

Of a different feather: two new species of featherheads from the *Ptilotus macrocephalus* (Amaranthaceae) complex

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Abstract. *Ptilotus macrocephalus* (R.Br.) Poir. (Amaranthaceae), commonly known as a featherhead, is a widespread and common species in many parts of Australia. In the present study, we assess morphological variation in *P. macrocephalus* throughout its geographic range and provide evidence for the recognition of two new species, namely, *P. psilorhachis* T.Hammer & R.W.Davis and *P. xerophilus* T.Hammer & R.W.Davis. Geospatial analyses indicated that these new species are partitioned ecologically and geographically.

Additional keywords: Australia, biogeography, ecology, taxonomy.

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Introduction

Ptilotus R.Br. comprises ~120 species, all of which are native to mainland Australia, with one species (*P. conicus* R.Br.) also occurring on the Lesser Sunda Islands and the Aru Islands, and one (*P. spathulatus* (R.Br.) Poir.) occurring in Tasmania. Species diversity is highest in arid and semi-arid regions, particularly in Western Australia (Hammer *et al.* 2015, 2018a).

Ptilotus macrocephalus (R.Br.) Poir., known by several common names, including featherheads and green mulla mulla, is a widespread species found throughout mainland Australia. It was one of six species first described by Brown (1810) in *Trichinium* R.Br. (as *T. macrocephalum* R.Br.), on the basis of a specimen from Victoria. Poiret (1816) synonymised *Trichinium* under *Ptilotus*, making the new combination *P. macrocephalus* (R.Br.) Poir. Moquin-Tandon (1849) rejected Poiret's synonymy and retained *Trichinium* and *Ptilotus* as two distinct genera but misapplied the name *T. macrocephalum* to specimens of *P. exaltatus* Nees (e.g. A. Cunningham 202 at MEL; see also Hammer *et al.* 2018b). Confusion between *T. macrocephalum* and *P. exaltatus* led Moquin-Tandon to describe *T. pachcephalum* Moq., also on the basis of a specimen from Victoria, and *T. angustifolium* Moq. from the Hunter River, New South Wales. Further confusion was created when Lindley (in Mitchell 1848) misapplied the name *T. fusiforme* R.Br. to specimens of *T. macrocephalum*.

Von Mueller (1868) followed Poiret (1816) by including *Trichinium* within *Ptilotus*. He recognised *T. macrocephalum sensu* Moquin-Tandon (1849) as a synonym of his own concept of *P. nobilis* (Lindl.) F.Muell., and considered *T. angustifolium*,

T. pachcephalum and *T. fusiforme sensu* Lindley (in Mitchell 1848) to be conspecific (including them under *P. pachcephalus* (Moq.) F.Muell.). Bentham (1870) recognised the similarity of *Ptilotus* and *Trichinium*, but, nevertheless, maintained them as separate genera and listed Mueller's *P. pachcephalus* as a synonym of *T. macrocephalum*. Black (1948) synonymised *Trichinium* under *Ptilotus*, reinstating the name *P. macrocephalus*, and this view has been followed by subsequent taxonomists. The phylogeny presented in Hammer *et al.* (2015) showed that all of Brown's original *Trichinium* species are nested within *Ptilotus*. *Ptilotus macrocephalus* is placed in an informal 'Clade D' and is closely related to *P. polystachyus* (Gaudich.) F.Muell., *P. giganteus* (A.Cunn. ex Moq.) R.W.Davis & R.Butcher and related species.

Bean (2008) noted that *P. macrocephalus* occurs across a wide range of environments, from arid regions of Western Australia and western Queensland to high-rainfall areas near the coast in eastern Australia, and is morphologically variable. He recorded that sepals (termed 'tepals' by Bean) are longest in plants from north-eastern Queensland, nearly as long in near-coastal areas of Queensland and New South Wales, and shortest in Western Australia; he considered this variation to be clinal. In the present study, we prefer to continue the use of the term 'sepals' to the previously used 'tepals' (Hammer 2018; Hammer *et al.* 2018a), because recent studies have clarified the calycine origin of the uniseriate perianth of the Caryophyllales (e.g. Ronse de Craene 2013), the corolla having been lost, and following the change in terminology for other genera in Amaranthaceae (e.g. Vrijdaghs *et al.* 2014; Borsch *et al.* 2018).

The present study critically examines morphological variation in *P. macrocephalus* across its range and shows that there is strong morphological evidence for the recognition of three distinct geographically and ecologically partitioned taxa.

Materials and methods

Morphological examinations

In total, 676 fertile specimens from the National Herbarium of Victoria (MEL), the National Herbarium of New South Wales (NSW), the Queensland Herbarium (BRI), the State Herbarium of South Australia (AD) and the Western Australian Herbarium (PERTH) were examined, including material from throughout the geographic range of *P. macrocephalus*. Specimens from the Northern Territory Herbarium (DNA) were not accessed, but an adequate amount of material collected from the Northern Territory was available from other herbaria. Important morphological characters were identified, and specimens categorised into three distinct morphotypes without *a priori* consideration of geography or habitat.

Geospatial analyses

Collection localities of all specimens examined were obtained from the Australasian Virtual Herbarium (<http://avh.chah.org.au/>, accessed 15 April 2019). Records with a georeferenced precision >10 km were discarded, leaving *n* = 427 samples (Table S1, available as Supplementary material to this paper). A geospatial dataset of 40 Bioclim climate variables from the CliMond dataset (Kriticos *et al.* 2012, 2014; see <https://www.climond.org>, accessed 15 April 2019) for each included locality was constructed using the Point Sampling Tool in QGIS (ver. 3.3, Open Source Geospatial Foundation Project, see <http://qgis.osgeo.org>, accessed 15 April 2019). Given the broadly allopatric and very wide ranges of the three morphotypes, climate variables were considered to be suitable for modelling their distributions. Maximum-entropy modelling (Maxent, ver. 3.4.1, see https://biodiversityinformatics.amnh.org/open_source/maxent/, accessed 1 May 2019; Phillips *et al.* 2004; Phillips and Dudík 2008) analyses were used to assess ecological and geographic partitioning between the three morphotypes (see also Hammer *et al.* 2018b). No feature selection was conducted on the data. Multiple occurrence records of each morphotype from any given 10- × 10-km cell were ignored. Bootstrapping was performed for each model with 10 replications and 25% of records were randomly withheld for model testing. All other settings were left as default. Model accuracy was assessed using the area under curve (AUC) statistic (Fielding and Bell 1997), and jackknife tests were used to assess variable importance. Taxon distribution maps were created using QGIS.

A principal-component analysis (PCA) was conducted on the geospatial dataset using the R statistical platform (ver. 3.5.1, R Foundation for Statistical Computing, Vienna, Austria, see <https://www.r-project.org/>, accessed 15 April 2019) in RStudio (ver. 1.1.456, RStudio, Inc., Boston, MA, USA, see <https://www.rstudio.com/>, accessed 15 April 2019), to determine whether the morphotypes occupied discrete environmental envelopes. Standardisation of the variables was implemented. The PCA was visualised using the R packages ggplot2 (see <https://ggplot2.tidyverse.org/>, accessed 15 April 2019; Wickham 2016)

and ggfortify (see <https://github.com/sinhrks/ggfortify>, accessed 15 April 2019; Tang *et al.* 2016).

Results

Morphological examinations

All specimens of *Ptilotus macrocephalus sens. lat.* (i.e. as currently circumscribed) examined could be reliably segregated into one of three morphotypes (Fig. 1), one of which included the type specimens of *T. macrocephalum*, *T. angustifolium* and *T. pachycephalum*. The morphotypes are distributed in (1) south-eastern Australia, from far south-eastern South Australia through Victoria and into eastern New South Wales, (2) arid parts of central and western Australia, closely associated with the Eremaean botanical province, and (3) eastern Queensland from west of Brisbane to near Cairns. The morphotypes are, hereafter, referred to as (1) *P. macrocephalus*, (2) *P. xerophilus* and (3) *P. psilorrhachis* (see Taxonomy section below). Distinguishing morphological characters are summarised in Table 1.

Plants of *P. macrocephalus* are perennial herbs with a woody, sometimes branching, taproot; many specimens appear to be long-lived (Fig. 1B) on the basis of scars and dead branches from previous seasons being retained on the crown. By contrast, the other two species have fleshy taproots and seem to be mainly annuals but may persist for several seasons given favourable conditions (Fig. 1D, F). Field observations of *P. xerophilus* in Western Australia, the Northern Territory and northern South Australia (T. A. Hammer, pers. obs.) and of *P. psilorrhachis* near Cairns, Queensland (P. J. H. Hurter, pers. comm.) confirm their primarily annual habit.

Inflorescences of *P. psilorrhachis* are markedly different from those of *P. macrocephalus* and *P. xerophilus*. A key feature of *P. psilorrhachis* is a glabrous or very sparsely hairy rachis (i.e. a few scattered hairs may be present). This is in distinct contrast to the densely villous or tomentose indumentum that obscures the surface of the rachis in the other two taxa. Flowers on pressed specimens of *P. psilorrhachis* are also loosely arranged, with the rachis being visible between the flowers (Fig. 1C), whereas flowers in *P. macrocephalus* and *P. xerophilus* are more tightly arranged, with the overlapping bracts and bracteoles obscuring the rachis (Fig. 1A, E).

Differences in sepal indumentum between species of *Ptilotus* are often informative (e.g. Hammer 2018; Hammer *et al.* 2018b). The indumentum on the abaxial surface of the sepals differs

Table 1. Summary of distinguishing morphological characters for the taxa in this study

| Character | <i>Ptilotus macrocephalus</i> | <i>P. psilorrhachis</i> | <i>P. xerophilus</i> |
|-------------------------|-------------------------------|---------------------------------|----------------------|
| Taproot woodiness | Woody | Fleshy | Fleshy |
| Rachis indumentum | Densely hairy | Glabrous or very sparsely hairy | Densely hairy |
| Flower arrangement | Tight | Loose | Tight |
| Adaxial sepal hairs | Present | Absent | Absent |
| Staminal cup hairs | Present | Present | Absent |
| Outer sepal length (mm) | 20–24 | 28–45 | 14–25 |
| Outer sepal width (mm) | 1.5–2.0 | 1.3–1.8 | 0.7–1.1 |



Fig. 1. Examples of the three taxa *in situ*. A. *Ptilotus macrocephalus* inflorescence in Victoria. B. *P. macrocephalus* perennial habit in Victoria. C. *P. psilorhachis* inflorescence in Queensland. D. *P. psilorhachis* annual habit in Queensland. E. *P. xerophilus* inflorescence in Western Australia. F. *P. xerophilus* annual habit in Western Australia. Photographs by G. Goods and M. Goods (A, B), J. Newland and R. Fryer (C, D) and T. Hammer (E, F).



Fig. 2. Longitudinal sections showing the adaxial surface of inner sepals (i.e. staminal cup attached) and abaxial surface of outer sepals for each of the three taxa. A. Inner sepal of *Ptilotus macrocephalus* (A.C.Beaglehole 86470, MEL 1620389). B. Outer sepal of *Ptilotus macrocephalus* (A.C.Beaglehole 86470, MEL 1620389). C. Inner sepal of *Ptilotus xerophilus* (D.J.Nelson 1742, MEL 2220885). D. Outer sepal of *Ptilotus xerophilus* (D.J.Nelson 1742, MEL 2220885). E. Inner sepal of *Ptilotus psilorhachis* (I.R.Telford & R.J. Rudd 11249, BRI AQ581412). F. Outer sepal of *Ptilotus psilorhachis* (I.R.Telford & R.J.Rudd 11249, BRI AQ581412). Scale bar: 5 mm.

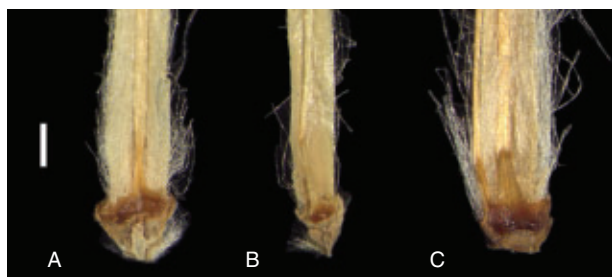


Fig. 3. Close up of the adaxial surface of the inner sepals, showing the differences in staminal cup and sepal indumentum (from Fig. 2). A. *Ptilotus macrocephalus* (A.C.Beaglehole 86470, MEL 1620389). B. *P. xerophilus* (D.J.Nelson 1742, MEL 2220885). C. *P. psilorhachis* (I.R.Telford & R.J. Rudd 11249, BRI AQ581412). Scale bar: 1 mm.

among the three taxa (Fig. 2). The hairs in *P. macrocephalus* and *P. psilorhachis* are long, spreading and verticillate for almost the entire length of the sepal (Fig. 2B, F), except for glabrous apices. In *P. xerophilus*, the hairs are short, appressed and simple in the lower half of the sepal (some specimens are almost glabrous), with only the upper half having long, spreading, verticillate hairs below the glabrous apices (Fig. 2C). These variations in abaxial sepal indumentum give the inflorescences a different appearance overall (Fig. 1). The indumentum within the flowers also varies

among the three taxa (Fig. 3). In *P. macrocephalus*, the inner sepals are adaxially villous and the apex of the staminal cup has simple hairs (Fig. 3A). In *P. xerophilus*, the adaxial surface of the inner sepals and staminal cup are glabrous (Fig. 3B). In *P. psilorhachis*, the inner sepals are adaxially glabrous and the apex of the staminal cup has simple hairs (Fig. 3C).

As Bean (2008) noted, there are clear differences in sepal length within *P. macrocephalus sens. lat.* (Fig. 2). The outer sepals of *P. psilorhachis* are noticeably longer (28–45 mm) than those of *P. macrocephalus sens. str.* (20–24 mm) and *P. xerophilus* (14–25 mm). Bean (2008) suggested that sepal length was clinal in *P. macrocephalus sens. lat.*, but we found no evidence of clinal change in sepal length in our concepts of *P. macrocephalus sens. str.* or *P. xerophilus*. There is a general clinal trend in sepal length in *P. psilorhachis* (with long sepals predominantly at the northern end of the range and shorter sepals in the south); however, we found that there were exceptions at both ends of the geographic range. In addition to the differences in sepal length, the outer sepals of *P. xerophilus* are narrower (0.7–1.1 mm wide) than those of *P. macrocephalus* (1.5–2.0 mm) and *P. psilorhachis* (1.3–1.8 mm).

Geospatial analyses

Ptilotus macrocephalus was represented in the geospatial dataset for the Maxent modelling by 130 specimens, *P. psilorhachis* by 35 specimens and *P. xerophilus* by 262 specimens.

The distribution model for *P. macrocephalus* largely fits its known distribution (Fig. 4A), with areas in the south-east of mainland Australia and in Tasmania fitting well with the climatic conditions modelled for the species. The model returned an average AUC of 0.899 with a standard deviation of 0.008. Variables contributing most to the model were Bio27 (radiation of coldest quarter; 34.8%) and Bio28 (annual mean moisture index; 29.5%). The highest probability areas were in eastern Victoria and eastern to central New South Wales; an apparent disjunction, on the basis of known specimens, between southern Victoria and the Northern and Central Tablelands of New South Wales appears to not be a sampling artefact, with reduced probabilities of occurrence in the gap. A specimen from Toowoomba in southern Queensland (BRI AQ0178569) was determined as *P. macrocephalus* in the present study, but it was not included in the geospatial analysis because of the georeferenced precision being >10 km.

The model for *P. psilorhachis* predicted its occurrence through much of eastern Queensland, with lower probabilities on Cape York Peninsula, extending west across the northern end of the Northern Territory (the ‘Top End’) to the Kimberley region of Western Australia (Fig. 4B). The model returned an average AUC of 0.976 with a standard deviation of 0.004. Variables contributing most to the model were Bio18 (precipitation of warmest quarter; 48.0%) and Bio28 (21.8%). There is an apparent gap between the occurrences of *P. psilorhachis* in northern Queensland inland of Cairns and southern Queensland, which may be due to under-collecting or perhaps indicates that the available habitats there are not suitable for the species. The distribution models of *P. macrocephalus* and *P. psilorhachis* overlap around the border of northern New South Wales and southern Queensland, but no specimens of *P. psilorhachis* are known from New South Wales.

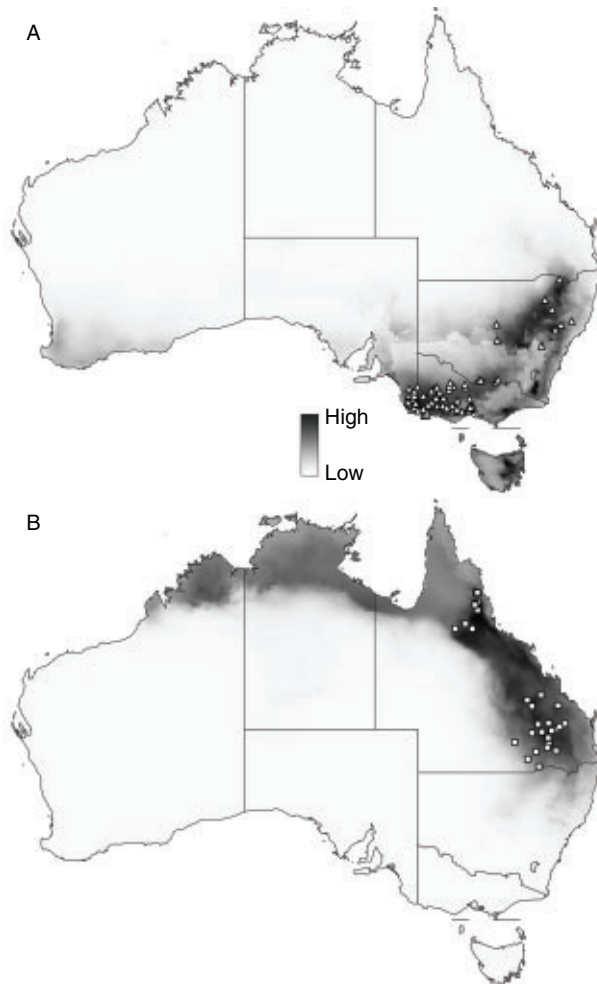


Fig. 4. Maps of the Maxent distribution models of the probability of occurrence. A. *Ptilotus macrocephalus*. B. *P. psilorhachis*. Points are the occurrence records used in the analysis for each taxon.

The model for *P. xerophilus* predicted its occurrence accurately throughout central and western Australia, excluding the far north, south and east (Fig. 5A). The model returned an average AUC of 0.791 with a standard deviation of 0.007. Variables that contributed most to the model were Bio21 (highest weekly radiation; 37.1%), Bio28 (22.9%) and Bio27 (12.4%). Narrow distributional gaps in northern South Australia and the south-eastern Northern Territory may be real on the basis of lower probabilities of modelled occurrence.

The species distribution models for each taxon were geographically allopatric or parapatric (Fig. 4, 5), with very little overlap at the margins of each. Across all three models, the variable Bio28 (annual mean moisture index) was an important predictor in driving the distribution of the taxa (Fig. 5B).

The PCA of the entire dataset shows that the three taxa, originally separated by differences in morphology, occupy discrete climatic envelopes (Fig. 6). *Ptilotus psilorhachis* occupies the largest climatic space of the three taxa, with specimens from southern Queensland and northern New South

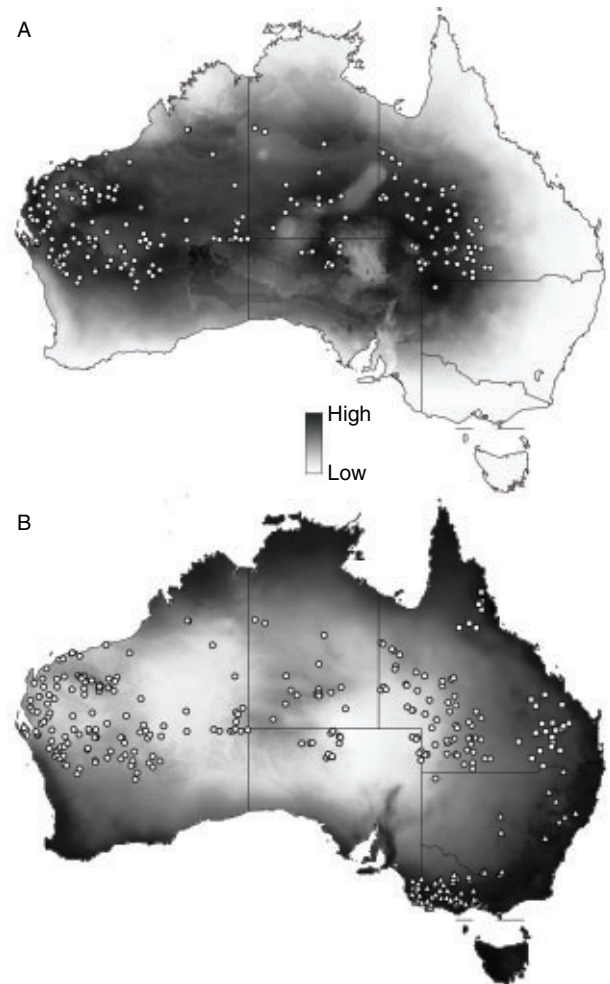


Fig. 5. A. Map of the Maxent distribution model of the probability of occurrence of *Ptilotus xerophilus*. B. The records of all three taxa plotted over a map of the variable Bio28, annual mean moisture index. Points are the occurrence records used in the analysis for each taxon: *P. macrocephalus* (triangles), *P. psilorhachis* (squares) and *P. xerophilus* (circles).

Wales being resolved disjunctly from those in northern Queensland and adjacent to a few specimens of *P. macrocephalus* from northern New South Wales. These latter specimens are also climatically disjunct from the main area of distribution of *P. macrocephalus* in Victoria.

Discussion

Geospatial analyses

Maxent modelling and the PCA ordination on the basis of environmental parameters showed that the three morphologically defined taxa are also ecologically partitioned, with the partitioning matching their distributions.

Because few specimens of *P. macrocephalus* from New South Wales were available for the geospatial analysis, the climatic space occupied by that species may be more continuous than is apparent in the current PCA (see Fig. 6), although the Maxent model showed that these occurrences in northern New South

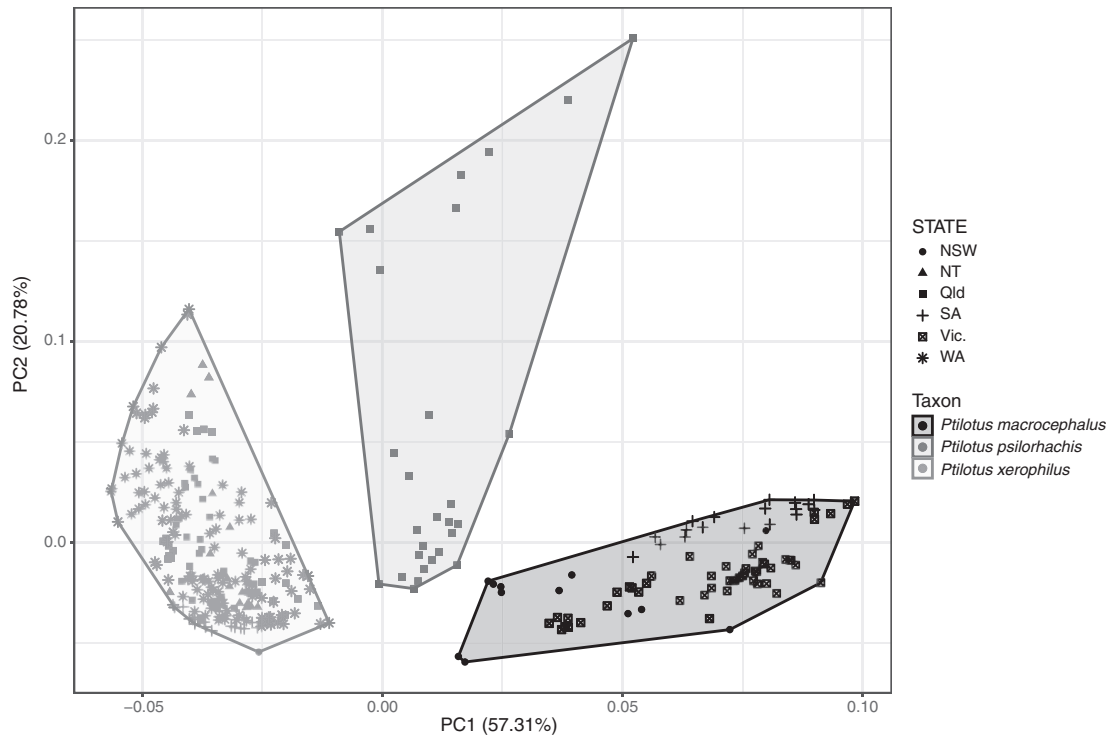


Fig. 6. Principal-component analysis (PCA) ordination of the geospatial dataset, with convex hulls representing the climatic space for each taxon.

Wales and those from Victoria may be separated by unsuitable environments on the Southern Tablelands and South-western Slopes. An apparent environmental disjunction between northern and southern populations of *P. psilorhachis* may be caused by under-collecting or by a lack of suitable habitat in these areas (Fig. 4B).

The distribution of *P. xerophilus* is disjunct from the other two taxa, and it is more clearly different, in ecology, from the other two species, which occur in noticeably higher-rainfall regions of Australia. Despite its wider geographic distribution, it occupied the smallest environmental envelope on the PCA (Fig. 6), further suggesting that the geographically narrow disjunctions in its modelled distribution in northern South Australia and the southern Northern Territory are likely to be real.

Phylogenetic relationships

A single specimen of *P. xerophilus* was included (as *P. macrocephalus sens. lat.*) in the phylogeny of Hammer *et al.* (2015), where it formed a clade with *P. beckerianus* (F.Muell.) F. Muell. ex J.M.Black, *P. distans* (R.Br.) Poir., *P. capensis* (Benl.) A.R.Bean, *P. fusiformis* (R.Br.) Poir., *P. giganteus* and *P. polystachyus*.

Relationships among some of these species remain unresolved or poorly supported, owing to a lack of sequence variation within the markers used for the phylogeny, perhaps indicating recent speciation within the group (Hammer *et al.* 2015). Taxonomic patterns within this group are complex, as evidenced by several new species being recognised recently, on the basis of discrete but subtle segregation of morphological

characters (e.g. *P. capensis* separated from *P. distans* by Bean 2008 and *P. giganteus* from *P. polystachyus* by Davis and Butcher 2010).

Because *P. macrocephalus sens. str.* and *P. psilorhachis* were not included in these phylogenies, their relationships to the other species in the clade are uncertain. The three taxa in *P. macrocephalus sens. lat.* recognised here may not comprise a monophyletic group.

Ptilotus distans, *P. capensis* and *P. giganteus* are distributed in the monsoonal tropics of northern Australia in the Top End of the Northern Territory, Cape York Peninsula to just south of Cairns, and the Kimberley region of Western Australia respectively. These areas all fall within the predicted area of distribution of *P. psilorhachis*. It is possible that all these species comprise a single Northern Australian radiation from a common ancestor adapted to the monsoon tropics.

Ptilotus beckerianus is a rare endemic in South Australia, occurring in the southern part of the Eyre Peninsula and on Kangaroo Island, west of and disjunct from the western edge of the range of *P. macrocephalus sens. str.* (i.e. occurrences in the Naracoorte Coastal Plain IBRA bioregion). Both species are perennial herbs with woody taproots (Black 1948). *Ptilotus beckerianus* is perhaps most morphologically similar to *P. macrocephalus sens. str.* within this clade and may be closely related, perhaps indicating a small southern radiation from a temperate-adapted ancestor. The species that are the sister group to the subclade that includes all these species (i.e. *P. clementii* (Farmer) Benl, *P. gardneri* Benl, *P. polystachyus*) all occur in northern arid or semi-arid areas (the last with a wide distribution, including temperate southern and monsoon-tropical

northern Australia). It is, thus, possible that the clade has diversified by recent peripatric or parapatric speciation from an arid-adapted common ancestor, with radiation into new tropical and temperate niches.

Taxonomic implications

The present study has demonstrated that, as currently circumscribed, *P. macrocephalus* sens. lat. includes three distinct taxa that are partitioned morphologically, geographically and ecologically. We consider the morphological differences among these species to be significant, and the ecological differences between these taxa add validation to the concept that they are distinctly evolving metapopulation lineages, as recognised by the general-lineage species concept (de Queiroz 2007). We, therefore, regard that these taxa are most appropriately recognised at species rank. Accordingly, we formally name and describe here the new species *P. psilorhachis* T.Hammer & R.W.Davis and *P. xerophilus* T.Hammer & R.W.Davis, and recircumscribe *P. macrocephalus* in the narrow sense as discussed above.

Taxonomy

Ptilotus macrocephalus (R.Br.) Poir., *Lam., Encycl. Suppl.* 4: 620 (1816)

Trichinium macrocephalum R.Br., *Prodr.* 415 (1810).

Type: Port Phillip [Victoria], *s. dat.*, *Anon. s.n.* (syn: BM 000895593, image! <https://plants.jstor.org/stable/10.5555/al.ap.specimen.bm000895593>; syn: GB 0047020, image! <https://plants.jstor.org/stable/10.5555/al.ap.specimen.gb-0047020>).

Trichinium angustifolium Moq. in A.L.P.P. de Candolle (ed.), *Prodr.* 13 (2): 293 (1849).

Type: New South Wales, the upper parts of Hunter River, 1825, *A. Cunningham s.n.* (syn: K 000356810, image! <https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000356810>; syn: P 00609981, image! <https://plants.jstor.org/stable/10.5555/al.ap.specimen.p00609981>; syn: G-DC (microfiche), *vide* Bean 2008).

Trichinium pachycephalum Moq. in A.L.P.P. de Candolle (ed.), *Prodr.* 13(2): 294 (1849); *Ptilotus pachycephalus* (Moq.) F.Muell., *Fragm.* 6 (49): 228 (1868).

Type: Port Phillip [Victoria], 20 Mar. 1840, *R.C. Gunn s.n.* (syn: P 00609982, image! <https://plants.jstor.org/stable/10.5555/al.ap.specimen.p00609982>).

Erect perennial *herbs* with a woody, sometimes branching, taproot, 30–50 cm high. *Stems* terete, ribbed, glabrous or glabrescent towards stem apex; hairs crisped-nodose or subverticillate. *Basal leaves* not seen. *Cauline leaves* linear-lanceolate to narrowly oblanceolate, sessile, 30–120 mm long, 2–14 mm wide, glabrous or glabrescent with sparse, verticillate hairs; margins entire, often undulate. *Inflorescences* spiciform, terminal, cylindrical, creamish-green (rarely with a pinkish flush), 30–90 mm long, 45–60 mm wide; rachis densely tomentose or sometimes villous; flowers tightly arranged on rachis; apex rounded or truncate. *Bracts* narrowly ovate to ovate, 7.5–11 mm long, 3.0–4.5 mm wide, transparent, glabrous or with verticillate hairs along the conspicuous, white or pale brown midrib; apex mucronate, the mucro 1.0–1.2 mm long; margins

entire. *Bracteoles* broadly ovate to obovate, 6.5–9.8 mm long, 3.2–5 mm wide, transparent, glabrous; midrib conspicuous, white; apex shortly mucronate, the mucro 0.1–0.2 mm long; margins serrate. *Outer sepals* lanceolate, 20–24 mm long, 1.5–2.0 mm wide, creamish-green (rarely with a pale pink flush towards apex), adaxially villous, abaxially villous with spreading verticillate hairs almost throughout; apex acute, glabrous. *Inner sepals* lanceolate, 19–23 mm long, 0.8–1.2 mm wide, with colour and indumentum as for outer. *Fertile stamens* 4; *filaments* cream, 15–19 mm long, unequal, filiform; *anthers* yellow, 1.2–2.0 mm long, 0.4–1.0 mm wide. *Staminode* 1, 0.5–3.5 mm long. *Staminal cup* symmetrical, unlobed, 0.4–0.5 mm long, strongly adnate to sepal tube, apically covered with simple hairs. *Ovary* obconical, 0.8–1.3 mm long, 1.0–1.8 mm wide, apically covered with simple hairs; stipe 1.0–2.0 mm long. *Style* sigmoidal, 17–22 mm long, cream, excentrically fixed on the ovary, verticillate-hairy on the lower half. *Stigma* capitate. *Seed* smooth, pale brown, ~2.7 mm long, ~1.5 mm wide. (Fig. 1A, B, 2A, B, 3A.)

Distribution and habitat

Ptilotus macrocephalus occurs from south-eastern South Australia, through central and northern Victoria, into central to eastern New South Wales, and just over the border into south-eastern Queensland (Fig. 4A). On the basis of herbarium label data, the species commonly inhabits open grasslands dominated by *Austrostipa* spp. and *Themeda triandra* on brown or reddish loamy soils derived from basalt in the south of its range. In the north of the range, it is recorded on north-facing hill slopes or on flats in open eucalyptus woodlands with stony, red or brown sandy or clayey loam soils.

Conservation status

Common in South Australia and Victoria; known occurrences in New South Wales are somewhat sporadic, many being older collections, indicating that it may be restricted in occurrence and uncommon in that state. The species may be rare in Queensland, occurring only near the border with New South Wales; therefore, its conservation status should be assessed.

Notes

The epithet of *Trichinium pachycephalum* deviates from the usual construction ('pachycephalum'), as it derives from the Greek noun *pachos* (thickness) rather than the more usual adjective *pachys* (thick). Although this construction is not strictly grammatically correct, it is valid under Art. 60.10 of the ICN (Turland *et al.* 2018) and is not a correctable orthographic error.

Selected specimens examined

QUEENSLAND. Toowoomba, *C.H. Hartmann s.n.* (BRI AQ0178569). **SOUTH AUSTRALIA.** Near Donovan's Landing, *B. Copley* 1807 (AD); Desert Camp Conservation Park, *D.J. Duval & M.K. Jones* 275A (AD); Mary Seymour Conservation Park, *H.P. Vonow* 2906 (AD). **NEW SOUTH WALES.** Carters Road, Pigna Barney, *N. Cobcroft s.n.* (NSW 441772); 8.2 miles [~13.2 km] W of Sandy Hollow on the Mudgee Road, *R.G. Coveny* 2451 (NSW); alongside Carters Road E of Boonara, *J.R. Hosking* 2125 (NSW); Goulburn River Valley, ~5 km SW of Baerami, *T.A. James, W. Bishop & S.V. Goodwin* 660 (NSW); Narrabri, *J.H. Maiden s.n.* (NSW 29487); near

Lake Urana, *W.E. Mulham* W975 (NSW). **VICTORIA.** Hawkes Road, *C.W. Ahrens* 40 (MEL); Hands Road, *C.W. Ahrens* 43 (MEL); Oliver's Lake Flora and Fauna Reserve, *A.C. Beauglehole* 86470 (AD); Grampian Mountains, *D. Keane* s.n. (AD 96947051); Werribee, *A. Morrison* 1467 (PERTH); 1.8 km upstream from Donovan, *R.D. Pearce* 395 (AD); Anglesea, *V. Stajsic* 99 (MEL); Willaura–Wickliffe road, *N.G. Walsh & Z. Smith* 5698 (MEL).

Ptilotus psilorhachis T. Hammer & R.W. Davis, sp. nov.

Type: Queensland, Emu Creek Station, 8.5 km NNE of Petford, 20 Jan. 2002, *P.I. Forster, R. Booth & R. Jensen* PIF 28204 (holo: BRI AQ555919!; iso: AD 142716!, MEL 2291403A!).

Erect annual or short-lived perennial *herbs* with fleshy taproot, 40–60 cm high. *Stems* terete, ribbed, glabrous or glabrescent towards stem apex; hairs crisped-nodose or subverticillate. *Basal leaves* not seen. *Cauline leaves* linear-lanceolate to narrowly oblanceolate, sessile, 20–120 mm long, 1–6 mm wide, glabrescent or with sparse, verticillate hairs; margins undulating or entire. *Inflorescences* spiciform, terminal, cylindrical, creamish-green (rarely with a pinkish flush), 40–100 mm long, 60–90 mm wide; rachis glabrous or very sparsely hairy; flowers loosely arranged on rachis; apex rounded or truncate. *Bracts* narrowly ovate to ovate, 9–12 mm long, 2.5–4 mm wide, transparent, glabrous or with verticillate hairs along midrib; midrib conspicuous, white or pale brown; apex mucronate, the mucro ~1 mm long; margins entire. *Bracteoles* obovate, 7–11.5 mm long, 2.5–5 mm wide, transparent, glabrous; midrib conspicuous, white; apex shortly mucronate, the mucro 0.1–0.2 mm long; margin serrate. *Outer sepals* lanceolate, 28–45 mm long, 1.3–1.8 mm wide, creamish-green or rarely with pale pink flush towards apex, adaxially villous, abaxially villous with spreading verticillate hairs; apex acute, glabrous. *Inner sepals* lanceolate, 27–42 mm long, 0.6–1.0 mm wide, creamish-green or rarely with pale pink flush towards apex, adaxially glabrous, abaxially villous with spreading verticillate hairs; apex acute, glabrous. *Fertile stamens* 4; *filaments* cream, 20–36 mm long, unequal, filiform; *anthers* yellow, 2.0–3.0 mm long, 0.5–1.0 mm wide. *Staminode* 1, 0.4–6 mm long. *Staminal cup* symmetrical, not lobed, 0.3–0.5 mm long, strongly adnate to sepal tube, the apex covered with simple hairs. *Ovary* obconical, 1.2–2.2 mm long, 1.4–2.0 mm wide, glabrous; stipe ~1 mm long. *Style* sigmoidal, 25–40 mm long, cream, excentrically fixed on the ovary, with verticillate hairs on lower half. *Stigma* capitate. *Seed* smooth, pale brown, 3.3–3.5 mm long, 1.9–2.0 mm wide. (Fig. 1C, D, 2E, F, 3C.)

Distribution and habitat

Ptilotus psilorhachis is distributed in eastern Queensland from west of Cairns south to west of Brisbane (Fig. 4B), including the IBRA subregions of Einasleigh Uplands, Brigalow Belt North and Brigalow Belt South. On the basis of herbarium label data, the species commonly inhabits open eucalypt woodlands, commonly dominated by *Eucalyptus populnea*, *E. crebra* or *E. leptophleba*, on flats with brown or red sandy or clayey loam soil, sometimes with a gravelly surface.

Etymology

From the Greek *psilos* (naked) and *rhachis* (a spine or rachis), referring to the conspicuous and glabrous or very sparsely hairy rachis characteristic of the species.

Conservation status

Ptilotus psilorhachis is common across its range and is not considered to be of conservation concern.

Selected specimens examined

QUEENSLAND. 3 km along Pearlinga road W of Mundubbera, *A.R. Bean* 11936 (BRI); 65 km from Mitchell on road to Bollon, *A.R. Bean* 24397 (BRI); 16.6 km along Roche Creek Road E of Wandoan, *A.R. Bean* 29487 (BRI); Gayndah Dirnbir, *E.W. Bick* s.n. (BRI AQ0178578); 'Potters Flats', ~52 km N of Yuleba, *C. Eddie* CPE2472 (BRI); ~1.5 km by road E of Dimbulah, *K.R. McDonald* KRM4927 (BRI); 40 miles [~64.4 km] S of Ayr on W bank of Burdekin River, *H.C. Seton* 5 (BRI); Lakeland Downs near Condamine, *K.M. Stephens, C. Thrupp & A. Daniel* s.n. (BRI AQ0855297); 4 km from Petford along road to Irvinebank, *I.R. Telford & R.J. Rudd* 11249 (BRI); Nangram Station, Condamine Highway, ~10 miles [~16 km] NE of Condamine, *W.G. Trapnell* s.n. (BRI AQ0178565); 4 km S of Mount Garnet on the Gunnawarra Road, *B.S. Wannan* 3998 (BRI); Old coal road between Gladstone and Biloela, *M. Worthington* 1676 (BRI).

Ptilotus xerophilus T. Hammer & R.W. Davis, sp. nov.

Type: Western Australia, 700 m south along Paynes Find–Yalgoo road from junction of Geraldton–Mount Magnet road, 26 Aug. 2018, *R. Davis & T. Hammer* RD12901 (holo: PERTH!; iso [to be distributed]: BRI!, CANB!).

Erect annual *herbs* with fleshy taproot, 20–120 cm high. *Stems* terete, ribbed, glabrous or glabrescent towards stem apex; hairs crisped-nodose or subverticillate. *Basal leaves* not seen. *Cauline leaves* linear-lanceolate to narrowly oblanceolate, sessile, 10–130 mm long, 2–8 mm wide, glabrescent or with sparse verticillate hairs; margins undulating or entire. *Inflorescences* spiciform, terminal, cylindrical, creamish-green or rarely with pinkish flush, 30–70 mm long, 32–50 mm wide, sweetly scented at night; rachis densely tomentose or sometimes villous; flowers tightly arranged on rachis; apex acute, rounded or truncate. *Bracts* ovate to broadly ovate, 6–10 mm long, 2.5–4.5 mm wide, transparent, glabrous or with verticillate hairs along midrib; midrib conspicuous, white or pale brown; apex mucronate, the mucro 0.5–0.6 mm long; margins entire. *Bracteoles* obovate, 5–9 mm long, 2–4 mm wide, transparent, glabrous; midrib conspicuous, white; apex shortly mucronate, the mucro ~0.1 mm long; margins serrate. *Outer sepals* linear to lanceolate, 14–25 mm long, 0.7–1.1 mm wide, creamish-green or rarely with pale pink flush towards apex, adaxially glabrous, abaxially villous with spreading verticillate hairs in the upper half, the indumentum sparse, short and appressed in lower half to one third; apex acute, glabrous. *Inner sepals* linear to lanceolate, 13–25 mm long, 0.5–0.8 mm wide, creamish-green or rarely with pale pink flush towards apex, adaxially glabrous, abaxially villous with spreading verticillate hairs, the indumentum sparse, short and appressed in lower half to one third; apex acute, glabrous. *Fertile stamens* 4; *filaments* cream, 11–20 mm long, unequal, filiform; *anthers* yellow, 1.3–2.0 mm long, 0.5–0.6 mm wide. *Staminode* 1, 0.5–4 mm long. *Staminal cup* symmetrical, not lobed, 0.2–0.4 mm long, strongly adnate to sepal tube, glabrous. *Ovary* obconical, 0.8–1.5 mm long, 1–1.5 mm wide, glabrous or with a row of simple hairs apically; stipe ~1 mm long. *Style* sigmoidal, 12–22 mm long, cream, excentrically fixed on the ovary, with verticillate hairs on

lower half. *Stigma* capitate. *Seed* smooth, pale brown, 1.8–2 mm long, 1.0–1.1 mm wide. (Fig. 1E, F, 2C, D, 3B.)

Distribution and habitat

Occurs throughout arid regions of Western Australia, Northern Territory and in northern South Australia, western Queensland and north-western New South Wales (Fig. 5A), typically on plains with clayey or loamy soils and often in open mulga shrublands.

Etymology

From the Greek *xeros* (dry) and *philia* (love), referring to the distribution of this species in lower-rainfall regions of Australia than that of the other two species in the *P. macrocephalus* complex, which occur in higher-rainfall regions of eastern Australia (see Fig. 5B).

Conservation status

The species is common in Western Australia, Northern Territory, South Australia and Queensland, but may be uncommon or rare in north-western New South Wales, with only a few specimens recorded from the north-western corner of the state, where its status should be assessed.

Notes

This species often occurs *en masse*, particularly in Western Australia. We consistently observed this species being visited by night-flying moths (e.g. in the family Erebididae) in Western Australia. Floral observations were also made in daylight, and no insect visitation was seen. The flowers of this species are conspicuously sweetly scented at night. The closely related species *P. polystachyus*, which is also green-flowered and night-scented, was also observed to be visited by moths at night. We suspect *P. xerophilus* and the related green-flowering species to be primarily pollinated by nocturnal moths (see also Hammer *et al.* 2018b).

Selected specimens examined

WESTERN AUSTRALIA. Eastern Hamersley Range, *N.Casson & E.M.Mattiske MCPL1002* (PERTH); 186 km S of Carnarvon on North West Coastal Highway, *R.Davis 10995* (PERTH); on Rio Tinto Rail Access Road, ~18 km N of of Nanutarra–Munjina road, *T.Hammer & S.Dillon TH30* (PERTH); Woolgorong Station Homestead Gate, *T.Hammer & R.Davis TH61* (PERTH); 80 km N of Mullewa, *T.Hammer & R.Davis TH65* (PERTH). **NORTHERN TERRITORY.** Ruby Gorge, Hale River, 112 km ENE of Alice Springs, *A.C.Beauglehole 20724* (AD); 11.6 miles [~18.7 km] NE of Frewena, *G.M.Chippendale 7346* (PERTH); Mount Olga, W side at Docker River road junction, *N.N.Donner 4408* (AD); ~5 km SE of Alice Springs, *J.Z.Weber 893* (AD). **SOUTH AUSTRALIA.** Cordillo Downs, *J.Bates 47179* (AD); Arckaringa Station, *P.J.Lang BSOP-441* (AD); on the Indulkana Range Plateau, *P.J.Lang & P.D.Canty BS23–29163* (AD); ~16 km W of Arckaringa Homestead along road to Evelyn Downs, *T.S.Te, D.J.Duval & D.E.Murfet 1021* (AD). **QUEENSLAND.** 7.2 km E of Stonehenge, *A.R.Bean 22437* (BRI); 40 km E of Quilpie towards Charleville, *A.R.Bean 29976* (BRI); Colwell Mackinlay, *D.M.Collings s.n.* (BRI AQ0178574); 67 km WNW of Mount Isa and 6 km N of Mingera, *P.L.Harris 281* (BRI); Idalia National Park, Hobbs Tank, *C.Morgan CM11* (BRI); ~11 km E of Scott's Tank, Diamantina National Park, *M.Mostert MM256* (BRI); Well Flat, 2 km S of Wathopa

Homestead, *J.L.Silcock JLS1522* (BRI). **NEW SOUTH WALES.** 5 miles [~8 km] W of Tibooburra, *G.M.Cunningham 1164* (NSW).

Key to species of the *P. macrocephalus* group

- 1 Inflorescence rachis densely villous or tomentose2
 Inflorescence rachis glabrous or with a few sparse hairs present *P. psilorhachis*
- 2 Perennial herb with a woody taproot; outer sepals >1.4 mm wide; abaxial sepal surface with spreading verticillate hairs on entire surface (except glabrous apices); hairs present on adaxial sepal surface; staminal cup hairs present *P. macrocephalus*
 Annual or short-lived perennial herb with fleshy taproot; outer sepal <1.2 mm wide; abaxial sepal surface with short appressed hairs on bottom half; hairs absent on adaxial sepal surface; staminal cup hairs absent *P. xerophilus*

Conflicts of interest

Kevin R. Thiele is an Associate Editor for *Australian Systematic Botany*. Despite this relationship, he did not at any stage have Associate Editor-level access to this manuscript while in peer review, as is the standard practice when handling manuscripts submitted by an editor to this journal. *Australian Systematic Botany* encourages its editors to publish in the journal and they are kept totally separate from the decision-making process for their manuscripts. The authors declare that they have no further conflicts of interest.

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