U18
Cryptogramma crispa-Athyrium distentifolium snow-bed

Synonymy
Cryptogrammeto-Athyrietum chionophilum McVean & Ratcliffe 1962.

Constant species
Alchemilla alpina, *Athyrium distentifolium*, *Cryptogramma crispa*, *Deschampsia cespitosa*, *D. flexuosa*, *Galium saxatile*, *Rumex acetosa*, *Saxifraga stellaris*, *Viola palustris*, *Barbilophozia floerkii*, *Hylocomium splendens*, *Hypnum callichroum*, *Kiaeria starkei*, *Polytrichum alpinum*, *Rhytidiadelphus loreus*, *Cladonia bellidiflora*.

Rare species
Athyrium distentifolium, *Kiaeria starkei*, *Polytrichum sexangulare*.

Physiognomy
The rare Arctic-Alpine fern, *Athyrium distentifolium*, occurs occasionally in some other vegetation types of snow-bound montane slopes, but it is most characteristic of this community, sometimes dominant in the field layer as small groups of densely-packed crowns distributed over the rocky ground that is the typical substrate here, or more patchily abundant over extensive areas. The fronds appear after the spring snow-melt, uncurling erect and moderately tall from the shuttlecock bunches, and they die down rapidly in autumn, although the herbage decays only slowly, the patches of red-brown often providing a clear marker of stands when the ground is exposed the following season. Very locally, on higher slopes, plants with smaller fronds and elbowed stipes, giving a strikingly spreading habit, have sometimes been distinguished as *A. flexile* (e.g. Page 1982). This seems to breed true, though it remains a taxon of doubtful status, perhaps a monstrous variant of *A. distentifolium* that has gained a firm hold in a few stations (Tutin *et al.* 1964).

Cryptogramma crispa is the other important plant of the community, quite often more abundant than *A. distentifolium*, particularly towards lower altitudes where it continues as a major pioneer on drier, more exposed screes than are usual here, and bigger clumps of this species can be very conspicuous in summer with their fresh green foliage. Other ferns are occasionally found, though not usually in any abundance: *Thelypteris phegopteris*, *T. limbosperma*, *Gymnocarpium dryopteris*, *Blechnum spicant* and *Dryopteris dilatata* have all been recorded as scattered individuals, and at lower altitudes there is a small overlap with the range of *Athyrium filix-femina*, a plant with pinnae usually less ascending than in *A. distentifolium*, and with a distinct indusium over the sorus.

Other vascular constants are *Deschampsia cespitosa* and *D. flexuosa*, which usually occur as scattered tussocks, *Alchemilla alpina*, *Galium saxatile*, *Saxifraga stellaris*, *Rumex acetosa* and *Viola palustris*. Also very common are *Omalotheca supina*, *Nardus stricta* and *Oxalis acetosella* with occasional plants of *Cerastium fontanum*, *Agrostis capillaris*, *Huperzia selago*, *Anthoxanthum odoratum* and the Arctic-Alpines *Carex bigelowii*, *Epilobium anagallidifolium*, *Juncus trifidus*, *Sibbaldia procumbens* and *Luzula spicata*.

Bryophytes are numerous and varied, though only *Rhytidiadelphus loreus* occurs with any great abundance, being sometimes the dominant of an extensive ground carpet among the rocks. Also very frequent, though usually with lower cover, are the montane mosses *Polytrichum alpinum*, *Hypnum callichroum* and *Kiaeria starkei*, *Hylocomium splendens* and the leafy hepatic *Barbilophozia floerkii*. Other common species are *Racomitrium lanuginosum*, *Rhytidiadelphus squarrosus*, *Dicranum fuscescens*, *D. majus*, *D. scoparium*, *Pleurozium schreberi*, *Plagiothecium undulatum*, *P. denticulatum*, *P. sylvaticum* and *Diplophyllum albicans* with occasional *Racomitrium canescens*, *Rhizomnium punctatum*, *Eurhynchium praelongum*, *Pogonatum urnigerum*, *Oligotrichum hercynicum*, *Hylocomium umbratum*, *Sphagnum capillifolium*, *Lophozia sudetica* and *Anastrepta orcadensis*. *Cladonia bellidiflora* is a constant but, apart from occasional *C. gracilis* and *Peltigera canina*, other lichens are rare.

Habitat

The *Cryptogramma-Athyrium* community is confined to high-altitude snow-beds on rocky ground with base-poor, humic soils in the cold, wet mountains of the Scottish Highlands. It is mainly western in its distribution, though with an important outlier on locally suitable ground in the eastern Grampians, occurring on stabilised block scree, among boulders and on ledges of mainly acidic rocks, sometimes forming quite large stands.

A. distentifolium, which gives this rather loose assemblage of plants its major focus, is an Arctic-Alpine fern, found in the uppermost vegetated zones of Scottish mountains, mostly between 600 and 1100 m (Page 1982). All the stands fall within the 21 °C mean annual maximum isotherm, indeed most occur inside the 20 °C isotherm (Conolly & Dahl 1970), and the species is probably confined by a requirement for low summer temperatures (Page 1982), a condition even more readily met on the sunless east- and north-facing slopes where the community is concentrated. The climate is also wet, most stands experiencing over 2400 mm precipitation annually (*Climatological Atlas* 1952) with more than 220 wet days yr^{-1} (Ratcliffe 1968), though in the low- and middle-alpine zones, where this kind of vegetation is most frequent, much of the winter share of this falls as snow, readily accumulating and persisting on sheltered aspects. And this is very important for the maintenance of the community, for *A. distentifolium* is a strongly chionophilous plant, depending on long, regular and deep snow-lie for protection against desiccation and frost (Page 1982).

Accumulation of snow over this vegetation probably reaches its maximum in March, with a speedy melt thereafter (McVean & Ratcliffe 1962), the single, sharp rise in temperature triggering the sudden flush of frond growth in the fern, which is then able to take maximum advantage of the brief, frost-free summer. The thick, dark mantle of the previous season's litter, through which the foliage uncurls, may also be of some importance in these early days, absorbing the weak spring sun and providing a buffer against any unseasonal chills (Page 1982). In the more oceanic western Highlands, it is probably the somewhat earlier melt, hastened along by warm spring rains, that prevents *A. distentifolium* descending, as many Arctic-Alpines do, to lower altitudes which have a suitably cool growing season for the plant (Page 1982). Towards the eastern Grampians, where precipitation drops to around 1600 mm yr^{-1} (*Climatological Atlas* 1952), with only 180 wet days annually (Ratcliffe 1968), it is probably the general dryness of climate that makes the community increasingly local. Here, it occurs only in the latest snow-beds of the Cairngorms and on Lochnagar, where long snow-lie is of crucial importance not only in providing shelter, but also in the redistribution of precipitation (McVean & Ratcliffe 1962).

The spring melt, together with any summer rain, helps keep the ground moist throughout the growing season, with the sheltered and often shaded aspect maintaining high humidity among the herbage. Typically, though, the soils here are free-draining, developing over pervious rocky terrain, generally quite steep, features that further restrict this kind of vegetation to particular stretches of snow-bound mountain slopes. The ground is characteristically stable, without the disruption that frost-heave or solifluction bring, the community being found most often among blocky talus or between large boulders, or on ledges of cliffs and ravines. Typically, too, the rocks are acidic, though a wide variety of exposures is colonised, including granites in the Cairngorms, quartzose schists, granulites and other siliceous rocks of the Dalradian and Moine series through the central Highlands and beyond the Great Glen, and Torridonian sandstone and Lewisian gneiss in the west. Over such substrates, the soils are often developed in pockets and are usually immature, sometimes comprising mixtures of humus, decaying sand fragments and inwashed silt, but often amounting to no more than fern remains and dense raw mor resting directly on the bedrock below. A surface pH of 3–4 has been recorded in such humic rankers (McVean & Ratcliffe 1962), which provide a very congenial medium for the growth of *A. distentifolium*: it is a calcifuge plant which readily spreads and branches beneath the slowly-decaying litter, gradually building up large clumps (Page 1982).

The associated flora of the *Cryptogramma-Athyrium* community reflects these habitat conditions. The other common dominant, *C. crispa*, has a broader climatic tolerance than *A. distentifolium*, and its abundance here can be seen as an extension, to higher sheltered altitudes, of its widespread occurrence on more stable, acidic screes right down through the sub-montane zone in the cool, oceanic parts of western Britain. Towards the middle-alpine zone, and especially in the drier and colder mountains of eastern Scotland, the characteristically late snow-lie is of great importance in helping this plant maintain its vigour at levels which would be otherwise uncongenial (Page 1982). It is tolerant of long and deep snow-cover and virtually confined to this vegetation type at higher altitudes (McVean & Ratcliffe 1962). Other associates are somewhat more catholic, being generally characteristic of moist, base-poor soils on snow-bound slopes at higher altitudes in the Scottish Highlands with particularly strong representation of plants from stable and well-irrigated ground around snow-fields. Species such as *Deschampsia cespitosa*, *D. flexuosa*, *Viola palustris*, *Alchemilla alpina*, *Rumex acetosa*, *Rhytidiadelphus loreus*, *Hylocomium splendens* and *Polytrichum alpinum*, for example, can be seen here as forming a kind of fragmented cover that over unbroken

stretches of humic soils fed by snow-melt thickens up into a continuous sward. The bouldery topography, dense fern growth and thick litter accumulation limit the challenge that the more robust of these plants can pose to the dominants, and also restricts the opportunity for abundant spread of the bryophytes that are so conspicuous on ground that is equally snow-bound, but where gentler and unbroken slopes carry gleyed podzolic soils often subject to churning and flow.

Zonation and succession

The *Cryptogramma-Athyrium* community is usually found as a visually distinct but quite integral component of suites of chionophilous vegetation types disposed over snow-bound slopes of varying rockiness, steepness and stability at higher altitudes through the Scottish Highlands. With the geographical shift eastwards, the community becomes much more local and there are some changes among the other elements represented in these patterns.

Wherever snow-bound slopes in the low- and middle-alpine zones are interrupted by crags or brows of acidic rocks, bouldery patches or tracts of block scree which retain their snow cover long and deep, the *Cryptogramma-Athyrium* community is likely to be represented, particularly through the western Highlands. Stands can be very small, just a few square metres in extent, or up to several hectares, although such bigger stretches tend to be rather heterogeneous, resolving into mosaics on closer inspection. Sometimes, the context for the community is some kind of high-altitude grassland or grass-heath, covering the less rocky slopes around, from which snow is blown clear or melts away earlier in the spring. The *Nardus-Carex* community, for example, commonly occupies moderately snow-bound slopes with impeded drainage up to about 900 m throughout the range of the *Cryptogramma-Athyrium* vegetation, and is often found on gentler and less sharply draining ground around it. With its heathy mixtures of *Nardus* and *Carex bigelowii*, however, and occasional local abundance of *Scirpus cespitosus*, the *Nardus-Carex* community is usually well defined. Closer in composition and especially associated with the fern beds through the western Highlands, is the *Deschampsia-Galium* grassland, which includes swards of peaty soils on cold, flushed slopes where snow-melt is often a major source of the irrigating waters. Ferns occur occasionally in this kind of vegetation, and small patches of the *Cryptogramma-Athyrium* community can mark out little groups of boulders within it. Moreover, with plants like *Deschampsia cespitosa*, *D. flexuosa*, *Galium saxatile*, *Alchemilla alpina*, *Viola palustris*, *Rumex acetosa* and bulkier mosses occurring frequently in both vegetation types, the similarities between them are sometimes very obvious, and there can be some interlocking where thin stretches of turf run in among blocky talus around the edges of screes. These kinds of pattern can be seen over the upper less calcareous exposures on Beinn Laoigh, on Bidean nam Bian, Beinn Eighe, Beinn Dearg, through the Affric–Cannich, Fannich and Letterewe hills and, in more fragmentary fashion, on Ben More Assynt to the north. It is in these mountains, too, that the floristic similarities between the *Cryptogramma-Athyrium* community and more oligotrophic tall-herb ledge vegetation are most apparent, and over the corrie slopes, screes and ledges of sites like Beinn Bhan, Beinn Eighe and the Letterewe Forest, the fern beds can be found in close association with both the *Luzula-Vaccinium* vegetation and *Deschampsia-Galium* swards perhaps partly derived from them by grazing. *A. distentifolium* can be locally abundant in the *Luzula-Vaccinium* community, as on the Coire na Poite ledge on Beinn Bhan, where flushing in an equable climate compensates for the shelter and humidity provided by longer snow-lie, and in such situations it can be quite hard to distinguish the vegetation from *Cryptogramma-Athyrium* beds.

Through the western Highlands, the moss-rich *Rhytidiadelphus* sub-community of the *Deschampsia-Galium* grassland often represents the most chionophilous kind of vegetation on gentler unbroken slopes with humic rankers and podzols kept wet and cold throughout the year by irrigation with melt and run-off. Where the *Cryptogramma-Athyrium* community occurs on rocky brows around such late snow-beds or among patches of boulders which are disposed between hollows, it is generally clearly defined by the abundance of ferns, but there can be a strong continuity between the ground carpet of the two vegetation types, with *R. loreus*, *H. splendens*, *Racomitrium lanuginosum*, *Polytrichum alpinum* and *Barbilophozia floerkii* frequent throughout. To the west of Creag Meagaidh and Ben Heasgarnich, where the *Cryptogramma-Athyrium* community is very local on snow-bound bouldery ground in the Cairngorms and on Lochnagar, the *Deschampsia-Galium* snow-beds are replaced by the *Carex-Polytrichum* type, swards which are not so strongly chionophilous as the fern beds, but sometimes found juxtaposed with them on gentle, ill-drained ground that carries longer snow cover than is usual for the *Nardus-Carex* grass-heath. *Deschampsia cespitosa*, *D. flexuosa* and bryophytes such as *Polytrichum alpinum*, *Dicranum fuscescens* and *Racomitrium lanuginosum* provide a measure of continuity here, but *Carex bigelowii* is usually at least a co-dominant in the swards and ferns are hardly every found.

Through much of the range of the *Cryptogramma-Athyrium* community, however, it is the *Polytrichum-Kiaeria* vegetation that is its most consistent companion in the very latest snow-beds. This comprises bryophyte-dominated swards with an abundance of mosses and hepatics that find, at most, a sparse representation in the fern beds, species such as *Kiaeria starkei*, *Polytrichum*

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sexangulare, *P. alpinum*, *Oligotrichum hercynicum* and *Barbilophozia floerkii* providing most of the ground cover, with but sparse occurrence of vascular plants like *Deschampsia cespitosa*, *Saxifraga stellaris* and *Omalotheca supina* and only very rare records for ferns. Typically, this vegetation occupies the sodden humic soils that cover quite steep slopes, snow-bound well into the late spring, through the middle-alpine zone. The ground is stable, though not rocky, and the community generally passes very sharply to the *Cryptogramma-Athyrium* vegetation where there is a bouldery surround above the snow-bed. More unstable soils, equally snow-bound, but subject to frost-heave and solifluction, may have the *Salix-Racomitrium* community, characterised by crusts of *Salix herbacea* and bryophytes, and mosaics of this and the *Polytrichum-Kiaeria* vegetation often occur together on the slopes below patches of the *Cryptogramma-Athyrium* vegetation. Through much of the range of the fern stands of this kind, the summit plateaus above the middle-alpine snow-beds have *Carex-Racomitrium* heath or fell-field, with the *Juncus-Racomitrium* heath replacing this through the Cairngorms.

Distribution

The *Cryptogramma-Athyrium* community is widespread but local through the western Highlands, with outlying stands in the Cairngorms and Lochnagar.

Affinities

The *Cryptogramma-Athyrium* community is largely based on McVean & Ratcliffe's (1962) *Cryptogrammeto-Athyrietum*, the only detailed diagnosis ever provided for this kind of vegetation. In this scheme, *Cryptogramma crispa* stands with no real chionophilous influence, such as are found down to low altitudes in western Britain, are separated off into the *Cryptogramma-Deschampsia* community, and no division is possible among the fern snow-bed data that we have on the basis of whether *Athyrium* or *Cryptogramma* is dominant. This treatment still differs, therefore, from that proposed by Nordhagen (1943) and Gjaerevøll (1956) for Scandinavia where distinct associations, an *Athyrietum* and a *Cryptogrammetum*, were characterised. The latter was described just from western Norway, the former from throughout Scandinavia with a subdivision according to whether the associates were tall herbs or small late snow-bed plants. The *Cryptogramma-Athyrium* community has considerable overlap with both of Gjaerevøll's (1956) associations, which experience similar snow-lie and edaphic conditions. Although both Gjaerevøll (1956) and Nordhagen (1943) placed their vegetation types among the late snow-beds of the Salicetalia herbaceae, a better locus for British stands of this kind seems to be among the more oligotrophic of the tall-herb and fern vegetation in the Cicerbition alpinae.

Floristic table U18

Cryptogramma crispa	V (4–7)	*Dicranum majus*	III (1–3)
Deschampsia cespitosa	V (2–4)	*Plagiothecium undulatum*	III (1–3)
Barbilophozia floerkii	V (1–4)	*Diplophyllum albicans*	III (1–4)
Athyrium distentifolium	V (2–8)	*Pleurozium schreberi*	III (1–3)
Galium saxatile	V (1–3)	*Nardus stricta*	III (1–3)
Deschampsia flexuosa	V (1–4)	*Oxalis acetosella*	III (1–3)
Alchemilla alpina	V (1–4)	*Plagiothecium denticulatum*	II (1–3)
Rhytidiadelphus loreus	V (1–4)	*Racomitrium canescens*	II (1–3)
Polytrichum alpinum	V (1–4)	*Thelypteris phegopteris*	II (2–3)
Hypnum callichroum	IV (1–4)	*Cladonia gracilis*	II (1–3)
Saxifraga stellaris	IV (1–3)	*Blechnum spicant*	II (2–4)
Cladonia bellidiflora	IV (1–3)	*Plagiothecium sylvaticum*	II (1–3)
Kiaeria starkei	IV (1–4)	*Cerastium fontanum*	II (1–2)
Rumex acetosa	IV (1–3)	*Epilobium anagallidifolium*	II (1–2)
Hylocomium splendens	IV (2–4)	*Rhizomnium punctatum*	II (2–4)
Viola palustris	IV (1–3)	*Agrostis capillaris*	II (2–3)
Racomitrium lanuginosum	III (1–4)	*Dicranum scoparium*	II (1–4)
Rhytidiadelphus squarrosus	III (1–4)	*Juncus trifidus*	II (2–3)
Dicranum fuscescens	III (1–6)	*Eurhynchium praelongum*	II (2–3)
Omalotheca supina	III (1–3)	*Lophozia sudetica*	II (2–3)
		Gymnocarpium dryopteris	II (3)

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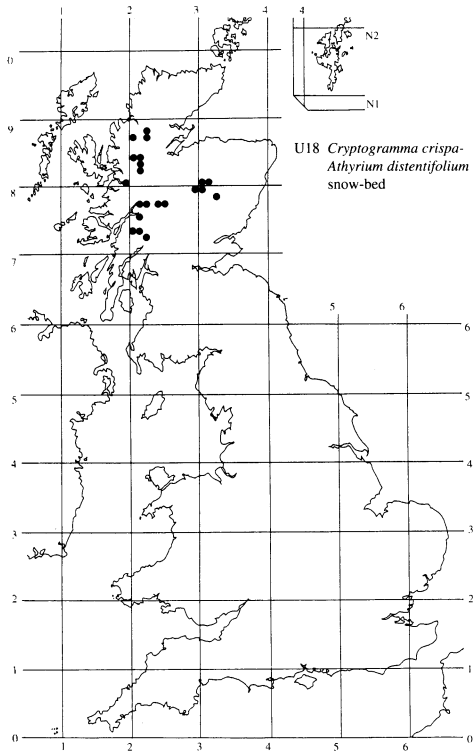
Floristic table U18 (*cont.*)

Dryopteris dilatata	II (2)
Carex bigelowii	II (1–3)
Peltigera canina	II (1–2)
Anastrepta orcadensis	II (1–3)
Pogonatum urnigerum	II (1–2)
Huperzia selago	II (1–3)
Vaccinium myrtillus	II (2)
Anthoxanthum odoratum	II (3)
Sphagnum capillifolium	II (2–4)
Hylocomium umbratum	II (3–4)
Oligotrichum hercynicum	II (1–3)
Luzula spicata	II (1)
Pohlia nutans	II (1–2)
Polytrichum sexangulare	I (1)
Polytrichum piliferum	I (1)
Sibbaldia procumbens	I (2)
Lophozia obtusa	I (1)
Drepanocladus uncinatus	I (1)
Tritomaria quinquedentata	I (2)
Oxyria digyna	I (2)
Racomitrium fasciculare	I (3)
Ptilidium ciliare	I (4)
Thelypteris limbosperma	I (3)
Number of samples	8
Number of species/sample	32 (22–43)
Vegetation height (cm)	13 (8–18)
Vegetation cover (%)	71 (50–100)
Altitude (m)	967 (823–1082)
Slope (°)	32 (20–50)



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