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# Resolution of a 35-year taxonomic dilemma: *Eucalyptus* sp. Howes Swamp Creek (Myrtaceae) from eastern Wollemi National Park, New South Wales

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# Abstract

The identity of a population of eucalypts from Howes Swamp Creek in the eastern part of Wollemi National Park in New South Wales has remained unresolved for over 35 years. Despite several workers inspecting both the site and the trees growing there over this period, little consensus has been achieved on its taxonomic status. Various suggestions have been made that the entity was a new species with affinities to *Eucalyptus dalrympleana*, *E. viminalis* or *E. bridgesiana*, and at one time the unpublished manuscript name *E. 'wollemiensis'* was used. Because of the perceived small population size and threats posed by wildfire and other factors, the entity phrase name *E.* sp. Howes Swamp Creek (M.Doherty 26) was listed as an endangered taxon in both Commonwealth and State threatened species legislation. Our investigations over the last few years, involving field, seedling, and herbarium studies, have determined the original reference specimen designated for the phrase name is *E. bridgesiana* × *E. viminalis*. Both parent species are present at the site, although the former species is seemingly very rare there. We recommend that *E.* sp. Howes Swamp Creek be removed from threatened species legislation, and that the names *E.* sp. Howes Swamp Creek (M.Doherty 26) and *E. 'wollemiensis'* ms be considered nomenclatural synonyms of *E. bridgesiana*.

# Introduction

During university studies undertaken by Michael Doherty within the Mellong Swamps region of eastern New South Wales in the mid-1980s, an anomalous, sterile eucalypt specimen (*M.Doherty 26*) was lodged at the National Herbarium of New South Wales (NSW). The identity of this specimen could not be determined by Doherty or others at that time, but it was recognised as belonging to *Eucalyptus* sect. *Maidenaria* based on the morphology of its juvenile leaves. Notes associated with this specimen stated that it was from a 'clump of juveniles, all with immature leaves'. A second collection from this site including buds and fruit was collected by Doherty in March 1988 (*M.Doherty 27*), with notes stating that it was from a 'population of juveniles and small adults (10 m) with sucker growth. Very few adult trees. Scattered "mallee-like" juveniles'. Eucalypt taxonomist

Ken Hill subsequently visited and collected from the site on three separate occasions over an eight-year period in the 1990s, ultimately referring to the population by the unpublished manuscript name *E. 'wollemiensis'*. Duplicate specimens collected by Hill in November 2000 and lodged at CANB have been re-determined there by Andrew Slee as *E. bridgesiana*.

Later gatherings from the population in 2017 by one of us (GP) noted small trees to 8 m in height showing superficial similarities to *E. viminalis*, but with inflorescences in 7s, and nearby young plants with cordate juvenile leaves. This combination of features (*viz.* cordate juvenile leaves and 7-flowered inflorescences), combined with the mostly smooth texture of the bark, confounded its positive identification. Over a 15-year period, notes associated with several collections (e.g. *M.Doherty 26* in 1985; *M.Doherty 27* in 1988; *K.D.Hill 5648B* in 2000) include observations that the area appears to be regularly burnt. In addition, our own observations made in 2009 and in more recent years (2019 and 2020) suggest that fire is indeed a regular occurrence, and while this has allowed ready collection of juvenile coppice growth, at the same time it has hindered the collection of flowering and fruiting material.

PlantNet (2022) refers to this population as *E*. sp. Howes Swamp Creek (M. Doherty 26), with additional notes under the entry for *E*. *bridgesiana* that it is nearest to this species but is poorly understood, and under *E*. *viminalis* that specimens from Howes Swamp exhibiting bluish juvenile leaves may represent a separate taxon. Klaphake (2012) has referred to the Howes Swamp Creek population as *E*. *bridgesiana*  $\times$  *E*. *viminalis* hybrids, while Slee *et al.* (2015) consider the plants to simply represent a population of *E*. *bridgesiana* with smaller than usual juvenile leaves and less prominently erect, exsert valves in the fruit. Bell (2008) and Hager and Benson (2010) both note the presence of the population under the unpublished name *E*. *'wollemiensis'* but offer no further taxonomic opinion.

In 2000, *E.* sp. Howes Swamp Creek (M. Doherty 26) was listed federally as endangered in the *Environment Protection and Biodiversity Conservation Act 1999* (Commonwealth of Australia 2000), having been previously listed as endangered in the NSW *Threatened Species Conservation Act 1995* (now replaced by the *Biodiversity Conservation Act 2016*) in 1995. Both listings were based on the few available herbarium records offering limited species knowledge, small population size and the threats posed to individuals by frequent fire (NSW Department of Planning and Environment 2019). In New South Wales, the taxon has been allocated to the 'data-deficient' stream of the Saving our Species conservation program, its uncertain taxonomy delaying the provision of management funding to ensure long-term survival.

Over the course of 35 years, specimens of *E*. sp. Howes Swamp Creek have been variously determined as *E*. *'wollemiensis'* ms, *E*. sp. aff. *dalrympleana*, *E*. sp. aff. *viminalis*, *E*. *bridgesiana*, and *E*. *bridgesiana*  $\times$  *E*. *viminalis* hybrids. It is clear that a resolution of its taxonomy is required, and hence this paper outlines the results of field and herbarium studies, including seedling trials, to determine the most appropriate taxonomic outcome.

### **Field investigations**

#### Habitat

Several visits to Howes Swamp Creek have been undertaken by the authors over a period of 30 years, with most effort expended over the last ten. Survey of the northern side of Howes Swamp Creek undertaken in 1992 by one of us (SB) failed to confidently locate *E*. sp. Howes Swamp Creek, with only *E*. *viminalis* being observed. Attempts made in 2009 by SB and DN to relocate the taxon on two separate occasions were thwarted by wildfire that had impacted the area, leaving little material worthy of collection or inspection. From 2016, further visits to the site were undertaken by GP, and in 2017 fertile material and juvenile leaves of both the purported taxon and *E. viminalis* were located and examined.

More detailed inspection of the site in late 2019 by SB and GP incorporated a targeted search of the northern side of Howes Swamp Creek, recording 14 individuals of the putative taxon. During this time, juvenile leaves from epicormic growth from all individuals were collected, together with buds, fruit and adult leaves on trees large enough to support these. Two kilometres of Howes Swamp Creek were examined, with individuals located only within a 500 m stretch (Fig. 1).

All located individuals occurred within a narrow band between the swampy riparian zone of Howes Swamp Creek and the nearby sandstone escarpment running parallel to the length of the creek. The occupied zone comprised a canopy of *Angophora floribunda*, with occasional small individuals of *E. parramattensis* subsp. *parramattensis* and *E. amplifolia* subsp. *amplifolia*, over an understorey of *Acacia parramattensis*, *Persoonia linearis*, *Grevillea mucronulata*, *Melaleuca thymifolia*, *Gompholobium latifolium*, *Pteridium esculentum*, *Monotoca scoparia* and *Dianella revoluta* (Fig. 2). Howes Swamp Creek itself at this point is dominated by emergent *E. amplifolia* subsp. *amplifolia*, over dense thickets of *Leptospermum juniperinum* and *Callistemon citrinus*. Upslope from the creek, dry open forest dominated by *E. piperita* occurs, with occasional individuals of *Corymbia eximia*. Upstream from the habitat supporting the purported taxon, *E. viminalis* is prominent, but this species is not present in the habitat occupied by *E. sp.* Howes Swamp Creek. Inspections further downstream of this area identified a dryer shrubby forest dominated by *E. racemosa*.

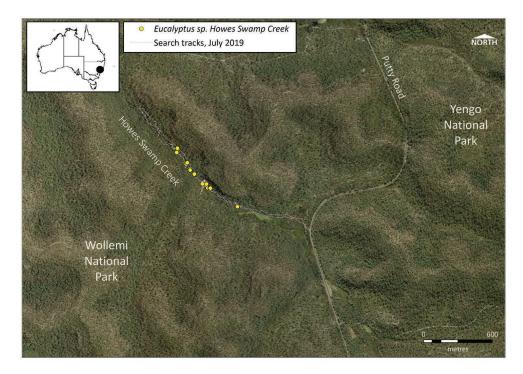


Fig. 1. Location of all individuals previously determined as Eucalyptus sp. Howes Swamp Creek.



**Fig. 2.** Habitat of *Eucalyptus* sp. Howes Swamp Creek, with one tree indicated by pink tape just right of centre. All other larger, rough-barked trees shown are *Angophora floribunda*.

#### Morphology

A wide range of juvenile leaf forms were evident in the 14 trees examined at the site in 2019. These ranged from the broadly cordate and alternate juvenile leaves typical of *E. bridgesiana*, to those with broad-lanceolate, opposite leaves more similar to *E. viminalis* (Fig. 3). Such variation within a relatively small area of habitat is suggestive of more than one taxon evident in the population. The colour of the juvenile foliage varied among individuals, with those nearer to the western edge of the population being glaucous and bluish like those of typical *E. bridgesiana*, while plants further east were greener like *E. viminalis*. The west-to-east shift was also evident in leaf shape, with the more cordate leaves (near to *E. bridgesiana*) grading to oblong-lanceolate and lanceolate forms closer to stands of pure *E. viminalis*.



**Fig. 3.** Variation in juvenile leaf morphology exhibited within the population in 2019: a. Tree 1, *Eucalyptus bridgesiana*, showing characteristic cordate leaves with alternate arrangement; b. Tree 7, *E. bridgesiana*  $\times$  *E. viminalis*, bluish tinge; c. Tree 11, *E. bridgesiana*  $\times$  *E. viminalis*, green tinge with broad leaves; d. Tree 6, *E. bridgesiana*  $\times$  *E. viminalis*, green tinge with narrower leaves.

Fertile material was only evident in one tree ('Tree 7') during our visit in 2019 (Fig. 4), and the buds obtained at that time were arranged in 7's (typical of *E. bridgesiana*). Fruit collected from that same tree in 2017 were within the range of variation expected for *E. bridgesiana* (Fig. 5), however juvenile leaves were intermediate between this species and *E. viminalis* (see Fig. 3b).

Two sapling-stage individuals observed in 2019, Trees 1 and 7, were of upright form and to c. 8 m high. Tree 7 exhibited rough, compacted bark on the basal third of the trunk, with the upper trunk and branches smooth. This form is typical of similarly aged *E. bridgesiana*, though the upper smooth bark shedding in short ribbons above basal rough bark is more reminiscent of *E. viminalis*. All the juveniles recorded in 2017 and 2019 were single- or multiple-trunked plants with a gnarled appearance, scarcely exceeding 2 m high and not bearing any fertile material. They all appeared to arise from lignotubers (Fig. 5), a trait known in both *E. bridgesiana* and *E. viminalis*, and no doubt this permitted these plants to survive the frequent fire regime of the area. Regular resprouting following fire may help to explain the apparent lack of mature *E. bridgesiana* in 2017 or 2019, with this isolated population continually reduced to coppice growth from aging lignotubers struggling to produce fertile material between fire events.



Fig. 4. Adult lanceolate foliage of *Eucalyptus bridgesiana* × E. viminalis, showing 7-flowered inflorescences (Tree 7).



**Fig. 5.** *Eucalyptus bridgesiana* × *E. viminalis*; fruit collected in 2017 (Tree 7, left), and bulbous lignotuber (Tree 1) in 2019 (right).

# Herbarium investigations

Examination of herbarium specimens at NSW shows a confusing history of name use for *E*. sp. Howes Swamp Creek. However, most specimens could be accommodated in two groups: 1) typical *E. bridgesiana*, and 2) hybrids with *E. viminalis* (Table 1). The earliest specimens, collected by Doherty from '800 m W of *Putty Rd*', including the reference specimen *M.Doherty 26*, consist of only juvenile foliage, with the cordate, amplexicaul juveniles clearly blue-green, crenulate and soon alternating on the stem, typical of *E. bridgesiana*. The specimens are noted as coming from a 'clump of juveniles, all with immature leaves', and from Doherty's second collection in 1988 (*M.Doherty 27*) as a '*Population of juveniles and small adults (10 m) with sucker* growth. Very few adult trees. Scattered "mallee-like" juveniles'. The 7-flowered, ovoid buds and hemispherical fruits with a raised annular disc on *M.Doherty 27*, collected 3 years later than *M.Doherty 26*, also align well with *E. bridgesiana*. Consequently, *E.* sp. Howes Swamp Creek (M. Doherty 26) is here considered a taxonomic synonym of *E. bridgesiana*.

Primary collector and number	Initial identification	Collection date	Location	Buds/ fruit?	Juvenile leaves?	Hill determination c. 2000	Our determination
M. Doherty 26	<i>E. dalrympleana</i> subsp. <i>dalrympleana</i> changed to <i>E.</i> sp. Howes Swamp Creek	19/07/1985	Howes Swamp Creek, 800 m west of Putty Road,	z	~	E. wollemiensis ms.	E. bridgesiana
M. Doherty 27	<i>E. dalrympleana</i> subsp. <i>dalrympleana</i> changed to <i>E.</i> sp. Howes Swamp Creek	12/03/1988	Howes Swamp Creek, 800 m west of Putty Road,	~	~	E. wollemiensis ms.	E. bridgesiana
K.D. Hill 4169	E. viminalis	15/06/1992	Howes Swamp Creek, N side, 500 m W of Windsor Road	~	z	E. aff. viminalis	E. viminalis
K.D. Hill 4170	E. viminalis	15/06/1992	Howes Swamp Creek, N side, 500 m W of Windsor Road	z	~	E. aff. viminalis	E. viminalis
K.D. Hill 4167	E. wollemiensis	15/06/1992	Howes Swamp Creek, N side, 800 m W of Windsor Road	~	z	E. wollemiensis ms.	E. bridgesiana
K.D. Hill 4168	E. wollemiensis	15/06/1992	Howes Swamp Creek, N side, 800 m W of Windsor Road	Z	×	E. wollemiensis ms.	E. bridgesiana
K.D. Hill 5018	E. wollemiensis	15/01/1999	Howes Swamp Creek, N side, 500 m W of Windsor Road	~	<u> </u>	E. aff. viminalis	E. bridgesiana × viminalis
K.D. Hill 5019	E. wollemiensis	15/01/1999	Howes Swamp Creek, N side, 500 m W of Windsor Road	٨	Z	E. aff. viminalis	E. bridgesiana × viminalis
K.D. Hill 5073	E. wollemiensis	5/11/1999	Howes Swamp.	Z	Y	E. aff. viminalis	E. bridgesiana × viminalis
K.D. Hill 5648A	E. wollemiensis	30/11/2000	Howes Swamp.	Υ	Z	E. wollemiensis ms.	E. bridgesiana
K.D. Hill 5648B	E. wollemiensis	30/11/2000	Howes Swamp.	Y	Z	E. wollemiensis ms.	E. bridgesiana
K.D. Hill 5648C	E. wollemiensis	30/11/2000	Howes Swamp.	Z	Y	E. wollemiensis ms.	E. bridgesiana
K.D. Hill 5650	E. wollemiensis	30/11/2000	Howes Swamp.	Z	Y	E. wollemiensis ms.	E. bridgesiana
K.D. Hill 5649	E. wollemiensis	30/11/2000	Howes Swamp.	Z	Y	E. wollemiensis ms.	E. bridgesiana
R.L. Johnstone 2758	E. sp. aff. <i>viminalis</i>	19/05/2010	<ul> <li>c. 500 metres west of the Putty Road on Howes Swamp Creek (north side of swamp)</li> </ul>	~	z	I	E. bridgesiana × viminalis
G.P. Phillips 133	E. sp. aff. <i>viminalis</i>	21/09/2016	Howes Swamp Creek, on river flat on N side of creek c. 650 m from Putty Rd	×	Z	I	E. bridgesiana × viminalis
G.P. Phillips 132	E. sp. Howes Swamp Creek	21/09/2016	Howes Swamp Creek, on North side of creek c. 700 m from Putty Rd	×	Z	I	E. bridgesiana × viminalis
G.P. Phillips 343	E. sp. Howes Swamp Creek	27/07/2017	N edge of Howes Swamp Creek, c. 1 km W of Putty Rd	Z	~	I	E. bridgesiana
G.P. Phillips 342	E. sp. Howes Swamp Creek	27/07/2017	N edge of Howes Swamp Creek, c. 1 km W of Putty Rd	×	z	I	E. bridgesiana × viminalis

Table 1. Herbarium specimens and proposed determinations.

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Seed Source Collection	Seedling Specimen Reference No.	Harvest Date	Collector	Leaf Shape	Leaf Colour	Leaf Margin	Leaf Arrangement	Leaf Arrangement Our Determination
K.D. Hill 5018	NSW 438624	9/03/2000	Anon. s.n.	Lanceolate to 30 mm wide	Blue-green	Entire	opposite	E. bridgesiana × viminalis
	NSW 438626	9/03/2000	Anon. s.n.	Lanceolate	Green	Entire	opposite	E. bridgesiana × viminalis
	NSW 518106	5/05/2000	Anon. s.n.	Lanceolate	Blue-green	Entire	opposite	E. bridgesiana × viminalis
	NSW 446535	1/11/2000	Anon. s.n.	Narrow-lanceolate	Green	Entire	opposite	E. bridgesiana × viminalis
	NSW 446536	1/11/2000	Anon. s.n.	Lanceolate	Green	Entire	opposite	E. bridgesiana × viminalis
	NSW 1115673	2/04/2021	G.P. Phillips <i>s.n</i> .	Lanceolate with 1 branch of ovate	Grey-green	Entire	alternate	E. bridgesiana × viminalis
	NSW 1115674	2/04/2021	G.P. Phillips <i>s.n</i> .	Lanceolate to 25 mm wide	Grey-green	Entire	opposite	E. bridgesiana × viminalis
	NSW 1115675	2/04/2021	G.P. Phillips s.n.	Narrow-lanceolate	Grey-green	Entire	opposite	E. bridgesiana × viminalis
	NSW 1115676	2/04/2021	G.P. Phillips s.n.	Narrow-lanceolate	Grey-green	Entire	opposite	E. bridgesiana × viminalis
	NSW 1115677	2/04/2021	G.P. Phillips s.n.	Lanceolate	Grey-green	Entire	opposite	E. bridgesiana × viminalis
K.D. Hill 5648A	NSW 518122	17/07/2001	Anon. s.n.	Ovate	Blue-grey	Crenulate	alternate	E. bridgesiana
	NSW 518123	1/03/2002	Anon. s.n.	Ovate	Blue-grey	Crenulate	alternate	E. bridgesiana

Table 2. Herbarium specimens of cultivated seedlings. Specimens held at NSW and grown from wild source seed collected from plants attributed to E sp. Howes Swamp Creek.

Ken Hill identified his 1992 collections as potentially comprising two taxa, including specimens sourced from the same area '800 m W of Windsor Rd' as collected by Doherty. Hill identified his material by proposing the manuscript name *E. 'wollemiensis'* for the specimens morphologically similar to Doherty's (*K.D.Hill* 4167 and *K.D.Hill* 4168) and *E.* sp. aff. *viminalis* for other material from the site (*K.D.Hill* 4169 and *K.D.Hill* 4170). Both taxa are represented as a pair of specimens from a mature plant as well as a nearby juvenile. The specimens matching Doherty's collections again display juvenile foliage, buds and immature fruit typical of *E. bridgesiana*. Hill's *E.* sp. aff. *viminalis* specimens though, despite his initial thoughts, appear typical of *E. viminalis*, bearing obovoid fruit with an obliquely raised disc, inflorescences in umbels of 3, and green, sessile, narrow-lanceolate juvenile leaves opposite for many nodes. These specimens are also only noted as being '500 m W of Windsor Rd' which approximates our observations of the known *E. viminalis* stand.

Hill's specimens from 1999 (K.D.Hill 5018, K.D.Hill 5019, K.D.Hill 5073) were also initially labelled by Hill as *E. 'wollemiensis'* ms before later being re-determined by him to *E.* sp. aff. *viminalis*. These all show much broader lanceolate juvenile leaves than typically found in *E. viminalis* despite the more typical buds and fruit of that species. Seed propagated by Hill and lodged as juvenile plants at NSW (Table 2) show characteristics consistent with *E. bridgesiana* × *E. viminalis* (grown from *K.D.Hill* 5018) or *E. bridgesiana* (grown from *K.D.Hill* 5648A).

## **Growth trials**

Seedlings grown by us, also sourced from *K.D.Hill 5018*, found all progeny were attributable to *E. bridgesiana* × *E. viminalis* (Table 3, Fig. 6). At 12 months of age, these seedlings had deteriorated in health considerably with 5 of 16 dying and 9 of the remaining 11 mildly to heavily scale infested and not progressing into mature growth phases. Several individuals produced shoots from their lignotubers, producing a number of weak basal stems which in most cases rapidly died off. Three randomly selected plants were maintained for a further 12 months but showed no further development or maturation despite regular removal of scale and daily watering. Reduced vigour and continual death of shoots and resprouting from their bases are suggestive of a weak hybrid origin.

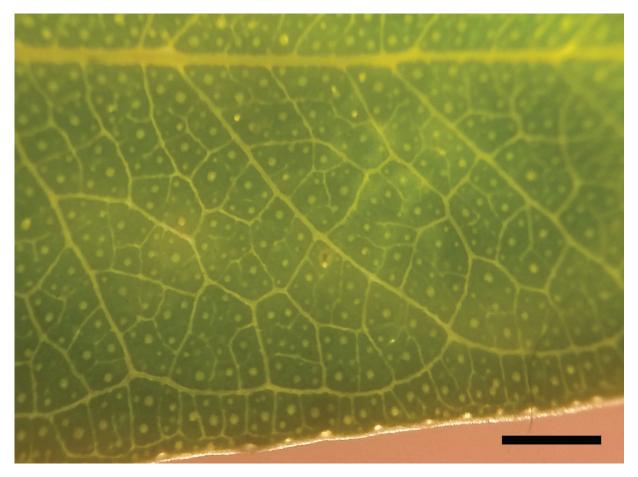


**Fig. 6.** Seedling variation from the single maternal genotype (*K.D.Hill 5018*) showing evidence of hybridisation. Plant 4 (a) shows leaves broader than expected for *E. viminalis* and broader than all other seedlings in the batch, while Plant 9 (b) shows branches producing ovate, disjunct foliage.

Table 3. Seedling trial measurements. Source material was held at the Australian PlantBank in cold storage at -20°C. A sample of 20 seeds was sown on water agar in petri dishes in February 2020 and germinated in a climate-controlled cabinet at 20°C with 12 hours of light daily. Seedlings were potted into standard potting mixture after germination at 22 to 30 days and transferred	to a heated glasshouse before finally moving into a polyhouse after 3 months. Seedlings were scored at 6 months of age. All plants had green, concolorous leaves that were sessile on the	lower nodes and with rounded bases on the upper stem. Plants marked * had scattered oil glands (the others were not measured).
Table 3. Seedling trial measurements. Source material was held at the Australi. 2020 and germinated in a climate-controlled cabinet at 20°C with 12 hours of lic	to a heated glasshouse before finally moving into a polyhouse after 3 month	lower nodes and with rounded bases on the upper stem. Plants marked * had

Height (mm)Nodes expandedPosition35613Opposite34715Opposite34715Opposite34512Opposite346512Opposite34613Opposite34614Opposite34713Opposite34511Opposite34713Opposite34713Opposite34514Opposite34511Opposite34713Opposite34714Opposite34713Opposite34714Opposite34714Opposite34714Opposite34414Opposite34414Opposite34414Opposite34414Opposite34414Opposite34414Opposite34414Opposite34414Opposite34414Opposite34414Opposite34414Opposite34414Opposite34414Opposite34414Opposite34414Opposite344140pposite344140pposite344140pposite344140pposite344140pposite344140pposite	No	Stem		Leaves	Lower Stem (lowest 6	st 6 nodes)			Upper Stem (above node 6)	e 6)	
356       13       Opposite         447       15       Opposite         395       12       Opposite & disjunct         315       12       Opposite & disjunct         400       13       Opposite & disjunct         315       11       Opposite & disjunct         315       11       Opposite & disjunct         315       11       Opposite         315       11       Opposite         315       11       Opposite         315       11       Opposite         315       13       Opposite         315       13       Opposite         315       13       Opposite         317       12       Opposite         318       11       Opposite         320       11       Opposite         330       13       Opposite		Height (mm)	Nodes expanded	Position	Lamina shape	Basal shape	Mean lamina width (mm)	Mean lamina length (mm)	Lamina shape	Mean lamina width (mm)	Mean lamina length (mm)
447       15       Opposite         395       12       Opposite & disjunct         395       12       Opposite & disjunct         465       12       Opposite & disjunct         315       11       Opposite         315       11       Opposite         315       11       Opposite         316       13       Opposite         375       13       Opposite         375       13       Opposite         375       13       Opposite         375       14       Opposite         375       13       Opposite         375       14       Opposite         375       11       Opposite         375       11       Opposite         375       11       Opposite         375       11       Opposite         375       14       Opposite         375       14       Opposite         375       14       Opposite         375       14	-	356	13	Opposite	narrow-lanceolate	amplexicaul	11	55	narrow-lanceolate	7	40
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465       12       Opposite & disjunct         400       13       Opposite & disjunct         315       11       Opposite         315       13       Opposite         317       13       Opposite         317       12       Opposite         317       12       Opposite         317       12       Opposite         310       11       Opposite         320       11       Opposite         320       12       Opposite	m	395	12	Opposite	lanceolate	amplexicaul	12	57	narrow-lanceolate	10	72
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417     13     Opposite       375     13     Opposite       375     13     Opposite       417     12     Opposite       365     14     Opposite       365     13     Opposite       330     11     Opposite       345     11     Opposite       345     11     Opposite       345     11     Opposite       345     14     Opposite	7	395	11	Opposite	narrow-lanceolate	amplexicaul	17	46	lanceolate	10	41
375     13     Opposite       417     12     Opposite       365     14     Opposite       365     14     Opposite       370     11     Opposite       345     11     Opposite       345     11     Opposite       345     11     Opposite       37     12     Opposite       397     12     Opposite       330     13     Opposite	*0	417	13	Opposite	lanceolate	rounded	14	55	narrow-lanceolate	11	63
417     12     Opposite       365     14     Opposite       365     14     Opposite       392     13     Opposite       330     11     Opposite       345     11     Opposite       345     11     Opposite       345     11     Opposite       345     11     Opposite       347     12     Opposite       347     12     Opposite       347     13     Opposite       347     14     Opposite       347     13     Opposite	*6	375	13	Opposite	lanceolate	rounded	16	50	lanceolate	10	33
365         14         Opposite           392         13         Opposite           330         11         Opposite           345         11         Opposite           345         11         Opposite           345         11         Opposite           345         11         Opposite           347         12         Opposite           397         13         Opposite	10	417	12	Opposite	lanceolate	rounded	19	68	lanceolate	12	56
392         13         Opposite           330         11         Opposite           345         11         Opposite           397         12         Opposite           397         12         Opposite           337         13         Opposite	11	365	14	Opposite	lanceolate	rounded	19	50	narrow-lanceolate	11	62
330         11         Opposite           345         11         Opposite           397         12         Opposite           432         14         Opposite <b>390 13</b> Opposite	12	392	13	Opposite	lanceolate	amplexicaul	I	I	narrow-lanceolate	12	52
345         11         Opposite           397         12         Opposite           432         14         Opposite           390         13         1	13	330	11	Opposite	lanceolate	amplexicaul	15	52	lanceolate	12	41
397         12         Opposite           432         14         Opposite           390         13	14	345	11	Opposite	broad-lanceolate	amplexicaul	19	57	lanceolate	10	27
432         14         Opposite           390         13         13	15*	397	12	Opposite	lanceolate	rounded	15	47	lanceolate	13	45
390	16	432	14	Opposite	narrow-lanceolate	amplexicaul	I	I	narrow-lanceolate	8	39
-	Mean		13				16.4	53.9		11.4	47.6

Visible oil gland frequency was also examined to provide additional supporting evidence of the hybrid nature in *E.* sp. Howes Swamp Creek. *Eucalyptus bridgesiana* (mean frequency 320 cm<sup>-2</sup>, scattered) and *E. viminalis* (mean frequency 900 cm<sup>-2</sup>, very numerous) differ considerably in oil gland density (Brooker and Nicolle 2013), and counts were undertaken of this trait on freshly grown seedlings. Despite most seedlings superficially resembling *E. viminalis*, a random selection of well-developed juvenile leaves from seven plants had a visible oil gland frequency in the range of 300 to 350 cm<sup>-2</sup> (Fig. 7), as would be expected from the 'scattered' oil gland frequency of *E. bridgesiana*.



**Fig. 7.** Visible oil gland frequency of a representative leaf (Plant 7) in seedlings grown from seed (from *K.D.Hill 5018*). This leaf shows a frequency of approximately 300 per cm<sup>2</sup> consistent with that seen in adult leaves of *E. bridgesiana*, despite superficial morphological resemblance to the most narrow-leaved juveniles of *E. viminalis*. Scale = 2 mm.

#### Discussion

Our investigations are now able to shed light on the convoluted taxonomic history of *E*. sp. Howes Swamp Creek (M.Doherty 26). Despite several names and taxonomic hypotheses being proposed over the years, the concept of *E*. sp. Howes Swamp Creek conflates two entities: 1) a small, disjunct and remnant stand of *E*. *bridgesiana*, which is now rare in the area and reduced to a few, stunted individuals after a history of repeated fire; and 2) a hybrid swarm of *E*. *bridgesiana*  $\times$  *E*. *viminalis*, comprising a number of plants of various forms and trait combinations, with evidence of back-crossing with the more prevalent *E*. *viminalis* which occurs upstream.

On review, the reference specimen for the phrase name *E*. sp. Howes Swamp Creek (M.Doherty 26), and several of the specimens included by Hill in the unpublished *E*. *'wollemiensis'* ms, are within the expected range of variation exhibited by *E*. *bridgesiana*. The combination of cordate to ovate, amplexicaul, blue-grey juvenile leaves with crenulate margins soon becoming disjunct on the stem is unique to this taxon among eucalypts in New South Wales and allows for positive identification from juvenile specimens alone. Other populations of *E*. *bridgesiana* have been linked to novel species previously, but when placed into context across the entire distribution of this species, their differences are questionable. For example, *E*. *saxicola* J.T.Hunter, a species described in 2001 based on material from exposed outcrops on Mount Canobolas in the central

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west of NSW, was differentiated from *E. bridgesiana* by its smaller stature, smaller juvenile leaves and slight differences in buds and fruit (Hunter 2001). However, *E. bridgesiana* exhibits wide variation in these features across its range and therefore populations exhibiting such subtle differences are insufficiently differentiated, potentially explainable by prevailing environmental conditions at specific sites (NSW Threatened Species Scientific Committee 2012; Slee *et al.* 2015). Both Slee *et al.* (2015) and Klaphake (2012) note that specimens from Howes Swamp Creek exhibiting similarly slight differences from typical *E. bridgesiana* do not fall outside of the expected variation of that species. The phrase name *E.* sp. Howes Swamp Creek (M.Doherty 26) should therefore be synonymised under that species. *Eucalyptus 'wollemiensis'* ms should be synonymised under *E. bridgesiana* × *viminalis* in part, given some specimens placed under that name by Hill are hybrids.

Examination of herbarium specimens collected over time and plants *in situ* suggest that the small population of *E. bridgesiana* at Howes Swamp Creek has persisted on the site despite its frequent fire history, though the evolutionary origin of this outlying population remains unknown. The nearest confirmed wild populations of *E. bridgesiana* occur some 34 km to the northwest in the Central Tablelands, so either a historical westerly range contraction to the drier, cooler higher altitudes of the tablelands has caused the isolation of this stand, or a chance dispersal to a novel habitat eastward has occurred. It is also possible that other small stands of *E. bridgesiana* remain undetected in the area given the large region of wilderness between these sites.

Hybrids are a relatively common feature in the eucalypts (e.g. Parsons and Kirkpatrick 1972; Potts and Reid 1983; Bennett 1995; Barbour et al. 2003; Hopper and McQuoid 2009), including parentage by E. viminalis which is known to hybridise with a number of other species including E. aggregata H.Deane & Maiden (Field 2008) and E. camaldulensis Dehnh. (Barson 1973). Some authors have argued for formal recognition of hybrids, particularly those where one or both parents have been removed through anthropogenic causes (e.g. Parsons and Zubrinich 2010), while others have investigated hybrid origins and questioned their conservation value. For example, Walker et al. (2009) analysed microsatellite variation in the West Australian E. × bennettiae D.J.Carr & S.G.M.Carr and suggested that the entity did not warrant conservation protection (although it currently still carries a P4 conservation code in that state). They examined key criteria in the context of Western Australian conservation policy to show that E. × bennettiae did not 'breed true' during germination experiments, was clonal and did not produce viable seed that maintained morphological features at the seedling stage (seedlings instead displaying segregation of parental characteristics), and hybrids were produced from a natural hybridisation process (not the result of anthropogenic disturbances). A similar conclusion can be applied to the *E. bridgesiana* × *E. viminalis* hybrid swarm at Howes Swamp Creek (but not E. sp. Howes Swamp Creek, synonymised here under E. bridgesiana), whereby seedling studies have shown wide variation in morphology, F1 plants observed in the field also show considerable variation, and a review of morphological traits evident in herbarium specimens collected over 35 years is explainable by the presence of this hybrid swarm.

The dominance of E. viminalis in Howes Swamp Creek, together with the restricted presence of E. bridgesiana in some locations, has in our opinion resulted in a population of hybrid forms showing varied morphology. This is particularly evident in the juvenile leaves of these hybrids, which on balance are more like *E. viminalis* than *E. bridgesiana*. We hypothesise that repeated back-crossing between these two postulated parent species has resulted in wide variation, and over time it is probable that the population will revert to more typical *E. viminalis*. From a conservation point of view, this means that little value is found in maintaining a conservation status for the hybrid entity as not only is it difficult to identify with its highly variable morphology, but the evidence of a post-zygotic barrier to reproduction resulting in reduced hybrid vigour and the continued back-crossing with *E. viminalis* means that decline in the population is a likely natural process. It is fortunate that the entire population lies within Wollemi National Park, as the only real threats to the remnant E. bridgesiana are likely to be repeated hot fires in quick succession and extended droughts as predicted through a changing climate. Despite this, most plants support well-developed lignotubers suggesting a history of resprouting following fire. Given the outcomes of our study, we propose that the endangered status of E. sp. Howes Swamp Creek (M.Doherty 26) be revoked, synonymising the reference specimen under E. bridgesiana, and recognising the wide morphological variation within the population at Howes Swamp Creek as a hybrid swarm between *E. bridgesiana* and *E. viminalis*.

#### Taxonomy

*Eucalyptus bridgesiana* R.T.Baker, *Proc. Linn. Soc. New South Wales* 23: 164 (1898). *Type*: New South Wales: Albury, 21 June 1897, *A.Andrews s.n.*; lecto: NSW 314589, designated by A.R.Bean, *Telopea* 12(3): 310 (2009).

*Eucalyptus stuartiana* var. *amblycorys* Blakely, *Key Eucalypts* 145 (1934); *E. bridgesiana* var. *amblycorys* (Blakely) Cameron, *Victorian Naturalist* 63: 41 (1946). *Type:* New South Wales: Tumut, January 1897, *E.Betche s.n.*; holo: NSW 315102; iso: HO 538775, *n.v.* 

*Eucalyptus saxicola* J.T.Hunter, *Telopea* 9(2): 403 (2001). *Type*: New South Wales: Central Tablelands: Mt Canobolas State Recreation Area, c. 14 km south-west of Orange, 33° 20' 11" S, 154° 58' 22" E, on margin of trachyte outcrop, 1200 m altitude, *J.T.Hunter* 8556, 2 June 1998; holo: NSW; iso: BRI, CANB, MEL, all *n.v.*, apparently not distributed.

Eucalyptus 'wollemiensis' ms, K.D. Hill; noted in Bell (2008) and Hager and Benson (2010), in part.

*Eucalyptus* sp. Howes Swamp Creek (M.Doherty 26), National Herbarium of New South Wales, PlantNET Flora of New South Wales Online https://plantnet.rbgsyd.nsw.gov.au/ (Accessed 17 May 2022).

**Specimens examined:** New South Wales: Central Coast: Howes Swamp Creek, 800 m west of Putty Road, Wollemi National Park, *M.Doherty 26*, 19 Jul 1985 (NSW 207054); Howes Swamp Creek, 800 m west of Putty Road, Wollemi National Park, *M.Doherty 27*, 12 Mar 1988 (NSW 207056); Howes Swamp Creek, N side, 500 m W of Windsor Road, *K.D.Hill 4167, L.A.S.Johnson & L.C.Stanberg*, 15 Jun 1992 (BRI *n.v.*, MEL 0231159A, NSW 256749); Howes Swamp Creek, N side, 500 m W of Windsor Road, *K.D.Hill 4167, L.A.S.Johnson & L.C.Stanberg*, 15 Jun 1992 (BRI *n.v.*, MEL 0231159A, NSW 256749); Howes Swamp Creek, N side, 500 m W of Windsor Road, *K.D.Hill 4168, L.A.S.Johnson & L.C.Stanberg*, 15 Jun 1992 (BRI *n.v.*, MEL 0231157A, NSW 256750); Howes Swamp, *K.D.Hill 5648A & L.C.Stanberg*, 30 Nov 2000 (NSW 449316); Howes Swamp, *K.D.Hill 5648B & L.C.Stanberg*, 30 Nov 2000 (AD *n.v.*, BRI *n.v.*, CANB *n.v.*, HO 529271, K *n.v.*, MEL *n.v.*, MO *n.v.*, NSW 449345); Howes Swamp, *K.D.Hill 5648C & L.C.Stanberg*, 30 Nov 2000 (CANB 584211.1, MEL *n.v.*, NSW 449348); Howes Swamp, *K.D.Hill 5649& L.C.Stanberg*, 30 Nov 2000 (CANB *n.v.*, MEL *n.v.*, NSW 449319); Howes Swamp, *K.D.Hill 5650& L.C.Stanberg*, 30 Nov 2000 (CANB *n.v.*, MEL *n.v.*, NSW 449348); Howes Swamp, *K.D.Hill 5649& L.C.Stanberg*, 30 Nov 2000 (CANB *n.v.*, MEL *n.v.*, NSW 449319); Howes Swamp, *K.D.Hill 5648A* (Howes Swamp), *Anon. s.n.*, 17 Jul 2001 (NSW 518122); Seedling grown from *K.D.Hill 5648A* (Howes Swamp), *Anon. s.n.*, 1 Mar 2001 (NSW 518123); N edge of Howes Swamp Creek, c. 1 km W of Putty Rd, *G.P.Phillips 343*, 27 Jul 2017 (NSW 999615).

#### Eucalyptus bridgesiana × E. viminalis

Eucalyptus 'wollemiensis' ms, K.D. Hill; noted in Bell (2008) and Hager and Benson (2010), in part.

*Eucalyptus* sp. Howes Swamp Creek, National Herbarium of New South Wales, PlantNET Flora of New South Wales Online https://plantnet.rbgsyd.nsw.gov.au/ (Accessed 17 May 2022), in part (as to the concept), but not including the reference specimen *M.Doherty 26*, which is *E. bridgesiana*.

Specimens examined: New South Wales: Central Coast: Howes Swamp Creek, N side, 500 m W of Windsor Road, K.D.Hill 5018 & M.Turton, 15 Jan 1999 (NSW 425911); Howes Swamp Creek, N side, 500 m W of Windsor Road, K.D.Hill 5019 & M.Turton, 15 Jan 1999 (AD n.v., BRI n.v., CANB 522143.1, DNA D0276752, HO 506652, K n.v., MEL 2068393A, MO n.v., NSW 425913, NY n.v., PERTH n.v.); Howes Swamp, K.D.Hill 5073& L.C.Stanberg, 15 Jan 1999 (BRI n.v., CANB n.v., NSW 437925); seedling grown from K.D.Hill 5018 (Howes Swamp Creek, N side, 500 m W of Windsor Road), Anon. s.n., 9 Mar 2000 (NSW438624); seedling grown from K.D.Hill 5018 (Howes Swamp Creek, N side, 500 m W of Windsor Road), Anon. s.n., 9 Mar 2000 (NSW438626); seedling grown from K.D.Hill 5018 (Howes Swamp Creek, N side, 500 m W of Windsor Road), Anon. s.n., 5 May 2000 (NSW 518106); seedling grown from K.D.Hill 5018 (Howes Swamp Creek, N side, 500 m W of Windsor Road), Anon. s.n., Nov 2000 (NSW446535); seedling grown from K.D.Hill 5018 (Howes Swamp Creek, N side, 500 m W of Windsor Road), Anon. s.n., Nov 2000 (NSW446536); c. 500 metres west of the Putty Road on Howes Swamp Creek (north side of swamp), R.L.Johnstone 2758, G.Errington, A.E.Orme, R.G.Coveny & J.P.Silk, 19 May 2010 (NSW 862275); Howes Swamp Creek, on North side of creek c. 700 m from Putty Rd, G.P.Phillips 132 & K.E. Willis, 21 Sep 2016 (NSW 988725); Howes Swamp Creek, on river flat on N side of creek c. 650 m from Putty Rd, G.P.Phillips 133 & K.E. Willis, 21 Sep 2016 (NSW 988728); N edge of Howes Swamp Creek, c. 1 km W of Putty Rd, G.P.Phillips 342, 27 Jul 2017 (CANB n.v., MEL n.v., NSW 999614); seedlings grown from K.D.Hill 5018 (Howes Swamp Creek, N side, 500 m W of Windsor Road), G.P.Phillips s.n., 2 Apr 2021 (NSW 1115673, NSW 1115674, NSW 1115675, NSW 1115676, NSW 1115677).

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