

The floral ecology of *Dianella caerulea* var. *assera* (Phormiaceae)

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Bernhardt, Peter¹ (National Herbarium of New South Wales, Royal Botanic Gardens, Sydney, Australia 2000) 1995. The floral ecology of *Dianella caerulea* var. *assera* (Phormiaceae). *Cunninghamia* 4(1): 9–20. Two populations of *Dianella caerulea* var. *assera* R. Henderson were observed over two years in eastern Australia. Both populations flowered in spring, with inflorescences opening only 5% of their flowers at the same time. Only 20% of all flowers on an inflorescence set fruit, suggesting that they do not self-pollinate. The nodding, nectarless flowers had elongated anthers, each opening via two terminal pores, and the anthers formed a loose cone around the style. Flowers were buzz-pollinated by female bees primarily in the families Anthophoridae (*Exoneura* spp.) and Halictidae (*Lasioglossum*, *Nomia* spp.). Bees less than 6 mm long (*Homalictus holochorous* and *Trigona* spp.) removed pollen from anthers, but did not contact stigmas while foraging. Examination of pollen loads indicated that most bees were polylectic foragers that had visited at least one nectar-secreting taxon (e.g. *Ceratopetalum gummifera*, *Haloragis* spp., papilionoid legumes, Myrtaceae) before foraging on *D. caerulea*. However, bees were never observed grasping, probing or combing the swollen, brightly coloured and papillate apices of the staminal filaments. The absence of this behaviour indicated that these structures did not function as nectaries or as a source of pseudopollen as proposed by earlier authorities.

Introduction

An examination of spring-flowering species in southern Australia suggests convergent and/or parallel trends in floral presentation. A conspicuous proportion of vernal herbs and shrubs produce flowers that nod on their scapes or pedicels and have brightly coloured perianths, emphasising yellow or blue-purple pigmentation. These perianth segments are often reflexed or are expanded so broadly that the androecium is fully exposed (see Cochrane et al. 1980; Willis et al. 1975).

The androecium of such flowers often contrasts sharply in colour to the perianth and consists of relatively few stamens (oligandrous) with porose-porate anthers (Vogel 1978; Gack 1979; Buchmann 1983; Faegri 1986). These elongated/inflated anthers are clustered to form a cone around the protruding style, or may form an arched and elevated tuft above the stigma or stigmas (e.g. *Hibbertia*; Bernhardt 1984, 1986). Dissection of these flowers shows an absence of nectaries, oileries or food bodies, indicating that pollen is the only edible reward offered (Buchmann 1983; Bernhardt 1984, 1986; Bernhardt & Burns-Balogh 1986).

Vogel (1978) reviewed this mode of floral presentation within many families of flowering plants and termed it the *Solanum*-type flower. The *Solanum*-type appears

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to be pandemic, as it has evolved independently within more than 65 angiosperm families (Buchmann 1982; Barth 1985) that are not confined to Australia. However, Vogel's initial descriptions of *Solanum*-type flowers included examples of many genera that are indigenous or endemic to Australia; e.g. *Arthropodium*, *Bulbine*, *Calectasia*, *Dianella*, *Hibbertia*, *Solanum*, *Sowerbaea*, *Stypantra*, *Xyris*, etc. Faegri (1986) much expanded the list of genera of *Solanum*-type flowers in Australia by examining specimens native to the south-west of the continent and suggested it was a particularly common, floral form in the Mediterranean south-west. In fact, *Solanum*-type flowers are so common in southern Australia that their mode of floral presentation appears to be exploited by some mimetic orchids that are cross-pollinated via pseudanthery (Bernhardt & Burns-Balogh 1986; Dafni & Bernhardt 1990).

In general, *Solanum*-type flowers are most likely to be buzz-pollinated. That is, pollen is repeatedly 'shaken' out of the terminal pores through the stereotyped vibration of flight muscles within the insect's thorax (Buchmann 1983). The major pollen vectors are female bees and, to a much lesser extent, large syrphid flies in the genus *Volucella*.

The study of buzz-pollination in Australia has been infrequent and inconsistent. A review of *Solanum*-type forms in the flora of south-eastern Australia would suggest, though, that it may be a particularly common mode of pollination in some petaloid monocots with a broad lilioid base. Of the genera listed above, *Dianella* would appear to make the most promising model of fieldwork. There are two reasons for this tentative conclusion.

First, *Dianella* species are widely distributed throughout coastal Australia, often forming dense, easily located, clonal colonies (Wilson 1993). They are common roadside perennials throughout the south-east (Bernhardt, personal observation). In fact, the genus has a broad but disjunctive distribution throughout Australasia, Indo-Malaysia and the islands of the South Pacific, and is also found as far west as Africa, Madagascar and the Mascarenes (Dahlgren et al. 1985). This phylogeography offers potential for future studies comparing the adaptive radiation of pollination mechanisms of allopatric species.

Second, pollination studies of *Dianella* species are required to clarify contradicting interpretations of androecium morphology. In most *Dianella* species the distal portion of each staminal filament is swollen, densely papillate and often referred to as a struma (*sensu* Henderson 1987). This structure has been interpreted as an androecial nectary (Daumann 1970; Dahlgren & Clifford 1982). In contrast, Vogel (1978) and Faegri (1986) interpreted strumae as shifts towards deception. It was assumed that the enlarged and gaudy struma made the smaller anther look larger and more attractive to prospective foragers. Neither hypothesis involved direct observation of pollinators on the flowers. Therefore, the following observations are presented to help clarify earlier hypotheses concerning the functions of floral organs in *Dianella*.

Materials and methods

Study sites

Two discontinuous populations of *Dianella caerulea* var. *assera* (*sensu* Henderson 1987) were observed weekly at sites in Royal National Park between November 1990 and October–November 1991. Description of sites follows Specht et al. (1974) for major plant communities at Royal National Park.

Site 1. Gray's Farm

Open riparian forest of wet sclerophyll grading to disturbed, dry sclerophyll. *Dianella caerulea* population in discrete clumps along roadside or within disrupted and successional sections colonised by mixed, shrubby Myrtaceae, *Hibbertia scandens* and *Pteridium esculentum*.

Site 2. Lady Carrington Track

Tall closed forest grading from dense, wet sclerophyll (*Syncarpia glomulifera* and rainforest elements) to warm-temperate rainforest. *Dianella caerulea* forming spreading rhizomatous colonies on exposed banks and in light gaps.

Recording data on reproductive features

Flowering shoots were selected while walking the entire length of each site. Since *Dianella* species are both rhizomatous and clonal, only every third flowering shoot was used for measurements in order to expand the sample of potential genotypes. Each inflorescence consists of an apical cluster of flowers (terminal florescence) and one or more side branches (paracladia). One side branch was selected on each inflorescence to represent the average number of flower buds or berries/branch. However, infructescences containing one or more obviously galled ovaries were not recorded for fruiting details. Vouchers have been deposited at the Missouri Botanical Garden (MO).

Flowers required for morphological examinations were stored in plastic bags or placed in vials containing 70% ethanol for long-term storage. Flowers were picked only on days when the perianth had expanded, exposing the androecium.

To sample floral odour, fresh flowers were placed in clean, glass vials and sealed for two hours. The vials were placed in a warm, sunny location, then reopened at the end of the two hour period and smelled (Buchmann et al. 1978). To determine the possible sites of scent glands (osmophores), fresh flowers of *D. caerulea* var. *assera*, *D. ensifolia* (Royal Botanic Garden Living Collection no. 781020) and *Dianella* sp. aff. *longifolia* (Royal Botanic Garden Living Collection no. 17047) were stained in a 1% solution of Neutral Red in distilled water for two hours, then washed in distilled water for 18 hours. The staminal filaments were checked for the presence of nectar secretions by observing fresh flowers under a dissecting microscope and by probing filament apices of flowers at field sites with microcapillary tubes.

Analyses of foraging insects

Foraging behaviour of prospective pollinators was observed over the days of field-work. Insects were collected from 9 am until 1 pm, as foraging behaviour became negligible by early afternoon. Insects were netted only if they were observed foraging on open flowers. Foraging is defined here as the active removal of pollen from the anthers, or the probing of floral organs with mouthparts. Insects were killed in jars containing fumes of ethyl acetate. To determine the deposition of pollen, each insect was observed under a dissecting microscope. To analyse pollen taxa carried by insects, each insect was placed on a clean glass slide and 'bathed' in a couple of drops of 100% ethanol. When the ethanol evaporated, the residue remaining on the slide was mounted in two or three drops of Calberla's fluid (Ogden et al. 1974). Identification of pollen was made under light microscopy. However, since different insects were killed in the same jar, contamination was possible. Therefore, a pollen taxon was not recorded as present unless more than 25 individual monads could be counted under each cover slip.

In contrast to the majority of lilioid monocots, the pollen of Phormiaceae are readily distinguished from the vast majority of angiosperm pollens in Australia, as they are both distinctly trichotomosulcate (Dahlgren & Clifford 1982; Dahlgren et al. 1985) and the monads appear to have such a thin exine that they always stain a light pink in the presence of Calberla's fluid (Bernhardt, personal observation). Although the genus *Stypandra* (Phormiaceae; *sensu* Dahlgren et al. 1985) is also distributed throughout eastern Australia, it was not found in either study site. Insects were washed, air-dried, measured (from base of mouthparts to abdomen tip), pinned, and labelled to cross-reference with their respective pollen slides. Insect vouchers were deposited in the National Museum of Victoria, Abbotsford.

Results

Inflorescence structure and floral phenology

Dianella caerulea var. *assera* has paniculate flowering shoots indicative of the genus. Each scape terminates in an apical cluster of flowers. Below this terminal florescence, the scape produces an average of seven alternative side branches or paracladia (Table 1). Each paracladium contains a similar number of flower buds as are found in the terminal florescence. Flowering began in late October and concluded by the end of November. Fruiting was contiguous with flowering and a paracladium often contained one or more ripe, blue berries, while flower buds continued to open on the same branch. The average number of fruits produced by a single infructescence deviated far more than any other reproductive feature recorded (Table 1). The conversion rate of individual flowers on a single inflorescence into fruits was approximately 20%.

The order in which individual flower buds opened within the same panicle was either subacropetal or did not follow any stereotyped program of anthesis. However, flowering within each paracladium was acropetal. The perianth of a flower opened

Table 1. Flower and fruit production of the inflorescences of *Dianella caerulea* var. *assera*

Reproductive structure	n ¹	Mean	Range	SD
Number of branches/inflorescence	32	7.9	3-13	2.2
Number of flowers/branch ²	43	8.0	2-23	5.2
Number of open flowers/inflorescences	52	3.5	1-12	2.8
Number of fruits/branch	27	2.6	1-9	16.3

¹n = The number of inflorescences sampled.

²Branch = either one paracladium or the terminal florescence on each inflorescence.

and withered within a 24 to 48 hour period. Over two seasons of observation no paracladium was found to have more than one open flower at a time. Only 5% of all flowers on an inflorescence were ever open at the same time and 44% of all branches on the same inflorescence displayed one open flower on the same day (Table 1).

Floral presentation, attractants and rewards. Open flowers of *D. caerulea* nodded on their pedicels (Fig. 1) or were held horizontally. Illustrations of flowers of *Dianella* species often depict the perianth as bell-like or funnellform, with tepals obscuring the androecium (e.g. see *D. ensifolia* and *D. nigra* in Dahlgren et al. 1985). This was not observed in populations of *D. caerulea* var. *assera*. The tepals of fresh, first-day flowers tended to be reflexive, exposing whole stamens to full view from the side (Fig. 1). The anthers formed a loose cone around the style. The stigma protruded from the centre of the anther cone. The style often curved or twisted below the tip of the anther cones, but there was no evidence of enantiomorphy as has been described in *Cyanella* and some *Solanum* species (Bowers 1975; Dulberger & Ornduff 1980). The anthers were extrorsive, each anther tip bearing two terminal pores (Fig. 1). There was no evidence of dimorphic pollen as in the enantiomorphic taxa discussed above (Dulberger 1981).

The pigmentation of floral organs was distinct and contrasting. Tepals of both whorls were blue with accentuated, dark-blue veins. The six stamens have blue filaments terminating in swollen, papillose, golden-orange tips embracing the greenish, straw-yellow anthers. The struma is about half the length of its anther, but each struma is about equal the length of the geniculate filament (Fig. 1). The globular ovary was a bright, polished green with a blue style and stigma.

When flowers were smelled on their inflorescences it was not possible to record a discernible scent. Flowers sampled two hours after they were placed in vials had a distinct but non-sweet odour reminiscent of baked pumpkin or squash.

In all three *Dianella* species sampled the strongest positive response to Neutral Red occurred repeatedly and consistently on the stigma, anther pores, pollen, inner surfaces of the tepals and on all strumae. The papillae of each struma turned an opaque, brick-red, while the geniculate filaments either showed no response (*Dianella* sp. aff. *longifolia*) or stained a translucent light pink (*D. caerulea* and *D. ensifolia*).

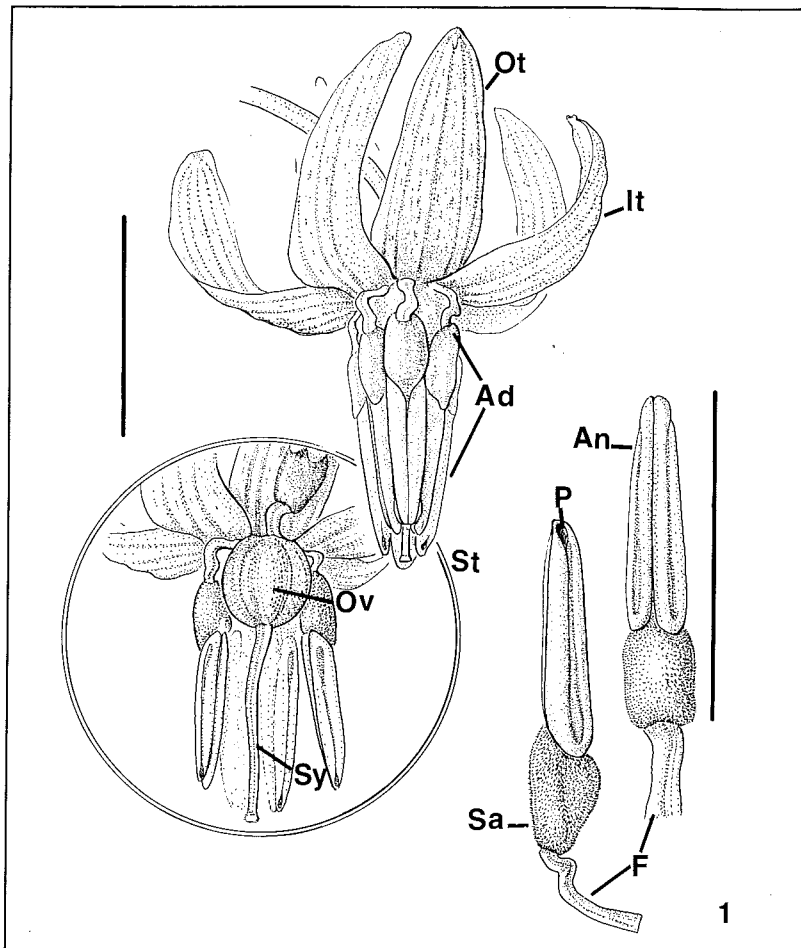


Fig. 1. The flower of *Dianella caerulea* var. *assera* (scale = 5 mm). Above, side presentation of flower, Ad = androecium; It = inner tepal; Ot = outer tepal; St = protruding stigma. Below left, side presentation of flower exposing the gynoecium, Ov = ovary; Sy = style. Lower right, stamens; An = anther; F = geniculate filament; P = pore; Sa = struma (note papillae).

The papillate surface of the strumae of *D. caerulea* var. *assera* remained dry over three seasons of sampling. No fluids were drawn into microcapillary tubes in the three species sampled and their strumae never felt damp or sticky.

Pollination mechanism

Female bees were the only successful pollen foragers on flowers of *D. caerulea* (Tables 1 and 2). Bees collected represented four out of the five families of Apoideae distributed throughout Australia (*sensu* Armstrong 1979). Bees observed at both sites rarely visited more than one open flower on each inflorescence, but regularly visited more than one inflorescence during a pollen foraging bout.

The introduced honey bee, *Apis mellifera* was observed to hover in front of the flowers, but rarely clung to the floral organs. The single *A. mellifera* collected on

Table 2. Pollen loads of bees collected on *Dianella caerulea* var. *assera*

Bee taxon	Bee length ¹	Pollen load		
		<i>Dianella</i> only	<i>Dianella</i> + other species	Other species (no <i>Dianella</i>)
Anthophoridae				
<i>Exoneura</i> spp.	6.5	1	5	1
Apidae				
<i>Apis mellifera</i>	14.0	0	0	1
<i>Trigona</i> spp.	4.5	4	5	0
Colletidae				
<i>Hylaeus</i> sp.	8.0	0	1	0
Halictidae				
<i>Homalictus holochorus</i>	5.0	0	1	0
<i>Lasioglossum</i> subgenera				
<i>Australictus</i> sp.	9.0	0	1	0
<i>Callalictus</i> sp.	9.0	1	2	
<i>Chilalictus</i>				
<i>L. convexum</i>	7.0	1	1	0
<i>Lasioglossum</i> spp.	6.0	0	0	1
<i>Nomia</i> spp.	11.5	0	2	0
Totals (n = 28)	-	6	18	3

¹ Mean length in mm

D. caerulea failed to carry the host plant's pollen (Table 1). No native bee was ever observed to land or perch on the strumae, attempt to scrape the papillae with their claws or probe them with their mouthparts.

Pollination was accomplished by bees at least 6 mm long or longer (Table 2) in the genera *Exoneura* (Anthophoridae), *Lasioglossum* and *Nomia* (Halictidae). All bees observed landed on the anthers and never on strumae or tepals. These insects always foraged upside down while clinging directly to the anthers, as even a horizontally held flower bent under the weight of the smallest foragers. *Exoneura* and the larger halictid bees appeared to shake the anthers using thoracic vibration. Pollen released from the anther pores was deposited ventrally on the bee's thorax. The bee combed this pollen off her thorax, depositing the grains between scopal hairs on the hind legs or into a patch of scopal hairs at the base of the abdomen. During the process of pollen collection the stigma contacted the bee's thorax or the base of the abdomen.

Although the *Hylaeus* species (Colletidae) carried *Dianella* pollen (Table 2), it was not observed to shake the androecium or contact the stigma. Bees less than 6 mm long regularly failed to contact the stigma while foraging for pollen. In particular, the eusocial *Trigona* species (subgenus *Tetragona*) were so small that worker bees regularly grasped the tip of only one anther on one flower at a time and scraped out

pollen by inserting a foreleg directly into the anther pores. No thoracic vibration was ever observed in *Trigona* on *Dianella* anthers.

The majority of bees collected on *D. caerulea* carried the pollen of more than one plant in flower in the study site (Table 2). All bees carrying mixed loads of pollen carried pollen from at least one nectar-producing species within the study site (Table 3; Figs. 2 and 3). The larger halictid bees (*Lasioglossum* and *Nomia* species) carried a maximum of four recognisable pollen taxa in their scopae with a mean of more than two pollen taxa/insect (n = nine bees bearing pollen). *Exoneura* species (Anthophoridae) carried a maximum of five pollen taxa with a mean of more than three pollen taxa/insect (n = six bees bearing pollen).

Discussion

The conversion of flowers into fruit is so low in *D. caerulea* var. *assera* it seems most likely that the rate of mechanical self-pollination (autogamy) is negligible in this taxon. Since anthers do not release pollen unless struck or shaken, pollination must be vector-mediated. The foraging pattern of insects combined with the flowering pattern of the plant suggests that a pollinator is more likely to deliver pollen from a second flowering shoot than from a second flower on the same inflorescence. In this respect, the adaptive phenology and morphology of the pollination system of *D. caerulea* var. *assera* overlaps broadly with some other buzz-pollinated taxa in the genera *Echeandia* (Bernhardt & Montalvo 1979), *Hibbertia* (Bernhardt 1984, 1986), *Dodecatheon* (Macior 1974) and *Solanum sensu stricto* (Macior 1974; Bowers 1976; Buchmann 1983). In all of these species the number of open flowers on an inflorescence at any time is always a fraction, compared to the original number of flower

Table 3. Pollen loads of bees carrying grains of *Dianella caerulea* mixed with the pollen of at least one more species

Bee taxon	Pollen taxa							
	CG+	DC-	HC-	HS+	MM+	PL+	SG+	UE+ ¹
<i>Exoneura</i> spp.	4	5	3	0	3	3	1	0
<i>Homalictus holochorous</i>	0	1	1	0	0	1	0	0
<i>Hylaeus</i> sp.	1	1	0	0	0	0	0	0
<i>Lasioglossum</i> subgenera								
<i>Australictus</i>	0	1	1	0	0	1	1	0
<i>Callalictus</i>	0	2	2	0	0	2	0	1
<i>Chilalictus</i>								
<i>L. convexum</i>	0	1	0	1	0	0	0	0
<i>Nomia</i> sp.	0	2	0	0	1	1	0	0
<i>Trigona</i> sp.	0	5	1	0	4	0	0	0
Totals (n = 18)	5	18	8	1	8	8	2	1

¹ CG = *Ceratopetalum gummifera*; DC = *Dianella caerulea*; HC = *Hibbertia scandens*; HS = *Haloragis* spp.; MM = Mixed, unidentified Myrtaceae (e.g. *Angophora*, *Baeckea*, *Eucalyptus*, *Kunzea*, *Leptospermum* spp.); PL = papilionoid legumes; SG = *Stylidium graminifolium*; UE = unidentified Epacridaceae (in tetrads); + = secretes floral nectar; - = no floral nectar.

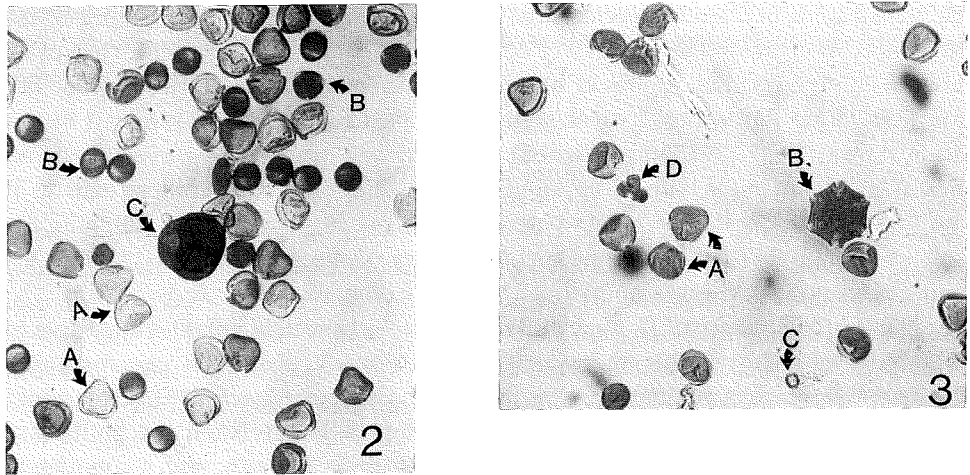


Fig. 2. Pollen grains from a section of the scopal load of a female *Lasioglossum* (subgenus *Callalictus*) X 98. A = *Dianella caerulea* var. *assera*; B = *Hibbertia scandens*; C = Unidentified Epacridaceae. Figure 3. Pollen grains from a section of the scopal load of a female *Exoneura* sp. X 98. A = *Dianella caerulea*; B = *Stylidium graminifolium*; C = *Ceratopetalum gummifera*; D = papilionoid legume.

buds produced by the inflorescence. This mode of flowering is known as the steady state syndrome (Gentry 1974).

The highly variable yet comparatively low rate of conversion of flowers into fruits converged with *Echeandia* (Bernhardt & Montalvo 1979), suggesting that *D. caerulea* was probably dependent on outbreeding (Richards 1986). The sharply contrasting pigmentation of the *D. caerulea* flower is largely duplicated in *Solanum* and *Dodecatheon* species. As in the majority of *Solanum*-type flowers, the perianth of *D. caerulea* expanded to expose the androecium. The staminal filaments were relatively short compared to the length of the anthers, and such anthers were clustered and positioned so that the bee could not extract pollen without contacting the stigma.

Both long-tongue (Anthophoridae) and short-tongue (Halictidae) families of bees pollinated *D. caerulea*, but this is also typical of *Solanum*-type flowers. When pollen is the only edible reward, the length of the bee's glossa (proboscis) is inconsequential and many *Solanum*-type flowers in the western hemisphere are also pollinated by long-tongue Apoidea, especially bumblebees (*Bombus* species) and anthophorids (Macior 1974; Bowers 1975; Bernhardt & Montalvo 1979; Buchmann 1983).

Dianella caerulea received a greater diversity of foragers in the halictid genus, *Lasioglossum* (four subgenera), than any nectarless, bee-pollinated species studied previously in southern Australia (e.g. Bernhardt 1984, 1986, 1989; Bernhardt & Burns-Balogh 1986). *Lasioglossum* species appear to be dominant foragers on many genera with nectarless flowers in Australia (Bernhardt 1989). The failure of *Apis mellifera* to remove pollen from *D. caerulea* has been recorded in other *Solanum*-type flowers (Buchmann 1983; Barth 1985).

Do the strumae of *Dianella* species have a recognisable function? The strumae of the three species examined are definitely not nectaries. This may not be indicative of all taxa in this genus, but it should be noted that nectariferous secretions were not found in living flowers of *D. revoluta* or *D. longifolia* var. *longifolia* examined by the author from 1990–1992 (unpublished). Furthermore, no bee was ever observed mistaking strumae for anthers by attempting to scrape off the papillose cells as if they were pseudopollen or, as has been observed of some female bees, scraping the calli or trichome brushes in some orchid flowers (Dafni & Bernhardt 1990) or the hairy staminodes of some species within the Commelinaceae (Faden 1992). The papillae on the strumae of *D. caerulea* did not appear to secrete volatiles attractive to male bees as on the anther connectives of *Cyphomandra endopogon* var. *endopogon* (Solanaceae) which is pollinated by neotropical euglossines (Gracie 1993). How could the strumae make the anthers of *D. caerulea* appear larger when the anthers of *D. caerulea* var. *assera* are twice as long as the strumae, smooth, and a completely different colour?

It should be noted that androecia bearing some form of ornamentation and/or distal swelling are extremely common in the flowers of petaloid monocots that are buzz-pollinated. In *Xyris* and *Commelina*, for example, fertile stamens alternate with ornamented-brushy staminodes (Vogel 1978; Faden 1992). However, in Australia some monocot genera with *Solanum*-type flowers have fertile stamens in which the filament tips are enlarged and/or ornamented, including *Arthropodium*, *Bulbine*, *Caesia*, *Dichopogon*, *Herpolirion*, *Tircoryne* (Vogel 1978; Dahlgren et al. 1985; Bernhardt & Burns-Balogh 1986, and descriptions by Willis 1978) and *Stypandra* (a sister genus of *Dianella*) (Dahlgren et al. 1985). All but *Herpolirion* are currently placed within only two families in the order Asparagales, suggesting a strong trend towards parallel evolution (Dahlgren et al. 1985).

In the flowers of these five genera and *Dianella* the colour of the swollen filaments or their ornaments often contrasts vividly with the anther colours. Since these flowers tend to nod on their pedicels, ornamented filaments probably contribute to the overall visual cue of the flower's profile or side view. Epidermal sculptures on each filament could also help mesh stamens together, keeping the anther tuft tightly clustered.

Strumae may also function as scent glands but further investigation is required to test this hypothesis. The oily pollen coat of insect-pollinated flowers usually serves as a matrix for pollen scents and such scents appear to attract some pollinators (Buchmann 1983; Bernhardt 1984, 1986; Dobson et al. 1990). However, the pollen grains of buzz-pollinated flowers are retained inside inflated chambers so pollen odours are not exposed directly to the air until after the grains are removed by the bees. Scents attracting female bees to the source of pollen in a *Solanum*-type flower could be secreted by the filament apices.

Swollen, stalked and ornamented appendages are very common in the Asclepiadaceae, Aristolochiaceae, Burmanniaceae and Orchidaceae and these structures have been identified as osmophores (Vogel 1990). Therefore, the positive response to the

Neutral Red test of the strumae of *Dianella* species suggests that they may serve as both visual and olfactory cues to female bees searching actively for inverted and dangling anthers.

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