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Three new species of northern Australian *Glycine* (Fabaceae, Phaseolae), *G. gracei*, *G. montis-douglas* and *G. syndetika*

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Abstract. Three new Australian diploid species in *Glycine* Willd. are described. Two of these (*Glycine gracei* B.E.Pfeil & Craven and *Glycine montis-douglas* B.E.Pfeil & Craven) are endemic to the Northern Territory whereas the third (*Glycine syndetika* B.E.Pfeil & Craven) is endemic to Queensland. *G. montis-douglas* is only known from one locality. The genetic affinities of *G. gracei* and *G. syndetika* are with other A genome species. The species *G. syndetika* is the closest relative of a diploid parent of the T2 allotetraploid race of the *G. tomentella s.l.* Hayata species complex, as well as of allotetraploid *G. pescadrensis* Hayata, which is here formally reinstated from synonymy. Images are included of the leaflet venation for several species discussed in the paper. Thus, the treatment incorporates evidence from morphology, cytology, DNA sequences and crossing experiments. A key to the subgenera and to the species within *Glycine* subgenus *Glycine* is provided, which includes all 25 described Australian taxa.

Introduction

In light of cytological, genetic and molecular evidence accumulated over the last 30 years, *Glycine tomentella* Hayata is now understood to be a genetically diverse assemblage (see Pfeil and Craven 2002). Cytologically, the complex includes diploid and polyploid taxa that form a network of shared genomes (Doyle *et al*. 2002). Species in *Glycine* have historically been grouped on the basis of chromosome affinity in synthetic hybrids, to produce a genome group system (Singh and Hymowitz 1985). Diploid individuals classified as *G. tomentella* and its near relatives have been designated as part of genome groups D, E and H (Hymowitz 2004); summarised in Table 1. The taxa comprising *G. tomentella s.l.* have been loosely united by possession of a denser indumentum than other *Glycine* Willd. species, straight pods at least until dehiscence, pinnate leaves, a racemose but clustered inflorescence, and a lack of adventitious roots. The diversity within the complex has not been taxonomically fully resolved, although some taxa allied with *G. tomentella* (in the H and I genome groups) have been recently described (Tindale 1986; Tindale and Craven 1988, 1993; Pfeil and Craven 2002).

The variation in chromosome number in the *G. tomentella* complex was recognised at least as early as 1978, with counts of $2n = 38$, 40, 78 and 80 reported (Newell and Hymowitz 1978). Groups of diploid and groups of tetraploid individuals within the species based on shared isozyme variation were later established (Doyle and Brown 1985) and subsequently confirmed by 5S repeat variation (Doyle and Brown 1989). These isozyme groups agreed with but subdivided the genome group designation, which has since been expanded (Singh *et al*. 1998; see Table 1). A hybridisation study focused on *G. tomentella* found that within isozyme groups hybrids were fertile, but hybrids between these isozyme groups were sterile (Doyle *et al*. 1986). Exceptions to this generalisation emerged later from better collections—hybrids between the two aneuploid ($2n = 38$) isozyme groups D1 and D2 from Queensland are fertile whereas some within the D5 isozyme group from Northern Australia are sterile (AHD Brown personal observation).

D4 Glycine tomentella

One of the diploid groups identified by isozyme variation, designated D4 (Table 1), was later found to be more genetically similar to species of genome group A (e.g. *G. clandestina* Wendl.) than to other *G. tomentella* genome or isozyme groups (Grant *et al*. 1984, 1986; Singh *et al*. 1988). Initial chloroplast DNA phylogenies using accessions from several *G. tomentella* isozyme groups placed these with other A genome species; however, the resolution of these phylogenies was poor within the A genome, and no discrimination could be made among *G. tomentella* isozyme

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Table 1. Species and genome groups to which plants classified as *Glycine tomentella* are related

Species	Genome group[A]	Isozyme group / Histone H3-D clade[B]
G. argyrea, *G. canescens*, *G. clandestina*, *G. gracei sp. nov.* (Daly Waters), *G. latrobeana*, *G. peratosa*, *G. rubiginosa*	A	A genome clade
G. tomentella in part	D	D3
G. tomentella in part	D_1	D5B
G. tomentella in part	D_2	D5A
G. syndetika sp. nov. (D4 *G. tomentella*)	D_3	D4 / A genome clade
G. tomentella in part	E	D1 and D2
G. arenaria, *G. hirticaulis*, *G. pindanica*, *G. pullenii*	H	D5B clade
G. montis-douglas	Not placed	Unknown

[A]Summarised by Hymowitz (2004).
[B]Summarised by Brown *et al*. (2002).

groups (Doyle *et al*. 1990*a*, 1990*b*). A later phylogenetic study using nuclear DNA sequences from the ITS region placed D4 *G. tomentella* with the A genome species (although only present in 51% of bootstrap pseudoreplicates) but clearly removed it from other diploid *G. tomentella* races, these being grouped together and with the I genome taxa in 73% of bootstrap pseudoreplicates (Singh *et al*. 1998). This finding was confirmed with robust (100%) bootstrap support from histone H3-D nuclear DNA with additional sampling within diploid *G. tomentella* isozyme groups (Brown *et al*. 2002).

Collections made near Daly Waters in the Northern Territory of Australia were initially classified as either *G. tabacina* Benth. AAB_2B_2 polyploids (= *G. pescadrensis* Hayata, below) or *G. canescens* F.J.Herm. They also share some morphological similarity with D4 *G. tomentella* plants. However, nothing further was known about them. While our current knowledge of the D4 isozyme group clearly demonstrates that it is a species distinct from the remainder of *G. tomentella*, formal recognition has not yet occurred. In this study we evaluate the taxonomic boundaries between D4 *G. tomentella* and the Daly Waters plants and their relationship to each other and the remainder of *Glycine*.

New Glycine tomentella *relative from Mt Douglas*

An unusual *Glycine* currently known only from Mt Douglas in the Northern Territory was first collected in 1999 by R.K. Harwood (Northern Territory Herbarium). It has a combination of features that make the plant unique in the genus. Additional collections made in 2001 have confirmed that a population of plants bearing this character combination exists. The taxonomic status of these plants is also evaluated here.

Glycine pescadrensis

Glycine pescadrensis Hayata originated from an allopolyploid between *G. stenophita* B.E.Pfeil & Tindale and D4 *G. tomentella* (Doyle *et al*. 2000). It occurs in eastern Australia, Taiwan and the Ryukyu Islands. Because this species has been the subject of many informal names and the name has also been placed in synonymy, we clarify the nomenclature of this species (below).

A key to Glycine

A key to *Glycine* focusing on subgenus *Glycine* (which includes all of the Australian species) is presented below. *Glycine* currently includes 27 described species by our recognition (two in subgenus *Soja* and 25 in subgenus *Glycine*). Although one more named species, *G. dolichocarpa* Tateishi & Ohashi, has not been seen by us, it is probably applicable to a tetraploid species ('race') of the *G. tomentella* complex, but has not been included in the key nor the number of species. The taxonomy of the tetraploid races of *G. tomentella* is beyond the scope of this paper.

Materials and methods

Morphology and nDNA sequences

All known relevant herbarium specimens held at the Australian National Herbarium and the Northern Territory Herbarium were examined for morphological information by a traditional taxonomic approach and used to prepare character descriptions of the three new species we describe (below). An isotype specimen of *G. pescadrensis* (at the Taiwan Forestry Research Institute, TAIF) was examined and compared with currently recognised taxa as well as unpublished taxon concepts. DNA for histone H3-D sequencing of Daly Waters plants and additional samples of other A genome species was extracted from either dried leaflets taken from herbarium specimens, silica dried leaflets, or from fresh leaflets taken from plants grown in a Cornell University glasshouse from bulked seed from the CSIRO germplasm collection held in Canberra. These sequences were compared with those of D4 *G. tomentella*, several accessions of other *G. tomentella* isozyme groups, and most other diploid species in subgenus *Glycine*. Available material of the *G. tomentella* relative from Mt Douglas did not yield consistent and reproducible sequences. DNA extraction, PCR conditions and sequencing phylogenetic analyses were as described by Doyle *et al*. (1999). New GenBank accession numbers are included in Table 2. Phylogenetic analyses were performed with Mr Bayes v.3.1.1 (Huelsenbeck and Ronquist 2001) and PAUP* v.4.10b (Swofford 1998). Bayesian analysis was run to two million generations using substitutions within 471 aligned nucleotides (GTR+I+G model) and nine binary coded indels (JC+G model with the coding = variable setting) as two partitions, with the shape parameter unlinked. After examining the likelihood *v.* generation plot, we discarded 400 trees as the burn-in and constructed a majority-rule consensus tree from the remaining 1601 trees. We also ran an analysis using a HKY+I+G model for substitutions and a JC model for indels, the results of which are practically identical to the first analysis and are not shown. Maximum parsimony bootstrapping was performed (after recoding the indels using 'A' and 'T' characters to allow inclusion in the same block) using 500 bootstrap replicates, with 10 random addition sequence replicates per bootstrap resample (holding a maximum of 50 trees per random addition sequence replicate).

Leaflet venation

Leaf venation images were recorded using a Nikon Coolpix 5000 5.0 megapixel digital camera attached to a Zeiss microscope and saved as maximum resolution TIFF files. Different magnification was accounted for by including in each photograph a scale ruler that served as the reference for image size adjustment in Adobe Photoshop 7.0. The absolute size and approximate brightness of each image was standardised with Photoshop (but no contrast adjustments were made), and only the red channel (includes only red light) was saved as a black and white image to highlight venation.

These leaf venation images provide a magnified examination of venation features that can generally be observed in the field with a hand lens using light from behind the leaf.

Cytology

Immature flower buds for chromosome analysis were fixed in ethanol : chloroform : glacial acetic acid (6 : 3 : 1) for 24 h and then transferred to 70% ethanol for storage. Anthers at the appropriate stage were dissected in a drop of FLP orcein (Jackson 1973), heated and squashed before observing under the microscope. Between 10 and 20 pollen mother cells were examined from each plant.

Results and discussion

D4 Glycine tomentella *and Daly Waters plants*

Although prior evidence from genetic, cytological, breeding and sequence data clearly show that the D4 isozyme group is a distinct taxon from other *G. tomentella* isozyme groups, morphological similarities have hindered its taxonomic recognition. It shares moderately dense and easily visible tertiary venation, a moderately dense indumentum on many parts, and a lack of stolonifery with other *G. tomentella* races. Some features that distinguish it from the remainder of *G. tomentella* include narrower leaflets and legumes with more seeds. Images of the leaflet venation variation, which is quite useful in helping distinguish among groups of *Glycine* species, are included (Figs 1–3). Species from the A genome, and diploid and tetraploid races of *G. tomentella* have been included for comparative purposes. We have observed a general consistency of venation features within species and qualitative differences among species that can be seen in these images (excluding only Daly Waters plants, which show intra-individual variation), although the limited number of samples within and among individuals precludes a robust statistical assessment of these differences. Leaflet venation variation is also used in the key to species and users of the key should refer to the images to help understand these features.

Table 2. Accession and GenBank numbers for new histone H3-D sequences

Species	Accession #	GenBank #
G. argyrea	G1626	DQ494159
G. canescens	G1301	DQ494166
G. canescens	G1672	DQ494167
G. clandestina	G1225	DQ494158
G. clandestina	G1031	DQ494160
G. clandestina	G1034	DQ494161
G. clandestina	G1123	DQ494157
G. clandestina	G1826	DQ494163
G. clandestina	G2688	DQ494162
G. gracei	G2536	DQ494153
G. gracei	G2538	DQ494154
G. gracei	G3124	DQ494168
G. latrobeana	G1387	DQ494170
G. latrobeana	G1390	DQ494169
G. peratosa	G2916	DQ494155
G. peratosa	G3144	DQ494156
G. rubiginosa	G1873	DQ494164
G. rubiginosa	G2393	DQ494165

D4 *Glycine tomentella* plants were only known from central to northern Queensland on the Great Dividing Range. We found that the plants from near Daly Waters in the Northern Territory are diploids (Fig. 4*a*) and are most closely related to D4 *G. tomentella* based on histone H3-D nDNA sequences (Fig. 5). Artificial hybrids between the Daly Waters plants and D4 *G. tomentella* plants are fertile and produce quantities of seed (data not shown).

Several morphological differences occur among these groups: Daly Waters plants have narrower leaflets (5–12 : 1, length : width) compared with D4 plants (2–3 : 1, length : width), the former has a loosely racemose inflorescence *v.* an inflorescence with flowers crowded towards the apex, mauve *v.* pink standard petals, black seed lacking tubercles *v.* red-brown seed with tubercles, and often lacking a leaf rachis (to make the leaves digitate) compared with the shortly pinnate leaves of D4 *G. tomentella* plants.

The two groups of accessions also have different histone H3-D sequences, although only sequences from Daly Waters form a monophyletic group. Their differences in sequence and morphology are consistent with their non-overlapping distributions, indicating the existence of two taxa. However, their close relationship and ability to produce fertile artificial hybrids suggests a recent shared origin. The lack of monophyly of D4 *G. tomentella* sequences suggests that the Daly Waters populations might have been derived by dispersal from a D4 population(s), although sampling of more loci and individuals is required to confirm this hypothesis.

The Daly Waters and D4 *G. tomentella* populations are described below as two new species: *Glycine gracei* B.E.Pfeil & Craven *sp. nov.* and *Glycine syndetika* B.E.Pfeil & Craven *sp. nov.* respectively, the latter name alluding to the link that this species represents between *G. tomentella* and *G. tabacina* polyploid complexes (e.g. fig. 8 in Doyle *et al*. 2002).

Glycine montis-douglas

Several features, including pinnate leaves, broad leaflets and dense venation, indicated that the novel collection from

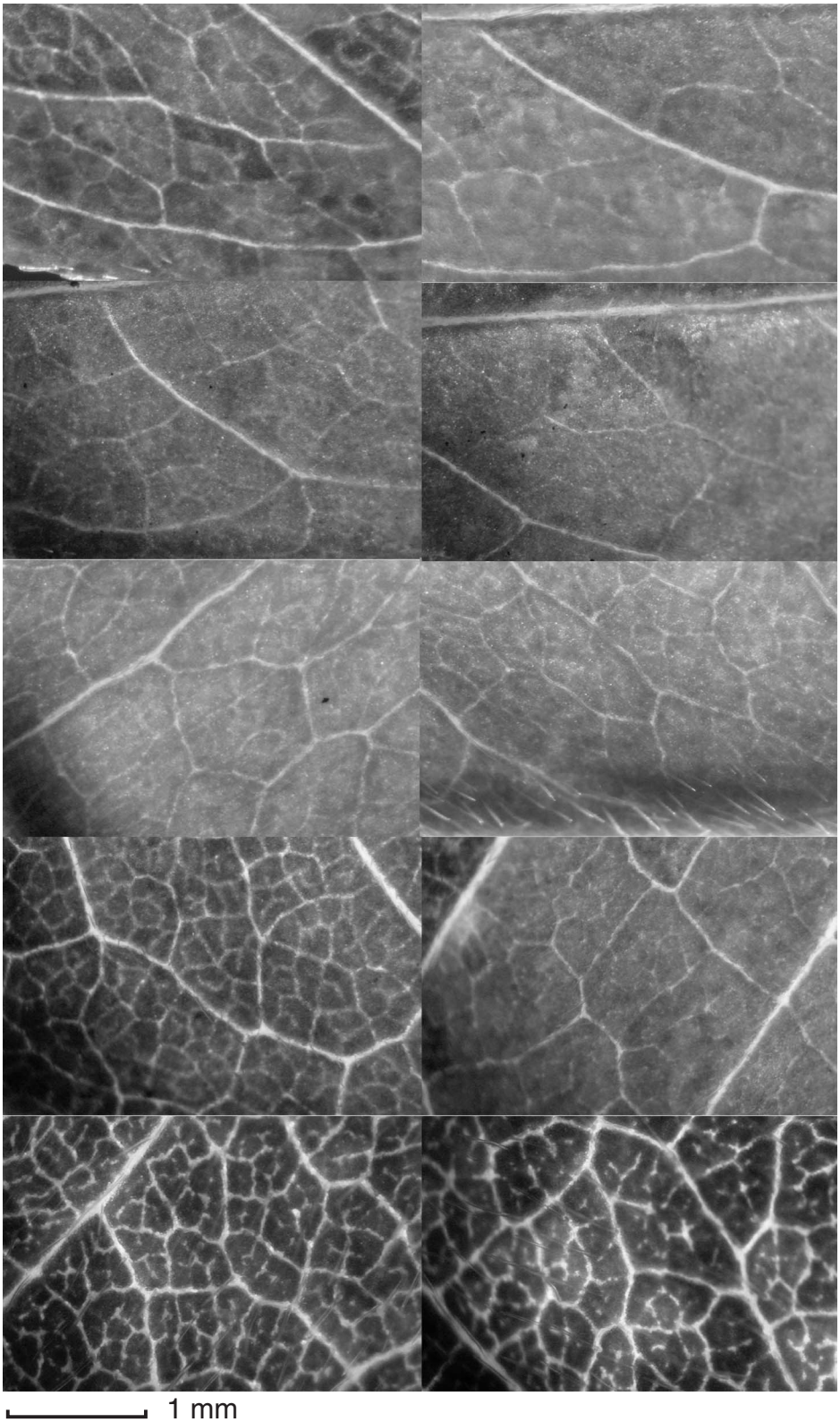

Fig. 1. A genome leaflet tertiary venation. Each horizontal pair of images are of two leaflets from the same individual. From top to bottom: G2940 (*G. aff clandestina* WA), G2972 (*G. aff canescens* WA), G1232 (*G. canescens* NSW), G2537 (*G. gracei* NT), G2321 (*G. syndetika* Qld). The tertiary venation density in the first three individuals is also typical of G1128 (*G. clandestina* NSW) and G3104 (*G. argyrea* NSW), whereas other A genome species (G2357, *G. rubiginosa* SA; G2916, *G. peratosa* WA) show lower venation density again (BE Pfeil unpubl. data).

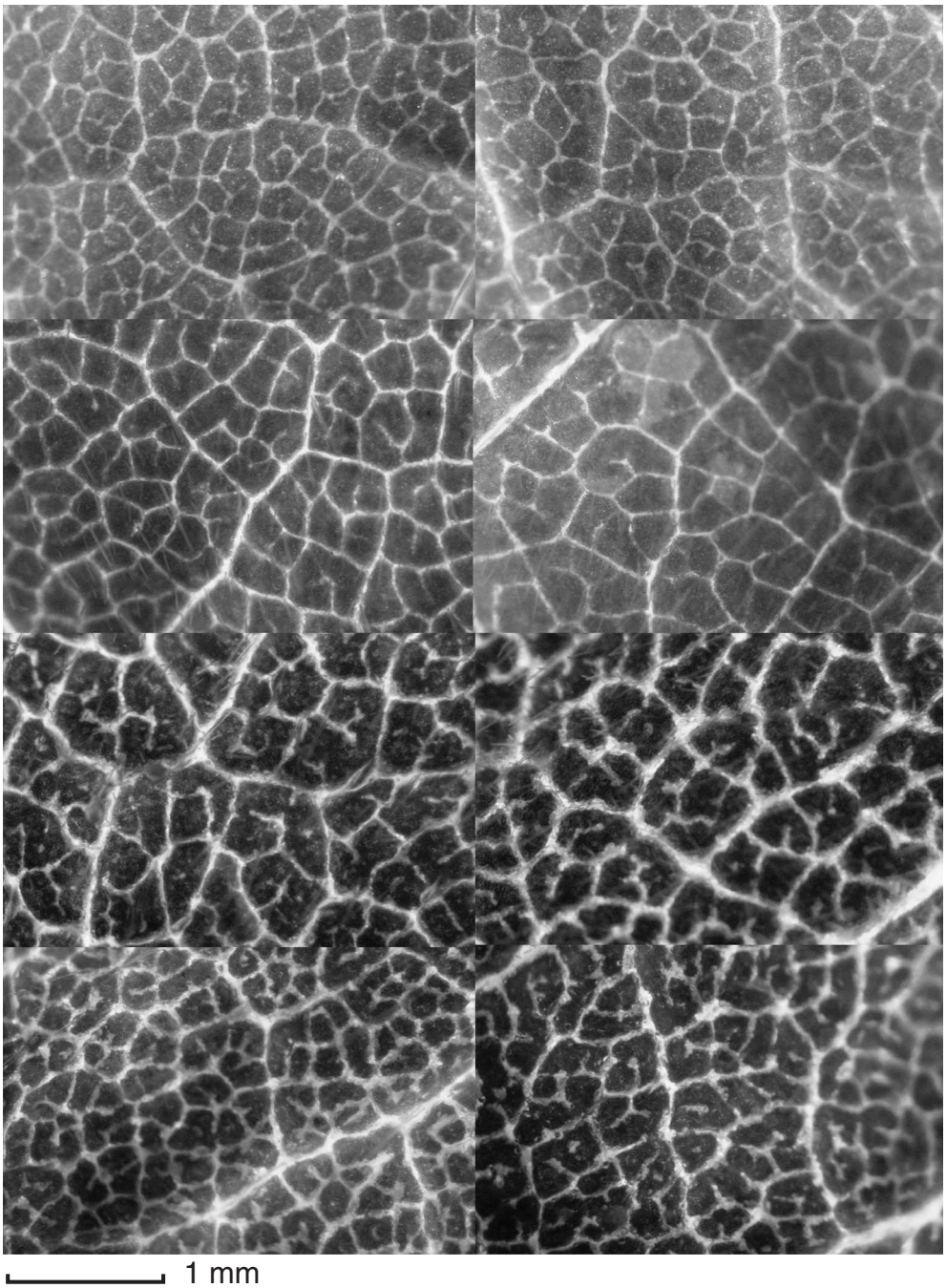

Fig. 2. *Glycine tomentella* diploid races leaflet tertiary venation. Each horizontal pair of images are of two leaflets from the same individual. From top to bottom: G1415 (D2 Qld), G1403 (D3 Qld), G2053 (D5A WA), G1932 (D5B WA). Each major clade of diploid *G. tomentella* has been sampled (Brown *et al.* 2002).

Mt Douglas has an affinity to the *G. tomentella* complex. However, other features, such as the capitate inflorescence, white corolla, and very prominent veins on the abaxial side of the leaflets, are also found in a species from the I genome, *G. albicans* Tindale & Craven, which is only known from northern Western Australia on the Mitchell Plateau. Unique to the Mt Douglas plant is that the flower-bearing portion of the inflorescence is held at right angles to the peduncle. The peduncle appears to grow along the ground until flowering is initiated, and then to grow vertically. Additional seed collections from the same area have been grown in cultivation by us where this feature has also been observed, although not as pronounced as in field-collected plants. These plants represent a new

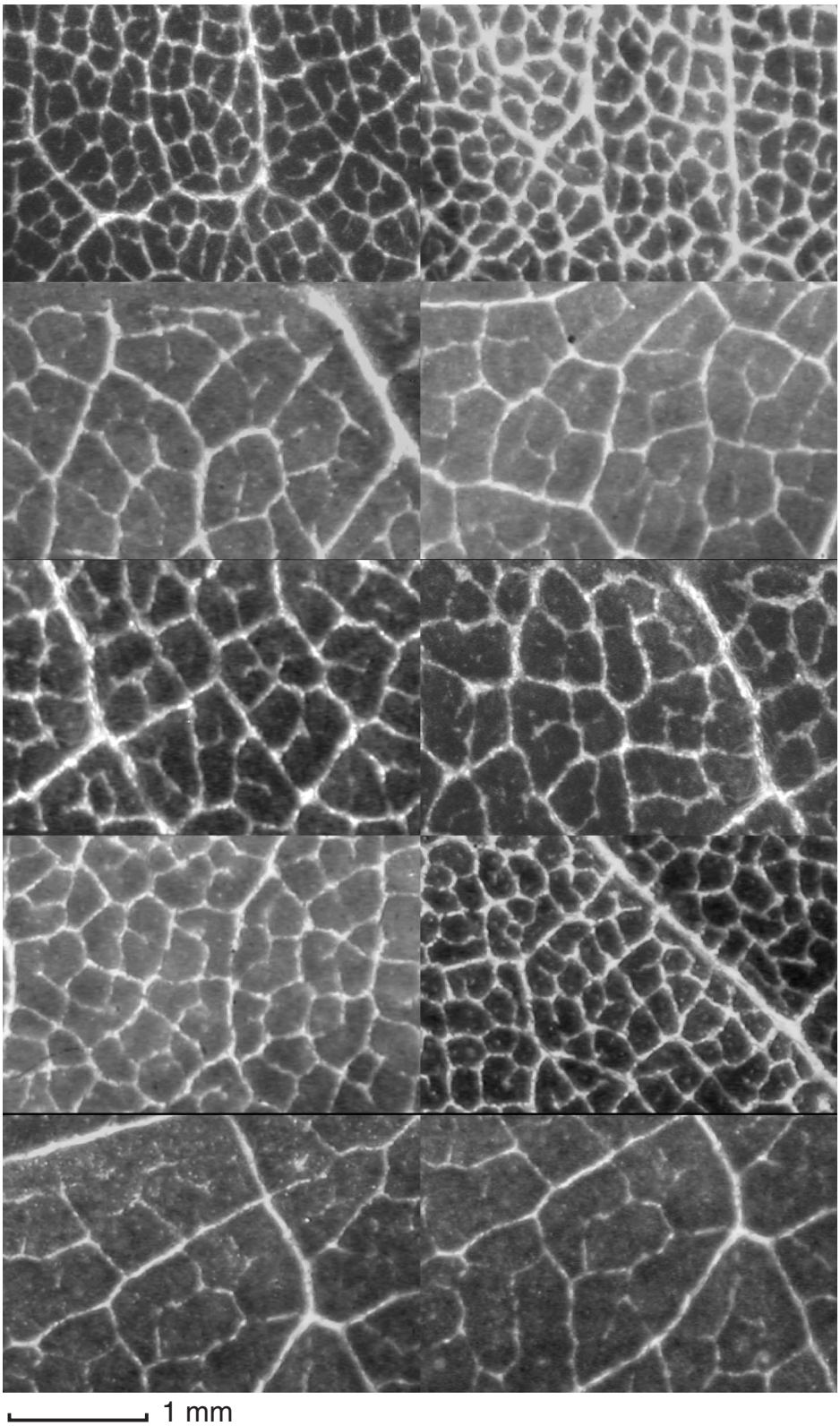

Fig. 3. *Glycine tomentella* tetraploid races leaflet tertiary venation. Each horizontal pair of panels is from the same individual. From top to bottom: G1136 (T1, which is D1 / 2 × D3 NSW), G1134 (T2, which is D3 × *G. syndetika* Qld), G1394 (T3, which is D3 × D5A Qld), G1350 (T4, which is D3 × D5B Taiwan), G1487 (T5, which is D1 / 2 × *G. clandestina* NSW). The tertiary venation density in both allopolyploids arising from A genome crosses to *G. tomentella* (T2 and T5) appears to be less than that of the other allopolyploids.

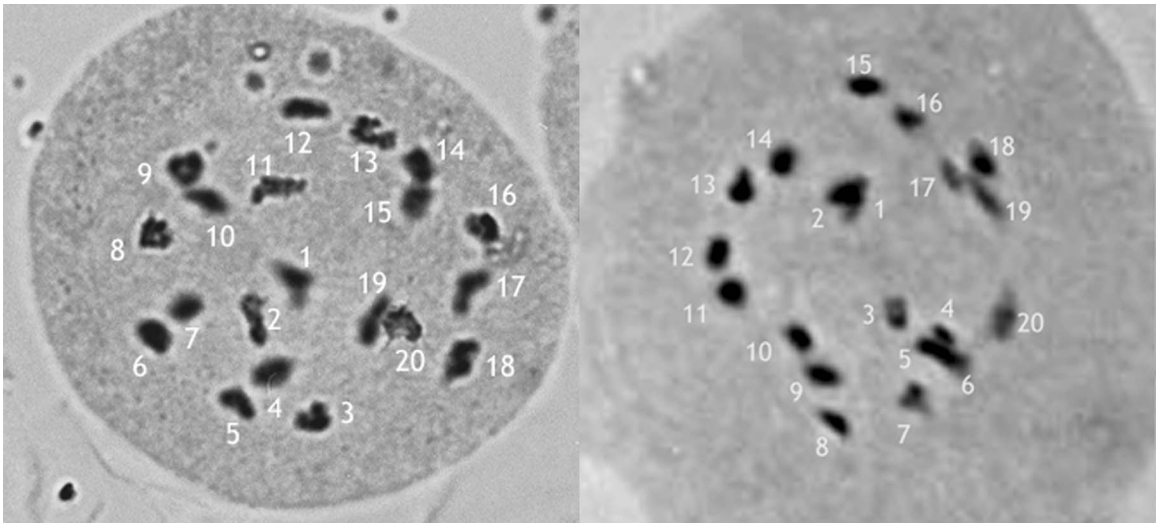

Fig. 4. Diakinesis in pollen mother cells of (*a*, left) *Glycine gracei* and (*b*, right) *Glycine montis-douglas* showing the regular formation of 20 bivalents.

species that is described here as *Glycine montis-douglas* B.E.Pfeil & Craven.

Taxonomy

Glycine gracei B.E.Pfeil & Craven, *sp. nov.*

A *G. tomentella* Hayata foliis brevipinnatis vel digitatis (rhachidibus 0–4 mm longa), foliolis angustioribus (longitudo : latitudo 5–12 : 1), inflorescentia laxe racemosa differt.

Type: Australia: Northern Territory: 201 km from the Stuart Highway at Daly [Waters] along Carpentaria Highway towards Borroloola, Lat. 16°42′S, Long. 135°28′E., 11 May 1987, *Grace, Craven & Second 280* (CANB, holo).

Climbing non-stoloniferous perennial herb. *Stem hairs* white to pale rusty, appressed or sometimes ascending, sparse to moderately dense; *stipules* up to 2.75 mm long and 1 mm wide, not fused, the hairs white to pale rusty, appressed, sparse to moderately dense. *Petioles* to 40 mm long (58 in cultivation), the hairs white to pale rusty, appressed or sometimes ascending, sparse to moderately dense. *Leaves* pinnately to digitately trifoliolate. *Lateral stipels* up to 1.75 mm long; *terminal stipels* present, up to 1.75 mm long; stipel hairs white to pale rusty, appressed to ascending, moderately dense to dense. *Petiolules* up to 1.25 mm long, the hairs white to pale rusty, ascending to ascending-spreading, moderately dense to dense. *Terminal rachis* 0–4 mm long. *Leaflets* up to 65 (73 in cultivation) mm long and 10 mm wide, linear, narrowly elliptic or narrowly ovate; margin flat; apex acute or obtuse and mucronate or mucronulate; terminal leaflets usually slightly larger than lateral leaflets. *Leaflet* length : width ratio 5–12.5 : 1. *Leaflet venation* brochidodromous; *secondary veins* obvious, especially abaxially, 20–50° from the mid-vein; reticulation visible but not pronounced, moderately dense (Fig. 1, fourth pair of panels from top). *Leaflet hairs*: *abaxial* mid-vein and lamina hairs white (to pale rusty on the mid-vein), appressed to ascending, moderately dense (rarely sparse); *adaxial* mid-vein and lamina hairs white, ascending, sparse to moderately dense.

Inflorescences racemose, flowers loosely arranged; each bract subtending a single flower. *Peduncles* up to 60 mm long, the hairs white to pale rusty, appressed to sometimes ascending, moderately dense; *bracts* up to 2 mm long and 0.5 mm wide, the hairs white to pale rusty, appressed to ascending, moderately dense. *Pedicels* up to 0.5 mm long, the hairs white, ascending to ascending-spreading, moderately dense; *bracteoles* up to 1.5 mm long, the hairs white to pale rusty, appressed, dense; bracteoles inserted at the base of the calyx or slightly below. *Calyx* 1.5–2 mm long and 1.25–1.5 mm wide, the sinus between the adaxial teeth up to 1 mm long; the calyx hairs white to pale rusty, appressed, dense. *Corolla*: standard petal pale mauve with a white to light green centre, wing and keel petals mauve; the standard 6 mm long and wide, without lobes on the lower edge; wings 4 mm long, keel 3 mm long. *Carpel hairs*: denser towards the apex of the carpels particularly on the upper and lower edge, but not forming a distinct collar.

Chasmogamous legumes (open pollinated) not seen. *Cleistogamous legumes* (self pollinated from an unopen flower with reduced petals) 30–40 mm long, 3.5–5 mm wide, brown when mature, initially straight but becoming twisted after dehiscence; the legume hairs white to pale rusty, appressed, sparse to moderately dense. Cleistogamous legumes solitary or sometimes on short peduncles to 12 mm long, not forming specialised aerial branches with pods

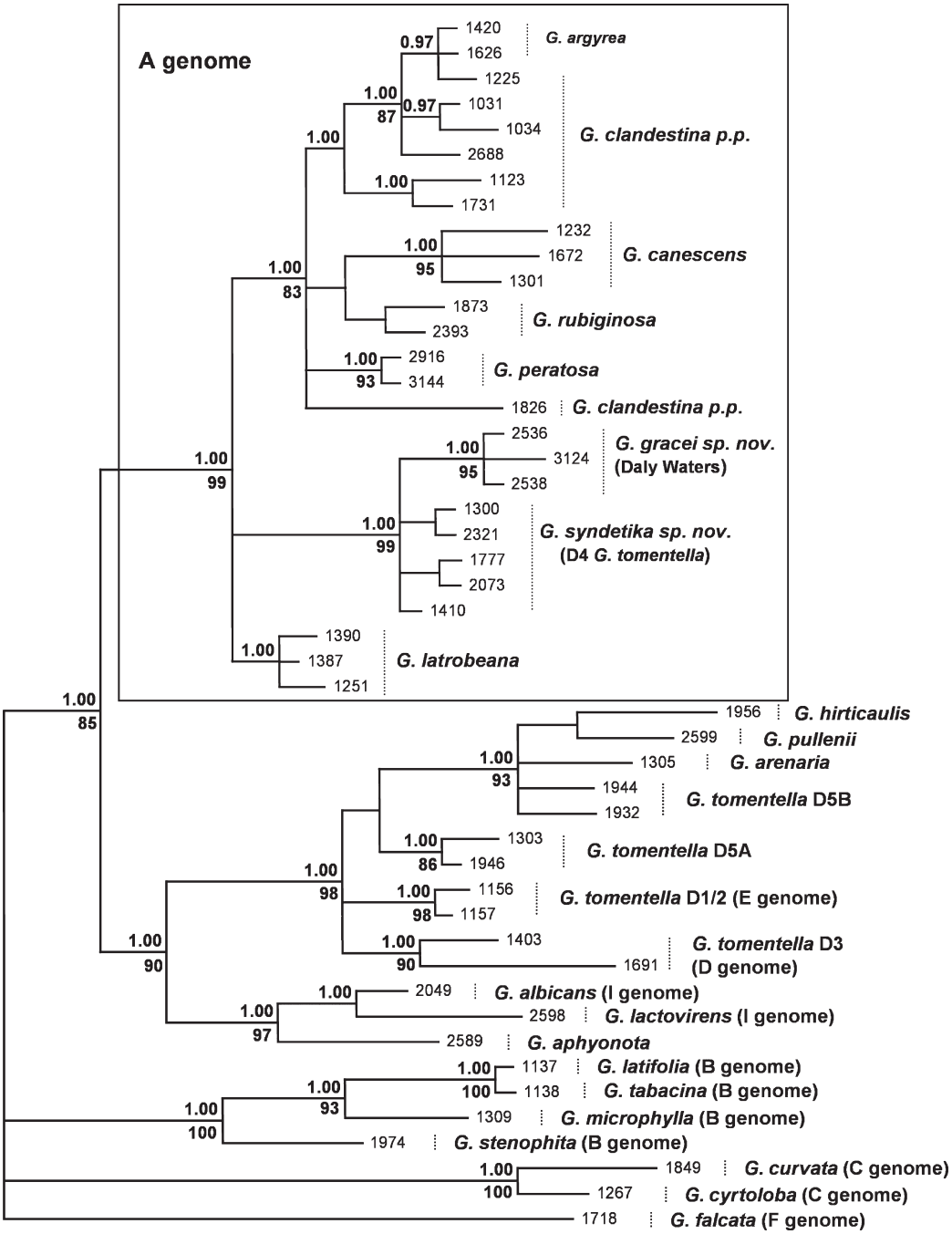

Fig. 5. Phylogeny of A genome *Glycine* species based on histone H3-D allele sequences indicating the close relationships of two of the new species, *G. gracei* and *G. syndetika*, with other A genome species. Bayesian topology and branch lengths are derived from a consensus of 1601 trees found in the stable part of the posterior probability distribution. Posterior probabilities of 0.95 and greater are shown above branches; parsimony bootstrap proportions of 80 and greater are shown below branches. The topology is unrooted, although the root probably lies along the branch leading to the F genome (Doyle *et al.* 1996).

in leaf litter. *Seeds* 4–6 (rarely 3–8) per cleistogamous legume, *c.* 3 mm long; black, not mottled, tubercles lacking; flattened barrel-shaped, with a square or shortly rectangular outline side-on, and a narrow elliptic outline end-on; surface rough (perisperm adheres), reticulation very rounded and smoothed over.

Cytological data

A chromosome count from this taxon (G3124, CSIRO germplasm number) found $2n = 40$ chromosomes with regular bivalent formation, confirming the diploid status of this plant (Fig. 5*a*) (RG Palmer, pers. comm.).

Distribution and habitat

The four wild collections known of this species occur between *c*. 50 and 250 km east of Daly Waters along the Carpentaria Highway and *c*. 150 km north of Daly Waters on Stuart Highway, NT. These plants have been found in grey-brown sandy loam on laterite and red clay.

Notes

This species does not produce litter pods. This species is named in honour of Jim Grace, formerly of CSIRO Plant Industry. His many collections, maintenance of cultivated material over many years, enthusiasm for and knowledge of the plants has ultimately contributed significantly to our understanding of *Glycine*.

Selected specimens

NORTHERN TERRITORY: 49.9 km from Stuart H'way at Daly Waters along Carpentaria H'way towards Borroloola, *Grace*, *Craven and Second 279*, 10.v.1987 (CANB); 244.7 km from Stuart Highway at Daly Waters along Carpentaria Highway towards Borroloola, *Grace*, *Craven and Second 281*, 11.v.1987 (CANB); 201.0 km from Stuart H'way at Daly River along Carpentaria H'way towards Borroloola, *Grace*, *Craven and Second 280*, 11.v.1987 (CANB); 2.5 km south of Gorrie South turn-off along Stuart Highway, *Short*, *P.S. and Dunlop*, *C.R. 4912*, 23.ii.1999 (CANB, DNA).

Glycine syndetika B.E.Pfeil & Craven, *sp. nov.*

A *G. gracei* B.E. Pfeil & Craven foliolis latioribus (longitudo: latitudo 2–3: 1), inflorescentia *versus* apicem subcongesta, petalis roseis, et semine porphyreo (perispermo medio-brunneo usque atrobrunneo) tuberculato differt.

Type: Australia: Queensland: 65 km S of the Georgetown–Mt Surprise turnoff, near Wy[a]ndotte property turnoff, Lat. 18°41′S, Long. 144°45′E, 29 July 1983, *Grace*, *Brown & Hymowitz 143* (CANB, holo).

Twining or climbing non-stoloniferous perennial herb. *Stem hairs* white to pale rusty, appressed to spreading, sparse to moderately dense; *stipules* up to 4 mm long and 1.5 mm wide, not fused, the hairs white to pale rusty, appressed to ascending, moderately dense. *Petioles* to 40 mm long (45 in cultivation), the hairs white to pale rusty, ascending to spreading, moderately dense to dense. *Leaves* pinnately trifoliolate. *Lateral stipels* up to 1.75 mm long; *terminal stipels* present, up to 1.75 mm long; stipel hairs white to pale rusty, ascending to spreading, moderately dense. *Petiolules* up to 1.5 mm long, the hairs white to rusty, ascending-spreading to spreading, moderately dense to dense. *Terminal rachis* 1–4 mm long (to 8 mm in cultivation). *Leaflets* up to 41 mm long (63 mm in cultivation) and 14 mm wide (22 mm in cultivation), elliptic, ovate, or sometimes narrowly elliptic; margin flat; apex acute or obtuse (rarely retuse), mucronate or mucronulate; terminal leaflets larger than lateral leaflets. *Leaflet* length : width ratio 2–3 : 1 (up to 4 : 1 in cultivation). *Leaflet venation* brochidodromous; *secondary veins* obvious, especially abaxially, 30–60° from the mid-vein; reticulation visible and somewhat pronounced (less so in cultivation), moderately dense (Fig. 1, bottom pair of panels). *Leaflet hairs*: *abaxial* mid-vein and lamina hairs white (to pale rusty on the mid-vein), ascending to ascending-spreading, moderately dense; *adaxial* mid-vein and lamina hairs white, ascending, moderately dense.

Inflorescences racemose, flowers somewhat clustered towards the apex; each bract subtending a single flower. *Peduncles* up to 35 mm long, the hairs white to pale rusty, ascending to ascending-spreading, moderately dense; *bracts* up to 1.5 mm long and 0.25 mm wide, the hairs white, ascending, moderately dense. *Pedicels* up to 0.5 mm long, the hairs white, ascending to ascending-spreading, moderately dense; *bracteoles* up to 1.5 mm long, the hairs white, ascending, moderately dense; bracteoles inserted at the base of the calyx or slightly below. *Calyx* 1.5–2.5 mm long and 1.25–1.75 mm wide, the sinus between the adaxial teeth up to 1 mm long; the calyx hairs white, appressed to ascending, moderately dense to dense. *Corolla* pink throughout; the standard petal 6 mm long and wide, without lobes on the lower edge; wings 4 mm long, keel 3 mm long. *Carpel hairs*: denser towards the apex of the carpels particularly on the upper and lower edge, but not forming a distinct collar.

Chasmogamous legumes not seen. *Cleistogamous legumes* 17–37 mm long, 3–4 mm wide, brown to dark brown when mature, initially straight but becoming twisted after dehiscence; the legume hairs white to rusty, ascending to ascending-spreading, sparse to moderately dense. Cleistogamous legumes solitary or paired in the leaf axils, not forming specialised aerial branches with pods in leaf litter. *Seeds* 4–9 per cleistogamous legume, *c*. 2–2.5 mm long; red-brown, with brown to dark brown tubercles (the perisperm can completely obscure the seed colour, leaving only a brown to dark brown appearance); flattened barrel-shaped, with a square or shortly rectangular outline side-on, and a narrow elliptic outline end-on; surface rough (perisperm adheres), with tubercles and irregular reticulation.

Cytological data

An accession from this species originally listed under *G. tomentella* (PI 441000, USDA, or G1300, CSIRO, germplasm numbers) was reported as having $2n = 40$ chromosomes (Newell and Hymowitz 1983) and later confirmed (Grant *et al*. 1984). Doyle *et al*. (1986) also reported G1410 as diploid.

Distribution and habitat

Distributed in Queensland south of Mt Surprise to west of Emerald. Grows in rocky sandy soils in open eucalypt woodland, from *c*. 300 to 600 m altitude.

Notes

Syndetikos is Greek for link. This species is a close relative of the parents of two tetraploids, *G. tomentella* T2 isozyme group and *G. pescadrensis*. This species does not produce litter pods. The collection by Morain, S.A. 171 (G1300 = PI 441000) is notable in the literature for its frequency of parenting success in artificial interspecific crosses (Newell and Hymowitz 1983; Grant *et al*. 1984, 1986; Singh and Hymowitz 1985; Doyle *et al*. 1986; Singh *et al*. 1988).

Selected specimens (of 8 known collections)

QUEENSLAND: 70km SE of Mt Garnet, North Kennedy District, *Morain*, *S.A.* 171, 2.xi.1967 (CANB); The Oasis, food and petrol stop 259 km north of Hughenden, 52 km NNW of Greenvale, *Grace*, *Brown and Hymowitz* 147, 30.vii.1983 (CANB); 3.3 km west of Greenvale, beside Red Bank Creek, *Grace*, *Brown and Hymowitz* 146, 30.vii.1983 (CANB).

Glycine montis-douglas B.E.Pfeil & Craven, *sp. nov.*

A *G. albicanti* Tindale & Craven habitu prostrato et foliis pinnatim trifoliolatis, et a *G. lactovirenti* Tindale & Craven foliis pinnatim trifoliolatis, calyce breviore (usque 2.5 mm longo), vexillo breviore (5 mm longo) et trichomatibus petioli et paginae abaxialis foliolorum albis differt.

Type: Australia: Australian Capital Territory: Canberra, cultivated in CSIRO greenhouse, 30 January 2003, *Craven 10445* (DNA, holo; A, B, BRI, CANB, K, L, NSW, P, US, iso), (Provenance: Northern Territory, Mt Douglas, *Craven*, *Hymowitz & Dixon 10403*).

Prostrate non-stoloniferous perennial herb. *Stem hairs* white to pale yellow, spreading, moderately dense; *stipules* to 2.5 mm long, 1.75 mm wide, not fused, the hairs white, appressed to ascending, moderately dense to dense. *Petioles* to 65 mm long, the hairs white, spreading, moderately dense to dense. *Leaves* pinnately trifoliolate. *Lateral stipels* to 2 mm long; *terminal stipels* present, to 1.25 mm long; stipel hairs white, ascending, moderately dense to dense. *Petiolules* to 3.5 mm long, the hairs white, spreading, moderately dense to dense. *Terminal rachis* to 18 mm long. *Leaflets* up to 62 mm long (to 70 mm in cultivation) and up to 54 mm wide, elliptical, obovate or ovate; margin flat; apex obtuse and usually mucronulate, rarely slightly retuse; terminal leaflets usually larger than lateral leaflets; lateral leaflets sometimes slightly asymmetric. *Leaflet* length : width ratio 1.1–1.6 : 1. *Leaflet venation* brochidodromous; *secondary veins* obvious, 30–50° from mid-vein; reticulation obvious, moderately dense. *Leaflet hairs*: abaxial mid-vein and lamina hairs white, spreading, moderately dense to dense; adaxial mid-vein and lamina hairs white, spreading, moderately dense.

Inflorescences terminally compressed ('capitate'), the chasmogamous flower-bearing portion held aloft vertically and usually at right angles to the peduncle, the latter growing along the ground; each bract subtending a single flower. *Peduncles* up to 80 mm long, the hairs white, spreading, dense; *bracts* up to 1.5 mm long and 0.5 mm wide, the hairs white, ascending, dense. *Pedicels* up to 1 mm long, the hairs white, appressed to ascending, dense; *bracteoles* up to 1.25 mm long, the hairs white, appressed to ascending, dense; bracteoles inserted at the base of the calyx. *Calyx* up to 2.5 mm long and 2 mm wide, the sinus between the adaxial teeth *c*. 0.75 mm long; the calyx hairs white, appressed to ascending, dense. *Standard petal* 5 mm long and 5 mm wide and with small lobes on the lower edge, white with green base; wing petals 4 mm long, greenish, keel petals 4 mm long, light purplish. *Carpel hairs*: evenly spread to halfway up the style.

Chasmogamous legumes 17–21 mm long and 5–6 mm wide, brown when mature, initially straight but becoming twisted after dehiscence; the legume hairs white, ascending to ascending-spreading, moderately dense. *Cleistogamous legumes* 8–10 mm long and 5–6 mm wide, borne on specialised aerial inflorescences derived from leaf axillary buds that penetrate the soil. *Seeds* 1–2 per chasmogamous legume (1 per cleistogamous legume), *c*. 5.5 mm long; dark brown–black; ellipsoidal; surface rough (the perisperm adheres), with small tubercles and sometimes with angular reticulation.

Cytological data

One individual of this species (*L.A. Craven*, *T. Hymowitz and D. Dixon 10402*) has been confirmed as a diploid, with $2n = 40$ chromosomes and normal bivalent pairing (Fig. 4*b*).

Distribution and habitat

This species is only known from Mt Douglas, NT, approx. 120 km SE of Darwin and approx. 40 km S of Annaburroo Station. It occurs on lower slopes and flats below sandstone in *Eucalyptus bleeseri* woodland with *Erythrophleum*, *Livistona inermis* and annual sorghum on dark sandy soil with a fine talus layer.

Notes

Flowers and immature fruit have been recorded in March, whereas mature cleistogamous fruit has been recorded in June. The species is very unusual in that it does not produce litter pods as do many other northern Australian species of *Glycine*. In the other litter pod species, it appears that the production of the branch systems from buds in the leaf axils, upon which cleistogamous flowers and fruit occur, is a spontaneous response to the stem becoming partly covered with leaf litter during heavy rain. In *G. montis-douglas*,

in contrast, the stems are mostly trailing across fine talus from the adjacent sandstone slopes and consequently do not become covered with leaf litter. Un- or little-branched leaf axillary shoots of this species grow vertically into the soil and then at a few cm depth develop cleistogamous flowers. The same phenomenon was observed by one of us (LAC) in June 2001 on stems of *G. hirticaulis* subsp. *leptosa* at the Howard Springs turnoff locality where the stems were not directly on the soil surface.

Selected specimens (all known wild collections)

NORTHERN TERRITORY: Mt Douglas, SW end, plot 1682, *R.K. Harwood 561*, 9.iii.1999 (DNA), Mount Douglas, *L.A. Craven*, *T. Hymowitz & D. Dixon 10402*, 4.vi.2001 (CANB); Mount Douglas, *L.A. Craven*, *T. Hymowitz & D. Dixon 10403*, 4.vi.2001 (CANB).

Glycine pescadrensis Hayata

Hayata, Ic. Pl. Formosanarum 9: 26. (1920). *Type*: Taiwan: Bokoto Isl, May 1909, *Kawakami s.n.* (TAIF, iso)

Glycine pescadrensis was synonymised with *G. clandestina* Wendl. by Hosokawa (1935). Hermann (1962) followed Hosokawa, although he stated that he had not had the opportunity to study type material; perhaps for this reason his synonymy was qualified with a question mark. More recently, Ohashi *et al*. (1991) and Tateishi and Ohashi (1992) placed *G. pescadrensis* in the synonymy of *G. tabacina* Benth. Tateishi and Ohashi (1992) indicated that they did this following the application of the name *G. tabacina* to the plant in the Penghu Islands by Chuang and Huang (1965). To establish accurately the application of the name *G. pescadrensis*, a search for type material was undertaken by LAC and BEP and an isotype specimen was located in the herbarium of the Taiwan Forestry Research Institute (TAIF) and borrowed for examination. The specimen is conspecific with a species that had been variously given the informal names '*G. tabacina* AAB_2B_2 polyploid' (Doyle *et al*. 1990*c*), '*G. tabacina* without adventitious roots' (Singh *et al*. 1987), '*G. pacifica* ms' (Pfeil and Tindale 2001), '*G. tabacina* taxon A' (Tindale 1991), and '*G. tabacina* 'L' polyploid' (the latter two occurring on herbarium annotations at CANB).

Glycine pescadrensis is a widely occurring species being in Taiwan, the Ryukyu Islands and Australia. The Australian distribution is disjunct, with the species occurring from Cape York Peninsula in Queensland south to central-eastern New South Wales.

Cytological data

The chromosome number of this species is $2n = 80$. This number has been reported for material held in the USDA (PI number) and CSIRO (G number) germplasm collections and listed under '*G. tabacina* without adventitious roots' in Table 1 of Singh *et al*. (1987) that we classify under this species (PI 440994 = G1430; PI 440996 = G1433 = *Grace 752*; PI 505195 = G1828 = *Grace 948*; PI 505200 = G1925 = *Grace 946*; the Grace collections are listed below).

Selected specimens

Cultivated specimens: ACT: cultivated at Canberra, *Grace 752*, [day and month unknown].1984 (CANB) (Provenance: Clarenza, 8 km S of Grafton, NSW, leg. *Wilson 11797*), cultivated at Canberra, *Grace 948*, 20.iii.1985 (CANB) (Provenance: Jump-up site, Weipa, Qld, leg. *Grace, Brown & Hymowitz*), ACT: cultivated at Canberra, *Grace 946*, 20.iii.1985 (CANB) (Provenance: Pine Tree Creek, 116 km N of Hughenden, leg. Grace, Brown & Hymowitz).

Wild-collected specimens: QUEENSLAND: W side of Burdekin Falls–Mingela road, 12 km N of Burdekin Falls, *Jobson 1111*, 8.iv.1990 (CANB), N bank of Warrego River, N of Charleville, W side of Highway 71, *Bruhl 253*, 3.v.1986 (CANB). NEW SOUTH WALES: Marshalls Ponds, 15 km N of Moree, *Grace & Brown 249*, 26.viii.1985 (CANB), Alroy Park, Singleton Heights, Hunter Valley, *Pullen & Grant 11080*, 10.xii.1984 (CANB).

Key to *Glycine*

1. Peduncle below lowest flower very reduced or absent; inflorescence racemose with short internodes; annual habit . . . . . subgenus *Soja* (Moench) F.J.Herm. (2 species; northern and central China, Korea, Japan, far eastern Russia, Taiwan)
   Peduncle clearly present below lowest flower (>2 cm long); inflorescence racemose, either loosely or terminally compressed; perennial habit . . . . subgenus *Glycine* (25 species; chiefly Australia, various islands of the southern western Pacific, Taiwan, Ryukyu Islands, Pescador Islands)

Key to subgenus *Glycine* (includes all Australian taxa)

1. Inflorescence terminally compressed ('capitate')
   2. Leaflet length : width <3 : 1
      3. Plant erect; leaflet abaxial surface hairs dense, abaxial areoli obscured by hairs; rhizome bearing cleistogamous fruit . . . . . *G. albicans* Tindale & Craven
      3: Plant prostrate; leaflet abaxial surface hairs moderately dense to dense, abaxial areoli not obscured by hairs; usually not rhizomatous (if so, then lacking cleistogamous fruit)
         4. Leaves digitately trifoliolate; calyx *c*. 5 mm long; standard petal 7–7.5 mm long; petiole and abaxial leaflet hairs cream or pale ferruginous . . . . . *G. lactovirens* Tindale & Craven
         4: Leaves pinnately trifoliolate; calyx up to 2.5 mm long; standard petal 5 mm long; petiole and abaxial leaflet hairs white . . . . . *G. montis-douglas* B.E.Pfeil & Craven
   2: Leaflet length : width >8 : 1
      5. Standard petal white; secondary veins 60–80° from mid-vein

6. Leaflets up to 14 mm wide, the margins flat or slightly recurved; hairs on stem, abaxial lamina and peduncle mostly short (up to 0.25 mm long) with scattered longer hairs (*c*. 0.75 mm long) present; stem hairs moderately dense; abaxial lamina sparsely to moderately densely hairy . . . . . *G. hirticaulis* Tindale & Craven subsp. *hirticaulis*
6: Leaflets up to 5 mm wide (rarely to 7 mm), the margins strongly recurved; hairs on stem, abaxial lamina and peduncle mostly present (*c*. 0.75 mm long); stem glabrous or sparsely hairy; abaxial lamina glabrous to sparsely hairy . . *G. hirticaulis* subsp. *leptosa* B.E.Pfeil
5: Standard petal pink, purple, mauve or blue; secondary veins 40–60° from mid-vein . . . . . *G. pindanica* Tindale & Craven
1: Inflorescence not terminally compressed, although sometimes the flowers crowded towards the apex
7. Fruit apex curved upwards at maturity, either sharply distally to include the last one or two seeds (*G. canescens*) or more gently to include most of the pod (other species)
8. Leaflet reticulation usually obvious (similar to Fig. 2); secondary veins ≥60° (Qld, coast and ranges)
9. Fruit without purple flecks at maturity; seed perisperm without tubercles, alveoli regular (circular to oval) . . . . . *G. curvata* Tindale
9: Fruit with purple flecks at maturity; seed perisperm with flattened tubercles, alveoli irregular . . . . . *G. cyrtoloba* Tindale
8: Leaflet reticulation obscure (similar to the top 3 panels in Fig. 1); secondary veins usually <60° (W of the Great Divide)
10. Seed smooth (perisperm not adhering); leaves digitately trifoliolate; rhizomatous; 1-seeded cleistogamous fruit on rhizomes . . . . . *G. falcata* Benth.
10: Seed rough (perisperm adhering); leaves pinnately to sometimes digitately trifoliolate (individuals generally have one type); not rhizomatous; 3- or more-seeded cleistogamous fruit axillary . . . . . *G. canescens* F.J.Herm.
7: Fruit straight, or only the very tip slightly curved with the curvature not including any seeds
11. Leaves digitately trifoliolate
12. Leaflet reticulation obvious
13. Seed tuberculate; plant stoloniferous or not
14. Leaflet length : width >12 : 1; fruit 3-seeded; plant not stoloniferous . . . . . *G. pindanica* Tindale & Craven
14: Leaflet length : width <7 : 1; fruit 4–6-seeded; plant stoloniferous . . . . . *G. microphylla* (Benth.) Tindale
13: Seed not tuberculate; plant not stoloniferous
15. Leaflet length : width 0.8–3.7 : 1; stipules fused on one side . . . . . *G. latrobeana* (Meisn.) Benth.
15: Leaflet length : width 5–12.5 : 1; stipules not fused . . . . . *G. gracei* B.E.Pfeil & Craven
12: Leaflet reticulation obscure or nearly so
16. Fruit 7–13-seeded and secondary veins >50°; eastern coast and ranges
17. Leaflet abaxial surfaces densely hairy; hairs white or sometimes pale rusty . . . . . *G. argyrea* Tindale
17: Leaflet abaxial surfaces sparse to moderately hairy; hairs white to rusty . . . . . *G. clandestina* J.C.Wendl.
16: Fruit ≤6-seeded and / or secondary veins <50°; rarely fruit up to 9-seeded and secondary veins up to 60°, but then in NT
18. Secondary veins obscure
19. Fruit 5–9-seeded, up to 30 mm long; seed surface smooth; leaflet adaxial surface hairs almost always absent . . . . . *G. rubiginosa* Tindale & B.E.Pfeil
19: Fruit 2–4-seeded, up to 18 mm long; seed surface rough; leaflet adaxial surface hairs sparse . . . . . *G. peratosa* B.E.Pfeil & Tindale
18: Secondary veins obvious
20. Terminal stipels absent; stipules partly fused on one side, broad +/− blunt . . . . . *G. latrobeana* (Meisn.) Benth.
20: Terminal stipels present; stipules free
21. Inflorescence loosely racemose; fruit 4–9-seeded; leaflet length : width ratio 5–12.5 : 1 . . . *G. gracei* B.E.Pfeil & Craven
21: Flowers crowded towards the inflorescence apex; fruit 3-seeded; leaflet length : width ratio >12 : 1 . . . . . *G. pindanica* Tindale & Craven
11: Leaves pinnately trifoliolate
22. Leaflet reticulation obscure; rachis < 4 mm long; not stoloniferous
23. Seed lacking tubercles . . . . . *G. gracei* B.E.Pfeil & Craven
23: Seed with tubercles
24. Fruit 7–13-seeded, up to 70 mm long; leaflet secondary veins obvious, 40–90°; leaflet length : width 2 : 1–50 : 1
25. Leaflet abaxial surfaces densely hairy; hairs white or sometimes pale rusty . . . . . *G. argyrea* Tindale
25: Leaflet abaxial surfaces sparse to moderately hairy; hairs white to rusty . . . . . *G. clandestina* J.C.Wendl.
24: Fruit 2–4-seeded, up to 18 mm long; leaflet secondary veins obscure, 40–60°; leaflet length : width 4 : 1–10 : 1 . . . . . *G. peratosa* B.E.Pfeil & Tindale
22: Leaflet reticulation usually obvious; rachis variable, often >4 mm long; sometimes stoloniferous
26. Seeds 4–5 mm long, orange or mottled orange-brown (perisperm partly adhering); peduncles <80 mm long, often <20 mm long . . . . . *G. pullenii* B.E.Pfeil, Tindale & Craven
26: Seeds <4 mm long, brown or black (perisperm usually completely adhering); peduncles variable, up to 200 mm long
27. Stoloniferous, adventitious root buds may be visible in axils of older stems, brown; leaflet length : width 1.3–7 : 1
28. Seeds with obvious raised tubercles (appearing granular under a microscope); leaflet length : width 1.3–2.2 : 1; plants moderately hairy on most parts . . . . . *G. latifolia* (Benth.) C.A.Newell & Hymowitz
28: Seeds with very obscure flattened tubercles; leaflet length : width 1.6–7 : 1; plants sparsely hairy on most parts
29. Seeds usually short barrel-shaped (rarely more or less spherical); leaflet length : width 1.6–4 : 1; secondary veins 30–60° from mid-vein (rarely to 70°) (east coast and tablelands) . . . . . *G. tabacina* (Labill.) Benth.
29: Seeds usually more or less spherical; leaflet length : width 2–7 : 1; secondary veins 60–80° from mid-vein (mainly east coast) . . . . . *G. microphylla* (Benth.) Tindale
27: Not stoloniferous, lacking adventitious root buds; leaflet length : width 1.1–20 : 1

30. Leaflet abaxial surfaces moderately to densely hairy, adaxial surfaces sparsely to densely hairy; adaxial calyx teeth usually 0.75–2 mm long; cleistogamous fruit either in leaf axils or on specialised branches arising from partly-covered aerial stems ('litter pods')
    31. Leaflet length : width 5–13 : 1; rachis <4 mm long
        32. Seed rough, tuberculate; standard petal purple to violet; fruit 1–2-seeded; able to produce litter pods ..... *G. arenaria* Tindale
        32: Seed non-tuberculate; standard petal pink to pale mauve; fruit more than 4-seeded; never producing litter pods ..... *G. gracei* B.E.Pfeil & Craven
    31: Leaflet length : width 1.1–6 : 1; rachis variable, up to 15 mm long
        33. Standard petals 4–5 × 4–5 mm; stem hairs white to grey-white, never pale rusty; stems quite robust, not herbaceous; inflorescences up to 30 mm long, with 3–5 flowers; terminal leaflets 2–3 times longer than lateral leaflets ..... *G. aphyonota* B.E.Pfeil
        33: Standard petals 5–9 × 4–8 mm; hairs on most parts white to pale rusty; stems herbaceous; inflorescences 20–80 mm long, with *c*. 5–15 flowers; terminal leaflets usually up to 2 times longer than lateral leaflets
            34. Leaf terminal rachis 0–4 mm long ..... *G. syndetika* B.E.Pfeil & Craven
            34: Leaf terminal rachis up to 15 mm long, usually longer than 4 mm
                35. Able to produce litter pods (cleistogamous fruit under leaf litter) ..... *G. tomentella* Hayata races D5B, T4
                35: Never producing litter pods ..... *G. tomentella* Hayata races D1–3, D5A, T1–3, T5–6)
30: Leaflet abaxial surfaces sparsely hairy, adaxial surfaces glabrous to sparsely hairy; adaxial calyx teeth 0.25–1 mm long; cleistogamous fruit in leaf axils only, 3–9-seeded
    36. Fruit usually up to 6-seeded (rarely 7-seeded); fruit usually up to 28 mm long (rarely to 30 mm); adaxial calyx teeth 0.25–0.5 mm long; diploid ($2n = 40$) ..... *G. stenophita* B.E.Pfeil & Tindale
    36: Fruit usually 6–9-seeded (rarely 4-seeded); fruit usually >28 mm long (rarely from 25 mm long); adaxial calyx teeth 0.25–1 mm long; tetraploid ($2n = 80$) ..... *G. pescadrensis* Hayata

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