The lichenicolous species of Odontotrema (syn. Lethariicola) (Ascomycota, Ostropales)

Paul DIEDERICH, Mikhail ZHURBENKO and Javier ETAYO

Abstract: The genus Lethariicola is shown to be a synonym of Odontotrema. Fifteen lichenicolous species are recognized: O. bryoriae sp. nov. (on Bryoria), O. cuculare comb. nov. (on Parmeliopsis hyperopta), O. figulinum comb. nov. (on Lecanora polytropa), O. intermedium sp. nov. (on Thannolia), O. lecanorae sp. nov. (on Lecanora), O. melaneliae sp. nov. (on Melanelia), O. ochrolechiae sp. nov. (on Ochrolechia), O. pertusariae sp. nov. (on Pertusaria hymenea), O. rhizocarpicola sp. nov. (on Rhizocarpon), O. santessonii sp. nov. (on Thannolia), O. sipei comb. nov. (on Letharia), O. themnoliae, sp. nov. (on Thannolia), O. sipei comb. nov. (on Letharia), O. thannoliae sp. nov. (on Thannolia), O. sipei comb. nov. (on Letharia), O. thermoliae sp. nov. (on Thannolia), O. sipei comb. nov. (on Letharia), O. thermoliae sp. nov. (on Thannolia), O. sipei comb. nov. (on Letharia), O. thermoliae sp. nov. (on Thannolia), and three undescribed species of Odontotrema, and the name is lectotypified on the species growing on Parmeliopsis. A key is given to all lichenicolous species of Odontotrema and Paralethariicola. © 2002 The British Lichen Society. Published by Elsevier Science Ltd. All rights reserved.

Key words: Lethariicola, lichenicolous fungi, Odontotrema, Ostrapales.

Introduction

The genus Lethariicola Grummann was described for the single species L. sipei Grummann, lichenicolous on Letharia vulpina in the USA (Oregon) (Grummann 1969). Hawksworth & Sherwood (1982) noticed the similarities with the genus Nvl., thev Odontotrema and subsequently included Lethariicola in the family Odontotremataceae, which was treated in more detail later by Sherwood-Pike (1987). Lumbsch & Hawksworth (1990) discovered that two additional names formerly included in Diploschistes belonged to the same genus, and they accepted two species, Lethariicola Lumbsch cucularis (Norman) & D. Hawksw., of which L. sipei was considered to

M. Zhurbenko: Lab. of the Systematics and Geography of Fungi, Komarov Botanical Institute, Russian Academy of Sciences, Professor Popov Str. 2, 197376 St. Petersburg, Russia. be a synonym, and *L. figulina* (Norman) Lumbsch & D. Hawksw. As a continuation of our monographic studies on lichenicolous Ostropales and Helotiales (Calatayud *et al.* 2001; Diederich & Etayo 2000; Etayo & Diederich 2000; Etayo *et al.* 2001), we herewith propose the synonymy of *Lethariicola* with *Odontotrema* and present a worldwide revision of the lichenicolous fungi that belong in the genus.

Material and Methods

The specimens examined are located in the institutional herbaria: AMNH, ASU, B, DUKE, E, GZU, IMI, K, LE, O, TRH and UPS, and in the personal collections of the authors.

The morphological characters (dimensions, colour, etc.) of dry herbarium specimens were studied and illustrated with a dissecting microscope at a magnification of $\times 40$ or $\times 80$. The microscopical examination (including all microscopical measurements) was carried out using hand-cut sections mounted in water. The excipular pigments were studied in water, 5% KOH and concentrated nitric acid. The iodine reaction was tested in Lugol's reagent, without (I) or with (KI) pretreatment with KOH. Spore guttules were examined in KOH. Ascospore measurements, ascoma and pore

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diameter, and ascomatal width are indicated as (minimum–) $\bar{X} - \sigma_x - \bar{X} + \sigma_x$ (-maximum), followed by the number of measurements (*n*); if possible, only mature ascospores were measured; the length/width ratio of ascospores is indicated as l/w and given in the same way, but the extreme values are omitted; in the key, extreme values are also mostly omitted. All measurements of asci and ascospores are based on dead cells.

Results

When Sherwood-Pike (1987) revised the family Odontotremataceae (Ostropales; type genus: Odontotrema), she accepted the monotypic genus Lethariicola as different from Odontotrema on the basis of 'a lichenicolous growth habit and very robust margin with poorly developed periphysoids'. With the discovery of many additional species referable to Lethariicola, some of them with a thin margin, others with a well-developed periphysoid layer, these differences can no longer be sustained, and the distinction between the two genera becomes questionable. We did not study the type species of Odontotrema, as the only known specimen is immature, and as a detailed description together with high quality illustrations were published by Sherwood-Pike (1987). The type species is similar in all aspects to the Lethariicola species studied by us, except that the ascospores are only 1-septate (a condition known from just two lichenicolous species), the ascomata are larger, 0.8-1.0 mm diam., and they are lignicolous. We studied one specimen of Odontotrema (on a leaf of cf. Dryas, intermixed with the type specimen of O. *intermedium*), which is almost indistinguishable from the published description of O. cassiopes (Rostr.) L. Holm, a species confined to dead leaves of Cassiope tetragona. This specimen is clearly congeneric with the lichenicolous species studied by us; it has 3-septate ascospores of $10-12 \times 3.3-4 \,\mu\text{m}$, like O. intermedium, but it is distinguished by smaller ascomata, 240-300 µm diam., and overall smaller dimensions of exciple, hymenium and asci. We conclude that there is no way to distinguish lichenicolous Lethariicola species from non-lichenicolous Odontotrema species, and that the former genus should best be

considered as a synonym of the latter. The genus *Odontotrema*, as circumscribed by Sherwood-Pike (1987), includes four species confined to phanerogam leaves or herbaceous stems, and six species inhabiting wood or bark. We herewith add 15 lichenicolous species, which are all highly specialized, each confined to one host genus. It should be noted that none of the wood- or barkinhabiting species were studied, and that some of them may also be lichenicolous on a lichen with an indistinct, endoxylic thallus.

described The recently monotypic genus Paralethariicola Calatayud, Etayo & Diederich, with one lichenicolous species growing on Aspicilia (Calatayud et al. 2001), is very similar to Odontotrema, but differs in several important characters, which are summarized in the key below. Lichenicolous specimens of Odontotrema have often been confused with Skyttea in the past, but they should easily be recognized using the key to all known lichenicolous ostropalean and helotialean taxa published by Diederich & Etayo (2000).

Species of Odontotrema have a remarkable geographical distribution. Most species are known only from boreal or alpine collections, with the exception of the type species, which curiously grows on wood of *Ilex* aquifolium in Corsica. Most lichenicolous species are from northern countries (Alaska, Iceland, Scotland, Scandinavia, northern Russia), apart from two Lecanora-inhabiting species collected in the Austrian Alps (O. lecanorae and Odontotrema sp. 3), the former also being known from Wyoming, USA, O. sipei from the USA (Oregon) and Canada, Odontotrema sp. 1 from the USA (Oregon) and Sweden, O. bryoriae from the USA (Washington), and O. santessonii, a common species in Iceland and Russia, has also been collected once in Peru at an altitude of c. 4000 m. A yet undescribed species on Usnea (Odontotrema sp. 2) has been collected by us in Papua New Guinea at 2400 m.

Most species do not cause any obvious damage to the host, except that the host cortex over immersed ascomata is eventually elevated or discarded. In *O. pertusariae*, the host thallus is often slightly damaged around 2002

the ascomata, which suggests that this species might be weakly pathogenic.

Odontotrema Nyl.

Mém. Soc. Imp. Sci. Nat. Cherbourg 5: 143 (1858); type: Odontotrema phacidioides Nyl.

Sphaeropezia Sacc., Bot. Centralbl. 18: 253 (1884); type: Sphaeropezia alpina (Sacc.) Sacc. [=Odontotrema alpinum (Sacc.) L. Holm].

Lethariicola Grummann, Sydowia 22: 221 (1969); type: Lethariicola sipei Grummann [=Odontotrema sipei (Grummann) Diederich].

The following description is based on the lichenicolous taxa studied in the present paper, and does not include the non-lichenicolous species, for which descriptions are available in Sherwood-Pike (1987).

Ascomata initially immersed in the host thallus, subspherical to slightly flattened, dark brown or blackish, cleistohymenial, i.e. at first completely closed, the upper, covering part of the exciple much thicker and more strongly pigmented than the lower part, the upper inner ascomatal cavity lined with periphysoids (Fig. 3A & B), opening by a pore, which in some species remains small, punctiform, hiding the disc, in others or in very old ascomata becoming larger and showing the shiny, whitish or greyish disc (Fig. 3C & D); margin of mature ascomata smooth or rugose, often radially fissured. Exciple laterally much thicker than basally, almost paraplectenchymatous, dark vellowish brown in outer lateral parts (pigment extracellular, granulose, dark yellowish brown, with a more or less distinct olivaceous or greyish olivaceous tinge in KOH, orange to red in HNO₃), medium yellowish brown in basal and inner lateral parts, with roundish or ellipsoid lumina and thick gelatinized walls (Fig. 5B), without hairs, or exceptionally with a few scattered, minuscule hair-like projections. Periphysoids usually present and well developed on the inner excipular layer, septate, branched, hyaline, I - and KI-, strongly swollen in KOH (Figs 3E, 5C); in a few species periphysoids indistinct. Hypothecium absent. Subhymenium hyaline, KI-, formed by interwoven hyphae. Hymenium hyaline, I+

briefly blue then red (with the exception of the upper part which is I+ persistently blue), KI+ blue, rarely I - and KI - (and then mentioned in the species descriptions). Epihymenium hyaline. Paraphyses filiform, simple or rarely branched, septate, cells 6-10 µm long, hyaline, 1-2 µm thick, apically often slightly thickened (Figs 1B, 5C). Asci elongate clavate to subcylindrical, outer layer and tholus I – and KI –, or laterally I+ briefly bluish then pale red (hemiamyloid) and KI+ pale blue, but apically I+ pale blue (eu-amyloid) and KI+ pale blue, often covered by an irregular KI+ blue gelatinous sheath, epiplasma KI+ deep orange, tholus c. $3-5 \,\mu\text{m}$ thick when dead, with a distinct ocular chamber, 8-spored (Figs 1B, 8B). Ascospores hyaline, 1-2seriate, usually narrowly ellipsoid, 3-septate, rarely 1- or pluriseptate or submuriform, not or slightly constricted at the septa; cells multi-guttulate; wall generally smooth at maturity; a thin perispore of up to $0.5 \,\mu\text{m}$ sometimes visible in KOH; wall and septa c. $0.5 \,\mu\text{m}$, KI – or KI+ blue (mainly in young ascospores); epiplasma KI - (yellow); septa with a small, not or hardly prominent torus (observed in water, not visible in KOH), and a thin lamella (Fig. 6). Conidiomata unknown.

Observations. Lichenicolous species of Odontotrema are very poor in useful taxonomic characters, and many of the species with 3-septate ascospores were therefore difficult to separate. All these species share similar ascomata, the same excipular structure and pigment, similar periphysoids, paraphyses, asci and ascospores, and only minor differences could be detected. Some of these characters appear to be variable within one species, and the small number of observations available did not allow an appreciation of their real variability. In particular, characters for which each measurement requires sectioning an additional ascoma, such as thickness of exciple or hymenium, or length of asci (which are usually similar in length within one ascoma, but different in other ascomata of a different degree of maturity), could not be adequately

studied in the many species for which no rich and abundant material was available.

One of the most important taxonomic characters proved to be the ascospore dimensions, although substantial differences could also be observed between different specimens of apparently the same species. Statistical analysis of the ascospore dimensions of all species were performed prior to taking decisions about species delimitation, and it was consequently possible to recognize a group of species with shorter ascospores, less than 12 µm in length, and a group with longer ascospores. Further, the length/width (l/w) ratio of the ascospores proved to be relatively constant within one species and allowed the separation from otherwise similar species. The amyloidity of ascospores may represent an additional character helping to distinguish species, but, in our experience, all or just 20% of all the ascospores from different specimens belonging to the same species may react KI+ blue. This reaction might be a function of the age of the ascospores or of the degree of maturity of the entire ascoma, and more studies are needed to understand this variability. In the key information on the KI-reaction is sometimes added, but always as a secondary character to distinguish taxa.

Other very useful characters are the dimensions of the ascomata and the ascomatal pore, and the width of the ascomatal margin. As the ascomatal diameter increases with age, this character is not constant within one species. The ascomatal pore is initially closed, then opens and becomes larger with age, and this character is also not constant within one species. Both ascomatal and pore diameter appear to be correlated with the age of the ascoma. Nevertheless, the measurement of the ascomatal and pore diameter of a large number of ascomata provides valuable information towards the characterization of a species. The width of the ascomatal margin is more difficult to interpret correctly: when young, the margin is half as wide as the ascomatal diameter (as the pore is still absent); later the ascoma opens and the margin either retreats from the centre, but stays more or less horizontal, and thus the width remains quite constant, or it becomes elevated and ultimately almost vertical, at which point it is the thickness rather than the width which is measured in surface view. As there is a continuum between both extremes, in the species descriptions the width of the margin, as observed in surface view, is indicated regardless of whether it is the width of a flat margin or the thickness of an elevated margin. Further characters of the ascomatal margin, such as colour, surface structure (smooth, rugose, striate, etc.), convexity, structure around the pore (dentate, rugose, irregular, etc.), often proved to be difficult to describe accurately, but nevertheless were of some help in characterizing certain species.

In view of the absence of taxonomically useful characters in some species groups, only the discovery of further material will show if our taxonomic treatment is accurate, or if the observed variability results from small adaptations to different hosts. Three entities within the group of species with 3-septate ascospores confined to *Lecanora*, and also those very similar species occurring on *Mycoblastus*, *Ochrolechia*, *Pertusaria* and *Usnea*, will therefore not be described formally, until more material becomes available.

Key to the lichenicolous species of Odontotrema and Paralethariicola

Inner excipular margin with hairs; ascus wall apically with a distinct KI+ blue ring; ascus apex distinctly flattened; paraphyses 2–3(–4) μm diam.; ascospores curved, falcate or slightly helicoid, with more or less pointed ends, 3-septate; on *Aspicilia* Paralethariicola aspiciliae Exciple without hairs; ascus wall without a KI+ blue ring; ascus apex rounded; paraphyses 1–2 μm diam.; ascospores in most species narrowly ellipsoid, with rounded ends, straight, not sigmoid, (1–)3(–8)-septate or submuriform ... 2

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2(1).	Ascospores 1-septate (exceptionally 2-septate), $2 \cdot 5 - 3 \cdot 5 \mu m$ wide $\dots \dots 3$ Ascospores with several septa (but sometimes intermixed with immature 0-2-septate ascospores), or submuriform, at least $3 \mu m$ wide $\dots \dots \dots 4$
3(2).	Ascospores $11\cdot0-14\cdot9 \times 2\cdot5-3\cdot2 \mu m$, l/w ratio $3\cdot8-5\cdot4$; ascomata $150-200 \mu m$, immersed to erumpent; lateral exciple <i>c</i> . $35 \mu m$; on <i>Thamnolia</i> O. thamnoliae Ascospores shorter, $7\cdot6-8\cdot8 \times 3\cdot1-3\cdot5 \mu m$, l/w ratio $2\cdot2-2\cdot7$; ascomata much larger, $310-410 \mu m$, superficial from an early stage; lateral exciple $75-85 \mu m$; on <i>Bryoria</i> O. bryoriae
4(2).	Ascospores $(3-)6-8(-9)$ -trans-septate, occasionally with 1–3 longitudinal or oblique septa, $15\cdot4-20\cdot4 \times 3\cdot6-4\cdot6 \mu m$, l/w ratio $3\cdot6-5\cdot2$; asci mostly $40-50 \mu m$; ascomata 280–380 μm ; on <i>Thamnolia</i> O. santessonii Ascospores shorter, 3–5-trans-septate, occasionally with 1–2 longitudinal or oblique septa, l/w ratio<3.5; asci usually over 50 $\mu m \log$ 5
5(4).	Ascospores submuriform, with 3–5 transverse and 1–2 longitudinal or oblique septa, $12\cdot3-14\cdot6 \times 6\cdot2-7\cdot4 \mu m$; on <i>Lecanora polytropa</i> O. figulinum Ascospores 3-trans-septate, exceptionally with one longitudinal septum, $3\cdot5-6 \mu m$ wide
6(5).	As cospores mostly $9-12 \mu m \log$; if up to $12.5 \mu m$, then less than $4.5 \mu m$ wide .
	As cospores at least $12 \mu\text{m}$ long and $4.5 \mu\text{m}$ wide
7(6).	Ascospores narrowly ellipsoid, $10.6-12.5 \times 3.4-4.1 \mu\text{m}$, I/w ratio $2.7-3.5$; on <i>Thamnolia</i> O. intermedium Ascospores broader, $9-12 \times 4.2-5.6 \mu\text{m}$, I/w ratio $1.8-2.6 \ldots \ldots 8$
8(7).	Ascospores broadly ellipsoid, $9\cdot 3-11\cdot 1 \times 4\cdot 8-5\cdot 6 \mu m$, l/w ratio $1\cdot 8-2\cdot 2$; hymenium KI+ blue; periphysoids indistinct; ascomatal margin striate, with numerous, narrow, radial fissures; ascomata $155-245 \mu m$; pore $30-60 \mu m$; margin $60-100 \mu m$; on <i>Rhizocarpon</i>
9(6).	Ascomata 350–640 μ m; lateral exciple 70–140 μ m thick 10 Ascomata 150–350 μ m; lateral exciple in most species less than 70 μ m 11
10(9).	Ascomata $(350-)360-480(-590) \mu m$; pore very small, often closed, $0-40(-105) \mu m$; ascospores $12 \cdot 2 - 13 \cdot 8 \times 4 \cdot 5 - 5 \cdot 0 \mu m$, l/w ratio $2 \cdot 6 - 2 \cdot 9$; on <i>Letharia</i> O. sipei Ascomata larger, $(450-)470-590(-640) \mu m$; pore larger, usually opened, $(0-)25-105(-160) \mu m$; ascospores longer, $14 \cdot 5 - 15 \cdot 9 \times 4 \cdot 7 - 5 \cdot 2 \mu m$, l/w ratio $2 \cdot 9 - 3 \cdot 3$; on <i>Parmeliopsis</i>
11(9).	Ascomata almost permanently immersed in gall-like swellings of the host of $170-350 \ \mu\text{m}$ diam., not exposed; lateral exciple $100-115 \ \mu\text{m}$; pore usually very small, $0-20 \ \mu\text{m}$, exceptionally larger; ascospores with a thin, hyaline, granulose ornamentation, relatively broad, $(5\cdot4-)5\cdot5-6\cdot1(-6\cdot3) \ \mu\text{m}$ wide, l/w ratio $2\cdot2-2\cdot5$; on <i>Melanelia</i> O. melaneliae Ascomata generally exposed at maturity; lateral exciple mostly less than 75 $\ \mu\text{m}$ (but up to 140 $\ \mu\text{m}$ in <i>O. ochrolechiae</i>); pore often larger; ascospores smooth-walled, often narrower, mostly less than $5\cdot5 \ \mu\text{m}$ wide (but up to 6 $\ \mu\text{m}$ in <i>Odontotrema</i> sp. 3), l/w ratio often larger 12

12(11).	Ascomatal pore relatively small compared to the ascomatal diameter, for most ascomata: $x>3y+110$ (where x=ascoma diam. and y=pore diam. in μ m); ascomata 230–330 μ m, those under 270 μ m with a pore of 0–40 μ m; exciple laterally 50–140 μ m; on <i>Ochrolechia</i> O. ochrolechiae Ascomatal pore relatively large, for most ascomata: $x<3y+110$ 13
13(12).	Ascomatal margin in surface view more or less flat, often slightly incurved towards the pore; ascomata (180–)210–290(–350) µm; pore (0–)20–80(–140) µm; on <i>Lecanora</i>
14(13).	Pore (0-)30-50(-60) μm; lateral exciple 35-65 μm; on Mycoblastus Odontotrema sp. 1 Pore (20-)35-110(-150) μm, c. 50% over 60 μm; lateral exciple 50-70 μm 15
15(14).	Margin of mature ascomata (surface view) 60–80 μm thick; hymenium KI+ blue; periphysoid layer poorly developed; perispore absent; on <i>Pertusaria hymenea</i>

Odontotrema bryoriae Diederich & Etayo sp. nov.

Odontotrema lichenicola in thallo Bryoriae vigens, insignis ascomatibus $310-410 \mu m$, poro $10-70 \mu m$, margine $140-180 \mu m$, ascosporis non amyloideis 1-septatis $7.6-8.8 \times 3.1-3.5 \mu m$.

Typus: USA, Washington, 25 mi W of Yakima, on *Bryoria fremontii*, 8 July 1986, *Rossman* (IMI 308462—holotypus).

(Figs 1, 2A)

Ascomata superficial from the beginning, roundish, subspherical, margin dark brown to blackish, smooth, more or less horizontal at maturity, sometimes slightly incurved around the pore, with some radial fissures, (275-) $310-410(-440) \mu m$; pore (0-)10-70(-120) μ m; margin (110–)140–180(–200) μ m (*n*= 26). Exciple laterally 75-85 µm, basally 25-60 µm thick, with lumina of 6-10 µm. Periphysoids up to 20 µm. Subhymenium 8-13 µm. Hymenium 50-70 µm. Paraphyses 1-1.5 µm thick, apically slightly swollen. Asci 40-60 \times 5-6 µm. Ascospores uniseriate, ellipsoid, with more or less pointed ends, 1-septate (exceptionally 2-septate), $(7\cdot4-)7\cdot6-8\cdot8(-9\cdot2)\times$ $(2\cdot 8-)3\cdot 1-3\cdot 5(-4\cdot 0) \ \mu m; \ l/w \ ratio \ 2\cdot 2-2\cdot 7$ (n=27); no perispore visible in KOH; wall and septa KI -.

Host. Bryoria fremontii (thallus).

Distribution. Known only from the type locality in the USA (Washington).

Observations. The type specimen of this species was included by Lumbsch & Hawksworth (1990)under Lethariicola cucularis. These authors stated that it was growing on Letharia vulpina intermixed with Bryoria fremontii, but that it does not colonize the Bryoria thallus. However, a careful examination showed that no Letharia is present in the collection received on loan from IMI, and that it grows entirely on Bryoria. The host is in a very poor condition, as it had apparently been lying on the ground for a long time, with most thalli dead and blackish, and many attacked by whitish moulds. Nevertheless the numerous ascomata are all in a good condition and fully mature, and the specimen can thus serve as a type. Lumbsch & Hawksworth (1990) obviously did not notice that the ascospores are 1-septate in this species and much smaller than those of O. cuculare, which were recorded as $14.5-17 \times 5-5.5 \,\mu\text{m}$ by these authors.

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FIG. 1. Odontotrema bryoriae (holotypus). A, habitus; B, asci and paraphyses (in H_2O). Scales: A=100 µm; B=10 µm.

Odontotrema bryoriae is easily distinguished from O. thamnoliae, the only other lichenicolous species of the genus with 1-septate ascospores, by the much shorter ascospores and larger ascomata. The two non-lichenicolous species of the genus with the same ascospore septation and ascomata less than 500 µm described by Sherwood-Pike (1987), O. oregonense Sherwood and O. phacidiellum Nyl., both have ascospores longer than 10 µm.

Odontotrema cuculare (Norman) Diederich comb. nov.

Limboria cucularis Norman, Öfvers. Kgl. Vetensk. Akad. Förh. 7: 804 (1870).—Lethariicola cucularis (Norman) Lumbsch & D. Hawksw., Bibl. Lichenol. 38: 327 (1990).—Diploschistes cucularis (Norman) Zahlbr., Cat. Lich. Univ. 2: 662 (1924); type: Norway, Alten, Melladal, on Parmeliopsis hyperopta, 1869, Norman (O lectotype: ascomata on P. hyperopta!, designated here).

Ascomata at first immersed in the host thallus, soon erumpent, roundish, margin

dark brown to blackish, smooth, $(450-)470-590(-640) \mu m$; pore $(0-)25-105(-160) \mu m$; margin $(200-)200-260(-300) \mu m$ (n=10). *Exciple* laterally 85–140 µm, basally 26– 35 µm thick, with lumina of 5–11 µm. Periphysoids up to 15 µm. Subhymenium 5–9 µm. Hymenium 75–90 µm. Paraphyses 1.5–2 µm thick, apically not distinctly swollen. Asci 80–90 × 5–7 µm. Ascospores ellipsoid to narrowly ellipsoid, 3-septate, (13.5-)14.5- $15.9(-17.0) \times (4.5-)4.7-5.2(-5.5) µm, 1/w$ ratio 2.9–3.3 (n=30); no perispore visible in KOH; wall and septa KI – .

Host. Parmeliopsis hyperopta (thallus).

Distribution. Known only from the type locality in Norway.

Observations. When Lumbsch & Hawksworth (1990) revised the genus Lethariicola, they adopted a rather wide species concept and included under the name L. cucularis, the type specimen of Odontotrema sipei, and even the type of O. bryoriae, which is distinguished by very small, 1-septate ascospores and much smaller ascomata. Furthermore, an examination of the type specimen of O. cuculare revealed that it consists of two distinct species, one with particularly large ascomata growing on Parmeliopsis, and the other with smaller ascomata growing on a sterile Ochrolechia. Although most of the ascomata are on Ochrolechia, we lectotypify the name O. cuculare here on the ascomata on Parmeliopsis, as those on Ochrolechia are mostly immature, almost completely closed, and often with no ascospores yet formed. We prefer to select another collection in a much better condition as the type of O. ochrolechiae. Furthermore, this is in agreement with the statement by Lumbsch and Hawksworth (1990) that the type of O. cuculare is growing on Parmeliopsis. It is not clear to us to which of the two host species the description and illustrations of the type of O. cuculare given by Lumbsch & Hawksworth (1990) refer. The large ascomata up to 700 µm and also the relatively long ascospores recorded in their



FIG. 2. Ascospores of some Odontotrema species (in H₂O). A, O. bryoriae (holotypus); B, O. intermedium (holotypus); C, O. lecanorae (holotypus); D, O. melaneliae (holotypus); E, O. ochrolechiae (holotypus); F, O. sipei (holotypus); G, Odontotrema sp. 1 (Coppins 6038, on Mycoblastus affinis); H, Odontotrema sp. 3 (Hafellner 23693, on Lecanora). Scale=10 μm.

description clearly refer to *O. cuculare*; the photographs, however, most probably represent *O. ochrolechiae*.

Odontotrema cuculare has the largest ascomata of all lichenicolous species of the genus. The differences from O. sipei, the only other lichenicolous species with large ascomata are given in the key.

Odontotrema figulinum (Norman) Diederich comb. nov.

Limboria figulina Norman, Öfvers. Kgl. Vetensk. Akad. Förh. 7: 804 (1870).—Lethariicola figulina (Norman) Lumbsch & D. Hawksw., Bibl. Lichenol. **38**: 331 (1990).—Diploschistes figulinus (Norman) Zahlbr., Cat. Lich. Univ. **2**: 662 (1924); type: Norway, Tromsö, on Lecanora polytropa, 1869, Norman (O—lecto- and isolectotype!, designated by Lumbsch & Hawksworth 1990).

(Fig. 7)

Ascomata partly immersed in the host thallus or hymenium, soon becoming superficial, roundish, black, smooth, not fissured, deeply urceolate, $(210-)250-360(-440) \mu m$ diam.; pore $(0-)20-90(-120) \mu m$; margin incurved towards the pore, (90-)110-140 $(-160) \mu m$ (n=25); disc whitish. Exciple laterally 40–65 μm , basally 11–24 μm thick, with lumina of 7–20 μm . Periphysoids $6-15 \times 1-3 \mu m$. Subhymenium 5–7 μm . Hymenium 60–90 μm . Paraphyses 1·3–1·5 μm thick, apically not or slightly thickened. Asci 68–82 × 11–15 µm. Ascospores ellipsoid, submuriform, with 3–5 transverse and 1–2 longitudinal or oblique septa, (12.0-)12.3- $14.6(-17.0) \times (5.8-)6.2-7.4(-8.7)$ µm, 1/w ratio 1.8-2.2 (n=56); perispore not observed; wall and septa I – , KI – .

Host. Lecanora polytropa, thallus and apothecia (margin and disc).

Distribution. Known only from the type locality in Norway.

Observations. Odontotrema figulinum is distinguished from all other species of the genus by its much broader, submuriform ascospores with 3–5 transverse and 1–2 longitudinal septa.

Odontotrema intermedium Diederich, Zhurb. & Etayo sp. nov.

Odontotrema lichenicola in thallo Thamnoliae vigens, insignis ascomatibus 320–460 μ m, poro 30–100 μ m, margine 130–180 μ m, ascosporis non amyloideis 3-septatis 10·6–12·5 × 3·4–4·1 μ m.

Typus: USA, NW Alaska, c. 140 km E of Kotzebue, middle Kobuk River by its left bank, Kobuk Valley Wilderness, NW margin of the Great Kobuk Sand Dunes, 67°05'N, 159°00'W, alt. 45 m, depression forested by Salix spp. and Picea glauca, on open hillock amongst Dryas integrifolia, lichens and mosses, on Thamnolia vermicularis, 13 August 2000, Zhurbenko 2002

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00218 (LE-holotypus; hb. Diederich, hb. Etayo-isotypi).

(Figs 2B, 3)

Ascomata initially immersed in the host and completely covered by a thin whitish layer of the host thallus, then erumpent, with thallus cover breaking into small pieces or splitting radially, almost mosaic- or star-like, finally superficial, with thallus remnants eventually disappearing, roundish, margin blackish, occasionally cracked around the pore, (225-)320-460(-540) µm diam.; pore (0-)30-100(-160) µm; margin (110-) $130-180(-210) \ \mu m \ (n=55)$. Exciple laterally 100–110 µm, basally 14–35 µm thick, with lumina of 4-7 µm. Periphysoids up to 28 µm; small, hvaline to brownish hairs up to 4 um long and 2 µm thick, occasionally present on the excipular margin, probably homologous to periphysoids. Subhymenium 10-15 µm. 60–70 µm. Paraphyses Hymenium 1.5-2 µm thick, apically up to 2.5 µm. Asci $60-75 \times 6.5-7.5 \,\mu\text{m}$. Ascospores narrowly 3-septate, (10.0-)10.6-12.5(ellipsoid, 13.5) × (3.0–)3.4–4.1(–4.5) µm, l/w ratio 2.7-3.5 (*n*=30); perispore not observed; wall and septa I - , KI - .

Host. Thamnolia vermicularis (thallus).

Distribution. Known only from the type locality in Alaska.

Observations. This species is easily separated from the other lichenicolous species with 3-septate ascospores by the much narrower and relative shorter ascospores, and from the two other species growing on *Thamnolia* by the 3-septate ascospores.

Odontotrema lecanorae Diederich & Marson sp. nov.

Odontotrema lichenicola in thallo Lecanorae vigens, insignis ascomatibus $180-440 \,\mu\text{m}$, poro $10-130 \,\mu\text{m}$, margine plano ad incurvato $70-170 \,\mu\text{m}$, ascosporis interdum amyloideis 3-septatis $10\cdot0-11\cdot5 \times 4\cdot2-5\cdot1 \,\mu\text{m}$.

Typus: Austria, Kärnten, Nationalpark Hohe Tauern, Glockner-Gruppe, NW-Grat des Großen Magrötzen Kops W ober dem Hochtor, knapp SW unter dem Grat, c. 2620 m, MTB 8943/1, Granatglimmerschiefer, auf SW-exponierten Schrofen und Blöcken, auf *Lecanora* sp., 30 August 1996, *Hafellner* 39850 (GZU—holotypus).

(Figs 2C, 4A & B, 5–7)

Ascomata initially immersed in the host thallus and apothecia, later superficial, roundish, dark brown, smooth or indistinctly striate, often slightly cracked around the pore, $(140-)180-440(-710) \mu m$ diam.; pore (0-)10-130(-270) µm; margin more or less flat, often slightly incurved towards the pore, but ascending when overmature, (50–) 70–170(–220) μm (*n*=41). *Exciple* laterally $80-110 \,\mu\text{m}$, basally $15-28 \,\mu\text{m}$ thick, with lumina of 4–10 µm. Periphysoids 10–17 µm. Subhymenium 7-17 µm. Hymenium 55-90 µm, KI+ blue reaction sometimes weak and only present in the upper part of the hymenium, or even absent. Paraphyses $1-2 \,\mu m$ thick, apically up to $2.5 \,\mu m$. Asci $50-86 \times 6-10 \,\mu\text{m}$. Ascospores ellipsoid to narrowly ellipsoid, 3-septate, (9.0-)10.0- $11.5(-13.2) \times (3.4) + 2.5 \cdot 1(-6.5) \,\mu\text{m}; \ l/w$ ratio $2 \cdot 1 - 2 \cdot 6$ (n=82); sometimes with a perispore of $0.5 \,\mu\text{m}$; wall and septa KI – or KI+ pale blue.

Hosts. An unidentified, saxicolous *Lecanora* species of the *L. muralis* group with small lobes, *Lecanora varia* and *Lecanora* sp. (probably close to *L. varia*: USA) (thallus and apothecia).

Distribution. Known from the Austrian Alps and the USA (Wyoming).

Observations. This species has shorter ascospores than most other lichenicolous Odontotrema species with 3-septate ascospores. They are similar in size to those of O. rhizocarpicola, which is distinguished by a combination of several characters (see key). Odontotrema sp. 3, also confined to Lecanora, has longer ascospores, and a hymenium and ascospores that are KI+ blue; O. figulinum, a species known from Lecanora polytropa, has broader, submuriform ascospores. The type specimen of O. lecanorae has larger ascomata



FIG. 3. Odontotrema intermedium (holotypus). A, young, almost closed ascoma in surface view; B, same ascoma in section, with hymenium almost entirely covered by the exciple, from which periphyses are descending; C, mature ascoma in surface view; D, same ascoma in section; E, detail of periphysoids. Scales: A & C=100 μ m, B & D=50 μ m; E=20 μ m.



Fig. 4. Ascomata of the Odontorrema species with 3-septate ascospores confined to Lecanora. A, O. lecanorae (holotypus); B, O. lecanorae (Nash 17364); C, Odontotrema sp. 3 (Hafellner 23693). Scale = 250 µm.



FIG. 5. Odontotrema lecanorae (holotypus). A, section through ascoma; B, excipular structure; C, periphysoids (left) and paraphyses (bottom). Scales: A=50 μm; B & C=10 μm.

than the material on *Lecanora varia*, which possibly represents a distinct species (Fig. 4).

Additional specimens examined: Austria: Kärnten, top of ridge SE of Greifenburg, 46°43'N, 13°08'E, alt. 1600–1800 m, on dead *Picea*, on *Lecanora varia*, 1978, *Nash* 17364 (ASU, GZU; the GZU specimen has different label information: 'Kärnische Alpen, Kärnten, Aufstieg von der Fürstlichen Alm zum Jaukengipfel, 1950–2000 m, trockenes Faulholz', but is nevertheless clearly part of the same collection).—**USA:** *Wyoming*: Grand Teton N. P., 200 m SW of Jenny Lake, on wood of *Pinus contorta*, on *Lecanora* gr. varia, vi 1996, Marson (hb. Diederich).

Odontotrema melaneliae Diederich & Zhurb. sp. nov.

Odontotrema lichenicola in thallo Melaneliae vigens, insignis ascomatibus immersis 170–350 µm, poro 0–20 µm, ascosporis amyloideis 3-septatis 12·8– $14\cdot4 \times 5\cdot5-6\cdot1$ µm.

Typus: Sweden, Härjedalen, Tännäs par., between Klinken and Girtibaunastugan, c. 5 km NW of Ramundbergets Fjällgard, 62°43'45"N, 12°18'30"E, alt. c. 800 m, on *Melanelia olivacea*, 9 August 1987, *Santesson* 31924 (UPS—holotypus).

(Fig. 2D)



FIG. 6. Odontotrema lecanorae (holotypus), ascospore with torus and lamella on each septum (in H_2O). Scale=5 μ m.

Ascomata immersed in the host hymenium or thallus, roundish, often \pm permanently covered by a thin, dark brown, smooth and shiny cortical layer of the host, which is darker than the host apothecial disc, convex, sometimes with a slightly constricted base, for a long time completely closed and thus appearing perithecioid, when mature opening by a minuscule pore, sometimes surrounded by several radially arranged cracks, $170-350 \,\mu\text{m}$ diam.; pore usually $0-20 \,\mu\text{m}$, only exceptionally becoming larger, up to 100 µm; ascomata, when exposed, dark brown to black. Exciple laterally 100-115 μ m, basally 15–35 μ m thick, with lumina of 7–12 μ m. Periphysoids 13–20 \times 1– 3 μm. Subhymenium 4·5–7 μm. Hymenium 70-85 µm. Paraphyses 1-1.5 µm thick, apically not thickened. Asci $60-85 \times 6.5 8.5 \,\mu\text{m}$. Ascospores ellipsoid, (1-)3-septate, exceptionally with one longitudinal sep- $(12-)12\cdot 8-14\cdot 4(-15\cdot 5) \times (5\cdot 4-)5\cdot 5$ tum, $6 \cdot 1(-6 \cdot 3) \mu m$; l/w ratio $2 \cdot 2 - 2 \cdot 5 \quad (n=30)$; sometimes with a $0.5\,\mu m$ thick perispore visible in KOH; wall covered by a very thin, hyaline, granulose ornamentation; wall and septa distinctly KI+ blue.

Hosts. Melanelia hepatizon and *M. olivacea*, generally on the disc of the apothecia, rarely on the thalline margin or on the thallus.

Distribution. Sweden and Alaska.

Observations. This species has a unique appearance as it is covered until maturity by

a dark brown, shiny, cortical layer of the host, and the ascomata are thus not or only rarely exposed and visible. This is, however, just a reaction of the particular host and not a diagnostic character of the new species. The species is distinguished from the other lichenicolous members of the genus with 3-septate ascospores and ascomata less than $350 \,\mu\text{m}$ by especially large ascospores, and thick lateral exciple and a small ascomatal pore (see identification key). Within the genus, this is the only known species to have ascospores with a thin ornamentation.

Additional specimens examined. **USA:** Alaska: Alaska Range, Denali National Park Wilderness, unnamed mountain at the headwaters of Hinnes Creek (near 11th mile of the Denali Park Road), 63°44'N, 149°07'W, alt. 1200 m, dwarf shrub (*Dryas*)-moss-lichen mountain tundra, on *Melanelia hepatizon*, 2000, *Zhurbenko* 00305 (LE).—**Sweden:** *Torne Lappmark*: The Torneträsk Area, Abisko, in the subalpine birch forest between the Scientific Research Station and the tarn 'Chara-sjön' (S of the station), on *Melanelia olivacea*, 1959, *Santesson* 13424c (UPS).

Odontotrema ochrolechiae Diederich, Holien & Zhurb. sp. nov.

Odontotrema lichenicola in thallo Ochrolechiae vigens, insignis ascomatibus $230-330 \mu m$, poro $5-50 \mu m$, margine $100-150 \mu m$, ascosporis amyloideis 3-septatis $12\cdot 1-14\cdot 4 \times 4\cdot 8-5\cdot 5 \mu m$.

Typus: Norway, S-Trøndelag, Trondheim, Bymarka, E-facing slope NE of Elgsethytta, UTM NR 610 331/ 1621 IV (WGS), 380 m, on *Ochrolechia* on decaying wood of *Picea*, 14 October 2000, *Holien* 8437 (TRH—holotypus; hb. Diederich—isotypus).

(Figs 2E, 8, 9)

Ascomata at first immersed in the host thallus, erumpent, roundish, margin dark brown to blackish, often slightly cracked around the minuscule pore, (180-)230-330(-400) µm diam.; pore (0-)5-50(-150) μm; margin (80-)100-150(-190) μm (n=107). Exciple laterally 50–140 µm, basally 24-36 µm thick, with lumina of 3.5-7 µm. Periphysoids present, but sparse, $7-9 \times 3-4 \,\mu\text{m}$, KI – . Subhymenium 4–6 μm . Hymenium 55–70 µm. Paraphyses 1–1.5 µm thick, apically not distinctly thickened. Asci $50-75 \times 9-14 \,\mu\text{m}$. Ascospores ellipsoid to



FIG. 7. As cospore length and width of the Odontotrema species confined to Lecanora: O. figulinum (\blacktriangle), O. lecanorae (\Box , holotypus; \diamondsuit , Nash 17364) and Odontotrema sp. 3 (\bigcirc).



FIG. 8. Odontotrema ochrolechiae (Zhurbenko 00316). A, habitus with different stages of development, almost naked ascoma on soralium; B, asci and paraphyses in H_2O (right) and in KOH (left); C, section through exciple. Scales: A=100 μ m; B=10 μ m; C=50 μ m.



FIG. 9. Ascoma diameter and pore diameter in *Odontotrema ochrolechiae* (\bigcirc) and *O. pertusariae* (\blacklozenge).

narrowly ellipsoid, 3-septate, $(10.8-)12\cdot 1-14\cdot 4(-16\cdot 0) \times (4\cdot 3-)4\cdot 8-5\cdot 5(-6) \mu m$, 1/w ratio $2\cdot 3-2\cdot 8$; no perispore visible in KOH; wall and septa distinctly KI+ blue.

Hosts. Ochrolechia species, including O. frigida (thallus).

Distribution. Norway, Sweden and the USA (Alaska).

Observations. Odontotrema ochrolechiae belongs to a group of very similar species, distinguished by a combination of minor characters. A large number of measurements of ascomata and pores in all known specimens of this and similar species show that the relative pore diameter is constantly smaller in O. ochrolechiae than in the similar O. pertusariae, Odontotrema sp. 1, Odontotrema sp. 2 and Odontotrema sp. 3 (Fig. 9).

The Norwegian specimen is part of the type of *O. cuculare* (see discussion under that species). In that specimen, most ascomata are immature, completely closed, and most contain no ascospores. Nevertheless, the ascomata are slightly larger $(290-410 \,\mu\text{m}, \text{pore } 0-60 \,\mu\text{m}, \text{margin } 140-190 \,\mu\text{m}, n=16)$

than in the three other known specimens of O. ochrolechiae (225–315 μ m, pore 10– 50 μ m, margin 100–140 μ m, n=91), and the lateral exciple is much thicker, up to 140 μ m, whilst in the three other specimens the lateral exciple is 50–60 μ m thick. Whether two distinct species are involved or not can be decided only when more specimens with larger ascomata and a thicker exciple are available.

Odontotrema ochrolechiae can easily be confused with Sagediopsis campsteriana (Linds.) D. Hawksw. & R. Sant., which also has 3-septate ascospores, and accompanies O. ochrolechiae in some of the specimens examined. Sagediopsis campsteriana is distinguished by true, permanently closed perithecia.

Additional specimens examined. Norway: Alten, Melladal, on Ochrolechia, 1869, Norman (O) [the same specimen includes the lectotype of Odontotrema cuculare on Parmeliopsis hyperopta].—Sweden: Härjedalen, Tännäs par., SW slope of Mt. Stora Mittakläppen (towards Mt. Gruvvålen), 940–980 m, on Ochrolechia frigida, 1977, Santesson 27933 (UPS).—USA: Alaska: Alaska Range, Denali National Park Wilderness, unnamed mountain at the headwaters of Hinnes Creek (near 11th mile of the Denali Park Road), 63°44'N, 149°07'W, alt. 1200 m, dwarf shrub (Dryas)-mosslichen mountain tundra, on Ochrolechia sp., 2000, Zhurbenko 00316 (LE, hb. Diederich, hb. Etayo).



FIG. 10. Odontotrema pertusariae (holotypus): A, immature (above) and mature (below) ascospores (in H₂O); B, asci and paraphyses (in H₂O); C, section through ascoma. Scales: A & B=10 μm, C=50 μm.

Odontotrema pertusariae Etayo, Diederich & Coppins sp. nov.

Skyttea sp. on Pertusaria, in Sherwood et al., Trans. Brit. Mycol. Soc. 75: 483 (1981 ['1980']).

Odontotrema lichenicola in thallo Pertusariae vigens, insignis ascomatibus 170–260 μ m, poro 40–110 μ m, margine ascendenti 60–80 μ m, ascosporis non amyloideis 1–3-septatis 12:5–15:4 × 4:7–5:5 μ m.

Typus: Great Britain, Scotland, Mid Perthshire (VC 88), N side of Loch Earn, Glen Beich, on *Corylus*, on *Pertusaria hymenea*, 26 August 1994, *Coppins & O'Dare* 16356 (E—holotypus).

(Figs 9, 10)

Ascomata immersed, at first closed, opening by dentate cracks, slightly erumpent, brownish black, $(140-)170-260(-310) \mu m$ diam.; pore relatively large, (20-)40-110 $(-150) \mu m$; margin ascending towards the pore, $(50-)60-80(-100) \mu m$ (n=28). Exciple laterally $50-65 \mu m$, basally $10-18 \mu m$ thick. Periphysoids poorly developed, 1-3-celled, $2 \cdot 5-3 \mu m$ thick. Subhymenium $18-25 \mu m$. Hymenium KI+ blue, $50-60 \mu m$. Paraphyses $1-1 \cdot 5 \mu m$ thick, apically not thickened. Asci $50-57 \times 7-11 \mu m$. Ascospores ellipsoid, 1-3septate, $(11 \cdot 5-)12 \cdot 5-15 \cdot 4(-16 \cdot 0) \times (4 \cdot 5-)$ 4.7-5.5(-6.0) µm; l/w ratio 2.4-3.2 (*n*=10); perispore not observed; wall and septa KI – .

Host. Pertusaria hymenea (thallus). In most collections, the host thallus is slightly damaged close to the apothecia, so that the species can be considered as a weak pathogen.

Distribution. Great Britain (Scotland), apparently not rare.

Observations. A sterile specimen of this new species (Coppins 3624) was reported by Sherwood et al. (1981: 483) as an undescribed species of Skyttea. The discovery of additional, fertile material, and a careful examination of the excipular structure show that this species belongs to the genus Odontotrema. It belongs to a group of very similar species of which the distinguishing features are given in the identification key.

A Scottish specimen of *Odontotrema* on *Pertusaria coronata* (VC 95, Moray: Grantown-on-Spey, Dreggie Woods, 38/ 022.281, alt. 245 m, 2001, *Coppins* 19916, E) was examined. It has smaller ascomata $(150-200 \ \mu m \ diam.)$ than specimens on *P. hymenea* and also a thinner margin, and might be a distinct undescribed species. Unfortunately, the ascomata are all too old and in a poor condition, and no paraphyses, asci or ascospores could be observed.

Additional specimens examined (all on P. hymenea). Great Britain: Scotland: V. C. 88, Mid Perthshire: Crieff, Drummond Park, Drummond Wood, 1978, Coppins 3624 (E, IMI 238252, hb. Diederich); ibid., 1991, Coppins 14324 (E). V. C. 89, East Perthshire: Milton Wood NNR, 1994, Coppins 16365 (E). V. C. 98, Argyll Main: Inverary, Glen Shira, N of Beinnbhuidhe House, 1996, Coppins 16889 (E, K, hb. Diederich).

Odontotrema rhizocarpicola Zhurb., Diederich & Himelbrant sp. nov.

Odontotrema lichenicola in thallo Rhizocarponis vigens, insignis ascomatibus $155-245 \mu m$, poro $30-60 \mu m$, margine $60-100 \mu m$, ascosporis non amyloideis (1–)3-septatis $9\cdot3-11\cdot1 \times 4\cdot8-5\cdot5 \mu m$.

Typus: Russia: Karelia Republic, Kandalaksha Gulf of the Beloe Sea, Keret Archipelago, Bolshoi Gorelyi Island, 66°18'N, 33°37'E, alt. 30 m, forested top of a rocky selga (=hill) in the centre of the island, on *Rhizocarpon geographicum*, 21 July 1998, *Himelbrant* (LE—holotypus; hb. Diederich-isotypus).

Ascomata immersed in the host thallus, later occasionally erumpent by one third, roundish, margin dark brown to blackish, strongly cracked and irregular around the pore, (140–)155–245(–300) µm; pore (30–) 30–60(–70) µm; margin (50–)60–100(–120) μm (n=20). Exciple laterally 60–110 μm , basally 15–25 μ m thick, with lumina of 3.5– 8 µm. Periphysoids indistinct. Subhymenium 5-9 um. Hymenium 50-80 um. Paraphyses $1.5-3 \,\mu\text{m}$ thick, apically up to $2.5 \,\mu\text{m}$. Asci $50-70 \times 6.5-13 \,\mu m.$ Ascospores (1-)3septate, septa sometimes oblique, (8.0-)9.3- $11 \cdot 1(-13 \cdot 5) \times (4 \cdot 5 -)4 \cdot 8 - 5 \cdot 6(-6 \cdot 5) \ \mu m; \ l/w$ ratio 1.8-2.2 (n=29); perispore $0.5 \mu m$; wall and septa KI -.

Host. Rhizocarpon geographicum (thallus).

Distribution. Russia, known only from the type locality on the Kola Peninsula.

Observations. This species is well characterized by its short but relatively broad ascospores, the small ascomata and the distinctly striate ascomatal margin. The differences between this species and the similar *O. lecanorae* are given in the key.

Odontotrema santessonii Zhurb., Etayo & Diederich sp. nov.

Odontotrema lichenicola in thallo Thamnoliae vigens, insignis ascomatibus 280–380 μ m, poro 55–125 μ m, margine 100–140 μ m, ascosporis non amyloideis (3–) 6–8(–9)-trans-septatis, 1–3 septis obliquis vel longitudinalibus, 15·4–20·4 × 3·6–4·6 μ m.

Typus: Russia, Chukchi Peninsula, mouth of the Chegitun River, *Dryas*-tundra on high river terrace, on *Thamnolia vermicularis* var. *subuliformis*, 12 August 1971, *Yurtsev* (LE 207696—holotypus; hb. Diederich—isotypus).

(Fig. 11)

Ascomata dispersed on the host thallus, immersed, at first closed, opening by marginal cracks, partly erumpent, with a



FIG. 11. Odontotrema santessonii (Demme s. n.): A, three ascomata on Thamnolia; B, ascospores (in H₂O); C, asci, ascospores and paraphyses (in H₂O). Scales: A=100 μm, B & C=10 μm.

constricted base, finally almost sessile, margin blackish, dull, fissured, (225-)280-380 (-440) µm diam.; pore (20-)55-125(-190) µm; margin (70-)100-140(-150) µm (n=28). Exciple laterally 45-55 µm, basally 15-25 µm. Periphysoids present but often indistinct. Subhymenium 8-14 µm. Hymenium 45-60 µm, I - (or indistinctly reddish), KI+ bluish. Paraphyses 1-1.5 µm thick, apically thickened 1.5-2.5 µm. Asci 40-50 (-55) × 813 µm. Ascospores fusiform, often asymmetrical, with the broadest part close to one apex, straight or slightly curved, trans-septate to submuriform, with (3-)6-8 (-9) transverse septa, occasionally with a longitudinal or oblique septum in 1–3 central 'cells', $(12\cdot5-)15\cdot4-20\cdot4(-23\cdot5) \times (3-) 3\cdot6-4\cdot6(-5)$ µm; l/w ratio $3\cdot6-5\cdot2$ (n=48); young, immature ascospores 1–3-transseptate; perispore not observed; wall c. $0\cdot3$ µm thick, KI – .

Host. Thamnolia vermicularis, incl. var. subuliformis.

Distribution. Known from the Russian Arctic, Iceland and Peru. Most probably widespread and common in Arctic regions.

Observations. Odontotrema santessonii differs from all known species of the genus by the longer and narrower, multiseptate to submuriform ascospores.

The ascospores in the Peruvian specimen are $16 \cdot 5 - 18 \times 5 - 5 \cdot 5 \mu m$, whilst those from Arctic specimens are slightly narrower, $15 \cdot 4 - 20 \cdot 4 \times 3 \cdot 6 - 4 \cdot 6 \mu m$. Whether the Peruvian population represents a distinct taxon or not can only be decided when more South American specimens become available.

Odontotrema santessonii is named after Professor Rolf Santesson in recognition of his continuous help and encouragements, and for allowing us to study his rich collections of lichenicolous fungi.

Additional specimens examined (all on Thamnolia vermicularis). Iceland: Central Highlands, just S of Hofsjökull Glacier, Jökulkriki below Ólafsfell Mt, 64°40'N, 18°50'W, alt. 620 m, vii 1972, Kristinsson (AMNH 15718); Eastern Iceland, Austur-Skaftafellssýsla, Súlusker Nunatak in Skaftafellsjökull Glacier, 64°05'N, 16°50'W, vii 1979, Biörnsson (AMNH 15703); Northern Iceland, Eyjafjarðarsýsla, Klængshóll Farm in Skiðadalur Valley, 65°48'N, 18°35'W, alt. 700-800 m, vi 1967, Kristinsson (AMNH 15724).-Peru: Prov. Tarma: Dept. Junin, 25-30 km (road distance) SE of Tarma, 11°33'S, 75°35'W, alt. c. 4000 m, 1981, Santesson P18:13 & Moberg (UPS).-Russia: The Kara Sea, Izvestii Tz. I. K. Archipelago, Sverdrup Island, viii 1992, Kozhevnikov (UPS); Taimyr Peninsula, Byrranga Mts, Levinson-Lessing Lake, 1994, Zhurbenko 94373b (LE 207477b, sub Stigmidium frigidum); Franz Josef Land, Hooker Island, on T. v. var. subuliformis, 1930, Demme s. n. (UPS).

Odontotrema sipei (Grummann) Diederich comb. nov.

Lethariicola sipei Grummann, Sydowia 22: 221 (1969); type: USA, Oregon, Crater Lake National Park, on Letharia vulpina, August 1953, Sipe 1227 (B—holotype!).

(Fig. 2F)

Ascomata at first immersed in the host thallus, soon erumpent, subspherical,

dark brown, initially smooth, outer layer often breaking through irregular fissures around the minuscule pore, (350-)360-480 $(-590) \mu m$; pore frequently closed, (0-)margin (170–)180–230 0–40(–105) μm; (-290) µm (n=20). Exciple laterally 70-100 µm, basally 25-50 µm thick, with lumina of $3.5-8 \,\mu\text{m}$. Periphysoids poorly developed, up to 10 µm. Subhymenium 5-8 µm. Hymenium 50-70 µm. Paraphyses $1-2 \mu m$ thick, apically not distinctly swollen. Asci 55–65 \times 5–7 µm. Ascospores ellipsoid to narrowly ellipsoid, 3-septate, (11.0-)12.2- $13.8(-14.5) \times (4.2) + 3.5 - 5.0(-5.0) \mu m$, l/w ratio $2 \cdot 6 - 2 \cdot 9$ (*n*=30); no perispore visible in KOH; wall and septa KI - .

Hosts. Letharia columbiana and L. vulpina (thallus).

Distribution. This species is known from the type locality in the USA (Oregon) and has been reported from two further collections from Canada (British Columbia) (Alstrup & Cole 1998; Goward *et al.* 1996).

Observations. This species was considered to be a synonym of Odontotrema cuculare by Lumbsch & Hawksworth (1990). For a discussion about the differences, see under O. cuculare and the key. In the original account of this species, pycnidia associated with the ascomata were illustrated (Grummann 1969), but it was not clear if they belonged to O. sipei. We carefully examined the type specimen and did not find any such pycnidia.

Odontotrema thamnoliae Zhurb., Diederich & Etayo sp. nov.

Odontotrema lichenicola in thallo Thamnoliae vigens, insignis ascomatibus $150-200 \,\mu$ m, poro $20-60 \,\mu$ m, margine $50-80 \,\mu$ m, ascosporis non amyloideis 1(-2)-septatis $11\cdot0-14\cdot9 \times 2\cdot5-3\cdot2 \,\mu$ m.

Typus: Russia, western part of Chukchi Peninsula, near Baranikha settlement, on *Thamnolia vermicularis* [with *Stigmidium frigidum*], June 1971, *Makarova* (LE 207695—holotypus).

(Fig. 12)

Ascomata dispersed or aggregated, immersed, at first closed, roundish or



FIG. 12. Odontotrema thannoliae (Zhurbenko 9777): A, host thallus with four erumpent ascomata, the lower one in section, showing the excipular structure; B, asci and paraphyses (in H_2O); C, ascospores in H_2O (left) and in KOH (right). Scales: A=100 µm; B & C=10 µm.

slightly ellipsoid, opening by marginal cracks, slightly (1/4 to 1/2) erumpent, occasionally sessile and slightly constricted at base, margin dull, blackish, fissured, (140-) 150-200(-290) µm diam.; pore (0-)20-60 (-85) µm; margin (50-)50-80(-110) µm (n=43). Exciple laterally c. 35 µm, basally c. 15 µm thick, with lumina of 4-6 µm. Periphysoids indistinct. Subhymenium 8-17 µm. Hymenium 43–55 µm. Paraphyses 1–2 µm thick. Asci 30-45 \times 7-10 um. Ascospores fusiform, straight or occasionally slightly curved, 1(-2)-septate, symmetrically tapering towards the narrow and rounded ends, (9.0-) $11.0-14.9(-18.0) \times (2.5-)2.5-3.2(-3.5)$ µm; 1/w ratio 3.8-5.4 (*n*=35); wall KI - .

Host. Thamnolia vermicularis, incl. var. subuliformis.

Distribution. Known from the Russian and Swedish Arctic.

Observations. This species is easily distinguished from the only other lichenicolous species and all the non-lichenicolous species of the genus with 1-septate ascospores by the very small ascomata and the relatively long ascospores.

We were initially confused by the presence of three species of *Odontotrema* growing on *Thamnolia*, and for some time we wondered if the material included here under *O. thamnoliae* might represent immature specimens of one of the other species. However, the differences between the three species are very constant, and no overlap of the diagnostic characters could be observed. Odontotrema sp. 1 (on Mycoblastus)

(Fig. 2G)

Ascomata immersed in the host thallus, later occasionally erumpent by one third, roundish, margin dark greyish brown, often slightly cracked around the minuscule pore, (140–)160–230(–250) µm diam.; pore (0–) 30-50(-60) µm; margin ascending towards the pore, $(50-)60-90(-100) \ \mu m \ (n=16)$. *Exciple* laterally $35-65 \mu m$, basally $8-13 \mu m$ thick, with lumina of 3.5-7 µm. Periphysoids $7-15 \times 3.5-4.5 \,\mu\text{m}$. Subhymenium 4-6.5 µm. Hymenium 55-70 µm. Paraphyses c. $1.5 \,\mu\text{m}$ thick, apically up to $2 \,\mu\text{m}$. Asci $50-60 \times 7-9 \,\mu\text{m}$. Ascospores ellipsoid to narrowly ellipsoid, 3-septate, (12.5-)13.9- $15.5(-16) \times (4.5-)4.9-5.4(-5.7)$ µm; 1/w ratio $2 \cdot 7 - 3 \cdot 1$ (*n*=25); no perispore visible in KOH; wall and septa distinctly KI+ blue.

Hosts. Mycoblastus affinis and M. sanguinarius (thallus).

Distribution. Known from Sweden and the USA.

Observations. This species is very similar to *O. pertusariae* and *Odontotrema* sp. 2. It is distinguished by the distinctly smaller pores of mature ascomata and the thinner lateral exciples (see key). As these differences might vanish with the discovery of additional material, we prefer not to describe the species formally here.

Specimens examined. Sweden: Norbotten, Korpilombola par., 15 km SSE of Kainulasjärvi, Vinsanlehto, 66°52'N, 22°35'E, alt. c. 120 m, on lignum of fallen conifer trunk, on *Mycoblastus affinis*, vii 1977, *Coppins* [6038] & *Tibell* (E).—USA: Oregon, Corvallis, Mary's Mt., on *M. sanguinarius*, vii 2002, *Miadlikowska* s.n. (DUKE, hb. Diederich).

Odontotrema sp. 2 (on Usnea)

Ascomata immersed in the host thallus, later erumpent to sometimes almost superficial, roundish, margin blackish, often distinctly cracked around the pore, (160-)215-275 $(-300) \mu m$ diam.; pore relatively large, $(20-)35-85(-100) \mu m$; margin ascending towards the pore, $(70-)80-110(-110) \mu m$

Additional specimens examined. Sweden: Torne Lappmark: the Torneträsk area, Mt Låktatjåkka, above the railway tunnel of Tornehamn, c. 500 m, alpine heath, viii 1947, Santesson (UPS).—Russia: Severnaya Zemlya, northern extremity of Bolshevik Is., western coast of Akhmatov Bay, 1996, Zhurbenko 96132 (LE 207716); northern coast of Chukchi Peninsula (coast of Chukchi Sea), eastern coast of Kolyuchinskaya Bay, just north of Cape Anayan, Tussock tundra, vii 1980, Katenin & Zhurbenko (LE); Taimyr Peninsula, mouth of Pyasina River, 1993, Kuvaev 2133 (UPS); Murmansk Region, Kola Peninsula, Barents Sea coast at the mouth of Voron'ya River, 1997, Zhurbenko 9777 (LE 207714).

(*n*=19). Exciple laterally 55–70 µm, basally 35–45 µm, with lumina of 3–9 µm. Periphysoids 6–23 × 2–3 µm. Subhymenium 8–12 µm. Hymenium 65–85 µm, I – , KI – . Paraphyses 1–1.5 µm thick, apically up to 2 µm. Asci 50–60 × 8–18 µm. Ascospores ellipsoid to narrowly ellipsoid, 3-septate, (12.9–)13.2–16.1(–18) × (4.8–)4.9–5.8 (–6.5) µm; l/w ratio 2.5–2.9 (*n*=20); a distinct perispore of 1 µm visible in water, up to 1.5 µm in KOH; wall and septa KI – .

Host. Developing over branches of *Usnea* sp., which are not or only slightly damaged by the fungus.

Distribution. Papua New Guinea.

Observations. This species is distinguished from Odontotrema pertusariae by the KI – hymenium and by a much thicker ascomatal margin (see key). As the only known specimen is very small (c. 30 ascomata on a few small branches of the host) and is very close to O. pertusariae, we prefer not to describe the species formally here, but to await the discovery of richer material.

Specimen examined: **Papua New Guinea:** Eastern Highlands Province: Mount Gahavisuka Provincial Park, 11 km N of Goroka, along trail to lookout, little disturbed mossy mountain forest, 6°01'S, 145°25'E, alt. 2400 m, on Usnea, 1992, Diederich 10499 (hb. Diederich).

Odontotrema sp. 3 (on Lecanora)

(Figs 2H, 4C, 7)

Ascomata partly immersed in the host thallus, roundish, margin dark brown, often slightly cracked around the minuscule pore, $(180-)210-290(-350) \mu m$; pore $(0-)20-80(-140) \mu m$; margin more or less flat, often slightly incurved towards the pore, $(70-)80-110(-130) \mu m$ (n=49). Exciple laterally 40-65 μm , basally 13–28 μm thick, with lumina of 4–9 μm . Periphysoids reduced, poorly developed, best observed in KOH, 0–1-septate. Subhymenium 7–12 μm . Hymenium 45–80 μm . Paraphyses 1–2 μm thick, apically up to 2.5 μm . Asci 40–70 × 7–14 μm . Ascospores ellipsoid to narrowly ellipsoid,

3-septate, $(11\cdot8-)13\cdot2-15\cdot6(-17\cdot0) \times (4\cdot6-)$ $5\cdot0-5\cdot8(-6\cdot0) \ \mu\text{m}$, l/w ratio $2\cdot4-2\cdot8 \ (n=88)$; a thin perispore of up to $0\cdot5 \ \mu\text{m}$ sometimes visible in KOH; wall KI+ blue (at least in young ascospores).

Hosts. Lecanora pulicaris and L. symmicta (thallus).

Distribution. Known from three localities in the Austrian Alps.

Observations. Odontotrema sp. 3 belongs to a group of very similar species, which are mainly separated on the basis of different ascomatal, pore and ascospore size and structure and form of the ascomatal margin (see key). The differences from the other species growing on *Lecanora* are also given in the key. This species was found on two *Lecanora* species that are not closely related, but no morphological differences between these populations could be observed. As the three known specimens are very small, we do not describe the species formally here.

Specimens examined: Austria: Steiermark: Schladminger Tauern, Kleinsölk-Obertal, Stubneralm, steile, felsige S-Abhänge des Säulecks, c. 1850 m, auf Rhododendron ferrugineum, auf Lecanora pulicaris, vi 1975, Mayrhofer & Remler s.n. (GZU); ibid., Lemperkar über der Putzentalalm, auf R. ferrugineum, auf L. symmicta coll., vii 1986, Mayrhofer & Scheuer s.n. (GZU);Niedere Tauern, Seckauer Tauern, Hochreichart-Massiv, am Weg vom Stubentörl zum Kleinen Reichart, c. 1965 m, Krummholzbestände, auf Pinus mugo, auf L. symmicta, ix 1975, Döbbeler, Hafellner [23693] & Poelt (GZU).

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