

FACTS AND SPECULATIONS ABOUT THE FACTORS
AFFECTING THE DISTRIBUTION OF ANTHRACOIDEA
SCIRPI AS A PARASITE OF TRICHOPHORUM
CAESPITOSUM

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1. *Introduction*

It might seem axiomatic that the parasitic fungi should have the same distribution as their hosts. However, this is not always so. Examples are known which clearly illustrate the situation, e.g. *Anthracoidea fischeri* (Karsten) Kukkonen (NANNFELDT & LINDBERG 1957), and *A. lasiocarpae* Lindeberg (KUKKONEN 1963). These examples suggest that the parasite has its own ecological requirements which differ from those of the host. The problem can be further analysed by introducing a new example, *A. scirpi* (Kühn) Kukkonen on *Trichophorum caespitosum* (L.) Hartm. subsp. *austriacus* (Palla) Hegi and subsp. *germanicus* (Palla) Hegi.

2. *Distribution of the parasite*

Most of the finds of *Anthracoidea scirpi* have been made in Norway where its distribution area extends from the southern biogeographical provinces Aust-Agder and Buskerud up to the northernmost province Finnmark (JØRSTAD 1963, p. 94). It is not found in Iceland, and in Sweden it has been found in four provinces only (LINDBERG 1959, p. 20). In Finland it has been encountered in the three northernmost provinces (LIRO 1938, pp. 44 and 531); a few additional locations are listed by KUKKONEN (1963, p. 70), the most recent ones being made in the summer of 1963 on expeditions directed by Dr. MÄKINEN from the Kevo Subarctic Research Station (Fig. 1). The smut has been found in the Hibirä Mts. in the Kola peninsula in the USSR (GUTNER 1941).

Anthracoidea scirpi has been found also in Central Europe. One specimen is given in COOKE'S Fungi Brit. Exs. The locality in Scotland mentioned by

KUKKONEN (1963, p. 70) was visited again in September, 1963, by Dr. HENDERSON and myself and specimens are deposited in Edinburgh and Turku (E & TUR). VIENNOT-BOURGIN (1956) mentions that the smut occurs in France without giving any precise information on the locality. The type locality in the Harz Mountains in Germany has been visited by many collectors and specimens are in several exsiccata (KUKKONEN l.c.). SCHELLENBERG (1911, p. 78) describes a specimen (ZT) from Switzerland, Kanton Bern, in which the smut is *A. scirpi* although his illustration shows clearly papillate spores. Another specimen collected in the same area is in Bern (BERN).

The specimens collected from Canada are listed by SAVILE (1952) and KUKKONEN (1963); the localities are in Nova Scotia, Quebec and the District of Mackenzie. The smut occurs also in Alaska and in Michigan according to FISCHER (1953, p. 63).

3. *Distribution of the host*

The host, *Trichophorum caespitosum*, occurs according to HYLANDER (1945, 1955) as two subspecies, subsp. *austriacus* and subsp. *germanicus*. The former includes the North American form, often called "var. *callosus* Bigel." (HYLANDER 1945, PORSILD 1957), and the latter the host of the type specimen (RABENHORST: "Fungi europei", no. 1698) named "*Scirpus caespitosus* var. *nemorosus* Roth." (HEGI 1901). The determination should, however, be checked, because both subspecies occur in the Brocken area in Harz Mts.

The subspecies *austriacus* is a boreal circumpolar plant (HULTÉN 1950). It is common in Finland, Sweden and Norway, and also in Iceland, Faeroe Islands, Ireland, and the northern parts of Great Britain. In south Europe it is found in north Portugal (and even in N.W. Africa?), in the Pyrenees, in Corsica and in the Alps, the easternmost locations being in Romania, Transylvania. It is also found in the south German mountains, in the Schwarzwald, and in the Thüringer Wald, the easternmost locations being in Polish Sudeten. It is rare in Holland, common in Denmark, rare in northern Germany and Poland and in the southern part of the east coast of the Baltic, and common in western Esthonia. It is rare in the vicinity of Leningrad (MEINSHAUSEN 1878, SHISHKIN 1955). It obviously does not cross the river Svir between lakes Ladoga and Onega (ELFVING 1878, HUSTICH 1945), but is common northwards in the area of granitic bedrock (NORRLIN 1871, HERLIN 1944, RAMENSKAJA 1960). The dots on both sides of Lake Ladoga in Fig. 1 give the most southeastern localities. It is common in the Kola peninsula and eastwards in European USSR (KRECHETOWICH 1935). It is said to be less common in east Siberia, but is mentioned to occur in the

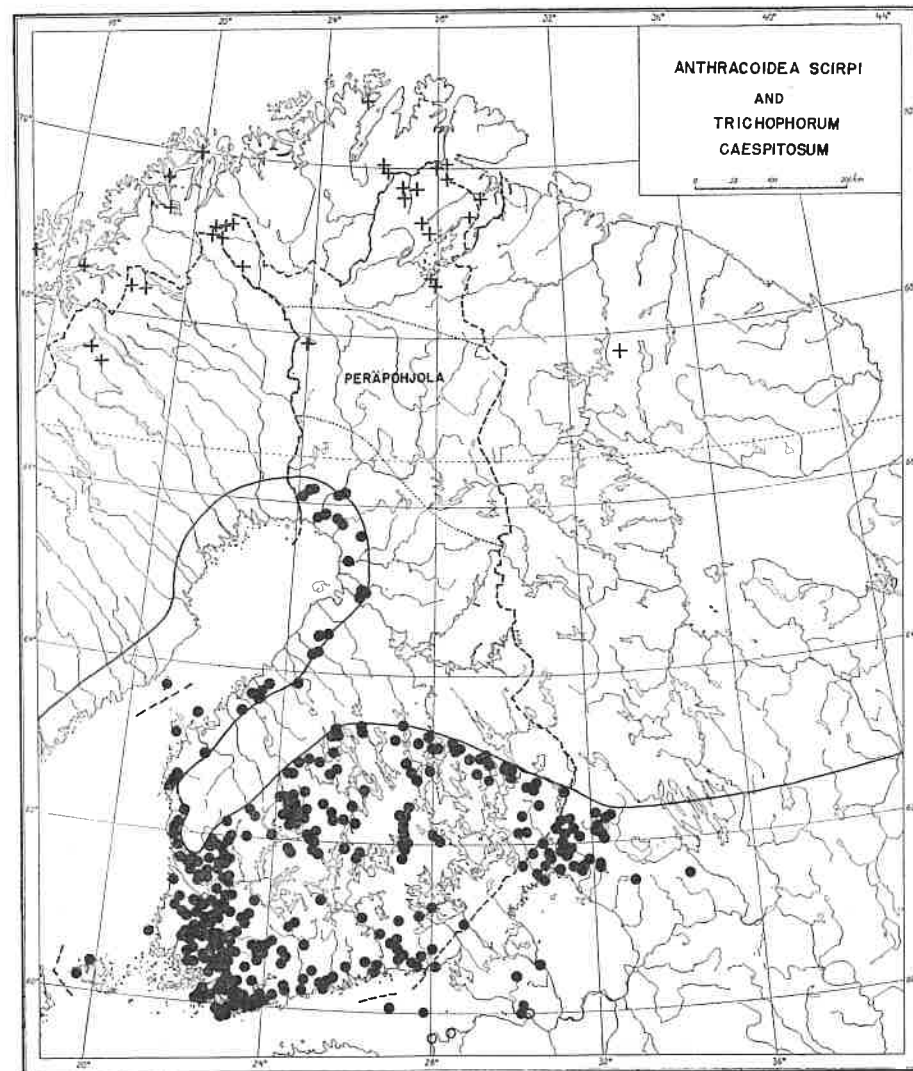


Fig. 1. Distribution of *Anthracoidea scirpi* (+) and *Trichophorum caespitosum* subsp. *austriacum* in Finland. *T. caespitosum* is common north of the solid line; along the coasts of the Gulf of Bothnia and south of the solid line it is occasional (•). Specimens in TUR and H were studied for the map and the localities given in the most important Finnish botanical periodicals are recorded. In south Finland, especially the unpublished data of Mr. P. ISOVIITA, M.Sc., have been important. The southernmost localities (o) are from HULTÉN's Atlas (1950). *T. caespitosum* is occasional also in Peräpohjola (RUUHIJÄRVI 1960), indicated by dotted lines, except in the Kuusamo area in its S.E. corner.

Altay Mts., in the Himalayas, and in Sakhalin, Kamchatka and Japan. The area of distribution in North America extends from Alaska to southern Baffin Land and along the Rockies to Colorado and on the eastern coast to the southern Allegheny Mts. In Greenland it occurs along both coasts up to the 70th parallel.

In Finland *Trichophorum caespitosum* occurs in the northern and central parts (Fig. 1), especially in the area of the "aapa" bogs (RUUHIJÄRVI 1960, p. 255). Its high frequency in this area has been pointed out by KYHKYNNEN (1919) and FAGERSTRÖM (1958). Southwards the area extends along the watershed Suomenselkä and the species is frequently found in the area of raised bogs in S.W. Finland to the coast (cf. EUROLA 1962, p. 115), and along the eastern watershed of Maanselkä to the raised bog area of North Karelia and in Russian Karelia at the N.E. corner of Lake Ladoga (EUROLA l.c., LINKOLA 1916, LUMIALA 1937).

The subsp. *germanicus* is a maritime plant of Europe. It is found in the southwestern coastal parts of Norway and Sweden. It is more common than subsp. *austriacum* in Denmark, Holland and the northern lowlands of Germany. It occurs also in Poland, France, England, Ireland, and Scotland and in the Orkney, Shetland and Faeroe Islands.

4. The habitats of the host in Finland

In central Finland *Trichophorum caespitosum* prefers oligotrophic bogs characterized especially by *Sphagnum papillosum* (RUUHIJÄRVI 1960, p. 257, EUROLA 1962, p. 127). In the same area *S. papillosum* may be replaced in certain types of bogs by *S. compactum* (RUUHIJÄRVI l.c., pp. 257—259, EUROLA l.c., p. 113), or towards the south and especially in the area of raised bogs by *S. balticum* (WARÉN 1926, EUROLA l.c., p. 133). However, in the south *T. caespitosum* is frequently associated also with *S. cuspidatum* (AUER 1937, 1944, EUROLA l.c., pp. 100 and 134). In the raised bogs *T. caespitosum* grows in deep pools made by the frost and which are rather dry in summer, mostly along the marginal slopes, but ascends sometimes to their level central area (PAASIO 1933, 1935). The bogs rich in *S. lindbergii* in north Finland bear a resemblance to *S. papillosum* bogs (KALELA 1939, pp. 507—508).

T. caespitosum does not occur so frequently in the bogs of Peräpohjola in Finnish Lapland (Fig. 1) as it does in central Finland, because the bogs are wetter and are heavily flooded in the spring (RUUHIJÄRVI 1960, p. 270). Also *S. papillosum* is absent. Instead *T. caespitosum* occurs in more eutrophic and minerotrophic fens, where *Sphagnum* species have been largely

displaced by Bryales mosses (RUUHIJÄRVI l.c., p. 102). Thus it is common in Kuusamo, in the fens on hill slopes (HAVAS 1961, p. 25). It is probably significant that at least certain types of Bryales bogs are rather dry late in summer, e.g. those in Kuusamo (HAVAS l.c., pp. 19—20), but also those in Fjeld Lapland (KALELA 1934, p. 424, KALLIOLA 1932, 1939, RUUHIJÄRVI l.c., pp. 287—288, SÖYRINKI 1938).

T. caespitosum occurs in Lapland also outside the bog habitats, viz. on wet mineral soil in the fjelds and along the river banks (KUJALA 1961, ROIVANEN 1923, SÖYRINKI l.c., p. 62).

5. The habitats of the parasite

There are no descriptions of plant communities in which the smutted *T. caespitosum* plants are found. However, some conclusions can be drawn on the basis of field observations.

Several collections of *A. scirpi* were made by the author in habitats where the host grew on mineral soil, e.g. on the southern slope of Saana fjeld in Enontekiö, beside a small rivulet above the tree-line, another in Inari Lapland on the bank of the River Tshiuttijoki, and a third one in Canada, near Great Whale River. Very obvious was the preferred habitat on Mt. Beinn Eighe in Northern Ross in Scotland, where the smut was abundant on the north-facing ledges of the bank of a rivulet above the tree-line, but was completely absent from the surrounding wet meadow, although the host grew abundantly.

A. scirpi has also been collected from some types of nutrient-rich fens, which obviously are best classified as Bryales bogs where low sedges grow, and which resemble the "*Scirpus austriacus*" bogs described by KALLIOLA (1939). It has been collected from such places, for example, S.E. of Saana fjeld and in Urtasjoki River Valley in N.W. Enontekiö and about one hundred km south of these in a muddy margin of an "aapa" bog. On the eastern bank of the River Diddno on the Norwegian side of the border with Finland in N.W. Enontekiö the smut was collected by the author from, at the time, dry peatland.

The smut has evidently never been found in a *Sphagnum* bog.

6. Discussion

1. A comparison of the world distributions of *A. scirpi* and its host, *T. caespitosum*, gives probably the impression that the distributions are identical. It should be remembered that the distribution of the parasite is

certainly not exactly known. However, there are also large gaps in the distribution of the parasite, because the smut seems to be unable to infect its host in the *Sphagnum* bogs of the lowlands. In Finland the smut is restricted to the northernmost provinces (Fig. 1). It is not found in the north German lowland either.

2. In central Finland *T. caespitosum* subsp. *austriacus* is a common species in *Sphagnum papillosum* bogs. It is often the characteristic plant and forms also large colonies. On the other hand, in the north German lowland *T. caespitosum* subsp. *germanicus* is a characteristic species in *Erica tetralix* heaths. In this respect the host fulfills also here the requirements evidently imposed on a primary host by an *Anthracoidea* species (NANNFELDT & LINDBERG 1957, KUKKONEN 1963). It thus is common and forms large colonies, which is supposed to guarantee survival of the parasite through fluctuations of climate in different seasons.

3. *T. caespitosum* occurs in southern and central Finland mainly in oligotrophic *Sphagnum* bogs, but in the north of Finland it is probably more common in Bryales bogs. Even if the smut is for some reason unable to infect its host in the *Sphagnum* bogs, there are, at least superficially, suitable Bryales bogs further south from the known distribution area of the smut, in Kuusamo for example.

4. It is very likely that wild plants have similar parasite-resistant races as have the cereals (LINDBERG 1959, p. 20). If so, it should be taken into consideration that the southern lowland plants or races occurring in *Sphagnum* bogs may be resistant to *A. scirpi*. This should be experimentally confirmed. Even if such races exist, it is hardly possible that these would be the primary reason for the present distribution of *A. scirpi*.

A. scirpi infects both subspecies of *T. caespitosum*, which are very different in their ecology. This is illustrated by *Puccinia confinis* Sydow, which produces its teliospores on subsp. *germanicus* in Norway, but never attacks subsp. *austriacus*, because the latter never grows together with *Solidago virgaurea*, the aecial host of the rust (JØRSTAD 1942, and in litt.).

As the smut occurring on subsp. *germanicus* may differ from the smut on subsp. *austriacus*, all Norwegian specimens of *A. scirpi* in Oslo (cited by JØRSTAD 1963) were studied, but no morphological character distinguishing the smuts on the two subspecies of the host was found. Instead it was noted that the Norwegian smuts as a whole were slightly different in having now and then clearly papillate spores, which have not been noticed in material previously studied (KUKKONEN 1963; cf. LINDBERG 1959 and BOLDOL & POELT 1963).

A. scirpi is thus able to infect, or probably more correctly, has been able to produce physiological variants that infect both subspecies of *T. caespitosum*. Why then has it not been able to infect the lowland forms in central and south Finland and in north Germany?

5. Very little is known about the requirements of the *Anthracoidea* species. SAVILE (1952, p. 411) points out that the *Anthracoidea* smuts prefer moist, northern, maritime, or alpine conditions. The distribution of *A. scirpi* as demonstrated above has maritime and alpine features. In addition, according to the author's experience, there has been open water in the vicinity in every location of *A. scirpi*, even outside the bogs. It is also well known that the abundance of *Anthracoidea* smuts varies considerably from year to year which may be caused by the fluctuations of the climate. For example, according to LIRO (1938, p. 531), *A. scirpi* may be frequently found in one summer, but is practically nonexistent in the next.

It is believed that the *Anthracoidea* spores need frost before germination occurs (LEHTOLA 1940). Experiments have shown that the germination is physiologically prevented in the same season; indeed, an afterripening period is needed, but during this frost is, at least in some cases, not a necessity (unpublished experiments). Spore germination has also some special requirements in regard to humidity, light and temperature (unpubl.).

It is now commonly believed that *Anthracoidea* species cause a local infection in the flowers of the host plant (SAVILE 1952, NANNFELDT & LINDERERG 1957, LINDBERG 1959, KUKKONEN 1961, 1963). In good accordance with this is the observation first made by LEHTOLA (1940) that the same spike of the host might be parasitized by two different *Anthracoidea* species. A preliminary infection experiment of the present author with germinated material gave satisfactory results. Accordingly, the infection may be caused by the sporidia or probably by the promycelia. These are both hygroscopic (KUKKONEN 1963, p. 40). Thus favourable local climatic conditions are needed for successful infection. These obviously should be moist, not too cold, and should prevail long enough. This is in good accordance with field observations.

6. If the *Anthracoidea* species infect their hosts through floral parts, which is probable, northern and alpine conditions are more favourable for the infection not only because they are humid, but also because the short season forces the two, in the south probably separated processes, viz. the spore germination of the parasite and the flowering of the host, closer together. In other words, the parasite and its host do not only have their own ecological requirements, but in order that the parasite would be able to infect, the requirements must also fit together.

7. Summary

The distribution of *Anthracoidea scirpi* and its host *Trichophorum caespitosum* has been studied. Although their distributions roughly resemble each other, the parasite does not infect the host in lowland habitats. There are, at least superficially, suitable habitats for the smut further south from its present area. Evidence has been found that the area where *A. scirpi* occurs is determined not only by the suitable northern and alpine climatic conditions, but also by the fact that the life cycles of the parasite and host must overlap.

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LARGER FUNGI ON DUNES IN FINLAND

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The first reports on the fungi of the Scandinavian dunes are from the 18th century, but only in this century have these fungi become objects of extensive geographical and ecological studies. There is also information on sand fungi from other European countries and from North and South Africa, North and South America, Asia, Australia and New Zealand. When O. ANDERSSON studied the vegetation of sand dunes in Sweden in 1944—50, he found some fungi new for that country. He found about twenty species of sand fungi. No special studies of the sand fungi in Finland have been carried out, but there are numerous observations on them. The first observations on fungi of the Finnish dunes are probably those on *Inocybe lacera*, *I. maritima*, *Laccaria laccata* and *Deconia (Psilocybe) atrorufa* which THESLEFF (1919, p. 77—78) states to be common on the dunes along the Gulf of Finland. After these observations the same and some new species have been found on the Finnish dunes, especially in the 1960's. The new ones are *Corynetes arenarius*, *Laccaria trullisata* f. *rugulospora*, *Inocybe lacera* var. *halophila*, *Scleroderma bovista* and *Tulostoma brumale*. The last-mentioned species was found by STENLID in Kökar and Jurmo (ANDERSSON 1950).

Corynetes arenarius (Rostr.) Dur. The irregularly clubshaped fruit-body is 1—5 cm long and 0.5—2 cm wide. The fertile part amounts to half of the entire black fruit-body. At the base of the stem there is a club- or bag-shaped formation consisting of mycelium strands with attached grains of sand. The fruit-bodies occur isolated or thickly clustered. Eight hyaline ascospores are found in the asci. The spores are straight or somewhat bent without septa. The paraphyses are club-shaped, bent at the tip, brown and septate. ANDERSSON (1950) found the size of the asci to be $110-160 \times 12-18 \mu$ and that of spores $25-30-35 \times 4-6(-6.5) \mu$. The asci and spores of one collection (from Yyteri) measured by Miss HEIKKILÄ (KALLIO & HEIKKILÄ 1964) were $124.3 \pm 0.09 \times 12.2 \pm 0.008 \mu$ (90 asci) and $33.3 \pm 0.3 \times 6.0 \pm 0.09 \mu$ (100 spores). It was she who found *Corynetes arenarius*, a new species in Finland, on dunes in Yyteri twenty kilometres west of the city of Pori ($61^{\circ}34' N.$). In