

Global Permian tetrapod biostratigraphy and biochronology

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Abstract: The most extensive Permian tetrapod (amphibian and reptile) fossil records from the western United States (New Mexico–Texas) and South Africa provide the basis for definition of 10 land-vertebrate faunachrons that encompass Permian time. These are (in ascending order): the Coyotean, Seymouran, Mitchellcreekian, Redtankian, Littlecrotonian, Kapteinskraalian, Gamkan, Hoedemakeraan, Steilkransian and Platbergian. These faunachrons provide a biochronological framework with which to determine and discuss the age relationships of Permian tetrapod faunas. Their correlation to the marine time scale and its numerical calibrations indicate that the Coyotean is a relatively long time interval of about 20 Ma, whereas most of the other faunachrons are much shorter, about 1–2 Ma long each. The Platbergian may also be relatively long, 14 Ma, although this is not certain. This suggests slow rates of terrestrial tetrapod faunal turnover during most of the Early Permian and late Middle to Late Permian, but more rapid rates of turnover during the latest Early and most of the Middle Permian, especially during the explosive initial diversification of therapsids.

Permian tetrapod (amphibian and reptile) fossils are widely distributed (Fig. 1) and have long provided a basis for non-marine biostratigraphy and biochronology (see reviews by Lucas 1998*a*, 2002, 2004). Here, I document a formal global Permian tetrapod biochronology that recognizes 10 time intervals (land-vertebrate faunachrons) (Lucas 2005*d*). This biochronology is based on the body-fossil record of tetrapods and provides a tetrapod-based time scale that can be used to determine and discuss the temporal relationships of Permian tetrapod assemblages. It can also be cross-correlated with reasonable precision to the standard global chronostratigraphical scale for the Permian, which is based on marine biostratigraphy. This correlation, which can be numerically calibrated, indicates a wide range of evolutionary turnover rates of tetrapods during the Permian.

Abbreviations and terminology

Biostratigraphy documents the distribution of fossils in strata, whereas biochronology is concerned with the temporal distribution of taxa. The following abbreviations are used in the text: FAD, first appearance datum (a biochronological event); HO, highest occurrence (a biostratigraphic datum); LAD, last appearance datum (a biochronological event); LVF, land-vertebrate faunachron; LO, lowest occurrence (a biostratigraphic datum); SGCS, standard global chronostratigraphic scale, which is the global time scale based on marine biostratigraphy (Wardlaw *et al.* 2004).

In this paper, pelycosaurian-grade (primitive basal) synapsids are simply referred to as pelycosaurids. Advanced basal synapsids are referred to as therapsids, and the term ‘reptile’ is used instead of ‘amniote’.

Problems and procedures

Most of the problems with developing a Palaeozoic (Late Devonian, Carboniferous and Permian) tetrapod biostratigraphy and biochronology reduce to one problem: the rarity or lack of good Palaeozoic tetrapod index fossils. Good index fossils are easily identified, abundant and have a broad geographical (facies) range but a short stratigraphical (temporal) range. Few, if any, Devonian–Carboniferous tetrapod genera or species meet these criteria (Carroll 1979; Lucas 2000). Only in the Permian do some Palaeozoic tetrapod taxa qualify as good index fossils, and most of these are of Middle to Late Permian age. Indeed, as tetrapod abundance, diversity and breadth of geographic distribution (globalization) increases through the Palaeozoic, the ability to use tetrapods in biostratigraphy and biochronology increases (Fig. 2).

Much of the published discussion of Palaeozoic tetrapod distribution has focused on ecological or taphonomic controls of their distribution. For example, many workers have stressed the differences between Palaeozoic tetrapod records in coal-bearing strata (‘coal measures’) and red beds (e.g. Rayner 1971), noting that it is difficult

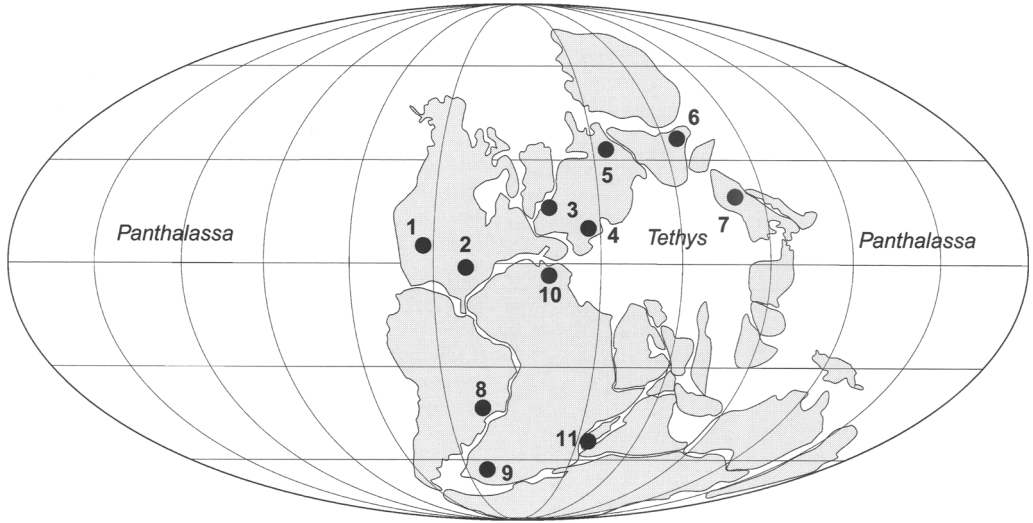


Fig. 1. Map of Permian Pangaea showing principal tetrapod localities. 1, western USA; 2, eastern USA (Dunkard); 3, Scotland; 4, western Europe (Rotliegend); 5, Russian Urals; 6, Junggur Basin, China; 7, Ordos Basin, China; 8, Paraná Basin, Brazil; 9, Karoo Basin, South Africa; 10, Morocco; 11, southern Madagascar.

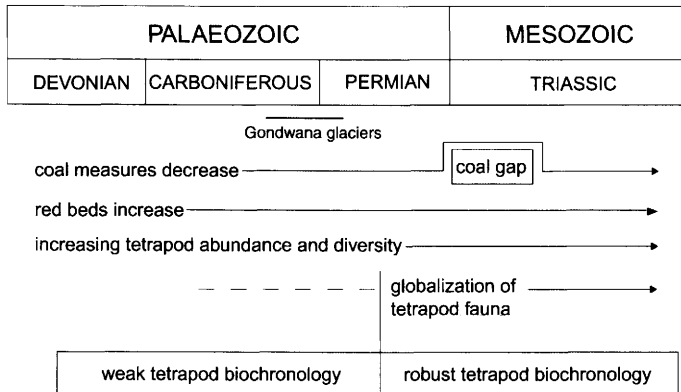


Fig. 2. Some parameters of the Devonian-Triassic world and an evaluation of the relative strength of tetrapod biochronology during that time interval.

to correlate between these two broadly conceived lithofacies. Other discussions explore in detail the sedimentological and taphonomical context of Palaeozoic tetrapod localities, indicating (or at least implying) that factors such as changes in climate or other environmental factors and taphonomic bias are the primary controls of Palaeozoic tetrapod distribution, not the actual temporal ranges of the tetrapod taxa themselves (e.g. Olson 1962; Olson & Vaughn 1970; Carroll 1979, 1997; Milner *et al.* 1986; Eberth *et al.* 2000). While these arguments have their merits – taphonomical and palaeoenvironmental factors do control the distributions of some tetrapod

taxa – all Palaeozoic tetrapod taxa had distinct stratigraphic (temporal) ranges that make them of potential use in biostratigraphy (biochronology). This is particularly the case for some Permian tetrapod taxa, and this allows development of a global biostratigraphy and biochronology based on the record of Permian tetrapods (Lucas 2002, 2005*d*).

The subdivision of Permian time documented here is a biochronological scheme of 10 land-vertebrate faunachrons (Fig. 3). Lucas (1998*b*) explained the conceptual and methodological basis of such a scheme. The beginning of each LVF is defined by the FAD of a tetrapod genus,

PER	EPOCH	LVFs	FADs	New Mexico, USA	Texas, USA	South Africa							
PERMIAN	LATE (Lopingian)	Platbergian	← <i>Lystrosaurus</i>			Balfour Formation							
		MIDDLE (Guadalupian)	Steilkransian			← <i>Dicynodon</i>			Teekloof Formation				
	Hoedemakeran		← <i>Oudenodon</i>										
	Gamkan		← <i>Tropidostoma</i>										
	Kapteinskraalian		← <i>Tapinocephalus</i>										
	EARLY (Cisuralian)		Littlecrotonian			← <i>Eodicynodon</i>					Abrahamskraal Formation		
			Redtankian			← <i>Angelosaurus</i>							
			Mitchellcreekian			← <i>Labidosaurus</i>							
			Seymourian			← <i>Mycterosaurus</i>							
			Coyotean			← <i>Seymouria</i>							
						← <i>Sphenacodon</i>							
		PENNSYLVANIAN											

PERMIAN	NEW MEXICO, USA	TEXAS, USA	SOUTH AFRICA				
MIDDLE (Guadalupian)							
				EARLY (Cisuralian)			

Fig. 3. The composite standard used to create a global tetrapod biochronology for the Permian.

so the end of an LVF is defined by the beginning of the succeeding LVF. The temporal succession of the FADs that define the beginnings of the LVFs is well established and allows all of Permian time to be encompassed by the LVFs. The primary basis for characterization of each LVF is a characteristic tetrapod assemblage that well represents the tetrapod fauna of the time interval. Robust index fossils of each LVF are temporally restricted, common, widespread and easily identified, so they do not include rare taxa restricted to a LVF, usually as a single record. The LVFs proposed here are the formalization (with some modification) of the biochronological scheme first proposed informally by Lucas (2002) and a detailed documentation of this scheme as presented by Lucas (2005d).

In this paper, the genus is the operational taxonomic unit for biostratigraphy. This is because most species-level taxa of Permian tetrapods are meaningless for correlation, as they are usually based on a single specimen or a local assemblage of well-preserved material and cannot be recognized at multiple localities (Williston 1915; Romer 1928). However, some species of Permian tetrapod genera (such as *Seymouria*

and *Bolosaurus*) are of use in correlation, and taxonomic revisions of some other genera (such as *Eryops* and *Dimetrodon*) should produce species-level taxa of value to biostratigraphy. For example, Werneburg (1989) has also argued that species lineages (chronocones) provide a more precise biostratigraphy than genus-based correlations. I agree with him in principle, but am unable to construct meaningful species lineages for most of the Permian tetrapod genera that are of value to a global biochronology. Nevertheless, where possible I do discuss species-level distinctions that are of use to correlation and that may be further developed to refine the biochronological framework proposed here.

The record of Permian tetrapods

The most extensive records of Permian tetrapods are from the western United States, western Europe, the Russian Urals, northern China and South Africa (Fig. 1). Relatively recent reviews of part or all of the Permian tetrapod record include Anderson & Cruickshank (1978), Olson (1989a), Milner (1990, 1993), Olson & Chudinov (1992),

Rubidge (1995a), Ivakhnenko *et al.* (1997), Berman *et al.* (1997), Lucas (1998a, 2002, 2004) and Rubidge & Sidor (2001). As extensive and long studied as the Permian record of tetrapods is, it is not without biases and imperfections. Most significant is the virtual geographic restriction of Early Permian tetrapods to the United States and western Europe, and the global gap in part of the Middle Permian tetrapod fossil record (Lucas 2004).

Note also that the biochronological framework proposed here has limitations. Thus, it cannot correlate endemic assemblages, such as that described from the Moradi Formation in Niger (Sidor *et al.* 2005), or isolated records, such as the discosauriscid seymouriamorph record from Tadjikistan (Ivakhnenko 1981).

Previous studies

Previous attempts to delineate a global tetrapod biostratigraphy or biochronology of the Permian are few (Fig. 4). Romer (1966, 1973) divided the Permian tetrapod record into three 'stages' that represent a three-fold subdivision of the Permian

into Early (= Cisuralian on the SGCS), Middle (= part of the Guadalupian on the SGCS) and Late (= latter part of Guadalupian and Lopingian on the SGCS). As Romer noted, 'cotylosaurs' (his sense) and pelycosaurs dominate the early stage, best known from North America and the western European Rotliegend. The intermediate stage is dominated by therapsids and known mostly from South Africa and the Russian Urals. The third stage (Romer also called it the 'final phase') is dominated by advanced therapsids known mostly from South Africa.

Romer, thus, was decades ahead of the marine biostratigraphers in recognizing a more logical division of the Permian into three time intervals (or Epochs) instead of two. Indeed, it is also amazing that some of the Early Permian tetrapod biochronology documented here was already presaged by a remarkable and little utilized article by Romer (1928). In this article, Romer identified five stratigraphic zones (0-4) based on tetrapod fossils from the Texas Lower Permian section, and his zones nearly correspond to the faunachrons used here. Thus, Romer's zone 0

Romer (1966, 1973)	Anderson & Cruickshank (1978)	Cooper (1982)	Efremov (1937, 1952) Russia	Ivakhnenko <i>et al.</i> (1997) Russia	Rubidge <i>et al.</i> (1995) South Africa		
final stage (Upper Permian)	endothiodontid/dicynodontid empire	17	Zone IV	Archosaurus rossicus Zone	Dicynodon Assemblage Zone		
		16		Cistecephalus Zone		Scutosaurus karpinskii Zone	
						Proelginia permiana Zone	
						Deltavjatia vjatkensis Zone	
intermediate stage (Middle Permian)	tapinocephalid empire	15	"Zone III"	Ulemosaurus svjagensis Zone	Tropidostoma Assemblage Zone		
		14		Robertia Zone	Estemmenosuchus uralensis Zone	Pristerognathus Assemblage Zone	
		13	Zone II	Parabradysaurus silantjevi Zone	Tapinocephalus Assemblage Zone		
		12		Otsheria Zone			
		early stage (Lower Permian)	edaphosaurid empire	11	Zone I	Clamorosaurus nocturnus Zone	Eodicynodon Assemblage Zone
				10		Dimacrodon Zone	
9	Titanophoneus Superzone			[Hatched]	[Hatched]		
8							
7							
6							
5							
4							
3							
2							
1							

Fig. 4. Previously proposed schemes of Permian tetrapod biostratigraphy and/or biochronology.

approximates to the Coyotean, his zones 1 and 2 approximate to the Seymouran, his zone 3 is the Mitchellcreekian and his zone 4 is the Redtankian.

Anderson & Cruickshank (1978) recognized the same broad global divisions as Romer (1966, 1973), but they recast them as 'empires' (essentially the same concept as the chronofaunas of Olson 1952). Anderson & Cruickshank (1978, charts 2.1–2.2) also listed 17 Permian tetrapod zones, but did not explicitly define them (Fig. 4). However, from their chart 2.1, it is clear that zones 1–12 are based on the classical Texas stratigraphic units (1 = Pueblo Formation; 2 = Moran Formation; 3 = Putnam Formation; 4 = Admiral Formation; 5 = Belle Plains Formation; 6 = Clyde Formation; 7 = Lueders Formation; 8 = Arroyo Formation; 9 = Vale Formation; 10 = Choza Formation; 11 = San Angelo Formation; 12 = Flowerpot Formation), while zones 13 and 14 are equivalent to the Russian zones proposed by Efremov (1937) (13 = Zone I; 14 = Zones II and III), and the youngest zones are those of the South African Karoo Basin (15 = *Tapinocephalus* Zone; 16 = *Cistecephalus* Zone; 17 = *Daptocephalus* [= *Dicynodon*] Zone).

Cooper (1982) published a Middle to Late Permian tetrapod biostratigraphy very similar to zones 11–17 of Anderson & Cruickshank (1978), but with different terminology (Fig. 4). Thus, Cooper's (1982) *Dimacrodon* Zone is based on the vertebrate fossil assemblages of the San Angelo and Flowerpot formations of Texas (Olson 1962), while his *Otsheria* Zone is equivalent to Russian Zone I, his *Venyukovia* Zone to Russian Zone II, and his *Robertia* Zone to the *Tapinocephalus* Zone. Cooper (1982) assigned the *Lystrosaurus* Zone to the Permian, although most workers consider it (or most of it) to be Triassic.

Lucas (2002) proposed an informal Permian tetrapod biochronology that consisted of 10 faunachrons, labeled A–J. The LVFs documented here are a formalization of this scheme with some modifications that correct errors in Lucas (2002) and reflect a more detailed understanding of the temporal distribution of Permian tetrapods (also see Lucas 2004). This article thus provides detailed documentation of the scheme formalized in brief by Lucas (2005*d*).

There have been no other explicit attempts to develop a global biostratigraphy or biochronology of Permian tetrapods, although correlation charts of the Permian tetrapod record are numerous (e.g. Romer 1966; Anderson 1981; Cheng 1981; Olson 1989*a*; Olson & Chudinov 1992). Nevertheless, two regional schemes of Permian tetrapod biostratigraphy have been

extremely important (Fig. 4). Efremov (e.g. 1937, 1940) proposed a succession of four tetrapod 'zones' for the Middle to Upper Permian of the Russian Urals. Olson (1957) provided a useful English-language review of this record (also see Olson 1962; Olson & Chudinov 1992). Zone I is also called the Ocherian dinocephalian complex, and Zone II is the Isheevan dinocephalian complex. 'Zone III' lacks tetrapods, and Zone IV has been called the pareiasaurian faunal complex.

Ivakhnenko *et al.* (1997; also see Golubev, 1998, 2005) recently recast the Russian Permian tetrapod record in a new biostratigraphical scheme. They recognized two 'superzones': a *Titanophoneus* 'Superzone' equivalent to Zones I and II of Efremov (1937), and a *Scutosaurus* 'Superzone' equivalent to Zone IV of Efremov (Fig. 4). These 'superzones' are divided into eight zones, largely based on the stratigraphical ranges of dinocephalians. Furthermore, two of the zones in the *Scutosaurus* Superzone are divided into subzones based on the succession of chroniosuchian temnospondyls (Golubev 1998). The recent summary of the Permian tetrapod record in the southeastern Urals (Tverdokhlebov *et al.* 2005) does not modify the existing scheme of tetrapod biostratigraphy in the Russian section.

Rubidge *et al.* (1995) reviewed the evolution of the biostratigraphic understanding of the South African succession of Permian tetrapod assemblage zones originally proposed by Broom (1906, 1907, 1909) and Watson (1914*a, b*) and later elaborated by Kitching (1977) and Keyser & Smith (1977–1978). The current succession recognizes six assemblage zones of Mid- to Late Permian age (Fig. 4).

Composite standard

The most extensive Lower Permian tetrapod record is from the western United States, especially from Texas, Oklahoma and New Mexico (e.g. Olson 1967; Simpson 1979; Hook 1989; Berman 1993). The New Mexican and Texas records are used here to construct the Early Permian tetrapod biochronology of five LVFs (Fig. 3).

Fossil vertebrates have been collected from the non-marine Permian red beds in north-central Texas since the 1870s (see historical review by Craddock & Hook 1989). The collected vertebrate fossils have been published extensively by E. D. Cope, E. C. Case, S. W. Williston, A. S. Romer and E. C. Olson, among others, and they provide the basis for much of what is known about the Early Permian evolution of tetrapods.

The lithostratigraphical nomenclature long applied to the Texas section was that of Plummer

Plummer and Moore (1921)		Hentz (1988)		this paper						
Clear Fork Group	Choza	Clear Fork Group	undivided	Clear Fork Group	Choza					
	Vale				Vale					
	Arroyo				Arroyo					
	Lueders									
	Wichita Group				Clyde	Wichita Group	Waggoner Ranch	Wichita Group	Waggoner Ranch	
					Belle Plains		Petrolia		Petrolia	
					Admiral		Nocona			
					Putnam		Archer City		Archer City	
					Moran		Bowie Group		Markley	Markley
					Pueblo					
					Harpersville					
					Thrifty					
	Cisco Group				Graham					

Fig. 5. Comparative lithostratigraphic nomenclature of the Lower Permian section in north-central Texas.

& Moore (1921), who named a series of rock formations of primarily marine origin, assigning them to the Cisco and Wichita groups of Pennsylvanian to Early Permian age (Fig. 5). Vertebrate palaeontologists, especially Romer (1928, 1935, 1958, 1974), readily placed vertebrate fossil localities in the Texas section into this lithostratigraphy. However, the vertebrate-fossil-bearing localities are mostly non-marine red beds split by thin marine limestone/shale horizons that correlate to, but are lithologically distinct from, the formations named by Plummer & Moore (1921).

Thus, Hentz (1988) justifiably created a new lithostratigraphical nomenclature for the Texas Permian red beds (Figs 5–6). Nevertheless, based on my field observations, two modifications need be made to his nomenclature.

(1) There is no significant (mappable) lithologic difference between the Archer City and

Nocona formations (Hentz & Brown 1987; Hentz 1988; Hentz, pers. comm. 2001), so they should not be regarded as separate lithostratigraphical units. I thus abandon the term Nocona Formation and include all strata in this interval in the Archer City Formation (Fig. 5).

(2) Similarly, there is no lithological basis for separating the Bowie Group of Hentz from the Wichita Group, so I abandon Bowie Group and extend the base of the Wichita Group downward to the base of the Markley Formation (Fig. 5).

These changes modify the lithostratigraphy of the Texas Lower Permian red beds proposed by Hentz so that all formations are mappable units, and groups are associated mappable units, in accordance with accepted stratigraphic practice (NACSN 1983; Owen 1987).

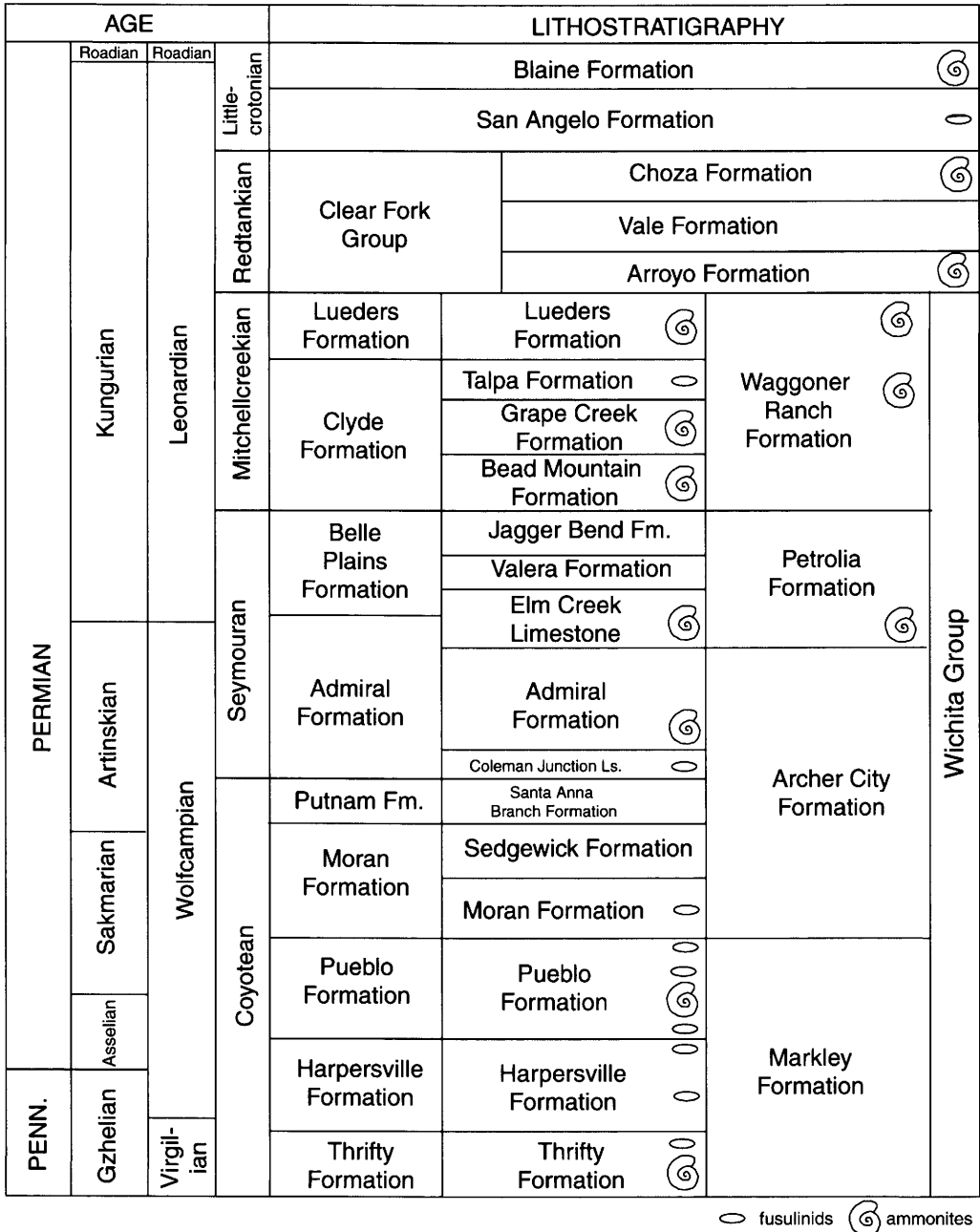


Fig. 6. Summary diagram of the Lower Permian section in north-central Texas showing cross-correlation of vertebrate biochronology and marine biostratigraphy. Formations on right of diagram are the tetrapod-bearing units.

The Texas Lower Permian red-bed section represents fluvial deposition on a broad coastal plain between a Permian seaway to the west and a series of ancestral Rocky Mountain uplifts (Ouachita, Arbuckle and Wichita) to the east and

northeast (e.g. Brown 1973; Hentz 1988, 1989). The non-marine red beds intertongue with, and are laterally equivalent to, marine strata, allowing cross-correlation of non-marine and marine biostratigraphies (Fig. 6). This means it

is possible to correlate directly a tetrapod biostratigraphy developed in the Texas red beds with a marine biostratigraphy based largely on fusulinids and ammonites (e.g. Böse 1917; Plummer & Moore 1921; Roth 1930; Dunbar & Skinner 1937; Plummer & Scott 1937; Henbest 1938; Lee *et al.* 1938; Miller & Furnish 1940; Skinner 1946; Miller & Youngquist 1947; Thompson 1954; Eardle 1960; Myers 1958, 1960, 1968; Kemp 1962; Kauffman & Roth 1966; Ross 1969; Vanderloop-Avery & Nestell 1984) and for which some conodont data are becoming available (Walsh & Barrick 2002; Wardlaw 2005).

The Texas section thus provides an excellent basis for Early Permian tetrapod biostratigraphy, and this biostratigraphy can be readily correlated to marine biostratigraphy (Fig. 6). However, this section has a glaring weakness in lacking an extensive record of tetrapods across the Pennsylvanian–Permian boundary. To remedy this, I have included the Pennsylvanian–Permian boundary record of tetrapods in north-central New Mexico (Rio Arriba County) to form a composite standard of New Mexico–Texas for the oldest Permian tetrapod faunachrons. The basis for this is as follows.

1. An extensive Upper Pennsylvanian tetrapod assemblage is known from the El Cobre Canyon Formation in the Cañon del Cobre of Rio Arriba County, New Mexico (Fig. 7). Co-occurring palynomorphs, megafossil plants and some of the tetrapod taxa themselves (such as *Desmatodon* and *Limnoscelis*) indicate an Upper Pennsylvanian age. (Vaughn 1963; Fracasso 1980; Hunt & Lucas 1992; Berman 1993; DiMichele & Chaney 2005; Lucas & Krainer 2005; Lucas *et al.* 2005b). This is the characteristic tetrapod assemblage of the Cobrean LVF of Lucas *et al.* (2005b).
2. Stratigraphically above this assemblage is a tetrapod assemblage that includes the LO of *Sphenacodon*. This assemblage, best known from the Arroyo del Agua area near Coyote in Rio Arriba County (Berman 1993; Lucas *et al.* 2005c), crosses the Virgilian–Wolfcampian boundary, so by the current time scale it is of latest Pennsylvanian to earliest Permian age. It has long been correlated (on a vertebrate palaeontological basis) to the lower part of the Wichita Group (Markley and lower Archer City formations) in Texas (e.g. Langston 1953; Romer 1960).
3. Stratigraphically higher, the LO of *Seymouria* is in the Arroyo del Agua Formation of the Cutler Group. It can be correlated to

the *Seymouria*-bearing interval of the Wichita Group in Texas (Lucas *et al.* 2005c).

Thus, the New Mexican record superposes tetrapod assemblages that are entirely latest Pennsylvanian, cross the Pennsylvanian–Permian boundary and are of Early Permian age (Fig. 7). When combined with the Texas record, the tetrapod succession encompasses the entire Early Permian (Fig. 3).

The Middle to Upper Permian tetrapod fossil record and its biostratigraphy in the Karoo Basin of South Africa has long provided the classic succession of Middle to Late Permian tetrapod assemblages (Fig. 8). Karoo tetrapod fossils were discovered in 1838 and have been extensively studied and published on since the 1850s. Reviews by Rubidge (1995b, 2005), Smith & Keyser (1995a–d) and Kitching (1995) recognize six successive assemblage zones based on tetrapods. Here, I recast five of the South African assemblage zones as biochronological units (LVFs), using the FAD of a widespread and characteristic tetrapod taxon to define the beginning of each faunachron. This provides five LVFs for most of Middle and Late Permian time (Fig. 3). Thus, the New Mexico–Texas and South African tetrapod records provide a composite standard by which Permian tetrapod biochronology is defined (Fig. 3). However, few data are now available that allow the South African Middle to Late Permian tetrapod record to be cross-correlated to the SGCS.

In the Ural foreland basin the Russian succession of Middle to Late Permian tetrapod assemblages broadly correlates to the Karoo succession and has two advantages: not only can the lowermost (Kazanian) Russian tetrapods be tied to marine biostratigraphy, but the Ilwara magnetostratigraphic event (see below) has been identified in the Russian Tatarian, which provides another way of correlating the Russian section to the SGCS. Unfortunately, prior to the LO of *Dicynodon* in the Russian section (just above the Ilwara event: Lozovsky *et al.* 2001), virtually all of its genus-level taxa are endemic and thus of limited biostratigraphical value. Rare exceptions include the parareptiles *Belebe* (also known in China) and *Macroleter* (reported from Oklahoma), but these provide only a limited basis for correlation. This is why long-standing attempts to correlate the Russian tetrapod assemblages to coeval assemblages in Gondwana (especially in the South African Karoo) have largely been based on assessments of the stage of evolution, usually expressed as family-level correlations (e.g. Rubidge 2005), not on low-level (genus or species) taxonomic identity, and thus

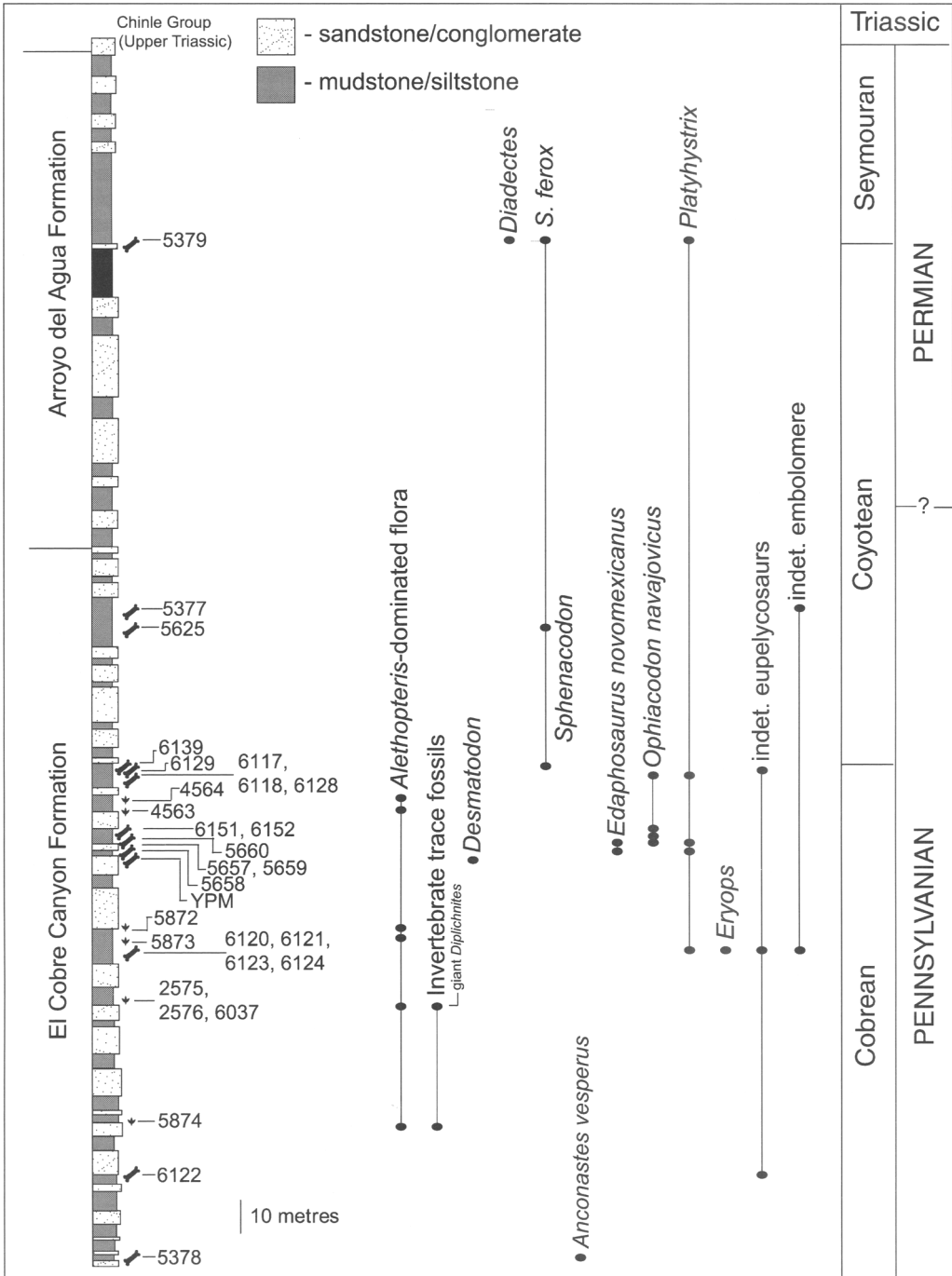


Fig. 7. Composite stratigraphic section of Cutler Group strata in El Cobre Canyon (Cañon del Cobre), northern New Mexico, and the distribution of vertebrate fossils and their ages (after Lucas *et al.* 2005b).

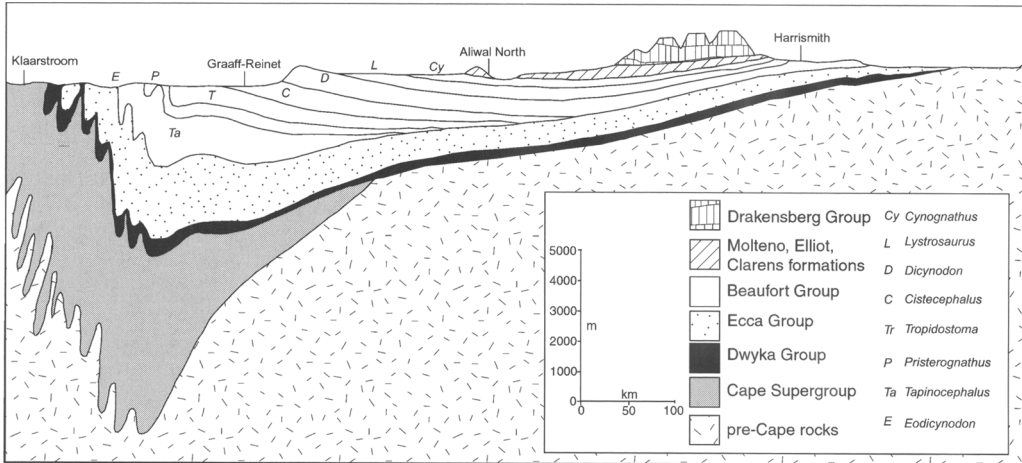


Fig. 8. Cross section showing distribution of vertebrate assemblage zones in the South African Karoo Basin (after Rubidge *et al.* 1995).

inherently imprecise and, to some, remain debatable. Therefore, I use the South African record as a more robust standard for Middle–Upper Permian vertebrate biostratigraphy than can be provided by the Russian record.

Land-vertebrate faunachrons

Coyotean LVF

Definition

The oldest interval of Permian time based on tetrapods is the Coyotean LVF. The name is for Coyote, New Mexico, near the many tetrapod bonebeds of Coyotean age in the upper part of the El Cobre Canyon Formation of the Cutler Group. Coyotean time begins with the FAD of the pelycosaur *Sphenacodon* and encompasses the Pennsylvanian–Permian boundary.

Index fossils

The eureptiles *Romeria* and *Protorothyris* are restricted to Coyotean time, as are the temnospondyls *Chenoprosopus*, *Edops*, *Neopteroplax*, *Neldasaurus* and *Breviodorsum* and the pelycosaur *Stereophallodon* (Fig. 9). However, none of these taxa are abundant or widespread enough to be robust index taxa.

Characteristic assemblage

The characteristic Coyotean assemblage is from the upper part of the El Cobre Canyon Formation (Cutler Group) in the Arroyo del Agua area of Rio Arriba County, New Mexico (Berman, 1993; Lucas *et al.* 2005c). It includes the temnospondyls *Eryops*, *Chenoprosopus*,

Zatrachys, *Platyhystrix*, *Broiliellus* and *Ecolsonia*, the microsaurs *Stegotretus*, an embolomere, a lepospondyl, the diadectomorphs *Diadectes* and *Tseajaia*, the parareptile *Bolosaurus*, the eureptile *Rhiodenticulatus*, the araeoscelid *Zarcasaurus* and the pelycosaur *Sphenacodon*, *Aerosaurus*, *Edaphosaurus*, *Oedaleops* and *Ophiacodon*. The temnospondyl and eureptile components of the Coyotean are distinct from those of the Seymourian.

Principal correlatives

In Texas, the tetrapod assemblage from the Markley and lower part of the Archer City formations of the Wichita Group is of Coyotean age. This assemblage includes diverse temnospondyls (e.g. *Eryops*, *Edops*, *Neldasaurus*, *Zatrachys* and *Trimerorhachis*), a few microsaurs and nectrideans, anthracosaurs (*Archeria*), the diadectomorph *Diadectes*, the eureptiles *Protorothyris* and *Romeria* and diverse pelycosaur (especially *Dimetrodon*, *Edaphosaurus* and *Stereophallodon*) (e.g. Hook, 1989 and references cited therein).

In the Arizona–Utah borderland (principally Monument Valley), the Halgaito Formation (Cutler Group) yields a Coyotean tetrapod assemblage that includes *Diplocaulus*, *Phlegethonia*?, a trimerorhachid, *Eryops*, *Platyhystrix*, *Archeria*, a limnoscelid, *Limnoscelis*, *Ophiacodon*, *Edaphosaurus*, *Sphenacodon* and an araeoscelid? (Vaughn 1962, 1964, 1965, 1966a, b, 1973; Frede *et al.* 1993; Sumida *et al.* 1999a, b). Sumida *et al.* (1999b) identified a single vertebra from the Halgaito Formation as *Seymouria*?, but this genus-level identification has been abandoned (S. Sumida, pers. comm. 2006).

TETRAPOD BIOSTRATIGRAPHY & BIOCHRONOLOGY

taxa	Coyotean	Seymouran	Mitchellcreekian	Redtankian	Littlecrotonian
<i>Acheloma</i>				●	
<i>Angelosaurus</i>					●
<i>Araeoscelis</i>		●	●	●	
<i>Archeria</i>	●	●	●		
<i>Aspidosaurus</i>				●	
<i>Bolosaurus</i>	●	●	●		
<i>Brachydectes</i>	●		●		
<i>Brevidorsum</i>	●				
<i>Broiliellus</i>	●	●		●	
<i>Cacops</i>			●	●	
<i>Captorhinus</i>	●	●	●	●	
<i>Carrolla</i>		●			
<i>Casea</i>				●	
<i>Caseoides</i>					●
<i>Chenoprosopus</i>	●				
<i>Cotylorhynchus</i>				●	●
<i>Crossotelos</i>			●		
<i>Ctenospondylus</i>		●			
<i>Cymatorhiza</i>					●
<i>Diadectes</i>	●	●	●	●	
<i>Dimetrodon</i>	●	●	●	●	●
<i>Diplocaulus</i>	●	●	●	●	●
<i>Ecolsonia</i>	●				
<i>Edaphosaurus</i>	●	●	●	●	
<i>Edops</i>	●				
<i>Eothyris</i>		●			
<i>Eryops</i>	●	●	●	●	
<i>Glaucosaurus</i>			●		
<i>Kahneria</i>					●
<i>Labidosaurikos</i>			●	●	
<i>Labidosaurus</i>				●	
<i>Lupeosaurus</i>	●	●			
<i>Macroleter</i>					●
<i>Mycterosaurus</i>			●		
<i>Neldasaurus</i>	●				
<i>Neopteroplax</i>	●				
<i>Ophiacodon</i>	●	●	●		
<i>Pantylus</i>	●		●		
<i>Pariotichus</i>		●			
<i>Parioxys</i>	●	●			
<i>Platyhystrix</i>	●	●			
<i>Protocaptorhinus</i>		●	●		
<i>Protorothyris</i>	●				
<i>Romeria</i>	●				
<i>Rothianiscus</i>					●
<i>Secodontosaurus</i>		●		●	
<i>Seymouria</i>		●	●	●	
<i>Slaughenhopia</i>					●
<i>Sphenacodon</i>	●	●			
<i>Stereophallodon</i>	●				
<i>Tersomius</i>	●	●	●		
<i>Trematopsis</i>				●	
<i>Trimerorhachis</i>	●	●	●	●	
<i>Tseajaia</i>	●	●			
<i>Varanodon</i>					●
<i>Varanosaurus</i>		●	●	●	
<i>Zatrachys</i>	●	●		●	

Fig. 9. Temporal ranges of selected genera of Early Permian tetrapods.

In southwestern Colorado, the upper part of the Cutler Formation yielded a Coyotean-age assemblage that includes *Eryops*, *Platyhystrix*, a seymouriid, *Diadectes*, a captorhinid?, a haplodontid and 'Mycterosaurus' (unreliable identification) (Lewis & Vaughn 1965; Wideman *et al.* 2005).

In the Lucero uplift of central New Mexico, the Red Tanks Member of the Bursum Formation yielded *Eryops*, *Trimerorhachis*, cf. *Archeria*, *Diadectes*, *Edaphosaurus*, *Sphenacodon* and *Dimetrodon* (Harris *et al.* 2004) – an assemblage of Coyotean age.

In southern Oklahoma, the upper part of the Oscar Group (especially the Waurika I locality) yielded a tetrapod assemblage of Coyotean age that includes *Diplocaulus*, *Trimerorhachis*, *Eryops*, *Archeria*, *Pantylus*, *Ophiacodon*, *Dimetrodon* and *Edaphosaurus* (Olson 1967; Simpson 1979).

In Brown County, Kansas, the Robinson locality in the upper Virgilian Soldier Creek Shale Member of the Bern Limestone yields a lysorophid, *Diplocaulus*, *Cricotus*, a trimerorhachid and cf. *Platyhystrix* (Foreman & Martin 1988). This assemblage may be of Coyotean age.

The Indian Cave Sandstone in Nemaha County, Nebraska, has yielded *Ophiderpeton*, *Phlegethontia*, *Captorhinus*, *Denderpetron* and a pelycosaur (Foreman & Martin 1988) – an assemblage that may be of Coyotean age. In Richardson County, Nebraska, the Eskridge Formation yields *Acropylus*, *Brachydectes*, a trimerorhachid, a microsauro, a diadectid and an edaphosaurid (Huttenlocker *et al.* 2005) and may also be of Coyotean age.

Tetrapods from the Washington Formation of the Dunkard Group in the west Virginia–Ohio–Pennsylvania borderland of the eastern United States (Moran 1952; Romer 1952; Olson 1975) include *Edops* (a Coyotean index taxon), as well as *Trimerorhachis*, *Diadectes*, *Edaphosaurus* and *Dimetrodon*, and are reasonably assigned a Coyotean age.

In Europe, some of the Rotliegend tetrapod assemblages (e.g. the lower *Protriton* and Gottlob horizons in the Thuringian forest) dominated by branchiosaurs (e.g. Boy 1993; Werneburg 1989, 2001) are apparently of Coyotean age, but the lack of shared taxa makes a direct tetrapod-based correlation impossible. The correlation, instead, must be based on other evidence which indicates that some of the Rotliegend tetrapod assemblages are of late Virgilian to middle Wolfcampian age (e.g. Roscher & Schneider 2005), which means they correlate to the Coyotean. The latest version of the Rotliegend amphibian zonation (Werneburg & Schneider 2006) recognizes nine

zones based on species chronoclines that provide correlations in the Czech Republic, Germany, France, Poland and Italy. This is a provincial biostratigraphy in the Rotliegend extensional basins of Europe in which amphibian zones 3–9 appear to overlap Coyotean time as here defined.

Steyer (2000) critiqued Werneburg's biostratigraphy by arguing that taphonomic and palaeoecological factors have more control over amphibian distributions than actual temporal ranges, and by critiquing the species-chronocline method of taxonomy. However, Steyer's assertions about palaeoecology and taphonomy are largely undocumented, and the species-chronocline method is the preferred method used in the micropalaeontological taxonomy of the fusulinids and conodonts, the two biostratigraphic workhorses of the Permian SGCS. In principle, an extensive record of European amphibians should be amenable to such methods.

Comments

Lucas (2002) defined an informal faunachron A that is, in part, equivalent to the Coyotean. However, in 2002, I used the FAD of *Eryops* to define the beginning of Coyotean time, which clearly predates the FAD of *Sphenacodon* (e.g. Vaughn 1958; Harris *et al.* 2004; Lucas *et al.* 2005b). By using the FAD of *Sphenacodon* to define the beginning of the Coyotean, its beginning is close to (but almost certainly precedes) the Pennsylvanian–Permian boundary, making the Coyotean a shorter time interval than faunachron A of Lucas (2002).

Note that the distribution of tetrapod taxa in the New Mexico and Texas sections indicates that the Coyotean is equivalent to part of the Virgilian and much of the Wolfcampian (Fig. 6). Thus, *Sphenacodon* has its LO in Virgilian strata of the Bursum Formation in central New Mexico (Harris *et al.* 2004), and Coyotean tetrapods are found throughout the Markley and lower part of the Archer City formations in Texas, which means that the Coyotean encompasses most of Wolfcampian time.

Seymourian LVF

Definition

The Seymourian LVF is the time interval between the Coyotean and Mitchellcreekian LVFs. The name is for the town of Seymour, Baylor County, Texas, near the characteristic assemblage of the Seymourian, which is from the upper part of the Archer City Formation. The Seymourian LVF begins with the FAD of the seymouriamorph *Seymouria*.

Index fossils

The microsaurs *Carrolla* and *Pariotichus*, and the pelycosaurs *Ctenospondylus* and *Eothyris*, are restricted to the Seymouran. However, none of these taxa are abundant or widespread enough to be robust index taxa. The FADs of *Protocaptorhinus*, *Seymouria*, *Varanosaurus*, *Secodontosaurus* and *Araeoscelis*, and the LADs of *Parioxys*, *Platyhystrix* and *Sphenacodon*, also distinguish the Seymouran LVF (Fig. 9).

The species *Seymouria sanjuanensis* may be the best index taxon of the Seymouran, as it is known from Utah, New Mexico and Germany. The younger species, *S. baylorensis*, is late Seymouran through Redtankian, and *S. grandis* is from the Redtankian (Olson 1980).

Characteristic assemblage

The characteristic assemblage of the Seymouran is from the upper Archer City ('Nocona') and Petrolia formations of the Wichita Group in Texas. This assemblage has temnospondyls similar to those of the Coyotean (but without *Edops* and *Neldasaurus*), the microsaurs *Carrolla* and *Pantylus*, a few neotridians, the anthracosaur *Archeria*, *Diadectes* and *Seymouria*, the eureptile *Protocaptorhinus*, diverse pelycosaurs (including the LOs of *Secodontosaurus* and *Varanosaurus*), the diapsid *Araeoscelis* and the parareptile *Bolosaurus* (see Hook 1989 and references cited therein).

Principal correlatives

In the Arizona–Utah borderland, the Organ Rock Shale (Cutler Group) yields a Seymouran tetrapod assemblage that includes *Seymouria*, *Eryops*, a trimerorhachid, a zatrachyd, the diadectomorphs *Tseajaia* and *Diadectes*, *Sphenacodon*, *Ophiacodon*, *Dimetrodon* and *Ctenospondylus* (Vaughn 1964, 1966a, b, 1973; Sumida *et al.* 1999a, b). The underlying Cedar Mesa Sandstone yields *Eryops* and *Sphenacodon* and could be either Coyotean or Seymouran in age.

In the Chama Basin of northern New Mexico, the superposition of Coyotean and Seymouran tetrapod assemblages is documented in the Arroyo del Agua Formation of the Cutler Group, where a Seymouran-age assemblage of *Seymouria*, *Sphenacodon*, *Diadectes*, *Platyhystrix* and an eryopid is stratigraphically above the characteristic Coyotean tetrapod assemblage (Lucas & Krainer 2005; Lucas *et al.* 2005c).

In northern Oklahoma, the Wellington Formation (especially the Perry and Orlando localities) yields an extensive tetrapod assemblage of Seymouran age that includes *Trimerorhachis*, *Zatrachys*, *Seymouria?*, *Brachydictes* (= *Lysorophus* of Wellstead 1991), *Eryops*,

Diplocaulus, *Broiliellus*, *Diadectes*, *Archeria*, *Ophiacodon*, *Captorhinus*, *Edaphosaurus* and *Dimetrodon* (Olson 1967; Simpson 1979).

In Kansas, various localities in the upper Council Grove Group (especially those in the Speiser Shale) yield a probable Seymouran-age assemblage that includes *Brachydictes*, *Diplocaulus*, *Trimerorhachis* and *Euryodus* (Foreman & Martin 1988).

The Greene Formation of the Dunkard Group (localities principally in western Ohio) overlies the Washington Formation and yields *Brachydictes*, *Trimerorhachis*, *Eryops*, *Edaphosaurus* and *Ctenospondylus* (Berman & Berman 1975; Berman 1978). *Ctenospondylus* is also known from the 'Belle Plains Formation' (Petrolia Formation) in Texas and the Organ Rock Shale, both of which are Seymouran-age records, and this suggests a Seymouran age for the *Ctenospondylus* occurrence in the Green Formation. However, based primarily on chondrichthyans, Lund (1975) correlated the Greene Formation to the lower Clear Fork Group of Texas, which suggests a Redtankian age.

Lower Permian red beds on Prince Edward Island in eastern Canada yield *Eryops*, *Seymouria*, *Diadectes* and a pelycosaur (Langston 1963; Spalding 1993), an assemblage of probable Seymouran age.

Berman & Martens (1993), Sumida *et al.* (1996, 1998), Berman *et al.* (2000, 2001, 2004) and Sumida *et al.* (2004), among others, documented tetrapods from the Tambach Formation of the Upper Rotliegend in Germany (also see Eberth *et al.* 2000), which include the trematopid *Tambachia*, *Seymouria*, the eureptile *Thuringothyris*, the diadectomorphs *Diadectes* and *Orobates*, the bolosaurid *Eudibamus*, a varanopid, a caseid and the pelycosaur *Dimetrodon*. This assemblage is of Seymouran age.

Comments

The Seymouran as used here is essentially the same as faunachron B of Lucas (2002). There is a substantial turn-over in the eureptile and pelycosaur components of the tetrapod fauna between the Coyotean and Seymouran (e.g. Romer & Price 1940, Clark & Carroll 1973; Heaton 1979; Hook 1989). Correlation of the Texas section indicates that the Seymouran straddles the Wolfcampian–Leonardian boundary (Fig. 6).

*Mitchellcreekian LVF**Definition*

The Mitchellcreekian LVF is the time interval between the Seymouran and Redtankian LVFs. The name is for Mitchell Creek near Lake Kemp

in Baylor County, Texas, which is near the characteristic tetrapod assemblage of the Mitchellcreekian in the Waggoner Ranch and Lueders formations. The Mitchellcreekian begins with the FAD of the pelycosaur *Mycterosaurus*.

Index fossils

The varanopid pelycosaur *Mycterosaurus* is not a common taxon, but it is known from Oklahoma, Texas and Ohio and is restricted to the Mitchellcreekian (Berman & Reisz [1982] note that its record in the Cutler Formation of Colorado [Lewis & Vaughn 1965] can be discounted). The nectridean *Crossotelos* and the pelycosaur *Glaucosaurus* are also restricted to Mitchellcreekian time but are not robust index taxa. The FAD of *Cacops* and the LADs of *Archeria*, *Bolosaurus*, *Brachyectes*, *Ophiacodon*, *Protocaptorhinus*, *Pantylus* and *Varanosaurus* also distinguish the Mitchellcreekian (Fig. 9).

Characteristic assemblage

The characteristic Mitchellcreekian tetrapod assemblage is from the Waggoner Ranch and Lueders formations in Texas. The characteristic assemblage has only a few temnospondyls (except for abundant armoured dissorophids), gymnarthrids, *Brachyectes*, an aistopod, abundant nectrideans (especially *Diplocaulus*), *Archeria* and *Diadectes*, eureptiles similar to those of Seymouran age, and diverse pelycosaur (see Hook 1989, and references cited therein).

Principal correlatives

Tetrapod assemblages of Mitchellcreekian age are currently known only from Texas and Oklahoma (Olson 1967; Simpson 1979; Hook 1989; Burkhalter & May 2002). In southern Oklahoma, the tetrapod assemblage from the lower-middle Garber Formation (especially the South Grandfield and Northeast Frederick sites) is of Mitchellcreekian age and includes *Trimerorhachis*, *Tersomius*, *Brachyectes*, *Diplocaulus*, *Archeria*, *Diadectes*, *Captorhinus*, *Labidosaurikos*, *Ophiacodon*, *Dimetrodon* and *Araeoscelis*. The Richards Spur locality (a fissure-fill in Ordovician limestone) may also be of Mitchellcreekian age and includes *Phlegethonia*, *Doleserpeton*, *Cacops*, *Tersomius*, *Seymouria*, diverse gymnarthrids, *Captorhinus*, *Mycterosaurus*, *Bolosaurus* and a caseid. Indeed, the bolosaurid from Richards Spur, *Bolosaurus grandis*, is larger and more derived than the Coyotean–Seymouran bolosaurid, *B. striatus*, so they may be an ancestor-descendent lineage of biostratigraphic value (Lucas *et al.* 2005a).

Comments

The Mitchellcreekian as used here is faunachron C of Lucas (2002). However, Lucas (2002) used

the FAD of '*Lysorophus*' (= *Brachyectes*) to define the beginning of his faunachron C because this corresponds to its LO in the Texas section. But, *Brachyectes* has older, Coyotean records outside of Texas (see above). The Mitchellcreekian is of Leonardian age (Fig. 6).

Redtankian LVF

Definition

The Redtankian LVF is the time interval between the Mitchellcreekian and Littlecrotonian LVFs. The name is for Red Tank, north of Seymour in Baylor County, Texas, near the characteristic tetrapod assemblage of the Redtankian, which is from the Clear Fork Group. The FAD of the eureptile *Labidosaurus* defines the beginning of the Redtankian.

Index fossils

Labidosaurus is an index fossil of Redtankian time but is rare. *Aspidosaurus*, *Casea*, *Acheloma* and *Trematopsis* are also restricted to the Redtankian, but they are not robust index taxa. The FADs of *Labidosaurikos* and *Cotylorhynchus* help to define the Redtankian, as do the LADs of *Araeoscelis*, *Broiliellus*, *Cacops*, *Captorhinus*, *Diadectes*, *Edaphosaurus*, *Eryops*, *Seymouria* and *Varanosaurus* (Fig. 9).

Characteristic assemblage

The characteristic Redtankian assemblage is from the Clear Fork Group (Arroyo, Vale and Choza formations) or Clear Fork Formation (where the three constituent formations are not distinct mappable units: Nelson *et al.* 2001) of Texas. It includes abundant *Brachyectes*, *Trimerorhachis* and *Diplocaulus*, as well as *Eryops*, *Trematops*, *Cacops*, *Trematopsis*, diverse dissorophids (including *Broiliellus*, *Aspidosaurus* and *Dissorophus*), diverse eureptiles (especially *Captorhinus*, '*Captorhnikos*', *Captorhinoides* and *Labidosaurus*), *Seymouria*, *Diadectes*, diverse pelycosaur (including *Casea*, *Dimetrodon*, *Varanosaurus*, *Secodontosaurus* and *Edaphosaurus*) and *Araeoscelis* (Olson 1952, 1954, 1958, 1989b; Olson & Mead 1982; Murry & Johnson 1987; Berman & Lucas, 2003).

Principal correlatives

Tetrapod assemblages of Redtankian age are currently known from Texas and Oklahoma. In Oklahoma, the LO of *Labidosaurus* is in the upper Garber Formation. The overlying Hennessey Group also yields a Redtankian assemblage that includes *Trematops*, *Tersomius*, *Trimerorhachis*, *Peroneodon*, *Brachyectes*, *Eryops*, *Captorhinus*, *Cotylorhynchus*, *Dimetrodon* and *Ophiacodon* (Olson 1967; Simpson 1979).

Comments

The Redtankian as used here is the same as faunachron D of Lucas (2002). Its characteristic assemblage is the classic Clear Fork Group chronofauna of Texas (Olson 1952) but, as will be discussed later, this chronofauna was of relatively short duration in geological time. The Redtankian is equivalent to part of the Leonardian (Fig. 6).

Littlecrotonian LVF

Definition

The Littlecrotonian LVF is the time interval between the Redtankian and Kapteinskraalian LVFs. The LVF derives its name from Little Croton Creek in Knox County, Texas, near the characteristic tetrapod assemblage in the San Angelo Formation. The FAD of the caseid pelycosaur *Angelosaurus* defines the beginning of the Littlecrotonian.

Index fossils

Most of the tetrapod genera of Littlecrotonian age are restricted to the time interval (Fig. 9), but only the 'microsaur' *Cymatorhiza*, the eurentile *Rothianiscus* (although it includes specimens that pertain to *Labidosaurikos*: Sumida, pers. comm. 2006) and the pelycosaur *Angelosaurus* are widely distributed in Texas–Oklahoma and thus may be relatively robust index taxa.

Characteristic assemblage

The youngest North American Leonardian tetrapod assemblage, from the San Angelo Formation of Texas (Olson & Beerbower 1953), is characteristic of this time interval. It is from localities in Knox, Foard and Hardeman counties in north-central Texas and includes the captorhinid *Rothianiscus*, the caseid pelycosaur *Caseoides Cotylorhynchus* and *Angelosaurus*, the sphenacodontids *Steppesaurus* and *Tappensaurus* and the putative therapsid *Dimacrodon*. Olson (1962) later added these taxa to the San Angelo tetrapod assemblage: the temnospondyl *Slaughenhopia*, the captorhinid *Kahneria*, the sphenacodont *Dimetrodon*, the caseid *Caseopsis* and the 'therapsids' *Knoxosaurus*, *Gorgodon*, *Eosyodon*, *Driveria* and *Mastersonia*. Olson (1962) also reassigned *Tappenosaurus* and *Steppesaurus*, along with *Dimacrodon*, to the Therapsida. Abundant and diverse caseids are characteristic of Littlecrotonian time. However, all the 'therapsid' taxa from this assemblage have been re-evaluated and deemed to be based on fragmentary pelycosaur fossils (Parrish *et al.* 1986; Sidor & Hopson 1995).

Principal correlatives

The Flowerpot Formation of Texas and the Chickasha Formation of Oklahoma yield

tetrapod assemblages of Littlecrotonian age (Olson 1962, 1965, 1967; Lucas 2004). Olson & Barghusen (1962) described vertebrate fossils from two localities in the Flowerpot Formation in Kingfisher County, Oklahoma, that yield the 'microsaur' *Cymatorhiza*, *Rothianiscus*, *Cotylorhynchus* and *Angelosaurus*.

Strata of the Chickasha Formation, which are laterally equivalent to the middle part of the Flowerpot Formation, yielded vertebrate fossils from about 20 localities, mostly in Blaine and Kingfisher counties, Oklahoma (Olson 1965). A single locality in McClain County, Oklahoma, also yielded unidentified bone from the Duncan Sandstone (Olson 1965). The Chickasha assemblage includes *Cymatorhiza*, the amphibians *Nannospondylus* and *Fayella*, *Rothianiscus*, *Cotylorhynchus*, *Angelosaurus* and the varanopid *Varanodon*. Olson (1972) subsequently added the nectridean *Diplocaulus* to this assemblage, and also described the supposed therapsid (actually a pelycosaur) *Watongia* (Olson 1974). Olson's (1980) *Seymouria agilis* from the Chickasha Formation assemblage has been reassigned to the parareptile *Macroleter*, a genus previously known only from Russia (Reisz & Laurin 2001).

Because Littlecrotonian time lasts until the beginning of the Kapteinskraalian, the gap between the Texas–Oklahoma assemblages just discussed and the oldest Kapteinskraalian assemblage ('Olson's gap') is of Littlecrotonian age (Fig. 3). The only tetrapod assemblage that may be in this gap is the Inta assemblage from the Pechora Basin in Russia. This assemblage is essentially an endemic amphibian fauna that resembles North American Early Permian amphibians in its stage of evolution, but cannot be otherwise correlated based on tetrapod biostratigraphy alone (Lucas 2004).

Comments

Olson (1962; and also Efremov 1956 and Olson & Chudinov 1992) consistently correlated the tetrapod assemblage of the San Angelo and Flowerpot formations with the oldest Middle Permian therapsid-bearing assemblages in Russia. This correlation was not based on shared low-level taxa (genera and species) but on the supposed abundance of therapsids in the Texas faunas and the presence of 'counterparts' (equivalent evolutionary grades) among the Texan and Russian amphibians and caseids. Recognition that all the San Angelo 'therapsid' fossils are actually pelycosaur fossils undermines this correlation and suggests that the therapsid-dominated faunas that are the oldest Permian assemblages in Russia and South Africa postdate the youngest North American Permian faunas

(e.g. Sidor & Hopson 1995). Marine biostratigraphy supports this, so there is a hiatus in the Permian tetrapod record ('Olson's gap') equivalent to part of Roadian time (Lucas 2004). Recently, Lozovsky (2005) has argued against this, but his arguments have been answered by Lucas (2005a).

Kapteinskraalian LVF

Definition

The Kapteinskraalian LVF is the time interval between the Littlecrotonian and Gamkan LVFs. The LVF derives its name from the Kapteinskraal River in South Africa, the type section of the *Eodicynodon* assemblage zone. The beginning of the Kapteinskraalian LVF is the FAD of the therapsid *Eodicynodon*.

Index fossils

Most of the tetrapod taxa of the characteristic Kapteinskraalian assemblage are limited to the LVF (Fig. 10), but lack a proven broad distribution (they are endemic to either South Africa or Russia) that would identify them as robust index

taxa. The most primitive anomodonts (e.g. *Eodicynodon*, *Otsheria* and *Patronomodon*) and dinocephalians (e.g. *Australosyodon*, *Tapinocaninus*) are indexes of the Kapteinskraalian, but no genus-level taxon is widespread. The first therapsids appear during Kapteinskraalian time.

Characteristic assemblage

The characteristic Kapteinskraalian assemblage is from the lower Abrahamskraal Formation, Beaufort Group, South Africa (Rubidge 1995b). The characteristic tetrapod assemblage is the *Eodicynodon* Assemblage Zone and includes temnospondyls, a gorgonopsian, the therocephalians *Glanosuchus* and *Alopecodon*, the anomodont *Patronomodon*, the dicynodont *Eodicynodon* and the dinocephalians *Tapinocaninus* and *Australosyodon* (Rubidge 1995b, 2005 and references cited therein).

Principal correlatives

The oldest Russian tetrapod assemblages of Kazanian age (Russian Zone I: Ocher assemblage and part of Mezen assemblages) yield basal anteosaurid dinocephalians and anomodonts

taxa	Kapteinskraalian	Gamkan	Hoedemakeraan	Steilkraansian	Platbergian
<i>Alopecodon</i>	•	•			
<i>Aulacephalodon</i>				•	
<i>Bradyosaurus</i>		•			
<i>Cistecephalus</i>				•	
<i>Dicynodon</i>					•
<i>Diictodon</i>		•	•	•	•
<i>Elliotsmithia</i>		•			
<i>Embrithosaurus</i>		•			
<i>Emydops</i>		•	•	•	•
<i>Endothiodon</i>		•	•	•	
<i>Eodicynodon</i>	•				
<i>Eunotosaurus</i>		•			
<i>Gorgonops</i>		•	•	•	
<i>Ictidosuchoides</i>		•	•	•	•
<i>Kingoria</i>			•	•	•
<i>Lycaenops</i>			•	•	•
<i>Otsheria</i>	•				
<i>Oudenodon</i>				•	•
<i>Pareiasaurus</i>		•	•	•	•
<i>Patronomodon</i>	•				
<i>Pelanomodon</i>					•
<i>Priesterodon</i>		•	•	•	•
<i>Priesterognathus</i>		•			
<i>Rhachiocephalus</i>			•	•	
<i>Rhinesuchus</i>		•	•	•	•
<i>Robertia</i>		•			
<i>Tapinocephalus</i>		•			
<i>Theriongnathus</i>					•
<i>Tropidostoma</i>			•		
<i>Youngina</i>			•	•	•

Fig. 10. Temporal ranges of selected genera of Mid- to Late Permian tetrapods.

(see Golubev 1998, 2005 for summaries). They predate the beginning of the Gamkan LVF and are therefore of Late Kapteinskraalian age.

Comments

The Kapteinskraalian as used here is faunachron F of Lucas (2002). The characteristic assemblage, the *Eodicynodon* assemblage zone in the Karoo Basin, is thought to be of Kazanian (Wordian) age, and older than the Russian Zone I and II assemblages (Rubidge & Hopson 1990; Lucas 2004; Rubidge 2005), but direct correlation with the SGCS is difficult. For many years, and by some today (Benton *et al.* 2004, fig. 1; Golubev 2005), Russian Zone II was thought to be the oldest therapsid fauna, but taxa from the *Eodicynodon* Assemblage Zone in South Africa are among the most primitive members of their groups; this is especially true of anomodonts and tapinocephaline dinocephalians (Rubidge 1993; Rubidge & Hopson 1996; Modesto *et al.* 1999, 2002, 2003; Modesto & Rubidge 2000; Modesto & Rychczynski 2000; Battail 2000; Rubidge & Sidor 2001). Thus, based on stage-of-evolution, the *Eodicynodon* Assemblage Zone is thought to be the oldest Mid-Permian tetrapod assemblage with therapsids. Given that no Early Permian tetrapod assemblage yields *bona fide* therapsids, it seems unlikely that the *Eodicynodon* assemblage zone is of Early Permian age. But, just how old it is in the Mid-Permian remains uncertain.

Gamkan LVF

Definition

The Gamkan LVF is the time interval between the Kapteinskraalian and Hoedemakeran LVFs. The name of the LVF is for the Gamka River, which adjoins the type locality of the *Tapinocephalus* assemblage zone. The beginning of the Gamkan LVF is the FAD of the dinocephalian *Tapinocephalus*.

Index fossils

Tapinocephalus, various other dinocephalians, *Eunotosaurus*, *Bradysaurus*, *Elliotsmithia*, *Pristerognathus* and *Robertia* are some of the better-known taxa restricted to the Gamkan but they are not robust index fossils. The FADs of *Diictodon*, *Endothiodon*, *Gorgonops*, *Ictidosuchoides*, *Pristerodon*, *Rhinesuchus* and *Emydops* and the LAD of *Alopecodon* help to define the Gamkan (Fig. 10). The Gamkan is the time of highest dinocephalian diversity.

Characteristic assemblage

The characteristic Gamkan tetrapod assemblage is from the upper Abrahamskraal and lower

Teekloof formations, Beaufort Group, South Africa. It combines those of the *Tapinocephalus* Assemblage Zone of Smith & Keyser (1995a) and the *Pristerognathus* Assemblage Zone of Smith & Keyser (1995b). It thus includes the temnospondyl *Rhinesuchus*, pareiasaurs (especially *Bradysaurus*), the pelycosaur *Elliotsmithia*, diverse dinocephalians (especially *Tapinocephalus*), the anomodont *Galeops*, dicynodonts (especially *Diictodon*), two biarmosuchians, several gorgonopsians and therocephalians (see Smith & Keyser 1995a, b and references cited therein).

Principal correlatives

In Zimbabwe, the Madumabisa Mudstones have yielded diverse dinocephalians (anteosaurids, tapinocephalids and *Criocephalosaurus*) (Boonstra 1946; Lepper *et al.* 2000) of probable Gamkan age.

The *Endothiodon* record in the K5 interval of the Ruhuhu Formation in the Ruhuhu depression in Tanzania may be of Gamkan age (Cox 1964; Gay & Cruickshank 1999).

Zone II (Isheev) of the Russian Permian (Ivakhnenko *et al.* 1997) has long been correlated to the South African *Tapinocephalus* zone (e.g. Chudinov 1975) based on shared evolutionary counterparts in biarmosuchians, anteosaurid and tapinocephalid dinocephalians and anomodonts and therefore is of Gamkan age.

In the Ordos Basin of northern China, the Xidagou Formation yields the temnospondyl *Anakamacops*, an *Intasuchus*-like temnospondyl, the anthracosaurs *Ingentidens* and *Phratochronis*, the bolosaur *Belebey* (also known from Russian Zone II), a captorhinid, the dinocephalians *Sinophoneus* and *Stenocybus* and the anomodont *Biseridens*. This is the *Biseridens* assemblage of probable Gamkan age (Lucas 2005b).

In the Paraná Basin of southern Brazil, the Posto Queimado and Aceguá tetrapod assemblages include diverse dinocephalians and *Pareiasaurus* and are of probable Gamkan age (Araújo 1985; Barbarena *et al.* 1985b; Lee 1997; Langer *et al.* 1998; Langer 2000; Cisneros *et al.* 2005).

Recently described tetrapods from intraformational conglomerates of the Buena Vista Formation in northeastern Uruguay (on the southern flank of the Paraná Basin) include the procolophonoid *Pintosaurus*, a supposed varanopid pelycosaur (though I doubt this identification) and a temnospondyl, and may be a single biostratigraphic assemblage of Gamkan age (Marsicano *et al.* 2000; Piñeiro *et al.* 2003, 2004). I base this very tentative conclusion largely on the fact that the Buena Vista Formation is

homotaxial to the Sango do Cabral Formation of Brazil and that the youngest varanopids are of Gamkan age (Modesto *et al.* 2001).

Comments

The Gamkan as used here is faunachron G of Lucas (2002). The fauna of the *Pristerognathus* Assemblage Zone is a depauperate subset of the *Tapinocephalus* Assemblage Zone, which I have not treated as distinctive, so it is considered to be of late Gamkan age. Boonstra (1969) divided his *Tapinocephalus* zone into three assemblages, lower, middle and upper (= *Pristerognathus* assemblage zone), so the potential exists for subdivision of the Gamkan LVF.

Hoedemakeran LVF

Definition

The Hoedemakeran LVF is the time interval between the Gamkan and Steilkransian LVFs. The name is for the Hoedemaker River in South Africa, near the type locality of the *Tropidostoma* assemblage zone. The Hoedemakeran LVF begins with the FAD of the dicynodont *Tropidostoma*.

Index fossils

Tropidostoma is an index taxon of Hoedemakeran time. The FADs of *Cistecephalus*, *Kingoria*, *Lycanops*, *Rhachiocephalus* and *Youngina* help to identify the Hoedemakeran (Fig. 10).

Characteristic assemblage

The characteristic Hoedemakeran assemblage is from the middle Teekloof Formation, Beaufort Group, South Africa. The characteristic tetrapod assemblage is much of the *Tropidostoma* Assemblage Zone (below the LO of *Cistecephalus*) of Smith & Keyser (1995c) and includes the temnospondyl *Rhinesuchus*, the pareiasaur *Pareiasaurus*, therocephalians (but no scylacosaurids), gorgonopsians and numerous dicynodonts, especially *Diictodon*, *Pristerodon*, *Tropidostoma* and *Endothiodon*.

Principal correlatives

The lower part of the Kawinga Formation in the Ruhuhu depression of Tanzania yields a temnospondyl?, a pareiasaur?, *Endothiodon*?, *Rhachiocephalus*, *Pristerodon*? and *Pachytegos*? (Gay & Cruickshank 1999) and may be of Hoedemakeran age.

In the Paraná Basin of southern Brazil, the Serra do Cadeao locality yielded rhinesuchids and *Endothiodon* and is probably of Hoedemakeran age (Barbarena & Araújo 1975; Barbarena & Dias 1998; Barbarena *et al.* 1985a, b; Barbarena 1998; Cisneros *et al.* 2005).

In Russia, all or part of the *Proelginia permiana* assemblage zone (*sensu* Golubev 2005) may be of Hoedemakeran age. The tetrapod assemblage includes chroniosuchids, 'procolophonids,' pareiasaurs, burnetiids, gorgonopids, dicynodonts and cynodonts.

Comments

The Hoedemakeran as used here is faunachron H of Lucas (2002). There is a substantial turnover of pareiasaurs at the beginning of the Hoedemakeran, and a very diverse dicynodont fauna characterizes this LVF.

Steilkransian LVF

Definition

The Steilkransian LVF is the time interval between the Hoedemakeran and Platbergian LVFs. The name is for the Steilkrans farm in South Africa, which is the type locality of the *Cistecephalus* assemblage zone. The Steilkransian LVF begins with the FAD of the dicynodont *Cistecephalus*.

Index fossils

Aulacephalodon is an index taxon of the Steilkransian. The FAD of *Oudenodon* and the LADs of *Cistecephalus*, *Endothiodon*, *Gorgonops* and *Rhachiocephalus* also help to identify the Steilkransian (Fig. 10).

Characteristic assemblage

The characteristic Steilkransian tetrapod assemblage is from the Upper Teekloof Formation, Beaufort Group, South Africa. The characteristic tetrapod assemblage thus combines the uppermost *Tropidostoma* Assemblage Zone and the *Cistecephalus* Assemblage Zone (Smith & Keyser 1995c, d) and includes the temnospondyl *Rhinesuchus*, captorhinids, therocephalians, a biarmosuchian and dicynodonts, especially *Diictodon*, *Cistecephalus*, *Emydops*, *Aulacephalodon* and *Oudenodon*.

Principal correlatives

Cistecephalus occurs in the Madumabisa Mudstone Formation of the Luangwa Valley in Zambia, and the closely related *Kawingasaurus* is present in the Kawinga Formation in the Ruhuhu depression of Tanzania (Gay & Cruickshank 1999), so these are records of probable Steilkransian age.

In Malawi, the Chiweta beds are coal-bearing strata of the Karoo Supergroup that yield *Endothiodon*, *Oudenodon* and a new biarmosuchian and are of probable Steilkransian age (Haughton 1926; Jacobs *et al.* 2005).

In southern Madagascar, south of the Isalo massif, the lower Sakamena Formation yields *Oudenodon*, *Rhinesuchus* and various endemic reptiles (Piveteau 1926; Mazin & King, 1991), and is probably of Steilkransian age.

In the Pranhita–Godavari Valley of India, the Kundaram Formation yields a captorhinid and the dicynodonts *Endothiodon*, *Pristerodon*, *Emydops*, *Cistecephalus* and *Oudenodon*, an assemblage of Steilkransian age (Ray 1999, 2001).

In northern China, the *Shihtienfenia* assemblage from the Shihezi Formation in Henana and the Sunjiagou Formation in Shanxi yields the temnospondyl *Bystrowiana* and various pareiasaurs, especially *Shihtienfenia* (Lucas 2005b). The pareiasaurs are most similar to characteristic Steilkransian pareiasaurs such as *Scutosaurus*, *Pareiasaurus* and *Pareiasuchus*, which suggests a tentative correlation (Lucas 2005b).

Comments

The Steilkransian as used here is faunachron I of Lucas (2002). Its boundaries are marked by significant evolutionary turn-over in pareiasaurs, gorgonopsians and therocephalians.

Platbergian LVF

Definition

The Platbergian LVF is the time interval between the Steilkransian and Lootsbergian LVFs (see Lucas 1998b for definition of the Lootsbergian). The name is for Platberg in South Africa, which is the type locality of the *Dicynodon* assemblage zone. The Platbergian LVF begins with the FAD of the dicynodont *Dicynodon*.

Index fossils

Dicynodon is the key index taxon of Platbergian time. *Pelanomodon* and *Theriognathus* are also restricted to Platbergian time. The LADs of *Oudenodon*, *Aulacephalodon* and a variety of tetrapod taxa that become extinct at or just before the Permo-Triassic boundary also help to identify the Platbergian (Fig. 10).

Characteristic assemblage

The characteristic tetrapod assemblage is from the uppermost Teekloof and the Balfour formations, Beaufort Group, South Africa. The characteristic assemblage combines the uppermost *Cistecephalus* Assemblage Zone and the *Dicynodon* Assemblage Zone (Kitching 1995), a tetrapod assemblage dominated by dicynodonts (especially *Dicynodon*, *Diictodon* and *Pelanomodon*) with some biamnosuchians, diverse gorgonopsians and therocephalians (especially *Theriognathus*) and cynodonts (especially *Procynosuchus*).

Principal correlatives

The broad distribution of *Dicynodon* establishes the Platbergian as the most widely recognizable (correlateable) of the Permian LVFs. Tetrapod assemblages of Platbergian age are:

- (1) Karoo Basin, South Africa, where specimens of *Dicynodon* first occur in the upper *Cistecephalus* Assemblage Zone and are the dominant tetrapod fossils in the *Dicynodon* Assemblage Zone of the Teekloof and Balfour formations (Kitching 1995);
- (2) part of the Kawinga Formation in the Ruhuhu Valley of Tanzania (Haughton 1932; Gay & Cruickshank 1999; Maisch & Gebauer 2005);
- (3) 'Horizon 5' of Boonstra in the Luangwa Valley, 4.8–6.4 km north of Nt'awere, Zambia (King & Jenkins, 1997);
- (4) Cutties Hillock Quarry, Elgin, Scotland (Newton 1893; King 1988) in the Cutties Hillock Sandstone Formation (Benton & Walker 1985);
- (5) the Hopeman Sandstone at Clashbach Quarry, Scotland (Clark 1999);
- (6) various localities of the Upper Sokolki assemblage and Vyatskyan assemblage of the Russian Upper Tatarian (Amalitzky 1922; Sushkin 1926; Ivakhnenko *et al.* 1997; Kurkin 1999; Kalandadze & Kurkin 2000; Golubev 2000; Lucas 2005b);
- (7) Quanzijie, Wutonggou and Guodikeng formations in the Junggur and Turpan basins, Xinjiang Province, China (Lucas 1998a, 2001, 2005a);
- (8) Sunan Formation, Gansu and Naobaogou Formation, Nei Monggol, both Ordos Basin, China (Lucas 1998a, 2001, 2005a; Li *et al.* 2000);
- (9) north of the Mekong River in the Luang–Prabang area of Laos (Battail *et al.* 1995; Battail 1997).

Comments

The Platbergian as used here is faunachron J of Lucas (2002). *Dicynodon* is a long recognized and extensively studied Permian dicynodont (King 1988). Nevertheless, the amount and significance of variation in the genus has never been fully documented and analysed, so that the species-level taxonomy of *Dicynodon* has remained open to discussion (Cluver & Hotton 1981; King 1988).

Recently, Angielczyk & Kurkin (2003) advocated a cladistic approach to the species-level taxonomy of *Dicynodon* that purports to split it into several genera that correspond to terminal nodes on a cladogram. Lucas & Kondrashov

(2004) referred to such an approach as 'cladotaxonomy', and defined a cladotaxon as a low-level taxon (genus or species) that corresponds to a clade in a cladistic analysis. Lucas (2005c) critiqued the cladotaxonomy of *Dicynodon* as basically typological, over-split, of little biological significance and premature.

With regard to alpha taxonomy, taxonomic identity should be demonstrated by morphological similarity analysed within the context of population variation. Such an analysis will produce species-level taxa of potential biological significance that can be organized into genera. This is preferable to the typology inherent to cladotaxonomy, which will recognize several genera in what was formerly *Dicynodon* based only on their perceived cladistic relationships. However, having said this, there still needs to be an extensive overhaul of the taxonomy of the genus *Dicynodon* to better assess its utility and the utility of its species in Permian biostratigraphy.

Cross-correlations

The Pennsylvanian–Permian boundary as currently defined falls within the Wolfcampian Stage, so the boundary is within the Coyotean LVF (Fig. 11). This is because the LO of *Sphenacodon* is Late Virgilian (Harris *et al.* 2004).

Sumida *et al.* (1999a, b) assigned a Late Pennsylvanian age to the Coyotean tetrapod assemblage of the Halgaito Formation of the Cutler Group in the Arizona–Utah borderland. They based this age assignment on Baars (1995, pp. 39–40), who stated that the mixed marine–non-marine strata of the Elephant Canyon Formation, the supposed lateral equivalent of the Halgaito Formation, is mostly of Late Pennsylvanian age. However, a review of the age data on and unresolved debate over the Elephant Canyon Formation (e.g. Welsh 1958; Baars 1962, 1987, 1991; Loope *et al.* 1990; Condon 1997) reveals a much more complex picture. Thus, whether or not the Elephant Canyon Formation is a valid lithostratigraphical unit is uncertain and, according to Condon (1997), the Halgaito Formation only correlates to the uppermost Elephant Canyon Formation (but see Baars 1987 for a different correlation). The Elephant Canyon Formation yields three temporally successive fusulinid assemblages: *Triticites*-dominated (Virgilian), *Schwagerina*-dominated (probably Bursum age, which is now latest Pennsylvanian) and *Pseudoschwagerina*-dominated (earliest Permian). Clearly, the Halgaito Formation and its tetrapod assemblage are close in age to the

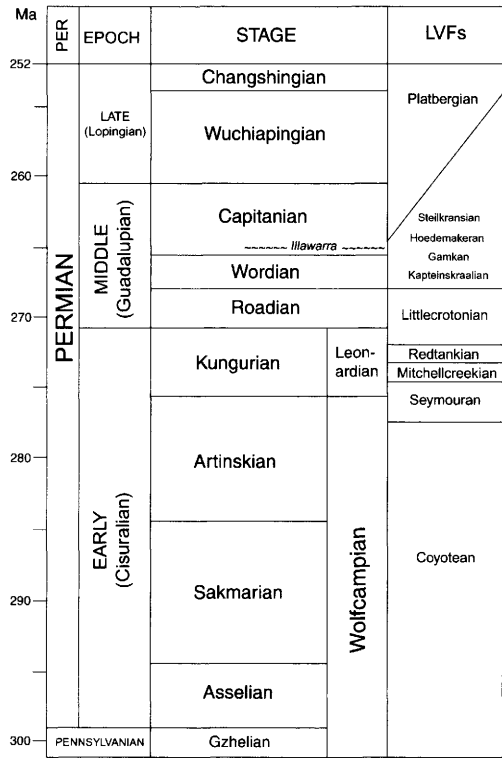


Fig. 11. Cross-correlation of the tetrapod biochronology proposed here to the SGCS of Wardlaw *et al.* (2004).

Pennsylvanian–Permian boundary, but it is not clear whether they are entirely Pennsylvanian or entirely Early Permian.

The Early Permian tetrapod record is restricted to North America and western Europe, so the biochronological scheme of Early Permian faunachrons has no current applicability outside of a Euramerican palaeoprovince. For most of the Coyotean, however, which was during the Gondwana glaciation, it is unlikely that any tetrapods lived in Gondwana.

Recent re-correlation of the North American Early Permian marine stages (Wolfcampian and Leonardian) to the standard Russian Cisuralian stages indicates that the Leonardian is only equivalent to the Kungurian, so the Wolfcampian is much longer than the Leonardian (Wardlaw *et al.* 2004). Numerical calibration of this part of the Permian time scale is imprecise, being based largely on interpolation between a cluster of radioisotopic ages near the Carboniferous–Permian boundary, an Artinskian U–Pb age from Russia of 280.3 ± 2.5 and the U–Pb age of the Capitanian base of

265.3 ± 0.2 Ma (Wardlaw *et al.* 2004). If the graphic correlation based on these numbers is used, then the Wolfcampian is about 23 Ma long (~ 276–299 Ma ago), and the Leonardian is only about 6 Ma long. This indicates that the Coyotean is 15–20 Ma long, whereas Seymouran time is closer to 5 Ma long. The three remaining Early Permian LVFs encompass less than 2 Ma each (Fig. 11). This suggests very little evolutionary turn-over in the tetrapod fauna during Coyotean time (a true chronofauna) followed by substantially higher faunal turn-over rates in the late Wolfcampian–Leonardian that may be related to the drier and more seasonal climates of the late Early Permian (e.g. Olson & Vaughn 1970).

At the Early–Middle Permian boundary, the basis for the LVFs shifts from North America to South Africa. I advocate recognition of a global gap between the youngest North American Permian tetrapods (San Angelo Formation and equivalents) and the oldest, therapsid-bearing faunas, those of Russian Zone I and the *Eodicynodon* Assemblage Zone of South Africa (Lucas 2004). Thus, Lucas (2004) explained in detail why the youngest North American Permian tetrapod assemblages (from the San Angelo, Flowerpot and Chickasha formations of Texas–Oklahoma) are late Leonardian in age. In brief, this is because intercalated marine strata yield Leonardian fusulinids, and overlying strata at the base of the Blaine Formation yield ammonoids of late Leonardian age (Fig. 6).

I have also accepted the argument (see above) that the *Eodicynodon* Assemblage Zone is probably the oldest therapsid-bearing assemblage, because it contains the most primitive therapsids. Therefore, I define the beginning of the Kapteinskraalian by the FAD of *Eodicynodon*, and consider the San Angelo assemblage to be older, and characteristic of the Littlecrotonian LVF (Fig. 11). Thus, the gap in the tetrapod record is equivalent to the younger part of the Littlecrotonian, which is part or all of the Rodian of the SGCS.

In the Russian Tatarian, the Illawara event is just below the LO of *Dicynodon*, which is approximately at the Urzhumian–Severodvinskian boundary, so this is ~ 265 Ma (Lozovsky *et al.* 2001; Menning 2001). If the LO of *Dicynodon* elsewhere is approximately synchronous (within resolution) with the Russian LO, then the Platbergian (= *Dicynodon* biochron of Lucas 1997) is very long, spanning about 14 Ma (~ 252–268 Ma ago). Furthermore, this indicates that the four Middle Permian LVFs, which are no older than Wordian, represent about 4 Ma of Permian time

(Fig. 11). Faunal turn-over rates would thus have been extremely high during the Wordian, with explosive diversifications of dinocephalians and therapsids.

Nevertheless, a very long Platbergian necessitates substantial differences in sedimentation rates in the Karoo basin succession. Thus, the *Tapinocephalus* zone has a maximum thickness of 2000 m, whereas the other zones are 200–600 m thick. If the 500-m thick *Dicynodon* assemblage zone in the Karoo is 14 Ma long, then the underlying tetrapod zones, with a combined maximum thickness of about 3500 m, are squeezed into an interval about 4 Ma long. The average sedimentation rates would thus be about 36 mm/1000 years during the Platbergian, and 875 mm/1000 years for the Kapteinskraalian–Steilkransian, average rates of sedimentation that are well within the range of average rates for fluvial systems (Schindel 1980, 1982; Sadler 1981). However, whether or not such drastic changes in sedimentation rates are possible in the Karoo section needs to be addressed.

It is also possible that the LO of *Dicynodon* in the Russian section is much older than its LO in the Karoo Basin, with its LO in the Karoo being the result of immigration. Finally, there is the problem of the taxonomy of *Dicynodon* discussed above. What is called *Dicynodon* at its LO in the Russian section may not be the same taxon at its LO in the Karoo section. At present, I lack the data to resolve the problems posed by cross-correlation of the Platbergian to the SGCS, so, on Figure 11, I show the Platbergian base as a diagonal line that covers the range of possibilities. This is an important problem that needs resolution.

Traditionally, the Permian–Triassic boundary has been placed at the FAD of the dicynodont *Lystrosaurus*. However, it is likely that the FAD of *Lystrosaurus* is actually latest Permian (Lucas 1998b; Hancox *et al.* 2002; Retallack *et al.* 2003). Therefore, the boundary is within the Lootsbergian LVF of Lucas (1998b), which immediately follows the Platbergian of this paper. Thus, like the Carboniferous–Permian boundary, the Permian–Triassic boundary does not correspond to an LVF boundary.

I am grateful to T. Hentz and A. Milner for unpublished information. Collaboration in the field and the museum with D. Berman, D. Chaney, S. Harris, A. Henrici and K. Krainer influenced the content of this paper. Reviews by D. Berman, S. Harris, S. Modesto, B. Rubidge, S. Sumida and R. Werneburg corrected many shortcomings in the manuscript and are gratefully acknowledged.

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