

# *Lystrosaurus* species composition across the Permo–Triassic boundary in the Karoo Basin of South Africa

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*Lystrosaurus* is one of the few therapsid genera that survived the end-Permian mass extinction, and the only genus to have done so in abundance. This study identifies which species of *Lystrosaurus* have been recovered from Permian and Triassic strata to determine changes in the species composition across the Permo–Triassic (P–T) boundary in the Karoo Basin of South Africa. Data generated from museum collections and recent fieldwork were used to stratigraphically arrange a total of 189 *Lystrosaurus* specimens to determine which species survived the extinction event. Results reveal that *L. curvatus* and *L. maccaigi* lived together on the Karoo floodplains immediately before the extinction event. *L. maccaigi* did not survive into the Triassic in South Africa. *L. curvatus* survived, but did not flourish and soon became extinct. Two new species of *Lystrosaurus*, *L. murrayi* and *L. declivis*, appeared in the Early Triassic. It is possible that *L. murrayi* and *L. declivis* occupied different niches to *L. maccaigi* and *L. curvatus*, and had special adaptations that were advantageous in an Early Triassic environment. We suggest that *L. maccaigi* may be used as a biostratigraphic marker to indicate latest Permian strata in South Africa and that, in support of previous proposals, the genus *Lystrosaurus* should not be used as a sole indicator of Triassic-aged strata. Our field data also show that *L. curvatus* may be regarded as a biostratigraphic indicator of the P–T boundary interval. □ *End-Permian extinction, Karoo Basin, Lystrosaurus, Permo–Triassic.*

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The end-Permian extinction, dated at 251.4 Ma (Bowring *et al.* 1998), is considered to be the most catastrophic of the five major Phanerozoic mass extinctions (Erwin 1994; Looy *et al.* 2001; Benton & Twitchett 2003). Suggested causes of the extinction include extraterrestrial impact (Becker *et al.* 2001), volcanism (Renne *et al.* 1995), oceanic anoxia (Wignall & Twitchett 1996; Isozaki 1997; Hotinski *et al.* 2001), oceanic overturn (Knoll *et al.* 1996), excessive methane release (Krull *et al.* 2000; Sheldon & Retallack 2002), global warming (Ward *et al.* 2000; Smith & Ward 2001), ecosystem collapse (Wang *et al.* 1994; Ward *et al.* 2000, 2005), oxygen stress (Retallack *et al.* 2003; Huey & Ward 2005) and complex combinations of these possibilities (Erwin 1994). However, the pattern of species disappearances across the Permo–Triassic (P–T) boundary is complicated, and conclusive evidence for any of these suggested causes has yet to be found.

The extinction caused approximately 90% of all marine species and 70% of all terrestrial vertebrate families to disappear (Maxwell 1992; Erwin 1994). Most studies examining the end-Permian extinction

have focused on marine organisms because their abundant fossils provide a high-resolution record of the extinction (Erwin 1994). Less is known about the effect on terrestrial vertebrates (Smith & Ward 2001; Benton *et al.* 2004), as the P–T boundary is difficult to locate in terrestrial rocks, although features such as a ‘global fungal spike’ (Eshet *et al.* 1995) and a ‘global coal gap’ (Retallack *et al.* 1996) at the boundary provide a more accurate fix. It has recently been found that the southern Karoo Basin of South Africa provides an uninterrupted terrestrial stratigraphic record from the Permian to the Triassic (shown by the gradational change from shale-dominated strata of the Permian Balfour Formation to sandstone-dominated Triassic Katberg Formation as well as the absence of a disconformity other than those usually found within fluvial sequences; Smith & Ward 2001), allowing changes in the abundance of terrestrial vertebrate taxa across the boundary to be examined. The most up-to-date field data position the P–T boundary in South Africa at approximately 40 stratigraphic metres below the base of the Katberg Formation (recognized by the last appearance datum



Fig. 1. Reconstruction of the genus *Lystrosaurus* (courtesy of C. Hunter).

of *Dicynodon lacerticeps*, a negative excursion in  $\delta^{13}\text{C}$  and a distinctive laminated sandstone-shale unit, MacLeod *et al.* 2000; Ward *et al.* 2000; Smith & Ward 2001).

By the end of the Permian, the Therapsida (advanced non-mammalian synapsids) were the dominant vertebrate fauna in southern Gondwana. Remains of a particularly diverse and numerous therapsid clade, the Dicynodontia, have been recovered in vast quantities from the uppermost Permian strata, but are almost completely absent from rocks that are Early Triassic in age (Kitching 1977; Smith 1995; Smith & Ward 2001). To date, *Lystrosaurus* is the only dicynodont genus to be found on either side of the P–T boundary (Smith & Ward 2001). More recently, the therocephalians *Tetracynodon*, *Moschorhinus* (Damiani *et al.* 2003a) and *Ictidosuchoides* (Smith & Botha 2005) have also been found in Late Permian as well as Early Triassic strata. However, *Lystrosaurus* is the only therapsid genus to be found in abundance.

*Lystrosaurus* is a well-known dicynodont (Fig. 1), remains of which have been recovered from Zambia, India, China, Mongolia, Russia, Antarctica, Australia and Laos (Kemp 1982; Gubin & Sinitza 1993; King 1993; King & Jenkins 1997; Retallack & Krull 1999), but it is particularly abundant in the Karoo Basin of South Africa (Rubidge 1995; Smith 1995). It is a medium- to large-sized genus with an average adult basal skull length ranging from 109 mm to 258 mm (depending on the species).

Historically, there has been much debate over the number of taxonomically valid *Lystrosaurus* species (e.g. Broom 1932; Brink 1951, 1986; Kitching 1968, 1977; Cluver 1971) with a total of 23 species being erected on South African specimens alone (King 1993). However, studies by Cosgriff *et al.* (1982) and King (1993) suggested that there were perhaps only six distinct species, namely *Lystrosaurus curvatus*, *L. platyceps*, *L. oviceps*, *L. maccaigi*, *L. murrayi*

and *L. declivis*. This number has recently been further reduced (on the basis of bivariate allometric analyses and principal components analyses; Grine *et al.*, 2006) to just four species (Fig. 2), with *L. platyceps* and *L. oviceps* being included under *L. curvatus*. The main features that characterize *L. curvatus* are particularly large orbits, a gently curved snout and the absence or weak development of a frontonasal ridge, longitudinal, premaxillary ridge and postorbital and prefrontal bosses (Fig. 2A) (Brink 1951; Cluver 1971). Unlike studies such as Ray (2005), Grine *et al.* (2006) consider *L. murrayi* and *L. declivis* to be distinct species based on the following characteristics. *L. murrayi* (Fig. 2B) has a notably short, curved snout; its postorbital bosses are absent and the anterior surface of the snout lies at right angles to the parieto-preparietal plane. Prefrontal bosses, a frontonasal ridge and longitudinal, premaxillary ridge are sometimes present, but only in a weakly developed state (Cluver 1971; Grine *et al.* 2006). *Lystrosaurus declivis* (Fig. 2C) is similar to *L. murrayi*, but differences include the presence of prefrontal bosses, a more prominent frontonasal ridge, and a longitudinal, premaxillary ridge (Cluver 1971; Grine *et al.* 2006). We agree with Grine *et al.* (2006) and also note that the length of the snout in *L. murrayi* is approximately equal to the length of the skull roof (from the frontonasal ridge to the occiput), whereas the snout of *L. declivis* is notably longer than the length of the skull roof. Both *L. murrayi* and *L. declivis* have two frontal grooves or depressions in an anterior-posterior direction, posterior to the frontonasal ridge. These grooves extend below the surface of the frontal bone, are present on all *L. murrayi* and *L. declivis* individuals and are found in both distorted and undistorted specimens. They are absent from *L. curvatus* and *L. maccaigi*. *Lystrosaurus maccaigi* (Fig. 2D) has been described as having relatively large orbits and markedly prominent pre- and postorbital bosses (Brink 1951; Cluver 1971). The facial surface slopes forward and down from its junction with the frontal plane, similar to *L. declivis* (Fig. 2C). However, the premaxillary plane lies at a sharper angle and the orbits of *L. maccaigi* are more upward and forward facing compared to *L. declivis*.

This study identifies the various *Lystrosaurus* species occurring in Permian and Triassic strata to determine the changes in species composition across the P–T boundary in South Africa.

## Material and methods

*Lystrosaurus* is one of the most abundant therapsids found in South African Karoo strata, which would

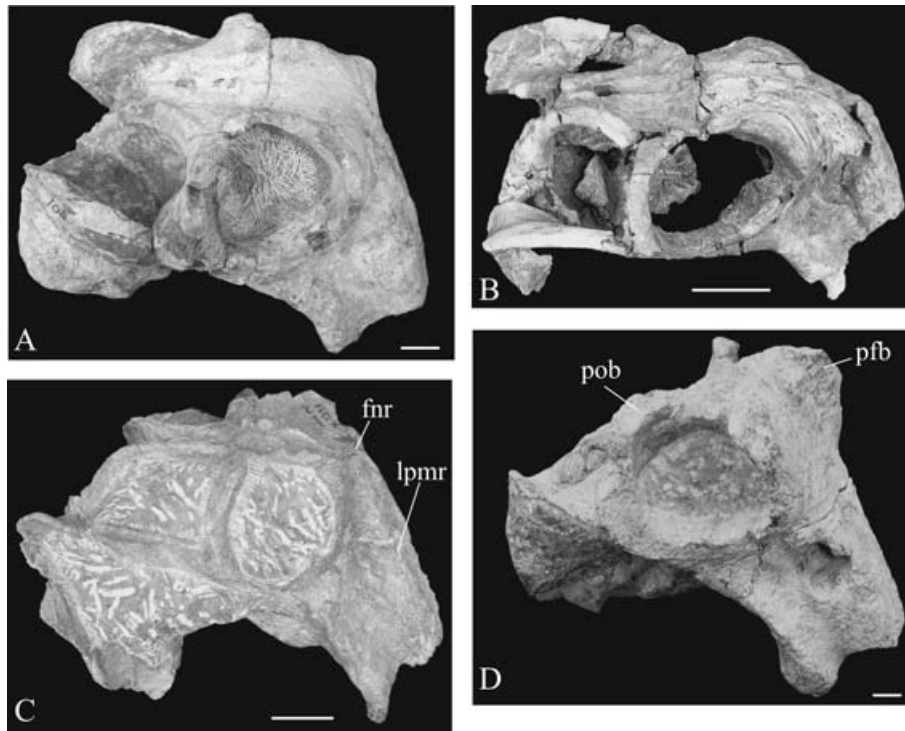


Fig. 2. Photographs of the four *Lystrosaurus* species proposed by Grine *et al.* (2006). Specimens housed in the Iziko South African Museum of Cape Town. □A. *L. curvatus* (SAM-PK-706). □B. *L. murrayi* (SAM-PK-K1495). □C. *L. declivis* (SAM-PK-K1398). □D. *L. maccaigi* (SAM-PK-K116). Scale bar = 3 cm. Abbreviations: fnr, frontonasal ridge; lpmr, longitudinal premaxillary ridge; pob, postorbital boss; pfb, prefrontal boss.

imply that a large sample size is available for study. However, a large amount of fossil material, previously identified as *Lystrosaurus*, is not associated with cranial material and/or is poorly preserved, thus preventing species identification. Thus, any museum specimen that could not be positively assigned to a *Lystrosaurus* species was excluded from this study. Another major difficulty with the museum collections was obtaining accurate locality data, and this too has caused many specimens to be excluded from this study.

*Lystrosaurus* specimens, kept in the collections of the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, (B/P/1/), Iziko South African Museum, Cape Town (SAM-PK-K), and the National Museum, Bloemfontein (NMQR), were examined. A total of 189 specimens were associated with detailed locality data and could be identified to species level. Species identifications follow the descriptions outlined above as formulated by Grine *et al.* (2006). The lithostratigraphic position of the locality of each specimen was determined from latest 1:250 000 scale geological maps compiled by the Regional Geology Division of the South African Council for Geosciences. Each specimen was then designated either

Permian or Triassic only if it was recovered from a farm containing only Permian or Triassic strata. Collectors were also personally contacted in some cases in order to confirm that the location of the specimen was correct. Twenty-one localities from the Graaff-Reinet, Middelburg, Colesburg, Venterstad, Bethulie, Albert, Estcourt, Bergville and Harrismith districts were used in the study (Fig. 3). In addition to the museum collection data, five detailed lithostratigraphical sections through the P–T boundary in the Graaff-Reinet (Lootsberg Pass, Old Wapadsberg Pass, Tweefontein farm) and Bethulie Districts (Bethel, Fairydale farms) were examined (compiled by R. M. H. Smith from 1992 to 2002). These detailed sections contain the exact stratigraphic positions (to an accuracy of 0.5 m) of every embedded *Lystrosaurus* fossil found at these localities.

## Biostratigraphy

General collecting of fossil-rich outcrops in the Late Permian Karoo strata has been taking place since the 1800s, however, it is only over the past ten years that systematic, inch-by-inch searching methods have

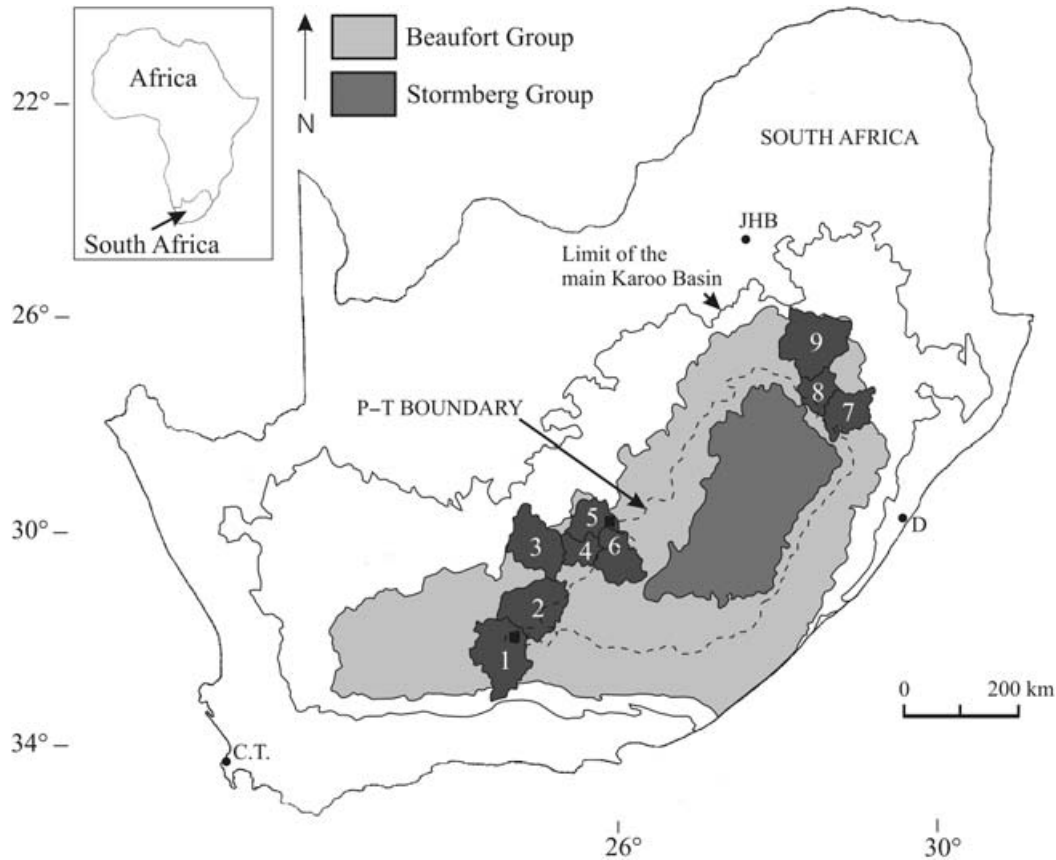


Fig. 3. Map of South Africa showing the location of the nine districts from where the study specimens were recovered. The districts include data from 21 different localities where *Lystrosaurus* skulls have been collected. Districts: 1, Graaff-Reinet; 2, Middelburg; 3, Colesburg; 4, Venterstad; 5, Bethulie; 6, Albert; 7, Estcourt; 8, Bergville; 9, Harrismith. Abbreviations: CT, Cape Town; D, Durban; JHB, Johannesburg.

been used, especially on the P-T boundary interval (i.e. the few metres of strata below and above the biostratigraphically defined boundary based on the extinction of the Permian fauna and the radiation of the Triassic fauna). The results from the museum collections and 75 *in situ* *Lystrosaurus* specimens logged to 5 m accuracy over an estimated 12 000 man hours show that only *L. maccaigi* and *L. curvatus* are present in the uppermost Permian strata of the *Dicynodon* Assemblage Zone and that three of the four species, namely *L. curvatus*, *L. murrayi* and *L. declivis*, are found in the lowermost Triassic strata of the *Lystrosaurus* Assemblage Zone (Figs 4–6).

Detailed biostratigraphy indicates that the range of *L. maccaigi* extends from 30 m below the P-T boundary to the boundary itself. It is limited to the upper Permian *Dicynodon* Assemblage Zone (Fig. 4) and is absent from the lower Triassic *Lystrosaurus* Assemblage Zone (Figs 4, 7). Positively identified individuals of *L. curvatus* have been found 8 m below the P-T boundary (in the *Dicynodon* Assemblage Zone) and the highest documented occurrence is

GROUP	FM	MEMBER (SACS)	BIOZONES Rubidge 1995	BIOZONES Hancox & Rubidge 2001	STAGE	PERIOD
BEAUFORT	KATBERG		<i>Cynognathus</i>	<i>Cynognathus</i> sub zone A	SCYTHIAN	TRIASSIC
			<i>Lystrosaurus</i>	<i>Lystrosaurus</i>		
	BALFOUR	Palingkloof			TATARIAN	PERMIAN
		Oudeberg	<i>Dicynodon</i>	<i>Dicynodon</i>		

Fig. 4. Summary of the biostratigraphy of the southern Karoo Basin indicating the stratigraphic position of the P-T boundary. The P-T boundary separates the *Dicynodon* Assemblage Zone (characterized by the presence of the dicynodont *Dicynodon* and the therapsid *Therapsid*) from the overlying *Lystrosaurus* Assemblage Zone (characterized by the abundance of *Lystrosaurus*, the presence of *Procolophon* and the absence of *Dicynodon*). Abbreviations: FM, Formation; SACS, South African Committee for Stratigraphy.

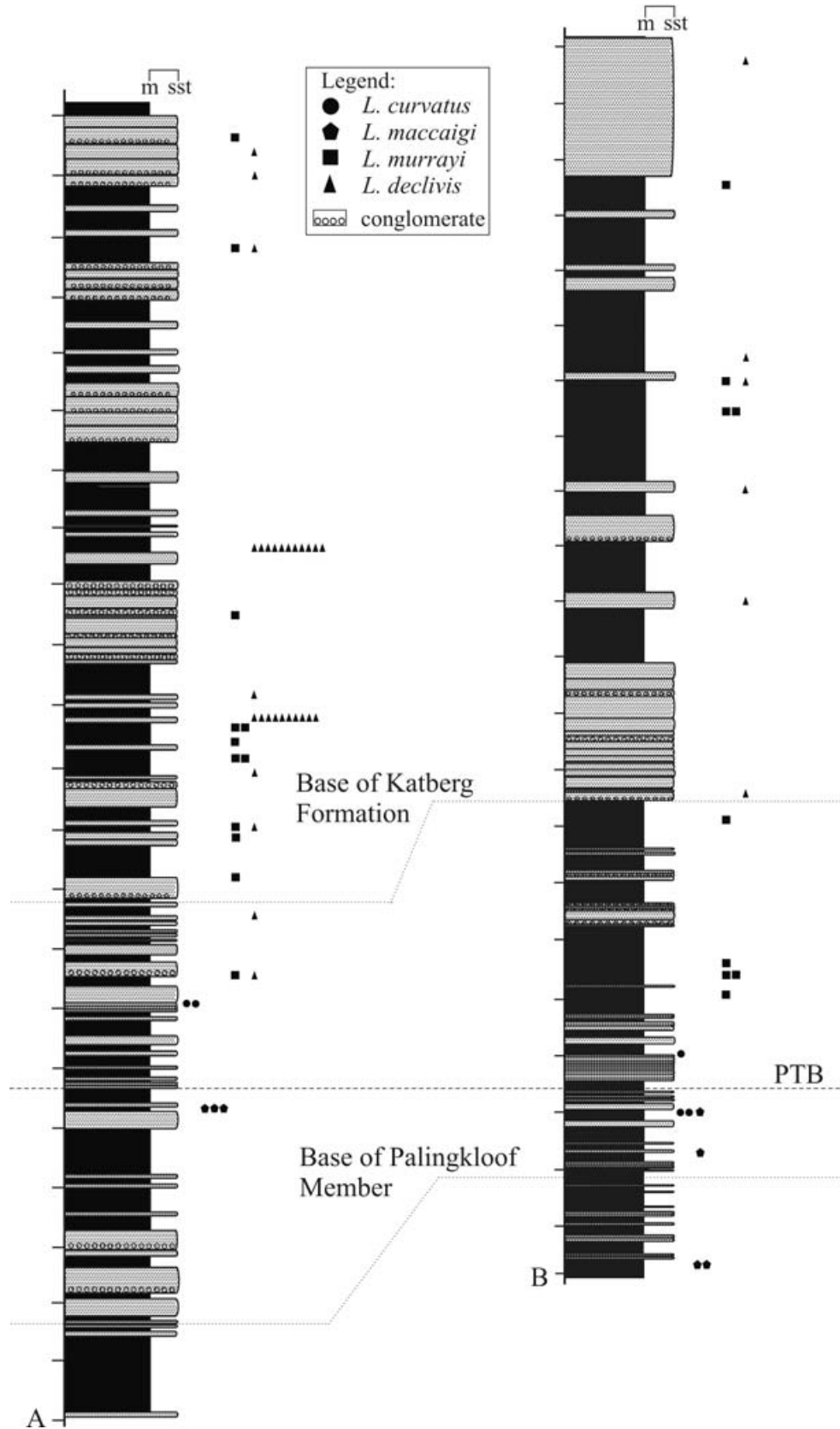


Fig. 5. Detailed lithostratigraphic sections from the Bethulie District showing the stratigraphic positions of the *in situ* *Lystrosaurus* skulls in relation to the Palingkloof Member, the P-T boundary and the Katberg Formation. □A. Fairydale □B. Bethel. Vertical scale tick marks represent 10 m.

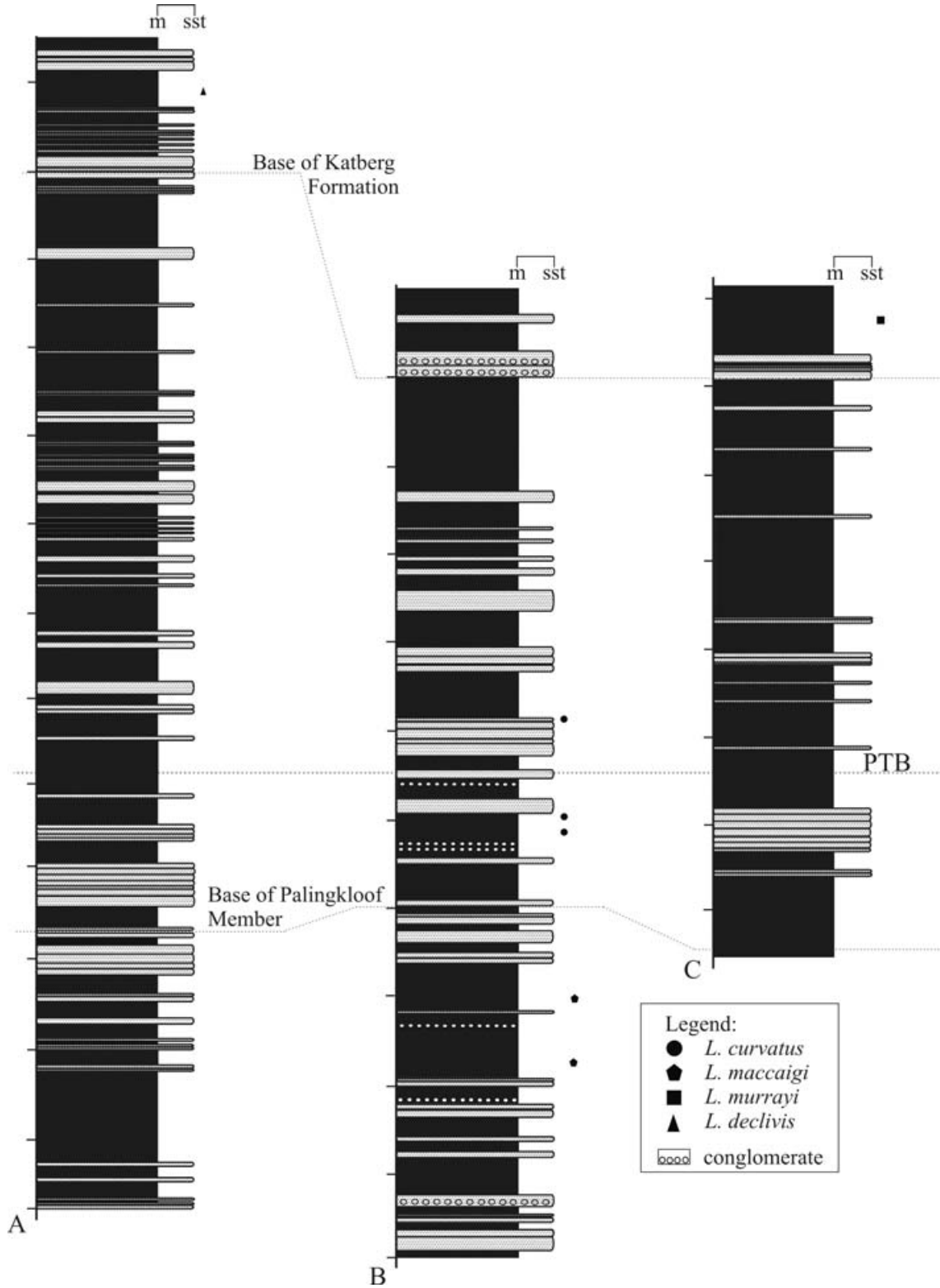


Fig. 6. Detailed lithostratigraphic sections from the Graaff-Reinet District, showing the stratigraphic positions of the *in situ* *Lystrosaurus* specimens in relation to the Palingkloof Member, the P-T boundary and the Katberg Formation. □A. Old Lootsberg Pass. □B. Old Wapadsberg Pass. □C. Tweefontein. Vertical scale tick marks represent 10 m.

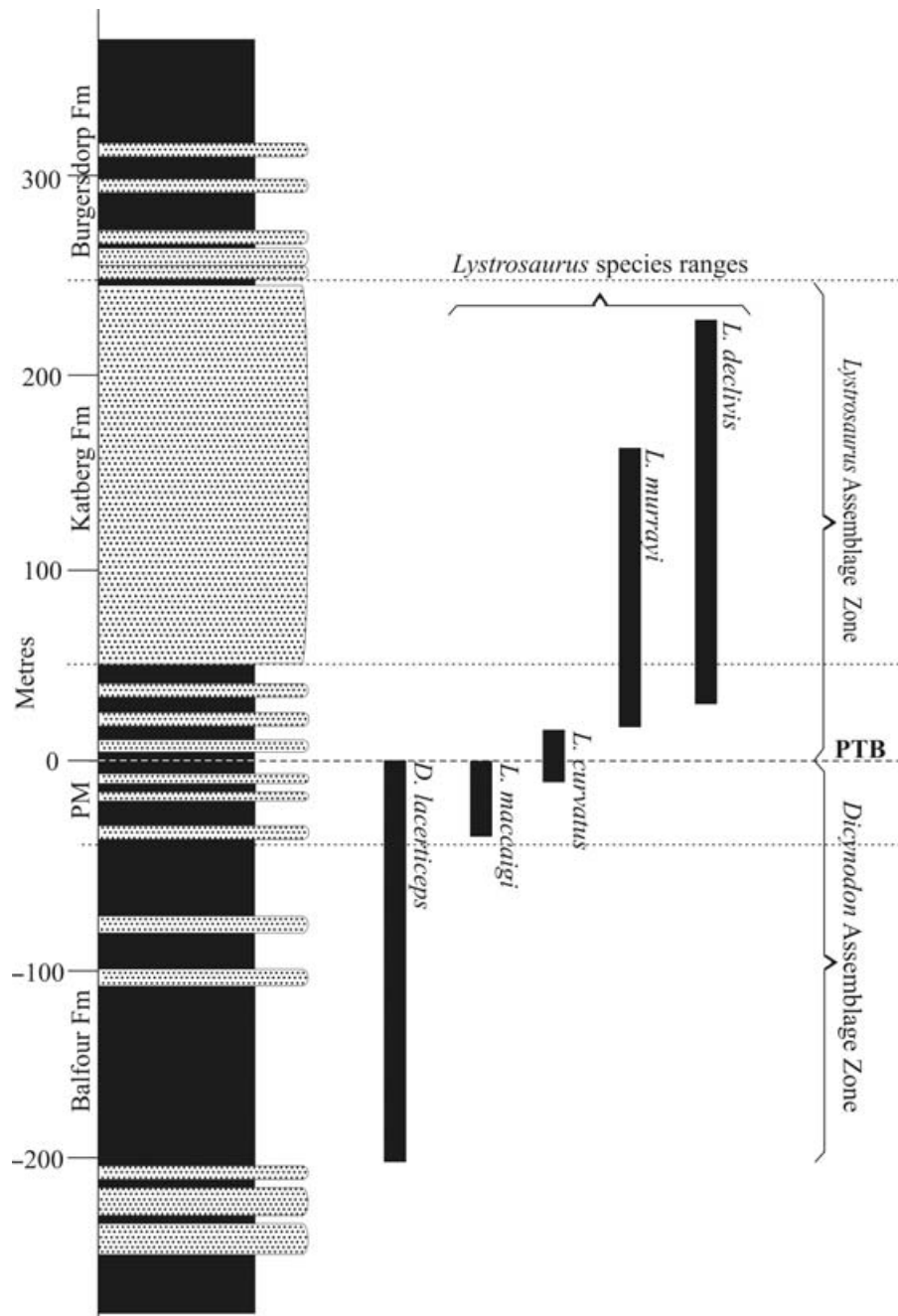


Fig. 7. Combined collection-based locality data with a composite stratigraphic section from the Bethulie and Graaff-Reinet localities. A compilation of the data shows that *L. maccaigi* is absent from lower Triassic strata in South Africa and *L. curvatus* ranges across the boundary into the lower Triassic portion of the Palingkloof Member, Balfour Formation. *Lystrosaurus murrayi* and *L. declivis* first appear in lower Triassic strata and their ranges extend into the Katberg Formation.

only 13 m above the boundary (in the *Lystrosaurus* Assemblage Zone), still within the strata of the Palingkloof Member, of the Balfour Formation (Fig. 7). *Lystrosaurus curvatus* has yet to be documented from the overlying Katberg Formation.

*Lystrosaurus murrayi* is first noted in the Lower Triassic portion of the Palingkloof Member at

approximately 16 m above the boundary and its range extends into the Early Triassic Katberg Formation to approximately 165 m above the P–T boundary (Fig. 7). Similarly, *L. declivis* is also first noted in lower Triassic strata. *L. declivis* extends from approximately 30 m above the boundary to 188 m into the Katberg Formation (Fig. 7).

## Correlation

The combined museum collection locality data and detailed field-based lithostratigraphic sections suggest that *L. maccaigi* appeared in the Karoo Basin in the latest Permian, but did not survive the end-Permian extinction in South Africa. Cosgriff *et al.* (1982) noted the presence of a *L. maccaigi* specimen from the lower Fremouw Formation in Antarctica, which has traditionally been assigned an Early Triassic age. However, the recent discovery of *Glossopteris*-dominated flora and absence of *Dicroidium* from Collinson Ridge in the lower Fremouw Formation has cast doubt on the age of the lower Fremouw Formation and a Late Permian age has now been proposed (McManus *et al.* 2002).

*L. curvatus* appeared during the latest Permian and survived the extinction. *L. murrayi* and *L. declivis* have not been documented from below the P–T boundary. *L. declivis* and *L. murrayi* both range from the upper Palingkloof member into the Early Triassic Katberg Formation (Fig. 7). Nine *L. curvatus* individuals were identified above the P–T boundary, whereas *L. murrayi* and *L. declivis* are significantly more abundant. While there may be more *L. curvatus* specimens yet to be discovered from above the P–T boundary, it is unlikely that this species will be found in similar numbers to *L. murrayi* and *L. declivis*. Thus, it appears that *L. murrayi* and *L. declivis* were more successful species than was *L. curvatus*.

## Discussion

### *Possible causes of changes in Lystrosaurus species composition*

There are several possible explanations for the observed changes in *Lystrosaurus* species composition across the South African Karoo P–T boundary, including factors such as preservational bias, preferential species survival and dispersal.

*Preservational bias.* – The rocks of the Upper Permian *Dicynodon* Assemblage Zone were deposited by high-sinuosity streams and comprise greenish-grey floodplain mudstones and subordinate, lenticular, channel sandstones. This evidence has been used to suggest that the environment consisted of meandering streams in a semi-arid climate (Smith *et al.* 1993; Smith 1995; Rubidge 1995). In contrast, the Lower Triassic palaeosols in the *Lystrosaurus* Assemblage Zone are mostly red in colour and numerous casts of desiccation cracks are evident. The palaeosols also have a slightly greater depth to calcic horizon than

those of the latest Permian. Retallack *et al.* (2003) interpret this as evidence of increased seasonal precipitation, combined with an increase in mean annual temperature and the onset of a monsoonal rainfall regime. This resulted in more strongly seasonal, yet highly unreliable, rainfall and increased storm intensity (Retallack *et al.* 2003). The depositional environment changed from high sinuosity, perennial rivers and shallow lacustrine environments on a cool, seasonally dry (i.e. predominantly wet) alluvial plain in the latest Permian to wide shallow, braided, ephemeral rivers on a hot, seasonally wet (i.e. predominantly dry) floodplain in the earliest Triassic (Smith 1995; Ward *et al.* 2000).

It might be expected that the dramatic change in climate between the latest Permian and the earliest Triassic would cause fossils to be less frequently preserved in Triassic rocks, as a more irregular rainfall regime does not usually facilitate conditions for good fossil preservation (due to increased weathering, low floodplain accretion rates and irregular bone burial events). However, the vertebrate fossils found in the *Lystrosaurus* Assemblage Zone are frequently found in clusters, consisting of numerous articulated and commonly curled-up skeletons (Kitching 1977; Rubidge 1995; Smith 1995). This mode of occurrence differs from the skeletons located in the *Dicynodon* Assemblage Zone, which are usually disarticulated and have commonly been scattered and transported. The change in taphonomic style has been attributed to a change in climate from seasonally dry floodplains with high water tables in the Late Permian (resulting in disarticulated and transported skeletons) to predominantly dry floodplains in the Early Triassic (Smith 1995; Retallack *et al.* 2003) resulting in behavioural aggregation around waterholes and bone accumulations as a result of drought-induced die-offs (Smith & MacLeod 1998). Although the taphonomic style differs from the Permian to the Triassic and there is a decrease in diversity, there is no decrease in the relative abundance of fossils (Kitching 1977). Thus, the absence of *L. maccaigi* and the rarity of *L. curvatus* in the Early Triassic are not likely due to a scarcity of Early Triassic fossils, particularly as *L. murrayi* and *L. declivis* are found in abundance in Lower Triassic strata.

*Preferential species survival.* – Large carnivores and herbivores appear to be particularly susceptible to mass extinctions (Kemp 1982). Large carnivores tend to have small population sizes and low speciation rates. They are generally highly mobile and thus, are more likely to disperse, which reduces the number of opportunities for isolated populations to form new species. Similarly, large herbivores also tend to have



low speciation rates because of their high mobility. However, they have higher population numbers and are therefore less susceptible to total extinction compared to large carnivores. Small herbivores also have high population numbers and tend to form new species more quickly as smaller animals are generally less mobile than large animals, leading to isolated populations forming new species. Small carnivores appear to be the least susceptible to mass extinctions as they have large population numbers, high speciation rates and are also less specialized compared to herbivores and therefore, occupy wider niches (Kemp 1982; Stanley 1990).

Large herbivores are relatively rare in the *Tropidostoma* and *Cistecephalus* Assemblage Zones of the Late Permian strata of the Karoo. They become more abundant and more diverse towards the end of the Permian in the overlying *Dicynodon* Assemblage Zone, but they are completely absent from the Early Triassic *Lystrosaurus* Assemblage Zone (King 1990). The large herbivorous therapsids are considered to be those with a skull length exceeding 300 mm (Haughton & Brink 1954; Cluver & Hotton 1981). In the *Dicynodon* Assemblage Zone in South Africa they include genera such as *Aulacephalodon*, *Dicynodon*, *Dinanomodon* and *Palanomodon*, all of which did not survive the end-Permian extinction (Rubidge 1995; Smith & Ward 2001). *L. maccaigi* lived alongside these Late Permian herbivores and is generally regarded as the largest *Lystrosaurus* species (Brink 1951; Cluver 1971) compared to the other three species (maximum basal length of 310 mm, compared to 230 mm in *L. curvatus*, 159 mm in *L. murrayi* (Grine *et al.*, 2006) and 160 mm in *L. declivis*). It is also the rarest of the four species. Large size tends to increase vulnerability to environmental change (Olson 1989), and as a rare, large herbivore, *L. maccaigi* may not have been able to adapt quickly enough (Stanley 1990) to cope with the dramatic change in climate over such a short period (possibly 50 000 years or less; Eshet *et al.* 1995; Rampino & Adler 1998; Smith & Ward 2001).

Alternatively, *L. maccaigi* may have had a different food preference to *L. curvatus*, *L. murrayi* and *L. declivis*. As *L. maccaigi* is significantly larger (up to twice the size) than the other three species, it would have occupied a different feeding niche. It has previously been suggested that *Lystrosaurus* was pre-adapted to feeding on the *Dicrodium*-dominated flora of the Early Triassic (King & Jenkins 1997) and drought-resistant horsetails (Smith 1995), but it is possible that, as such a large animal, *L. maccaigi* was dependent on the taller, larger elements of the *Glossopteris* flora, which did not survive the end-Permian extinction.

Remains of *L. curvatus* have been recovered from the latest Permian and earliest Triassic Palingkloof Member of the Balfour Formation and have yet to be found in the Katberg Formation. At present, its narrow range spans the P–T boundary and as such, can tentatively be regarded as an indicator fossil of the boundary interval. *L. curvatus* is considered to be the least derived of the *Lystrosaurus* species, as it appears to be morphologically closest to the rest of the Permian dicynodonts (Brink 1951; Cluver 1971; King & Jenkins 1997). Thus, *L. curvatus* may have been able to survive the end-Permian extinction as one of the more generalized species, which are thought to be less susceptible to environmental change compared to more derived species (Stanley 1990).

It is notable that *L. murrayi* and *L. declivis* are not only present in lower Triassic strata, but are also highly abundant. Most of the large carnivorous species did not survive the extinction and most of the carnivorous species in the *Lystrosaurus* Assemblage Zone are small (body length less than 60 cm) and probably did not offer much predation pressure on the Early Triassic *L. murrayi* and *L. declivis* populations. *Moschorhinus*, a 1.5-m-long therocephalian and the large archosauriform *Proterosuchus* appear to have been the only carnivorous species capable of preying on adult *L. murrayi* and *L. declivis* individuals. It is likely that the extinction of the Permian gorgonopsians also played a significant role in allowing *L. murrayi* and *L. declivis* to flourish during the Early Triassic.

It has also been suggested that *Lystrosaurus* had an expanded chest, thick ribs and elongated neural spines, possibly indicating the presence of enlarged lungs (Retallack *et al.* 2003). This feature would have increased its respiratory capability and may have been advantageous in a hypoxic early Triassic environment (Retallack *et al.* 2003). However, although a brief examination of neural spine height on several Permian and Triassic dicynodonts has found that Triassic dicynodonts do appear to have relatively longer neural spines compared to Permian taxa (K. Angielczyk, personal communication, 2006), there are no data to support Retallack *et al.*'s (2003) suggestion that *Lystrosaurus* had an expanded chest and thicker ribs compared to Permian dicynodonts. Furthermore, King (1990) found the thorax of *Lystrosaurus* to be similar to that of the Permian dicynodont *Diictodon*. The presence of elongated neural spines may be associated with posture, locomotion or even body size and is not necessarily related to respiratory efficiency (K. Angielczyk, personal communication, 2006). Further study on the postcrania of Permian and Triassic dicynodonts is required before any such hypotheses on dicynodont respiration can be made.

Another possible reason for the change in species composition across the P–T boundary is that each *Lystrosaurus* species may have occupied a different microhabitat. It has long been suggested that *Lystrosaurus* had adaptations for digging and may even have burrowed (Groenewald 1991; King & Cluver 1991; Miller *et al.* 2001). More recently, several *Lystrosaurus* skeletons were found in large scratch-digger burrows at the Bethulie section in Triassic aged strata (Retallack *et al.* 2003). Such an adaptation may have been used to escape the severe environmental conditions and has been documented and suggested as a means of survival for other taxa including *Procolophon*, *Diictodon*, *Thrinaxodon* and *Trirachodon* (Smith 1987; Groenewald *et al.* 2001; Damiani *et al.* 2003b). Thus, as fossorial (burrowing) animals, *L. curvatus*, *L. murrayi* and *L. declivis* may have been pre-adapted to surviving extreme environmental conditions such as prolonged drought.

The specific behaviour of an animal may also influence its preservation potential after death (Behrensmeyer *et al.* 2000), thus leading to increased/decreased abundance in the fossil record. For example, skeletons of animals that live and die in burrows along the edges of watercourses are more likely to be buried by overbank floods in articulation (King 1990). However, *L. murrayi* and *L. declivis* are significantly more abundant compared to other fossorial contemporaneous taxa such as *Procolophon* or *Thrinaxodon*, thus, in this case, the abundance of these two species is more likely to be due to true abundance and not preservation bias. It should be noted however, that if the abundance of *Lystrosaurus* is due to true abundance, then a fossorial lifestyle is not likely to be the sole reason for the success of *L. murrayi* and *L. declivis*. If a fossorial lifestyle played such a significant role in their survival, it would be expected that other fossorial taxa would be as abundant in the *Lystrosaurus* Assemblage Zone, but specimens of *L. murrayi* and *L. declivis* outnumber other taxa by orders of magnitude. A recent study conducted by Ray *et al.* (2005), on the basis of bone histology, suggested that *Lystrosaurus* was adapted to an aquatic or semi-aquatic lifestyle rather than a fossorial one. However, if this is the case, and *Lystrosaurus* was successful because of such a lifestyle, it would also be expected that contemporaneous semi-aquatic amphibians be as abundant in the fossil record as *Lystrosaurus*. However, although there is evidence of an increase in amphibians in the Karoo Basin during the Triassic, their numbers still do not approach those of *L. murrayi* and *L. declivis*.

*Dispersal.* – Several authors have noted that the appearance of *Lystrosaurus* in the fossil record is

relatively sudden, and they have suggested that the genus may have migrated into the South African Karoo Basin (e.g. Kitching 1977; Smith 1995; King & Jenkins 1997).

On the basis of a skull, identified as *L. curvatus*, from the Madumabisa Mudstones of Zambia, King & Jenkins (1997) suggested that *L. curvatus* was an immigrant to the South African Karoo basin. The Madumabisa Mudstones are thought to correlate with the Upper Permian *Cistecephalus* and *Dicynodon* Assemblage Zones of the main Karoo Basin (Rubidge 1995) and the Cuttie's Hillock Formation at Elgin in Scotland, for which a latest Permian age has been suggested (Benton & Walker 1985). The discovery of *L. curvatus* in the Upper Permian Madumabisa Mudstones of Zambia and the previously assumed absence of this species in South African Upper Permian strata lead to the suggestion that *L. curvatus* dispersed into South Africa (King & Jenkins 1997). However, the results in this study indicate that *L. curvatus* was already present in South Africa during the Late Permian and thus, did not necessarily disperse southwards into the Karoo Basin.

King & Jenkins (1997) observed that *Lystrosaurus* has no obvious South African ancestor. Since then, a basal member of the lystrosaurian lineage has been described from the *Dicynodon* Assemblage Zone of KwaZulu-Natal in South Africa (Maisch 2002). Maisch (2002) described a new Late Permian dicynodont, *Kwazulusaurus shakai*, and used cladistics to compare it with several dicynodonts, including *L. murrayi*. He concluded that *Kwazulusaurus* represents the most basal member of the lystrosaurian lineage and that *Lystrosaurus* and *Kwazulusaurus* are sister taxa. On the basis of the short and relatively deep, squared-off snout, reduction of the ectopterygoid (Maisch 2002), absence of a longitudinal premaxillary ridge, postorbital and prefrontal bosses (personal observation), Maisch (2002) noted that *K. shakai* is strikingly similar to *L. curvatus*. *Kwazulusaurus* may, thus, represent one of the Permian taxa that leads to *L. curvatus*. If this is the case, it is unlikely that the ancestor of *L. maccaigi* is similar to that of *L. curvatus*. Cluver (1971) noted that *L. maccaigi* is a relatively morphologically derived species of *Lystrosaurus*, and its sudden appearance in the fossil record without an obvious ancestor suggests that *L. maccaigi* dispersed into the area and did not originate from the South African Karoo Basin. A similar hypothesis has been proposed for the sudden appearance of other *Lystrosaurus* zone taxa such as *Prolacerta*, archosauriforms and rhynchosaurs (Reisz *et al.* 2000).

Liu *et al.* (2002) noted similarities between the Chinese species of *Lystrosaurus* and those found in

South Africa, but acknowledged that the Chinese *Lystrosaurus* taxonomy requires further examination before any comparisons between the two lineages can be made. Similarly, Ray (2005) also noted that several of the Indian *Lystrosaurus* species require further examination. Until this is done, no detailed comparisons between the Chinese, Indian and South African species or hypotheses regarding the origin of the genus *Lystrosaurus* can be made.

Although factors such as reduced carnivore populations, lifestyle adaptation or dispersal may have played a role in aiding the survival of *Lystrosaurus*, the most likely reason for the remarkable abundance of the Triassic *Lystrosaurus* is probably their feeding strategy and/or food preference, possibly for a *Dicroidium*-type flora or horsetails that were present (albeit as a minority) in the Permian. It is possible that *Lystrosaurus* occupied small *Dicroidium*-dominated niches during the Permian and once *Dicroidium* became the dominant flora during the Triassic, *L. murrayi* and *L. declivis* were able to increase in number and flourish. *Lystrosaurus maccaigi* and *L. curvatus* did not thrive during the Triassic possibly due to large size (in *L. maccaigi*) or differences in food preference.

### Implications for South African biostratigraphy

Traditionally, *Lystrosaurus* skeletal remains in the South African Karoo Supergroup have been used to indicate Triassic-aged strata (Rubidge 1995). However, the identification of an overlap between the ranges of *Lystrosaurus* and *Dicynodon* in the Karoo Basin (Hotton 1967; Kitching 1977; Smith 1995) and a *L. curvatus* skull from Permian strata in Zambia (King & Jenkins 1997) made it evident that *Lystrosaurus* could no longer be used as a solely Triassic indicator. Mixed *Dicynodon*-*Lystrosaurus* faunas have also been reported from the Guodikeng Formation of Xinjiang in China (Cheng 1993). It is now well established that the rocks of the lowermost portion of the range of *Lystrosaurus* are Upper Permian (MacLeod *et al.* 2000; Hancox & Rubidge 2001; Smith & Ward 2001).

The findings in this study agree with those of King & Jenkins (1997) that the genus *Lystrosaurus* should not be used as a sole indicator of Lower Triassic strata. However, we propose that individual *Lystrosaurus* species may still be used as biostratigraphical markers.

*L. maccaigi* is limited to the uppermost Permian Palingkloof Member and becomes extinct in the P-T boundary event beds. *L. curvatus* is also limited to the Palingkloof Member and its narrow range spans the P-T boundary such that it may be used as a

biostratigraphic indicator of the boundary interval. *L. murrayi* and *L. declivis* first appear in the upper Palingkloof Member and extend into the Katberg Formation. They are the only two *Lystrosaurus* species to occur in Early Triassic strata in abundance.

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