

Two New Endemic Australian Genera in the Tribe *Brongniartieae* (Fabaceae) to Accommodate Two Species Formerly Included in *Templetonia* R. Br.

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Abstract

Chemical and molecular data confirm the anomalous position within *Templetonia* R. Br. of *T. biloba* (Benth.) Polhill and *T. incana* J.H. Ross. Two new genera, *Cristonia* and *Thinicola*, are described to accommodate *Templetonia biloba* and *Templetonia incana* respectively, and the relevant new combinations are made.

Introduction

Although the circumscription of a number of genera await clarification, our understanding of the phylogenetic relationships at various taxonomic levels within the tribes *Mirbelieae*, *Bossiaeeae* and the Australian genera of the *Brongniartieae* has advanced considerably in recent decades (Lee, 1973; Polhill 1976, 1981; Arroyo, 1981; Crisp & Weston 1987, 1995; Polhill, 1994; Chappill, 1995; Doyle, 1995; Crisp *et al.*, in press).

Polhill (1976, 1981), on the basis of differences in anther and seed characters, divided the genera in the *Bossiaeeae* into two groups which he termed the *Templetonia* group (*Hovea* R. Br., *Lamprolobium* Benth., *Plagiocarpus* Benth. and *Templetonia* R. Br.) and the *Bossiaea* group (*Aenictophyton* A.T. Lee, *Bossiaea* Vent., *Goodia* Salisb., *Muelleranthus* Hutch., *Platylobium* Sm. and *Ptychosema* Benth.). The *Templetonia* group was characterised by having alternately basifixed and dorsifixed anthers with narrow inconspicuous connectives, seeds with an aril in the form of a collar or cap, often with a lip, straight radicles, and a tendency to accumulate quinolizidine alkaloids. In contrast, in the *Bossiaea* group the anthers are uniform in size, all dorsifixed, with perceptible brown connectives, seeds generally with hooded cap-like arils, inflexed radicles, and a tendency to accumulate canavanine. Arroyo (1981) and Polhill (1981) commented upon the close resemblance of some elements of the *Bossiaeeae* to the *Mirbelieae* on the one hand, and to the *Brongniartieae* on the other, and each suggested that the similarities may reflect a phylogenetic relationship.

The study of Crisp and Weston (1987) revealed clearly that the *Bossiaeeae* as previously circumscribed is polyphyletic. In order to remedy this situation, the *Templetonia* group of genera was transferred from the *Bossiaeeae* to the *Brongniartieae* with which it was found to share six strong synapomorphies. The more narrowly defined *Bossiaeeae* formed a monophyletic sister group to the *Mirbelieae*. However, although not strongly supported, there is some evidence from molecular data (Crisp *et al.*, in press) that the *Bossiaeeae* and *Mirbelieae* are not monophyletic sister taxa, and that the *Bossiaeeae* is nested within the *Mirbelieae*. The *Bossiaeeae* lineage has the same embryo-sac type (*Polygonum*-type with giant antipodals) as the *Daviesia* group of the *Mirbelieae*. Contrary to previous assumptions, the *Brongniartieae* is not closely allied to the *Bossiaeeae* or to the *Mirbelieae*.

In addition to modifying the circumscription of the *Bossiaeeae* and *Brongniartieae*, Crisp and Weston (1987) highlighted (i) the anomalous position within *Templetonia* of *T. biloba* (Benth.) Polhill and *T. incana* J.H. Ross, (ii) the fact that the two species are not closely related to each other, (iii) are more closely related to *Lamprolobium*, *Plagiocarpus* and *Hovea* than they are to *Templetonia*, (iv) and the need for further work to establish the phylogenetic status of these two species (see Fig. 1). As a consequence,

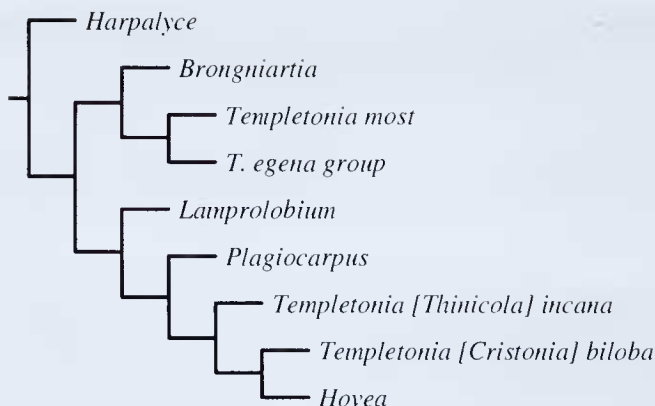


Figure 1. A portion of a cladogram taken from Crisp and Weston (1987) showing relationships between *Thiicola incana*, *Cristonia biloba*, and other exemplars of the *Brongniartieae*.

an endeavour was made to assemble additional collections and data relating to these two anomalous species of *Templetonia*, specifically chemical and molecular data, to try and establish their phylogenetic position. This paper summarises this work.

Results

ALKALOID DATA

Surveys of the alkaloids in *T. biloba* (Greinwald *et al.*, 1995b) and *T. incana* (Greinwald *et al.*, 1996a) revealed that both *T. biloba* and *T. incana* lack the ormosanine-type alkaloids that are typical constituents of the other species of *Templetonia* analysed, a finding that supports the removal of these species from *Templetonia*. *Templetonia biloba* was found to accumulate mainly α -pyridone alkaloids and tetrahydrocytisine derivatives with a fully saturated ring A. The co-occurrence of these compounds characterised *T. biloba* and it was concluded that tetrahydrocytisine and *N*-methyltetrahydrocytisine could be regarded as marker alkaloids for *T. biloba* because they represent quite rare constituents (Greinwald *et al.*, 1995b). In contrast to *T. biloba*, quinolizidine alkaloids were absent from all *Bossiaea* species studied where tyramine was found as major component of several species (Greinwald *et al.*, 1995b). This is significant because *T. biloba* was described initially as a species of *Bossiaea* before being transferred to *Templetonia* by Polhill (1976).

Templetonia incana was found to accumulate mainly α -pyridone alkaloids, together with smaller amounts of bicyclic quinolizidine alkaloids and the bipiperidyl alkaloid ammodendrine. *Templetonia incana* lacks the tetrahydrocytisine derivatives with a fully saturated ring A, that are typical constituents of *T. biloba*. The differences in the chemical profiles of *T. biloba* and *T. incana* reinforce the conclusion reached by Crisp & Weston (1987) that the two species are not sister species.

In terms of suggesting the possible affinities of *T. incana* and *T. biloba*, the alkaloid data are incomplete and, in part, inconclusive, but nevertheless provide some pointers. The data suggest that *T. incana* and *T. biloba* are more closely related to *Plagiocarpus* and *Lamprolobium* than they are to the other species of *Templetonia* or to *Hovea* (Greinwald *et al.*, 1995a). Among the Australian members of the *Brongniartieae*, ormosanine-type alkaloids have been reported only in *Hovea* and *Templetonia* (excluding *T. incana* and *T. biloba*).

Available data indicate that *T. incana*, *T. biloba* and *Plagiocarpus* have a similar

combination of quinolizidine alkaloids. Both *T. incana* and *Plagiocarpus* accumulate bicyclic quinolizidine alkaloids and mainly α -pyridone bases, and the presence of hydroxysparteines in *T. incana* and *Plagiocarpus* suggests a relationship between the taxa (Greinwald *et al.*, 1995a). The discovery of several hydroxysparteines in *T. incana* was significant because these compounds are absent from *T. biloba* and *Lamprolobium* (Greinwald *et al.*, 1996a). Although *Plagiocarpus* and *Lamprolobium* both accumulate bicyclic quinolizidine alkaloids and α -pyridones, *Lamprolobium* has the ability to produce the rather rare alkaloid lamprolobine and accumulates lower amounts of sparteine derivatives than *Plagiocarpus*.

The alkaloid pattern of *T. biloba* also exhibits a combination of bicyclic quinolizidine alkaloids and α -pyridones, but differs from that of *Plagiocarpus* by the absence of hydroxysparteine and by the presence of tetrahydrocytisine derivatives, therefore suggesting a more distant relationship to *Plagiocarpus* than is evident for *T. incana*. The presence of tetrahydrocytisine and its derivatives in *T. biloba* contrasts with the alkaloid profile of *Lamprolobium* (Greinwald *et al.*, 1995b).

To sum up, the alkaloid data suggest that *T. incana* and *T. biloba* are not closely allied, and that their affinities are with *Plagiocarpus* and *Lamprolobium* rather than with *Templetonia* or *Hovea*. It was postulated (Greinwald *et al.*, 1996b), that the detection of lamprolobine in the leaves of *Brongniartia sousae* Dorado might reflect a relationship between *Brongniartia* and *Lamprolobium* as this alkaloid is known from very few sources. Arroyo (1976) drew attention to certain similarities between *Lamprolobium* and section *Brasilianae* of *Harpalyce*, but the alkaloid data provide no insight. The alkaloid profiles of *Brongniartia* and *Harpalyce* showed significant qualitative differences (Greinwald *et al.*, 1996b). A more comprehensive analysis of the alkaloid data in the *Brongniartieae* is given in Grimes *et al.* (in preparation).

MOLECULAR DATA

Nuclear DNA from the 5S ribosomal DNA gene and spacer region and the first internal transcribed spacer region (ITS-1) of the 45S ribosomal DNA cistron of 23 taxa were sequenced (Thompson, 1999; Thompson *et al.*, in press). On the basis of the ITS-1 rDNA sequence data, and using *Bossiaea cinerea* and *Platylobium formosum* as outgroups, the members of the *Brongniartieae* form a strongly supported clade (Fig. 2). Within the *Brongniartieae*, *Harpalyce* is basal and sister to a strongly supported clade containing the remainder of the ingroup taxa. Within this clade of ingroup taxa, *Brongniartia* and *Plagiocarpus* form a clade, and *B. flava* and *P. axillaris* are sister taxa. *Lamprolobium grandiflorum*, *Templetonia incana* and *T. biloba* form a clade and there was moderate jackknife support for the pairing of *L. grandiflorum* and *T. incana*.

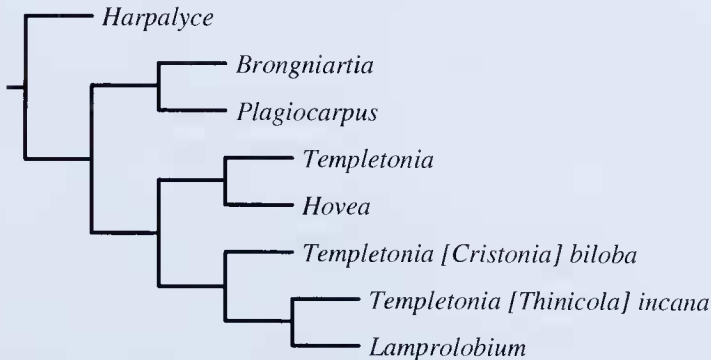


Figure 2. A portion of a cladogram taken from Thompson (1999) showing relationships between *Thinicola incana*, *Cristonia biloba*, and other exemplars of the *Brongniartieae*.

Deleting *Bossiaea* and *Platylobium* from the data set and changing the outgroup to *Harpalyce brasiliensis* resulted in a tree that differed in only a few ways from the previous one. The clade comprising *Brongniartia flava*, *B. pringlei* and *Plagiocarpus axillaris*, although unresolved, was more strongly supported, but the clade of the previous tree comprising *Lamprolobium grandiflorum*, *Templetonia incana* and *T. biloba* is collapsed and forms part of a polychotomy with the remaining ingroup taxa. *Brongniartia* appears to be more closely related to some of the Australian members of the *Brongniartieae* than it is to *Harpalyce*, the other American member of the tribe.

To sum up, the molecular data suggest that *Harpalyce* occupies an isolated position in the tribe, that *Brongniartia* and *Plagiocarpus* form a clade, and that *Lamprolobium*, *Templetonia incana* and *T. biloba* form a clade.

Discussion

The molecular and alkaloid data relating to *T. incana* and *T. biloba* are apparently contradictory. The alkaloid data suggest that the affinities of *T. incana* are with *Plagiocarpus* and that *T. biloba*, although not as closely allied as *T. incana*, also has affinities with *Plagiocarpus* rather than with *Lamprolobium* or the remaining species of *Templetonia*. On the other hand, the molecular data indicate that the affinity of *T. incana* and *T. biloba* is with *Lamprolobium* rather than with *Plagiocarpus* or the remaining *Templetonia* species, and that the affinities of *Plagiocarpus* are with *Brongniartia*.

The American genus *Harpalyce* is morphologically well circumscribed, has several unique character states, no evident close extant relative in the tribe, and its affinities are not clear. Molecular data suggest that *Brongniartia*, the only other American genus until now included in the tribe *Brongniartieae*, is more closely related to the Australian members of the tribe than it is to *Harpalyce*. However, it is evident (Hu *et al.*, 2000) that the neotropical genera *Poecilanthus* and *Cyclobium*, previously considered part of the *Millettieae*, should be included in the *Brongniartieae*. Although the molecular data associated *Brongniartia* with *Plagiocarpus*, morphologically the genera are very dissimilar. In *Brongniartia* the calyx is more or less bilabiate, the vexillar stamen-filament is free, the flowers are large, and mostly in the orange-red-purple-violet range of the colour spectrum, the pods are oblong to obovate-oblong and compressed, and the leaves are imparipinnately compound. In *Plagiocarpus*, on the other hand, the calyx is not bilabiate, the vexillar stamen-filament is not free, the flowers are small and yellow, the pods are obliquely ellipsoid and turgid, and the leaves are mostly digitately trifoliate.

Molecular data supported the sister relationship of *Lamprolobium* with *T. incana*, and associated *T. biloba* more closely with *Lamprolobium* than with *Plagiocarpus*. *Lamprolobium*, a ditypic genus, is confined in distribution to north-eastern Queensland, and *T. incana* to the sandy desert regions of Western Australia. Morphologically *Lamprolobium* and *T. incana* are dissimilar. *Lamprolobium* is distinguished readily by the calyx which is circumscissile basally, a unique character state in the tribe *Brongniartieae*, the flowers are small and yellowish, and the leaves are imparipinnately compound. In contrast, *T. incana* has large essentially red flowers that are adapted to bird pollination, and simple leaves.

All of the available evidence supports the exclusion from *Templetonia* of *T. incana* and *T. biloba*. The decision to do so is adopted here. The result of this decision to exclude *T. biloba* and *T. incana* from *Templetonia* is that the two species have to be accommodated elsewhere, either within an existing genus or genera or in a new genus or in new genera. Although the affinities of *T. biloba* and *T. incana* remain unclear, it appears most likely that they form part of a clade with the genus *Lamprolobium*. It could be argued perhaps that the two species should be accommodated within the ditypic *Lamprolobium*. However, this is not considered an appropriate option as neither species possesses a basally circumscissile calyx, the character state that is unique to *Lamprolobium*. Little is to be

gained by transferring two species that were anomalous within *Templetonia* to *Lamprolobium* where likewise they will be anomalous. *Templetonia biloba* and *T. incana* are not closely related to each other and consequently each is transferred to a new monotypic genus. The necessary changes are effected below.

Taxonomy

Cristonia J.H. Ross, *genus nov.*, a speciebus omnibus *Templetoniae* foliis simplicibus apice bilobo manifeste plerumque, lobis calycis superis connatis in limbum truncatum productis, bracteolis linearibus herbaceis; a *Plagiocarpus* foliis simplicibus corollis flavis et purpureo-fuscis, leguminibus oblongis; a *Lamprolobio* foliis simplicibus, corollis flavis et purpureo-fuscis, calycibus non basaliter circumscissis; a *Thinicola* foliis apice bilobo manifeste, corollis flavis et purpureo-fuscis, lobis calycibus superis connatis in limbum truncatum productis, stipulis magnis oblique ovatis orbiculatis vel obovato-oblongis persistentibus foliaceis destititis differt.

Typical species: C. biloba

Cristonia differs from all species of *Templetonia* in having simple leaves that are usually distinctly bilobed apically, the 2 upper calyx-lobes united into a truncate limb, and linear herbaceous bracteoles; from *Plagiocarpus* in having simple leaves, large yellow and purplish-brown corollas, and oblong pods; from *Lamprolobium* in having simple leaves, yellow and purplish-brown corollas, and calyces that are not basally circumscissile; and from *Thinicola* in having leaves that are usually distinctly bilobed apically, the standard petal pale yellow internally with a broad purplish-brown zone around the throat, and the 2 upper calyx-lobes united into a truncate limb. Furthermore, the vegetative parts, pedicels and external surface of the calyces in *C. biloba* lack the dense spreading silvery hairs that are so conspicuous in *Thinicola*, and *C. biloba* lacks the large obliquely ovate, orbicular or obovate-oblong persistent foliaceous stipules of *Thinicola incana*.

Cristonia biloba (Benth.) J. H. Ross, *comb. nov.* *Bossiaea biloba* Benth. in Endl. *et al.*, Enum. Pl. Nov. Holl. 36 (1837). *Templetonia biloba* (Benth.) Polhill, Bot. Syst. 1: 309 (1976); Ross, Muelleria 5: 6–8, figs. 3 & 4 (1982). *Type*: Western Australia, King Georges Sound, Hügel (holotype W).

Bossiaea biloba var. *stenophylla* Meisn. in Lehm., Pl. Preiss. 1: 85 (1844). *Type*: Western Australia, Swan River, J. Drummond 264 (isotypes MEL, W).

Cristonia biloba occurs in Western Australia along the coastal plain and in the Darling Range from the vicinity of Perth northwards to Shark Bay. Although relatively widespread, plants are seldom common and, when not in flower, are easily overlooked.

The hairs on the exterior of the calyx in *C. biloba* are often dark brown, a feature shared with many species of *Hovea*. The two upper united calyx-lobes in *Lamprolobium* are reminiscent of those in *C. biloba*.

The name *Cristonia* is a contraction and acknowledges the contribution of Michael D. Crisp and Peter H. Weston whose joint studies have advanced significantly our understanding of the tribes *Mirbelieae*, *Bossiaeeae* and *Brongniartieae*. The bilobed leaf apices of *C. biloba* symbolise this joint contribution.

Thinicola J.H. Ross, *genus nov.*, a speciebus omnibus *Templetoniae* partibus vegetativis pedicellis pagina externa calycis pilis densis effusis argenteis vestitis, stipulis magnis oblique ovatis orbiculatis vel obovato-oblongis persistentibus foliaceis, floribus magnis pendulis rubris admodum (*T. retusa* similitudine sed forma differt), bracteolis linearibus herbaceis; a *Plagiocarpus* et *Lamprolobio* foliis simplicibus, stipulis magnis persistentibus,

floribus magnis rubris admodum; a *Cristonia* partibus vegetativis pedicellis pagina externa calycis pilis densis effusis argenteis vestitis, foliis non apice bilobis, stipulis magnis persistentibus, floribus magnis rubris admodum differt.

Typical species: T. incana

Thinicola differs from all species of *Templetonia* in having the vegetative parts, pedicels and the external surface of the calyces clothed with dense spreading silvery hairs, large obliquely ovate, orbicular or obovate-oblong persistent foliaceous stipules, large, pendulous and essentially red flowers (also in *T. retusa* but the shape of the corolla differs), distinctive auricles at the apex of the standard claw, and linear herbaceous bracteoles; from *Plagiocarpus* and *Lamprolobium* in having simple leaves, large persistent stipules, and large essentially red flowers; and from *Cristonia* in having the vegetative parts, pedicels and external surface of the calyces clothed with dense spreading silvery hairs, leaves not bilobed apically, large persistent stipules, and large essentially red flowers. Unlike *Lamprolobium*, *Thinicola* does not have basally circumscissile calyces.

Thinicola incana (J.H. Ross) J.H. Ross, *comb. nov.* *Templetonia incana* J.H. Ross, *Muelleria* 4: 247–249, fig. 1 (1980). *Type*: Western Australia, red sand dune 19 miles ENE of Jupiter Well, 28.vii.1967, A.S. George 9065, (holotype PERTH; isotypes AD, CANB, K, MEL, PERTH).

Thinicola incana occurs on the crest of dunes in the Gibson, Great and Little Sandy Deserts in Western Australia. Sometimes grows in association with *Crotalaria cunninghamii* with which it is easily mistaken from a distance on account of the superficially similar foliage.

When first described, mature pods and seeds were unknown. This deficiency has been remedied. Pods oblong, 2.4–3.2 cm long, 1.2–1.5 cm wide, valves yellowish-brown when mature, inconspicuously transversely venose, shiny, glabrous, flattened, apically apiculate, dehiscent. Seeds elliptic to ovate or occasionally almost rounded, 5.3–6.6 mm long, 3–4.4(–5.7) mm wide, 3–4.2 mm thick, straw- to chestnut-brown, the small hilum surrounded by a cap-like aril.

The name *Thinicola* is derived from the Latin 'thinimi' meaning 'dune', and 'cola' meaning 'dweller', and refers to the preferred habitat of *T. incana* on the crests of sand dunes.

Key to the Australian genera of the *Brongniartieae*

1. Leaves all or mostly 3–5(–7)-foliolate; leaflets elliptic- to obovate-oblong, oblong, obovate, narrowly elliptic to narrowly ovate, never linear-terete or filiform2
1. Leaves simple, unifoliolate, reduced to scales or imparipinnate but then leaflets linear-terete to filiform3
2. Leaves imparipinnately compound, usually 3–5(–7)-foliolate, but distal leaves often unifoliolate; calyx circumscissile basally; pods oblong*Lamprolobium*
2. Leaves digitately 3-foliolate; calyx not circumscissile basally; pods obliquely ellipsoid*Plagiocarpus*
3. Leaves simple, unifoliolate, reduced to scales or imparipinnately compound and the leaflets linear-terete to filiform; bracteoles ovate, papery*Templetonia*
3. Leaves simple; bracteoles linear to ovate but not papery4
4. Corolla (except for markings in throat of standard) blue, purple or mauve, rarely white; pods not or scarcely longer than broad; aril 3 or more times as long as broad*Hovea*
4. Corolla yellow with purplish-brown markings or essentially red; pods oblong, much longer than broad; aril nearly circular to elliptic5

5. Subshrub to 0.5 m high; branchlets sparingly to densely clothed with villous hairs; leaves linear to linear-cuneate or cuneate-oblong, typically bilobed apically; stipules absent; corolla yellow with purplish-brown markings; 2 upper calyx-lobes fused into a truncate limb *Cristonia*
5. Shrub to 3 m high; branchlets and leaves densely clothed with spreading silvery hairs; leaves elliptic, ovate or elliptic-oblong, rounded, obtuse to slightly emarginate and apiculate apically; stipules large, conspicuous; corolla essentially red but often partially pale cream or yellow; 2 upper calyx-lobes larger than the lower 3 but not fused into a truncate limb *Thinicola*

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