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THE ORIGINS OF THE DINOSAURS†

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The dinosaurs were one of the most successful groups of animals of all time, dominating terrestrial faunas from the Late Triassic to the end of the Cretaceous (225–65 Myr.). Their success has often been attributed to competitive advantage of their gait or physiology in comparison with their ecological predecessors, the mammal-like reptiles, rhynchosaurs and thecodontians. Recent researches suggest, however, that the dinosaurs rose to dominance only after a major mass extinction event and that large-scale competition need not be invoked.

KEY WORDS: Dinosaurs, Triassic, competition, macroevolution, thecodontians, synapsids.

INTRODUCTION

One of the joys of palaeontology (the study of ancient life on earth) is that one's object of study are all dead and usually extinct. Without living representatives, it is possible to let the mind wander freely in imagining what they were like in life—how did they walk, how did they eat, what colour were they? However, non-palaeontologists have a more morbid interest in the life of the past. All they want to know is "why did they die out?" This is true of dinosaurs in particular, but I think that more than enough has been written on that subject recently. I will try here to tackle the diametrically opposite question of how the dinosaurs arose in the first place.

Interestingly enough, the origin of the dinosaurs is a subject on which most current books and papers are rather reticent. The author may state that it is hard to describe the origin of the dinosaurs because we don't know enough about the ecology of their early days. Another problem seems to be that no-one is very sure about just which the first dinosaur was, as there is great confusion about the relationships of the most primitive dinosaurs and their dinosaur-like ancestors. It is frequently argued, indeed, that the dinosaurs are not even a natural group, that they arose from a variety of different ancestors and have no particularly close relationship to each other.

These were the views that I was taught and the whole area of study seemed to be fraught with problems. However, in the past four or five years a number of palaeontologists, working both in North America and in Europe, have started to tackle two major aspects of the question of the origin of the dinosaurs, namely analyses of the major faunal replacements that took place at that time and of the evolutionary relationships of the earliest dinosaurs.

FAUNAL REPLACEMENTS IN THE TRIASSIC

The dinosaurs first came on the scene in some abundance in the Late Triassic, about

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215–225 million years ago. Palaeontologists recognised some time ago that this initial radiation of the dinosaurs was part of a major faunal replacement on the land, during which a whole assemblage of animals disappeared and a new assemblage came on the scene. Colbert (1949, 1958a, b) described the extinction of a range of early amphibians and reptiles, such as labyrinthodonts, procolophonids, "protorosaurs," rhynchosaurs, thecodontians and most mammal-like reptiles during the Late Triassic, or at the very end of the Triassic period at the Triassic-Jurassic boundary. These forms had dominated terrestrial faunas for millions of years in the Permian and Triassic periods. They were replaced by new groups, such as the lissamphibians (frogs and salamanders), turtles, lepidosaurs (lizards and their relatives), crocodiles, dinosaurs and mammals (Figure 1).

The key question is whether the faunal replacement in the Late Triassic was a long drawn-out affair which might have involved large-scale "competition" between the old and the new animals, or whether the replacement was opportunistic, in that the "old" animals became extinct and the "new" ones radiated into empty adaptive space. The great replacement event that took place 155 million years later, at the Cretaceous-Tertiary boundary, is generally reckoned to have been opportunistic, since the dinosaurs died out relatively abruptly and the small hairy mammals "took their chance" and evolved rapidly to take over many of the adaptive roles formerly held by dinosaurs. Very few people now believe the theory that the mammals directly

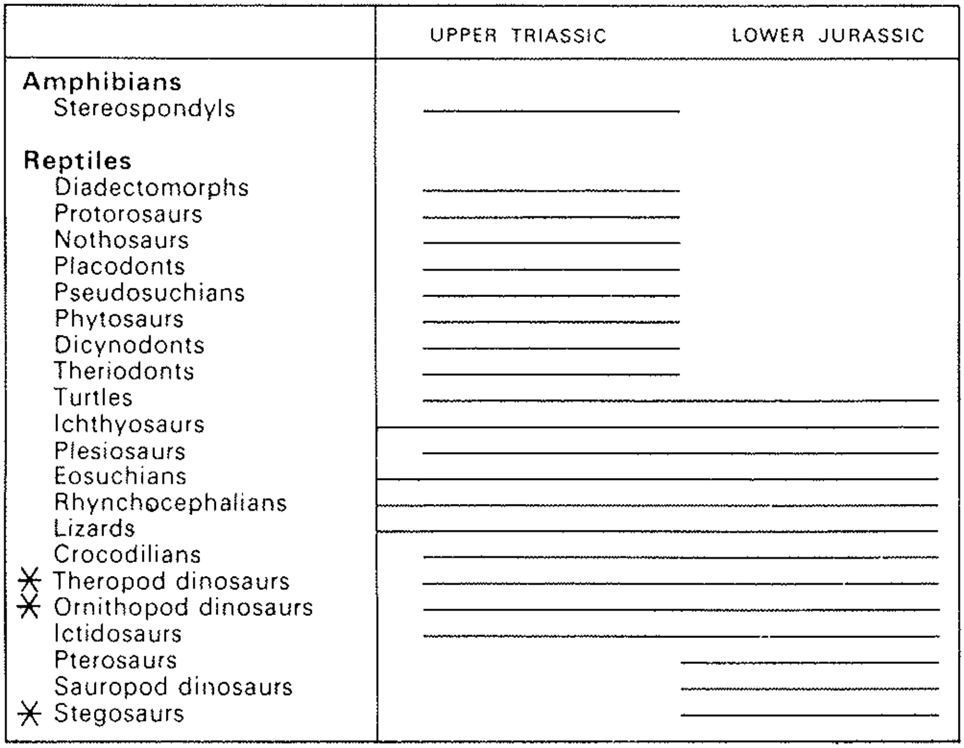

Figure 1 A mass extinction amongst non-marine tetrapods at the end of the Triassic has been recognized for a long time. Edwin H. Colbert summarised the major faunal turn-overs at that time which heralded the origin of the dinosaurs, pterosaurs, crocodiles, turtles and mammals. (After Colbert, 1966.)

competed with the dinosaurs and drove them to extinction by eating their food supplies, or preying on their eggs.

However, a large-scale competitive model has become rather entrenched in the literature on dinosaur origins. The development of this view can be traced in papers published after 1950. In 1949, Colbert recognized that the origin or radiation of several of the "new" groups in the Late Triassic and Jurassic did not result from competition. For example, the phytosaurs "were a highly successful and very dominant group of reptiles in the final phases of Triassic history," but they died out for unknown reasons. The crocodiles, which were already present as small terrestrial carnivores, radiated into various aquatic niches after the extinction of the phytosaurs, so competition was not responsible. However, in a later account, Colbert (1958a) concluded that some of the groups disappeared at the end of the Triassic because of competition with newly evolved forms. Thus, "eosuchians" (early "lizard-like" forms) "crowded out" the procolophonids, and the thecodontians (which include ancestors of the crocodiles and the dinosaurs) may have outcompeted the mammal-like reptiles. Colbert had special problems in accounting for the extinction of the thecodontians: "they were well adapted to their environment, and they were widely distributed over several continents in great numbers." He could not explain how the small early dinosaurs and crocodiles could possibly have "competed" with the thecodontians and the phytosaurs. However, by 1969 Colbert (1969, pp. 166–167) argued that the thecodontians were eliminated by competitive pressure from their descendants, the dinosaurs, and likewise, that the mammal-like reptiles "vanished because of the highly progressive nature of their descendants [the mammals]. They evolved themselves into oblivion."

In a typical competitive model (e.g. Charig, 1984), it is stated that in carnivorous niches, the thecodontians progressively replaced the mammal-like reptiles during the Early and Middle Triassic, and that the thecodontians in turn were replaced by the theropod dinosaurs as dominant meat-eaters. In herbivore niches, the mammal-like reptiles were replaced by a group of specialised plant-eating thecodontians, the aetosaurs, and by the rhynchosaurs, a group of remarkable beaked reptiles that were distantly related to the thecodontians. Finally, in the Late Triassic, the plant-eating prosauropod dinosaurs took over. In both cases, the whole relay of competitive replacements lasted for 10–35 million years (Figure 2A).

What competitive advantages did the "new" animals (e.g. the dinosaurs) have over the "old" (e.g. the mammal-like reptiles)? Several authors have linked the replacement to major environmental changes that were taking place in the Late Triassic. In particular, the habitats in which fossil reptiles and amphibians are found appear to have become more arid. The kinds of theories that have been presented for the competitive success of the dinosaurs over the thecodontians and the mammal-like reptiles depend on ideas about their physiology. For example, it was argued that dinosaurs were warm-blooded and that their naked skin allowed them to lose heat in the new arid climates (Cox, 1967, Crompton, 1968). The hairy mammal-like reptiles simply overheated. A related suggestion was that the dinosaurs, like living birds and many reptiles, excreted their waste as uric acid instead of as urea, which uses a great deal of water, as in living mammals. This was a key to water-retention in times of aridity (Robinson, 1971; Hotton, 1980). Some other authors have stated that the key competitive advantage of the dinosaurs was improved locomotor ability—an erect posture, which allowed greater speed than the primitive sprawling gait of their ancestors (Bakker, 1971; Charig, 1972, 1984). Further suggestions have been that the dinosaurs were fully warm-blooded, or endothermic (Bakker, 1971, 1972, 1980),

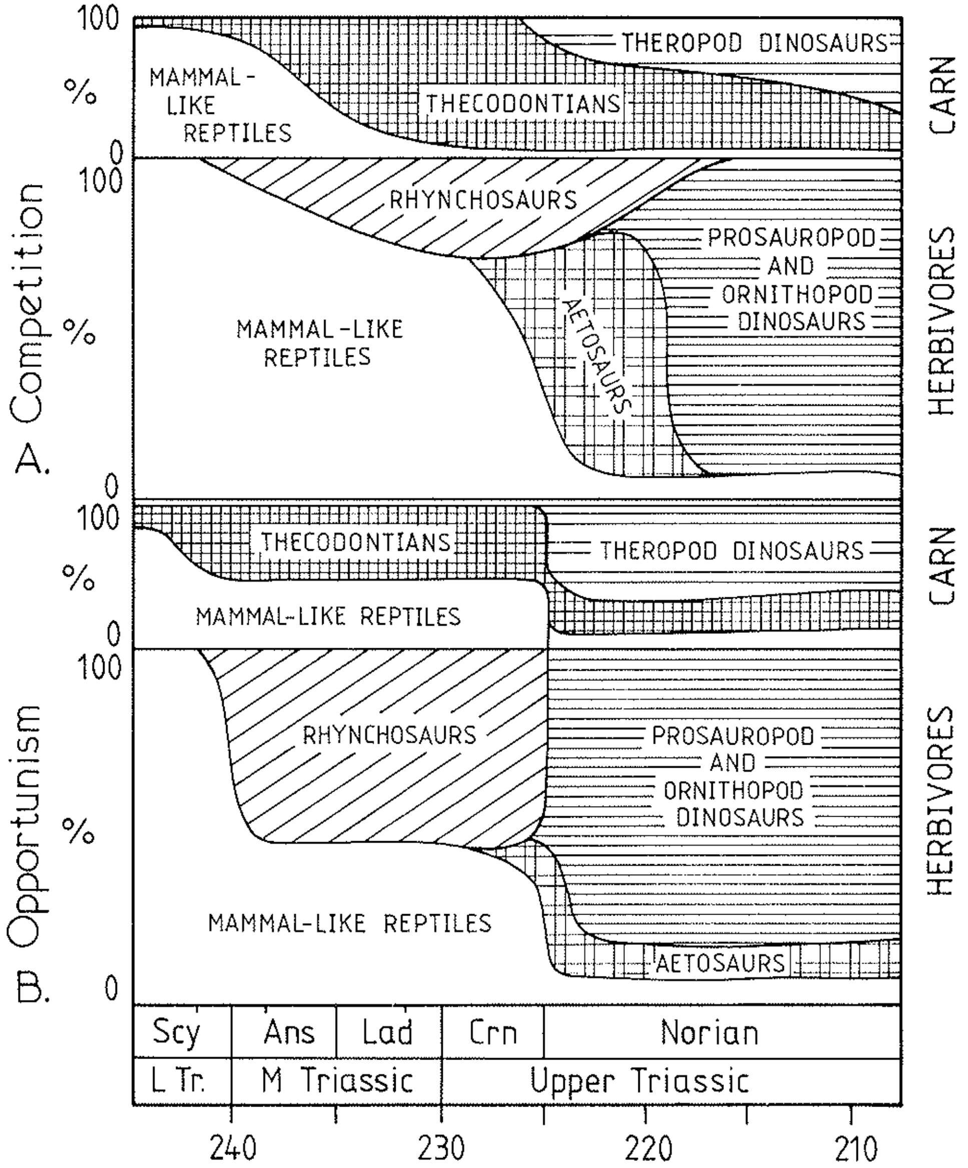

Figure 2 Two views of the evolution of Triassic non-marine tetrapods. According to one interpretation (*A*), the mammal-like reptiles were replaced over several million years by the competitively superior thecodontians and rhynchosaurs. These were replaced in turn by the dinosaurs. According to another interpretation (*B*), the mammal like reptiles were replaced in part, but not by overwhelming competition. The mammal-like reptiles, thecodontians and rhynchosaurs became largely extinct during the end-Carnian extinction event, and the dinosaurs then radiated opportunistically. These diagrams are based on assessments of the relative abundance of specimens within fossil faunas. Abbreviations: Ans Anisian; CARN Carnivores; Crn Carnian; Lad Ladinian; L Tr Lower Triassic; M Middle; Scy Scythian. Allowance has been made for the problems of selective preservation and fossilisation [After Charig, 1984 (upper); Benton, 1983a, b, 1986a (lower)].

or that they had a kind of warm-bloodedness that depended on their great body size, termed inertial homeothermy (Spotila *et al.*, 1973; Benton, 1979; Spotila, 1980). The list of "explanations" for the success of the dinosaurs could fill several pages. Is there any solution to this question of the origin and success of the early dinosaurs?

EXTINCTION AND OPPORTUNISM

The hypothesis that the origin of the dinosaurs resulted from their successful competition with all comers has been challenged. Several detailed analyses of the fossil record in the Triassic and Early Jurassic (Tucker and Benton, 1982; Benton, 1983a, b, 1984a, 1985a, b, 1986a, c; Olsen and Sues, 1986) now point to mass extinction and opportunism.

In one study (Benton, 1983a), an attempt was made to plot the relative abundances of the major groups of tetrapods (amphibians, reptiles and mammals) through the Triassic (245–208 million years ago). Details of the numbers of skulls, or of complete skeletons, in each major dated fauna around the world were compiled. It was then possible to calculate the percentage representation of each family at different times during this time span and to follow their relative fates (Figure 2B). It turned out that there was no evidence at all for competition. The carnivorous thecodontians never successfully took over from the carnivorous mammal-like, reptiles. Indeed, a wide range of families of thecodontians and mammal-like reptiles and the rhynchosaurs died out at the same time, about 225 million years ago. The dinosaurs, which were already present as rare faunal elements, then radiated widely during the next 5–10 million years. The extinction occurred clearly *before* the radiation, which seems to have been opportunistic, rather than competitive (Figure 2A, B).

Further evidence in support of this view has come from studies of mass extinction events in general and the Late Triassic event(s) in particular. Indeed, the Late Triassic mass extinction turns out to have been just as serious as the more famous end Cretaceous event. Sepkoski (1984) calculated that 23% of all marine families died out in the Late Triassic and certain groups were particularly heavily affected, such as the sponges, gastropods, bivalves, cephalopods, brachiopods and marine reptiles. In non-marine situations, freshwater fish and a wide variety of amphibians and reptiles disappeared as outlined above (see also Benton, 1985a, b). Terrestrial plants, however, were apparently little affected (Knoll, 1984).

The Late Triassic fossil record of non-marine tetrapod families has now been analysed in some detail (Benton, 1986a, c; Olsen and Sues, 1986; Olsen *et al.*, 1987), and two extinction events have been identified (Figure 3a), one at the end of the Carnian stage (225 million years ago) and one at the end of the Norian stage, at the Triassic–Jurassic boundary (208 million years ago). During each event, at least seven families disappeared, but the extinction rates for the end-Carnian event are the greater since the maximum time involved was less than for the end-Norian event (Figure 3b, c).

The evidence of a number of different studies points clearly to a major mass extinction amongst non-marine tetrapods at the end of the Carnian stage. The dinosaurs radiated extensively during the Norian and continued to diversify in the Jurassic, after the second, smaller, end-Norian event.

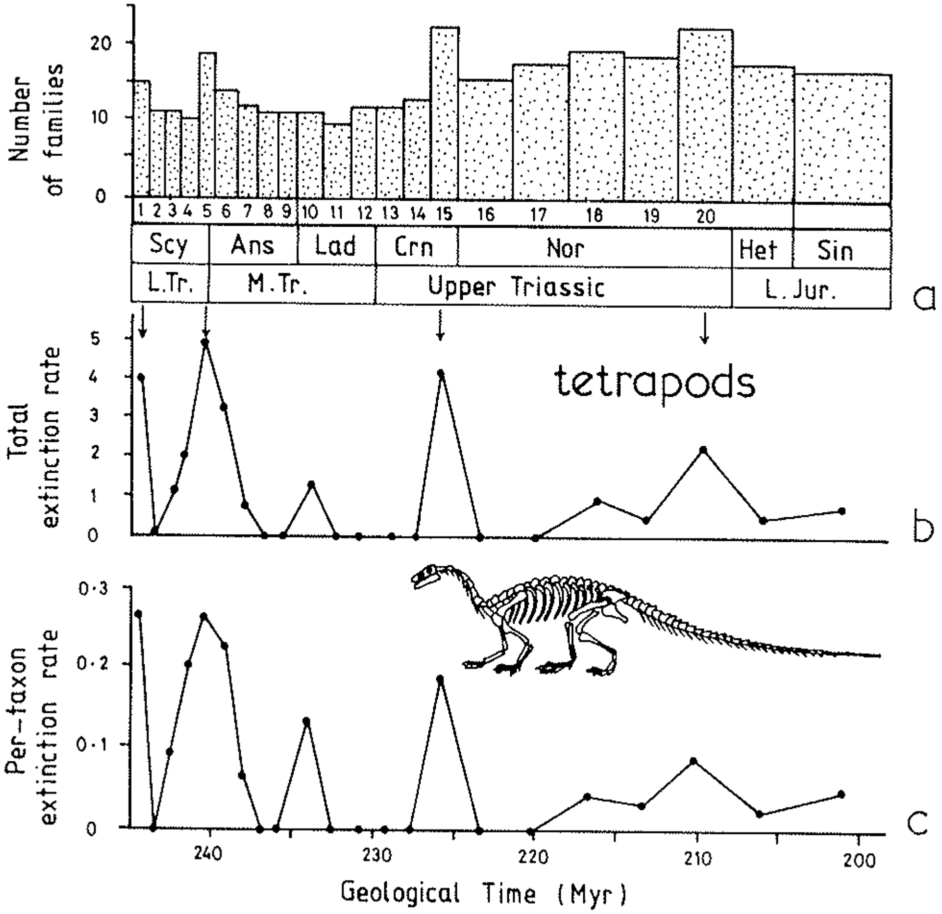

Figure 3 Mass extinctions amongst families of Triassic non-marine tetrapods. The total diversity (number of families), plotted against stratigraphic units, shows drops in the Early Triassic, at the end of the Early Triassic, at the end of the Carnian and at the end of the Norian (a). These drops correspond to high total extinction rates (= numbers of families dying out per million years) (b) and to higher per-taxon extinction rates (= numbers of families dying out per million years per number of families at risk) (c). Abbreviations: Het Hettangian; L. Jur Lower Jurassic; Nor Norian; Sin Sinemurian; others as in Figure 2.

REPTILES OF THE LATE TRIASSIC

The key episodes of faunal turnover about the time of the origin and radiation of the dinosaurs are represented in reptile-bearing geological formations in various parts of the world. Typical examples include the Santa Maria Formation of Brazil and the Ischigualasto Formation of Argentina. The faunal lists of both formations are similar and they are assigned similar dates, the Santa Maria being possibly slightly older (? Middle Carnian) than the Ischigualasto (? Middle–Late Carnian).

The dominant animals in both formations are species of the rhynchosaur *Scaphonyx*. This 1.5 metre long animal has a broad head with a downturned "beak," and the general bodily proportions of a pig. *Scaphonyx* probably fed on tough vegetation, such as the contemporary seed ferns, ferns, cycadophytes, horse tails and lycopods.

The other major plant-eaters of this time were the dicynodonts *Ischigualastia* and *Dinodontosaurus*, which were massive cow-sized herbivores, the last of the large mammal-like reptiles. There were also some plant-eating aetosaurs, curious plated animals that probably looked like crocodiles, but fed on roots and tubers that they grubbed up. The meat-eaters included rauisuchids, 2–4 metre long animals with teeth like steak-knives, as well as smaller crocodile-like forms, mammal-like reptiles and a number of possible early dinosaurs. These are *Staurikosaurus* from the Santa Maria Formation and *Herrerasaurus, Ischisaurus and Pisanosaurus* from the Ischigualasto Formation.

EARLY DINOSAURS AND ERECT GAIT

The first of these early dinosaurs, *Staurikosaurus*, is known from only one partial skeleton (Galton, 1977) that consists of a vertebral column and a partial hindlimb (Figure 4a). These indicate a lightly built animal that was about 2.1 metres long in life and it is assumed that it was an active, fast-moving hunter that probably fed on the smaller mammal-like reptiles that are found with it.

Herrerasaurus was a heavier animal (Figure 4b) about three metres long (Galton, 1977; Bonaparte, 1978). It is known from four skeletons which have not yet been fully described, but it was clearly a powerful predator.

Ischisaurus (Figure 4c) is very poorly known (Bonaparte, 1978), being represented by only two incomplete skeletons.

Pisanosaurus, a small animal, about one metre long in all, is known from a partial skull and skeleton (Figure 4d). In the jaws, the teeth are closely spaced and leaf-shaped, which suggests a plant-eating diet.

Why are these four animals called dinosaurs, especially when the fossils are rather incomplete? All four show one or more of a suite of innovations that set the dinosaurs off from their ancestral stocks amongst the thecodontian archosaurs. These innovations are largely to do with the acquisition of erect gait (Charig, 1972; Parrish, 1984, 1986).

The first archosaurs of the Early Triassic still generally had the primitive sprawling gait (Figure 5) that is seen today in lizards and salamanders. The arms and legs stick out sideways so that the upper part of each limb is roughly horizontal. A number of later archosaurs show an apparent advance over the sprawling condition. Their upper limbs slope partly downwards and the body is raised off the ground. When modern crocodiles run they adopt this intermediate posture in the semi-erect gait (Figure 5a). In the erect posture (Figure 5a), the limbs are tucked right beneath the body, as in mammals and birds. "Erect" does not mean bipedal of course—the alternative term, parasagittal, expresses the idea that the limbs are held in closer to the middle axis of the body. In the erect posture, the weight of the body is transmitted straight down through the limbs, rather than sideways and downwards, as in the sprawling and semi-erect postures, which can put a tremendous strain on the knee and elbow joints. The erect posture then allows great body weights to be achieved—as in dinosaurs and some mammals—weights that would be impossible in a sprawler.

In animals with an erect gait, there are a number of anatomical innovations in the hip region, the leg and the foot, all of which relate to their specialised posture. The most obvious features are around the joint between the femur (the thigh bone) and the hip (Figure 5b, c). The head of the femur is well developed and ball-like and bent inwards towards the hip. The socket into which it fits, the acetabulum, is deep and

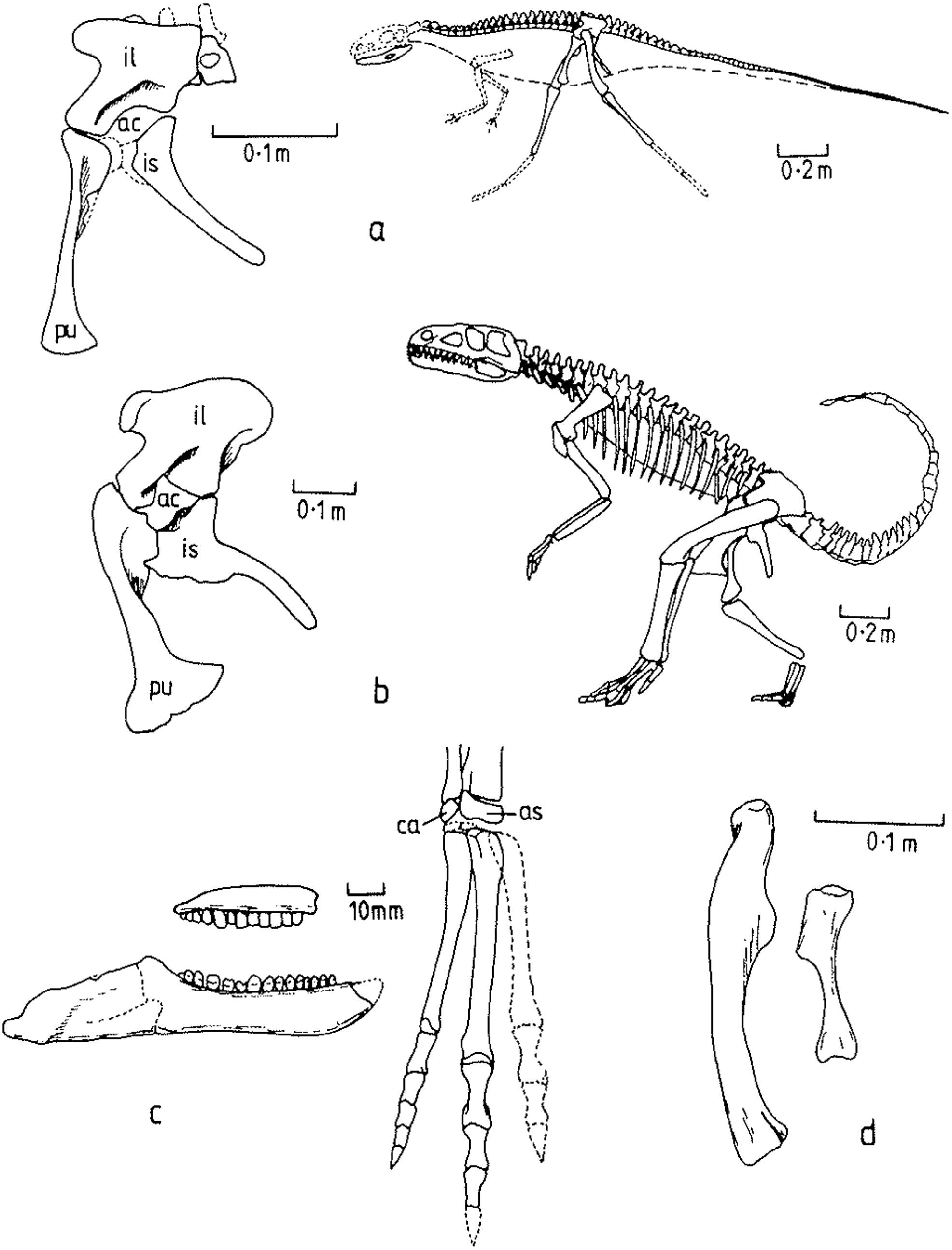

Figure 4 The earliest dinosaurs. (a) *Staurikosaurus pricei* from the Santa Maria Formation of Brazil; (b) *Herrerasaurus ischigualastensis;* (c) *Ischisaurus cattoi*; and (d) *Pisanosaurus mertii*, all from the Ischigualasto Formation of Argentina. A skeletal restoration and side view of the pelvis are shown for *Staurikosaurus* and *Herrerasaurus, Ischisaurus* is represented by a femur (left) and a humerus (right). *Pisanosaurus* is represented by toothed elements of the upper and lower jaw (left) and by a foot and ankle region (right). Abbreviations: ac, acetabulum; as, astragalus; ca, calcaneum; il, ilium; is, ischium; pu, pubis. (After Bonaparte, 1976, 1978; Galton, 1977).

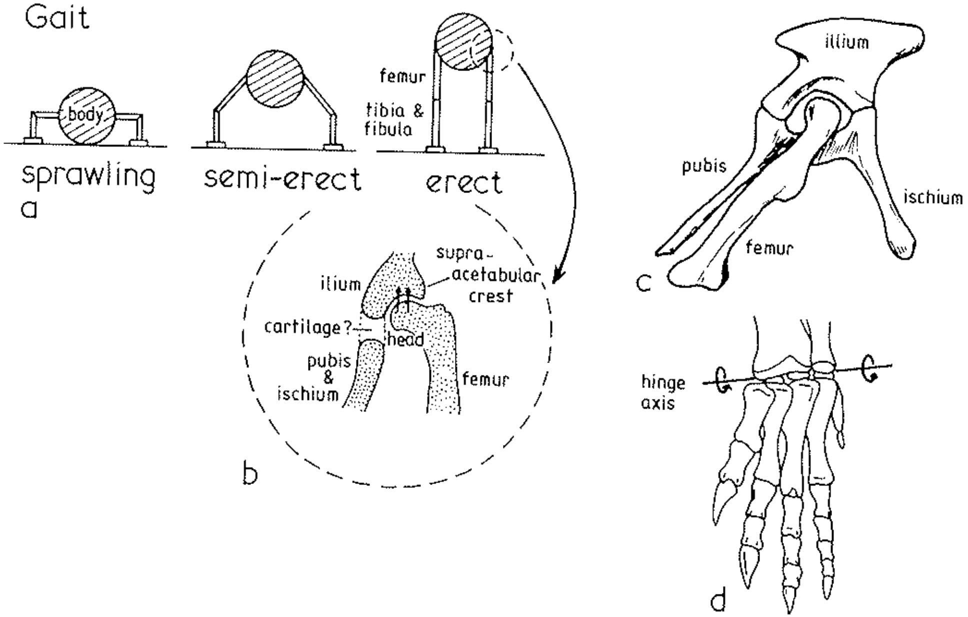

Figure 5 Hind limb posture and adaptations in dinosaurs and their ancestors. The primitive sprawling, the intermediate semi-erect and the advanced erect posture are shown in diagrammatic cross-sections of animals (a). The inturned head of the femur and the deep socket-like acetabulum are characteristics of an erect dinosaur (b). A side view of the hip region of a prosauropod dinosaur shows the perforate acetabulum and the femur in a forward position (c). The foot of a prosauropod shows the simple hinge in the ankle joint and the reduced outer toes (d). (After Charig, 1972.)

there is a strong ridge above it, the supra-acetabular crest, which prevents the femur from slipping out. In many cases, the acetabulum becomes perforated.

The femur, lower limb and foot are also modified as a result of the erect gait. There is a very clear fourth trochanter, a sharp ridge that is the attachment point for the muscles that pull the leg backwards in walking (Figure 5c). Dinosaurs have additional bony knobs, the greater and lesser trochanters, for the attachment of other muscles (Figure 5b). The knee joint is at a different angle in the erect dinosaurs compared with the sprawling thecodontians. It is now in a straight line between the hip and the foot instead of being placed at an angle. The main shin bone, the tibia, is twisted and there is a notch at the bottom which interlocks with the ankle bones.

The dinosaur ankle is a simple hinge-like joint (Figure 5d). The two upper bones of the ankle, the astragalus and calcaneum, are more or less attached to the tibia and the rest of the ankle bones form part of the foot. In sprawling and semi-erect forms, there is much more rotation between the ankle bones and the astragalus and calcaneum had a complex joint between them. The foot of erect dinosaurs (Figure 5d) is roughly symmetrical, with the middle toe (III) the longest. The outer toes (I and V) are often reduced in size, or even absent in some later dinosaurs. These changes are connected with the erect posture and the fact that dinosaurs stood up on their toes (digitigrade posture) instead of putting the sole of the foot flat on the ground (plantigrade posture), the primitive condition.

The four early dinosaurs all show one or more of the dinosaur innovations that have just been described. For example, *Staurikosaurus* has a deep perforated

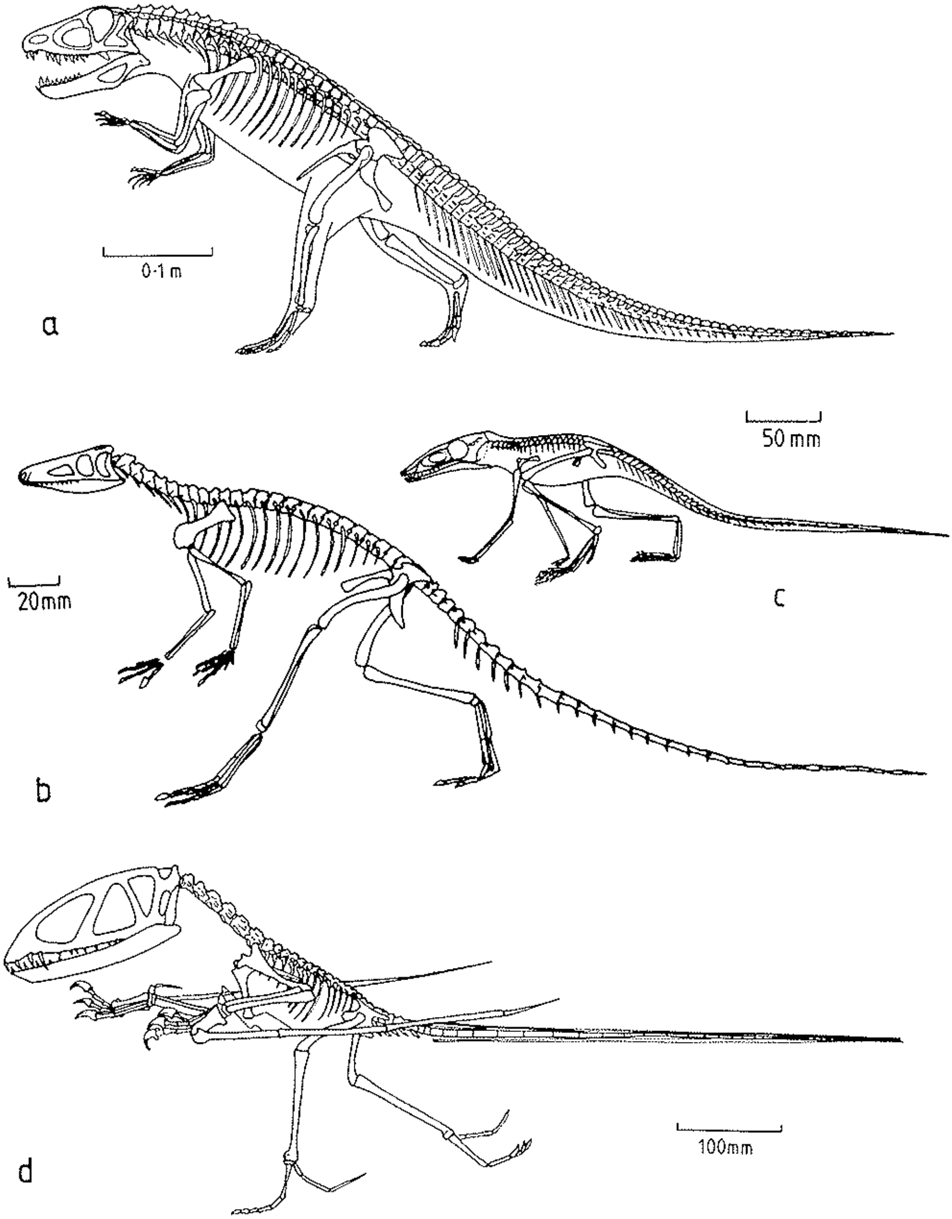

Figure 6 Some close relatives of the dinosaurs. Skeletal reconstruction of (a) *Ornithosuchus longidens* from the Lossiemouth Sandstone Formation of Scotland; (b) *Lagosuchus talampayensis* from the Chañares Formation of Argentina; (c) *Scleromochlus taylori* from the Lossiemouth Sandstone Formation of Scotland and (d) the pterosaur *Dimorphodon macronyx* from the Liassic of England. (After Walker, 1964; Bonaparte 1978; Padian, 1983.)

acetabulum, a supra-acetabular crest, a ball-like femoral head, a clear fourth trochanter and a notched tibia. *Herrerasaurus* shows these characters, as well as a reduced inner toe (I). The limb bones of *Ischisaurus* and *Pisanosaurus* are less well known, but they show a few of the dinosaurian specialisations.

Until recently, most people have tried to assign these early forms to one of the major sub-groups of dinosaurs. For example, *Staurikosaurus, Herrerasaurus* and *Ischisaurus* have been variously assigned to the Theropoda (later meat-eaters) or to the Sauropodomorpha (medium to large-sized mainly quadrupedal plant-eaters with long necks), and *Pisanosaurus* has been placed in the Ornithopoda (bipedal plant-eaters). Unfortunately, none of the four genera has any diagnostic characters of these dinosaur sub-groups. More recently, several authors (e.g. Paul, 1984; Gauthier and Padian, 1985; Gauthier, 1986; Benton and Norman, 1988) have recognised that all four genera are more primitive than the major groupings and that they lie outside the main dinosaurian assemblage.

What of the closest relatives of these early dinosaurs? Here, the choice is very broad: there are the ornithosuchids, moderate-sized carnivores from Scotland (Figure 6a) and close relatives from the Carnian and Norian of Argentina; the small long-limbed *Lagosuchus* from the Ladinian (late Middle Triassic) of Argentina (Figure 6b); the tiny, 0.25 m long *Scleromochlus* from the Carnian of Scotland (Figure 6c); and possibly even the flying pterosaurs (Figure 6d) which arose in the Norian and appear to share many advanced features with the dinosaurs. How can we sort out all of these animals in order to answer the question: just what was the oldest dinosaur?

CLADISTIC ANALYSIS

A number of authors have hit on the same solution to this problem in the last few years. What is required is some method of classification that allows us to sort out the different fossil species into a pattern that reflects their evolution. Although the skeletons are incomplete, it was possible to say, for example that *Staurikosaurus* has a dinosaur-like hip and hind limb. A number of specific features may be listed, such as the perforated acetabulum, the inwardly-turned ball-like head on the femur, the fourth trochanter, the notch on the tibia for the ankle bones and so on. Palaeontologists pick up on these particular characters because they are *advanced*, or *derived*, in comparison with other tetrapods. Only dinosaurs have this set of derived characters: other tetrapods either have the primitive characters of non-perforate acetabulum, non-inturned femur head and no fourth trochanter, or they have entirely different derived characters of their own.

Interestingly enough, in this example, it seems to be possible to define ever-smaller inclusive groups, or sub-sets, that have a particular sub-set of derived characters such as the perforated acetabulum (only slightly open in ornithosuchids, admittedly), the supra-acetabular crest above it, sharply developed fourth trochanter and so on. The dinosaurs have all of these *plus* some others, such as the fully perforated acetabulum, the fourth trochanter located low on the femur and the main ankle bone (the astragalus) with a clear process that rises into a pit on the tibia. A subset of the Dinosauria excluding *Herrerasaurus, Staurikosaurus*, and other primitite forms has yet more derived characters: the presence of three or more vertebrae over the hip (sacral vertebrae: all other forms have the primitive number of two); the lesser trochanter, near the head of the femur, is a spike or crest. It is possible to proceed through all of the later dinosaurs in this way, defining ever-smaller subsets in terms of their shared derived characters.

This kind of character analysis, in which primitive and derived characters are assessed, and an hierarchial arrangement of nested (inclusive) sets is built up is called a *cladistic analysis.* Cladistics (Hennig, 1966; Eldredge and Cracraft 1980; Wiley, 1981) is a method of working out relationships between organisms and it is now widely used in classifying vertebrates. The pattern of nested groups is usually shown as a cladogram (Figure 7). The cladogram is simply a summary of the nested sets and it can include conveniently a vast amount of information. In this example, the major groups are noted—Ornithosuchia, Dinosauria, Pterosauria and so on—and the derived characters at each branching point are listed. Further details of this cladistic

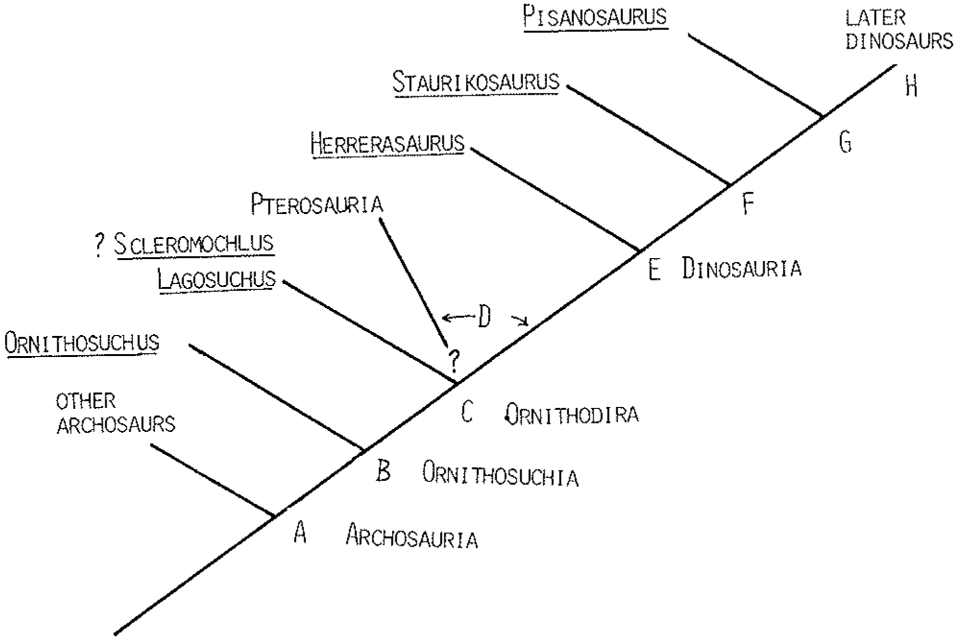

Figure 7 The relationships of the dinosaurs shown as a cladogram. The inclusive nested arrangement of the groupings is clearly indicated, with ever smaller sub-sets towards the right. The Dinosauria is included in the Ornithosuchia (Gauthier and Padian, 1985; Gauthier, 1986), all of which are characterised by a number of specialisations in the skull and skeleton. These in turn fall within the Archosauria, a major group that includes dinosaurs, crocodiles, pterosaurs, "thecodontians" and birds. Each branching point is marked by the acquisition of a number of specialisations, or derived characters, that are not seen in any other tetrapods. The major characters that relate to the acquisition of erect gait are listed in sequence. (A) ARCHOSAURIA. Possession of a fourth trochanter on the femur. (B) ORNITHOSUCHIA. Acetabulum is perforated; supra-acetabular crest on the ilium; proximal head of the femur is turned inwards; lesser trochanter on the femur; fourth trochanter is a sharp flange; knee articulates at 90°, stance is digitigrade. (C) ORNITHODIRA. Habitual bipedality (ratio of length of forelimb:hindlimb = 0.5); fourth trochanter is an aliform process; femur is shorter than the tibia; fibula is greatly reduced; mesotarsal ankle joint (simple hinge); calcaneum has no tuber; ascending process on the astragalus which fits between the tibia and fibula; metatarsals II–IV are closely bunched as a unit; metatarsals II–IV are elongated. (D) Proximal head of the femur is fully offset with a distinct neck; distal end of the femur forms two subterminal condyles. (E) DINOSAURIA. Acetabulum is fully open; fourth trochanter occurs low on the femur, ascending process of the astragalus is well developed; prominent cnemial crest on the tibia. (F) Reduced contact between the pubis and ischium. (G) Tibia is twisted. (H) Presence of three or more sacral vertebrae; lesser trochanter is a spike or a crest.

analysis may be found in Benton (1984b), Padian (1984), Gauthier and Padian (1985), Gauthier (1986), Benton and Clark (1988), and Benton and Norman (1988).

It should be noted that this cladogram is provisional. Many of the specimens are incomplete and all of the characters cannot be assessed in each sub-grouping. There are also cases in which it is hard at present to decide upon the correct distribution of derived characters. For example, the relationships of *Lagosuchus*, the Pterosauria and the Dinosauria are not clear at present because there are roughly equal numbers of derived characters in favour of the two options of pairing Pterosauria more closely with Dinosauria and *Lagosuchus* with Dinosauria.

The cladogram can be converted quite readily into an *evolutionary*, or *phylogenetic, tree* by the addition of information about the ages of specimens (Figure 8). This highlights the sequence and timing of events. The dinosaurs probably diverged from their closest relatives, the pterosaurs, *Lagosuchus* and the ornithosuchids, some time in the Late Ladinian or Early Carnian, thus from 228–232 million years ago.

THE FIRST DINOSAUR

We are nearly ready to answer the question posed earlier: what was the first dinosaur? However, there is one final problem to clear up, a problem that arises because of the incompleteness of many fossils; namely that there are dozens of supposed early dinosaur specimens that have not even been mentioned here yet. Most of these specimens are highly fragmentary—odd teeth, toe bones, chunks of jaw and so on. However, if the palaeontological literature of the twentieth century is to be believed, there is a full extensive record of dinosaurs known from the Early Triassic onwards. For example, the eminent German paleontologist Friedrich von Huene in 1932 listed ten named dinosaurs from the early part of the Middle Triassic of Germany. Is the evolutionary tree in Figure 8 here entirely wrong?

I have re-examined as many of these supposed early dinosaur specimens as I can, and it turns out that they can be either positively identified as prolacertiforms (a group of "lizard"-like animals) or thecodontians, or they lack all diagnostic characters (Benton, 1986b, c). One particular group, from the Middle and Late Triassic of most parts of the world, the Teratosauridae, was thought to have been an important early radiation of large carnivorous dinosaurs. Most of these specimens belong to a thecodontian group called the Rauisuchia which had no special relationship to the dinosaurs at all.

Intensive research is now going on in rocks of Carnian age in many parts of the world and probable dinosaurs (many are still unnamed and undescribed) have now been found as far afield as Scotland, Morocco, South Africa, Canada (Nova Scotia) and the United States (Arizona, Texas, North Carolina, Pennsylvania). The oldest known, named, dinosaur would seem to be *Staurikosaurus pricei* from the Santa Maria Formation of Rio Grande do Sul Province, Brazil.

The fact that the oldest named dinosaurs come from South America and that *Lagosuchus*, one of the closest relatives of Dinosauria, also comes from South America, might suggest that the group arose in that continent. In any case, primitive dinosaurs appear to have had a virtually worldwide distribution by the end of Carnian times. The first large dinosaurs, the prosauropods such as *Plateosaurus* which reached lengths of up to five metres, appeared in the early to middle Norian, about five million years later. They are known first from Germany and then radiated worldwide in the late Norian and especially in the Early Jurassic. Ornithischian

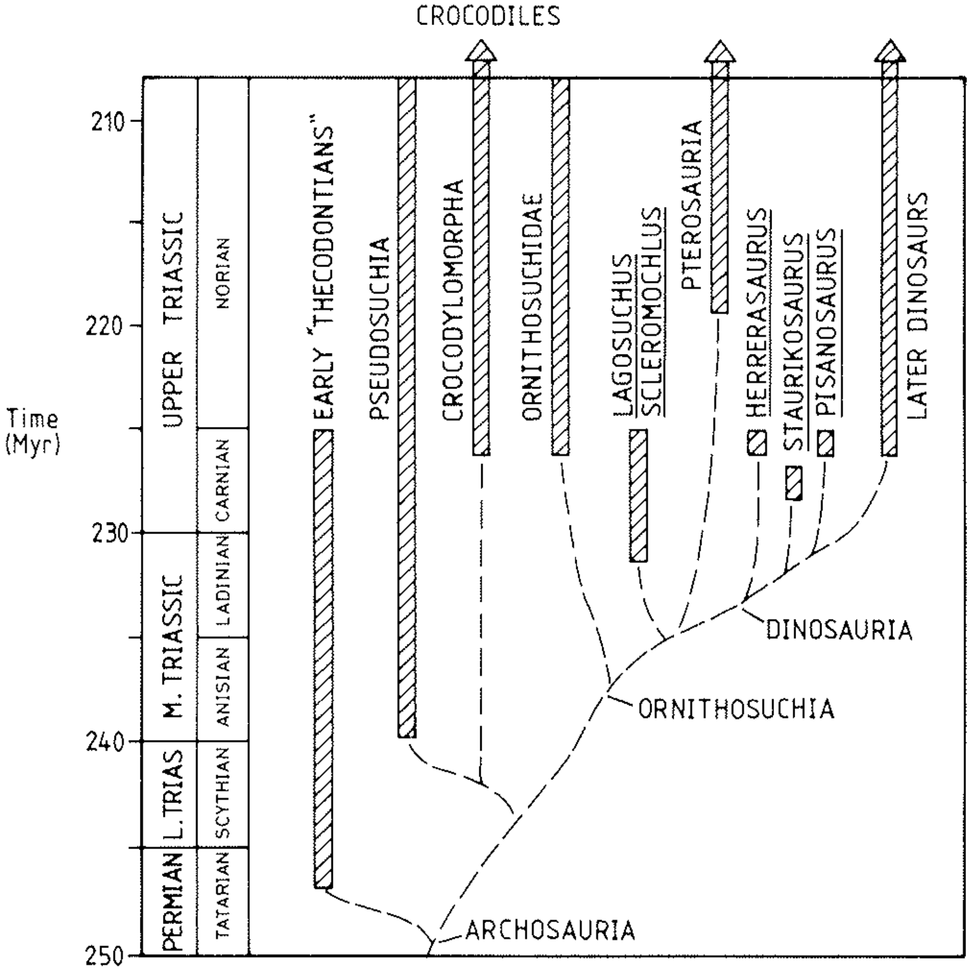

Figure 8 The key features of archosaur evolution took place during the Triassic. This phylogenetic tree is based on the cladogram in Figure 7, with the addition of stratigraphic information. The Archosauria arose in the Late Permian and several primitive groups lived through the Early and Middle Triassic. In the Early Triassic, the main lineage split into a crocodile-like group and a dinosaur-like group. The crocodile-like forms include the pseudosuchians—herbivores (aetosaurs) and carnivores (rauisuchians) of the Middle and Late Triassic, as well as the Crocodylomorpha, the crocodilians themselves. The dinosaur-like group (the Ornithosuchia) gave off a number of branches in the Middle and Late Triassic, the Ornithosuchidae, *Lagosuchus*, the Pterosauria and finally the Dinosauria. The oldest known dinosaur dates from the mid Carnian, but the Dinosauria may have arisen in the Ladinian.

dinosaurs—the bipedal plant-eaters and all the armoured forms—probably did not appear until the Early Jurassic. The first radiations of prosauropods apparently occurred after the end-Carnian extinction event and these were members of the first truly dinosaur-dominated faunas. Further diversification of the Dinosauria in the Early Jurassic again followed a mass extinction event, that at the end of the Norian.

The whole area of research encapsulated in the title of this article is presently very exciting. Our views have changed tremendously in the last few years as a result of more rigorous analyses of faunal replacement and mass extinctions and as a result of the application of cladistic analysis to the reconstruction of phylogeny. The conclusions that have been outlined here are clearly only provisional, but I hope they are a little more satisfactory than the rather evasive answers that used to be given to the persistent question: just how did the dinosaurs originate?

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