

Three subspecies of Bracken, *Pteridium aquilinum* (L.) Kuhn, in Britain

C. N. PAGE

Royal Botanic Garden, Edinburgh, EH3 5LR

ABSTRACT

Two additional native subspecies of *Pteridium aquilinum* (Bracken) are added to the single hitherto known taxon of this genus in the British flora. These are *Pteridium aquilinum* (L.) Kuhn subsp. **latiusculum** (Desv.) C. N. Page, **comb. et stat. nov.**, known previously to have its nearest location in Scandinavia, now found to occur in the Scottish native pinewoods, and *Pteridium aquilinum* (L.) Kuhn subsp. **atlanticum** C. N. Page, **subsp. nov.**, recently discovered on the Atlantic fringes of western Scotland and described here for the first time. Both these brackens are distinct from the widespread and common British bracken, to which the subspecific epithet *Pteridium aquilinum* (L.) Kuhn subsp. *aquilinum* is here restricted, and from which they are distinguished.

The theory is proposed that subsp. *aquilinum* may be the hybrid between subsp. *atlanticum* and subsp. *latiusculum*.

INTRODUCTION

This paper reports the addition of two taxa of bracken new to the British flora. These are *Pteridium aquilinum* (L.) Kuhn subsp. *latiusculum* (Desv.) C. N. Page, **comb. et stat. nov.**, known previously to have its nearest stations in Scandinavia, but which has been found to be present in the Scottish native pinewoods, and *Pteridium aquilinum* subsp. *atlanticum* C. N. Page, **subsp. nov.**, recently discovered in limited areas of the Atlantic fringe of western Scotland.

Both have been found by the author in the last few years, and their morphology, ecology and seasonal behaviour have now been followed in the field over a number of seasons. These observations show that each of these brackens differs strongly from the other, as well as from the widespread *P. aquilinum* subsp. *aquilinum*, not only in morphology but also in ecology and seasonal behaviour, with the most diagnostic structural differences apparent during the period of frond emergence in spring and during frond senescence in autumn and winter. Hence the new taxa may be most easy to locate initially at these times of the year.

The morphology of each of these new taxa suggests that subsp. *aquilinum* is strikingly intermediate between them, and the theory is proposed here that subsp. *aquilinum* may be of hybrid origin between subsp. *latiusculum* and subsp. *atlanticum*. The continuing occurrence of some hybridization and very possibly introgression of subsp. *aquilinum* back to both the other taxa is suggested by the field evidence, indicating one possible source of the variability of the widespread and vigorous subsp. *aquilinum*. The native British material of the latter is known to be genotypically as well as phenotypically variable (Page 1982 a & b, 1986; Hadfield & Dyer 1986; Wolf *et al.* 1988), and introgression is a phenomenon which itself is extremely rare in ferns (Walker 1958, 1979; Lovis 1977).

DESCRIPTIONS

Pteridium aquilinum* (L.) Kuhn subsp. *latiusculum* (Desv.) C. N. Page, **comb. et stat. nov.*

Pteris latiuscula Desv., *Mem. Soc. Linn. Paris* 6 (2): 303 (1827)

Pteridium aquilinum (L.) Kuhn var. *latiusculum* (Desv.) Underw. ex Heller, *Cat. N. Am. Pl.*, 3rd ed., 17 (1909)



A



B

FIGURE 1. *Pteridium aquilinum*. A, subsp. *latiusculum*; B, subsp. *atlanticum*.

VOUCHER: Scotland: East-Inverness-shire, Rothiemurchus Forest near Loch an Eilean, in native pinewood, 4 June 1983, C. N. Page 17,049 (E, PTH, GL, ABD).

Fronds to 80 cm or somewhat more; stipe usually short, erect, slender (seldom exceeding 4 mm diam.), initially wiry, tough, rigid and remaining so throughout the season, broken stipes only weakly mucilaginous; rachis usually strongly deflexed at the junction of stipe and first pinna-pair into a shallowly ascending to nearly horizontal angle, thereafter remaining inclined and approximately straight for the full length of the blade; pinnae expanding very rapidly and almost simultaneously throughout the frond in spring, their expanding croziers regularly and tightly coiled, with a tomentum of sparse, short-lived white hairs and very numerous and distinctive long, cinnamon-coloured hairs which are long-persistent throughout the rachis, pinna midribs and pinnule midribs during the expansion phases of the frond; newly expanding pinnae and pinnules at once obliquely ascending, stiff and rigid; expanded blades broadly triangular, ternate to subternate, tripinnate to tripinnate-pinnatifid, bright grass green on all surfaces and scarcely glossy above, their pinnae not rotated from the plane of the rachis but pinna midribs and pinnules all constantly somewhat distally angled, each straight (never drooping at the tips even when freshly flushed) and obliquely assurgent; fronds turning bright red-brown in autumn, and usually mostly remaining standing, with rather little decay, until the end of winter or the following spring.

The especially distinctive features of this bracken are its extremely early-season and rapid frond expansion rate (Fig. 1A), harsh and wiry texture of stipe and frond from the outset, nearly simultaneous pinna-pair expansion throughout each blade, steeply inclined blade orientation from the first pinna pair, obliquely ascending rigid pinnae to the expanding fronds, and the very abundant presence of numerous, long, cinnamon-coloured hairs over the frond and pinna croziers, giving them a conspicuously red-brown coloration during their brief expansion phase. Indeed, the simultaneous flushing of the pinnae, the bright green colour of the blade, the angled blade and pinna orientation and the cinnamon-coloured croziers combine to make this plant distinctive and easily recognizable even from a distance.

***Pteridium aquilinum* (L.) Kuhn subsp. *atlanticum* C. N. Page, subsp. nov.** TYPE: Scotland: North-east Arran, Clyde Isles (v.c. 100), c. 15 m. alt., on Carboniferous limestone, 4 June 1987, C. N. Page 29,020 (holotype E, isotypes PTH, GL, ABD).

Pinnae frondarum accurate in ordine ad apices versus extendentes; crociae (apices circinnati) tomento denso e squamis longis albo-argenteis indutae, pilis rufis carentibus; laminae extensae ovato-triangularae, numquam ternatae.

Pinnae of fronds expanding in a strongly sequenced acropetal succession, the croziers with a dense tomentum of long, silver-white hairs, without red hairs; the expanded blades ovate-triangular, never ternate.

Fronds to 120 cm or more; stipe usually tall, erect, thick (c. 6–9 mm diam.), initially soft, turgidly succulent with broken surfaces abundantly mucilaginous, eventually becoming toughly succulent; rachis deflexed only slightly and equally at each successive pinna-pair junction, the several lowermost increments of the rachis thus nearly erect; pinnae of the whole blade expanding very slowly and in a strongly sequenced acropetal progression of successive pinna pairs (never simultaneously throughout the frond); frond and pinna croziers large, only loosely and irregularly coiled during expansion phases, and conspicuously covered on the expanding rachis and pinna and pinnule midribs with a very dense and abundant tomentum of long, bright silver-white hairs of silky texture, without any intermixed red hairs, the white tomentum persisting in sparser form through the expansion phases of the frond to become progressively lost by maturity; fully expanded blades ovate-triangular, never ternate, usually bipinnate-pinnatifid, dull green and usually glossy above, paler beneath, the pinnae horizontally inserted on near-vertical rachis (especially those in the lowermost half of the frond); pinnae and pinnules mostly perpendicularly inserted (neither oblique nor assurgent), spreading horizontally from their bases and laxly drooping towards their tips (especially during expansion but remaining arching downward throughout the life of the frond);

fronds turning pale tan-brown in autumn and senescing and decaying rapidly following the first severe frosts.

The especially distinctive features of this bracken are its late-season and sometimes particularly slow frond expansion rate (Fig. 1B), strongly sequenced unrolling of successive pinna pairs, initially vertical orientation of the blade with horizontally inclined pinnae, nearly perpendicular pinna and pinnule insertion angles, very succulent early-season stipe and rachis, soft frond texture and lax pinnae-tips to the expanding fronds, and the very abundant capping to the expanding croziers by silver-white hairs, lacking totally in red hairs, giving the croziers of this subspecies a conspicuously white-capped appearance during their long expansion phase. Indeed, the white croziers coupled with the late-season flushing of vertical fronds make this plant especially conspicuous during its early-season growth.

NOMENCLATURE

The type of the species belongs to the common, vigorous morph which is widespread in Europe (Sheffield *et al.*, 1989). The epithet subsp. *aquilinum* is thus restricted to this morph.

The two taxa added here to the British flora are treated as additional subspecies of *P. aquilinum* because of their strong and largely discontinuous morphological (and corresponding ecological) distinctions from the widespread variant, indicating a more distant relationship to it (see below). Indeed, it might be justifiable to treat each of the three native British brackens as separate species, but I have not done so for lack, as yet, of evidence of sufficient distinction at genetic or cytological level, and because of the occurrence of widespread intergradient variants which I suspect may prove to be fully fertile (although neither the subspecies nor apparent hybrids have been found to be spore-productive through the succession of several climatically dull, wet summers in Scotland, through which they have been studied).

ECOLOGY

Although their distribution is as yet imperfectly known, both these new taxa of bracken appear to be native and are probably ancient members of the British flora. Both also appear to be significantly less vigorous than is subsp. *aquilinum*, and the colonies of both are relatively local and limited in extent. Beyond these basic similarities, however, available information suggests that the ecology of the two new brackens, like their morphology, contrasts in several significant aspects.

Subsp. *latiusculum* is as yet known in Britain only from limited areas of relict Scottish native pinewood vegetation (*Pinus sylvestris* L.) with an understorey of native juniper (*Juniperus communis* L.), in the vicinity of Rothiemurchus, Speyside (Page 1988). Here it forms open, low-canopied stands over small areas, the edges of which abut on to, and partly intermingle with, much more extensive and taller-growing stands of subsp. *aquilinum*, which is present throughout much of the pinewoods around it. Compared with adjacent subsp. *aquilinum*, the stands of subsp. *latiusculum* are lower-growing and notably more open and, despite their more horizontally-inclined blades, more light penetrates to the ground beneath. Here a continuous ground-flora of grasses, mosses and associated pinewood species persists. The soil is deep and acidic, with a peaty surface layer developed over very much deeper fluvio-glacial outwash sands and gravels of largely granitic origin. The persistence of the fronds (and especially their stipes) in a more or less standing position through the winter months probably helps to ensure that ground vegetation beneath is not heavily swamped by a decaying frond-blanket, in contrast to that beneath stands of nearby subsp. *aquilinum*, whose stipes normally readily collapse.

Subsp. *atlanticum*, as here described, is as yet known only from very limited areas of Scottish limestone grassland at very low altitude near western coasts (Arran and Kintyre). In each site it forms fairly open, low to moderately high-canopied stands over little more than a few hundred square metres, abutting on to much denser and generally taller-growing stands of subsp. *aquilinum*, which are locally extensive. Its particularly slow rate of expansion results, in dull summers, in fronds which are still unfurling at their tips (and thus can seem almost indefinitely growing) while the several lower pinnae of the same fronds are senescing at the end of the season. In such summers, fronds may thus fail to expand completely, and this may be a normal condition at its Scottish latitudes. The stands of subsp. *atlanticum* are also rather more open than are those of subsp.

aquilinum nearby, with a more continuous ground flora of basic grassland species. The soil is very shallow in places, with significant areas of outcropping rock. That the whole of the range of this plant appears to correspond exclusively to areas of outcropping Carboniferous limestone rock overlain by a thin limestone soil, appears to be one of the most notable aspects of the ecology of this taxon, and is unusual for bracken anywhere. Indeed, off the limestone, subsp. *atlanticum* is replaced immediately by subsp. *aquilinum* or by hybrids and introgressants with it, all of which appear not to succeed on the limestone. Indeed, it seems likely that it is just this ecological distinction which has been responsible for the survival of subsp. *atlanticum* in these sites, even when closely surrounded by extensive more vigorous subsp. *aquilinum*.

DISCUSSION

The addition of these two new taxa to the British flora, and the presence also of suspected hybrids between each and subsp. *aquilinum*, further supplements the view previously expressed (Page 1982a, 1986) that, in Britain at least, bracken is anything but a totally uniform plant.

The occurrence of subsp. *latiusculum* in Scottish pinewoods suggests that this subspecies is also native and relictual. Indeed, outside the British Isles, the known range of this taxon stretches in a broad band across far northern Europe and Asia to the Orient, and across northern North America (Tryon 1941; Page 1976). It is thus essentially the bracken of the northern boreal conifer forests of the world, and its discovery within the range of an ancient native pinewood in Scotland, and its rapid spring frond extension and apparent substantial frost-hardiness, all seem aspects of its ecology entirely in accord with this general range.

The occurrence of subsp. *atlanticum* in remote sites of relatively undisturbed vegetation on the Atlantic fringes of western Scotland similarly suggests that this taxon is also native. Its apparent total restriction to outcrops of limestone is unusual in the range of the genus, while its late and extremely slow rates of frond expansion and apparent high frost sensitivity seem to indicate also a likely requirement for a long growing season. Further, its known sites, only at low altitude in mild western climates, occur close to sites for other ferns of highly Atlantic range (including on nearby, more acidic rock areas, *Dryopteris aemula* and the three native filmy ferns), and suggest that this bracken too may well be a plant of essentially southerly and Atlantic affinity. In this connection, it is interesting to note that Jermy (pers. comm. 1989) reports similar open bracken stands at 1000 m alt. in the Picos d'Europa, northern Spain, where fronds with characteristically silvery tips were still unfurling in early August. He notes further that these plants too occur in an area where other Atlantic pteridophytes are prevalent, notably the rare *Stenogramma pozoi*, *Trichomanes speciosum* and *Dryopteris guanchica*. The possibility of subsp. *atlanticum* occurring in other southerly localities both within and beyond the British Isles thus now seems an important area to which further field study might be usefully directed.

The report by Löve & Kjellqvist (1972) of an allegedly limestone-dwelling bracken occurring in the western Mediterranean basin (named *Pteridium herediae* (Clemente ex Colmeiro) Löve & Kjellqvist) needs to be mentioned here, although it is, regrettably, impossible from the brief and incomplete published descriptions of this plant and from the lack of any known type material (see Sheffield *et al.* 1989) to compare this plant with subsp. *atlanticum*.

POSSIBLE INTERRELATIONSHIPS

The respective morphologies and ecologies of the two subspecies of bracken reported here are highly distinctive. Between these morphological and ecological extremes, subsp. *aquilinum* appears to be intermediate. Indeed, much of the variability of subsp. *aquilinum*, where other than environmentally induced, reflects different combinations of characters and ecologies which are represented in 'pure' form only by the two taxa discussed here.

For these reasons, the theory is proposed here that the widespread and common *Pteridium aquilinum* subsp. *aquilinum* may be the genetically stabilized hybrid between subsp. *latiusculum* and subsp. *atlanticum*, its vigour and variability resulting from heterosis, presumed polytopic origins and possible widespread superimposed introgression.

Further study of the taxa in question is now proceeding at Edinburgh to investigate their suspected interrelationships experimentally.

ACKNOWLEDGMENTS

I am grateful to A. C. Jermy (BM) and Dr A. F. Dyer (Edinburgh) for comments made in the field, and to them and B. L. Burt (Edinburgh), Dr T. G. Walker (Newcastle) and Dr E. Sheffield (Manchester) for helpful comments on the manuscript, and to B. L. Burt for latinization of the diagnosis.

REFERENCES

- HADFIELD, P. & DYER, A. (1986). Polymorphism of cyanogenesis in British populations of bracken (*Pteridium aquilinum* (L.) Kuhn.), in SMITH, R. T. & TAYLOR, J. A., eds. *Bracken. Ecology, land use and control technology*, pp. 293–300. Carnforth.
- LÖVE, A. & KJELLQVIST, E. (1972). Cytotaxonomy of Spanish plants. 1. Introduction: Pteridophytes and Gymnospermae. *Lagascalia* 2: 23–25.
- LOVIS, J. D. (1977). Evolutionary patterns and processes in ferns. *Adv. Bot. Res.* 4: 229–415.
- PAGE, C. N. (1976). The taxonomy and phylogeography of bracken – a review. *Bot. J. Linn. Soc.* 73: 1–34.
- PAGE, C. N. (1982a). *The ferns of Britain and Ireland*. Cambridge.
- PAGE, C. N. (1982b). The history and spread of bracken in Britain. *Proc. Roy. Soc. Edinb.* 81B: 3–10.
- PAGE, C. N. (1986). The strategies of Bracken as a permanent ecological opportunist, in SMITH, R. T. & TAYLOR, J. A., eds. *Bracken. Ecology, land use and control technology*, pp. 173–181. Carnforth.
- PAGE, C. N. (1988). *Ferns. Their habitats in the landscape of Britain and Ireland*. London.
- SHEFFIELD, E., WOLF, P. G., HAUFLE, C. H., RANKER, T., & JERMY, A. C. (1989). A re-evaluation of plants referred to as *Pteridium herediae*. *Bot. J. Linn. Soc.* 99: 377–386.
- TRYON, R. (1941). A revision of the genus *Pteridium*. *Rhodora* 43: 1–41, 47–67.
- WALKER, T. G. (1958). Hybridization in some species of *Pteris* L. *Evolution* 12: 82–92.
- WALKER, T. G. (1979). The cytogenetics of ferns, in DYER, A. F., ed. *The experimental biology of Pteridophytes*, pp. 87–132. London.
- WOLF, P. G., HAUFLE, C. H. & SHEFFIELD, E. (1988). Electrophoretic variation and mating system of the clonal weed *Pteridium aquilinum* (L.) Kuhn (Bracken). *Evolution* 42: 1350–1355.

(Accepted January 1989)