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A revision of the genus *Pachysoma* M'Leay with an evaluation of the subtribe Pachysomina Ferreira and its genera (Coleoptera: Scarabaeidae)

by

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The validity of the subtribe Pachysomina is questioned and *Mnematium* M'Leay and *Neopachysoma* Ferreira are synonymized with *Pachysoma* M'Leay. Four new species synonymies are proposed and the ten South African species are mapped and discussed. Morphological characters are illustrated; a key to species and a table of character states of 28 characters for 13 species are provided.

INTRODUCTION

The wingless true scarabaeids of South West Africa and Namaqualand were last revised by Ferreira (1953a). Since then one synonymy (Ferreira 1966) and one new species (Zunino 1977) have been published. From a survey of the Central Namib desert which was conducted by members of our department over the past four years, much new material of these species has been accumulated. Combined with the extensive collections of the Transvaal Museum and the Dung Beetle Research Unit (CSIRO) as well as the material and types from the old collections in Europe, this material permitted us to map the known distributions of all species and assess their morphological variation.

The African wingless scarabaeids are of particular evolutionary and zoogeographical interest. Balthasar (1963) and others regard them as primitive within the Scarabaeinae, and close to the Neotropical Eucraniini. In Africa they have a polarized north-south distribution, that has been recorded for various old Coleoptera-groups (Balthasar 1963; Endrödy-Younga 1978; Holm 1978; 1979). Lastly, their Cape to Namib distribution is of interest in view of the close historical link between these two biomes (Endrödy-Younga 1978; Holm 1979).

The species treated in this paper have been adequately described and redescribed in previous papers and only supplementary notes are provided here. Although the revisions by Ferreira (1953a, b) are profusely and neatly illustrated the proportions of some of the drawings are not quite accurate and we have therefore redrawn the most important structures with the aid of a *camera lucida*. Types which could not be traced or were not seen are quoted in parentheses.

Abbreviations of institutes are explained in the acknowledgements. Localities under material examined are given as on the labels and grid references are added to prevent ambiguity.

STATUS OF THE SUBTRIBE PACHYSOMINA FERREIRA, 1953

The four characters on which the subtribe is based are: aptery; absence of humeral calli; semi-contiguous metacoxae; short metasternum. Genera included are *Pachysoma* M'Leay, *Neopachysoma* Ferreira, *Mnematium* M'Leay and *Neomnematium* Janssens. The type genus is *Pachysoma* M'Leay (by tautonomy). Of the subtribal characters, the first two are obviously related and aptery is the only character the four genera share which *Scarabaeus* L. does not. Since aptery involves a reduction rather than a unique acquisition, and the same reduction is known from quite unrelated (e.g. *Circellium* Latreille) and closely related Scarabaeinae (e.g. Eucraniini), and is quite widespread among lamellicorns in general (e.g. Trogidae, Lucanidae and Acanthoceridae), there is little reason to suppose that it constitutes a synapomorph for the Pachysomina. The aptery is also developed to widely varying degrees among the Pachysomina (Table 1).

The semi-contiguous mesocoxae are not consistent within the subtribe. Arrow (1919) pointed out that *M. silenus* Gray has the mesocoxae well apart, and so has *M. rotundipenne* (Holdhaus). In the southern species, there are cases of completely contiguous mesocoxae. Furthermore, the relative width between mesocoxae differs more between e.g. species of *Pachylomera* Kirby and *Kheper* Janssens (both Scarabaeina Ferreira) than between *Pachylomera* and *Pachysoma*.

The length of the metasternum is equally variable among the Scarabaeini. There are *Kheper* species which have it as short as most Pachysomina and shorter than *M. rotundipenne*. It should also be borne in mind that aptery mostly results in a general shortening of the abdomen, and that the shortening of the metasternum in most Pachysomina may just be one more consequence of aptery, rather than an independent character.

We therefore conclude that, for lack of any demonstrably synapomorphic character, the subtribe Pachysomina has no phylogenetic justification.

PACHYSOMA M'Leay

Pachysoma M'Leay, 1821: 507. Type-species *Pachysoma hippocrates* M'Leay.
Mnematium M'Leay, 1821: 506 **syn. nov.** Type-species *Mnematium ritchiei* M'Leay.
Irrorhotides Shipp, 1896: 116. Type-species *Irrorhotides fryi* Shipp.
Neopachysoma Ferreira, 1953a: 37 **syn. nov.** Type-species *Pachysoma denticolle* Péringuey.

Arrow (1919) pointed out that the distinction between *Mnematium* M'Leay and *Pachysoma* M'Leay was untenable. Ferreira (1969) separated the two genera on the shape of the genae and the length of the third segment of the maxillary palp.

The shape of the genae is extremely variable in *Pachysoma* and *Neopachysoma* and it is apparent that the species of *Mnematium* are closer to *N. denticolle* (Péringuey), *P. bennigseni* Felsche and *P. schinzi* Fairmaire, then these three are to *P. aesculapius* Olivier or *P. hippocrates* M'Leay (figs 5–29). The relative length of the third segment of the maxillary palp varies independently of the genus between the species of *Pachysoma* and *Neopachysoma* (figs 8–29) and there is no meaningful difference between this range on the one hand and that of *Mnematium* on the other. Although in *Mnematium* the mean length of the third segment is shorter and the fourth longer than in *Pachysoma*, there is little difference between e.g. *P. striatum* (fig. 18) and *P. ritchiei* (fig. 6).

Although Balthasar (1963) recognized *Mnematium* as a valid genus he did not distinguish it from *Pachysoma*, and separated it from the other Scarabaeini on primary and secondary characters of aptery. He commented that the genus is untenable in relation to *Scarabaeus* L.

The behaviour of *Mnematium* is unfortunately not, to our knowledge, recorded. It would be interesting to know whether they drag dung pellets forward like *Pachysoma* species, or roll them backwards like *Scarabaeus* species.

According to Ferreira (1953a, 1966 & 1969) the genus *Neopachysoma* Ferreira is distinguished from *Pachysoma* by the following characters: shape of genae; lengths of third and fourth segment of maxillary palp; groove on outside of last segment of maxillary palp; subapical projection on inside of protibia; convexity of mesofemur; sinuosity on outside of mesotibia; height of insertion of tarsus on metafemur.

The shape of the genae and the lengths of the palpal segments vary too much for a sensible grouping of species into two genera (figs 7–29). The groove on the last segment of the maxillary palp is reduced in the *Neopachysoma* species, but in a gradient from *N. rotundigena* to *N. rodriguesi*. The subapical denticulate projection on the inside of the protibia is well developed in the three Neopachysoma species, but a gradient of development of this character can be seen in the *Pachysoma* species, from *P. fitzsimonsi* to *P. bennigseni* to *P. striatum* (in the latter in the male only). The further increase and backward shift of this structure goes from *N. rotundigena* to *N. rodriguesi* and *N. denticolle* (figs 30–66). In these three species, sexual dimorphism of this character is present but not as marked as in *P. striatum*. (It is also interesting to note that the structure recurs in *Drepanopodus* Janssens and to a lesser degree in certain *Scarabaeus* species.) The characters of convexity of the mesofemur, formation of the outside of the mesotibia and insertion of the metatarsus (figs 71–83) all vary by degrees between the species, and prohibit a clear separation.

We must conclude that *Neopachysoma* does not seem to be warranted as a genus, but should rather be regarded as a species group similar to those that include *hippocrates* and *aesculapius* or *ritchiei*, *silenus* and *rotundipenne*.

The genus *Irrorhotides* Shipp is a junior synonym of *Pachysoma*. We have not seen *Neomnematium* Janssens which occurs in Madagascar and cannot treat it at present. The *Pachysoma* elytron mentioned by Ferreira (1966) from Somalia could not be found in the collection of the Transvaal Museum. It would be interesting to know how Ferreira determined it to be a *Pachysoma* rather than a *Mnematium*.

Pachysoma cancer (Arrow) (described as *Mnematium cancer*) is an exceptional species, both in its distribution in south east Angola and in morphology. The profemur has well-pronounced spines, similar to *Pachylomera*, while the general size is double that of the other large *Pachysoma* species. If any *Pachysoma* species warrants a separate genus it would be this one.

Lastly, with many *Scarabaeus* species we examined we failed to find reliable morphological characters to separate *Pachysoma s. lat.* from *Scarabaeus*, other than aptery and associated characters. Aptery need not be (and probably is not) holophyletic in *Pachysoma*, as pointed out above. Since it is beyond the scope of this study and our experience in the Scarabaeinae to define the relationship between *Pachysoma* and *Scarabaeus* categorically, and since the southern species at least show a very different behaviour, we provisionally treat *Pachysoma* as a valid, although possibly paraphyletic

Pachysoma granulatum Ferreira, 1953b: 6; Ferreira 1966: 59; Ferreira 1969: 20.
HOLOTYPE: ALLOTYPE; 2 PARATYPES: Daberas Dunes, Gt Namaqualand: TM; 2
PARATYPES: ditto: BM.

Length 16,5–18,5 mm; width 10,5–12,5 mm. This species agrees with P. *denticolle* in size and in having deeply striate elytra and the pronotum with three depressions. The genae (fig. 15) and tarsi (fig. 75) are also similar to those of P. *denticolle*, but their profemurs differ, as those of *P. bennigseni* lack sexual dimorphism (fig. 47). It shares the bristles on the posterior edge of the last abdominal segment with *P. denticolle*, *P. rotundigena* and *P. rodriguesi* and forms a transition from the species allocated by Ferreira to *Neopachysoma* and to *Pachysoma* respectively in all characters which separate these two groups. Some specimens have discernible rudiments of the transverse brushes on the outside of the metatibia (fig. 75) and males have the protuberances on the sides of the abdominal segments as in *P. fitzsimonsi*.

P. granulatum was described by Ferreira (1953b) and sybsequently synonymized by the same authoress (Ferreira 1966 and 1969).

This species occurs from just south of the Orange River along the coast to Spencer Bay. In the south it is sympatric with *P. gariepinus*, but inhabits the looser sanddunes, while in the north it is sympatric with *P. denticolle* and inhabits the coastal sanddunes and sand flats whereas *P. denticolle* lives in the inland dunes. Near Lüderitz, where both species occur, a few specimens of *P. denticolle* have been collected which have some characteristics which are similar to those of *P. bennigseni* (reduction of red on elytra; transverse rugosity of elytra; larger size). These have been described as *Neopachysoma penrithae* by Zunino (1977) and could either be remnants of a transitional or intermediate form, or be hybrids between the two species (see *P. denticolle* below). Foraging and tunneling is very similar to that by *P. gariepinus* (see above).

MATERIAL EXAMINED. (24 unsexed specimens): SOUTH WEST AFRICA: Spencer Bay Water, SE 25 14 Dd, 14.i.1974, Endrödy-Younga (TM); Buchuberg Lüderitz, SE 27 15 Dd, 1972. C.J.C. (SM): Spencer Bay, Noordhoek, Brakvlei, SE 25 14 Dd, 17.i.1973 (UP); Agate Beach Lüderitz, SE 26 15 Ca, 19.i.1973, M. K. Jensen (UP); Daberas Dunes, Gt. Namaqualand, SE 28 16 Bb, v.1953, C. Koch (TM); Oranjemund, Lüderitz, SE 28 16 Cb, 25–27.xi.1972 (SM); 10 km N Oranjemund, SE 28 16 Ad, vii.1978, E. Holm (UP); Oranjemund, SE 28 16 Cb, vii.1978, I. Bruwer (UP); 10 km N Oranjemund, SE 28 16 Ad, vii.1978, E. Holm (UP). SOUTH AFRICA. CAPE PROVINCE. 10 km S Alexander Bay, SE 28 16 Ca, vii.1978, E. Holm (UP).

Pachysoma rotundigena Felsche, figs 1; 11; 12; 43–46; 72

HOLOTYPE: DRE
Type locality: Sinclair, South West Africa.
Pachysoma rotundigena Felsche, 1907: 273; Péringuey 1908: 555; Gillet 1911: 6.
Neopachysoma rotundigena: Ferreira 1953a: 43; Ferreira 1966: 60; Ferreira 1969: 25; Zunino 1977: 15.

Length 21, 5–24,5 mm; width 13, 5–15 mm. This species can easily be distinguished from the sympatric *P. fitzsimonsi* by the lack of the basal ridge on the elytra; the presence of a bifurcate spur and a subapical projection on the inside of the protibia (figs 43; 44); the presence of setae on the edge of the last abdominal sternite. It differs from the much larger *P. rodriguesi* in having the tibiae black, the protibial spur

bifurcate in the female (fig. 44) and the striation on the shiny elytra virtually obsolete. The genae are without points and are finely serrated (fig. 11). The legs are stout as in *P. aesculapius* but lack the external brushes and have the insertion of the tarsus relatively high up (figs 71; 72). The basal ridge on the elytra is absent and the metatarsal claws are long.

This species occurs in the overgrown marginal inland dunes of the southern Namib dune area. Foraging has not been observed.

MATERIAL EXAMINED. (33 unsexed specimens): SOUTH WEST AFRICA: S. W. Helmeringhausen, SE 26 16 Ab3, viii.1978, E. Holm (UP); Koichab East, SE 26 16 Bb, vii.1978, Dept. Entomology (UP); Kanaän 104, Lüderitz, SE 25 16 Cc, 6–7.x.1972 (SM); Namib Park, SE Corner, SE 23 15 Da, 26.xi.1974, Endrödy-Younga (TM); Namtib 70 m NW Aus, Gt. Namaqualand, SE 25 16 Cc, Koch & van Son (TM); Namib Farm Kanaän, SE 25 16 Cc, S. Mothlasedi (TM); Gorrasis 99 Lüderitz, SE 25 15 Bd, 25–31.i.1974 (SM); Sesriem 137 Maltahöhe, SE 24 15 Dc, 5–6.iv.1972 (SM); E. Awasib, SE 25 15 Bbl, 11.vii.1976 Dept. Entomology (UP); Sesriem dunes, SE 24 15 Db, 5.v.1972, I. O. Prozesky (TM).

Pachysoma rodriguesi (Ferreira) **comb. nov.** figs 4; 9; 10; 3–38;

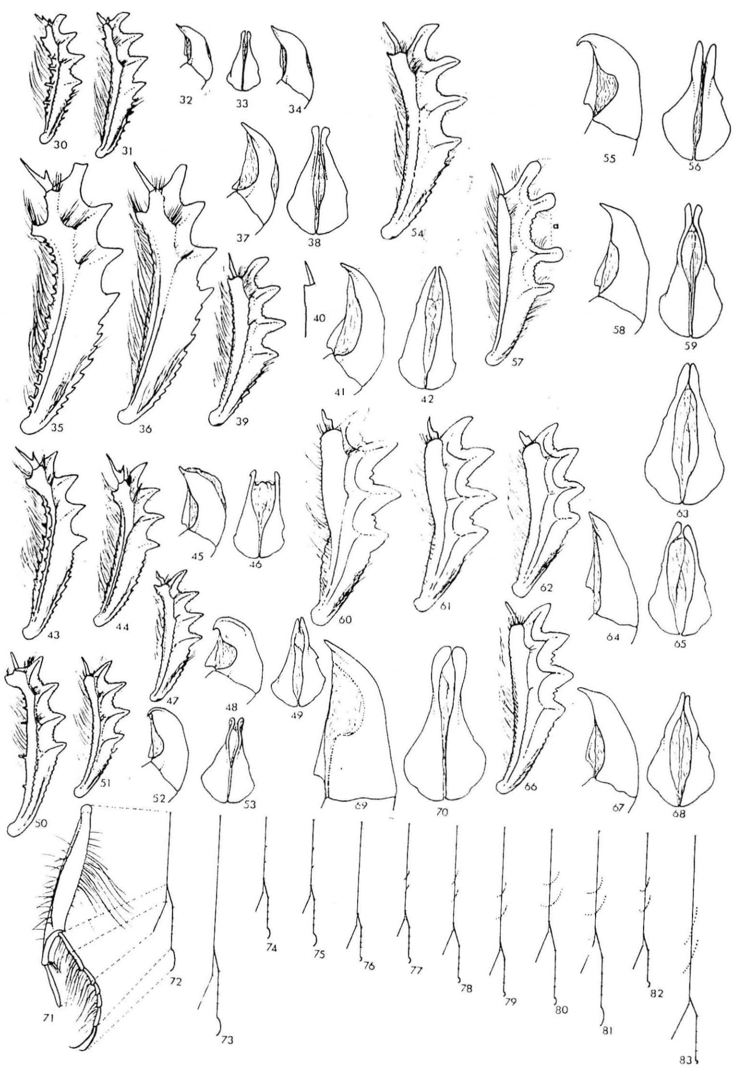
HOLOTYPE, PARATYPE: TM
Type locality, Namtib, near Aus, South West Africa.
Neopachysoma rodriguesi Ferreira, 1953a: 44; Ferreira 1966: 60; Ferreira 1969: 25; Zunino 1977: 15.

Length 28,0–35,5 mm; width 16,0–22,5 mm. *P. rodriguesi* has several unique characters: the frons has a median tubercle (fig. 9); tibiae and tarsi are reddish and the pronotum has a sharp point on either side of the rear margin. Sexual dimorphism of the protibiae is marked (figs 35; 36) and the profemur is dilated in the male. Metatarsal claws are long and transverse external brushes on the metatibia are absent (fig. 73). The basal ridge on the elytra is absent and the impressions on the pronotum are as in *P. bennigseni* and *P. denticolle*.

Together with *P. denticolle*, *P. rodriguesi* inhabits the whole central Namib dune area, and these two species represent the psammophilous and deserticolous extremes of the genus in habits and morphology. *P. rodriguesi* forages mainly on *Oryx gazella* droppings and is often found cradling and dragging several balls in the crook of the hindlegs while walking forward. Burrows extend down into moist sand for up to half a metre. The burrows are characteristic, with drag marks leading towards them and with a characteristic pile of sand at the entrance. Sand is pushed forward out of the burrows with the protibiae, head and pronotum together. Pairs of beetles are often found in burrows. In summer they have a bimodal diurnal activity and often dig temporary shelters at midday. Mating was observed above ground in the afternoon.

While the subdesert mostly supports ungulates the wingless scarabaeids could presumably be active at least once in every season, but rainfall in the Namib dune area is scattered and low, and ungulates may not move into a particular area for as long as two or three years. This would make a special adaptation for a prolonged quiescence necessary in the cases of *P. rodriguesi* and *P. denticolle*.

A very curious record is the one female specimen collected at Buffelsrivier in Namaqualand by Endrödy-Younga. This specimen does not differ significantly from the northern ones (except in having the tubercle on the frons rather reduced) and the locality would need verification.



MATERIAL EXAMINED. (37 unsexed specimens): SOUTH WEST AFRICA: N-E Tsondab Plains, SE 23 15 Cc2, 15.vii.1976, Dept. Entomology (UP); 9 km W Awasib, SE 25 15 Ad, 8.vi.1969 (SM); Namib Expedition, SE 25 15 Ac4, i.1977, Holm, Kirsten, Scholtz (UP); Koichab Pan, SE 26 15 Bc, 20,i.1966 (SM); Dunes nr Harus Lüderitz, SE 25 15 Ac, 9.v.1969 (SM); St. Francis Bay, SE 25 14 Bbl. 8.vii.1976, Dept. Entomology (UP); Namib Expedition, SE 23 15 Cc, i.1977, Holm, Kirsten, Scholtz (UP); N-Uri Hauchab, SE 25 15 Ac2, 6.vii.1976, Dept. Entomology (UP); Tsondap, SE 24 15 Bal, 11.vii.1975, Dept. Entomology (UP); Namtib Dunes, 35 m E Neisib, Aus distr., SE 25 16 Dc, 1.v.1972, L. & O. Prozesky (TM); N-Tsondab plains, SE 23 15 Ccl, 14.vii.1976, Dept. Entomology (UP); N-Awasib, SE 25 15 Bc3, 4.vii.1976, Dept. Entomology (UP); Harusberg, SE 25 15 Ac, v.1969 (SM); Sossusvlei Lüderitz, SE 24 13 Cb, 6.iv.1974, W. Wendt, H. Roth (SM); Lüderitz, SE 25 14 Bb, 17.ix.1971 (SM); SE-Tsondab Plains, SE 23 15 Cc4, 15.vii.1976, Dept Entomology (UP); Namib Expedition, SE 25 15 Cd2, i.1977, Holm, Kirsten, Scholtz (UP); E-Awasib, SE 25 15 Bbl, 11.vii.1976, Dept Entomology (UP); Homeb 10 m ESE Gobabeb, SE 23 15 Cb, 23–25.i.1972 (BM): SW Helmeringhausen, SE 26 16 Ab3, vii.1978. E. Holm (UP); W Guinasibberg, SE 25 15 Ad2, 6.vii.1976, Dept Entomology (UP); S Gobabeb, SE 23 15 Ca3, 14.vii.1976, Dept. Entomology, (UP); Namib Expedition, SE 25 15 Aa4, i.1977, Holm, Kirsten, Scholtz, (UP); Koichab West, SE 26 15 Bc, vii.1978, E. Holm (UP); Kanaän, SE 25 16 Cc. 7.v.1977, Endrödy-Younga (TM); SOUTH AFRICA. CAPE PROVINCE: Buffelsrivier, SE 29 17 Cb, 4.x.1976, Endrödy-Younga (TM).

Pachysoma denticolle Péringuey, figs 2; 7; 8; 30–34; 74

LECTOTYPE: UP
Type locality: Walvis Bay, South West Africa.
Pachysoma denticolle Péringuey, 1888: 93; Péringuey 1900: 77 Gillet 1911: 6.
Neopachysoma denticolle: Ferreira 1953a: 37; Ferreira 1966: 60; Ferreira 1969: 25; Zunino 1977: 15.
Neopachysoma penrithae Zunino, 1977: 15, **Syn. nov.**
HOLOTYPE: Lüderitz, SE 26 15 Ca: SM (PARATYPE: Süd-Namib: Coll. Zunino).

Figs 30–83. Tibiae (from above), tarsi and aedeagi of *Pachysoma* species. 30–34. *P. denticolle*. 30. Protibia male. 31. Protibia female. 32. Aedeagus lateral. 33. Aedeagus dorsal. 34. Aedeagus lateral (*penrithae*). 35–38. *P. rodriguesi*. 35. Protibia male. 36. Protibia female. 37. Aedeagus lateral. 38. Aedeagus dorsal. 39–42. *P. fitzsimonsi*. 39. Protibia male. 40. Distal end protibia female. 41. Aedeagus lateral. 42. Aedeagus dorsal. 43–46. *P. rotundigena*. 43. Protibia male. 44. Protibia female. 45. Aedeagus lateral. 46. Aedeagus dorsal. 47–49. *P. bennigseni*. 47. Protibia. 48. Aedeagus lateral. 49. Aedeagus dorsal. 50–53. *P. striatum*. 50. Protibia male. 51. Protibia female. 52. Aedeagus lateral. 53. Aedeagus dorsal. 54–56. *P. gariepinus*. 54. Protibia male. 55. Aedeagus lateral. 56. Aedeagus dorsal. 57–59. *P. schinzi*. 57. Protibia male (with distance 'a' less in female). 58. Aedeagus lateral. 59. Aedeagus dorsal. 60–65. *P. hippocrates*. 60. Protibia male (from Darling). 61. Protibia female (from Karoovlei). 62. Protibia male (from Wallekraal = *hessei*). 63. Aedeagus dorsal (from Darling). 64. Aedeagus lateral (from Wallekraal). 65. Aedeagus dorsal (from Wallekraal). 66–68. *P. aesculapius*. 66. Protibia. 67. Aedeagus lateral. 68. Aedeagus dorsal. 69–70. *P. richiei*. 69. Aedeagus lateral. 70. Aedeagus dorsal. 71. Metatibia of *P. rotundigena* (from the outside). 72–83. Proportionate lengths of metatibia, spur, tarsal segments and tarsal claw. 72. *P. rotundigena*. 73. *P. rodriguesi*. 74. *P. denticolle*. 75. *P. bennigseni*. 76. *P. fitzsimonsi*. 77. *P. gariepinus*. 78. *P. striatum*. 79. *P. schinzi*. 80. *P. aesculapius*. 81. *P. hippocrates*. 82. *P. rotundipenne*. 83. *P. cancer*.

Length 14,0–18,0 mm; width 8,5–12,0 mm. This is the smallest *Pachysoma* species and most specimens have the orange elytra of the typical form. A black form occurs on the coast and a full range of intermediates occur. Elytra are strongly striate, without a basal ridge and with more or less developed single rows of granules on the costae. The pronotum has a median and an oblique lateral depression on the disc. These depressions are shiny and unsculptured. Genae are moderately pointed and finely serrated on the outside (fig. 7). In most other features *P. denticolle* resembles *P. rodriguesi*.

The type of *P. denticolle*, which Ferreira (1953a) could not trace, was found in the Péringuey collection at the University of Pretoria. The specimen fits the original description and bears the label 'Walfisch Bay, Nightingale'. This specimen was not marked as a type. The black specimen from 'Ganab' which Ferreira (1953a) mentioned and which was marked 'Type' by Péringuey is not mentioned in the original description. It is possible that the labels of the two specimens became interchanged. We designated the 'Walfisch Bay' specimen as lectotype.

We have examined the female holotype of *P. penrithae* (Zunino) as well as a male from the same locality. Zunino (1977) mentioned the following differences between *P. denticolle* and *P. penrithae*: shape of median clypeal teeth; elytral sculpture; coloration of elytra, epipleura and pseudo-epipleura. The first of these characters is variable within the species and clypeal teeth are susceptible to wear. The elytral sculpture and profile are the only significant differences between the two forms, with the profile flatter and transverse rugosity and granules more pronounced in *P. penrithae*. With only a few specimens of *P. penrithae* known it is difficult to evaluate these differences. One possibility is that *P. penrithae* represents a clinal extreme since all features which differ between them vary to some extent from one locality to another. A second possibility is that a subspecies is involved but distributional evidence for this is insufficient at present. Lastly, the specimens may be hybrids between *P. denticolle* and *P. bennigseni* (see above). The coloration of the elytra and epipleura varies in *P. denticolle* (the holotype has black epipleura and pseudo-epipleura as in *penrithae*) and the genitalia do not differ significantly between the two forms (figs 32–34 and Zunino 1977 fig. 2) with variation in *P. denticolle s. str.* taken into account.

P. denticolle only occurs in the dunes in the central Namib, sympatric with *P. rodriguesi*. Their habits are similar but *P. denticolle* takes mainly hare dung and only one pellet is dragged at a time. On occasions this species also collects mice and chameleon droppings and vegetable matter (grass blades, *Monsonia* sp. leaves etc.). In these cases the forage is picked up with the hind legs and pressed to the underside of the abdomen. This heterogenous diet strengthens our suspicions that the *Pachysoma* species feed on the fungi which grow on the forage stored in the moist sand.

MATERIAL EXAMINED. (78 unsexed specimens): SOUTH WEST AFRICA: N-Awasib, SE 25 15 Bc3, 4.vii.1976, Dept. Entomology (UP); N-Uri-Hauchab, SE 25 15 Ac2, 6.vii.1976 Dept. Entomology (UP); Tsondab, SE 24 15 Bal, 11.vii.1975, Dept. Entomology (UP); Tsondab, SE 23 15 Dcl, 12.vii.1975, Dept. Entomology (UP); N-E Tsondap Plains, SE 23 15 Cc2, 15.vii.1976, Dept. Entomology (UP); W Tsondap Plains, SE 23 14 Dd2, 14.vii.1976, Dept. Entomology (UP); N-Tsondap Plains, SE 23 15 Ccl, 14.vii.1976, Dept. Entomology (UP); Namib Expedition, SE 25 15 Cd2, Jan. 1977, Holm, Korsten, Scholtz (UP); Namib Expedition, SE 24 15 Ccl, Jan. 1977, Holm, Kirsten, Scholtz (UP); N-Guinnasibberg, SE 25 15 Ba3, 5.vii.1976, Dept.

Entomology (UP); SE-Guinasibberg, SE 25 15 Bcl, 4.vii.1976, Dept. Entomology (UP); SE-Tsondap Plains, SE 23 15 Cc4, 15.vii.1976, Dept. Entomology (UP); E. Awasib, SE 25 15 Bbl, 11.vii.1976, Dept. Entomology (UP); Sossus Vlei, SE 24 15 Da3, 14.vii.1975, Dept. Entomology (UP); E-Awasib, SE 25 15 Bbl, 11.vii.1976, Dept. Entomology (UP); Namib, Spencer Bay, N-Hook, SE 25 15 Db, 11.i.1974, Endrödy-Younga, (TM); Walvisbaai, 8 km S of town, SE 22 14 Dc, 19.xi.1974, Endrödy-Younga (TM); Dunes S of Rechenberg, 30 km N-E Lüderitz, SE 26 16 Ad, ix.1963, W. D. Haacke (TM); Sandwich Harbour, SE 23 14 Bc 28.xii.1962, W. Criess (TM); Namib Expedition, SE 26 15 Ab4, Jan. 1977, Holm, Kirsten, Scholtz (UP); Lüderitz, SE 26 15 Ca4, 16.vii.1974, Dept. Entomology (UP); Namtib, 70 m NW of Aus, Gt. Namaqualand, SE 25 16 Dd, Koch & van Son (TM); Awasib dunes E, Lüderitz, SE 25 15 Ba, 29–30.i.1974 (SM); Koichab West, SE 26 15 Bc, Dept. Entomology (UP); Sossusvlei, SE 24 15 Cb, 4.vii.1978, L. A. Wessels (UP); Namib, Farm Kanaan, SE 25 16 Cc, 7.v.1977, Endrödy-Younga (TM); Namib, Spencer Bay Water, SE 25 14 Dd, 14.i.1974, Endrödy-Younga (TM); Sesriem 137, Maltahöhe, SE 24 15 Dc, 5–8.iv.1972; Walfisch, Dec. 1893 (SAM).

DISCUSSION

In Table 1 we have recorded 28 characters of the *Pachysoma* species which differ between species, and presented their relative states. This list could be extended to include more characters (e.g. metasternum, mesotibia, mesocoxae) but is adequate to illustrate our findings on the relationships between species.

Decisions on what the primitive states of characters are, were problematical. Out-group comparison proved to be of some use, but since *Pachysoma* is supposed to be primitive in the Scarabaeini which in turn is primitive in the Scarabaeidae, establishing unequivocal plesiomorphs by reference to more primitive forms was impossible. Even structures which only occur in *Pachysoma* species could not be regarded as apomorphic. Atrophy and those structures associated with atrophy were easier to interpret. In some cases we could not classify characters at all and these were not considered for the totals at the end of the table.

Table 1 illustrates that: (1) few characters show a significant gap in variation between species; (2) characters which unite the species of one group either show gradation or recur in the remainder of the species groups, no matter how the species are grouped; (3) there are also no convincing separations between any groupings of species when total apomorphism is considered; and (4) although acquired characters and reduced characters correlate, reductions seem to outweigh acquisitions in the more primitive (least apomorphic) species (*P. ritchiei*, *P. rotundipenne* and *P. aesculapius*) while the opposite is true of the furthest evolved species (*P. rodriguesi*, *P. rotundigena*, *P. denticolle* and *P. bennigseni*).

We therefore fail to see phylogenetically discreet groupings of species in *Pachysoma* but rather suggest a number of evolutionary trends which may but need not have a phylogenetic basis. The best expressed is that which starts in *P. rodriguesi* and *P. denticolle*, while *P. hippocrates*, *P. schinzi*, *P. ritchiei* and *P. cancer* all constitute terminal forms of different trends. All the terminal forms (except *P. schinzi*) are also geographically terminal or isolated.

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TABLE 1. Morphological characters of *Pachysoma*. Degree of development or reduction is ranked by numbers between 0 and 4, with the total range of variation within the genus as the scale. Probable newly-developed structures are indicated with an asterisk, while probable reductions are indicated by numbers in parentheses. The rest of the numbers relate to characters which could not be defined as either. 1 reduction of pointed genae, 2 increase in serration of genae, 3 relative length of third/fourth segment of maxillary palp, 4 reduction of setation on second segment of maxillary palp, 5 reduction of groove on last segment of maxillary palp, 6 autapomorphs: frontal protuberance (*P. rodriguesi*); clypeal horns (*P. schinzi*); no ventral clypeal spine (*P. cancer*), 7 granulation on disc, 8 posterior margin from convex to concave, 9 development of lateral serration, 10 development of depressions on disc, 11 decrease in recess for head, 12 striation from absent to deep, 13 width between two lateral rims from broad to narrow, 14 rear profile flat to round, 15 length relative to pronotum from long to short, 16 basal ridge well-developed to reduced, 17 development and proximal shift of projection on the inside, 18 reduction of denticulation on the inside, 19 reduction of denticulation on the proximal half of the outside, 20 spur from simple to forked, 21 development of sexual dimorphism, 22 increase in length of tarsal claws relative to last tarsal segment, 23 reduction of the two combs of bristles on the underside of the tibia, 24 position of tarsus on tibia low to high, 25 reduction in length of hindwing relative to elytra, 26 paramere points flat to pointed to hooked, 27 parameres depressed above, 28 setae on posterior margin absent to dense.

	Head						Pronotum					Elvtra					Protibia					Metatibia and Tarsus			Hind wing	Aedaegus		Last abdominal Sternite	Totals of ratings for reduction	Totals of ratings for development*
	(1)	2*	3*	(4)	(5)	6	7	8	9*	10*	(11)	12	13*	(14)	(15)	(16)	17*	(18)	(19)	20*	21*	22*	(23)	24*	(25)	26*	27*	28*		
P. rodriguesi	4	2	4	3	4	4*	4	2	1	1	1	0	4	4	3	4	4	4	0	4	4	3	4	4	1	1	1	4	38	30
P. rotundigena	1	2	3	3	2	—	1	2	3	1	4	0	4	1	2	1	3	4	0	4	3	1	1	3	4	4	1	3	35	41
P. denticolle	2	2	1	3	3	—	4	2	4	4	1	1	3	1	1	1	4	1	0	1	4	3	3	3	4	1	3	3	29	42
P. benningseni	2	4	2	1	0	—	1	2	3	3	3	1	2	0	0	1	2	2	0	2	0	3	3	3	4	3	1	1	19	32
P. gariepinus	3	3	3	0	0	—	4	3	2	0	1	3	0	2	0	4	1	1	0	1	0	1	2	0	3	2	1	1	16	15
P. striatum	4	0	0	3	0	—	2	2	2	0	3	2	1	3	0	4	2	1	1	0	4	2	3	2	3	1	1	0	27	17
P. fitzsimonsi	3	3	2	3	0	—	3	3	2	[illegible]	2	3	3	3	1	2	1	0	2	1	0	1	4	3	4	2	1	0	24	20
P. schinzi	0	4	2	1	0	4*	0	4	2	0	1	0	1	1	2	3	0	2	4	0	2	2	1	2	2	0	1	0	20	20
P. hippocrates	4	0	1	3	0	—	2	4	0	0	1	0	3	3	3	1	0	0	3	4	1	4	0	1	4	0	0	0	22	14
P. aesculapius	4	0	1	2	0	—	3	4	1	0	1	1	3	3	3	1	0	2	2	0	0	0	0	0	3	1	0	0	21	5
P. rotundipenne	0	0	0	3	0	—	0	0	3	0	1	2	1	0	4	0	0	1	0	0	0	1	1	2	0	0	0	0	10	7
P. richiei	1	0	0	4	0	—	0	1	2	0	2	2	3	0	2	0	0	1	0	0	0	0	1	2	1	0	0	0	12	7
P. cancer	0	1	2	4	0	(4)	0	2	1	0	0	0	4	1	1	2	0	1	3	0	[illegible]	0	1	0	0	0	0	0	17	8