

Comparative floral presentation and bee-pollination in two *Sprengelia* species (Ericaceae)

Karen A. Johnson* and Peter B. McQuillan

School of Geography and Environmental Studies, University of Tasmania, Private Bag 78, Hobart, Tasmania 7001, Australia.

*Corresponding author. E-mail: johnsonk@utas.edu.au

Abstract: Pollination by sonication is unusual in the Styphelioideae, family Ericaceae. *Sprengelia incarnata* and *Sprengelia propinqua* have floral characteristics that suggested they might be adapted to buzz pollination. Both species have florally similar nectarless flowers except that the stamens of *Sprengelia propinqua* spread widely after the flower opens, while those of *Sprengelia incarnata* cohere in the centre of the flower. To test whether sonication occurs, we observed bee behaviour at the flowers of both plant species, documented potential pollinators, and examined their floral and pollen attributes. We found that *Sprengelia incarnata* had smaller and drier pollen than *Sprengelia propinqua*. We found that *Sprengelia incarnata* was sonicated by native bees in the families Apidae (*Exoneura*), Halictidae (*Lasioglossum*) and Colletidae (*Leioproctus*, *Euryglossa*). *Sprengelia propinqua* was also visited by bees from the Apidae (*Exoneura*) and Halictidae (*Lasioglossum*), but pollen was collected by scraping. The introduced *Apis mellifera* (Apidae) foraged at *Sprengelia propinqua* but ignored *Sprengelia incarnata*. The two *Sprengelia* species shared some genera of potential pollinators, but appeared to have diverged enough in their floral and pollen characters to elicit different behaviours from the native and introduced bees.

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Introduction

The interactions between plants and pollinators are thought to be responsible for much of the diversity in angiosperm flower morphology, with many floral traits associated with particular animal behaviours (Lawrence et al., 2001). The flowers of buzz-pollinated plants are a notable example of this phenomenon. Furthermore, it has been proposed that flowers with small, dry pollen typical of buzz-pollination may represent a transitional stage to anemophily (Buchmann, 1983), and phylogenetic analyses suggest that the evolution of anemophily is more likely in groups with these traits (Culley et al., 2002).

Buzz-pollination is widespread among angiosperms. In the Australian flora, buzz pollination occurs in a range of genera including *Hibbertia* (Bernhardt, 1984; Bernhardt, 1986), *Thelymitra* (Bernhardt & Burns-Balogh, 1986), *Dianella* (Bernhardt, 1995), *Tetralochea* (Driscoll, 2003) and *Solanum* (Anderson & Symon, 1988). In the Styphelioideae, buzz-pollination has been confirmed for *Conostephium* and hypothesised for *Coleanthera myrtoides* Stschegl., *Rupicola*

species, some *Leucopogon* species, *Richea milliganii* (Hook.f.) F.Muell., and *Sprengelia incarnata* Sm. (Houston & Ladd, 2002; Ladd, 2006). A range of floral characteristics that make up the traits of buzz-pollinated flowers have been elucidated (Buchmann, 1983; Harder, 1990). In the Australian taxa, buzz-pollinated flowers have been observed to have either exposed anthers (solanooid-type), or anthers hidden by the petals (Houston & Ladd, 2002). They typically have purple or blue petals and yellow anthers, or white petals and purple anthers (Houston & Ladd, 2002).

Buzz pollination occurs when a bee vibrates its thoracic flight muscles over the anthers, vibrating dry pollen onto its body (Harder, 1998; Houston & Ladd, 2002; Thorp, 2000). Buzz pollination or sonication of flowers by bees has been associated with porocidal anthers such as those in the Ericaceae. Most Ericaceae have two-lobed anthers that dehisce by introrse or terminal pores (Curtis, 1963; Stephens, 2004), an important preadaptation to buzz pollination in ericads such as *Vaccinium stamineum* L. (Cane et al., 1985). In contrast to the rest of the Ericaceae, the subfamily Styphelioideae (epacrids) generally have unilocular anthers

that open by a single longitudinal slit (Curtis, 1963). However, the more basal genera, *Prionotes*, *Sprengelia* and *Richea* can have bilocular anthers that dehisce by a single slit (Crayn et al., 1998; Curtis, 1963) giving them characteristics of both ericads and epacrids.

Although the epacrids do not have apically porose anthers, the following characters are thought to make the widespread *Sprengelia incarnata* a candidate for sonication: nectarless flowers, anthers that dehisce introrsely from an elongated pore, and stamens that cohere and move as a unit (Houston & Ladd, 2002). With the exception of this last character, the Tasmanian endemic *Sprengelia propinqua* A.Cunn. ex DC. shares these attributes. Until recently, *Sprengelia incarnata* and *Sprengelia propinqua* were considered to be a single variable species (Buchanan, 2009; Buchanan, 2005; Curtis, 1963). However, the stamens in *Sprengelia propinqua* are free (Curtis, 1963), generally separating and spreading away from the central position after the flower opens.

Sonication has been observed to occur, regardless of different stamen morphologies and arrangements. For instance, in Java, *Xylocopa* bees buzz-pollinate three *Dillenia* species: *Dillenia suffruticosa* Martelli, where the stamens form a cone; and *Dillenia alata* (D.C) Martelli and *Dillenia philippinensis* Rolfe which have spreading stylar branches and both long and short stamens. On this evidence, *Sprengelia propinqua* may also be a candidate for sonication (Endress, 1997). We tested the hypothesis that the flowers of *Sprengelia incarnata* and *Sprengelia propinqua* are sonicated by native bees, examined floral morphology and pollen tackiness, and documented potential pollinators.

Methods

Study species and sites

Sprengelia propinqua was split from *Sprengelia incarnata* based on floral characters including free rather than cohering stamens and solely white flowers rather than bi-coloured pink and white flowers (Curtis, 1963; Walsh & Entwisle, 1996). The flowers of both species are hermaphroditic and nectarless. *Sprengelia propinqua* is a prominent species in moorland in southwest Tasmania while *Sprengelia incarnata* is a locally dominant species occurring throughout southeastern Australia and Tasmania. Observations on *Sprengelia incarnata* were made in buttongrass (*Gymnoschoenus sphaerocephalus* (R.Br.) Hook.f.) hummock sedgeland in the Peter Murrell Nature Reserve (43°00'45"S 147°18'43"E); in heathy *Eucalyptus tenuiramis* Miq. woodland with buttongrass present in the understorey, near Egg and Bacon Bay (43°14'45"S; 147°06'19"E); in similar vegetation on the Tasman Peninsula (43°01'23"S; 147°53'41"E) and in the Tasmanian Wilderness World Heritage Area (WHA) where it co-occurs with *Sprengelia propinqua* (42°57'18"S; 146°21'23"E). Observations on *Sprengelia propinqua* were made in buttongrass hummock sedgeland in the WHA

(42°55'26"S; 146°21'34"E and 42°53'03"S; 146°22'52"E). An *Apis mellifera* L. (introduced honeybee) hive was present within 100 m of one *Sprengelia propinqua* study site.

For the purpose of our study plants closely fitting the descriptions of *Sprengelia incarnata* and *Sprengelia propinqua* were chosen for examination (Curtis, 1963; Walsh & Entwisle, 1996). Plants with intermediate floral morphology occur in the western study area. Vascular plant nomenclature follows Buchanan (2009); and author names follow those on The International Plant Names Index (www.ipni.org – accessed 19 May 2010). Monthly climate averages for rainfall, temperature, relative humidity and wind speed for our study sites are given in Table 1.

Floral morphology and pollen

Twenty specimens of each species were randomly selected from material housed at the Tasmanian Herbarium, Hobart (Appendix 1). Floral morphology was compared by measuring (to an accuracy of 0.5 mm) sepal, petal, style, stamen and anther length under a dissecting microscope. We used the Student's 2-sample t-test to determine if there were significant differences in the size of floral parts of *Sprengelia incarnata* and *Sprengelia propinqua*. All tests were performed in MINITAB 15.

To determine if there were any differences in the pollen of *Sprengelia incarnata* and *Sprengelia propinqua*, pollen samples from a live plant of each species (from Peter Murrell Reserve and WHA sites respectively) were examined under a Scanning Electron Microscope (SEM) at 5000x magnification at the Central Science Laboratory at the University of Tasmania. Maximum pollen grain diameter and tackiness were recorded. Tackiness in *Sprengelia* species was determined by whether pollen grains occurred separately (dry) or adhered to each other (sticky).

Flower visitors

Observations on flower visitors were made in person (while walking amongst flowers) and by video camera (Panasonic Digital Video Camera, model number NV-GS70, 1.7 mega pixel, 500x digital zoom) mounted on a tripod. A pollinator is defined as an animal that collects pollen and deposits it onto conspecific stigmas of other plants (Pellmyr, 2002). In contrast, a flower visitor is an animal at a flower that either does not contact the reproductive parts of the flower and/or does not travel between plants. For the purpose of our study, we defined a potential pollinator as an animal that we observed to contact the reproductive organs of a plant, actively removed pollen from the anthers, and move between conspecific species. In addition to the 'solanoid' *Sprengelia* flower-form that enables easy observation of insects contacting and removing pollen from the anthers, the *Sprengelia* pollen is different in colour from many of the sympatric co-flowering plant species including *Pimelea*, *Hibbertia*, *Aotus* and *Pultenaea*. Potential buzz pollination

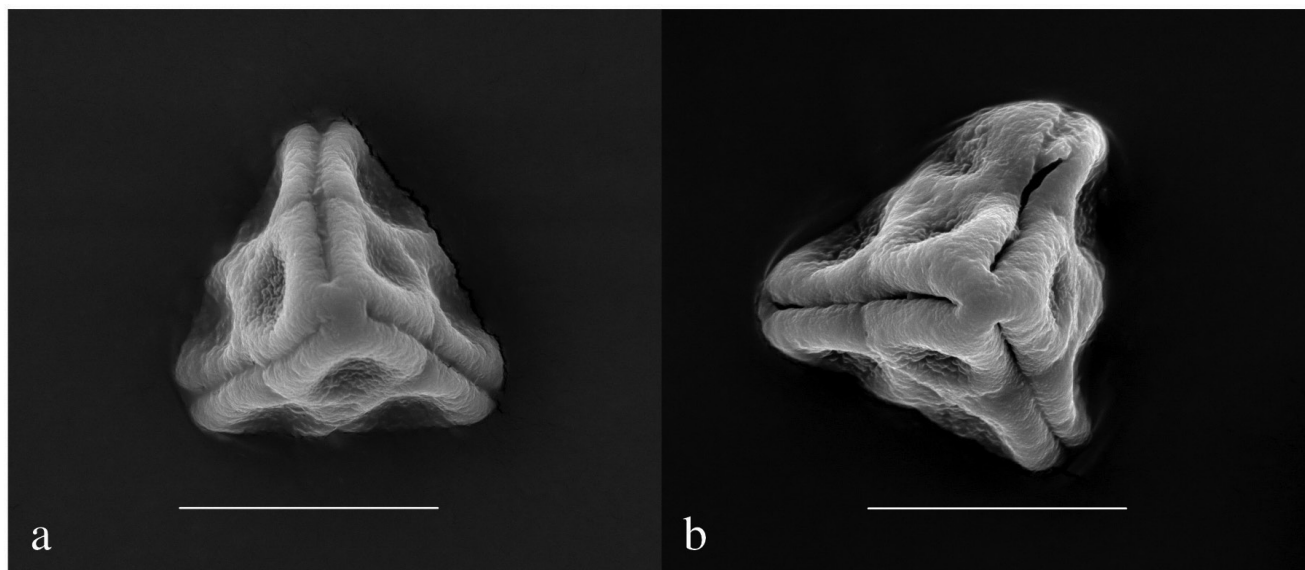


Fig. 1. *Sprengelia incarnata* pollen grain; B. *Sprengelia propinqua* pollen grain (scale bar approx. 20 μ m)

was identified by a bee hunching over a flower's anthers with wings held back along the line of its body, and by an audible buzzing (Harder, 1998; Houston & Ladd, 2002; Thorp, 2000).

Observations were made on clear and relatively warm (> 18 °C) days. Observations were made on *Sprengelia incarnata* between 10 am and 4 pm on 9 Oct 2008, 29 Sep, 4 Oct, 10 Oct and 8 Nov 2009 during its peak flowering period. Observations were made on *Sprengelia propinqua* between 11 am and 3 pm on 23 Oct, 1 Nov, 5 Nov, 13 Nov, 19 Nov 2008 and 8 Nov 2009 during its peak flowering period.

Samples of the foraging insects were collected by netting, or captured straight into a plastic screw-top container wetted with ethanol. Insects were killed and stored in screw-top vials with 70% ethanol. Bees were identified to genus under a dissecting microscope using the key of Michener (1965) and the Hingston bee collection which holds specimens determined by Dr. Ken Walker (National Museum of Victoria). Together with potential pollinators collected during

our survey, the Hingston collection is housed at the School of Geography and Environmental Studies Laboratory, UTAS. Flies were identified using Colless and McAlpine (1991) and butterflies using Braby (2004). Other invertebrates were identified using Zborowski and Storey (2003) and Daley (2007).

Results

Floral morphology and pollen

There was no overlap in the size of floral parts with *Sprengelia incarnata* being smaller in all parts (Table 2). Observation of pollen under the SEM revealed that the grains of *Sprengelia incarnata* occurred separately, indicating that they were dry, while the grains of *Sprengelia propinqua*, commonly adhered to form clumps indicating that the pollen was sticky. *Sprengelia propinqua* pollen was larger (ca 10%) than *Sprengelia incarnata* pollen, but had a similar morphology (Fig.1).

Table 1. Monthly climate averages for *Sprengelia* sites

(Note: All figures are from the closest climate stations on the Bureau of Meteorology website (www.bom.gov.au/weather/tas – accessed on 18 May 2010. These were Hobart, Dover, Port Arthur, and an average from the Strathgordon and Maydena Post Office climate sites).

Species and sites	Flowering time	Rainfall mm	Days rain \geq 1 mm	Wind km/h 3 pm	Temp °C 3pm	% RH 3 pm
<i>Sprengelia incarnata</i> (Peter Murrell)	Sept–Oct	61	9	18	15	56
<i>Sprengelia incarnata</i> (Egg and Bacon Bay)	Sept–Oct	85	7	15	14	63
<i>Sprengelia incarnata</i> (Tasman Peninsula)	Sept–Oct	104	14	22	12	65
<i>Sprengelia incarnata</i> (WHA)	Sept–Oct	161	16	11	13	62
<i>Sprengelia propinqua</i> (WHA)	Oct–Nov	161	16	11	13	62



Fig. 2. *Lasioglossum* (Parasphcodes) bees on *Sprengelia incarnata* showing: A. folded wing position; B. hunched position during sonication; C. pollen accumulation; and D. anther position in *Sprengelia propinqua*

Table 2. Comparison of floral presentation in *Sprengelia incarnata* and *Sprengelia propinqua* in Tasmania

Floral presentation	<i>S. incarnata</i>	<i>S. propinqua</i>
Floral measurements (mean mm \pm SE)*		
- Stamen	3.0 \pm 0.04	4.8 \pm 0.16
- Anther	1.6 \pm 0.06	3.4 \pm 0.15
- Style	3.7 \pm 0.06	6.0 \pm 0.90
- Petal	4.2 \pm 0.09	6.6 \pm 0.25
- Sepal	4.5 \pm 0.09	7.2 \pm 0.22
Flower colour	bicoloured pink and white	white
Flower position on stem	terminal	terminal
Flower heads	upright	upright
Stamen position	cohering in centre of flower	spreading widely as flower matures
Flowering time	Sep–Oct–Nov	Oct–Nov

**S. incarnata* and *S. propinqua* are significantly different in the size of all floral characters as follows: stamen ($t = -10.98$, $P < 0.001$, $DF = 22$), anther ($t = -11.42$, $P < 0.001$, $DF = 24$), style ($t = -11.30$, $P < 0.001$, $DF = 22$), petal ($t = -9.35$, $P < 0.001$, $DF = 24$), sepal ($t = -11.04$, $P < 0.001$, $DF = 25$).

Flower visitors

Sprengelia incarnata was repeatedly observed being sonicated by native bees (Fig. 2; Table 3). *Lasioglossum* species and *Exoneura* species were the main visitors (>100 observations). During sonication the bees collected large amounts of pale-coloured pollen on their legs and bodies and moved between *Sprengelia incarnata* plants. A thick layer of pollen was collected on the hind legs (femur, tibia and basitarsus) and abdominal sternites with additional pollen also scattered on body hairs outside these areas, including the head. Bees were observed to groom themselves after sonication, moving pollen from the thorax to abdomen with the aid of the front legs. The pollen-covered abdomen was observed to contact a flower's stigma in a manner consistent with a potential pollinator (Fig. 2C). Hoverflies (Syrphidae) were present at the study sites and two individuals contacted the anthers and appeared to collect pollen from *Sprengelia incarnata*. However, they were not observed to move between *Sprengelia incarnata* flowers. An introduced bumble bee queen, *Bombus terrestris* (L.), was observed to visit five flowers but was not observed to collect pollen. *Apis mellifera* (honeybees) were present and active at all sites during observations. They visited three flowers of *Sprengelia incarnata* over three separate occasions but did not collect pollen. Generally they flew past

Sprengelia incarnata without landing on the flowers. They frequently collected pollen from sympatric plants including *Euryomyrtus ramosissima* (A.Cunn.) Trudgen, *Leucopogon collinus* (Labill.) R.Br., *Pimelea linifolia* Sm., *Pultenaea stricta* Sims, and *Aotus ericoides* (Vent.) G.Don when native bees were buzzing *Sprengelia incarnata*. Native bees also visited some of these sympatric plants.

No bees were observed to sonicate *Sprengelia propinqua*. *Apis mellifera* and *Lasioglossum* species were the main visitors (> 100 observations). Hoverflies (*Simosyrphus* species and *Melangyna* species) were also prominent visitors. *Exoneura* species was present but was only observed visiting *Epacris corymbiflora* Hook.f. Macleays' swallowtail butterfly (*Graphium macleayanus* (Leach)) visited *Sprengelia propinqua* and bobbed its head up and down in the same way it did to extract nectar from, and potentially pollinate, *Epacris corymbiflora*. On one occasion it probed a number of flowers on one plant. However, it was not observed to move between *Sprengelia propinqua* plants, making it a visitor, rather than a potential pollinator. In contrast, *Graphium macleayanus* regularly moved between *Epacris corymbiflora* plants (> 50 observations). *Graphium macleayanus* is known to be predominantly a nectar feeder, which makes it unlikely to be a regular forager on, and pollinator of, the nectarless *Sprengelia propinqua*. During observations on 23 Oct and 1 Nov 2008 at the site near the apiary, *Apis mellifera* was the only species active on *Sprengelia propinqua* and native bees were not observed.

Table 3. Potential pollinators and flower visitors for *Sprengelia incarnata* and *Sprengelia propinqua* in Tasmania

(i) = introduced, p = potential pollinator, + = buzz pollination, fv = flower visitor

Animal	<i>S. incarnata</i>	<i>S. propinqua</i>
Bees		
<i>Euryglossa</i> sp.	p +	
<i>Exoneura</i> sp.	p +	
<i>Lasioglossum</i> (Chilalictus) sp.	p +	p
<i>Lasioglossum</i> (Parasphcodes) sp.	p +	p
<i>Leioproctus</i> sp.	p +	
(i) <i>Apis mellifera</i> L.	fv	p
(i) <i>Bombus terrestris</i> (L.)	fv	p?
Flies		
Syrphidae	p?	p
<i>Musca vetustissima</i> Walker		fv
Tachinid fly (long-legged)		fv
Tachinid fly (short-legged)	fv	fv
Butterflies and moths		
<i>Junonia villida</i> (Fabricius)	fv	
<i>Graphium macleayanus</i> (Leach)		fv
<i>Melitulias graphicata</i> (Walker)		fv
Beetles		
Elateridae	fv	fv
<i>Paropsis</i> sp.	fv	
<i>Chauliognathus tricolor</i> (Castelnau)		fv
Other		
<i>Diaea</i> sp.	fv	fv
Pentatomidae (unidentified shield bug)	fv	fv
Thripidae (unidentified thrip)	fv	fv
Curculionidae (unidentified weevil)	fv	

Discussion

We have confirmed that pollen is collected from *Sprengelia incarnata* by sonication, as predicted by Houston & Ladd (2002) and scraped from *Sprengelia propinqua*. *Sprengelia propinqua* was not observed to be sonicated. Regardless of differences in flower size, pollen tackiness, stamen morphology and arrangement, *Sprengelia incarnata* and *Sprengelia propinqua* have overlapping floral visitor profiles with *Lasioglossum* bees being prominent potential pollinators of both plants.

Sonication of *Sprengelia incarnata* is undertaken by at least four native bee genera in Tasmania. With the exception of *Euryglossa*, bees from these genera are known to sonicate a range of plants in Australia. *Leioproctus* species have been observed to buzz *Conostephium drummondii* (Stschegl.) C.A.Gardner, *Conostephium pendulum*, *Conostephium minus* Lindl., *Conostephium roei* Benth. (Houston & Ladd, 2002) and *Hibbertia fasciculata* (Bernhardt, 1986). *Lasioglossum* species have been observed to buzz, *Conostephium roei* (Houston & Ladd, 2002), *Hibbertia stricta* (DC.) F.Muell. (Bernhardt, 1984), *Hibbertia fasciculata* DC. (Bernhardt, 1986), *Thelymitra nuda* R.Br. (Bernhardt & Burns-Balogh, 1986), *Melastoma affine* D.Don (Gross, 1993), *Dianella caerulea* var. *assera* R.J.F.Hend. (Bernhardt 1995) and *Tetratheca juncea* Sm. (Driscoll, 2003). *Exoneura* species are

buzz-pollinators of *Dianella caerulea* var. *assera* (Bernhardt 1995) and *Tetraloche juncea* (Driscoll, 2003). Gross (1993) observed that bees from the genera *Amegilla*, *Lestis*, *Nomia* and *Xylocopa* were also capable of collecting pollen, via sonication, although they did not always do so. At least nine bee families are known globally to contain buzz-pollinators (Thorp, 2000).

Lasioglossum species and the introduced honeybee collected pollen from *Sprengelia propinqua* by scraping rather than sonication. Honeybees are not known to collect pollen by sonication (Thorp, 2000), and they ignored the flowers of *Sprengelia incarnata*. Honeybees have also been found to ignore the flowers of the buzz-pollinated *Conostephium pendulum* (Houston & Ladd, 2002) and *Dianella* species (Duncan et al., 2004). The introduced *Bombus terrestris* is a known buzz-pollinator (Dupont & Olesen, 2006) but was not observed to sonicate either *Sprengelia* species. *Exoneura* species has not been observed to visit *Sprengelia propinqua*, although it is present at these sites. *Euryglossa* species and *Leioproctus* species have not been observed at the *Sprengelia propinqua* sites and it is currently unknown if their geographic range extends into southwest Tasmania. Of the four native bee genera observed during survey, *Lasioglossum* species and *Exoneura* species are floral generalists but some *Euryglossa* species and *Leioproctus* species are known to be oligolectic (Houston, 2000). In Tasmania, these four bee genera represent important pollinators of a range of plant species, particularly from the Fabaceae and Ericaceae (Hingston collection held at University of Tasmania).

On some occasions pollinator activity was absent at *Sprengelia incarnata* even though known buzz-pollinators were scraping pollen from other plants nearby. The absence of pollinator activity on *Conostephium* flowers has also been observed on many occasions (Houston & Ladd, 2002). This could be a result of either pollinators seeking nectar, which is not offered by *Sprengelia*; or perhaps unfavourable climatic conditions for mobilising pollen. In general, foraging bees must either rely on honey reserves available prior to foraging – *Apis mellifera* can load up on supplies before leaving the nest – or divide their foraging bouts between nectarless and nectariferous flowers – like the majority of bee taxa (Bernhardt, 1989). In contrast to the polylectic nature of many native bee taxa, *Apis mellifera* workers usually collect pure pollen loads (Bernhardt et al., 1984). As the honeybee has a preference for foraging on some native plant species and not others, and is likely to collect pure pollen loads, it has the potential to impact not only on the floral evolution of individual native plant species, particularly those with nectarless flowers, but the entire native flora of Australia. Both *Sprengelia incarnata* and *Sprengelia propinqua* occur with co-flowering nectar-producing plants and honeybees were prevalent at all study sites; honeybee hives were present at the Tasmanian Wilderness World Heritage Area study sites.

In contrast to the other buzz-pollinated epacrid, *Conostephium*, which has hidden anthers and a pendulous, tubular corolla– *Sprengelia incarnata* resembles a ‘solanoid’ flower. However like *Conostephium*, *Sprengelia incarnata* does not have the usual colouration associated with many buzz-pollinated plants – yellow anthers and purple or blue petals (Houston & Ladd, 2002) – instead it has pale anthers and bicoloured white and pink petals. Given that a variety of floral morphologies and stamen arrangements are known to be sonicated, it is possible that the presence of drier (and possibly smaller) pollen enables collection by sonication at *Sprengelia incarnata*. It is probable that tacky pollen, such as that of *Sprengelia propinqua*, would be difficult to mobilise by sonication. In the Styphelioideae, the pollen of the buzz-pollinated *Conostephium pendulum* was found to be dry as was that of the readily mobilised, wind-dispersed pollen of *Richea procera* (F.Muell.)F.Muell and *Richea sprengelioides* (R.Br.)F.Muell. (Houston & Ladd, 2002; Ladd, 2006). This contrasts with the sticky pollen of the bird-pollinated *Prionotes cerinthoides* (Labill.)R.Br. (Johnson et al., 2010) and the likely mammal-pollinated, *Acrotriche serrulata* R.Br. (Johnson et al., 2011).

Houston & Ladd (2002) observed that the buzz-pollination syndrome was present in phylogenetically separated parts of the Styphelioideae. They confirmed that pollen was collected via sonication from *Conostephium* in the tribe Styphelieae. Now, we have confirmed that pollen is also collected by sonication from *Sprengelia incarnata* in the tribe Cosmelieae. Thus, there has been independent development of flowers suitable for this form of pollen collection in the Styphelioideae. Although there is currently no phylogenetic hypothesis for the genus *Sprengelia*, it is possible that *Sprengelia incarnata* with a floral form suitable for sonication was derived from a *Sprengelia propinqua*-type ancestor exhibiting the more common tacky pollen and spreading anthers. The intergradation of floral presentation between these two species could be viewed as supporting evidence for such a hypothesis.

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Appendix 1. Tasmanian Herbarium, Hobart (HO) voucher specimens

Sprengelia incarnata 2608, 5168, 5719, 5720, 5721, 5775, 5783, 5801, 5802, 8605, 51876, 72097, 79848, 89782, 94825, 106431, 119960, 400831, 405983, 407896; and

Sprengelia propinqua 2473, 5757, 5763, 5799, 5804, 58204, 76339, 77618, 89566, 119893, 120776, 120813, 121824, 123685, 315596, 401194, 402889, 403717, 404484, 406328.