GLOBAL TRIASSIC TETRAPOD BIOSTRATIGRAPHY AND BIOCHRONOLOGY: 2007 STATUS

SPENCER G. LUCAS[1], ADRIAN P. HUNT[1], ANDREW B. HECKERT[2] AND JUSTIN A. SPIELMANN[1]

[1] New Mexico Museum of Natural History, 1801 Mountain Road NW, Albuquerque, NM 87104-1375;
[2] Department of Geology, Appalachian State University, ASU Box 32067, Boone, NC 28608-2067

Abstract—The global Triassic timescale based on tetrapod biochronology remains a robust tool for both global and regional age assignment and correlation. The Lootsbergian and Nonesian land-vertebrate faunachrons (LVFs) are of Early Triassic age; cross correlation of part of the Lootsbergian to the Olenekian and all or part of the Nonesian to the Anisian lacks support. In the South African Karoo basin, both the Lootsbergian and the Nonesian can and should be subdivided into sub-LVFs. The upper part of the South African *Cynognathus* zone, previously considered Nonesian in age, is younger, of Perovkan age. We redefine the beginning of the Perovkan as the first appearance datum of the temnospondyl *Eocyclotosaurus*, which resolves uncertainties in the correlation of *Eocyclotosaurus* assemblages and shansiodont assemblages. The Berdyankian LVF equates to parts of Ladinian and Carnian time. Rejection of recent cladotaxonomy of phytosaurs and an incorrect claim of a Revueltian record of the temnospondyl *Metoposaurus*, as well as newly established stratigraphic ranges and new taxonomy of aetosaurs, have improved correlation and temporal resolution within the interval Otischalkian-Apachean. This further supports separation of the Otischalkian and Adamanian and runs contrary to suggestions to merge the two LVFs as a single Ischigualastian LVF. Though readily recognized and correlated in western North America, the Apachean LVF remains the most problematic LVF for global correlation. A recent purported test of the Triassic LVFS based on GIS is rejected as invalid because it is replete with internal inconsistencies, factual errors and questionable interpretations. Continued careful biostratigraphy in the field and improved alpha taxonomies that are not cladotaxonomies will further develop, elaborate and test the Triassic timescale based on tetrapod evolution.

INTRODUCTION

Although the use of tetrapod fossils for biostratigraphy had a long tradition, Lucas (1990) first discussed the possibility and desirability of developing a global Triassic timescale based on tetrapod evolutionary events. Lucas and Hunt (1993) subsequently proposed a series of four land-vertebrate faunachrons (LVFs) for most of Late Triassic time based on a succession of four tetrapod fossil assemblages ("faunas") in the Chinle Group of the western United States. Huber et al. (1993) also proposed a set of LVFs for the Upper Triassic tetrapod assemblages of the Newark Supergroup in eastern North America. Lucas (1993) proposed four LVFs for the Early-Middle Triassic tetrapod assemblages of northern China. Lucas et al. (1997a) presented revised definitions of some of the Late Triassic LVFs.

Lucas (1998) consolidated these earlier works and presented a comprehensive global Triassic tetrapod biochronology (Fig. 1). This scheme, which divides Triassic time based on tetrapod evolution, has now been tested and refined over nearly a decade. Here, we discuss the current status of the Triassic tetrapod-based timescale, reviewing new data and analyses and addressing some of the comments and critiques of some other workers.

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

THE LAND VERTEBRATE FAUNACHRONS

Lootsbergian

Lucas (1998) defined the Lootsbergian LVF as the time between the FADs of the dicynodont *Lystrosaurus* and the cynodont *Cynognathus* (Fig. 1). In essence, it is the time equivalent to the "*Lystrosaurus* zone" of longstanding usage. Based on its principal index fossil *Lystrosaurus*, Lootsbergian-age tetrapod assemblages have long been identified in South Africa, Russia, India, China and Antarctica (see references in Lucas, 1998). Recognition of and correlation within the Lootsbergian appears to be one of the most biostratigraphically stable parts of the Triassic tetra-

pod timescale.

Nevertheless, three issues merit consideration based on recent work: (1) what is the relationship of the beginning of the Lootsbergian to the Permo-Triassic boundary (PTB)?; (2) what is the precise correlation of the Lootsbergian to the standard global chronostratigraphic scale (SGCS)?; and (3) can the Lootsbergian LVF be subdivided?

Unlike almost all of the Triassic marine stage boundaries, the base of the Triassic (= 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. Nevertheless, at present there is no precise basis for correlating the beginning of the Lootsbergian (the FAD of *Lystrosaurus*, long considered a nonmarine proxy for the beginning of the Triassic) to the FAD of *H. parvus*.

Magnetostratigraphic data indicate that the PTB is in a normal polarity chron in marine sections, and a normal polarity chron also encompasses the LO of *Lystrosaurus* in the Karoo basin of South Africa and the Junggur basin of northwestern China (Ogg, 2004; Steiner, 2006). However, this only suggests contemporaneity within the duration of the normal chron (assuming, of course, that it is, in fact, the same normal chron), not synchrony.

Most who equate the *Lystrosaurus* FAD to the Permo-Triassic boundary do so by assuming a single mass extinction in the nonmarine and marine realms is the Permo-Triassic boundary (e.g., Retallack et al., 2003). Similar circular reasoning has been used to identify the Triassic-Jurassic boundary in nonmarine strata (see critique of Lucas and Tanner, 2006). Such circular reasoning overlooks two facts: (1) the largest marine extinction at Meishan actually is below the LO of *Hindeodus parvus*; and (2) it is not at all clear that the LO of *Lystrosaurus* is coincident with a terrestrial mass extinction. Thus, the stratigraphic overlap of *Dicynodon*, the classic youngest Permian dicynodont, and *Lystrosaurus* is well (and repeatedly) documented in South Africa and northwestern China. Plant-based criteria used to identify the Permo-Triassic boundary do not coin-

230

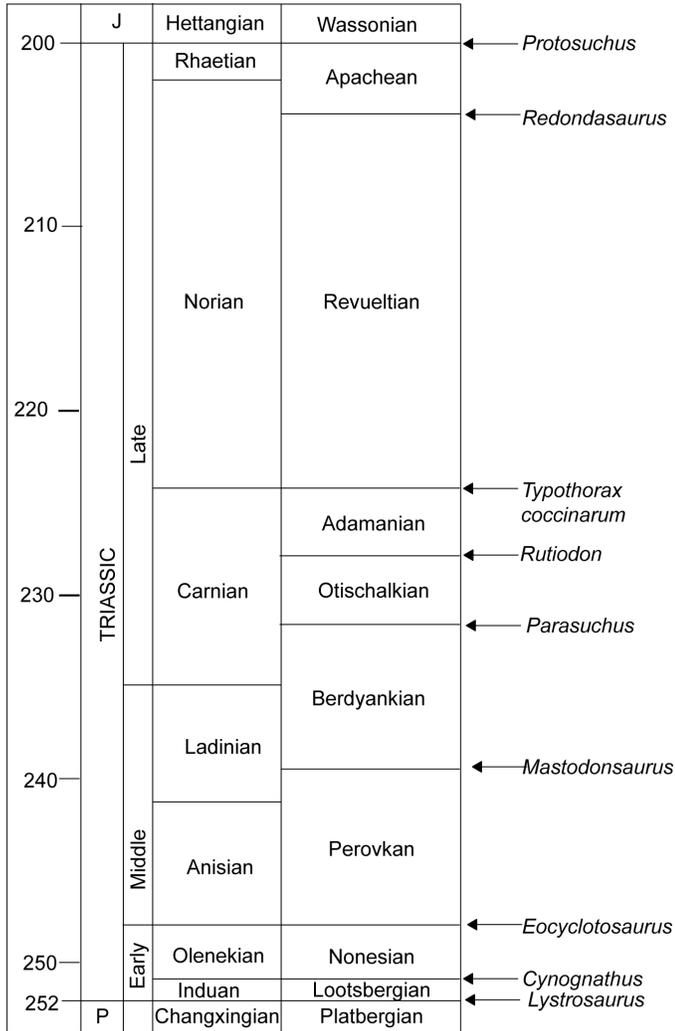| Ma	Period	Epoch	Stage	LVF	Defining taxon
200	J		Hettangian	Wassonian	← Protosuchus
			Rhaetian	Apachean	← Redondasaurus
210	TRIASSIC	Late	Norian	Revueltian	
220					
			Carnian	Adamanian	← Typothorax coccinarum
					← Rutiodon
230				Otischalkian	← Parasuchus
			Ladinian	Berdyankian	
240		Middle		Perovkan	← Mastodonsaurus
			Anisian		
					← Eocyclotosaurus
250		Early	Olenekian	Nonesian	← Cynognathus
252			Induan	Lootsbergian	← Lystrosaurus
	P		Changxingian	Platbergian	

FIGURE 1. The Triassic timescale based on tetrapod evolution showing taxa that define the beginning of each LVF on the right, and correlation of the LVFs to the SGCS.

cide with the LO of *Lystrosaurus* (Hancox et al., 2002). Most of the tetrapod extinctions that occur close to the LO of *Lystrosaurus* are, in fact, stratigraphically below it, and are lesser in number than some of the tetrapod turnovers lower and higher in the section (e.g., King, 1990, 1991; Lucas, 1994). At present, we continue to believe that the beginning of the Lootsbergian is close to the Permo-Triassic boundary, but current data do not demonstrate a precise equivalence.

Correlation of the Lootsbergian to at least part of the marine Induan Stage is clear (Lucas, 1998). 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 (Lucas, 1998). 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 assigned a Lootsbergian age]…is actually latest Spathian or Spathian-Anisian in age." This undocumented statement is also remarkable considering that 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, 1993a, 1998, 2001). In another example, 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*. The more likely possibility that Damiani et al. (2000) simply extended the range of that trematosaurid back into the Induan was not considered by them.

Lootsbergian time encompasses both the "*Lystrosaurus* zone" and "*Procolophon* zone" of classic usage (e.g., Broom, 1906). Thus, there may be two or three distinct tetrapod assemblages (at least in the Karoo basin) within the Lootsbergian (the stratigraphic distribution of the cynodont *Thrinaxodon* may be useful here: Groenewald and Kitching, 1995), and this should provide a basis for subdivision of the LVF.

Nonesian

Lucas (1998) defined the Nonesian as the time between the FAD of the cynodont *Cynognathus* and the FAD of the dicynodont *Shansiodon*. In essence, it was intended to be the time equivalent to the South African "*Cynognathus* zone" of classic usage. 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 Spathian strata in the Mangyshlak Peninsula of western Kazakstan (e.g., Lozovsky and Shishkin, 1974).

During the 1990s, careful biostratigraphy in the Karoo basin by John Hancox and collaborators demonstrated that the classic "*Cynognathus* zone" consists of three stratigraphically discrete assemblages (e.g., Hancox et al., 1995, 2000; Hancox, 2000). These assemblages have been called subzones A, B and C by Hancox et al. (1995), and the upper is clearly Perovkan in age (Hancox, 2000). This means the South African Nonesian (which encompasses subzones A and B) is divisible into two biochronological units (Hancox, 2000). However, correlation of these subzones to the Olenekian-Anisian remains somewhat problematic, and the alternatives are well discussed by Hancox (2000). We regard subzones A and B as Early Triassic and C as Anisian, but the jury is still out on whether B could be, at least in part, early Anisian. The important point is that recognizing subzone C as Perovkan does not affect the definition of the Nonesian, it only means that considering all of the "*Cynognathus* zone" to be Nonesian (Lucas, 1998) was incorrect.

Perovkan

Lucas (1998) 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 Formation, so the land-vertebrate biochronology shifts here from superposed South African assemblages (the characteristic assemblages of the Lootsbergian and Nonesian LVFs) to superposed Russian assemblages (the characteristic assemblages of the Perovkan and Berdyankian LVFs). This geographic shift poses problems for the biochronology, particularly in demonstrating the temporal succession (not overlap) of Nonesian and Perovkan-age assemblages. Indeed, the reassignment of the upper "*Cynognathus* zone" to the Perovkan LVF just discussed well reflects such problems.

Shishkin (2000) argued (on weak evidence) that the Donguz Formation tetrapod assemblage is actually late Anisian, so it is younger than the *Eocyclotosaurus* assemblage that well represents the Perovkan in western Europe and North America and is of unambiguous early Anisian age (Lucas and Schoch, 2002). A more circumspect reading of the data (e.g., Ivakhenko et al., 1997) simply regards the Donguz assemblage as Anisian, with no more precise age correlation.

Lucas (1993b) argued that the LO of the dicynodont *Shansiodon* is Anisian, and this is why Lucas (1998) used it to define the beginning of the Perovkan. If the LO of *Shansiodon* is actually younger than the LO of *Eocyclotosaurus*, then *Eocyclotosaurus* is of Nonesian age. This is not easily resolved, but we do note that the LO of *Kannemeyeria* in China predates the LO of *Shansiodon*, as it does in South Africa, and there is no evidence that the youngest Nonesian assemblage in South Africa (subzone B of Hancox et al., 1995) is equivalent to the *Eocyclotosaurus* zone. It is

also important to realize that Shishkin's (2000) arguments are based on his own ideas of temnospondyl evolutionary trajectories (not shared, for example, by Schoch and Milner, 2000) and his willingness to readily correlate nonmarine strata to the SGCS based on conchostracans, nonmarine ostracods and other data that we consider of low biostratigraphic reliability.

Nevertheless, we do recognize 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 reduce ambiguity here is to redefine the beginning of the Perovkan as the FAD of *Eocyclotosaurus*, and we do so (Fig. 1). Nesbitt (2003) has demonstrated that the rauisuchian *Arizonasuarus* is widely distributed and relatively easily recognized, so it can be added to the list of Perovkan index taxa.

Berdyankian

Lucas (1998) defined the Berdyankian LVF as the interval between the FAD of the temnospondyl *Mastodonsaurus* and the FAD of the phytosaur *Paleorhinus* (now correctly called *Parasuchus*). As Lucas (1998) noted, 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 land-vertebrate "age" of Bonaparte, 1966, 1967). Recognition of Berdyankian-age assemblages in Russian and Germany is rendered easy by the presence of the key index taxon *Mastodonsaurus* (Lucas, 1999)

The Brazilian and Argentinian *Dinodontosaurus* assemblages are unambiguously correlated to each other, and have generally been considered Ladinian based on flimsy palynostratigraphic evidence (see reviews by Lucas and Harris, 1996 and 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 and Wild, 1995; Lucas, 1998). At present, this South American-European correlation remains weakly supported and merits further study. This may be one area where magnetostratigraphy (in South America) is needed.

A much better knowledge of Berdyankian assemblages now can be had from German sections where *Mastodonsaurus* extends through the Lettenkeuper (Schoch, 1999; Lucas, 1999). This firmly establishes the Berdyankian as representing a portion of Ladinian time. Particularly significant are newly collected bone beds in the Lettenkeuper, which have yielded a diverse assemblage of tetrapods, including *Plagiosuchus*, *Gerrothorax*, *Mastodonsaurus*, *Kupferzellia*, trematosaurids, almasaurids, *Batrachotomus*, various archosaurs and a cynodont (e.g., Schoch, 2002).

Otischalkian

The Otischalkian LVF was defined as the time between the FADs of the phytosaurs *Parasuchus* (=*Paleorhinus*) and *Rutiodon* (Lucas and Hunt,1993; Lucas et al., 1997a; Lucas, 1998). 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 and Lucas, 1991a), so that this name should be regarded as the senior synonym of *Paleorhinus* (see Lucas et al., 2007a). Furthermore, even though Hunt and Lucas (1991a) provided a careful taxonomic revision of *Parasuchus*, and provided a clear diagnosis of the genus that has never been contested, some cladotaxonomists 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 (Rayfield et al., 2005). We reject such a cladotaxonomic approach to primitive phytosaur taxonomy and recognize *Parasuchus* as a diagnosable genus widespread in Otischalkian strata (Lucas et al., 2007a). However, there is one record of *Paleorhinus* in what we have regarded as oldest Adamanian

strata, at the *Placerias*/Downs quarries in the Bluewater Creek Formation of the Chinle Group in Arizona (Lucas et al., 1997a). Also, note that the aetosaur *Stagonolepis* is now known to have Otischalkian records in Poland (Dzik, 2001) and in Germany (Heckert and Lucas, 2000), so it is no longer an index fossil of the Adamanian LVF (see below).

The Otischalkian index taxa *Longosuchus* (= *Lucasuchus*) and *Doswellia* still stand. *Metoposaurus* also has only Otischalkian records, though Milner and Schoch (2004) recently claimed its presence in the Revueltian Stubensandstein of Germany. They based this claim on a skull acquired by the British Museum in 1862, listed in the museum records as coming from "the Middle Keuper near Stuttgart, Württemburg." Fraas (1889, p. 137) stated the skull came from "Feuerbacher Heide bei Stuttgart" and provided a brief description of the skull, which had never been illustrated. Despite this description, Milner and Schoch (2004, p. 244) stated that "it is questionable if Fraas ever saw the specimen." Feuerbacher Heide was a small community that is now part of greater Stuttgart, where stone quarries in the Schilfsandstein yielded many tetrapod specimens including *Metoposaurus*, the phytosaur *Zanclodon arenaceus* and the sphenosuchian *Dyoplax* (e.g., Hunt, 1993; Lucas et al., 1998a; Hungerbühler, 2001b). Thus, it makes eminent sense for the British Museum metoposaur skull to have come from a stone quarry at Feuerbacher Heide, as stated by Fraas, who had a detailed firsthand knowledge of the Feuerbacher localities and fossils.

Nevertheless, Milner and Schoch (2004) claimed that the BMNH skull came from the Middle Stubensandstein at Aixheim. They based this conclusion on the preservation of the specimen, stating that the "three dimensional creamy-white bone" and "green coarse sandstone" of the BMNH specimen excludes its provenance as Schilfsandstein. However, not all specimens from the Schilfsandstein are black, crushed bone as Milner and Schoch (2004) claim (see for example, the type of *Zanclodon arenaceus*: Hungerbühler, 2001b, figs. 1-2), and "green coarse sandstone" does not exclude the Schilfsandstein lithologically.

Indeed, the original locality data with the British Museum skull preclude its provenance as middle Stubensandstein at Aixheim. Thus, Aixheim is not near Stuttgart, it is ~90 km to the SSW (Hungerbühler, 1998, fig. 1). In 1862, Aixheim would have been at least a two-day journey by horse from Stuttgart, and thus would not have been described as "near Stuttgart." Furthermore, the original attribution to the "Middle Keuper" excludes the Stubensandstein, as the Schilfsandstein was traditionally considered Middle Keuper in Baden-Württemberg (Geyer and Gwinner, 1991). Finally, no well provenanced German metoposaur has ever been found in the Stubensandstein; all are from the Schilfsandstein-Lehrberg Schichten interval (Lucas, 1999). Thus, we conclude that Milner and Schoch's (2004) claim that the British Museum skull is from the Stubensandstein, and thus Revueltian in age, is based on specious reasoning and reject it.

The last Otischalkian index fossil listed by Lucas (1998) is the phytosaur *Angistorhinus*. Its records are Otischalkian (Long and Murry, 1995) except one, near Lamy, New Mexico, where it co-occurs with *Rutiodon* in the earliest Adamanian (Hunt et al., 1993). This overlap of Otischalkian and Adamanian index fossils (as at the *Placerias* quarry in Arizona) is what may be expected in as good a fossil record as the Chinle Group.

The occurrence of a specimen of *Parasuchus* in marine Upper Carnian (Tuvalian) strata in Austria cross-correlates the Otischalkian, in part, to the late Carnian (Hunt and Lucas, 1991a). However, some Otischalkian tetrapods (e.g., those from the Schilfsandstein) are as old as early Carnian (late Julian), so a cross correlation of the Otischalkian to part of the early and part of the late Carnian is best supported by the data (Fig. 1).

We see the Otischalkian as one of the best supported and most globally correlatable of the LVFs; it represents a slice of Carnian time readily recognized in North America, Europe, North Africa and India. Indeed, Heckert and Lucas (2006) demonstrated that, although some vertebrate taxa do co-occur in strata of both Otischalkian and Adamanian

age, there are many microvertebrate taxa that are known only from strata of Adamanian age (see below). Rayfield et al. (2005, p. 347), however, claimed that the Otischalkian "cannot act a global biochronological unit" principally based on their endorsement of the cladotaxonomy of *Parasuchus/Paleorhinus* and their acceptance of Milner and Schoch's (2004) incorrect report of *Metoposaurus* in the Revueltian Stubensandstein.

Adamanian

Lucas (1998) defined the Adamanian LVF as the time between the FADs of the phytosaurs *Rutiodon* and *Pseudopalatus*. He listed as 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 an update of these index taxa.

Stagonolepis now has well-documented records in the Otischalkian assemblage at Krasiejów in southern Poland (Dzik, 1991; Lucas et al., 2007b). This lends support to Heckert and Lucas' (2000) conclusion that *Ebrachosaurus singularis* Kuhn, 1936, from the Otischalkian German Blasensandstein (type destroyed in World War II) was based on specimens of *Stagonolepis*. These European Otischalkian records of *Stagonolepis* thus raise the possibility that its stratigraphically lowest records in North America, such as at the *Placerias*/Downs quarries in Arizona, may also be Otischalkian (and thus the record of *Paleorhinus* there would also be Otischalkian).

Extensive revisions of rhynchosaurs (Langer and Schultz, 2000; Langer et al., 2000a, b) indicate that specimens previously assigned to *Scaphonyx* are dominantly *Hyperodapedon*. Lucas et al. (2002a) reviewed these records in detail and demonstrated that a *Hyperodapedon* biochron is of Otischalkian and Adamanian age. Thus, at the generic level, rhynchosaurs can no longer be used to discriminate the Otischalkian and Adamanian.

Largely based on this, Langer (2005a, 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 (2005b) dismissed phytosaur-based distinctions of the Otischalkian and Adamanian, basing his rejection largely on the cladotaxonomy of primitive phytosaurs "documented" in published abstracts by Hungerbühler (2001a; Hungerbühler and Chatterjee, 2002). Langer (2005b) also rejected aetosaur-based correlations based on the taxonomy of South American aetosaurs published by Lucas and Heckert (2001) and Heckert and Lucas (2002). This is particularly significant, as Langer (2005b, p. 228) repudiates the work by claiming, without any documentation, that "*Stagonolepis wellesi* lacks a unique ornamentation pattern of its dorsal paramedian osteoderms," contrary to the published work of Lucas and Heckert, as well as those of Long and Ballew (1989), Parrish (1994), Long and Murry (1995) and Parker (2007), among others. Unlike Langer, we prefer to base our taxonomic conclusions on well justified and documented, published work based on the study of fossils, especially where there is a consensus among all experts, not on single sentence opinions that lack supporting data.

Langer (2005b) 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., 2007b). Rayfield et al. (2005) also argued for amalgamation of the Otischalkian and Adamanian based largely on the same arguments as Langer (2005a, b).

What these workers also fail 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 Otischalkian and Adamanian time; and (3) identification of distinct Otischalkian and/or Adamanian assemblages has been achieved in North America, South America, Europe, India and North Africa. The fact that Langer (2005b) and Rayfield et al. (2005) cannot accept a well-documented alpha taxonomy of Otischalkian and Adamanian index fossils (which they have not studied) is not a valid reason to amalgamate 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 recognized new records in strata of Adamanian age. These new data are principally from the Petrified Forest National Park in Arizona (Heckert and Lucas, 2002; Hunt et al., 2002; Woody, 2003; Heckert, 2004; Woody and Parker, 2004; Heckert et al., 2005) and the extensive exposures of the Chinle Group in east-central New Mexico (Hunt and Lucas, 1995; Lucas et al., 2002b), with other records from the Tecovas and Trujillo formations in Texas (Heckert, 2004; Heckert et al., 2006; Martz and Small, 2006). Clearly, there is a "transitional" fauna between the Adamanian and Revueltian lvfs (Woody and Parker, 2004), and this prompted Hunt et al. (2005) to subdivide the Adamanian into two sub-faunachrons, St. Johnsian (older) and Lamyan (younger), of regional biochronological significance.

Heckert and Lucas (2006) built upon the microvertebrate collections documented by Heckert (2001, 2004) and demonstrated that there are multiple microvertebrate index taxa of Adamanian (St. Johnsian) time, including the xenacanth "*Xenacanthus*" *moorei*, the enigmatic vertebrate *Colognathus obscurus* and the archosaurs (possibly ornithischian dinosaurs) *Tecovasaurus murryi*, *Crosbysaurus harrisae*, and *Krzyzanowskisaurus hunti*.

Revueltian

Lucas (1998) defined the Revueltian as the time interval between the FADs of the phytosaurs *Pseudopalatus* and *Redondasaurus*. However, Hunt et al. (2005) redefined the beginning of the Revueltian as the FAD of the aetosaur *Typothorax coccinarum*, and we endorse this decision (Fig. 1).

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

Typothorax, *Aetosaurus* and *Pseudopalatus*-grade phytosaurs were listed as Revueltian index fossils (Lucas, 1998). However, recognition of an older, Adamanian species of *Typothorax*, *T. antiquum*, by Lucas et al. (2002b) 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*. Parker (2007) has stated without explanation that *T. antiquum* cannot be distinguished from *T. coccinarum* but we dismiss his undocumented claim and refer to the diagnosis provided by Lucas et al. (2002b).

Rayfield et al. (2005, table 1, p. 340) claim that there is a single osteoderm of *T. coccinarum* from the Tres Lagunas Member of the Santa Rosa Formation of New Mexico, citing both Long and Murry (1995) and Lucas et al. (2002b) as the sources of this record. However, a careful reading of Lucas et al. (2002b) reveals there are no *T. coccinarum* fossils known from the Tres Lagunas Member; indeed, the record claimed by Long and Murry (1995, p. 234) is of a specimen of *T. antiquum* from the younger (but still Adamanian) Garita Creek Formation. *T. coccinarum* thus 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., 2002b) creates the first place in the Triassic tetrapod biochronology that the beginning of a LVF can be defined by a true species-level evolutionary event, not the appearance of

a genus-level taxon. This was another impetus to redefine the beginning of the Revueltian as the FAD of *T. coccinarum*.

Aetosaurus is one of the most robust tetrapod index fossils of the Triassic. Lucas et al. (1998b) 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*, well reflected by Rayfield et al. (2005), claims that because *Aetosaurus* has been portrayed as the plesiomorphic sister taxon of other aetosaurs in cladistic analyses (e.g., Heckert and Lucas, 2000) it "must" have a long ghost lineage that therefore renders it useless in biostratigraphy. This is clearly specious cladotaxonomic reasoning (Lucas et al., 1999). 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, any alternative cladogram of aetosaurs, for example, one that views *Aetosaurus* as a highly derived, dwarfed and simplified form, would produce a very different "ghost lineage."

Rayfield et al. (2005, p. 339) further claim "there is some disagreement over the status of supposed '*Aetosaurus*' remains" but provide no explanation, citation, or justification of this remark. We know of no such disagreement in the primary literature on *Aetosaurus* (e.g., O. Fraas, 1877; Huene, 1921; Walker, 1961; Wild, 1989; Heckert and Lucas, 1998; Small, 1998; Lucas et al., 1998b, 1999) or on aetosaurs in general (Walker, 1961; Parrish, 1994; Heckert et al., 1996; Heckert and Lucas, 2000; Parker, 2007). We conclude that there is no valid reason to question the use of *Aetosaurus* as a Revueltian index taxon.

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 Ballew, 1989; Long and Murry, 1995; and Hungerbühler, 2002).

Heckert and Lucas (1996) first suggested that *Revueltosaurus* might serve as an index taxon of Revueltian time. At that time they (and all other published literature) considered *Revueltosaurus*, which was known solely from teeth, 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 and Lucas (2006) then showed that *R. callenderi* is restricted to strata of Revueltian (Barrancan) age, and is therefore an index taxon of the Revueltian.

The preceding example is important not so much because it reaffirms the validity of the Revueltian, but because it demonstrates the relative unimportance of phylogeny in biostratigraphy. Indeed, just as the vast majority of the geologic time scale (with all periods save the Ordovician named prior to Darwin's publication of the *Origin of Species*) was constructed with no knowledge of evolution *per se*, the changing phylogenetic position of *Revueltosaurus* alters neither its biostratigraphic significance nor its biochronological utility. Biostratigraphically, what is important about *Revueltosaurus* is that it is distinctive (easily identified), relatively common and/or widespread, and known from a relatively restricted stratigraphic interval. Whether it is an ornithischian (as previously supposed) or a crurotarsan (the current hypothesis) is irrelevant to its biostratigraphic potential, regardless of how interesting the evolutionary questions related to its phylogenetic position may be.

Hunt (1994, 2001) divided the Revueltian 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 and Lucas, 2006).

Apachean

The Apachean LVF was defined as the time between the FADs of the phytosaur *Redondasaurus* and the crocodylomorph *Protosuchus*. As Lucas (1998) noted, the Apachean is very difficult to correlate outside of North America because of latest Triassic endemism, and Rayfield et al. (2005, p. 348) correctly described the Apachean as "useful as a regional, but not global, biochronological unit."

Lucas (1998) listed three Apachean index fossils: the aetosaur *Redondasuchus*, the phytosaur *Redondasaurus* and the dinosaur *Riojasaurus*. Restricted to Argentina, *Riojasaurus* is not a robust index fossil of the Apachean, but the Apachean is readily distinguished in North America by its primary index fossils, *Redondasaurus* and *Redondasuchus*. However, some workers (Long and 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*, although Martz (2002) did recognize *Redondasuchus* as a distinct species of *Typothorax*, *T. reseri*.

Long and Murry (1995) did not consider the supratemporal fenestra being visible in dorsal view a taxonomically useful character, which could be used to distinguish *Redondasaurus* from *Pseudopalatus* (=*Arribasuchus*). Spielmann et al. (2006a) demonstrated that in the various photographic plates used to illustrate the skulls of *Pseudopalatus*, the supratemporal fenestra can always be seen in dorsal view, usually as slits medial to the squamosals (Long and Murry, 1995, fig. 40A-C). Thus, they considered "supratemporal fenestrae that are essentially concealed in dorsal view" is a character that distinguishes *Redondasaurus* as a genus separate from *Pseudopalatus* (= *Arribasuchus*). This interpretation of *Redondasaurus* as distinct from *Pseudopalatus* was also advocated by the taxonomic analysis of Hungerbühler (2002).

Redondasuchus reseri (Hunt and Lucas, 1991b; Heckert et al., 1996) was identified as a juvenile *Typothorax coccinarum* by Long and Murry (1995) and Martz (2002). They suggested that the paramedian osteoderms illustrated by Hunt and Lucas (1991b) were osteoderms of the cervical or caudal region of the carapace. They also attributed the extreme flexure of the paramedian osteoderms of *R. reseri* to postmortem distortion. Spielmann et al. (2006b) reaffirmed the validity of *Redondasuchus* and noted that many paramedian osteoderms of *Redondasuchus* are not crushed or deformed and still exhibit their characteristic flexure.

Lehman and Chatterjee (2005; also see Lehman, 1994) reported a revised Upper Triassic tetrapod biostratigraphy in West Texas using an interpretation of lithostratigraphy that is unique to them (contrary to all previous published stratigraphy and geologic mapping) and was previously refuted by Lucas et al. (1994). Thus, in reading Lehman and Chatterjee (2005) it is necessary to realize that the lithostratigraphy has been retrofitted to an undocumented model of Chinle Group sedimentation in West Texas, one in which relatively fine-grained strata to the west and north (distal or basinal deposits) are assumed to correlate to relatively coarse-grained strata to the east and south (proximal or basin edge deposits). This assumption allows the type Otischalkian tetrapod assemblage near Big Spring to be correlated to the Revueltian assemblages near Post. Previous work on Chinle lithostratigraphy in West Texas, including our own, arrived at different correlations than do Lehman and Chatterjee (2005). Indeed, pioneering work by Drake (1892) produced more credible lithostratigraphic correlations of the West Texas Upper Triassic strata than do Lehman and Chatterjee (2005).

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., 1997b; Lucas and Tanner, 2007). Improved magnetostratigraphy and recognition of *Aetosaurus* in lower Rock Point Formation strata in Colorado (Small, 1998) and New Mexico (unpublished data) also lead us to suggest that Apachean time may not

simply equate to the Rhaetian, but may also include late Norian strata. However, as we have long stressed (e.g., Lucas and Hunt, 1993; Lucas, 1998; Lucas and Tanner, 2007), cross-correlation of the Apachean age rocks in the America Southwest to the SGCS is particularly difficult.

DISCUSSION

The global Triassic timescale based on tetrapod evolution developed in the 1990s has been critiqued 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, and we believe the extensive taxonomies we and others developed for many of the Triassic index taxa, especially metoposaurs, phytosaurs and aetosaurs, provide a sound basis for their use in biostratigraphy. Much of the criticism of these taxonomies comes from cladotaxonomists who are developing a typological, oversplit and biologically uninformative alpha taxonomy of many Triassic tetrapods.

Here, we resolve 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 remain largely because in much of the nonmarine Triassic section few data can be relied on for cross correlation to the marine timescale.

Clearly, we need a nonmarine Triassic tetrapod biochronology with which to 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. Most of the criticisms of the scheme have come from cladotaxonomists who believe that imaginary "ghost lineages" somehow constrain biostratigraphic correlation or from those incapable of undertaking accurate lithostratigraphic and biostratigraphic correlations. Rayfield et al. (2005) represents a flawed synopsis of these criticisms, and further couched their review as a "GIS test" of the Triassic tetrapod biochronology (but see the Appendix). This literature review-based test, however, is replete with errors of commission and omission that undermine its use as an evaluation of Triassic tetrapod biochronology, As the work reviewed here demonstrates, that biochronology will continue to be elaborated, refined and evaluated by careful work in the field and museum.

REFERENCES

Ash, S. R., 1980, Upper Triassic floral zones of North America; *in* Dilcher, D. L. and Taylor, T. N., eds., Biostratigraphy of fossil plants: Stroudsburg, Dowden, Hutchinson and Ross, p. 153-170.

Ash, S. R., 1987, The Upper Triassic red bed flora of the Colorado Plateau, western United States: Journal of the Arizona-Nevada Academy of Science, v. 22, p. 95-105.

Ballew, K. L., 1989, A phylogenetic analysis of Phytosauria from the Late Triassic of the western United States; *in* Lucas, S. G. and Hunt, A. P., eds., The dawn of the age of dinosaurs in the American Southwest: Albuquerque, New Mexico Museum of Natural History, p. 309-339.

Barnosky, A. D. and Carrasco, M. A., 2000, MIOMAP: A GIS-linked database for assessing effects of environmental perturbations on mammal evolution and biogeography: Journal of Vertebrate Paleontology, v. 20, supplement to no. 3, p. 28A.

Bonaparte, J. F., 1966, Chronological survey of the tetrapod-bearing Triassic of Argentina: Breviora, no. 251, 13 p.

Bonaparte, J. F., 1967, Cronología de algunas formaciones Triásicas de Argentina: Basada en restos de tetrápodos: Associacion Geologica de Argentina Revista, v. 21, p. 20-38.

Broom, R., 1906, On the Permian and Triassic faunas of South Africa: Geological Magazine (5), v. 3, p. 29-30.

Chatterjee, S., 2001, *Parasuchus hislopi* Lydekker, 1885 (Reptilia, Archosauria): proposed replacement of the lectotype by a neotype: Bulletin of Zoological Nomenclature, v. 58, p. 34-36.

Cheng, Z., 1981, Permo-Triassic continental deposits and vertebrate faunas of China; *in* Cresswell, M. M. and Vella, P., eds., Gondwana Five. Rotterdam, A. A. Balkema, p. 65-70.

Damiani, R., Neveling, J., Hancox, J., and Rubidge, B., 2000, First trematosaurid temnospondyl from the *Lystrosaurus* assemblage zone of South Africa and its biostratigraphic implications: Geological Magazine, v. 137, p. 659-665.

Drake, N. F., 1892, Stratigraphy of the Triassic of West Texas: Geological Survey of Texas, Third Annual Report, p. 227-247.

Dzik, J., 2001, A new *Paleorhinus* fauna in the early Late Triassic of Poland: Journal of Vertebrate Paleontology, v. 21, p. 625-627.

Fara, E. and Hungerbühler, A., 2000, *Paleorhinus magnoculus* from the Upper Triassic of Morocco: a juvenile primitive phytosaur (Archosauria): Comptes Rendus Académie des Sciences, Paris, Sciences de la Terre et des Planetes, v. 331, p. 831-836.

Fraas, E., 1889, Die Labyrinthodonten der Schwäbischen Trias: Palaeontographica, v. 36, p. 1-158.

Fraas, E., 1896, Die schwäbischen Trias-Saurier: Festgabe des Königlichen Naturalien-Cabinets in Stuttgart: Stuttgart, Schweizerbart, 18 p.

Fraas, O., 1877, *Aetosaurus ferratus* Fr. Die gepanzerte Vogel-Echse aus dem Stubensandstein bei Stuttgart: Festschrift zur Feier des vierhundertjährigen Jubiläums der Eberhard-Karls-Universität zu Tübingen, Wurttembergische naturwissenschaftliche Jahreshefte, v. 33, p. 1-22.

Geyer, O. F. and Gwinner, M. P., 1991, Geologie von Baden-Württemberg. Stuttgart, E. Schweizerbart'she Verlagsbuchhandlung, 482 p.

Groenewald, G. H. and Kitching, J. W., 1995, Biostratigraphy of the *Lystrosaurus* Assemblage Zone: South African Committee for Stratigraphy Biostratigraphy Series, no. 1, p. 35-39.

Hallam, A. 2002, How catastrophic was the end-Triassic mass extinction?: Lethaia, v. 35, p. 147-157.

Hancox, P. J., 2000, The continental Triassic of South Africa: Zentralblatt für Geologie und Paläontologie Teil I 1998, v. 11-12, p. 1285-1234.

Hancox, P. J., Damiani, R. J., and Rubidge, B. S., 2000, First occurrence of *Paracyclotosaurus* (Temnospondyli, Capitosauridae) in the Karoo Basin of South Africa and its biostratigraphic significance: South African Journal of Science, v. 96, p. 135-137.

Hancox, P. J., Shishkin, M. A., Rubidge, B. S. and Kitching, J. W., 1995, A threefold subdivision of the *Cynognathus* assemblage zone (Beaufort Group, South Africa) and its palaeogeographical implications: South African Journal of Science, v. 91, p. 143-144.

Heckert, A. B., 2001, The microvertebrate record of the Upper Triassic (Carnian) lower Chinle Group, southwestern U.S.A. and the early evolution of dinosaurs [Ph.D. thesis]: University of New Mexico, 465 p.

Heckert, A. B., 2004, Late Triassic microvertebrates from the lower Chinle Group (Otischalkian-Adamanian: Carnian): New Mexico Museum of Natural History and Science, Bulletin 27, 170 p.

Heckert, A. B., and Lucas, S. G., 1997, First use of ornithischian dinosaurs for biostratigraphic zonation of the Upper Triassic: Albertiana, v. 20, p. 58-63.

Heckert, A. B., and Lucas, S. G., 1998, First occurrence of *Aetosaurus* (Reptilia:Archosauria) in the Upper Triassic Chinle Group (USA) and its biochronological significance: Neues Jahrbuch für Geologie und Paläontologie Monatshefte, v. 1998, p. 604-612.

Heckert, A.B., and Lucas, S.G., 2000, Taxonomy, phylogeny, biostratigraphy, biochronology, paleobiogeography, and evolution of the Late Tri-

assic Aetosauria (Archosauria:Crurotarsi): Zentralblatt für Geologie und Paläontologie Teil I 1998 Heft 11-12, p. 1539-1587.

Heckert, A.B., and Lucas, S.G., 2002, Revised Upper Triassic stratigraphy of the Petrified Forest National Park, Arizona, U.S.A.: New Mexico Museum of Natural History and Science, Bulletin 21, p. 1-36.

Heckert, A. B., and Lucas, S. G., 2006, Micro- and small vertebrate biostratigraphy and biochronology of the Upper Triassic Chinle Group, southwestern USA: New Mexico Museum of Natural History and Science, Bulletin 37, p. 94-104.

Heckert, A. B., Hunt, A. P., and Lucas, S. G., 1996, Redescription of *Redondasuchus reseri*, a Late Triassic aetosaur (Reptilia:Archosauria) from New Mexico (U.S.A) and the biochronology and phylogeny of aetosaurs: Geobios, v. 29, p. 619-632.

Heckert, A. B., Lucas, S. G., and Hunt, A. P., 2005, Triassic vertebrate fossils in Arizona: New Mexico Museum of Natural History and Science Bulletin, v. 29, p. 16-44.

Heckert, A. B., Spielmann, J. A., Lucas, S. G. and Hunt, A. P., 2007, Biostratigraphic utility of the Upper Triassic Aetosaur *Tecovasuchus* (Archosauria:Stagonolepididae), an index taxon of St. Johnsian (Adamanian:Late Carnian) time: New Mexico Museum of Natural History and Science, Bulletin 41, this volume.

Heckert, A. B., Lucas, S. G., Rinehart, L. F., Spielmann, J. A., Hunt, A. P., and Kahle, R., 2006, Revision of the archosauromorph reptile *Trilophosaurus*, with a description of the first skull of *Trilophosaurus jacobsi*, from the Upper Triassic Chinle Group, West Texas, U.S.A.: Palaeontology, v. 49, p. 621-640.

Huber, P., Lucas, S. G., and Hunt, A. P., 1993, Vertebrate biochronology of the Newark Supergroup Triassic, eastern North America: New Mexico Museum of Natural History and Science, Bulletin 3, p. 179-186.

Huene, F. v., 1921, Neue Pseudosuchier un Coleurosaurier aus dem württembergischen Keuper: Acta Zoologica, v. 2, p. 329-403.

Hungerbühler, A., 1998, Cranial anatomy and diversity of the Norian phytosaurs of Southwestern Germany [Ph.D. thesis]: University of Bristol, 453 p.

Hungerbühler, A., 2001a, Status and phylogenetic relationships of the Late Triassic phytosaur *Rutiodon carolinensis*: Journal of Vertebrate Paleontology, v. 21, supplement to no. 3, p. 64A.

Hungerbühler, A., 2001b, The status and phylogenetic relationships of "*Zanclodon*" *arenaceus*: the earliest known phytosaur?: Paläontologische Zeitschrift, v. 75, p. 97-112.

Hungerbühler, A., 2002, The Late Triassic phytosaur *Mystriosuchus westphali*, with a revision of the genus: Palaeontology, v. 45, p. 377-418.

Hungerbühler, A. and Chatterjee, S., 2002, New phytosaurs from the upper Triassic of India: Journal of Vertebrate Paleontology, v. 22, supplement to no. 3, p. 68A.

Hungerbühler, A., Chatterjee, S. and Cunningham, D. P., 2002, A new phytosaur species from the Triassic of West Texas: New information on cranial anatomy, taxonomy, and sexual dimorphism in Pseudopalatinae: Journal of Vertebrate Paleontology, v. 23, supplement to no. 3, p. 63A-64A.

Hunt, A. P., 1989, A new ?ornithischian dinosaur from the Bull Canyon Formation (Upper Triassic) of east-central New Mexico;, *in* Lucas, S. G., and Hunt, A. P., eds., Dawn of the age of dinosaurs in the American Southwest: Albuquerque, New Mexico Museum of Natural History, p. 355-358.

Hunt, A.P., 1993, Revision of the Metoposauridae (Amphibia: Temnospondyli) and description of a new genus from western North America: Museum of Northern Arizona, Bulletin 59, p. 67-97.

Hunt, A P., 1994, Vertebrate paleontology and biostratigraphy of the Bull Canyon Formation (Chinle Group: Norian), east-central New Mexico with revisions of the families Metoposauridae (Amphibia: Temnospondyli) and Parasuchidae (Reptilia: Archosauria) [Ph.D. dissertation]: Albuquerque, University of New Mexico, 403 p.

Hunt, A. P., 2001, The vertebrate fauna, biostratigraphy and biochronology of the type Revueltian land-vertebrate faunachron, Bull Canyon Formation (Upper Triassic), east-central New Mexico: New Mexico Geological Society, Guidebook 52, p. 123-151.

Hunt, A. P., and Lucas, S. G., 1991a, The *Paleorhinus* biochron and the correlation of the non-marine Upper Triassic of Pangaea: Palaeontology, v. 34, p. 487-501.

Hunt, A. P. and Lucas, S. G., 1991b, A new aetosaur from the Redonda Formation (Late Triassic: middle Norian) of east-central New Mexico, USA. Neues Jahrbuch für Geologie und Paläontologie Monatshefte, v. 1991, p. 728-736.

Hunt, A. P. and Lucas, S. G., 1995,Vertebrate paleontology and biochronology of the lower Chinle Group (Upper Triassic), Santa Fe County, north-central New Mexico: New Mexico Geological Society, Guidebook 46, p. 243-246.

Hunt, A. P., Lucas, S. G. and Bircheff, P., 1993, Biochronological significance of the co-occurrence of the phytosaurs (Reptilia: Archosauria) *Angistorhinus* and *Rutiodon* in the Los Esteros Member of the Santa Rosa Formation, Santa Fe County, New Mexico, USA: New Mexico Museum of Natural History and Science, Bulletin, p. 203-204.

Hunt, A.P., Lucas, S.G., and Heckert, A.B., 2002, A Revueltian (Norian) phytosaur from the Sonsela Member of the Petrified Forest Formation (Chinle Group: Upper Triassic), Petrified Forest National Park, Arizona: New Mexico Museum of Natural History and Science, Bulletin 21, 165-169.

Hunt, A. P., Lucas, S. G., and Heckert, A. B., 2005, Definition and correlation of the Lamyan: A new biochronological unit for the nonmarine late Carnian (Late Triassic: New Mexico Geological Society Guidebook, v. 56, p. 357-366.

Ivakhhnenko, M. F., Golubev, V. K., Gubin, Y. M., Kalandadze, N. N., Novikov, I. V., Sennikov, A. G. and Rautian, A. S., 1997, Permskiye i Triasoviye tetrapodi vostochnoi Evropi [Permian and Triassic tetrapods of eastern Europe]. Moscow, GEOS, 216 p.

King, G. M., 1990, Dicynodonts and the end Permian event: Palaeontologica Africana, v. 27, p. 31-39.

King, G. M., 1991, Terrestrial tetrapods and the end Permian event: a comparison of analyses: Historical Biology, v. 5, p. 239-255.

Kirby, R.E., 1989, Late Triassic vertebrate localities of the Owl Rock member (Chinle Formation) in the Ward Terrace area of northern Arizona; *in* Lucas, S.G. and Hunt, A.P., eds., Dawn of the age of dinosaurs in the American Southwest, New Mexico Museum of Natural History, Albuquerque, p. 12-28.

Kirby, R.E., 1991, A vertebrate fauna from the Upper Triassic Owl Rock Member of the Chinle Formation in northern Arizona [M.S. thesis]: Northern Arizona University, Flagstaff, 476 p.

Kirby, R.E., 1993, Relationships of Late Triassic basin evolution and faunal replacement events in the southwestern United States: Perspectives from the upper part of the Chinle Formation in northern Arizona: New Mexico Museum of Natural History and Science, Bulletin 3, p. 233-242.

Kuhn, O., 1936, Weitere Parasuchier und Labyrinthodonten aus dem Blasensandstein des mittleren Keuper von Ebrach: Palaeontographica A, v. 83, p. 61-98.

Langer, M. C., 2005a, Studies on continental late Triassic tetrapod biochronology. I. The type locality of *Saturnalia tupiniquim* and the faunal succession in South Brazil: Journal of South American Earth Sciences, v. 19, p. 205-218.

Langer, M. C., 2005b, Studies on continental late Triassic tetrapod biochronology. II. The Ischigualastian and a Carnian global correlation: Journal of South American Earth Sciences, v. 19, p. 219-239.

Langer, M. C., and Schultz, C. L., 2000, A new species of the Late Triassic rhynchosaur *Hyperodapedon* from the Santa Maria Formation of south Brazil: Palaeontology, v. 43, p. 633-652.

Langer, M., Boniface, M., Cuny, G., and Barbieri, L., 2000a, The phylogenetic position of *Isalorhynchus genovefae*, a Late Triassic rhynchosaur from Madagascar: Annales de Paléontologie, v. 86, p. 101-127.

Langer, M. C., Ferigolo, J., and Schultz, C. L., 2000b, Heterochrony and tooth evolution in hyperodapedontine rhynchosaurs (Reptila, Diapsida): Lethaia, v. 33, p. 119-128.

Lehman, T. M., 1994, The saga of the Dockum Group and the case of the Texas/New Mexico boundary fault: New Mexico Bureau of Mines & Mineral Resources, Bulletin, v. 150, p. 37-51.

Lehman, T., and Chatterjee, S., 2005, Depositional setting and vertebrate

biostratigraphy of the Triassic Dockum Group of Texas: Journal of Earth Systems Science, v. 114, p. 325-351.

Long, R. A. and Ballew, K. L., 1985, Aetosaur dermal armor from the Late Triassic of southwestern North America, with special reference to material from the Chinle Formation of Petrified Forest National Park: Museum of Northern Arizona, Bulletin 54, p. 35-68.

Long, R. A. and Murry, P. A., 1995, Late Triassic (Carnian and Norian) tetrapods from the southwestern United States: New Mexico Museum of Natural History and Science, Bulletin 4, 254 p.

Lozovsky, V. R. and Shishkin, M. A. 1974. Pervaya nakhodkha labirintodontov v nizhnem Triase Mangyshlaka [First discovery of a labyrinthodont in the Lower Triassic of Mangyshlak]. Doklady Akademiya Nauk SSSR, 214: 169-172.

Lucas, S. G., 1990, Toward a vertebrate biochronology of the Triassic: Albertiana, v. 8, p. 36-41.

Lucas, S. G. 1993a, Vertebrate biochronology of the Triassic of China: New Mexico Museum of Natural History and Science, Bulletin 3, p. 301-306.

Lucas, S. G. 1993b, The Shansiodon biochron, Middle Triassic of Pangea: Albertiana, v. 11, p. 40-42.

Lucas, S. G., 1994, Triassic tetrapod extinctions and the compiled correlation effect: Canadian Society of Petroleum Geologists, Memoir 17, p. 869-875.

Lucas, S. G., 1997, Upper Triassic Chinle Group, western United states: A nonmarine standard for Late Triassic time; in Dickins, J. M. et al., eds., Late Paleozoic and early Mesozoic circum-Pacific events and their global correlation: Cambridge, Cambridge University Press, p. 209-228.

Lucas, S. G., 1998, Global Triassic tetrapod biostratigraphy and biochronology: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 143, p. 347-384.

Lucas, S. G., 1999, Tetrapod-based correlation of the nonmarine Triassic: Zentralblatt für Geologie und Paläontologie Teil I, v. 7-8, p. 497-521.

Lucas, S. G., 2001, Chinese fossil vertebrates. New York, Columbia University Press, 375 p.

Lucas, S. G., 2002, A new dicynodont from the Triassic of Brazil and the tetrapod biochronology of the Brazilian Triassic: New Mexico Museum of Natural History and Science, Bulletin 21, p. 131-141.

Lucas, S. G. and Harris, S. K. 1996. Taxonomic and biochronological significance of specimens of the Triassic dicynodont Dinodontosaurus Romer, 1943 in the Tübingen collection. Paläontologische Zeitschrift, 70: 603-622.

Lucas, S. G., and Heckert, A. B., 2001, The aetosaur Stagonolepis from the Upper Triassic of Brazil and its biochronological significance: Neues Jahrbuch für Geologie und Paläontologie Monatsheft, v. 2001, p. 719-732.

Lucas, S. G. and Huber, P., 2003, Vertebrate biostratigraphy and biochronology of the nonmarine Triassic; in LeTourneau, P. M. and Oolsen, P. E., eds., The great rift valleys of Pangea in eastern North America. Volume 2. Sedimentology and paleontology: New York, Columbia University Press, p. 143-191.

Lucas, S. G. and Hunt, A. P. 1993. Tetrapod biochronology of the Chinle Group (Upper Triassic), western United States. New Mexico Museum of Natural History and Science, Bulletin 3, p. 327-329.

Lucas, S. G., and Schoch, R. R., 2002, Triassic temnospondyl biostratigraphy, biochronology and correlation of the German Buntsandstein and North American Moenkopi Formation: Lethaia, v. 35, p. 97-106.

Lucas, S. G. and Tanner, L. H., 2004, Late Triassic extinction events: Albertiana, no. 31, p. 31-40.

Lucas, S. G. and Tanner, L. H., 2006, Fossil vertebrates and the position of the Triassic-Jurassic boundary: Journal of Vertebrate Paleontology, v. 26, supplement to no. 3, p. 91A.

Lucas, S. G., and Tanner, L. H., 2007, Tetrapod biostratigraphy and biochronology of the Triassic-Jurassic transition on the southern Colorado Plateau, USA: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 244, p. 242-256.

Lucas, S. G. and Wild, R. 1995. A Middle Triassic dicynodont from Germany and the biochronology of Triassic dicynodonts. Stuttgarter Beiträge zur Naturkunde, 220: 1-16.

Lucas, S. G., Anderson, O. J. and Hunt, A. P. 1994. Triassic stratigraphy and correlations, southern High Plains of New Mexico-Texas. New Mexico Bureau of Mines and Mineral Resources Bulletin, 150: 105-126.

Lucas, S. G., Heckert, A. B. and Harris, J. D., 1999, Biostratigraphic correlation based on cladistic phylogeny: An unparsimonious exercise: Geological Society of America, Abstracts with Programs, v. 31, p. 42.

Lucas, S. G., Heckert, A. B., and Hotton, N., III, 2002a, The rhynchosaur Hyperodapedon from the Upper Triassic Wyoming and its global biochronological significance: New Mexico Museum of Natural History and Science Bulletin, v. 21, p. 149-156.

Lucas, S. G., Heckert, A. B., and Huber, P., 1998b, Aetosaurus (Archosauromorpha) from the Upper Triassic of the Newark Supergroup and its biochronological significance: Palaeontology, v. 41, p. 1215-1230.

Lucas, S. G., Heckert, A. B. and Hunt, A. P.,1997a, Stratigraphy and biochronology of the Late Triassic Placerias quarry, eastern Arizona (U.S.A.): Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, v. 203, p. 23-46.

Lucas, S.G., Heckert, A.B., and Hunt, A.P., 2002b, A new species of the aetosaur Typothorax (Archosauria: Stagonolepididae) from the Upper Triassic of east-central New Mexico: New Mexico Museum of Natural History and Science, Bulletin 21, p. 221-234.

Lucas, S. G., Heckert, A. B. and Rinehart, L. F., 2007a, A giant skull, ontogenetic variation and taxonomic validity of the Late Triassic phytosaur Parasuchus: New Mexico Museum of Natural History and Science, Bulletin 41, this volume.

Lucas, S. G., Spielmann, J. A. and Hunt, A. P., 2007b, Biochronological significance of Late Triassic tetrapods from Krasiejów, Poland: New Mexico Museum of Natural History and Science, Bulletin 41, this volume.

Lucas, S. G., Wild, R. and Hunt, A. P., 1998a, Dyoplax O. FRAAS, a Triassic sphenosuchian from Germany: Stuttgarter Beiträge zur Naturkunde , no,. B263, 13 p.

Lucas, S. G., Heckert, A. B., Estep, J. W. and Anderson, O. J., 1997b, Stratigraphy of the Upper Triassic Chinle Group, Four Corners region: New Mexico Geological Society, Guidebook 48, p. 81-107.

Lucas, S. G., Heckert, A. B., Fraser, N. C., and Huber, P., 1999, Aetosaurus from the Upper Triassic of Great Britain and its biochronological significance: Neues Jahrbuch für Geologie und Paläontologie Monatshefte, v. 1999, p. 568-576.

Martz, J. W., 2002, The morphology and ontogeny of Typothorax coccinarum (Archosauria, Stagonolepididae) from the Upper Triassic of the American Southwest [M.S. thesis]: Texas Tech University, 279 p.

Martz, J. W., and Small, B. J., 2006, Tecovasuchus chatterjeei, a new aetosaur (Archosauria: Stagonolepididae) from the Tecovas Formation (Carnian, Upper Triassic) of Texas: Journal of Vertebrate Paleontology, v. 26, p. 308-320.

Martz, J., Mueller, W. and Small, B., 2003, Two new aetosaurs (Archosauria, Stagonolepididae) from the Uppwer Triassic of Texas and Colorado, and problems in aetosaur identification and taxonomy: Journal of Vertebrate Paleontology, v. 23, supplement to no. 3, p. 76A.

Milner, A. R., and Schoch, R. R., 2004, The latest metoposaurid amphibians from Europe: Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, v. 232, p. 231-252.

Nesbitt, S. J., 2003, Arizonasaurus and its implications for archosaur divergence: Proceedings of the Royal Society of London, B; Biology Letters, v. 03BL138, p. 1-4.

Ogg, J. G., 2004, The Triassic, in Gradstein, F. G., Ogg, J. G., and Smith, A. G., eds., A Geologic Time Scale 2004: Cambridge, Cambridge University Press.

Padian, K., 1990, The ornithischian form genus Revueltosaurus from the Petrified Forest of Arizona (Late Triassic: Norian; Chinle Formation): Journal of Vertebrate Paleontology, v. 10, p. 268-269.

Parker, W. G., 2007, Reassessment of the aetosaur 'Desmatosuchus' chamaensis with a reanalysis of the phylogeny of the Aetosauria (Archosauria: Pseudosuchia): Journal of Systematic Palaeontology, v. 5, p. 43-67.

Parker, W. G., Irmis, R. B., Nesbitt, S. J., Martz, J. W., and Browne, L. S., 2005, The Late Triassic pseudosuchian Revueltosaurus callenderi and

its implications of the diversity of early ornithischian dinosaurs: Proceedings of the Royal Society of London, B; Biology Letters, v. 272, p. 963-969.

Parrish, J. M., 1994, Cranial osteology of *Longosuchus meadei* and the phylogeny and distribution of the Aetosauria: Journal of Vertebrate Paleontology, v. 14, p. 196-209.

Rayfield, E. J., Barrett, P. M., McDonnell, R. A., and Willis, K. J., 2005, A geographical information system (GIS) study of Triassic vertebrate biochronology: Geological Magazine, v. 142, p. 327-354.

Retallack, G. J., Smith, R. M. H. and Ward, P. D., 2003, Vertebrate extinction across Permian-Triassic boundary in Karoo basin, South Africa: Geological Society of America Bulletin, v. 115, p. 1133-1152.

Schoch, R. R., 1999, Comparative osteology of *Mastodonsaurus giganteus* (Jaeger, 1828) from the Middle Triassic (Lettenkeuper: Longobardian) of Germany (Baden-Württemberg, Bayern, Thüringen): Stuttgarter Beiträge zur Naturkunde B, v. 278, p. 175.

Schoch, R. R., 2002, Stratigraphie und Taphonomie wirbeltierreicher Schichten im Unterkeuper (Mitteltrias) von Velberg (SW-Deutschland): Stuttgarter Beiträge zur Naturkunde B, no. 318, 30 p.

Schoch, R. R., and Milner, A. R., 2000, Sterospondyli: Stem-Sterospondyli, Rhinesuchidae, Rhytidostea, Trematosauroidea, Capitosauroidea, Encyclopedia of Paleoherpetology: München, Verlag Dr. Friedrich Pfeil, p. 203.

Schultz, C. L., 2005, Biostratigraphy of the non-marine Triassic: Is a global correlation based on tetrapod faunas possible?; *in* Koutsoukos, E. A. M., ed., Applied stratigraphy: Dordrecht, Springer, p. 123-145.

Shishkin, M. A., 2000, Olenekian-Anisian boundary in the history of land tetrapods; in Gradinaru, E., ed., Workshop on the Lower-Middle Triassic (Olenekian-Anisian) boundary, 7-10 June, Tulcea, Romania: Bucharest, Romanian National Committee of Geologists, p. 60-69.

Small, B. J., 1998, The occurrence of *Aetosaurus* in the Chinle Formation (Late Triassic, U.S.A.) and its biochronological significance: Neues Jahrbuch für Geologie und Paläontologie Monatshefte, v. 1998, p. 2

Spielmann, J. A., Lucas, S. G. and Hunt, A. P., 2006a, The vertebrate macrofauna of the Upper Triassic (Apachean) Redonda Formation, east-central New MexicoNew Mexico Museum of Natural History and Science, Bulletin 37, p. 502-509

Spielmann, J. A., Hunt, A. P., Lucas, S. G. and Heckert, A. B., 2006b, Revision of *Redondasuchus* (Archosauria: Aetosauria) from the Upper Triassic Redonda Formation, New Mexico, with description of a new species: New Mexico Museum of Natural History and Science, Bulletin 37, p. 583-587.

Spielmann, J. A., Lucas, S. G. and Heckert, A. B., 2007, Tetrapod fauna of the Upper Triassic (Revueltian) Owl Rock Formation, Chinle Group, Arizona: New Mexico Museum of Natural History and Science, Bulletin 41, this volume.

Steiner, M. B., 2006, The magnetic polarity time scale across the Permian-Triassic boundary: Geological Society, London, Special Publications, v. 265, p. 15-38.

Sulej, T., 2002, Species discrimination of the Late Triassic temnospondyl amphibian *Metoposaurus diagnosticus*: Acta Palaeontologica Polonica, v. 47, p. 535-546.

Tanner, L. H., Lucas, S. G. and Chapman, M. G., 2004. Assessing the record and causes of Late Triassic extinctions: Earth-Science Reviews, v. 65, p. 103-139.

Walker, A. D., 1961, Triassic reptiles from the Elgin area: *Stagonolepis*, *Dasygnathus*, and their allies: Philosophical Transactions of the Royal Society of London, B, v. 244, p. 103-204.

Wild, R., 1989., *Aetosaurus* (Reptilia: Thecodontia) from the Upper Triassic (Norian) of Cene near Bergamo, Italy, with a revision of the genus: Rivista del Museo Civico di Scienze Naturali, v. 14, p. 1-24.

Woody, D. T., 2003, Revised geological assessment of the Sonsela Member, Chinle Formation, Petrified Forest National Park, Arizona [M. S. thesis]: Flagstaff, Northern Arizona University, 205 p.

Woody, D. and Parker, W. G., 2004, Evidence for a transitional fauna within the Sonsela Member of the Chinle Formation, Petrified Forest National Park, Arizona: Journal of Vertebrate Paleontology, v. 24,supplement to no. 3, p. 132A.

Yin, H., Zhang, K., Tong, J., Yang, Z. and Wu, S., 2001, The global stratotype section and point (GSSP) of the Permian-Triassic boundary: Episodes, v. 24, p. 102-114.

APPENDIX

Rayfield et al. (2005) presented a putative "GIS study/test" of the Triassic tetrapod biostratigraphy and biochronology we developed in the 1990s (see text). Here, we review this article in detail to demonstrate that it is replete with factual errors, selective use of the literature, misrepresentations and misinterpretations. Page numbers used as headings here and figure and table callouts refer to Rayfield et al. (2005). "The text" refers to the preceding body of our article.

Page 327

1. The "massive and abrupt extinction of marine animals" at the Triassic-Jurassic boundary (TJB) has been called into question by Hallam (2002), Tanner et al. (2004) and Lucas and Tanner (2004), literature not cited by Rayfield et al.

2. Lucas (1994) did not argue for "a gradual, possibly competitive replacement" of tetrapods across the TJB.

3. "The standard stage-level division of the Triassic is based upon the stratigraphical distribution of ammonites in the European Alps" is erroneous. The current SGCS recognizes several stages defined on non-Alpine stratotypes, such as Induan and Olenekian. One of the two agreed-on GSSP's for the Triassic stages (base Induan) is defined by conodont biostratigraphy in China, and conodont biostratigraphy will define others.

Page 328

4. "Eight 'Land Vertebrate Faunachrons' ('LVFS') were identified, each comprising successive assemblage zones of Triassic tetrapod fossils" is misleading. The LVFs are time intervals between the FADs of key taxa. They have a characteristic tetrapod assemblage, but they are not temporally coextensive with assemblage zones of tetrapod fossils.

5. The "aim to test the LVF concept for the first time, using a Geographical Information Systems (GIS-based) approach" misleads on two accounts. First, there have already been many published tests of the LVF concept prior to Rayfield et al. (see the text), and, second, GIS is not able to test biochronology (see below).

Page 329

6. Figure 2 fails to account for Lucas et al.'s (2002a) reappraisal of the distribution of *Hyperodapedon*, although this is later referred to in the text.

7. The reference to Barnosky and Carrasco (2000) implies that somehow their GIS database (MIOMAP) has some relevance to biochronology, but it is not being used to evaluate biochronology simply because GIS cannot make such evaluations.

PAGES 330-333 (TABLE 1)

Many of the age assignments of the index taxa to the SGCS are identical to ours. However, the table contains numerous errors:

8. There is no verified record of *Mastodonsaurus* in the Bromsgrove Sandstone Formation.

9. Similarly, *Mastodonsaurus* is not known from the Schilfsandstein.

10. *Paleorhinus* (=*Parasuchus*) has no record in the middle Pekin Formation.

11. *Paleorhinus* (=*Parasuchus*) has no record in the Tecovas Formation.

12. *Metoposaurus* has no verifiable record in the Baldy Hill Formation.

13. *Metoposaurus* has no record in the Middle Stubensandstein (see the text).

14. *Rutiodon* does not occur in the lower Bull Canyon Formation.

15. *Rutiodon* has no record in the Owl Rock Formation.

16. *Rutiodon* has no record in the Grès à Avicula Contorta.

17. *Typothorax coccinarum* has no record in the Tres Lagunas Member of the Santa Rosa Formation (see the text).

18. There are no records of *Typothorax coccinarum* in the Trujillo Formation.

19. *Typothorax coccinarum* is not known from the Redonda Formation.

20. *Typothorax coccinarum* (indeed, no aetosaur) has ever been documented from the Sloan Canyon Formation.

21. There is no evidence that the aetosaur record in "Lithofaces Association II" of the Deep River Basin, North Carolina is late Carnian. The cited correlation is based on fishes and "magnetostratigraphy in prep.," neither of which reliably indicate a late Carnian age.

Page 334

22. It is interesting that "Early Triassic LVFs are not considered herein…because most of their known assemblages occur outside of the western Northern Hemisphere" even though the same could certainly be said of the Berdyankian LVF.

23. The analysis is so frought with basic errors (see comments on Table 1 above) that the claim that "our chosen area and timeframe offer enough information to provide a thorough test of the validity of Middle and Late Triassic LVFs" is questionable.

24. Supposedly "care was taken to ensure that taxon and formation ages were estimated using tetrapod and megafloral-biochronology-independent means (e.g., magnetostratigraphy, radiometric dating, palynology) in order to avoid circularity and non-independence of data (Tables 1, 2)." But, not enough care was taken to produces tables free of numerous errors (see comments on Table 1, above and Table 2, below). Furthermore, are palynological ages really independent of megafloral ages? And, how do you assign a late Norian-Rhaetain age to the Sloan Canyon Formation based on "tetrapod trackways" only (as is done in Table 1), and then claim this "correlation" is independent of vertebrate biostratigraphy?

25. The claim is made that through a "GIS database analysis" the "distribution of type LVF assemblage taxa and key index taxa…through space and time using attribute selection…" is being evaluated. In reality, once a time ordering of tetrapod assemblages is achieved, the distribution of taxa can be determined without GIS. So, to claim that GIS is somehow being used to evaluate the biochronology is to claim for GIS something it cannot do and is not needed to do.

26. How megafloral data can be used "in testing LVF stability" is impossible to understand. Does conodont biostratigraphy test the stability of ammonite biostratigraphy?

Page 335

27. Some of the errors in Table 1 are incorporated into the temporal ranges in Figure 3. However, the figure actually indicates very robust index fossils for the Otischalkian, for example, so it does not support (contradicts) the later claim that the Otischalkian is not a useful biochronologic unit.

28. We agree that grade-level correlations are less desirable than shared alpha taxa, but to state that "ghost lineages between sister-taxa may persist for millions of years, such that taxa related at the familial level need not exist in the same temporal range" is to present an assumed and undocumented hypothetical with regard to erythrosuchid-based Middle Triassic correlations.

Page 336

29. Were the Moenkopi erythrosuchid identified as *Shanisuchus*, it would support a China-western North America correlation, which is a global terrestrial correlation across Middle Triassic Pangea. Contrary to what is said by Rayfield et al., this would make *Shanisuchus* a quite useful Perovkan index taxon.

30. We do not consider "regional" to equate to "western Northern Hemisphere" (=North America and Europe). This strikes us as a geographical area larger than a "region."

31. "None of the five index taxa [of the Beryankian LVF] are present in North America" is true but misleading, simply because no Berdyankian-age tetrapod assemblage has ever been found in North America.

32. The Berdyankian is Ladinian-Carnian in age, so the statement that the Berdyankian index taxon *Exaeretodon* "ranges from Ladinian- to Carnian-aged strata in South America" is irrelevant to its utility as an index taxon.

33. As above, there are no documented records of *Mastondonsaurus* in the Bromsgrove Sandstone Formation or in the Schilfsandstein. Therefore, the statement that "*Mastondonsaurus* appears not to be a temporally restricted index taxon" is false.

Page 337

34. The temporal ranges claimed for *Macronemus* and *Ticinosuchus* (also see Fig. 3) are much longer than their actual ranges.

35. The cladotaxonomic conclusions of Fara and Hungerbühler (2000) and Hungerbühler (2001b) used by Rayfield et al. to undermine the taxonomy of *Paleorhinus* (=*Parasuchus*) have been refuted by Lucas et al. (2007a).

36. The statement that "*Paleorhinus* has not been diagnosed in terms of derived character states; its diagnostic feature, the position of the external naris relative to the antorbital fenestra, is plesiomorphic" is not followed up, but presumably represents the cladotaxonomic reasoning discussed above in the text and rejected by us.

37. In Table 1 *Paleorhinus* is listed as having a marine Carnian record in the Austrian Opponitzer Schichten, and here it is claimed the specimen

"may represent an indeterminate small basal phytosaur." Which is it?

38. The Bluewater Creek record of *Paleorhinus* (=*Parasuchus*) may be Otischalkian, as discussed in the text.

39. Milner and Schoch's (2004) claim of a *Metoposaurus* record in the Stubensandstein, quoted here, is discussed at length in the text and rejected.

Page 338

40. "The taxonomic instability of both taxa [*Paleorhinus* and *Metoposaurus*] renders them problematic global biochronological markers," yet the "taxonomic instability" of *Metoposaurus* is in no way discussed.

41. Again, "the taxonomic status of both genera [*Metoposaurus* and *Paleorhinus*] needs further attention before they can be used confidently for global biochronology," yet not even a cladotaxonomic comment is presented by Rayfield et al. regarding the taxonomy of *Metoposaurus*.

42. As documented by Lucas et al. (2007b), *Stagonolepis* now has a known temporal range of Otischalkian-Adamanian, obviating much of the text on page 338.

43. Martz et al. (2003) are cited as indicating that there are "problems in identifying aetosaurs from isolated and incomplete scutes" (but see Heckert et al., 2007), and then it is claimed this is a factor that "hinder[s] the potential of *Stagonolepis* as a useful global Adamanian index fossil." Yet, no published identifications of *Stagonolepis* are actually questioned by Rayfield et al.

44. *Paleorhinus* and *Rutiodon* do not co-occur in the Tecovas Formation in West Texas; they are stratigraphically separate in West Texas (Hunt and Lucas, 1991).

Page 339

45. There are no records of *Paleorhinus* in the middle Pekin Formation of the Newark Supergroup (also see Table 1).

46. There are no records of *Rutiodon* in the Owl Rock Formation in Arizona. The reference cited for this record (Kirby, 1989) makes no definite assignment of an Owl Rock phytosaur to *Rutiodon*. In fact, all subsequent workers have assigned the Owl Rock phytosaurs to *Pseudopalatus* (Kirby, 1991, 1993; Spielmann et al., 2007).

47. Interestingly, *Rutiodon*? is listed from the Grès à Avicula Contorta in France, but here it is acknowledged that this record – based on isolated teeth and a premaxilla – has been dismissed as an unjustified identification (Lucas and Huber, 2003), yet at the same time it is presented as a possible Norian record of *Rutiodon* (also see Fig. 7). Which is it?

48. The conclusion that "there is, therefore, a strong argument for amalgamating the Northern Hemisphere Otischalkian-Adamanian biochrons into a coarser late Carnian unit" does not follow from preceding text. Indeed, once the obvious errors are removed from Table 1 and Figure 3, Rayfield et al.'s (2005) own analysis does not support their conclusion.

49. The statement "there is some disagreement over the status of supposed '*Aetosaurus*' remains" finds no support in the work of those who have actually studied aetosaurs (see the text).

50. The unfounded claim that *Aetosaurus* has a long "ghost lineage" and "therefore, one should expect to find *Aetosaurus* in pre-Norian strata" is made here and addressed above in the text.

Page 340

51. Had Rayfield et al. carefully read Lucas et al. (2002b), they would not repeat the error (also see Table 1) of claiming that *Typothorax coccinarum* has a "late Carnian" record in New Mexico.

52. The errors (Table 1) regarding Apachean records of *Typothorax* (especially in the Sloan Canyon Formation of New Mexico, where no aetosaur fossil has ever been found) are repeated here.

53. On the one hand, an abstract by Hungerbühler et al. (2003) is cited as authority that *Redondasaurus* is a synonym of *Pseudopalatus*, yet a published article by Hungerbühler (2002) upholding the distinctiveness of *Redondasaurus* is ignored, clearly demonstrating a selective citing of the relevant scientific literature.

54. The megafloral analysis begun here is heavily rooted in circular correlation built into Table 2 – such as using the plant megafossils to determine the ages of the plant megafossils (example: *Eoginkoites* from the Popo Agie Formation in Table 2). This directly contradicts the statement in point 24 above.

Page 341

55. The ranges claimed and depicted in Figure 4 and Table 2 should be compared to the Chinle Group megafloral ranges depicted by Lucas (1997, fig. 23.8). Lucas compiled the actual lithostratigraphic ordering of the megafossil plant genera in the Chinle Group and provide better temporal resolution of the megaflora than Table 2 of Rayfield et al.

56. Rayfield et al. evaluate an out-of-date plant biostratigraphy based on Ash (1980), overlooking Ash (1987), who subdivided his *Dinophyton* floral zone into lower (*Dinophyton*) and upper (*Sanmiguelia*) floral zones. This is part of the reason why some of the "*Dinophyton* floral zone" records listed in Table 2 are erroneously recorded as Norian.

57. The statement that "megafloral records do not allow recognition of distinct Carnian-aged Otischalkian and Adamanian biochrons" is misleading, as Otischalkian and Adamanian are based on vertebrate evolution, not plant evolution. Furthermore, Lucas' (1997) analysis of Chinle plant distribution suggests that there are distinct megafloras in Otischalkian and Adamanian strata.

58. Again, the succeeding statement that "megafloral records neither support nor contradict the LVF biochron divisions proposed for these intervals [Anisian-Ladinian, Norian-Rhaetian]" is irrelevant to tetrapod biostratigraphy.

Pages 342-343

59. Some of the problems/errors in Table 2 have already been discussed above. Claims of Norian records of *Pagiophyllum* and *Dinophyton* are erroneous (Ash, 1980; Lucas, 1997).

60. The claim that "the distribution of the Otischalkian index taxa *Metoposaurus* and *Angistorhinus* appears to be influenced by depositional environment" is based on a very imprecise and error-laden assessment, and readily rejected (see below).

61. "*Metoposaurus* is found in various high-energy environments." But, on the one hand, Rayfield et al. claim that *Metoposaurus* records in the western USA, Nova Scotia and western Europe are "generally found in conglomeratic or channel sandstone deposits" or in "braided river channels." On the other hand they cite Milner and Schoch (2004) as authority that "German *Metoposaurus* remains were more abundant in the playa lake environments [low energy] of the Lehrbergschichten…" Which is it?

62. The statement that "*Angistorhinus* tends to be deposited [sic, how is a fossil taxon deposited?] in low-energy settings such as the floodplain or low-energy stream deposits" is largely a taphonomic artifact, as a complete enough skull of a phytosaur to be identified as *Angistorhinus* is unlikely to be preserved in a high energy deposit.

63. Figure 5, a supposed "GIS-derived correlation of *Metoposaurus* to high-energy environments and *Angistorhinus* to low-energy environments" is replete with errors. Thus, *Metoposaurus* records in the "playa lake environments" of the German Lehrbergschichten and the marine "Raibl beds Dolomia di Forni" are "high-energy environments" equated by the figure to the fluvial environments of the Blasensandstein, Kieselsandstein and Schilfsandstein. The unverified record of *Metoposaurus* in the Baldy Hill Formation of Oklahoma (see above) is incorporated into the figure. In the map of part of the western USA, the geographic region from Santa Rosa, New Mexico through northeastern Arizona/southeastern Utah is shown on the map (Fig. 5a) as "perceived ocean," even though the Chinle deposits within the "ocean" are also labeled as "conglomeratic or channel sandstone depositional environments." (It has long been known that the Late Triassic shoreline of western Pangea is much farther west than shown in Figure 5a). Clearly, the figure is full of errors that undermine its value as a "GIS derived correlation."

64. "Analysis of Otischalkian taxa reveals that the aetosaur *Longosuchus* is only found in association with coals." Yet, there are no coals in the Upper Triassic of West Texas, where most *Longosuchus* records occur, or associated with its Moroccan record as well. Only in North Carolina are there coal beds in the same depositional basin as *Longosuchus* fossils, though there is no clear association of the tetrapod with a coal bed (which could lead to the kind of paleoclimatic influences that Rayfield et al. hope to make).

65. The follow-up statement that "*Longosuchus* has the potential to act a regional index taxon for North American Otischalkian time if further occurrences appear outside of humid, coal-containing environments" can be dimissed.

66. Figure 6 also embodies many errors, such as omitting the record of *Redondasaurus* in the Wingate Sandstone of southeastern Utah (Lucas et al., 1997b). Note that the western North American seaway shown in Figure 5a is absent in Figure 6a (and Figures 7a and 8a), though all are supposedly derived from the same paleogeographic base map.

67. The statement that "Otischalkian *Paleorhinus* and Adamanian *Rutiodon* only co-occur in warm temperate or tropical environments" misleads, as the taxa have only one co-occurrence in the Chinle Group of Arizona (see text).

68. The statement "*Paleorhinus* is found without *Rutiodon* in the Popo Agie Formation of the western USA" is supposed to convey climate information, but *Rutiodon* does not occur in the Popo Agie Formation because it is Otischalkian, and thus, by definition, pre-dates *Rutiodon* records (also see Table 1).

69. The succeeding statements that "in warmer, wetter climes, an increase in resource availability enabled both taxa [*Paleorhinus* and *Rutiodon*] to co-exist" and "resource depletion in arid conditions may have resulted in *Paleorhinus* succeeding in the western USA, whereas *Rutiodon* succeeded in the east" are unsupportable, given the near total temporal separation of the two genera.

70. Given that there are no Upper Triassic coal deposits in the American Southwest, the statement that "both *Rutiodon* and *Stagonolepis* are found in association with coal deposits across southern North America" is incorrect. The continuation, that they are found "in arid European deposits" is incorrect for several reasons, including there are no European *Rutiodon* records, and *Stagonolepis* records in Europe are in the lower part of the Middle Keuper, a wet interval of sedimentation. Finally, the claim that *Rutiodon* and *Stagonolepis* are found in association with "calcretes and evaporates in the northern basins of the Newark Supergroup" also lacks a factual basis, especially because *Stagonolepis* is not known from any of the Newark basins.

71. The statement that *Aetosaurus* "tends to prefer arid environments" lacks supporting data and is false based on our own documentation of its distribution (e.g., Lucas et al., 1998b).

72. Given the erroneous base maps, incorrect correlations, inconsistencies and imprecise level of discrimination of depositional environments and climatic indicators, it is not surprising that "identifying climatic biases that might have acted on megafloral distribution is also problematic." The entire analysis is problematic because its database is inadequate.

73. Errors in Figures 7 and 8 have been discussed above; their largest error is that both figures do not accurately depict the distributions of the taxa whose distribution is being analyzed.

74. The discussion of megafloral restrictions to depositional environments and climate is meaningless, as no information on the taphonomic biases (taphofacies) of the megaplant records are considered.

75. The text repeats reference to the erroneous Revueltian records of *Dinophyton* and *Pagiophyllum* listed in Table 2.

76. The conclusions reiterate many of the mistakes, misrepresentations and misinterpretations of the previous text. Given the sheer quantity of errors in the text of Rayfield et al. (see above), almost all of the conclusions of the article can be rejected.