Pollination function transferred: modified tepals of *Albuca* (Hyacinthaceae) serve as secondary stigmas

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- **Background and Aims** The stigma, a structure which serves as a site for pollen receipt and germination, has been assumed to have evolved once, as a modification of carpels, in early angiosperms. Here it is shown that a functional stigma has evolved secondarily from modified tepals in some *Albuca* species (Hyacinthaceae).
- **Methods** Deposition of pollen on *Albuca* floral organs by bees was recorded. Pollen germination and fruit set was measured in flowers that had pollen deposited solely on their tepals or had their tepal tips experimentally isolated or removed after pollination.
- **Key Results** Leafcutter bees deposit pollen onto the papillate apices of the inner tepals of *Albuca* flowers. Pollen germinates in tepal-derived fluid secreted 2 or 3 d after anthesis and pollen tubes subsequently penetrate the style during flower wilting. Application of cross-pollen to the inner tepal apices of *A. setosa* flowers led to high fruit set. No fruits were produced in pollinated flowers in which the inner tepals were mechanically isolated or removed.
- **Conclusions** Pollen capture by tepals in the *Albuca* clade probably evolved in response to selection for floral morphology that maximizes the accuracy of pollen transfer. These findings show how pollination function can be transferred among floral organs, and shed light on how the original angiosperm stigma developed from sporophylls.

**Key words:** Hyacinthaceae, Ornithogaloideae, pollen, pollen germination, pollen receipt, pollen tube, pollination, sexual interference.

**INTRODUCTION**

Accurate transfer of angiosperm pollen by animal vectors usually requires that anthers and stigmas contact the same site on the animal’s body, and yet be separated physically to avoid self-pollination (Barrett, 1990, 2002). This problem is easily solved in plants with bilaterally symmetrical flowers, as they orient visitors predictably, allowing anthers and stigma to be separated spatially (herkogamy) or temporally (dichogamy), yet aligned in the same plane to ensure efficient pollen transfer (Neal et al., 1998). In contrast, anthers of tubular actinomorphic flowers are typically placed in a ring around the entrance to the tube, while the stigma occupies a central position, leading to inefficient pollen transfer because pollinators that crawl into the tube receive pollen on the side of their body which is opposite to the stigma. One solution commonly adopted by plants with actinomorphic flowers is secondary pollen presentation on the style which ensures that pollen is deposited on the same surface of the pollinator that contacts the stigma (Yeo, 1993). Here we demonstrate the existence of another solution – pollen deposition on the perianth – which enables efficient pollen transfer in some actinomorphic flowers.

Flowers of the African hyacinth genus *Albuca* (slime lilies) have long intrigued plant reproductive biologists on account of their tightly closed inner tepals with apices covered in papillae. In a remarkable paper that was overlooked by subsequent authors, Wilson (1891) speculated that pollen from visiting bumblebees was deposited onto the papillate tepal apices of ‘*Albuca corymbosa*’, a South African species that had been planted at his home in Scotland. He speculated that this pollen would be ‘carried forward to the stigma by it [the tepal] when the bee has retired’. Eighty years later, Fluellen (1974) found that germination of *Albuca* pollen required secretions from the tepal apices and that pollen applied to stigmas failed to germinate if the tepal apices had been removed or prevented from closing onto the stigmas. She also noted that papillae on the tepals were very similar in external structure to those on the primary stigma. Like Wilson (1891), Fluellen speculated that pollen could be deposited onto the tepal apices, but she lacked observations of pollinators and suggested that future experiments should be conducted to establish whether pollen deposition onto the tepal apices would indeed affect fertilization (Fluellen, 1974; Kingston, 1998). A different interpretation of the *Albuca* flower was offered by Westerkamp (in Yeo, 1993) and Manning et al. (2002) who both suggested that the papillate style of *Albuca* may function in secondary pollen presentation. However, Westerkamp and Classen-Bockhoff (2007) later suggested that pollen would be deposited directly on the tepals of *Albuca* flowers. Thus, various authors have suggested that the modified inner tepals of *Albuca* serve a stigmatic function, but conclusive evidence has been lacking.

Our preliminary field observations of two *Albuca* species – *A. canadensis* (L.) F.M.Leight. (= *A. maxima* Burm.f.) and
A. setosa Jacq — in their native habitats in South Africa were in accordance with Wilson’s (1891) suggestion that visiting bees deposit pollen on the apices of the inner tepals. To test the hypothesis that the inner tepals of Albuca flowers serve the function of a stigma, we examined the following predictions: (a) bee visitors should deposit pollen mainly on the papillae at the apex of the inner tepals; (b) pollen should germinate on the inner tepals; (c) pollen deposited on the tepals should successfully fertilize ovules.

MATERIALS AND METHODS

Study species and field sites

Flowers of Albuca have spreading outer tepals and connivent inner tepals which form a chamber around the style and stamens (Figs 1B and 2A). The three well-developed inner stamens are always shorter than the style and have introrse anthers with filaments joined to the inner tepals. The two species included in this study represent different modifications of the three outer stamens in the genus. In A. canadensis (Fig. 1), these stamens are vestigial and reduced to staminodes, while in A. setosa, these stamens produce pollen, but are reduced in size (Fig. 2A). In both species a standing crop of approx. 1–5 μL of nectar secreted from septal nectaries is presented in a cup-shaped modification of the base of the stamen filaments.

Observations and manipulative experiments were conducted in a large (>300 plants) population of A. setosa in natural grassland on the Pietermaritzburg campus of the University of KwaZulu-Natal, South Africa during 2008–2010. Additional observations of pollinators were made in populations of approx. 500 A. setosa plants at Wahroonga Farm, KwaZulu-Natal, in 2008, approx. 150 A. setosa plants at Blinkwater, KwaZulu Natal, in 2005, 2008 and 2010, and approx. 200 A. canadensis plants (Fig. 1A) at Nieuwoudtville, in the Namaqualand region, in 2002, 2003 and 2008. The A. setosa complex is highly variable and plants at the three study sites for this species varied considerably in overall stature and flower size (smallest at the university population and largest at Wahroonga). Voucher specimens of plants from each population were deposited in the Bews Herbarium (NU) in Pietermaritzburg.

Pollinators and pollen loads

We observed the identity and behaviour of insect visitors to determine the mechanism of pollen transfer (60 h in the A. setosa populations in KwaZulu-Natal and 20 h in the A. canadensis population). Flower-visiting insects were captured and pollen was removed separately from the thorax and abdominal scopae with small blocks of fuchsin gel which were melted onto microscope slides, as described by Beattie (1971), to count the Albuca pollen grains available for pollination (thoracic loads) and nest provisioning (scopal loads). To determine if A. canadensis pollen is collected from flowers and used to provision brood cells, the pollen composition of all eight cells in a single nest of its principal pollinator, the leaf-cutter bee Megachile reicherti, was analysed in September 2006, using the methods described by Timmermann and Kuhlmann (2008).

Pollen deposition on flowers during single visits

To determine experimentally whether bees deposit pollen on the inner tepals, we bagged inflorescences with unopened buds on ten A. setosa plants at the university site and, after anthesis,
allowed 16 virgin flowers to each receive a single visit by a leafcutter bee (the most common and effective pollinator; Table 1). These flowers were then transferred individually in vials to a laboratory where we counted pollen grains deposited on the inner tepals and the stigma/style. Albuca grains are large (approx. 100 μm) and yellow, and thus easy to distinguish from a tepal’s white papillae, and were counted under a dissecting microscope. Pollen is less distinguishable from a stigma’s yellow papillae and was counted by immersing styles in 200 μL of ethanol with 20 μL of fuchsin stain (1 % dilution), and estimating the total pollen count from the number of pollen grains in five 20-μL subsamples. Identical procedures were applied to unvisited flowers, allowing us to estimate how much self-pollen was present on inner tepals and the style prior to bee visits and how much pollen bees subsequently deposited on these flower parts. Statistical comparisons of the mean number of pollen grains deposited on flower parts prior to and after single visits by megachilid bees were conducted using t-tests implemented in SPSS 19 (IBM Corp.).

To investigate the mechanism of pollen uptake from anthers by bees and its deposition on flower parts, UV reflective dye (DayGlo Colour Corp., Cleveland, OH, USA) was applied with a toothpick onto the anthers of three A. canadensis flowers and the scutum (dorsal thorax) of three male Megachile reicherti leafcutter bees. Bees that had previously visited dyed flowers and flowers visited by bees with dye applied to their scutae were examined to determine the sites of dye deposition.

**Patterns of floral anthesis and pollen germination**

We monitored 30 individual flowers marked from the bud stage on ten plants of A. setosa and noted the timing of flower opening and closing, as well as the initiation of secretions from the apices of the inner tepals and final flower wilting.

Using fluorescence microscopy to visualize pollen tubes, we investigated the occurrence and timing of germination of
Wahroonga

Amegilla capensis (Friese) Apidae ♀ 1 (1) 0.0 ± 0.0 na
Amegilla barkeri Megachilidae ♀ 13 (12) 59.5 ± 0.0 41.2 ± 36.7
Nomia sp. Halictidae ♂ 1 (1) 88.0 ± 0.0 nr
Mega
gale iantho
tera (Fabricius) Megachilidae ♀ 1 (1) 0.0 ± 0.0 na

Blinkwater

Megachile bucephala (Fabricius) Megachilidae ♀ 1 (1) 88.0 ± 0.0 nr
Megachile ianthoptera (Fabricius) Megachilidae ♀ 2 (2) nr 38.5 ± 4.3

nr, data not recorded; na, not applicable.

A. setosa pollen on the inner tepals and primary stigma. We examined the apices of inner tepals and styles from seven flowers collected prior to wilting (1200–1600 h), the apices of inner tepals and styles from five flowers collected after wilting (approx. 2100 h), and the apices of inner tepals from four recently wilted flowers, in which contact between the tepals and style had been prevented, using a paper sleeve around the style. Tepals and styles were fixed in Carnoy’s solution for 24 h and then stored in 70% alcohol. Pistils were softened in 1 mol L⁻¹ NaOH for 15 h, rinsed in distilled water for 1 h and stained in a 0.1% solution of aniline blue in 0.1 mol L⁻¹ K₂HPO₄ for about 48 h. Flower parts were then mounted in a drop of stain solution on a microscope slide and squashed under a coverslip. Pollen tubes were viewed using an Olympus Provis AX70 fluorescent microscope with an illuminating wavelength of 365 nm.

**Controlled pollination**

Controlled hand-pollinations were conducted on both *Albuca* species to determine the extent to which they are reliant on pollinator visits for seed production and whether or not they are genetically self-incompatible. In the case of *A. setosa* plants at the university site we also tested whether pollen deposition on tepal apices alone leads to fertilization. Inflorescences of 18 *A. setosa* plants were bagged during bud stage. Following anthesis, flowers on each inflorescence were assigned randomly to be self-pollinated using pollen from the same plant, cross-pollinated with pollen from a plant at least 3 m away or left unmanipulated as a test of autonomous self-fertilization. Pollen was applied solely to the tepal apices and not to the stigma. We also recorded fruit set in naturally pollinated flowers. Controlled hand-pollinations using the same treatment groups were also conducted using six *A. canadensis* plants that had been bagged at the bud stage. However, as controlled pollinations involving *A. canadensis* were intended only as a test of the breeding system, pollen was applied liberally to both the tepal apices and the primary stigma. For both species, we compared the frequency of fruit set of flowers in treatment groups using chi-square contingency tests implemented in SPSS 19 (IBM Corp.). Means for seed set per fruit in naturally and cross-pollinated flowers of *A. setosa* were compared using a t-test implemented in SPSS 19 (IBM Corp.).

**Floral manipulation to test the stigma function of tepals**

To determine whether the papillate tepal apices of *Albuca* are required for fertilization, we conducted two separate experiments, each of which involved comparison of fruit set of flowers, in which the inner tepals were prevented from contacting the style, to fruit set of unmanipulated flowers in which the inner tepals could contact the style. These experiments were conducted in the university *A. setosa* population during 2010, and all the flowers used in these experiments had been pollinated naturally (assessed by the presence of large amounts of pollen on the tepal apices) but had not yet wilted prior to the experiment. In the first experiment, we excised the papillate apices of the inner tepals of one flower on each of 20 plants with fine scissors and removed the apices of the outer tepals of a one flower on each of 20 additional plants as a control for the effects of physical damage. In the second experiment, the styles of one flower on each of 20 plants were enclosed in paper tubes to prevent contact with the inner tepals, and an additional un-manipulated flower on each of 20 additional plants was marked as a control. In both experiments, experimental flowers were marked with small pieces of uniquely coloured thread and then bagged to
avoid interference from subsequent pollinator visits. Fruit set was assessed after 2 weeks. The frequency of fruit set in manipulated and control treatments was compared using chi-square contingency tests implemented in SPSS 19 (IBM Corp.).

RESULTS

Pollinators and pollen loads

Leafcutter bees (Megachile: Megachilidae) were overwhelmingly the most common visitors of flowers of both Albuca study species. We observed >100 individual foraging bouts by megachilid bees on A. setosa plants across the three sites for this species and approx. 30 foraging bouts by megachilid bees on A. canadensis plants at the Nieuwoudtville site. These bees could prise open the tightly closed inner tepals of Albuca flowers with their heads (Fig. 1B) (Supplementary Data Video) and accessed the nectar by clambering down the style. As they enter the flower, pollen already on their thorax is deposited on the inner-tepal apex (Figs 1C and 2B, D), and then, as they crawl further into the flower, pollen from one of the anthers is deposited on the dorsal surface of their thoraces. When feeding on nectar at the base of the filament, one of the inner tepals and its associated stamen is widely deflected (Fig. 2C). Bees usually exited the flowers sideways, rather than backing up in a reverse direction, and the stamen and tepal then return to their original position.

Several megachilid species were captured on flowers of A. setosa across the three study sites (Table 1 and Supplementary Data Video). Honey bees Apis mellifera scutellata were observed visiting A. setosa flowers at the university site, and were observed unsuccessfully attempting to enter flowers at the other two sites. Bees captured on both Albuca species carried pollen on the scutum, which is contacted by an anther when they enter the flowers (Figs 1B and 2B). Overall, the various Megachile species carried more Albuca pollen on their thorax than did honey bees (Table 1). Scopal pollen loads were dominated by Albuca pollen, with the highest percentage being recorded for honey bees (Table 1).

Only a small set of large bees that have the sufficient size and the skills accessed the tightly closed flowers of A. canadensis (Fig. 1B). Megachile (Chalicodoma) reicherti (Brauns) is the principal pollinator and both males and females frequently visited flowers for nectar throughout the observation period. Males were often seen patrolling around patches of flowering A. canadensis plants. Additional infrequent visitors included Xylocopa rufitarsis Lepeletier (Apidae) in 2003 and a single Plesianthidium (Carinanthidium) cariniventre (Friese) (Megachilidae). Interestingly, no large Anthophora bees were observed visiting A. canadensis flowers, despite their relative abundance during flowering time. Apis mellifera capensis could not open A. canadensis flowers, despite trying for several minutes. A dead honeybee was found, apparently trapped, in one flower. Scopal pollen loads of only one of seven female M. reicherti contained Albuca pollen (30% of all pollen grains) and eight brood cells from a single M. reicherti nest lacked Albuca pollen.

Pollen deposition on flowers during single visits

During single visits to previously bagged (virgin) flowers of A. setosa, Megachile bees deposited an average (± s.e.) of 92 ± 11.1 Albuca pollen grains on the apex of the inner tepals that were prised open, whereas there were no Albuca pollen grains on the inner tepals of unvisited flowers (t_{15} = 8.2, P < 0.0001, equal variances not assumed; Fig. 3A). On flowers that were visited by bees, inner tepals that were not prised open (because those particular pollination chambers on the flowers were not entered) had only 7.56 ± 2.7 Albuca pollen grains, as opposed to the 92 ± 11.1 grains found on tepals that were prised open when bees entered the associated pollination chamber (t_{30} = 7.36, P < 0.0001). Many self-pollen grains were present on the style and stigma of unvisited flowers, and the number of pollen grains on these flower parts did not increase significantly after bee visits (t_{23} = 1.14, P = 0.26; Fig. 3B). All Megachile bees (five observations) that
Patterns of floral anthesis and pollen germination

*Albuca setosa* flowers opened for two successive days. The outer tepals close at the end of the first day of anthesis and open again at approx. 0700 h on the following morning. During the afternoon (approx. 1700 h) of the second day of anthesis, the inner tepals produce an obvious secretion (Fig. 2F), causing any adhering pollen grains to hydrate and become rounded (they have ovoid shape in their unhydrated state). By late afternoon (approx. 1800 h) the flowers are shrivelled, although the apices of the inner tepals remain moist and become closely appressed to the stigma.

No pollen tubes were visible on the inner tepals and styles of pollinated flowers during the first day and second morning of anthesis, indicating that there is delayed pollen germination. However, wilted flowers had many (100–300) germinated pollen grains with pollen tubes exceeding 100 μm on their inner tepals and stigmas. We also observed similar numbers of germinated pollen grains with pollen tubes on wilted inner tepals that had been prevented from contacting the stigma (Fig. 2G, H).

Controlled pollination

Application of cross-pollen to the apices of the inner tepals of *A. canadensis* had pigment grains attached to their vertex and scutum and flowers visited by marked bees (three observations) had pigment deposited exclusively on the tepal apices.

Floral manipulation to test the stigma function of tepals

Flowers of *A. setosa* for which the inner tepals were prevented from contacting the style, either by use of a paper sleeve barrier or by removal of the tepal apices, failed to set fruits, whereas fruits were set in 31–39% of control flowers (Table 2).

### Table 2. The effects of manipulation of inner tepals on the frequency of fruit set in flowers of *Albuca setosa*

<table>
<thead>
<tr>
<th>Manipulation</th>
<th>Manipulated</th>
<th>Control</th>
<th>$\chi^2$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tepal apex and style separated with paper sleeve</td>
<td>0 (21)</td>
<td>38.8 (18)</td>
<td>7.48</td>
<td>0.006</td>
</tr>
<tr>
<td>Removed tepal apex</td>
<td>0 (18)</td>
<td>31.2 (16)*</td>
<td>4.33</td>
<td>0.03</td>
</tr>
</tbody>
</table>

* Control flowers had the apices of the outer tepals removed.

DISCUSSION

The inner tepals of *Albuca* flowers clearly perform the primary functions of a stigma in being responsible for pollen receipt and germination (Fig. 4). Our observations of pollen receipt after a single bee visit support Wilson's prediction that 'pollen will be placed on the papillose apex of the segment' (Wilson, 1891), although he was mistaken in thinking that pollen would be 'carried forward to the stigma by it [the tepal apex] when the bee has retired'. Instead, pollen deposited by bees remains on the tepal apices and germinates there only when flowers senesce (Figs 2G, H and 4). As first shown by Fluellen (1974), fluid secreted by the apex of senescing inner tepals stimulates germination of *Albuca* pollen; we also demonstrated that pollen deposited solely on the inner tepal apex germinates, fertilizes ovules and enables subsequent seed production. Together these results provide the first confirmed case of a stigmatic function for petals in angiosperm flowers.

Observations of pollinators under natural conditions were required to reveal the unique floral mechanism of *Albuca*. These observations indicate that flowers of both study species are specialized for pollination by megachilid bees as a functional group (cf. Fenster et al., 2004), though not to any megachilid species specifically. *Albuca* flowers are effectively divided in three functional pollination chambers (meranthia) that are each operated individually when bees prise open one of the inner tepals with their heads (Figs 2B and 4). This subdivision of the flowers into separate pollination chambers is a parallel to the floral mechanisms found in some Iridaceae, such as Iris and Moraea (Goldblatt et al., 2005). Although both *Albuca* species have the same pollination mechanism, the behaviour of their pollinating bees differed. In *A. setosa*, bees visited flowers for nectar, but observations and analysis of their scopal loads indicated that they also collected pollen from the secondary stamens which are visible in Fig. 2A. In *A. canadensis*, the secondary stamens are reduced to mere staminodes and bees visited flowers of this species for nectar rather than for pollen, as shown by observations of both male and female bees on flowers and the almost complete lack of pollen in female scopal pollen loads and brood cells of *M. reicherti*.
Our controlled pollination experiments revealed that *A. setosa* is strictly self-incompatible, while *A. canadensis* is self-compatible, but not capable of autonomous self-fertilization. Variation in breeding systems among *Albuca* species was also reported by Fluellen (1974) who found that *A. scabromarginata* De Wildem., *A. sudanica* A. Chev., and *A. fibrotunicata* Gledhill & Oyewole were self-incompatible, while *A. abyssinica* Jacq. (= *A. angolensis*) was self-compatible. Self-sterility was reported for *Albuca kirkii* (Bak.) Brenan by Knudtzon and Stedje (1986) who also commented on the variability in self-incompatibility among cytotypes of *A. abyssinica*.

The pathway leading to the evolution of stigmatic petals in *Albuca* can be inferred from the pollination mechanisms of closely related genera. Available phylogenies for the Ornithogaloidea indicate that the closest living relatives of *Albuca* are species of *Stellarioideae* and *Colionox* (Manning et al., 2009; Martinez-Azorin et al., 2011) which do not have closed inner tepals that restrict access to nectar (Fig. 2I). Fluellen (1974) showed that delayed pollen germination is widespread in the tribe that includes these genera. Pollen in these species is captured conventionally on the stigma but there is, intriguingly, evidence that secretions from the inner tepals play a role in pollen germination. As noted by Fluellen (1974), there are papillae on the tepal apices of *Ornithogalum umbellatum* Thunb. and *Stellarioideae* (*Ornithogalum*) *tenuifolia* (F. Delaroche), respectively, and these tepals close onto the stigma during wilting. As in *Albuca*, the inner tepals of *Stellarioideae* appear to play a key role in pollen germination. Flowers of *S. tenuifolia* which have their inner tepal apices removed fail to set fruit, while those which have the outer tepal apices removed set fruit normally (S. D. Johnson and A. Jürgens, unpubl. res.). This finding, in conjunction with Fluellen’s observation that delayed pollen germination and papillate tepals are widespread in the Ornithogaloideae, suggests that tepal secretions and delayed pollen germination evolved prior to pollen capture by tepals in the *Albuca* clade.

This raises interesting questions about the selective factors that led to the evolution of the *Albuca*-type floral morphology with closed inner tepals. Although further experimentation is required, we believe that the *Albuca* flower evolved because of selection for greater precision in pollen transfer (cf. Armbruster et al., 2009). In *Albuca* species, approx. 4–6% of pollen removed from flowers reaches stigmas on other plants (S. D. Johnson and A. Jürgens, unpubl. res.), which is
an order of magnitude greater than the average efficiency of pollen transfer in plants with granular pollen and conventional stigmas (Harder and Johnson, 2008). Flowers of the Ornithogalum–Stellarioïdes type are usually unspecialized (Fig. 2I) and have relatively generalized pollination systems in which insects deposit pollen on the primary stigma haphazardly (S. D. Johnson and A. Jürgens, unpubl. res.), whereas in Albuca, pollinators are filtered out by the floral morphology and those that can prise open in the inner tepals are forced to adopt a position that apparently results in very precise pollen transfer. Few steps may be required for the evolution of the Albuca-type flower, and probably involved suppression of the daily opening of the inner tepals. The connivent placement of the inner tepals appears to be a novel adaptation linked to their stigma function. However, the overall structure of the inner tepals, including their secretion of fluids that stimulate pollen germination, can be considered an exaptation in the sense of Gould and Vrba (1982) of a shift in the function of a pre-existing trait.

Fluellen (1974) earlier suggested that if the inner tepals of Albuca were shown to be the site of pollen deposition they could be described as a ‘secondary stigma’ (Kingston, 1998). This is an extension of the terminology of secondary pollen presentation when the style assumes the function of the anther. Flowers of some Sebaea species (Gentianaceae), for instance, have a secondary stigma on the style below the primary stigma (Marloth, 1909; Hill, 1913), but this is derived from carpels and thus not independently derived from the primary stigma. Wang et al. (2004) showed that self-pollination in flowers of Caulokaempferia coenobialis (Zingiberaceae) is achieved when pollen is transferred from anthers to the stigma by an oily film derived from pollenkitt that slides along the style, but germination occurs in the conventional stigma. Endress (1979) reported a case of transfer of true stigma function (a site for pollen receipt and germination) to a mucilage produced by floral cup tissue in Tambourissa religiosa (Monimiaceae) and described this plug of mucilage at the entrance to the floral cup as a ‘hyperstigma’. Tambourissa and Albuca are thus the only cases known to us of a secondary stigma derived from non-carpellar tissue, and Albuca the only case where the secondary stigma is derived from tepals.

**SUPPLEMENTARY DATA**

Supplementary data are available online at www.aob.oxfordjournals.org and consist of a video showing megachilid bees entering the flowers of Albuca setosa and depositing pollen on the inner tepals.

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**LITERATURE CITED**


