# A Geographical Information System (GIS) study of Triassic vertebrate biochronology

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**Abstract** – Geographical Information Systems (GIS) have been applied extensively to analyse spatial data relating to varied environmental issues, but have not so far been used to address biostratigraphical or macroevolutionary questions over extended spatial and temporal scales. Here, we use GIS techniques to test the stability, validity and utility of proposed Middle and Late Triassic 'Land Vertebrate Faunachrons' (LVFs), a global biostratigraphical framework based upon terrestrial/freshwater tetrapod occurrences. A database of tetrapod and megafloral localities was constructed for North America and Western Europe that also incorporated information on relevant palaeoenvironmental variables. This database was subjected to various spatial analysis techniques. Our GIS analysis found support at a global level for *Eocyclotosaurus* as an Anisian index taxon and probably *Aetosaurus* as a Norian indicator. Other tetrapod taxa are useful biostratigraphical/biochronological markers on a regional basis, such as *Longosuchus* and *Doswellia* for Late Carnian time. Other potential index fossils are hampered, however, by taxonomic instability (*Mastodonsaurus*, *Metoposaurus*, *Typothorax*, *Paleorhinus*, *Pseudopalatus*, *Redondasaurus*, *Redondasuchus*) and/or are not clearly restricted in temporal distribution (*Paleorhinus*, *Angistorhinus*, *Stagonolepis*, *Metoposaurus* and *Rutiodon*). This leads to instability in LVF diagnosis. We found only in the western Northern Hemisphere is there some evidence for an Anisian–Ladinian biochronological unit amalgamating the Perovkan and Berdyankian LVFs, and a possible late Carnian unit integrating the Otischalkian and Adamanian.

Megaplants are generally not useful for biostratigraphical correlation in the Middle and Upper Triassic of the study area, but there is some evidence for a Carnian-age floral assemblage that corresponds to the combined Otischalkian and Adamanian LVFs. Environmental biases do not appear to strongly affect the spatial distribution of either the tetrapods or megaplants that have been proposed as index taxa in biostratigraphical schemes, though several examples of apparent environmental bias were detected by the analysis. Consequently, we argue that further revision and refinement of Middle and Late Triassic LVFs is needed before they can be used to support global or multi-regional biostratigraphical correlations. Caution should therefore be exercised when using the current scheme as a platform for macroevolutionary or palaeoecological hypotheses. Finally, this study demonstrates the potential of GIS as a powerful tool for tackling palaeontological questions over extended timescales.

Keywords: Triassic, tetrapods, biostratigraphy, Geographic Information Systems.

## 1. Introduction

The Triassic/Jurassic boundary ($\sim$ 200 Ma: Gradstein, Ogg & Smith, 2005; Kent & Olsen, 1999; Olsen & Kent, 1999) was marked by a massive and abrupt extinction of marine animals (Hallam, 1981, 1990; Raup & Sepkoski, 1982). In the terrestrial realm, communities of basal synapsids, basal archosaurs, parareptiles and early tetrapods that had been relatively stable for much of the Triassic were replaced by an essentially modern fauna consisting of mammals, crocodilians, dinosaurs and turtles (e.g. Colbert, 1958; Olsen & Galton, 1977; Benton, 1986*a*, 1994; Olsen &

Sues, 1986). Three hypotheses have been proposed to explain the tempo and mode of this dramatic change in the terrestrial vertebrate fauna: a catastrophic event during the Triassic (Benton, 1986*a,b*, 1994; Simms, Ruffell & Johnson, 1994); a catastrophic event commensurate with the marine event at the Triassic/Jurassic boundary, perhaps linked to an extra-terrestrial bolide impact (Olsen, Shubin & Anders, 1987; Olsen *et al.* 2002; Weems, 1992); or a gradual, possibly competitive replacement (Charig, 1984; Lucas, 1994).

Studies of faunal turnover during the Triassic and across the Triassic/Jurassic boundary are confounded by the lack of resolution in early Mesozoic continental stratigraphy. The standard stage-level division of the Triassic is based upon the stratigraphical distribution of ammonites in the European Alps (Tozer, 1967, 1974,

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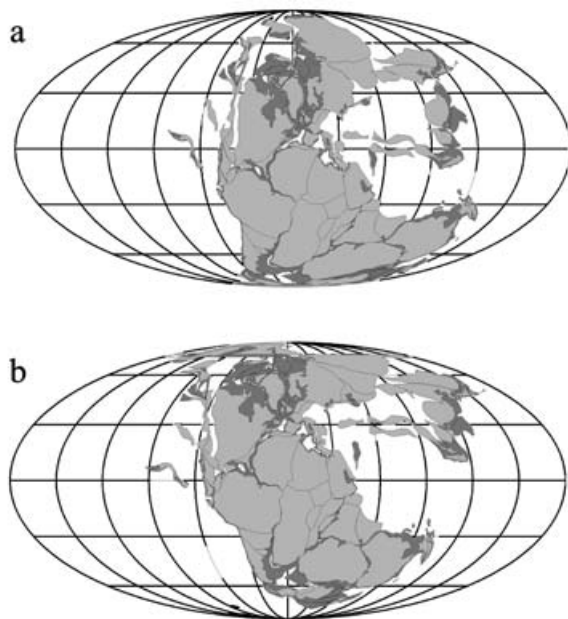
Figure 1. Middle and Late Triassic continental reconstruction. (a) 240 Ma (Anisian). (b) 200 Ma (approximate date of the Triassic/Jurassic boundary after Gradstein, Ogg & Smith, 2005). Dark grey areas are continental margin; light grey areas are continental shelf. Mollweide projection, after Scotese (2001).

1979), and detailed biostratigraphical correlations between Alpine and other marine strata are possible. Informative terrestrial sequences, such as the type Triassic strata of the Germanic Basin, generally cannot be linked directly with the marine biostratigraphical timescale due to a lack of shared index fossils. As a consequence, resolution beyond the stage level is rarely achieved in the terrestrial realm (Olsen & Sues, 1986). Furthermore, the Germanic strata consist of Lower and Upper Triassic terrestrial units (Buntsandstein and Keuper, respectively) that flank Middle Triassic marine Muschelkalk strata. This marine intrusion is not present in the Middle Triassic continental strata of North America and some European localities, further confounding attempts at stratigraphical resolution. Correlation between palynological zones and the Alpine ammonite sequence holds the possibility to resolve continental stratigraphy (Benton, 1994, fig. 22.1), but total congruence has not yet been achieved.

The coalescence of the supercontinent Pangaea in the Permian (approximately 292–253 Ma, Fig. 1; Smith, Smith & Funnell, 1994) increased the potential for global biotic exchange, such that widely distributed families dominated early Mesozoic tetrapod assemblages (Shubin & Sues, 1991). By exploiting family- and generic-level dispersal, the presence or absence of fossil vertebrates, especially tetrapods, has been used for many years in attempts to correlate Triassic non-marine strata. Tetrapod biochronology and biostratigraphy is based on the premise that particular

tetrapod fossil assemblages can characterize specific intervals of time. Terrestrial tetrapod biostratigraphy has been used to categorize South African faunal divisions (Kitching, 1977; Kitching & Raath, 1984; Rubidge, 1995), Russian Permo-Triassic faunas (Ochev & Shishkin, 1989; Shishkin *et al.* 2000), Cenozoic North American 'Land Mammal Ages' (Wood *et al.* 1941), and Chinese (Dong, 1992; Lucas, 1996*a,b*, 2001), Argentine (Bonaparte, 1982) and North American Mesozoic faunas (Huber, Lucas & Hunt, 1993*a*; Lucas & Hunt, 1993).

Lucas (1998*a*, refined in part in Lucas, Heckert & Hunt, 2001; Lucas & Heckert, 2002; Lucas & Schoch, 2002; Lucas & Huber, 2003) proposed an extensive global Triassic tetrapod biochronology. Eight 'Land Vertebrate Faunachrons' ('LVFs') were identified, each comprising successive assemblage zones of Triassic tetrapod fossils (Fig. 2). LVFs are defined by the First Appearance Datum (FAD) of a specific tetrapod genus, and are characterized by a type tetrapod fossil assemblage (Fig. 2). Within an LVF, correlations are made between the type assemblage and other non-marine assemblages on the basis of shared index fossils (Fig. 2). Magnetostratigraphy and palynology (where available) and occasional preservation of terrestrial taxa in marine assemblages can link biochronology to the standard global chronostratigraphical timescale (Table 1). Tetrapod biostratigraphies have subsequently been used to date terrestrial sequences of ambiguous age.

A standard biostratigraphical timescale is a crucial component in assessing the pattern of evolutionary change throughout the Triassic Period and across the Triassic/Jurassic boundary extinction event. It is, therefore, extremely important that LVFs represent, to the best of our current knowledge, accurate biochronological and biostratigraphical units. All biochronological hypotheses are fluid and subject to change with new fossil discoveries and advances in independent dating resolution. Global biochronological units should, however, remain intact when additional fossil assemblage data are considered, and taxa within a unit should not be erroneously grouped together on the basis of possible ecological or environmental biases in the fossil record.

In this paper we aim to test the LVF concept for the first time, using a Geographical Information System (GIS)-based approach. The aims of the analysis are three-fold. Firstly, index fossils should be temporally restricted, numerically abundant and spatially widespread. We investigate whether LVF index fossils meet these criteria, particularly when assemblages of a similar age, not included in the original LVF definitions, are considered. Secondly, we explore whether lithological, palaeoecological and climatic data influence assemblage composition, and the effect that such influences may have upon LVF stability. Finally, we investigate whether biostratigraphical

| EPOCH | AGE | LVF | FAD | INDEX FOSSILS |
|---|---|---|---|---|
| | RHAETIAN | APACHEAN | *Redondasaurus* | *Redondasaurus, Redondasuchus, Riojasaurus* |
| LATE | NORIAN | REVUELTIAN | *Pseudopalatus* | *Typothorax, Aetosaurus, Pseudopalatus*-grade phytosaurs |
| | CARNIAN | ADAMANIAN | *Rutiodon* | *Scaphonyx (Hyperodapedon), Stagonolepis, Rutiodon*-grade phytosaurs |
| | | OTISCHALKIAN | *Paleorhinus* | *Paleorhinus, Angistorhinus, Longosuchus (=Lucasuchus), Metoposaurus, Doswellia* |
| MIDDLE | LADINIAN | BERDYANKIAN | *Mastodonsaurus* | *Dinodontosaurus, Mastodonsaurus, Exaeretodon, Massetognathus, Stahleckeria* |
| | ANISIAN | PEROVKAN | *Shansiodon* | *Eryosuchus, Eocyclotosaurus, Shansiodon, Scalenodon, Parakannemeyeria, Sinokannemeyeria, Kannemeyeria simocephalus* |
| EARLY | OLENIKIAN | NONESIAN | *Cynognathus* | *Parotosuchus, Trematosuchus, Erythrosuchus, Cynognathus, Diademodon, Trirachodon, Kannemeyeria cristarhynchus* |
| | INDUAN | LOOTSBERGIAN | *Lystrosaurus* | *Wetlugasaurus, Tupilakosaurus, Luzocephalus, Lydekkerina, Procolophon, Lystrosaurus, Scaloposaurus, Thrinaxodon, Proterosuchus, Prolacerta* |

*(TRIASSIC PERIOD spans the left margin of all age rows.)*

Figure 2. Correlation of global Land Vertebrate Faunachrons (LVFs) to the standard global chronostratigraphical timescale. First Appearance Datum (FAD) taxa signify the onset of a particular LVF. Index fossils (and type assemblages, of which details are not shown here, but see text) characterize each LVF. The end of each LVF is defined by the appearance of the FAD taxon of the subsequent LVF. Shaded area indicates LVFs considered in this study. Figure modified and expanded after Lucas (1998*a*). Note that most occurrences of *Scaphonyx* are now assigned to *Hyperodapedon* (Langer *et al.* 2000).

signals from Triassic floral records are congruent with faunal biostratigraphy. The results have wide-ranging implications for the correlation of Triassic non-marine strata to the global chronostratigraphical timescale, and the subsequent formulation of hypotheses of evolutionary turnover.

We have used the spatial data-handling capabilities of a GIS to address these questions. A GIS is a computer-based system for storing, managing and analysing data describing positions and objects on the Earth's surface. GIS plays an important role in understanding spatial patterns and dynamics and is used in practical applications such as public utilities mapping, the maintenance of demographic records and environmental management (including palaeontological and geological resources: e.g. Fiorillo *et al.* 2002; Garcia-Bajo & Lawley, 2003). The advantage of a GIS over standard database analysis techniques is that it

supports inventorying, querying and analysis of spatial relationships across layers of mapped information. Through this, spatial patterns, the distribution of key variables, and the aggregation of multiple variables at a point in space may be identified.

By focusing upon palaeontological data through time, a temporal aspect is also incorporated into our analysis. Unlike most GIS applications, the time-scales considered in this study are so large that the movements of geographical locations, caused by plate tectonics, need to be accounted for. GIS is currently being used to assess mammalian evolution and distribution during the Miocene and Quaternary (e.g. Barnosky & Carrasco, 2000), but to our knowledge we present here the first use of GIS to generate a database of multiple vertebrate orders and floral records in order to address macroevolutionary questions and biostratigraphical correlation over an extensive geological timescale.

Table 1. Occurrence, age estimate, dating source and correlating LVF for all Middle and Late Triassic LVF index taxon datapoints in western Europe and North America; where Correlating LVF is highlighted in bold, index taxon is occurring outside prescribed temporal range of Lucas (1998a)

| Index taxon | Occurrence | Age estimates | Dating source | Correlating LVF |
|---|---|---|---|---|
| *Eocyclotosaurus* | Moenkopi Fm. | Early Anisian | Conchostracans (Ash & Morales, 1993; Kozur, Mahler & Sell, 1993) | Perovkan |
| *Eocyclotosaurus* | Otter Sandstone Fm. | Early–late Anisian | Magnetostratigraphy (Hounslow & McIntosh, 2003) | Perovkan |
| *Eocyclotosaurus* | Upper Buntsandstein, Germany | Early Anisian | Conodonts and conchostracans (Kozur, 1993a,b) | Perovkan |
| *Eocyclotosaurus* | Grès à meules, Grès à Voltzia, Buntsandstein | Early Anisian | Conchostracans (Kozur, 1975, 1993b; Kozur, Mahler & Sell, 1993) | Perovkan |
| *Mastodonsaurus* | Uppermost Muschelkalk | Early Ladinian | Palynology (Visscher, Brugman & Van Houte, 1993) | Berdyankian |
| *Mastodonsaurus* | Lettenkeuper Fm. | Early–late Ladinian | Palynology and sequence stratigraphy (Visscher, Brugman & Van Houte, 1993; Geiger & Hopping, 1968; Aigner & Bachmann, 1992) | Berdyankian |
| *Mastodonsaurus* | Bromsgrove Sandstone Fm. | Early–middle Anisian | Palynology (Warrington *et al.* 1980; Benton *et al.* 1994) | **Perovkan** |
| *Mastodonsaurus?* | Schilfsandstein | Middle–late Carnian | Palaeoclimatological correlations, palynology, magnetostratigraphy (reviewed Benton, 1994), sequence stratigraphy (Aigner & Bachmann, 1992; summarized Reinhardt & Ricken, 2000) | **Otischalkian** |
| *Paleorhinus* | Colorado City Fm./member | Middle–late Carnian | Only biochronology available | Otischalkian |
| *Paleorhinus* | Camp Springs Fm./member | Early late Carnian–late Carnian | Palynology (Dunay & Fisher, 1979) | Otischalkian |
| *Paleorhinus* | Popo Agie Fm. | Middle Carnian–late Carnian | *Eoginkgoites* floral zone (Ash, 1980), lithostratigraphy and vertebrate biochronology (Lucas, 1991) | Otischalkian |
| *Paleorhinus?* | Middle Pekin Fm. | Late Carnian | Palynology (Litwin & Ash, 1993) | Otischalkian |
| *Paleorhinus* | Opponitzer Schichten | Late Carnian | Ammonites and palynology (Hunt & Lucas, 1991a) | Otischalkian |
| *Paleorhinus* | Tecovas Fm. | Early late Carnian–late Carnian | Palynology (Dunay & Fisher, 1979) | **Adamanian** |
| *Paleorhinus* | Lower Bluewater Creek Fm.* | Late Carnian | Palynology, magnetostratigraphy (Litwin, Traverse & Ash, 1991; Molina-Garza *et al.* 1991) | **Adamanian** |
| *Paleorhinus* | Blasensandstein, Weser Fm. | Late Carnian–early Norian | Palaeoclimatological correlations, palynology, magnetostratigraphy (reviewed Benton, 1994), sequence stratigraphy (Aigner & Bachmann, 1992) | **Adamanian/ Revueltian?** |
| *Metoposaurus* | Camp Springs | Early late Carnian–late Carnian | Palynology (Dunay & Fisher, 1979) | Otischalkian |
| *Metoposaurus* | Wolfville Fm. | Late Carnian | Biochronology (Huber, Lucas & Hunt, 1993a) | Otischalkian |
| *Metoposaurus* | Schilfsandstein | Middle–late Carnian | Palaeoclimatological correlations, palynology, magnetostratigraphy (reviewed Benton, 1994), sequence stratigraphy (Aigner & Bachmann, 1992; summarized Reinhardt & Ricken, 2000) | Otischalkian or earlier |
| *Metoposaurus* | Lehrberg-schichten, Weser Fm. | Late Carnian | Palaeoclimatological correlations, palynology, magnetostratigraphy (reviewed Benton, 1994), sequence stratigraphy (Aigner & Bachmann, 1992; summarized Reinhardt & Ricken, 2000) | Otischalkian/ **Adamanian** |
| *Metoposaurus* | Raibl beds, Dolomia di Forni | Carnian | Palynology (Blendinger, 1988) Conodonts linked to ammonite scale (Roghi, Mietto & Dalla Vecchia, 1995) | Otischalkian/ **Adamanian** |
| *Metoposaurus* | Baldy Hill Fm. | Late Carnian–early Norian | Sequence stratigraphy (Lucas, Hunt & Hayden, 1987) | **Adamanian/ Revueltian** |

Table 1. *Continued.*

| Index taxon | Occurrence | Age estimates | Dating source | Correlating LVF |
|---|---|---|---|---|
| *Metoposaurus* | Kieselsandstein, Weser Fm. | Late Carnian–early Norian | Palaeoclimatological correlations, palynology, magnetostratigraphy (reviewed Benton, 1994), sequence stratigraphy (Aigner & Bachmann, 1992; summarized Reinhardt & Ricken, 2000) | **Adamanian/ Revueltian** |
| *Metoposaurus* | Blasensandstein, Weser Fm. | Late Carnian–early Norian | Palaeoclimatological correlations, palynology, magnetostratigraphy (reviewed Benton, 1994), sequence stratigraphy (Aigner & Bachmann, 1992; summarized Reinhardt & Ricken, 2000) | **Adamanian/ Revueltian** |
| *Metoposaurus* | Middle Stubensandstein Arnstadt Fm. | Early–middle Norian | Palaeoclimatological correlations, palynology, magnetostratigraphy (reviewed Benton, 1994), sequence stratigraphy (Aigner & Bachmann, 1992; summarized Reinhardt & Ricken, 2000) | **Revueltian** |
| *Angistorhinus* | Colorado City | Middle–late Carnian | Palynology (Litwin, Traverse & Ash, 1991; Cornet, 1993) | Otischalkian |
| *Angistorhinus* | Popo Agie | Middle Carnian–late Carnian | *Eoginkgoites* flora zone (Hunt & Lucas, 1991*b*) | Otischalkian |
| *Angistorhinus* | Los Esteros member, Santa Rosa Fm. | Latest Carnian | Sequence stratigraphy and biostratigraphy: plants and tetrapods (Lucas, Heckert & Hunt, 2001) | **Adamanian** |
| *Longosuchus* | Colorado City Fm. | Middle–late Carnian | Palynology (Litwin, Traverse & Ash, 1991; Cornet, 1993) | Otischalkian |
| *Longosuchus* | Middle Pekin Fm. | Late Carnian | Palynology (Litwin & Ash, 1993) | Otischalkian |
| *Doswellia* | Doswell Fm. | Late Carnian | Fish and tetrapod biostratigraphy (LeTourneau, Huber & Olsen, 1998), palynology (Litwin & Weems, 1992). | Otischalkian |
| *Doswellia* | Colorado City Fm. | Middle–late Carnian | Palynology (Litwin, Traverse & Ash, 1991; Cornet, 1993) | Otischalkian |
| *Rutiodon?* | Middle Pekin Fm. | Middle?–late Carnian | Palynology (Litwin & Ash, 1993) | **Otischalkian** |
| *Rutiodon* | Stockton Fm. | Middle–late Carnian | Magnetostratigraphy (Kent & Olsen, 1999), palynology and plant megafossils (Luttrell, 1989) | **Otischalkian**/ Adamanian† |
| *Rutiodon* | Blue Mesa member, Petrified Forest Fm. | Late Carnian | Palynology (Litwin, Traverse & Ash, 1991), sequence stratigraphy (Lucas, 1993) | Adamanian |
| *Rutiodon* | Lower Bluewater Creek Fm.* | Late Carnian | Palynology, magnetostratigraphy (Litwin, Traverse & Ash, 1991; Molina-Garza *et al.* 1991) | Adamanian |
| *Rutiodon* | Lower Tecovas Fm. | Early late–late Carnian | Palynology (Dunay & Fisher, 1979) | Adamanian |
| *Rutiodon* | Los Esteros member, Santa Rosa Fm. | Latest Carnian | Sequence stratigraphy and biostratigraphy: plants and tetrapods (Lucas, Heckert & Hunt, 2001) | Adamanian |
| *Rutiodon* | Lockatong Fm. | Late Carnian | Magnetostratigraphy (Kent & Olsen, 1999) | Adamanian |
| *Rutiodon?* | Upper Cow Branch Fm. | Late Carnian | Palynology (Litwin & Ash, 1993; Traverse, 1987) | Adamanian |
| *Rutiodon* | Cumnock Fm. | Late Carnian | Palynology (Litwin & Ash, 1993) | Adamanian |
| *Rutiodon* | New Oxford Fm. | Late Carnian | Palynology (Cornet, 1993; Litwin, Traverse & Ash, 1991) | Adamanian |
| *Rutiodon?* | Lower Bull Canyon Fm. | Early–middle Norian | Ostracods, sequence stratigraphy, magnetostratigraphy (summarized in Lucas, 1997, 1998*a*; Lucas, Heckert & Hunt, 2001; Molina-Garza *et al.* 1991; Molina-Garza, Geissman & Lucas, 1993). | **Revueltian** |
| *Rutiodon?* | Owl Rock Fm. | Norian | Palynology (Litwin, Traverse & Ash, 1991) and sequence stratigraphy (Lucas, 1993) | **Revueltian** |
| *Rutiodon?* | Grès à Avicula Contorta | Norian–Rhaetian | Palynology (Schuurman, 1977; Sigogneau-Russell & Hahn, 1994) | **Revueltian/ Apachean?** |
| *Stagonolepis?* | Wolfville Fm. | Late Carnian | Biochronology (Huber, Lucas & Hunt, 1993*a*) | **Otischalkian** |

Table 1. *Continued.*

| Index taxon | Occurrence | Age estimates | Dating source | Correlating LVF |
|---|---|---|---|---|
| *Stagonolepis* | Blasensandstein, Weser Fm. | Late Carnian–early Norian | Palaeoclimatological correlations, palynology, magnetostratigraphy (reviewed Benton, 1994), sequence stratigraphy (Aigner & Bachmann, 1992) | **Otischalkian** |
| *Stagonolepis* | Blue Mesa member, Petrified Forest Fm. | Late Carnian | Palynology (Litwin, Traverse & Ash, 1991), sequence stratigraphy (Lucas, 1993) | Adamanian |
| *Stagonolepis* | Lower Bluewater Creek Fm.* AZ, NM | Late Carnian | Palynology, magnetostratigraphy (Litwin, Traverse & Ash, 1991; Molina-Garza *et al.* 1991) | Adamanian |
| *Stagonolepis* | Los Esteros member, Santa Rosa Fm. | Latest Carnian | Sequence stratigraphy and biostratigraphy: plants and tetrapods (Lucas, Heckert & Hunt, 2001) | Adamanian |
| *Stagonolepis* | Lower Tecovas Fm. | Early late–late Carnian | Palynology (Dunay & Fisher, 1979) | Adamanian |
| *Stagonolepis* | Lossiemouth Sandstone | Late Carnian | Only biochronology available (Benton & Spencer, 1995; Heckert & Lucas, 2002) | Adamanian |
| *Hyperodapedon/ Scaphyonx* | Wolfville Fm. | Late Carnian | Biochronology (Huber, Lucas & Hunt, 1993a) | **Otischalkian** |
| *Hyperodapedon/ Scaphyonx* | Popo Agie | Middle Carnian–late Carnian | *Eoginkgoites* flora zone (Hunt & Lucas, 1991b) | **Otischalkian** |
| *Typothorax coccinarum?* | Tres Lagunas member, Santa Rosa Fm. | Late Carnian | Sequence stratigraphy and vertebrate biochronology (Lucas, Heckert & Hunt, 2001) | **Adamanian** |
| *Typothorax sp.* | Bull Canyon Fm. | Early–middle Norian | Ostracods, sequence stratigraphy, magnetostratigraphy (summarized in Lucas, 1997, 1998a; Lucas, Heckert & Hunt, 2001; Molina-Garza *et al.* 1991; Molina-Garza, Geissman & Lucas, 1993). | Revueltian |
| *Typothorax coccinarum* | Upper Petrified Forest Fm. AZ, NM | Early–middle Norian | Palynology (Litwin, 1987; Litwin, Traverse & Ash, 1991), unionid bivalves (Lucas *et al.* 2003) | Revueltian |
| *Typothorax coccinarum* | Owl Rock Fm. | Norian | Palynology (Litwin, Traverse & Ash, 1991) and sequence stratigraphy (Lucas, 1993, 1997). | Revueltian |
| *Typothorax coccinarum* | Trujillo Fm. | Early–middle Norian | Sequence stratigraphy, vertebrate biochronology (Lucas, Heckert & Hunt, 2001), magnetostratigraphy (Molina-Garza *et al.* 1991; Molina-Garza, Geissman & Lucas, 1993) | Revueltian |
| *Typothorax coccinarum* | Cooper Canyon Fm. | Early Norian | Sequence stratigraphy and faunal correlates (Chatterjee, 1986, Small, 1989) | Revueltian |
| *Typothorax coccinarum/ Redondasuchus ?* | Redonda Fm. | Late Norian–Rhaetian | Magnetostratigraphy (Molina-Garza *et al.* 1996), biostratigraphy: plants, invertebrates, ostracods and tetrapods (Lucas, Heckert & Hunt, 2001) | **Apachean** |
| *Typothorax coccinarum/ Redondasuchus ?* | Sloan Canyon Fm. | Late Norian–Rhaetian | Tetrapod trackways (Lockley & Hunt, 1993) | **Apachean** |
| *Pseudopalatus*-grade phytosaur | Bull Canyon Fm. | Early–middle Norian | Ostracods, sequence stratigraphy, magnetostratigraphy (summarized in Lucas, 1997, 1998a; Lucas, Heckert & Hunt, 2001; Molina-Garza *et al.* 1991; Molina-Garza, Geissman & Lucas, 1993). | Revueltian |
| *Pseudopalatus*-grade phytosaur | Upper Petrified Forest Fm. | Early–middle Norian | Palynology (Litwin, 1987; Litwin, Traverse & Ash, 1991), unionid bivalves (Lucas *et al.* 2003) | Revueltian |
| *Pseudopalatus*-grade phytosaur | Owl Rock Fm. | Norian | Palynology (Litwin, Traverse & Ash, 1991) and sequence stratigraphy (Lucas, 1993, 1997). | Revueltian |
| *Pseudopalatus*-grade phytosaur | Cooper Canyon Fm. | Early Norian | Sequence stratigraphy and faunal correlates (Chatterjee, 1986, Small, 1989) | Revueltian |

Table 1. *Continued.*

| Index taxon | Occurrence | Age estimates | Dating source | Correlating LVF |
|---|---|---|---|---|
| *Pseudopalatus/ Nicrosaurus*-grade phytosaur | Trujillo Fm. | Early–middle Norian | Sequence stratigraphy, vertebrate biochronology (Lucas, Heckert & Hunt, 2001); magnetostratigraphy (Molina-Garza *et al.* 1991; Molina-Garza, Geissman & Lucas, 1993) | Revueltian |
| *Aetosaurus/Stegomus* # | Lithofacies Association II | Late Carnian–early Norian | Fish correlate (*Turseodus*) (Olsen, Schlisch & Gore, 1989), magnetostratigraphy in prep. (cited in Sues *et al.* 2003) | **Adamanian**/ Revueltian |
| *Aetosaurus* # | Lower Passaic Fm. | Early–middle Norian | Magnetostratigraphy (Kent & Olsen, 1999) | Revueltian |
| *Aetosaurus* # | Middle New Haven Fm. | Norian | Palynology and U–Pb dating (Cornet & Traverse, 1975; Wang *et al.* 1998) | Revueltian |
| *Aetosaurus* ‡ | Lower Bull Canyon Fm. | Early–middle Norian | Ostracods, sequence stratigraphy, magnetostratigraphy (summarized in Lucas, 1997, 1998; Lucas, Heckert & Hunt, 2001; Molina-Garza *et al.* 1991; Molina-Garza, Geissman & Lucas, 1993) | Revueltian |
| *Aetosaurus* | Main Elk Creek locality, Colorado | Early–middle Norian | Similar sediments, but no other dating except vertebrate comparisons (Small, 2001) | Revueltian |
| *Aetosaurus* | Cromhall Quarry Fissure Fill | ?–late Norian | Faunal correlates (summarized in Fraser, 1994) | Revueltian |
| *Aetosaurus* | Lower and Middle Stubensandstein, Arnstadt Fm. | Early–middle Norian | Palaeoclimatological correlations, palynology, magnetostratigraphy (reviewed Benton, 1994), sequence stratigraphy (Aigner & Bachmann, 1992; summarized Reinhardt & Ricken, 2000) | Revueltian |
| *Aetosaurus* | Calcare di Zorzino | Middle Norian | Correlation to ammonite series (Jadoul *et al.* 1994; Roghi, Mietto & Dalla Vecchia, 1995) | Revueltian |
| *Aetosaurus* | Upper Fleming Fjord Fm. | Middle–late Norian | Invertebrates, palynology then refined with faunal composition data (Jenkins *et al.* 1994) | Revueltian |
| *Redondauchus* | Upper Redonda Fm. | Late Norian–Rhaetian | Magnetostratigraphy (Molina-Garza *et al.* 1996), tetrapod biostratigraphy (Lucas, Heckert & Hunt, 2001) | Apachean |
| *Redondasaurus* | Redonda Fm. | Late Norian–Rhaetian | Magnetostratigraphy (Molina-Garza *et al.* 1996), biostratigraphy: plants, invertebrates, ostracods and tetrapods (Lucas, Heckert & Hunt, 2001) | Apachean |
| *Redondasaurus* | Uppermost Travesser Fm. | Norian–Rhaetian | Sequence stratigraphy, faunal correlates and palaeopole data (Hunt, 1991; Hunt & Lucas, 1993; Long & Murry, 1995) | Apachean |
| *Redondasaurus* | Rock Point Fm./member (including Church Rock Fm.) | Norian–Rhaetian | Palynomorphs (Lucas *et al.* 2003; Litwin, Traverse & Ash, 1991), magnetostratigraphy (Molina-Garza, Geissman & Lucas, 1999), faunal correlation to Redonda Fm. (Hunt & Lucas, 1993) | Apachean |

We followed the convention of Lucas (1993) in elevating the Chinle Formation to Group status so as to facilitate direct comparisons between taxa, however, we did not feel it appropriate to degrade the Dockum Group to formation status (*contra* Lucas, 1993), and therefore retained formation and member names to clearly distinguish between different localities in this group.
*Some authors consider the *Placerias* quarry to be lower Petrified Forest Formation, late Carnian (Fiorillo & Padian, 1993). Lucas, Heckert & Huber (1997) disagree and place the *Placerias* Quarry in the older Bluewater Creek Formation.
† Classed as Adamanian as part of the correlative provincial LVF Conewagian (Huber, Lucas & Hunt, 1993*a*), even though palynostratigraphy, plant megafossils and magnetostratigraphy date the upper Stockton as middle–late Carnian – typically Otischalkian time and palynostratigraphy dates the Doswell Formation to early–middle Carnian.
#Considered to be *Stegomus* by some authors (Sues & Baird, 1993; Sues *et al.* 2003); assigned to *Aetosaurus* by Lucas, Heckert & Huber (1998); Heckert & Lucas (1999).
‡ Listed as Stagonolepididae indet. by Long & Murry (1995).
Abbreviations: AZ – Arizona; NM – New Mexico.

## 2. Materials and methods

### 2.a. Data collection and processing

Following a review of the relevant literature, a database incorporating information on vertebrate faunas and megafloras was constructed for Middle to Late Triassic fossil localities in North America and Western Europe. There are known problems with generic-level identification of certain taxa crucial to the various LVF definitions (for example, see Schoch & Milner, 2000). Therefore, during database assembly, we followed the taxonomic designations of Lucas (1998*a*) except where conflict arises, as discussed later in the text. Early Triassic LVFs are not considered herein (Fig. 2) because most of their known assemblages occur outside of the western Northern Hemisphere. Although spatially and temporally limited, our chosen area and timeframe offer enough information to provide a thorough test of the validity of Middle and Late Triassic LVFs.

Each fossil occurrence was treated as an individual datum, consisting of a latitude–longitude reference and appropriate taxonomic information; over 5000 records were generated. By convention, additional data assigned to a spatial datum (a vertebrate or megafloral fossil occurrence) is known in a GIS as an 'attribute'. In this analysis, lithostratigraphical information (locality, horizon, unit), age estimation of strata (bracketed by youngest and oldest estimated age), lithology and palaeoecology were attributed to each datum whenever possible. In order to account for the position of the continents in the Middle to Late Triassic (Fig. 1), modern day latitude–longitude coordinates were converted to palaeolatitude–longitude coordinates at 20 Ma intervals (240 Ma, 220 Ma, 200 Ma) using PointTracker software (Scotese, 2001). Coordinate conversion accuracy was checked by converting modern latitude–longitude data for capital cities (London, Berlin, etc.) into palaeolatitude–longitude co-ordinates, which were then plotted onto appropriate palaeo-plate reconstructions (Scotese, 2001). Care was taken to ensure that taxon and formation ages were estimated using tetrapod and megafloral biochronology-independent means (e.g. magnetostratigraphy, radiometric dating, palynology) in order to avoid circularity and non-independence of data (Tables 1, 2).

Lithological climatic indicators and climate bands derived from General Circulation Models (only available for relatively coarse-scaled units of time, either 'Late Triassic' (C. R. Scotese, unpub. data, 2002, see http://www.scotese.com) or 'Carnian' (Wilson *et al.* 1994)) were assigned appropriate palaeolatitude–longitude spatial markers before digitizing, using CartaLinx and MapInfo (Version 5.6), to generate GIS-compatible outline maps. Areal extent maps of European and North American Middle and Late Triassic outcrops were digitized and made GIS-compatible in the same manner.

In the ArcMap subprogram of GIS software ArcView 8.1 (ESRI), climatic and areal extent maps were overlaid onto ArcView compatible 20 Ma interval plate boundary reconstructions (e.g. Fig. 1; Scotese, 2001). Faunal and floral point occurrences (including their taxonomic, lithological, ecological and dating attributes) could then be overlaid on these base maps to create an overview of the ecological configuration of each assemblage and locality. By analysing this data using GIS, these LVFs could be tested.

### 2.b. GIS database analysis

The first stage of the analysis involved creating a 'whole-evidence' map of fauna, flora, climate, lithology and palaeoecology for each locality assigned to a specific LVF. This stage involved an 'attribute selection' process, where a key attribute variable (e.g. formation name or taxon name) can be searched for in multiple databases. All taxa associated with the key variable can then be selected and plotted onto the appropriate palaeogeographical reconstruction. The distribution of type LVF assemblage taxa and key index taxa (Fig. 2) through space and time was examined using attribute selection, in order to test the utility of proposed index taxa, and therefore the validity of the LVF.

Subsequently, we tested whether macrofloral records showed any evidence of temporal and/or spatial restriction, and their consequent utility in biostratigraphical correlation and in testing LVF stability. Attribute selection and overlay analysis (where multiple datasets are overlaid onto the same palaeogeographical reconstruction and variables are selected for based on spatial relationships) were used to address these questions.

If these analyses identified apparently valid biochronological units of fauna and flora, lithological, palaeoecological and climatic data were then consulted in order to determine whether these biochronological correlations could be linked to specific environmental factors. Fauna and flora specific to a particular environment make poor index fossils, as environment, rather than temporal restriction, may be dictating their appearance and distribution. Attribute selection processes enabled us to investigate whether groups of taxa, regardless of temporal or spatial distribution, were linked by possible environmental preferences, rather than shared age *per se*.

## 3. Results and discussion

### 3.a. Faunal correlates

True index fossils should be temporally restricted, common and widespread. This analysis revealed that while some index fossils used to define LVFs (Fig. 2; Huber, Lucas & Hunt, 1993*a*; Lucas & Hunt, 1993;
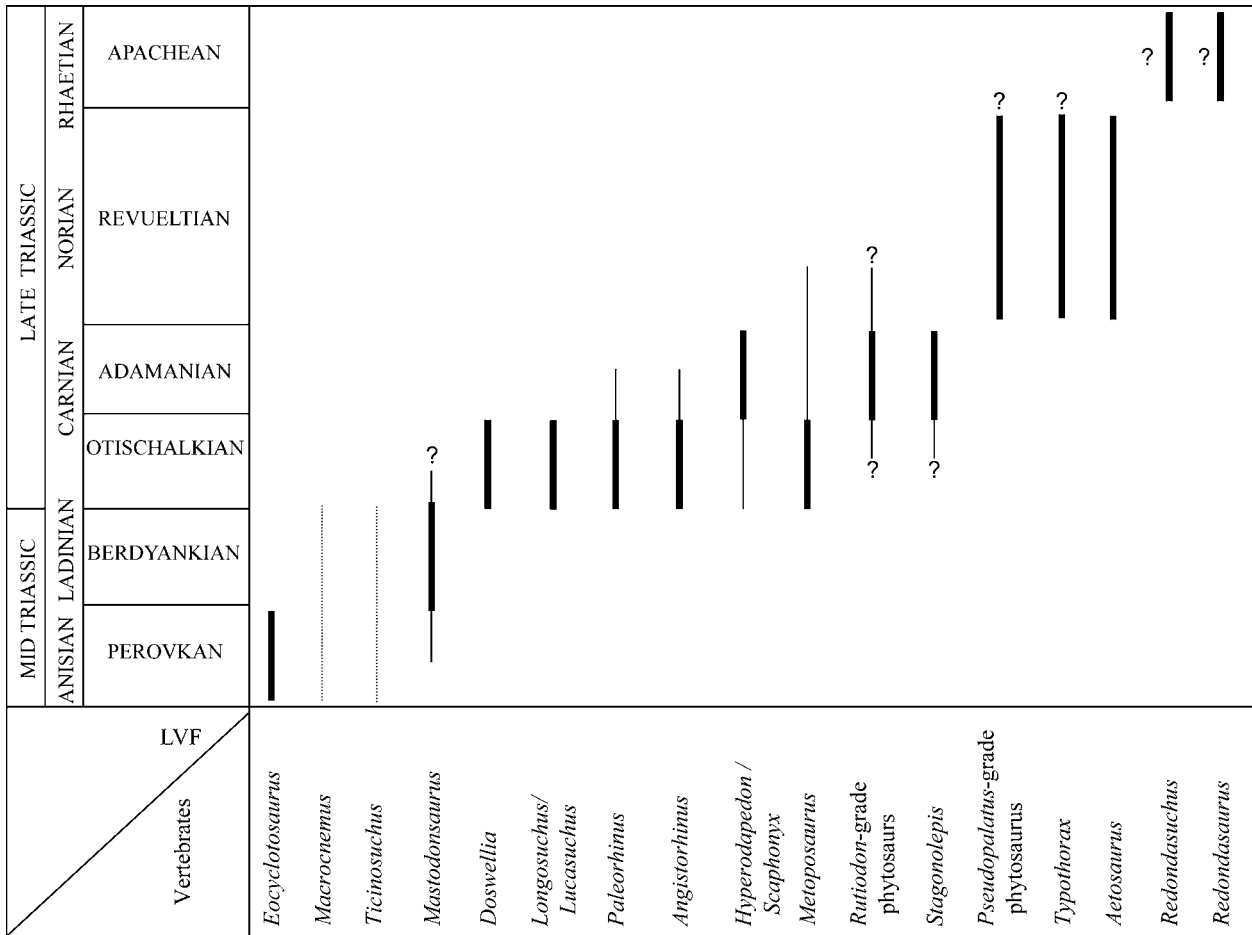
Figure 3. Temporal ranges of LVF index fossils in North America and Western Europe. Thick black line indicates extent of index taxon in associated LVF; thin black line shows full range of index taxon; dotted line signifies potential new index taxa discussed in the text; question mark denotes possible record. See Table 1 for further details.

Lucas, 1998*a*) meet these criteria, others do not. Figure 3 documents the temporal range of LVF index fossils and potential index marker taxa and, as such, highlights both the strengths and weaknesses associated with particular LVF index taxon assemblages.

### 3.a.1. Perovkan LVF

The onset of the Perovkan LVF is determined by the FAD of the dicynodont *Shansiodon* and is characterized by seven index taxa and a type assemblage from the Donguz deposits of the Russian Urals (Fig. 2). Of the seven proposed Perovkan index taxa, only the temnospondyl *Eocyclotosaurus* is present in western Europe and North America (Table 1). *Eocyclotosaurus* is, however, absent from the type assemblage. Consequently, this geographical distribution of taxa would appear to indicate that there is a divide between eastern and western tetrapod faunas during Perovkan time with little interchange of taxa, potentially hindering biostratigraphical correlation. This makes definition of a global biochron problematic.

Lucas (1998*a*) suggested eastern and western faunas were also linked through the presence of a '*Shansisuchus*-like' erythrosuchid in the *Eocyclotosaurus*-bearing Anton Chico Member of the Moenkopi Formation of North America, and the combined presence of *Shansisuchus* and the Perovkan index taxon *Shansiodon* in the Ermaying Formation of China (Lucas, Estep & Hunt, 1998). The North American '*Shansisuchus*-like' taxon appears to be referable to the Erythrosuchidae, but could not be assigned to *Shansisuchus* due to a lack of diagnostic features. In any case, such grade-level associations are problematic, as ghost lineages between sister-taxa may persist for millions of years, such that taxa related at the familial level need not exist in the same temporal range (discussed in more detail in Sections 3.a.4 and 3.a.5). The only previously known erythrosuchid from North America, *Arizonasaurus babbiti* (Welles, 1947; Hunt, 1993; Lucas, Estep & Hunt, 1998) from the penecontemporaneous Holbrook Member of the Moenkopi Formation, has been re-identified recently as a ctenosauriscid archosaur on the basis of new material (Nesbitt, 2003), removing the only other

evidence for the presence of erythrosuchids in the Middle to Late Triassic of North America. Were the Anton Chico erythrosuchid to be confidently identified as *Shansisuchus*, *Shansisuchus* itself is not a Perovkan index taxon, but merely a genus that could provide a potential linkage to a *Shansiodon*-bearing unit in China. All of these factors indicate that the link between the Chinese and North American faunas, and more generally between Eastern and Western Hemisphere faunas is weak. As the best evidence for the proposed Anisian age of the Perovkan comes from the association between *Eocyclotosaurus* and an early Anisian conodont fauna in Germanic marine facies (Lucas, 1998*a*), the lack of linkage between eastern and western faunas has implications for age correlation to other Perovkan assemblages.

These results notwithstanding, *Eocyclotosaurus* appears to be a potentially valid index taxon for western Northern Hemisphere Anisian time (as suggested by Milner *et al.* 1990). It is found only in the Anisian (Ash & Morales, 1993; Kozur, Mahler & Sell, 1993) Moenkopi Formation in western North America, the early Anisian (Kozur, 1975, 1993*a*,*b*; Kozur, Mahler & Sell, 1993) Upper Buntsandstein of Germany and France, and the Anisian-age Otter Sandstone of Devon, United Kingdom (Hounslow & McIntosh, 2003; Table 1; Fig. 3). Hence, it appears that the Perovkan LVF has biostratigraphical utility on a regional, western Northern Hemisphere level, but may not be recognizable globally, at least on the basis of current criteria and evidence.

### 3.a.2. Berdyankian LVF

The FAD of *Mastodonsaurus* marks the beginning of the Berdyankian LVF, which is linked to the Ladinian stage of the global chronostratigraphical timescale (Lucas, 1998*a*; Fig. 2, Table 1). *Mastodonsaurus* is the only Berdyankian index taxon found in the type assemblage, the Bukobay Formation of Russia. None of the five index taxa are present in North America. One is endemic to South America (the traversodontid *Massetognathus*), whilst the traversodontid *Exaeretodon* is found in India (Chatterjee, 1982) and ranges from Ladinian- to Carnian-aged strata in South America. The utility of the remaining index taxa (the dicynodonts *Dinodontosaurus* and *Stahleckeria*) is considered here.

*Dinodontosaurus* is absent from the type Russian assemblage; however, Lucas (1998*a*) cites the presence of a '*Dinodontosaurus*-like' humerus in the Vitriolschiefer of the Lettenkeuper (Lucas & Wild, 1995) as linking northern faunas to the Ischichuca (Chañares) Formation of Argentina and the lower Santa Maria Formation of Brazil, both of which contain identifiable *Dinodontosaurus* remains. Linking the type Russian assemblage to the South American faunas using *Dinodontosaurus* in this manner requires an intermediate step, using the shared presence of

*Mastodonsaurus* in Russia and Germany to initially link these two assemblages. It is the case, however, that the German dicynodont cannot be referred to either the genus *Dinodontosaurus*, or to any other known Triassic dicynodont as it lacks any autapomorphic features that would permit its generic-level identification (Lucas & Wild, 1995). As a result, the existence of *Dinodontosaurus* outside South America and therefore its utility as a *global* index taxon is questionable as it relies upon a weakly supported 'grade-level' association.

Lucas (1998*a*) also suggests that Russian and South American faunas can be linked directly via the presence of *Stahleckeria* in Brazilian assemblages and the occurrence of '*Elephantosaurus jachimovitschi*' in the Russian Bukobay type assemblage. '*Elephantosaurus*' is known only from a fragment of skull roof (Vyushkov, 1969), and most closely resembles *Stahleckeria*, hence the apparent faunal linkage (Lucas, 1998*a*). However, previous work has implied that '*Elephantosaurus*' is morphologically distinct from *Stahleckeria* and cannot be ascribed to this genus (Lucas & Wild, 1995). Moreover, *Elephantosaurus* is currently considered a *nomen dubium* (King, 1988). In the absence of convincing evidence to the contrary, it is possible that *Dinodontosaurus* and *Stahleckeria* are endemic to South America. If correct, four of the five Berdyankian index taxa are South American, restricting their potential to act as index taxa in global correlations.

*Mastodonsaurus*, the remaining Berdyankian index taxon, links the type Russian Bukobay Formation to the German Lettenkeuper (Figs 2, 3, Table 1), although German and Russian forms are at least distinct species (*M. giganteus* and *M. torvus*, respectively). As age estimates for the Lettenkeuper range from early to mid-late Ladinian (Benton, 1994; Lucas, 1998*a*), Lucas (1998*a*) assigned a Ladinian age to the Berdyankian. However, although *Mastodonsaurus* links Russian and European faunas, there is evidence to suggest it is not temporally restricted to 'Berdyankian/Ladinian time'. *Mastodonsaurus* occurs in the Anisian Bromsgrove Sandstone Formation of the United Kingdom (Schoch & Milner, 2000; Schoch, 1999), although other British mastodonsaurid material (from the Anisian Otter Sandstone Formation) has not been formally reassessed in light of the assignment of German Anisian '*Mastodonsaurus*' material to *Heptasaurus* (Schoch, 1999; Lucas & Schoch, 2002), and must be treated with caution. There is, however, a possible record of *Mastodonsaurus* in the Carnian Schilfsandstein of Germany (Schoch, 2000; Table 1), although this is regarded elsewhere as Mastodonsauridae indet. (Schoch & Milner, 2000). Regardless of the status of Carnian records, *Mastodonsaurus* appears not to be a temporally restricted index taxon. Whilst the majority of specimens are found in the Ladinian, Anisian records from the United Kingdom hamper the use of *Mastodonsaurus* as a consistent indicator of Berdyankian time. This curtails the usefulness of the Berdyankian as a

Ladinian biochronological unit. Global correlation of Beryankian faunas hinges on taxonomic resolution of *Mastodonsaurus* and the taxonomic status of Northern Hemisphere *Dinodontosaurus* and *Stahleckeria* material.

Ladinian-aged rocks are probably absent from North America, meaning this region cannot be linked directly to the Berdyankian LVF. Nevertheless, the Lower Wolfville Formation of the Fundy Basin, Nova Scotia, yields a fauna of temnospondyls, archosaurs, archosauromorphs, procolophonids and synapsids (Table 1; Shubin & Sues, 1991), some of which are common to European assemblages over a wider time interval. Our analysis revealed that, in the western Northern Hemisphere, a broader Middle Triassic Anisian to Ladinian interval could possibly be characterized by the presence of *Eocyclotosaurus* and two further taxa: the prolacertiform *Macrocnemus* and the rauisuchid *Ticinosuchus* (Fig. 3). The prolacertiform *Tanystropheus* is also common to Anisian–Ladinian assemblages, but the genus persists into the Norian in Italy, hence diminishing its biostratigraphical utility (Dalla Vecchia, 2000). The aforementioned taxa link the Moenkopi Formation, the Upper Buntsandstein, the Otter Sandstone and the Grenzbitumenzone of Switzerland and Italy, thus supporting Shubin & Sues' (1991) cluster analysis correlation of Middle Triassic faunal assemblages. Interestingly, North American faunas appear intermediate in composition between the temnospondyl-rich western European and Russian faunas and the archosaur-rich South American assemblages. The distinctness of eastern and western Northern Hemisphere faunas may be attributable to a postulated Middle Triassic epicontinental seaway between eastern Russian and western European island faunas (Smith, Smith & Funnell, 1994).

In conclusion, the temporal range of *Mastodonsaurus*, combined with largely endemic index taxa, and the doubtful taxonomic status of the German '*Dinodontosaurus*' and the Russian '*Stahleckeria*', means that Russian and European faunas cannot be directly correlated to South American faunas, with the result that the Berdyankian LVF is presently not useful for global biostratigraphical correlation. *Eocyclotosaurus* is a useful index taxon for the western Northern Hemisphere, and a broader regional Middle Triassic time interval may be identified, defined on the basis of North American and western European assemblages.

### 3.a.3. Otischalkian LVF

The FAD of the phytosaur *Paleorhinus* marks the onset of the Otischalkian, the first Late Triassic LVF (Fig. 2). There is a marked shift in assemblage composition, with a suite of new clades present, including phytosaurs and aetosaurs, which help to characterize the transition from faunas of Middle to Late Triassic age (Figs 2, 3, Table 1). As the type assemblage (from the Colorado City Formation of the Dockum Group) and all five index taxa are found in the United States, the Otischalkian provides a thorough coverage of western North American biochronology. Furthermore, *Paleorhinus* and/or the temnospondyl *Metoposaurus* are also found in the eastern United States, Europe, Morocco and India (Table 1), thereby placing portions of the Newark Supergroup, the German Schilfsandstein, Blasensandstein, perhaps the Kieselsandstein, and the basal portion of the Indian Maleri Formation into the Otischalkian biochron (Lucas, 1998a) There are potential problems with this chronology, however, as the only African occurrence of *Paleorhinus*, in the Moroccan Irohalene Member of the Timesgadiouine Formation, is disputed due to the juvenile nature of the only known specimen (Fara & Hungerbühler, 2000), although *Angistorhinus* (another Otischalkian index taxon) is also present in this deposit. Furthermore, it has been proposed that the Indian '*Paleorhinus*' material cannot be synonymized with North American *Paleorhinus* as currently defined, and could be assigned to *Parasuchus*, as a distinct genus (Hungerbühler, 2001). Furthermore, *Paleorhinus* has not been diagnosed in terms of derived character states; its diagnostic feature, the position of the external naris relative to the antorbital fenestra, is plesiomorphic (H.-D. Sues, pers. comm. 2004).

The occurrence of *Paleorhinus* in Tuvalian (late Carnian) Austrian marine strata (Hunt & Lucas, 1991a; Table 1) provides a benchmark age for the Otischalkian. The specimen, originally *Francosuchus*? *trauthi*, is a rostral fragment, and may represent simply an indeterminate small basal phytosaur (Sues, pers. comm. 2004). Sequence stratigraphy, magnetostratigraphy and palynostratigraphy broaden Otischalkian time to late Julian–early Tuvalian (early to late Carnian) in age (Lucas, 1998a). There is, however, a record of *Paleorhinus* in non-Otischalkian linked strata; the Adamanian-age lower Bluewater Creek Formation at the *Placerias*/Downs quarries (Table 1, Figs 3, 7; see Section 3.a.4). Consequently, *Paleorhinus* is not exclusively restricted to Otischalkian strata (Fig. 3).

*Metoposaurus* has recently been described from the early to middle Norian, middle Stubensandstein of Germany (Milner & Schoch, 2004), and as noted by these authors, this extends the range of *Metoposaurus* from middle Carnian to middle Norian, throughout the Otischalkian, Adamanian and Revueltian biochrons, hence diminishing the stratigraphical utility of the genus. Records of *Metoposaurus* from the Kieselsandstein and probably the Blasensandstein of Germany have been used previously (Lucas, 1998a) to assign a Late Carnian age to these strata, yet the discovery of younger specimens highlights the inherent circularity imposed when using index taxa in which the upper and lower extent of temporal ranges are unknown.

The global integrity of the Otischalkian biochron depends primarily upon the temporal restriction of *Paleorhinus* and *Metoposaurus*. The taxonomic instability of both taxa renders them problematic global biochronological markers. *Paleorhinus* is generally restricted to Otischalkian strata, yet an occurrence in Adamanian-linked strata calls into question the usefulness of this taxon as a definitive index fossil.

Of the remaining three index taxa, the phytosaur *Angistorhinus* and the aetosaur *Longosuchus* are known from North America and Morocco (Lucas, 1998*b*; Dutuit, 1977) and *Angistorhinus* may also be present in Algeria (Jalil, Lucas & Hunt, 1995). As a result, these taxa would be useful for global biochronology, although *Angistorhinus* is known also from Adamanian-linked strata of the Los Esteros Member of the Santa Rosa Formation (Hunt, Lucas & Bircheff, 1993; Table 1, Fig. 3), as noted by Lucas & Huber (2003), and is therefore not temporally restricted. There is a possibility that the aetosaur *Longosuchus* and basal archosauriform *Doswellia* may be useful as regional index fossils in North America. These taxa are restricted to strata dated by palynostratigraphy to the middle or more probably late Carnian (Litwin, Traverse & Ash, 1991; Cornet, 1993; Litwin & Ash, 1993) (Table 1; Fig. 3), although *Doswellia*, the fifth index taxon, is of little global utility as it is currently restricted to the United States.

To summarize, *Metoposaurus*-like and *Paleorhinus*-like taxa are indeed dotted over the globe during the Carnian. However, the taxonomic status of both genera needs further attention before they can be used confidently for global biochronology. Furthermore, *Paleorhinus* and *Metoposaurus* persist into Adamanian and Revueltian-linked strata, an issue considered again below (Section 3.a.4). *Longosuchus* and *Angistorhinus* are potentially interesting, being found in North America and Morocco, yet *Angistorhinus* is not temporally restricted to Otischalkian time. *Doswellia* is restricted to the United States and is useful at a regional but not global level.

### 3.a.4. *Adamanian LVF*

The Blue Mesa Member of the Petrified Forest Formation, Chinle Group, western North America, yields the type Adamanian assemblage (Table 1, Fig. 2). Two of the three index taxa used to define the Adamanian (the aetosaur *Stagonolepis* and '*Rutiodon*-grade' phytosaurs) are found in the Blue Mesa Member and a number of other units across western and eastern North America. The use of '*Rutiodon*-grade' phytosaurs is problematic, in our opinion, as this grade grouping also potentially includes *Leptosuchus* (considered a junior synonym of *Rutiodon* by Ballew, 1989) and *Smilosuchus* (*contra* Long & Murry, 1995). Moreover, correlations based on 'grade level' referrals are poorly supported for reasons discussed previously.

The shared presence of *Stagonolepis* links the North American faunas to the Lossiemouth Sandstone of Scotland (Table 1). Furthermore, Heckert & Lucas (1996, 2002) note that *Aetosauroides* from the Argentine Ischigualasto Formation and the Brazilian Santa Maria Formation represents a junior subjective synonym of *Stagonolepis*, thereby linking North and South American faunas and placing all localities into the Adamanian biochron. However, the presence of *Stagonolepis* in the German Blasensandstein is taken by Heckert & Lucas (2002) to infer an Adamanian age for this horizon, but the Blasensandstein also contains *Paleorhinus* and for this reason had previously been assigned to the Otischalkian biochron (Lucas, 1998*a*; see Section 3.a.3). Clearly, index taxa from successive North American biochrons co-exist in the German strata, suggesting that index taxa of general utility in the former region have a different temporal distribution on the European continent. Does *Stagonolepis* indicate an Adamanian age for the Blasensandstein, or does *Paleorhinus* provide a stronger case for an Otischalkian assignment? Sequence stratigraphy of the German Keuper suggests the Blasensandstein is latest Carnian, in keeping with an Adamanian age, yet this devalues the utility of *Paleorhinus* as an Otischalkian indicator. Additionally, *Paleorhinus* and *Stagonolepis* co-exist in the Bluewater Creek Formation of the Chinle Group, although Heckert & Lucas (2000) note that this overlap occurs at the base of the formation at the transition from Otischalkian- to Adamanian-aged strata. In general, although *Stagonolepis* fulfils the criterion of widespread geographical distribution, its temporal range is blurred and extends beyond typical Adamanian boundaries when considered globally. On the basis of this evidence, the same problems also apply to the use of *Paleorhinus*. Furthermore, Martz, Mueller & Small (2003) point out the problems in identifying aetosaurs from isolated and incomplete scutes, as recently discovered North American aetosaur species possess scutes with varying morphology, attributable to multiple taxa. In our opinion, all these factors hinder the potential of *Stagonolepis* as a useful global Adamanian index fossil.

The FAD of *Rutiodon* marks the onset of the Adamanian (Fig. 2), however, *Paleorhinus* (an Otischalkian index taxon) and *Rutiodon* co-exist at two or possibly three North American localities. Both taxa are found in the typically Adamanian Tecovas Formation (although specimens are found at separate localities), and the Bluewater Creek Formation at the *Placerias*/Downs quarries (Table 1, Fig. 3). Hunt & Lucas (1991*a*) and Lucas (1997) acknowledge these facts, pointing out that overlap occurs at the base of the Bluewater Creek and Tecovas, where *Paleorhinus* records are fragmentary and *Rutiodon* is more common, in association with *Stagonolepis*. Lucas (1997) denotes this period as a '*Paleorhinus*, *Angistorhinus* and *Rutiodon* overlap biochron'. Localities such as the

Chinle that are rich in specimens offer the chance to examine relative abundance of various taxa and subsequently deduce whether the biochron represents Otischalkian, Adamanian or an overlap period. In localities that typically yield fewer, fragmentary remains, such as the Newark Supergroup and the German Keuper, multiple taxa may not be available for comparison, making it impossible to deduce to which biochronological unit a single specimen of, for example, *Paleorhinus*, may belong. A third possible co-occurrence of *Rutiodon* and *Paleorhinus* (as ?*Paleorhinus* indet.) occurs in the typically Otischalkian middle Pekin Formation of the Newark Supergroup (Table 1; Huber, Lucas & Hunt, 1993*a*,*b*). If correct, this presumably represents the overlap biochron, yet the middle Pekin also contains *Longosuchus*, an Otischalkian index taxon. Can *Longosuchus* therefore reliably represent early late Carnian time? A record of *Rutiodon* in the Revueltian Bull Canyon formation (Hunt & Lucas, 1989) may prove to have been misidentified, yet there is a further possible record of *Rutiodon* alongside *Typothorax* in the Norian Owl Rock Formation in northern Arizona (Kirby, 1989). A report of isolated teeth and an undiagnostic phytosaur premaxilla attributed to *Rutiodon* from the Norian–Rhaetian 'Grès à Avicula Contorta' (Buffetaut & Wouters, 1986) was dismissed as an unjustified identification (Lucas & Huber, 2003). It is presently unclear whether any of these records will lead to a positive identification of *Rutiodon* in the Norian.

Lucas (1998*a*) proposed the rhynchosaur *Scaphonyx* as the third Adamanian index taxon. Recent taxonomic revisions have assigned most *Scaphonyx* and some hyperodapedontid material from the Otischalkian (lower Maleri Formation of India and middle Wolfville Formation of Nova Scotia), the Adamanian (Lossiemouth Sandstone of Scotland, Ischigualasto Formation of Argentina and Santa Maria Formation of Brazil), and the Late Carnian of Zimbabwe and Tanzania, to the genus *Hyperodapedon* (Langer & Schultz, 2000; Langer *et al.* 2000; Langer, Ferigolo & Schultz, 2000). New discoveries have revealed the presence of *Hyperodapedon* in the Otischalkian Popo Agie Formation of Wyoming (alongside *Paleorhinus* and *Angistorhinus*: Lucas, Heckert & Hotton, 2002) and the Late Carnian of Madagascar (Langer *et al.* 2000).

Consequently, *Scaphonyx*/*Hyperodapedon* is not a useful index taxon at the fine level of resolution proposed by Lucas (1998*a*), as it is found alongside both Otischalkian and Adamanian index taxa. Lucas & Heckert (2002) and Lucas, Heckert & Hotton (2002) recognize this fact, and argue for the presence of a global *Hyperodapedon* biochron, representing a broader Otischalkian–Adamanian time zone (in addition to retaining the Otischalkian and Adamanian biochron units). Our investigation is in agreement with the former proposition and has also shown that *Stagonolepis* and possibly *Rutiodon* display a propensity for Otischalkian faunas. There is, therefore, a strong argument for amalgamating the Northern Hemisphere Otischalkian–Adamanian biochrons into a coarser late Carnian unit, as suggested for South American faunas by Langer (2003). Our megafloral analysis also supports this proposition (see Section 3.b.1). However, taxonomic problems still exist: the assignment of the Madagascan rhynchosaur *Isalorhynchus genovefae* to *Hyperodapedon* has recently been called into question (Whatley, 2003). Furthermore, it has been suggested that *Hyperodapedon* is a paraphyletic taxon, as Nova Scotian and Brazilian forms differ from other rhynchosaurs assigned to *Hyperodapedon* in the derived absence of lingual teeth on the dentary (H.-D. Sues, pers. comm. 2004).

### 3.a.5. Revueltian LVF

The Revueltian type assemblage, the Bull Canyon Formation of east-central New Mexico, contains all three Revueltian index taxa: the aetosaurs *Aetosaurus* and *Typothorax* and '*Pseudopalatus*-grade' phytosaurs (Table 1, Fig. 2). There is some disagreement over the status of the latter two index taxa, which according to some authors extend into Apachean-aged strata (see Section 3.a.6). However, as currently defined, the third taxon *Aetosaurus* is restricted to well-dated early to middle Norian-aged localities, and is additionally found in Europe and Greenland (Fig. 3, Table 1), although there is some disagreement over the status of supposed '*Aetosaurus*' remains. In addition to a record of *Aetosaurus* from the Elk Creek locality of Colorado (Small, 1998), the presence of this taxon in the Norian of North America depends upon the re-identification of *Stegomus arcuatus* in the New Haven Formation (Sues & Baird, 1993), Passaic Formation (Baird, 1986; Huber, Lucas & Hunt, 1993*b*) and Durham Sub-basin (Huber, Lucas & Hunt, 1993*b*) as subjective junior synonyms of *Aetosaurus arcuatus* (Lucas, Estep & Hunt, 1998; Heckert & Lucas, 1999) and the referral of Bull Canyon Formation material identified as Stagonolepididae indet. (Long & Murry, 1995) to *Aetosaurus* (Lucas & Heckert, 1997; Heckert & Lucas, 1998) (Table 1). If these re-identifications hold true, *Aetosaurus* is a valid index fossil on a global scale for early to middle Norian aged North American and European strata. However, several of these suggested referrals are disputed based in part on the fact that *Aetosaurus* is the sister taxon to all other known, predominantly Carnian, stagonolepid aetosaurs. Therefore, one should expect to find *Aetosaurus* in pre-Norian strata (Sues *et al*. 2003). Lucas, Heckert & Harris (1999) dispute these claims based on the lack of evidence of ghost lineage taxa in the fossil record.

As *Typothorax* and *Pseudopalatus* are endemic to western North America, they are of little global value, although they may hold regional biostratigraphical

utility. Previous records of *Typothorax* from Ada-manian-aged strata of the Los Esteros Member of the Santa Rosa Formation and the Garita Creek Formation, both of New Mexico, have been assigned to a distinct Carnian species: *T. antiquum* (Lucas, Heckert & Hunt, 2002). With the exception of a single paramedian scute assigned to *T. coccinarum*, apparently from the Late Carnian Tres Lagunas Member of the Santa Rosa Formation (Long & Murry, 1995), all records of *T. coccinarum sensu* Lucas, Heckert & Hunt (2002) pertain to Norian, Revueltian-age strata. Nevertheless, this taxonomic scheme is not accepted universally, and the validity of *Typothorax* as a Norian indicator has been challenged (see Section 3.a.6); thus, the Revueltian LVF may not be a stable division.

### 3.a.6. *Apachean LVF*

The Apachean is characterized by a regionally restricted type assemblage containing little material identifiable to familial or generic level except for the proposed index taxa *Redondasaurus* (a phytosaur with two species: *R. bermani* and *R. gregorii*) and the aetosaur *Redondasuchus reseri* (Fig. 2, Table 1). The Apachean is currently of limited utility as a global chronological unit since the index taxa are restricted to western North America. A third proposed index taxon, the prosauropod *Riojasaurus*, is found in only two Argentine localities (Bonaparte, 1996; Weishampel *et al*. 2004).

*Redondasaurus* and *Redondasuchus* could potentially act as useful regional index taxa, but conflict exists over their generic level assignment. Hunt & Lucas (1993) regard *Pseudopalatus* and *Redondasaurus* as distinct phytosaur genera on the basis of differences in supratemporal fenestra shape. Furthermore, Hunt & Lucas (1991*a*) and Heckert, Hunt & Lucas (1996) suggested that the aetosaurs *Typothorax coccinarum* and *Redondasuchus reseri* could be distinguished from each other on the basis of paramedian scute morphology. Following this taxonomic scheme, *Pseudopalatus* and *Typothorax* act as valid Revueltian index taxa, while *Redondasaurus* and *Redondasuchus* characterize the Apachean LVF (Lucas, 1998*a*). However, Ballew (1989) and Long & Murry (1995) do not consider *Redondasaurus* and *Redondasuchus* distinct from *Pseudopalatus* and *Typothorax*, respectively. The latter authors therefore advocate the persistence of *Typothorax* and *Pseudopalatus* into the Apachean/Rhaetian Sloan Canyon and Redonda formations (Table 1). Hungerbühler, Chatterjee & Cunningham (2003) describe a new species of phytosaur from the Norian Cooper Canyon Formation of Texas, with supratemporal morphology intermediate between that of *Pseudopalatus* and *Redondasaurus*. Phylogenetic analysis places this new taxon as sister group to *R. gregori*, whilst *R. bermani* is outgroup to a *Pseudopalatus* clade. *Redondasaurus* is therefore considered a subjective

junior synonym of *Pseudopalatus* (Hungerbühler, Chatterjee & Cunningham, 2003). These results support claims by Long & Murry (1995) that whilst *R. gregorii* is conspecific with *Pseudopalatus pristinus*, *R. bermani* represents a small specimen of *Arribasuchus buceros* (which Ziegler, Lucas & Heckert, 2002, consider a subjective junior synonym of *Pseudopalatus*).

If the taxonomic conclusions of Hunt & Lucas (1991*a*, 1993), Heckert, Hunt & Lucas (1996), Lucas (1998*a*) and Ziegler, Lucas & Heckert (2002) are correct, then *Typothorax* might be restricted to Norian time (apart from a possible Late Carnian occurrence in the Tres Lagunas member, Table 1) and *Pseudopalatus* may be restricted to Revueltian assemblages, thus upholding the stability (at a regional level) of the Revueltian and Apachean LVFs. In contrast, if Long & Murry (1995) and Hungerbühler, Chatterjee & Cunningham (2003) are correct, Revueltian and Apachean LVFs cannot be distinguished as discrete biochronological units except for the presence or absence of *Aetosaurus*. Such taxon identification disputes highlight how taxonomic conflicts can influence and undermine the validity of LVFs.

### 3.b. **Megafloral correlates**

In this study, we also aimed to test whether these tetrapod-based biostratigraphical correlations were supported or contradicted by those based on megafloral occurrences. Analysis of our megafloral database revealed that floral records generally consist of endemic time-restricted forms or widespread, long-lived genera. Identifying spatially and temporally restricted megafloral records was therefore difficult. Some authors have claimed that megafloral fossils are inadequate tools for zonation due to their longer temporal ranges and the rarity of useful fossils (Cornet, 1993). Our analysis provides support for this view, as only nine potentially useful megafloral taxa, all associated with predominately Carnian-age strata, were identified. Lack of collected specimens, paucity of published information and complex climatic effects as yet undetected or unresolved (particularly in the case of eastern USA lake varve systems) may account for difficulties with this analysis.

On the basis of current information, it has not been possible to find any megafloral genera that are spatially widespread yet temporally restricted to stage level in the Middle or Late Triassic across both North America and Western Europe (Fig. 4; Table 2). Within North America, six genera and three species do appear to be temporally restricted (Fig. 4, Table 2). The cycad *Macrotaeniopteris* and the lycopods *Chinlea* and possibly *Leptocyclotes* are restricted to late Carnian and Adamanian-linked deposits (although data are sparse) and the remaining records are typically found in both Otischalkian- and Adamanian-aged rocks,
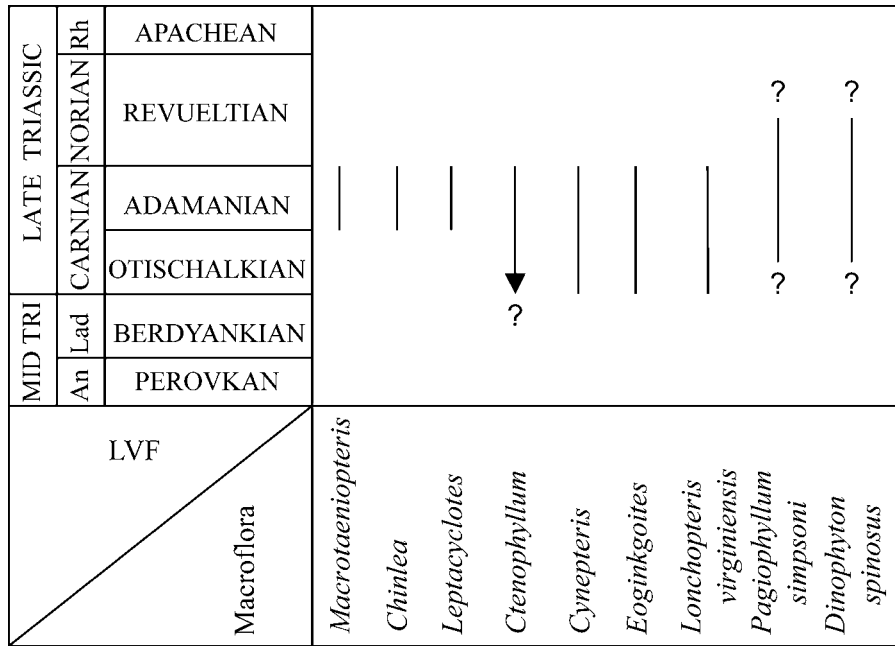
Figure 4. Floral distribution across LVFs. GIS database attribute queries were used to identify all floral records that were geographically widespread and temporally restricted. An – Anisian; Lad – Ladinian; Rh – Rhaetian. See Table 2 for further details.

with occasional Revueltian records (Table 2). All but one taxon (*Chinlea*) are found in both eastern and western North America, supporting the existence of a continental, but not global, megafloral assemblage (Fig. 4, Table 2).

### 3.b.1. Megafloral zones and possible correlations

Ash (1980) tentatively proposed three Late Triassic megafloral zones in North America: the middle Carnian *Eoginkgoites* zone, the late Carnian *Dinophyton* zone and an unnamed Rhaeto-Liassic zone equivalent to the *Thaumatopteris* zone of Greenland. Zones were correlated with the Germanic Triassic stages using associated pollen and spores. Typically the Shinarump, Temple Mountain, Popo Agie, Cumnock, Pekin and Stockton formations have been attributed to the *Eoginkgoites* zone. The Dolores, lower Petrified Forest, Tecovas, Trujillo, Santa Rosa and New Oxford formations are attributed to the *Dinophyton* zone (Table 2). Axsmith & Kroehler (1989) recorded the discovery of *Dinophyton* in the *Eoginkgoites* zone, and our analysis has revealed that *Eoginkgoites* and *Dinophyton* zone assemblages are frequently linked by the common presence of other key megaflora taxa (Table 2). In particular, taxa from the *Eoginkgoites*-zone Pekin, Cumnock and Shinarump formations are frequently found in *Dinophyton* assemblages such as the New Oxford Formation. Our findings are supported by recent reassessment of Newark sequence strata dating, where strata typically assigned to distinct floral zones are now considered to be temporally equivalent late Carnian units. For example, palynological dating has re-assigned the middle Pekin and the upper middle New Oxford Formation to the late Carnian (Cornet, 1993; Litwin & Ash, 1993; Table 2) and the Cumnock and Shinarump formations are now dated as late, rather than middle Carnian (Parrish, 1989; Godefroit & Battail, 1997; Olsen *et al.* 2002; Table 2). Our analysis revealed that taxa from both the *Eoginkgoites* and *Dinophyton* floral zones frequently co-occur in the same stratigraphical units, supporting the proposed lack of temporal distinction between late Carnian LVFs. Consequently, megafloral records do not allow recognition of distinct Carnian-aged Otischalkian and Adamanian biochrons. This observation parallels the result obtained from consideration of the tetrapod data, which also fails to recognize a clear distinction between these LVFs, suggesting that they could be combined with each other (Fig. 3, Table 1). As for other Middle to Late Triassic time intervals, there are no clear megafloral biostratigraphical signals for Middle (Anisian–Ladinian) and the majority of Late Triassic (late Norian–Rhaetian) time. Therefore, megafloral records neither support nor contradict the LVF biochron divisions proposed for these intervals.

### 3.c. Palaeoecological bias

Ecological and facies bias can influence the distribution and occurrence of taxa. Using information on palaeoecology and palaeoenvironmental setting for each tetrapod occurrence, potentially useful index taxa (both floral and faunal) were assessed in order to see if they were subject to any possible environmental bias. Most taxa did not exhibit any biases, and were found in a wide variety of terrestrial, and occasionally near-shore marine, environments.

Table 2. *Occurrence, age estimate, floral zone, dating source and correlating LVF for all Middle and Late Triassic floral records that appear temporally restricted to between one and three LVFs in western Europe and North America; correlating LVF is assigned to formational unit based upon index faunal occurrences (see Table 1)*

| Floral record | Occurrence | Age estimate | Floral zone (after Ash, 1980) | Dating source | Correlating LVF |
|---|---|---|---|---|---|
| *Macrotaeniopteris* | Cumnock Fm. | Late Carnian | *Eoginkgoites* | Palynology (Litwin & Ash, 1993) | Adamanian |
| *Macrotaeniopteris* | Upper Middle New Oxford Fm. | Late Carnian | *Dinophyton* | Palynology (Cornet, 1993; Litwin, Traverse & Ash, 1991) | Adamanian |
| *Macrotaeniopteris* | Lower Petrified Forest Fm. | Late Carnian | *Dinophyton* | Palynology, sequence stratigraphy, magnetostratigraphy (summarized in Lucas, 1998a). | Adamanian |
| *Chinlea* | Lower Petrified Forest Fm., multiple localities | Late Carnian | *Dinophyton* | Palynology, sequence stratigraphy, magnetostratigraphy (summarized in Lucas, 1998a). | Adamanian |
| *Cynepteris* | Many localities, Richmond Basin | Early–middle Carnian | *Eoginkgoites* | Palynology (Cornet, 1989, 1993) | Otischalkian |
| *Cynepteris* | Middle Pekin Fm. | Late Carnian | *Eoginkgoites* | Palynology (Litwin & Ash, 1993) | Otischalkian |
| *Cynepteris* | Cumnock Fm. | Late Carnian | *Eoginkgoites* | Palynology (Litwin & Ash, 1993) | Adamanian |
| *Cynepteris* | Upper Middle New Oxford Fm. | Late Carnian | *Dinophyton* | Palynology (Cornet, 1993; Litwin, Traverse & Ash, 1991) | Adamanian |
| *Cynepteris* | Blue Mesa member, Petrified Forest Fm. | Late Carnian | *Dinophyton* | Palynology (Litwin, Traverse & Ash, 1991), sequence stratigraphy (Lucas, 1993) | Adamanian |
| *Cynepteris* | Shinarump Fm. AZ and UT | Late Carnian | *Eoginkgoites* | Palynology (Litwin *in* Parrish, 1989) | Otischalkian |
| *Cynepteris* | Monitor Butte Fm. NM | Late Carnian | *Dinophyton* | Palynology (Litwin *in* Parrish, 1989) | Otischalkian/ Adamanian |
| *Cynepteris* | Santa Rosa Fm. | Late Carnian | *Dinophyton* | Sequence stratigraphy (summarized Benton, 1994; Hunt, Lucas & Bircheff, 1993; Long & Murry, 1995) | Adamanian |
| *Ctenophyllum* | Many localities, Richmond Basin | Early–middle Carnian | *Eoginkgoites* | Palynology (Cornet, 1989, 1993) | Otischalkian |
| *Ctenophyllum* | Lower Pekin Fm. | Early–late Carnian | *Eoginkgoites* | Palynology (Litwin & Ash, 1993) | Otischalkian |
| *Ctenophyllum* | Cumnock Fm. | Late Carnian | *Eoginkgoites* | Palynology (Litwin & Ash, 1993) | Adamanian |
| *Ctenophyllum* | Upper Middle New Oxford Fm. | Late Carnian | *Dinophyton* | Palynology (Cornet, 1993; Litwin, Traverse & Ash, 1991) | Adamanian |
| *Ctenophyllum* | Shinarump Fm. AZ | Late Carnian | *Eoginkgoites* | Palynology (Litwin *in* Parrish, 1989) | Otischalkian |
| *Eoginkgoites* | Middle Pekin Fm. | Late Carnian | *Eoginkgoites* | Palynology (Litwin & Ash, 1993) | Otischalkian |
| *Eoginkgoites* | Upper Stockton Fm. | Middle–late Carnian | *Eoginkgoites* | Magnetostratigraphy (Kent & Olsen, 1999), palynology and plant megafossils (Luttrell, 1989) | Adamanian |
| *Eoginkgoites* | Shinarump Fm. AZ and UT | Late Carnian | *Eoginkgoites* | Palynology (Litwin *in* Parrish, 1989) | Otischalkian |
| *Eoginkgoites* | Temple Mountain Fm. | Middle–late Carnian | *Eoginkgoites* | Palynology (Litwin, Traverse & Ash, 1991) | Otischalkian |
| *Eoginkgoites* | Popo Agie Fm. | Middle–late Carnian | *Eoginkgoites* | *Eoginkgoites* flora zone (Hunt & Lucas, 1991b) | Otischalkian |
| *Lonchopteris virginiensis* | Upper Cow Branch Fm. | Late Carnian | Unspecified | Palynology (Litwin & Ash, 1993; Traverse, 1987) | Adamanian |
| *Lonchopteris sp.* | Middle Pekin Fm. | Late Carnian | *Eoginkgoites* | Palynology (Litwin & Ash, 1993) | Otischalkian |
| *Lonchopteris virginiensis* | Blue Mesa member, Petrified Forest Fm. | Late Carnian | *Dinophyton* | Palynology (Litwin, Traverse & Ash, 1991), sequence stratigraphy (Lucas, 1993) | Adamanian |
| *Leptacyclotes* | Upper Cow Branch Fm. | Late Carnian | Unspecified | Palynology (Litwin & Ash, 1993; Traverse, 1987) | Adamanian |

Table 2. *Continued.*

| Floral record | Occurrence | Age estimate | Floral zone (after Ash, 1980) | Dating source | Correlating LVF |
|---|---|---|---|---|---|
| *Leptacyclotes* | Blue Mesa member, Petrified Forest Fm. | Late Carnian | *Dinophyton* | Palynology (Litwin, Traverse & Ash, 1991), sequence stratigraphy (Lucas, 1993) | Adamanian |
| *Pagiophyllum simpsoni* | Upper Cow Branch Fm. | Late Carnian | Unspecified | Palynology (Litwin & Ash, 1993; Traverse, 1987) | Adamanian |
| *Pagiophyllum simpsoni* | Upper Stockton Fm. | Middle–late Carnian | *Eoginkgoites* | Magnetostratigraphy (Kent & Olsen, 1999), palynology and plant megafossils (Luttrell, 1989) | Adamanian |
| *Pagiophyllum simpsoni* | Upper Middle New Oxford Fm. | Late Carnian | *Dinophyton* | Palynology (Cornet, 1993; Litwin, Traverse & Ash, 1991) | Adamanian |
| *Pagiophyllum simpsoni* | Tecovas Fm. | Early late Carnian–latest Carnian | *Dinophyton* | Palynology (Dunay & Fisher, 1979) | Otischalkian/Adamanian |
| *Pagiophyllum simpsoni* | Trujillo Fm. | Early–middle Norian | *Dinophyton* | Sequence stratigraphy, vertebrate biochronology (Lucas, Heckert & Hunt, 2001), magnetostratigraphy (Molina-Garza *et al.* 1991; Molina-Garza, Geissman & Lucas, 1993) | Revueltian |
| *Pagiophyllum simpsoni* | Lower Petrified Forest Fm., Blue Mesa member | Late Carnian | *Dinophyton* | Palynology, sequence stratigraphy, magnetostratigraphy (summarized in Lucas, 1998*a*). | Adamanian |
| *Pagiophyllum simpsoni* | Upper Petrified Forest Fm., Painted Desert member | Early–middle Norian | Unspecified | Palynology (Litwin, 1987) | Revueltian |
| *Pagiophyllum simpsoni* | Monitor Butte Fm. NM | Late Carnian | *Dinophyton* | Palynology (Litwin *in* Parrish, 1989) | Otischalkian/Adamanian |
| *Dinophyton spinosus* | Middle Pekin Fm. | Late Carnian | *Eoginkgoites* | Palynology (Litwin & Ash, 1993) | Otischalkian |
| *Dinophyton spinosus* | Upper Stockton Fm. | Middle–late Carnian | *Eoginkgoites* | Magnetostratigraphy (Kent & Olsen, 1999), palynology and plant megafossils (Luttrell, 1989) | Adamanian |
| *Dinophyton spinosus* | Upper Middle New Oxford Fm. | Late Carnian | *Dinophyton* | Palynology (Cornet, 1993; Litwin, Traverse & Ash, 1991) | Adamanian |
| *Dinophyton spinosus* | Tecovas Fm. | Early late Carnian–latest Carnian | *Dinophyton* | Palynology (Dunay & Fisher, 1979) | Adamanian |
| *Dinophyton spinosus* | Lower Petrified Forest Fm., Blue Mesa member | Late Carnian | *Dinophyton* | Palynology, sequence stratigraphy, magnetostratigraphy (summarized in Lucas, 1998*a*). | Adamanian |
| *Dinophyton spinosus* | Upper Petrified Forest Fm., Painted Desert member | Early–middle Norian | Unspecified | Palynology (Litwin, 1987) | Revueltian |
| *Dinophyton spinosus* | Monitor Butte Fm. NM | Late Carnian | *Dinophyton* | Palynology (Litwin *in* Parrish, 1989) | Otischalkian/Adamanian |
| *Dinophyton spinosus* | Santa Rosa Fm. | Late Carnian | *Dinophyton* | Sequence stratigraphy (summarized Benton, 1994; Hunt, Lucas & Bircheff, 1993; Long & Murry, 1995) | Adamanian |

Abbreviations: AZ – Arizona; NM – New Mexico; UT – Utah.

There are exceptions to this rule, however. The distribution of the Otischalkian index taxa *Metoposaurus* and *Angistorhinus* appears to be influenced by depositional environment (Fig. 5). *Metoposaurus* is found in various high-energy environments: in the western USA it is generally found in conglomeritic or channel sandstone deposits, and remains in Nova Scotia and western Europe tend to be deposited in braided river channels (although Milner & Schoch, 2004, noted German *Metoposaurus* remains were more abundant in
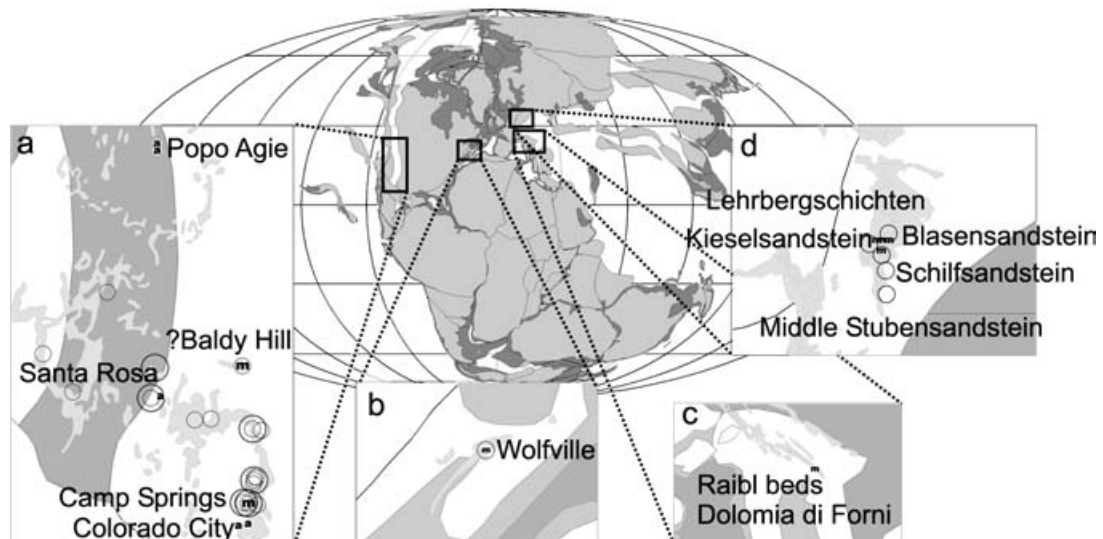
Figure 5. Possible facies bias in Otischalkian index taxa. GIS-derived correlation of *Metoposaurus* to high-energy environments and *Angistorhinus* to low-energy environments. Central map is a 220 Ma plate reconstruction, Mollweide projection. (a) Western North America. (b) Fundy basin, Nova Scotia, eastern North America. (c) Northern Italy, Europe. (d) Germanic basin, Europe. Light grey outlined regions indicate areal extent of Middle and Late Triassic outcrops as currently known; mid-grey is continental margin; dark grey is perceived ocean. m – *Metoposaurus* occurrence; a – *Angistorhinus* occurrence. Open black circle indicates Carnian or Norian-aged conglomeritic or channel sandstone depositional environments. Latitude/longitude references for fossil occurrence and outcrop data have been adjusted to reflect depositional position at 220 Ma. Although *Metoposaurus* and *Angistorhinus* exist in close proximity, taxa never co-occur in the same depositional environment.

the playa lake environments of the Lehrbergschichten than other Carnian and Norian fluviate deposits). In contrast, *Angistorhinus* tends to be deposited in low-energy settings such as the floodplain or low-energy stream deposits of the Los Esteros member of the Santa Rosa Formation (Hunt, Lucas & Bircheff, 1993; Fig. 5; Table 1). *Metoposaurus* and *Angistorhinus* are both found in the Carnian of western North America and occur in close proximity to each other, but are never found in the same depositional environment (Fig. 5). It was established previously that neither taxon is temporally restricted (see Section 3.a.3), and evidence for facies bias further diminishes their potential as useful index taxa.

Facies bias is not clearly observed in the distribution of Perovkan or Berdyankian index taxa and is not discussed further here. The Adamanian taxa *Stagonolepis*, *Buettneria* and *Poposaurus* and the Revueltian index taxon *Pseudopalatus* are generally found in fluvial deposits, although the correlation is not strong. Lucas (1998*a*) cites facies bias to explain the apparent endemism of Apachean index taxa *Redondasaurus* and *Redondasuchus* and their absence from the mainly lacustrine deposits of the eastern USA. Although restricted to western North America, results from this study indicate that these two taxa are found in a wide range of depositional environments, including lacustrine settings (Fig. 6). An absence of facies bias potentially increases the usefulness of these taxa as index fossils, but their global utility is restricted by their endemism (see above).

Of the ten floral correlates identified (Section 3.b), most show no evidence of environmental bias or are known from too few occurrences for bias to be tested. The strongest suggestion of bias concerns the cycad *Macrotaeniopteris*, which is found preferentially in low-oxygen pond, marsh or bog deposits. The osmundacean fern *Lonchopteris* and the lycopods *Leptacyclotes* and *Chinlea* are found exclusively in deep-water lacustrine, pond or bog and floodplain environments.

**3.d. Climatic bias**

Lithological indicators of climate and climatic zones were only available for either the Carnian stage or an amalgamated 'Late Triassic' timeframe (see Section 2). Subtleties in climate change postulated to occur during the Carnian or at the Carnian–Norian boundary (Simms, Ruffell & Johnson, 1994) cannot be detected, and dispute over whether Late Triassic weather systems were zonal and/or monsoonal further hampers study of possible correlations between faunal and floral composition and climate (Parrish, Ziegler & Scotese, 1982; Parrish, 1993; Wilson *et al.* 1994; Olsen & Kent, 1996; Kent & Olsen, 2000). Differing interpretations of Late Triassic lithological climatic indicators offer conflicting scenarios; for example, indicators of humidity, like coals, and arid markers, such as evaporites and calcretes, co-exist in some regions (e.g. see Fig. 8). This effect may be due to lack of temporal resolution in the data, with
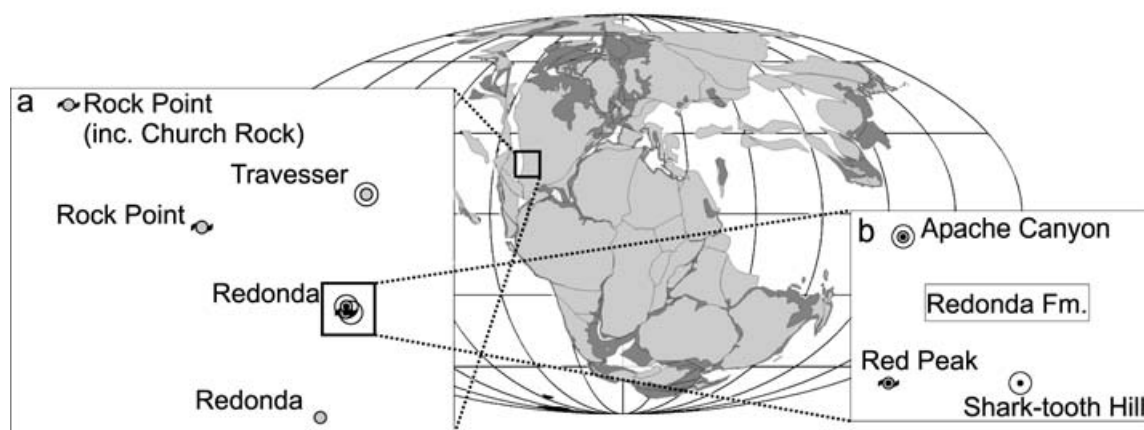
Figure 6. Facies bias in Apachean index taxa. Central map is a 200 Ma-plate reconstruction. Grey circle – *Redondasaurus*; smaller black circle – *Redondasuchus*; large open black circle indicates Rhaetian aged conglomerate and channel sandstone facies; ∼ – lower energy Rhaetian aged siltstone and mudstone facies. (a) Western North America (close up of inset square on main map). Labels indicate formation name. (b) Close-up of inset square in (a), Redonda Formation *Redondasaurus* and *Redondasuchus* point occurrences with quarry or locality yielding specimen labelled. *Redondasaurus* and *Redondasuchus* are found in a variety of depositional environments (*contra* Lucas, 1998*a*).

the map depicting climatic conditions that changed over time as the North American continent drifted northwards during Late Triassic times (Kent & Olsen, 2000). Alternatively, such lithological indicators may reflect a real signal caused by seasonally alternating periods of intense rainfall followed by aridity under a monsoonal regime (Parrish, Ziegler & Scotese, 1982). It is difficult, therefore, to interpret results gained from mapping faunal and floral occurrences onto lithological indicators of climate. An attempt is made here, however, the results are preliminary and must be treated with caution.

Although a lack of information on Middle Triassic climate records hinders the identification of climatic bias, it appears that, generally, the distributions of Perovkan and Berdyankian index taxa, as outlined in Lucas (1998*a*), are unaffected by this factor. These index taxa would have had the potential to act as reliable LVF index markers if they were temporally restricted (though as discussed previously, this criterion is not met in some instances). Analysis of Otischalkian taxa reveals that the aetosaur *Longosuchus* is only found in association with coals (although too few occurrences are known to document a significant association), whilst *Doswellia* does not exhibit environmental bias. *Longosuchus* has the potential to act as a regional index taxon for North American Otischalkian time if further occurrences appear outside of humid, coal-containing environments.

Using lithological climate indicators as a guide, the Otischalkian *Paleorhinus* and Adamanian *Rutiodon* only co-occur in warm temperate or tropical environments. Both taxa are found in supposedly arid northerly North American climes, but our results suggest that they do not co-occur in these environments. *Paleorhinus* is found without *Rutiodon* in the Popo Agie

Formation of the western USA, whilst only *Rutiodon* occurs in deposits recording similar environments in the Gettysburg and Newark basins of the eastern USA (Fig. 7). It could be argued that in warmer, wetter climes, an increase in resource availability enabled both taxa to co-exist. Resource depletion in arid conditions may have resulted in *Paleorhinus* succeeding in the western USA, whereas *Rutiodon* succeeded in the east.

Plotting localities that have yielded the Adamanian index fossils *Rutiodon*, *Stagonolepis* and *Hyperodapedon* onto a map of Late Triassic lithological climate indicators reveals no climatic biases (Fig. 8). Both *Rutiodon* and *Stagonolepis* are found in association with coal deposits across southern North America, calcretes and evaporites in the northern basins of the Newark Supergroup, and in arid European deposits (Fig. 8). Distributions of Revueltian and Apachean faunal index taxa are not influenced by climatic bias, except for *Aetosaurus*, which tends to prefer arid environments, although this correlation is not definitive.

Identifying climatic biases that might have acted on megafloral distribution is also problematic, as many records occur in areas yielding both calcretes and coals (see Fig. 8 for the close association between humid and arid indicators). Most Newark Supergroup deposits display orbitally controlled, climatically induced cyclical variations in lithofacies that are related to water depth. Deep-water fine-grained black shales reflect warmer, more humid conditions during periods of lake transgression, while red to buff-coloured deposits grading into mudflats containing roots and reptile footprints reflect increasingly arid and upland conditions during periods of regression (Olsen *et al.* 1996; Kent & Olsen, 1999). Western North American deposits yielding many megafloral fossils, such as the Petrified Forest
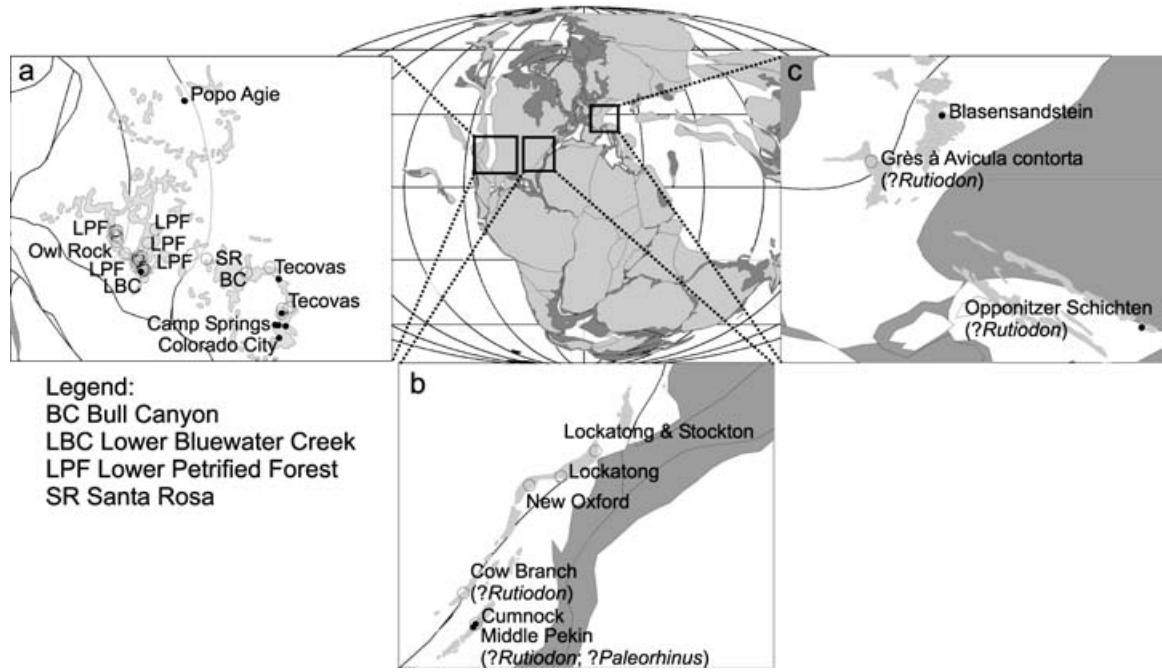
Figure 7. Distribution of *Paleorhinus* and *Rutiodon*-grade phytosaurs (including *Leptosuchus* and *Smilosuchus*; after Lucas, 1998*a*) in the Carnian (Otischalkian and Adamanian LVFs). Central map is a 220 Ma plate reconstruction. Open circle – *Rutiodon*; black circle – *Paleorhinus*; question mark indicates possible record of taxon; enclosed light grey areas indicate current areal extent of Upper Triassic strata *in situ* 220 Ma; dark grey regions indicate ocean. (a) Chinle Group deposits in western North America. (b) Newark Supergroup deposits, with large basins named, eastern North America. (c) Germanic basin, Europe. In all cases, large black text indicates formation in which taxon point occurrence is recorded. *Paleorhinus* and *Rutiodon* co-exist at two or possibly three localities: the Tecovas Formation (alongside *Metoposaurus*); the Bluewater Creek Formation at the *Placerias*/Downs quarries; and possibly the Middle Pekin Formation.
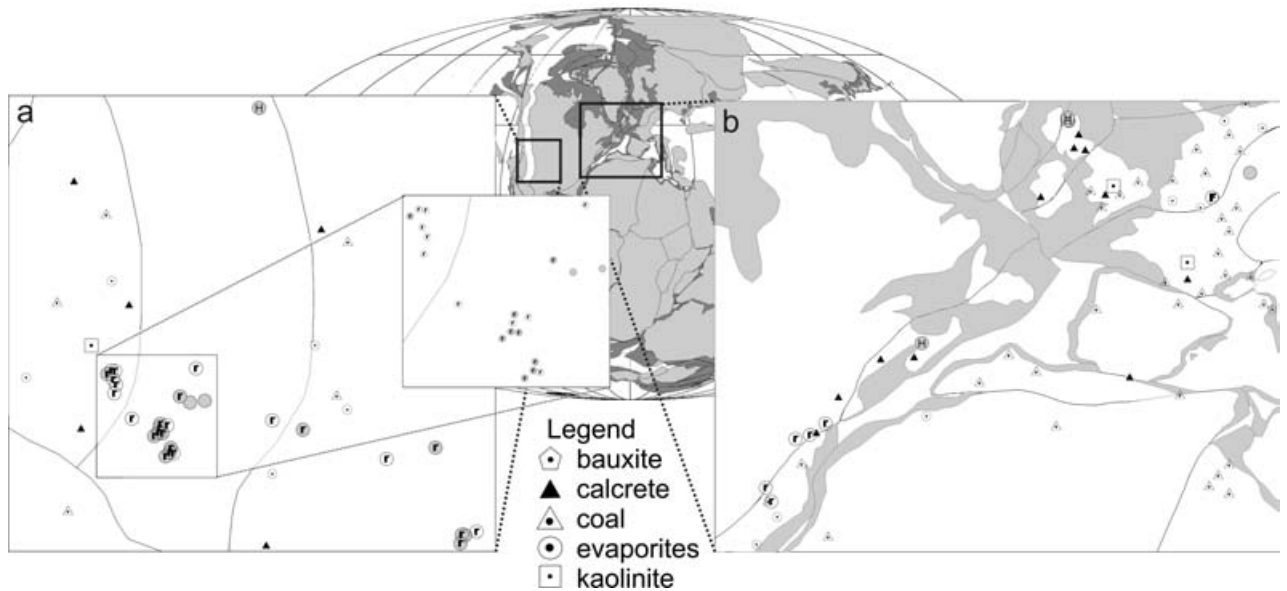


Figure 8. Investigating climatic bias in Adamanian index taxa *Rutiodon* and *Rutiodon*-grade phytosaurs (including *Leptosuchus* and *Smilosuchus*; after Lucas, 1998*a*) (small 'r' surrounded with open circle); *Stagonolepis* (empty grey circle); *Hyperodapedon* (letter 'H' in empty circle); co-occurrence of *Rutiodon* and *Stagonolepis* indicated by small 'r' in grey circle; *Stagonolepis* and *Hyperodapedon* by 'H' in grey circle. Central map and insets represent 220 Ma plate reconstructions. See key for lithological indicators: in some regions arid indicators (e.g. evaporites) occur in close proximity to humid indicators (e.g. coals). See text for possible explanation. (a) Close-up of western North America (with inset for clarity). (b) Close-up of eastern North America and western Europe.

Formation, have been identified as mainly humid (Ash, 1972; Parrish, 1989; but see Gottesfeld, 1972 for an alternative interpretation). Megafloral distribution has been linked to depositional environment, which in turn may be indicative of climate (Cornet, 1993; Weems & Olsen, 1997). Our results indicate that five of the nine potentially biochronologically useful megafloral taxa exhibit bias towards humid environments, although data are limited. These taxa comprise cycads, lycopods and ferns (although not all ferns are restricted to humid settings). The conifer *Pagiophyllum simpsoni* is restricted to shallow lacustrine and floodplain environments. These observations support the suggestion that climatic bias has some influence on floral assemblage type, as would be expected, particularly in the cyclical Newark deposits, although the remaining five megafloral taxa appear unaffected by climatic bias. The lycopod *Chinlea* is found only in Adamanian-age strata and may act as a useful indicator of late Carnian time, although only four point occurrences are recorded (Daugherty, 1941; Ash, 1972, 1980). The cynepteridacean fern *Cynepteris*, the bennettitalean *Ctenophyllum*, the cycadophyte *Eoginkgoites* and the osmundacean fern *Lonchopteris virginiensis* are all found in both Otischalkian- and Adamanian-age strata, and may be useful indicators of Carnian time (Fig. 4), although Chaney, Mamay & DiMichelle (1998) recorded cf. *Ctenophyllum* from the Early Permian of Texas. *Pagiophyllum simpsoni*, *Zamites powelli* and *Dinophyton spinosus* range through Otischalkian, Adamanian and Revueltian deposits (Fig. 4), and therefore have little stage-level correlative power.

## 4. Conclusions

This study has investigated the stability and utility of global Land Vertebrate Faunachrons as tools for biostratigraphical correlation between discrete stratigraphical units over broad intra- and intercontinental areas. By using GIS we have been able to combine and simultaneously analyse information from a combination of point data (e.g. faunal occurrences) and spatial maps (e.g. climatic banding and lithological indicators) in ways not possible using more conventional database analysis techniques. The results of this investigation cast doubt upon the utility of some of the index fossils that have been proposed to characterize distinct LVFs. Consequently, the utility and coherence of the majority of the proposed Middle and Late Triassic LVFs is questioned, particularly in terms of their correlative power on a global scale.

This analysis indicates that the Perovkan, Berdyankian, Otischalkian, Adamanian and Apachean LVFs cannot act as global biochronological units. The Norian-age Revueltian LVF appears to be a useful global biochron, based solely upon the index taxon *Aetosaurus* (as, notwithstanding taxonomic problems

associated with the generic level identification of *Typothorax* and '*Pseudopalatus*-grade' phytosaurs, these index taxa are endemic to the western United States). *Aetosaurus* is temporally restricted and, although it displays a slight preference for arid environments, does not exhibit strong environmental bias in its distribution. Its utility would be considerably decreased, however, if controversial referrals of American taxa to *Aetosaurus* were excluded from the biostratigraphical scheme.

The referral of fragmentary, isolated and/or poorly preserved specimens lacking the diagnostic character states that would allow them to be assigned with confidence to a particular index taxon is problematic for LVF definition. The use of '*Shansisuchus*-like' and '*Dinodontosaurus*-like' specimens to provide taxonomic and temporal linkage between global faunas is a major problem in defining the Middle Triassic Perovkan and Berdyankian LVFs, and the integrity of these biochrons is hampered by a lack of index taxa that are widely distributed geographically, but restricted temporally. An east–west division in faunal composition observed during the Perovkan results in type Russian deposits that cannot be linked directly to western European and North American assemblages. *Eocyclotosaurus* is restricted to the Anisian, but can only act as a regional, western Northern Hemisphere marker of Anisian/Perovkan time. The Berdyankian cannot be extended to North American faunas, as the temporal range of *Mastodonsaurus* extends into Anisian-aged Perovkan strata, and on a global level, North American Ladinian-aged deposits are unknown. Furthermore, links between Russian and South American faunas are based on loose second-order linkages (see examples above) or specimens of uncertain taxonomic status, such as '*Elephantosaurus*'. In a step towards resolving this problem, we have been able to identify three taxa that appear to characterize Anisian to Ladinian time in the western Northern Hemisphere.

Accurate identification of taxa is a prerequisite of any biostratigraphical scheme. Proposed index taxa should be defined on the basis of unambiguous diagnostic features and identifications of specimens should rely on these criteria, rather than on general phenotypic resemblance. Associating index taxa on the basis of 'grade-level' similarities is problematic in this regard. Such 'grades' are often loosely defined and based on the presence of a suite of widely distributed (plesiomorphic) character states that may be present in a nexus of closely related taxa. As a result, it may not be possible to identify the particular index taxon of interest definitively, but may erroneously lead to the use of a distinct, but phenotypically similar (or closely related) taxon, which itself may have limited biostratigraphical utility. This lack of precision in the identification of specimens not only directly undermines the use of such 'grade-level' taxa in biostratigraphical correlations,

but also has other deleterious effects. For example, such identifications invoke problems with taxon ghost-lineages, such that closely related taxa, which may be phenotypically similar (differing from each other in only a small number of character states), may not exist in the same temporal zone. Furthermore, phylogenetic history may indicate that index taxa have a broader temporal range than suggested by the current fossil record, as may be the case for *Aetosaurus*. As a result, we strongly advocate the abandonment of 'grade-level' associations when attempting biostratigraphical correlation.

Although the Otischalkian and Adamanian LVFs both possess globally distributed index taxa, these taxa are not temporally restricted. In fact, Otischalkian and Adamanian taxa tend to be found alongside each other in the same assemblages, thereby merging the boundaries between these Carnian-age LVFs. Megafloral distributions also support a continuous Otischalkian–Adamanian biochron at a global level. There is a case for a North American regional Otischalkian biochron based upon *Longosuchus* and *Doswellia*, but *Longosuchus* may be biased towards occurrences in humid localities (although more data are needed to support this suggestion). *Chinlea* may indicate a possible Adamanian megafloral biochron, but again data are currently limited.

As currently defined, the Apachean is useful as a regional, but not global, biochronological unit. Of the three Apachean index taxa, the prosauropod *Riojasaurus* is present only in Argentina. *Redondasaurus* and *Redondasuchus* are restricted to western North America and have the potential to define a regional Rhaetian/Apachean biochron if the generic separation of these taxa from *Pseudopalatus* and *Typothorax*, respectively, withstands future scrutiny.

Generally, the proposed members of the index faunas exhibit little facies bias, an observation that would increase their potential for use as index taxa. Analysis of climatic bias is hampered by a general lack of temporally resolved data, and by widespread endemism, temporal longevity and the suggestion of small-scale environmental control in megafloral assemblages (particularly in the lacustrine sequences of the Newark Supergroup). Provisional results support merging the tentatively established *Dinophyton* and *Eoginkgoites* zones in North America.

Although this analysis has revealed many problems in the use of tetrapods in biochronology, in many cases these fossils represent a potentially useful source of biochronological data in terrestrial deposits that lack other conventional index taxa (e.g. ammonites, conodonts). Further testing of the proposed biochronology appears to be needed, particularly with reference to independent dating methods, for example, the increased application of magnetostratigraphical dating techniques across the Chinle Group and in additional Newark Supergroup basins. In addition, further fossil

collecting and continuing taxonomic resolution will provide a more stable framework on which to build a tetrapod-based biochronology.

This analysis has focused on faunal and floral records for the western Northern Hemisphere, thereby excluding Early Triassic LVFs that are based mainly on African and Chinese faunas. Consequently, we do not comment on the validity of these biochrons herein, though their validity also requires testing and may provide fertile ground for future work. For example, although not useful global biochronological units, it is possible that some proposed Middle Triassic LVFs may be useful regional biochrons for the Eastern Hemisphere, particularly for Russian and Chinese faunas. Also, extending this analysis to proposed Early Jurassic LVFs (Lucas, 1996*a,b*, 1998*a*; Marzolf & Lucas, 1996) would allow more rigorously based investigations into patterns of extinction and survival across the Triassic–Jurassic boundary.

GIS has proved to be a useful tool in facilitating the identification of spatial and temporal relationships between Triassic fauna and flora. We have been able to identify that, as currently defined, some LVF units have the potential to act as regional biochronological indicators, with the proviso that definitions are adjusted to account for more restricted taxon ranges (in both space and time) and a reduced number of informative index taxa. This demonstrates that GIS has the potential to become a powerful tool in the testing of palaeoecological and macroevolutionary patterns.

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