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J. Holtan-Hartwig

The lichen genus *Peltigera*, exclusive of the *P. canina* group, in Norway

1993

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Seventeen species of the lichen genus *Peltigera*, exclusive of the *P. canina* group, are accepted from Norway. Their morphology, chemistry, ecology, and distribution in Norway are presented, and a key to the species is provided. *Peltigera retifoveata* is reported as new to Norway and a new species, *P.* sp. 1, which belongs to the *P. aphthosa* group, is treated but not formally described.

Different morphotypes of *P. aphthosa*, *P. malacea*, and *P. neopolydactyla* and different chemotypes of *P. aphthosa*, *P. elisabethae*, *P. horizontalis*, *P. malacea*, *P. neopolydactyla*, *P. scabrosa*, and *P.* sp. 1 are described. Correlations between several morphotypes and chemotypes are shown, but these are not treated as taxonomic units, although they probably are biological species.

Phototype pairs in *P. aphthosa, P. britannica*, and *P. venosa* are described, and the close relationship between the two first mentioned and *P. malacea* is pointed out.

Keywords: Chemotypes, Distribution, Ecology, Lichens, Lichen substances, Morphotypes, Norway, *Peltigera*, Phototype pairs, Taxonomy.

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INTRODUCTION

Linnaeus (1753) described three species that today are included in the genus *Peltigera*: *Lichen aphthosus*, *L. caninus* and *L. venosus*. Willdenow (1787) introduced the genus *Peltigera* based on the two first mentioned species, of which *P. canina* later has been chosen as the type species (Lanjouw et al. 1966). Acharius (1810; as *Peltidea*) treated six species and ten varieties. Nylander (1861) accepted nine species in Scandinavia: *Peltigera aphthosa*, *P. canina*, *P. horizontalis*, *P. malacea*, *P. polydactyla*, *P. pulverulenta* (today called *P. scabrosa*), *P. rufescens*, *P. spuria* (= *P. didactyla*) and *P. venosa*, and in addition some varieties.

Although several species are common and have frequently been collected, the genus long remained poorly understood. During the years 1926–1942 Gyelnik introduced a great number of taxa, especially at the infraspecific level, which were often poorly grounded. Some of these have later been shown to be distinct taxa, others have been reduced to synonymy, but most of them are still unresolved.

In Norway, Lynge (1910) accepted eight species, and also some infraspecific taxa of *P. canina*. Later Lynge (1921) treated 13 species, of which 12 are accepted at present: *P. aphthosa*, *P. canina*, *P. erumpens* (= *P. didactyla*), *P. horizontalis*, *P. lepidophora*, *P. malacea*, *P. polydactyla*, *P. praetextata*, *P. rufescens*, *P. scabrosa*, *P. scutata* (= *P. collina*), *P. spuria* (= *P. didactyla*), and *P. venosa*. Magnusson (1936) included the same taxa as Lynge (1921) and in addition *P. leucophlebia*. Dahl & Krog (1973) added *P. degenii*, and Krog et al. (1980) *P. elisabethae*, *P. hymenina* (= *P. lactucifolia*), *P. kristinssonii*, *P. membranacea*, *P. neckeri*, and *P. neopolydactyla* among the Norwegian species, bringing the number up to 20. Tønsberg & Holtan-Hartwig (1983) separated *P. britannica* from *P. aphthosa*, and Holtan-Hartwig (1988) described *P. frippii* and *P. scabrosella*. In the present work, *P. retifoveata* is reported as new to Norway and an apparently undescribed species, belonging to the *P. aphthosa* group, is treated but not formally described.

A key to the European species was given by Vitikainen (1981), and the chemistry of the *Peltigera aphthosa* group in Norway was described by Tønsberg & Holtan-Hartwig (1983). A survey of the chemistry of the British species was presented by White & James (1987).

The chemistry of *Peltigera* has been poorly investigated in comparison with other common genera of macrolichens. Zopf (1909) analyzed the chemistry of twelve species of *Peltigera*, mainly collected in the Alps, and reported peltigerin, peltidactylin and zeorin along with some other substances. Huneck & Tümmler (1965) found peltigerin to be identical with tenuiorin, a substance already known from *Lobaria*.

The first modern chemotaxonomic study of *Peltigera* was made by Kurokawa et al. (1966). They studied the chemistry of the Japanese species and some European and American populations by means of TLC. In spite of taxonomic and methodological problems, Kurokawa et al.'s (1966) results clearly indicated that the chemistry in *Peltigera* was taxonomically important. Kurokawa et al. (1966) reported dolichorrhizin from *P. dolichorrhiza* (Nyl.) Nyl. and phlebic acid A and phlebic acid B from *P. aphthosa*.

Takahashi et al. (1969, 1970) revised the structure of phlebic acid A and phlebic acid B as 28-acetoxy-22-hydroxyhopan-23-oic acid and 22-hydroxyhopan-23-oic acid, respectively. Furthermore, they found dolichorrhizin to be identical to 15α-acetoxyhopan-22-ol, a substance originally isolated from *Pseudocyphellaria billardieri* (Delise) Räsänen (Corbett & Young 1966b). Huneck et al. (1973) identified Zopf's original substance of peltidactylin as 7ß-

acetoxyhopan-22-ol, this substance was also already known from *P. billardieri* (Corbett & Young 1966a). Maass (1975) studied the occurrence of phenols in *Peltigera aphthosa* by means of NMR and two-dimensional TLC, and reported tenuiorin, evernic acid, gyrophoric acid, methyl evernic acid, methyl gyrophoric acid, methyl lecanoric acid, methyl orcellinic acid, and 4-O-methyl gyrophoric acid.

Tønsberg & Holtan-Hartwig (1983) presented the chemistry of the *P. aphthosa* group, exclusive of *P. malacea* and *P.* sp. 1, in Norway, and reported for the first time hopane-15α,22-diol and the occurrence of chemotypes, from the genus. The chemistry of *P. retifoveata* was reported by Vitikainen (1985). In a booklet on microchemical techniques (White & James 1985), the chemistry of *P. lactucifolia*, *P. polydactyla* and *P. neckeri* was given as an example on how terpenoids can be helpful in the identification of closely allied species. The last mentioned species was said to contain hopane-6α,7ß,22-triol, which was the first report of this triterpenoid from *Peltigera*. White & James (1987) later, however, stated that the identification of hopane-6α,7ß,22-triol in *P. neckeri* was based on a misidentification, but reported the triterpenoid from *P. collina* and *P. polydactyla* instead. Holtan-Hartwig (1988) presented the chemistry of *P. frippii*, *P. malacea*, *P. neckeri*, *P. scabrosa* and *P. scabrosella*. Bachelor et al. (1990) isolated two new terpenoides from *P. aphthosa*. These terpenoids were designated phlebic acid C and phlebic acid D, and were determined to be 7β-acetoxy-22-hydroxyhopan-27-oic acid and 22-hydroxyhopan-27-oic acid, respectively. No attempts have been made to compare these terpenoids with terpenoids occurring in the Norwegian *Peltigera* species.

The aim of the present work is to study the taxonomy, chemistry, ecology, and distribution of the Norwegian *Peltigera* species producing secondary substances, with the exception of *P. didactyla*. The Norwegian *Peltigera* species not included in this study comprise a morphologically and anatomically delimited unit which is here named the *P. canina* group. In Norway it consists of *P. canina* (L.) Willd., *P. degenii* Gyelnik, *P. didactyla* (With.) Laundon, *P. kristinssonii* Vitik., *P. lepidophora* (Nyl.) Bitter, *P. membranacea* (Ach.) Nyl., *P. praetextata* (Flörke) Zopf, and *P. rufescens* (Weiss) Humboldt. Studies of the nomenclature were considered beyond the scope of the present work.

MATERIAL AND METHODS

MATERIAL

This study is based on all relevant material of *Peltigera* in the Norwegian herbaria BG, O, TRH, and TROM, and includes *c.* 2500 specimens. In addition, I have examined private collections made by H.C. Gjerlaug (Ridabu). Some few Norwegian collections in S and in UPS have also been included.

Parts of the material in TNS used by Kurokawa et al. (1966) for their chemical analyses, some specimens in CANL studied by Brodo & Richardson (1978) in their phototype work, and the type material of *Peltigera avenosa* Gyelnik, *P. lyngei* Gyelnik, and *P. variolosa* f. *britannica* Gyelnik, all in UPS, were also studied. My own collections comprises *c.* 800 specimens and are deposited in O.

METHODS

Field work

Intensive field work, mainly in the southwestern, western and central part of southeastern Norway, was carried out in 1980 and 1981. During the years 1982–1989, I have collected *Peltigera* spp. in all counties of Norway.

Morphology and anatomy

The morphological descriptions are made from dry material, unless otherwise stated. Binocular lenses (magnification 6–32x) and a light microscope (100–1000x) were used for morphological and anatomical studies, respectively. A freezing microtome was used for preparing anatomical sections. Spores were studied in squash preparations mounted in lactophenol cotton blue. Only spores with 3 or more septa were regarded as mature and selected for measurements.

Chemistry

Approximately 2300 specimens were subjected to thin-layer chromatography (TLC), mainly according to the standard techniques described by Culberson & Kristinsson (1970) and Culberson (1972), modified by Menlove (1974). Among the standard solvent systems, only system C (referred to as TA in the present study; toluene/acetic acid: 200/30) satisfactorily separated the terpenoids in *Peltigera*. A new solvent system, EHF (diethyl ether/hexane/formic acid: 300/100/3), was developed especially for the terpenoids of *Peltigera* (Tønsberg & Holtan-Hartwig 1983). This solvent system resembles system G of Culberson et al. (1981),

but gives a better separation of *Peltigera* terpenoids. Identification of substances was made by comparison with other species with known chemical constitution, partly with authentic material from the study by Kurokawa et al. (1966). The terpenoids were numbered from 1 to 41. Some numbers are not included in this study; these are substances occurring in low concentrations and hence of little diagnostic value with the present method, or occurring in extra-Norwegian species only.

Small thallus fragments were extracted in hexane, diethyl ether, or acetone for *c.* 5 minutes. Hexane was used in order to avoid trailing by the depsides, which could otherwise mask the terpenoids. This extracting agent does not solve polar compounds as well as diethyl ether and acetone, however. The extracts were spotted on to precoated Merck silica gel 60 F_{254} aluminium plates and eluated in the solvent systems TA and EHF. The chromatograms were

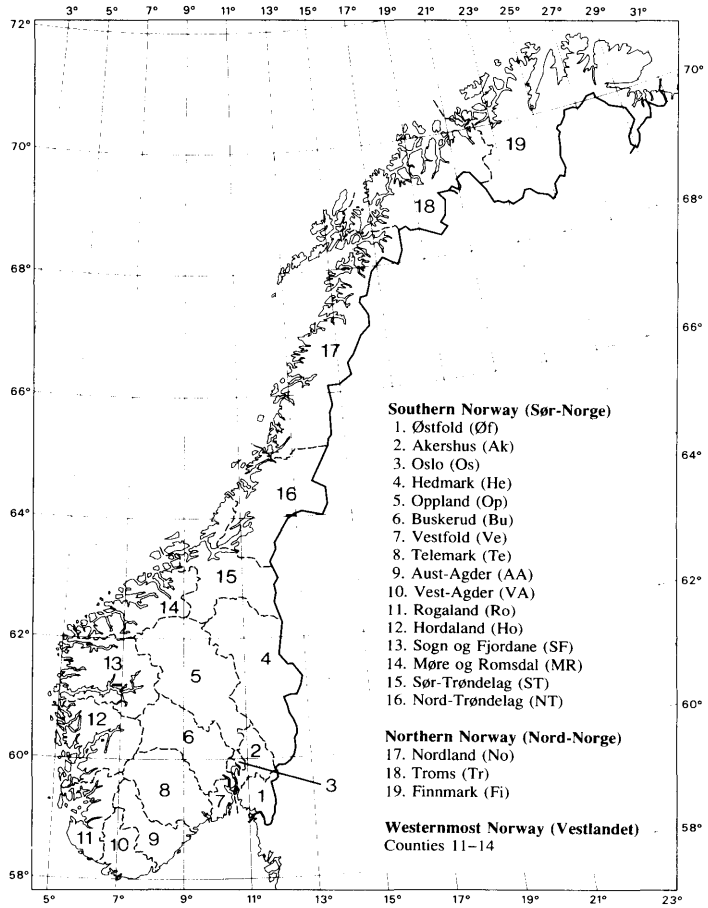


Fig. 1. Norwegian counties and their abbreviations, and geographical terms.

often eluated two or three consecutive times in each solvent system in order to obtain optimal separation of the substances. The chromatograms were air dried between each eluation. For two-dimensional chromatography, EHF was used for the first direction and TA for the second direction; both directions were eluated twice.

The chromatograms were developed by spraying with 10% sulphuric acid and heating in 3–5 min. in an oven at 110 °C. They were studied in daylight and in ultra-violet light (350 nm) for observation of characteristic colours.

Descriptions of the species and geographical terms

Spore measurements are given in the form

$$(L_{min}-)\ L-1.5*SD_l-\mathit{L}-L+1.5*SD_l\ (-L_{max}) \times W_{min}-W_{max}$$

where L is the arithmetic mean and SD_l the sample standard deviation (division by n-1) of spore length. Numbers given for length and width are rounded to the nearest 1 µm and 0.5 µm, respectively. The counties in which a species has been recorded, are listed under the heading 'Counties', in a strict order in accordance with Fig. 1, which also gives the abbreviated form used in 'Specimens seen'.

All information about distribution is based on material I have seen. Only collections provided with sufficiently precise localization have been used for distribution maps and diagrams showing the vertical distribution.

Definitions of geographical terms are evident from Fig. 1.

RESULTS AND DISCUSSION

MORPHOLOGY

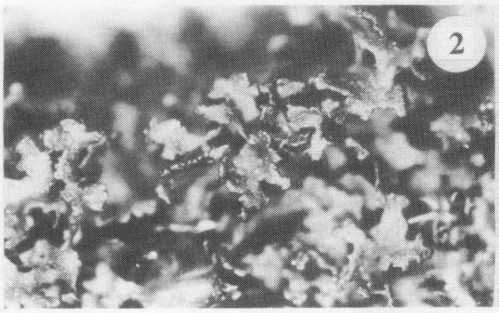
Thallus

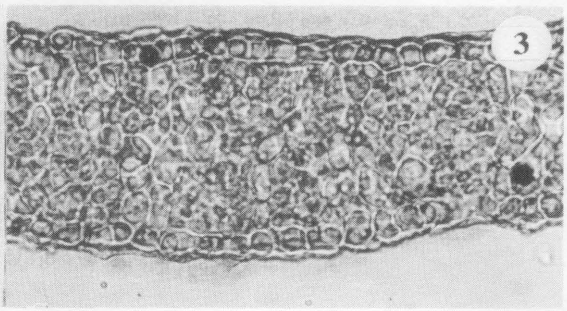
All species, except for the blue-green phototype of *Peltigera venosa*, had a heteromerous, foliose, and lobed thallus with a corticate upper side and an ecorticate lower side. In *P. venosa*, vertical sections of the blue-green phototype showed a homoiomerous, paraplectenchymatic medullary tissue and one-layered upper and lower cortices (Figs 2–3). The size (diameter) of the thallus varied from *c.* 3 cm in *P. venosa* to *c.* 60 cm in *P. aphthosa*.

Lobes

The lobes normally grew radially from the center of the thallus. In some species they were distinctly imbricate. The margins were more or less sinuose and ascending to involute.

The width and the length of primary lobes varied only slightly from one species to another. The visual impression of the lobe width, however, is more based on thallus sections formed by the more or less regular cracking occurring in all species. The cracks developed between the primary lobes and grew towards the center of the thallus. Repetitive inward crackings, and the ratio between growth of primary lobes and the speed of cracking, produce the secondary lobe pattern. In some species, e.g. *P. neopolydactyla*, the thallus sections consisted of 3–4 primary lobes, in others, e.g. *P. malacea,* usually of only one primary lobe. The variation between species seems to be genetically controlled, and the width of the thallus sections is a taxonomically useful character. In this study the term lobe is used for a thallus section delimited by two neighboring cracks. Lobe width is measured between the starting points for these cracks. The length of the lobes has not been measured since the thallus usually disintegrates from the center.





Figs 2–3. Blue-green phototype, *Peltigera venosa*, Hordaland, Holtan-Hartwig 2223 (O). Fig. 2. Habit. 13×. Fig. 3. Vertical section showing a homoiomerous thallus, paraplectenchymatic tissue and one-layered cortices. 306×.

Upper side

The colour of the upper side was greyish blue, bluish green, yellowish green, yellowish brown or brown. The brown colour was caused by cortical pigments, other colours by the photobiont.

Hairs occurred in all the species of the *P. aphthosa* group, i.e. *P. aphthosa*, *P. britannica*, *P. leucophlebia*, *P. malacea* and *P.* sp. 1. In these species, except for the last mentioned, the hairs were more or less erect, sparsely branched, thick-walled and short-celled. In *P.* sp. 1 the hairs were less erect and more branched. In *Peltigera retifoveata* they were appressed, richly branched, thin-walled and long-celled and similar to those usually found in the *P. canina* group.

The upper side was scabrous in *P. malacea* morphotype B, *P. scabrosa*, and *P. scabrosella*; often scabrous in *P. collina*; and smooth in all other species.

Pruina usually occurred near the lobe ends, especially in *P. collina*, *P. frippii*, *P. malacea* and *P. neckeri*, but could also be sparsely present in most of the other species.

Maculae occurred in varying amounts and were especially prominent in the blue-green phototypes of *P. aphthosa* and *P. britannica*, and also occurred in *P. frippii*.

Phyllidia

The cephalodia of *Peltigera britannica* (Fig. 8), which were dorsiventral, shell-shaped and loosely attached to the upper side of thallus, could also be regarded as phyllidia. They resembled the phyllidia of *P. praetextata* (*P. canina* group), and functioned as diaspores when detached from the thallus.

Most of the species had the ability to produce lobules at places where the thallus was damaged. These regeneration lobules were not distinctly dorsiventral, and were smaller and more globose than the phyllidia found in *Peltigera britannica* and *P. praetextata*.

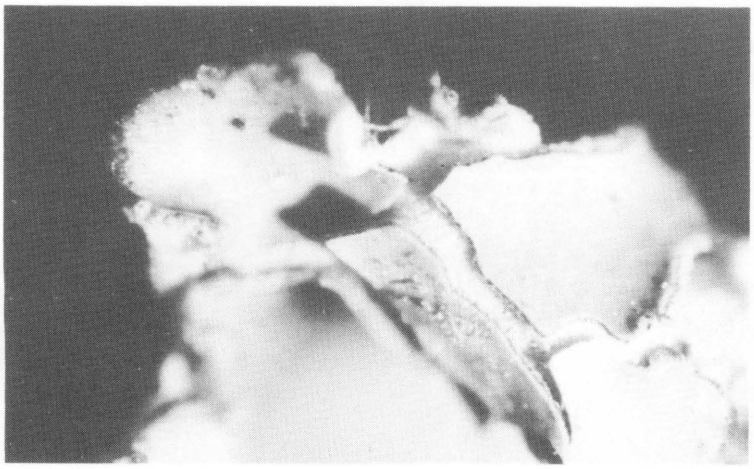
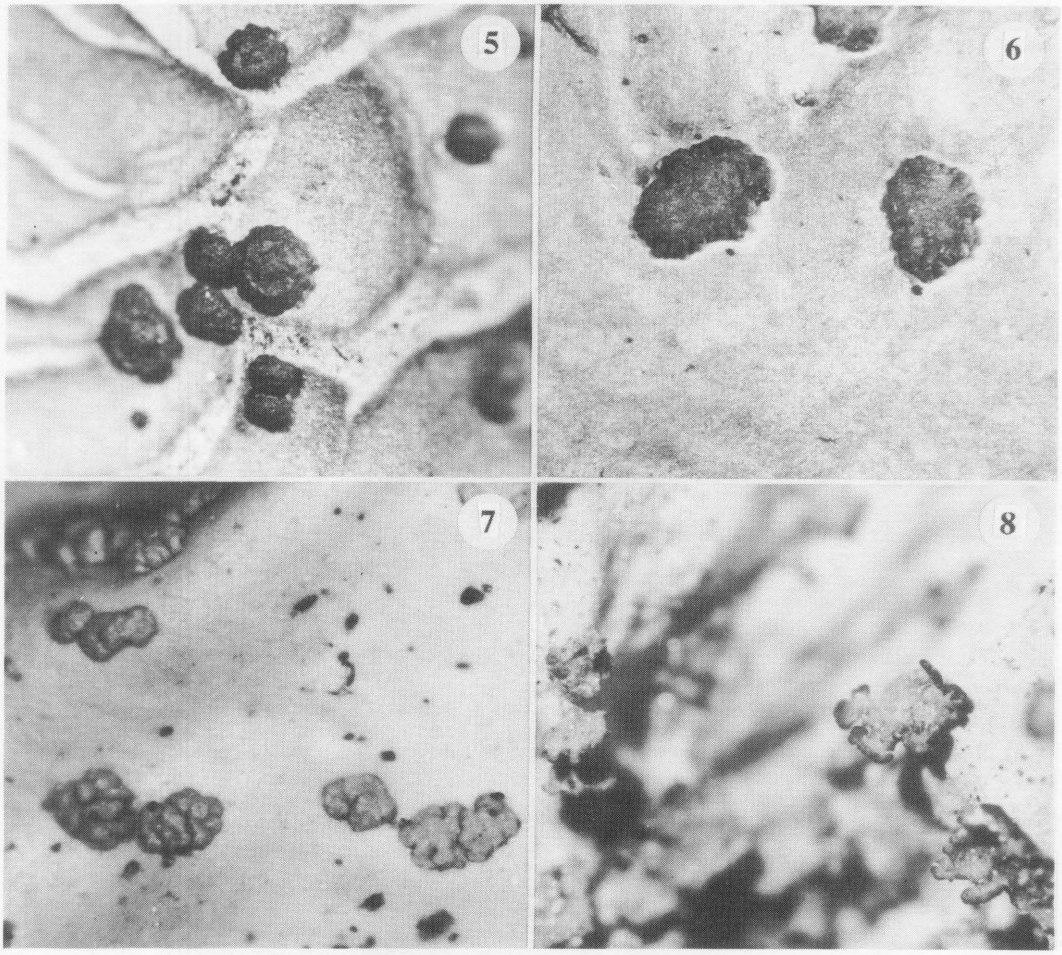


Fig. 4. Schizidia, *Peltigera elisabethae*. 22×.



Figs 5–8. Types of cephalodia. Fig. 5. Wart-shaped, *Peltigera aphthosa*. 22×. Fig. 6. Plane, *P. aphthosa*. 11×. Fig. 7. Cerebriform, *P. leucophlebia*. 20×. Fig. 8. Shell-shaped, *P. britannica*. 18×.

Schizidia

Schizidia occurred only in *P. elisabethae*. They were produced along cracks between thallus sections and along laminal fissures. Cortex, the algal layer, and a part of the medulla stripped off in small, 0.2–2.2 mm wide, irregular flakes (Fig. 4). Later, regeneration lobules were often produced along the scars of detached schizidia.

Soralia

Soralia occurred only in *P. collina*. They were marginal and linear, more rarely laminal and orbicular. The soredia were coarse and often more or less corticate.

Cephalodia

Cephalodia were always present in species containing green algae as photobiont. These were either attached to the upper side (*P. aphthosa*, *P. britannica*, *P. leucophlebia*, and *P.* sp. 1) or to the lower side (*P. venosa*) of the thallus. Cephalodia attached to the upper side of thallus may be divided into four morphological types: wart-shaped, plane, cerebriform and shell-shaped.

The wart-shaped cephalodia were convex with only slightly incised margins and a smooth central area. In *P. aphthosa* morphotype B and C, the cephalodia remained convex even when old (Fig. 5). In morphotype A, however, they often became plane and appressed (Fig. 6).

The cerebriform cephalodia were convex, more incised and had a more or less uneven central area (Fig. 7). This type did not show the same tendency of becoming flattened as the wart-shaped cephalodia. Both types were firmly attached to the upper side of thallus. The cerebriform type occurred in *P. leucophlebia* and *P.* sp. 1.

The shell-shaped cephalodia were plane to concave with toothed, free margins (Fig. 8). They easily fell off when subjected to mechanical stress, leaving white scars. This type occurred in *P. britannica*.

In *P. venosa*, the cephalodia were attached to the veins on the lower side of the thallus. They were globose, often with a tendency to become flattened, sometimes subfoliose, with age. These subfoliose cephalodia were loosely attached and easily fell off when subjected to mechanical stress.

Photobiont

Peltigera aphthosa, *P. britannica*, *P. leucophlebia*, *P. venosa*, and *P.* sp. 1, contained light green to yellowish green, unicellular algae, probably *Coccomyxa*, as main photobiont. The remainder of the studied species contained cyanobacteria, probably *Nostoc*. The colour of the cyanobacteria was green, blue-green, emerald green, greenish grey, bluish grey, or greyish blue. Most species contained cyanobacteria of only one of these colour forms. However, in *P. malacea*, *P. neckeri*, *P. neopolydactyla*, and *P. retifoveata* two or more colour forms occurred. In e.g. *P. neopolydactyla*, thalli containing emerald green, blue-green or greyish blue cyanobacteria were common. Whether the different colour forms of cyanobacteria represent separate taxa or a single taxon becoming modified by symbiosis with different mycobiont taxa, is not known. The constancy and significance of the observed colour variation requires further study.

Pilema and veins

All species (except the blue-green phototype of *P. venosa*) had a tissue of more or less pigmented hyphae on the lower side of the thallus. This tissue is referred to as the pilema in this study. In some species, the pilema was differentiated into distinct veins or a network of veins with medullary interstices. In other species, the pilema covered the entire lower side of the thallus.

Two main types of pilema occurred among the Norwegian *Peltigera* species. The first type occurred in all species included in this study. It was composed of more or less unoriented or partly parallel, not conglutinated hyphae. The pilema varied from forming broad, flat veins to covering the entire lower side.

The second type occurred in the *P. canina* group only, where the pilema was differentiated into cylindrical veins with the central parts composed of parallel hyphae in which the walls were conglutinated. The outer part of the veins consisted of branched hyphae or hyphae branching at right angles from the veins.

The constancy and the significance of the two types of pilema requires further study.

Attachment

The pigmentation, form and distribution of the rhizines are diagnostically useful characters. However, these characters have to be used with care; the rhizines often became unrecognizable in contact with the substrate and they often dissolved into separate hyphae or small fascicles of hyphae. Usually, the young rhizines emerged in small, compact groups in the actively growing parts of the lobes, reaching their ultimate form and distribution when the lobes reached maturity. Thus it is important to examine mature rhizines which are free from the substrate.

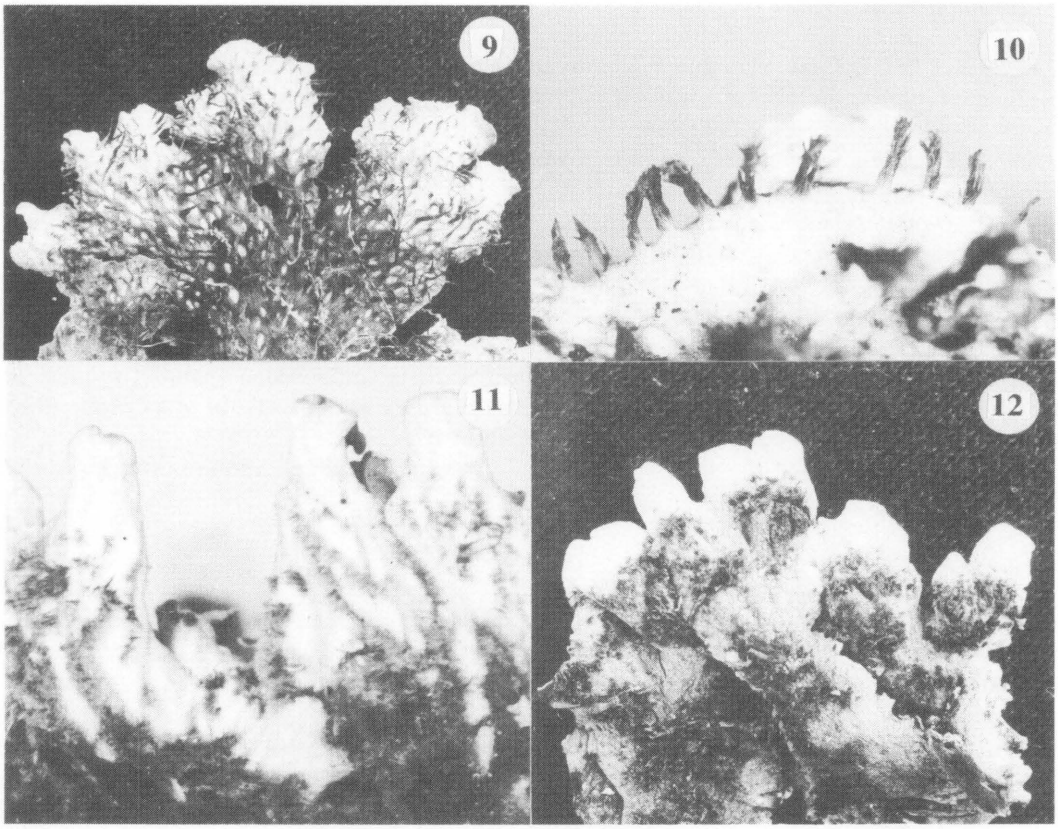
Rhizines occurred in all species except *P. venosa*. The rhizines varied from thin and rarely branched (predominant type in, e.g., *P. lactucifolia* and *P. scabrosella*) to thick and often branched. The thick rhizines were often more or less irregular and are termed bush shaped (predominate type in e.g. *P. neckeri*). In other species (*P. elisabethae*, *P. horizontalis* (Fig. 10) and *P. scabrosa*), they were more regular and are termed shaving-brush shaped.

The rhizines were termed separate if their bases were clearly separated (Figs 9–10), confluent if their bases were close together (Figs 11–12). The rhizines were evenly scattered over the lower side (Fig. 9), arranged in rows (Fig. 11), in groups (Fig. 12) or in concentric lines (Fig. 10). The colour varied from white to brownish black.

In *P. venosa* the thallus was attached by a thick, basal rhizoid (Fig. 90).

Phototype pairs

In Peltigerales several species are able to produce well-developed thalli both with green algae and with cyanobacteria. Several terms have been applied for these thalli, e.g. 'lichen chimeras', 'composite thalli', 'joined thalli', 'chimeroid associations', 'phototype pairs', and 'photosymbiodeme'. In this work the term 'phototype' will be used both for lobes and free thalli containing a specific photobiont in species known to occur in two types, i.e. having either cyanobacteria (blue-green phototype) or green algae (green phototype) as the main photobiont.



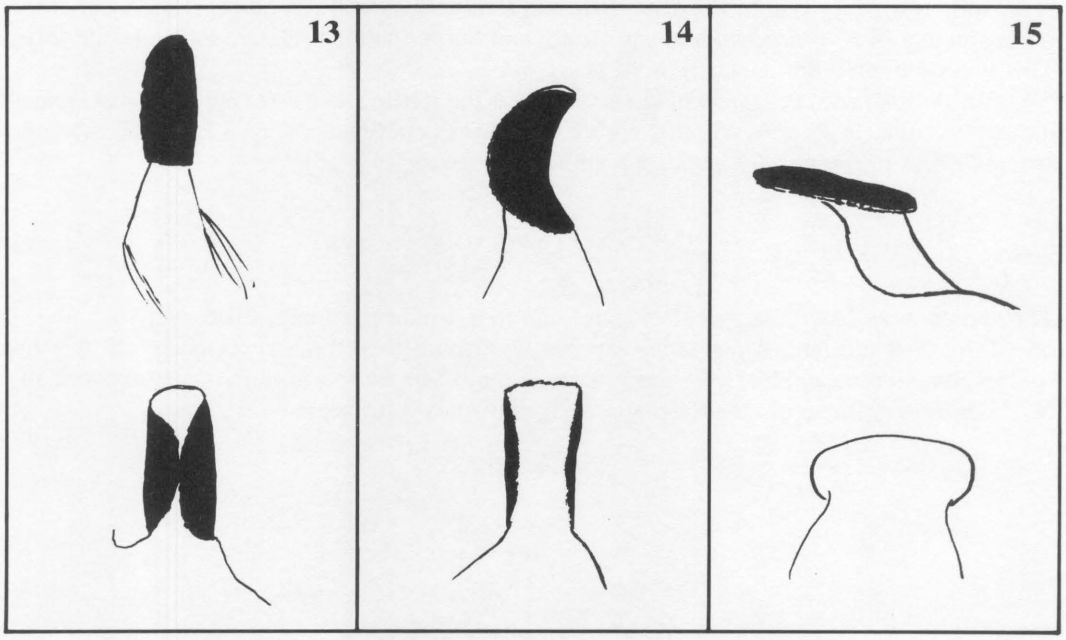
Figs 9–12. Rhizines. Fig. 9. Separate, evenly distributed, *Peltigera neopolydactyla*. 1.1×. Fig. 10. Separate, in concentric lines (only one line is visible in the figure), *P. horizontalis*. 2.3×. Fig. 11. Confluent, in rows, *P. frippii*. 6.1×. Fig. 12. Confluent, in groups, *P. malacea*. 1.3×.

The occurrence of phototype pairs in *Peltigera* was for the first time reported by James & Henssen (1976), based on material communicated by O. Vitikainen. Later, Brodo & Richardson (1978; '*P. aphthosa*'), Tønsberg & Holtan-Hartwig (1983; *P. aphthosa*, *P. britannica*, and *P. venosa*), and Ott (1988; *P. venosa*) have given detailed descriptions of phototype pairs.

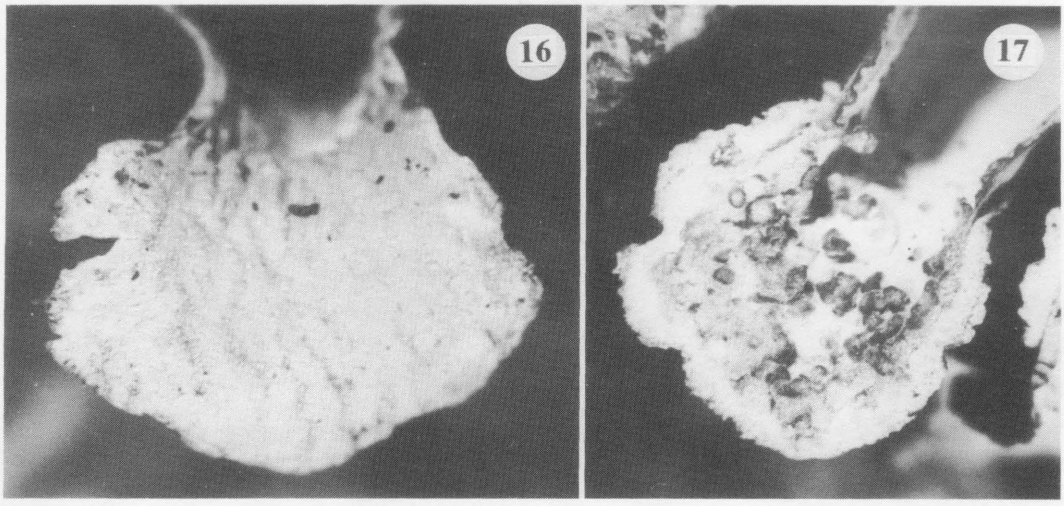
Phototype pairs occurred in *P. aphthosa*, *P. britannica*, and *P. venosa*.

Apothecia

The apothecia were attached to the margin of the upper side on narrow, more or less elongated and ascending, flat or canaliculate lobes. The apothecial discs were isodiametric to broadly ellipsoid. In most species the discs were oriented parallel to the upper side of the fertile lobe, and were laterally revolute. These apothecia are termed saddle- or finger-shaped, depending on whether being curved or straight, respectively (Figs 13–14). Intermediates between these



Figs 13–15. Semi-schematic outline of apothecia. Fig. 13. Finger-shaped. Fig. 14. Saddle-shaped. Fig. 15. Horizontal.



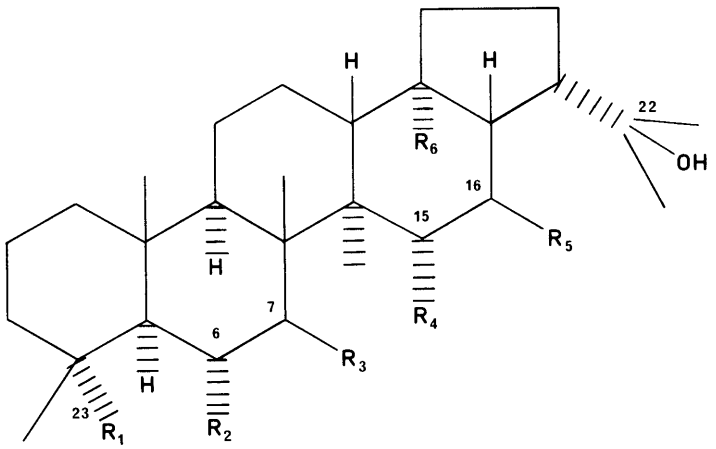
Figs 16–17. Underside of apothecia. 5.6×. Fig. 16. Patches of cortical tissue, *P.* sp. 1. Fig. 17. Continuous cortex, *Peltigera aphthosa.*

types did, however, exist. In *P. elisabethae* and *P. horizontalis* the apothecial discs were more or less plane, in *P. venosa* concave to plane, and borne inclined relative to the fertile lobes. This type is termed horizontal (Fig. 15).

In *P. aphthosa*, *P. leucophlebia* and *P.* sp. 1 the fertile lobes were corticate just beneath the apothecium. In *P. aphthosa* this cortex was always continuous (Fig. 17), in the two other species always present only as patches of cortical tissue (Fig. 16).

Spores

The spores were colorless, 3-septate (rarely up to 6-septate), smooth, fusiform to acicular, *c.* 25–100 x 3–8 µm, and 8 per ascus. Spores with more than three septa occurred in a few species, but were rare. Most previous reports of multi-septate spores in *Peltigera* are probably based on observations of cytoplasmatic bridges mistaken for septa.



	R_1	R_2	R_3	R_4	R_5	R_6	
10:	CH_3	H	OAc	H	H	H	7ß-acetoxyhopan-22-ol (peltidactylin)
12:	CH_3	H	H	OAc	H	H	15α-acetoxyhopan-22-ol (dolichorrhizin)
15:	CH_3	OH	H	H	H	H	hopane-6α,22-diol (zeorin)
16:	COOH	H	H	H	H	OAc	28-acetoxy-22-hydroxyhopan-23-carboxylic acid (phlebic acid A)
17:	COOH	H	H	H	H	H	22-hydroxyhopan-23-carboxylic acid (phlebic acid B)
20:	CH_3	OH	OH	H	H	H	hopane-6α,7ß,22-triol
35:	CH_3	H	H	OH	H	H	hopane-15α,22-diol

Fig. 18. Chemical structure of pentacyclic hopane and the identified terpenoids. Data compiled from Wilkins & James (1979) and Takahashi et al. (1969, 1970).

Tab. 1. R_f-values and characterization in daylight and ultraviolet light (350 nm) of lichen substances in *Peltigera*, by eluation in the solvent systems EHF and TA and development by sulphuric acid and heat. The terpenoids are designated by a number (1-41). Trivial names and abbreviated structural names of the identified terpenoids are given in parentheses. d1 is an unidentified depside in *P. venosa*, h - hopane, "→" means "oxidated to".

Substance	R_f (x100) EHF	TA	Colour in daylight	Colour in UV_{350}
28	3	5	grey → bluish grey	pinkish brown
27	4	3	reddish brown	light brown
41	8	8	greyish brown → bluish violet	pale yellowish brown → greyish brown
38	13	7	greyish brown → bluish violet	pale yellowish brown → greyish brown
20 (h-6α,7ß,22-triol)	15	16	greyish brown → bluish violet	pale yellowish brown → greyish brown
35 (h-15α,22-diol)	17	18	yellowish brown → reddish brown	yellowish brown
24	19	8	greyish brown	reddish brown
23	25	14	greyish brown	yellowish brown
16 (phlebic acid A)	26	21	greyish green	turquoise
13	27	28	ochraceous	ochraceous
37	31	19	greyish brown → bluish violet	pale yellowish brown → greyish brown
17 (phlebic acid B)	34	27	greyish green	turquoise
21	35	20	reddish brown	reddish brown
18	38	19	pink	reddish pink
32	39	20	reddish brown → pale violet	pinkish brown
19	39	23	greyish violet	pale pink
30	40	15	reddish brown	yellowish brown
22	42	20	pinkish brown	reddish brown
15 (zeorin)	43	28	greyish brown → greyish violet	reddish brown
33	43	28	pale turquoise	pale turquoise
25	47	38	pale orange	light blue
31	48	25	greyish violet	pink
gyrophoric acid	50	19	yellow	yellowish green
12 (dolicorrhizin)	50	35	light brown → brown violet	pinkish brown
14	52	44	yellowish brown	bluish white
40	54	32	pink	reddish pink
10 (peltidactylin)	55	40	reddish brown → bluish violet	yellowish brown → bluish black
9	55	43	reddish brown	yellowish brown
36	56	35	pale orange	bluish white
methyl gyrophoric acid	56	35	yellow	greenish yellow
39	56	43	reddish brown	reddish brown
7	60	47	reddish brown	reddish brown
d1	62	54	yellow	greenish yellow
6	63	45	greyish brown	light brown
tenuiorin	68	55	yellow	greenish yellow
methyl lecanoric acid	68	55	yellow	greenish yellow
evernic acid	68	55	yellow	greenish yellow
methyl evernic acid	68	55	yellow	greenish yellow
5	73	38	pink → dirty brown	reddish pink → brownish orange
4	73	42	reddish violet → light brown	red → brownish orange
3	83	51	pale yellow or colourless	cornflower blue
2	88	52	reddish violet → colourless	reddish pink → signal yellow
1	93	55	brownish red → pale brown	brownish orannge → signal yellow

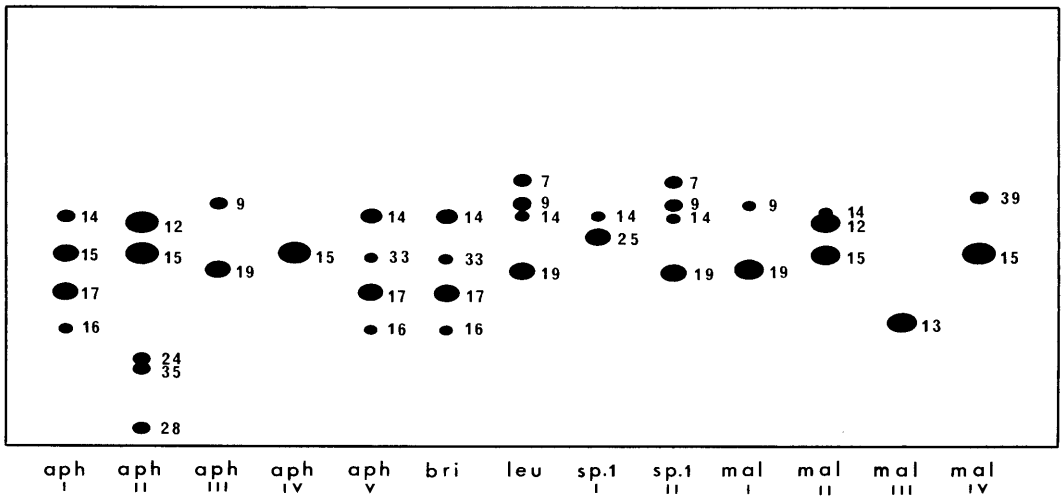


Fig. 19. Chromatogram, developed in solvent system EHF, showing terpenoids occurring in the species of the *Peltigera aphthosa*-group. **aph**, *P. aphthosa*; **bri**, *P. britannica*; **leu**, *P. leucophlebia*; **sp. 1**, *P.* sp. 1; **mal**, *P. malacea*. Chemotypes are designated by Roman numerals.

Pycnidia

Pycnidia occurred sporadically and seemed not to be diagnostically important. They were attached near the lobe tips, partly immersed to sessile, and dark brown to black. The pycnoconidia were drop-shaped to foot-shaped, 6–11 x 2–4 µm.

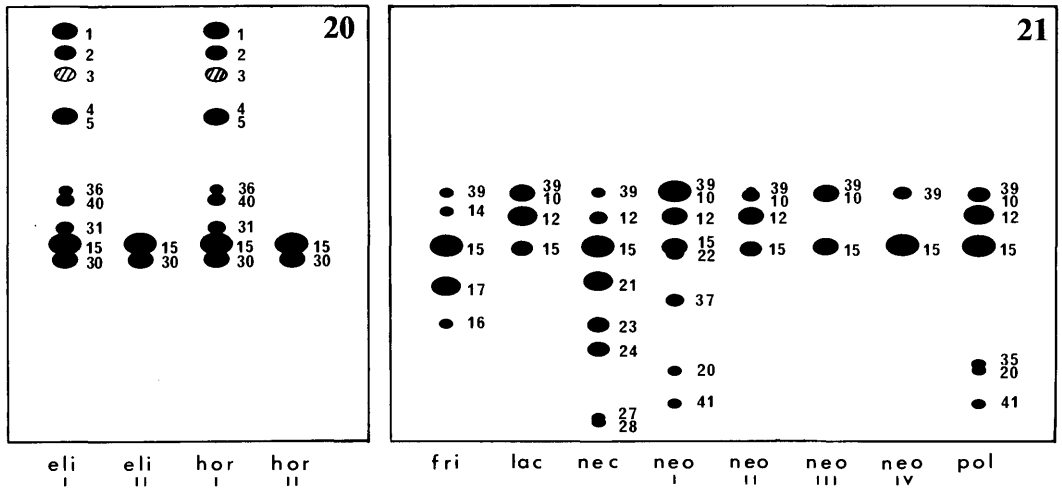
CHEMISTRY

Results

All studied species contained a great number of secondary metabolites. In this study only substances with sufficient concentration to be used diagnostically are included.

The identified substances all belonged to the major classes depsides and triterpenoids. Six of the seven included depsides and seven of the 36 included terpenoids were identified. The identified terpenoids were all pentacyclic hopanes. Fig. 18 shows the structures of pentacyclic hopane and the identified terpenoids.

With exception of *P. venosa*, all species had the same set of depsides, here called the tenuiorin-aggregate: Evernic acid, gyrophoric acid, methyl evernic acid, methyl gyrophoric acid, methyl lecanoric acid, and tenuiorin. *Peltigera venosa* contained the entire tenuiorin-aggregate, and in addition an unidentified depside-like substance designated d1. Methyl gyrophoric acid and tenuiorin always occurred in high concentrations in all species, the other depsides usually in low concentrations. In *P. neopolydactyla* chemotypes II and III, gyrophoric



Figs 20–21. Chromatograms, developed in solvent system EHF, showing terpenoids occurring in the species of the *Peltigera horizontalis*-group and the *Peltigera polydactyla* group. Fig. 20. The *P. horizontalis* group. **eli**, *P. elisabethae*; **hor**, *P. horizontalis*. Fig. 21 The *P. polydactyla*-group. **fri**, *P. frippii*; **lac**, *P. lactucifolia*; **nec**, *P. neckeri*; **neo**, *P. neopolydactyla*; **pol**, *P. polydactyla*. Chemotypes are designated by Roman numerals.

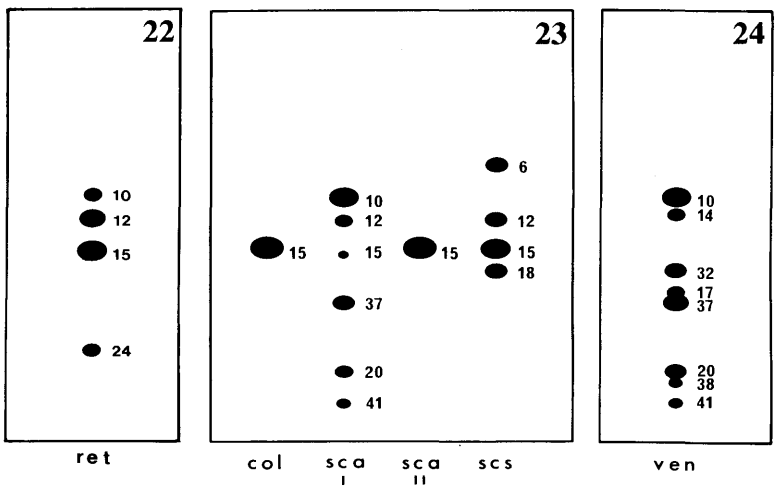


Fig. 22–24. Chromatograms, developed in solvent system EHF, showing terpenoids occurring in the species of the *Peltigera retifoveata* group, the *P. scabrosa* group, and the *P. venosa* group. Fig. 22. The *P. retifoveata* group. **ret**, *P. retifoveata*. Fig. 23. The *P. scabrosa* group. **col**, *P. collina*; **sca**, *P. scabrosa*; **scs**, *P. scabrosella*. Fig. 24. The *P. venosa* group. **ven**, *P. venosa*. Chemotypes are designated by Roman numerals.

Tab. 2. Terpenoids in Norwegian species of *Peltigera*. +, major substance; (+), minor substance. Numbers of terpenoids in accordance with Tab. 1.

Species/chemotype	1	2	3	4	5	6	7	9	10	12	13	14	15	16	17	18	19	20	21	22	23	24	25	27	28	30	31	32	33	35	36	37	38	39	40	41
P. aphthosa I	.	.	.	.	.	.	.	.	.	.	.	+	+	(+)	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
P. aphthosa II	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	+	.	.	.	.	.	.
P. aphthosa III	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
P. aphthosa IV	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
P. aphthosa V	.	.	.	.	.	.	.	.	.	.	.	+	.	(+)	+	.	.	.	.	.	.	.	.	.	.	.	.	.	(+)	.	.	.	.	.	.	.
P. britannica	.	.	.	.	.	.	.	.	.	.	.	+	.	(+)	+	.	.	.	.	.	.	.	.	.	.	.	.	.	(+)	.	.	.	.	.	.	.
P. collina	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
P. elisabethae I	+	+	+	+	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	(+)	.	.	.	+	.
P. elisabethae II	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
P. frippii	.	.	.	.	.	.	.	.	.	.	.	+	+	(+)	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
P. horizontalis I	+	+	+	+	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	(+)	.	.	.	+	.
P. horizontalis II	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
P. lactucifolia	.	.	.	.	.	.	.	.	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	(+)	.	.
P. leucophlebia	.	.	.	.	.	.	+	+	.	.	.	(+)	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
P. malacea I	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
P. malacea II	.	.	.	.	.	.	.	.	.	+	.	(+)	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
P. malacea III	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
P. malacea IV	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
P. neckeri	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	+	.	+	+	.	(+)	(+)	.	.	.	.	.	.	.	.	(+)	.	.
P. neopolydactyla I	.	.	.	.	.	.	.	.	+	+	.	.	+	.	.	.	.	(+)	.	(+)	.	.	.	.	.	.	.	.	.	.	.	+	.	(+)	.	(+)
P. neopolydactyla II	.	.	.	.	.	.	.	.	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	(+)	.	.
P. neopolydactyla III	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	(+)	.	.
P. neopolydactyla IV	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
P. polydactyla	.	.	.	.	.	.	.	.	+	+	.	.	+	.	.	.	.	(+)	.	.	.	.	.	.	.	.	.	.	.	(+)	.	.	.	(+)	.	(+)
P. retifoveata	.	.	.	.	.	.	.	.	(+)	+	.	.	+	.	.	.	.	.	.	.	.	(+)	.	.	.	.	.	.	.	.	.	.	.	.	.	.
P. scabrosa I	.	.	.	.	.	.	.	.	+	+	.	.	(+)	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	(+)
P. scabrosa II	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
P. scabrosella	.	.	.	.	.	+	.	.	.	+	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
P. venosa	.	.	.	.	.	.	.	.	+	.	.	+	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	+	.	.	+	(+)	.	.	(+)
P. sp. 1 I	.	.	.	.	.	.	.	.	.	.	.	(+)	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
P. sp. 1 II	.	.	.	.	.	.	+	+	.	.	.	(+)	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	1	2	3	4	5	6	7	9	10	12	13	14	15	16	17	18	19	20	21	22	23	24	25	27	28	30	31	32	33	35	36	37	38	39	40	41

acid always occurred in high concentration.

Tab. 1 shows the R_f-values and colours in daylight and ultra-violet light after eluation in the solvent systems EHF and TA, followed by spraying with sulphuric acid. Tab. 2 shows the occurrence of terpenoids in the treated species, and Figs 19–24 show the appearances of the substances on the chromatograms.

Discussion

The genus *Peltigera* consists partly of species containing depsides and terpenoids, and partly of species lacking secondary substances. The last mentioned belong to the *P. canina* group, which is characterized by the correlation between this absence of secondary substances and the morphology and anatomy of the species. The chemically anomalous *Peltigera didactyla*, containing depsides in the soralia, is here placed in the *P. canina* group for morphological and anatomical reasons.

For the *Peltigera* species treated here, only the terpenoids have important diagnostic value. The set of terpenoids is often species specific and provides good diagnostic characters. Several substances often occur in too low concentration for safe identification by TLC, however. A single terpenoid may occur in different species, and some species are represented by several chemotypes. On the other hand, some sets of terpenoids are unique for a species or chemotype, e.g. in *P. malacea* chemotype III and *P. scabrosella*. The chemical variation between some species is apparently chemosyndromic, e.g. between *P. lactucifolia*, *P. neopolydactyla*, and *P. polydactyla*, where the variation seems to be caused by different concentrations of terpenoids in the same set of substances. Among the terpenoid-containing species, no acid deficient chemotype is found. Morphologically similar species are often represented by similar chemotypes, e.g. *Peltigera aphthosa* and *P. britannica*; *P. elisabethae* and *P. horizontalis*; *P. lactucifolia*, *P. neopolydactyla*, and *P. polydactyla*; and *P. leucophlebia* and *P.* sp. 1.

ECOLOGY AND DISTRIBUTION

Humidity, temperature, nutrient availability, and interspecific competition seem to be the most important factors governing the distribution of the *Peltigera* species. Most species grow on the ground. They are mainly muscicolous, rarely terricolous. Typical habitats in Norway are moss-rich, east- to north-facing slopes, rock-faces, overgrown paths, road cuts, abandoned gardens, and ecotones between cultivated land and undisturbed vegetation.

The species may be exacting with respect to the type of moss cover. For instance, *P. aphthosa* usually grows on a thick and fluffy moss-cover, whereas *P. leucophlebia* usually grows on a thin to medium thick, compact moss-cover. The type of moss-cover apparently determines the degree of contact with the ground, and it appears that species with a high demand for nutrients or humidity often grow on a thin or compact moss-cover or close to the ground. This probably gives the thallus easy access to nutrients and humidity. *Peltigera elisabethae* and *P. polydactyla* sometimes grow on moss-covered rocks in river beds and river banks were they become inundated in periods of flood. *Peltigera collina*, on the other hand, often grows on moss-covered trunks of deciduous trees, and also occurs on thin twigs of

Tab. 3. *Peltigera* species grouped according to their distribution in Norway, including an account of the vertical distribution (main altitudinal range, highest record within parentheses).

Distribution	Species	Altitudinal range (m)
Ubiquitous	*P. leucophlebia*	0-1400 (1700)
	P. elisabethae	0-700 (960)
	P. scabrosa	0-1500 (1550)
	P. neckeri	0-1200 (1600)
	P. polydactyla	0-1000 (1500)
	P. venosa	0-1400 (1650)
Widely distributed with higher frequency along the coast	*P. collina*	0-900 (1200)
	P. scabrosella	0-300 (1290)
Coastal	*P. britannica*	0-100 (840)
	P. lactucifolia	0-150 (920)
Southern	*P. horizontalis*	0-200 (520)
Eastern	*P. frippii*	0-1000 (1650)
	P. retifoveata	860
	P. sp. 1	200-1000 (1220)
Boreal to arctic-alpine	*P. aphthosa*	0-1400 (1840)
	P. neopolydactyla	0-1400 (1500)
	P. malacea	0-1200 (1650)

spruce in '*Lobarion*-communities' in the humid area of Trøndelag. *Peltigera horizontalis* may grow on moss-covered deciduous trees, especially near the tree base.

The subalpine region is particularly rich in species, and contains all Norwegian *Peltigera* species (also including the *P. canina* group), with the exception of *P. horizontalis*. In mountain areas, the species occurs in habitats where the competition from higher plants appears to be limited.

A grouping of the species according to their distribution in Norway is given in Tab. 3.

TAXONOMIC CONSIDERATIONS

Subdivision of the genus

Most authors have applied photobiont as a main character for their subdivision of the genus. This is unfortunate and makes no sense in *Peltigera* where there exists mycobionts able to produce thalli both with green algae and cyanobacteria.

I have made no formal subdivision because this will require a global study of the genus and a more close study of anatomic characters, which is beyond the scope of this work. The subdivision presented here (Tab. 4) is primarily meant as a practical grouping of the Norwegian species. However, the subdivision will hopefully also reflect to some extent their phylogenetic relations. See Tab. 5 for comparison of the groups.

Peltigera aphthosa *group*. The group is mainly characterized by the occurrence of erect, thick-walled and simple hairs on the upper side. All the species, with the exception of *P. malacea*, have a green algae as main photobiont and incorporates in addition cyanobacteria in external cephalodia. *Peltigera malacea* contains cyanobacteria as photobiont and is morphologically very similar to the blue-green phototype of both *P. aphthosa* and *P. britannica*.

Peltigera canina *group*. The group is mainly characterized by the occurrence of cylindrical veins with the central parts composed of parallel hyphae in which the walls are conglutinated. The outer parts of the veins are composed of branched hyphae or hyphae branching in right angels from the veins. Most species have appressed, thin-walled and branched hairs on the upper side. Secondary metabolites are lacking except in *P. didactyla* which contains depsides in the soralia.

Peltigera horizontalis *group*. The group is mainly characterized by having plane

Tab. 4. Subdivision of Norwegian *Peltigera* species into species groups.

Species group	Species
Peltigera aphthosa group	*P. aphthosa, P. britannica, P. leucophlebia, P. malacea,* P. sp. 1
Peltigera canina group	*P. canina, P. degenii, P. didactyla, P. kristinssonii, P. lepidophora, P. membranacea, P. praetextata, P. rufescens*
Peltigera horizontalis group	*P. elisabethae, P. horizontalis*
Peltigera polydactyla group	*P. frippii, P. lactucifolia, P. neckeri. P. neopolydactyla, P. polydactyla*
Peltigera retifoveata group	*P. retifoveata*
Peltigera scabrosa group	*P. collina, P. scabrosa, P. scabrosella*
Peltigera venosa group	*P. venosa*

Tab. 5. Characters applied for subdivision of *Peltigera* into groups. 1 - *Peltigera aphthosa* group, 2 -*P. canina* group, 3 - *P. horizontalis* group, 4 - *P. polydactyla* group, 5 - *P. retifoveata* group, 6 - *P. scabrosa* group, 7 - *P. venosa* group.

Character	Character state	Group						
		1	2	3	4	5	6	7
Apothecial disc	finger/saddle-shaped	+	+	–	+	+	+	–
	horizontal	–	–	+	–	–	–	+
Spores	acicular	+	+	–	+	+	+	–
	fusiform	–	–	+	–	–	–	+
Upper side	smooth	+/–	+/–	+	+	+	–	+
	scabrous	+/–	+/–	–	–	–	+	–
	with hairs	+	+/–	–	–	+	–	–
	without hairs	–	+/–	+	+	–	+	+
Attachment	rhizines	+	+	+	+	+	+	–
	rhizoid	–	–	–	–	–	–	+
Hyphae of veins	free	+	–	+	+	+	+	+
	conglutinated	–	+	–	–	–	–	–
Chemistry	terpenoids	+	–	+	+	+	+	+
	depsides	+	+/–	+	+	+	+	+

apothecial discs which are borne inclined to the lobes. The spores are fusiform.

Peltigera polydactyla *group*. The group is mainly characterized by the following combination of characters: Naked and smooth upper side and saddle- or finger-shaped apothecia. *Peltigera frippii* has never been found fertile, and its inclusion in the group is uncertain.

Peltigera retifoveata *group*. *Peltigera retifoveata* resembles most species in the *P. canina* group by having *P. canina*-like hairs on the upper side, but differs markedly by containing terpenoids, and by having veins in which the hyphal walls are more or less non-conglutinated. It is placed in a group of its own, by possessing this unique combination of characters.

Peltigera scabrosa *group*. The group is mainly characterized by having an upper side that is distinctly scabrous, at least towards the lobe-ends. Some *P. collina* specimens have a smooth upper side, thus the inclusion of this species in the group is uncertain.

Peltigera venosa *group*. *Peltigera venosa* is placed in a group of its own, mainly because it lacks rhizines and is attached by a rhizoid. The apothecial disc is horizontal. The blue-green phototype of *P. venosa* differs from all the other examined species in the genus by having a paraplectenchymatic thallus and by having a lower cortex. This may suggest that the species holds an isolated position in the genus.

The species concept

Difficulties in carrying out experimental studies have kept the species concept in lichenology morphological (i.e., also including anatomical and chemical characters). Morphological continuity within the species and morphological discontinuity between species are used as the main species criteria. A biological species concept based on internal or external breeding barriers is thus not yet applicable.

Some lichenologists use chemical discontinuity alone as criterion for the rank of species. A chemical difference may be based on a difference in one or only a few genes, so that the variation is a result of simple recombination in a outbreeding population. Thus such 'chemical species' may be biologically meaningless. When chemical differences between two populations are correlated with differences in morphology, ecology and distribution, it is reasonable to suppose that the differences are maintained by lack of gene exchange.

Within a biological species, one may, nevertheless, expect to find different chemotypes with obscure morphological characteristics and different ecological preferences, if the different genotypes producing different chemotypes have unequal adaption values to certain habitats. This may be so when genes coding for secondary metabolites are linked to genes coding for morphological and/or ecological features, or when a large set of genes are coding in a synergetic manner for a large number of features (both chemical, morphological and ecological). Theoretically one may imagine that a strong selective force from the environment may maintain a correlation between morphology, chemistry and ecology that apparently will justify giving chemotypes rank of species.

In the present work a such variation is described in the genus *Peltigera*. In *P. aphthosa*, *P. malacea*, and *P. neopolydactyla* several chemotypes exist which are morphologically, ecologically, and distributionally definable. Whether this is due to the chemotypes really being discrete biological species, in other words, examples of "sibling species" (as discussed in lichens by W.L. Culberson (1986)), or a result of strong selection within a biological species, is uncertain. At present, we do not know to what extent gene exchange really does occur in *Peltigera* populations. The individuals may mainly be autogamic, or even apogamic, making the term "biological species" irrelevant.

However, it seems unlikely that a natural selective force can be so strong that a correlation between morphology, chemistry and ecology can be maintained without the occurrence of intermediate forms in intermediate habitats. The chemotypes (morphotypes) have a uniform morphology and ecology throughout the whole investigated area. In *P. aphthosa* I have found mixed stands of up to three chemotypes at the same locality, although in separate microhabitats, and still with their morphological traits intact.

Suggesting that the *Peltigera* species are allogamic, it seems likely that the observed variation of chemotypes is due to genetic barriers between them. Several chemotypes in *Peltigera* are then to be considered biological species. Many of them may be recognized morphologically, after a long time of experience, and fits well with the term "sibling species". They are not considered as separate taxonomic species in this work, partly because each biological species not necessarily has to be accepted as a taxonomic species (see discussion by Grant 1981: 86-90), and partly because it is still uncertain whether they actually represent biological species or not.

TAXONOMY

KEY TO THE SPECIES

GP = Green phototype
BGP = Blue-green phototype

1 Thallus homoiomerous, without veins, resembling a small *Leptogium* . . . . . *P. venosa* (BGP)
1 Thallus heteromerous, usually with veins, not resembling a small *Leptogium* . . 2

2(1) Photobiont green algae; cephalodia present 3
2 Photobiont cyanobacteria; cephalodia absent 7

3(2) Thallus up to 3 cm in diam.; cephalodia attached to the lower side of the thallus; thallus without rhizines, attached by one basal rhizoid . . . . . *P. venosa* (GP)
3 Thallus usually more than 6 cm in diam.; cephalodia attached to the upper side of the thallus; thallus with rhizines, without basal rhizoid 4

4(3) Cephalodia shell-shaped, with free margins, loosely attached *P. britannica* (GP)
4 Cephalodia flat, wart-shaped or cerebriform, without free margins, firmly attached 5

5(4) Fertile lobes continuously corticate on the lower side of the ascocarps; cephalodia wart-shaped or flat; rhizines often confluent . . . . . *P. aphthosa* (GP)
5 Fertile lobes only with patches of cortical tissue on the lower side of the ascocarps; cephalodia cerebriform; rhizines usually separate 6

6(5) Upper side of thallus with erect hairs only towards the margins *P. leucophlebia*
6 Upper side of thallus with erect to appressed hairs also in the center . . . *P.* sp. 1

7(2) Thallus with marginal, linear soralia, sometimes also with laminal, orbicular soralia . . . . . *P. collina*
7 Thallus without soralia 8

8(7) Upper side of thallus with hairs, at least towards the lobe-ends 9
8 Upper side of thallus without hairs 12

9(8) Thallus without secondary lobes containing green photobiont; phlebic acid A and B lacking 10
9 Thallus usually with few or several secondary lobes that contain green photobiont; phlebic acid A and B usually present 11

10(9) Upper side of thallus hairy only towards the lobe-ends; hairs erect . . *P. malacea*
10 Upper side of thallus hairy also in the center; hairs appressed . . . *P. retifoveata*

11(9) Upper side usually glossy centrally; photobiont bluish grey; zeorin or unknown terpenoid 19 present ..... *P. aphthosa* (BGP)
11 Upper side usually dull centrally; photobiont greenish; zeorin and unknown terpenoid 19 absent ..... *P. britannica* (BGP)

12(8) Upper side distinctly scabrous, at least towards the lobe-ends 13
12 Upper side smooth 14

13(12) Rhizines pale as young; lower side pale in the center ..... *P. scabrosella*
13 Rhizines dark as young; lower side dark in the center ..... *P. scabrosa*

14(12) Lower side with distinct veins or network of veins 15
14 Lower side without distinct veins or network of veins 18

15(14) Veins more or less parallel to fan-shaped, moderately anastomosing, on the average as wide as the interstices; rhizines confluent, often in rows ..... *P. frippii*
15 Veins frequently anastomosing, on the average wider than the interstices; rhizines different 16

16(15) Veins yellowish brown, distinctly pigmented all the way to the lobe-ends; rhizines often confluent, unevenly distributed or arranged in short rows; lobe-edges crisped and torn ..... *P. polydactyla*
16 Veins greyish brown to dark brown, not distinctly pigmented all the way to the lobe-ends; rhizines separate; lobe-edges not crisped and torn 17

17(16) Apothecial disc mostly plane, horizontal; rhizines often arranged in concentric lines; peltidactylin absent ..... *P. horizontalis*
17 Apothecial disc revolute, saddle-shaped to finger-shaped; rhizines not arranged in concentric lines; peltidactylin present ..... *P. neopolydactyla*

18(14) Lower side pale ochraceous or greyish brown; rhizines slender, slightly branched 19
18 Lower side dark brown to black; rhizines bush-shaped or shaped like a shaving brush 20

19(18) Lower side pale ochraceous; rhizines up to 6 mm; lobes narrow and acute ..... *P. lactucifolia*
19 Lower side pale brownish grey: rhizines up to 12 mm: lobes broad and rounded ..... *P. neopolydactyla*

20(18) Thallus with schizidia ..... *P. elisabethae*
20 Thallus without schizidia 21

21(20) Apothecial disc reddish brown; photobiont emerald green ..... *P. neopolydactyla*
21 Apothecial disc black; photobiont bluish grey or green ..... *P. neckeri*

DESCRIPTIONS OF THE SPECIES

Peltigera aphthosa (L.) Willd.

Fl. berol. prodr.: 347 (1787).
Lichen aphthosus L., Sp. pl. 2: 1148 (1753).

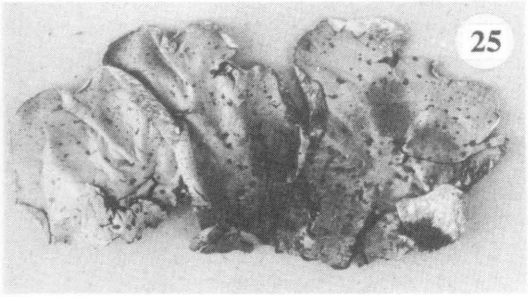
Figs 25-26.

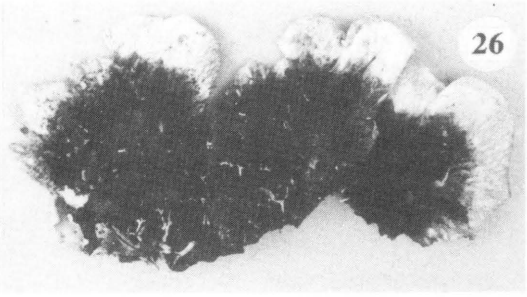
Description, green phototype. *Thallus* large, thick, up to 45 (–60) cm diam. Lobes 2.0–4.5 cm wide, deeply boat-shaped or plane with ascending to involute edges, evenly rounded. Upper side greyish green, with colorless to light brown and more or less erect hairs towards the margin, usually lacking hairs towards the center; cephalodia up to 2 mm diam., greyish blue to brown, flat or convex and wart-shaped, with a smooth central area. Lower side with a pale, broad marginal zone, towards the center dark brown to black, lacking veins. Rhizines dark brown to black, simple to bush-shaped, often confluent. Photobiont green algae; colour bright yellowish green. *Apothecia* not uncommon, mostly saddle-shaped, on elongated and revolute lobes; disc dark reddish brown, up to 1.2 mm diam.; lower side continuously corticate. Spores narrowly acicular, 3-septate, (48–) 58–*67*–77 (–84) × 4.5–5.5 µm; SD_I=6.5. Pycnidia not seen.

Chemistry, green phototype. *Chemotype I*: Tenuiorin-aggregate, zeorin (15), phlebic acid A (16; trace) and B (17), unidentified terpenoid 14; *chemotype II*: Tenuiorin-aggregate, dolichorrhizin (12), zeorin (15), hopane-15α,22-diol (35), unidentified terpenoids 24, 28; *chemotype III*: Tenuiorin-aggregate, unidentified terpenoids 9 and 19; *chemotype IV*: Tenuiorin-aggregate, zeorin (15); *chemotype V*: Tenuiorin-aggregate, phlebic acid A (16; trace) and B (17), unidentified terpenoids 14 and 33 (trace).

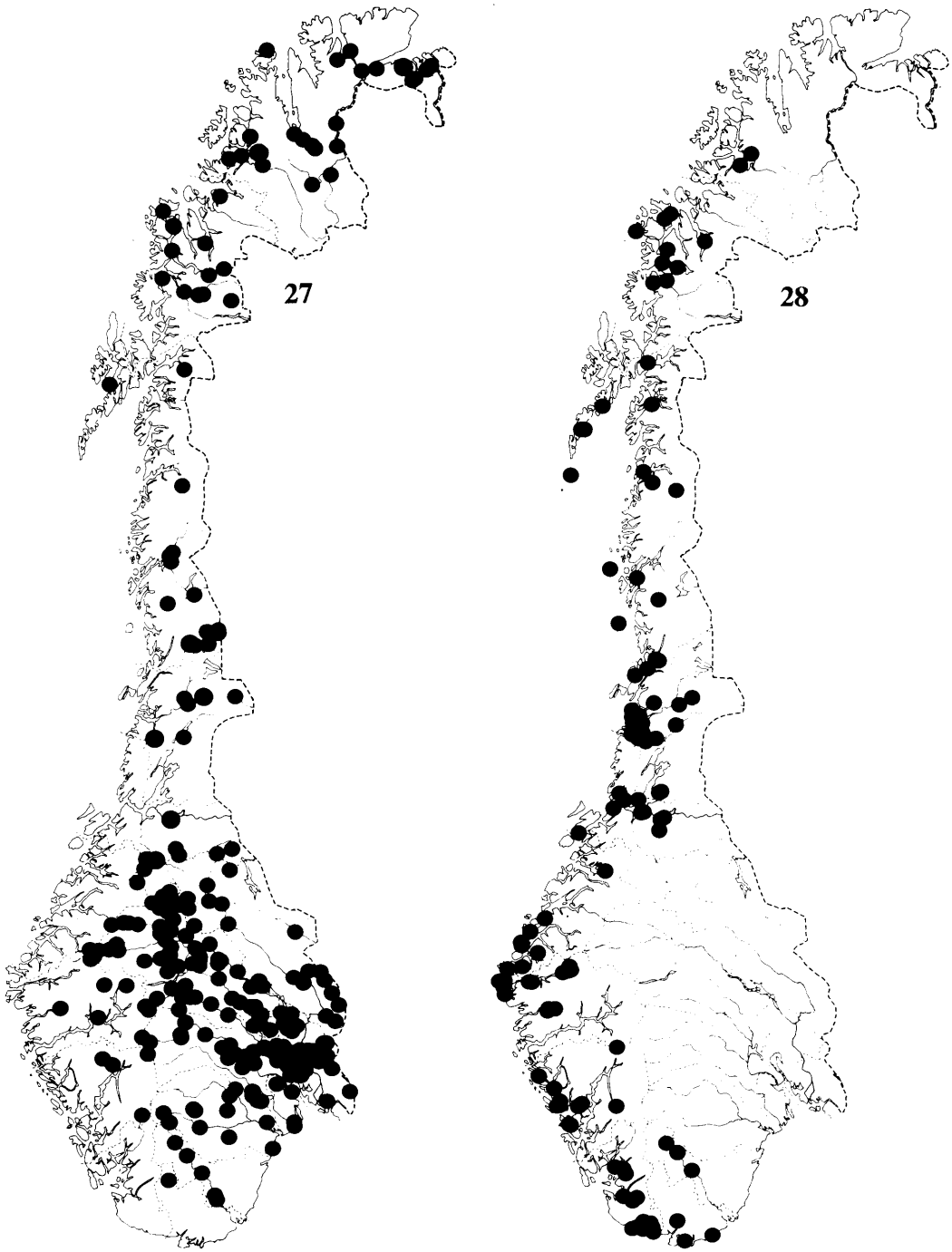
Description, blue-green phototype. *Thallus* up to 30 (–45) cm diam. Lobes 1.0 (–3.0) cm wide, regularly rounded with ascending edges. Upper side greyish blue, sometimes with brown areas, maculate, smooth and more or less glossy towards the center, with colorless to pale brown and more or less erect hairs towards the margins, sometimes with lobes of the green phototype attached. Lower side with a broad and pale marginal zone, dark brown to black towards the center, without veins, usually with small, submarginally attached lobes of the green phototype. Rhizines dark brown to black, simple to bush-shaped, often confluent. Photobiont cyanobacteria; colour greyish blue. *Apothecia* and pycnidia not seen.

Chemistry, blue-green phototype. Tenuiorin-aggregate, zeorin (15), phlebic acid A (16;

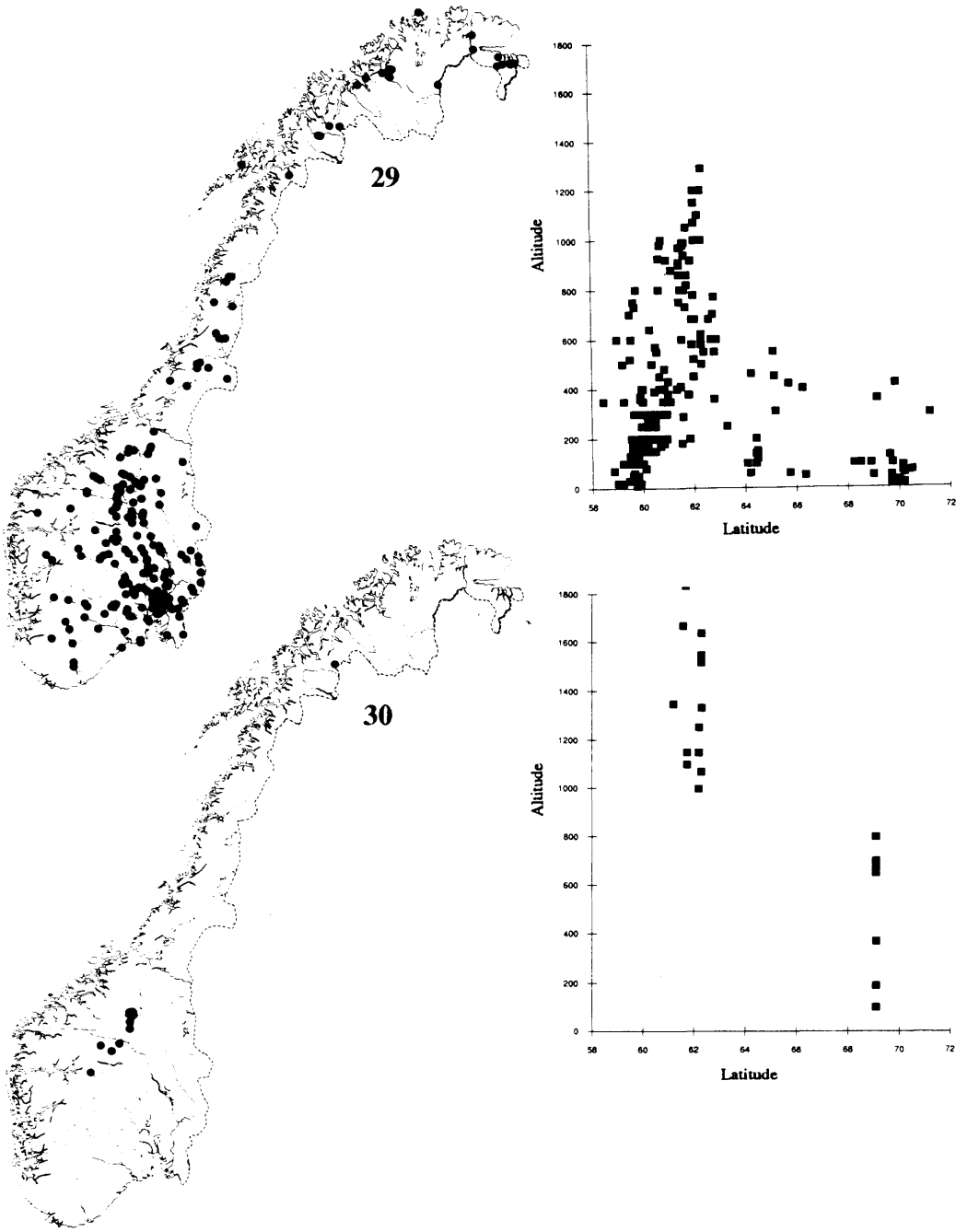




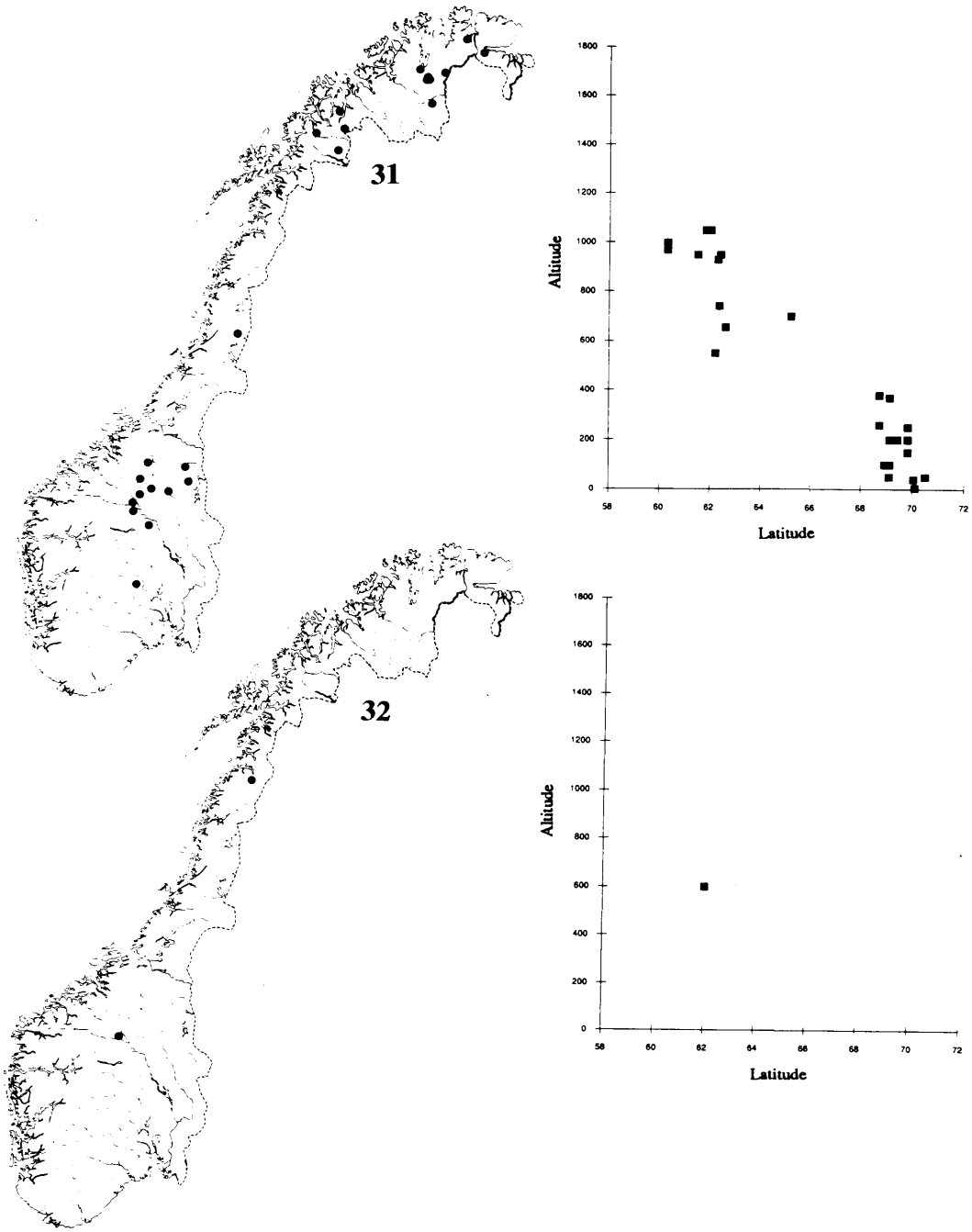
Figs 25–26. *Peltigera aphthosa*, morphotype A, Troms, Holtan-Hartwig 4336 (O). 0.6×.



Figs 27–28. Norwegian distribution. Fig. 27. *Peltigera aphthosa*. Fig. 28. *P. britannica*.



Figs 29–30. Horizontal and vertical distribution of chemotype I and II of *Peltigera aphthosa*. Fig. 29. Chemotype I. Fig. 30. Chemotype II.



Figs 31–32. Horizontal and vertical distribution of chemotype III and IV of *Peltigera aphthosa*. Fig. 31. Chemotype III. Fig. 32. Chemotype IV.

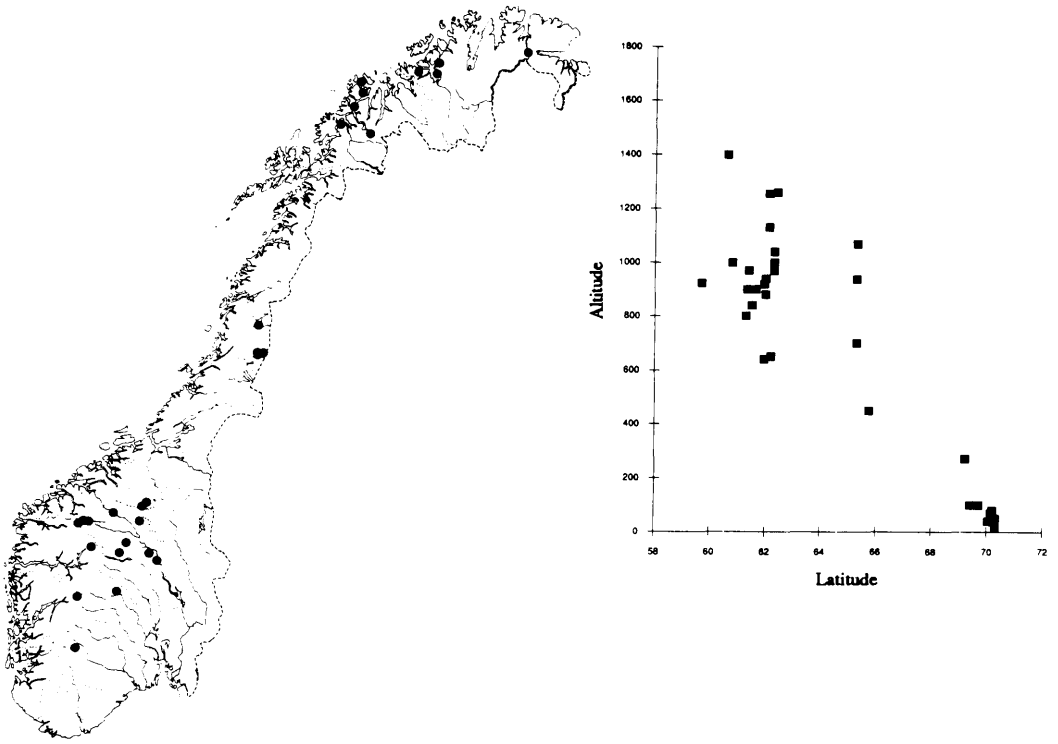


Fig. 33. Horizontal and vertical distribution of chemotype V of *Peltigera aphthosa*.

trace) and B (17), unidentified terpenoid 14. Tenuiorin-aggregate, unidentified terpenoids 9 and 19.

Variation. According to the chemical variation and the morphological variation in thallus size and shape of the lobes and cephalodia, the species is here divided into five chemotypes and three morphotypes.

Morphotype A: Thallus large, up to 60 cm diam.; lobes broad, boat-shaped, with ascending edges; cephalodia varying from plane to wart-shaped on the same individual. – Chemotype I.

Morphotype B: Thallus small, up to 20 cm diam.; lobes more narrow, flat, with involute edges; cephalodia always wart-shaped. – Chemotype II.

Morphotype C: Thallus and lobes as in morphotype A; cephalodia always wart-shaped. – Chemotypes III, IV, and V.

Affinities. *Peltigera aphthosa* is related to *P. britannica*, *P. leucophlebia* and *P.* sp. 1, and may easily be confused with the two last mentioned. Fertile specimens are readily distinguished by the continuous cortex on the lower side of the ascocarp in *P. aphthosa* (Fig. 17) in contrast to the scattered patches of cortical tissue in *P. leucophlebia* and *P.* sp. 1 (Fig. 16). Sterile specimens of *P. leucophlebia* without or with a poorly developed network of veins may be difficult to distinguish from *P. aphthosa*. However, the cephalodia of *P. leucophlebia* are always convex and cerebriform, whereas those of *P. aphthosa* are either plane and wart-shaped (morphotype A) or exclusively wart-shaped (morphotypes B and C). The rhizines of the former species are separate, those of the latter are often confluent. For distinguishing

Tab. 6. Comparison of species containing green photobiont in the *Peltigera aphthosa* group.

Character	*P. aphthosa*	*P. britannica*	*P. leucophlebia*	*P.* sp. 1
Margin	not undulate	sometimes faintly undulate	usually distinctly undulate	always distinctly undulate
Mature cephalodia	flat or wart-shaped, firmely attached	shell-shaped, frequently detaching causing white scars	cerebriform, firmly attached	cerebriform, firmly attached
Hairs	± erect, usually only towards the lobe-ends	± erect, usually only towards the lobe-ends	± erect, usually only towards the lobe-ends	± appressed, usually all the way to the center of thallus
Pilema	continuous	usually continuous	as a network of veins or continuous	continuous or interrupted by large pale circular to oblong areas
Apothecia	not uncommon; fertile lobes continuously corticate on the lower side of the ascocarps	unknown	not uncommon, fertile lobes patchyly corticate on the lower side of the ascocarps	not uncommon, fertile lobes patchyly corticate on the lower side of the ascocarps
Development of blue-green phototype	from the under side of the green phototype	from the cephalodia	unknown	unknown
Terpenoids	chemotype I: 14, 15, 16 (trace), 17 chemotype II: 12, 15, 24, 28, 35 chemotype III: 9, 19 chemotype IV: 15 chemotype V: 14, 16 (trace), 17, 33 (trace)	14, 16 (trace), 17, 33 (trace)	7, 9, 14 (trace), 19	chemotype I: 14 (trace), 25 chemotype II: 7, 9, 14 (trace), 19

characters against *P. britannica* and *P.* sp. 1, see under these species. A comparison between the four species is given in Tab. 6.

The blue-green phototype of *P. aphthosa* is morphologically similar to specimens of the blue-green phototype of *P. britannica* and specimens of *P. malacea*. For a comparison, see

under the two last mentioned.

Ecology and distribution. *Peltigera aphthosa* is common throughout the country, except for coastal areas from Aust-Agder to Nordland (Fig. 27). It usually grows on the ground on a thick layer of mosses in *Vaccinium*-rich, mixed coniferous forests and in subalpine and low-alpine shrub and dwarf-shrub vegetation. **Counties**: Østfold–Vest-Agder, Hordaland–Finnmark.

The different chemotypes have distinct distribution patterns (Figs 29–33) and ecological requirements.

Morphotype A: This morphotype only consists of chemotype I. It normally grows on the ground, on thick and fluffy layers of mosses which are often composed of *Hylocomnium splendens* and *Pleurozium schreberi*. Typical habitats are *Vaccinium*-rich mixed coniferous forests, *Betula nana*- and *Juniperus communis*-dominated vegetation in subalpine *Betula*-forests, and low alpine heaths. This morphotype is by far the most common one of *P. aphthosa* and occurs throughout the whole distribution area of the species in Norway, although it is rare in Finnmark. Its altitudinal distribution ranges from about sea level to 1290 m (Fig. 29).

Morphotype B: This morphotype only consists of chemotype II. It grows on and among mosses, often in close contact with the ground, and often in sites with a well-developed soil layer. The habitat is not as dry as for morphotype A, and is often dominated by grasses and short mosses. The morphotype may be calciphilous. In northern Norway it is known only from a small area (Troms, Mt Paras; 100–800 m alt.); in southern Norway only from low-alpine to high-alpine regions (1000–1840 m alt.) (Fig. 30).

Morphotype C: This morphotype consists of chemotypes III, IV, and V. Chemotype III often grows on a thick layer of mosses in the same vegetation types as for chemotype I, but is only found in subalpine and low-alpine regions. The chemotype has an eastern distribution in Norway (Fig. 31) and is mainly collected in habitats rich in calcareous rocks. In Norway, chemotype IV is only known from two localities (Nordland, Saltdalen and Oppland, Mt Nonshaugen) (Fig. 32). Chemotype V usually grows on a thick layer of mosses, often on stones and boulders, but is otherwise ecologically similar to chemotype I. In southern Norway and in Nordland it has been collected from inland habitats, but in Troms and Finnmark it has been collected close to the sea (up to 270 m alt.) (Fig. 33).

Note. The blue-green phototype of *P. aphthosa* has only been recorded from seven localities in Norway, always sterile. Among these, only one collection belonged to chemotype III. The blue-green thalli have always been found associated with green lobes. The two phototypes are chemically and morphologically relatively similar.

The Arctic material of *P. aphthosa* in O consists of specimens from Iceland (10, all chemotype V), Greenland (13 chemotype I, 7 chemotype II, 1 chemotype IV, and 5 chemotype V), Svalbard (9 chemotype II and 2 chemotype III), and Novaya Zemlya (2, both chemotype II). This supports the assumption of an Arctic-alpine distribution pattern of chemotype II. Chemotype V occurs in southern Norway in inland areas from 500 to 1400 m alt., but in Northern Norway only in coastal areas. (Fig. 33).

Specimens seen. *Chemotype I*: Øs (BG: 1, O: 4); Ak (O: 29, TROM: 1); Os (BG: 2, O: 16); He (O: 18, TRH: 1, TROM: 1); Op (BG: 2, O: 60, TRH: 1, TROM: 1); Bu (BG: 2, O: 17, TRH: 1), Ve (O: 4, TRH: 2), Te (O: 10); AA (O: 2); VA (BG: 1); Ho (BG: 2, O: 5); SF (BG: 1, O: 3); MR (O: 1); ST (BG: 5, O: 13, TRH: 10); No (BG: 4, O: 1, TRH: 2, TROM: 2); Tr (O: 5); Fi (BG: 8, O: 9, TRH: 1). *Chemotype II*: Op (O: 11); SF (O: 1); ST (O: 5); Tr (O: 7). *Chemotype III*: He (O: 3); Op (O: 3, TRH: 1); Bu (O: 2); ST (O: 4); No (BG: 1); Tr (O: 7); Fi (BG: 1, O: 7, TROM: 1). *Chemotype IV*: Op (O: 1); No (O: 2). *Chemotype V*: Op (O: 9); Bu (O: 1); Te (O: 1); Ho (O: 1); SF (O: 3); ST (O: 4); No (O: 3, TROM: 1); Tr (BG: 2, O: 3, TRH: 1, TROM: 1); Fi (BG: 2, O: 2).

Peltigera britannica (Gyelnik) Holt.-Hartw. & Tønsb.

Nord. J. Bot. 3: 685 (1983).
Peltigera variolosa f. *britannica* Gyelnik, Annls mycol. 30: 453 (1932).

Figs 34–35.

Description, green phototype. *Thallus* large, up to 40 cm diam. Lobes 2.0–3.0 cm wide, evenly rounded; edges moderately involute. Upper side greyish green, sometimes with brown areas, with pale to pale brown, more or less erect hairs towards the lobe margins, centrally without hairs; cephalodia usually up to 2 (–3) mm diam., greyish blue to brown, shell-shaped, flat to concave, often with dentate, free edges, falling off easily and leaving white scars. Lower side with a broad pale marginal zone, centrally dark brown to black, usually without veins. Rhizines dark brown to black, simple to bush-shaped, often confluent. Photobiont green algae; colour bright yellowish green. *Apothecia* and pycnidia not seen.

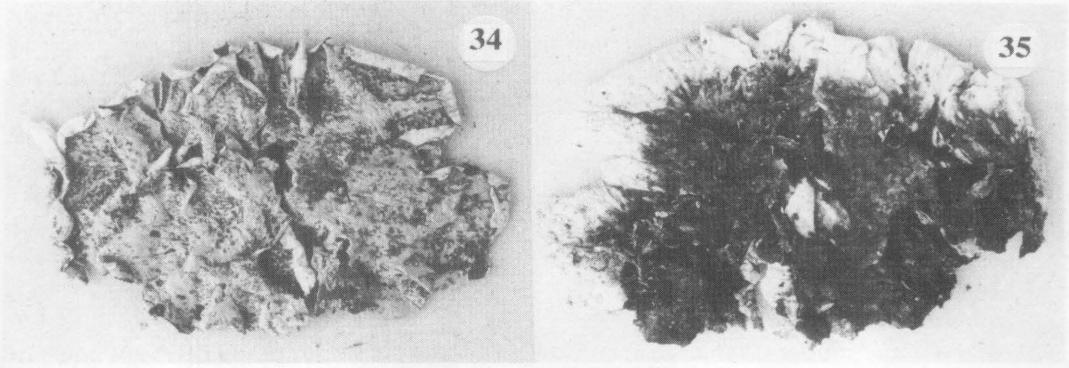
Chemistry, green phototype. Tenuiorin-aggregate, phlebic acid A (16; trace) and B (17), unidentified terpenoids 14 and 33 (trace).

Description, blue-green phototype. *Thallus* up to 30 cm diam. Lobes 1.5–2.0 cm wide, evenly rounded; edges often dentate. Upper side bluish grey to brown, maculate, with pale to brown and more or less erect hairs (especially towards the lobe margins), usually with lobes of the green phototype attached. Lower side with a wide pale marginal zone, centrally dark brown to black, without veins, usually with lobes of the green phototype attached. Rhizines dark brown to black, simple to bush-shaped, often confluent and dissolved into single hyphae. Photobiont cyanobacteria; colour blue-green. *Apothecia* and pycnidia not seen.

Chemistry, blue-green phototype. Tenuiorin-aggregate, phlebic acid A (16: trace) and B (17), unidentified terpenoids 14 and 33 (trace).

Variation. Both phototypes show only little variation. The green phototype varies in the differentiation of the pilema. Usually the thallus consists of a dominating green phototype with the blue-green phototype represented as cephalodia only. The cephalodia may either fall off and start independent growth, or they may continue growing on the parent thallus forming larger lobes.

Affinities. *Peltigera britannica* is related to *P. aphthosa*, *P. leucophlebia* and *P.* sp. 1. The green phototype of *P. britannica* has shell-shaped cephalodia which easily detach and



Figs 34–35. *Peltigera britannica*, Sogn og Fjordane, 1949, Størmer (O). Fig. 34. 0.9×. Fig. 35. 1.1×.

leave white scars in the cortex, whereas the green phototypes of the other species have wart-shaped, plane or cerebriform cephalodia which are firmly attached to the cortex. For additional distinguishing characters, see Tab. 6.

The blue-green phototype of *P. britannica* can usually be distinguished from the corresponding phototype of *P. aphthosa* by the more dull and more densely hairy upper side, and the more greenish colour. For comparison with *P. malacea*, see that species.

Ecology and distribution. *Peltigera britannica* usually grows on north- to westfacing, more or less vertical rock-faces, in habitats with high air humidity or a moist substrate covered by a thin moss layer. The species is distributed along the coast from Aust-Agder to Finnmark (Fig. 28). It rarely occurs above 100 m alt., but has been collected at 800–900 m alt. both in Setesdalen (Aust-Agder) and in Flåmsdalen (Hordaland). **Counties**: Aust-Agder–Finnmark.

Note. In *P. britannica* the blue-green phototype is common, especially in humid and shady habitats. The species has never been found fertile. In dry habitats the cephalodia usually reach only 2 (–3) mm in diameter when attached to the parent thallus. If moisture is sufficient, the attached cephalodia may continue growing on the dying and disintegrating parent thallus. Blue-green thalli probably also develop from detached cephalodia. Green lobes will usually develop on the upper and lower sides of the blue-green thallus, giving a cyclic alternation of the two phototypes. The two phototypes are chemically and morphologically relatively similar.

Peltigera britannica was described by Gyelnik (1932) as *P. variolosa* f. *britannica*, and raised to specific rank by Tønsberg & Holtan-Hartwig (1983). In addition to the Norwegian material, I have also seen specimens from Great Britain, Portugal and Canada (British Columbia).

Specimens seen. AA (O: 3); VA (O: 3, UPS: 2); Ro (BG: 3, O: 29); Ho (BG: 11, O: 5, UPS: 1); SF (BG: 3, O: 21); MR (BG: 1, O: 8); ST (BG: 16, O: 7, TRH: 5); NT (BG: 5, O: 2, TRH: 21); No (BG: 11, O: 9, TRH: 1, TROM: 3, UPS: 2); Tr (BG: 3, O: 7, TROM: 3, UPS: 1); Fi (BG: 1, O: 1).

Peltigera collina (Ach.) Schrader

J. Bot. 1: 78 (1801).
Lichen collinus Ach., Lichenogr. suec. prodr.: 162 (1798).

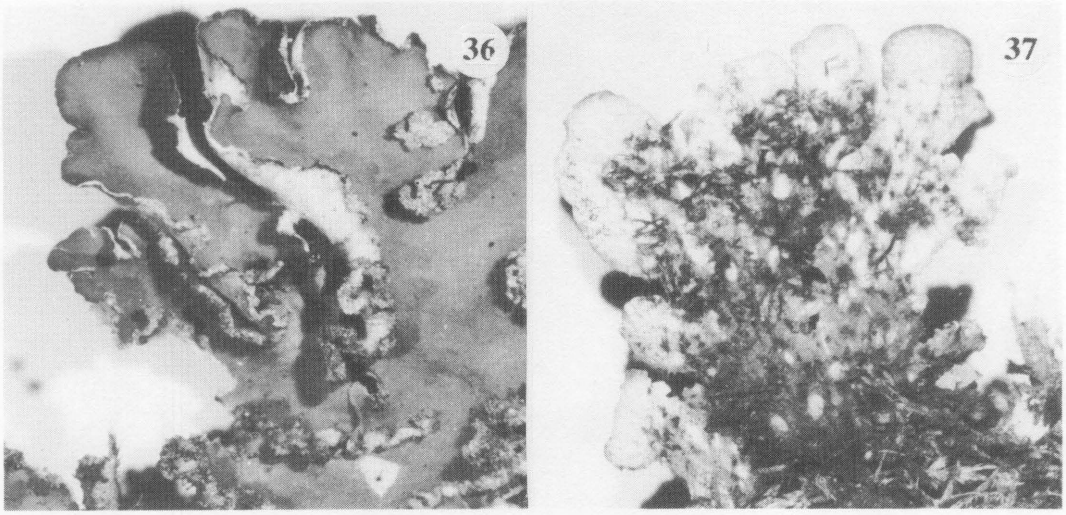
Fig. 36–37.

Description. *Thallus* small, up to 20 cm diam. Lobes narrow, 0.5–1.0 (–2.0) cm wide, ascending, moderately involute; margins undulating, with linear soralia; soredia coarse. Upper side brown, greyish brown or grey, smooth in the central part, often scabrous and pruinose towards the margins, sometimes with laminal, orbicular soralia. Lower side with a pale marginal zone, with a network of dark brown, plane veins in the central part or with a more or less continuous, dark brown pilema. Rhizines colorless to pale brown, thin, tapering or divided, often confluent. Photobiont cyanobacteria; colour greenish grey. *Apothecia* not common, finger-shaped, on non-elongated lobes; discs black, thick, often rugose, up to 5 mm diam. Spores acicular, 3-septate, (43–) 46–56–66 (–72) × 4.0–4.5 µm; SD_i=6.6. Pycnidia not common, attached to the lobe margins; pycnoconidia drop-shaped to foot-shaped, 6.0–8.0 × 2.3–3.8 µm.

Chemistry. Tenuiorin-aggregate, zeorin (15).

Variation. *Peltigera collina* is not a variable species. In some specimens the pilema are continuous and not differentiated into a network of veins.

Affinities. *Peltigera collina* is the only Norwegian *Peltigera*-species having marginal



Figs 36–37. *Peltigera collina*, Sogn og Fjordane, Holtan-Hartwig 1600 (O). Fig. 36. 4.3×. Fig. 37. 3.1×.

soralia. Here it is placed in the *P. scabrosa* group because of the scabrous upper side, but the species also shows affinities with the *P. polydactyla* group.

Ecology and distribution. The species grows on moss-covered bark of deciduous trees, mainly *Fraxinus excelsior*, *Populus tremula*, *Salix caprea*, *Sorbus aucuparia* and *Alnus incana*, and on moss-covered rock faces and rock boulders. It occurs on thin *Picea abies* twigs in Lobarion communities in the humid area of Trøndelag. *Peltigera collina* is most common along the coast of southern Norway and occurs only scattered in the inland and throughout northern Norway as far north as Alta (Fig. 38). Its vertical distribution ranges from almost sea level to *c.* 1300 m. **Counties**: Østfold–Finnmark.

Specimens seen. Øs (BG: 1, O: 6); Ak (BG: 2, O: 22, TRH: 2); Os (O: 9, TRH: 2); He (O: 1); Op (BG: 1, O: 4, TRH: 6); Bu (BG: 1, O: 9); Ve (O: 1, TRH: 7); Te (O: 4); AA (BG: 1, O: 10, TRH: 3, TROM: 1); VA (BG: 1, O: 9); Ro (BG: 3, O: 18, TRH: 1); Ho (BG: 15, O: 16, TRH: 1, TROM: 1); SF (BG: 4, O: 11); MR (O: 10); ST (O: 7, TRH: 8); NT (O: 9, TRH: 15); No (O: 4, TRH: 3 TROM: 1); Tr (BG: 1, O: 5); Fi (O: 2).

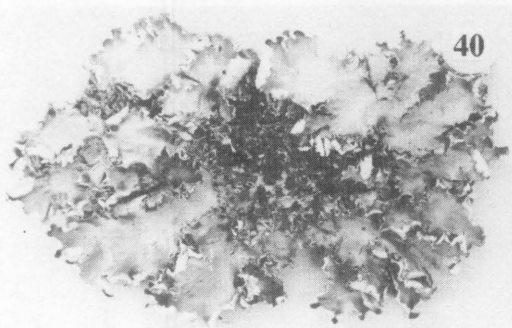
Peltigera elisabethae Gyelnik

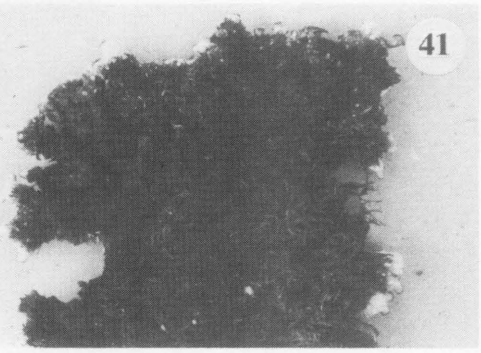
Bot. Közl. 24: 135 (1927).

Fig. 40–41.

Description. *Thallus* medium sized, up to 30 cm diam. Lobes 1.0–1.5 (–2.0) cm wide, moderately ascending, moderately involute; edges curled. Upper side greyish blue, brownish grey or brown, smooth, glossy, with submarginal or more rarely laminal schizidia. Lower side with a broad, pale marginal zone and a dark brown to blackish brown central zone with small, greyish white, circular to oblong areas. Rhizines dark brown to black, thick, shaving-brush shaped, separate, often arranged in concentric rows. Photobiont cyanobacteria; colour bluish grey. *Apothecia* rare, horizontal, on shortly elongated lobes; disk reddish brown to black,

Figs 38–39. Norwegian distribution. Fig. 38. *Peltigera collina*. Fig. 39. *P. elisabethae*.





Figs 40–41. *Peltigera elisabethae*, Finnmark, Holtan-Hartwig 4383 (O). Fig. 40. 0.5×. Fig. 41. 0.7×.

plane, up to 9 mm diam. Spores fusiform, 3-septate, (26–) 29–*34*–39 (–43) × 5.5–7.0 µm; SD_I=3.4. Pycnidia not seen.

Chemistry. *Chemotype I*: Tenuiorin-aggregate, zeorin (15), unidentified terpenoids 1, 2, 3, 4, 5, 30, 31, 36 (trace), and 40; *chemotype II*: Tenuiorin-aggregate, zeorin (15), unidentified terpenoid 30.

Variation. *Peltigera elisabethae* is not a variable species. The width of the lobes and the colour of the thallus varies somewhat, probably in response to the humidity and illumination at the site. Schizidia are mainly developed laterally on the lobes. They are highly irregular in size and shape; being formed by cortex, algal layer, and a part of the medulla peeled off as small scales. Schizidia may also be produced along laminal cracks. Regeneration lobules are also often found along these cracks.

Two chemotypes occur in Norway (see above).

Affinities. *Peltigera elisabethae* is characterized by the occurrence of schizidia and the dark, almost continuous pilema. It is closely related to the habitually similar *P. horizontalis*, distinguishable by the pilema forming a well-developed network of veins and by lacking schizidia.

Peltigera elisabethae may also be confused with *P. neckeri*. Both species have a more or less continuous, brownish black pilema and a white marginal zone, but *P. neckeri* lacks schizidia. The rhizines of *P. elisabethae* are shaving-brush shaped and separate, in *P. neckeri* bush-shaped and often confluent. *Peltigera neckeri* is often fertile and has revolute, ascending apothecia. The two species are also chemically distinct.

Ecology and distribution. *Peltigera elisabethae* usually grows on calcareous or nutrient-rich stones and soil covered by mosses, often somewhat shaded. The major habitats are sides of large boulders, the base of rock walls, and rock faces in the inundation zone along brooks and rivers. The species is common in the calcareous areas in southern Norway and in Troms (Fig. 39), but is probably overlooked and may have a wider distribution than presently known. *Peltigera elisabethae* has been collected from about the sea level to 1000 m. **Counties**: Østfold–Aust-Agder, Hordaland–Nord-Trøndelag, Troms, Finnmark.

Chemotype I occurs throughout the total distributional area of the species in Norway (Fig. 42), chemotype II only scattered in southern Norway (Fig. 43).

Note. No correlations between chemotype and the morphological variation and ecological preferences were observed.

Figs 42–43. Distribution of the chemotypes of *Peltigera elisabethae*. Fig. 42. Chemotype I. Fig. 43. Chemotype II.

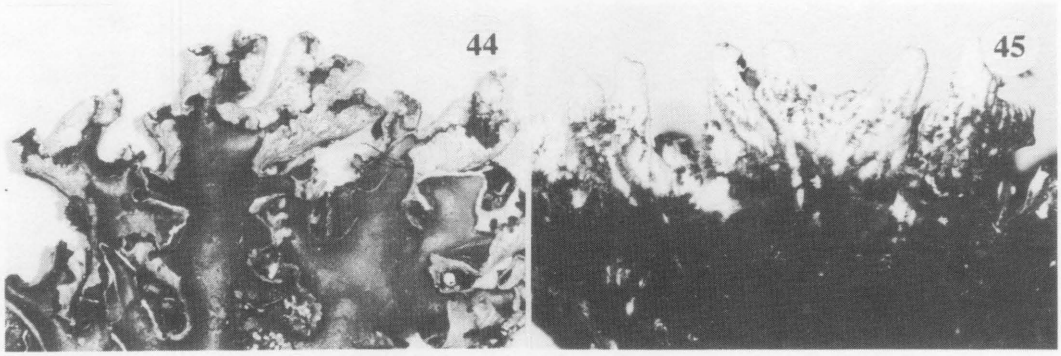
Specimens seen. *Chemotype I*: Øs (O: 1); Ak (O: 1); Os (O: 4); He (O: 1); Op (O: 18, TRH: 6); Bu (O: 6); Te (O: 1); AA (O: 2); Ho (O: 1); SF (O: 1); MR (O: 2); ST (BG: 1, O: 1); NT (O: 1); Tr (O: 4); Fi (O: 2, TROM: 1). *Chemotype II*: Os (O: 2); He (O: 1); Op (TRH: 2); Bu (O: 7); Ho (BG: 1); NT (O: 2).

Peltigera frippii Holt.-Hartw.

Lichenologist 20: 11 (1988).

Fig. 44-45.

Description. *Thallus* small, up to 15 cm diam., fragile. Lobes rather narrow, up to 1.0 (–2.0) cm wide, more or less imbricate, irregularly and frequently deeply incised; margins ascending to involute, curled and torn. Upper side greyish brown to brown, more or less dull to glossy, smooth, maculate when moist, often faintly pruinose towards the lobe tips. Lower



Figs 44–45. *Peltigera frippii*, Hedmark, holotypus. Fig. 44. 2.7×. Fig. 45. 3.0×.

side blackish brown in central part, pale brown to colorless towards the margins; veins colorless to blackish brown, parallel to fan-shaped. Rhizines medium brown to blackish brown, short, bush-shaped, frequently confluent, arranged in rows. Photobiont cyanobacteria; colour blue-green. *Apothecia* and pycnidia not seen.

Chemistry. Tenuiorin-aggregate, zeorin (15), phlebic acid A (16; trace) and B (17), unidentified terpenoids 14 and 39.

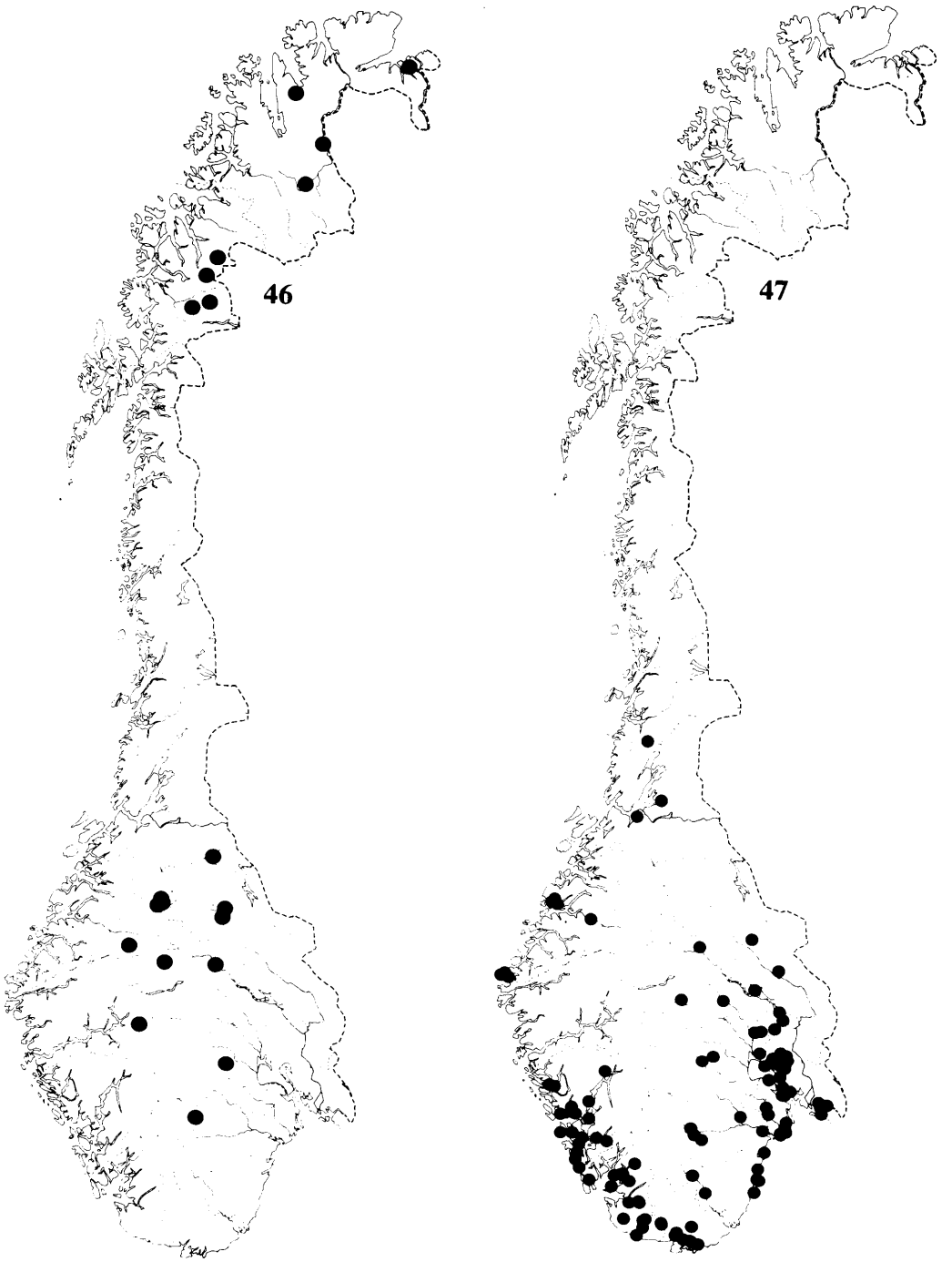
Affinities. *Peltigera frippii* is characterized by the short and narrow lobes with ascending to involute, curled and torn margins, the maculate upper side, the parallel to fan-shaped veins, and the confluent rhizines which are arranged in rows. It may be confused with *P. malacea* and *P. neckeri*, but differs morphologically from the former mainly in the absence of tomentum on the upper side and the presence of more or less distinct veins on the lower side. It differs morphologically from the latter mainly in the maculate upper side and its more crispy appearance.

Peltigera frippii is chemically distinct from all European species of the genus, except from chemotype I of *P. aphthosa*. The unidentified terpenoid 39, however, is possibly absent from *P. aphthosa*. *Peltigera frippii* differs from the blue-green phototype of that species especially in the absence of hair on the upper side, the more fragile thallus, and the narrower and more incised lobes.

Ecology and distribution. The species apparently has a wide ecological amplitude. It grows on both sandy and humus-rich soil covered by a thin moss cover, and has most frequently been collected in low dwarf-shrub vegetation, on road-sides and on riverbanks. It is presently known from inland localities in the boreal and the alpine regions of Norway (Fig. 46), and is apparently a rare species. Its vertical distribution ranges from 130 to 1600 m alt. **Counties**: Hedmark–Telemark, Sogn og Fjordane, Sør-Trøndelag, Troms, Finnmark.

Note. The species has recently been described by Holtan-Hartwig (1988) and is so far only known from Norway.

Specimens seen. He (O: 1, hb. Gjerlaug: 1); Op (O: 2, TRH: 1); Bu (O: 3); Te (O: 1); SF (O: 2); ST (O: 9); Tr (O: 5); Fi (O: 4).



Figs 46–47. Norwegian distribution. Fig. 46. *Peltigera frippii*. Fig. 47. *P. horizontalis*.

Peltigera horizontalis (Huds.) Baumg.

Flora lips.: 562 (1790).
Lichen horizontalis Huds., Fl. angl.: 548 (1762).

Fig. 48–49.

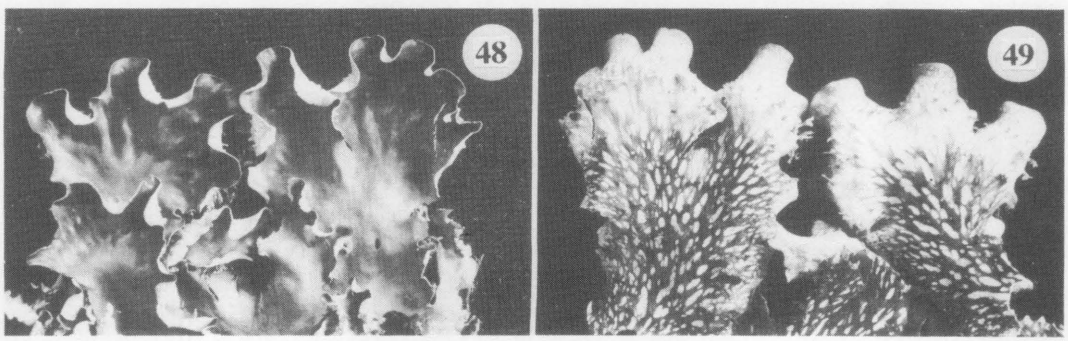
Description. *Thallus* medium sized to large, up to 40 cm diam. Lobes 2.0–2.5 (-3.0) cm wide; margins moderately ascending, moderately involute. Upper side usually bluish grey, sometimes with brown areas, more rarely brown, smooth, glossy, often with small depressions above the rhizines. Lower side with a broad and pale marginal zone, towards the center with a distinct network of dark brown to brownish black, plane veins and numerous white oblong interstices. Rhizines dark brown to black, thick, shaving-brush shaped, separate, often arranged in concentric rows. Photobiont cyanobacteria; colour greyish blue. *Apothecia* common, horizontal, on shortly elongated lobes; discs reddish brown to black, plane, up to 9 mm diam. Spores fusiform, 3-septate, (29–) 30–*36*–43 (–48) × 5.5–7.0 µm; SD_I=4.3. Pycnidia not seen.

Chemistry. *Chemotype I*: Tenuiorin-aggregate, zeorin (15), unidentified terpenoids 1, 2, 3, 4, 5, 30, 31, 36 (trace), and 40; *Chemotype II*: Tenuiorin-aggregate, zeorin (15), unidentified terpenoid 30.

Variation. *Peltigera horizontalis* is not a variable species. The colour and width of the lobes varies somewhat, probably in response to the illumination and humidity at the site. Two chemotype are known from Norway (see above).

Affinities. The species is closely related to *P. elisabethae*, and differs morphologically by having a pilema forming a distinct network of veins and by lacking schizidia. The two species have also different distributions and different ecological requirements.

Peltigera horizontalis has often been confused with *P. polydactyla* s. str. Fertile specimens are easily distinguished by the shape and attachment of the apothecia. In *P. polydactyla* the apothecial disc is revolute and parallel with the upper side of the fertile lobe (Fig. 13). In *P. horizontalis* the apothecial disc is more or less plane and inclined (Fig. 15). Sterile specimens can be distinguished by how far the pigmentation of the veins reach towards the lobe margins and by the type and distribution of the rhizines. In *P. horizontalis* the veins are unpigmented near the lobe margins, and the rhizines are thick, shaving-brush shaped, separate, and often arranged in concentric lines. In *P. polydactyla* the veins are pigmented all the way out to the lobe margins, the rhizines are thin and more or less confluent, and not arranged in concentric lines. The two species are also chemically different.



Figs 48–49. *Peltigera horizontalis*, Oslo, Holtan-Hartwig 4526 (O). 1.1×.

Figs 50–51. Distribution of the chemotypes of *Peltigera horizontalis*. Fig. 50. Chemotype I. Fig. 51. Chemotype II.

Ecology and distribution. *Peltigera horizontalis* usually grows on moss covered, weakly to moderately inclining rock faces or on the base of deciduous trees, often in shaded habitats. The species is thermophilous, and is common along the coast of southern Norway as far north as Sogn og Fjordane (Fig. 47). Scattered collections have been made northwards to Overhalla in Nord-Trøndelag. In eastern Norway it is most common in the southern areas, but also occurs in the inland valleys as far north as Ringebu, Oppland. Most collections have been made below 300 m, while the highest recorded altitude is 520 m. **Counties**: Østfold–Nord-Trøndelag.

The two chemotypes have relatively congruent distribution areas in Norway (Figs 50–51), but chemotype I is somewhat more common.

Specimens seen. *Chemotype I*: Øs (O: 5); Ak (BG: 1, O: 19); Os (BG: 3, O: 16, TROM: 1); He (O: 3); Op (O: 2); Bu (O: 8); Ve (BG: 1, O: 9, TRH: 4); Te (O: 5); AA (BG: 1, O: 8); VA (O: 6); Ro (BG: 1, O: 13); Ho (BG: 11, O: 17); SF (BG: 3, O: 1); MR (BG: 2, O: 6); ST (TRH: 1); NT (O: 1, TRH: 1). *Chemotype II*: Øs (O: 1); Op (O: 4); Ve (O: 1); Te (O: 1); VA (O: 7); Ro (O: 6); Ho (BG: 5, O: 8).

Peltigera lactucifolia (With.) Laundon

Lichenologist 16: 221 (1984).
Lichen lactucifolius With., Bot. arr. veg. Gr. Brit. 1, 2: 718 (1776).

Fig. 52–53.

Description. *Thallus* small to medium sized, up to 25 cm diam., thin. Lobes imbricate, acute, 1.0–2.0 (–4.0) cm wide, with ascending and often involute margins. Upper side brown, more rarely greyish blue, moderately glossy. Lower side pale with diffuse, plane, broad, pale ochraceous veins. Rhizines white to brown, thin, simple, separate. Photobiont cyanobacteria; colour bluish grey. *Apothecia* not uncommon, saddle-shaped, on shortly elongated lobes; discs dark brown, usually less than 6 mm diam. Spores acicular, 3-septate, (53–) 58–66–75 (–79) × 3.5–4.0 µm; SD_i=6.0. Pycnidia not seen.

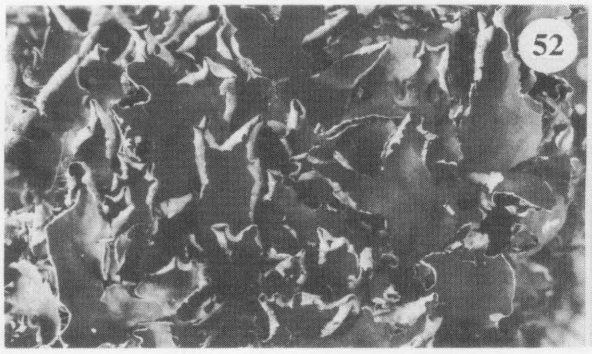
Chemistry. Tenuiorin-aggregate, peltidactylin (10), dolichorrhizin (12), zeorin (15), unidentified terpenoid 39 (trace).

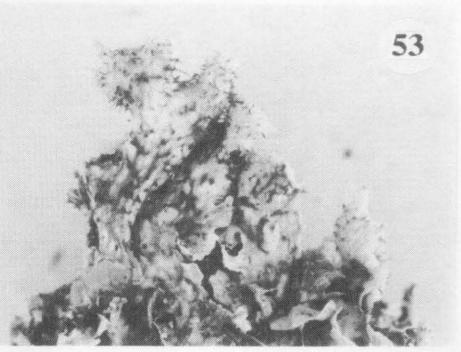
Variation. *Peltigera lactucifolia* shows extensive variation in the width of the lobes; this is probably in response to the humidity at the site.

Affinities. *Peltigera lactucifolia* is related to *P. neckeri*, *P. neopolydactyla* and *P. polydactyla*, and may most easily be confused with *P. neopolydactyla*. *Peltigera lactucifolia* is characterized by having narrow, imbricate lobes with involute margins giving the lobes an acute appearance. The lower side lacks veins, or has broad, diffuse, ochraceous veins. In *P. neopolydactyla* the lobes are broad, not imbricate, evenly rounded and moderately involute, and the lower side usually has a distinct greyish brown to dark brown network of veins. The pale lower side of *P. lactucifolia* distinguishes it both from *P. neckeri*, which always has a brownish black lower side, and *P. polydactyla*, which has a distinct brown pigmented network of veins with numerous white, circular to oblong interstices. The distinguishing characters between the species in the *P. polydactyla* group are summarized in Tab. 7.

Peltigera lactucifolia may be confused with *P. scabrosella* in habit. Both have acute lobes with involute edges and diffuse, ochraceous veins. In *P. lactucifolia*, however, the upper side is always smooth, in *P. scabrosella* scabrous. The two species are also chemically distinct.

Ecology and distribution. *P. lactucifolia* grows mainly on moss-covered rock faces and weakly inclining rocks. The species occurs in a broad zone along the coast from Østfold to

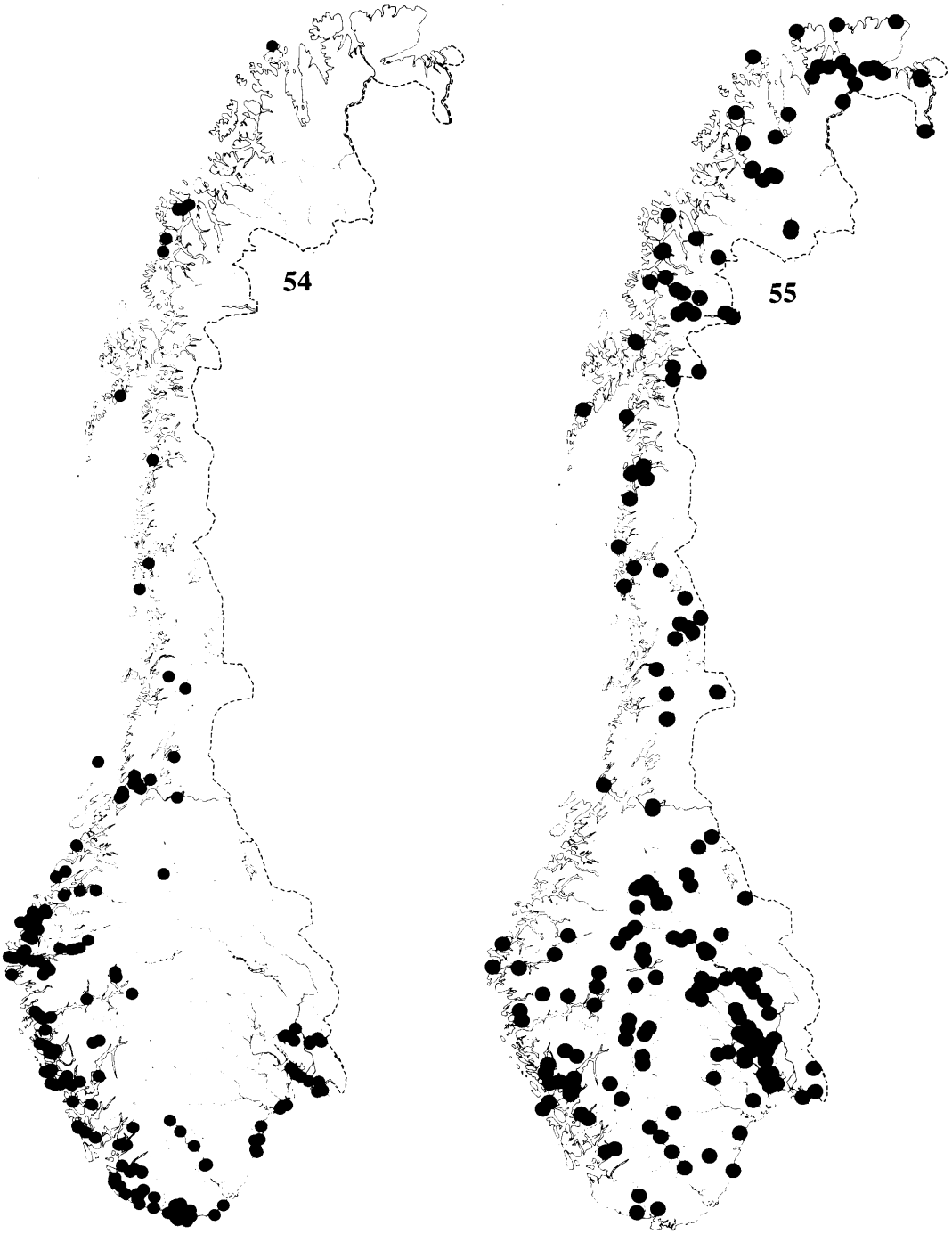




Figs 52–53. *Peltigera lactucifolia*, Rogaland, Holtan-Hartwig 284 (O). Fig. 52. 1.1×. Fig. 53. 1.5×.

Tab. 7. Comparison of the species in the *Peltigera polydactyla* group.

Character	*P. frippii*	*P. lactucifolia*	*P. neckeri*	*P. neopolydactyla*	*P. polydactyla*
Lobes	1.0 (–2.0) cm wide, acute; margins curled and torn	1.0–2.0 (–4.0) cm wide, acute; margins entire	2.0–3.0 (–4.5) cm wide, rounded; margins entire	2.5–4.0 (–6.0) cm wide, rounded; margins entire	1.0–2.0 (–3.5) cm wide, rounded; margins crisped and torn
Veins	usually distinct, pale to brownish black, narrow, weakly anastomosing, weakly pigmented towards the lobe-ends	indistinct, white to ochraceous, broad, anastomosing, unpigmented towards lobe-ends	usually lacking, with a continuous, brownish black pilema which is un-pigmentet towards lobe-ends	greyish brown to brownish black network with few to numerous white interstices, weakly pigmented towards lobe-ends	brownish network with numerous white interstices, distinctly pigmented all the way to the lobe-ends
Rhizines	brownish black, bush-shaped, confluent, in rows	white to pale brown, simple, separate	brownish black, bush-shaped, often confluent	brownish black, simple to bush-shaped, separate	pale brown to brown, simple, often thin and divided, often confluent
Apothecia	unknown	on shortly elongated lobes; discs reddish brown, saddle-shaped, usually up to 6 mm	on shortly elongated lobes; discs black, finger-shape, usually up to 9 mm	on elongated lobes; discs reddish brown, saddle- to finger-shaped, usually up to 9 mm	on elongated lobes; discs reddish brown, finger-shaped, usually up to 9 mm
Spores (µm)	unknown	(53–) 58–*66*–75 (–79)	(41–) 43–*48*–53 (–53)	(50–) 59–*73*–86 (–100)	(48–) 50–*58*–66 (–67)
Terpen-oids	14, 15, 16 (trace), 17, 39	10, 12, 15, 39 (trace)	12, 15, 21, 23, 24, 27 (trace), 28 (trace), 39 (trace)	chemotype I: 10, 12, 15, 20 (trace), 22 (trace), 37, 39 (trace), 41 (trace) chemotype II: 10, 12, 15, 39 (trace) chemotype III: 10, 15, 39 (trace) chemotype IV: 15, 39	10, 12, 15, 20 (trace), 35 (trace), 39 (trace), 41 (trace)



Figs 54–55. Norwegian distribution. Fig. 54. *Peltigera lactucifolia*. Fig. 55. *P. leucophlebia*.

Finnmark (Fig. 54). It is rare north of Oslo, but becomes more common southwards on both sides of the Oslo Fjord. It is common in coastal areas of southern Østfold. It reaches its highest abundance in westernmost Norway. Most localities are situated below 150 m alt., but it has been collected up to about 900 m (Setesdalen and Drivdalen). **Counties**: Østfold–Oslo, Vestfold-Finnmark.

Note. *P. lactucifolia* was reported from Norway for the first time by Krog et al. (1980). The species is mapped for Europe by Vitikainen (1987).

Specimens seen. Øs (O: 16); Ak (O: 2); Os (O: 5); Ve (O: 5); Te (O: 2); AA (O: 14); VA (BG: 1, O: 20); Ro (O: 34); Ho (BG: 41, O: 10); SF (BG: 4, O: 37); MR (O: 19, TRH: 3); ST (BG: 2, O: 7, TRH: 2); NT (BG: 2, O: 2); No (O: 4); Tr (O: 3, TROM: 3); Fi (BG: 2).

Peltigera leucophlebia (Nyl.) Gyelnik

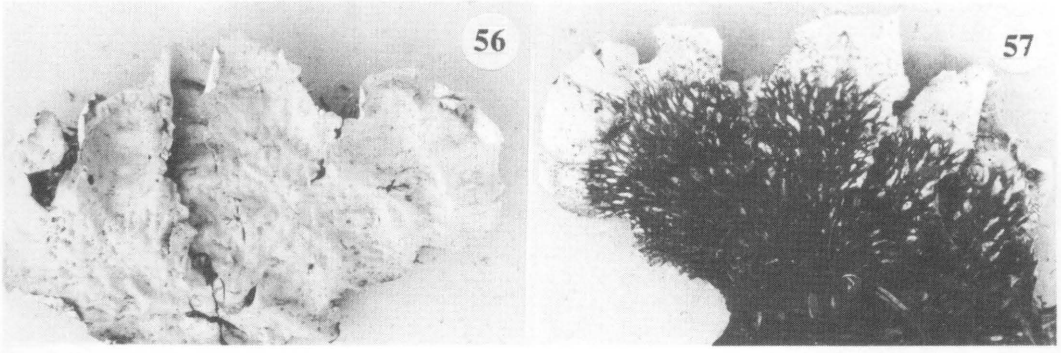
Magyar bot. Lapok 24: 79 (1926).
Peltigera aphthosa v. *leucophlebia* Nyl., Syn. meth. lich. 1: 323 (1860).

Fig. 56–57.

Description. *Thallus* medium sized, up to 25 cm diam., thin and fragile. Lobes 2.0–3.5 cm wide, irregularly incised; margins moderately ascending, curled. Upper side often finely wrinkled and bumpy, greyish green, sometimes with brown patches, hairless towards the center, with pale to light brown more or less erect hairs towards the lobe margins; cephalodia greyish blue or brown, convex, cerebriform, up to 1.2 mm diam. Lower side with a pale marginal zone, in the central part with a network of dark brown to black veins and white, oblong to circular interstices or with a continuous, dark brown to black pilema. Rhizines dark brown to black, bush-shaped, usually separate. Photobiont green algae; colour bright yellowish green. *Apothecia* not uncommon, saddle- to finger-shaped, on elongated lobes; the area beneath the apothecium with patches of cortex; discs reddish brown to black, up to 9 mm diam. Spores acicular, 3-septate, (46–) 50–59–68 (–72) × 5.0-6.0 µm; SD_i=6.0. Pycnidia not seen.

Chemistry. Tenuiorin-aggregate, unidentified terpenoids 7, 9, 14 (trace), and 19.

Variation. The species shows some morphological variation. Specimens from sheltered, moss-rich lowland habitats are usually fragile, thin, foveate and broad-lobed, with a distinct dark brown to black network of veins. Alpine specimens, especially those growing on soil,



Figs 56–57. *Peltigera leucophlebia*, Nord-Trøndelag, Holtan-Hartwig 1495 (O). 0.6×.

often have a thicker thallus and a more diffuse network of veins. The species shows considerable variation in the curliness of the lobe edges. The cephalodia are always convex, cerebriform and show little variation.

Affinities. *Peltigera leucophlebia* is related to *P. aphthosa*, *P. britannica* and *P.* sp. 1; see *P. aphthosa* and *P.* sp. 1 for discussion, and Tab. 6 for the distinguishing characters between the species in the *P. aphthosa* group.

Ecology and distribution. The species mainly grows on rock-faces, soil, and rocks, with a thin and compact moss-cover, and favours habitats with seepage of ground water rich in calcium or other nutrients. It prefers shaded habitats and avoids poor and dry vegetation types. *Peltigera leucophlebia* is common throughout the whole country (Fig. 55). Its vertical distribution ranges from almost sea level to 1700 m alt. **Counties**: Østfold–Finnmark.

Specimens seen. Øs (BG: 1, O: 4); Ak (BG: 3, O: 8, TRH: 2); Os (BG: 1, O: 10, TRH: 2); He (BG: 2, O: 9); Op (BG: 1, O: 31, TRH: 5, TROM); Bu (BG: 2, O: 17); Ve (O: 4); Te (O: 4); AA (O: 6); VA (O: 2); Ro (O: 3); Ho (BG: 11, O: 15); SF (BG: 7 O: 10); MR (O: 2); ST (BG: 2, O: 29, TRH: 4); NT (O: 1, TRH: 3); No (BG: 2, O: 12, TRH: 2 TROM: 9); Tr (BG: 6, O: 10, TROM: 3); Fi (BG: 8, O: 26, TRH: 3).

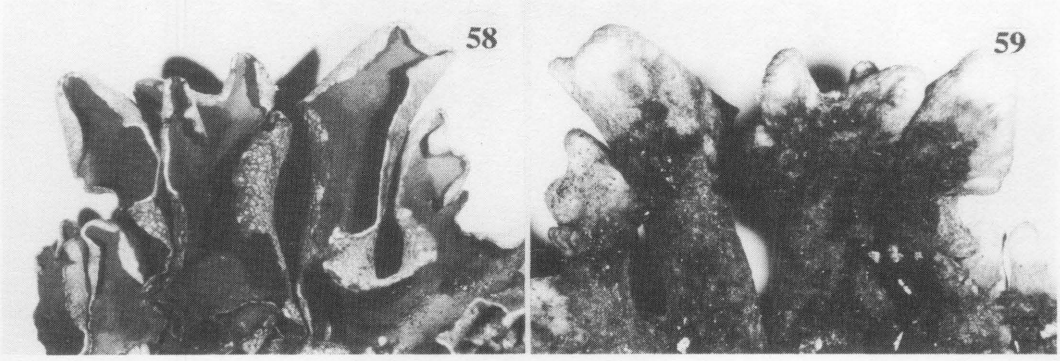
Peltigera malacea (Ach.) Funck

Crypt. Gewächse 33: 5 (1827).
Peltidea malacea Ach., Syn. meth. lich.: 240 (1814).

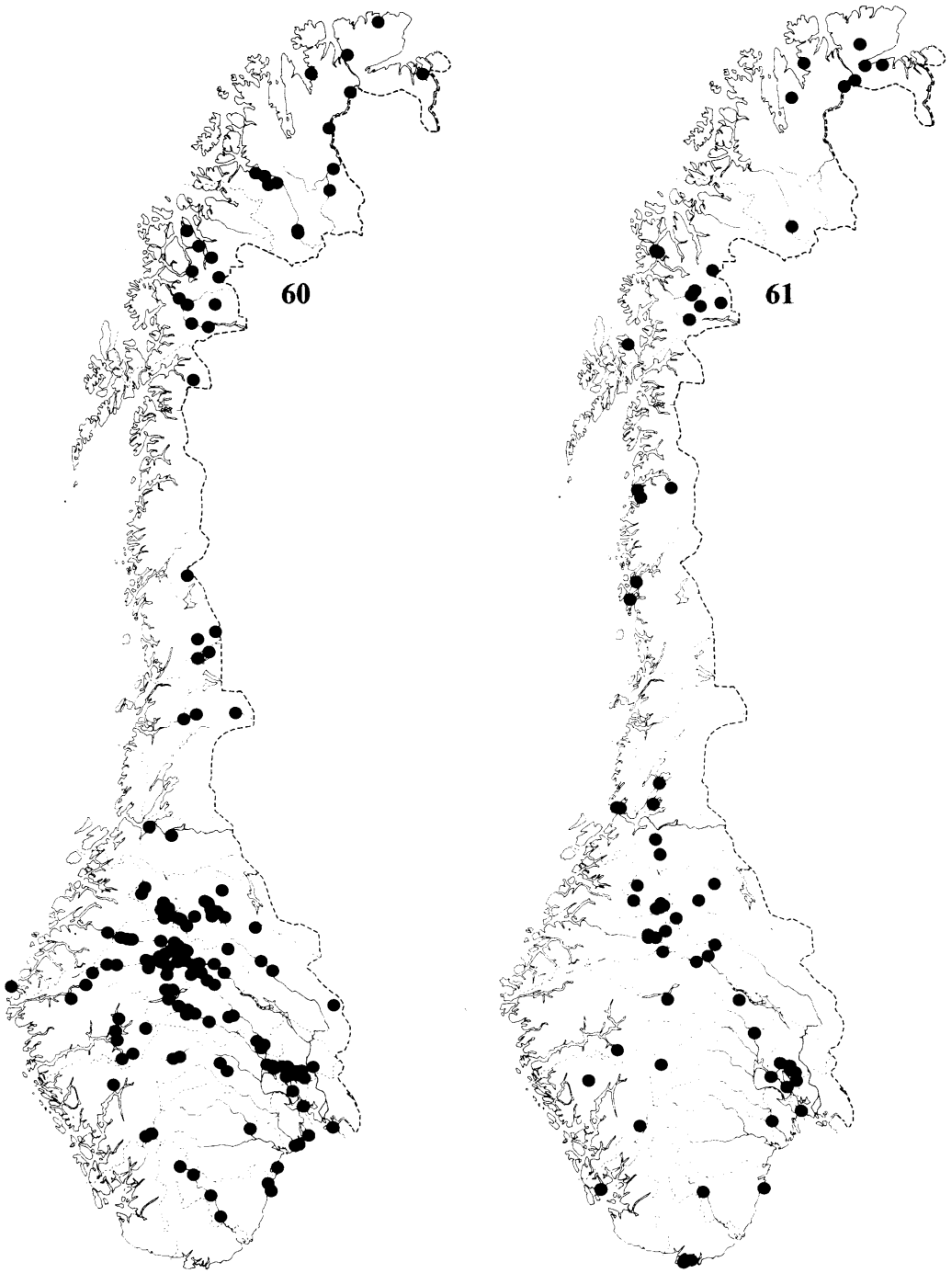
Figs 58–59.

Description. *Thallus* thick, medium sized, up to 30 cm diam., loosely attached to the substrate. Lobes 1.0–1.5 (–2.0) cm wide, imbricate, deeply incised with ascending lateral margins. Upper side greyish brown to grey, mainly dull, with more or less erect hairs towards the lobe margins, sometimes scabrous and pruinose. Lower side brown to dark brown, with a broad pale marginal zone; without veins. Rhizines dark brown to black, short, bush-shaped, unevenly distributed, often confluent and arranged in groups. Photobiont cyanobacteria; colour bluish grey or blue-green to green. *Apothecia* not common, saddle-shaped, on shortly elongated lobes; discs dark reddish brown, up to 7 mm diam. Spores acicular, 3-septate, (48–) 52–*63*–73 (–79) × 4.0–5.0 µm; SD_l=6.8. Pycnidia not seen.

Chemistry. *Chemotype I*: Tenuiorin-aggregate, unidentified terpenoids 9, 19; *chemotype*



Figs 58–59. *Peltigera malacea*, morphotype A, Oppland, Holtan-Hartwig 554 (O). Fig. 58. 2.5×. Fig. 59. 2.8×.



Figs 60–61. Norwegian distribution. Fig. 60. *Peltigera malacea*. Fig. 61. *P. neckeri*.

II: Tenuiorin-aggregate, dolichorrhizin (12), zeorin (15), unidentified terpenoid 14 (trace); *chemotype III*: Tenuiorin-aggregate, unidentified terpenoid 13; *chemotype IV*: Tenuiorin-aggregate, zeorin (15), unidentified terpenoid 39.

Variation. Specimens of *P. malacea* can, according to morphological differences, roughly be divided in 3 groups.

Morphotype A: Thallus medium broad-lobed, medium thick; upper side smooth, densely covered with hairs towards the lobe-ends; cyanobacteria blue-green to green; rarely fertile. - Chemotypes II and III.

Morphotype B: Thallus broad-lobed, thick; upper side scabrous and with hairs towards the lobe-ends; cyanobacteria greyish blue; often fertile. - Chemotypes I and IV.

Morphotype C: Thallus medium broad-lobed, thin to medium thick; upper side smooth and more or less shiny, sparsely provided with hairs towards the lobe-ends; cyanobacteria green; rarely fertile. - Chemotype I.

Affinities. *Peltigera malacea* is apparently most closely related to *P. aphthosa*. The two species have a similar morphology, chemistry, ecology and distribution. The same type of hair is found on the upper side, and both have a continuous pilema. Chemotypes I, II and IV are identical, or very similar to, chemotypes III, IV and II of *P. aphthosa*, respectively, and both species have a boreal-alpine distribution.

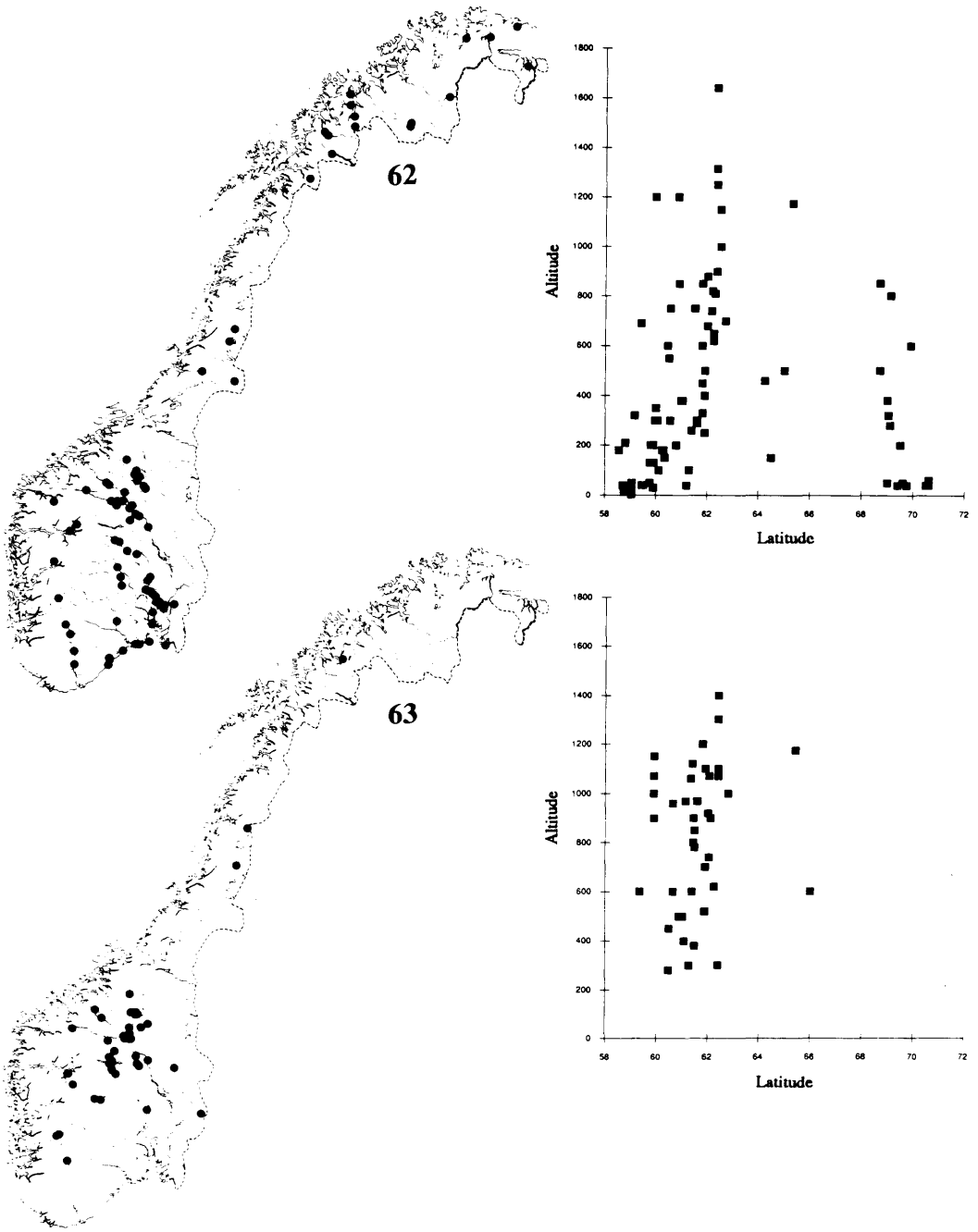
Peltigera malacea resembles the blue-green phototypes of *P. aphthosa* and *P. britannica*. The blue-green phototype of *P. aphthosa* has a bluish grey colour like that found in morphotype B of *P. malacea*, but the species can be distinguished by the upper side which is smooth in *P. aphthosa* and scabrous in morphotype B of *P. malacea*. Chemotype III of *P. aphthosa* (corresponds to chemotype I in *P. malacea*) is only known from a single collection as a blue-green phototype, and chemotype II of *P. aphthosa* (corresponds to chemotype IV in *P. malacea*) is not known as blue-green phototype in Norway.

The blue-green phototype of *P. britannica* and morphotypes A and C of *P. malacea* has a photobiont with a similar greenish colour, and this phototype of *P. britannica* can usually not be distinguished morphologically from *P. malacea*. The blue-green phototype in *P. britannica*, however, is nearly always associated with the green phototype. Chemically, *P. britannica* is different from all the chemotypes of *P. malacea*.

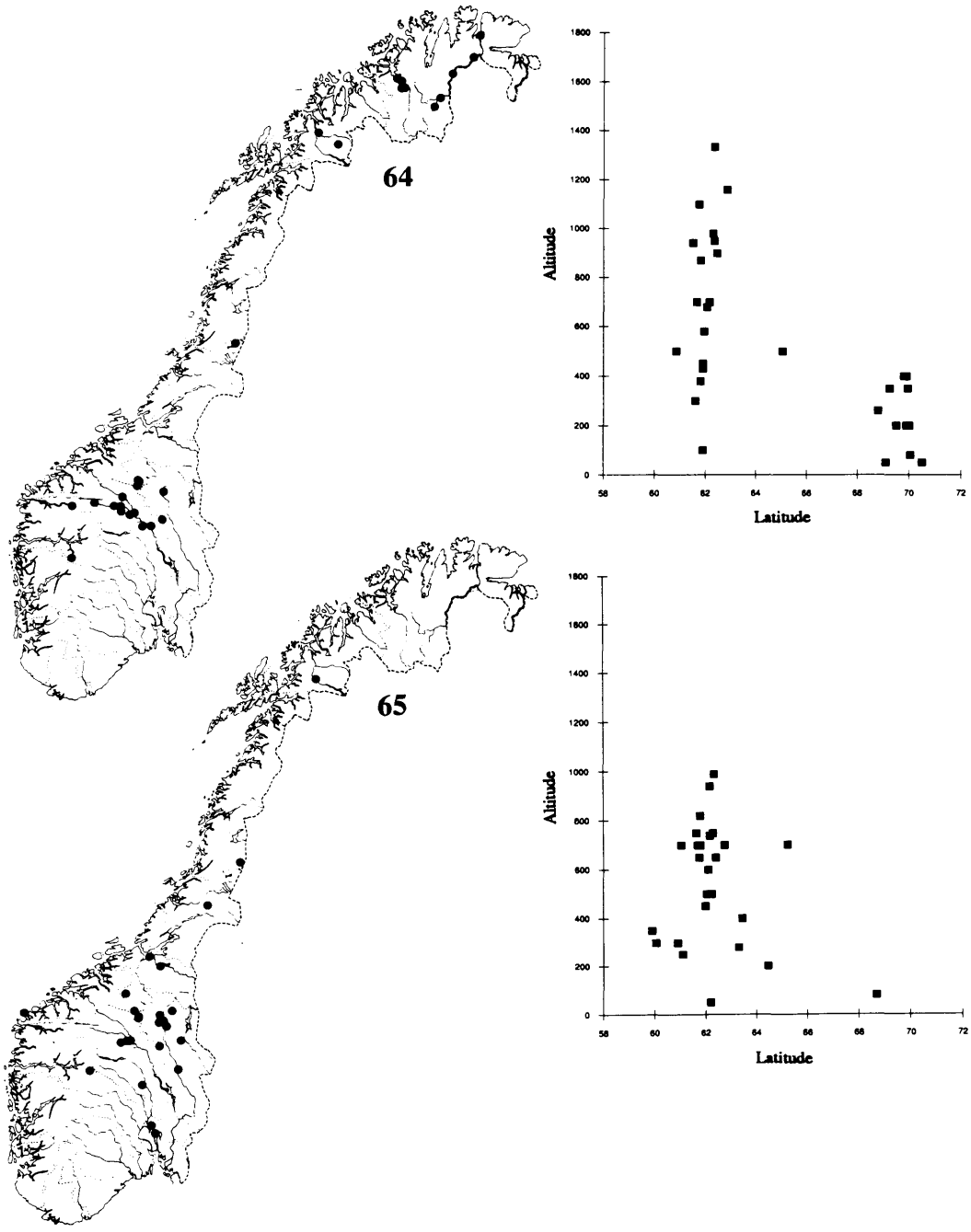
Ecology and distribution. *Peltigera malacea* usually grows on moss- and humus-covered rocks and soil in pine forests, heaths, and subalpine birch forests; often exposed to light and in relatively dry habitats. It rarely occurs on vertical rock faces. The species is common in the inland throughout the country, and has not been found along the coast of westernmost Norway (there is one collection from Stad, but this is probably from an alpine area; cf. Fig. 60). Its vertical distribution ranges from almost sea level to about 1650 m. **Counties**: Østfold–Aust-Agder, Hordaland–Finnmark.

The four chemotypes have somewhat different distribution areas. Chemotype I occurs throughout the whole range of the species in Norway, and is found from almost sea level to 1650 m (Fig. 62). Chemotype II is known from the central parts of southern Norway, two localities in Nord-Trøndelag, and one locality in Troms; it has been collected from 270 to 1400 m (Fig. 63). Chemotype III is known from the northern parts of central southern Norway and the inner parts of Sogn, Nord-Trøndelag, Troms and Finnmark; it has been collected from about sea level to 1340 m (Fig. 64). Chemotype IV is known from the inner parts of southern Norway from Oslo to Nord-Trøndelag, and from inner Sogn, Stadlandet and inner Troms; it has been collected from almost sea level to 1000 m alt. (Fig. 65).

The different morphotypes also differ somewhat with respect to distribution. Morphotype A consists of chemotypes II and III (see above). Morphotype B consists of parts of chemotype



Figs 62–63. Horizontal and vertical distribution of chemotype I and II of *Peltigera malacea*. Fig. 62. Chemotype I. Fig. 63. Chemotype II.



Figs 64–65. Horizontal and vertical distribution of chemotype III and IV of *Peltigera malacea*. Fig. 64. Chemotype III. Fig. 65. Chemotype IV.

I and the entire chemotype IV, and occurs throughout the main part of the distribution of these chemotypes. However, the morphotype is lacking in the lowlands and in the southernmost localities. Morphotype C contains the remaining part of chemotype I; it occurs throughout the whole distribution area of this chemotype. Morphotype C is hence the only morphotype that is common in the lowlands of southern Norway; the other morphotypes are mainly boreal to arctic alpine.

Note. In addition to Norwegian material, I have examined 10 specimens from Central Europe which all proved to belong to chemotype I and morphotype C.

Specimens seen. *Chemotype I*: Øs (O: 4); Ak (O: 8); Os (BG: 2, O: 7, TRH: 1); He (O: 3); Op (BG: 2, O: 20, TRH: 1, TROM: 1); Bu (BG: 1, O: 6); Ve (O: 3); Te (O: 2); AA (O: 6); Ho (BG: 1, O: 2); SF (O: 3); ST (BG: 1, O: 7, TRH: 2); NT (O: 5, TRH: 1); No (TROM: 1); Tr (BG: 4, O: 7); Fi (BG: 1, O: 9, TROM: 1). *Chemotype II*: He (BG: 1, O: 4); Op (O: 17, TRH: 1); Bu (O: 2); AA (O: 1); Ho (O: 3); SF (BG: 1, O: 3); MR (O: 1); ST (O: 5, TRH: 1); No (O: 2); Tr (BG: 1, O: 1). *Chemotype III*: He (O: 1); Op (O: 12); SF (O: 2); ST (O: 3, TRH: 1 TROM: 1); NT (O: 1); Tr (O: 3); Fi (BG: 1, O: 10). *Chemotype IV*: Os (O: 1, He (BG: 2, O: 12, TROM: 1); Op (BG: 2, O: 4, TRH: 1); Bu (O: 1); SF (BG: 1, O: 2); ST (O: 1, TRH: 3); NT (O: 1); No (O: 1); Tr (O: 1).

Peltigera neckeri Hepp ex Müll. Arg.

Mém. Soc. Phys. Hist. nat. Genève 16: 370 (1862).

Fig. 66–67.

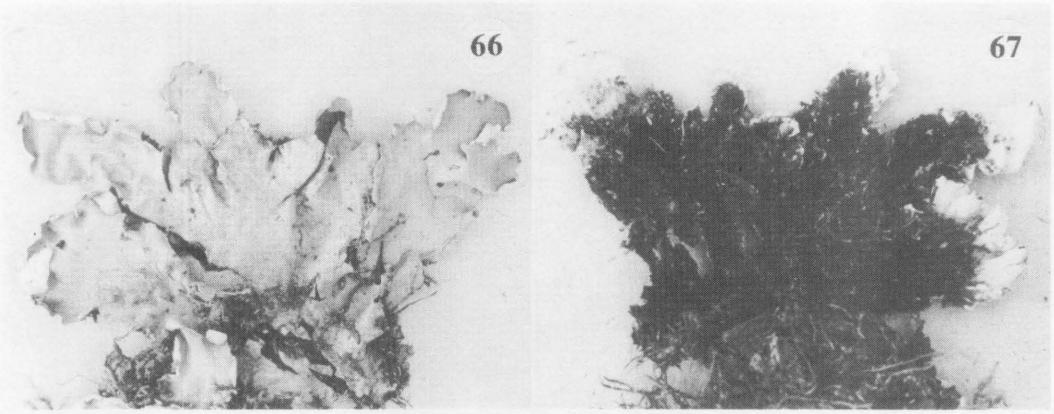
Description. *Thallus* rigid, small to medium sized, up to 20 cm diam. Lobes usually irregularly and deeply incised, 2.0–3.0 (–4.5) cm wide; margins moderately ascending. Upper side greyish blue to brown, shiny, often faintly pruinose towards the lobe-ends. Underside dark brown to black, with a broad, pale zone towards the lobe margins; usually without veins or sometimes with few, plane, broad veins transitional between the dark central zone and the pale marginal zone. Rhizines dark brown to black, bush-shaped, often confluent. Photobiont cyanobacteria; colour green or bluish grey. *Apothecia* not uncommon, finger-shaped, on shortly elongated lobes; discs black, thick, up to 9 mm diam. Spores acicular, 3-septate, (41–) 43–*48*–53 (–53) × 3.5–4.0 µm; SD_i=3.5. Pycnidia not common, attached to the lobe margins; pycnoconidia drop-shaped to foot-shaped, 6–11 × 2–3 µm.

Chemistry. Tenuiorin-aggregate, dolichorrhizin (12), zeorin (15), unidentified terpenoids 21, 23, 24, 27 (trace), 28 (trace), and 39 (trace).

Variations. *Peltigera neckeri* is not a variable species. The colour of the photobiont is usually bluish grey, more rarely green.

Affinities. *Peltigera neckeri* belongs to the *P. polydactyla* group, and is generally easily separated from the other species; see Tab. 7 for distinguishing characters between the species in this group.

The species is characterized by the usually continuous, dark brown to black pilema; some individuals have small, white areas where the pilema is missing. The transition from the dark central area to the pale marginal zone is very distinct. *Peltigera neckeri* is the only species of the *P. polydactyla* group with pure black apothecial discs. It has shorter spores than the other species of the group. Some specimens of morphotype A of *P. neopolydactyla* have an 'overgrown' network of veins, and hence resemble *P. neckeri*. These specimens can be distinguished morphologically by the lower side which has a more gradual transition from the dark central area to the pale marginal zone, and the rhizines that are more separate. In *P. neckeri* the rhizines are often confluent. The photobiont of morphotype A of *P. neopolydactyla*



Figs 66–67. *Peltigera neckeri*, Troms, Holtan-Hartwig 4334 (O). 0.8×.

is usually emerald green or more rarely bluish grey; in *P. neckeri* the photobiont is usually bluish grey or more rarely green. Fertile individuals of *P. neopolydactyla* have reddish brown apothecial discs; in *P. neckeri* the disc is black. *Peltigera neckeri* is chemically distinct from all other Norwegian species of the genus.

Habitually, *P. neckeri* may be confused with *P. elisabethae*; see the treatment of that species for comparison.

Ecology and distribution. *Peltigera neckeri* usually grows on stones and soil on calciferous or otherwise nutrient rich grounds, with a thin moss cover. It often occurs in habitats dominated by short grasses, in roadsides, in or near *Salix*-scrubs in eutrophic vegetation, subalpine meadows, tufts in mires, and on boulders. It is rarely found on vertical rock faces. *Peltigera neckeri* occurs scattered throughout the country, but is apparently rare along the west coast of southern Norway (Fig. 61). Its vertical distribution ranges from almost sea level to 1600 m. **Counties**: Østfold–Vestfold, Aust-Agder–Finnmark.

Note. *Peltigera neckeri* was for the first time recorded from Norway by Krog et al. (1980). It is mapped for Europe by Vitikainen (1987).

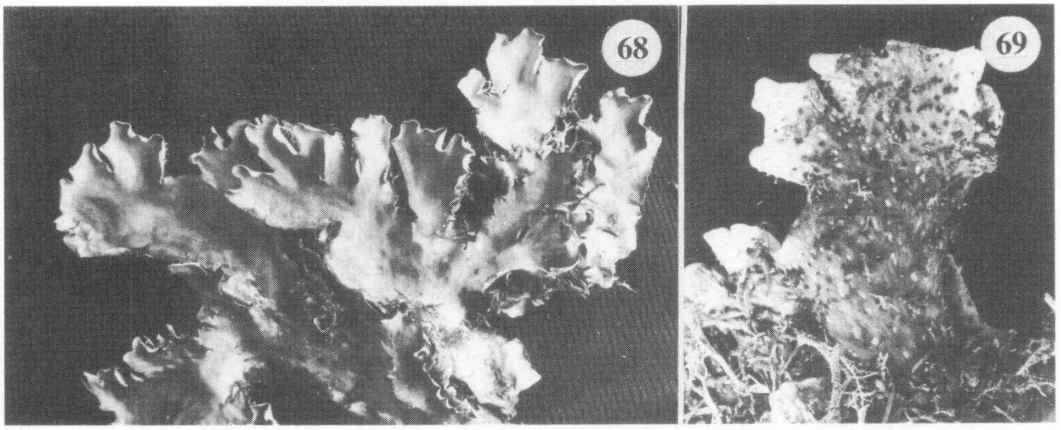
Specimens seen. Øs (O: 1); Ak (O: 2); Os (O: 7, TRH: 1); He (O: 4); Op (O: 13); Bu (O: 2); Ve (O: 1); AA: (O: 2); VA (BG: 1, O: 1); Ro (BG: 1); Ho (BG: 2, O: 2); SF (O: 1); MR (O: 1); ST (BG: 1, O: 14, TRH: 1); NT (BG: 1, TRH: 1); No (O: 3, TROM: 2); Tr (BG: 1, O: 9, TRH: 1); Fi (O: 8).

Peltigera neopolydactyla (Gyelnik) Gyelnik

Revue bryol. lichénol. 5: 71 (1932).
Peltigera polydactyla v. *neopolydactyla* Gyelnik, Magyar Bot. Lapok 31: 46 (1932).

Fig. 68–69.

Description. *Thallus* large, up to 40 cm diam. Lobes rounded, 2.5–4.0 (–6.0) cm wide, margins slightly ascending, rarely involute. Upper side usually grey, greyish blue or greenish grey, more rarely brown; turning emerald green or greyish blue when moist. Lower side usually with a network of greyish brown to dark brown, broad veins and few to numerous white, circular to oblong interstices, with a broad pale marginal zone. Rhizines brown to



Figs 68–69. *Peltigera neopolydactyla*, morphotype A, Buskerud, Holtan-Hartwig 771 (O). Fig. 68. 0.5×. Fig. 69. 0.9×.

brownish black, medium long to long, simple to bush-shaped, separate. Photobiont cyanobacteria; colour greyish blue, blue-green or emerald green. *Apothecia* common, saddle-to finger-shaped, on elongated lobes; discs mainly reddish brown, up to 9 mm diam. Spores acicular, 3-septate, rarely 4-septate, (50–) 59–*73*–86 (–100) × 4.0 µm; SD_l=8.9. Pycnidia not seen.

Chemistry. *Chemotype I*: Tenuiorin-aggregate, peltidactylin (10), dolichorrhizin (12), zeorin (15), hopane-6α,7ß,22-triol (20; trace), unidentified terpenoids 22 (trace), 37, 39 (trace), and 41 (trace); *chemotype II*: Tenuiorin-aggregate, peltidactylin (10), dolichorrhizin (12), zeorin (15), unidentified terpenoid 39 (trace); *chemotype III*: Tenuiorin-aggregate, peltidactylin (10), zeorin (15), unidentified terpenoid 39 (trace) ; *chemotype IV*: Tenuiorin-aggregate, zeorin (15), unidentified terpenoid 39.

Variation. *Peltigera neopolydactyla* is a somewhat variable species. Three different morphotypes may be recognized. Intermediate forms exist, but are rare.

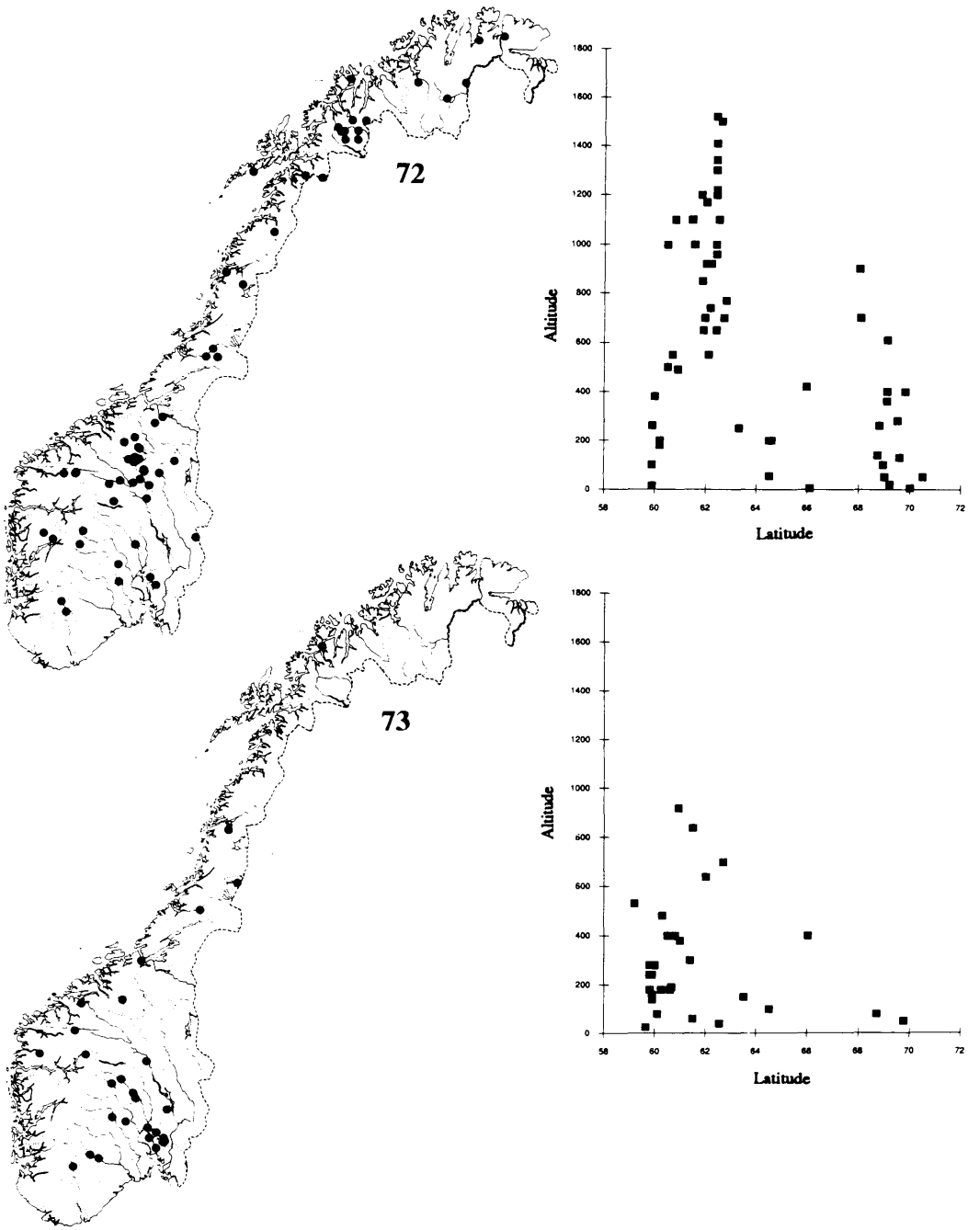
Morphotype A: Thallus thick and rigid, without regular wrinkles; upper side greyish green to grey, emerald green when moist; lower side with a greyish brown to brownish black network of veins (interstices sometimes secondarily overgrown by the veins) and bush-shaped, medium long rhizines; cyanobacteria emerald green. – Chemotype I.

Morphotype B: Thallus thin; upper side greyish blue, with short wrinkles; lower side with a pale brown, less distinct network of veins and long, only slightly branched rhizines; cyanobacteria greyish blue. – Chemotypes II, III, IV.

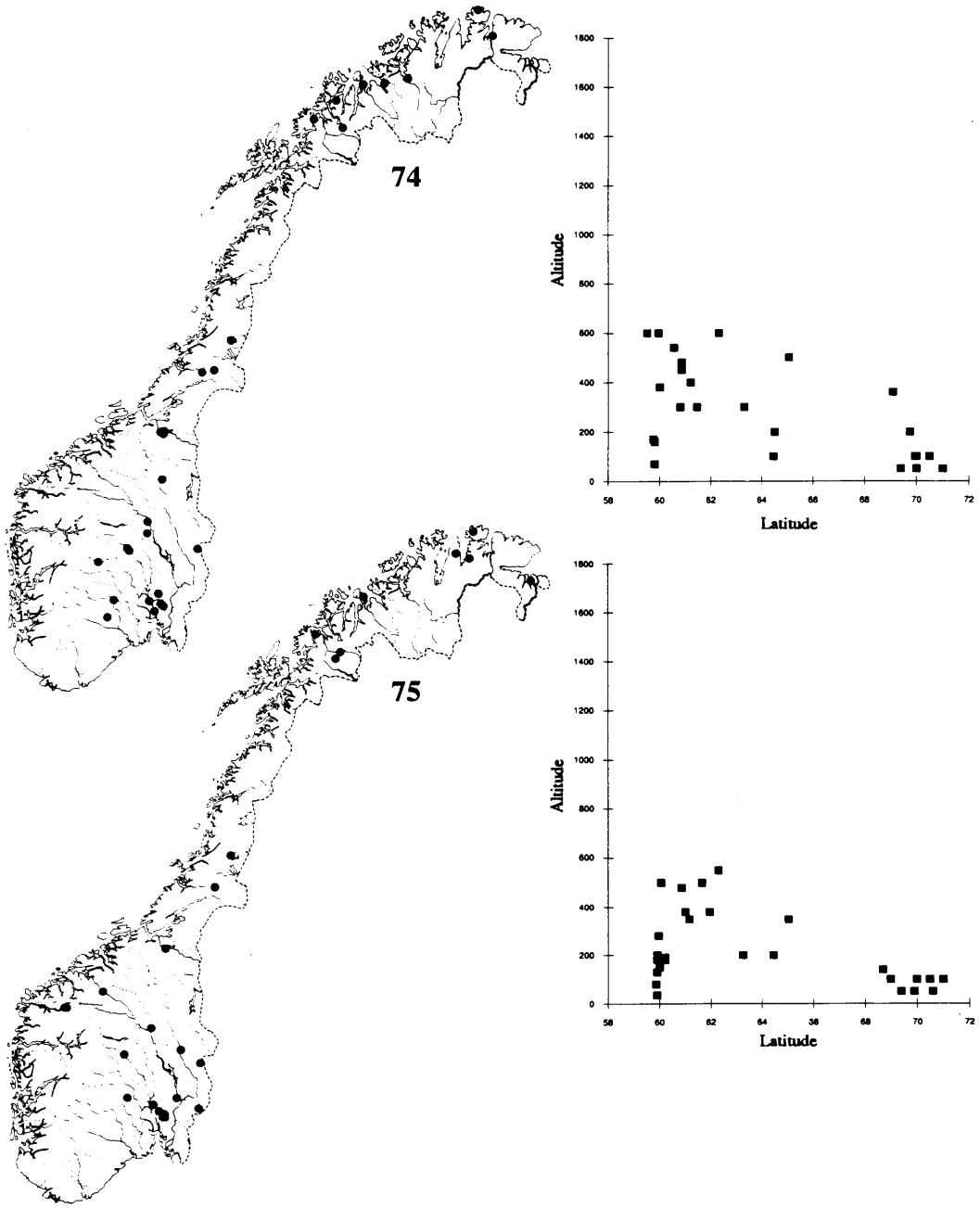
Morphotype C: Thallus medium thick; upper side greyish brown to brown, with long wrinkles; lower side with a medium brown network of veins and thick, bush-shaped to slightly branched, medium long rhizines; cyanobacteria greyish blue or blue-green. – Chemotype IV.

Affinities. *Peltigera neopolydactyla* belongs in the *P. polydactyla* group. See *P. lactucifolia*, *P. neckeri*, and *P. polydactyla* for taxonomic discussions, and Tab. 7 for a comparison of distinguishing characters in the *P. polydactyla* group. *Peltigera neopolydactyla* may also be confused with *P. degenii* (*P. canina* group), but that species may be distinguished by its cylindrical veins which are much narrower than the interstices, and the absence of secondary metabolites. In *P. neopolydactyla* the veins are flat and usually broader than the interstices.

Figs 70–71. Norwegian distribution. Fig. 70. *Peltigera neopolydactyla*. Fig. 71. *P. polydactyla*.



Figs 72–73. Horizontal and vertical distribution of chemotype I and II of *Peltigera neopolydactyla*. Fig. 72. Chemotype I. Fig. 73. Chemotype II.



Figs 74–75. Horizontal and vertical distribution of chemotype III and IV of *Peltigera neopolydactyla*. Fig. 74. Chemotype III. Fig. 75. Chemotype IV.

Ecology and distribution. *Peltigera neopolydactyla* usually grows in sites with a well-developed moss cover; on the ground, on stones and on inclining rock faces. It occurs in spruce forests, mixed coniferous forests, deciduous forests, and subalpine birch forests. Above the timber line, it is often found in moist, gently sloping, grass-dominated vegetation. The species is quite common throughout the whole country, but it has not been recorded from Vest-Agder, Rogaland and the outermost coast from Hordaland to Sør-Trøndelag (Fig. 70). Its vertical distribution ranges from almost sea level to about 1500 m. **Counties**: Akershus–Aust-Agder, Hordaland–Finnmark.

The different chemotypes have slightly different distribution patterns (Figs 72–75) and ecological requirements.

Morphotype A (corresponds to chemotype I) is distributed throughout the whole area of the species in Norway, both horizontally and vertically (Fig. 72). It is most often found on a thick layer of mosses in open mixed coniferous forests or in moist, subalpine or alpine grass-dominated vegetation.

Morphotype B occurs in spruce forests and shaded, humid places in deciduous forests. All records are from below 920 m. It comprises chemotypes II, III and partly IV, all with a wide distribution (Figs 73–75). Chemotype II is rare in northern Norway and chemotype III has not been recorded from westernmost Norway.

Morphotype C consists of chemotype IV (partly) and has scattered occurrences throughout the whole area of the chemotype. It has been collected from almost sea level to about 550 m. It is often found on a thin moss-cover on the ground, usually more strongly exposed to light than the other two morphotypes.

Note. *Peltigera neopolydactyla* was mentioned from Norway for the first time by Tønsberg et al. (1979). A map of its European distribution is found in Vitikainen (1987).

Specimens seen. *Chemotype I*: Os (O: 6); He (O: 7); Op (O: 8); Bu (O: 6); AA (O: 2); Ho (BG: 1, O: 1); SF (O: 3); ST (O: 9, TRH: 7); NT (O: 3); No (BG: 1, O: 4, TROM: 1); Tr (O: 11); Fi (O: 5). *Chemotype II*: Ak (O: 7); Os (O: 2); Op (O: 8); Bu (O: 4); Te (O: 2); AA (O: 1); SF (O: 4); MR (O: 1); ST (O: 2, TRH: 1); NT (O: 1); No (O: 1); Tr (BG: 1, O: 1). *Chemotype III*: Ak (O: 2); Os (O: 1, He (O: 3, TRH: 1); Op (O: 5); Bu (O: 3); Te (O: 2); ST (TRH: 2); NT (O: 4); Tr (BG: 2, O: 4); Fi (BG: 1, O: 1, TRH: 1). *Chemotype IV*: Os (O: 6); He (O: 3); Op (BG: 1, O: 7); SF (O: 1); ST (TRH: 3); NT (O: 2); Tr (O: 5); Fi (O: 4).

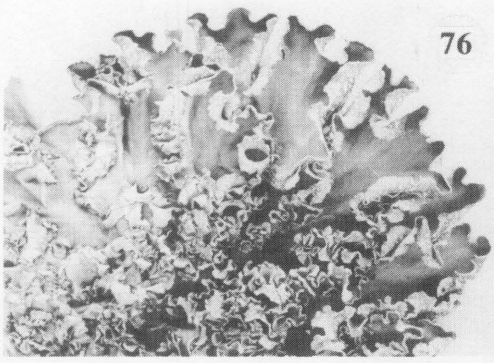
Peltigera polydactyla (Necker) Hoffm.

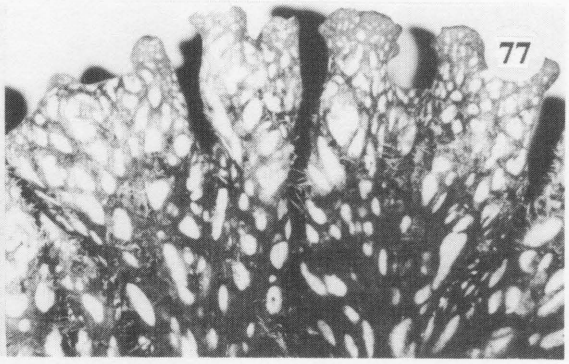
Descr. pl. cl. crypt. 1: 19 (1790).
Lichen polydactyla Necker, Meth. musc.: 85 (1771), *"polydactylon"*.

Fig. 76–77.

Description. *Thallus* medium large, up to 30 cm diam. Lobes 1.0–2.0 (–3.5) cm wide, deeply incised; lateral margins soon becoming crisped and torn (often loosing fragments). Upper side brown, often with a yellowish tinge, more rarely greyish brown, smooth, shiny. Lower side with a network of brown, flat veins and numerous, intensely white, circular to oblong interstices; veins distinctly pigmented all the way to the lobe-ends. Rhizines pale brown to dark brown, thin and divided, often confluent. Photobiont cyanobacteria; colour blue-green. *Apothecia* not uncommon, finger-shaped, on elongated lobes; discs dark brown, up to 9 mm diam. Spores acicular, 3-septate or rarely 5-septate, (48–) 50–58–66 (–67) × 4.0–5.0 µm; SD_i=5.3. Pycnidia not common, attached marginally near the lobe-ends; pycnoconidia narrowly ellipsoid to foot-shaped, 8–11 × 2.0–2.5 µm.

Chemistry. Tenuiorin-aggregate, peltidactylin (10), dolichorrhizin (12), zeorin (15),





Figs 76–77. *Peltigera polydactyla*, Sør-Trøndelag, Holtan-Hartwig 415 (O). Fig. 76. 1.0×. Fig. 77. 2.2×.

hopane-6α,7ß,22-triol (20; trace), hopane-15α,22-diol (35; trace), unidentified terpenoids 39 (trace) and 41 (trace).

Variation. *Peltigera polydactyla* is not a variable species.

Affinities. *Peltigera polydactyla* is related to *P. lactucifolia*, *P. neckeri*, and *P. neopolydactyla*. These taxa have been poorly understood, and by most authors referred to *P. polydactyla* or *P. horizontalis*. The species is recognized by the characteristic yellowish tinge of the brown thallus, its crisped and torn lateral lobe margins, and the flat, yellowish brown network of veins (with purely white interstices) which are pigmented all the way to the lobe-ends. *P. lactucifolia* and *P. neckeri* are separated from *P. polydactyla* by lack of veins and by a pale lower side in the former and a dark lower side in the latter. *Peltigera neopolydactyla* rarely has the yellowish brown upper side characteristic of *P. polydactyla*, the lobe margins are not crisped and torn, and the veins are not as deeply pigmented near the lobe-ends (giving the lower side a paler marginal zone). For a comparison of distinguishing characters between the species in the *P. polydactyla* group, see Tab. 7.

Peltigera polydactyla has often been confused with *P. horizontalis*; see the latter species for a comparison.

Ecology and distribution. *Peltigera polydactyla* usually grows on moss-covered, sandy soils in relatively exposed sites; on the ground, on inclining rock faces, in the inundation zones in brooks and rivers, at lake shores, and in road cuts. The species is common throughout the whole country as far north as Alta, but rarer in westernmost Norway (Fig. 71). *Peltigera polydactyla* rarely grows above 1000 m alt., but is collected up to 1500 m. **Counties**: Østfold–Finnmark.

Note. The European distribution is mapped by Vitikainen (1987).

Specimens seen. Øs (BG: 1, O: 4); Ak (O: 4, TROM: 1); Os (O: 5); He (O: 4, TRH: 1); Op (O: 31, TRH: 1); Bu (BG: 2, O: 10); Ve (O: 1); Te (O: 3); AA (O: 9); VA (O: 1); Ro (O: 2); Ho (BG: 1, O: 3); SF (O: 5); MR (BG: 1, O: 13); ST (O: 7, TRH: 2); NT (O: 3, TRH: 2); No (O: 6); Tr (BG: 2, O: 6, TROM: 4); Fi (O: 1).

Peltigera retifoveata Vitik.

Annls bot. fenn. 22: 296 (1985).

Fig. 78–79.

Description. *Thallus* medium sized, up to 20 cm diam. Lobes 1,5–2,0 (–3.0) cm wide; margins partly descending, partly ascending. Upper side bluish grey to grey, often with brown patches, dull, with appressed hairs towards the margins. Lower side with a white marginal zone, centrally ochraceous to pale dirty brown; veins broad and hairy; interstices often pit-like and often divided by secondary veins. Rhizines pale to dark brown, simple to bush-shaped, long, separate, densely covered with short branches. Photobiont cyanobacteria; colour green or blue-green. *Apothecia* not seen. Pycnidia not seen.

Chemistry. Tenuiorin-aggregate, peltidactylin (10; trace), dolichorrhizin (12), zeorin (15), unidentified terpenoid 24 (trace).

Variation. Moistened thalli show some variation in colour, mainly due to the colour of the photobiont.

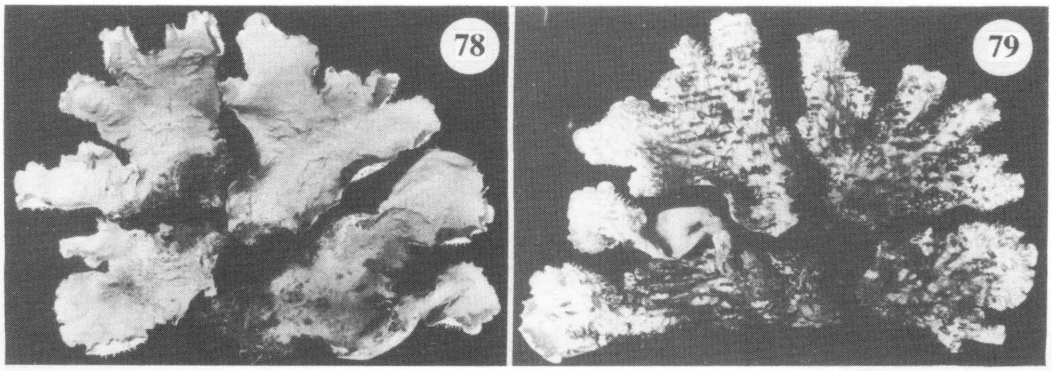
Affinities. *Peltigera retifoveata* may be confused both with *P. canina* and *P. membranacea*, these species may be distinguished by more strongly foveate upper sides, distinctly down-turned margins, narrower veins and absence of secondary substances.

Ecology and distribution. The only known locality is situated in a continental area of southern Norway (Fig. 80) where the species grew on thick moss layers in a subalpine birch forest. **County**: Oppland.

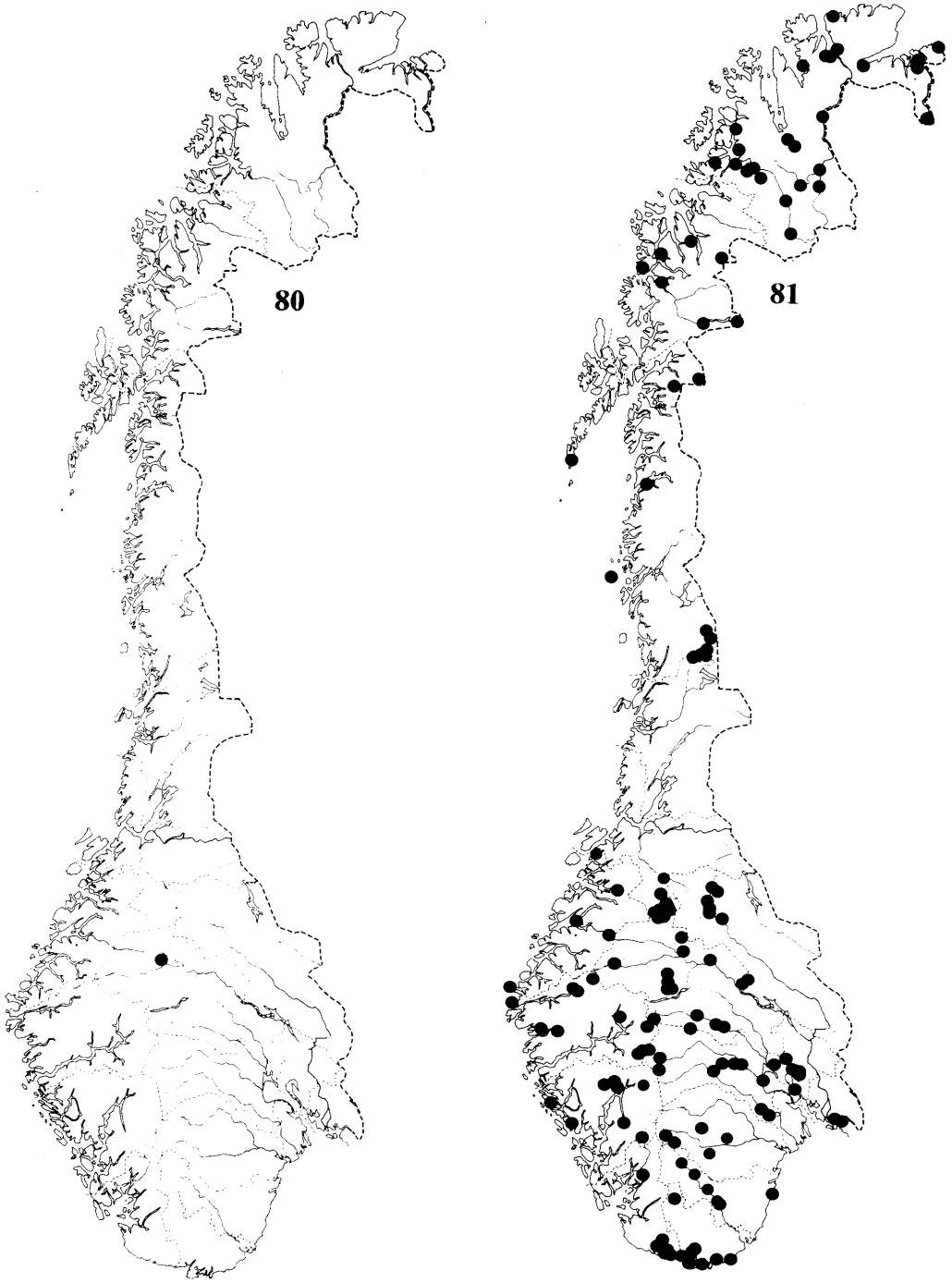
Note. *Peltigera retifoveata* is here reported as new to Norway.

The species was described and mapped by Vitikainen (1985) who reported it to have an essentially disjunct circumboreal range. In Europe it is rare, with two known localities in Finland and one uncertain record from Sweden.

Specimens seen: Norway, Oppland, Vågå, Dalgrovi, in the western part of the valley Jønndalen, *c.* 10 km NW of Vågåmo, 12 August 1989, Holtan-Hartwig 4644; 11 August 1992, Holtan-Hartwig 4671, 4672.



Figs 78–79. *Peltigera retifoveata*, Oppland, Holtan-Hartwig 4672 (O). 0.5×.



Figs 80–81. Norwegian distribution. Fig. 80. *Peltigera retifoveata*. Fig. 81. *P. scabrosa*.

Peltigera scabrosa Th. Fr.

Lich. arct.: 45 (1860).

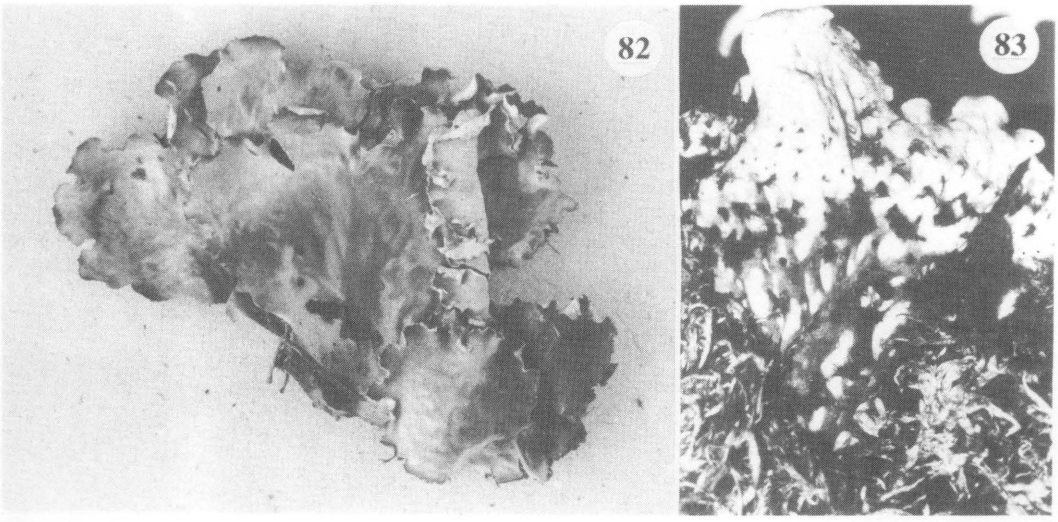
Figs 82–83.

Description. *Thallus* medium large to large, up to 35 cm diam., loosely attached to the substrate. Lobes rounded; margins moderately ascending, 2.0–3.0 (–4.5) cm wide. Upper side grey, greyish brown to yellowish brown, green when moist, dull, scabrous. Lower side with grey to ochraceous brown veins, dark brown to black in the center; interstices white to greyish brown, few to numerous. Rhizines soon becoming pigmented, dark brown to black, thick, shaving-brush shaped, separate, often growing together at their tips and then forming a more or less continuous mat. Photobiont cyanobacteria; colour green. *Apothecia* not common, saddle-shaped, on shortly elongated lobes; discs dark reddish brown, up to 8 mm diam. Spores acicular, 3-septate, (55–) 63–77–92 (–103) × 3.5–4.5 µm; SD_l=9.7. Pycnidia not seen.

Chemistry. *Chemotype I*: Tenuiorin-aggregate, peltidactylin (10), dolichorrhizin (12), zeorin (15; trace), hopane-6α,7ß-22-triol (20), unidentified terpenoids 37 and 41 (trace); *Chemotype II*: Tenuiorin-aggregate, zeorin (15).

Variation. The species is not very variable. Specimens of chemotype II are on the average more broad-lobed than specimens of chemotype I.

Affinities. *Peltigera scabrosa* is closely related to *P. scabrosella*, and differs morphologically from the latter mainly by having broader, more rounded lobes with moderately ascending margins, rhizines which soon become pigmented, and a network of veins that are dark brown to black in the center. *Peltigera scabrosella* has more narrow, acute lobes usually with involute margins, rhizines which are unpigmented when young, and diffuse veins that are pale all the way to the center. In *P. scabrosa*, the thallus is usually loosely attached to the substrate, in *P. scabrosella* the thallus is more firmly attached. The species are also chemically different.



Figs 82–83. *Peltigera scabrosa*. Fig. 82. Oppland, Holtan-Hartwig 516 (O). 0.8×. Fig. 83. Oppland, Holtan-Hartwig 630 (O). 2.2×.

Figs 84–85. Distribution of the chemotypes of *Peltigera scabrosa*. Fig. 84. Chemotype I. Fig. 85. Chemotype II.

Ecology and distribution. The species grows on the ground, on inclining faces of rock outcrops, and on boulders, with well-depeloped moss cover. In the lowlands of southern Norway it often occurs on humid, shaded, rock faces with northerly to easterly aspect in moss-rich deciduous and spruce forests. At higher altitudes and northwards it often grows on sloping ground in humid, moss-rich sites in alpine heath and dwarf-shrub vegetation. *Peltigera scabrosa* is common throughout the country (Fig. 81), and its vertical distribution ranges from almost sea level to 1800 m.

Chemotype I occurs throughout the total distributional area of the species in Norway (Fig. 84), chemotype II is scattered and recorded from southern Norway only (Fig. 85). **Counties**: Østfold–Finnmark.

Note. Preliminary studies suggest that chemotype II has a eastern distribution in Scandinavia.

Specimens seen. *Chemotype I*: Øs (O: 2, TRH: 1)); Ak (O: 1); Os (O: 6, TRH: 2); He (O: 11, TRH: 3, TROM 1); Op (O: 12, TRH: 1, TROM: 1); Bu (O: 16, TRH: 1); Te (O: 3); AA (O: 5); VA (BG: 1, O: 7); Ro

(BG: 1, O: 13); Ho (BG: 5, O: 6, TROM: 1); SF (BG: 1, O: 14); MR (O: 3, TRH: 1); ST (O: 13, TRH: 1); NT (O: 4, TRH: 1); No (BG: 2, O: 4, TROM: 2); Tr (BG: 3, O: 5, TROM: 1); Fi (BG: 7, O: 27, TRH: 1, TROM: 2). *Chemotype II*: Ak (O: 1); He (O: 1, TRH: 1); Bu (O: 1); Te (O: 2); Ho (O: 2); ST (BG: 1); NT (TRH: 1).

Peltigera scabrosella Holt.-Hartw.

Lichenologist 20: 15 (1988).

Fig. 86–87.

Description. *Thallus* small to medium sized, up to 25 cm diam., closely attached to the substrate. Lobes usually distinctly imbricate, acute, relatively short and narrow; margins ascending, somewhat irregularly involute. Upper side grey to greyish brown, scabrous. Lower side pale, veins diffuse, ochraceous brown. Rhizines simple, slender, white to pale brown, usually dissolved into a mess of simple hyphae at the zone of contact with the substrate. Photobiont cyanobacteria; colour blue-green or green. *Apothecia* not uncommon, distally involute or plane, attached to shortly elongated lobes or directly to the main lobes; discs reddish brown, up to 5 mm diam. Spores acicular, 3-septate, (67–) 75–*86*–98 (–101) × 3.5–4.5 µm. Pycnidia not seen.

Chemistry. Tenuiorin-aggregate, dolichorrhizin (12), zeorin (15), unidentified terpenoids 6 and 18.

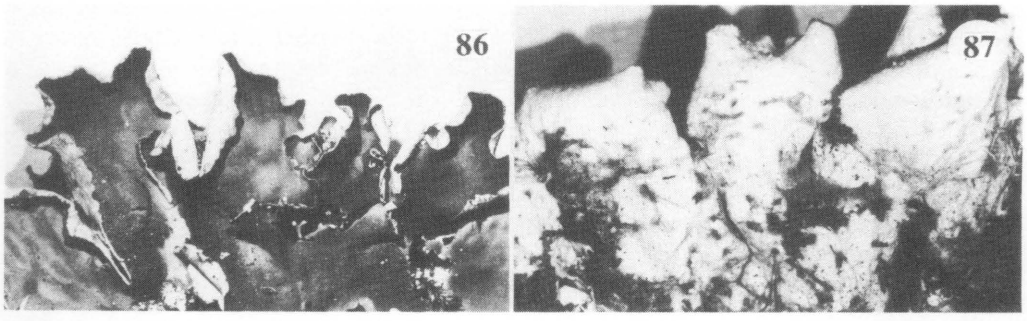
Variation. The species is not very variable. Some specimens are only slightly scabrous.

Affinities. *Peltigera scabrosella* is characterized by narrow and acute lobes with irregularly involute margins, rhizines which are unpigmented when young, and a pilema which is pale all the way to the center of the lower side. Typically, the rhizines tend to dissolve into a mess of simple hyphae, thereby attaching the thallus firmly to the substrate. *Peltigera scabrosella* is closely related to *P. scabrosa*. For comparison, see that species.

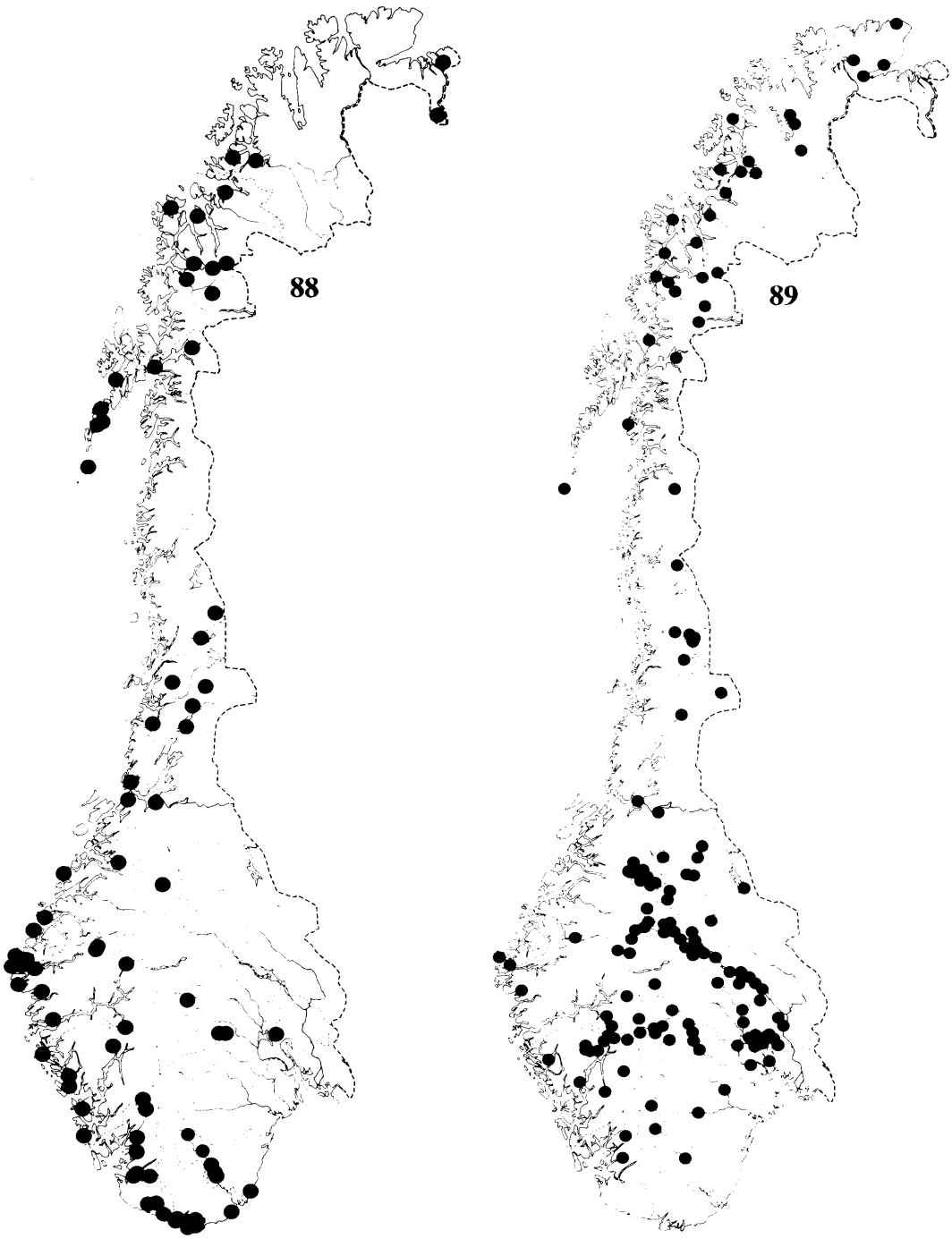
Peltigera scabrosella may habitually be confused with *P. lactucifolia*, but that species is never scabrous.

Ecology and distribution. The species is most frequently found closely attached to mosses on steep to vertical rock walls, seemingly preferring surfaces with trickling water. In the alpine region it may also occur as a muscicole on the ground in snow-beds.

The species is fairly common along the coast, and also occurs in humid localities in the eastern parts of the country (Fig. 88). It is often accompanied by *P. scabrosa*, which generally



Figs 86–87. *Peltigera scabrosella*. Fig. 86. Vest-Agder, Holtan-Hartwig 224 (O). 1.9×. Fig. 87. Sør-Trøndelag, Holtan-Hartwig 422 (O). 3.0×.



Figs 88–89. Norwegian distribution. Fig. 88. *Peltigera scabrosella*. Fig. 89. *Peltigera venosa*.

occupies drier microsites and has a more ubiquitous distribution in Norway. The altitude ranges from about sea-level to 1600 m. **Counties**: Oslo, Oppland, Buskerud, Aust-Agder–Finnmark.

Note. *Peltigera scabrosella* was recently described by Holtan-Hartwig (1988), and is so far known from Norway, Finland, and Southwest Greenland.

Specimens seen. Os (O: 1); Op (O: 1); Bu (O: 4); AA (O: 6); VA (O: 10); Ro (O: 15); Ho (BG: 2, O: 4); SF (BG: 2, O: 15); MR (BG: 1, O: 2, TRH: 1); ST (O: 4); NT (O: 7, TRH: 1); No (O: 9); Tr (BG: 1, O: 13); Fi (O: 4).

Peltigera venosa (L.) Hoffm.

Descr. pl. cl. crypt. 1: 31 (1790).
Lichen venosus L., Sp. Pl. 2: 1148 (1753).

Fig. 90.

Description, green phototype. *Thallus* small, auriculate, up to 3 cm diam., attached to the substrate with a single, thick, basal rhizoid. Upper side greyish green, intensely green when moist, shiny. Lower side with dark brown, broad, more or less fan-shaped veins radiating from the rhizoid; cephalodia bluish grey to brown, spherical to flattened, arranged in groups and attached to the veins. Photobiont green alga; colour bright yellowish green. *Apothecia* almost always present, concave to plane, on non-elongated lobes; discs dark brown, up to 9 mm diam. Spores fusiform, (31–) 32–*38*–44 (–46) × 6.5–7.5 µm; SD_i=4.1. Pycnidia not seen.

Chemistry, green phototype. Tenuiorin-aggregate, unidentified depside d1, peltidactylin (10), hopane-6α,7ß-22-triol (20), unidentified terpenoids 14, 17, 32, 37, 38 (trace) and 41 (trace).

Description, blue-green phototype. *Thallus* up to 1 cm diam, homoiomerous. Lobes ascending, up to 1 mm wide, deeply incised; margin crenulate. Upper and lower sides corticate, medium brown, smooth. Cortex one-layered, usually consisting of pigmented and somewhat thick-walled cells with round to oblong, rather small luminae. The area between the upper and lower cortices consists of a paraplectenchymatic tissue which is composed of cells of variable size, but mostly larger than the cells of the cortices. Photobiont cyanobacteria; colour greenish grey; cells in clusters or more or less evenly distributed throughout the thallus.

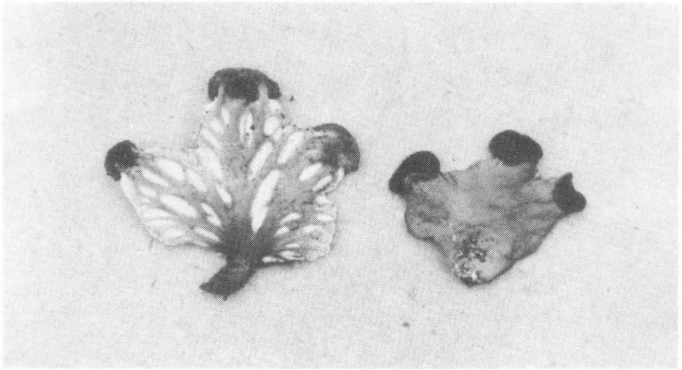


Fig. 90. *Peltigera venosa*, Buskerud, 1971, Elven (O). 1.6×.

Apothecia and pycnidia not seen.

Chemistry, blue-green phototype. No lichen substances.

Variation. None of the two *P. venosa* phototypes shows significant morphological variation.

Affinities. *Peltigera venosa* can hardly be confused with any other *Peltigera* species. The blue-green phototype (Figs 2–3) is habitually similar to a small *Leptogium* species, and has an anatomic structure similar to that of *Leptogium* sect. *Homodium*.

Ecology and distribution. *Peltigera venosa* usually grows on naked or slightly moss-covered soil and gravel, often in shade, and favors habitats with seepage of ground water rich in calcium or other minerals. The species often occurs on protruding ridges, especially in the subalpine zone, in crevices in rock walls, on boulders, at the base of rock walls, in screes, in road-sides, paths, and riverbanks. It prefers habitats where landslides, erosion and solifluction steadily expose new mineral soil and/or retard closure of the vegetation. *Peltigera venosa* occurs scattered throughout the whole country (Fig. 89), and is most common in calcareous areas in the subalpine and low alpine regions. Its vertical distribution ranges from almost sea level to 1650 m. **Counties**: Akershus–Buskerud, Telemark, Aust-Agder, Rogaland-Finnmark.

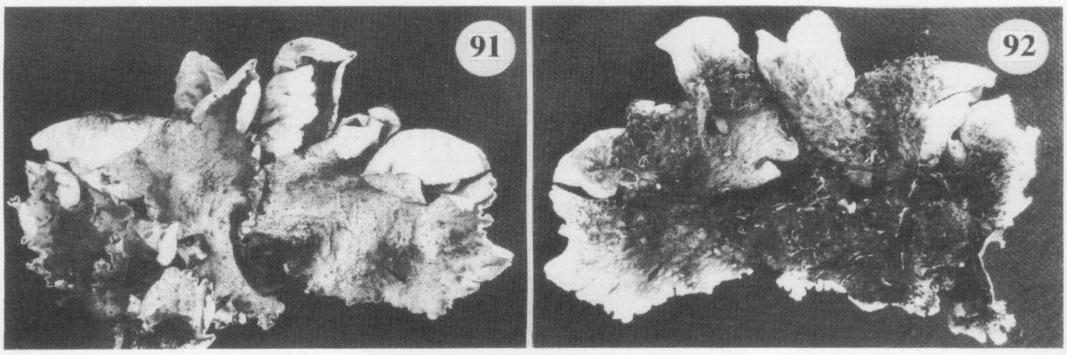
Note. In *P. venosa* the blue-green phototype (Figs 2–3) is relatively common, but never found fertile. A detailed description of the development of phototype pairs in *P. venosa* was given by Ott (1988).

Specimens seen. Ak (O: 5); Os (BG: 1, O: 6); He (BG: 1, O: 10, TROM: 1); Op (BG: 2, O: 24, TRH: 2); Bu (BG: 3, O: 16, TRH: 1); Te (O: 4); AA (O: 2); Ro (O: 2); Ho (BG: 3, O: 14); SF (BG: 1, O: 7); MR (BG: 1); ST (O: 23, TRH: 5); NT (BG: 2, O: 2, TRH: 2); No (BG: 1, O: 6, TRH: 1, TROM: 1); Tr (BG: 5, O: 12); Fi (BG: 4, O: 14).

Peltigera sp. 1

Figs 91–92.

Description. *Thallus* large, up to 30 cm diam. Lobes 3.0–4.0 (–6.0) cm wide, boat-shaped; margins ascending and crenulate. Upper side pale greyish green, often finely furrowed and bumpy, usually with hyaline, appressed to erect hairs to the center; cephalodia usually greyish blue, cerebriform, up to 1.0 mm diam. Lower side with an irregular pattern of depressions, with a more or less continuous, dark brown to black pilema, and with a broad, pale zone towards the margins. Rhizines dark brown to black, bush-shaped, mainly separate.



Figs 91–92. *Peltigera* sp. 1, Sør-Trøndelag, Holtan-Hartwig 2824 (O). 0.4×.

Fig. 93. Norwegian distribution. *Peltigera* sp. 1. (●) chemotype I, (★) chemotype II.

Photobiont green algae; colour bright yellowish green. *Apothecia* not uncommon, saddle- to finger-shaped, on elongated lobes; the area beneath the apothecium with patches of cortex; disc reddish brown, up to 10 mm diam. Spores acicular, 3-septate, (55–) 55–59–62 (–62) × 4.5–5.0 µm; SD_l=2.4. Pycnidia not seen.

Chemistry. *Chemotype I*: Tenuiorin-aggregate, unidentified terpenoids 14 (trace) and 25; *Chemotype II*: Tenuiorin-aggregate, unidentified terpenoids 7, 9, 14 (trace) and 19.

Variation. The species is not variable.

Affinities. *Peltigera* sp. 1 belongs to the *P. aphthosa* group, and differs morphologically from the other species of this group by having broader lobes, hairs occurring over almost the whole upper side of thallus, and an irregular pattern of depressions on the lower side. The hairs differ from those found in the other species of the group by being more strongly appressed and by being thin-walled and more strongly branched. Chemotype I is different from all Norwegian *Peltigera* species, but chemotype II is identical to the single chemotype of *P. leucophlebia*. See Tab. 6 for a comparison of distinguishing characters in the *P. aphthosa* group.

The Asiatic species *P. nigripunctata* Bitter, which also belongs to the *P. aphthosa* group, has a chemistry similar that of chemotype I of *P.* sp. 1, but the apothecia are inclined and the pilema is differentiated to a distinct network of veins.

Ecology and distribution. The species occurs on the ground on well-developed, fluffy moss-covers in subalpine birch forests and in low-alpine dwarf-shrub vegetation. It is so far only known from seven localities in Norway (Fig. 93) and three localities in Alaska (O). **Counties**: Oppland, Sør-Trøndelag, Finnmark.

Note. All examined collections from Alaska belonged to chemotype I. Formal description of this species awaits nomenclatural studies in the *P. aphthosa* group.

Specimens seen. *Chemotype I*: Op (BG: 1); ST (O: 3, TRH: 1, TROM: 1); Fi (BG: 1, O: 2). *Chemotype II*: Fi (TROM: 1).

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