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J. Middelborg & J. Mattsson

Crustaceous lichenized species of
the Caliciales in Norway.

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Thirty-nine species are recognized in the lichen genera *Calicium* Pers., *Chaenotheca* (Th.Fr.) Th.Fr., *Cyphelium* Ach., *Microcalicium* Vain. emend. Tibell, *Sclerophora* Chevall., and *Thelomma* Massal. emend. Tibell in Norway. The genus *Cybebe* is reduced to synonymy with *Chaenotheca*, and the new combinations *Chaenotheca gracilentata* (Ach.) Mattsson & Middelborg and *Sclerophora coniophaea* (Norm.) Mattsson & Middelborg are proposed. Three families are recognized, the Caliciaceae, the Coniocybaceae, and the Microcaliciaceae. The chemistry is described, and a number of unidentified secondary substances are characterized by their Rf values. The ecology and distribution of the species are described. Keys are given to the genera and species, and distribution maps for Norway are provided. *Calicium adaequatum* Nyl., *Calicium adpersum* Pers., *Calicium corynellum* Ach., *Calicium parvum* Tibell, *Chaenotheca carthusiae* (Harm.) Lett., and *Microcalicium ahlneri* Tibell are reported new to Norway.

Keywords: Caliciales, Distribution, Ecology, Lichens, Lichen substances, Norway, Taxonomy.

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INTRODUCTION

The first species to be validly described in the Caliciales was *Chaenotheca furfuracea* (as *Mucor furfuraceus*) by Linnaeus in 1753. Persoon (1794) established the genus *Calicium*. A more thorough revision and delimitation was made by Acharius (1815-1817), who described *Coniocybe* and *Cyphelium*. These genera were placed in the family Calicioidea together with *Calicium*. During the same century Chevallier (1826) described *Sclerophora* and Massalongo (1860) described *Thelomma*. Fries (1861) gave an up-to-date presentation of the genera in the Caliciales and also gave a description of *Chaenotheca*. In the following century Vainio (1927) established *Microcalicium*. Schmidt (1970b) segregated the saprophytic species with active spore dispersal in the new family Mycocaliciaceae Schmidt. Tibell (1984) placed the species belonging to *Coniocybe* in *Chaenotheca* and *Sclerophora*, and in the new genus *Cybebe*.

J. M. Norman was the first Norwegian who made taxonomic investigations in the Caliciales. He described the macrolichen *Tholurna dissimilis* (Norm.) Norm. (Norman 1861) and the tiny, but beautiful crustaceous species *Coniocybe coniophaea* Norm. (Norman 1868), syn *Sclerophora coniophaea* (Norm.) Mattsson & Middelborg.

L. Tibell has made extensive taxonomic and nomenclatural studies in the Caliciales in Sweden (Tibell 1977, 1978b, 1980a), Europe (Tibell 1971), and in other regions (Tibell 1975, 1976b, 1978a and 1980b). He has recently given a comprehensive taxonomic reappraisal of the Caliciales together with a historical survey (Tibell 1984). A list of the Caliciales species occurring in Sweden and Norway is given by Santesson (1984).

The primary aim of our study has been to investigate the Norwegian distribution of the species, the ecology, and the secondary substances occurring in the Norwegian members of the crustaceous Caliciales. Taxonomic problems that arose during the study have been dealt with.

We have studied the crustaceous genera with passive spore dispersal in the Caliciales, i.e. *Calicium*, *Chaenotheca*, *Cyphelium*, *Microcalicium*, *Sclerophora*, and *Thelomma*. *Sphinctrina* Fr. has not been included, partly because there is only one collection from Norway, and partly because the genus has recently been studied in Europe by Löfgren & Tibell (1979). The non-lichenized species in the Mycocaliciaceae have not been included. The macrolichen genera *Sphaerophorus* Pers. and *Tholurna* Norm. are well known from earlier studies in Norway (Krog et al. 1980), and are not included in this study.

MATERIAL AND METHODS

We have examined approximately 1000 specimens in the herbaria BG, O, S, TRH, TROM, and UPS, and in the private herbaria of Gunnar Degelius and Tor Tønsberg. Field studies have been carried out in South, Central, and North Norway during 1984 and 1985. Our collections, about 450 specimens, are deposited in O.

The morphological studies were carried out with binocular lenses at 10 to 30x magnifications. Detailed analyses of the spore surfaces were done by scanning electron microscopy (SEM) and transmission electron microscopy (TEM). The anatomy has been studied with the aid of light microscopes at 125x, 500x, and 1250x magnifications. Both squash preparations and sections cut on a freezing microtome were used. Preparations of spores and algae were studied in water and 2% KOH. The spore surfaces were most easily investigated in a solution of lactophenol-cotton blue. Optimum resolution was achieved with an oil immersion condenser. The majority of the specimens have been microscopically investigated. Measurements of apothecia and spores were made, and when our results were in accordance with those of Tibell (1971, 1981) we have adopted his results. The iodine reaction of the apothecia in *Calicium adaequatum* and *C. subquercinum* was studied in a solution of iodine/potassium iodide (I).

Thin-layer chromatography (TLC) was performed in accordance with the methods of Culberson & Kristinsson (1970), Culberson (1972), and Culberson & Johnson (1982). Spot tests with paraphenylene diamine (PD) and 10% potassium hydroxide (K) have been performed. Polarized light was used to locate crystals of lichen substances in the apothecia.

The nomenclature follows Tibell (1984, 1981) except for the combinations *Chaenotheca gracilentia* (Ach.) Mattsson & Middelborg and *Sclerophora coniophaea* (Norm.) Mattsson & Middelborg which are proposed in this study. The combination *Chaenotheca sulphurea* (Retz.) has been used for the species *Coniocybe sulphurea* (Retz.) Nyl. (see p. 50).

A list of localities is available on request from the Botanical Museum, Oslo.

RESULTS AND DISCUSSION

MORPHOLOGY AND ANATOMY

Thallus

There are three main types of thallus in the species examined. The shape of the thallus within a single species frequently shows a wide variation.

(1) Endosubstratal thallus. The algae and hyphae are totally immersed in the substrate. When immersed in lignum, the thallus is called endoxylic.

(2) Sorediose/granular thallus. The thallus is rather thin and consists of small, ecorticate or pseudocorticate granules consisting of algae surrounded by hyphae.

(3) Verrucose/squamulose thallus. The thallus is rather thick, and the algae and hyphae are covered by a thin cortex.

Phycobionts

Three types of algae are found in the Caliciales (Tibell 1984). In the Norwegian species the following genera are represented.

(1) *Trebouxia* and *Dictyochloropsis* belong to the Chlorococcales. They have a quite similar appearance. *Trebouxia* occurs in *Calicium*, *Cyphelium*, *Thelomma*, and in some *Chaenotheca* species. *Dictyochloropsis* occurs in *Chaenotheca brunneola* (Tschermak-Woess 1978). The cells are bright green, single and almost globose (diameter 10-15 μm). They often form tetrads (Fig. 1).

(2) *Stichococcus* occurs in some *Chaenotheca* species. The cells are bright green and form chains. Each cell is small (less than 10 μm) and narrowly ellipsoidal. They divide transversely (Fig. 2).

(3) *Trentepohlia* occurs in *Sclerophora* and in some *Chaenotheca* species not known from Norway. The cells are reddish green and form loose chains. Each cell is large (more than 10 μm) and broadly ellipsoid. They divide transversely (Fig. 3).

Apothecia

Apothecia are frequent in the majority of the species with the exception of *Thelomma ocellatum*. Only two fertile specimens of *T. ocellatum* have been collected in Norway.

The apothecia are stalked (in *Calicium*, *Chaenotheca*, *Sclerophora*, and part of the species in *Microcalicium*); or sessile or immersed (in *Cyphelium*, *Thelomma*, and *Microcalicium disseminatum*). The stalked apothecia consist of a stalk (0.3-3.5 mm tall) and a capitulum. There is frequently a wide variation in a single species with respect to stalk length. Some species, e.g. *Calicium viride*, have stout apothecia,

Fig. 1. *Trebouxia*. From *Calicium viride*, Hedmark, Ringsaker, Mesnali, Mattsson 395 (O).

Fig. 2. *Stichococcus*. From *Chaenotheca trichialis*, Telemark, Grenland, Mattsson & Middelborg 245 (O).

Fig. 3. *Trentepohlia*. From *Sclerophora coniophaea*, Finnmark, Alta, Middelborg 326 (O).

others like *Chaenotheca gracilentia* have slender apothecia. The hyphae of the stalk are dark brown and irregularly arranged in *Calicium* and *Microcalicium*; and medium or pale brown and periclinally arranged in *Chaenotheca* and *Sclerophora*.

The tissue containing the hymenium in an apothecium forms the excipulum. It is usually well developed, but poorly developed in some *Chaenotheca* and *Sclerophora* species. In some *Sclerophora* species the excipulum forms a collar (Tibell 1984, Fig. 12 C). The excipulum consists of globular cells in *Calicium*, *Cyphelium*, *Microcalicium* and *Thelomma*, and elongated cells in *Chaenotheca* and *Sclerophora*.

The mazaedium consists of a spore mass formed by the hymenium. The spores are released from the asci as a dry, loose powdery mass on the hymenium. This is caused by the prototunicate asci. The result is a passive dispersal of the spores, which is characteristic for all species in the Caliciales, except species in the Microcaliciaceae. The colour of the mazaedium depends on the colour of the spores. Species in *Calicium*, *Cyphelium*, and *Thelomma* have a black mazaedium, species in *Microcalicium* have a greenish black mazaedium, and species in *Chaenotheca* and *Sclerophora* have a brown mazaedium. Sometimes the mazaedium is stabilized by sclerotized hyphae (in *Microcalicium*).

The pruina may either form a ring on the excipulum margin or it may cover the lower side of the excipulum, or even the whole stalk. The colour of the pruina may be white, brown, reddish brown or yellow (pulvinic acid derivatives). The pruina may be K+ or K-.

Asci

The asci are prototunicate and dissolve before the spores reach maturity. The spores continue maturing in the mazaedium. According to Tibell (1984), the asci lack apical structures, with the exception of species in the Microcaliciaceae. The asci may be cylindrical, clavate, or of irregular shape. They are formed singly, or, in some *Chaenotheca* species and in *Microcalicium*, in chains (catenulate). Croziers are often present in the formation of asci, but absent in *Chaenotheca gracilentia* and in *Microcalicium*. The asci contain eight spores.

Spores

In *Calicium*, *Cyphelium*, and *Thelomma*, the spores are broadly ellipsoid, 8-28 μm long, one-septate often with a constricted septum, and dark brown. In *Microcalicium* the spores are narrowly ellipsoid, 5-15 μm long, 1-3-7-septate and green. In *Chaenotheca* and *Sclerophora* the spores are non-septate and pale brown; globose or ellipsoid, 5-9 μm long in the former, and globose in the latter.

In *Sclerophora* the spore surface is reticulate (Figs 8, 11), in *Chaenotheca* cracked (Fig. 4) and in *Microcalicium* there are spirally arranged ridges. The spore surface in *Calicium* (Figs 5, 6, 7) and *Cyphelium* may be more or less cracked, spirally arranged, or almost smooth.

Figs 4-7. SEM photographs of spores. The rules are 1 μ m. Fig. 4. *Chaenotheca gracilentia*, Norway, Oppland, Dovre, Skjellestad, 1948, Ahlner (S). Fig. 5. *Calicium abietinum*, Norway, Troms, Målselv, Likkavarre, 1911, Lynge (O). Fig. 6. *Calicium glaucellum*, Norway, Vest-Agder, Lyngdal, Kvellandsfossen, Mattsson & Middelborg 267 (O). Fig. 7. *Calicium salicinum*, Norway, Oppland, Gausdal, Ormtjernkampen, Mattsson & Middelborg 211 (O).

Figs 8-11. EM photographs of spores. The rules are 1 μ m. Fig. 8. SEM of *Sclerophora coniophaea*, Norway, Finnmark, Alta, Middelborg 326 (O). Fig. 9. TEM in ascus of *S. coniophaea*, and Fig. 10. TEM of *S. coniophaea*, both Sweden, Uppland, Söderfors, Älvkarleby, Tibell 15650 (UPS), photo L. Tibell. Fig. 11. SEM of *S. nivea*, Norway, Telemark, Kragerø, Mattsson & Middelborg 253a (O).

CHEMISTRY

Previous reports of secondary substances in the Caliciales are summarized by Culberson (1969) and Culberson et al. (1977). The most recent reports are from Tibell (1971, 1980b, 1984 and 1985). Chemical pathways are listed in Culberson et al. (1977).

The following secondary substances in species occurring in Norway have been reported:

Table 1. Secondary substances in *Calicium*, *Chaenotheca*, *Cyphelium*, *Sclerophora* and *Thelomma*.

Substances	Caliciaceae			Coniocybaceae	
	Calicium	Cyphelium	Thelomma	Chaenotheca	Sclerophora
Rhizocarpic acid	+	+	-	-	-
Epanorin	+	+	-	-	-
Vulpinic acid	+	+	-	+	-
Pulvinic acid	-	-	-	+	-
Pulvinic dilactone	-	-	-	+	-
Usnic acid	+	-	-	-	-
Atranorin	+	-	+	+	-
Diffractaic acid	+	-	-	-	-
Baeomycesic acid	-	-	-	+	-
Squamatic acid	-	-	-	+	-
Norstictic acid	+	+	+	-	-
Anthraquinoid pigments	-	-	-	+	+
Unknown triterpenoid	-	-	-	+	-
Glaucellum unknown	+	-	-	-	-
Inquinans unknown 1	-	+	-	-	-
Inquinans unknown 2	+	+	-	-	-
Inquinans unknown 3	+	+	-	+	-
Tigillare unknown 1	-	+	-	-	-
Tigillare unknown 2	-	+	-	-	-
Carthusiae unknown	-	-	-	+	-
Ferruginea unknown 1	-	-	-	+	-
Ferruginea unknown 2	-	-	-	+	-
Gracilenta unknown 1	-	-	-	+	-
Gracilenta unknown 2	-	-	-	+	-
Stemonea unknown	-	-	-	+	-
Subroscida unknown	-	-	-	+	-
Trichialis unknown 1	-	-	-	+	-
Trichialis unknown 2	-	-	-	+	-

Table 2. Secondary substances in *Calicium*. Parentheses show substances that occur sporadically.

	Number of specimens	Rhizocarpic acid	Epanorin	Vulpinic acid	Usnic acid	Atranorin	Diffractic acid	Norstictic acid	Glaucellum unknown	Inquinans unknown 2	Inquinans unknown 3	No secondary substances
<i>C. abietinum</i>	2	-	-	-	-	-	-	-	-	-	-	+
<i>C. adaequatum</i>	1	-	-	-	-	-	-	-	-	-	-	+
<i>C. adspersum</i>	4 ¹	-	-	+	-	-	-	+	-	-	-	-
<i>C. corynellum</i>	5 ²	+	-	-	(+)	(+)	-	-	-	-	-	-
<i>C. denigratum</i>	4	-	-	-	-	-	-	-	-	-	-	+
<i>C. glaucellum</i>	14	-	-	-	-	-	-	-	+	-	-	-
<i>C. parvum</i>	2	-	-	-	-	-	+	-	-	-	+	-
<i>C. quercinum</i>	1	-	-	-	-	-	-	-	-	-	-	+
<i>C. salicinum</i>	4	-	-	-	-	-	-	+	-	-	-	-
<i>C. subquercinum</i>	5	-	-	-	-	-	-	-	-	+	-	-
<i>C. trabinellum</i>	8	-	-	+	-	-	-	-	-	-	-	-
<i>C. viride</i>	17	+	+	-	-	-	-	-	-	-	-	-

- 1) Including two Nordic specimens from outside Norway.
- 2) Three Nordic specimens (Norway 1, Sweden 2) contain usnic acid, two Central European specimens (Austria 1, Yugoslavia 1) contain atranorin.

In *Calicium* - norstictic acid (*C. adspersum*); vulpinic acid (*C. adspersum*, *C. trabinellum*); rhizocarpic acid (*C. viride*).

In *Chaenotheca* - vulpinic acid (*C. carthusiae*, *C. chrysocephala*, *C. laevigata*, *C. phaeocephala*, *C. subroscida*); baeymycesic acid (*C. brunneola*); unknown a and c (*C. stemonea*); anthraquinoid pigment (*C. ferruginea*).

In *Cyphelium* - usnic acid, atranorin, unidentified substance (K⁺ reddish-brown), and unidentified yellow pigment (*C. inquinans*); rhizocarpic acid (*C. pinicola* and *C. tigillare*).

In *Sclerophora* - anthraquinoid pigments.

In *Thelomma* - usnic acid, rhizocarpic acid and epanorin (*T. ocellatum*).

The main secondary substances that we have identified with the aid of TLC, are listed in Tables 1, 2, 3, and 4. Several unidentified substances were encountered in addition to the identified ones. The main characteristics of these substances are listed in Table 5. The appearances of the unidentified substances on TLC chromatograms are shown in Fig. 12.

Table 3. Secondary substances in *Chaenotheca*. Parentheses show substances that occur sporadically.

	Number of specimens	Vulpinic acid	Pulvinic acid	Pulvinic dilactone	Atranorin	Baeomycesic acid	Squamatic acid	Anthraquinoid pigments	Unknown triterpenoid	Carthusiae unknown	Ferruginea unknown 1	Ferruginea unknown 2	Gracillenta unknown 1	Gracillenta unknown 2	Inquinans unknown 3	Stemonea unknown	Subroscida unknown	Trichialis unknown 1	Trichialis unknown 2	No. secondary substances
<i>C. brunneola</i>	5	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. carthusiae</i>	4	+	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	+	-
<i>C. chrysocephala</i>	12	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. cinerea</i>	2	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>C. ferruginea</i>	7	-	-	-	(+)	-	-	+	-	-	+	+	-	-	-	-	(+)	-	-	-
<i>C. furfuracea</i>	13	+	+	+	(+)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. gracilenta</i>	5	-	-	-	-	-	-	-	+	-	-	-	+	+	+	-	-	-	-	-
<i>C. gracillima</i>	3	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. laevigata</i>	3	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. phaeocephala</i>	4	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. stemonea</i>	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
<i>C. subroscida</i>	6	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>C. sulphurea</i>	3	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. trichialis</i>	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-
<i>C. xyloxena</i>	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+

Identified secondary substances

Shikimic acid pathway: The pulvinic acid derivatives are produced here. These substances occur in both *Calicium*, *Chaenotheca*, and *Cyphelium*.

Vulpinic acid is present in the pruina in *Calicium* (*C. adspersum*, *C. trabinellum*), *Chaenotheca* (*C. carthusiae*, *C. chrysocephala* - also in thallus, *C. furfuracea* - also in thallus, *C. laevigata*, *C. phaeocephala*, *C. subroscida*, *C. sulphurea* - also in thallus), and *Cyphelium* (*C. lucidum* - in thallus from an Austrian specimen).

Pulvinic acid and pulvinic dilactone are present in the thallus of *Chaenotheca* (*C. chrysocephala* and *C. furfuracea*). We have only found pulvinic acid, not pulvinic dilactone in *C. sulphurea*, maybe because of sparse collections.

Rhizocarpic acid is present in thallus both in *Calicium* (*C. corynellum*, *C. viride*) and *Cyphelium* (*C. notarisi* - a Swedish specimen, *C. pinicola*, and *C. tigillare*). The report of rhizocarpic acid from *Chaenotheca furfuracea* (as *Coniocybe furfuracea*) by Bendz et al. (1965) has not been confirmed.

Epanorin occurs together with rhizocarpic acid except in *Calicium corynellum*.

It is noteworthy that vulpinic acid occurs in both the Caliciaceae and the Coniocybaceae, while rhizocarpic acid and epanorin only occur in the Caliciaceae, and pulvinic acid and pulvinic dilactone only occur in the Coniocybaceae.

Acetate-polymalonate pathway: Phenolic carboxylic acid derivatives are produced here. In β -orcinol series the paradesides atranorin, baeomycesic acid, diffractaic acid, and squamatic acid occur. Atranorin has been detected in *Calicium*

Table 4. Secondary substances in *Cyphelium*, *Microcalicium*, and *Sclerophora*. Parentheses show substances that occur sporadically.

	Number of specimens	Rhizocarpic acid	Epanorin	Vulpinic acid	Norstictic acid	Inquinans unknown 1	Inquinans unknown 2	Inquinans unknown 3	Tigillare unknown 1	Tigillare unknown 2	Anthraquinoid pigments	No secondary substances
<i>C. inquinans</i>	7 ₁	-	-	-	-	+	+	+	-	-	-	-
<i>C. karelicum</i>	4 ₁	-	-	-	-	(+)	+	(+)	-	-	-	-
<i>C. lucidum</i>	1 ₂	-	-	+	-	-	-	-	-	-	-	-
<i>C. notarisii</i>	1 ₃	+	+	-	-	-	-	-	-	-	-	-
<i>C. pinicola</i>	7	+	+	-	(+)	-	-	-	-	-	-	-
<i>C. tigillare</i>	11	+	+	-	-	-	-	-	+	+	-	-
<i>M. ahlneri</i>	1	-	-	-	-	-	-	-	-	-	-	+
<i>M. arrenarium</i>	2	-	-	-	-	-	-	-	-	-	-	+
<i>M. disseminatum</i>	3	-	-	-	-	-	-	-	-	-	-	+
<i>S. coniophaea</i>	8	-	-	-	-	-	-	-	-	-	+	-
<i>S. farinacea</i>	2	-	-	-	-	-	-	-	-	-	+	-
<i>S. nivea</i>	4	-	-	-	-	-	-	-	-	-	+	-
<i>S. peronella</i>	1	-	-	-	-	-	-	-	-	-	+	-

1) Including one specimen from Karelen, Finland

2) Tyrol, Austria

3) Södermanland, Sweden

(*C. corynellum* - Central European specimens), in *Chaenotheca* (*C. cinerea*, *C. ferruginea* - sporadic, and *C. furfuracea* - sporadic), and in *Thelomma* (*T. ocellatum* - sporadic). Baeomycesic acid and squamatic acid occur in *Chaenotheca* (*C. brunneola*). Diffractaic acid is present in *Calicium* (*C. parvum*).

Among β -orcinol depsidones, norstictic acid occurs in *Calicium* (*C. adpersum*, *C. salicinum*), and *Cyphelium* (*C. pinicola* - sporadic).

Usnic acid is only present in the Nordic specimens of *Calicium corynellum*.

Anthraquinoid pigments occur in *Chaenotheca* (*C. ferruginea*, and *C. gracillima*), and *Sclerophora* (all four species). With the exception of the pigment in *Chaenotheca ferruginea*, the anthraquinoids are omitted from Fig.12.

Mevalonic acid pathway: Triterpenoids are produced here. Triterpenoid has only been found in one species in *Chaenotheca* (*C. gracilentia*).

Table 5. Characteristic features of the secondary substances encountered in *Calicium*, *Chaenotheca* and *Cyphelium*.

	R _f - classes			UV	Spot coloration with H ₂ SO ₄ and heat
	TDA	HEF	TA		
Squamatic acid	2	3	3	+ blue	yellowish brown
Ferruginea pigment	2	5	1		red pigment
Pulvinic acid	2	5	2	+ orange	yellow pigment
Ferruginea unknown 1	3	2-3	2-3	+ blue	colourless
Ferruginea unknown 2	3	3	2-3	+ blue	colourless
Baeomycetic acid	3-4	5	5		yellowish brown
Norstictic acid	4	4	4		yellowish brown
Gracilenta unknown 1	4	4	5-6		colourless
Diffractaic acid	4	6	5-6		brown
Glaucellum unknown	4	6	5-6		brown
Stemonea unknown	4	6	6		orange
Inquinans unknown 1	5	3	5	++ blue	colourless
Carthusiae unknown	5	3	5-6		pale brown
Trichialis unknown 1	5	3	6		brown
Subroscida unknown	5	5	6		brown, turns grey
Trichialis unknown 2	5	5	6		brown
Tigillare unknown 1	5	6	6		pale brown
Tigillare unknown 2	5	6	6		pale brown
Epanorin	6	5	6		yellow pigment
Gracilenta unknown 2	6	5	6		colourless
Unknown triterpenoid	6	5	6		pale brown
Rhizocarpic acid	6	5	6		yellow pigment
Inquinans unknown 2	6	6	6		brown
Utric acid	6	6	6		greenish grey
Vulpinic acid	6-7	6	8		yellow pigment
Atranorin	7	7	7		yellowish brown
Inquinans unknown 3	7	7	7	++ blue	colourless
Pulvinic dilactone	8	8	8		yellow pigment

Unidentified secondary substances

Calicium: glaucellum unknown occurs in *C. glaucellum*; inquinans unknown 2 in *C. subquercinum*; and inquinans unknown 3 in *C. parvum*.

Chaenotheca: carthusiae unknown, and trichialis unknown 2 occur in *C. carthusiae*; ferruginea unknown 1, ferruginea unknown 2, and a yellowish red anthraquinoid pigment in *C. ferruginea*; gracilenta unknown 1, gracilenta unknown 2, inquinans unknown 3, and an unknown triterpenoid in *C. gracilenta*; stemonea unknown in *C. stemonea*; subroscida unknown in *C. subroscida*, *C. cinerea* - sporadic, and *C. ferruginea* - sporadic; trichialis unknown 1, and trichialis unknown 2 in *C. trichialis*.

Cyphelium: inquinans unknown 1, inquinans unknown 2, and inquinans unknown 3 in *C. inquinans*; inquinans unknown 1 - sporadic, inquinans unknown 2, and inquinans unknown 3 - sporadic in *C. karelicum*; tigillare unknown 1, and tigillare unknown 2 in *C. tigillare*.

Fig. 12. Chromatogram in solvent systems TDA, HEF, and TA of the unknown secondary substances encountered, with the addition of vulpinic acid, rhizocarpic acid, and epanorin. A,K - References. B - *Calicium glaucellum*. C - *Chaenotheca gracilentia*. D - *Chaenotheca ferruginea*. E - *Chaenotheca stemonea*. F - *Chaenotheca subroscida*. G - *Chaenotheca trichialis*. H - *Chaenotheca carthusiae*. I - *Cyphelium inquinans*. J - *Cyphelium tigillare*. 1-22 Secondary substances: 1 - norstictic

A few species lack secondary substances: *Calicium abietinum*, *C. adaequatum*, *C. denigratum*, *C. quercinum*, *Chaenotheca xyloxena*, and all species in *Microcalicium*.

Sporadic spots frequently occur on the TLC diagrams. Lichens often grow intermingled, and other species may therefore influence the result.

ECOLOGY

Ecological factors

On the basis of our field knowledge, we have made a list of ecological factors we find significant for the distribution of the Caliciales species:

(1) Microclimatic humidity. This is perhaps the most important ecological factor for explaining the distribution of the Caliciales species. The microclimatic humidity is primarily a product of topography and vegetation, not of precipitation.

(2) Substrate. There are great differences between the species in their ability to grow on various substrates. Some species are very specific regarding substrate, while species with a wider ecological amplitude with regard to substrate, may grow on both organic and inorganic substrates. The most common substrates are lignum, bark, bryophytes and siliceous rock.

(3) Light. Some species grow on lignum exposed to high light intensity, some may grow in root caves with a very low light intensity, and others may grow intermediate. Several species seem to tolerate low light intensity because of the correlation with high humidity.

(4) Degree of decomposition of lignum. Whether the lignum is deciduous or coniferous seems to be of less importance. More important is probably the degree of decomposition of the substrate. Slightly decomposed lignum is hard, acid and dry, while well decomposed lignum is softer, more acid and has a higher water capacity (Barkman 1969).

(5) Dispersal. Most of the species, especially the endosubstratic ones, depend on spore dispersal. The spores are not actively dispersed, but stay in the mazaedium. Short distance dispersal may happen by means of tiny animals like mites. Dispersal of thallus fragments occurs in the sorediose/granular species e.g. *Chaenotheca furfuracea*, *C. stemonea* and *C. subroscida*.

acid. 2 - atranorin. 3 - glaucellum unknown. 4. - gracilentia unknown 1. 5 - gracilentia unknown 2. 6 - unknown triterpenoid. 7 - inquinans unknown 3. 8 - red pigment. 9 - ferruginea unknown 1. 10 - ferruginea unknown 2. 11 - stemonea unknown. 12 - subroscida unknown. 13 - vulpinic acid. 14 - trichialis unknown 1. 15 - trichialis unknown 2. 16 - carthusiae unknown. 17 - inquinans unknown 1. 18 - inquinans unknown 2. 19 - tigillare unknown 1. 20 - tigillare unknown 2. 21 - rhizocarpic acid. 22 - epanorin.

(6) Continuity of the environment. Perhaps a combination of stable humidity and small temperature amplitude is of importance in climax forests with a high ecological continuity. It is probable that e.g. *Chaenotheca subroscida* and *Cyphelium karelicum* demand old spruce forests, while *Chaenotheca chrysocephala* also thrives in younger forests. National parks usually have a high frequency of Caliciales species.

(7) Pollution or influence of urban areas. Several species avoid urban areas. This may be due to air pollution or other environmental factors produced by towns. Many Caliciales species probably do not tolerate the dryness and the short continuity of the environment in the urban areas. However, according to Barkman (1969), *Chaenotheca ferruginea* has extended in urban areas in Europe. We have not found this species to be very frequent in the surroundings of Oslo.

(8) Competition. Bryophytes and lichens (especially *Gladonia* spp.) are competitors for the Caliciales species. On the Norwegian west coast, with oceanic conditions, bryophytes are abundant on stems and stumps. In the central and eastern parts of Fennoscandia, with more continental conditions, *Gladonia* spp. overgrow stumps and leave little room for the Caliciales species.

Ecological groups

We have divided the species into ecological groups (Table 6). There are gradual transitions between these groups in nature, and this division is merely an aid in the interest of simplicity.

Comments on the substrate groups in Table 6.

(1) Various substrates. Species within this group grow on lignum, oligotrophic bark, bryophytes or siliceous rock. They are found well protected in root caves or under overhangs. In spite of lacking direct precipitation, the habitats are moist. The soil absorbs water and keeps humidity high. Because of the shade and almost no wind, there is little evaporation. Temperature does not fluctuate much. This contributes to a stable microclimate.

(2) Lignum and oligotrophic bark. Lignum has several features in common with oligotrophic bark, i.e. bark of *Betula*, *Quercus*, *Pinus* and *Picea*. It is acid, hard, has a low water capacity, much tannin, and a low electrolytic concentration (Barkman 1969). Species which are growing under very humid conditions, are mainly found under old stumps. *Chaenotheca trichialis* is mostly corticolous on *Picea*. *Microcalicium disseminatum* grows as a parasite or parasymbiont on Caliciales species (mostly *Chaenotheca* spp.), as a parasite on algae, or as a saprophyte on lignum or oligotrophic bark. *Chaenotheca subroscida* and *Cyphelium karelicum* are usually corticolous on *Picea* in old forests, often near the base of old trunks or under huge branches. *Chaenotheca chrysocephala* grows in younger forests with lower humidity and shorter continuity of the environment. It is a common species on twigs of *Picea*. In the western parts of Norway *Picea* is lacking, and *Pinus* is the most common substrate for *C. chrysocephala*.

Table 6. Species classified by substrate and humidity.
(see text for explanation)

Substrate	Species	Very humid	Humid	Mode- rately humid	Dry
1) Various	Ch. furfuracea	_____			
	Ch. gracilentia	_____			
	Mi. arenarium	_____			
2) Lignum and oligotrophic bark	Ca. subquercinum	_____			
	Ch. stemonea	_____			
	Ch. sulphurea	_____			
	Sc. coniophaea	_____			
	Ch. trichialis	_____			
	Mi. disseminatum	_____			
	Ch. subroscida		_____		
	Cy. karelicum		_____		
	Ca. viride		_____		
	Ch. ferruginea		_____		
	Ca. adspersum			_____	
	Ca. quercinum			_____	
	Ch. chrysocephala			_____	
	Ch. phaeocephala			_____	
3) Lignum	Ch. brunneola	_____			
	Ch. gracillima	_____			
	Ch. laevigata	_____			
	Mi. ahlneri	_____			
	Ca. glaucellum		_____		
	Ca. salicinum		_____		
	Cy. inquinans		_____		
	Ch. carthusiae		_____		
	Ch. xyloxena		_____		
	Ca. denigratum				_____
	Ca. trabinellum				_____
	Cy. pinicola				_____
	Cy. tigillare				_____
	Th. ocellatum				_____
4) Siliceous rock	Ca. corynellum	_____			
5) Alnus twigs	Ca. adaequatum		_____		
6) Eutrophic bark	Sc. farinacea			_____	
	Sc. nivea			_____	

Calicium viride and *Chaenotheca ferruginea* have a wide ecological amplitude with regard to humidity. *Calicium viride* is often corticolous on *Picea*, while *Chaenotheca ferruginea* is mostly corticolous on *Pinus*.

Calicium adspersum, *C. quercinum* and *Chaenotheca phaeocephala* are usually corticolous on old, isolated trunks of *Quercus*, or they grow on slightly decomposed lignum.

(3) Lignum. The lignicolous species occurring in very humid habitats grow in sheltered places, inside or under well decomposed stumps. The other species occur in more exposed habitats, and the lignum is often less decomposed.

Calicium glaucellum and *C. salicinum* have a wide ecological amplitude with regard to humidity. *C. glaucellum* is sometimes corticolous on *Picea* and *C. salicinum* is sometimes corticolous on *Quercus*.

Calicium denigratum, *C. trabinellum*, *Cyphelium pinicola* and *C. tigillare* are the most xerophytic species. They grow on exposed, ecorticate twigs or old fences, usually *Pinus*.

Thelomma ocellatum also occurs on dry lignum. It is ornithocoprophilous and has been collected in Norway on worked timber only. It prefers wooden posts and roofs.

(4) Siliceous rock. *Calicium corynellum* grows on siliceous rock under overhangs.

(5) Twigs of *Alnus*. *Calicium adaequatum* is corticolous on rather young twigs of *Alnus*.

(6) Eutrophic bark. *Sclerophora farinacea* and *S. nivea* favour old, isolated trees of *Fraxinus*, *Ulmus*, *Acer*, and *Tilia*. The eutrophic bark of these trees is slightly acid, soft, has a high water capacity, little tannin, and a high electrolytic concentration (Barkman 1969).

(7) There is a miscellaneous group consisting of *Calicium abietinum*, *Calicium parvum*, *Chaenotheca cinerea*, and *Sclerophora peronella*. We have not classified these species owing to lack of field experience, and because only a few collections have been made in Norway.

FENNOSCANDIAN DISTRIBUTION

For evaluation of the floristic distribution patterns within Fennoscandia we use a system suggested by Bendiksen & Halvorsen (1981) and Økland & Bendiksen (1985). This system includes vegetation zones as described by Ahti et al. (1968). We have placed the species in groups according to the overall appearance of their Fennoscandian distribution patterns as far as it has been possible to ascertain it.

Bendiksen and Halvorsen (1981) divide the Fennoscandian vascular plant flora into five elements: Western, southern, south-eastern, eastern and alpine. In addition we have one group of species with a ubiquitous distribution pattern in Fennoscandia, and a remainder group consisting of species with poorly known distribution patterns. We have added our own data to the known Swedish distributions (Tibell 1977, 1978b, 1980a, Santesson 1984 and Ingeløg et al. 1984) plus scattered information from Denmark and Finland (Tibell 1969, 1976a, 1978a and 1980b). Our distribution data from Norway are found in the chapter TAXONOMY under the description of the species, and maps are provided in Figs 15-49.

Fig. 13 shows the total number of species in the seven groups mentioned above. Note the high number of eastern species (16) and the absence of western species (0). Some reasons for this are suggested in the discussion of the eastern

Fig. 13. The number of species in seven distributional groups. W - western element. A - alpine element. A2 - boreal-alpine species. SE - south-eastern element. SE3 - Slightly south-eastern species. R - rest group. U - ubiquitous species. S - southern element. S2 - southern species. S3 - slightly southern species. S4 - widely distributed species with southern tendency. E - eastern element. E1 - eastern species. E2 - slightly eastern species.

element below.

Western element

There are no species in Norway belonging to the western element.

Southern element

Factors that may influence the distribution of species belonging to the southern element are: (1) the distribution of the substrate. Several of the lichens are restricted to deciduous trees having a southern distribution in Fennoscandia e.g. *Ulmus*, *Fraxinus*, and *Quercus*. (2) Low temperatures in the summer or low temperatures in the winter may also be delimiting.

The southern element is divided into four groups:

S 1 Strongly southern species. No species occur in this group.

S 2 Southern species. Five species occur in this group:

Calicium adspersum (Fig. 16)

Calicium quercinum (Fig. 19)

Sclerophora farinacea (Fig. 47)

Sclerophora nivea (Fig. 48)

Sclerophora peronella (Fig. 47)

Species in this group occur in the temperate and hemiboreal vegetation zones.

S 3 Slightly southern species, including two species:

Calicium corynellum (Fig. 16)

Chaenotheca carthusiae (Fig. 25)

Species in this group occur in the temperate, hemiboreal, and south boreal vegetation zones.

S 4 Widely distributed species with southern tendency, also including two species:

Calicium glaucellum (Fig. 18)

Chaenotheca ferruginea (Fig. 28)

Species in this group occur in the temperate, hemiboreal, south boreal, and middle boreal vegetation zones.

South-eastern element

High summer temperatures seem to be important for species belonging to the south-eastern element, although low winter temperatures cannot be disregarded.

The south-eastern element is divided into four groups:

SE 1 Strongly south-eastern species. No species occur in this group.

SE 2 South-eastern species. No species in this group.

SE 3 Slightly south-eastern species.

Chaenotheca phaeocephala (Fig. 33).

The species in this group occur as far north as the Nordland province, and they may reach the inner fjords of the Norwegian west coast. (In Sweden *Chaenotheca phaeocephala* has been collected as far north as Lule Lappmark).

SE 4 Widely distributed species with south-eastern tendency. No species occur in this group.

Eastern element

Several factors have been suggested as important for the distribution of species in the eastern element: (1) The distribution of the substrate. Some of the lichens (*Chaenotheca subroscida* and *Cyphelium karelicum*) prefer *Picea* which has an

eastern distribution in Fennoscandia. (2) Low humidity may be significant for some, but not for all species. (3) The snow cover may influence some species. (4) Competition, especially from bryophytes, may be of considerable importance at the Norwegian west coast.

Species belonging to the eastern element fall into different ecological groups. *Calicium denigratum*, *C. trabinellum*, *Cyphelium tigillare* and *Thelomma ocellatum* occur on dry lignum in exposed habitats, while the other species grow under very humid or humid conditions. They occur in root caves, on well decomposed lignum of stumps, or they are corticolous in humid forests. The eastern element is divided into two groups:

E 1 Eastern species. This group includes 10 species:

Calicium adaequatum (Fig. 16)
Calicium denigratum (Fig. 17)
Chaenotheca gracillima (Fig. 31)
Chaenotheca laevigata (Fig. 32)
Chaenotheca subroscida (Fig. 35)
Chaenotheca sulphurea (Fig. 36)
Cyphelium karelicum (Fig. 40)
Microcalicium ahlneri (Fig. 43)
Microcalicium disseminatum (Fig. 45)
Sclerophora coniophaea (Fig. 46)

E 2 Slightly eastern species, including four species.

Calicium trabinellum (Fig. 22)
Chaenotheca xyloxena (Fig. 38)
Cyphelium tigillare (Fig. 42)
Thelomma ocellatum (Fig. 49)

The species in group E 2 reach the inner fjords of the Norwegian west coast while the species in group E 1 only reach the mountain chain.

Alpine element

Species belonging here probably do not tolerate high summer temperatures.

The alpine element is divided into three groups.

A 1 Pronounced alpine species. No species occur in this group.

A 2 Boreal-alpine species.

Cyphelium pinicola (Fig. 41).

The species in this group are mostly distributed in alpine areas, but may also occur in the boreal vegetation zones.

Cyphelium pinicola grows in the most continental areas of Norway. It seems to have a disjunct distribution. The substrate (*Pinus*) is widely distributed in Norway, and climatic factors must be restricting the distribution of *C. pinicola*.

A 3 Southern hemiboreal-alpine species. No species occur in this group.

Ubiquitous species

These are widely distributed species in Fennoscandia.

Calicium viride (Fig. 23)
Calicium salicinum (Fig. 20)
Chaenotheca brunneola (Fig. 24)
Chaenotheca chrysocephala (Fig. 26)
Chaenotheca furfuracea (Fig. 29)
Chaenotheca gracilentia (Fig. 30)
Chaenotheca stemonea (Fig. 34)
Chaenotheca trichialis (Fig. 37)
Cyphelium inquinans (Fig. 39)

Remainder

These species have been collected only a few times in Fennoscandia, and their distribution patterns are still insufficiently known:

Calicium abietinum (Fig. 15)
Calicium parvum (Fig. 19)
Calicium subquercinum (Fig. 21)
Chaenotheca cinerea (Fig. 27)
Microcalicium arenarium (Fig. 44)

CLASSIFICATION

Tibell (1984) has proposed the following classification of the Caliciales.

Caliciaceae	Coniocybaceae	Microcaliciaceae	Sclerophoraceae
<i>Calicium</i>	<i>Chaenotheca</i>	<i>Microcalicium</i>	<i>Sclerophora</i>
<i>Cyphelium</i>	<i>Cybebe</i>		
<i>Thelomma</i>			

We suggest a modified version.

Caliciaceae	Coniocybaceae	Microcaliciaceae
<i>Calicium</i>	<i>Chaenotheca</i>	<i>Microcalicium</i>
<i>Cyphelium</i>	<i>Sclerophora</i>	
<i>Thelomma</i>		

Description of the Caliciaceae Fée.

Thallus crustaceous. Phycobiont *Trebouxia*. Apothecia stalked, sessile, or immersed. Mazaedium black. Excipulum well developed, thick or thin. Pruina absent or present. Asci cylindrical or clavate; formed singly, croziers present. Spores one-septate, ellipsoid, dark brown with a surface of irregular cracks, spirally arranged ridges, or almost smooth.

Description of the Coniocybaceae Reichenb.

Thallus crustaceous. Phycobionts *Dictyochloropsis*, *Stichococcus*, *Trebouxia*, or *Trentepohlia*. Apothecia stalked. Mazaedium brown or pale brown. Excipulum well developed or poorly developed, collar absent or present. Pruina usually present. Asci cylindrical or of irregular shape; catenulate or formed singly, croziers present or absent. Spores non-septate, globose or ellipsoid, brown or pale brown with a reticulate or cracked surface.

Description of the Microcaliciaceae Tibell

Parasites or parasymbionts on Caliciales species, parasites on algae, or saprophytes on bark or lignum. Apothecia stalked or sessile. Mazaedium greenish black. Excipulum well developed. Pruina absent. Asci cylindrical; catenulate, croziers absent. Spores 1-3-7-septate, ellipsoid, green with a surface of spirally arranged ridges.

DELIMITATION OF *CHAENOTHECA* (Th.Fr.) Th.Fr. VERSUS *CYBEBE* Tibell AND *SCLEROPHORA* Chevall.

Tibell (1984) has revised the taxonomy of the Caliciales. He placed the species belonging to *Coniocybe* in *Chaenotheca* and in *Sclerophora* and established the monotypic genus *Cybebe*. He also gave a description of the families.

Description of *Chaenotheca*

Chaenotheca is a heterogeneous genus. The thallus may be endo-substratal, or episubstratal of various forms. The phycobionts are *Dictyochloropsis*, *Stichococcus*, *Trebouxia*, or *Trentepohlia*. The apothecia are stalked, 0.5-3.0 mm tall. The hyphae of the stalk are brown, and periclinally arranged. The excipulum is poorly or well developed, without collar. The mazaedium is brown. The asci are cylindrical, or of irregular shape. They are either catenulate or formed singly, and croziers are present in the formation of the ascus. The spores are globose, or ellipsoid, non-septate, and brown with a surface of irregular cracks. The identified secondary substances occurring in *Chaenotheca* are vulpinic acid, pulvinic acid, pulvinic

dilactone, atranorin, baeomycesic acid, squamatic acid, and anthraquinoid pigments.

Description of *Cybebe*

Cybebe is a monotypic genus containing *Cybebe gracilentata* (Ach.) Tibell, syn. *Chaenotheca gracilentata* (Ach.) Mattsson & Middelborg, syn. *Coniocybe gracilentata* (Ach.) Ach. The thallus is episubstratal, granular. The phycobiont is *Stichococcus*. The apothecia are stalked, 2.4-3.5 mm tall. The hyphae of the stalk are brown, and periclinally arranged. The excipulum is poorly developed without collar. The mazaedium is greyish brown. The asci are cylindrical, catenulate, and croziers are absent in the formation of ascus. The spores are globose and pale brown, with a surface of irregular cracks. We have observed four unidentified secondary substances.

Description of *Sclerophora*

The thallus is endosubstratal. The phycobiont is *Trentepohlia*. The apothecia are stalked, 0.4-1.5 mm tall. The hyphae of the stalk are pale brown, and periclinally arranged. The excipulum is poorly or well developed, a collar is present or absent. The mazaedium is pale brown. The asci are cylindrical. They are formed singly, and croziers are present in the formation of the ascus. The spores are globose, non-septate, and pale brown with a reticulate surface. Anthraquinoid pigments occur in the apothecia.

The delimitation of *Chaenotheca* versus *Cybebe*

According to the descriptions given above, *Cybebe* differs from *Chaenotheca* mainly in having an ascus formation without croziers (Nadvornik 1941, Schmidt 1970a). Tibell (1984) also emphasizes the small and pale spores and the lack of secondary substances. We wish to stress the similarities between *Chaenotheca* and *Cybebe* in ascocarp structure, excipulum structure, spore structure and the catenulate asci. Catenulate asci are rare among lichenized fungi, in the Caliciales being known from *Chaenotheca*, *Cybebe* and *Microcalicium* only. *Microcalicium* differs from the two other genera in several morphological characters. The presence of catenulate asci in *Microcalicium* and *Chaenotheca* can thus be regarded as a result of parallel evolution. However, in our opinion the formation of catenulate asci in *Chaenotheca* and *Cybebe* has evolved once, and we regard *Chaenotheca* and *Cybebe* as a monophyletic group. The absence of croziers in *Cybebe* is probably a secondary feature that has been established after the formation of catenulate asci. In our opinion the catenulate asci, the small and slightly cracked spores, the poorly developed excipulum and the lack of vulpinic acid link *Cybebe* to *Chaenotheca* subgenus *Chaenotheca*.

In a chemical investigation of *Cybebe* (see p. 14) we have observed four unidentified secondary substances. It is our opinion that the unidentified substances should not be used in the separation of *Cybebe* from the chemically heterogeneous *Chaenotheca*.

In SEM, spores of *Cybebe* (Fig. 4) show the same surface pattern as *Chaenotheca* spp. (Tibell 1980b). The surface consists of cracks and irregular areas.

Thus we do not accept *Cybebe* at generic level but regard it as synonymous with *Chaenotheca*.

The delimitation of *Chaenotheca* versus *Sclerophora*

According to the descriptions given above, *Sclerophora* differs from *Chaenotheca* in having an endosubstratal thallus, *Trentepohlia* as phycobiont, and an excipulum structure like a collar surrounding the stalk. The spores in *Sclerophora* have a reticulate surface, and anthraquinoid pigments always occur in the apothecia; while *Chaenotheca* spores have a cracked surface and vulpinic acid or anthraquinoid pigments occur in the apothecia.

An examination of *Chaenotheca* spp., however, shows that some species have an endosubstratal thallus (*C. xyloxena*), *Trentepohlia* as phycobiont (*C. hispidula*), and anthraquinoid pigments in the apothecia (*C. ferruginea*, *C. gracillima*). An examination of *Sclerophora* spp. shows that *S. peronella* lacks a collar, and has an excipular structure similar to that of several *Chaenotheca* species, e.g. *C. stemonea*.

The main difference between the two genera is the ontogeny of the spore walls. According to Tibell (1984) *Chaenotheca* spores have an "ornamentation formed by rupturing of the primary wall". *Sclerophora* spores have an "ornamentation formed by intraplasma-lemmatic irregularities of the outer surface of the spore wall". We have compared SEM photographs of spores in two *Sclerophora* species (Figs 8, 11). They are clearly distinct from *Chaenotheca* spores (Tibell 1980b).

According to the treatment above, the ontogeny of the spore walls is the only feature which clearly separates *Sclerophora* and *Chaenotheca*. We find this insufficient for placing *Sclerophora* in the monotypic family Sclerophoraceae Tibell, and we therefore place *Sclerophora* with *Chaenotheca* in the Coniocybaceae.

TAXONOMY

KEY TO THE CRUSTACEOUS GENERA OF CALICIALES IN NORWAY

- 1 Hymenium pale brown or brown.....2
 1 Hymenium black or greenish black.....3
 2(1) Phycobiont *Trentepohlia*. Spores globose with a reticulate surface.....*Sclerophora*
 2 Phycobiont *Stichococcus* or belonging to the *Chlorococcales*. Spores ellipsoid or globose with a cracked surface.....*Chaenotheca*
 3(1) Mazaedium absent. Asci persistent or dissolving late...4
 3 Mazaedium present. Asci dissolving at an early stage...5
 4(3) Parasites/parasymbionts on *Pertusaria*. Apothecia almost sessile.....[*Sphinctrina*]*
 4 Saprophytes. Apothecia stalked.....[*Mycocaliciaceae* (*Chaenothecopsis*, *Mycocalicium*, *Phaeocalicium*, *Stenocybe*)]*
 5(3) Apothecia sessile or immersed.....6
 5 Apothecia stalked.....8
 6(5) Apothecia sessile. Mazaedium greenish black. A saprophyte, parasite on algae or parasite/parasymbiont on Caliciales species.....*Microcalicium disseminatum*
 6 Apothecia sessile or immersed. Mazaedium black. Lichenized.....7
 7(6) Apothecia usually absent. Thallus with black isidia in globular areas. Medulla I+ dark blue..*Thelomma ocellatum*
 7 Apothecia common. Isidia absent. Medulla I-....*Cyphelium*
 8(5) Mazaedium black. Spores 8-16 μm long. Lichenized.....*Calicium*
 8 Mazaedium greenish black or dark brown. Spores 5-8 μm long. Saprophytes or parasites on algae....*Microcalicium*

* Not included in the following treatment.

Italicized province names in the following treatment indicate a first report.

CALICIUM Pers.

Thallus endosubstratal or granular, green to grey. Phycobiont *Trebouxia*. Apothecia black or rarely dark brown, stalked. Excipulum well developed. Mazaedium black. Pruina on the apothecium brown, yellow, white, or absent. Asci cylindrical or clavate. Spores one-septate, ellipsoid, dark brown with a surface of spirally arranged ridges or more or less irregular cracks.

Key to the species

- 1 Pruina on apothecium yellow.....2
- 1 Pruina on apothecium absent or of other colour.....3
- 2(1) Thallus granular, grey. Asci clavate. Spores with a surface of spirally arranged ridges.....*C. adspersum*
- 2 Thallus endosubstratal. Asci cylindrical. Spores with a surface of irregular cracks.....*C. trabinellum*
- 3(1) Pruina brown, on the lower side of excipulum. Apothecia stout, large (0.9-1.9 mm).....4
- 3 Pruina absent or pruina white on excipulum margin. Apothecia smaller (0.4-1.3 mm).....5
- 4(3) Thallus granular, green. Asci clavate. Spores with a surface of irregular cracks.....*C. viride*
- 4 Thallus endosubstratal. Asci cylindrical. Spores with a surface of spirally arranged ridges.....*C. salicinum*
- 5(3) Thallus episubstratal, well developed, yellowish or greyish green.....6
- 5 Thallus endosubstratal; or very poorly developed, green.....7
- 6(5) Thallus yellowish green, farinaceous-granular. Apothecia very short (0.3-0.5 mm).....*C. corynellum*
- 6 Thallus greyish green, verrucose-granular. Apothecia medium (0.7-1.0 mm).....*C. quercinum*
- 7(5) Apothecium stalk I+ blue.....8
- 7 Apothecium stalk I-.....9
- 8(7) Stalk black. Apothecia medium (0.8-1.3 mm). Pruina white on excipular margin.....*C. subquercinum*
- 8 Stalk dark brown. Apothecia small (0.4-0.7 mm). Pruina absent.....*C. adaequatum*
- 9(7) Asci clavate. Pruina white on excipular margin.*C. parvum*
- 9 Asci cylindrical. Pruina white on excipular margin, or pruina absent.10
- 10(9) Pruina white on excipular margin. Spores with a surface of irregular cracks (Fig. 8).....*C. glaucellum*
- 10 Pruina absent. Spore surface various.....11
- 11(10) Stalk black or dark brown, medium (0.6-0.9 mm). Spores with a warty surface (Fig. 7).....*C. abietinum*
- 11 Stalk black, long (0.7-1.3 mm). Spores with a slightly cracked surface.....*C. denigratum*

1. *Calicium abietinum* Pers.

Morphology and anatomy. Thallus endoxylic. Phycobiont *Trebouxia*. Apothecia black or dark brown, of medium height (0.6-0.9 mm). Pruina absent. Asci cylindrical. Spores 11.5-15.0 x 5-7 μ m with an irregular warty surface.

Chemistry. No secondary substances found.

Ecology. *C. abietinum* is lignicolous.

Distribution. A rarely collected species, in Norway known from two localities only (Fig. 15). Tibell (1975) reports *C. abietinum* as a southern species in Europe. The collection from Troms province does not fit into this pattern.

Figs 14-15. Provinces in Norway and species distribution. Fig. 14. Provinces in Norway. 1 - Østfold (Østf). 2 - Akershus (Akh). 3 - Hedmark (Hedm). 4 - Oppland (Oppl). 5 - Buskerud (Busk). 6 - Vestfold (Vestf). 7 - Telemark (Tel). 8 - Aust-Agder (A-Agd). 9 - Vest-Agder (V-Agd). 10 - Rogaland (Rog). 11 - Hordaland (Hord). 12 - Sogn og Fjordane (S & F). 13 - Møre og Romsdal (M & R). 14 - Sør-Trøndelag (S-Trønd). 15 - Nord-Trøndelag (N-Trønd). 16 - Nordland (Nordl). 17 - Troms (Troms). 18 - Finnmark (Finnm). Abbreviations used in text are given in brackets. Fig. 15. *Calicium abietinum*.

Akh, Troms.

Taxonomical notes. *Calicium abietinum* is very similar to *C. glaucellum*. *C. abietinum* has no pruina and may have a dark brown apothecium. *C. glaucellum* usually has a white pruina on the excipular margin and always has a black apothecium. The spores in *C. glaucellum* are slightly smaller. In SEM, spores of *C. abietinum* (Fig. 7) show an irregular warty pattern, those of *C. glaucellum* (Fig. 8) a surface of coarser cracks.

2. *Calicium adaequatum* Nyl.

Morphology and anatomy. Thallus endosubstratal. Phycobiont *Trebouxia*. Apothecia dark brown, I+ blue, small (0.4-0.7 mm). Pruina absent. Asci cylindrical. Spores 11-14 x 5-7 μ m with a surface of spirally arranged ridges.

Chemistry. No secondary substances found.

Ecology. *C. adaequatum* is corticolous on twigs of *Alnus incana* in humid habitats.

Distribution. A rarely collected species, in Norway known from one collection only (Fig. 16).

Oppl. New to Norway.

3. *Calicium adpersum* Pers.

Morphology and anatomy. Thallus granular, grey, PD+ orange, K+ red. Phycobiont *Trebouxia*. Apothecia black, stout (0.6-1.0 mm). Pruina yellow on the capitulum. Asci clavate. Spores 13-16 x 5.5-6.5 μ m with a surface of spirally arranged ridges.

Chemistry. The thallus contains norstictic acid, and the yellow pruina vulpinic acid. This is in accordance with Tibell (1975).

Ecology. *C. adpersum* is corticolous on old *Quercus* trunks in moderately humid habitats.

Distribution. A rarely collected species, in Norway known from one locality only (Fig. 16).

Vestf. New to Norway.

4. *Calicium corynellum* Ach.

Morphology and anatomy. Thallus farinaceous-granular, yellowish green. Phycobiont *Trebouxia*. Apothecia black, very short (0.3-0.5 mm). Pruina white, faint, on the lower side of excipulum. Asci clavate. Spores 12-16 x 4-6 μ m with a cracked surface.

Chemistry. We have found rhizocarpic acid in the thallus. In the Scandinavian specimens usnic acid also occurs. In the Central European specimens atranorin occurs instead of usnic acid.

Ecology. *C. corynellum* grows on siliceous rock under overhangs in very humid habitats.

Distribution. A rarely collected species, in Norway known from one collection only (Fig. 16).

Figs 16-17. Species distributions. Fig. 16. *Calicium adaequatum* (▲), *C. adpersum* (●), and *C. conynellum* (■). Fig. 17. *C. denigratum*.

Akh. New to Norway.

5. *Calicium denigratum* (Vain.) Tibell

Morphology and anatomy. Thallus endoxylic. Phycobiont *Trebouxia*. Apothecia black, medium or long (0.7-1.3 mm). Pruina absent. Asci cylindrical. Spores 11.0-13.5 x 6.0-7.5 μm with few irregular cracks on the surface.

Chemistry. No secondary substances found.

Ecology. *C. denigratum* is lignicolous, especially on *Pinus* in dry habitats.

Distribution. The species has an eastern distribution in Norway (Fig. 17).

Hedm, Oppl, N-Trønd, Troms, Finnmark.

6. *Calicium glaucellum* Ach.

Morphology and anatomy. Thallus endosubstratal or granular, green, thin. Phycobiont *Trebouxia*. Apothecia black, medium (0.5-0.9 mm). Pruina white on excipular margin or rarely absent. Asci cylindrical. Spores 10.5-13.0 x 5.0-6.5 μm with irregular cracks and ridges on the surface.

Chemistry. *Glaucellum* unknown occurs in the thallus.

Ecology. *C. glaucellum* is lignicolous; or more rarely corticolous on *Picea*. The habitat varies from humid to dry.

Distribution. A common species with a wide distribution in Norway, avoiding the northernmost areas only (Fig. 18).

Østf, Akh, Hedm, Oppl, Busk, Vestf, Tel, A-Agd, V-Agd, Rog, Hord, M & R, N-Trønd, Nordl, Troms.

Taxonomical notes. See *C. abietinum*, p. 33.

7. *Calicium parvum* Tibell

Morphology and anatomy. Thallus granular, grey, thin. Phycobiont *Trebouxia*. Apothecia black, medium (0.5-0.8 mm). Pruina white on excipular margin. Asci clavate. Spores 8-11 x 3.5-4.5 μm with irregular cracks on the surface. Pycnidia present, black. Pycnoconidia ellipsoid, 2.0-3.0 x 1.0-1.5 μm .

Chemistry. We have found diffractaic acid and inquinans unknown 3 (UV++ blue) in the thallus.

Ecology. *C. parvum* is corticolous on *Pinus* or *Picea*.

Distribution. A rarely collected species, in Norway known from one collection only (Fig. 19). The previous report from Akershus province (Tibell 1975) represents a specimen collected in Sweden.

Oppl. New to Norway.

8. *Calicium quercinum* Pers.

Morphology and anatomy. Thallus verrucose-granular, greyish green, thick. Phycobiont *Trebouxia*. Apothecia black, medium (0.7-1.0 mm). Pruina white on excipular margin. Asci cylindrical. Spores 9-11 x 4-5 μm with a surface of spirally

Figs 18-19. Species distributions. Fig. 18. *Calicium glau-cellum*. Fig. 19. *C. parvum* (■) and *C. quercinum* (●).

arranged ridges.

Chemistry. No secondary substances found.

Ecology. *C. quercinum* is corticolous on old *Quercus* trunks in moderately humid habitats.

Distribution. A rarely collected species, in Norway known from one collection only (Fig. 19).

Akh.

9. *Calicium salicinum* Pers.

Morphology and anatomy. Thallus endosubstratal, PD+ orange, K+ red. Phycobiont *Trebouxia*. Apothecia black, large (0.9-1.5 mm). Pruina brown on the lower side of the excipulum. Asci cylindrical. Spores 8-11 x 4-5 μ m with a surface of spirally arranged ridges (Fig. 9).

Chemistry. We have found norstictic acid in the thallus.

Ecology. *C. salicinum* is lignicolous; or rarely corticolous on *Quercus*. The habitat varies from humid to dry.

Distribution. The species seems to have a wide distribution in Norway (Fig. 20).

Akh, Hedm, Oppl, Busk, Vestf, Tel, A-Agd, Hord, S-Trønd, Nordl, Troms, Finnmark.

10. *Calicium subquercinum* Asah.

Morphology and anatomy. Thallus endosubstratal or granular, grey, thin. Phycobiont *Trebouxia*. Apothecia black, medium (0.8-1.3 mm). Pruina white on excipular margin. Asci clavate. Spores 9-11 x 4-5 μ m with a warty surface. In contrast to most other Caliciales species, semimature spores within the asci are non-septate.

Chemistry. We have found one substance, iniquinans unknown 2, in the thallus.

Ecology. *C. subquercinum* is lignicolous or corticolous in very humid habitats. It has been collected once on siliceous rock.

Distribution. The species has often been collected at Ringebu, Oppl., otherwise rarely (Fig. 21).

Hedm, Oppl, Hord.

11. *Calicium trabinellum* Ach.

Morphology and anatomy. Thallus endoxylic. Phycobiont *Trebouxia*. Apothecia black, medium (0.6-0.9 mm). Pruina yellow on excipular margin. Asci cylindrical. Spores 10.0-11.5 x 5-6 μ m with a surface of irregular cracks.

Chemistry. We have found vulpinic acid in the yellow pruina. This is in accordance with Tibell (1975).

Ecology. *C. trabinellum* is lignicolous, especially on *Picea* in dry habitats.

Distribution. A common species with a slightly eastern distribution in Norway (Fig. 22).

Figs 20-21. Species distributions. Fig. 20. *Calicium salicinum*.
Fig. 21. *C. subquercinum*.

Figs 22-23. Species distributions. Fig. 22. *Calicium trabi-nellum*. Fig. 23. *C. viride*.

Akh, Hedm, Oppl, Busk, Tel, A-Agd, Hord, M & R, S-Trønd, N-Trønd, Nordl, Troms, Finnm.

12. *Calicium viride* Pers.

Morphology and anatomy. Thallus granular, green, usually thick. Phycobiont *Trebouxia*. Apothecia black, large (1.1-1.9 mm). Pruina brown on the lower side of excipulum. Asci clavate. Spores 12.5-13.5 x 6-7 μ m with a surface of irregular cracks.

Chemistry. We have found rhizocarpic acid and epanorin in the thallus.

Ecology. *C. viride* is lignicolous or corticolous on both deciduous and coniferous trees. It has a wide ecological amplitude with regard to humidity.

Distribution. A common species with a wide distribution in Norway (Fig. 23).

Østf, Akh, Hedm, Oppl, Busk, Vestf, Tel, A-Agd, Hord, M & R, S-Trønd, N-Trønd, Nordl, Troms, Finnm.

CHAENOTHECA (Th.Fr.) Th.Fr.

Thallus endosubstratal or episubstratal, granular, farinaceous, verrucose or squamulose. Thalline colour green, yellow or grey. Phycobiont *Dictyochloropsis* or *Trebouxia* (Chlorococcales), *Stichococcus* or *Trentepohlia* (Tibell 1980b). Apothecia black or dark brown, stalked. Excipulum well or poorly developed. Mazaedium medium or pale brown. Pruina on the apothecium yellow, yellowish green, white or reddish brown; or absent. Asci cylindrical or irregular; catenulate or formed singly, croziers present or absent. Spores globose or ellipsoid, non-septate, brown. Spore surface with irregular cracks.

Key to the species

- 1 Phycobiont Chlorococcales.....2
- 1 Phycobiont *Stichococcus*.....7
- 2(1) Pruina yellow.....3
- 2 Pruina white or absent.....6
- 3(2) Spores ellipsoid.....4
- 3 Spores globose.....5
- 4(3) Thallus yellow, verrucose or granular. Apothecia short (0.6-1.3 mm).....*C. chrysocephala*
- 4 Thallus endosubstratal. Apothecia long (0.9-1.9 mm).....*C. laevigata*
- 5(3) Thallus greenish brown, verrucose or squamulose. Apothecia stout. Lignicolous, or corticolous on *Quercus*.....*C. phaeocephala*
- 5 Thallus greyish white, granular. Apothecia slender. Corticolous on *Picea*.....*C. subroscida*
- 6(2) Thallus greyish, granular, often with yellow, K+ red spots. Excipulum well developed. Spores 6-7.5 μ m.....*C. ferruginea*

- 6 Thallus endosubstratal. Excipulum poorly developed. Spores 3.5-4.5 μ m.....*C. brunneola*
- 7(1) Pruina yellowish green or bright yellow.....8
- 7 Pruina white or reddish brown.....10
- 8(7) Pruina bright yellow. Thallus greyish green. Spores ellipsoid.....*C. carthusiae*
- 8 Pruina yellowish green. Thallus endosubstratal or yellowish green. Spores globose.....9
- 9(8) Thallus yellowish green. Apothecia long (1.6-2.7 mm). Mazaedium pale brown.....*C. furfuracea*
- 9 Thallus endosubstratal. Apothecia short (0.4-1.4 mm). Mazaedium dark brown.....*C. sulphurea*
- 10(7) Apothecia flexuose, very long and slender (1.6-3.5 mm)11
- 10 Apothecia not flexuose, shorter and stouter.....12
- 11(10) Thallus farinaceous, greyish green. Pruina white, faint, K-, on the lower side of excipulum. Mazaedium greyish brown.....*C. gracilentia*
- 11 Thallus endosubstratal. Pruina reddish brown, K+ violet, on the upper part of the apothecium. Mazaedium brown....*C. gracillima*
- 12(10) Thallus granular, greyish white. Pruina white, dense, covering the whole apothecium.....*C. cinerea*
- 12 Thallus endosubstratal or green. Pruina white, faint, on the lower side of excipulum.....13
- 13(12) Thallus endosubstratal.....*C. xyloxena*
- 13 Thallus episubstratal.....14
- 14(13) Thallus verrucose or squamulose, greyish green. Apothecia large (1.0-1.9 mm). Excipulum well developed.*C. trichialis*
- 14 Thallus farinaceous, green. Apothecia medium (0.8-1.4 mm). Excipulum poorly developed.....*C. stemonea*

Appendix: Species known from Sweden, but not from Norway:

C. hispidula (Ach.) Zahlbr. Thallus endosubstratal. Phycobiont *Trentepohlia*. Excipulum well developed. Pruina yellow. Spores globose.

1. *Chaenotheca brunneola* (Ach.) Mull.Arg.

Morphology and anatomy. Thallus endosubstratal. Phycobiont *Dictyo chloropsis* (Tschermak-Woess 1978). Apothecia black, medium (0.6-1.6 mm), sometimes branched. Excipulum poorly developed. Pruina absent or white, on the lower side of excipulum. Spores globose, 3.4-4.6 μ m, with a slightly cracked surface.

Chemistry. We have found baeomycesic acid and squamatic acid in the thallus. Tibell (1980b) reported baeomycesic acid.

Ecology. *C. brunneola* occurs mostly on well decomposed lignum in very humid habitats. It has been collected on oligotrophic bark a few times.

Distribution. The species seems to have a wide distribution in Norway (Fig. 24).

Figs 24-25. Species distributions. Fig. 24. *Chaenotheca brunneola*. Fig. 25. *C. carthusiae*.

Akh, Hedm, Oppl, Vestf, Tel, Hord, N-Trønd, Nordl, Troms.

2. *Chaenotheca carthusiae* (Harm.) Lett.

Morphology and anatomy. Thallus granular or verrucose, greenish grey. Phycobiont *Stichococcus*. Apothecia black, small (0.5-1.0 mm). Excipulum well developed. Pruina yellow, covering the upper part of the apothecia. Spores ellipsoid, 4.8-7.7 x 2.7-3.6 μ m, with a roughly cracked surface.

Chemistry. We have found vulpinic acid in the yellow pruina and *carthusiae* unknown and *trichialis* unknown 2 in the thallus. Tibell (1980b) reported vulpinic acid in the pruina.

Ecology. *C. carthusiae* is lignicolous in humid habitats. We have always found it in association with *C. trichialis*.

Distribution. The species has a slightly southern distribution in Norway (Fig. 25). The previous report from Finnmark (Tibell 1973) represents *C. laevigata*.

Busk, A-Agd, V-Agd, Rog, Nordl. New to Norway.

3. *Chaenotheca chrysocephala* (Turn. ex Ach.) Th.Fr.

Morphology and anatomy. Thallus granular, yellow. Phycobiont *Trebouxia* (Tschermak-Woess 1978). Apothecia black, medium (0.6-1.3 mm). Excipulum well developed. Pruina yellow on the lower side of excipulum. Spores ellipsoid, 6.2-9.0 x 3.8-4.8 μ m, with a roughly cracked surface.

Chemistry. We have found vulpinic acid, pulvinic acid and pulvinic dilactone in the thallus. Tibell (1980b) reported vulpinic acid.

Ecology. *C. chrysocephala* is mainly corticolous on *Picea* in moderately humid habitats, but has also been collected on *Pinus* and lignum. It thrives in rather young forests and seems to tolerate modern forestry. It is often parasitized by *Chaenothecopsis concosiata* (Nadv.) Schmidt.

Distribution. The species has a wide distribution in Norway and is one of the most common Caliciales species (Fig. 26).

Akh, Hedm, Oppl, Busk, Vestf, Tel, A-Agd, V-Agd, Hord, S-Trønd, N-Trønd, Nordl, Troms, Finnmark.

4. *Chaenotheca cinerea* (Pers.) Tibell

Morphology and anatomy. Thallus granular, grey. Phycobiont *Stichococcus*. Apothecia brown, short (0.6-1.0 mm). Excipulum well developed. Pruina white, covering the upper part of the apothecia. Spores globose, 4.6-5.6 μ m, with a slightly cracked surface.

Chemistry. We have found atranorin and subroscida unknown in the thallus.

Ecology. *C. cinerea* has been collected on dead bryophytes in Norway.

Distribution. A rarely collected species, in Norway only known from Ringebu, Oppl. (Fig. 27).

Figs 26-27. Species distributions. Fig. 26. *Chaenotheca chrysocephala*. Fig. 27. *C. cinerea*.

Oppl.

5. *Chaenotheca ferruginea* (Turn. ex Sm.) Migula

Morphology and anatomy. Thallus granular, greyish green with yellow, K+ red, spots. Phycobiont *Trebouxia*. Apothecia black, medium (0.8-1.7 mm). Excipulum well developed. Pruina absent. Spores globose, 5.6-7.7 μm , with a roughly cracked surface.

Chemistry. We have found ferruginea unknown 1 and 2 in the thallus, and a yellowish red, K+ red, pigment in smaller areas on the thallus. Sometimes the thallus also contains subroscida unknown or atranorin. The mazaedium also contains a K+ red pigment. Tibell (1980b) reported a K+ red pigment from the thallus and the mazaedium.

Ecology. *C. ferruginea* is frequently found corticolous on *Pinus*. It is lignicolous or corticolous, and has also been collected a few times on burnt lignum. The habitat varies from humid to dry.

Distribution. The species has a southern tendency in Norway (Fig. 28).

Østf, Akh, Hedm, Oppl, Busk, Tel, A-Agd, V-Agd, Troms.

6. *Chaenotheca furfuracea* (L.) Tibell

Synonym: *Coniocybe furfuracea* (L.) Ach.

Morphology and anatomy. Thallus farinaceous, yellowish green. Phycobiont *Stichococcus*. Apothecia black, long (1.6-2.7 mm) and slender. Excipulum poorly developed. Mazaedium pale brown. Pruina yellowish green, covering the whole apothecium. Spores globose, 2.3-3.1 μm , with a reticulately cracked surface.

Chemistry. We have found vulpinic acid, pulvinic acid and pulvinic dilactone in the thallus and the pruina.

Ecology. *C. furfuracea* grows in shaded and very humid habitats. It has been collected on various substrates such as bark, lignum, bryophytes, roots and siliceous rock.

Distribution. The species has a wide distribution in Norway, and is one of the most common Caliciales species (Fig. 29).

Østf, Akh, Hedm, Oppl, Busk, Vestf, Tel, Hord, S&F, M&R, S-Trønd, N-Trønd, Nordl, Troms, Finnmark.

7. *Chaenotheca gracilentia* (Ach.) Mattsson & Middelborg comb. nov.

Basionym: *Calicium gracilentum* Ach. Lichenographia Universalis (1810), p.243. Synonyms: *Coniocybe gracilentia* (Ach.) Ach., *Cybebe gracilentia* (Ach.) Tibell

Morphology and anatomy. Thallus farinaceous, greyish green. Phycobiont *Stichococcus*. Apothecia black, flexuose, very long (2.4-3.5 mm) and slender. Excipulum poorly developed. Pruina greyish, faint, on the lower side of excipulum. Spores globose, 2.5-3.0 μm , with a slightly cracked surface.

Figs 28-29. Species distributions. Fig. 28. *Chaenotheca ferruginea*. Fig. 29. *C. furfuracea*.

Figs 30-31. Species distributions. Fig. 30. *Chaenotheca gracilentia*. Fig. 31. *C. gracillima*.

Chemistry. We have found an unknown triterpenoid, *gracilentia* unknown 1 & 2 and *inquinans* unknown 3 in the thallus. According to Tibell (1984) no secondary substances are found.

Ecology. *C. gracilentia* grows in very humid and shaded habitats. It has mostly been collected on bark, roots and bryophytes, but also on siliceous rock.

Distribution. The species seems to have a wide distribution in Norway (Fig. 30).

Oppl, Hord, N-Trønd, Troms, Finnm.

Taxonomical notes. We do not recognize *Cybebe* Tibell at generic level (see p. 28).

8. *Chaenotheca gracillima* (Vain.) Tibell

Synonym: *Coniocybe gracillima* Vain.

Morphology and anatomy. Thallus endosubstratal. Phycobiont *Stichococcus*. Apothecia black, flexuose, long (1.6-2.5 mm) and slender. Excipulum poorly developed. Pruina reddish brown, K+ violet, on excipulum and the upper part of the stalk. Spores globose, 2.6-3.2 μm , with a slightly cracked surface.

Chemistry. The pruina contains a reddish brown, K+ violet, pigment.

Ecology. *C. gracillima* is usually lignicolous in very humid habitats and on well decomposed lignum.

Distribution. The species seems to have an eastern distribution in Norway (Fig. 31).

Hedm, Oppl, N-Trønd, Nordl, Troms.

9. *Chaenotheca laevigata* Nadv.

Morphology and anatomy. Thallus endosubstratal. Phycobiont *Trebouxia*. Apothecia long (0.9-1.9 mm) and slender. Excipulum well developed. Pruina yellow, on excipulum and the upper part of the stalk. Spores ellipsoid, 5.5-6.3 x 3.2-3.6 μm , with a roughly cracked surface.

Chemistry. We have found vulpinic acid in the pruina. This is in accordance with Tibell (1980b).

Ecology. *C. laevigata* shows a preference for lignum of *Picea* in very humid habitats.

Distribution. A rarely collected species, probably with an eastern distribution in Norway (Fig. 32).

Oppl, Hedm, Finnm.

10. *Chaenotheca phaeocephala* (Ach.) Th.Fr.

Morphology and anatomy. Thallus verrucose, squamulose, greenish brown. Phycobiont *Trebouxia*. Apothecia dark brown, small/medium (0.5-1.2 mm), stout. Excipulum well developed. Pruina yellow, on the lower side of excipulum. Spores globose, 5.6-7.2 μm , with a cracked surface.

Figs 32-33. Species distributions. Fig. 32. *Chaenotheca laevigata*. Fig. 33. *C. phaeocephala*.

Chemistry. The pruina contains vulpinic acid. This is in accordance with Tibell (1980b).

Ecology. *C. phaeocephala* is corticolous on *Quercus* trunks; or rarely lignicolous. The habitat is moderately humid.

Distribution. The species has a slightly south-eastern distribution in Norway (Fig. 33).

Akh, Hedm, Busk, Tel.

11. *Chaenotheca stemonea* (Ach.) Müll. Arg.

Morphology and anatomy. Thallus farinaceous, green. Phycobiont *Stichococcus*. Apothecia black, small/medium (0.8-1.4 mm). Excipulum poorly developed. Pruina white on the lower side of excipulum. Spores globose, 3.5-4.9 μm , with a cracked surface.

Chemistry. We have found stemonea unknown in the thallus. Tibell (1980b) reported two unknowns, but there is no information about Rf values.

Ecology. *C. stemonea* is corticolous or lignicolous in shaded and very humid habitats.

Distribution. The species seems to have a wide distribution in Norway (Fig. 34).

Akh, Hedm, Oppl, V-Agd, Hord, Troms.

12. *Chaenotheca subroscida* (Eitn.) Zahlbr.

Morphology and anatomy. Thallus granular, greyish white. Phycobiont *Trebouxia*. Apothecia black, medium (0.8-1.5 mm). Excipulum well developed. Pruina yellow, on the lower side of excipulum. Spores globose, 6.0-7.3 μm , with a cracked surface.

Chemistry. We have found vulpinic acid in the pruina, and subroscida unknown in the thallus. Tibell (1980b) reported vulpinic acid.

Ecology. *C. subroscida* is usually corticolous on *Picea* in old forests.

Distribution. The species has an eastern distribution in Norway (Fig. 35).

Hedm, Oppl, Busk, Nordl.

13. *Chaenotheca sulphurea* (Retz.)

Synonym: *Coniocybe sulphurea* (Retz.) Nyl.

Morphology and anatomy. Thallus endosubstratal. Phycobiont *Stichococcus*. Apothecia black, medium (0.4-1.4 mm). Excipulum poorly developed. Mazaedium dark brown (darker than that of *C. furfuracea*). Pruina yellowish green, covering the whole apothecium. Spores globose, 2.8-3.7 μm , with a slightly cracked surface.

Chemistry. We have found vulpinic acid and pulvinic acid in the pruina.

Ecology. *C. sulphurea* is lignicolous or corticolous in very humid habitats.

Figs 34-35. Species distributions. Fig. 34. *Chaenotheca stemonea*. Fig. 35. *C. subroscida*.

Figs 36-37. Species distributions. Fig. 36. *Chaenotheca sulphurea*. Fig. 37. *C. trichialis*.

Distribution. The species seems to have an eastern distribution in Norway (Fig. 36).

Hedm, Oppl, Troms.

Nomenclatural note. The nomenclature of the species *Coniocybe sulphurea* (Retz.) Nyl. is confusing (Tibell 1984). The species evidently belongs to the genus *Chaenotheca*, and we have chosen to use *Chaenotheca sulphurea* as a preliminary name without making a formal combination since it is not certain that *Chaenotheca sulphurea* has priority.

14. *Chaenotheca trichialis* (Ach.) Th.Fr.

Morphology and anatomy. Thallus squamulose or granular, greyish green. Phycobiont *Stichococcus*. Apothecia black, large (1.0-1.9 mm). Excipulum well developed. Pruina white, on the lower side of excipulum. Spores globose, 4.0-5.0 μm , with a slightly cracked surface.

Chemistry. We have found *trichialis* unknown 1 and *trichialis* unknown 2 in the thallus.

Ecology. *C. trichialis* is often corticolous on *Picea*. It is lignicolous or corticolous on coniferous or deciduous trees. The humidity of the habitats varies from humid to dry.

Distribution. The species has a wide distribution in Norway (Fig. 37).

Østf, Akh, Oppl, Busk, Tel, A-Agd, V-Agd, Rog, Hord, S-Trønd, N-Trønd, Nordl, Troms, Finnmark.

15. *Chaenotheca xyloxena* Nád. v.

Morphology and anatomy. Thallus endoxylic. Phycobiont *Stichococcus*. Apothecia black, slender, long (0.9-1.5 mm). Excipulum well developed. Pruina white, on the lower side of excipulum. Spores globose, 3.1-3.8 μm , with a slightly cracked surface.

Chemistry. No secondary substances found.

Ecology. *C. xyloxena* is lignicolous in rather humid habitats.

Distribution. The species has a slightly eastern distribution in Norway (Fig. 38).

Østf, Akh, Oppl, Busk, Vestf, Hord, Nordl, Troms.

CYPHELIUM Ach.

Thallus episubstratal, verrucose, yellow, grey or greenish grey. Phycobiont *Trebouxia*. Apothecia black, sessile or immersed. Excipulum thin, or thick at the base. Mazaedium black. Pruina white on excipular margin, or absent. Asci cylindrical or broadly clavate. Spores one-septate, dark brown with a surface of irregular cracks or almost smooth.

Figs 38-39. Species distributions. Fig. 38. *Chaenotheca xyloxena*. Fig. 39. *Cyphelium inquinans*.

Key to the species

- 1 Thallus yellow.....2
- 1 Thallus grey or greenish grey.....3
- 2(1) Apothecia immersed. Excipulum thin at the base. Asci clavate*C. tigillare*
- 2 Apothecia sessile. Excipulum thick at the base. Asci cylindrical.....*C. pinicola*
- 3(1) Thallus grey, thick. Spores with a smooth surface.....*C. inquinans*
- 3 Thallus greenish grey, thin. Spores with a roughly cracked surface.....*C. karelicum*

Appendix: Species known from Sweden, but not from Norway:

C. notarissii (Tul.) Blomb. & Forss. Thallus yellow. Apothecia immersed. Excipulum thin. Asci clavate. Spores submuriform, with a smooth surface.

C. sessile (Pers. ex. Merat) Trevis. Parasite/parasymbiont on *Pertusaria*. Apothecia sessile. Excipulum thick. Asci clavate. Spores with a cracked surface.

C. trachylioides (Nyl. ex. Deichm. Branth & Rost.) Erichs. Thallus grey. Apothecia immersed. Excipulum thin. Asci clavate. Spores with a smooth surface.

1. *Cyphelium inquinans* (Sm.) Trevis.

Morphology and anatomy. Thallus verrucose, grey, usually thick, K+ red, PD+ orange. Phycobiont *Trebouxia*. Apothecia black, sessile, diameter 1.5-2.5 mm. Excipulum thick. Pruina white on excipular margin. Asci cylindrical. Spores 14-19 x 8-11 μ m, with an almost smooth surface.

Chemistry. We have found three secondary substances in the thallus: *Inquinans* unknown 1, *inquinans* unknown 2 and *inquinans* unknown 3. None of these are usnic acid, atranorin or pigments. Tibell (1969) reported usnic acid, atranorin, an unidentified substance (K+ reddish brown), and an unidentified yellow pigment.

Ecology. *C. inquinans* is usually lignicolous in moderately humid habitats. It is also corticolous, especially on *Picea*.

Distribution. The species seems have a wide distribution in Norway (Fig. 39).

Akh, Hedm, Oppl, Busk, Hord, N-Trønd, Nordl, Troms, Finnmark.

2. *Cyphelium karelicum* (Vain.) Ras.

Morphology and anatomy. Thallus verrucose, greenish grey, thin. Phycobiont *Trebouxia*. Apothecia black, sessile, diameter 0.4-0.7 mm. Excipulum thick. Pruina white on excipular margin. Asci cylindrical. Spores 13-17 x 8-11 μ m, with a roughly cracked surface. The septum is constricted.

Figs 40-41. Species distributions. Fig. 40. *Cyphelium karelicum*. Fig. 41. *C. pinicola*.

Chemistry. We have always found inquinans unknown 2 and sometimes inquinans unknown 1 and inquinans unknown 3 in the thallus.

Ecology. *C. karelicum* is usually corticolous on *Picea* in old forests.

Distribution. A rarely collected species, probably with an eastern distribution in Norway (Fig. 40).

Hedm, Oppl, N-Trønd.

3. *Cyphelium pinicola* Tibell

Morphology and anatomy. Thallus verrucose, yellow, thick. Phycobiont *Trebouxia*. Apothecia black, sessile, diameter 0.4-0.6 mm. Excipulum thick. Pruina absent. Asci cylindrical. Spores 13-17 x 7-9 μ m, with an almost smooth surface.

Chemistry. We have found rhizocarpic acid and epanorin in the thallus. Two out of seven specimens examined also contained norstictic acid. Tibell (1969) reported rhizocarpic acid.

Ecology. *C. pinicola* is lignicolous on dry twigs of *Pinus*. It has been collected once on bark of *Betula*.

Distribution. The species grows in the most continental areas in Norway (see p. 25) and seems to have a disjunct distribution (Fig. 41).

Hedm, Oppl, M&R, S-Trønd, Troms.

4. *Cyphelium tigillare* (Ach.) Ach.

Morphology and anatomy. Thallus verrucose, yellow. Phycobiont *Trebouxia*. Apothecia black, immersed, diameter 0.5-0.8 mm. Excipulum thin. Asci clavate. Spores 17-21 x 9-11 μ m, with an almost smooth surface.

Chemistry. We have found rhizocarpic acid, epanorin, tigillare unknown 1 and tigillare unknown 2 in the thallus. Tibell (1969) reported rhizocarpic acid.

Ecology. *C. tigillare* is lignicolous in dry habitats. It often occurs on worked timber.

Distribution. A common species with a slightly eastern distribution in Norway (Fig. 42). Akh, Hedm, Oppl, Busk, Tel, Rog, Hord, S-Trønd, Nordl, Troms, Finnm.

MICROCALICIUM Vain.

Thallus endosubstratal, saprophytic on lignum, parasymbiotic, or parasitic on algae or lichens. Apothecia black, sessile or stalked. Excipulum well developed. Mazaedium greenish black or dark brown, sclerotized hyphae present or absent. Pruina absent. The mazaedium contains a probably intracellular, greenish, K⁺ brown pigment. Asci cylindrical, formed in chains without croziers (Schmidt 1970a). Spores ellipsoid, greenish, 1-3(-7)-septate with a surface of spirally arranged ridges. Pycnidia present or absent.

Figs 42-43. Species distributions. Fig. 42. *Cyphelium tigillare*. Fig. 43. *Microcalicium ahlneri*.

Key to the species

- 1 Apothecia sessile. Spores 9-15 μm long.....*M. disseminatum*
- 1 Apothecia stalked. Spores 6-8 μm long.....2
- 2(1) Lignicolous. Mazaedium greenish black, with sclerotized hyphae.....*M. ahlneri*
- 2 Saxicolous, or on roots. Mazaedium dark brown or greenish black, without sclerotized hyphae.....*M. arenarium*

1. *Microcalicium ahlneri* Tibell

Morphology and anatomy. A saprophyte, or parasite on green algae. Apothecia black, short (0.4-1.1 mm). Mazaedium greenish black with sclerotized hyphae. Pruina absent. Asci cylindrical. Spores ellipsoid, 1-septate, 5.7-7.0 x 2.2-2.8 μm , with a surface of spirally arranged ridges. Pycnidia absent.

Chemistry. No secondary substances found.

Ecology. *M. ahlneri* occurs on well decomposed lignum in very humid habitats.

Distribution. The species seems to have an eastern distribution in Norway (Fig. 43).

Hedm, Oppl. New to Norway.

2. *Microcalicium arenarium* (Hampe ex. Massal.) Tibell

Morphology and anatomy. A parasite on green algae or parasymbiont on *Lecidea lucida* (Ach.) Ach. Apothecia black, of medium height (0.6-1.8 mm). Mazaedium dark brown or greenish black, without sclerotized hyphae. Pruina absent. Asci cylindrical. Spores ellipsoid, 1-septate, 6.7-8.2 x 2.3-2.9 μm , with a surface of spirally arranged ridges. Pycnidia absent.

Chemistry. No secondary substances found.

Ecology. *M. arenarium* has been collected on roots, siliceous rock or on *Lecidea lucida* in very humid habitats.

Distribution. A rarely collected species in Norway (Fig. 44).

Oppl, Busk, S&F, Nordl.

3. *Microcalicium disseminatum* (Ach.) Vain.

Synonym: *Microcalicium subpedicellatum* (Schaer.) Tibell.

Morphology and anatomy. A parasite/parasymbiont on algae or on Caliciales species, or a saprophyte. Apothecia black, sessile. Mazaedium greenish black, protruding, with sclerotized hyphae. Asci cylindrical. Spores ellipsoid, 1-3(-7)-septate, 11.5-15.0 x 3.4-4.2 μm , with a surface of spirally arranged ridges. Pycnidia present, black. Pycnoconidia ellipsoid, 2-3 x 2 μm .

Chemistry. No secondary substances found.

Ecology. *M. disseminatum* is lignicolous or corticolous on *Picea*, or grows on Caliciales species (it has been found on *Chaenotheca chrysocephala*, *C. ferruginea*, *C. stemonea* and *C. trichialis* in Norway). It grows under humid conditions.

Figs 44-45. Species distributions. Fig. 44. *Microcalicium arenarium*. Fig. 45. *M. disseminatum*.

Distribution. The species has an eastern distribution in Norway (Fig. 45).

Hedm, Oppl, Busk, Tel, N-Trønd, Finnm.

SCLEROPHORA Chevall.

Thallus endosubstratal. Phycobiont *Trentepohlia*. Apothecia brown or pale, stalked. Excipulum poorly or well developed, with or without a collar. Mazaedium pale brown. Pruina yellow, reddish-brown or violet, K- or K+ violet. Asci cylindrical. Spores globose, pale, with a reticulate surface.

Key to the species

- 1 Apothecia pale or white, small (0.4-0.8 mm).....2
- 1 Apothecia brown, medium (0.7-1.5 mm).....3
- 2(1) Apothecia pale. Pruina reddish-brown, K+ violet. Spores 3.0-3.6 μm*S. peronella*
- 2 Apothecia white. Pruina yellow, K-. Spores 7.2-8.4 μm*S. nivea*
- 3(1) Pruina on capitulum, violet, K-. Spores 6.6-7.8 μm*S. farinacea*
- 3 Pruina on the whole apothecium, reddish-brown, K+ violet. Spores 4.7-6.3 μm*S. coniophaea*

1. *Sclerophora coniophaea* (Norm.) Mattsson & Middelborg comb. nov.

Basionym: *Coniocybe coniophaea* Norm. K. Norske

Vidensk.-Selsk. Skr. 5 (1868), p. 362. Synonym: *Chaenotheca coniophaea* (Norm.) Tibell.

Morphology and anatomy. Thallus endosubstratal. Phycobiont *Trentepohlia*. Apothecia brown, of medium height (0.9-1.5 mm). Excipulum well developed, without collar. Pruina on the whole apothecium, reddish-brown, K+ violet. Asci cylindrical. Spores globose, 4.7-6.3 μm , with a reticulate surface.

Chemistry. The pruina and hymenium contain a reddish-brown, K+ violet, pigment.

Ecology. *S. coniophaea* is lignicolous or corticolous in very humid habitats.

Distribution. The species has an eastern distribution in Norway, and is common in the northern parts of the country (Fig. 46). Tibell (1978b) reported it from deciduous trees in southern parts of Sweden.

Hedm, Nordl, Troms, Finnm.

Taxonomical notes. We have discussed the delimitation of *Chaenotheca* versus *Sclerophora* (see p. 29). The most significant distinction between the two genera was found to be the ontogeny of the spore walls. We have compared SEM photographs of spores in *S. coniophaea* (Fig. 10) and *S. nivea* (Fig. 13). They are clearly distinct from *Chaenotheca* spores (Tibell 1980b). TEM photograph of *S. coniophaea* (Fig. 11) show

Figs 46-47. Species distributions. Fig. 46. *Sclerophora coniophaea*. Fig. 47. *S. farinacea* (●) and *S. peronella* (■).

the plasmalemma of the spores winding in and out in an early stage in the ascus. This corresponds with the ontogeny of *Sclerophora* spores. Note the plasmalemma on the surface of mature spores (Fig. 12). Thus, in our opinion this species belongs to the genus *Sclerophora*.

2. *Sclerophora farinacea* (Chevall.) Chevall.

Synonym: *Coniocybe farinacea* (Chevall.) Nyl.

Morphology and anatomy. Thallus endosubstratal. Phycobiont *Trentepohlia*. Apothecia brown, of medium height (0.7-1.2 mm). Excipulum well developed, with collar. Pruina on capitulum, violet, K-. Asci cylindrical. Spores globose, 6.6-7.8 μm , with a reticulate surface.

Chemistry. The pruina and hymenium contain a violet, K-, pigment.

Ecology. *S. farinacea* has been collected on bark of *Ulmus*, *Fraxinus* and *Tilia* in Norway.

Distribution. A rarely collected species (Fig. 47). All collections are from the last century.

Akh.

3. *Sclerophora nivea* (Hoffm.) Tibell

Synonym: *Coniocybe pallida* (Pers.) Fr.

Morphology and anatomy. Thallus endosubstratal. Phycobiont *Trentepohlia*. Apothecia pale, almost white, small (0.4-0.7 mm). Excipulum well developed, with collar. Pruina on the whole apothecium, yellow, K-. Asci cylindrical. Spores globose, 7.2-8.4 μm , with a reticulate surface.

Chemistry. The pruina and hymenium contain a yellow, K-, pigment.

Ecology. *S. nivea* occurs on eutrophic bark of deciduous trees in moderately humid habitats.

Distribution. The species has a southern distribution in Norway (Fig. 48).

Akh, Busk, Tel, V-Agd, Hord, N-Trønd.

4. *Sclerophora peronella* (Ach.) Tibell

Synonym: *Coniocybe peronella* (Ach.) Tibell

Morphology and anatomy. Thallus endosubstratal. Phycobiont *Trentepohlia*. Apothecia pale brown, darker in the centre, small (0.5-0.8 mm). Excipulum poorly developed, without collar. Pruina on capitulum reddish-brown, K+ violet. Asci cylindrical. Spores globose, 3.0-3.6 μm , with a reticulately cracked surface.

Chemistry. The pruina contains a reddish-brown, K+ violet, pigment.

Ecology. *S. peronella* has been collected on lignum of *Fraxinus*.

Figs 48-49. Species distributions. Fig. 48. *Sclerophora nivea*.
Fig. 49. *Thelomma ocellatum*.

Distribution. A rarely collected species, in Norway known from one collection only (Fig. 47).

Hord.

THELOMMA Massal. emend. Tibell

1. *Thelomma ocellatum* (Körber) Tibell

Morphology and anatomy. Thallus verrucose, grey. Black isidia occur in globular areas. Medulla I+ dark blue. Phycobiont *Trebouxia*, Chlorococcales. Apothecia immersed, very rare in Norway. Mazaedium black. Excipulum thick at the base. Pruina absent. Asci cylindrical. Spores ellipsoid, 22-28 x 12-15 μm , one-septate with an almost smooth surface.

Chemistry. Secondary substances usually absent, but some specimens contained either atranorin or norstictic acid in the thallus. Tibell (1976b) reported usnic acid, epanorin and rhizocarpic acid.

Ecology. *T. ocellatum* is lignicolous on worked timber in exposed habitats (fence posts, wooden roofs etc.). It is an ornithocoprophilous species.

Distribution. The species seems to have a slightly eastern distribution in Norway (Fig. 49). The collections from Nordland province (Degelius 1982) do not fit into this pattern.

Østf, Akh, Hedm, Oppl, Busk, Tel, Hord, S&F, M&R, Nordl, Troms, Finnmark.

Remarks. This is the first report of a fertile *T. ocellatum* in Fennoscandia. There are two fertile specimens collected in Norway: Sogn & Fjordane, Aurland, 1968, Øvstedal; and Oppland, Vågå, Veomoan, Mattsson & Middelborg 553. Our collection is from an old wooden fence. The thallus is well developed, but isidia are less frequent than usual. Apothecia are rare, only three apothecia were found in this collection. The other collection contains only one apothecium. Fertile specimens are more common in Central Europe (Tibell 1976b).

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