CLIMATIC CHANGE, HABITAT MODIFICATION AND RELATIVE AGE OF DUNG BEETLE TAXA (COLEOPTERA: SCARABAEIDAE, HYDROPHILIDAE, HISTERIDAE, STAPHYLINIDAE) IN THE SOUTH-WESTERN CAPE

I. Text

by

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ABSTRACT

1. Climatic isolation due to the inception of winter rainfall climate in the Pliocene, three million years before present, and recent widespread clearance of the ubiquitous indigenous shrubland have probably shaped both the taxonomic composition and the functional relationships of the dung beetle fauna in the south-western Cape.

2. Steep cross climatic gradients in species richness and abundance extend northwards from the south-western Cape where the most favourable period for activity during spring is much cooler than the mid-summer activity period in the summer rainfall region in the Transvaal which the winter rainfall system has probably displaced to the north.

3. Exceptions to this gradient are recorded in some groups of dung Coleoptera on the west coast of the south-western Cape where abundance is boosted by cold-adapted species breeding in the absence of competition in early spring.

4. The higher taxa of dung beetles in the south-western Cape may be ranked from the Scarabaeinae/Coprinae through the Aphodiinae and Histeridae to the Staphylinidae/Hydrophilidae which represents a sequence from more specialist to more generalist spatial distribution.

5. Over the same sequence, a trend from low to greater taxonomic similarity with Transvaal species assemblages is recorded.

6. This taxonomic sequence may be related to relative specialization of the higher taxa to coprophilous habits and their relative age in the fauna of the south-western Cape.

7. The detailed geographical distribution data available for the Scarabaeinae and Coprinae has facilitated the identification of groups endemic to the winter and bimodal rainfall regions of South Africa and others with a more widespread occurrence.

8. Data for geographical distribution and habitat associations of Scarabaeinae and Coprinae suggest that species from the summer rainfall region have recently dispersed into the south-western Cape in response to clearance of the natural shrubland.

9. Owing to the strong association with indigenous shrubland shown by some of the endemic species, the widespread clearance of indigenous vegetation is a cause for concern for survival of much of the insect fauna endemic to the south-western Cape.

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INTRODUCTION

Members of four families of Coleoptera (Scarabaeidae, Hydrophilidae, Histeridae, Staphylinidae) are abundant in dung in southern Africa. The Scarabaeidae comprise entirely coprophagous taxa many of which tunnel in the soil and breed in the dung that they, or other species, bury. Relatively few scarabaeids breed within the dung pad. The other families comprise primarily predatory taxa and a few coprophages. All of these species are pad-dwellers which breed within the dung pad.

For convenience, the dung Coleoptera may be subdivided into six groups on both taxonomic and functional grounds. Three of the groups are coprophagous comprising, (i) the predominantly dung-burying Scarabaeidae: Scarabaeinae/Coprinae, (ii) the dung-burying or pad-dwelling Scarabaeidae: Aphodiinae and (iii), the pad-dwelling Staphylinidae: Oxytelinae. The other three pad-dwelling groups show predatory habits as larvae, as in (i) the Hydrophilidae, or as both larvae and adults, as in (ii) the Histeridae and, (iii) several subfamilies of Staphylinidae. The functional relationships between the groups, including the inhibitory influence of dung burial on breeding by pad-dwelling species, are summarized in Table I1 and reviewed in detail in Appendix 1. The evolutionary and biogeographical history of the groups is reviewed in Appendix 2 with particular emphasis on the Scarabaeinae and Coprinae.

The spatial distribution of dung beetle species has been shown to be strongly influenced at a regional level by climate (Kirk & Ridsdill Smith 1986) and at a local level by habitat, including vegetation type (e.g. Howden & Nealis 1975, Nealis 1977, Lumaret 1983, Doube 1983, Davis *et al.* 1988). Therefore, the development during the Pliocene of a climatic system characterized by winter rainfall in the western Cape (Deacon 1983) and bimodal rainfall during spring and autumn in the eastern Cape, which is associated with the development of shrubland as the dominant vegetation-type, was probably responsible for the appearance of the endemic dung beetle elements described by Davis (1987). This climatic system, dominated by the prevailing westerly winds, probably superseded a summer rainfall system dominated by easterly winds which still prevail to the north of the winter rainfall region. North-south oscillations of these climatic belts during the glacial cycles of the Pleistocene (Tyson 1986) probably resulted in extensive waves of expansion, contraction and translocation of species ranges leading to isolation of populations and their subsequent speciation.

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Recent widespread clearance of indigenous shrubland, which was the dominant vegetation type in the south-western Cape (Acocks 1975), and its replacement by vegetation of differing physiognomy has also probably had a strong influence on beetle distribution (Davis 1987). Therefore, the present study attempts to identify the relative contribution of climatic change and recent physical disturbances in determining the composition of species assemblages of dung beetles in the region with a view to predicting the relative age of the component groups and identifying those worthy of conservation effort.

The relatively older elements in the south-western Cape may be identified by their specialist characteristics in that they show low fecundity, restricted geographical range and are often more strongly associated with the dominant indigenous shrubland than the younger generalist elements which show high fecundity and a wide geographical range. By definition, geographical distribution of endemic elements in the present study are restricted to regions receiving autumn/winter /spring rainfall. Thus, the higher the taxonomic levels of the endemism, the more distant the taxonomic relationships to species also occurring in the adjoining summer rainfall region. Although the seasonal activity of the older elements usually reaches a maximum during periods of suitable temperature and rainfall conditions both younger and older groups may display activity patterns which are out of phase with optimum climatic conditions.

Although the study is predominantly biogeographical in approach detailed geographical distribution data is only available for the Scarabaeinae/Coprinae. Therefore, predictions of a biogeographical nature involving species assemblages of the other five higher taxa have been based on a comparison of their seasonal and spatial distributions within a small area in the south-western Cape. This is supported by comparison with species assemblages in a small area of the Transvaal.

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STUDY SITES AND TRAPPING METHODS

Abstract

1. Two study sites near Pretoria in the Transvaal were located in a summer rainfall climatic area, type II3d (Walter & Lieth 1964), on deep sand in both open woodland and grassland.
2. Eleven study sites in the south-western Cape were distributed between two winter rainfall climatic areas, type IV in the Cape of Good Hope Peninsula and type III(IV)a (Walter & Lieth 1964) on the west coast. The west coast could be divided into two subregions, the coastal belt of deep calcareous sand and the Darling Hills comprising predominantly sandy soils with a higher clay fraction. Vegetation at the sites formed a gradient from low, dense pasture to taller sparser shrubland. The five pasture sites were distributed between all three subregions whereas the six shrubland sites were located only in the Cape of Good Hope Peninsula and on the west coastal belt.
3. Pitfall traps baited with cattle dung were used to sample dung beetle fauna over 24h periods once a week in the Transvaal, irrespective of weather (three traps/site), and on three sunny occasions per month in the south-western Cape (ten traps/site) for one year.
4. A further 13 study sites used for back-up studies in the south-western Cape were concentrated into three localities, three in the Cape of Good Hope Peninsula, six on the west coastal plain and four in the Darling Hills. These sites comprised different combinations of pasture (five sites) and shrubland (eight sites) habitats. Five traps at each site were baited on one 24h occasion each month over six months.

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Climatic regimes

Southern Africa may be partitioned into four major climatic regions based on the seasonal occurrence of rainfall (Davis 1987, derived from Walter & Lieth 1964). The present study has been conducted at sites in two of these four regions. One set of 11 sites was situated in the south-western Cape in the vicinity of Cape Town (Winter rainfall region) and another two sites were situated in the Transvaal near Pretoria (Summer rainfall region, area 2) (Fig. M1). The regions in which traps were placed constitute opposite extremes along a climatic gradient across southern Africa.

In the South-western Cape, peak rainfall generally coincides with the coolest temperatures of the year during June and July whereas in the Transvaal peak rainfall generally coincides with the warmest temperatures of the year during December and January. Sites in the summer rainfall region in the Transvaal fall within a single climatic area designated type II3d by Walter & Lieth (1964) (Fig. M1). However, sites in the winter rainfall region in the south-western Cape straddle both climatic types IV and III(IV)a (Walter & Lieth 1964). Besides variation in the seasonal occurrence of rainfall, the main differences between these climatic types are much warmer temperatures in type II3d than in types IV and III(IV)a whereas cooler temperatures and higher rainfall differentiate type IV from type III(IV)a. Examples of seasonal distribution of temperature and rainfall in each of the three climate types are shown in Figure M2 as averages over a series of years and in Figure M3 as actual values recorded during the trapping period. Above average rainfall was recorded during the earlier part of the trapping period in the south-western Cape whereas overall rainfall was below average during the trapping period in the Tranvaal (Fig. M3).

Density and height of vegetation

In each climatic regime sites were located on sandy soils in both natural woodland or shrubland habitats and in improved pastures where shrubs or trees had been replaced by grass.

A quantitative study was made of the vegetation only at sites in the south-western Cape. Density of the vegetation was determined by walking along transects and counting the number of paces for which vegetation touched the tip of the foot compared with the number in which vegetation was absent. Variability in the height of the vegetation was determined by measuring the distance from the centres of each trap at which vegetation obscured graduations on a pole at a height of 5, 15, 30cm and upwards at 20cm intervals. Four sets of measurements were taken around each trap along 3m lines leading east, south, west and north. Thus, a total of 40 sets of measurements was taken from the ten traps at each study site. The vegetation height index for each site was derived from the sum of values for the

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average height of the vegetation in each height class times the number of observations in that class.

Transvaal sites

Trapping sites in the summer rainfall region were situated on the farm Boekenhoutskloof (25°34'S 28°29'E) (Fig. M1) which lies at *c.* 1150m a.s.l. The deep sands of the area support an open woodland described as broad-orthophyll plains bushveld (Werger & Coetzee 1978) which constitutes part of the woodland and grassland system of the Sudano-zambezian biogeographical region which extends over much of warm temperate and tropical subsaharan Africa. One trapping site was situated in each of the two habitat-types investigated in the present study. Density and variability in height of the vegetation were not measured but height of the trees is estimated to have varied from 5-10m and is taller than any vegetation encountered at sites in the south-western Cape.

Sites in the south-western Cape

Trapping sites in the winter rainfall region were placed on various farms and reserves between 10-150m a.s.l (Fig. M4). The three sites situated in the cooler, moister climate type IV were located on deep acid sands on the Cape of Good Hope Peninsula. Vegetation in the area is relatively less modified than that in much of the rest of the south-western Cape. Indigenous shrubland is still widespread with farm pastures forming part of a large island of grossly modified vegetation sandwiched between the mountains and the Cape of Good Hope Nature Reserve. Grass at the single site in pasture (farm Bonne Attente) was characterized by dense cover and very low profile (Fig. M5) whereas fynbos replacing recently burnt shrubland in the reserve (2-3yr old) also showed fairly dense cover but with a profile resembling rank grass. The site in more mature shrubland in the reserve (9-10yr old) was characterized by reduced cover and more variable but fairly low profile. Both shrubland sites were dominated by restioid and ericoid shrubs. Periodic burning of these shrubs is conducted as part of the management policy of the reserve. The entire area is frequently exposed to high coastal winds.

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The portion of the warmer drier climate type III(IV)a in which eight trapping sites were located on the west coast may be divided into two areas, the coastal plain and the Darling Hills. Traps on the coastal plain were placed on deep calcareous sands resulting from a Pliocene marine regression (Hendey 1983) on which much indigenous shrubland remains and pasture is relatively uncommon, occurring mainly in small islands. The single site placed in a pasture island in the coastal region (West Coast National Park) was characterized by fairly dense cover and very low profile (Fig. M5). Shrubland sites on the coastal plain were quite different and although physiognomic structure of the vegetation was variable, the profile was much higher and density of cover lower than in pasture. The single shrubland site on the coastal flats was dominated by restioid vegetation (farm Modderrivier) which showed a lower profile than the shrubs on the dunes which comprised fynbos, karroid, Namib and afromontane elements (Taylor 1978) (West Coast National Park [coastal], farm Pampoenvlei [landward edge of coastal plain]). Some traps at Pampoenvlei (sandy loam) were placed on soil with a much higher clay fraction than on the coastal plain. Both sites at Pampoenvlei were in a sheltered kloof which was noticeably warmer than the other sites.

Traps in the Darling Hills, where most natural vegetation has been removed and replaced by a mosaic of pastures and arable land, were placed on predominantly sandy soils with a higher clay fraction. Each of the pasture sites was characterized by dense, low profile cover and, thus, varied only slightly in vegetative characteristics (Fig. M5). There were, however, broad differences in edaphic attributes. The predominantly sandy, well-drained soils of the coast-facing hillside (farm Groote Post) were in sharp contrast to the gritty soils containing a greater clay fraction on the landward side of the Darling Hills (farms Waylands and Oranjefontein). Both of the landward sites showed a high water table as evidenced by occasional retention of water in the bases of the traps. This was particularly noticeable at Oranjefontein where surface moisture persisted into early summer and probably reduced surface temperatures compared with drier nearby sites.

Trapping methods

Trapping methods were broadly similar in both the south-western Cape and the Transvaal. However, owing to the greater abundance of the fauna and

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the warmer temperatures in the Transvaal, fewer traps and a slightly different method of bait presentation were used.

Standardized pitfall traps were used for all trapping (Fig. M6). These comprised a container dug into the soil over which was placed a flat metal plate with a large hole machined from its centre. On each trapping occasion a preserving jar containing 3-6cm of water mixed with a little detergent to immobilize the catch, was placed in the base of the container. A funnel constructed from a metal lampshade with its apex machined out was suspended over the jar by its rim which was slightly larger than the hole in the metal plate. A 0,5*L* bait of cattle dung wrapped in chiffon to exclude insects was supported over the funnel by two lengths of 10 gauge wire.

In the Transvaal, three traps were placed in each habitat and baited early in the morning with fresh dung. These baits were replaced during the late afternoon in order to present fresh dung to both diurnal and crepuscular fauna. Times of baiting varied slightly with season owing to differences in day-length. Trapping was conducted for 24h from Monday to Tuesday each week for one year from November 1983 to October 1984 irrespective of weather conditions.

In the south-western Cape, ten traps were placed in each habitat and baited on three 24h occasions during sunny weather each month for one year from August 1987 till July 1988. Traps were baited only once during each trapping occasion owing to the distance between sites. Baiting commenced during the early morning in the Cape of Good Hope Nature Reserve and was completed by about midday in the Darling Hills on each trapping occasion. Dung baits were stored deep-frozen and defrosted over the 48h-24h before use.

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Specific influence of habitat modification

Limitations were imposed on the direct comparison of species abundances between most sites owing to difficulties in separating the influence of broad climatic variation from that of habitat variables. Therefore, a further set of 13 sites, concentrated in three different areas, was chosen to verify conclusions concerning the influence of replacement of indigenous shrubs by vegetation with differing physiognomy. Sites were selected on the Cape of Good Hope Peninsula, the Rondeberg strip on the west coastal plain and on the farm Groote Post in the Darling Hills (Fig. M7).

On the Cape of Good Hope Peninsula, a comparison was made between the Cape of Good Hope Nature Reserve in which indigenous shrubland is present and cattle absent, and the farm Bonne Attente where cattle are present and indigenous shrubland has been largely replaced by pasture although secondary shrubland occurs in places close to relatively undisturbed indigenous vegetation of the adjoining mountainside. Traps were placed (1) near the main gateway of the reserve where low profile shrubland results from the burning of firebreaks, (2) immediately across the road in a pasture on Bonne Attente and (3) just beyond the pasture in secondary shrubland with a greater amount of high vegetation than that in the reserve as indicated by the larger vegetative height index (Fig. M8).

On the Rondeberg strip, a comparison was made between the beetle fauna of different height classes of indigenous shrubland, large habitat islands cleared of natural shrubs, and shrubland of exotic *Acacia* originating from Australia (Stirton 1983). Traps in indigenous shrubland were placed (1) on dunes dominated by tall shrubs, (2) dunes dominated by lower shrubs in loosely packed, well-drained sand and (3) on coastal flats dominated by restioid shrubs (Fig. M8). Vegetative density was similar at all three shrubland sites and only the height and physiognomy of the vegetation varied. Traps in the pasture islands cleared of natural restioid shrubland were situated (4) in a field established at least ten years previously which had been recently harrowed, and (5) in a broad strip of grassland with patches of *Mesembryanthemum*. Apart from the very low vegetative profile, vegetative density in pasture also differed from shrubland sites being much lower in the harrowed field and much higher in the pasture. The sixth site, in shrubland of exotic *Acacia*, showed a similar canopy density to indigenous shrubland but was much taller (Fig. M8) with very little surface cover. The six trapping sites were situated along a 2km line parallel to the coast across the farms Modderrivier, Rondeberg and Vygevlei (Fig. M7).

On the farm Groote Post, the beetle fauna of sites in alternating strips of (1) tall restioid shrubland and (2) equally sparse low profile pasture cover was compared with that of larger areas consisting of (3) restioid and ericoid shrubland and (4) dense pasture cover (Fig. M8). This study determined to what extent dung beetles discriminated between indigenous shrubland and areas cleared of shrubs. The most suitable area was unfortunately on a shallowly inclined hillside on which the three lower sites were noticeably warmer than the more exposed site of extensive pasture.

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CHAPTER 1

INFLUENCE OF CLIMATE ON SPECIES RICHNESS, ABUNDANCE AND SEASONAL DISTRIBUTION OF DUNG BEETLES IN SOUTHERN AFRICA

Abstract

1. Annual activity of six higher taxonomic groupings (Scarabaeinae/Coprinae, Aphodiinae, Oxytelinae, Histeridae, Hydrophilidae, predatory Staphylinidae) has been studied in pasture and shrubland/open woodland habitats, in winter rainfall climates of the Cape of Good Hope Peninsula and the west coast of the south-western Cape and, in the summer rainfall climate of the Transvaal bushveld.
2. Species richness of most higher taxa increases across a gradient from the cooler south-western Cape to the warmer Transvaal and may be due to increasing seasonal and diel duration of favourable temperatures which results especially in relatively greater numbers of crepuscular/nocturnally active species in the Transvaal.
3. The steeper slope of this trend in the Scarabaeinae/Coprinae may reflect the greater spatial dispersal of dung-burying elements compared to the other higher taxa whose activities are predominantly restricted to the dung pad.
4. Abundance of most higher taxa in shrubland or open woodland also increases across this climatic temperature gradient but in pasture greatest abundance of four higher taxa was recorded on the cool west coast and may be related to lower levels of dung burial providing competitive release for pad-breeding elements resulting in their increased relative abundance particularly during early spring.
5. Largely similar patterns of relative abundance of predatory groups indicates that the predator/prey systems are comparable in each of the habitats in the three climate types.
6. Broad heterogeneity in patterns of relative abundance between the same habitat and climate types in coprophagous groups reflect the changing relationships between these taxa relative to climate.
7. Significantly greater within site variation in annual trap catches in the south-western Cape may be due to greater seasonality than in the Transvaal.
8. Seasonal peaks in activity by the most abundant groups of taxa were maximized towards the most favourable seasonal conditions during the mid-summer rainy season in the Transvaal and towards the increasing temperatures and declining rainfall of spring in the south-western Cape.

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9. Atypical seasonal activity peaks by some groups during early winter or early spring in both the Transvaal and the south-western Cape may represent taxa evolved under cooler past climatic conditions when winter rainfall occurred over wider areas of southern Africa.

10. Greater consistency in seasonal activity peaks of the higher taxa in the Transvaal which occurred during December and January may reflect the predominantly summer rainfall origins of the fauna.

11. Greater variation in seasonal activity peaks of higher taxa in the south-western Cape may result from the wider climatic origins of the fauna with spring peaks in coprophagous taxa probably numerically dominated by winter rainfall elements and early summer, mid-summer and early winter peaks in predatory groups reflecting greater numbers of species also recorded from the summer rainfall region.

The climate of southern Africa results from seasonal periodicity in the relative influence of two major air flow systems, the easterlies and the westerlies (Tyson 1986). Strengthening and northward expansion of the westerlies during winter and southward expansion of the easterlies during summer coincide with seasonal increases in waves of disturbance in these air currents which bring rainfall. Waves of disturbance in the easterlies show an annual cycle of variation with maxima in mid-summer and control summer rainfall over the interior plateau of South Africa (Harrison 1986). Waves of disturbance in the westerlies show a bimodal annual cycle of variation with maxima in autumn (March-May) and spring (September-November) (Tyson 1986). They are responsible for the remaining rainfall particularly in coastal regions where contribution of the westerly component increases to the south.

The net result of these various influences is a seasonal gradient in occurrence of peak rainfall from the north-east to the south-west over southern Africa. For instance, peak rainfall in the central Transvaal is during mid-summer in December and January, in the northern Cape it is during late summer in March and in the south-western Cape during mid-winter in June and July. Peaks in rainfall in the eastern Cape show the same bimodal periodicity as the maxima in disturbance of westerly air waves, one in autumn during March-May and the other in spring during September-November. These equate to the rainfall patterns in the four major climatic regions of southern Africa recognized by Davis (1987) and derived from the climatic classification of Walter & Lieth (1964).

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The northward expansion of westerly air currents (Tyson 1986) about 3 MYBP (million years before present) (Deacon 1983) probably displaced the summer rainfall system towards the Transvaal. The resulting seasonal differences in the distribution of rainfall in the south-western Cape and the Transvaal represent systems which are, in essence, climatic opposites. The composition and seasonal activity of the dung beetle fauna of the south-western Cape is, therefore, compared with that of the Transvaal and possible reasons for the differences are presented.

Analytical methods

Data from 13 study sites, three in climate type IV on the Cape of Good Hope Peninsula, eight in climate type III(IV)a on the west coast of the south-western Cape and two in climate type II3d in the southern-central Transvaal bushveld were used for the analysis of the seasonal distribution of species.

Relationships between the seasonal distributions of species within each taxonomic grouping in each climatic area were determined by first constructing data matrices for each of four higher taxonomic groupings (Scarabaeinae/ Coprinae, Aphodiinae, Staphylinidae/Hydrophilidae, Histeridae) in each of the three climatic areas. These comprised the mean abundance per trap per month for each of the more abundant species. In order to emphasize principal distributional trends, uncommon species were deleted from the analyses according to the trapping intensity in each of the climatic areas. In the Cape of Good Hope Peninsula, those species whose sum of monthly means was <0,15 were deleted. For the west coast samples the level of deletion was <0,06 and for the Transvaal <0,51. Data for each species in the resulting matrices were converted to percentage seasonal distribution to give equal weighting to each species.

The Clustan computer package was used for the analysis (Wishart 1984). The procedure was as follows. Similarity matrices were constructed from each data set using the squared euclidean distance similarity coefficient. These matrices were subjected to cluster analysis using an agglomerative technique, group average sorting. The results were summarized as dendrograms and histograms (Addendum, Figs AD1-7.).

Groups of species showing similar seasonal distribution were defined from the dendrograms (Addendum, Figs AD1-3.) and ranked according to group abundance. Mean data for those groups showing greatest abundance (>7% of total

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abundance) or comprising >10 species were subjected to a second cluster analysis in order to determine principal seasonal trends.

Cross climatic trends in species richness

In order to compare trends across climatic regions, values for species richness and abundance were standardized by conversion to ratios. Steepness of trends was compared using the slope of lines fitted to the ratios by linear regression.

Species richness increases across a climatic gradient from the cooler climate type IV to the warmer type II3d in all higher taxa except pasture hydrophilids (Table 1.1.). As dung beetle activity is correlated with rainy periods (e.g. Halffter & Matthews 1966, Davis 1989b), it is probable that both the higher summer temperatures of the Transvaal and their coincidence with summer rainfall has provided a wider range of favourable conditions leading to greater species richness than that recorded in the cooler south-western Cape where the warmest annual temperatures coincide with the dry season.

The greater number of species in the Transvaal is probably also explained by the longer daily duration of higher temperatures favourable for dung beetle activity since warm temperatures after nightfall support a much larger number of crepuscular and nocturnally active taxa than in the cooler south-western Cape (Table 1.2.). In the Transvaal, numbers are evenly distributed between diurnal and crepuscular/nocturnal flight activity in four groups including the Scarabaeinae/Coprinae. This is in marked contrast to the same group in the south-western Cape where diurnal species predominate and all but two of the crepuscular/nocturnal species have probably recently dispersed into the area from the summer rainfall region (Chapter 5).

In general, the slope of the trend in species richness is steeper for species assemblages of shrubland/open woodland than for those of pastures (Table 1.1.). This may be the result of exceptionally low species richness in the shrubland of the Cape of Good Hope Nature Reserve due to the absence of cattle. The similar magnitude of the difference between species richness at pasture and shrubland/open woodland sites on the cool west coast of the south-western Cape and in the warmer Transvaal would tend to support this suggestion (Table 1.3.) when compared to the greater difference shown between habitats in the Cape of Good Hope Peninsula.

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The slope of the trend to greater species richness in both habitat-types towards the Transvaal is much greater in the Scarabaeinae/Coprinae than in the other five higher taxa (Table 1.1.). This may be related to the lower spatial restriction on dung-burying/ball-rolling taxa which disperse away from the dung. Activity of the other species groups is largely limited to the pads. A similar explanation is offered by Hanski & Hammond (1986) to explain shallow latitudinal gradients in species richness of dung-breeding Staphylinidae from temperate regions to the tropics in the northern hemisphere.

Cross climatic trends in abundance

Trends in abundance across the climatic gradient from cooler climate type IV to the warmer type II3d differed somewhat between habitats (Table 1.4.). In the shrubland/ open woodland, the trend to greater abundance in the Transvaal is very much steeper than in pasture in all groups except the Oxytelinae. This may be partly related to the absence of cattle from the shrubland of the Cape of Good Hope Nature Reserve and the presence of only a small population of buck which drop collections of dung pellets that are unsuitable for beetles which breed within dung. Therefore, as shown for species richness, the steeper slope of the trend in shrubland may be the result of an exceptionally low abundance of dung beetles in the reserve. The greater similarity of the magnitude of differences in abundance of five higher taxa between pasture and shrubland/open woodland on the cool west coast of the south-western Cape and in the warmer Transvaal (Table 1.5.) would tend to support this suggestion when compared to the much greater difference shown between habitats in the cool Cape of Good Hope Peninsula. The increased abundance of most groups in Transvaal open woodland sites, compared to the Cape (Table 1.4.), is probably also partly due to the coincidence of rainfall with longer seasonal duration of high temperatures favourable for the exploitation of dung. On the other hand, the distinctly greater abundance of most higher taxa in open woodland as opposed to Transvaal pasture sites (Table 1.5.) may reflect the presence of shade which reduces the rate of desiccation in some pads thus influencing the abundance of both pad-breeding and dung-burying taxa.

The greater abundance shown by four out of the six higher taxa in cool west coast pastures (Table 1.4.) may be related to differences in the amount of dung removed from pads in the cooler south-western Cape and warmer Transvaal

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climate-types. Dung removal has been shown to reduce breeding success of Coleoptera which breed within dung pads both in the laboratory for Staphylinidae (Roth 1983) and in the field for pad-breeding species of Coprinae (Davis 1989b).

Abundance of dung-burying Scarabaeinae/Coprinae is relatively low on the west coast (Fig. 1.1., Table 1.4.) particularly the large Coprinae (Coprina, Dichotomiina, Onitini) which bury relatively larger amounts of dung than most other taxa and comprise only 1,9% of the Scarabaeine/coprine fauna of the south-western Cape compared to 11,9% in the Transvaal. This results in a much lower level of dung removal than in the Transvaal (Fig. 1.2.).

Although dung removal levels were equally low in the cool Cape of Good Hope Peninsula (personal observation), warmer spring temperatures probably account for the greater population density of the pad-breeding groups on the west coast. This is particularly true of the Oxytelinae and the Aphodiinae in which *Anotylus caffer* and *Coptochirus brachypterus*, respectively, showed extreme numerical dominance during spring and may represent examples of density compensation in the absence of competition by other cold-adapted taxa.

It is interesting to note that the numerically dominant Cape oxyteline, *A. caffer*, is, respectively, 12 and 2,4 times larger than its Transvaal counterparts, *A. latiusculus* and *A. okahandjanus* so that biomass of this group in the south-western Cape is relatively even greater than in the Transvaal. Thus, selection of oxyteline taxa in the south-western Cape and the Transvaal seems to favour different body sizes.

It is unclear why the trend to greater abundance on the west coast is only recorded for the Oxytelinae in shrubland but this may be related to the more patchy distribution of favourable temperatures due to the partially shaded nature of the shrubland habitat. Position of shaded patches and duration spent in shade will vary with the diel movement of the sun in relation to vegetative profile creating great heterogeneity in insolation of the soil surface.

The relative abundance of the six higher taxa indicates differences between predators and coprophages in their response to the climatic gradient (Fig. 1.1.). Largely similar patterns of relative abundance for the three higher predatory taxa suggests that the predator/prey systems are comparable in most situations. However, the three higher coprophagous taxa show four different patterns of relative abundance indicating much greater variation in their relationships. As discussed above, this may reflect different relative breeding success of elements which breed within dung pads under conditions of low percentage dung burial and

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low temperatures in the Cape of Good Hope Peninsula, higher temperatures and low percentage dung burial on the west coast and high temperatures and high percentage dung burial in the Transvaal.

Within site variation around the mean abundance per trap for the six higher taxa on each trapping occasion over the course of one year was significantly different between the two habitat and three climate types (F = 10,904, d.f. = 5,30, P<0,001, Analysis of variance) (Table 1.6.). The source of the variance was the greater within site variation at habitats in the south-western Cape climate types. This may be connected with the greater seasonality under the winter rainfall system which is probably expressed by a greater frequency of conditions unfavourable for activity, even during periods of peak abundance during the cool spring, compared with those in the warmer Transvaal.

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Seasonal distribution of dung beetles in different climatic regions

The more species rich or abundant species groups (Addendum, Figs AD1-7.) showed four principal seasonal trends at the 40% level of similarity (Fig. 1.3.). Two of these comprised the greatest number of groups and presumably showed maximization to the most favourable periods for activity in either the winter or summer rainfall climatic regions (Fig. 1.4.). Activity peaks of most south-western Cape taxonomic groups (Group A) were concentrated into a three month period from September to November during spring and early summer which was characterized by decreasing rainfall and increasing temperatures. Activity peaks of most Transvaal species groups (Group B) were concentrated into a three month mid-summer period between December and February which coincided with annual peaks in temperature and rainfall. However, this group also included three groupings of taxa in the south-western Cape where their mid-summer activity period coincided with the dry season which was unfavourable for activity by dung beetles. These groupings (SCWCB, STWCB, HIGHB) were, thus, characterized by relatively low abundance and mainly (90%) comprised species known to occur in the summer rainfall region.

Activity peaks of comparatively few groups occurred during the cool autumn and early winter or during early spring in both the Transvaal and the south-western Cape (Groups C,D). Although examples in Figure 1.3. were restricted to the Aphodiinae and Histeridae, groups of relatively uncommon Scarabaeinae/Coprinae and Staphylinidae/ Hydrophilidae also showed similar seasonal patterns of activity (Addendum, Figs AD1-3., 6, 7.).

The autumn-active Aphodiinae of the Transvaal were distinctive in that they showed greater generic richness (*Aphodius* (*Bodilus*), *Colobopterus*, *Pseudoxymus*, *Drepanocanthus*, *Coptochirus*) and were, therefore, taxonomically distinct from the summer-active group (*Aphodius*, *Colobopterus*) (Addendum, Fig. AD3c.). The autumn or early spring active aphodine fauna of the south-western Cape was taxonomically closer (*Aphodius*, *Drepanocanthus*, *Coptochirus*) to the autumn-active group in the Transvaal than to the summer-active group (Addendum, Figs AD1c., AD2c.). The cold-adapted autumn or spring-active groups in the south-western Cape showed great abundance (Fig. 1.3.) and comprised up to three species of *Coptochirus* occurring sympatrically at a single study site, including the species recorded in the Transvaal although this may be a close but taxonomically separable relative. The relatively less abundant, dry-season, autumn- active, Transvaal group may, therefore, include seasonal relicts resulting from northwards expansion of the winter rainfall climate during glacial periods.

There was a greater consistency in the seasonal distribution of the six higher taxa in the Transvaal than in the south-western Cape (Fig. 1.5a-f.) which may reflect the summer rainfall origin of most of the Transvaal fauna. Seasonal peaks in activity of all groups occurred during December and January. Weather during the trapping period was atypical (Fig. M3) in that rainfall declined and temperature correspondingly increased from November leading to unseasonal drought which was most intense in February. Whereas results for February may, therefore, have been atypically low, the overall seasonal pattern of activity corresponds closely to seasonal variation in dung removal activity by Transvaal Scarabaeinae/Coprinae (Davis 1989b) during years of higher rainfall.

The greater variability of seasonal peaks in activity by the six higher taxa on the west coast of the south-western Cape may reflect the mixed origins of the fauna from both the winter and summer rainfall regions. The coprophagous groups, Scarabaeinae/Coprinae, Aphodiinae, Oxytelinae, are clearly numerically dominated by cold-adapted, predominantly winter rainfall elements as evidenced by their spring peaks in activity (Fig. 1.5a-c.). However, the predatory groups show peaks in seasonal activity biased towards warmer weather at the end or beginning of the rainy season (Fig. 1.5e,f.) or in the middle of the dry season (Fig. 1.5d.). These groups are known to include more species in common with the trapping sites in the Transvaal than most of the coprophagous higher taxa (Table 1.7.). Activity in

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climate type IV on the Cape of Good Hope Peninsula was comparable to that on the west coast in all groups except the Aphodiinae which have been discussed above in relation to Figure 1.3.

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CHAPTER 2

SPATIAL DISTRIBUTION OF COPROPHILOUS COLEOPTERA IN THE SOUTH-WESTERN CAPE

Abstract

1. A trend from relatively discriminate to a more widespread spatial distribution was shown across a taxonomic gradient from the Scarabaeinae/Coprinae through the Aphodiinae and Histeridae to the Staphylinidae/Hydrophilidae.
2. In a set of study sites subject to different climatic conditions but situated on a similar soil type, this result was largely a response to vegetation-type comprising indigenous shrubland or pasture with which the shrubs have been recently replaced.
3. With the removal of data for single superabundant and widespread species from the Aphodiinae and Staphylinidae/Hydrophilidae, respectively, principal components analysis showed that in all higher taxa the fauna of the shrubland sites showed the closest correlation to the factor accounting for the greatest amount of variance which is consistent with the greater spatial heterogeneity in this habitat-type.
4. Species groups with distributions skewed towards either shrubland or pasture were shown for all taxa but a greater number of statistically significant associations with shrubland or pasture were shown for the Scarabaeinae/Coprinae than for other higher taxa which showed only pasture specialists.
5. This trend was consistent with the taxonomic gradient in spatial distribution of higher taxa and may reflect the relative specialization to, and age of, coprophilous habits in each higher taxon and their relative age in the fauna of the south-western Cape.

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The spatial distribution of dung beetles is influenced principally by climate (Kirk & Ridsdill Smith 1986), soil-type (e.g. Nealis 1977) and vegetation-type (e.g. Howden & Nealis 1975, Cambefort 1982a, Doube 1983, Lumaret 1983). In the present study, trapping sites were distributed across two climatic areas of the south-western Cape (types IV, III(IV)a in two principal vegetation-types, shrubland and pasture. An effort was made to standardize soil-type by selecting sites on sand or predominantly sandy soils. Therefore, the analysis of spatial distribution was expected to be mainly influenced by climate and vegetation-type although microclimatic variables induced by edaphic attributes, particularly the high water table at several sites, were also expected to be influential. The results were used to determine relative spatial specialization in higher taxa and are discussed in terms of their relative specialization to coprophily and their relative age in the fauna of the south-western Cape.

Analytical methods

The manner in which space was partitioned by the taxonomic groupings was determined by first constructing data matrices comprising mean abundance per trap for each species of each grouping in each of the 11 trapping sites. Size of the matrices was as follows, 11 habitats by 45 species for the Scarabaeinae/Coprinae, 11 X 31 for the Histeridae, 11 X 34 for the Aphodiinae, and 11 X 87 for the Staphylinidae/Hydrophilidae. Principal components analyses (PCA) were conducted on these matrices to determine the relationships between the fauna of different localities. Eigenvectors were rotated using the varimax method. The CRISP computer package was used for this analysis.

Relationships between the spatial distributions of individual species were determined by first deleting those species whose sum of mean abundances/trap across the 11 sites was <0,04. This reduced the size of the matrices to 11 X 37 for the Scarabaeinae/Coprinae, 11 X 22 for the Histeridae, 11 X 23 for the Aphodiinae, and 11 X 47 for the Staphylinidae/Hydrophilidae. Abundances across the 11 sites were converted to percentages to give equal weighting to the distribution of each species. These matrices were subjected to cluster analysis using the Clustan computer package as described in analytical methods (Chapter 1).

Groups of species showing similar spatial distribution were defined from the dendrograms derived from this analysis (Addendum, Figs AD8., AD9.). To determine principal trends in habitat associations, the more abundant (>15% of total abundance for each taxon) or more species rich groups (>9 species) were subjected to a second cluster analysis.

Owing to the great climatic variation across the area occupied by the trapping sites, only the shrubland and pasture sites in West Coast National Park were sufficiently close (3-400m) for direct comparison of beetle abundance to be made with any degree of confidence that vegetation-type was the only variable influencing their distributions. Therefore, the mean number of beetles/trap on each

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of 36 trapping occasions in shrubland was compared with those in the adjacent pasture site for 38 species from four different families.

Comparison of spatial partitioning by higher taxa

Higher taxa of dung beetles show a trend from greater to lesser discrimination in spatial distribution (Table 2.1.). The Scarabaeinae/Coprinae are strongly influenced by three factors, the Histeridae and Aphodiinae by two and the Staphylinidae/Hydrophilidae by one. This probably results from an increasing percentage of spatial generalists included in each taxon across the gradient from Scarabaeinae/Coprinae to Staphylinidae/Hydrophilidae. Increasing generalization in spatial distribution across the same gradient probably also accounts for the decreasing degree of separation between clusters of data points in the ordination plots (Fig. 2.1.).

Proximity or distance between ordination data points represent similarity or dissimilarity of the faunal composition at each study site. Data points formed at least two loose but distinct clusters for each higher taxon except the most generalist, the Staphylinidae/Hydrophilidae, which formed a single cluster of sites. Separate clusters were each dominated by either pasture or shrubland sites, which indicates that vegetation-type probably accounts for the greatest amount of variance in spatial distribution with some within cluster separation possibly influenced by climate.

The Scarabaeinae/Coprinae show clear faunal separation between shrubland and pasture sites except at the pasture island in West Coast National Park where the fauna is very close to that of the surrounding shrubland (Fig. 2.1a.). PCA has divided the sites into west coastal plain sandveld situations resulting from a marine regression in the Pliocene (Hendey 1983), shrubland sites on the peninsula showing their own distinctive faunal composition and, pasture localities in the Darling Hills and the Cape of Good Hope Peninsula. Ordination of spatial distribution data for the Histeridae produced a cluster of sites on the west coastal plain of Pliocene origin dominated by shrubland but including the pasture island in West Coast National Park and a second cluster of sites in the Darling Hills and the Cape of Good Hope Peninsula dominated by either pasture or fynbos (Fig. 2.1b.).

In the other two higher taxonomic groupings regional influence in faunal affinities is less apparent. A similar fauna of Aphodiinae was indicated at all

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grassland sites and also at two of the lower profile, Restio-dominated, shrubland sites (Fig. 2.1c.) in the 2-3yr old fynbos on the Cape of Good Hope Peninsula and on the west coastal plain at Modderrivier. Two distinct elements of shrubland associated Aphodiinae were also indicated by the separation of fauna at the older 9-10yr old fynbos in the Cape of Good Hope Nature Reserve and those on dunes of the west coastal plain where the shrubs were taller and both taxonomically distinct and structurally denser than those at Modderrivier. The Staphylinidae/Hydrophilidae apparently showed extreme generalization with no clear separation of pasture and shrubland sites on the basis of faunal composition.

The trend to generalization in distribution shown by the Aphodiinae and the Staphylinidae/Hydrophilidae (Table 2.1., Fig. 2.1c,d.) is strongly influenced by the extreme abundance and widespread occurrence, respectively, of *Coptochirus brachypterus* and *Anotylus caffer*. Removal of data for *C. brachypterus* from a second PCA of spatial distribution of the Aphodiinae produced radically different results (Fig. 2.1e.) to those in the first analysis (Fig. 2.1c.). Results for the second analysis are extremely close to those shown for the Scarabaeinae/Coprinae (Fig. 2.1a.) indicating a high degree of spatial discrimination in the remaining aphodine species. A second PCA conducted on the spatial distribution of the Staphylinidae/Hydrophilidae after removal of the data for *A. caffer* shows that the group distribution of the less abundant species remains more generalist than in other higher taxa (Table 2.1., Fig. 2.1f.). However, faunal separation relative to vegetation type is more accentuated resulting in distinct polarity of pasture and shrubland sites within a loose single cluster of all sites except Bonne Attente (Fig. 2.1d,f.).

Over the taxonomic gradient shown in Table 2.1., the first analyses showed a trend for clusters dominated by shrubland sites to show closest correlation to the factor accounting for the greatest amount of variance in the Scarabaeinae/Coprinae and the Histeridae and for clusters dominated by pasture sites to show closest correlation to the factor accounting for the greatest amount of variance in the Aphodiinae and probably the Staphylinidae/Hydrophilidae. In the second analyses, after removal of the species showing extreme abundance, clusters dominated by shrubland sites showed closest correlation to the factor accounting for the greatest amount of variance in all higher taxa. This is consistent with the expectation that greater heterogeneity in faunal distribution would be associated with the greater spatial heterogeneity at shrubland sites, i.e. a mosaic of shaded and relatively unshaded situations. The reason for the greater variance amongst the

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fauna at pasture sites for Aphodiinae and Staphylinidae/Hydrophilidae in the initial analyses is the high relative abundance of *C. brachypterus* and *A. caffer* at pasture sites in the Darling Hills (Fig. AD8c., Group C; AD8d., Group A) compared to their occurrence in other (coastal) pasture sites and in shrubland.

Separation of data points within the principal clusters seems to represent sites influenced by cooler temperatures. This has produced the greatest response in the Scarabaeinae/Coprinae and little response in the Staphylinidae/Hydrophilidae. In the Scarabaeinae/Coprinae the separation of sites on the west coastal plain from those in the Cape of Good Hope Nature Reserve along Factor 1, reflects general similarity coupled with specific differences in the composition of the fauna probably related to climate type. Within cluster separation of fauna along Factors 1 and 2 in other higher taxa involves the same coastal sites in the cool Cape of Good Hope Peninsula or that at Oranjefontein with its high water table (Fig. 2.1b-f.).

Factor 3 may represent variation in faunal composition and relative abundance induced by differences in soil surface temperature between sites. Although this is speculative in the absence of surface temperature records, greatest correlation to the factor was shown by the fauna of the two low profile shrubland (fynbos) sites which occupied very exposed situations on the Cape of Good Hope Peninsula. Correlation to this factor was also shown to a lesser extent by the fauna at most other coastal sites (Fig. 2.1a.) and also, especially, by that in the pasture at Oranjefontein where the water table was extremely high. This would cause very cool surface temperatures due to loss of latent heat by evaporation and possibly accounts for the differences in the seasonal activity by *Euoniticellus triangulatus* between sites in the Darling Hills. At Oranjefontein, *E. triangulatus* showed a somewhat leptokurtic curve of activity concentrated into mid-summer, whereas at drier nearby sites, particularly at Groote Post, it was abundant throughout the dry season forming a platykurtic curve of activity.

Despite increasing spatial generalization across the taxonomic gradient shown in Table 2.1., abundant or species rich groups associated with either pasture or shrubland were demonstrated for all higher taxa (Figs 2.2., 2.3.). However, the distribution of species richness and abundance between the shrubland and pasture groups was consistent with the taxonomic gradient shown by higher taxa. In particular, species richness was fairly evenly shared between shrubland and pasture groups in all higher taxa except the Staphylinidae/Hydrophilidae in which the majority of the species occurred in groups with distribution skewed towards

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pasture (Table 2.2.). Abundance of groups showing a bias to either shrubland or pasture distribution (>60% of numbers) were fairly similar in the Scarabaeinae/ Coprinae and the Histeridae but in the Aphodiinae and the Staphylinidae/Hydrophilidae, the greatest percentage of total abundance occurred in groups with distributions biased towards pasture (Table 2.2.). The most abundant groups biased towards shrubland distribution in the Histeridae and the Aphodiinae (Addendum, Fig. AD8b., Group C; AD8c., Group B), which occupy an intermediate position on the higher taxonomic gradient (Table 2.1.), also both showed some abundance in the dry pastures of the West Coast National Park and Groote Post.

The trend shown by habitat associations of the individual species of higher taxa (Table 2.3.) was also consistent with the higher taxonomic gradient from discriminant to more generalized spatial distribution (Table 2.1.). Statistically significant associations with vegetation type were shown by 63,6% of the Scarabaeinae/Coprinae compared with only 18,5% for the other taxa. Both pasture and shrubland associations were demonstrated for the more abundant Scarabaeinae/Coprinae but only pasture specialists were shown for the other groups.

On the assumption that radiation and specialization of habit occurs as a function of time, it is suggested that the taxonomic gradient in spatial distribution (Table 2.1.) may reflect the relative age of coprophilous habits in each higher taxon. The most discriminate group, the Scarabaeinae/Coprinae, are known to be predominantly coprophagous at subfamily level and to have Gondwanaland origins (Halffter & Matthews 1966) whereas coprophilous habits in the Aphodiinae are thought to be more recent since many taxa are saprophages (Halffter & Matthews 1966). Coprophilous habits in the Hydrophilidae are probably also recent as they show predominantly aquatic habits whereas the staphylinid subfamilies, Oxytelinae and Tachyporinae are known to be generalist frequenters of decaying matter including dung (Britton 1970).

It is probable that shrubland was the dominant physiognomic vegetation type when Europeans first arrived in the south-western Cape (Acocks 1975). Since that time much of the shrubland has been cleared for agricultural purposes. In cattle pastures it has been replaced by grassland . In the present study, distinct shrubland elements have been shown for all higher taxa (Figs 2.1., 2.2.) but statistically significant associations with shrubland have been shown for only the Scarabaeinae/Coprinae (Table 2.2.) which are the spatially most discriminant group (Table 2.1.). In the Aphodiinae and, especially, the Staphylinidae/Hydrophilidae,

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distributions of a majority of species are skewed towards occurrence in pasture. Owing to their distributional bias to an apparently younger vegetation type, this may represent a more recent colonization of the area than in the Gondwanaland Scarabaeinae/Coprinae, at least in the lowlands where the study was conducted.

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CHAPTER 3

GENERALISTS AND SPECIALISTS IN THE DUNG BEETLE FAUNA OF THE SOUTH-WESTERN CAPE

Abstract

1. Generalists are characterized by high fecundity and wide geographical range, specialists by low fecundity and restricted geographical range.
2. Indices representing relative generalization/specialization of species assemblages of higher taxa at each study site have been derived from data on spatial distribution and potential fecundity (number of follicles in the ovary) by two different methods.
3. In method one, each index was derived by summing the products of a species percentage abundance in each assemblage times its coefficient of variation (mean/standard deviation) across 11 study sites.
4. In method two, each index was derived by summing the products of a species percentage abundance in each assemblage times its rank position determined from combined data sets on size of geographical range in southern Africa and number of follicles in the ovary.
5. Distribution of rank series of coefficients of variation or size of geographical range for species assemblages of higher taxa from 11 study sites in the south-western Cape were best described by exponential curves which are well known to describe population growth.
6. This is not surprising since generalist and specialist attributes are by definition linked to differential rates of population growth which in turn influence size of geographical range.
7. Scarabaeinae/Coprinae comprised significantly more specialist species than the Histeridae, Aphodiinae and Staphylinidae which is consistent with the relative spatial discrimination of the taxa and their relative specialization to coprophilous habits.
8. Assemblages of Scarabaeinae/Coprinae comprised significantly more specialist species in indigenous shrubland than in pasture with which shrubs have been recently replaced.

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Each species of animal has a bionomic strategy characterized by the combined parameters of size, longevity, fecundity, range and migration habit (Southwood 1976). Species biased towards *r*-strategy show high fecundity, a high intrinsic natural rate of population increase (*r*) and short generation time. This leads to rapid growth in population size which increases intraspecific competition and tends to expand the species range (Giller 1984) thus favouring opportunistic and adaptable habits. Species biased towards *K*-strategy show low fecundity, low values of *r*, and low rates of mortality and recruitment of filials. Through increased interaction with its resources (Stearns 1977) fitness of such populations maximizes towards the carrying capacity (*K*) of the habitat (Southwood 1976) with the passage of time resulting in competitive superiority over the narrow niche width that they occupy. They occur in predictable situations and are often large, long-lived and may exhibit parental care. In general, *K*-strategists breed slowly and occupy restricted ranges whereas *r*-strategists tend to breed rapidly and occupy large ranges (Southwood 1976). *K*-strategists tend to be sensitive to change, therefore, clearance of indigenous shrubland in the south-western Cape and its replacement by a physiognomically different vegetation type is likely to have been detrimental to *K*-strategists and favourable to the more adaptable *r*-strategists.

Use of the terms *r* and *K*-selection have been criticized by Stearns (1977) on mathematical grounds. The term, *r*, can be expressed quantitatively as a function of life history traits and is, therefore, a population parameter. In contrast, *K* is a composite of the population, its resources and their interaction (Stearns 1977). It is not a population parameter. Thus, whilst the *r* - *K* continuum (Pianka 1970) has philosophical value it has no mathematical validity as it has not been possible to express *r* and *K* in common terms. Many modern workers have circumvented this problem by using the terms, "generalist" (substitutes for *r*-strategists) and "specialist" (substitutes for *K*-strategist), which carry no mathematical implications.

Generalization/specialization may be implied using relative values of *r*, the intrinsic rate of increase of natural population size. However, obtaining data for the calculation of this parameter is a time-consuming exercise. Therefore, the present chapter examines several ways of quantifying generalist or more specialist attributes from the size of species ranges or the number of follicles in the ovary (potential fecundity). The results are used to examine relative generalization/specialization in different taxonomic groups in different habitats. They support the findings of Chapter 2 which indicate a taxonomic gradient between

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higher taxa which has been linked to the relative age of coprophilous habits and to habitat associations of the fauna of the south-western Cape.

Analytical methods

Two principal methods have been developed to produce indices of relative generalization/specialization of faunal elements in the south-western Cape. One of these has been derived entirely from the spatial distribution data collected for the six higher taxonomic groupings during the present study. The other index has been derived using this data in conjunction with geographical distribution data for Scarabaeinae/Coprinae in southern Africa and data on the number of follicles in their ovaries which is probably related to potential fecundity. Method two has been used only for the Scarabaeinae/Coprinae since available geographical distribution and breeding data for the other five higher taxonomic groupings is inadequate.

The geographical distribution of the 45 species of Scarabaeinae/Coprinae recorded in the south-western Cape during the present study has been quantified by summing the number of degree squares of latitude and longitude in which each species was recorded south of latitude 15° S in southern Africa. The information has been drawn from the reference collection of the former CSIRO Dung Beetle Research Unit which was amassed over a period of 15 years (Davis 1986) and from published distribution records for the subtribe Canthonina (Scholtz & Howden 1987a,b, Howden & Scholtz 1987). The results have been allotted a number from one upwards according to their rank position from smallest to largest distributional range.

It has been noted that the number of follicles in the ovaries of Scarabaeinae/Coprinae varies from few in *Scarabaeus* and *Copris* to many more in *Onthophagus* (Halffter & Matthews 1966). This trend seems to parallel a trend from specialized nesting behaviour featuring low fecundity and parental care to relatively more generalized behaviour incorporating higher fecundity and production of many broods which are immediately abandoned by the parent. This suggests that the number of follicles in the ovary is likely to be proportional to the relative generalization/specialization of the species. Therefore, the number of follicles in the ovaries of 28 of the 45 species of Scarabaeinae/Coprinae recorded in the south-western Cape during the present study were determined by dissection and the mean

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results allotted a rank number from smallest to largest value as for geographical distribution data.

To combine these two data sets, mean rank positions were calculated for those species for which both geographical distribution and potential fecundity data were available. Where necessary, these rank numbers were rearranged in sequence with the rank positions for those species for which only geographical distribution data was available.

Spatial distribution data from the 11 study sites in the south-western Cape was prepared by converting real abundance of individual species to percentage of total abundance in each species assemblage of the six higher taxonomic groupings in order to give equal weighting to the fauna at each study site. These percentage values for each species were then multiplied by an integer derived for each species from either method one or two. In method one, these integers were the coefficients of variation (mean/standard deviation) in spatial distribution across the 11 study sites for each species. In method two, each integer was the mean rank position occupied by that species as calculated from the combined rank series of size of geographical range and numbers of follicles in the ovary. The products of percentage abundance times the integer were summed for each species assemblage to produce an index of relative generalization/specialization. In each case, the smaller the index, the relatively greater the specialization.

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Distributional trends shown by generalists and specialists

Generalist or specialist habits are by definition linked to the rate of population growth which in turn is linked to the size of geographical range. In the present study, generalization/specialization has been quantified for assemblages of higher taxa using the coefficient of variation in spatial distribution across 11 study sites in the south-western Cape and for the Scarabaeinae/Coprinae using size of geographical range within southern Africa. If these attributes are ranked from smallest (most specialist) to largest (most generalist) values, the distributions are mostly best described by exponential curves (Table 3.1., Figs 3.1., 3.2.). Such curves are well known to define population growth.

Clear differences in relative generalization/specialization were shown between different higher taxa (F = 210,15, d.f. = 5,60, P<0,001, Analysis of variance) (Table 3.2.). Although the hydrophilids appeared to have the most specialist distribution, this is thought to represent a patchy marginal occurrence in the south-western Cape since most of the six species recorded are known to be widespread in the summer rainfall region to the north. If the results for the Staphylinidae and Hydrophilidae were combined, then the taxonomic sequence from specialist to more generalist fauna was the same as that shown by principal components analysis (PCA) of spatial distribution of the higher taxa in the south-western Cape (Chapter 2).

Although the method supported the findings of PCA, it was not useful for demonstrating differences in habitat associations probably because the coefficients of variation were derived from distributions over too small a geographic area. For instance, larger coefficients of variation (more generalist) were shown for some species endemic to the winter and bimodal rainfall regions which occurred in both shrubland and pasture than for those which occurred over much wider areas but were found mainly in pastures in the south-western Cape. Only predatory Staphylinidae were shown to be significantly more specialized and that in pasture situations. This may represent more limited penetration into shrubland in this group (Chapter 2).

The second method which could be developed only for the Scarabaeinae/Coprinae used geographical distribution data throughout southern Africa in conjunction with data for potential fecundity. The indices derived from this method clearly showed that the fauna in indigenous shrubland was significantly more specialist than that in pasture with which native shrubs have been recently replaced (Table 3.3.).

Rank species abundance of higher taxa at each site was best described by exponential curves (Table 3.4., Fig. 3.3.). This is, of course, the same as the straight line relationship in rank log. abundance which describes species diversity patterns. A straight line is the well-known distribution of exponential data expressed in terms of logarithms.

However, species assemblages in any given habitat, of course, comprise a mixture of specialists and generalists which are better adapted to that site and are, therefore, competitively superior to some generalists and possibly some specialists at the margins of their distributional range. This explains why the most abundant species at each pasture and shrubland site was relatively generalist (Table 3.5.) and why there is no correlation between rank position for the 12 most abundant species and values for their relative generalization/specialization based on size of geographical range at either shrubland (r = 0,119; d.f. = 11; not

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significant) or pasture sites (r = 0,368; d.f. = 11; not significant). However, there were significantly more specialist elements in the rank series of the 12 most abundant species at shrubland sites than at pasture sites (Table 3.5.).

Discussion

On a purely philosophical level, *r* and *K* may be defined as directional forces on a theoretical continuum. In terms of the taxon cycle, or "taxon pump", animals and plants evolve from generalist towards specialist, particularly in isolated populations at the edges of species ranges (Ricklefs & Cox 1972) or on islands (Wilson 1961). This suggests that there must be a permanent pool of flora and fauna with relatively generalist habits. This will be associated predominantly with large, spatially heterogeneous areas which favour adaptability such as the summer rainfall region of tropical and warm temperate southern Africa. The inception of winter rainfall climate and the development of shrubland as the dominant physiognomic vegetation type in the south-western Cape has provided the selective pressure for a specialized dung beetle fauna in the region. This geographically small, climatic island lies at the southern margins of the large, diverse region of summer rainfall climate.

Maximization towards the carrying capacity of a habitat requires time. Therefore the more specialized a taxon in a given situation, the older it is likely to be. This suggests that the Scarabaeinae/Coprinae which are known to have Gondwanaland origins contain older evolutionary elements than the other higher taxa with the dung Staphylinidae represented by relatively young taxa in the south-western Cape.

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distribution model is widely used in entomological research and seems to apply mainly in situations where one or a few factors dominate the ecology of the species assemblage (Magurran 1988) as in the present data set (Chapter 2). Most species assemblages studied by ecologists conform to the log. normal pattern of species abundance which may be said to characterize a large, mature and varied natural species assemblage (Magurran 1988). The fourth distribution pattern is described by MacArthur's broken stick model and is strongly subject to sample size. It characterizes even sharing of resources and is primarily applicable to narrowly-defined assemblages of taxonomically related organisms. Thus, one extreme of the gradient between models represents harsh environmental circumstances, the other, narrow definition of the species assemblage.

Comparison of diversity between localities is facilitated by the use of single indices for each site based on the proportional abundance of the species. However, comparison of rank species abundance plots is better (Magurran 1988) since they incorporate all the variables in the rank sequence and are, therefore, more accurate than indices which tend to be biased towards either rare (species richness) or common species (numerical dominance) (Peet 1974). In the present study, diversity indices have been used to compare trends in different habitats and cluster analysis has been used to characterize groups showing similar rank species abundance sequences. Plots are used as examples to illustrate diversity in these groups.

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Analytical methods

Equal sampling intensity, as in the present study, is a prerequisite for the use of indices to compare diversity between different sites (Magurran 1988). Numerous diversity indices exist and although some are mathematically sophisticated, May (1975) concluded that the simple Berger-Parker dominance index was, "as good as any and better than most". This dominance index is used to compare diversity in pasture and shrubland sites in the present study and is defined by

$$d = Nmax / N$$

in which N is the total abundance and Nmax is the abundance of the commonest species. This has been expressed in the form of the reciprocal, 1/d.

The use of plots to characterize species abundance relationships at a large number of sites is impractical. Therefore, two identical data matrices were prepared comprising rank abundance of the species in each of the six higher taxa at the 11 localities from which samples were taken in the south-western Cape. As species richness in the 66 rows of data ranged from two to 43, in each case, zeroes were used to fill in the blanks and create a matrix of 66 X 43. These matrices were each treated in different ways. Values of total abundance in one matrix were converted to a log.10 scale. Values of abundance in the other matrix were converted to percentage distributions of numbers along each row (i.e. percentage distribution of numbers between species of each higher taxon at each site). Cluster analysis was conducted on these matrices using the Clustan computer package as described in analytical methods (Chapter 1).

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Diversity in different habitats

Diversity is the observable result of how resources are partitioned by the taxa present at any given locality. It is expressed in terms of two parameters, species richness and evenness (equitability) in distribution of numbers between the species. A trend from low through intermediate to high species richness was shown in both the three coprophagous and the three predatory higher taxa which was roughly paralleled by trends to greater evenness in diversity over the same taxonomic sequences (Table 4.1.). Size, feeding, breeding behaviour and interaction between the various groups are probably responsible for these numerical relationships.

Species richness was greater in pastures in all groups except the Scarabaeinae/Coprinae whereas variation in evenness between habitats in four groups showed no clear trend. This was not such a consistent relationship between natural shrubland and disturbed pasture habitats as that shown for ants in burnt and more mature fynbos where both species richness and evenness were greater in the disturbed (burnt) habitat (Donelly & Giliomee 1985).

The results reflect the two different responses shown to disturbance of habitat by dung beetles which leads to extreme dominance or increased evenness. Significantly greater diversity of shrubland Aphodiinae is due to the extreme dominance of the early spring-active *Coptochirus brachypterus* in some pastures. Together with the oxyteline, *Anotylus caffer*, which showed extreme dominance during early spring in both pasture and shrubland, this may represent density compensation due to competitive release (Chapter 1). Similar observations of dung Staphylinidae interpreted as density compensation have been made in cool, montane situations in Sarawak (Hanski & Hammond 1986). Greater evenness in diversity of Scarabaeinae/Coprinae in pastures largely reflects the spatial overlap of three abundant species of *Euoniticellus*. These have probably recently expanded their ranges into the south-western Cape in response to the clearance of natural shrubland (Chapter 5) after evolution in isolation in warmer climates to the north where overlap is much reduced due to their differing climatic associations.

The present data set indicates a significant relationship between species richness and the Berger-Parker dominance index (Fig. 4.1.) which is contrary to the findings of Magurran (1988). This accounts for a greater amount of the variation in pasture (Fig. 4.1b.), where it is best described by an exponential curve, than in shrubland where it is best described by a multiplicative curve (Fig. 4.1a.). The reasons for the greater variance between diversity indices of the different groups in shrubland is uncertain but may possibly be linked to the greater between site vegetative heterogeneity.

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Diversity in different taxonomic groups

Cluster analysis is a convenient method of summarizing similarities in diversity between many study sites. The two different treatments of rank species abundance data produce quite different results. Analysis of logged data (Fig. 4.2.), in which variance was low emphasized species richness whereas analysis of data in which values were converted to percentage distributions (Fig. 4.3.), and the variance was, thus, higher, emphasized dominance.

At the 60% level of similarity, the dendrogram derived from analysis of logged data showed three groups of low, intermediate and high species richness (Fig. 4.2., Groups A,B,C; Table 4.2.). Each group showed two subgroups of lower and higher diversity at the 80% level of similarity. Rank species richness of these subgroups was paralleled by a trend to increasing size of the dominance index (Table 4,2.). Rank species abundance plots drawn for examples from each group indicated that Group B1, which comprised mainly Oxytelinae and was characterized by low species richness and extreme dominance, best fitted a geometric series model (Fig. 4.4a.). This may reflect the harsh conditions under which the numerically dominant species of oxyteline is able to breed within dung pads during early spring. The remainder of the subgroups show log series distributions approaching lognormal with increasing species richness (Fig. 4.4b-f.). This probably reflects the few factors which influence the distribution of the species (Chapter 2). One example of low species richness (narrowly defined assemblage) and high evenness in Group B2 was shown to fit a broken stick model which is characterized by even sharing of resources between species (Fig. 4.5.).

At the 60% level of similarity, the dendrogram derived from analysis of percentage abundance data showed two groups of high and low dominance each of which was divisible into two subgroups of high and low species richness (Fig. 4.3., Table 4.3.). However, comparison of logged data, which emphasizes species richness, is probably the better method since the separation between assemblages showing low species richness and high dominance with geometric series distributions and those showing higher species richness with log series distribution (Figs 4.2., 4.4.) was more consistent than that produced by analysis of percentage data (Fig. 4.3.).

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CHAPTER 5

REGIONAL ASSOCIATIONS AND ORIGINS OF SCARABAEINAE AND COPRINAE IN THE SOUTH-WESTERN CAPE

Abstract

1. A total of 45 species of Scarabaeinae and Coprinae was recorded at 11 study sites in the winter rainfall region in the south-western Cape.
2. Principle components analysis of their geographical range has defined three species groups and seven species with dissimilar distributions which have been treated as a fourth group.
3. Two of these groups comprising 34 species were endemic to the winter and bimodal rainfall regions of South Africa where they showed extreme numerical dominance in indigenous shrubland and were biased towards diurnal flight activity in the spring.
4. The other two groups comprising 11 species were also widespread in the adjacent summer rainfall region and showed either diurnal or crepuscular/nocturnal flight activity mainly in summer in farm pastures where shrubs have been recently replaced by grass.
5. These biota are taxonomically distinct from the endemic groups and have probably recently dispersed from the summer rainfall into the winter rainfall region via western and eastern coastal corridors in response to the clearance of the formerly ubiquitous native shrubs.
6. This suggestion is supported by their limited penetration into indigenous shrubland and may be related to unfavourable temperature regimes in this habitat.
7. This results in a fauna which is taxonomically different from that of the summer rainfall region and which differs markedly between habitats, unlike that of the Transvaal.
8. This may reflect the climatic isolation of the south-western Cape and the former absence of pasture habitats from the region compared to the Transvaal where both natural grassland and open woodland habitats occur in close proximity.

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The Scarabaeine/Coprine dung beetle fauna of the south-western Cape comprises two distinct groups with characteristic regional, vegetational, and seasonal associations (Davis 1987). This major dichotomy in the fauna may result from the recent large-scale clearance of indigenous shrubland which seems to favour elements widespread in the adjacent summer rainfall region leading to lower relative abundance of endemic winter rainfall elements in pastures. Differences between the fauna of the summer and winter rainfall regions and between habitat associations of summer and winter rainfall elements have, therefore, been examined in some detail. Findings support the contention that clearance of natural shrubland and its replacement by a physiognomically different vegetation type has strongly influenced faunal composition in the south-western Cape.

Study sites and data sets

Relative abundance of tribes of Scarabaeinae/Coprinae in different regions and the seasonal distribution of groups in different habitats and climates was determined using data from the 11 original widely-distributed study sites. Habitat associations were verified using data from the second set of 13 sites concentrated in three small areas.

Analytical methods

The distribution of the 45 Scarabaeinae and Coprinae recorded at the 11 trapping sites in the south-western Cape has been plotted according to their presence or absence from all degree squares of latitude and longitude south of latitude 15°S in southern Africa from which collections were made. Data has been drawn from the reference collections of the former CSIRO Dung Beetle Research Unit (now lodged with the National Collection of Insects, Pretoria) and from published distribution records for Canthonina (Scholtz & Howden 1987a, b, Howden & Scholtz 1987). These results were used to produce a data matrix of 45 species by the number of degree squares occupied by these species in each of the four climatic regions derived from Walter & Lieth (1964) by Davis (1987). Principal components analysis (PCA) was conducted on these matrices using the Clustan computer package.

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Comparison of Transvaal and south-western Cape scarabaeine/coprine fauna

The taxonomic composition of the scarabaeine and coprine fauna was similar in each climate type of the winter rainfall region but differed markedly to that in the summer rainfall region (Table 5.1.). The winter rainfall fauna was dominated taxonomically by species of Scarabaeina and Canthonina (Scarabaeinae) whereas in the Transvaal species of Onthophagini (Coprinae) were numerically dominant. Members of two old world tribes, common elsewhere in Africa, were absent in the south-western Cape (Gymnopleurina) or represented only on the warmer west coast by a single species (Sisyphina). Since both of these subtribes comprise relatively small ball-rolling species like the Canthonina of Gondwanaland origin, they may have displaced the canthonines elsewhere or represent an ecological equivalent in warmer areas preventing expansion of range by the canthonines.

Relative abundance of tribal and subtribal elements differed between both climate type and habitat (Fig. 5.1.). In the winter rainfall region, patterns of relative abundance differed between habitats but were similar between climate types. In the Transvaal, patterns of relative abundance were similar between habitats but differed from distributional patterns in the winter rainfall region.

The shrubland biota of the south-western Cape comprises winter and spring active taxa. Large and small ball-rolling Scarabaeinae are prominent together with small, possibly kleptoparasitic, Scarabaeinae and small, tunneling coprine elements. Clearance of shrubland and its replacement by pasture generally has resulted in the addition of spring or summer-active, tunneling coprines of the tribe Oniticellini and the loss of large, ball-rolling Scarabaeina, although the brief abundance of *Scarabaeus suri* at Groote Post was an exception to this trend. Pastures in the south-western Cape therefore show greater similarity to the Transvaal biota which are dominated by summer-active Coprinae particularly Onthophagini and Oniticellini.

Analysis of geographical and habitat associations of Scarabaeinae and Coprinae recorded in the south-western Cape

An analysis of the geographical distribution of the 45 species of Scarabaeinae and Coprinae recorded in the south-western Cape during the present

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study has identified three species groups and seven species with a relatively dissimilar geographical range which have been treated as a fourth group (Fig. 5.2.).

The 31 species of Group 1 were endemic to the winter and bimodal rainfall regions of South Africa and occurred abundantly in all habitats and climate types studied in the south-western Cape (Figs 5.3., Table 5.2.). They showed maximum activity in spring (Figs 5.4., 5.5.) during a period of increasing temperatures and declining rainfall. *Copris fidius* and *Onitis confusus* are atypical of Group 1 since they are known to be widespread in the summer rainfall region. However, they fall into the group because they were poorly represented outside of winter and bimodal rainfall regions in the collections from which the distribution data were drawn.

The three species of Group 3 also showed a centre of distribution in the winter and bimodal rainfall regions with maximum activity during spring (Figs 5.3., 5.4.). However, they also showed a wide spring distribution in the arid karoo which extends across the southern part of the summer rainfall region. This may explain their marginal occurrence in the moist climate type IV on the Cape of Good Hope Peninsula (Table 5.2.). On the drier west coast, they were equally abundant in shrubland and pasture (t = 0,37, d.f. = 11, n.s.), like the members of Group 1.

The four species of Group 2 show a centre of distribution in the summer rainfall region (Fig.5.3a.) with a distributional bias towards the arid western regions of southern Africa (Fig. 5.3b.) where the geographical ranges of three species (Fig. 5.2., Group 2 a,b,c.) extend across the Kalahari or the Pre-Namib sandveld. High relative abundance of Group 2 in the winter rainfall region and summer rainfall region, area 1 (Fig. 5.3b.), suggest a west coast dispersal route into the south-western Cape. Dispersal from hot, arid areas of western and central southern Africa is further indicated by the failure of the group to penetrate to the cool, moist climate type IV of the Cape of Good Hope Peninsula and its relatively marginal occurrence on the cool, dry west coast (Table 5.2.). The greater abundance of the group in shrubland (t = 1,18, d.f. = 11, n.s.) where it shows an early summer peak in activity (Fig. 5.4.) was the result of the numerical dominance of *Scarabaeus proboscideos* which was recorded principally at the warmest of the shrubland sites on sand at Pampoenvlei.

Species 4-10 are widespread in southern Africa. Like the 79 species at study sites in the Transvaal for which distribution data was available, their distribution is biased towards the moister eastern seaboard of Africa in summer rainfall region, area 2 (Fig. 5.3a.). Higher relative abundance and overlapping

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distributions of species 4-10 in the bimodal rainfall region may indicate a dispersal route to the south-western Cape via the eastern Cape (Fig. 5.3b.). This distributional pattern of relative abundance in records of the group was not duplicated by species 1-79 of the Transvaal data set. Species 4-10 showed only marginal occurrence in shrubland and were significantly more abundant in pasture in both climate types of the south-western Cape (IV: $t = 2,21$, d.f. $= 11$, $P<0,05$; III(IV)a: $t = 3,32$, d.f. $= 11$, $P<0,05$) (Fig. 5.4.).

Unlike the other groups, there were differences in the seasonal distribution of species 4-10 in the different climate types (Figs 5.4., 5.5.). On the warmer west coast, peaks in activity occurred during mid-summer as in the Transvaal and showed little seasonal overlap with the other groups. However, on the Cape of Good Hope Peninsula, the only abundant member of the group, *Euoniticellus triangulatus*, showed broad seasonal overlap with Group 1 species during spring. This was quite unlike its seasonal activity on the west coast (Chapter 2).

Further distributional trends shown by Groups 1 and 3, with their strongly endemic character in the winter and bimodal rainfall regions, and Group 2 plus species 4-10, with their generalist distribution in southern Africa, extend to taxonomic composition, diel flight activity and habitat associations.

Taxonomic composition of the two groupings shows a strong tendency to differ at the tribal or subtribal level (Table 5.3.). Groups 1 and 3 comprise all of the species in subtribes of Gondwanaland origin, most of the remaining ball-rolling Scarabaeinae and all of the Onthophagini present at the 11 original study sites. Group 2 plus species 4-10 are dominated by Coprinae and, if the probably misplaced *Onitis confusus* is grouped with the other summer rainfall elements, they comprise all of the Oniticellini and the Onitini. This suggests a separate wave of radiation in these groups (Chapter 7).

Distribution of diel flight activity patterns in Group 2 and species 4-10 show similarities to those of Transvaal species but differs markedly to those of Groups 1 and 3 (Table 5.4.). The bias to diurnal flight activity in Groups 1 and 3 is perhaps an adaptation to the cool temperatures of their spring activity period. Increased relative abundance of crepuscular/nocturnal species in the other grouping may be largely related to the warmer temperatures of their summer activity period and reflect their origin from a warmer climatic region. It is interesting to note that both species of ball-rolling Scarabaeina, *Scarabaeus proboscideos* and *S. satyrus*, which have recently dispersed from the summer to the winter rainfall region have

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crepuscular/nocturnal habits and are active during summer. They, therefore, do not show temporal overlap with endemic ball-rolling taxa.

The strongly endemic Groups 1 and 3 showed extreme numerical dominance over Group 2/species 4-10 in indigenous shrubland ($t = 2,65$, d.f. $= 5$, $P < 0,05$) whereas recently created pasture sites were much more favourable for both spring and summer activity by Group 2/species 4-10 leading to a more even numerical balance between these groups and Groups 1 and 3 ($t = 0,87$, d.f. $= 4$, n.s.) (Table 5.5.). The pasture island in West Coast National Park was an exception to this trend in that its faunal composition appeared to be strongly influenced by the surrounding shrubland. The overall trend shown by numerical balance of the groupings at sites of indigenous shrubland was much more consistent than at disturbed pasture sites.

Comparison of group distributions across habitats in close proximity to one another supported findings drawn from sites occurring under a wide range of climatic conditions. Although Groups 1 and 3 are composed of some generalist species together with many shrubland and a few pasture specialists (Chapter 2), at the group level, overall abundance was fairly similar in both shrubland and pasture (Fig. 5.6.). They were, however, rare in the exotic *Acacia* shrubland of Australian origin which is physiognomically different to indigenous shrubs (Fig. M8).

The strong association of Group 2 plus species 4-10 with pasture was confirmed on both the coastal Rondeberg strip and the farm Groote Post in the Darling Hills where discrimination was shown even between alternating 16,8±0,8m wide strips of shrubland and pasture. The only abundant member of species 4-10 occurring in the Cape of Good Hope Peninsula, *Euoniticellus triangulatus*, also showed strong association with pasture (Fig. 5.6.). Abundance of this species was significantly lower at shrubland sites irrespective of the presence of cattle in shrubland on the farm Bonne Attente and their absence from the Cape of Good Hope Nature Reserve. Therefore, the presence of shrubland seems to be the most important factor largely excluding this summer rainfall element from the reserve and the absence of a suitable dung type rather less important.

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Discussion

Regional differences in relative abundance of tribes and subtribes in the scarabaeine/coprine fauna of the Transvaal and the south-western Cape carry several implications. Clearance of trees to create pasture had little influence on patterns of relative abundance between habitats in the Transvaal (Fig. 5.1.). This may reflect the proximity of natural grassland habitats at only slightly higher altitude on the highveld and the more equitable temperature distribution between habitats during seasonal peaks in dung beetle activity. However, in the south-western Cape, distinct differences were shown in faunal composition between indigenous shrubland and pasture with which shrubs have been replaced after their clearance. The fauna as a whole, has been shown to consist of two major groupings of species, one with a strongly endemic character, the other with a more generalist distribution throughout southern Africa. The high level of taxonomic dissimilarity between these groupings (Table 5.3.), the strongly endemic character of species assemblages in shrubland (Table 5.5.) and the strong pasture associations of Group 2 and species 4-10, which have apparently recently dispersed into the south-western Cape from the summer rainfall region, suggest that shrubland and natural grassland have not coexisted in the extreme south-western Cape for an appreciable period.

This raises questions as to the abundance or, indeed, the presence of Group 2 and species 4-10 in the south-western Cape prior to the widespread clearance of natural shrubland. The strong pasture associations of this grouping suggest that they were uncommon in the winter rainfall region until recently whereas the scale of taxonomic differences between species 4-10 and the endemic fauna suggest that its members evolved in isolation presumably under warmer summer rainfall climatic regimes to the north (Chapter 4). Observations and published data on other species suggest that temperature distribution between unshaded and partly shaded habitats may be responsible for pasture associations in Group 2 and species 4-10 in the south-western Cape.

In a study of the crepuscular/nocturnal, African, summer rainfall species, *Onthophagus gazella*, which has been introduced into Texas in the USA, Fincher *et al.* (1986) found that this species showed extreme pasture associations in 1979 but much greater relative abundance in a wooded pasture during the following year which was much hotter. The authors suggest that intraspecific competition resulting from the greater population density in 1980 contributed to the expansion of its range and increased abundance in the woodland pasture. However, it is

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probable that the warmer temperatures of 1980 also facilitated immigration into the woodland.

Key (1981) has shown similar changes in vegetation associations of dung beetles (Aphodiinae) in Norway where known shade specialists at warmer lower altitudes were numerically dominant in cool exposed situations at higher altitudes.

Finally, *Euoniticellus intermedius*, which is a member of the pasture-associated species 4-10 in the south-western Cape, is much more abundant in open woodland than in grassland on sandveld in the warmer Transvaal (Davis unpublished data).

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CHAPTER 6

SEASONAL BREEDING STRATEGIES OF SCARABAEINAE AND COPRINAE IN THE SOUTH-WESTERN CAPE

Abstract

1. Two principal breeding strategies are shown by the Scarabaeinae and Coprinae of the Mediterranean-type climatic region in the south-western Cape.

2. One strategy features a long breeding period in which 8-12 months separates activity peaks of sclerotized and teneral individuals. It is characteristic of larger species which are numerically dominated by elements recently dispersed into the south-western Cape from the summer rainfall region of South Africa.

3. The other strategy features a short breeding period in which 1-6 months separates activity peaks of sclerotized and callow individuals. It is characteristic of smaller species which are numerically dominated by elements endemic, or largely restricted, to the winter and bimodal rainfall regions of South Africa.

4. Examples of annual breeding cycles of endemic species show apparent univoltinism and breeding specializations. In the few, large, winter-active, endemic species with long breeding cycles, ovarian maturation is probably delayed until spring whereas in some small spring-breeding species ovarian maturation is probably arrested prior to summer dormancy in filials produced in late spring/early summer.

5. Examples of annual breeding cycles of summer rainfall elements show relatively generalist breeding activity characterized by the presence of gravid females throughout the activity period and possible partial bivoltinism.

6. Evidence suggests that those species showing long breeding cycles pass unfavourable periods mainly as larvae whereas those showing short breeding cycles undergo dormancy as adults.

7. Selection for small species showing a short generation time and oversummering/overwintering as adults may be a more suitable strategy for exploiting a short period of favourable breeding conditions during spring when increasing temperatures are paralleled by decreasing rainfall.

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Probable northward displacement of a summer rainfall climatic system with the inception of a winter rainfall climate (Tyson 1986) has strongly influenced the taxonomic composition of the dung beetle fauna of the south-western Cape (Davis 1987). It has probably also influenced the annual breeding cycles of the fauna. Obtaining standardized laboratory breeding data for the many species of Scarabaeinae and Coprinae recorded was not possible in the time available. Therefore, a field study has been made of the variation in periods of time between annual peaks in abundance of sclerotized and teneral specimens of the more abundant species. This is defined as the annual breeding strategy of the species.

Methods

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The recruitment of filials into populations of Scarabaeinae and Coprinae may be identified from the hardness of the exoskeleton. In the present study, specimens were classified as freshly-emerged, young and callow (teneral) if the disc of the prothorax could be depressed under gentle pressure or, fully sclerotized older and possibly mature if there was strong resistance to distortion of the cuticle. This proved a quick, easy and reliable method for showing broad seasonal changes in age structure of populations in a large multispecies data set.

Seasonal distribution data for sclerotized and teneral specimens of 21 species of Scarabaeinae and Coprinae recorded at eight study sites on the west coast of the south-western Cape over one year have been used to compare their annual breeding strategies. Because the species showed periods of abundance in different seasons, it was necessary to standardize the data. This was done by placing values for the month of peak abundance of sclerotized specimens into the first column of the data matrix and moving preceding values, if any, to the end of the line. Data for callow specimens of each species were rearranged according to the changes made to sclerotized material. Data for callow material was, thus, standardized to reflect the duration of time between activity peaks in sclerotized and teneral specimens with seasonal variation between species removed.

Monthly values for each species in the data set for tenerals were converted to percentage distributions to give equal weighting to each species and principal components analysis (PCA) was conducted on the data to compare annual breeding strategies in the different taxa. A minimum spanning tree showing relationships between data points on an ordination plot derived from the PCA was dentition worn down to stumps. These graduations are equivalent to stages zero, 1-3 and 4-6 of Edwards (1986). This aging method was unsuitable for specialized genera such as *Scarabaeus* which probably burrow less frequently than more generalist taxa such as *Onitis* and *Onthophagus*.

Annual breeding strategies

Two principal annual breeding strategies in Scarabaeinae and Coprinae on the west coast of the south-western Cape are suggested by the bimodal distribution of the number of months between peaks in abundance of sclerotized and teneral material (Fig. 6.1.). A long period between peaks or their simultaneous occurrence suggests an annual cycle in which progeny pass through unfavourable periods as larvae whereas a short period between peaks suggests that filials are produced rapidly and undergo dormancy as adults during unfavourable periods.

Ordination of the standardized annual distribution data for teneral material indicates three main clusters of data points (Fig. 6.2.). Species 1a-3a and 3b-6 form clusters which are mostly positively correlated to Factor 2. They mainly comprise small species with short breeding cycles which are endemic to the winter and bimodal rainfall regions (Table 6.1.). Species 8-12d form a cluster which is negatively correlated to Factor 2 and comprises larger species with long breeding cycles which have mostly dispersed into the south-western Cape from the summer rainfall region relatively recently (Chapter 5).

Detailed examples of annual breeding strategies indicate that endemic species are univoltine with breeding specializations whereas the summer rainfall elements are relatively generalist breeders and, perhaps, partially bivoltine.

Many members of the tribe Scarabaeini show breeding specializations which include low numbers of follicles in the ovary, low brood ball production (Sato & Imamori 1986a,b, 1987) and tend the broods during larval development (e.g. Sato & Imamori 1987, Edwards 1988). This may explain why autumn populations of *Scarabaeus rugosus* are represented by oversummered, older, sclerotized parous individuals followed by the winter and spring appearance of teneral filial material (Fig. 6.3a.). This sequence of events is paralleled by a significant increase in the number of follicles in the ovary ($P<0,05$, Scheffes tests) which reached a peak in October and November and coincided with a reduction in the abundance of nulliparous individuals in the population. This possibly signifies specialization to a

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spring breeding period in which younger material commences breeding leaving some older and possibly senescent females still feeding from dung pads. *Copris anceus* showed a similar specialized breeding cycle. Both of these large species are considered older elements in the fauna endemic to the winter rainfall region (Chapter 7), few of which showed a long breeding cycle.

Although members of the genus, *Onthophagus*, are more generalist in their breeding biology than *Scarabaeus, O. cameloides* shows a breeding cycle with specializations which are well suited to the winter rainfall climate of the south-western Cape despite its marginal occurrence in the southern parts of the summer rainfall region. The virtual absence of tenerals in the predominantly young spring population (Fig. 6.3b.) indicates oversummering and overwintering as adults. As spring progresses, the population ages as evidenced by the increasing amounts of tibial wear and the increasing proportion of parous individuals. This trend is paralleled by a significant decrease in the numbers of follicles in the ovary ($P < 0,05$, Scheffes tests). Follicle numbers remain high throughout the breeding period which reflects continuous breeding characteristic of *Onthophagus* with their relatively unspecialized nesting behaviour (Halffter & Edmonds 1982). The clear break in age structure patterns between October and November presumably represents mortality of a senescent population and its replacement by teneral, nulliparous, filial individuals with little tibial wear. As the ovaries of filials remained in vestigial undifferentiated condition throughout the two month period in which they were recorded, even in fully sclerotized individuals, delayed maturation may be shown as an adaptation to the imminent oversummering and overwintering as adults in a Mediterranean-type climatic system.

Members of the genus, *Onitis*, also show continuous breeding habits and relatively unspecialized nesting behaviour (Halffter & Edmonds 1982) which, in *O. aygulus*, is reflected by the similar numbers of follicles in the ovary throughout its period of activity. The predominantly young, early summer population comprising many callow, nulliparous individuals with undifferentiated ovaries (Fig. 6.3c.) suggests overwintering is mainly as larvae. As summer progresses, the population ages as indicated by the increasing amounts of tibial wear, decline in recruitment of tenerals and decrease in relative abundance of nulliparous individuals. However, the slight increase in recruitment which interrupts this trend during February (Fig. 6.3c.) may indicate partial bivoltinism. Unlike, *O. cameloides*, individuals with fully gravid ovaries were recorded throughout the activity period of *O. aygulus*. Thus, the breeding cycle in this widespread species is more generalist than that of the endemic

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or relatively endemic species in the south-western Cape.

This generalist pattern of apparent partial bivoltinism is similar in other summer rainfall elements, including *Onitis caffer*, which shows an autumn/winter/spring activity period in the south-western Cape. Although there was a clear break between early and late season trends in age structure of populations of *Chironitis scabrosus*, the presence of follicles in the ovaries of young specimens late in their activity period suggests that there is no arrest of ovarian development in this species due to endogenous factors. Most of these species have populations dominated by teneral adults at the commencement of their period of activity indicating passage through unfavourable periods as larvae. The one exception is *Euoniticellus triangulatus* which apparently overwinters as adults. This species showed typical summer activity on the west coast of the south-western Cape but was the only abundant summer rainfall element in the cooler climate of the Cape of Good Hope Peninsula where it showed typical spring patterns of activity similar to those of endemic species (Chapter 5).

Generation time in insects is known to be positively correlated to body size (Gaston 1988). However, size and, duration of the period between peaks in abundance of sclerotized and teneral individuals in the present data set were not significantly correlated ($r = 0{,}388$; d.f. = 20; $P < 0{,}10$).

The fauna of endemic Scarabaeinae and Coprinae in the south-western Cape contains relatively few large species with long breeding cycles and most of those which occur are thought to be relatively old elements, *c.f. Scarabaeus rugosus, Copris anceus*, possibly descended from ancestral stock already present at the inception of the winter rainfall climate some 3 MYBP (Deacon 1983) (Chapter 7).

Under the winter rainfall system, selection seems to have been mainly for smaller spring-active species with relatively short generation times which oversummer as adults. It may be an advantage to be immediately active as an adult to fully exploit the short period of cool but favourable spring conditions when temperatures are increasing but rainfall declining. Possible autumn/winter breeding exceptions to the general trend in endemic species seem to be mostly represented by relictual elements (Chapter 7) whereas most summer rainfall elements with long breeding cycles characterize the species which have recently dispersed into the area in response to clearance of indigenous shrubland (Chapter 5).

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CHAPTER 7

DISCUSSION: EVOLUTIONARY AND GEOGRAPHICAL ORIGINS OF THE DUNG BEETLE FAUNA OF THE SOUTH-WESTERN CAPE

Abstract

1. Five levels of endemism or generalization in geographical distribution may be recognized in the scarabaeine/coprine dung beetle fauna of the south-western Cape.
2. These comprise taxa endemic at generic level, taxa endemic at species level with or without close relatives in the adjacent summer rainfall region, species which are largely endemic but with a marginal distribution in the summer rainfall region and, species which have probably recently dispersed into the south-western Cape from the summer rainfall region.
3. The oldest elements of Scarabaeinae/Coprinae in the south-western Cape may originate from stock which pre-dates the inception of the winter rainfall system in the Pliocene. They include elements of Gondwanaland origin and some taxa with old world affinities.
4. A number of older species are probably derived from elements resulting from speciation after colonization of coastal sands exposed by a marine regression in the Pliocene.
5. Other elements probably result from expansion and contraction of range, isolation of populations and speciation due to north/south climatic oscillation in response to cyclic advance and retreat of polar glaciation during the Pleistocene.
6. Recent widespread clearance of indigenous shrubland in the south-western Cape and its partial replacement by pastures has probably resulted in the expansion of range and increase in population size by species of Scarabaeinae/Coprinae from the summer rainfall region.
7. The other higher taxa in dung, Aphodiinae, Histeridae, Staphylinidae and Hydrophilidae, probably represent more recent elements in dung in the south-western Cape owing to a lower degree of spatial discrimination and specialization and, particularly in predatory taxa, a much higher degree of similarity to the fauna in the Transvaal.

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As the evolutionary history of some dung beetle elements present in the modern fauna of the south-western Cape can be traced back to a Gondwanaland origin (Appendix 2), a brief review of the effects of geological and climatic change in southern Africa from the late Mesozoic through the Tertiary and Quaternary periods is relevant.

The modern history of the south-western Cape may be said to date from the Mesozoic fragmentation of Gondwanaland which resulted in the area becoming a continental margin fronted by ocean as early as the mid-Cretaceous (*c.* 100 MYBP) (Hendey 1983). Subsequent climatic and vegetational history is most complex although several principal factors of importance may be identified. These include the 15 degree northward drift of the African continent which by the late Miocene had probably caused the southward elimination of most so-called temperate elements of Gondwanaland origin which may still be identified in southern regions of South America, in Australia (Axelrod & Raven 1978) and in New Zealand. However, perhaps the most important events influencing the modern flora and fauna of southern Africa were those concerning Antarctica and oceanic currents in the South Atlantic.

During the Tertiary period (*c.* 65-1,8 MYBP), a general decline in temperature and rainfall has occurred (Shackleton & Kennet 1975, Tyson 1986) which has been marked by greater cooling of temperatures in the higher latitudes relative to those of tropical regions. In the southern hemisphere, this seems to be linked to the late Oligocene or early Miocene thermal isolation of Antarctica after its separation from South America which resulted in the establishment of a circum-Antarctic current. This current prevented the penetration of warm water and associated air masses into higher latitudes (Tyson 1986) resulting in increasing frigidity and formation of the southern polar ice cap. The development of cold currents emanating from polar regions was responsible for the increasing latitudinal thermal stratification and was probably linked to a northward shift in the circum-global belt of westerly winds in the southern hemisphere (Tyson 1986). The northwards expansion of the westerlies and the strengthening of the cold Benguela current along the western coast of southern Africa have had a strong climatic influence (Hendey 1983) particularly in the south-western Cape where the Mediterranean climatic system of warm dry summers and cool wet winters is thought to have commenced some 3 MYBP (Deacon 1983) during the mid-Pliocene. To the north the climate of southern Africa becomes increasingly more influenced by the warm Agulhas current which flows down the east coast from the tropics and is

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associated with easterly air flow. Interplay between these two systems results in the present seasonal distribution of winter rainfall in the south-western Cape and summer rainfall to the north (Chapter 1).

Vegetational responses to climatic change in the south-western Cape have been various. Evidence indicates that with increasing cooling of the climate, forests of the warm and wet early Tertiary retreated to centres of refuge during the late Miocene (Axelrod & Raven 1978, Tyson 1986) and were replaced by more xeric types of vegetation. The first strong development of fynbos vegetation occurred in the early Pliocene (Coetzee & Rodgers 1982) with grasses important in the plant assemblages of the late Pliocene (Coetzee 1986) resulting in a grass/shrub/forest mosaic (Hendey 1983, Tyson 1986).

The absolute age of the modern dung beetle fauna in the south-western Cape is difficult to assess. However, the inception of the winter rainfall system and the concomitant vegetational changes probably provided a principal selection pressure. Increasing polar glaciation which led to the development of this climatic system may also have been linked to a marked decrease in sea level during the Pliocene which exposed much of the calcareous coastal sandveld to the north and east of Cape Town (Hendey 1983). This caused southward deflection of the warm Agulhas current and as a result the west coast became drier (Taylor 1978). Thus, the western and southern coastal regions have been populated relatively recently probably under changing conditions. As a result, they may have acted as a centre for speciation from stock extant before the inception of winter rainfall climate and may be responsible for some of the endemism in the dung fauna of the south-western Cape.

Subsequently, during the later Pliocene and the Quaternary period, there have been cyclical climatic changes linked with advance and retreat of polar glaciation (Deacon 1983, Tyson 1986). Oxygen isotope analysis of samples from sea-bottom core deposits of the last ice age imply that in cooling phases expansion of glaciation results in the northward shift of the westerly wind belt of the southern hemisphere (Tyson 1986). As a result, bimodal rainfall patterns may have expanded across the southern Cape due to the more northerly influence of rain bearing autumn and spring westerly air flow and winter rainfall probably expanded further inland. During the warmer interglacial phases as at the present , the westerlies have moved south, the winter and bimodal rainfall regions have contracted and late summer rainfall has become dominant over a wider area of south-western southern Africa.

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The possible effects of these changes on vegetation has generated much discussion. Van Zinderen Bakker (1978) has hypothesized cyclical vegetation changes coeval with these climatic oscillations. His suggestion that shrubland is the dominant form of vegetation during warm interglacials changing to grassland during cool glacial maxima may be true of more exposed situations (Deacon 1983). For instance, the fossil mammal record of the last glacial includes some grazing forms (Klein 1983) whereas charcoal in stratified hearths of prehistoric man in the eastern Cape indicates woodland prior to 42000yr before present with woody composites the main fuel from 32000 to 14000yr before present which includes the last glacial maximum, and woodland returning thereafter (Deacon *et al.* 1983). However, more detailed information on vegetation changes is unavailable due to the paucity of fossil pollen and other plant deposits in the south-western Cape. Thus, the influence of past changes in climate and vegetation type on the modern dung beetle fauna may only be surmised.

It seems that in the recent historical past, shrubland was the dominant vegetation-type in the south-western Cape (Acocks 1975). However, since the arrival of Europeans several hundred years ago, vast amounts of this indigenous shrubland have been cleared for farming purposes and replaced by a physiognomically much different flora. This has markedly influenced the faunal composition of species assemblages of Scarabaeinae/Coprinae in the south-western Cape (Davis 1987).

It seems likely that these waves of climatic change, since the mid Pliocene, have caused expansion, contraction and intermingling of the ranges of flora (Taylor 1978) and fauna. The different levels of endemism or generalization shown by dung beetles in the south-western Cape are correlated to the relative age of the faunal elements particularly as it has been suggested that specialization is a function of time spent under a limited range of conditions. Relative age may be inferred from a combination of both taxonomic and distributional parameters including, species richness of genera, taxonomic level of endemism, taxonomic proximity of relatives in other regions, size of range, and seasonal association. Relative age of the Scarabaeinae/Coprinae in the south-western Cape is considered in some detail. Relative endemism/generalization in the other higher taxa is briefly discussed.

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Relative age of Scarabaeinae/Coprinae in the south-western Cape

The 45 species of Scararabaeinae/Coprinae recorded at the 11 study sites in the south-western Cape comprised five species groups on the basis of their taxonomic and geographical associations (Table 7.1.). This somewhat qualitative assessment is partly supported by the multivariate analysis of the geographical associations of the same 45 species in Chapter 5.

Groups A-C are equivalent to Group 1 (Chapter 5) minus *Copris fidius* and *Onitis confusus* which show widespread distributions similar to species 4-10. They comprise taxa endemic to the winter and bimodal rainfall regions either at generic level (Group A) or species level (Groups B, C). The endemic species are either taxonomically isolated (Group B) or have close relatives in the summer rainfall region (Group C). Members of all three groups appear to include derived species possibly restricted to the calcareous sands of Pliocene origin on the west coast. Group D comprises species with activity patterns typical of the winter and bimodal rainfall regions which also show spring activity in the arid southern parts of the summer rainfall region. They are equivalent to Group 3 (Chapter 5) and appear to be recently evolved taxa whose ranges may be relicts of northward expansion of winter rainfall climate during previous glacial periods. Group E comprises widespread taxa in which the same species are found in both the winter, bimodal and summer rainfall regions. They are equivalent to Group 2/species 4-10 and appear to have dispersed into the winter rainfall region mainly in response to the recent clearance of indigenous vegetation (Chapter 5).

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The sequence of presentation of these five groups is thought to be roughly correlated with the relative age of their ancestral stock in the fauna of the winter rainfall region. Accordingly they show a gradation from winter through spring to summer orientated seasonal activity (Table 7.2.). They also show a gradation from low to higher numbers of follicles in the ovary (i.e. specialist to more generalist breeders) (Table 7.1.). Coprine species numerically dominate the oldest and the youngest groups whereas scarabaeines dominate the remainder.

The supposed oldest elements in the scarabaeine/coprine fauna of the south-western Cape are endemic at generic level (Group A) and belong entirely to subtribes of Gondwanaland origin. The canthonine genus, *Aphengoecus*, is represented by just two locally-occurring species in the south-western Cape whereas the dichotomine genus, *Macroderes*, is represented by 13 species occupying a coastal range from Namaqualand to the eastern Cape. It is unclear whether species distributions are allopatric or disjunct. The pronounced hemispherical dorso-ventral profile of the group members may be related to conservation of heat and be associated with their cool-weather seasonal activity (Table 7.2.).

Members of Group B are clearly endemic to the winter and bimodal rainfall regions at species level but claims of their relative taxonomic isolation within their respective genera are somewhat qualitative in the virtual absence of detailed numerical taxonomic studies. The species represent higher taxa of both Gondwanaland and old world origin. Some of these, such as *Sarophorus tuberculatus* (Dichotomiina) and *Sceliages brittoni* (Scarabaeina), belong to species poor genera which appear to show disjunct species distributions. The remaining taxa belong to relatively species rich genera, *Epirinus* (Canthonina), *Scarabaeus* (Scarabaeina), *Copris* (Coprina), *Onthophagus* (Onthophagini), which often show only marginal overlap between distributions of other congeneric Group B species.

Members of Group C are also clearly endemic to the winter and bimodal rainfall regions at species level but are considered to have close relatives in the summer rainfall region and, therefore, belong to recognizable species groups. Higher taxa of either Gondwanaland or old world origin are prominent. Lower taxa all belong to species rich genera but some, like *Kheper* (Scarabaeina) and *Neosisyphus* (Sisyphina), are represented by single species in the south-western Cape, others by several species with overlapping distributions, *Epirinus*, *Odontoloma* (Canthonina), *Scarabaeus*, *Onthophagus*. To the north, relatives within each species group often occupy allopatric or disjunct distributions often in higher lying areas.

The two subtribes of Gondwanaland origin appear to differ in their evolutionary history in the south-western Cape. The soil-tunneling dichotomines show a somewhat relictual status in the region with *Macroderes* endemic at generic level and the strongly tubercular *Sarophorus tuberculatus* only remotely related to the other three species of *Sarophorus* which are themselves restricted to south-eastern Africa (Ferreira 1972). This suggests that there has been no recent radiation in this subtribe within the south-western Cape. Although throughout the rest of Africa, many of the dichotomine genera are dietary or behavioural specialists, e.g. *Coptorhina* (mycetophages), *Pedaria* (possible kleptocoprids), *Paraphytus* (saproxylophages), they occupy broad geographical ranges and many are species rich some with overlapping species distributions.

The ball-rolling canthonines as a subtribe are largely restricted to southern Africa with only one widespread tropical genus, *Anachalcos*, and some forest relicts in east Africa (Scholtz & Howden 1987a). Although endemism to the

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winter and bimodal rainfall regions is high in the canthonine species recorded in the present study, most belonged to two species rich genera (*Epirinus* and *Odontoloma*) which also occur in the cooler parts of the summer rainfall region (Scholtz & Howden 1987b, Howden & Scholtz 1987). As the greatest number of species occur in the winter and bimodal rainfall regions, summer rainfall elements may represent a northward expansion of their range during Pleistocene glacial cycles and speciation in populations now isolated in higher lying areas. Since many African canthonines show relictual forest distributions in southern Africa, they may originate from cool temperate forest stock which entered Africa by a southern route as indicated by Halffter (1974).

Thus, Gondwanaland groups in the south-western Cape probably represent descendants of stock already present at the inception of winter rainfall climate some of which are apparently restricted to calcareous Pliocene sand on the west coast, e.g. *Macroderes* sp. a, *Epirinus bentoi*, *E. scrobiculatus*, *Odontoloma pusillum*. Since northward radiation, which was possibly in response to cooler climatic phases, has only occurred in small ball-rolling canthonines, the presence of small soil-tunneling *Onthophagus* in cooler areas may be a reason for the relictual status and apparent lack of a similar radiation in small soil-tunneling dichotomines. All Gondwanaland species are of small size and show early winter or early spring peaks in abundance during May/June or August (Table 7.1.).

Various patterns of evolutionary history are indicated by the distributions of the remaining taxa and their relatives which are of old world origin. Other than a few small soil-tunneling *Onthophagus* with early spring peaks in abundance during August, most old world endemic taxa are larger than species of Gondwanaland groups and show mid to late spring activity peaks between September and November (Table 7.1.).

The few large species which show greatest abundance during early spring in August are probably descendants of stock which was isolated in the south-western Cape by the inception of the winter rainfall climate, e.g. *Scarabaeus rugosus*, *Copris capensis*, *C. anceus*. Some of the same or other species are derived elements apparently restricted to the west coast sandveld of Pliocene age (*Copris anceus*, *Scarabaeus aesculapius*, *Sceliages brittoni*, *Neosisyphus quadricollis*). The late spring peaks in activity of most of these and other large old world taxa may indicate their more recent recruitment into the endemic fauna of the south-western Cape.

The same, or additional, species probably resulted from the expansion of their ranges within southern Africa, subsequent contraction or translocation of

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range of populations leading to their isolation in cooler areas and speciation in response to Pleistocene climatic oscillation (e.g. *Neosisyphus quadricollis*, *Onthophagus giraffa*, *Scarabaeus canaliculatus*, *S. spretus*). According to Brain (1981) their have been at least 17 such glacial and interglacial events in southern Africa in the past 1,7 million years. Fossil evidence indicates that reorganization of species ranges and their recombination into new species assemblages has also occurred naturally in other insects, mammals and plants on most continents including North America, Europe, Asia and Africa as a result of the glacial cycles (Matthews 1975, Livingstone 1975, Guthrie 1986, Graham & Lundelius 1986).

Finally, there has been the recent dispersal of modern, predominantly summer active elements from the summer rainfall region probably via coastal corridors in response to the clearance of indigenous shrubland (Table 7.1., Group E; Chapter 5).

Distribution patterns of endemic taxa and their close relatives are difficult to categorize. The group of *Scarabaeus* (Mostert & Holm 1982) formerly separated as the genus, *Pachysoma*, show a west coastal range from Swakopmund to Cape Town and are clearly separable into three taxonomic groups (Fig. 7.1.) based on numerical taxonomic data published by Holm & Scholtz (1979). The south western Cape taxa, *S. aesculapius* and *S. hippocrates*, are separated from all but a summer rainfall element from southern Namibia, *S. schinzi*. A western range extending into the Pre-Namib and the Kalahari is also shown by *Scarabaeus canaliculatus* and its relatives (Fig. 7.2.). Most other groups show a broad southern African distribution as for the west Cape, east Cape and central eastern highland range of *Scarabaeus spretus* and its relatives (Fig. 7.3.), or a south-western Cape, eastern Cape distribution extending into the central eastern highland blocks of southern Africa shown by *Onthophagus giraffa* and allied taxa (Fig. 7.4.). The west Cape, Transvaal highveld and north Natal coastal range of *Kheper bonellii* and its relatives (Davis 1986) is another distributional pattern. These illustrations serve to demonstrate the complexity of the evolutionary history of the dung beetle fauna in the south-western Cape.

The recent radiation of Onitini and Oniticellini into cattle pastures of the south-western Cape from the summer rainfall region is responsible for the broad taxonomic dissimilarity between summer rainfall and endemic elements. In dung preference trapping, species of onitine and oniticelline genera, *Onitis deceptor* and *Euoniticellus intermedius*, showed a strong association with cattle dung in the Transvaal (Davis unpublished data). Owing to the great difference in consistency

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APPENDIX 1

COMPOSITION AND OUTLINE ECOLOGY OF DUNG FAUNA WITH EMPHASIS ON DUNG COLEOPTERA

Abstract

1. Dung is a distinctive food resource and microhabitat which attracts a wide range of behaviourly diverse taxa characteristic of dung or decomposing matter in general.
2. Dung contains a species rich fauna since it is distributed as a patchy micro-environment in different macrohabitats and has a temporary and rapidly changing but renewable nature which enhances the possibilities of coexistence by many taxa.
3. It is especially attractive to coprophagous Diptera and Coleoptera, their dipteran, coleopteran and acarine predators and their coleopteran and hymenopteran parasitoids.
4. Breeding habits of dung Coleoptera vary from burial of dung (some coprophages), use of dung buried by other taxa (kleptoparasitism) (some coprophages) or breeding within the dropping in situ (some coprophages and all predators and parasitoids). Dung Diptera also breed within the dropping.
5. Spatial organisation of dung fauna is a response to soil type, vegetation type and climate. Temporal organisation is a response to weather, season, diel rhythms and age of the dung. Trophic organisation is in response to dung type.
6. Successional occurrence of taxa with age of the dung from specialist dung fauna (stage 1) through generalist fauna of decomposing matter (stage 2) to invasion by the soil fauna (stage 3) shows similarities to world wide spatio-temporal organisation of insects in dung with specialists dominant in favourable seasons and climates, fauna of decomposing matter dominant in marginal seasons and climates and soil fauna dominant when or where dung fauna are poorly represented.
7. Possibilities for coexistence are high in the cool temperate dung fauna but these decrease towards the tropics where burial of dung and the consequent removal or pre-emption of the breeding and feeding resource of pad-dwellers become more important.

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Taxonomic composition and general habits of dung fauna

Dung attracts a distinctive and species rich fauna which is numerically dominated by members of the insect orders Coleoptera and Diptera (Africa: Hafez 1939a; North America: Mohr 1943, Valiela 1974, Merritt & Anderson 1977, Harris & Blume 1986; Australia: Snowball 1944). Species of 31 dipteran and 16 coleopteran families have been recorded from cattle dung by these authors and the list is certainly incomplete (see Hanski & Hammond 1986). Despite the taxonomic diversity, members of only four families of Coleoptera (Scarabaeidae, Staphylinidae, Histeridae, Hydrophilidae) and several families of Diptera are numerically dominant in most situations. These taxa comprise two trophic groups, feeders on dung, decomposing matter or fungi (coprophages, saprophages, necrophages, mycetophages), and predators of these taxa. Dung Scarabaeidae and larvae of most dipteran taxa are coprophagous (Halffter & Matthews 1966, Merritt 1976, Koskela & Hanski 1977) whereas both adults and larval members of the other three beetle families and a few muscid and anthomyiid dipteran larvae are predatory (Merritt 1976, Koskela & Hanski 1977). Exceptions to the latter group include adult hydrophilids and members of several staphylinid subfamilies, including the Oxytelinae, which are considered to be coprophages, saprophages or necrophages (Koskela & Hanski 1977, Hanski & Hammond 1986).

Dung constitutes a temporary habitat comprising partially digested plant or animal matter. Therefore, in addition to the dung specialists (coprophages and their predators) it also attracts colonists of naturally decomposing vegetable and animal matter (saprophages, necrophages and their predators) and their parasitoids. Members of the soil fauna and free-living, foraging predators are also attracted to animal droppings. In most regions, specialist taxa numerically dominate the dung fauna. These not only comprise the Coleoptera and Diptera discussed above but often also include hymenopterous parasitoids of the immature stages of flies (Figg *et al.* 1983, Harris & Summerlin 1984, Hoyer 1986) and predatory phoretic Acarina (Hafez 1939b, Mohr 1943), which are transported from pad to pad by dung Coleoptera. However, many of the families which colonize dung are known to represent generalist frequenters of decomposing vegetable or animal matter (Britton 1970, Colless & McAlpine 1970) and these may predominate under climatically or seasonally unfavourable conditions. For instance, Diptera: Psychodidae are abundant in dung during autumn in Europe (Laurence 1954,

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Koskela & Hanski 1977), whereas Coleoptera: Ptilidae and Catopinae are abundant in cool montane conditions in Sarawak (Hanski & Hammond 1986).

Under extreme conditions, members of the soil fauna may predominate in dung. For instance, fresh cattle dung may be consumed by colonies of termites (Isoptera: Termitidae) (Ferrar & Watson 1970, Davis personal observation) during the dry season in warm temperate and tropical regions or colonized by ants (Hymenoptera: Formicidae) under desert conditions (Schoenly 1983). Under cool mid-winter conditions, Collembola have been observed to colonize cattle pads in large numbers in both the Mediterranean-type climatic areas of south-western Australia (Snowball 1944) and south-western South Africa (Davis personal observation). The soil fauna of soil mites and Collembola is also numerically dominant in the winter rainfall climate of Chile where the dung fauna is depauperate (Covarrubias *et al.* 1982).

Free-living predators representing several families often forage on dung. These include staphylinids (Snowball 1944, Alcock & Forsyth 1988), carabids (Wingo *et al.* 1974), ants, spiders (Arachnida: Aranaeidae) and omnivorous or predatory crickets (Orthoptera: Gryllidae) (Wingo *et al.* 1974, Schoenly 1983). A specialized form of predation is shown by flies of the family Asilidae which await and prey on members of the dung fauna as they arrive at the dropping (Bernon 1981).

Fresh dung is colonized by the characteristic specialist fauna. The surface fauna consists predominantly of adult Diptera (Mohr 1943) with the addition of ball-rolling scarabaeine dung beetles in warmer climates. The internal fauna comprises larval Diptera and both adult and larval Coleoptera including coprine dung beetles. Of the coprophagous taxa, larval Diptera complete their development within the pad and pupate at the base of the dropping or superficially in the soil. Habits and breeding strategies of the dung Coleoptera are described in more detail below.

General habits and breeding strategies of dung Coleoptera

The coprophagous dung beetles show degrees of association with coprophilous habits. The scarabaeid subfamilies, Scarabaeinae and Coprinae are predominantly coprophagous (Halffter & Matthews 1966) but also include necrophages (Halffter & Matthews 1966), mycetophages (e.g. Bornemissza 1971)

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and saprophages (e.g. Monteith & Storey 1981). Members of the scarabaeid subfamily, Aphodiinae, on the other hand, are predominantly saprophagous (Halffter & Edmonds 1982) although many species are dung specialists (Hanski & Koskela 1977). It seems that the staphylinid subfamily, Oxytelinae, is probably fairly generalist in its microhabitat associations (Koskela & Hanski 1977, Hanski & Hammond 1986). Predatory dung beetles may also be fairly generalist in their microhabitat associations and are predators, especially, of the immature stages of dung-breeding flies.

Coprophagous dung beetles show three principal breeding strategies. They either bury dung in which eggs are laid (broods), they lay their eggs in the broods of dung-burying beetles or they breed within the dropping in situ. Dung-burying taxa of the family Scarabaeidae remove dung to the ends of tunnels excavated in the soil beneath animal droppings (Coprinae) or roll a portion of dung some distance from the dropping before burial in the soil (Scarabaeinae). Eggs are laid in portions of buried dung termed broods which may be irregular ovoids packed into the end of the tunnel or regular ovoids modelled within a chamber (Halffter & Matthews 1966, Halffter 1977, Halffter & Edmonds 1982). A number of small coprine species have been recorded from brood balls and brood ovoids of scarabaeine (Halffter & Matthews 1966, Hammond 1976) and coprine (Martinez 1959, Halffter 1959) dung beetles. As it is presumed that their immatures develop in the host broods, this behaviour is termed kleptoparasitism. These habits appear to be widespread in coprine species of small size, few of which other than the oniticelline genus, *Drepanocerus* (Lumaret & Cambefort 1980), have been recorded to bury dung.

Breeding entirely within the dung pad in situ is quite uncommon in the Scarabaeinae and Coprinae but has been described for a few genera of the tribe, Oniticellini (Gardner 1929, Bornemissza 1969, Davis 1977, 1989a, Cambefort 1982b, Rougon & Rougon 1982, 1983, Klemperer 1983). In all cases, development of immatures was completed within modelled broods. Shallow burial of broods is also infrequently observed in some oniticelline genera (Cambefort 1980, Cambefort & Lumaret 1983, Lumaret & Moretto 1983) and in the scarabaeine tribe, Eurysternini (Halffter *et al.* 1980).

The scarabaeid subfamily, Aphodiinae, shows similar breeding strategies to those outlined for the Coprinae, i.e. burial of dung, kleptoparasitism or breeding within cells in the pads (Bernon 1981). However, the relative distribution of these habits between taxa may differ to the Coprinae and the modelling of buried dung is not so elaborate. Breeding strategies of the staphylinid subfamily, Oxytelinae, are unknown but are probably completed within the dung pad in situ.

Life histories of the predatory dung beetles are largely completed within the confines of the pad (e.g. Hafez 1939b, c, Summerlin *et al.* 1981, 1984). It appears that predatory Staphylinidae are unable to burrow in the dung since they use pre-existing burrows (Mohr 1943). However, some species are undoubtedly dung specialists (Hanski & Koskela 1977, Davis unpublished data) whereas other species are more generalist in their macrohabitat associations (Hanski & Hammond 1986). Adults have been recorded as predators of eggs, larvae and pupariae of Diptera (Staphylininae, Aleocharinae, Tachyporinae) (Merritt 1976), adult Collembola (Steninae) and mites (Eusthetinae) (Hanski & Hammond 1986). Although larval Staphylininae have been recorded as predators of fly larvae and mites in dung (Hafez 1939b), some of the Aleocharinae are pupal parasitoids of flies (Drea 1966, Wingo *et al.* 1967, Thomas & Morgan 1972, Figg *et al.* 1983).

Some species of Histeridae are dung specialists, others found in dung are also strongly attracted to carrion (Davis unpublished data). Adult Histerinae are known as predators of larval and pupal Diptera. Their eggs and pupariae are located in the soil beneath the dung, whereas the larvae are predators of dipteran larvae and pupariae within the pads (Bornemissza 1968, Summerlin *et al.* 1981, 1984).

Unlike the other groups showing predatory habits, adult Hydrophilidae are coprophagous but larval *Sphaeridium* are considered to be predators by recent authors (Bourne & Hays 1968, Koskela & Hanski 1977). Eggs larvae and pupariae are all found in the dung (Hafez 1939c).

Partitioning of space by dung fauna

The spatial distribution of dung beetles is strongly influenced by various physical parameters. Climate, chiefly comprising annual temperature and rainfall distribution, influences the occurrence of dung beetles on a regional level. Habitat, chiefly comprising soil and vegetation type influences dung beetle distribution on a local level.

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Latitudinal changes in old world species assemblages in dung

From temperate to tropical latitudes there are changes in both the taxonomic structure of species assemblages in dung and in the importance of dung burial as an ecological factor. Coleoptera of the cool temperate dung fauna of Finland are numerically dominated by Aphodiinae, Hydrophilidae and Staphylinidae (Hanski & Koskela 1977). Histeridae are not abundant nor is dung burial an important ecological factor. In warmer temperate regions and the tropics, the complexity of the assemblages of coprophilous Coleoptera is increased taxonomically by the incorporation of further groups (Scarabaeinae, Coprinae) and ecologically by the effects of seasonally extensive dung burial by these taxa (e.g. Davis 1989b) which may pre-empt the breeding resource of pad-dwelling groups (Roth 1983, Davis 1989b).

Comparison of published totals for species richness across latitudinal gradients is ecologically unsound due to the number of variables involved. In addition to climatic variation, these include differences in sizes of study area, bait types, habitats, trapping periods and trapping intensity. However, general trends may be clearly inferred from the magnitude of some of the differences. Scarabaeinae, Coprinae (none in Finland, 17 species in Corsica, 131 species in the Ivory Coast - Hanski & Koskela 1977, Lumaret 1980, Cambefort 1982a) and Histeridae (four species in Finland, 21 species in South Africa - Hanski & Koskela 1977, Davis *et al.* 1988) are predominantly warm temperate and tropical elements. Aphodiinae, Staphylinidae and Hydrophilidae have both a cool temperate and a tropical distribution. Species richness of Aphodiinae (18 species in Finland, 41 species in the Transvaal, South Africa - Hanski & Koskela 1977, Davis unpublished data) appears to increase towards the tropics. That of the Staphylinidae and Hydrophilidae, whose activities are confined to the dung (134 and 16 species respectively in Finland, 100 and 13 species respectively in South Africa - Hanski & Koskela 1977, Davis *et al.* 1988), appears to be similar across latitudinal gradients.

Regional climatic gradients

The regional distribution of dung beetles is chiefly influenced by climatic factors. For instance, species assemblages of dung beetles (Scarabaeinae, Coprinae) are organized according to climate in Spain (Kirk & Ridsdill Smith 1986).

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Along similar lines of latitude in east Africa, organization of species assemblages of Scarabaeinae and Coprinae appears to be strongly influenced by altitude and annual rainfall regime (Davis & Dewhurst unpublished data). Altitude and its effect on temperature may also influence habitat associations in *Aphodius* since species previously described as shade specialists at lower altitudes were characteristic of unshaded situations at higher altitudes in Norway (Key 1981).

Local partitioning of space

Dung is distributed as a patchy environment which increases spatial variance and facilitates the coexistence of large numbers of species (Hanski 1981). Other factors decreasing spatial overlap are specialization to a particular habitat and behaviour of the fauna which may remain in the dung or engage in dispersal away from the dropping.

The site of deposition influences the species composition of the fauna by which it is colonized. Many species of Scarabaeinae, Coprinae (Nealis 1977, Lumaret 1980, 1983, Cambefort 1982a, Doube 1983), Aphodiinae, Staphylinidae, Histeridae and Hydrophilidae (Rainio 1966, Hanski & Koskela 1977, Davis *et al.* 1988) show clear associations with particular soil types or with physiognomic structure of the vegetation.

Dung beetles (all taxa) have partitioned both the horizontal plane (soil surface) and the vertical plane (Scarabaeinae, Coprinae). Below the soil surface, depth of burial of the broods varies between species of Coprinae (Lumaret 1983, Edwards 1987) which excavate their tunnels under the dropping, either vertically or at an angle away from the dung. Most Scarabaeinae seem to bury their broods relatively shallowly and this may be related to horizontal dispersal of the breeding sites away from the dropping and the consequent reduction in competition for breeding space. In tropical African rain forests, some species of Scarabaeinae and Coprinae are most abundant at 10-20m above the soil surface in the vegetation (Walter 1983). They are uncommon at ground level particularly in the rainy season when dung beetles are most abundant. Perching behaviour in forest vegetation has also been recorded for Neotropical and Australian dung beetles (Howden & Nealis 1978).

Soil type is defined especially by grain size and mineral composition. Grain size influences the soil's capacity for water retention and the rate of drainage.

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Moisture content of soil has been shown to influence nesting behaviour of *Euoniticellus intermedius* (Reiche) (Coprinae) which produced diffuse nests in moist soil and concentrated clusters of broods in drier soil (Rougon & Rougon 1983). Soil type has also been shown to influence survival of immature stages in *Phanaeus* spp. (Coprinae) (Fincher 1973).

Although hardness of soils varies with the moisture content from rainfall, overall harness of fine-grained soils is greater than that of coarse-grained soil (Davis unpublished data). In *Phanaeus* spp., increase in the clay fraction of the soil was positively correlated with the number of broods produced and negatively correlated with the depth of their burial (Fincher 1973). Thus, space available for partitioning by species burying dung under the dropping would be reduced on clay and may be one reason for variation in the composition of species assemblages relative to soil type.

Both vegetative cover and vegetative profile influence dung beetle distribution (e.g. Howden & Nealis 1975, Lumaret 1980, Cambefort 1982a). Shade from high profile vegetation probably influences microclimatic variables around the droppings such as temperature, light intensity and humidity (Landin 1961, Doube 1983, Lumaret 1983). As both soil and vegetation type influence the composition of species assemblages, it is not surprising that they also influence dung burial in warm temperate regions with greatest burial on unshaded sand and least on shaded clay (Davis *et al.* 1988). Although this has the capacity to disrupt the activities of beetles breeding in the dung, there is much short term variation in the amounts buried (Davis unpublished data) which would allow some spatial separation of buriers and dung pad breeders.

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Temporal partitioning by dung fauna

Seasonal occurrence

Activity by the specialist members of the dung fauna is greatest during warm wet periods. Therefore, in most temperate regions the dung fauna is abundant during summer (Mohr 1943, Valiela 1974, Hanski & Koskela 1977) but limited during the winter (McDaniel and Balsbaugh 1968). In regions of Mediterranean-type climate, activity is mainly during spring and autumn (Krausse 1907a, b, Lumaret 1983, Davis 1987) whereas in warm temperate and tropical climates it is mainly during the rainy season (Halffter & Matthews 1966, Kingston 1977, Cambefort 1982a, Davis 1989b).

Since seasonal changes in the size of bushflies in south-western Australia was correlated with seasonal variation in pasture growth which influenced the nutrient value of the dung (Matthiessen & Hayles 1983), activity in dung beetles is probably maximized towards the main growth period in the local vegetation. This may partly explain why peak seasonal activity by Scarabaeinae and Coprinae in South Africa was during spring in the Mediterranean-type climate of the south-western Cape (Davis 1987) and during the early summer portion of the rainy season in the Transvaal (Davis 1989b).

Faunal succession with age of the dung

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Dung fauna arrives in a recognizable succession (Mohr 1943, Valiela 1974, Koskela & Hanski 1977, Hanski & Koskela 1977) attracted by olfaction (Mohr 1943, Halffter & Matthews 1966) to volatile compounds (Shibuya & Inouchi 1982). Chemical structure of these volatile compounds changes with the age of the dung (Yasuhara *et al.* 1984) and parallels the process of desiccation. Time of colonization and duration of residence by dung fauna varies with the original moisture content of the dung (Mohr 1943) and its rate of drying (Davis 1989b). The rate of desiccation in each pad varies with temperature, humidity and disruption of the pad by dung fauna (Davis 1989b) which is dependent on season, weather and insolation. In general, abundance, biomass and diversity of the fauna decreases with age of the pad whereas differences in species composition between individual droppings increase with age (Koskela & Hanski 1977). The initial rate of colonization, at least, is more rapid in unshaded than in shaded situations (Koskela & Hanski 1977).

Dung is a temporary habitat in which most of the faunal succession occurs over a fairly short period. Three stages in the succession have been recognized by Mohr (1943) and Koskela & Hanski (1977). The short early stage of the succession in cattle pads is dominated by dung specialists. Later in the succession facultative dung breeders, which are also commonly found in other types of decomposing matter, are observed followed, finally, by invasion by members of the soil fauna. In warm temperate and tropical regions, this succession may be disrupted by dung-burying beetles which are able to remove entire (1*L*) pads within 24h (Davis unpublished data). However, moderate amounts of dung removal appear to have little effect on the abundance of dung pad-dwelling taxa (Davis *et al.* 1988) although their breeding success is reduced (Roth 1983) under laboratory conditions.

Colonization of dung by abundant coprophagous taxa is bimodal (Mohr 1943, Hanski & Koskela 1977). Large muscids, anthomyiids and sarcophagids rapidly became abundant and quickly declined in number on cattle pads in North America whereas small sepsids and sphaerocerids slowly increased to peak numbers (Mohr 1943). The first peak in numbers of European coprophagous beetles comprised large dung specialists (*Aphodius* spp., *Sphaeridium* spp.) which showed a short period of residence (Hanski & Koskela 1977). The second peak comprised smaller mainly generalist saprophages with a longer period of residence (Oxytelinae, Proteinae, *Cercyon* spp.). Dung-burying beetles (Coprinae) in South Africa also showed species arriving either early or slightly later in the succession (Doube *et al.* 1988).

Colonization of dung by predatory taxa is apparently unimodal and remains at a high rate for longer than that of coprophagous species (Koskela & Hanski 1977). This perhaps reflects the build-up of prey populations which, for specialists, probably bears an inverse relationship to deterioration of the dung. Even so, some predatory species show an early peak in the succession, others a later peak (Wingo *et al.* 1974). Specialist dung predators (larvae of *Sphaeridium* spp., *Hister* spp., some *Philonthus* spp.) may be associated with the first wave of specialist dung fly larvae and other predators with more generalist flies of the second group. Many flies lay eggs within minutes of pad deposition whereas dung sarcophagids are viviparous (Mohr 1943). *Sphaeridium* spp. are also present very early in the succession (personal observation), lay eggs rapidly and have often developed to pupal stage with the first flies (Mohr 1943).

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Diel flight activity

Patterns of diel flight activity of the dung fauna show clear distributional trends in northern Europe (Koskela 1979). In specialist coprophages (*Sphaeridium* spp. *Aphodius* spp.) and large predators, unimodal, mostly diurnal flight activity was shown whereas generalist coprophages (*Cercyon* spp., Oxytelinae) and smaller predators (Aleocharinae) mostly show bimodal more or less crepuscular flight activity. This pattern changes with season so that the bimodal distribution during the long period of daily flight activity during the warm summer became unimodal during the cooler autumn when the daily flight period was shorter. Duration of flight activity was also shorter in shaded than in unshaded habitats. These results are presumably related to differences in the distribution of favourable temperatures for flight activity between habitats and seasons.

Trophic partitioning by dung fauna

Dung constitutes a distinct resource type in an array of different forms of decomposing animal and vegetable matter. It is, therefore, visited by a specialist dung fauna in addition to generalist elements of the fauna colonizing decomposing matter. Dung may be divided into three general types dependent on vertebrate diet and digestive system. Dung of non-ruminant herbivores, e.g. elephant, rhinoceros, horse, zebra, is coarse-fibred in comparison to that of ruminant herbivores, e.g. cattle, buffalo, wildebeest. Dung texture of omnivorous and carnivorous vertebrates also often lacks obvious fibre but the odour is markedly different to that of herbivore dung indicating a quite different chemical structure of the volatiles. As attraction to dung is by olfaction (Halffter & Matthews 1966) it is suggested that odour is the primary control of trophic partitioning.

Dung type has been clearly partitioned by many species of the dung fauna both coprophages, predators, Coleoptera and Diptera (Hafez 1939a, Rainio 1966, Fincher *et al.* 1970, Gordon & Cartwright 1974, Pitkin 1986, Davis unpublished data). Some more generalist species found on omnivore dung are also common on carrion. Some found on herbivore dung are also well represented in naturally rotting vegetation (Davis unpublished data).

Dung has also been partitioned according to size of the dropping and, perhaps, behaviour of the dung beetles (Peck & Howden 1984). Large beetles and small species which bury dung under the dropping were associated with large baits. Small ball-rolling beetles tended to favour small baits.

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APPENDIX 2

EVOLUTION AND BIOGEOGRAPHY OF DUNG BEETLES IN RELATION TO VERTEBRATE DUNG TYPES WITH EMPHASIS ON THE SCARABAEINAE AND COPRINAE

Abstract

1. Specialist dung beetles probably evolved in response to regular occurrence of increasing densities of dung.
2. Some elements of the Scarabaeinae and Coprinae show a true Gondwanaland distribution whereas all other taxa show a more restricted distribution and are clearly of more recent origin.
3. The Gondwanaland distribution of the subtribe Canthonina (Scarabaeinae) and the Dichotomiina (Coprinae) implies a Mesozoic origin during the era of the dinosaurs as the dominant terrestrial vertebrates.
4. However, distribution data suggest that most diversification of modern dung beetle taxa has occurred since the fragmentation of Gondwanaland presumably in response to increasing size and physico-chemical diversification of mammalian dung types.
5. Association with dung at lower taxonomic levels in Staphylinidae, Histeridae, Hydrophilidae and Aphodiinae together with generalization on other types of rotting matter shown by many taxa, indicates a more recent adoption of coprophilous habits than in the Scarabaeinae and Coprinae which show highly evolved dung-nesting behaviour.
6. This probably occurred only with the increase in size of mammalian dung types during the Tertiary which allowed the generalist endocoprid lifestyle exhibited by many small predatory and coprophagous taxa.
7. By far the greatest diversity and endemism of scarabaeine and coprine genera occurs in the southern continents which argues for the southern derivation of the fauna in northern continents.
8. However, local patterns of dung beetle evolution and biogeography have been in accordance with the geological, climatic, vegetational and coprological history of the continental block.

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9. The highly endemic scarabaeine and coprine fauna of the long isolated island continent of Australia is characterized by low diversity of taxa which is possibly related to the universality of the pellet droppings of the native mammals. Gondwanaland groups (Canthonina, Dichotomiina) dominate in terms of generic richness and occur primarily in the forests. More recently arrived vicariant groups from Asia (Onthophagini) are well represented in unshaded situations which have expanded with the progressive cooling and drying of the climate since the Miocene.

10. The highly endemic fauna of South America, which was isolated for much of the Tertiary until the Pliocene, is characterized by much higher diversity of taxa than Australia. Indigenous diversification of taxa (Phanaeina, Ennearabdina, Eucraniina, Eurysternini) has added to the Gondwanaland groups (Canthonina, Dichotomiina) possibly in response to early Tertiary diversification of endemic mammals, their dung types and the size range of droppings. Gondwanaland groups still dominate in terms of generic richness and are primarily restricted to forests which have probably undergone recent expansion. However, recent radiation into unshaded habitats has also occurred. Increasing aridity in the south resulting from a rain shadow induced by uplift of the Andes may be responsible for the presence of a few southern relict groups. Pliocene interchange of fauna with North America has allowed invasion of elements ultimately of old world origin probably via Asia. The fauna of North America is depauperate and has been derived from the old world, perhaps together with mammal invasions during the Miocene and Pliocene, and probably more recently from South America during the Pliocene to present.

11. The fauna of Africa is the most diverse of all the continents with Gondwanaland groups (Canthonina, Dichotomiina) dominated in terms of abundance and generic richness by indigenous diversification of taxa possibly in response to diversification of mammalian dung types and increase in their size during the early-mid Tertiary, e.g. Proboscidea, and again in the late Tertiary, e.g. Bovini. This provides greater diversity of native dung types than in Australia and South America. Retreat of forest during the later Tertiary and widespread uplift resulted in a dung beetle fauna primarily centred in unshaded situations. High generic endemism compared with the rest of the old world indicates a predominantly African origin for the Palaearctic and Oriental fauna which have probably dispersed to North and South America (Coprina, Onthophagini, Oniticellini, Sisyphina) and Australia (Onthophagini) via occasional land bridges or island archipelagos.

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12. Scarabaeinae and Coprinae of island groups are generally dominated by Gondwanaland elements. Proximity of large land masses determines whether more recent vicariant elements have been added naturally to the fauna. Madagascar and Caribbean islands have a fauna of both Gondwanaland and more recent elements. The isolated island group of New Caledonia has only a fauna of Gondwanaland elements.

The modern insect fauna of dung comprises four main families in terms of numerical abundance (Scarabaeidae, Staphylinidae, Histeridae, Hydrophilidae) which comprise two main trophic groups, coprophages and predators feeding principally on the immature stages of coprophagous dung-breeding flies.

These show degrees of association with dung ranging from specialization to a particular type of dung to generalization on various forms of decomposing animal and vegetable matter (Davis unpublished data). Certain Scarabaeidae show a large degree of specialization to coprophagy at the subfamily (Scarabaeinae, Coprinae) or tribal (Geotrupinae, Geotrupini) level (Halffter & Matthews 1966, Halffter & Edmonds 1982). However, predominantly predatory groups (Staphylinidae, Histeridae, Hydrophilidae) and the coprophagous Aphodiinae only show specialization at the species level and many species found in dung are microhabitat and dietary generalists (Hanski & Koskela 1977, Hanski & Hammond 1986). As, broadly speaking, evolutionary distant influences are expressed at higher taxonomic levels than evolutionary recent influences, it is suggested that the coprophagous Scarabaeinae and Coprinae are more ancient colonists of dung than the other coprophagous and predominantly predatory groups. It is considered likely that the Scarabaeinae and Coprinae have evolved with the dung of large vertebrates commencing with the utilization of pellets whereas predatory groups are associated with the later evolution of large dung masses suitable for the support of an endocoprid predator/prey system or suitable for breeding within the dung (some Aphodiinae, Oxytelinae).

Dung specialists probably evolved with dung type which is linked to the evolutionary history of mammals. Mammal dispersal is known to be closely linked to continental drift (Eisenberg 1981) which is consistent with the viewpoint of Cooper (1977) who suggests that continental drift has shaped the geological, climatic and bio-evolutionary history of the planet.

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A synopsis of the main events in continental drift, a suggested time scale, and their influence on palaeoclimate, flora and fauna, is provided by Axelrod & Raven (1978), Lillegraven *et al.* (1979), Cox & Moore (1985) and Tyson (1986). Fragmentation of the supercontinent Pangaea, which formerly comprised all of the world's major land masses and which commenced some 150-170 million years before present (MYBP) has induced climatic evolution and great vegetational change. In the early stages of this fragmentation during Mesozoic times (Triassic - Cretaceous) the world was warm with an absence of pronounced latitudinal temperature gradients. However, the separation of fragments of the southern supercontinent of Gondwanaland and the northern supercontinent of Laurasia, from Cretaceous times onwards, led to a worldwide trend towards cooling during the Tertiary, particularly in the higher latitudes. This resulted in the development of a distinct latitudinal temperature gradient and the formation of polar ice caps. These changes paralleled the closure of the circum-latitudinal oceanic circulation of the Tethys of Mesozoic times and its replacement by north/south cellular circulation systems in the modern oceans. With the cooling trend during the Tertiary, there were concomitant changes in vegetation and fauna. In many regions, the forests of the warmer and wetter early Tertiary opened out into vegetation types physiognomically better suited to the cooler drier climate especially during the Miocene. As a response to this selective pressure, the emphasis changed from small, mainly arboreal forest mammals to large, terrestrial grazing forms better suited to shrubland and grassland. The production of large dung masses in unshaded situations by these larger terrestrial forms would have had great influence on dung beetle evolution as forest elements gave way to new groups in the open situations, particularly in Africa.

This section discusses the possible effects of changes in physical characteristics of dung type on the evolution of habits in dung beetles. It also examines the influence of continental drift on the evolution and dispersal of mammals and their dung types in relation to the biogeography of dung beetles, principally Scarabaeinae and Coprinae.

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Origin and evolution of coprophilous habits

The evolutionary sequence of events in specialization to coprophagy by the modern dung fauna remains speculative. It presumably commenced as a response by the ancestors of small coprophagous taxa such as the Scarabaeinae and

Coprinae to increasing densities of dung pellets dropped by the small early vertebrate taxa. Increasing size and physico-chemical variability of droppings probably led to the diversification of scarabaeid taxa and the colonization of dung by additional elements characteristic of rotting material by virtue of their pre-adaptation, particularly larval Diptera and their staphylinid and histerid predators. Hydrophilid dung beetles, which belong to a predominantly aquatic family, may have evolved from colonists of dung dropped at watering points. Predatory groups appear to be comparatively recent elements since the association is at a low taxonomic level and many taxa remain generalist inhabitants of rotting matter. This argues for the comparatively recent appearance of these groups in large mammalian droppings.

A wide range of breeding behaviour is shown by dung taxa from relatively unspecialized to extreme specialization. The probable most recent colonists in terms of evolutionary time show the most unspecialized breeding behaviour in dung. In these taxa, which comprise predatory groups and some Aphodiinae, the eggs are laid in or under the dung (Hafez 1939b, c, Klemperer 1980, Summerlin *et al.* 1981, 1984). The larvae are free-living or confined to a cell in the dung. Various other behavioural patterns are known. The larva of *Aphodius rufipes* (L.) lives freely in the dung until the third instar when it constructs a short tunnel in the soil from which it commutes to the dung pad or colonizes dung buried in the soil by other coprophages (Klemperer 1980). However, some *Aphodius* and *Colobopterus* provision for larvae by burying dung in shallow shafts immediately under the dropping (Bernon 1981, Yoshida & Katakura unpublished manuscript). The eggs are laid in the soil close to the dung. According to Edmonds (1983) it is burial of dung by adults for their food requirements which has led to provisioning for larval Scarabaeinae and Coprinae. Increase in the complexity of provisioning and nesting behaviour by these taxa has been paralleled by a decrease in fecundity with the ovaries reduced to a single left ovariole and the number of follicles present ranging from about 17 to only one or two in Afrotropical species (Davis personal observation). This indicates extreme specialization to breeding in dung.

Broadly speaking, the Scarabaeidae have fossorial associations if not as adults then usually in the larval stage. It is probable that the ultimate ancestors of the group were fossorial saprophages. In modern Aphodiinae, which are considered to be relatively recent colonists of dung, saprophagy is considered to be the primitive condition and coprophagy the derived behaviour whereas in the Scarabaeinae and Coprinae, coprophagy is considered primitive and all other diets

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derived (Halffter & Edmonds 1982). This viewpoint has been challenged by Cambefort and Walter (1985) who suggest that saproxylophagous breeding in the dichotomine genus, *Paraphytus*, is primitive behaviour. This hypothesis is based on the Gondwanaland distribution of its generic relatives and the presence of three mandibular larval teeth as opposed to two which is the derived or apomorphic condition found in most other scarabaeine and coprine larvae. There is probably insufficient evidence to support this suggestion since, as pointed out by the authors, both attributes are also common to another dichotomine genus, *Heliocopris* (Cambefort & Lumaret 1986), which shows coprophagous habits. To the converse, there is insufficient evidence to disprove the suggestion. Thus, the genus may represent an early radiation by saprophagous ancestors or a secondary specialization by coprophagous ancestors.

Behavioural (Halffter & Edmonds 1982) and morphological (Zunino 1983) evidence indicate that the Scarabaeinae and Coprinae diverged early in their evolutionary history. Differences in the pattern of behavioural response to dung is probably the source of this divergence since the Scarabaeinae remove dung to another site before burial whereas Coprinae bury dung at the site of its deposition. Thus, ball-rolling might either be a result of primitive foraging behaviour, a response to competition at the dropping or both. Although speculation concerning the early evolutionary stages of these habits is all that is now possible, a logical sequence of events suggest a progression from generalist saprophage to specialist association with dung combined with the evolution of provisioning for larvae.

Provisioning for larval Scarabaeinae and Coprinae is characterized by complex nesting behaviour. It is suggested that dung moisture content and competition have been the principal evolutionary pressures increasing the complexity of this behaviour. Broods are modelled from fresh dung by compression and elimination of excess moisture so that dung water content is much reduced during nest construction (Edwards 1988, Davis 1989a). This reduction is about 20% in broods of *Oniticellus egregius* Klug constructed from horse dung and 30% in those made from cattle dung. Similar percentage reductions have been recorded for *Onitis* spp. (Edwards 1988). As drainage of moisture from artificial brood balls into the soil appear to increase survival and growth rates in larvae of *Onitis caffer* Boheman (Edwards & Aschenborn 1985) much of the behaviour involved in brood construction may be related to provision of a suitable dung plasticity.

Most coprine beetles bury dung at the end of tunnels under the droppings. In its most basic form dung is compressed directly into the end of the tunnel so that excess moisture soaks into the tunnel wall. Because of the gradual addition of dung directly from the dropping, the rate of burial by such species is relatively slow, e.g. *Euoniticellus, Onthophagus, Onitis* (Doube In press). In other species, the rapid removal of dung into a subterranean store may be a response to exposure to resource pre-emption. As such behaviour demands space for the reworking of the dung it has presumably been accompanied by the evolution of chamber construction. In its simplest form the end of the tunnel is expanded, e.g. *Gromphas* (Halffter & Edmonds 1982). However, in the more highly evolved genus, *Heliocopris*, dung is at first buried in a shallow tunnel and later transferred from storage to a deeply excavated chamber where broods are cut from a compressed dung cake (Klemperer & Boulton 1976). In chambers, the broods are exposed to the air which may increase the rate of desiccation and allow fungal growth. Thus, those of most species are enveloped in a soil shell. Prolonged parental attendance of broods produced in chambers has been a natural progression from this behaviour, e.g *Copris* (e.g. Tyndale Biscoe 1983).

Chamber construction is almost universal in scarabaeine subtribes (Halffter & Edmonds 1982), which mostly remove all their immediate dung requirements as a ball which is rolled away and buried some at distance from the dropping. Chamber construction is, perhaps, again related to the necessity of a space in which to rework the dung and eliminate excess moisture. Most taxa coat their broods in soil shells (Halffter & Edmonds 1982). Sisyphina are an exception but many species of *Neosisyphus* are known to construct their broods at the soil surface and bury them directly into the soil or abandon them on the surface (Paschalidis 1974).

In the Coprinae, a trend from burial of dung in unelaborated tunnels through chamber construction to parental care of broods is seen in two tribes, i.e. Oniticellini (e.g. Davis 1989a) and Coprini (e.g. Tyndale Biscoe 1983, Halffter & Edmonds 1982). In the Scarabaeinae, chamber construction is more usual and parental care more widespread (e.g. Halffter *et al.* 1980, Halffter *et al.* 1984, Sato & Imamori 1987, Edwards 1988). The widely divergent origins of these taxa (Zunino 1983) suggest the independent evolution of similar habits on several occasions which constitute marked evolutionary parallelism.

The trend to parental care is interpreted as subsocial behaviour by some authors (Klemperer 1982, 1983, Sato 1988) but evidence indicates that there is a trend to diversification (Lumaret 1983, Edwards 1987) rather than aggregation of

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breeding sites in Scarabaeinae and Coprinae. Therefore, it seems unlikely that this can be accepted as true subsocial behaviour.

Zunino (1983) has indicated that *Onitis, Gromphas* and *Phanaeus*, which are currently considered as coprine taxa, are in fact derived from scarabaeine taxa based on a study of their aedeagi. If the morphology of aedeagi accurately reflects the phylogeny of the subfamilies, taxonomic reorganization and modification to concepts of behavioural evolution in these taxa will be required.

Timescale of evolution of coprophilous habits

The production of vertebrate dung at a sufficient rate and density to support a specialist dung fauna presumably occurred before the late Cretaceous fragmentation of Gondwanaland as determined from the present distribution of the Canthonina and Dichotomiina which indicates a Gondwanaland origin. This places the early evolution of the Scarabaeinae and Coprinae firmly in the era of the dinosaurs which became extinct only at the end of the Cretaceous. Dinosaurs have usually been considered as cold-blooded and, therefore, to have a low metabolic rate. Low body temperature is correlated with a slow rate of digestion. This decreases by 400% over a temperature range of 36,5-16,5°C (Bakker 1986). Dietary studies on modern crocodiles, which are distant cold-blooded relatives of the dinosaurs, showed that the stomach was often empty or nearly so (Bakker 1986) implying a sporadic mode of feeding and consequently a slow rate of dung production. However, Bakker (1986) has provided detailed evidence for endothermy and a high rate of metabolism in dinosaurs. This evidence includes the high density of haversian canals in both mammal and dinosaur bones which are presumed to be associated with a rapid rate of growth, low predator/prey ratios in mammals and dinosaurs compared with fossil amphibians which is presumed to be associated with the greater energy requirements of individual endothermic predators and, the high walking speed of modern mammal and extinct dinosaurs compared with modern and extinct amphibia as calculated from recent and fossil footprints. Thus, dung production in dinosaurs would have been slow if they were poikilotherms or rapid and copious if they were endothermic. However, the absence of fossil evidence for or against a dinosaur dung fauna restricts all comment to the purely speculative. It can only be concluded that the extant Scarabaeinae and Coprinae may have evolved

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directly from saprophagous ancestors or from part of an established specialist dung fauna.

Whatever its initial origins, late Mesozoic and Tertiary evolution of the modern dung fauna has clearly been associated with the radiation of mammal taxa and diversification of their dung types. This is supported by observations that traps baited with modern reptile and amphibian dung in Panama are very poor attractants for dung beetles in comparison to those baited with mammal dung (Young 1981). The present distribution of taxa in southern continents implies that the first specialized dung fauna associated with pellets evolved before the fragmentation of Gondwanaland was complete. Relatively low diversity of Gondwanaland Scarabaeinae and Coprinae (one subtribe in each subfamily) may indicate limited early diversification in relation to pellets (see comments on modern Australian fauna) dropped by Mesozoic mammals which were all small (Lillegraven 1972). Subsequent diversification has probably occurred with the early Tertiary evolution and increase in size of non-ruminant herbivores voiding large, coarse-fibred droppings which followed the extinction of the dinosaurs at the end of the Cretaceous. This must have occurred after the fragmentation of Gondwanaland owing to the restricted distribution of most of the species rich taxa. Finally, a further principal radiation of taxa primarily evolved from within extant higher taxa (i.e. a recent event) has occurred with the appearance of large ruminant herbivores voiding large, fine-fibred droppings. Elements of the first two main waves of adaptive radiation may constitute the fauna of omnivore and carnivore dung.

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Evolutionary history of Scarabaeinae and Coprinae with emphasis on southern continents

A discussion of the world-wide distribution of dung Coleoptera other than Scarabaeinae, Coprinae and Geotrupinae is not possible at present as the alpha taxonomy is incomplete or the distribution data have not been suitably collated. It can only be noted here that Aphodiinae and predatory families show a temperate and tropical distribution but are poorly represented in Australia (Doube 1986) which lacks a native vertebrate fauna dropping large masses of dung (Bornemissza 1976). Also, compared with the old world, generic richness of dung Aphodiinae is low in the Americas where only *Aphodius* and *Ataenius* have been recorded in various studies of dung fauna (Howden & Nealis 1975, Peck & Howden 1984, Fincher *et al.* 1986, Harris & Blume 1986).

The geographical distribution of the Geotrupinae has been summarized by Halffter (1974) and the feeding habits by Halffter & Edmonds (1982) and Britton (1970). The group clearly has ancient origins with the addition of more recent elements. Of the four tribes, the Bolboceratini (mycetophages found in dung in Australia) have a fairly cosmopolitan distribution although it is composed of elements with differing biogeographical origins, some of which may be Gondwanian. The other tribes have slightly more restricted distributions. The Athyreini (mycetophages) are found predominantly in south and central America and also in Africa and the Oriental region. The Geotrupini (coprophages) are holarctic in distribution and the Lethyrini (phytophages) Palaearctic, mainly in Asia. The restriction of coprophagous habits to the tribe, Geotrupini, indicate that coprophagy is a recent development in the subfamily.

The Scarabaeinae and Coprinae have a cosmopolitan distribution in warm temperate and tropical regions. Coprophagous habits are widespread in each subfamily and therefore of ancient occurrence. The most recently published list of genera (Halffter & Edmonds 1982) has been used to produce a matrix depicting numbers of genera per tribe or subtribe in the various biogeographical regions. For the purposes of this study, Madagascar has been designated as a distinct biogeographical entity. This matrix has been analyzed using an agglomerative clustering technique, group average linking, in conjunction with the Bray-Curtis coefficient of similarity. The results have been used to produce a graphic representation of the relationships between the distributions of the various tribes and subtribes and, between the fauna of the biogeographical areas (Figs A2.1., A2.2.).

Like the Geotrupinae, the Scarabaeinae and Coprinae have ancient origins with the addition of more recent elements. At the 60% level of similarity (Fig. A2.1.), five groups of tribal/subtribal distributional relationships are indicated for the Scarabaeinae and Coprinae. Group A comprises the Canthonina and Dichotomiina which are considered to have a Gondwanaland origin (Halffter & Matthews 1966, Matthews 1974, Halffter 1974) and to be composed of heterogeneous elements (Matthews 1976). They numerically dominate the Neotropical, Australian and Malagasy generic fauna at generic level (Table A2.1.). Whereas Group A is abundant in Africa in terms of number of genera (28), the fauna is numerically dominated by the elements of Group B, the group which

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predominates in the old world (Table A2.1.). Groups C and D comprise elements mainly or entirely restricted to the Neotropical region and Group E is native to Madagascar. The Nearctic region is depauperate in genera and has been colonized by a few elements from both the Neotropical and the old world fauna. It is suggested that Groups B-E are more recent elements due to their more restricted distribution. This is unlikely to result from selective extinction on some continents.

Figure A2.2. shows that the scarabaeine and coprine fauna of the old world (Africa, Europe, Asia) are comparatively close and although they differ from those of Australia, the Americas and Madagascar, there are reasonable similarities. In the old world, where modern land links exist, similarities occur at generic level and rarely at species level. On the other continents which are broadly separated from one another and the old world by sea, similarities are at the slightly higher level of subtribe or, occasionally, genus. The relatively close taxonomic relationships between the fauna of widely separated land masses are consistent with the theory of continental drift which maintains that the earth's crust is divided into tectonic plates which are in movement relative to one another by addition or subtraction of material at the plate margins. A large body of evidence indicates that all the land masses were once connected and have since separated and, in some cases, recombined to produce the modern continental distributions. During the Tertiary, all southern continents have spent varying periods in isolation as a result of continental drift. It is suggested therefore that waves of adaptive radiation and dispersal in dung beetles associated with climatic and vegetational changes have been influenced by local evolution of vertebrates dropping dung of differing characteristics and limited by the availability of suitable land links.

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Adaptive radiation

Biogeographical distribution of a group may provide information concerning its past adaptive radiations. This concept maintains that species often expand their ranges, sometimes over very wide areas, perhaps in response to favourable conditions induced by climatic and associated changes. Further change may isolate populations of this species through retreat to refugia so that genetic input is restricted to that evolved in response to local conditions. In time, differences between population groups in isolated areas may be sufficient to separate them taxonomically at species level or greater. Further cycles of expansion and contraction of range may result in intermingling and sympatry between these new species. Alternatively, if some of these new species become too specialized to be able to adapt to local change and are unable to move to a more favourable area or track a favourable climatic type then extinction occurs resulting in gaps in the original range of the radiated group and leading to a typical relict distribution.

Various predictions or hypotheses may arise from this concept. The most recent radiations will comprise single species with a very wide range. Slightly less recent radiations will comprise a species group within a genus composed of a few wide-ranging but largely allopatric species. Fairly recent radiations will comprise genera with a very wide range composed of numerous species incorporating both allopatric and sympatric distributions. Ancient radiations will be recognized from a genus or higher taxon, perhaps with a broad-based distribution, but composed of few species each usually with a local, restricted and disjunct distribution. Recent radiation in elements of ancient taxa may be recognized by characteristics of their distribution as defined above (e.g. *Eurysternus*, a single genus separated from other Scarabaeinae at tribal level with 22 sympatric and allopatric species throughout South America which is perhaps related to the recent expansion of rainforest described below). In the following accounts of dung beetle biogeography, these predictions are used as methods to define the relative age of faunal elements.

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Mammals and Scarabaeinae/Coprinae of Australia

Australia is considered to have been virtually isolated from other continents since its separation from Antarctica in the Palaeocene/Eocene (Clemens 1979) or the Oligocene (Axelrod & Raven 1978). From the Oligocene it has moved northwards to its present position close to the island arcs of Indonesia. Its native mammal fauna is composed almost entirely of metatherians (Marsupalia). High diversity of Oligocene and Miocene fossils suggest that marsupials were resident in Australia prior to its separation from South America/Antarctica (Clemens 1979). Diversity of the modern fauna is mainly at species level (Murray 1986) but extinctions within the last 100,000yr have reduced the number of large genera (74kg body weight) from 19 to three (Martin 1986). Most groups have been of small or moderate size except for an evolutionary brief trend to gigantism in the diprotodonts and some kangaroos (Lillegraven 1979). Modern marsupials have a generally lower rate of metabolism than eutherians (Clemens 1979) and drop their dung as pellets. The scarabaeine and coprine fauna is limited to fairly small ball-rolling and small dung-burying forms of only four higher taxa, Canthonina, Coprina, Dichotomiina and Onthophagini. These taxa are probably predominantly coprophagous (Matthews 1972, 1974, 1976).

The Canthonina constitute the generically richest elements and with endemism at generic level are considered the oldest members of the Australian dung beetle fauna (Matthews 1974). They probably have an entirely Gondwanaland origin although a partly northern route cannot be ruled out (Matthews 1976) since, for instance, the genus, *Lepanus*, appears to extend to Java and is closely related to *Panelus*, a genus which extends from Japan to Africa (Matthews 1974). They are divisible into two groups on morphological criteria which may be partly supported by behavioural characteristics (Matthews 1974). Members of all but one genus of the so-called non-mentophiline group have been observed to make balls. Members of the other and structurally most heterogeneous mentophiline group have never been observed to make balls but use only pellets dropped preformed by the mammal fauna. This may be primitive behaviour predating the evolution of ball making (Matthews 1974). However, it might also represent aberrant behaviour associated with the universality of pellet droppings amongst native marsupials. At least one member of this group, *Cephalodesmius armiger* (Westwood), is now known to make balls cut from a cake of rotting vegetation constructed by the parent (Monteith & Storey 1981). Also the particular morphological characters used to separate the mentophiline group is known in genera on other continents, one species of which, the Afrotropical *Anachalcos convexus*, is known to construct balls of dung from cattle pads (Davis personal observation). Therefore, the morphological characters in question are not necessarily associated with absence of ball-making either within or outside of Australia.

At the beginning of the Miocene (20 MYBP), rainforest was dominant in Australia (Kershaw 1986) but with continuing decrease in temperatures prevalent during the Tertiary (Tyson 1986) and a probable decrease in rainfall, forest began to open into grassland from the early Miocene (Kershaw 1986). From the Pliocene to the Pleistocene, replacement of forest by open eucalypt woodland in the east was matched by the expansion of arid assemblages of sclerophyllous and grassland elements elsewhere (Kershaw 1986, Hope 1986).

The Canthonina are found predominantly in rain or sclerophyll forest (84% of species) and are rarities in pastures (Matthews 1974) which conforms with

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the antiquity of the group considering the former dominance of rainforest in and prior to the Miocene. They are considered to be the products of long isolation and have radiated into niches normally occupied by the Coprini which are poorly represented in Australia. This may indicate later arrival of the Coprina which are traceable from only one invasion but which are also mainly forest elements (Matthews 1976). As the Coprina are a predominantly old world group, Matthews (1976) has postulated an African origin for the Australian genera. Considering their endemism at the generic level this would have been an ancient occurrence but probably after the fragmentation of Gondwanaland since there are no Coprina in South America other than the recently-arrived and almost cosmopolitan genus, *Copris*. However, as coprina-like genera occur in the Dichotomiina, a Gondwanaland group represented by one genus in Australia (*Demarziella*, cited as *Notopedaria*) perhaps further study of Coprina and Dichotomiina genera would be useful, particularly since one of the Australian Coprina genera, *Coptodactylus*, possesses aedeagi which are morphologically closer to the dichotomine genus, *Pedaria*, than to *Copris* (Zunino 1983).

Matthews (1976) links *Demarziella* to the Afro-Oriental genera, *Pedaria* and *Paraphytus*, as the closest modern relatives. Many external morphological differences between *Pedaria* species are quite subtle but a study of the aedeagi shows broad morphological variation between most of *circa* 30 Afrotropical species examined (Davis personal observation) indicating a long evolutionary history. The aedeagi of *Pedaria* are broadly different to those figured for *Demarziella* by Matthews (1976). Whereas *Pedaria* and *Demarziella* may have similar kleptoparasitic habits on the broods of other dung beetles (Hammond 1976, Davis personal observation), at least one species of *Paraphytus*, which is morphologically almost indistinguishable from *Pedaria* (Matthews 1976), is saproxylophagous (Cambefort & Walter 1985). Therefore, divergence of these genera probably occurred a long time ago.

The Onthophagini, which show endemism at only the species level, are considered to be the most recent addition to the Australian dung beetle fauna (Matthews 1972). They constitute over 50% of Australian scarab species. Matthews has recognized 34 groups some with a restricted distribution, others widespread. This probably represents a long period of invasion over sea via the Indonesian island archipelago. Some species have a forest distribution but many also occur in shrubland and grassland. This may represent arrival and adaptive radiation with the retreat of rainforest and its replacement by structurally more open forms of

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vegetation. This may have paralleled the invasion of Laurasian or Indo-Malayan plant elements which has occurred since the Miocene (Kershaw 1986).

Mammals and Scarabaeinae/Coprinae of South and North America (Neotropical, Nearctic regions)

Review of dung beetle biogeography in the Americas

Distribution and origin of the modern insect fauna of the Americas has been reviewed by Halffter (1974). South America may be divided into three principal biogeographical provinces. The Guyano-Brazilian region which has had a tropical climate since the end of the Mesozoic is the dominant centre of dispersal of the modern Neotropical insect fauna and shows some affinities with that of Africa. The Araucanian region, which includes Patagonian and Chilean temperate forests, is dominated by Palaeantarctic elements with affinities closer to the insect fauna of southern Australia and New Zealand than to the Neotropical region. The Andean-Patagonian region results from the significant uplift of the Andes due to a bout of orogenics 12 MYBP which has continued to and beyond the Pliocene causing progressive development of a rain shadow and xeric conditions in south eastern South America (Simpson 1980, Marshall *et al.* 1982). The insect fauna of this region is derived from the Guyano-Brazilian region, the Araucanian region and so-called Palaeoamerican elements which have close north American and old world affinities. The insect fauna of South America is, however, predominantly of Gondwanaland origin. Dung beetles are concentrated especially in the Guyano-Brazilian region and also occur in the Andean-Patagonian region.

South America was virtually isolated from other land masses from the Eocene (Halffter 1974) until the late Miocene/Pliocene (Simpson 1980). Although close to north America throughout this period with intervening island chains, present land links were only re-established in the Pliocene. The scarabaeine and coprine fauna is, thus, dominated by Gondwanaland elements (Canthonina, Dichotomiina) with the addition of native elements (Phanaeina, Ennearabdina, Eurysternini, Eucraniina) which, perhaps, evolved in response to increase in diversity of dung types dropped by native South American mammals (see below). The remainder of the fauna comprises so-called Palaeoamerican elements derived from North America and, ultimately, old world taxa. According to Halffter (1974),

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these elements have an origin between the Triassic and the Palaeocene although a recent review of this hypothesis places their origin at between the end of the Mesozoic and the Miocene (Kohlmann & Halffter 1988).

The insect fauna of the warmer regions of North America, e.g. U.S.A., comprise Nearctic elements related to Palearctic groups at generic level or lower, northern Holarctic groups restricted to mountains towards the south, and Neotropical groups which have spread north from South America. The Neotropical groups are held to consist of two groups (Halffter 1974), one of recent occurrence since the Pliocene and another of ancient occurrence before the Eocene.

In Mexico, just to the north of the point of contiguity between the North and South American tectonic plates, there is a zone of transition between the Nearctic and Neotropical insect fauna. This is characterized by Neotropical elements in the lower coastal regions and by Mexican plateau (Miocene origin) endemics at higher altitudes. These are related to South American groups and tend not to occur in highlands occupied by elements with a northerly Nearctic/Holarctic or, so-called, Palaeoamerican origin.

The so-called Palaeoamerican elements (Halffter 1974) comprise taxa which are abundant in North and central America and less so in South America. They consist both of Nearctic groups and others with a wide distribution in the old world (Africa, Eurasia). They are composed of two subgroups, one widespread in both high mountains and lowlands in Mexico with a wide distribution in North and South America, the other with a relict distribution. Relict Scarabaeine and coprine species are found in California, Florida and Caribbean islands, Mexico and central America. In the Scarabaeinae and Coprinae, examples of Palaeoamerican distribution are supposedly shown by the genera, *Copris, Onthophagus* (wide distribution), *Sisyphus, Euoniticellus* and *Liatongus* (latter two both cited as *Oniticellus*) (relict distribution) (Halffter 1964, 1974). All of these genera also have a wide distribution in the old world. Nearctic/Holarctic elements in dung beetles are differentiated from these Palaeoamerican elements by a distribution restricted to North America and the Mexican highlands, e.g. *Geotrupes.*

The category of Palaeoamerican and the time scale of intercontinental exchange of faunal elements (Halffter 1974) require some examination. From their modern distribution, Palaeoamerican elements are interpreted as ancient taxa present since some time between the Triassic and Palaeocene (Halffter 1974) or the end of the Mesozoic and the Miocene (Kohlmann & Halffter 1988). Most Neotropical elements in North America are also considered

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to have entered the continent before the Eocene with some additional species in the same genera arriving after the Pliocene re-establishment of land links. Halffter (1974) suggests that this indicates a much slower evolutionary rate in insects (speciation only) than in mammals (diversification to ordinal rank in some groups) over the same 50 MY period. Even though species turnover is known to be greater in mammals than in cold-blooded groups such as reptiles (Bakker 1986), this seems an extraordinarily slow rate of evolution for insects particularly considering the observation that oceanic islands with an age of 11 MY or greater may support endemic genera of dung beetles (Paulian 1987). Neotropical and Palaeoamerican groups are held to have evolved contemporaneously and sympatrically during much of the Tertiary. However, Gondwanaland Neotropical groups are separated from extra-American taxa at generic level whereas Palaeoamerican taxa are separated only at species level. This is somewhat anomalous. The genera, *Canthon, Deltochilum* (Canthonina), *Ateuchus, Dichotomius* (Dichotomiina) and *Phanaeus* (Phanaeina) with a Neotropical origin, which are supposed to incorporate both ancient and recent taxa, have a very widespread geographical distribution. This incorporates tropical rainforest, tropical deciduous forest, arid areas and high plains in central/southern America and various North American habitats to the Canadian border area. Widespread distribution at low taxonomic level is usually indicative of a recent adaptive radiation as has been shown for the genus, *Ateuchus* (Kohlmann & Halffter 1988), rather than ancient occurrence. In view of these observations, a modified interpretation of dung beetle biogeography in the Americas is proposed below. It is suggested that, at least in the Scarabaeinae and Coprinae, all intercontinental exchange between North and South America has occurred since late Miocene/Pliocene times, that between Asia and North America occurred in the Miocene and Pliocene coeval with mammal invasions (see below), and that present distributions result from the rapid and cyclic changes in climate in the intervening 5-8 MY. Palaeoamerican and Nearctic/Holarctic elements are, therefore, separated in age by only a few million years but with different origins and different levels of penetration into central and South America. The same applies to Neotropical elements which have penetrated into North America.

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Origins of dung beetle taxa in the Americas

Three main stages may be recognized in the history of mammalian evolution in South America based on the fossil record (Simpson 1980). Firstly, an adaptive radiation in comparative isolation during the Palaeocene and Eocene gave rise to a fauna of strongly endemic character (Marsupalia, Xenarthra, Notoungulata) but more diverse than that of Australia. Secondly, the appearance, perhaps via island arcs, of Rodentia and Primates during the early Oligocene led to rodent diversification matched by decline in the diversity of Notoungulate taxa. Thirdly, the Pliocene was marked by the interchange of South and North American faunal elements after the re-establishment of land links and the Pleistocene by gigantism in native South American taxa. Some large South American herbivores which spread north included glyptodonts (siliceous grass-eating relatives of the armadillos up to 3,6m long) and ground sloths. Large herbivores which spread south from North America included gomphotheres, camelids and equids. Gomphothere proboscideans occurred throughout South America in the Pleistocene. *Stegomastodon* and equids were characteristic of the Argentinian pampas. They are now all extinct. Halffter & Matthews (1966) suggest that the extinction of this megafauna, the consequent absence of herds of large mammals until the recent introduction of domestic livestock and the paucity of large forest mammals, largely account for the displacement of Scarabaeinae and Coprinae towards necrophagy in South America.

Marsupials occurred in South America in the late Cretaceous and are abundant in the Palaeocene fossil record (Clemens 1979). Although there is no direct evidence on their time of arrival in Australia (Clemens 1979) they may have migrated via a southern route if any import may be attached to the paucity of marsupial fossils in the old world (only a few in western European deposits). Australia split from Antarctica in the Palaeocene or Eocene (Clemens 1979) which might warrant a tentative suggestion that canthonines and, perhaps, dichotomines were the only dung beetles extant at the time as no other groups common to South America have been recorded in Australia except the recently arrived *Onthophagus*.

The Palaeocene and Eocene adaptive radiation occurred in three groups of mammals (Simpson 1980). One of these was the metatherian marsupials, relatives of the pellet-dropping mammals which support the limited scarabaeine and coprine fauna of Australia. The other groups comprise the herbivorous eutherian Xenarthra, to which belong the modern sloths and armadillos, and the

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Notoungulata, a now extinct taxon. Both groups were probably derived from Condylarthra (Simpson 1980), a mammal group also found as fossils in western North America (Eisenberg 1981). Some members of these eutherian groups achieved a fairly large size by the early Oligocene (Simpson 1980) and presumably dropped sizeable amounts of dung. For instance, fossil droppings of the recent, but now extinct, Shasta Ground Sloth are known to have been large and coarse.

Some evidence exists for the contemporaneous occurrence of typically Neotropical dung beetle taxa which may be associated with the diversification of these mammals. Fossil brood balls recovered from sediments of probable Oligocene and Miocene age in Argentina are mostly characteristic of the modern genus, *Phanaeus* (Phanaeina) (Halffter 1974). There is only one modern species of *Dichotomius* (Dichotomiina) known to Halffter to which they might be attributed. Frenguelli (1938a, b, 1939) considered similar balls to represent those of *Megathopa* (now *Megathopa* and *Malagoniella*) (Canthonina).

In addition to elements with a Gondwanaland distribution (Canthonina, Dichotomiina), the typically Neotropical groups are also separated from extra-American Scarabaeinae and Coprinae at subtribal or tribal level. This, it is suggested, indicates that they are old elements evolved soon after the isolation of South America, i.e. Eucraniina, Eurysternini, Ennearabdina, Phanaeina. The former three of these groups show specialized behaviour but are predominantly dung taxa (Halffter & Matthews 1966). Eurysternini breed in chambers excavated at the dung/earth interface (Halffter *et al*. 1980). All three extant genera of Eucraniina hold their food between the two front legs in order to carry it to their burrows (Halffter & Matthews 1966). The single extant genus of the Ennearabdina is especially associated with caprine dung (Halffter & Matthews 1966). The fourth subtribe, the Phanaeina, is the only group whose species both tunnel near the dung or may also commonly roll dung away from the pad (Halffter *et al*. 1974). The morphology of their aedeagi places them within the ball-rolling scarabaeine group rather than the tunnelling Coprinae according to Zunino (1983). The same study indicated that Eurysternini and Eucraniina are strongly divergent from the other scarabaeine taxa although the 20 or 22 species of the single eurysternine genus, *Eurysternus*, are widespread with overlapping distributions throughout central and South America (Jessop 1985) which suggests recent radiation.

Unlike the strongly endemic character and limited distributions of the Australian canthonine fauna in which 10 of the 16 genera comprise three or less species with a trend to flightlessness in 13 genera (Matthews 1974), 14 out of 25

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canthonine genera in South America have a broadly Neotropical or Nearctic distribution (Halffter 1974) suggesting greater recent diversification. This trend has also been emulated by some phanaeine (*Phanaeus*) and dichotomine genera (*Dichotomius, Ateuchus*) which are predominantly coprophagous (Halffter & Matthews 1966) and of relatively large size. It is suggested that this radiation may be related to the late Tertiary mammal megafauna and the great American interchange of fauna. This agrees with the viewpoint of Janzen (1983) who considers that the present dung beetle fauna may be a remnant of that supported by the American megafauna until its extinction 12-10,000 yr BP (Martin 1986) or 10-8000yr BP (Marshall *et al.* 1982) during a period of major climatic change (Bradbury *et al.* 1981).

The Palaeocene mammal fauna of North America is derived from eight basic groups compared with three in South America (Simpson 1980). Romer (1966) indicates that early adaptive radiations during the Palaeocene and Eocene culminated in extinction of archaic taxa (Condylarthra, Multituberculata and early radiations of modern taxa) at the end of the Eocene which gave the Oligocene mammal fauna a more modern composition. The end of the Miocene was marked by the arrival of proboscideans in North America via a land bridge from Eurasia across the modern Bering Straits (Beringia). The Pliocene/Pleistocene was marked by the arrival of mammoths, bison, sheep and goats across Beringia in the north and the interchange between south and north American biota in the south. Despite this long history of diverse mammalian fauna, all dung beetle taxa show relationships to extra-North American groups, mainly at generic level (different species only in North America) which indicates recent arrival of the fauna. Neotropical elements probably radiated during the interchange as discussed above, old world elements probably arrived with the mammal invasions via Beringia during the Miocene and the Plio/Pleistocene. This hypothesis is supported by taxonomic evidence since the 23 species of *Copris* in America belong to two distinct groups, which probably indicates two invasions of taxa from Asia. This division is not reflected in the old world fauna (Matthews 1961).

Recent climatic changes have markedly influenced the present distribution of flora and fauna. In North America, vegetational changes have been towards the expansion of grassland with the opposite trend in South America where forest has expanded in range (Graham & Lundelius 1986). Expansion of rainforest was an ongoing event 8000yr before present in Venezuela (Bradbury *et al.* 1981) although, by way of contrast, increasing desertification has been the rule in

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Patagonia (Simpson 1980, Marshall *et al.* 1982). Influences of climatic changes in North America have been reviewed by Guthrie (1986) and amount to a recent reorganization of taxa into modern species assemblages. Taxa once sympatric and now only occurring in the arctic north or temperate south include flora, mammals and insects. Similar broad changes in range have occurred in dung beetle distributions during the last 20,000yr (Miller *et al.* 1981) as determined from the present occurrence of species recorded as fossils in Pleistocene deposits at Rancho La Brea. Two of the species are probably extinct as there are no recent records. One of these species is *Copris pristinus* Pierce. The present distribution of *Copris* is restricted to the east of longitude 100° W, *c.* 1600km to the east of Rancho La Brea. The closest relatives of the extinct *Onthophagus* appear to be modern Mexican taxa. Of two species of *Canthon* recorded in the fossil record, the range of one has retreated from the winter rainfall area of California. A fifth fossil attributable to the genus, *Phanaeus*, is the very large head of a very minor male (Miller *et al.* 1981). As large dung beetles have been shown to be associated with larger amounts of dung (Peck & Howden 1984), I tentatively suggest that the size of these remains may be associated with the volume of megafaunal droppings.

Recent climatic and vegetational changes together with intermingling of Nearctic and Neotropical dung beetle fauna may also possibly account for Antillean and central American relict distributions of some Nearctic taxa ultimately derived from the old world, e.g. *Euoniticellus* spp. (Oniticellina) in California and in Florida, Cuba, Jamaica; *Sisyphus* spp. (Sisyphina) in tropical coastal refugia in Mexico and Nicaragua. The highly specialized *Liatongus monstrosus* recovered from ant's nests of the genus, *Atta*, in Mexico (Halffter 1964), the record of *Anoplodrepanus*, a genus endemic to Jamaica but ascribed to the old world subtribe, Drepanocerina and the presence of unrelated brachypterous species of *Onthophagus* in montane forests in Mexico and central America (Zunino & Halffter 1988) may possibly originate from an earlier Miocene invasion of dung beetles from Asia via North America. All of these elements are only remotely related to the other Neotropical elements.

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Mammals and Scarabaeinae/Coprinae in the old world (Africa, Eurasia - Afrotropical, Palaearctic, Oriental regions)

Various biogeographical provinces have been proposed for Africa, particularly for plants (Werger 1978) but there seems to be no general consensus of opinion. In the absence of an accepted biogeographical framework or a numerical analysis of dung beetle distribution in Africa, a qualitative assessment of their biogeography is all that is possible.

One biogeographical region is undoubtedly delimited by the winter and bimodal rainfall areas of southern Africa (Climate types IV and V according to Walter & Lieth 1964) due to the high endemism of the scarabaeine and coprine taxa associated with the native vegetation (Davis 1987). As regional distribution of dung beetles is clearly related to climate (Kirk & Ridsdill Smith 1986, Davis & Dewhurst unpublished data), the climatic classification of Walter & Lieth (1964) is probably a reasonable guide to dung beetle biogeography in Africa as any system of regional division. For instance, climate type I largely defines the present or former extent of tropical rainforest which has probably acted as a biogeographical barrier during much of recent evolutionary history and may explain the broad differences between west African (Cambefort 1982a) (climate type II north) and Zairois (Walter 1978) (climate type II south) species assemblages. Climate type II south may probably be separated into a drier eastern seaboard region extending from southern to eastern Africa and a moister southern west central region. The arid region in the north east of Africa (climate type III north) support a number of endemic Scarabaeina (Ferreira 1972) and other taxa (Davis & Dewhurst unpublished data). It may have some remote affinities with the arid region of Namibia and central South Africa (climate type III south) due to the existence of an arid corridor linking the two during the Pleistocene (Endrody-Younga 1978, Bigalke 1978, Winterbottom 1978). For instance, the genus, *Platyonitis*, comprises two species on the coastal plain of Kenya and one other in Ovamboland and southern Angola. A similar dry corridor may have separated Zairois and West African rainforest blocks on occasions in the past (Cox & Moore 1985). This may have acted as a route for interchange of fauna between southern and western Africa. For instance, *Copris laius* has a west and central African distribution but its closest four relatives occur well to the south of the rainforest occupying a disjunct distribution in southern Africa (Nguyen-Phung & Cambefort 1987).

There has been great climatic and geological change in Africa during the Tertiary which has been reviewed by Axelrod & Raven (1978). From the late Cretaceous into the early Tertiary, moist air was more prevalent over Africa than at present due to various factors including its more southerly position. Together with its relatively low altitude, this supported broad bands of rainforest and savanna woodland stretching from the west to the east coast interrupted only by a shallow sea in parts of the Sahara. As the continent drifted north, vegetational bands shifted to the south resulting in the elimination of southern temperate rainforest with its probable Palaeantarctic affinities. Major volcanism during the late Oligocene/early Miocene produced minor uplift and commenced the development of the east African rift valley system. Coupled with the mid-Miocene joining of the African tectonic plate to Arabia, this led to gradually drier climate, progressive retreat of the forests and their replacement by more xeric woodland and savanna. Further major uplift in the late Pliocene/early Pleistocene raised circumferential mountains and plateaux in east and southern Africa by appreciable amounts. Two periods of biotic reorganization and rapid speciation were correlated with these Miocene and Plio/Pleistocene changes in topography and climate. Thus, because of the relative youth of most highland blocks, oldest relict or residual taxa are likely to occur in lowlands, particularly in forests.

The evolutionary history of mammals in Africa during the Tertiary has been reviewed by Maglio (1978) and Bigalke (1978). It was closely linked to that of Eurasia and took the form of long periods of isolation punctuated by brief periods of interchange thought to have occurred in the late Oligocene/early Miocene, late Miocene and late Pliocene (Cooke 1972, Coryndon & Savage 1973). This may account for the greater endemism of mammal families in Africa during the earlier Tertiary, particularly in the Eocene and Oligocene, compared with later ages of the era.

Palaeocene and early Eocene mammal stocks were derived from the north and comprised Condylarthra, carnivorous Creodonta and Prosimian Primates. Subsequent adaptive radiations of condylarth derivatives during the later Eocene and Oligocene gave rise to several endemic groups, in particular the Proboscidea, which had achieved great diversity of taxa and large size by the Miocene when they first appear in the fossil record outside of Africa. Similar adaptive radiations of the Primates gave rise to three endemic families which first appear in the fossil record in the Oligocene. In the late Oligocene/early Miocene, the arrival of various mammal groups including Suidae, Canidae and Felidae from Europe,

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Rhinocerotidae, Giraffidae and Bovidae from Asia accompanied the commencement of geological and climatic change in Africa. These arrivals were followed by those of hyaenids and equids which first appear in the fossil record of the late Miocene. During the Pliocene/Pleistocene bout of orogenics, new forms evolved, particularly in the bovids and suids, which replaced archaic taxa. Thus, during the course of early evolutionary history of mammals in Africa, pellets and omnivore droppings would have been present followed by the appearance of large coarse-fibred droppings with the increase in size of non-ruminant herbivores, e.g. Proboscidea and (later) Rhinocerotidae. The appearance of large, fine-fibred droppings of large ruminants would have been a very recent event as fossil African Bovini have been first recorded from only the late Miocene (*Bos*), early Pleistocene (*Pelorovis*) and late Pleistocene (*Syncerus*). Following the establishment of canthonine and dichotomine dung beetles, it is suggested that adaptive radiations occurred with the appearance of large, coarse-fibred droppings and the much later appearance of large, moist, fine-fibred droppings.

The great abundance of these different dung types up until the recent past coupled with varied topography is presumed to be the reason for the great diversity of scarabaeine and coprine taxa in the old world, particularly in Africa. Much of this diversity is due to the evolution of new taxa (Scarabaeinae: Scarabaeina, Gymnopleurina, Sisyphina; Coprinae: Onitini, Oniticellini, Onthophagini, Coprina) subsequent to the fragmentation of Gondwanaland. As a result, the Gondwanaland groups (Canthonina, Dichotomiina) comprise only 33% of the genera in Africa.

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The modern distributions of the two subtribes of Gondwanaland origin indicate that they have each had a quite different evolutionary history in Africa with the canthonines showing greater relictual status than the dichotomines. Distributions of most canthonines are restricted or centred on southern Africa (Scholtz & Howden 1987a, b, Howden & Scholtz 1987) with species of a few genera showing distributions mainly on mountains of the east coastal plain of Africa as far north as Ethiopia and a few others with an arid region distribution extending northwards to northern Namibia. Of the 17 genera described for Africa, only one, *Anachalcos*, has a tropical centre of distribution. Distribution records for the 14 Afrotropical genera of Dichotomiina (Ferreira 1972) show that they have a predominantly warm temperate and tropical occurrence and are well represented in west and central Africa unlike the Canthonina. This may indicate a more northerly route of entry to Africa. Of the Afrotropical canthonine genera, nine are monotypic diversification of taxa with a Sino-Tibetan and, ultimately, Palaearctic origin. Only the Onthophagini, which have invaded Australia from Asia over a period of time (Matthews 1972), show marked difference to taxa from other biogeographical regions (Paulian 1987). The Afrotropical origin of the bulk of the Palaearctic and Oriental fauna is supported by Table A2.5. which indicates significantly higher generic endemism in Africa than in Eurasia. Three or four tribes/subtribes show greater endemism than the remainder. These taxa include the two subtribes with a Gondwanaland origin, the Canthonina and Dichotomiina, plus the Onitini and, perhaps, the Scarabaeina which are restricted to the old world.

Mammals and Scarabaeinae/Coprinae of tropical islands: New Caledonia, Madagascar and the Antilles

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The fauna of tropical islands in three oceans was studied by Paulian (1987). These were numerically dominated by genera of Gondwanaland origin with the addition of vicariant elements apparently commensurate with the proximity of large land masses. Thus, the fauna of New Caledonia, which has been broadly isolated by land subsidence and the formation of the Coral Sea, comprises only Canthonina, a Gondwanaland group. Endemism is largely at generic level although there is one genus in common with the fauna of Australia to which the New Caledonian fauna shows close affinities.

The fauna of Madagascar, which is at some distance from the east coast of Africa, is almost entirely endemic and is composed predominantly of Canthonina (13 genera: 158 species), an endemic subtribe of the Oniticellini (Helictopleurina - two genera: 53 species) and a few Onthophagini and Scarabaeina. Paulian (1987) has proposed that the canthonines were present before the fragmentation of Gondwanaland, that a single Miocene invasion via rafting or an island archipelago gave rise to the Helictopleurina and that a second during the Pliocene/Pleistocene resulted in the arrival of a few Scarabaeina and Onthophagini. The Canthonina and Helictopleurina are found predominantly in forest (79,5% and 58%, respectively) and are less diverse in the arid south-western region which is considered to be of more recent origin.

Extant Malagasy dung beetles have presumably diversified with the endemic vertebrate fauna. Excluding the relatively recently arrived river hog (*Potamochoerus*) and Hippopotamus, this fauna was dominated by lemurs, large ratite birds, viverrid carnivores and rodents (Mahe 1972). Lemurs are related to fossil primates known elsewhere from the Eocene and Oligocene. They are considered to be pre-Miocene arrivals in Madagascar due to the absence of the more recent Lorisiformes and have radiated throughout the forests. Before the arrival of man, the savanna areas were dominated by a vertebrate fauna of ratite birds, archaelemurs (semi-terrestrial) and giant tortoises (Dewar 1986). These are all now extinct and replaced by domestic livestock.

The Antilles lie at variable distance from the American mainland which may account for the fact that there are only two genera in common between the Greater and Lesser Antilles which suggests differing origins according to Paulian (1987). Endemism in the more isolated Greater Antilles is at species and generic level whereas that in the Lesser Antilles is at species level. The fauna of the Greater Antilles (Canthonina, Onthophagini, Oniticellini, Phanaeina) is derived from six invasions between the Miocene and the Pliocene (Paulian 1987). Paulian suggests that the fauna is derived from central and North America and whilst this is probably true of later arrivals and that of *Anoplodrepanus*, a genus closely related to the old-world Drepanocerina, the endemic canthonines are probably derived from the fauna of South America as it is likely that the canthonines only dispersed into North America during the faunal interchange with South America in the Pliocene. This is supported by the fact that there is only one endemic canthonine genus in the whole of North America. The fauna of the Lesser Antilles (Canthonina, Dichotomiina, Onthophagini) has probably been recently derived from that of nearby South America owing to the slight differentiation from mainland species and their low diversification (Paulian 1987).

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Trends in scarabaeine/coprine biogeography

The lower species richness within canthonine genera of Australia and southern Africa suggests a more relictual status than that of South American members of this Gondwanaland group. In Australia, this may be due to limited diversification of dung type since the Mesozoic, recent large-scale extinction of Marsupials (Martin 1986) and colonization of unshaded situations by vicariant Onthophagini. In Africa, this may be due to diversification of the Scarabaeina, Gymnopleurina and Sisyphina which show similar ball-rolling habits to the Canthonina. In South America, where these old world subtribes are virtually absent, there has been recent diversification in Canthonina which have dispersed into North America. The southern African distribution of canthonines supports the southern route of dispersal proposed by Halffter (1974) whereas the principally tropical distribution of dichotomines in South America and Africa suggests a more northerly possibly later dispersal by this group, particularly since they are taxonomically poorly represented in Australia where canthonines occupy some dichotomine and coprine niches (Matthews 1974). The diversification of small to medium sized, dung-burying Onthophagini, Oniticellini, Onitini and Coprina may account for the relictual status or dietary specialization in many surviving small-sized African Dichotomiina except the recently evolved, large dung-burying genus, *Heliocopris* which has few competitors in its size range. High diversity of dichotomine dung-frequenting taxa is seen in South America where Onthophagini are probably recent arrivals during the Pliocene interchange of fauna with North America.

Greatest diversity of dung beetles is seen in Africa and Eurasia where the diversity of native dung types is greater than in South America and, particularly, Australia. An African origin for the Gondwanaland and post-Gondwanaland Eurasian fauna seems likely due to higher endemism in Africa. From Asia it is probable that old world dung beetles have dispersed with the mammals into North then South America (Onthophagini, Coprina, Oniticellini, Sisyphina) and into Australia (Onthophagini and possibly Dichotomiina/Coprina plus some Canthonina) during the later Tertiary. The South American fauna shows limited dispersal only into North America perhaps due to its isolation until the recent past and its predominantly tropical origin.

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APPENDIX 3

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Three new Afrotropical dung beetles (Coleoptera: Scarabaeinae) in the genera, *Kheper* Janssens, *Gymnopleurus* Illiger and *Onitis* Fabricius, with notes on related species.

by

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Kheper zurstrasseni **sp. nov.** from South Africa, *Gymnopleurus particolor* **sp. nov.** from west Africa and *Onitis autumnalis* **sp. nov.** from south east Africa, are described and their relationships discussed. *K. clericus* (Boheman) is redescribed and its geographical distribution is illustrated on a map together with those of the closely-related *K. zurstrasseni* and *K. bonellii* (MacLeay). A key is provided to separate *O. autumnalis* from six closely-related species and the geographical distribution of all seven species is depicted by maps.

In 1970, the Commonwealth Scientific and Industrial Research Organization (CSIRO) established the Dung Beetle Research Unit (DBRU) in Pretoria, South Africa, to study and select species of dung-burying beetles suitable for introduction into Australia (Bornemissza 1976). During the 16 years of the DBRU's existence a large reference collection of these beetles (Scarabaeinae) has been amassed. This now numbers approximately 50000 specimens belonging to about 850 species. These were collected mainly in Nigeria, Kenya, Tanzania and Africa south of the River Zambezi.

The present publication describes species from this collection and those of the National Collection of Insects, Pretoria, the South African Museum, Cape Town, the British Museum (Natural History), London, and the Muséum National d'Histoire Naturelle, Paris. In particular, it includes the redescription of *Kheper clericus* (Boheman), formerly known only by the female holotype; the description of a new *Kheper* Janssens which has been confused with *K. clericus*; the description of a new *Onitus* Fabricius, previously confused with *O. caffer* Boheman; and the description of a new *Gymnopleurus* Illiger.

Genus *KHEPER* Janssens, 1940

The Afrotropical and Oriental genus, *Kheper*, was described by Janssens (1940a) in a partial revision of the tribe, Scarabaeini. Besides diagnostic features of the genus, a key to all the known species was included in this publication. There has been no subsequent revision of these taxa.

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Kheper clericus (Boheman), Figs 1–3, 12

Ateuchus clericus Boheman, 1857. *Insecta caffrariae* **2:** 167.
Kheper clericus (Boheman): Janssens, 1940a.

MALE. Black with a muted, non-metallic sheen; all hairs and setae deep brown or black, tips of setae sometimes tan. Length, 17–29 mm; mean, 23 mm (n = 17); maximum width, 9–16 mm; mean, 13 mm.

Head. Anterior margins of clypeus and genae sexdentate; tips of clypeal teeth smooth (× 10); clypeus and genae with raised, acute ridging enclosing elongate and ovoid, scalloped depressions; frons very slightly raised, rounded, rugose and micropunctate; vertex coarsely pitted, somewhat rugose laterally. Frontal suture slightly raised laterally, effaced medially; clypeo-genal sutures incised and smooth.

Thorax. Dense, anterior and lateral macrogranulation of pronotal disc merging into lunate and umbilicate macropunctation medially; macropunctation usually becoming fine, sparse and roughly isodiametric posteriorly on disc, but sometimes remaining coarse especially in smaller specimens; small, ill-defined, posterior, mid-longitudinal area of disc (approximately 5%) lacking macropunctation (Fig. 1). Entire disc with very fine, contiguous micrograņulation (× 20); micrograņulation becoming gradually overlaid by micropunctation posteriorly. Metasternum smooth medially, moderately punctate and pilose laterally; metasternal protuberance rounded, smooth ventrally with moderately dense asperate granules and pilosity laterally. Elytra fairly smooth (× 0), but densely micrograņular with incipient microrugosity not elevated (× 20); striae fairly distinct (× 10); interstriae with very sparse, fine punctation (× 20) loosely arranged in 2 rows per interstria. Dorsal surface of fore tibia with a small denticle at the base of tibial tooth 2. Internal superior ridge of hind tibia with a row of long setae; median setae longer and more densely packed.

Abdomen. Sternites predominantly smooth with a little coarse punctation laterally on sternites 1, 5 and 6; sternites 2, 3 and 4 with a row of short but distinct (× 10) densely packed setae antero-laterally. Pygidium moderately punctate; aedeagus as in Figs 2, 3.

FEMALE. Length, 18–25 mm, mean, 23 mm (n = 14). Only slightly different from male; setae on internal superior ridge of hind tibia of uniform density; setae antero-laterally on sternites 2, 3 and 4 sparse and indistinct (× 10).

MATERIAL EXAMINED. Information in square brackets is not cited on the locality labels of the specimens. Holotype ♀: SOUTH AFRICA, Natal, Caffraria, J. Wahlb[erg]. Other material: 1 ♂ and 2 ♀♀, Hluhluwe G. R. [= Game Reserve] [28°–28° 09′ S, 32°–32° 09′ E], 15.xi.74, G. Tribe; 1 ♂, Umfolozi G. R. [28° 14′–26′ S, 31° 43′–58′ E], 29.x.73, Tribe and Temby; 1 ♀, Mkuzi G. R. [27° 34′–46′ S, 32° 04′–22′ E], 15.xi.74, G. Tribe. 1 ♂ and 1 ♀, Mkuzi G. R., (Tinley's Dam/ Nhlonhlela), 23.x.73, Tribe and Temby; 1 ♀, Hluhluwe G. R., (Seme), 24.xii.73, A. L. V. Davis; 1 ♀, Mkuzi G. R., (Vulture Pan), 22.xii.73, A. L. V. Davis; 1 ♂ and 1 ♀, Umfolozi G. R., 1–3.xi.76, G. Bernon; 15 ♂♂ and 8 ♀♀, Mkuzi G. R., 27–29.x.81, Edwards and Bridgens; 1 ♂ and 1 ♀, Mkuzi G. R., 23–26.iii.83, P. B. Edwards; 1 ♀, Mkuzi G. R., 23–25.v.83, P. B. Edwards. Holotype in the Naturhistoriska Riksmuseet, Stockholm.

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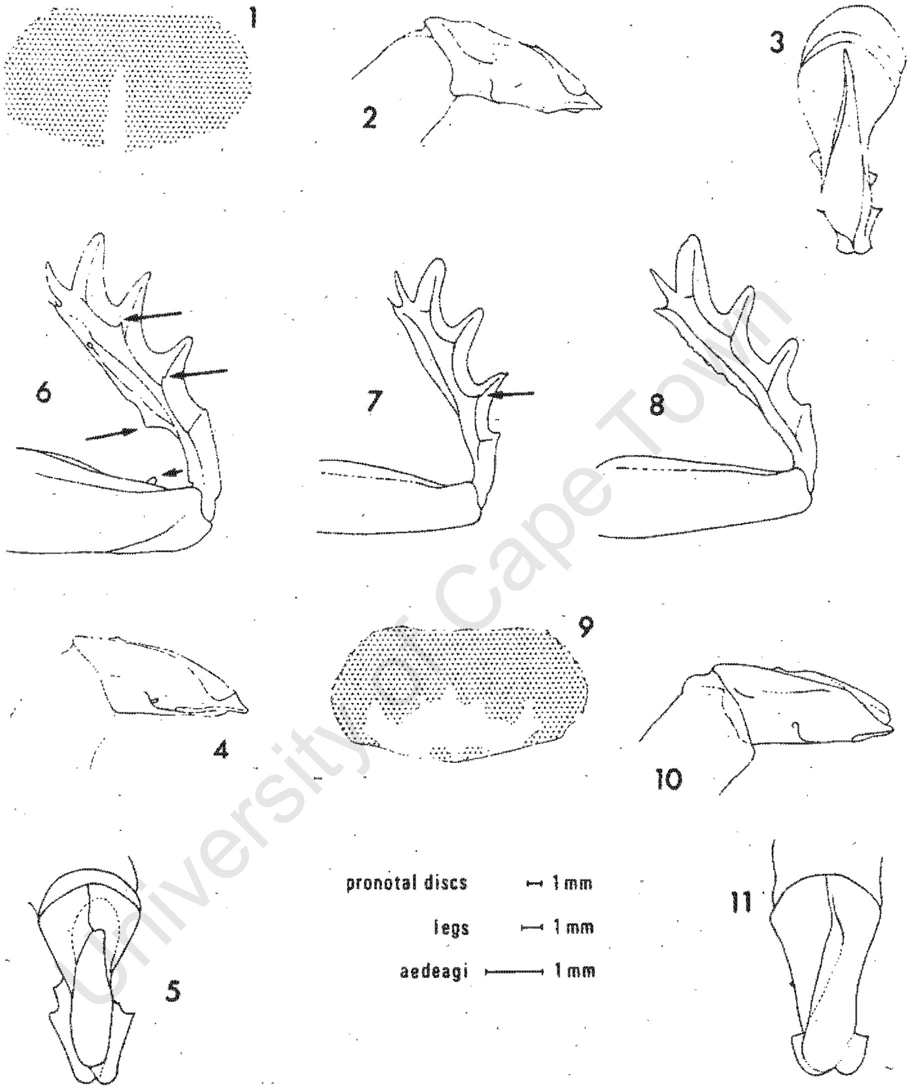

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Figs 1–11. *Kheper* spp. 1–3. *K. clericus* (Boheman); 1. pronotal disc, dorsal view; 2–3. aedeagus; 2. left paramere, lateral view; 3. ventral view. 4–5. *K. zurstrasseni* **sp. nov.**, aedeagus; 4. left paramere, lateral view; 5. ventral view. 6–8. Right forelegs of 3 Kheper spp., dorsal views showing diagnostic features of 3 species groups indicated by arrows; 6. *K. lamarcki* (MacLeay); 7. *K. nigroaeneus* (Boheman); 8. *K. cupreus* (Castelnau). 9–11. *K. bonellii* (MacLeay); 9. pronotal disc, dorsal view; 10–11. aedeagus; 10. left paramere, lateral view; 11. ventral view.

Kheper zurstrasseni sp. nov., Figs 4, 5, 12

Scarabaeus clericus (Boheman): Péringuey, 1902.
Kheper clericus (Boheman): Ferreira, 1972.

This species has been previously misidentified as *K. clericus* as discussed below.

MALE. Colour of body and hairs as for *K. clericus*. Length, 24–25 mm; mean, 24 mm (n = 3); maximum width, 14 mm.

Head. Similar to *K. clericus* in every respect.

Thorax. Prothoracic disc, metasternum and legs similar to *K. clericus*. Interstriae of elytra densely microgranular with dense, clearly elevated microrugosity (× 20); when present, very sparse, fine punctation predominantly obscured by microrugosity.

Abdomen. Similar to *K. clericus* in every respect except aedeagus (Figs 4, 5).

FEMALE. Length, 22–23 mm; mean, 22 mm (n = 4). Only slightly different from male as in *K. clericus*.

The new species is named for Dr R. zur Strassen of the Forschungsinstitut und Naturmuseum, Senckenberg, Frankfurt am Main, West Germany, in recognition of his excellent work in scarabaeine taxonomy.

MATERIAL EXAMINED. Information in square brackets is not cited on the locality labels of the specimens. Holotype ♂: SOUTH AFRICA: Transvaal, Pretoria [25° 45′ S, 28° 12′ E], 21.ii.36, E. C. G. Bedford. Paratypes: 1 ♀, Pretoria, 21.ii.36, E. Bedford; 1 ♂, Transvaal, [?] J. Hume; 1 ♂ and 2 ♀♀, Potchefst[room] Dist[rict] [26° 44′ S, 27° 04′ E]; 1 ♀, no data. Holotype and 4 paratypes in the National Collection of Insects, Pretoria; 2 paratypes in the South African Museum, Cape Town.

IDENTITY OF *KHEPER* MATERIAL EXAMINED. The new species belongs to a group of 3 close relatives which are endemic to South Africa. These species comprise, *K. bonellii* (MacLeay), *K. clericus* (Boheman) and *K. zurstrasseni* sp. nov. Material from the south west of Cape Province is undoubtedly *K. bonellii* but there is some confusion in published work between the identity of *K. clericus* and the new species.

Ateuchus clericus was described by Boheman (1857) and ultimately assigned to the genus *Kheper* (Janssens 1940a) via the genus *Scarabaeus* L. The holotype was collected by J. Wahlberg (etiquette reads, "J. WAHLB.") in "Caffraria". Material labelled in this way is considered to have been collected in Natal (R. Oberprieler, pers. comm.).

The holotype of *K. clericus* represents the same species as material in the reference collection of the DBRU which originates from the game reserves of northern Natal. Since *K. clericus* was formerly known from a single female specimen, I have used the holotype and the additional male and female material from the game reserves to redescribe the species.

Péringuey (1902) and Ferreira (1972) cited *clericus* from Potchefstroom, Pretoria and Zebediela in the Transvaal. I have attempted to trace this material in the National Collection of Insects and the Transvaal Museum in Pretoria and in the South African Museum in Cape Town. Although these institutions hold determined material of *clericus* from the above localities, none of the specimens can with certainty be recognized as those cited by Péringuey and Ferreira. A single specimen from Potchefstroom in the National Collection determined as *K. clericus* by Ferreira in 1951 also bears a label reading, "Ateuchus clericus Boh. compared with type", possibly in Péringuey's handwriting. The labels on the remaining material of *clericus* from Potchefstroom and Pretoria which are lodged in the National Collection of Insects and the South African Museum, do not state the determining authority. All of this material has been misidentified and is, in fact, *K. zurstrasseni* sp. nov. A specimen from Zebediela (24° 18′ S, 29° 19′ E) determined as *K. clericus* by Ferreira in 1964 and lodged with the Transvaal Museum, is a melanic example of *K. nigroaeneus* (Boheman).

Relationships. The Afrotropical species of *Kheper* may be divided into 3 groups on the presence or absence of spines and denticles on the fore legs (Janssens 1940a) (Figs 6–8). The group typified by *K. lamarcki* (MacLeay), has a spine on the antero-inferior ridge of the fore femur, another on the internal superior ridge of the fore tibia and single denticles projecting from the dorsal surface of the fore tibia at the bases of tibial teeth 2 and 3 (Fig. 6). The group typified by *K. nigroaeneus* (Boheman), lacks spines on the femur and inner margin of the fore tibia and is characterized by a single denticle only at the base of tibial tooth 2 (Fig. 7). The third group, typified by *K. cupreus* (Castlenau), lacks all the spines and denticles described for the other 2 groups (Fig. 8).

K. zurstrasseni has a single denticle on the dorsal surface of the fore tibia at the base of tibial tooth 2 and, therefore, belongs to the *K. nigroaeneus* group. It has close affinities to *K. clericus* (Boheman) and *K. bonellii* (MacLeay). Descriptions of differences between these species and *K. zurstrasseni* are based on examinations of the holotype or syntype of each species. The external morphology of *K. clericus* differs from that of *K. zurstrasseni* only in having sparse but clear (×20), fine punctation over most of the elytra and, interstriae with incipient microrugosity which is not raised (×20). The aedeagi of the 2 species are, however, quite different (Figs 2, 3, 4, 5). *K. bonellii* differs from *K. zurstrasseni* in a number of features including the lack of macrogranulation or macropunctation on the posterior 40% of the pronotal disc (Fig. 9), the sparsely microgranular pygidium, the discrete microgranules on the elytra, the acute, vestigial horn on the frons and the morphology of the aedeagus (Figs 10, 11).

The other species of the *K. nigroaeneus* group also differ clearly from *K. zurstrasseni* and may be separated using Janssens' key (1940a). These species are, *K. nigroaeneus* (Boheman), *K. pustulosus* (Gerstaecker), *K. aeratus* (Gerstaecker), *K. festivus* (Harold), *K. asceticus* (Gillet), *K. laevistriatus* (Fairemaire), *K. porosus* (Bates) and *K. intermedius* (Gillet).

Janssens (1940a) considers *K. paganus* (Harold) to be a synonym of *K. festivus*. I have examined specimens of *Kheper* collected in Angola (ex DBRU collection) which were identified as *K. paganus* by R. zur Strassen in 1975, and have compared them with material of *K. festivus*. I am in agreement with zur Strassen that *K. paganus* is a valid species. However, this decision needs to be confirmed by comparison of the holotypes.

Distribution. There is no overlap between the geographical distributions of *K. bonellii*, *K. clericus* and *K. zurstrasseni* (based on material in the reference collections of the Dung Beetle Research Unit, the National Collection of Insects, Pretoria, and the South African Museum, Cape Town) (Fig. 12). *K. bonellii* is restricted to the winter rainfall region of South Africa (rainy season from April to October) where it has been

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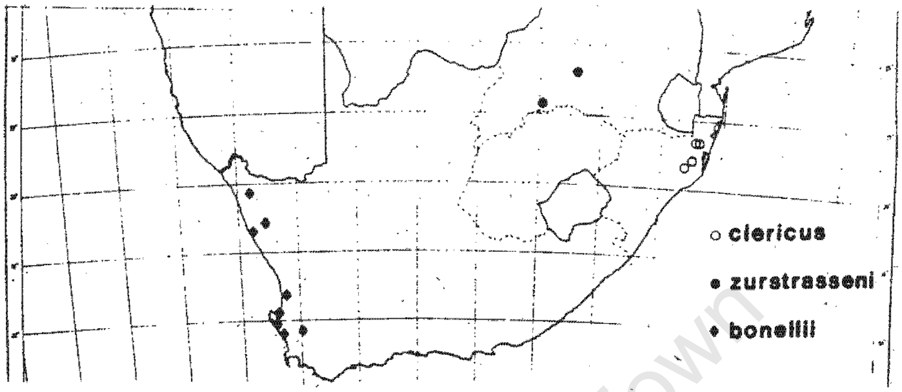

Fig. 12. Geographical distribution of *Kheper bonellii* (MacLeay), *K. clericus* (Boheman) and *K. zurstrasseni* **sp. nov.**

collected on sandy soils and deep sand. It is active predominantly during September and October although one specimen has been recorded during December. *K. clericus* has been found only in the Natal lowlands in the summer rainfall region of South Africa (rainy season from October to April) where it occurs on clay-loam (Makatini). It has been recorded during each month between September and May although peak abundance was observed in October and again in January (B. M. Doube, pers. comm.). *K. zurstrasseni* occurs on the Transvaal highveld in the summer rainfall region of South Africa.

Genus *GYMNOPLEURUS* Illiger, 1803

The Palaearctic, Afrotropical and Oriental genus, *Gymnopleurus s. str.*, was last revised by Janssens (1940b). In this publication, the diagnostic features of the genus were given and a key to all the known species was provided. In recent years, a further 4 valid species have been described, *G. andreaei* Ferreira, *G. imitator* Balthasar, *G. nyankpalensis* Endrödi and *G. rhodesianus* Balthasar.

Gymnopleurus particolor sp. nov., Figs 13–16

MALE. Pronotal disc and dorsal surface of head magenta with a pale green metallic sheen; elytra, legs and pectus green or deep blue with a blue or blue-green metallic sheen. Length, 4–10 mm; mean, 8 mm (n = 10); maximum width, 2–5 mm; mean, 4 mm.

Head. Lateral margins of strongly bidentate clypeus weakly sinuous, genal margin rounded. Clypeus with dense, submarginal, elongate, scalloped depressions and posteriorly-directed, peg-like setae (× 45), posterior part of clypeus densely granular; genae granular; lateral granulation of vertex merging into umbilicate pits sublaterally. Mid-longitudinal line of head smooth, weakly raised and rounded except for short submarginal part of clypeus; smooth area becoming broad and weakly dome-like on the vertex. Clypeo-genal sutures distinct, moderately raised; frontal sutures raised laterally, effaced medially.

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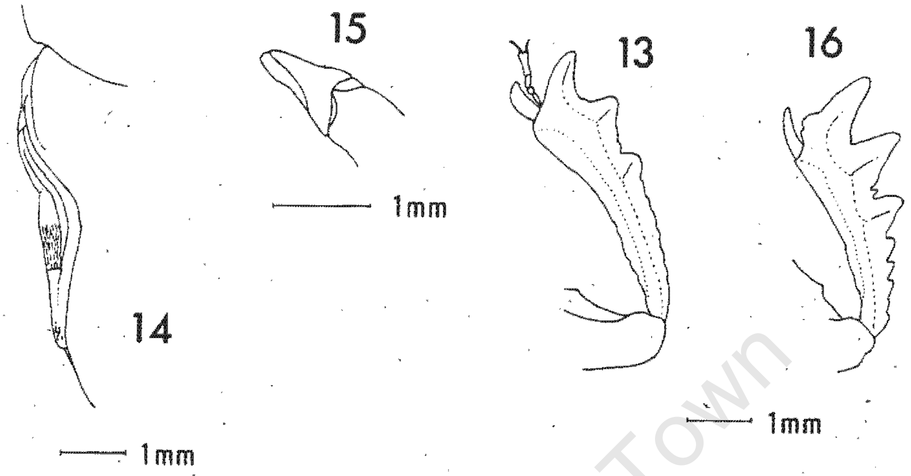

Figs 13–16. *Gymnopleurus particolor* **sp. nov.**; 14. ♀, emargination of left elytrum, epimeral ridge; 13. ♂, right fore tibia, dorsal view; 15. aedeagus, right paramere, lateral view; 16. ♀, right fore tibia, dorsal view.

Thorax. Pronotal disc strongly convex with sparse lunate and umbilicate punctation in an ill-defined pattern, distinctive features being, two small mid-sublateral patches of dense punctation, increasing density of pits towards antero-lateral angles merging into asperate granulation at the angles (× 30), sparse punctation or raspy asperate granules laterally, ill-defined apunctate areas medially and sub-laterally and, an indistinct median groove between the anterior and basal margins often visible only posteriorly. Lateral impressions deep. Metasternum smooth medially, densely granular laterally (× 20) with abundant white silky hairs; metasternal protuberance rounded, granular laterally. Elytra convex, lateral margins rounded in humeral region; interstria 1 without visible (× 0) surface sculpture; interstria 2 with several large, only slightly raised, rounded humps in longitudinal series; interstriae 3–9 with ill-defined sparse lunate pits; interstriae 4–9 with dense, coarse, rugose microgranulation and micropunctation (× 45). Anterior inferior ridge of fore femur with a very small, obtuse, medio-distal projection (× 20); terminal spur of fore tibia bulbous (Fig. 13); median femur punctate and setose ventrally; hind femur densely punctate with abundant fine white hairs ventrally.

Abdomen. Epimeres 1 and 2, exposed by lateral emargination of the elytra, bearing 2 indistinct patches of fine white hairs (× 10); epimeral ridge as in Fig. 14. Sternites densely microgranular with large, sparsely setiferous, asperate granules laterally (× 40). Pygidium marginate and finely rugose (× 30); aedeagus as in Fig. 15.

Female. Length, 8–9 mm; mean, 8 mm (n = 4). Almost identical to male, differing only in the slightly shorter and broader fore tibia with an acute terminal spine (Fig. 16).

Material examined. Information in square brackets not cited on locality labels of specimens. Holotype ♂: GHANA (cited as Gold Coast): 9 ♂♂ and 5 ♀♀ paratypes, Yapi [= New Tamale, 9° 10′ N, 1° 02′ W], x.1915, J. J. Simpson. NIGER: 1 ♂ paratype, Niamey [13° 31′ N, 2° 20′ E], 1977, D. Rougon. All specimens from Ghana in the British Museum (Natural History), London. Specimen from Niger in the Muséum National d'Histoire Naturelle, Paris.

RELATIONSHIPS. *G. particolor* sp. nov. has affinities with the species allied to *G. virens* Erichson. These species are characterized by a smooth, clearly apunctate and agranular mid-line of the head which is slightly raised and rounded from behind the bidentate clypeal margin to the basal ridge of the vertex. All of the species in the group are monochromatic except for the new species and *G. bicolor* Latreille which are bichromatic.

Descriptions of differences between *G. particolor* and other species are based on examinations of the holotypes of *G. virens* Erichson ssp. *sternalis* Müller, *G. sericeifrons* Fairemaire, *G. ignitus* Klug var. *nigrocupreus* Janssens and additional, reliably-identified material. *G. virens* differs from *G. particolor* only in its uniform colour, in the greater density of the punctation medially on its pronotal disc and in the dense asperate granulation and rugosity laterally on the disc. Other close relatives are more clearly different. *G. sericeifrons* differs from *G. particolor* in having very fine, isodiametric punctation medially on the pronotal disc and fine white hairs entirely covering the dorsal surface of the head. *G. ignitus* differs from *G. particolor* in having dense, coarse, u-shaped punctation and smooth apunctate areas arranged in a distinct pattern on the pronotal disc.

The other species of the *G. virens* group also differ clearly from *G. particolor* and may be separated using Janssens' key (1940b). These species are, *G. fulgidus* Olivier, *G. bicolor* Latreille, *G. aenescens* Weidemann, *G. elegans* Klug, *G. foricarius* Garreta and the only known oriental member of the group, *G. koenigi* Fabricius.

Genus *ONITIS* Fabricius, 1798

The Afrotropical species of this Palaearctic, Afrotropical and Oriental genus were last revised by Ferreira (1978). In this publication, a key to the genera of the tribe Onitini was provided together with keys to the groups and species of the genus, *Onitis*, and redescriptions of each Afrotropical species.

Onitis autumnalis sp. nov., Figs 17–21, 28

Onitis caffer Boheman: Ferreira, 1978, *ex parte* (misidentification of material from Zimbabwe).

MALE. Black with a strong sheen, very inconspicuously metallic; all pilosity tan. Length, 10–19 mm; mean, 16 mm (n = 20); maximum width, 5–10 mm; mean, 9 mm.

Head. Arcuate margin of clypeus very weakly bidentate anteriorly; clypeus with coarse isodiametric or weakly ovoid punctation, becoming finer and more sparse posteriorly; genae sparsely and inconspicuously micropunctate; vertex with coarse but shallow punctation (× 20), basal margin forming a bisinuate ridge, somewhat effaced medially. Clypeo-genal and frontal sutures entire and strongly raised. Clypeal carina and tubercle of the vertex raised and prominent; tubercle of the vertex almost equidistant between frontal carina and basal margin of vertex (Fig. 17).

Thorax. Pronotal disc strongly convex with dense, coarse, squamose granulation mid-anteriorly extending to antero-lateral angles, becoming finer, more sparse

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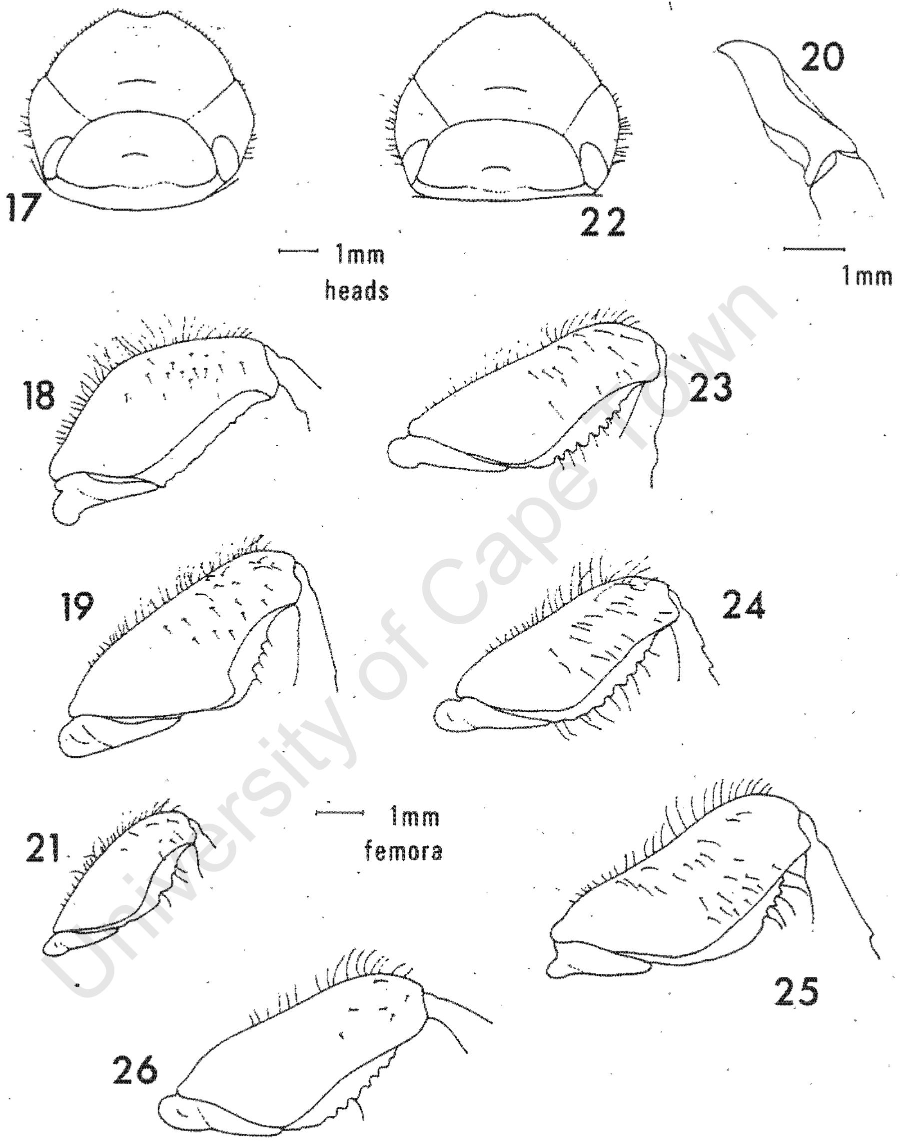

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Figs 17–26. *Onitis* spp. 17–21. *O. autumnalis* **sp. nov.**; 17. ♂, head, dorsal view; 20. aedeagus, right paramere, lateral view; 18. ♂, right median femur, ventral view; 19. major ♂, right hind femur, ventral view; 21. minor ♂, right hind femur, ventral view. 22. *O. caffer* (Boheman), ♂, head, dorsal view. 23–26. major ♂, right hind femora, ventral views; 23. *O. caffer* Boheman; 24. *O. perpunctatus* Balthasar; 25. *O. confusus* Boheman; 26. *O. anthracinus* Felsche.

and asperate mid-posteriorly; towards post-lateral angles, granulation grading sequentially into gradually finer and more sparse lunate, umbilicate and then isodiametric punctation; disc densely micrognanular between basal impressions; basal and lateral impressions deep. Metasternum abundantly punctate and pilose anteriorly with more sparse punctation and shorter hairs posteriorly, bearing a distinct, mid-sternal groove extending from near anterior margin almost to basal margin. Elytra convex, declivous laterally; striae incised and marginate, interstriae slightly convex and finely punctate with shallow, oblique, elongate depressions, density and coarseness variable between individuals. Fore tibia elongate, tip strongly recurved inwards in larger specimens; posterior superior ridge of median femur crenulate (Fig. 18); posterior margin of posterior femur produced into an obtuse, proximo-median lobe with distal crenulation of the posterior superior ridge, proximal portion of superior ridge entire (Fig. 19); each metacoxa with a large spur protruding under the trochanter.

Abdomen. Final sternite narrowing medially. Pygidium marginate with mid-transverse band of fine, pilose punctation; aedeagus as in Fig. 20.

Variation in males. As usual in *Onitis*, there is morphological variation and reduction in prominence of the secondary sexual characters of the males with the decreasing size of the specimens (Fig. 21).

FEMALE. Length, 13–18 mm; mean, 16 mm (n = 20). Clypeus with discrete, short, carinate granules anterior to clypeal carina; each metacoxa lacks spur under the trochanter. Otherwise the usual sexual dimorphism in *Onitis*. Fore tibia short and wedge-shaped, broad end distal; posterior superior ridges of median and hind legs only with minute, barely visible (× 10) crenulation; final sternite without mid-sternal narrowing.

MATERIAL EXAMINED. In addition to my own labels, 18 of the 32 paratypes listed below also bear labels reading 'Onitis caffer Boh., M. C. Ferreira det., 19'. In the following list, information in square brackets is not cited on the locality labels of the specimens. Holotype ♂: ZIMBABWE (cited as Rhod[esia]): and 2 ♀♀ paratypes. Inyanga, 30 km W [18° 26′ S, 32° 28′ E], 16.iv.73, H. H. Aschenborn. Other paratypes: 1 ♂, Salisbury [= Harare], 5 mi E [17° 52′ S, 31° 09′ E], 8.iv.71, Bornemissza and Aschenborn; 7 ♂♂ and 7 ♀♀, Chipinga [= Chipinge], 12 mi N [20° 08′ S, 32° 35′ E], 20.iv.71, Bornemissza and Aschenborn, 1 ♂, Silverstreams Riv[er] Bridge [19° 57′ S, 32° 43′ E], Rhodesian highlands, 21.iv.71, Bornemissza and Aschenborn; 1 ♂, Chipinga, 10 mi N [20° 08′ S, 32° 26′ E], 21.iv.71, Bornemissza and Aschenborn; 2 ♂♂ and 2 ♀♀, Umtali [= Mutare], 11 km S [19° 01′ S, 32° 38′ E], 15.iv.73, H. H. Aschenborn; 1 ♀, Chipinga, 20 mi N [19° 57′ S, 32° 43′ E], 20.iv.71, Bornemissza and Aschenborn; 2 ♂♂ and 6 ♀♀, Vumba Area, 11 mi SE Umtali [19° 06′ S, 32° 41′ E], 5,200 ft [1600 m], 9.iv.71, Bornemissza and Aschenborn. Other material: 11 ♂♂ and 5 ♀♀, Umtali, 22 mi N [18° 40′ S, 32° 43′ E], 9.iv.71, Bornemissza and Aschenborn; 21 ♂♂ and 11 ♀♀, Silverstreams Riv. Bridge, 3 mi N [19° 56′ S, 32° 44′ E], 21.iv.71, Rhodesian highlands, Bornemissza and Aschenborn. Holotype in the National Collection of Insects, Pretoria; 20 paratypes in the collection of the Dung Beetle Research Unit, Pretoria and 4 paratypes in each of the following institutes, British Museum (Natural History), London; Australian National Insect Collection, Canberra and Muséum National d'Histoire Naturelle, Paris.

IDENTITY OF *ONITIS* MATERIAL EXAMINED. Of the 81 specimens of *O. autumnalis*

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cited in this paper, 48 have been previously identified as *O. caffer* Boheman by M. C. Ferreira. As none of the identification labels is dated it is not possible to ascertain whether this material includes any of the 12 specimens from Zimbabwe (ex DBRU collection) identified as *O. caffer* by Ferreira (1978). However, it is probable that these misidentified specimens have been included in the type series of *O. autumnalis* since a large amount of material on loan to Ferreira was returned to the DBRU in July 1978 and, 22 specimens of *O. autumnalis*, cited in the present paper, were collected on the same dates and at the same localities as the 12 specimens.

Evidence that these 12 specimens were misidentified is provided by Ferreira's drawings and text (1978). Firstly, whereas Figure 254 is representative of the hind femur of male *O. caffer*, the hind femur depicted by Figure 261 is undoubtedly that of *O. autumnalis*. Secondly, Ferreira (1978) did note differences in the femoral morphology of males from the Zimbabwe material but suggested that these might represent the characters for major males of *O. caffer*. This is unlikely since similarly sized specimens of *O. caffer* from South Africa bear consistently different armament on the hind femora.

As all material from Zimbabwe which I have examined, is clearly *O. autumnalis*, this raises questions concerning the identity of material from Cafumpe, Moçambique (19° 06′ S, 33° 34′ E) (Fig. 27), cited as *O. caffer* Boheman by Gomes Alves (1950). Since I have not examined this material I am only able to point out that Cafumpe is close to the known geographical range of *O. autumnalis* but distant from that of *O. caffer* (Fig. 27).

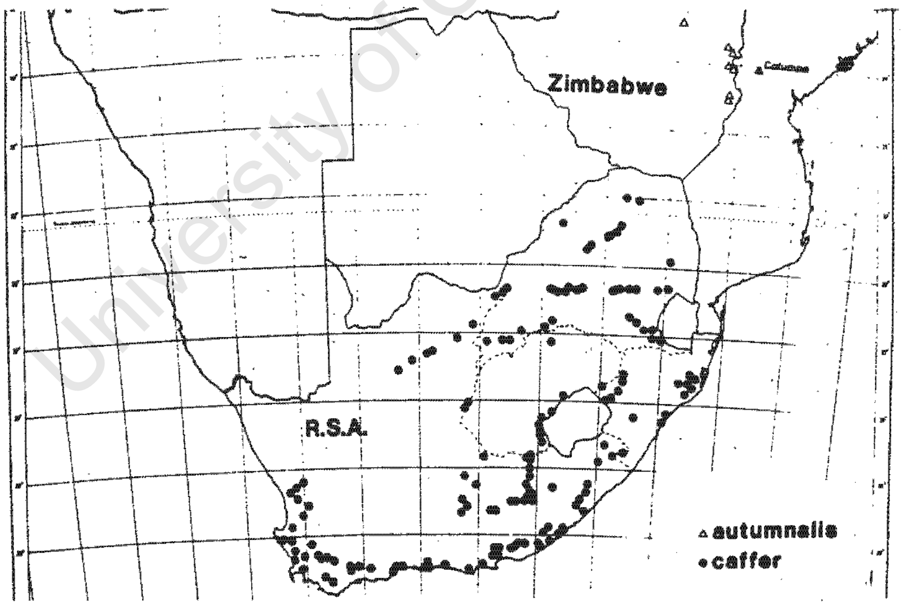

Fig. 27. Geographical distribution of *Onitis caffer* Boheman and *O. autumnalis* **sp. nov.** and the location of Cafumpe, Moçambique.

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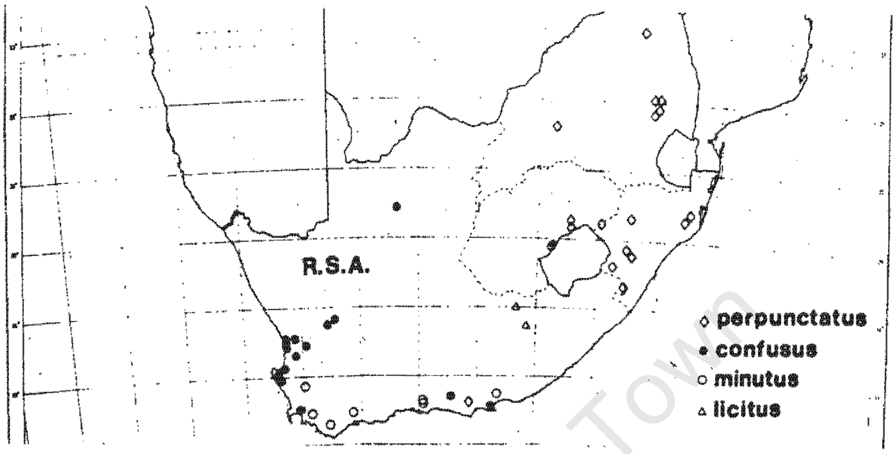

Fig. 28. Geographical distribution of 4 *Onitis* spp.; *O. perpunctatus* Balthasar, *O. confusus* Boheman, *O. licitus* Péringuey and *O. minutus* Lansberge.

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RELATIONSHIPS. Janssens (1937) has separated the *Onitis* into a total of 20 groups subsequently reduced to 19 by Ferreira (1978). The new species belongs to Group VII. With the exception of females from Groups VIII and X, the species of Group VII differ from all Afrotropical members of the other groups by one or more of the following characters: clypeal carina present; frontal suture entire; tubercle present on vertex well anterior to basal margin and well posterior to carinate frontal suture; basal margin of vertex not strongly raised medially; with the exception of *O. perpunctatus* Balthasar, pronotal disc not entirely granular; metacoxa with spine under trochanter in males.

Descriptions of difference between *O. autumnalis* and closely-related species are based on material used for the redescription of each species by Ferreira (1978). *O. autumnalis* is closely allied to *O. caffer* and *O. perpunctatus*. In both sexes of *O. caffer* the vertex differs from that of the new species in being sparsely micrognanular and in having a more posteriorly positioned tubercle (Fig. 22). The hind femur of males lacks a posterior lobular protrusion (Fig. 23) and the posterior superior ridge is almost entirely denticulate. Both sexes of *O. perpunctatus* differ from *O. autumnalis* in that the vertex, genae (× 30) and the pronotal disc are entirely granular although umbilicate depressions between granules on the discs of some specimens may equally be interpreted as punctation. The morphology of the hind femur in males (Fig. 24) is similar to that of *O. caffer*.

Key to the Afrotropical species of *Onitis* belonging to Janssens' Group VII (males and females).

1 Pronotal disc almost entirely punctate or, granular anteriorly and entirely punctate posteriorly 2

— Pronotal disc entirely or partially granular, if partially granular, granulation always present mid-posteriorly 3

2 Pronotal disc granular at anterolateral angles and between basal impressions (× 20): otherwise entirely punctate in both sexes; in males, posterior superior ridge of hind femur carinate terminating distally in 3–7 denticles (Fig. 25) . . . . *confusus* Boheman

— Pronotal disc granular at anterolateral angles, otherwise entirely punctate in male including between basal impressions (× 20); in female, pronotal disc granular anteriorly and punctate posteriorly; in males, posterior superior ridge of hind femur entirely crenulate, denticles nine or more in number (Fig. 26) .... *anthracinus* Felsche

3 Entirely metallic green or metallic green with brown elytra and pygidium 4

— Entirely black 5

4 Entirely metallic green, sometimes with a rosy metallic sheen; in male, space between teeth 2 and 3 of fore tibia, 1,5 times greater than that between teeth 3 and 4 .... *licitis* Péringuey

— Elytra and pygidium brown, sometimes with a muted green metallic sheen, rest of body metallic green, sometimes with a cupreous metallic sheen; teeth of fore tibia equidistant .... *minutus* Lansberge

5 Genae granular (× 30); pronotal disc entirely granular, sometimes with umbilicate depressions between granules; interstriae of elytra coarsely and densely punctate .... *perpunctatus* Balthasar

— Genae with shallow pits (× 30); pronotal disc becoming distinctly punctate towards postlateral angles; punctation of elytral interstriae often fine but if coarse then also with shallow, elongate depressions 6

6 Vertex with shallow pits (× 30); tubercle of vertex only slightly closer (approx. 0,2 times) to basal ridge of vertex than to frontal carina (Fig. 17); in male, crenulate posterior superior ridge of hind femur distal to lobular posterior extension of femoral margin (Fig. 20), denticles 4–6 in number .... *autumnalis* **sp. nov.**

— Vertex with sparse microgranulation (× 30), somewhat rugose in female; tubercle of vertex approximately 2,0 times closer to basal ridge of vertex than to frontal carina (Fig. 22); in male, crenulate posterior superior ridge of hind femur not distal to a lobular posterior extension of femoral margin (Fig. 23), denticles 5–9 in number .... *caffer* Boheman

Distribution. The geographical distribution of the new species and its six Afrotropical relatives in Group VII (according to material in the reference collection of the Dung Beetle Research Unit) is shown by Figures 27–29. The two tropical members of the group, *O. autumnalis* and *O. anthracinus,* both have highland distributions. Apart from *O. perpunctatus,* which has been collected predominantly between November and February, most reference material of Group VII has been collected during the cooler months of the year (March–October). The two species with the most southerly distribution, *O. licitus* (H. H. Aschenborn, pers. comm.) and *O. minutus* are both day-flying. All other Afrotropical *Onitis* with known flight periods are principally dusk-flying, including *O. caffer* and *O. confusus.* Other *Onitis* spp. with day-flying habits have only been recorded at the northern limits of the generic range, e.g. *O. numida* Castelnau in north Africa and *O. humerosus* (Pallas) in Iran (G. F. Bornemissza, pers. comm.).

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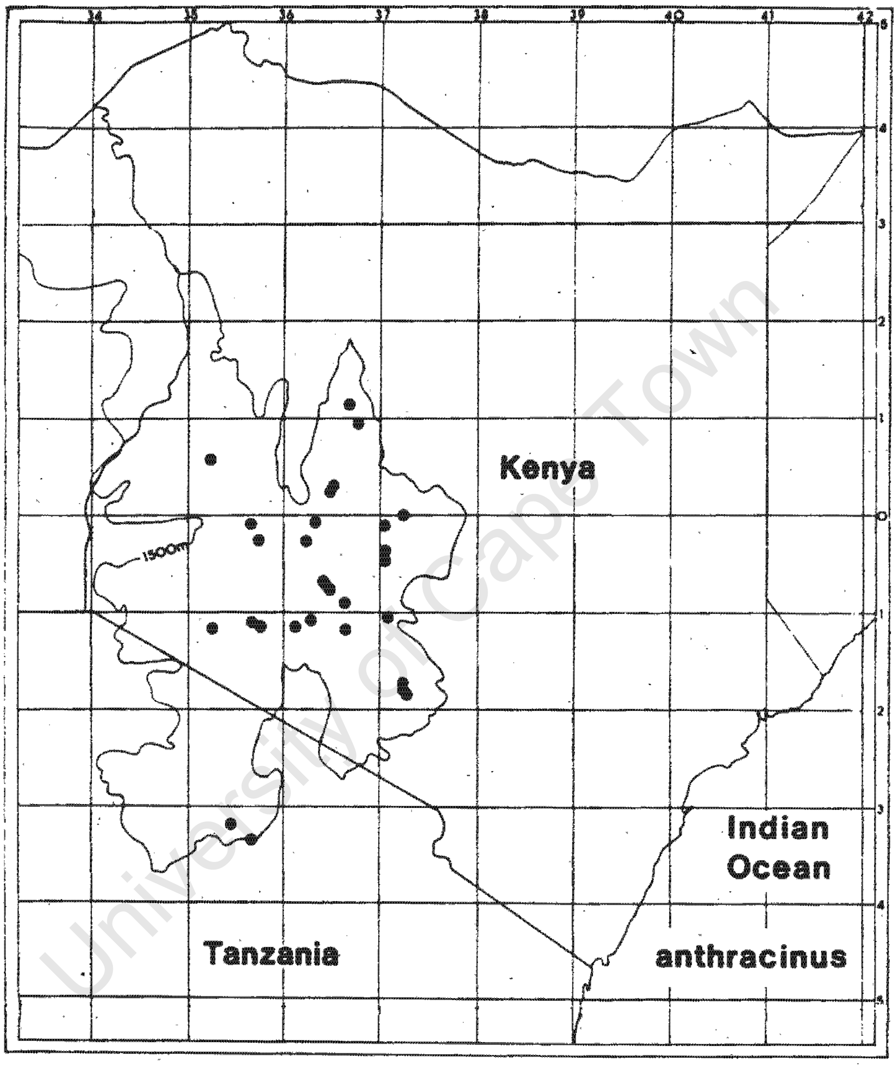

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Fig. 29. Geographical distribution of *Onitis anthracinus* Felsche in relation to the 1500 m contour in Kenya and northern Tanzania.

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APPENDIX 4

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Geographical distribution of dung beetles (Coleoptera: Scarabaeidae) and their seasonal activity in south-western Cape Province

by

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A total of 30 species of dung beetles was recorded in indigenous shrubland near Langebaan and a pasture of Kikuyu grass near Paarl over a period of 13 months. These species were divided into 2 groups according to their distribution between the rainfall regions of southern Africa. Group 1, which was numerically dominant at Langebaan, was largely endemic to the winter and bimodal rainfall regions and was principally active during the winter rainy season in the south-western Cape. Group 2, which was numerically dominant at Paarl, was widespread in the winter, bimodal and summer rainfall regions and was principally active during the summer dry season and beginning of the rainy season in the south-western Cape. The potential of these beetles as control agents of the dung-breeding bush fly in south-western Australia is discussed.

INTRODUCTION

Bornemissza (1960) recommended that exotic, dung-burying beetles (Scarabaeidae: Scarabaeinae) should be introduced into Australia to remove cattle pads which foul pastures and act as breeding sites for the fly pests, *Haematobia irritans exigua* (de Meijere) (buffalo fly) and *Musca vetustissima* Walker (bush fly). Dung beetles with potential as control agents of the bush fly in the mediterranean climatic region of south-western Australia are being sought in roughly homoclimatic areas of southern Europe and south-western Cape Province in South Africa. Those species selected must show peaks in abundance which coincide with the increase in numbers of the bush fly during spring in south-western Australia (Ridsdill Smith & Matthiessen 1984).

The seasonal distribution of dung beetle fauna in regions with mediterranean-type climate has been previously studied in both southern Europe (Krausse 1907a, b, Lumaret 1983) and south-western Australia (Ridsdill Smith & Hall 1984a, b). The present study examines the seasonal activity of dung beetles in the south-western Cape. As much of the native vegetation has been cleared from this region, traps were placed in both indigenous shrubland and in a pasture of introduced Kikuyu grass *(Pennisetum clandestinum)*. The geographical distribution of the species recorded was plotted on maps of southern Africa and compared with their seasonal activity patterns in the south-western Cape.

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METHODS

Study sites and trapping method

The study site in indigenous shrubland was situated on deep sand on the farm, 'Geelbek' (33° 10′ S 18° 08′ E), near Langebaan. This shrubland was described as dense strandveld scrub by Acocks (1975) and is characterised by a vegetative profile of up to 3 m and a vegetative cover of approximately 40%.

The study site in Kikuyu grass was situated on sandy loam on the farm, 'Nantes Herd' (33° 40′ S 18° 48′ E), near Paarl in an area totally cleared of native vegetation. Kikuyu grass differs from the shrubland it replaces not only in its low vegetative profile of a few centimetres but also in its 100% vegetative cover. A small part of this study site retained green grass throughout the dry season due to seepage from a pumphouse. Pipe irrigation of this study site was observed on a single occasion.

There were climatic differences between the two sites. The farm, 'Geelbek', is situated at sea level on the west coast which results in a less extreme annual range in mean monthly temperatures (max. 28°C, min. 7°C at Langebaanweg) than at Paarl (max. 30°C, min. 6°C) which lies inland at an altitude of *c.* 140m a.s.l. The average annual rainfall also differs between sites with *c.* 300 mm at Langebaan and *c.* 600 mm at Paarl.

Seasonal distribution of dung beetles at Langebaan and Paarl was studied for 13 months between April 1979 and April 1980. At each study site, 10 pitfall traps were placed 2–3 m apart and baited with *c.* 1 L of fresh cattle dung for 24 h each week. Because the study sites were 120 km apart, the traps at each were baited on different days of the week.

Distribution of dung beetles in relation to climatic zones

Over the last 16 years a large reference collection of scarabaeine dung beetles has been amassed by the Dung Beetle Research Unit. This collection currently contains *c.* 850 species from over 2500 localities, mostly in southern Africa. The distribution of the dung beetle species trapped during the present study was plotted in relation to the major climatic regions of southern Africa. These regions were derived by reducing the 19 temperature/rainfall zones proposed for the area by Walter & Lieth (1964), to four regions based solely on the seasonal occurrence of rainfall.

The seasonal distribution of rainfall at one site in each of the four regions is shown by Figure 1. In the winter rainfall region (WR) of the western Cape, peak rainfall is during mid-winter (usually June or July) whereas in the bimodal rainfall region (BR) in the southern and eastern Cape, peaks in rainfall occur during spring (usually September-November) and in late summer or autumn (usually March-May). In summer rainfall region one (SR1), which comprises southern South West Africa and central South Africa, peak rainfall occurs during late summer (usually in March). In summer rainfall region two (SR2), which comprises Botswana, northern South Africa and northern South West Africa, rainfall is fairly evenly distributed throughout the rainy season with a peak in mid-summer (usually December or January).

RESULTS

A total of 30 species of Scarabaeinae was trapped (Table 1). These were divided into two groups on the basis of their distribution between the four rainfall regions

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TABLE 1. Distribution of 30 species of dung beetles in southern Africa and total numbers recorded in indigenous shrubland at Langebaan and in a pasture of Kikuyu grass at Paarl over a period of 13 months.

GROUP 1. Species restricted or largely restricted to the winter rainfall (WR) and bimodal rainfall (BR) regions

Species	Total numbers	
	LANGEBAAN Indigenous shrubland	PAARL Kikuyu grass
Pachysoma hippocrates MacLeay	3	
Kheper bonellii (MacLeay)	15	
Scarabaeus rugosus (Hausman)	1948	
S. intricatus Fabricius	44	
S. suri (Hausman)	2	
Sceliages brittoni zur Strassen	6	
Sisyphus quadricollis Peringuey	1	
Epirinus aeneas Weideman	82	
E. bentoi Ferreira	47	
E. flagellatus (Fabricius)	1	
Odontoloma dentinum (Harold)	3	24
O. pusillum Howden & Scholtz	86	
Odontoloma sp.	1	
Copris anceus Olivier	442	
C. capensis Waterhouse	4	
Macroderes sp.	6	
Sarophorus tuberculatus (Castelnau)	20	
Onthophagus cameloides d'Orbigny	3	12
O. giraffa Hausman	36	
O. immundus Boheman		4
O. minutus Boheman	1366	
Total	4107	40
Number of traps x number of trapping occasions	552	543

GROUP 2. Species of the winter; bimodal and summer rainfall (SR1, SR2) regions

Species	Total numbers	
	LANGEBAAN Indigenous shrubland	PAARL Kikuyu grass
Onitis aygulus (Fabricius)	52	28
O. caffer Boheman	7	27
O. confusus Boheman	11	
Chironitis scabrosus (Fabricius)	22	1
Onthophagus binodis Thunberg		90
O. gazella Fabricius		69
Euoniticellus africanus (Harold)		7
E. intermedius (Reiche)	80	569
E. triangulatus (Harold)		368
Total	172	1159
Number of traps x number of trapping occasions	552	543

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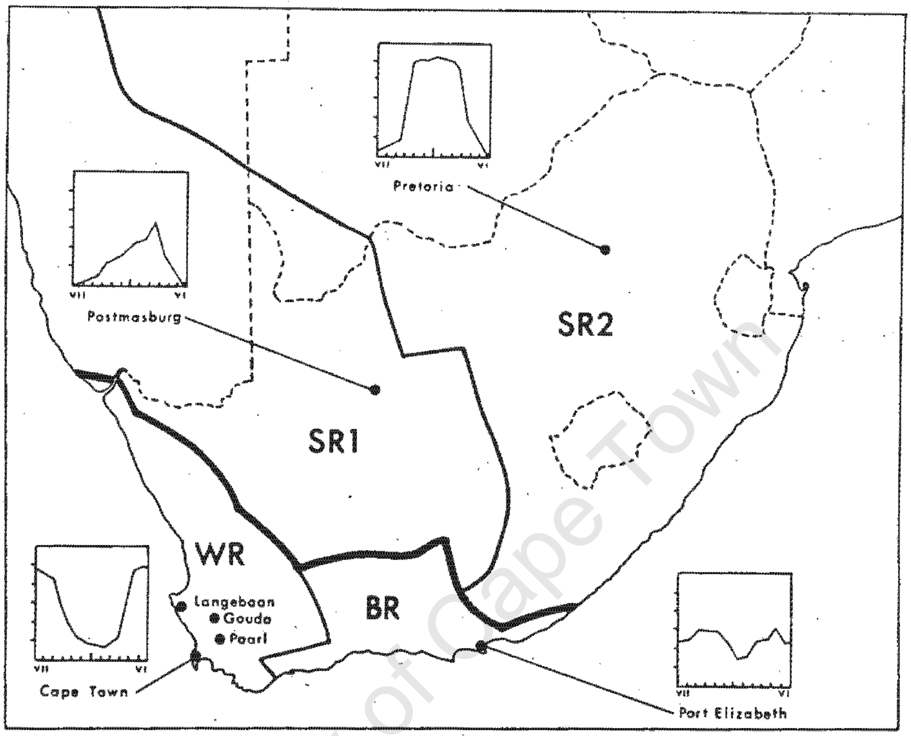

Fig. 1. The four rainfall regions of southern Africa (derived from Walter & Lieth 1964) with examples of seasonal rainfall from each region and the location of trapping sites in south-western Cape Province. WR = winter rainfall. BR = bimodal rainfall. SR = summer rainfall (areas 1 and 2).

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of southern Africa (Figs 1–4). Group 1 comprises 18 species restricted to the winter (WR) and bimodal rainfall (BR) regions (Fig. 2) plus three species with a marginal distribution in the southern parts of the summer rainfall (SR1, SR2) region in addition to their occurrence in the winter and bimodal rainfall regions (Fig. 3). Group 2 comprises nine species with a wide distribution in the winter, bimodal and summer rainfall regions (Fig. 4).

Group 1 comprised 96% of the total numbers recorded in indigenous shrubland at Langebaan (Table 1) and was predominantly active during the winter rainy season (Fig. 5). At the beginning of the rainy season in autumn (April-May) there was an increase in abundance which reached a maximum during spring (August-October). Activity declined rapidly at the beginning of the dry season (November-December) and remained low until the beginning of the following rainy season (April). This seasonal distribution reflects the August, September or October peaks in activity of all the more abundant ($n > 20$) Group 1 species except *Epirinus aeneas* which shows a peak in activity during May (Table 2). Group 1 comprised only 3% of the total numbers recorded

TABLE 2. Seasonal occurrence of the most abundant species (n > 20) of Group 1 dung beetles in the south-western Cape and the size of each species expressed as mean dry mass.

Species	Mean/trap × 100			Month of maximum activity	*Mean dry mass (g) per specimen
	Early rainy season Apr.-Jul.	Late rainy season Aug.-Nov.	Dry season Dec.-Mar.		
LANGEBAAN					
Epirinus aeneas	32	18	0	May	0,019
Copris anceus	87	169	7	Aug.	0,253
Onthophagus minutus	234	523	41	Aug.	0,007
O. giraffa	6	13	1	Sept.	0,032
Odontoloma pusillum	15	30	0	Sept.	0,002
Sarophorus tuberculatus	0	11	0	Sept.	0,020
Epirinus bentoi	0	28	3	Sept.	0,014
Scarabaeus rugosus	279	802	4	Oct.	0,339
S. intricatus	1	18	6	Oct.	0,043
PAARL					
Odontoloma dentinum	1	11	0	Oct.	0,002

*Derived from 10 specimens for each species.
Mass indicates potential usefulness for dung removal.

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TABLE 3. Seasonal occurrence of the most abundant species (n > 20) of Group 2 dung beetles in the south-western Cape and the size of each species expressed as mean dry mass.

Species	Mean/trap × 100			Month of max. (or 2nd to max.) activity	* Mean dry mass (g) per specimen
	Early rainy season Apr.-Jul.	Late rainy season Aug.-Nov.	Dry season Dec.-Mar.		
LANGEBAAN					
Euoniticellus intermedius	25	6	10	April	0,010
Chironitis scabrosus	0	1	13	Dec.	0,063
Onitis aygulus	4	1	28	Feb.	0,256
PAARL					
Onthophagus gazella	25	0	14	April	0,039
Euoniticellus intermedius	26	19	23	May	
Onitis caffer	15	3	0	May	0,223
Euoniticellus triangulatus	62	69	90	April (Nov.)	0,009
Onthophagus binodis	14	12	30	April (Dec.)	0,027
Onitis aygulus	1	1	16	Dec.	

*Derived from 10 specimens for each species.
Mass indicates potential usefulness for dung removal.

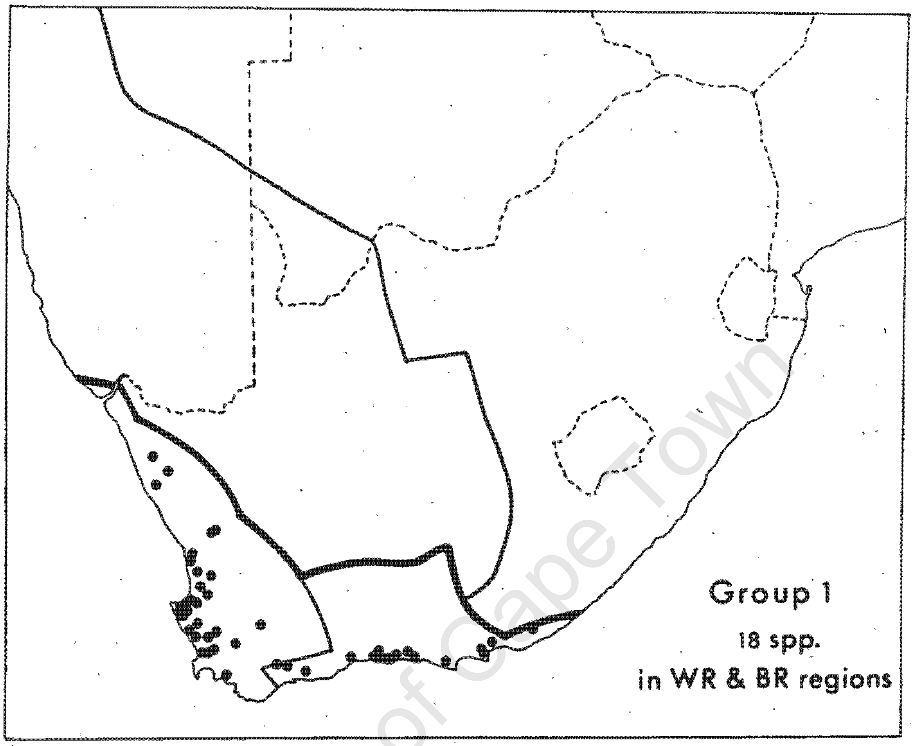

Fig. 2. The combined distribution of 18 species of dung beetles in Group 1 (all those listed in Table 1 minus those cited in Fig. 3) in the winter and bimodal rainfall regions of South Africa.

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in Kikuyu grass at Paarl. These numbers were too low to assess seasonal distribution (Fig. 6).

Group 2 comprised 97% of the total numbers recorded at Paarl (Table 1) and showed bimodal seasonal activity (Fig. 6). The greatest peak in abundance was at the beginning of the rainy season in 1979 (April-May). This was followed by a decline in activity during the latter half of the rainy season (June-October). A second and smaller peak in abundance occurred at the beginning of the dry season (November-December) followed by decline in activity during the latter half of the dry season. No increase in activity was recorded in April 1980. Group 2 comprised only 4% of the total numbers recorded at Langebaan. The activity period from December to May was similar to that of Group 2 at Paarl (Figs 5, 6).

The seasonal distributions recorded for the more abundant (n > 20) species of Group 2 are summarized in Table 3. Activity by *Onitis caffer* was restricted to the rainy season. *Onthophagus gazella, O. binodis, Euoniticellus intermedius* and *E. triangulatus*, were relatively abundant in both the rainy and the dry season whereas activity by *Onitis aygulus* and *Chironitis scabrosus* was largely restricted to the dry season.

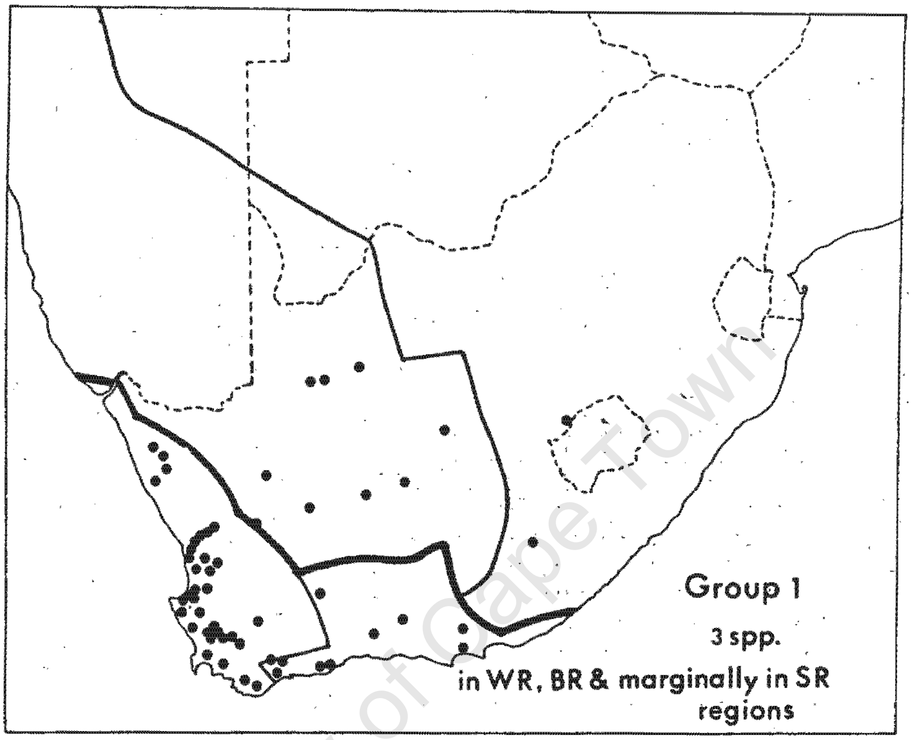

Fig. 3. The combined distribution of three Group 1 species of dung beetles, *Epirinus aeneas*, *E. flagellatus* and *Onthophagus cameloides*, between the four rainfall regions of southern Africa.

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DISCUSSION

Two faunal groups of dung beetles have been shown to occur in the mediterranean climatic region of the south-western Cape. A relationship has been shown between their geographical and seasonal distributions. It is suggested that in addition to seasonal activity, the vegetation associations of these groups will strongly influence their potential as control agents of the bushfly in south-western Australia.

Geographical and seasonal distribution

The virtual restriction of Group 1 species to the winter and bimodal rainfall regions is reflected by their seasonal activity which is largely during the winter rainy season in the south-western Cape. The minor peak in activity by Group 1 species at the beginning of the rainy season (autumn) and the major peak late in the rainy season (spring) is similar to that of the dung beetles of southern Europe (Krausse 1907a, b, Lumaret 1983). However, the overall seasonal pattern of activity in southern France differs from that in the south-western Cape, presumably due to the lower mean annual temperature, much shorter dry season and correspondingly longer rainy season. In south-western Australia, seasonal peaks in abundance of dung beetles were variable be-

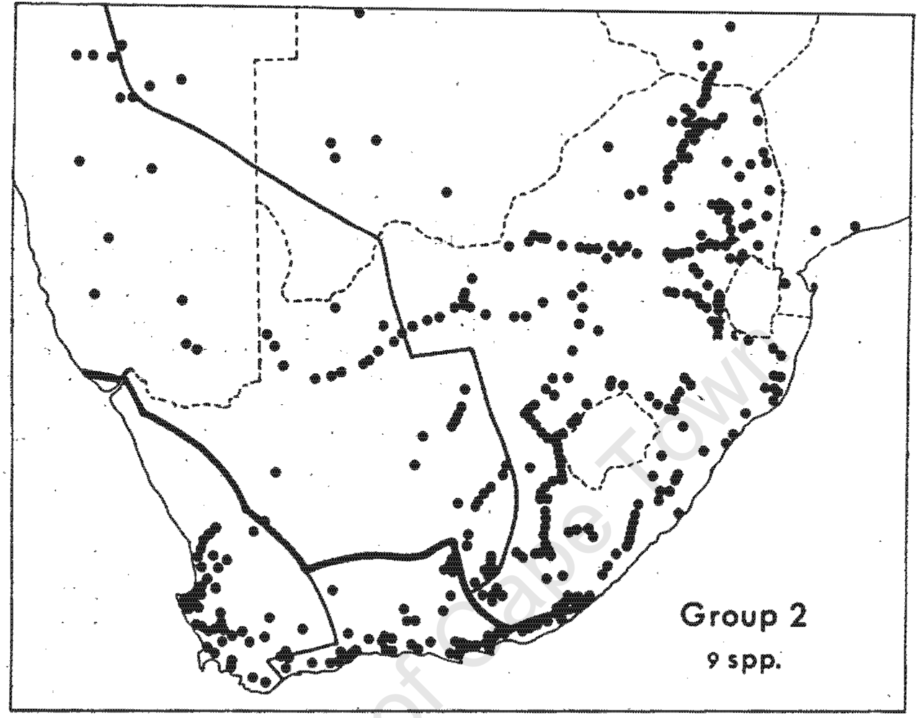

Fig. 4. The combined distribution of the nine species of dung beetles in Group 2 (see Table 1) between the four rainfall regions of southern Africa.

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tween localities with either a single peak in spring, a single peak in autumn or a major peak in autumn and a minor peak in spring (Ridsdill Smith & Hall 1984a, b).

Group 2 shows a wider geographical range (Figs 2, 3, 4) and a broader seasonal distribution (Tables 2, 3) than Group 1 but overall abundance was much lower (Table 1). This may be because greatest activity by dung beetles is during rainy periods (Krausse 1907a, b, Halffter & Matthews 1966, Kingston 1977, Cambefort 1982, Lumaret 1983) whereas, in the south-western Cape, the main activity period of Group 2 species is during the warmer, predominantly dry months (Fig. 6). Furthermore, the present study was conducted in virtually non-irrigated situations so that there was little dry-season soil moisture. The occurrence of Group 2 at Langebaan and Paarl may be associated with the moderate to high rainfall coastal belt of the southern Cape which connects the south-western Cape to the moist summer rainfall region. In contrast, no naturally-occurring dung beetles with Group 2 activity patterns have been recorded in south-western Australia (Ridsdill Smith and Hall 1984a, b) which is isolated from moist summer rainfall regions by the arid centre of the continent.

Effects of habitat and farming practice on distribution of dung beetles

Much of the shrubland indigenous to the south-western Cape has been cleared. In perennial cattle pastures it is often replaced either by a sparse cover of natural

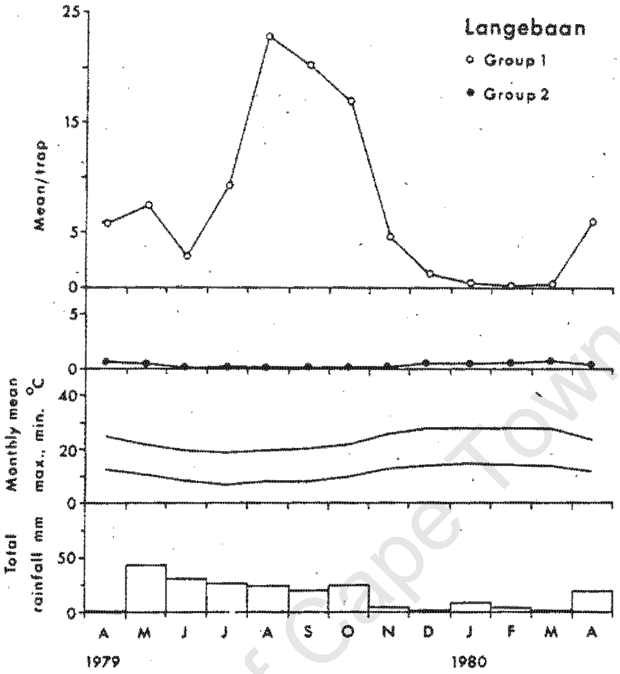

Fig. 5. Seasonal distribution of Group 1 and Group 2 dung beetles in indigenous shrubland near Langebaan with seasonal temperature and rainfall data from Langebaanweg (climatic data courtesy of the Weather Bureau of South Africa).

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herbs and grasses or by a dense cover of Kikuyu grass usually under irrigation during the dry season. In herbs and grasses at Langebaan and at Gouda (33° 16′ S 19° 02′ E), numerical balance of Group 1 (*c.* 60%) and Group 2 (*c.* 40%) (Davis, unpubl. data) was intermediate to the extreme distributions of the groups in indigenous shrubland and Kikuyu grass. These differences in faunal composition parallel increasing modification of the native habitat. As vegetation type, soil type and climate differed between trapping sites in the present study, further work is necessary to determine the causes of these differences.

Selection of dung beetle species for introduction into Australia

Of the seven species of dung beetles that have been introduced into south-western Australia and become established (Ridsdill Smith & Matthiessen 1984), *Onitis aygulus, Onthophagus binodis* and *Euoniticellus intermedius* were recorded during the present study. These three species belong to Group 2 which shows summer and autumn activity in the south-western Cape. A similar activity period is shown by the entire group of exotic species introduced into south-western Australia. This postdates the spring increase in the abundance of the bushfly (Ridsdill Smith & Matthiessen 1984) which these species were introduced to control. The present study has identified spring-active species belonging to Group 1 in the south-western Cape but they may be associated

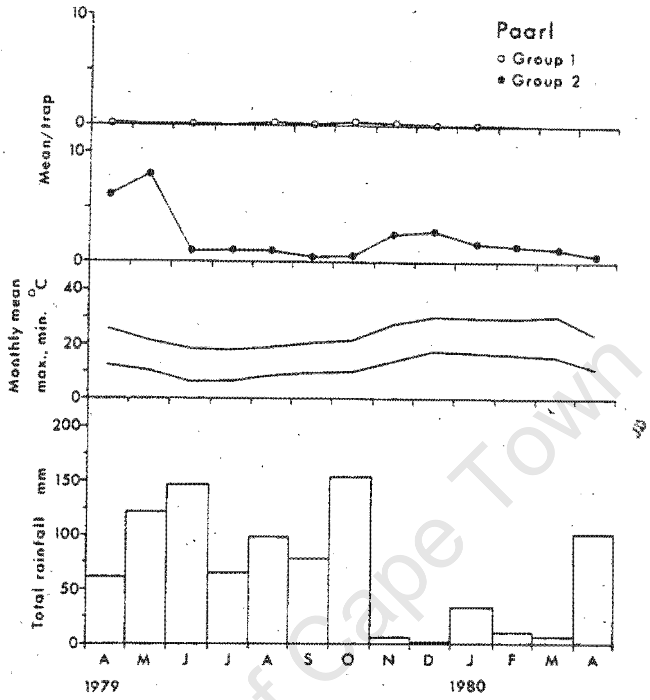

Fig. 6. Seasonal distribution of Group 1 and Group 2 dung beetles in Kikuyu grass near Paarl with temperature and rainfall data for Paarl (climatic data courtesy of the Weather Bureau of South Africa).

with indigenous shrubland which would make them unsuitable for introduction into pasture habitats in Australia.

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APPENDIX 5

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Habitat associations and seasonal abundance of coprophilous Coleoptera (Staphylinidae, Hydrophilidae and Histeridae) in the Hluhluwe region of South Africa

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Abstract

A total of 134 species of Coleoptera (100 of staphylinids, 13 of hydrophilids and 21 of histerids) was extracted from pads of cattle dung placed in four contrasting habitats in both Hluhluwe Game Reserve, Natal, South Africa, and the surrounding pastoral regions. Pads were exposed to colonists for 24 h on eight occasions over one year. Forty-six species and species complexes were captured in numbers sufficient to permit analysis of their distribution patterns. Of 27 species significantly influenced by vegetation type, 22 were more abundant in unshaded situations and five more abundant in situations shaded by high profile vegetation. The total numbers of individual predatory staphylinids were evenly distributed between vegetation types, but members of coprophagous staphylinid and other predatory taxa were more numerous in unshaded situations. Of 13 species significantly influenced by soil type, six were more abundant on clay and seven more abundant on deep sand. The total numbers of individual coprophagous oxyteline staphylinids were greater on clay than on sand, but the members of predatory taxa, including staphylinids, were evenly distributed across soil types. Of 14 species showing significant seasonal changes in abundance, 13 were more abundant in hot wet months and one in cool dry months. The total numbers of hydrophilid individuals were greater in the cool dry season, but the other taxa were active predominantly in the rainy season. Most species were present in similar numbers in both the game reserve and pastoral regions. Enclosure of dung pads within wiremesh cones to exclude large dung-burying beetles resulted in reduced colonization by most beetle species regardless of their size.

Introduction

Predatory and parasitic species of Coleoptera from southern Africa are considered to have potential as control agents of the dung-breeding buffalo fly, *Haematobia irritans exigua* de Meijere, in Australia (Doube, 1986) where it is a serious blood-sucking pest of cattle. Cattle are a relatively recent introduction into Australia (Waterhouse, 1974), and the beetle fauna associated with their dung is depauperate compared with a climatically equivalent area of Africa (Doube, 1986). The African dung beetle fauna includes many

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predatory and parasitic species belonging to the families Staphylinidae, Hydrophilidae and Histeridae. Beetles from these three families have been shown to reduce breeding success of *Haematobia* spp. in both southern Africa (Fay & Doube, 1983; Doube & Huxham, 1987) and North America (Bourne & Hays, 1968; Blume *et al.*, 1970; Thomas & Morgan, 1972; Macqueen & Beirne, 1975; Harris & Oliver, 1979; Roth, 1982, 1983; Summerlin *et al.*, 1984).

Information on the relative abundance and habitat associations of predatory beetles is essential for the selection of suitable species for introduction into Australia. Clear associations with different vegetation types have been shown for species of Staphylinidae, Hydrophilidae and Histeridae in both Texas, USA (Hunter *et al.* 1986), and in cooler regions such as Finland (Rainio, 1966; Koskela, 1972; Koskela & Hanski, 1977; Hanski & Koskela, 1977). However, there is no published work on the habitat associations of these taxa in Africa.

In the present study, the soil and vegetation associations of the more abundant coprophilous species in these families were examined in northern Natal, South Africa. The seasonal abundance of these species was also examined, and comparisons were made between the fauna in Hluhluwe Game Reserve and the surrounding pastoral district. Results are presented for representatives of groups known to contain mainly predatory species and also for members of the staphylinid subfamily Oxytelinae, which are generally considered to be coprophagous (Koskela & Hanski, 1977).

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Methods

Study sites

Study sites were located in an area 15 × 30 km near the village of Hluhluwe (20°02'S, 32°17'E) in the northern lowlands of Natal. This area varies from 50 to 150 m above sea level. The mean annual rainfall ranges from 750–925 mm and falls predominantly during the hottest months of the year (November–March) (Weather Bureau, undated). The region is homoclimatic with coastal central Queensland in Australia (Walter & Lieth, 1964) where *H. i. exigua* is abundant during summer.

Four habitats, defined according to soil type and physical characteristics of the vegetation, were selected for study, and each habitat was represented by four sampling sites. Two sites for each habitat were in Hluhluwe Game Reserve, and two were on nearby cattle farms. A description of the 16 sites is presented in Table I.

TABLE I. *The soil and vegetative characteristics of the areas surrounding the 16 study sites selected in the Hluhluwe region*

Habitat	Hluhluwe Game Reserve*	Farms near Hluhluwe**
Unshaded situations on clay or clay-loam	Site 1. Extensive area of dense grassland in the Inzimane Valley (clay). Site 2. Extensive area of dense grass replacing cleared shrub-woodland near Memorial Gate (clay).	Sites 1 & 2. Extensive area of dense grassland in degraded shrub-woodland (clay-loam (Makatini)).
Shaded situations on clay or clay-loam	Site 1. Well-shaded isolated thicket at edge of grassland in the Inzimane Valley (clay). Site 2. Well-shaded riverine woodland with dense low canopy and relatively open understorey near Memorial Gate (clay).	Sites 1 & 2. Poorly shaded thickets in degraded open shrub-woodland (clay-loam (Makatini)).
Unshaded situations on deep sand	Sites 1 & 2. Unshaded patches of sparse grass cover in open shrub-woodland in the Inzimane Valley.	Sites 1 & 2. Extensive area of sparse grassland replacing cleared dense shrub-woodland with a few well-dispersed clumps of relict woodland.
Shaded situations on deep sand	Sites 1 & 2. Moderately shaded thickets in open shrub-woodland in the Inzimane Valley.	Sites 1 & 2. Extensive area of moderately shaded, dense shrub-woodland.

* Memorial Gate and the Inzimane Valley are 19 and 27 km, respectively, west-south-west of Hluhluwe.
** The clay-loam area and the deep sand area are 5 and 15 km, respectively, south of Hluhluwe.

Sampling procedures

Beetles were sampled on eight occasions between December 1981 and December 1982. Fresh dung baits were placed on the soil surface for 24-h periods, and the beetle colonists present at the end of the exposure period were extracted and counted. In December 1981, sampling was conducted only at the eight study sites in Hluhluwe Game Reserve. On subesequent occasions, samples were taken from all 16 study sites. Whenever possible, sampling was conducted on sunny days to minimize the effects of weather on the numbers of beetles caught.

On each sampling occasion, freshly-voided, beetle-free, cattle dung was collected in Pretoria during the early morning. This was transported to the study area in large plastic tubs which were sealed to minimize crusting and oxidation of the dung. Dung baits were placed in the field within 2 h of sunrise on the morning following arrival in Natal. In order to provide similar bait for both diurnal and crepuscular beetles, dung pads were collected and replaced with fresh pads during the 2 h before sunset. The replacement pads were collected the next morning within 2 h of sunrise. Immediately before collection, the amount of dung which had been removed from each pad by dung-burying beetles was estimated visually. After collection, all pads were placed in insect-proof, ventilated boxes together with any loose soil from under the pad and then transported to the laboratories in Pretoria where they were placed in Berlese-type extraction funnels. During the subsequent three days, the dung and soil dried out and the emergent beetles were collected in 70% alcohol.

Dung removal by scarabaeine beetles can be both rapid and substantial. Such removal activity may influence colonization and residence in dung pads by other coprophilous beetles. Therefore, dung baits were treated in one of two different ways. In treatment 1, a single 0·5-litre pad of dung was placed on the bare soil surface at each of the 16 study sites. In treatment 2, a duplicate series of pads was placed adjacent to the treatment 1 pad at all study sites and was enclosed within a cone (diameter: 46 cm; height at apex: 25 cm) of 3-mm-gauge wiremesh. These cones were designed to exclude the majority of dung-burying beetles and thus reduce dung burial whilst allowing the smaller coprophagous and predacious species to have access to the pads.

On each 24-h sampling occasion for each of treatments 1 and 2, 32 pads were placed in the field. These comprised one day-exposed and one night-exposed pad at each of the four sites in each of the four habitats. Because only eight Berlese-type funnels were available to extract the dung fauna from each of treatments 1 and 2, it was necessary to pool some samples. Therefore, the day and night pads were pooled for each site, and the pads from replicate sites within habitats were also pooled. This resulted in 8 × 2-litre samples of uncovered dung (treatment 1) which represented the same four habitat types both inside and outside the game reserve. The covered pads in treatment 2 were pooled in a similar manner.

Analysis of data

Data for the most abundant species extracted from unenclosed pads were analysed for associations with soil type, vegetation type, season and locality. Total numbers for each species were calculated for each of the eight sampling occasions in the reserve and the seven occasions on the farms to give 15 separate totals. The 15 totals were each subdivided into numbers on clay-loam and numbers on deep sand to give 15 paired data sets for each species. Data on distribution between unshaded and shaded vegetation types were treated in the same manner. Wilcoxon signed-ranks tests were conducted on these data. The unequal numbers of observations in different seasons (nine observations in the hot wet months of November–March and six in the cool dry months of May–September) and localities (eight observations in the game reserve and seven on the cattle farms) were analysed using Mann-Whitney *U* tests.

During the summer, there is often substantial dung removal from pads on deep sand but a much lower level of removal from pads on clay-loam. The potentially asymmetric effect of dung removal by Scarabaeinae on colonization of dung pads by other coprophilous beetles was examined by comparing the distribution of total numbers recorded from

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unenclosed (some dung removal) and enclosed pads (minimal dung removal) on deep sand (high scarabaeid numbers) and on clay soils (low scarabaeid numbers) using 2 × 2 contingency tests. In those instances where the chi square was statistically significant, a separate analysis was conducted on the habitat and seasonal data for enclosed pads in which dung removal was minimal in all treatments.

The influence of wiremesh cones on colonization of dung pads by predatory beetles and oxyteline Staphylinidae was tested by comparing the numbers recorded in unenclosed and enclosed pads using Wilcoxon signed-ranks tests.

Results

A total of 26 606 beetles was extracted from unenclosed sample pads. These comprised 134 species, representing 100 species of Staphylinidae (22 163 individuals), 13 species of Hydrophilidae (3557 individuals) and 21 species of Histeridae (886 individuals). The Staphylinidae consisted of 79 putative predatory species from five subfamilies (2640 individuals) and 19 species of coprophagous Oxytelinae (19 523 individuals). Analysis of habitat associations and seasonal distribution was restricted to the 44 species and two species complexes (two species in each) for which 20 or more individuals were recorded. The remaining 86 species are listed in Table II.

Thirty-two of the 46 species and species complexes showed significant associations ($P<0\cdot05$) with either vegetative cover (27 species), soil type (13 species) or both (eight species). At $P<0\cdot10$, a further four species showed associations with soil type and two with vegetation type (Appendix). Most staphylinid and all hydrophilid and histerid species that showed a significant association with vegetative cover were more abundant in unshaded than shaded situations. The numbers of species showing significant associations with sand and clay soil were similar in all groups except the histerids in which only sand specialists were demonstrated. Overall, 28 species showed no association with soil type and 16 showed no association with vegetation type.

Fourteen out of 46 species and species complexes showed significant ($P<0\cdot05$) seasonal changes in abundance, and trends in a further four species were significant at $P<0\cdot10$ (Appendix). The majority of staphylinid and all hydrophilid and histerid species that showed a significant seasonal trend in activity were more abundant in hot wet months than cool dry ones.

There was little difference in the occurrence of species between Hluhluwe Game Reserve and nearby pastoral situations. Only three out of 46 species and species complexes were significantly more abundant in the reserve ($P<0\cdot05$) and three significantly more abundant on the farms.

The total numbers of individuals from different taxa varied with habitat and season (Table III). The oxyteline staphylinids were most abundant during summer in unshaded situations on clay soils. The predacious staphylinids also showed a distinct seasonal association with hot wet months but were relatively evenly distributed across soil types and vegetative cover. In contrast, the hydrophilids were most abundant during the cool dry months in unshaded situations, although they showed little soil preference. The histerids were most abundant in unshaded situations during the hot wet season and were evenly distributed between soil types.

The amount of dung removed from sample pads by dung-burying beetles varied with season, soil type and treatment of the pads (Table IV). The removal of dung was negligible in all situations during the five cool dry months and moderate from unenclosed pads on deep sand during the seven hot wet months. In the latter period, dung removal was 60% or more in 28% of pads and 90% or more in 10% of pads. In contrast, little dung was removed from unenclosed pads on clay and from pads enclosed within wiremesh cones on both soil types.

The contingency analysis of the asymmetric effect of dung removal on colonization of pads showed significant heterogeneity in the distribution of ten species and species complexes (Appendix). In these cases, data on associations with soil type, vegetative cover, seasonal abundance and locality were re-analysed using the results from enclosed pads, i.e. those

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TABLE II. *Species of Staphylinidae, Hydrophilidae and Histeridae of which less than 20 species were taken from unenclosed pads of cattle dung in the Hluhluwe region*

Species	Total numbers Unenclosed pads	 Enclosed pads
STAPHYLINIDAE		
Staphylininae		
Philonthus reinecki Schubert (318)	5	2
P. capeneri Last (301)	2	0
P. parvicornis Fauvel (315)	10	1
P. mivutanus Tottenham (310)	1	0
P. nairobiensis Fauvel (312)	10	4
P. densecaudatus Bernhauer (305)	4	1
P. ventralis (Gravenhorst) (325)	1	0
P. caffer Boheman (303)	15	17
Philonthus 4 spp.	3	3
Philonthus (*Spatulonthus*) *maskinius* Tottenham (308)	8	0
P. (*S.*) *bisignatus* Boheman (302)	11	10
P. (*S.*) *peregrinus* Fauvel (316)	5	3
Gabronthus 2 spp.	13	12
Gabrius huendus Tottenham (350)	3	0
Xantholininae		
Phacophallus sp. b (605)	2	0
Thyreocephalus sp. (620)	1	2
Aleocharinae		
Aleochara bicoloripennis Bernhauer (103)	1	0
A. crassa Baudi (107)	4	0
A. puberula Klug (108)	12	9
Aleochara 2 spp.	3	0
Macrophthalmodites melanocephalus Scheerpeltz (175)	6	23
Atheta ?provincialis Cameron (136)	19	41
Atheta 6 spp.	17	15
Atheta indeterm.	4	3
Tinotus minutus Bernhauer (178)	19	15
Falagria coarcticollis Fauvel (160)	11	8
F. crucifera Bernhauer (161)	0	1
F. capicola Tottenham (163)	5	0
F. pseudosulcata Tottenham (166)	2	1
F. liliputana Tottenham (165)	0	1
Eusteniamorpha sp. (164)	3	0
Cordalia ?obscura (Gravenhorst) (172)	12	11
Aleocharinae indeterm. 3 spp.	9	9
Paederinae		
Rugilus minimus (Bernhauer) (520)	7	5
Rugilus 2 spp.	1	1
Lithocharis 5 spp.	29	38
Oxytelinae		
Oxytelus bidentulus Fauvel (220)	19	12
O. simulator Eppelsheim (224)	18	5
O. kawaensis Cameron (239)	1	0
Oxytelus 2 spp.	18	20
Anotylus miriceps (Fauvel) (204)	2	2
A. caffer (Erichson) (202)	0	1
Anotylus 4 spp.	35	25
Carpelimus sp. (251)	9	11
Bledius sp. (253)	1	0
HYDROPHILIDAE		
Sphaeridium senegalense Castelnau (715)	7	0
Sphaeridium sp. a (713)	10	6
Cercyon 2 spp.	33	6
Cryptopleurum sp. (721)	2	0
HISTERIDAE		
Abraeus bacanioformis Bickhardt (802)	11	5
Abraeus 2 spp.	4	1
Saprinus cupreus Erichson (870)	1	0
Tribulus amnicola Lewis (890)	1	1
Atholus sp.	10	2
Hister furciger Marseul (831)	14	1
H. tropicus Paykull (838)	5	1
H. nomas Erichson (835)	2	0
H. ignavus Fåhraeus (832)	4	2
H. obesus Marseul (836)	3	0
Pactolinus caffer (Erichson) (857)	1	0
Macrolister gigas Paykull (854)	1	0
Acritus 2 spp.	4	0

The number in brackets after each species name is the Dung Beetle Research Unit code number for specimens of that species lodged with the Australian National Insect Collection, Canberra.

TABLE III. *The distribution of coprophilous beetles in relation to soil type (clay vs sand), vegetative cover (shaded vs unshaded) and season of year (hot wet: November to March vs cool dry: May to September)*

	Percentage of total number trapped			
	On clay soil	In unshaded situations	During the hot wet season	Total nos
Oxyteline staphylinids	74·7	80·1	62·4	19419
Other staphylinids*	54·6	52·8	70·1	2382
Hydrophilidae	55·7	89·4	29·3	3505
Histeridae	53·4	74·6	90·4	825

The data refer only to the 46 most abundant species (see text).
* Comprising the subfamilies Staphylininae, Xantholininae, Aleocharinae, Tachyporinae and Paederinae.

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TABLE IV. *The mean percentage removal of cattle dung from sample pads placed in the Hluhluwe region between December 1981 and December 1982*

		Mean percentage of dung removed			
		Deep sand		Clay and clay-loam	
Season	Treatment of sample pads	Unshaded	Shaded	Unshaded	Shaded
Hot wet months (November–March)	Unenclosed	39	26	17	8
	Enclosed by wiremesh	10	7	4	0
Cool dry months (May–September)	Unenclosed	6	1	1	0
	Enclosed by wiremesh	0	0	0	0

with minimal dung removal. In no case did this second analysis give a result substantially different from that derived using the data for unenclosed pads.

The enclosure of pads by meshwork cones reduced the number of beetle colonists overall by 37% and was statistically significant ($P<0{\cdot}05$) in the case of 26 species (Appendix).

Discussion

This study has demonstrated clear habitat associations and changes in seasonal abundance for a number of coprophilous staphylinid, hydrophilid and histerid beetles, many of which belong to genera known to contain predators or parasites of dung-breeding flies. As the Hluhluwe area is roughly homoclimatic with coastal central Queensland, it is likely that many of these species could become established in Australia. Coastal Queensland has a substantial cattle industry based chiefly in open pastures on clay-loam where *H. i. exigua* is both abundant and pestilent, particularly during summer. Several species of predatory dung beetles from the Hluhluwe region were shown to be associated with clay soils in unshaded situations (Appendix). These species may have potential to augment control of *H. i. exigua* in Queensland where there is a deficiency in the predatory dung beetle fauna (Doube, 1986). A number of these species from the Hluhluwe area have been shown readily to kill the immatures of the closely-related, African buffalo fly, *H. thirouxi potans* (Bezzi), in laboratory experiments (Doube & Huxham, 1987).

The biological response which determines the habitat associations observed for coprophilous staphylinids, hydrophilids and histerids in the Hluhluwe area remains unknown. In other groups of dung beetles, differences in distribution of numbers between baits exposed directly to the sun and those shaded by tall vegetation have been attributed to microclimatic variables such as humidity, dung temperature and light intensity (e.g. Landin, 1961; Howden & Nealis, 1975; Doube, 1983; Lumaret, 1983). Lumaret (1980) found that scarabaeine dung beetles were distributed according to the height and density of vegetation in Corsica. The manner in which shade influences the dung micro-habitat was illustrated by Key (1982), who showed that, in cool exposed habitats at high altitude in Norway, dung beetle species previously described as shade specialists in low-lying regions were numerically dominant over species previously described as associated with unshaded situations at low altitude.

An explanation for the soil associations observed at Hluhluwe is rather more tentative than that for vegetation associations since most staphylinid, hydrophilid and histerid species enter the soil beneath dung pads only in order to pupate and, perhaps in some cases, to oviposit or escape harsh conditions. Soil type may directly affect pupal survival in these taxa since it is known to affect the survival of immature scarabaeine dung beetles (Fincher, 1973). Indirect influences of soil type on predator abundance are also a possibility. Roth (1983) has shown that activity by dung-burying beetles reduces breeding success of the staphylinid *Philonthus flavolimbatus* Erichson in America. The much greater dung burial in deep sand in the Hluhluwe area might therefore have a greater influence on breeding by predatory taxa than on clay. It can only be concluded that a complex of local factors is

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probably responsible for observed soil associations in some predatory taxa since, for example, *Cilea intermedia* Last was significantly associated with clay in the Hluhluwe area ($P<0{\cdot}05$) but was seven times as abundant on deep sand as on clay near Pretoria (Davis, unpubl. data).

Reduced levels of colonization of mesh-covered dung pads by most species is presumably a response to the wire mesh and the modified microhabitat around the pads. For example, on a sunny afternoon, light intensity was almost 50% lower under the cones than in direct sunlight. As the overall influence of the cones on species distribution is unclear, we did not use data from enclosed pads in the analysis of habitat associations except for those species for which the level of dung removal appeared to influence the number of pad colonists.

The present study constitutes a preliminary investigation of habitat associations and seasonal abundance of the predatory dung beetle fauna in the Hluhluwe area. Sampling was conducted in only a small range of habitats in a limited area on few occasions at irregular intervals. Although species with potential as control agents of *H. i. exigua* in Australia were identified, data were sufficient to analyse the distributions of less than 40% of the species recorded. Hence there is a need for further information on the predatory dung beetle fauna of the Natal lowlands, particularly in view of apparently inconclusive evidence on soil associations in some species.

Acknowledgements

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APPENDIX. DISTRIBUTION OF 44 SPECIES AND TWO SPECIES COMPLEXES OF COPROPHILOUS BEETLES BETWEEN DIFFERENT SOIL TYPES, VEGETATION TYPES, SEASONS, LOCALITIES AND PAD TREATMENTS IN THE HLUHLUWE REGION

Species		Total numbers in unenclosed pads				Association				Total numbers	
		Unshaded sand	Shaded sand	Unshaded clay	Shaded clay	Soil	Vegetation	Season	Locality	Unenclosed pads	Enclosed pads
STAPHYLINIDAE											
Staphylininae											
Philonthus natalensis Boheman (314)		3	0	19	3	clay*	unshaded*	none	none	25	10
P. (Spatulonthus) sanamus Tottenham (319)		24	2	35	10	none	unshaded*	none	none	71*	21
P. (S.) minutus Boheman (309)		46	11	80	34	none	unshaded*	hot wet*	none	171*	61
Gabronthus mgogoricus Tottenham (360)		42	25	25	49	none	none	hot wet*	none	141*	53
Gabrius sp. a (351)		2	91	0	135	none	shaded*	hot wet*	none	228	174
Xantholininae											
Phacophallus sp. a (604)		28	6	12	11	none	none	hot wet*	none	57*	11
Aleocharinae											
Aleochara mahugi (Likovsky) (109)		26	4	15	1	none	unshaded*	hot wet*	reserve	46*	11
A. trivialis Kraatz (118)		80	4	26	4	none	unshaded*	none	none	114*	57
A. afra (Eichelbaum) (106)		8	36	15	19	none	shaded	hot wet*	farms	78	40
A. sublaevipennis Fauvel (117)		10	0	24	2	none	unshaded*	none	none	36	18
Atheta viatica Fauvel (145)		24	0	0	0	sand	unshaded	none	none	24	25
A. graciosa Scheerpeltz (134)		2	1	14	3	clay	unshaded*	none	none	20	26
A. ruparia Cameron (137)		0	66	4	14	none	shaded*	none	none	84	50
A. nigerrima (Aubé) (135)	u	13	2	10	2	none	unshaded*	none	none	27	20
	c					(none)	(none)	(none)	(none)		
Atheta (Acrotona) sp. (130)		73	20	11	9	sand*	none	none	none	113*	55
Atheta (Microdota) sp. a (131)[b]	u	6	48	3	17	sand	shaded*	none	none	74	48
	c					(sand)	(shaded*)	(none)	(farms)		
Atheta (Microdota) sp. b (132)		33	24	53	44	none	none	cool dry	none	155	104
Tinotus clavicornis Cameron (177)		27	11	0	2	sand*	none	none	farms*	40*	15
Aleocharine sp. a (150)		0	92	0	2	sand*	shaded*	none	farms*	94	36
Aleocharine sp. b (179)		1	2	3	20	none	none	none	none	26*	5
Falagria kawaensis (Cameron) (162)[b]	u	7	8	2	3	none	none	none	none	20	40
	c					(none)	(none)	(none)	(none)		
Autalia capensis Tottenham (170)		15	17	13	38	none	none	none	none	83	52
Tachyporinae											
Cilea ?medialis Tottenham (402)		0	41	7	51	none	shaded*	hot wet*	reserve*	99	95
C. ?sculpta (Bernhauer) (404)		15	19	73	6	none	unshaded*	hot wet*	none	113*	47
C. intermedia Last (401)[b]	u	3	20	35	20	clay*	none	none	reserve*	78	101
	c					(clay*)	(none)	(none)	(reserve*)		
C. ?picta (Erichson) (403)		34	10	238	53	clay*	unshaded*	none	none	335*	173
Paederinae											
Lithocharis kawaensis Cameron (501)		0	0	16	14	clay	none	none	none	30	13

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Species		Total numbers in unenclosed pads				Association				Total numbers	
		Unshaded sand	Shaded sand	Unshaded clay	Shaded clay	Soil	Vegetation	Season	Locality	Unenclosed pads	Enclosed pads
Oxytelinae											
Oxytelus puncticeps Kraatz (223)[h]	u	10	8	30	62	none	none	cool dry*	none	110*	31
						(none)	(shaded)	(cool dry*)	none		
O. varipennis Kraatz (230)[h] & *O. depauperatus* Wollaston (221)	u	170	9	628	66	clay*	unshaded*	none	none	873*	406
	c					(clay*)	(unshaded*)	(none)	(none)		
O. planus Fauvel (222)		79	171	60	29	none	none	hot wet*	none	339*	159
Anotylus okahandjanus (Bernhauer) (205)		70	23	5	0	sand*	unshaded*	none	none	98	185
A. latiusculus (Kraatz) (203)[h]	u	2325	279	8948	1555	clay	unshaded*	none	none	13107*	10411
	c					(clay*)	(unshaded*)	(none)	(none)		
A. bacillus (Bernhauer) (201)[h]	u	1394	382	1837	1279	none	unshaded*	none	none	4892*	2550
	c					(none)	(unshaded*)	(none)	(none)		
HYDROPHILIDAE											
Sphaeridium caffrum Castelnau (711)		467	2	284	28	clay*	unshaded*	none	none	781*	33
S. ornatum Boheman (714)		39	0	15	0	none	unshaded*	hot wet*	none	54*	8
S. exile Boheman (712)		8	0	11	1	none	unshaded*	none	reserve*	20*	4
Sphaeridium sp. b (716)		51	1	4	0	sand*	unshaded*	none	farms*	56	7
Cercyon atricapillus (Marsham) (701)		908	41	390	67	sand	unshaded*	none	none	1406*	745
C. hova Régimbart (702)		75	5	248	72	clay*	none	none	none	400	146
Cryptopleurum suturatum Régimbart (720)		9	1	162	5	none	none	hot wet*	none	177*	16
Pachysternum capense (Mulsant) (730)[h]	u	279	65	183	84	none	none	none	none	611*	126
	c					(none)	(none)	(none)	(none)	(none)	
HISTERIDAE											
Chaetabraeus setulosus (Fåhraeus) (820)		10	2	3	5	none	none	hot wet	none	20	6
C. spiculator (Thérond) (821)	u	154	8	229	8	none	unshaded*	hot wet*	none	399*	67
	c					(none)	(unshaded*)	(hot wet)	(none)		
Abraeus curtulus Fåhraeus (801) & *Abraeus* sp. nr *curtulus* (804)		91	105	59	60	sand*	unshaded	hot wet*	none	315*	69
Hypocacculus metallescens (Erichson) (861)		18	0	8	0	none	unshaded*	hot wet	none	26*	1
Acritus ?apicestrigosus Bickhardt (810)		32	21	11	1	sand*	unshaded*	hot wet*	none	65*	32

*Statistically significant association with soil type, vegetation type, season, locality or pad treatment ($P<0{\cdot}05$) (Wilcoxon signed-ranks tests and Mann-Whitney *U* tests). Association without asterisk indicates a statistically significant preference for soil type, vegetation type, season or locality ($P<0{\cdot}10$).

'None' indicates no significant association.

[h] Species in which there was statistically significant heterogeneity in distribution of numbers between pad treatments on different soil types ($P<0{\cdot}05$), indicating a possible influence of dung removal on numbers recorded (2 × 2 contingency tests).

u Data from unenclosed dung pads.

c Data from enclosed dung pads.

The number in brackets after each species name is the Dung Beetle Research Unit code number for specimens of that species lodged with the Australian National Insect Collection, Canberra.

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APPENDIX 6

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Nesting of Afrotropical *Oniticellus* (Coleoptera, Scarabaeidae) and its evolutionary trend from soil to dung

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ABSTRACT. 1. *Oniticellus egregius* Klug constructs brood ovoids of dung in the soil immediately under the edge of animal droppings. Each successive brood ovoid is enveloped within a soil shell. After completion of brood construction, loose earth is cleared from around the broods to produce a brood chamber. The immatures are then abandoned as eggs or first instar larvae.

2. *O.planatus* Castelnau and *O.formosus* Chevrolat usually construct brood balls of dung within animal droppings. Each brood is progressively enlarged by the addition of further dung after egg-laying. This enlargement is slight in *O.planatus* and marked in *O.formosus*. Parental females of both species remain in the brood chambers during development of the immatures which are abandoned principally as pupae.

3. Under very moist experimental conditions, *O.planatus* buries dung and constructs broods shallowly in the soil. Such nests are frequently connected to the pad by a short tunnel.

4. From a consideration of behavioural patterns it is suggested that the specialized nesting habits of these species have been derived from those of dung-burying ancestors similar to the modern genus, *Euoniticellus*, through reduction and loss of tunnelling in the soil.

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Key words. Nesting, Coleoptera, Scarabaeidae, *Oniticellus*, dung, evolution.

Introduction

Species of the subfamily Scarabaeinae show complex nesting behaviour. The majority of species are coprophilous and lay their eggs in modelled portions of dung, termed broods. The broods of most scarabaeine taxa are constructed at the ends of tunnels in the soil. However, nesting behaviour of the genus, *Oniticellus* (tribe Oniticellini, subtribe Oniticellina), is exceptional in that broods are constructed within or immediately beneath the dropping (Gardner, 1929; Bornemissza, 1969; Davis, 1977; Rougon & Rougon, 1982, 1983; Lumaret & Moretto, 1983; Klemperer, 1983). Other members of the subtribe nest in a similar manner to *Oniticellus* as in the genus, *Tragiscus* (Davis, 1977), or they construct brood ovoids from dung packed into the branched tips of tunnels as in the genera, *Euoniticellus* (Rougon & Rougon, 1982, 1983;

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tion of *O.planatus*, ten pairs of beetles were introduced into 0.5 litre pads of cattle dung to which water had been added to give a moisture content of 84.1% by mass. These pads were placed in plastic containers (11×11×13.5cm deep) on an 8cm deep layer of slightly moistened sand (3.7% water content by mass) so that the pads almost completely covered the surface of the sand. After 14 days the position of the brood chambers was recorded.

Results

Nesting behaviour of Oniticellus egregius

Brood construction by *O.egregius* is illustrated in Fig. 1. The female excavated a small pit in the soil under the edge of the dropping (Fig. 1a). This was lined with dung (Fig. 1b) which she compressed against the sides of the pit using the fore-legs and the head which are dorso-ventrally flattened. An egg was laid at the base of the pit supported on its end by a colloidal mass of dung particles (Fig. 1c). The top of the brood was sealed with dung to enclose the egg within a chamber (Fig. 1d) and the soil adhering to the outside was pressed down to form a shell (Fig. 1e). Further brood ovoids were constructed in the same manner adjacent to the first (Fig. 1f). In fresh horse dung, *O.egregius* commenced breeding on days 1 or 2 (Fig. 2). The number of broods produced by each female increased steeply from days 1 to 4. Over the same period there was a decrease in the number of females disturbed in the act of brood construction. Between days 4 and 6, loose soil was cleared from around the broods to produce a brood chamber with a single entrance (Fig. 1g). The female then abandoned the chamber and departed from the dung. At this time the immatures were mostly eggs or first instar larvae (Table 1). During nesting, the mean length of brood ovoids on day 2 was significantly greater ($P<0.05$) (Scheffe's tests) than those on days 3–6 (Fig. 3). In fresh cattle dung, *O.egregius* shredded and constructed pits in the edge of the pad over days 1–3. Breeding by some females commenced on days 2–3 but 30% of females had still not started brood construction by day 3. Results beyond day 3 have not been reported due to high mortality.

Duration of residence in cattle dung during breeding was slightly longer than that in horse dung (Table 1). Females resided in both dung types for slightly longer periods than males. The mean size of the broods produced in cattle dung on dry soil was about 23% larger than those from horse dung on moist soil (Fig. 3). Although mean moisture content of fresh horse dung (70.00±0.9% by mass, $n=6$) was less than that of fresh cattle dung used for breeding *O.egregius* (77.3±0.8%, $n=3$), the mean moisture content of brood ovoids over days 1–6 was similar for both dung types (50.1±4.3% in horse dung, $n=57$; 48.0±4.0% in cattle dung, $n=16$). In both

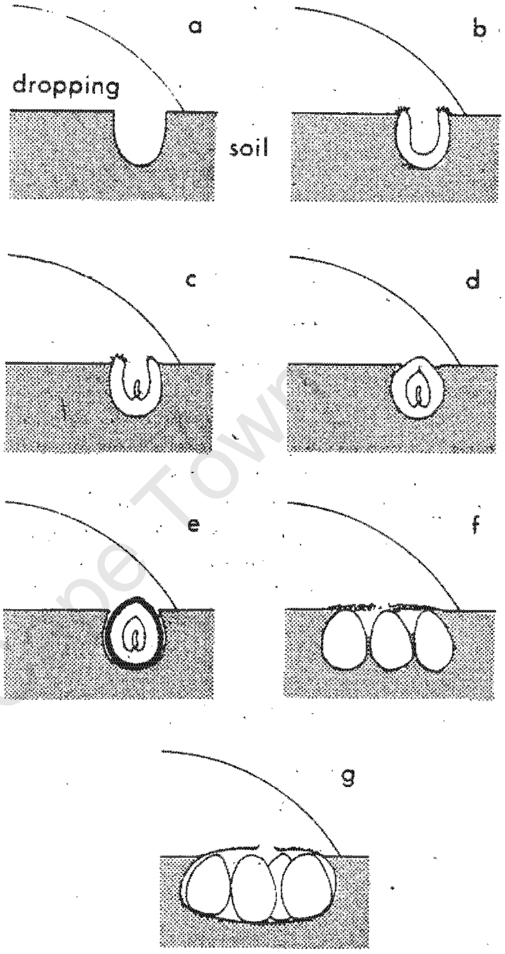

FIG. 1. Manner of brood ovoid construction by *Oniticellus egregius* Klug: (a) pit excavated in soil; (b) pit lined with dung; (c) egg laid; (d) brood sealed; (e) brood enveloped in soil shell; (f) more broods constructed; (g) loose soil cleared from around broods to form chamber.

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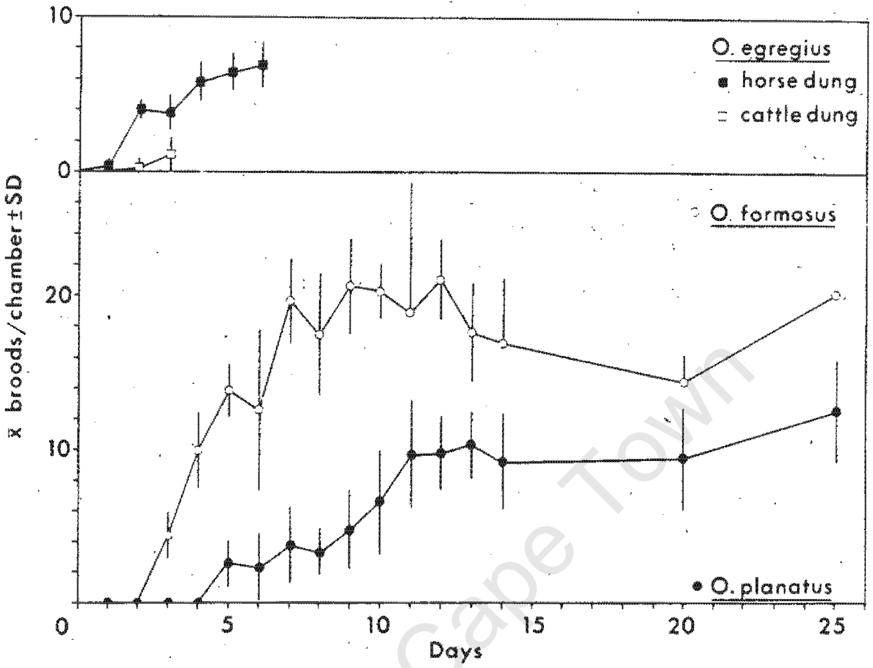

FIG. 2. Mean number ±SD of brood ovoids and balls per brood chamber on different days during nesting by *Oniticellus* spp. (see method 2).

dung types the majority of brood chambers were positioned wholly within the soil under the edge of the dropping (Table 2).

Nesting behaviour of Oniticellus planatus

Females of *O.planatus* tunnelled the edges of fresh cattle pads over days 1–11. Brood construction commenced between days 5 and 12 and is illustrated in Fig. 4. A small area in the dung was shredded (Fig. 4a). Some of the shreds were pressed against the base of the incipient brood chamber to form a thick circular mat (Fig. 4b). The female compressed the centre of this mat of shreds then laid an egg supported on its end by a colloidal mass of dung particles (Fig. 4c). The egg was enclosed within a chamber to produce a roughly spherical brood ball (Fig. 4d). Further brood balls were constructed in a similar manner adjacent to the first. The completed brood chamber was smooth-walled with a single entrance and little or no loose dung fibre between the snugly-fitting brood balls (Fig. 4e). The mean number of brood balls per chamber and the number of females in the nest showed a steady increase until day 11 (Fig. 2). Between days 12 and 14, 20 and 25, all females were found in the nest. At the time of emergence of parental females from the dung pad (Table 1), the immatures were largely pupae or callow adults. Between days 5 and 14 of nesting, there was a slight but steady increase in the mean diameter of the broods (Fig. 3). The broods on days 12–14 were about 20% larger than those on days 5 and 6. Except for the comparison between days 5 (due to low sample size, $n=5$ broods) and 12, these differences were significant ($P<0.05$) (Scheffe's tests). There was also a significant decrease in mean diameter of brood balls ($P<0.05$) from days 13 and 14 to days 20 and 25. The moisture content of the broods over days 5–14 was 65.0±3.0% by mass ($n=83$). Duration of residence in dung pads by males was much shorter than that of females (Table 1).

In natural cattle dung with a mean moisture content of 78.9±1.6% by mass ($n=16$), brood chambers of *O.planatus* were mostly constructed wholly within the pad (Table 2). In very moist dung (84.1%), *O.planatus* constructed brood chambers wholly within the soil, in most cases connected to the pad by a short dung-lined tunnel up to 2.5 cm long.

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TABLE 1. Duration of residence in dung by *Oniticellus* spp. during nesting at 30°C and stage of development of immatures at the time of departure of the parental female (see method 1).

Species and treatment	Duration of residence in dung (days) (x̄ (SD))		Developmental stage of immatures at departure time of parental females (x̄ per brood chamber (SD))								No. of brood chambers observed
	Males	Females	Egg	First instar larva	Second instar larva	Third instar larva	Prepupa	Pupa	Callow adult	Filial adult (emerged)	
Horse dung											
O.egregius	4.2 (0.9)	5.1 (0.9)	2.0 (1.4)	2.3 (1.4)	0.2 (0.6)	0	0	0	0	0	14
Cattle dung											
O.egregius	5.5 (1.1)	6.3 (0.7)	—*	—	—	—	—	—	—	—	7
O.planatus	10.5 (3.0)	31.1 (3.9)	0	0	0	0.1 (0.3)	0.9 (2.3)	7.9 (3.5)	2.3 (3.2)	1.1 (3.5)	11
O.formosus	14.7 (3.9)	28.6 (3.3)	0	0	0	0.5 (1.3)	1.4 (2.6)	11.5 (4.3)	0	0	8

* No observations made

Nesting behaviour of Oniticellus formosus

Females of *O.formosus* shredded the edges of fresh cattle pads over days 1–3. Breeding commenced on days 3–4. A single observation was made of a circular mat of dung shreds which was presumed to be a brood under construction in a manner similar to that of *O.planatus*. Loose dung fibre lay between brood balls in the completed brood chamber. The number of brood balls per chamber increased between days 3 and 7 (Fig. 2). Between days 4–14, 20 and 25, the majority of females were found in the nest. When parental females left the pads, the immatures were largely pupae (Table 1). Between days 3 and 14 of nesting, there was a steady increase of up to 80% in the diameter of brood balls (Fig. 3). Most daily increases in diameters of broods were significantly different from one another ($P<0.05$) (Scheffe's tests). There was a significant decrease in diameter of broods from days 13–14 to days 20 and 25 ($P<0.05$). The initial size of brood balls of *O.formosus* was about 25% smaller than those of *O.planatus*, but those of days 13–14 were about 10% larger (Fig. 3). The mean moisture content of the broods between days 3 and 14 was 65.1±2.5% by mass ($n=120$) and, like the duration of residence in dung pads by males (Table 1), was similar to that of *O.planatus*. Brood chambers were mostly constructed wholly within the edges of dung pads with the pad forming the inner walls and a mass of shreds the outer walls (Table 2).

Discussion

Influence of study methods on nesting behaviour of Oniticellus

In the laboratory, most brood chambers of *O.planatus* were constructed within the dung and those of *O.formosus* in a mass of shreds at the edge of the pad (Table 2). In the field, brood chambers of *O.planatus* often straddle the dung/earth interface (Cambefort, 1982) and those of *O.formosus* are positioned deeply within the pad (Rougon & Rougon, 1982, 1983) without extensive external shredding. The differences probably result from laboratory methods in which *Oniticellus* species were introduced into fresh dung which was dried by constant, high, ambient temperature whereas in the field, *O.planatus* and *O.formosus* colonize older

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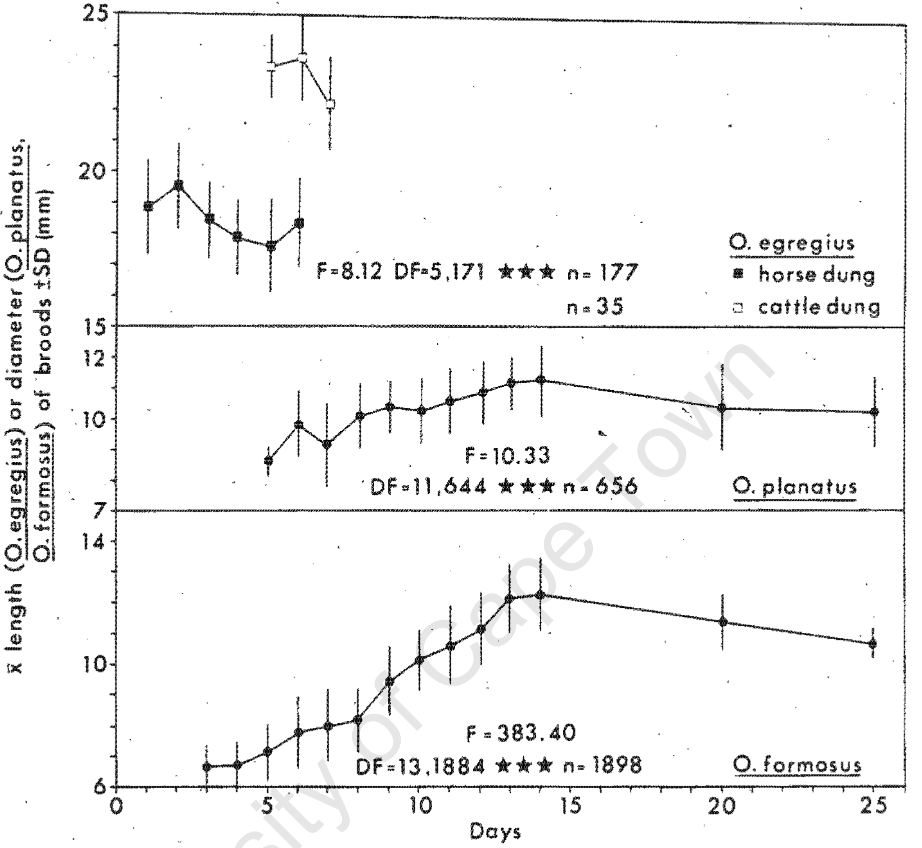

FIG. 3. Mean length ±SD of brood ovoids (*Oniticellus egregius* Klug) and mean diameter ±SD of brood balls (*O.planatus* Castelnau and *O.formosus* Chevrolat) on different days during nesting. Results of analysis of variance in size of broods with time (***$P<0.001$).

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TABLE 2. Variation in position of brood chambers of *Oniticellus* spp. under different dung and soil treatments.

Species	Treatment	Position of brood chamber (%)					No. of observations
		A	B	C	D	E	
O.egregius	Horse dung, moist soil, large container	0	84.4	11.3	4.3	0	115
O.egregius	Cattle dung, dry soil, large container	0	61.1	27.8	11.1	0	18
O.planatus		0	4.4	13.3	80.0	2.3	90
O.formosus		0	0	4.8	1.6	93.6	125
O.planatus	Watered-down cattle dung, moist sand, small container	77.8	22.2	0	0	0	9

(A) Wholly within soil, connected to dung pad via short tunnel. (B) Wholly within soil, opening directly into dung pad. (C) Half in soil, half in dung pad. (D) Wholly within dung pad. (E) At edge of pad, in mass of dung shreds.

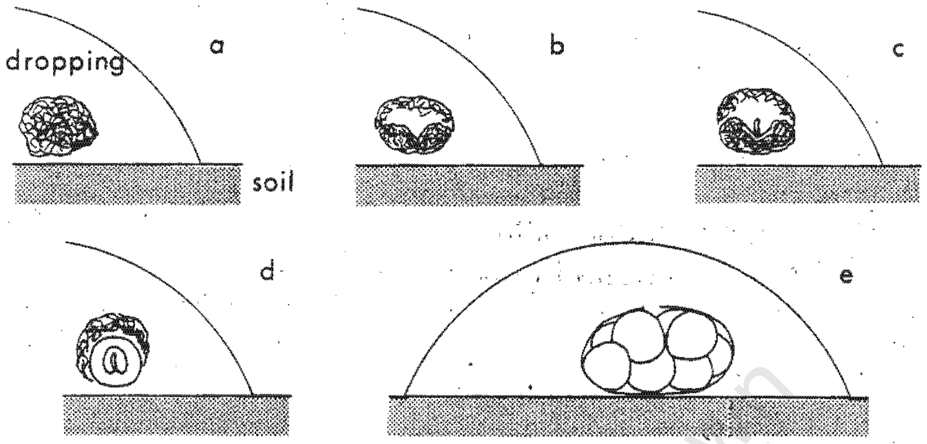

FIG. 4. Manner of brood ball construction by *Oniticellus planatus* Castelnau: (a) small area of dung shredded; (b) mat of shreds constructed and centre of mat compressed; (c) egg laid; (d) brood sealed and rounded off; (e) more broods constructed in chamber.

TABLE 3. Summary of morphological and behavioural characteristics of three Afrotropical *Oniticellus* spp.

Species	Size of prosternal spur	Tunnelling or shredding behaviour in dung	Soil shell around broods	Position of brood chamber	Linear increase in size of broods after egg-laying	Main developmental stage of immatures at parental departure
O.egregius	Large	Shredding	Present	Soil	None	Egg/first instar larva
O.planatus	Small	Tunnelling	Absent	Dung	20%	Pupa
O.formosus	Very small	Shredding	Absent	Dung	80%	Pupa

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dung (Rougon & Rougon, 1982; Davis, unpublished data) which is dried by exposure to radiant heat from the sun in addition to ambient temperature. In contrast to the other two species, nesting behaviour of *O.egregius* was observed to be similar in both the laboratory and the field.

In the laboratory, commencement of breeding by *O.formosus* was synchronized whereas there was a wide range in commencement times of breeding in *O.planatus*. Shredding activity by *O.formosus* probably accelerated dung desiccation allowing an early start to nesting, whereas the tunnelling activity of *O.planatus* would have had little effect on dung desiccation with a consequent variable delay in the initiation of brood production dependent on the moisture content of the pad.

O.planatus and *O.formosus* produced between 2 and 3 times more broods in 14-day-old laboratory pads (Fig. 2) than in 14-day-old field pads for which a combined mean of 5.5±4.0 *Oniticellus* brood balls was recorded (Davis, unpublished data). This was probably a consequence of the dung drying more slowly in the laboratory and hence remaining suitable for brood production for a longer period. Variations in the number of broods per nest in both the laboratory and the field is probably due to differences in the initial moisture content of the dung and the rate at which it dried. Differences in the ages of parent females probably also influenced the numbers of broods per nest as Davis (1977) has shown that mean brood production per female increases up to the third chamber per life history in both *O.formosus* and *O.planatus* then declines.

Specializations in the nesting behaviour of Oniticellus

Surface nesting habits and their associated behavioural specializations are a radical departure from the comparatively simple nesting behaviour of some closely-related oniticelline genera, e.g. *Euoniticellus*, in which brood ovoids are produced by packing dung into the tips of tunnels in the soil. The broods of most other Scarabaeinae are also constructed from dung buried in tunnels excavated under the dropping or from portions of dung rolled some distance from the dropping before burial. The only genera showing similar surface nesting habits to *Oniticellus* are some proximal relatives in the Oniticellini, e.g. *Tragiscus* (Davis, 1977), *Drepanocerus* (Lumaret & Cambefort, 1980; Cambefort & Lumaret, 1983), *Drepanoplatynus* (Cambefort & Lumaret, 1983), *Cyptochirus* (Cambefort, 1981) and the distantly related eurysternine, *Eurysternus* (Halffter, 1977; Halffter *et al.*, 1980). Species of this central and southern American genus construct brood balls within chambers straddling the dung/earth interface. Their nests are superficially convergent with those of some *Oniticellus*. However, nesting behaviour differs in many details as might be expected given the differing evolutionary lineage of the two genera (Zunino, 1983). Behavioural evidence for their positions in the phylogeny of the Scarabaeinae is provided by the manner of ball construction. Balls of *Eurysternus caribaeus* (Herbst) are cut from dung (Halffter *et al.*, 1980) in a manner typical of ball-rolling genera. However, balls and ovoids of *Oniticellus* are built from particles of dung similarly to those of the closely related genus, *Onthophagus* (Zunino, 1983).

The nesting specializations of *Oniticellus* species have possibly developed in response to the extreme physical conditions encountered through nesting within or immediately beneath dung. These specializations include the housing of broods within a chamber, cf. all *Oniticellus*, the coating of brood ovoids with a soil shell, cf. *O.egregius*, and the progressive addition of dung to brood balls after egg-laying as a stage in the parental care of the broods, cf. *O.planatus* and *O.formosus*. Similar specializations in the nesting of a number of distantly related, soil-tunnelling genera of diverse evolutionary lineage (Zunino, 1983), e.g. *Copris, Canthon* (Halffter & Edmonds, 1982), have probably been acquired independently.

Genera of several scarabaeine tribes construct brood ovoids or balls in a chamber, i.e. Oniticellini, Coprini, Scarabaeini, Eurysternini. As a rule, the broods of non-brooding species are coated in a soil shell as in *O.egregius*, *Phanaeus* spp. (Halffter & Edmonds, 1982) and *Cartharsius* spp. (Halffter & Edmonds, 1982, quoting G. F. Bornemissza and H. H. Aschenborn) although there are exceptions, e.g. *Catharsius molossus* (L.) which neither tends its broods nor coats them in a soil shell. In brooding species, the broods are naked as in *O.planatus*, *O.formosus* and *Cephalodesmius armiger* Westwood (Monteith & Storey, 1981) with further dung added later or naked at first with a soil shell added during larval development, e.g. *Copris* spp. (Halffter & Edmonds, 1982), *Synapsis tmolus* (Fisher) (Siyazov, 1913), *Heliocopris hamadryas* (Fabricius) and *H.japetus* (Klug) (Klemperer & Boulton, 1976). Again, exceptions have been recorded, e.g. *Copris boucardi* Harold, which coats its broods with a soil shell before oviposition (Halffter & Edmonds, 1982).

Soil shells around broods may serve a number of functions. They probably reduce desiccation and inhibit fungal growth (Halffter & Matthews, 1966). They may protect the broods of *O.rhadamistus* (Fabricius) against termites (Lumaret & Moretto, 1983). According to Cambefort (1982), the broods of *O.cinctus* (Fabricius) are enveloped in a clay shell although neither Bornemissza (1969) nor Klemperer (1983) record similar observations.

The progressive addition of dung to brood balls after egg-laying is an uncommon behavioural characteristic in the Scarabaeinae. Besides *O.planatus* and *O.formosus* it has only been recorded in other oniticelline species, *O.cinctus* (Klemperer, 1983), *O.pictus* Hausman and *Tragiscus dimidiatus* Klug (Davis, 1977) and the Australian canthonine, *Cephalodesmius armiger* (Monteith & Storey, 1981). This mechanism may increase viability of the broods by reducing desiccation of the larval food supply. It would thus have a similar function to a soil shell. Differences in the amount of increase in brood diameter between species may be related to differences in nest position or climatic distribution. No biologically significant trend could be recognized in the differences between sizes of *O.egregius* broods.

Parental care has been recorded from the Oniticellini, Coprini, Scarabaeini and Eurysternini. The advantages gained from parental presence during the development of immature *O.planatus* and *O.formosus* remain unclear. However, the removal of brooding females from

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the nests of *Copris* species appears to decrease the viability of the broods (Halffter & Edmonds, 1982). Some of the functions of parental care are probably similar to that of a soil shell, e.g. retarding the growth of fungus (von Lengerken, 1954; Halffter & Edmonds, 1982). Other functions include orientation and defence of the broods and repairs to the nest, cf. *Copris lunaris* (L.) (Klemperer, 1982). Indirect parental care of immature Scarabaeinae has been identified as subsocial behaviour by some authors (Klemperer, 1982, 1983; Sato & Imamori, 1987). However, this remains at a primitive level compared with many social Hymenoptera (Klemperer, 1982).

The role of *Oniticellus* males in nest construction remains uncertain. In the earlier part of the nesting cycle, males of *O.planatus* were often recorded together with the female in the brood chamber, whereas the males of *O.formosus* were often recovered from dung shreds bordering the brood chamber. Males of *O.egregius* were usually recovered from the dung although they were occasionally found with the broods or together with the female in a brood under construction.

Trends in nesting behaviour in Oniticellus

Davis (1977) recognized three groups within the genus, *Oniticellus*, based on morphological and behavioural differences. *O.egregius* and the Oriental *O.rhadamistus* (Lumaret & Moretto, 1983), which comprise group 1, have a large prosternal spur and construct brood ovoids or balls in chambers in the soil immediately under the edge of droppings. Individual broods of both species are enveloped in a soil shell. *O.pseudoplanatus* Balthasar (Cambefort, 1982), *O.planatus* and the Oriental *O.cinctus* (Gardner, 1929; Bornemissza, 1969; Cambefort, 1982; Klemperer, 1983), comprise group 2. The prosternal spur is very small and each species constructs brood balls within chambers in dung pads or straddling the dung/earth interface. Most authors do not record a soil shell around the broods. *O.pictus* (Davis, 1977) and *O.formosus* (Rougon & Rougon, 1982, 1983) which comprise part of group 3, have a vestigial prosternal spur and construct brood balls within chambers in dung pads. Nesting behaviour of the Oriental, *O.tessellatus* Harold, the third member of group 3 has not been described. Janssens (1953) considers that there has been an evolutionary trend towards reduction of the prosternal spur in *Oniticellus* species. If correct, this would point to a parallel trend in brood chamber position from soil to pad.

Morphological and behavioural characteristics of three Afrotropical species of *Oniticellus* are summarized in Table 3. This updates a similar table published in Halffter & Edmonds (1982).

Evolution of nesting behaviour in Oniticellus

Cambefort (1982) and Cambefort & Lumaret (1983) have suggested that the nesting behaviour of *Drepanoplatynus* and *Drepanocerus* (subtribe Drepanocerina) represents the ancestral breeding pattern of the Oniticellini. This is perhaps because these species produce single brood ovoids either in a pit immediately under dung (Cambefort & Lumaret, 1983) or at the end of a short tunnel under dung (Lumaret & Cambefort, 1980). This is considered to be the simplest nesting behaviour shown by the Scarabaeinae (Halffter & Edmonds, 1982).

According to Cambefort (1982) and Cambefort & Lumaret (1983), two evolutionary pathways have been followed from this type of nesting. One has led to the soil-tunnelling genera, *Euoniticellus, Liatongus* and *Tiniocellus* (subtribe Oniticellina). The other has led to soil surface nesting of *Oniticellus* and *Tragiscus* (Oniticellina) via *Cyptochirus* (Drepanocerina), a genus which produces multiple broods in a soil-coated dung cake housed in a chamber immediately under dung (Cambefort, 1981). As pointed out by Cambefort himself (1982), this hypothesis transcends the accepted taxonomic relationships of the genera by intermingling elements of the two main subtribes. It is therefore suggested that the specialized nesting behaviour of *Oniticellus* has, in fact, evolved directly from dung-burying ancestors similar to the modern genus, *Euoniticellus*. This is consistent with both the taxonomy of the Oniticellini and with experimental evidence.

All three species of *Oniticellus* examined during the present study construct broods in the same basic manner. Dung is compressed against the earth or pad to form a dung-walled cup in which an egg is laid. This egg is then enclosed within a chamber to form a brood. This is essentially the manner of brood construction in most Oniticellini and Onthophagini studied to date, many of which produced their broods at the ends of tunnels in the soil. It is suggested that *Oniticellus* species have evolved from such ancestors through reduction or loss of tunnelling into the earth. This trend has been paralleled by the development of breeding specializations.

This conclusion is supported by behavioural characteristics of all three species examined in the present study. *O.egregius* still packs dung into pits in the soil as a first stage in brood construction. Its behaviour is less complex than that of *O.planatus* whose nests are usually intimately associated with dung pads. However, under certain experimental conditions, *O.planatus* abandoned its normal behaviour and constructed a nest in the soil connected to the pad by a short tunnel. Manipulation of dung and soil moisture failed to alter the dung nesting habits of *O.formosus* which is considered to show the most highly evolved behaviour of the three species studied.

In conclusion, nesting in *Oniticellus* may best be viewed as a direct progression from relatively simple behaviour incorporating specializations which are convergent with those in a number of other distantly related genera. Such parallelism in the evolution of nesting behaviour in the Scarabaeinae may explain the partial lack of congruency between the evolutionary dendrogram based on nesting patterns (Halffter & Matthews, 1966; Halffter, 1977; Halffter & Edmonds, 1982) and that based on morphology of genitalia (Zunino, 1983) assuming that the latter accurately reflects the phylogeny of the Scarabaeinae.

Acknowledgments

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APPENDIX 7

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Residence and breeding of *Oniticellus* (Coleoptera: Scarabaeidae) within cattle pads: inhibition by dung-burying beetles

by

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Oniticellus planatus Castelnau and *Oniticellus formosus* Chevrolat showed year-round activity in the Transvaal although their patterns of abundance, colonization and residence in cattle dung varied seasonally. During the warm, rainy season (October–April), when there was extensive burial of dung by soil-tunnelling Scarabaeinae, mean numbers of *O. planatus* were greatest in three day old sample pads and those of *O. formosus* in three day and seven day old sample pads. During the cool, dry season, when there was little dung removal, mean numbers of both species were greatest in 14 day old sample pads. Monthly totals of *Oniticellus* from all sample pads were greatest in the dry season. Overall population density was low. Mean numbers of *Oniticellus* brood chambers constructed in dung pads varied inversely with percentage dung removal. Peak breeding success was recorded late in the dry season (August, September) when dung burial was negligible. However, low numbers of broods were recorded early in the dry season despite low burial. It is suggested that breeding by the two species is seasonally inhibited by exploitation competition for dung with dung-burying Scarabaeinae (resource pre-emption) and by cool temperatures early in the dry season.

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INTRODUCTION

Coprophilous beetles of the subfamily Scarabaeinae lay their eggs in modelled portions of dung, termed broods. The fashioning, morphology and siting of these broods is often characteristic of a genus or a species group. Most coprophilous Scarabaeinae excavate brood tunnels directly under the animal droppings being exploited or roll a portion of dung a distance from the dropping before burying and reworking it into a brood ball (Halffter & Matthews 1966, Bornemissza 1969, Halffter 1977, Halffter & Edmonds 1982). However, species of the genus *Oniticellus* Serville construct their broods in chambers within or immediately under dung (Gardner 1929, Bornemissza 1969, Davis 1977, 1989, Cambefort 1982, Rougon & Rougon 1982, 1983, Lumaret & Moretto 1982, Cambefort & Lumaret 1983, Klemperer 1983). The females of most *Oniticellus* spp., including those of *O. planatus* Castelnau and *O. formosus* Chevrolat (Davis 1989) remain with the immatures during their development.

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Past ecological work on *Oniticellus* has been largely confined to studies of their nesting behaviour. Such nidification within dung pads exposes them to possible competitive interaction with dung-burying beetles. Therefore, in the present study, seasonal patterns of dung colonization and breeding activity by adult *O. planatus* and *O. formosus* have been compared with seasonal fluctuation in dung burial by other Scarabaeinae.

METHODS

The study was conducted near De Wildt (25°38′ S 28°53′ E), 35 km west of Pretoria. De Wildt lies at an altitude of about 1300 m and receives a mean annual rainfall of about 700 mm which falls predominantly in summer between October and April. Beetle activity was examined in a field of grassland bordered by citrus orchards on three sides and by further grassland on the other. The field was grazed by up to ten head of cattle and the soil type varied from deep sand to sandy loam.

Beetle activity was monitored once a month between December 1973 and March 1975. This period comprises an entire dry season (May–September 1974) and 1,6 rainy seasons (December 1973–April 1974, October 1974–March 1975). On each monitoring occasion 60 × 1,5 ℓ amounts of fresh, homogenised cattle dung with a standard water content of about 78% by mass were arranged in a 12 × 5 grid at the study site. These pads were placed on the bare soil surface between clumps of grass and were 4 m apart along the lines of 12. The rows were 14 m apart. Fifteen pads, three per row, were collected after three, seven, 14 and 21 days' exposure to beetle activity together with any loose underlying soil. On each of these occasions, percentage removal of dung from all the pads remaining in the field was estimated by eye. The pads were removed to the laboratory where *Oniticellus* brood balls and adult beetles were extracted by breaking up and sieving the remnants if the pads were fairly dry. If the pads were wet, they were first examined for brood balls then broken up under water to float out adult *Oniticellus*. Captured *Oniticellus* were released at the study site only after the completion of each 21 day monitoring exercise to avoid possibility of their immediate recapture. As no specialist predators were observed, predation pressure on adult *Oniticellus* would presumably be light given their low population density. Thus, the effects of short-term removal of a proportion of the population from predation would be minimal.

Visual estimation is a somewhat subjective method of measuring dung removal. However, in a recent study (Davis unpubl. data), the mean error between visual estimation and quantitative assessment of dung removal from the same 187 cattle pads was only 9,8 ± 9,2%. This suggests that the estimation of dung removal by eye was made with a fair degree of accuracy in the present study. This gives validity to interpretation of *Oniticellus* data made in relation to dung burial data.

RESULTS

The amount of dung removed from pads after 21 days' exposure to dung beetle activity followed a seasonal pattern (Fig. 1a–c). Greatest dung removal was during the rainy seasons and early dry season (December 1973–June 1974, October 1974–March 1975). Although dung removal during the rainy season of 1973/75 was much greater than that of 1974/75, greatest removal occurred in the early to mid-rainy season in each case. Except for May 1974, little dung was removed during the cool, dry season (May–September).

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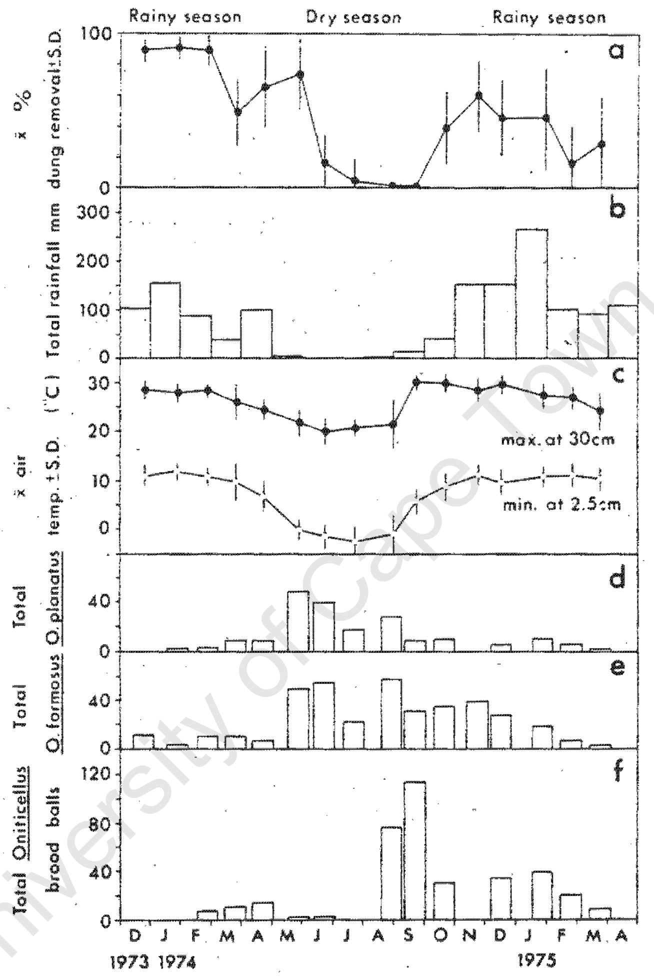

Fig. 1a–f. Seasonal pattern of dung removal from 21 day old monitoring pads and seasonal activity of *Oniticellus* spp. at De Wildt with meteorological data from the nearby Hartebeestpoort Agricultural Station (25° 35′ S 27° 49′ E). (Totals of beetles and broods are from all 60 pads exposed during each 21 days sampling period. Temperature measurements are those recorded during sampling periods only).

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The seasonal pattern in occurrence of adult *Oniticellus* spp. and their brood balls differed to that of dung removal (Fig. 1b–f). Total monthly numbers of *O. planatus* were greatest during the dry season (Fig. 1b, d) whereas those of *O. formosus* were greatest during the dry season and early part of the rainy season in 1974–75 (Fig. 1b, e). A peak in total monthly numbers of *Oniticellus* brood balls was recorded at the end of the dry season in August and September (Fig. 1b, f). Few brood balls were recorded during the early part of the cool, dry season or during the rainy season of 1973/74 when there were high levels of dung removal (Fig. 1a, f). During the rainy season of 1974–75, when dung removal was much lower, brood ball construction by *Oniticellus* was much greater.

The frequency distribution of *Oniticellus* in relation to age of pads varied significantly ($P < 0,01$) and also showed seasonal differences (Fig. 2). In the warm, rainy season when large amounts of dung were rapidly removed from the pads, peak numbers of *O. planatus* were recorded from the three day samples and highest numbers of *O. formosus* from the three and seven day samples. In the cool, dry season when dung removal was low, and took place over a long period, peak numbers of both species were recorded from 14 day samples. Although the numbers of *Oniticellus* per colonized pad were low (Table 1), there was some spatial overlap between the two species. This was greater during the dry season when 72,2% of the adult *O. planatus* and 54,4% of the adult *O. formosus* occupied the same pads. In the rainy season only 20,4% of the *O. planatus* coexisted with 8,2% of the *O. formosus*.

TABLE 1. Frequency distribution of *Oniticellus* spp. between colonized 1,5 ℓ cattle pads at De Wildt from December 1973 until March 1975.

Species	No. of adults/pad (%)							No. of pads colonized
	1	2	3	4	5–8	10	14	
O. planatus	65,6	21,8	5,9	3,4	2,5	0,8	0	119
O. formosus	61,4	16,8	11,7	4,1	5,6	0	0,5	197

Several trends in brood construction by *Oniticellus* were noted. Out of 75 observations of pads containing brood chambers, 70 contained a single chamber, four contained two chambers and only one pad contained three chambers. Most brood chambers were recorded from 14 and 21 day old pads ($H = 28,381$, d.f. = 2, $P < 0,001$, Kruskal-Wallis test) (Table 2). The mean number of brood chambers in these older pads decreased with increasing dung removal ($H = 35,008$, d.f. = 4, $P < 0,001$, Kruskal-Wallis test) (Table 3). However, there was no significant difference ($H = 5,473$, d.f. = 4, n.s., Kruskal-Wallis test) between the mean number of brood balls per chamber in different dung removal classes (Table 3). Although a range of 1–19 broods per chamber was recorded, mean numbers were low (Tables 2, 3).

DISCUSSION

Laboratory cultures of *O. planatus* and *O. formosus* have been bred continuously throughout the year (personal observations) so it is probable that the fluctuations in breeding activity by field populations of the two species are entirely influenced by exogenous factors. These are primarily, availability of unburied dung, ambient temperature and rainfall. The inverse relationship which was shown between dung removal and

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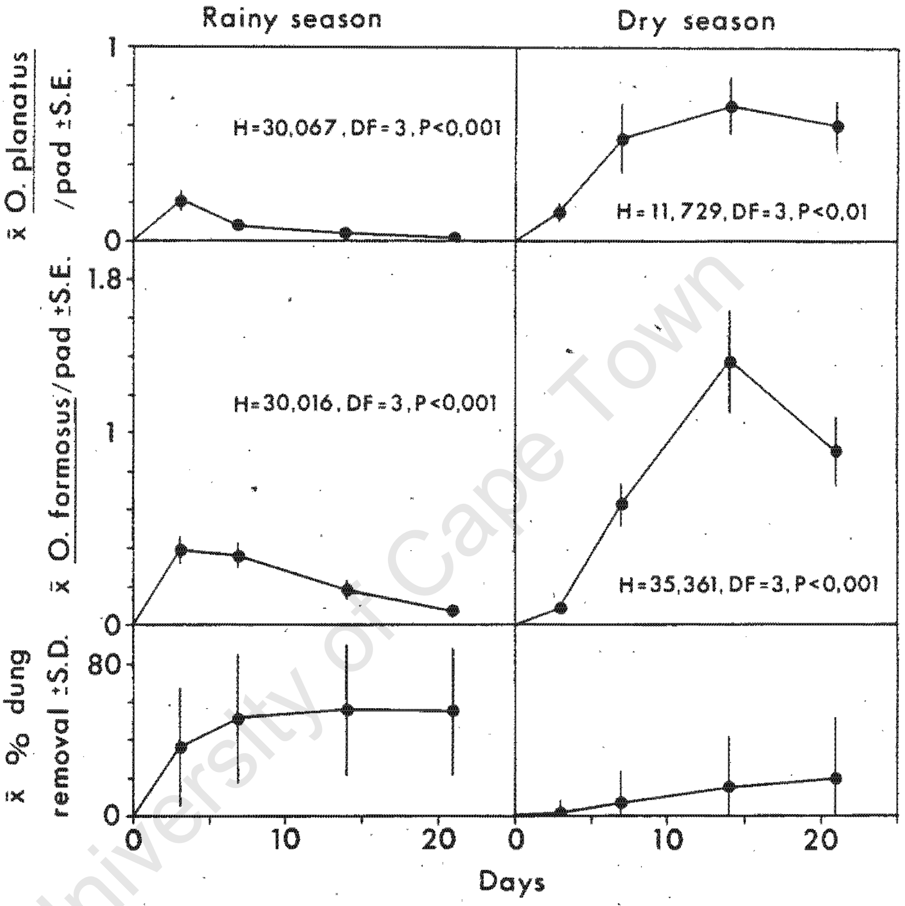

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Fig. 2. Colonization patterns of *Oniticellus* spp. and dung removal from cattle pads at De Wildt during a single cool, dry season (May–September 1974) and 1,6 warm, rainy seasons (December 1973–April 1974 and October 1974–March 1975). Results of Kruskal-Wallis tests on differences in frequency distribution of *Oniticellus* spp. with age of sample pads.

TABLE 2. The production of brood balls by *Oniticellus* in 1,5 ℓ pads of cattle dung at De Wildt between December 1973 and March 1975, in relation to age of dung.

Pad age (days)	No. pads	No. brood chambers	Total no. broods	$\bar{x}$ no. (S.D.) broods/ chamber	$\bar{x}$ no. (S.D.) chambers/ pad*
3	240	0	0	0	0
7	236	5	12	2,4 (0,8)	0,02 (0,14) a
14	235	35	194	5,5 (4,0)	0,15 (0,39) b
21	227	41	150	3,7 (2,6)	0,18 (0,43) b

* Values followed by a different letter differed significantly ($p < 0{,}001$) (Kruskal-Wallis tests used as multiple range tests).

TABLE 3. Brood ball and brood chamber production in relation to dung removal from 1,5 ℓ cattle pads left in the field for 14 and 21 days (pooled data) at De Wildt between December 1973 and March 1975.

Percentage dung removal classes	Total no. pads	Total no. brood chambers	Total no. brood balls	$\bar{x}$ no. (S.D.) broods/ chamber	$\bar{x}$ no. (S.D.) chambers/ pad*
0–20	196	56	275	4,9 (3,6)	0,29 (0,53) a
21–40	43	7	24	3,4 (3,4)	0,16 (0,37) ab
41–60	35	4	14	3,5 (2,4)	0,11 (0,32) ab
61–80	76	7	29	4,1 (3,5)	0,09 (0,29) b
81–100	113	2	2	1,0 (0)	0,02 (0,13) c

* Values followed by a different letter differed significantly ($p < 0{,}05$) (Kruskal-Wallis tests used as multiple range tests).

production of *Oniticellus* brood chambers points to competition between dung-burying Scarabaeinae and *Oniticellus* spp. seeking breeding space. It is likely that interference competition between the two groups was minimal since most *Oniticellus* broods were constructed in pads with an age of > 7 days (Table 2) whereas, during the rainy season, most dung was removed from pads soon after deposition (Fig. 2). Most reduction in brood construction by *Oniticellus* due to the removal of dung from cattle pads may therefore be ascribed to exploitation competition or, expressing the relationship more accurately, to resource pre-emption.

Although early removal of dung probably renders many pads unsuitable for residence and breeding by *Oniticellus*, brood balls were constructed with equal facility in both intact and partially disrupted pads (Table 3). Breeding in shredded pads may, however, lower the chances of larval survival in *Oniticellus*. At the beginning of the rainy season in October 1974, high egg and first instar larval mortality was noted in broods constructed in the highly disturbed and rapidly desiccating 21 day old pads. The parental females, which normally tend the immatures during development (Davis 1989), appeared to have abandoned these broods.

Low temperatures during May and June 1974 probably also inhibited brood production in *Oniticellus*. Although mean minimum temperatures were equally low during August when large numbers of broods were produced, variations in temperature were relatively large compared with the consistently low temperatures during the earlier part of the dry season.

Unlike most dung beetles which are active mainly during the rainy season (e.g. Halffter & Matthews 1966), *Oniticellus* spp. remained active throughout all seasons. Therefore it is probable that rainfall affected activity by these species mainly through its influence on temperature.

The disruption of dung has a similar effect on the other insects which breed within animal droppings. Roth (1983) has shown that breeding success of *Philonthus flavolimbatus* Erichson (Coleoptera, Staphylinidae) in North America is reduced in the presence of dung burial activity by *Onthophagus* spp. (Coleoptera, Scarabaeinae). Dung burial by scarab beetles has also been shown to reduce survival and cause stunting in dung-breeding Diptera (e.g. Bornemissza 1970, Ridsdill Smith 1981, Ridsdill Smith *et al.* 1986). On the other hand, Afrotropical *Aphodius (Bodilus)* spp. (Coleoptera, Aphodiinae), which breed within cells in the dung (Bernon 1981), are restricted to dry season activity in the Transvaal (Davis unpubl. data) and so largely avoid competitive interaction with dung-burying beetles.

Low density of *Oniticellus* brood chambers in cattle pads may be a function of low population density of adults. However, this does not rule out intraspecific competition for breeding space since many of the 30–40% of pads containing more than one individual of the same species (Table 1), contained more than one female. Interspecific competition for breeding space between *Oniticellus* species is also possible, particularly late in the dry season (August, September) when 72,9% of the adult *O. planatus* coexisted in the same pads as 36,8% of the *O. formosus*. However, competition between the two species may be reduced by partial separation of breeding sites as *O. formosus* breed deeply within dung pads (Rougon & Rougon 1982) whereas *O. planatus* brood chambers often straddle the dung/earth interface (Cambefort 1982).

In conclusion, seasonal differences in colonization of dung pads and breeding by *O. planatus* and *O. formosus* are probably influenced principally by dung removal and temperature. Brood balls are constructed predominantly within older dung pads which is highly specialized nesting behaviour (Davis 1989). This is susceptible to inhibition by the extensive and rapid removal of fresh dung which is frequently encountered during warm, wet periods (Table 3, Fig. 1a–c). Greatest breeding success is thus restricted to warm periods of low dung removal (Fig. 1a–c, f) especially the warm days late in the dry season when conditions are unfavourable for dung-burying beetles. Such pressures have probably selected for year-round activity and opportunistic breeding habits by both *Oniticellus* species which may compensate for low population density.

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CLIMATIC CHANGE, HABITAT MODIFICATION AND RELATIVE AGE OF DUNG BEETLE TAXA (COLEOPTERA: SCARABAEIDAE, HYDROPHILIDAE, HISTERIDAE, STAPHYLINIDAE) IN THE SOUTH-WESTERN CAPE

II. Tables and Figures

by

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Thesis submitted to the Department of Zoology, University of
Cape Town in fulfillment of the requirements for the degree
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INDEX

Chapter

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Table I1. Characteristics of the six most abundant groups of Coleoptera recorded from dung in the south-western Cape.

Size	Mean dry weight (gm) (S.D.) [n] of species in		Trophic habit	Taxa	Breeding habit
	S-W Cape	Transvaal			
Often large	0,17 (0,002) [28]	0,19 (0,45) [85]	Coprophagous	Scarabaeidae: Scarabaeinae/ Coprinae	Mostly bury dung, some kleptoparasitic**, few breed within dung
Mostly small	0,002 (0,0013) [16]	0,0027 (0,0035) [34]	Coprophagous	Scarabaeidae: Aphodiinae	Bury or breed within dung or kleptoparasitic
Small	0,00036 (0,000025) [3]	0,00019 (0,00013) [10]	Coprophagous	Staphylinidae: Oxytelinae	Breed within dung
Mostly small	0,0029 (0,0019) [3]	0,00096 (0,001) [5]	* Mostly predatory	Hydrophilidae	Breed within dung
Mostly small	0,0066 (0,0079) [15]	0,021 (0,038) [16]	Mostly predatory	Histeridae	Breed within dung
Mostly small	0,0025 (0,0058) [25]	0,00072 (0,0012) [50]	Mostly predatory	***Staphylinidae: Other subfamilies	Breed within dung

*Feeding especially on the immature stages of coprophilous Diptera.

**Kleptocoprid species breed in dung buried by other dung beetles.

***Subfamilies Staphylininae, Aleocharinae, Tachyporinae, Xantholininae, Paederinae.

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Figure M1. The seasonal distribution of rainfall in the four principal climatic regions of southern Africa and the location of climatic subregions in which trapping sites were placed.
WR = Winter rainfall, BR = Bimodal rainfall, SR = Summer rainfall.

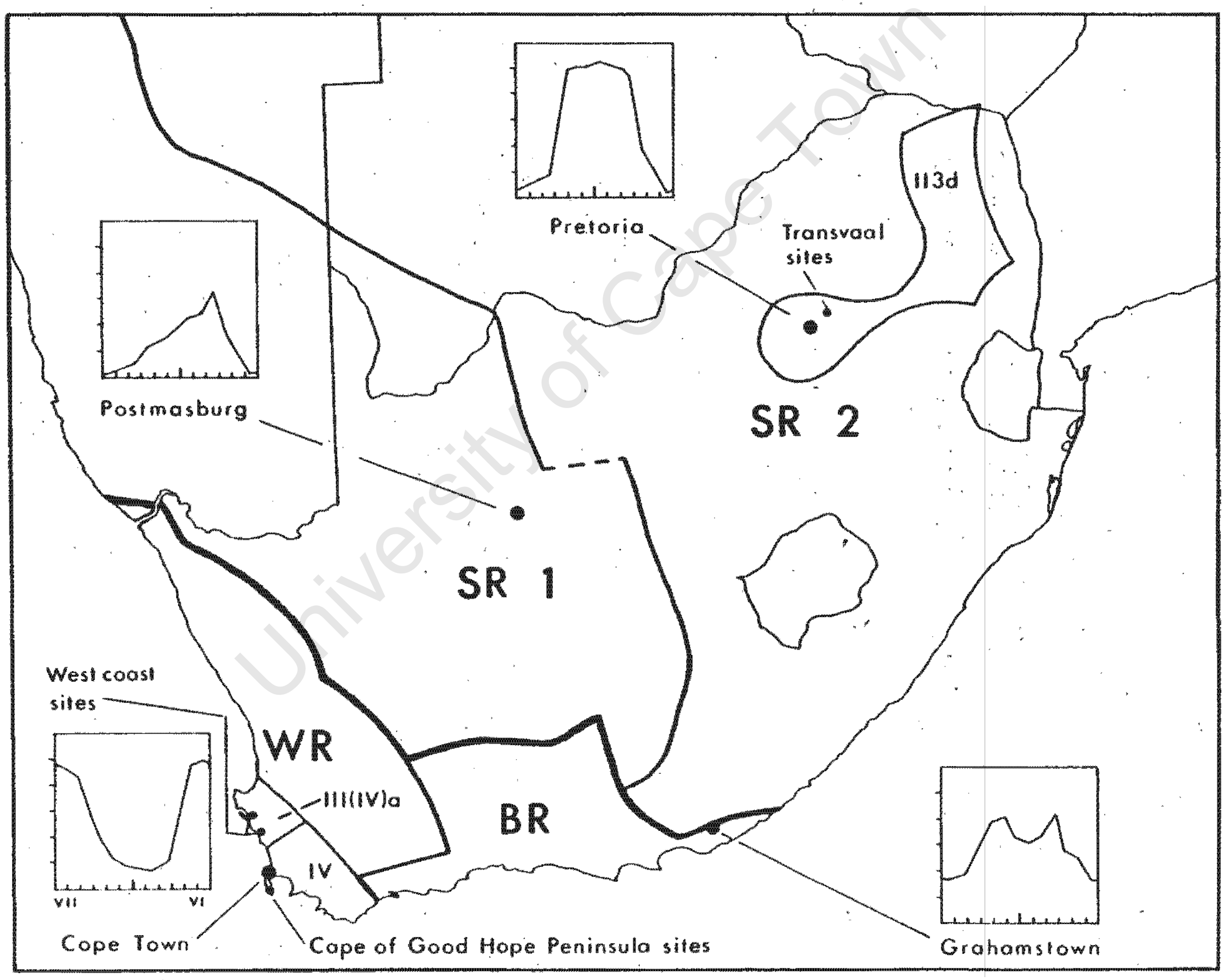

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Figure M2. Long-term temperature and rainfall data for four localities in three climatic subregions of southern Africa in which trapping sites were placed.

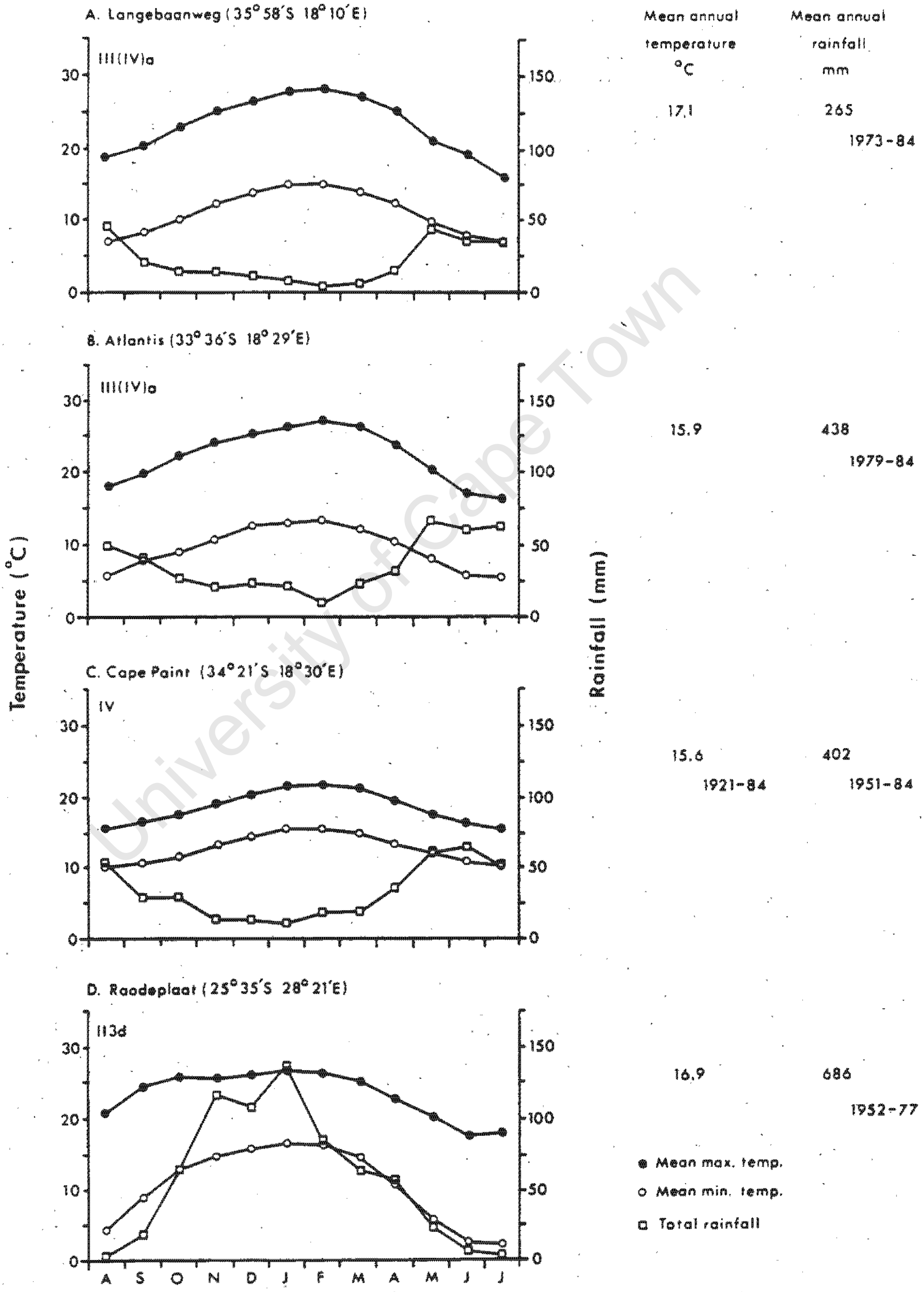

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Figure M3. Temperature and rainfall data for four localities in three climatic subregions of southern Africa during the period in which trapping was conducted.

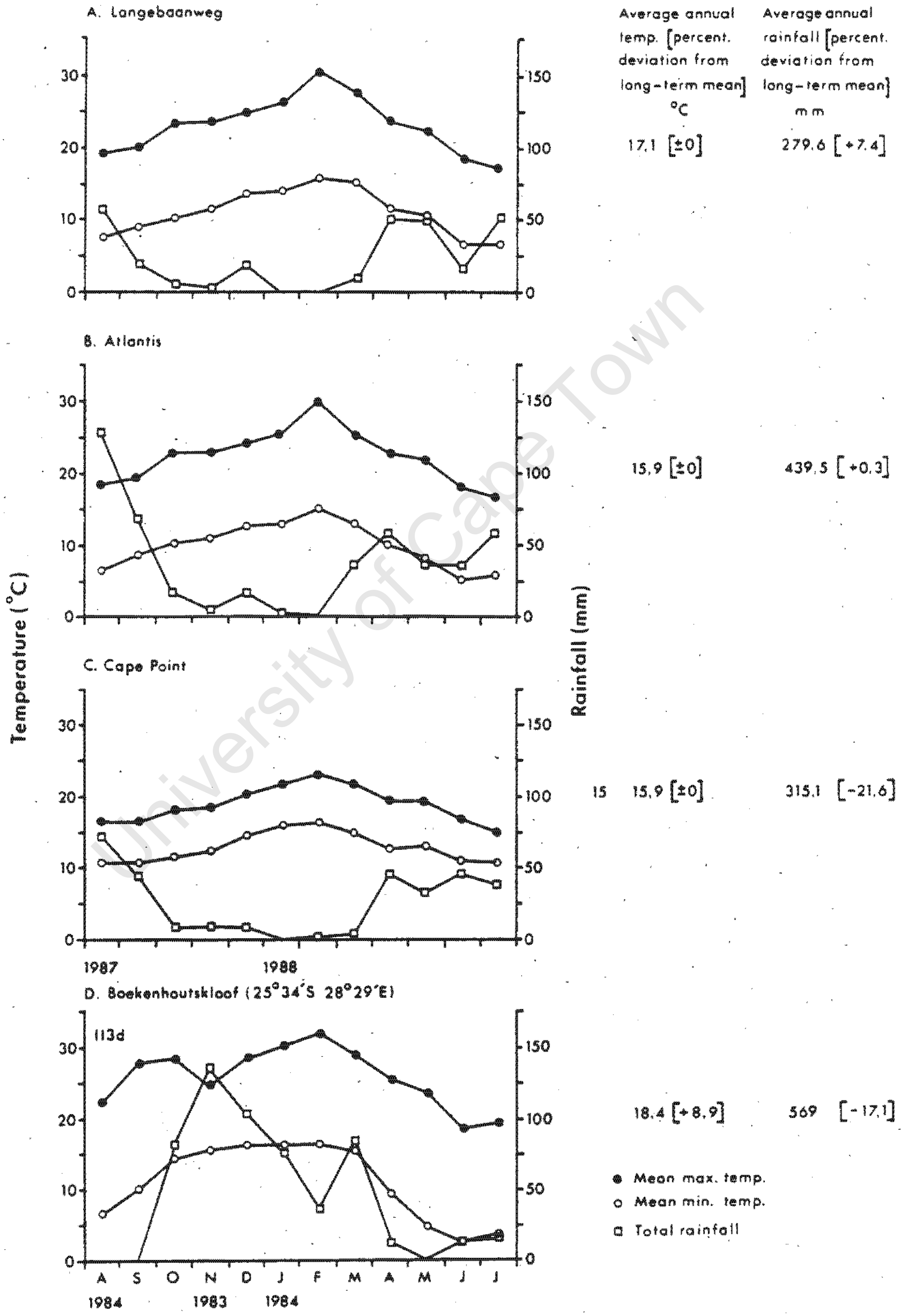

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Figure M4. Location of trapping sites in the south-western Cape in relation to climatic and rainfall regimes.

Key

1. Cape of Good Hope Nature Reserve, 9-10yr old fynbos.
2. Cape of Good Hope Nature Reserve, 2-3yr old fynbos.
3. Bonne Attente.
4. Modderrivier.

5,6. West Coast National Park.

7. Waylands.
8. Oranjefontein.

9,10. Pampoenvlei.

11. Groote Post.

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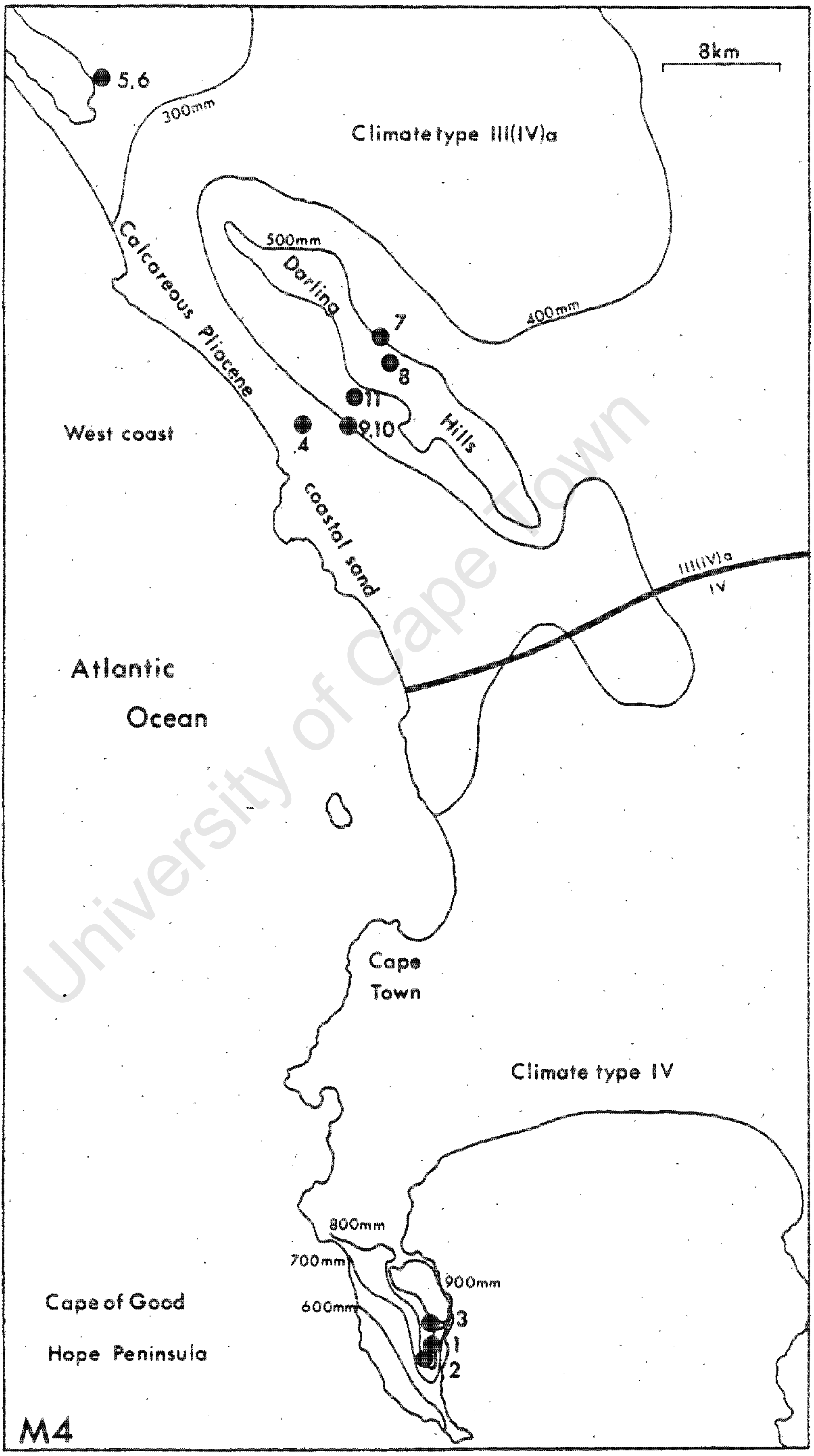

M4

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Figure M5. Variability in height and density of vegetation at trapping sites in the south-western Cape.*

	Locality	Vegetation	Grid reference	Vegetative density (%)	Vegetative Height index
a.	Groote Post	Pasture	33°16'S 18°25'E	93	5
b.	Bonne Attente	Pasture	34°16'S 18°28'E	100	25
c.	Waylands	Pasture	33°24'S 18°26'E	100	45
d.	West Coast National Park	Pasture	33°10'S 18°08'E	89	225
e.	Oranjefontein	Pasture	33°25'S 18°26'E	99	545
f.	Cape of Good Hope Nature Reserve	2-3yr old fynbos	34°18'S 18°27'E	95	1640
g.	Cape of Good Hope Nature Reserve	9-10yr old fynbos	34°18'S 18°27'E	81	1990
h.	Modderrivier	Restioid shrubland	33°28'S 18°20'E	68	3485
i.	Pampoenvlei (sand)	Proteoid/ sclerophyll shrubland	33°28'S 18°24'E	56	4060
j.	West Coast National Park	Sclerophyll shrubland	33°10'S 18°08'E	65	5095
k.	Pampoenvlei (sandy loam)	Sclerophyll shrubland	33°28'S 18°24'E	69	7155

*For site numbers, see Figure M4.

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M5

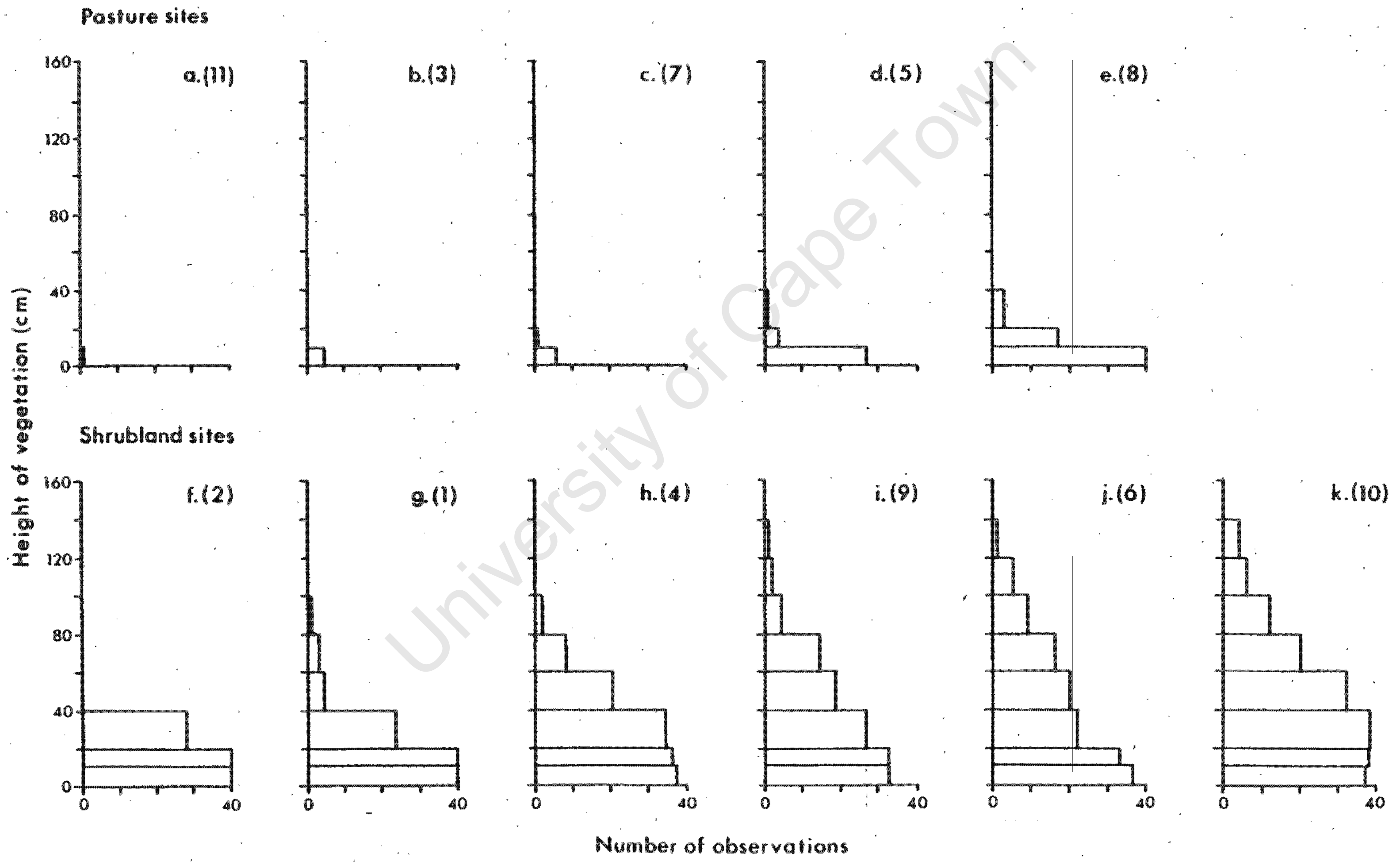

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Figure M6. Transverse section through a standardized baited pitfall trap.

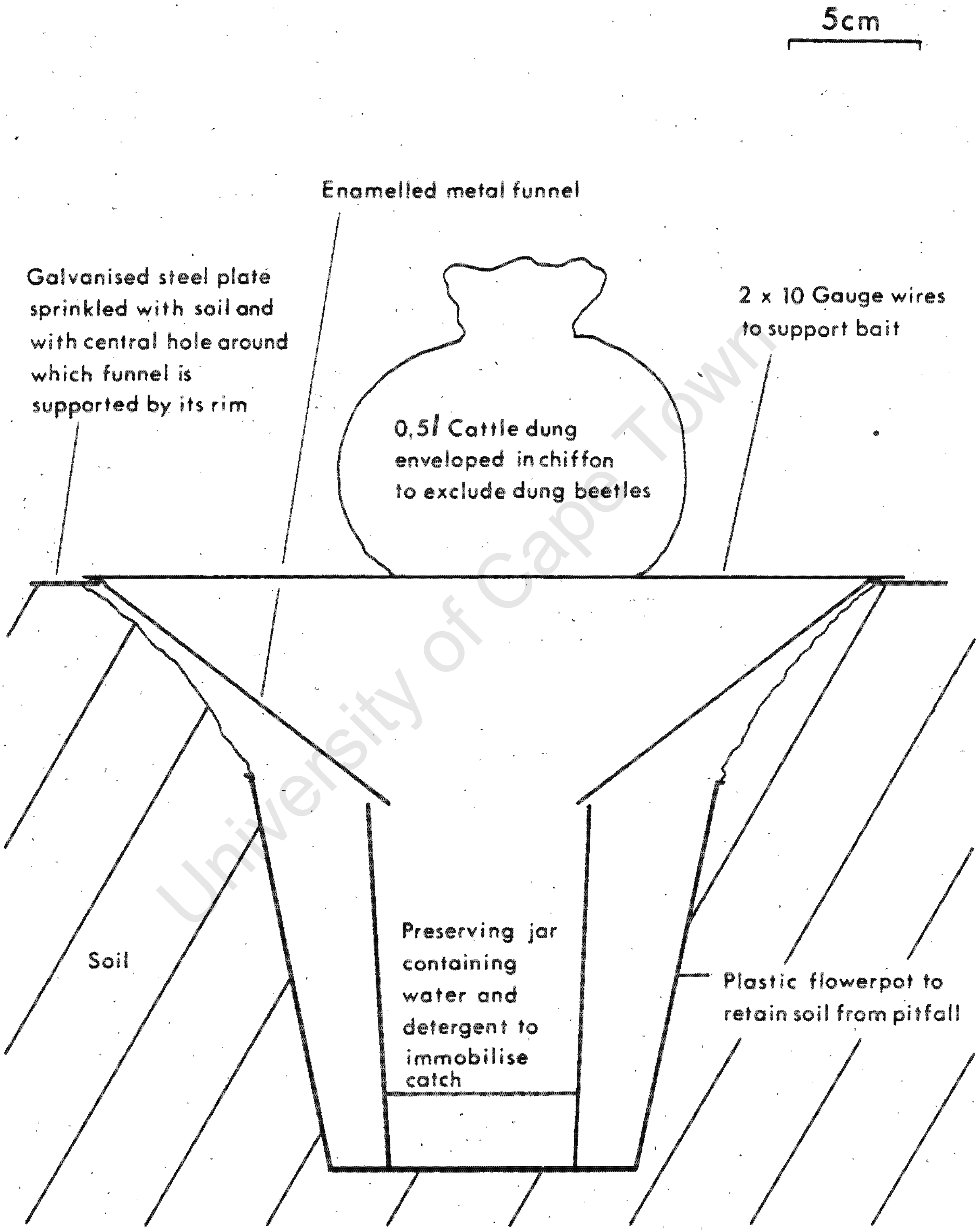

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Figure M7. Location of trapping sites used in follow-up studies in the south-western Cape in relation to climatic and rainfall regimes.

Cape of Good Hope Peninsula

1. Cape of Good Hope Nature Reserve.

2,3. Bonne Attente.

Rondeberg Strip

1,2. Modderrivier.

3-5. Rondeberg.

6. Vygevlei.

Groote Post

1-4. Groote Post.

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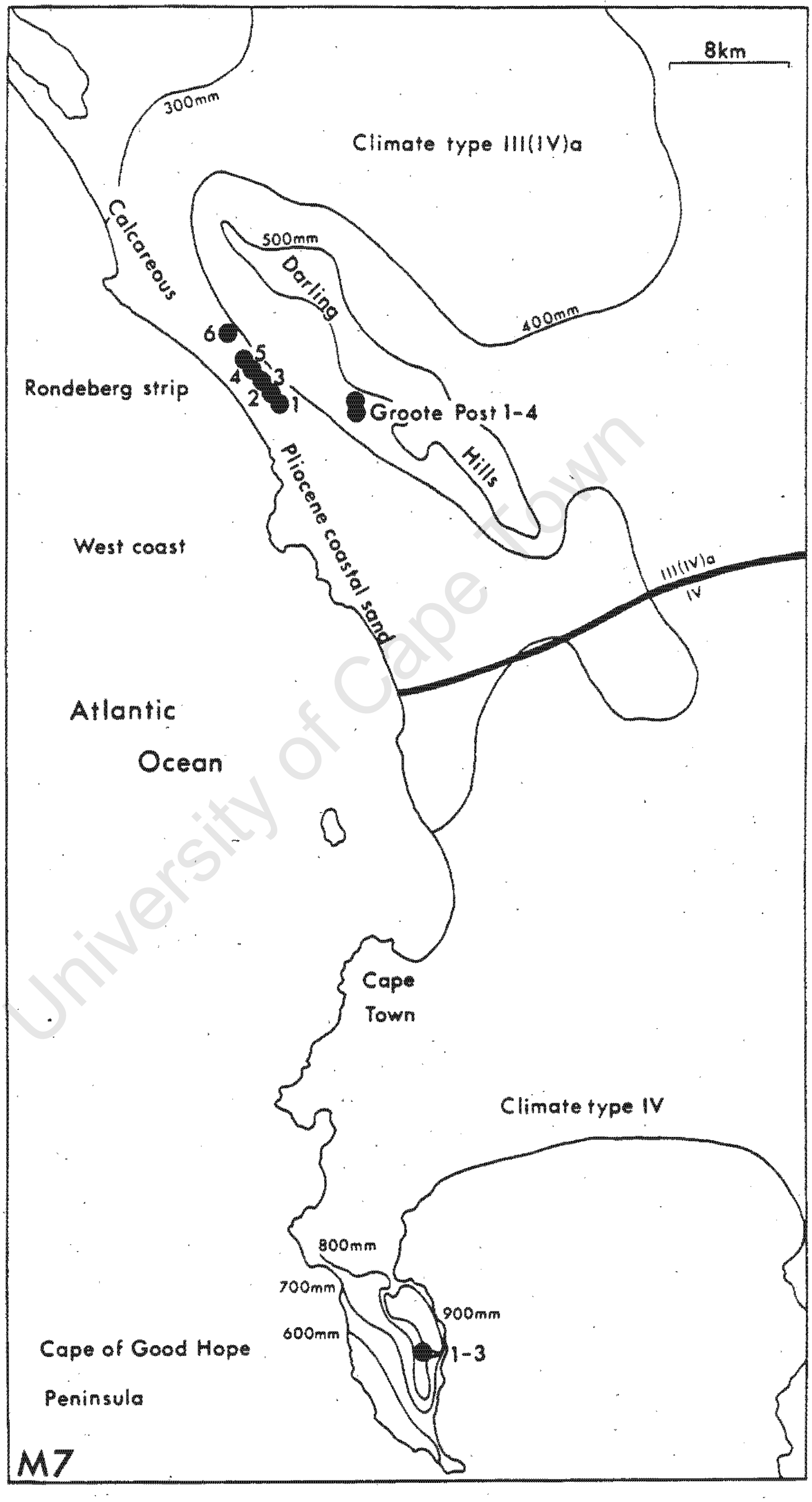

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Figure M8. Variability in height and density of vegetation across trap lines in the Cape of Good Hope Peninsula, Rondeberg Strip and Farm Groote Post.

	Locality	Vegetation	Vegetative density (%)	Vegetative height index (x2)
A.	**Cape of Good Hope Peninsula 34°15'S 18°28'E**			
1.	Cape of Good Hope Nature Reserve	Degraded restioid fynbos	69	1590
2.	Bonne Attente	Pasture	100	50
3.	Bonne Attente	Secondary sclerophyll shrubland	68	2870
B.	**Rondeberg Strip 33°25'S 18°17'E**			
1.	Modderrivier	Sclerophyll shrubland	70	10780
2.	Modderrivier	Sclerophyll shrubland	68	6180
3.	Rondeberg	Restioid shrubland	70	4830
4.	Rondeberg	Pasture	52	270
5.	Rondeberg	Harrowed field	92	690
6.	Vygevlei	Exotic *Acacia* shrubland	66	15900
C.	**Groote Post 33°16'S 18°25'E**			
1.	Groote Post	Pasture strips	66	560
2.	Groote Post	Restioid shrubland strips	66	4930
3.	Groote Post	Sclerophyll shrubland	78	4140
4.	Groote Post	Pasture	93	20

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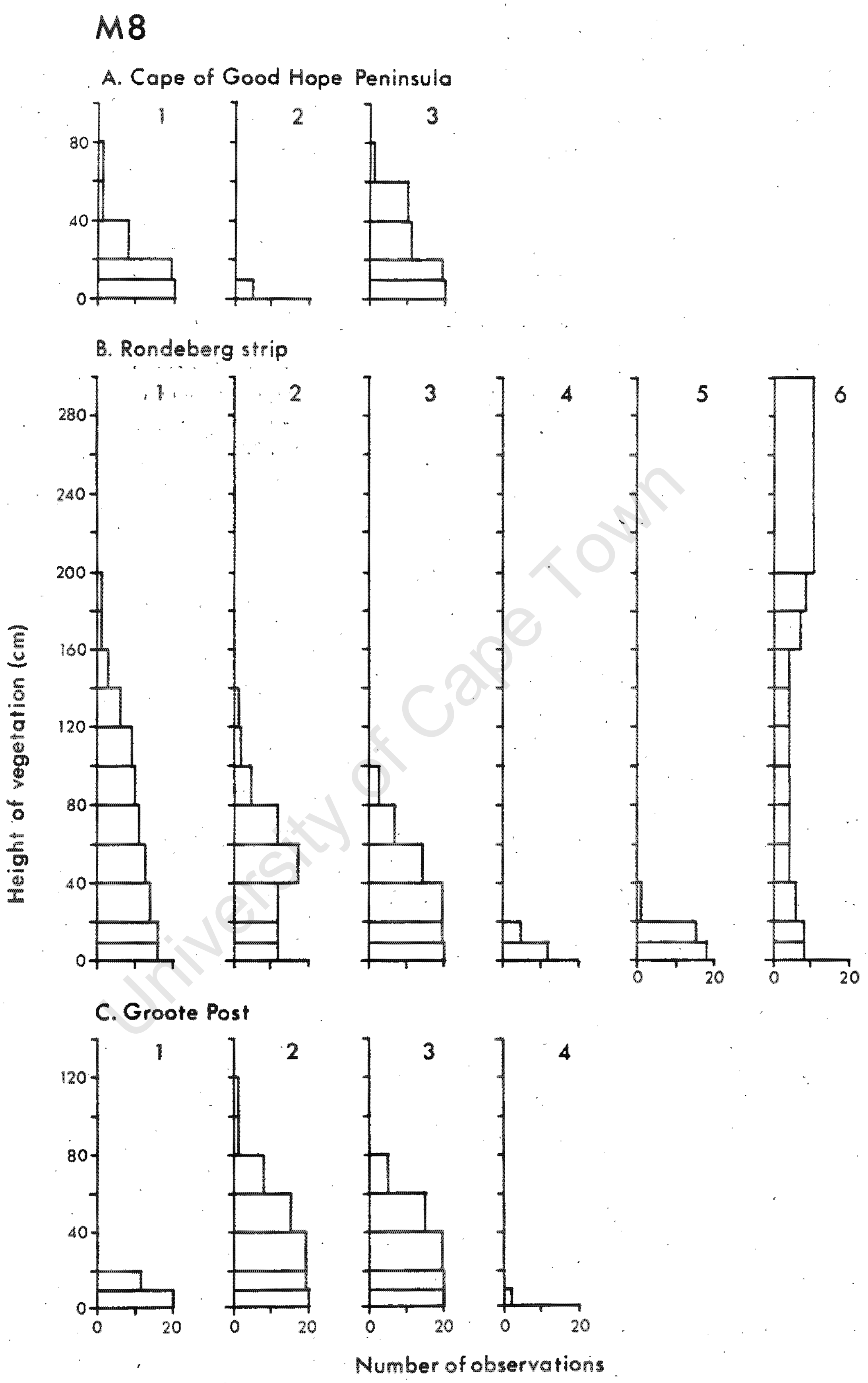

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Table 1.1. Changes in species richness of six higher taxa of dung Coleoptera across three climatic regions of southern Africa in two different habitat-types.

Family/ subfamily	Mean number of species/trapping site (S.D.)						Ratios of species richness across climate types		Slope of trend fitted to ratios by linear regression	
	Pasture in Climate type			Shrubland in Climate type						
	IV*	III(IV)a	II3d	IV	III(IV)a	II3d	Pasture	Shrubland/ open woodland	Pasture	Shrubland/ open woodland
Staphylinidae: Oxytelinae	5,0	4,3 (0,8)	9,0	2,5 (0,5)	3,5 (0,9)	9,0	1 : 0,9 : 1,8	1 : 1,4 : 3,6	0,4	1,3
Scarabaeidae: Aphodiinae	15,0	19,8 (2,3)	32,0	13,0 (0,5)	17,3 (0,4)	28,0	1 : 1,3 : 2,1	1 : 1,3 : 2,2	0,6	0,6
Scarabaeidae: Scarabaeinae/ Coprinae	14,0	28,0 (3,7)	81,0	12,5 (0,5)	20,0 (2,7)	77,0	1 : 2,0 : 5,8	1 : 1,6 : 6,2	2,4	2,6
Hydrophilidae	6,0	6,0 (0,0)	6,0	2,5 (0,5)	4,5 (1,1)	6,0	1 : 1,0 : 1,0	1 : 1,8 : 2,4	0,0	0,7
Histeridae	16,0	16,0 (1,7)	22,0	7,0 (0,0)	15,3 (2,9)	18,0	1 : 1,0 : 1,4	1 : 2,2 : 2,6	0,2	0,8
Staphylinidae: predatory subfamilies**	28,0	40,0 (1,9)	53,0	24,0 (4,0)	37,3 (4,4)	52,0	1 : 1,4 : 1,9	1 : 1,6 : 2,2	0,5	0,6

*Climate type IV: Cape of Good Hope Peninsula, south-western Cape.
Climate type III(IV)a: West coast of south-western Cape.
Climate type II3d: Transvaal bushveld.

**Staphylininae, Aleocharinae, Paederinae, Xantholininae, Tachyporinae.

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Table 1.2. Relative abundance of diurnal and crepuscular/nocturnally active taxa of dung Coleoptera.

Family/ subfamily	No. of species for which information available (% of total no. recorded for group)	Percentage distribution	
		Diurnal	Crepuscular/ nocturnal
Transvaal bushveld			
Scarabaeinae/ Coprinae	91 (100,0)	41,8	58,2
Aphodiinae	26 (78,8)	23,1	76,9
Oxytelinae	8 (80,0)	50,0	50,0
Hydrophilidae	5 (71,4)	40,0	60,0
Histeridae	16 (61,5)	100,0	0,0
Staphylinidae (predatory subfamilies)	44 (72,1)	50,0	50,0
South-western Cape			
Scarabaeinae/ Coprinae	45 (100,0)	87,8	22,2

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Table 1.3. Magnitude of the difference in species richness of six higher taxa of dung Coleoptera between two habitats across three climate types.

Locality	Ratio of mean number of species (S.D.)		
	Pasture		Shrubland/open woodland
Climate type IV, Cape of Good Hope Peninsula south-western Cape	*a 1,7 (0,6)	:	1
Climate type III(IV)a, West coast of south-western Cape	ab 1,2 (0,1)	:	1
Climate type II3d, Transvaal bushveld	b 1,1 (0,1)	:	1

*Ratios differed significantly (F = 5,24; d.f. = 2,15; P<0,02; Analysis of variance).

Values coded by a different letter differed significantly (P<0,05; Scheffe's tests).

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Table 1.4. Changes in abundance of six higher taxa of dung Coleoptera across three climatic regions of southern Africa in two different habitat-types.

Family/ subfamily	Mean number of individuals/trap (S.D.)						Ratios of abundance across climate types		Slope of trend fitted to ratios by linear regression	
	Pasture in Climate type			Shrubland/open woodland in Climate type						
	IV*	III(IV)a	II3d	IV	III(IV)a	II3d	Pasture	Shrubland/ open woodland	Pasture	Shrubland/ open woodland
Staphylinidae: Oxytelinae	34,9 (21,9)	102,3 (197,0)	75,6 (82,4)	9,0 (24,4)	98,7 (269,6)	75,5 (82,2)	1 : 2,9 : 2,2	1 : 11,8 : 3,0	0,6	3,7
Scarabaeidae: Aphodiinae	9,9 (21,9)	59,5 (166,5)	34,4 (53,1)	3,8 (20,9)	17,3 (51,1)	22,7 (28,7)	1 : 6,0 : 3,5	1 : 4,6 : 6,0	1,3	2,5
Scarabaeidae: Scarabaeinae/ Coprinae	23,9 (64,0)	12,5 (17,0)	49,8 (66,3)	2,7 (5,8)	13,2 (15,2)	97,7 (126,1)	1 : 0,5 : 2,1	1 : 4,9 : 36,2	0,6	17,6
Hydrophilidae	3,3 (13,3)	5,7 (20,0)	2,2 (5,4)	0,1 (0,4)	0,2 (0,7)	3,5 (6,1)	1 : 1,7 : 0,7	1 : 1,2 : 35,0	-0,2	17,0
Histeridae	1,1 (2,4)	5,4 (12,0)	5,3 (7,3)	0,2 (0,9)	5,9 (13,1)	13,4 (16,5)	1 : 4,9 : 4,8	1 : 29,5 : 67,0	1,9	33,0
Staphylinidae: predatory subfamilies**	3,6 (7,4)	16,2 (29,0)	26,0 (23,3)	1,4 (3,5)	15,2 (43,1)	36,3 (30,4)	1 : 4,5 : 7,2	1 : 10,9 : 25,9	3,1	12,5

*Climate type IV: Cape of Good Hope Peninsula, south-western Cape.
Climate type III(IV)a: West coast of south-western Cape.
Climate type II3d: Transvaal bushveld.
**Staphylininae, Aleocharinae, Paederinae, Xantholininae, Tachyporinae.

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Table 1.5. Magnitude of the difference in mean abundance per trap of six higher taxa of dung Coleoptera between two habitats across three climate types.

Locality	Ratio of mean abundance/trap (S.D.)		
	Pasture		Shrubland/open woodland
Climate type IV, Cape of Good Hope Peninsula, south-western Cape	9,4 (10,8) **a [4,7 (2,3)]*	:	1
Climate type III(IV)a, West coast of south-western Cape	6,0 (10,1) b [1,5 (1,0)]	:	1
Climate type II3d, Transvaal bushveld	0,8 (0,4) b [1,1 (0,1)]	:	1

*Ratios for five higher taxa, excluding data for the Hydrophilidae which showed extreme differences in abundance between habitat types in the south-western Cape.

**Ratios differed significantly (F = 7,80; d.f. = 2,12; P<0,01; Analysis of variance).

Values coded by a different letter differed significantly (P<0,05; Scheffe's tests).

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Figure 1.1. Percentage distribution of numbers between six higher taxa of dung beetles in two habitat-types in three climatic subregions of southern Africa.

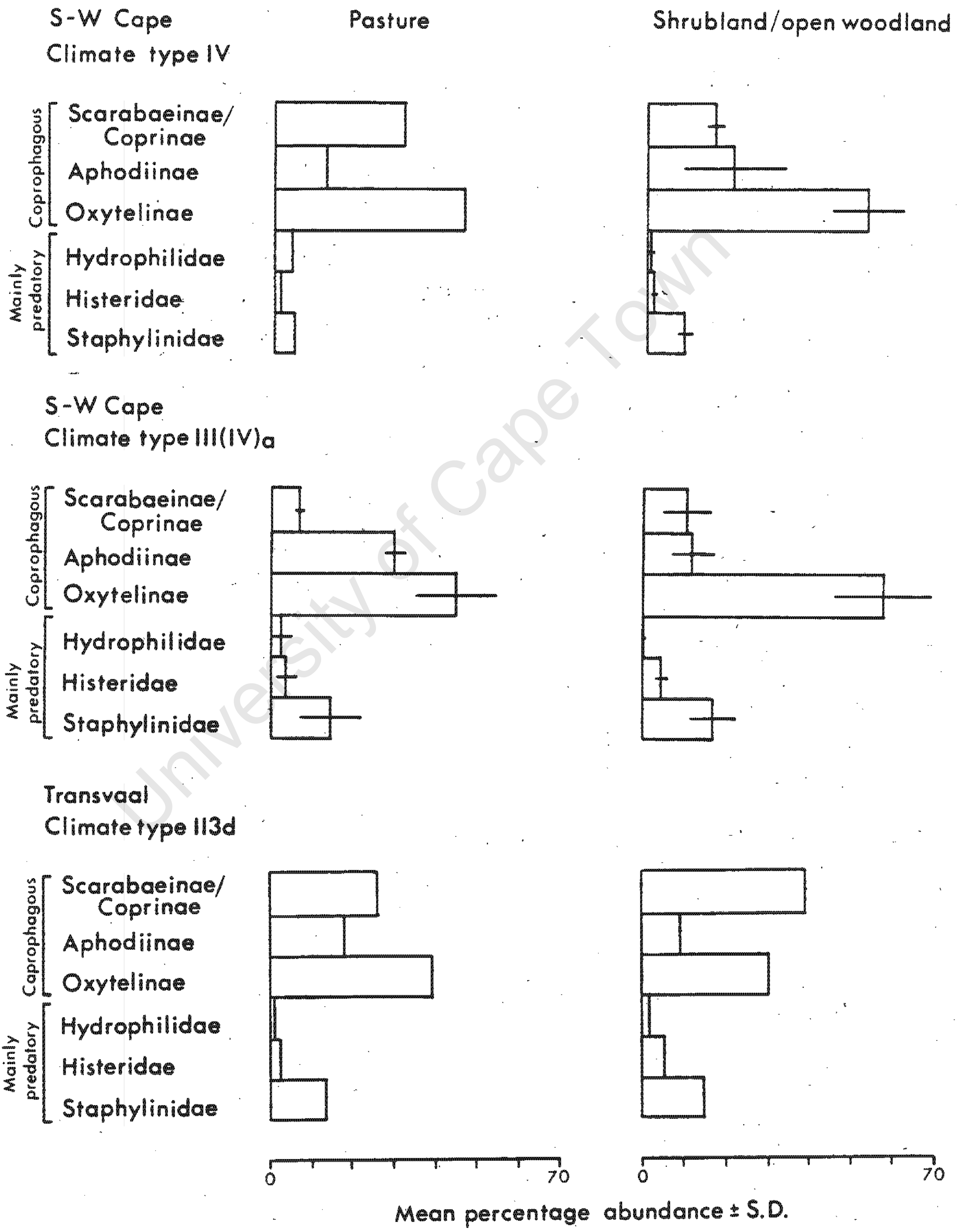

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Figure 1.2. Amount and seasonal variation in dung removal from cattle pads in two regions of southern Africa.

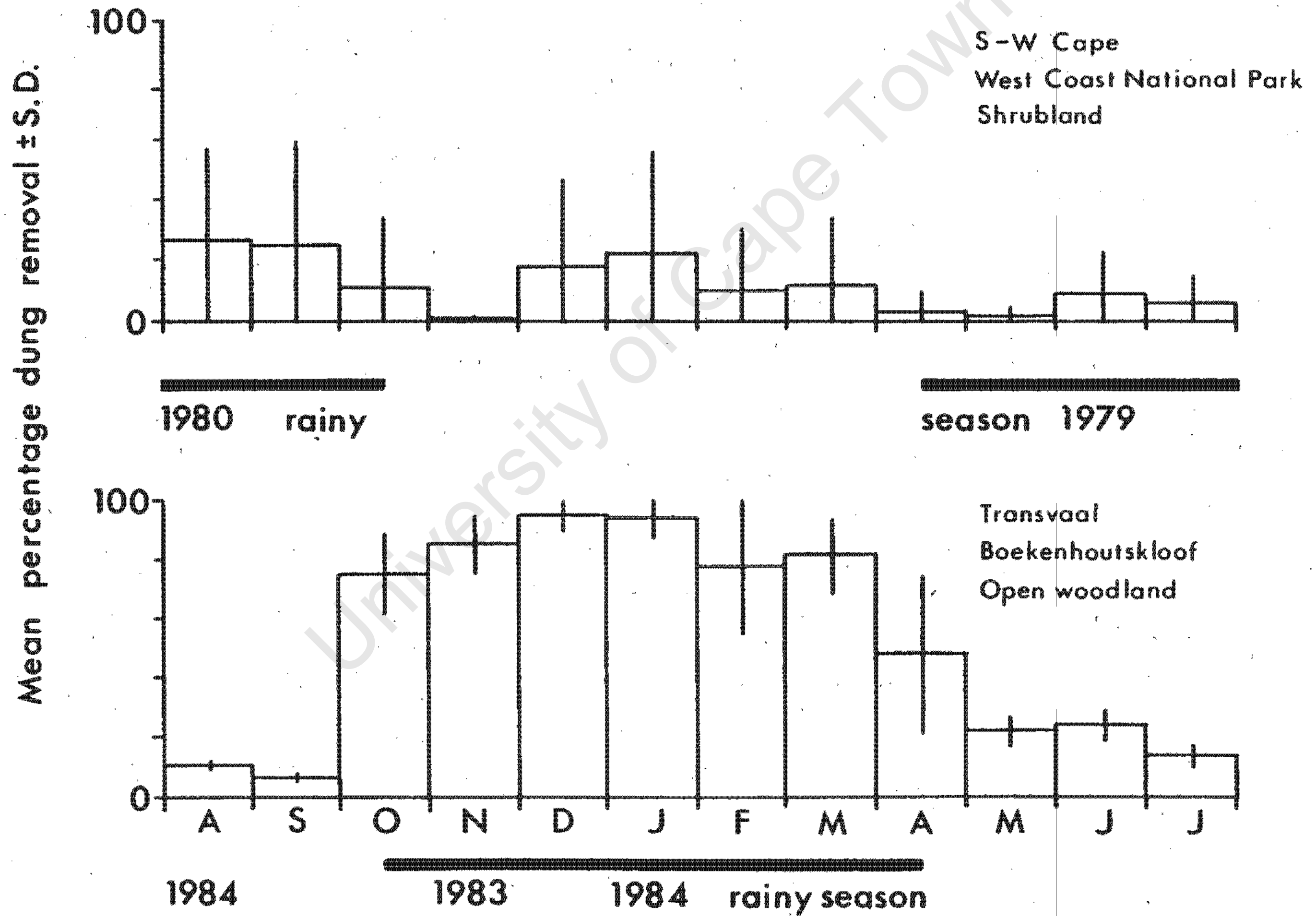

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Table 1.6. Coefficient of variation (mean/standard deviation) in mean abundance/trap of six higher taxa of dung Coleoptera between two habitats across three climatic regions.

Locality	Mean coefficient of variation (S.D.)	
	Pasture	Shrubland/open woodland
Climate type IV, Cape of Good Hope Peninsula, south-western Cape	0,402 (0,079) a*	0,308 (0,118) a
Climate type III(IV)a, West coast of south-western Cape	0,484 (0,146) a	0,387 (0,087) a
Climate type II3d, Transvaal bushveld	0,761 (0,020) b	0,844 (0,187) b

*Within site variation between trap catches coded by a different letter differed significantly (P<0,05) (confidence intervals).

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Figure 1.3. Dendrogram showing trends in seasonal distribution of abundant or species rich groups of southern African dung Coleoptera.*

Key to column headings

Activity peak = Month of maximum abundance.

PTA = Percentage of the total numbers recorded for the taxon in each climatic region.

Taxon

SC = Scarabaeinae/Coprinae.
A = Aphodiinae.
HI = Histeridae.
ST = Staphylinidae/Hydrophilidae.

Climatic region

GH = Climate type IV, Cape of Good Hope Peninsula, south-western Cape.
WC = Climate type III(IV)a, West coast of south-western Cape.
TVL = Climate type II3d, Transvaal bushveld.

Group = Regional groups derived from cluster analysis of seasonal distribution data of the more abundant species (see Addendum, Figs AD1-7.).

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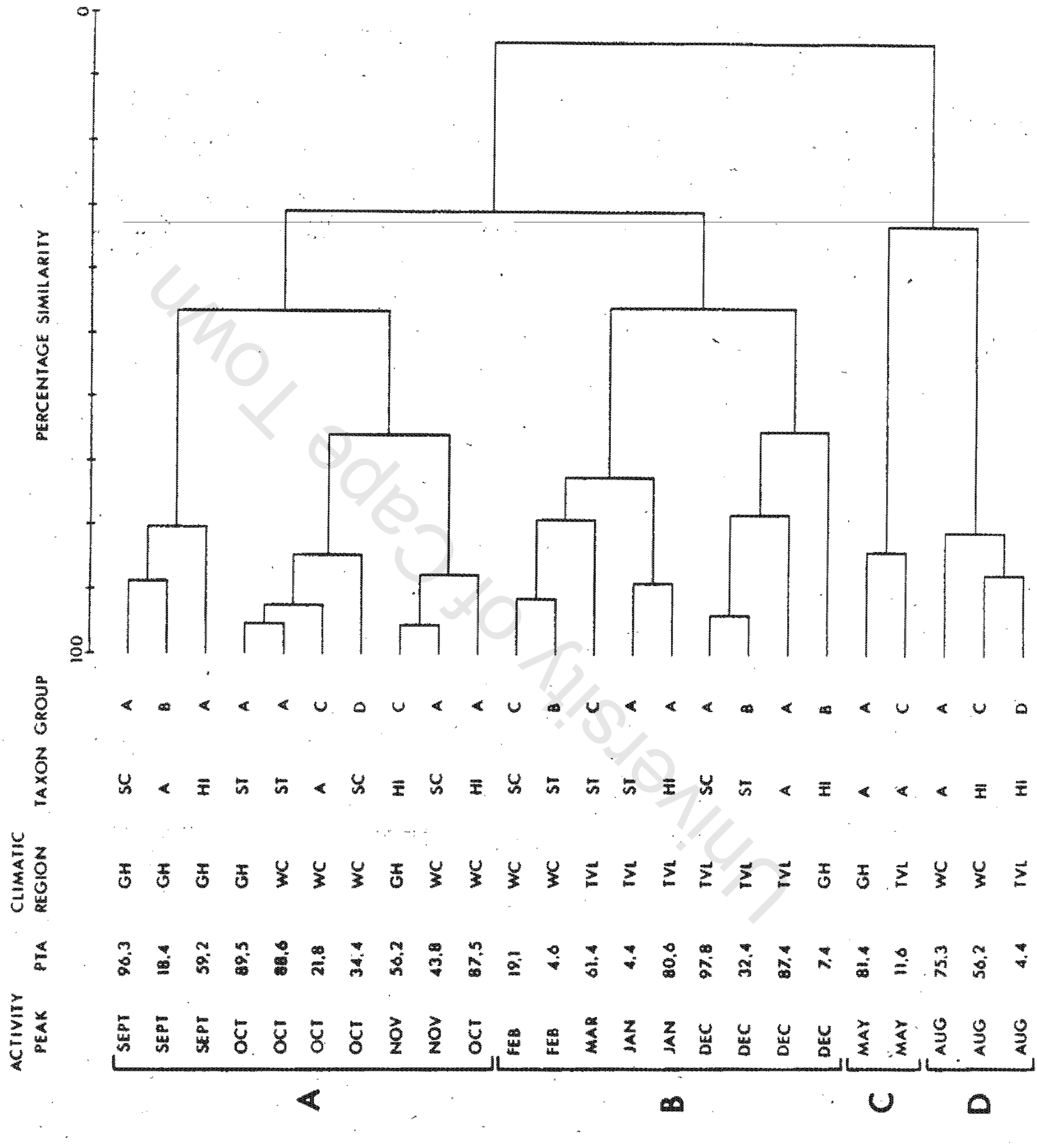
1.3.



ACTIVITY PEAK	PTA	CLIMATIC REGION	TAXON	TAXON GROUP	
SEPT	96,3	GH	SC	A	A
SEPT	18,4	GH	A	B	
SEPT	59,2	GH	HI	A	
OCT	89,5	GH	ST	A	
OCT	88,6	WC	ST	A	
OCT	21,8	WC	A	C	
OCT	34,4	WC	SC	D	
NOV	56,2	GH	HI	C	
NOV	43,8	WC	SC	A	
OCT	87,5	WC	HI	A	
FEB	19,1	WC	SC	C	B
FEB	4,6	WC	ST	B	
MAR	61,4	TVL	ST	C	
JAN	4,4	TVL	ST	A	
JAN	80,6	TVL	HI	A	
DEC	97,8	TVL	SC	A	
DEC	32,4	TVL	ST	B	
DEC	87,4	TVL	A	A	
DEC	7,4	GH	HI	B	
MAY	81,4	GH	A	A	C
MAY	11,6	TVL	A	C	
AUG	75,3	WC	A	A	D
AUG	56,2	WC	HI	C	
AUG	4,4	TVL	HI	D	

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Figure 1.4. Overall seasonal distribution patterns shown by groups of four higher taxonomic groupings of dung beetles from three different climatic regions derived from cluster analysis (Figure 1.3.)

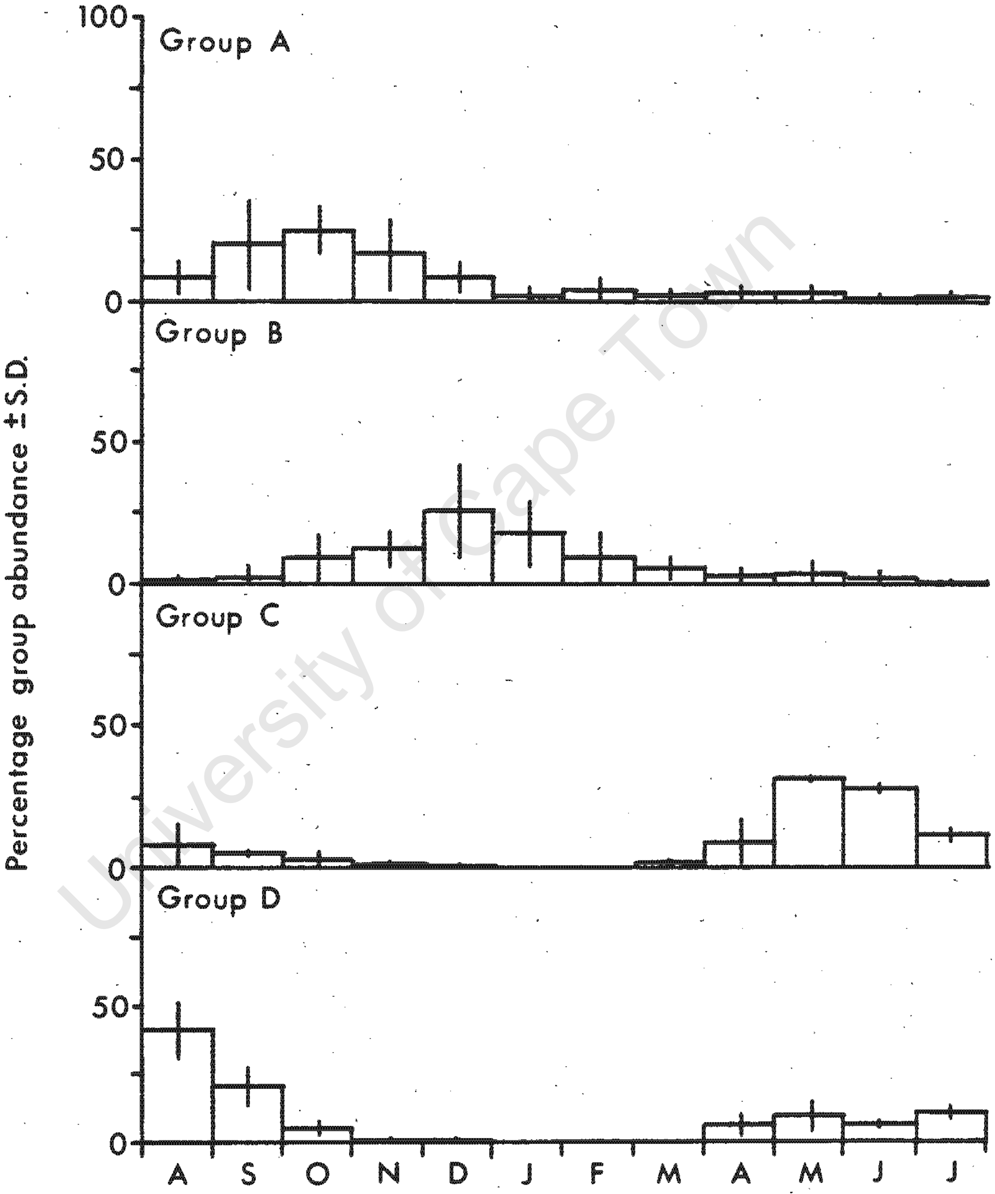

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Figure 1.5. Seasonal variation in abundance of six higher taxa of dung beetles in two climatic subregions of southern Africa.

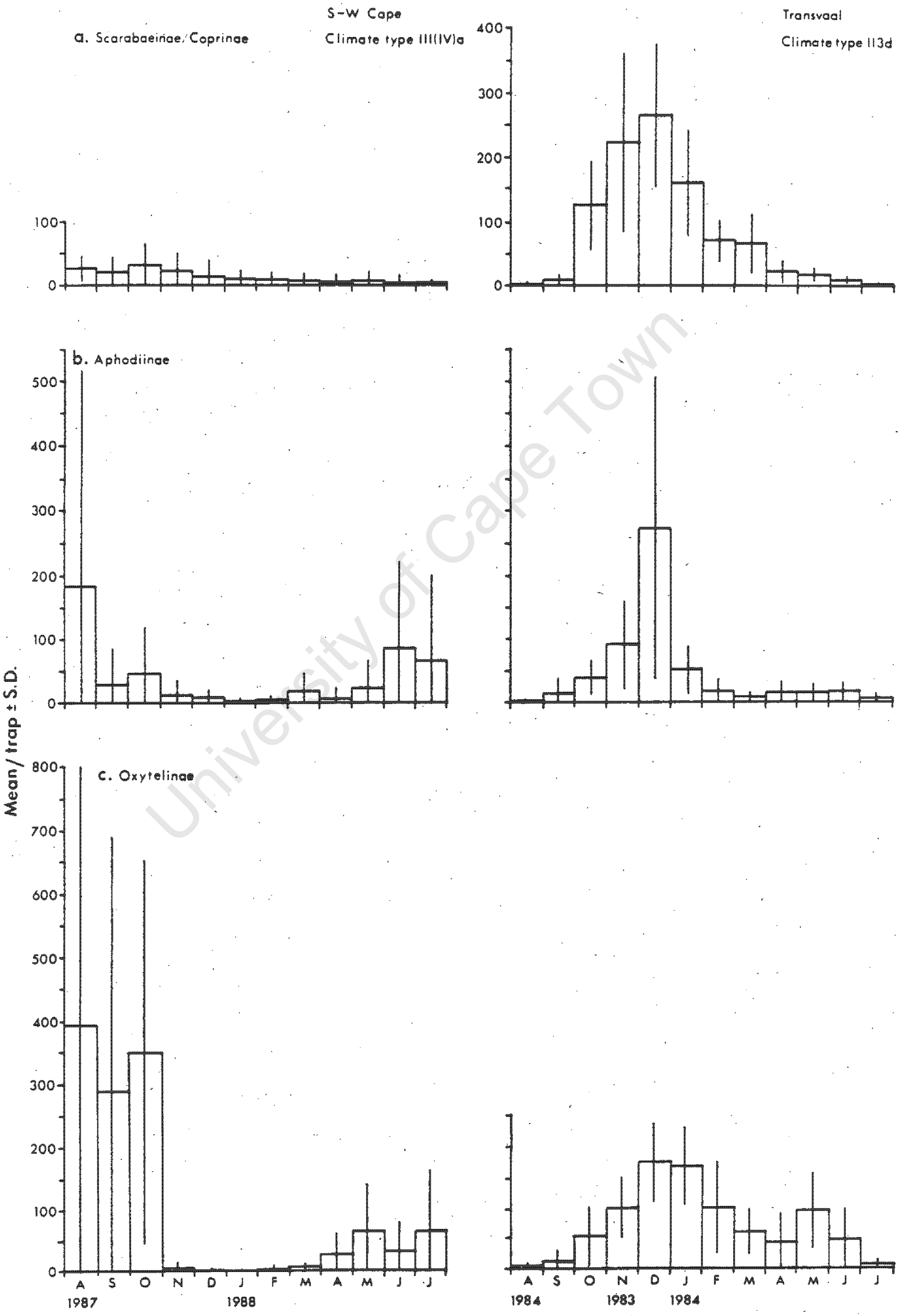

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Figure 1.5. cont.

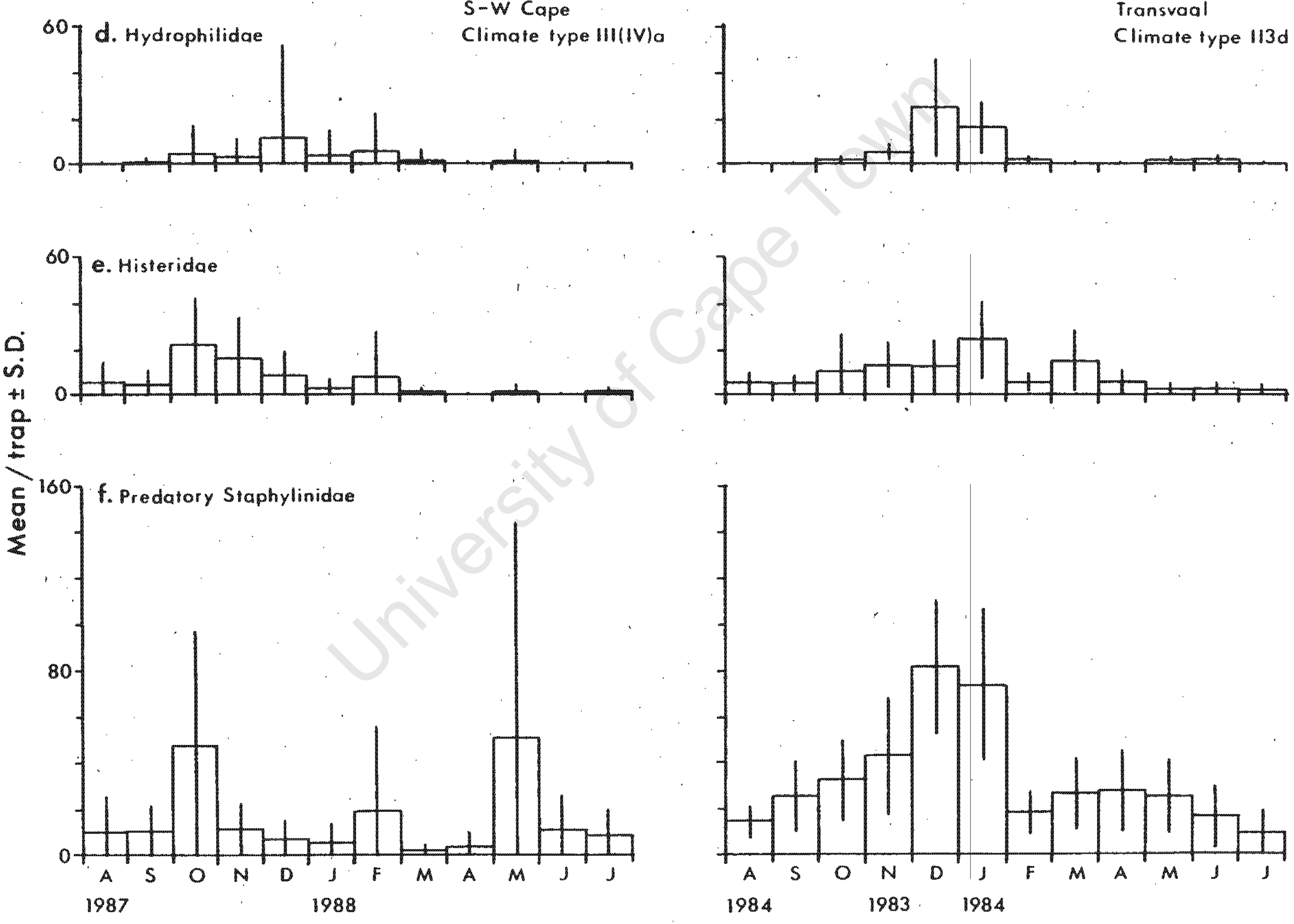

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Table 1.7. Similarities between dung beetle fauna in the south-western Cape and the Transvaal bushveld on sand.

Family/ Subfamily	Total number of species in S-W Cape	Number of species common to S-W Cape and Tvl	Percentage of species common to S-W Cape and Tvl
Scarabaeidae: Scarabaeinae/ Coprinae	45	4	8,9
Scarabaeidae: Aphodiinae	34	3	8,8
Staphylinidae: Oxytelinae	8	4	50,0
Hydrophilidae	7	4	57,0
Histeridae	31	6	19,4
Staphylinidae: predatory subfamilies*	67	21	31,3

*Staphylininae, Aleocharinae, Paederinae, Xantholininae, Tachyporinae.

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Table 2.1. Amount of the total variance accounted for by the first three factors in principal components analyses of the distribution of four taxonomic groupings of dung beetles across 11 habitats in the south-western Cape.

	Percentage of total variance			
	Scarabaeinae Coprinae	Histeridae	Aphodiinae	Staphylinidae Hydrophilidae
U.C.**				
Factor 1	41,5	52,8	70,5 (46,3)*	98,9 (84,2)
Factor 2	27,6	24,8	17,2 (24,2)	0,9 (9,1)
Factor 3	20,5	9,7	8,2 (13,7)	0,2 (4,7)
Total %	89,6	87,3	95,9 (84,2)	100,0 (98,0)
V.R.C.***				
Factor 1	37,3	46,2	57,7 (33,8)	59,5 (51,8)
Factor 2	26,9	30,7	28,1 (32,1)	44,0 (37,2)
Factor 3	25,5	10,5	10,0 (18,2)	0,0 (9,2)
Total %	89,7	87,4	95,6 (84,1)	99,5 (98,2)

*Results in parenthesis refer to PCAs conducted after the removal of data for *Coptochirus brachypterus* from the Aphodiinae and *Anotylus caffer* from the Staphylinidae.

**U.C. = Unrotated components.

***V.R.C. = Varimax rotated component loadings.

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Figure 2.1. Ordination plots derived from principal components analysis of the distribution of four higher taxonomic groups of dung beetles across 11 habitats in the south-western Cape with varimax rotation.

Three dimensional plots

a. Scarabaeinae/Coprinae.

Two dimensional plots

b. Histeridae.

c. Aphodiinae (including data for *Coptochirus brachypterus*).

d. Staphylinidae/Hydrophilidae (including data for *Anotylus caffer*).

e. Aphodiinae (excluding data for *Coptochirus brachypterus*).

f. Staphylinidae/Hydrophilidae (excluding data for *Anotylus caffer*).

Key

1. Cape of Good Hope Nature Reserve (9-10yr old fynbos).
2. Cape of Good Hope Nature Reserve (2-3yr old fynbos).
3. Bonne Attente, pasture.
4. Modderrivier, shrubland.
5. West Coast National Park, pasture.
6. West Coast National Park, shrubland.
7. Waylands, pasture.
8. Oranjefontein, pasture.
9. Pampoenvlei, shrubland on sand.
10. Pampoenvlei, shrubland on sandy loam.
11. Groote Post, pasture.

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2.1.

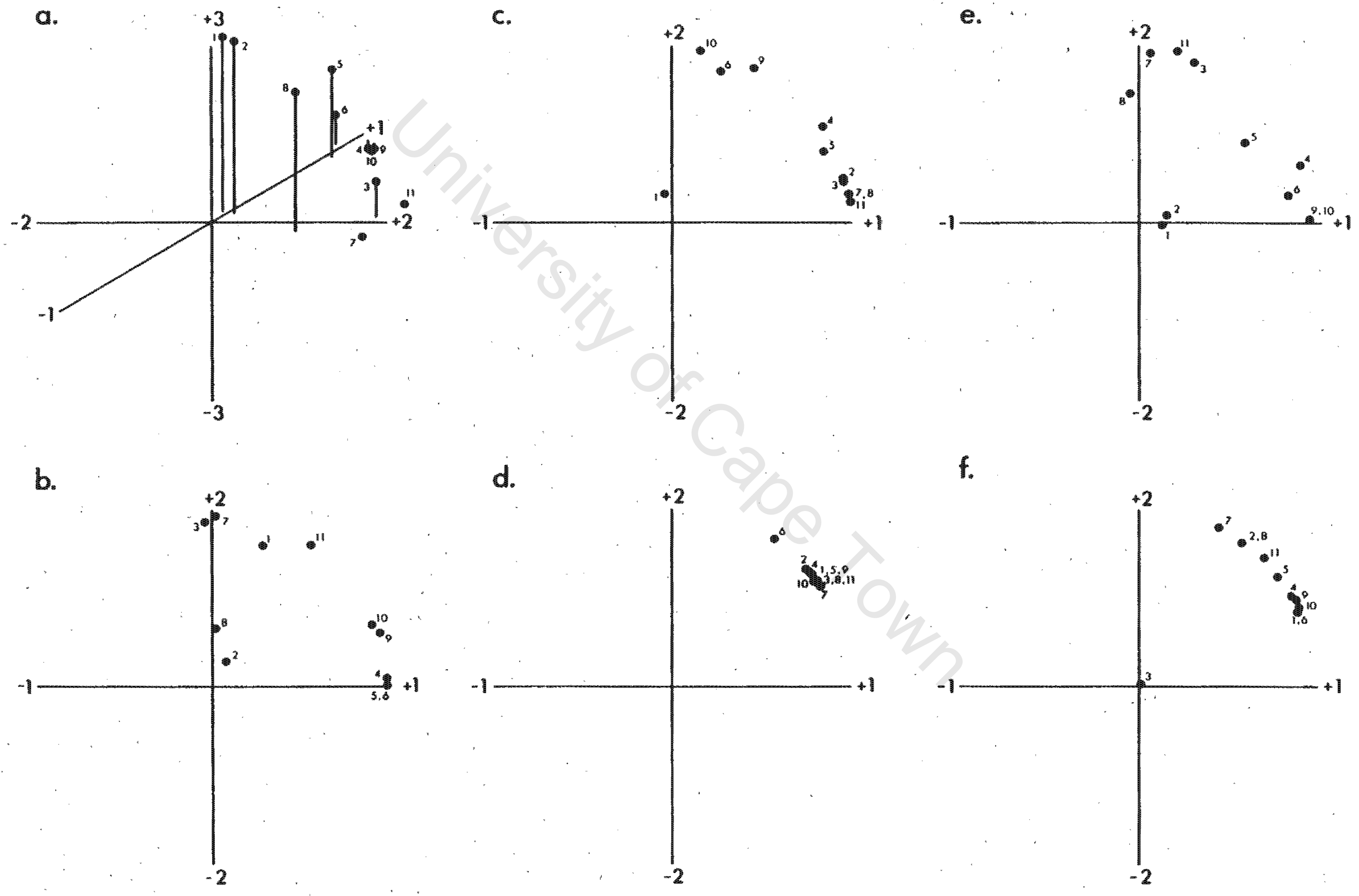

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Figure 2.2. Dendrogram showing trends in spatial distribution of abundant or species rich groups of dung Coleoptera in the south-western Cape.

PTA = Percentage of total faunal abundance (see Addendum Fig. AD9.).

TAXON
SC = Scarabaeinae/Coprinae.
HI = Histeridae.
A = Aphodiinae.
ST = Staphylinidae/Hydrophilidae.

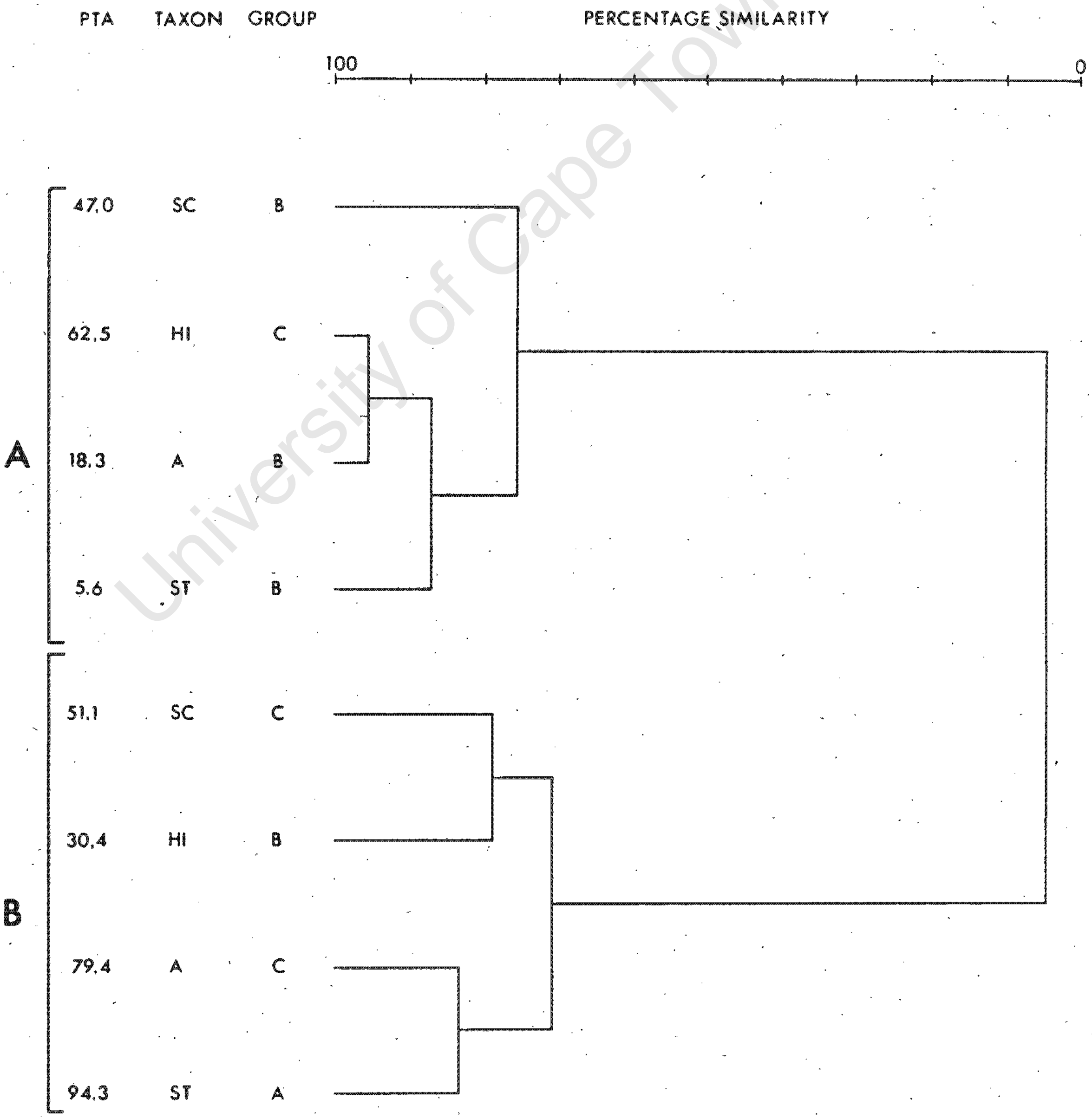

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Figure 2.3. Overall spatial distribution patterns shown by groups of four higher taxonomic groupings of dung beetles in the south-western Cape as derived from cluster analysis (Figure 2.2.).

Pasture sites: GP = Groote Post, BA = Bonne Attente, W = Waylands, WCG = West Coast National Park, O = Oranjefontein.

Shrubland sites: GHR = Cape of Good Hope Nature Reserve, 2-3yr old fynbos, GHM = Cape of Good Hope Nature Reserve, 9-10yr old fynbos, M = Modderrivier, PS = Pampoenvlei (sand), WCS = West Coast National Park, PL = Pampoenvlei (Sandy loam).

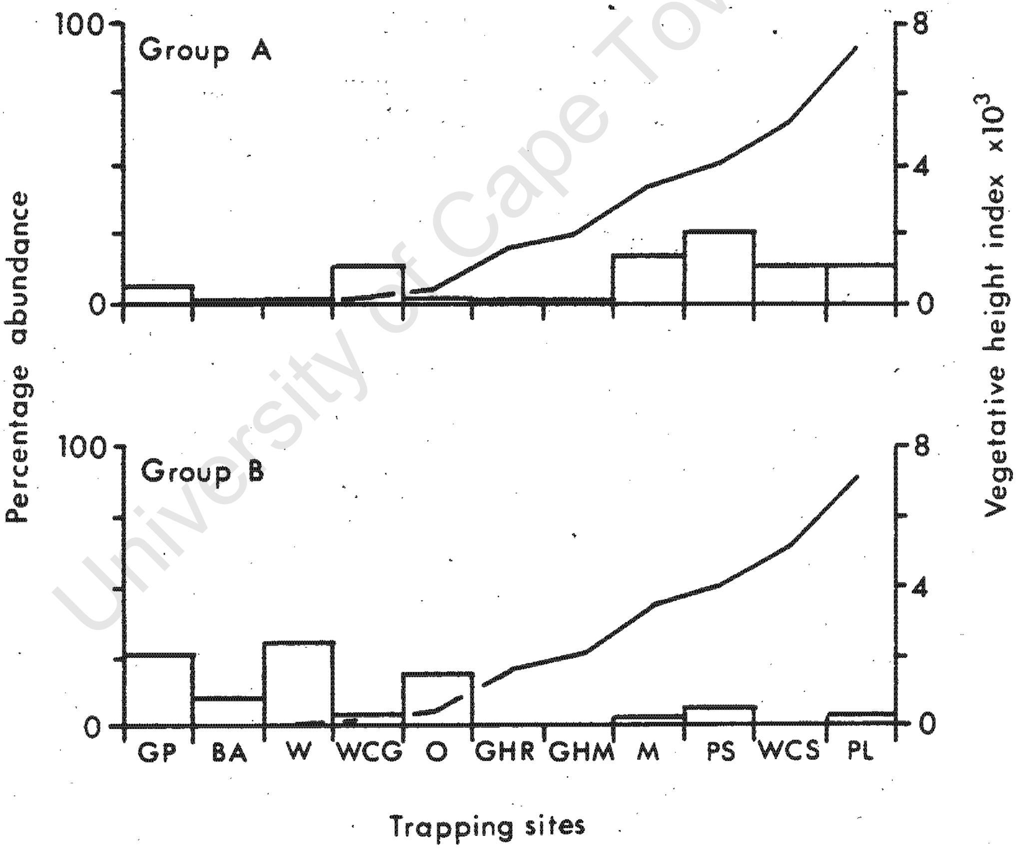

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Table 2.2. Distribution of species richness and abundance between groups of higher taxa of dung beetles derived from cluster analysis of their spatial distribution between vegetation types.*

Family/ subfamily	Total number of species in groups with distributions skewed towards:		Total percentage abundance of species in groups with distributions skewed towards:	
	Shrubland	Pasture	Shrubland	Pasture
Scarabaeinae/ Coprinae	15	22	51,5	48,5
Histeridae	12	10	63,4	36,6
Aphodiinae	11	12	18,4	81,6
Staphylinidae/ Hydrophilidae	10	37	5,6	94,4

*See Addendum, Figures AD8. and AD9.

Table 2.3. Habitat associations of the more abundant dung Coleoptera in West Coast National Park.

	Percentage of taxa			
Family/ subfamily	Associated with shrubland (P<0,05)*	Associated with pasture (P<0,05)*	No significant association	Number of taxa
Scarabaeidae: Scarabaeinae/ Coprinae	36,4	27,3	36,4	11
Scarabaeidae: Aphodiinae	0,0	11,1	88,9	9
Staphylinidae/ Hydrophilidae/ Histeridae	0,0	16,7	83,3	18

*t tests

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Table 3.1. Values of r squared for regression on rank position of coefficients of variation in spatial distribution across 11 trapping sites for four taxonomic groups in the south-western Cape using four different models.

Family/ subfamily	Values of r squared (%)			
	Regression model			
	Multiplicative	Linear	Reciprocal	Exponential
Scarabaeinae/ Coprinae	77,9	93,3	97,0	98,1
Aphodiinae	76,3	87,4	97,9	97,3
Histeridae	67,1	90,1	93,1	95,5
Staphylinidae/ Hydrophilidae	79,8	92,4	92,7	96,1

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Figure 3.1. Regression on rank position and coefficient of variation in distribution of species of dung beetles from four higher taxa between 11 trapping sites in the south-western Cape.

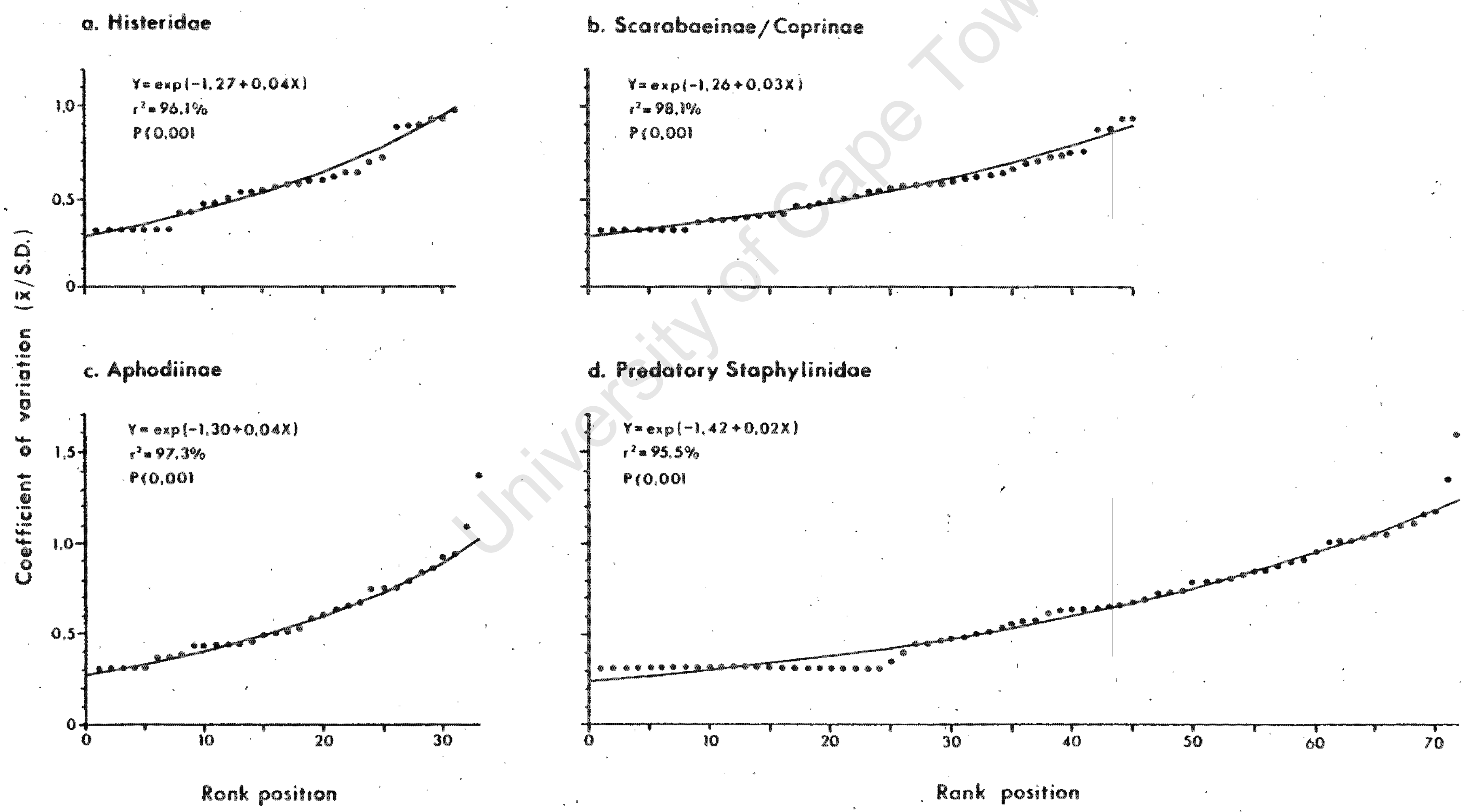

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Figure 3.2. Regression on rank position and size of geographical range in southern Africa for 45 species of Scarabaeinae/Coprinae recorded at 11 trapping sites in the south-western Cape.

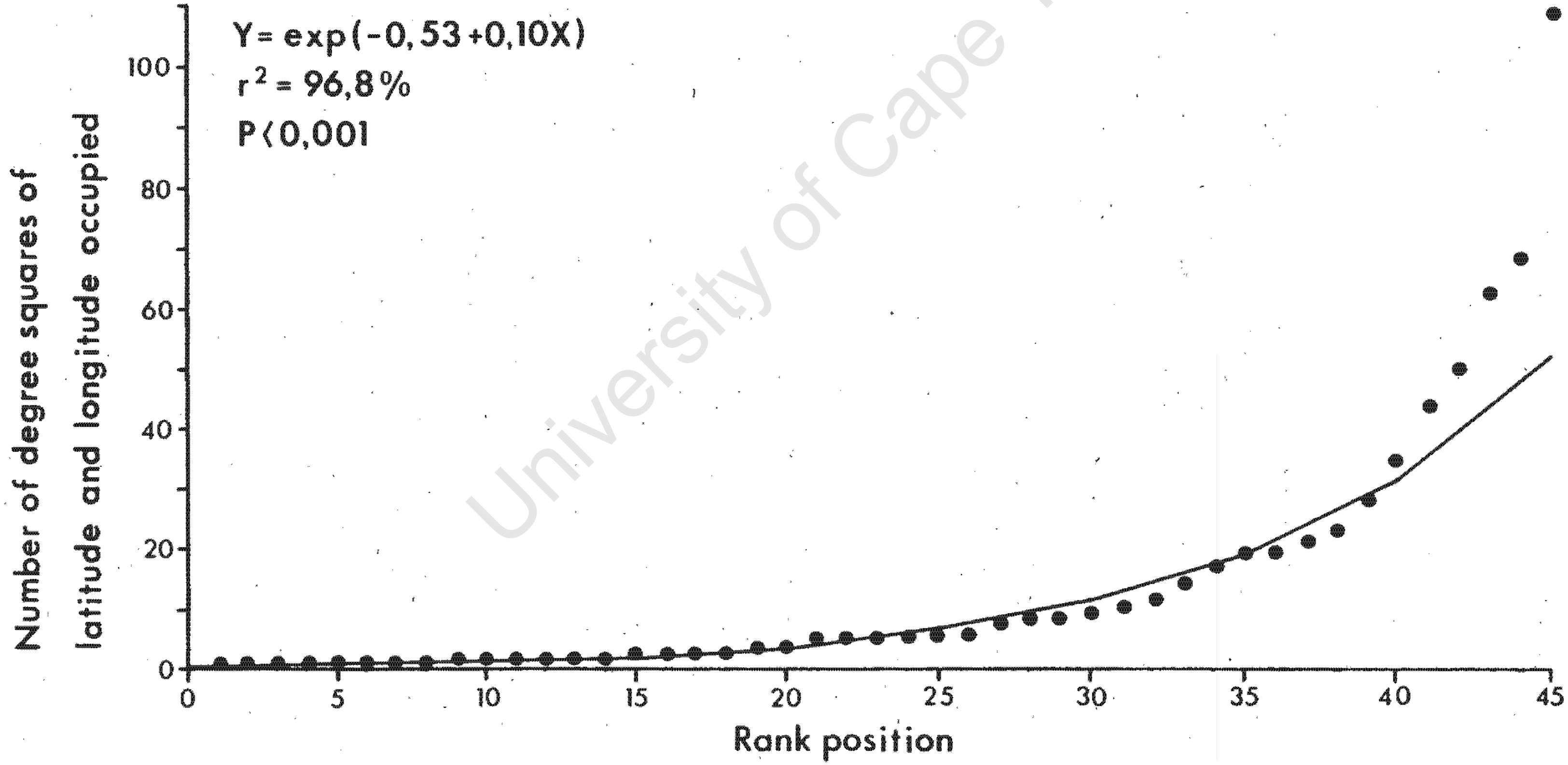

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Table 3.2. Mean values for an index representing relative generalization/ specialization of six higher taxa of dung beetles at 11 study sites in the south-western Cape.

Family/ subfamily	Mean index values (S.D.) for 11 study sites**	Mean index values (S.D.) for six shrubland sites	Mean index values (S.D.) for five pasture sites
Hydrophilidae	59,20 (4,02) a***	60,57 (4,84)	57,43 (1,33)
Scarabaeidae: Scarabaeinae/ Coprinae	70,74 (4,49) b	71,79 (1,16)	69,48 (6,31)
Histeridae	77,87 (11,24) c	77,48 (12,44)	78,35 (9,57)
Scarabaeidae: Aphodiinae	78,82 (4,96) c	76,84 (5,41)	81,20 (2,96)
Staphylinidae: (predatory subfamilies)	95,85 (5,98) d	99,44 (0,52)	*91,55 (6,65)
Staphylinidae: Oxytelinae	138,52 (0,95) e	138,98 (0,07)	137,97 (1,19)
Staphylinidae/ Hydrophilidae	130,17 (5,03)	132,18 (3,81)	127,76 (5,25)

*Significantly more specialist fauna relative to vegetation type ($P<0,05$, t tests)

**Values for species assemblages at each site derived from summing values for the percentage of total abundance for each species times the coefficient of variation (mean/standard deviation) in distribution across 11 study sites.

***Numbers followed by a different letter differed significantly ($P<0,05$, LSD intervals)

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Table 3.3. Values for a faunal generalization/specialization index* at 11 habitats in the south-western Cape.

Locality	Index for shrubland sites	Locality	Index for pasture sites
Cape of Good Hope Nature Reserve (9-10 yr old fynbos)	2034,2	Bonne Attente	2632,0
Cape of Good Hope Nature Reserve (2-3yr old fynbos)	2037,0	West Coast National Park	2072,3
Modderrivier	2034,0	Waylands	2787,6
West Coast National Park	1695,7	Oranjefontein	2524,7
Pampoenvlei (sand)	2133,2	Groote Post	2437,5
Pampoenvlei (sandy loam)	2166,2		
Mean (S.D.)	2016,8 (152,8)**		2490,8 (239,7)

*See text for derivation

**Significantly more specialist fauna (H = 5,63, d.f. = 5, P<0,02, Kruskal-Wallis test).

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Figure 3.3. Regression on rank percentage species abundance for four species assemblages of dung beetles showing different levels of numerical dominance by the most abundant species.

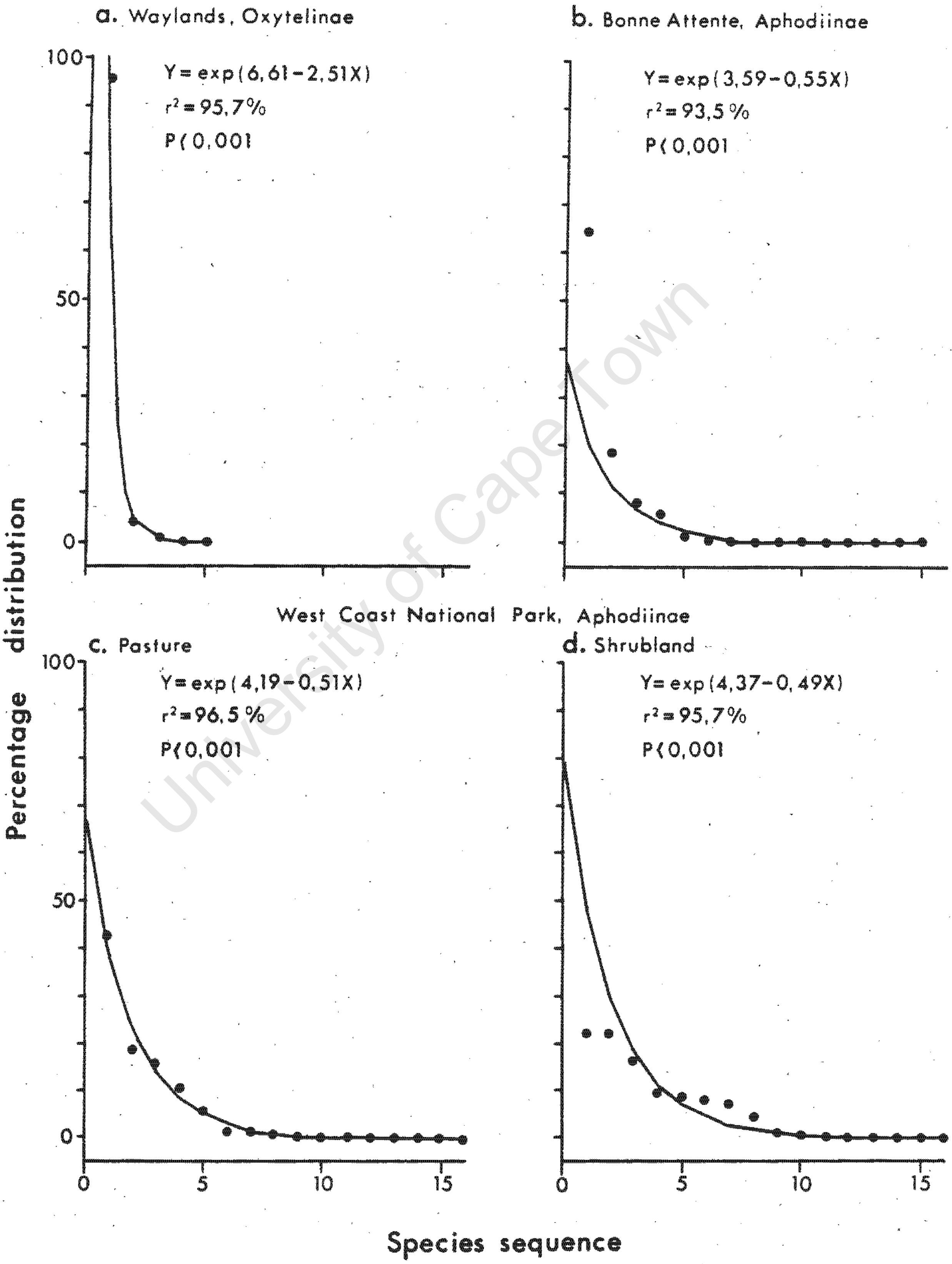

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Table 3.4. Values of r squared for regression on rank percentage species abundance of four species assemblages of dung beetles using four different regression models.

Species assemblage	Value of r squared (%)				Percentage abundance of numerically dominant species
	Regression model				
	Linear	Reciprocal	Multiplicative	Exponential	
Waylands Oxytelinae	53,2	80,3	95,9	95,7	95,6
Bonne Attente Aphodiinae	36,2	78,2	96,1	93,5	64,3
West Coast National Park Aphodiinae	56,3	38,4	84,9	96,9	42,2
West Coast National Park Aphodiinae	78,4	66,4	76,5	95,7	22,1

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Table 3.5. Generalization/specialization of Scarabaeinae/Coprinae at the first 12 levels of rank abundance for the fauna at 11 study sites in the south-western Cape.

Rank abundance level	Mean rank level (S.D.) based on size of geographical range from 1-45	
	Shrubland sites	Pasture sites
1	28,3 (1,9)	35,4 (6,9)
2	14,7 (7,5)	27,8 (9,4)
3	22,7 (6,6)	29,8 (7,9)
4	23,7 (9,7)	33,6 (14,0)
5	26,3 (10,5)	32,0 (7,3)
6	31,0 (4,6)	35,6 (4,8)
7	19,5 (15,4)	29,4 (15,3)
8	13,0 (5,7)	28,0 (11,6)
9	16,3 (9,6)	33,4 (7,0)
10	14,7 (12,9)	24,6 (8,1)
11	24,7 (13,3)	31,8 (7,6)
12	28,0 (11,9)	28,2 (10,0)
Mean (S.D.)	21,9 (5,9)*	30,8 (3,2)

*Significantly more specialised fauna in shrubland (H = 11,03, d.f. = 10, P<0,001, Kruskal-Wallis test).

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Table 4.1. Species richness and diversity of six higher taxa of dung beetles in shrubland and pasture in the south-western Cape.

Family/ subfamily	Mean species richness (S.D.)		Mean diversity (S.D.) defined by the reciprocal of the Berger-Parker dominance index (1/d)	
	Shrubland	Pasture	Shrubland	Pasture
Staphylinidae: Oxytelinae	3,5 (0,9)	4,4 (0,8)	1,00 (0,00)	1,02 (0,02)
Scarabaeidae: Aphodiinae	15,8 (2,1)	18,8 (2,8)	2,75 (1,03)*	1,47 (0,46)
Scarabaeidae: Scarabaeinae/ Coprinae	22,8 (7,9)	19,2 (3,3)	2,11 (0,92)	3,18 (0,86)
Hydrophilidae	3,7 (1,1)	6,0 (0,0)	1,65 (0,27)*	1,27 (0,13)
Histeridae	12,5 (4,5)	16,0 (1,6)	1,80 (0,66)	1,78 (0,38)
Staphylinidae: predatory subfamilies	33,3 (7,2)	37,6 (5,0)	2,84 (1,24)	4,83 (1,45)

*Species richness or diversity differed significantly between habitat types ($P < 0,05$, unpaired t tests).

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Figure 4.1. Regression on species richness and the Berger-Parker dominance index for species assemblages of dung beetles from six higher taxa at shrubland and pasture sites in the south-western Cape.

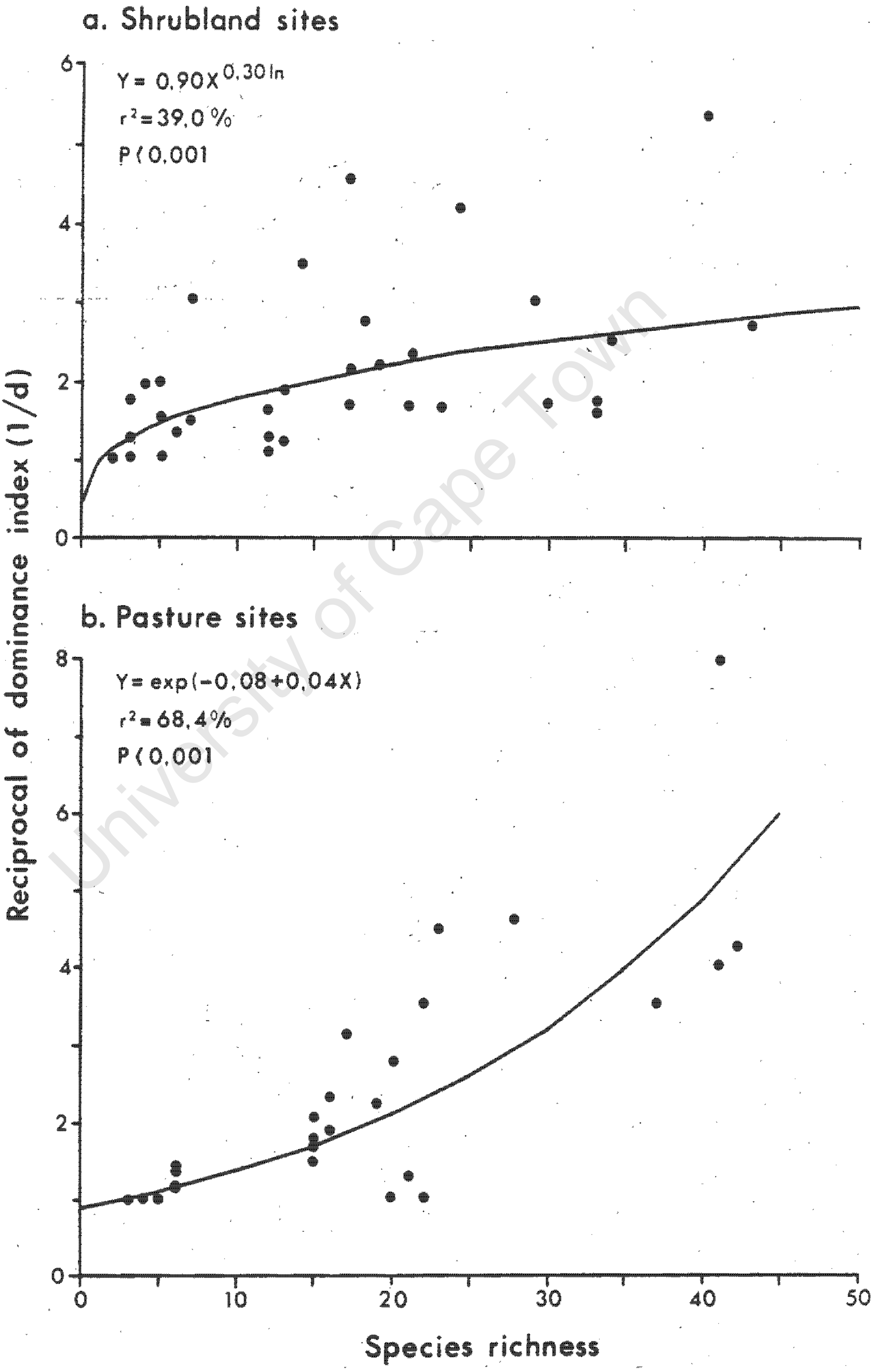

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Figure 4.2. Dendrogram showing the degree of similarity between rank species abundance sequences in species assemblages of six higher taxa of dung beetles from 11 habitats in the south-western Cape derived from cluster analysis of log.10 transformed data.

Figure 4.3. Dendrogram showing the degree of similarity between rank species abundance sequences in species assemblages of six higher taxa of dung beetles from 11 habitats in the south-western Cape derived from cluster analysis of data transformed to percentage abundance.

SPP.N = Species richness.

1/D = Reciprocal of Berger-Parker dominance index.

SITE
GHM = Cape of Good Hope Nature Reserve, 9-10yr old fynbos.
GHR = Cape of Good Hope Nature Reserve, 2-3yr old fynbos.
WCG = West Coast National Park, Pasture.
WCS = West Coast National Park, Shrubland.
O = Oranjefontein.
M = Modderrivier.
GP = Groote Post.
PL = Pampoenvlei (sandy loam).
W = Waylands.
BA = Bonne Attente.
PS = Pampoenvlei (sand).

TAXON
SC = Scarabaeinae/Coprinae.
ST = Predatory Staphylinidae.
HI = Histeridae.
A = Aphodiinae.
HY = Hydrophilidae.
O = Oxytelinae.

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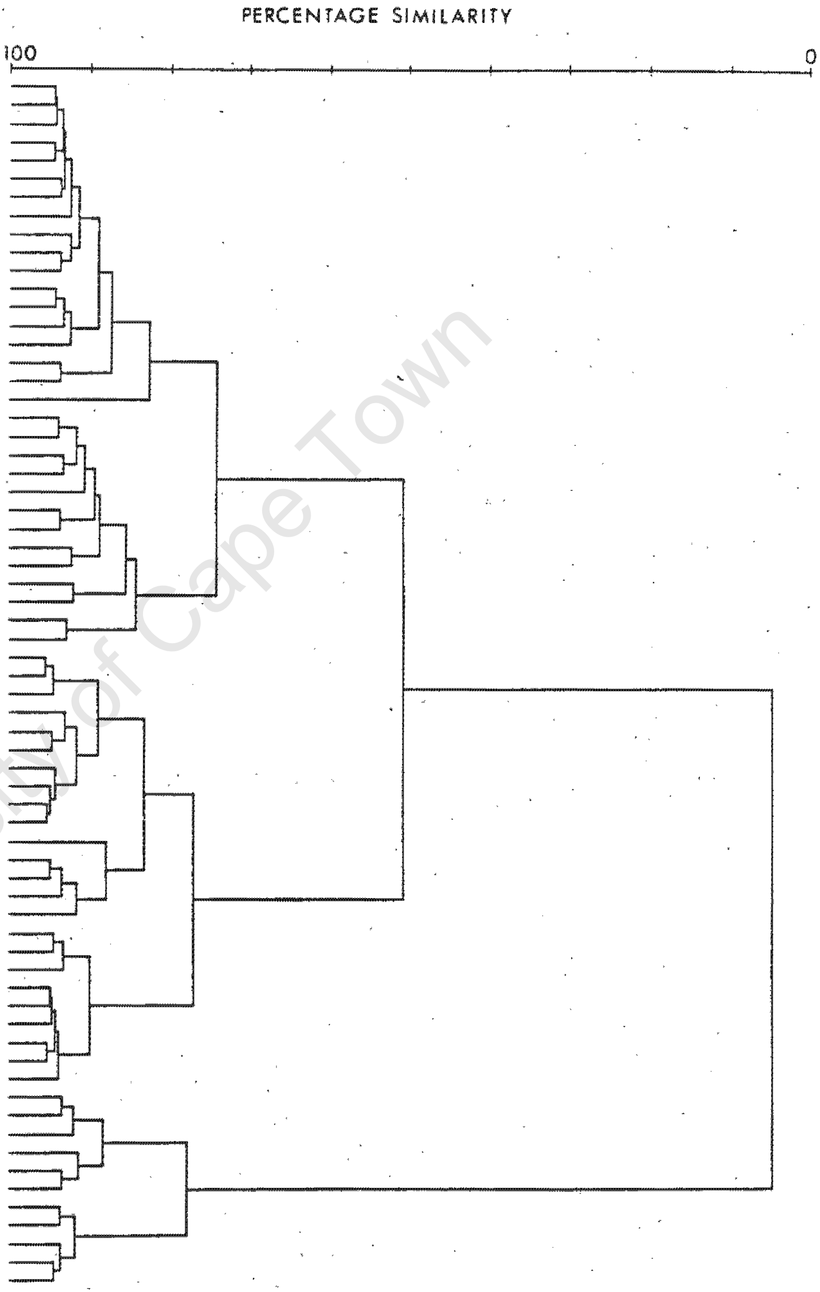
4.2.

	SPP. N	1/D	SITE	TAXON
A1	12	1,63	GHM	SC
	15	2,07	O	HI
	13	1,88	GHR	SC
	15	1.25	WCG	HI
	15	1,42	W	HI
	12	1,29	GHR	A
	13	1,24	M	HI
	15	1,56	BA	A
	14	3.57	GHM	A
	16	1,89	BA	HI
	12	1,10	WCB	HI
	21	2,32	PL	A
	19	2,21	PL	HI
	19	2,26	GP	HI
	17	1,69	PS	HI
	29	3,02	GHM	ST
	21	1,68	GHR	ST
	14	1,60	BA	SC
A2	22	3,57	WCG	SC
	20	2,77	O	SC
	17	3,16	W	SC
	17	2,14	M	A
	21	1,31	GP	A
	16	2.32	WCG	A
	18	2,77	PS	A
	24	4,17	WCB	SC
	17	4,53	WCB	A
	20	1,10	W	A
	22	1,05	O	A
	23	1,66	PL	SC
	28	4,64	BA	ST
B1	3	1,00	GHM	O
	2	1,00	GHR	O
	3	1.00	WCB	O
	5	1,01	BA	O
	4	1,01	O	O
	5	1,00	PL	O
	3	1,00	M	O
	3	1,01	WCG	O
	3	1.00	PS	O
	5	1,00	GP	O
	5	1,05	W	O
	6	1,13	BA	HY
	6	1,40	GP	HY
	6	1,19	O	HY
	6	1,16	W	HY
B2	3	1,31	GHM	HY
	3	1,76	M	HY
	6	1,33	GHR	HY
	6	1,45	WCG	HY
	5	1,54	PS	HY
	7	1,50	GHR	HI
	4	1,93	WCB	HY
	5	2,00	PL	HY
	7	3,03	GHM	HI
C1	33	1,60	M	SC
	37	3,54	WCG	ST
	30	1,73	PS	SC
	23	4,51	GP	SC
	34	2,52	M	ST
	33	1,74	WCB	ST
C2	41	4,05	W	ST
	42	4,27	O	ST
	43	2,68	PS	ST
	40	5,39	PL	ST
	41	7,64	GP	ST



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4.3.

	SPP. N	1/D	SITE	TAXON
A1	12	1.63	GHM	SC
	30	1.93	PS	SC
	33	1.74	WCB	ST
	25	1.66	PL	SC
	29	1.68	GHR	ST
	33	1.60	M	SC
	15	1.56	BA	A
	6	1.54	PS	HY
	17	1.69	PS	HI
	7	1.50	GHR	HI
	15	1.29	GHR	A
	21	1.31	GP	A
	6	1.45	WCG	HY
	6	1.40	GP	HY
	15	1.42	W	HI
	3	1.31	GHM	HY
	3	1.33	GHR	HY
A2	20	1.10	W	A
	6	1.13	BA	HY
	12	1.10	WCB	HI
	6	1.16	W	HY
	6	1.19	O	HY
	13	1.24	M	HI
	15	1.25	WCG	HI
	22	1.05	O	A
	5	1.05	W	O
	3	1.00	GHM	O
	3	1.00	WCB	O
	2	1.00	GHR	O
	3	1.00	M	O
	5	1.01	BA	O
	3	1.00	PS	O
	5	1.00	PL	O
	5	1.00	GP	O
	3	1.01	WCG	O
	4	1.01	O	O
B1	13	1.88	GHR	SC
	7	1.89	BA	HI
	17	2.14	M	A
	17	2.32	PL	A
	19	2.21	PL	HI
	16	2.33	WCG	A
	14	1.91	BA	SC
	5	2.00	PL	HY
	4	1.93	WCB	HY
	15	2.07	O	HI
	34	2.52	M	ST
	43	2.68	PS	ST
	3	1.76	M	HY
	22	3.57	WCG	SC
	17	3.16	W	SC
	14	3.47	GHM	A
	7	3.03	GHM	HI
	20	2.77	O	SC
	29	3.02	GHM	ST
	18	2.77	PS	A
	19	2.26	GP	HI
B2	24	4.17	WCB	SC
	17	4.53	WCB	A
	28	4.64	BA	ST
	37	3.54	WCG	ST
	23	4.51	GP	SC
	41	4.05	W	ST
	41	4.27	O	ST
	43	5.39	PL	ST
	41	7.64	GP	ST

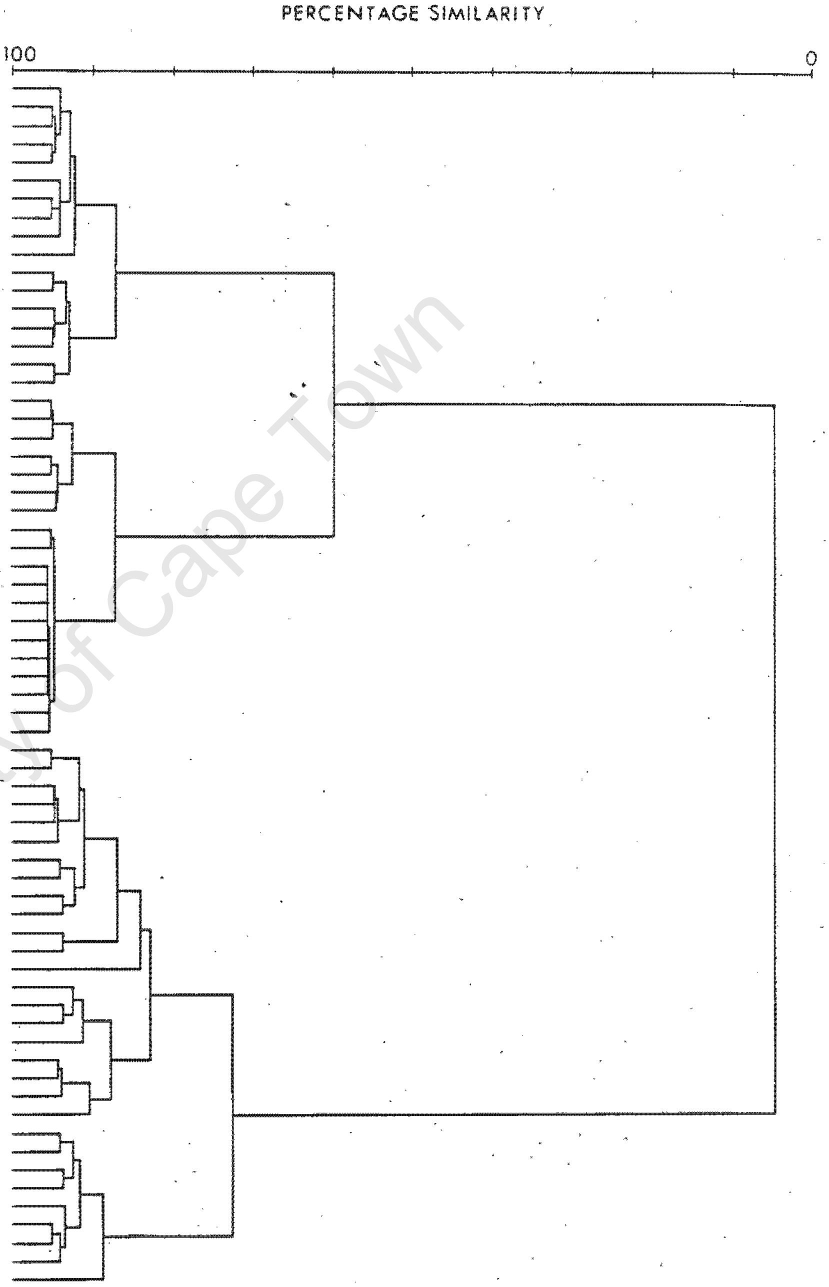

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Table 4.2. Mean species richness and diversity (reciprocal of the Berger-Parker dominance index) in groups of dung beetle taxa from different habitats derived from cluster analysis of ranked species abundance sequences (log.10 values).

Groups	Mean species richness (S.D.)	Mean diversity (1/d) (S.D.)	Number of habitats
B1	4,3 (1,4) a*	1,06 (0,11) a**	15
B2	5,1 (1,5) a	1,76 (0,51) ab	9
A1	16,2 (4,2) b	1,87 (0,61) ab	18
A2	20,4 (3,3) c	2,71 (1,21) b	13
C1	31,7 (4,4) d	2,61 (1,08) b	6
C2	41,2 (1,0) e	4,81 (1,66) c	5

*Species richness differed significantly between groups (F = 153,84; d.f. = 5,60; P<0,001; Analysis of variance).

**Dominance differed significantly between groups (F = 14,98; d.f. = 5,60; P<0,001; Analysis of variance).

Values in each vertical sequence coded by a different letter differed significantly (P<0,05, Scheffe's tests).

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Figure 4.4. Rank species abundance plots for six species assemblages of dung beetles showing diversity patterns in groups derived from cluster analysis of 66 rank species abundance sequences.

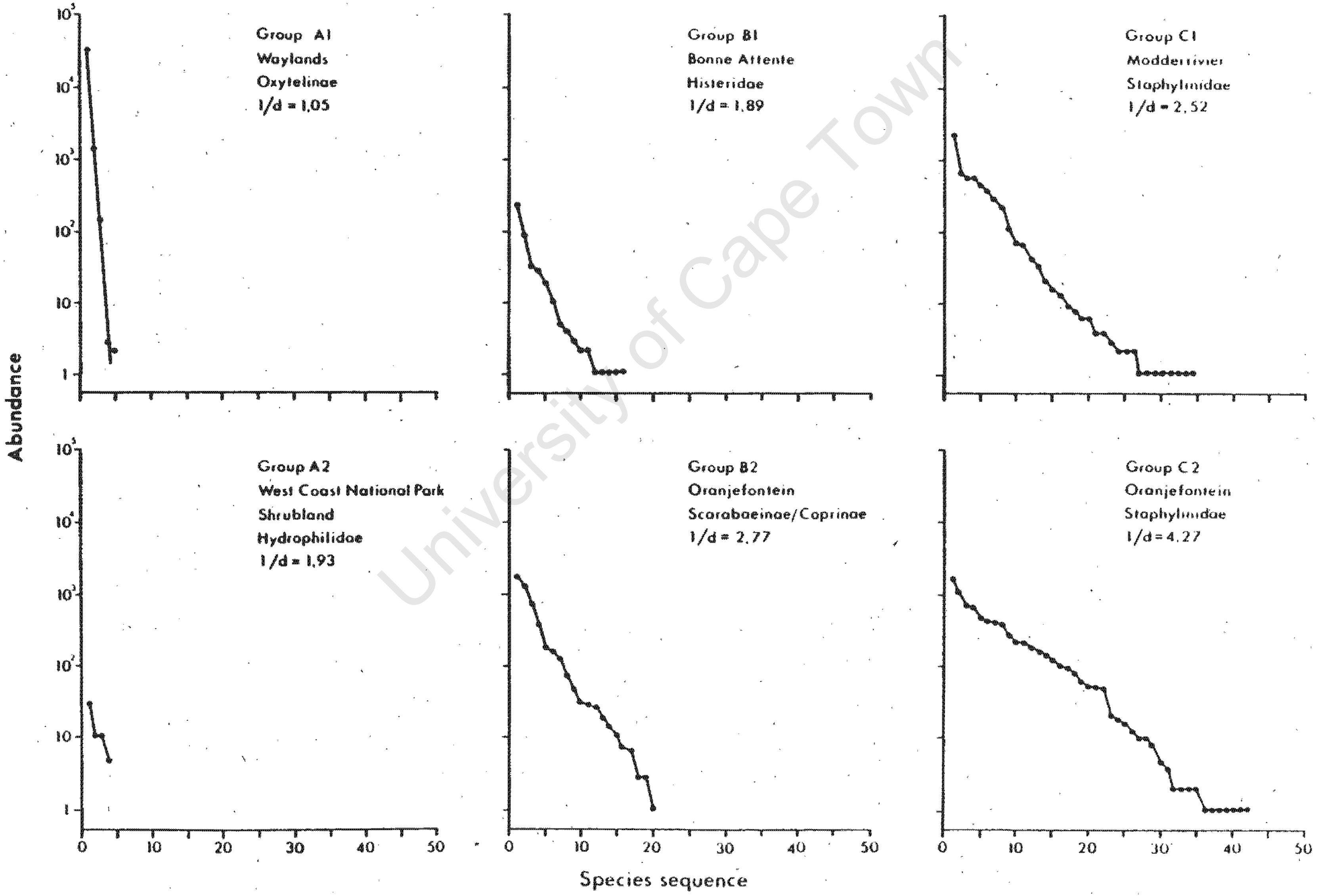

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Figure 4.5. Rank species abundance plot for the Histeridae at the Cape of Good Hope Nature Reserve in 9-10yr old fynbos.

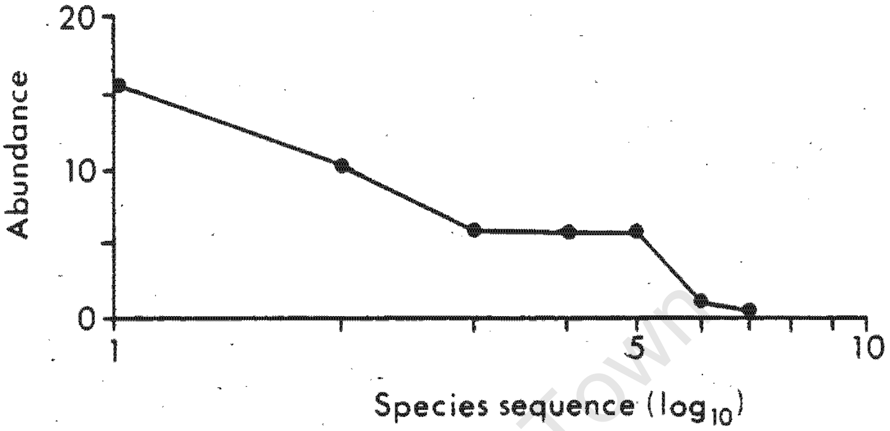

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Table 4.3. Mean species richness and diversity (reciprocal of the Berger-Parker dominance index) in groups of dung beetle taxa from different habitats derived from cluster analysis of ranked species abundance sequences (percentage abundance values).

Groups	Mean species richness (S.D.)	Mean diversity (1/d) (S.D.)	Mean % abundance of numerically dominant species (S.D.)	Number of habitats
A2	7,4 (5,8) a*	1,07 (0,08) a**	94,4 (7,0)	19
A1	16,2 (10,3) b	1,52 (0,15) a	66,5 (6,8)	18
B1	16,8 (9,5) b	2,46 (0,53) b	42,5 (8,6)	21
B2	32,8 (9,3) c	4,75 (1,13) c	22,0 (4,0)	9

*Species richness differed significantly between groups (F = 15,89; d.f. = 3,62; P<0,001; Analysis of variance).

**Dominance differed significantly between groups (F = 105,00; d.f. = 3,62; P<0,001; Analysis of variance).

Values in each vertical sequence coded by a different letter differed significantly (P<0,05, Scheffe's tests).

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Table 5.1. Distribution of scarabaeine and coprine species between tribes and subtribes in three climatic areas of southern Africa

Tribe/ subtribe	Percentage distribution of numbers of species		
	Climate type IV Cape of Good Hope Peninsula, south-western Cape	Climate type III(IV)a West coast of south-western Cape	Climate type II3d Transvaal bushveld
Scarabaeina	22,2	25,0	9,9
Canthonina	27,8	25,0	2,2
Sisyphina	0,0	2,5	3,3
Gymnopleurina	0,0	0,0	3,3
Coprina	16,7	10,0	11,0
Dichotomiina	5,6	7,5	5,5
Onitini	11,1	12,5	8,8
Onthophagini	11,1	10,0	44,0
Oniticellini	5,6	7,5	12,1
Total number of species	18	40	91

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Figure 5.1. Percentage distribution of numbers between the tribes and subtribes of Scarabaeinae and Coprinae in two habitat-types in three climatic subregions of southern Africa.

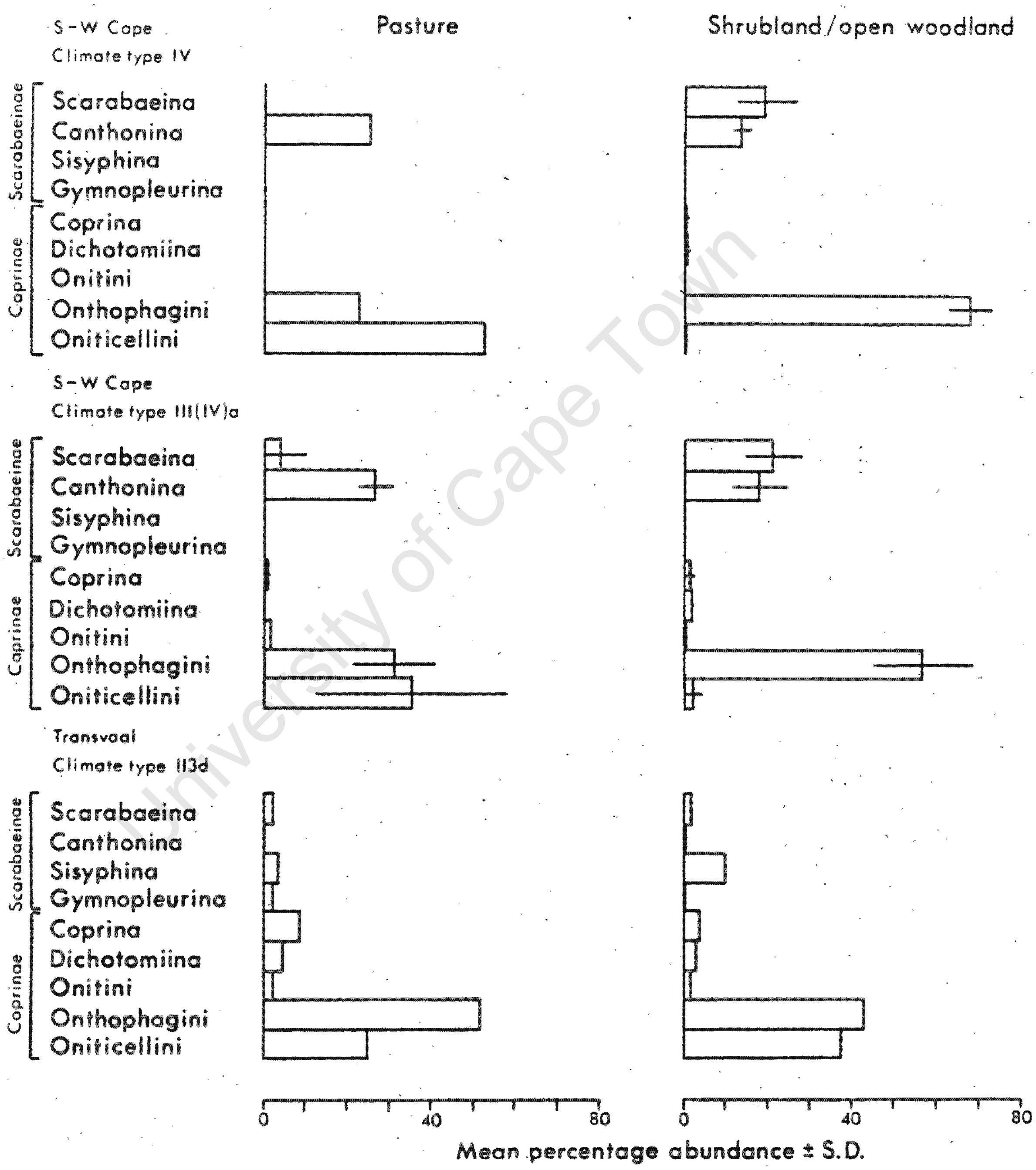

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Figure 5.2. Ordination plot derived from principal components analysis of the distribution of 45 south-western Cape species of Scarabaeinae and Coprinae across four climatic regions of southern Africa with groups of similar distribution outlined by the Clustan computer package.

Key

Group 1
- a. *Scarabaeus aesculapius, S. hippocrates, Epirinus bentoi, Odontoloma pusillum, Sisyphus quadricollis, Copris anceus.*
- b. *Scarabaeus rugosus, Epirinus comosus.*
- c. *Scarabaeus intricatus, Kheper bonellii, Epirinus scrobiculatus, Odontoloma dentinum, Aphengoecus multiserratus.*
- d. *Sceliages brittoni, Epirinus granulatus, Epirinus* sp. (undescribed), *Odontoloma* spp. a, b, *Macroderes* spp. a, b, c.
- e. *Scarabaeus canaliculatus, S. spretus.*
- f. *Scarabaeus suri.*
- g. *Sarophorus tuberculatus.*
- h. *Onthophagus immundus.*
- i. *Onthophagus minutus.*
- j. *Onthophagus giraffa.*
- k. *Copris capensis.*
- l. *Copris fidius.*
- m. *Onitis confusus.*

Group 2
- a. *Scarabaeus proboscideos.*
- b. *Scarabaeus satyrus.*
- c. *Metacatharsius latifrons.*
- d. *Chironitis hoplosternus.*

Group 3
- a. *Epirinus aeneus.*
- b. *Epirinus flagellatus.*
- c. *Onthophagus cameloides.*

Species 4-10

4. *Catharsius tricornutus.*
5. *Onitis aygulus.*
6. *Onitis caffer.*
7. *Chironitis scabrosus.*
8. *Euoniticellus intermedius.*
9. *Euoniticellus triangulatus.*
10. *Euoniticellus africanus.*

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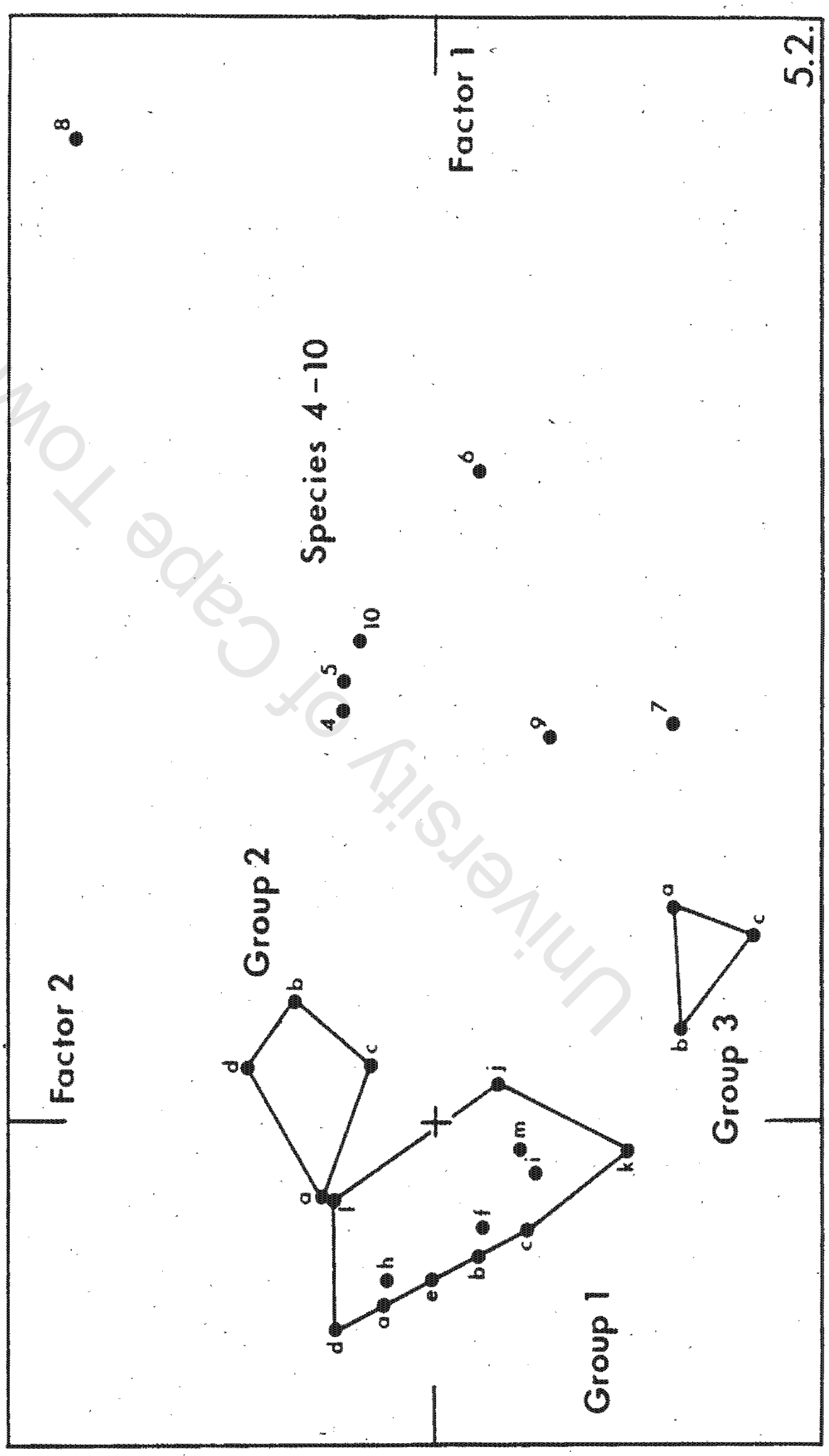

5.2.

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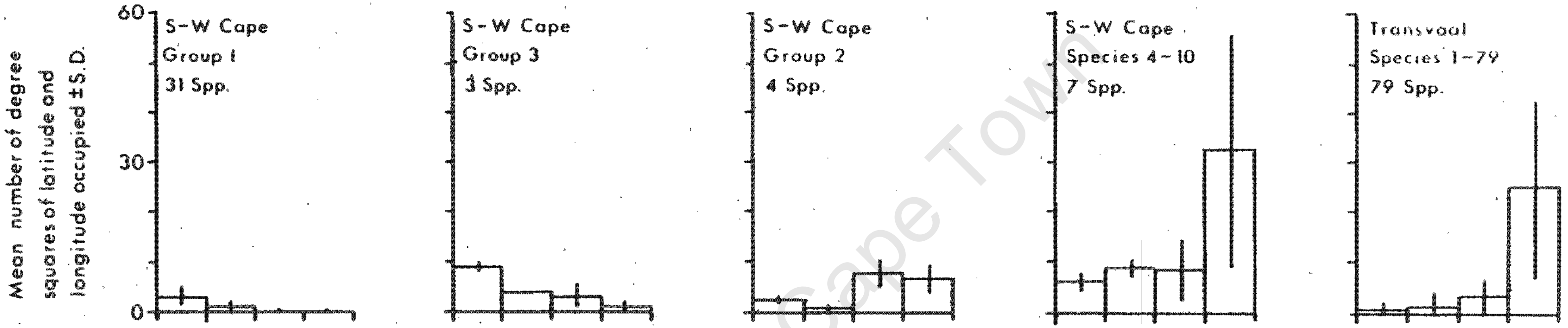
Figure 5.3. Distribution of five species groupings of Scarabaeinae/Coprinae between the four principal climatic regions of southern Africa.

a. Abundance



b. Relative abundance

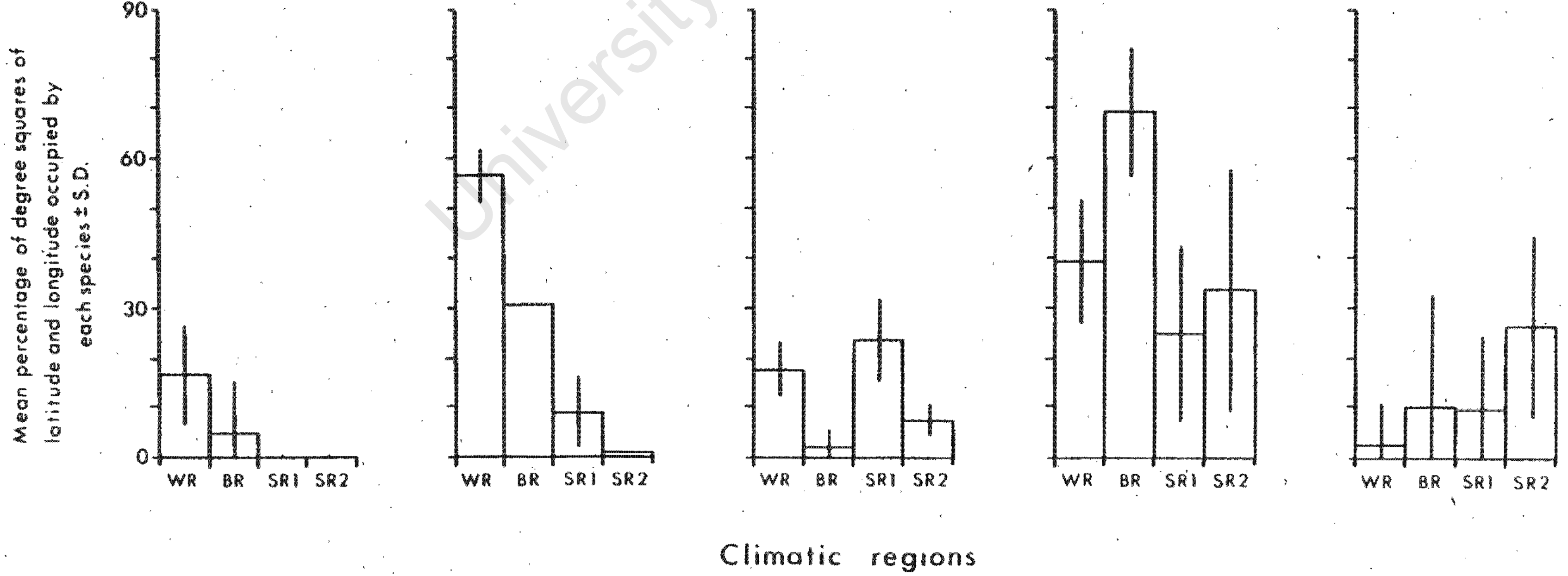


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Table 5.2. Distribution of groups of Scarabaeinae/Coprinae defined by principal components analysis between different habitats and climate types in the south-western Cape.

Group	Mean number/trap (S.D.)			
	Climate type IV		Climate type III(IV)a	
	Shrubland	Pasture	Shrubland	Pasture
Group 1	4,4 (8,1)	11,2 (26,7)	11,8 (22,8)	6,5 (13,8)
Group 2	0,0	0,0	0,1 (0,4)	0,03 (0,2)
Group 3	0,1 (0,4)	0,1 (0,3)	1,1 (2,6)	1,3 (3,3)
Species 4-10	0,01 (0,07)	12,5 (41,5)	0,3 (1,1)	4,8 (8,9)

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Figure 5.4. Seasonal distribution of four species groups of Scarabaeinae/Coprinae at trapping sites on the west coast of the south-western Cape in climate type III(IV)a.

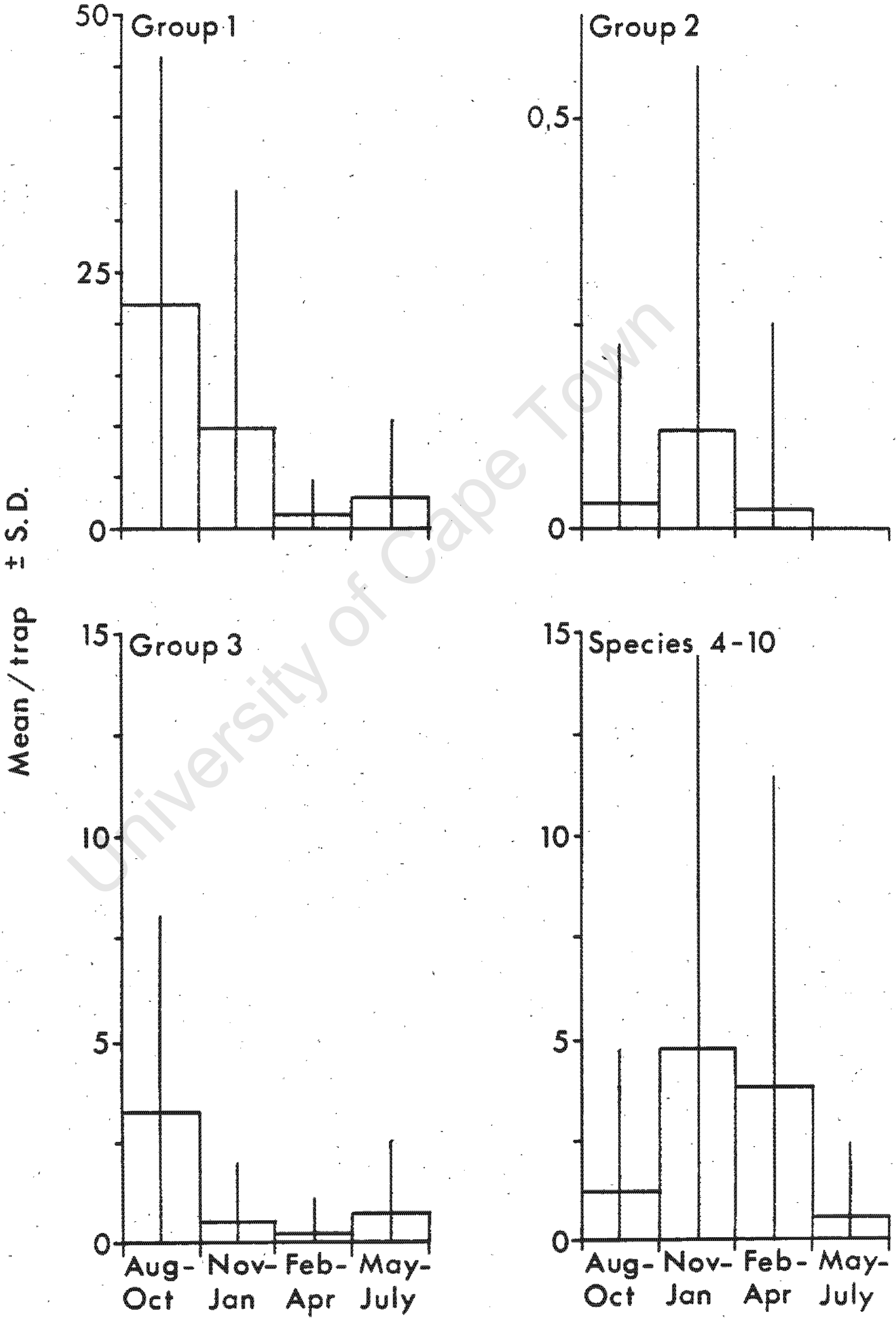

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Figure 5.5. Seasonal distribution of two species groups of Scarabaeinae/Coprinae at trapping sites on the Cape of Good Hope Peninsula in Climate type IV.

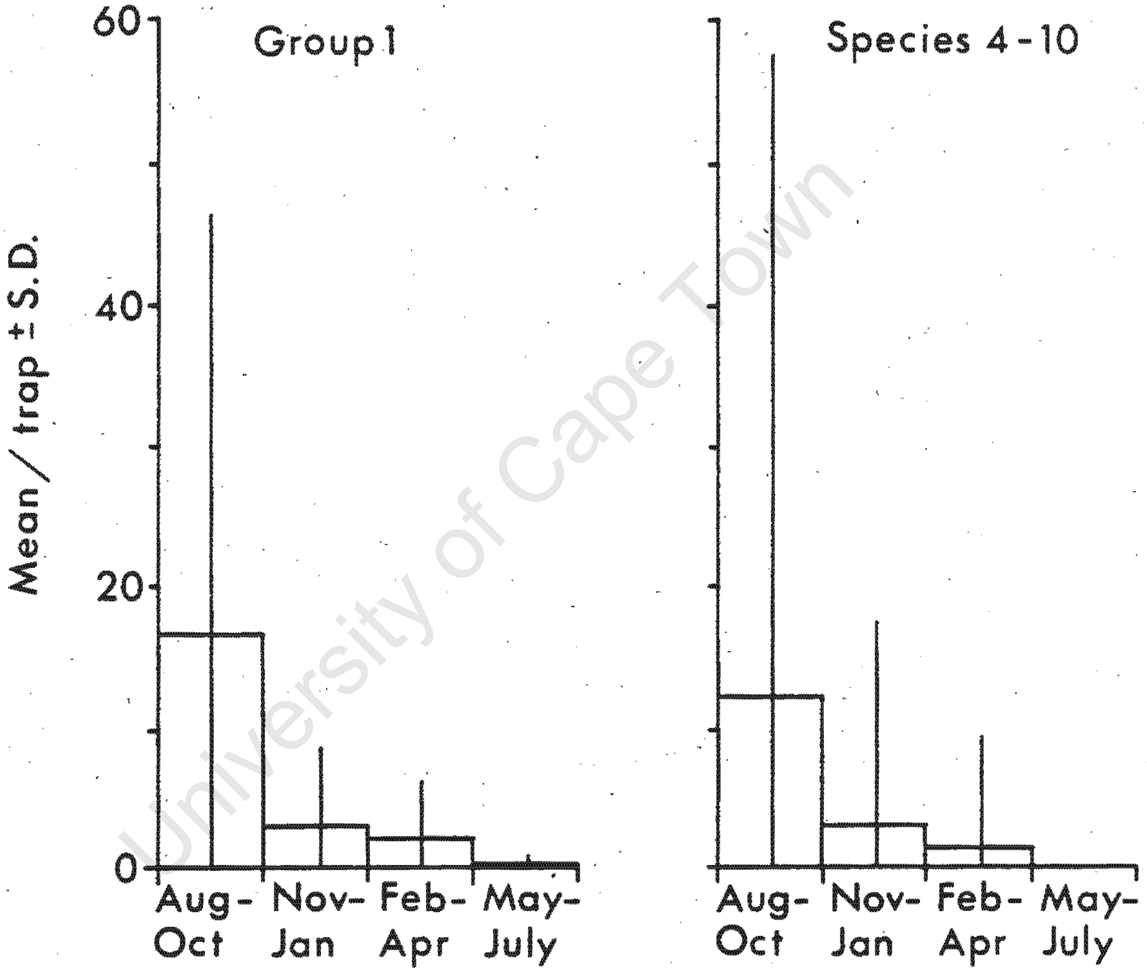

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Table 5.3. Species composition of groups of Scarabaeinae and Coprinae derived from principal components analysis of their geographical distribution across four climatic regions of southern Africa.

Tribe/ subtribe	Number of species		Percentage distribution of species	
	Groups 1 & 3	Group 2 Species 4-10	Groups 1 & 3	Group 2 Species 4-10
Scarabaeina	9	2	81,8	18,2
Canthonina	12	0	100,0	0,0
Sisyphina	1	0	100,0	0,0
Dichotomiina	4	0	100,0	0,0
Coprina	3	2	60,0	40,0
Onitini	1	4	20,0	80,0
Onthophagini	4	0	100,0	0,0
Oniticellini	0	3	0,0	100,0

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Table 5.4. Diel flight activity of groups of Scarabaeinae and Coprinae derived from principal components analysis of their geographical distribution across four climatic regions of southern Africa.

Flight activity	Percentage distribution of flight activity		
	South-western Cape		Transvaal
	Groups 1 & 3	Group 2 Species 4-10	Species 1-79
Crepuscular/ nocturnal	11,8 (6,3)*	54,6 (61,5)	57,0
Diurnal	88,2 (93,7)	45,4 (38,5)	43,0

*Values in parenthesis indicate percentage distribution of flight activity if *Copris fidius* and *Onitis confusus* are placed with Group 2/species 4-10. Both of these species have probably recently dispersed into the south-western Cape from the summer rainfall region.

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Table 5.5. Relative abundance of scarabaeine/coprine Groups 1 and 3, and Group 2/species 4-10 in two habitat types in the south-western Cape.

Shrubland sites	Mean number/ trap	Percentage distribution between		Pasture sites	Mean number/ trap	Percentage distribution between	
		Groups 1 & 3	Group 2 Species 4-10			Groups 1 & 3	Group 2 Species 4-10
Climate type IV				**Climate type IV**			
Cape of Good Hope Nature Reserve (9-10yr old fynbos)	2,7	99,7	0,3	**Bonne Attente**	24,3	47,7	52,5
Cape of Good Hope Nature Reserve (2-3yr old fynbos)	2,7	99,9	0,1				
Climate type III(IV)a				**Climate type III(IV)a**			
West Coast National Park	7,4	98,9	1,1	**West Coast National Park**	8,9	92,9	7,1
Modderrivier	24,0	99,4	0,6	**Waylands**	12,3	35,7	64,3
Pampoenvlei (sand)	17,1	93,2	6,8	**Oranjefontein**	13,6	73,4	26,6
Pampoenvlei (sandy loam)	4,8	96,7	3,3	**Groote Post**	15,4	53,4	46,6
Mean percentage occurrence (S.D.)	9,8 (8,0)	98,0 (2,2)*	2,0 (2,4)	**Mean percentage occurrence (S.D.)**	14,9 (5,2)	60,6 (20,2)	39,4 (20,3)

*Significant difference in abundance between groups ($t = 2{,}65$; d.f. = 5; $P < 0{,}05$, t test) based on comparison of mean number/trap.

Figure 5.6. Distribution of dung Scarabaeinae/Coprinae along trap lines in the Rondeberg Strip, the farm Groote Post and the Cape of Good Hope Peninsula.

a, c. Rondeberg Strip

Key to sites

1. Modderrivier, Sclerophyll shrubland.
2. Modderrivier, Sclerophyll shrubland.
3. Rondeberg, Restioid shrubland.
4. Rondeberg, Harrowed field.
5. Rondeberg, Pasture.
6. Vygevlei, Exotic *Acacia* shrubland.

b, d. Groote Post

Key to sites

1. Pasture strips.
2. Sclerophyll shrubland strips.
3. Sclerophyll shrubland.
4. Pasture.

e. Cape of Good Hope Peninsula

Key to sites

1. Cape of Good Hope Nature Reserve, Gateway, Sclerophyll shrubland.
2. Bonne Attente, Pasture.
3. Bonne Attente, Sclerophyll shrubland.

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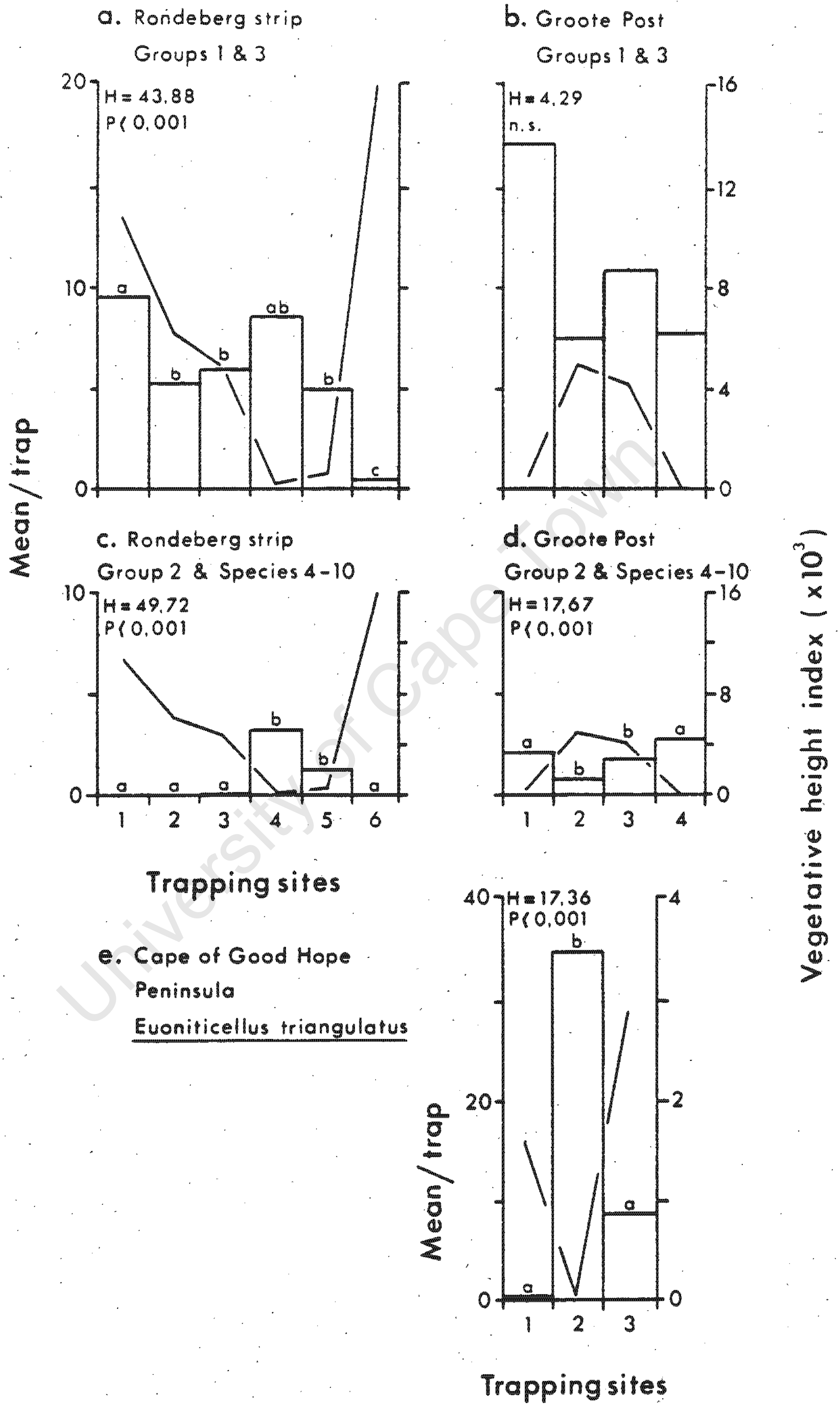
5.6.



a. Rondeberg strip
Groups 1 & 3

b. Groote Post
Groups 1 & 3

c. Rondeberg strip
Group 2 & Species 4-10

d. Groote Post
Group 2 & Species 4-10

e. Cape of Good Hope
Peninsula
Euoniticellus triangulatus

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Figure 6.1. Breeding strategies of 21 species of Scarabaeinae/Coprinae recorded on the west coast of the south-western Cape.

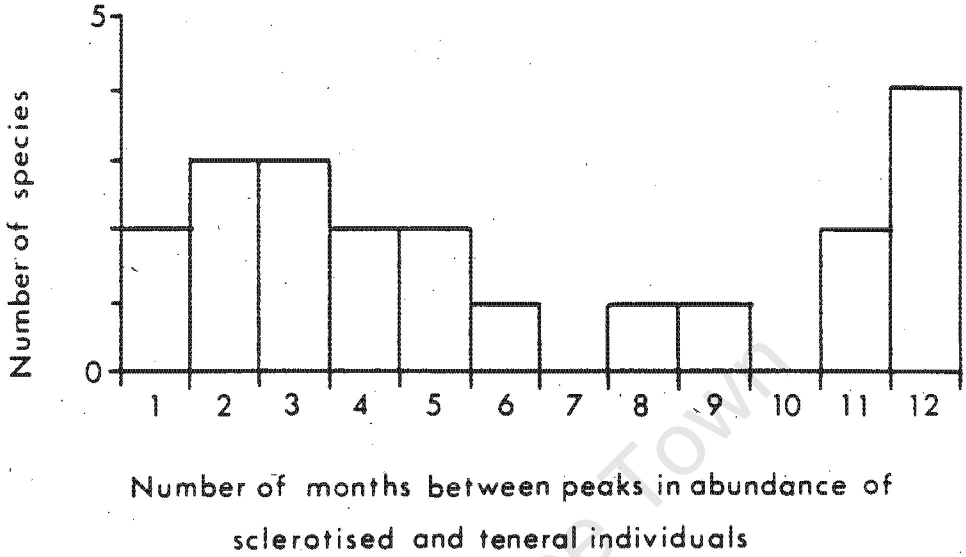

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Figure 6.2. Ordination plot with data points joined by a minimum spanning tree fitted by the Clustan computer package showing trends in the duration of time between seasonal peaks in abundance of sclerotised and callow filial adults of 21 species of Scarabaeinae/Coprinae on the west coast of the south-western Cape.

Key to the species in which code numbers represent the duration in months between seasonal peaks in abundance of sclerotised and filial adults.

			Group*
Species 1a-3a	1a.	*Scarabaeus suri*	1
	b.	*Odontoloma dentinum*	1
	2a.	*Onthophagus immundus*	1
	b.	*Epirinus aeneus*	1
	c.	*E. flagellatus*	1
	3a.	*Metacatharsius latifrons*	2
Species 3b-6	3b.	*Onthophagus minutus*	1
	c.	*Epirinus bentoi*	1
	4a.	*Onthophagus cameloides*	3
	b.	*Epirinus granulatus*	1
	5a.	*Odontoloma pusillum*	1
	b.	*Scarabaeus intricatus*	1
	6.	*Onthophagus giraffa*	1
Species 8-12d	8.	*Scarabaeus rugosus*	1
	9.	*Onitis aygulus*	4-10
	11a.	*Euoniticellus intermedius*	4-10
	b.	*E. triangulatus*	4-10
	12a.	*Scarabaeus proboscideos*	4-10
	b.	*Chironitis scabrosus*	4-10
	c.	*Kheper bonellii*	1
	d.	*Euoniticellus africanus*	4-10

*Groups 1 and 3 are endemic to the winter and bimodal rainfall regions. Group 2 and Species 4-10 are also widespread in the summer rainfall region.

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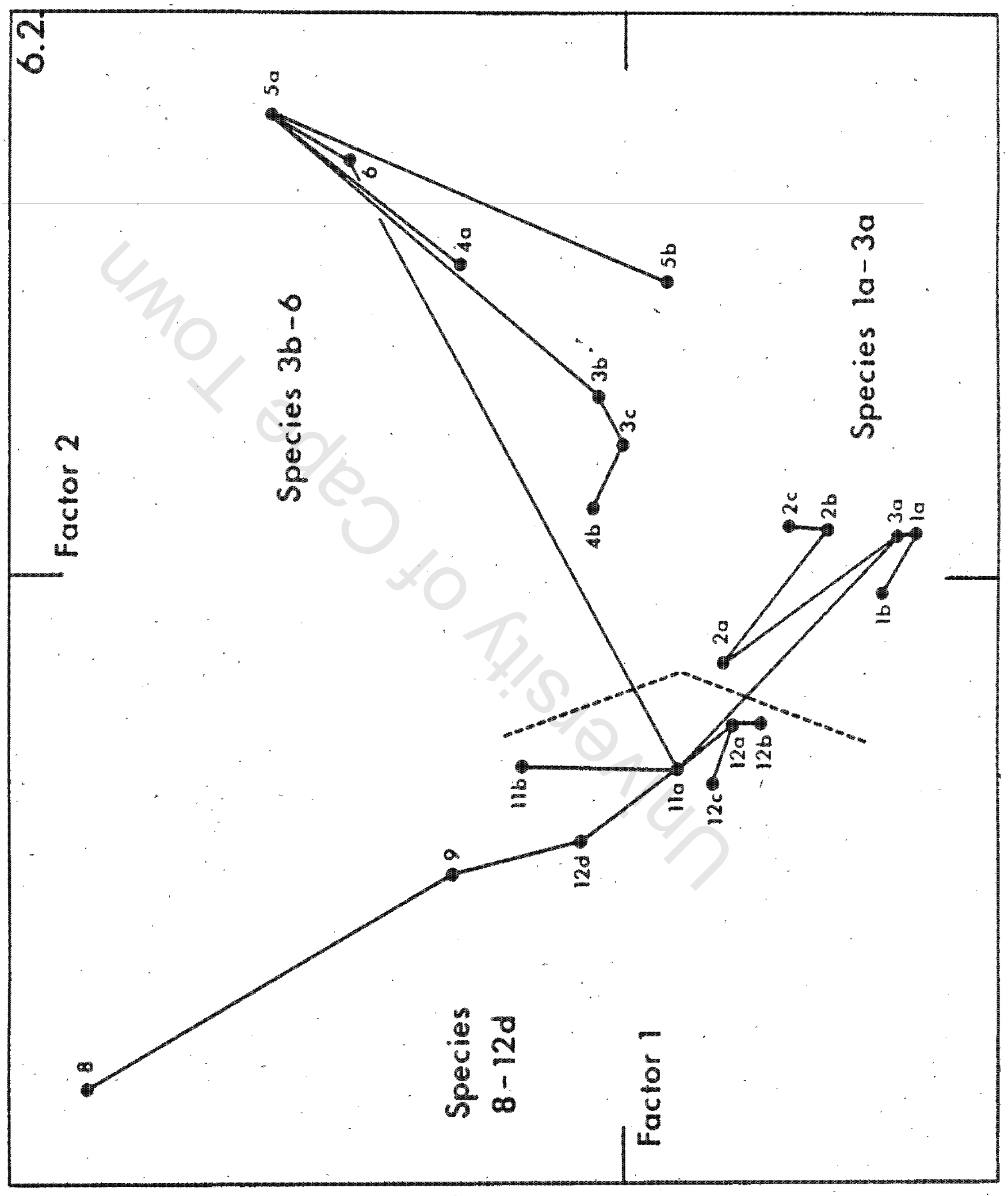

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Table 6.1. Size and geographical origin of three groupings of species defined in terms of the duration of time between peaks in abundance of sclerotised and callow filial adults on the west coast of the south-western Cape.

	Species 1-3a	Species 3b-6	Species 8-12d
Mean size of species (S.D.) (gm dry wt)	0,095 (0,168)	0,022 (0,017)	0,275 (0,279)
Range in size of species (gm dry wt)	0,002-0,468	0,001-0,048	0,009-0,71
Percentage of species comprising winter and bimodal rainfall elements (Group 1, 3)	83,3	100,0	25,0
Percentage of species comprising summer rainfall elements (Group 2/species 4-10)	16,7	0,0	75,0
Number of species	6	7	8

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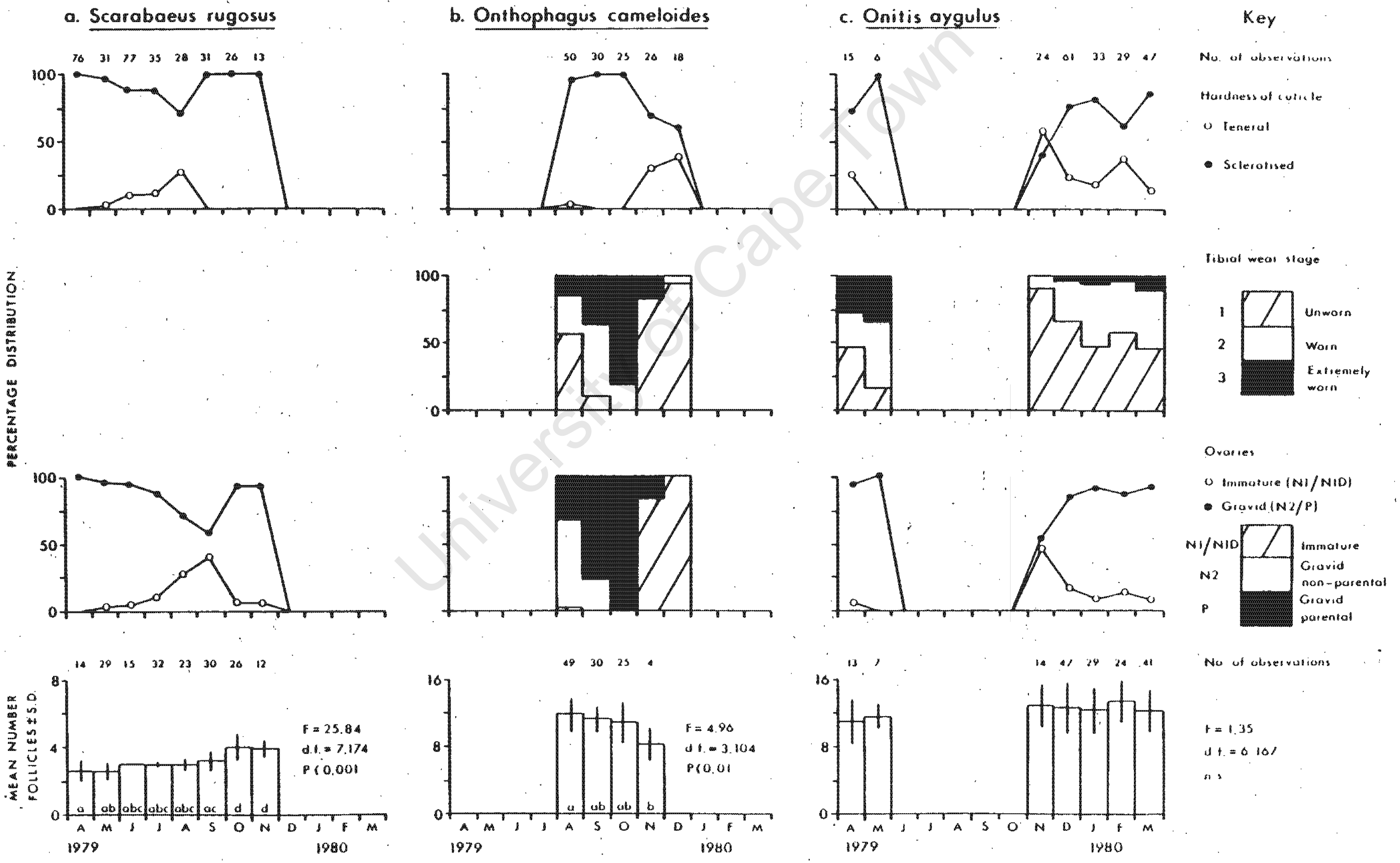
Figure 6.3. Breeding strategies of three species of Scarabaeinae and Coprinae recorded in the south-western Cape.



a. Scarabaeus rugosus

b. Onthophagus cameloides

c. Onitis aygulus

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Table 7.1. Level of endemism, month of peak abundance and fecundity in 45 species of **Scarabaeinae**/Coprinae recorded at 11 localities in the south-western Cape.

	Endemic to winter and bimodal rainfall regions at generic level	Endemic to winter and bimodal rainfall regions at species level with no close relatives in the summer rainfall region	Endemic to winter and bimodal rainfall regions at species level with close relatives in the summer rainfall region	Distribution centred in the winter and bimodal rainfall regions with marginal occurrence in the summer rainfall region	Distribution centred in the winter and bimodal rainfall regions with marginal occurrence in the summer rainfall region
	Group A	Group B	Group C	Group D	Group E
Known distribution in the winter rainfall region	*Aphengoecus multiserratus* (Aug.) *Macroderes* sp. a (May) *Macroderes* sp. b (Aug.) *Macroderes* sp. c (Aug.)	*Scarabaeus rugosus* (May)* *S. aesculapius* (Oct.) *S. hippocrates* (Sept.) *Sceliages brittoni* (Sept.) *Epirinus* sp. (June) *Epirinus comosus* (Aug.) *E. granulatus* (May) *E. bentoi* (Aug.) *Copris anceus* (Aug.) *Onthophagus immundus* (Aug.)	*Kheper bonellii* (Sept.) *Scarabaeus intricatus* (Oct.) *S. canaliculatus* (Nov.) *S. spretus* (Sept.) *Epirinus scrobiculatus* (May) *Odontoloma dentinum* (Aug.) *O. pusillum* (May) *Odontoloma* sp. a (Aug.) *Odontoloma* sp. b (Aug.) *Sisyphus quadricollis* (Oct.)		
Known distribution in the winter and bimodal rainfall regions		*Copris capensis* (Aug.) *Sarophorus tuberculatus* (Aug.)	*Scarabaeus suri* (Nov.) *Onthophagus giraffa* (Sept.) *O. minutus* (Aug.)		
Known distribution all rainfall regions				*Epirinus aeneus* (Aug.) *E. flagellatus* (Aug.) *Onthophagus cameloides* (Aug.)	*Scarabaeus proboscideus* (Oct.) *S. satyrus* (Dec.) *Copris fidius* (Dec.) *Catharsius tricornutus* (Oct.) *Metacatharsius latifrons* (Nov.) *Onitis confusus* (Apr.) *O. aygulus* (Nov.) *O. caffer* (May) *Chironitis scabrosus* (Dec.) *Chironitis hoplosternus* (Dec.) *Euoniticellus africanus* (Jan.) *E. intermedius* (Jan.) *E. triangulatus* (Jan.)
Mean number of follicles/ovary	4,5	2,8	4,1	6,3	11.3
Number of scarabaeine spp.	1	8	11	2	2
Number of coprine spp.	3	4	2	1	11

***Month of greatest abundance**

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Table 7.2. Seasonal peaks in abundance of groups of Scarabaeinae/Coprinae based on the two months of greatest abundance of each species.

	Percentage distribution												
Group	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	Number of species
Group A		28,6	28,6		28,6	14,3							4
Group B		4,9	4,9	4,9	28,2	23,9	19,0	9,2	4,9				12
Group C		7,8			23,8	20,2	23,8	20,2	4,2				13
Group D					50,0		50,0						3
Group E	4,5	4,5			4,5		8,4	17.3	21,8	21,8	17,3		13

Group A: Endemic to the winter and bimodal rainfall regions at generic level.
Group B: Endemic to the winter and bimodal rainfall regions with no close relatives in the summer rainfall region.
Group C: Endemic to the winter and bimodal rainfall regions with close relatives in the summer rainfall region.
Group D: Distribution centred in the winter and bimodal rainfall regions with marginal occurrence in the summer rainfall region.
Group E: Distribution centred in the summer rainfall region but also widespread in the winter and bimodal rainfall regions.

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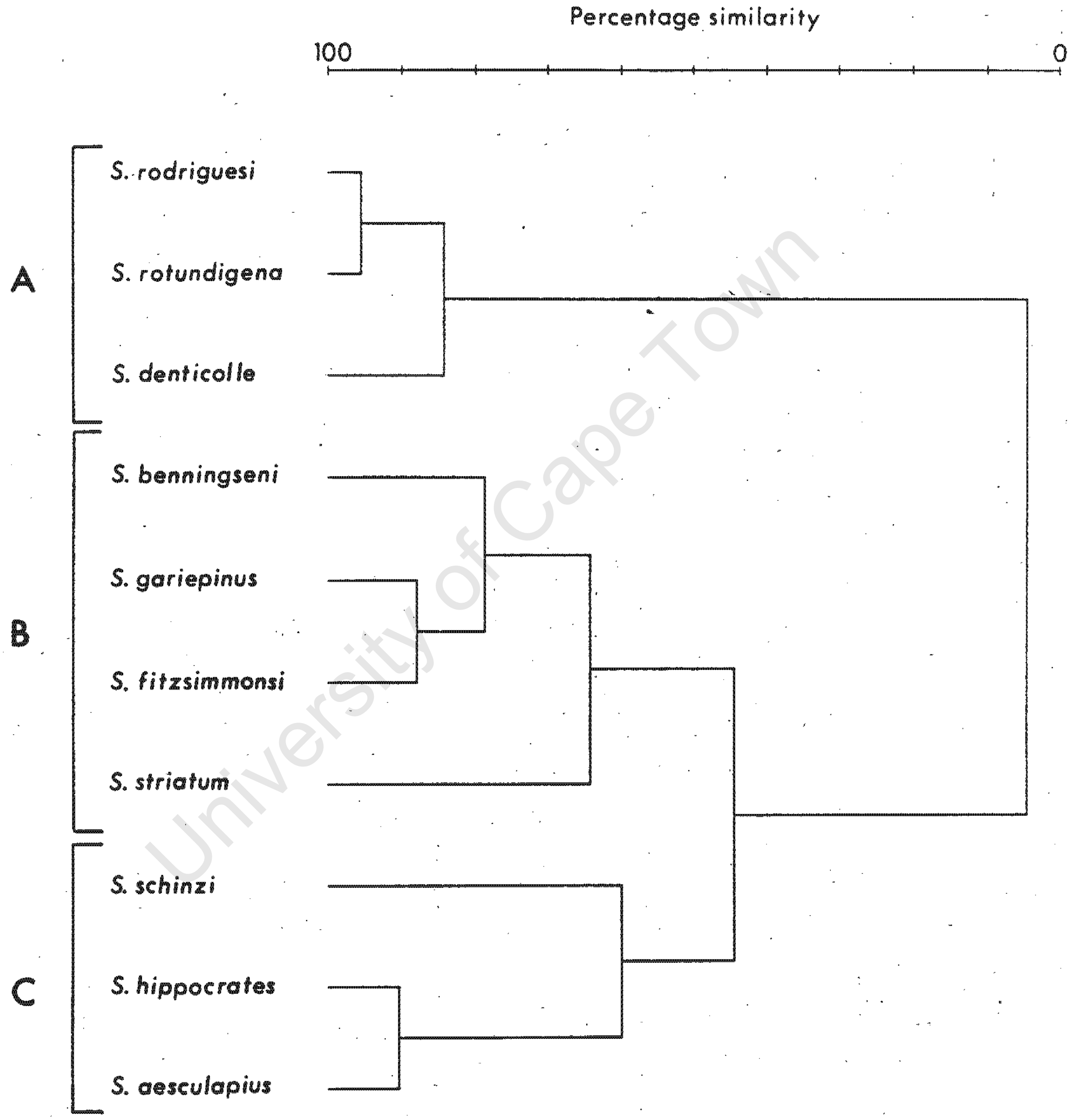
Figure 7.1. Dendrogram showing the taxonomic relationships between ten species of flightless *Scarabaeus* endemic to the west coast of southern Africa.



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Figures 7.2.-7.4. Principal distribution patterns shown by species of Scarabaeinae/ Coprinae in the south-western Cape and by their close relatives in the summer rainfall region.

7.2. Kalahari and arid west coast distribution shown by *Scarabaeus canaliculatus* and close relatives.

7.3. Allopatric distributions throughout South Africa shown by *Scarabaeus spretus* and close relatives.

7.4. Coastal southern Cape, eastern seaboard highland and coastal forest distribution shown by *Onthophagus giraffa* and close relatives.

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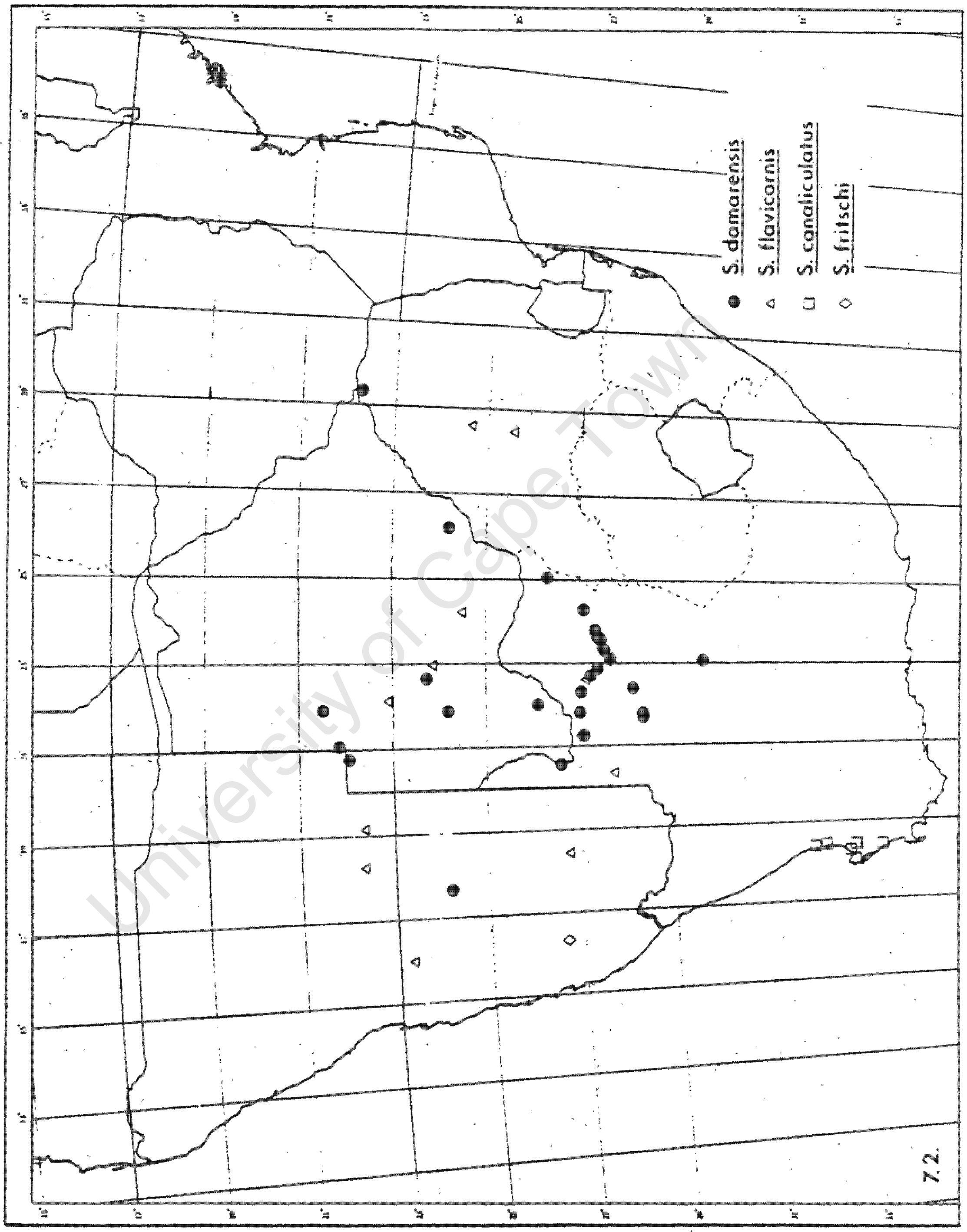

7.2.

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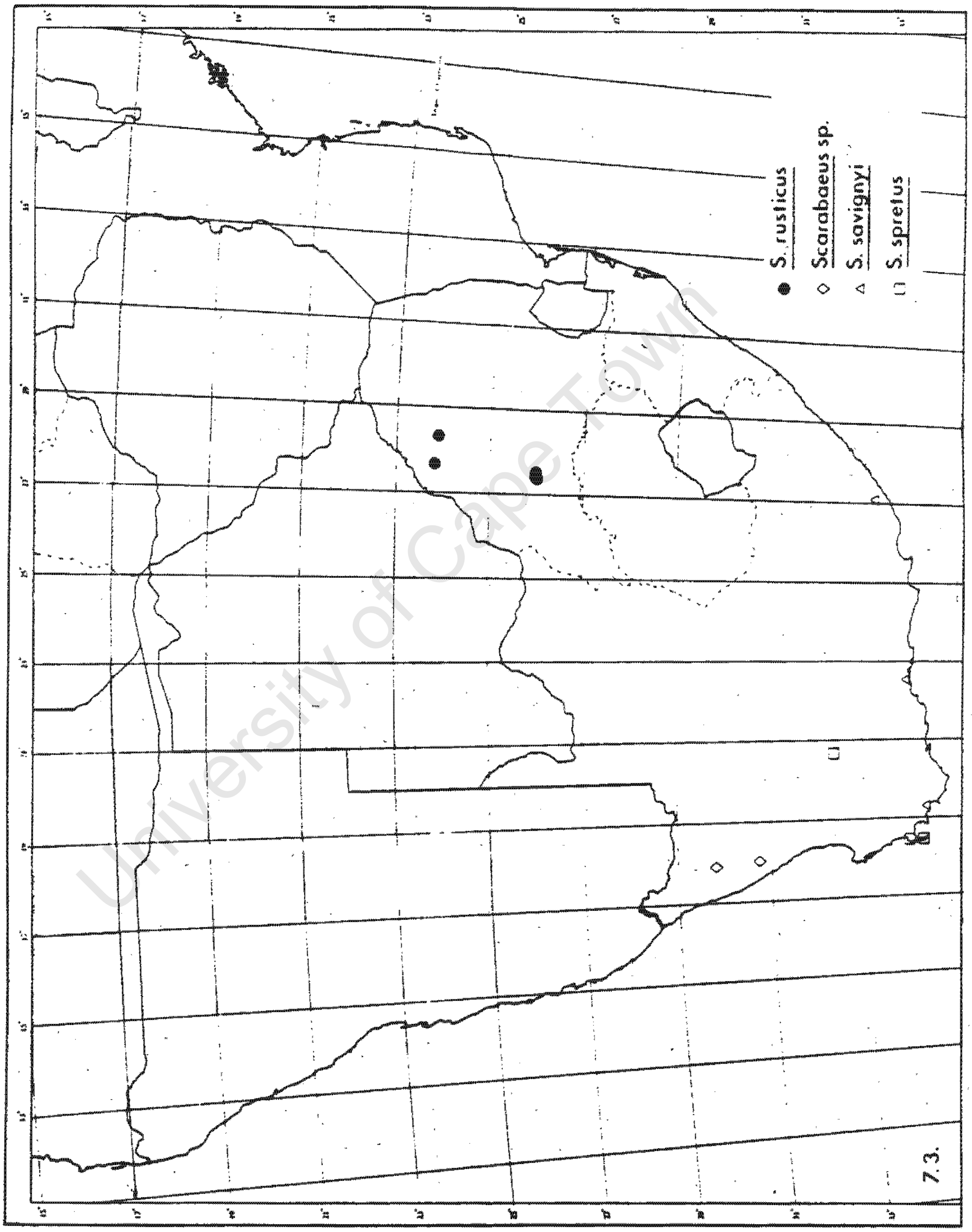

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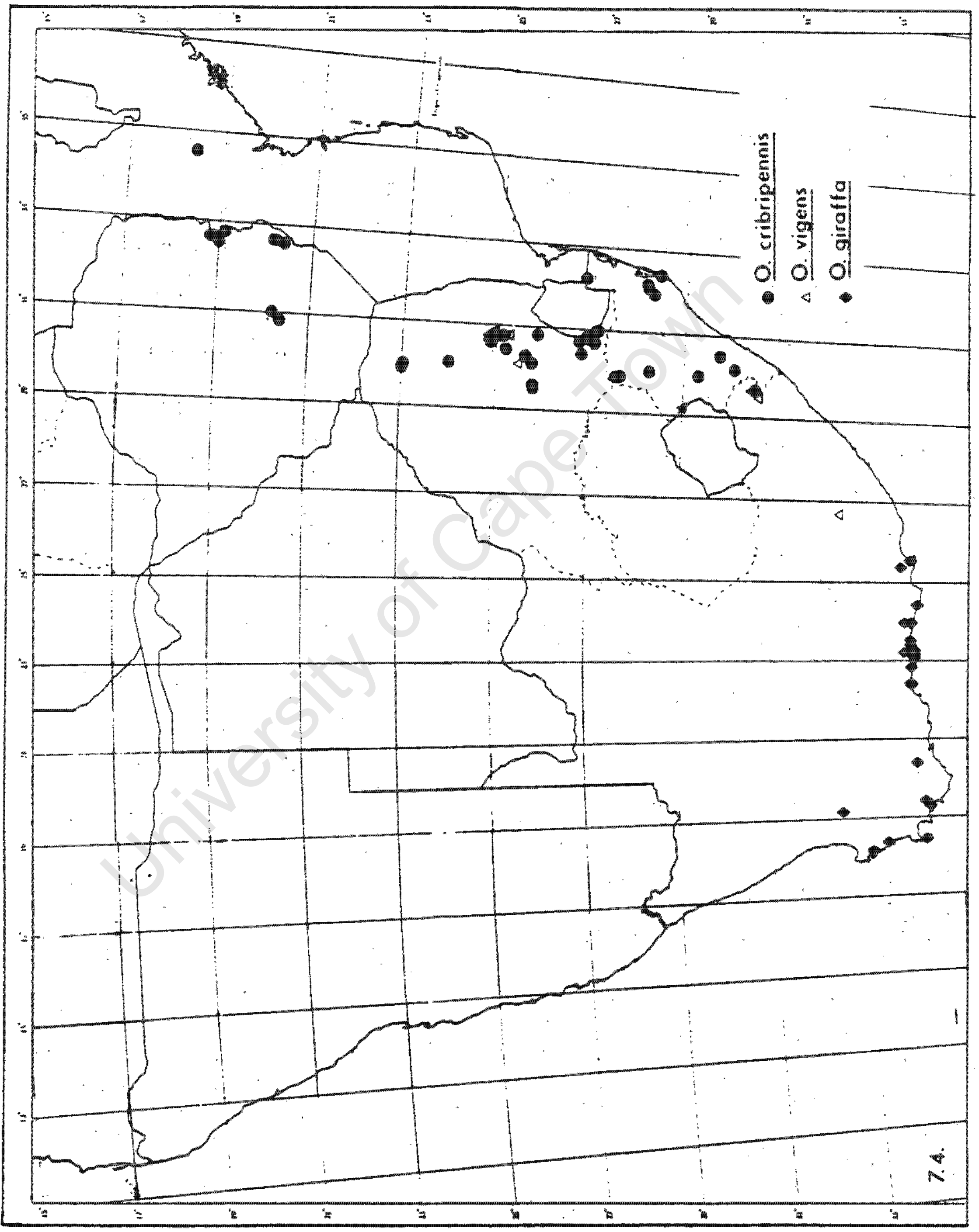

7.4.

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Figure A2.1. Dendrogram showing relationships between the distribution of tribes and subtribes of Scarabaeinae and Coprinae derived from cluster analysis of the number of genera in different biogeographical regions.

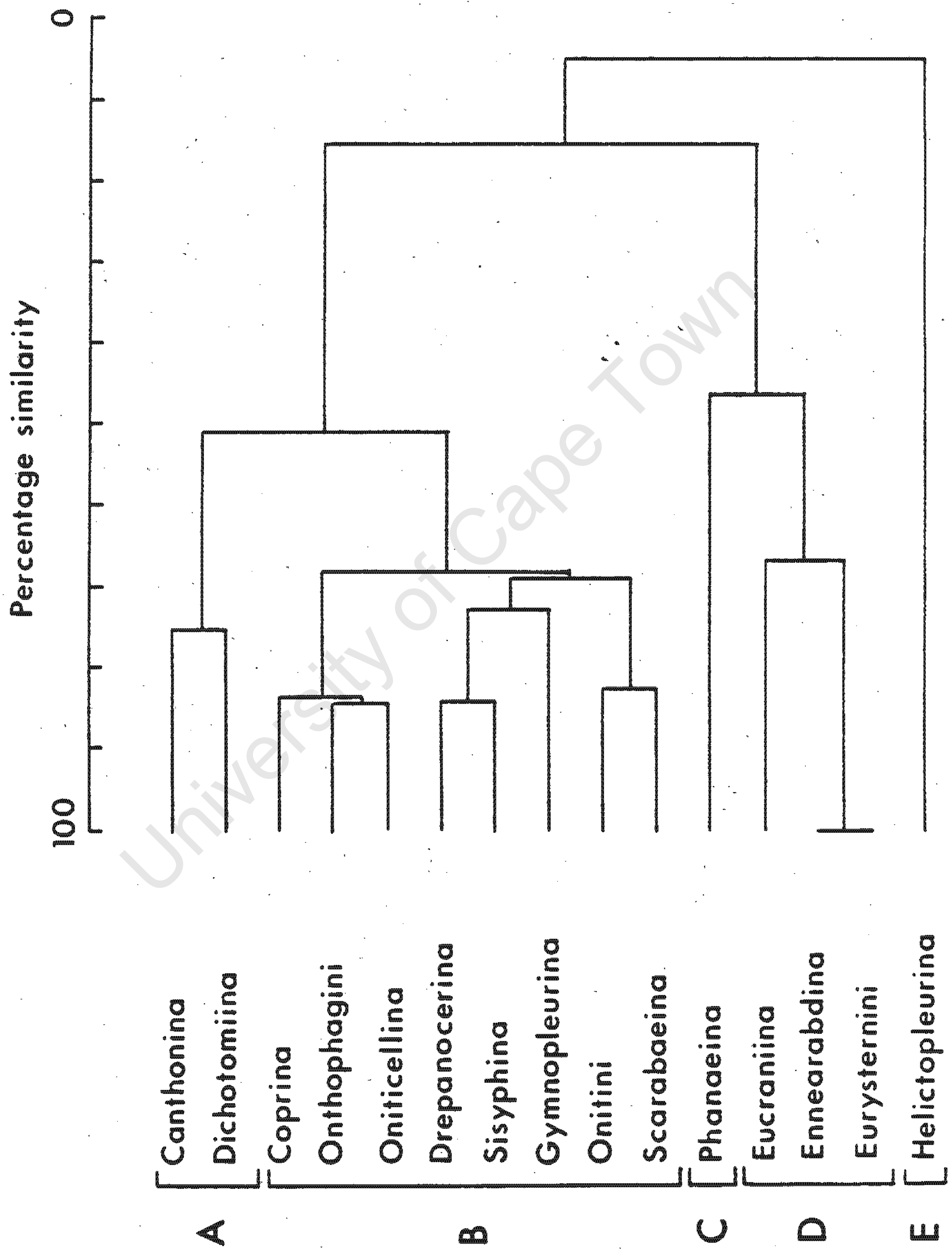

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Figure A2.2. Dendrogram showing relationships between the scarabaeinae and coprine fauna in different biogeographical regions as derived from cluster analysis of the number of genera in the different tribes and subtribes.

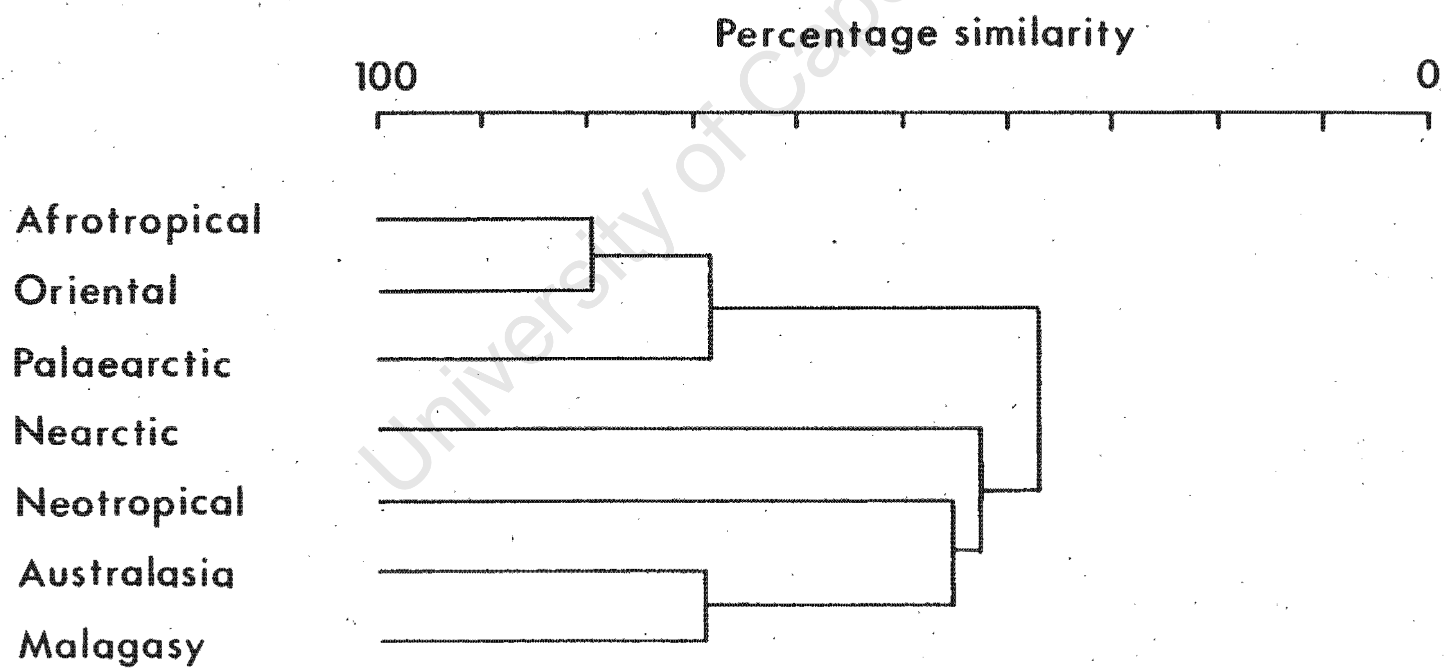

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Table A2.1. Biogeographical distribution of tribal/subtribal groups derived from cluster analysis.*

Group	Percentage of total number of genera in each biogeographical region						
	Afrotropical	Oriental	Palaearctic	Nearctic	Neotropical	Australia	Madagascar
Group A	32,9	25,7	5,9	50,0	72,5	87,5	77,8
Group B	67,1	74,3	94,1	33,3	7,3	12,5	11,1
Group C	0,0	0,0	0,0	16,7	13,0	0,0	0,0
Group D	0,0	0,0	0,0	0,0	7,3	0,0	0,0
Group E	0,0	0,0	0,0	0,0	0,0	0,0	11,1
Total number of genera	85	35	17	6	69	24	18

*See Figure A2.1.

Data derived from Halffter & Edmonds (1982) except the dichotomine genera, *Parapinotis* and *Xinidium*, treated as a single genus due to synonymy (Cambefort 1983).

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Table A2.2. Association of Afrotropical onitine genera with dung type.^

Genera of Onitini	Number of species examined	Number of collections in which species were recorded (correction for bias in distribution of observations between dung types)		
		Coarse-fibred non-ruminant dung**	Fine-fibred ruminant dung***	
Species poor genera				
Aptychonitis	1	12	0	
Anonychonitis	1	4	0	
Gilletellus	1	0	1*	
Heteronitis	4	61	6	(1,1)
Megalonitis	1	5	0	
Platyonitis	3	7	4	(0,8)
Pseudochironitis	2	23	11	(2,1)
Tropidonitis	1	2	0	
Total	14	114	22	(4,1)
Species rich genera				
Chironitis	10	47	218	(40,7)
Onitis	58	311	1770	(330,3)
Total	68	358	1988	(371,0)

^Data from the collection records of the CSIRO Dung Beetle Research Unit, now lodged with the National Collection of Insects, Pretoria, South Africa.

*Springbok dung.

**Elephant, rhinoceros, zebra, horse, donkey, camel, warthog and hippopotamus dung (331 observations).

***Cattle, buffalo and wildebeest dung (1774 observations).

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Table A2.3. Species richness of Afrotropical Scarabaeine and coprine genera.*

Tribe/subtribe	Number of genera comprising			
	1-5 spp.	6-10 spp.	11-30 spp.	>31 spp.
Canthonina	16	1	2	0
Scarabaeina	0	1	2	1
Sisyphina	0	0	2	0
Gymnopleurina	0	0	2	1
Dichotomiina	5	5	3	1
Coprina	3	0	3	0
Onitini	16	1	0	1
Onthophagini	2	1	1	4
Oniticellini	6	0	3	0

*Derived from Ferreira (1972).

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Table A2.4. Rank percentage representation of scarabaeine and coprine taxa in West Africa (Nigeria and longitudes west).*

Tribe/subtribe	Percentage in West Africa	
	Genera (n)	Species (n)
Canthonina	11,8 (2)	6,5 (5)
Scarabaeina	25,0 (2)	7,8 (9)
Onitini	31,6 (6)	12,3 (9)
Coprina	40,0 (2)	13,9 (31)
Dichotomiina	57,1 (8)	12,5 (20)
Oniticellini	66,7 (7)	31,2 (19)
Onthophagini	87,5 (7)	22,0 (189)
Sisyphina	100,0 (3)	28,1 (9)
Gymnopleurina	100,0 (3)	21,7 (13)

*Comprises approximately 20% of the land area of Africa.
Data derived from Ferreira (1972).

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Table A2.5. Distribution and degree of endemism in genera of Scarabaeinae and Coprinae in the Old World.^

Tribe/ subtribe	Biogeographical distribution of genera		
	Afrotropical endemics	Palaearctic and Oriental endemics	All regions Afro-Oriental Afro-Palaearctic
Canthonina	13	2	2
Scarabaeina	6	1	2
Sisyphina	0	0	2
Gymnopleurina	0	1	3
Coprina	3	1	2
Dichotomiina	10	2	3
Onitini	16	1	2
Onthophagini	4	3	6
Oniticellini	4	0	5
Total	56*	11	27

^Data derived from Halffter & Edmonds (1982).

*Significantly more endemic genera in the Afrotropical region than in the Palaearctic/Oriental regions (t = 2,63, d.f. = 16, $P < 0{,}02$, t test).

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ADDENDUM

Figures AD1-AD3. Dendrograms showing similarities between the seasonal distribution of species of dung beetles from four higher taxonomic groups in three climatic regions of southern Africa.

AD1. Climate type IV. Cape of Good Hope Peninsula, south-western Cape.
AD2. Climate type III(IV)a. West coast of south-western Cape.
AD3. Climate type II3d. Southern central Transvaal bushveld.

Taxon	Level of percentage similarity at which groups were defined		
	AD1	AD2	AD3
a. Scarabaeinae/Coprinae	60%	53%	60%
b. Histeridae	70%	55%	70%
c. Aphodiinae	45%	50%	50%
d. Staphylinidae/Hydrophilidae	45%	58%	48%

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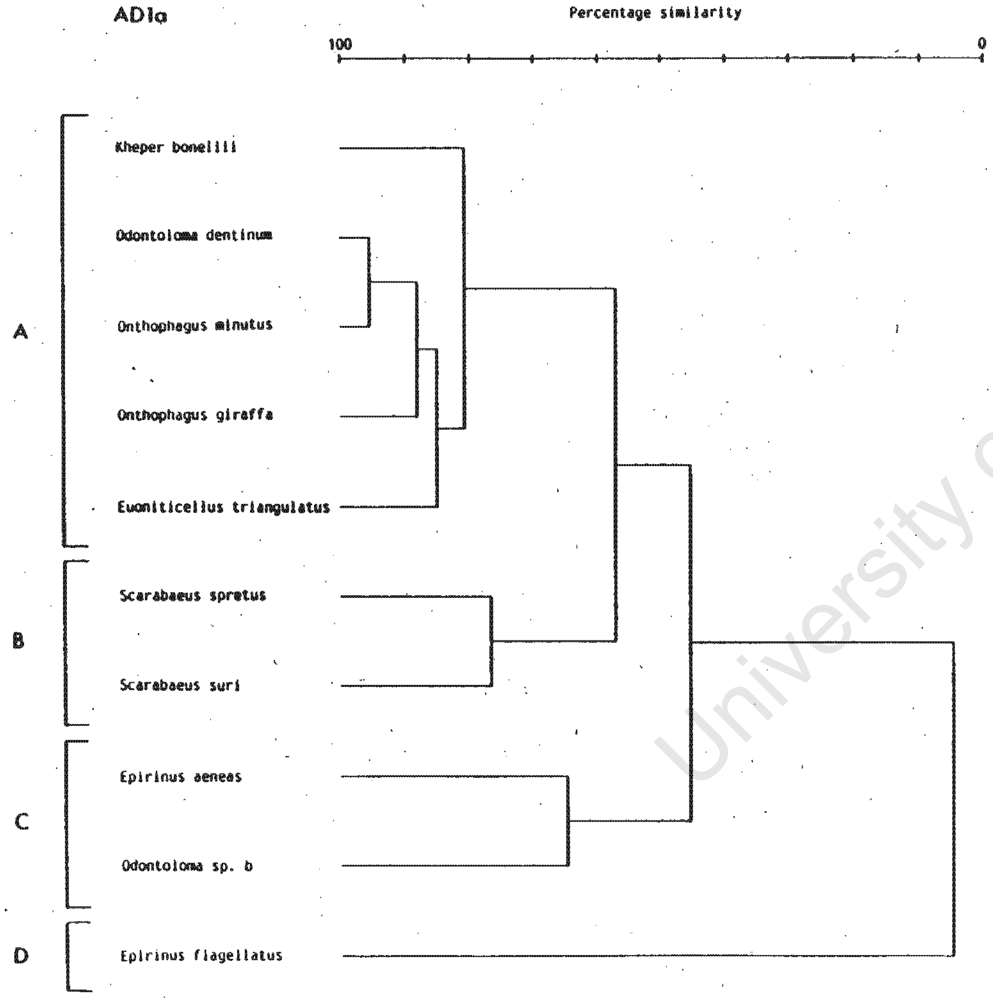
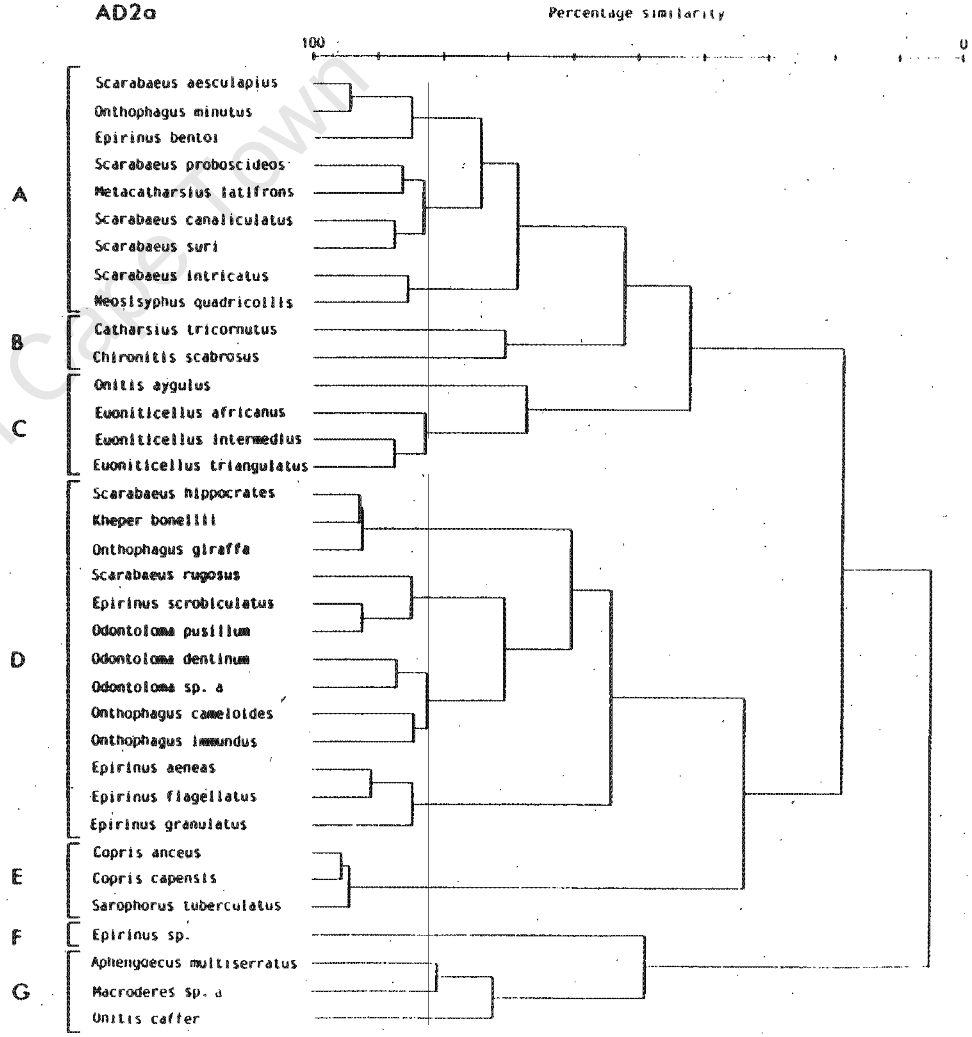
AD1a



AD2a



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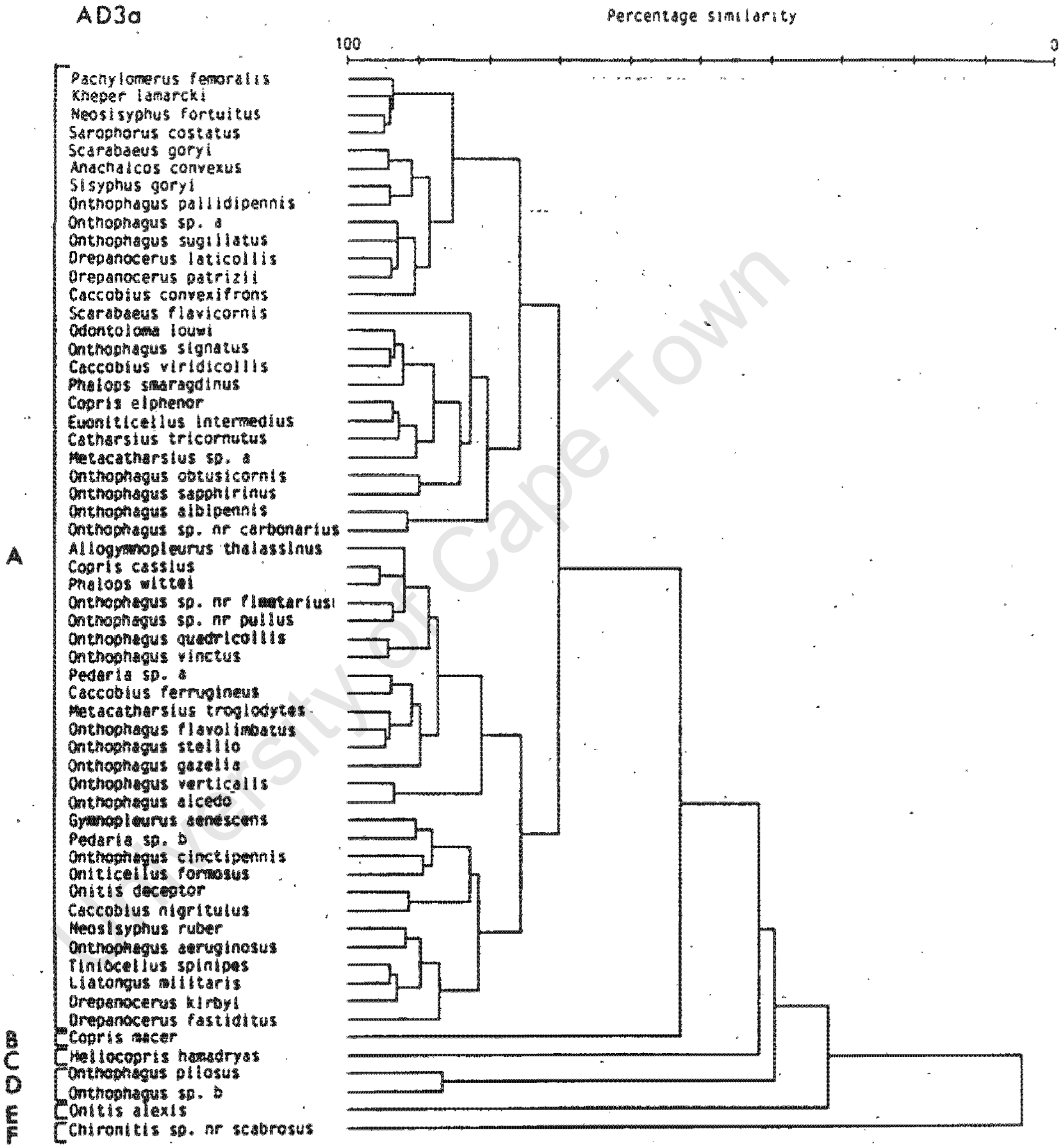

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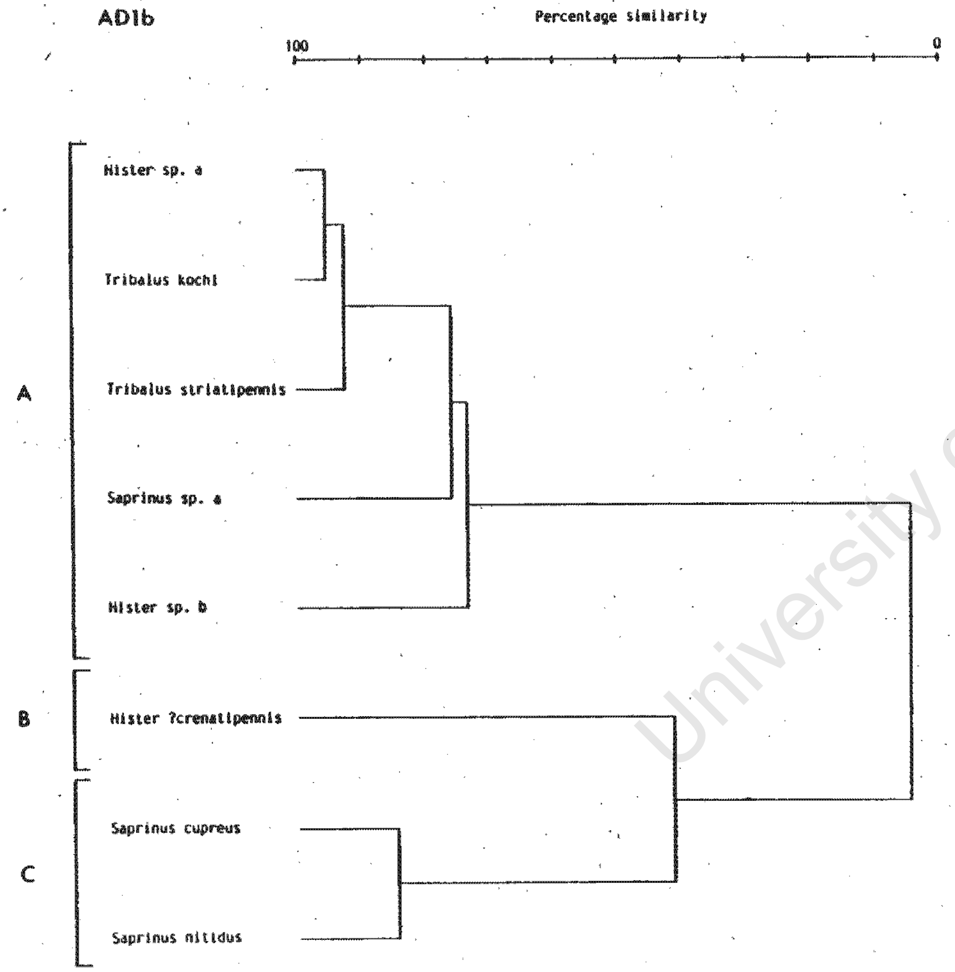

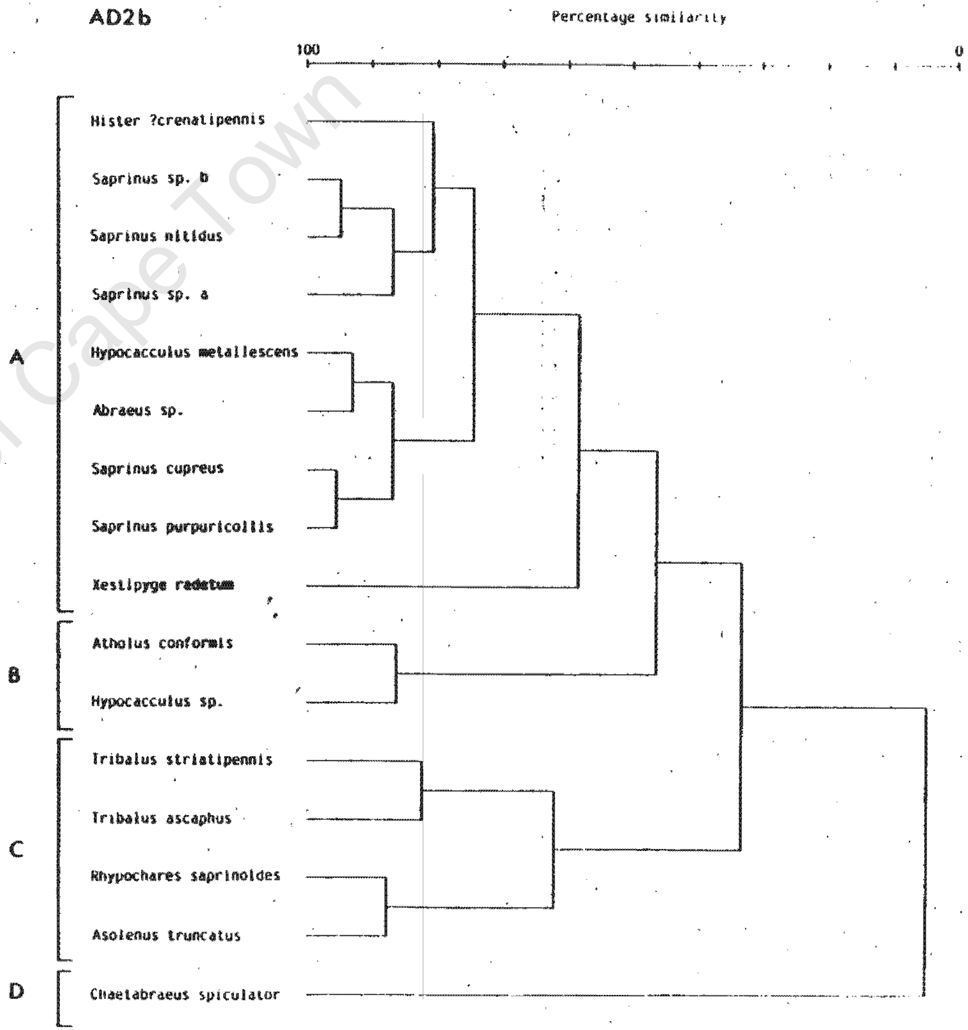

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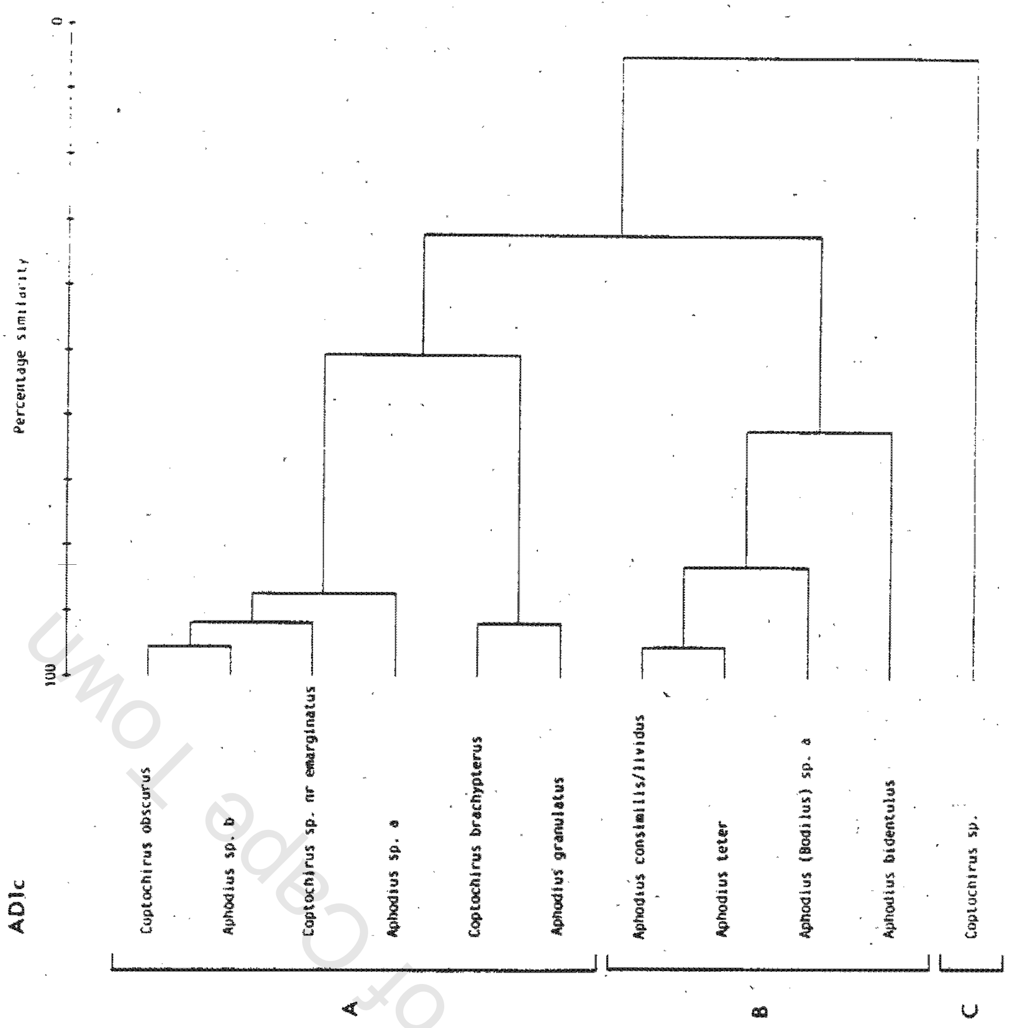

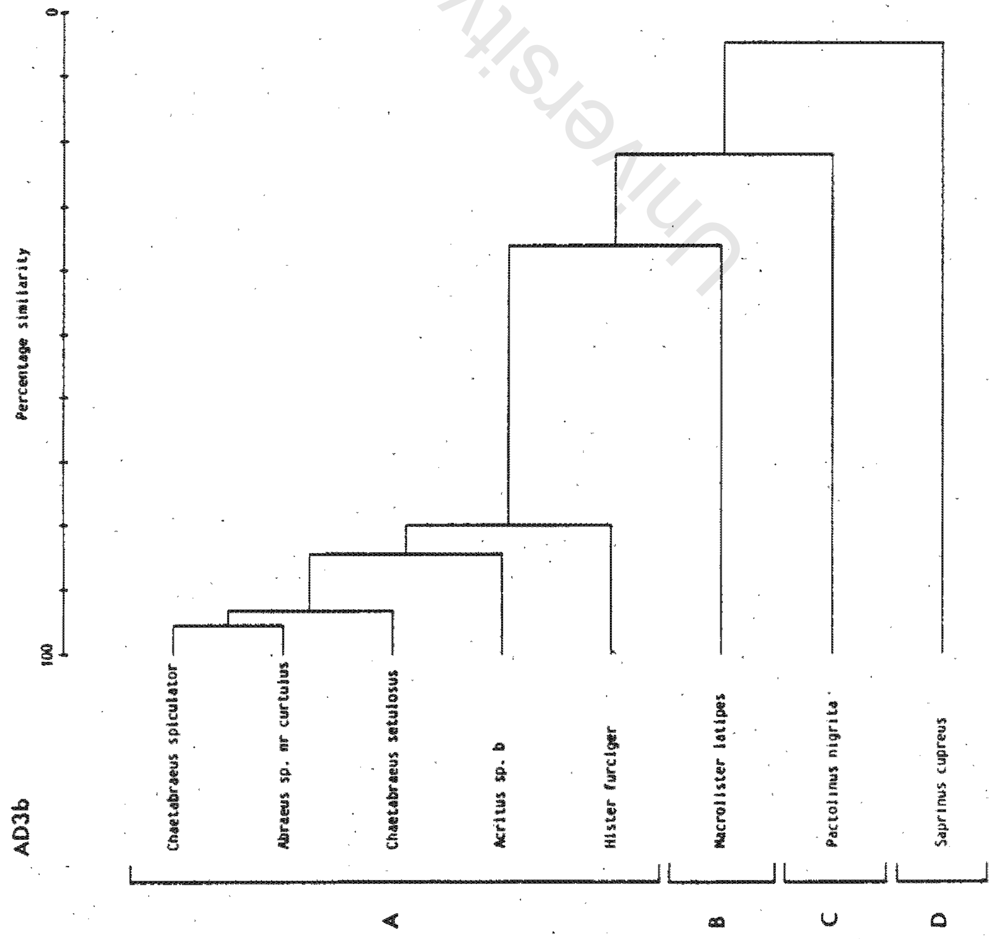

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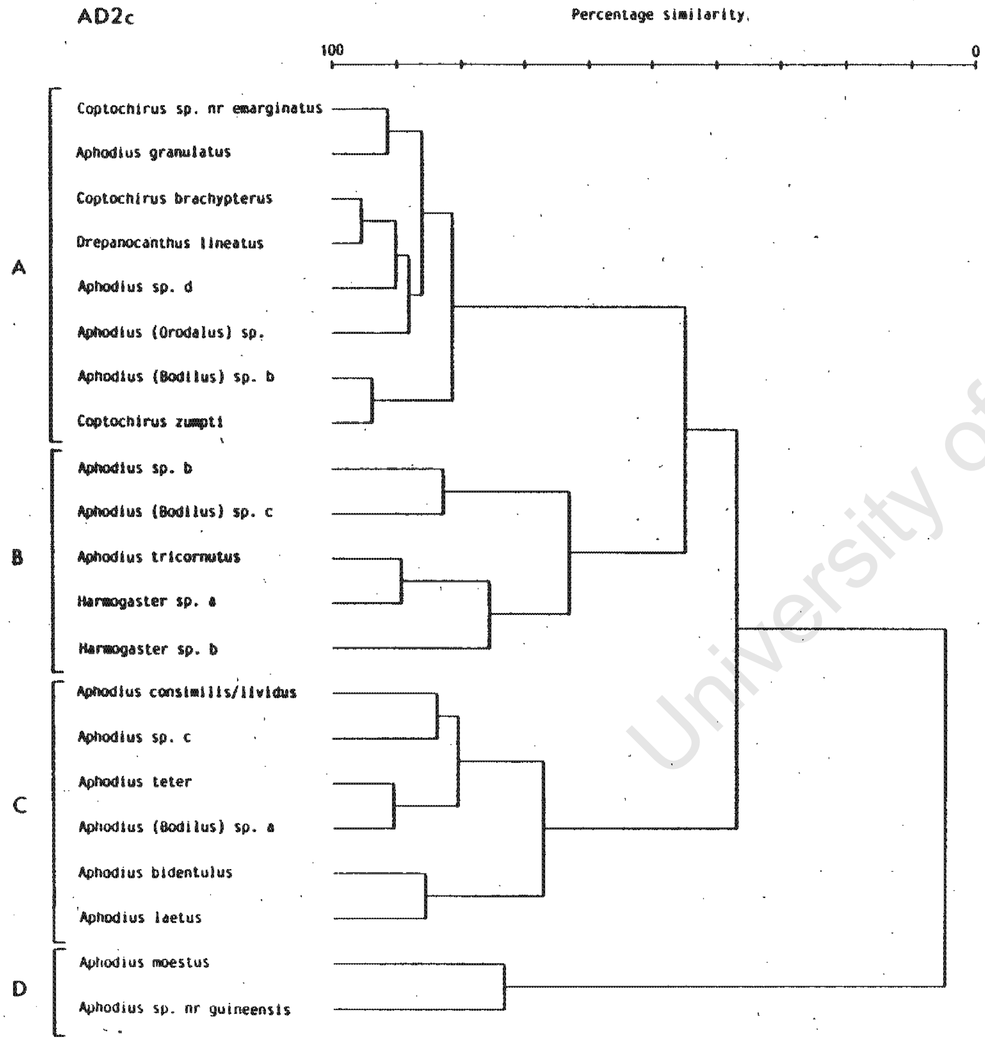
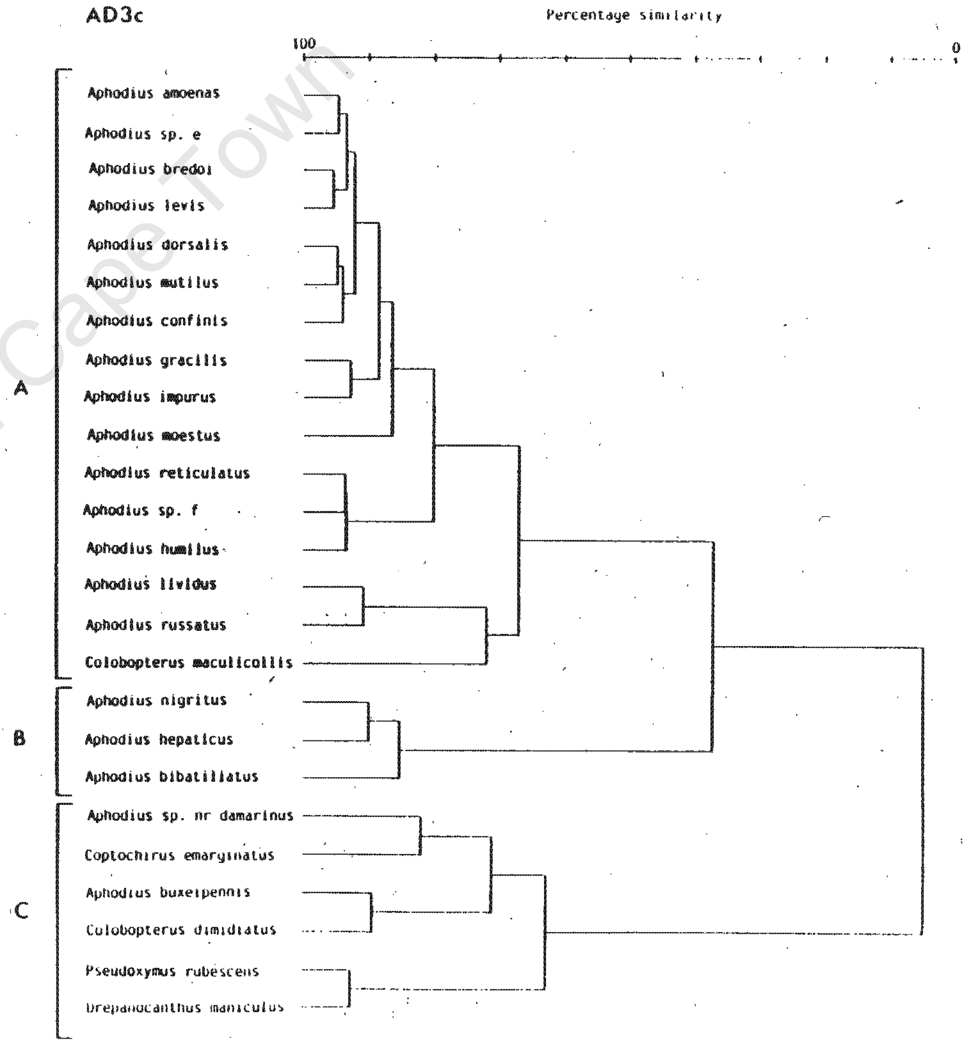
AD2c



AD3c



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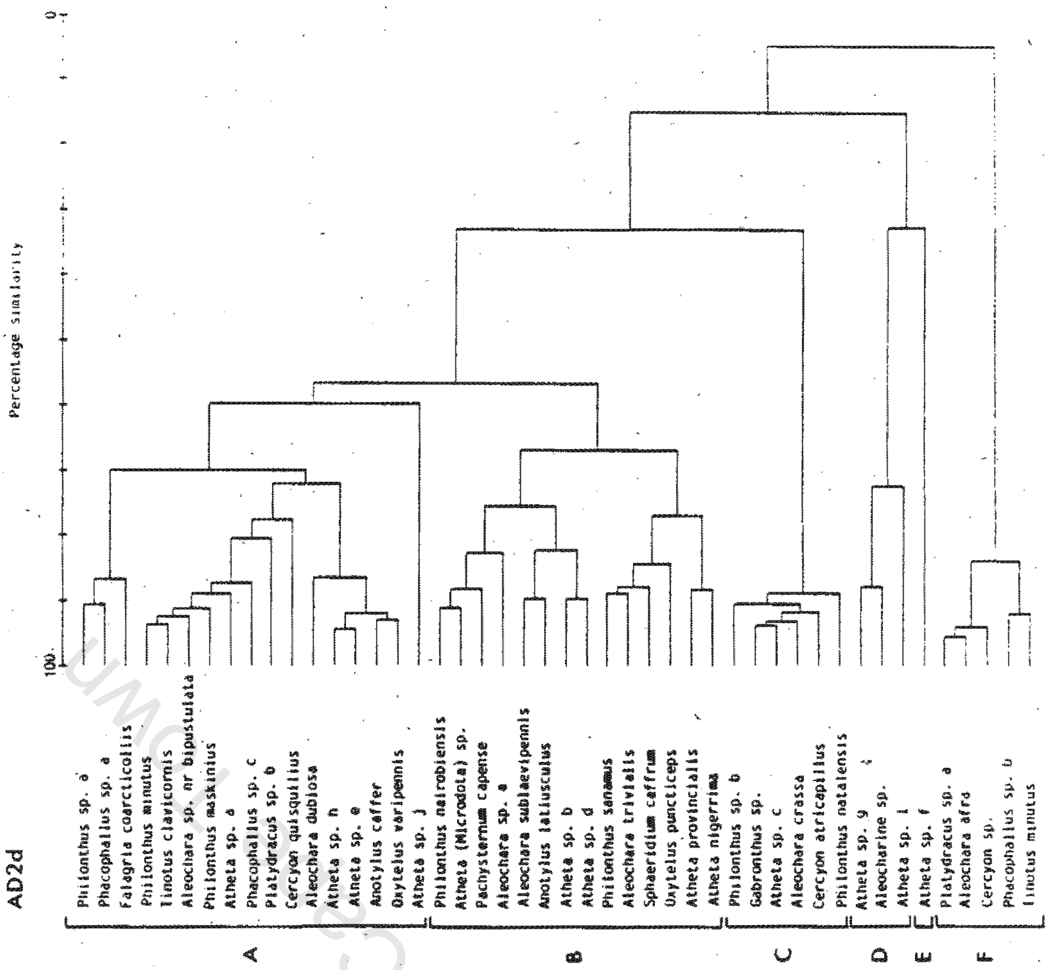

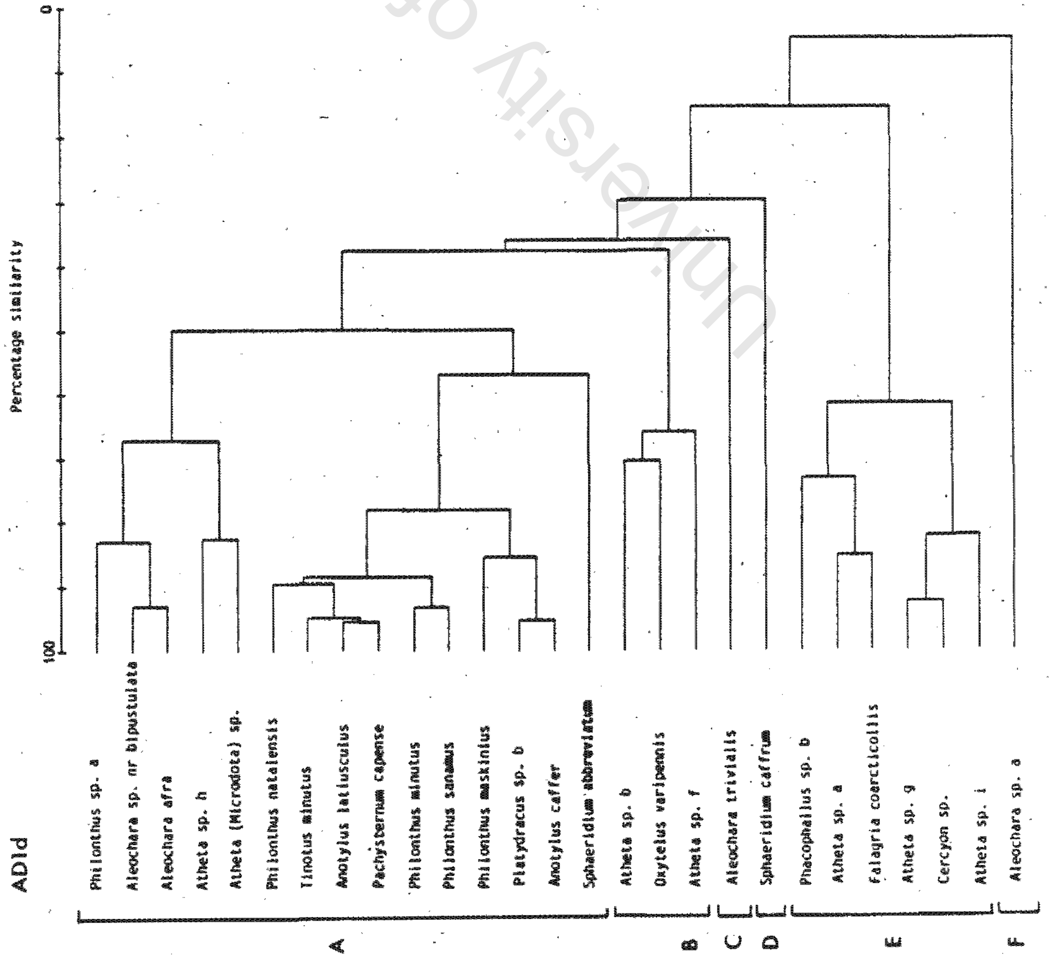

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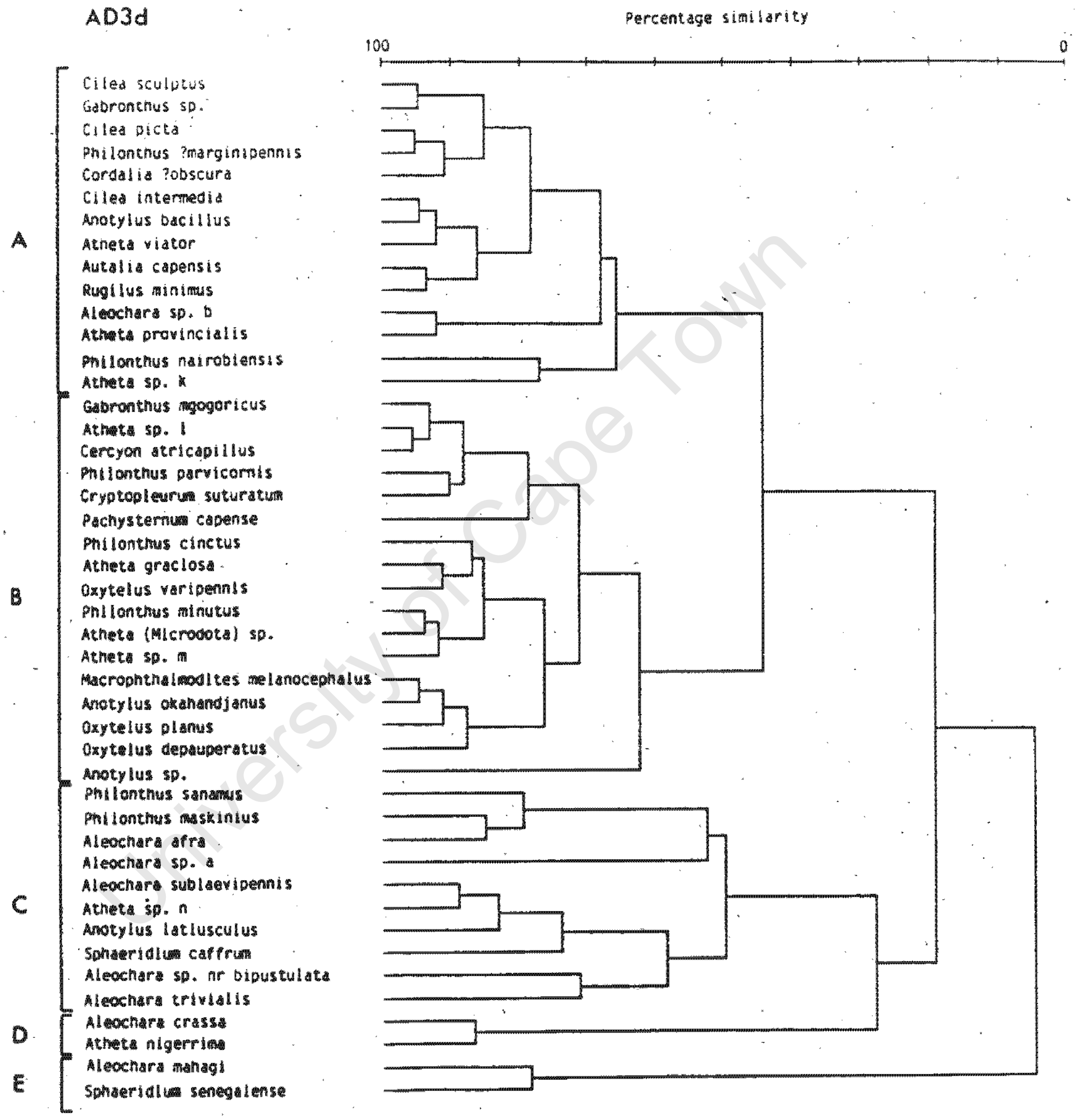

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Figures AD4-AD7. Seasonal distribution of species groups of four higher taxa of dung beetles in three climatic regions of southern Africa derived from cluster analysis.

AD4. Scarabaeinae/Coprinae.

AD5. Histeridae.

AD6. Aphodiinae.

AD7. Staphylinidae/Hydrophilidae.

a. Climate type IV. Cape of Good Hope Peninsula, south-western Cape.
b. Climate type III(IV)a. West coast of south-western Cape.
c. Climate type II3d. Southern central Transvaal bushveld.

*PTA = Percentage of total abundance in climatic region.
Groups above the broad line were used in the analysis of trends in seasonal distribution summarized in Figure 1.3.

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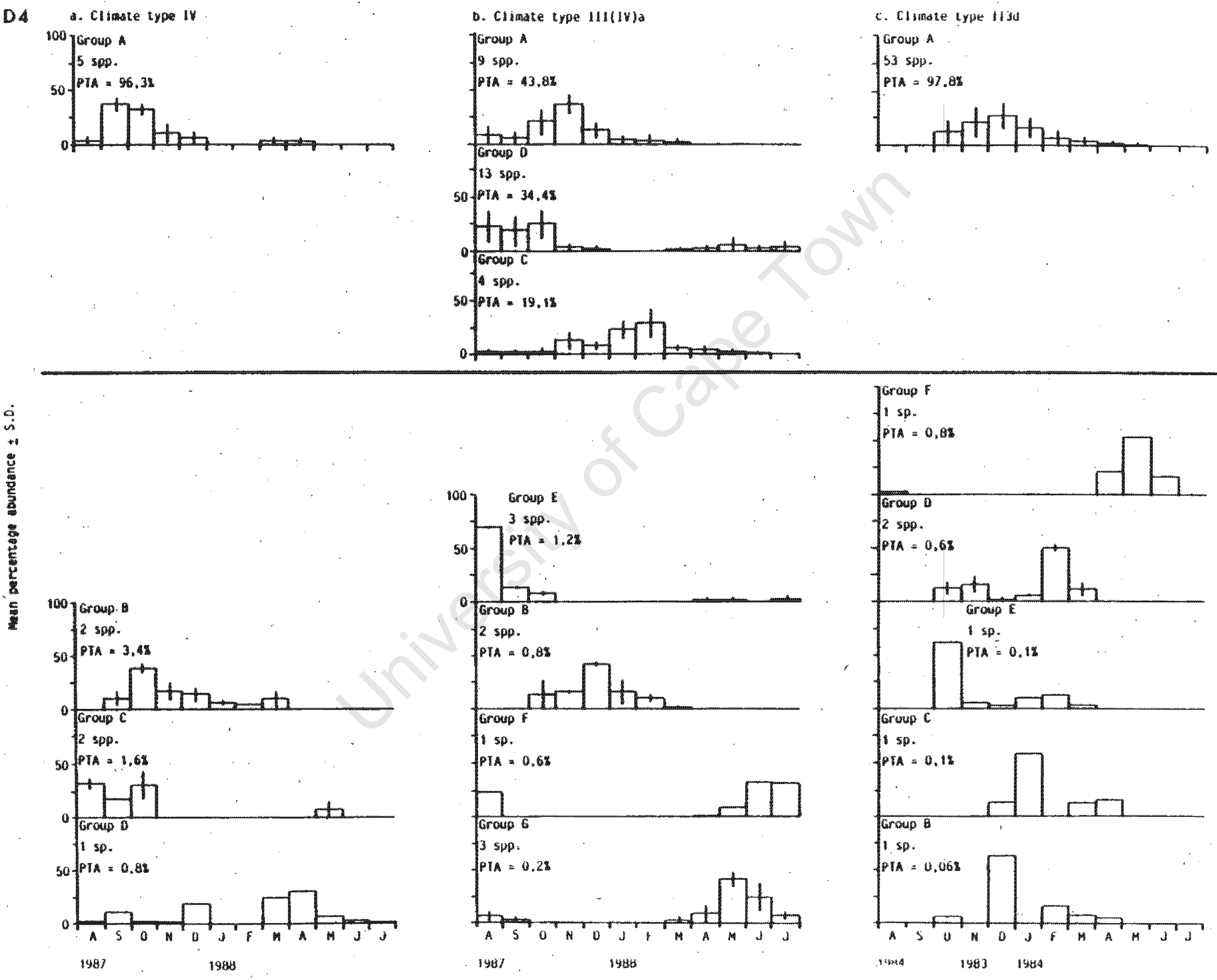
AD4



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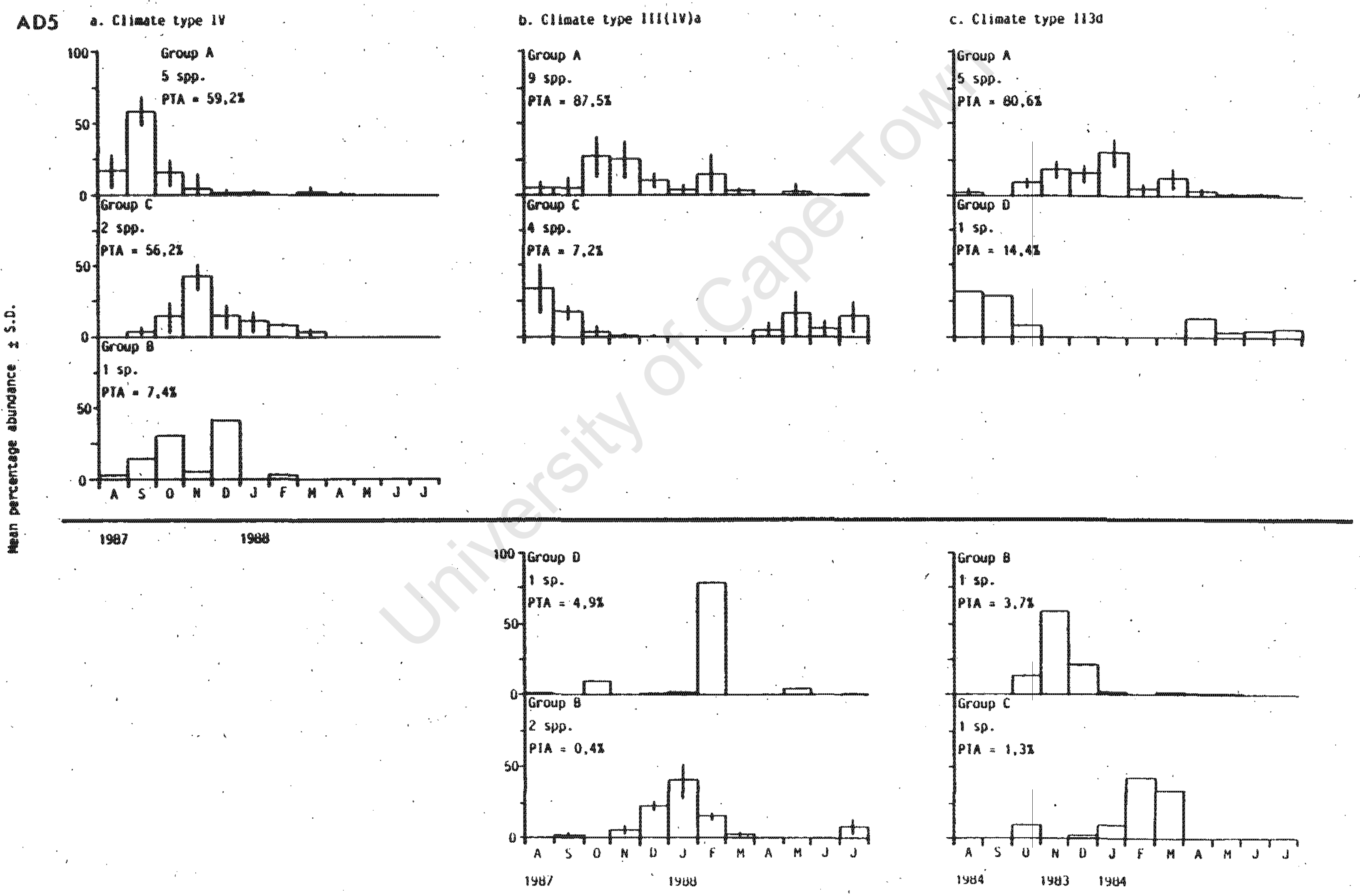

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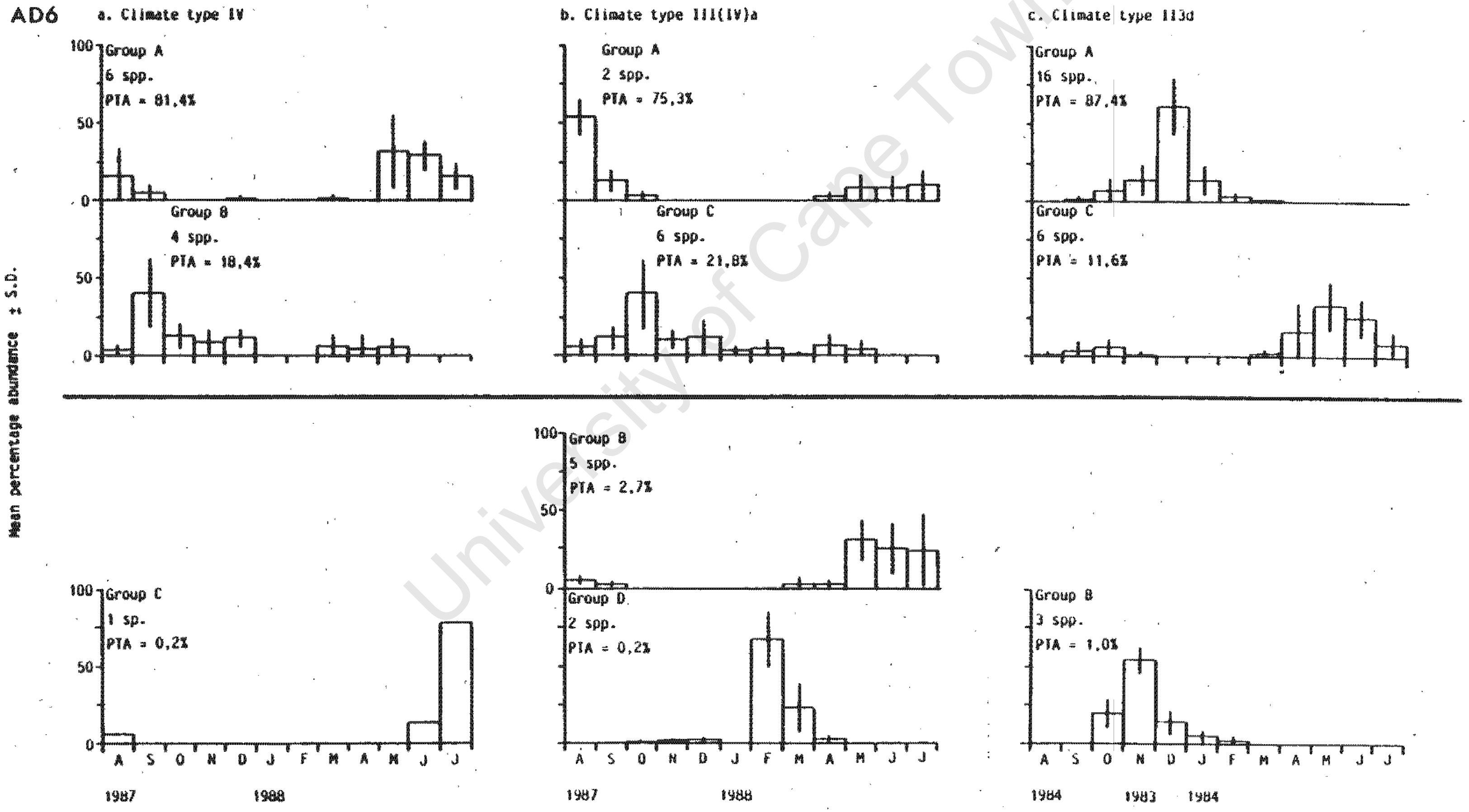
AD6



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AD7

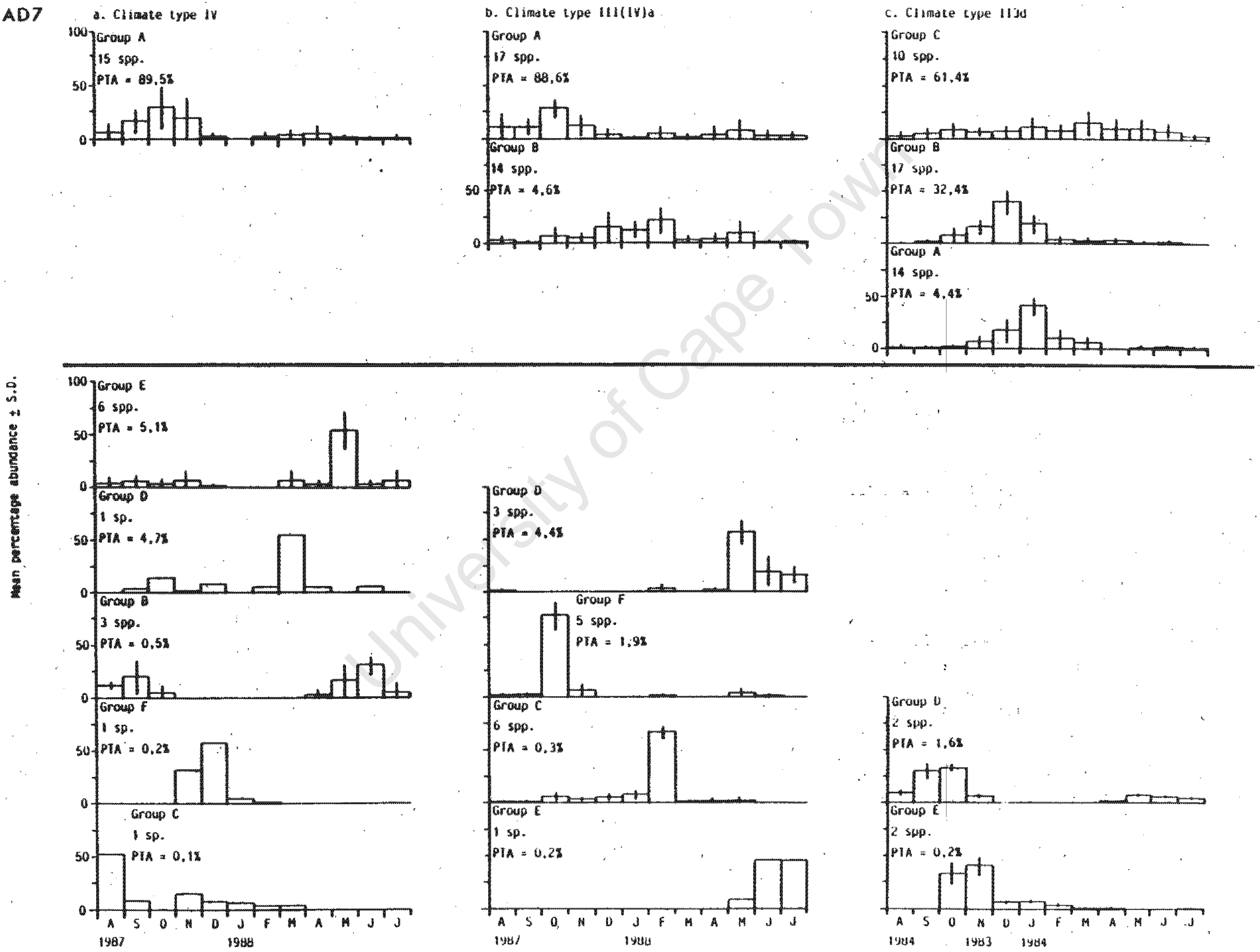

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Figure AD8.Dendrograms showing similarities between the spatial distribution of species of dung Coleoptera in four higher taxonomic groups across 11 habitats in the south-western Cape.

a. Scarabaeinae/Coprinae.
b. Histeridae.
c. Aphodiinae.
d. Staphylinidae hydrophilidae.

Figure AD9. Spatial distribution of species groups of four higher taxa of dung beetles derived from cluster analysis in relation to vegetation height across 11 habitats in the south-western Cape.

Taxon	Percentage level of similarity at which groups were defined
a. Scarabaeinae/Coprinae	43%
b. Histeridae	60%
c. Aphodiinae	70%
d. Staphylinidae/Hydrophilidae	65%

*Significant association with vegetation type (P<0,05, Kuskal-Wallis tests).
***Pasture sites*: GP = Groote Post, BA = Bonne Attente, W = Waylands, WCG = West Coast National Park, O = Oranjefontein.
Shrubland sites: GHR = Cape of Good Hope Nature Reserve, 2-3yr old fynbos, GHM = Cape of Good Hope Nature Reserve, 9-10yr old fynbos, M = Modderrivier, PS = Pampoenvlei (sand), WCS = West Coast National Park, PL = Pampoenvlei (Sandy loam).

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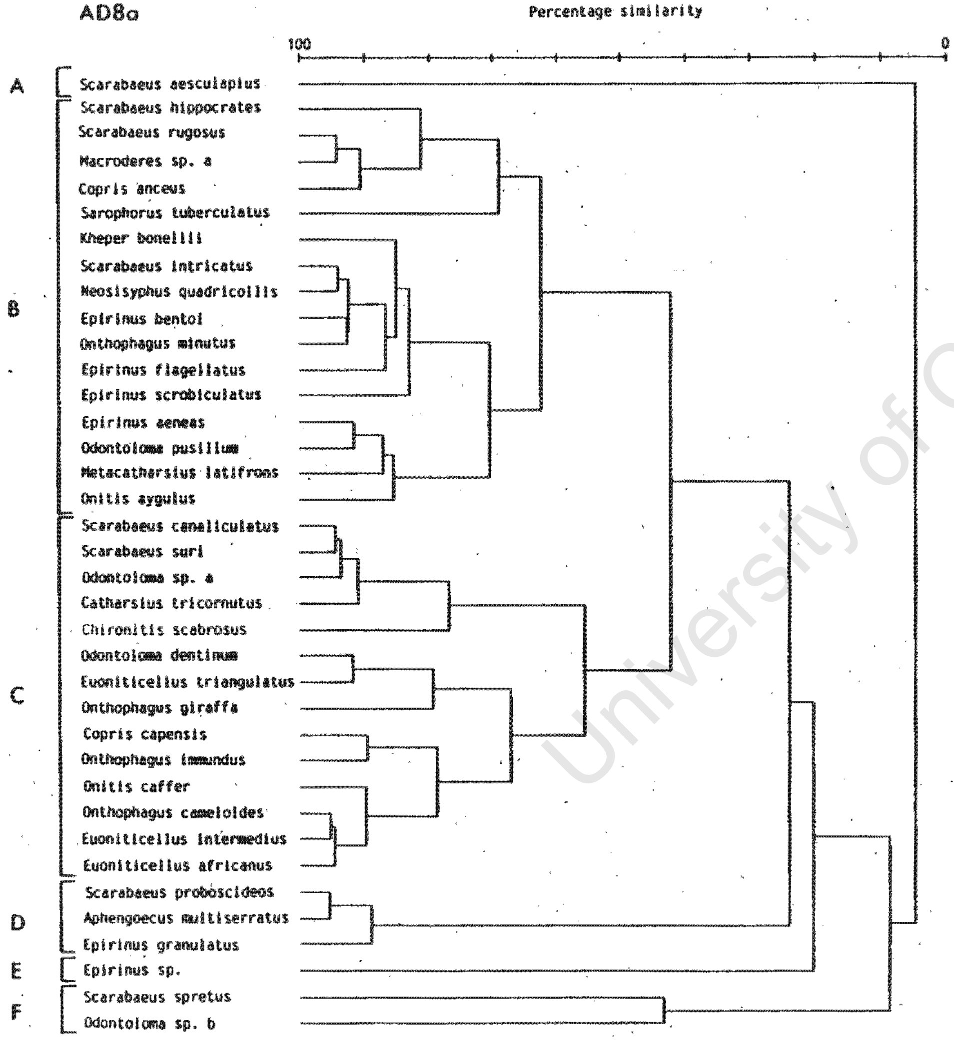
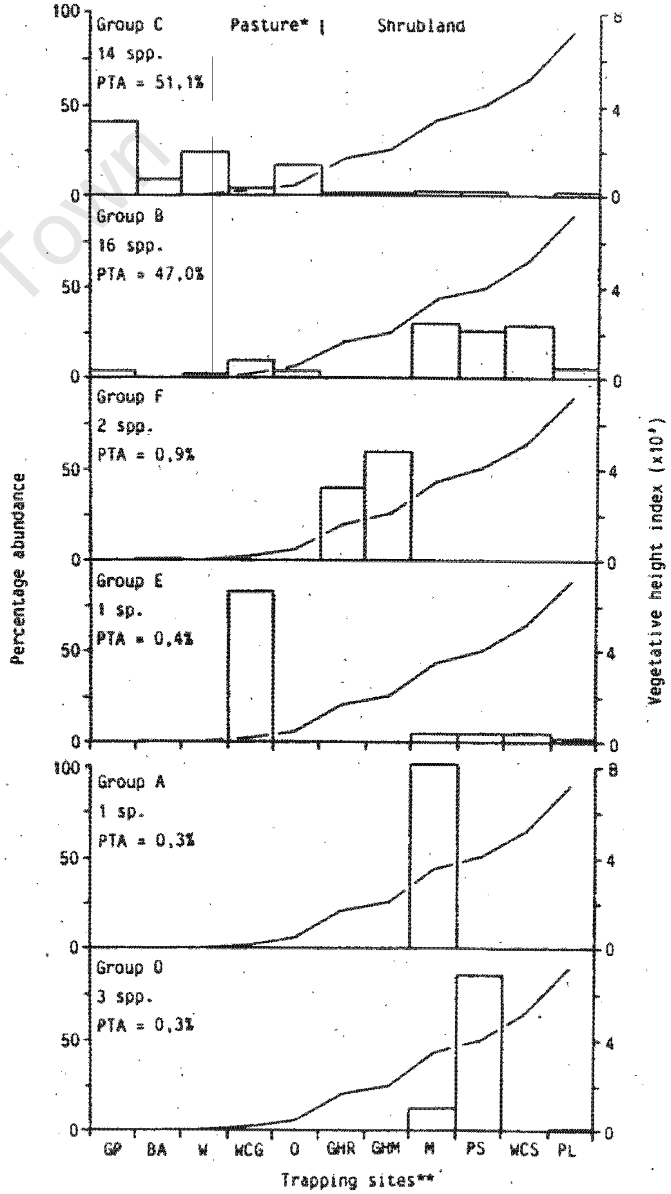
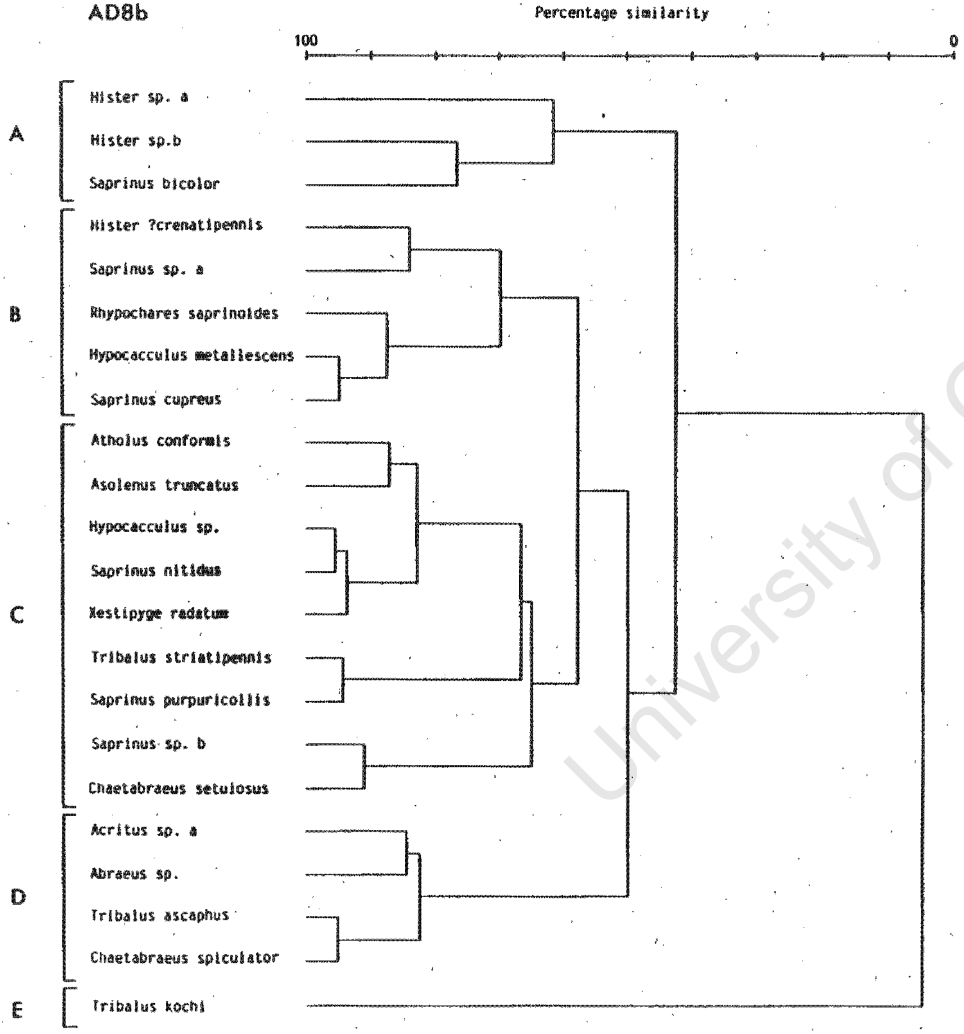
AD8a


Percentage similarity
100
0
A
B
C
D
E
F
Scarabaeus aesculapius
Scarabaeus hippocrates
Scarabaeus rugosus
Macroderes sp. a
Copris anceus
Sarophorus tuberculatus
Kheper bonellii
Scarabaeus intricatus
Neosisyphus quadricollis
Epirinus bentoi
Onthophagus minutus
Epirinus flagellatus
Epirinus scrobiculatus
Epirinus aeneas
Odontoloma pusillum
Metacatharsius latifrons
Onitis aygulus
Scarabaeus canaliculatus
Scarabaeus suri
Odontoloma sp. a
Catharsius tricornutus
Chironitis scabrosus
Odontoloma dentinum
Euoniticellus triangulatus
Onthophagus giraffa
Copris capensis
Onthophagus immundus
Onitis caffer
Onthophagus cameloides
Euoniticellus intermedius
Euoniticellus africanus
Scarabaeus proboscideos
Aphengoecus multiserratus
Epirinus granulatus
Epirinus sp.
Scarabaeus spretus
Odontoloma sp. b

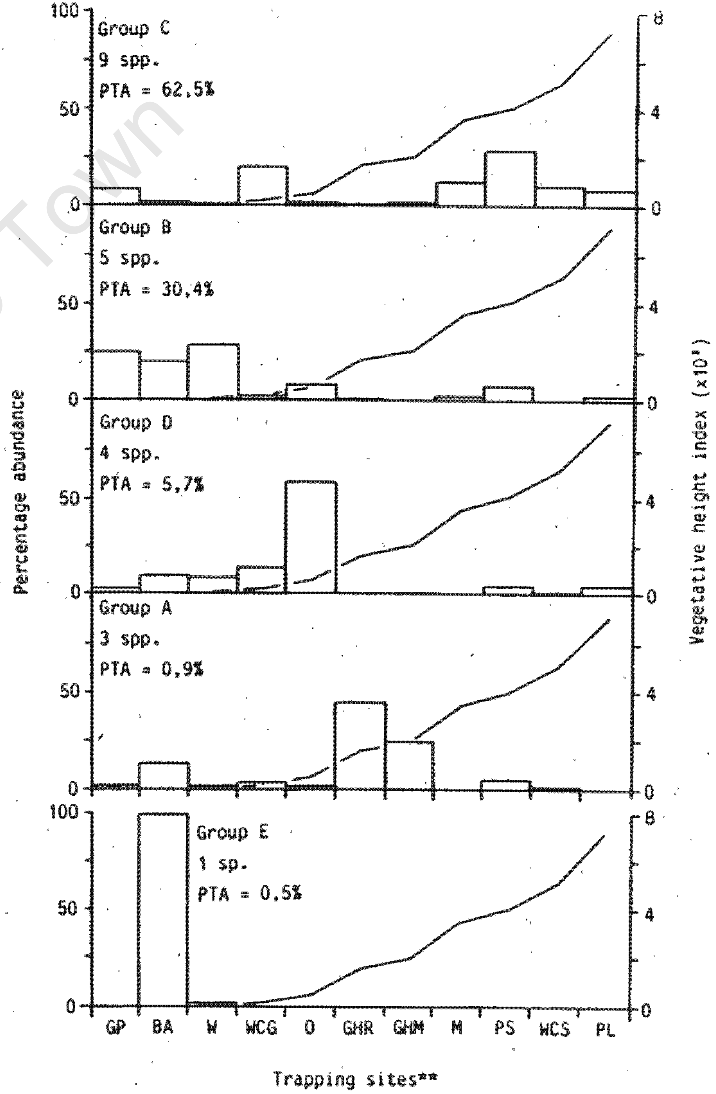
AD9a.


Pasture* | Shrubland
Group C
14 spp.
PTA = 51,1%
Group B
16 spp.
PTA = 47,0%
Group F
2 spp.
PTA = 0,9%
Group E
1 sp.
PTA = 0,4%
Group A
1 sp.
PTA = 0,3%
Group D
3 spp.
PTA = 0,3%
Percentage abundance
100
50
0
Vegetative height index (x10⁴)
8
4
0
GP
BA
W
WCG
O
GHR
GHM
M
PS
WCS
PL
Trapping sites**

AD8b



AD9b.



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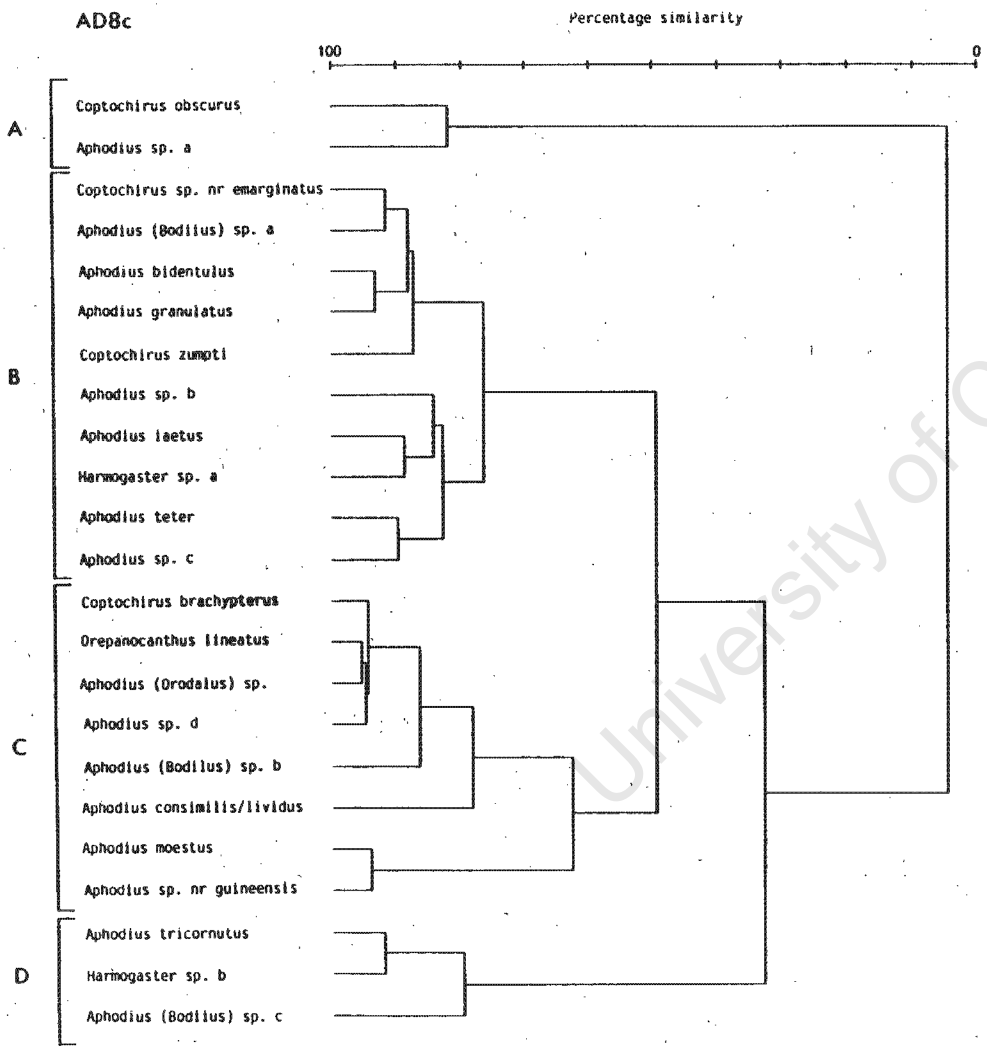
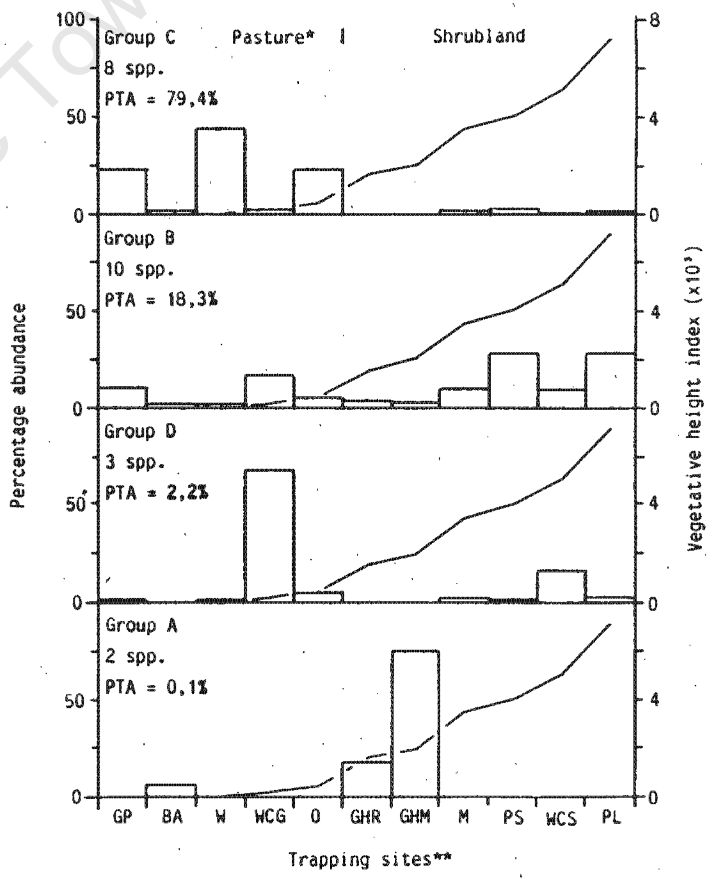
AD8c



AD9c.



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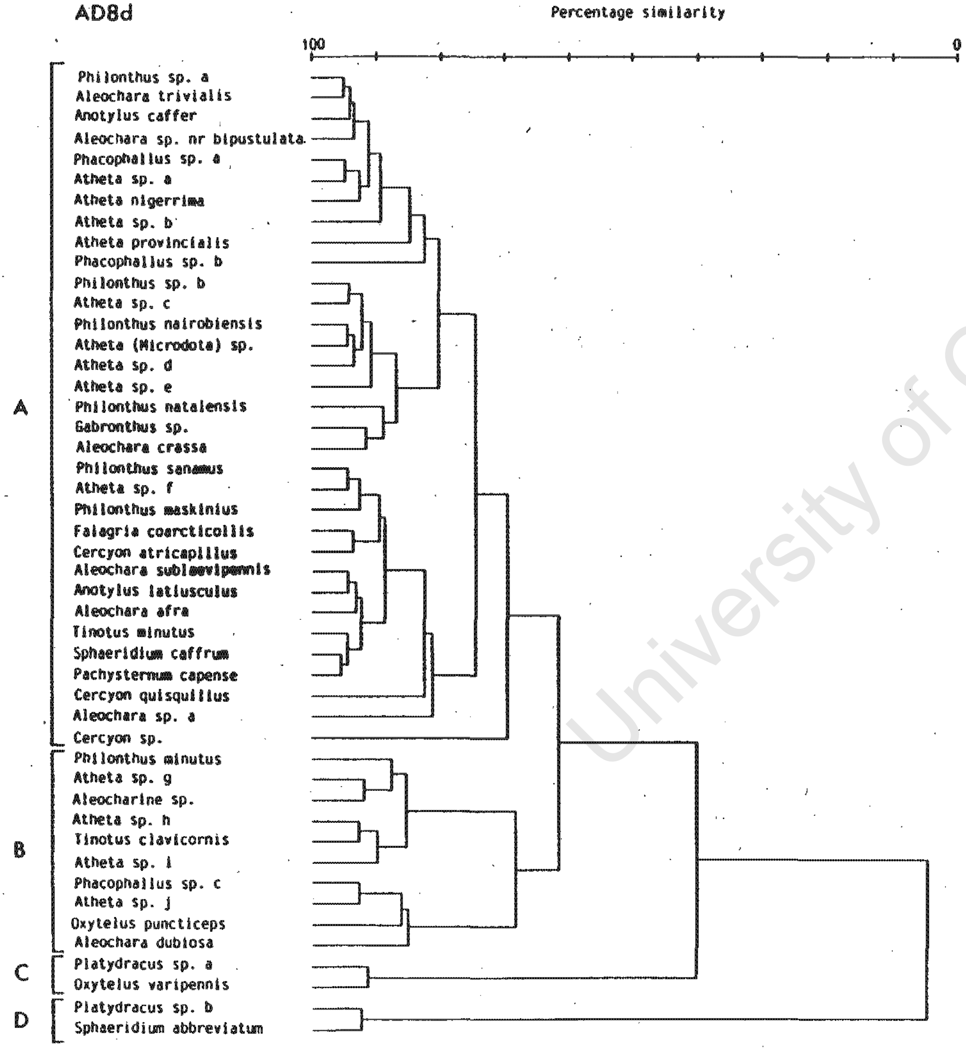
AD8d



AD9d.

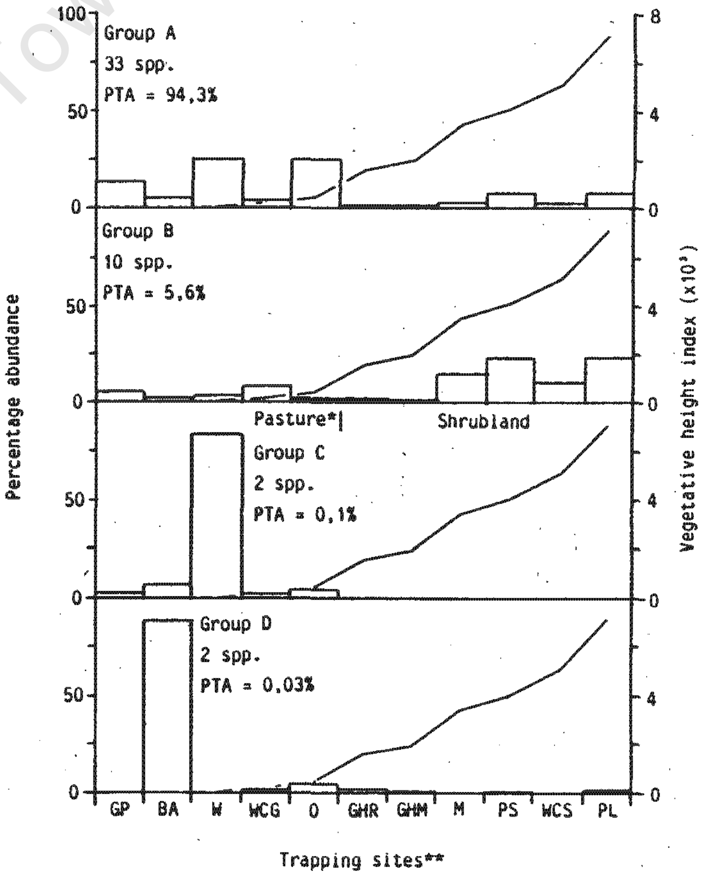


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Table AD1. Species of dung beetles recorded in the south-western Cape and their coefficients of variation in spatial distribution (mean/S.D.) across 11 study sites.

Taxa	Coeff.of variation	Mean no. of follicles/ovary (S.D.) [n]	*No. of degree squares occupied
SCARABAEIDAE: SCARABAEINAE			
Scarabaeina			
Kheper bonellii (M'Leay)	0,708	2,8 (0,4) [13]	5
Scarabaeus aesculapius (Olivier)	0,316	2,0 [1]	2
S. canaliculatus Fairmaire	0,376	2,3 (0,5) [3]	3
S. hippocrates (M'Leay)	0,376		2
S. intricatus (Fabricius)	0,568	2,1 (1,0) [14]	5
S. proboscideos Guerin	0,405		11
S. rugosus (Hausman)	0,536	3,2 (0,8) [183]	4
S. satyrus (Boheman)	0,316		21
S. spretus zur Strassen	0,442	2,0 (0,0) [3]	3
S. suri (Hausman)	0,390	2,4 (0,5) [10]	5
Sceliages brittoni zur Strassen	0,471		1
Canthonina			
Epirinus aeneus Weidemann	1,028	3,3 (0,5) [3]	19
E. bentoi Ferreira	0,623	3,0 [1]	2
E. comosus Peringuey	0,316		4
E. flagellatus (Fabricius)	0,923	4,2 (0,8) [5]	14
E. granulatus Scholtz & Howden	0,316		1
E. scrobiculatus Harold	0,560		5
Epirinus sp.	0,392	1,2 (0,4) [5]	1
Odontoloma dentinum Harold	0,726		5
Odontoloma sp. a	0,443		1
Odontoloma sp. b	0,359		1
Aphengoecus multiserratus Scholtz & Howden	0,403		5
Sisyphina			
Neosisyphus quadricollis Gory	0,488	4,0 [1]	2

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Table AD1. cont.

Taxa	Coeff.of variation	Mean no. of follicles/ovary (S.D.) [n]	*No. of degree squares occupied
SCARABAEIDAE: COPRINAE			
Coprini: Coprina			
Catharsius tricornutus de Geer	0,499	7,0 [1]	62
Copris anceus Olivier	0,657	3,6 (1,0) [69]	2
C. capensis Waterhouse	0,534	3,9 (1,2) [9]	8
C. fidius (Olivier)	0,379		8
Metacatharsius latifrons Harold	0,742		19
Coprini: Dichotomiina			
Macroderes sp. a	0,487		1
Macroderes sp. b	0,316	6,0 [1]	1
Macroderes sp. c	0,316	3,0 [1]	1
Sarophorus tuberculatus (Harold)	0,605		3
Onitini			
Chironitis hoplosternus (Harold)	0,316	11,0 (1,0) [2]	23
C. scabrosus (Fabricius)	0,586	9,2 (1,8) [29]	28
Onitis aygulus (Fabricius)	0,866	12,3 (2,6) [93]	35
O. caffer Boheman	0,553	17,7 (3,7) [407]	68
O. confusus Boheman	0,316	20,9 (3,1) [12]	9
Onthophagini			
Onthophagus cameloides d'Orbigny	0,685	11,3 (2,2) [108]	17
O. giraffa Hausman	0,864	8,1 (1,5) [14]	10
O. immundus Boheman	0,555		3
O. minutus Hausman	0,738	8,8 (1,1) [6]	7
Oniticellini: Oniticellina			
Euoniticellus africanus (Castelnau)	0,618	8,9 (1,7) [34]	50
E. intermedius (Reiche)	0,637	7,4 (1,7) [310]	109
E. triangulatus (Harold)	0,570	7,2 (1,6) [214]	44

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Table AD1. cont.

Taxa	Coeff. of variation
SCARABAEIDAE: APHODIINAE	
Aphodius (*Amidorus*) *granulatus* Boheman	0,674
A. (*Amoecius*) *bidentulus* Harold	0,583
A. (*A.*) *tricornutus*	0,441
A. (*Bodilus*) *laetus* Weidemann	1,089
A. (*Bodilus*) sp. a	0,540
A. (*Bodilus*) sp. b	0,756
A. (*Bodilus*) sp. c	0,504
A. (*Bodilus*) sp. d	0,510
A. (*Calaphodius*) *moestus* Fabricius	0,446
A. (*Nialus*) *lividus* Olivier/ *consimilus* Boheman	0,754
A. (*Orodalus*) sp.	0,660
A. (*Pharaphodius*) sp. nr *guineensis*	0,376
A. (*Pleuraphodius*) *teter* Roth	0,858
Aphodius sp. a	0,442
Aphodius sp. b	1,366
Aphodius sp. c	0,792
Aphodius sp. d	0,602
Aphodius sp. e	0.461
Aphodius sp. f	0,519
Aphodius sp. g	0,316
Aphodius sp. h	0,316
Colobopterus (*Colobopterus*) *maculicollis* Reiche	0,451
C. brachypterus Harold	0,838
Coptochirus sp. nr *emarginatus*	0,922
Coptochirus obscurus	0,372
C. zumpti Petrovitz	0,746
Coptochirus sp.	0,316
Drepanocanthus lineatus Weidemann	0,636
Harmogaster sp. a	0,938
Harmogaster sp. b	0,385
Harmogaster sp. c	0,451
Harmogaster sp. d	0,316
Rhyssemus sp.	0,316
HISTERIDAE	
Histerinae	
Atholus conformis	0,572
Hister ?crenatipennis	0,584
Hister sp. a	0,413
Hister sp. b	0,495
Hypocacculus metallescens (Erichson)	0,880
H. roeri	0,413
Abraeinae	
Abreus bacanioformis Bickhardt	0,316
Abreus sp. a	0,632
Acritus sp. a	0,591
Acritus sp. b	0,316
Chaetabraeus setulosus (Fahraeus)	0,709
C. spiculator (Therond)	0,468

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Table AD1. cont.

Taxa	Coeff. of variation		Coeff. of variation
HISTERIDAE			
Histerinae		**Tribalinae**	
Hypocacculus ?rubricatus	0,316	*Atribalus mixtus*	0,686
Hypocacculus sp. a	0,923	*Tribalus ascaphus*	0,460
Hypocacculus sp. b	0,566	*T. kochi*	0,321
Hypocacculus sp. c	0,316	*T. striatipennis*	0,549
Saprininae			
Saprinus cupreus Erichson	0,897		
S. bicolor	1,077		
S. nitidus	0,893		
S. purpuricollis	0,538	*Asolenus truncatus*	0,630
Saprinus sp. a	0,608	*Monoplius imitator*	0,316
Saprinus sp. b	0,531	*Rhypochares saprinoides*	0,528
Saprinus sp. c	0,316	*Xestipyge radatum*	0,921
HYDROPHILIDAE			
Cercyon atricapillus (Marsham)	0,669	*Pachysternum capense* (Mulsant)	0,526
C. quisquilius (L.)	0,575	*Sphaeridium abbreviatum* Boheman	0,330
Cercyon sp. a	0,691	*S. caffrum* Castelnau	0,565
Cercyon sp. b	0,880		
STAPHYLINIDAE: OXYTELINAE			
Anotylus caffer (Erichson)	1,391	*Oxytelus depauperatus* Wollaston	0,316
A. latiusculus (Kraatz)	0,628	*O. puncticeps* Kraatz	0,596
Bledius sp.	0,553	*O. varipennis* Kraatz	0,422
Oxytelus sp. a	0,584		
Oxytelus sp. b	0.316		

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Table AD1. cont.

Taxa	Coeff. of variation		Coeff. of variation
STAPHYLINIDAE: (PREDATORY TAXA)			
Staphylininae		**Aleocharinae**	
?Gabrius sp.	0,316	*Aleochara afra* (Eichelbaum)	0,784
Gabronthus ?alluaudanus	0,510	*Aleochara* sp. nr *bipustulata* a	1,045
G. mgogoricus Tottenham	0,316	*Aleochara* sp. nr *bipustulata* b	0,535
Gabronthus sp. a	0,316	*A. crassa* Baudi	0,630
Philonthus caffer (Boheman)	0,679	*A. dubiosa*	0,502
P. nairobiensis Fauvel	1,047	*A. puberula* Klug	0,442
P. natalensis Boheman	0,613	*A. sublaevipennis* Fauvel	0,554
P. (*Spatulonthus*) *maskinius*		*A. trivialis* Kraatz	1,170
Tottenham	0,883	*Aleochara* sp. a	0,471
P. (*S.*) *minutus* Boheman	1,101	*Atheta nigerrima* (Aube)	1,020
P. (*S.*) *peregrinus* Fauvel	0,316	*A ?provincialis* Cameron	0,729
P. (*S.*) *sanamus* Tottenham	0,843	*Atheta* sp. a	1,165
Philonthus sp. a	1,335	*Atheta* sp. b	1,599
Philonthus sp. b	0,721	*Atheta* sp. c	0,694
Philonthus sp. c	0,796	*Atheta* sp. d	0,790
Philonthus sp. d	0,316	*Atheta* sp. e	0,957
Philonthus sp. e	0,316	*Atheta* sp. f	0.842
Platydracus sp. a	0,449	*Atheta* sp. g	1,032
Platydracus sp. b	0,397	*Atheta* sp. h	1,010
Platydracus sp. c	0,460	*Atheta* sp. i	0,638
Platydracus sp. d	0,316	*Atheta* sp. j	0,828
Staphylininae ?genus sp. a	0,316	*Atheta* sp. k	0,651
Staphylininae ?genus sp. b	0,316	*Atheta* sp. p	0,316
Xantholininae		*Atheta* sp. q	0,657
Phacophallus sp. a	1,096	*Atheta* sp. r	0,316
Phacophallus sp. b	1,004	*Atheta* sp. s	0,316
Phacophallus sp. c	0,720	*Atheta* sp. t	0,316
Phacophallus sp. d	0,316	*Atheta* sp. u	0,316
Xantholininae ?genus sp.	0,566	*Atheta* sp. v	0,316

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Table AD1. cont.

Taxa	Coeff. of variation		Coeff. of variation
STAPHYLINIDAE: (PREDATORY TAXA)			
Paederinae		**Aleocharinae**	
Lithocharis sp. a	0,566	*Atheta* sp. w	0,471
Rugilus sp. a	0,316	*Atheta* sp. x	0,316
Rugilus sp. b	0,316	*Atheta* (*Microdota*) sp.	0,908
Rugilus sp. c	0,316	*Tinotus clavicornis* Cameron	0,784
Paederinae ?genus sp. a	0,316	*T. minutus* Bernhauer	0,630
Falagria coarticollis Fauvel	0.645	Aleocharinae ?genus sp. a	0,874
		Aleocharinae ?genus sp. b	0,316
?Subfamily		Aleocharinae ?genus sp. c	0,316
?genus sp.	0,316	Aleocharinae ?genus sp. d	0,442

*Number of degree squares of longitude and latitude occupied in southern Africa south of latitude 15°S

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Table AD2. Species of dung beetles recorded at two study sites on deep sand in open woodland and in pasture on the farm Boekenhoutskloof (25°34'S 28°29'E) in the Transvaal.

SCARABAEIDAE: SCARABAEINAE

Scarabaeini: Scarabaeina

- *Kheper lamarcki* (M'Leay)
- *Pachylomerus femoralis* Kirby
- *P. opaca* Lansberge
- *Scarabaeus ambiguus* (Boheman)
- *S. bohemani* Harold
- *S. flavicornis* (Boheman)
- *S. goryi* Castelnau
- *S. inquisitus* Peringuey
- *S. zambesianus Peringuey*

Scarabaeini: Gymnopleurina

- *Allogymnopleurus thalassinus* Klug
- *Garreta nitens* (Olivier)
- *Gymnopleurus aenescens* Weidemann

Scarabaeini: Sisyphina

- *Neosisyphus fortuitus* Peringuey
- *N. ruber* Paschalidis
- *Sisyphus goryi* Harold

Scarabaeini: Canthonina

- *Anachalcos convexus* Boheman
- *Odontoloma louwi* Scholtz & Howden

SCARABAEIDAE: COPRINAE

Coprini: Dichotomiina

- *Sarophorus costatus* (Fahraeus)
- *Pedaria* sp. a
- *Pedaria* sp. b
- *Heliocopris japetus* Klug
- *H. hamadryas* (Fabricius)

Coprini: Coprina

- *Catharsius tricornutus* de Geer
- *C. sesostris* Waterhouse
- *Copris cassius* Peringuey
- *C. denticulatus* Nguyen-Phung
- *C. elphenor* Klug
- *C. evanidus* Klug
- *C. macer* Peringuey
- *Metacatharsius troglodytes* Boheman
- *Metacatharsius* sp. a
- *Metacatharsius* sp. b

Onthophagini

- *Caccobius convexifrons* Raffray
- *C. ferrugineus* Fahraeus
- *C. nigritulus* Klug
- *C. viridicollis* Fahraeus
- *Caccobius* sp.
- *Onthophagus aequepubens* d'Orbigny
- *O. aeruginosus* Roth
- *O. albipodex* d'Orbigny
- *O. aschenborni* Frey
- *Onthophagus* sp. nr *carbonarius*
- *O. cinctipennis* Quedenfeldt
- *O. cribripennis* d'Orbigny
- *O. ebenus* Peringuey
- *O. flavolimbatus* d'Orbigny
- *O. gazella* (Fabricius)
- *O. interstitialis* Fahraeus

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Table AD2. cont.

SCARABAEIDAE: COPRINAE

Onitini

Onitis alexis Klug
O. caffer Boheman
O. deceptor Peringuey
O. fulgidus Klug
O. setosus Lansberge
O. tortuosus Houston
O. viridulus Peringuey
Chironitis sp. nr *scabrosus*

Oniticellini: Oniticellina

Oniticellus egregius Klug
O. formosus Chevrolat
O. planatus Castelnau
Euoniticellus intermedius (Reiche)
E. triangulatus (Harold)
Liatongus militaris (Castelnau)
Tiniocellus spinipes (Roth)

Oniticellini: Drepanocerina

Drepanocerus fastiditus Peringuey
D. kirbyi (Kirby)
D. laticollis Fahraeus
D. patrizii (Boucomont)

Onthophagini

Onthophagus leroyi d'Orbigny
O. obtusicornis Fahraeus
O. pallidipennis Fahraeus
O. pilosus Fahraeus
O. pugionatus Fahraeus
Onthophagus sp. nr *pullus* a
Onthophagus sp. nr *pullus* b
O. quadrinodosus Fahraeus
O. rasipennis d'Orbigny
O. signatus Fahraeus
Onthophagus sp. nr *sugillatus*
O. stellio Erichson
O. verticalis Fahraeus
O. vinctus Erichson
Onthophagus sp. a
Onthophagus sp. b
Onthophagus sp. c
Onthophagus sp. d
Phalops boschas Klug
P. dregei Harold
P. smaragdinus Harold
P. wittei Harold
Proagoderus alcedo d'Orbigny
P. sapphirinus Peringuey

SCARABAEIDAE: APHODIINAE

Aphodius (*Aganocrossus*) *amoenas* *Boheman*
A. (*Blackburneus*) *bernoni* Endrodi
A. (*Bodilus*) *buxeipennis* Harold
A. (*B.*) *laetus* Weidemann
A. (*Bodilus*) sp. nr *damarinus*

Aphodius (*Pleuraphodius*) *bibatillatus* Petrovitz
A. (*P.*) *confinis* Schmidt
A. (*P.*) *levis* Schmidt
A. (*P.*) *mutilus* Schmidt
A. (*P.*) *reticulatus* Endrodi

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Table AD2. cont.

SCARABAEIDAE: APHODIINAE

Aphodius (*Bodilus*) sp. a
A. (*Bodilus*) sp. b
A. (*Calaphodius*) *moestus* Fabricius
A. (*Erytus*) *gracilis* Boheman
A. (*Hemicyclium*) *planatus*
A. (*Mesontoplatys*) *dorsalis* Klug
A. (*Nialus*) *lividus* Olivier
A. (*N.*) *nigritus* Fabricius
A. (*Nobius*) *hepaticus* Roth
A. (*Orodalus*) *bredoi* Endrodi
A. (*Pharaphodius*) *guineensis* Klug
A. (*P.*) *impurus* Roth
A. (*P.*) *russatus* Erichson
Aphodius (*Pleuraphodius*) sp.
A. (*Trichaphodius*) *humilis* Roth
A. (*T.*) *calcaratus* Boheman
Aphodius sp. i
Colobopterus (*Colobopterus*) *maculicollis* Reiche
C. (*Megateloides*) *dimidiatus* Roth
C. (*Teuchestes*) *analis* Fabricius
Coptochirus emarginatus Germar
Drepanocanthus maniculus Petrovitz
D. nasutus Harold
Pseudoxymus rubescens Petrovitz

STAPHYLINIDAE: OXYTELINAE

Anotylus bacillus (Bernhauer)
A. latiusculus (Kraatz)
A. okahandjanus (Bernhauer)
Anotylus sp. a
Anotylus sp. b
Oxytelus depauperatus Wollaston
O. planus Fauvel
O. puncticeps Kraatz
O. varipennis Kraatz
Oxytelus sp. c

HYDROPHILIDAE

Cercyon atricapillus (Marsham)
Cercyon sp. c
Cercyon sp. b
Cryptopleurum suturatum Regimbart
Pachysternum capense (Mulsant)
Sphaeridium caffrum Castelnau
S. senegalense Castelnau

HISTERIDAE

Abraeinae

Abreus bacanioformis Bickhardt
Abreus sp. nr *curtulus*

Histerinae

Adelopygus nickerli Schmidt
Atholus conformis

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Table AD2. cont.

HISTERIDAE

Abraeinae
- *Acritus* sp. c
- *Acritus* sp. d
- *Acritus* sp. e
- *Chaetabraeus spiculator* (Therond)
- *C. setulosus* (Fahraeus)

Saprininae
- *Saprinus cupreus* Erichson
- *Saprinus* sp. c
- *Saprinus* sp. d
- *Saprinus* sp. e
- *Saprinus* sp. f
- *Saprinus* sp. g
- *Saprinus* sp. h

Histerinae
- *Hister furciger* Marseul
- *H. ignavus* Fahraeus
- *H. lentulus* Erichson
- *Hister* sp. c
- *Hypocacculus metallescens* (Erichson)
- *Macrolister latipes* (Palisot de Beauvois)
- *Pactolinus caffer* (Erichson)
- *P. nigrita* (Erichson)
- *Pelorurus fraudator* Lewis

Tribalinae
- *Tribalus amnicola* Lewis

STAPHYLINIDAE (PREDATORY TAXA)

Tachyporinae
- *Cilea ?sculpta* (Bernhauer)
- *C. ?exilis*
- *C. ?picta* (Erichson)
- *C. intermedia* Last

Xantholininae
- *Phacophallus politus*

Staphylininae
- *Gabronthus mgogoricus* Tottenham
- *G. ?alluaudanus*
- *Philonthus caffer* (Boheman)
- *P. cinctus* Fauvel
- *P. hospes* Erichson
- *P. ?marginipennis* Wollaston
- *P. natalensis* Boheman
- *P. nairobiensis* Fauvel

Aleocharinae
- *Aleochara afra* (Eichelbaum)
- *A. bicoloripennis* Bernhauer
- *Aleochara* sp. nr *bipustulata sp. a*
- *Aleochara* sp. nr *bipustulata* sp. b
- *A. crassa* Baudi
- *A. mahagi* (Likovsky)
- *A. puberula* Klug
- *A. sublaevipennis* Fauvel
- *A. trivialis* Kraatz
- *Aleochara* sp. b
- *Aleochara* sp. c
- *Atheta graciosa* Scheerpeltz
- *A. nigerrima* (Aube)
- *A. ?provincialis* Cameron
- *A. ruparia* Cameron

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Table AD2. cont.

STAPHYLINIDAE (PREDATORY TAXA)

Staphylininae

- *Philonthus parvicornis* Fauvel
- *P. reinecki* Schubert
- *P.* (*Spatulonthus*) *bisignatus* Boheman
- *P.* (*S.*) *maskinius* Tottenham
- *P.* (*S.*) *minutus* Boheman
- *P.* (*S.*) *sanamus* Tottenham
- *Platydracus* sp. e
- Staphylininae ?genus sp. c

Paederinae

- *Lithocharis ?kawaensis* Cameron
- *Lithocharis* sp.
- *Rugilus minimus* (Bernhauer)
- *Rugilus* sp. d
- Paederinae ?genus sp. b

Aleocharinae

- *Atheta viatica* Fauvel
- *Atheta* (*Microdota*) sp.
- *Atheta* sp. l
- *Atheta* sp. m
- *Atheta* sp. n
- *Atheta* sp. o
- *Atheta* sp. z
- *Atheta* sp. aa
- *Atheta* sp. ab
- *Atheta* sp. ac
- *Autalia capensis* Tottenham
- *Cordalia ?obscura* (Gravenhorst)
- *Falagria coarticollis* Fauvel
- *F. kawaensis* (Cameron)
- *Macrophthalmodites melanocephalus* Scheerpeltz
- *Schistogenia methneri* Bernhauer
- *Tinotus clavicornis* Cameron
- *T. minutus* Bernhauer
- Aleocharinae ?genus sp. d
- Aleocharinae ?genus sp. e

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