

## MORPHOTYPE AND CONFLICTING TAXONOMIES IN *PTERIDIUM* (DENNSTAEDTIACEAE: PTERIDOPHYTA)

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### ABSTRACT

Conflicting taxonomic treatments of the diploid bracken ferns of the Laurasian lineage within *Pteridium* are briefly reviewed. The infraspecific entities recognised in this section of the genus can be separated on morphological, phenological and physiological criteria into two main groups referred to respectively as 'aquilinum' and 'latiusculum' morphotypes. Evidence of gene flow between morphotypes is discussed, including the finding from DNA studies that taxa of the 'aquilinum' and 'latiusculum' morphotypes in each major geographic region are more closely related to the contrasting morphotype from the same region than to the corresponding morphotype from another region. It is proposed here that the 'aquilinum' and 'latiusculum' morphotypes may be regarded as mediated by a simple genetic polymorphism involving alternative pleiotropic alleles at a single major morphogenetic locus comparable to those previously described in *Athyrium* and postulated in *Asplenium* and *Pteridium*, but other possible models are discussed.

It is concluded that *P. aquilinum* is best treated as a single species containing at present 11 subspecies.

### INTRODUCTION

A vigorous ongoing polemic continues to cloud taxonomic treatment of the diploid ( $2n = 104$ ; Wolf *et al.*, 1987, 1988) bracken ferns [*Pteridium aquilinum* (L.) Kuhn] comprising a Laurasian lineage within the genus. Thomson and colleagues (Thomson, 2004; Thomson *et al.*, 2005; Thomson *et al.*, 2008; *contra* Thomson, 2000) regard *P. aquilinum* as a grouping of 11 subspecies (Table 1) that in general correspond to varieties within Tryon's (1941) *P. aquilinum* subsp. *aquilinum*. In contrast, certain other contemporary classifications are based on separation of these taxa into two phenotypic groups designated here as the 'aquilinum' and 'latiusculum' morphotypes (Table 1). Page (1997) and coauthors (Page & Mill, 1995; Gureyeva & Page 2005) regard these 'aquilinum' and 'latiusculum' morphotypic groups as multi-species complexes represented in Europe by *P. aquilinum* and by *P. pinetorum* C.N. Page & R.R. Mill respectively, each with several subspecies. Fraser-Jenkins (1997), on the other hand, recognises *P. latiusculum* (Desv.) Hieron. ex R.E.Fr. at species level and accords subspecific rank to *P. latiusculum* subsp. *pinetorum* (C.N. Page & R.R. Mill) Fraser-Jenk. Stace (1997) and Karlsson (2000) group the European 'aquilinum' phenotypes as *P. aquilinum* subsp. *aquilinum* and those of 'latiusculum' as *P. aquilinum* subsp. *latiusculum* (Desv.) Hultén. Shorina & Perestoronina (2000) distinguish the European 'latiusculum' morphotype as *P. aquilinum* var. *pinetorum* (C.N. Page & R.R.

**Table 1:** Geographic distribution and current subspecific nomenclature of northern hemisphere diploid ( $2n = 104$ ) bracken taxa indicating ‘aquilinum’ or ‘latiusculum’ morphotype, together with Tryon’s (1941) varietal names for reference.

Geographic region/ morphotype	<i>P. aquilinum</i> subspecies	<i>P. aquilinum</i> variety
<b>Europe</b>		
‘aquilinum’	<i>aquilinum</i>	<i>aquilinum</i>
‘latiusculum’	<i>pinetorum</i> (C.N. Page & R.R. Mill) J.A. Thomson <sup>1,2</sup>	<i>latiusculum</i> (Desv.) Underw. ex Heller
<b>Asia</b>		
‘aquilinum’	<i>wightianum</i> (Wall. ex J. Agardh) Shieh <sup>3</sup>	<i>wightianum</i> (J. Agardh) R. Tryon
‘latiusculum’	<i>japonicum</i> (Nakai) A. Löve & D. Löve <sup>1</sup>	<i>latiusculum</i> (Desv.) Underw. ex Heller
<b>Africa</b>		
‘aquilinum’	<i>capense</i> (Thunb.) C. Chr. <sup>4</sup>	<i>aquilinum</i>
‘latiusculum’	<i>centrali-africanum</i> Hieron. ex R.E. Fr. <sup>4</sup>	<i>africanum</i> Bonap.
<b>North America</b>		
‘latiusculum’	<i>feei</i> (W. Schaffn. ex Fée) J.A. Thomson, Mickel & K. Mehlreter <sup>5</sup>	<i>feei</i> (W.Schaffn. ex Fée) Maxon ex Yuncker
	<i>latiusculum</i> (Desv.) Hultén auct. Thomson (2004) <sup>1</sup>	<i>latiusculum</i> (Desv.) Underw. ex Heller
	<i>pseudocaudatum</i> (Clute) Hultén <sup>5</sup>	<i>pseudocaudatum</i> (Clute) Heller
	<i>pubescens</i> (Underw.) J.A. Thomson, Mickel & K. Mehlreter <sup>5</sup>	<i>pubescens</i> Underw.
<b>Hawaiian Islands</b>		
‘intermediate’	<i>decompositum</i> (Gaudich.) Lamoureux ex J.A. Thomson <sup>1</sup>	<i>decompositum</i> (Gaudich.) R. Tryon

<sup>1</sup> Thomson, 2004

<sup>2</sup> Also referred to as *P. aquilinum* subsp. *latiusculum* (Desv.) Hultén; *P. aquilinum* var. *pinetorum* (C.N. Page & R.R. Mill) Perestor.; *P. pinetorum* C.N. Page & R.R. Mill; *P. latiusculum* subsp. *pinetorum* (C.N. Page & R.R. Mill) Fraser-Jenk.

<sup>3</sup> Also referred to as *P. revolutum* (Blume) Nakai

<sup>4</sup> Thomson *et al.*, 2005

<sup>5</sup> Thomson *et al.*, 2008

Mill) Perestor.

A dearth of useful discriminatory characters often leads to difficulties in pteridophyte taxonomy, especially in the case of low order taxa that may be separated on as few as one single character (Perrie & Brownsey, 2005). In many fern species the segmental units represented at successive levels by frond, pinna, pinnule, and even pinnulet, form a repetitive hierarchical series for which a feature expressed at one level may not be independent of a corresponding feature scored at another segmental level. In general, such attributes should be treated as relating to a single character, and may well share a common genetic basis. Examples are evident in the morphometric documentation of the relative number, size, shape and spacing of pinnae, pinnules and pinnulets in subspecies of *Pteridium aquilinum* (L.) Kuhn (Thomson *et al.*, 2005; Thomson *et al.*, 2008). Further, many commonly used features of indumentum, false indusium and laminal segmentation are extremely labile, being affected by age, shading, water-logging and other environmental conditions (Ashcroft & Sheffield, 1999; Karlsson, 2000; Thomson *et al.*, 2005; Thomson *et al.*, 2008) and must be employed quantitatively and with caution.

Three recent re-evaluations of disputed taxonomic treatments in ferns highlight the contribution that genetic evidence, either directly from breeding experiments or indirectly from molecular data, may make to more consistent and objective assignment of taxonomic rank. In *Athyrium distentifolium* Tausch ex Opiz (Woodsiaceae), morphotype 'flexile' is endemic to Scotland and is found only at localities where 'distentifolium' is also present (McHaffie *et al.*, 2001). Sporophytes of the 'flexile' phenotype are distinguished from 'distentifolium' by frond morphology, position of sori and response to nutrients. The two phenotypes are controlled by alleles of a single major gene with pleiotropic effects expressed in both gametophyte and sporophyte, the 'flexile' morphotype being recessive to 'distentifolium'. In one natural population the frequency of the recessive allele was about 0.4. The two morphotypes were originally described as separate species but McHaffie and colleagues recommend a taxonomic status not higher than variety.

In *Asplenium hookerianum* Colenso (Aspleniaceae), morphotype 'hookerianum' occurs in Australia and New Zealand and is distinguished from the endemic New Zealand morphotype 'colensoi' which has consistently narrower pinnules. Stands in New Zealand commonly comprise morphotype 'hookerianum' alone or co-occurring with 'colensoi': 'colensoi' by itself is rare (Perrie & Brownsey, 2005). The two forms were originally described as separate species. Neither nuclear genomic fingerprinting by AFLP nor the chloroplast sequence results separated the specimens according to morphotype. Geographic source accounts for much more of the total DNA-sequence variation than pinnule morphology in both the AFLP data (29% of genetic variation *versus* 0%) and the chloroplast haplotype data (58% of genetic variation *versus* 3%; Perrie & Brownsey, 2005). Plants of contrasting morphotype originating from close sites are more similar to each other genetically than to plants of the their own morphotype from distant sites. The phenotypic stability of plants of the two morphotypes even when growing intertwined in the field argues against a major role for environmental variables, and 'colensoi' is purported to breed true from spores (Perrie & Brownsey, 2005). It appears probable that morphotypic variation in *Asplenium*, like that in *Athyrium*, results from a simple genetic polymorphism based on allelic variation at a single locus. Perrie & Brownsey (2005) conclude that there is no significant genetic discontinuity between the two morphotypes, and no justification for separating them at

higher than varietal or form rank.

Within *P. aquilinum* in North America, the status of the two eastern taxa now designated subsp. *latiusculum* and subsp. *pseudocaudatum* (Table 1) proved contentious until detailed analyses of morphology and isozyme complements were made by Speer & Hilu (1999) and Speer *et al.* (1999). These taxa are clearly distinct on morphological and distributional grounds (Speer & Hilu, 1999; Thomson *et al.*, 2008). Over their main east-coast range, 'latiusculum' is more abundant in the northern states, 'pseudocaudatum' in the south (Speer & Hilu, 1999), with only very few narrow zones of overlap where intermediates suggesting introgression are seen. Detailed isozyme analyses showed unrestricted gene flow between the two morphotypes at one such zone of co-occurrence (Speer *et al.*, 1999). Speer and colleagues postulate that the 'latiusculum' and 'pseudocaudatum' phenotypes may be controlled by alternative alleles at a single genetic locus with pleiotropic effects. If the 'latiusculum' phenotype is dominant and determined by an allele with high frequency in the north of its range, while the recessive allele for the 'pseudocaudatum' phenotype is at high frequency or fixed in the south, the roughly equal frequencies of the two forms observed in the North Carolina piedmont would correspond to a frequency of about 0.7 for the recessive allele (Speer *et al.*, 1999). Strong selective pressure in relation to environmental features and habitat preference are indicated, with a taxonomic ranking of subspecies for the two morphotypes (Thomson *et al.*, 2008).

#### CHARACTERISATION OF GENERALISED 'AQUILINUM' AND 'LATIUSCULUM' MORPHOTYPES IN *PTERIDIUM*

Characters that reflect the relative number, relative size, spacing and shape of laminal segments at blade, pinna, pinnule and pinnulet levels (Thomson, 2000; Thomson *et al.*, 2005; Thomson *et al.*, 2008), are particularly effective in discriminating a 'latiusculum'-like group of taxa from an 'aquilinum'-like phenotypic group.

**The 'aquilinum' morphotype:** Blade long, ovate to linear, typically 2-3 times the length of the longest pinna which is generally one of the third to the fifth pair from the lamina base towards the tip. Pinnae, pinnules (and less markedly pinnulets), relatively long and narrow; typically 13-18 pinnules in the basal half of the longest pinna. Pinnae and pinnules commonly inserted on rachis and costa at 70-90°. Frond expansion gradual, progressing from base to apex. Basal 1-2 pinna pairs often marcescent before expansion of the distal pinnae is complete. Frond axes relatively thick and fibrous; dense stands leave heavy, often partially upright, litter in winter that is slow to collapse next season.

**The 'latiusculum' morphotype:** Blade short, broadly triangular, typically 1-1.5 times the length of the longest pinna which is generally one of the first or second pair from the base towards the tip. Pinnae, pinnules (and less markedly, pinnulets) relatively short and broad; typically 6-9 pinnules in the basal half of the longest pinna. Basal segment(s) of each order sometimes much reduced, even vestigial. Pinnae and pinnules commonly inserted on rachis and costa at 45-70°. Frond expansion rapid, often almost synchronous, although progressive from base to apex. Basal pinna pairs not marcescent before frond expansion is complete. Frond axes relatively thin, not heavily fibrous; dense stands leave thin litter in winter that collapses readily next season.

The ovate to linear form of the expanded blade and pinna in 'aquilinum' morphotypes results from both the shorter length of the lowest pinna and pinnule pair(s) compared with those placed more centrally and the relatively higher number of these

segments on the frond axis and costa respectively. The broadly triangular frond blade and pinna of the ‘latiusculum’ morphotype could be envisaged as derived from the ‘aquilinum’ type by loss of pinna and pinnule pairs from the base of blade and pinna upwards, a process which would at the same time increase the apparent length, relative to more distal segments, of the pinnae/pinnules which thus become the basal or near basal components. Overall the ‘latiusculum’ morphotype appears to reflect adaptation to conditions providing a short growing season.

Where zones of contact or parapatry occur locally, as in Europe (Rumsey *et al.*, 1991; Karlsson, 2000), NE Asia (Tryon, 1941), and Africa (Verdcourt, 2000), recurrent field observations of morphological intermediates provide evidence of recent, probably ongoing, interbreeding between ‘aquilinum’ and ‘latiusculum’ morphotypes. Multi-locus isozyme marker studies also reveal gene flow between multiple genets (Bridges *et al.*, 1998) of subsp. *pinetorum* in Scotland and local populations of subsp. *aquilinum* (Rumsey *et al.*, 1991).

DNA fingerprinting using the Arbitrarily Primed Polymerase Chain Reaction (AP-PCR) and Inter Simple Sequence Repeat (ISSR) procedures show that genomic similarity is higher between ‘aquilinum’ and ‘latiusculum’ morphotypes from the same geographic region than either is with morphotypes of its own group from other regions (Thomson *et al.*, 2005; Thomson *et al.*, 2008). Thus subspp. *capense* and *centrali-africanum* from sub-Saharan Africa are more similar genomically than *capense* is to *aquilinum* of Europe or *centrali-africanum* is to the N American *latiusculum* (Thomson *et al.*, 2005; Thomson *et al.*, 2008). Similarly, subspp. *pinetorum* and *aquilinum* of Europe share more genomic markers than *pinetorum* shares with *latiusculum* of North America (Thomson, 2000; Thomson *et al.*, 2005). Chloroplast genome haplotype for the *rps4-trnS* region based on presence or absence of one or both of two 5-base direct repeats is not concordant with the ‘aquilinum’ or ‘latiusculum’ morphotypic groupings (Thomson *et al.*, 2005; Thomson *et al.*, 2008). For example, the haplotypes (Type A or B, Thomson *et al.*, 2005) of three geographically contiguous ‘latiusculum’ and ‘aquilinum’ morphotype pairs are: subspp. *pinetorum/aquilinum* (Europe) respectively Types A and B, subspp. *centrali-africanum/capense* (Africa) both Type B, and subspp. *japonicum/wightianum* (NE Asia) both Type A.

These findings provide strong evidence against a taxonomy based on separation of ‘latiusculum’ and ‘aquilinum’ clades (Thomson *et al.*, 2008), and in particular argue against recognition of ‘latiusculum’ or ‘aquilinum’ as reproductively-separated groupings that individually merit full species status. Within *Pteridium aquilinum* as recognised here (Table 1), reticulate phylogenetic relationships overlie evolutionary trends presumably based on diversification and local adaptation.

### IS THE ‘AQUILINUM’ VERSUS ‘LATIUSCULUM’ DISTINCTION A SIMPLE GENETIC POLYMORPHISM?

Descriptively, the morphological polymorphisms analysed in *Athyrium* (McHaffie *et al.*, 2001) and postulated in both *Asplenium* (Perrie & Brownsey, 2005) and *Pteridium* (Speer *et al.*, 1999) behave as if based on variant alleles of major genes, with allele frequencies being maintained by balancing selection pressures in particular environments and/or differentially in the gametophyte or sporophyte stage. The contention that the ‘aquilinum’ *versus* ‘latiusculum’ contrast also represents a genetic polymorphism is supported by distributional data (Table 1), the genetic relationships of the contrasting morphotypes in areas of overlap, and evidence that laminal segment

morphology at frond, pinna, pinnule and even pinnulet levels is hierarchically repetitive and likely to be under control of a common gene or genes with alternative, apparently pleiotropic, alleles. Definitive characterisation of the genetic basis of morphotype in bracken must await integrated breeding and molecular analyses. The loci involved are, however, clearly distinct from those responsible for the small-scale morphological variants often collected and cultivated by growers (see, for example, Andersson, 1927) that are rare in natural populations, with very low allele frequencies maintained by recurrent mutation opposing negative selection (McHaffie *et al.*, 2001).

While for descriptive purposes morphotypic variation in the ferns discussed here may be adequately treated in terms of single locus polymorphisms with pleiotropy, functional and structural molecular analyses of the loci responsible are now required to reveal how the underlying developmental process are controlled. In general, the more numerous and diverse the multiple phenotypic effects involving disparate morphological and physiological characteristics that appear to be under single gene control, the more an explanation invoking pleiotropy becomes questionable. In the present cases we therefore need to consider other possible models of gene structure such as that exemplified by the complex S locus responsible for self-incompatibility (SI)/compatibility (SC) in a number of families of flowering plants such as Brassicaceae. This super-locus provides co-ordinated unitary genetic control over multiple aspects of SI mediated by tightly linked co-adapted sequence segments collectively forming an S haplotype (Charlesworth *et al.*, 2005). Multiple developmental, cellular, physiological and biochemical processes in different S phenotypes are mediated by the alternative S haplotypes represented in polymorphic populations or in different taxa (Bechsgaard *et al.*, 2006; Sherman-Broyles *et al.*, 2007). The several features characterising each S phenotype are controlled by distinct sequence elements and do not involve pleiotropy. Where aspects of phenotype are controlled by a complex super-locus or through a stepwise multigene pathway, multiple mutations may appear as a single event if a mutation acting at an early step blocks expression of accumulated changes effective later in the pathway. If features distinguishing allopatric morphotypes are subject to selection, the allelic variants responsible will be expected to change in frequency more rapidly than 'neutral' genomic elements. Phenotypic features under positive selection are likely to become fixed faster than other genomic segments so that the probability of finding DNA sequence markers correlating with morphotype is expected to be low, increasing with the time of separation of the contrasting forms. In *Asplenium*, Perrie & Brownsey (2005) found that neither AFLP fingerprinting of the nuclear genome nor chloroplast sequence data grouped the plants analysed according to their morphotype. In *Pteridium*, Thomson (2000) identified markers detected by AP-PCR that are specific to subsp. *wightianum* (as *P. revolutum*) and other markers that are specific to subsp. *capense* [misnamed by Thomson (2000) as *P. aquilinum* var. *africanum*; see Thomson *et al.*, 2005). These major markers are in both cases restricted in occurrence to geographically localised taxa here regarded as of subspecific status, and neither is shared by other 'aquilinum' morphotypes. Distinctive alleles, supergene haplotypes and/or modified dominance relations may account for the 'intermediate' morphotype of subsp. *decompositum* (Table 1) in which genomic elements of both subsp. *japonicum* ('latiusculum') and subsp. *wightianum* ('aquilinum') are present (Thomson, 2000).

### CONCLUSIONS

In most taxonomic investigations of ferns, especially where multiple taxa must be considered, controlled breeding experiments of the kind so admirably applied in *Athyrium* (McHaffie *et al.*, 2001) are not practicable. More widely feasible are genomic comparisons based on methodologies such as AP-PCR (RAPD), AFLP, ISSR, or microsatellite analyses. If plants of taxon A from locality 1 are more closely related genetically to plants of taxon B from locality 1 than to taxon A plants from localities 2...n, and/or a comparable situation holds for the relationships of taxon B, there is *prima facie* evidence of recent and/or ongoing gene flow between the taxa that is likely to be inconsistent with the degree of reproductive isolation normally associated with full specific status. Rather, such a situation strongly suggests that the taxa concerned should be accorded infraspecific rank, for example as subspecies, varieties, or forms (Perrie & Brownsey, 2005; Thomson *et al.*, 2008).

The work of McHaffie and colleagues on the ‘distentifolium’/‘flexile’ polymorphism in *Athyrium* represents an extraordinary contribution to our understanding of fern morphogenetics by showing how morphological and physiological studies of the gametophyte as well as the sporophyte may reveal at these two life stages ‘antagonistic pleiotropy’ (Shaw, 2001) that determines allele frequencies in natural populations through otherwise unsuspected opposing positive and negative selective pressures. However, as pointed out above, questions remain open regarding the structure of the genetic loci involved in the control of fern morphotype, and thus on the strict applicability of the term pleiotropy in these cases.

*P. aquilinum* appears at present to be best treated as a single species containing 11 subspecies as listed in Table 1. Further morphometric and genetic studies are needed to clarify the status of a number of named taxa described from many parts of Eurasia which on present evidence should, if named, be ascribed varietal, form or ecotype rankings (Stace, 1997).

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