CHAPTER 4

CONCLUSION AND SUMMARY

The cladistic analysis of *Scarabaeus (Pachysoma)* MacLeay reveals that *Pachysoma* represents a derived clade of the large and variable genus *Scarabaeus* Linnaeus. Desert animals are renowned for exhibiting an array of behavioural, physiological and morphological adaptations to their environment (Louw and Seely 1982, Cloudsley-Thompson 1983, 1991, Wilson 1989, Costa 1995, Somme 1995, Henschel 1997). Thus when one considers the selective effect of an arid environment, it is not surprising that *S. (Pachysoma)* evolved from a *Scarabaeus/Mnematium*-like ancestor adapted to the specific environmental conditions of the Namib Desert. Their dragging foraging strategy, diet of dry dung and detritus, reduced mesocoxal distance and well-developed psammophily and aptery are all indications of the biological and morphological changes that *S. (Pachysoma)* species have undergone. This specialisation is also evident in the flying genera of the tribe Scarabaeini that appear to have radiated into other feeding niches. These include *Kheper*, *Drepanopodus* and *Scarabaeus (Scarabaeus)* as predominately wet dung feeders; *Scarabaeus (Scarabaeolus)* as wet dung and carrion feeders; *Sceliages* as millipede feeders and *Pachylomerus* with a mixed diet of wet dung, fruit and carrion.

The morphological ancestor of *S. (Pachysoma)* (see figure 1 in chapter 2), undoubtedly similar to a *Mnematium* species, must have inhabited arid areas. *Mnematium*, unlike *S. (Pachysoma)*, has not undergone such extensive morphological and biological adaptation to their xeric environment. This is evident from their mouthpart morphology, intermediate between dry and wet dung feeding. Additionally, *Mnematium* species show slight psammophilous adaptation (i.e. long leg setae and spatulate mesospurs as present in *S. (Pachysoma)*), and the degree of morphological reduction is slight. For example, degree of brachyptery varies among *Mnematium cancer, Mnematium silenus* and *Mnematium ritchiei* while in *S. (Pachysoma)* species it is uniformly advanced.

The polyphyletic origin of wing loss (figure 1 chapter 2) displayed in the tree topology supports hypotheses proposed by Holm and Scholtz (1979) and Mostert and Holm (1982), that aptery has evolved more than once within the Scarabaeini. Consequently there is no justification for the Pachysomina subtribe composed of four flightless groups, *Pachysoma, Neopachysoma, Mnematium* and *Neomnematium* (see Ferreira 1953). This is evident by the size of *Mnematium* wing buds in *M. ritchiei* (see Zunino 1984), semi-contiguous mesocoxae in *M. silenus* and presence of a mesosternal ridge in *M. ritchiei* and *M. silenus*. Based on figure 1 in chapter 2, elevating *Pachysoma* to generic level would make the genus *Scarabaeus* paraphyletic. Unfortunately, *Scarabaeus* is still paraphyletic with the continued recognition of *Kheper, Drepanopodus* and *Sceliages*. However, for practical purposes *Pachysoma* is proposed as a subgenus of *Scarabaeus*. The inclusion of *Scarabaeus (Scarabaeolus) scholtzi* and *M. silenus* (*sensu* Mostert and Holm 1982) in the subgenus *Scarabaeolus* (*sensu* Balthasar 1965) makes *Mnematium* polyphyletic and is thus regarded as synonymous with *Scarabaeus*. Lacking

synapomorphies for *Neomnematium* and *Neopachysoma*, these genera are included as synonyms with *Scarabaeus (Scarabaeus)* and *Scarabaeus (Pachysoma)*, respectively. It is beyond the scope of this study to alter the generic status of *Kheper*, *Sceliages* and *Drepanopodus*, but their retention as valid genera makes *Scarabaeus* paraphyletic, and a system of subgenera to include them within *Scarabaeus* is thus suggested to future workers.

Five modes of food relocation have been recorded in the Scarabaeini. The four main clades of the cladogram (figure 1 chapter 2) include one or more of these relocation strategies. Of interest is that the 'super-telecoprid' *Kheper*, which only roll, is apical, while taxa with more than one form of relocation behaviour are more basal in the tree (e.g. *Pachylomerus*, *Scarabaeus galenus* and *Scarabaeus catenatus*), while the *Pachysoma* clade represents derived draggers. A morphological change associated with aptery is a reduction in the mesocoxal distance (see Scholtz 1981). However, taxa with reduced mesocoxal distance also have aberrant or multi-strategy relocation behaviours. Thus, there may be an association between the mesocoxal distance and the predominant mode of foraging.

A sandy substrate is required by *S. (Pachysoma)* species to rehydrate their dry food, but flying taxa with aberrant relocation strategies (*Pachysoma* which drag food forward can also be classified as aberrant relocators in the telecoprid sense) also prefer a sandy substrate (see Sato 1997).

Scarabaeus (Pachysoma) are restricted to the semiarid to arid coastal sands of southern Africa (see figure 1 chapter 3). The remaining flightless Scarabaeini have also been recorded from similar xeric areas (see figure 2 chapter 3), suggesting an association between wing loss and aridity in the Scarabaeini.

The subgenus contains 13 species, of which 2 are described as new. Types (lectotype and paralectotypes) are designated and rediscovered types listed in the abstract of chapter 3 and discussed in that same chapter. The revision illustrates the clinal morphology of most *S. (Pachysoma)* species. The large number of *Scarabaeus (Pachysoma) hippocrates* specimens examined, covering most of their range, is an especially good example of the clinal gradation of morphology over their distribution. Unless detected, this can lead to misinterpretations of species boundaries. For example, the proposed species, *Neopachysoma penrithae* Zunino and subspecies *Scarabaeus (P.) denticollis penrithae*, represent the southern extreme of a clinal population when sufficient material is available for study (see *S. (P.) denticollis* comments in chapter 3). *Scarabaeus (Pachysoma) glentoni* and *Scarabaeus (Pachysoma) endroedyi* appear to represent a vicariance speciation event, with the Olifants River as the boundary separating these species and two populations of *S. (P.) hippocrates*. *S. (P.) glentoni* is especially interesting as this species hardly differs from *S. (P.) hippocrates* externally, but has male genitalia that are strikingly different (see figures 58a,b,c and 59a,b,c in chapter 3).

To date, nine of the 13 species of *S. (Pachysoma)* have been observed only dragging dry dung and detritus forward (see species' biology in chapter 3). Although, there is a single record of *Scarabaeus (Pachysoma) gariepinus* making and rolling a dung ball from fresh dung (Mostert and Holm 1982). Howeve[illegible] f field work was this observed,

even when fresh dung was offerred. However, the foraging strategies as exbited by *S. galenus* (Tribe 1976, Halffter and Halffter 1989, Doube 1990, Ybarrondo and Heinrich 1996) and *S. catenatus* (Sato 1997, 1998) suggest that modification of ball rolling could lead to dragging.

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OPSOMMING

Die filogenetiese geldigheid van *Pachysoma* MacLeay, 1821, word kladisties ondersoek. Die kladistiese analise van 64 volwasse karakters van 37 taksa sluit wat alle genera van die Scarabaeini (behalwe die monotipiese *Madateuchus* Paulian, 1953) insluit, dui aan dat sommige huidig erkende genera (nl. *Sceliages* Westwood, 1837; *Kheper* Janssens, 1940; en *Drepanopodus* Janssens, 1940) 'n polifiletiese oorsprong het. *Pachysoma* behels 'n monofiletiese klade van hoogs gevorderde ('derived') *Scarabaeus* Linnaeus, 1758. Om nomenklaturale stabiliteit in die Scarabaeini te bevorder is dit wenslik om *Pachysoma* as 'n subgenus van 'n uitgebreide genus *Scarabaeus* Linnaeus, 1758 te beskou. *Neopachysoma* Ferreira, 1953; *Mnematium* MacLeay, 1821 en *Neomnematium* Janssens, 1938 word behou as sinonieme van *Scarabaeus sensu latu*. Die unieke biologie van *Pachysoma* word geïnterperteer in die lig van aanpassings tot droë toestande, en is deels afkomstig van balrolgedrag en voeding op nat mis. Daar word gepostuleer dat die verdorring van die Namibwoestyn die evolusie van *Pachysoma* vanaf 'n *Scarabaeus*-tipe voorouer geïnisiëer het, terwyl duinbewegings hul huidige verspreiding verklaar. Dit blyk dat die evolusie van vluglosheid bemiddel word deur 'n verwantskap tussen droë mis- en detritusvoeding, uitsonderlike hervestigingstrategieë, en die teenwoordigheid in droë, sanderige habitatte. Die evolusionêre geskiedenis van *Pachysoma* word bespreek aan die hand van die filogenetiese analise, geografiese verspreidings, biologie, substraat, en voedselversamelingsstrategie.

Die subgenus *Scarabaeus (Pachysoma)* MacLeay word hersien. Al 13 spesies van die subgenus is endemies tot die weskus van suidelike Afrika. 'n Sleutel tot al die spesies is saamgestel en hul verspreidings is gekarteer. Twee nuwe spesies, *Scarabaeus (Pachysoma) endroedyi* en *Scarabaeus (Pachysoma) glentoni*, word van die suid-westelike Kaap Provinsie beskryf. Die subspesie *S. (P.) denticollis penrithae* (Zunino) word gesinoniemiseer met *S. (P.) denticollis denticollis* (Péringuey). Die sinonimie van *S. (P.) hessei* (Ferreira) met *S. (P.) hippocrates* (MacLeay) word bevestig. *Scarabaeus (P.) valeflorae* (Ferreira), voorheen gereken 'n sinoniem van *S. (P.) schinzi* (Fairmaire) word herstel as 'n geldige spesie. Die vermiste tipereeks van *S. (P.) hessei* (Ferreira) word nagespeur. 'n Lektotipe word aangewys vir *S. (P.) aesculapius* Olivier, en drie paralektotipes word aangewys vir *S. (P.) marginatus* (Péringuey). Aantekeninge oor die tipereekse, verspreidingsrekords, morfologiese variasie en bekende biologie van al die vluglose Scarabaeini word gegee. 'n Oorsiglys van die geldige spesies en die sinonieme van *Pachysoma, Neopachysoma, Mnematium* en *Neomnematium* word ingesluit.

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