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Alpha and sigma taxonomy of *Lystrosaurus murrayi* and *L. declivis*, Triassic dicynodonts (Therapsida) from the Karoo Basin, South Africa

Permo-Triassic dicynodont (Therapsid) fossils attributed to the genus *Lystrosaurus*[1] are known from the South African Karoo Basin, including two Triassic taxa referred to as *L. (Dicynodon) murrayi*[2] and *L. (Ptychognathus) declivis*[3]. Distinction of the two taxa has been recognised inter alia by Brink[4], Cluver and King[5], Botha and Smith[6], Grine et al.[7] and Botha-Brink et al.[8] However, in this instance, the appropriateness of alpha taxonomy may be questioned, recognising that boundaries between these species of *Lystrosaurus* are not necessarily clear, especially for specimens close to the time of divergence postdating the Permo-Triassic boundary, 252 million years ago. The question has arisen as to whether only one species occurred.[9] Thackeray[10] proposed the following hypotheses:

- H_T – that one species existed and
- H_{BB} – that there were two taxa, clearly distinct at the species level.

Both hypotheses need to be considered in the light of a statement by Camp[11]: 'traditional data were unable to distinguish between *L. murrayi* and *L. declivis* without overlapping measurements in regions where the geometric morphometric analyses indicated they differed most'. Irrespective of which statistical methods are used for taxonomic purposes, it is essential to have some kind of definition of a species that can be applied in palaeontological contexts, to address opposing views held by 'alpha taxonomists' who assume clear boundaries between species[12], and 'sigma taxonomists'[13-15] who do not.

Appeals have been made for the use of a statistical (probabilistic) definition of a species, using morphometric analyses whereby measurements of any Specimen A are compared (through least squares linear regression) with those of any Specimen B, and vice versa.[14-16] The standard error of the m coefficient (sem) in equations of the form $y=mx+c$ is calculated to reflect the degree of morphological similarity or dissimilarity when pairs of crania are compared. Notably, for large samples of conspecific modern taxa (used for reference purposes), there is a normal distribution of log-transformed sem values.[17]

In the case of conspecifics, a mean log sem value of -1.61 ± 0.1 has been calculated from anatomical measurements obtained from more than 70 modern taxa.[14,17] As it has been replicated from independent sets of data, for extinct and extant taxa[14, 18], it can be considered to reflect the typical degree of morphological variability in vertebrate taxa across evolutionary time and geographical space. As such, a mean log sem value (T) of -1.61 ± 0.1 has been proposed as a probabilistic definition of a species applicable in palaeontological contexts.[14] This morphometric approach has the potential to address taxonomic issues regarding Triassic specimens of *Lystrosaurus*. Examples are given here for selected specimens.

Ideally, complete and well-preserved holotypes for *L. murrayi* and *L. declivis* should be used for taxonomic purposes. Unfortunately, the holotypes for these two species described respectively by Huxley[2] and Owen[3], and curated at the Natural History Museum in London, are not sufficiently complete to allow detailed morphometric analyses based on many cranial dimensions. On the basis of morphology alone, Broom[19] questioned whether the (incomplete) holotype of *L. declivis*[3] was the same species represented by the (incomplete) holotype of *L. murrayi*[2]. In this study, cranial measurements of other (well-preserved, more complete) specimens attributed to either *L. murrayi* or *L. declivis* are analysed with a view to identifying potential neotypes on the basis of log sem statistics.

Materials

The specimens in this study are well-preserved crania of *Lystrosaurus*, selected on the basis of a relatively high number of measurable dimensions among the specimens classified by Camp[11] who indicates whether there is consensus between her identifications and those of others. These specimens are:

- NMNH 23349 attributed to *L. murrayi* (consensus identification), curated at the National Museum of Natural History, Smithsonian Institution, Washington.
- BMNH 36221 attributed to *L. declivis* (consensus identification), curated at the Natural History Museum in London.
- NMNH 12690, the identification of which is uncertain (*L. murrayi*/*declivis*), curated at the National Museum of Natural History, Smithsonian Institution, Washington.

These specimens are sufficiently well preserved to measure about 30 dimensions based on anatomical landmarks.[11] The 20 variables common to all three specimens are listed in Table 1.

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Table 1: Cranial dimensions used in this study. Reference numbers (with definitions) are those given by Camp[11]

Reference number	Definition
1	Basal cranial length
2	Anterior skull length
3	Posterior skull length
4	Pineal foramen length
5/6	Arc/chord length of frontal
7/8	Arc/chord length of nasal
9/10	Arc/chord length of premaxilla
12	Orbit height
13	Anterior-posterior snout length
14	Anterior-posterior length between anterior borders of orbit and nares
15	Dorsoventral height between ventral margins of orbit and nares
16	Dorsoventral snout height
17	Dorsoventral height of caniniform process
18	Minimum interorbital width
19	Maximum width across lateral margins of prefrontals
20	Minimum internarial width
21	Maximum width across lateral margins of caniniform processes
22	Maximum width across anterior quadrate foramina
23	Maximum anterior-posterior length of temporal fossae
24	Maximum width of temporal fossae
25	Minimum width of braincase
27	Maximum width across lateral margins of squamosals
39	Minimum medio-lateral width between tusks
42	Anterior-posterior length of interpterygoid fossa
43	Anterior-posterior length from interpterygoid fossa to occipital condyles
45	Anterior-posterior length from tip of snout to posterior margin of quadrate
46	Minimum medio-lateral width of pterygoids

Methods

Pairwise comparisons of cranial measurements are made using least squares linear regression analysis to calculate log sem values associated with specimens attributed to *L. murrayi* (a 'consensus' identification for NMNH 23349) and to *L. declivis* (a 'consensus' identification for BMNH 36221). Log sem values are also calculated for comparisons with NMNH 12690, the identification of which is not certain.

Results

Log sem values for pairwise comparisons are as follows, in increasing order:

- NMNH 12690 (*x*-axis) versus NMNH 23349 (*y*-axis)
  Log sem = **-1.474**
- NMNH 23349 (*x*-axis) versus NMNH 12690 (*y*-axis)
  Log sem = **-1.419**
- NMNH 12690 (*x*-axis) versus BMNH 36221 (*y*-axis)
  Log sem = **-1.104**
- NMNH 23349 (*x*-axis) versus BMNH 36221 (*y*-axis)
  Log sem = **-1.017**
- BMNH 36221 (*x*-axis) versus NMNH 23349 (*y*-axis)
  Log sem = **-1.014**
- BMNH 36221 (*x*-axis) versus NMNH 12690 (*y*-axis)
  Log sem = **-1.008**

Discussion and conclusions

Relatively low log sem values (ranging between -1.474 and -1.419) are obtained when NMNH 23349 (attributed to *L. murrayi*, 'consensus identification') is compared against NMNH 12690 (with uncertain status). In relation to the probabilistic definition of a species (T=-1.61±0.1), the two specimens may be conspecific because the mean log sem value of -1.446 falls within the 95% confidence limits for a species. However, this log sem value is near the upper limit, such that in terms of degrees of variation, it is relatively close to being different at a species level. This proximity is important in the context of a view that there may not be a distinct boundary between *L. murrayi* and *L. declivis*.

On the basis of an impressive sample of almost 200 crania of Triassic *Lystrosaurus* studied by Botha-Brink et al.[8], it has been demonstrated that the mean basal skull length of specimens attributed to *L. murrayi* is not significantly different from the mean basal skull length dimension of specimens attributed to *L. declivis*[10]. The mean values (and the associated standard deviations) are almost identical, as if one species was being sampled from the same kind of populations. In addition to the morphometric data presented here, based on as many as 20 variables per specimen, this result is relevant to the possibility that no distinct boundary exists between the two taxa at a species level, in the context of both temporal and spatial variability.

Do at least some crania represent different taxa at the level of a species? High log sem values (ranging between -1.020 and -1.014) are in fact obtained when BMNH 36221 (attributed to *L. declivis*, 'consensus' identification) is compared against NMNH 23349 (*L. murrayi*, 'consensus' identification). In relation to the probabilistic definition of a species (T = -1.61±0.1), these particular well-preserved specimens have a high probability of being different at a species level as the mean log sem value of -1.017 falls undoubtedly well outside the upper 95% confidence limit for a species. As such, these results for at least two particular specimens serve to refute the hypothesis (H_T) that all specimens attributed to either *L. declivis* or to *L. murrayi* represent only one species.[10] It could be concluded that *L. murrayi* is indeed represented by NMNH 23349, and that *L. declivis* is represented by BMNH 36221.

However, not all comparisons may necessarily reflect differences at a species level. In the case of closely related taxa, log sem values can serve to quantify *degrees* of similarity if not distinguish differences in *kind*. For instance, the relatively low mean log sem value of -1.446 obtained for the comparison between NMNH 12690 (previously identified uncertainly as *Lystrosaurus murray*/*declivis*) and NMNH 23349 indicates that the former specimen is relatively closer to *L. murrayi* (represented by NMNH 23349) than it is to *L. declivis* (represented by BMNH 36221), as a higher log sem value is obtained when the latter is compared to NMNH 12690.

Specimens such as NMNH 12690, whose identification has been uncertain (*L. murray/declivis*), may be those which fall within a spectrum of variability associated with two species which diverged close to the time of the Permo-Triassic boundary, 252 million years ago, but which may have hybridised. Hybridisation is recognised as a phenomenon that is much more common than previously thought.[15]

Because NMNH 23349 and BMNH 36221 are recognised here as being distinct at a species level for Triassic specimens of *Lystrosaurus*, on the basis of a probabilistic definition of a species (T=-1.61±0.1), and because they are sufficiently complete to allow many measurements per specimen, they are recommended as potential neotypes for *L. murrayi* and *L. declivis*, respectively.

When and if neotypes are formally described, they can be used as reference specimens to assess the *probability* that other Triassic fossils of *Lystrosaurus* do or do not belong to *L. murrayi* or *L. declivis*. The examples given above relate to sigma taxonomy[13-15], where sigma is the Greek letter Σ (S for spectrum), as opposed to alpha taxonomy[12] which assumes clear boundaries between species.

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