

Molecular phylogenetics reveals a new species of *Prostanthera* from tropical Queensland with links to more southerly taxa

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Abstract

Prostanthera eungella B.J.Conn & K.M.Proft (Lamiaceae) is described as a new species from the South Kennedy botanical region of northern Queensland. Concatenated nuclear (ETS) and chloroplast (*trnH-psbA*) sequence data for 38 species of *Prostanthera* were analysed using maximum-likelihood and Bayesian-inference methods. These combined data recovered *P. eungella* as part of a polytomy that included *P. galbraithiae*, *P. howelliae*, and a *P. tallowa* + *P. lasianthos* clade. A detailed description, photograph of the holotype specimen, and distribution map of *P. eungella* are provided.

Introduction

The Eungella plateau, c. 80 km west of Mackay (Eungella 21° 7' 52.3"S, 148° 29' 30.5"E), Queensland (Australia), is an isolated, Carboniferous massif comprising intrusions of the Urannah volcanic complex. Reaching elevations of 950–1259 m, it has an annual average precipitation of 2240 mm, rarely falling as snow on the higher peaks. Vegetation changes rapidly from complex lowland rainforest in the east of the plateau through to grassy eucalypt woodland in the west.

There is growing evidence that the Eungella plateau represents a significant area of biotic endemism (Kitching and Ashton 2013, Low 1993). Many plant species are restricted to the plateau and its surrounds, with some endemic plants associated with endemic fauna (Forster and Sankowsky 1995), whereas others reach their geographic limit in this region (Rossetto *et al.* 2007).

The taxonomic status and phylogenetic relationship of plants of *Prostanthera* (Lamiaceae: Westringieae) occurring in the Eungella district, South Kennedy botanical region (*sensu* Anonymous 1975) of Queensland, have remained unclear since first collected in 1992. These collections were gathered from open eucalypt forests and from the margin of rainforest. They have been tentatively identified as *Prostanthera lasianthos* Labill., presumably based on their toothed leaves which are superficially similar. However, their inclusion in that geographically widespread, morphologically variable species complex of *P. lasianthos* represents a disjunction of more than 700 km north of the most northerly populations of this species. Although collections from near Eungella were morphologically distinct from any other known species of *Prostanthera*, its affinities were unclear because morphological similarities do not always co-vary with genetic differences. For example, a

recent molecular phylogeny of *Prostanthera* (Wilson *et al.* 2012) found that *P. tallowa* B.J.Conn is sister to *P. lasianthos*, even though it has certain morphological features that suggested a strong similarity to *P. linearis* R.Br. (Conn and Wilson 2012). Therefore, both chloroplast and nuclear DNA data were used to investigate the affinities of the plants of *Prostanthera* occurring in the Eungella region.

Materials and methods

Taxon sampling

Forty-eight taxa of *Prostanthera*, representing 44 published species, were sampled for genetic analysis (Table 1), with 26 of these sequences being new to this study. The selection of the two outgroup species (*Hemigenia purpurea* R.Br. and *Westringia longifolia* R.Br.) was based on the known sister relationship between these species and *Prostanthera* (Wilson *et al.* 2012). The genetic samples were either collected specifically for this study, dried in silica gel and stored at 4°C, or were taken from dried herbarium vouchers. The *Prostanthera* species included were based on Wilson *et al.* (2012), as well as other unpublished analyses by these authors, to represent the known phylogenetic and morphological diversity of the genus.

Acquisition of sequences

Sequences stored in GenBank (<http://www.ncbi.nlm.nih.gov/genbank/>), as provided by Wilson *et al.* (2012), were included to supplement the sequences extracted in this study (Table 1). Silica dried leaf material was used as a source for plant cellular DNA extraction using the DNeasy Plant Mini kit protocol (Qiagen, Hilden, Germany). A MyCycler thermal cycler (BioRad Laboratories Inc., Australia) was used for PCR amplification. A reaction mix for PCR consisted of 2.5 µL of 10X NH₄ buffer, 1.2 µL of 2.4mM MgCl₂, 0.5 µL of each 0.25mM dNTP, 0.5 µL of each primer, 0.25 µL of BIOTAQ™ (Bioline, www.bioline.com) and 18.05 µL of H₂O. Genomic DNA (1 µL) was added to complete a reaction volume of 26 µL. Non-coding chloroplast sequence was amplified from the *trnH-psbA* intergenic spacer using primers *trnH* (GUG) (Tate and Simpson 2003) and *psbAF* (Sang *et al.* 1997). The *trnH-psbA* intergenic spacer was chosen because its relatively high proportion of informative sites means that it is commonly used in phylogenetic analyses at the interspecific level (Shaw *et al.* 2005). The fast-evolving non-coding nuclear external transcribed spacer (ETS) was amplified using the 18S-E (Baldwin and Markos 1998) and ETS-PROS2 (Wilson *et al.* 2012) primers. The PCR protocol used similar methods to those used by Wilson *et al.* (2012); although annealing temperature was set to 53°C for amplification of the *trnH-psbA* intergenic spacer. Clean-up and sequencing reactions were performed by Macrogen (Seoul, Korea), using BigDye® Terminator v3.1 Cycle Sequencing Ready Reaction Kits and an Applied Biosystems 3730xl DNA Analyzer (ABI Biosystems, www.appliedbiosystems.com).

Double-stranded DNA consensus sequences were assembled using Sequencher® 4.5 (Gene Codes Corporation). A base in the ETS marker that was ambiguous due to overlapping base peaks was coded as polymorphic rather than uncertain. MUSCLE (Edgar 2004) on the CIPRES portal (Miller 2010) was used for sequence alignment after which BioEdit 5.0.9 (Hall 1999) was used for final editing. A concatenated alignment of the *trnH-psbA* intergenic spacer and ETS datasets was completed using Sequence Matrix (Vaidya *et al.* 2011).

Analyses

Maximum likelihood (ML) analyses were performed using RAxML-HPC2 version 8 (Stamatakis 2006, 2014) and Bayesian inference analyses were performed with MrBayes version 3.2.4 (Huelsenbeck and Ronquist 2001) on the CIPRES portal (Miller 2010). RAxML implements the GTR+Γ model in ML analyses. Maximum Likelihood analysis used a 1000-replicate bootstrap to estimate nodal support. For Bayesian analyses, substitution models for each partition were unlinked, and the number of substitution types was set to 6 and the rate variation across sites was set as gamma-distributed. Default program settings specified *a priori* probabilities for other parameters. For each analysis, two independent Metropolis coupled MCMC were run, each with one heated and three cold chains run, for 5 million generations and sampled every 1000th generation. Log likelihood scores were plotted using Tracer v1.6 (Rambaut *et al.* 2014) to estimate the burn-in duration (30000 generations). A majority-rule consensus constructed from the total 10000 trees from Bayesian analysis, as well as bootstrap values from ML analyses, were visualized using FigTree v1.4.0. (<http://tree.bio.ed.ac.uk/>). Posterior probability (PP) values of ≥ 95% (Larget and Simon 1999) and bootstrap (BS) values of ≥ 75% were considered as significant support.

Table 1. Chloroplast (*trnH-psbA*) and nuclear (ETS) markers amplified for species of *Prostanthera*, *Hemigenia purpurea* and *Westringia longifolia* (Westringiaceae: Lamiaceae). GenBank accessions are given for each marker. *H* = *Hemigenia*; *P* = *Prostanthera*; *W* = *Westringia*; * = new accessions for this study

Taxon	Collection details	<i>trnH-psbA</i>	ETS
<i>H. purpurea</i>	Wilson 122	–	JX047602
<i>P. albohirta</i> *	Ford 6174	KU563336	KU532856
<i>P. althoferi</i> *	Wilson 271	KU563337	KU532857
<i>P. althoferi</i> *	Wilson 360	KU563338	KU532858
<i>P. ammophila</i> *	Te 854	KU563339	KU532859
<i>P. askania</i>	Anon. AB873115	–	JX047626
<i>P. athertoniana</i> *	Ford 1835	KU563340	KU532860
<i>P. baxteri</i> *	Wilson 380	KU563341	KU532861
<i>P. caerulea</i>	Anon. AB790000	–	JX047647
<i>P. campbellii</i> *	Perkins WA101	KU563342	KU532862
<i>P. canaliculata</i> *	Hislop, Davis, Mills 178–7	KU563343	KU532863
<i>P. centralis</i> *	Wilson 417	KU563344	KU532864
<i>P. clotteniana</i> *	Ford 5982	KU563345	KU532865
<i>P. cruciflora</i>	Wilson 13	–	JX047631
<i>P. densa</i>	Wilson 173	KF145103	KF112049
<i>P. denticulata</i>	Wilson 241	–	JX047679
<i>P. eckersleyana</i> *	Horn 2508	KU563346	KU532866
<i>P. eungella</i> *	McDonald 5131	KU563347	KU532867
<i>P. galbraithiae</i>	Conn 5222	–	JX047667
<i>P. granitica</i>	Wilson 162	KU563349	JX047639
<i>P. hindii</i>	Washington 98/3	–	JX047645
<i>P. hirtula</i>	Wilson 170	–	JX047648
<i>P. howelliae</i>	Wilson 135	–	JX047644
<i>P. laricoides</i> *	Edinger 6582	KU563351	KU532868
<i>P. lasianthos Grampians</i> *	Conn 5311	KU563352	KU532869
<i>P. lasianthos Mt Field</i> *	Henwood 864	KU563353	KU532871
<i>P. lasianthos Mt Tomah</i>	Wilson 44	KU563354	JX047663
<i>P. lasianthos Mt Wilson</i> *	Proft 3	KU563355	KU532870
<i>P. linearis</i>	Wilson 137	–	JX047666
<i>P. marifolia</i>	Conn 4380	KF145108	JX047657
<i>P. mulliganensis</i> *	Clarkson 5241	KU563356	KU532872
<i>P. nivea</i>	Wilson 61	KU563357	JX047651
<i>P. nudula</i> *	Latz 24527	KU563358	KU532873
<i>P. patens</i> *	Markey & Dillon 3715	KU563359	KU532874
<i>P. phyllicifolia</i>	Wilson 107	–	JX047643
<i>P. porcata</i>	Wilson 106	–	JX047613
<i>P. prostantheroides</i> *	Wilson 333	KU563360	KU532875
<i>P. prunelloides</i>	Wilson 113	–	JX047650
<i>P. rhombea</i>	Wilson 123	–	JX047637
<i>P. ringens</i>	Wilson 153	–	JX047605
<i>P. scutata</i> *	Porter 320	KU563362	KU532876
<i>P. scutellarioides</i>	Wilson 110	–	JX047642
<i>P. serpyllifolia</i> subsp. <i>microphylla</i> *	Byrne 3929	KU563363	KU532877
<i>P. serpyllifolia</i> subsp. <i>serpyllifolia</i> *	Pigott s.n.	KU563364	KU532878
<i>P. striatiflora</i>	Johnstone s.n.	–	JX047676
<i>P. tallowa</i>	Wilson 234	KF692284	JX047664
<i>P. tallowa</i> *	Wilson 236	KU563365	KU532879
<i>P. verticillaris</i> *	Wilson 388	KU563366	KU532880
<i>P. violacea</i> *	Wilson 401	KU563367	KU532881
<i>W. longifolia</i> *	Wilson 458	KU563368	KU532882

Results

Data statistics

The total length of the *trnH-psbA* alignment was 482 characters. Several regions could not be aligned unambiguously, and were excluded from analysis. The final alignment consisted of 379 sites, of which 31 (8% of total alignment) of 74 variable sites were parsimony informative. The ETS alignment of 430 sites also contained regions that could not be aligned unambiguously. These regions were excluded from the final alignment that consisted of 358 sites, of which 164 were parsimony-informative sites (45.8% of total alignment) out of 241 variable sites. A test for compositional homogeneity using a Chi-square test revealed that the *trnH-psbA* alignment ($\chi^2 = 14.5$; $p = 1.0$; A = 35.4, C = 12.3, G = 17.0, T = 35.3) and the ETS alignment ($\chi^2 = 50.4$; $p = 1.0$; A = 25.2, C = 28.6, G = 27.6, T = 19) did not significantly deviate from compositional homogeneity.

Tree topology

The phylogeny obtained by the analysis of the combined *trnH-psbA* intergenic spacer and ETS (Fig. 1) agrees broadly with that recovered from the three-marker dataset of Wilson et al. (2012). Our results depict a well-supported clade (Bayesian posterior probabilities (PP) 1.0; Bootstrap (BS) 91%) congruent with clade 'C' of Wilson et al. (2012), and confirms a sister relationship between the narrow endemic *P. tallowa* and a broad geographic representation of *P. lasianthos s. str.* However, unlike the phylogeny of Wilson et al. (2012), which used different chloroplast markers and showed a strongly supported *P. lasianthos s. str.* clade, our results gave relatively weak support for a monophyletic *P. lasianthos s. str.* clade (PP = 0.88; BS = 69%). Our single accession of *Prostanthera* from the Eungella region of Queensland (as *P. eungella sp. nov.*) was placed outside *P. lasianthos s. str.* in a polytomy with *P. galbraithiae* B.J.Conn, *P. howellii* Blakely s. str., and the *P. tallowa* + *P. lasianthos s. str.* clade. It had a weakly supported sister relationship (BS = 65%) with the *P. tallowa* + *P. lasianthos s. str.* clade.

Our analysis indicates clearly that our sample of *P. eungella* is not a component of the geographically widespread and morphologically variable *P. lasianthos* species complex. *Prostanthera galbraithiae* and *P. howelliae* have consistently formed a sequential sister relationship with a clade comprising *P. tallowa* and *P. lasianthos s. str.* (Wilson et al. 2012). Although all of these taxa, together with *P. eungella*, form a well-supported clade in this phylogeny (PP = 1.0; BS = 91%), the precise phylogenetic relationships within this clade remain to be resolved. Regardless of the true phylogenetic relationship amongst *P. galbraithiae*, *P. howelliae* and *P. eungella*, it is clear that the latter is not part of a clade comprising the nominant form of *P. lasianthos*, and nor is it morphologically similar to *P. galbraithiae* or *P. howelliae*.

Discussion

The fauna and flora of the Eungella rainforest and fringing open *Eucalyptus* forests consists of several unique elements as well as widespread species that are conspicuous by their absence (Winter and McDonald 1986). There are several faunal species that have their northern limits in this area, such as the Regent Bowerbird, the Golden-crowned snake, the Dwarf Crowned snake, the Tusked Frog, the Great Barred Frog, and several skinks. Examples of northern faunal species with their southern limits in the Eungella region include the Buff-breasted Paradise Kingfisher, the White-browed Robin, and the *Lampropholis basiliscus* skink (all taken from Winter and McDonald 1986). Species of trees have similar geographical patterns to those of the fauna. For example, *Syzygium resa* (B.Hyland) Craven & Biffin (Craven et al. 2006) and *S. wesa* B.Hyland (Hyland 1983) have their southern limits in the Eungella area (Craven et al. 2006). In contrast, *Eucalyptus andrewsii* Maiden and *E. campanulata* R.T.Baker & H.G.Sm. reach their northern limit in this region, and both form part of the floristic association from which *P. eungella* has been collected. Other northern species with limits in the Eungella area include: *Bleasdalea bleasdalei* (F.Muell.) A.C.Sm. & J.E.Haas (Weston 1995, as *Gevuina bleasdalei* F.Muell.), and *Cryptocarya corrugata* C.T.White & W.D.Francis and *C. murrayi* F.Muell. (Hyland 2007). Southern species of Lauraceae that have their northern limits at Eungella include *Cryptocarya glaucescens* R.Br. (Hyland 2007) and *C. macdonaldii* B.Hyland (Hyland 1989).

Prostanthera eungella has phylogenetic affinities with more southern elements of the genus (Fig. 1), rather than with the more northern species *P. albohirta* C.T.White, *P. athertoniana* B.J.Conn & T.C.Wilson, *P. clotteniana* (F.M.Bailey) A.R.Bean and *P. mulliganensis* B.J.Conn & T.C.Wilson (none of which nest within clade 'C', Wilson et al. 2012, Fig. 1). When considering only the phylogenetic affinities amongst *P. galbraithiae*, *P. howelliae* and *P. eungella*, the Eungella accession could be considered as being part of a more broadly circumscribed *P. galbraithiae* or *P. howelliae*. Although these species, together with *P. eungella*, form a well-supported clade (PP = 1.0; BS = 91%), the sister relationships of *P. eungella* are unclear.



Fig. 1. 50% majority rule phylogram from Bayesian analysis of the concatenated *trnH-psbA* and ETS sequence data for *Prostanthera* including *Hemigenia purpurea* and *Westringia longifolia* as outgroup representatives. Bayesian analysis posterior probabilities of >0.95 from Mr Bayes are reported as thickened branches and Maximum likelihood bootstrap values $\geq 75\%$ are reported above branches.

Prostanthera galbraithiae is restricted to heathy open forest and heathy woodland of the Gippsland Plains, Victoria (Conn 1998, 1999), and is characterised by having sessile, very narrowly ovate or oblong leaves that are more or less strongly revolute; corolla deep mauve to purple, with maroon dots at base of lobes and in mouth and throat, with an abaxial median lobe approximately the same width as the lateral lobes, and distinctly papillate anthers that lack an appendage. In contrast, *P. howelliae* s. str. (referred to as '*P. howelliae*-2' in Wilson et al. 2012) ranges from Gippsland (Victoria) to northern New South Wales in dry woodlands. It is characterised by narrowly ovate leaves with an entire, recurved margin, and short petioles (c. 0.1 mm long); anthers lacking an appendage, but each loculus has a basal tuft of coarse hairs; pink-mauve to purple-mauve corolla, with dark red, maroon or purple dots in throat, with an abaxial median lobe broader than the lateral lobes. Wilson et al. (2012) refer to a second accession of *P. howelliae* (as '*P. howelliae*-1') from the Goonoo State Forest (New South Wales) which has larger leaves than the nominant form. The phylogenetic affinities of this accession are with *P. discussata* and *P. granitica*. Since the taxonomic status of the Goonoo taxon has not been fully resolved, it was not included in the current study,

Prostanthera eungella is readily morphologically separable from *P. galbraithiae* and *P. howelliae* by its longer petioles (4 mm), toothed leaf margin, mostly white to pale mauve corolla, and anther appendages 2–2.3 mm long. On the basis of morphological differences and phylogenetic relationships we here describe as new, *P. eungella* to accommodate accessions of *Prostanthera* from the Eungella region of Queensland.

Taxonomy

Prostanthera eungella B.J.Conn & K.M.Proft, sp. nov.

Holotype: Australia: Queensland: South Kennedy: Swamp Ridge Road, c. 6.7 km NW of Eungella township, W. McDonald 5131 & A.R. Bean, 24 May 1992 (NSW452207!); iso: AD, BRI-AQ543531!, CANB, K, MEL.

Erect shrub up to c. 1 m high. *Branches* subterete (slightly flattened laterally), with shallow lateral grooves within each axil to the next upper node, sparsely to moderately hairy [20–25 hairs/mm²], particularly between lateral grooves and at nodes; hairs mostly antrorse, subappressed, ± straight, 0.05–0.2 mm long, white; moderately glandular [20–30 glands/mm²]. *Leaves* dark green above, paler below, glabrous, except hairs restricted to midvein of adaxial surface (hairs retrorse or spreading, less frequently antrorse, subappressed, ± straight, up to 0.2 mm long), moderately glandular [20–50 glands/mm²] (glands more distinctive on abaxial surface), aromatic (when crushed); *petiole* 4 mm long; *lamina* narrowly ovate, 39.5–44.5 mm long, 10.5–11.5 mm wide [length to width ratio 3.7–3.9, length of maximum width from base to total lamina length ratio 0.2–0.3]; base cuneate, slightly oblique; margin with up to 6 teeth (teeth mostly on distal half of margin, ± directed forward, 0.5 mm long, 0.5(–1) mm wide at base); apex attenuate; venation indistinct to faint, midrib slightly raised on abaxial surface. *Inflorescence* frondose, unbranched to 1-branched, hence conflorescence uni- or dibotryoidal; uniflorescence botryoidal; 6–20(–40)-flowered [per conflorescence]. *Pherophylls* not persistent, narrowly ovate, abruptly tapering at apex, c. 2 mm long. *Pedicel* 2–4 mm long, glandular, glabrous or often with scattered hairs. *Prophylls* persistent, inserted just below the calyx [a_1 axis to anthopodium ratio c. 4], opposite, linear, 1.5 mm long; base tapering; margin entire, usually partially fringed with hairs; apex attenuate; venation not visible. *Calyx* green; outer surface glabrous or with an occasional hair, densely glandular; inner surface glabrous except near margin of lobes densely hairy [at least 200 hairs/mm²], sometimes ± restricted to near margin; hairs antrorse, appressed, white, c. 0.1 mm long; *tube* 2.5–3 mm long; *abaxial lobe* 2–2.5 mm long, apex rounded; *adaxial lobe* c. 2 mm long, apex rounded. *Corolla* 10–12 mm long, white in tube, mauve distally with dull orange tinge; outer surface glabrous basally, moderately to densely hairy distally [20–60 hairs/mm²], hairs 0.3–0.6 mm long, spreading to antrorse, straight to slightly curled, moderately to densely glandular; inner surface glabrous basally, mouth and base of lobes (sometimes throughout) sparsely hairy [16–20 hairs/mm²], hairs 0.2–0.4 mm long; *tube* 5.5 mm long; *abaxial median lobes* broadly spatulate, 6–8 mm long, c. 7 mm wide [length to width ratio 0.9–1.1], apex irregular and rounded, bilobed (sinus c. 1 mm long); *lateral lobes* oblong to slightly obovate, 4.5 mm long, 2.5 mm wide, apex slightly irregular, rounded to slightly retuse; *adaxial median lobe-pair* depressed ovate c. 4.5 mm long, c. 7.5 mm wide [length to width ratio c. 0.6], apex rounded, irregular, bilobed (sinus 1–1.5 mm long). *Stamens* with filaments 4–4.5 mm long, anthers c. 1 mm long, connective extended to form 1 basal appendage 2–2.3 mm long. Disc c. 0.4 mm long. *Pistil* 7–9 mm long, often glandular; *ovary* cylindrical obovoid, 0.4–0.6 mm long, diameter at base 0.2–0.4 mm, lobes 0.1–0.2 mm long; *style* 7.5–10.5 mm long; *stigma lobes* 0.4–0.7 mm long. *Fruiting calyx* slightly enlarged (abaxial lobe up to c. 3.5 mm long; adaxial lobe 2.5–3 mm long. *Mature mericarps* not seen. **Fig. 2**

Distribution: Known only from the Eungella region, west of Mackay, northern Queensland. **Fig. 3**



Fig. 2. Photograph of holotype of *Prostanthera eungella* B.J.Conn & K.M.Proft (held at NSW).

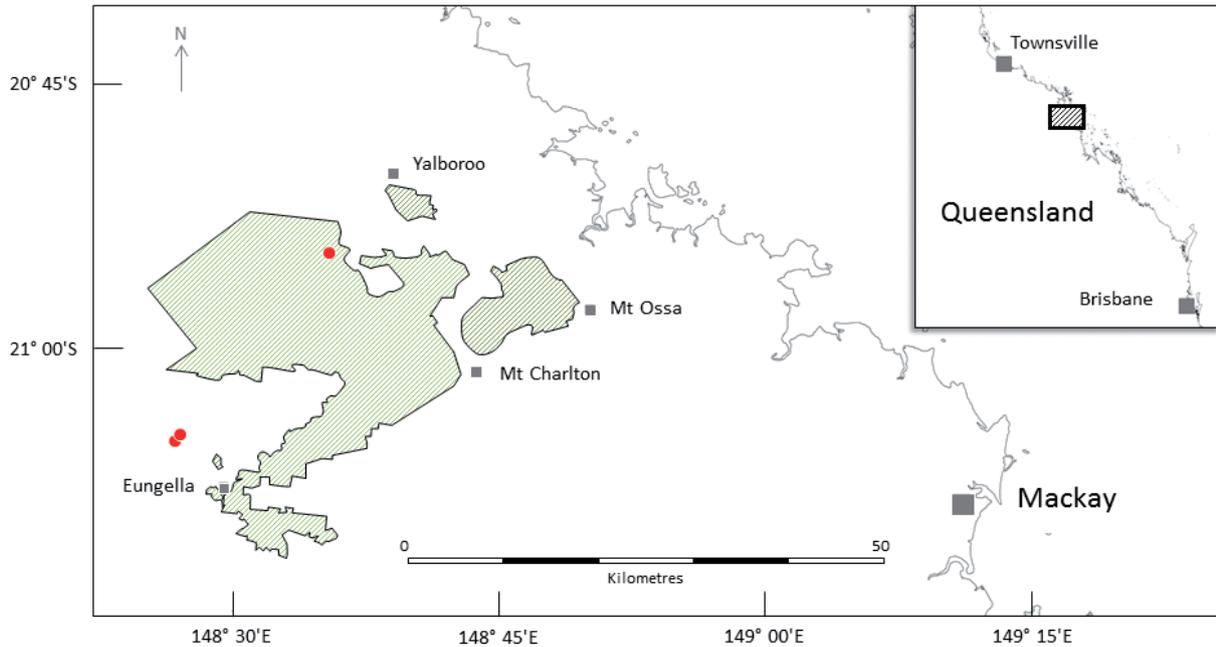


Fig. 3. Distribution map of *Prostanthera eungella*, west of Mackay, South Kennedy region, Queensland. The current known localities of *P. eungella* are marked by red dots. The Eungella National Park boundary is outlined and shaded with green hatching.

Habitat: Open-forest of *Eucalyptus campanulata* R.T.Baker & H.G.Sm., *Corymbia intermedia* (R.Baker) K.D.Hill & L.A.S.Johnson with lower tree layer of *Allocasuarina littoralis* (Salisb.) L.A.S.Johnson; altitude 1000 m (McDonald 5131); *Eucalyptus andrewsii* Maiden open forest on dark brown loam-clay on granite (Pollock 222); and edge of rainforest (Foreman AE110); grassy to layered open forest with *Glochidion ferdinandi*, *Kennedia rubicunda*, Poaceae, *Pteridium*, *Rubus*, on grey brown gravelly loam clay on metamorphosed granite (Bruhl 3199).

Flowering/fruiting: recorded as flowering in May and December, and fruiting in December.

Additional specimens: QUEENSLAND: SOUTH KENNEDY: W Eungella Range, Schumanns Road, c. 1.1 km E of Swampy Ridge radar installation, A.B. Pollock 222, 25 Jun 1995 (BRI-AQ639028); Eungella National Park: Peak 996, Dicks Tableland, near Eungella, P. Foreman AE110, 26 Dec 1993 (BRI-AQ632038); NE of Eungella, beyond Schumanns Road, S of radar installation, J.J. Bruhl 3199 & C.J. Prychid, 12 Dec 2012 (NE99199).

Etymology: The specific epithet refers to the Eungella area of Queensland where this species is known to occur.

Conservation status: Data deficient: recorded as scarce (Pollock 222), assumed to be afforded some protection since recorded from the Eungella National Park.

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