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geography, and ecology of the
piliferous *Campylopus* species
in the
Netherlands and N. W. Germany

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**NOTES ON THE TAXONOMY, GEOGRAPHY, AND
ECOLOGY OF THE PILIFEROUS *CAMPYLOPUS*
SPECIES IN THE NETHERLANDS AND
N.W. GERMANY**

by

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INTRODUCTION

On July 1, 1962 mr. A. MABELIS collected material of a *Campylopus* near Tongeren (Neth.), which was then identified by the present author as *C. introflexus* Brid., a species not previously recorded for the Netherlands. On July 21, 1962 the locality was revisited by A. MABELIS and the author and a number of vegetation records were made. A second Dutch locality was discovered by the author at Kraloo on 9-5-1963 and a third at Kampina by A. MABELIS, which was visited again by mr. A. MABELIS and the author on September 21, 1963. In all stations vegetation records have been made.

At that time I was ignorant of the fact that GIACOMINI (1955) had reestablished the existence of two closely related species, which since 1869 had been considered synonymous, viz. the mainly Africo-Indian *C. polytrichoides* de Not., also occurring in S. and W. Europe, and the American-Australian species *C. introflexus* Brid., with

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a single European station in Finistère (Brittanny, France). RICHARDS (1963) added many British localities of *C. introflexus*. Both species occur in Great-Britain. In view of these publications the Dutch specimens of "*introflexus*" have been reexamined with the result that the material from Kraloo and Kampina indeed belongs to *C. introflexus*, the Tongeren specimens to *C. polytrichoides*. This means that in a short interval two species of the same genus have been added to the Dutch moss flora. For *C. polytrichoides* it also means an extension of its known natural area in Europe, Tongeren being its northernmost locality on the continent. As to *C. introflexus*, the two Dutch localities are the second and third on the Eurasian continent.

Both GIACOMINI and RICHARDS paid attention to the ecology of the two species. It is interesting to compare them with our field observations. Since the third Dutch *Campylopus* species with piliferous leaves, *C. brevipilus* Br. et Schimp., is often found associated with them, and little was known so far concerning its ecology in the Netherlands, special attention has also been paid to this species and the results are included in our geographical and ecological considerations. First, however, some critical remarks should be made regarding the morphology and anatomy of *C. introflexus* and *polytrichoides*, in view of their taxonomic status.

TAXONOMIC REMARKS CONCERNING *C. introflexus* AND *polytrichoides*

GIACOMINI has thoroughly discussed the morphological differences between these species and their varieties. He also summarized the more important characters in a table (l.c., p. 35). RICHARDS gave a literal translation in English, so there is no need to reproduce it here. In the text RICHARDS added a difference in colour which, according to him, "is sometimes striking". He described it as "usually dark green or with a golden tinge in *C. polytrichoides*; olive green or dusky, seldom with any golden tinge in *C. introflexus*". GIACOMINI, however, held a more or less opposite view on this matter: *C. polytrichoides* having "cespi olivaceo-bruni,

fino a fulvo-rossastri, per lo più con una caratteristica lucentezza metallica”, *C. introflexus* having a “color giallo-verdognolo, fino al giallo-oro, con lucentezza più o meno notevole, talora con tinta bruno-chiara fino a scura”. So we must assume either that one of the authors has made an error, or that in Great-Britain the colour differences are more or less reversed, in which case these differences would be hardly reliable for taxonomic purposes. That would explain why the authors omitted them from the table. We shall follow here the monographer GIACOMINI, but use this character with caution.

We may add some differences taken from the detailed descriptions and drawings to scale by GIACOMINI, but omitted from his table and ignored by RICHARDS. The comal leaves in *C. introflexus* are 3.0-3.3 mm (hairpoint excluded) \times 0.73-0.91 mm (at base 0.64-0.82 mm wide), those of *C. polytrichoides* 3.5 (2.5-6) \times 0.55-0.82 mm (at base 0.5-0.7 mm wide). The hyaline border ascends the leaf margin to (more than) $\frac{1}{2}$ of the leaf length (hair point excluded) in *C. introflexus*, and reaches only $\frac{1}{5}$ — $\frac{1}{3}$ ($-\frac{1}{2}$) of the leaf length in *C. polytrichoides*.

The most important vegetative diagnostic characters, however, seem to be the relative length of the convolute part of the leaves, the relative width of the nerve, the direction of the hair points in dry state, and the cell structure of the nerve in cross section. In Europe we have often to rely upon these characters since fruits of *C. polytrichoides* are extremely rare here. In Great-Britain fruits of *C. introflexus* seem to be common. Among the three Dutch collections only the *introflexus* specimens of Kraloo were fertile, but with immature capsules.

In Great-Britain *C. polytrichoides* grows in small patches on undisturbed, often stony soil in warm dry situations, whereas *C. introflexus* is sometimes observed to form extensive carpets and it most frequently grows in disturbed habitats like cut peat or burnt ground. Now it is remarkable that at Tongeren *C. polytrichoides* forms extensive carpets in a recently burnt heath! The colour (yellow green or golden green), if we follow GIACOMINI'S

opinion, and the deflexed hair points also speak in favour of *C. introflexus*. However, the colour does not seem to be so important, and with regard to the hair points RICHARDS remarked that "this character is somewhat variable... In *C. polytrichoides* the hair points if long may be somewhat reflexed, though not usually as regularly or at so large an angle as *C. introflexus* where many of them are at 90° or more to the rest of the leaf". In the Tongeren specimens the hair points of the apical leaves are at 0°-80° with the lamina and only in some apical leaves¹ up to 110°. Most of them are at an angle between 45° and 70°.

Mr. J. LAMBINON (Liège, Belgium) kindly forwarded me specimens of *C. polytrichoides* from the only Belgian locality (Kalmpthout) and from S. France (départ. Aveyron). A duplicate of the former (same collector, date, locality, and habitat) had been identified and cited as *C. polytrichoides* by GIACOMINI himself; the latter specimen (collected in 1961, after GIACOMINI's publication) comes from a region where only *C. polytrichoides* occurs. The Belgian material has straight hair points, but the stems are slender, the colour is dull, the leaves are only 2.4-3.5 mm long and the nerve is 1/3 - 1/5 of the leaf width (*C. introflexus* characters). All other characters are those of *C. polytrichoides*. The S. French material, however, is typical *C. polytrichoides* in every respect, but for the hair points, part of which are distinctly reflexed!

In the author's opinion, therefore, the character of the straight or deflexed hair points is not decisive. Both specimens are considered to be *C. polytrichoides*. The same view is held regarding the Tongeren material, for the following reasons: the habit is robust, the plants are very glossy, the leaves are 3.2-4.5 × 0.68-0.89 mm, with convolute margins in the whole upper 1/3-1/2 part. The hyaline border reaches up to 1/3-1/2 of the leaf, the nerve is 2/3 of the leaf width throughout the leaf. I made nume-

1. Leaf characters, discussed in this paper, always refer to comal leaves of sterile stems, if not stated otherwise.

rous cross sections, all of which showed three distinct layers and stereidiform cells in clear cut groups of 3-5. In fact, the section of the leaf nerve is identical with that of the Belgian and French specimens. Like the British plants, the Dutch specimens belong to ssp. *polytrichoides* Giac. var. *genuinus* Giac.

The habitat, it is true, is quite different from normal *C. polytrichoides*, but so is the habitat of the Belgian specimens. The label mentions: "sur le sable humide des dunes à Kalmphouth (prov. Anvers)". It is probably the addition "Anvers" which gave GIACOMINI and RICHARDS the wrong impression that the moss grew here "on littoral dunes" (which in Belgium are strongly calcareous). In fact, the Kalmphouth dunes are non-calcareous, acid inland dunes of fluvioglacial sand, i.e. the same habitat type as near Tongeren, only still less typical of *C. polytrichoides*, being humid.

The Dutch material of *C. introflexus* fairly answers the description of that species. The specimens of Kampina are dull olive green. The leaves are $2.1-2.6 \times 0.41-0.77$ mm, as a rule with strongly deflexed hair points ($60^\circ - 120^\circ$), often with slightly or not convolute margins and with a nerve occupying $1/3 - 1/2$ of the leaf width; in cross section stereidiform cells are hardly distinguishable, those present possess wide lumina and do not form alternating groups.

The Kraloo material, which was collected in a much wetter habitat, was remarkably dark green to blackish, almost like *C. atrovirens*. It had very slender stems with distant innovations. The leaves measured $2.2 - 3.2 \times (0.44 -) 0.79 - 0.91$ mm and had a hyaline border along $\frac{1}{2}$ or more of the leaf length. The margin was not convolute or only so at apex. Width and anatomy of the nerve the same as in the Kampina specimens. Many hair points were erect; their angle with the lamina varied from 0° to 90° . The setae of the immature fruits were 5-8 mm long, as they should be in *introflexus*.

It seems to me that the colour of the two species in the Ne-

therlands resembles more that of the British than that of the Southern European specimens.

GEOGRAPHICAL CONSIDERATIONS

As pointed out above, *C. polytrichoides* is a palaeotropical species, occurring in India, Sumatra and Java, all over the African continent and in S. and S. W. Europe. In Great-Britain it has been known for a long time from a very limited and apparently unchanging area in W. Ireland, Wales, Cornwall, S. Devon, and the Channel Islands, with a single locality as far North as Argyll (W. Scotland). On the European continent it is common in Ticino (S. Switzerland), Italy, Spain, and Portugal. In France the species is limited to the S., the Centre and the W., but it is rare outside the mediterranean region (BOULAY, 1877). The northernmost stations are near Paris and in Normandy (GIACOMINI, 1955). Outside this area so far only one isolated locality was known at Kalmphout (Belgium), on the Dutch border N. of Antwerp, 330 km from its nearest locality in France. After its discovery in 1884 it has never been found again here nor anywhere else in Belgium.

The Dutch locality of Tongeren is not far from Epe, a village on the Veluwe (prov. Guelders), 40 km N. of Arnhem. This is 150 km from Kalmphout and the northernmost locality of this species, now known on the European continent. It is amazing that *C. polytrichoides* should occur here in such quantities at such a distance from its main area, for outside Spain and Portugal it has never been found fruiting in Europe. The species also lacks means of vegetative propagation. In this connection it may be significant that in the last three decades other mediterranean and mediterranean—southern atlantic species have been discovered in the Netherlands, such as *Convolvulus lineatus*, *Erica vagans*, *E. ciliaris*, and *E. scoparia*. The two last-named were found in the North (isl. of Terschelling), far from their main

area, which seems quite comparable to the case of *Campylopus polytrichoides*.

Campylopus introflexus is a neotropical and antarctic species, occurring in New Zealand, Australia, Kerguelen, Falkland Islands, S., Central and North America. Until recently only one European locality was known, viz. Menez-Hom in Brittany. This induced GIACOMINI to speak of a very interesting disjunction, similar to that of some *Sphagnum* species (in a letter to mr. STÖRMER, cf. STÖRMER, 1958). He probably had *Sphagnum pylaei* in mind. In the light of new evidence, however, it seems more likely that the species has been introduced there by man. RICHARDS (1963) pointed out that *C. introflexus* had not been recorded for Great-Britain until 1941 and that it is rapidly spreading now all over the British Isles: the author cited no less than 86 localities!

The spreading was already observed by LACEY (1957) and in the period 1958-1961 no less than 20 new localities were recorded in the "New Vice-County Records" compiled by mrs. PATON and regularly published in the Transactions of the British Bryological Society. Although neither LACEY nor PATON distinguished between *C. polytrichoides* and *C. introflexus*, these records are likely to refer to *C. introflexus* since only this species is spreading and also since the habitat data of the new records are in full agreement with the requirements of *C. introflexus*, not with *C. polytrichoides*. After RICHARDS' publication 13 more localities of *C. introflexus* have been discovered in Great-Britain and only one of *C. polytrichoides* over a period of two years. KING (1964) actually observed spreading of the species in one particular Irish locality over the period 1942-1961.

The two Dutch localities are:

1. Kampina, E. part of the 'Kampinase heide', a nature reserve near Boxtel (between 's Hertogenbosch and Eindhoven, prov. of N. Brabant).

2. 'Kraloose heide', a nature reserve near Ruinen (between Assen and Meppel, prov. of Drenthe).

In the first locality the species grows in very small quantities

and lacks fruits, in the second it is quite abundant and fertile. Since *C. introflexus* fruits abundantly in Great-Britain, it is likely to have come here naturally: the very light spores probably can be carried over considerable distances and the predominantly westerly winds are favourable for a rapid eastward extension.

The case is quite comparable to that of the South African moss *Orthodontium lineare* Schwaegr., which was first introduced in England, too, (Liverpool around 1916) and equally made its first appearance on the continent in the Netherlands (first find in 1943), having spread now at least as far as E. Germany. Lately it is becoming a very common species in the Netherlands (BARKMAN, 1962). Similar things may be expected to happen to *Campylopus introflexus*. If this species should spread also to Southern Europe, where *C. polytrichoides* is found fruiting, hybridisation might occur, which would present a most interesting case. This is even possible elsewhere, for *C. polytrichoides* has been found with antheridia in Cornwall and near Tongeren (Neth.); both male and female gametangia seem to be common on the continent (RICHARDS, 1963).

Although it is now likely that *C. introflexus* did not originally have an amphi-atlantic disjunction, its area still has some puzzling aspects. Being able to thrive in a cold climate like the Scottish Highlands and the N. Netherlands, and even in real arctic conditions like Patagonia and Kerguelen, one wonders why it should be restricted to the Southern United States (California, Arizona, Texas, Alabama, Georgia, Tennessee, Ohio), the more so since it is able to grow there at considerable altitudes (GROUT, 1937)!

ECOLOGICAL CONSIDERATIONS

For sake of comparison the vegetation records of the three piliferous species have been united into one table (table I), but the species will be discussed separately. From other countries complete phytosociological records have only been published by GIACOMINI (1951) for the insubrian region (S. Switzerland and

N. Italy), dealing with *C. polytrichoides*, and by JONAS (1935) for N. W. Germany (*C. brevipilus*).

a) *Campylopus polytrichoides*

Near Tongeren this species grows in an extensive heath on undulating soil of ice-pushed preglacial sand. The sand is coarse, gravelly and slightly loamy, acid and poor in minerals, though not so poor as the cover sand on which *C. introflexus* and *brevipilus* have been found. It is also better drained. The profile is a humus podzol with a humus layer of 1-1.5 cm, except in record no. 2, made on drift sand, where it measured only 0-0.5 cm. The low dunes were covered with *Calluna* heath, the wet depressions with *Erica tetralix* heath. The whole area had been burnt not long before. Consequently the vegetation (dwarf shrub layer) still had an open character, particularly in the dry *Calluna* heath.

Record 1: dry, low hummock, flat. Dead branches of cut pine trees scattered everywhere.

Record 2: slope of young sand dune, exp. SW, 5°-10°.

Record 3: N exposed slope, 17°-30°.

Record 4: flat, moist depression.

As will be seen by inspection of table I, *Campylopus polytrichoides* decreases in abundance from left to right, i.e. with increasing soil moisture and increasing coverage of the shrub layer. Yet, although *C. polytrichoides* is mainly found in open spots, this circumstance can hardly explain its decrease, for even in record no. 4 the open spots still have a total coverage of 15%, whereas *C. polytrichoides* covers less than 0.1%.

Campylopus brevipilus, which as a rule has the same preference for open spots, strongly increases from left to right. The opposite behaviour of the two species is easily explained by the xerophilous character of *C. polytrichoides* and the hygrophilous character of *C. brevipilus*, as is well known from other localities and from the literature. Outside the sample plots the same phe-

nomenon was observed. It is, therefore, curious that near Antwerp *C. polytrichoides* has been found on humid sand.

The habitat of this species in Great-Britain and S. Europe is quite different from ours, the only points in common being that it is everywhere confined to warm, dry, probably acid, mineral soil. According to AMANN (1928) it is exclusively calciphobous in Switzerland, but only found on neutral soil (pH 7.0). There is good reason, however, to doubt this observation since the pH was determined colorimetrically and since AMANN also placed strongly acidiphytic species like *Dicranum majus*, *Ptilium crista-castrensis*, *Sphagnum fuscum*, and *S. rubellum* in this group of neutrophilous mosses. The measurements probably refer to the subsoil. AMANN did not mention *C. polytrichoides* for heath vegetation. According to JÄEGGLI (1950) the species is restricted to siliceous rocks in the hottest valleys of Ticino, between 250 and 650 m altitude.

It is therefore not surprising that the community is quite different from the Dutch, too. AMANN published one record; none of the nine associated species grows together with *C. polytrichoides* in the Netherlands, eight do not even occur in our country. JÄEGGLI cited 9 associated species, 5 of which are indigeneous in the Netherlands; only two species are also associated with *C. polytrichoides* near Tongeren, viz. *Campylopus fragilis* and *Polytrichum piliferum*.

GIACOMINI (1951) described a special association for N. Italy, the *Campylopodietum polytrichoidis* (alliance *Campylopodion*), based on 4 records with a total of 14 species, of which only one (*Polytrichum piliferum*) is also present in our records. GIACOMINI (1955) described the habitat of the species as: 'on dry soil in coastal and inland areas, on sunny siliceous rocks, particularly in the garigue on the top of earth-covered rocky outcrops; sometimes also on loamy-sandy soil', The moss often grows in crevices of strongly sloping rock faces. It does not stand irrigation with surface water, only with rain water. Yet, it seems to be restricted to parts of the mediterranean region with a high precipitation rate.

In Spain and Portugal *C. polytrichoides* has also been found in ericaceous vegetation (*Erica cinerea*, *Polytrichum juniperinum* etc.). According to BOULAY (1877) the moss grows on dry, siliceous soil in S. France; it is rather common on loam, sand, and sandstone. BOULAY gives a list of 11 associated species on sandstone, among which only *Polytrichum juniperinum* and *P. piliferum* are equally present in the Dutch community. In Great-Britain the species is found "in rather dry or intermittently moist stony situations, or in rock crevices, usually with a south, south-western or south-eastern aspect". "In nearly all its British localities the substratum is probably acid". (RICHARDS, l.c.).

b) *Campylopus introflexus*

Only two records could be made to include this species. At Kampina (rec. 5) the species grew in a small *Calluna*-heath, surrounded by coppice, on poor, dry, level soil, consisting of fine fluvioglacial cover sand. The profile was a podzol with 2.5 cm of dark brown humus on top. The heath had not recently been burnt or cut and there were scattered seedlings of oak and birch. *Campylopus introflexus* was scarce and confined to a small open spot in the *Calluna*-heath.

At Kraloo (rec. 6) the moss in question grew in a very extensive wet heath in a blown-out depression of fine cover sand with a strongly developed low humus podzol and a thick layer of peaty humus. This heath is inundated each winter. It had been burnt 6 years ago. *Campylopus introflexus* was very abundant here. In view of the difference in habitat it is not surprising that the vegetation in these localities was rather different, too (cf. table I).

According to RICHARDS *C. introflexus* is found on peat in blanket bogs, moist heath, etc., occasionally on circumneutral fen peat (pH 6.5-7.0), together with such plants as *Filipendula ulmaria*, *Comarum palustre*, *Menyanthes trifoliata*, *Parnassia palustris*, *Campylium stellatum* a.o. (LACEY, 1957). RICHARDS remarked that

it is "possibly less oligotrophic and calcifuge than *C. polytrichoides*" and "certainly less restricted to dry, well-drained situations". The soil is often disturbed by burning, peat cutting, etc. It is a pioneer which can rapidly colonize bare soil. TANSLEY (1953) mentioned neither *C. polytrichoides* nor *C. introflexus*. STÖRMER (1958) described the only French locality as "a dry *Erica cinerea*-heath". It should be remembered, however, that the locality (Menez-Hom, alt. 330 m, near the coast) has a very high rain-fall and probably a high air humidity.

c) *Campylopus brevipilus*

Table I gives 13 records with this species, of which 4 with either *C. polytrichoides* or *C. introflexus*, already discussed above. The data of the other records (all in the province of Drenthe) are the following:

7. Kraloo, low hill in large area of wet heath. S. aspect 0°-3°, fine cover sand, burned in March, 3 years before (1 year after the fire no *C. brevipilus* was present yet).

8. Wijster-Spier, level heath on fine, humose cover sand, burnt 6 years before.

9. Kraloo, heath on E aspect 5°, same soil type, burnt probably 3 years before.

10. Nuil (Ruinen), heath on podzolic cover sand with thick layer of peaty humus. Burnt the year before, in May.

11. Holthe (near Westerbork), open spot in moist *Calluna*-heath, where sods have recently been cut. Not burnt. Humus-rich cover sand.

12. 'Sliekerveen' near Lheebroek (Beilen). Same soil type as no. 10; sods have recently been cut. Not recently burnt.

13. Dwingeloo, extensive wet heath on fine, blown-out sand (heavily podzolised). Not burnt or cut for many years.

14. Bunner Veen (Norg-Roden), old, tall *Calluna*-heath on partly reclaimed, drained peat bog. Not recently burnt or cut.

15. Bonge Veen (*ibidem*), open, muddy spot on partly reclaimed peat.

The data show that of all species *Campylopus brevipilus* is the most hygrophytic one. Contrary to *C. polytrichoides* and *introflexus*, which have only been found on mineral soil (sand) in the Netherlands, *C. brevipilus* occurs both on sandy soil and on peat. This is in accordance with its atlantic distribution in Europe.

HERZOG (1926, p. 87) may be quoted here: "*Campylopus brevipilus* begleitet die atlantische Heide vom westlichen Mittelerranbecken bis zum südlichen Norwegen, ohne irgendwo beträchtlich in den Kontinent vorzurücken". TIMM (1928) gave a more detailed description of the area: Algeria, Sardinia, SW. Portugal, N.W. Spain, France (mainly in the W.), Great-Britain, Netherlands, W. Germany from Westphalia to Schleswig-Holstein, Denmark, W. Norway from Jäderen (S. of Stavanger) to Fosen (NW. of Trondhjem, 63° 52' N. lat.). We may add Ticino (S. Switzerland; only one locality, viz. Faido. Fide JAEGGLI, 1950) and Belgium (DEMARET and CASTAGNE, 1961). The latter authors also mention the Azores and Madeira.

It seems to be extremely abundant in NW. Germany: "In der ostfriesischen Moorheide ist *C. brevipilus* stellenweise so häufig dass dort die Kinder dieses Moos zum Spielen benützen" (TIMM, 1928). One is therefore surprised at its relative rarity in the Netherlands. Only 25 localities are known, mostly dating back to the last century; only 4 localities date from 1900 or later (AGSTERIBBE, 1950), but the species has probably been somewhat overlooked, for I could add 6 more localities. Yet, the species is probably becoming rarer. Recent Dutch specimens are generally more stunted and show a tendency to reduction of the hair points (*f. epilosus*). DEMARET and CASTAGNE cited no more than 9 localities for Belgium, of which only 4 date from the 20th century; since 1922 the species has not been found any more.

All authors (BROTHERUS, DIXON, MOENKEMEYER, AMANN, TIMM, TANSLEY, RILSTONE, AGSTERIBBE, DEMARET and CASTAGNE) agree

that *C. brevipilus* is a species of moist heaths and peat bogs. TIMM added: 'on sterile, black peat'. The most detailed information regarding its habitat has been given by TANSLEY (1953) and JONAS (1935). In Somerset it is found in wet places of peat bogs, associated with *Eriophorum angustifolium*, in N. England (Pen-nines) in heath moors, in Surrey in *Calluna*-heath, in an early stage after heath fires, together with *Polytrichum piliferum* (second stage; the first stage is formed by *Ceratodon purpureus*, *Funaria hygrometrica*, and *Tortula subulata*). After 2-3 years the *Campylopus brevipilus* stage is succeeded by lichens.

In the Netherlands the species is very rare in bogs and most frequent in burnt, moist to wet heaths, especially if the heath has been burnt in (early) summer, i.e. at a time when the soil is superficially dry so that the top humus layer has been burnt, too. This was probably also the case in Surrey, for *Funaria hygrometrica* only develops on charcoal. Curiously enough, this moss is absent from our records, as well as from those made by JONAS (see below). No correlation could be detected between the cover percentage of *Campylopus brevipilus* and the number of years since the last fire. It may be abundant even in heaths which have been burnt 6 years ago. Also, the species, although less frequent, may be equally abundant on heaths which have not been burnt at all, both where sods have recently been cut and where this has not taken place.

PHYTOSOCIOLOGICAL CONSIDERATIONS

In spite of considerable floristic differences,¹ all records of table I have in common that they represent acidophilous, oligotraphent pioneer communities. This is obvious from the presence of typical pioneer species such as *Lecidea granulosa* and *uliginosa* on dry soil, *Zygonium ericetorum* on wet soil. The *Cladonia*-species of the subgenus *Cenomyce* also characterise an

1. This is evident from the small ratio: average number of species/total number of species, which is 20.5/82; i. e. table I has a homogeneity coefficient of only 0.25.

early (although not the first) stage of recolonisation. Their great number (14 spp.!) is significant and so is the small number (2) of *Cladonia*'s of the subgenus *Cladina*, indicative of terminal heath and bog stages. *Cladonia impexa*, abundant in every mature heath, is remarkably scarce.

Among bryophytes the acrocarpous mosses, particularly *Campylopus fragilis*, *Pohlia nutans*, *Polytrichum piliferum*, *P. juniperinum*, and *Dicranella heteromalla*, as well as the liverwort *Cephalozia starkei*, characterise early stages of colonisation. In all records the acrocarpous mosses greatly outnumber the pleurocarps. *Pleurozium schreberi*, which is abundant to dominant in all mature heaths, is lacking entirely. *Hypnum cupressiforme* var. *ericetorum* of which the same can be said, has low degrees of both constancy and abundance.

If we compare now the communities of the three piliferous *Campylopus* species, the following differences can be observed:

a) *Campylopus polytrichoides* - community.

Characterised by the differential species *Campylopus fragilis* and *Lecidea granulosa* (group 1) and the absence of *Zygodonium ericetorum*, *Erica tetralix*, *Molinia coerulea*, and *Carex panicea* (3).

b) *Campylopus introflexus* - community.

Intermediate between a (presence of species of group 2) and c (presence of species of group 3).

c) *Campylopus brevipilus* - community.

Characterised by the differential species *Gymnocolea inflata*, *Cephalozia connivens*, and *Palmogloea protuberans* (4) and by the absence of *Polytrichum piliferum* and *Cladonia cornuto-radiata* (2), which do occur in both a and b.

The numbers of records are as yet insufficient to justify the establishment of definitive associations. One can only say that

the records with *C. polytrichoides* are most allied to the *Biatorretum uliginosae* (Langerfeldt) Klem., with transitions towards the next stage in the sere, the *Cladonietum dstrictae* Langerfeldt (cf. KLEMENT, 1955).

Still less can be said of the *C. introflexus* - "community" since we have only two, rather different records. Record no. 5 is somewhat allied to the *Cladonietum cenoteae* Frey (fragmentary). It may well be that with the expected geographical spread of this species, it will also spread in an ecological sense, i.e. to various communities, as is already the case in Great-Britain.

Campylopus brevipilus is often found associated with other *Campylopus* species: *C. polytrichoides*, *C. introflexus*, *C. flexuosus*, and/or *C. fragilis*, in the Netherlands. Already A. BRAUN in 1847 found it together with *C. polytrichoides* near Fontainebleau (TIMM, 1928). In NW. Germany JONAS (1935) found it occasionally with *C. flexuosus* only (which, according to TIMM, is the normal situation in Norway). In the "Grosses Ahlenmoor" (NW. Germany) this author found it mixed with *C. pyriformis*, which, however, seems to be exceptional, also in that area. In the heath moors of N. England TANSLEY mentioned the combination of *C. brevipilus*, *C. flexuosus*, *C. fragilis*, *C. pyriformis* and *C. atrovirens*. *C. fragilis* is an atlantic species, too; *C. atrovirens* is still more strictly atlantic, being absent from the Netherlands, Germany, Belgium, and France.

In the Netherlands *C. brevipilus* apparently occurs in two distinct communities, one in moist heaths (records 3, 4, 6-9), the other on bare peat in drained bogs (records 12-15). The records 10 and 11, made in moist heaths with peaty soil, are intermediate.

c 1. *The heath community* has at least five differential species:

Pohlia nutans, (only here with fruits; greatest abundance here), *Polytrichum juniperinum*, *Cephaloziella starkei*, *Lecidea granulosa*, and *Carex pilulifera* (5).

TABLE I

No. of vegetation record	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Campylopus brevipilus communities		
Original field no. of record	2644	2645	2646	2647	2899	2780	2829	2648	2747	2649	3082	3133	3073	2864	2862			
Vegetation type	C	Co	C	C	Cm	CE	Cm	CE	CE	E	E	Es	Es	E	E			
Soil type	gS	dS	gS	gS	fS	fS	fS	fS	fS	PS	fS	PS	PS	P	P			
Soil humidity	d	d	md	mm	md	m	d	md	md	mm	mm	m	w	m	w			
Recent human influence	b	b	b	b	—	b	b	b	b	b	c	c	—	—	—			
Sample plot area in sq. m.	12	5	9	15	0.4	6	35	20	24	16	0.4	15	30	24	0.24			
Number of species	24	24	24	20	17	26	19	21	17	24	14	26	22	17	13			
Total coverage moss layer in %	90	90	90	85	100	90	60	40	75	90	100	70	75	50	100			
Total coverage dwarf shrub layer in %	50	30	65	85	1	75	60	95	90	60	15	65	95	75	25			
<i>Moss layer:</i>																		
Campylopus polytrichoides	2a.3	1.2 ^δ	+2	r.2												II ^r	—	—
Campylopus introflexus					+1.2	3.4fr										—	I ^s	—
Campylopus brevipilus		+2	2b.3	4.5		+2	+1	2b.3	3.3	3.3	4.5	+2	2m.2	3.4	3.3	V ^s	V ^s	V ^{s.2}
(1) Campylopus fragilis	2a.3	2a.3	2a.3	+2		2m.2				2b.3				+2		III ^{s.2}	—	I ^r
(1) (5) Lecidea granulosa	3.4fr	3.3	2b.3	2a.3		r.1	1.1	2a.2fr	1.2	1.2						V ^{s.2}	—	—
(2) } Polytrichum piliferum	1.3fr	4.5fr	1.3fr			2a.2fr										II ^{s.2}	—	—
(2) } Cladonia cornuto-radiata	r.1 ¹															—	—	—
(3) Zygonium ericetorum					2a.2	3.4				3.4	3.4	3.4			3.3	II ^s	II ^s	IV ^s
(4) Palmogloea protuberans						1.2			2b.3	2a.2	1.2	2a.2	r.1	2b.3		III ^{s.2}	II ^s	I ^r
(4) (6) Gymnocolea inflata						+1				2b.3fr	2b.3	2m.2			3.4	II ^s	IV ^s	II ^s
(4) (6) Cephalozia connivens						+2				2m.2		1.2	+2	+2	+2	II ^s	II ^{s.1}	II ^s
(5) } Pohlia nutans	2m.2fr	2m.2fr	2m.2fr	1.2fr	4.4fr	2b.3fr	2a.3fr	2a.2fr	1.2fr	2a.3fr			r.2	+2	+2	V ^s fr	II ^r	II ^r
(5) } Polytrichum juniperinum	+2			+1		+1	+3	1.1	2m.2fr	+2					+1	IV ^s	—	I ^r
(5) } Cephaloziella starkei			1.2	+2	2m.2fr	2m.2	1.2	2m.2	2a.2		2m.2				1.2	V ^{s.2}	—	I ^r
(6) } Odontoschisma sphagni													+2	2a.2	+2	—	II ^s	III ^{s.1}
(6) } Sphagnum compactum	+2				+2					(+3)			2a.3	2a.2		I ^r	V ^{s.2}	—
(6) } Cladonia squamosa			r.1										1.2		1.3	I ^r	II ^s	I ^r
Cladonia bacillaris	1.2					+1										I ^r	—	—
Cladonia coccifera var. pleurota	+2	+2		1.1	+2	r.2fr			+2fr	+2	1.2		r.1	2a.3fr		IV ^s	I ^r	I ^r
Cladonia crispata						+1fr			1.2 ^s	2b.2			+2	+2		III ^s	I ^r	I ^r
Cladonia dstricta		1.1														—	—	—
Cladonia foliacea		2a.2														—	—	—
Cladonia floerkeana	2m.2fr ^s	1.2 ^s	+2 ^s	2m.2fr ^s	2b.3fr ^s	r.1fr	+2 ^s	1.2fr	+2fr	2m.2fr			+2fr	1.1fr		IV ^s	III ^s	II ^{s.1}
Cladonia glauca			+1	+1	1.1	r.1fr										III ^{s.1}	—	—
Cladonia gracilis	r.2	+2	+2							1.2			r.1	2m.2		II ^{s.1}	I ^r	I ^r
Cladonia impexa	+1	+1	+1	+1 ^o			r.1	r.1	r.1				1.1-2	+1		IV ^s	II ^s	II ^s
Cladonia macilenta	+2 ^s	+2	+1	1.2fr	2a.3fr		r.1fr	1.2					r.2	+1fr		III ^s	I ^r	II ^s
Cladonia pyxidata var. chlorophaea	1.2	+2	1.2	+1	2m.3fr		r.1 ^r	r.1					r.1	+2		III ^s	IV ^{s.1}	II ^s
Cladonia strepsilis										+1						II ^r	II ^s	—
Cladonia sylvatica		+1				r.1										—	II ^s	—
Cladonia uncialis		+1														—	II ^s	—
Cornicularia aculeata		+2														—	II ^s	—
Lecidea uliginosa	2b.3fr	2a.2	3.3	2b.3			4.4fr			2b.2fr				1.2		III ^s	—	I ^r
Parmelia physodes	+1	r.1														—	I ^r	I ^r
Campylopus flexuosus	2b.4							2a.3					+2			I ^r	II ^s	—
Dicranella cerviculata										+2						I ^r	I ^r	I ^r
Dicranella heteromalla					1.2											—	—	—
Dicranum scoparium					+2		+1-2						1.3			I ^r	IV ^s	—
Dicranum spurium					1.2		r.1									I ^r	I ^r	—
Hypnum cupressiforme var. ericetorum										+2			1.3			II ^s	V ^{s.2}	I ^r
Leucobryum glaucum		r.2	2b.3							+2			1.3			II ^s	III ^s	—
Polytrichum gracile				1.1	+1	r.1										I ^r	—	—
Polytrichum commune var. perigoniale	+2		1.2		+1	1.1	2m.4fr		1.2							IV ^s	—	I ^r
Sphagnum cuspidatum															1.1	—	—	II ^s
Sphagnum fallax									1.1 ^o							I ^r	—	—
Sphagnum molle												1.2				—	II ^s	—
Sphagnum molluscum													4.4			—	II ^s	—
Calypogeia sphagnicola																—	I ^r	—
Mylia anomala										2m.3	+2				1.1	II ^s	I ^r	I ^r
Telaranea setacea														1.2		—	I ^r	II ^s
Calluna vulgaris	1.1k		+1k	+1k		+1k				2m.2k						—	I ^r	—
Carex pilulifera			r.1k													—	I ^r	—
Erica tetralix										1.1k				2m.1k		—	I ^r	—
Pinus sylvestris				r.1k												—	—	—
<i>Dwarf shrub layer:</i>																		
(3) } Erica tetralix			+2fl	1.2fl		3-4.3fr	2a.3fl	3.2fl	2b.2fr	2b.3fl	1.1j	2b.2fl	5.5fl	2a.2fl	1.1j	V ^s	V ^s	V ^{s.2}
(3) } Molinia coerulea					+1j	2b.3fr	1.3	+2	+2	2a.3fr	+1j	2a.2fl	1.1-2fl		2b.2j	III ^{s.2}	V ^s	V ^{s.2}
(3) } Carex panicea						2b.3fl						+1	1.2			IV ^{s.2}	III ^s	—
(5) Carex pilulifera		+1	1.2fr				2a.2fr	2b.2	2m.2fr	(+2)						IV ^{s.2}	—	—
Agrostis canina var. montana			+2fl													I ^r	—	—
Amelanchier laevis						(+2j)								r.1j		—	I ^r	—
Betula pubescens			(r.1k)				r.1k									II ^r	I ^r	II ^s
Betula verrucosa				r.1j												I ^r	—	—
Calluna vulgaris	3-4.2	3.2	4.3	5.5	+1j	3.2	4.4j	4.5	5.5	3.4	2b.3j	3.3		4.5	2a.2 ^o	V ^s	V ^{s.2}	V ^s
Carex arenaria	+2															—	—	—
Carex nigra							+1fr									I ^r	I ^r	II ^s
Drosera intermedia													+1fl			—	I ^r	—
Drosera rotundifolia													2m.2fl		+2	—	IV ^s	II ^s
Epilobium angustifolium									(+2j)							(I ^r)	—	—
Eriophorum angustifolium													+1 ^o			—	I ^r	IV ^{s.1}
Festuca ovina ssp. tenuifolia		1.2	+2fr													I ^r	—	—
Genista anglica	1.1								(+2fr)							(I ^r)	—	—
Genista pilosa	1.1	1.2 ^o														—	—	—
Juncus effusus																—	I ^r	—
Juncus squarrosus						+1							r.1 ^o fr			I ^r	—	

c 2. The peat community has at least six differential species:

Gymnocolea inflata, *Odontoschisma sphagni*, *Cephalozia con-nivens*, *Sphagnum compactum*, *Zygogonium ericetorum*, and *Cladonia squamosa* (6).

The latter is most closely allied with the 'Dicranella cerviculata-Campylopus pyriformis-Assoziation' Herzog 1943 (cf. von HÜBSCHMANN, 1957),, equally occurring on bare peat, but there are many differences. The dominant and constant species *Dicranella cerviculata*, for instance, is very rare here, and so are *Telaranea setacea* and *Mylia anomala*. *Cladonia incrassata*, *Polytrichum gracile* a.o. are even completely absent from the *C. brevipilus*-community on peat.

JONAS (1935) was the only author who described a *Campylopus brevipilus*-sociation. His records were made in a region (Hümmling) situated close to the Dutch (Drentian) border. The species is found there both near heath pools and in extensive raised bogs, invariably on denuded soil owing to fire, watererosion or winderosion. The species is infrequent in the wet bog hollows with *Zygogonium*, dominant in the inactive degenerating hummock phase ("Stillstandskomplex") of the bog cycle. This is the *C. brevipilus*-sociation. In the bogs JONAS found this sociation only near the relatively dry margin, where the whole bog vegetation had been destroyed through erosion by wind, loaded with drift-sand from neighbouring dunes. Here the sociation occupies moist peat, avoiding both dry and wet places. He also found it at the margin of heath pools bordering upon *Ericetum* heath, sometimes in a zone 5 m wide and in tall turfs 15-20 cm deep!

JONAS refers only to 3 records (l.c., p. 95, nos. 1-3), but throughout his book records with *C. brevipilus* on peaty soil can be found, 12 in total. If we compare these records with our *C. brevipilus*-records on peaty soil (nos. 12-15 of table I), we find considerable differences. No less than 23 species are mentioned in JONAS' records and not in ours; 15 of them were found only once. The others are: *Sphagnum papillosum* III¹; *Cladonia furcata* II¹; *C. tenuis* I^{+ -1}, *C. papillaria* I⁺, *C. incrassata* I⁺,

Sphagnum recurvum I²; *Gentiana pneumonanthe* II⁺ and *Potentilla erecta* II⁺.

There are some striking differences, above all the complete absence from the NW. German records of *Pohlia nutans* and *Cephalozia connivens*; further the absence of *Campylopus flexuosus*, *Cladonia coccifera*, *C. macilenta*, *C. gracilis* and *C. crispata*. On the other hand *C. sylvatica*, *C. uncialis*, *C. strepsilis*, *C. furcata*, *C. tenuis*, *C. papillaria*, *C. incrassata*, *Sphagnum papillosum*, *Gentiana pneumonanthe* and *Potentilla erecta*, to mention only the more important species, do not occur in the Dutch records. *Eriophorum angustifolium* is much more frequent in the NW. German records. This is partly explained by the different situation in NW. Germany, especially at the time of JONAS' research (1930-1933) when extensive living raised bogs still existed, showing the complete regeneration complex, including denuded areas (stationary and degenerative phases) not present (any more) in the Netherlands. The *Sphagnum* bogs E of the river Ems have, for that matter, never been so seriously affected by drainage and fire for the cultivation of buckwheat as have the Dutch bogs.

The infiltration of the bogs with drift sand on the other hand may well explain the presence of *Nardo-Galion* species like *Gentiana*, *Pedicularis*, *Potentilla*, etc. This contact situation (ecotone) is not encountered any more in the N. Netherlands.

JONAS' records, too, can be divided into two communities, one in heaths with peaty soil and near heath pools, the other on raised bogs. The former corresponds to our records 12 and 13, the latter to our records 14 and 15. On this basis our *Campylopus brevipilus* community on peat can be divided into two communities, so that this species occurs in at least three communities in the N. Netherlands and NW. Germany. (Our heath community is not mentioned by JONAS). These communities are:

c 1. *Campylopus brevipilus* community on dry to moderately moist sandy soil (table I, rec. 3, 4, 6-11).

c 2. Ditto on moist to wet peaty sand (table I, rec. 12 and 13; JONAS 70/4, 100/6, 100/13, 100/14, 100/15, 95/3¹).

c 3. Ditto on moist to wet, denuded peat (table I, rec. 14 and 15; JONAS 36/4, 95/1, 95/2, 95/4, 95/5, and 95/6).

At the right end of table I we have given the degrees of constancy (five classes, Roman figures) and average cover degrees (Arab figures) of the component species for each of the three communities (the cover degrees are average values only of those records where a species did occur).

Campylopus brevipilus is about equally abundant in c 1 — c 3, its coverage figures ranging from + to 4 in c 1, from + to 3 in c 2, from + to 5 in c 3.

Community c 1 is characterised by the absence of *Odontoschisma sphagni* and *Drosera rotundifolia* (occurring in c 2 and c 3), by the lower constancy of *Molinia coerulea* and by the differential species *Campylopus fragilis*, *Polytrichum piliferum*, *Juniperinum* and *perigoniale*, *Pohlia nutans*, *Cephaloziella starkei*, *Lecidea granulosa* and *uliginosa*, *Cladonia coccifera* var. *pleurota*, *Cl. crispata*, *Cl. glauca*, *Cl. macilenta* and *Carex pilulifera* (*Genisteto-Callunetum!*).

Community c 2 is characterised by the differential species: *Gymnocolea inflata*, *Sphagnum compactum*, *S. molle*, *S. molluscum*, *Dicranum scoparium*, *Hypnum cupressiforme* var. *erectorum*, *Cladonia sylvatica*, *Cl. uncialis*, *Cornicularia aculeata*, *Scirpus caespitosus*, *Drosera rotundifolia*, *Narthecium ossifragum*, and *Pedicularis sylvatica* (cf. table I), as well as the species *Cladonia furcata* (— II¹⁻² —), *Cl. tenuis* (— II^{+ -1} —), *Gentiana pneumonanthe* (— II⁺ —), and *Potentilla erecta* (— II⁺ —). (*Eriacetum tetralicis!*).

Community c 3 is characterised by the absence or lesser abundance (or constancy) of *Campylopus flexuosus*, *Leucobryum glaucum*, *Cladonia floerkeana*, *Cl. pyxidata* var. *chlorophaea*, *Cl. strepsilis* and *Carex panicea* (typical of c 1 and c 2), and by the

1. The first figure refers to the page, the second to the number of the record on that page.

differential species *Zygonium ericetorum*, *Sphagnum cuspidatum*, *S. papillosum* (— II⁺ II²), *Carex nigra* and *Eriophorum angustifolium*.

SUMMARY AND CONCLUSIONS

1. In 1962 and 1963 *Campylopus polytrichoides* de Not. and *C. introflexus* Brid. were discovered in the Netherlands, in one and two localities respectively.

2. Since these mosses are often found associated with the third indigenous piliferous species of the genus, *C. brevipilus* Br. et Schimp., they have been treated together. The present paper reviews the existing literature and discusses the taxonomy, geographical distribution and dispersal, habitat and community types of the three mosses (cf. table I).

3. The Dutch specimens of *Campylopus polytrichoides* are somewhat abnormal as to colour, direction of hair points (deflexed!) and habitat. All other characters agree with *C. polytrichoides*. It is pointed out that the direction of the hair points is not fully reliable as a diagnostic character. The abnormal habitat is the same as that of typical *polytrichoides* from Belgium.

4. *C. polytrichoides* is a palaeotropical species, occurring in Europe mainly in the S. and SW. The Tongeren locality (Neth.) is the northernmost on the continent, 150 km from the nearest (isolated) locality and 480 km from the next (main area).

5. *C. introflexus* is an antarctic and neotropical species, recently introduced in Great-Britain where it is rapidly spreading now. Apart from a single station in France the two Dutch finds are the first on the European continent. A rapid extension is expected here. Attention is drawn upon the curious southern distribution in the U.S.A.

6. *C. brevipilus* has long been known from the Netherlands. Its area is atlantic and west-mediterranean. In contrast with *C. introflexus* it seems to become rarer, at least in the Netherlands and Belgium.

7. All three species occur in open pioneer communities on acid oligotrophic soils.

8. In the Netherlands *C. polytrichoides* has only been found on coarse, gravelly, ice-pushed, preglacial sand, *C. introflexus* on fine fluvioglacial and postglacial cover sand, *C. brevipilus* on both substrata and also on peaty sand and bare peat (*Sphagnum* bogs). In this order the hygrophily of the species increases.

9. The numbers of available records do not yet permit the establishment of definite associations. The floristic composition and the differences between the communities of the three species will be evident from table I. Both the *C. polytrichoides*-community (rec. 1-4) and the *C. brevipilus*-community (rec. 7-15) have specific differential species [groups (1) and (4) respectively]. The *C. introflexus* records (nos. 5 and 6) are intermediate and lack specific differential species.

10. The *C. polytrichoides*-community is most closely allied to the *Biatoretum uliginosae*. The records with *C. brevipilus* (including those of JONAS from NW. Germany) belong to three distinct communities (c 1-3, each with 8 records; cf. last three columns of table I), viz. (c 1) on dry to moderately moist sand, (c 2) on moist to wet peaty sand, (c 3) on moist to wet denuded peat, each with a number of differential species; (c 1) is most allied with pioneer stages (after fire) of the *Genisteto-Callunetum (molinitosum)*, (c 2) with those of the *Ericetum tetralicis*, (c 3) with the *Dicranella cerviculata - Campylopus pyriformis* - association of bare peat. The differences in floristic composition between these communities in Drenthe (North Netherlands) and Emsland (NW. Germany) are pointed out.

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Legend of Table 1:

- Vegetation types: Co = Corynephorum;
C = Genisteto-Callunetum typicum (dry Calluna-heath);
Cm = G.-C. molinietosum (moist Calluna-heath);
CE = Intermediate between G.-C. and Ericetum (Calluna-Erica heath);
E = Ericetum tetralicis;
Es = Ericetum sphagnetosum.
- Soil types: gS = gravelly, coarse sand (preglacial);
dS = drift sand;
fS = fine cover sand (glacial);
PS = sand with thick layer of peaty humus;
P = peat.
- Soil humidity: d = dry;
md = moderately dry;
mm = moderately moist;
m = moist;
w = wet.
- Human influence: — = none;
b = recently burnt;
c = sods recently cut
= seedling.