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Notes

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Abstract: The Triassic timescale based on nonmarine tetrapod biostratigraphy and biochronology divides Triassic time into eight land-vertebrate faunachrons (LVFs) with boundaries defined by the first appearance datums (FADs) of tetrapod genera or, in two cases, the FADs of a tetrapod species. Definition and characterization of these LVFs is updated here as follows: the beginning of the Lootsbergian LVF = FAD of *Lystrosaurus*; the beginning of the Nonesian = FAD *Cynognathus*; the beginning of the Perovkan LVF = FAD *Eocyclotosaurus*; the beginning of the Berdyankian LVF = FAD *Mastodonsaurus giganteus*; the beginning of the Otischalkian LVF = FAD *Parasuchus*; the beginning of the Adamanian LVF = FAD *Rutiodon*; the beginning of the Revueltian LVF = FAD *Typothorax coccinarum*; and the beginning of the Apachean LVF = FAD *Redondasaurus*. The end of the Apachean (= beginning of the Wasonian LVF, near the beginning of the Jurassic) is the FAD of the crocodylomorph *Protosuchus*. The Early Triassic tetrapod LVFs, Lootsbergian and Nonesian, have characteristic tetrapod assemblages in the Karoo basin of South Africa, the *Lystrosaurus* assemblage zone and the lower two-thirds of the *Cynognathus* assemblage zone, respectively. The Middle Triassic LVFs, Perovkan and Berdyankian, have characteristic assemblages from the Russian Ural foreland basin, the tetrapod assemblages of the Donguz and the Bukobay svitas, respectively. The Late Triassic LVFs, Otischalkian, Adamanian, Revueltian and Apachean, have characteristic assemblages in the Chinle basin of the western USA, the tetrapod assemblages of the Colorado City Formation of Texas, Blue Mesa Member of the Petrified Forest Formation in Arizona, and Bull Canyon and Redonda formations in New Mexico. Since the Triassic LVFs were introduced, several subdivisions have been proposed: Lootsbergian can be divided into three sub-LVFs, Nonesian into two, Adamanian into two and Revueltian into three. However, successful inter-regional correlation of most of these sub-LVFs remains to be demonstrated. Occasional records of nonmarine Triassic tetrapods in marine strata, palynostratigraphy, conchostracan biostratigraphy, magnetostratigraphy and radioisotopic ages provide some basis for correlation of the LVFs to the standard global chronostratigraphic scale. These data indicate that Lootsbergian = uppermost Changshingian, Induan and possibly earliest Olenekian; Nonesian = much of the Olenekian; Perovkan = most of the Anisian; Berdyankian = latest Anisian? and Ladinian; Otischalkian = early to late Carnian; Adamanian = most of the late Carnian; Revueltian = early–middle Norian; and Apachean = late Norian–Rhaetian. The Triassic timescale based on tetrapod biostratigraphy and biochronology remains a robust tool for the correlation of nonmarine Triassic tetrapod assemblages independent of the marine timescale.

Triassic tetrapod (amphibian and reptile) fossils have long been used in biostratigraphy, a tradition extending back to at least the 1870s. Lucas (1990) advocated developing a global Triassic timescale based on tetrapod evolution, and subsequently Lucas (1998*a*) presented a comprehensive global Triassic tetrapod biochronology (Fig. 1). This biochronological timescale divides the Triassic into eight time intervals (land-vertebrate faunachrons, LVFs) based on successive changes in faunal composition driven by tetrapod evolution. This model has been tested and refined for more than a decade. Here, I present the current status of the Triassic tetrapod-based timescale, incorporating new data, analyses and modifications published since 1998.

In this paper: FAD = first appearance datum; HO = highest occurrence; LO = lowest occurrence; LMA = land–mammal 'age'; LVA = land-vertebrate 'age'; LVF = land–vertebrate faunachron; and SGCS = standard global chronostratigraphic scale (the marine timescale).

Previous studies

Although tetrapods have been used to correlate nonmarine Triassic strata since the 1800s, before the 1990s few attempts were made to establish a global tetrapod biostratigraphy or biochronology of the Triassic (Fig. 2). In the late 1800s, some workers did use tetrapod fossils to correlate

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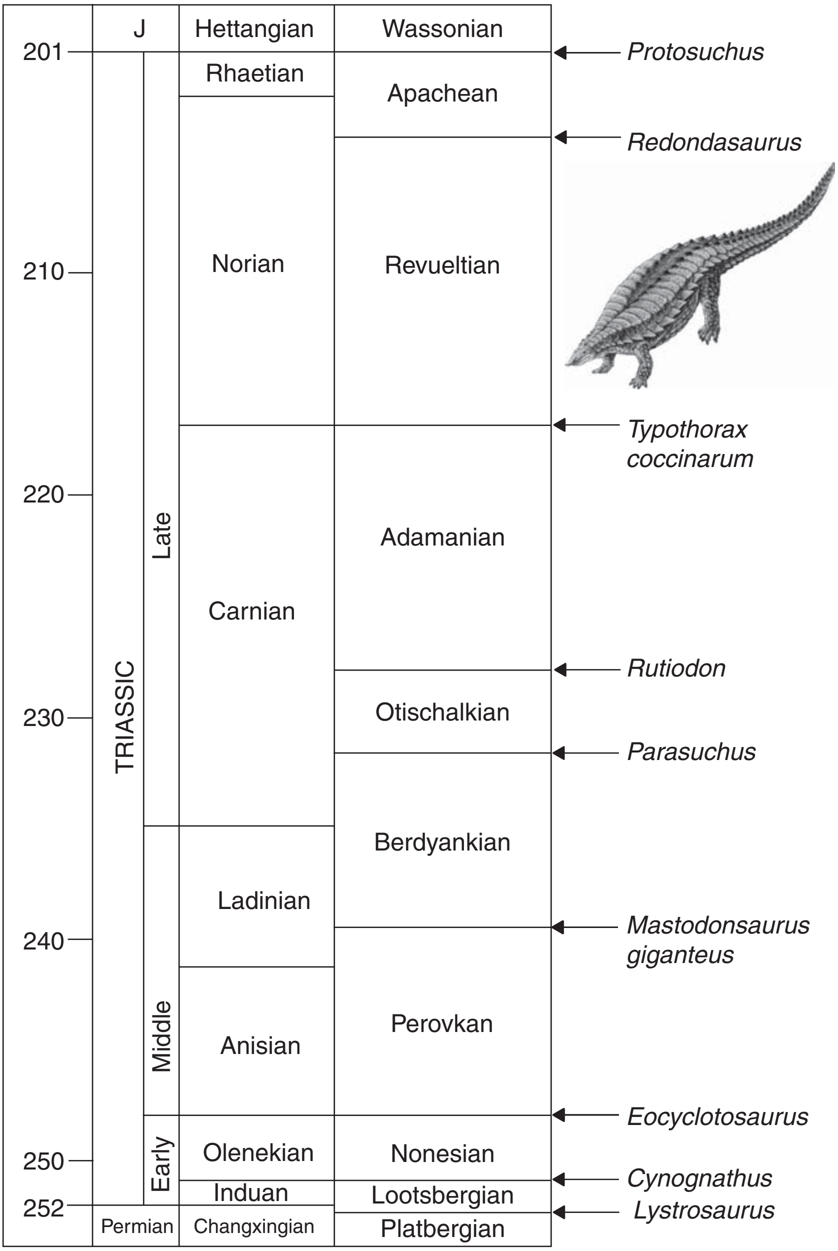
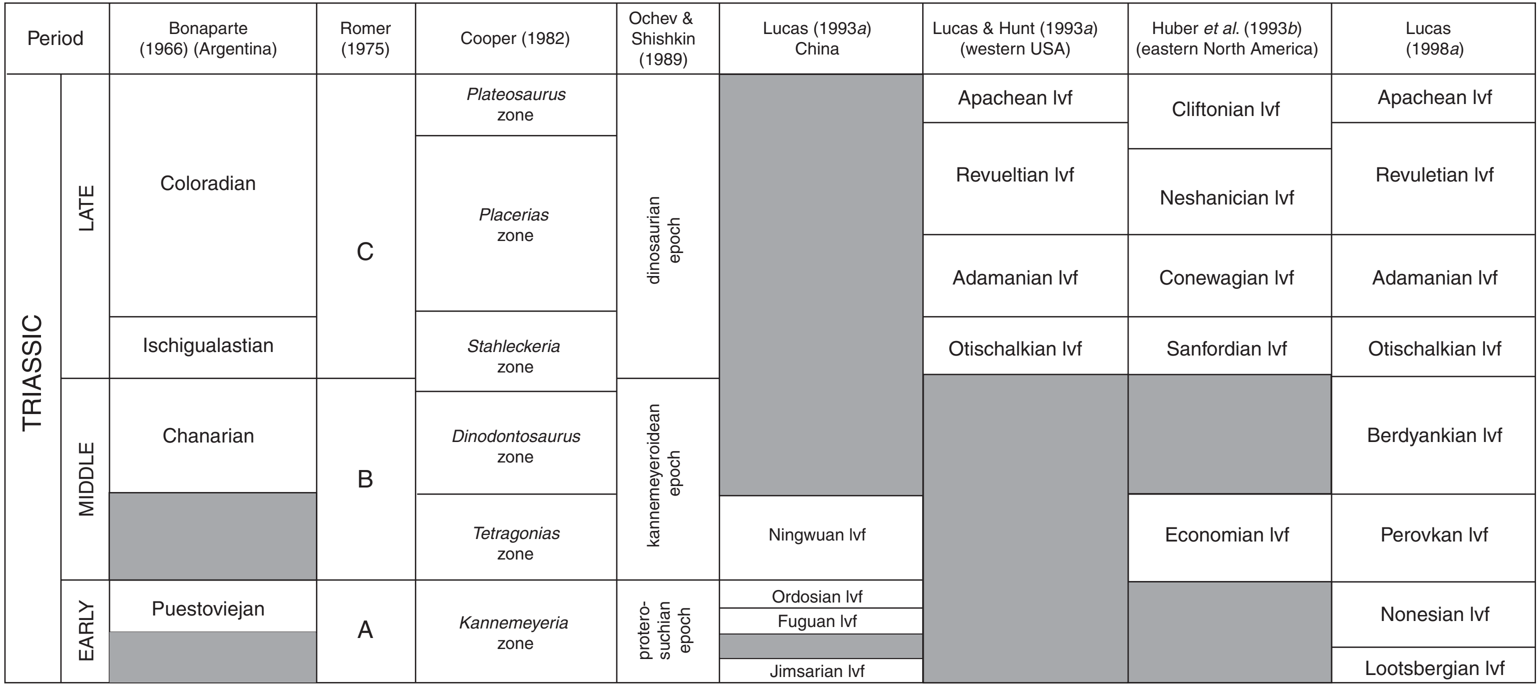


Fig. 1. The Triassic timescale based on tetrapod biostratigraphy and biochronology. Restoration of *Typothorax* by Matt Celeskey.

nonmarine Triassic strata on a broad scale, for example, Cope (1875) who correlated part of the German Keuper to the Upper Triassic strata of the American Southwest based on shared taxa of fossil reptiles such as the phytosaur '*Belodon*'.

Broom (1906, 1907, 1909) introduced the earliest, and perhaps the most influential, Triassic tetrapod biostratigraphy, for the Lower Triassic of the Karoo basin in South Africa. He identified three successive biostratigraphic intervals, the *Lystrosaurus*, *Procolophon* and *Cynognathus* 'beds'. Watson (1914*a*, *b*) later termed these 'zones' and, since Kitching (1970), the *Lystrosaurus* and *Procolophon* zones have been combined into a



Period		Bonaparte (1966) (Argentina)	Romer (1975)	Cooper (1982)	Ochev & Shishkin (1989)	Lucas (1993*a*) China	Lucas & Hunt (1993*a*) (western USA)	Huber *et al.* (1993*b*) (eastern North America)	Lucas (1998*a*)
TRIASSIC	LATE	Coloradian Ischigualastian	C	*Plateosaurus* zone *Placerias* zone *Stahleckeria* zone	dinosaurian epoch		Apachean lvf Revueltian lvf Adamanian lvf Otischalkian lvf	Cliftonian lvf Neshanician lvf Conewagian lvf Sanfordian lvf	Apachean lvf Revuletian lvf Adamanian lvf Otischalkian lvf
	MIDDLE	Chanarian	B	*Dinodontosaurus* zone *Tetragonias* zone	kannemeyeroidean epoch	Ningwuan lvf		Economian lvf	Berdyankian lvf Perovkan lvf
	EARLY	Puestoviejan	A	*Kannemeyeria* zone	protero-suchian epoch	Ordosian lvf Fuguan lvf Jimsarian lvf			Nonesian lvf Lootsbergian lvf

Fig. 2. Previous tetrapod-based subdivisions of Triassic time.

single, *Lystrosaurus* zone (e.g. Rubidge *et al.* 1995; Botha & Smith 2007). Recognition elsewhere of the *Lystrosaurus* and/or *Cynognathus* 'beds' or 'zones' has long been possible in Antarctica, South America, India, China and/or Russia because some Early Triassic tetrapod taxa are virtually cosmopolitan, especially the genera *Lystrosaurus* and *Cynognathus* (Lucas 1998*a*).

Romer (1975; also see Cox 1973) presented the first global Triassic tetrapod biochronology, by identifying three successive Triassic land–vertebrate 'faunas': A, Early Triassic; B, Middle Triassic; and C, Late Triassic (Fig. 2). Cosgriff (1984) divided Romer's division A into A1 (= *Lystrosaurus* biochron) and A2 (= *Cynognathus* biochron). Ochev & Shishkin (1989; also see Anderson & Cruickshank 1978) recognized the same intervals as Romer, but chose to name them the: A, proterosuchian epoch; B, kannemeyerioidean epoch; C, and dinosaurian epoch.

Cooper (1982) proposed a more detailed global tetrapod biostratigraphy of the Triassic than did Romer and other workers of the 1970s and 1980s (Fig. 2). In this, he recognized a succession of six Triassic zones based largely on a perceived stratigraphic succession of dicynodonts (Lucas & Wild 1995 later presented a revized Triassic dicynodont biozonation). Subsequent workers have not adopted Cooper's zonation. Indeed, prior to Lucas (1998*a*), the concept of a global Triassic tetrapod biostratigraphy and biochronology had not progressed beyond Romer (1975).

Tetrapod-based subdivisions of Triassic time have been proposed as local, provincial biochronologies for Argentina, North America and China. Bonaparte (1966, 1967, 1982) introduced a set of 'provincial ages' for the Triassic of Argentina, but he never defined these terms (Fig. 2). However, since then Lucas & Harris (1996) have defined the Chanarian as a LVF, and Langer (2005*b*) has defined the Ischigualastian as a LVF. Lucas (1993*a*) proposed a succession of LVFs for the Chinese Early–Middle Triassic tetrapod record. At about the same time, Lucas & Hunt (1993*a*) proposed Late Triassic LVFs based on the Chinle Group tetrapod record from the western United States, and Huber *et al.* (1993*b*) proposed Middle–Late Triassic LVFs based on the Newark Supergroup record of eastern North America (Fig. 2). Lucas *et al.* (1997*a*) since then have presented revized definitions of some of the Late Triassic LVFs proposed by Lucas & Hunt (1993*a*).

Lucas & Huber (2003) reviewed global Late Triassic tetrapod biochronology and demonstrated the broad applicability of the LVFs proposed by Lucas and Hunt (1993*a*; also see Lucas 1997*a*). Lucas *et al.* (2007*e*) reviewed the status of the Triassic timescale based on patterns of tetrapod evolution and made some necessary modifications that are incorporated and elaborated upon here.

Vertebrate biostratigraphy and biochronology

The term LMA has long referred to intervals of geological (mostly Cenozoic) time characterized by distinctive mammalian fossil assemblages. LMAs have been defined to encompass Cenozoic time intervals on most of the world's continents (Savage & Russell 1983), and for the Late Cretaceous of western North America (Cifelli *et al.* 2004). However, more broadly-based LVA or LVF have been introduced for parts of the Mesozoic record of Asia, South America and North America (Lucas 1997*b*, 2008). Thus, LVAs or LVFs have been proposed for the Triassic and Jurassic of China (Lucas 1993*a*, 1996); the Triassic of Argentina (Bonaparte 1966); the Late Triassic of western North America (Lucas & Hunt 1993*a*); the Middle Triassic–Early Jurassic of eastern North America (Huber *et al.* 1993*a*; Lucas & Huber 2003; Lucas & Tanner 2007*a*, *b*); the Late Jurassic–Early Cretaceous of western North America (Lucas 1993*e*); the Late Cretaceous of western North America (Russell 1964, 1975; Sullivan & Lucas 2003, 2006); the Late Jurassic-Cretaceous of Mongolia and China (Jerzykiewicz & Russell 1991; Lucas & Estep 1998; Lucas 2006*a*); and the Cretaceous of Argentina (Leanza *et al.* 2004). Russell (1993) proposed marine vertebrate ages for the Cretaceous of western North America.

Mammals are not the only tetrapods that can be used to recognize intervals of geologic time. In the Mesozoic, especially prior to the Late Cretaceous, when mammal fossils are very rare, non-mammalian tetrapods can be biochronologically useful. For this reason, some workers use the term LVA. Because LMAs and LVAs are not formal ages in stratigraphy, Lucas (1993*a*) introduced the term faunachron (essentially the same concept as Dunbar & Rodgers' [1957] 'faunichron') to refer to the time interval that is equivalent to the duration of a 'fauna'. I, thus, use the more precise term LVF instead of LMA or LVA.

LVFs are biochronological units, and I define their beginnings by biochronological events. Each LVF begins with the FAD of a tetrapod index taxon, usually a genus, though species are used if they provide greater biostratigraphic resolution. In so doing, the end of an LVF is defined by the beginning of the succeeding LVF, which is the FAD of another tetrapod index taxon. This is a precise way to define LVF boundaries. LVFs thus are interval biochrons.

A distinctive assemblage of vertebrate fossils characterizes each LVF. The name of the LVF is a geographical name taken from the place where (or very close to where) the characteristic example of the vertebrate fossil assemblage was collected. Many LMA and LVA names have been taken from the rock formation in which the fossils are found, and the rock formation name is based on a place name. However, using the rock formation name may cause confusion because it can imply that the LMA or LVA refers to the entire duration of deposition of the formation and not just to the duration of interval in which the vertebrate fossil assemblage is found, which is often much shorter. It is less confusing to choose another place name for the LMA or LVA. For example, the Late Triassic Ischigualastian LVA of Argentina (Bonaparte 1966) was named for the Ischigualasto Formation, but the Ischigualastian LVF vertebrates do not occur throughout the Ischigualasto Formation, which is potentially confusing. In contrast, the Late Triassic Adamanian LVF of western North America (Lucas & Hunt 1993*a*) is named after Adamana, where the fossils occur, not after the Blue Mesa Member of the Petrified Forest Formation, which contains the characteristic fossil assemblage. This prevents confusion between the concept of a formation and the concept of a LVF.

The characteristic tetrapod assemblage is the primary basis for characterization of the LVF. Index fossils identified here meet the criteria of true index fossils (temporally restricted, common, widespread, easily identified) and do not include endemic or rare taxa that happen to be restricted to a LVF, usually as single records. Principal correlatives of the characteristic tetrapod assemblage of each LVF are listed in this article. These are tetrapod assemblages that are reasonably well studied, diverse and unambiguously correlated. Although I make a strong effort here to correlate the LVFs to the SGCS, the tetrapod biochronology of the Triassic is a timescale independent of the SGCS. It is also important to keep in mind that, although global LVF's could not be defined today due to the wide separation of most of the continents, in the Triassic Pangaean world it was possible for at least some of the land vertebrates to spread across most of the world's land area. Some degree of endemism is apparent, but it was not so great as to prevent definition of global or near-global faunachrons.

Triassic land–vertebrate faunachrons

Introduction

The Triassic tetrapod timescale is based on tetrapod assemblages from the Karoo basin in South Africa (Early Triassic: Lootsbergian–Nonesian), the Ural foreland basin in Russia (Middle Triassic: Perovkan–Berdyankian) and the Chinle basin of the western USA (Upper Triassic: Otsichalkian–Apachean) (Fig. 3). The Karoo basin contains the tetrapod assemblages characteristic of the Lootsbergian and Nonesian LVFs. These assemblages are stratigraphically superposed and are thus demonstrably time successive; they are the classic *Lystrosaurus* assemblage zone and most of the *Cynognathus*

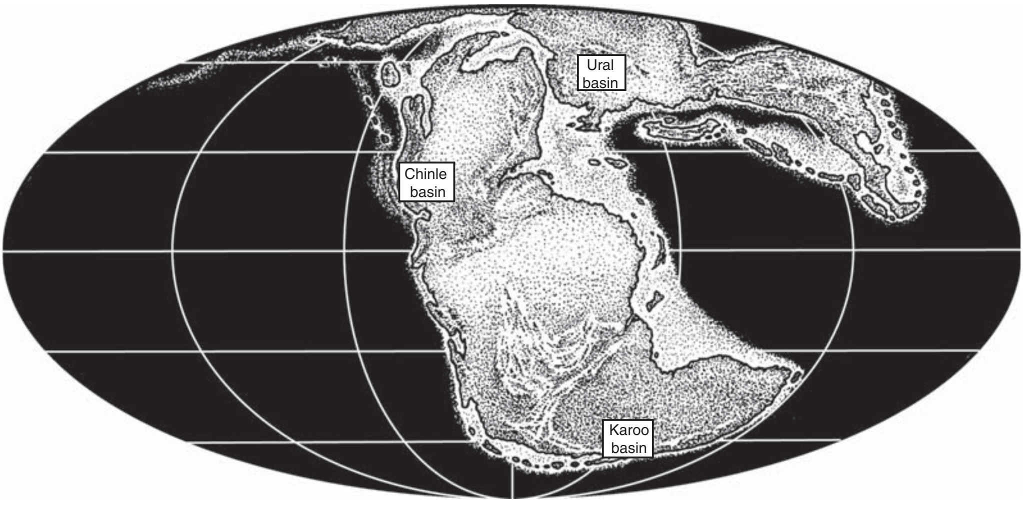


Fig. 3. Map of Triassic Pangaea showing the three areas that provide the fossils and strata that form the standards for the Triassic tetrapod timescale: Karoo basin, South Africa (Lootsbergian and Nonesian), Russian Urals basin (Perovkan and Berdyankian) and Chinle basin (Otischalkian, Adamanian, Revueltian and Apachean). Base map drawn by Matt Celeskey.

assemblage zone (e.g. Rubidge *et al.* 1995; Groenewald & Kitching 1995; Kitching 1995; Hancox & Rubidge 1997; Hancox 2000; Smith & Botha 2005; and Botha & Smith 2007 provide an overview). These assemblages include amphibians, parareptiles, dicynodonts and cynodonts particularly useful for broad correlation.

The South African Triassic tetrapod record contains a long hiatus between the uppermost strata of the Lower Triassic *Cynognathus* assemblage zone and southern African rocks that contain tetrapods of certain Late Triassic age (notably the lower Elliot Formation: Lucas & Hancox 2001). This forces the tetrapod biochronological standards for Middle Triassic time to be moved elsewhere. For this part of the standards, Lucas (1998*a*) used two superposed tetrapod assemblages from the Russian Ural foreland basin (e.g. Shishkin *et al.* 1995*b*, 2000*a*, *b*; Ivakhnenko *et al.* 1997; Novikov *et al.* 2000; Battail & Surkov 2000; Gower & Sennikov 2000; Spencer & Benton 2000; Ivakhnenko 2008*a*, *b*, *c*; Sennikov 2008; Tatarinov 2008) as the basis for the Middle Triassic Perovkan and Berdyankian LVFs. The presence of some temporal overlap between the top of the South African section (upper *Cynognathus* Zone) and the Urals foreland basin section makes correlation between these sections considerably easier. The Russian assemblages yield amphibians, archosaurs and dicynodonts of value for broad correlation. No Upper Triassic tetrapod assemblages are known from the Russian Ural foreland basin (e.g. Shishkin *et al.* 2000*b*), so the tetrapod biochronology standard for Late Triassic time again must be moved elsewhere.

The Chinle Group strata of the American Southwest provide the best studied and most complete record for defining the Late Triassic LVFs: Otischalkian, Adamanian, Revueltian and Apachean. Of great importance, tetrapod assemblages from Texas (Otischalkian characteristic assemblage), Arizona (Adamanian characteristic assemblage) and New Mexico (Revueltian and Apachean characteristic assemblages) are stratigraphically superposed and thus are time successive (e.g. Lucas 1993*c*, 1997*a*; Lucas *et al.* 2001; Heckert & Lucas 2002*a*, *b*, 2003; Heckert 2004; Heckert *et al.* 2005*a*, *b*; Parker *et al.* 2006). The Chinle assemblages yield phytosaurs, aetosaurs and metoposaurs useful for broad correlation, and a burgeoning microvertebrate biostratigraphy also supports ths macrovertebrate-based correlation (Heckert 2004; Heckert & Lucas 2006).

Lootsbergian LVF

Definition. Lucas (1998*a*) introduced the term Lootsbergian LVF for the time between the FAD of the dicynodont *Lystrosaurus* and the FAD of the cynodont *Cynognathus* (Fig. 1). Its characteristic tetrapod assemblage is the *Lystrosaurus* Assemblage Zone found in the Balfour (Palingkloof Member), Katberg and Burgersdorp (lower part) formations of the Karoo basin of South Africa (e.g. Groenewald & Kitching 1995; Damiani *et al.* 2003; Smith & Botha 2005; Botha & Smith 2006, 2007). This assemblage zone has a type locality designated by Groenewald & Kitching (1995) around Lootsberg Pass. Lootsbergian time begins with the FAD of *Lystrosaurus*, which is the end of the Late Permian Platbergian LVF of Lucas (2005, 2006*b*). The end of the Lootsbergian is equivalent to the beginning of the Nonesian LVF, which is defined by the FAD of *Cynognathus*.

Broom (1906) introduced two successive zones – *Lystrosaurus* and *Procolophon* – that Kitching (1970, 1977) later combined into a single, *Lystrosaurus* Zone. Keyser (1979) referred to this same zone as the *Lystrosaurus-Thrinaxodon* Assemblage Zone. The original name *Lystrosaurus* Zone (or Assemblage Zone) continues to be used (e.g. Groenewald & Kitching 1995; Lucas 1998*a*; Damiani *et al.* 2001; Botha & Smith 2006, 2007; Smith & Botha 2005).

Characteristic tetrapod fossil assemblage. The characteristic tetrapod fossil assemblage of the Lootsbergian LVF is the *Lystrosaurus* Assemblage Zone of the Karoo basin, South Africa. It consists of amphibians, parareptiles, prolacertiforms, archosaurs, dicynodonts, therocephalians and cynodonts.

Kitching (1977) reviewed the *Lystrosaurus* Assemblage Zone localities, Groenewald & Kitching (1995) provided a synopsis of the stratigraphic ranges of the genera, and Botha & Smith (2006, fig. 7) have presented the most recent data. The *Lystrosaurus* Assemblage Zone has long provided a standard for correlation of the oldest Triassic tetrapod assemblages, so it logically serves as the basis for the oldest Triassic LVF (though it encompasses the Permo-Triassic boundary and includes some uppermost Permian strata, see below).

Index fossils. The following tetrapod genera are restricted to Lootsbergian time and are widespread and/or common enough to be useful as index fossils (Fig. 4): the amphibians *Wetlugasaurus*, *Tupilakosaurus*, *Luzocephalus*, and *Lydekkerina*; the parareptile *Procolophon*; the prolacertiform *Prolacerta;* the archosaur *Proterosuchus* (= *Chasmatosaurus*); the dicynodont *Lystrosaurus*; and the cynodonts *Scaloposaurus* and *Thrinaxodon*.

Principal correlatives. Recognition of and correlation within the Lootsbergian is one of the most stable parts of the Triassic tetrapod timescale. Thus, the terms *Lystrosaurus* zone, beds or fauna

taxa	Lootsbergian	Nonesian	Perovkan	Berdyankian
amphibians:				
Eocyclotosaurus			●	
Eryosuchus			●	
Luzocephalus	●			
Lydekkerina	●			
Mastodonsaurus			●	●
Odenwaldia		●		
Paracyclotosaurus			●	
Parotosuchus		●		
Trematosaurus		●		
Trematosuchus		●		
Tupilakosaurus	●			
Wetlugasaurus	●			
parareptile:				
Procolophon	●			
prolacertiform:				
Prolacerta	●			
archosaurs:				
Arizonasaurus			●	
Erythrosuchus		●	●	
dicynodonts:				
Kannemeyeria		●	●	
Lystrosaurus	●			
Parakannemeyeria			●	
Shansiodon			●	
Sinokannemeyeria			●	
Stahleckeria				●
cynodonts:				
Cynognathus		●	●	
Diademodon		●	●	
Massetognathus				●
Scalenodon			●	
Scaloposaurus	●			
Thrinaxodon	●			
Trirachodon		●		

Fig. 4. Temporal ranges of selected genera of Early and Middle Triassic tetrapods.

have long been applied to a wide geographical range of strata/fossils of Lootsbergian age.

Most significant correlatives are the vertebrate fossil assemblages of the: Wordy Creek Formation, eastern Greenland; Vokhmian, Sludkian and Ustmylian horizons of the Vetluga Series, Russian Urals; upper Guodikeng and lower Jiucaiyuan formations, Junggur basin, China; Heshanggou Formation, Ordos basin, China; Panchet Formation, India; Sanga do Cabral Formation, Paraná basin, Brazil; Rewan Formation, SE Galilee basin, Australia; Arcadia Formation, SW Bowen basin, Australia; and lower part of Fremouw Formation, Antarctica. Note that the alleged *Lystrosaurus* record from Laos (Repelin 1923; Piveteau 1938) has been re-identified as the Late Permian dicynodont *Dicynodon* (Battail *et al.* 1995; Battail 1997).

The Wordy Creek Formation in eastern Greenland yields the amphibians *Luzocephalus*, *Wetlugasaurus* and *Tupilakosaurus* (Säve-Söderbergh 1935; Nielsen 1954) and thus is of Lootsbergian age. These strata also yield Induan ammonites, and are key to correlation of the Lootsbergian to part of the Induan (see below).

In the Russian Urals, the Lootsbergian interval is equivalent to Zone V of Efremov (1937, 1952), which has most recently been called the Vokhmian, Sludkian and Ustmylian horizons of the Vetlugan Series (Superhorizon) (Ivakhnenko *et al.* 1997; Shishkin *et al.* 2000*b*). Tetrapod taxa include anthracosaurs, the temnospondyls *Luzocephalus, Benthosuchus*, *Wetlugasaurus* and *Tupilakosaurus*, procolophonids, a prolacertiform, the proterosuchid *Chasmatosuchus* and other (mostly fragmentary) archosaurs and the dicynodont *Lystrosaurus* (Shishkin *et al.* 1995*b*; Ivakhnenko *et al.* 1997; Battail & Surkov 2000; Gower & Sennikov 2000; Novikov *et al.* 2000; Shishkin *et al.* 2000*a*, *b*; Spencer & Benton 2000).

In northwestern China, land-vertebrates of Lootsbergian age come from the upper part of the Guodikeng Formation and the lowermost Jiucaiyuan Formation (both in the Cangfanggou Group) near Jimsar NE of Urumqi in western Xinjiang (e.g. Cheng 1981; Metcalfe *et al.* 2009). These vertebrates are the '*Lystrosaurus* fauna' of northwestern China of some workers (e.g. Sun 1972), and they provided the basis for the Jimsarian LVF of Lucas (1993*a*). Taxa present are a prolacertid, a ?procolophonid, the proterosuchian *Proterosuchus* (= *Chasmatosaurus*), a regisaurid therocephalian and the dicynodont *Lystrosaurus*, of which seven species have been named, most of which are invalid (Colbert 1974; Colbert & Kitching 1977; Lucas 2001).

In the Ordos basin of north–central China, near Fugu, Shanxi, the upper part of the Heshanggou Formation yields a vertebrate fauna that was the basis of the Fuguan LVF of Lucas (1993*a*). Taxa present are indeterminate capitosauroids, procolophonids, an erythrosuchid and an ordosiid therocephalian; based primarily on the procolophonids, these are of likely Lootsbergian age.

In India, the Panchet Formation along the Damodar River northwest of Calcutta has produced a Lootsbergian vertebrate assemblage that includes a lydekkerinid, ?benthosuchid, ?capitosaurids, an indobrachyopid, trematosaurids, a procolophonid, the proterosuchian *Proterosuchus* and *Lystrosaurus* (Lydekker 1882; Sahni & Huene 1958; Tripathi 1961, 1969; Tripathi & Satsangi 1963; Hughes 1963; Ray 2005).

In southern Brazil, the Sanga do Cabral Formation in the Paraná basin yields a rhytidosteid amphibian, indeterminate temnospondyls, *Procolophon*, ?thrinaxodontids and ?*Lystrosaurus* (e.g. Barbarena *et al.* 1985; Lucas 2002; Abdala *et al.* 2002; Cisneros 2008*a*, *b*; Cisneros & Schultz 2002; Dias-da-Silva *et al.* 2005, 2006*a*, *b*; Dias-da-Silva & Marsicano 2006; Dias-da-Silva & Schultz 2008). A putative Permian tetrapod record from the Buena Vista Formation of Uruguay (Piñeiro *et al.* 2003, 2004, 2007) is more likely correlative to the Lootsbergian Sanga do Cabral assemblage (Dias-da-Silva *et al.* 2006*b*).

In eastern Australia, the Arcadia Formation (SW Bowen basin) and the Rewan Formation (SE Galilee basin) yield small assemblages of tetrapods of Lootsbergian age. The Arcadia Formation assemblage encompasses a diversity of mostly endemic amphibians, including fragmentary lydekkerinids, a primitive procolophonid, a possible *Prolacerta*, an archosaur similar to *Proterosuchus* and ?*Lystrosaurus* (e.g. Bartholomai 1979; King 1983; Thulborn 1983; Warren 1991; Damiani 2001; Warren *et al.* 2006). In the SE Galilee basin, the occurrence of *Lydekkerina* in the Rewan Formation supports a Lootsbergian age assignment (Warren *et al.* 2006).

Southwest of the Transantarctic Mountains in southern Antarctica, the lower part of the Fremouw Formation yields a vertebrate fossil assemblage of Lootsbergian age that includes temnospondyls, a rhytidosteid, the procolophonid *Procolophon*, the prolacertiform *Prolacerta*, a proterosuchid or erythrosuchid, a rauisuchian, the dicynodonts *Myosaurus* and *Lystrosaurus*, the cynodont *Thrinaxodon* and scaloposaurs (e.g. Colbert 1972, 1991; Hammer 1990; Collinson *et al.* 2006). This Lootsbergian assemblage has been referred to as the lower Fremouw fauna or lower tetrapod fauna of the Fremouw Formation (Colbert 1972, 1991).

Comments. Most Lootsbergian vertebrate fossil assemblages are readily recognized by the presence of *Lystrosaurus. Procolophon* and *Proterosuchus* are also important to the correlation of Lootsbergian tetrapod assemblages. However, temnospondyl-dominated assemblages occur that lack *Lystrosaurus* and thus are more difficult to correlate. I have used the temporal overlap of *Lystrosaurus* and the amphibians *Tupilakosaurus* and *Luzocephalus* in Russian strata as the primary basis for equating Lootsbergian dicynodont-dominated assemblages with temnospondyl-dominated assemblages.

Cosgriff (1984) assigned several temnospondyl-dominated assemblages to his A1 'horizon' (= Lootsbergian), even though these lack any index taxa of the Lootsbergian: the Knocklofty Sandstone/Shale in SE Tasmania (Cosgriff 1974), the Sticky Keep Formation in Svalbard (Wiman 1910, 1915; Nilsson 1942, 1943; Cox & Smith 1973), the upper Andavakoera Formation (Middle Sakamena Group or Formation) in NW Madagascar (Lehman 1961, 1966; Steyer 2002; Maganuco & Pasini 2009) and the Arcadia Formation of southern Queensland (Warren 1991). Except for the Arcadia Formation, I assign these assemblages a Nonesian age (see below).

Lootsbergian time encompasses both the '*Lystrosaurus* zone' and '*Procolophon* zone' of classic usage (e.g. Broom 1906). Thus, two distinct tetrapod assemblages (at least in the Karoo basin) can be recognized within the Lootsbergian, simply based on the stratigraphic distribution of *Procolophon*.

According to Botha & Smith (2007), all records of *Lystrosaurus maccaigi* in the Karoo basin are Permian (they co-occur with the Permian dicynodont *Dicynodon*), whereas *L. curvatus* straddles the Permo-Triassic boundary, and records of *L. murrayi* and *L. declivus* are Triassic. This provides a basis for a threefold subdivision of the Lootsbergian (Fig. 5): (1) Lootsbergian A is the time of overlap of *Dicynodon* and *Lystrosaurus*; (2) Lootsbergian B is the succeeding interval with *Lystrosaurus* without *Procolophon*; and (3) Lootsbergian C is the temporal overlap of *Lystrosaurus* and *Procolophon*. These subdivisions have some value outside of the Karoo basin. For example, in the Guodikeng Formation in the Junggur basin of northwestern China, there is a stratigraphic overlap of *Lystrosaurus* and *Dicynodon* (Lootsbergian A) followed by an interval of *Lystrosaurus* without *Procolophon* (Lootsbergian B) (Cheng 1981; Metcalfe *et al.* 2009). Indeed, in northwestern China, the co-occurrence of *Lystrosaurus* and *Dicynodon* at Dalongkou was first assigned to the upper Changhsingian *Falsisca postera* conchostracan zone and uppermost part of the *F. eotriassica* conchostracan zone by Kozur (1998*a*, *b*) (see also Kozur & Weems 2010). Therefore, a formal subdivision of the Lootsbergian into sub-LVFs has merit and should provide more precise correlation within the Lootsbergian interval.

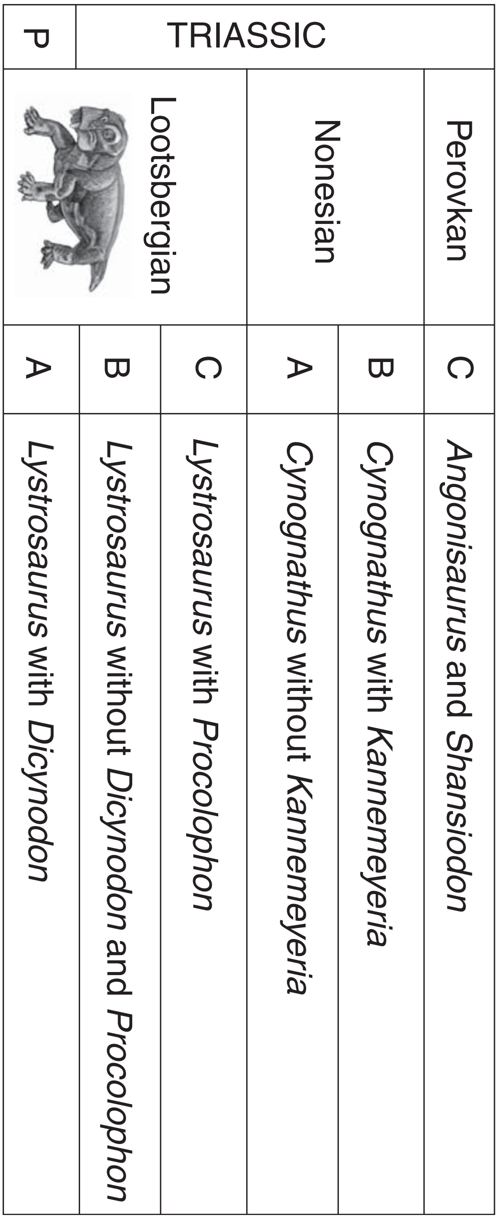


Fig. 5. Subdivisions of the Lootsbergian and Nonesian LVFs (based primarily on Hancox 2000). Restoration of *Lystrosaurus* by Matt Celeskey.

Nonesian LVF

Definition. The term Nonesian LVF refers to the time between the FAD of the cynodont *Cynognathus* and the FAD of the amphibian *Eocyclotosaurus*. The characteristic tetrapod assemblage is found in the lower two-thirds of the *Cynognathus* Assemblage Zone, which is from the upper two-thirds of the Burgersdorp Formation in the Karoo basin of South Africa (e.g. Kitching 1995; Hancox *et al.* 1995; Hancox 2000). The type section of the *Cynognathus* Assemblage Zone encompasses Nonesi's Nek, from which the name Nonesian is derived (Kitching 1995). Nonesian time begins with the FAD of *Cynognathus*, which is the end of the Lootsbergian LVF. The end of the Nonesian is the beginning of the Perovkan LVF, which is defined by the FAD of *Eocyclotosaurus*.

Broom (1906, 1907) coined the name *Cynognathus* 'beds', which was later transmuted to 'zone' by other workers (Watson 1914*a*, *b*; Kitching 1970, 1977). Keyser & Smith (1978) renamed it the *Kannemeyeria* Assemblage Zone, and Keyser (1979) termed it the *Kannemeyeria–Diademodon* Assemblage Zone. Kitching (1984) called it the *Cynognathus–Diademodon* Assemblage Zone. The term *Cynognathus* Assemblage Zone has been used most recently (e.g. Kitching 1995; Rubidge *et al.* 1995; Lucas 1998*a*; Hancox 2000).

Characteristic tetrapod assemblage. The characteristic assemblage of the Nonesian LVF occurs in subzones A and B of the *Cynognathus* Assemblage Zone of the Karoo basin (Hancox 2000) (Fig. 5). The tetrapod taxa present are amphibians, including *Parotosuchus, Wellesaurus* and *Trematosuchus*, captorhinids, a ?sphenodontid (or ?procolophonid), rhynchosaurs, the archosaurs *Erythrosuchus* and *Euparkeria*, the dicynodonts *Kannemeyeria* and *Kombuisia*, therocephalians and cynodonts, including *Cynognathus*, *Diademodon* and *Trirachodon* (e.g. Kitching 1977, 1995; Hancox & Rubidge 1994; Hancox *et al.* 1995; Shishkin *et al.* 1995*a*; Damiani 2001; Damiani & Rubidge 2003; Abdala *et al.* 2005).

Index fossils. The following tetrapod genera are restricted to Nonesian time and are widespread and/or common enough to be considered index fossils (Fig. 4): the amphibians *Parotosuchus*, *Odenwaldia*, *Wellesaurus*, *Trematosaurus* and *Trematosuchus* and the cynodont *Trirachodon*. The LOs of the the archosaur *Erythrosuchus*, the cynodonts *Cynognathus* and *Diademodon* and of the dicynodont *Kannemeyeria* are in the Nonesian. The species *K. simocephalus* is restricted to Nonesian time, but the species *K. cristarhynchus* is younger, of Perovkan age.

Principal correlatives. Principal correlatives of the type *Cynognathus* Assemblage Zone are: Wupatki and Torrey formations of the Moenkopi Group/Formation, Utah/Arizona, USA; Sticky Keep Formation of Svalbard, Arctic Norway; Middle Buntsandstein (upper Volpriehausen, Hardegsen and Solling formations), Germany; Petropavlovsk Formation (Yarenskiy horizon) in the Russian Urals; lower part of Ermaying Formation, Ordos basin, China; Puesto Viejo and Rio Mendoza formations, Argentina; base of the Lower Sandstone of the Zarzaitine Series in Algeria; lower N'tawere Formation, Zambia; K7 horizon of the Kingori Sandstone, Tanzania; and upper Fremouw Formation, Antarctica.

The Torrey Formation of the Moenkopi Group in Utah, USA, has yielded a skull of *Parotosuchus* (Lucas & Schoch 2002). Specimens of *Wellesaurus* as well as an *Odenwaldia*-like form are from the Wupatki Member of the Moenkopi Formation in Arizona (Damiani 2001; Lucas & Schoch 2002; Heckert *et al.* 2005*a*; Nesbitt 2005). These records of Nonesian index taxa are of late Olenekian age (see below).

In the Germanic basin, the Middle Buntsandstein (upper Volpriehausen, Hardegsen and Solling formations) yields fossils of *Parotosuchus, Oldenwaldia* and *Trematosaurus*, indicative of a Nonesian age (e.g. Schroeder 1913; Werneburg 1993; Lucas 1999; Schoch & Werneburg 1999; Lucas & Schoch 2002; Schoch 2008). Specifically, *Odenwaldia* occurs only in the Solling Formation, and *Trematosaurus* is common in the Hardegsen Formation and present in the Solling Formation. *Parotosuchus* is known from the Hardegsen and the Solling formations. One specimen of *Parotosuchus* (the holotype of *P. helgolandicus*) is known from the uppermost Volpriehausen Formation, from the upper *Gerviellia* beds assigned by Kozur & Bachmann (2008), based on conchostracans, to the Spathian.

Temnospondyls of the Sticky Keep Formaton in Svalbard co-occur with early Olenekian (Smithian) ammonites (Buchanen *et al.* 1965; Tozer 1967). The temnospondyls are: *Sasenisaurus, Peltostega*, *Aphanerama* (= *Lonchorhynchus*), *Lyrocephaliscus*, *Teretrema* and *Boreaosaurus* (Wiman 1910, 1915, 1916; Nilsson 1942, 1943; Cox & Smith 1973). Such an acme in trematosaur diversity may characterize the Nonesian. I assign a Nonesian age to the Sticky Keep tetrapods based mostly on the marine evidence that they are Olenekian and that the Nonesian is equivalent to at least part of the Olenekian (see below).

The Petropavlovsk svita in the Russian Urals (Yarenskiy horizon) yields anthracosaurs, temnospondyls (including *Parotosuchus*), procolophonids, a prolacertid, and various archosaurs, including erythrosuchids and rauisuchids (Shishkin *et al.* 1995*b*, 2000*a*, *b*; Ivakhnenko *et al.* 1997; Battail & Surkov 2000; Gower & Sennikov 2000; Novikov *et al.* 2000; Spencer & Benton 2000). The *Parotosuchus* record is the primary basis for a Nonesian age assignment.

In China, the lower Ermaying Formation in the Ordos basin produces a vertebrate fauna upon which Lucas (1993*a*) based the Ordosian LVF. Taxa present are a procolophonid, a proterosuchian, euparkeriids, a therocephalian and the dicynodonts *Parakannemeyeria* and *Kannemeyeri*a (= *Shaanbeikannemeyeria*) (Lucas 2001). The *Kannemeyeria* record as well as the overall composition of the assemblage suggest a Nonesian age.

In Argentina, the upper part of the Puesto Viejo Formation produces the dicynodont *Kannemeyeria*, a traversodontid and *Cynognathus* (Bonaparte 1970, 1978, 1982). The co-occurrence of *Cynognathus* and *Kannemeyeria* supports a Nonesian age assignment. The correlative fauna from the middle part of the Rio Mendoza Formation (but see Zavattieri & Arcucci 2007 for a different correlation) includes *Kannemeyeria* (*Vinceria andina* Bonaparte is not *Shansiodon*, as Lucas [1993*e*] suggested, but instead is *Kannemeyeria*), traversodontids and a galeosaurid.

Bonaparte (1981) described dicynodonts and proterosuchian postcrania from the lower part of the Puesto Viejo Formation. He referred to them as the Agua de los Burros local fauna. He assigned the dicynodonts to '*Vinceria*' (= *Kannemeyeria*) and claimed correlation to the *Lystrosaurus* Assemblage Zone based on a mean value of K/Ar ages of 232 ± 4 Ma from basalts and tuffs that bracket the fossils (Valencio *et al.* 1975, fig. 2). Given that we now know that the Induan is approximately 251–252 Ma (Bachmann & Kozur 2004; Kozur & Weems 2010; Mundil *et al.* 2010), the Argentinian dates (which are Carnian by current Triassic timescale calibration) do not support Bonaparte's correlation, nor do the fossils, which instead suggest a Nonesian age.

The base of the Lower Sandstone of the Zarzaitine Series in southeastern Algeria yields the amphibians *Odenwaldia* and '*Wellesaurus*' (an indeterminate heylerosaurid according to Damiani 2001) as well as a ?brachyopid, trematosaurid and the prolacertiform *Jesairosaurus* (Lehman 1957, 1971; Welles 1993; Jalil 1990, 1993, 1994, 1997, 1999). The record of *Odenwaldia* supports a Nonesian age assignment.

The lower part of the N'tawere Formation in Zambia produces *Diademodon* and *Kannemeyeria* (Crozier 1970). In the Ruhuhu Valley of Tanzania, the K7 horizon of the Kingori Sandstone Formation of Stockley (1932) yields *Kannemeyeria* (Cruickshank 1986). These are likely (though not definitively) Nonesian records.

In Antarctica, the upper part of the Fremouw Formation yields capitosaurid temnospondyls including *Parotosuchus*, *Cynognathus*, a diademodontid and a kannemeyeriid (Colbert 1991; Hammer 1988, 1990, 1995; Damiani 2001; Collinson *et al.* 2006). This has long been regarded as an assemblage of the '*Cynognathus* zone', and is of Nonesian age.

Comments. Most Nonesian vertebrate assemblages have long been recognized by the presence of *Cynognathus* and/or *Diademodon*, but these taxa have temporal ranges that extend into the Perovkan. *Parotosuchus* is a key temnospondyl taxon to correlate many Nonesian assemblages (Damiani 2001). The temporal succession of *Kannemeyeria* species is important, with *K. simocephalus* restricted to the Nonesian and *K. cristarhynchus* a Perovkan taxon.

Kitching (1977) reviewed the *Cynognathus* Assemblage Zone localities, and Kitching (1995) and Hancox (2000) provided a synopsis of the stratigraphic ranges of the genera. Watson (1942) and Kitching (1977) subdivided the *Cynognathus* Assemblage Zone into two subzones. Hancox & Rubidge (1994), Hancox *et al.* (1995), Shishkin *et al.* (1995*a*), Hancox (2000; Hancox *et al.* 1995, 2000) and Abdala *et al.* (2005) divided the *Cynognathus* Assemblage Zone into three stratigraphically discrete assemblages (Fig. 5). These assemblages have been called subzones A, B and C by Hancox *et al.* (1995), and the upper one is now assigned a Perovkan age (Hancox 2000; Abdala *et al.* 2005; Lucas *et al.* 2007*e*). This means that the South African Nonesian (which encompasses subzones A and B) is divisible into two biochronological units (Hancox 2000). A more important point is that recognizing subzone C as Perovkan means that not all of the classically-recognized '*Cynognathus* zone' is Nonesian.

Following Hancox (2000), the Nonesian can be subdivided into older (Nonesian A) and younger (Nonesian B) sub-LVFs (Fig. 5). Nonesian A begins with the FAD of *Cynognathus*, and Nonesian B begins with the FAD of *Kannemeyeria*. The FAD of *Eocyclotosaurus* (beginning of the Perovkan LVF) is the end of Nonesian B. In the Karoo basin, where *Eocyclotosaurus* is so far unknown, the LO of shansiodont dicynodonts approximates the beginning of Perovkan time (Fig. 5). In Nonesian A time in the Karoo basin, the amphibian *Kestrosaurus* is common and associated with *Trematosuchus* as well as theriodonts, *Cynognathus*, *Diademodon*, *Trirachodon* and *Bauria*. During Nonesian B time, characteristic taxa are *Parotosuchus*, *Kannemeyeria*, *Cynognathus*, *Diademodon*, *Trirachodon*, *Bauria*, *Erythrosuchus* and *Euparkeria*. Most of the Nonesian correlative tetrapod assemblages (see above) include *Kannemeyeria*, so they are of Nonesian B age.

Perovkan LVF

Definition. The term Perovkan LVF refers to the time interval between the FADs of the amphibians *Eocyclotosaurus* and *Mastodonsaurus giganteus* (Fig. 1). The characteristic tetrapod assemblage is the vertebrate fossil assemblage of the Donguz svita (*Eryosuchus* fauna) in the Russian Urals (Shishkin *et al.* 1995*b*, 2000*b*; Ivahknenko *et al.* 1997). Lucas (1998*a*) termed this the *Shansiodon* Assemblage Zone, after the distinctive dicynodont *Shansiodon* (= *Rhinodicynodon*). These fossils are from an approximately 175-m-thick section exposed in the Donguz River drainage near the city of Perovka, from which the name of the LVF is taken (Lucas 1998*a*, fig. 8). The beginning of the Perovkan is defined by the FAD of the amphibian *Eocyclotosaurus*. The end of the Perovkan LVF is the beginning of the Berdyankian LVF, which is defined by the FAD of the amphibian *Mastodonsaurus giganteus*.

Lucas (1998*a*) originally defined the beginning of Perovkan time as the FAD of the dicynodont *Shansiodon*. However, Shishkin (2000) has argued that the type assemblage of the Perovkan LVF is late Anisian, so it is younger than the *Eocyclotosaurus* assemblage that typically represents the Perovkan in western Europe and North America and is of unambiguous early Anisian age (Lucas & Schoch 2002). A more circumspect reading of the same data (e.g. Ivakhenko *et al.* 1997) simply regards the Donguz assemblage as Anisian, with no more precise correlation to the SGCS.

Lucas (1993*d*) argued that the LO of the dicynodont *Shansiodon* is Anisian, and this is why Lucas (1998*a*) used it to define the beginning of the Perovkan. However, if the LO of *Shansiodon* is actually younger than the LO of *Eocyclotosaurus*, then records of *Eocyclotosaurus* (Upper Buntsandstein in Germany and France, upper Moenkopi Group in USA) are of Nonesian age. The temporal succession of *Eocyclotosaurus* and *Shansiodon* is not easily resolved, but Lucas *et al.* (2007*e*) noted that the LO of *Kannemeyeria* in China predates the LO of *Shansiodon*, and in South Africa the LO of *Kannemeyria* predates the LO of shansiodonts (Fig. 5), and there is no conclusive evidence that the youngest Nonesian assemblage in South Africa (subzone B of Hancox *et al.* 1995) is equivalent to the *Eocyclotosaurus* zone. Lucas *et al.* (2007*e*) therefore recognized problems in establishing the temporal succession of Perovkan assemblages, but believe all are broadly Anisian, and some (part of American Moenkopi Group, German Röt Formation) are clearly early Anisian. The easiest way to remove ambiguity here is to redefine the beginning of the Perovkan as the FAD of *Eocyclotosaurus*, as did Lucas *et al.* (2007*e*).

Characteristic tetrapod assemblage. Three principal sites in the Donguz svita produce the following taxa: various amphibians, including *Eryosuchus, Bukobaja, Plagiosternum* and *Plagioscutum*, a procolophonid, a prolacertid, a proterosuchid, the erythrosuchid *Erythrosuchus*, rauisuchids, a euparkeriid, the dicynodonts *Kannemeyeria* (= *Rhadiodromus*, *Rabidosaurus*, *Edaxosaurus*, *Calleonassus* and *Rhinocerocephalus*) and *Shansiodon* (= *Rhinodicynodon*), therocephalians, the cynodonts *Scalenodon*, *Antecosuchus* and a traversodontid (Shishkin *et al.* 1995*b*, 2000*a*, *b*; Ivakhnenko *et al.* 1997; Surkov 1999; Battail & Surkov 2000; Gower & Sennikov 2000; Spencer & Benton 2000; Tverdokhlebov *et al.* 2002).

Index fossils. The following tetrapod genera are common and/or widespread enough to be useful index taxa of the Perovkan (Fig. 4): the amphibians *Eryosuchus*, *Eocyclotosaurus* and *Paracyclotosaurus*, the archosaur *Arizonasaurus*, the cynodont *Scalenodon* and the dicynodonts *Shansiodon*, *Parakannemeyeria* and *Sinokannemeyeria*. *Kannemeyria christarhynchus* is a Perovkan index fossil, and the HOs of *Kannemeyeria*, *Cynognathus* and *Diademodon* are Perovkan.

Principal correlatives. Principal correlatives of the type Perovkan assemblage are from the Holbrook and Anton Chico members of the Moenkopi Formation, Arizona–New Mexico USA; lower part of Wolfville Formation at Lower Economy, Fundy basin, Nova Scotia, Canada; Otter Sandstone of the United Kingdom; Upper Buntsandstein (Röt Formation), Germany-France; lower Kelamayi Formation, Junggur basin, Xinjiang, China; upper Ermaying Formation, Ordos Basin, China; Yerrapalli Formation, India; Lower Zarzaitine Formation, Algeria; upper part of the Burgersdorp Formation in the Karoo basin of South Africa; Omingonde Formation, Namibia; and lower Manda Formation, Tanzania.

The Holbrook and Anton Chico members of the Moenkopi Formation, in Arizona–New Mexico, USA, yield the characteristic Perovkan capitosauroid amphibian *Eocyclotosaurus*, very similar to *E. lehmanni* from the Upper Buntsandstein (Röt Formation), as well as other capitosaurs, brachyopids, and the ctenosauriscid *Arizonasaurus* (Lucas & Morales 1985; Lucas & Hunt 1987; Morales 1987; Schoch 2000*b*; Boy *et al.* 2001; Lucas & Schoch 2002; Heckert *et al.* 2005*a*; Nesbitt 2005). A *Shansisuchus*-like erythrosuchian from the Anton Chico Member in New Mexico (Lucas *et al.* 1998*b*; Nesbitt *et al.* 2006) is consistent with a Perovkan age assignment.

In the Fundy basin of Nova Scotia, Canada, the lower part of the Wolfville Formation (also referred to as the 'Lower Economy Beds') yields a small tetrapod assemblage that was the basis of the Economian LVF of Huber *et al.* (1993*b*). The presence of a trematosaur (cf. *Cosgriffius*) and the lepidosaur cf. *Tanystropheus* suggests a possible Perovkan age (Lucas & Huber 2003).

The Otter Sandstone in Devon, United Kingdom, yields the temnospondyl *Eocyclotosaurus*, the rhynchosaur *Fodonyx*, the prolacertiform *Tanystropheus*, a procolophonid, a rauisuchian and a ?ctenosauriscid archosaur (Benton *et al.* 1994; Hone & Benton 2008). As Milner *et al.* (1990) stressed, '*Mastodonsaurus*' *lavisi* Seeley from the Otter Sandstone is a *nomen dubium* upon which it is risky to draw stratigraphic conclusions, so I do not consider it a Perovkan record of *Mastodonsaurus*. Indeed, Damiani (2001) considered the type material of '*M.*' *lavisi* to be indeterminate.

In Germany and France, the Upper Buntsandstein (Röt Formation) yields *Eocyclotosaurus* (Heyler 1969, 1976; Ortlam 1970; Kamphausen & Morales 1981; Lucas & Schoch 2002) and is of Perovkan age.

In the Junggur basin of Xinjiang, China, the lower part of the Kelamayi (= Karamay) Formation produces a vertebrate fauna that consists of indeterminate labyrinthodonts (including the holotype of the *nomen dubium* '*Parotosaurus*' [= *Parotosuchus*] *turfanensis* Young: Lucas & Hunt 1993*b*), a euparkeriid, an erythrosuchid and the dicynodonts *Parakannemeyeria* and *Xiyukannemeyeria* (Liu & Li 2003; Liu 2004). The bauriid therapsid *Traversodontoides* from Jiyuan, Henan may also be of Perovkan age (Cheng 1981; Sun 1989).

The upper part of the Ermaying Formation in the Ordos basin in northern China produces what has been called the Perovkan-age '*Sinokannemeyeria* fauna' or 'kannemeyeriid fauna' of China (e.g. Sun 1972; Cheng 1981; Lucas 2001). Lucas (1993*a*) based the Ningwuan LVF on this assemblage. The vertebrate fossil assemblage includes indeterminate labyrinthodonts, a procolophonid, erythrosuchids, an ?ornithosuchid, a ?euparkeriid, a cynodont, and the dicynodonts *Shansiodon, Sinokannemeyeria* and *Parakannemeyeria* (Lucas 2001).

In the Pranhita–Godavari Valley of India, the Yerrapalli Formation yields an assemblage of Perovkan age. It includes the amphibian *Eryosuchus*, the rhynchosaur *Mesodapedon*, a prolacertid, the archosaur *Erythrosuchus*, a raisuchid, the dicynodonts *Wadiasaurus* and *Kannmeyeria* (= *Rechnisaurus*), and a trirachodontid, (e.g. Roychowdhury 1970*a*, *b*; Chatterjee 1980*b*; Damiani 2001; Sen 2003, 2005; Bandyopadhyay & Sengupta 2006).

The Omingonde Formation in Namibia produced a Perovkan-age assemblage that includes an eryopoid temnospondyl, the dicynodonts *Kannemeyeria cristarhynchus*, *Dolichuranus*, and *Rhopalorhinus*, a bauriamorph, and cynodonts, including ?*Cynognathus*, *Diademodon* and *Trirachodon* (Keyser 1973*a*, *b*, 1978; Pickford 1995; Smith & Swartt 2002).

In the Karoo basin of South Africa, the upper part of the Burgersdorp Formation yields the upper part of the *Cynognathus* Assemblage Zone (subzone C of Hancox 2000, see discussion above and Fig. 5). Characteristic taxa are the amphibian *Paracylotosaurus*, the dicynodonts *Cynognathus*, *Diademodon* and *Cricodon*, and the dicynodonts *Angonisaurus* and *Kannemeyeria*, which support a Perovkan age assignment (e.g. Hancox & Rubidge 1994, 1996; Damiani 2001; Damiani & Hancox 2003; Abdala *et al.* 2005). *Paracylotosaurus* is also known from the Denwa Formation in the Satpura basin, India and the Wianamatta Group of the Sydney basin, Australia (Damiani & Hancox 2003), so these may also be Perovkan records.

The lower Manda Formation in Tanzania produces the amphibian *Eryosuchus*, the rhynchosaur *Stenaulorhynchus*, the archosaur '*Mandasuchus*', the dicynodonts *Shansiodon* (= *Tetragonius*) and *Angonisaurus* and the cynodont *Scalenodon* (Huene 1938*a*, *b*; Crompton 1955; Cruickshank 1965, 1967; Cox & Li 1983; Damiani 2001). This is a Perovkan assemblage.

Comments. Lucas (1998*a*) defined the Perovkan LVF as the time between the FAD of the dicynodont *Shansiodon* and the FAD of the temnospondyl *Mastodonsaurus*. Its characteristic assemblage is the tetrapod fauna from the Russian Donguz svita, so the land-vertebrate biochronology shifts here from superposed South African assemblages (the characteristic assemblages of the Lootsbergian and Nonesian LVFs) to the superposed Russian assemblages (the characteristic assemblages of the Perovkan and Berdyankian LVFs). This geographical shift poses problems for the biochronology, particularly in demonstrating the temporal succession (and not overlap) of Nonesian and Perovkan assemblages. Indeed, the reassignment of the upper '*Cynognathus* zone' to the Perovkan LVF discussed above directly reflects such problems (Hancox 2000; Abdala *et al.* 2005; Lucas *et al.* 2007*e*). The easiest way to reduce ambiguity here was to redefine the beginning of the Perovkan as the FAD of *Eocyclotosaurus* (Lucas et al. 2007*e*).

Perovkan tetrapod assemblages are best known in Russia and China where they contain numerous dicynodonts. Correlatives are either dicynodont dominated (Manda Formation, upper Burgersdorp Formation) or amphibian dominated (upper Moenkopi, upper Buntsandstein).

Berdyankian LVF

Definition. The term Berdyankian LVF is the time interval between the FAD of the amphibian *Mastodonsaurus giganteus* and the FAD of the phytosaur *Parasuchus* (= *Paleorhinus*) (Fig. 1). The characteristic tetrapod assemblage is the vertebrate fossil assemblage of the Bukobay svita in the Russian Urals (e.g. Ivakhnenko *et al.* 1997; Shishkin *et al.* 2000*b*). Relevant vertebrate-fossil localities are near the Berdyank River, from which the LVF takes its name. The characteristic Berdyankian tetrapod assemblage is directly superposed on the characteristic Perovkan assemblage. The beginning of the Berdyankian is defined by the FAD of *Mastodonsaurus giganteus*, whereas the end of the Berdyankian is the beginning of the Otischalkian, which is defined by the FAD of *Parasuchus*.

Characteristic tetrapod assemblage. The assemblage from the Bukobay Formation includes an anthracosaur, the amphibians *Mastodonsaurus*, *Bukobaja*, ?*Cyclotosaurus*, *Plagioscutum* and *Plagiosternum*, an erythrosuchid, a rauisuchid, and the dicynodonts '*Elephantosaurus jachimovitschi*' Vyushkov (a *Stahleckeria*-like form) and a generically indeterminate kannemeyeriid (Shishkin *et al.* 1995*b*, 2000*a*, *b*; Ivakhnenko *et al.* 1997; Battail & Surkov 2000; Gower & Sennikov 2000).

Index fossils. The following tetrapod genera are common and/or widespread enough to be index fossils of the Berdyankian (Fig. 4): the cynodont *Massetognathus* and the dicynodonts *Dinodontosaurus* and *Stahleckeria*. The LO of the amphibian *Mastodonsaurus giganteus* is Berdyankian. An acme in plagiosaur diversity and abundance characterizes Berdyankian time. No procolophonids are known from Berdyankian strata (Cisneros 2008*a*), but this must be due to a lack of discovery, not a real absence, as both pre- and post-Berdyankian procolophonids are known.

Principal correlatives. The Lettenkohle (Lettenkeuper, Lower Keuper, Erfurt Formation) in Germany and the Chanarian LVF localities in Argentina and Brazil are the principal correlatives of the Berdyankian type assemblage. The Lettenkohle record is important because it establishes the Ladinian age of at least part of the Berdyankian (see below). The Lettenkohle fossils are from the Grenze bonebed, the laterally equivalent/overlying Vitriolschiefer and the Kupferzell locality, so they are above the unconformity that separates the Keuper from the underlying Muschelkalk. Lettenkohle tetrapods include a chroniosuchian, the amphibians *Mastodonsaurus giganteus*, *Callistomordax*, *Plagiosternum, Plagiosuchus* and *Kupferzella*, the rauisuchian *Batrachotomus*, the prolacertiform *Tanystropheus* and small cynodonts (e.g. Wild 1978, 1980; Schoch 1997, 2000*a*; Lucas 1999; Schoch & Werneburg 1999; Witzmann *et al.* 2008; Damiani *et al.* 2009; Gower & Schoch 2009). A *Dinodontosaurus*-like humerus from the Vitriolschiefer (Lucas & Wild 1995) may link the Lettenkohle to the South American Chanarian. However, a *Dinodontosaurus*-like radius is also known from the upper Anisian interval of the Muschelkalk in Germany, so this may indicate that the Berdyankian also encompasses part of late Anisian time (Lucas 2007*b*).

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

The lower part of the Santa Maria Formation in the Paraná basin of Rio Grande do Sul, Brazil yields vertebrate fossil assemblages from Candelaria and Chiniquá considered by Barberena (1977) and Barberena *et al.* (1985) to be two different local faunas of different ages. Lucas (2002) regarded them as a single biostratigraphic assemblage that includes a procolophonid, archosaurs, the dicynodonts *Dinodontosaurus* and *Stahleckeria*, chiniquodontids, and the traversodontids *Massetognathus*, *Belesodon*, *Traversodon*, *Exaeretodon*, *Santacruzodo*, *Protuberum* and *Probelesodon* (e.g. Abdala & Ribeiro 2003; Cisneros *et al.* 2004; Langer *et al.* 2007; Reichel *et al.* 2009). This assemblage and the Chanarian type assemblage in Argentina are assigned a Berdyankian age based largely on their dicynodonts and traversodontids and their stratigraphic position, which places them between the Nonesian and the Adamanian.

Comments. Previously, I used the FAD of the genus *Mastodonsaurus* to define the beginning of the Berdyankian. This was based on a taxonomy in which *Mastodonsaurus* (typified by the species *M. giganteus*) was distinguished from the older (Perovkan) *Heptasaurus* (e.g. Schoch 1999; Schoch & Milner 2000). However, taxonomists who study these amphibians have suggested that *Mastodonsaurus* and *Heptasaurus* be combined into a single genus, *Mastodonsaurus* (Rayfield *et al.* 2009). Thus, I now use the FAD of the species *M. giganteus* to define the beginning of the Berdyankian so as not to be subject to the shifting opinions of taxonomists revising the genus-level taxonomy of stereospondyl amphibians. This preserves the original intent of the Berdyankian, as no temnospondyl worker has advocated the synonymy of *Heptasaurus cappelensis* and *Mastodonsaurus giganteus* at the species-level.

As noted by Lucas (1998*a*), global correlations within the Berdyankian interval are confounded by the near endemism of South American tetrapod assemblages that are apparently of this age (the *Dinodontosaurus* faunas of Argentina and Brazil, classically assigned to the Chanarian LVA of Bonaparte 1966, 1967). Recognition of Berdyankian-age assemblages in Russia and Germany is rendered easy by the presence of the key taxon *Mastodonsaurus giganteus* (Lucas 1999).

The Berdyankian is difficult to correlate globally, largely because of a paucity of tetrapod assemblages of this age. Two clusters of localities (European and South American) are equated, largely on the basis of the Lettenkohle dicynodont and the conclusion that '*Elephantosaurus*' is a 'stahleckeriid', possibly a synonym of *Stahleckeria* (Lucas & Wild 1995). The South American Chanarian LVF thus is the provincial secondary standard correlative to the Berdyankian.

The Berdyankian may be relatively long, at least correlative to the latest Anisian and Ladinian (see below). Nevertheless, Berdyankian tetrapod fossil assemblages probably only represent the earlier part of this time interval. Indeed, the paucity of tetrapod assemblages of Berdyankian age represents one of the most substantial deficits in the global record of Triassic tetrapods. This is an important deficit because many characteristic Late Triassic tetrapod taxa, such as metoposaurs, phytosaurs, aetosaurs and dinosaurs, so far lack evolutionary antecedents that should occur in Berdyankian-age strata.

Otischalkian LVF

Definition. The Otischalkian LVF is the time interval between the FADs of the phytosaurs *Parasuchus* (= *Paleorhinus*) and *Rutiodon* (Fig. 1). Lucas & Hunt (1993*a*) proposed the Otischalkian LVF based on the vertebrate fossil assemblage of the Colorado City Formation of the Chinle Group near the defunct town of Otis Chalk, Howard County, Texas, USA (Lucas & Anderson 1993*a*, *b*, 1994, 1995; Lucas *et al.* 1993, 1994, 1997*a*). The beginning of the Otischalkian is the FAD of *Parasuchus*. The end of the Otischalkian is the beginning of the Adamanian, which is defined by the FAD of the phytosaur *Rutiodon*.

Characteristic tetrapod assemblage. The characteristic tetrapod assemblage of the Otischalkian is the assemblage of vertebrate fossils from just north of the defunct town of Otis Chalk in Howard County, Texas. Lucas *et al.* (1993) reviewed the fauna, which is from the Colorado City Formation of the Chinle Group. The following taxa are present: the amphibians *Latiscopus*, *Buettneria* and *Apachesaurus*, a procolophonid, the rhynchosaur *Otischalkia*, the archosaurs *Doswellia*, *Trilophosaurus* (= *Malerisaurus*) and *Poposaurus*, the aetosaurs *Longosuchus* (= *Lucasuchus*) and *Coahomasuchus*, and the phytosaurs *Parasuchus* and *Angistorhinus* (Lucas *et al.* 1993; Long & Murry 1995; Heckert & Lucas 1999; Spielmann *et al.* 2006*c*).

Index fossils. The following tetrapod genera are restricted to Otischalkian time and are widespread and/or common enough to be useful as index fossils (Fig. 6): the aetosaur *Longosuchus*, and the archosaur *Doswellia*. *Parasuchus* and *Angistorhinus* are mostly of Otischalkian age, but also have early Adamanian records. The dicynodont *Placerias* has both Otischalkian and earliest Adamanian records. The LOs of the widespread temnospondyl *Metoposaurus* and of the rhynchosaur *Hyperodapedon* are Otischalkian, and these taxa are also known in Adamanian strata (Lucas *et al.* 2002*a*, 2007*e*).

Principal correlatives. Besides Chinle Group correlatives, principal Otischalkian vertebrate assemblages are from the Sanfordian interval of the Newark Supergroup basins of eastern North America; Schilfsandstein (Stuttgart Formation) of the German Keuper; the Irohalene Member (T4) of the Timesgadiouine Formation, Argana Group, Morocco; and the basal part of the Maleri Formation, Pranhita–Godavari Valley, India.

Otischalkian principal correlatives and the characteristic tetrapod assemblage encompass a broad geographical range of Chinle Group outcrops in Wyoming, New Mexico and Texas. They occur in units of the lower part of the Chinle Group that have been correlated with each other on a lithostratigraphic basis (Lucas 1993*b*). The most well-known principal correlative of the type Otischalkian fauna in the Chinle Group is the vertebrate-fossil assemblage from the Popo Agie Formation of Wyoming, principally Fremont County (Branson & Mehl 1928; Mehl 1928; Colbert 1957; Lucas 1994; Lucas *et al.* 2002*a*) that includes the amphibian *Buettneria*, the phytosaurs *Parasuchus* and *Angistorhinus*, the aetosaur *Desmatosuchus*, the archosaurs *Poposaurus* and *Heptasuchus*, the rhynchosaur *Hyperodapedon*, and the dicynodont *Placerias*. A less well-known principal correlative is the small assemblage from the Salitral Formation in Rio Arriba County, New Mexico that consists of a metoposaur, *Longosuchus*, a phytosaur, and an indeterminate dinosaur (Lucas & Hunt 1992). Heckert (2004; Heckert & Lucas 2006) provided some microvertebrate basis for recognition of the Otischalkian in Chinle Group strata, such as the LO of the 'dinosaur' *Protecovasaurus* and the archosaur *Trilophosaurus buettneri* (also see Spielmann *et al.* 2008).

In the Newark Supergroup of eastern North America, the stratigraphically lower formations of the Deep River, Gettysburg, Newark and Fundy basins contain two distinct vertebrate fossil assemblages. The older of these was used by Huber *et al.* (1993*b*) as the basis of the Sanfordian LVF, after the characteristic assemblage from the middle Pekin Formation in the Sanford sub-basin of the Deep River basin complex. An age-equivalent assemblage from the middle Wolfville Formation (Fundy basin) is also assigned to this LVF. The collective Newark tetrapod fauna of this Sanfordian LVF includes the amphibian *Metoposaurus*, procolophonids, the traversodontids *Arctotraversodon* and *Plinthogomphodon*, the dicynodont *Placerias*, the rhynchosaur *Hyperodapedon*, the archosaur

taxa	Otischalkian	Adamanian	Revueltian	Apachean
amphibians:				
Apachesaurus		●	●	●
Buettneria	●	●	●	●
Metoposaurus	●	●		
phytosaurs:				
Angistorhinus	●	●		
Mystriosuchus			●	
Nicrosaurus			●	
Parasuchus	●	●		
Pseudopalatus			●	
Redondasaurus				●
Rutiodon		●		
aetosaurs:				
Aetosaurus			●	
Desmatosuchus	●	●		
Longosuchus	●			
Paratypothorax		●	●	
Redondasuchus				●
Rioarribasuchus		●		
Stagonolepis	●	●		
Typothorax		●	●	
others:				
Doswellia	●			
Eudimorphodon			●	
Hyperodapedon	●	●		
Placerias	●	●		
Revueltosaurus			●	
Riojasaurus				●

Fig. 6. Temporal ranges of selected genera of Late Triassic tetrapods.

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

In Germany, the Schilfsandstein produces *Metoposaurus* and *Parasuchus* but lacks *Stagonolepis*, so it can be assigned an Otischalkian age (Hunt & Lucas 1991; Lucas 1999; Schoch & Werneburg 1999; Hungerbühler 2001*b*).

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

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

Comments. The Otischalkian LVF was originally defined as the time between the FADs of the phytosaurs *Parasuchus* (= *Paleorhinus*) and *Rutiodon* (Lucas & Hunt 1993*a*; Lucas *et al.* 1997*a*; Lucas 1998*a*). It is important to note that a little advertised petition to the International Commission on Zoological Nomenclature by Chatterjee (2001) resulted in establishing a diagnostic lectotype for *Parasuchus* (long a *nomen dubium*: Hunt & Lucas 1991), so that this name should be regarded as the senior synonym of *Paleorhinus* (Lucas *et al.* 2007*c*). Furthermore, even though Hunt & Lucas (1991) provided a careful taxonomic revision of *Parasuchus*, and provided a clear diagnosis of the genus that has never been contested, some taxonomists have relegated all primitive phytosaurs to a metataxon (grade) and then claimed these phytosaurs (long and widely known as *Paleorhinus*/*Parasuchus*) are of no value to biostratigraphy (e.g. Fara & Hungerbühler 2000; Rayfield *et al.* 2005, 2009). I reject such an approach to primitive phytosaur taxonomy and recognize *Parasuchus* as a diagnosable genus (Lucas *et al.* 2007*c*).

I have long regarded *Parasuchus* as a robust index taxon of the Otischalkian (Hunt & Lucas 1991; Lucas *et al.* 2007*c, d*). However, recently developed Upper Triassic conchostracan biostratigraphy (Kozur & Weems 2005, 2007) and European records of the characteristic Adamanian aetosaur *Stagonolepis* suggest that some *Parasuchus* records should be considered early Adamanian in age (Kozur & Weems 2005). Thus, if all *Stagonolepis* records are regarded as Adamanian (as they were by Lucas 1998*a*), and the conchostracan-based correlations of the Adamanian are accepted, then records of *Parasuchus* from the German Kieselsandstein and Blasensandstein and the Polish Krasiejów locality are Adamanian. This is also consistent with the Chinle Group record of *Parasuchus* at the *Placerias*/Downs quarries in the Bluewater Creek Formation of the Chinle Group in Arizona, in what I have regarded as oldest Adamanian strata (Lucas *et al.* 1997*a*). Thus, recognizing that *Parasuchus* records are not strictly Otischalkian (some are early Adamanian: Fig. 6), and that *Stagonolepis* records are strictly Adamanian, clarifies correlation in the Otischalkian–Adamanian interval.

The Otischalkian index taxa *Longosuchus* (= *Lucasuchus*) and *Doswellia* still stand. *Metoposaurus* also has only Otischalkian and early Adamanian records, though Milner & Schoch (2004) recently claimed its presence in the Revueltian Stubensandstein of Germany, a claim that met a detailed refutation from Lucas *et al.* (2007*e*). The last Otischalkian index fossil listed by Lucas (1998*a*) is the phytosaur *Angistorhinus*. Its records are Otischalkian (Long & Murry 1995) except one, near Lamy, New Mexico, USA, where it co-occurs with *Rutiodon* in the earliest Adamanian (Hunt *et al.* 1993, 2005) (Fig. 7).

Adamanian LVF

Definition. The Adamanian is the time interval between the FAD of the phytosaur *Rutiodon* and the FAD of the aetosaur *Typothorax coccinarum* (Fig. 1). Lucas & Hunt (1993*a*) based the Adamanian LVF on the vertebrate fauna of the Blue Mesa Member of the Petrified Forest Formation in the Petrified Forest National Park, Arizona, USA (Lucas 1993*b*; Lucas & Hunt 1993*a*; Lucas *et al.* 1997*a*). Lucas (1998*a*) termed this the *Rutiodon* Assemblage Zone. The beginning of the Adamanian is defined as the FAD of the phytosaur *Rutiodon*. The end of the Adamanian is the beginning of the Revueltian, which is defined by the FAD of the aetosaur *T. coccinarum.*

Characteristic tetrapod assemblage. The characteristic tetrapod assemblage of the Adamanian is the assemblage of vertebrate fossils found in the Blue Mesa Member of the Petrified Forest Formation in the Petrified Forest National Park, near the defunct railroad siding of Adamana, Arizona. Recent faunal lists have been provided by Murry & Long (1989), Long & Murry (1995), Heckert *et al.* (2005*a*) and Parker *et al.* (2006). The fauna includes the following tetrapods: the amphibians *Apachesaurus* and *Buettneria*, the aetosaurs *Desmatosuchus*

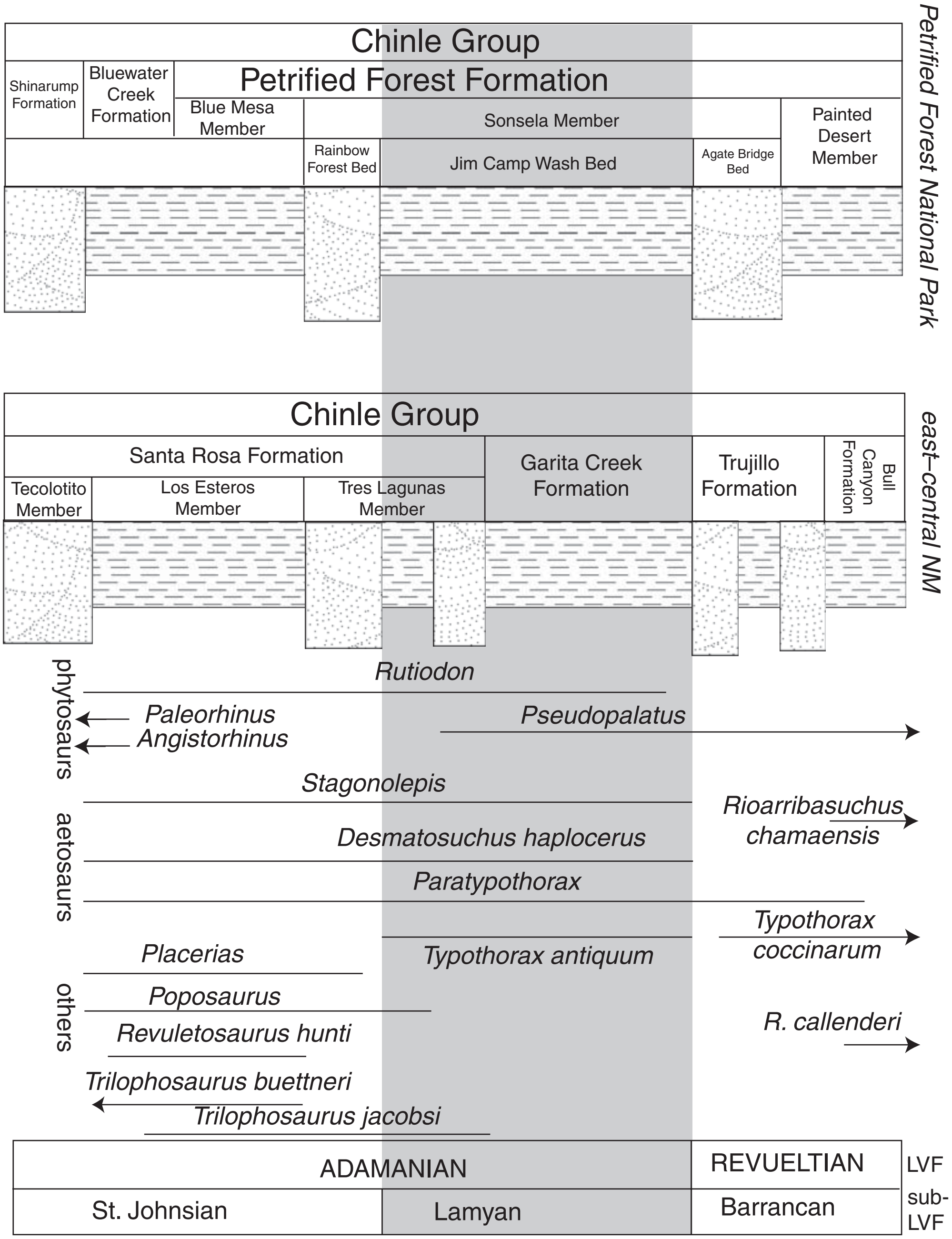


Fig. 7. Lithostratigraphy and tetrapod biostratigraphy of the Adamanian and Revueltian intervals in east–central New Mexico and in the Petrified Forest National Park, Arizona. The Lamyan interval is shaded (after Hunt *et al.* 2005).

(= *Acaenasuchus*), *Stagonolepis*, *Adamanasuchus* and *Paratypothorax*, *Rutiodon*-grade phytosaurs (including *Leptosuchus* and *Smilosuchus*), the rauisuchian *Postosuchus*, the archosaurs *Hesperosuchus*, *Acallosuchus*, *Parrishea* and *Vancleavea*, and the dicynodont *Placerias*, as well as many microvertebrate taxa.

Index fossils. The following tetrapod genera are restricted to Adamanian time and are widespread and/or common enough to be useful as index fossils (Fig. 6): *Rutiodon*-grade phytosaurs, including *Leptosuchus* and *Smilosuchus*, the trilophosaurid archosaur *Spinosuchus* and the aetosaur *Stagonolepis*. The HO of dicynodonts was long thought to be Adamanian. However, there is a putative Cretaceous record from Australia (Thulborn & Turner 2003), and Dzik *et al.* (2008) recently reported a Triassic dicynodont from Poland in strata they deemed Rhaetian based on palaeobotany. The HO of the widespread rhynchosaur *Hyperodapedon* is Adamanian (Lucas & Heckert 2001; Lucas *et al.* 2002*a*) (Fig. 8). Within the Chinle Group, various microvertebrate taxa, including *Colognathus*, *Tecovasurus*, and *Crosbysaurus*, are index taxa of the Adamanian (Heckert 2004; Heckert & Lucas 2006).

Principal Correlatives. Besides the Chinle Group correlatives, major Adamanian faunas are those of the Conewagian interval of the Newark Supergroup basins of eastern North America; Lossiemouth Sandstone Formation, Scotland; Lehrberg Schichten interval of the German Keuper; the Krasiejów locality in Poland; Ischigualasto Formation, Argentina; and upper Santa Maria Formation, Brazil.

In the Chinle Group, Adamanian vertebrates are widespread and include the vertebrate fossil assemblages of the *Placerias* and Downs' quarries, Bluewater Creek Formation, Arizona (Camp & Welles 1956; Kaye & Padian 1994; Long & Murry 1995; Lucas *et al.* 1997*a*; Heckert 2004; Heckert *et al.* 2005*a*); the Bluewater Creek Formation and Blue Mesa Member of the Petrified Foreset Formation in the Blue Hills, Arizona; the Bluewater Creek Formation and Blue Mesa Member of the Petrified Forest Formation, McKinley and Cibola counties, New Mexico (Heckert 1997); the Los Esteros and Tres Lagunas members, Santa Rosa Formation, vicinity of Lamy, Santa Fe County, New Mexico (Hunt *et al.* 2005) (Fig. 7); Garita Creek Formation, Santa Rosa and vicinity, Guadalupe County, New Mexico (Hunt & Lucas 1993*a*); and Tecovas Formation, West Texas (Murry 1986, 1989; Long & Murry 1995).

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

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

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

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

The tetrapod assemblage of the Lossiemouth Sandstone Formation of Grampian (Elgin) Scotland comes from small quarries and the coastal section at Lossiemouth. Benton & Spencer (1995) provided a

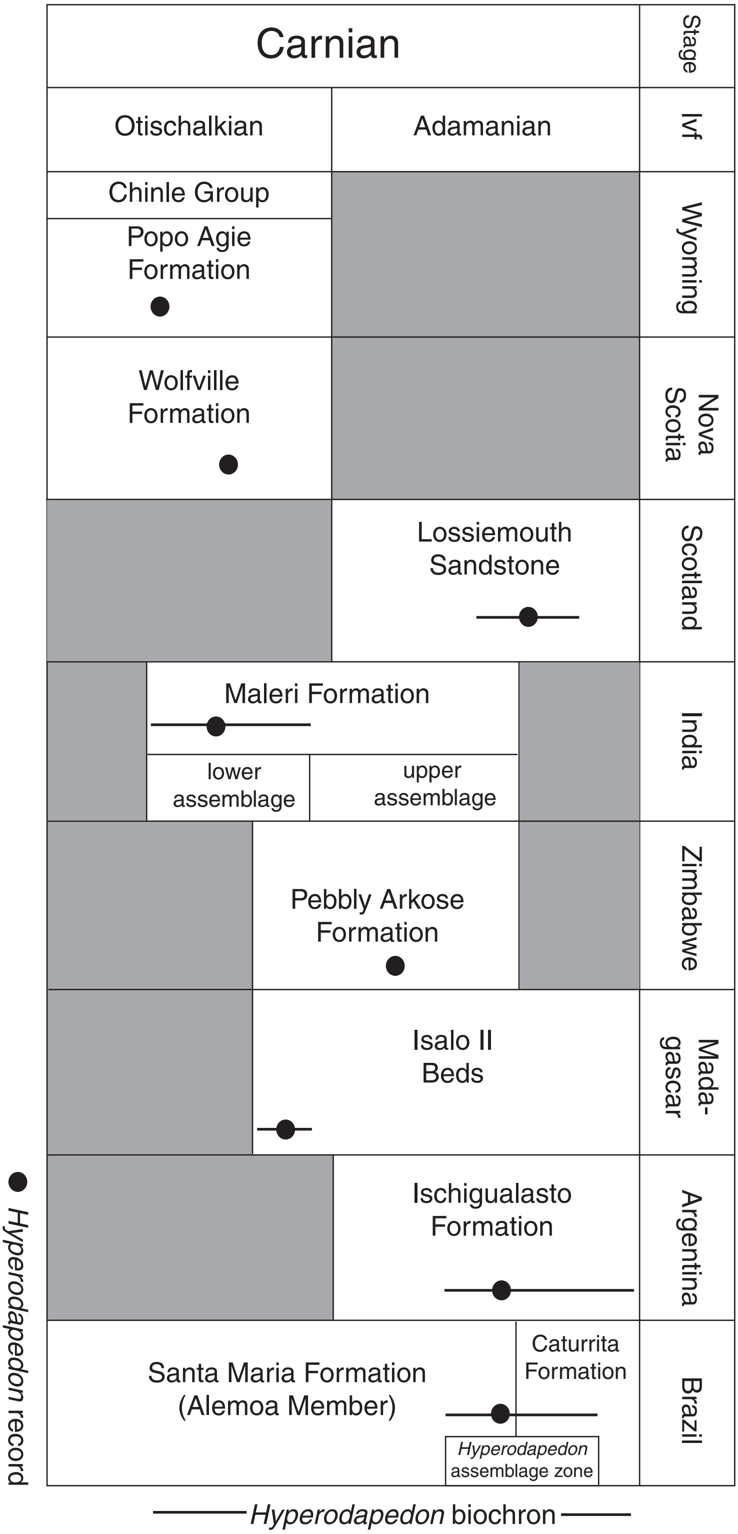


Fig. 8. Global correlation of *Hyperodapedon* localities, which identify a *Hyperodapedon* biochron of Otischalkian–Adamanian age.

detailed summary and indicate that all sites come from a narrow stratigraphic range, so I treat the vertebrates as a single biostratigraphic assemblage. It includes the procolophonid *Leptopleuron*, the sphenodontid *Brachyrhinodon*, the rhynchosaur *Hyperodapedon*, the aetosaur *Stagonolepis*, the ornithosuchid *Ornithosuchus*, the crocodylomorph *Erpetosuchus*, the probable ornithodiran *Scleromochlus* and the 'dinosaur' *Saltopus*. The presence of *Hyperodapedon* and *Stagonolepis* supports correlation of this assemblage to the Chinle Group Adamanian.

In Germany, the stratigraphic interval between the Schilfsandstein and the Stubensandstein (Lehrberg Schichten, Blasensandstein and Kieselsandandstein) produces *Stagonolepis*, *Parasuchus* and *Metoposaurus* (e.g. Lucas 1999), and is assigned an Adamanian age (Kozur & Weems 2005).

In Poland, the Krasiejów tetrapod assemblage includes the amphibians *Cyclotosaurus* and *Metoposaurus*, the phytosaur *Parasuchus*, the aetosaur *Stagonolepis*, the rauisuchian *Teratosaurus* and the dinosauriform *Silesaurus* (Dzik 2001, 2003; Sulej 2002, 2005, 2007; Sulej & Majer 2005; Dzik & Sulej 2007; Lucas *et al.* 2007*d*). This assemblage is from strata *c.* 80 m above the Reed Sandstone (a Schilfsandstein equivalent) that are homotaxial to the German Lehrberg Schichten and is of Adamanian age.

In Argentina, the Ischigualasto Formation is 500–900 m thick and consists of drab mudstones, tuffs and sandstones that produce an extensive tetrapod assemblage including: the amphibian *Promastodonosaurus*, the archosaurs *Saurosuchus, Sillosuchus*, and *Proterochampsa*, the aetosaur *Stagonolepis* (= *Aetosauroides*), the rhynchosaur *Hyperodapedon*, the dinosaurs *Herrerasaurus* (= ?*Ischisaurus* = *Frenguellisaurus*), *Eoraptor* and *Pisanosaurus*, the chiniquodontid cynodont *Chiniquodon*, the gomphodont cynodonts *Exeraetodon*, *Proexaraetodon*, and *Ischignathus* and the dicynodont *Ischigualastia* (e.g. Cabrera 1944; Reig 1959, 1961, 1963; Casamiquela 1960, 1962; Cox 1965; Bonaparte 1976; Rogers *et al.* 1993; Sereno *et al.* 1993; Bonaparte 1997; Alcober & Parrish 1997; Heckert & Lucas 2002*c*). The assemblage slightly overlaps and mostly overlies the Herr Toba bentonite that yielded a ^{40}Ar/^{39}Ar age of 227.8 ± 0.3 Ma (Rogers *et al.* 1993), which was 'recalculated' to 231.4 Ma by Irmis and Mundil (2008).

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

The tetrapod assemblage of the Caturrita Formation, which overlies the Santa Maria Formation, includes a mastodonsauroid amphibian, the sphenodont *Clevosaurus*, the rhynchosaur *Hyperodapedon*, the proterochampsid *Proterochampsa*, the dinosaurs *Guabisaurus* and *Saccasaurus*, a phytosaur, the cynodonts *Exaeretodon* and *Riograndia*, the dicynodont *Ischigualastia* (= *Jachaleria*) and cynodonts (Araújo & Gonzaga 1980; Barbarena *et al.* 1985; Dornelles 1990; Bonaparte *et al.* 1999, 2001; Kischlat & Lucas 2003; Ferigolo & Langer 2006; Bonaparte & Sues 2006; Bonaparte *et al.* 2007; Langer *et al.* 2007; Dias-da-Silva *et al.* 2009).

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

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

In western Madagascar, the Isalo group ('Groupe d l'Isalo' of Besarie 1930; also see Besarie & Collignon 1960, 1971) has long been divided into Isalo I, Isalo II and Isalo III based on perceived geological age. The Isalo II strata yield Late Triassic tetrapods, including metoposaurs, sphenodontids, phytosaurs, the rhynchosaur *Hyperodapedon*, the aetosaur *Desmatosuchus*, the archosaur *Azendohsaurus*, cynodonts and dicynodonts (Guth 1963; Westphal 1970; Dutuit 1978; Buffetaut 1983; Flynn *et al.* 1999, 2000, 2008; Langer *et al.* 2000*a*; Lucas *et al.* 2002*a*; Burmeister *et al.* 2006). The stratigraphic range of the Isalo II tetrapods is *c.* 1200 m, but the rhynchosaur *Hyperodapedon* is one of the stratigraphically lowest taxa in the assemblage. This means the Isalo assemblage is no older than Otischalkian and, based on the *Desmatosuchus* record, likely to be Adamanian.

Comments. Lucas (1998*a*) listed as Adamanian index fossils the rhynchosaur *Scaphonyx*, the aetosaur *Stagonolepis* and *Rutiodon*-grade phytosaurs (including *Leptosuchus* and *Smilosuchus*). The dicynodont *Ischigualastia* (= *Jachaleria*) was also considered an Adamanian index taxon. Taxonomic revisions and range extensions have necessitated a reconsideration of some of these index taxa.

Stagonolepis now co-occurs with *Parasuchus* at Krasiejów in southern Poland (Dzik 2001; Lucas *et al.* 2007*d*). This lends support to Heckert & Lucas' (2000) conclusion that *Ebrachosaurus singularis* Kuhn 1936, from the Adamanian German Blasensandstein (type destroyed in World War II), was based on specimens of *Stagonolepis*. These European Adamanian records of *Stagonolepis* are consistent with regarding its stratigraphically lowest records in North America, such as at the *Placerias*/Downs quarries in Arizona, as early Adamanian (Lucas *et al.* 1997*a*).

An extensive revision of Late Triassic rhynchosaurs (Langer & Schultz 2000; Langer *et al.* 2000*a*, *b*) indicates that specimens previously assigned to *Scaphonyx* are mostly of *Hyperodapedon*. Lucas *et al.* (2002*a*) reviewed these records in detail and demonstrated that a *Hyperodapedon* biochron is of Otischalkian and Adamanian age (Fig. 8). Thus, the rhynchosaur *Hyperodapedon* cannot be used to discriminate the Otischalkian and Adamanian.

Largely based on this, Langer (2005*a*, *b*; also see Schultz 2005) claimed that the Otischalkian and Adamanian cannot be distinguished and they should be abandoned and replaced by a single LVF, the Ischigualastian. To do so, Langer (2005*b*) dismissed phytosaur-based distinctions of the Otischalkian and Adamanian, basing his rejection largely on the cladotaxonomy of primitive phytosaurs advocated in published abstracts by Hungerbühler (2001*a*; Hungerbühler & Chatterjee 2002). Langer (2005*b*) also rejected aetosaur-based correlations based on the taxonomy of South American aetosaurs published by Heckert & Lucas (2000) and Lucas & Heckert (2001). Thus, Langer (2005*b*, p. 228) states that '*Stagonolepis wellesi* lacks a unique ornamentation pattern of its dorsal paramedian osteoderms', contrary to the published work of Lucas & Heckert, as well as those of Long & Ballew (1985), Parrish (1994), Long & Murry (1995) and Parker (2007), among others.

Langer (2005*b*) also used the conclusions of Sulej (2002) regarding the taxonomy of *Metoposaurus* and *Buettneria* to question using amphibians to distinguish the Otischalkian and Adamanian. However, a review of the metoposaur specimens described by Sulej (2002) does not support some of his basic anatomical observations or his taxonomy (Lucas *et al.* 2007*d*). Rayfield *et al.* (2005, 2009) also argued for merging of the Otischalkian and Adamanian based largely on the same arguments as Langer (2005*b*), but Lucas *et al.* (2007*e*) have presented a detailed refutation of their arguments.

What these workers have failed to recognize is that: (1) Otischalkian and Adamanian tetrapod assemblages are stratigraphically superposed and readily distinguished in the Chinle Group of the American Southwest; (2) there is no evidence that the 'Ischigualastian' of South America is Otischalkian and much more evidence that it is Adamanian, so Ischigualastian should not be redefined to encompass both Otischalkian and Adamanian time; and (3) recognition of distinct Otischalkian and/or Adamanian assemblages has been achieved in North America, South America, Europe, India and North Africa (e.g. Fig. 8). The fact that Langer (2005*b*) and Rayfield *et al.* (2005, 2009) do not accept a well-documented alpha taxonomy of Otischalkian and Adamanian index fossils is not a valid reason to merge the Otischalkian and Adamanian LVFs.

Recent work in the Chinle Group of the western USA has refined the stratigraphic ranges of known tetrapod taxa and has produced new records in strata of Adamanian age. These new data are principally from the Petrified Forest National Park in Arizona (Heckert & Lucas 2002*a*; Hunt *et al.* 2002; Woody 2003, 2006; Heckert 2004; Woody & Parker 2004; Heckert *et al.* 2005*a*) and the extensive exposures of the Chinle Group in east–central New Mexico (Lucas *et al.* 2001, 2002*b*), though there are also other new records from the Tecovas and Trujillo formations in Texas (Heckert 2004; Heckert *et al.* 2006; Martz & Small 2006). Clearly, there is a 'transitional' fauna between the Adamanian and Revueltian LVFs (Woody & Parker 2004), and this prompted Hunt *et al.* (2005) to subdivide the Adamanian into two subfaunachrons, St. Johnsian (older) and Lamyan (younger), of regional biochronological significance (Fig. 7). The aetosaur *Tecovasuchus* is a St. Johnsian index taxon (Heckert *et al.* 2007*b*), whereas the aetosaur *Typothorax antiquum* is a Lamyan index taxon (Hunt *et al.* 2005).

Heckert & Lucas (2006) built upon the microvertebrate collections documented by Heckert (2001, 2004) to demonstrate that there are multiple microvertebrate index taxa of Adamanian (St. Johnsian) time, including the xenacanth '*Xenacanthus*' *moorei*, the enigmatic tetrapod *Colognathus obscurus* and the archosaurs (possibly ornithischian dinosaurs) *Tecovasaurus murryi*, *Crosbysaurus harrisae*, and *Krzyzanowskisaurus hunti*. So far, these taxa are presently known only from the Chinle Group of the American Southwest, so they may not be of broad biostratigraphic utility.

Revueltian

Definition. The Revueltian is the time interval between the FAD of the aetosaur *Typothorax coccinarum* and the FAD of the phytosaur *Redondasaurus* (Fig. 1). Lucas & Hunt (1993*a*) introduced the term Revueltian LVF to refer to the time equivalent to the vertebrate fossil assemblage of the Bull Canyon Formation in east–central, New Mexico, USA (Lucas *et al.* 1985; Hunt 1994, 2001; Hunt & Lucas 1997). Lucas (1998*a*) termed this the *Pseudopalatus* Assemblage Zone. The name of the LVF is for Revuelto Creek, one of the key collecting areas in eastern New Mexico. Revueltian time begins with the FAD of the aetosaur *T. coccinarum*. The end of the Revueltian is the beginning of the Apachean, which is defined by the FAD of the phytosaur *Redondasaurus*.

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

Index fossils. The following tetrapod taxa are restricted to Revueltian time and are widespread and/or common enough to be useful as index fossils: the crurotarsan *Revueltosaurus*, the aetosaurs *Aetosaurus, Rioarribasuchus* and *Typothorax coccinarum*, and *Pseudopalatus*-grade phytosaurs. The pterosaur *Eudimorphodon* is present in Revueltian assemblages in Italy and Greenland (e.g. Jenkins *et al.* 2001; Dalla Vecchia 2003, 2006) and can also be considered a Revueltian index taxon (but see Dalla Vecchia 2009). The stratigraphic co-occurrence of dinosaurs and dinosauromorphs (Sullivan & Lucas 1999; Ezcurra 2006; Irmis *et al.* 2007; Nesbitt *et al.* 2007, 2009; Spielmann *et al.* 2007*b*; Nesbitt & Chatterjee 2008) also aids in recognition of Revueltian time.

Principal correlatives. Besides Chinle Group assemblages, which are primarily from Texas, New Mexico and Arizona (e.g. Zeigler *et al.* 2003; Heckert *et al.* 2005*a*, *b*; Parker *et al.* 2006; Spielmann *et al.* 2007*a*, *b*; Nesbitt & Stocker 2008), the principal Revueltian tetrapod assemblages are those of the Newark Supergroup of eastern North America of Neshanician and Cliftonian (part) age; Ørsted Dal Member of the Fleming Fjord Formation, Greenland; Stubensandstein (Löwenstein Formation) of the German Keuper; Calcare di Zorzino (Zorzino Limestone) and Dolomia di Forni (Forni Dolomite), northern Italy; and lower part of Dharmaran Formation, India.

In West Texas-eastern New Mexico, the Bull Canyon Formation of the Chinle Group yields extensive assemblages of Revueltian tetrapods, including the characteristic tetrapod assemblage (e.g. Hunt 2001; Lehman & Chatterjee 2005). In the Chama basin of north–central New Mexico, the Petrified Forest Formation of the Chinle Group also yields Revueltian tetrapods, especially from the Snyder and Canjilon phytosaur-dominated bonebeds (Zeigler *et al.* 2003; Heckert *et al.* 2005*b*; Nesbitt & Stocker 2008). In northern Arizona, two Chinle Group units, the Painted Desert Member of the Petrified Forest Formation and the overlying Owl Rock Formation, have produced numerous Revueltian fossils, especially from the Petrified Forest National Park and from localities on Ward's Terrace north of Flagstaff (e.g. Kirby 1989, 1991, 1993; Heckert *et al.* 2005*a*; Spielmann *et al.* 2007*a*).

In eastern North America, the provincial Neshanician LVF is based on a limited fossil assemblage typified by the aetosaur *Aetosaurus arcuatus* (Lucas *et al.*1998*a*; Lucas & Huber 2003). This taxon is present in 'Lithofacies Association II' of the Chatham Group (Durham sub-basin of the Deep River basin), the Newark Basin (range zone: Warford through Neshanic Members of the lower Passaic Formation), and the middle New Haven Arkose of central Connecticut. Other vertebrates from the Neshanician LVF include indeterminate metoposaurid and phytosaur teeth, skull and scute fragments (e.g. '*Belodon validus*'), a rauisuchian, crocodylomorph, traversodontid and a sphenodontid (lower New Haven Arkose) as well as a dominance of the primitive neopterygian *Semionotus* sp. over other fish taxa, a trend also apparent in age-equivalent strata of the Chinle Group and German Keuper (Huber *et al.* 1993*c*; Lucas & Huber 2003).

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

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

In Germany, the best known and most diverse Keuper tetrapod assemblage is that of the Lower Stubensandstein (Löwenstein Formation). This assemblage includes the amphibians *Cyclotosaurus* and *Gerrothorax*, the earliest European turtles (*Proganochelys* and *Proterochersis*), *Pseudopalatus*-grade phytosaurs (*Nicrosaurus*), the aetosaurs *Aetosaurus* and *Paratypothorax*, rauisuchians (*Teratosaurus*), theropod dinosaurs, and the prosauropod dinosaurs *Sellosaurus* and *Thecodontosaurus* (e.g. Benton 1993; Hungerbühler 1998; Lucas 1999; Schoch & Werneburg 1999; Schoch 2007). The phytosaurs, aetosaurs, and rauisuchians provide a strong basis for assigning a Revueltian age to the Lower Stubensandstein (Lucas & Hunt 1993*a*; Hunt 1994; Lucas 1999). The younger, Middle and Upper Stubensandstein, produce a similar, but less diverse assemblage, so I also assign them a Revueltian age. Whether or not the lowest occurrence of *Mystriosuchus* in the Middle Stubensandstein is of biochronologic significance is not clear. The assemblages of the Upper Stubensandstein and Knollenmergel (Trössingen Formation) are almost entirely dinosaurian – 95% or more of the fossils are of dinosaurs (Benton 1986, 1991). This contrasts sharply with the Lower and Middle Stubensandstein assemblages, in which dinosaurs are a much smaller percentage of the fossils collected. However, I regard this change to dinosaur domination as largely a local facies/taphonomic effect, not a biochronologically significant event (Hunt 1991). It seems likely, but not certain, that the Knollenmergel assemblage is of Apachean age (see below).

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

The other Italian Late Triassic tetrapod sites are in the Forni Dolomite (Dolomia di Forni) in the Veneto Prealps of northeastern Italy. They yield the drepanosaurids *Drepanosaurus* and *Megalancosaurus*, and the pterosaurs *Eudimorphodon* and *Preondactylus* (Dalla Vecchia 1995) and a specimen of *Langobardisaurus* under study by S. Renesto (written commun. 2009). The presence of *Eudimorphodon* supports a Revueltian age assignment.

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

Comments. Hunt & Lucas (1993*c*) suggested that, perhaps along the lines of the Cliftonian-Neshanician subdivision used in the Newark Supergroup, the Revueltian merits subdivision, and Hunt (1994, 2001) subdivided it into three sub-LVFs of regional utility. Two of these, the Barrancan (early Revueltian) and Lucianoan (later Revueltian) are readily correlated in the western USA using various index fossils (e.g. Heckert & Lucas 2006).

Some of the discussion of the Revueltian has focused on whether or not it is readily distinguished from the next younger Apachean LVF (Long & Murry 1995; Rayfield *et al.* 2005, 2009). These discussions are rooted in taxonomic arguments, as the type assemblages of the Revueltian and Apachean are stratigraphically superposed in east–central New Mexico, USA and thus are obviously time successive.

Typothorax, *Aetosaurus* and *Pseudopalatus*-grade phytosaurs were listed as Revueltian index fossils by Lucas (1998*a*). However, recognition of an older, Adamanian species of *Typothorax*, *T. antiquum*, by Lucas *et al.* (2002*b*) has modified this; it is the species *T. coccinarum* that is a Revueltian index fossil, and this is part of what prompted Hunt *et al.* (2005) to redefine the beginning of the Revueltian as the FAD of *T. coccinarum*, a decision followed by Lucas *et al.* (2007*e*) and also used here.

Typothorax coccinarum stands as a robust index fossil of the Revueltian across the Chinle Group. Indeed, its likely descent from *T. antiquum* as part of an anagenetic evolutionary lineage (Lucas *et al.* 2002*b*) is significant to the Triassic tetrapod biochronology in that the beginning of a LVF can be defined by a true species-level evolutionary event, not the appearance of a genus-level taxon.

Aetosaurus is one of the most robust index fossils of the Triassic tetrapod timescale (Fig. 9). Lucas *et al.* (1998*b*) presented a detailed taxonomic revision based on study of all North American and European specimens. *Aetosaurus* has a marine record in the middle Norian of northern Italy (Wild 1989), and all of its nonmarine records are Revueltian. Criticism of the use of *Aetosaurus*, typified by Rayfield *et al.* (2005, 2009), is based on the claim that because *Aetosaurus* has been portrayed as the plesiomorphic sister taxon of other aetosaurs in cladistic analyses (e.g. Heckert & Lucas 2000) it 'must' have a long ghost lineage that therefore renders it useless in biostratigraphy. I regard this as specious cladotaxonomic reasoning (Lucas *et al.* 1999*a*, 2007*c*, *e*). Thus, the position of a taxon on a cladogram has nothing to do with its biostratigraphic utility unless all the assumptions of the cladogram – and the existence of a ghost lineage is nothing more than an assumption – are brought into the biostratigraphic analysis. Indeed, an alternative interpretation of the Heckert & Lucas (2000) cladogram of aetosaurs, one that views *Aetosaurus* as a highly derived, dwarfed and simplified form, would produce a very different 'ghost lineage'.

Aetosaurus thus is a taxonomically stable and robust Revueltian index fossil (e.g. Fraas 1877; Huene 1921; Walker 1961; Wild 1989; Parrish 1994; Heckert *et al.* 1996, 2007*a*; Heckert & Lucas 1998; Small 1998; Lucas *et al.* 1998*b*, 1999*a*; Heckert & Lucas 2000; Parker 2007). *Pseudopalatus*-grade phytosaurs include *Pseudopalatus*, *Nicrosaurus* and *Mystriosuchus*, all taxa restricted to Revueltian time. Like the use of *Rutiodon*-grade phytosaurs to identify the Adamanian, this is a convenient and concise way to refer to a group of broadly contemporaneous phytosaur taxa whose stratigraphic ranges are well established, but whose genus- and species-level nomenclature remain in flux (compare, e.g. the differing phytosaur taxonomies of Ballew 1989; Hunt 1994; Long & Murry 1995; and Hungerbühler 2002).

Heckert & Lucas (1997) suggested that *Revueltosaurus* might serve as an index taxon of Revueltian time. At that time *Revueltosaurus*, which was known solely from teeth, was considered to be an ornithischian dinosaur. Parker *et al.* (2005) documented associated skulls and postcrania of *Revueltosaurus callenderi*, demonstrating that that taxon is actually a crurotarsan archosaur. However, they noted that, following Hunt (1989), Padian (1990) and others, the teeth are indeed diagnostic, and the taxon is valid. Heckert & Lucas (2006) then showed that in the Chinle Group *Revuletosaurus* is restricted to strata of Revueltian age.

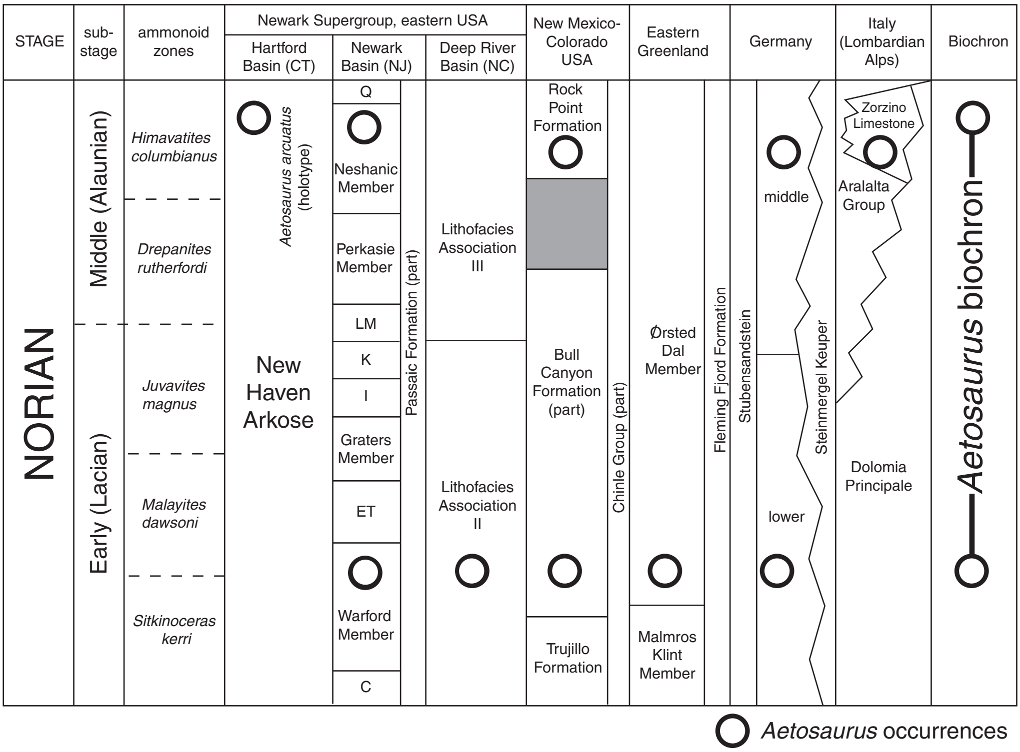


Fig. 9. Global correlation of *Aetosaurus* localities, which identify an *Aetosaurus* biochron of Revueltian age.

This demonstrates the irrelevance of the assumed position of a taxon in a phylogeny to biostratigraphy. The changing phylogenetic position of *Revueltosaurus* alters neither its biostratigraphic significance nor its biochronological utility. What is biostratigraphically important about *Revueltosaurus* is that it is distinctive (easily identified), relatively common and/or widespread, and known from a restricted stratigraphic interval. Whether it is an ornithischian (as previously supposed) or a crurotarsan (the current phylogenetic hypothesis) is irrelevant to its biostratigraphic and biochronological utility.

Apachean

Definition. The Apachean LVF is the time interval between the FAD of the phytosaur *Redondasaurus* and the FAD of the crocodylomorph *Protosuchus* (Fig. 1). Lucas & Hunt (1993*a*) introduced the term Apachean LVF to refer to the time equivalent to the vertebrate fossil assemblage of the Redonda Formation (Chinle Group) in east–central New Mexico, USA (Lucas *et al.* 1985; Hunt 1994; Hunt & Lucas 1997; Lucas 1998*a*; Lucas *et al.* 2001; Spielmann *et al.* 2006*a*, *b*). Apachean time begins with the FAD of the phytosaur *Redondasaurus*. The end of Apachean time is the beginning of the Wassonian LVF, which is the FAD of the crocodylomorph *Protosuchus* (Lucas & Huber 2003; Lucas & Tanner 2007*a*, *b*).

Characteristic tetrapod assemblage. The characteristic tetrapod assemblage of the Apachean LVF is from the Redonda Formation of the Chinle Group in Guadalupe and Quay Counties, New Mexico, USA. The following taxa are present: the amphibian *Apachesaurus*, a sphenodontid, a procolophonid, the phytosaur *Redondasaurus*, the aetosaur *Redondasuchus*, the rauisuchian *Redondavenator*, the sphenosuchian *Vancleavea*, a rauisuchian, theropod dinosaurs and a ?cynodont (e.g. Hunt 1994; Hunt & Lucas 1993*b*, 1997; Heckert *et al.* 2001; Hunt *et al.* 2005; Spielmann *et al.* 2006*a*, *b*).

Index fossils. The following tetrapod genera are restricted to Apachean time and are widespread and/or common enough to be useful as index fossils: the phytosaur *Redondasaurus*, the aetosaur *Redondasuchus* and the dinosaur *Riojasaurus.*

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

At Ghost Ranch in New Mexico, the Whitaker quarry bone bed is dominated by skeletons of the theropod dinosaur *Coelophysis bauri* (Colbert 1989). Nevertheless, it also includes the sphenodont *Whitakersaurus*, at least one drepanosaur, a rauisuchian skeleton (cf. *Postosuchus*), the sphenosuchians *Hesperosuchus* and *Vancleavea*, the chatterjeeid *Shuvosaurus* (= *Effigia*) and the phytosaur *Redondasaurus* (e.g. Hunt & Lucas 1993*b*; Clark *et al.* 2000; Harris & Downs 2002; Hungerbühler 2002; Hunt *et al.* 2002; Lucas *et al.* 2003; Rinehart *et al.* 2004; Nesbitt 2007; Lucas *et al.* 2005, 2007*e*; Heckert *et al.* 2008; Renesto *et al.* 2009).

In Argentina, the Los Colorados Formation consists of siliciclastic red beds approximately 800 m thick. Near its base, a single tetrapod fossil – a dicynodont skull, the holotype of '*Jachaleria*' *colorata* Bonaparte 1970 – was collected. The remainder of the tetrapod fossils from the Los Colorados Formation are from its middle and upper parts but have not been stratigraphically organized. The assemblage includes the turtle *Palaeochersis*, the ornithosuchid *Riojasuchus*, the aetosaur *Neoaetosauroides*, the rauisuchid *Fasolasuchus*, the crocodylomorphs *Hemiprotosuchus* and *Pseudhesperosuchus*, the prosauropod dinosaurs *Riojasaurus* and *Coloradisaurus*, the theropod dinosaur *Zupaysaurus* and the tritheledontid cynodont *Chaliminia* (e.g. Bonaparte 1970, 1971, 1978, 1980, 1997; Lucas & Hunt 1994; Rougier *et al.* 1995; Arcucci *et al.* 2004). The correlative Quebrada del Barro and El Tranquilo formations also produce prosauropods (e.g. *Riojasaurus*, '*Mussaurus*') (Casamiquela 1980; Bonaparte & Vince 1979; Bonaparte & Pumares 1995). The Los Colorados assemblage clearly is of Late Triassic age (Arcucci *et al.* 2004) and must be post-Ischigualastian. However, its endemism makes it difficult to correlate precisely. I tentatively consider it an Apachean correlative based primarily on its abundant prosauropods.

The age of the tetrapod assemblage from the Lower Elliott Formation in South Africa has long been considered Late Triassic. Lucas & Hancox (2001) reviewed the age of this assemblage, which is dominated by sauropodomorph dinosaurs, but also has rare amphibians (a large chigutisaurid), a possible rauisuchian (*Basutodon*), the ornithischian dinosaur *Eocursor*, a traversodontid (*Scalenodontoides*) and the characteristic Late Triassic footprint ichnogenus *Brachychirotherium* (Kitching & Raath 1984; Lucas & Hancox 2001; Butler *et al.* 2007). This is the '*Euskelosaurus* range zone' of Kitching & Raath (1984), the youngest Triassic tetrapod assemblage in the Karoo basin. Yates (2003) re-evaluated the prosauropods of the Lower Elliott Formation and concluded that most are indeterminate sauropodomorphs or basal sauropods. He noted similarities of indeterminate prosauropods from the Lower Elliott Formation to *Riojasaurus* from the Los Colorados Formation of Argentina, and similarities between the basal sauropod *Antetonitrus* from South Africa and *Lessemsaurus* from Argentina (Yates & Kitching 2003). These conclusions suggest a Lower Elliott–Los Colorados correlation, and thus a tentative Apachean age assignment.

In the United Kingdom, fissure fills such as Durdham Down in Clifton yield fossils that include phytosaurs, aetosaurs, dinosauriforms and dinosaurs (e.g. Fraser 1994; Fraser *et al.* 2002; Galton 2005, 2007*a*, *b*; Whiteside & Marshall 2008). Unfortunately, other than a tentative record of *Aetosaurus* based on a single osteoderm (Lucas *et al.* 1999*b*), the fissure fill tetrapods are mostly endemic taxa of no biochronological significance or cosmopolitan taxa with long age ranges, such as the sphenodontian *Clevosaurus*. Recently, Whiteside & Marshall (2008), based primarily on the palynoflora, assigned the Tytherington fissure fill a Rhaetian age, and extrapolated this age to the other fissures. If this Rhaetian age is correct, then the fissure fill tetrapods are of Apachean age. However, as Lucas & Hunt (1994, p. 340) noted, 'a single age should not necessarily be assigned to the fossils from one fissure and . . . . individual fossils from the fissures may range in age from middle Carnian to Sinemurian'. Therefore, I continue to regard as problematic the precise age of the Triassic tetrapod assemblages from the British fissure fills.

Comments. The Apachean is the most difficult Triassic LVF to correlate globally. This almost certainly reflects a provincialization of the global tetrapod fauna near the end of the Triassic. Some of the apparent endemism of Apachean land-vertebrate assemblages may also be due to facies, sampling and taphonomic biases. Thus, rather than recognize a global Apachean LVF, it may ultimately be necessary to recognize two or more provincial LVFs during this time interval.

There is no evidence that any part of the Apachean is of Jurassic age. The FAD of the crocodylomorph *Protosuchus*, which defines the beginning of the next LVF, the Wassonian, appears to correspond closely to the beginning of the Jurassic (Lucas & Tanner 2007*a*, *b*). Thus, *Protosuchus* occurs in units assigned an Early Jurassic based on diverse evidence: the McCoy Brook Formation (Newark Supergroup), the upper Stormberg Group of South Africa and the upper part of the Dinosaur Canyon Member of the Moenave Formation in Utah-Arizona (Colbert & Mook 1951; Sues *et al.* 1996; Lucas *et al.* 2005; Lucas & Tanner 2007*a*, *b*). The Moenave record of *Protosuchus* is stratigraphically superposed above Apachean body fossil assemblages of the uppermost Chinle Group (Lucas *et al.* 1997*b*, 2005; Lucas & Tanner 2007*a*, *b*). Furthermore, it is correlative to the Lower Jurassic conchostracan assemblages from the Whitmore Point Member of the Moenave Formation (Lucas & Tanner 2007*a*; Kozur & Weems 2010). Relatively recent recognition that Apachean-age strata extend above the Chinle Group into part of the Moenave–Wingate (lower Glen Canyon Group) lithosome has been based, in part, on the occurrence of a *Redondasaurus* skull in the lower part of the Wingate Sandstone in southeastern Utah (Lucas *et al.* 1997*b*; Lucas & Tanner 2007*a*, *b*). (Note that Spielmann *et al.* 2007*a*, fig. 8A–B illustrated a cast of this skull and mistakenly attributed it to the Revueltian Owl Rock Formation).

Lucas (1998*a*) listed three Apachean index fossils: the aetosaur *Redondasuchus*, the phytosaur *Redondasaurus* and the dinosaur *Riojasaurus. Riojasaurus* is known from Argentina and may be present in the Lower Elliott Formation in South Africa. The Apachean is readily distinguished in North America by its primary index fossils, *Redondasaurus* and *Redondasuchus*. However, some workers (Long & Murry 1995; Martz 2002) have questioned the validity of *Redondasaurus* and *Redondasuchus*, proclaiming the former a synonym of *Pseudopalatus* and the latter a synonym of *Typothorax.* Nevertheless, Heckert *et al.* (2001) and Spielmann *et al.* (2006*a*, *b*) reaffirmed the distinctiveness and validity of *Redondasuchus* and *Redondasaurus*, and Hungerbühler (2002) also recognized *Redondasaurus* as distinct from *Pseudopalatus*.

Correlation of the LVFs to the Marine SGCS

Introduction

Records of nonmarine Triassic tetrapods in marine strata (Lucas & Heckert 2000), palynostratigraphy, magnetostratigraphy and radioisotopic ages provide some basis for correlation of the LVFs to the standard global chronostratigraphic scale (Fig. 10). Nevertheless, reliable data for this correlation remain relatively sparse, so the correlation of the LVFs to the SGCS is still imprecise in many time intervals.

Lootsbergian

The base of the Triassic (= Permo-Triassic boundary [PTB], = base of Induan Stage) has been formally defined by the FAD of the conodont *Hindeodus parvus* at a global stratotype section and point (GSSP) located at Meishan in southern China (Yin *et al.* 2001). This means it is possible to attempt to correlate a potential Triassic base in the nonmarine section to a fixed, agreed-upon point in the marine timescale.

It is important to ask how the Lootsbergian correlates to the marine PTB in order to establish the synchrony or diachroneity of marine and nonmarine events across the PTB. However, such correlation is not simple, because no sections are known where strata bearing terrestrial tetrapods can be directly correlated (say by interfingering lithostratigraphy) to the marine record across the PTB. Thus, magnetostratigraphy, isotope stratigraphy, conchostracan biostratigraphy and palynostratigraphy have been used to correlate the nonmarine and marine records across the PTB. Lucas (2009) provides a detailed discussion of this correlation, which is briefly reviewed here.

There is a well documented negative $\delta^{13}C$ excursion at the PTB in marine sections that closely coincides with the major extinction that precedes the formally-defined PTB (e.g. Payne *et al.* 2004; Yin *et al.* 2005, 2007; Richoz 2006). Diverse analyses indicate that the marine PTB is within the lower third of a long normal-polarity chron (e.g. Ogg 2004; Steiner 2006; Hounslow & Muttoni 2010). Palynostratigraphy has also been used by some to correlate marine to nonmarine sections at the PTB (e.g. Morante 1996; Looy *et al.* 1999, 2001; Twitchett *et al.* 2001; Collinson *et al.* 2006), particularly the fungal abundance spike documented in marine and nonmarine sections that some have considered to correspond to the PTB marine mass extinction (e.g. Eshet *et al.* 1995; Visscher *et al.* 1996; Steiner *et al.* 2003).

In the conchostracan biostratigraphy, which is well correlated with the marine scale, the PTB coincides with the boundary between the *Falsisca postera* Zone and the *Falsisca verchojanica* Zone (Kozur 1998*a*, *b*, 1999; Bachmann & Kozur 2004; Kozur & Weems 2010). As in the marine section, this conchostracan zonal boundary lies in the lower third of a long normal magnetostratigaphic zone that straddles the PTB, and it is characterized by a minimum in $\delta^{13}C$ in continental beds (Bachmann &

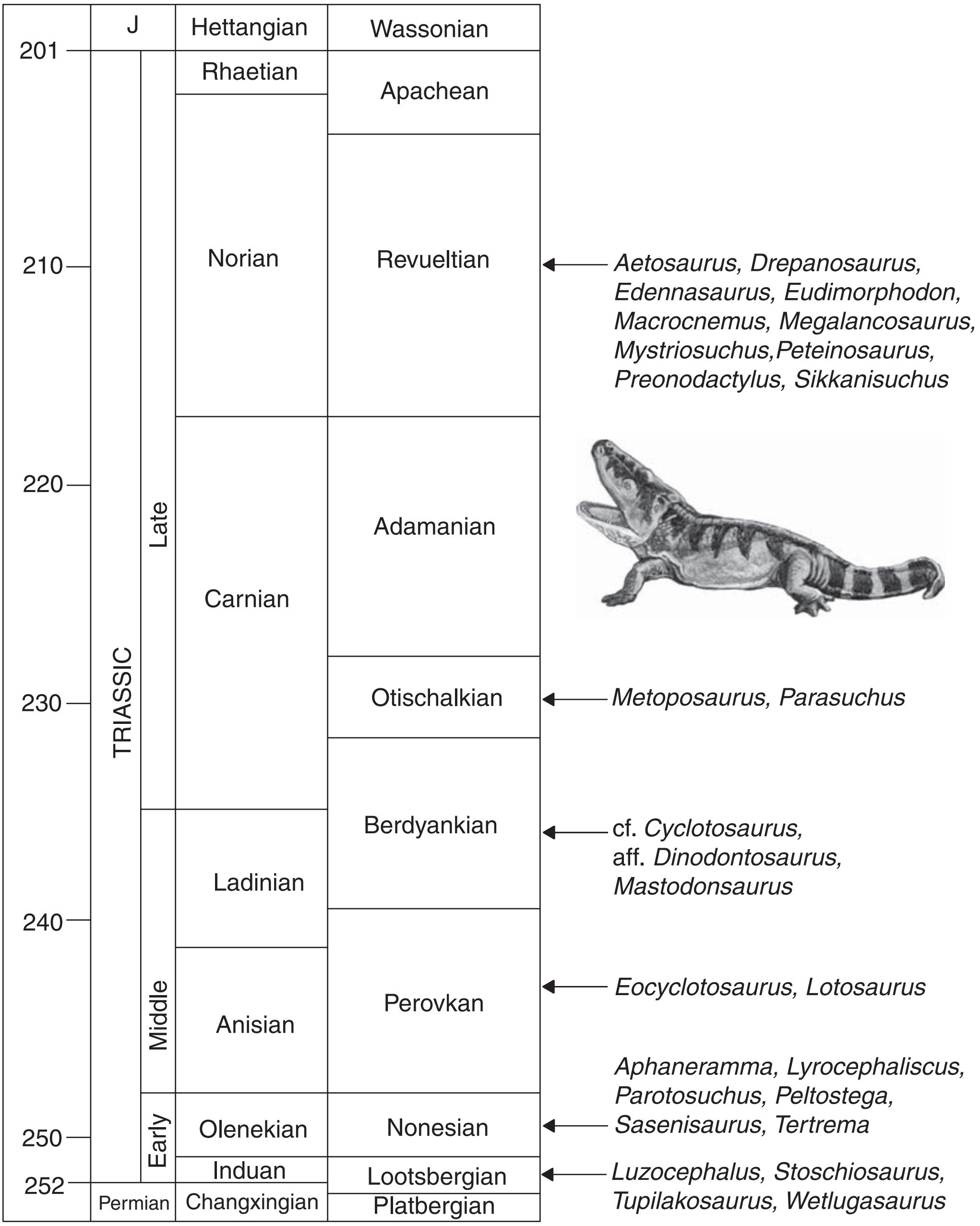


Fig. 10. Marine records of Triassic nonmarine tetrapod correlated to the marine SGCS and the Triassic land–vertebrate faunachrons. See Lucas & Heckert (2000) for details. Restoration of *Eocyclotosaurus* by Matt Celeskey.

Kozur 2004; Korte & Kozur 2005*b*). This minimum in $\delta^{13}C$ occurs in continental lakes without facies changes, and the conchostracan boundary occurs in the Dalongkou section in northwestern China close to the HO of *Dicynodon* (Kozur 1998*a*, *b*; Metcalfe *et al.* 2009; Kozur & Weems 2010).

At the Meishan section in southern China, a sharp drop in $\delta^{13}C$ values coincides with the maximum amount of marine extinction, and this mass extinction and carbon isotope excursion are older than the PTB defined by the lowest occurrence of the conodont *Hindeodus parvus* (Fig. 11).

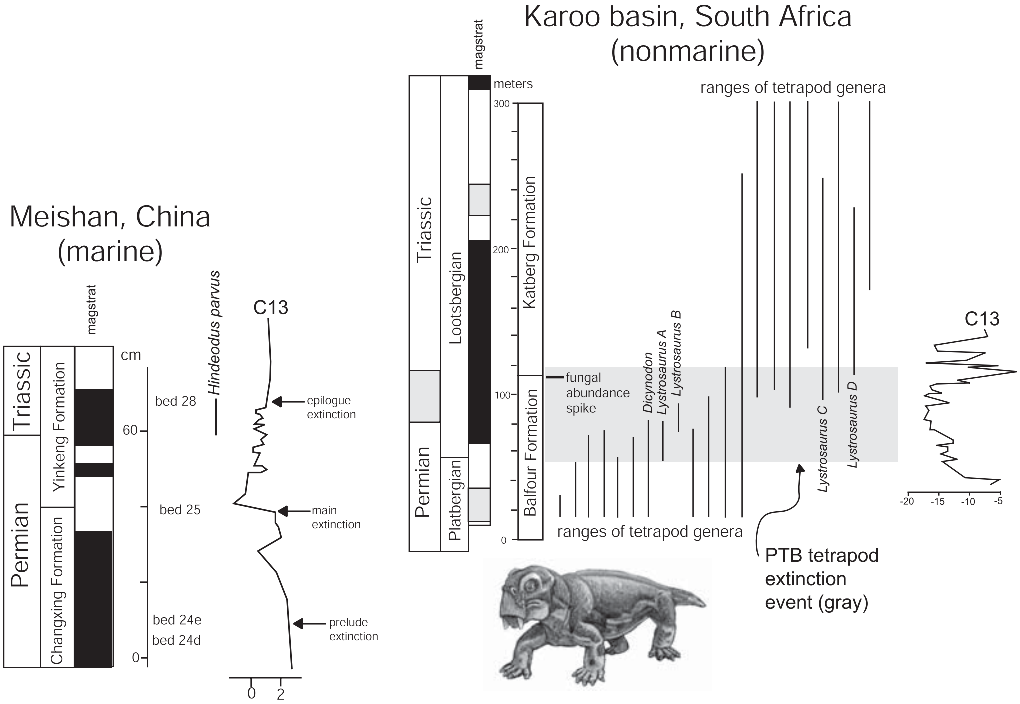


Fig. 11. Magnetostratigraphic correlation of marine PTB section at Meishan, China (based on Yin *et al.* 2005) to PTB tetrapod extinction interval in Karoo basin of South Africa (based on Ward *et al.* 2005). The sections are correlated at the base of the normal polarity magnetozone that encompasses the PTB. However, they are not scaled to each other based on time intervals or section thickness, so the only certain point of correlation indicated is the base of the normal polarity magnetozone that encompasses the PTB. From Lucas (2009). Restoration of *Lystrosaurus* by Matt Celeskey.

However, in sections without a weathered boundary clay (e.g. Shahreza, Iran, and Gerenavár, Bükk Mts, Hungary) or without a boundary clay, the δ^{13}C minimum lies around the FAD of *H. parvus*, at the PTB (Korte & Kozur 2005*a*). In the Karoo basin of South Africa, δ^{13}C isotope data through the PTB have been used to correlate to the marine δ^{13}C excursion (MacLeod *et al.* 2000; Ward *et al.* 2005). However, these isotope data do not convincingly support the conclusion that the highest occurrence of *Dicynodon* in the Karoo basin is equivalent to the PTB. Indeed, Tabor *et al.* (2007) recently published an analysis of δ^{13}C across the PTB in the Karoo basin and argued that changes in that record are driven by local facies changes and are not a reflection of atmospheric carbon values. Therefore, the δ^{13}C record in the Karoo basin cannot be reliably correlated to the δ^{13}C record in marine strata across the PTB. However, at Dalongkou in northwestern China the HO of *Dicynodon* is close to the PTB defined and correlated to the marine scale by conchostracans. Therefore, the minimum in δ^{13}C in the Karoo basin may be a primary signal, and the HO of *Dicynodon* is close to the PTB.

The PTB marine extinction took place during a relatively long interval of normal magnetic polarity that straddles the PTB, well documented in a variety of marine sections (Ogg 2004; Steiner 2006) as well as in continental sections (Szurlies 2004; Bachmann & Kozur 2004). In the Karoo basin there is an interval of normal polarity that encompasses the highest occurrence of *Dicynodon* and is part of the stratigraphically thick (*c.* 60 m) interval of low δ^{13}C values (Schwindt *et al.* 2003; De Kock & Kirschvink 2004; Ward *et al.* 2005; Steiner 2006) (Fig. 11). These magnetostratigraphic data indicate that the lowest occurrence of *Lystrosaurus* (in an interval of reversed polarity) is older than the PTB (as already suggested by King & Jenkins 1997; Kozur 1998*a*, *b*; and Botha & Smith 2007, among others), and that the highest occurrence of *Dicynodon* is closer to the PTB (Fig. 11).

I favour the magnetostratigraphic correlation of the Meishan and Karoo sections, and it is consistent with all other available correlation data. The correlation indicates that in the Karoo basin the base of the Lootsbergian (LO of *Lystrosaurus*) pre-dates the main marine extinction event. The LO of

Lystrosaurus cannot be used to place the PTB in nonmarine sections; the highest occurrence of *Dicynodon* is a much better proxy for the PTB.

Thus, the earliest Lootsbergian is of latest Permian (Changshingian) age. Correlation of the rest of the Lootsbergian to at least part of the marine Induan Stage is clear (Lucas 1998*a*; Lucas *et al.* 2007*e*). However, whether the Lootsbergian equates to part, all or more than Induan time is not possible to determine with the available data. The Wordy Creek Formation in eastern Greenland has a record of Lootsbergian amphibians interbedded with marine late Griesbachian–early Dienerian (middle Induan) age strata. Thus, the stratigraphically lowest record of *Luzocephalus* here is in the *Ophiceras commune* ammonite zone, and the genus extends up through the '*Proptychites rosenkrantzi* Zone'. Most of the Wordy Creek Formation amphibians come from the younger '*Anodontophora fassarensis* beds', which are the youngest Lower Triassic strata in this section (Nielsen 1935; Säve-Söderbergh 1935). This indicates a range of *Luzocephalus* from late Griesbachian through early Dienerian (middle Induan), but the other temnospondyl taxa are of middle or late Dienerian (late Induan) age (Trümpy 1961; Silberling & Tozer 1968; Tozer 1994). *Luzocephalus*, *Tupilakosaurus*, and *Wetlugasaurus* occur in the Vokhmian Horizon of the Vetlugian Series of the Russian Urals. This fauna includes *Lystrosaurus*, an index taxon of the Lootsbergian land–vertebrate faunachron, so the amphibian records from Greenland establish a middle–late Induan age for at least part of Lootsbergian time.

In northwestern Madagascar the upper part of the marine Andavakoera Formation (Dienerian) yields a diverse assemblage of temnospondyls: ?*Benthosuchus*, ?*Wetlugasaurus*, *Mahavisaurus*, *Aphaneramma*, *Ifasaurus*, *Tertrema*, *Tertremoides*, *Trematosaurus*, *Wantzosaurus* and *Deltacephalus* (Swinton 1956; Lehman 1961, 1966, 1979). The *Benthosuchus* and *Wetlugasaurus* identifications are not reliable (Cosgriff 1984; Damiani 2001), though the amphibians from the Andavakoera Formation may be of Lootsbergian age. This may indicate correlation of part of the Lootsbergian and the Dienerian.

Shishkin (2000, p. 65) asserted that the Lootsbergian includes assemblages younger than Induan, but no credible data support his claim. For example, he stated (p. 65) that 'the Hesshanggou assemblage of China [which Lucas 1998*a* assigned a Lootsbergian age] ... is actually latest Spathian or Spathian–Anisian in age'. However, there is no direct way to correlate Hesshanggou Formation red beds in Shanxi (long correlated by Chinese workers to the '*Procolophon* zone' of the Karoo: Cheng 1981) to the SGCS (Lucas 1993*a*, 1998*a*, 2001; Lucas *et al.* 2007*e*). In another case, Damiani *et al.* (2000) reported a generically-indeterminate trematosaurid jaw from the South African Lootsbergian strata and claimed it extends Lootsbergian time up to the late Olenekian, largely because of its resemblance to Olenekian *Trematosaurus*. An equally likely possibility is that Damiani *et al.* (2000) simply documented an Induan-age trematosaurid. Thus, the possibility exists that Lootsbergian time is as young as early Olenekian, but no reliable data are known to support a Lootsbergian–Olenekian correlation.

Nonesian

Cross correlation of the Nonesian to at least part of the Olenekian is clear because of the occurrence of the Nonesian index temnospondyl *Parotosuchus* in marine upper Olenekian (Spathian) strata in the Mangyshlak Peninsula of western Kazakstan. Thus, from Mangyshlak, Lozovsky & Shishkin (1974) documented *Parotosuchus sequester* from marine upper Olenekian (Spathian) strata that yield *Tirolites* and other ammonites. *Parotosuchus* is an index taxon of Nonesian time, and the Kazak record thus provides a direct Nonesian-late Olenekian correlation. Furthermore, a Spathian conchostracan fauna of the Germanic Basin in the Hardegsen Formation (with *Parotosuchus*) is well correlated with marine beds in Hungary (with Spathian ammonoids) and northern Siberia (Kozur & Weems 2010).

In the western USA, the Nonesian Torrey Formation of the Moenkopi Group overlies the early Olenekian (Smithian) ammonite-bearing Sinbad Formation, whereas the Nonesian Wupatki Member of the Moenkopi Formation is clearly younger than the late Olenekian (Spathian) Virgin Limestone (e.g. McKee 1954; Blakey 1974; Morales 1987; Steiner *et al.* 1993; Lucas & Schoch 2002; Goodspeed & Lucas 2007; Lucas *et al.* 2007*a*). This suggests a Smithian–Spathian (Olenekian) age for the Moenkopi Nonesian tetrapods, and supports a broad Nonesian–Olenekian correlation.

The Sticky Keep Formation in Svalbard yields amphibians that co-occur here with early Olenekian (Smithian) ammonites (Buchanen *et al.* 1965; Tozer 1967). The amphibians are: *Sasenisaurus*, *Peltostega*, *Aphaneramma*, *Lyrocephaliscus*, *Teretrema* and *Boreaosaurus* (Wiman 1910, 1915; Nilsson 1942, 1943; Cox & Smith 1973). These trematosaurs are believed to have been euryhaline amphibians that may have actually lived in marine environments. They also reflect a high diversity and abundance of trematosaurs characteristic of the Nonesian. However, the Svalbard trematosaur taxa are mostly endemic and thus only provide stage-of-evolution evidence for an Olenekian–Nonesian cross-correlation.

Perovkan

A fairly direct correlation can be made of some Perovkan tetrapod assemblages to the SGCS (Lucas & Schoch 2002). Thus, strata of the Röt Formation (Upper Buntsandstein) in southwestern Germany–eastern France are lower Anisian marginal marine to interbedded nonmarine/marine facies of well-established age because of their close physical relationship to the Lower Muschelkalk. Indeed, marine facies of the lower Röt contain early Anisian conodonts, the early Anisian (Aegean) ammonoid *Beneckeia tenuis* and age-diagnostic holothurian sclerites (e.g. Kozur 1993), and magnetostratigraphic correlation of the Röt Formation to marine magnetostratigraphy indicates an early Anisian age (Szurlies 2007; Hounslow *et al.* 2008). Furthermore, conchostracans of the Röt correlate with Aegean and lower Bithynian marine intercalations (Kozur & Weems 2010). The common amphibian from the Röt Formation, *Eocyclotosaurus*, is an index taxon of the Perovkan found in both Europe and the western United States (e.g. Ortlam 1970; Morales 1987; Lucas & Schoch 2002). The Röt records of *Eocyclotosaurus* thus provide a Perovkan–early Anisian correlation.

The Gogolin Formation (lowermost Muschelkalk) in Polish Silesia yields fragmentary temnospondyl and archosaur fossils that include the types of *Mentosaurus waltheri*, *Eurycervix posthumus*, and '*Xestorrhytias perrini*', all of which are indeterminate mastodonsaurids, and the rauisuchian *Zanclodon silesiacus* Jaekel, based on a single tooth. Ammonite biostratigraphy places the Gogolin Formation in the lower Anisian (e.g. Kaim & Niedźwiedzki 1999). The tetrapod material, however, is too fragmentary to be of much biochronological utility. Nevertheless, the available material closely resembles some of the tetrapods from the Upper Buntsandstein (Röt Formation) of southwestern Germany–eastern France, and thus supports a Perovkan–early Anisian correlation.

Magentostratigraphic correlation of the Perovkan Otter Sandstone in Great Britain indicates it is of late Anisian age (Hounslow & McIntosh 2003). Abdala *et al.* (2005) assigned the Perovkan *Cynognathus* zone C in the Karoo basin to the late Anisian based largely on the palynological content of its probable correlatives, such as the Wianamatta Group in the Sydney basin of Australia. Thus, there is good evidence that the Perovkan is equivalent to most of Anisian time.

Berdyankian

The German section provides the best data for a Berdyankian–Ladinian correlation. Thus, the Berdyankian taxon *Mastodonsaurus giganteus* ranges from the Upper Muschelkalk through the Lettenkeuper, strata of late Ladinian (Longobardian) age (Schoch 1999).

The lower Ladinian Partnach Formation of western Austria yielded a temnospondyl jaw fragment that Sander & Meyer (1991) identified as cf. *Cyclotosaurus* sp. However, this specimen could just as well belong to *Mastodonsaurus* (cf. Schoch 1999), so it is of limited biochronological significance.

Stur (1873) reported ?*Mastodonsaurus giganteus* from the Lunz Sandstone in the Austrian Alps. This is an early Carnian (Julian) record, broadly correlative to the German Schilfsandstein. However, I have examined the material Stur described, and it is not diagnostic of *M. giganteus*; it could just as well belong to *Cyclotosaurus*. Therefore, this record also is of limited biochronologic significance.

The Brazilian and Argentinian *Dinodontosaurus* assemblages are unambiguously correlated to each other, and have generally been considered Ladinian based on flimsy palynostratigraphic evidence (Lucas & Harris 1996; Lucas 2002). Tetrapod evidence to correlate the *Dinodontosaurus* assemblages to the European Berdyankian is also not robust; it consists of fragmentary remains of *Dinodontosaurus*-grade and *Stahleckeria*-grade dicynodonts from the German Muschelkalk and Russian Bukobay Formation, respectively, not on shared alpha taxa (Lucas & Wild 1995; Lucas 1998*a*; Lucas *et al.* 2007*b*). At present, this South American–European correlation remains weakly supported and merits further study. This is one area where magnetostratigraphy (in South America) will be of assistance.

Thus, all available robust data for correlating the Berdyankian to the SGCS indicate that it is equivalent to the late Ladinian. This may indicate that there is a global gap equivalent to the early Ladinian in the Triassic tetrapod record.

Otischalkian

There are two records of Otischalkian tetrapod index taxa in marine strata in Austria that support an Otischalkian–Carnian correlation:

1. Raibler Schichten, Austria: Koken (1913) described *Metoposaurus santaecrucis* from a conglomeratic sandstone in the upper part of the Raibler Schichten. This is an early Carnian (Julian) record, and thus correlates part of the Otischalkian (index taxon = *Metoposaurus*) to the early Carnian.

2. Opponitzer Schichten, Austria: Huene (1939) described a skull fragment of the phytosaur *Parasuchus* (= *Francosuchus*) from the lower part of the Opponitzer Schichten (Kalk) near Lunz, Austria. The occurrence is of late Carnian (Tuvalian) age (Janoscheck & Matura 1980), but it cannot be tied

precisely to a particular ammonite zone (Hunt & Lucas 1991).

In Germany, Otischalkian tetrapods from the Schilfsandstein are as old as early Carnian (late Julian). Palynostratigraphy assigns a late Carnian age to the lower Chinle Group, including the strata of Otischalkian age, and an early Carnian age to the oldest Sanfordian strata of the Newark Supergroup (Litwin *et al.* 1991, 1993; Cornet 1993). Sequence stratigraphy of the Chinle Group advocated by Lucas (1991, 1993*b*), Lucas & Marzolf (1993) and Lucas & Huber (1994) assigns lower Chinle Group strata to a single sequence, the Shinarump–Blue Mesa sequence. This sequence can be correlated to a late Carnian marine sequence in Nevada (Lupe & Silberling 1985; Lucas & Huber 1994), and recent studies of detrital zircons are consistent with these correlations (Dickinson & Gehrels 2008; Dickinson *et al.* 2009). Magnetostratigraphy correlates lower Chinle Group strata to the late Carnian portion of the Newark Supergroup magnetostratigraphy (Kent *et al.* 1995; Molina-Garza *et al.* 1996; Muttoni *et al.* 2004). Therefore, the Otischalkian clearly is Carnian, equivalent to the early Carnian and part of the late Carnian.

Adamanian

I have long considered the Adamanian to be of late Carnian age based on palynostratigraphy, sequence stratigraphy and magnetostratigraphy (see references cited above under marine cross-correlation of the Otischalkian). In West Texas, Otischalkian and Adamanian tetrapod assemblages are stratigraphically superposed (Lucas 1993*b*; Lucas & Anderson 1993*a*, *b*, 1994, 1995; Lucas *et al.* 1993, 1994). Therefore, Adamanian time is younger than the Otischalkian. Revueltian vertebrates are stratigraphically above Adamanian vertebrates in Arizona, New Mexico and Texas. Therefore, Adamanian vertebrates are either the youngest Carnian vertebrates known or the oldest Norian vertebrates known (or both).

Kozur & Weems (2007, 2010) discussed at length the biostratigraphic evidence to support a late Carnian (Tuvalian) correlation of the Adamanian. This is the concordance of three biostratigraphies – palynostratigraphy, conchostracan biostratigraphy and vertebrate biostratigraphy – that all indicate that the Adamanian is Tuvalian. Particularly significant is the record in the Newark Supergroup of eastern North America, where, for decades, palynostratigraphy placed the Carnian–Norian boundary at or just above the base of the Passaic Formation (at the Warford Member), a placement supported by conchostracan and tetrapod biostratigraphy (and by megafossil plant biostratigraphy: Ash 1980, 1987) (see summary by Huber *et al.* 1993*a*). Correlations to the Chinle Group based on palynomorphs, conchostracans and tetrapods indicate that the Adamanian LVF is older than the base of the Passaic Formation. Based on counting cycles in the Newark, the estimated age of the Passaic Formation base (and the base of the Norian) is about 217 Ma (Kent & Olsen 1999), but in this counting a complete Rhaetian was assumed. However, according to Kozur & Weems (2005, 2007), most of the Rhaetian is missing in the Passaic Formation, where only the uppermost precession cycle of *c.* 20 000 years yielded uppermost Rhaetian conchostracans, whereas below these beds late Norian conchostacans are present.

Recent correlations of Newark magnetostratigraphy, however, have been used to argue for a much older Norian base in the Newark section (Muttoni *et al.* 2004), one that would be close to the base of the Lockatong Formation, with an estimated age of *c.* 228 Ma based on Newark cycle counting. Furthermore, in an abstract, Irmis & Mundil (2008) reported a $^{206}\mathrm{Pb}/^{238}\mathrm{U}$ age of 219.2 ± 0.7 Ma for an Adamanian horizon of the Chinle Group in west–central New Mexico. On face value, the Chinle date and the interpretation of Newark magnetostratigraphy of Muttoni *et al.* (2004) indicate that the Adamanian is Norian.

Nevertheless, the correlations Muttoni *et al.* (2004) propose between the Newark and the marine Late Triassic magnetostratigraphy from Pizzo Mondello are fraught with problems, mostly because the marine section contains far fewer magnetochrons than does the presumed age-equivalent interval of the Newark. Furthermore, the correlation has abandoned the only well-documented biostratigraphic datum in the Newark that allows a correlation to marine strata: the Carnian–Norian boundary at the approximate base of the Passaic Formation (see above). Thus, the proposed Pizzo Mondello-Newark magnetostratigraphic correlation lacks an independent biostratigraphic datum by which to correlate. Furthermore, the Pizza Mondelo marine section is thin (*c.* 430 m of limestone-dominated section represent late Carnian and much of Norian time) in comparison to the more than 4-km-thick Newark section. Therefore, it is not surprising that the Pizzo Mondello section yields a magnetostratigraphic record that does not directly correspond, in both reversal frequency and pattern, to the Newark section. I thus believe there is real reason to question the reliability of the magnetostratigraphic correlations advocated by Muttoni *et al.* (2004).

I maintain a late Carnian (Tuvalian) age for the Adamanian, choosing biostratigraphic data over what I judge to be less reliable correlations based on magnetostratigraphy. As for the date reported in an abstract by Irmis & Mundil (2008), without supporting data its reliability cannot be fully evaluated.

However, if it is a reliable age, it dates part of the late Carnian to *c.* 219 Ma, which means the base of the Norian would be younger than 219 Ma, in agreement with the 217 Ma age suggested by Kent & Olsen (1999), and the Norian is not as long as concluded by Muttoni *et al.* (2004).

Revueltian

Two Italian records are critical to correlation of the Revueltian to part of the Norian:

1. Zorzino Limestone, Lombardian Alps, Italy: The Zorzino Limestone (Calcare de Zorzino) has been correlated to the mid-Norian (uppermost Alaunian) *Himavatites columbianus* ammonite zone (Jadoul *et al.* 1994; Roghi *et al.* 1995). Nonmarine tetrapods from this unit at the Cêne and Endenna quarries in Lombardy include the Revueltian index taxa *Mystriosuchus*, *Aetosaurus* and *Eudimorphodon* (Wild 1989; Renesto 2006).

2. Forni Dolomite, Veneto Prealps, Italy: the Forni Dolomite (Dolomia di Forni) in northeastern Italy is the same age as the Zorzino Limestone, mid-Norian (Roghi *et al.* 1995). Its nonmarine tetrapods include the Revuletian index taxon *Eudimorphodon* (Dalla Vecchia 1995). The Italian records thus provide direct evidence that at least part of the Revueltian = middle Norian (Alaunian). I consider the Revueltian to correlate approximately with the early-middle Norian, which is consistent with the Italian data (Lucas 1997*a*).

Palynostratigraphy, magnetostratigraphy and sequence stratigraphy suggest the characteristic Revueltian tetrapod assemblage in the Chinle Group of New Mexico, USA, is of Norian age (Lucas 1997*a*, 1998*a*). Based on stratigraphic position (Huber *et al.* 1993*b*; Lucas & Huber 2003), magnetostratigraphy (Witte *et al.* 1991; Kent *et al.* 1995; Muttoni *et al.* 2004), and palynomorphs (Cornet 1977), the Neshanician LVF in the Newark Supergroup of eastern North America is of early to middle Norian or just of middle Norian age. Stratigraphic position (Huber *et al.* 1993*b*; Lucas & Huber 1993), magnetostratigraphy (Witte *et al.* 1991; Kent *et al.* 1995; Muttoni *et al.* 2004), and palynomorphs (Cornet 1977; Fowell & Olsen 1993; Lucas & Tanner 2007*b*) indicate the Cliftonian LVF is of late Norian–Rhaetian age. Thus, a Norian correlation of the Revueltian is certain, with well supported correlation to the early and middle Norian.

Apachean

Apachean time is post-Revueltian (*c.* mid-Norian) and pre-Jurassic. Magnetostratigraphy of the uppermost Chinle Group in the Four Corners and in eastern New Mexico (Reeve & Helsley 1972; Molina-Garza *et al.* 1996, 2003), correlated to the Newark Supergroup magnetostratigraphy (Kent *et al.* 1995; Muttoni *et al.* 2004; Hounslow & Muttoni 2010, this volume), also suggests the Apachean is latest Triassic ('Norian–Rhaetian').

Earlier arguments that the Apachean is equivalent to the Rhaetian (Hunt 1993; Lucas 1993*b*, 1998*a*) cannot be sustained in the light of new data. These arguments were largely based on a stage-of-evolution assessment of the Apachean phytosaur *Redondasaurus*. This phytosaur is more derived than the Knollenmergel (late Norian) phytosaurs of the German Keuper, so *Redondasaurus* was therefore assigned a Rhaetian age. However, the Norian aetosaur *Aetosaurus* occurs in Rock Point strata in Colorado (Small 1998) and Rock Point strata in New Mexico, and the Rock Point palynomorphs suggest a Norian age (Litwin *et al.* 1991). Clearly, the Apachean is younger than the Revueltian (early–middle Norian), so I regard it as late Norian to Rhaetian in age (Lucas *et al.* 2005, 2007*e*; Lucas & Tanner 2007*a*, *b*).

The stratigraphically highest Apachean assemblage from the American Southwest is in the Dinosaur Canyon Member of the Moenave Formation and laterally equivalent Wingate Sandstone (Lucas *et al.* 2005, 2006; Lucas & Tanner 2007*a*, *b*). There are several compelling reasons to assign a Late Triassic age to this assemblage: (1) the Apachean phytosaur *Redondasaurus* is present, and no phytosaur is known from Jurassic strata; (2) the footprint ichnogenus *Brachychirotherium* is present and not known anywhere from Jurassic strata; (3) the lower Dinosaur Canyon Member is laterally equivalent to strata of well established Late Triassic age (upper Rock Point Formation of the Chinle Group); (4) the Wingate Formation basal contact is gradational with underlying Upper Triassic strata of the Rock Point Formation; and (5) magnetostratigraphy of the Dinosaur Canyon interval is reasonably correlated to the magnetostratigraphy of uppermost Triassic strata of the Newark Supergroup in eastern North America (Molina-Garza *et al.* 2003).

Although it is possible to assign the Dinosaur Canyon assemblage to the Late Triassic, its precise correlation to the marine timescale is uncertain. Probably it equates to part or all of Rhaetian time, simply because the Dinosaur Canyon interval is the youngest Triassic interval on the Colorado Plateau and is conformably overlain by strata that apparently correlate to the earliest part of the Early Jurassic (Hettangian) (Lucas & Tanner 2007*a*, *b*; Kozur & Weems 2010). This supports a correlation of the Apachean with the late Norian–Rhaetian.

Triassic Footprint Biostratigraphy

In this volume, Klein & Lucas (2010) present a Triassic footprint biostratigraphy and biochronology that build on, revize and synthesize previous efforts, including those of Haubold (1969, 1971, 1984, 1986), Demathieu & Haubold (1972, 1974), Olsen (1980, 1983), Lockley & Hunt (1995), Hunt & Lucas (2007*a*, *b*), Lucas (2003, 2007*a*) and Klein & Haubold (2007). Triassic tetrapod footprints have a Pangaea-wide distribution; they are known from North and South America, Greenland, Europe, North Africa, China, Australia, Antarctica and South Africa. They often occur in nonmarine Triassic strata that lack well-preserved body fossils, so their biostratigraphic utility has been of some interest.

In Triassic strata, several characteristic footprint assemblages and ichnotaxa have restricted stratigraphic ranges and thus represent distinct time intervals. Key Triassic footprint ichnotaxa are archosaur tracks: *Rotodactylus*, the chirotherian ichnotaxa *Protochirotherium*, *Synaptichnium*, *Isochirotherium*, *Chirotherium*, *Brachychirotherium* and grallatorids (theropod dinosaur tracks). Nevertheless, non-archosaur footprints are common, especially the ichnotaxa *Rhynchosauroides*, *Procolophonichnium*, *Capitosauroides* and several dicynodont-related or mammal-like forms that dominate some footprint assemblages.

From the temporal distribution pattern Klein & Lucas (2010) identified five distinct tetrapod-footprint-based biochrons: (1) dicynodont tracks (Lootsbergian); (2) *Protochirotherium* (*Synaptichnium*): also includes *Rhynchosauroides* and *Procolophonichnium* (Nonesian); (3) *Chirotherium barthii*, also includes *C. sickleri*, *Isochirotherium*, *Synaptichnium*, *Rotodactylus*, *Rhynchosauroides*, *Procolophonichnium*, dicynodont tracks and *Capitosauroides* (Nonesian–Perovkan); (4) *Atreipus–Grallator* ('*Coelurosaurichnus*'), which also includes *Synaptichnium*, *Isochirotherium*, *Sphingopus*, *Parachirotherium*, *Rhynchosauroides*, *Procolophonichnium* (Perovkan–Berdyankian); and (5) *Brachychirotherium*, which also includes *Atreipus–Grallator*, *Grallator*, *Eubrontes*, *Apatopus*, *Rhynchosauroides*, dicynodont tracks (Otischalkian–Apachean).

Tetrapod footprints are thus useful for Triassic biostratigraphy and biochronology, but, compared to the tetrapod body fossil record with eight biochrons, the five footprint-based biochrons provide less temporal resolution. Nevertheless, in nonmarine Triassic strata where body fossils are rare, footprints can be useful for biostratigraphy and biochronology.

Conclusion

The global Triassic timescale based on tetrapod evolution developed in the 1990s has been criticized because of: (1) perceived problems with the alpha taxonomy of some of its index fossils; (2) possible temporal overlap of the Nonesian and Perovkan LVFs; (3) changes and additions to the stratigraphic ranges of some index taxa; and (4) perceived problems of correlation to the SGCS.

Taxonomic disagreements lie at the heart of many arguments over biostratigraphy, but I believe that the extensive taxonomies developed for many of the Triassic index taxa, especially temnospondyls, phytosaurs, aetosaurs, dicynodonts and cynodonts, provide a sound basis for their use in biostratigraphy. Shifting opinions about taxonomy of these tetrapods will remain, and that will always affect correlations based on tetrapod fossils.

Lucas *et al.* (2007*e*) resolved the problems of potential overlap or gaps around the Nonesian–Perovkan boundary by redefining the beginning of the Perovkan to obviate such problems. Stratigraphic range extensions and changes are the regular outgrowth of collecting and careful biostratigraphic study in the field. They always force adjustments to any biochronological scheme rooted in sound biostratigraphy. Problems with correlation of the Triassic LVFs to the SGCS persist largely because in much of the nonmarine Triassic section few reliable data are available for correlation to the marine timescale.

Clearly, we need a nonmarine Triassic tetrapod biochronology with which to correctly sequence the history of tetrapod evolution on land. Advances in the scheme proposed in the 1990s have come from new fossil discoveries, more detailed biostratigraphy and additional alpha taxonomic studies based on sound evolutionary taxonomic principles. As the work reviewed here demonstrates, the global Triassic timescale based on tetrapod biochronology remains a robust tool for both global and regional age-assignment and correlation.

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