ancestor, and that the group included all the descendants of that ancestor. This view was commonly held during most of the nineteenth century, but it was shaken by Harry Seeley's demonstration in 1887 that there were two major dinosaur groups, the Saurischia and Ornithischia, distinguished by the nature of their pelvic arrangements (see Chapter 3, this volume).

Perhaps, thought Seeley, the Saurischia and Ornithischia were distinct evolutionary branches that had arisen from separate ancestors. Seeley was merely espousing a commonly held view at the time called the persistence of types, a view promoted especially by Thomas Henry Huxley. The idea was that large changes in form could not happen readily in evolution, and the fossil record showed how major groups retained their main characteristics for long periods of time. Hence, paleontologists had to look for very long periods of initial evolution that led up to each major group, and often these initial spans of evolution were missing from the fossil record.

Seeley's view dominated during most of the twentieth century, and many dinosaur paleontologists made it even more complex. Not only had the Saurischia and Ornithischia evolved from separate ancestors, but so too had some of the subdivisions within those two groups, probably the two saurischian groups, the Theropoda and Sauropodomorpha, and possibly even some of the main ornithischian groups known in 1900, the Ornithopoda, Ceratopsia, Stegosauria, and Ankylosauria. In the end, the dinosaurs became merely an assemblage of large extinct reptiles of the Mesozoic that shared little in common. Hence, dinosaurs were seen as a polyphyletic group, deriving from two, three, or more sources among the basal archosaurs (reviewed in Benton 2004).

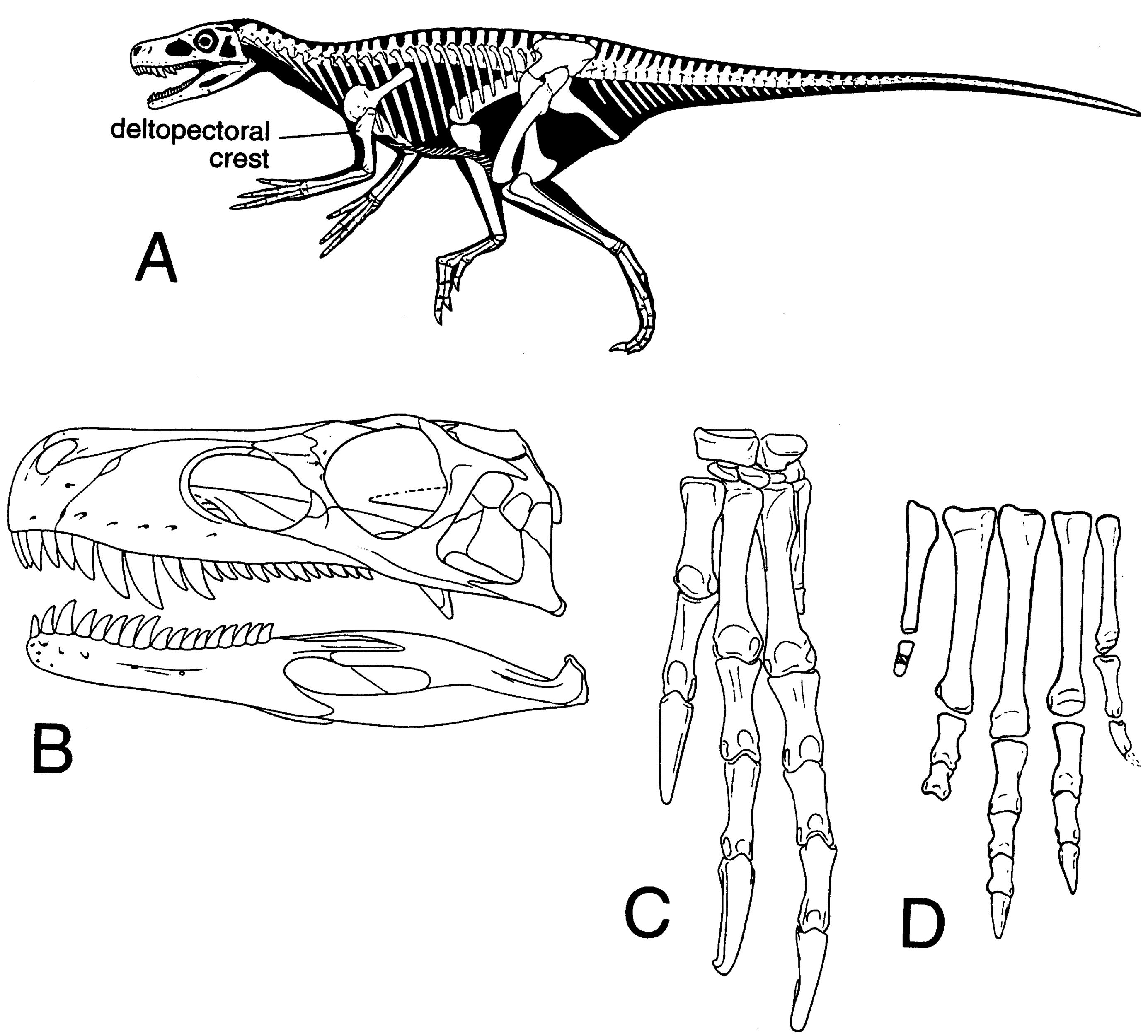
The collapse of the polyphyletic view came quickly and dramatically in about 1984 (Fig. 18.1). This had been presaged in short papers by Bakker and Galton (1974) and Bonaparte (1976), who saw many unique characters shared by both saurischian and ornithischian dinosaurs. Some brief papers published in 1984 were followed by more substantial accounts (Gauthier 1986; Sereno 1986; Novas 1989, 1994; Benton 1990); all applied strictly cladistic approaches to the data, and they independently agreed strongly that the Dinosauria of Owen (1842) is a monophyletic group, defined by a number of synapomorphies, including the following:

- Possible absence of a postfrontal bone (Fig. 18.2B).
- Jugal branching backward into two distinct processes to contact the quadratojugal (Fig. 18.2B).
- Temporal musculature extending anteriorly onto the skull roof, marked by a distinct fossa on the frontal bone.
- Epipophyses (additional facets on the postzygapophyses) on the cervical vertebrae.
- Elongate deltopectoral crest on the humerus (Fig. 18.2A).
- Possible three or fewer phalanges in the fourth finger of the hand (Fig. 18.2C).
- Fully open acetabulum (Figs. 18.2A, 18.3A).
- Possible brevis shelf on the ventral surface of the postacetabular part of the ilium.
- Asymmetrical fourth trochanter with a steeply angled distal margin on the femur.
- Articulation facet for the fibula occupying less than 30% of the transverse width of the astragalus.

Three of these 10 characters are listed as "possible" because incomplete knowledge of basal dinosauromorphs such as *Marasuchus* and *Eucoelophysis* makes their placement uncertain (Benton 1999, 2004; Langer and Benton 2006; Brusatte et al. 2010; Langer et al. 2010; Nesbitt 2011).

Many other dinosaurian features arose lower down the cladogram in close outgroups of Dinosauria, such as *Marasuchus*, *Silesaurus*, *Eucoelophysis*, and Pterosauria (see Parrish, Chapter 17 in this volume). These include several characters that were given by Gauthier (1986), Benton and Clark

18.2. The early dinosaur *Herrerasaurus ischigualastensis* from the Ischigualasto Formation of Argentina. A, Skeleton in side view; B, skull in side view; C, left hand viewed from above; D, right foot viewed from above. A–C, based on Sereno (1994); D, based on Novas (1994).

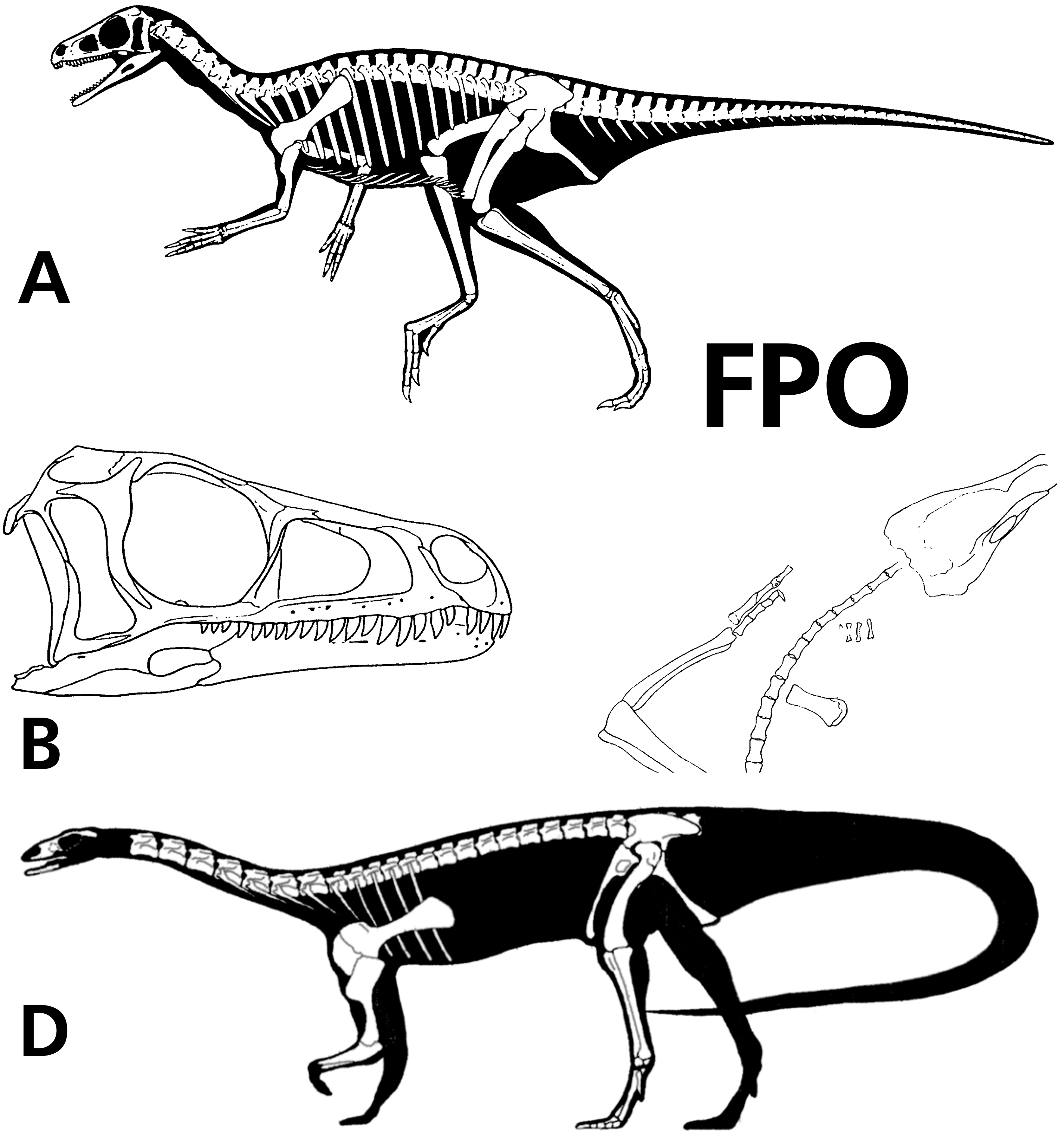


(1988), and Novas (1996) as dinosaurian synapomorphies: elongate vomers, an elongate scapula, a symmetrical hand, three or more sacral vertebrae, and the ascending astragalar process and attachment site on the anterior face of the tibia. These have been dropped because they are seen in other basal archosaurs or they are not convincingly present in all dinosaurs—for example, *Herrerasaurus* has two sacral vertebrae, whereas ornithosuchids, *Scleromochlus*, *Silesaurus*, and Pterosauria apparently have three.

What Is the Oldest Dinosaur?

Over the years, many claims have been made about the date of the first dinosaurs. Earliest supposed records have been based on isolated bones, groups of bones, and footprints from Middle Triassic, Lower Triassic, and even Permian rocks. With a clear cladistic definition of the Dinosauria, it should now be possible to weed these out.

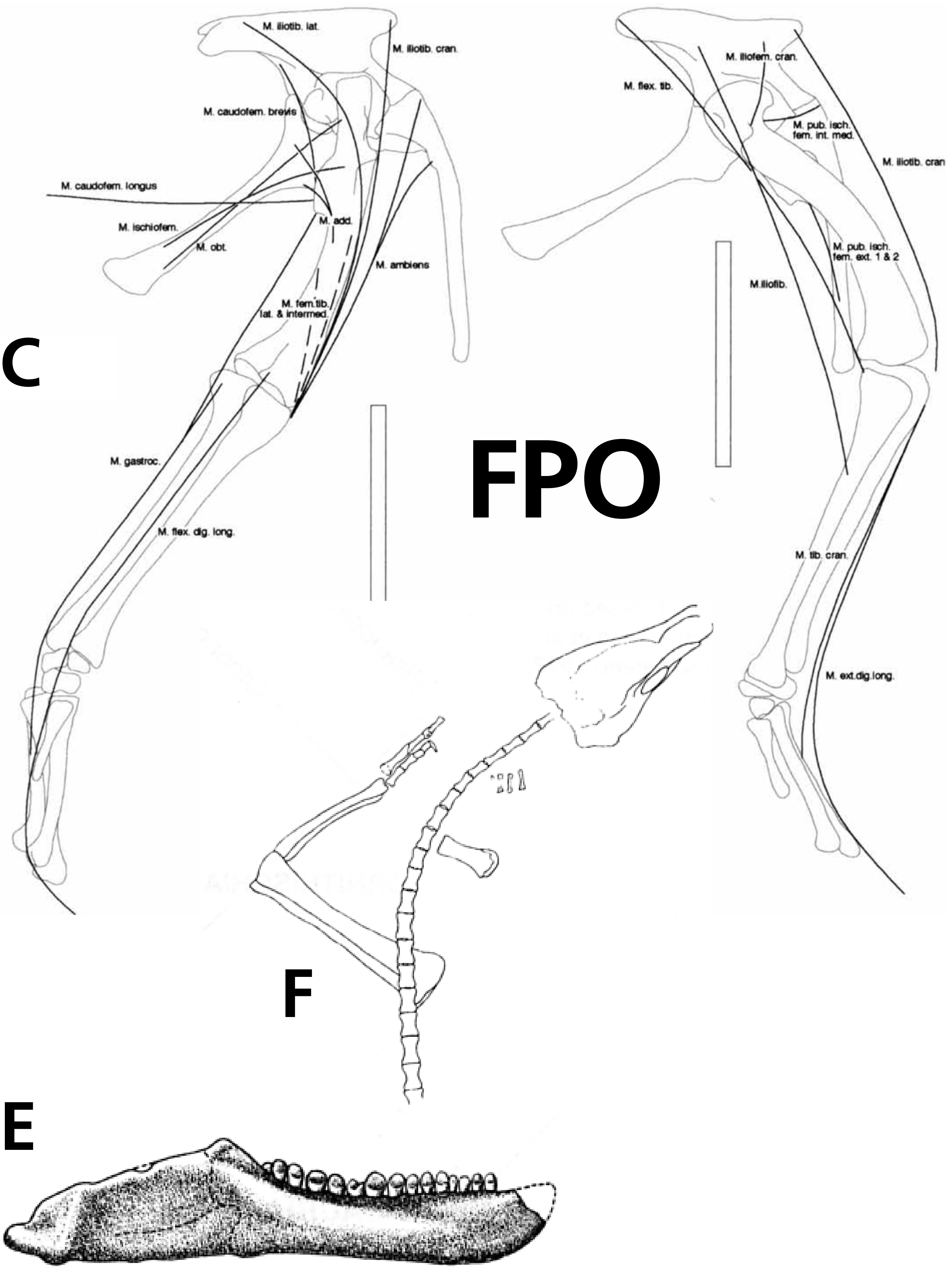
Many supposed early dinosaurs were described on the basis of isolated vertebrae, skull elements, and limb bones from the Triassic of Germany.



18.3. Early dinosaurs. A, B, Skeleton and skull of *Eoraptor lunensis* from the Ischigualasto Formation of Argentina, both in side view. C, D, Restored skeleton and hind limb of *Saturnalia tupinquim,* both in side view; the hind limb shows key muscles in backswing and forward positions of the stride. E, F, Partial skeleton and lower jaw of *Pisanosaurus mertii* from the Ischigualasto Formation of Argentina. A, B, Based on Sereno et al. (1993); C, D, based on Langer (2003); E, F, based on Bonaparte (1976).

Many of these elements have turned out to belong to prolacertiforms, to belong to rauisuchid archosaurs, or to be indeterminate (Benton 1986a).

Unusually early records of dinosaurs based on footprints extend back into the Middle and Lower Triassic, and even the Permian. These early finds have all been based on three-toed footprints, with no indication of a palm print, a good indication that the trace was made by a dinosaur standing up on its toes (the digitigrade posture), since most other Permo-Triassic tetrapods left plantigrade four- and five-toed prints. However, some of these


C
M. iliotib. lat.
M. iliotib. cran.
M. caudofem. brevis
M. caudofem. longus
M. ischiofem.
M. obt.
M. add.
M. ambiens
M. fem.tib. lat. & intermed.
M. gastroc.
M. flex. dig. long.
M. iliofem. cran.
M. flex. tib.
M. pub. isch. fem. int. med.
M. iliotib. cran
M. pub. isch. fem. ext. 1 & 2
M.iliofib.
M. tib. cran.
M. ext.dig.long.
FPO
F
E

early records have turned out to be either broken fragments of five-toed prints, invertebrate tracks (king crabs leave tiny "three-toed" impressions), or inorganic sedimentary structures (King and Benton 1996). Newer reports, however, identify convincing trackways of well-preserved three-toed digitigrade footprints from the Lower and Middle Triassic of Europe (Brusatte et al. 2011), and it is yet to be clarified whether these were made by dinosaurs, or more likely, by basal dinosauromorphs that had already adopted the upright digitigrade posture before Dinosauria emerged.

The report of the silesaurid dinosauromorph *Asilisaurus* in the late Anisian of Tanzania (Nesbitt et al. 2010) shows a much earlier origin of Dinosauromorpha than had been assumed previously (*Marasuchus* is Ladinian; *Silesaurus* and *Eucoelophysis* are Carnian and Norian, respectively), and suggests that true Dinosauria ought to extend back to that time as well, although convincing fossils to fill that gap have yet to be found.

The First Dinosaurs

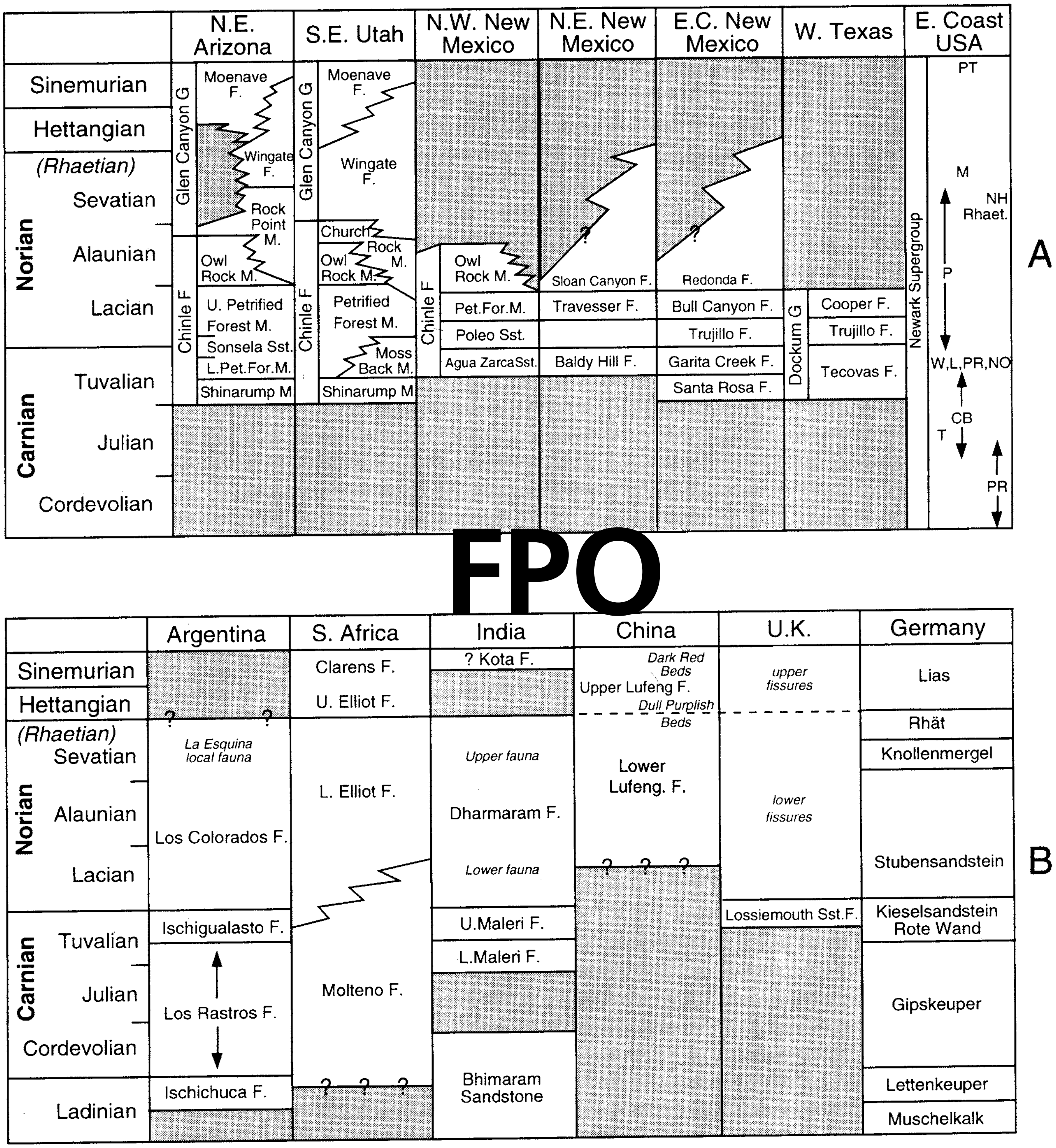
The first unquestionable dinosaurs are all Carnian in age, and late Carnian at that (Fig. 18.4). Although rare elements in their faunas, late Carnian dinosaurs are now known from many parts of the world, and these are detailed here. Most of the specimens are incomplete, and they will be summarized briefly first, followed by a fuller account of the superb South American early dinosaurs.

The only possible Carnian dinosaur from Europe is *Saltopus* from the Lossiemouth Sandstone Formation of Elgin, Scotland, but the single specimen is equivocal, and it is most probably a nondinosaurian ornithodiran (Benton and Walker 2011). From Africa comes *Azendohsaurus* from the Argana Formation of Morocco, based on a tooth (Gauffre 1993), but with such limited material that its identity is open to question. Some small prosauropod jaws from Madagascar (Flynn et al. 1999) have been presented as representing possibly the oldest known dinosaur. The remains are clearly dinosaurian; dating of the fossiliferous unit is uncertain but is likely Carnian. *Alwalkeria* from the Maleri Formation of India, based on a partial skull and skeleton, appears to be a small theropod (Chatterjee 1987).

A number of dinosaurs have been reported from the Carnian of North America, but most are based on isolated elements. However, many have been misidentified; most are likely from basal archosaurs or the basal diapsid *Trilophosaurus*, or are simply nondiagnostic (Irmis et al. 2007; Nesbitt et al. 2007). Named forms include the supposed theropods *Camposaurus*, *Caseosaurus*, and *Eucoeolophysis* and the ornithischian *Tecovasaurus*, which were all probably basal dinosauromorphs.

The late Carnian Santa Maria and Caturrita formations of Brazil, and the Ischigualasto Formation of Argentina have been much more productive than all the other units of the same age elsewhere in the world. This, as well as the fact that *Marasuchus* and *Lagerpeton*, close outgroups of the Dinosauria, are exclusively South American, suggests that the dinosaurs perhaps arose in that continent (Langer et al. 2010).

The Santa Maria Formation is the source of *Staurikosaurus pricei*, *Saturnalia tupinquim*, and *Teyuwasu barbarenai*, and the Caturrita Formation of *Guabiasaurus candelariensis*. The Ischigualasto Formation is even better known as the source of *Herrerasaurus ischigualastensis*, *Eoraptor lunensis*,



Eodromaeus murphi, and *Pisanosaurus mertii*. These Carnian dinosaurs were moderately sized animals, all lightweight bipeds, mostly 1–2 m long.

Staurikosaurus and *Hererrasaurus* are members of the Family Herrerasauridae. *Herrerasaurus* (Fig. 18.2) is known in some detail (Novas 1989, 1992, 1994; Sereno and Novas 1992, 1994; Sereno 1994) from 11 specimens, including some partial skeletons. These show a slender lightweight biped (Fig. 18.2) ranging in length from 3 to 6 m. The skull (Fig. 18.2B) is narrow and low. There is a sliding joint in each lower jaw, which allowed the jaws to flex and grasp struggling prey. The neck is slender. The forelimbs are less

18.4. Stratigraphy of vertebrate-bearing sequences in the Late Triassic and earliest Jurassic of North America (A) and various parts of Gondwanaland (B). The dates are based largely on comparisons of tetrapods with the German sequence by Olsen et al. (1987, 1990), Benton (1994a, 1994b), and others. CB = Cow Branch Formation; L = Lockatong Formation; M = McCoy Brook Formation; NH = New Haven Arkose; NO = New Oxford Formation; P = Passaic Formation; PK = Pekin Formation; PT = Portland Formation; T = Turkey Branch Formation; W = Wolfville Formation. Modified from Benton (1994a).

than half the length of the hind limbs, and the hand is elongated. Digits IV and V of the hand (Fig. 18.4C) are reduced, and the long penultimate phalanges of the hand indicate that it was adapted for grasping. There are two sacral vertebrae, one less than the normal dinosaurian condition, and the acetabulum is perforate. The femur has an inturned subrectangular head to fit into the pelvic bowl, and the tibia bears a cnemial crest. The foot (Fig. 18.2D) is digitigrade (the animal stands high on its toes), the calcaneum is reduced in size, and the astragalus bears an ascending process on the front of the tibia. Two other species from the Ischigualasto Formation, *Ischisaurus cattoi* and *Frenguellisaurus ischigualastensis*, are probably synonyms of *Herrerasaurus ischigualastensis*. *Staurikosaurus* is similar, but it differs from *Herrerasaurus* in the shape of the ilium and the distal outline of the tibia. *Eoraptor* is another small carnivorous dinosaur (Fig. 18.3A, B), but only 1 m long (Sereno et al. 1993). It has a lower snout than *Herrerasaurus*, there is no intramandibular joint, and the hand is shorter. Otherwise, *Eoraptor* differs from other basal dinosaurs in being generally more primitive rather than in possessing a great many unique features. Finally, *Eodromaeus murphi* has been described as a basal theropod (Martínez et al. 2011).

Panphagia protos, *Saturnalia tupinquim*, and *Teyuwasu barbarenai* were all described as basal sauropodomorphs. *Panphagia* (Martínez and Alcober 2009) is based on a single partial skeleton of an animal originally about 1.3 m long. It appears to be the most basal sauropodomorph so far described, sharing many features with *Saturnalia*, but also sharing hollow bones, sublanceolate teeth, and overall proportions with *Eoraptor*.

Saturnalia is known from three skeletons, only partly described so far (Langer et al. 1999; Langer 2003; Langer and Benton 2006). *Saturnalia* has small, leaf-shaped serrated-edged teeth, characteristic of prosauropods. There are at least two sacral vertebrae, and possibly a third, caudosacral, element. The pelvic elements are similar to other early dinosaurs: a short ilium, with an extended anterior process and a short posterior process, and a largely closed acetabulum. The pubis and ischium are long and slender, and the pubes meet in the midline in a deep pubic apron. The femur is sigmoid, with an inturned head, and the tibia is straight. The ankle is dinosaurian, and there are five digits on the foot, the fifth most reduced (Fig. 18.3C, D). *Teyuwasu* has been described only briefly on the basis of a dinosaurian femur and tibia (Kischlat 1999) and is probably not a validly established taxon.

Guabiasaurus candelariensis was described (Bonaparte et al. 1999, 2007) on the basis of some vertebrae, a scapulocoracoid, and hip and hind limb elements as a basal saurischian ancestral to the sauropodomorphs, although Langer (2000) suggested it might be a basal theropod. Two sacral vertebrae are preserved, but there was probably at least a third. The scapula is slender. The acetabulum is only partially open, and the hind limb elements are similar to those of *Herrerasaurus*.

Pisanosaurus is another tiny dinosaur (Bonaparte 1976) known from incomplete remains (Fig. 18.3E, F). The lower jaw (Fig. 18.3F) indicates that this specimen is an ornithischian dinosaur: the teeth are broad and diamond shaped, with a spatulate outer face, and there is a prominent shelf along the outer face of the lower jaw that marks the bottom of a soft cheek. The hind limb and foot appear dinosaurian, with a reduced calcaneum, an ascending process on the astragalus, and a functionally three-toed digitigrade foot.

Finally, *Eocursor parvus* is the most complete Triassic ornithischian yet described, based on a selection of skeletal elements, including skull fragments, spinal elements, pelvis, long leg bones, and unusually large grasping hands. Together, these indicate an animal about 1 m long (Butler et al. 2007; Butler 2010). The skull, poorly known in *Pisanosaurus*, is similar to Early Jurassic basal ornithischians in *Eocursor*, with a slightly inset tooth row (implying possible cheeks) and low, triangular teeth.

Relationships of the First Dinosaurs: Saurischia and Ornithischia

The systematics of the early dinosaurs has been disputed. For example, *Herrerasaurus* and *Staurikosaurus* were formerly regarded as primitive forms that were neither saurischians nor ornithischians. However, Sereno and Novas (1992, 1994), Sereno et al. (1993), Novas (1994), and Sereno (1994) argued that the Herrerasauridae and *Eoraptor* are basal theropods (Fig. 18.1), not least because they share the intramandibular joint (Fig. 18.4A). However, many other characters of theropods are absent. A new cladistic analysis of basal dinosaurs by Langer (2004; Langer and Benton 2006; Langer et al. 2010) places *Eoraptor* and Herrerasauridae as basal saurischians, successive outgroups to the clade compirisng Theropoda and Sauroporomorpha). In a further migration of *Eoraptor,* Martínez et al. (2011) class it as a sauropodomorph!

The Saurischia may be diagnosed by a number of characters of the skull, vertebrae, and limbs (Gauthier 1986; Sereno et al. 1993), including the following: the jugal overlaps the lacrimal; the thumb is robust; the bases of metacarpals III and IV lie on the palmar surfaces of manual digits III and IV, respectively; and the calcaneal proximal articular face is concave. The shape of the saurischian pelvis (Fig. 18.2A) is not useful diagnostically because this pattern is primitive and shared with the ancestors of the dinosaurs, and indeed with most other reptiles.

The Saurischia may include Herrerasauridae and *Eoraptor* as basal taxa, and then the two major clades, Theropoda and Sauropodomorpha. *Guaibasaurus* turns out to be the basal theropod, and *Panphagia* is the basal sauropodomorph, lying immediately below *Saturnalia* (Langer et al. 1999; Langer and Benton 2006; Brusatte et al. 2010; Langer et al. 2010).

The Ornithischia has long been recognized as a monophyletic group; ornithischians are diagnosed by the presence of triangular teeth, with the largest tooth in the middle of the tooth row. In addition, there is a coronoid process behind the tooth row in the lower jaw (Fig. 18.3F) and a reduced external/mandibular fenestra (cf. Fig. 18.3B, a saurischian, and 18.3F, an ornithischian). The classic ornithischian trademark, a predentary bone at the front of the lower jaw, is not seen in *Pisanosaurus* (Fig. 18.3F) or *Eocursor,* in both cases because of poor preservation, but both are widely accepted as basal ornithischians.

Stratigraphy

In early accounts of the history of vertebrate life on land during the Triassic (e.g., Colbert 1958; Romer 1970), the stratigraphic schemes were little more refined than lower, middle, and upper. Even in later accounts (e.g., Bonaparte 1982; Benton 1983; Charig 1984), there was little improvement, and most of the stratigraphic assignments of tetrapod-bearing rock units were based on comparisons of the vertebrates themselves. It is little use in attempts to study patterns of evolution to sequence faunas in terms of the nature of the faunas themselves!

The standard stratigraphic scheme for the Triassic rocks is based on ammonoids (Tozer 1974, 1979) and hence can only be applied to marine rocks. There is an independent palynological scheme, based on pollen and spores, for dating continental Triassic rocks (e.g., Visscher and Brugman 1981; Roghi et al. 2009; Smith 2009), but this scheme is not always reliable. Continental Triassic rocks have been correlated here and there with the marine scheme by using isolated tetrapod finds and other crossover evidence, and this has led to a more independent dating scheme for Triassic terrestrial tetrapod faunas (Ochev and Shishkin 1989; Benton 1991, 1994a, 1994b; Brusatte et al. 2010). Radiometric dating of volcanic layers associated with the Ischigualasto Formation (Rogers et al. 1993) gave a date of 227 million years ago (mya), which is in good agreement with biostratigraphic assumptions. This has been revised to a range of 231.4 and 225.9 mya, based on dating multiple volcanic ash beds (Martínez et al. 2011). Current work involving the establishment of further radiometric dates (e.g., Furin et al. 2006), as well as magnetostratigraphy (determining the reversed and normal magnetization of rocks through time; e.g., Muttoni et al. 2004) are providing firmer correlations between terrestrial and marine rocks (Brusatte et al. 2010; Langer et al. 2010), and these suggest that many vertebrate-bearing units formerly assigned to the late Carnian now move up to the early Norian, and the Norian stage extends in duration to some 20 million years. The correlations of major tetrapod faunas of the Late Triassic are shown in Figure 18.4.

Ecological Models for the Origin of the Dinosaurs

A major faunal turnover took place on land during the Late Triassic. Various long-established groups, sometimes termed paleotetrapods (synapsids, "thecodontians," temnospondyl amphibians, rhynchosaurs, prolacertiforms, procolophonids), were replaced by new reptilian types, sometimes termed neotetrapods (turtles, crocodilians, dinosaurs, pterosaurs, lepidosaurs, mammals). It had long been assumed that this replacement was a long, drawn-out affair involving competition (Bonaparte 1982; Charig 1984), with the dinosaurs leading the way in driving out the synapsids, rhynchosaurs, and "thecodontians." The success of the dinosaurs was explained by their superior adaptations, such as their upright posture, their initial bipedalism, their speed and intelligence, or their posited endothermy.

I have opposed this assumption of long-term competitive replacement (Benton 1983, 1986a, 1991, 1994a, 1994b, 2004). First evidence came from quantitative studies of tetrapod faunas through the Triassic (Benton 1983), which did not show a long-term decline of paleotetrapod groups and a matching rise of neotetrapod groups. Indeed, new groups generally did not supplant previously existing groups. The study revealed that there was a dramatic changeover from late Carnian and early Norian faunas that contain rare dinosaurs, to those in the mid- and late Norian (Fig. 18.4), where dinosaurs dominate.

Later studies (Benton 1986a, 1991, 1994b) clarified this changeover. Redating suggested that this event happened at the Carnian–Norian boundary, then dated at about 220 mya. Further redating (e.g., Muttoni et al. 2004; Brusatte et al. 2010) has moved the Carnian–Norian boundary down to 227–228 mya, but the turnover event that affected vertebrates remains at about 220 mya, now somewhere between the early and late Norian, as originally indicated using older conventions by Benton (1983).

During this terrestrial extinction event, the kannemeyeriid dicynodonts, chiniquodontids, traversodontids, and rhynchosaurs all died out or diminished sharply in diversity and abundance (single, isolated survivors of some of these groups in the later Norian hardly constitute continuing dominance!). These four families had made up 40–80% of all the late Carnian and early Norian faunas, representing the dominant medium- and large-size herbivores worldwide. Other groups that disappeared at this time were temnospondyl amphibians (Mastodonsauridae, Trematosauridae), archosauromorphs (Prolacertidae), basal archosaurs (Proterochampsidae, Scleromochlidae), and dinosaurs (Herrerasauridae, Pisanosauridae). Hence, 10 of the 24 late Carnian families died out (a loss of 42%), and continental tetrapod faunas were dramatically depleted in terms of diversity and abundance.

A detailed study of the Ischigualasto Formation by Rogers et al. (1993), subsequently updated by Martínez et al. (2011), confirmed the view that there was no long-term ecological replacement of paleotetrapods by neotetrapods because members of both assemblages coexist without evidence of a decline of the former and a rise of the latter. Dinosaurs appear early in the Ischigualasto sequence, but they never increase above a diversity of three or four species, nor a percentage representation of 6% of all specimens collected.

There were other extinctions during this time among marine organisms (foraminifera, ammonoids, bivalves, bryozoans, conodonts, coral reefs, echinoids, and crinoids; Benton 1986b; Hallam and Wignall 1997). At this time, there was a worldwide series of climatic changes from humid to arid (Simms and Ruffell 1990). These may have been triggered by events associated with the beginning of rifting of the supercontinent Pangaea. Major floral changes occurred too, with the disappearance of the *Dicroidium* floras of southern continents, and the spread worldwide of northern conifer-dominated floras. Perhaps the drying climates favored conifers over seed ferns such as *Dicroidium*, and perhaps the dominant Carnian herbivores were unable to adapt to new kinds of vegetation, and died out.

The origin and early expansion of dinosaurs has been assessed by comparisons of diversity and disparity change (Brusatte et al. 2008a, 2008b). Disparity is the morphological diversity of a group, representing body design, diet, and lifestyle. When dinosaurs and crurotarsans in the Late Triassic were compared, it emerged that crurotarsans were twice as disparate as dinosaurs (Fig. 18.6). In other words, the crurotarsans were experimenting with many more different ways to make a living, more so than the dinosaurs. These results show that during the first 30 million years of their history, dinosaurs were living alongside and sharing niches with a group (the crurotarsans) that was evolving at the same pace and exploring twice the number of different lifestyles. This pattern held across the entire 30 million years that dinosaurs and crurotarsans lived side by side. Thus, there is no evidence that dinosaurs were doing anything better than crurotarsans. Both groups were doing quite well, but it actually was the crurotarsans that were doing better in one key trait (disparity), as well as being more diverse and abundant.

First Radiation of the Dinosaurs

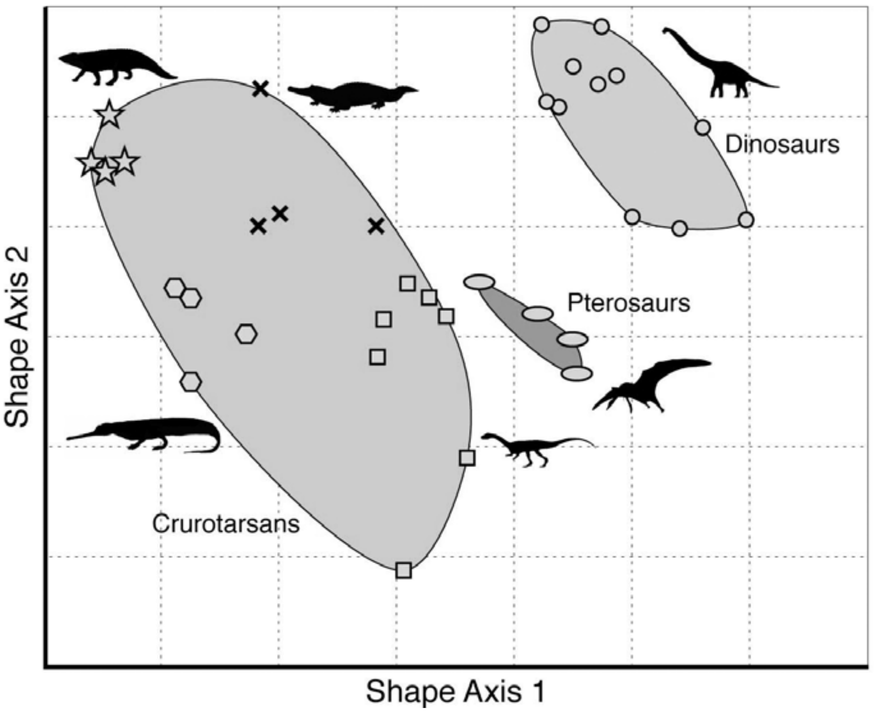
Dinosaurs diversified to a limited extent during the late Carnian and early Norian, and increasingly after the early Norian extinction event. In the middle and late Norian, for the first time, mass accumulations of dinosaur skeletons are found – for example, the famous death assemblage of several hundred individuals of the theropod *Coelophysis* at Ghost Ranch, New Mexico, in the Upper Petrified Forest Member of the Chinle Formation. For the first time too, dinosaurs became relatively diverse, and they began to exhibit that feature for which the group is famous: large size. Specimens of *Plateosaurus* from the Stubensandstein and Knollenmergel of Germany reached lengths of 6–8 m. Overall, dinosaurs had switched from being minor players in the late Carnian and early Norian, at faunal abundances of less than 6%, to being the dominant land reptiles, with abundances of 25–60% in the middle and late Norian.

The end-Triassic mass extinction event, 200 mya, had major effects on life in the sea and on land (Hallam and Wignall 1997). The end-Triassic event has been explained as the result of an impact, analogous to the Cretaceous–Tertiary impact that caused the final extinction of Dinosauria, by Olsen et al. (1990, 2002) and Bice et al. (1992). A major impact crater, the Manicouagan structure in Quebec, was identified as the smoking gun for a catastrophic extraterrestrial impact at the Triassic–Jurassic boundary (Olsen et al. 1990). Shocked quartz was found at a Tr-J boundary section in Italy (Bice et al. 1992), as well as an iridium anomaly and a fern spike in the eastern United States (Olsen et al. 2002), all three classic evidence for the Cretaceous–Tertiary impact. However, none of these indicators of impact at the Triassic–Jurassic boundary is particularly convincing. First, the Manicouagan impact structure was redated (Hodych and Dunning 1992) away from the Tr-J boundary (200 mya) with an age of 214 mya (Fig. 18.5). Second, the nature of the lamellae in the shocked quartz was not adequate to rule out other explanations, such as a volcanic source for the material (Bice et al. 1992). Third, the iridium anomaly and fern spike are modest in comparison with Cretaceous–Tertiary examples (Olsen et al. 2002).

Period	Stage	Boundary date (Ma)	**Events**
Jurassic	Hettangian		
Late Triassic	Norian	20	Triassic-Jurassic mass extinction
			214-Ma Manicouagan impact
		220	Carnian-Norian mass extinction
	Carnian		228-Ma Ischigualasto dinosaurs
		230	

Note: Ma = million years ago.

18.5. Timescale of major events in the Late Triassic, showing the time line of the early dinosaurs from the Ischigualasto Formation of Argentina, the current date of the Manicouagan impact (shaded circle, and age range indicated), and the two mass extinctions (asterisks). Evolution of the major archosaur groups through the Triassic, showing the major groups plotted against their occurrences in time, and with postulated relationships, based on cladograms in Benton (2004). Ans. = Anisian; J. = Jurassic; Lad. = Ladinian; P. = Permian; Rht. = Rhaetian.



18.6. The morphospace occupied by crurotarsans was much larger than that occupied by dinosaurs or pterosaurs during the Carnian and Norian (230–200 mya), the time when dinosaurs were supposedly outcompeting the crurotarsans. Note that the extremely small morphospace occupied by the Late Triassic pterosaurs reflects their uniform range of form. (Redrafted from Brusatte et al. 2008a.)

Current evidence suggests that the end-Triassic event was geologically sudden (Deenen et al. 2010) and probably closely linked to massive volcanic eruptions of the Central Atlantic Magmatic Province (Whiteside et al. 2010), which produced a few degrees of global warming (Hallam and Wignall 1997; McElwain et al. 1999; Whiteside et al. 2010). Global warming led to stagnation of the oceans with anoxia on the seabed, and a calcification crisis occurred as surfaced water became more acid. On land, the volcanic gases, mixed with atmospheric water, fell as acid rain, presumably killing plants in huge quantities, and so damaging the bases of food chains.

The global expansion of dinosaurs was evidently a three-step phenomenon, with splitting of the main lineages (Ornithischia, Theropoda, Sauropodomorpha) in the Carnian, expansion of dinosaurian diversity and abundance from two or three species and up to 6% of individuals in late Carnian and early Norian faunas to four or five species and 25–60% of faunal composition in the middle and late Norian, and finally radiation of further theropod and sauropodomorphs, as well as ornithischians in the earliest Jurassic.

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