Chapter 10
Late Triassic Terrestrial Tetrapods: Biostratigraphy, Biochronology and Biotic Events

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Abstract The fossil record of Late Triassic tetrapods can be organized biostratigraphically and biochronologically into five, temporally successive land-vertebrate faunachrons (LVFs) that encompass Late Triassic time (in ascending order): Berdyankian, Otischalkian, Adamanian, Revueltian and Apachean. An up-to-date review of the age constraints on Late Triassic tetrapod fossil assemblages and correlation within the framework of the LVFs is presented. This makes possible a much more accurate evaluation of the timing of biotic events of Late Triassic tetrapod evolution, including: (1) Otischalkian, HO (highest occurrence) of almasaurids and chroniosuchians?, LOs (lowest occurrences) of crocodylomorphs and dinosaurs; (2) Adamanian, HO of mastodonsaurids and trematosaurids, LO of mammals; (3) Revueltian, HOs of capitosaurids, rhynchosaurs and dicynodonts; and (4) Apachean, HOs of metoposaurids, plagiosaurids and aetosaurs. The LO of turtles is Early Triassic or older, and the HO of phytosaurs is an Early Jurassic record. There is no compelling evidence of tetrapod mass extinctions at either the Carnian-Norian or the Triassic-Jurassic boundaries.

Keywords Late Triassic • Tetrapods • Berdyankian • Otischalkian • Adamanian • Revueltian • Apachean • Dinosaurs • Extinctions

10.1 Introduction

The Late Triassic was a major juncture in the evolution of terrestrial tetrapods (amphibians and reptiles) marked by many evolutionary events, including the oldest records of crocodylomorphs, pterosaurs, dinosaurs and mammals. It was also an interval of extinctions of some important tetrapod taxa, notably most of the

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temnospondyl amphibians and all of the crurotarsan archosaurs (“thecodonts” of older terminology). Much of the recent literature on Late Triassic terrestrial tetrapods takes a phylogenetic and taxonomic approach, which means it focuses on the origin, phylogenetic relationships and evolution of a particular taxon or taxa. Such an approach takes place within the context of phylogenetic (cladistic) analysis that dominates the discussion of the evolution of Late Triassic terrestrial tetrapods.

My approach here focuses on establishing the timing of biotic events in the evolution of Late Triassic terrestrial tetrapods. First, I review the temporal succession of Late Triassic terrestrial tetrapod assemblages to provide the most precise global correlation and temporal ordering possible. Within that framework, I then discuss key biotic (origination and extinction) events in the Late Triassic history of terrestrial tetrapods.

10.2 Temporal Framework

I organize the Late Triassic fossil record of terrestrial tetrapods within the temporal framework of land-vertebrate faunachrons (LVFs) developed by Lucas and Hunt (1993a), Lucas (1998, 2010) and Lucas et al. (2007a). This framework identifies five LVFs that encompass Late Triassic time (ascending order): Berdyankian, Otischalkian, Adamanian, Revueltian and Apachean (Fig. 10.1). All Late Triassic terrestrial tetrapod assemblages can be assigned to a LVF based on the genus-level taxa present in each assemblage, so the LVFs provided a means of ordering and correlating Late Triassic tetrapod assemblages that is independent of the standard global chronostratigraphic scale (SGCS, also sometimes called the “marine timescale”). Nevertheless, the cross correlation of the LVFs to the SGCS is important because it allows the tetrapod record to be correlated to physical events well constrained by marine biostratigraphy. However, that cross correlation is complicated, in places debatable, and at several points imprecise (Lucas and Heckert 2000; Lucas 2010).

The base of the Upper Triassic Series (base of the Carnian Stage) is defined by its GSSP (global stratotype section and point) at Prati di Stuori/Stuores Wiesen in northern Italy, with the primary signal the FAD (first appearance datum) of the ammonoid *Daxatina canadensis* (Mietto et al. 2012). Radioisotopic ages from Ladinian-age rocks indicate that the base of the Carnian is ~237 Ma (Mundil et al. 2010; Ogg 2012; Ogg et al. 2014; Lucas 2017b). However, direct correlation of the base of the Carnian to the LVFs is only possible in the Germanic basin, where the Carnian base is located in the middle Keuper (Gipskeuper) at about the base of the upper Grabfeld Formation (Bachmann and Kozur 2004; Kozur and Bachmann 2005, 2008). The Berdyankian tetrapod assemblage from the lower Keuper (Lettenkohle = Erfurt Formation) and the oldest Otischalkian tetrapod assemblage in the Schilfsandstein (Stuttgart Formation), which is “middle” Carnian in age, indicate the base of the Carnian correlates to a point in Berdyankian time. However, no tetrapod assemblage is known from the upper part of the Gipskeuper, so the tetrapod succession across the Ladinian-Carnian boundary is not clear in the Germanic basin.

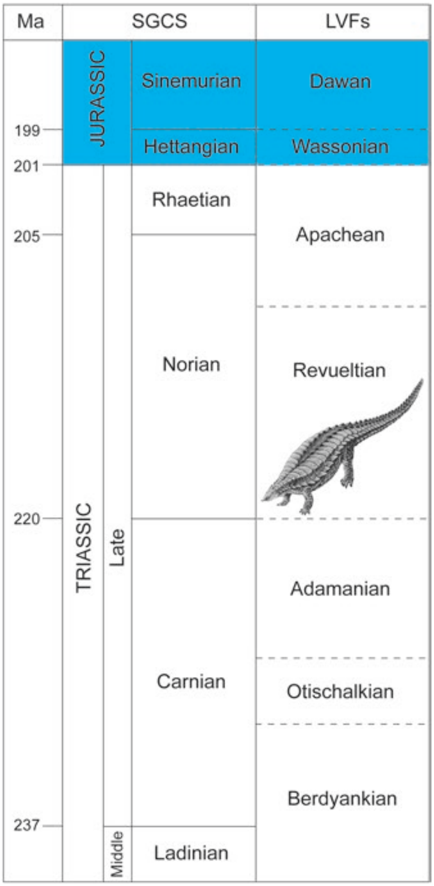

Fig. 10.1 Late Triassic land-vertebrate faunachrons (LVFs) and their correlation to the Standard Global Chronostratigraphic Scale (SGCS). After Lucas and Tanner (2015). See Lucas (2017b) for further details, especially of the numerical calibration shown here

The age of the base of the Otischalkian is well constrained as being during Carnian time, co-eval with the mid-Carnian wet episode, which is late Julian, and close in age to 231 Ma (e.g., Ruffell et al. 2016). Thus, the base of the Otischalkian in the Germanic basin is in the mid-Carnian Schilfsandstein, and that is the oldest possible age of the Otischalkian type assemblage from the basal Chinle Group in the western USA.

There is no agreed on GSSP for the base of the Norian, but that base will likely be defined using conodont biostratigraphy in western Canada or Sicily. The expectation is that the definition will be close to the longstanding working definition, which equates the base of the Norian to the base of the North American *Stikinoceras kerri* ammonoid zone (Orchard 2010, 2014). I have long advocated the equivalence or near equivalence of the base of the Norian and the beginning of the Revueltian LVF (Lucas 1998, 2010, 2015; Lucas et al. 2012). However, the "long Norian" of Muttoni et al. (2004, 2010), based on a magnetostratigraphic correlation, makes the base of the Norian much older (about 227–228 Ma) and places it within the Adamanian LVF. Lucas et al. (2012) provided a lengthy refutation of the "long Norian," placing the base of the Norian close to 220 Ma, and that correlation is followed here (Fig. 10.1). However, numerical ages that constrain the age of the base of the Norian are mostly from detrital zircons and are fraught with inconsistencies and contradictions discussed at length by Lucas et al. (2012) and Lucas (2017b). Recent work by Kohút et al. (2017) provides detrital zircon ages from Central Europe that indicate the base of the Norian is close to 221 Ma, but more data are needed to resolve fully the numerical age of the Carnian-Norian boundary.

Like the Norian, the Rhaetian base has no agreed on GSSP, though it will be defined based on the FAD (first appearance datum) of the conodont *Misikella posthernsteini*. Currently, there are two candidate GSSP sections, at Steinbergkogel in Austria, and in the Lagonegro basin of southern Italy (Krystyn et al. 2007a, b; Rigo et al. 2016; Bertinelli et al. 2016). The Apachean LVF encompasses the Norian-Rhaetian boundary, based on conchostracan biostratigraphy, magnetostratigraphic correlations and the presence of the aetosaur *Aetosaurus* in Apachean strata (Lucas 2010; Weems and Lucas 2015). Thus, Lucas (2010) regarded the Apachean as late Norian-Rhaetian.

Magnetostratigraphy, palynostratigraphy, conchostracan biostratigraphy and vertebrate biostratigraphy indicate the beginning of the Wassonian LVF is very close to the base of the Hettangian (Kozur and Weems 2005, 2007, 2010; Lucas and Tanner 2007b; Cirilli et al. 2009). Thus, I regard the Apachean-Wassonian boundary as a good approximation of the Triassic-Jurassic boundary (Fig. 10.1).

10.3 Biofacies and Biases

During the Early and Middle Triassic, terrestrial tetrapod assemblages can be divided into amphibian dominated and dicynodont dominated (Lucas and Hunt 1993b). These two kinds of assemblages likely are biofacies that represent aquatic (including shallow marine), amphibian-dominated communities and terrestrial, dicynodont-dominated communities. This dichotomy mostly ends in Berdyankian time, when the dicynodont dominated assemblages largely disappear, though they do persist into the Adamanian in South America (see below). The different composition of the tetrapod assemblages of each biofacies makes difficult direct comparisons and correlation of assemblages of the two different biofacies.

Late Triassic terrestrial tetrapod assemblages have been collected and studied for nearly 200 years, going back to the earliest studies in the Germanic basin during the early 1800s. Nevertheless, it is clear that the temporal coverage of Late Triassic time provided by terrestrial tetrapod assemblages is patchy at best. Lucas (1997) advocated using the Chinle Group tetrapod assemblages from the western USA as the standard succession of Late Triassic tetrapod assemblages. Indeed, the Otischalkian, Adamanian, Revueltian and Apachean LVFs are based primarily on Chinle Group assemblages (Lucas and Hunt 1993a; Lucas 1998, 2010; Lucas et al. 2007a). But, the Chinle Group is a succession of fluvial strata no more than 600 m thick that encompasses most of Late Triassic time, 30 million years or more. Therefore, a priori, the Chinle succession must be riddled with hiatuses ranging from paraconformities to substantial unconformities (Lucas 1993; Lucas and Spielmann 2013). This means the succession of Chinle Group tetrapod assemblages provides "snapshots" of the Late Triassic record, not a continuous and complete succession of assemblages.

Indeed, numerical calibration of the Late Triassic LVFs indicates that they are about 2–10 million years long (Fig. 10.1). Thus, at the level of LVF, the temporal resolution is poor. Subdivision of the Adamanian and Revueltian LVFs has been proposed in the Chinle Group section (Hunt 1991; Hunt et al. 2005), but these subdivisions cannot readily be correlated to other non-Chinle assemblages. This means that plotting vectors of tetrapod evolution within each LVF is difficult to impossible, so the comparisons are between LVFs, not within them.

10.4 Late Triassic Terrestrial Tetrapod Record

Terrestrial tetrapod fossil assemblages have a broad paleogeographic distribution over what was Late Triassic Pangea (Fig. 10.2). Here, I review the composition and correlation (Figs. 10.3 and 10.4) of these assemblages.

10.4.1 Berdyankian Tetrapod Assemblages

Berdyankian-age tetrapod assemblages are known from Russia (the assemblage characteristic of the LVF), Germany, Argentina, Brazil and Namibia (Figs. 10.2 and 10.3). The characteristic assemblage from the Bukobay Formation in the Russian Ural foreland basin includes an anthracosaur, the amphibians *Mastodonsaurus*, *Bukobaja*, *Cyclotosaurus*?, *Plagioscutum* and *Plagiosternum,* an erythrosuchid, a rauisuchid, and the dicynodonts "*Elephantosaurus jachimovitschi*" Vyushkov (a *Stahleckeria*-like form) and a generically indeterminate kannemeyeriid (e.g., Shishkin et al. 1995, 2000a, b; Ivakhhnenko et al. 1997; Gower and Sennikov 2000).

The Lettenkohle (Lettenkeuper, Lower Keuper, Erfurt Formation) in Germany and the Chanarian LVF localities in Argentina and Brazil are the principal correlatives of the Berdyankian type assemblage. The Lettenkohle record is important because it establishes the Ladinian age of at least part of the Berdyankian (see above). The Lettenkohle fossils are from the Grenze bonebed, the laterally equivalent/overlying Vitriolschiefer and the Kupferzell locality, so they are above the unconformity that separates the Keuper from the underlying Muschelkalk. Lettenkohle tetrapods include a chroniosuchian, the amphibians *Mastodonsaurus giganteus*, *Callistomordax*, *Plagiosternum, Plagiosuchus* and *Kupferzella*, the rauisuchian *Batrachotomus*, the prolacertiform *Tanystropheus* and small cynodonts (e.g., Wild 1978, 1980; Schoch 1997, 2000; Lucas 1999; Schoch and Werneburg 1999; Damiani et al. 2009; Gower and Schoch 2009).

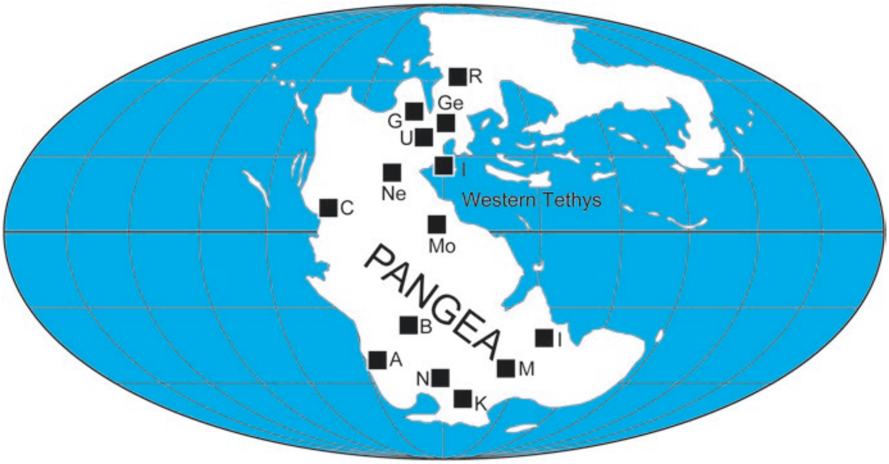

Fig. 10.2 Map of Late Triassic Pangea showing locations of principal tetrapod assemblages discussed in the text. Localities are: A = Argentina, B = Brazil, C = Chinle basin, western USA, G = Greenland, Ge = Germanic basin, I = Northern Italy, In = India, K = Karoo basin, South Africa, M = Madagascar, N = Namibia, Ne = Newark Supergroup, eastern North America, R = Russian Urals, U = United Kingdom

The Chañares local fauna from the Ischichuca (formerly Chañares) Formation of the Ischigualasto-Villa Unión basin of northwestern Argentina includes various archosaurs such as *Lagerpeton, Marasuchus* and *Chanaresuchus*, the dicynodont *Dinodontosaurus*, the traversodontid *Massetognathus*, the chiniquodontid *Chiniquodon* and the probainognathid *Probainognathus* (Bonaparte 1970, 1997; Romer 1973; Sereno and Arcucci 1993, 1994; Lucas and Harris 1996; Arcucci and Marsicano 1998; Hsiou et al. 2002; Mancuso et al. 2014). Bonaparte (1966, 1967, 1982) based the Chanarian "provincial age" on this assemblage.

Marsicano et al. (2016) reported U-Pb ages on detrital zircons of ~236–234 Ma for the Chanarian tetrapod assemblage, which, on face value indicate that they are early Carnian. However, as they noted, the "samples contain complex age inventories" (Marsicano et al. 2016: 511), so the reliability of the reported ages are open to question. However, if accurate, these ages indicate that the Chanarian tetrapod assemblage is likely of early Carnian age.

The lower part of the Santa Maria Formation in the Paraná basin of Rio Grande do Sul, Brazil, yields vertebrate fossil assemblages from Candelaria and Chiniquá considered by Barberena (1977) and Barberena et al. (1985) to be two different local faunas of different ages. Lucas (2002, 2010) regarded them as a single biostratigraphic assemblage that includes a procolophonid, archosaurs, including *Tarjadia* (=*Archaeopelta* Desojo et al. 2011; Lucas et al. 2013), the dicynodonts *Dinodontosaurus* and *Stahleckeria*, chiniquodontids, and the traversodontids *Massetognathus, Belesodon, Traversodon*, *Exaeretodon, Santacruzodo, Protuberum* and *Probelesodon* (e.g., Abdala and Ribeiro 2003; Cisneros et al. 2004; Langer et al. 2007; Reichel et al. 2009). This assemblage and the Chanarian type assemblage in

Fig. 10.3 Correlation chart of Berdyankian-Adamanian tetrapod assemblages

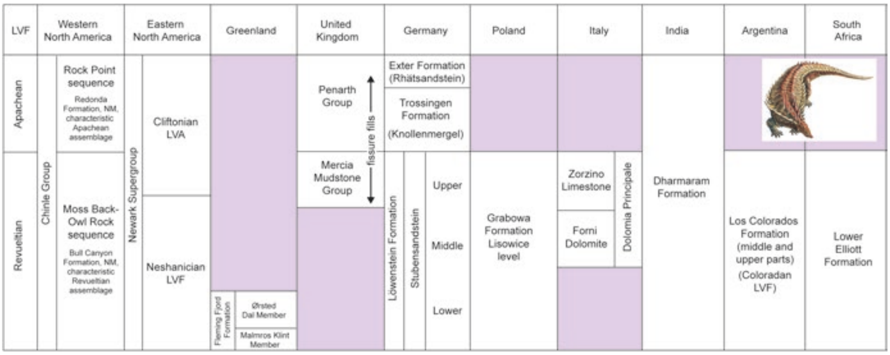

Fig. 10.4 Correlation chart of Revueltian-Apachean tetrapod assemblages

Argentina are assigned a Berdyankian age based largely on their dicynodonts and traversodontids and their stratigraphic position, which places them between tetrapod assemblages of Nonesian and Adamanian age.

The upper part of the Omingonde Formation in Namibia produces a tetrapod assemblage that includes an eryopoid temnospondyl, the dicynodonts *Kannemeyeria, Dolichuranus,* and *Rhopalorhinus*, a bauriamorph, and cynodonts (Keyser 1973a, b, 1978; Pickford 1995; Smith and Swartt 2002) that was long considered Perovkan in age (e.g., Lucas 2010). However, recent work has identified the cynodont *Chiniquodon* and the dicynodont *Stahleckeria* in the upper part of the Omingonde Formation (e.g., Abdala and Smith 2009; Abdala et al. 2013). This supports correlation to Berdyankian assemblages in South America, as detailed by Abdala et al. (2013).

Global correlation of tetrapod assemblages within the Berdyankian (Fig. 10.3) is problematic in part because of the biofacies problems outlined above. Thus, the Argentinian and Brazilian tetrapod assemblages are dicynodont-cynodont dominated and readily correlated to each other. The German and Russian assemblages are amphibian dominated and also readily correlated to each other. But, correlation of the tetrapod assemblages from the two biofacies to each other is less certain, though all of these assemblage do fall into a time interval between Perovkan and Otischalkian.

10.4.2 Otischalkian Tetrapod Assemblages

Otischalkian tetrapod assemblages are broadly distributed: in western and eastern North America, Germany, India, Morocco and possibly Kyrgyzstan (Figs. 10.2 and 10.3). The characteristic tetrapod assemblage of the Otischalkian is the assemblage of vertebrate fossils from just north of the defunct town of Otis Chalk in Howard County, Texas (Fig. 10.3). Lucas et al. (1993) and Long and Murry (1995) reviewed the fauna, which is from the Colorado City Formation of the Chinle Group. The following taxa are present: the amphibians *Latiscopus, Buettneria* and *Apachesaurus*, a procolophonid, the rhynchosaur *Otischalkia*, the archosaurs *Doswellia, Trilophosaurus* (=*Malerisaurus*) and *Poposaurus*, the aetosaurs *Longosuchus* (=*Lucasuchus*) and *Coahomasuchus*, the phytosaurs *Parasuchus* and *Angistorhinus* and the dinosaur *Lepidus* (Lucas et al. 1993; Long and Murry 1995; Heckert and Lucas 1999; Spielmann et al. 2006c; Nesbitt and Ezcurra 2015).

Otischalkian tetrapod assemblages are found across a broad geographic range of Chinle Group outcrops in Wyoming, New Mexico and Texas. The most well-known principal correlative of the type Otischalkian fauna in the Chinle Group is the vertebrate-fossil assemblage from the Popo Agie Formation of Wyoming (Branson and Mehl 1928; Mehl 1928; Colbert 1957; Lucas 1994; Lucas et al. 2002) that includes the metoposaurid *Koskinonodon*, the phytosaurs *Parasuchus* and *Angistorhinus*, the aetosaur *Desmatosuchus,* the archosaurs *Poposaurus* and *Heptasuchus*, the rhynchosaur *Hyperodapedon*, and the dicynodont *Placerias*. A less well-known principal correlative is the small assemblage from the Salitral Formation in Rio Arriba County, New Mexico, that consists of a metoposaur, *Longosuchus*, a phytosaur, and an indeterminate dinosaur (Lucas and Hunt 1992). Heckert (2004) provided some microvertebrate basis for recognition of the Otischalkian in Chinle Group strata, such as the LO of the "dinosaur" *Protecovasaurus* and the archosaur *Trilophosaurus buettneri* (also see Spielmann et al. 2008). Outside of the Chinle Group, Otischalkian assemblages are also known from the Newark Supergroup in eastern North America, the Germanic basin, Morocco, India and, possibly, Kyrgyzstan.

In the Newark Supergroup of eastern North America, the stratigraphically lower formations of the Deep River, Gettysburg, Newark and Fundy basins contain two distinct vertebrate fossil assemblages. The older of these was used by Huber et al. (1993b) as the basis of the Sanfordian LVF, after the characteristic assemblage from the Passaic ("Sanford") Formation in the Sanford sub-basin of the Deep River basin complex (see Weems et al. 2016 for a revised lithostratigraphy of the Newark Supergroup used throughout this article). An age-equivalent assemblage from the Passaic Formation (Fundy basin) is also assigned to this LVF. The collective Newark tetrapod fauna of the Sanfordian LVF includes a metoposaurid, the trematosauroid *Calamops,* procolophonids, the traversodontids *Arctotraversodon* and *Plinthogomphodon*, the dicynodont *Placerias*, the rhynchosaur *Hyperodapedon*, the archosaur *Doswellia*, the aetosaurs *Desmatosuchus* and *Longosuchus*, indeterminate rauisuchians ("*Zamotus*"), the rauisuchian *Postosuchus*, the "sphenosuchian"

Dromicosuchus, indeterminate phytosaur fragments and fragmentary dinosaur remains (e.g., Cope 1871; Olsen et al. 1989; Hunt and Lucas 1990; Huber et al. 1993a; Hunt 1993; Sues et al. 1994, 1999, 2003; Langer et al. 2000; Lucas et al. 2002; Peyer et al. 2008; Dilkes and Sues 2009; Sues and Schoch 2013). The Sanfordian correlates with the Chinle Group Otischalkian LVF based on the shared presence of *Koskinonodon*, *Hyperodapedon*, *Desmatosuchus*, *Longosuchus*, *Doswellia*, and *Placerias*.

In Germany, the Schilfsandstein (Stuttgart Formation) produces *Metoposaurus* and *Parasuchus* but lacks *Stagonolepis*, so it can be assigned an Otischalkian age (Hunt and Lucas 1991; Lucas 1999; Schoch and Werneburg 1999; Hungerbühler 2001; Kimmig and Arp 2010). Note that the Schilfsandstein is the age of the Carnian wet episode, which is "middle" Carnian (late Julian) in age (e. g., Hornung et al. 2007; Ruffell et al. 2016).

The 500-m-thick Irohalene Member of the Timesgadiouine Formation (interval T-5 of Dutuit 1966; Tixeront 1971) has produced most of the Late Triassic vertebrate fauna from Morocco. It contains the majority of vertebrate fossil localities described by Dutuit (1972, 1976, 1977, 1988, 1989a, b). Most of these occur in the lower part of the member, and they have produced a moderately diverse assemblage that includes the amphibians *Almasaurus* and *Dutuitosaurus*, the phytosaur *Parasuchus*, the aetosaur *Longosuchus*, the dicynodont *Placerias* (=*Moghreberia*, =*Azarifeneria*: Cox 1991; Lucas and Wild 1995) and the archosauromorph *Azendohsaurus* (Gauffre 1993; Lucas 1998; Jalil 1999; Flynn et al. 2010). Several of Dutuit's (1976) localities are in the upper part of the Irohalene Member, which is a distinct faunal horizon that includes the amphibian *Arganasaurus*, the phytosaur *Angistorhinus*, and the dicynodont *Placerias*. The presence of *Parasuchus*, *Angistorhinus, Longosuchus* and *Placerias* supports assigning the Irohalene Member tetrapod assemblage(s) an Otischalkian age.

In the Pranhita-Godavari Valley of India, the basal Maleri Formation produces a tetrapod assemblage that includes the amphibian *Metoposaurus*, the rhynchosaur *Paradapedon*, the phytosaur *Parasuchus*, the archosaur "*Malerisaurus*," an aetosaur, the theropod dinosaur *Alwalkeria*, a prosauropod ("cf. *Massospondylus*" of Kutty and Sengupta 1989), a large dicynodont, and the cynodont *Exeraetodon* (e.g., von Huene 1940; Jain et al. 1964; Roychowdhury 1965; Chatterjee 1967, 1974, 1978, 1980, 1982, 1987; Chatterjee and Roychowdhury 1974; Jain and Roychowdhury 1987; Bandyopadyhay and Sengupta 2006; Spielmann et al. 2006c; Kammerer et al. 2016). This is the only well-described Upper Triassic tetrapod assemblage from the Pranhita-Godavari Valley. It includes *Parasuchus* and *Metoposaurus*, taxa indicative of an Otischalkian age.

Northeast of the Pranhita-Godavari valley, in the Rewa basin of India, the Tiki Formation yields an Otischalkian tetrapod assemblage. This includes *Metoposaurus*, *Parasuchus*, the rhynchosaur *Hyperodapedon*, the supposed agamid lizard *Tikiguana*, the cynodont *Rewacodon* and the supposed mammals *Tikitherium* and *Gondwanodon* (e.g., Datta and Das 1996; Datta 2005; Mukherjee et al. 2012).

In the Fergana basin of Kyrgyzstan, the upper part of the Madygen Formation yields a tetrapod assemblage usually assigned a Ladinian-Carnian age based on the associated paleoflora (e.g., Dobruskina 1995a). Voigt et al. (2017) recently reported a U-Pb age of 237 ± 2 Ma on six concordant zircons from a pyroclastic bed stratigraphically below the tetrapod assemblage, which suggests the tetrapods may be of Carnian age. However, the entire tetrapod assemblage from the Madygen Formation is endemic and of no value to biostratigraphy. It consists of the amphibian *Triassurus*, the reptiliomorph *Madygenerpeton*, the unusual diapsids *Sharovipteryx, Kyrgyzsaurus* and *Longisquama* and the cynodont *Madygenia* (Sharov 1970, 1971; Ivakhnenko 1978; Tatarinov 2005; Unwin et al. 2000; Schoch et al. 2010; Alifanov and Kurochkin 2011). The assemblage may be of Otischalkian age, but more precise data are needed to confirm this.

10.4.3 Adamanian Tetrapod Assemblages

The characteristic tetrapod assemblage of the Adamanian is the assemblage of vertebrate fossils found in the Blue Mesa Member of the Petrified Forest Formation in the Petrified Forest National Park, near the defunct railroad siding of Adamana, Arizona (Fig. 10.3). Recent faunal lists have been provided by Murry and Long (1989), Long and Murry (1995), Heckert et al. (2005) and Parker et al. (2006). The fauna includes the following tetrapods: the amphibians *Apachesaurus* and *Koskinonodon*, the aetosaurs *Desmatosuchus* (=*Acaenasuchus*), *Stagonolepis*, *Adamanasuchus* and *Paratypothorax*, *Rutiodon*-grade phytosaurs (including *Leptosuchus* and *Smilosuchus*), the rauisuchian *Postosuchus*, the archosaurs *Hesperosuchus, Acallosuchus*, *Parrishea* and *Vancleavea*, and the dicynodont *Placerias*, as well as many microvertebrate taxa.

Besides the Chinle Group correlatives, major Adamanian faunas are those of the Conewagian interval of the Newark Supergroup basins of eastern North America; Lossiemouth Sandstone Formation, Scotland; Lehrberg Schichten-Obere Bunte Mergel interval of the German Keuper; the Krasiejów locality in Poland; Ischigualasto Formation, Argentina; and upper Santa Maria Formation and Caturitta Formation, Brazil (Fig. 10.3).

In the Chinle Group, Adamanian vertebrates are widespread and include the vertebrate fossil assemblages of the *Placerias* and Downs' quarries, Bluewater Creek Formation, Arizona (Camp and Welles 1956; Kaye and Padian 1994; Long and Murry 1995; Lucas et al. 1997; Heckert 2004; Heckert et al. 2005); the Bluewater Creek Formation and Blue Mesa Member of the Petrified Forest Formation in the Blue Hills, Arizona; the Bluewater Creek Formation and Blue Mesa Member of the Petrified Forest Formation, McKinley and Cibola counties, New Mexico (Heckert 1997); the Los Esteros and Tres Lagunas members, Santa Rosa Formation, and the Garita Creek Formation in the vicinity of Lamy, Santa Fe County, New Mexico (Hunt et al. 2005; Lucas et al. 2010); Garita Creek Formation, Santa Rosa and vicinity, Guadalupe County, New Mexico (Hunt and Lucas 1993a); and Tecovas Formation, West Texas (Murry 1986, 1989; Long and Murry 1995; Lucas et al. 2016).

The fauna at the *Placerias* and Downs' quarries has been discussed by Kaye and Padian (1994), Long and Murry (1995), Lucas et al. (1997) and Heckert (2004). It includes the amphibians *Koskinonodon* and *Apachesaurus*, the prolacertiform *Gwyneddosaurus* (=*Tanytrachelos*), the phytosaurs *Parasuchus* and *Rutiodon*/*Leptosuchus*, the aetosaurs *Stagonolepis* and *Desmatosuchus* (=*Acaenasuchus*), the rauisuchid *Postosuchus*, the archosaurs *Trilophosaurus, Acallosaurus, Poposaurus, Chatterjeea, Hesperosuchus, Tecovasaurus* and cf. *Uatchitodon*, an indeterminate ceratosaur and the dicynodont *Placerias*.

A U-Pb age recently reported from Chinle Group strata at the *Placerias*/Downs' quarries by Ramezani et al. (2014) is not consistent with earlier published ages. This is an age of 219.39 ± 0.16 Ma from near the base of the Chinle Group at the *Placerias* fossil locality in Arizona. Stratigraphic position puts this age well below a series of ages in the 220–227 Ma range reported by Ramezani et al. (2011) and Atchley et al. (2013). To explain this contradiction, Ramezani et al. (2014) claim massive lateral facies changes in the lower Chinle lithosome, and even conclude that "geochronological correlation independent of conventional stratigraphic methods [lithostratigraphy, biostratigraphy] is the only viable means for deciphering the depositional history of rock similar to the Chinle Formation" (p. 995). I prefer instead to rely on a century of geologic mapping, detailed lithostratigraphic analysis and the biostratigraphy of palynomorphs, conchostracans and vertebrates (e.g., Heckert and Lucas 2002 and references cited therein) that demonstrates that the *Placerias* quarry numerical age of Ramezani et al. (2014) is stratigraphically below many older numerical ages. Thus, the *Placerias* quarry age published by Ramezani et al. (2014) is anomalously young, likely due to postcrystallization lead loss, and should be ignored.

The following tetrapod taxa are known from the Los Esteros Member, Santa Rosa Formation, near Lamy, New Mexico: the amphibian *Apachesaurus*, the phytosaurs *Rutiodon* and *Angistorhinus*, the aetosaurs *Desmatosuchus, Tecovasuchus* and *Stagonolepis* and the dicynodont cf. *Ischigualastia* (Hunt and Lucas 1993a, 1994; Hunt et al. 2005; Heckert et al. 2007). The overlying Garita Creek Formation contains the following taxa: the amphibian *Koskinonodon*, phytosaurs, rauisuchians, and the aetosaurs *Desmatosuchus, Stagonolepis* and *Paratypothorax* (Hunt et al. 2005; Lucas et al. 2010).

The Tecovas Formation of West Texas yields the following tetrapod taxa: the amphibians *Koskinonodon* and *Apachesaurus*, the probable tetrapod *Colognathus*, the archosauromorphs *Trilophosaurus*, *Spinosuchus, Parrishea, Tecovasaurus*, and *Crosbysaurus*, the phytosaurs *Rutiodon, Leptosuchus* and *Smilosuchus,* the aetosaurs *Desmatosuchus* and *Stagonolepis*, the rauisuchian *Postosuchus*, and the oldest known mammal, *Adelobasileus* (Lucas and Luo 1993; Lucas et al. 1994, 2016; Long and Murry 1995; Spielmann et al. 2008, 2013).

In the Deep River basin of North Carolina, an assemblage of the Conewagian LVF from the Cumnock Member of the Lockatong Formation (cf. Weems et al., 2016) is superposed on the characteristic Sanfordian assemblage. Conewagian assemblages are characterized by the tetrapod assemblage in the basal Lockatong (="Gettysburg") Formation (Kozur and Weems 2010) along Little Conewago Creek in south-central Pennsylvania (Gettysburg basin: Huber et al. 1993b; Sullivan et al. 1995; Lucas and Sullivan 1997) and also are known from the Lockatong (="Cow Branch") Formation (Dan River basin), and upper Stockton and Lockatong formations (Newark basin). The most widespread and characteristic Conewagian tetrapod is the phytosaur *Rutiodon*, which co-occurs with the amphibian *Koskinonodon*, archosaurs of uncertain affinity, the problematic reptile *Colognathus*, an aetosaur (*Desmatosuchus*), one or more "ornithischian dinosaurs" (e.g., *Pekinosaurus, Crosbysaurus, Revueltosaurus* and *Galtonia*), the archosaurs *Uatchitodon* and *Gwyneddosaurus* (=*Tanytrachelos*), lepidosaurs, including the single record of the gliding lepidosauromorph *Icarosaurus* and cynodonts, including aff. *Boreogomphodon* and *Microconodon* (e.g., Emmons 1856; Olsen 1980, 1988; Olsen et al. 1989; Sues 1992; Huber et al. 1993a; Hunt 1993; Hunt and Lucas 1994; Doyle and Sues 1995; Lucas and Huber 2003; Heckert et al. 2012). Conewagian assemblages correlate with the Adamanian LVF of the Chinle Group, based on the shared presence of *Koskinonodon*, *Colognathus*, *Uatchitodon*, *Rutiodon* and other *Rutiodon*-grade phytosaurs (*Smilosuchus* of Long and Murry 1995), *Desmatosuchus* and broadly similar "ornithischian dinosaurs" (e.g., Murry and Long 1989; Lucas et al. 1992, 1997, 2016; Huber et al. 1993b; Hunt 1993; Hunt and Lucas 1994; Heckert 2004; Heckert et al. 2012).

The tetrapod assemblage of the Lossiemouth Sandstone Formation of Grampian (Elgin) Scotland comes from small quarries and the coastal section at Lossiemouth. Benton and Spencer (1995; also see Fraser 2006) provided a detailed summary that indicates that all sites come from a narrow stratigraphic interval, so they are a single biostratigraphic assemblage. It includes the procolophonid *Leptopleuron*, the sphenodontid *Brachyrhinodon*, the rhynchosaur *Hyperodapedon*, the aetosaur *Stagonolepis*, the ornithosuchid *Ornithosuchus*, the crocodylomorph *Erpetosuchus*, the probable ornithodiran *Scleromochlus* and the "dinosaur" *Saltopus*. The presence of *Hyperodapedon* and *Stagonolepis* supports assigning this assemblage an Adamanian age.

In Germany, strata in the interval between the Schilfsandstein and the Stubensandstein (Lehrberg Schichten, Blasensandstein and Kieselsandandstein) produce *Stagonolepis*, *Parasuchus* and *Metoposaurus* (e.g., Lucas 1999), and are assigned an Adamanian age (Kozur and Weems 2005).

Kear et al. (2016) recently identified a temnospondyl skull fragment as *Cyclotosaurus* from the DeGeerdalen Formation in Svalbard. These are marine strata assigned a middle-late Carnian age based on ammonoids. Thus, if correctly identified, this would be the oldest record of *Cyclotosaurus*, which is otherwise known from Revueltian (Norian) strata.

The Polish fossil record of Late Triassic tetrapods advanced greatly during the 1990s, when scientific study of the extensive bonebed in the Krasiejów clay pity near Ople began, and much has been published since (see especially the reviews by Dzik and Sulej 2007; Szulc et al. 2015). The Krasiejów tetrapod assemblage includes the amphibians *Cyclotosaurus* and *Metoposaurus*, the phytosaur *Parasuchus*, the aetosaur *Stagonolepis*, the rauisuchian *Teratosaurus* and the dinosauriform *Silesaurus* (Dzik 2001, 2003; Sulej 2002, 2005, 2007, 2010; Sulej and

Majer 2005; Dzik and Sulej 2007; Lucas et al. 2007b*;* Szulc et al. 2015; Lucas 2015). This assemblage is from strata ~80 m above the Reed Sandstone (a Schilfsandstein equivalent) that are homotaxial to the German Lehrberg Schichten and is of Adamanian age (Lucas 2015).

In Argentina, the Ischigualasto Formation is 500–900 m thick and consists of drab mudstones, tuffs and sandstones that produce an extensive tetrapod assemblage, including: the amphibian *Promastodonsaurus*, the archosaurs *Saurosuchus, Sillosuchus*, and *Proterochampsa*, the ornithosuchid *Venaticosuchus*, the aetosaur *Stagonolepis* (=*Aetosauroides*), the rhynchosaur *Hyperodapedon*, the dinosaurs *Herrerasaurus* (=*Ischisaurus*? =*Frenguellisaurus*), *Eoraptor* and *Pisanosaurus,* the chiniquodontid cynodont *Chiniquodon*, the gomphodont cynodonts *Exeraetodon*, *Proexaraetodon*, and *Ischignathus* and the dicynodont *Ischigualastia* (e.g., Cabrera 1944; Reig 1959, 1961, 1963; Casamiquela 1960, 1962; Cox 1965; Bonaparte 1976, 1997; Rogers et al. 1993; Sereno et al. 1993; Alcober and Parrish 1997; Heckert and Lucas 2002; Baczko and Ezcurra 2013). This assemblage was the basis of the Ischigualastian land-vertebrate "age" of Bonaparte (1966, 1967, 1982).

Martínez et al. (2013) reviewed the stratigraphic distribution of the tetrapod fossils in the Ischigualasto Formation to show that most are from the lower 300 m of the formation. They also reviewed the radioisotopic ages associated with the Ischigualasto Formation tetrapods (e. g., Valencio et al. 1975; Rogers et al. 1993; Currie et al. 2009) to assign them an age range of ~226–231 Ma. This suggests a late Carnian (Tuvalian) age, which fits well with the conclusion that the Ischigualasto tetrapods are of Adamanian age (Lucas 2010; Lucas et al. 2012).

In northwestern Argentina, the Puesto Viejo Group contains a tetrapod assemblage that includes *Kannemeyeria* and *Cynognathus* and has long been considered to be of Nonesian (late Olenekian) age (e. g., Lucas 2010). However, Ottone et al. (2014) reported a SHRIMP 238 U/206Pb age of 235.8 ± 2.0 Ma from a rhyolitic tuff in the approximate middle of the Puesto Viejo succession. They accepted this numerical age as evidence of the Carnian age of the Puesto Viejo tetrapod assemblage. Instead, it is much more likely that the age reported by Ottone et al. (2014) is simply incorrect (too young) and does not indicate that Nonesian tetrapods (including the classic *Cynognathus* Assemblage Zone of the South African Karoo) are of Late Triassic age.

In Brazil, the principal Upper Triassic vertebrate assemblage from the Santa Maria Formation is from the vicinity of Santa Maria City. This is the Rhynchocephalia assemblage zone of Barberena (1977) or the *Scaphonyx* assemblage of Barberena et al. (1985), from the upper part of the Santa Maria Formation. The assemblage consists of abundant fossils of the rhynchosaur *Hyperodapedon* and the aetosaur *Stagonolepis* (=*Aetosauroides*); traversodontids, proterochampsids; the archetypal rauisuchian *Rauisuchus* and the primitive dinosaur *Staurikosaurus* (Barberena et al. 1985; Lucas 2002; Lucas and Heckert 2001; Abdala et al. 2001; Langer et al. 2007; Raugust et al. 2013; Melo et al. 2015). Clearly, the presence of *Scaphonyx* and *Stagonolepis* supports correlation with the vertebrates of the Ischigualasto Formation in Argentina, and therefore an Adamanian (=Ischigualastian) age (Lucas and Heckert 2001; Heckert and Lucas 2002; Lucas 2002, 2010).

Abdala et al. (2001) identified a "traversodontid biozone" (later termed the *Santacruzodon* Assemblage Zone) intermediate between the *Dinodontosaurus* and *Hyperodapedon* assemblages of the Santa Maria Formation. This biozone yielded the cynodont *Menadon*, also found in the Isalo II strata of Madagascar (Melo et al. 2015). Abdala et al. (2001) and Melo et al. (2015) consider the *Santacruzodon* Assemblage Zone to be of Ladinian or early Carnian age. However, correlation to Isalo II suggests an age of Adamanian, which is late Carnian. Furthermore, there is no lithostratigraphic basis for placing the so-called *Santacruzodo*n Assemblage Zone between the *Dinodontosaurus* and *Hyperodapedon* assemblages (cf. Langer et al. 2007). In effect, the *Santacruzodon* Assemblage Zone is a hypothetical biostratigraphic construct based on a single locality that is the same age as the *Hyperodapedon* assemblage of the Santa Maria Formation. The *Santacruzodon* Assemblage Zone should be abandoned.

The tetrapod assemblage of the Caturrita Formation, which overlies the Santa Maria Formation, includes a mastodonsauroid amphibian, the procolophonid *Soturnia*, the sphenodont *Clevosaurus*, the lepidosaur *Cargninia*, the rhynchosaur *Hyperodapedon*, the proterochampsid *Proterochampsa*, the supposed pterosaur *Faxinalipterus* (but see Dalla Vecchia 2013), the dinosaurs *Unaysaurus* and *Guaibisaurus*, the dinosauriform *Saccasaurus*, a phytosaur, the cynodonts *Exaeretodon* and *Riograndia*, the dicynodont *Ischigualastia* (=*Jachaleria*) and diverse cynodonts (Araújo and Gonzaga 1980; Barberena et al. 1985; Dornelles 1990; Bonaparte et al. 1999, 2001, 2007, 2010a, b; Cisneros and Schultz 2003; Kischlat and Lucas 2003; Leal et al. 2003; Ferigolo and Langer 2006; Bonaparte and Sues 2006; Langer et al. 2007; Dias-da-Silva et al. 2009; Soares et al. 2011).

Philipp et al. (2013), in an extended abstract, reported U-Pb ages on 13 zircons from an ash bed (though Schultz et al. 2016 referred to these as "detrital zircons") that form an isochron of 236 ± 3.5 Ma. This ash bed is approximately at the stratigraphic level of the "*Santacruzodon* assemblage," so it suggests an age close to the Ladinian-Carnian boundary between the Berdyankian and Adamanian tetrapod assemblages of the Santa Maria Formation. Further publication of the analytical data associated with these ages is needed to assess their accuracy.

Most South American workers (e.g., Bonaparte 1982; Barberena et al. 1985; Langer 2005a, b; Rubert and Schultz 2004; Dias-da-Silva et al. 2007; Langer et al. 2007; Soares et al. 2011) advocate dividing the Brazilian Upper Triassic tetrapod succession into two biostratigraphically distinct assemblages largely based on their judgment that the dicynodonts *Jachaleria* and *Ischigualastia* are not the same taxon. They, therefore, correlate the Brazilian Caturrita Formation to the Argentinian Los Colorados Formation. Langer (2005b) also claimed that the Ischigualastian = Otischalkian + Adamanian, largely based on not recognizing the temporal range of *Hyperodapedon* as longer than the temporal range of the Ischigualastian. I do not accept either evaluation of the Brazilian Upper Triassic tetrapod biostratigraphy (Lucas 2002, 2010). Thus, I regard the Caturitta Formation as a correlative of the Ischigualasto Formation, so it is Adamanian, of late Carnian age.

In the Pranhita-Godavari Valley of India, the upper vertebrate fossil assemblage from the Maleri Formation is stratigraphically above the lower assemblage, but its stratigraphic range is not clear. This upper assemblage includes an aetosaur, prosauropods and a large dicynodont. Chigutisaurid amphibians (*Compsocerops* and *Kuttycephalus*: Sengupta 1995) and a "*Rutiodon*-like" phytosaur are also present (Bandyopadhyay and Sengupta 2006). Therefore, this assemblage may be Adamanian, but needs further documentation.

In western Madagascar, the Isalo group ("Groupe d l'Isalo" of Besarie 1930; also see Besarie and Collignon 1960, 1971) has long been divided into Isalo I, Isalo II and Isalo III based on perceived geologic age. The Isalo II strata yield Late Triassic tetrapods, including metoposaurs, sphenodontids, phytosaurs, dinosaurs, the rhynchosaur *Hyperodapedon*, the aetosaur *Desmatosuchus*, the archosaur *Azendohsaurus*, various cynodonts (including the traversodontids *Dadadon* and *Menadon*) and a dicynodont (Guth 1963; Westphal 1970; Dutuit 1978; Buffetaut 1983; Flynn et al. 1999, 2000, 2008; Lucas et al. 2002; Flynn and Wyss 2003; Burmeister et al. 2006; Kammerer et al. 2010; Ranovharimanana et al. 2011). The stratigraphic range of the Isalo II tetrapods is about 1200 m, but the rhynchosaur *Hyperodapedon* is one of the stratigraphically lowest taxa in the assemblage. This means the Isalo II assemblage is no older than Otischalkian and, based on the *Desmatosuchus* record, likely to be Adamanian. Flynn and collaborators (e.g., Flynn and Wyss 2003) advocate an older age, perhaps as old as Ladinian, for the Isalo II assemblage, but no data support that conclusion.

10.4.4 Revueltian Tetrapod Assemblages

The characteristic tetrapod assemblage of the Revueltian is that of the Bull Canyon Formation in east-central New Mexico (Fig. 10.4), and the following taxa are present: the amphibian *Apachesaurus*, the turtle *Chinlechely*s, the phytosaur *Pseudopalatus* and other *Pseudopalatus*-grade phytosaurs, the aetosaurs *Rioarribasuchus*, *Paratypothorax*, *Typothorax coccinarum* and *Aetosaurus*, the suchian *Revueltosaurus*, the "dinosaur" *Lucianosaurus*, the rauisuchian *Postosuchus*, the chatterjeeids *Shuvosaurus* (=*Effigia*) and *Chatterjeea*, the sphenosuchian *Hesperosuchus* and the cynodont *Pseudotriconodon* (e.g., Hunt 1994, 2001; Lucas et al. 2001; Joyce et al. 2009).

In the Chama basin of north-central New Mexico, the Petrified Forest Formation of the Chinle Group also yields Revueltian tetrapods, especially from the Snyder, Hayden and Canjilon phytosaur-dominated bonebeds (Sullivan and Lucas 1999; Zeigler et al. 2003; Heckert et al. 2005; Ezcurra 2006; Nesbitt and Stocker 2008). In northern Arizona, two Chinle Group units, the Painted Desert Member of the Petrified Forest Formation and the overlying Owl Rock Formation, have produced numerous Revueltian fossils, especially from the Petrified Forest National Park and from localities on Ward's Terrace north of Flagstaff (e.g., Kirby 1989, 1991, 1993; Heckert et al. 2005; Spielmann et al. 2007).

Outside of the Chinle Group, Revueltian tetrapod assemblages are known from the Newark Supergroup in eastern North America, Greenland, the Germanic basin, (including eastern Poland), northern Italy, India, Argentina and South Africa (Fig. 10.4). In eastern North America, the provincial Neshanician LVF is based on a limited fossil assemblage typified by the aetosaur *Aetosaurus arcuatus* (Lucas et al. 1998; Lucas and Huber 2003). This taxon is present in the Passaic Formation in the Durham sub-basin of the Deep River basin, the Newark Basin (range zone: Warford through Neshanic members of the lower Passaic Formation), and the middle Sugarlof Member of the Passaic Formation of central Connecticut. Other vertebrates from the Neshanician LVF include indeterminate metoposaurid and phytosaur teeth, skull and scute fragments (e.g. "*Belodon validus*"), a rauisuchian, a crocodylomorph, a traversodontid and a sphenodontid. The dominance of the primitive neopterygian *Semionotus* sp. over other fish taxa is a trend also apparent in age-equivalent strata of the Chinle Group and German Keuper (Huber et al. 1993c; Lucas and Huber 2003).

The Cliftonian LVF is based on a low-diversity assemblage defined by the distribution of the procolophonid *Hypsognathus fenneri*. This taxon is common in the type area, from the middle (?Mettlars Member) to the upper (?Member TT) Passaic Formation of the northern Newark basin (e.g., Baird 1986). It is also known from the upper Passaic Formation of the Hartford basin, central Connecticut, and the basal Blomidon Formation in the Fundy basin, Nova Scotia (Sues et al. 1997). The Fundy basin specimen of *Hypsognathus* was obtained from pebble conglomerate at the base of the Blomidon Formation, which unconformably overlies the Wolfville Formation. The only other vertebrates that occur in the interval of Cliftonian age are indeterminate phytosaur remains (including the holotype of "*Clepsysaurus pennsylvanicus*" Lea 1851) from the Ukrainian Member of the Passaic Formation in the Newark basin, moderately diverse tetrapod footprint assemblages at many horizons in the Passaic Formation (e.g., Szajna and Silvestri 1996; Lucas and Sullivan 2006), and an indeterminate sphenodontid from the upper Passaic Formation (Olsen 1980; Sues and Baird 1993; Lucas and Huber 2003).

The Malmros Klint and overlying Ørsted Dal members of the Fleming Fjord Formation in eastern Greenland yield tetrapod fossils of Revueltian age (Jenkins et al. 1994, 1997, 2001, 2008; Clemmensen et al. 2016). The Malmros Klint Member has produced fragmentary fossils of plagiosaurid amphibians, the amphibian *Cyclotosaurus*, phytosaur bones and the prosauropod dinosaur *Plateosaurus*. The Ørsted Dal Member assemblage is much more diverse: the amphibians *Gerrothorax* and *Cyclotosaurus*, the turtle cf. *Proganochelys*, unidentified sphenodontians, the aetosaurs *Aetosaurus* and *Paratypothorax*, the pterosaur *Eudimorphodon*, the prosauropod dinosaur "*Plateosaurus*," a theropod dinosaur, theropod dinosaur footprints (*Grallator*), and the mammals *Kuehneotherium*, cf. *Brachyzostrodon*? and *Haramiyavia*. As Jenkins et al. (1994) argued, this assemblage shares many taxa with the German Stubensandstein. More specifically, other than *Plateosaurus*, most taxa from the Ørsted Dal Member are known in the Lower Stubensandstein, to which I correlate the Greenland assemblage (Fig. 10.4).

In Germany, the best known and most diverse Keuper tetrapod assemblage is that of the Lower Stubensandstein (Löwenstein Formation). This assemblage includes the amphibians *Cyclotosaurus* and *Gerrothorax*, the turtles *Proganochelys* and *Proterochersis*, *Pseudopalatus*-grade phytosaurs (*Nicrosaurus*), the aetosaurs *Aetosaurus* and *Paratypothorax*, rauisuchians (*Teratosaurus*), theropod dinosaurs, and the prosauropod dinosaurs *Sellosaurus* and *Thecodontosaurus* (e.g., Benton 1993; Hungerbühler 1998; Lucas 1999; Schoch and Werneburg 1999; Schoch 2007; Kimmig and Arp 2010). The phytosaurs, aetosaurs, and rauisuchians provide a strong basis for assigning a Revueltian age to the Lower Stubensandstein (Lucas and Hunt 1993a; Hunt 1994; Lucas 1999). The younger, Middle and Upper Stubensandstein, produce a similar, but less diverse assemblage, so I also assign them a Revueltian age (Lucas 1999). Whether or not the lowest occurrence of *Mystriosuchus* in the Middle Stubensandstein is of biochronologic significance is not clear.

The tetrapod assemblages of the Upper Stubensandstein and Knollenmergel (Trossingen Formation) are almost entirely dinosaurian—95% or more of the fossils are of dinosaurs (Benton 1986, 1991). This contrasts sharply with the Lower and Middle Stubensandstein assemblages, in which dinosaurs are a much smaller percentage of the fossils collected. However, I regard this change to dinosaur domination as largely a local facies/taphonomic effect, not a biochronologically significant event (Hunt 1991). It seems likely but not certain that the Knollenmergel assemblage is of Apachean age (see below).

In eastern Poland, Dzik et al. (2008) announced the discovery of an Upper Triassic bonebed at the Lipie Slaski clay pit near Lubliniec. This bonebed yields an assemblage dominated by dicynodonts and archosaurs. There are three other correlative fossil vertebrate localities in Silesia. Another bonebed in the Woźniki clay pit yield vertebrates similar to those from Lipie (Sulej et al. 2011). Sulej et al. (2011) correlated the Woźniki assemblage with the Krasiejów locality, but Szulc et al. (2015) argue convincingly that the Woźniki assemblage and the Lipie assemblage are stratigraphically equivalent and subsume it under what they call the Lisowice level. Bones from Poręba were discovered in 2008 and include amphibians, turtles, and aetosaurs, among others, and have in part been described (Sulej et al. 2012; Niedźwiedzki et al. 2014). This locality, and very recently discovered bones from another locality at Zawiercie, are stratigraphically equated to Lipie (Szulc et al. 2015). Thus, the Lisowice level comprises the fossil vertebrate localities at Lipie, Woźniki, Poręba and Zawiercie.

Biochronologically significant tetrapod taxa reported and/or documented from the Lisowice level include the amphibians *Cyclotosaurus* and *Gerrothorax*, the turtle cf. *Proterochersis*, an aetosaur I judge to be *Paratypothorax* (Lucas 2015) and a large dicynodont (Dzik et al. 2008; Sulej et al. 2012; Niedźwiedzki et al. 2012, 2014; Świło et al. 2014). Szulc et al. (2015) represents the first explicit correlation of the Lipie bonebed to the Triassic LVFs, assigning it a Revueltian age.

In the Lombardian Alps of northern Italy, after the regional progradation of platform carbonates during the early-middle Norian (Dolomia Principale), extensional tectonism produced intraplatform depressions occupied by patch reefs, turbiditic debris flows and lagoonal to freshwater facies (Jadoul 1985; Jadoul et al. 1994). Tetrapods from these intraplatform strata, the Zorzino Limestone at the Cene and Endenna quarries in Lombardy, are the diapsids *Endennasaurus* and *Vallesaurus,* the prolacertiform *Longobardisaurus*, the rhynchocephalian *Diphydontosaurus*, the drepanosaurids *Drepanosaurus* and *Megalancosaurus*, the phytosaur *Mystriosuchus*, the aetosaur *Aetosaurus,* the pterosaurs *Eudimorphodon* and *Peteinosaurus* and the placodont *Psephoderma* (e.g., Wild 1989; Pinna 1993; Renesto 2006; Renesto et al. 2010). In Germany, *Mystriosuchus* is well known from the Middle Stubensandstein (Hungerbühler 2002) and *Aetosaurus* from the Lower-Middle Stubensandstein, so a Revueltian age of the Zorzino Limestone is certain. The Calcare di Zorzino also crops out in Austria, where it yields specimens of *Langobardisaurus* and the pterosaur *Austriadactylus* (Dalla Vecchia 2009, 2013). Also, in Austria, unpublished specimens of *Mystriosuchus* are known from Totes Gebirge (possibly Dachstein) (Buffetaut 1993).

The other Italian Late Triassic tetrapod sites are in the Forni Dolomite (Dolomia di Forni) in the Veneto Prealps of northeastern Italy. They yield the drepanosaurids *Drepanosaurus* and *Megalancosaurus,* the pterosaurs *Eudimorphodon* and *Preondactylus* (Dalla Vecchia 1995, 2003, 2006) and a specimen of *Langobardisaurus*. The presence of *Eudimorphodon* supports a Revueltian age assignment.

Upper Triassic tetrapod assemblages from the Indian Subcontinent come from the Pranhita-Godavari Valley of south-central India. Several summaries (Jain et al. 1964; Kutty 1969; Kutty and Roychowdhury 1970; Sengupta 1970; Jain and Roychowdhury 1987; Yadagiri and Rao 1987; Kutty et al. 1988; Kutty and Sengupta 1989; Bandyopadhyay and Roychowdhury 1996; Bandyopadyhay and Sengupta 2006; Kammerer et al. 2016) have been published, but other than the lower Maleri assemblage (see above), relatively few of the fossils have been adequately documented in print, forcing me to rely largely on unsubstantiated genus-level identifications to evaluate the ages of the tetrapod assemblages. A case in point is the Dharmaram Formation, which yields two stratigraphically discrete vertebrate fossil assemblages (lower and upper). The stratigraphic range of the lower assemblage has not been published, and it includes a phytosaur that Kutty and Sengupta (1989: table 2) list as *Nicrosaurus*, aetosaurs, including a so-called "*Paratypothorax*-like" form, and prosauropod dinosaurs. Based primarily on the supposed *Nicrosaurus* record, I consider the lower assemblage of the Dharmaram Formation a possible Revueltian correlative.

I formerly and tentatively regarded the Coloradan LVF of Argentina and the tetrapod assemblage of the Lower Elliot Formation in South Africa as of Apachean age. In Argentina, the Los Colorados Formation consists of siliciclastic red beds approximately 800 m thick. Near its base, a single tetrapod fossil—a dicynodont skull, the holotype of "*Jachaleria*" *colorata* Bonaparte 1970—was collected. I regard *Jachaleria* as a synonym of *Ischigualastia*, so it is likely the lower part of the Los Colorados Formation is of Adamanian age.

The remainder of the tetrapod fossils from the Los Colorados Formation are from its middle and upper parts but have not been stratigraphically organized. The assemblage includes the turtle *Palaeochersis*, the ornithosuchid *Riojasuchus,* the aetosaur "*Neoaetosauroides*" (see below), the rauisuchid *Fasolasuchus*, the crocodylomorphs *Hemiprotosuchus* and *Pseudhesperosuchus*, the prosauropod dinosaurs *Riojasaurus* and *Coloradisaurus*, the theropod dinosaur *Zupaysaurus* and the tritheledontid cynodont *Chaliminia* (e.g., Bonaparte 1970, 1971, 1978, 1980, 1997; Lucas and Hunt 1994; Rougier et al. 1995; Arcucci et al. 2004). The correlative Quebrada del Barro and El Tranquilo formations also produce prosauropods (e.g., *Riojasaurus*, "*Mussaurus*") (Bonaparte and Vince 1979; Casamiquela 1980; Bonaparte and Pumares 1995). The Los Colorados assemblage clearly is of Late Triassic age (Arcucci et al. 2004) and must be post-Ischigualastian. However, its endemism makes it difficult to correlate precisely. I tentatively considered it an Apachean correlative based primarily on its abundant prosauropods. However, the possibility that it is Revueltian needs to be considered, especially given the similarity of *Neoaetosauroides* to *Aetosaurus*.

Indeed, having now had the opportunity to study the type material of *Neoaetosauroides engaeus* firsthand, it is abundantly clear that *Neoaetosauroides* is a junior synonym of *Aetosaurus*. Thus, the armor plates of *Neoaetosauroides* (Fig. 10.5) display all of the diagnostic features of the armor of *Aetosaurus* (cf. Fraas 1877; Heckert and Lucas 2000; Schoch 2007). To wit, the dorsal paramedian plates are moderately wide (width/length = 2.4–3.1) and possess a radial pattern of elongate ridges and pits and a low dorsal boss near the posterior margin of the plate (Fig. 10.5). The work of Desojo and Baéz (2007: text-fig. 5) makes it clear that the skulls of *Neoaetosauroides* and *Aetosaurus* have virtually identical suture patterns and proportions. This synonymy will be documented in greater detail elsewhere. But, I draw attention to it here because *Aetosaurus* is an index taxon of the Revuletian LVF. Thus, its presence in the middle-upper Los Colorados Formation indicates a Revueltian age.

Kent et al. (2014) presented a magnetostratigraphy of the Los Colorados Formation based on limited sampling of only 52 geomagnetic sites with a stratigraphic spacing of 10 m or more. The 15 polarity intervals identified were pattern matched to the E8-E15 interval of the Newark section, which, if correctly correlated, means the Los Colorados Formation crosses the Carnian-Norian boundary (is of Adamanian-Revueltian age). This is consistent with my interpretation that the Los Colorados is of Adamanian-Revueltian age. Nevertheless, I have little confidence in the pattern matching to the Newark magnetostratigraphy of so few and such widely spaced samples from the Los Colorados Formation.

The age of the tetrapod assemblage from the Lower Elliott Formation in South Africa has long been considered Late Triassic. Lucas and Hancox (2001) reviewed the age of this assemblage, which is dominated by sauropodomorph dinosaurs, but also has rare amphibians (a large chigutisaurid), a possible rauisuchian (*Basutodon*), the ornithischian dinosaur *Eocursor*, a traversodontid (*Scalenodontoides*) and the characteristic Late Triassic footprint ichnogenus *Brachychirotherium* (Kitching and Raath 1984; Lucas and Hancox 2001; Butler et al. 2007). This is the "*Euskelosaurus* range zone" of Kitching and Raath (1984), the youngest Triassic tetrapod assemblage in the Karoo basin. Yates (2003) re-evaluated the prosauropods of the Lower Elliott Formation and concluded that most are indeterminate sauropodomorphs or

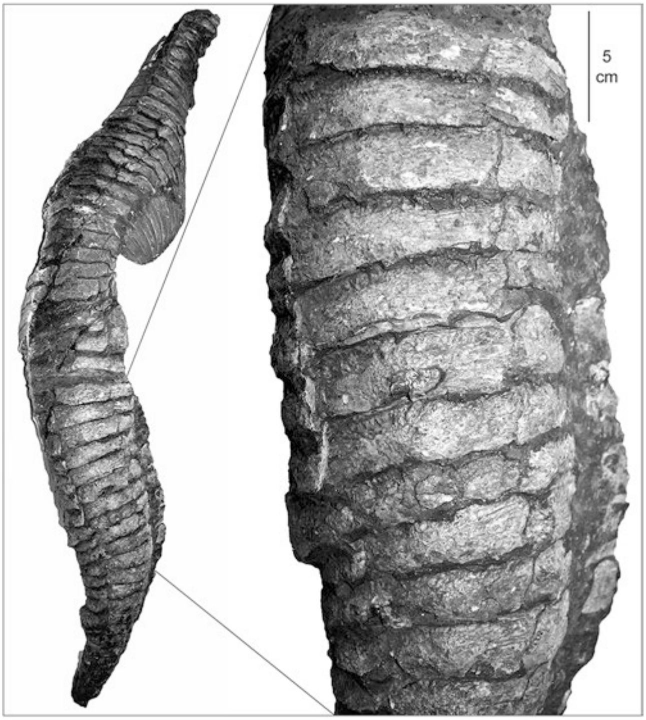

Fig. 10.5 Part of the holotype of *Aetosaurus* (“*Neoaetosauroides*”) *engaeus*, Instituto Miguel Lillo, Tucuman, Argentina, PVL 3525. On *left* is a dorsal view of the dorsal armor, and on the *right* is a detail of part of the armor showing paramedian and lateral plates of the posterior dorsal to sacral region

basal sauropods. He noted similarities of indeterminate prosauropods from the Lower Elliott Formation to *Riojasaurus* from the Los Colorados Formation of Argentina, and similarities between the basal sauropod *Antetonitrus* from South Africa and *Lessemsaurus* from Argentina (Yates and Kitching 2003). These conclusions suggest a Lower Elliott-Los Colorados correlation, and thus a tentative Revueltian age assignment.

10.4.5 Apachean Tetrapod Assemblages

The characteristic tetrapod assemblage of the Apachean LVF is from the Redonda Formation of the Chinle Group in Guadalupe and Quay Counties, New Mexico, USA. The following taxa are present: the amphibian *Apachesaurus*, a sphenodontid, a procolophonid, the phytosaur *Redondasaurus*, the aetosaurs *Redondasuchus* and *Apachesuchus*, the rauisuchian *Redondavenator*, the archosauriform *Vancleavea*, theropod dinosaurs and the cynodont *Redondagnathus* (e.g., Hunt 1994; Hunt and

Lucas 1993b, 1997; Heckert et al. 2001; Hunt et al. 2005; Spielmann et al. 2006a, b; Spielmann and Lucas 2012).

Principal correlatives of the type Apachean assemblage are the Whitaker quarry in the Rock Point Formation of the Chinle Group at Ghost Ranch, New Mexico, the Cliftonian LVF assemblages (in part) of the Newark Supergroup, the Knollenmergel (Trossingen Formation), time-equivalent upper Arnstadt Formation and the "Rhaetian Bonebed" (Exter Formation) of the Germanic Basin (Fig. 10.4). Some of the fissure-fill assemblages in the uppermost Mercia Mudstone Group and/or lowermost Penarth Group of the United Kingdom (Fraser 1994; Benton and Spencer 1995; Whiteside and Marshall 2008) may be Apachean correlatives. Some of the so-called Rhaetian vertebrate sites in France, such as Saint-Nicolas-de-Port, may be Apachean correlatives as well (Lucas and Huber 2003).

At Ghost Ranch in New Mexico, the Whitaker quarry bone bed is dominated by skeletons of the theropod dinosaur *Coelophysis bauri* (Colbert 1989; Rinehart et al. 2009). Nevertheless, it also includes the sphenodont *Whitakersaurus*, at least one drepanosaur, a rauisuchian skeleton (cf. *Postosuchus*), the sphenosuchians *Hesperosuchus* and *Vancleavea*, the chatterjeeid *Shuvosaurus* (=*Effigia*), the phytosaur *Redondasaurus* and the theropod dinosaur *Daemonosaurus* (e.g., Hunt and Lucas 1993b; Clark et al. 2000; Harris and Downs 2002; Hungerbühler 2002; Hunt et al. 2002; Lucas et al. 2003; Nesbitt 2007; Lucas et al. 2005; Heckert et al. 2008; Renesto et al. 2009; Rinehart et al. 2009; Sues et al. 2011).

A recently discovered bonebed (the "Saints and Sinners Lagerstätte") in the Wingate Sandstone (which is the lower part of the "Nugget Sandstone" of Sprinkle et al., 2011) of northeastern Utah includes fossils of sphenodonts, sphenosuchians, drepanosaurs, theropod dinosaurs and a pterosaur, yet to be described (Britt et al. 2016: table 1). Given its stratigraphic position, this bonebed is likely of Apachean age.

The uppermost Triassic strata of the Newark Supergroup in eastern North America yield a low diversity tetrapod assemblage of mostly fragmentary material that defies precise identification. The tetrapods present include the procolophonid *Hypsognathus*, sphenodontids, indeterminate phytosaurs and the synapsid *Oligokyphus* (e.g., Gilmore 1928; Baird 1986; Huber et al. 1993b; Fedak et al. 2015). These are the tetrapods of the Cliftonian LVF of Huber et al. (1993b) and at least some are of likely Apachean age.

In the United Kingdom, fissure fills such as Durdham Down in Clifton yield fossils that include phytosaurs, aetosaurs, dinosauriforms and dinosaurs (e.g., Fraser 1994, 2006; Fraser et al. 2002; Galton 2005, 2007a, b; Whiteside and Marshall 2008). Unfortunately, other than a tentative record of *Aetosaurus* based on a single osteoderm (Lucas et al. 1999), the fissure fill tetrapods are mostly endemic taxa of no biochronological significance or cosmopolitan taxa with long age ranges, such as the sphenodontian *Clevosaurus*.

Whiteside and Marshall (2008), based primarily on the palynoflora, assigned the Tytherington fissure fill a Rhaetian age, and extrapolated this age to the other fissures. If this Rhaetian age is correct, then the fissure fill tetrapods are of Apachean age. However, as Lucas and Hunt (1994: 340) noted, "a single age should not necessarily be assigned to the fossils from one fissure and…individual fossils from the fissures may range in age from middle Carnian to Sinemurian." Therefore, I continue to regard as problematic the precise age of the Triassic tetrapod assemblages from the British fissure fills.

10.4.6 Wassonian LVF

Lucas and Huber (2003) introduced the Wassonian LVF, and Lucas and Tanner (2007a) defined is as the time interval between the FAD of the crocodylomorph *Protosuchus*, and the beginning of the Dawan LVF, which is defined by the FAD of the theropod dinosaur *Megapnosaurus* (Lucas 2008). The FAD of *Protosuchus* in Arizona, Nova Scotia and South Africa appears to be lowermost Jurassic, so I take the beginning of the Wassonian LVF to approximate the Triassic-Jurassic boundary (Fig. 10.1). Most Early Jurassic tetrapod assemblages, however, are younger, of Dawan (~Sinemurian) age (Lucas 2008).

10.5 Late Triassic Tetrapod Footprints and Bromalites

The Upper Triassic record of tetrapod footprints was reviewed by Klein and Lucas (2010a) and is also reviewed by Hunt et al. (2017), so I do not review it here. It only resolves into one or two biochronological units, and is thus of much less significance to Late Triassic tetrapod biochronology than is the body-fossil record (e.g., Lucas 2007; Hunt and Lucas 2007; Klein and Lucas 2010a). Similarly, the Late Triassic bromalite (principally coprolite) record has some biochronological utility, but, like the footprint record, it resolves Late Triassic time rather poorly (see Hunt et al. 2017).

Brachychirotherium (*sensu stricto*), the footprint of aetosaurs (Fig. 10.6; Lucas and Heckert 2011), appears at the beginning of the Otischalkian. It is a characteristic ichnotaxon of the Late Triassic, together with *Atreipus-Grallator* (quadrupedal to bipedal trackways), *Grallator* and *Eubrontes* (bipedal trackways), the latter all attributed to theropods, except for *Atreipus*, which may also have had an ornithischian trackmaker. The stratigraphic upper limit of *Brachychirotherium* is the Triassic-Jurassic boundary (end of the Apachean); there is no evidence of *Brachychirotherium* in post-Triassic strata (Rainforth 2003; Lucas and Tanner 2007a, b, 2015).

Late Triassic tetrapod footprint assemblages are characteristically archosaur-dominated, particularly by chirothere and theropod tracks, but also feature the oldest records of sauropodomorph tracks. They thus mirror the overall pattern of the body fossil record but provide much less detailed insight into Late Triassic tetrapod distribution and evolution.

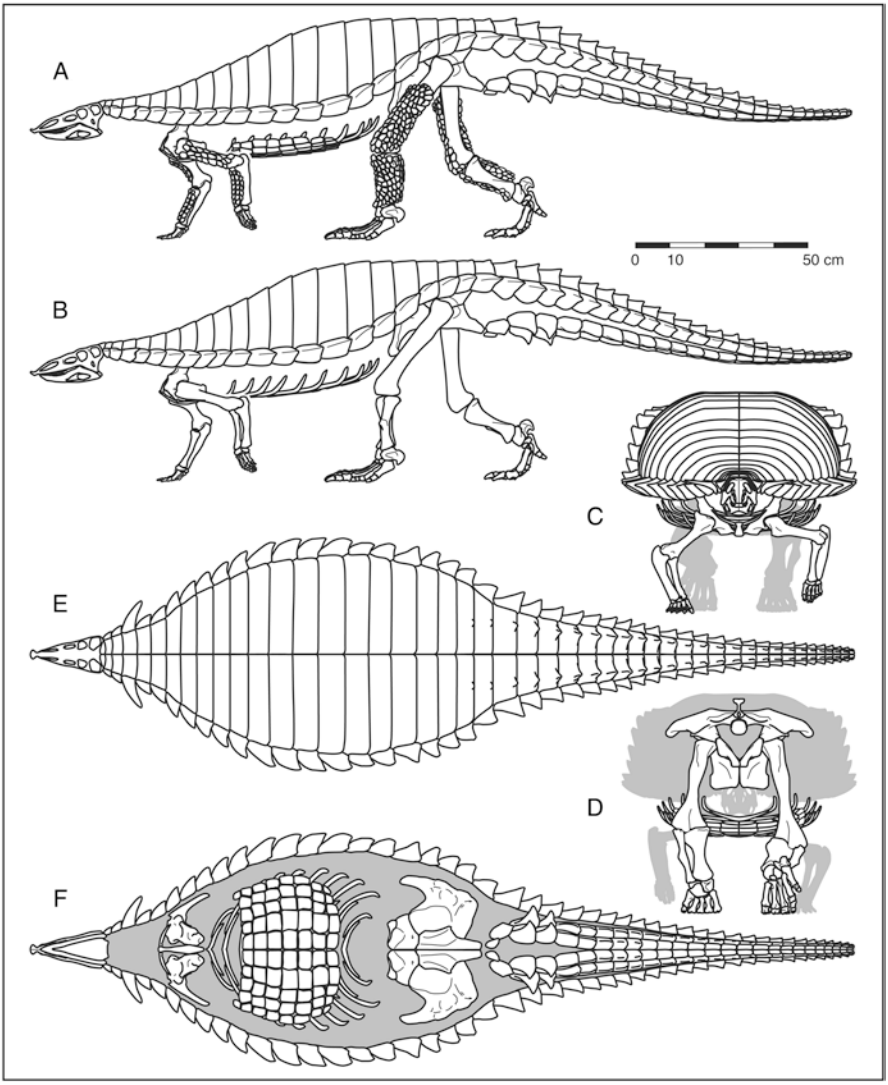

Fig. 10.6 The skeleton of the aetosaur *Typothorax coccinarum* as the trackmaker of *Brachychirotherium*, in lateral (**a**, **b**), anterior (**c**), posterior (**d**), dorsal (**e**) and ventral (**f**) views. After Lucas and Heckert (2011)

10.6 Biotic Events

10.6.1 Introduction

The Late Triassic has long been recognized as a critical juncture in the evolution of terrestrial tetrapods because it was an interval of both important originations and extinctions (e.g., Fraser 2006; Sues and Fraser 2010). Here, I discuss the nature and timing of some of these events (Figs. 10.7, 10.8, 10.9, 10.10, 10.11, 10.12, and 10.13).

10.6.2 Archosaurs Rise to Dominance

The Berdyankian is the time of most of the youngest, dicynodont-dominated tetrapod assemblages. These assemblages are primarily from Argentina and Brazil and are dominated by fossils of dicynodonts (mostly the genus *Dinodontosaurus*), rhynchosaurs and traversodontid cynodonts. Fossils of amphibians and archosaurs are much less common constituents of these assemblages.

In contrast, the amphibian biofacies of Berdyankian time is dominated by mastodonsaurids and plagiosaurs, with much lesser numbers of prolacertiforms, archosaurs and small cynodonts. These assemblages are best known from the Germanic basin and from Russia. An acme in plagiosaur diversity and abundance in these assemblages characterizes Berdyankian time. No procolophonids are known from Berdyankian strata, but this must be due to a lack of discovery, not a real absence, as both pre- and post-Berdyankian procolophonids are known.

Otischalkian tetrapod assemblages are different from Berdyankian assemblages in being dominated by archosaur fossils, particularly of phytosaurs and aetosaurs. Indeed, it is during Otischalkian time, about 15 million years after the end-Permian extinctions that archosaur-dominated tetrapod fossil assemblages first appear. Thus, the old idea (e.g., Benton 1991; McGhee et al. 2004) that the Permo-Triassic extinctions were characterized by the takeover of many terrestrial tetrapod niches by archosauromorphs is erroneous (also see Lucas 2017a).

A new group of temnospondyls, the metoposaurs, is also abundant during Otischalkian time. It is striking how uniform in overall composition the Otischalkian tetrapod assemblages are, from North America, Western Europe, Morocco and India. This implies a degree of cosmopolitanism and no major biofacies differences.

The beginning of the Otischalkian essentially corresponds or overlaps the onset of the Carnian humid episode (e. g., Ruffell et al. 2016). Two groups of dominantly amphibious/aquatic tetrapods are abundant at this time, the metoposaurs and the phytosaurs. This may be a real acme as a response to wetter climates, but that conclusion may be confounded by taphonomy—preferential preservation of aquatic tetrapods by widespread river systems of the Carnian "pluvial." That caveat aside, metoposaurs and phytosaurs are the dominant components of almost all Otischalkian and younger Late Triassic tetrapod assemblages.

The overall character of many Adamanian tetrapod assemblages is very similar to Otischalkian assemblages—domination by fossils of metoposaurs, phytosaurs and aetosaurs. However, Adamanian tetrapod assemblages from Argentina and Brazil are dominated by dicynodonts, cynodonts and rhynchosaurs, with few to no phytosaurs and metoposaurs. Nevertheless, aetosaurs are common in these assemblages.

Fig. 10.7 Restoration of the Late Triassic metoposaurid amphibian *Koskinonodon* (artwork by Matt Celeskey)

Fig. 10.8 Restorations of the female (above) and male (below) heads of the phytosaur *Pseudopalatus*, showing the cranial sexual dimorphism evident in population samples of this phytosaur (artwork by Matt Celeskey)

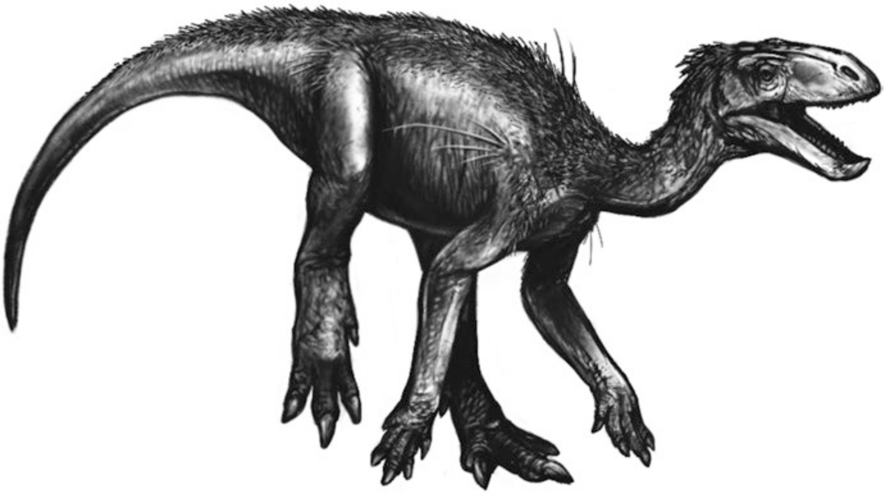

Fig. 10.9 The Late Triassic dinosauromorph *Silesaurus* has a foot structure that would make tracks like those of early theropod dinosaurs (artwork by Matt Celeskey)

Revueltian and Apachean tetrapod assemblages are also dominated mostly by archosaurs and metoposaurs. In some assemblages, dinosaurs are very abundant, and it is clear that the diversification of the dinosaurs had already begun by Revueltian time (Hunt 1991).

10.6.3 Temnospondyl Diminishment and Extinctions

The Late Triassic was the last interval of any substantial temnospondyl diversity (Milner 1990, 1993; Schoch and Milner 2000; Schoch 2008, 2014) (Fig. 10.7). It is also clear that this diversity collapsed stepwise throughout the Late Triassic, so that by Jurassic time few temnospondyl clades remained (Fig. 10.13). The lissamphibian radiation had begun in the Early Triassic (e.g., Rage and Roček 1989), though no definite lissamphibian fossils are known from the Upper Triassic, with the possible exception of *Triassurus* from Madygen (Ivakhnenko 1978).

The Late Triassic temnospondyl families are the Brachyopidae, Capitosauridae, Chigutisauridae, Almasauridae, Mastodonsauridae, Metoposauridae, Plagiosauridae and Trematosauridae. All are families of low diversity following much greater temnospondyl diversity earlier in the Permian and Triassic (Milner 1990; Ruta and Benton 2008). The record of almasaurids ends in the Otischalkian, and that of mastodonsaurids and trematosaurids ends in the Adamanian. Capitosaurid records are no younger than Revueltian, and metoposaurids and plagiosaurids have records that end in the Apachean. Brachyopids continued into the Jurassic, whereas chigutisaurids continued to the Cretaceous. Chroniosuchians have their last record at Madygen

Fig. 10.10 One of the last dicynodonts, Adamanian *Placerias*, attacked by a phytosaur (artwork by Matt Celeskey)

during the Otischalkian(?). Clearly, old ideas of a major extinction of temnospondyls at the end of the Triassic can be abandoned (Lucas and Tanner 2015).

10.6.4 Turtle Origins

The oldest turtles were long considered to be Revueltian in age. Best known is *Proganochelys* from Germany (Gaffney 1990), and Revueltian or younger turtle records are also known from Poland, Thailand, Greenland, the USA and South America (e.g., Lucas et al. 2000; Joyce et al. 2009; Joyce 2017). Recently added to this record is *Odontochelys* from marine lower Carnian strata in China (Li et al. 2008) and a supposed Ladinian turtle, *Pappochelys* from Germany (Schoch and

Fig. 10.11 Restoration of the oldest mammal, *Adelobasileus* (artwork by Matt Celeskey)

Fig. 10.12 The drepanosaur *Hypuronector* (artwork by Matt Celeskey)

Sues 2015). Furthermore, the middle Permian *Eunotosaurus*, with expanded ribs, originally proposed as a close turtle relative by Watson (1914), is now being placed back into that position (Lyson et al. 2010, 2012, 2013, 2016).

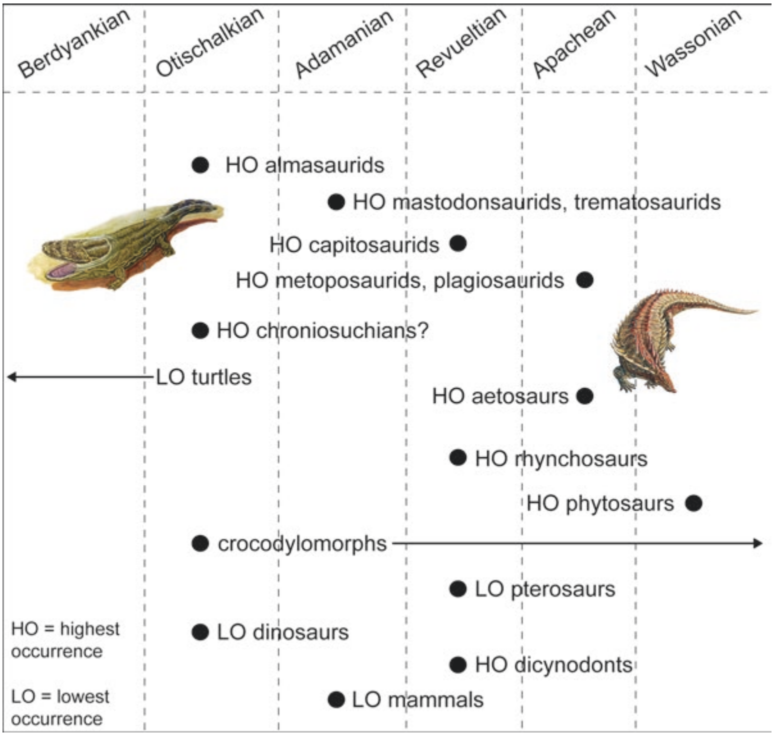

Fig. 10.13 Timing of the records of some important biotic events in the Late Triassic evolution of terrestrial tetrapods

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Much overlooked in the discussion of turtle origins is their footprint record, which begins in the late Early Triassic (Spathian) (Rühle v. Lilienstern 1939; Haubold 1971; Lovelace and Lovelace 2012; Thomson and Lovelace 2014; Lichtig et al. 2017). Thus, recent claims that *Odontochelys* or *Pappochelys* are the oldest turtles are incorrect—the oldest turtle fossils (footprints) are of Early Triassic (Nonesian) age. They thus predate the oldest body fossils of turtles (and I do not consider *Pappochelys* to be a turtle; it is a placodont) by at least 10 million years. The origin of turtles thus is not, as long thought, a Late Triassic event, but took place much earlier (Fig. 10.13).

10.6.5 Rhynchosaurs

Rhynchosaurs are a Triassic group of herbivorous archosauromorphs that were most diverse during the Middle Triassic. Indeed, Romer (1966) long argued that together with gomphodont cynodonts they were dominant elements of Middle Triassic tetrapod assemblages. However, rhynchosaurs were of low diversity during the Late Triassic, known from only a few genera. Most interesting is the very cosmopolitan *Hyperodapedon* found in Otischalkian-Adamanian assemblages in North America, western Europe, India, South America, Africa and Madagascar (Lucas et al. 2002).

The rhynchosaur genus *Otischalkia* is known from Otischalkian-Revueltian strata of the Chinle Group in the western USA (Hunt and Lucas 1991; Long and Murry 1995; Spielmann et al. 2013; Lucas et al. 2016). The Revueltian record of *Otischalkia* is the only bona fide Norian record of a rhynchosaur, and demonstrates that they did not go extinct at the Carnian-Norian boundary, as long thought (e.g., Benton 1991).

Schultz et al. (2016: fig. 10) recently presented what I regard as an erroneous time calibration of Late Triassic rhynchosaurs. Thus, they show "*Isalorhynchus*" (a synonym of *Hyperodapedon*) predating *Hyperodapedon* during the Carnian. They show *Teyumbatia* (a cladotaxon named and described by Montefeltro et al. 2010, 2013, likely synonymous with *Hyperodapedon;* cf. Azevedo and Schultz 1987) as Norian, though the fossil is from the Adamanian Caturitta Formation and therefore of Carnian age (see above). Schultz et al. (2016) also uniquely claim that *Otischalkia* is not diagnostically a rhynchosaur. Clearly, my view of Late Triassic rhynchosaur distribution differs markedly from that of Schultz et al. (2016), though all agree that rhynchosaur diversity was low during the Late Triassic.

10.6.6 Phytosaurs and Aetosaurs

Recent analysis identifies Middle Triassic *Diandongosuchus* as the oldest phytosaur and cladotaxonomically splits many long-recognized phytosaur genera into multiple genera (e. g., Stocker 2012; Stocker and Butler 2013; Butler et al. 2014; Stocker et al. 2017). This work ignores important factors of biological variation in phytosaurs (e.g., Fig. 10.8; Kimmig and Spielmann 2011) and will need substantial revision. The peak of phytosaur diversity was during the Adamanian-Revueltian, with perhaps no more than one genus surviving into Apachean time. A phytosaur snout fragment from the Lower Jurassic of the UK is the stratigraphically highest phytosaur fossil not clearly reworked, so it suggests phytosaur survival across the Triassic-Jurassic boundary (Maisch and Kapitzke 2010) (Fig. 10.13).

Aetosaur taxonomy is similarly being overspilt by cladotaxonomy (Desojo et al. 2013) and will need revision. The oldest aetosaur records are Otischalkian, with an acme during the Adamanian-Revueltian. Most of the evidence of Apachean aetosaurs is based on the footprint ichnogenus *Brachychirotherium* (see above).

Assemblages dominated by metoposaurs, phytosaurs and/or aetosaurs characterize much of the Late Triassic tetrapod record. Clearly, a taphonomic overprint is at least in part responsible for this. Metoposaurs and phytosaurs were amphibious tetrapods that would have been preferentially preserved/fossilized in the fluvial sediments from which comes most of the Late Triassic tetrapod fossil record. Nevertheless, before the Otischalkian no such metoposaur/phytosaur/aetosaur assemblages are known, though these groups likely had a Middle Triassic ancestry. The abundance and ubiquity of metoposaurs and phytosaurs is a Late Triassic phenomenon across Pangea, with the exception of South America.

10.6.7 Crocodylomorphs

The oldest crocodylomorphs are sphenosuchans, with a record that begins in the Otischalkian (Lucas et al. 1998). Among them are taxa well-known from comprehensive cranial and postcranial material such as *Hesperosuchus*, *Sphenosuchus*, *Saltoposuchus, Dibothrosuchus* and *Protosuchus* (e. g., Colbert and Mook 1951; Colbert 1952; Crush 1984; Parrish 1991; Sereno and Wild 1992; Wu and Chatterjee 1993; Lucas et al. 1998; Clark et al. 2004). These early crocodiles have long been interpreted as lightly built cursorial and fully terrestrial forms.

No substantial change takes place in the Sphenosuchia across the Triassic-Jurassic boundary (Klein and Lucas 2015). What does occur much later, definitely in the Late Jurassic, perhaps as early as the Middle Jurassic, is the appearance of aquatic/amphibious crocodylians. The body fossil and footprint records document this (e.g., Lockley et al. 2010; Klein and Lucas 2010b, 2015). Clearly, the aquatic predator niches now associated with crocodylians were not occupied by crocodylomorphs during the Late Triassic-Early Jurassic. Phytosaurs occupied at least some of those niches during the Late Triassic (Hunt 1989).

10.6.8 Pterosaur Origins

Pterosaurs appear suddenly and completely adapted to flight during the Late Triassic. The lack of antecedents has made the origin and precise phylogenetic placement of pterosaurs somewhat unclear. Certainly pterosaurs are archosaurs, and most (but not all) analyses place them close to dinosaurs (see Hone and Benton 2008; Dalla Vecchia 2013 for reviews). *Scleromochlus* from the Adamanian of Scotland has been considered to be related to the ancestry of pterosaurs by some (e.g., Padian 1984), but others have dismissed that idea (e.g., Sereno 1991).

The oldest complete and reliable skeletal records of pterosaurs are Revueltian, from Italy, but isolated teeth and bones of Adamanian age have also been identified (with less certainty) as pterosaur (see Barrett et al. 2008; Dalla Vecchia 2013). *Faxinalipterus* from the Adamanian of Brazil, a supposed pterosaur (Bonaparte et al. 2010b), is not demonstrably a pterosaur according to Dalla Vecchia (2013). Given the phylogenetic analysis and their temporal distribution it seems that, as with dinosaur origins (see below), pterosaur origins was likely a Middle Triassic event for which we need a fossil record. However, on face value, the pterosaur first appearance is a sudden one during the Revuletian of forms very similar to the long-tailed, non-pterodactyloid pterosaurs of the Jurassic.

10.6.9 Dinosaur Origins

Understanding dinosaur origins has been beset by three problems: (1) semantic, namely what is and what is not a dinosaur; (2) cladistic—disagreements over the phylogeny of dinosaur origins, confounded by an inability to sort out convergence; and (3) biochronologic—disagreements over the actual age of the "oldest dinosaur." Despite these problems, all agree that the oldest dinosaur body fossils are Carnian (e.g. Langer et al. 2009; Lucas 2010; Benton 2012; Nesbitt and Ezcurra 2015). More precisely, they are Otischalkian, from the Chinle Group in the western USA (*Lepidus*) and the Maleri Formation of India (*Alwalkeria*). Otischalkian or Adamanian records of "dinosaurs" (*Azendohsaurus*) from Morocco and Madagascar have been discounted as not being based on dinosaurs (see Langer 2014 for discussion). Records from South America are Adamanian, so they are not the oldest records of dinosaur body fossils (contra Langer et al. 2009; Langer 2014).

The footprint record of the earliest dinosaurs also does not demonstrate dinosaurs older than Carnian. This, despite diverse claims (one of the most recent being by Marsicano et al. 2007) that tridactyl, apparently mesaxonic footprints from Middle Triassic strata are dinosaurian. Most of these are tridactyl remnants of chirothere tracks (see review by Klein and Lucas 2010a). Also, some could be the tracks of dinosauromorphs (Fig. 10.9) or of ornithodirans close to dinosaur origins, as discussed by Marsicano et al. (2007).

Particularly misleading, however, was the claim of dinosauromorph tracks in the Lower Triassic of Poland (Brusatte et al. 2011). This claim was based on the ichnogenus *Protorodactylus*, which is barely, if at all distinguishable from *Rhynchosauroides* (Klein and Niedzwiedźki 2012). The so-called "dinosauromorph" tracks of Brusatte et al. (2011) thus are most likely the tracks of lepidosauromorphs.

To conclude, the oldest dinosaur fossils are Carnian, more specifically of Otischalkian age. Importantly, they are not from South America, as many have erroneously claimed, though, clearly, much more remains to be discovered of dinosaur origins.

10.6.10 Dicynodont Diminishment and Extinction

The dinocephalian extinction event near the end of the middle Permian opened up the tetrapod herbivore niches to dicynodonts (Lucas 2017a). During the late Permian and Early Triassic, successive tetrapod assemblages were dominated by a single dicynodont genus, most famously *Lystrosaurus* of the earliest Triassic. However, other than in South America, by Berdyankian time dicynodont domination of the tetrapod herbivore niches had diminished (Fig. 10.10). Dicynodont diversity was low in the Late Triassic, with only one-two genera per LVF, and dicynodonts are only abundant in some South American assemblages. Late Triassic dicynodonts are also known from mass death assemblages in Arizona, Morocco and Poland.

The tetrapod herbivore niches occupied by dicynodonts may have been taken over by herbivorous aetosaurs, rhynchosaurs, prosauropod dinosaurs and cynodonts. However, the feeding mechanism of these herbivores are very different than those of dicynodonts, so replacement seems unlikely.

The HO (highest occurrence) of dicynodonts was long thought to be Adamanian. However, there is a putative Cretaceous record from Australia (Thulborn and Turner 2003), though it seems extremely doubtful. Dzik et al. (2008) recently reported a Triassic dicynodont from Poland in strata they deemed Rhaetian based on paleobotany, but that are Revueltian (Lucas 2015). These are the youngest known dicynodonts (Fig. 10.13).

10.6.11 Cynodont Evolution and Mammal Origins

The first cynodonts appear at about the end of the middle Permian and gradually increased in generic diversity through the Permo-Triassic boundary, the prelude to a much greater diversification during the Middle-Late Triassic (e. g., Abdala and Ribeiro 2010; Smith et al. 2012; Ruta et al. 2013; Abdala and Gaetano 2017). Late Triassic cynodont families are primarily the Traversodontidae, Trithelodontidae and Tritylodontidae. Traversodontids were most diverse (~ 17 genera), mostly of Adamanian age and mostly known from Gondwana (Liu and Abdala 2014). The only well-documented, post-Adamanian traversodontid is *Scalenodontoides* from the Revueltian Lower Elliott Formation of South Africa.

Tritylodontids were very mammal-like, especially in their postcranial anatomy. Their first appearance is during the Revueltian. However, most of their diversity is Early Jurassic. Trithelodontids (including the “dromatheres”) were also not very diverse during the Late Triassic, but they most likely include the ancestors of mammals.

For decades, the oldest mammals were considered to be of Late Triassic age, notably *Morganucodon* from the British fissure fills. Cladistic analysis of the earliest mammals by Rowe (1988), however, changed that by redefining Mammalia as a crown clade consisting of the common ancestor of living monotremes and therians.

Cladistic analysis also “made” mammals monophyletic, even though such authorities as Olson and Simpson had entertained the possibility of a polyphyletic Mammalia. Questions of mammal origins had long been deeply emeshed in functional-adaptive analyses of the biology of the transition, particularly changes in the auditory and masticatory apparatuses. In the abiological world of numerical cladistics, these questions were trivialized as “essentialist” and not of scientific interest (Rowe and Gauthier, 1992; DeQuieroz 1994).

Miao (1991) provided a pointed discussion of these issues, rejecting cladistic redefinition of the Mammalia (also see Lucas 1992). Following Lucas and Luo (1993), I define Mammalia as the monophyletic group that includes *Adelobasileus* (Fig. 10.11), *Sinoconodon* and *Morganucodon* in the Mammalia.

Thus, I recognize a monophyletic Mammalia defined primarily by the biologically significant novelty of a petrosal promontorium, likely with a coiled cochlea. The oldest mammal thus is *Adelobasileus* from the Adamanian of Texas, USA (Lucas and Luo 1993). Potentially older mammals may be known from teeth from the Tiki Formation of India (Datta and Das 1996; Datta 2005). Mammal origins from a trithelodontid cynodont seem likely, and this was a Late Triassic event.

During the Revueltian-Apachean there was a diversification of morganucodontids, haramiyids and "symmetrodonts," particularly in Europe (Kielan-Jaworowska et al. 2004; Luo 2011; Debuysschere et al. 2015). Moganucodonts achieved a Pangean distribution and were small (less than 100 g estimated body weight) insectivores represented by 16 genera. All of the well known morganucodontid genera cross the Triassic-Jurassic boundary.

10.6.12 Oddities

There are a variety of highly specialized, ergo bizarre, Late Triassic diapsids. These include drepanosaurs (Fig. 10.12), trilophosaurs and the possible gliders *Icarosaurus*, *Sharovipteryx* and *Longisquama*. Most or all of these taxa defy precise classification and lack antecedents that would connect them morphologically to more generalized ancestors. They demonstrate just how incomplete our knowledge is of the Late Triassic tetrapod record. In effect, they are end members of clades that have been little sampled.

10.6.13 Provinciality

There have been at least two views of tetrapod paleobiogeography across Late Triassic Pangea. The traditional view is one of cosmopolitanism, and whatever provinciality existed was the difference between Laurussian archosaur-dominated assemblages and Gondwanan therapsid-dominated assemblages (e. g., Romer 1966; Cox 1973). More recent studies argue for a distinction between Laurussian and Gondwanan tetrapod assemblages largely predicated on floral differences or for provinciality driven by paleoatitude (zonal climate belts) (Ezcurra 2010; Whiteside et al. 2011).

Shubin and Sues (1991) inferred tetrapod cosmopolitanism during the Middle Triassic followed by latitudinal variation that correlated to long-recognized paleofloral differences (e.g., Dobruskina 1995b; Artabe et al. 2003). However, their correlation of tetrapod assemblages (see especially Shubin and Sues 1991: fig. 3) is fraught with inaccuracies. Furthermore, their analysis identifies India and Madagascar as having affinities with the tetrapod assemblages of Europe and North America, even though the floras of India and Madagascar are Gondwanan (*Dicroidium* dominated).

Whiteside et al. (2011) claimed latitudinal differences between tetrapod faunas as due to the differences between areas in which sedimentation was driven by ~10 kyr cycles (cynodont-dominated) and those driven by ~20 kyr cycles (procolophonid-dominated). Their analysis was based on the tetrapod record of the Newark Supergroup in which there is essentially no temporal overlap between older, cynodont-dominated assemblages and younger procolophonid-dominated assemblages. Clearly, the differences between these assemblages could be due to their different geological ages, not to paleolatituidinal differences.

Ezcurra (2010) analyzed the paleobiogeography of Triassic tetrapods for three time slices: Middle Triassic, "Ischigualastian" and "Coloradan." Like Shubin and Sues (1991), his analysis identified Middle Triassic cosmopolitanism. Interestingly, his analysis of the "Ischigualastian" linked India and Europe but not North America, despite the great similarity between North American and European tetrapod assemblages. In general, his analysis employs too coarse of temporal resolution to identify meaningful paleobiogeographic differences.

The correlations advocated here indicate that the strikingly distinct Late Triassic tetrapod assemblages are those from the Berdyankian-Adamanian of South America. Whether or not these assemblages, dominated by dicynodonts, represent a distinct province or a distinct facies, however, is difficult to determine. Given the inland nature of deposition in the South American basins that produce these assemblages, the possibility that they are just representatives of the dicynodont-dominated biofacies seen earlier in the Triassic (see discussion above) needs to be entertained. Otherwise, the Late Triassic tetrapod record seems to demonstrate much cosmopolitanism.

10.7 Conclusion: Late Triassic Extinctions

Colbert (1958) long ago drew attention to the striking differences between Late Triassic and Early Jurassic tetrapod faunas. Late Triassic tetrapod faunas are populated by many "thecodonts," notably phytosaurs, aetosaurs and rauisuchians. Dinosaurs were not major components of most Late Triassic tetrapod faunas, and metoposaurs dominated the amphibians. In strong contrast, Early Jurassic tetrapod faunas are dinosaur dominated, with various crocodylomorphs, and totally lack "thecodonts" and metoposaurs, taxa that suffered extinction across the Triassic-Jurassic boundary. The question has been when and how did these extinctions take place.

Lucas and Tanner (2015) recently analyzed the Late Triassic tetrapod extinctions to conclude that they were not a single extinction at the Triassic-Jurassic boundary. There is also no evidence of a tetrapod extinction across the Carnian-Norian boundary (e.g. Lucas 1994; Sues and Fraser 2010).

Using the best temporal resolution, the Late Triassic looks like a prolonged interval of stepwise tetrapod extinctions and low origination rates. However, none of these is a mass extinction, and no reliable data support continued claims of a tetrapod extinction just before or at the end of the Triassic (contra Kent et al. 2017). With new and more detailed stratigraphic data, the perceived Triassic-Jurassic boundary tetrapod extinction is mostly an artifact of coarse temporal resolution, the compiled correlation effect. The amphibian, archosaur and synapsid extinctions of the Late Triassic were not concentrated at the Triassic-Jurassic boundary, but instead occurred stepwise, beginning in the Norian and extending into the Hettangian (Fig. 10.13; Lucas and Tanner 2015).

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