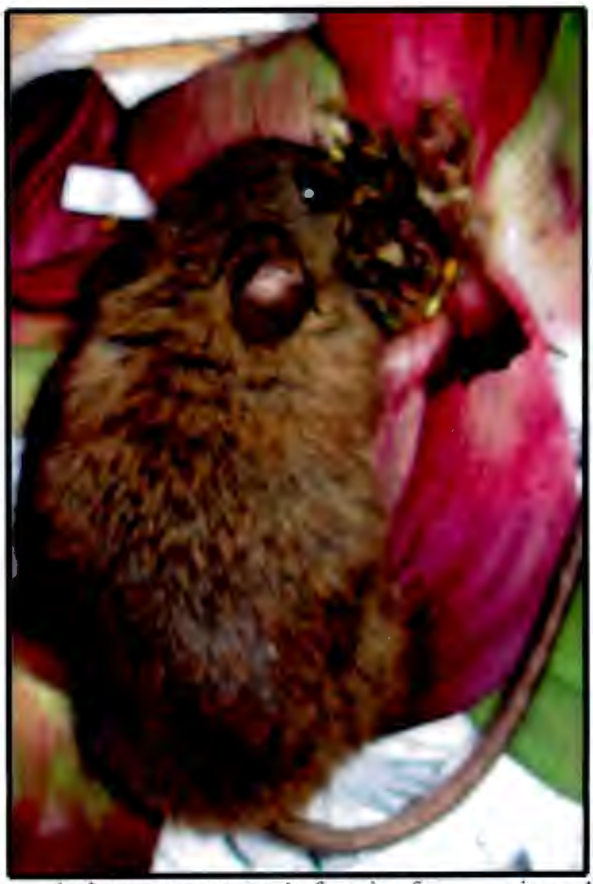
Rodent Pollination in *Androcymbium latifolium* (Colchicaceae)

Ciara Kleizen

Supervisor: Jeremy Midgley
University of Cape Town



Namaqualand Rock Mouse, *Aethomys namaquensis*, foraging for nectar in an *Androcymbium latifolium* inflorescence. Photograph by author.

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Anti-plagiarism Declaration

I declare that this thesis is my own work. It is being submitted for the Degree of Honours in Botany at the University of Cape Town. It has not been submitted before for any other project or degree.

Signed by candidate

Ciara Kleizen

Abstract

The repeated discovery of rodent pollination (therophily) has lead to the concept of a rodent pollination syndrome. The adaptive plant traits that characterize this syndrome include flowers packed tightly into geoflorous and cryptic inflorescences, nocturnal anthesis and production of copious amounts of sugar-rich nectar and pollen as well as a musky odour. *Androcymbium latifolium* (Colchicaceae), a geophyte that occurs in the semiarid Succulent karoo region of South Africa, exhibits several of the therophilous traits. Experiments were conducted investigating the hypothesis that this species is rodent pollinated. Several lines of evidence were found to support this hypothesis. These include: the almost exclusive presence of *A. latifolium* pollen in the scats of live-trapped *Aethomys namaquensis* rodents and in the fuschin gelatine swabs from the rostrum area of the rodents; and observations of captive *A. namaquensis* individuals foraging for nectar non-destructively in *A. latifolium* inflorescences. The exclusion of rodents from inflorescences resulted in a significant decrease in seed set compared to control plants. This result indicated that rodents do contribute to pollination success of *A. latifolium*, however, in the absence of rodents, the flowers self-pollinate, indicating a facultative selfing strategy. Therefore, *A. latifolium* displays an opportunistic life history attracting rodents to the sugar-rich nectar when other food sources are scarce. This is supported by the observation that the seed set of *A. latifolium* decreases as the distance from the rodents nesting site increases. This study presents substantial evidence for therophily in *A. latifolium*, making this species the first species in the family Colchicaceae, and the second geophyte in the world to be rodent pollinated.

Introduction

Rodent pollination (therophily) is one of the most unexpected interactions between plants and animals (Johnson *et al.* 2001). Until recently, all of the research conducted on the subject of rodent pollination in the south-western Cape has been on Proteaceae species (Rourke and Wiens, 1977; Wiens and Rourke, 1978; Wiens *et al.* 1983; Wiens, 1985). Rebelo and Breytenbach (1987) compiled a list of 36 putatively rodent pollinated Proteaceae species, of which three species [*P. amplexicaulos*, *P. humiflora* (Wiens and Rourke, 1978; Fleming and Nicolson, 2002) and *P. subulifolia* (Rourke and Wiens, 1977)] have been experimentally proven. The only Namaqualand species proposed by Rebelo and Breytenbach (1987), as a possible rodent pollinated species, is *Aloe claviflora* Burchell (Aspholdelaceae). *Massonia depressa (Hyacinthaceae)* is the first species that occurs in the semiarid Succulent karoo region of South Africa, that has been shown to be rodent pollinated (Johnson *et al.* 2001). Here, I report the discovery of rodent pollination in *Androcymbium latifolium*, a species that occurs in the semiarid Succulent karoo region. This is the second record of a rodent pollinated geophyte.

In order to measure the effectiveness of rodents as pollinators, there are six types of data that are sought: (1) observations of regular and non-destructive visits to the flowers; (2) substantial loads of pollen need to occur on the fur or in the faeces; (3) the pollen transported on the animal needs to come into contact with the stigma of a flower (Carthew and Goldingay, 1997, Johnson *et al.* 2001); (4) rare insect and bird visitation to the flowers; (5) reduced fecundity when the rodents are excluded from the flowers; and finally, (6) the nectar production, scent production and floral anthesis should occur at times that correspond with the activity times of the rodents and preclude the successful nectar foraging by birds and insects (Rourke and Wiens, 1977; Johnson *et al.* 2001).

Various authors (Carpenter, 1987; Turner, 1982) have attempted to define the traits that distinguish the rodent pollination "syndrome". Plants adapted for rodent pollination tend to have flowers that are dull in colour (Johnson *et al.* 2001), are robust and cup-shaped, and are hidden deep within foliage (cryptic). The flowers are also positioned near ground level (geoflorous) (Wiens and Rourke, 1978). The heads

of the flowers tend to be strongly attached to the stems (Rourke and Wiens, 1977), and produce copious amounts of nectar (Johnson *et al.* 2001). The flowering heads are odiferous, which are often characterized as having a "yeasty" odour (presumably the initial attracting mechanism). The sense of smell is well developed in rodents, and in view of the hidden position of these inflorescences, odour must be the primary attractant (Rourke and Wiens, 1977). The time of flowering of rodent pollinated plants tends to be late winter, so the flowering might correlate with a low point in the food cycle of the rodents (Rourke and Wiens, 1977), therefore the nectar in the inflorescences will provide a good supply of nutrients. This syndrome is also characterised by a distinctive 10 mm stigma-nectar distance (Rebelo and Breytenbach, 1987; Wiens *et al.* 1983).

Species of the genus *Androcymbium* Willd. (Colchicaceae) are geophytes with an annual vegetative cycle, and pass the unfavourable period buried like a tunicated corm (Membrives *et al.* 2002, Membrives *et al.* 2003). Hardly any research has been conducted on the reproductive biology of southern African *Androcymbium* species. The only published reference shows the pollination system of *A. capense*, which is insect pollinated (Membrives *et al.* 2002). The species *Androcymbium latifolium* has many features in common with proven rodent pollinated species. However, until now there has been no investigation into the pollination system or reproductive biology of this species. The primary aim of this study was to test the hypothesis that *A. latifolium* is rodent pollinated. In this investigation, the following questions were asked: 1) Do rodents visit *A. latifolium*? 2) Does rodent visitation to *A. latifolium* flowers result in seed set? 3) Does the distribution of rodents have an effect on the distribution of *A. latifolium* plants?

Materials and Methods

Study site

This study was carried out at a site in Glen Lyon farm in the town of Niewoudtville in the semiarid Succulent Karoo region of South Africa (31°249' S, 019 °0924' E, elevation 774m). A large population (<1000) of *A. latifolium* occurred behind a large dolerite ridge, known locally as Kameel Koppie which is situated in heavy red dolerite clay soils. This habitat is dominated by geophytes and annuals with very few shrubs (Proches *et al.* 2006).

Rodent Trapping

On the site behind Kameel Koppie, live trapping of rodents was carried out over three consecutive nights (8th, 9th and 10th of August). A total of 84 gutter pipe traps were used each night. Therefore, there was a total of 252 trap nights. For each of the trapping nights, four transects, 20 metres apart and consisting of 16 traps each, were laid out amongst the *A. latifolium* population, moving up an inclining slope. On the first and second trapping nights, 20 traps were laid out in Kameel Koppie, of which 10 were positioned in the open, and 10 were positioned next to rocks or boulders. After the first and second trapping nights, it appeared as though rodents most commonly occurred in the rocky areas on the dolerite ridges. Therefore, on the third trapping night the traps that were positioned in the open in Kameel Koppie (10 traps) were moved to another rocky dolerite ridge that is approximately one kilometre behind Kameel Koppie. These traps were also positioned next to rocks or boulders. The traps were set up each evening between 17h00 and 18h00pm; and then checked the following morning between 7h00 and 8h00am.

The traps were baited with peanut-butter and rolled oats. It has been proposed that peanut-butter and oats combined with red wine results in a higher trapping success rate (Midgley, pers. comm.). On the third trapping night, two out of the four transects were baited with peanut-butter rolled with oats and red wine. The 10 traps set out in the dolerite ridge behind Kameel Koppie, were also baited with red wine, peanut butter and oats.

Two more trapping nights were conducted on the 1st and 2nd of September. Four transects of five traps each were laid out in the open plains ("vlakte") in the Niewoudtville Flower Reserve (31°2156' S, 019 °0852' E, elevation 772m). Therefore, there were a total of 40 trap nights in the Niewoudtville Flower Reserve.

Observations

As it is virtually impossible to observe rodents in the field at night (cf. Wiens *et al.* 1983), I released two captured *Aethomys namaquensis* individuals, each in a glass tank, at 10h00. A gutter pipe trap was placed in each tank and the floor was covered in shredded paper to provide warmth. Four *A. latifolium* flowers and two *A. burchelli* flowers were placed in each tank in the evening, at 18h00. The observation tanks were placed in a dark and quiet room. The foraging behaviour of each individual was filmed and photographed from 18h00 until 24h00. This observation experiment was conducted twice, on two consecutive nights. On both of the nights, fresh flowers were placed into the tanks. The same two *A. namaquensis* individuals were used on both observation nights. During the day, before the second evening of observations, the rodents were fed rolled peanut-butter and oats.

In the field, a total of six hours was spent observing a population of *A. latifolium* plants. Notes were taken on any observed animal interactions, such as insects feeding from the flowers.

Pollen transfer and Consumption

The quantification of pollen grains in scats indicates the proportion, by volume, of pollen in other indigestible diet components (nectar is digested completely). Pollen may be ingested directly, through feeding, or indirectly through grooming (Fleming and Nicolson, 2002). Captured rodents were identified and temporarily placed in a plastic bag with a hole in one corner through which the snout of the rodent protruded. The fur just around the nose of each trapped rodent was swabbed for 10 seconds with a small block of fuschin gelatine (Beattie, 1971). Each of the fuschin gelatine samples was then melted onto a slide and then examined microscopically (40X magnification) for the presence of pollen. Permanent slides of *A. latifolium* pollen were made from

fresh flowers, for comparison with the collected samples. Rodent scats were collected from the traps and stored in 70% alcohol in epindorphs. The scats were broken up with forceps. The solution of faeces and alcohol was then mixed in a vortex mixer. This solution was then poured through a 38μm soil sieve. A drop of liquid fuschin gelatine was added to a small sample of the liquid solution on a slide. The slides were examined at 40X magnification and the number of pollen grains was counted over four scans of the length of the coverslip.

A kolmogorov-Smirnov test and a Levene's test were conducted testing for normality and equal variance respectively. A kruskal wallis ANOVA and median test was then conducted in Statistica (version 7, Statsoft Inc.). This was done in order to test for significant differences between the abundance of the pollen species in both the scat samples and the fuschin gelatine samples.

Exclusion of rodents from flowers

To determine the effects of excluding small mammal visitation from *A. latifolium* plants on seed production, 28 pairs of newly opened plants were selected. One plant per pair was enclosed in a cage made from chicken wire, and the control plant was labelled with a marker. The wire exclosure effectively excluded rodents from the flower, but allowed easy access to insects.

When the flowers were at the end of their flowering season, the seed set of the enclosed plants and the control plants were compared. Each of the ovaries per flower was dissected, for all flowers per inflorescence, by cutting transversely through the ovary with a sharp, thin blade. In order to determine seed set, the number of seeds per ovary was counted.

A kolmogorov-Smirnov test and a Levene's test were conducted testing for normality and equal variance respectively; then a Mann-Whitney U test was performed in Statistica (version 7, Statsoft Inc.), investigating the difference between the seed set of the flowers inside the exclosures and the control flowers.

Stigma-nectar distances

A total of 25 flowers were collected and one measurement was taken per flower of the distance between the nectar accumulation "trough" and the stigmatic groove. A digital vernier caliper was used to measure the distances.

Number of seeds per ovule in relation to distance from a dolerite ridge

The rodent trapping data indicated that most small mammals were captured within the dolerite out-crops. This lead to the expectation that the seed set should decrease as the distance from the dolerite out-crops increases. A total of ten inflorescences were collected approximately every ten metres, along a transect of 85 metres. The transect started at a dolerite ridge moving away from the peak of the ridge down a declining slope. Each of the inflorescences was then dissected into its separate flowers and the number of seeds per ovary was counted.

Results

Rodent trapping

Over a total of 292 trap nights set at three different habitat types, there was a 15% trap success rate at the dolerite out-crops on Glen Lyon farm (Table 1), a 0% trap success rate on the open slope in Glen Lyon farm, and a 0% trap success rate from the traps set on the "vlakte" in the Niewoudtville Flower Reserve. The nine captured rodents were all *A. namaquensis* (Namaqualand Rock mice) individuals.

Table 1: Number and location of rodent captured.

Date	Number of individuals caught	Location of traps
8-Aug	0	-
9-Aug	5	Kameel Koppie
10-Aug	2	Kameel Koppie
	2	Ridge behind Kameel Koppie
1-Sep	0	-
2-Sep	0	-

Since there was a 0% trapping success rate on the slope, it appeared as though the bait which included wine, in half of the traps, was not more attractive to rodents. The 10 traps set with the wine bait in a dolerite ridge resulted in the trapping of two individuals. However, the 10 traps baited without wine also resulted in the trapping of two rodents. Therefore, the addition of wine to the bait did not appear to have an effect on the success of the trapping.

Observations

On the first evening, the *A. namaquensis* individuals in the observation tanks came out from hiding inside the open gutter pipe traps approximately 30 minutes after placing the flowers in the tanks. They were observed to run around the Perspex tank, trying to escape. Both rodents did not seem interested in feeding from the *A. latifolium* flowers. During the evening, both rodents ate the anthers, stigma and red bracts of all four *A. latifolium* flowers, only leaving the green leaves untouched. All of the *A. burchelli* flowers were also completely untouched by both rodents. During the

evening, both rodents were observed to jump up against the walls of the tanks, presumably trying to escape.

The following day, peanut-butter balls rolled with oats was placed in the tanks, and both rodents ate two balls of this food. In the evening, approximately 20 minutes after placing the freshly picked flowers into the tanks, both *A. namaquensis* individuals came out from inside the open traps and moved immediately towards the *A. latifolium* flowers. Both individuals foraged repeatedly from the *A. latifolium* flowers, and completely ignored the *A. burchelli* flowers. The rodents inserted their snouts into the gaps between the anthers, deep enough to be able to reach the nectar at the base of the anthers. They then moved their heads in and out of the flower in a fast pumping motion. It is presumed that the rodents are lapping up the viscous nectar during this motion. In this process, the pollen is moved from the tips of the anthers to the snouts of the foraging rodent. Both rodents moved around repeating this process with all of the *A. latifolium* flowers in the tank. (Video clip 1 in appendix). One of the rodents was observed to wet-preen its snout and ears with its forepaws after foraging from the *A. latifolium* flowers in the tank (Video clip 2, see appendix). On this evening, both rodents were calm and did not try to escape from the tank by jumping against the walls of the tank, and neither of the individuals ate the flowers like they had on the first night of observations. One of the rodents was observed to eat from the base of the *A. latifolium* inflorescence. This rodent nibbled from the base of the flowers, and it appeared as though the rodent was interested in the base of the anthers (Video clip 3, see appendix).

Pollen transfer and Consumption

There were three species of pollen that occurred in the *A. namaquensis* scats, *A. latifolium*, a triporate pollen and a pollen species from the family Asteraceae, subfamily Asteroideae. Due to the position of the triporate pollen and the pollen belonging to the subfamily Asteroideae, in the permanent slides, they could not be identified further. The pollen found in the scats was almost exclusively *A. latifolium* pollen, and was found to be significantly more abundant when compared to the other two pollen species ($H = 20.81251$, $df = 2$, $p < 0.05$) (Figure 1A). The pollen count from the fuschin gelatine samples showed that *A. latifolium* was the most abundant.

Androcymbium latifolium pollen was significantly more abundant than the triporate pollen. However, *A. latifolium* was not significantly more abundant than the pollen from the subfamily Asteroideae ($H = 9.961746$, $df = 2$, $p < 0.05$) (Figure 1B).

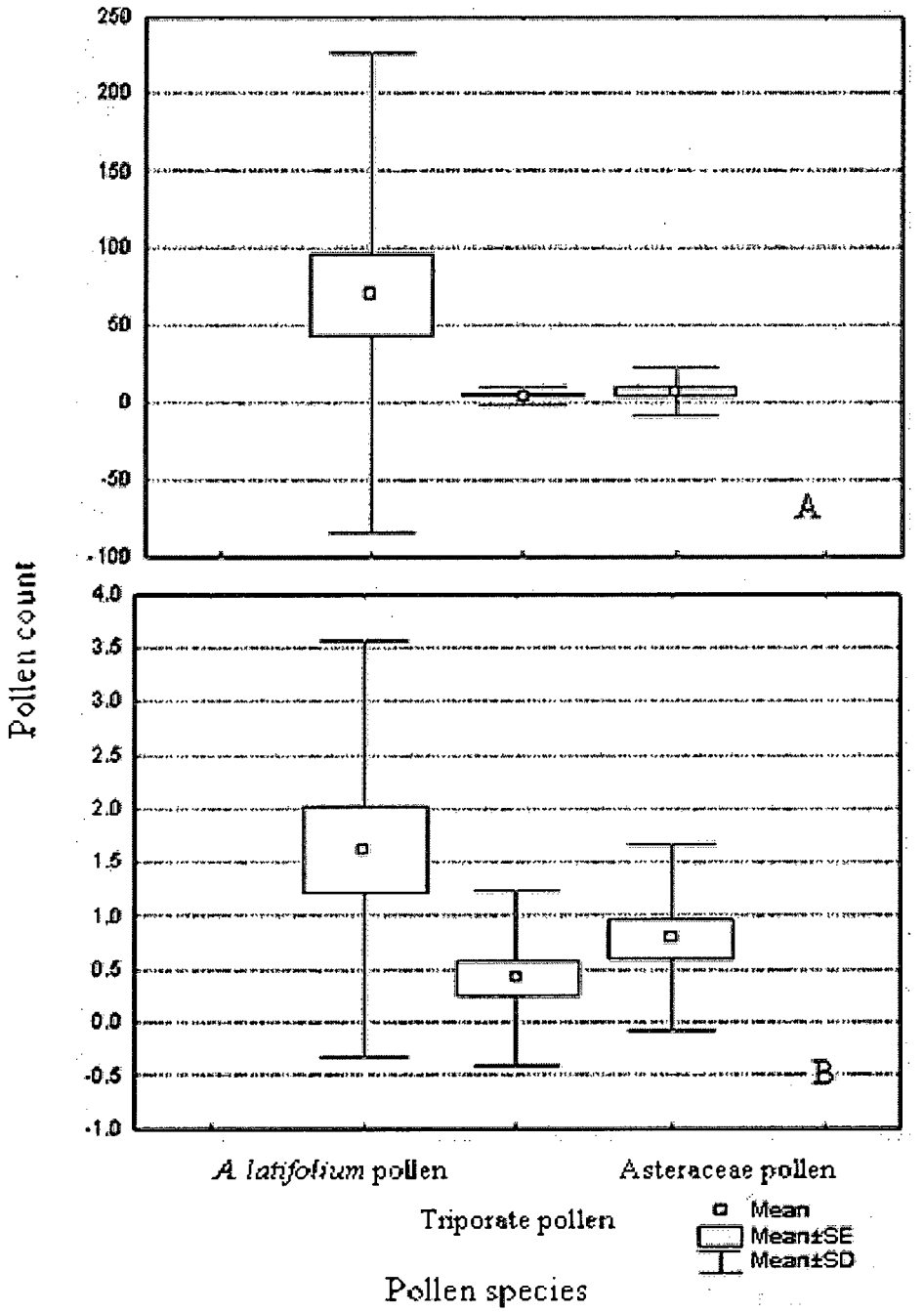

Figure 1. – **A**. Then mean pollen count for each of the pollen species in the captured rodents' scats. **B**. The mean pollen count for each of the pollen species seen in the fuschin gelatine samples from the captured rodents.

Figure 2. – A. An *A. latifolium* inflorescence consisting of two flowers. **B.** A portion of the *A. latifolium* population behind Kameel Koppie, showing the geoflorous inflorescences. **C, D & E.** *Aethomys namaquensis* inserting its snout into an *A. latifolium* inflorescence.

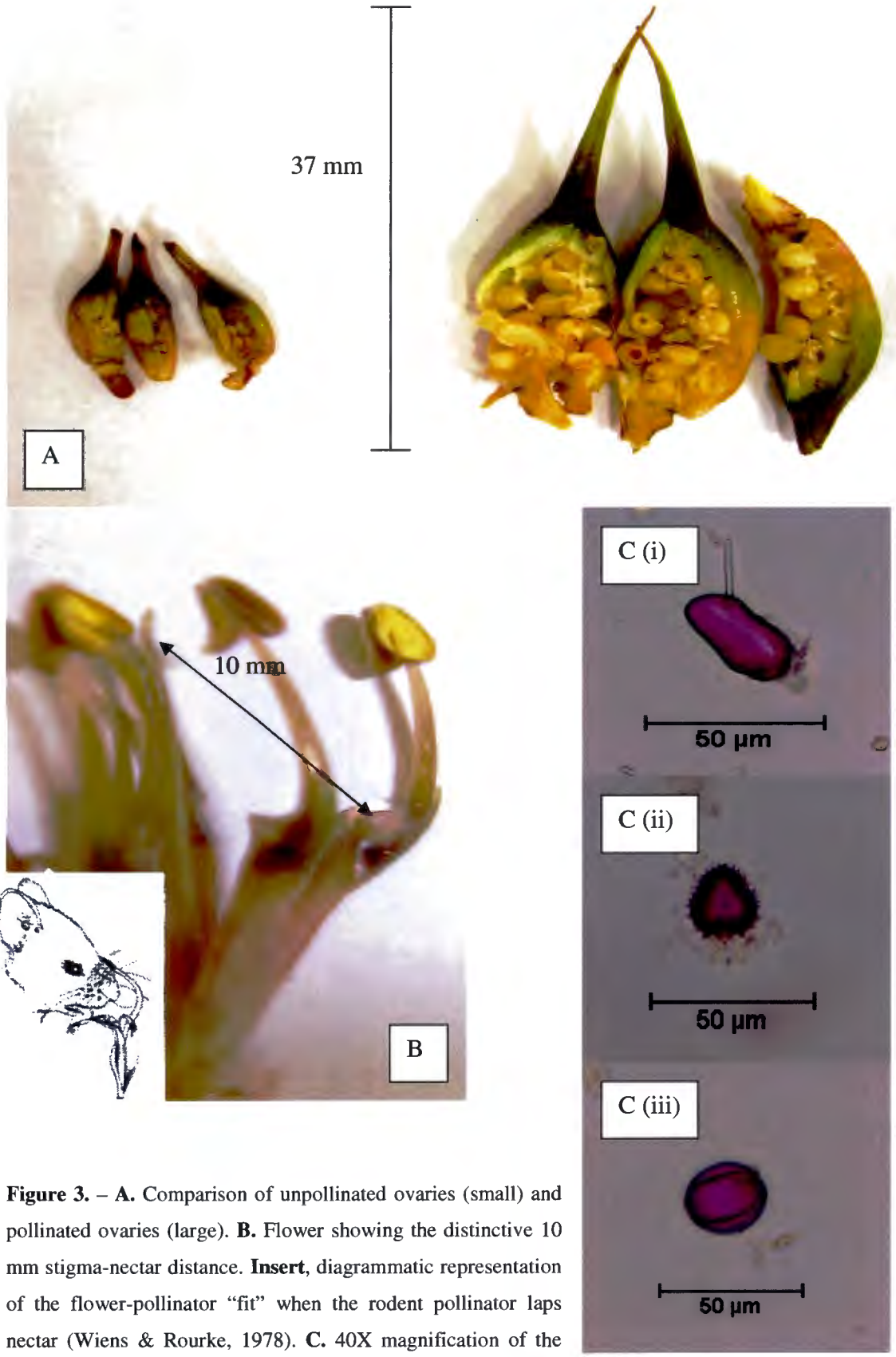

Figure 3. – **A.** Comparison of unpollinated ovaries (small) and pollinated ovaries (large). **B.** Flower showing the distinctive 10 mm stigma-nectar distance. **Insert**, diagrammatic representation of the flower-pollinator "fit" when the rodent pollinator laps nectar (Wiens & Rourke, 1978). **C.** 40X magnification of the three pollen species identified in the scat samples and the fuschin gelatine samples: *A. latifolium* (i), Asteraceae pollen (ii) and a triporate pollen (iii).

Exclusion of rodents from flowers

Approximately one month after setting up the exclosures and marking the respective control plants, the plants were picked for analysis. Out of the 28 exclusion pairs, only eight were viable for analysis (29% of the original exclusion pairs). Most of the exclosures had been knocked over, and many of the control plants had been eaten, presumably both by porcupines. Evidence for this was the shallow pits left in the soil from digging for the bulb by the animal. The plants enclosed by a cage did set seed. However, the average number of seeds per ovary was significantly higher in the flowers of the control plants ($U = 3.00$, $p < 0.05$). Seed set was reduced by 20% on inflorescences where rodent visitation was excluded (Table 2).

Table 2. The number of seeds per flower in the enclosed and control inflorescences.

exclosure	flower	seeds/flower	control	flower	seeds/flower
1	1	16	1	1	38
	2	1		2	26
2	1	0	2	1	27
	2	0		2	74
3	1	9	3	1	64
	2	37		2	19
4	1	2	4	1	54
	2	3		2	72
5	1	0	5	1	66
6	1	4	6	1	73
	2	34			
7	1	3	7	1	113
				2	159
8	1	0	8	1	98
	2	76			
	average	13.2		average	67.9
	SE	5.9		SE	10.8

On retrieving the flowers for seed set analysis, it was apparent that the flowers inside the exclosures flowered for longer than their respective control flowers. All of the control flowers were in the stage where the bracts had wilted off, and the stigma and anthers of the flowers were brown in colour. A few of the flowers inside the exclosures still had intact pink bracts, and the anthers and stigma of the flowers were not as brown as in the control flowers. On dissecting the flowers, the number of seeds was counted by hand. The pollinated flowers (control flowers) had very swollen

ovaries compared to those of the unpollinated flowers (flowers inside the exclosures) (Figure 3A), and the seeds were very different in size. No data was collected however, on seed size, because of the unequal phenologies of the flowers inside the exclosures and the control flowers.

Stigma-nectar distances

All of the 25 flowers measured had a stigma-nectar distance of greater than 10 mm in length (average, SE: 12.58 mm, 0.45).

Number of seeds per ovule in relation to distance from the koppie

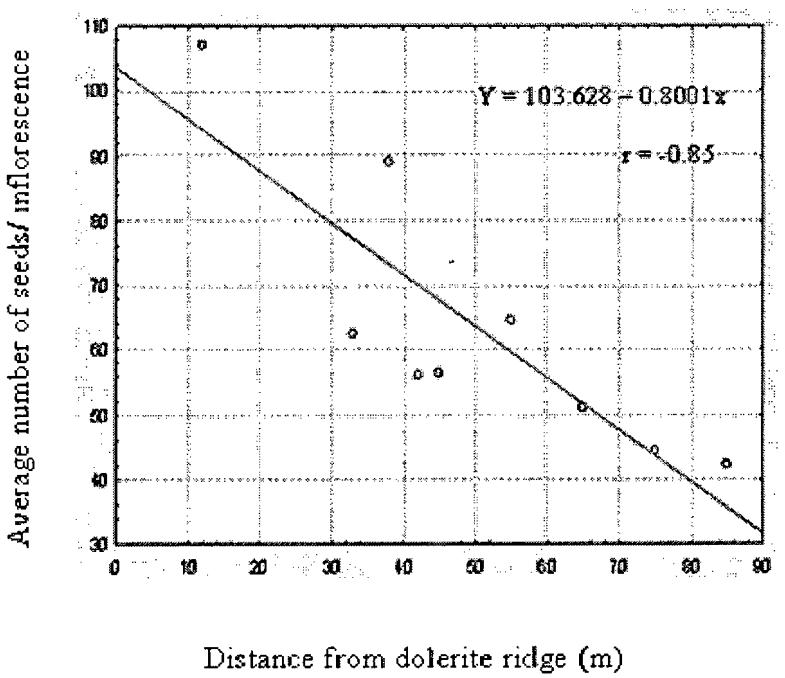

Figure 4. Relationship between the distance away from a dolerite ridge and the seed set of flowers, measured over an 85 metre long transect.

As the distance increased from the rocky peak of a dolerite ridge, the area where *A. namaquensis* individuals reside (assumed from the capturing data), the seed set success of the flowers declines. There is a significant correlation between the distance from the dolerite ridge and the average number of seeds per flower (r = -0.85) (Figure 4).

Discussion

Traits of the therophilous floral syndrome in *A. latifolium*

The flowers of *A. latifolium* show many of the traits defined as traits characterizing the therophilous syndrome (Carpenter, 1978). *Androcymbium latifolium* flowers from late winter till the end of spring (Membrives *et al.* 2002). The flowers are tightly packed into inflorescences, and these geoflorous flowers are strongly attached to the soil (Figure 2A & 2B). Membrives *et al.* (2002) showed the nocturnal anthesis and nectar production of *A. latifolium*; as they found that nectar production was between 18h00 and 9h00. From visual investigation, it was clear that copious amounts of nectar were being secreted by these flowers. It has been stated that the *A. latifolium* flowers do have a yeast-like odour (Membrives *et al.* 2002).

The ten millimetre rule that states that therolphilous plants have an effective 10 mm stigma-nectar distance (Rebelo and Breytenbach, 1987; Wiens *et al.* 1983) was observed, with an average distance of 12.58 mm. This distance correlates closely with the rostrum length of the major rodent pollinator (Wiens *et al.* 1983). This rule is observed, even in very large flowers, such as *Protea cryophila*, which has style length of 80 to 90 mm. In this protea, the nectar pool is raised in the perianth tube (Rebelo and Breytenbach, 1987). This stigma-nectar distance allows for a pollinator-flower "fit;" and this "fit" allows for the sticky pollen to be transferred from the rostrum of the rodent onto the stigmatic slit (Figure 3B). The style and the filaments of *A. latifolium* flowers are relatively thick and strong (Figure 2A). This may allow for forceful manipulation by the rodent, while minimising the risk of damage (Wiens and Rourke, 1978).

Evidence for rodent visitation to *A. latifolium* inflorescences

The therophilous traits described above may provide the first lines of evidence for the hypothesis that *A. latifolium* is rodent pollinated. The pollen found in the scats was almost exclusively *A. latifolium* pollen (figure 1A). The pollen in the scats is presumably ingested after grooming. As from the observations of rodent foraging in the Perspex tanks; no attempt was made by the rodents to feed directly on the pollen

from the anthers; and one of the rodents was filmed wet-preening itself following nectar feeding from all of the inflorescences in the tank (Video clip 2, see appendix). *Androcymbium latifolium* pollen was also the most abundant pollen in the fuschin gelatine samples (figure 1B). An experimental error occurred during the swabbing of the block of fuschin gelatine. The gelatine was swabbed for approximately 10 seconds on the fur immediately surrounding the nose of the rodents. However, in order to obtain a more accurate measure of the presence of pollen on the fur, the gelatine block should have been swabbed on the rostrum; as this is the position on the head of the rodent where the pollen would be deposited from the anther. It is predicted that if the gelatine block had been swabbed on the rostrum of the rodents, the pollen counts would have resulted in significantly higher pollen grain numbers.

In addition to the indirect evidence for rodent pollination mentioned above; the most convincing evidence comes from the video footage showing *A. namaquensis* individuals (family Muridae, subfamily Murinae), known to be nocturnal and generalist foragers (Johnson *et al.* 2001), foraging for nectar in *A. latifolium* inflorescences. The second night of observations of captive *Aethomys* mice in tanks with *A. latifolium* plants showed that the rodents fed non-destructively on the nectar in the flowers. The movement of the rodent's head in and out of the flower indicates a lapping motion. The "troughlike" structure containing the nectar, at the base of the filament, probably facilitates the lapping by the rodents (seen in Figure 3B). During this action, pollen was visibly dusted onto the snouts of the foraging rodent, which moved between the inflorescences in the tank (Video clip 1, see appendix). The rodents' movements between the *A. latifolium* individuals in the tanks, illustrates their ability to cross pollinate flowers (Carthew and Goldingay, 1997). There is a potential drawback to *Aethomys* as a pollinator: these rodents are herbivorous/granivorous, and so include plant material in their diet (Monadjem, 1997). On the first night of observations, the rodents ate all the parts of the plants placed in the observation tanks, except the green leaves. This shows that this species can be destructive to *A. latifolium* plants. It is assumed that the rodents did not eat the green leaves because of the presence of the toxic alkaloid, colchicine. This alkaloid is present in all species in the family Colchicaceae (Alali *et al.* 2004). It is likely that the rodents displayed such destructive behaviour because they were merely extremely hungry. The rodents had been trapped in the gutter pipe traps, and placed into the observation tanks the

following morning, without any food in the tanks. The rodents probably did not feed on the ball of peanut-better and oats in the trap, due to stress. Both rodents fed on rolled peanut-butter and oats during the day after the first night of observations, and so by the second evening of observations, the rodents were probably in a calm state and were not extremely hungry, similar to being in the wild. It is presumed that since these rodents are generalist hervivores/granivores, individuals most probably always have some food supply that is edible. Some rodent pollinated Proteaceae species have compensated for highly destructive rodents by increasing the number of reproductive units per inflorescence far beyond the number necessary to maintain successful reproductive levels (Rourke and Wiens, 1977). The population of *A. latifolium* was estimated to having over 1000 inflorescences, so it is possible that each *A. latifolium* plant is also compensating for the sometimes destructive behaviour of *A. namaquensis* by increasing the number of inflorescences per plant. The observation of the captive rodents biting from the base of two of the inflorescences on the second night of observations could display the ability of this species to be destructive. However, during this action, the rodents seemed to be interested in feeding from the base of the anthers. It is possible that this section of the anther contains nectar. Many rodent pollinated plants have nectar channelling from the inflorescence into the ground (Rebelo and Breytanbach, 1987). In the field, rodents would not be able to access this part of the plant because it is secured into the ground. However, in the observation tanks, this channel of the nectar may have been exposed for the rodent (Video clip 3, see appendix).

One of the original possible explanations for the bright red colour of the bracts could be that they are a warning sign for the toxin, colchicine. However, since both rodent individuals ate the red bracts of the inflorescences on the first night of observations, and were apparently unaffected; it is assumed that colchicine is not present in toxic concentrations in the red bracts. The other possible explanation may be that this bright colour is an attracting mechanism. This study has shown that when rodents are very hungry, the bracts may be seen as food. The bright colour of the bracts contrasts the light green colour of the anthers and styles of the flowers and may therefore also act as a target for rodents. Originally, one of the proposed traits of the therophilous syndrome was that flowers should be cryptic and or dull coloured, because of the nocturnal activity of rodents (Carpenter, 1978). However, like *A. latifolium*, many

nonflying mammal pollinated proteas are geoflorous, but do not have cryptic heads, (eg. *P. cryophila*) (Wiens *et al.* 1983). The significance of the target formed by the contrasting colours, is clearly visible to the naked eye even in the dark, but their perception by rodents is unknown (Rebelo and Breytenbach, 1987), although it is presumed that differences in shades of colours are apparent to mammals (Wiens *et al.* 1983).

The effect of rodents on seed set

O'Farrell (2005) showed that the vast majority of the rodent individuals captured across several habitat types, were captured in dolerite ridges. *Aethomys namaquensis* was the most abundant species in this habitat type (92% of the total number of individuals captured). *Aethomys namaquensis* was not caught in any of the other habitat types he investigated (renosterveld, transformed renosterveld and dolerite plains). In my experiment, *A. namaquensis* was the only species captured. This suggests that *Aethomys namaquensis* is the main pollinator of *A. latifolium*. However, *A. latifolium* does not only occur on the dolerite ridges, like *A. namaquensis*. Another population of *A. latifolium* occurred on Glen Lyon farm on tillite soil, on the outskirts of a patch of transformed renosterveld. O'Farrell (2005) found that the short-tailed Gerbil, *Desmodillus auricularis*, is the most common rodent species that occurred in this habitat type. Another population of *A. latifolium* occurred on dolerite plains in the Niewoudtville flower reserve. Two nights of trapping were conducted in this site. No individuals were captured in this experiment. According to O'Farrell (2005), the Cape gerbil, *Tatera afra*, Kreb's fat mouse, *Steatomys krebsii*, and the white-tailed mouse, *Mystromys albitcaudatus*, all occur on dolerite plains. Therefore, if *A. latifolium* occurs on the habitat types: dolerite ridges, dolerite plains and transformed renosterveld habitat type, *A. namaquensis*, which only occurs on dolerite ridges, cannot be the only rodent pollinator. The *A. latifolium* population at the dolerite ridge, Kameel Koppie, was significantly larger than the other populations mentioned above. Therefore, it could be that since *A. namaquensis* is more abundant than the other rodent species in the Namaqualand region, *A. latifolium* reproduces more successfully when in the habitat type of *A. namaquensis*.