

SHORT COMMUNICATION

Elevation of *Eucalyptus gardneri* subsp. *ravensthorpensis*, and notes on relationships between obligate-seeder and resprouter members of subseries *Levispermae* (Myrtaceae)

Eucalyptus subseries *Levispermae* Brooker (subg. *Symphyomyrtus*, section *Bisectae*, series *Levispermae*; Brooker 2000; the *E. redunca* superspecies of Brooker & Hopper 1991) consists of nine terminal taxa with distributions in the wheatbelt and southern coastal regions of Western Australia (Figure 1). In the revision of the broader series *Levispermae* by Brooker and Hopper (1991), five species were recognised with four of these consisting of two subspecies each. Important characters for distinguishing taxa are growth form (related specifically to whether the taxon develops a lignotuber), mature leaf colour, glossiness and width, and operculum length, noting that there is little differentiation in fruit traits (Brooker & Hopper 1991). Currently recognised taxa, noting lignotuber states, are *E. gardneri* Maiden subsp. *gardneri* (obligate-seeder), *E. gardneri* subsp. *ravensthorpensis* Brooker & Hopper (obligate-seeder), *E. densa* Brooker & Hopper subsp. *densa* (obligate-seeder), *E. densa* subsp. *improcera* Brooker & Hopper (lignotuber-resprouter), *E. pluricaulis* Brooker & Hopper subsp. *pluricaulis* (lignotuber-resprouter), *E. pluricaulis* subsp. *porphyrea* Brooker & Hopper (lignotuber-resprouter), *E. varia* Brooker & Hopper subsp. *varia* (lignotuber-resprouter), *E. varia* subsp. *salsuginosa* Brooker & Hopper (lignotuber-resprouter) and *E. redunca* Schauer (lignotuber-resprouter). Elevation

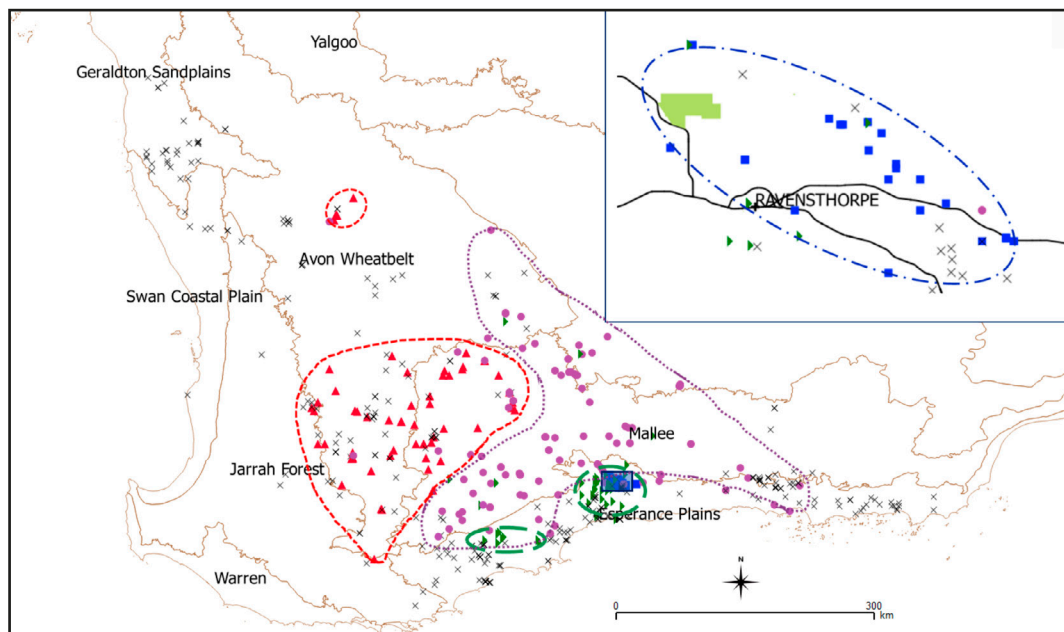


Figure 1. Distribution of specimens held in the Western Australian Herbarium as at 29 May 2019 and approximate range of *Eucalyptus ravensthorpensis* (■; dash-dot line), *E. gardneri* (▲; short-dash line), *E. densa* (●; dotted line), *E. improcera* (▶; long-dash line) and other taxa (×; all lignotuber-resprouter; *E. redunca*, *E. pluricaulis* and *E. varia*, using the taxonomy of Brooker & Hopper 1991) of the subseries *Levispermae*, in the context of IBRA Regions. The insert shows the Ravensthorpe Range area with major roads and conservation estate (shaded ■), to which *E. ravensthorpensis* is endemic.

of *E. improcera* (Brooker & Hopper) D.Nicolle & M.E.French, along with new combinations affecting *E. pluricaulis* and *E. redunca*, were recently proposed by French and Nicolle (2019), although they cited no new data supporting these novel taxonomic arrangements.

The taxonomic concept applied by Brooker and Hopper (1991) considered morphological differences and the degree of apparent reproductive isolation when in sympatry. Of particular relevance to this paper is their treatment as subspecies of those allopatric taxa with ‘minor morphological distinctions’. Thus, two subspecies with allopatric distributions were recognised in *E. gardneri* and *E. densa*, distinguished respectively primarily by differences in operculum length and growth form/lignotuber state.

In a study investigating whether lignotuber state differences (i.e. lignotuber-resprouter vs. obligate-seeder) between otherwise morphologically essentially identical eucalypt populations were representative of broader genetic distinctiveness, Gosper *et al.* (2019) sampled multiple individuals of multiple populations of all nine terminal taxa of *E.* subseries *Levispermae* using high-density, genome-wide markers. They found that the subseries as currently recognised was monophyletic, that taxa differing in lignotuber state formed discrete phylogenetic lineages, that all obligate-seeder terminal taxa were monophyletic and strongly differentiated from each other and all lignotuber-resprouter taxa, and hence that lignotuber state is a more strongly conserved character than other morphological differences such as leaf traits. Conversely, monophyly among many of the lignotuber-resprouter taxa within the subseries was not supported (Gosper *et al.* 2019).

Neither *E. gardneri* nor *E. densa* (*sensu lato* i.e. including *E. improcera*) were recovered as monophyletic at the species level in phylogenetic trees (Figure 2; Gosper *et al.* 2019). Gosper *et al.* (2019) found high levels of bootstrap support for monophyly of the ancestor of *E. gardneri* subsp. *ravensthorpensis* as one of the two earliest branches of *E.* subseries *Levispermae* (outgroups included *E. clivicola* and *E. phaenophylla* from the series *Levispermae*). The next branch, again with high support, separated hypothesized ancestors of the two remaining obligate-seeder members of the subseries (*E. gardneri* subsp. *gardneri* and *E. densa* subsp. *densa*) from those of the lignotuber-resprouter taxa, including *E. densa* subsp. *improcera*, *Eucalyptus gardneri* subsp. *gardneri* and *E. densa* subsp. *densa* were recovered as monophyletic with strong levels of support. These results were reflected in levels of divergence in Principal Coordinate Analysis (PCoA) of genetic variation.

The combination of consistent morphological trait differences and the genetic results described above lead us to conclude that the appropriate taxonomic treatment is for the two subspecies within *E. gardneri* and *E. densa* (*sensu lato*) to be recognised at the species level; as *E. gardneri*, *E. ravensthorpensis*, *E. densa*, and *E. improcera*. An argument could be made that the parphyly or polyphyly (depending on tree construction method) of *E. improcera* with some other lignotuber-resprouter members of the subseries, but with whom it is morphologically distinct (Gosper *et al.* 2019), also demands re-assignment of these taxa. However, the absence of clear correlation between morphological characters and genetic relationships among lignotuber-resprouter members of the subseries *Levispermae* (Gosper *et al.* 2019) renders taxonomic decisions concerning these entities problematic. Other studies using high-density genetic markers in eucalypts have similarly recovered non-monophyletic arrangements between populations of currently recognised terminal taxa (Jones *et al.* 2016; Rutherford *et al.* 2016), bringing into focus the challenge of integrating traditional and phylogenomic taxonomic approaches in *Eucalyptus*. Recent and ongoing speciation, incomplete lineage sorting, introgression and/or hybridisation have been reasons proffered for the lack of commonality between *Eucalyptus* genomic phylogenies and morphology-based taxonomic arrangements (Larcombe *et al.* 2015; Bradbury *et al.* 2016; Jones *et al.* 2016). Consequently, we tentatively retain *E. improcera* as a distinct entity pending further taxonomic research, supporting its elevation by French and Nicolle (2019).

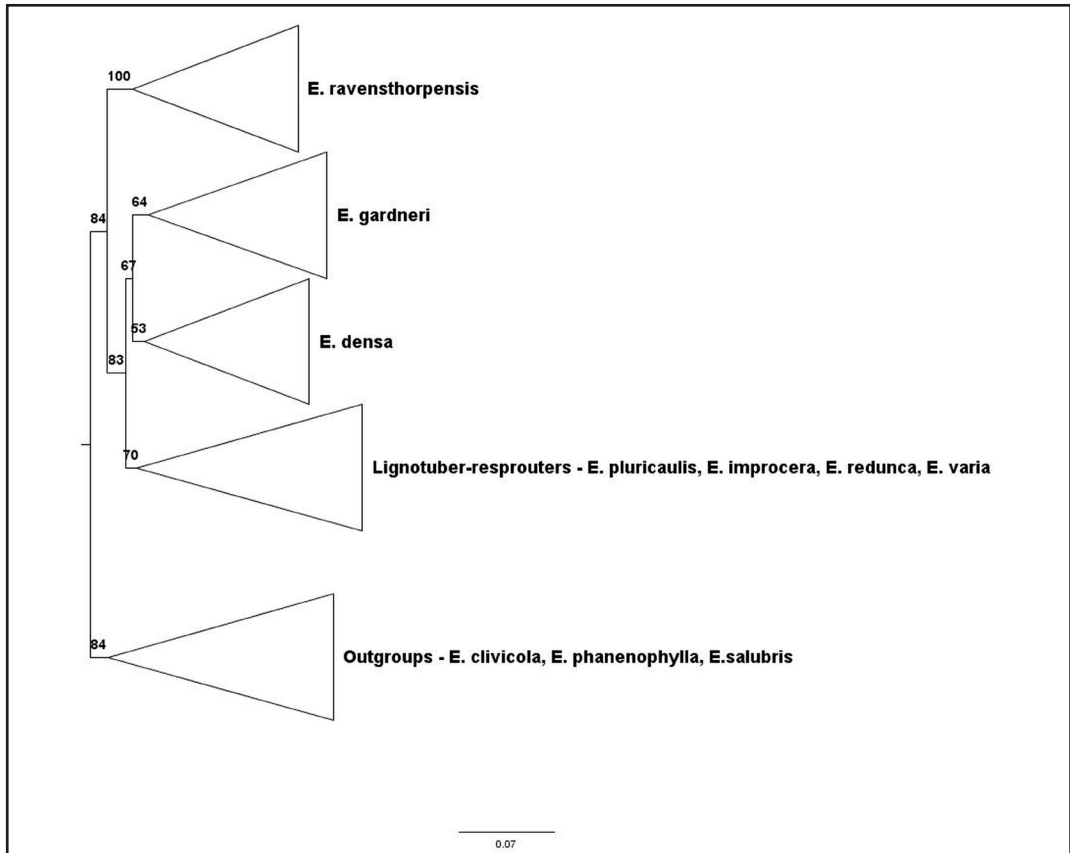


Figure 2. Simplified phylogenetic tree of *Eucalyptus* subseries *Levispermae* based on genomic DNA sequenced using DArTseq and produced using maximum likelihood (see Gosper *et al.* 2019 for more details). Numbers above branches show bootstrap percentages and triangles at the tips of the tree represent clades containing multiple samples of the same taxon or taxa, noting that for the clades ‘Outgroups’ and ‘Lignotuber-resprouters’ (using the taxonomy of Brooker & Hopper 1991 excepting *E. improcera*) not all taxa within each clade reconstructed as monophyletic at the taxon level.

The position of the *E. ravensthorpensis* clade as sister to all others in the subseries *Levispermae* in the phylogenetic trees presented by Gosper *et al.* (2019) supports the proposition of Brooker and Hopper (1991) that the species may be a relictual taxon within the subseries (Figure 2). *Eucalyptus ravensthorpensis* has shorter opercula than all other members of the subseries but similar to taxa of the broader series *Levispermae* (Brooker & Hopper 1991; Gosper *et al.* 2019) (Figure 3C). After the node separating the ancestor of *E. ravensthorpensis*, long opercula appear to have evolved in the subseries *Levispermae* and were subsequently retained in all other taxa. Further, *E. ravensthorpensis* is restricted to the Ravensthorpe Range; a centre of diversity for the series *Levispermae* and within the richest area for eucalypts nationally (Brooker & Hopper 1991; González-Orozco *et al.* 2014; Figure 1). Significantly for a putatively relictual taxon, the Ravensthorpe Range provides a complex mixture of ancient lateritic, greenstone, mafic and ultramafic uplands (OCBILs) with more recently derived colluvial slopes, with topographic intricacies producing fine-scale variation in water availability and disturbance regimes (Hopper 1979, 2009; Markey *et al.* 2012).

These four taxa have largely allopatric distributions in the Ravensthorpe area and north into the southern and central wheatbelt (Figure 1). Taxon, distribution and habitat descriptions, and diagnostic features, outlined in Brooker and Hopper (1991) remain valid.



Figure 3. *Eucalyptus ravensthorpensis*. A – habitat on breakaways of the Ravensthorpe Range; B – tree (obligate-seeder) habit in situ; C – leaf and bud morphology, noting the less elongate opercula than other members of the subseries *Levispermae*. Images of C.R. Gosper CRG 0008, S.M. Prober & C.J. Yates (B, C). Photographs by C.R. Gosper.

Eucalyptus ravensthorpensis* (Brooker & Hopper) C.R.Gosper & Hopper, *comb. et stat. nov.

Eucalyptus gardneri subsp. *ravensthorpensis* Brooker & Hopper, *Nuytsia* 8(1): 145 (1991). *Type*: Ravensthorpe Range, ca. 5 km E of Ravensthorpe, 800 m ENE of Highway 1 along Carlingup Road, then 800 m NNW to regenerating gravel pit [Western Australia], 10 April 1991, *S.D. Hopper* 7929 (*holo*: PERTH 07534701; *iso*: CANB 687856, MEL 2340062, NSW 595295).

Selected specimens: WESTERN AUSTRALIA [localities withheld for conservation reasons]: 7 Apr. 1995, M.I.H. Brooker 12204 W (AD, CANB, NSW, PERTH); 14 Mar. 2017, C.R. Gosper CRG 0008, S.M. Prober & C.J. Yates (PERTH) (Figure 3); 14 Mar. 2017, C.R. Gosper CRG 0009, S.M. Prober & C.J. Yates (PERTH); 14 Mar. 2017, C.R. Gosper CRG 0010, S.M. Prober & C.J. Yates (PERTH); 14 Mar. 2017, C.R. Gosper CRG 0011, S.M. Prober & C.J. Yates (PERTH); 7 Jan. 2008, L.S.J. Sweedman 7313 (K, PERTH).

Conservation status. Recently re-listed as Priority Four under Conservation Codes for Western Australian Flora (Smith & Jones 2018), under the name *E. gardneri* subsp. *ravensthorpensis*. Restricted in distribution to the Ravensthorpe Range and recognised as a short-range endemic taxon, although locally abundant in suitable habitat (Markey *et al.* 2012). Known from Overshot Hill NR (Markey *et al.* 2011; French & Nicolle 2019; although no PERTH specimens from this location; Figure 1). All populations occur in areas prospective for mining.

Acknowledgements

We thank Julia Percy-Bower for extracting specimen records from the Western Australian Herbarium database and for facilitating inspection of herbarium specimens, Bronwyn Macdonald for undertaking DNA extractions, and Nathan McQuoid for field checking of plant identifications.

References

- Bradbury, D., Grayling, P.M., MacDonald, B., Hankinson, M. & Byrne, M. (2016). Clonality, interspecific hybridisation and inbreeding in a rare mallee eucalypt, *Eucalyptus absita* (Myrtaceae), and implications for conservation. *Conservation Genetics* 17: 193–205.
- Brooker, M.I.H. (2000). A new classification of the genus *Eucalyptus* L'Her. (Myrtaceae). *Australian Systematic Botany* 13: 79–148.
- Brooker, M.I.H. & Hopper, S.D. (1991). A taxonomic revision of *Eucalyptus wandoo*, *E. redunca* and allied species (*E. series Levispermae* Maiden - Myrtaceae) in Western Australia. *Nuytsia* 8: 1–189.
- French, M. & Nicolle, D. (2019). *Eucalypts of Western Australia: the south-west coast and ranges*. (Scott Print: Perth.)
- González-Orozco, C.E., Thornhill, A.H., Knerr, N., Laffan, S. & Miller, J.T. (2014). Biogeographical regions and phytogeography of the eucalypts. *Diversity & Distributions* 20: 46–58.
- Gosper, C.R., Hopley, T., Byrne, M., Hopper, S.D., Prober, S.M. & Yates, C.J. (2019). Phylogenomics shows lignotuber state is taxonomically informative in closely related eucalypts. *Molecular Phylogenetics and Evolution* 135: 236–248.
- Hopper, S.D. (1979). Biogeographical aspects of speciation in the southwest Australian flora. *Annual Review of Ecology and Systematics* 10: 399–422.
- Hopper, S.D. (2009). OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. *Plant and Soil* 322: 49–86.
- Jones, R.C., Nicolle, D., Steane, D.A., Vaillancourt, R.E. & Potts, B.M. (2016). High density, genome-wide markers and intra-specific replication yield an unprecedented phylogenetic reconstruction of a globally significant, speciose lineage of *Eucalyptus*. *Molecular Phylogenetics & Evolution* 105: 63–85.
- Larcombe, M.J., Holland, B., Steane, D.A., Jones, R.C., Nicolle, D., Vaillancourt, R.E. & Potts, B.M. (2015). Patterns of reproductive isolation in *Eucalyptus* - a phylogenetic perspective. *Molecular Biology & Evolution* 32: 1833–1846.
- Markey, A., Kern, S. & Gibson, N. (2012). Floristic communities of the Ravensthorpe Range, Western Australia. *Conservation Science Western Australia* 8: 187–239.
- Markey, A., Wilkins, C., Allen, J., Kern, S. & Rathbone, D. (2011). *Report on the conservation status of 74 taxa from the Ravensthorpe Range*. (Department of Environment and Conservation: Kensington.)
- Rutherford, S., Wilson, P.G., Rossetto, M. & Bonser, S.P. (2016). Phylogenomics of the green ash eucalypts (Myrtaceae): a tale of reticulate evolution and misidentification. *Australian Systematic Botany* 28: 326–354.

Smith, M.G. & Jones, A. (2018). Threatened and Priority Flora list 5 December 2018. Department of Parks and Wildlife. <https://www.dpaw.wa.gov.au/plants-and-animals/threatened-species-and-communities/threatened-plants> [accessed 16 August 2018].

Carl R. Gosper^{1,2,4}, Tara Hopley¹, Margaret Byrne¹, Stephen D. Hopper³, Suzanne M. Prober² and Colin J. Yates¹

¹Biodiversity and Conservation Science, Department of Biodiversity, Conservation and Attractions, Locked Bag 104, Bentley Delivery Centre, Western Australia 6983

²CSIRO Land and Water, Private Bag 5, Wembley, Western Australia 6913

³Centre of Excellence in Natural Resource Management, The University of Western Australia, Foreshore House, Proudlove Parade, Albany, Western Australia 6330

⁴Corresponding author, email: carl.gosper@dbca.wa.gov.au