mula 2. Thus, if the methods presented in this paper are correctly employed, a litter estimate will be needed for method 1.

3. 7. Estimating consumption

The extent to which lichen stands are grazed by reindeer varies with the time and place. Nevertheless, it is theoretically possible to estimate consumption. The observations should include the biomass of the grazed stand over several years, the net production rate of the biomass and its litter formation rate. It should then be possible to calculate the consumption rate. The model treatment similar to those of OLSON (1963) or GORE & OLSON (1968) might be useful.

The following simpler method could also be tried: the biomass of a lichen pasture is measured late in autumn when the lichen growth is just stopping; the following biomass measurement is made early in spring before considerable growth has occurred. Consumption (G) is calculated simply with the following formula:

(7) $G \approx B_a - B_s$,

where B_a = biomass in autumn,
B_s = biomass in spring.

The possible errors of this method include the following: if the true living biomass is measured, the dying of the lowest living internode in spring decreases the biomass. But in the grazed stands the lichens are generally so young that this error is not serious, though it should be corrected. The area to be studied in this way should be rather heavily grazed. Otherwise random variation can produce misleading results. In addition, when using this method, one should be sure that the grazing and trampling happens only in winter and that the growth early in spring when the snow is melting does not invalidate the result. Growing in boxes under snow in enclosures may be expected to give good correction coefficients. If sampling is continued for many years the result will be more reliable, and, in addition, some useful material for other estimates may be obtained.

Acknowledgements. The author gratefully acknowledges receiving mathematical advice from Mr. JUSSI TAMMISOLA, M. Sc. The work was supported financially by the Finnish State Council of Natural Sciences. The author is indebted to Mrs. ANNA A. DAMSTRÖM, M. A., for correcting the English language.

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Rep. Kevo Subarctic Res. Stat. 7, 47—56. 1971

Studies on the morphological variation of the lichen Cladonia uncialis

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Received July 5, 1970 Printed March 25, 1971

Abstract

KÄRENLAMPI, LAURI & PELKONEN, MIRJA. (Botany Dept., Univ., Turku 50, Finland) Studies on the morphological variation of the lichen Cladonia uncialis. REP KEVO SUBARCTIC RES STAT 7. 47—56. Illus. 1971. — Morphological observations were made on the material of 29 Finnish mass collections. In addition 961 herbarium specimens were seen. The following characters were studied: branching pattern, length/breadth ratio of internodes, percentage of axils with perforations, percentage area of algal layer, and presence or absence of pycnidia and apothecia. An evaluation of these characters was attempted. It appeared most realistic to consider the variation in terms of the *deme* terminology, and different ecophenoclinodemes were recognized. In addition, the following nomenclatural solution was proposed: *Cladonia uncialis* (L.) Wigg. var. *uncialis* (branching predominantly tri- to tetrachotomous or representing higher levels of polytomy, mainly continental in distribution), and *C. uncialis* (L.) Wigg. var. *dicraea* Kär. & Pelk., n. comb. (branching predominantly dichotomous, mainly maritime in distribution).

This paper is a continuation of the introductory report of KÄRENLAMPI (1964). Most of the observations for the present work were made by the junior author. Attention is paid to characters of *Cladonia uncialis,* with the aim of assessing their taxonomic value. An attempt is made to discover whether any discontinuities exist in their distribution and whether there are any correlations between them. In addition, the regional distribution of the characters is considered. Finally, a taxonomic decision is attempted.

1. Material and methods

The material of this study included 29 collections from different localities in Finland. These comprised 9—27 specimens each. Every specimen consisted of a tuft of numerous podetia, which evidently belonged to one clone and were generally very uniform. 13 of the collections came from the southwestern archipelago, 4 from the area between the archipelago and the more continental interior, 9 from the interior and 3 from Lapland (the map in the Fig. 5 shows the collection localities). The total number of specimens measured amounts 355.

In addition 961 herbarium specimens were seen. They included specimens in TUR (Turku), H (Helsinki) and GB (Göteborg).

The morphological observations were made on the material of the collections. From every specimen two representative podetia were selected. 3—4 of the topmost internodes were examined. The presence or absence of a perforation at the axil was observed and the number of branches per node counted. The length and thickness (diameter) of the internodes were measured under a binocular microscope, and the ratio of the length to the thickness was used as a character. The youngest internode was generally not considered. In addition, the percentage area of the green algal layer was estimated and the presence or absence of pycnidia and apothecia was noted. All this was done using moistened lichens. The measurements of the length and breadth of the ascospores were made in water.

2. Results

2.1. *Number of branches*

Fig. 1 shows the distribution of the specimens according to the number of branches per node. The material from the archipelago (A) has very low numbers of branches and the range of variation is narrow. The material from the interior (C) has a much higher mean and the range of variation is wide. The material from the zone between the archipelago and the continental interior (B) seems to be partly similar to that of archipelago and partly intermediate between the populations of the archipelago and the interior. The material from Lapland (D) seems to have its own distribution pattern with a relatively low mean and a narrow range of variation.

The analysis of variance (nested classification) showed that the differences between the populations and the differences between the areas are both significant at the 0.1 % level (see Table 1).

Table 1. Results of the analysis of variance of the characters which can be parametrically tested.

	Differences between populations			Differences between the four areas		
	f_1	f_2	F	f_1	f_2	F
Number of branches	25	321	7.60***	3	25	235.4 ***
Length/thickness ratio	»	»	2.70***	»	»	30.85***
Area of algal layer	»	»	6.22***	»	»	11.64***

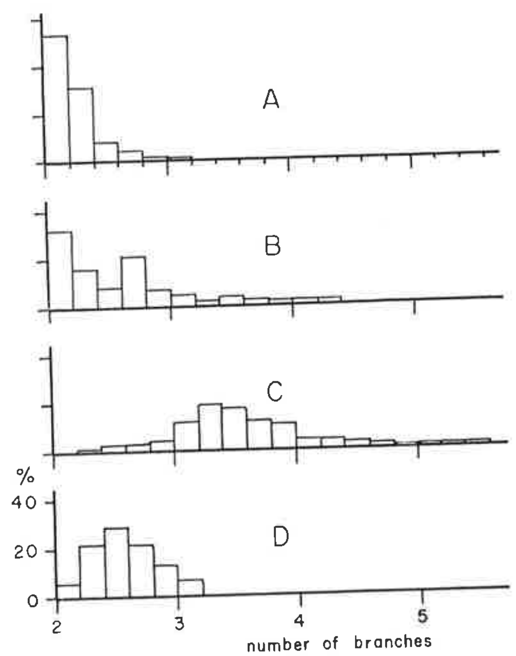


Fig. 1. Distribution of the material in relation to the number of branches. (A, archipelago, B: maritime zone between archipelago and continental interior, C: interior, D: Lapland.)

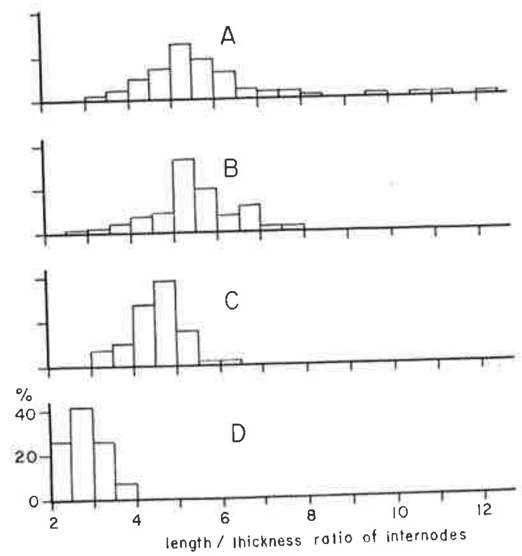


Fig. 2. Distribution of material in relation to the length/thickness ratio of the internodes. (A: archipelago, B: maritime zone between archipelago and continental interior, C: interior, D: Lapland.)

When all the material of the collections is united, no discontinuity can be found in the distribution curve. The variation must therefore be considered clinal.

2.2. *Length to thickness ratio of internodes*

Fig. 2 shows the results of the measurements of the length to thickness ratio of the internodes. The material from the archipelago (A) has quite a high mean and a wide range of variation. Very long, slender podetia are sometimes found. The interior of Finland (C) has a lower mean and a narrower range of variation. The material from the zone between the archipelago and the continental interior (B) resembles that of the archipelago. The material from Lapland (D) has a distinctive frequency distribution, the lichens having very short, thick internodes.

The analysis of variance showed that the differences between the populations and the differences between the areas are both significant at the 0.1 % level (see Table 1).

When all the material of the collections is united, some discontinuity is found, a gap existing between the material from Lapland and that from the other areas. This may be the effect of the long distance between Lapland and the other collection sites. This character also seems to display clinal variation.

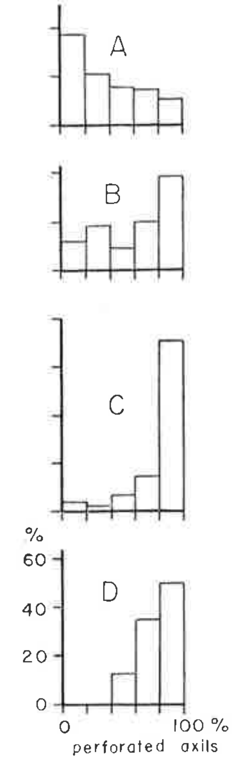
2.3. *Perforation at axil*

Fig. 3 shows the results of the observations of the perforations at the axils. In the material from the archipelago (A) the axils are very often non-perforate, but in 10 % of the specimens more than 80 % of the axils were found to be perforate. The material from the interior (C) has a more discontinuous distribution, because the proportion of the class with the greatest percentage of perforated axils is very high. The material from maritime zone (B) seems to be more like that of the more continental interior, but, as in the archipelago, specimens with a small percentage of perforated axils are common, and there are even fewer specimens with 40—60 per cent than in the archipelago. The material from Lapland (D) again has its own rather distinctive distribution pattern.

This character also seems to display clinal variation.

2.4. *Algal layer area percentage*

Fig. 4 shows the percentages of the areas of the specimens covered by the algal layer. The material from the archipelago (A) has the highest mean. The others form a series with decreasing means. No differences are found in the range of variation. The specimens were collected at the same time of the year, at the height of summer, and no differences should be caused by possible seasonal variations in the algal content.



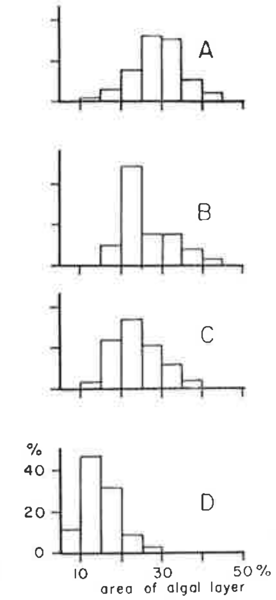


Fig. 3 (left). Distribution of material in relation to the percentage of perforated axils.

Fig. 4 (right). Distribution of material in relation to the percentage area of algal layer. (A: archipelago, B: zone between arcipelago and continent, C: Central Finland, D: Lapland.)

The analysis of variance showed that the differences between the populations and the differences between the areas are both significant at the 0.1 % level (see Table 1). When all the material is united, no discontinuity can be found in the distribution curve. The variation of this character seems to be clinal.

2.5. *Apothecia and pycnidia*

The distributions of the specimens according to the presence or absence of apothecia and pycnidia are shown in Table 2. It is very clearly seen that the percentage of lichens bearing pycnidia is correlated with the percentage of lichens bearing apothecia. Every specimen with apothecia was found to bear pycnidia, too. It seems clear that the pycnidium and the apothecium represent successive developmental stages.

Table 2. Presence of pycnidia and apothecia in the four populations of *Cladonia uncialis*.

	Percentage of specimens with pycnidia	Percentage of specimens with apothecia
Archipelago	34.4	1.4
Archipelago — interior	41.4	2.8
Interior	100.0	10.0
Lapland	100.0	29.0

Some measurements were made of the ascospores, and the results are shown in Table 3. No significant differences could be found. It was difficult to find spores to measure in the material from the archipelago, because many of the rare apothecia contained no spores.

Table 3. Means of the ascospore measurements in *Cladonia uncialis*.

	Mean length in µm	Mean breadth in µm
Archipelago	13.4	3.5
Archipelago — interior	13.0	3.8
Interior	13.8	3.6
Lapland	13.4	3.5
—»—	13.4	4.0

2.6. »*Goodness*» *of the observed characters*

According to Davis & Heywood (1965: 119) the »good» characters are those that (1) are not subject to wide variation within the samples being considered; (2) do not have a high intrinsic genetic variability; (3) are not easily susceptible to environmental modification; (4) show consistency.

(1) Some of the observed characters show wide variation, e.g. the number of branches per node in the populations from the interior of Finland and the length to thickness ratio of the internodes in the populations from the archipelago. Nevertheless, the analysis of variance showed that there are very significant differences between the populations and areas. We can conclude that in this respect the characters are, at least, not »bad». This conclusion is not inconsistent with the fact that the variation of the characters is considered to be clinal.

(2) The second criterion is difficult to apply, but it must be regarded as possible that the high variability of the characters of some populations, e.g. of the number of branches in the population from the interior (see Fig. 1 C), may be genetic in origin. The branching seems to vary between different levels of polytomy rather than between dichotomy and polytomy.

(3) As regards the susceptibility to environmental modifications, the following points may be noted. In some cases, e.g. in south-eastern Finland, specimens which were similar to the archipelago type were found growing side by side with specimens clearly belonging to the type from the interior. The environment was the same, but the lichens differed morphologically. On the other hand, in some cases the specimens clearly showed modifications. For example, in the archipelago lichens collected from moist mossy places on some rocks were found to have higher numbers of branches and higher percentages of open axils, than the specimens from dry localities, although they by no means resembled the inland type. There are also cases where the environment has been changed (transplantations, tree felling), but no resultant changes have been observed in the plants, at least not in the mature lichens, which rather begin to degenerate.

The branching pattern changes when the podetium develops. Fig. 7 shows regenerating podetia. The specimen comes from

Lapland and has evidently been broken by grazing reindeer. At this early stage the branching is clearly dichotomous, though in the mature specimens of the same area, a considerable proportion of the axils are trichotomous or display higher levels of polytomy. Moreover, at the later stages the number of branches often becomes very high, this change being correlated with the presence of apothecia. The reasons for this phenomenon are not known. The different branching trends of the early and late stages, cannot have seriously affected the results of this study, because the material generally did not include any very young or very senescent specimens.

The length/thickness ratio is probably modified by the environment. The lichens with the longest and most slender internodes were found in very dry heath forest in the archipelago. The area of the algal layer is also very probably modified by the environment.

The lack of demonstrable discontinuities in the variation of the characters might be taken to mean that it is mainly the result of environmental modification. We must remember that the choice of the collection localities was not random and that the representation of the different parts of the distribution area is not proportional. So we do not know the exact distribution of the characters.

We can conclude that the variation in the branching pattern is probably much less dependent on environmental than on genetic factors, but that the other characters are possibly not equally satisfactory in this respect.

(4) A character shows consistency when it is correlated with others. Table 4 shows the rank correlation coefficients obtained for the observed characters. It is seen that there are many very significant correlations. This emphasizes the »goodness» of the observed characters. We must, of course, bear in mind the possibility that some of the characters

Table 4. Spearman rank correlation coefficients for the observed characters.

	1	2	3	4
1. Number of branches	—			
2. Percentage of perforated axils	0.90***	—		
3. Percentage of specimens with pycnidia	0.91***	0.88***	—	
4. Percentage area of algal layer	—0.40*	—0.60***	—0.46**	—
5. Length/thickness ratio of internodes	—0.63***	—0.62***	—0.77***	0.35

may be necessary correlates, but probably there are no mathematically correlated characters in the observations: in other words, it is unlikely that the same character has been counted more than once by assessing it in a different way. However, the characters probably are, to some extent, functionally or ecologically correlated. According to Davis & Haywood (1965: 130), »in assessing overall similarity, for example, such correlated characters cannot be ignored since they contribute to general resemblance, no matter what the cause.»

2.7. *Relationships between the characters*

Table 4 presents the rank correlations between the characters. Fig. 5 gives a pictorial scatter diagram, showing the mean values of the populations and their collection localities. Fig. 6 contains drawings illustrating the variation, and the values obtained for two of the characters (number of branches per node and length/thickness ratio). It also shows the distribution of the material into different classes.

Relationships between the characters are found to be as follows: The material from the archipelago has a high length/thickness ratio (long slender podetia) and a low number of branches (nearly dichotomous); a high percentage of its surface area is covered by the algal layer, and a low percentage of the axils have perforations. The material from the interior of Finland has a lower length/thickness ratio, a higher number of branches (trichotomous to tetrachotomous); the areal percentage of the algal layer is lower and a higher percentage of the axils are perforate. The material from Lapland has a very low length/thickness ratio; the

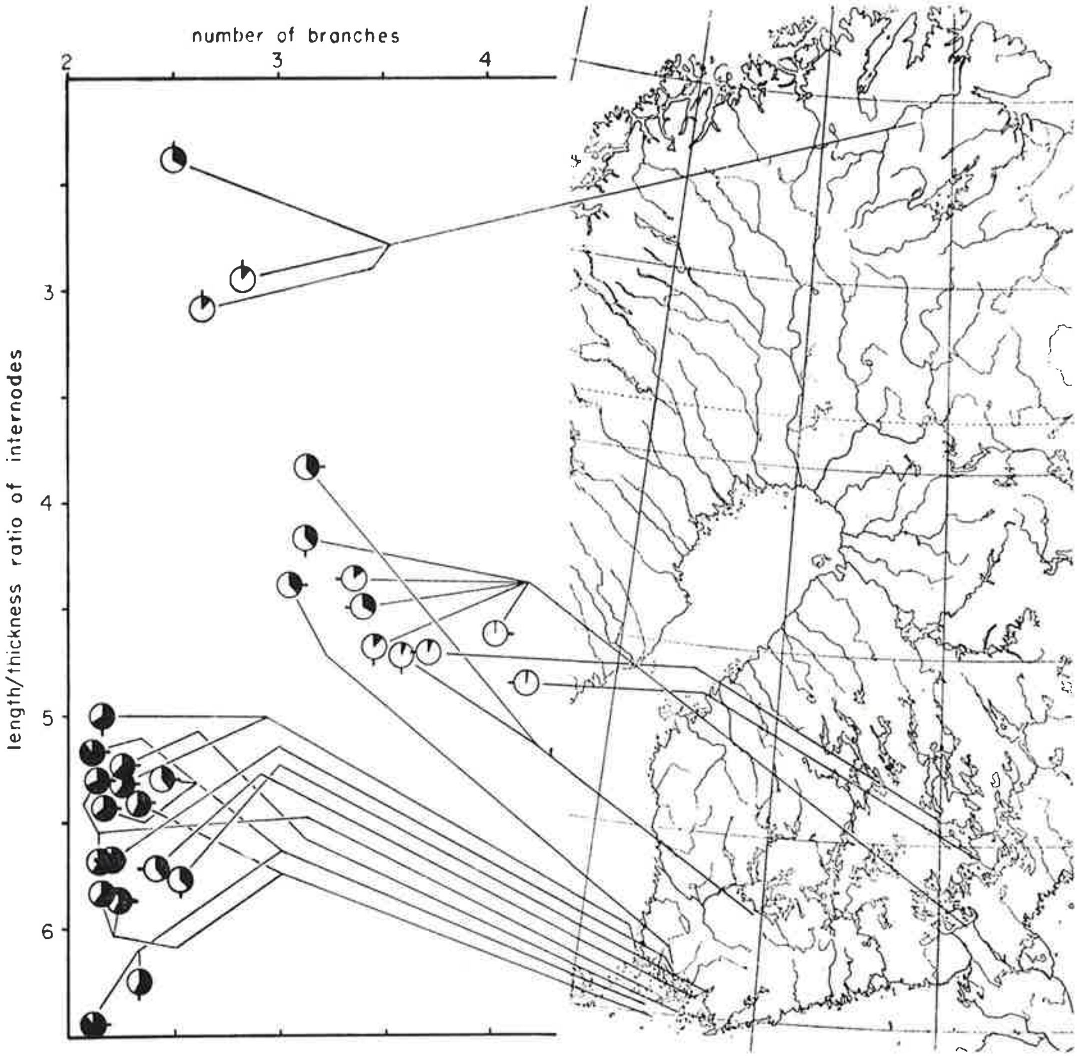


Fig. 5. Pictorial scatter diagram of the distribution and correlations of the observed characters, and map showing the collection localities of the populations. The white segments of the circles show the proportion of the perforated axils. The short line shows the percentage of the area covered by the algal layer; to the right: more than 30 per cent, downwards: 25—30 per cent, to the left: 20—25 per cent, upwards: less than 20 per cent. All values are averages of population measurements.

number of branches averages 2,5—3,0 the areal percentage of the algal layer is low and a high percentage of the axils are perforate.

The clines between these three »centres» are thought to be as follows: The cline from the archipelago to the interior of Finland is relatively discontinuous, in other words, the change is quite abrupt. The cline between the archipelago deme and the Lapponian deme does not appear to be discontinuous, judging from this material. The cline between the Lapponian and the inland deme is not thought to be discontinuous, though the selection of the sampling localities has left a gap between Lapland and the areas representing the interior of Finland.

Fig. 8 contains some additional drawings of *C. uncialis*. *a* shows a specimen displaying a high level of polytomy. *c* and *d* represent

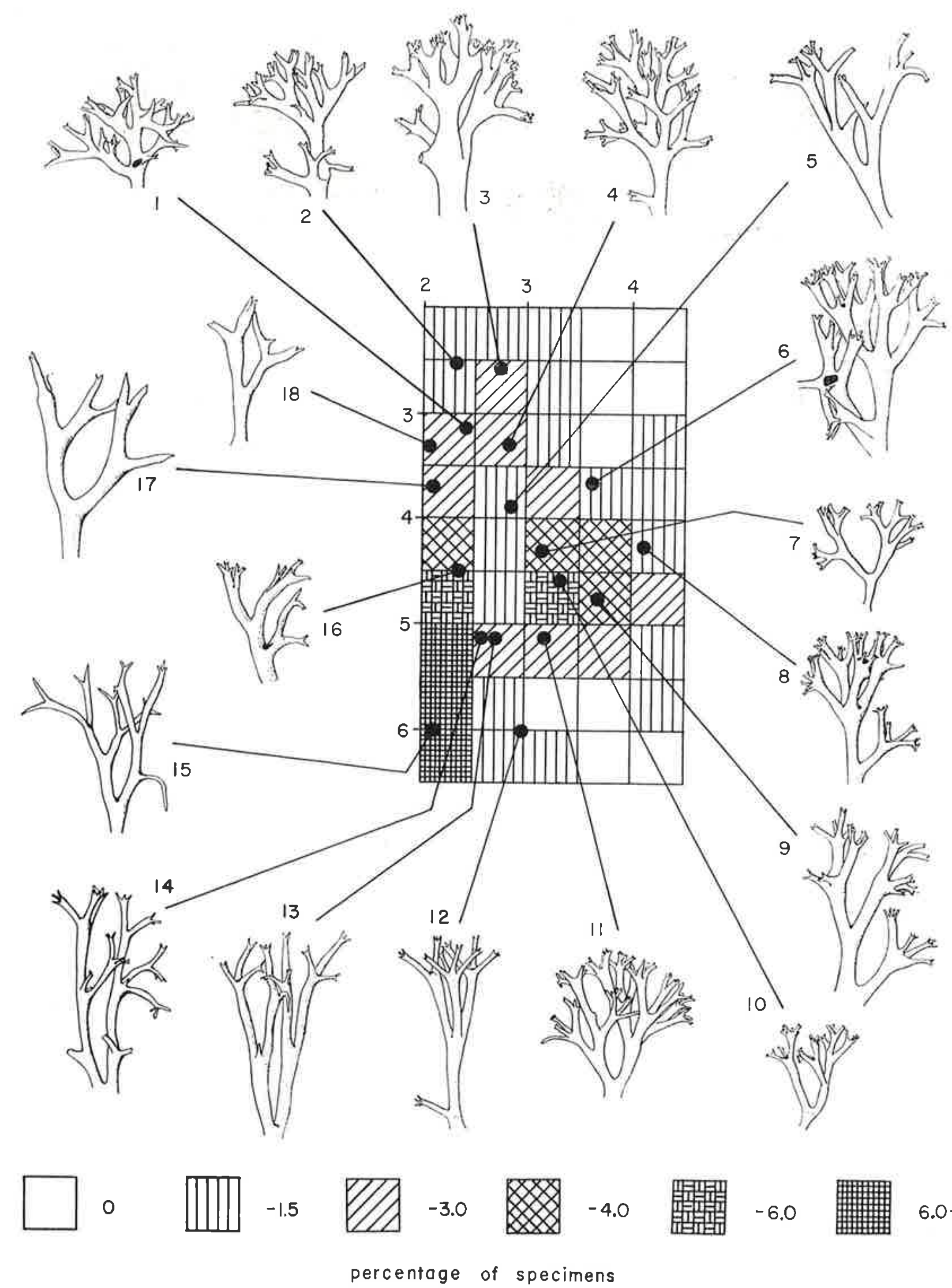


Fig. 6. The axes of the diagram in the centre are the same as those of Fig. 5. In addition the figure shows the percentages of specimens in the classes into which the range of variation is divided, and drawings of typical specimens.

the long, slender dichotomous populations from the dry heaths in the Finnish archipelago. *b* represents the form sometimes found in Arctic coastal regions.

2.7. *Variation and the environment*

The different phenoclinodemes described above have diffent environments, in other words, they are also different ecodemes. The environment of the populations from the archipelago is generally sunny and windy. They grow on open rocks or rocks in sparse pine stands.

The environment of the populations from the interior of Finland is more sheltered from the sun and wind. The localities in Lapland where the collections were made are more like localities representing the interior.

The environmental gradient between the archipelago and the interior is thought to be abrupt like the variation taking place along it. The environmental gradient between the southern interior and Lapland appears to parallel the gentle gradation in morphological characters. The populations of the open mountains in Lapland participate in the cline between the archipelago deme and the Lapponian lowland deme, and their environment lies on the gradient between the areas on the Nothern Atlantic coast and the more continental parts of Lapland.

In addition, it must be mentioned that some specimens of *Cladonia uncialis* found on lakeside rocks in the interior of Finland are similar to those from the archipelago.

The morphological differences between the specimens from maritime and more continental areas in Newfoundland (material of Dr. TEUVO AHTI) were found to be similar to those between specimens from corresponding areas in Finland. In the archipelago of Finland both the atmospheric humidity and the rainfall are relatively low, so that the dichotomous branching appears unlikely to be an adaptation to a moist maritime climate. Rather, the maritime type of morphology seems to occur in open, windy localities. It may be pointed out that the fact that a character has adaptational value need not prevent it from being useful taxonomically.

We can conclude that the observed variation is correlated with changes in the environment. The populations seem to belong to ecoclines. No attempt can be made here to identify the most important environmental factors. We only can outline the environmental complex that is connected with the phenoclinodemes.

3. Taxonomic conclusions

Figs. 6 and 7 show the pictorial scatter diagram of the studied Finnish populations and the sites of collection. The authors consider that the predominantly dichotomous group from the archipelago might constitute one taxon and the more polytomous group from the interior and Lapland constitute another taxon.

In selecting the unit of classification we must remember that the variation is not discontinuous, and therefore not all the specimens can easily be assigned to one or the other group. Secondly, the environmental conditions vary throughout the distribution areas of the groups and both are subject to environmental modification. Both groups are quite heterogeneous, and a more widely collected material might give a somewhat different result. Accordingly, we must admit that the taxonomy of *Cladonia uncialis* is

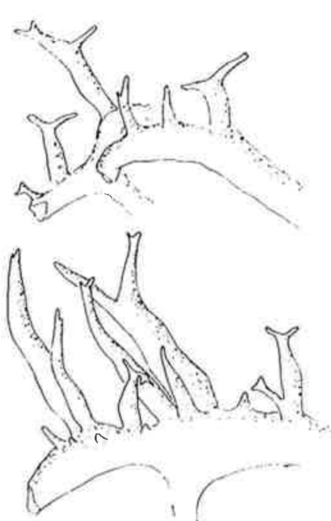


Fig. 7. Regeneration of *Cladonia uncialis.*

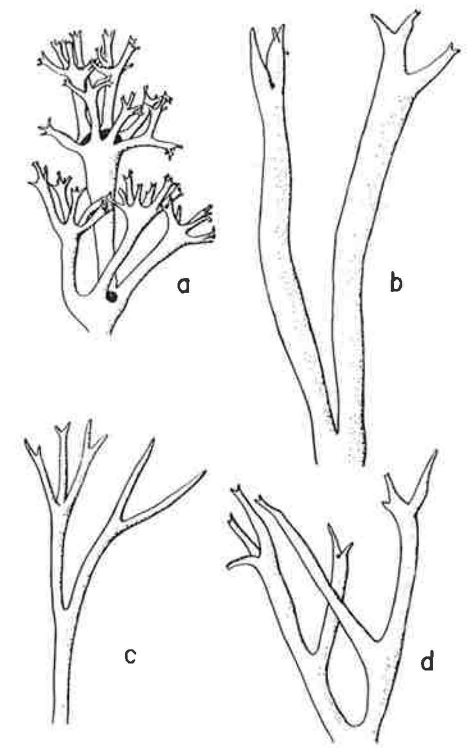


Fig. 8. Additional drawings of *Cladonia uncialis.* See text.

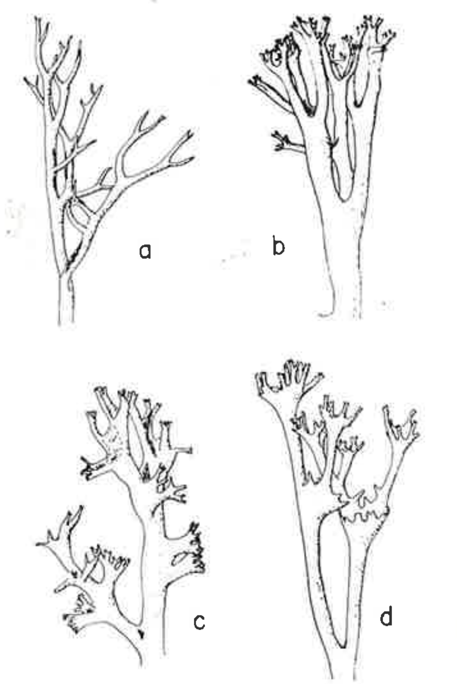


Fig. 9. Drawings of *Cladonia amaurocraea.*

still in the pioneer phase, and that varietal status is perhaps most suitable for the taxa separated.

In fact, we feel that at this stage the best solution might be to employ the *deme* terminology (see GILMOUR 1960) and to describe the groups as ecophenoclinodemes. They are ecologically and phenologically different and the variation is clinal. Further studies may throw more light on their nature and give a better basis for classification.

In any case, the following nomenclatural solution is proposed:

Cladonia uncialis (L.) Wigg. var. **uncialis** *Basionym: Lichen uncialis* L., Spec. Plant. 1153. 1753. — *Type* (lectotype): Sweden (LINN, no. 1273 × 247, seen on microfilm. No. 1273 × 246 belongs to *C. amaurocraea,* see VAINIO 1886.)

Description: Branching predominantly tricho- to tetrachotomous or displaying higher level of polytomy. Length/thickness ratio of internodes less than 5. Percentage of area covered by algal layer relatively low. Pycnidia and apothecia common.

Distribution: Cladonia uncialis is a boreal circumpolar species. *C. uncialis* var. *uncialis* inhabits continental wooded areas.

Cladonia uncialis (L.) Wigg. var. **dicraea** Kär. & Pelk., n. comb. *Basionym: Baeomyces uncialis B. dicraeus* Ach., Meth. Lich. 353. 1803. — Type (lectotype): Sweden? (H-ACH).

Description: Branching predominantly dichotomous. Length to thickness ratio more than 3. Percentage of perforated axils less than sixty. Percentage of area covered by algal layer relatively high. Pycnidia and apothecia rare.

Distribution: Unlike var. *uncialis,* var. *dicraea* occurs in the climatically maritime areas. In the mountain areas and near the northern and southern limits of the range the distributional trends are not clearly defined.

According to AHTI (1965) the British specimens belong to this variety.

Appendix: Differences between *C. uncialis* and *C. amaurocraea.*

Fig. 9 contains drawings of some typical specimens of *Cladonia amaurocraea.* The morphological differences between the Finnish material of *C. amaurocraea* and that of *C. uncialis* are as follows:

C. amaurocraea:

1. in the dichotomous podetia internodes curved in towards the centre of the axil
2. branching of more anisotomous type
3. perforations at axils not regularly rounded
4. apothecia large
5. thallus harder
6. sometimes forming cups

C. uncialis:

1. corresponding internodes straight or curved away from the centre of the axil
2. branching of more isotomous type
3. perforations rounded
4. apothecia small
5. thallus more fragile
6. always cupless.

The dubious specimens were identified with the aid of the microchemical chrystal test (*C. amaurocraea:* barbatic acid). The results are very similar to those of PIŠUT (1959), but our observations on the perforations at axils are slightly different, and characters 2 and 5 are additional to those mentioned by PIŠUT.

Acknowledgements: Our sincerest thanks are due to Dr. TEUVO AHTI for his most kind guidance. We are indebted to Mrs. ANNA A. DAMSTRÖM, M. A., for correcting the English language.

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Rep. Kevo Subarctic Res. Stat. 7, 57—59. 1971

On the abundance relations of mesofaunal groups in the ground layer of three subarctic habitats

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Received February 25, 1970 Printed March 25, 1971

Abstract

KOPONEN, SEPPO. (Zoology Dept., Univ., Turku 50, Finland) On the abundance relations of mesofaunal groups in the ground layer of three subarctic habitats. REP KEVO SUBARCTIC RES STAT 7. 57—59. Illus. 1971. — The abundance of gastropods, centipedes, harvestmen, spiders, and insects in the ground layer of pine forest, birch forest, and subalpine heath was investigated by pitfall trapping and sifting at Kevo (69° 45' N., 27° E.), Finnish Lapland, in the summer of 1969.

The productivity of three terrestrial ecosystems has been studied at Kevo Subarctic Research Station (69° 45' N., 27° E.) from 1968 onwards (International Biological Programme, see KALLIO & KÄRENLAMPI 1968). Some investigations on the mesofauna of the ground layer in these three habitats were carried out by myself in the summer of 1969. The animal groups included in this study are gastropods, centipedes, harvestmen, spiders, and insects.

1. The study habitats

The study habitats are pine forest (*Pinus silvestris*), birch forest (*Betula »tortuosa»*), and subalpine heath. The moss layer of the pine forest is patchy and thin (*Pleurozium schreberi, Dicranum fuscescens,* and *Ptilidium ciliare*), and there are also needle litter and some lichens (*Cladonia alpesris, Cl. mitis,* and *Stereocaulon paschale*). The moss layer of the birch forest is very thick (10—15 cm) and consists of *Pleurozium schreberi* and *Hylocomium splendens.* There is also some birch leaf litter. The ground layer of he subalpine heath is very sparse. *Stereocaulon paschale* is dominant in the study area and there are also some occurrences of *Dicranum fuscescens, Arctostaphylos alpina,* and *Empetrum hermaphroditum.* The pine forest lies 90 m above sea level, the birch forest 130 m, and the subalpine heath 330 m. The surface of Lake Kevojärvi is 75 m above sea level.

2. Methods and material

The main collecting method was pitfall trapping. Ethylene glycol was used in the traps with a cleaning agent (»Raino») to decrease the great surface tension of the glycol. In each study area there were 20 traps about 2—3 m apart. The trapping periods were as follows:

pine forest	July 2 — September 8 (1969)
birch forest	June 20 — September 8
subalpine heath	July 1 — September 10

Since pitfall trapping depends on the active locomotion of the animals, the results of this method reveal the activity relations of the animal groups studied rather than their numerical abundance (cf. e.g. BALOGH 1958: 231). However, the activity of different animal groups, especially the carnivorous ones, is a rather good indicator of their importance in the ecosystem. The moss and litter layer of quadrats chosen in the pine and birch forests was sifted in July 1969. The size of the quadrats was 25 x 25 cm.

The total material of this study consists of 6689 individuals, 6473 caught by traps and 216 by sifting.