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The beginning of the 'Age of Dinosaurs': a brief overview of terrestrial biotic changes during the Triassic

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ABSTRACT: The first appearance of dinosaurs during the early Late Triassic coincided with marked faunal changes in terrestrial ecosystems. Most of the major groups of extant tetrapods (or their proximate sister-taxa), including mammaliaforms, crocodyliform archosaurs, lepidosaurs and turtles, also first appeared in the fossil record during the Late Triassic. On the other hand, a number of Palaeozoic 'holdovers', such as procolophonid parareptiles, dicynodont therapsids and many groups of temnospondyls, vanished near or at the end of the Triassic. The tempo and mode of this faunal turnover have long been debated, but there has been growing acceptance of a rather sudden event, although the precise dating of such an event remains controversial. However, new discoveries have cast doubt on this assumption. The persistence of non-dinosaurian dinosauromorphs alongside dinosaurs well into Norian times hints at a more protracted turnover. New data on Triassic insect assemblages indicate that turnover among insects may also have been more protracted and possibly not co-incident with the faunal changes among tetrapods. Future work directed toward improved absolute age assessments for major faunal assemblages will be critical for a better understanding of the transition from therapsid-dominated to dinosaur-dominated communities during the early Mesozoic.

KEY WORDS: extinctions, insects, Pangaea

The Triassic Period represents a major turning point in the history of life on land. Bracketed by the largest mass extinction of all time near or at the end of the preceding Permian Period, and by another major extinction event near or at its end, the Triassic can be viewed as a time of extraordinary change and innovation in vertebrate evolution (Sues & Fraser 2010). However, it goes much further than that – the Triassic can justifiably be considered the 'Dawn of the Modern World'. At the beginning of this period, there are few if any terrestrial tetrapods with close links to the principal extant groups. Yet, by the beginning of the Jurassic Period, there are lepidosaurs, turtles, modern amphibians and close relatives of present-day mammals and crocodylians (Sues *et al.* 1994). Sphenodontian lepidosaurs were already widely distributed across Pangaea during the Late Triassic (Bonaparte & Sues 2006). Admittedly, many of these forms still differ considerably from the extant representatives of these clades. For example, the earliest crocodyliforms were fully terrestrial, highly cursorial carnivores rather than amphibious predators. But other forms, such as turtles, would already have been readily recognisable as members of their respective clades.

Alberti (1834) first coined the term 'Trias' for a tripartite succession of sedimentary rock units in southern Germany (in ascending order): Buntsandstein, Muschelkalk and Keuper. He noted that similar deposits were widely distributed across Europe and already suspected their presence in India and North America. Alberti's threefold lithostratigraphic succession corresponds roughly to the current standard division of the Triassic into Lower, Middle and Upper Triassic series.

Following on this tripartite division, Romer (1966) grouped Triassic terrestrial vertebrate assemblages into three major successive 'faunas'. His Early Triassic Fauna 'A' was still dominated by therapsids, but archosauriform and basal archosaurian reptiles were already present, along with other less common faunal elements. Romer's Middle Triassic Fauna 'B' was dominated by gomphodont cynodonts and rhynchosaurs, and there was a major diversification of archosaurs, including dinosaurian precursors. Finally, dinosaurs, along with various groups of non-dinosaurian archosaurs, dominated Romer's Late Triassic Fauna 'C', but therapsids were only a relatively minor faunal component. Although admittedly oversimplified, these divisions illustrate the principal change that took place among terrestrial tetrapod communities during the Triassic – the replacement of therapsids as the dominant terrestrial tetrapods by archosaurian reptiles.

In the introduction to an edited volume, Padian (1986) noted that Triassic vertebrate assemblages comprised three main and successive components: 'holdovers', 'indigenous' taxa that appear to be entirely restricted to this period, and 'modern' elements.

Recent work suggests that insects also started to show a shift towards modern forms some time during the Triassic. For example, some Late Triassic beetles, dipterans and thysanopterans (thrips) are already remarkably similar to extant representatives of these groups (Fraser & Grimaldi 2003; Grimaldi & Engel 2005; Blagoderov *et al.* 2007). Similar to Romer's threefold division of Triassic tetrapod communities, Shcherbakov (2008) recently divided Triassic insect assemblages into three groups. He identified a low-diversity group of assemblages from the Early Triassic, which comprised taxa related to those from the Late Permian, as well as a few endemic forms. Shcherbakov argued that the peak

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diversification of Triassic insects occurred during the Middle and early Late Triassic (Carnian). He noted an abundance of Triassic endemic forms, but also the first known occurrences of certain extant orders and families. Finally, according to Shcherbakov, groups with affinities to later Mesozoic taxa and a number of aquatic forms characterise apparently less diverse insect assemblages of latest Triassic (Norian and Rhaetian) age.

It was against this background that dinosaurs and their closest relatives first appeared. Thus, the 'Beginning of the Age of Dinosaurs' is another commonly-used designation for the Triassic Period. In the present paper, different views on the nature of the biotic changes during the Triassic will be outlined briefly, with an emphasis on the fossil record of terrestrial vertebrates. Additional discoveries continuously provide new insights into our understanding of this critical period in the history of life on Earth. Improved radiometric dating, discoveries of new insect and plant assemblages and, in particular, new investigations of Middle and early Late Triassic fossil-bearing continental strata worldwide suggest that much remains to be learned about the origin of dinosaurs and its context.

1. Triassic tetrapod faunas

1.1. Early Triassic

The Early Triassic was a time of biotic recovery from the end-Permian mass extinction (Looy *et al.* 1999; Benton & Twitchett 2003; Smith & Botha 2005; Sahney & Benton 2008). Initially, diversity levels of vertebrate terrestrial faunas appear to have been quite low, with assemblages dominated by a few taxa that attained wide geographic distribution. Consequently, the earliest Triassic tetrapod assemblages are fairly uniform in composition across Pangaea. The best-known example is the dicynodont therapsid *Lystrosaurus*, which is known from South Africa, Antarctica, China, India and Russia (Colbert 1982). The small parareptile *Procolophon* and basal archosauriform reptiles such as *Proterosuchus* were similarly widespread (Rubidge 2005). However, recent discoveries suggest that Early Triassic tetrapod assemblages may have been more diverse than traditionally assumed (e.g., Damiani *et al.* 2003). Although therapsids attained much lower taxonomic diversity than during the Late Permian, they were still the most abundant land vertebrates in many regions of Pangaea. However, they were only minor elements (if present at all) in Early Triassic tetrapod assemblages from Russia, Germany and Australia, in which temnospondyls predominated. Sahney and Benton (2008) argued that there was an initial increase in cosmopolitanism immediately following the end-Permian event. However, these authors claimed that it declined again through the rest of the Early and Middle Triassic, which other authors (e.g., Ezcurra 2010) would dispute.

1.2. Middle Triassic

The composition of terrestrial tetrapod communities changed dramatically during the Middle Triassic. Considerable faunal uniformity was still present across Pangaea, but there are certainly ecological and possibly taphonomic differences among known assemblages. Archosauromorph reptiles, especially rhynchosaurs, rapidly increased in diversity and abundance. New discoveries from the Moenkopi Formation of Arizona and the Lifua Member of the 'Manda beds' of Tanzania, respectively, indicate that the two principal lineages of Archosauria – one leading to dinosaurs including birds (Ornithodira) and the other leading to crocodylians (Crurotarsi) – extended back to at least Anisian times (Nesbitt 2003; Nesbitt *et al.* 2010). Two groups of therapsids, kannemeyeriiform dicynodonts and gomphodont cynodonts, each attained considerable abundance and diversity, especially in Gondwana.

1.3. Late Triassic

Late Triassic tetrapod assemblages provide evidence for a major change from 'archaic' forms (palaeotetrapods *sensu* Charig 1980) to more 'modern' taxa (neotetrapods *sensu* Charig 1980). The former include both Permian 'holdovers' such as dicynodont therapsids, procolophonid parareptiles and chroniosuchian anthracosaurs, as well as groups entirely restricted to the Triassic, such as most crurotarsan archosaurs (Fig. 1). On the other hand, crocodyliforms, lepidosaurs, mammaliaforms and turtles first appeared and subsequently became key elements of tetrapod communities worldwide in the later Mesozoic. (The oldest frogs, salamanders and caecilians are definitely known from the Early Jurassic but, based on their phylogenetic relationships, must have first appeared during the Triassic as well.) The oldest known dinosaurs and pterosaurs also date from the Late Triassic. As birds are clearly derived from maniraptoran theropods, dinosaurs really should also be counted among the 'modern' tetrapod groups.

2. Tempo and causes of faunal turnover

The tempo and mode of the aforementioned faunal changes have long been the subject of much debate. While it is generally accepted that there was indeed a major faunal turnover, researchers have proposed different scenarios to explain the observed changes.

Charig (1980, 1984) argued for a gradual transition and interpreted the observed faunal changes as the result of direct competition between the various groups of tetrapods. He suggested that the upright stance of dinosaurs was somehow 'superior' to the sprawling posture retained by most more basal archosaurs such as aetosaurs and phytosaurs. An alternative scenario posited that the archaic forms died out first and other groups then occupied the vacated ecological niches (Benton 1987, 1991). In recent years much more has been written on this subject. For example, Brusatte *et al.* (2008) compared evolutionary rates and morphological disparity of basal dinosaurs and crurotarsan archosaurs and found that dinosaurs apparently exhibited lower disparity and an indistinguishable rate of character evolution. They suggested that historical contingency rather than competitive superiority was the primary factor in the rise of dinosaurs. Some attention has also been given to potential regional variations. For example, Irmis *et al.* (2007b) showed that the replacement of more basal archosaurs by dinosaurs did not occur suddenly at high latitudes. They also found no support for the 'competition' hypothesis.

The end-Triassic extinction event has long been considered one of the five mass extinctions during the Phanerozoic with profound effects in the marine realm (e.g., Newell 1962; Raup & Sepkoski 1982; Hallam & Wignall 1997; Bambach *et al.* 2004). Although there is also no disputing that vertebrate life on land was also greatly affected, as first suggested by Colbert (1958), the precise timing and nature of the event is more controversial. Two major schools of thought have developed. The first argues for a single mass extinction on land at the end of the Triassic (Olsen & Sues 1986; Olsen *et al.* 1987, 2002), whereas the second favours an additional, possibly more severe extinction event at the end of the Carnian (Benton 1986, 1991). Benton (1983, 1986) argued that this end-Carnian event may

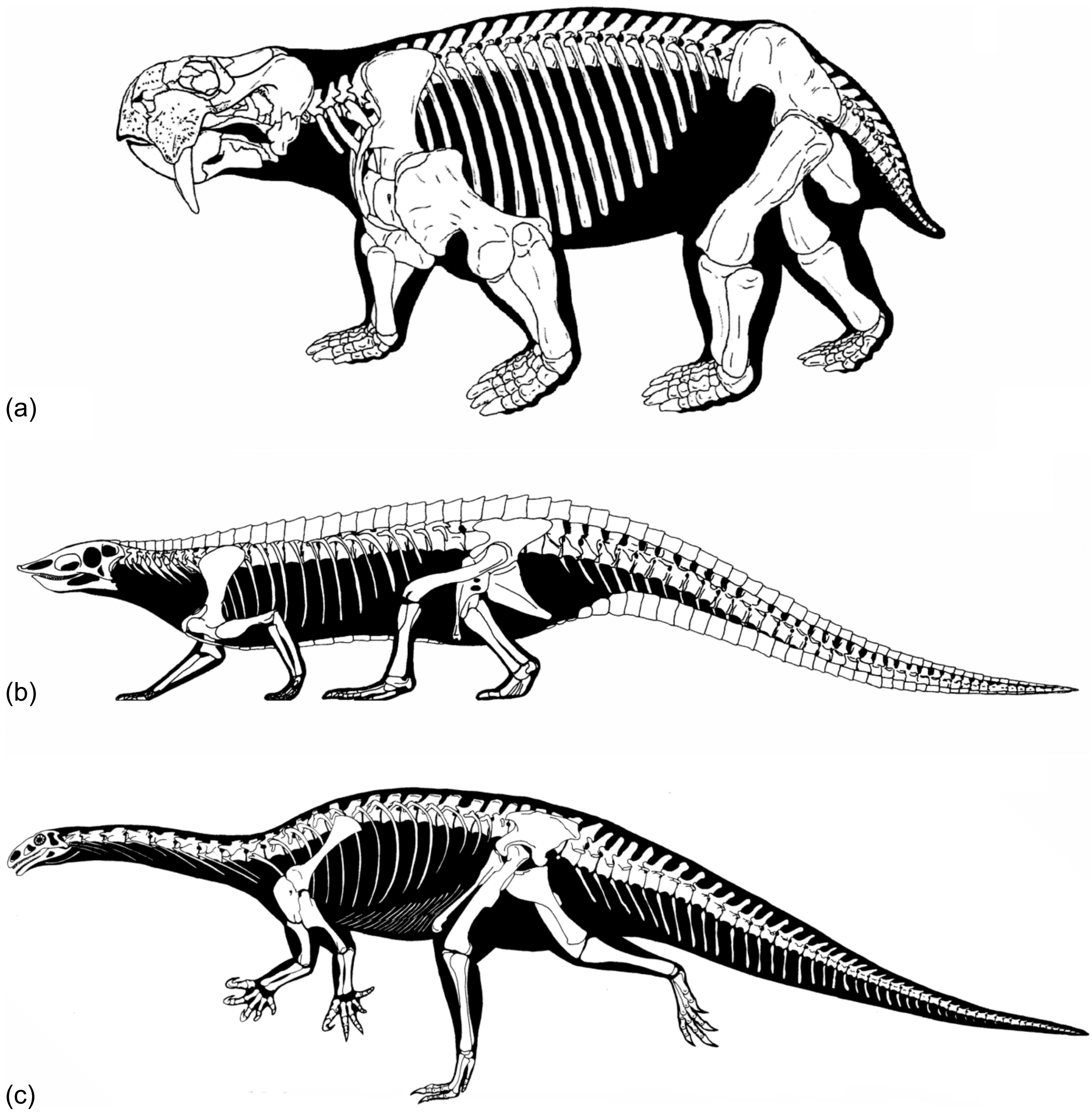

Figure 1 Skeletal reconstructions (with body silhouettes) of Late Triassic tetrapods to illustrate the three categories of Triassic terrestrial tetrapods discussed in the text: (a) Example of Palaeozoic 'holdover': dicynodont therapsid *Dinodontosaurus* (Santa Maria Formation, Brazil). Length up to 3 m. Courtesy of L. Morato; (b) Example of exclusively Triassic group: aetosaur *Stagonolepis* (Lossiemouth Sandstone Formation, Scotland). Length up to 2·1 m. Modified from Walker (1961); (c) Dinosaur: sauropodomorph *Plateosaurus* (Trossingen Formation, Germany). Length up to 9 m. Modified from Weishampel & Westphal (1986).

have been more instrumental in triggering the initial diversification of dinosaurs. However, recent studies have found little evidence for an end-Carnian extinction among continental tetrapods. For example, kannemeyeriiform dicynodonts were cited as one of the groups that vanished at the end of the Carnian, but the discovery of a large kannemeyeriid from the upper Norian or Rhaetian of Poland (Dzik *et al.* 2008) has established that this group persisted to the end of the Triassic. Furthermore, many allegedly Carnian-age occurrences have now been re-dated as Norian, based on a new time-scale developed by Muttoni *et al.* (2004). In this context it is worth noting that Anderson and Cruickshank (1979) and Benton (1983) proposed an early or middle Norian extinction. Without question, support for an end-Triassic terrestrial extinction event has increased. For example, Olsen *et al.* (2002) documented significant changes in the taxonomic composition of tetrapod trackway assemblages from the Newark Supergroup at the end of the Triassic (but see Lucas & Tanner 2007).

Many researchers now implicate the Chicxulub impact in Mexico as the proximate cause of the extinction of non-avian dinosaurs and many other taxa at the end of the Cretaceous, although others (e.g., Archibald *et al.* 2009) disagree with this conclusion, arguing for multiple causes for this mass extinction. Similarly, some authors have argued that the impact of an extraterrestrial object may have facilitated the initial rise of dinosaurs to dominance during the early Mesozoic (Olsen *et al.*

Figure 2 Map of eastern Québec (Canada) showing circular lake representing the present-day outline of the Norian-age Manicouagan impact crater and its drainage. Details modified from physiographic map at http://atlas.gc.ca.

1987). The Manicouagan impact, which left a crater with an estimated original diameter of perhaps 100 km in Québec, was once proposed as a possible cause for the end-Triassic extinction (Olsen *et al.* 1987; Fig. 2). However, consistent U–Pb dates of 214 ± 1 Ma (Hodych & Dunning 1992) and ca. 215·5 Ma (Ramezani *et al.* 2005) for the impact-melt rock firmly place this impact in the Norian, well before the end of the Triassic. Spray *et al.* (1998) linked smaller impact craters from Obolon (Ukraine) and Rochechouart (France) to the Manicouagan event, but the precise dating of the latter two features remains very uncertain (Schmieder & Buchner 2008). Given the magnitude of the Manicouagan impact, it is curious that no clear evidence of a biotic disturbance in the Newark Supergroup or elsewhere has been found to date. However, Parker (this volume) has recently noted possibly coeval changes among tetrapod assemblages from the Chinle Formation of the American Southwest (Parker & Martz 2011).

Although no undisputed end-Triassic impact crater has been identified to date, some indirect evidence has been cited in support of such an impact. Bice *et al.* (1992) reported the discovery of shocked quartz from Triassic–Jurassic boundary deposits in Italy, but Hallam & Wignall (1997) and Olsen *et al.* (2002) have questioned this record. Walkden *et al.* (2002) discovered pseudomorphs of melt spherules in a calcareous mud within a Late Triassic red-bed succession in SW Britain and interpreted this layer as a deposit of impact ejecta. However, based on the chemical composition of associated garnet crystals, Thackrey *et al.* (2009) argued that the Manicouagan impact was the likely source of these ejecta. Olsen *et al.* (2002) reported slightly elevated levels of iridium in latest Triassic strata of the Newark Supergroup in the Newark basin in Pennsylvania, as well as a dramatic increase in the abundance of fern spores (which is considered an indicator of significant ecological disturbance). Both phenomena could be potential indicators of an impact event based on similar changes at the Cretaceous–Palaeogene boundary. The evidence for an end-Triassic impact remains unconvincing, and large-scale volcanic activity could have generated similar biotic disturbances and even left a comparable geochemical signature. The recognition of a Central Atlantic Magmatic Province (CAMP), which formed around the radiometrically determined Triassic–Jurassic boundary (Marzoli *et al.* 1999), is significant in this context. This igneous province, possibly the largest of the entire Phanerozoic, resulted from more or less synchronous eruptions of vast flood basalts from a common magma reservoir, which was possibly supplied by a mantle plume, along the pre-Atlantic rift zone (Fig. 3). Radiometric dates for the CAMP basalts cluster around 200 Ma. There has been some question whether the formation of CAMP coincided with (or even predated) the end-Triassic extinction event (Whiteside *et al.* 2007).The most recent research tends to support the hypothesis that the volcanic eruptions coincided with the extinctions in the marine realm (Deenan *et al.* 2009; Whiteside *et al.* 2010). Hallam (2002; see also Hallam & Wignall 1999) noted the possibility that the plume activity could have led to changes in sea level that, in turn, would have caused increased rates of extinction in marine ecosystems.

3. Ages and correlations

Any global analyses of biotic changes must rely heavily on well-constrained dates for and robust correlations between different sequences of fossiliferous strata around the globe. Inevitably, few if any continuous sections representing significant intervals of time document the fossil record of Triassic terrestrial life. Correlation of continental strata is often limited to biostratigraphic methods, with the inevitable problem of circular reasoning.

Biostratigraphy. Pollen and spores have long been widely employed for the correlation of Triassic continental strata (e.g., Litwin *et al.* 1991; Heunisch 1999). However, their

Figure 3 Simplified map of Late Triassic Pangaea with pre-Atlantic rift zone (light stippling) and probable extent of flood basalts of the Central Atlantic Magmatic Province (CAMP; darker stippling). Courtesy of P. E. Olsen (Columbia University).

biostratigraphic use is not without problems. In particular, the composition of floras reflects local and regional environmental conditions, especially differences in temperature and precipitation. Furthermore, pollen and spores are susceptible to destruction under oxidising conditions – a common feature of early Mesozoic continental depositional environments, many of which formed red beds.

Many researchers have used tetrapod fossils for intercontinental correlation of Triassic continental sequences. In recent years, Lucas and his associates (Lucas 1998, 1999; Lucas & Huber 2003) have been particularly active advocates of the use of Triassic tetrapods for both regional and global correlations. Lucas (1998) proposed and defined a series of eight successive land-vertebrate faunachrons (LVFs) for the Triassic Period. Each LVF was characterised by the first appearance datum (FAD) in the fossil record of a particular tetrapod taxon. For example, the first (oldest) LVF of the continental Triassic, the Lootsbergian, was defined on the first appearance of the dicynodont *Lystrosaurus*. However, Rayfield *et al.* (2005, 2009; but see Lucas *et al.* 2007) and others (e.g., Parker 2007) have argued that several of Lucas's LVFs are problematical because their purported index fossils have a longer stratigraphic ranges than originally assumed, or have a more restricted geographic distribution, or the taxonomic status of these fossils is uncertain. Langer (2005) has also been critical of the use of land-vertebrate faunachrons. Only with additional and better radiometric data will it be possible to calibrate schemes for biostratigraphic zonation more accurately against a chronostratigraphic standard and assess the relative merits of each proposed zonation scheme (Irmis & Mundil 2008).

Magnetostratigraphy. One particularly promising development in recent years has been the use of magnetostratigraphy for the correlation of Triassic strata. Using radiometric dates of rocks for precise calibration, an astrochronology can be developed, as exemplified by the elegant work by Olsen and Kent in the Newark Supergroup of eastern North America (e.g. Kent *et al.* 1995; Olsen *et al.* 1996; Olsen & Kent 2000). Of particular interest are current studies that link these data with the results of research undertaken outside North America. For example, using palaeomagnetic data in concert with biostratigraphic and chemostratigraphic information from an extensive section of Late Triassic marine strata at Pizzo Mondello in the Sicani Mountains of Sicily, Muttoni *et al.* (2004) presented two correlation options with the Newark astrochronological polarity time scale. Significantly, their preferred ('long Norian') option results in a much longer Norian stage than previously assumed, pushing the lower boundary for the Norian back by some 20 million years to 227–228 Ma (Fig. 4). Most recently, Muttoni *et al.* (2010) placed the beginning of the Rhaetian stage somewhere between 210 and 207 Ma, based on new magnetostratigraphic data from the southern European Alps. This revised chronology has profound implications for the correlations of many continental sequences. For example, many fossil assemblages long dated as Carnian are now considered early Norian in age (although this obviously does not affect the absolute age of the horizons in question).

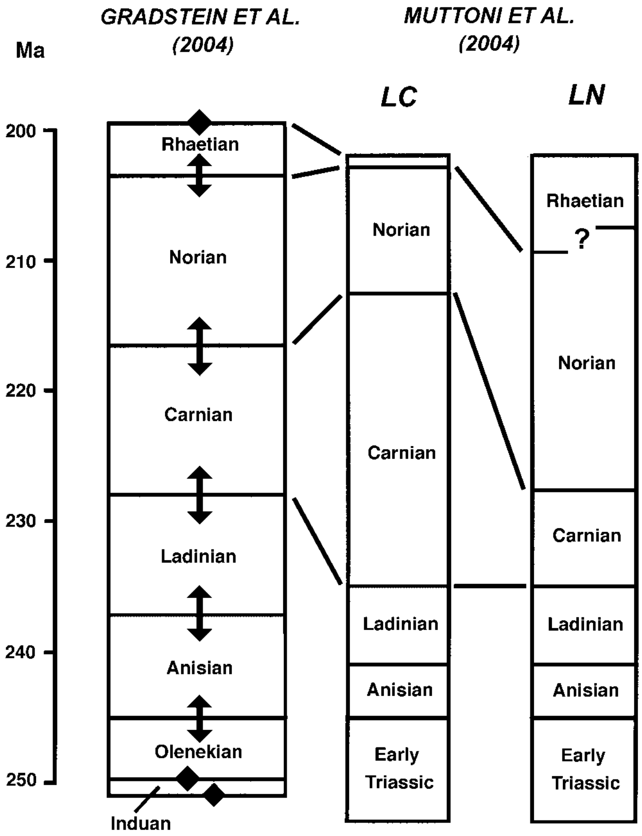

Figure 4 Comparison of the time scale for the Triassic Period by Gradstein *et al.* (2004) and two alternative time scales based on the work by Muttoni *et al.* (2004). Arrows in the scale by Gradstein *et al.* (2004) indicate ranges in age of boundaries between the stages. Modified from a diagram by Dickinson & Gehrels (http://gsa.confex.com/gsa/responses/2008CD/283.ppt).

4. Dinosaurs and dinosauromorphs

Based on several lines of stratigraphic evidence, Olsen & Galton (1977) re-dated many of Romer's (1966) 'C' assemblages as Early Jurassic. As a result, dinosaurs were less common in Late Triassic assemblages than traditionally assumed. Nesbitt *et al.* (2007) further underscored this point in their review of dinosaurian taxa reported from the Late Triassic of North America. Using explicitly apomorphy-based criteria for specimen identification, these authors concluded that many of the published records, particularly those assigned to sauropodomorphs, were either misidentified or devoid of diagnostic features, and that Late Triassic dinosaurs were much less common and diverse in North America than previously assumed. There are also no longer any confirmed reports of Late Triassic ornithischians in North America; indeed, most of the reported Triassic occurrences of these dinosaurs worldwide are problematical (Irmis *et al.* 2007a). *Pisanosaurus* from the Ischigualasto Formation of Argentina is known only from a single, poorly preserved skeleton, and its interpretation remains controversial. Although *Eocursor* from the lower Elliot Formation of South Africa is undoubtedly an ornithischian (Butler *et al.* 2007), the age of this formation is poorly constrained.

Irmis *et al.* (2007b) demonstrated the persistence of non-dinosaurian dinosauriforms well into the Late Triassic in North America. Until recently, such forms, especially *Marasuchus* and *Lagerpeton* from the Ladinian-age Chañares Formation of Argentina, were thought to be restricted to the Middle Triassic. The discovery of the Norian-age lagerpetid *Dromomeron*, co-existing with undisputed theropod dinosaurs, has changed our perspective on the early evolutionary history of dinosaurs (Irmis *et al.* 2007b). Other new discoveries such as the Anisian-age silesaurid *Asilisaurus* (Nesbitt *et al.* 2010) establish that the early evolution of dinosauriforms extended far back to the Early Triassic, as has long been argued on the basis of trackways referable to ichnotaxa such as *Rotodactylus* (e.g., Haubold 1983). These finds also revealed that the current knowledge of Triassic tetrapod faunas is much more limited than previously realised.

There exists remarkable convergence between certain crurotarsan archosaurs and dinosaurs – for example, the Rhaetian-age ‘rauisuchian’ *Effigia* from the Chinle Formation of New Mexico (Nesbitt 2007) is remarkably similar to contemporary theropod dinosaurs in body form and many anatomical features (Fig. 5). Basal crocodylomorphs had fully erect limb posture (Parrish 1987). Such resemblances negate previous claims that dinosaurs had a ‘superior’ stance and gait compared to crurotarsans. Other explanations must be sought for one of these groups surviving to diversify during the Jurassic whereas the other did not. The broad temporal overlap of dinosauriforms and dinosaurs with various derived crurotarsans of remarkably dinosaur-like appearance should also put to rest lingering notions of competitive replacement of non-dinosaurian archosaurs by dinosaurs.

5. The Triassic fossil record as a whole

Most attention has focused on the fossil record of terrestrial vertebrates in analyses of the end-Triassic biotic changes, but tetrapods are just one component of the Triassic continental ecosystems. What about insects and plants? Does the Triassic record of marine ecosystems tell a similar story?

5.1. The fossil record of insects

The fossil record for Early Triassic insects is still poor, although several sites have been reported from European Russia. The known assemblages are characterised by low taxonomic diversity and tend to be dominated by one or two groups. For example, beetles dominate the richest Early Triassic assemblage, Babiy Kamen’ (Shcherbakov 2008). The number of individual insect fossils recovered to date tends to be in the hundreds rather than the thousands.

The fossil record for insects from the Middle and Late Triassic is much more extensive, with sites in the Madygen Formation of Kyrgyzstan and the Molteno Formation of South Africa each yielding thousands of specimens. The Anisian-age Grés á Voltzia of eastern France and several horizons in Australia (Mt Crosby and Blackstone formations and Ipswich Coal Measures; Jell 2004) are also rich sources of insect fossils. The Grés á Voltzia has yielded a diverse insect assemblage comprising Protorthoptera, Blattodea, Coleoptera, Ephemeroptera and Hemiptera, as well as the oldest known representatives of Diptera (Gall & Grauvogel-Stamm 1999; Béthoux *et al.* 2005). More than 500 species of insects have been formally named from the Middle or Upper Triassic Madygen Formation. Dipterans (Shcherbakov *et al.* 1995) and xyeloid hymenopterans (Rasnitsyn 1969) have also been reported, along with putative trichopterans and curculionoid beetles.

The insects from the Molteno Formation (Anderson *et al.* 1993a, b) are mostly known only from isolated wings, which hint at a considerable taxonomic diversity; however, full assessment of that diversity must await more comprehensive taxonomic study. Blattodea and Coleoptera are the two most common groups of insects in the Molteno assemblage. Curiously, only a single indeterminate dipteran has been identified from this assemblage to date (Blagoderov *et al.* 2007). The insect assemblages from some of the classic Triassic localities in Australia (Jell 2004) have not been re-examined in recent decades. According to Shcherbakov (2008), they contain fewer Triassic endemics.

One of the most important occurrences of Late Triassic insects is the Solite Quarry in the Norian-age Cow Branch Formation (Newark Supergroup) of Virginia (Fraser & Grimaldi 2003). Renowned for its abundance of largely complete insect fossils, this locality has yielded the oldest known records for many major groups of extant insects, including staphylinid beetles, thysanopterans (thrips), and belostomatid water bugs (Fig. 6). The diversity of dipterans from the Solite Quarry (Fig. 7) is unexpectedly high, with 16 species in eight families, of which four are still extant (Blagoderov *et al.* 2007). The Solite assemblage also represents the oldest known diverse record of aquatic insects.

Surveys of the Middle and Late Triassic insect assemblages indicate that many of the principal groups of present-day insects evolved and/or first diversified during the Triassic (Béthoux *et al.* 2005; Grimaldi & Engel 2005). Interestingly, the initial appearance of these ‘modern’ taxa seems to have occurred somewhat in advance of the vertebrates. Given the great diversity of dipterans at Solite, it seems likely that their origins date much further back in time. Whether the same is true for other modern groups such as thysanopterans (Grimaldi *et al.* 2004) or staphylinid beetles is still not clear. Shcherbakov (2008) highlighted the similarity of the Solite insect assemblage to Rhaetian and Early Jurassic insect assemblages elsewhere. He suggested that the transition to more ‘modern’ insect communities may have begun in the palaeoequatorial zones and then spread to higher palaeolatitudes.

5.2. The marine realm

It has long been argued that a dramatic faunal turnover occurred in marine ecosystems near or at the end of the Triassic Period. Hallam (1981) found that bivalves underwent a significant extinction at the end of the Triassic. Johnson and Simms (1989) noted major losses of diversity among pectinoid bivalves and crinoids, but mainly during the Carnian. Similarly, bryozoans (Schäfer & Fois 1987) and echinoids (Smith 1990) both suffered major declines in diversity during the Carnian. In a comprehensive review, Hallam (2002) noted that the end of the Triassic marked the disappearance of the ceratite ammonoids, conodonts, most calcareous demo-

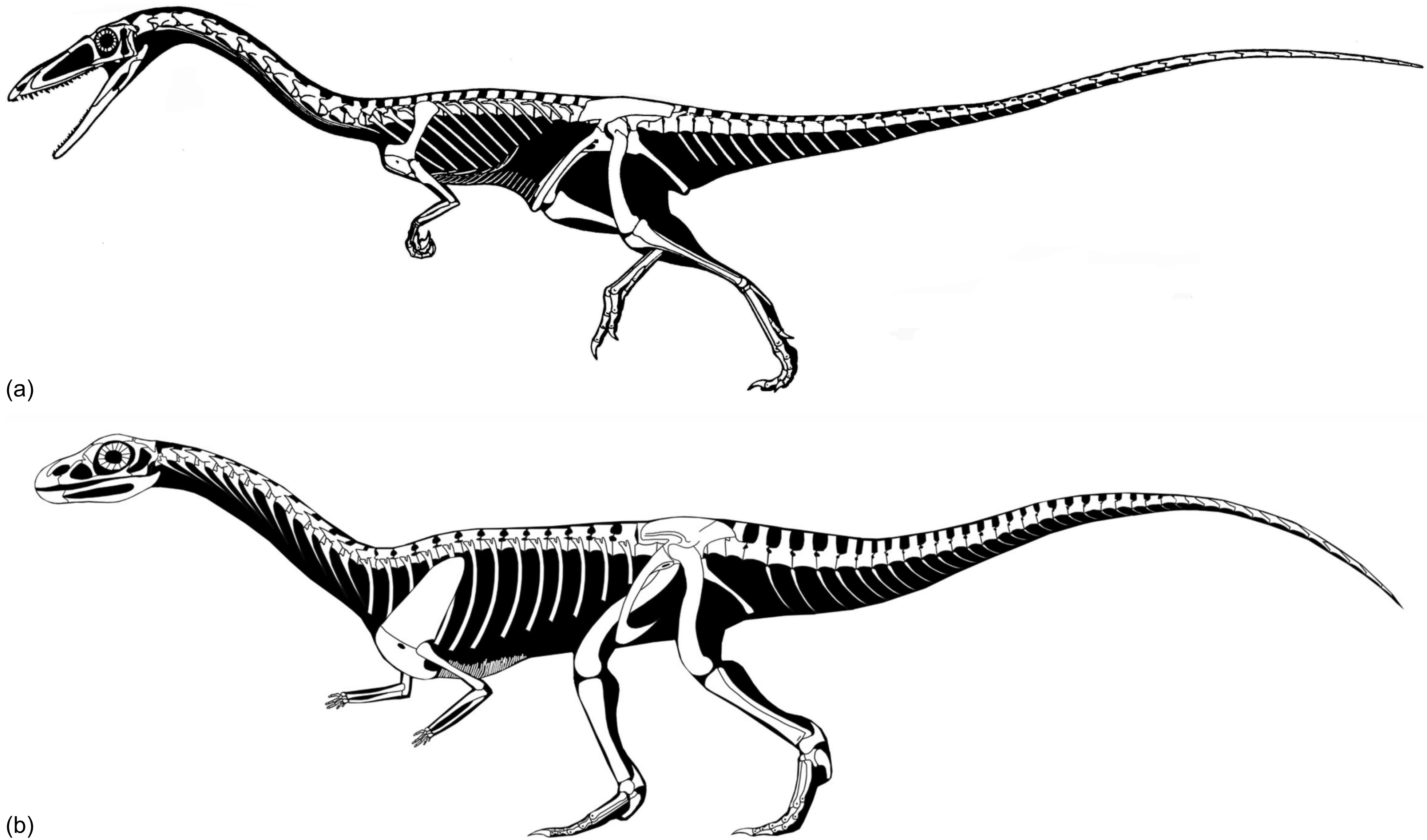

Figure 5 Convergence in body plan between (a) the theropod dinosaur *Coelophysis* and (b) the ‘rauisuchian’ crurotarsan *Effigia*. Both taxa are known from the Upper Triassic Chinle Formation of Ghost Ranch, New Mexico. Reconstruction of *Coelophysis* from Paul (1993) and reconstruction of *Effigia* courtesy of S. J. Nesbitt (University of Texas at Austin). *Coelophysis* reached a length of up to 3 m; *Effigia* attained a length of about 2 m.

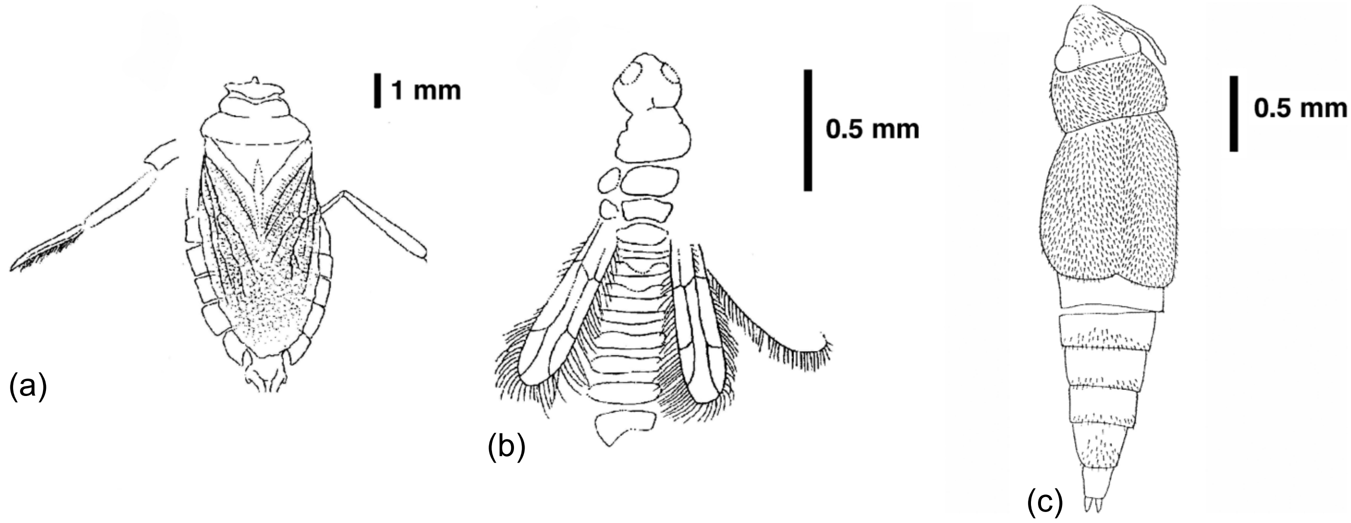

Figure 6 Late Triassic representatives of three extant insect clades from the Cow Branch Formation of the Solite Quarry, Virginia (USA): (a) Belostomatid water bug; (b) Thysanopteran *Triassothrips*; (c) Staphylinid beetle. From Fraser and Grimaldi (2003).

sponges, and various important groups of bivalves and brachiopods. In some regions, there was also a significant increase in extinction rates among dinoflagellates and radiolarians, but Hallam noted that it remains to be established if these changes were global rather than regional in nature. He argued that there was a substantially higher rate of extinction among marine animals during the Rhaetian as compared to the preceding Norian stage. Kiessling *et al.* (2007) also proposed a major extinction during the Rhaetian. However, they suggested that this event apparently had only a limited ecological impact outside the heavily affected reef ecosystems. Benson *et al.* (2010) found no evidence for an end-Triassic extinction event among marine tetrapods although Benton (pers. comm.) has questioned their methodology and findings.

5.3. Floras

Flowering plants (angiosperms) dominate present-day terrestrial floras. Currently, the oldest known undisputed angiosperms are Early Cretaceous in age (Friis *et al.* 2006). However, estimates of the divergence time based on molecular data suggest a much earlier origin for angiosperms, possibly as far back as the Triassic or even the Permian (Magallón 2010). Some authors have interpreted the enigmatic *Sanmiguelia* from the Upper Triassic of the American Southwest as an angiosperm with palm-like foliage (Brown 1956; Tidwell *et al.* 1977; Cornet 1986), but this interpretation remains controversial (Read & Hickey 1972). Another alleged angiosperm, *Pannaulika* from the Norian-age Cow Branch Formation of the Solite Quarry (Cornet 1993), is possibly based on a partial leaf of a dipteridaceous fern (B. Axsmith, pers. comm.). Currently there exists no unequivocal fossil evidence for the existence of Triassic angiosperms, and thus the Triassic cannot be regarded as marking the first appearance of truly modern floras. However, Middle to Late Triassic terrestrial plant assemblages do show the successive appearance of new groups such as the bennettitaleans (which are thought to be closely related to angiosperms) as well as the first members of extant clades of ferns (Dipteridaceae, Matoniaceae) and conifers (Kerp 2000).

Major floral changes occurred near or at the end of the Triassic. For example, the rich fossil record of plants from the Jameson Land Basin of East Greenland documents significant and abrupt turnover in floras at the Triassic–Jurassic boundary (McElwain *et al.* 2007, 2009). However, this change apparently did not lead to a mass extinction of family-level taxa but rather to changes in community diversity and ecology. Late Triassic high-diversity forests dominated by the broad-leaved conifer *Podozamites* and various bennettitaleans (*Anomozamites*, *Pterophyllum*) gave way to lower-diversity forests with the ginkgophyte *Sphenobaeira*, the gymnosperm *Czekanowskia*, and the osmundaceous fern *Todites*. Kürschner *et al.* (2007) and Bonis *et al.* (2009) showed that gymnosperm forests adjacent to the Eiberg Basin in Austria were gradually replaced by ferns and fern-associated vegetation. McElwain *et al.* (2007) also observed a gradual decline in plant diversity at the genus and species level below the Triassic–Jurassic boundary, which is inconsistent with a catastrophic extinction. On the other hand, new analyses of the records of pollen and spores and of plant macrofossils from East Greenland indicate that there may have been an abrupt biodiversity loss at the Triassic–Jurassic boundary after all, and Mander *et al.* (2010) suggest that this pattern of change was more widespread (see Fowell & Olsen 1993; Olsen *et al.* 2002). Clearly more work is needed, but currently the fossil record of plants is inconsistent with that for terrestrial vertebrates and does not provide unambiguous evidence for an end-Triassic mass extinction.

There were also well-established floral differences between Gondwana and Laurasia during the Triassic. In particular, corystospermalean foliage of the form taxon *Dicroidium* is widespread and often extremely abundant in plant assemblages from Gondwana, where it is frequently found in association with reproductive structures such as *Umkomasia*. Yet, *Dicroidium* is not definitely known from Laurasia to date, although *Umkomasia* has recently been reported from the Upper Triassic of northern China (Zan *et al.* 2008). Although the latter find indicates a wider distribution of corystospermaleans than previously assumed, they must still be considered a predominantly Gondwanan group. Among tetrapods, the superficially crocodile-like phytosaurs are widespread and common elements of Laurasian tetrapod assemblages. The recent referral of a jaw fragment from the Upper Triassic of southern Brazil to phytosaurs (Kischlat & Lucas 2003) is intriguing if controversial. However, given their well-established occurrence in both India and Madagascar, phytosaurs clearly did exist in some parts of Gondwana, but apparently never attained a significant role in tetrapod communities from the southern regions of Pangaea.

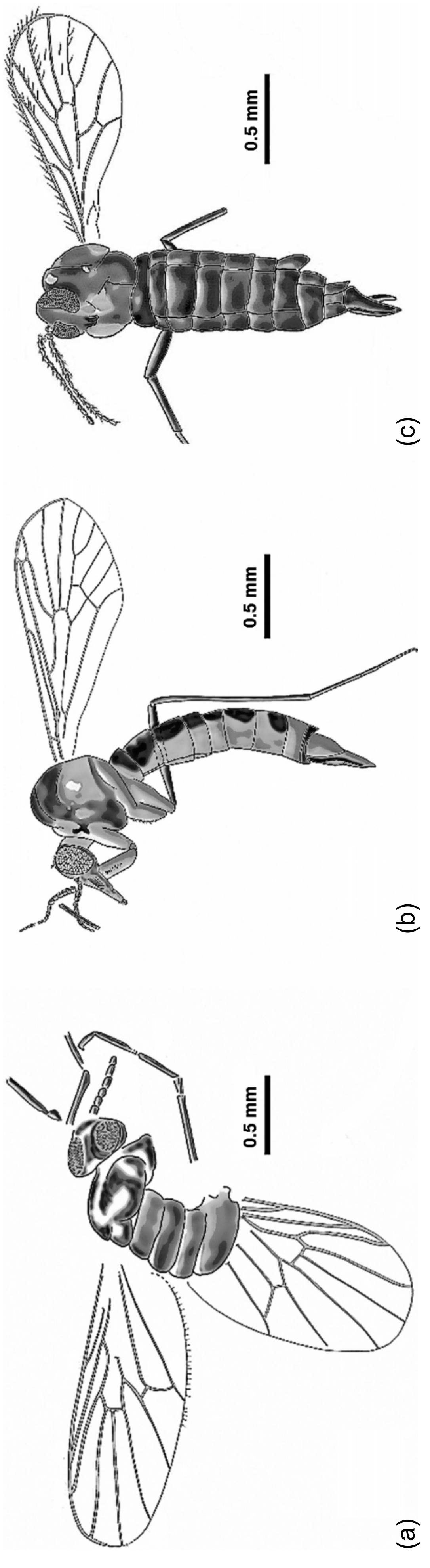

Figure 7 Late Triassic (Norian) representatives of three clades of Diptera from the Cow Branch Formation of the Solite Quarry, Virginia (USA): (a) Stem brachyceran *Prosechamyia*; (b) Tipulomorph *Metarchilimonia*; (c) Psychodomorph *Triassopsychoda*. From Blagoderov *et al.* (2007).

6. Conclusions

Triassic tetrapod assemblages have long been considered fairly uniform in taxonomic composition across the globe. Such uniformity is not surprising in view of the existence of Pangaea and the apparent absence of major physical obstacles to the dispersal of animals and plants. However, Romer (1966) already cited several transitional assemblages as well as regional differences between tetrapod communities. The recent study by Ezcurra (2010) argued for a Pangaean pattern of tetrapod distribution with a number of cosmopolitan groups during the Middle Triassic. During the early Late Triassic, his analysis suggests a strongly palaeolatitudinally-influenced pattern of distribution for some tetrapod lineages. During the latest Triassic, Gondwanan tetrapod assemblages appeared more similar to each other than to Laurasian ones. These conclusions are intriguing, but require further testing with more complete taxonomic coverage. Certainly, major differences in continental faunas and floras existed between Gondwana and Laurasia. Furthermore, the tetrapod assemblages from North America, especially during the Late Triassic, differ from those from other regions of Laurasia. Particularly noteworthy is the apparent absence of sauropodomorphs from North America during the Late Triassic, although these dinosaurs are very common in more or less coeval strata in Europe, Greenland, Argentina and South Africa (Galton & Upchurch 2004; Rowe *et al.* in press). Yet, there are also a number of shared tetrapod taxa between Laurasia and Gondwana: for example, closely related, possibly congeneric aetosaurs are known from Scotland and Argentina (Heckert & Lucas 2002), and the sphenodontian *Clevosaurus* has been reported from the Late Triassic of southwest Britain and Brazil (Bonaparte & Sues 2006).

The currently available data suggest that many of the principal groups of extant terrestrial vertebrates and insects evolved soon after the end-Permian extinction event. Moreover, many of them co-existed with taxa apparently restricted to the Triassic, such as most non-dinosaurian archosaurs, for millions of years. Thus, the causes of the selective demise of certain groups at the end of the Triassic pose an intriguing research problem. Undoubtedly, as we are able to refine the absolute ages for an increasing number of fossiliferous continental strata, our perspective on the tempo and mode of these biotic changes will change considerably. We are currently witnessing a veritable torrent of new discoveries, and some of these may profoundly affect our understanding of the evolution of terrestrial ecosystems at the beginning of the Mesozoic Era. However, what will not change is the fact that the Triassic Period was truly a time of transition between ancient and modern ecosystems on land – a fascinating story that we are only beginning to tell.

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