Telopea 13(1-2) 77–92

Walwhalleya jacobsiana (Poaceae, Paniceae), a new, rare species of grass from South Australia

Jeremy J. Bruhl and R.D.B. (Wal) Whalley

Botany and N.C.W. Beadle Herbarium, School of Environmental and Rural Science, University of New England, Armidale NSW 2351 Australia
Author for correspondence: jbruhl@une.edu.au; rwhalley@une.edu.au

Abstract

Phenetic (ordination and cluster) analysis using an extensive morphometric character set of all three species of the grass genus *Walwhalleya* (*W. pungens*, *W. subxerophylla* and *W. proluta*) and the monospecific *Homopholis* (*H. belsonii*) corroborated intuitive recognition of a new species, '*Walwhalleya* sp. Flinders Ranges'. The new species is characterised in part by prominently strigose upper glumes and lower lemmas. Known only from two gatherings, and likely rare, we assign it the IUCN conservation status of 'data deficient'. We name this new species ***Walwhalleya jacobsiana*** in honour of Surrey Jacobs.

Introduction

Previous phenetic and cladistic analyses of some members of Paniceae resulted in the erection of the new genus *Walwhalleya* (K.E.Wills & J.J.Bruhl) K.E.Wills & J.J.Bruhl (syn. *Whalleya* K.E.Wills & J.J.Bruhl, *nom. illeg. non Whalleya* J.D.Rogers, Y.M.Ju & F. San Martín). The genus includes *Walwhalleya proluta* (F.Muell.) K.E.Wills & J.J.Bruhl, *W. subxerophylla* (Domin) K.E.Wills & J.J.Bruhl and the newly described *W. pungens* (K.E.Wills & J.J.Bruhl) K.E.Wills & J.J.Bruhl. *Homopholis* C.E.Hubb., from which *Walwhalleya* was separated, was restricted to the type species, *H. belsonii* C.E.Hubb. (Webster 1987; Wills et al. 2000; Bruhl et al. 2006).

In preparing to return loans for our previous studies of these grasses (Wills et al. 2000; Bruhl et al. 2006), we examined 120 specimens of *Walwhalleya proluta* from MEL and 65 specimens from AD that had not been used in the previous analyses. Two gatherings from the Flinders Ranges appeared to be distinctly different from the rest of the specimens, and we intuitively segregated them as a putative new species. We also observed unrecorded variation in spikelet indumentum in some other specimens. The aim of the present study was to investigate the extent of morphological variation among the additional 185 specimens, and their taxonomic status.

 ISSN0312-9764

Materials and Methods

Selection of specimens: thirty five specimens (Table 1) were used as operational taxonomic units (OTUs) (cf. Wills et al. 2000), including additional material of *Walwhalleya proluta* from AD and MEL to sample the range of indumentum on the glumes and lower lemma, including the two morphologically distinct specimens from AD. Selection of OTUs was biased towards presence of good vegetative and flowering material. An additional specimen each of *W. pungens* and *Homopholis belsonii* was selected to verify that the scoring of characters in the new study by RDBW was consistent with that of Wills (1996). All the original specimens examined by Wills (1996) were reassessed in this study for extra characters.

Character selection: the original data set used by Wills et al. (2000) was reduced to only include vegetative, inflorescence and spikelet morphological characters. OTUs of other genera and species such as *Digitaria coenicola* (F.Muell.) Hughes, *Panicum effusum* R.Br. and *P. queenslandicum* Domin, included in Wills et al. (2000), were omitted here. Attributes from the original study rendered invariant in the present data set were removed. Obvious differences apparent in the indumentum of the glumes and lemmas among the new specimens prompted the addition of further characters (see asterisks in Table 2). A total of 82 characters were used in the analyses (Table 2). Characters were scored on dried herbarium specimens or rehydrated material for some of the spikelet characters. Methods for morphology, micromorphology and anatomy follow Wills et al. (2000).

Analyses: a single data matrix was constructed for all characters (Appendix 1). Cluster and ordination analyses were undertaken using PATN V. 3.03 (Blatant Fabrications Pty. Ltd). All characters were given equal weighting in the analyses. Gower Metric was used for the association measure. Phenograms were produced using flexible UPGMA with β=-0.1. Three dimensional ordination plots of semi-strong hybrid multidimensional scaling (SSH MDS) were generated. 'Number of iterations' was increased to 1000 to minimise stress in the ordination. Phenograms, ordination scatter plots and plots of correlation of characters with ordination pattern (PCC) were produced directly from PATN and figures colour-coded using Adobe Illustrator CS3 v. 13.0. The criteria for accepting the putative species as distinct entities were 1) the OTUs representing the putative species formed a discrete group distinct from all other groups of OTUs in both cluster and ordination analyses and 2) the two OTUs within this group exhibited minimal dissimilarity compared with known species included in the analyses (see Wills et al. 2000; Plunkett et al. 2009).

Table 1. Vouchers for specimens in phenetic analyses. Species: OTU, voucher.

Homopholis belsonii: HB1, ***R. Tremont 4*** (NE); HB2, ***R. Tremont 5*** (NE); HB3, ***R. Tremont 1*** (NE); HB4, ***R. Tremont 3*** (NE); HB5, AD 99040158; HB6, ***R. Tremont 2*** (NE); ***Walwhalleya proluta***: WPR1, MEL 1620815; WPR2, MEL 1564746; WPR3, AD 98446400; WPR4, MEL 570575; WPR5, MEL 1620817; WPR6, AD 97507128; WPR7, AD 97636285; WPR10, MEL 1620816; WPR11, AD 98665088; WPR12, MEL 1511529; WPR13, ***N.C.W. Beadle s.n.***, 2 Nov. 1970 (NE 24894); WPR14, AQ 418275; WPR15, NSW 365202; WPR16, MEL 225501; WPR17, NSW 221763; WPR18, NSW 355220; ***Walwhalleya* sp. Flinders Ranges**: WPR8, AD 97021093; WPR9, AD 97215110; ***W. pungens***: WPU1, ***K.E. Wills 100*** (NE); WPU2, ***K.E. Wills 83b*** (NE); WPU3, ***K.E. Wills 108*** (NE); WPU4, ***K.E. Wills 69b*** (NE); WPU5, ***J.R. Hosking 1622*** (NE67741); WPU6, ***K.E. Wills 69a*** (NE); ***W. subxerophylla***: WS1, AQ 425324; WS2, NSW 220377; WS3, NSW 254088; WS4, NE 8579; WS5, ***M. Driver s.n.***, Sep. 1978 (NE 40105).

Results and Discussion

Phenetic patterns from SSH MDS ordination and UPGMA clustering (Figs 1 & 2) are essentially the same and recover the same groups as we intuitively predicted and are consistent with those of previous analyses of the group by Wills et al. (2000). The stress value of the ordination is very low (0.0607) and most of the characters correlate strongly with the ordination space (Table 3).

Five distinct groupings of OTUs were obtained. One group, whose OTUs had not been previously analysed, represents the two Herbarium AD specimens from the Flinders Ranges allocated by AD to *Homopholis proluta*. This group appears more similar to *W. subxerophylla* than to either *W. proluta* or *W. pungens* phenetically (Figs 1 & 2) and morphologically (Fig. 3) and is here referred to as *Walwhalleya* sp. Flinders Ranges until formally described below. This new species is readily distinguished, with the aid of a hand lens, from other members of the genus by strigose upper glumes and lower lemmas of its spikelets (Fig. 3).

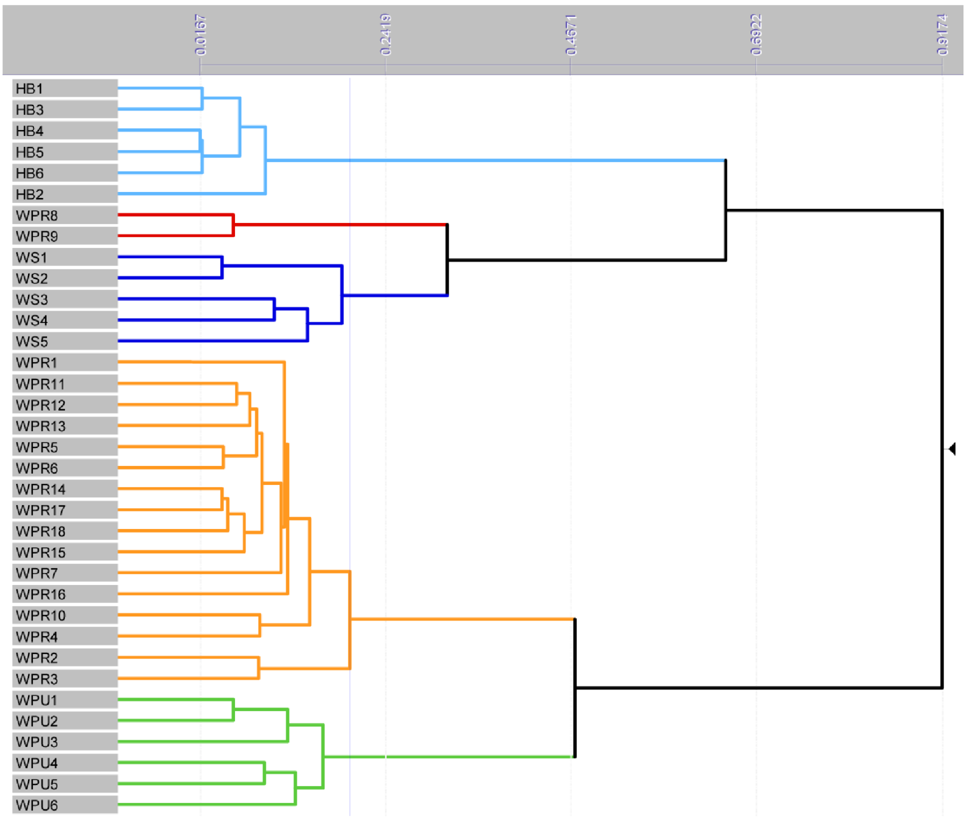

Fig. 1. Phenogram based on Gower association and flexible UPGMA with β=-0.1 of OTUs of *Homopholis* and *Walwhalleya*. HB= ***Homopholis belsonii***, WPR= ***Walwhalleya proluta***, **WS=** ***W. subxerophylla***, WPU= *W. pungens*. Following analyses **WPR8 and WPR9** were assigned to ***Walwhalleya*** **sp. Flinders Ranges**. See Table 1 for vouchers.

Table 2. Morphological characters used for ordination and cluster analyses of *Walwhalleya* and *Homopholis*. * = Characters additional to those used in the analysis by Wills et al. (2000).

No.	Character: States
Vegetative	
1.	plants: stoloniferous/not stoloniferous
2.	auricle: present/absent
3.	ligule length (mm)
4.	leaf width (mm)
5.	leaf tip: pungent/not pungent
6.	leaf blade adaxial surface: hairy/not hairy
Inflorescence	
7.	inflorescence at maturity: fully exserted/not fully exserted
8.	primary inflorescence branches: spreading/not spreading
9.	primary inflorescence branches degree of secondary branching: many/not many
10.	primary inflorescence branches: spikelets appressed/not appressed
11.	primary inflorescence branches: spikelets ascending/not ascending
12.	primary inflorescence branches at lowermost inflorescence node: whorled/not whorled
13.	pedicels: flexuose/not flexuose
14.	spikelet: number on a typical lowermost branch
Spikelet	
15.	spikelet shape: lanceolate/not lanceolate
16.	spikelet length (mm)
17.	spikelet width (mm)
18.	spikelet length to width ratio
19.	lower glume length (mm)
20.	lower glume shape: triangular/not triangular
21.	lower glume shape: ovate/not ovate
22.	lower glume shape: lanceolate/not lanceolate
23.	lower glume shape: elliptic/not elliptic
24.	lower glume number of nerves
25.	lower glume texture: rough/not rough
26.	lower glume apex shape: long acuminate/not long acuminate
27.	lower glume apex shape: acuminate/not acuminate
28.	lower glume apex shape: acute/not acute
29.	lower glume apex shape: rounded/not rounded
30.	*lower glume intercostal indumentum in the upper third: present/not present
31.	*lower glume intercostal indumentum in the lower two thirds: present/not present
32.	*lower glume vein indumentum scabrous/not scabrous
33.	*lower glume mid vein indumentum in upper third: present/not present
34.	*lower glume mid vein indumentum in lower two thirds: present/not present
35.	*lower glume lateral vein indumentum in upper third: present/not present
36.	*lower glume lateral vein indumentum in lower two thirds: present/not present
37.	lower glume ratio to spikelet length
38.	upper glume length (mm)

39. upper glume number of nerves
40. upper glume texture: membranous/not membranous
41. upper glume texture: chartaceous/not chartaceous
42. upper glume: hairy/not hairy
43. *upper glume intercostal indumentum type: scabrous/not scabrous
44. *upper glume intercostal indumentum: strigose/not strigose
45. *upper glume intercostal indumentum in upper third: present/not present
46. *upper glume intercostal indumentum in lower two thirds: present/not present
47. *upper glume vein indumentum: scabrous/not scabrous
48. *upper glume vein indumentum: strigose/not strigose
49. *upper glume mid vein indumentum in upper third: presents/not present
50. *upper glume mid vein indumentum in lower two thirds: present/not present
51. *upper glume lateral vein indumentum in upper third: present/not present
52. *upper glume lateral vein indumentum in lower two thirds: present/not present
53. lower lemma texture: membranous/not membranous
54. lower lemma texture: chartaceous/not chartaceous
55. lower lemma apex shape: long acuminate/not long acuminate
56. lower lemma apex shape: acuminate/not acuminate
57. lower lemma apex shape: acute/not acute
58. lower lemma nerves: producing slit-like interspaces/not producing slit-like interspaces
59. *lower lemma intercostal indumentum type: scabrous/not scabrous
60. *lower lemma intercostal indumentum type: strigose/not strigose
61. *lower lemma intercostal indumentum in upper third: present/not present
62. *lower lemma intercostal indumentum in lower two thirds: present/not present
63. *lower lemma vein indumentum: scabrous/not scabrous
64. *lower lemma vein indumentum: strigose/not strigose
65. *lower lemma mid vein indumentum in upper third: present/not present
66. *lower lemma mid vein indumentum in lower two thirds: present/not present
67. *lower lemma lateral vein indumentum in upper third: present/not present
68. *lower lemma lateral vein indumentum in lower two thirds: present/not present
69. lower lemma number of nerves
70. upper lemma colour at maturity: brown/not brown
71. upper lemma texture: cartilaginous/not cartilaginous
72. upper lemma texture: indurate/not indurate
73. upper lemma surface ornamentation: smooth/not smooth
74. upper lemma surface ornamentation: minutely muricate/not minutely muricate
75. upper lemma surface ornamentation distribution: regular/not regular
76. upper lemma margins recurved: thinner than body/not thinner than body
77. upper lemma apex: shortly beaked/not shortly beaked
78. upper lemma with a membranous point: yes/no
79. upper floret shorter than lower floret: yes/no
80. upper lemma length (mm)
81. upper palea with a prominent keel: yes/no
82. lodicule length (μm)

Here, *W. proluta* and *W. pungens* are more similar to each other than to other members of *Walwhalleya* and *Homopholis*, whereas Wills et al. (2000) found *W. pungens* and *W. subxerophylla* to be more similar. Also, in the present study *H. belsonii* appears more similar to *W. subxerophylla* and *W.* sp. Flinders Ranges than to *W. proluta* and *W. pungens* by contrast to Wills et al. (2000). Based on exploratory analyses where we have removed some OTUs/characters (not presented), the differences between our present and previous findings largely result from the inclusion here of *Walwhalleya* sp. Flinders Ranges and the expanded use of characters capturing features of the indumentum on the glumes and lemmas. Lower stress values obtained here, despite an increase in number of attributes, lends confidence to our main findings.

Nevertheless, neither pattern of similarity is unreasonable based on current knowledge of the geographic distributions of the species of *Walwhalleya* (see Australia's Virtual Herbarium, www.ersa.edu.au/avh/), and we do not interpret these phenetic results as an estimation of phylogeny. Rather, we will collaborate with others on molecular phylogenetics to test and extend the earlier (Wills et al 2000) non-molecular phylogeny of the group. New collections of *Walwhalleya* sp. Flinders Ranges will be useful towards this purpose and in the better assessment of its rarity. So, we encourage a search for this new and rare member of the South Australian flora.

Conclusions

There is clear evidence from morphology and phenetic analysis confirming intuitive assessment of the recognition of a fourth species of *Walwhalleya*: *W.* sp. Flinders Ranges, which we formally name below. Given the widespread and thorough wetting

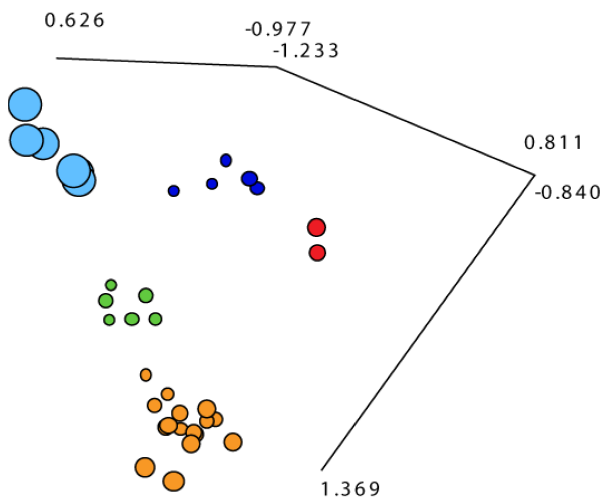

Fig. 2. 3D-ordination of semi-strong hybrid multidimensional scaling for OTUs of *Homopholis* and *Walwhalleya*. Stress = 0.0607. From top left hand, clockwise: ***Homopholis belsonii***, ***Walwhalleya subxerophylla***, ***Walwhalleya* sp. Flinders Ranges**, ***W. proluta***, ***W. pungens***.

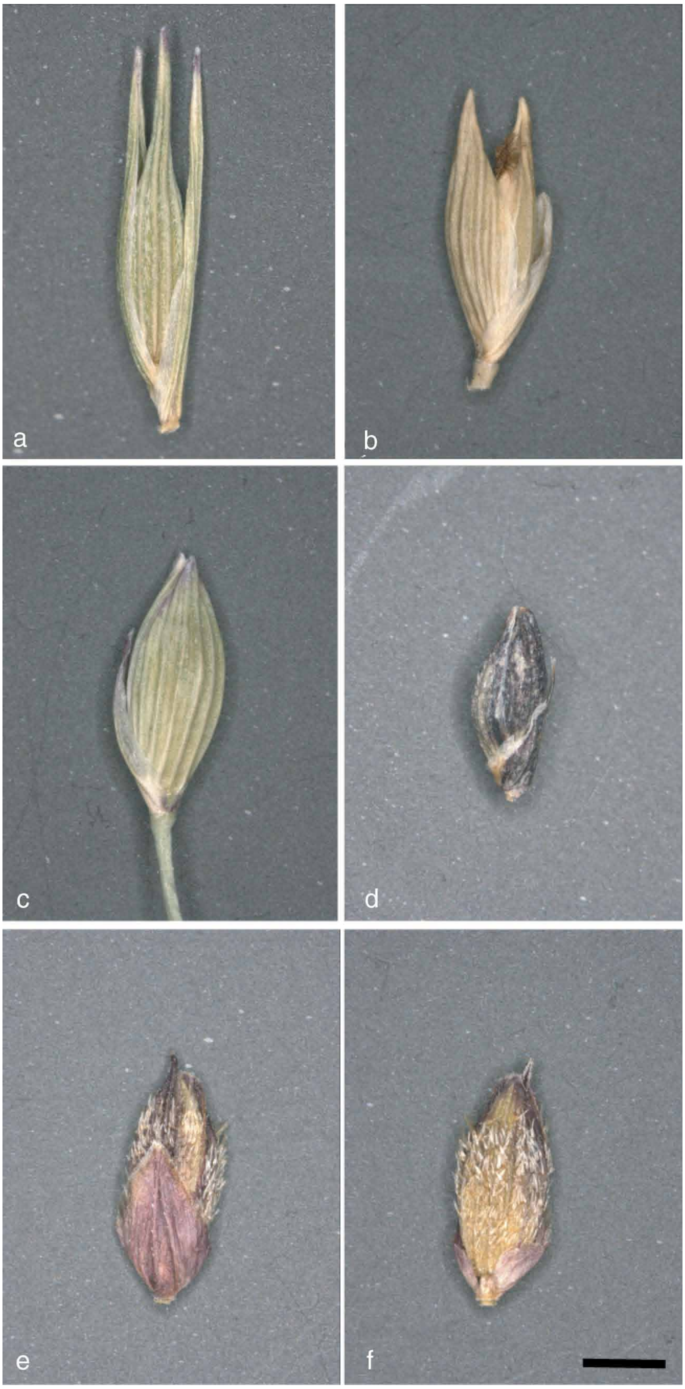

Fig. 3. Spikelets of the study group species. **a,** *Homopholis belsonii* (*R.Tremont 3*, NE); **b,** *Walwhalleya proluta* (AD 97507128); **c,** *W. pungens* (*K.E.Wills 69b*, NE); **d,** *W. subxerophylla* (NE 8579); **e, f,** *W*. sp. Flinders Ranges (AD 97215110). Scale bar: **a–f** = 1 mm.

Table 3. PCC values with correlation of attributes with ordination space of 70% or more, for SSH MDS ordination of *Walwhalleya* and *Homopholis*; see Fig. 2. * = characters additional to those used in the analysis by Wills et al. (2000); see Table 1.

No.	Character	X	Y	Z	r-squared
23	lower glume shape: elliptic/not elliptic	-0.776	0.63	0.007	0.92
44	*upper glume intercostal indumentum: strigose/not strigose	0.776	-0.63	-0.007	0.92
67	*lower lemma lateral vein indumentum in upper third: present/not present	0.776	-0.63	-0.007	0.92
63	*lower lemma vein indumentum: scabrous/not scabrous	0.84	-0.534	0.093	0.88
65	*lower lemma mid vein indumentum in upper third: present/not present	0.84	-0.534	0.093	0.88
6	leaf blade adaxial surface: hairy/not hairy	-0.075	0.928	-0.365	0.85
15	spikelet shape: lanceolate/not lanceolate	0.075	-0.928	0.365	0.85
22	lower glume shape: lanceolate/not lanceolate	0.075	-0.928	0.365	0.85
26	lower glume apex shape: long acuminate/not long acuminate	0.075	-0.928	0.365	0.85
55	lower lemma apex shape: long acuminate/not long acuminate	0.075	-0.928	0.365	0.85
75	upper lemma surface ornamentation distribution: regular/not regular	-0.075	0.928	-0.365	0.85
60	*lower lemma intercostal indumentum type: strigose/not strigose	0.708	-0.671	0.219	0.84
56	lower lemma apex shape: acuminate/not acuminate	-0.747	0.64	-0.18	0.80
9	primary inflorescence branches degree of secondary branching: many/not	-0.981	0.039	-0.192	0.80
47	*upper glume vein indumentum: scabrous/not scabrous	0.98	-0.199	-0.013	0.80
49	*upper glume mid vein indumentum in upper third: presents/not present	0.98	-0.199	-0.013	0.80
51	*upper glume lateral vein indumentum in upper third: present/not present	0.98	-0.199	-0.013	0.80
5	leaf tip: pungent/not pungent	-0.755	0.637	-0.157	0.78
19	lower glume length (mm)	-0.083	-0.725	0.684	0.75
46	*upper glume intercostal indumentum in lower two thirds: present/not present	0.998	-0.014	0.067	0.75
45	*upper glume intercostal indumentum in upper third: present/not present	0.608	0.792	-0.061	0.73
24	lower glume number of nerves	-0.054	-0.69	0.722	0.72
38	upper glume length (mm)	-0.227	-0.718	0.658	0.71
61	*lower lemma intercostal indumentum in upper third: present/not present	0.579	0.805	-0.129	0.69
74	upper lemma surface ornamentation: minutely muricate/not minutely muricate	-0.015	0.959	-0.283	0.69
16	spikelet length (mm)	-0.196	-0.691	0.696	0.69

of much of inland Australia in 2010 and the consequent fabulous growth of grasses and other herbs, we encourage collection of high quality specimens (and data) of grasses from these areas to aid the assessment of their distribution and to maximise the chance of discovery of new species of Poaceae.

Taxonomy

Walwhalleya jacobsiana R.D.B.Whalley & J.J.Bruhl, ***sp. nov.***

W. subxerophila (Domin) K.E.Wills & J.J.Bruhl *affinis, sed gluma supera et lemmate infero strigosa inter nervos differt.*

Type: South Australia. Flinders Range[s], north, Oraparinna National Park, Hans Heysen Range. c. 18 km west-north-west of Oraparinna homestead. 17 Sep. 1971, *E.N.S. Jackson 1880*; holo: AD; iso: BRI, CANB, K, MEL, MO, NE, NSW, PERTH, PRE, SI, US. Fig. 4.

Plants hermaphrodite; perennial; non-rhizomatous; *cataphylls* absent. *Flowering culms* erect; clumped; 10–20 cm tall; mostly sparingly branched; inflorescences terminal, solitary; 4–8 noded. *Flowering culm nodes* glabrous. *Mid-culm internodes* hollow; glabrous; shorter than the associated leaf sheaths. *Auricles* absent. *Mid-culm leaves* not distinctly distichous. *Mid-culm sheaths* rounded at the back; glabrous; sheath margins non-ciliate; sheath nerves smooth. *Ligule* a membrane; 1.5–2.8 mm long; erose, or entire; apically rounded to truncate. *Collar* glabrous. *Mid-culm leaf blades* involute; 4–10 × 1.6–2.5 mm; linear; adaxially hairy, scabrous; not noticeably thickened and spongy; tapering to a narrow apex (sharp, spine-like); non-ciliate basally; with scabrous margins; without tubercle-based hairs.

Inflorescence a panicle usually fully exserted at maturity (apparent in *R.Callen s.n. 8 Oct. 1969,* AD). *Main inflorescence axis* present; 40–80 mm long; scabrous. *Primary inflorescence branches* initially appressed, spreading with maturity; whorled at the lowermost inflorescence node; with few secondary branches; axils hairy; (15–)30–50 × 0.2–0.5 mm; distinctly grooved or angled; not winged; smooth on the faces; lacking papilla-based setae; scabrous on the angles. *Spikelet-bearing branches* not basally adnate to the rachis; terminating in a spikelet. Spikelets initially appressed to the branches, later ascending; arranged singly on the branches; not secund. *Bristles* absent. *Pedicels* present; 15–50 mm long; distinctly angled; scabrous; flexuose or straight. *Pedicel apices* glabrous; concave, cupuliform. Disarticulation at the base of the spikelet. *Callus* not differentiated. Spikelets not overlapping; solitary; 1–3 on a typical lowermost branch; not embedded in the rachis; not diverging from the axis.

Spikelets dorsiventrally compressed; ellipsoid; 2.5–2.9 × 1.1–1.3 mm. *First glume* present; 1.7–2.1 mm long (*c.* 0.6–0.7 × spikelet length); ovate; encircling the spikelet base; not inflated at the base; 5–7-nerved; membranous; veins scabrous in the upper third; acute to acuminate; rachilla pronounced between the first and second glume. *Second glume* 2.2–2.6 mm long; elliptic; 7–9-nerved; rounded on the back; chartaceous; margins neither noticeably flared nor hyaline, non-ciliate; with both intercostal and vein indumentum, intercostae strigose, vein indumentum both scabrous and strigose; acute, muticous; *c.* 1 × the length of the lower lemma. *Lower floret* neuter. *Lower lemma* elliptic; lacking distinct transverse nerves; not keeled; chartaceous; lacking a hyaline area at the base; internerve spaces equal; 7–9-nerved, nerves not anastomosing apically, without slit-like interspacing, pronounced; margins non-ciliate, thin; intercostal indumentum

Fig. 4. Image of holotype of *Walwhalleya jacobsiana* (AD 97215110). Inflorescences at various stages towards maturity.

strigose, vein indumentum both scabrous and strigose; acute, muticous. *Palea of lower floret* absent or minute. *Rachilla* not well developed between the lower and upper floret. *Upper floret* perfect; shorter than the lower floret. *Upper lemma* 1.7–2.1 mm long; indurate; very finely muricate; elliptic; rounded on the back; obscurely nerved; margins recurved and not noticeably thinner than the body (at maturity); glabrous; base without special modifications; the apex not differentiated into a membranous green point; lacking an apical crest; recurved apically; acuminate; apiculate. *Palea of upper floret* indurate; very finely muricate; with the base neither swollen nor protruding; with obscure nerves; enclosed at its apex by the lemma. *Lodicules* well developed; plicate; 8.5–11 µm long. *Anthers* 3. *Styles* basally free. *Rachilla* not prolonged beyond the upper floret. *Differentiated cleistogamous spikelets* absent.

Abaxial epidermis of leaf blade: costal/intercostal zonation conspicuous; veins scabrid. Epidermis with differentiated long and short cells. Long cells similar in shape and wall thickness costally and intercostally. *Microhairs* present, 25–50 x 5–8.8 µm at the septum; confined to the non-stomatal files; adjacent to the costal zone and in the middle of the costal zone; panicoid-type; elongated; clearly two-celled; inflated and rounded; having both cells more or less the same shape. Distal cells blunt. Basal cell base neither constricted nor expanded; parallel-sided. Microhair apical cells 12.5–27.5 µm long. Microhair ratio of apical cell to total length 0.3–0.62. Microhair ratio of width at septum to total length 0.14–0.3. *Stomata* common; 30.0–32.5 µm long.

Photosynthetic pathway: C_3 inferred from a 'maximum cells distant count' of >1 (see Hattersley and Watson 1975)

Distribution and habitat: known only from the Flinders Ranges: Heysen Range of Flinders Ranges National Park, Oraparinna Section and Gammon Range of Vulkathunha-Gammon Ranges National Park. No direct habitat information is available, but the species grows in a semi-arid region and is recorded from a hillside making it likely that it occurs in open woodlands and/or herbfields.

Only other specimen known: South Australia: northern Flinders Range[s], north side of Gammon Range, *R. Callen s.n.*, 8 Oct. 1969 (AD97021093).

Phenology: flowers: Sep–Oct; fruits: Sep–Oct.

Conservation status: *Walwhalleya jacobsiana* is known only from two gatherings, one each from Heysen Range and Gammon Ranges in the Flinders Ranges, separated by c. 50 km. Given the lack of data, the species should be considered 'data deficient' (DD) according to IUCN 2001 criteria (www.iucnredlist.org/technical-documents/categories-and-criteria/2001-categories-criteria), which is also used by South Australia's Department of Environment and Heritage to assess rare and threatened species (National Parks and Wildlife Council 2003). Nevertheless, based on number of collections in this reasonably well botanised area, the species is likely rare. Priority should be given to refind the species and commence assessment of its conservation status. Good rains in 2010 provide a timely opportunity to commence this search. The species is conserved in Flinders Ranges National Park, Oraparinna Section and Vulkathunha-Gammon Ranges National Park.

Etymology: we have named this species in honour of Herbarium NSW agrostologist Surrey Jacobs, who has been over decades an inspiration to workers in native grasses, and a friend and colleague of us both.

Key to Species of *Walwhalleya*

1 Spikelets < 2.9 mm long; lower lemma scabrous or strigose between nerves; fertile lemma subequal to lower lemma **2**

1* Spikelets ≥ 3 mm long; lower lemma glabrous between nerves; fertile lemma shorter than lower lemma **3**

2 Upper glume and lower lemma with strigose hairs between nerves, lower lemma nerves without spicules .... ***W. jacobsiana***

2* Upper glume and lower lemma without strigose hairs between nerves, lower lemma nerves with spicules .... ***W. subxerophila***

3 Mid-culm leaf blades flat; upper glume glabrous, acuminate .... ***W. proluta***

3* Mid-culm leaf blades involute; upper glume scabrous, acute .... ***W. pungens***

Acknowledgments

We thank Ian Telford (NE) and Frances Quinn (UNE) for helpful comments on a draft of the manuscript; Lyn Craven (CANB) for Latin translation; Nigel Andrew (UNE) for use of Leica MZ16A; Herbaria AD and MEL for extended loans and permission to sample specimens; Jürgen Kellermann and Helen Vonow (AD) for a copy of the SA Discussion paper and useful feedback; NSW for previous loans of relevant material and access to specimens at NSW; specimen data was accessed from Australia's Virtual Herbarium with permission of the Council of Heads of Australasian Herbaria Inc.; and referees and editorial committee for their helpful comments. We acknowledge use of the N.C.W. Beadle Herbarium (NE) and research facilities within the School of Environmental & Rural Science, UNE.

References

Bruhl JJ, Wilson PG & Wills KE (2006) Grass not fungus: *Walwhalleya nom. nov.* (Poaceae, Paniceae). *Australian Systematic Botany* 19: 327–328.

Hattersley PW, Watson L (1975) Anatomical parameters for predicting photosynthetic pathways of grass leaves: The 'maximum lateral cell count' and the 'maximum cells distance count'. *Phytomorphology* 25: 325–333.

National Parks and Wildlife Council (2003) Review of the status of threatened species in South Australia: Proposed schedules under the South Australian National Parks and Wildlife Act 1972: Discussion Paper. (Dept for Environment & Heritage, S.A.: Adelaide) [Sept. 2003].

Plunkett GT, Bruhl JJ, Telford IRH (2009) Two new, sympatric species of *Wahlenbergia* (Campanulaceae) from the New England Tableland escarpment, New South Wales, Australia. *Australian Systematic Botany* 22: 319–331.

Webster RD (1987) The Australian Paniceae (Poaceae). (J. Kramer: Berlin)

Wills KE (1996) Systematic studies in *Homopholis* (Poaceae: Panicoideae: Paniceae). Graduate Diploma in Science Thesis, Botany, University of New England Armidale, NSW.

Wills KE, Whalley RDB & Bruhl JJ (2000) Systematic studies in Paniceae (Poaceae): *Homopholis* and *Whalleya* gen. et. sp. nov. *Australian Systematic Botany* 13: 437–468.

Manuscript received 20 March 2010, accepted 16 September 2010

Appendix 1.

Data set for phenetic analysis of Homopholis and Walwhalleya. See Table 1 for characters relating to the numbers in header row. Empty cells are missing data. See table 1 for vouchers.

OTU	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
HB1	1		1.4	2.7	0	0	0.5	1	0	0	1	0	0	2.5	1	5.2	0.9	5.7	4.9
HB2	1	0	1.4	2.2	0	0	1	0	0			0	0	1.5	1	5.5	0.9	6.2	5.4
HB3	1	0	1.3	2.3	0	0	0.5	1	0	0	1	0	0	2.7	1	4.9	1.0	5.1	4.7
HB4	1	0	1.1	2.2	0	0	0.5	1	0	0	1	0	0	1.3	1	4.6	0.9	5.3	4.5
HB5	1	0	2.0	2.8	0	0	0.5	1	0	0	1	0	0	2.0	1	5.1	1.1	4.6	4.8
HB6	1	0	1.3	2.0	0	0	1	1	0	0	1	0	0	2.0	1	5.7	1.0	5.7	5.7
WPR1	0	0	2.5	2.7	1	1	0	0	1	1	1		0.5	7.6	0	3.3	1.1	2.9	2.5
WPR10	0	0	2.6	4.0	1	1	0	0	1	1	1	0	0.5	15.0	0	3.7	1.3	2.8	3.0
WPR11	0	0	3.0	3.3	1	1	0	1	1	1	1	0	0.5	5.8	0	3.5	1.3	2.7	2.3
WPR12	0	0	2.3	4.1	1	1	0.5	1	1	0	1		0.5	15.3	0	3.4	1.1	3.0	2.3
WPR13	0	0	1.7	3.6	1	1	0	1	1	0	1	0	0.5	6.0	0	3.0	1.1	2.8	2.2
WPR14	0	0	2.8	4.1	1	1	0	0	1	0	1	0	0.5	17.0	0	3.2	1.2	2.7	2.4
WPR15	0	0	2.4	3.1	1	1	0.5	1	1	0	1	0	0.5	11.8	0	2.3	0.8	2.7	1.6
WPR16	0	0	2.6	5.2	1	1	0	0	1	0	1	0	0.5	18.0	0	3.5	1.1	3.2	2.7
WPR17	0	0	2.5	4.2	1	1	0	0	1	0	1	0	0.5	63.0	0	3.2	1.0	3.2	2.1
WPR18	0	0	2.3	3.9	1	1	0.5	1	1	0	1	0	0.5	16.5	0	3.5	1.1	3.1	2.3
WPR2	0	0	2.0	4.1	1	1	0	1	1	1	1	0	0.5	15.2	0	3.4	1.1	3.0	2.2
WPR3	0	0	3.2	3.0	1	1	0.5	1	1	1	1	0	0.5	4.4	0	3.2	1.2	2.7	2.1
WPR4	0	0	4.0	3.8	1	1	0.5	1	1	1	1		0.5	12.3	0	3.9	1.3	3.3	3.4
WPR5	0	0	2.5	3.0	1	1	0.5	1	1	1	1	0	0.5	8.0	0	3.5	1.1	3.2	2.9
WPR6	0	0	2.3	3.1	1	1	1	1	1	1	1	0	0.5	7.0	0	3.5	1.2	2.8	2.5
WPR7	0	0	4.1	3.0	1	1	0	1	1	0	1		0.5	6.6	0	3.4	1.1	3.1	2.7
WPR8	0	0	2.7	2.2	1	1	1	1	0	0	1	1	0.5	2.4	0	2.7	1.3	2.1	1.7
WPR9	0	0	1.6	1.8	1	1	0	0	0	1	0	0	0.5	3.3	0	2.9	1.2	2.5	2.0
WPU1	1	0	1.2	2.6	1	1	0.5	1	0	0	1	0	1	2.4	0	3.5	1.6	2.3	2.6
WPU2	1	0	1.1	2.2	1	1	1	1	0	0	1	0	0.5	1.0	0	3.2	1.4	2.3	2.5
WPU3	0	0	1.4	2.4	1	1	1	1	0	0	1	0	0.5	2.2	0	3.3	1.4	2.4	2.3
WPU4		0	1.5	2.5	1	1	0	0	0	0	1	0	0.5	1.3	0	3.3	1.4	2.4	2.4
WPU5	0	0	1.8	1.9	1	1	0	1	0	0	1	0	0.5	2.4	0	3.3	1.4	2.4	2.5
WPU6	1	1	1.4	2.4	1	1		0	0	0	1	0	0.5	3.0	0	3.4	1.2	2.8	2.6
WS1	0	0	1.1	3.0	0	1	0.5	1	0	1	0	1	0.5	4.6	0	2.1	1.0		1.6
WS2	0	0	2.8	3.8	0	1	0	0	0	1	0	1	1	8.2	0	2.5	1.1	2.4	2.2
WS3	0	0	1.9	2.2	0	1	0	0	0	1	0	1	1	7.0	0	2.6	1.0	2.5	1.7
WS4	0	1	1.8	2.2	0	1	0.5	0	0	1	1	0.5	0.5	25.0	0	2.3	1.1	2.2	1.7
WS5	0	1	2.1	2.0	0	1	0.5	0	0	1	1	0.5	0.5	4.5	0	2.4	1.1	2.3	1.9

OTU	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**
HB1	0	0	1	0	7	0	1	0	0	0	1	1	1	1	1	1	1	0.95	5.1	7	1
HB2	0	0	1	0	7	0	1	0	0	0	1	1	1	1	1	1	1	1.00	4.8	7	1
HB3	0	0	1	0	7	0	1	0	0	0	1	1	1	1	1	1	1	0.95	4.7	7	1
HB4	0	0	1	0	7	0	1	0	0	0	1	1	1	1	1	1	1	0.98	4.5	7	0
HB5	0	0	1	0	7	0	1	0	0	0	1	1	1	1	1	1	1	0.97	4.6	7	0
HB6	0	0	1	0	7	0	1	0	0	0	1	1	1	1	1	1	1	1.00	5.2	7	0
WPR1	0	0	0	1	5	0	0	0	1	1	1	1	0	0	0	0	0	0.76	3.0	9	0
WPR10	0	0	0	1	5	0	0	1	0	0	0	0	1	1	0	0	0	0.83	3.4	9	0
WPR11	0	0	0	1	5	0	0	0	0	1	1	0	1	1	0	1	0	0.68	3.1	9	0
WPR12	0	0	0	1	5	0	0	0	1	1	1	0	1	1	0	1	0	0.68	3.3	7	0
WPR13	0	0	0	1	5	0	0	0	1	1	1	0	1	1	0	1	0	0.74	2.7	9	0
WPR14	0	0	0	1	5	0	0	0	1	1	0	0	1	1	0	0	0	0.74	3.2	9	0
WPR15	0	0	0	1	5	0	0	0	1	1	0	0	1	1	1	1	1	0.72	3.4	9	0
WPR16	0	0	0	1	4.8	0	0	0	1	1	1	0	1	1	0	1	0	0.79	3.5	9	0
WPR17	0	0	0	1	5	0	0	0	1	1	0	0	1	1	0	1	0	0.65	3.2	9	0
WPR18	0	0	0	1	5	0	0	0	1	1	0	0	1	1	0	1	0	0.65	3.3	9	0
WPR2	0	0	0	1	5	0	0	0	1	1	1	1	0	0	0	0	0	0.66	3.1	9	0
WPR3	0	0	0	1	5	0	0	0	1	1	0	0	1	1	0	0	0	0.67	2.9	9	0
WPR4	0	0	0	1	5	0	0	1	0	0	1	0	1	1	0	1	0	0.86	3.7	9	0
WPR5	0	0	0	1	5	0	0	0	1	0	0	0	1	1	0	0	0	0.83	3.2	9	0
WPR6	0	0	0	1	5	0	0	0	1	0	1	0	1	1	0	0	0	0.73	3.2	7	0
WPR7	0	0	0	1	7	0	0	0	1	0	0	0	1	1	0	1	0	0.81	3.1	9	0
WPR8	0	1	0	0	5	0	0	0	1	0	0	0	1	1	0	1	0	0.65	2.3	9	0
WPR9	0	1	0	0	7	0	0	0	1	0	0	0	1	1	0	1	1	0.67	2.5	7	0
WPU1	0	0	0	1	5	0	0	0	1	1	1	1	1	1	0	1	0	0.73	3.4	8.6	0
WPU2	0	0	0	1	5.4	0	0	0	1	1	1	1	1	1	0	1	0	0.76	3.2	9	0
WPU3	0	0	0	1	5	0	0	0	1	1	1	1	1	1	1	1	1	0.70	3.2	8.5	0
WPU4	0	0	0	1	5	0	0	0	1	1	1	1	1	1	1	1	1	0.73	3.1	9	1
WPU5	0	0	0	1	5	0	0	0	0	1	1	1	1	1	1	1	1	0.77	2.9	9	1
WPU6	0	0	0	1	5	0	0	0	1	1	1	1	1	1	0	1	0	0.76	3.4	8.5	0
WS1	1	1	0	0	5	1	0	0	1	0	1	1	1	1	1	1	1	0.75	2.1	9	0
WS2	1	1	0	0	5	1	0	0	1	0	1	1	1	1	1	1	1	0.68	2.5	9.5	0
WS3	1	1	0	0	4	1	0	0	1	1	1	1	1	1	1	1	1	0.67	2.5	8	1
WS4	1	1	0	0	4	1	0	0	1	1	1	1	1	1	1	1	1	0.73	2.3	9	1
WS5	1	1	0	0	4	1	0	0	1	0	1	1	1	1	1	1	1	0.78	2.5	8.5	1

OTU	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**	**61**
HB1	0	1	0	1	0	1	1	0	1	0	1	0	0	1	1	0	01	0	1	0	1
HB2	1	1	0	1	0	1	1	0	1	0	1	0	1	1	1	0	0	1	0	1	0
HB3	0	1	0	1	0	1	1	0	1	0	1	0	0	1	1	0	0	1	0	1	0
HB4	1	1	0	1	0	1	1	0	1	0	1	0	0	1	1	0	0	1	0	1	0
HB5	1	1	0	1	0	1	1	0	1	0	1	0	0	1	1	0	0	1	0	1	0
HB6	1	1	0	1	0	1	1	0	1	0	1	0	0	1	1	0	0	1	0	1	0
WPR1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
WPR10	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
WPR11	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
WPR12	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
WPR13	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1
WPR14	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0
WPR15	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0
WPR16	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
WPR17	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
WPR18	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0
WPR2	1	1	1	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1
WPR3	1	1	1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1
WPR4	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
WPR5	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
WPR6	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
WPR7	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
WPR8	1	1	0	1	0	1	1	1	1	1	1	1	0	1	0	0	1	0	0	1	0
WPR9	1	1	0	1	0	1	1	1	1	1	1	1	0	1	0	0	1	0	0	1	0
WPU1	1	1	1	0	1	1	1	0	1	0	1	0	0	1	0	1	1	0	1	0	1
WPU2	1	1	1	0	1	1	1	0	1	0	1	0	0	1	0	1	1	0	1	0	1
WPU3	1	1	1	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1
WPU4	0	1	1	0	1	1	1	0	1	0	1	0	1	0	0	1	0	0	1	0	1
WPU5	0	1	1	0	1	1	1	0	1	0	1	0	0	1	0	1	0	0	1	0	1
WPU6	1	1	1	0	1	1	1	0	1	0	1	0	1	1	0	1	0	0	1	0	1
WS1	1	1	0	1	1	1	1	0	1	1	1	1	0	1	0	0	1	0	0	1	1
WS2	1	1	0	1	1	1	1	0	1	1	1	1	0	1	0	0	1	0	0	1	1
WS3	0	1	0	1	1	1	1	0	1	1	1	1	1	0	0	0	1	0	0	1	1
WS4	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	0	1	0	1
WS5	0	1	1	1	1	1	1	1	1	0	1	0	1	0	0	1	1	0	1	1	1

OTU	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82
HB1	1	0	1	0	1	0	7	0	1	0	1	0		0	1	1	1	2.7	0		
HB2	1	1	0	1	0	1	0	7	0	1	0	1	0		0	1	1	1	2.7	0	
HB3	1	1	0	1	0	1	0	7	0	1	0	1	0		0	1	1	1	2.7	0	
HB4	1	1	0	1	0	1	0	7	0	1	0	1	0		0	1	1	1	2.6	0	8
HB5	1	1	0	1	0	1	0	7	0	1	0	1	0		0	1	1	1	2.7	0	12.5
HB6	1	1	0	1	0	1	0	7	0	1	0	1	0		0	1	1	1	2.8	0	11
WPR1	0	0	0	0	0	0	0	7	0	0	1	1	1	1	0	1	1	1	2.1	0	10.5
WPR10	0	0	0	0	0	0	0	9	1	0	1	1	1	1	0	0	0	1	2.3	0	11.5
WPR11	0	0	0	0	0	0	0	7	0	0	1	0	1	1	0	1	1	1	2.0	0	11
WPR12	0	0	0	0	0	0	0	7	0	0	1	1	1	1	0	1	1	1	2.2	0	11
WPR13	0	0	0	0	0	0	0	7	0	0	1	1	0	0	1	1	1	1	2.2	0	6.5
WPR14	0	0	0	0	0	0	0	7	0	0	1	1	1	0	1	1	1	1	2.1	0	8.5
WPR15	0	0	0	0	0	0	0	8	0	0	1	1	1	0	0	1	1	1	2.1	0	10
WPR16	0	0	0	0	0	0	0		0			1	1	0	0	1	1	0	2.3	0	10
WPR17	0	0	0	0	0	0	0	7	0	0	1	1	1	0	1	1	1	1	2.1	0	9.5
WPR18	0	0	0	0	0	0	0		0	0	1	1	1	0	1	1	1	1	2.1	0	8.5
WPR2	1	0	0	0	0	0	0	7	0	0	1	1	1	1	0	1	1	1	2.0	0	11
WPR3	0	0	0	0	0	0	0	7	0	0	1	1	1	1	0	1	1	1	2.2	0	9
WPR4	0	0	0	0	0	0	0	7	1	0	1	1	1	1	0	0	1	1	2.5	0	5
WPR5	0	0	0	0	0	0	0	7	1	0	1	1	1	1	0	0	1	1	2.3	0	10.5
WPR6	0	0	0	0	0	0	0	7	0	0	1	1	1	1	0	1	1	1	2.2	0	10
WPR7	0	0	0	0	0	0	0	7	0	0	1	1	1	1	0	1	1	0	2.1	1	6.5
WPR8	1	1	1	1	1	1	1	9	1	0	1	0	1	1	0	1	1	1	1.8	1	11
WPR9	1	1	1	1	1	1	1	7	1	0	1	0	1	1	0	1	1	1	2.1	1	8.5
WPU1	1	1	0	1	0	0	0	8	0	0	1	1	1	0	1	1	1	1	2.8	0	13
WPU2	1	0	0	0	0	0	0		0	1	0	1	1	0	1	1	1	1	2.6	0	11
WPU3	1	0	0	0	0	0	0	9	0	0	1	1	1	0	1	1	1	1	2.6	0	
WPU4	1	0	0	0	0	0	0	8.5	0			1	1	0		1	1	1	2.6	0	11
WPU5	1	0	0	0	0	0	0	7	0	0	1	1	1	0		1	1	1	2.4	0	17.5
WPU6	1	0	0	0	0	0	0	7.5				1	1	0		1	1	1	2.6	0	15
WS1	1	1	0	1	1	1	1	9	0	0	1	0	1	0	0	0	1	0	1.9	0	12
WS2	1	1	0	1	1	1	1	9	0	0	1	0	1	0	1	0	1	0	2.1	0	11
WS3	1	1	0	1	1	1	1	8	0			0	1	0		1	1	0	2.1	0	13
WS4	1	1	0	1	1	1	1	8	0	0	1	0	1	0	0	1	1	0	2.0	0	14
WS5	0	1	0	1	0	1	0	8	0	0	1	0	1	0	1	1	1	0	2.1	0	13