

A global hiatus in the Middle Permian tetrapod fossil record

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ABSTRACT: For about a half century, most vertebrate paleontologists have correlated the youngest Permian tetrapod assemblages in North America, which are from the San Angelo, Flowerpot and Chickasha formations in Texas-Oklahoma, to the oldest therapsid-bearing assemblages of the Russian Kazanian. This correlation was not based on shared low-level taxa (genera and species), but on the supposed therapsids in the American faunas and the presence of some “counterparts” (equivalent evolutionary grade) among the American and Russian captorhinids and caseid pelycosaurs. Marine biostratigraphy indicates that the youngest tetrapod assemblages in Texas-Oklahoma are of Kungurian (late Leonardian) age, whereas the base of the Kazanian is no older than late Roadian. Thus, a very real hiatus in the global tetrapod record, previously named Olson’s gap, is evident between the youngest, pelycosaur-dominated assemblages of North America and the oldest, therapsid-dominated tetrapod assemblages of Russia. This hiatus is equivalent to most of Roadian time, and is at least two million years long. A review of the global record of Permian tetrapod body fossils and footprints reveals that this is a hiatus of global extent. Olson’s gap corresponds to a significant remodelling of the Permian tetrapod fauna.

INTRODUCTION

The global record of Permian tetrapod fossils (text-fig. 1) encompasses a significant geographic discontinuity. Early Permian tetrapods have their most extensive fossil record in the western United States (especially Texas and Oklahoma) and a much less extensive record in western Europe (especially Germany and the Czech Republic). In contrast, the most extensive fossil records of Middle and Late Permian tetrapods are from South Africa (Karoo basin) and Russia (Ural Mountains foreland), but do not overlie significant records of older, Early Permian tetrapods. Other records of Permian tetrapods, from Brazil, India, China and other locations, are assemblages of limited diversity that do not encompass significant intervals of Permian time (Lucas 1998).

Thus, a complete understanding of Permian tetrapod evolution must bridge a geographic gap between the most significant record of Early Permian tetrapods, in the western USA, and the most significant records of Middle-Late Permian tetrapods, in Russia and South Africa. Furthermore, the temporal relationship between the youngest American and the oldest Russian or South African tetrapod assemblages must be established.

Beginning with Olson (1955, 1962) and Efremov (1956), it has generally been believed that the correlation of the youngest American and oldest Russian assemblages had been accomplished, though the fossil record of early Middle Permian tetrapods remains sparse (e.g., Milner 1993, Benton 1993, Lucas 1998). Supposedly the youngest North American Permian tetrapods, of presumed Guadalupian age, are correlated directly to the oldest Russian Kazanian tetrapod assemblages (Olson 1990). Here, I argue otherwise by demonstrating that a hiatus, equivalent to part of the Middle Permian, exists in the global Permian tetrapod fossil record. This hiatus has been termed Olson’s gap (Lucas and Heckert 2001), a significant deficit in the Permian history of tetrapod evolution.

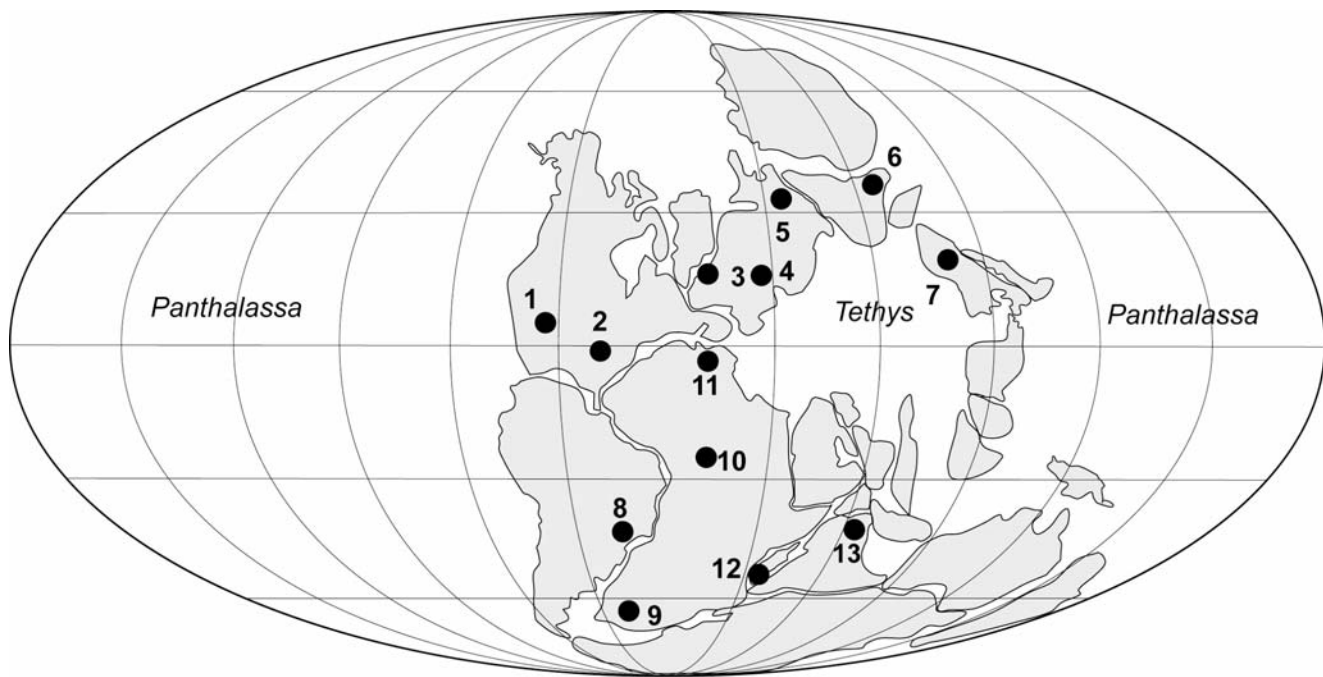
PERMIAN TIMESCALE

Three Permian timescales are relevant to this article (text-fig. 2). The standard global chronostratigraphic scale (SGCS) is that advocated by the Subcommittee on Permian Stratigraphy of the International Commission on Stratigraphy, International Union of Geological Sciences (e.g., Glenister et al. 1992, Wardlaw 1999). This is the global marine standard composed of three series divided into nine stages. Two provincial, or secondary (*sensu* Cope 1996) timescales are useful here—an American and a Russian scale (text-fig. 2). The American Leonardian stage, based on a marine stratotype, spans much of the Early Permian. In Russia, the Ufimian, Kazanian and Tatarian Stages have stratotypes that are a mixture of marine and nonmarine strata and span the entire Middle and Late Permian.

Numerical calibration of the Permian timescale is imprecise because only a handful of reliable radioisotopic ages can be unambiguously correlated to the SGCS. Relevant to this paper is an age of ~ 265 Ma that calibrates the Wordian-Capitanian boundary (Bowring et al. 1998). Duration of the Roadian and Wordian has been estimated by Wardlaw (1999), with each stage equivalent to one conodont zone assumed to be of about two million years duration. However, other estimates assign each stage a longer duration of about three to five million years (e.g., Menning 2001).

AGE AND CORRELATION: NORTH AMERICA

Permian tetrapod fossils have been collected in the western United States, especially Texas and Oklahoma (text-fig. 3), since the 1800s (Hook 1989). The most extensive and best known assemblages are of unquestioned Early Permian age. They come primarily from rocks of the Bowie, Wichita and Clear Fork groups in Texas that intertongue with or are laterally equivalent to marine strata of Wolfcampian-Leonardian age (e.g., Hentz 1988, Hook 1989, Lucas 1998) (text-fig. 4). Less extensive, age-equivalent assemblages are known from the Cutler Group and correlative strata in the Four Corners states of



TEXT-FIGURE 1

Map of Permian Pangea (after Li et al. 1993) showing principal tetrapod localities mentioned in the text. 1 = western USA; 2 = eastern USA (Dunkard) ; 3 = Scotland; 4 = Western Europe (Rotliegendes); 5 = Russian Urals; 6 = Junggur basin, China; 7 = Ordos basin, China; 8 = Paraná basin, Brazil; 9 = Karoo basin, South Africa; 10 = Niger; 11 = Morocco; 12 = southern Madagascar; 13 = Kashmir, India. Less extensive Permian tetrapod assemblages from Zimbabwe, Zambia, Malawi, and Australia are not shown.

New Mexico, Colorado and Utah, from the Dunkard Group of the West Virginia-Ohio-Pennsylvania borderland and from Prince Edward Island in eastern Canada (e.g., Berman 1993, Lucas 1998, 2004, Sumida et al. 1999). The stratigraphically highest (and youngest) Permian tetrapod assemblages in the American Permian are from the San Angelo, Flowerpot and Chickasha formations of Texas-Oklahoma (text-figs. 3-4).

Olson and Beerbower (1953) described the vertebrate fossil assemblage from the San Angelo Formation, which is from localities in Knox, Foard and Hardeman Counties in north-central Texas (text-fig. 3). It includes the xenacanth shark *Xenacanthus*, the captorhinid *Rothianiscus multidonta* (Olson and Beerbower), the caseid pelycosaur *Caseoides sanangelensis* Olson and Beerbower, *Cotylorhynchus hancocki* Olson and Beerbower and *Angelosaurus dolani* Olson and Beerbower, the sphenacodontids *Steppesaurus gurleyi* Olson and Beerbower and *Tappensaurus magnus* Olson and Beerbower and the putative therapsid *Dimacrodon hottoni* Olson and Beerbower. Olson (1962) later added these new taxa to the San Angelo tetrapod assemblage: the temnospondyl *Slaughenhopia texensis*, the captorhinid *Kahneria seltina*, the sphenacodont *Dimetrodon angeloensis*, the caseids *Angelosaurus greeni* and *Caseopsis agilis* and the “therapsids” *Knoxosaurus niteckii*, *Gorgodon minutus*, *Eosyodon hudsoni*, *Driveria ponderosa* and *Mastersonia magnus*. Olson (1962) also reassigned *Tappensaurus* and *Steppesaurus*, with *Dimacrodon*, to the Therapsida.

Olson and Barghusen (1962) described vertebrate fossils from two localities in the Flowerpot Formation in Kingfisher County, Oklahoma (text-fig. 3). These represent the “microsaur” *Cymatorhiza kittsi* Olson and Barghusen, *Rothianiscus multidonta*, *Cotylorhynchus bransoni* Olson and Barghusen and *Angelosaurus romeri* Olson and Barghusen.

Strata of the Chickasha Formation, which are laterally equivalent to the middle part of the Flowerpot Formation (text-fig. 4), yielded vertebrate fossils from about 20 localities, mostly in Blaine and Kingfisher Counties, Oklahoma (Olson 1965) (text-fig. 3). A single locality in McClain County, Oklahoma also yielded unidentified bone from the Duncan Sandstone (Olson, 1965). The Chickasha assemblage includes the xenacanth *Xenacanthus* sp., indeterminate palaeoniscoid fish, *Cymatorhiza kittsi*, the amphibians *Nannospondylus stewarti* Olson and *Fayella chickashaensis* Olson, *Rothianiscus robusta* Olson, *Cotylorhynchus bransoni*, *Angelosaurus romeri* and the varanopsid *Varanodon agilis* Olson. Olson (1972) subsequently added the nectridean *Diplocaulus parvus* to this assemblage, and Olson (1974) described the supposed therapsid *Watongia meieri*. Olson’s (1980) *Seymouria agilis* from the Chickasha Formation assemblage has recently been reassigned to the parareptile *Macroleter*, a genus previously known only from Russia (Reisz and Laurin 2001).

In discussing the composition and age of these assemblages, Olson emphasized the differences between the tetrapods found in the San Angelo, Flowerpot and Chickasha formations, although the fossils come from a single, relatively narrow stratigraphic interval (text-fig. 4). Furthermore, all three formations yield tetrapod fossil assemblages dominated by caseid pelycosaur, and they share genera, including *Cymatorhiza*, *Rothianiscus*, *Cotylorhynchus* and *Angelosaurus*. Therefore, I feel justified in treating the vertebrate fossils from the San Angelo, Flowerpot and Chickasha formations as a single biostratigraphic assemblage of one age, as did Olson in his later work (e.g., Olson and Chudinov 1992).

The “therapsids” that Olson described from the San Angelo and Chickasha formations were based on fragmentary specimens

and have been considered of questionable affinity, though their assignment to the Therapsida was long upheld by many workers (e.g., Sigogneau-Russell 1989). Nevertheless, recent re-evaluation of these “therapsid” taxa has deemed them to be based on fragmentary pelycosaur fossils (Parrish et al. 1986, Sidor and Hopson 1995). I agree with this assessment (also see Battail, 2000), and thus conclude that there are no demonstrable therapsid taxa from the San Angelo or Chickasha formations.

There are three ways to determine the age of the vertebrate fossils from the San Angelo, Flowerpot and Chickasha formations and correlate them to the SGCS: (1) marine biostratigraphic evidence of the age of the Blaine Formation; (2) fusulinid evidence of the age of the San Angelo Formation; and (3) lithostratigraphic, event and sequence stratigraphic correlation of the Blaine Formation and underlying strata. All three indicate that these youngest North American Permian tetrapods are of late Early Permian (late Leonardian/Kungurian) age.

Blaine Formation biostratigraphy

The minimum age of the tetrapod assemblages of the San Angelo, Flowerpot and Chickasha formations is directly constrained by the age of the overlying Blaine Formation (text-fig. 4), marine strata that yield invertebrate fossils, including ammonoids. In Oklahoma, the Blaine Formation of Gould (1902, 1905) is 25–30 m of interbedded gypsum, dolomite and reddish brown silty shale (Fay 1962, 1964). It conformably overlies the Flowerpot Formation and is conformably overlain by the Dog Creek Shale (Fay 1962, 1964) (text-fig. 4). The Chickasha Formation is also conformably overlain by the Blaine in Oklahoma, though, locally, clastic tongues of the Chickasha are laterally equivalent to or overlie the Blaine. However, the Chickasha and Flowerpot vertebrate localities in Oklahoma are stratigraphically below the Blaine (Olson and Beerbower 1953, Fay 1964, Olson 1965). In north-central Texas, the Blaine Formation is as much as 210 m thick and conformably overlies the San Angelo Formation (Jones 1971) (text-fig. 4).

Plummer and Scott (1937) first documented ammonoids from various horizons in the Blaine Formation in Texas. They reported *Eumedlicottia burckhardti* (Böse), *Eumedlicottia crotonensis* Plummer and Scott, *Perrinites gouldi* Plummer and Scott, *Perrinites hilli* (Smith) and *Stacheoceras* n. sp. and identified them as part of a *Perrinites hilli* assemblage of earliest Guadalupian age, largely because of the supposed presence of *Eumedlicottia burckhardti*. However, Miller and Furnish (1940) revised the taxonomy of the Blaine ammonoids and considered them to be of Leonardian age, listing them as *Propinacoceras knighti* Miller and Furnish, *Medlicottia whitneyi* Böse, *Metalegoceras?* sp., *Stacheoceras?* sp. and *Perrinites hilli* (Smith).

Clifton (1942) documented 37 species of invertebrates from the Blaine Formation and overlying Dog Creek Shale at localities in Texas and Oklahoma. These are mostly brachiopods, bivalves and cephalopods, including the ammonoids *Propinacoceras knighti* Miller and Furnish, *Medlicottia whitneyi* Böse, *Medlicottia* sp., *Pseudogastriceras texanum* Clifton, *Adrianites newelli* Miller and Furnish, *Agathiceras girtyi* Böse and *Perrinites hilli* (Smith). He, too, assigned the Blaine a Leonardian age based on these fossils.

Perrinites was long the standard ammonoid of the Leonardian Formation (Böse 1919, Adams et al. 1939, Glenister and Fur-

Ma	PERMIAN			SGCS	USA	RUSSIA
	EARLY	MIDDLE	LATE			
251				Changshingian		
255			Lopingian	Wuchiapingian	Ochoan	Tatarian
260				Capitanian	Capitanian	
265		Guadalupian		Wordian	Wordian	Kazanian
				Roadian	Roadian	Ufimian
270				Kungurian		Kungurian
275				Leonardian		Leonardian
280		Cisuralian		Artinskian		Artinskian
285				Sakmarian		Sakmarian
				Wolfcampian		Wolfcampian
290				Asselian	"Bursumian"	Asselian

TEXT-FIGURE 2

Permian marine timescales relevant to this article. The standard global chronostratigraphic scale (SGCS) is from Wardlaw (1999), as is the numerical calibration, which is tentative. Correlation of the North American and Russian scales to the SGCS is that of Glenister et al. (1992), Kozur (1995) and Kotlyar (2000).

nish 1981). However, its youngest records in the Glass Mountains of West Texas are in the stratotype of the Roadian stage, the Road Canyon Formation, formerly called the “First Limestone” of the Word Formation (King 1931, Clifton 1945, 1946, King 1947, Cooper and Grant 1964, 1966). There have been two views of the taxonomy of the *Perrinites* of the Road Canyon Formation. They have either been assigned to *P. hilli* or to a separate, more advanced species, *P. vidriensis* Böse.

Indeed, the most recent revision of *Perrinites*, by Tharalson (1984), identifies *Perrinites hilli* (Smith), which has its type specimens from the Blaine Formation and is also known from the Leonardian Choza Formation of the Clear Fork Group, and *P. vidriensis* Böse, known from the upper part of the Leonardian Cathedral Mountain and Skinner Ranch formations and the Roadian lower Road Canyon Formation. Thus, by Tharalson’s (1984) taxonomy, *Perrinites hilli* from the Blaine Formation indicates a Leonardian age.

Jones (1971) agreed with Miller and Furnish (1940) and Clifton (1942, 1945, 1946) in assigning the Blaine a Leonardian age. However, he claimed that Skinner (1946, p. 1863) indicated a Guadalupian age for the Blaine based on the fusulines *Parafusulina rothi*, *P. lineata*, *P. sellardsi* and *P. deliciosensis* found in subsurface rocks correlated to the San Andres Formation. Nevertheless, no fusulinids have been reported from the Blaine Formation, and Skinner merely listed these taxa as coming from subsurface strata of the San Andres, not the Blaine. Skinner (1946) did, indeed, correlate the Blaine and San Andres, and, given that he considered the San Andres to be of Wordian age, he assigned the Blaine a Wordian age. Nevertheless, this forced him to regard Leonardian index taxa such as *Perrinites hilli* known from the Blaine as “holdovers” (Skinner 1946, p. 1865).



TEXT-FIGURE 3
Distribution of uppermost Lower, Middle and Upper Permian strata in Texas-Oklahoma (strata of the Pease River Group and equivalents) and adjacent areas (after Mear 1984) and principal localities of the San Angelo, Flowerpot and Chickasha tetrapod assemblages.

Thus, a straightforward interpretation of Blaine invertebrate biostratigraphy indicates it is of Leonardian age.

Recently, DiMichele et al. (2001, p. 450) claimed that the ammonoids from the Blaine Formation have stratigraphic ranges that only overlap in Guadalupian strata, and thus suggest a Guadalupian age for all but the lowermost Blaine. This claim, however, was based on two oversights. First, DiMichele et al. (2001) stated that *Eumedlicottia burckhardti* Plummer and Scott, a characteristic Wordian ammonoid, is present in the Blaine, based on the report of Plummer and Scott (1937, p. 19, 20, 21, 397). However, they overlooked that Miller and Furnish (1940, p. 55) reassigned this record, as well as the Blaine species *Eumedlicottia crotonensis* Plummer and Scott (see Plummer and Scott 1937, p. 19, 21, 82-84, 85, 398, pl. 6, figs. 7-11), to *Medlicottia whitneyi*. There are no records of *Eumedlicottia burckhardti* from the Blaine Formation.

Furthermore, DiMichele et al. (2001, p. 450) claimed that the overlap zone of the six taxa of Blaine ammonoids reported by Clifton (1942) is Wordian, using the range charts of Zhou et al. (1996). This is incorrect. According to Zhou et al. (1996), the range of *Medlicottia* is Sakmarian-Wordian, *Propinacoceras* is Artinskian-Wordian, *Pseudogastriceras* is Wuchiapingian-Changshingian, *Adrianites* is Wordian, *Agathiceras* is Moscovian-Wordian and *Perrinites* is Artinskian-Roadian. Not only is there no overlap zone of all these taxa, but the taxa *Pseudogastriceras* and *Adrianites* as used by Zhou et al. (1996) are vastly revised taxonomically compared to the way those names were used by Clifton (1942) (B. Glenister, C. Spinosa, written commun., 2001). Moreover, according to Miller and Furnish (1940, p. 84, 114), the genera *Pseudo-*

gastriceras and *Adrianites*, as then construed, had Wolfcampian and/or Leonardian records.

In conclusion, ammonoid biostratigraphy indicates a Leonardian age for the Blaine Formation. This means that the vertebrate fossils of the San Angelo, Flowerpot and Chickasha formations cannot be younger than Leonardian. Given that these units overlie a thick section of Leonardian strata (upper Wichita Group and Clear Fork Group), a late Leonardian age for the Blaine, San Angelo, Flowerpot and Chickasha formations seems certain (text-fig. 4).

Fusulinids

There is some compelling evidence from fusulinids of the age of the San Angelo Formation. Thus, Skinner (1946, p. 1863) reported the characteristic upper Leonardian fusulinid *Schubertella melonica* Dunbar and Skinner from subsurface samples of limestone beds of the San Angelo Formation (also see DiMichele et al. 2000). Furthermore, Skinner (1946, p. 1863) reported the typical upper Leonardian fusulinid *Parafusulina fountaini* Dunbar and Skinner from the "Holt Pay," a limestone immediately above the San Angelo (= Glorieta) Formation in Ector County, Texas. Skinner's (1946) reports, however, were not documented by illustrations of fossils, but Wilde et al. (2001) have recently documented the middle-upper Leonardian fusulinid *Parafusulina brooksensis* Ross from the "Holt Pay." These fusulinid records are consistent with Blaine ammonoid biostratigraphy, which indicates that the San Angelo Formation, and its Oklahoma correlatives, are of Leonardian age.

Lithostratigraphic and Event Stratigraphic Correlation

A third way to correlate the Blaine and underlying San Angelo and correlative units is through a physical stratigraphic correlation across the Midland basin from eastern New Mexico to north-central Texas (text-fig. 5). This correlation indicates that the Glorieta Sandstone of eastern New Mexico is equivalent to the San Angelo Formation, and the base of the San Andres Formation of eastern New Mexico represents the same marine transgressive event as the base of the Blaine (text-fig. 5). A large literature exists that documents this correlation, and it is well represented by Page and Adams (1940), Hills (1942, 1972), King (1942) and Mear (1963, 1984). Thus, Hills (1942, figs. 7-8) presented a correlation of surface and subsurface sections from southeastern New Mexico across Texas to Oklahoma showing the correlation of the Glorieta to the San Angelo and Flowerpot formations and the lower San Andres to the Blaine and Dog Creek formations. He thus reconstructed the paleogeography of Blaine time as a single extensive marine seaway that covered parts of New Mexico, Texas and Oklahoma and simultaneously deposited the San Andres and Blaine formations (Hills 1942, fig. 5).

In his classic monograph on the correlation of Permian strata in New Mexico and Texas, King (1942) also advocated the physical equivalence of the Glorieta Sandstone and the San Angelo Formation. He cited (p. 694) a personal communication from J. W. Skinner that Leonardian fusulinids were found in wells in Borden County, Texas in "beds approximately equivalent to the Blaine and Dog Creek formations." King therefore concluded the Blaine is of Leonardian age. He questioned early workers (Beede and Bentley 1921, Beede and Christner 1926), who considered the San Angelo base to be an unconformity, though subsequent authors have generally upheld the presence of an unconformity at the base of the San Angelo Formation (e.g., Ross 1987). King (1942, p. 698-699) also discussed broader

problems of correlation based on ammonoids and concluded that the Blaine and Dog Creek ammonoids are Leonardian.

Correlation of the Blaine and the San Andres has been taken by some to indicate the Blaine is Guadalupian, despite the ammonoid evidence to the contrary (e.g., Dunbar et al. 1960). Fay (1964) well represents this literature. He considered the Flowerpot, Blaine and Dog Creek to be of Guadalupian age, and he correlated the Oklahoma Flowerpot to the San Angelo Formation of Texas and to the Glorieta Sandstone of New Mexico, citing King (1942, p. 695, pl. 2) as the primary basis for the correlation.

Indeed, most of the problem with determining the age of the Blaine is derived from a longstanding disagreement about the age of the correlative San Andres Formation, assigned by some a Guadalupian age, along with the underlying and intertongued Glorieta Sandstone. However, recent detailed biostratigraphic work, especially with conodonts, indicates that the Glorieta and the lower San Andres are late Leonardian, whereas the upper San Andres is Guadalupian (Sarg and Lehmann 1986, Kerans et al. 1993, Fitchen 1993, Sonnenfeld 1993, Lambert et al. 2000). Conodonts indicate the lower San Andres Formation is in the *Neostreptognathodus sulcopicatus* Zone of late Leonardian age (Kerans et al. 1993, Wardlaw 1995, 2000).

Thus, the initial San Andres transgression, which is homotaxial with the Blaine, is Leonardian, and the Glorieta base, which is disconformable on the Yeso, is equivalent to the base of the San Angelo Formation (text-fig. 5). Another way to state this is to recognize that the unconformity at the bases of the Glorieta and San Angelo is the sequence boundary beneath the lower (or lower to middle) San Andres sequence that includes the Blaine (Sarg and Lehmann 1986, Ross 1987, Kerans et al. 1993). Lithostratigraphic correlation of the San Angelo-Blaine with the Glorieta-lower San Andres thus is consistent with biostratigraphic evidence that the San Angelo and Blaine are of late Leonardian age.

AGE AND CORRELATION: RUSSIA

Permian tetrapod fossils from the Russian Ural foreland are from an outcrop belt that extends more than 1500 km north-south (text-fig. 6). These fossils come from more than 500 localities, of which approximately 120 are of biostratigraphic value because they contain identifiable fossils (Golubev 1998). Virtually all of the localities are in Kazanian or Tatarian sediments.

Efremov (1937, 1940, 1952, and others) proposed a biostratigraphic scheme for the succession of Permian tetrapod fossils in the Urals region (text-fig. 7). He divided the record into four zones (although the vertebrate fossils originally assigned to Zone III were eventually shown to belong to Zone II. Efremov and Vyushkov (1955) organized this record into two phases or complexes, dinocephalian and pareiasaurian (text-fig. 7). Subsequent workers little altered this scheme, though it was renamed by Chudinov (e.g., 1975, 1983) as three assemblages or complexes— Ocher Deinocephalian or Ochersky, Isheevo Deinocephalian or Isheevsky and North Dvina Pareiasaur or Severodvinsky (text-fig. 7). Ivakhnenko (1990a, b, c) and Ivakhnenko et al. (1997) have proposed new biostratigraphic schemes that are a reorganization and further subdivision of the older zonation (text-fig. 7). Critical to this discussion is the age and correlation of the oldest therapsid-dominated assemblages in Russia.

LITHOSTRATIGRAPHIC NOMENCLATURE				STAGE	
Pease River Group	Dog Creek Shale	Chickasha Formation		LEONARDIAN	
	Blaine Formation				
	San Angelo Formation				Flowerpot Formation
					Duncan Sandstone
Clear Fork Group	Choza Formation	Hentz (1988)			
	Vale Formation				
	Arroyo Formation				
Wichita Group	Lueders Formation	Wichita Group	Waggoner Ranch Formation		
	Clyde Formation		Petrolia Formation		
	Belle Plains Formation		Nocona Formation		
	Admiral Formation	Bowie Group	Archer City Formation		
	Putnam Formation		Markley Formation		
	Moran Formation				
	Pueblo Formation				
			WOLF CAMPIAN		

TEXT-FIGURE 4
Stratigraphy of Permian tetrapod-bearing formations in Texas-Oklahoma based on Olson (1962), Hentz (1988) and Hook (1989). The nomenclature of the Bowie and Wichita Groups of Hentz (1988), on the right, is contrasted with that of earlier workers, on the left.

Oldest Therapsid Assemblages

The stratigraphically lowest, and hence the oldest, therapsid-dominated tetrapod assemblage in the Russian section is the Golyusherma locality (text-figs. 6, 8). It yields a tetrapod assemblage of archegosaurids, melosaurids, bolosaurids, captorhinids, leporophids and primitive estemmosuchid and anteosaurid therapsids (Konzhukova 1955, Golubev 1992, 1998, Ivakhnenko 1995). The Golyusherma locality can be lithostratigraphically correlated to the Baitugan horizon at the base of the Kazanian (Golubev 1998) (text-fig. 8). Thus it is, without question, the stratigraphically lowest and hence the oldest, therapsid-bearing tetrapod assemblage in the Russian section, and it is of early Kazanian age.

In Bashkirstan, a locality at the Santagulovo Mine (text-fig. 6) may be equally old. It comes from strata intercalated with basal Kazanian marine limestones, and yields fragmentary remains of temnospondyls, the dinocephalian "*Brithopus*" and phreatosuchids (e.g., Efremov 1954, Efremov and Vyushkov 1955, Olson 1962, Modesto and Rychczynski 2000). These specimens were collected early in mining activities, so their exact stratigraphic provenance is somewhat uncertain (Olson 1957), though their association with brachiopod-bearing limestones of early Kazanian age seems clear. These specimens may be as old as Golyusherma, but are not older. Thus, the oldest

STAGE	East-central New Mexico	Glass Mountains	North-central Texas	Central Oklahoma
Leonardian	San Andres Formation	Cathedral Mountain Formation	Whitehorse Fm.	Dog Creek Fm.
	Glorieta Sandstone		Blaine Fm.	Blaine Fm.
	Yeso Formation		San Angelo Fm.	Flowerpot Formation Chickasha Formation
	upper member of Abo Formation	Skinner Ranch Formation	Choza Formation	Hennessey Group
	Bone Springs Limestone		Vale Formation	
	middle member of Abo Formation		Hess Formation	Arroyo Formation
Wolf-campian			Leuders Formation	
			Clyde Formation	Wellington Formation
			Belle Plains Formation	Oscar Formation
		Lenox Hills Formation	Admiral Formation	

TEXT-FIGURE 5
Correlation of Leonardian strata from eastern New Mexico to Oklahoma (text-fig. 3) (based in part on Simpson 1973, Ross 1987 and Kerans et al. 1993).

therapsid-bearing tetrapod assemblages in the Russian section are of early Kazanian age.

Slightly younger assemblages include Belebey, Ocher and Mezen (text-fig. 8), and are some of the classic Kazanian therapsid-dominated assemblages of the Russian section. They are of late Kazanian age (e.g., Lozovsky 1992, 2003, Ivakhnenko et al. 1997, Golubev 1998) (text-fig. 8). These are the bulk of the Zone I and II assemblages, and they are dominated by diverse therapsids, especially anteosaurids and anomodonts (also see Ivakhnenko 1990a, b).

Inta Assemblage

In Russia, there is a tetrapod assemblage older than the Kazanian relevant to this discussion. This is the Inta River assemblage from the Pechora basin, well to the northeast of the classic Kazanian tetrapod localities (text-fig. 6). This assemblage is essentially an amphibian fauna originally described by Konzjukova (1953) and assigned by her to the Early Permian. Later workers place it in the Sheshminsky horizon of the upper Ufimian, which means it is earliest Middle Permian in age (Gubin 1984, 1986, Lozovsky 1992, 2003, Olson and Chudinov 1992, Ivakhnenko et al. 1997, Kotlyar 2000). Indeed, the type localities of the Inta fauna (Inta and Pechora) are in the upper part of the Intinskoy svita, a unit of well-established Ufimian age (Muravyev 1972, Chuvashov et al. 1995, Golubev 1999, Kotlyar 2000).

Gubin (1998) and Shishkin et al. (2000) noted the similarity of the Inta amphibians to Upper Pennsylvanian-Early Permian amphibians in North America and Western Europe. The fauna is mostly endemic intasuchids and Early Permian holdovers of eryopoids. Ivakhnenko (1990b) added a captorhinid to the Inta fauna, but this is actually from Asselian strata on the Mylva River (Modesto and Rybczynski 2000). Significantly, Inta lacks therapsids, so it does not extend the Russian therapsid record back to pre-Kazanian strata.

Global correlation of Ufimian-Kazanian

The volume by Esaulova et al. (1998) includes extensive reviews of Ufimian and Kazanian nonmarine bivalves, ostracods, fishes, ichthyoliths, charophytes, macroflora, palynomorphs and terrestrial vertebrates. Most of these fossils are endemic to the Russian section and/or are shallow marine or nonmarine taxa of no value to a correlation to the SGCS. Nevertheless, some marine intervals in the Ufimian and Kazanian strata locally contain marine fossils useful to their global correlation.

Based on various data, including ammonoids, non-fusulinid foraminiferans, brachiopods and marine bivalves from the Russian section, and sequence stratigraphic correlations, the beginning of Roadian time is generally correlated to a horizon within the Russian Ufimian (between the Solikamsk and Sheshma horizons); and the Kazanian is correlated approximately to the Wordian, with some workers regarding its base as upper Roadian and/or its top as lowermost Capitanian (e.g., Ross and Ross 1988, 1995, Dickins 1992, Kozur 1992, 1993a, Jin et al. 1994, Leonova 1998, Archbold 1999, Grunt 1999, Pronina 1999, Byakov 1999, Kotlyar 1999, 2000). The most convincing biostratigraphic data to support, and refine, these correlations come from conodonts.

Thus, Kozur (1975) described the conodont *Stepanovites meyeri* from the Russian Kazanian, and this taxon was reassigned to the Wordian-Capitanian taxon *Merrillina divergens* (Bender and Stoppel) by Wardlaw and Collinson (1986). More recently, Chalimbada and Silantiev (1998) reported conodonts from shallow marine strata of the type Kazanian. These are from southeast of Kazan along the Kama River and are: (1) *Sweetina triticum* Wardlaw and Collinson from the lowermost Kazanian (Baitugan horizon); and (2) *Merrillina divergens* from the upper Kazanian. In North America, *Sweetina triticum* has a stratigraphic range of upper Roadian and lower Wordian, whereas the range of *Merrillina divergens* is uppermost Wordian-lowermost Capitanian (Wardlaw and Collinson 1986, Kozur 1995, Wardlaw 1995, 2000).

Kozur (1998) did not accept reassignment of *Stepanovites meyeri* to *Merrillina divergens*, and he differed on the taxonomic identification of the conodonts described by Chalimbada and Silantiev (1998). Nevertheless, he did not question that they indicate a late Roadian-Wordian correlation for the Kazanian. The conodont data thus are consistent with other data that indicate the base of the Kazanian is no older than late Roadian and that most of the Kazanian is Wordian. Indeed, the late Roadian-early Wordian conodont *Sweetina triticum* occurs in marine strata of the Baitugan horizon that can be directly correlated to Golyusherma, the oldest Russian therapsid assemblage. Thus, on the SGCS, the oldest Russian therapsid-bearing tetrapod assemblages are no older than late Roadian and may be as young as early Wordian (also see Lozovsky 2003).

CORRELATION: NORTH AMERICA TO RUSSIA

Based on the above discussion, correlation of the youngest North American and the oldest Russian Permian tetrapod records can be undertaken based on marine biostratigraphy (text-fig. 9). The presence of the Illawara magnetic reversal in the North American Capitanian and Russian Tatarian is consistent with this correlation (e.g., Menning 2001). This correlation indicates a temporal gap between the youngest North American pelycosaur-dominated assemblages and the oldest Russian therapsid-dominated assemblages. This gap is in small part filled temporally by the Inta assemblage, though it lacks

therapsids. Nevertheless, a hiatus, equivalent to much of Roadian time, and therefore at least two million years long, does exist between the American and Russian assemblages, and has been termed Olson's gap (Lucas and Heckert 2001).

BRIDGING THE GAP

Other Permian Tetrapod Assemblages

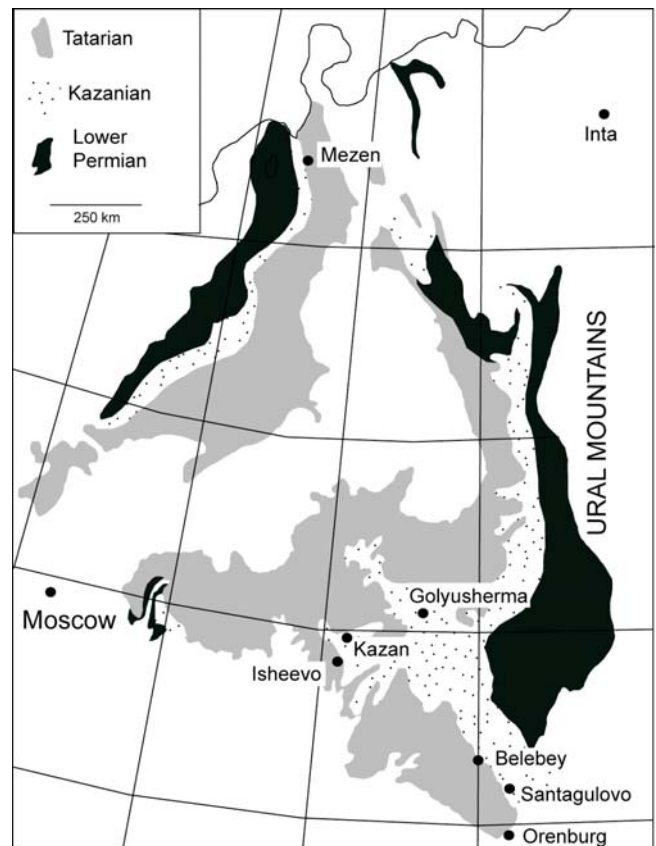
Outside of North America and Russia, can Olson's gap be filled? A review of the temporal distribution of Permian tetrapods suggests not (text-fig. 10).

South America. Relatively few Permian tetrapods are known from South America. In the Parnaíba basin of northern Brazil, Price (1948) described the archegosaurid temnospondyl *Prionosuchus* from the Pedra do Fogo Formation and assigned it an Early Permian age (also see Barberena 1972). Cox and Hutchinson (1991) re-evaluated *Prionosuchus* and noted it is a derived archegosaurid, possibly synonymous with *Platyoposaurus*, a Kazanian taxon. Therefore, they advocated a "Middle Permian" age for the Pedra do Fogo Formation, though precise correlation to the SGCS is uncertain.

In the Paraná basin of southeastern Brazil, Middle Permian tetrapods from the Rio do Rasto Formation are rhinesuchid temnospondyls, the pareiasaur *Provelosaurus*, fragmentary dinocephalians and the dicynodont *Endothiodon* (Barberena et al. 1985, Langer 2000). Barberena et al. (1980, 1985) correlated this assemblage to the South African *Cistecephalus* Assemblage Zone, but Langer (2000) suggested an older age, correlating it to either the *Eodicynodon* or *Tapinocephalus* Assemblage Zones in South Africa. However, neither correlation suggests an age older than Kazanian, so no Brazilian tetrapod assemblage fills Olson's gap (text-fig. 10).

Western Europe. Nonmarine Upper Carboniferous and Lower Permian strata were deposited in Western Europe in a series of small, intermontane basins during the Variscan orogeny. These are the Rotliegend sediments that have long been considered Lower Permian, though Kozur (1984) placed the base of the Permian in the upper part of the lower Rotliegend. Most of the tetrapod record here is from the upper Rotliegend and thus is of Early Permian age (e.g., Werneburg 1989, Boy 1993, Berman et al. 1997). The stratigraphically highest Rotliegend tetrapod body fossil assemblage is from the Bromacker quarry in the Tambach Formation in Germany. Berman and Martens (1993), Sumida et al. (1996, 1998) and Berman et al. (2001) documented tetrapods from the Tambach Formation (also see Eberth et al. 2000), which are the protorothyridid *Thuringothyris*, the seymouriamorph *Seymouria*, the diadectomorph *Diadectes*, the trematopid *Tambachia* and the pelycosaur *Dimetrodon*. This assemblage shares taxa with and is approximately equivalent to the late Wolfcampian Nocona Formation in Texas (Berman et al. 2001).

Some Upper Permian tetrapods are also known from Western Europe, especially those from Cutties Hillock Quarry in Great Britain. Here, the dicynodonts *Dicynodon* (= *Gordonia*) and *Pelanomodon* (= *Geikia*), and the pareiasaur *Elginia*, are present (Benton and Spencer 1995). This assemblage is equivalent to the *Dicynodon* assemblage zone of the South African Karoo (Lucas 1998) and thus of Tatarian age on the Russian scale. No Permian tetrapod assemblage from Western Europe fills Olson's gap (text-fig. 10).



TEXT-FIGURE 6

Distribution of Permian strata in the Russian Ural foreland and location of key tetrapod localities discussed in the text (after Olson 1962 and Nalivkin 1966).

China. China's fossil record of Permian vertebrates is confined to occurrences of Middle-Late Permian age from two areas of northern China, the Junggur basin of Xinjiang and the Ordos basin of Shaanxi, Henan, Gansu and Nei Monggol. Middle-Late Permian vertebrate fossil assemblages from these areas are dominated by dinocephalians, dicynodonts and/or pareiasaurs (Cheng 1981, Lucas 1998). They appear to represent two time intervals.

The oldest time interval is best known from a quarry developed in the upper part of the Xidagou Formation at Dashankou in Gansu. To date, the following taxa have been reported: the dissorophid temnospondyl *Anakamacops petrolicus* Li and Cheng, an *Intasuchus*-like temnospondyl, the anthracosaurs *Ingentidens corridoricus* Cheng and Li and *Phratochronis gilianensis* Cheng and Li, the bolosaurid *Belebey vegrandis* Ivakhnenko, an undescribed captorhinid, the dinocephalians *Sinophoneus yumenensis* Cheng and Li and *Stenocybus acidentatus* Cheng and Li, and the "eotitanosuchian" *Biseridens qilianicus* Li and Cheng (Li and Cheng 1995a, b, 1997a, b, 1999, Cheng and Li 1996, 1997). Li and Cheng (1995b) correlated this assemblage to the *Tapinocephalus* Assemblage Zone of the South African Karoo and Russian Zones I and II. This correlation is supported by a shared taxon (*Belebey*) and overall faunal similarity, and indicates a Kazanian age. The pareiasaur-dominated assemblages from the Shihezi Formation in Henan and the Sunjiagou Formation in Shanxi are no older than the Dashankou assemblage (Li and Cheng 1995b).

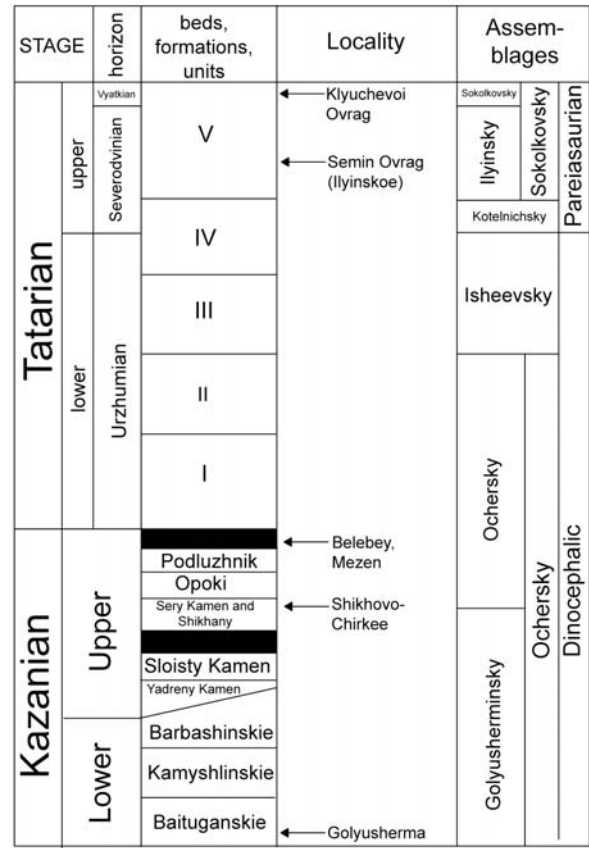
Efremov (1937)	Chudinov (1975)	Ivakhnenko et al. (1997)	
Zone IV	North Dvina Pareiasaur Complex	Scutosaurus Superzone	Archosaurus rossicus Zone
			Scutosaurus karpinskii Zone
			Proelginia permiana Zone
			Deltavjatia vjatkensis Zone
"Zone III"	fauna not known		
Zone II	Ishevo Deinocephalian Complex	Titanophoneus Superzone	Ulemosaurus svijagensis Zone
			Estemmenosuchus uralensis Zone
			Parabradysaurus silantjevi Zone
Zone I	Ocher Deinocephalian Complex		Clamosaurus nucturnus Zone

TEXT-FIGURE 7
Different proposed biostratigraphic zonations of the Russian Kazanian-Tatarian tetrapod assemblages.

China's youngest Permian vertebrates are principally from the lower Cangfanggou Group (Quanzijie Formation, Wutonggou Formation and overlying lower-middle Guodikeng Formation) in Xinjiang. They are dominated by the dicynodont *Dicynodon*, clearly correlate to the *Dicynodon* Assemblage Zone of the South African Karoo (Cheng 1981, Lucas 1998) and thus are of Tatarian age on the Russian scale. No pre-Kazanian Permian tetrapods are known from China (text-fig. 10).

Incidentally, I reject recent arguments by Angielczyk and Kurkin (2003) that *Dicynodon* may not be used to correlate Upper Permian strata because cladistic analysis suggests the genus is paraphyletic. This is because the cladistic analysis of *Dicynodon* presented by Angielczyk and Kurkin (2003) only incorporates a handful of *Dicynodon* specimens and in no way analyzes the populational variation characteristic of this well known and polymorphic genus. Their cladogram thus does not present a valid analysis of the alpha taxonomy of *Dicynodon* that is relevant to the use of the genus in biostratigraphy.

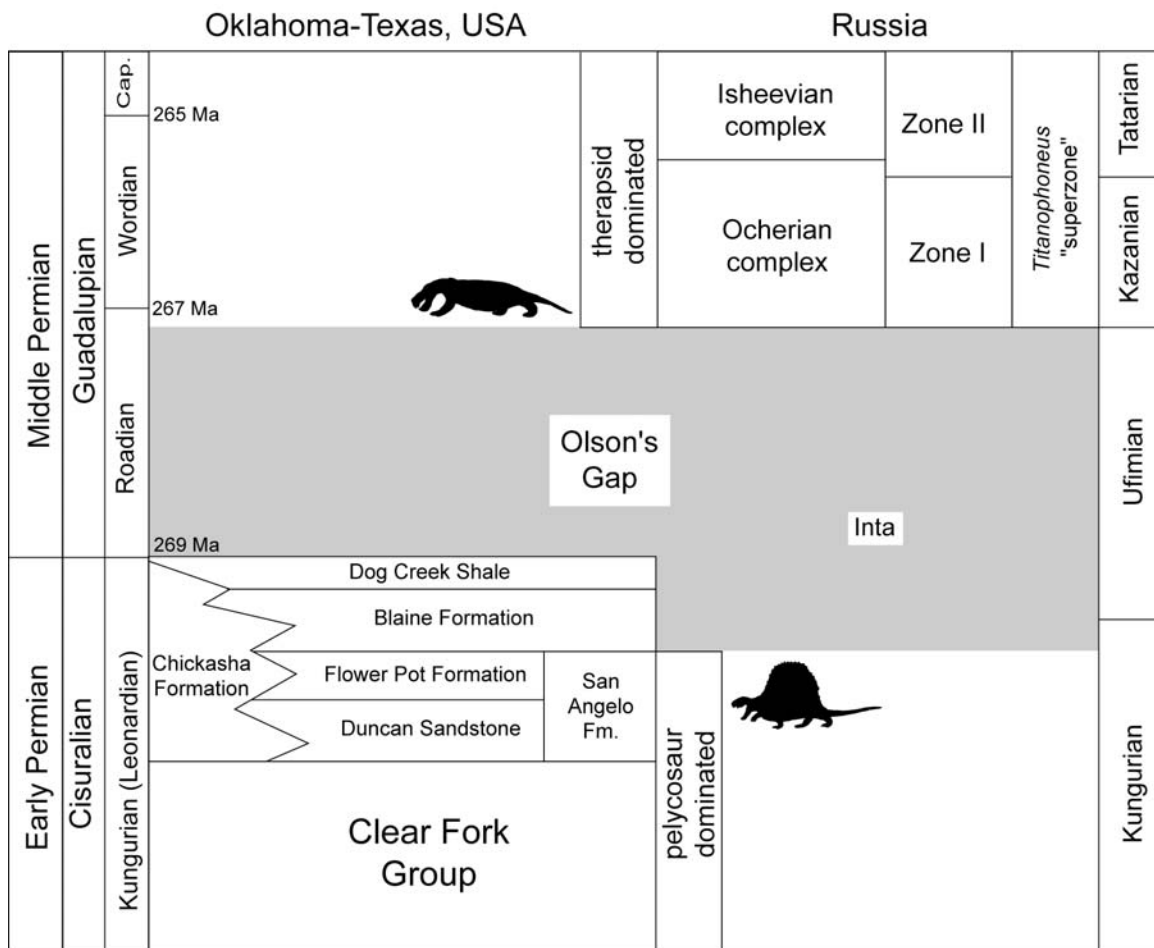
South Africa. The Permian vertebrate record and its biostratigraphy in the Karoo basin of South Africa has long provided a classic succession of Middle to Late Permian tetrapod faunas. Recent reviews by Rubidge (1995), Smith and Keyser (1995a, b, c, d) and Kitching (1995) recognize six successive assemblage zones based on tetrapods (also see Hancox and Rubidge, 2001). The oldest is the *Eodicynodon* Assemblage Zone of Rubidge (1995), and the characteristic assemblage is from the lower Abrahamskraal Formation. It includes temnospondyls, a gorgonopsian, the therocephalians *Glanosuchus* and *Alopecodon*, the anomodont *Patranomodon*, the dicynodont *Eodicynodon* and the dinocephalians *Tapinocaninus* and *Australosydon*.



TEXT-FIGURE 8
Stratigraphic distribution of the key Russian Kazanian and Tatarian tetrapod assemblages (after Golubev 1998, 1999).

Taxa from the *Eodicynodon* Assemblage Zone in South Africa are among the most primitive members of their groups, especially the dicynodonts and tapinocephaline dinocephalians (Rubidge and Hopson 1990, 1996, Rubidge 1993). Thus, based on stage-of-evolution, the *Eodicynodon* Assemblage Zone may be older than the Russian Zone II assemblages, though it is not clearly older than Zone I, and thus pre-Kazanian. Unfortunately, there is no other way at present to correlate the *Eodicynodon* Assemblage Zone directly to the SGCS, though there is no evidence that it is older than Russian Zone I (text-fig. 10).

Other African Records. Outside of South Africa, other continental African records of Permian tetrapods are isolated occurrences or small assemblages. (1) Taquet (1969) reported the captorhinomorph *Moradisaurus grandis* from Niger and assigned it a Late Permian age, and Sidor et al. (2003a,b) also reported a "Late Permian" captorhinomorph-dominated assemblage (including an endemic pareiasaur) from the Moradi Formation in northern Niger; (2) Gaffney and McKenna (1979) reported the captorhinomorph *Procaptorhinus* associated with endothiodontids from the Madumabisa Mudstones in Zimbabwe (also see Lepper et al., 2000), suggesting correlation in the range of the *Pristerognathus* through *Cistecephalus* Assemblage Zones in South Africa; and (3) the temnospondyl *Diplocaulus minimus* and the captorhinid *Acrodonta irerhi* (this



TEXT-FIGURE 9
Correlation of youngest North American and oldest Russian Permian tetrapod assemblages and duration of Olson's gap.

taxon also includes elements of a pareiasaur: Sidor et al., 2003b) are from the lower Argana Group (level T2) in Morocco (e.g., Dutuit 1988, Jalil and Dutuit 1996). These records may be of Kazanian age, as Jalil and Dutuit (1996) argued, but the presence of *Diplocaulus*, restricted to the Early Permian in the USA, may indicate an older age. Also, a tetrapod assemblage correlated to the *Dicynodon* Assemblage Zone is known from Zambia (King and Jenkins 1997).

Madagascar. South of the Isalo Massif in southern Madagascar, two low-diversity assemblages of temnospondyls (e.g., *Rhinesuchus*) and reptiles (*Tangasaurus*, *Hovasaurus*, *Coelurosauravus*) are known (e.g., Piveteau 1926). They have long been correlated to the "Endothiodon" (= *Tropidostoma* Assemblage Zone) and *Cistecephalus* zones of the South African Karoo (Piveteau 1926, Wescott and Diggins 1998; Smith 2000).

India. Woodward (1905) and Tewari (1962) described specimens of the temnospondyls *Archegosaurus*, *Actinodon* and *Lysipterygium* from the "Lower Gondwana" ("Gangamopteris Beds") of Kashmir, of probable Early Permian age. However, Milner (1993) noted these may be younger records of Middle or Late Permian age. Indeed, Werneburg and Schneider (1996) reviewed this temnospondyl assemblage, which is from the Mamal Formation, and assigned it an Ufimian-Tatarian age

based on intercalated marine invertebrate assemblages, though a precise age assignment within this broad range apparently cannot be made (text-fig. 10).

Kutty (1972) and Ray (1999, 2000, 2001) reported a Permian tetrapod assemblage from the Kundaram Formation in the Pranhita-Godavari Valley. It includes specimens of *Endothiodon* and *Cistecephalus*, and thus can be broadly correlated to the *Tropidostoma* and *Cistecephalus* Assemblage Zones of the South African Karoo (Werneburg and Schneider 1996; Ray, 2001). The Indian tetrapod record thus does not bridge Olson's gap (text-fig. 10).

Australia. The only Permian tetrapod body fossil from Australia is the rhytidosteid temnospondyl *Trucheosaurus major* (Woodward) from the Glen Davis Formation in New South Wales; this is supposedly a Late Permian (Dzhulfian) record (Warren 1991, Marsicano and Warren 1998).

Permian Tetrapod Footprint Assemblages

Often, where the tetrapod body fossil record is sparse or absent, footprints fill the gap. This is not, however, the case with Olson's gap, which is overlapped by an even longer gap in the Permian tetrapod footprint record (text-fig. 11).

PER	EPOCH	South African Assemblage Zones	Texas, USA	Western Europe	Russia	China	India	Brazil	South Africa				
PERMIAN	LATE (Lopingian)	<i>Dicynodon</i>		Cutties Hillock Sandstone F.	Zone IV	lower Cangfanggou Group (Xinjiang)			Balfour Formation				
		<i>Cistecephalus</i>		Zones I and II		Kundaram Formation			Teekloof Formation				
	<i>Pristerognathus & Tropidostoma</i>	Rio do Rasto Formation			Abrahamskraal Formation								
	<i>Tapinocephalus</i>			Xidagou F. (Gansu), Shihezi F. (Henan), Sunjiagou F. (Shanxi)									
	<i>Eodicynodon</i>												
	Olson's gap												
	EARLY (Cisuralian)	San Angelo Formation											
		Choza F.											Clear Fork Group
		Vale F.											
		Arroyo F.											
Waggoner Ranch/ Lueders formations		Wichita Group	Eisenach F.				Upper Rotliegend						
Petrolia F.			Tambach F.										
Nocona F.		Bowie Group	Lower Rotliegend										
Archer City F.													
Markley F.													

TEXT-FIGURE 10
Global correlation of principal Permian tetrapod-bearing units. See text for discussion.

Early Permian tetrapod footprints have extensive fossil records in the western USA (especially Texas, New Mexico and Arizona) and in the European Rotliegendes (e.g., Haubold 1971, 1984, 2000, Lucas and Heckert 1995, Hunt and Lucas 1998, Lucas 2002b, Arduini et al. 2003, Santi 2003). In North America, the youngest Permian tetrapod footprint assemblages are from the San Angelo and Blaine formations in Texas, and include tracks of seymouriamorphs and pelycosaurs (Pittman et al. 1996). More limited assemblages are known from the Russian Caucasus and Argentina (Melchor 1997, Lucas et al. 1999). Despite some claims to the contrary (e.g., Ellenberger 1983, Santi 2003), there is no compelling evidence that any of these assemblages is younger than Kungurian on the SGCS, and most are older (Kozur 1993b; Haubold and Lucas 2001, Lucas 2002b, Cassinis 2003).

Younger Permian tetrapod footprint records are fewer in number and restricted to relatively young Permian strata. These are limited records from the European Zechstein, the Karoo basin in South Africa and the Russian Tatarian (e.g., Haubold 1984, Haubold and Lucas 2001, Tverdokhlebov et al. 1997), none of which is older than Capitanian on the SGCS. Indeed, the only substantial Late Permian tetrapod footprint assemblage, from the Val Gardena Sandstone in Italy (e.g., Conti et al. 1977), is directly related to marine strata of Late Permian (Dzhulfian = Wuchiapingian) age (e.g., Kozur 1993b).

Thus, there is a substantial temporal gap between Early Permian tetrapod footprint assemblages, and Middle-Late Permian assemblages, which, at their oldest, may be of Capitanian age (text-fig. 11). This means that the Permian tetrapod footprint record does not fill Olson's gap and reveals an even larger gap of its own, spanning nearly the entire Middle Permian.

Miscorrelations

About half a century ago, Olson (1955, 1962) believed he had bridged the gap between the North American and Russian Permian tetrapod assemblages. Like Efremov (1956), he thought he had done that with the discovery of the tetrapods of the San Angelo, Flowerpot and Chickasha formations. This conclusion was reinforced in Olson's mind by workers who considered the Blaine to be Guadalupian (see above), as well as the palynology of the Flowerpot Formation (Wilson 1962), which yielded a palynoflora more similar to that of the European Zechstein than to the Rotliegendes.

In his classic monograph on Late Permian tetrapods from the USA and USSR, Olson (1962) considered the base of the Kazanian and Guadalupian to be correlative (also see Olson 1975). This is now known to be incorrect. Furthermore, Olson reviewed at length the data on the age and correlation of the San Angelo, Flowerpot, Chickasha and Blaine formations and concluded they are Guadalupian in age. This, too, is not correct. However, given the two incorrect age assignments, Olson concluded that the San Angelo-Flowerpot-Chickasha tetrapods and the Russian Zone I and II assemblages are correlative (also see Olson and Chudinov 1992).

Indeed, Olson (1962, p. 156) even went so far as to state that "vertebrates appear to provide the most reliable evidence for correlation of North American and Russian Permian." This, despite the fact that no genera or species were shared between the American and Russian tetrapod assemblages. Olson (1962, 1975), nevertheless, did point to "parallelism" in the caseids, some captorhinids and "therapsids," explicitly equating the North American caseids *Cotylorhynchus* and *Angelosaurus* with Russian *Ennatosaurus*, the North American captorhinid *Kahneria* with Russian *Hecatogomphius* and the North American "therapsid" *Eosyodon* with Russian *Syodon*. Olson (1955) also argued that the "gigantism" of the San Angelo taxa found a

Arizona	New Mexico	Texas	Germany	France	Italy	AGE		footprint biochrons
					Bellerophon Formation	Lopingian	Late Permian	<i>Rhynchosauroides</i> biochron
				La Lieude Formation	Val Gardena Sandstone			
						Guadalupian	Middle Permian	
Kaibab Formation	San Andres Formation	Whitehorse Formation				Cisuralian	Early Permian	<i>Dromopus</i> biochron
Coconino Sandstone	Glorieta Sandstone	Blaine Formation		Rabejac Formation	Tregiovo Formation			
Schnebbly Hill Formation	Yeso Formation	San Angelo Formation						
		Choza Formation						
		Vale Formation						
Hermit Shale	Abo Formation	Arroyo Formation			Collio Formation			
Esplanade Sandstone	Sangre de Cristo Formation	Wichita Group	Tambach Formation					
			Lower Rotliegend	Viala Formation				

TEXT-FIGURE 11
Global correlation of selected tetrapod track-bearing strata of Permian age (after Lucas 2002b).

parallel in equally large Russian Kazanian taxa. In effect, Olson correlated by evolutionary grades, not by shared genera or species (index taxa).

This same correlation has re-emerged recently in the work of Lozovsky (2001, 2003) who, like Olson, equates the Chickasha assemblage with the Kazanian tetrapods based on some evolutionary-grade similarities of Chickasha and Russian tetrapod taxa. Reisz and Laurin (2001) followed suit when documenting the presence of the reptile *Macroleter* in the Chickasha Formation of Oklahoma. They concluded “that the Chickasha Formation ... belongs to the Guadalupian, and that it is equivalent in age to the late Kazanian, or early Tatarian of the Russian platform” (p. 1231). Based on this mis-correlation of the Chickasha Formation with the upper Kazanian, Reisz and Laurin (2001) state that the *Macroleter* from the Chickasha Formation “is the first evidence of the northern dvinosaurid-chroniosuchid prov-

ince in North America” and “thus the first direct evidence of tetrapod faunal interchange between North America and Russia” (p. 1232). These conclusions, however, should be reconsidered.

Marine biostratigraphy indicates that the Chickasha Formation is substantially older than the Russian upper Kazanian, so the records of *Macroleter* in North America and Russia are temporally disjunct by millions of years (text-fig. 9). Indeed, based on a phylogenetic analysis of parareptiles, Modesto (2000; also see Reisz and Laurin 2001, fig. 10) indicated that a common ancestor of *Macroleter* and *Procolophon* must exist in the Early Permian, so the presence of *Macroleter* or a similar basal procolophonid in the American Lower Permian is not surprising. Reisz and Laurin (2002), in a reply to a discussion of their original article by Lucas (2002a), simply reiterated their

correlation of the Chickasha to Mezen, despite the evidence to the contrary.

EVOLUTIONARY SIGNIFICANCE OF OLSON'S GAP

To this point, I have discussed Olson's gap as a temporal hiatus in the Permian tetrapod fossil record. However, Olson's gap is also an evolutionary break between two substantially different global tetrapod faunas. Thus, it is marked by a dramatic remodelling of the Permian tetrapod fauna, from pelycosaur dominated to therapsid dominated. A few antecedents of the therapsid-dominated assemblages of the Middle-Late Permian are known from the American Permian, including the Chickasha record of *Macroleter* already discussed, and the Leonardian (Artinskian) record of *Tetraceratops*, possibly the oldest therapsid (Laurin and Reisz 1996), though this is not certain (Conrad and Sidor 2001). And, a few elements of the Russian Kazanian tetrapod assemblages are relicts of groups that are diverse in the American Early Permian, for example the caseid pelycosaur. Nevertheless, there remains a crucial hiatus in the Middle Permian tetrapod record during which a major remodelling of the global tetrapod fauna took place, one for which a fossil record remains to be discovered.

The idea that three distinct phases of tetrapod evolution can be recognized in the Permian dates back at least to Romer (1966, table 2) and has been developed along evolutionary, paleobiogeographic and/or paleoecologic lines by Bakker (1977, 1980), Anderson and Cruickshank (1978), Olson (1989) and Olson and Chudinov (1992), among others. Three phases (variously called complexes, chronofaunas, dynasties or empires by previous workers) of Permian tetrapod evolution can be identified. (1) Early Permian; (2) Middle Permian (Kazanian); and (3) Late Permian (Tatarian).

Most Early Permian tetrapods are holdovers from the Late Carboniferous. They identify a single paleobiogeographic province (the edaphosaurid empire of Anderson and Cruickshank [1978] or the edaphosaur-neotridian province of Milner [1993]) from the southern region of Euramerica close to the paleoequator. Lepospondyls, anthracosaurs, seymouriamorphs, cotylosaurs and a variety of pelycosaur are characteristic Early Permian tetrapods. These are the tetrapods that precede Olson's gap.

The first therapsid-dominated faunas appear suddenly during the early Kazanian, marking what Bakker (1980) aptly termed the "Kazanian revolution" in tetrapod evolution. The Kazanian amphibian fauna consists of some Early Permian holdovers with only a few new appearances (Milner 1990). By the Kazanian, the diapsid reptiles had diversified into their two great clades, the lepidosauromorphs (younginids and tangasaurids) and the archosauromorphs (protorosaurids and proterosuchids). Synapsid reptiles numerically dominated Kazanian tetrapod faunas. Especially abundant were the herbivorous dinocephalians and early anomodonts. Anderson and Cruickshank (1978) identified the Kazanian fauna as the first fully terrestrial tetrapod fauna and termed it the tapinocephalid empire.

The sudden appearance of the Kazanian tetrapod fauna is at least partially a reflection of Olson's gap. Modesto et al. (1999) and Modesto and Rubidge (2000) have recently argued that anomodont therapsids may have originated in Gondwana because of the diversity of their most primitive representatives in South Africa. This interesting idea should be tested by a search for fossils in Gondwana that will fill Olson's gap.

Olson's gap thus marks a major remodelling of the tetrapod fauna, one that happens suddenly with few antecedents. As Olson set out to do more than half a century ago, there is a real need to search for fossils that fill this gap. Only new discoveries that fill Olson's gap will provide a reasonably continuous record of Permian tetrapod evolution.

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REFERENCES

- ADAMS, J. E., CHENEY, M. F., DEFORD, R. K., DICKEY, R. I., DUNBAR, C. O., HILLS, J. M., KING, R. E., LLOYD, R. E., MILLER, A. K., and NEEDHAM, C. E., 1939. Standard Permian section of North America. *American Association of Petroleum Geologists Bulletin*, 23: 1673-1681.
- ANDERSON, J. M. and CRUICKSHANK, A. R. I., 1978. The biostratigraphy of the Permian and the Triassic. Part 5. A review of the classification and distribution of Permo-Triassic tetrapods. *Palaeontologica Africana*, 21: 15-44.
- ANGIELCZYK, K. D. and KURKIN, A. A. 2003. Has the utility of *Dicynodon* for Late Permian terrestrial biostratigraphy been overstated? *Geology*, 31: 363-366.
- ARCHBOLD, N. W., 1999. The Australian Permian. Correlations with the Russian Permian sequences. In: Burov, B. V., N. K. Esaulova and V. S. Gubareva Eds. *Proceedings of International Symposium "Upper Permian Stratotypes of the Volga Region."* Moscow, GEOS: 53-70.
- ARDUINI, P., KRIEGER, C., ROSSI, M. and SANTI, G., 2003. Early Permian vertebrate ichnoassociation in the Scioc Valley, Orobic basin (Lombardy, northern Italy). *Neues Jahrbuch für Geologie, Paläontologie und Geologie Monatshefte*, 2003: 385-399.
- BAKKER, R. T., 1977. Tetrapod mass extinctions—a model of the regulation of speciation rates and immigration by cycles of topographic diversity. In: Hallam, A. Ed. *Patterns of Evolution as Illustrated by the Fossil Record*. Amsterdam, Elsevier: 439-468.
- , 1980. Dinosaur heresy—dinosaur renaissance why we need endothermic archosaurs for a comprehensive theory of bioenergetic evolution. In: Thomas, R. D. K. and Olson, E. C. Eds., *A Cold Look at the Warm-blooded Dinosaurs*. Washington, D.C.: American Association for the Advancement of Science, 351-462.
- BARBERENA, M. C., 1972. South American late Paleozoic tetrapods. *Anais Academia Brasileira de Ciências Suplemento*, 44: 67-75.
- BARBERENA, M. C., ARAÚJO, D. C. and LAVINA, E. L., 1985. Late Permian and Triassic tetrapods of southern Brazil. *National Geographic Research*, 1: 5-20.
- BARBERENA, M. C., CORREIA, N. D. R. and AUMOND, J. J., 1980. Contribuição à estratigrafia e bioestratigrafia do Grupo Passa Dois na Serra do Cadeado (Nordeste do Paraná, Brasil). *Revista Brasileira de Geociências*, 10: 268-275.
- BATTAIL, B. 2000. A comparison of Late Permian Gondwanan and Laurasian amniote faunas. *Journal of African Earth Sciences*, 31:165-174.
- BEEDE, J. W. and BENTLEY, W. P., 1921. The geology of Coke County. *University of Texas Bulletin*, 1850: 1-82.

- BEEDE, J. W. and CHRISTNER, D. D., 1926. The San Angelo Formation; the geology of Foard County. *University of Texas Bulletin*, 2607: 5-53.
- BENTON, M. J., 1993. Reptilia. In Benton, M. J. Ed. *The Fossil Record* 2. London, Chapman and Hall: 681-715.
- BENTON, M. J. and SPENCER, P. S., 1995. *Fossil Reptiles of Great Britain*. Chapman and Hall, London.
- BERMAN, D. S., 1993. Lower Permian vertebrate localities of New Mexico and their assemblages. *New Mexico Museum of Natural History and Science Bulletin*, 2: 11-21.
- BERMAN, D. S. and MARTENS, T., 1993. First occurrence of *Seymouria* (Amphibia. Batrachosauria) in the Lower Permian Rotliegend of central Germany. *Annals of the Carnegie Museum*, 62: 63-79.
- BERMAN, D. S., SUMIDA, S. S. and LOMBARD, R. E., 1997. Biogeography of primitive amniotes. In: Sumida, S. S. and Martin, K. L. M. Eds. *Amniote Origins*. San Diego: Academic Press, 85-139.
- BERMAN, D. S., REISZ, R. R., MARTENS, T. and HENRICI, A. C., 2001. A new species of *Dimetrodon* (Synapsida. Sphenacodontidae) from the Lower Permian of Germany records first occurrence of genus outside of North America. *Canadian Journal of Earth Sciences*, 38: 803-812.
- BÖSE, E., 1919. The Permo-Carboniferous ammonoids of the Glass Mountains, West Texas, and their stratigraphic significance. *University of Texas Bulletin*, 1762: 1-241.
- BOWRING, S. A., ERWIN, D. H., JIN, Y. G., MARTIN, M. W., DAVIDEK, K. and WANG, W., 1998. U/Pb zircon geochronology and tempo of the end-Permian mass extinction. *Science*, 280: 1039-1045.
- BOY, J., 1993. Synopsis of the tetrapods from the Rotliegend (Lower Permian) in the Saar-Nahe basin (SW-Germany). *Pollichia*, 29: 155-169.
- BYAKOV, A. S., 1999. Correlation of the marine Upper Permian of the boreal realm by molluscs and possibly equivalent bivalves in north-eastern Asia and non-boreal regions. In: Burov, B. V., Esaulova, N. K. and Gubareva, V. S. Eds. *Proceedings of International Symposium "Upper Permian Stratotypes of the Volga Region."* Moscow, GEOS:222-227.
- CASSINIS, G., 2003. Towards a stratigraphic reference table for the continental Permian of Italy. *Bolletina della Società Italiano Volume Speciale*, 2: 153-168.
- CHALIMBADA, V. G. and SILANTIEV, V. V., 1998. Conodonts from the Upper Permian type strata of European Russia. *Proceedings of the Royal Society of Victoria*, 110: 137-145.
- CHENG, Z., 1981. Permo-Triassic continental deposits and vertebrate faunas of China. In: Cresswell, N. N and Vella, P. Eds. *Gondwana Five*. Rotterdam, A. A. Balkema: 65-70.
- CHENG, Z. and LI, J., 1996. First record of a primitive anteosaurid dinocephalian from the Upper Permian of Gansu, China. *Vertebrata Palasiatica*, 34: 123-134.
- , 1997. A new genus of primitive dinocephalian – the third report on Late Permian Dashankou lower tetrapod fauna. *Vertebrata Palasiatica*, 35: 35-43.
- CHUDINOV, P. K., 1975. New facts about the fauna of the Upper Permian of the USSR. *Journal of Geology*, 73: 117-130.
- , 1983. Early therapsids. *Trudy Paleontologicheskovo Instituta*, 202: 1-227.
- CHUVASHOV, B. I., KANEV, G. P., KOLODA, N. A. and CHERMYNKH, V. A., 1995. Terrestrial outcrops of the Lower and Upper Permian. In: Chuvashov, B. I. Ed. *Guidebook to the Excursion to Permian Outcrops on the Kozhim River*. Moscow, Paleontological Institute: 21-40.
- CLIFTON, R. L., 1942. Invertebrate faunas from the Blaine and Dog Creek formations of the Permian Leonard Series. *Journal of Paleontology*, 16: 685-699.
- , 1945. Permian Word Formation. Its faunal and stratigraphic correlatives, Texas. *American Association of Petroleum Geologists Bulletin*, 29: 1766-1776.
- , 1946. Middle Permian Cephalopoda from Texas and New Mexico. *Journal of Paleontology*, 20: 556-559.
- CONRAD, J. and SIDOR, C., 2001. Re-evaluation of *Tetraceratops insignis* (Synapsida. Sphenacodontia). *Journal of Vertebrate Paleontology*, 21 (3): 42A.
- CONTI, M. A., LEONARDI, G., MARIOTTI, N. and NICOSIA, U., 1977. Tetrapod footprints of the Val Gardena Sandstone (North Italy). Their paleontological, stratigraphic and paleoenvironmental meaning. *Palaeontographica Italica*, 70: 1-79.
- COOPER, G. A. and GRANT, R. E., 1964. New Permian stratigraphic units in Glass Mountains, West Texas. *American Association of Petroleum Geologists Bulletin*, 48: 1581-1588.
- , 1966. Permian rock units in the Glass Mountains, West Texas. *U. S. Geological Survey Bulletin*, 1244-E: E1-E9.
- COPE, J. C. W., 1996. The role of the secondary standard in stratigraphy. *Geological Magazine*, 1996: 107-110.
- COX, C. B. and HUTCHINSON, P., 1991. Fishes and amphibians from the Late Permian Pedra do Fogo Formation of northern Brazil. *Palaeontology*, 34: 561-573.
- DICKINS, J. M., 1992. Permian geology of Gondwana countries. *International Geology Review*, 34: 986-1000
- DIMICHELE, W. A., CHANEY, D. S., DIXON, W. H., NELSON, W. J. and HOOK, R., W., 2000. An Early Permian coastal flora from the central basin platform of Gaines County, West Texas. *Palaos*, 15: 524-534.
- DIMICHELE, W. A., MAMAY, S. H. CHANEY, D. S. HOOK, R. W. and NELSON, W. J., 2001. An Early Permian flora with Late Permian and Mesozoic affinities from north-central Texas. *Journal of Paleontology*, 75: 449-460.
- DUNBAR, C. O., BAKER, A. A., COOPER, G. A., KING, P. B., MCKEE, E. D., MILLER, A. K., MOORE, R. C., NEWELL, N. D., ROMER, A. S., SELLARDS, E. H., SKINNER, J. W., THOMAS, H. D. and WHEELER, H. E., 1960. Correlation of the Permian formations of North America. *Geological Society of America Bulletin*, 71: 1763-1806.
- DUTUIT, J-M., 1988. *Diplocaulus minimus* n. sp. (Amphibia. Nectridea), lépospondyle de la Formation d'Argana, dans l'Atlas marocain. *Compte Rendus de l'Académie des Sciences Paris*, 307: 851-854.
- EBERTH, D. A., BERMAN, D. S., SUMIDA, S. S. and HOPF, H., 2000. Lower Permian terrestrial paleoenvironments and vertebrate paleoecology of the Tambach basin (Thuringia, central Germany). The upland holy grail. *Palaos*, 15: 293-313.

- EFREMOV, I. A., 1937. On the stratigraphic subdivision of the continental Permian and Triassic of the USSR on the basis of the fauna of early Tetrapoda. *Doklady Akademiyi Nauk SSSR*, 16: 121-126.
- , 1940. Preliminary description of new Permian and Triassic terrestrial vertebrates from the USSR. *Trudy Paleontologicheskaya Instituta*, 10: 1-140.
- , 1952. On the stratigraphy of the Permian red beds of the USSR based on terrestrial vertebrates. *Izvestiya Akademiyi Nauk SSSR Geology Series*, 6: 49-75.
- , 1954. Fauna of terrestrial vertebrates in the Permian metalliferous sands of the western pre-Urals. *Trudy Paleontologicheskoye Instituta*, 44: 1-416.
- , 1956. American elements in the fauna of the USSR. *Doklady Akademiyi Nauk SSSR*, 111: 1091-1094.
- EFREMOV, I. A. and VYUSHKOV, B. P., 1955. Catalogue of Permian and Triassic localities of terrestrial vertebrates in the territory of the USSR. *Trudy Paleontologicheskoye Instituta*, 46: 1-185.
- ELLENBERGER, P., 1983. Sur la zonation ichnologique du Permien moyen (Saxonien) et du Permien inferieur (Autunien) du bassin de Lodève (Hérault). *Compte Rendus de l'Académie des Sciences Paris*, 297: 553-558.
- ESAULOVA, N. K., LOZOVSKY, V. R. and ROZANOV, A. YU., eds., 1998. *Stratotypes and Reference Sections of the Upper Permian in the Regions of the Volga and Kama Rivers*. Moscow: GEOS.
- FAY, R. O., 1962. Geology and mineral resources Blaine County, Oklahoma. *Oklahoma Geological Survey Bulletin*, 89: 1-258.
- , 1964. The Blaine and related formations of northwestern Oklahoma and southern Kansas. *Oklahoma Geological Survey Bulletin*, 98: 1-238.
- FITCHEN, W. M., 1993. Sequence stratigraphic framework of the upper San Andres Formation and equivalent basinal strata in the Brokenoff Mountains, Otero County, New Mexico. In: Love, D. W., Hawley, J. W., Kues, B. S., Adams, J. W., Austin, G. S. and Barker, J. M. Eds. *Carlsbad Region, New Mexico and West Texas. New Mexico Geological Society Guidebook, 44th Field Conference*. Socorro, New Mexico Geological Society: 185-193.
- GAFFNEY, E. S. and MCKENNA, M. C., 1979. A Late Permian captorhinid from Rhodesia. *American Museum Novitates*, 2688: 1-15.
- GLENISTER, B. F. and FURNISH, W. M., 1981. Permian ammonoids. In: House, M. R. and Senior, J. R. Eds. *The Ammonoidea. The Systematics Association Special Volume*, 18: 49-64.
- GLENISTER, B. F., BOYD, D. W., FURNISH, W. M., GRANT, R. E., HARRIS, M. T., KOZUR, H., LAMBERT, L. L., NASSICHUK, W. W., NEWELL, N. D., PRAY, L. C., SPINOSA, C., WARDLAW, B. R., WILDE, G. L. and YANCEY, T. M., 1992. The Guadalupian. Proposed international standard for a Middle Permian Series. *International Geology Review*, 34: 857-888.
- GOLUBEV, V. K., 1992. The lower Kazanian tetrapod locality Goyusherma (Udmurtiya). *Byulletin MOIP Otdel Geologiy*, 67: 131.
- , 1998. Terrestrial vertebrates. In: Esaulova, N. K., Lozovsky, V. R. and Rozanov, A. Yu. Eds. *Stratotypes and reference sections of the Upper Permian in the regions of the Volga and Kama Rivers*. Moscow: GEOS, 227-235.
- , 1999. Biostratigraphy of the Upper Permian of European Russia based on terrestrial vertebrates and problems of the correlation of Permian outcrops. In: Burov, B. V., Esaulova, N. K. and Gubareva, V. S. Eds. *Proceedings of International Symposium "Upper Permian Stratotypes of the Volga Region."* Moscow, GEOS: 228-240.
- GOULD, C. N., 1902. General geology of Oklahoma. *Oklahoma Department of Geology and Natural History Biennial Report*, 2: 17-137.
- , 1905. Geology and water resources of Oklahoma. U. S. *Geological Survey Water-supply and Irrigation Paper*, 148: 1-178.
- GRUNT, T. A., 1999. Discussion of the problems of the stage subdivision of the upper part of the Permian System. In: Burov, B. V., Esaulova, N. K. and Gubareva, V. S. Eds. *Proceedings of International Symposium "Upper Permian Stratotypes of the Volga Region."* Moscow: GEOS, 129-145.
- GUBIN, Y. M., 1984. The systematic position of the intasuchids. *Paleontological Journal*, 1984(2): 70-75.
- , 1986. New data on the archegosaurids of the East European platform. *Paleontological Journal*, 1986(2): 118-120.
- , 1998. Permian amphibians of northern Russia. In: Ginter, M. and Wilson, M. V. H. Eds. *Circum-Arctic Paleozoic Faunas and Faecies*. Warsaw: Warsaw University, 17-18.
- HANCOX, P. J. and RUBIDGE, B. S. 2001. Breakthroughs in the biodiversity, biogeography, biostratigraphy, and basin analysis of the Beaufort Group. *Journal of African Earth Sciences*, 33: 563-577.
- HAUBOLD, H., 1971. Ichnia amphibiorum et reptiliorum fossilium. *Handbook of Paleoherpetology*, 18: 1-124.
- , 1984. *Saurierfahrten*. Wittenberg Lutherstadt, A Ziemsen Verlag.
- , 2000. Tetrapodenfahrten aus dem Perm-Kennntnisstand und Progress 2000. *Hallesches Jahrbuch für Geowissenschaften*, 22: 1-16.
- HAUBOLD, H. and LUCAS, S. G., 2001. Early Permian tetrapod tracks – preservation, taxonomy, and Euramerican distribution. *Natura Bresciana*, 25: 27-34.
- HENTZ, T. F., 1988. Lithostratigraphy and paleoenvironments of Upper Paleozoic continental red beds, north-central Texas. Bowie (new) and Wichita (revised) Groups. *The University of Texas at Austin, Bureau of Economic Geology, Report of Investigations*, 170: 1-55.
- HILLS, J. M., 1942. Rhythm of Permian seas—a paleogeographic study. *American Association of Petroleum Geologists Bulletin*, 26: 217-255.
- , 1972. Late Paleozoic sedimentation in West Texas Permian basin. *American Association of Petroleum Geologists Bulletin*, 56: 2303-2322.
- HOOKE, R. W., 1989. Stratigraphic distribution of tetrapods in the Bowie and Wichita groups, Permo-Carboniferous of north-central Texas. In: Hook, R. W., Ed., *Permo-Carboniferous vertebrate paleontology, lithostratigraphy, and depositional environments of north-central Texas*. Austin, Society of Vertebrate Paleontology: 47-53.
- HUNT, A. P. and LUCAS, S. G., 1998. Implications of the cosmopolitanism of Permian tetrapod ichnofaunas. *New Mexico Museum of Natural History and Science Bulletin*, 12: 55-57.
- IVAKHNENKO, M. F., 1990a. Late Paleozoic tetrapod faunal complex from outcrops of the Mezen River basin. *Paleontological Journal*, 4: 81-90.

- , 1990b. Early Permian faunal elements in the tetrapod faunal complexes of Eastern Europe. *Paleontological Journal*, 2: 102-111.
- , 1990c. Tetrapod faunal complexes in the Late Permian of eastern Europe. *Byulletin MOIP Otdel Geologii*, 65: 55-60.
- , 1995. Primitive dinocephalians-titanosuchians from the Late Permian of eastern Europe. *Paleontological Journal*, 3: 98-105.
- IVAKHNENKO, M. F., GOLUBYEV, V. K., GUBIN, YU. M., KALANDADZE, N. N., NOVIKOV, I. V., SENNIKOV, A. G. and RAUTIAN, A. S. 1997. *Permian and Triassic Tetrapods of Eastern Europe*. Moscow: GEOS.
- JALIL, N. and DUTUIT, J.-M., 1996. Permian captorhinid reptiles from the Argana Formation, Morocco. *Palaeontology*, 39: 907-918.
- JIN, Y., GLENISTER, B. F., KOTLYAR, G. V. and SHENG, J., 1994. An operational scheme of Permian chronostratigraphy. *Palaeoworld*, 4: 1-13.
- JONES, J. O., 1971. The Blaine Formation of North Texas. Ph. D. dissertation, University of Iowa.
- KERANS, C., FITCHEN, W. M., GARDNER, M. H. and WARDLAW, B. R., 1993. A contribution to the evolving stratigraphic framework of Middle Permian strata of the Delaware basin, Texas and New Mexico. In: Love, D. W., Hawley, J. W., Kues, B. S., Adams, J. W., Austin, G. S. and Barker, J. M., Eds., Carlsbad Region, New Mexico and West Texas. *New Mexico Geological Society Guidebook, 44th Field Conference*. Socorro, New Mexico Geological Society: 175-184.
- KING, G. M. and JENKINS, I. 1997. The dicynodont *Lystrosaurus* from the Upper Permian of Zambia: Evolutionary and stratigraphic implications. *Palaeontology*, 40: 149-156.
- KING, P. B., 1942. Permian of West Texas and southeastern New Mexico. *American Association of Petroleum Geologists Bulletin*, 26: 535-763.
- , 1947. Permian correlations. *American Association of Petroleum Geologists Bulletin*, 31: 774-777.
- KING, R. E., 1931. The geology of the Glass Mountains, Texas; Part 2, faunal summary and correlation of the Permian formations, with description of Brachiopoda. *University of Texas Bulletin*, 3042: 1-245.
- KITCHING, J. W., 1995. Biostratigraphy of the *Dicynodon* Assemblage Zone. *South African Committee for Stratigraphy Biostratigraphic Series*, 1: 29-34.
- KONZHUKOVA, YE. D., 1953. Lower Permian fauna of terrestrial tetrapods from the northern pre-Urals (Inta River basin). *Doklady Akademii Nauk SSSR*, 89: 723-726.
- , 1955. Permian and Triassic labyrinthodonts from Povolzhya and the Pre-Urals. *Trudy Paleontologicheskovo Instituta*, 49: 5-88.
- KOTLYAR, G. V., 1999. Late Permian chronostratigraphic standard. Reality and problems. In: Burov, B. V., Esaulova, N. K. and Gubareva, V. S. Eds. *Proceedings of International Symposium "Upper Permian Stratotypes of the Volga Region."* Moscow: GEOS, 23-32.
- , 2000. Permian of the Russia and CIS and its interregional correlation. In: Yin, H., Dickens, J. M., Shi, G. R. and Tong, J., Eds., *Permian-Triassic evolution of Tethys and western circum-Pacific*. Amsterdam: Elsevier, 17-35.
- KOZUR, H., 1975. Beiträge zur Conodontenfauna des Perm. *Geologisch-Paläontologische Mitteilungen Innsbruck*, 5: 1-44.
- , 1984. Carboniferous-Permian boundary in marine and continental sediments. *Compte Rendus 9e Congres International Stratigraphie et Geologie Carbonifere*, 2: 577-586.
- , 1992. Boundaries and stage subdivision of the mid-Permian (Guadalupian Series) in the light of new micropaleontological data. *International Geology Review*, 34: 907-932.
- , 1993a. Boundaries and subdivision of the Permian System. *Occasional Publications ESRI New Series*, 9B: 139-156.
- , 1993b. Application of the "parastratigraphic" and international scale for the continental Permian of Europe. *Pollichia*, 29: 9-22.
- , 1995. Permian conodont zonation and its importance for the Permian stratigraphic standard scale. *Geologische Paläontologische Mitteilungen Innsbruck*, 20: 165-205.
- , 1998. The Permian conodont biochronology. Progress and problems. *Proceedings Royal Society Victoria*, 110: 197-220.
- KUTTY, T. S., 1972. Permian reptilian fauna from India. *Nature*, 237: 462-463.
- LAMBERT, L. L., LEHRMANN, D. J. and HARRIS, M. T., 2000. Correlation of the Road Canyon and Cutoff formations, West Texas, and its relevance to establishing an international Middle Permian (Guadalupian) Series. *Smithsonian Contributions to Earth Sciences*, 34: 153-173.
- LANGER, M. C., 2000. The first record of dinocephalians in South America. Late Permian (Rio do Rasto Formation) of the Paraná basin, Brazil. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 215: 69-95.
- LAURIN, M. and REISZ, R. R., 1996. The osteology and relationships of *Tetraceratops insignis*, the oldest known therapsid. *Journal of Vertebrate Paleontology*, 16: 95-102.
- LEONOVA, T. B., 1998. Permian ammonoids of Russia and Australia. *Proceedings of the Royal Society of Victoria*, 110: 157-162.
- LEPPER, J., RAATH, M. A. and RUBIDGE, B. S. 2000. A diverse dinocephalian fauna from Zimbabwe. *South African Journal of Science*, 96: 403-405.
- LI, J. and CHENG, Z., 1995a. The first discovery of bolosaurs from Upper Permian of China. *Vertebrata Palasiatica*, 33: 17-23.
- , 1995b. A new Late Permian vertebrate fauna from Dashankou, Gansu with comments on Permian and Triassic vertebrate assemblage zones of China. In: Sun, A. and Wang, Y. Eds. *Sixth symposium on Mesozoic terrestrial ecosystems and biota, short papers*. Beijing, China Ocean Press: 33-37.
- , 1997a. A captorhinid from the Upper Permian of Nei Mongol, China. In: Tong, Y. Ed. *Evidence for evolution—essays in honor of Prof. Chungchien Young on the hundredth anniversary of his birth*. Beijing, China Ocean Press: 119-124.
- , 1997b. First discovery of eotitanosuchian (Therapsida, Synapsida) of China. *Vertebrata Palasiatica*, 35: 268-282.
- , 1999. New anthracosaur and temnospondyl amphibians from Gansu, China—the fifth report on Late Permian Dashankou lower tetrapod fauna. *Vertebrata Palasiatica*, 37: 234-247.
- LI, Z., POWELL, C. M. AND TRENCH, A., 1993. Palaeozoic global reconstructions. In Long, J. Ed. *Palaeozoic Vertebrate Biostratigraphy and Biogeography*. London, Belhaven Press: 25-53.

- LOZOVSKY, V. R., 1992. The Permian-Triassic boundary in continental series of Laurasia and its correlation with the marine scale. *International Geology Review*, 34: 1008-1014.
- , 2001. Some problems and new achievements in the long distance correlations of the continental Permian of Pangea. *Stratigraphic and Structural Evolution of the Late Carboniferous to Triassic Continental and Marine Successions in Tuscany (Italy)*, *Regional Reports and General Correlation*, Abstracts: 52-53.
- , 2003. Correlation of the continental Permian of northern Pangea: A review. *Bolletina della Società Italiano Volume Speciale*, 2: 239-244.
- LUCAS, S. G., 1998. Toward a tetrapod biochronology of the Permian. *New Mexico Museum of Natural History and Science Bulletin*, 12: 71-91.
- , 2002a. The reptile *Macroleter*: First vertebrate evidence for correlation of Upper Permian continental strata of North America and Russia: Discussion. *Geological Society of America Bulletin*, 114: 1174-1175.
- , 2002b. Global Permian tetrapod footprint biostratigraphy and biochronology. *Pernophiles*, 41: 30-34.
- , 2004. Late Paleozoic tetrapod biochronology in the western United States. *Geological Society of America Abstracts with Programs*, 36(4): 18.
- LUCAS, S. G. and HECKERT, A. B., eds., 1995. Early Permian footprints and facies. *New Mexico Museum of Natural History and Science Bulletin*, 6: 1-301.
- , 2001. Olson's gap: A global hiatus in the record of Middle Permian tetrapods. *Journal of Vertebrate Paleontology*, 21(3): 75A.
- LUCAS, S. G., LOZOVSKY, V. R. and SHISHKIN, M. A., 1999. Tetrapod footprints from Early Permian redbeds of the northern Caucasus, Russia. *Ichnos*, 6: 277-281.
- MARSICANO, C. A. and WARREN, A., 1998. The first Palaeozoic rhytidosteid. *Trucheosaurus major* (Woodward) from the Late Permian of Australia, and a reassessment of the Rhytidosteidae (Amphibia, Temnospondyli). *Bulletin of the Natural History Museum London (Geology)*, 54: 147-154.
- MEAR, C. E., 1963. Stratigraphy of Permian outcrops, Coke County, Texas. *American Association of Petroleum Geologists Bulletin*, 47: 1952-1962.
- , 1984. Stratigraphy of Upper Permian rocks, Midland basin and eastern shelf, Texas. In Grover, G., Jr., Ed., *Lower Permian to Upper Pliocene Carbonate and Clastic Facies, Southern Eastern Shelf Texas. Midland, Permian Basin Section*. Society of Economic Paleontologists and Mineralogists, 89-93.
- MELCHOR, R. N., 1997. Permian tetrapod ichnofaunas from Argentina. Further evidence from redbed shallow lacustrine and aeolian vertebrate ichnofacies. *Abstracts and Papers, Workshop Ichnofacies and Ichnotaxonomy of the Terrestrial Permian*, Halle: 59-60.
- MENNING, M., 2001. A Permian time scale 2000 and correlation of marine and continental sequences using the Illawara reversal (265 Ma). *Natura Bresciana*, 25: 355-362.
- MILLER, A. K. and FURNISH, W. M., 1940. Permian ammonoids of the Guadalupe Mountains region and adjacent areas. *Geological Society of America Special Paper*, 26: 1-242.
- MILNER, A. R., 1990. The radiations of temnospondyl amphibians. In: Taylor, P. D. and Larwood G. P., Eds., *Major evolutionary radiations*. Oxford: Clarendon Press, 321-349.
- , 1993. Biogeography of Palaeozoic tetrapods. In Long, J. A., Ed., *Palaeozoic vertebrate biostratigraphy and biogeography*. London: Belhaven Press, 324-353.
- MODESTO, S. P., 2000. *Eumotosaurus africanus* and the Gondwanan ancestry of anapsid reptiles. *Palaeontologia Africana*, 36: 15-20.
- MODESTO, S. P. and RUBIDGE, B., 2000. A basal anomodont therapsid from the Lower Beaufort Group, Upper Permian of South Africa. *Journal of Vertebrate Paleontology*, 20: 515-521.
- MODESTO, S. P. and RYBCZYNSKI, N., 2000. The amniote faunas of the Russian Permian. Implications for Late Permian terrestrial vertebrate biostratigraphy. In: Benton, M. J., Shishkin, M. A., Unwin, D. M. and Kurochkin, E. N., Eds., *The age of dinosaurs in Russia and Mongolia*. Cambridge, Cambridge University Press: 17-34.
- MODESTO, S. P., RUBIDGE, B. S. and WELMAN, J., 1999. The most basal anomodont therapsid and the primacy of Gondawana in the evolution of the anomodonts. *Proceedings Royal Society of London*, B266: 331-337.
- MURAVYEV, I. S., 1972. *Stratigraphy and living conditions of Permian foraminiferans from outcrops in the Prechora Pre-Urals*. Kazan, Izdatelstvo Kazan Un-ta,.
- NALIVKIN, D. V., 1966. *Geological map of the USSR*. Moscow, Ministerstvo Geologii SSSR.
- OLSON, E. C., 1955. Parallelism in the evolution of the Permian reptilian faunas of the Old and New Worlds. *Fieldiana Zoology*, 37: 385-401.
- , 1957. Catalogue of localities of Permian and Triassic terrestrial vertebrates of the territories of the U. S. S. R. *Journal of Geology*, 65: 196-226.
- , 1962. Late Permian terrestrial vertebrates, U.S.A. and U.S.S.R. *Transactions of the American Philosophical Society New Series*, 52: 1-223.
- , 1965. Chickasha vertebrates. *Oklahoma Geological Survey Circular*, 70: 1-70.
- , 1972. *Diplocaulus parvus*, n. sp. (Amphibia, Nectridea) from the Chickasha Formation (Permian, Guadalupian) of Oklahoma. *Journal of Paleontology*, 46: 656-659.
- , 1974. On the source of the therapsids. *Annals South African Museum*, 64: 27-46.
- , 1975. Vertebrates and some problems of Permo-Carboniferous geochronology. In: Cys, J. M. and Toomey, D. F., Eds., *Permian exploration, boundaries, and stratigraphy. Midland, Permian Basin. Section Society of Economic Paleontologists and Mineralogists*: 98-103.
- , 1980. The North American Seymouriidae. In: Jacobs, L. L., Ed., *Aspects of vertebrate history*. Flagstaff, Museum of Northern Arizona Press: 137-152.
- , 1989. Problems of Permo-Triassic terrestrial extinctions. *Historical Biology*, 2: 17-35.
- , 1990. *The other side of the medal. A paleobiologist reflects on the art and serendipity of science*. Blacksburg: McDonald and Woodward.

- OLSON, E. C. and BARGHUSEN, H., 1962. Vertebrates from the Flowerpot Formation, Permian of Oklahoma. *Oklahoma Geological Survey Circular*, 59: 5-48.
- OLSON, E. C. and BEERBOWER, J. R., 1953. The San Angelo Formation, Permian of Texas, and its vertebrates. *Journal of Geology*, 61: 389-423.
- OLSON, E. C. and CHUDINOV, P., 1992. Upper Permian terrestrial vertebrates of the USA and Russia. 1991. *International Geology Review*, 34: 1143-1160.
- PAGE, L. R. and ADAMS, J. E., 1940. Stratigraphy, eastern Midland Basin. *American Association of Petroleum Geologists Bulletin*, 24: 52-64.
- PARRISH, J.M., PARRISH, J. T. and ZIEGLER, A. M., 1986. Permian-Triassic paleogeography and paleoclimatology and implications for therapsid distribution. In: Hotton, N. III, MacLean, P. D. Roth, J. J. and Roth, E. C., Eds., *The ecology and biology of mammal-like reptiles*. Washington, D.C., Smithsonian Institution Press: 109-131.
- PITTMAN, J. G., SCHULTZ-PITTMAN, R., LOCKLEY, M. G. and WESTGATE, J. W., 1996. Two Permian footprint localities at San Angelo, Texas. *Journal of Vertebrate Paleontology*, 16(3): 58A.
- PIVETEAU, J., 1926. Paléontologie de Madagascar, XIII. Amphibiens et reptiles Permians. *Annales de Paléontologie*, 15: 1-128.
- PLUMMER, F. B. and SCOTT, G., 1937. The geology of Texas. Volume III. Part 1. Upper Paleozoic ammonites in Texas. *The University of Texas Bulletin*, 3701: 13-516.
- PRICE, L. I., 1948. Um anfíbio labirintodonte de Formação Pedra do Fogo, estado do Maranhão. *Boletim Divisão de Geologia e Mineralogia, Departamento Nacional de Produção Mineral, Rio de Janeiro*, 124: 1-32.
- PRONINA, G. P., 1999. Correlation of Upper Permian outcrops of the Boreal realm by small foraminiferans. In Burov, B. V., Esaulova, N. K. and Gubareva, V. S., Eds., *Proceedings of International Symposium "Upper Permian Stratotypes of the Volga Region."* Moscow: GEOS, 182-191.
- RAY, S. 1999. Permian reptilian fauna from the Kundaram Formation, Pranhita-Godavari Valley, India. *Journal of African earth Sciences*, 29: 211-218.
- , 2000. Endothiodont dicynodonts from the Late Permian Kundaram formation, India. *Palaeontology*, 43: 375-404.
- , 2001. Small Permian dicynodonts from India. *Palaeontological Research*, 5: 177-191.
- REISZ, R. R. and LAURIN, M., 2001. The reptile *Macroleter*, the first vertebrate evidence for correlation of Upper Permian continental strata of North America and Russia. *Geological Society of America Bulletin*, 113: 1229-1233.
- , 2002. The reptile *Macroleter*: First vertebrate evidence for correlation of Upper Permian continental strata of North America and Russia: Reply. *Geological Society of America Bulletin*, 114: 1176-1177.
- ROMER, A. S., 1966. *Vertebrate paleontology*. Third edition. Chicago, University of Chicago Press.
- ROSS, C. A., 1987. Leonardian Series (Permian), Glass Mountains, West Texas. In Cromwell, D. and Mazzullo, L., Eds., *The Leonardian Facies in W. Texas and S. E. New Mexico and guidebook to the Glass Mountains, West Texas*. Midland, Permian Basin Section Society of Economic Paleontologists and Mineralogists: 25-33.
- ROSS, C. A. and ROSS, J. P. R., 1988. Late Paleozoic transgressive-regressive deposition. *Society of Economic Paleontologists and Mineralogists Special Publication*, 42: 227-247.
- , 1995. Permian sequence stratigraphy. In: Scholle, P. A., Peryt, T. M. and Ulmer-Scholle, D. S. Eds. *The Permian of Northern Pangea Volume 1. Paleogeography, Paleoclimates, Stratigraphy*. Berlin: Springer-Verlag, 98-123.
- RUBIDGE, B. S., 1993. New South African fossil links with earliest mammal-like reptile (therapsid) faunas from Russia. *South African Journal of Science*, 89: 460-461.
- , 1995. Biostratigraphy of the *Eodicynodon* Assemblage Zone. *South African Committee for Stratigraphy, Biostratigraphic Series*, 1: 3-7.
- RUBIDGE, B. S. and HOPSON, J. A., 1990. A new anomodont therapsid from South Africa and its bearing on the ancestry of *Dicynodontia*. *South African Journal of Science*, 86: 43-45.
- , 1996. A primitive anomodont therapsid from the base of the Beaufort Group (Upper Permian) of South Africa. *Zoological Journal of the Linnean Society*, 117: 115-139.
- SANTI, G., 2003. Early Permian tetrapod footprints from the Orobic basin (southern Alps-northern Italy). Data, problems, hypotheses. *Bolletina della Società Italiano Volume Speciale*, 2: 59-66.
- SARG, J. F. and LEHMANN, P. J., 1986. Lower-middle Guadalupian facies and stratigraphy, San Andres/Grayburg formations, Guadalupe Mountains, New Mexico. In: Moore, G. E. and Wilde, G. L., Eds., *San Andres/Grayburg formations. Lower-Middle Guadalupian facies, stratigraphy and reservoir geometries, Guadalupe Mountains, New Mexico*. Midland, Permian Basin Section Society of Economic Paleontologists and Mineralogists, 1-8.
- SHISHKIN, M. A., NOVIKOV, I. V. and GUBIN, Y. M., 2000. Permian and Triassic temnospondyls from Russia. In: Benton, M. J., Shishkin, M. A., Unwin, D. M. and Kurochkin, E. N., Eds., *The age of dinosaurs in Russia and Mongolia*. Cambridge, Cambridge University Press: 35-59.
- SIDOR, C. A. and HOPSON, J. A., 1995. The taxonomic status of the Upper Permian eotheriodont therapsids of the San Angelo Formation (Guadalupian), Texas. *Journal of Vertebrate Paleontology*, 15(3): 53A.
- SIDOR, C. A., LARSSON, H., STEYER, J., O'KEEFE, R. and SMITH, R., 2003a. Late Permian tetrapods from the Sahara. *Journal of Vertebrate Paleontology*, 23(3): 97A.
- SIDOR, C. A., BLACKBURN, D. C. and GADO, B. 2003b. The vertebrate fauna of the Upper Permian of Niger—II. Preliminary description of a new pareiasaur. *Paleontologia Africana*, 39: 45-52.
- SIGOGNEAU-RUSSELL, D., 1989. Theriodonta I Phthinosuchia, Biarmosuchia, Eotitanosuchia, Gorgonopsia. *Handbook of Paleoherpology*, 17B/I: 1-127.
- SIMPSON, L. C., 1973. Preliminary correlation of the Lower Permian of north Texas and Oklahoma. *Shale Shaker*, 74: 68-72.
- SKINNER, J. W., 1946. Correlation of Permian of West Texas and southeast New Mexico. *American Association of Petroleum Geologists Bulletin*, 30: 1857-1874.
- SMITH, R. M. H., 2000. Sedimentology and taphonomy of Late Permian vertebrate fossil localities in southwestern Madagascar. *Palaeontologia Africana*, 36: 25-41.

- SMITH, R. M. H. and KEYSER, A. W., 1995a. Biostratigraphy of the *Tapinocephalus* Assemblage Zone. *South African Committee for Stratigraphy Biostratigraphic Series*, 1: 8-12.
- , 1995b. Biostratigraphy of the *Pristerognathus* Assemblage Zone. *South African Committee for Stratigraphy Biostratigraphic Series*, 1: 13-17.
- , 1995c. Biostratigraphy of the *Tropidostoma* Assemblage Zone. *South African Committee for Stratigraphy Biostratigraphic Series*, 1: 18-22.
- , 1995d. Biostratigraphy of the *Cistecephalus* Assemblage Zone. *South African Committee for Stratigraphy Biostratigraphic Series*, 1: 23-28.
- SONNENFELD, M. D., 1993. Anatomy of offlap. Upper San Andres Formation (Permian, Guadalupian), Last Chance Canyon, Guadalupe Mountains, New Mexico. In: Love, D. W., Hawley, J. W., Kues, B. S., Adams, J. W., Austin, G. S. and Barker, J. M., Eds., *Carlsbad Region, New Mexico and West Texas. New Mexico Geological Society Guidebook, 44th Field Conference*. Socorro, New Mexico Geological Society: 195-203.
- SUMIDA, S. S., BERMAN, D. S. and MARTENS, T., 1996. Biostratigraphic correlations between the Lower Permian of North America and central Europe using the first record of an assemblage of terrestrial tetrapods from Germany. *PaleoBios*, 17: 1-12.
- , 1998. A new trematopid amphibian from the Lower Permian of central Germany. *Palaeontology*, 41: 605-629.
- SUMIDA, S. S., LOMBARD, R. E., BERMAN, D. S. and HENRICI, A. C., 1999. Late Paleozoic aminotes and their near relatives from Utah and northeastern Arizona, with comments on the Permian-Pennsylvanian boundary in Utah and northern Arizona. In Gillette, D. D., Ed., *Vertebrate paleontology in Utah. Utah Geological Survey Miscellaneous Publication*, 99-1: 31-43.
- TAQUET, P., 1969. Première découverte en Afrique d'un reptile captorhinomorphe (cotylosaurien). *Compte Rendus de l'Académie Science Paris D*, 268: 779-781.
- TEWARI, A. P., 1962. On a new species of *Archegosaurus*, from the Lower Gondwana of Kashmir. *Records of the Geological Survey of India*, 89: 427-434.
- THARALSON, D. B., 1984. Revision of the Permian ammonoid family Perrinitidae. *Journal of Paleontology*, 58: 804-833.
- TVERDOKHLEBOV, V. P., TVERDOKHLEBOVA, G. I., BENTON, M. J. and STORRS, G. W., 1997. First record of footprints of terrestrial vertebrates from the Upper Permian of the Cis-Urals, Russia. *Palaeontology*, 40: 157-166.
- WARDLAW, B. R., 1995. Permian conodonts. In: Scholle, P. A., Peryt, T. M. and Ulmer-Scholle, D. S., Eds., *The Permian of northern Pangea Volume 1. paleogeography, paleoclimates, stratigraphy*. Berlin: Springer-Verlag, 186-195.
- , 1999. Notes from the SPS chair. *Permophiles*, 35: 1-2.
- , 2000. Guadalupian conodont biostratigraphy of the Glass and Del Norte Mountains. *Smithsonian Contributions to Earth Sciences*, 32: 37-87.
- WARDLAW, B. R., and COLLINSON, J. W., 1986. Paleontology and deposition of the Phosphoria Formation. *Contributions to Geology University of Wyoming*, 24: 107-142.
- WARREN, A., 1991. Australian fossil amphibians. In: Vickers-Rich, P., Monaghan, J. M., Baird R. F. and Rich, T. H., Eds., *Vertebrate palaeontology of Australasia*. Melbourne, Monash University: 569-590.
- WERNEBURG, R., 1989. Some notes to systematic, phylogeny and biostratigraphy of labyrinthodont amphibians from the Upper Carboniferous and Lower Permian in central Europe. *Acta Musei Reginae Hradecensis Scientiae Naturales*, 22: 117-129.
- WERNEBURG, R., and SCHNEIDER, J., 1996. The Permian temnospondyl amphibians of India. *Special Papers in Palaeontology*, 52: 105-128.
- WESCOTT, W. A. and DIGGENS, J. N., 1998. Depositional history and stratigraphical evolution of the Sakamena Group (middle Karoo Supergroup) in the southern Morondova basin, Madagascar. *Journal of African Earth Sciences*, 24: 585-601.
- WILDE, G. L., ELLIOTT, T. L., HILL, R. B. and SCHNEIDER, R., 2001. Age of the "Holt Pay" and its relationship to the Cutoff Formation, Apache Mountains, Culberson County, Texas. In: Viveiros, J. J. and Ingram, S. M., Eds., *The Pennsylvanian basin. Microns to satellites looking for oil and gas at all scales*. Midland, West Texas Geological Society: 251-257.
- WILSON, L. R., 1962. Permian plant microfossils from the Flowerpot Formation, Greer County, Oklahoma. *Oklahoma State Geological Survey Circular*, 49: 1-49.
- WOODWARD, A. S., 1905. Permo-Carboniferous plants and vertebrates from Kashmir. II. Fishes and labyrinthodonts. *Memoirs of the Geological Survey of India Palaeontologica Indica*, 11: 10-11.
- ZHOU, Z., GLENISTER, B. F., FURNISH, W. M. and SPINOSA, C., 1996. Multi-episodal extinction and ecological differentiation of Permian ammonoids. *Permophiles*, 29: 52-62.

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