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Dung beetle (*Scarabaeus* (*Pachysoma*)) biology and immature stages: reversal to ancestral states under desert conditions (Coleoptera: Scarabaeidae)?

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The unique feeding biology of the unusual flightless Namib Desert dung beetle species belonging to *Scarabaeus* (*Pachysoma*) MacLeay (Scarabaeidae: Scarabaeinae) has been studied in the past but in this report we document breeding biology, larval feeding and immature morphology for the first time. Females provision burrows with fragments of dry herbivore dung and detritus, in which the larvae develop and on which they feed. This is a novel deviation, and a probable reversal to the ancestral state, from the obligatory brood ball constructed from wet dung in which scarab larvae usually develop. The free-living larvae and pupae have several unique attributes that distinguish them from relatives that develop within the confines of a brood ball and provide additional support for monophyly of the group. Many of these also appear as reversals to a probable ancestral condition. Unique larval characters include a left mandible with two teeth, the absence of a 'coprine' hump, small spiracles, and two- or indistinctly three-segmented antennae. Those unique to the pupa are the presence of peculiar prothoracic projections, the absence of lateral tergal supporting projections on the abdomen, and the perpendicular elytra and wings relative to the median bodyline. © 2004 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2004, **83**, 453–460.

ADDITIONAL KEYWORDS: ball-rollers – flightless – free-living – monophyletic – Namib Desert – unique.

INTRODUCTION

The extraordinary evolutionary success of dung beetles (Scarabaeidae: Scarabaeinae) is readily explained by a variety of behavioural, morphological and physiological adaptations (Halffter & Matthews, 1966; Halffter & Edmonds, 1982; Hanski & Cambefort, 1991). Some of the more obvious ones are the following. Adult dung beetles feed on minute particles of dung filtered from the liquid portion of the food source (Holter, Scholtz & Wardhaugh, 2002). Because wet dung is an ephemeral resource, the ability to fly and to locate fresh dung quickly is critical. Furthermore, most species have evolved specialized food relocation behaviour, i.e. the ability to move dung quickly from competitors by employing different relocation strategies, for example, making and rolling dung balls (see Doube, 1990, for a review and details of the different functional groups). Typically, the species dig underground burrows that they provide with food for the larvae, and in some cases the female remains with the brood until maturity. This nidification behaviour and subsequent parental care entail high investment by the adults (especially the female). In these cases the brood mass is kept free of pathogenic fungi (Halffter & Matthews, 1966); in others the larva is provisioned with food as it grows (e.g. *Cephalodesmius*; Monteith & Storey, 1981). In all members of the Scarabaeinae there is extreme reduction in fecundity – species have only one ovary (Ritcher & Baker, 1974; Halffter & Edmonds, 1982) and the larger ball-rollers may produce fewer than 20 eggs per female, and often only one or two per season (Hanski & Cambefort, 1991; Sato, 1997). This typically results in an extreme K-selection reproductive strategy.

Dung beetle larvae are characterized by a suite of morphological adaptations to facilitate living and feeding within a confined space such as a brood ball or

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dung plug (Halffter & Matthews, 1966; Edmonds & Halffter, 1978). Some structures are reduced in comparison with free-living scarabaeid larvae such as those of Aphodiinae, Melolonthinae, Rutelinae and Dynastinae. These include sparse body and rastal setae, reduced and barely functional legs and weakly developed mouthparts. Other special adaptations include enlargement of the dorsum of all or some of the first six abdominal segments to form the 'coprine hump' that accommodates the enlarged hind gut, which functions as a fermentation chamber, a flattened anal abdominal area (Fabre's trowel), and well-developed spiracles (adapted from Halffter & Matthews, 1966).

Of the five currently recognized Scarabaeini genera (Mostert & Scholtz, 1986; Harrison & Philips, 2003) only larvae of *Scarabaeus* (Ronchetti, 1949; Medvedev & Medvedev, 1958; Oberholzer, 1959; Paulian & Lumaret, 1975; Edmonds & Halffter, 1978), *Kheper* (Palestrini & Barbero, 1992) and *Sceliages* (Forgie, Grebennikov & Scholtz, 2002) have been described. The most recent reviews of dung beetle larvae include those of Edmonds & Halffter (1972, 1978) and the comprehensive, but broader work of Ritcher (1945, 1966).

Scarabaeus (*Pachysoma*) MacLeay, 1821, includes 13 species of flightless dung beetles endemic to the sandy coastal strip of desert of south-western Africa stretching from Cape Town (33°55′S, 18°25′E) in South Africa to Walvis Bay (22°58′S, 14°30′E) in Namibia (Holm & Scholtz, 1979; Harrison, Scholtz & Chown, 2003). The group is unique in the Scarabaeini because all species are flightless (see Scholtz, 2000, for a review on flightlessness in desert scarabaeoids) and feed and breed only on dry food (e.g. dung pellets and detritus), while related genera *Kheper*, *Scarabaeus* (Halffter & Edmonds, 1982; Sato & Imamori, 1986a, b, 1987, 1988; Edwards & Aschenborn, 1988), *Pachylomerus*, *Drepanopodus* (Tribe, 1976; Mostert & Scholtz, 1986) and *Sceliages* (Forgie *et al*., 2002) feed on wet food (e.g. fresh dung and carrion). Typically, food selection and foraging behaviour in *S*. (*Pachysoma*) species is as follows (Scholtz, 1989). Beetles walk or run around in seemingly random fashion searching for dry dung pellets or plant detritus. Once food is located a holding-chamber is excavated. Food is then collected, held by the hind legs and dragged forward to the holding-chamber. This is repeated numerous times, until sufficient food has been collected. Foraging behaviour requires accurate navigation to enable the beetle to locate its burrow repeatedly, something it achieves using polarized light as a cue to aid the navigation (Dacke *et al*., 2002). After sufficient food has been collected the burrow is dug deeper, ending in a second chamber below the moisture line in the soil. The food is then moved from the holding-chamber to the feeding or nesting-chamber. Finally the nest entrance and tunnel are blocked with sand. This foraging strategy differs significantly from flying members of the tribe Scarabaeini, which all form a ball at a fresh dung source (or pieces of millipede in the case of *Sceliages*), roll it backwards (butt it forwards in *Sceliages*) to a suitable site where it is buried and fed on, or bred in, i.e. typical telecoprid behaviour (Doube, 1990; Forgie *et al*., 2002).

This led us to the question of how *S. (Pachysoma)* species make a brood ball that is otherwise obligatory for ball-rollers, from the fragments of dry dung and detritus they collect. We also report the first known case of a non-encapsulated mode of life (i.e. 'free-living') in *S. (Pachysoma)* larvae, which was previously unknown for the group, the tribe Scarabaeini, and for ball-rolling dung beetles as a whole. Furthermore, we provide the first description of mature larvae and pupae of two, and one *S. (Pachysoma)*, species, respectively. Their unique morphological characters are highlighted and the phylogenetic affinities of *S. (Pachysoma)* within the tribe Scarabaeini based on larval morphology are discussed.

MATERIAL AND METHODS

COLLECTION AND REARING

Adults of three species, *S. (Pachysoma) striatus* (Castelnau, 1840), *S. (Pachysoma) hippocrates* (MacLeay, 1821), and *S. (Pachysoma) gariepinus* (Ferreira, 1953), were collected from coastal South Africa and Namibia (see material examined for locality and dates). Pairs excavated from their burrows were set up in 20 L round (31.0 × 33.5 cm) buckets or 5 L square (285 × 210 × 210 mm) bins in sand from the collection site. Field-collected dry dung pellets (mainly sheep) and wind-accumulated detritus were fed to the beetles. Three pairs of each species were used in 1996 and five pairs of each in 1998. Food was provided *ad libitum* and about 100 mL of water were sprayed onto the sand weekly for the three-month rearing period (approximately October to December). All terraria were maintained indoors at room temperature (about 25 °C) with a natural day and night cycle (about 14 : 10 h).

The specimens are deposited in the University of Pretoria (UPSA) and Transvaal Museum (TMSA) collections as specified below.

Scarabaeus (Pachysoma) striatus (Castelnau, 1840)
Three (probably) third-instar larvae (two partly damaged), two pupae (one severely damaged). Material reared *ex ovo* (the date from collection to preservation of larva is included) from adults collected in South Africa: Namaqualand, Strand Fontein 499, Bitter

River dunes, 30°33′01S 17°26′21E, 28.viii.1996–24.i.1997, site 71, interdune slack, white/red sand, leg. det. J. du G. Harrison (3 TMSA); Sand Kop 322, 29°39′55S 17°10′34E, 9.ix.1998–2.xii.1998, site 113, vegetated dune, red sand, leg. det. C.H. Scholtz (2 UPSA).

S. (P.) gariepinus (Ferreira, 1953)
Three (probably) third-instar larvae (one damaged). Material reared *ex ovo* (the date from collection to preservation of larva is given) from adults collected in South Africa: Namaqualand, Farm 600, Bakenskop, 28°57′11S 17°01′59E, 26.x.1996–28.i.1997, leg., det. J. du G. Harrison, site 112, vegetated dune, red sand (1 TMSA); Bontekoe 197, 29°33′34S 17°19′44E, 13.xi.1996–23.i.1997, leg., det. J. du G. Harrison, site 116, Buffels River valley, coarse river sand (1 TMSA); Namibia: Hohenfels, 28°30′S 16°37′E, 8.ix.1998–3.xii.1998, leg., det. C.H.Scholtz, dunes (1 TMSA).

PRESERVATION AND DISSECTION

Larvae and pupae were placed into boiling water, left for three minutes, then preserved in 70% ethanol. Two larvae of each species were cleared in a solution of hot KOH before disarticulation. Dissected sections were mounted in glycerol and studied on microscope slides under dissecting and compound microscopes (magnifying up to 600×). Pupae were studied intact in 70% ethanol under a dissecting microscope. Morphological terms used here follow Böving (1936), Ritcher (1966), Edmonds & Halffter (1978; for numeration see pp. 308–310) and Lawrence (1991: 147–177).

Edmonds & Halffter (1978) provided detailed diagnoses and descriptions of morphological characters shared by all Scarabaeinae larvae known to them. *S. (Pachysoma)* larvae share the majority of these characters. Consequently, in the larval descriptions that follow only characters whose states differ from those previously described are indicated (numeration follows Edmonds & Halffter, 1978).

RESULTS

Three larvae each of *S. (P.) gariepinus* and *S. (P.) striatus,* and two pupae of *S. (P.) striatus* were reared. *S. (P.) hippocrates* did not breed. For both species reared there was no evidence of a brood ball or pear to contain the larvae that were in the sand close to loose nest material consisting of larval or adult frass and/or a decomposed plug of dry dung and detritus. The two *S. (P.) striatus* pupae were on their backs in the sand, surrounded by a fragile case constructed from sand grains cemented together. Adults were not close to either larvae or pupae.

DESCRIPTION OF LARVAE

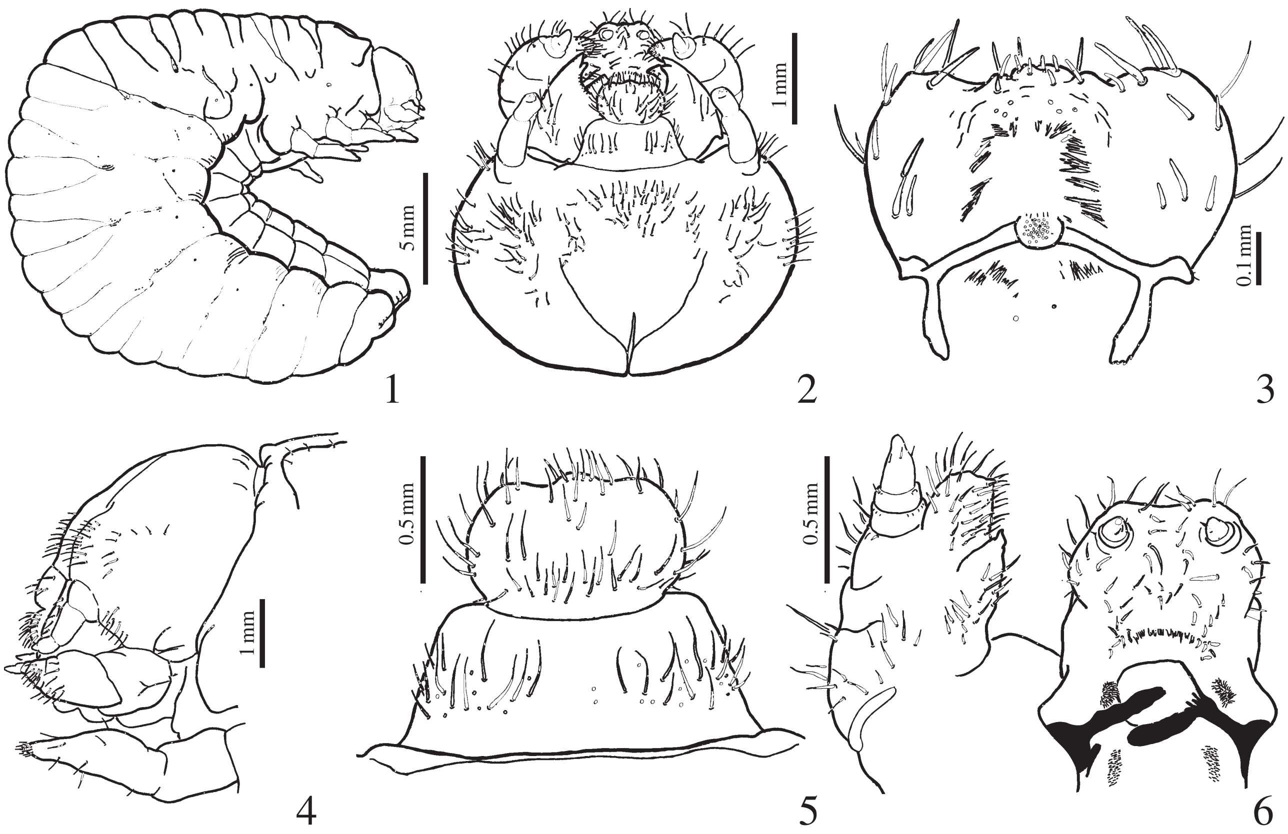
The larvae share the diagnostic Scarabaeinae larval characters that were described by Edmonds & Halffter (1978), except for the following: (1) diameter of abdominal segments three to five gradually greater than those of anterior body segments and thus body not appearing strongly expanded dorsally ('humped'), i.e. coprine hump reduced (Fig. 1); (7) tormae united mesially (Fig. 3); (8) mesophoba consisting of two separate groups of cuticular spines on left and right sides of haptolachus (Fig. 3); (9) incisor lobes of both mandibles with two apical teeth (Figs 7–12); (10) lateral area of mandible (scrobis) with about ten setae (Figs 7–12); (13) uncus of lacinia not toothed basally (Fig. 6); (14) dorsal surface of stipes with irregular row of about three to five conical teeth along basal margin ('stridulatory teeth') or these teeth completely lacking (Fig. 6); (15) hypopharyngeal area with relatively small group of fine setae left and right form two dissimilar hypopharyngeal sclerites ('oncyli') (Fig. 6); (16) antenna two- or indistinctly three-segmented (Figs 2, 4, 19, 20, 25, 26), (17) apex of second antennomere with flat sensory area (Figs 13, 14, 19, 20, 25); (19) thorax with two pairs of spiracles, metathoracic spiracles vestigial (Fig. 1); all functional spiracles markedly reduced in size compared to those of other Scarabaeinae larvae; (21) legs two- or indistinctly three-segmented (Figs 17, 18); (22) apex of each leg with (Figs 27, 28) or without (Figs 15, 16) papilla and distinct pair of terminal setae; apex of each leg with 18–20 similar setae (Figs 15, 16); (25) venter of last abdominal segment without rows or patches of setae (Fig. 22).

Larvae of *S. (Pachysoma) striatus* and *S. (P.) gariepinus* can be distinguished as follows:

– Antenna two-segmented with minute remnant of segment III at apex of antennomere II (Figs 19, 20); dorsal surface of stipes without conical teeth along basal margin ('stridulatory' teeth; Fig. 6); small lateral group of setae on hypopharynx as in Figure 6; apices of legs without papillae and distinct pair of terminal setae (Figs 15, 16); head width 2.08–2.16 mm (*N* = 3) – *S. (P.) striatus* (Castelnau).
–* Antenna indistinctly three-segmented (Figs 25, 26); dorsal surface of stipes with three-to-five conical teeth along basal margin ('stridulatory teeth'); small lateral group of setae on hypopharynx about twice longer than in Fig. 6; apices of legs with papillae and distinct pair of terminal setae (Figs 27, 28); head width 2.39–2.54 mm (*N* = 3) – *S. (P.) gariepinus* (Ferreira).

DESCRIPTION OF PUPA

Pupa exarate (Figs 22, 23) is creamy-white. Both elytra and fully developed hind wings are present; elytra are relatively short, not covering hind tibiae,



Figures 1–6. Mature larvae of *Scarabaeus* (*Pachysoma*). Fig. 1, *S.* (*P.) striatus*, habitus, lateral view; Fig. 2, *S.* (*P.) striatus*, head, dorsal view; Fig. 3, *S.* (*P.) striatus*, epipharynx, ventral view; Fig. 4, *S.* (*P.) gariepinus*, head with part of prothorax, lateral view; Fig. 5, (*S*). (*P.) striatus*, labrum and clypeus, dorsal view; Fig. 6, *S.* (*P.) striatus*, left maxilla and labium, dorsal view.

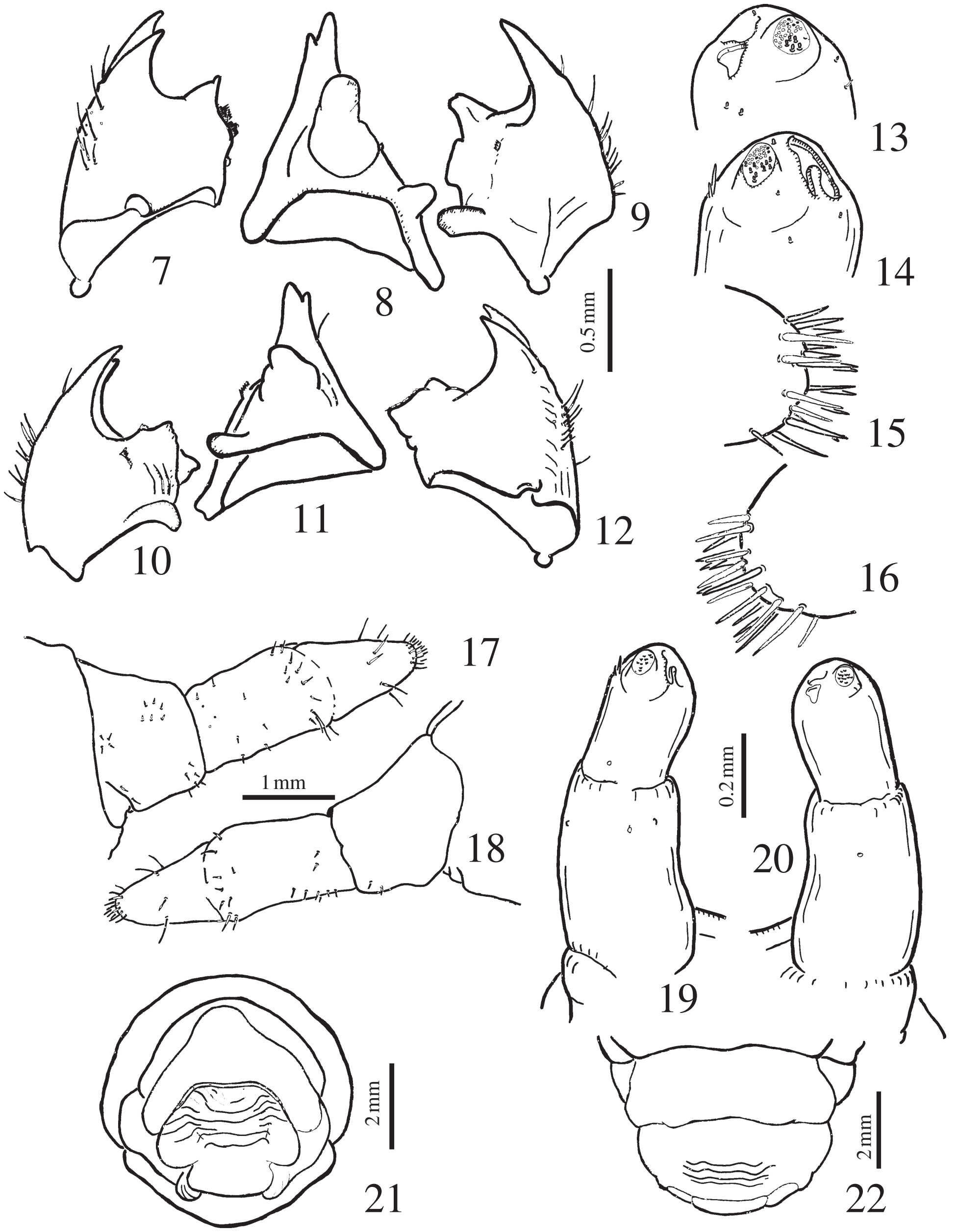
directed nearly perpendicular to the body. Lateral tergal projections are absent. Dorsal tergal projections are weakly developed and presented as medial tergal ridges with short projections at the middle. Pteronotal projections on meso- and metanotum are absent. Paired caudal projections are present and weakly developed. The pronotal supporting system consists of three rounded projections on the dorsal surface of the prothorax, located in small depressions (Fig. 23). The abdomen has eight spiracles on each side of segments I-VII; those on segments I-III are larger and darker, apparently functional, while the remaining spiracles appear nonfunctional.

DISCUSSION

In their review of dung beetle larvae (Scarabaeidae: Scarabaeinae) Edmonds & Halffter (1978) characterized *Scarabaeus* larvae as follows: (1) sensory area of third antennomere flat; (2) chaetopariae each with six-to-eight setae; (3) lateral area of mandibles with four-to-seven setae (one in *S. radama*); (4) uncus of lacinia not toothed (observed in *S. affinis* only); (5) pronotum with distinct shields bearing anterior angles; (6) legs not terminated by papillae; (7) third abdominal segment lacking dosomedian prominence; (8) raster indistinct, venter of last abdominal segment with few, minute setae (visible only under high magnification); (9) tormae of labrum not united mesially.

The larvae of the two species described here share all of the above characteristics with *Scarabaeus sensu stricto*, but differences include the following characters that probably represent autapomorphies for the subgenus. The left mandible has two apical teeth, as opposed to three in its relatives, the evenly curved body is without the very characteristic coprine hump, the spiracles are relatively small, and the antennae are two- or indistinctly three-segmented. *Scarabaeus s.s.* larvae have distinctly three-segmented antennae.

Pupae of *S. (P.) striatus* also possess three unique and apparently apomorphic characters. The lateral tergal supporting projections that are present on the abdomen of *Scarabaeus sensu stricto* pupae are absent in *Scarabaeus* (*Pachysoma*) pupae. The latter also

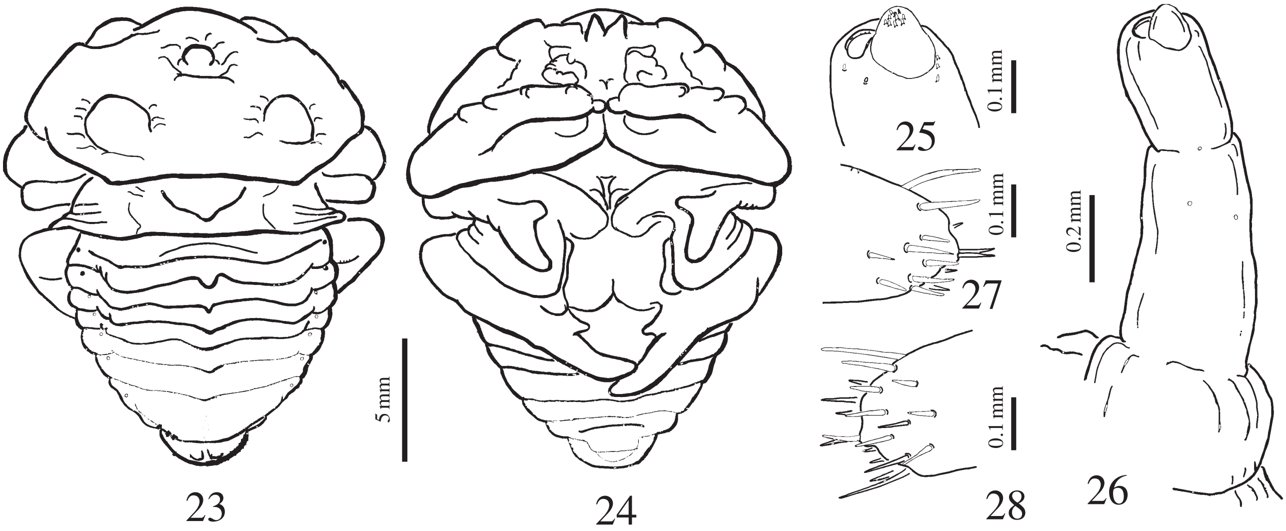


Figures 7–22. Mature larvae of *Scarabaeus* (*Pachysoma*) *striatus*, details. Figs 7–9, left mandible, dorsal, mesial and ventral views, respectively; Figs 10–12, right mandible, ventral, mesial and dorsal views, respectively; Figs 13, 14, apices on left and right antennae, respectively, dorsal view; Figs 15, 16, apices of left foreleg, anterior and posterior views, respectively; Figs 17, 18, left foreleg, anterior and posterior views, respectively; Figs 19, 20, left and right antennae, respectively, dorsal view; Fig. 21, abdominal segment X and IX, posterior view; Fig. 22, abdominal segment X and IX, ventral view.

have peculiar prothoracic projections that are absent in the former. In *Scarabaeus* (*Pachysoma*) pupae the elytra and hind wings lie perpendicular to the median bodyline whereas they are roughly parallel in *Scarabaeus s.s.* pupae.

These seven characters give strong support to regard *S. (Pachysoma)* as a monophyletic lineage. An independent adult morphological phylogeny (Harrison & Philips, 2003) that included all of the Scarabaeini genera and subgenera also found *S.* (*Pachysoma*) to be a monophyletic clade, sister to *Scarabaeus*.

These characters in *S. (Pachysoma)* immatures appear to represent reductions or reversals to an ancestral way of life and may be interpreted as adap-



Figures 23–28. Immature stages of *Scarabaeus* (*Pachysoma*) spp. Figs 23, 24: *S.* (*P.) striatus*, pupa, habitus, dorsal and ventral views, respectively; Figs 25–28: *S.* (*P.) gariepinus*, mature larva; Fig. 25: antennomere three and apex of antennomere two with sensory area, right antenna, dorsal; Fig. 26, right antennal palpifer and antenna, dorsal; Figs 27, 28, apices of left foreleg, anterior and posterior views, respectively.

tations to a free-living lifestyle necessitated by the harsh environment. A reduced number of antennal segments is presumably still adequate for tactile movements in the soil. Maxillary stridulatory teeth, which are thought to be used in communication with the adult female outside the ball (Edmonds & Halffter, 1978), may become reduced in the absence of the need to communicate. The stiff abdominal setae, presumably used to aid locomotion in the ball, are lost in the free-living larvae. Large spiracles, which are apparently necessary to enable respiration in the oxygen-poor environment of the brood-ball, are superfluous in the free-living situation. Smaller spiracles may also be more efficient at excluding fine soil particles that are largely absent in a ball, and may restrict the loss of moisture from the trachea, something that is more likely to occur in loose sand rather than in the confines of a ball. The coprine hump, which is so characteristic of larvae living in brood-balls, and is thought to aid locomotion inside the ball, is lost in free-living larvae, as is the highly modified lobular anal segment (Fabre's trowel) that is used for plastering faeces on the cavity wall in the ball, and in ball-repair (Edmonds & Halffter, 1978).

The only other scarabaeine dung beetle known to us that has a free-living life style and unspecialized body shape is *Liatongus monstrosus* (Bates) (Oniticellini). It is an obligate associate of the leaf cutter ant, *Atta mexicana* Smith, in Mexico (Halffter & Edmonds, 1982). Adult females dig tunnels underneath the *A. mexicana* refuse dumps and fill the tunnel with the ants' refuse (decomposing fungus garden remains and dead ants) (Halffter & Edmonds, 1982). The relevance of *L. monstrosus* biology here is that it is an unrelated (i.e. separate tribe) taxon to *S. (Pachysoma)*, which feeds on detritus, does not occur in a brood ball, and consequently, has similar unspecialized body form.

The nesting biology of the distantly related *Geotrupes (Thorectes) sericeus* (Scarabaeoidea: Geotrupidae) (Klemperer & Lumaret, 1985) may provide some insight into the biology of flightless species nesting in sand and feeding on dry dung, as occurs in all *S. (Pachysoma)* species. Female *G. sericeus* lay an egg at the terminal end of a chamber before provisioning it with a plug of dry rabbit pellets. The egg chamber is thus outside the dung mass and the larvae are free-living. Related species, *G. albarracinus* and *G. laevigatus*, which nest in soil, have their egg chamber within a brood mass of wet sheep dung (Klemperer & Lumaret, 1985). Klemperer & Lumaret (1985) suggest that '… ovipositing outside the brood mass may have a selective advantage where nests are made during the wet season in sandy environments. Water is more likely to drain away from a chamber in sand, but an egg inside a dung mass is more likely to "drown". This is because the dung mass will retain water by capillary suction …'. Scholtz (1989) demonstrated capillary action with dry pellets buried by *S. (P.) striatus* in wet sand. Other Geotrupidae that nest in sand, viz. *Typhaeus typhoeus* and *Ceratophyus hoffmannseggi*, always oviposit outside the brood chamber (Klemperer & Lumaret, 1985). *G. sericeus* pupate inside the original brood chamber but *T. typhoeus*, which prefer sandy soils (Brussaard & Visser, 1987), pupate in the surrounding sand, as do the *S. (Pachysoma) striatus* pupae described here.

To conclude, we propose that the unique suite of adaptations exhibited by *S. (Pachysoma)* species has been selected for in response to the arid conditions to which they are exposed. These include the unusual feeding biology and immature morphology reported on here for the first time, as well as the well-documented loss of flight and unique feeding biology in adults (Scholtz, 1989). The reversal from feeding and breeding in wet dung to dry dung and detritus (the probable ancestral condition; Scholtz & Chown, 1995) was necessitated by the availability of only the latter materials which are not pliable enough for manipulation into a dung ball for rolling or nesting. In order to exploit this resource, *S. (Pachysoma)* species have modified their relocation strategy from rolling a single large ball backwards to dragging numerous small food fragments forwards, often over a large area, towards their preconstructed burrows and navigating using polarized light as an orientation cue. Furthermore, evolving a larval life-style in which the larva can move freely within a tunnel loosely packed with dry dung and detritus solves the second obstacle of manipulating the fragmented larval food into a ball. Finally, this free-living life-style in *S.* (*Pachysoma*) immatures is facilitated by a reversal to the less specialized morphological attributes documented here.

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