Phylogeography of *Scarabaeus (Pachysoma)* Macleay (Scarabaeidae: Scarabaeinae).

By

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To David, Gillian, Michael and Ian with love……

"Do molecules and morphology give the same picture of the history of life, or two or more distorted views of the same picture, or two quite different pictures?"
Patterson (1988)

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Abstract

Scarabaeus (Pachysoma) consists of 13 flightless dung beetle species endemic to the arid west coast of southern Africa. *Scarabaeus (Pachysoma)* are unique in their feeding and foraging habits, in that they randomly search for dry dung/detritus which, when found, is dragged forwards, and buried in a pre-constructed holding chamber, as opposed to the convention of rolling it backwards. This action is repeated to provision the chamber after which the nest is expanded to below the moisture line to allow the stored food to re-hydrate. Poor vagility, taxonomic contention - seen in *Scarabaeus* taxonomy - and conservation concern, made *Scarabaeus (Pachysoma)* an ideal group of beetles to study both the phylogenetics and potential influences that anthropogenic and environmental changes have had on structuring the species and populations thereof.

Both molecular and morphological data were used as individual datasets and combined in a total evidence approach. Biogeographic inferences were made based on recent detailed Namib biogeography and the ages of the species were estimated using the molecular clock method. A phylogeographic study was done on three of the species of *Scarabaeus (Pachysoma)* – *S. (P.) hippocrates*, *S. (P.) gariepinus* and *S. (P.) denticollis* - that had previously shown south-north morphological clinal variation. Lastly, an attempt was made to isolate microsatellite loci for *Scarabaeus*, in the hope of characterising genetic diversity within and between populations of the same species.

Scarabaeus (*Pachysoma)* was found to be monophyletic within *Scarabaeus* and was therefore classified as a derived subgenus thereof. Morphologically *Scarabaeus (Pachysoma)* was shown to have 13 species while at a molecular level strong resolution for 11 of the 13

was obtained. *S. (P.) hippocrates* and *S. (P.) glentoni* formed a species complex the hippocrates/glentoni complex. The combined phylogenetic tree showed good overall support for all 13 species. Both the morphological and molecular data partition phylogenies show congruence with the combined phylogeny, lending support for combining datasets.

Scarabaeus (Pachysoma) appears to have arisen 2.9 million years ago. The formation of advective fog is a consistent water source for Desert dwelling organisms and appears to be associated with *Scarabaeus (Pachysoma)* radiation into inhospitable areas. Analysis of gene flow revealed large amounts of south-north movement, lending support for movement of psammophilous taxa with their substratum, the barchan dune.

Population demographics of the three species, *S. (P.) hippocrates, S. (P.) gariepinus* and *S. (P.) denticollis*, chosen for this study differed greatly except in areas of geographic similarity. Major rivers appear to have acted as gene barriers, allowing for distinct genetic entities to be identified within the three species. Phylogeographic partitioning was supported by an AMOVA analysis. All three species were shown to have undergone historical population expansion dating back to the Pleistocene era. Nested Clade Analysis indicated that allopatric speciation; isolation by distance and continuous range expansion could be the factors having affected overall population structure. Recent events show that human induced factors, environmental barriers and reduced vagility have influenced the species population structure.

Four potentially polymorphic loci were isolated for *Scarabaeus* using the FIASCO protocol. Identification of at least one additional locus is needed in order to obtain statistical significance for future studies directed at uncovering recent population dynamics.

Keywords: *Scarabaeus*, Cytochrome oxidase I, Morphology, Phylogeny, Combined, Phylogeography, Namib Desert, Total Evidence, Microsatellites, Coleoptera

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Disclaimer

The present study is a continuation of a study done by James du Gueslin Harrison (1999), all the morphological data was provided by him. Each of the chapters within this study, except for Chapter 5, have been written up in paper format for different journals, hence the format for each chapter may differ slightly.

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