



Do specimens attributed to *Lystrosaurus murrayi* and *L. declivis* (Triassic Therapsida) represent one species?

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Lystrosaurus murrayi and *L. declivis* are two dicynodont (Therapsida, or mammal-like reptile) species commonly represented in Triassic deposits which are referred to as the 'Lystrosaurus Assemblage Zone' of the South African Karoo, postdating the Permo-Triassic boundary at 252 million years ago. The holotypes of these two species are curated in the Natural History Museum in London. Unfortunately, both are fragmentary (personal observation). Despite the fragmentary condition of the holotypes, Cluver¹, Cluver and King² and Brink³ accepted the view that at least two species of *Lystrosaurus* (*L. murrayi* and *L. declivis*) could be distinguished.

Lystrosaurus murrayi was first described by Thomas Henry Huxley in 1859. A year later, Richard Owen described a similar specimen as *L. declivis*. Recognising similarities in the two holotypes, Broom⁴ regarded Owen's specimen as 'probably' representing the same species as that which was described by Huxley in 1859. This view is consistent with those of Thackeray et al.⁵ By contrast, Botha-Brink et al.⁶ retain the view that two Triassic taxa of *Lystrosaurus* can be distinguished. In an impressive study, they examined as many as 97 crania attributed by them to *L. murrayi*, and 99 crania attributed to *L. declivis*.⁶

Two hypotheses

Thackeray's hypothesis addressed in this paper (H_1) is that specimens attributed to one or other of the two Triassic species are conspecific. H_{BB} is the alternative hypothesis (reflected for example by Botha-Brink et al.⁶) which is that two distinct Triassic species of *Lystrosaurus* can be recognised.

In order to test these two hypotheses, attention was given to the maximum basal skull length (BSL) dimensions in a total of 196 specimens of *Lystrosaurus* in Triassic deposits.⁶ Two other species of *Lystrosaurus* (*L. maccaigi* and *L. curvatus*), both of which occur in Permian deposits, were not considered here but deserve attention in future studies.

A summary of measurements obtained for BSL for specimens examined by Botha-Brink et al.⁶ and attributed by them to two Triassic species of *Lystrosaurus*, is given in Table 1. The results presented in Table 1 can be used to determine whether H_1 is supported.

Table 1: Comparison of basal skull length measurements for *Lystrosaurus murrayi* and *L. declivis*

	<i>Lystrosaurus murrayi</i>	<i>Lystrosaurus declivis</i>
Number of crania	97	99
Mean basal skull length (mm)	106.7	118.1
Standard deviation	31.1	30.0
Coefficient of variation	29.1	25.2

From Table 1, the following observations are made:

1. The mean BSL dimensions in specimens attributed to *L. murrayi* (106.7 mm) is only slightly smaller than that for specimens attributed to *L. declivis* (118.1 mm).
2. The means are not significantly different (Students *t*-test, $p=0.05$).
3. The standard deviations are almost identical (31.1 and 30.0 mm).
4. The coefficients of variation are almost identical (29.1 and 25.2).

Two important additional observations are:

5. Specimens attributed to the two species are both represented in the *Lystrosaurus* Assemblage Zone, with *L. declivis* apparently occurring only slightly later than *L. murrayi*, which apparently occurs first at the time of the Permo-Triassic boundary, 252 million years ago.⁶ Notably, the specimens are coeval in most of the *Lystrosaurus* Assemblage Zone.
6. Specimens attributed to *L. murrayi* and *L. declivis* both display an 'early breeding pattern', which is associated with relatively low percentages of large individuals in the *Lystrosaurus* assemblages in Triassic deposits.⁶

It can be concluded that H_1 is supported by all six of these observations.

Further analyses should be undertaken on measurements in addition to BSL to test H_1 , using a morphometric analysis of the kind developed by Thackeray et al.⁷, updated by Thackeray⁸ and discussed by Thackeray and Schrein⁹ in the context of a probabilistic definition of a species, related to sigma taxonomy^{10,11}, as opposed to

the general tendency to use alpha taxonomy¹² whereby specimens are classified in terms of discrete taxa, assuming clear boundaries between them.

The six observations presented here, in support of H_T, are consistent with the view held by Broom⁴ who stated that Owen's specimen attributed by him to *L. declivis* was 'probably' the same species represented by the holotype of *L. murrayi* described by Huxley in 1859. The six observations presented here are also consistent with those of Cosgriff et al.¹³

Thackeray et al.⁵ suggested that much of the variability in specimens attributed to *L. murrayi* and *L. declivis* may be a result of sexual dimorphism (associated in part with 'bossing' on crania above the orbits), or ontogeny within one species. It was indicated that bosses were likely to occur primarily in male specimens, as reflected by the following statement: 'Where supraorbital bosses are present, these occur mainly in relatively large individuals. We consider the presence of supraorbital bosses in almost 50% of large individuals and the absence of such bosses in about 50% of similar-sized individuals attributed to the same species, as a potential indication of differences between adult males and females'⁵.

If only one species of *Lystrosaurus* species is represented in Triassic deposits of the South African Karoo, as hypothesised through H_T, the nomen '*murrayi*' would have precedence over '*declivis*' according to rules of nomenclature, as Huxley's specimen was described in 1859, a year earlier than that reported formally by Owen. A possibility to be considered is that *L. murrayi* and *L. declivis* are components within a chronospecies, recognising also the importance of hybridisation in a diversity of modern taxa.⁹

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