Nicotiana paulineana, a new Australian species in Nicotiana section Suaveolentes

Julia Bally AB, Claire E. Marks C, Hyungtaek Jung A,E, Fangzhi Jia D, Sally Roden A,B, Tal Cooper A,B, Ed Newbigin C and Peter M. Waterhouse ID A,B,D,F

A Centre for Agriculture and the Bioeconomy, Queensland University of Technology, Brisbane, Qld 4001, Australia.
B School of Biology and Environmental Science, Queensland University of Technology, Brisbane, Qld 4001, Australia.
C School of BioSciences, The University of Melbourne, Melbourne, Vic. 3010, Australia.
D School of Biological Sciences, The University of Sydney, Sydney, NSW 2006, Australia.
E Present address: School of Biological Sciences, The University of Queensland, Saint Lucia, Qld 4072, Australia.
F Corresponding author. Email: peter.waterhouse@qut.edu.au

Abstract. Nicotiana is found predominantly in the Americas and Australia, but also has representatives in Africa and the Pacific Islands. All native Australian Nicotiana species belong to section Suaveolentes. The number of species in this section is uncertain and subject to revision. An example of this uncertainty is the taxonomic status of a South Australian Nicotiana accession colloquially termed ‘Corunna’. Here, we report sequences for nuclear and plastid markers for N. sp. Corunna (D.E. Symon 17088) and accessions of two other Australian species, N. buridgeae and N. benthamiana. Phylogenetic comparison of these sequences with those of other members of Nicotiana places all three taxa in N. section Suaveolentes and shows that ‘Corunna’ represents a distinct phylogenetic lineage in a well supported clade along with N. goodspeedii, N. maritima, N. amplexicaulis and N. suaveolentes. Phenetic analysis of floral characters also supports recognition of N. sp. Corunna (D.E. Symon 17088) as a distinct species, which we describe here as Nicotiana paulineana Newbigin & P.M. Waterh., sp. nov. The enlarged molecular dataset described here contributes to a better understanding of taxonomic relationships within the section.

Keywords: Nicotiana, Suaveolentes, phylogenetic tree, plastid genome, classification, new species.

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Introduction

The nightshade or Solanaceae family is widely distributed across all temperate and tropical continents. The family contains many of the world’s most important agricultural species, such as potatoes, tomatoes, eggplants and tobacco. It also includes several important model species used in plant research, including Nicotiana benthamiana Domin and Petunia Juss. (Bomarely et al. 2012; Vandenbussche et al. 2016; Bally et al. 2018). The Solanaceae consists of ~100 genera and 2800 species and relationships within the family have been the subject of repeated phylogenetic revision (D’Arcy 1979; Olmstead et al. 2008).

Nicotiana L. is one of the larger genera in the Solanaceae that includes mainly annual, non-woody plants, and includes various species commonly referred to as ‘tobacco plants’. The genus Nicotiana includes 86 species in 13 sections distributed across tropical and temperate regions, with most being native to South and North America (Knapp et al. 2004). With currently ~35 species, section Suaveolentes Goodsp. is a monophyletic group of ancient allopolyploid origin and the largest of the Nicotiana sections (Leitch et al. 2008; Clarkson et al. 2010). Unlike other Nicotiana sections, Suaveolentes contains no American taxa and is native to Australia (26 recognised species), the Pacific (three species) and Africa (one species). Australian Suaveolentes taxa are widespread across the continent, especially in the arid zone (Knapp et al. 2004; Chase et al. 2018a).

The number of species in section Suaveolentes is currently subject to revision (Chase et al. 2018a). Misidentification of available N. section Suaveolentes seed and herbarium material is common, with estimates ranging from 23% to at least 50% (Marks et al. 2011a; Chase et al. 2018a). For instance, several Western Australian accessions previously described as N. umbratica N.T. Burb. appear to represent a recently described species, N. karijini M.W. Chase & Christenh. (Chase and Christenhusz 2018), and several inland South
Australian tobaccos previously attributed to *N. maritima* H.-M.Wheeler belong to the novel taxa *N. yandinga* M.W. Chase & Christenh. and *N. fauciicola* M.W.Chase & Christenh. (Chase et al. 2018b, 2018c).

As well as misidentified material, there are also undescribed species in *N. section Suaveolentes* (Chase et al. 2018a). One example is an accession related to *N. goodspeedii* H.-M.Wheeler that was collected by the noted Australian botanist D. E. Symon in 2004 and is currently named *Nicotiana* sp. Corunna (D.E.Symon 17088) Symon after the property (Corunna Station, near Iron Knob in South Australia) where it was found. A subsequent morphological study of *N*. sp. Corunna (D.E.Symon 17088) by Marks (2010), using plants grown from seed collected by Symon, concluded that it was sufficiently distinctive to be recognised as a new species. Here, we resolve the taxonomic status of *N*. sp. Corunna (D.E.Symon 17088) by further characterising plants grown from Symon’s original seed. On the basis of plastid and nuclear DNA sequences, we show that *N*. sp. Corunna (D.E.Symon 17088) is a distinct species, which we have called *N. paulineana*. We also provide sequence data for *N. burbidgeae* and *N. benthamiana*, two Australian species that have rarely appeared in phylogenetic treatments of *N. section Suaveolentes* (Chase et al. 2003; Clarkson et al. 2010).

**Materials and methods**

**Plant material and DNA sequencing**

DNA sequences for the *Nicotiana* species shown in Table S2 were obtained from GenBank (www.ncbi.nlm.nih.gov/genbank). Although *N. suaveolens* Lehm. and *N. exigua* H.-M.Wheeler are considered conspecific (Horton 1981), the sequences lodged in GenBank under these names for *matK*, *ITS* and the two *GS* paralogs are not identical, and thus the original species names were retained and have been treated here as independent taxa. The voucher material for these sequences should be re-examined to confirm their identities.

Twelve species of *Nicotiana*, including the undescribed *N*. sp. Corunna (D.E.Symon 17088) and *N. burbidgeae*, were propagated for at least two generations, confirmed to have the morphological features diagnostic of the taxon, and used for DNA extraction. Total genomic DNA was extracted from leaf tissues using the CTAB method (Clarke 2009) and amplified with a high-fidelity *Taq* polymerase and the primers described in Table S1 of the Supplementary material, using a touchdown cycling technique and annealing temperatures of 50–55°C. For species without existing sequence information, the nuclear DNA regions amplified were the internal transcribed spacer of *rRNA* (*ITS*), the long and short forms of the chloroplast-expressed glutamine synthetase (*GSL* and *GSS* respectively; Clarkson et al. 2010), RNA-dependent RNA polymerase 1 (*RDR1*; Bally et al. 2015) and alcohol dehydrogenase C locus (*ADHC*); and the plastid region amplified was *matK*. Because nuclear and chloroplast DNA sequences were not available for *N*. sp. Corunna (D.E.Symon 17088) or *N. burbidgeae*, regions of ribosomal *ITS* and *matK* from these accessions, and also from *N. benthamiana*, were amplified and sequenced (Table S2). Cycle sequence reactions, performed with BigDye Terminator (ver. 3.1, Applied Biosystems) at suggested cycling conditions, were purified with an ethanol and EDTA precipitation. After purification, the amplified fragments were run on a Life Technologies 3500 Genetic Analyser at the Central Analytical Research Facility Genomics Laboratory at the Queensland University of Technology. Analysis of output chromatograms and further preliminary sequence editing was conducted using Geneious (ver. R11, Biomatters, New Zealand, see www.geneious.com; Kearse et al. 2012).

**Sequence alignment and phylogenetic analyses**

Gene sequences were aligned (Fig. S1 of the Supplementary material) using MUSCLE (ver. 3.8.31, see http://www.drive5.com/muscle/; Edgar 2004), followed by manual adjustments in BioEdit (ver. 7.2.6, see https://bioedit.software.informer.com/). For concatenation, the sequences were appended in the following order: *ITS, matK, GSL, GSS, RDR1* and *ADHC*. The Akaike information criteria in ModelFinder in IQ-TREE (ver. 1.5.4, see http://www.iqtree.org/; Kalyaanamoorthy et al. 2017) and jModelTest2 (ver. 2.1.10, see https://github.com/ddarriba/jmodeltest2/; Darriba et al. 2012) were used to estimate the best-fit substitution models. Model selection and the parameters used are described in Table S3. Phylogenetic analyses of individual and concatenated gene sequences were based on maximum likelihood implemented by a rapid and effective stochastic algorithm in IQ-TREE (Trifinopoulos et al. 2016) including partition files. Additional phylogenetic trees for concatenated data of all six genes were built through Bayesian inference as implemented in MrBayes (ver. 3.2.6, see https://github.com/NBISweden/MrBayes/; Ronquist et al. 2012) including partition files. The final consensus trees were displayed using FigTree (ver. 1.4.3, see https://github.com/rambaut/figtree/releases/tag/release_1_3/).

**Morphological assessment of flowers and phenetic analysis**

Marks et al. (2011a) reported measurements of 21 floral character states from a range of *N. section Suaveolentes* taxa, with each measurement being based on a minimum of 10 biological replicates. Measurements for selected taxa were extracted from those reported in this paper and data matrices of floral characters were subject to principal-component analysis (PCA) using R (ver. 3.5.0, R Foundation for Statistical Computing, Vienna, Austria) and the package factoextra (ver. 1.0.3, see https://CRAN.R-project.org/package=factoextra/).

**Results**

**Phylogenetic analyses**

A maximum-likelihood analysis (Fig. 1) was performed using the concatenated *ITS* and *matK* sequences for *N. burbidgeae*, *N. benthamiana* and *N*. sp. Corunna (D.E.Symon 17088), and equivalent sequences from other *Nicotiana* taxa and from the Australian genus *Anthocercis* Labill. (Solanaeae: Anthocercideae) as the designated outgroup (Clarkson et al. 2010). The trees produced with *ITS* or *matK* sequences alone are shown in Fig. S1 and S2. For the concatenated tree, the total number of nucleotides used was 2213, of which 406 were
variable. *Nicotiana* formed a well supported clade made up of several lineages and the branching pattern shown in Fig. 1 was consistent with previous analyses of this genus (e.g. see Clarkson et al. 2010). The branching pattern of the ITS tree was like that of the concatenated tree but the *matK* tree had fewer resolved nodes. All trees placed members of *N.* section *Suaveolentes* in a well supported lineage that included *N.* *benthaliana,* *N.* burlbidgeae and *N.* sp. Corunna (D.E. Symon 17088). *Nicotiana benthaliana* was sister to *N.* excelsior (J.M.Black) J.M.Black (bootstrap support (BS) = 100%) and *N.* *excelsior* (J.M.Black) J.M.Black (bootstrap support (BS) = 100%). *N.* *excelsior* was sister to *N.* *umbratica* and *N.* *fragrans* in a well supported lineage that included *N.* *excelsior* and its synonym *N.* *exigua*.

To further confirm *N.* sp. Corunna (D.E.Symon 17088) as a distinct species, additional nuclear sequences were obtained. Species in the allopolyploid *N.* section *Suaveolentes* retain both parental copies of the nuclear-encoded, chloroplast-expressed glutamine synthetase, and the paralogs, called *GSL* and *GSS,* have previously been used to determine phylogenetic relationships (Clarkson et al. 2010). As well as *N.* sp. Corunna (D.E.Symon 17088), *GSL* and *GSS* sequences were obtained for *N.* burlbidgeae, *N.* benthaliana and *N.* *roslata* (S.Moore) Domin and added to the existing *N.* section *Suaveolentes* sequence dataset (Table S2). Regions of a further two genes, *RDR1* and *ADHC,* were either sequenced from these species or retrieved from GenBank. Most species in *N.* section *Suaveolentes* appear to have retained only one of the parental copies of these genes (Kelly et al. 2013; Bally et al. 2015, 2018). Consistent with this, there were no polymorphisms observed in the amplified *ADHC* and *RDR1* products for any accession. The sequences of all six gene regions (*ITS, matK, GSL, GSS, RDR1* and *ADHC*) were used to generate phylogenetic trees for each individual gene region (Fig. S1–S6) and for a concatenation of all six (Fig. 2); their counterpart sequences from *Anthocercis gracilis* Benth., *Anthocercis sylvicola* T.D.Macfarl. & Ward.-Johnson, *Symonanthus bancroftii* (F.Muell.) Haegi or *N.* tabacum L. and *N.* sylvestris Spég. were used as outgroups, depending on availability. As previously encountered in phylogenetic trees of members of the *N.* section
Suaveolentes using different sequence datasets (Clarkson et al. 2010; Marks et al. 2011a), the patterns from the different gene-region sequences had several conflicting branches. Nevertheless, in each tree, with one exception, *N*. sp. Corunna (D.E.Symon 17088) was distinct from other members of *N*. section Suaveolentes. On the basis of the ADHC sequences, *N*. sp. Corunna (D.E.Symon 17088) was not distinct from *N*.burbidgeae. Using the tree generated from the concatenated sequences, among *N*. section Suaveolentes, the African species *N*. africana Merxm. and the New Caledonian species *N*. fragrans Hook. were sister to a well supported clade that contained all the Australian members. Most nodes in the Australian Suaveolentes clade were poorly supported and only two clades, being composed of more derived species, were well resolved. Species in these two groups generally have fewer chromosomes than do other members of the section. In Fig. 2, these clades are labelled A (six species; BS = 81%, posterior probability (PP) = 0.99) and B (4 species; BS = 99%, PP = 1). Clade A and Clade B are well supported as sisters (BS = 100%, PP = 1) in the tree. *Nicotiana* sp. Corunna (D.E.Symon 17088) forms a clade with *N*. goodspeedii, *N*. maritima, *N*. exigua, *N*. amplexicaulis N.T. Burb. and *N*. suaveolens. Although both are placed in Clade A, *N*. suaveolens and its synonym *N*. exigua do not cluster together. Clade B contains *N*. excelsior, *N*. rosulata, *N*. rotundifolia Lindl., and *N*. velutina H.-M.Wheeler.

Phenetic analysis of floral characters

Because DNA-based phylogenies pointed to *N*. sp. Corunna (D.E.Symon 17088) being a distinct species, a phenetic analysis of flowers was performed to obtain further evidence for it being a new species and to find characters that could be potentially useful in its identification. A PCA biplot (Fig. 2, inset) was constructed using *N*. sp. Corunna (D.E.Symon 17088) and the three species (*N*. goodspeedii,
*Nicotiana* maritima and *N. velutina*) that overlap its geographic distribution (Fig. 3) and with its sequence-based cladistic sister, *N. amplexicaulis*. *Nicotiana* sp. Corunna (D.E. Symon 17088) flower characters formed a cluster that was well separated from *N. goodspeedii*, *N. velutina* and *N. amplexicaulis*, and predominantly separated from *N. maritima*. *Nicotiana* sp. Corunna (D.E. Symon 17088) was readily distinguished from *N. goodspeedii*, by its shorter stamens, smaller floral tubes and calyx, and thinner corollas; it was distinguishable from *N. velutina* by its shorter calyx length and narrower corolla limb diameter. A PCA that uses all the species described in Marks et al. (2011) is shown in Fig. S7.

**Discussion**

The status of a potential new species, namely, *N. sp. Corunna* (D.E. Symon 17088) within *N. section Suaveolentes*, has remained unverified for many years, predominantly because of a lack of sequence information. This lack of information has been redressed by determining the ITS, matK, GSL, GSS, RDR1 and ADHC sequences from *N. sp. Corunna* (D.E. Symon 17088) and comparing these sequences with their counterparts from members of the *N. section Suaveolentes*. The new sequence information identifies *N. sp. Corunna* (D.E. Symon 17088) as a distinct terminal taxon.

Three well recognised members of *N. section Suaveolentes* (*N. maritima*, *N. goodspeedii* and *N. velutina*) have distributions that intersect with *N. sp. Corunna* (D.E. Symon 17088); however, of the three, only *N. goodspeedii* has the same chromosome number (*n* = 16) as does *N. sp. Corunna* (D.E. Symon 17088) and none has flowers that are identical to those of *N. sp. Corunna* (D.E. Symon 17088), as demonstrated in the PCA. *Nicotiana maritima* has recently been recircumscribed following recognition of a new species, *N. yandinga* (Chase et al. 2018b), that occurs in the vicinity of *N. sp. Corunna* (D.E. Symon 17088) (Fig. 4A). However, *N. yandinga* has features, such as indumentum and a genome of 21 chromosome pairs (Chase et al. 2018b), that distinguish it from *N. sp. Corunna* (D.E. Symon 17088). Altogether, this provides strong evidence that *N. sp. Corunna* (D.E. Symon 17088) merits recognition as a new species that we name as *N. paulineana*, sp. nov., and describe below. This posthumously fulfills an ambition of the highly respected Australian plant taxonomist, David Symon. His obituary (Barker 2013) listed several projects.

![Fig. 3. *Nicotiana paulineana* showing phyllotaxis, leaf form, flower structure, capsule and seed. Photograph inset: flower showing deeply cleft corolla lobes and approach herkogamy.](image-url)
that he regarded as unfinished, one of which was obtaining evidence for the recognition of *N*. sp. Corunna (D.E.Symon 17088) as a new species.

**Taxonomy**

*Nicotiana paulineana* Newbigin & P.M.Waterh., sp. nov.

Type: Cultivated. Victoria. Melbourne University, Parkville, glasshouse on Natural Philosophy Building, 25 June 2007, C.E.Marks 299 (holo: MELU D106463). Plants glabrous, erect, annual, 0.4–1 m high. Initially single-stemmed, commonly developing several branched stems. Seedlings with cotyledons 6–7 mm long. Basal leaves rosulate, petiolate, attenuate, 10–30 cm long. Eglandular trichomes with one single gland cell on the calyx. Panicles loosely decompound, major branching long, rapidly ascendant. Calyx 5–7 mm long, appressed to tube. Corolla slightly zygomorphic, lobes emarginate, spreading; corolla limb lobes pure white inside, with a green to yellow vein running down the back of each lobe; floral tube broadening above calyx, 15–25 mm long exclusive of limb, 2–3 mm wide, often purplish. Stamens all included, 4 anthers at or close to one level, near mouth of corolla, anther of 5th stamen 2–3 mm lower; filaments inserted in lower half of corolla. Capsule not constricted or thickened, no seeds retained. Seeds reinform, sinuous seeds testa, 0.9 mm long, brown. Chromosome number 16 pairs.

**Notes**

This species can be distinguished from *Nicotiana goodspeedii* and *N. maritima* by its narrower leaf shape and more deeply cleft corolla lobes (Fig. 3) and from *N. maritima* by its lack of a woolly indumentum.

The holotype is a flowering specimen taken from the plant used by Marks *et al.* (2011b) to assess the chromosome number. Additional notes on the specimen lodged at The University of Melbourne Herbarium (MELUD106464) say ‘Hydroponically grown for chromosome count, actual plant used for count…’, ‘cultivated from seed supplied by David Symon (AD) with provenance’, ‘grown from Symon 17088’. David Symon indicated to Claire Marks that this seed lot came from Corunna Station and has the provenance described for D.E. Symon s.n. (AD 169037), a specimen grown from a wild collection from Corunna Station.

**Distribution and habitat**

The five known collection locations of *N. paulineana* are all from South Australia within a 50-km radius south of Port Augusta, and its habitat is primarily vegetated natural and

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**Fig. 4.** Distribution of *Nicotiana* species in Groups A and B of Fig. 2B. A. Distribution of *N. paulineana* and *N. yandinga* based on records in the Atlas of Living Australia (ala.org.au). B. Distribution of *N. amplexicaulis*, *N. velutina*, *N. goodspeedii*, *N. maritima*, *N. suaveolens* and *N. rotundifolia* based on Burbidge (Burbidge 1960), Horton (Horton 1981), Chase (Chase *et al.* 2018b), and records in the Atlas of Living Australia (ala.org.au). Overlapping distributions are denoted by colours (black, green and purple) and, in the magnified region (A), the locations of *N. yandinga* and *N. paulineana* are shown as red and blue pins respectively.
semi-natural terrestrial vegetation in coastal South Australia. All collections have been made in association with drainage lines and usually below rocky outcrops. Recorded growing in association with the native species Allocausarina sp., Atriplex cinerea, Austrostipa nitida, A. scabra subsp. scabra, Callitris glaucophylla, Cassinia sp., Cheilanthes lasiophylla, Dodonaea sp., Encyphaena tomentosa var. tomentosa, Eremophila glabra subsp. glabra, Erodium crinitum, Eucalyptus camaldulensis, E. socialis, Esocarpos sp., Geranium sp., Goodenia havelandii, Heliotropium asperrum, Hydrocotyle trachycarpa, Isolepis congria, Lemooria burkittii, Levenhockia dubia, Milloia perpusilla, Myoporum sp., Sida sp., Spathyphyllum sp., Some sites are noted to have numerous, Scaevola spinescens, Sida sp., Vittadina sp., Wahlenbergia gracilenta and Zygocephalum sp. The presence of these weeds indicates a degradation of habitat for this localised species.

Etymology
This species is named after Professor Pauline Yvonne Ladiges AO FAA, a botanist distinguished for her studies on the systematics, biogeography and ecology of Australian plants, particularly the eucalypts, and who has greatly contributed to the study of Australian *Nicotiana*.

Other specimens examined
SOUTH AUSTRALIA: Mt Remarkable National Park, Carrichtera annua, Conyza sp., Echium plantagineum, Galenia pubescens, Hypochaeris glabra, Lactuca sp., Marrubium vulgare, Solanum elaeagnifolium, Trifolium angustifolium, T. arvense, Verbascum sp. and Vulpia myuros f. myuros, The authors thank Dr Melodina Fabillo (Queensland University of Technology) for her assistance with MrBayes analyses, Assoc. Prof. Mike Bayly (University of Melbourne) for helpful discussions and advice, and Tanya Hoolihan for drawing the botanical illustration in Fig. 3.

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