U21
Cryptogramma crispa-Deschampsia flexuosa community

Synonymy
Cryptogramma crispa vegetation Leach 1930; *Cryptogrammetum crispae* Jenny-Lips 1930.

Constant species
Cryptogramma crispa, Deschampsia flexuosa, Festuca ovina, Galium saxatile, Campylopus flexuosus, Polytrichum formosum.

Rare species
Cryptogramma crispa.

Physiognomy
The *Cryptogramma crispa-Deschampsia flexuosa* community comprises pioneer vegetation of screes and tumbled boulders in which *Cryptogramma crispa* is the most abundant plant. Young stands have very few associates, beyond the patches of encrusting lithophytes such as *Racomitrium fasciculare* and *Andreaea rupestris* and cushions of bryophytes like *Diplophyllum albicans, Racomitrium lanuginosum* and *R. heterostichum* which are early invaders of the fragments of detritus that collect among the talus. These latter, particularly *Diplophyllum*, appear to provide a congenial surface for the development of the fern prothalli and sporophytes and, if there is some stability to the substrate, *Cryptogramma* can grow into clumps more than a metre or so across, the bright green patches of the curled and crispy foliage being distinct even from a distance. It is in this stage of growth, as the fronds decay each autumn but remain attached to the rhizomes accumulating a mass of root-bound humus, that the associated flora begins to develop, though many stands have a somewhat fragmentary composition, particularly where there is periodic shifting of the talus.

Among these plants, small tufts of fine-leaved grasses such as *Deschampsia flexuosa* and *Festuca ovina* (including *F. vivipara* at higher altitudes) are very common and sometimes moderately abundant, with more occasionally a little *Nardus stricta, Anthoxanthum odoratum, Agrostis capillaris* and *A. canina*. *Galium saxatile* is constant and can form quite extensive patches and there are frequent individuals of *Oxalis acetosella* and *Huperzia selago* with, less commonly, *Diphasium alpinum, Rumex acetosella, Digitalis purpurea* and *Potentilla erecta*. Some stands are invaded by *Vaccinium myrtillus, Calluna vulgaris* or *Erica cinerea* but the cover of these sub-shrubs is never more than locally abundant.

Quite an extensive and varied bryophyte flora can develop among the patches of this vegetation subsequent to establishment of the fern, particularly where there is abundant shelter and shade. The most frequent species, apart from the early invaders, *Diplophyllum* and *Racomitrium* spp., are *Campylopus paradoxus, Polytrichum formosum, Dicranum scoparium, D. majus, Hypnum cupressiforme, Pleurozium schreberi, Rhytidiadelphus loreus, Polytrichum alpinum, Pogonatum urnigerum, Plagiothecium undulatum, Ptilidium ciliare, Isopterygium elegans, Lophozia ventricosa* and *Barbilophozia floerkii*. Some lichens can also be patchily abundant, with occasional records for *Cladonia impexa, C. squamosa, C. uncialis* and *C. furcata*.

Habitat
The *Cryptogramma-Deschampsia* community is a colonising vegetation of screes and boulder fields composed of hard, acidic rocks at moderate altitudes through the cool and more oceanic mountains of western and northern Britain. In regions where it is most abundant, fragmentary stands can also be found on walls, bridges and buildings made of suitable rocks.

Cryptogramma is a relatively oceanic plant (Page 1982), concentrated in Britain in those mountain ranges where there is some protection against extremes of cold and desiccation. At higher altitudes, and particularly in drier regions like the east-central Highlands, long snow-lie is of great importance in providing locally suitable habitats and, in such situations, the fern is invariably found as a member of the chionophilous *Cryptogramma-Athyrium* community. Below about 600 m, however, *Cryptogramma* is characteristic of areas with a fairly equable temperature regime and a generally humid climate. Most stands of the community experience cool summers, with mean annual maxima of 26 °C

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or less (Conolly & Dahl 1970) and annual accumulated temperatures of around 1100 day-degrees C or less (Page 1982). The winters are quite cold, with the fern becoming very scarce in the very mild south-west of Britain, but conditions are not unduly harsh: even in the hills of the north-west of Scotland, late frosts are not very frequent, particularly where *Cryptogramma* comes down to just 100 m or so above sea-level along the Ross-shire coast. Throughout this climatic zone, which includes mid and north Wales, the Pennines and Lake District, the Cheviots, the Southern Uplands and most of the Highlands, precipitation is high, mostly above 1600 mm yr^{-1} (*Climatological Atlas* 1962) with over 160 wet days annually (Ratcliffe 1968), and the typical sheltered bouldery topography further enhances local humidity.

Cryptogramma is further confined within these regions to sites with bare, rocky ground weathered from hard, acidic exposures. It is strongly calcifuge, though quite a diversity of rock types provide congenial chemical and physical conditions for its invasion. It is particularly associated with screes and boulder fields of various sandstones and grits, for example, and of granites and slates, but also occurs on quartzose granulites and schists, gneiss and some shales. It generally avoids smaller, shifting talus, such as characterises the active upper and central parts of screes, being better able to thrive along the flanks and lower edges of fans of detritus where there is greater stability, or to get a hold below large boulders where these hold up or divert moving rock fragments. The bottoms of cliffs can provide similar sheltered situations and, from such places, *Cryptogramma* can spread on to ledges. Artificial rocky habitats, like banks and boundary walls, bridges or buildings, provided they are built of suitable materials, can also offer crevices for invasion, although the development of the associated flora tends to be very fragmentary there.

In such open, rocky habitats, *Cryptogramma* can be an early coloniser, though it is probably greatly assisted in its establishment by the accumulation of appreciable amounts of wind-blown detritus and rock fragments, or the growth of bryophyte cushions in sheltered crevices and, certainly, for development of the prothallus and sporophyte, protection from wind and sun are essential. Subsequent enrichment of the species assemblage is very dependent on the accumulation of fern humus itself and, though the fronds die down quickly with the first sharp frosts of autumn, the slow incorporation of the litter results in the formation of a mass of raw mor, generally of pH 4–5, which is but slowly integrated with the rotting mineral material. The particular composition of at least the early stages in the development of the community is probably strongly influenced by chance invasion of the associates, but these are all plants tolerant of base-poor, oligotrophic, humic soils, with a persistent lithophyte element continuing to colonise the bare rock surfaces. Grasses that can grow as small tussocks, such as *D. flexuosa*, *F. ovina*, *Nardus*, *Anthoxanthum* and *Agrostis* spp., fare especially well, as do chamaephyte and rhizomatous herbs like *G. saxatile*, *H. selago*, *Diphasium alpinum* and *O. acetosella*, together with a range of more calcifuge bryophytes. Ericoid subshrubs can also gain a hold, though these may presage further successional development to some kind of heath. Around the margins of screes, rhizomatous plants can be especially prominent as invaders of established *Cryptogramma-Deschampsia* stands, with *V. myrtillus* and, near deeper colluvial soils, *Pteridium aquilinum*, especially widespread. At the but moderate altitudes characteristic of this community, an Arctic-Alpine influence in the vegetation is scarcely visible, a marked contrast with *Cryptogramma-Athyrium* beds.

The structural organisation of the vegetation is strongly controlled by the disposition of spaces among the rock fragments and the stability of the mass of detritus. Many stands remain as slowly-expanding but discrete patches studded across the surface of screes and bouldery hillsides, but particularly striking patterns can develop where stands extend downslope in the shelter of large blocks of talus or from the bases of cliffs, a phenomenon well described from the Lake District by Leach (1930). Then, actively-moving material on either side limits the vegetation laterally, attenuates the stand below and tends to build up a little alongside the stripe, leaving it in a shallow depression. More drastic movements of debris can leave stands partly covered with rock or pulled apart into fragments, able to re-establish themselves if stability is restored.

Eminently suitable sites for the development of the *Cryptogramma-Deschampsia* community on the gritstone screes of the southern Pennines may have lost this community through atmospheric pollution, something to which the fern may be especially vulnerable along the southern fringe of its British distribution.

Zonation and succession

The *Cryptogramma-Deschampsia* community is typically found with lithophyte vegetation and heaths in the early stages of succession on talus and boulders of hard, acidic rocks. The progression of the sere can be set back in any stage by shifting of the detritus but, even where it advances far, the influence of grazing or burning generally prevents the establishment of forest, deflecting the succession to plagioclimax pasture or heath, which communities now usually occupy the bulk of the stabilised slopes around stands of the community.

Epilithic lichen assemblages, generally grouped in the Leprarion chlorinae or Lecideion tumidae alliances according to whether they comprise shade or sun species (James *et al.* 1977), are often the first colonisers of the surfaces of the kinds of rocks among which the *Cryptogramma-Deschampsia* community eventually develops,

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and they can persist in mosaics with this vegetation over any remaining exposed rocks. Then, there are rock-surface bryophytes, notably *Andreaea rupestris* and *Racomitrium fasciculare*, which also make an early appearance though these do not seem to provide a congenial surface for subsequent invaders and cannot really be considered to play an active part in succession. They may, however, persist long. Other mosses, such as *Racomitrium heterostichum* and *Dicranella heteromalla*, may play a subsidiary role in helping to disintegrate mineral material but it is only with the appearance of the pioneers of sheltered crevices, notably *Diplophyllum*, that the progression to the *Cryptogramma-Deschampsia* community can be really seen as initiated.

Developments beyond the establishment of the community depend first on the stability of the substrate and, indeed, in many cases, the sere is repeatedly set back by slipping of the talus or tumbling of boulders on to the vegetation. But where this does not happen, the natural successor to the *Cryptogramma-Deschampsia* community is probably some kind of heath. *Calluna*, *E. cinerea* and *V. myrtillus* can all invade stabilised patches of this vegetation and, where competition from these and vigorously growing grasses becomes severe, *Cryptogramma* suffers and eventually dies out. Towards lower altitudes and particularly in more oceanic regions, the *Calluna-Erica* heath can succeed the fern vegetation with the *Calluna-Vaccinium* heath favouring the cooler, more humid environment of higher altitudes and shaded aspects, the *Vaccinium-Deschampsia* heath becoming important towards the uppermost limit of this community's range. Where such vegetation types develop among existing *Cryptogramma-Deschampsia* stands, species such as *D. flexuosa*, *F. ovina*, *Anthoxanthum*, *Agrostis* spp., *Nardus* and *Galium saxatile* all provide a strong floristic continuity, but the sub-shrubs become dominant and among them there is often an increase in bulky pleurocarpous mosses or lichens at the expense of the smaller acrocarps represented among the fern patches.

Within the forest zone, the natural climax of such a succession is the *Quercus-Betula-Dicranum* woodland and young saplings of the characteristic tree species of this community, *Betula pubescens* and *Sorbus aucuparia* in particular, with *Quercus petraea* occurring more rarely, can sometimes be found invading stable stretches of scree. This is a rare phenomenon, though, partly because of the scarcity of seed-parents over many upland slopes, but also because of the virtually ubiquitous occurrence of grazing. Subsequent succession beyond the *Cryptogramma-Deschampsia* community, then, is likely to be deflected to swards like the *Festuca-Agrostis-Galium* grassland, where the fine-leaved grass associates of the fern beds become the dominant element in the vegetation. Or, where burning also plays some part in the land management, *Calluna*-dominated stands of the heaths may be more or less permanently maintained and mosaics of such grassland and heaths often make up much of the closed vegetation around open screes where the *Cryptogramma-Deschampsia* community persists. A further important element in such patterns is *Pteridium-Galium* vegetation, a very widespread community now where colluvial soils have been cleared of forest through the upland fringes, and one which is able to invade up screes where these are reasonably stable, overwhelming such stands of *Cryptogramma-Deschampsia* vegetation as occur there.

Distribution

The community is found throughout the range of *Cryptogramma* below altitudes of about 600 m, being replaced on higher ground by the *Cryptogramma-Athyrium* vegetation.

Affinities

The *Cryptogramma-Deschampsia* community contains the kind of pioneer calcifuge fern vegetation that fell outside the scope of McVean & Ratcliffe's (1962) enquiry, but which was a central element in the successional stages described from acid screes in the Lake District by Leach (1930). In phytosociological schemes, *Cryptogramma* is regarded as a character species of the Androsacetalia alpinae, pioneer vegetation of siliceous screes (Ellenberg 1978), although central European stands have a much more obvious montane element than is found here.

Floristic table U21

Cryptogramma crispa	V (4–6)	*Vaccinium myrtillus*	III (1–7)
Deschampsia flexuosa	V (1–5)	*Oxalis acetosella*	III (1–3)
Festuca ovina	V (1–4)	*Huperzia selago*	III (1–2)
Galium saxatile	V (1–4)	*Dicranum scoparium*	III (1–3)
Campylopus paradoxus	IV (1–4)	*Hypnum cupressiforme*	III (1–4)
Polytrichum formosum	IV (1–4)	*Barbilophozia floerkii*	II (1–3)
Diplophyllum albicans	III (1–4)	*Pleurozium schreberi*	II (1–3)
Racomitrium lanuginosum	III (1–4)	*Lophozia ventricosa*	II (1–2)
Nardus stricta	III (1–4)	*Racomitrium fasciculare*	II (1–3)

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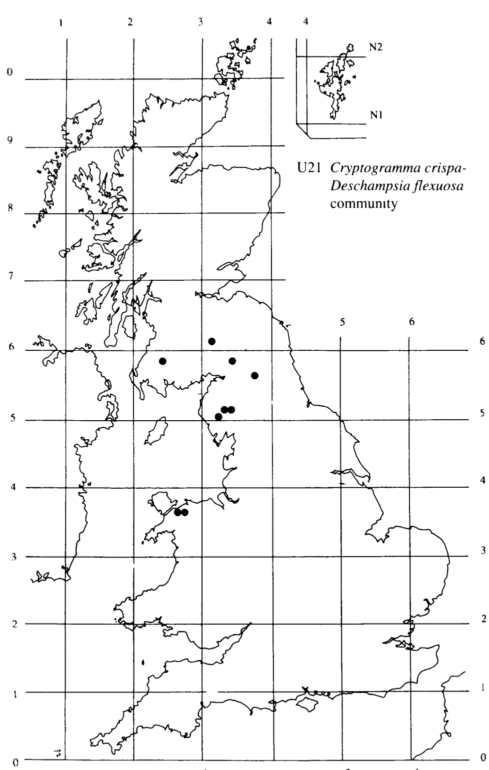
Floristic table U21 (*cont.*)

Anthoxanthum odoratum	II (1–3)
Cladonia impexa	II (1–4)
Cladonia squamosa	II (1–3)
Calluna vulgaris	II (1–5)
Rhytidiadelphus loreus	II (1–3)
Polytrichum alpinum	II (1–3)
Pogonatum urnigerum	II (1–3)
Dicranum majus	II (1–3)
Plagiothecium undulatum	II (1–3)
Agrostis capillaris	II (4)
Ptilidium ciliare	II (1–2)
Agrostis canina	II (1–3)
Cladonia uncialis	II (1–2)
Isopterygium elegans	II (1–3)
Erica cinerea	II (1–4)
Diphasium alpinum	II (1–2)
Racomitrium heterostichum	II (2)
Rhytidiadelphus squarrosus	I (1)
Pohlia nutans	I (1)
Rumex acetosella	I (1)
Nardia scalaris	I (1)
Dicranella heteromalla	I (1)
Thelypteris limbosperma	I (4)
Sphagnum subnitens	I (1)
Mnium hornum	I (1)
Polytrichum alpestre	I (1)
Cladonia furcata	I (1)
Cornicularia aculeata	I (1)
Isothecium myosuroides	I (1)
Digitalis purpurea	I (1)
Empetrum nigrum	I (5)
Grimmia donniana	I (1)
Polytrichum juniperinum	I (1)
Potentilla erecta	I (1)
Cephaloziella hampeana	I (1)
Cephalozia bicuspidata	I (1)
Number of samples	8
Number of species/sample	20 (8–31)
Vegetation height (cm)	21 (9–30)
Vegetation cover (%)	47 (10–70)
Altitude (m)	474 (255–620)
Slope (°)	50 (25–80)



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