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Genetics of white-flowered cultivars derived from *Watsonia borbonica* (Iridaceae)

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Abstract

Breeding experiments suggest that the occurrence of white (acyanic) flowers in several cultivars derived from *Watsonia borbonica* (Pourr.) Goldblatt is determined by a single recessive allele. Many *Watsonia* cultivars have been characterised simply as 'white-flowered'; but descriptions based on several characters are necessary if cultivars with unique genotypes are to be differentiated without ambiguity.

Keywords: *Watsonia*, Iridaceae, cultivated plants

Introduction

The chemical pathways by which flavonoids, including the red to blue coloured anthocyanins, are synthesised in plants have been thoroughly documented (Winkel-Shirley 2001). As these pathways are similar throughout the angiosperms, mutations with analogous effects on flower colour may be found in various genera. Species that normally produce anthocyanin-pigmented flowers will produce white or cream flowers when a mutation blocks any one of several steps in anthocyanin synthesis (Harrison & Stickland 1974; Mato et al. 2000). The superficially similar white flowers of various cultivars bred from the same species may therefore result from independent mutations at different loci. For example, Onozaki et al. (1999) were able to classify various cultivars of *Dianthus caryophyllus* bearing pure white or ivory-white flowers into three groups according to the stage at which anthocyanin synthesis is blocked by the absence of a necessary enzyme. A block may occur at the formation of chalcones by the enzyme chalcone synthase. Another, and later, stage that may be blocked is the conversion of flavanones to dihydroflavonols by flavanone 3-hydroxylase; in the absence of this enzyme, flavanones accumulate and are then converted to flavones by an alternative pathway involving flavanone isomerase (Onozaki et al., 1999). Although almost colourless, these flavones can be detected by the bright yellow colour produced when the flower is exposed to ammonia gas (Buxton 1932). This colour rapidly fades when the ammonia is removed, being due to a reversible auxochromic reaction (Tilley 2000).

The term albino has sometimes been applied to white-flowered mutants within species that typically bear conspicuously pigmented flowers. However, albinism in plants may also mean the absence of all pigments including chlorophyll. To avoid ambiguity here, I have followed current practice in using the term acyanic, i.e. lacking anthocyanins.

Plants with anthocyanin-pigmented flowers normally produce at least traces of red-purple pigmentation in the leaves and stems, particularly under conditions of stress. However, acyanic variants typically have pure green leaves and stems as these also lack anthocyanins. Armitage (1945) listed 100 species from the flora of Britain that demonstrate this colour polymorphism in both flowers and vegetative organs.

Perianth colour in *Watsonia* species typically ranges from pale pink or mauve-pink to intense red, purple or orange, due to the presence of various concentrations of anthocyanin pigments. The cultivars bred from these species show a somewhat wider range, from pastel pinks to mauve, purple, maroon, salmon, vermilion or combinations of these colours. The only anthocyanins so far characterised from *Watsonia* species are the orange to red pelargonidin derivatives (Harborne 1963). But the colours of mauve and purple must be due to another anthocyanin. This may be delphinidin, as its colourless precursor protodelphinidin and the corresponding flavonol myricetin have been isolated from leaves of the mauve-pink flowered *W. borbonica* (Williams et al. 1986). The range of flower colours in the genus implies that anthocyanin synthesis is influenced by several loci. However, a mutation that blocks all anthocyanin production is necessarily epistatic to all of these loci, resulting in unpigmented white flowers.

The **acyanic syndrome** in *Watsonia* is here defined as: Leaf bases and margins green; inflorescence axis green; floral bracts green-herbaceous to brown-scarious; perianth pure white or with a faint fugitive pink tinge; anthers cream.

In comparison, the **cyanic wild-type** has: Leaf bases green or suffused with red; leaf margins green to red-brown; inflorescence axis green to deep red or purple; floral bracts green-herbaceous to red, purple or scarious; perianth coloured pink, red, orange or purple; anthers purple.

The degree of anthocyanin pigmentation in the foliage and inflorescence axis of cyanic *Watsonia* varies widely with genotype and environment, being strongest in plants grown in full sun. The purple anthers are a more uniform character, with pollen grains and the anther wall darkly pigmented even in plants grown in the shade or with pale pink perianths. Anthers of acyanic *Watsonia* are cream in appearance due to the pale yellow pollen enclosed in a colourless anther wall.

This study aims to investigate the genetic basis of the acyanic syndrome in *Watsonia* and to resolve whether this basis is the same in the various acyanic accessions available for study.

Materials and methods

The following clonal accessions were used in experimental crosses and/or tests for flavones:

- *Watsonia aletroides* (Burm.f.) Ker Gawl. Perianth red; anthers purple; from a suburban Adelaide garden, and within the circumscription of this species by Goldblatt (1989).
- *Watsonia hysterantha* Mathews & L.Bolus Perianth vermilion-red; anthers purple; grown from wild-collected seed imported from South Africa, and within the circumscription of this species by Goldblatt (1989).
- *Watsonia meriana* (L.) Mill. var. *meriana*. Perianth vermilion-red; anthers purple; within the circumscription of this species by Goldblatt (1989). Collected from a naturalised population at Hahndorf (Cooke 1998a).
- *Watsonia borbonica* (Pourr.) Goldblatt 'Arderne's White'. Perianth white; perianth lobes 30–37 mm long; style exceeding anthers; anthers cream. (Fig. 1) From a suburban Adelaide garden, and closely matching the illustration of this cultivar in Goldblatt (1989), notably in the almost equilateral orientation of the stamens and the obovoid, very obtuse capsule. Also matched to a photograph of the isolectotype of *W. ardernei* Mathews & L.Bolus.
- *Watsonia* 'Lilac Towers'. Perianth deep pink; anthers purple; a cultivar derived from *W. borbonica* and probably also *W. meriana* (Cooke 2005).
- *Watsonia* 'Jessie'. Perianth flesh-pink; anthers purple; a cultivar derived from *W. borbonica* and *W. meriana* (Cooke 1998b).
- *Watsonia* 'Leng'. Perianth mauve-pink; anthers purple; a cultivar derived mainly from *W. borbonica* (Cooke 1998b).
- *Watsonia* 'Ivory Towers'. Perianth white, showing a fugitive pink tinge when opening at low temperatures; perianth lobes 32–40 mm long; style exceeding anthers; anthers cream. A commercially available cultivar (Tesselaar 2000) with a similar morphology to *W. borbonica*.
- *Watsonia* Accession 5. Perianth white; style equal to anthers; anthers cream; differing morphologically from 'Arderne's White' most visibly in the shorter, broader and slightly gibbous perianth tube and the more densely



Fig. 1. *Watsonia borbonica* 'Arderne's White', from material used in this study.

- branched inflorescence; from a suburban Adelaide garden.
- *Watsonia* Accession 17. Perianth white, showing a pink tinge when opening at low temperatures; style shorter than anthers; anthers cream. Collected from a roadside at Longwood, South Australia, resembling descriptions of Cronin's 'Ballarat' cited by Cooke (1998b) and with a similar morphology to *W. borbonica*.
- *Watsonia* Accession 36. Perianth pink; anthers purple; from a suburban Adelaide garden resembling descriptions of Cronin's 'Australia' cited by Cooke (1998b) and with a similar morphology to *W. borbonica*.
- *Watsonia* Accession 89. Perianth sometimes pink-tinged in bud but opening pure white; perianth lobes 36–42 mm long; style subequal to anthers; anthers cream. Cronin material (Cooke 1998b), with a similar morphology to *W. borbonica* from a former nursery at Chudleigh Park Gardens, Victoria.
- *Watsonia* Accession 91. Perianth white; perianth lobes 36–45 mm long; style exceeding anthers; anthers cream. Cronin material from Chudleigh Park Gardens, and resembling descriptions of Cronin's 'Hobart' cited by Cooke (1998b), with a similar morphology to *W. borbonica*.

1. Experimental crosses

Flowers of all the above are protandrous, usually remaining open for 4-5 days: the anthers dehisce on day 1, a few hours after anthesis, and the stigmas become receptive on day 3. Flowers to be used as ovule parents were emasculated just before anthesis and the style enclosed in a 3 cm length of plastic drinking straw. Pollen was transferred from newly dehisced anthers of the pollen parent using a toothpick on days 2 and 3.

Seed was sown in the autumn after its production, in trays of Nu-Erth™ potting mix (pH approximately 6) with added Nitrophoska™ fertilizer and potassium sulphate. Plants were grown to flowering size outdoors in 300 mm pots of the same mixture; they began to flower in either the second or third spring after germination.

2. Test for flavone accumulation

Freshly picked flowers of each acyanic *Watsonia* accession and 7 white or cream flowered control species were suspended in a enclosed 500 ml jars over 10 ml of 50 g/L ammonia solution. Flowers were scored for any colour change after 20 minutes, as irreversible blackening and necrosis occurs if exposure to ammonia continues beyond this time. A flower was also removed from the ammonia gas after 20 minutes and allowed to stand in air for 90 minutes.

Results

1. Experimental crosses

Table 1 lists the crosses made between *Watsonia* accessions. The F₁ generations were scored for acyanic or cyanic pigmentation.

It was also observed that all F₁ progeny of *W. borbonica* 'Arderne's White' × *W. meriana* had a mauve-pink (RHS 66C) perianth colour similar to wild-type *W. borbonica* rather than the vermilion red of the pollen parent.

F₂ generations were then bred from some of the individual progeny from crosses 1, 2 and 3 above. The results are summarised in Table 3.

2. Test for flavone accumulation

Results for 15 acyanic *Watsonia* and 6 white or cream flowered species from other genera are listed in Table 3.

In contrast to the bright yellow reaction in most of the control species, each of the acyanic *Watsonia* flowers tested showed only localised areas of faint grey-yellow at 20 minutes exposure before blackening completely within two hours. It is concluded that significant levels of flavone accumulation do not occur in these flowers.

Discussion

From Table 1, it will be seen that:

- F₁ crosses with a cyanic wild-type species as one parent produced only cyanic progeny (crosses 1 to 5).
- An F₁ cross between one cyanic cultivated form and an acyanic produced almost equal numbers of cyanic and acyanic (cross 6).
- F₁ crosses between two acyanic plants produced only acyanic progeny (crosses 7 and 8).
- F₁ crosses among three cyanic named cultivars produced a minority of acyanic progeny (crosses 9 and 10).

The ratios of cyanic: acyanic observed in the F₁ generations are consistent with the hypothesis that acyanic flowers are determined by a single locus with alleles here symbolised as *a* (acyanic, recessive) and *A* (cyanic, dominant). Genotypes inferred from this hypothesis for the accessions used are shown in Table 2. It is deduced that the related species (*W. aletroides*, *W. hysteroantha* and *W. meriana*) are most probably homozygous for the dominant cyanic *A* allele; the acyanic plants (*W. borbonica* 'Arderne's White', accession 5, accession 17, accession 91) are most probably homozygous for the recessive *a*; and the four cultivars with cyanic pigmentation (*W. 'Jessie'*, *W. 'Leng'*, *W. 'Lilac Towers'*, accession 36) would be heterozygous. It was not possible to test this hypothesis in the most direct way by self-pollinating the putative heterozygotes due to the high degree of self-incompatibility in *Watsonia*. Instead, the F₂ generation of three crosses using *W. 'Lilac Towers'* was used as a test: the reappearance of a minority of acyanic plants in some of the F₂ derived from each of the F₁ crosses 1–3 (Table 3) supports the hypothesis. Fortuitously, the outcome of F₁ crosses of *W. 'Jessie'* with *W. 'Leng'* or *W. 'Lilac Towers'* approached the ratio of 3:1 expected in crosses between parents heterozygous for a single locus. However, in view of the small numbers of plants grown

Table 1. F₁ crosses between cyanic (coloured) and acyanic (white-flowered) *Watsonia* accessions.

Cross no.	Ovule parent	Pollen parent	Numbers of progeny	
			Cyanic	Acyanic
1	<i>W. 'Lilac Towers'</i> (cyanic)	<i>W. aletroides</i> (cyanic)	12	0
2	<i>W. 'Lilac Towers'</i> (cyanic)	<i>W. hysteroantha</i> (cyanic)	28	0
3	<i>W. 'Lilac Towers'</i> (cyanic)	<i>W. meriana</i> (cyanic)	23	0
4	<i>W. borbonica</i> 'Arderne's White' (acyanic)	<i>W. meriana</i> (cyanic)	4	0
5	accession 91 (acyanic)	<i>W. hysteroantha</i> (cyanic)	8	0
6	accession 36 (cyanic)	<i>W. borbonica</i> 'Arderne's White' (acyanic)	7	8
7	accession 5 (acyanic)	<i>W. borbonica</i> 'Arderne's White' (acyanic)	0	15
8	accession 17 (acyanic)	<i>W. borbonica</i> 'Arderne's White' (acyanic)	0	18
9	<i>W. 'Jessie'</i> (cyanic)	<i>W. 'Lilac Towers'</i> (cyanic)	6	2
10	<i>W. 'Leng'</i> (cyanic)	<i>W. 'Jessie'</i> (cyanic)	7	2

Table 2. Genotypes of *Watsonia* accessions, dominant **A** (coloured) and recessive **a** (acyanic) inferred from Tab. 1.

<i>Watsonia aletroides</i>	AA
<i>W. hysterantha</i>	AA
<i>W. meriana</i>	AA
<i>W. borbonica</i> 'Arderne's White'	aa
Accession 5	aa
Accession 17	aa
Accession 91	aa
<i>Watsonia</i> 'Jessie'	Aa
<i>Watsonia</i> 'Leng'	Aa
<i>Watsonia</i> 'Lilac Towers'	Aa
Accession 36	Aa

to flowering size, a statistical analysis was not justified and the results are presented here as qualitative pedigree data.

When opening in cool overcast weather, flowers of some of the acyanics (for example, accession 17) develop a pink tinge that can be accentuated by keeping buds close to anthesis in a refrigerator at 4°C for 24 hours. The possibility that these acyanics are due to a complementary mutation at a separate locus is eliminated by the results of cross 7, which produced only acyanic progeny (Table 1). If two loci had been involved, only cyanic progeny would have been expected from this cross. On the other hand, the possibility that more than one mutation with the same effect has occurred independently at the same locus cannot be ruled out. The **A** locus in *Watsonia* presents a parallel to the **C** locus described by Brieger & Mangelsdorf (1926) in *Nicotiana sanderae*, where homozygous recessives are also acyanic and produce white flowers that may become pink tinged at low temperatures.

None of the acyanic *Watsonia* accessions examined accumulated visible amounts of either the bright yellow chalcones or the paler yellow flavonols. Nor did any of them show the clear, bright yellow reaction with ammonia diagnostic of flavone accumulation (Table 4). It is therefore concluded that their acyanic state is not due to the absence or down-regulation of flavanone 3-hydroxylase, but that flavonoid synthesis is blocked at some earlier stage of the biosynthetic pathway. This conclusion is consistent with the inference that the acyanic state in all these plants is determined by a mutation at the same locus. It is further hypothesised that this mutation may act by down-regulating or inhibiting the production of chalcone synthase, consequently preventing the formation of anthocyanins or other coloured flavonoids.

Many *Watsonia* cultivars have been characterised in horticultural literature and catalogues simply as 'white-flowered'. However, a named cultivar of an ornamental perennial is normally a vegetatively propagated clone (or genet) with fixed horticultural properties due to the identical genotype of all ramets bearing that name. If ambiguity is to be avoided, the names of such cultivars must be supported by a description based on several

Table 3. F2 crosses between progeny of *Watsonia* 'Lilac Towers'; parents are identified by the cross numbers 1–3 from Tab. 1, with letters distinguishing individual plants selected from each of these F1 crosses.

Ovule parent	Pollen parent	Numbers of progeny	
		Cyanic	Acyanic
1g	1b	5	2
2b	2g	4	0
2g	2h	6	2
2h	2i	7	3
2i	2j	8	0
3c	3b	13	3
3i	3f	19	0

characters, and ideally by a type specimen and molecular data as well. Ornamental cultivars are selected for flower colour and form, as well as for vegetative growth traits that make them 'gardenable', i.e. convenient for use in gardens. Other characters that are not directly selected may be useful indicators to distinguish similar cultivars. In *Watsonia* hybrids, such characters include the relative length of the style, shape of floral bracts, orientation of stamens and shape of the seed capsule.

Cultonomy

Watsonia borbonica (Pouret.) Goldblatt 'Arderne's White' B.Mathew

Kew Mag. 11: 39 (1994) ut *Watsonia borbonica* (Pouret.) Goldblatt subsp. *ardernei* (Sander) Goldblatt 'Arderne's White'.

Watsonia ardernei Sander, Sander's New Plants for 1897 18–20 & fig. (1897). — *Watsonia borbonica* subsp. *ardernei* (Sander) Goldblatt, Ann. Kirstenbosch Bot. Gard. 19: 35 (1989), pro parte. — **Lectotype:** Illustration in Sander's New Plants for 1897, fide Goldblatt, Ann. Missouri Bot. Gard. 74: 572 (1987).

Watsonia ardernei Mathews & L.Bolus, Ann. Bolus Herb. 4: 25–26 (1925), nom. illeg. non Sander (1897). — **Lectotype:** South Africa, Cape, Romans River Farm, Tulbagh Distr. (cult. Kirstenbosch), *Tredgold s.n.* (BOL 17839), n.v., fide Goldblatt, Ann. Missouri Bot. Gard. 74: 572 (1987). **Isolectotype:** PRE 89215-0 ex BOL 17839, n.v., photo seen.

Watsonia pyramidata 'Ardernei' Marais, Kew Bull. 34: 172 (1980).

Watsonia alba Arderne, Garden (London, 1871–1927) 63: 229 (1893). — **Lectotype:** Illustration in Garden (London 1871–1927), fide Goldblatt, Ann. Kirstenbosch Bot. Gard. 19: 35 (1989).

Watsonia iridifolia Ker Gawl. var. *obrienii* N.E.Br. Gard. Chron. ser. 3, 6: 350 (1889), as '*obrienii*' — **Lectotype:** "from the garden of J. O'Brien, Sept 3 1889" (K 320450), fide Goldblatt, Ann. Kirstenbosch Bot. Gard. 19: 35 (1989), n.v., photo seen. **Isolectotype:** K 320451, n.v., photo seen.

Watsonia obrienii Tubergen, Gard. Chron. ser. 3, 16: 701 (1894), nom. nud.

Illustration. L.Bolus, Fl. Pl. South Africa 19: t. 750 (1939), as *W. ardernei* Mathews & L.Bolus; Goldblatt, Ann. Kirstenbosch Bot. Gard. 19: t. 3., as *W. borbonica* subsp. *ardernei* (Sander) Goldblatt.

Typification. The lectotype illustration of *W. ardernei* Sander is a monochrome photolithograph of a gouache painting showing little detail as it was produced for a retail catalogue. The subject is compressed, with the scapes shortened so the inflorescences arise near ground level. The illustration confirms that the plant is a *Watsonia* with the facies of *W. borbonica*, broad ensiform leaves and white flowers with relatively long perianth tubes, but there is no scale and such details as stamen arrangement are not indicated. This illustration was designated as the lectotype by Goldblatt (1987) and later reconfirmed (Goldblatt, 1989). The lectotype illustration of *W. alba* Arderne is a steel engraving showing flowers resembling those of 'Arderne's White' in closeup, but with no detail of stamens or style. The lectotypes of *W. iridifolia* Ker Gawl. var. *obrieni* N.E.Br. and *W. ardernei* Mathews & L.Bolus agree in all essentials, consistent with statements that they are from the same vegetatively propagated stock.

Nomenclatural history

The origin and synonymy of the original acyanic mutant of *Watsonia borbonica* has been covered by Goldblatt (1989) and Mathew (1994). A single acyanic plant of this species was collected from a pink-flowered population at Romans River farm, Cape Province by H.M. Arderne who grew it on his property 'The Hill' at Claremont, Capetown. Around 1888, James O'Brien of Harrow introduced the clone to England and propagated it as *W. iridifolia* var. *obrienii* (Brown 1889).

It was exhibited at the Royal Horticultural Society on 17 September 1889 and illustrated by Hogg (1889). However, the same acyanic clone was re-introduced into England by Robert Templeman in 1891. After attracting much attention at Kew Gardens, it was marketed in the 1890s by Wallace & Co. of Colchester as *W. iridifolia ardernei* (Watson 1896). It was recognised at the time (Watson 1896) that the epithets *ardernei* and *obrieni* referred to the same plant, and this was reconfirmed by Goldblatt (1989).

A potential conflict between the nomenclatural codes for cultivated and wild plants arose because Goldblatt (1989) published the combination *W. borbonica* subsp. *ardernei*, also based on *W. ardernei* Mathews & L.Bolus, for one of the wild variants of *W. borbonica*. Recognising that the name 'Ardernei' was not available for the acyanic cultivar, Mathew (1994) formally published the cultivar name 'Arderne's White' in conformity with the International Code of Nomenclature for Cultivated Plants (Brickell et al. 2004). However, his reference to this plant as "the white watsonia" glossed over the existence of other white-flowered cultivars derived from *W. borbonica*.

Watsonia alba Arderne is a synonym based on the same clone from Romans River (Goldblatt 1989). However, the name *W. alba* was already in horticultural use for at least one other white or almost-white watsonia cultivated in England and Australia before the Romans River plant was introduced. By 1871 the Adelaide Botanic Garden was growing a plant listed as '*Watsonia alba* Ker Gawl.' (Schomburgk 1871);

Table 4. Results of ammonia test for 15 acyanic *Watsonia* and 6 white or cream flowered species in other genera.

	colour reaction after 20 minutes in ammonia	colour reaction after a further 90 minutes in air
Controls		
<i>Argyranthemum frutescens</i> (L.)Sch. Bip.	bright clear yellow	fade to white
<i>Freesia alba</i> (Baker)Gumbl.	bright clear yellow	fade to white
<i>Gladiolus</i> 'Blushing Bride'	faint yellow-grey	fade to cream
<i>Iris albicans</i> Lange	bright clear yellow	fade to white
<i>Rosa banksiae</i> W.T. Aiton	bright clear yellow	fade to cream
<i>Spiraea cantoniensis</i> Lour.	bright clear yellow	fade to white
Acyanic <i>Watsonia</i>		
<i>W. borbonica</i> 'Arderne's White'	faint yellow-grey	fade to off-white
<i>W.</i> 'Ivory Towers'	faint yellow-grey	fade to off-white
accession 5	faint yellow-grey	fade to off-white
accession 17	faint yellow-grey	fade to off-white
accession 89	faint yellow-grey	fade to off-white
accession 91	faint yellow-grey	fade to off-white
acyanic progeny from cross 5	faint yellow-grey	fade to off-white
acyanic progeny from cross 6	faint yellow-grey	fade to off-white
acyanic progeny from cross 7	faint yellow-grey	fade to off-white
acyanic progeny from cross 8	faint yellow-grey	fade to off-white
acyanic progeny from cross 9	faint yellow-grey	fade to off-white
acyanic progeny from cross 11	faint yellow-grey	fade to off-white
acyanic progeny from cross 13	faint yellow-grey	fade to off-white
acyanic progeny from cross 14	faint yellow-grey	fade to off-white
acyanic progeny from cross 16	faint yellow-grey	fade to off-white

however, no valid publication of this name can be traced. It is unlikely to be a misprint for *W. roseoalba* (Jacq.) Ker Gawl., a pink and cream flowered species which has been reduced to synonymy under *W. humilis* Mill. by Goldblatt (1989), who also showed that it was based on *Gladiolus roseoalbus* Jacq. A white-flowered plant similar to *W. borbonica* grown at Thomas Ware's Hale Farm Nurseries in Tottenham, England, was also illustrated as *W. alba* (Anon 1880). Hogg (1884) at first described this flower as pure white, but O'Brien (quoted in Hogg 1889) later averred that his own introduction was the only pure white *Watsonia* and that all others, including by implication those known as *W. alba*, were pink tinged. It may be due to the confusion surrounding the epithet *alba* that Goldblatt (1989) chose *ardernei* as the epithet for the northern subspecies of *W. borbonica*.

The application of the names 'Alba' and 'O'Brienii' to white watsonias in early Australian nursery catalogues is uncertain; for example, Brunning (1905) offered two distinct cultivars under these names in the same catalogue. The uncertainty is compounded by the fact that the closely related species *W. versfeldii* Mathews & L. Bolus was not recognised as distinct from *W. borbonica* until 1922 (Goldblatt 1989). As an acyanic form of *W. versfeldii* has been found naturalised in Victoria (Cooke 1986), this may be the plant to which Brunning applied one or the other of these names.

'Arderne's White' reached the USA from Europe, and was used by Luther Burbank in a breeding program that produced several white cultivars including 'Royal White' and 'Vesta' between 1908 and 1917 (Howard 1945).

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