



sommerfeltia

13

G. Gulden & E.W. Hanssen

Distribution and ecology of stipitate hydnceous fungi
in Norway,
with special reference to the question of decline

1992



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Since a decline in stipitate hydneous fungi has been reported in some parts of Europe, their occurrence in Norway merits consideration. The present study was intended to determine whether decline has taken place in Norway, and to form a basis for future monitoring of a group of organisms which may include important bioindicators of airborne pollution.

Twenty-eight species are recognised in Norway, belonging to the genera *Auriscalpium* (1), *Bankera* (2), *Hydnellum* (10), *Hydnum* (2), *Phellodon* (4), and *Sarcodon* (9). They are most common in eastern parts of Norway, and eutrophic spruce forests are the preferred habitats. Distribution maps and information on habitat preferences for each species are provided. The species are ranged in five groups according to their distributional patterns, occurrence in vegetational regions, and distributions in other parts of Eurasia. Factors regulating the occurrence of the species are discussed for each group.

An evaluation of the frequency of the species through the decades back to 1950 is presented. There is so far no strong evidence for decline of these fungi in Norway. However, there is a statistically significant decrease in observations of the three *Hydnellum* species: *H. aurantiacum*, *H. peckii*, and *H. suaveolens*.

Keywords: *Auriscalpium*, *Bankera*, Bioindicator, Distribution, Ecology, *Hydnellum*, *Hydnum*, Monitoring, Mycorrhiza, Norway, *Phellodon*, *Sarcodon*, Stipitate Hydneous Fungi.

Gro Gulden, Botanical Garden and Museum, University of Oslo, Trondheimsvn. 23B, N-0562 Oslo.

Even W. Hanssen, Bjerkeset s., N-3624 Lyngdal i Numedal.

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INTRODUCTION

The taxonomy and main distribution in Europe of *Hydnum* species and their relatives (referred to in this paper as "stipitate hydneous fungi") are well known thanks to the prodigious contribution by Maas Geesteranus which culminated in the monograph "Die terrestrischen Stachelpilze Europas" (1975). Less attention has been paid to the ecology of the group, for instance, knowledge of their mycorrhizal status is still insufficient: the classical taxonomic studies of these fungi, e.g., Maas Geesteranus (1975), do not touch the mycorrhizal question. However, evidence has been presented recently strongly suggesting that species of the genera *Bankera*, *Hydnellum*, *Hydnum*, *Phellodon*, and *Sarcodon* are ectomycorrhizal (Ogawa 1981, Otto 1989, Agerer 1991). Danielson (1984) even succeeded in synthesizing ectomycorrhizas between *Bankera fuligineo-alba* and *Pinus banksiana*.

A decline of macromycetes, including many stipitate hydneous fungi, in Central Europe, was not reported before the mid-1970s (Wojewoda 1976, Dörfelt & Kreisel 1977, Bas 1978, Winterhoff 1978, Doll 1979, Benkert 1982). Today ample documentation of this trend exists (Arnolds 1985, 1988, 1989a, 1989b, 1989c, Winterhoff & Krieglsteiner 1984, Derbsch & Schmitt 1987, Fellner 1988, Cudlín & Kropáček 1990) and nearly all stipitate hydneous species are included in Red data lists from European countries and regions (cf. Tab. 1).

The decline in the hydneous mycoflora has been particularly dramatic in the Netherlands, where eight species are regarded extinct and six additional species presently occur in less than 10% of their former localities (Arnolds 1989a). The decline could be traced back to the 1950s. In certain vegetation types, e.g. the moss- and lichen-rich pine forest on acid, sandy soils (Cladonio-Pinetum), it started more than a decade before a deterioration of the green vegetation became evident. Supply of air-borne nitrogen to the forest soils has been considered the main cause of the decline, and a combination of acidification and nitrogen supply may have been particularly harmful (Arnolds 1989a).

The ectomycorrhizal fungi are essential to the vitality and the distribution of the temperate forests (Moser 1967). Under environmental stress, as in large parts of West and Central Europe today, the ectomycorrhizal forests depend upon their mycorrhizal symbionts for survival (Meyer 1988, 1989). The stipitate hydneous fungi may be important early indicators of forest decline (Arnolds 1989a).

Ever since Maas Geesteranus revised the Norwegian herbarium material and presented an identification key (Maas Geesteranus & Eckblad 1962), hydneous fungi have been rather extensively collected in Norway. One result of this was the study by Gulden and Stordal (1973), focusing ecology and distribution.

The Norwegian south coast has for decades received heavy loads of long-distance airborne acid rain and also considerable nitrogen deposition. The mean annual nitrogen deposition has been approximately 20 kg ha⁻¹yr⁻¹ since 1973, and the deposition of excess sulphur in the period 1970-80 has been 94 me m⁻²yr⁻¹ (corresponding to 46 kg ha⁻¹ yr⁻¹) according to estimates by Aune et al. (1989). No clear signs of forest decline or degradation of plant communities have till now been demonstrated, but fish death in the lakes has been recorded since the 1970s (Baker, J. P. et al. 1990).

The aims of the present study are to provide data on the present distribution and ecological requirements of stipitate hydneous fungi in a part of Europe still relatively little influenced by air pollution, to trace changes, if any, in the distribution and abundance in

Norway during the last decades, and to provide a basis for future monitoring of these fungi in Norway.

MATERIALS AND METHODS

The group of "stipitate hydnaceous funig" is defined in accordance with Maas Geesteranus (1975), except that the corticiaceous *Sistotrema confluens* has been excluded. The other "outsider", *Auriscalpium vulgare*, is included, since it is mostly studied by collectors of hydnaceous species.

The material consisted of about 1200 collections deposited in the Norwegian herbaria in Oslo (O), Bergen (BG), Trondheim (TRH), and Tromsø (TROM), and of about 550 additional records considered reliable, originating mainly from Mr. Jens Stordal. Some records were drawn from Norwegian mycological and botanical journals, e.g. *Agarica*, *Blekksoppen*, *Blyttia*, *Polarflokken*, and *Våre Nyttevekster*. Many records from around the turn of the century were found in the works of A. Blytt (1905) and Egeland (1912, 1913, 1914). Records (not confirmed by material) are marked with open circles on the maps. Voucher material and notes are collectively referred to in the text as "finds", "records", or "observations". Personal experience from collecting of these fungi over many years (not always documented by voucher material), has also been reflected in the text.

Material of hydnaceous fungi has not been systematically sampled. There is for instance an over-representation of collections from the south-eastern part of the country, where most people are living. Collecting frequency has also changed. Before 1960 there was little mycological activity in Norway, except for a period around the turn of the century in the tradition of A. Blytt. During the 1950s Mr. Stordal was more or less alone in collecting and taking notes on macromycetes. A remarkable rise in interest in macromycetes occurred in the 1960s parallel to the expansion in university positions. Routines for publishing finds from excursions, courses, mushroom controllers, etc. have changed. The habit of printing foray lists more or less ended around 1980. As a whole, we consider the material badly suited for statistical treatment and we prefer to reproduce the original data such as dots on the maps and levels on histograms, rather than applying formal statistical tests. A chi square test (Fisher 1950) has, however, been used in a few cases.

Main sources for information on distribution have been Maas Geesteranus (1975), supplemented by Nikolajeva (1961), Phillips (1981), Ulvinen et al. (1981), Strid (1983, 1984, 1985, 1991), Jülich (1984), Ryman & Holmåsén (1984), Breitenbach & Kränzlin (1986), Buczacki (1989), and Petersen & Vesterholt (1990). Several other sources have also been consulted. M. Nunez, Oslo, E. Ohenoja, Oulu, and R. Watling, Edinburgh have supplied information on occurrence of hydnaceous fungi in Spain, Finland, and Great Britain. Red data lists consulted were:

Austria, A: Krisai 1986.

Denmark, DK: Vesterholt & Knudsen 1990.

Germany, D: Benkert 1982 (G.D.R.), Lettau 1982 (Schleswig-Holstein),

Winterhoff & Krieglsteiner 1984 (Baden-Württemberg), Runge 1987 (Nordrhein-Westfalen), Wöldecke 1987 (Niedersachsen and Bremen), Hirsch et al. 1988 (Thüringen).

Netherlands, NL: Arnolds 1989c.

Poland, PL: Wojewoda & Ławrynowicz 1986

Sweden, S: Databanken för hotade arter & Naturvårdsverket 1991.

The system of vegetation regions is according to Dahl et al. (1986). Rough boundaries for vegetations regions in Norway are outlined in Figs 28, 35, and 38. Boundaries in Fennoscandia are outlined in Koski-Kotiranta & Niemelä (1987). The nomenclature of forest types follows Kielland-Lund (1981).

The abundance of each species in each decade from 1950 to 1989 is given in histograms. Since finds from before 1950 were generally few, they were lumped as one column in the histograms. The categories "common", "not common", and "rare" in Tab. 1 were ascribed to the species according to a combined evaluation of number of observations, occurrence in vegetation regions, and distribution.

common - > 120 observations, occurrence in 5 vegetation regions, and in all parts of the country.

not common - 30-120 observations, occurrence in 3-4 vegetation regions.

rare - 1-30 observations.

RESULTS

NUMBER AND RELATIVE ABUNDANCE OF SPECIES

By 1991, 28 species of stipitate hydneous species were known to occur in Norway. Two new species, *Hydnellum scrobiculatum* (Fr.) P. Karst. and *Sarcodon glaucopus* Maas G. & Nannf., were added since the last revision (Gulden & Stordal 1973). One additional species, *Hydnellum ferrugipes* Coker, was recorded from Norway by Maas Geesteranus (1978). However, the difference between this and *H. caeruleum* is doubtful (see p. 34).

Six stipitate hydneous species are regarded as common in Norway (Tab. 1). Ten species are considered not common. Twelve species, or 43 % of the species, are rare.

DISTRIBUTION

The maps (Figs 28-53) roughly indicate the Norwegian distribution of the individual species. A grouping of the species according to their distributional patterns in Norway is shown below.

(1) Species restricted to the Norwegian south coast

Hydnellum compactum (Fig. 35)

Phellodon confluens (Fig. 43)

(2) Species restricted to South Norway, not predominantly eastern

Bankera fuligineo-alba (Fig. 31)

Sarcodon scabrosus (Fig. 52)

(3) Species restricted to South and Central Norway, not predominantly eastern

Hydnellum concrescens (Fig. 36)

Phellodon melaleucus (Fig. 44)

(4) Species restricted to East Norway

Hydnellum geogenium (Fig. 38)

Hydnellum scrobiculatum (2 observations; Fig. 42)

Sarcodon fennicus (Fig. 47)

Sarcodon fuligineo-violaceus (1 observation; Fig. 42)

Sarcodon glaucopus (1 observation; Fig. 42)

Sarcodon martioflavus (Fig. 51)

(5) Species predominantly occurring in East Norway

Bankera violascens (Fig. 32)
Hydnellum aurantiacum (Fig. 33)
Hydnellum ferrugineum (Fig. 37)
Hydnellum mirabile (Fig. 39)
Hydnellum peckii (Fig. 40)
Hydnellum suaveolens (Fig. 41)
Phellodon niger (Fig. 45)
Phellodon tomentosus (Fig. 46)
Sarcodon leucopus (Fig. 49)
Sarcodon lundellii (Fig. 50)
Sarcodon versipellis (Fig. 53)

(6) Species more or less equally represented in all parts of the country

Auriscalpium vulgare (Fig. 28)
Hydnum repandum (Fig. 29)
Hydnum rufescens (Fig. 30)
Hydnellum caeruleum (Fig. 34)
Sarcodon imbricatus (Fig. 48)

Considering the low collecting frequency in western districts, it appeared that *Bankera fuligineo-alba* and *Phellodon melaleucus* might be considered somewhat oceanic. No species exhibited a northern distribution. Altogether 14 species had a dominance of finds in the eastern or southeastern parts of the country.

OCCURRENCE IN VEGETATION REGIONS

The concept of vegetation regions has proved fruitful for the vascular higher plants, supplying information principally on the temperature requirements of the plants, and, in particular, on the ability of the species to grow at higher elevations, i.e., information which is not shown by the maps.

The hydnaceous species occurred in all vegetation regions up to the alpine region (cf. Tab. 1). Two species were collected only in the south, within the two mildest climate regions. Three others were only found in the boreo-nemoral region. In this region 27 of the 28 species occurred, i.e., all except *Sarcodon glaucopus*. The southern boreal region had 22 species. Sixteen species occurred in the middle boreal region, and only three ascended to the northern boreal region. Of these three, however, *Phellodon tomentosus* occurred only once in the region. One species, *Hydnum rufescens*, had two records from *Betula nana* scrubs just above the timber line. We do not consider this a truly alpine species.

The correspondence between distribution of the stipitate hydnaceous species and their occurrence in the vegetation regions was generally good. For instance, none of the species was found further to the north than could be expected from their occurrence in the vegetation

regions. However, some species could be expected to grow further north, viz., *Bankera fuligineo-alba*, *Hydnellum ferrugineum*, *Phellodon tomentosus*, *Sarcodon fennicus*, and *S. scabrosus*, a pattern also suggested by their distribution in other parts of Fennoscandia.

The concept of vegetation regions does not take into account the restrictions caused by factors like mycorrhizal associates and edaphic conditions; hence, we often observed a restriction of individual members of the group to sections of the vegetation regions.

ECOLOGY

Habitat ecology

Judging from literature accounts and our own preliminary studies, we consider the included genera, except *Auriscalpium*, to be ectomycorrhizal. The stipitate hydneous fungi are, according to our data and experience, mainly associated with spruce (*Picea abies*) in Norway. Some species appear exclusively to grow with spruce. Most of the *Hydnellum* and *Phellodon*, and about half of the *Sarcodon* species were typical of spruce forests. Pine forests (*Pinus sylvestris*) and mixed coniferous forests also accommodate many hydneous species. A grouping of the species according to the preferred tree species, gave the following result:

(1) Spruce forest species

Hydnellum geogenium
Hydnellum mirabile
Hydnellum suaveolens
Sarcodon fuligineo-violasceus
Sarcodon martioflavus
Sarcodon versipellis

(2) Species preferring spruce forests, but also occurring in pine or deciduous forests, mainly oak (*Quercus robur* and *Q. petraea*)

Bankera violascens (*Pinus*)
Hydnellum ferrugineum (*Pinus*)
Hydnellum peckii (*Pinus*)
Phellodon niger (*Pinus*)
Phellodon tomentosus (*Pinus*)
Sarcodon lundellii (*Pinus*)
Hydnellum scrobiculatum (deciduous species)
Hydnellum concretescens (*Quercus*, *Pinus*)
Phellodon melaleucus (*Quercus*, *Pinus*)

(3) Species preferring pine (*Pinus sylvestris*) forests, but also occurring in spruce (*Picea abies*) forests

Tab. 1. Summary of species characteristics. Distributional patterns refer to geographical groups 1-5 defined in text, pp. 20-21. Vegetation regions according to Dahl et al. (1986): N - nemoral region, BN - boreonemoral region, SB - southern boreal region, MB - middle boreal region, NB - northern boreal region. Edaphic requirements: c - calcicolous, e - eutrophic, o - oligotrophic, w - with wide tolerance. Abundance as defined on p. 9. Red list column lists all countries in which the species in question is considered as threatened. Trend - trend in Norway according to this study: + - increasing, 0 - status quo, - - decreasing, ? - data insufficient (one collection).

Species	Distri- butional pattern	Vegetation region					Associated tree(s)	Edaphic demands	Abundance	Red lists (countries)	Trend
		N	BN	SB	MB	NB					
<i>Auriscalpium vulgare</i>	5	*	*	*	*	-	pine (spruce)	(o)e	common	NL	0
<i>Bankera fuligineo-alba</i>	2	*	*	*	*	-	pine (spruce)	o(w)	not common	D, DK, NL, PL	+
<i>B. violascens</i>	4	*	*	*	*	-	spruce (pine)	w	not common	D, DK, PL	+
<i>Hydnellum aurantiacum</i>	4	*	*	*	*	-	spruce (pine/deciduous)	w	not common	D, DK, NL, PL	-
<i>H. caeruleum</i>	5	*	*	*	*	-	pine (spruce)	o	not common	D, DK, NL, PL	+
<i>H. compactum</i>	1	*	*	-	-	-	oak	w	rare	NL, S	+
<i>H. concrescens</i>	2	*	*	*	-	-	spruce/oak (pine)	w	not common	D, DK, NL, PL	+
<i>H. ferrugineum</i>	2	*	*	*	*	-	spruce (pine)	w	not common	D, DK, NL, PL	0
<i>H. geogenium</i>	3	*	*	*	-	-	spruce	e-c	not common	D, PL, S	0
<i>H. mirabile</i>	3	-	*	-	-	-	spruce	c	rare	S	-
<i>H. peckii</i>	4	*	*	*	*	-	spruce (pine)	(o)e	not common	D, DK, NL	-
<i>H. scrobiculatum</i>	2	-	*	-	-	-	spruce (deciduous)	e-c	rare	D, DK, PL	0
<i>H. suaveolens</i>	4	*	*	*	*	-	spruce	(o)e	common	D, PL	-
<i>Hydnum repandum</i>	5	*	*	*	*	*	coniferous/deciduous	w	common	NL	-
<i>H. rufescens</i>	5	*	*	*	*	*	coniferous/deciduous	w	common	NL	-
<i>Phellodon confluens</i>	1	*	*	-	-	-	oak	o	rare	D, DK, NL, S	+
<i>P. melaleucus</i>	2	*	*	*	*	-	spruce (oak, pine)	w	not common	D, DK, NL, S	0
<i>P. niger</i>	3	-	*	*	-	-	spruce (pine)	(o)e	rare	D, DK, NL, PL	0
<i>P. tomentosus</i>	5	*	*	*	*	*	spruce (pine)	w	common	D, DK, NL, PL	0
<i>Sarcodon fennicus</i>	4	-	*	*	-	-	pine (spruce)		rare	S	0
<i>S. fuligineo-violaceus</i>	2	-	*	-	-	-	spruce	e	rare	D, S	?
<i>S. glaucopus</i>	2	-	-	-	*	-			rare	DK, S, PL	?
<i>S. imbricatum</i>	5	*	*	*	*	-	spruce (pine/deciduous)	(o)e	common	D, DK, NL, PL	0
<i>S. leucopus</i>	3	*	*	*	-	-	pine (spruce)	e-c	rare	D, S	+
<i>S. lundellii</i>	3	*	*	*	*	-	spruce (pine)	e-c	rare		+
<i>S. martioflavus</i>	3	-	*	*	-	-	spruce	e-c	rare	D, S	+
<i>S. scabrosus</i>	2	-	*	*	-	-	pine (spruce/deciduous)	o	rare	D, DK, NL	0
<i>S. versipellis</i>	3	-	*	*	*	-	spruce	(o)e	not common	D, S	0

Auriscalpium vulgare
Bankera fuligineo-alba
Hydnellum caeruleum
Sarcodon fennicus (?)
Sarcodon leucopus

(4) Mainly coniferous forest species, but occurring also in various types of deciduous forests

Hydnellum aurantiacum (*Picea*)
Hydnum repandum
Hydnum rufescens
Sarcodon imbricatus (*Picea*)
Sarcodon scabrosus

(5) Species preferring oak (*Quercus robur*, *Q. petraea*) forests

Hydnellum compactum
Phellodon confluens

Successional patterns

Little information on forest stand age has until recently been given on Norwegian herbarium labels, undoubtedly because most forests have been mixed age stands. However, surprisingly many of the collections had references to spruce and pine plantations, although again often without indications of stand age. Forest stands recognised as plantations, and spruce plantations outside the natural spruce area are mostly young or medium aged, generally not more than 50 years. With the growing interest in nature conservation, it has become more common in recent years to indicate mature forest habitats on the labels as well. Based on the annotations, the following groups could be recognised:

(1) Species recorded from sites with planted spruce (*Picea abies*), with trees less than 20 years old

Hydnellum geogenium
Hydnellum peckii

(2) Species recorded from forests with young trees

Bankera violascens (*Pinus sylvestris*)
Hydnellum compactum (*Quercus*)
Hydnellum conrescens

(3) Species recorded from spruce plantations or stands with spruce outside its natural area (i.e. with young- to medium-aged trees)

Bankera fuligineo-alba
Bankera violascens
Hydnellum mirabile
Hydnellum peckii
Hydnellum suaveolens
Hydnum repandum
Hydnum rufescens
Phellodon melaleucus
Sarcodon imbricatus
Sarcodon versipellis

(4) Species recorded from pine plantations

Bankera violascens (*Pinus sylvestris*)
Hydnum repandum (*Pinus sylvestris*)
Hydnum rufescens (*Pinus sylvestris*)
Auriscalpium vulgare (*Pinus mugo*)

(5) Species recorded from mature forests

Bankera violascens
Hydnellum aurantiacum
Hydnellum conrescens
Hydnellum ferrugineum
Hydnellum geogenium
Hydnellum mirabile
Hydnellum peckii
Hydnellum suaveolens
Hydnum repandum
Hydnum rufescens
Phellodon tomentosus
Sarcodon lundellii
Sarcodon martioflavus
Sarcodon versipellis

Edaphic preferences

Surprisingly many of the species had been collected on calcareous bedrock. For instance, 14 of the 28 stipitate hydneous species known in Norway have been collected on a small calcareous (Cambro-Silurian) island in the Oslofjord in South-East Norway, Bjørkøya, ca. 1 km long and ascending to 68 m.

Many species exhibited wide tolerances in soil nutrient status and have been collected in eutrophic vegetations types, e.g., Melico-Piceetum, as well as in poor types such as Eupiceetum and Vaccinio-Pinetum. Eutrophic coniferous forests appear, however, to be the preferred habitats for many species: Seven species occurred mainly, or only in rich habitats or in sites with calcareous bedrock, viz., *Hydnellum geogenium*, *H. mirabile*, *H. scrobiculatum*,



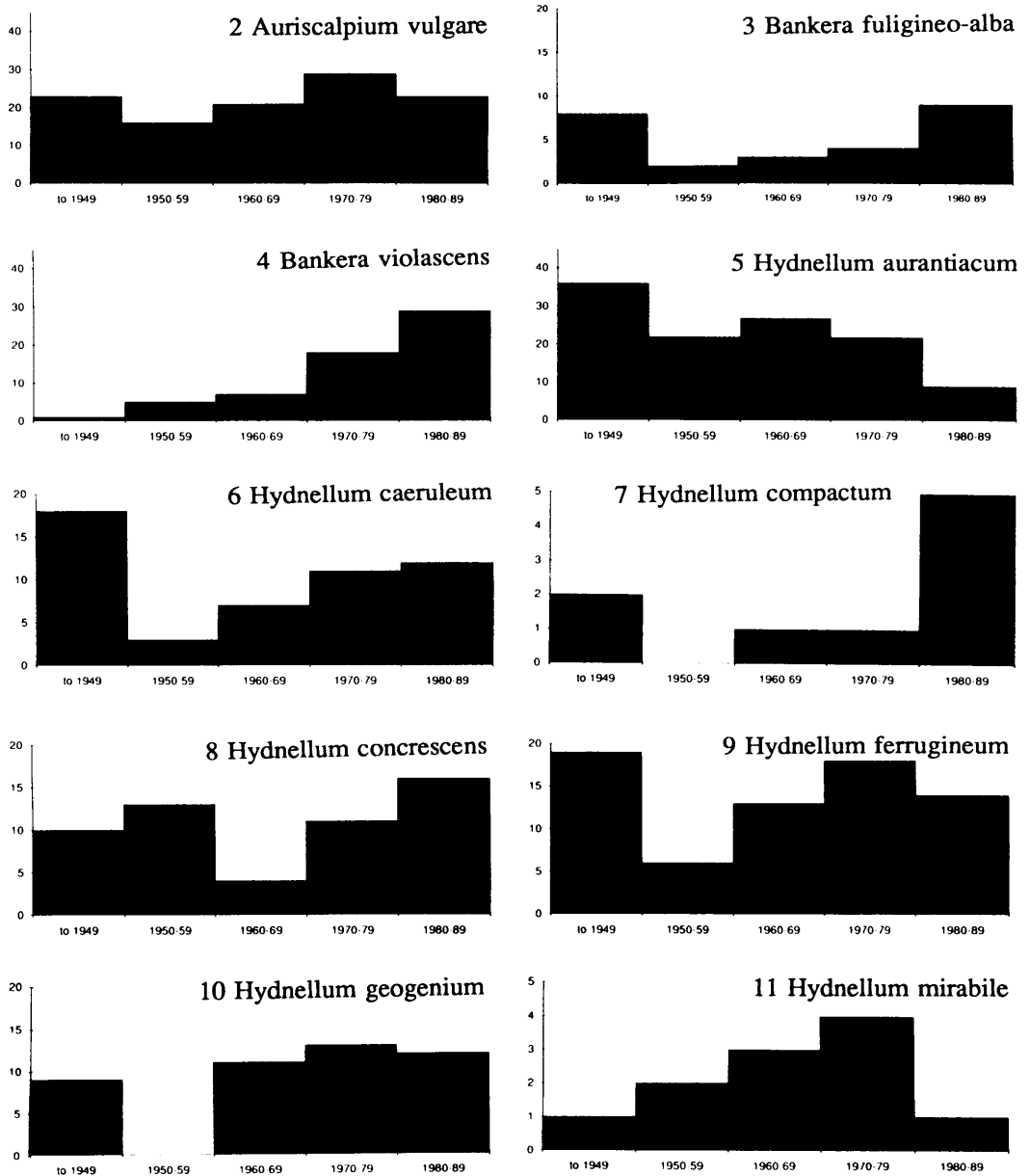
Fig. 1. Histogram showing the number of recorded finds of stipitate hydneous fungi in each decade from 1950 to 1989. The first column shows the number of observed finds up to 1949.

Sarcodon fuligineo-violaceus, *S. leucopus*, *S. lundellii* and *S. martioflavus*. Another group of six tended to prefer eutrophic habitats, but also occurred in poorer sites: *Auriscalpium vulgare*, *Hydnellum peckii*, *H. suaveolens*, *Phellodon niger*, *Sarcodon imbricatus*, and *S. versipellis*. Five species appeared to prefer oligotrophic sites: *Bankera fuligineo-alba*, *Hydnellum caeruleum*, *Phellodon confluens*, and *S. scabrosus*.

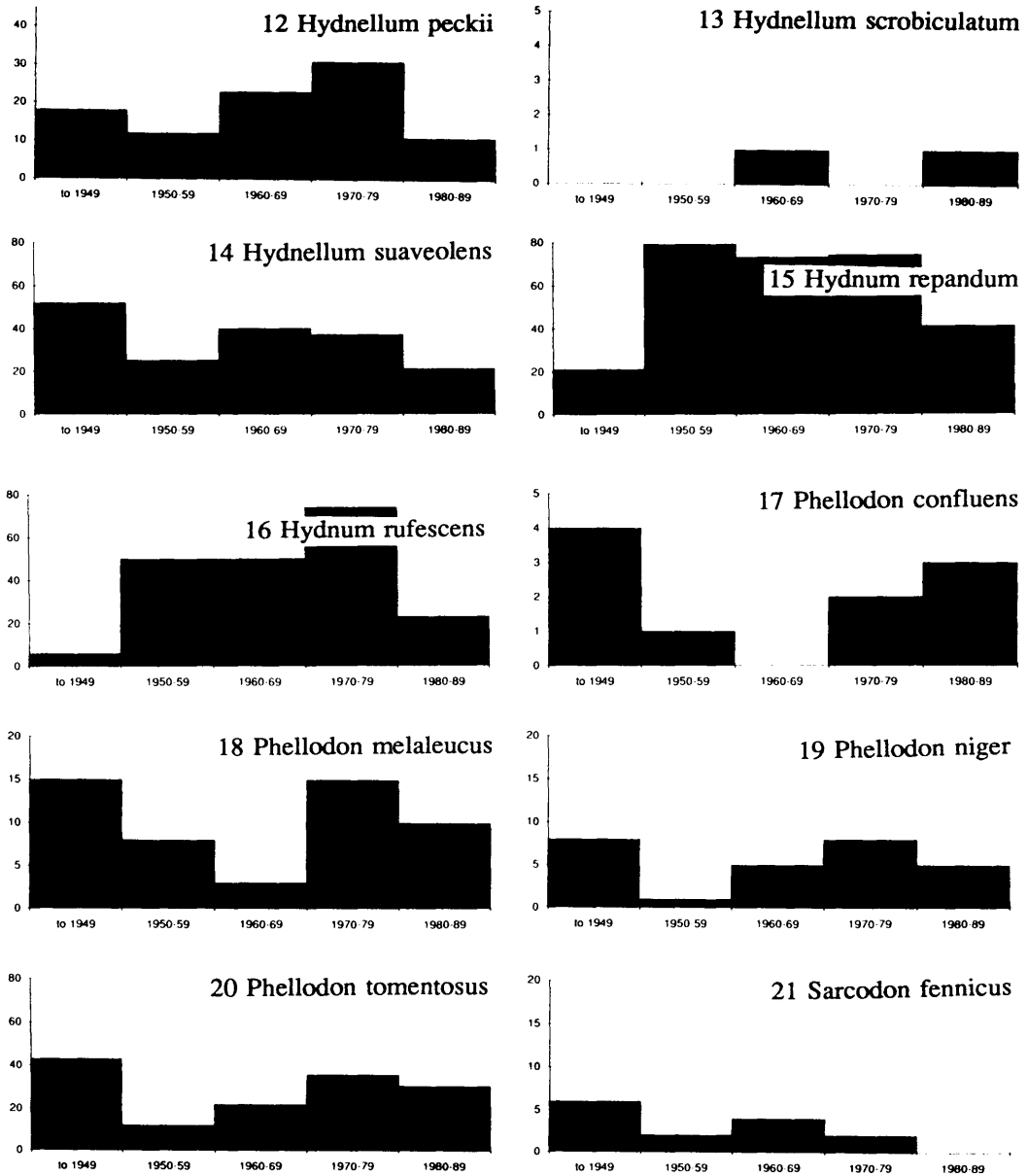
FREQUENCY OF OBSERVATIONS

Fig. 1 shows the total number of records of stipitate hydneous species in each decade from 1950 (and the total number of finds before this year). The number of observations in each of the last three decades has a peak in the 1970s of about 140 observations.

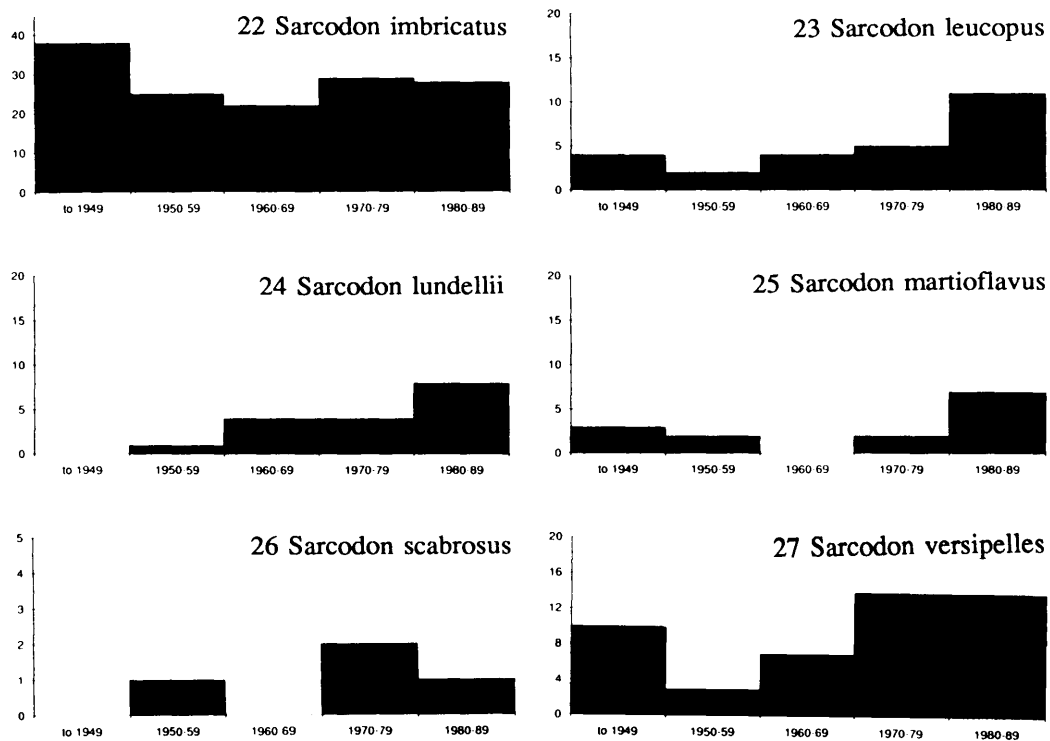
Figs 2-27 show the number of finds for each species in each decade. Of the more common species, referred to as "common" and "not common" in Tab. 1, four were represented with more finds in the recent period(s), five had fewer finds, and seven had about the same number of finds. Most of the "rare" species had been collected more frequently - or only - in the recent period(s).



Figs 2-11. Histograms showing the number of recorded finds of individual species in each decade from 1950 to 1989. The first column in each histogram shows the number of observed finds up to 1949.



Figs 12-21. Histograms showing the number of recorded finds of individual species in each decade from 1950 to 1989. The first column in each histogram shows the number of observed finds up to 1949.



Figs 22-27. Histograms showing the number of recorded finds of individual species in each decade from 1950 to 1989. The first column in each histogram shows the number of observed finds up to 1949.

DISCUSSION

NUMBER OF SPECIES

The 28 stipitate hydneous species growing in Norway represent about 65% of the European species. All of the species found in Norway also occur in Sweden (Strid 1983, 1984, 1985). Sweden has four additional and rare species: *Hydneum auratile* (Britz) Maas G., *H. gracilipes* (Karst.) Karst., *H. spongiosipes* (Peck) Pouzar, and *Hydneum albidum* Peck, which should be looked for in Norway. *Hydneum cumulatum* K. Harrison, a species quite recently recognised in Europe (Maas Geesteranus 1975) and reported from Denmark (Vesterholt & Knudsen 1990), probably could occur in Norway. Some species growing e.g., in the Netherlands and Great Britain, are missing in Norway, but probably could occur on the south-west coast.

DISTRIBUTION AND OCCURRENCE IN VEGETATION REGIONS

For many of the species the distributional potential in Norway is probably wider than indicated by the maps. This is indicated in some cases by asymmetry between distribution pattern and occurrence in vegetation regions. Some species with similar distribution patterns in Norway do not have similar distributions in Europe as a whole. *Hydneum geogenium* and *Sarcodon fennicus*, for instance, both with distributions restricted to South-East Norway, have widely different distributions in Europe. *Hydneum geogenium* occurs at its northern limit in Norway, while *S. fennicus* has a wide distribution towards the north-east in Eurasia, and occurs at its south-western limit in Norway.

By taking into consideration such features, we have arrived at the following five geographical groups for the stipitate hydneous species:

Group 1 - southern coastal species, restricted to the nemoral and boreo-nemoral regions, present in all parts of Europe:

Hydneum compactum (Fig. 35)

Phellodon confluens (Fig. 43)

Group 2 - southern species, extending northwards to Central Norway, ascending to the southern boreal or the middle boreal region, present in all parts of Europe:

Bankera fuligineo-alba (Fig. 31)

Hydneum conrescens (Fig. 36)

Hydneum ferrugineum (Fig. 37)

Hydneum scrobiculatum (Fig. 42)

Phellodon melaleucus (Fig. 44)

Sarcodon fuligineo-violaceus (Fig. 42)

Sarcodon glaucopus (Fig. 42)

Sarcodon scabrosus (Fig. 52)

Group 3 - south-eastern species, extending northwards to Central Norway, ascending to the southern boreal or the middle boreal region, absent or rare in West Europe:

Hydnellum geogenium (Fig. 38)

Hydnellum mirabile (Fig. 39)

Phellodon niger (Fig. 45)

Sarcodon leucopus (Fig. 49)

Sarcodon lundellii (Fig. 50)

Sarcodon martioflavus (Fig. 51)

Sarcodon versipellis (Fig. 53)

Group 4 - eastern species, extending to North Norway, ascending to the southern boreal or the middle boreal region, absent or rare in West Europe:

Bankera violascens (Fig. 32)

Hydnellum aurantiacum (Fig. 33)

Hydnellum peckii (Fig. 40)

Hydnellum suaveolens (Fig. 41)

Sarcodon fennicus (Fig. 47)

Group 5 - ubiquitous species, extending to North Norway, ascending to the middle boreal or the northern boreal region, present in all parts of Europe:

Auriscalpium vulgare (Fig. 28)

Hydnellum caeruleum (Fig. 34)

Hydnum repandum (Fig. 29)

Hydnum rufescens (Fig. 30)

Phellodon tomentosus (Fig. 46)

Sarcodon imbricatus (Fig. 48)

Sensitivity to winter frost generally limits the distribution of vascular plants, probably also fungi, towards the north and east. Species requiring mild winters tend to follow the south and west Norwegian coast northwards, and to be absent or have a very limited distribution in South-East Norway. Judging from the maps, only the two species of group 1, *Hydnellum compactum* and *Phellodon confluens*, appear to be restricted primarily by the winter frosts in Norway.

The species of group 2 have a wide distribution in Europe, albeit some of them appears to be rare everywhere, i.e., *Sarcodon fuligineo-violaceus* and *S. glaucopus*. Their different extensions northwards and upwards in colder vegetation regions is probably restricted by summer temperature requirements.

The distribution maps show that eastern parts of Norway are comparatively very rich in stipitate hydneous fungi. An over-representation of finds in South-East Norway, due to more extensive collecting, has probably influenced the picture. However, many species which

are rare or absent in more southern and western parts of Europe occur in South-East Norway. For instance, at least seven of the species occurring in East Norway are not known from Great Britain, thirteen are not known from the Netherlands, and ten are not known from Denmark.

In South-East Norway two groups of "eastern" species occur, (i) a group of species present in all parts of South and Central Europe and extending northwards as far as Fennoscandia, and (ii) a group of widely distributed species in North-East Europe and Asia, extending south-westwards to South-East Norway or further, i.e., the typical boreal species which are more or less confined to the north-eastern coniferous forests in Europe. They tend to be absent or rare in North-West Europe, e.g., Great Britain, Denmark, and the Netherlands.

The species of group 3 belong to the group of southern species extending northwards. Like the vascular plants with corresponding distribution type, they clearly prefer habitats on calcareous rock at their northern limit. They represent a thermophilous element. These species do not extend much further north in Sweden and Finland than in Norway. *Sarcodon leucopus* has an odd outpost in Iceland, which does not fit with the general pattern. *Sarcodon lundellii* has so far not been recorded in southern parts of Europe. *Phellodon niger* has a few odd finds in northern Fennoscandia which fit badly with its generally very clear southeastern distribution in Fennoscandia.

The species of group 4, represent the boreal element. They have all a wide distribution in North-East Fennoscandia where they extend considerably further to the north than in Norway. They extend southwards in Europe and tend to be absent or rare in countries of North-West Europe. *Sarcodon fennicus* has not yet been recorded further south than Fennoscandia. Requirement for permanent frost or snow cover during the winter season appears to be essential for vascular plants with similar distributional limits in Europe (Conolly & Dahl 1970, Salvesen 1988, Salvesen 1989). Ohenoja & Tuokkola (1990) have demonstrated that correlations exist between winter temperatures, snow cover, and basidiomycete fruitbody production in North Finland.

The species of group 5 are apparently not restricted by climatic factors in Norway. *Phellodon tomentosus*, which is dominant in eastern parts of South Norway, is widely distributed in western as well as eastern Europe, and hence referred to this group. We consider the eastern dominance in Norway to reflect its clear preference for spruce in Norway. *Hydnum rufescens* tends to be a more continental species than *H. repandum*. It is much more rare further south in Europe than *H. repandum*, and tends to prefer montane regions (Arnolds 1989a).

Remarkably many of the species, at least 10, extend considerably further northwards in Sweden and Finland than in Norway, where they also reach colder vegetation regions. The causes for this remain unclear to us, unless there has been insufficient collecting in the northern and middle boreal regions in Norway. These regions are represented by much larger areas in Sweden and Finland, and in Norway they are situated beyond the main collecting areas in South-East Norway.

ECOLOGY

Arnolds (1989a) states that in the Netherlands there are three main types of habitats for the stipitate hydneous fungi: (i) plantations of Scots pine on dry, acid sand dunes, (ii) oak

forests on very poor, acid sand, and (iii) roadsides with old trees of oak and birch. Doll (1979) considers oligotrophic pine forests to be typical habitats of the terricolous hydneous fungi in northern Germany (Mecklenburg) and this may also be the situation in large parts of lowland, Central Europe. In addition, mixed deciduous forests, especially oak and beech forests of the more acid types, seem to be preferred. The picture changes at higher altitudes southwards, where spruce associations becomes more common. Of the 27 stipitate hydneous fungi included by Breitenbach & Kränzlin (1986) from Switzerland, *Bankera violascens*, *Hydnellum geogenium*, *H. suaveolens*, and *Sarcodon imbricatum* are indicated as exclusively spruce forest species.

The strong preference of *Sarcodon* species for spruce in Fennoscandia was already pointed out by Maas Geesteranus & Nannfeldt (1969). In fact, the genera *Hydnellum* and *Phellodon* are even more strongly associated with spruce in Norway. The preference for spruce may be another reason for the clear dominance of finds in South-East Norway, since *Picea abies* occurs naturally mainly in the eastern parts of Norway. Some of the eastern species of groups 3 and 4 above, also occur in Great Britain, albeit rarely and mainly (only ?) in northern districts, i.e. *Hydnellum aurantiacum*, *H. peckii*, *H. suaveolens*, and *Phellodon niger*. Hence, climate is hardly the main limiting cause for their eastern dominance in Norway. Rather a shortness of a suitable mycorrhizal partner is reflected. *Hydnellum suaveolens* seems to be exclusively associated with spruce. Apart from a clear preference for spruce in Norway, the other three can grow also with pine, and *H. aurantiacum* and *Phellodon niger* with deciduous trees as well.

Many of the stipitate hydneous species tend to shift preference from deciduous forests further south in Europe to coniferous forests in Fennoscandia. Arnolds (1989a) indicates this shift for *Hydnellum conrescens*, *Phellodon niger*, *Hydnum repandum*, and *Sarcodon scabrosus*. This apparently also applies to *Phellodon niger* and *Hydnum rufescens*. Another remarkable switch is observed with the *Bankera* species, where *B. violascens* tends to shift from spruce to pine towards north and west, and *B. fuligineo-alba* occasionally occurs with spruce.

In the Netherlands the ectomycorrhizal hydneous species are restricted to mature forest stands with trees over 40 years old (Arnolds 1989a). With reference to Danielson (1984) Arnolds assumes they belong to the late stage mycorrhizal symbionts. In Norway at least five species occur in young forest stands (cf. p. 14), and some more species probably have been collected in forest stands with relatively young trees (cf. gr. (3), p. 14-15).

A remarkable difference is seen between the edaphic preferences of the stipitate hydneous species in Norway (Fennoscandia) as compared to lowland parts of Central Europe. Maas Geesteranus (1975, General part: 10), states that all stipitate hydneous species occur on acid ground in Europe. Arnolds (1989a) maintains that in the Netherlands they mainly grow in habitats on acid soils. Only *Auriscalpium vulgare* and the two *Hydnum* species are reported from rich soils (Arnolds 1989b). In Fennoscandia, however, preference for calcareous sites has been recognised for several species (Ryman & Holmåsén 1984, Strid 1984, 1985). Thirteen species are more or less eutrophic in Norway, cf. p. 15 and Tab. 1. Only four of these occur in the Netherlands (*Hydnellum compactum*, *H. peckii*, *Phellodon niger*, and *Sarcodon imbricatus*), where they all are typical of oligotrophic sites (Arnolds 1989b).

The pronounced preference for eutrophic and calcareous habitats of the hydneous species in Norway, may also have contributed to the eastern dominance seen on the maps, since the bedrocks of most western districts in South Norway are acid.

THE QUESTION OF DECLINE

The southernmost coastal districts of Norway have received the largest amounts of air pollution and this is the region where trends of decline should be expected the first. Too few collections from this part of the country, however, have made a comparison of temporal trends impossible. Reasons for the low numbers may partly be low collecting and partly shortness of suitable habitats. Mixed deciduous and pine forests on acid bedrock dominate, and the resulting habitats are not preferred by most hydneous fungi in Norway.

There is no obvious decline in the flora of stipitate hydneous fungi in Norway, when seen as a group. The total reduction in finds from the 1970s to the 1980s amounts to 134 (Fig. 1). A reduction of 84 is contributed by the two common species *Hydnum repandum* and *H. rufescens* alone. More species show increasing or unchanging tendencies over time, rather than decreasing (Tab. 1), and observed reductions are never dramatic (cf. Figs 2-27). There is, however, a trend towards reduction among the more common species, and increase among the rarer species. All the "common" species show decline or a maintenance of status quo, while as many as five of the "rare" species have increased and only one has decreased. We believe this different trend between the "common" and the "rare" species reflects a shifting interest along with progress in the mycological exploration of the country.

We regard only the "common" and "not common" species as represented by sufficient data to permit statistical evaluation of possible changes. Five of these show a tendency of decline, viz., *Hydnum repandum*, *H. rufescens*, *Hydnellum aurantiacum*, *H. peckii*, and *H. suaveolens*. Changes in collecting and reporting routines mostly affect common species and probably account for the decline of the two *Hydnum* species. We do not think the three *Hydnellum* species have been ignored in the same way. Applying the chi square test to a comparison of the proportion of observations in the 1980s with the pre-1980 proportions, indicated significant declines for *H. aurantiacum* ($p < 0.001$), *H. suaveolens* ($p < 0.005$), and *H. peckii* ($p < 0.02$). Although these figures suggest a significant decline in the species mentioned, some caution must be applied to the statistics, since they relate to three of a total of 26 species (in the test *H. repandum* and *H. rufescens* were excluded). The "declining" *Hydnellum* species are all ranged in group 4 (p. 21). Their main distribution is eastern, in Fennoscandia as well as further south in Europe. In western parts of Norway their presence is marginal. Common features are confinement to or preference for spruce, and preference for eutrophic habitats.

The species considered extinct in the Netherlands, which grow in Norway, are all ranged in group 4 and group 5 of our classification, except for *Bankera fuligineo-alba* of group 2. Some of these species probably occurred outside their climatically optimal area in the Netherlands. A further stress caused by human activities may easily have erased the populations.

Arnolds (1989a) recorded a much stronger decline of species associated with conifers than with deciduous trees, and the strongest decline among species typically growing in the most acid soils. *Hydnellum aurantiacum* and *H. peckii* are both considered extinct in the Netherlands, last found in 1954 (Arnolds 1989a). They were both typical of acid soils, and associated with conifers. In Norway, however, they prefer eutrophic habitats. The same is true for *H. suaveolens*, which is unknown from the Netherlands. None of the typically oligotrophic species has declining trends in Norway.

Hydnellum peckii is listed as threatened with extinction in eastern Germany (Benkert

1982). *Hydnellum aurantiacum* is considered extinct in parts of northern Germany (Wöldecke 1987) and endangered in Denmark (Vesterholt & Knudsen 1990). *Hydnellum suaveolens*, which still appears to be the most common of the *Hydnellum* species in Norway, was not observed for decades in the former DDR according to Otto (1989). It is considered vulnerable in Poland (Wojewoda & Ławrynowicz 1986). Observations from Norway and the general trend in Europe make these three species particularly interesting objects for future monitoring.

SPECIES CONSIDERED

FAM. AURISCALPIACEAE Maas G., GEN. AURISCALPIUM S.F. Gray

Auriscalpium vulgare S.F. Gray
Figs 2, 28.

Distribution: Some 60 Norwegian finds have been added since Koski-Kotiranta & Niemelä (1987) published its distribution in Fennoscandia, but the resulting pattern is in all essentials the same. The species is distributed fairly evenly over southern and central parts of Norway, but with very few records in southern coastal districts. There are only two finds from North Norway, and its northernmost known locality is Alta (Finnmark), at 70° N. *Auriscalpium vulgare* occurs with about the same frequency in the different vegetation regions, from the nemoral to the southern boreal region, and becomes rare in the middle boreal region. However, it follows this region to its northernmost outpost, Alta.

Ecology: Nine finds were made on spruce cones (*Picea abies*), while the specimens of the remaining 110 finds were probably all growing on pine cones (*Pinus sylvestris*). One find was from a *Pinus mugo* plantation. There is little information on soil and vegetation on the herbarium labels, except for notes with six of the collections that they were found on calcareous ground or in eutrophic vegetation types. However, several more collections are from regions with calcareous bedrock.

Temporal trend: The number of finds in Norway during the recent decades has been fairly constant.

Extra-territorial occurrence: The species has a wide distribution over the northern Hemisphere (Koski-Kotiranta & Niemelä 1987). In Finland it extends to the northern boreal region, where it is rare (Koski-Kotiranta & Niemelä 1987). According to Arnolds (1989a) it has been widespread and common in the Netherlands up to about 1960, but it has now become rare in regions with acid, pleistocene soils with low buffer-capacity. On the other hand, it has recently become established in some young coniferous plantations on calcareous sands in newly reclaimed polders. Pine (*Pinus sylvestris*) is its main host. The proportion of finds on spruce cones (*Picea abies*) in Fennoscandia as a whole is about 10% (Koski-Kotiranta & Niemelä 1987).

FAM. HYDNACEAE Chev., GEN. HYDNUM L. : Fr.

Both *H. repandum* and *H. rufescens* are common in Norway and certainly under-represented in herbaria due to their commonness. A third species of the genus, *H. albidum* Peck, is known in Europe only from Czechoslovakia, Germany, Denmark, and Sweden, and has not yet been found in Norway.

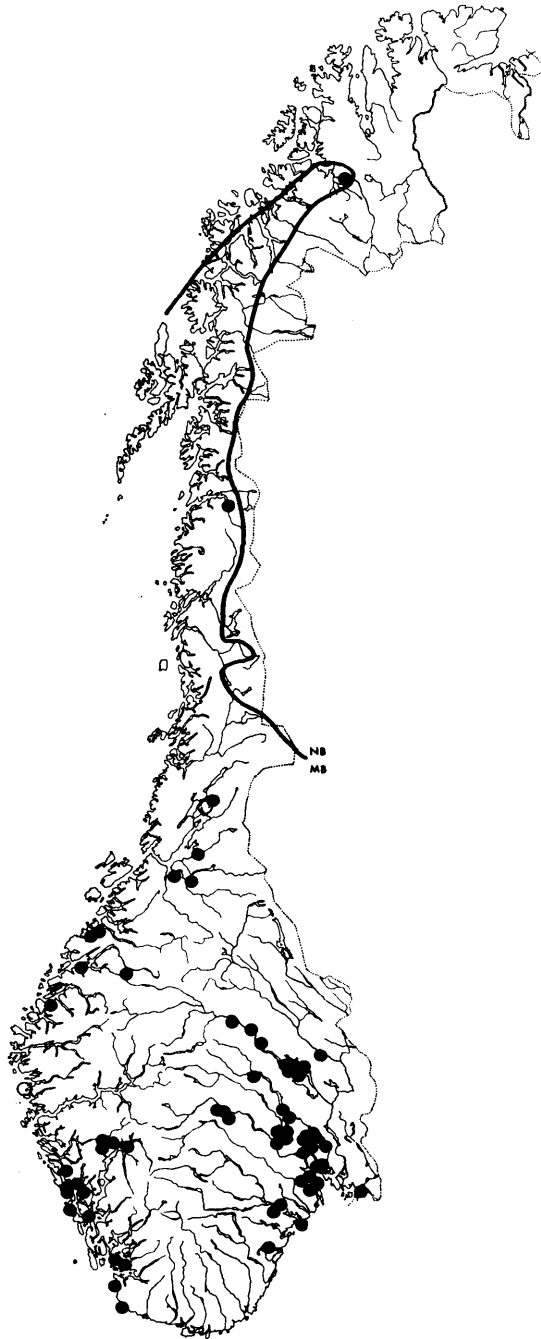


Fig. 28. Distribution map. *Auriscalpium vulgare*. The border between the middle and northern boreal regions in North Norway is indicated.

Hydnum repandum L. : Fr.

Figs 15, 29.

Distribution: The species occurs in all parts of the country, with the northernmost known locality near Alta (Finnmark) at 70° N. It occurs in all vegetation regions up to the timberline.

Ecology: At the timberline it is generally associated with *Betula*. For the rest it has mostly been found in spruce and mixed forests, but also in pine forests, and deciduous forests without conifers, often with oak (*Quercus robur* and *Q. petraea*), beech (*Fagus sylvatica*), and hazel (*Coryllus avellana*). It is recorded from spruce plantations as well as from old forests. It grows in humus, and most finds are from poor to intermediate sites, although it also occurs in eutrophic sites.

Temporal trend: This is probably the most common hydneaceous species in Norway. There are considerably fewer finds in the last decade than in the three previous ones, cf. comments p. 24.

Extra-territorial occurrence: *Hydnum repandum* is also common in Central Europe, but has become rarer in recent years, e.g., in the Netherlands (Arnolds 1989a) and parts of Germany. In Saarland (western Germany) it has disappeared completely from numerous forest sites (Schmitt 1987). In the Netherlands, this species and *H. rufescens* are the only two mycorrhizal hydneaceous species reported to grow not only in poor sites, but also in richer soils (Arnolds 1989a, 1989b).

Hydnum rufescens Fr. : Fr.

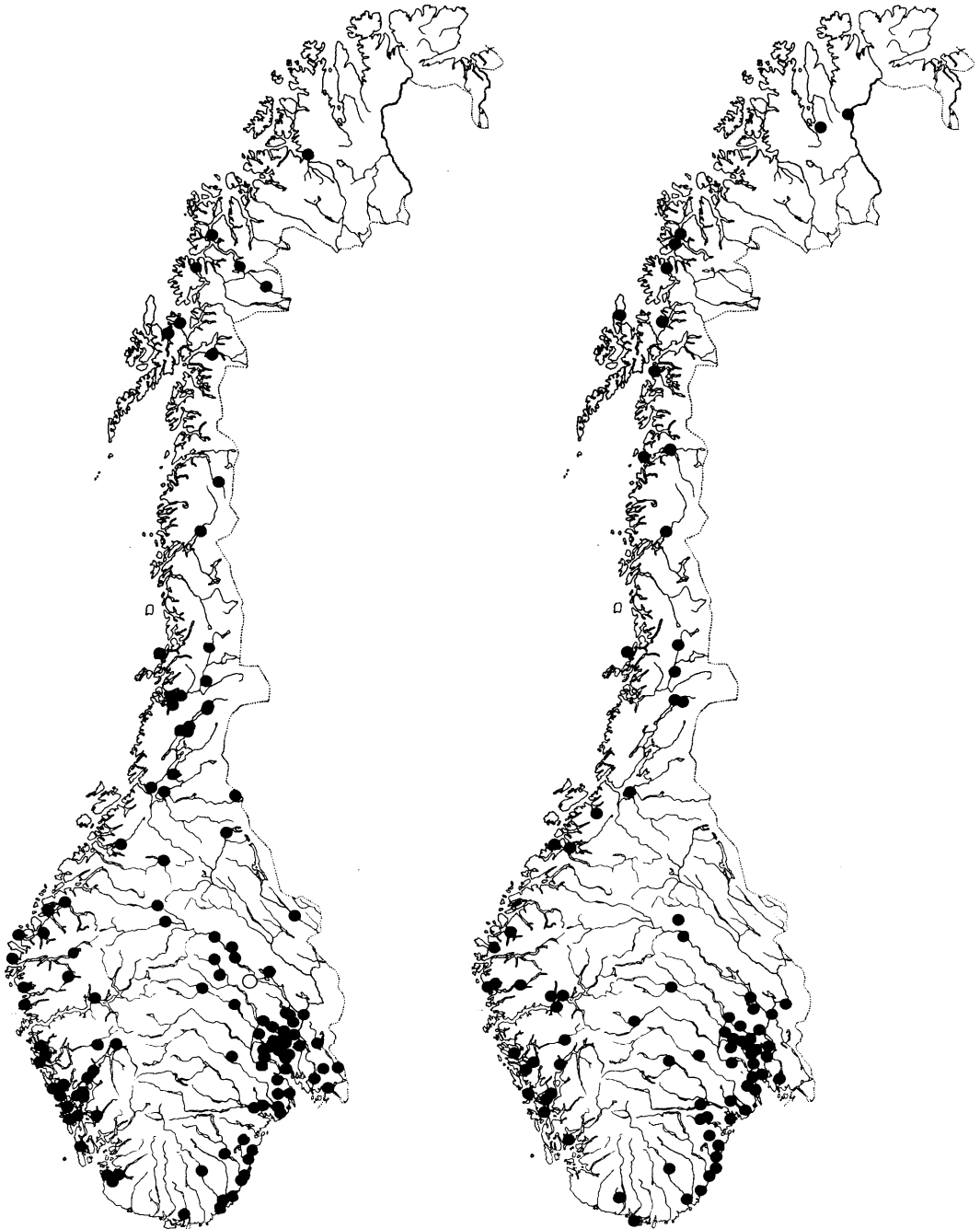
Figs 16, 30.

Distribution: The pattern is much the same as for the previous species. Its northernmost known locality is Lakselv (Finnmark), slightly north of 70° N. It has been collected twice above the timberline, up to 1150 m, growing with *Betula nana*, *Juniperus communis*, and *Dryas octopetala*.

Ecology: Most collections are from spruce and pine forests, in plantations as well as old forests. It also grows in deciduous forests with many different deciduous tree species. It has also been reported from pastures, and rather frequently from moist habitats. It grows on humus and seems to have a wide pH tolerance, but may prefer slightly richer soils.

Temporal trend: This is a really common mushroom in Norway, but there are relatively very few reported finds from the last decade, cf. comments p. 24.

Extra-territorial occurrence: *Hydnum rufescens* is known from all European countries, but seems to be more common in upland sites than in the lowlands (Maas Geesteranus 1975). Apparently it becomes rare towards the west in Europe, where it is much rarer than *H. repandum*. In Great Britain it is considered uncommon or occasional (Phillips 1981, Buczacki 1989). In the Netherlands it is, and probably always has been, rare. According to Arnolds (1989a) there is only one record from the Netherlands after 1983.



Figs 29-30. Distribution maps. Fig. 29. *Hydnum repandum*. Fig. 30. *H. rufescens*.

FAM. THELEPHORACEAE Chev., GEN. BANKERA Coker & Beers ex Pouz.

Bankera fuligineo-alba (Schmidt : Fr.) Pouz.

Figs 3, 31.

Distribution: There are scattered finds from all parts of South Norway, north to Molde (Møre & Romsdal) at 62° 45' N. A relatively large proportion of finds are from the west coast. The species ascends to the middle boreal region, in the south-eastern valleys to about 700 m.

Ecology: Most finds are from pine forests, often dry with mosses and lichens, but some have been made in spruce forests, in mixed pine and spruce forests, and in coniferous forests mixed with *Betula*. It has been collected in a young pine plantation and in spruce plantations in West Norway. For one collection calcareous ground is indicated. Sands and other inorganic soils may be preferred.

Temporal trend: There are relatively many finds from the last decade.

Extra-territorial occurrence: The species has been found much further to the north in Sweden and Finland than in Norway, and according to Strid (1983) it is even more common northwards in Sweden than in the southern parts. In Finland it extends northwards to the limit of the pine in Lapland (E. Ohenoja, pers. comm.). It has a wide distribution in Europe (Maas Geesteranus 1975) and in the Soviet Union (Nikolajeva 1961). In the Netherlands *B. fuligineo-alba* has not been observed since 1968 and is considered extinct (Arnolds 1989a). Originally it was not rare. The species is included in Red data lists from Germany, Poland, and Denmark.

Comments: *Bankera fuligineo-alba* is generally considered as strictly associated with pine (cf. Maas Geesteranus 1975), and as a typical species of dry pine forests on acid, sandy soils (Arnolds 1989a, 1989b). Its habitat range is more diverse in Norway than elsewhere in Europe, both with regard to edaphic conditions and associated tree genera.

Danielson (1984) was able to synthesize ectomycorrhizas of *B. fuligineo-alba* and jack pine (*Pinus banksiana*).

Bankera violascens (Alb. & Schwein. : Fr.) Pouz.

Figs 4, 32.

Distribution: The distribution in Norway is eastern, except for five finds on the west coast. There are also scattered finds from North Norway, with the northernmost from Alta (Finnmark), close to 70° N, at the northern limit of the middle boreal region. In the southeast it ascends to 700 m, which is at the upper limit of the middle boreal region.

Ecology: *B. violascens* is associated in the first place with spruce, but north of the northern limit of spruce it has been collected eight times in pine forests. Also one collection from the south coast, Onsøy (Østfold), was made in a (young) pine plantation. The localities on the west coast are also outside the natural distribution area of the spruce. Here the species was found twice in spruce plantations. *Bankera violascens* has been found in eutrophic sites (e.g., tall-herb spruce forest, low-herb spruce forest, and pine forest on calcareous ground), as well as in oligotrophic *Vaccinium* dominated spruce forest types. Moister habitats are fairly often referred to. It grows in young and old forests.

Temporal trend: There is an increasing number of finds through the last decades.



Figs 31-32. Distribution maps. Fig. 31. *Bankera fuligineo-alba*. Fig. 32. *B. violascens*.

Extra-territorial occurrence: Strid (1983) reports *B. fuligineo-alba* as the more common *Bankera* species in North Sweden. In Finland it follows the spruce northwards to its limit in Central Lapland (E. Ohenoja, pers. comm.). Compared to *B. fuligineo-alba*, *B. violascens* has a more continental distribution in Europe. It grows in Denmark and Spain (Petersen & Vesterholt 1990, M. Nunez pers. comm.), but is not on record from the Netherlands, nor from Great Britain (Arnolds 1989a, R. Watling pers. comm.). In Germany, Poland and Denmark it is included in Red data lists.

Comments: In Norway the *Bankera* species do not strictly follow the general pattern in Europe with *B. fuligineo-alba* confined to pine forests and *B. violascens* to spruce forests. Especially in the north and west, *B. violascens* changes its habitat ecology and grows with pine. In the west, *B. fuligineo-alba* also tends to shift associated tree, from pine to spruce. *Bankera violascens* is the more common species in Norway, and it extends considerably further to the north than *B. fuligineo-alba*, quite opposite to what it does in Sweden.

Otto (1989) has demonstrated ectomycorrhizal association between *B. violascens* and *Picea abies*.

FAM. THELEPHORACEAE, GEN. HYDNELLUM P. Karst.

With ten species, this is the largest genus of stipitate hydneaceous fungi in Norway.

Hydnellum aurantiacum (Batsch : Fr.) P. Karst.
Figs 5, 33.

Distribution: The distribution is mainly eastern in Norway, extending northwards to Nord-Trøndelag (Central Norway). There is one odd record from the south-west coast, made by Blytt (1905; Finnøy, Rogaland). In the south-eastern valleys it ascends to ca. 600 m, i.e., the middle boreal region. The record of *Hydnellum aurantiacum* from pine forest at Tronfjell (Henning 1885) possibly represents a northern boreal site.

Ecology: The finds are almost exclusively from spruce and mixed forests, ranging from the poor *Vaccinium myrtillus* type to eutrophic types, e.g., Melico-Piceetum. Three times it has been collected in pine forests, and according to the herbarium labels, once in a deciduous forest.

Temporal trend: There are many collections from the three decades between 1950 and 1980, but relatively few from the 1980s.

Extra-territorial occurrence: *Hydnellum aurantiacum* extends north to Central Lapland in Finland (Kallio & Kankainen 1964). In Sweden it is more common in northern parts than in the south and south-western parts (Ryman & Holmåsen 1984). Its distribution in Europe is mainly eastern. It is rare in Denmark (Petersen & Vesterholt 1990) and rare, predominantly northern in Great Britain (Buczacki 1989). A preference for spruce does not seem to be present in other parts of Europe; pine is more often reported. In some parts it also grows in mixed deciduous forests. In the Netherlands it is very rare and found exclusively in pine forests on acid sand. It has not been collected there since 1954 and is considered as probably extinct (Arnolds 1989b). *Hydnellum aurantiacum* is included in Red data lists from the



Figs 33-34. Distribution maps. Fig. 33. *Hydnellum aurantiacum*. Fig. 34. *H. caeruleum*.

Netherlands, Germany, Poland, and Denmark.

Hydnellum caeruleum (Hornem.) P. Karst.

Figs 6, 34.

Distribution: The distribution in Norway is generally eastern, but six finds have been made on the west coast. There is a large gap (> 800 km) between the southern finds in Norway, north to Trøndelag, and a single find in Finnmark (Alta), at 70° N, but the distribution is more or less continuous through northern Sweden and Finland. It ascends to ca. 600 m, i. e., the middle boreal region.

Ecology: *H. caeruleum* is a typical species of poor, dry pine forests (Cladonio-Pinetum and Barbilophozio-Pinetum). Most of the Norwegian collections are from such pine and mixed coniferous forests. Three finds are from spruce forests, and one is from a site with *Betula* and *Juniperus*. Typically it grows on litter, among mosses, *Cladonia* and *Calluna*.

Temporal trend: The species is not common in Norway, in spite of the abundance of its favoured vegetation types. Finds have increased since the 1950s.

Extra-territorial occurrence: *Hydnellum caeruleum* is rather common in pine and spruce forests in Sweden and Finland (Strid 1984, E. Ohenoja, pers. comm.). In Finland it follows the pine northwards to its limit in the northern boreal region in Utsjoki, Inari Lapland (Ryman & Holmåsén 1984, E. Ohenoja, pers. comm.). According to Maas Geesteranus (1975) *H. caeruleum* grows in coniferous forests, rarely in beech forests, in all parts of Europe. It seems to become more common eastwards. In Great Britain it is rare and confined to the Highland pine forests (Phillips 1981). In the Netherlands it has become very rare since 1950, and was observed most recently in 1956 (Arnolds 1989a). It is included in Red data lists from the Netherlands, Germany, Poland, and Denmark.

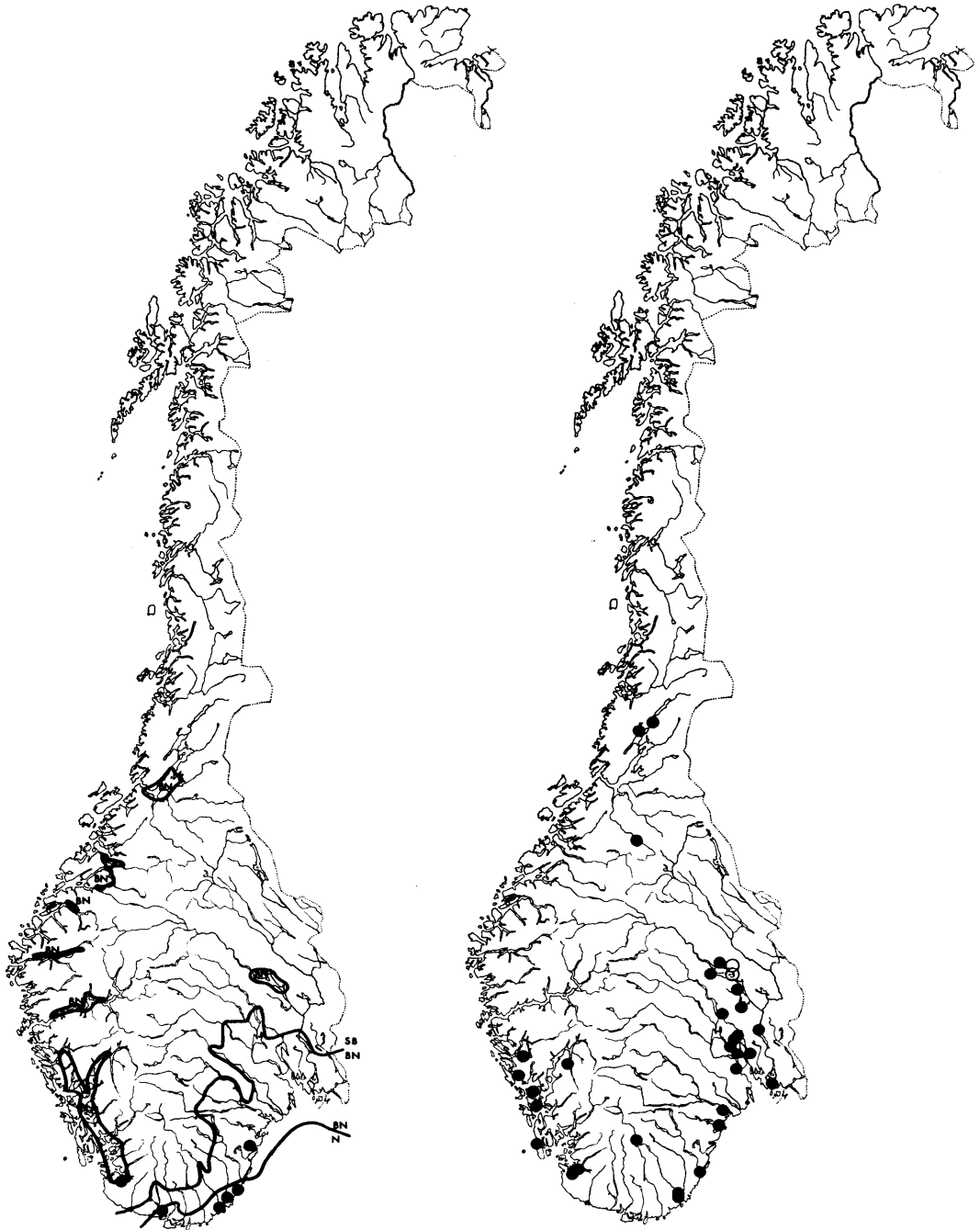
Comments: The North American species *Hydnellum ferrugipes* Coker closely resembles *H. caeruleum*. According to Maas Geesteranus they can be distinguished mainly by the lack of clamps in *H. ferrugipes*. This species was first recognised in Europe (France) in 1976 by Maas Geesteranus (1976), and a find from Lindås (Hordaland, W Norway) was published two years later (Maas Geesteranus 1978). Also several finds of the species from all parts of Finland were recorded.

When closer studied, quite a few more of the Norwegian collections filed as *H. caeruleum* turned out to lack clamps, or at least to have very few clamps. The criterion of clamps, however, seems to be of doubtful value. Baird (1986) found "rare to locally abundant" clamps in the type specimen of *H. ferrugipes*. Since no other good criteria for distinction are known, we consider *H. ferrugipes* a doubtful taxon.

Hydnellum compactum (Pers. : Fr.) P. Karst.

Figs 7, 35.

Distribution: In Norway this species is strictly southern and coastal, restricted to the nemoral and boreo-nemoral regions. Its distribution fits well into the "southern oak forest element" of macrofungi in Norway described by Brandrud (1986), including species like *Albatrellus cristatus*, *Collybia fusipes*, *Cortinarius orellanus*, *C. humicola*, *Phylloporus rhodoxanthus*, *Tricholoma pardinum*, and *T. ustaloides*.



Figs 35-36. Distribution maps. Fig. 35. *Hydnellum compactum*. The border between the nemoral and the boreo-nemoral region and the border between the boreo-nemoral and the southern boreal region are indicated. Fig. 36. *H. concrescens*.

Ecology: *H. compactum* has been collected in dense oak forest with young trees. There is little information on edaphic conditions with the material.

Temporal trend: Most of the finds are from the last decade.

Extra-territorial occurrence: *Hydnellum compactum* is associated with trees of the order Fagales further south in Europe (Maas Geesteranus 1975). The indication of *Pinus sylvestris* as accompanying tree by Arnolds (1989b) is odd. In southern parts of Scandinavia it is rare and at its northern limit. It does not occur in Finland (E. Ohenoja, pers. comm.). Its presence in Great Britain is questionable. In the Netherlands the species has strongly decreased and has only been observed three times since 1973 (Arnolds 1989a). It is included as rare in the Dutch and the Swedish Red data lists.

Hydnellum conrescens (Pers.) Banker

Figs 9, 37.

Distribution: The species grows in South and Central Norway north to Verran (Nord-Trøndelag) in inner Trondheimsfjord. The distribution is mainly eastern, but there are quite a few finds on the north-west coast between Bergen and Stavanger. It ascends to the upper limit of the southern boreal region.

Ecology: The finds are mainly from eutrophic spruce and oak forests; e.g., Melico-Piceetum. Calcareous ground is indicated. One find is from a poor, *Vaccinium*-rich pine forest. It has been collected under young oak shrubs as well as in old forests of oak and spruce.

Temporal trend: The species has been collected relatively often in the last decade.

Extra-territorial occurrence: *H. conrescens* is apparently at its northern limit in Fennoscandia. It is considered fairly common in Sweden (Ryman & Holmåsén 1984), and rather rare in Finland, where it extends to the northern boreal region in Central Lapland (E. Ohenoja, pers. comm.). Maas Geesteranus (1975) records *H. conrescens* from most European countries, growing in deciduous and coniferous forests. According to Arnolds (1989a, 1989b) the species grows with deciduous trees and shrubs in the south, and tends to switch to conifers towards the north in Europe. Otto (1989) reports hyphal connexions between *H. conrescens* and roots of *Picea abies* in Germany. According to Arnolds (1989a) it has strongly decreased in the eastern and southern parts of the Netherlands with originally strongly acid soils. The species is included in Red data lists from the Netherlands, Germany, Poland, and Denmark.

Hydnellum ferrugineum (Fr. : Fr.) P. Karst.

Figs 9, 36.

Distribution: The distribution in Norway is southern, with the northernmost find at Molde (Møre & Romsdal). So far it has rather surprisingly not been found in the wide Central Norwegian spruce forest areas in Trøndelag. The finds are predominantly from South-East Norway, but the number of finds from the west coast is not negligible. In the south-eastern valleys it ascends to ca. 500 m and thus reaches the middle boreal region. A wider distribution towards the north in Norway than indicated by the map, is to be expected on account of its presence in middle boreal habitats. It is one of the more common *Hydnellum* species.

Ecology: The finds are from spruce and pine forests. The species has been collected in eutrophic (Melico-Piceetum) as well as in oligotrophic (Barbilophozio-Pinetum) coniferous



Figs 37-38. Distribution maps. Fig. 37. *Hydnellum ferrugineum*. Fig. 38. *Hydnellum geogenium*. The border between the middle boreal and the northern boreal region is indicated.

forests. One collection is annotated as from old forest.

Temporal trend: The number of finds in the last decade is about the same as in the previous two decades.

Extra-territorial occurrence: *Hydnellum ferrugineum* is also fairly common in Sweden and Finland. It grows further to the north in eastern Fennoscandia (Ryman & Holmåsén 1984). In Finland it follows the pine northwards to its northern limit in the northern boreal region, Inari Lapland (E. Ohenoja, pers. comm.). Towards the northeast *H. ferrugineum* is more common in pine than in spruce forests, preferring poor and dryish pine heaths. Maas Geesteranus (1975) records *H. ferrugineum* from most parts of Europe, but states that it is absent in the Netherlands, and that it possibly also is absent in the extremely western parts of Great Britain, Belgium, north-western Germany and north-western France. Arnolds (1989c), on the other hand, records *H. ferrugineum* as previously rare in the Netherlands and now (probably) extinct. The species is included in Red data lists from the Netherlands, Germany, Poland, and Denmark.

Hydnellum geogenium (Fr.) Banker
Figs 10, 38.

Distribution: The distribution in Norway is south-eastern with a single outpost in Central Norway. Most finds are within the boreo-nemoral region; one or two finds originate from the southern boreal region.

Ecology: The species seems to be confined to spruce, and it often grows in moist and mossy sites among decaying needles. The finds are mainly from sites on calcareous ground or from eutrophic to intermediate forests. One collection is from an acid spruce forest. It grows in young plantations as well as old forests. The distribution in Norway seems to be restricted by climatic factors, since its area is very limited compared to the area of natural spruce forests.

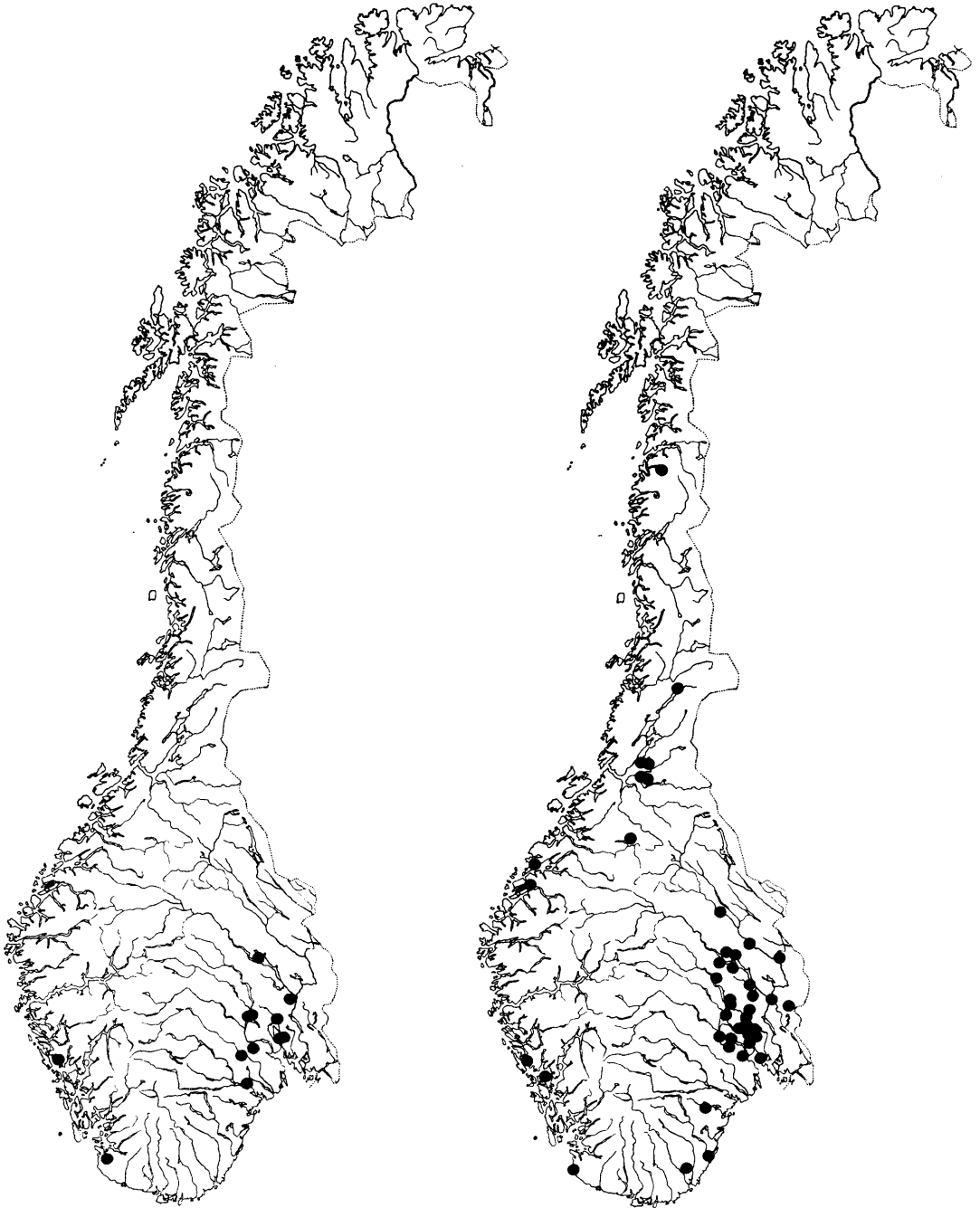
Temporal trends: The number of finds has been rather constant over the last three decades.

Extra-territorial occurrence: In Fennoscandia it does not appear to enter colder vegetation regions than the southern boreal region. The distribution in Fennoscandia as a whole is south-eastern, as seen from the map in Ryman & Holmåsén (1984). *Hydnellum geogenium* is an eastern species in Europe, at its northern limit in Fennoscandia, not recorded from Denmark, Great Britain, or Spain (Petersen & Vesterholt 1990, R. Watling, pers. comm., M. Nunez, pers. comm.). The species is included in Red data lists from Germany, Poland, and Sweden.

Hydnellum mirabile (Fr.) P. Karst.
Figs 11, 39.

Distribution: The species is rare in Norway, occurring mainly in the south-east, in the lower parts around the Oslofjord and north to lake Mjøsa. It is also known from two stations on the south-west coast. All finds are within the boreo-nemoral region.

Ecology: Five of the eleven finds of *H. mirabile* are from spruce forests, and with another two "coniferous forest" is indicated. On the west coast it grows in spruce plantations.



Figs 39-40. Distribution maps. Fig. 39. *Hydnellum mirabile*. Fig. 40. *H. peckii*.

One find is from a calcareous habitat, otherwise there is no information with the material as to the bedrock, soils or forest types.

Temporal trend: There is a decrease in finds the last decade.

Extra-territorial occurrence: The finds on the Norwegian south-west coast probably represent western outposts in Europe. In Sweden and Finland the species is also very rare. It has been found north to Norrland in Sweden (Strid 1984), where it occurs in coniferous forests, probably in the middle boreal region. Ryman & Holmåsén (1984) suggest a preference for calcareous habitats. The species is not recorded from Great Britain, the Netherlands, or Spain (Arnolds 1989a, R. Watling, pers. comm., M. Nunez, pers. comm.). The species is rare also in eastern parts of Europe. It is included as rare in the Swedish Red data list.

Hydnellum peckii Banker apud Peck
Figs 12, 40.

Distribution: The distribution is mainly eastern, extending northwards in North Norway to Beiarn (Nordland) at 67 °N. Only five finds are from the west coast. In South Norway it reaches 500 m, i.e., sites in the middle boreal region.

Ecology: Most finds are from spruce forests. The North Norwegian and some West Norwegian collections are from spruce plantations outside the naturally occurring spruce forests. Many collections have also been made in mixed coniferous forests. One of the western finds is from a pine forest. In the east only two collections are reported from pine forests. Many finds are from intermediate to rich sites, e.g., low-herb spruce forests, but it also grows in poor sites, e.g., a *Vaccinium* rich pine forest. It occurs in young plantations as well as in climax forests.

Temporal trend: After *H. suaveolens*, *H. peckii* is the most common and widespread *Hydnellum* species in Norway. The number of finds in the last decade is only about one third of the number in the previous decade.

Extra-territorial occurrence: The species is also rather common in Sweden and Finland, growing in coniferous forests to the northernmost parts of the countries (Ryman & Holmåsén 1984, E. Ohenoja, pers. comm.). It appears to have a mainly eastern distribution in Europe. In Great Britain it is uncommon and only known from the Scottish pine woods (Phillips 1981). Arnolds (1989a) records only three localities in the Netherlands, where it was last observed in 1954. The species is listed as strongly endangered in Germany and vulnerable in Denmark.

Hydnellum scrobiculatum (Fr.) P. Karst.
Figs 13, 42.

Distribution: There are only two Norwegian collections, both from the inner part of the Oslofjord region, South-East Norway, in the boreo-nemoral region.

Ecology: Both finds are from mixed spruce and deciduous woods on calcareous soils.

Extra-territorial occurrence: By the present recognition of *H. scrobiculatum* in Norway, it is known from all the Nordic countries, but as a rare species occurring in the south only (Strid 1991). It appears restricted to the hemiboreal and southern boreal regions in Fennoscandia. *Hydnellum scrobiculatum* occurs in western and eastern parts of Europe



Figs 41-42. Distribution maps. Fig. 41. *Hydnellum suaveolens*. Fig. 42. *Hydnellum scrobiculatum* (dot), *Sarcodon glaucopus* (triangle), and *S. fuligineo-violaceus* (star).

(Phillips 1981, Jülich 1984), but appears to be rare or much confused with other species. It is included in Red data lists from western and eastern Germany, Poland, and Denmark. In Poland it is considered extinct (Wojewoda & Ławrynowicz 1986).

Comments: *Hydnellum scrobiculatum* has been much confused with e.g., *H. conrescens*, *H. ferrugineum*, and *H. peckii*. There are several records of the species in Norwegian literature, but most material has turned out not to belong to *H. scrobiculatum*.

Hydnellum suaveolens (Scop. : Fr.) P. Karst.

Figs 14, 41.

Distribution: The main distribution in Norway is eastern. The species is common in the south-east, where it has been found up to 700 m, and in Central Norway (Trøndelag). It extends northwards to Bodø (Nordland), slightly north of 67° N. There are very few records from the south and west coast. *Hydnellum suaveolens* is a typical species of the southern boreal region, but it ascends to the middle boreal region.

Ecology: All the annotated collections originate from spruce forests, or spruce forest with scattered pine and birch. Spruce needles are found with all collections. Many of the annotated finds have been made in intermediate to rich forests, a few in oligotrophic types. It typically grows among moss and decaying litter.

Temporal trend: This is the most common *Hydnellum* species in Norway. There is a steady decreasing number of finds since the 1950s and a rather strong decrease in the last decade.

Extra-territorial occurrence: The species is also rather common in South and Central Sweden (Ryman & Holmåsen 1984), but also here it appears to be restricted northwards and upwards to middle boreal habitats. In Finland it is a rather rare species, extending northwards to the inner part of the Gulf of Bothnia (E. Ohenoja, pers. comm.). In general the species seems to be rather common in eastern parts of Europe, and to be more or less absent from western parts (Maas Geesteranus 1975). It is a rare northern species in Great Britain (Buczacki 1989), and there are no records from the Netherlands and Denmark. It extends eastwards beyond the Urals in the Soviet Union (Nikolajeva 1961). According to Otto (1989) the species has not been seen in the former DDR for decades. It is included in German and Polish Red data lists.

FAM. THELEPHORACEAE, GEN. PHELLODON P. Karst.

All four European *Phellodon* species occur in Norway. Only *P. tomentosus* belongs to the more common stipitate hydneaceous fungi.

Phellodon confluens (Pers.) Pouz.

Figs 17, 43.

Distribution: The distribution is southern and coastal in Norway. The species is



Figs 43-44. Distribution maps. Fig. 43. *Phellodon confluens*. Fig. 44. *P. melaleucus*.

restricted to the nemoral and boreo-nemoral regions. It is rare and at its northern limit in Norway.

Ecology: All finds are from deciduous forests; in most cases oak forests are indicated, but occasionally *Populus tremula*. There is sparse information with the material, but the species seems to prefer relatively poor and dry sites in Norway.

Temporal trend: A few more finds were made in the last decade than in the two previous.

Extra-territorial occurrence: *Phellodon confluens* is rare also in Sweden, occurring only in the southern parts, in oak and beech forests on the southern west coast (Ryman & Holmåsen 1984). It has not been found in Finland (E. Ohenoja, pers. comm.). According to Maas Geesteranus (1975) *P. confluens* is known from most European countries. In the Netherlands it was previously rather common and one of the characteristic hydneaceous species in shrubby oak forests on acid sands. However, since 1971 it has been observed only three times (Arnolds 1989a). The species is included in Red data lists from the Netherlands, western Germany, Denmark, and Sweden.

Phellodon melaleucus (Sw. apud Fr. : Fr.) P. Karst.
Figs 18, 44.

Distribution: The distribution is southern in Norway, with a single find in Central Norway (Trondheim, Sør-Trøndelag). It ascends to the middle boreal region.

Ecology: *P. melaleucus* has mainly been found in spruce forests, but has also been noted in mixed forests with e.g., pine and oak. The scattered finds on the west coast are almost all from sites with planted spruce. Apparently it has a wide pH tolerance. The species has been collected on humus, in thick needle carpets, and on old ant hills.

Temporal trend: The number of finds is about the same the two last decades.

Extra-territorial occurrence: In Sweden, like in Norway, *P. melaleucus* is rare and with a fairly southern distribution (Strid 1983, Ryman & Holmåsen 1984). In Finland it extends north to the Arctic circle (E. Ohenoja, pers. comm.) where it enters the middle boreal region. According to Maas Geesteranus (1975) it occurs all over Europe, in deciduous and in coniferous forests. It was formerly fairly common in the Netherlands, but is now considered quite rare (Arnolds 1989a). The species is included in Red data lists from the Netherlands, Germany, Denmark, and Sweden.

Phellodon niger (Fr. : Fr.) P. Karst.
Figs 19, 45.

Distribution: The species is rare in Norway. Present finds indicate a south-eastern distribution. There is one collection possibly belonging to *P. niger* from the west coast, but the material is in bad condition and a definite identification is impossible. Most of the finds are from the boreo-nemoral region, some from the southern boreal region.

Ecology: The finds, as far as they are annotated, are mainly from spruce forests, and eutrophic types. We have collected it also in pine forests on acid soil (Barbilophozio-Pinetum). Most of the collections are from districts with calcareous bedrock. Its predominantly south-eastern occurrence suggests a requirement for relatively high summer temperatures.



Figs 45-46. Distribution maps. Fig. 45. *Phellodon niger*. Fig. 46. *P. tomentosus*.

Temporal trend: The number of finds is about the same through the three latest decades.

Extra-territorial occurrence: In Sweden and Finland its main distribution is also in southern districts (Strid 1983, Ryman & Holmåsén 1984). The record from the Koillismaa biological province in Finland (Ulvinen et al. 1981), in the middle or northern boreal region, represents a northern outpost. The species has a wide distribution in Europe, mainly from coniferous forests, from areas with either acid or calcareous soils (Maas Geesteranus 1975). In the Netherlands it was never common, and has strongly declined with only three records made since 1972 (Arnolds 1989a). It is included in Red data lists from the Netherlands, Germany, Poland, and Denmark.

Comments: Otto (1989) has traced mycorrhizal connexions between *P. niger* and roots of *Picea abies*.

Phellodon tomentosus (L. : Fr.) Banker
Figs 20, 46.

Distribution: The distribution is mainly eastern with many finds in South-East and Central Norway. There are two finds from North Norway, where it reaches Rana (Nordland) somewhat north of 66° N, and two from the west coast near Ålesund. In the south-east it has been found up to 900 m, in the northern boreal region.

Ecology: With few exceptions the finds are from spruce forests. This holds true also for the two northern ones, which are from an area where naturally occurring spruce is at its northern limit. The finds from the west coast, and some of the eastern finds as well, are from pine forests. *Phellodon tomentosus* has been found in rich, intermediate and poor forest types. It has been collected on humus, often among moss, in needle carpets, and also on an old ant hill. No finds from young forests, but several from old forests are indicated.

Temporal trend: It is the most common and widespread *Phellodon* species in Norway. The number of finds has not changed much over the three last decades.

Extra-territorial occurrence: *Phellodon tomentosus* is also the most common *Phellodon* in other parts of Fennoscandia, where it extends northwards to Lapland (Ryman & Holmåsén 1984, E. Ohenoja, pers. comm.). It occurs in all parts of Europe (Maas Geesteranus 1975), but seems to be more common in continental regions. According to Arnolds (1989a) it was once fairly common in the Netherlands, but it is now probably extinct (last observation made in 1956). The species is included in Red data lists from the Netherlands, Germany, Poland, and Denmark.

FAM. THELEPHORACEAE, GEN. SARCODON *P. Karst.*

The genus is well represented in Norway with nine species, but only one of them, *S. imbricatus*, is common.



Figs 47-48. Distribution maps. Fig. 47. *Sarcodon fennicus*. Fig. 48. *S. imbricatus*.

Sarcodon fennicus (P. Karst.) P. Karst.

Figs 21, 47.

Distribution: The species is restricted to the south-eastern part of the country, where it is known from nine localities in the boreo-nemoral and southern boreal regions.

Temporal trend: There are few finds in all decades, except for the 1980s when there were none.

Ecology: The finds are from spruce, pine, and mixed coniferous forests. There is no reference to the edaphic conditions with the material.

Extra-territorial occurrence: The species is also rare in Sweden, but extends slightly further north there. Strid (1985) refers most finds to pine forests. In Finland it is also rare, but it extends northwards further than the Arctic circle. The specimens recorded as *S. fennicus* from northernmost Finland (Kallio & Kankainen 1964) belong to *S. scabrosus* (E. Ohenoja, pers. comm.). Nikolajeva (1961) records relatively many finds from the Soviet Union, including some east of the Urals. We are unaware of records of this species from other parts of Europe. *Sarcodon fennicus* is included in the Swedish Red data list as needing care.

Sarcodon fuligineo-violaceus (Kalchbr. ap. Fr.) Pat.

Fig. 42.

Distribution and Ecology: The species is known from only one locality, Hole (Buskerud, South-East Norway, 1967) in the boreo-nemoral region. Here it was found under spruce in a mixed coniferous forest on calcareous ground (Gulden & Stordal 1973).

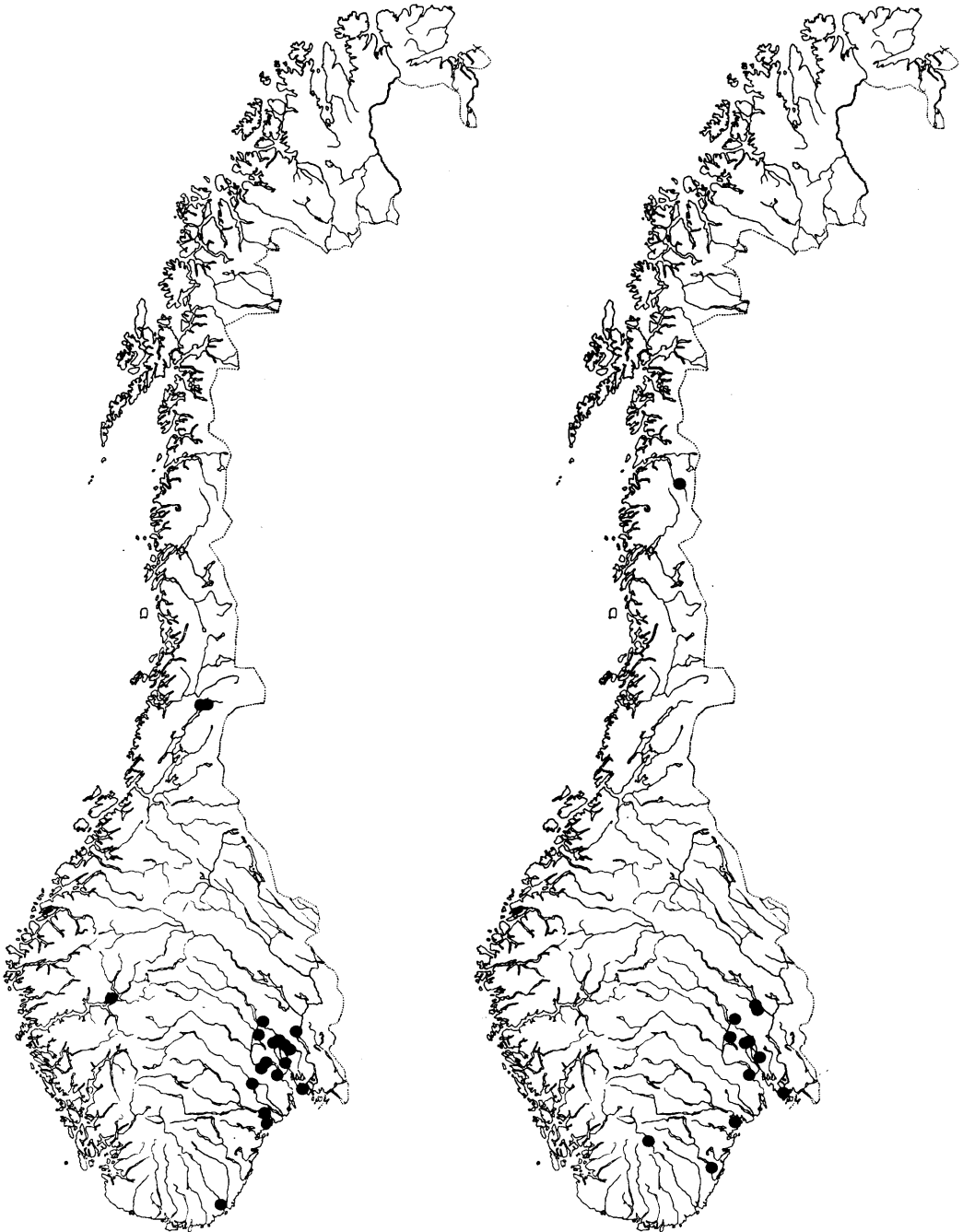
Extra-territorial occurrence: The species has been found a few times in Sweden, in coniferous forests on calcareous ground, north to Jämtland (Strid 1985), but not yet in Finland (Strid 1991). The find in Jämtland probably represents a northern boreal habitat. It is a rare species in all parts of Europe, occurring west to Great Britain and south to Spain and Greece (Maas Geesteranus 1975, Jülich 1984, Nunez, pers. comm.). Nikolajeva (1961) records the species from the island of Sakhalin in the easternmost USSR. *S. fuligineo-violaceus* is included in Red data lists from Germany and Sweden.

Sarcodon glaucopus Maas G. & Nannf.

Fig. 42.

Distribution: There is only one collection of this species from South-East Norway (Eggedal, Buskerud, 1988), from the middle boreal region and without notes on ecology.

Extra-territorial occurrence: It is also rare in Sweden, known from coniferous forests in south-eastern parts. In Finland it is rather common in dry coniferous forests, and in North Finland even more common than *S. imbricatus* (E. Ohenoja, pers. comm.). It extends northwards to the Koillismaa biological province near the Arctic circle (Ulvinen et al. 1981). Outside Fennoscandia it is known from Great Britain (R. Watling, pers. comm.), Denmark, Poland, Switzerland, and Italy (Jülich 1984). *Sarcodon glaucopus* is included in Red data lists and considered extinct in Poland and Denmark, and needing care in Sweden.



Figs 49-50. Distribution maps. Fig. 49. *Sarcodon leucopus*. Fig. 50. *S. lundellii*.

Sarcodon imbricatus (L. : Fr.) P. Karst.

Figs 22, 48.

Distribution: The species is widespread in Norway and especially common in the eastern parts. There are few finds from the southern coastal regions, and Mr. Stordal has noted that the species is rare in Vest-Agder (note on herbarium label). In North Norway it extends northwards almost to Narvik (Nordland), north of 68° N, but there are rather few finds. It grows in all vegetation regions up to the upper limit of the middle boreal region (e.g., ca. 700 m at Dovre, Oppland).

Ecology: *Sarcodon imbricatus* seems to be most common in eutrophic spruce forests, e.g., Melico-Piceetum. Many other finds are from spruce forests mixed with deciduous trees or with pine. It is also quite common in pine forests. One collection is from an *Alnus-Salix* scrub. It occurs in sites on calcareous ground as well in acid, sandy habitats. There are finds from spruce plantations on the west coast.

Temporal trend: After the two *Hydnum* species, this is the most common hydneous species in Norway. The number of finds has been stable from 1950 to 1989.

Extra-territorial occurrence: *Sarcodon imbricatus* is common in the other Fennoscandian countries as well, but in Sweden it is considered rare in the southernmost and northernmost parts (Strid 1985). In Finland, it grows as far north as the Koillismaa biological province (Ulvinen et al. 1981). *Sarcodon imbricatus* has been very common in large parts of Europe, and it still was in the late 1960s according to Maas Geesteranus & Nannfeldt (1969). It was sold in European markets in tons (Arnolds 1989a) and it is the most frequently illustrated *Sarcodon* species (Maas Geesteranus 1975). However, in Denmark it is rare, as it is also in Great Britain, where it is somewhat more common in Scotland than further south (Phillips 1981). Apparently the species is naturally less common in western parts of Europe than towards east.

Arnolds (1989a) records a dramatic decline of *S. imbricatus* in the Netherlands, where it has only been collected in three districts since 1972 and was seen most recently in 1985. In Denmark it is considered vulnerable (Vesterholt & Knudsen 1990). The species is included in Red data lists from the Netherlands, Germany, Poland and Denmark.

Comments: There appears to be a switch from pine to spruce as the main associated tree from western Europe to Norway. Agerer (1991) has described the mycorrhizas of *S. imbricatus* in great detail.

Sarcodon leucopus (Pers.) Maas G. & Nannf.

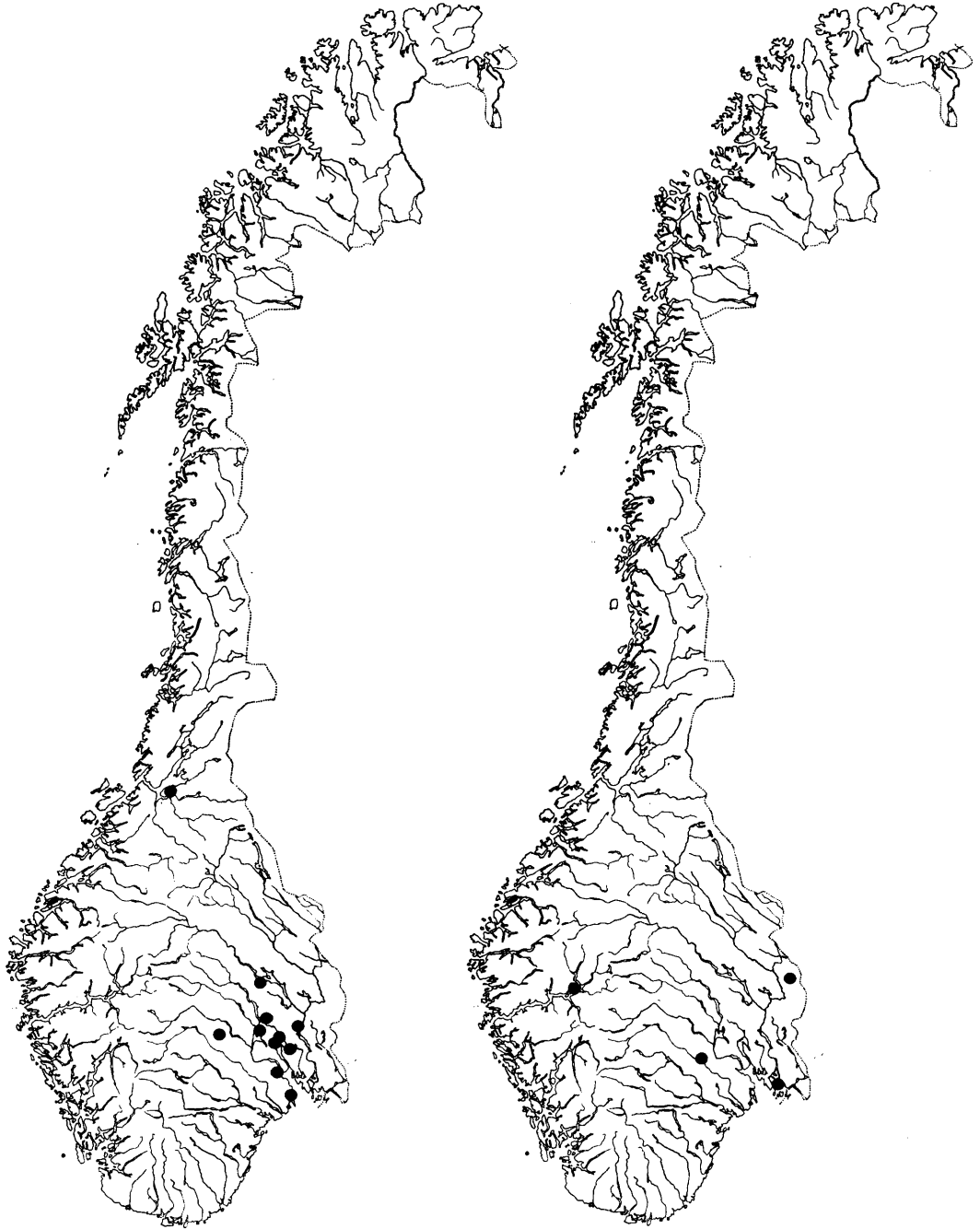
Figs 23, 49.

Distribution: The main distribution in Norway is south-eastern. There is one collection from Kristiansand (Vest-Agder) on the south coast, one from the inner Sognefjord (Sogn & Fjordane) in West Norway, and two collections from Central Norway. The species ascends to the southern boreal region.

Ecology: The finds are nearly all from pine forests on calcareous ground (Melico-Piceetum pinetosum). A few are from rich spruce forests, sometimes mixed with pines.

Temporal trend: The species is rare but there are an increasing number of finds from more recent years.

Extra-territorial occurrence: The species is also rare in other parts of Europe. Its



Figs 51-52. Distribution maps. Fig. 51. *Sarcodon martioflavus*. Fig. 52. *Sarcodon scabrosus*.

strongly eastern distributional tendency in Norway may seem odd, since the species also occurs in Iceland (Hallgrímsson 1963, Maas Geestermaus 1976) (collected in heaths among *Empetrum* spp. and *Arctostaphylos uva-ursi*). In Sweden and Finland it is southern, growing in coniferous forests on calcareous bedrock (Strid 1985, E. Ohenoja, pers. comm.). It appears to be absent from most western parts of Europe, e.g., Great Britain, Denmark, the Netherlands, Spain (Arnolds 1989a, Petersen & Vesterholt 1990, M. Nunez, pers. comm., R. Watling, pers. comm.). The species is included in Red data lists from Germany and Sweden.

Sarcodon lundellii Maas G. & Nannf.

Figs 24, 50.

Distribution: The species has a south-eastern distribution in Norway, with a single find in North Norway. The northern locality, Storjord at the entrance of Junkerdalen (Saltal, Nordland) at 67 °N, lies more than 700 km north of the southern distribution area. Junkerdalen is a well known locality for southern, thermophilous plants. *Sarcodon lundellii* ascends to the middle boreal region.

Ecology: Most annotated finds are from coniferous forests, mainly spruce forests, on calcareous ground or in eutrophic vegetation types. One collection is from a sandy pine forest with *Vaccinium myrtillus*. One collection is from an old, intermediate to rich spruce forest.

Temporal trend: There has been a small but steady increase in finds from the 1950s to present.

Extra-territorial occurrence: The species has so far not been recorded from outside Fennoscandia. In Sweden it is locally not uncommon, especially in the eastern parts, e.g., on the calcareous island Gotland. The species is rare in Finland, ascending to the middle boreal region in Central Finland (E. Ohenoja, pers. comm.).

Sarcodon martioflavus (Snell et al.) Maas G.

Figs 25, 51.

Distribution: The species is only known from the south-eastern, lowland part of the country, with the exception of a single collection from Central Norway (Trondheim, Sør-Trøndelag). The finds are from the boreo-nemoral and the southern boreal regions.

Temporal trend: Seven of the 14 Norwegian finds have been made the last decade.

Ecology: Old, eutrophic spruce forest seems to be the typical habitats of *S. martioflavus*. One find is from a *Vaccinium myrtillus* dominated spruce forest.

Extra-territorial occurrence: The species is rare also in Sweden. It has been found on calcareous ground in western parts of Central Sweden, north to Jämtland, where it probably occurred in the northern boreal region. The Swedish finds connect with the southern and northern distribution areas in Norway. It is very rare in Finland, occurring in spruce forest in South Finland (E. Ohenoja, pers. comm.). *Sarcodon martioflavus* appears to be an eastern species in Europe. Outside Fennoscandia it is known from Germany and Switzerland. It is included in Red data lists from Germany and Sweden.



Fig. 53. Distribution map. *Sarcodon versipellis*.

Sarcodon scabrosus (Fr.) P. Karst.
Figs 26, 52.

Distribution: Three collections are from South-East Norway. One is from the innermost part of Sognefjorden (Sogn & Fjordane, West Norway), with a fairly continental climate. It occurs in the boreo-nemoral and the southern boreal regions.

Ecology: The annotated finds are from a mixed oak-hazel-pine forest, a *Vaccinium myrtillus* spruce forest, and a pine forest on sandy, fluvial deposits.

Extra-territorial occurrence: The species also seems to be rare in Sweden, and is mainly found in coniferous forests. It extends considerably further north in Sweden, to Norrbotten (Ryman & Holmåsen 1984, Strid 1985). In Finland it is a rather common species, more common than *S. imbricatus*, growing in dry pine forests north to Lapland (E. Ohenoja, pers. comm.), and ascending to the northern boreal region. According to Maas Geesteranus & Nannfeldt (1969) *S. scabrosus* differs from most other *Sarcodon* species in Scandinavia by preferring the drier pine forests to the mossy spruce forests, where *Sarcodon* species generally grow. *Sarcodon scabrosus* is known from most European countries. Arnolds (1989a) records an apparent increase of this species in the Netherlands, but doubts whether this pattern is real. The species is included in Red data lists from the Netherlands, Germany, and Denmark.

Comments: A shift in preference from coniferous to deciduous forests (especially with oak) takes place from Fennoscandia to more southern parts of Europe.

Sarcodon versipellis (Fr.) Quél.
Figs 27, 53.

Distribution: The distribution is mainly eastern in Norway, with two finds on the south coast and a single one on the south-west coast. It extends northwards to Namsos (Nord-Trøndelag, Central Norway). It has been found from the boreo-nemoral to the middle boreal regions.

Ecology: Most finds are from spruce forests; Melico-Piceetum and Eu-Piceetum types are indicated. It also grows in mixed spruce-deciduous forests. It occurs in spruce plantations outside the natural area of the spruce. It is also found old forests. The edaphic tolerance may be wide.

Temporal trend: *Sarcodon versipellis* is (after *S. imbricatus*) the second most common *Sarcodon* in Norway. There are more finds in the last two decades than in any previous decade.

Extra-territorial occurrence: The species appears to be eastern in Europe (cf. Jülich 1984). According to Strid (1985) it is rare in Sweden, most common in central parts, and absent from the south. It occurs in Jämtland, probably in the northern boreal region. Its presence in Finland is uncertain (Strid 1991). The species is included in Red data lists from eastern Germany and Sweden.

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