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<td>Article Type:</td>
<td>Original Research Paper</td>
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<td>Keywords:</td>
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| Funding Information: |
Morphometric comparison of British *Pseudorchis albida* with Icelandic *P. straminea* (Orchidaceae: Orchidinae)

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Introduction

*Pseudorchis* Séguié (1754) has long been a taxonomic and nomenclatural football at the genus level, the more recent questions revolving around whether it merited distinction from the genus *Gymnadenia* (e.g. Bateman *et al.*, 2006, 2018) and, if so, whether *Pseudorchis* or *Leucorchis* had nomenclatural priority. DNA data have in recent years shown that *Pseudorchis* does indeed merit genus-level distinction, though they have not yet conclusively demonstrated whether it is sister genus to *Gymnadenia*
plus Dactylorhiza or to Platanthera plus Galearis (Bateman et al., 2018). Once it had been shown conclusively that the Greco-Bulgarian endemic 'P. frivaldii should in fact be included in Gymnadenia (Bateman et al., 2006), the main debate at the species level became whether or not the more northerly circumboreal populations should be segregated from Pseudorchis albida (L.) A. & D. Löve (1969) under the epithet straminea Fernald (1926). Logically downstream of this fundamental issue lay two further questions: (1) whether this segregated taxon should be treated at species, subspecies or varietal rank, and (2) whether the epithet straminea should encompass high-altitude populations of Pseudorchis from central and southern Europe that are often awarded the infraspecific epithet tricuspis Beck (1890, p. 209) (e.g. Reinhammar, 1998; Reinhammar & Hedrén, 1998) – the alternative, more recently popular view being that straminea should instead be restricted to cold-temperate and palearctic populations (e.g. Klein, 2000; Wucherfennig, 2002; Baumann et al., 2005; Delforge, 2006, 2016).

The main driver of current interest in Pseudorchis has been its rapid recent decline across much of Europe. By the turn of the last century, Pseudorchis was designated as threatened in 13 European countries (Reinhammar et al., 2002; see also Global Biodiversity Information Facility, 2015). Its decline has commonly been attributed to destruction or degradation of habitat, though given the circum-boreal distribution of Pseudorchis, it is tempting to speculate that climate change may also have played a significant role, particularly at lower altitudes.

The decline of P. albida has been especially precipitous in the British Isles (e.g. Duffy et al., 2009). In the UK, regional extirpations have led to a recent geographic distribution that shows comparative concentrations in the northern Pennines and northern half of Ireland, but its headquarters in the British Isles undoubtedly resides in northern and western Scotland (Preston et al., 2002; Stace et al., 2015); P. albida is designated Vulnerable on the UK Red List (Cheffings & Farrell, 2005). The species is designated Endangered in Ireland (Curtis & McGough, 1988; Curtis & Thompson, 2009), where it has become a serious cause for concern (Duffy et al., 2011). Our present study also confirmed previous reports that most surviving populations are small and still diminishing.

A further motivation for our study was provided two decades ago by the late Derek Turner Ettlinger. Although there exists a general consensus that Pseudorchis populations within the British Isles are all attributable to P. albida s.s., Ettlinger (1997, p. 58) argued that "in northern Scotland and Orkney it would be worth keeping an eye open for ssp. straminea . . . , a plant of alpine areas and the far north which occurs as near [to Britain] as the Faeroes islands." The identity of Pseudorchis populations within the British Isles was further questioned and rendered more complex by Harrap & Harrap (2009, p. 239), who noted that "the distribution and abundance of [var. tricuspis] in the British Isles has not been studied." We agree that these taxa should be sought in Britain and Ireland. But as yet, do we actually know what we are looking for?

Materials and Methods

Study populations

Table 1 summarises locality details for eight populations of P. albida studied by us in northern England (two) and Scotland (six), plus the three populations of P. straminea studied by us in the southwest quadrant of Iceland during an expedition that was oriented primarily toward studying the co-occurring orchid Platanthera hyperborea...
(Bateman et al., 2015). We had hoped to measure ten plants per study population, but this proved feasible in only four populations, and only one (Glencairn: Fig. 1a) exceeded 30 flowering plants. Icelandic populations proved especially difficult to detect, though the species is mapped as being more frequent in the north and east of the country (Global Biodiversity Information Facility, 2015). Flowering occurred consistently in the second half of June, barely overlapping into July in Iceland. All three Icelandic study localities are best characterised as heathland (Fig. 1e, f), as are the Scottish sites of Ardnish (coastal) and Balvattan (upland); the remainder of the UK sites are more accurately described as rough pasture (Fig. 1a, b). Soils were typically neutral to mildly acidic, and in many cases appeared unusually rich in heavy metals. The orchid most commonly associated with Pseudorchis in both Britain and Iceland was Dactylorhiza maculata, together with Gymnadenia borealis in the UK (Fig. 1c) and Platanthera hyperborea in Iceland (Bateman & Rudall, 2015).

**Morphometrics**

The comparatively simple micromorphology of Pseudorchis, epitomised by the absence of any discrete markings on either floral or vegetative organs (Fig. 2), reduced the number of credible macromorphological characters that could usefully be measured to just 36 (Table 2). Moreover, five of the characters carried forward to this reduced suite also ultimately proved to be invariant (italicised in Table 2), leaving just 31 characters for inclusion in the multivariate analyses. They described the stem and inflorescence (4 characters), leaves (8), bracts and ovary (5), labellum (11) and spur (3). They can alternatively be categorised as metric (19), meristic (3), multistate-scalar (8), or bistate (1). The colour of the lower half of the labellum was matched to the closest colour block(s) of the Royal Horticultural Society Colour Chart and later converted to three quantified variables recognised by the Commission Internationale de l'Eclairage (CIE).

Data for individual plants were summarised in an Excel v14.7 spreadsheet. Means, sample standard deviations and coefficients of variation were calculated for all measured plants of each of the two putative species (Table 2). Univariate analyses were summarised and presented using Deltagraph v5.6 (SPSS/Red Rock software).

The matrix of 65 plants × 31 characters (total 2,015 cells) contained only 19 missing values (0.9%), half of which reflected bract cell parameters of five of the ten Glencairn plants measured. The data were analysed at two demographic levels: first as all 65 individual plants, but also as mean values for all study populations that yielded measurements from three or more plants (this restriction excluded the Glendrynoch population of P. albida and the Skogar population of P. straminea).

For each of the two sets of analyses, the assembled data were analysed by multivariate methods using Genstat v14 (Payne et al., 2011). They were employed to compute a symmetrical matrix that quantified the similarities of pairs of data sets (i.e. plants) using the Gower Similarity Coefficient (Gower, 1971) on unweighted data sets scaled to unit variance. The matrix was in turn used to construct a minimum spanning tree (Gower & Ross, 1969) and subsequently to calculate principal coordinates (Gower, 1966, 1985) – compound vectors that incorporate positively or negatively correlated characters that are most variable and therefore potentially diagnostic. Principal coordinates are especially effective for simultaneously analysing heterogeneous suites of morphological characters and can comfortably accommodate missing values.

**Scanning electron microscopy**
SEM study was confined to single inflorescences from Scotland (P. albida) and Iceland (P. straminea). Preparation for SEM involved selecting flowers from each preserved inflorescence for dehydration through an alcohol series to 100% ethanol. They were then stabilised using an Autosamdi 815B critical-point drier, mounted onto stubs using double-sided adhesive tape, coated with platinum using an Emtech K550X sputter-coater, and examined under a Hitachi cold-field emission SEM S-4700-II at 2 kV. The resulting images were recorded digitally for subsequent enhancement in Adobe Photoshop. SEM images of P. albida were supplemented with those obtained through light microscopy using a Nikon Shuttlepix P-MFSC digital imaging system (not shown).

Results

Scanning electron microscopy
SEM study demonstrates that the unusually small and campanulate flowers of Pseudorchis are simpler in construction than those of most other genera in subtribe Orchidinae. There is little differentiation between the lateral petals and sepals (Fig. 4a), and the epidermal cells of all perianth segments are near-uniform in size and appearance (Fig. 3d). Within the short, cylindrical, blunt-tipped, downwardly-oriented spur (Fig. 3c), papillae are barely discernible and striated cells are confined to the spur entrance (Bell et al., 2009).

SEM study is particularly useful for elucidating gynostemia. That of Pseudorchis is strikingly compact, and in consequence the anther locules appear oversized (Fig. 3a) (Bateman et al., 2006). The connective linking distally the parallel locules is short, and the viscidia are brought into close juxtaposition by upward invagination of the rostellar ridge (Figs. 3a, b, 4b). Lateral auricles are comparatively well-developed (Figs. 3a, 4a), and the stigmatic surfaces are represented by horizontally elongate regions located immediately lateral to, and slightly above, the vertically compressed spur entrance (see also Claessens & Kleynen, 2011; Jersaková et al., 2011). The pollinaria are inverted cones that consist largely of massulae forming the pollinium (Fig. 4b); the caudicles are short as to be almost absent, and the translucent oblong viscidia are similarly small and seemingly under-developed (Fig. 4b; see also Claessens & Kleynen, 2011, p. 311). They are usually described as "naked", but Claessens & Kleynen reported that they are enclosed by a diaphanous membrane. Upon reaching maturity, the parallel pair of thin anther locules loosen, leaving the 0.5–0.6(–0.7) mm-long pollinaria unusually exposed (Figs. 3b, 4b). The pollinia are bisected almost to the base and typically consist of ca 50 massulae (Figs. 3e, 4b); individual pollen grains bear reticulate ornamentation on their distal hemispheres, and once adhering en masse to the stigma readily germinate to produce robust pollen tubes (Fig. 3e, f) (see also Schill & Pfeiffer, 1977).

These SEM images demonstrate that the statement of Bateman et al. (2006, p. 114) that "P. albida lacks the lappet-like stigmatic surface that is a feature not only of G. frivaldii but also of other species of Gymnadenia s.s." was simplistic. The contrast is rather that the lappet-like lateral stigmatic surfaces of Gymnadenia are obviously bipartite, the pale translucent stigmatic lobes being readily distinguished from labellar "shoulders" that extend vertically behind the stigmatic surface. The stigmatic lobes of Pseudorchis are of a simpler construction (see also Claessens & Kleynen, 2011, p. 293). However, the SEM studies were performed primarily in search of characters other than size differences that might reliably differentiate between P. albida and P. straminea – no such characters were identified.

4
Morphometrics: multivariate analyses

Figure 5 illustrate the first two principal coordinates derived from data for individual plants. The first two coordinates together account for a remarkable 46% of the total variance, and work together to describe a diagonal relationship between plants of *P. albida* and those of *P. straminea*. A clear morphological discontinuity separates the two putative species, whereas little population-level differentiation is evident within either species. The notable exception is the Balvattan population of *P. albida*, which is partly separated from other populations of *P. albida* on the first coordinate and wholly separated on the second coordinate, the gap being partially bridged by the Keltneyburn and Ardnish populations (Fig. 5).

The first coordinate was dictated almost entirely by 11 metric characters that described the greater sizes of both the vegetative and floral organs of plants located toward the right-hand side of the plot. The two exceptions were the degree of concavity of the labellum (also indirectly a size-related character: see Discussion) and the less hooded leaf tips of *P. straminea*. The second coordinate was dictated entirely by the subtle colour difference between the yellowish-green labella of *P. straminea* (RHS 4B–4C: Primrose Yellow) and the greenish-yellow labella of *P. albida* (RHS 150A–B–C, 151C: Sap/Citron Green) as viewed under natural light. It is noteworthy that use of flash photography evokes a very different impression of flower colour in this genus, the flowers appearing much greener in the shorter wavelength bluish light emitted by a typical camera flash (compare Fig. 2b, e versus 2c, f). Lower-order principal coordinates were of little value; the third coordinate (9.2%) was dominated by subtle differences in the number of sheathing leaves, and the fourth coordinate (7.8%) combined shape of uppermost leaf with number of flowers.

The first two coordinates based on mean values for populations (Fig. 6) encompassed an even greater 62% of the total variance, and once again identified a clear morphological discontinuity separating *P. straminea* from *P. albida*. Most of the populations of *P. albida* form a cluster in the top-left of the plot, centred on Keltneyburn. Once again, the Balvattan population forms an outlier, linked to Keltneyburn by a weaker branch on the minimum spanning tree. Floral dimensions and bract length once again contribute to the first coordinate, where they are joined by the paler leaves and less concave labella of *P. straminea*. The second coordinate, which separated Balvattan, was dominated by the somewhat positively correlated characters of flower number and inflorescence length. Once again, lower-level coordinates were of little value, the third coordinate (12.9%) representing C.I.E. colour coordinate ‘x’ (i.e. the green–yellow axis) and the fourth coordinate (10.1%) representing spur width plus the position of the longest leaf along the stem.

Morphometrics: univariate analyses

Of the 31 variable characters, 14 provided significant differences between *P. albida* and *P. straminea* (boldface in Table 2). They encompassed most of the characters that contributed to the principal coordinates plots of individual plants (Fig. 5), together with leaf colour and, to a lesser degree, bract marginal cell shape.

Four of the metric characters most useful for separating *P. albida* and *P. straminea* are further explored as box-plots: labellum length, labellum width, basal bract length and length of longest leaf (Fig. 7). For each character, the 25th–75th percentile boxes for the two species do not overlap but the 10th–90th percentile whiskers do overlap, thereby demonstrating that all of these characters are indicative of species identity but cannot be deemed conclusively diagnostic.
When plotted together (Fig. 8), the characters most effective at separating Balvattan (Fig. 2g) from other populations of *P. albida* – plant height (125±27 mm) and inflorescence length (26±6 mm) – do not fully separate all plants measured in this population; rather, its largest plants overlap in size with the smallest plants from the Glencairn, Keltneyburn and Ardnish populations. Moreover, the impression of shorter stems and inflorescences in the Balvattan population (Fig. 2g) was probably enhanced by the fact that it was the only population that we measured prior to peak flowering; indeed, the majority of study populations were measured beyond peak flowering. Nonetheless, the narrow stems (2.1±0.3 mm) and short (41±7 mm), basally concentrated leaves of the plants make clear that environmental factors also contributed to their dwarifism in this unusually exposed location, contrasting most strongly with the most vegetatively vigorous, less exposed population nearby at Speybridge. Thus, we suspect that ecophenotypy has contributed to their modest stature.

The two population of *P. albida* from the northern Pennines of England, Stainmore and especially Asby, have somewhat longer labella (means 2.6–2.7 mm vs 2.0–2.4 mm) and spurs (means 1.7–1.8 mm vs 1.5–1.6 mm) than any Scottish population, and were colour matched as being slightly darker-flowered; they also had on average less hooded leaf apices. Marginal bracts also varied considerably in both size and shape. Otherwise, the pattern between populations evident in our results is one of similarity more than one of difference. This statement also applies to our study populations of *P. straminea*, though the slightly less exposed Vogar population had on average larger labella and leaves than that at Solheimajökull.

**Discussion**

*Are albida and straminea different species?*

Opinions regarding this question differ enormously, and even the same observer’s published view can change through time. *Pseudorchis straminea* has for most of its existence been treated as a variety or a subspecies under multiple epithets. The best informed observer, Reinhammar, initially argued that *straminea* merited the status of full species because in Sweden it could be distinguished on the basis of morphology, allozymes and habitat preference (Reinhammar, 1995; Reinhammar & Hedrén, 1998). However, his commitment was weakened by his morphometric analysis of herbarium specimens that included material from the Alps, as it appeared to suggest slight morphological overlap between *P. straminea* and *P. albida* centred on the Alps (Reinhammar, 1998; Reinhammar *et al.*, 2002; Jersaková *et al.*, 2013). One of us (RB) has travelled the converse taxonomic route through the last two decades, initially believing that *straminea* was more appropriately treated as a subspecies of *albida* (Bateman *et al.*, 2003) but, on the basis of the results of the present study, now believing that *straminea* is more appropriately treated as a species.

Most other observers did not gather explicit data to support their chosen taxonomic positions, but a brief survey of the literature is nonetheless illuminating. *Pseudorchis straminea* has for most of its existence been treated as a variety or a subspecies under multiple epithets. The taxonomic concept of *straminea* arose in Canada (Fernald, 1926 onward) before spreading to Iceland (Löve, 1950 onward), Norway/Sweden (Hylander, 1966 onward), and most controversially to the Alps (Mossberg & Nilsson, 1982 onward) (reviewed by Reinhammar, 1995, 1998). In recent years, *straminea* has often been treated as a full species in Scandinavia, being regarded by most observers as the only *Pseudorchis* taxon present in Iceland (though...
ironically, the most recent flora of Iceland recognises only *P. albida*: Kristinsson, 2010). *Straminea* is also perceived as the most frequent *Pseudorchis* taxon occurring in Norway (e.g. Strann & Bjerke, 2010) and Sweden (e.g. Mossberg & Nilsson, 1982). Although species status for *straminea* was also advocated by Delforge (2006, 2016) in his European orchid monograph, elsewhere in Europe it has become more common to view *straminea* as as subspecies of *P. albida* (e.g. Buttler, 1991; Kreutz, 2004; Jersakova et al., 2013). And in spite of the facts that (a) our data imply that populations of *straminea* are more distinct from *albida* in Iceland than those located elsewhere in Scandinavia, and (b) plants similar to those in Iceland appear to characterise populations in Greenland and Newfoundland, Luer (1975) awarded *straminea* only the status of variety in his monograph of North American orchids.

Following up on a local study by Nilsson (1976), Reinhammar (1995) pursued a morphometric study of *straminea* in Sweden. Reinhammar & Hedrén (1998) reinforced this more traditional work with a molecular comparison of four populations of *P. albida* plus two populations of *P. straminea*. Interspecific variation in allozymes was much greater than intraspecific variation, the data leading the authors to speculate that the species diverged between 2.3 Ma and 1.1 Ma and represented two separate waves of postglacial immigration into Sweden, *P. straminea* preceding *P. albida*.

However, Reinhammar’s (1998) corresponding morphometric analysis yielded contrasting results. It was performed on a geographic pot pourri of herbarium specimens that were measured for 18 metric characters, many of them likely to suffer from positive correlation and all of them guaranteed to suffer from increased measuring error relative to in situ plants (Bateman et al., 2013; Parnell et al., 2013). The resulting canonical variates analysis clearly separated the two species, but this algorithm automatically maximises perceived distance between pre-ordained groups. The more objective principal components analysis showed slight overlap between *P. albida* and *P. straminea*, caused largely by herbarium specimens originally collected in the Alps. This overlap, though modest, was nonetheless sufficient to encourage Reinhammar (1998) to renounce his previous assertions of species status for *P. straminea* and demote it to a subspecies (though its species status was later reinstated by Reinhammar et al., 2002).

We chose to revisit this topic because our analysis applies to a much wider range of morphological characters measured on live plants using a similarly objective algorithm – principal coordinates analysis based on Gower’s similarity coefficient. And our results reveal a clear and reliable discontinuity in overall morphology between the two taxa, irrespective of whether they are analysed at individual or population level (Figs. 5, 6). Admittedly, the distinction between the two species in our analysis owes much to differences in flower size between British and Icelandic plants (Table 2). On the other hand, the analysis of Reinhammar (1998) and descriptions provided by Luer (1975) together suggest that the larger Icelandic plants are paralleled by most of the populations of *Pseudorchis* that occur in Greenland and Newfoundland.

It is unfortunate that our sampling did not include Continental populations, because the greatest outstanding issue is determining whether montane populations from central Europe that have larger and more yellowish flowers than *P. albida* have greater affinity with *P. albida* or *P. straminea*. Reinhammar (1995, 1998) understandably assigned them to *P. straminea* as a result of his multivariate morphometric study. However, Klein (2000) – using more traditional taxonomic methods but with broad geographic sampling – soon argued that they should instead be established as a third subspecies alongside *albida* and *straminea*, placing these
populations under the epithet *tricuspis* that he resurrected from Beck (1890). This
taxonomy is still advocated by online 'go-to' database 'The Plant List', but taxonomic
opinions on *tricuspis* extend from subspecies (Moore, 1980; Reinhammar, 1998;
Klein, 2000; Bournérias & Prat, 2005; Perazza, 2016) through varietas (Kreutz, 2004;
Delforge, 2006, 2016; Jersaková et al., 2013) to forma (Landwehr, 1977). It has since
become commonplace to assign *tricuspis* (a taxon particularly well-illustrated by
Perazza & Lorenz, 2013, pp. 366–7) to *P. albida* s.s.

It is our impression that distinguishing characters of *tricuspis* are, at best, few
(cf. Reinhammar, 1998; Reinhammar et al., 2002; Klein, 2000; Baumann et al., 2005;
Jersaková et al., 2011). Published tables comparing the two taxa show considerable
overlap in supposedly taxonomically useful characters such as plant height, leaf
number, inflorescence length, bract length, flower and leaf posture, leaving as the
most commonly used character the length (more accurately, the areal extent) of the
lateral lobes of the labellum relative to that of the central lobe. Flower colour also
appears to be problematic, Jersakova et al. (2011, their Table 1) comparing the
"greenish-white to yellowish-white" flowers of *albida* s.s., the "yellowish-white"
flowers of *straminea* and the "cream-white to yellowish-white" flowers of *tricuspis*.
And like *straminea*, *tricuspis* also reputedly prefers soils that are comparatively rich
in calcium carbonate (or perhaps heavy metals?). It is tempting to speculate that these
subtle differences in flower colour observed among *Pseudorchis* populations may
represent nothing more than contrasting soil chemistries.

In this context, it has recently been suggested (G. Preston, pers. comm., 2017)
that our ecophenotypically dwarfed study population at Balvattan contains some
individuals that could potentially be attributed to "var. *tricuspis*", primarily on the
basis of their unusually prominent lateral labellar lobes. If prominent lateral lobes are
all that is required for identification as var. (perhaps more appropriately forma) *tricuspis*
then this name could indeed be applied. But if other characters are viewed as diagnostic
then they cannot – for example, the Balvattan plants lack the yellow colouration so
well illustrated by Perezza & Lorenz (2013). A degree of molecular divergence would
be a helpful indicator of its taxonomic merit.

**DNA to the rescue yet again?**

In recent years, it has become traditional for molecular data to play a pre-eminent role
in resolving obvious cases of uncertain species boundaries. However, our attempt to
gather together from disparate sources DNA sequence data for *Pseudorchis* was
disappointing; we found that we were able to compare the two species for nrITS plus
two plastid regions also commonly used for phylogeny reconstruction, but only one
sequence (or, in the case of *trnL*-F, two sequences) was available for each region and
each species (Fig. 9). Consequently, any comparison made is entirely typological.
Unsurprisingly, the most slowly mutating region analysed, *rbcL*, yielded only one
SNP in comparison of 1,234 bases. *TrnL*-F performed little better, its 662 bases
yielding only a single SNP plus a slightly shorter poly-A region that appeared to be
two bases shorter in the Scottish plant of *P. albida*. It is perhaps therefore
unsurprising that Duffy et al. (2011) found no difference in plastid microsatellites
between four Irish populations of *P. albida* and a single Swedish accession of *P.
straminea*.

As usual, the largely non-coding ITS provided greater discrimination, yielding
seven SNPs in 652 bases, five occurring in ITS2 (Fig. 9). This molecular disparity
between the species of 1.1% is, in truth, somewhat more than the "negligible ITS
divergence" that was too casually dismissed by Bateman et al. (2003, p. 10); this
disparity actually matches in degree that recorded between some indisputable species of the closely related genera Gymnadenia and Dactylorhiza (cf. Bateman et al., 2003, 2018).

The greatest weakness of molecular studies pursued thus far is that none of the relevant sequences was generated from plants collected outside Scandinavia or the British Isles. In particular, to the best of our knowledge, no sequences are currently available for subs. / var. tricuspis – potentially a “missing link” between P. albida s.s. and P. straminea (cf. Reinhammar, 1998; Klein, 2000).

How are P. albida and P. straminea best distinguished?

On the basis of the data given in Table 2, P. straminea would be predicted to possess the following features distinguishing it from P. albida s.s.: Labellum primrose yellow, exceeding 2.7 mm long and 2.5 mm wide, lateral lobes considerably narrower than central lobe, spur exceeding 1.8 mm. Basal bracts exceeding 9 mm, floral bracts exceeding 7 mm. Leaves yellowish-green with negligible apical hooding, longest exceeding 57 mm. In addition, the possibility that the two species possess contrasting scents merits further exploration.

As expected, comparison with our morphometric data revealed many apparent errors or exaggerations in published descriptions of one or both Pseudorchis species, particularly with regard to the shapes and sizes of floral parts and bracts. For example, the claim by Bateman & Rudall (2015) that the labella of P. straminea are "more deeply three lobed" than those of P. albida is not upheld by the data but instead reflects the visual impact of the smaller size of the lateral lobes of the latter (the labellum sinuses represent on average 44–50% of the length of the central lobe in P. albida but only 36–41% in P. straminea). Nor did our data (Table 2) support the assertion of Reinhammar (1998; repeated by Jersaková, 2013) that tooth-like bract cells found toward the apex of each bract are "dense and symmetrical" in P. albida but "sparse and asymmetrical" in P. straminea; our study rather suggested that the entire spectrum of bract margin micromorphologies could be obtained merely by combining our Ardnish and Glencairn populations of P. albida. Bract-cell size also varies considerably, both within and between populations, and appears uncorrelated with cell shape.

A useful summary table comparing several phenotypic features of albida s.s., straminea and tricuspis was compiled by Jersaková et al. (2013) from information presented by Reinhammar (1998) and Klein (2000). Values for most characters in this table are a good match with our data in the case of P. albida, but the majority of those for P. straminea are dissimilar – our mean values for plant height, inflorescence length, bract length, flower number (almost), and labellum dimensions exceed the maximum value specified in the table of Jersaková et al. (2013), and thereby increase our perception of the morphological distinctiveness of the two species. In contrast, we were unable to detect the supposed less obovate leaves, more secund inflorescence, more prominent central labellar lobe, and more cylindrical spur attributed by past authors to P. straminea.

Autecology

Pseudorchis straminea prefers higher latitudes and/or higher altitudes than does P. albida (Reinhammar, 1995, 1998; Reinhammar et al., 2002; Jersakova et al., 2013). Several authors have commented on the different soil preferences of the two species, both species favouring nutrient-poor and often disturbed soils but P. straminea also showing a requirement for soils that contain carbonate or heavy metals (Reinhammar,
1998; Reinhammar et al., 2002; Jersaková et al., 2011; Bateman & Rudall, 2015). As well as disturbed soils, disturbed 'metastable' vegetation also appears to be important to these species. For example, in 1983 we estimated that 500 flowering plants appeared at Balvattan and 150 at Keltneyburn, whereas the corresponding numbers in 2015 were 20 and eight (Table 1); at both localities, the vegetation had become more rank in the intervening years. And at Ardnish, we were able to find only three etiolated plants struggling to emerge from within the now rampant sward of Calluna vulgaris. It seems likely that soil preference contributed to the remarkable total of 66 fungal (DNA-circumscribed) species identified by Kohout et al. (2013) on the tapered root-tubers of five high-altitude Czech populations attributed to P. albida, suggesting low specificity of mycorrhizal associates.

Reinhammar et al. (2002) argued that P. albida flowers somewhat earlier than P. straminea in central Sweden, but our comparison of P. albida in Scotland and P. straminea in Iceland suggests contemporaneous flowering once minor adjustments had been for latitude and altitude (Table 1).

Both Pseudorchis species generate modest amounts of nectar within their spurs and emit fragrances detectably by humans; that of P. albida is most commonly described as "faint and vanilla-like", whereas that of P. straminea was said by Reinhammar (1998, p. 365) to be "strong and spicy"; 58 compounds, dominantly terpenoids, were said by Jersaková et al. (2011) to form the scent cocktail of Czech populations of P. albida s.l. Microlepidopterans of at least five genera have been observed transporting pollinaria, which are often removed singly by becoming attached approximately mid-way along the visiting insects' proboscis (Claessens & Keynen, 2011; see also Baumann & Baumann, 2002). Field observers have reported both facultative autogamy (including cleistogamy: e.g. Hagerup, 1951, 1952) and extensive geitonogamy (Claessens & Kleyen, 2011). The short receptive period and rapid senescence of individual flowers, comparatively successful fruit-set (typically 70–90%), and low within-population variation in allozymes reported by Reinhammar & Hedrén (1998), are all consistent with 'mixed-economy' pollination. Vegetative reproduction has repeatedly been stated to be minimal, yet it was evident – albeit at a comparatively low level – in several of our study populations (e.g. Glencairn: Fig. 2a).

A putative hybrid reported between Pseudorchis albida and Platanthera chlorantha at the Keltneyburn locality (McKean, 1982) was rapidly re-interpreted as a mutant individual of the latter (Bateman, 1985). More convincing are rare reports of its hybrid with Dactylorhiza maculata (× Pseudorhiza bruniana), most frequently from the Scottish Isles, though there is a larger number of credible UK records of the hybrid with the often co-occurring Gymnadenia borealis (a hybrid combination not yet formally named: Jersaková et al., 2011; Stace et al., 2015). Indeed, we measured such a plant during our morphometric survey of the Stainmore population (Fig. 2h). In Continental Europe, hybrids have been recorded between Pseudorchis and several species of both Dactylorhiza and Gymnadenia s.l. (including the former genus Nigritella: Gerbaud & Schmid, 1999; Oddone et al., 2016). Given the occurrence of several intergeneric hybrids involving Pseudorchis, it should come as no surprise if gene-flow is eventually proven to occur between P. albida and P. straminea in situations where they co-occur or, more frequently, are juxtaposed. A modest amount of gene-flow could be sufficient to explain the apparently greater distinctiveness of P. straminea in Iceland, Greenland and Newfoundland, where P. albida s.s. does not occur.
Broader evolutionary issues
To the best of our knowledge, the chromosomes of Pseudorchis have not been subject to detailed study using modern methods, despite having proven through molecular phylogeny reconstruction to be highly conserved features. The chromosomal complement of P. straminea was long ago determined as 2n = 42 (Löve & Löve, 1969), which suggests that Pseudorchis is plesiomorphic in this character compared with the 2n = 40 that delimits the derived sister-genus pairing of Gymnadenia and Dactylorhiza (Bateman et al., 2003). However, many subsequent authors hedged their bets by representing the chromosome count of Pseudorchis albida as both 2n = 42 and 2n = 40 (e.g. Moore, 1980; Sundermann, 1980; Sheviak, 2002; Delforge, 2006, 2016) or even emphasising 2n = 40 at the expense of 2n = 42 (Bournérias & Prat, 2005). In contrast, Klein (2000) presented three counts of 2n = 42 for tricuspis, and a recent review of the genus by Jersaková et al. (2013, p. 1290) argued forcefully that albida, straminea and tricuspis all uniformly possess 2n = 42 (also Baumann et al., 2005).

Bateman et al. (2006, 2018) argued that the failure of many taxonomists to recognise that frivaldii is a species of Gymnadenia rather than Pseudorchis was a result of morphological convergence between small-flowered species of the two genera, and that this convergence was in turn necessary for evolution to successfully generate greatly downsized orchid flowers that remained functional. The present data offer further insights into the consequences of such floral downsizing. Firstly, the inflorescences of Pseudorchis appear ‘untidy’ – this impression is gained partly because they are often slightly secund but mainly because resupination (the 180° torsion of the ovary that renders the labellum lowermost) is far from perfectly executed in these small flowers. This failure may reflect the fact that the pedicel that is the usual site of resupination is so short in Pseudorchis, thus forcing the ovary to take on the role and leading to suboptimal outcomes (Fig. 3C).

The compact nature of the flowers also encourages only partial opening, necessitating a campanulate form, and this in turn structurally constrains the component organs of the flower – for example, we suspect that the typically less concave labella of P. straminea compared with those of P. albida simply reflects the greater labellum size of the former, projecting further beyond the other perianth segments. Certainly, the repeated miniaturisation of flowers evident in the taper-tubered orchid genera challenges Delforge’s (2006, p. 149) assertion that Pseudorchis is “similar to the common ancestor of the genera Platanthera and Gymnadenia”; current evidence suggests that its unusually small flowers are a derived rather than a primitive feature of subtribe Orchidinae.

Summary

(1) Pseudorchis clearly merits continued recognition at genus level, though it remains uncertain whether the genus is more closely related to Platanthera plus Galearis or Gymnadenia plus Dactylorhiza (Bateman et al., 2018).

(2) On present evidence, the boreal Pseudorchis straminea merits separation from the sub-boreal P. albida as a distinct species (cf. Reinhammar, 1995; Reinhammar & Hedrén, 1998; Delforge, 2006), rather than the subspecific status that it has more commonly received in recent literature. Ironically, the Flora of Iceland (Kristinsson, 2010) simply attributes all Icelandic populations to P. albida.

(3) The so-called P. albida var. (or subsp.) tricuspis from central and southern European montane habitats remains potentially pivotal to confirming the species
status provisionally awarded to *P. straminea*, yet *straminea* and especially *tricuspsis* have received remarkably little scientific attention since the groundwork was laid down two decades ago by L.-G. Reinhammar and E. Klein. Depending on how it is delimited, *tricuspsis* could potentially be sufficiently distinct to merit species status, or it could be a trivial divergent morph arising sporadically and iteratively across the geographic range of the nominate species.

(4) The slight morphometric overlap identified in multivariate plots by Reinhammar (1998), and caused primarily by Alpine specimens of *tricuspsis*, is insufficient evidence to reject the hypothesis that *P. albida* and *P. straminea* are separate species. For example, greater phenotypic overlap is evident among *Gymnadenia conopsea* s.s., *G. densiflora* and *G. borealis*, which nonetheless clearly merit species-level status by virtue of their reliably distinct DNA profiles (Bateman et al., 2006, 2018).

(5) The revised diagnostic characters (both morphological and molecular) presented here should in future permit more effective identification of *P. albida* and *P. straminea*, building on the previous work of Reinhammar (1995, 1998; Reinhammar & Hedrén, 1998) and Klein (2000).

(6) *Pseudorchis straminea* should continue to be sought in the British Isles. However, there seems little point is seeking *tricusps* at present, as its delimiting characters, affinities, geographic distribution and most appropriate taxonomic status all remain insufficiently clear. Robust taxonomy based on synthesis of morphological and molecular data-sets is an essential pre-requisite for accurate field recording.

(7) Our anecdotal evidence supports more nuanced studies in showing that *P. albida* is declining rapidly within the British Isles, as it is across much of its geographic range. Although it is often stated that excessive habitat disturbance (or loss) is the main cause of this decline, insufficient disturbance may be equally problematic. Climate change provides a likely additional detrimental influence, driving the species back toward higher latitudes and/or altitudes.

(8) *Pseudorchis* most likely originated through floral miniaturisation and consequent simplification. The fact that plants at the most exposed Scottish locality are ecophenotypically dwarfed encouraged us to recognise *straminea* at species level, as first principles would suggest that this plant of exposed boreal habitats would produce flowers smaller than those of the more southerly *P. albida*, rather than the larger flowers documented here.

(9) Although phylogenetic philosophy requires egalitarian perception of *P. albida* and *P. straminea* as sister-species, their molecular and morphological similarity, their comparative recency of divergence, and the potential absence from the genus of a third species combine to identify this as a case of speciation where distinguishing ancestor from descendant becomes a credible objective, given adequate interdisciplinary study. Such a study could also address the intriguing suggestion of Reinhammar & Hedrén (1998) that *P. straminea* and *P. albida* may represent successive waves of northward migration across Europe. But first, the ongoing enigma posed by *tricusps* must be resolved.

**Acknowledgements**

RB and ID are grateful to Alan Gendle for guiding them around Cumbrian *Pseudorchis* sites in 2014, and to Grahaone Preston for his intriguing 2027 observations on the Balvattan population. RB and PR kindly thank the Botanical Research Fund for once again subsidising their fieldwork – on this occasion, their
2014 excursion to Iceland. RB dedicates this paper to Anthony Bowley, a little of whose extraordinary biology teaching in the 1970s did eventually rub off.

References

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Plant List, the. 2017. The plant list: a working list of all plant species. www.theplantlist.org


[FIGURE CAPTIONS]

Figure 1 Pseudorchis habitats. (A) Glencairn – the locality maintaining by far the largest of our study populations of P. albida. (B) Stainmore – a typical rough pasture habitat of P. albida. (C) Balvattan, where P. albida occurs alongside its most frequent orchid associate, Gymnadenia borealis. (D) Asby – three imprisoned plants of P. albida epitomise the typical fate of a rapidly declining species. (E) Glacial outwash habitat of P. straminea at Solheimajökull, Iceland. (F) Lava cliff habitat of P. straminea at Skogarfoss, Iceland. All images: R. Bateman.
Figure 2 Pseudorchis plants. (A) Vigorous plants of *P. albida* at hill pasture, Glencairn. (B) Flowers of *P. albida* photographed under natural light, Speybridge. (C) Flowers of *P. albida* photographed using flash, Keltneyburn. (D) Isolated plant of *P. straminea* at Skogafoss, Iceland. (E) Flowers of *P. straminea* photographed under natural light, Skogar. (F) Flowers of *P. straminea* photographed using flash, Skogar. (G) Less vigorous plants of *P. albida* at exposed juniper heath, Balvattan. (H) Natural bigeneric hybrid formed between *P. albida* and *Gymnadenia borealis* at Stainmore. All images: R. Bateman.

Figure 3 Scanning electron micrographs of *Pseudorchis albida* flowers from Scotland. (A, B) Gynostemia featuring invaginated rostellum, lateral stigmatic lobes, auricles, and comparing undehisced (A) and dehisced (B) loculi. (C) Lateral view of opening bud showing the short, blunt spur and resupinate ovary. (D) Adaxial surface of labellum showing the uniformity of the epidermal cells. (E) Pollinium massulae adhering to stigmatic lobe. (F) Enlargement of massulae showing the reticulate distal tectum and germinating pollen tubes (pt) of individual pollen grains. All images: P. Rudall. Scales: (A) and (B) = 100 μm, (C) = 1 mm, (D) = 200 μm, (E) and (F) = 100 μm.

Figure 4 Scanning electron micrographs of *Pseudorchis straminea* flowers from Iceland. (A, C) Contrasting views of a mature flower that has been artificially opened out to better illustrate structures within. (B) Enlargement of gynostemium featuring the exceptionally compact pollinaria and invaginated rostellum. All images: P. Rudall. Scales: (A) and (C) = 1 mm, (B) = 100 μm.

Figure 5 Principal coordinates plot for individual plants. Superimposed contributing characters are listed in order of decreasing contribution, the arrows indicating the direction of increased value for each character. The key lists localities sequentially from south to north. Circles denote *P. albida*, triangles denote *P. straminea*.

Figure 6 Principal coordinates plot for population mean values. Superimposed contributing characters are listed in order of decreasing contribution, the arrows indicating the direction of increased value for each character. A minimum spanning tree based on Gower similarity coefficients is superimposed upon the plot; branch strentths are indicated in the key.

Figure 7 Box plots comparing values in *P. albida* and *P. straminea* for (A) labellum length, (B) labellum width, (C) basal bract length, and (D) longest leaf length. Spots denote mean values. The black box is terminated by the 25th and 75th percentiles; the horizontal line within the box denotes the 50th percentile, and the extended ‘whiskers’ mark the 10th and 90th percentiles.

Figure 8 Bivariate scattergram of plant height versus inflorescence length for Pseudorchis individuals. The key lists localities sequentially from south to north.

Figure 9 Sequence differences apparently distinguishing representative samples of *P. albida* and *P. straminea* for nuclear ribosomal ITS plus the plastid regions *rbcL* and *trnL-F*. Italicised numbers indicate alignment positions. Sources of data – ITS: both sequences derived from Bateman et al. (2003). *trnL-F*: one sequence
of each species from Bateman et al. (2018), plus one sequence of *P. albida* from Soininen et al. (2009: GQ245349). *rbcL*; sequences of *P. albida* (KF997412, 2013) and *P. straminea* (FN870908, 2010) uploaded to GenBank by the Savolainen Laboratory at Imperial College, London.

**Table 1** Details of study populations. All measurements were taken during 2014 or 2015, except Balvattan Hill (1996). Flowering period has been adjusted for unusually early (2014) or late (2015) seasons; the number preceding the forward slash is the month, the succeeding numbers denote the weeks of that month.

**Table 2** Comparison of mean and sample standard deviation values for 36 morphometric characters measured from 55 British plants of *Pseudorchis albida* and ten Icelandic plants of *P. straminea*. Metric measurements are given in mm (except cell diameter, μm). The five italicised characters proved to be invariant and so were excluded from analyses. The 14 boldface characters distinguish the two species. Scalar characters were scored as follows: C6 – Lip widest close to base (1) : middle (2) : apex (3). C7 – Lip slightly concave (1) : flat (2) : slightly convex (3). C14 – Spur slightly down-curved (4) : strongly down-curved (5). C15 – Lateral sepals project slightly below horizontal (1) : slightly above horizontal (2). C19 – Cells barrel-shaped (1) : slightly angular (2) : tooth-like (3). C30 – Longest leaf inserted above widest (1) : longest leaf is widest (2). A more detailed account of character measurement can be found in Bateman & Denholm (1985).
Table 2 Comparison of mean and sample standard deviation values for 36 morphometric characters measured from 55 British plants of *Pseudorchis albida* and ten Icelandic plants of *P. straminea*. Metric measurements are given in mm (except cell diameter, μm). The five italicised characters proved to be invariant and so were excluded from analyses. The 14 boldface characters distinguish the two species. Scalar characters were scored as follows: C6 – Lip widest close to base of labellum (1) : middle (2) apex (3). C7 – Lip slightly concave (1) : flat (2) : slightly convex (3). C14 – Spur slightly down-curved (4) : strongly down-curved (5). C15 – Lateral sepal project slightly below horizontal (1) : slightly above horizontal (2). C19 – Cells barrel-shaped (1) : slightly angular (2) : tooth-like (3). C30 – Longest leaf inserted above widest (1) : longest leaf is widest (2). A more detailed account of character measurement can be found in Bateman & Denholm (1985).

<table>
<thead>
<tr>
<th>No.</th>
<th>Character</th>
<th><em>Ps. albida</em></th>
<th>SSD</th>
<th><em>Ps. straminea</em></th>
<th>SSD</th>
</tr>
</thead>
<tbody>
<tr>
<td>C1</td>
<td>Lip length to central lobe</td>
<td>2.34</td>
<td>0.28</td>
<td>3.43</td>
<td>0.63</td>
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<td>C2</td>
<td>Lip sinuses absent : present</td>
<td>1.0</td>
<td></td>
<td>1.0</td>
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<td>C3</td>
<td>Lip length to base of sinuses</td>
<td>1.24</td>
<td>0.21</td>
<td>2.12</td>
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<td>Lip length to lateral lobe</td>
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<td>0.35</td>
<td>2.87</td>
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<td>Lip width</td>
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<td>0.14</td>
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<td>C6</td>
<td>Lip outline shape</td>
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<td>C7</td>
<td>Lip lateral lobe reflexion</td>
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<td></td>
<td>2.1</td>
<td></td>
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<td>Lip base colour, x</td>
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<td>29</td>
<td>375</td>
<td>0</td>
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<td>C9</td>
<td>Lip base colour, y</td>
<td>448</td>
<td>35</td>
<td>420</td>
<td>0</td>
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<td>C10</td>
<td>Lip base colour, reflectivity (Y)</td>
<td>72.3</td>
<td>12.0</td>
<td>85</td>
<td>0</td>
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<td>C11</td>
<td>Lip, indentation of lateral lobes</td>
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<td>0</td>
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<tr>
<td>C12</td>
<td>Spur length</td>
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<td>0.21</td>
<td>2.16</td>
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<td>C13</td>
<td>Spur width halfway along length</td>
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<td>0.74</td>
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</tr>
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<td>C14</td>
<td>Spur curvature</td>
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<td>5.0</td>
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<tr>
<td>C15</td>
<td>Lateral sepal position (v. vertical)</td>
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<td>C16</td>
<td>Basal bract length</td>
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<td>2.12</td>
<td>10.7</td>
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<td>C17</td>
<td>Floral bract length</td>
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<td>C18</td>
<td>Bract margin cell diameter</td>
<td>79.5</td>
<td>10.6</td>
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<td>C19</td>
<td>Bract margin cell shape</td>
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<td></td>
<td>1.3</td>
<td></td>
</tr>
<tr>
<td>C20</td>
<td>Plant height</td>
<td>195</td>
<td>28</td>
<td>211</td>
<td>35</td>
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<tr>
<td>C21</td>
<td>Inflorescence length</td>
<td>46.6</td>
<td>12.7</td>
<td>51.4</td>
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<td>C22</td>
<td>Ovary length</td>
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<td>4.7</td>
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</tr>
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<td>C23</td>
<td>Number of flowers</td>
<td>34.7</td>
<td>2.1</td>
<td>34.5</td>
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<td>C24</td>
<td>Stem diameter</td>
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<td>0.07</td>
<td>2.92</td>
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<tr>
<td>C25</td>
<td>Number of sheathing leaves</td>
<td>3.55</td>
<td></td>
<td>3.7</td>
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</tr>
<tr>
<td>C26</td>
<td>Number of non-sheathing leaves</td>
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<td>2.0</td>
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<tr>
<td>C27</td>
<td>Basal sheath absent : present</td>
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<td></td>
<td>0</td>
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<tr>
<td>C28</td>
<td>Longest leaf length</td>
<td>51.6</td>
<td>7.1</td>
<td>67.2</td>
<td>11.6</td>
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<td>C29</td>
<td>Widest leaf width</td>
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<td>17.9</td>
<td>3.8</td>
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<td>C30</td>
<td>Relative posn. longest : widest If</td>
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<td>1.1</td>
<td></td>
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<tr>
<td>C31</td>
<td>Distance of longest If above ground</td>
<td>2.16</td>
<td>1.58</td>
<td>2.1</td>
<td>1.3</td>
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<td></td>
<td>Description</td>
<td>Value1</td>
<td>Value2</td>
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<td>--------</td>
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<td>C32</td>
<td>Shape uppermost leaf</td>
<td>3.84</td>
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<td>C33</td>
<td>Shape longest leaf</td>
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<td>4.0</td>
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<tr>
<td>C34</td>
<td>Shape lowest leaf</td>
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<td>C35</td>
<td>Leaf hooded tips</td>
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</tr>
<tr>
<td>C36</td>
<td>Leaf colour</td>
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<td>Species</td>
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</table>

Ps. albida          T G A T C A A T — — T
Ps. straminea       C T C C T G C C A A G
Table 1  Details of study populations. All measurements were taken during 2014 or 2015, except Balvattan Hill (1996). Flowering period has been adjusted for unusually early (2014) or late (2015) seasons; the number preceding the forward slash is the month, the succeeding numbers denote the weeks of that month.

<table>
<thead>
<tr>
<th>Locality</th>
<th>Grid reference (UK) or Latitude plus Longitude</th>
<th>Altitude (m asl)</th>
<th>Soil parent materials</th>
<th>Flowering period</th>
<th>Appx. no. fl. plants</th>
<th>No. of plants measured</th>
</tr>
</thead>
<tbody>
<tr>
<td>Little ASBY pasture, W Kirkby Stephen, SE Cumbria, vc 69</td>
<td>NY 698102</td>
<td>285</td>
<td>Carboniferous limestone?</td>
<td>6/2–3</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Rough pasture S STAINMORE, E Brough, SE Cumbria, vc 69</td>
<td>NY 85–13–</td>
<td>ca 300</td>
<td>Carboniferous limestone?</td>
<td>6/3–4</td>
<td>30</td>
<td>10</td>
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<tr>
<td>Grassy knoll, KELTNEYBURN Reserve, nr Fortingall, Perth, vc 88</td>
<td>NN 771496</td>
<td>165</td>
<td>Mine talus/glacial till/Cambrian psam.</td>
<td>6/3</td>
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<td>Heath, BALVATTAN Hill, SE Aviemore, Rothiemurchus, Highland, vc 96</td>
<td>NH 914090</td>
<td>320</td>
<td>Sandy blanket head/Moine Schist</td>
<td>6/4</td>
<td>20</td>
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<td>Rough pasture, GLENCAIRN, S Boat of Garten, Highland, vc 96</td>
<td>NH 941162</td>
<td>215</td>
<td>Glacial sands /Cambrian psam.</td>
<td>6/4</td>
<td>500</td>
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<td>Grassy knoll, SW SPEYBRIDGE, S Grantown, Highland, vc 95</td>
<td>NJ 025255</td>
<td>205</td>
<td>Glaciofluvial sands/Precambrian gneiss</td>
<td>6/4</td>
<td>30</td>
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<td>Heath, ARDNISH peninsula, NE Broadford, Skye, vc 104</td>
<td>NG 666239</td>
<td>4</td>
<td>Raised beach sands/Jurassic limestone</td>
<td>6/3–4</td>
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<tr>
<td>Rough pasture, GLENDRYNOCH, E Drynoch, W Sligachan, Skye, vc 104</td>
<td>NG 416311</td>
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<td>Alluvium/Paleogene granite</td>
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<tr>
<td>Moorland, S SOLHEIMAJÖKULL glacier, NW Vik, SC Iceland</td>
<td>N63° 31' 39.4 W19° 22' 06.7</td>
<td>110</td>
<td>Glacial outwash/Late Pleistocene lavas</td>
<td>6/3–4</td>
<td>4</td>
<td>4</td>
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<tr>
<td>Cliffs, Skogaross, W SKOGAR, SC Iceland</td>
<td>N63° 31' 52.9 W19° 30' 44.3</td>
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<td>Late Pleistocene volcanic ash</td>
<td>7/1–2</td>
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<td>Heath, T-junction S Route 41, E Keflavik, SW VOGAR, SW Iceland</td>
<td>N63° 56' 51.2 W22° 25' 45.0</td>
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<td>Late Pleistocene lavas</td>
<td>6/4–7/1</td>
<td>15</td>
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