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The Age of Transformation: *The Triassic Period and the Rise of Today's Land Vertebrate Fauna*

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Introduction

The Triassic Period (about 251 to 200 million years ago on the most recent geological timescales) was revolutionary in two senses. First, faunal turnover among terrestrial tetrapods was greater, by some measures, than at any other time in history. In addition, independent advances in locomotion, growth rates, and associated physiological features in two major lineages of tetrapods, derived nonmammalian synapsids (therapsids) and the ornithodiran archosaurs, were more profound than at any other time during the evolutionary history of continental tetrapods. (Only the emergence of tetrapods onto land during the Devonian Period is comparable.)

Here we describe the principal changes in communities of continental tetrapods during the Triassic and how they unfolded over some 50 million years. Different groups dominated different global regions, changes in the tetrapod faunas through time were not in lockstep, and several waves of faunal replacement took place (Padian 1986, 2013; Fraser 2006; Sues and Fraser 2010; Irmis 2011; Irmis et al. 2007). Although we want to avoid overgeneralizing, we stress that these observations and inferences are based on a fossil record that is necessarily incomplete, but is surprisingly good in many respects.

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The first taxonomic shift happened after the diversity crisis at the end of the Permian. Late Paleozoic terrestrial communities had been dominated by stem-amphibians (temnospondyls) and nonmammalian synapsids (Kemp 1982, 2005; Ruta and Benton 2008). Reptiles remained a minor component of many Permian faunas. The best-known groups were the aquatic mesosaurs, the vaguely lizard-like millerosaurs, bolosaurs, and procolophonoids, and the large and robust pareiasaurs, along with some still poorly known groups of diapsid reptiles. All but the pareiasaurs were small animals, rarely exceeding 50 cm in total length. They were considerably smaller than most therapsids of the Late Permian.

During the Triassic, both continental and marine ecosystems changed in many ways. Reptiles rapidly diversified and by the Middle Triassic became dominant in many communities of continental tetrapods, increasingly relegating synapsids to rather minor roles for the remainder of the Mesozoic Era. Reptilian groups diversified into a range of functional and ecological roles unmatched in the history of tetrapods on land, and only rivaled by Cenozoic mammals. Although crown-group mammals themselves did not evolve until the Late Triassic, many key cranial, dental, locomotory, and physiological features of the mammalian lineage appeared earlier (see below). With the exception of the birds, all major extant tetrapod groups, as well as many others that have since become extinct, first appeared during the Triassic. Even so, some characteristic avian features had already appeared in theropod dinosaurs during the Late Triassic.

In this paper we want to tell the story of Triassic tetrapods from two perspectives. First, we review briefly the macroevolutionary patterns and phylogenetic relationships of the groups that took over the terrestrial realm during this period. We then want to recast these groups in functional and ecological terms, to show the extent of convergence and divergence in major community roles, and to emphasize how critical the environment of the Triassic was (in both abiotic and biotic senses) in fostering continental vertebrate diversity. The important take-away message is that the present-day continental vertebrate biotas are difficult to understand fully without reference to the Triassic, the most functionally and ecologically diverse period in

the history of terrestrial tetrapods, when most of these revolutionary changes began.

Phylogenetic Relationships of Triassic Tetrapods

Triassic tetrapod diversity was far too great to encompass in a single diagram. The most fundamental division is between Amphibia *sensu lato*, represented in the Triassic by various groups of stem-amphibians (including stem-frogs), and Amniota. Amniota (fig. 20.1) comprises two principal lineages, Reptilia and Synapsida. Reptilia comprises a few Paleozoic “holdovers” plus Diapsida, which includes the great reptilian radiations of the Mesozoic Era. Synapsida comprises mammals and their relatives, which (contrary to the traditional parlance of “mammal-like reptiles”) were never part of the reptiles. The two major lineages of Triassic Synapsida are Anomodontia and Cynodontia (including mammals). Within Diapsida there are two major groups: one leading to extant lizards, snakes, and rhynchocephalians (Lepidosauria) and their various relatives (Lepidosauromorpha), and the other leading to the crocodylian and dinosaur-bird lineages (Archosauria) and their diverse, mostly Triassic relatives (Archosauromorpha). During the Triassic, Archosauromorpha (including Archosauria) was the taxonomically and ecologically most diverse clade of tetrapods on land, and they will provide most of the examples that we cite in the following sections. Space is too limited for us to describe all these animals in detail here, but readers are referred to Benton (2014), Fraser (2006), and Sues and Fraser (2010) for more detailed introductions to most of them. In the following section we show how these groups can be sorted into three global “faunas” that replaced each other successively during the Triassic. Then we will explore the ecological roles that they played.

Triassic Faunal Turnover

Three general continental tetrapod faunas dominated the Triassic. These faunas were not cohesive phylogenetically, but represent successive collections of groups that dominated at particular times (fig. 20.2). The first group comprises “Paleozoic holdovers,” taxa that were diverse during the Permian and survived the end-Permian extinction to proliferate further during

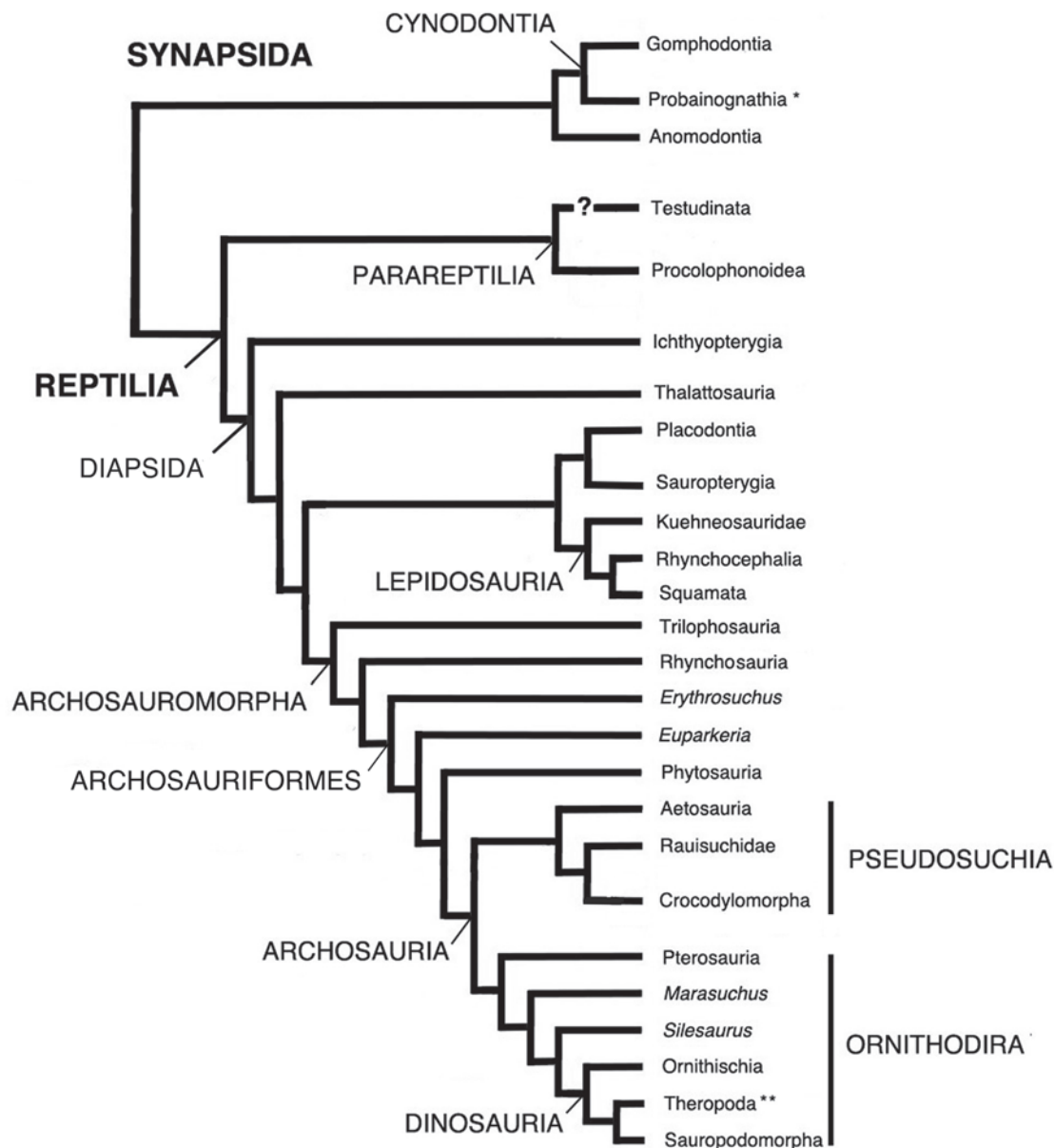


FIG. 20.1 Hypothesis of interrelationships of major groups of Triassic amniote tetrapods mentioned in the text. Combined from various sources. The placement of turtles (Testudinata) remains highly controversial. Probainognathia (*) includes mammals and their closest relatives (Mammaliaformes), and Theropoda (**) includes birds and their closest relatives (Avialae).

the Triassic. The second is called “indigenous” Triassic taxa, so named because they originated and became extinct during the Triassic. The third is the “living” fauna (we avoid the term “modern”), which comprises groups that first appeared during the Triassic but radiated much more extensively thereafter. Some representative types are pictured in figures 20.3 and 20.4.

The Late Paleozoic “Holdover” Fauna

The end-Permian diversity crisis included the disappearance of some temnospondyl stem-amphibians and gorgonopsian and dinocephalian synapsids. Some groups of reptiles (bolosaurs, millerosaurs, mesosaurs) and basal synapsids (sphenacodontids) had become

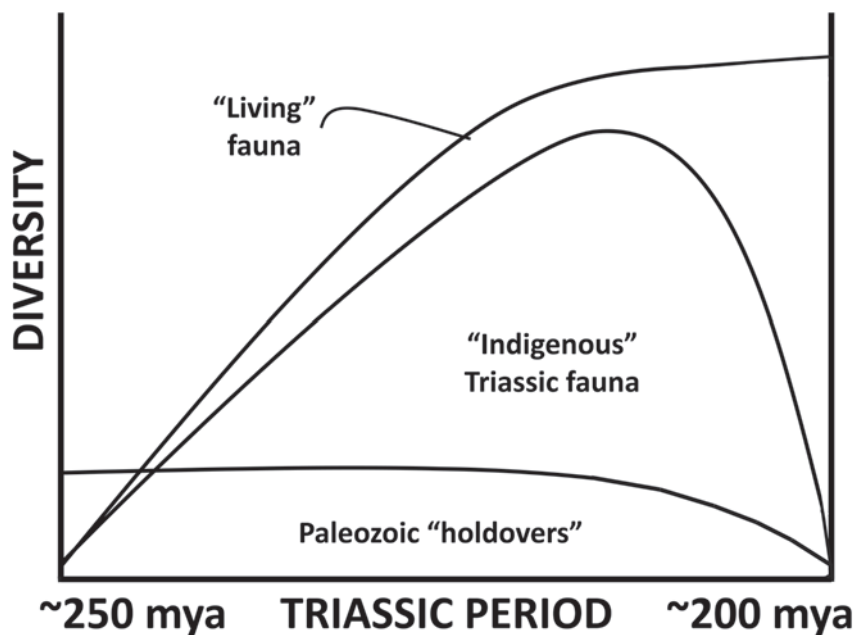


FIG. 20.2 Schematic depiction of three “evolutionary faunas” of Triassic terrestrial vertebrates: the Paleozoic “holdovers,” the “Indigenous” Triassic fauna, and the “Living” fauna. Estimated diversity correlates with morphological and ecological disparity rather than with Linnean taxonomic categories.

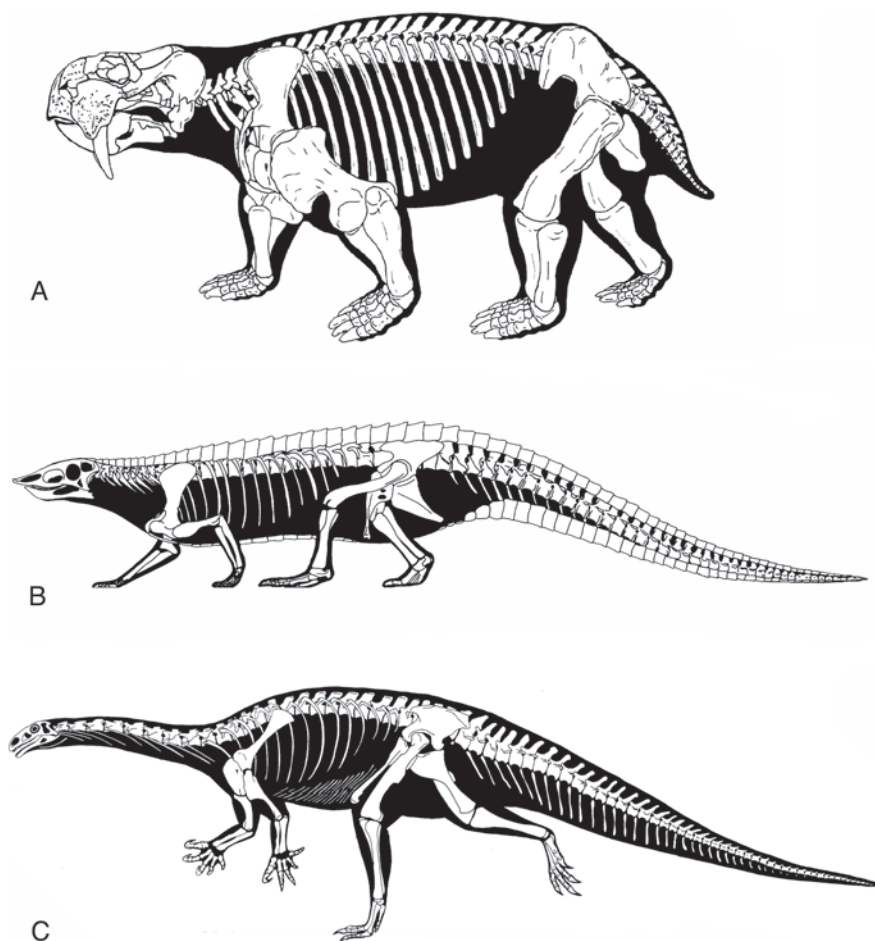


FIG. 20.3 Reconstructed skeletons (with body outline in black) of large Triassic herbivores. Top: Paleozoic “holdover”—dicynodont therapsid *Dinodontosaurus* (courtesy of Leonardo Morato); total length up to 3 m. Center: “Indigenous”—aetosaurian pseudosuchian *Stagonolepis* (modified from Walker 1961); total length up to 2.1 m. Bottom: “Living fauna”—sauropodomorph dinosaur *Plateosaurus* (modified from Weishampel and Westphal 1986); total length up to 9 m.



FIG. 20.4 Reconstructed skeletons (with body outline in black) of Triassic carnivores. Top: "Living fauna"—theropod dinosaur *Coelophysis* (from Paul 1993); total length up to 3 m. Bottom: "Indigenous"—rauisuchid pseudosuchian *Postosuchus* (courtesy of Jonathan Weinbaum), shown in bipedal pose; total length up to 5 m.

extinct before the end of the Permian. Other synapsid groups, such as dicynodonts and therocephalians, suffered major losses in diversity although some lineages (in the case of dicynodonts, at least four: Kemp 2005) did survive into the Triassic. Among temnospondyls, several mostly aquatic lineages persisted (Ruta and Benton 2008). Chroniosuchians, a lineage of armored non-amniote anthracosaurs, survived into the late Middle Triassic (Witzmann et al. 2008). Procolophonoids and archosauromorph reptiles survived the end-Permian crisis, although they are poorly known in the Permian. Both archosauromorph (bird-crocodylian) and lepidosauromorph (sphenodontian-squamate) lineages must have arisen in the Permian, but they are all but absent from the fossil record, so these "ghost lineages" must be inferred by phylogenetic analysis (e.g., Modesto et al. 2001). The effects of the end-Permian biotic crisis on other groups are still difficult to elucidate because much remains to be learned about reptilian diversity during the later part of the Permian and the timing of the originations and extinctions of various groups.

The "Indigenous" Triassic Fauna

By "indigenous" we mean groups that appeared and died out within the Triassic, and mostly within even a part of it. In the interest of space we refer readers to the summaries by Kemp (2005), Fraser (2006), and Sues and Fraser (2010) for details about the diversity and anatomy of particular groups.

We noted above that some temnospondyl and therapsid lineages survived the end-Permian crisis. These lineages evolved into new groups during the Triassic, although most of them became extinct by the end of the Triassic. Among temnospondyls, Stereospondyli comprised a wide range of sizes and body plans, ranging from superficially salamander- or crocodile-like stem-amphibians with long and narrow snouts to the peculiar plagiosaurs, whose heads were much wider than long. Among therapsids, the kannemeyeriiform dicynodonts became typically large (up to at least 3 m long) herbivores in many Middle and Late Triassic tetrapod communities. Cynodont therapsids, on the other hand, included two major groups, the omnivorous or herbivorous gomphodonts and the carnivorous/insectivorous probainognathians, which likely included the ultimate precursors of mammals (Hopson and Kitching 2001).

The Triassic Period was the apex in the evolution of major body types of archosauromorph reptiles, particularly the more basal forms. Archosauromorpha comprises Archosauria, which includes crocodylians, dinosaurs, and pterosaurs, and a host of other non-archosaurian groups that died out by the end of the Triassic (Gauthier 1986; Nesbitt 2011). Some 34 known archosauromorph lineages first diversified during the Triassic (although some may have first appeared in the Permian), but all except crocodylians, dinosaurs, and pterosaurs (unless turtles are also included in this clade) became extinct by the end of the Triassic (Nesbitt 2011, fig. 58). Examples include two clades

of presumably plant-eating forms, the rhynchosaurs and trilophosaurs, and a host of semiaquatic to fully aquatic archosauriform reptiles. Among archosaurs themselves, recent discoveries from late Early and early Middle Triassic strata have established that the division between pseudosuchians (crocodile-line archosaurs) and ornithomirans (bird-line archosaurs) had already taken place by the early Middle Triassic (Nesbitt et al. 2010; Nesbitt 2011). Pseudosuchians comprised mostly medium-sized to large carnivores and herbivores (2–9 m in length).

The Triassic also witnessed the appearance of several reptilian groups that adapted to life in the sea (discussed below). Of these, only ichthyosaurs and plesiosaurs survived through the end of the Triassic and diversified during the Jurassic Period.

The relationships of all these groups are shown in fig. 20.1, but this barely scratches the surface of the morphological and ecological diversity (including substantial convergence) of these “indigenous” Triassic tetrapod groups.

The Living (Triassic to Recent) Fauna

Almost every major group of living terrestrial tetrapods (or their immediate stem-forms) evolved by the end of the Triassic. (A “major group” is one with considerable diversity and a distinct ecological role through some extent of geological time.) These groups comprise dinosaurs (including birds) and pterosaurs, as well as crocodylians, turtles, lepidosaurs, the groups of extant amphibians (frogs, salamanders, and caecilians), and mammals. Some groups, such as lizards and snakes, still have no recognized Triassic fossil record but can be safely inferred as “ghost lineages” because their sister taxa (as implied by phylogenetic analyses) were already present. (The oldest sphenodontians, the sister group of squamates, date from the late Middle Triassic; Jones et al. 2013.) If these missing groups were present, we can perhaps not recognize them because they had not yet evolved the characteristics that we use to diagnose them. It is also important to stress that the first, earliest members of extant tetrapod groups often looked quite different from their extant relatives and performed different ecological roles. For example, based on extant taxa, we think of crocodylians as aquatic or amphibious

ambush predators. However, Triassic crocodylomorphs were mostly small to medium-sized (often less than a meter in length), lightly built terrestrial forms such as *Terrestrisuchus* and *Hesperosuchus*. They had an erect stance and a parasagittal gait, and their limb proportions suggest cursoriality. Crocodylomorphs apparently did not become aquatic until the Early Jurassic, when they first invaded both freshwater and marine environments.

In this evolutionary fauna we also include groups such as nonavian dinosaurs and pterosaurs, which survived the Triassic and flourished during the remainder of the Mesozoic (nearly 140 million years). The marine ichthyosaurs and plesiosaurs and their relatives followed the same pattern. All of them evolved by the early Middle Triassic, some 240 million years ago, and plesiosaurs survived until about 66 million years ago.

Triassic Functional-Ecological Revolutions

Two Roads to Erect Stance and Parasagittal Gait: Synapsids and Reptiles

The locomotion of an animal says much about its way of life, its surroundings, and its physiology. A habitually erect stance implies that a considerable level of energy is going into maintaining that position, compared to a sprawling posture in which the animal is often resting its body on the ground. Animals with long, parasagittally oriented limb segments are generally capable of fast running, which implies an energy budget for short bursts of speed or sustained chases at variable speeds.

During the Triassic, the two principal clades of amniotes, the synapsids and the reptiles, independently evolved erect stance and parasagittal gait in some lineages. They did so in somewhat different ways, though they began from similar starting points. These advances in the synapsids led to the mammalian condition—which primitively was not cursorial but a more generalized gait capable of walking and climbing (Jenkins 1971a). Among reptiles these advances are manifested in Ornithodira, the bird-line archosaurian clade that includes dinosaurs and pterosaurs. As we will see, the crocodile-line archosaurian clade also evolved a kind of upright posture and possibly parasagittal gait, but in a different way.

Synapsids

Kemp (2005) summarized the evolutionary history of synapsid gait from the earliest amniotes of the Late Carboniferous to the basal mammaliaforms of the Late Triassic. During the Permian Period, early (“pelycosaurian”) synapsids such as *Dimetrodon* greatly reduced or lost the lateral undulation of the vertebral column that characterized all basal tetrapods. The loss of axial flexibility accompanied the evolution of long, ventrally directed ribs that anchored muscles that aided in resisting axial sagging. The shoulder socket had a wide, complex shape that restricted movement of the humerus to the anteroposterior axis (Jenkins 1971a). As the humerus was drawn backward in the step cycle, the radius and ulna twisted to accommodate this motion while the hand remained planted; the radius rotated against the humerus while the ulna rotated on the wrist.

The pelvic girdle and hind limb were similarly primitive. The acetabulum was shallow and wide, and the femur, like the humerus, mostly moved in an anteroposterior direction. The femur could also be raised, lowered, and rotated. The lower leg seems to have been oriented ventrolaterally with respect to the knee. The tibia had a broad articular surface that contacted the distal end of the femur, whereas the fibula contacted only the posterolateral corner of this end. Conversely, the tibia articulated with the ankle only on the medial side of the astragalus, whereas the fibula broadly contacted both the astragalus and calcaneum (Kemp 2005). Thus, the posture was essentially sprawling, and the gait was rotatory (Padian et al. 2010).

The emergence of therapsids during the Permian brought important cranial and dental changes, but also substantial changes in posture and gait shared by today’s mammals (Kemp 2005). The shoulder girdle became more lightly built and less intimately connected to the ribs, allowing longer strides. The glenoid fossa was altered from a “corkscrew shape” to a dorsoventrally bifaceted notch that faced posteroventrally, much as in dinosaurs and certain other archosaurs. Kemp (1982) related these changes to the greater functional separation of the shoulder girdle from the ribcage, and the need to evolve separate muscular systems for connecting the anterior girdle to the body and moving the forelimbs in locomotion. The articular surface of the humeral head

was no longer a spiral but a long hemicylinder. As it rolled anteriorly over the glenoid, while the humerus was retracted, the bone also pronated nearly 90°. At the elbow, the radius rotated against the axis formed by the humerus and ulna, whereas, at the wrist, the ulna rotated and the radius did not. This combination, as in basal synapsids, produced an effective anchoring of the manus, which was probably plantigrade because both the metacarpals and phalanges were short.

The hind limb of early therapsids brought a new innovation in the ability to bring about both a rotatory and a more or less parasagittal gait (Kemp 1978, 1982; Sues 1986; for terminology see Padian et al. 2010). The latter style of gait approximates the mammalian condition in having the knees face more or less forward, but the elbows still faced laterally rather than posteriorly. This is a function of the orientation of the femur, which could be adducted for parasagittal gait and abducted for a more rotatory gait. The flexibility was made possible by a distinct, medially offset femoral head and a femoral shaft with a sigmoid curvature, such that the femoral head was offset approximately 90° to the distal condyles of the femur (Padian 1983, 1986). The femoral head articulated with the acetabulum so that both kinds of gaits could be accommodated, much as in extant crocodylians (Brinkman 1980) and perhaps other pseudosuchians (Bonaparte 1984). The difference is that archosaurian reptiles evolved these features in the Triassic, whereas synapsids had evolved them by the Late Permian.

However, the Triassic is when most of the evolution of Cynodontia, which includes mammals and their closest relatives, took place (Hopson and Kitching 2001). Therefore we have to ask what changes in posture and locomotion occurred then, and whether they were important to the diversification and success of the immediate precursors of mammals. In fact, the overall architecture of the girdles and limbs had not changed substantially from the condition in early therapsids, regardless of the numerous changes in the skull and dentition. Larger muscles and modified articulations seem to have facilitated more powerful and maneuverable limb movements, but the hind limb seems to have reduced its ability to produce a rotatory gait, as evidenced by the strongly offset femoral head and the evolution of the mammal-like greater trochanter,

as well as modification of the geometry of the pelvic bones (Kemp 1982, 2005). The closest lineages to mammals (tritheledontid and tritylodontid cynodonts: Sues and Jenkins 2006) evolved pelves that were even more “mammalian” with the reduction and even loss of the posterior portion of the iliac blade and development of the characteristic anterodorsal prong. At the same time, the pubis and ischium formed a more extensive ventral connection, and the obturator foramen became enlarged. But just as important were the changes in the pectoral girdle and forelimb. The coracoid was reduced, and the humeral head became bulbous, forming with the glenoid a ball-and-socket joint capable of a range of motions. Jenkins (1971a) showed that the humerus was more adducted, bringing the forelimb more underneath the body like the hind limb, with the elbow now directed posteriorly.

By the end of the Triassic, therefore, many mammalian-grade structures and functions had arisen. However, Jenkins (1971a, 1971b) showed that truly “cursorial” abilities did not appear until well into the history of crown-group mammals, and that early Mesozoic mammaliaforms did not have all features of the posture and gait present in crown-group mammals. Bramble and Jenkins (1989) charted the assembly of basal and derived cynodont locomotory features, noting that the hind limb and girdle took on “mammalian” characteristics before the forelimb and girdle did. They inferred that, as the limbs adopted a more parasagittally oriented stance, the possibility of developing asynchronous gaits (such as galloping) increased. The reduction of the posterior dorsal ribs has been linked with the evolution of a mammal-like diaphragm, which would have been critical to the efficiency of certain gaits (Carrier 1987).

Reptiles

Late Paleozoic reptiles were generally small, and had a sprawling posture and rotatory gait in both forelimbs and hind limbs. As with synapsids and basal tetrapods in general, the power for terrestrial locomotion mainly came from the hind limbs, while the forelimbs mainly supported the front end of the body and kept it off the ground and moving.

The fossil record of amniote trackways from the late Paleozoic (e.g., Haubold 1971) reflects trackmakers with widely spread limbs engaging in rotatory locomotion.

Narrow trackways with footprints close to the body midline are rare (i.e., some examples of *Rotodactylus*). However, most reptilian trackways from the Early Triassic are not close to the midline, their pace angulations are high, and their toes point anterolaterally instead of anteriorly, all of which suggests that their makers retained the basal tetrapod rotatory locomotion pattern.

Functional studies of Triassic archosauriforms suggest that the basal condition for the clade was a sprawling stance and rotatory gait. However, among Archosauria, two independent ways of reaching relatively erect stance and parasagittal gait evolved, at least in the hind limb (Sullivan, this volume), within Pseudosuchia and Ornithosuchia.

Bonaparte (1984) and Parrish (1986, 1987) showed that in some pseudosuchians an erect stance and parasagittal gait was achieved much as it was in the bird-line archosaurs; others accomplished it by having a slightly inturned head of the femur nested in the acetabulum underneath a laterally deflected iliac blade. This allowed the femur to be adducted so that the knee faced nearly forward. But the slightly inturned femoral head allowed the femur to be abducted as well, so that the more sprawling posture typical of basal archosauromorphs could be retained. Present-day crocodylians can execute both sprawling and relatively erect postures (Brinkman 1980). Parrish (1986) argued on the basis of careful reconstruction of the possible excursions at the limb joints that the ability to walk parasagittally first appeared in aetosaurs among pseudosuchians. This was reasonable because the joints of phytosaurs appeared to be too generalized to support a parasagittal gait. However, if the Triassic trackways known as *Apatopus* were made by phytosaurs, as Baird (1957) first suggested, the trackmaker most likely had an erect stance and parasagittal gait, because the limbs were brought in close to the body (Padian et al. 2010). If this interpretation holds, then parasagittal gait is a basal feature of Pseudosuchia. Nesbitt (2011) recently reevaluated the phylogeny of Archosauriformes and recovered phytosaurs outside Archosauria proper, in which case parasagittal gait would be primitive for the whole group.

This makes even more sense if we consider Ornithodira (the group within Ornithosuchia that includes most bird-line archosaurs), the sister taxon to Pseudosuchia, which had a very different functional-

evolutionary history. All ornithodirans appear to have had an erect stance and parasagittal gait, and they were most likely bipedal from their inception (Padian 1983, 2008; Nesbitt 2011). Traits that support this interpretation include a femur with a head that is distinctly offset from the shaft, a femoral shaft with a double (rather than simply sigmoid) curvature that reflected antero-posterior excursion, a reduced fibula (reflecting a lack of the torsion seen in animals with a rotatory gait), a mesotarsal ankle joint, an elongated metatarsus (reflecting habitual digitigrady, another sign of extended limb excursion common to cursorial animals using a parasagittal gait), and long digits. These features certainly appeared by the Middle Triassic with the earliest known ornithodirans (Sereni 1991). It is notable that dinosaurs and pterosaurs survived the end-Triassic extinctions and diversified extensively throughout the Mesozoic Era, whereas all pseudosuchians except crocodylomorphs became extinct. The pseudosuchian innovation of the buttressed ilium overhanging the hip joint can be seen as promoting versatility in gait (presumably the parasagittal gait allowed longer strides and more rapid progression) without requiring a fundamental change in physiology (they could still sprawl when not progressing quickly). However, the ornithodiran condition of mandatory erect posture and parasagittal gait seems to have required a commitment not just to rapid locomotion but to higher supporting metabolic levels, which we will explore below.

Two Roads to High Metabolic Rates: Synapsids and Reptiles

Although the term “warm-blooded” is widely used in professional and popular scientific works, it has no precise meaning, and has been used to refer to a variety of physiological syndromes that have different underlying causes and are not necessarily correlated. Present-day birds and mammals are considered “warm-blooded,” but their physiological systems are very different. It is likely that many features commonly considered characteristic of “warm-bloodedness” evolved in archosaurian reptiles (specifically ornithodirans) during the Triassic, but whether many of those features evolved in synapsids before the Jurassic is less clear.

Rather than using “warm-blooded” versus “cold-blooded,” we define and contrast three sets of terms.

Endothermic denotes that an animal generates most of its body heat itself, usually by burning calories. *Ectothermic* denotes that it gets most of the heat needed to run metabolic processes from external sources such as the sun. The body temperature of a *poikilothermic* tetrapod fluctuates significantly, even over the course of a single day whereas a *homeothermic* animal has a relatively constant body temperature (although many homeotherms can actively lower their body temperatures for daily periods, a syndrome called “heterothermy”). A *tachymetabolic* animal has relatively high metabolic rates, because its biochemical processes work at higher rates than those of *bradymetabolic* animals. There is no dichotomous distinction between any of these contrasting terms, nor are there absolute quantitative ranges into which the categories fall. Historically, birds and mammals have been considered “warm-blooded” (i.e., with a relatively high body temperature), endothermic, homeothermic, and tachymetabolic. Whereas this characterization is simplistic and there are many deviations and combinations, animals that do not fit these descriptions have generally been labeled by their antonyms. And taxonomic terms have come to bring their own typological baggage: “reptiles” are held to be “cold-blooded,” but birds evolved from and are themselves reptiles, so the generalization of “cold-blooded” is meaningless in evolutionary terms.

Among extinct animals it is difficult to assess endothermy, because we have no direct indication of the source of metabolic heat, although isotopic ratios of carbon and oxygen (as well as other elements such as calcium and phosphorus) in fossilized hard tissues may provide indirect evidence of body temperature (e.g., Eagle et al. 2010). The stability of body temperature (homeothermy) is also difficult to specify: although birds are generally considered “warm-blooded,” many of them actively lower their temperature for parts of the day. We cannot tell whether extinct animals did the same. Metabolic rate, however, is a slightly different story, because it is a partial determinant of growth rate: generally speaking, to grow quickly, an animal needs a high metabolic rate to sustain the processes of growth. However, although most slowly growing animals have lower metabolic rates, a slowly growing animal does not have to have low metabolic rates: among mammals, primates grow relatively slowly yet they are not bradymetabolic. Generally, in studying the growth rates

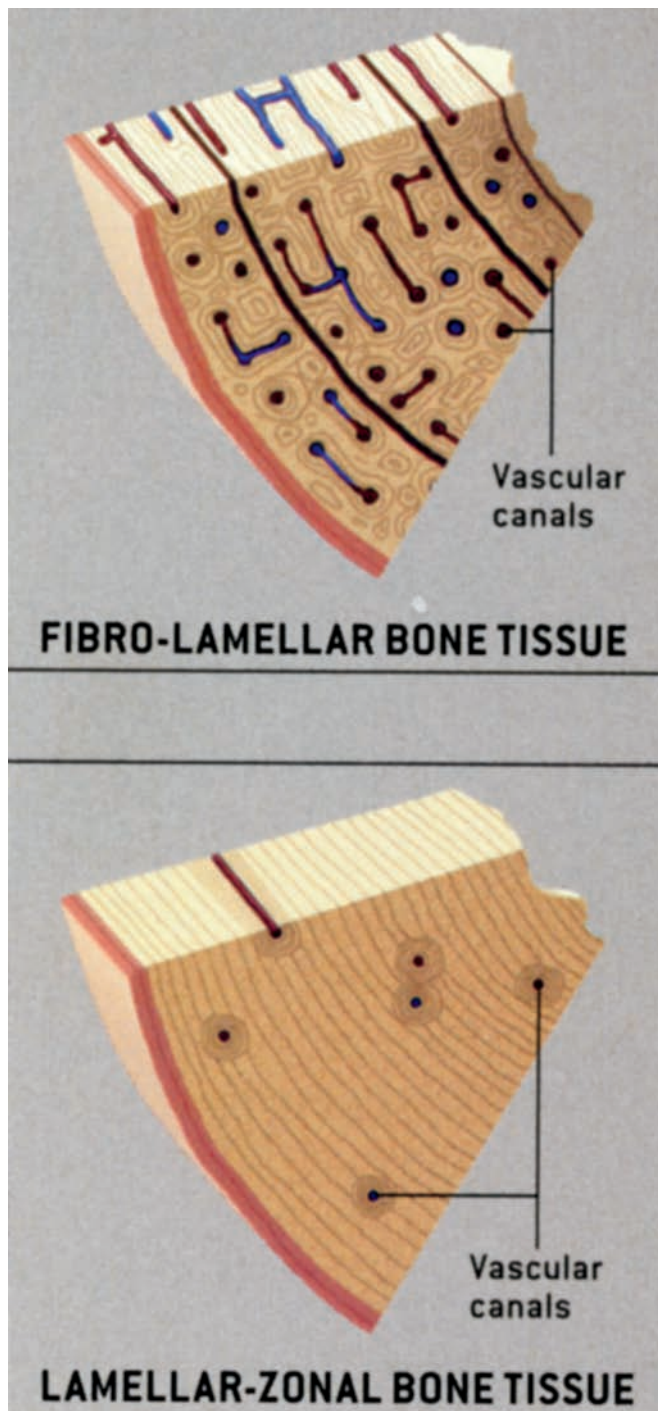


FIG. 20.5 Contrast between rapidly growing “fibro-lamellar” bone tissue found in most dinosaurs and mammals, and “lamellar-zonal” tissue that is more prevalent in other reptiles and amphibians. The red and blue circles and lines represent vascular canals, which are more numerous in fibro-lamellar bone and generally reflect higher growth rates and underlying metabolic rates. From Horner et al. (2005), reprinted by courtesy of Scientific American.

of extinct tetrapods, paleobiologists have been able to say only that if an animal is growing rapidly, its metabolic rates were probably relatively high (Padian et al. 2001).

Vertebrate bone preserves a direct indication of growth rate by the expression of certain tissue types that reflect the rate of growth (e.g., Castanet et al. 1996). These rates are normalized on the basis of experimental measurements taken from present-day species, and are usually expressed as microns of new bone deposition per day. In most extant non-avian reptiles and amphibians, cortical bone is deposited at a rate of $2\ \mu\text{m}$ or less per day. In present-day birds and mammals, that rate can be five to ten times higher or more. Even the fabric of the bone tissue looks different between these two general groups (fig. 20.5). Compared to the bone tissue of mammals and birds, amphibian and reptilian bone typically has fewer vascular canals, the tiny spaces where the osteocytes resided are generally smaller, fewer, and circumferentially aligned, and the circumferential rest lines that mark annual growth periods are closer together and more distinct, and may even manifest themselves in annuli of bone tissue with few or no canals and osteocytes. The faster-growing bone of mammals and birds not only has more vascular canals; in contrast to the sparser canals that generally run longitudinally in amphibian and reptile bone, the canals in mammal and bird bone can also extend circumferentially and radially, and can often connect with each other (Padian and Lamm 2012).

The high growth rates found in extant birds and mammals are absent in the fossil record of most tetrapods, with some exceptions. Among reptiles, the ornithomirans are most conspicuous (Padian et al. 2001, 2004). Among synapsids, somewhat higher growth rates seem to evolve in the therapsids, but mammals grow at even higher rates, especially the placentals (de Ricqlès 1969, 1972, 1974, 1980; Chinsamy-Turan 2011). Also in the Triassic, archosauromorph reptiles began to show higher rates of bone deposition, more osteocytes, vascular canals with more complex structure, and a greater preponderance of rapidly growing fibro-lamellar bone than in other reptiles (Werning et al. 2011). Among these animals, dinosaurs and pterosaurs reached rates comparable to those of mammals and birds, and the largest species grew most rapidly, a common feature of tetrapods (Padian et al. 2001). And these

histological advances tend to be correlated with the advent of advances in posture and gait that were detailed above. In the Triassic, therefore, a revolution of sorts occurred in both the posture and gait and the growth and metabolic regimes of advanced synapsids and archosaurs, particularly ornithomirans. These functional and metabolic changes signaled a commitment to “living fast,” as it were—establishing energy budgets that required a constant supply of high-quality food sources, whether plant or animal. Ecologists would see these commitments as risky, and perhaps they are. But the groups of animals that made these commitments went on to dominate all later communities of tetrapods on land.

Ecological Roles and Diversification during the Triassic

Given the large number of tetrapod clades that evolved during the Triassic Period, and given some of their functional and metabolic innovations, it was inevitable that ecological diversification would follow. The interesting thing about continental tetrapods in the Triassic is that so many independent groups repeatedly exploited the same adaptive zones—and often for the first time. For example, before the Triassic there had been no active fliers among tetrapods and few undisputed marine reptiles. What follows is a brief catalog of some of the major adaptive types, with remarks on the peculiarities of adaptations and also structural differences among the groups. For details see Fraser (2006) and Sues and Fraser (2010).

We begin with three generalizations. First, many or most taxa mentioned here are likely to have been trophic generalists, and even omnivores; we have no way of telling. Both biologists and paleobiologists often make sharp distinctions among (and even within) dietary categories, but countless studies on extant tetrapods show that these categories represent a continuum. Many herbivores consume animal protein, and many predominantly carnivorous animals occasionally feed on plants. Second, carnivory (with an emphasis on small prey consumed whole) or omnivory represented the plesiomorphic condition among tetrapods in general and tetrapods in particular, and the clades that populated the Triassic are no exception. There were at least 10 independent evolutionary forays into herbivory

among Triassic tetrapods (Reisz and Sues 2000). Until the reign of the dinosaurs during the Jurassic and Cretaceous, when carnivorous and herbivorous taxa were closely similar in diversity, and, in terms of numbers of individuals, herbivores must have greatly outnumbered carnivores in terrestrial tetrapod communities (as they do today), carnivory was more the rule and herbivory the exception. Some late Paleozoic basal synapsids (casseids and edaphosaurs) predominantly subsisted on plants, and pareiasaurs, at least some proclophionids, and larger captorhinids took this route among reptiles. Dicynodont therapsids were the most taxonomically diverse group of late Paleozoic herbivores. But the Triassic is the first period in Earth’s history when herbivores really diversified morphologically in communities of terrestrial tetrapods across a variety of major clades. And they included both synapsids and reptiles. Third, these ecological innovations not only occurred in different clades but at different times during the Triassic (which lasted about 50 million years). For example, some macrocarnivores evolved in the Early Triassic, others in the Middle Triassic, and yet others in the Late Triassic.

What we learn from the Triassic diversification of trophic groups among tetrapods is that the simple conical, often labiolingually flattened teeth that we usually interpret as indicative of carnivory turn out to be both the generalized condition for most groups and likely quite versatile for dietary preferences. Examples of some of these varied feeding types are shown in figures 20.6 and 20.7 and summarized in table 20.1.

Generalized Smaller Carnivores

We use this term broadly to include small to medium-sized tetrapods with a (presumably) mostly carnivorous diet, probably subsisting on arthropods and small tetrapods (including juveniles of larger species) that could be dispatched using the jaws and swallowed more or less whole. Our best clues to this inference come from the form of the teeth and shape of the skull. Among many smaller taxa presumed to qualify here (such as *Marasuchus*, *Lewisuchus*, and *Dromomeron*), little is as yet known of the skull and jaws. Where known, the skulls tend to be “long and low,” to use a common descriptor; this means that they are two to three times as long in total as they are high at the orbit, and they tend

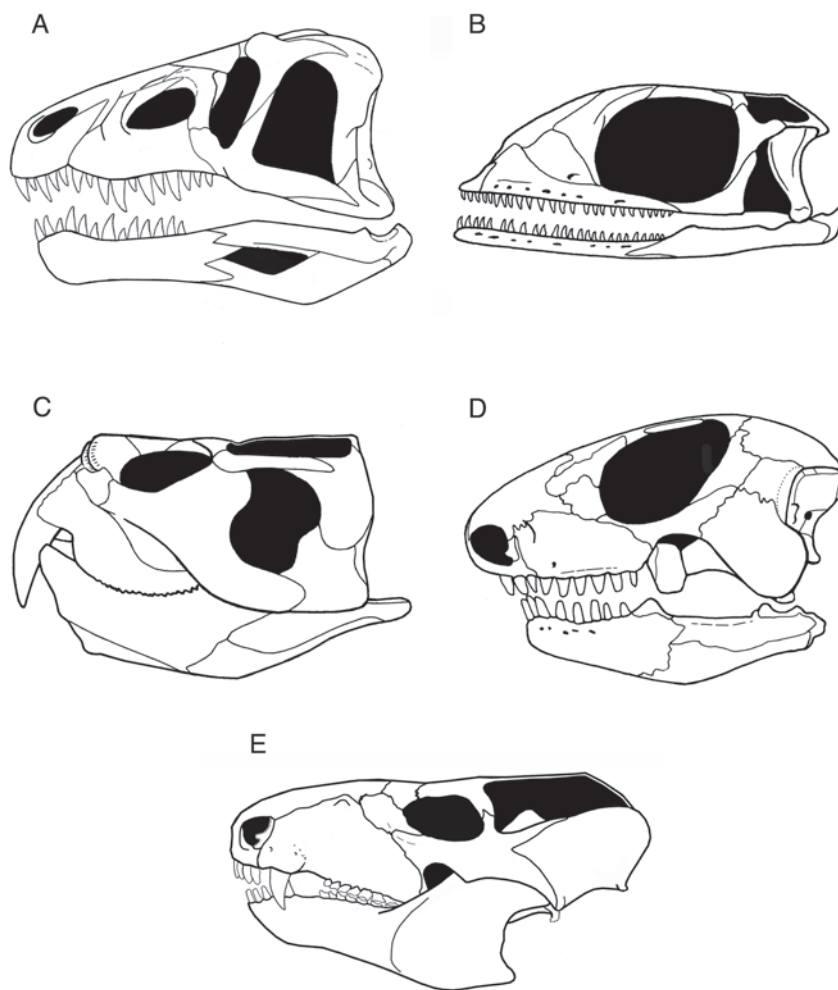


FIG. 20.6 Skulls of Triassic land-dwelling carnivorous and herbivorous tetrapods in left lateral view. (A) Large carnivore: archosauriform *Erythrosuchus* (modified from Gower 2003). (B) Small carnivore/insectivore: lepidosauromorph “*Kuehneosaurus*” (modified from Robinson 1962). (C) Large herbivore: rhynchosaurian archosauromorph *Hyperodapedon* (modified from Benton 1983). (D) Small herbivore: procolophonid parareptile *Procolophon* (modified from Carroll and Lindsay 1985). (E) Large herbivore: cynodont therapsid *Traversodon* (modified from Barberena 1981).

to taper steadily in height toward the tip of the snout. The tooth crowns are more or less conical to labiolingually flattened, often recurved, and they may have cutting edges on the mesial and (or) distal edges, which often are serrated. The teeth are relatively small and numerous in the jaws. Examples of this trophic morph include the Late Triassic ornithodiran *Scleromochlus* (20 cm long), the early crocodylomorph *Terrestriisuchus* (50 cm long), the earliest well-known archosauriform *Proterosuchus* (about 1.5 m long), and the theropod dinosaur *Coelophysis* (up to 3 m long). Among synapsids, many cynodonts (e.g., *Thrinaxodon*) have dentitions suggesting that they ate arthropods and small tetrapods, and this may have been the plesiomorphic diet for the Triassic-Jurassic lineages that were the closest relatives to true mammals (tritheledontids and morganucodontids).

Terrestrial Macrocarivores

We use the term “macrocarnivore” to denote a predator that takes prey of a substantial percentage of its own body size, prey that would have to be killed and bitten into smaller pieces, rather than simply swallowed whole, as predators that hunt smaller game would do with their food. These are mostly large animals (with a length of 2 m or more), often with a proportionately large head relative to body size. Skull length tends to be about twice its height at the orbit. Furthermore, skull height stays relatively high throughout the length of the skull. The teeth are large, typically labiolingually flattened and with serrated cutting edges, deeply implanted, and rather few in number in the jaw. The early Middle Triassic cynodont *Cynognathus*, which attained a skull length of more than 40 cm and has blade-like

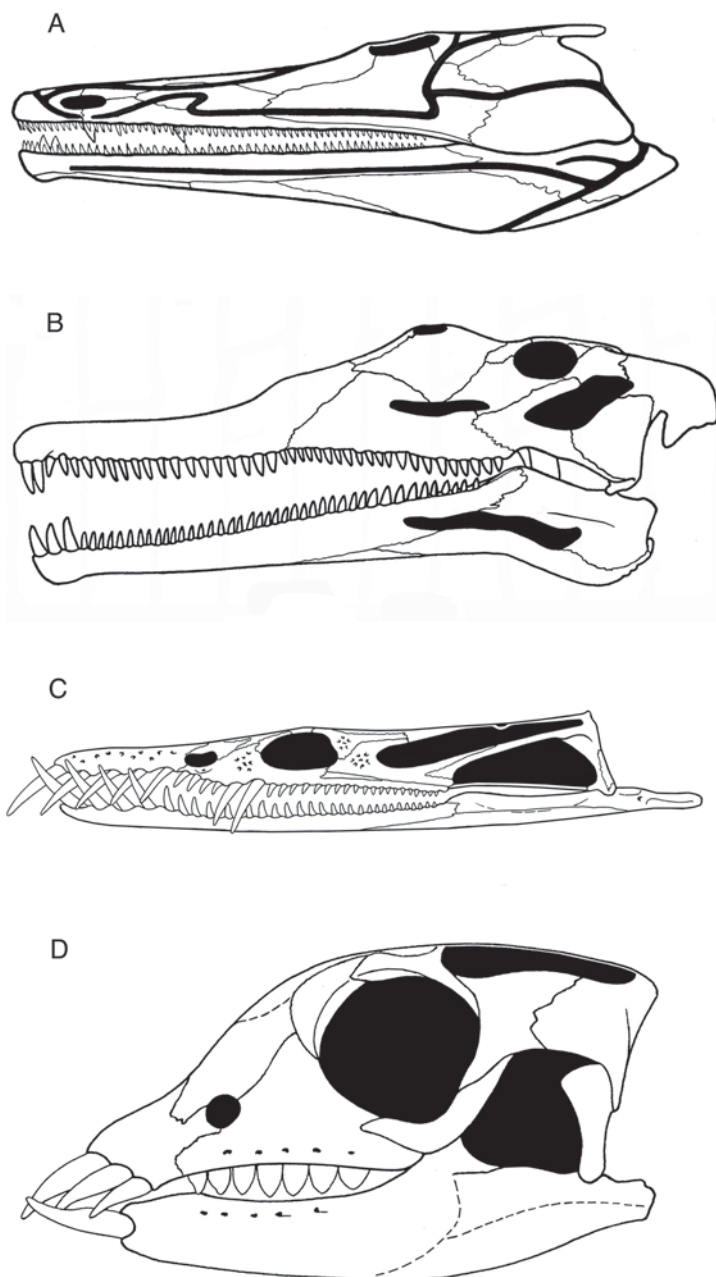


FIG. 20.7 Skulls of Triassic freshwater and marine tetrapods in left lateral view. (A) Freshwater carnivore: temnospondyl *Benthosuchus* (from Bystrov and Efremov 1940). (B) Freshwater carnivore: phytosaurian archosauriform *Machaerops* (modified from Colbert 1947). (C) Marine carnivore: nothosaurid sauropterygian *Nothosaurus* (modified from Rieppel 2000b). (D) Marine durophage: placodont *Paraplocodus* (modified from Rieppel 2000a).

“cheek” teeth with recurved, serrated cusps, was a macrocarnivore. In archosauriforms with this skull shape the antorbital and (or) narial opening may be relatively large. Examples of archosauromorph macrocarnivores include erythrosuchids (up to 5 m), ornithosuchids (up to 3 m long), the basal dinosaur *Herrerasaurus* (up to 4 m long), as well as poposaurids and rauisuchids (as defined by Nesbitt 2011; 5 m or more in length). Of these, *Herrerasaurus* and *Poposaurus* were obligate bipeds. Most of the other forms mentioned (with the

exception of the erythrosuchids) are often considered facultatively bipedal, largely because their hind limbs are considerably longer and more robust than their forelimbs. This is not unusual for reptiles, however, regardless of size. During rapid locomotion the forelimbs may have been unable to keep pace with the powerful hind limbs and may have simply been lifted off the ground. By itself, however, limb disparity is insufficient to infer bipedality. *Herrerasaurus*, like all ornithodirans, had an erect stance and parasagittal gait

TABLE 20.1 Partial listing of Triassic tetrapod lineages, grouped by generalized trophic/ecological categories

Generalized smaller carnivores	Some proterosuchids, protorosaurs, small pseudosuchians, crocodylomorphs, lagerpetids, lagosuchids, small theropods, miscellaneous ornithodirans, turtles, chiniquodontid and possibly tritheledontid cynodonts
Terrestrial macrocarnivores	Some erythrosuchids, ornithosuchids, larger pseudosuchians, poposaurids, large theropods, cynognathid therapsids
Freshwater carnivores	Various temnospondyl stem-amphibians, proterosuchids, proterochampsids, phytosaurs, choristoderans, some protorosaurs, somedrepanosaurids, <i>Vancleavea</i> , doswelliids
Marine reptiles	Sauropterygians (placodonts, plesiosaurs, nothosaurs, pistosaurs, pachypleurosaurids), ichthyosaurs, thalattosaurs, saurosphargids, some protorosaurs
Herbivores	Rhynchosaurs, trilophosaurs, aetosaurs, silesaurids, revueltosaurids, some sauropodomorphs, [ornithischians,] procolophonids, dicynodonts, gomphodont cynodonts
Aerial reptiles	Pterosaurs (flyers), kuehneosaurids, <i>Mecistotrachelos</i> , <i>Sharovipteryx</i> (gliders)

Note: These taxa are not of equivalent “Linnean” ranks or of comparable taxonomic diversity. Names in brackets represent ghost lineages.

because the structure of its hip joint restricted femoral excursion to a fore-and-aft plane, and the other joints of the hind limb acted as hinges (Sullivan, this volume).

Aquatic Carnivores

During the Triassic at least six lineages of reptiles adopted a semiaquatic or fully aquatic existence in freshwater. Some (proterosuchids, proterochampsids, phytosaurs) were relatively large (up to 7 m in length) carnivores with peg-like or conical teeth. Their skulls were typically long, particularly in the antorbital region. The snouts tended to be attenuated, sometimes gavial-like, which suggests a diet of fish. The jaws often held a large number of teeth: phytosaurs, for example, have up to 40 functional teeth in each jaw quadrant. Phytosaurs looked much like crocodylians superficially, and were either the most basal pseudosuchians or outside that entire clade. Their snouts were narrow and long, and the external narial openings in front of the eyes were on a raised prominence of the nasal bones. The back of the skull was wide transversely. Choristoderans, which probably evolved in the Triassic but became common only during the later Mesozoic and Paleogene, shared many of these features and also had a wide posterior region of the skull.

A range of generally smaller (less than 1 m body length) reptiles also invaded the freshwater environ-

ments of lakes, streams, and ponds. They generally lacked the long snouts of the larger fish-eaters mentioned above, and had smaller skulls and simpler teeth. A group of archosauromorph reptiles called protorosaurs diversified into freshwater (and marine) environments. *Tanytrachelos* (20 cm long) was one of them. Other aquatic archosauromorphs include drepanosaurids such as the deep-tailed *Hypuronector* (about 15 cm long) and the archosauriform *Vancleavea* (about 1 m long), which had extensive dermal armor and a deep tail. Unusual for this trophic category, *Vancleavea* has a short skull with large, somewhat recurved teeth of varying size. *Vancleavea* and perhaps doswelliids adopted at least semiaquatic modes of life. There were doubtless many other forms of small aquatic tetrapods, because those mentioned in this paragraph only came to light within the past few decades. Triassic microvertebrate assemblages (e.g., Kaye and Padian 1994) preserve teeth and skeletal elements from taxa that are so far unidentified, suggesting a further unrecognized diversity of aquatic tetrapods.

In addition to these reptiles, it should be noted that most Triassic temnospondyl stem-amphibians were probably aquatic or mostly so. They range in size from less than 1 m to more than 5 m in length, and skull shapes range from long and attenuated to wider than long. Typical Triassic members include metoposaurids, which are found in many Late Triassic freshwater deposits in North America and Europe. Metoposaurids have

large, flat skulls with rather small, anteriorly placed, and dorsally facing eyes. The first stem-frogs (*Triadobatrachus*, *Czatkobatrachus*) are known from the Early Triassic, and it may be presumed that they were at least partly aquatic.

The Return to the Sea

Not only did at least four reptilian groups return to the sea during the Triassic; they did so in completely different ways. In each case, we have as yet no evidence that the groups first ventured into freshwater and then moved on to marine environments. It seems rather that freshwater forms evolved inland in lakes and streams, and marine taxa in brackish or marine settings, because in most cases their earliest members are found in near-shore marine environments.

Placodonts have short, broad, and robust skulls, often with procumbent teeth at the front of the jaws and massive crushing teeth at the back of the jaws and especially on the palate. *Placodus* and related forms probably swam using undulation of the tail. Some derived placodonts had turtle-like dermal armor and probably swam by paddling. Most placodonts probably subsisted on hard-shelled marine invertebrates that were attached to the substrate. A poorly known lineage superficially similar in some respects to both placodonts and sauropterygians, Saurosphargidae (Li et al. 2011), represents yet another lineage of marine Triassic reptiles.

Although they were very different from other marine reptiles, placodonts may be most closely related to the long-necked plesiosaurs and their relatives, collectively known as Sauropterygia (Rieppel 2000a, 2000b, 2002). The Triassic members of this group include pachypleurosaurs, nothosaurs, and pistosaurs (the sister group to plesiosaurs). The small (usually less than 1 m long) pachypleurosaurs have small skulls with broad, rounded snouts and uniform dentitions. *Nothosaurus* was larger (up to 4 m long); its skull could attain a length of 50 cm. The snout is elongated with “pincer” jaws and a heterodont “fish-trap” dentition (Rieppel 2000b). Although their limbs became increasingly flipper-like, pachypleurosaurs and nothosaurs probably still relied on the tail as their principal means of propulsion, in contrast to plesiosaurs, which seem to have had a more or less rigid body and swam using both fore- and hind limbs that were modified as flippers (Robinson

1975; Braun and Reif 1985). Specialized sauropterygians extended their necks by increasing the number of cervical vertebrae: some Cretaceous plesiosaurs had more than 70.

Thalattosaurs were superficially similar to and probably related to sauropterygians. Generally rather lizard-like in body form, they have somewhat modified limbs and laterally flattened, deep tails, which, together with their occurrence in marine deposits, suggest an aquatic existence. The skulls were robust and had tapering, often deflected snouts.

Here then is an example of the dynamic tension between phylogenetic unity and morphological and ecological diversification: the thalattosaurs, placodonts, saurosphargids, pachypleurosaurs, nothosaurs, pistosaurs, and plesiosaurs (even only considering Triassic forms) were far more different from each other morphologically and ecologically than the “adaptive radiations” one commonly hears labeling extant cichlid fishes or dung beetles; yet these bizarre marine reptiles may have all had a single phylogenetic origin. Their rapid diversification exemplifies how unusual the Triassic Period was.

Ichthyosaurs are the most widely known Mesozoic marine reptiles, but their familiar dolphin- or tuna-like body shape did not become widely established until the Jurassic (Motani 2005). The earliest known ichthyosaurs were small, long-bodied forms such as *Utatsusaurus*, which swam using undulations of the body and tail (Braun and Reif 1985); they are known from near-shore marine environments. A variety of later Triassic ichthyosaurs such as *Shonisaurus* and *Cymbospondylus* attained large size (10 m or longer) and have long heads, deep bodies with strange, distally expanded ribs, and long, narrow forefins. These were open-water forms. Early ichthyosaurs were ecologically diverse; they are generally thought to have been active swimmers preying on fishes or cephalopods, but the more basal forms were probably not pursuit predators and may have favored a varied diet of invertebrates.

In addition to these major groups, several other reptilian clades invaded the seas. The protorosaurs that were mentioned above as aquatic foragers had several members that became large and lived in nearshore environments, including *Macrocnemus* and *Tanystropheus*, which had a neck that made up half its body length (up to 6 m) but still comprised the same basic number of

vertebrae shared by most other reptiles. Rather unexpectedly, the oldest known stem-turtle, *Odontochelys* from early Late Triassic marine deposits in China, has a shell comprising dorsal neural plates (and expanded dorsal ribs) and a fully developed ventral plastron (Li et al. 2008). Its shell may represent an intermediate stage in the evolution of the typical turtle shell (Lyson et al. 2013). Geologically slightly younger turtles such as *Proganochelys* appear to have been terrestrial, with both upper and lower shells (Joyce and Gauthier 2004).

As noted above, stem-crocodylians do not seem to have become aquatic until the Jurassic. However, the basal crocodile-line archosaur *Qianosuchus* from early Middle Triassic marine deposits in China already has a laterally flattened and dorsoventrally deep tail, which is suitable for swimming, although its skull appears to be that of a terrestrial carnivore.

All told, Triassic reptiles diversified quickly to exploit a range of food sources in several kinds of marine environments, evolving a diversity of body plans not only among, but even within, major lineages such as ichthyosaurs and sauropterygians.

Herbivores

As the phylogeny (fig. 20.1) shows, herbivory is a secondary specialization from carnivory/insectivory that independently evolved numerous times, and the transition usually seems to have involved an omnivorous phase, although we have little evidence of the actual transitions in many groups. Basal sauropodomorph (“prosauropod”) dinosaurs, which together with the carnivorous theropods make up the clade Saurischia, are a good example. It now appears that the earliest sauropodomorphs such as the aptly named *Panphagia* (“eats everything”) still had teeth suggestive of omnivory (Martínez and Alcober 2009). The teeth of *Panphagia* have triangular crowns like those of many herbivorous dinosaurs, but they also have finely serrated mesial and distal cutting edges, as well as labial and lingual keels that suggest puncturing as well as slicing. More derived sauropodomorphs such as *Plateosaurus* have more typical lanceolate, labiolingually flattened tooth crowns with coarser serrations, reminiscent of those in present-day plant-eating iguanid lizards.

The dentitions of some early ornithischian dinosaurs such as *Lesothosaurus* (an Early Jurassic form)

have simpler conical or recurved teeth at the front of the jaws (again suggestive of carnivorous or omnivorous ancestry). However, recent work indicates that ornithischian dinosaurs were very rare during the Triassic (Irmis et al. 2007). *Pisanosaurus*, from the early Late Triassic of Argentina, has long been considered the earliest ornithischian, but the only known specimen is poorly preserved and its phylogenetic status must be considered uncertain. Irmis et al. (2007, 5) reviewed the case of the missing Triassic ornithischians, and pointed out that “supposed ornithischian dental synapomorphies such as low, triangular tooth crowns, the separation of the crown and root by a distinct neck, and the presence of asymmetrical teeth with serrated denticles, also occur in other Late Triassic archosaurs, including aetosaurs (Walker 1961), *Silesaurus* (Dzik 2003) and now *R[evueltosaurus] callenderi* (Parker et al. 2005). Thus, these character-states cannot be used to assign isolated teeth to the Ornithischia.” This poses a major problem, first because most alleged Triassic ornithischian specimens (now almost all eliminated as ornithischian) are teeth, and, second, because ornithischians are considered the sister taxon to saurischians, the two groups must be equally ancient. Good material of one taxon, *Eocursor*, was described from strata of possibly Late Triassic age in South Africa (Butler et al. 2007), but the age of this record is poorly constrained.

Other taxa with more or less ornithischian-like teeth have been considered herbivores, including aetosaurs (and their relative *Revueltosaurus*) and silesaurids. Aetosaurs were basal crocodile-line archosaurs (Nesbitt 2011). Their bodies were protected by extensive dermal armor dorsally and ventrally, occasionally with prominent spikes in the shoulder region. The jaws were typically edentulous in front. Some forms have a beveled snout, which suggested rooting to some authors. Teeth assigned to *Revueltosaurus* were originally thought to belong to ornithischian dinosaurs, but when associated skeletal remains were eventually found, the tooth-bearer turned out to be a crocodile-line archosaur closely related to aetosaurs (Parker et al. 2005). Silesaurids were first thought to be ornithischians, but they were instead close relatives of dinosaurs, quadrupedal and apparently herbivorous (Dzik 2003; Nesbitt et al. 2010).

Other Triassic lineages that apparently evolved herbivory include two basal archosauromorph groups

(Reisz and Sues 2000). Rhynchosaurs were among the most unusual Triassic tetrapods. The skull has a downturned upper beak formed by the premaxillae, and the anterior ends of the dentaries are turned up. The maxillae each bear two or more rows of teeth bordering a groove into which the mandibular tooth row fits. The back of the skull is transversely wide, presumably to accommodate powerful jaw-closing musculature. On the other hand, the jaws of *Trilophosaurus* and *Teraterpeton* are edentulous at the front and have transversely broad molar-like teeth with cusps. The cheek region of the skull is deep and lacks a lower temporal opening.

Procolophonoid parareptiles were diverse during the Triassic. *Procolophon* and its Triassic relatives (Procolophonidae) have transversely broad teeth at the back of the jaws and incisor-like teeth at the front. The teeth at the back of the jaws interdigitated during jaw closure and have prominent apical crests and often cusps.

This makes at least eight independent major lineages of herbivorous reptiles known from the Triassic Period, and we can add at least two more lineages of herbivorous therapsids to this total. Gomphodont cynodonts have transversely wide, molar-like teeth at the back of the jaws. In many Triassic forms, the tooth crowns had several cusps and the upper and lower “cheek teeth” met in precise occlusion: the lower teeth met the upper ones and moved upward and backward. Gomphodonts were mostly smaller forms but a few Late Triassic forms such as *Exaeretodon* attained a length of at least 2 m. Triassic dicynodonts for the most part lack teeth. In a turtle-like manner, a keratinous beak covered the front of the snout. Food was sliced between the occluding halves of the beak by a posteriorly directed jaw motion, which was facilitated by a sliding jaw joint. The kannemeyeriiform dicynodonts became important elements in communities of Triassic terrestrial tetrapods. They often attained large body size, with a length of up to 3 m and a weight of at least one metric ton (e.g., *Stahleckeria*).

Perhaps the most striking thing about these 10 or more independent lineages of herbivorous Triassic tetrapods is that the teeth and jaws were different in each, and likely the occlusal mechanics were also different according to the shape of the food-processing apparatus and the type of plants being consumed. This diversity pales by comparison in extant herbivorous reptiles and mammals.

Aerial Reptiles

We distinguish gliders (which are mostly passive fliers) from true flyers, who power themselves through the air by means of a flight stroke. There is no evidence that any group of active flyers among tetrapods is related to gliders or passed through a gliding stage during the evolution of active flight (Padian 1985; pace Dudley et al. 2007). Pterosaurs were the first group of tetrapods to evolve active flight. To date, at least seven lineages are known from the Late Triassic (Dalla Vecchia 2013). Early pterosaurs typically have long jaws, often with multi-cusped teeth at the back of the jaws and large fangs near the front. Fish remains have been found in the gut regions of some Triassic pterosaur skeletons. Even the most basal pterosaurs are already fully winged and capable of active flight; they apparently descended from bipedal ornithodirans (Padian 2008). Late Triassic forms such as *Eudimorphodon* and *Peteinosaurus* still have wingspans of well under 1 m. Jurassic pterosaurs had simpler teeth but otherwise resembled their Triassic precursors in wing shape and skeletal structure.

In contrast, gliding seems to have evolved independently in at least three groups of small Triassic reptiles. The Late Triassic kuehneosaurids such as *Icarosaurus* were distantly related to lepidosaurs (Evans and Jones 2010). They have greatly elongated thoracic ribs upon which a gliding membrane of skin was stretched, much like in the present-day lizards of the genus *Draco*. The Late Triassic *Mecistotrachelos* was a long-necked (possible) archosauromorph with elongated ribs for gliding (Fraser et al. 2007). The Middle or Late Triassic *Sharovipteryx* has an extensive skin fold stretched between its hind limbs, which some workers have interpreted as a feature for parachuting or gliding. (Its forelimbs are small but poorly known.) Another small diapsid, *Longisquama*, which lived alongside *Sharovipteryx*, has long, recurved, blade-like epidermal structures along its back that have reminded some workers of bird feathers. However, there is nothing really feather-like about these structures, which form a single row along the midline of the back and had nothing to do with gliding or active flight. Nevertheless, this degree of diversification of aerial tetrapods into one flying lineage and at least three gliding ones has only been exceeded during the Cenozoic, with the great diversification of birds and the evolution of the flying bats and a great variety of

gliding marsupials, rodents, and dermopterans (Dudley et al. 2007).

Smaller Tetrapods and Their Varied Roles

As in present-day continental ecosystems, small tetrapods played important ecological roles in the Triassic, including small carnivores/insectivores (generally a size-dependent category), omnivores, and herbivores, but the players were different. Based on the presence of Early Triassic stem-frogs (such as *Triadobatrachus*), frogs must have existed during the Triassic but have no known fossil record until the Early Jurassic. Thus, their sister taxon, comprising newts and salamanders (caudates) must have been present as well, but, with the possible exception of the Middle or Late Triassic *Triasurus*, their fossil record begins in the Middle Jurassic.

Among Lepidosauria, squamates (lizards and snakes) are so far unknown from the Triassic, but their sister group, the sphenodontians (Rhynchocephalia, restricted today to the genus *Sphenodon*), dates back to the Middle Triassic and diversified during the Late Triassic (Jones et al. 2013). Some sphenodontians were probably insectivores/carnivores, but others fed on plants (Jones 2008).

Triassic mammaliaforms and haramiyid mammals were small (5–10 g) and presumably insectivorous, as were the closely related tritheledontid and brasilodontid cynodonts (Kemp 2005).

Among now-extinct groups of small tetrapods, procolophonids and gomphodont cynodonts appear to have been predominantly herbivorous (Fraser 2006; Sues and Fraser 2010).

Carnivores included a variety of small ornithodiran archosaurs, such as *Marasuchus*, as well as others more closely related to crocodylians, such as *Gracilisuchus*. All these animals are known from at least partial skeletons. But much remains to be learned about the diversity and structure of many other Triassic small tetrapods. Recovery of their skeletal remains usually requires breaking up and sieving bulk samples of bone-bearing sedimentary rock. In one example, the *Place-rias* Quarry in the Upper Triassic of Arizona, the known diversity of vertebrates was tripled by analysis of microvertebrate remains (Kaye and Padian 1994). The problem is that the processing of the fossil-bearing matrix dissociates and often damages bones and teeth to

a point where anatomical and taxonomic identification of the elements can become difficult if not impossible.

Functional Ecology and the Structure of Triassic Communities

Given the morphological and taxonomic diversity of Triassic land-dwelling tetrapods, what can we learn about the diversity and evolution of their communities and how they were structured? The reconstruction of “food webs” and other diagrams of trophic flow in communities is difficult because we cannot directly observe diets (except when food remains are preserved in a digestive tract); diets may change with size through the lifetime of an animal or even seasonally; and we cannot presume that a given animal lived in a particular environment of deposition merely because it was preserved there (it could have washed or been carried in, for example).

Generally speaking, carnivores feed on all members of a community that they encounter, depending on body size and ontogenetic stage. Small carnivores feed on small vertebrates and insects, again dependent in part on body size. Herbivores flourish and diversify depending on availability of plants, but there is little evidence of specific herbivores eating specific plants. Aquatic and semiaquatic animals presumably fed on fishes and invertebrates, but unless their jaws (e.g., placodonts) or body forms (e.g., thunniform ichthyosaurs) are obviously specialized for feeding or locomotory strategies, it is difficult to go beyond generalizations.

Size Increase and Ecological Diversification

The median body size of Triassic tetrapods was substantially greater than those of their Permian predecessors, partly because there were more large taxa in the Triassic. The largest known Permian tetrapods included the dinocephalian and some dicynodont synapsids and, among reptiles, pareiasaurs (up to 3 m in length). During the Triassic certain stereospondyl stem-amphibians, kannemeyeriiform dicynodonts, the archosauriform *Erythrosuchus*, phytosaurs, crocodile-line archosaurs (aetosaurs, ornithosuchids, rauisuchids), and saurischian dinosaurs attained lengths of up to 5 m and sometimes more (particularly the largest phytosaurs, rauisuchids, and sauropodomorphs). Most of these

taxa did not reach large body size by growing quickly through high metabolic levels; exceptions were the sauropodomorphs and possibly the erythrosuchians. Most of these large taxa grew slowly and took many years to reach full size (de Ricqlès et al. 2008). Apart from the large stem-amphibians and dicynodonts, whose lineages persisted with new members from the Permian to the Triassic, the vast majority of new large animals in the Triassic were reptiles. They include members of proterosuchids, erythrosuchids, trilophosaurs, rhynchosaurs, protorosaurs, phytosaurs, aetosaurs, paracrocodylomorphs, and sauropodomorphs. It can be presumed that these animals became larger because their food sources were abundant enough throughout the year to enable them to do so. Larger size enables resistance to smaller predators for prey species, and access to a greater range of prey (including larger prey) for predators. Expanding the upper limits of size in communities has other important effects on community diversity: both smaller species and the young of larger forms can play similar roles.

How Stable Were Triassic Continental Vertebrate Communities?

“Stability” is a difficult question for community ecologists who study diversity in the short term. Throughout the Triassic, some notable changes took place. The overriding theme is that whereas ecological roles diversified in the Triassic, from one temporal interval to the next (and also geographically), ecological roles may have been filled by members of either the same or different clades (or both) as those from the previous interval.

As detailed above, Triassic communities of continental tetrapods had three major components: late Paleozoic “holdovers,” “indigenous” Triassic taxa that diversified and became extinct during that period, and “living” groups that came to dominate more recent communities. During the Triassic, one clade of predominantly aquatic stem-amphibians, Stereospondyli, diversified, but most other temnospondyl lineages had vanished by the end of the Permian. Derived synapsids (therapsids), however, had a relatively smaller role in these ecosystems, because the reptiles (which had been restricted to mostly small forms during the Permian) greatly diversified and because therapsids declined

in diversity during the Triassic. However, two groups flourished during the Triassic: cynodonts (ranging from *Thrinaxodon* to *Exaeretodon* to *Morganucodon*) and certain dicynodonts (especially *Lystrosaurus* and kannemeyeriiforms) (Kemp 2005).

Although Early Triassic tetrapod communities were still taxonomically dominated by therapsids and temnospondyls, reptiles were diversifying even then, and, by the early Middle Triassic, they clearly were in ascendancy. By the Late Triassic, reptiles had become the dominant tetrapods in continental ecosystems. Archosauromorph reptiles, whose phylogeny is detailed in figure 20.1, were the principal component of this Late Triassic diversification. In other words, there was a turnover of taxa not only in terms of species within clades, but also of clades that dominated ecological roles. The latter did not include dinosaurs: there were only a few small to medium-sized carnivorous theropods and some medium-sized to large, predominantly herbivorous sauropodomorphs. Had life ended after the Triassic, dinosaurs would not have appeared as interesting as many other groups of the time.

Despite the apparent absence of major topographic barriers, Pangaea was not a homogenous place. Many tetrapod taxa were restricted to some regions, more diverse in certain regions, and existed for longer periods of time in some regions than in others. Some of this differentiation may have been latitudinal: for example, Whiteside et al. (2011) argued for latitudinal differences in the distribution of procolophonid parareptiles and gomphodont cynodonts from the Late Triassic in eastern North America. Dinosaurs did not replace their relatives as quickly or at the same times in low latitudes as in higher ones (Irmis et al. 2007). As interesting, and just as problematic, is that although theropod dinosaurs ranged widely across Pangaea during the Late Triassic, sauropodomorph dinosaurs were abundant in Europe, southern Africa, and South America during that time but are unknown from North America. When sauropodomorphs finally did appear in North America during the Early Jurassic, they seem to represent lineages that came from three different geographic areas (Rowe et al. 2011). The question of stability in Triassic continental ecosystems requires understanding that different groups occupied different roles in time and space, and that phylogeny and biogeography are important components of the mix.

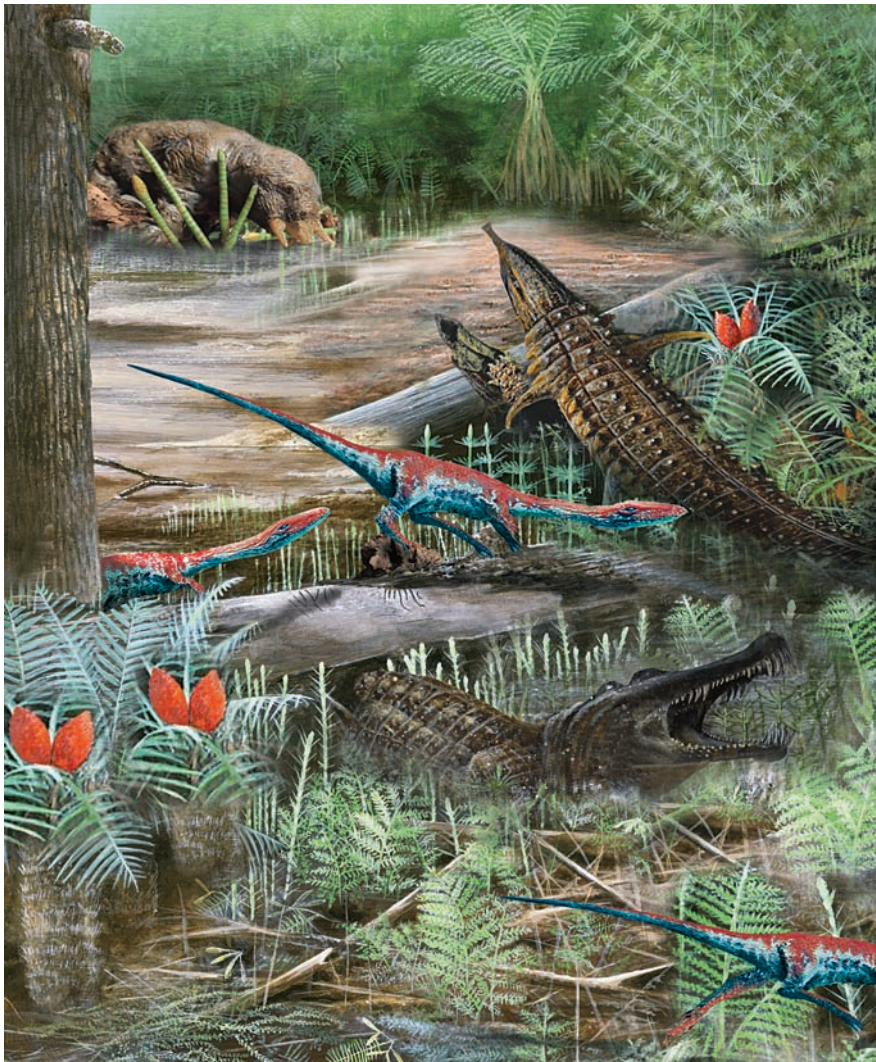


FIG. 20.8 Reconstruction of a Late Triassic habitat with various tetrapods in what is now the American Southwest. The dicynodont therapsid *Placerias* (in the upper left corner, drinking) represents one of the geologically youngest members of this group of “Paleozoic holdovers.” The heavily armored aetosaur *Desmatosuchus* (near the center of the scene, raising itself on a tree stump) and the crocodile-like phytosaur *Machaerops* (partially concealed under a fallen tree) both represent “indigenous” groups of reptiles that did not survive the end-Triassic extinction event. Three early theropod dinosaurs, representing the “living fauna,” scurry across the scene. Image courtesy of and copyright by Mary A. Parrish (National Museum of Natural History).

What Caused the Triassic Faunal Changes?

In brief, there is no satisfactory causal explanation for the taxonomic and ecological revolutions that occurred during the Triassic, and perhaps we should not expect to be able to divine them (Padian 2013). Climate change has often been invoked as a driver of biotic change in Triassic tetrapod communities. Earlier studies attempted to explain the evolutionary success of diapsid reptiles over synapsids by climatic factors. Following the late Paleozoic “Icehouse” world, global climates during the Triassic Period were for the most part warm and became increasingly dry, especially toward the end of this period. Robinson (1971) hypothesized that Triassic climates favored diapsids over synapsids in part because the former were able to excrete nitrogen with little loss of water. Extant reptiles and birds excrete

nitrogen in the form of uric acid, either as a nearly dry pellet (in lizards) or as a paste (in birds). By contrast, present-day mammals (and presumably their synapsid precursors) almost exclusively excrete nitrogen as urea, which requires copious amounts of water to be removed from the body. Given increasingly drier climatic conditions during the early Mesozoic, the water-saving disposal of nitrogen waste in archosaurs could have conferred a competitive advantage on these reptiles.

Irmis (2011) argued that climatic changes as currently understood during the Triassic could not account for the observed patterns of taxonomic change, although there were regional and latitudinal differences in which particular taxa survived and coexisted (Irmis et al. 2007). Throughout the Triassic, differential extinction favored some groups over others, though we do not know the ecological and environmental causes

of these changes. We know that nonmammalian synapsids and temnospondyls declined in taxonomic and ecological diversity compared to reptiles during the Triassic. We have no way to test hypotheses of competition among these groups, nor their implication that the surviving taxa must have been somehow competitively superior. The notion that dinosaurs simply got a “lucky break” (Brusatte et al. 2008) is intriguing but untestable. The traditional idea of “competitive superiority” of archosaurian reptiles, particularly dinosaurs, does not hold water because early dinosaurs coexisted with their relatives (Irmis et al. 2007) and with likely pseudosuchian competitors for more than 20 million years in some regions.

The Triassic—a Time of Functional and Ecological Innovation

The singular importance of the Triassic Period for the evolution of continental tetrapods consists not simply of the explosion of lineages, but of the diversifications of functional form and ecological exploitation. The taxonomic component of that diversity mainly comprised a burgeoning of archosauromorph reptiles, culminating

in the loss at the end of the Triassic of most groups of “indigenous” Triassic tetrapod groups and the survival of dinosaurs, pterosaurs, and the reptilian groups that would dominate the rest of the Mesozoic and Cenozoic eras, along with the other components of living tetrapod communities.

The ecological diversity of Triassic reptiles can best be expressed by considering the number of independent evolutionary iterations of particular ecomorphs, notably terrestrial macrocarnivores and herbivores. Marine reptiles comprised entirely separate evolutionary radiations into varied body plans. With the exception of the “Cambrian explosion” and its effects on the diversification of multicellular animals, it is difficult to think of another period in the history of life that witnessed so much rapid diversification. Even the Cenozoic radiations of mammals, although different in many respects, did not exceed the Triassic diversification of terrestrial tetrapods. The replacement of late Paleozoic “holdovers,” first by “indigenous” Triassic groups and then by representatives of the “living fauna” that has dominated since the early Mesozoic, resembles the waves of mammalian groups that replaced each other from the Paleocene to the Neogene.

* * *

Acknowledgments

We salute the late Farish Jenkins for having been the very model of a scientist, teacher, colleague, and friend for more than four decades. As much as he distinguished himself through elegant experimental research on vertebrate locomotion, his annual forays into the field greatly enriched the record of early Mesozoic vertebrate life and encouraged others to follow his lead. Every paper written by Farish tells a compelling story, weaving an exquisite narrative of functional evolution that integrates morphology, paleontology, and physiology in an innovative manner. He explored the Triassic for 30 years because he knew it held the secrets to the early evolution and assembly of the mammalian body plan and its physiological components, and he was wildly successful. Few can claim such a diverse legacy

or set such a fine example as both a researcher and teacher.

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