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Another overlooked boreal clubmoss *Spinulum annotinum* subsp. *alpestre* (Lycopodiaceae) in Scotland

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Abstract
Following the discovery of *Lycopodium lagopus* (Laest. ex Hartm.) Zinserl. ex Kusen in Scotland (Rumsey 2007), a second previously overlooked clubmoss is reported. We follow World Flora Online and the Pteridophyte Phylogeny Group in transferring *Lycopodium annotinum* (L.) to the genus *Spinulum* (A. Haines), and recognise two subspecies, *S. annotinum* subsp. *annotinum* (L.) A. Haines and *S. annotinum* subsp. *alpestre* (Hartm.) Uotila, both of which occur in Scotland. Subsp. *alpestre* is restricted to exposed sites at high altitudes. The previous suggestion that this plant is synonymous with *S. canadense* (Nessel) A. Haines is shown to be incorrect. Although these high altitude Scottish plants are closer to *S. subarcticum* (V. Vassil.) A. Haines, we choose to recognise them at subsp. rank. The extent to which any morphological gradations along an altitudinal gradient represent hybridisation as opposed to clinal variation requires resolution. *Spinulum annotinum* s.l. is recorded at altitudes >750 m in vice-counties 88, 89, 90, 92, 94, 96, 97, 98, 99 and 105 strongly suggestive that the montane boreal subspecies may be more widely distributed than the more limited area investigated in this preliminary study. A specimen collected in north Wales in 1773 (VC49) is subsp. *alpestre*.

Keywords
Lycopodium annotinum; Cairngorms National Park; clinal variation; altitudinal variation

Introduction

In Great Britain (GB) *Spinulum annotinum* (L.) A.Haines (*Lycopodium annotinum* (L.)) (Interrupted Clubmoss) is recorded from 24 vice-counties and 170 hectads post-1999 (Fig. 1). It is very rare outwith the Scottish Highlands and was known at only one site in England post-1999, until the discovery of a plant in S.W. Yorkshire in December 2025. It is extinct in Wales and has not been recorded from Ireland.

While British Floras, from Clapham et al (1952) to Stace (2019) do not refer to any infraspecific taxa within *L. annotinum*, internationally it is widely accepted that there are two taxa, though there is disagreement about their appropriate rank and genus.

- *Lycopodium annotinum* (L.) subsp. *annotinum* and *Lycopodium annotinum* subsp. *alpestre* (C.Hartm.) Á.Löve & D.Löve, Flora Europaea (Tutin et al, 1993) and Flora Nordica (Jonsell, 2000).
- *Lycopodium annotinum* (L.) and *Lycopodium dubium* Zoëga (Plants of the World Online, 2025)

- *Spinulum annotinum* subsp. *annotinum* (L.) A.Haines and *Spinulum annotinum* (L.) A.Haines subsp. *dubium* (Zoëga) J.H.Xue, Chepinoga & K.P.Ma, The World Ferns Checklist (Hassler, M., 1994 - 2025)
- *Spinulum annotinum* subsp. *annotinum* (L.) A.Haines and *Spinulum annotinum* subsp. *alpestre* (Hartm.) Uotila, WFO (2025).

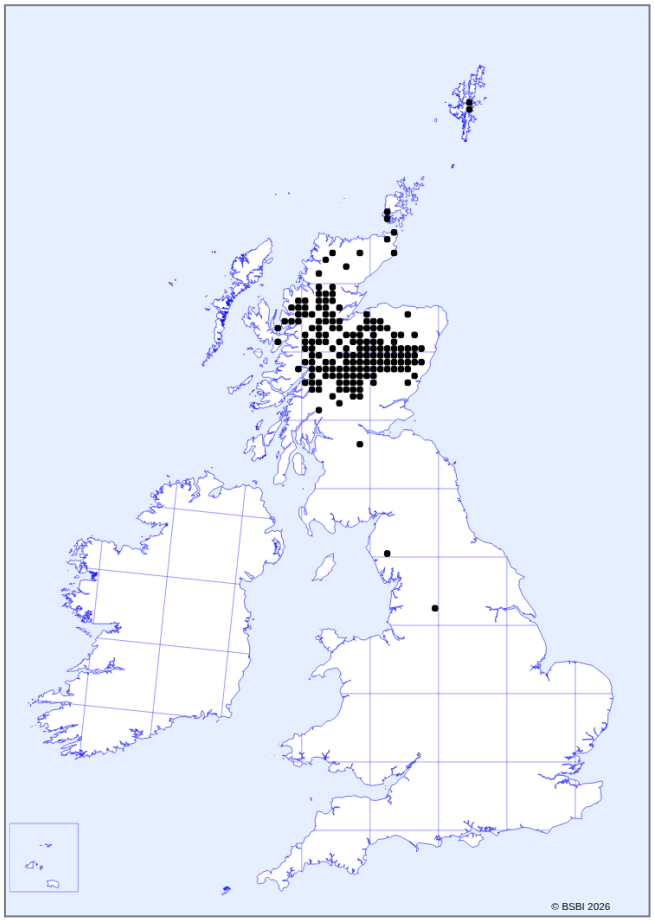


Figure 1. *Spinulum* (*Lycopodium*) *annotinum* post-1999 hectad distribution in GB (using data on the BSBI DDb at 08/06/2026)

Taxonomic Classification of *Lycopodiaceae*

Lycopodium annotinum was transferred to the newly created genus *Spinulum* by Haines (2003). Øllgaard (1987) had treated the species that Haines placed in *Spinulum* as section *Annotina* in the genus *Lycopodium*. He stated that "[the sections of *Lycopodium*] are equally distinct and accordingly should have the same rank". Given that *Diphasiastrum* (Holub) had been separated from *Lycopodium*, Haines argued that it was necessary to recognise *Spinulum* in order to create a consistent nomenclatural system in which all of the discrete lycopod groups are provided with the same rank. There is clear morphological support for the segregation of *Spinulum* from *Lycopodium* e.g.

- Species of *Spinulum* have upright shoots with leaves arranged in alternating pseudowhorls of 4 or 5 (vs. 6–10 in *Lycopodium* s.s.).
- Each leaf is tipped with a minute, but firm, spinule (vs. tipped by a long, colourless hair or with a membranous apex).
- The strobili are sessile at the apex of upright shoots (vs. borne on simple or branched stalks).

Herrera et al (2022) using morphological and DNA sequence datasets presented the phylogenetic relationships of *Lycopodiaceae* genera, which also supported *Spinulum* as being distinct from *Lycopodium*.

An attempt at a consensus classification of lycophytes and ferns down to genus level was proposed by the Pteridophyte Phylogeny Group (PPG I, 2016) and has been further revised on the basis of new molecular evidence (PPG II, in prep.). Based on strict monophyly, and with an apparent desire to see long divergent lineages recognised at generic rather than infrageneric level, the new classification often sees a narrower generic concept adopted. This includes the recognition by PPG of the genus *Spinulum*. The consensus taxonomy from PPG has been adopted by World Flora Online (WFO). The taxonomic view presented by Plants of the World Online, the most widely consulted online nomenclatural resource, is currently in marked contrast to the consensus view of the pteridophytic community. In this paper we follow WFO in recognising the genus *Spinulum*, with two subspecies (subsp. *annotinum* and subsp. *alpestre*) both of which occur in Scotland.

Discovery of *Spinulum annotinum* subsp. *alpestre* in Scotland

Following the reporting of *Lycopodium lagopus* (Laest. ex Hartm.) Zinserl. ex Kusen as new to Britain (Rumsey, 2007), Stewart Taylor while searching for *L. lagopus*, photographed an unusual form of *S. annotinum* at two sites in the Cairngorms (Fig. 2), which at the time (2008) Andy Amphlett (AA) thought were a candidate for subsp. *alpestre*.



Figure 2. *Spinulum annotinum* subsp. *alpestre*. Photo by S. Taylor. Abernethy Forest NNR: Bynack Beg: upper Coire Dubh VC96 altitude 900 m NJ0389306900, 21/09/2008

Photos were sent to Fred Rumsey (FR), however AA did not, at that time, follow up Taylor's observations in the field. The possibility of the occurrence of subsp. *alpestre* had already been suggested to FR by John Edgington, based on observations he had made, but it was felt that more evidence was needed before declaring the discovery of a novel taxon to GB.

In BSBI Atlas 2020 (Stroh *et al.*, 2023) FR wrote "In exposed sites at high altitudes, plants approaching *L. annotinum* subsp. *alpestre* (syn. *L. dubium*, also called *Spinulum canadense*) may occur, mirroring the situation with *L. lagopus* and *L. clavatum*. Further research is needed".

In July 2025, accompanied by Liz Amphlett (LA), AA was plant recording in Coire an Lochain (VC96) and came across examples of *S. annotinum* that also seemed to be subsp. *alpestre*. His interest rekindled, AA & LA next went to the upper part of Coire na Ciste (Cairngorm, VC96) and found clear examples of what AA was becoming confident were subsp. *alpestre*. Photographs and measurements were sent to FR who replied "I think (that is) great progress - good to have some figures and data to back things up and it certainly looks like a reasonable claim can be made that we have pukka subsp. *alpestre*". AA continued to search for *S. annotinum*, both in montane habitats (with LA) and at lower altitudes, hoping to clarify differences between the two subspecies, and to discern if intermediates occurred.

Features distinguishing subsp. *annotinum* and *alpestre* in European literature are given in Table 1.

Table 1. *Lycopodium annotinum* subspecies, from Flora Nordica Volume 1 (Jonsell, 2000), and Flora Europaea, Vol. 1, 2nd ed. (Tutin *et al.*, 1993)

	subsp. *annotinum*	**subsp. *alpestre***
Main shoots	Mostly on the ground	Mostly within the litter layer
Branches (length cm)	10-25	4-20
Branches (width mm)	10-16 (10-15)	4-10 (3-7)
Yearly growth	Cylindrical	Ellipsoid
Leaves	Spreading or reflexed (linear-lanceolate or linear, patent or deflexed)	Appressed, sometimes only loosely so (linear-subulate, patent to appressed)
Leaves (length mm)	4-10 (5-10)	2.5-6 (3-7)
Leaves	Green (thin, dull green)	Pale or brownish-green (thick)
Leaves (margin)	Serrate (coarsely toothed, apex acute)	Entire (nearly entire, apex acuminate)
Strobilus (length cm)	1.5-4 (1.5-3.0)	0.5-2 (0.5-1.5)
Habitat	Open to fairly shady *Pinus*, *Picea* or *Betula* forest, also by pools or mires; rare in open heathland	Alpine heath, subalpine *Betula* forest (Arctic and subarctic Europe southwards to 60^{o} N)

Altitudinal distribution of *S. annotinum* in Great Britain

In Great Britain, *S. annotinum* has been recorded from 1276 100 m grid cells of the Ordnance Survey (all years). The mean altitudes of the recorded grid references (excluding duplicate records) in each 100 m grid cell were calculated: median 612 m (inter quartile range 466-732 m). Altitudes were calculated within the BSBI database, which uses the SRTM 90 m Digital Elevation Model, except for Shetland, where altitudes were obtained from Ordnance Survey (OS) maps (Ordnance Survey, 2025).

In Great Britain, the species is most frequent between 400-750 m altitude (Fig. 3). Within the Cairngorms National Park the peak frequency is between 650-750 m, while outwith the CNP boundary, peak frequency is between 400-600 m. Only very exceptionally is it recorded at more than 1000 m altitude. A Welch's T-test was conducted to compare the mean altitude of locations at 100 m precision or better (excluding duplicate records) between the two areas (Non-CNP mean = 516.35 m, n = 787; CNP mean = 687.97 m, n = 834). The mean altitudes are statistically significantly different, $t = -20.17$, $p < 0.001$.

In the Cairngorms, altitudinal limits of '*potential-natural* woodland and scrub zones, *sensu* Peterken (1981, 1996) can be described as follows (from Amphlett, 2024). The '*forest line*' (also known as the '*timber line*'), the altitudinal limit of erect tree growth above which trees become wind-pruned and increasingly stunted, is (depending on exposure) at (500) - 560 - (590) m. The '*treeline*', defined as the altitude of the uppermost trees with a minimum height of 2 m is at (610) - 650 - (690) m. The *montane scrub* zone extends from *c*.650 m to the *scrub line* at 950 - (1000) m, above which tall-shrub species cease to grow or are no more than occasional in montane (alpine) zone vegetation.

Therefore, in the Cairngorms, *S. annotinum* is most frequent within the (potential) montane scrub zone, but also occurs at lower altitudes (including in woodland) and at higher altitudes in the low alpine zone.

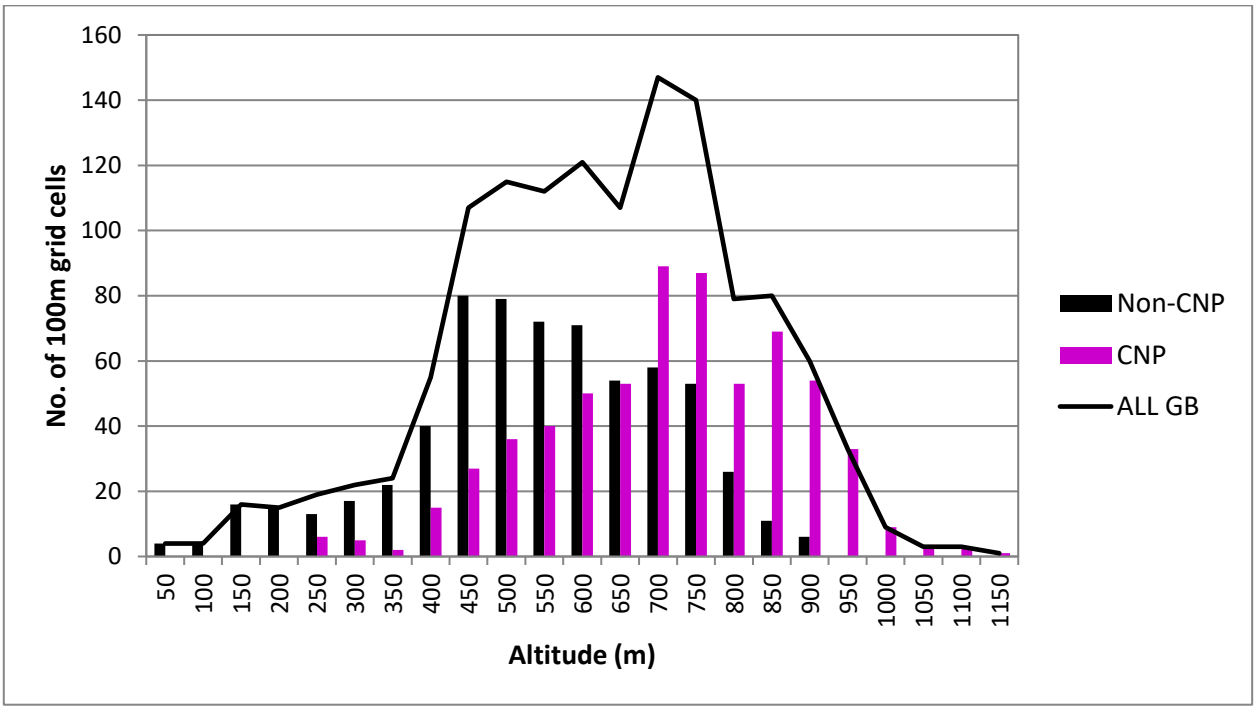


Figure 3. Altitudinal distribution of *Spinulum annotinum* in Great Britain, comparing recorded locations within the Cairngorms National Park vs outwith the CNP boundary (using data on the BSBI DDb at 08/06/2026)

Methods

29 patches / stands of *S. annotinum* were located, between 219 m and 1137 m altitude, in 16 monads (1 km Ordnance Survey grid squares) in vice-counties 94, 95 and 96 (Fig. 4, Table 2). Fieldwork was undertaken between 30 July and 24 August 2025.

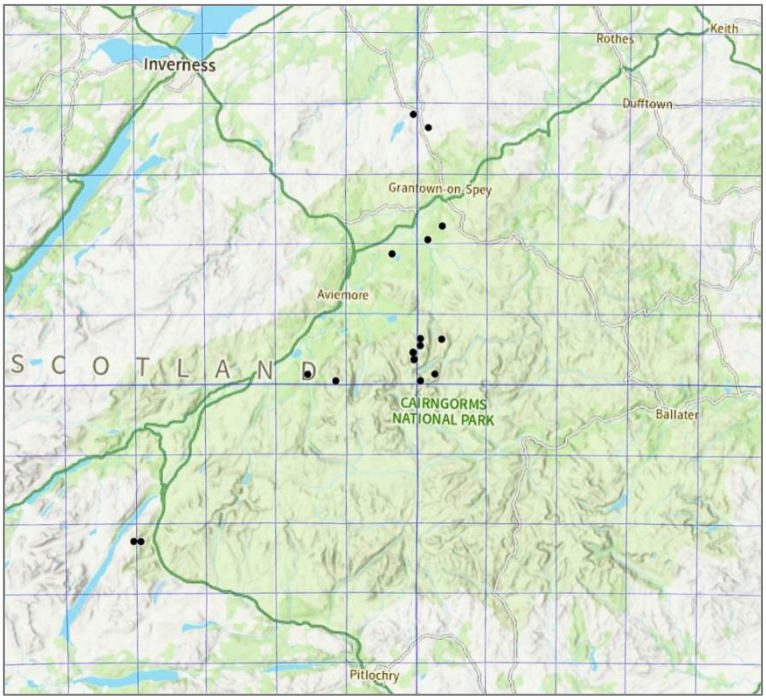


Figure 4. Locations of sampled *Spinulum annotinum* stands

Of these stands, 25 were visited by AA and Lewis Donaghy (LD) provided material and photographs from four stands. The following variables were recorded:

- Altitude – from OS maps.
- Branch length.
- Habitat.
- Leaf colour.
- Leaf hair points - present or absent (usually only present at apex of branches without strobili).
- Leaf length (mm) - at midpoint of annual growth. Leaf length of subsp. *annotinum* was measured to the nearest 1 mm. Leaf length of putative subsp. *alpestre* was measured to the nearest 0.5 mm under a stereo microscope at x10 magnification. (The dense slightly imbricate leaves of these plants made measurement with a ruler in the field impractical). The leaf lengths of subsp*. alpestre* were measured in a straight line from the leaf tip to the point where the leaf attaches to the branch.
- Leaf maximum width. A small sample measured to the nearest 0.1 mm under a stereo microscope at x10 magnification.
- Leaf apical angle. A small sample. Leaves were scanned and the angle measured on a computer monitor.
- Leaf margin - entire, irregular, very weakly serrate, weakly serrate or serrate

Table 2. Locations of *Spinulum annotinum* subsp. *annotinum* and subsp. *alpestre*

Subspecies	Location	VC	Gridref	Altitude (m)	Date	Recorder
annotinum	Abernethy Forest NNR	96	NH9668218436	219	2025-08-06	AA
annotinum	Nethybridge: School Wood	95	NJ01542069	236	2025-07-31	AA
annotinum	Inshriach Forest	96	NH8483401701	270	2025-08-02	AA
annotinum	Dava Moor	95	NH9926438241	294	2025-08-01	AA
annotinum	Heatherbell (NE of)	95	NJ0116836753	320	2025-08-01	AA
annotinum	Craigmore Wood	95	NJ0396422723	388	2025-08-07	AA
annotinum	Craigmore Wood	95	NJ0392722711	389	2025-08-07	AA
annotinum	Craigmore Wood	95	NJ0394622692	393	2025-08-07	AA
alpestre	Allt Coire Fhar (N. of)	96	NN6005877525	627	2025-08-22	AA, LA
alpestre	Allt Coire Fhar (N. of)	96	NN5979877411	664	2025-08-22	AA, LA
alpestre	Allt Coire Fhar (N. of)	96	NN5941777051	747	2025-08-22	AA, LA
alpestre	Invereshie & Inshriach NNR	96	NH8826100114	778	2025-08-24	AA, LA
alpestre	Coire an t-Sneachda	96	NH9903704292	831	2025-08-10	AA
alpestre	Coire an t-Sneachda	96	NH9904204288	833	2025-08-10	AA
alpestre	Coire an t-Sneachda	96	NH9917303965	866	2025-08-10	AA
alpestre	Creagan Dubh (monad)	96	NJ0078306391	872	2025-07-30	AA, LA
alpestre	Coire an t-Sneachda	96	NH9915703855	882	2025-08-10	AA
alpestre	Bynack Beg: upper Coire Dubh	96	NJ0392407014	884	2008-09-25	ST
alpestre	Abernethy Forest NNR	96	NJ0391506957	891	2025-08-16	AA
alpestre	Abernethy Forest NNR	96	NJ0390306913	898	2025-08-16	AA
alpestre	Abernethy Forest NNR	96	NJ0390306913	898	2025-08-16	AA
alpestre	Bynack Beg: upper Coire Dubh	96	NJ0389306900	900	2008-09-21	ST
alpestre	Creagan Dubh (monad)	96	NJ0074106183	905	2025-07-30	AA, LA
alpestre	Upper Coire na Ciste	96	NJ0049505768	915	2008-09-19	ST
alpestre	Creagan Dubh (monad)	96	NJ0064106020	917	2025-07-30	AA, LA
alpestre	Upper Coire na Ciste	96	NJ0056205876	921	2025-07-30	AA, LA
alpestre	Coire an t-Sneachda	96	NH9942903680	923	2025-08-10	AA
alpestre	Loch Etchachan (N. of)	94	NJ0097300836	928	2025-08-18	LD
alpestre	Coire Cas	96	NH9965004540	940	2025-08-18	LD
alpestre	Upper Coire na Ciste	96	NJ0060005780	946	2025-07-30	AA, LA
alpestre	Beinn Mheadhoin	94	NJ0249401537	1122	2025-08-17	LD
alpestre	Beinn Mheadhoin	94	NJ0244501538	1137	2025-08-17	LD

- Leaf orientation - Spreading (± horizontal), Spreading to below horizontal (drooping), Spreading to slightly above horizontal, S-shaped ascending or ± straight, above horizontal (typically at 45°)
- Leaf shape - Lanceolate, narrowly lanceolate or very narrowly lanceolate
- Shoot width - at midpoint of annual growth, to the nearest 1 mm.
- Shoot shape of annual growths. Parallel, ± parallel, tapering, narrow ellipse or elliptical.

- Spore size (µm) - the maximum widths of 10 spores per sample were measured at x400 using a calibrated eyepiece micrometer.
- Stomata on adaxial side of leaf - counted at x45 magnification using a stereo microscope, with incident illumination set at an acute angle. Leaves were selected from the midpoint of annual growth.
- Strobilus length - measured from tip of uppermost leaf to apex of strobilus, to the nearest 1 mm.

Results

A summary of the data collected is in Table 3. Photographs of the two subspecies are in Figs. 5-9 (subsp. *annotinum*) and Figs. 10-18 (subsp. *alpestre*). Scans of leaves are in Figs. 19-21 subsp. *annotinum*, Figs. 22-26 subsp. *alpestre*. Photographs of *S. canadense* (Nessel) A.Haines are in Figs. 27-28.

Table 3. Data from 29 populations of *Spinulum annotinum*

	Subsp. *annotinum*	**Subsp. *alpestre***
Altitude (m)	219-393	627-1137
Branch length (cm) mean (95% CL)	18.0 (± 4.14) (n=15, 5 populations)	6.8 (± 0.62) (n=62, 15 populations)
Habitat	Forest (7), moorland (1)	Montane (21)
Leaf colour	Yellow green (2) Dark green (6) Leaf apex straw, with / without brownish tip (0)	Yellow green (20) Dark green (0) Leaf apex straw, with / without brownish tip (17)
Leaf hair points	Present (4), absent (3)	Present (15), absent (4)
Leaf length (mm), mean (95% CL)	7.1 (± 0.24) (n=79, 8 populations)	4.7 (± 0.10) (n=180, 19 populations)
Leaf length (mm) (10th-90th percentiles)	6-9	4-6
Leaf maximum width (mm) (median)	1.0 (range 0.8-1.2) n = 9	1.2 (range 1.0-1.4) n = 15
Leaf apical angle (degrees) (median)	30 (range 20-35) n = 9	35 (range 25-40) n = 15
Leaf margin (modal state in bold)	Entire (5) Irregular (4) Very weakly serrate (0) Weakly serrate (4) **Serrate** (6) (n=7)	Entire (13) **Irregular** (18) Very weakly serrate (5) Weakly serrate (9) Serrate (0) (n=19)
Leaf orientation viewed from side (modal state in bold)	**Spreading (± horizontal)** (8), Spreading to below horizontal (drooping) (3) Spreading to slightly above horizontal (2) S-shaped ascending (0) ± straight (above horizontal) (0) (n=8)	Spreading (± horizontal) (1) Spreading to below horizontal (drooping) (0) Spreading to slightly above horizontal (0) **S-shaped ascending** (18) ± straight (above horizontal) (6) (n=19)

Leaf shape	Lanceolate (1) Narrowly lanceolate (1) Very narrowly lanceolate (5) (n=7)	Lanceolate (11) Narrowly lanceolate (11) Very narrowly lanceolate (0) (n=19)
Shoot width (mm), mean (95% CL)	14.4 (± 0.47) (n=75, 8 populations)	7.3 (± 0.27) (n=203, 19 populations)
Shoot width (mm), (10th-90th percentiles)	12-17	5-10
Shoot shape of annual growths	Parallel (5) ± parallel (3) Tapering (1) Narrow ellipse (0) Elliptical (0)	Parallel (0) ± parallel (13) Tapering (10) Narrow ellipse (2) Elliptical (8)
Spore size (µm), mean (95% CL)	35.0 (± 0.47) (n=40, 10 spores from each of 4 populations)	34.5 (± 0.58) (n=40, 10 spores from each of 4 populations)
Stomata on adaxial side of leaf, mean (95% CL by bootstrapping with replacement, 1000 samples)	11.0 (6.9-15.7) (n=58, 8 populations)	24.7 (18.5-31.0) (n=46, 12 populations)
Stomata on adaxial side of leaf, (10th-90th percentiles)	0-35	3-55
Strobilus length (mm), mean (95% CL)	31.2 (± 1.61) (n=105, 7 populations)	15.6 (± 0.70) (n=240, 18 populations)
Strobilus length (mm), (10th-90th percentiles)	21-43	9-23

Specimens of most of the plants examined have been retained and will be passed on to **E**.

Discussion

Habitat

Subsp. *annotinum* was recorded in forests dominated by *Pinus sylvestris* L. (Scots Pine) (7) and at one location on moorland. All 21 populations of subsp. *alpinum* were from montane habitats, the lowest (627 m) being at the potential treeline, as defined above (Amphlett, 2024).

Altitude

In this study, recorded populations of subsp*. annotinum* occurred from 219-393 m altitude, median 307 m, and populations of subsp. *alpestre* from 627-1137 m, median 898 m.

Branch length

Branch lengths were only measured from specimens collected. However, these samples were sufficient to demonstrate that subsp*. annotinum* has longer mean branch length (± 95% CL): 18.0 cm (± 4.14) vs 6.8 cm (± 0.62), subsp. *alpestre*.

Leaf colour.

Six of the eight populations of subsp. *annotinum* had dark green leaves, the other two had yellow green leaves. All 20 of the subsp. *alpestre* populations had yellow green leaves. The

difference is highly significant; Fisher's Exact Test p = 0.00007432. 17 of the 20 subsp. *alpestre* populations had leaf apices straw-colour with or without brownish tips.

Leaf hair points
Hair points at leaf tips occurred in 19 of 26 samples. Only leaves on branches were examined, and hair points were usually restricted to the apex of branches, so only branches lacking cones were checked. There was no significant difference in the proportion of samples with and without hair points between the two subspecies. Fisher's exact test p = 0.3401. However, in the field hair points on subsp*. alpestre* were often particularly obvious.

Leaf length
Mean leaf length (± 95% CL), at the midpoint of annual growths, differed between the two subspecies: subsp. *annotinum* 7.1 (± 0.24) vs subsp. *alpestre* 4.7 (± 0.10). The 10th-90th percentiles of leaf lengths also distinguish the two subspecies: subsp. *annotinum* 6-9 mm and subsp*. alpestre* 4-6 mm.

Leaf maximum width
Leaves of subsp. *annotinum* tend to be slightly narrower than those of subsp. *alpestre*: 1.0 (range 0.8-1.2) cf 1.2 (range 1.0-1.4).

Leaf apical angle
The apical angle of leaves was slightly more acute in subsp. *annotinum* cf. subsp*. alpestre*: 30˚ (range 20-35) cf 35° (range 25-40).

Leaf margin
Leaf margins were assigned to one or more of five categories: entire, irregular, very weakly serrate, weakly serrate or serrate. Leaves were examined under a stereo microscope at x10 with incident and transmitted light. In the field with a hand lens, leaves scored here as having an 'irregular' margin would most likely be categorised as 'entire'. An initial analysis found no significant difference between the two subspecies in the proportion of populations with all leaves with entire or irregular margins and those with margins with any degree of serration (Fisher's exact test p = 0.14560657). However, the proportion of populations with any leaf margins categorised as 'serrate' vs those with only weak serrations or less did differ between the two subspecies (Fisher's exact test p = 0.00176345). Five of seven samples of subsp. *annotinum* had at least some leaves with obvious serrations, which might be termed coarsely serrate. In contrast only one of 19 samples of subsp. *alpestre* had any leaves that were described as serrate, and then only as "irregularly serrate".

Leaf orientation
18 of 19 samples of subsp. *alpestre* had at least some branch leaves S-shaped ascending (Fig. 12), while zero of eight samples of subsp*. annotinum* had leaves with that orientation. The difference is highly significant, Fisher's exact test p = 0.00000405.

Leaf shape
Five of seven samples of subsp*. annotinum* had leaves categorised as 'very narrowly lanceolate'. These leaves were almost parallel sided in their proximal half (see Fig. 9). None of the 19 samples of subsp. *alpestre* had leaves of this shape. The difference is highly

significant, Fisher's exact test p = 0.00031925. 11 of 19 samples of subsp. *alpestre* had leaves categorised as lanceolate (Fig. 12), the remainder as narrowly lanceolate.

Shoot width
Mean shoot width (mm) (± 95% CL) differed between the two subspecies: subsp. *annotinum* 14.4 (± 0.47), subsp. *alpestre* 7.3 (± 0.27). The 10th-90th percentiles of shoot widths separate the two subspecies: subsp. *annotinum* 12-17 mm, subsp*. alpestre* 5-10 mm.

Shoot shape of annual growths.
In subsp*. annotinum* annual growths, between the winter bud constrictions, are ± parallel sided, and the winter bud constrictions are narrow and abrupt (Figs. 7 and 8), hence annual growth is rectangular, viewed from the side. In *subsp. alpestre*, the winter bud constrictions are more gradual, the leaves below a constriction becoming more upright, more congested (almost imbricate) and eventually smaller (Fig. 12). When the annual growth is short, the shape can approximate to an ellipse (Figs. 13 and 14). When annual growth is longer, the shape is ± parallel sided but still tapers towards the winter bud constriction (Figs. 15, 16 and 17). In subsp. *annotinum* seven of eight samples had all annual growths (±) parallel sided, while in subsp. *alpestre* only two of 20 samples had annual growths of that shape. The difference is highly significant, Fisher's exact test p = 0.00022297.

Spore size
Mean spore size (µm) (± 95% CL) did not differ between the two subspecies: subsp. *annotinum* 35.0 (± 0.47), and subsp. *alpestre* 34.5 (± 0.58). All spores examined were fully formed.

Stomata on adaxial side of leaf
Haines (2003) noted a difference in the number of stomata on the adaxial side of leaves, between *S. annotinum* and *S. canadense*. The latter species is currently synonymised with subsp. *alpestre* (WFO, 2025). He wrote "In *S. annotinum*, the adaxial (i.e., upper) surface of the trophophylls (leaves) show a rapid reduction in the number of stomates moving apically above the winter bud constriction. In general, within 4 or 5 pseudowhorls of trophophylls above the winter bud constriction, the adaxial surface will lack stomates completely. In *S. canadense*, there is no reduction in the number of stomates on the adaxial surface of trophophylls located above the winter bud constrictions (i.e., all the trophophylls show abundant stomates on the upper side)".

Examining leaves from approximately the midpoint of annual growths, the mean number (95% CL) of stomata on the adaxial surface did differ between the two subspecies: subsp. *annotinum* 11.0 (6.9-15.7) and subsp. *alpestre* 24.7 (18.5-31.0). Counts were extremely variable, and as the standard deviation was larger than the mean of the samples, the 95% confidence limits were obtained by bootstrapping. Although the means differed, the 10th-90th percentiles overlapped almost completely: subsp*. annotinum* 0-35 and subsp. *alpestre* 3-55.

Strobilus length

Mean (± 95% CL) strobilus length (mm) differed between the two subspecies: subsp. *annotinum* 31.2 (± 1.61) and subsp. *alpestre* 15.6 (± 0.70). The 10th - 90th percentiles only overlapped slightly: subsp. *annotinum* 21-43 and subsp*. alpestre* 9-23.



Figure 5. *Spinulum annotinum subsp. annotinum*. Nethybridge: School Wood VC95 NJ01542069



Figure 6. *Spinulum annotinum* subsp*. annotinum*. Craigmore Wood VC95 NJ0394622692 ⌀ 16 m



Figure 7. *Spinulum annotinum* subsp. *annotinum.* Craigmore Wood VC95 NJ0392722711 ⌀ 22 m



Figure 8. *Spinulum annotinum* subsp. *annotinum*. Nethybridge: School Wood VC95 NJ01542069



Figure 9. *Spinulum annotinum* subsp*. annotinum*. Craigmore Wood VC95 NJ0396422723



Figure 10. *Spinulum annotinum* subsp. *alpestre*. Coire an t-Sneachda VC96 altitude 923 m NH9942903680 ⌀ 6 m



Figure 11. *Spinulum annotinum* subsp. *alpestre*. Creagan Dubh (monad) VC96 altitude 917 m NJ0064106020 ⌀ 6 m



Figure 12. *Spinulum annotinum* subsp. *alpestre*. Invereshie & Inshriach NNR VC96 altitude 778 m NH8826100114 ⌀ 6 m



Figure 13. *Spinulum annotinum* subsp. *alpestre.* Abernethy Forest NNR VC96 altitude 898 m NJ0390306913 ⌀ 8 m



Figure 14. *Spinulum annotinum* subsp. *alpestre*. Upper Coire na Ciste VC96 altitude 921 m NJ0056205876



Figure 15. *Spinulum annotinum* subsp. *alpestre*. Coire an t-Sneachda VC96 altitude 833 m NH9904204288 ⌀ 6 m



Figure 16. *Spinulum annotinum* subsp. *alpestre*. Invereshie & Inshriach NNR VC96 altitude 778 m NH8826100114 ⌀ 6 m





Figure 17. *Spinulum annotinum* subsp. *alpestre*. Allt Coire Fhar (N. of) VC96 altitude 664 m NN5979877411 ⌀ 6 m
Two specimens from different patches at same location.



Figure 18. *Spinulum annotinum* subsp. *alpestre*. Coire an t-Sneachda VC96 altitude 831 m NH9903704292 ⌀ 6 m

Scans of leaves from approximately the midpoint of annual growths. All images are to the same scale.



Figure 19. Subspecies *annotinum*. Nethybridge: School Wood. NJ01542069. Altitude 236 m.



Figure 20. Subspecies *annotinum*. Craigmore Wood 1. NJ0396422723. Altitude 388 m.



Figure 21. Subspecies *annotinum*. Craigmore Wood 3. NJ0392722711. Altitude 389 m.



Figure 22. Subspecies *alpestre*. Allt Coire Fhar (N. of). NN6005877525, Altitude 627 m.



Figure 23. Subspecies *alpestre*. Coire an t-Sneachda 1. NH9903704292. Altitude 831 m.



Figure 24. Subspecies *alpestre*. Coire an t-Sneachda 3. NH9917303965. Altitude 866 m.



Figure 25. Subspecies *alpestre*. Abernethy Forest NNR: Upper Coire Dubh. NJ03106957. Altitude 891 m.



Figure 26. Subspecies *alpestre*. Upper Coire na Ciste. NJ0060005780. Altitude 946 m.

Comparison with non-European species

Values obtained from the study of the Scottish specimens are here compared with those collated by Arthur Haines (*S. annotinum*, *S. canadense* and *S. subarcticum* (V. Vassil.) A. Haines) and used in an unpublished key kindly provided to us, and data from Chen *et al.*, 2017 (*S. lioui* Li Bing Zhang & H. He).

Subsp. *annotinum*. Strobilus length 21-43 mm (10th - 90th percentiles), n = 105, is within the typical range of Haines' values for *S. annotinum* 17-43 mm. Leaf length 6-9 mm (10th - 90th percentiles), n = 79, is almost identical to Haines' typical values of 5.8-8.8 mm for *S. annotinum*.

Subsp. *alpestre*. Strobilus length 9-23 mm (10th - 90th percentiles) is similar to the 5-17(-22) mm of *S. canadense* /*S. subarcticum* and shorter than the 20-33 mm for *S. lioui*. Leaf width, median 1.2 (range 1.0-1.4) n = 15, is within the typical range of *S. subarcticum* (from Haines), 0.9–1.4 mm., [cf. 0.5–0.9(–1) mm wide in *S. canadense*; 0.7-1.3 mm in *S. lioui*]. Apical angle, median 35 degrees (range 25-40) n = 15, is within the range of *S. subarcticum*, 16–42 degrees, [cf. 5-23 degrees in *S. canadense*].

Leaves immediately apical to winter bud constrictions are widest near to the middle, agreeing with Haines' description of *S. subarcticum*. Those of *S. canadense* are lanceolate to triangular or narrow-ovate, widest well below the middle. In *S. lioui* they are described as acicular.

As previously discussed, counts of stomata on the adaxial surface (from leaves at midpoint of annual growths) were extremely variable. Although the means differed, the 10th-90th percentiles overlapped almost completely: subsp. *annotinum* 0-35 and subsp. *alpestre* 3-55.

Haines discriminated between *S. canadense* and *S. subarcticum* on the basis of usually less than 40 stomates per ½ adaxial trophophyll surface vs more than 40.

The number of leaves per pseudowhorl has not been investigated. This is difficult with pressed specimens, and the somewhat imbricate leaves of subsp. *alpestre* makes this more difficult still.

In conclusion, Scottish specimens of subsp. *alpestre* match *S. subarcticum* better than *S. canadense* or *S. lioui* in terms of leaf width, leaf apical angle, and shape of leaves immediately apical to winter bud constrictions.



Figure 27. *Spinulum canadense* (Nessel) A.Haines. © Arthur Haines, Native Plant Trust, from https://gobotany.nativeplanttrust.org/species/spinulum/canadense/



Figure 28. *Spinulum canadense* © Arthur Haines, Native Plant Trust, from https://gobotany.nativeplanttrust.org/species/spinulum/canadense/

Taxonomic considerations and further work

Kurtto & Uotila, (2019) commented that "The widespread Northern Hemisphere lycophytes, *Diphasiastrum complanatum* (L.) Holub, *Huperzia selago* (L.) Bernh. ex Schrank & Mart., *Lycopodium clavatum* L. and *Spinulum annotinum*, each have a more or less distinct south – north pattern of morphological variation, resulting in morphologically recognized northern races. ... In North Europe the distinctness of the variation differs between the genera, but all these taxa are connected to the corresponding southern races by frequent intermediates. Consequently, the races have been treated mostly as subspecies in North Europe and the subspecies rank seems most appropriate pending further research". Although in the Flora of North America (Wagner & Beitel, 1993) suggested the observed variation was environmentally induced, *S. annotinum* is treated in the Panarctic flora (Elven *et al.*, 2011), and in most European Floras, as having two subspecies. The typical subspecies (subsp. *annotinum*) occurring in the more southern range, while subsp. *alpestre* (Hartm.) Uotila occupies more northern (arctic) areas. A broad hybrid zone apparently occurs where these two subspecies meet and material from this area, including Newfoundland and Labrador (Meades & Brouillet, 2026), Greenland, and Kamchatka, was described as *L. annotinum* var. *pungens* Desv. ex Spring (Wagner & Beitel, 1993; Elven *et al.* 2011). Note that the authority of var. *pungens* should be cited as Desv. ex Spring, since the name in Desvaux's original 1827 publication was an invalid *nomen nudum*. The name *L. annotinum* var. *pungens* Bach.Pyl. ex Desv. (1827) is also invalid, as this name was listed in synonymy; Bachelot de la Pylaie did not make a valid publication in this taxon, so

combinations with Bach.Pyl. listed as the basionym are in error, as noted by Meades & Brouillet, 2026.

While the most profound differences are seen to occur between the southern and boreal forms, it is true that subtler differences exist between the boreal forms in the different circum-boreal geographic regions. In this respect there are parallels with the pan-boreal fern Bracken *Pteridium aquilinum* (L.) Kuhn, see for example Wolf *et al.*, 2019. Haines (2003) chose to recognise American and northern Asiatic forms of the boreal Interrupted Clubmoss at specific level, as *S. canadense* and *S. subarcticum*. Subsequently Chinese authors have segregated a further taxon, initially discriminated as *L. pseudopungens* H.S. Kung & Li Bing Zhang. It is suggested however that that name is synonymous with *S. canadense*, which led to the novel epithet *S. lioui* being published for the Chinese species (Chen *et al.*, 2017). The many invalid and superfluous names created for these plants and the resulting erroneous synonymisations has added nomenclatural confusion to an already challenging taxonomic situation. At least 39 names have been applied at species, subspecies, variety and forma ranks. From our morphological study Scottish (and European) boreal material, which we choose to treat as *S. annotinum* subsp. *alpestre*, equates more closely to Haines' *S. subarcticum* than to his *S. canadense*, with which it has hitherto been synonymised, or to Chen *et al.*'s *S. lioui*. Further work is clearly necessary before a satisfactory conclusion can be reached as to the ranking and distinctiveness of these apparently geographically defined entities. The extent to which intergradations represent hybridisation as opposed to clinal variation also requires resolution and will determine the taxonomic response.

This study has demonstrated that both subsp*. annotinum* and subsp. *alpestre* occur in Scotland. *Spinulum annotinum* s.l. is recorded at altitudes >750 m in vice-counties 88, 89, 90, 92, 94, 96, 97, 98, 99 and 105 strongly suggestive that the montane boreal subspecies may be more widely distributed than the more limited area investigated in this preliminary study. Vice-County Recorders are accordingly encouraged to keep a look out for plants of subsp. *alpestre* elsewhere.

In addition, further searches for plants at intermediate altitudes, *c*.400-600 m, are needed to clarify the limits of the two subspecies, and the possible occurrence of intermediate forms.

Long extinct in Wales, there is a specimen of *S. annotinum* collected in 1773 by Joseph Banks (BM 001184311), from 'Immediately above Llyn y Cŵn, about 200 yards up the side of the hill'. This is in monad SH6358, in VC49. The altitude would have been between 750-800 m. Although not as extreme as some of the examples seen in the Cairngorms, we consider this specimen to be subsp. *alpestre*.

Examination of further herbarium specimens may bring to light additional locations for subsp. *alpestre*. Pressed specimens of the two subspecies are typically very different in appearance (Fig. 29). In the field, plants of subsp. *annotinum* have leaves that are mostly spreading ± horizontally, sometimes slightly drooping to below horizontal. When pressed, in most instances the central leaves of a shoot point downwards, and the lateral leaves are spreading. In contrast, plants of subsp. *alpestre* have central leaves pointing upwards when pressed, with lateral leaves ascending with their apices curved upwards. In pressed specimens the winter bud constrictions also differ, those in subsp. *annotinum* are messier in appearance, more abrupt, with leaves variously oriented, while those of subsp. *alpestre* are obvious, more gradual, the leaves below a constriction becoming more upright, more congested (almost imbricate) and eventually smaller.



Figure 29. *Spinulum annotinum*, appearance of pressed specimens Left subsp. *annotinum*, Right subsp. *alpestre* (specimens at same scale)

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