Lecideoid lecanoralean ascomycetes invading *Rhizocarpon* subgen. *Rhizocarpon* taxa, with special emphasis on cryptothalline species

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Abstract: A reinvestigation of the types of *Lecidea halacsyi* Steiner and *Lecidea intrudens* H.Magn., both inhabiting yellow *Rhizocarpon* species, has revealed that these species are not conspecific and belong to different genera. On the other hand, none of them is identical with *Scoliciosporum intrusum* (Th.Fr.) Hafellner as it has been argued in several recent floras and checklists. *Lecidea intrudens* represents a cryptothalline lichenicolous *Carbonea* species identical with *C. halacsyi* sensu Hafellner & Sancho. *Lecidea halacsyi* Steiner is also endocapylic but does not belong to *Carbonea*. However, for the meanwhile the generic relationship of this species remains unclear. Both species are treated in detail. The new combination *C. intrudens* (H.Magn.) Hafellner is proposed. For *Lecidea halacsyi* Steiner a lectotype is designated.
All together, five fertile lecideoid fungi are known so far that are able to invade taxa of *Rhizocarpon* subgen. *Rhizocarpon*. These species are partly lichenized with a well-developed thallus, partly parasitic/parasymbiotic without a visible thallus. A key to lecideoid lecanoralean fungi invading yellow *Rhizocarpon* species is presented.

Zusammenfassung: Eine Untersuchung der Typusbelege von *Lecidea halacsyi* Steiner und *Lecidea intrudens* H.Magn., beide lichenicol auf gelben *Rhizocarpon*-Arten, hat gezeigt, dass jene nicht konspezifisch sind und zu verschiedenen Gattungen gehören. Andererseits ist auch keine der beiden identisch mit *Scoliciosporum intrusum* (Th.Fr.) Hafellner, eine Vermutung, die in einigen rezenten Floren und Checklisten geäußert wird. *Lecidea intrudens* stellt eine cryptothalline lichenicole *Carbonea*-Art dar und ist identisch mit *C. halacsyi* sensu Hafellner & Sancho. *Lecidea halacsyi* Steiner ist ebenfalls endocapylisch, gehört allerdings nicht zu *Carbonea*. Die generische Zugehörigkeit von *Lecidea halacsyi* bleibt vorerst unklar. Von beiden Arten wird eine detailierte Beschreibung verfasst. Die neue Kombination *C. intrudens* (H.Magn.) Hafellner wird vorgeschlagen. Für *Lecidea halacsyi* Steiner wird ein Lectotypus festgelegt.
Insgesamt sind zur Zeit fünf fertile, lecideoide lecanorale Schlauchpilze bekannt, die imstande sind, Arten von *Rhizocarpon* subgen. *Rhizocarpon* zu besiedeln. Diese sind teilweise lichenisiert und besitzen einen gut entwickelten Thallus, teilweise parasitisch/parasymbiotisch und dann ohne sichtbaren Thallus. Ein Bestimmungsschlüssel für lecideoide lecanorale Pilze, die gelbe *Rhizocarpon*-Arten besiedeln, wird vorgelegt.

Key Words: Ascomycotina, Lecanorales, lichenicolous fungi, taxonomy

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1. Introduction

For a long time lecideoid lichenicolous fungi have been classified in *Nesolechia* (VOUAUX 1913, KEISSLER 1930). With the improvement of the knowledge about the taxonomy of *Lecidea* and superficially similar genera, a basis for a critical restudy of the lichenicolous lecideoid taxa was laid, resulting in some astonishing insights, including the following:

- *Lecidea* s. str. is a genus relatively poor in lichenicolous species, all of these are lichenized (see e.g. HERTEL 1995).
- *Nesolechia* s. str. is a genus relatively poor in species and infraspecific taxa, all of them are lichenicolous. By some mycologists the genus is merged with *Phacopsis* (see e.g. TRIEBEL & RAMBOLD 1988, TRIEBEL et al. 1995).
- Several further lecideoid genera have their own evolutionary lineages towards lichenicolous growth, including *Carbonea*, *Lecidella*, *Rimularia*, *Miriquidica* (see e.g. HERTEL & RAMBOLD 1987, 1990)
- With *Cecidonia* a further entirely lichenicolous species group could be distinguished on generic rank (TRIEBEL & RAMBOLD 1988).
- Some lecideoid lichenicolous species have been recognized as members of primarily non-lecideoid genera, e.g. *Scoliciosporum* (HAFELLNER 2004).

For a considerable number of species with lecideoid apothecia it has been shown that they belong to *Carbonea*, including both lichenized and cryptothalline/?parasymbiotic taxa. *Carbonea* was first established on the rank of subgenus (HERTEL 1967) and later raised to genus level (HERTEL 1983). The lichenized, non-lichenicolous *Carbonea atronivea* (Arnold) Hertel is the type species. Soon it became evident that some lichenicolous lecanoralean fungi also belong to *Carbonea*, the first ones transferred here were the widely distributed and well known *Carbonea vitellinaria* (Nyl.) Hertel and C. supersparsa (Nyl.) Hertel (HERTEL 1983).

Carbonea species play also a role as invaders of yellow-green *Rhizocarpon* taxa (see e.g. RAMBOLD & TRIEBEL 1992). Two of them are lichenized. The widely distributed but rare *Carbonea assimilis* (Körb.) Hafellner & Hertel [in Wirth] is relatively well known as a non host-specific invader of silicicolous, crustose lichens, including *Rhizocarpon geographicum* (HERTEL 1969: 324, sub *Lecidea assimilis*). A further lichenicolous lichen taxon was recognized as belonging to *Carbonea* by ANDREEV (2003), i.e. *Carbonea invadens* (H.Magn.) Andreev. This species, which at least starts its development on *Rhizocarpon geographicum*, is so far only known from arctic Russia.

Beside these evidently lichenized *Carbonea* species, also infections by cryptothalline (non-lichenized parasitic/parasymbiotic) lecanoralean lecideoid fungi have been found on yellow *Rhizocarpons* and have regularly been reported in recent times. Although the occurrence of such infections is known for a long time (e.g. STEINER 1894, MAGNUSSON 1946) the taxonomy of the involved species was not clear so far. In attempts to determine such specimens mainly two names (and their nomenclatural synonyms) have been used, *Carbonea intrusa* or *Carbonea halacsyi*. The former recently has been recognized as belonging to *Scoliciosporum* (HAFELLNER 2004). The application of the latter name remained unclear.

A critical reinvestigation of relevant specimens, as well as a comparison with type specimens and with representative specimens of similar species has shown that, beside

Scoliciosporum intrusum, two further species belonging to two different genera are involved, one *Carbonea* and one species of unclear relationship. Although a *Carbonea* monograph has been announced by Knoph et al. several times since more than one decade (e.g. in RAMBOLD & TRIEBEL 1992), it seems to be justified to publish our own results of this peculiar group of species, as the author is responsible for the repeated use of one of the specific names, which turned out to be wrong, and because some synonymisations have been published in recent years by the colleagues in Munich and other lichenologists at various occasions (KNOPH et al. 2004, RAMBOLD & TRIEBEL 1992, SANTESSON 1993, SANTESSON et al. 2004), which in the opinion of the author are wrong, too.

2. Material and methods

Dried herbarium specimens cited together with the treatments of the species have been examined. External morphology was studied with a dissecting microscope (WILD M3, 6,4x - 40x), anatomical studies of the thallus and the ascomata were carried out under the light microscope (LEICA DMRE, 100x–1000x). Sectioning was performed with a freezing microtome (LEITZ, sections of 12–15 mm) but squash preparations were also used, especially for ascus analysis. Preparations were mounted in water. When necessary, contrasting was performed by a pretreatment with lactic acid-cotton blue (MERCK 13741). Amyloid reactions in hymenia were observed both progressively and regressively by the use of Lugol's reagent (MERCK 9261). Sections and squash preparations were not pretreated with KOH (K), unless otherwise stated. Measurements refer to dimensions in tap water.

Secondary chemistry of non-crystallized apothecial pigments was tested according to MEYER & PRINTZEN (2000) and the nomenclature there proposed is applied.

Abbreviations for institutional herbaria follow HOLMGREN et al. (1990). Abbreviations of author names are those proposed by BRUMMITT & POWELL (1992).

The following selected specimens have been used for comparison:

Adelolecia pilati (Hepp) Hertel & Hafellner
Austria: Steiermark, [Steirisches Randgebirge], „Lavanttaler Alpen“, Koralpe, Handalpe N über der Weinebene, 1750–1850 m, GF 9156/3, freistehende Felsen (sog. „Öfen“), 2. VIII. 1986, leg. J. Poelt & C. Roux (GZU). - Steiermark, Steirisches Randgebirge, Koralpe, am Rücken Moserkogel – Glashüttenkogel E der Handalpe, NE über Glashütten, 1730–1750 m, GF 9156, Gneisfelsen, 7. XI. 1992, leg. J. Poelt (GZU). - Steiermark: Niedere Tauern, Schladminger Tauern, Pleschnitzzinken SW von Gröbming, am Gipfel, ca. 2110 m, 47°22’25’’N / 13°51’25’’E, GF 8649/1; NW-exponierte Schieferschrofen, 2. IV. 1985, leg. J. Hafellner no. 13037 (GZU). - Kärnten: Kreuzeck-Gruppe, Knoten Berg NE vom Hochtristenhaus, S-seitige Abbrüche, [46°46’50’’N / 13°06’45’’E], 2150–2210 m, GF 9244/2, 15. VII. 1978, leg. J. Poelt (GZU). - **Italy**: Südtirol: [Zentralalpen, Ötztaler Alpen], Langtauferer Tal E des Reschenpasses, E von Melag, 1920 m, Fe-hältige Blöcke, 18. IV. 1984, leg. J. Hafellner no. 12400 (GZU).

Carbonea aggregantula (Müll.Arg.) Diederich & Triebel (all on *Lecanora polytropa*)
Austria: Steiermark: Niedere Tauern, Schladminger Tauern, Anstieg vom Hauser Kaibling auf den Höchstein, S von Haus/Ennstal, S-Abhänge knapp unter dem Gipfel, ca. 2450 m, [47°20’45’’N / 13°47’30’’E, GF 8648/4], 8. X. 1977, leg. J. Hafellner no. 3424 & E. Wind (GZU). - Kärnten: Nationalpark Hohe Tauern, Schober-Gruppe, hinterstes Gradental W von Döllach, Umgebung der Ad. Noßberger Hütte, ca. 2500 m, GF 9042/2, auf Gneisschrofen, 8. VII. 1988, leg. J. Hafellner & M. Walther (GZU). - **Italy**: Trentino-Alto Adige, prov. Trento, Southern Alps, Dolomiti, Passo di Rolle N of San Martino di Castrozza, northern slopes of the mountain Tognazza, 46°17’20–25’’N / 11°47’05–15’’E, ca. 2100 m; low outcrops of siliceous rocks in subalpine pastures, on inclined rock faces exposed to the N, 1. IX. 2002, leg. J. Hafellner no. 61136 (GZU).

Carbonea assimilis (Körb.) Hafellner & Hertel
Austria: Salzburg, Lungau, Niedere Tauern, Radstädter Tauern, Aufstieg vom Großeck zum Speiereck, W von Mauterndorf, ca. 2000 m, Kalkschiefer, auf *Tephromela atra*, 22. VII. 1982, leg. J. Hafellner no. 9947 (herb. Hafellner). - **Spain**: Prov. Madrid, Sierra de Guadarrama, SE vom Puerto de los Cotos, 2150 m, Felsköpfe an einem Geländegrat aus Gneis, auf *Lecidea lapicida* var. *pantherina*, 8. IX. 1980, leg. J. Hafellner no. 10897 (GZU).

Carbonea supersparsa (Nyl.) Hertel (all on *Lecanora polytropa* if not otherwiese stated)
Austria: Tirol, Osttirol, Nationalpark Hohe Tauern, Glockner-Gruppe, E ober Kals, am Steig von der Nigglalm zum Peischlachtörl, ca. 2300 m, GF 8942/3, 47°00’50’’N / 12°42’40’’E; S-exponierte Hänge mit alpinen Matten mit kleinen Schrofen, auf Glimmerschieferschrofen (teilweise Ca-hältig), 17. VII. 1997, leg. J. Hafellner no. 47097 (herb. Hafellner). - Salzburg: Hohe Tauern, Hüttwinkl Tal S von Rauris, Kolm-Saigurn am Nordfuß des Sonnblicks, ober dem Ammererhof, ca. 1650 m, 27. V. 1978, leg. J. Hafellner no. 3395 (herb. Hafellner). - Salzburg: Niedere Tauern, Schladminger Tauern, Lungau, SW-seitige Abbrüche der Zinkwand, im Bereich des W-Endes des Erzganges, 47°16’10’’N / 13°40’55’’E, ca. 2300 m, GF 8748/1; Steilabbrüche erzhältigen Gesteins, auf steilen Neigungsflächen, auf *Lecanora soralifera*, 6. VII. 1995, leg. J. Hafellner no. 50385 & M. Möslinger (GZU). - Steiermark: Gurktaler Alpen, Frauenalpe S von Murau, Zwergstrauchheiden und Schieferblöcke am Oberberg, [47°04’30’’N / 14°09’20’’E], 1750–1800 m, GF 8950, 18. VI. 1978, leg. J. Hafellner no. 3399 (GZU). - **Portugal**: Beira Baixa, Serra da Estrêla, an der Straße von Manteigas nach Covilhã, N von Penhas da Saúde, ca. 1600 m, auf einem Silikatblock, 22. IX. 1983, leg. F. Brunner, ex herb. Hafellner no. 10808 (GZU). - **Italy**: Trentino-Alto Adige, prov. Trento, Southern Alps, Dolomiti, Passo di Rolle N of San Martino di Castrozza, northern slopes of the mountain Tognazza, 46°17’20–25’’N / 11°47’05–15’’E, ca. 2100 m; low outcrops of siliceous rocks in subalpine pastures, on inclined rock faces exposed to the N, 1. IX. 2002, leg. J. Hafellner no. 61133 (GZU).

Carbonea vitellinaria (Nyl.) Hertel (all on *Candelariella vitellina* coll.)
EUROPE, Austria: Tirol: Osttirol, Nationalpark Hohe Tauern, Venediger-Gruppe, Innergschlöß NW von Matrei, kurz E vom Venedigerhaus, am orographisch linken Ufer des Gschlöß Baches, ca. 1690 m, 47°07’35’’N / 12°27’40’’E, GF 8840/4; Blöcke in einer subalpinen Weide, auf Neigungsflächen von Glimmerschieferblöcken, 4. IX. 1998, leg. J. Hafellner no. 46665 (GZU). - Salzburg: Nationalpark Hohe Tauern, Ankogel Gruppe, Greilkopf, knapp N unter dem Westgrat, E ober der Hagener Hütte, 47°01’30’’N / 13°05’50’’E, 2500 m, GF 8944/4; alpine Matten über Glimmerschiefer, auf niederen Glimmerschieferschrofen, 27. VIII. 1994, leg. J. Hafellner no. 33005 (GZU). - Kärnten: Hohe Tauern, Kreuzeck Gruppe, bei der Gerbershütte, ca. 2350 m, auf Grünschiefer, 2. XI. 1986, leg. W. Petutschnig (GZU). - Kärnten: Karnische Alpen, Bergmassive SW von Kötschach-Mauthen, kurz N unter dem Giramondopaß am Abstieg zur Oberen Wolayer Alm, ca. 1900 m, 46°37’45’’N / 12° 50’05’’E, GF 9343/3; alpine Matten mit zerstreuten Schieferblöcken, an Neigungsflächen, 15. VII. 1998, leg. J. Hafellner no. 45784 (GZU). - Steiermark, Steirisches Randgebirge, Koralpe, Bärental Alm, ca. 1700 m, GF 9155/4, Silikatblöcke, 1. VIII. 1989, leg. M. Matzer no. 103 et al. (GZU). - Burgenland, [Bernsteiner Gebirge], Wenzelanger-Sattel zwischen Bernstein und Redlschlag, Steinstückel, 720–820 m, GF 8563, Serpentin / Föhrenmischwald, 24. VI. 1984, leg. J. Poelt (GZU). - **Italy**: Piemonte, Prov. Cuneo: Alpi Cozie, crest SW above Colle dell' Agnello, 44°40’55’’N / 06° 58’35’’E, ca. 2830 m; outcrops of calcareous schists on steep slope exposed to the SE, on banks of calcareous schist, 25. VII. 2000, leg. J. Hafellner no. 59429 (herb. Hafellner). - [Friuli-Venezia Giulia], Prov. Udine, [Südalpen], Karnische Alpen, Mt. Crostis N von Comeglians, am Grat W vom Gipfel, ca. 2240 m; alpine Matten und Schrofen, auf niederen Silikatschrofen, 17. VIII. 1994, leg. J. Hafellner no. 36794 (GZU). – **ASIA, Turkey**: [Eastern Anatolia, Agri prov.], Südflanke des Ararat, über Ganikor-Su, in der Nähe von Dogubayasit, 2900 m, VIII. 1969, leg. T. Schauer (GZU). - **Syria**: Südsyrien, Dschebel Arab, ca. 1700 m, 1989, leg. H. Pölzl (GZU). – **NORTH AMERICA, U.S.A.**: Colorado, Clear Creek Co., summit of Squaw Mountain SSE of Idaho Springs, 39°41’N / 105°29’30’’W, siliceous rocks, 5. IX. 1977, leg. R. Anderson & J. Poelt (GZU).

Scoliciosporum intrusum (Th.Fr.) Hafellner
See Hafellner (2004)!

Toninia episema (Nyl.) Timdal (on *Aspicilia calcarea* coll. if not otherwise stated)
EUROPE, France: Dept. Sarthe, Alpes Mancelles-Sud, S von Alençon, SW von Fresnay-sur-Sarthe an der D 310, Kalkfelsen im Propriété Hiron, ca. 100 m, 11. VII. 1980, leg. J. Hafellner no. 8678 (herb. Hafellner). - Dept. Var, SW von la Cadière-d'Azur, ca. 3 km N der Straße von Bandol nach La Ciotat, 180 m, Kalk, 14. V. 1980, leg. J. Hafellner no. 8358 (herb. Hafellner). - Dept. Bouches-du-Rhône, Massif de la Sainte Baume, Col de l'Espigoulier NE von Aubagne, 720 m; Garrigue über Kalk, 11. V. 1980, leg. A. Bellemère & J. Hafellner no. 8547 (herb. Hafellner). - **Italy**: Toscana, Prov. Pisa, Monte Pisano, unterste W-exponierte Hänge SE von S. Giuliano Terme bei der Ortschaft Asciano, ca. 20 m, Kalk, 28. X. 1978, leg. J. Poelt (GZU). - Toskanischer Archipel, Insel Elba, Mittel-Elba, Monte Orello N von Lacona, S-exponierte Kalkfelsen in Macchie, 100–250 m, 28. VIII. 1982, leg. H. Mayrhofer no. 3952 (GZU). - Ligurien, oberhalb von Laigueglia, ca. 100 m, auf Flyschmergel, 24. IV. 1963, leg. M. Steiner (GZU). - Basilicata, Prov. Potenza, Trockenhänge ca. 2,5 km E der Autobahnausfahrt Lauria Sud, E vom Autobahntunnel, ca. 800 m, Kalk, 3. VI. 1979, leg. J. Hafellner no. 4699 (GZU). - **Croatia** („Jugoslawien"): Dalmatien, Insel Korčula, unweit des Hotels Repos SE der Stadt Korčula, niedrige Kalkfelsen, VIII. 1969, leg. J. Poelt no. 7409 (GZU). - Dalmatien, zwischen Zadar und Posedarje, am W Ortsrand von Murvica, 80 m, Kalk, 9. VI. 1973, leg. G. Zehetleitner (herb. Hafellner). – **AFRICA, Tunisia**: Halbinsel Bon, N von Korbous bei Ain Atrous, Felshänge an der Straße, 18. IV. 1982, leg. J. Poelt (GZU). - **Canary Islands**: Lanzarote, El Charco, 7–8 km NE of Arrecife, on *Aspicilia* spec., 24. XII. 1979, leg. R. Santesson no. 29986 (UPS). - Tenerife, Teno-Gebirge, NW unter Teno Alto am Steig hinab zur Nordküste, hoch oberhalb von Las Casas (kurz E der Punta de Teno), 18°21'05''N / 16°54'20''W, ca. 400 m; Vulkanitschrofen im Sukkulentenbusch, auf Neigungsflächen von Basaltfelsen, auf *Aspicilia* spec., 16. XII. 1998 bzw. 26. IV. 2005, leg. J. Hafellner no. 64240 (herb. Hafellner).

3. Results

Lecidea halacsyi J.Steiner, Denkschr. Akad. Wiss. Wien, math.-nat. Cl., 61: 529 (1894).

Syn.: *Nesolechia halacsyi* (J.Steiner) J.Steiner, Sitzungsber. Akad. Wiss. Wien, math.-nat. Cl., 107, 1. Abt.: 155 (1898). - *Carbonea halacsyi* (J.Steiner) Hafellner & Sancho, Herzogia 8: 365 (1990) non *Carbonea halacsyi* sensu Hafellner & Sancho.

Typus: Graecia, Peristeri, 1894, leg. Halacsy (W-lectotype)! Lectotype designated here.

Note: Together with the protologue, two collections originating from two localities are mentioned. The protologue itself includes characters of both of these two collections. Of these two collection sites, two specimens – both of the locality "Peristeri" – could be located in W. The two specimens are labeled as "typus". No specimen of *Lecidea halacsyi* from the locality named "Kyllene" could be traced in W (U. Passauer, in litt.). Therefore one of the samples from "Peristeri" (specimen with the acquisition number 19347) is selected as lectotype. The other one (acquisition number 19379) most likely is a duplicate, as seen from the rock type and the morphotype of the host lichen, and therefore probably represents an "isolectotype". See also the remarks below!

Icon.: Fig. 1 in this publication (longitudinal section of apothecium), Fig. 3a in this publication (ascus stained with Lugol's solution)

Exs.: -

Description (from STEINER 1894 and own observations): **Biology**: Lichenicolous. Infection marked by the presence of apothecia on the narrow prothallus stripes between host areolae, mostly without visible damage to the host, but here and there host areolae adjacent to apothecia somewhat bleaching. **Thallus** not discernable from the outside,

vegetative hyphae c. 3–5 µm in diam., extruding from the apothecia and penetrating the dark plectenchyma below the apothecia, I(Lugol)– and therefore distinguishable from hyphae of the host. **Apothecia** not agglomerated, often arranged in rows along the fissures between the areolae of the host, black, dull, with flat to slightly convex discs, most apothecia with visible margin, 0.2–0.4 mm in diam.; **exciple** composed of radiating hyphae forming an amphithecium, without medullary layer, intensely pigmented, pigments deposited in the intercellular spaces, outer zone green-black, inner zone dark red-brown, together c. 40–50 µm thick; **hypothecium** pale throughout, brownish in the upper part, c. 100–150 µm high; **hymenium** hyaline to brownish (colour resulting mainly from old asci), c. 50–55 µm high; **epihymenium** blue-green-black, for reactions see below. **Asci** clavate, of *Bacidia*-type, that is with an euamyloid tholus provided with an ocular chamber and a non-amyloid conical central body, 8-spored, 35–45 x 10–15 µm (excluding the gelatinous caps). **Paraphyses** c. 50–55 µm long and c. 2–3 µm thick, mostly unbranched and without anastomoses, conglutinated, paraphysal cells relatively short, terminal cells slightly enlarged and surrounded by blue-green pigment (Pigmenthauben sec. KILIAS 1981). **Ascospores** hyaline, non-septate, ellipsoid to almost oblong, non-halonate (perispore not discernable in LM), 8–12 x 3–5 µm (9–16 x 4–6 µm sec. STEINER 1894), length-width-ratio about 2,5–2,9–3,3. **Pycnidia** not observed.

Secondary chemistry: Not tested with TLC, no crystals visible in polarized light; vegetative hyphae I(Lugol)–; ascal wall I(Lugol)+ blue (outermost layer and tholus), hymenial gel I(Lugol)+ blue, turning red-brown at higher concentration; inner zone of exciple, upper part of hypothecium, and hymenium K+ purple, N+ orange-brown (atra-red sec. MEYER & PRINTZEN 2000); outer zone of exciple and epihymenium K+ dark blue-green, N+ purple-violet (cinereorufa-green sec. MEYER & PRINTZEN 2000).

Hosts: On the thallus of *Rhizocarpon geographicum*

Distribution: The species is so far known only from two mountain ranges in Greece. The records so far known indicate a meridional-oromediterranean distribution pattern, but data are still to scarce for a decision on this matter.

Earlier records: STEINER (1898: 53–54, sub *Nesolechia halacsyi*) mentions a third locality in Greece (Oeta, leg. Nider), however the corresponding specimen could not be traced in W (Passauer, in litt.). VOUAUX (1913) only repeats the data given by the describer. Records of *Carbonea halacsyi* from 1990 onwards from various countries, mainly by the author, refer to *Carbonea intrudens* (see below).

Remarks:

"*Lecidea*" *halacsyi* is certainly not a member of *Lecidea* s. str. and evidently does not belong to *Carbonea* either, which was the first guess (HAFELLNER & SANCHO 1990). *Carbonea* species are easily distinguished by their asci of *Lecanora*-type and *Lecidea* species are provided with *Lecidea*-type asci (HAFELLNER 1984).

Lecideoid lecanoralean fungi with *Bacidia*-type asci are so far arranged in the genera *Adelolecia* and *Calvitimela* (by some authors regarded as belonging to *Tephromela*). However, none of these genera seems to be an adaequate solution for this taxonomic problem.

Arguments for an inclusion in *Adelolecia* would be its asci of *Bacidia*-type combined with non-septate ascospores and the presence of certain non-crystallized apothecial pigments, *Lecidea*-Grün (cinereorufa-green sensu MEYER & PRINTZEN 2000) and *Lecanora*-Rot (atra-red sensu MEYER & PRINTZEN 2000). But as all known *Adelolecia* species have predominantly blue-green hyphal pigments in the outer exciple

(without an inner zone pigmented with atra-red) and lichenicolous behaviour so far is not known in that genus, we hesitate to combine the species into *Adelolecia*.

Regardless of ascospore septation, a closer relationship with *Toninia episema* (Nyl.) Timdal (syn. *Catillaria e*., *Scutula e*.) seemed possible. For this species and a few others HAFELLNER (1984) had proposed the genus *Kiliasia*, which TIMDAL (1991) included in *Toninia* later on. In fact, spores of some *Toninia* species remain non-septate for a relatively long time, but finally they usually become at least 1-septate. In the generic description TIMDAL (1991: 31) gives the spores as simple to 7-(9-)septate. Simple to 1-septate ascospores are typical for e.g. *Toninina himalayana* Timdal and *T. tristis* (Th.Fr.) Th.Fr. In *Toninia* also parasitism is relatively frequent, although this behaviour is often overlooked, especially when the *Toninia* itself is lichenized. In most cases the host species are lichenized with cyanobacteria, but there are also exceptions, e.g. *T. aromatica*, which grows on a range of lichens lichenized with coccal green algae. Several *Toninia* species, however, are regular parasites without a lichenized thallus. Their hosts are also lichenized either with cyanobacteria (e.g. *Degelia plumbea* in *T. plumbina* (Anzi) Hafellner & Timdal, *Collema multipartitum* in *Toninia collematicola* Timdal) or with coccal green algae (e.g. *Aspicilia calcarea* agg. in *T. episema*, species of *Lecanora subfusca*-group in *T. subfuscae* (Arnold) Timdal). Arguments against an inclusion of this species in *Toninia* are, beside the permanently non-septate ascospores the apothecial pigments (none of the *Toninia* pigments as defined by MEYER & PRINTZEN 2000 is present, but pigments unknown in *Toninia* occur), the paraphyses not easily separated in squash preparations, and – from the ecological point of view – the very acid substrate, because most of the *Toninia* species grow on calcareous rocks and soils. However, concerning the substrate preferences, there are some exceptions, e.g. *T. bullata* and *T. ruginosa*, which grow also on acidic rocks (TIMDAL 1991: 20). As "*Lecidea*" *halacsyi* is a lichenicolous species with reduced thallus, the pH of the substrate might be of minor importance, as in the case of *Toninia episema*, which was also found on *Aspicilia* taxa growing upon volcanic rocks.

For some cryptothalline lecideoid species, including *Lecidea campestricola* Nyl. and *Nesolechia cerasina* Müll.Arg., a relationship with *Tephromela atra* was postulated (RAMBOLD & TRIEBEL 1992, RAMBOLD 1993) thus they were interpreted as a lecideoid, lichenicolous branch in a typically lecanoroid lichenized genus. However, of *Tephromela* we have a narrower and in our opinion more natural concept, which excludes at least the majority of lecideoid species ever placed in that genus. For the *Lecidea armeniaca* group the genus *Calvitimela* was introduced (HAFELLNER & TÜRK 2001). Possibly these species will prove to be more closely related, although it is not very likely.

Other lecanoralean lecideoid genera including lichenicolous species, such as *Phacopsis*, *Rimularia*, and *Cecidonia* do exhibit other character states in ascus structure, excipulum texture as well as in colour and reactions of non-soluble pigments impregnating parts of the apothecia. Therefore they were not taken into consideration for a more natural placement of "*Lecidea*" *halacsyi*.

Thus, for the time being, the affinities of "*Lecidea*" *halacsyi* on genus level remain unclear.

As already mentioned, STEINER (1894) in the protologue has pointed out some differences between the two specimens which are also indicated in the diagnosis. So the specimen from Peristeri should have a darker hypothecium and hymenium and the hymenium is said to give a slightly different iodine reaction than the one from Kyllene. As no material from Kyllene was available, it remains unclear, whether this falls within the range of modification or possibly the two collections belong to different taxa. With the characters given for the Kyllene collection it is at least evident that it cannot belong to Carbonea intrudens (see below).

On the lectotype specimen also small thalli of *Candelariella vitellina* and traces of other, undeterminable lichens are present. However, the distribution of the *Carbonea* apothecia clearly indicates that the host is the *Rhizocarpon* and not the *Candelariella*, nor another lichen species. A more thorough investigation of the apothecial characters confirms that the lichenicolous fungus is not *Carbonea vitellinaria* but a different species.

At an earlier occasion (HAFELLNER & SANCHO 1990) we had given "Kyllene" as the type locality. This was done without a reexamination of authentic material. The need of a lectotypification was not indicated. As no herbarium was indicated, in which the type material is conserved, this "typification" in invalid under the rules of the code (ICBN 9.20).

Steiner (l.c., all sub *Lecidea*) has compared his species with *Carbonea supersparsa* but not with *C. aggregantula*, a species not mentioned by Steiner. *Carbonea halacsyi* sensu Hafellner & Sancho is in fact not very similar to *C. supersparsa* but shows similarities with *C. aggregantula*, Therefore some doubts remained whether both Steiner and we had the same species in our hands or not.

The reinvestigation of the type has revealed that the species described by Steiner and the *Carbonea* which we reported from a number of localities in Europe under the name *Carbonea halacsyi*, are not conspecific. Therefore *Carbonea halacsyi* (Steiner) Hafellner & Sancho is a nomenclatural synonym of the species treated here under its original name. On the other hand we were in need of a name for *Carbonea halacsyi* sensu Hafellner & Sancho. Fortunately, it needs not to be described as new, because this species was already described by MAGNUSSON (1946) as *Lecidea intrudens* H.Magn., and *Carbonea intrudens* is the correct name for it. See below!

For characters separating the lichenicolous endokapylic (cryptothalline) lecideoid species growing on *Rhizocarpon* subgen. *Rhizocarpon* from each other and both species from the epikapylic *Scoliciosporum intrusum* see HAFELLNER (2004) and below (in the text and table 1).

Having also flat apothecia, "*Lecidea*" *halacsyi* is morphologically similar to *Carbonea supersparsa* (a cryptothalline lichenicolous species mainly on species of the *Lecanora polytropa* group) and *C. vitellinaria* (a cryptothalline lichenicolous species on saxicolous populations of species of the *Candelariella vitellina* group). "*Lecidea*" *halacsyi* can be distinguished from both *Carbonea* species e.g. by its *Bacidia*-type asci.

KEISSLER (1920, 1930, sub *Nesolechia*) regarded the species as identical with *Lecidea verrucariae* Nyl., an opinion neither followed by consecutive mycologists nor in this publication. *Lecidea verrucariae* is now placed in the genus *Toninia* (RAMBOLD & TRIEBEL 1992: 170).

Further specimens seen: **Greece**: same locality as lectotype probably representing an isolectotype, on *Rhizocarpon geographicum* (W).

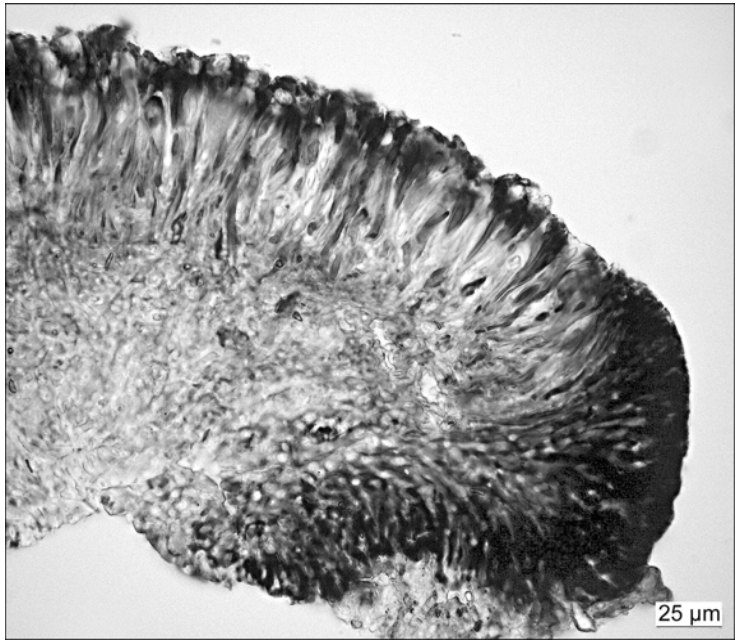

Fig. 1: "*Lecidea*" *halacsyi*: cross section of apothecium, unstained (from lectotype, phot. J. Hafellner)

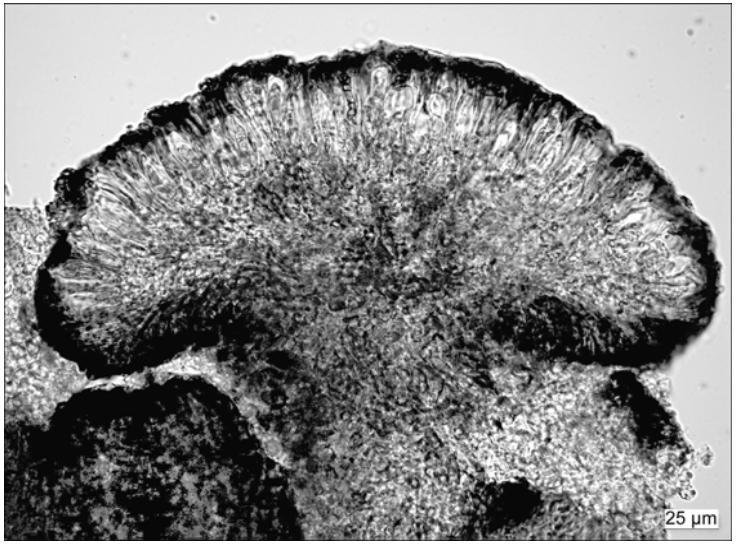

Fig. 2: *Carbonea intrudens*: cross section of apothecium, unstained (from Hafellner 24253, phot. J. Hafellner)

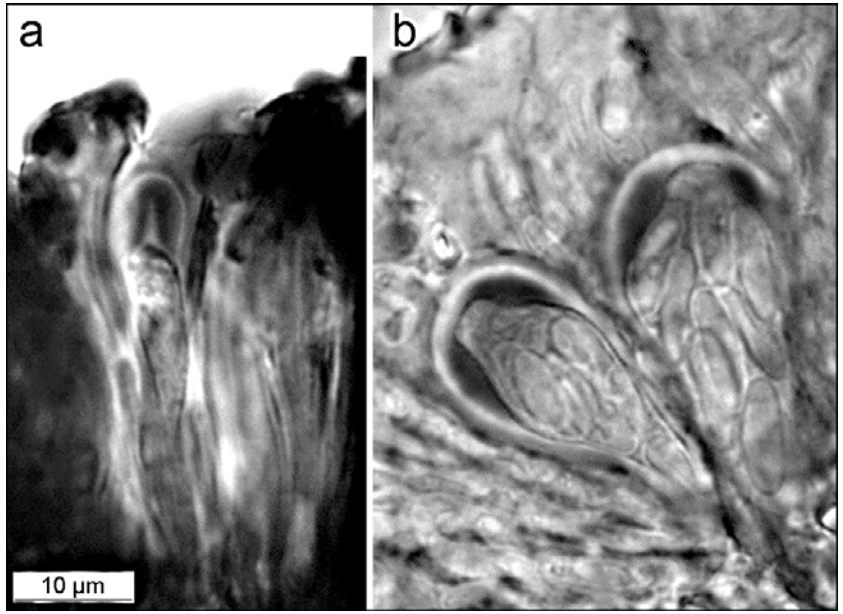

Fig. 3: a) "*Lecidea*" *halacsyi*: immature ascus, stained with I(Lugol) (from lectotype, phot. J. Hafellner). – b) *Carbonea intrudens*: mature asci, stained with I(Lugol) (from Hafellner 62306, phot. J. Hafellner)

Carbonea intrudens (H.Magn.) Hafellner comb. nov.

Bas.: *Lecidea intrudens* H.Magn., Ark. Bot. 33A(1): 53 (1946).

Typus: Sweden, Lycksele Lappmark, Stensele, Sandvik, 400 m, among boulders in the wood, upon *Rhizocarpon geographicum*, 2. VII. 1924, leg. Magnusson no. 7706 (UPS-holotype)!

Syn.: *Carbonea halacsyi* sensu Hafellner & Sancho non *Lecidea halacsyi* J.Steiner

Icon.: Hertel 1970: 408 fig. 9 (drawing of longitudinal section of apothecium); fig. 2 in this publication (longitudinal section of apothecium), fig. 3b in this publication (asci stained with Lugol's solution)

Exs.: -

Description (from MAGNUSSON 1946, HERTEL 1970 and own observations): **Biology**: Lichenicolous. Infection marked by tiny black areas on host areolae or without visible damage on the prothallus. **Thallus** not discernable from the outside, present as a plectenchymatic cushion below the apothecia, vegetative hyphae visible below the apothecia in longitudinal section, brown but pigmentation fading further down, forming a dense tri-dimensional net, c. 5–7 µm in diam., I(Lugol)–, (acc. to MAGNUSSON, l.c., proper thallus verruciform, up to 150 µm thick, inside a mixture of brownish lumps, containing yellowish-green algal cells, 6–8 µm in diam.). **Apothecia** in small dense

groups on the edge of areolae of the host or on the prothallus in between, black, convex from the beginning, somewhat glossy, broadly attached, without distinct margin, 0,3–0,5 mm in diam., groups up to 1,5 mm in diam.; **exciple** dark brown, getting more intense to carbonized towards the outside, c. 30–45 µm across, at least when young exciple composed of radially arranged hyphae; **hypothecium** dark brown to brown, 50– 80 µm high, of intricate hyphae; **hymenium** hyaline, c. 40–50 µm high, in the upper half with bluish tinge verging to dull blue-green or emerald green in the uppermost zone (c. 10 µm) and forming an epihymenium. **Asci** clavate, of *Lecanora*-type, 8-spored, 25–35 x 11–14 µm (15–17 µm acc. to MAGNUSSON, l.c.). Some **paraphyses** unbranched or others with some branches and anastomoses, conglutinated, c. 2–2,5 µm in diam., with slightly enlarged tips, surrounded by blue-green pigment, tips embedded in pigmented gel, in the gel pigment of same type but less intensely coloured, I(Lugol)–. **Ascospores** hyaline, non-septate, old spores not rarely with one thin septum, ellipsoid to oblong, 8–12(–16) x 3,5–5 µm, length-width-index about 3, non-halonate, perispore not discernable in LM. **Pycnidia** not observed.

Secondary chemistry: Not tested with TLC, no crystals visible in polarized light; vegetative hyphae I(Lugol)-; ascal wall I(Lugol)+ blue (outermost layer and tholus); hymenial gel I(Lugol)+ blue turning red-brown with higher concentration; exciple and hypothecium K-, N+ vividly orange-brown (leptoclinoides-brown sec. MEYER & PRINTZEN 2000); epihymenium K+ vividly blue-green, N+ for a short time intensely blue, then purple-violet (cinereorufa-green sec. MEYER & PRINTZEN 2000).

Hosts: On various morphotypes of *Rhizocarpon geographicum*, sometimes treated as subspecific taxa, rarely also on other species of *Rhizocarpon* subgen. *Rhizocarpon*, e.g. *R. alpicola*

Distribution and earlier records: Up to the 1970ies the species was known only from the type locality (HERTEL 1970). In the meanwhile many further collections came to our knowledge but almost all of them have erroneously been published under other names. Data from the herbarium labels suggest a subarctic–boreal to meridional–oro- to cryomediterranean distribution pattern, at least in Europe. With certainity *C. intrudens* is so far known from Norway (HAFELLNER 1993, sub *C. halacsyi*), Sweden, Austria (BOOM et al. 1996, HAFELLNER 1991, 2000, 2002, HAFELLNER & SANCHO 1990, HAFELLNER & TÜRK 1995, HAFELLNER et al. 2004, HOFMANN et al. 1995, all sub *C. halacsyi*), Italy (TRETIACH & HAFELLNER 2000, sub *C. halacsyi*), and Spain (HAFELLNER & SANCHO 1990, sub *C. halacsyi*).

In North America it is known from Greenland (see below). A further record which might refer to this species originates from Canada (Alberta) (see BEDER & OGILVIE 1967, sub *Lecidea intrudens* on *Rhizocarpon geographicum*), but the corresponding specimen needs to be revised.

The species was erroneously reported from southern France (CLAUZADE & RONDON 1961, sub *Lecidea intrudens* on *Lecanora gangaleoides*), as already HERTEL (1970) has stated and as it is indicated by the host species mentioned. But a later record from France (Auvergne) (HOUMEAU & ROUX 1980: 98, sub *Lecidea aggregatula* (sic!) on *Rhizocarpon geographicum* agg.) may be correct.

Remarks:

The type of *Lecidea intrudens* has been reinvestigated by HERTEL (1970: 424). We also looked at it under the dissecting microscope to confirm the assumption that the type is identical with the other specimens cited below. However, as the type specimen is very tiny and a detailed description is given by HERTEL (1970), we did not make any further sections. Thus, own observations of anatomical characters included in the description given above refer to non-type material.

In recent times *Lecidea intrudens* has been mentioned among the synonyms of *Carbonea intrusa* (now *Scoliciosporum intrusum*) (see e.g. RAMBOLD & TRIEBEL 1992, SANTESSON et al. 2004). For distinguishing characters between *Carbonea intrudens* and *Scoliciosporum intrusum* see HAFELLNER (2004) and table 1.

ARNOLD (1876: 359, sub "*Lecidea* – – (n. sp. videtur)"), accompanied by a description fitting quite well to *C. intrudens*) evidently was the first who recognized the presence of the species on *Rhizocarpon geographicum*. This first mention is based on a specimen from a locality in Northern Tyrol (Austria). Later the same author reported the species also from a locality now in Italy (Trentino) (ARNOLD 1880: 105). Both records are also included in the compilation by MAGNUS (1905: 356). However, as the specimens were not available to us, some uncertainty remains, if this our assumption is correct.

Interestingly, Lettau, who studied lichens from many different places in the Alps and also has investigated very carefully the lichenicolous taxa, did not mention any collection that might refer to *Carbonea intrudens* (LETTAU 1958).

With its convex, often aggregated apothecia *C. intrudens* is morphologically similar to *C. aggregantula* (a cryptothalline lichenicolous species mainly on species of the *Lecanora polytropa* group). *C. intrudens* can be distinguished from *C. aggregantula* by the conspicuous black basal cushion, on which the apothecia develop, and by the somewhat longer ascospores.

Furthermore, in order to avoid confusion, it is worth mentioning that Magnusson described also a *Lecanora intrudens* (MAGNUSSON 1942). This species has later been recognized as belonging to *Miriquidica* (HERTEL & RAMBOLD 1987).

Lichenicolous fungi on *Carbonea intrudens*: In a collection from northern Italy (Hafellner 61134, see below) the hymenia at least partly have been found infested by *Intralichen christiansenii* (D.Hawksw.) D.Hawksw. & M.S.Cole.

Further specimens seen (all on *Rhizocarpon geographicum* if not otherwise indicated):
EUROPE: **Austria: Tirol**: Ötztaler Alpen, Glockturm-Kamm, Platztal E ober Pfunds, Grat zwischen dem Schönjöchl und dem Arzkopf, ober dem verfallenen Bergwerk, ca. 2800 m, GF 9029; teilweise Fe-reicher Schiefer und Rasenbänder, auf Schrofen an Steilflächen, 4. IX. 1991, leg. J. Hafellner no. 30300 (GZU). - Osttirol, Karnische Alpen, am Steig aus dem hintersten Obertilliacher Tal auf den Hegetriegel, Klapfalm, ca. 1900 m, GF 9341/1, [subalpine Weiden mit Baumgruppen und einigen Blöcken], auf teilweise Ca-hältigen Schieferblöcken, 8. IX. 1989, leg. J. Hafellner no. 28790 (GZU). - Osttirol, Nationalpark Hohe Tauern, Venediger-Gruppe, Innergschlöß NW von Matrei, kurz E vom Venedigerhaus, am orographisch linken Ufer des Gschlöß Baches, ca. 1690 m, 47°07'35''N / 12°27' 40''E, GF 8840/4; Blöcke in einer subalpinen Weide, auf Neigungsflächen von Glimmerschieferblöcken, 3. IX. 1998, leg. J. Hafellner no. 46684 (GZU). - **Salzburg**: Gurktaler Alpen, E-Hänge der Friesenhals Höhe ober dem Rosanin See, [46°57'05''N / 13°46'35''E], ca. 2150 m, GF 9048/2; schrofendurchsetzte alpine Rasen, auf Schrofen aus einer silikatischen Breckzie, 14. VIII. 1989, leg. J. Hafellner no. 63954 & M. Magnes (GZU). - **Kärnten**: Nationalpark Hohe Tauern, Ankogel-Gruppe, Tauerntal NW von Mallnitz, am Weg von der Jamnigalm auf die Hagener Hütte, 2100–2200 m, GF 8944/4, 28. VII. 1989, leg. J. Hafellner no. 24253 & R. Türk (herb. Hafellner). - Nationalpark Nockberge, Klomnock N von Bad Kleinkirchheim, am Nordgrat gegen die

Schiestelscharte, knapp unter dem Gipfel, [46°53'00''N / 13°47'20''E], ca. 2250 m, GF 9148/2; Glimmerschiefer, auf NW-exponierten Felsschrofen; 28. VIII. 1994, leg. J. Hafellner no. 33377 (GZU). - Nationalpark Nockberge, Stileck, ca. 30 m W/NW unter dem Gipfel, 46°52'30''N / 13°38'20''E, ca. 2170 m, GF 9147/2, Granat-Glimmerschiefer-Felsblock in alpinen Rasen, auf *Rhizocarpon alpicola*, 6. IX. 1989, leg. W. Petutschnig (GZU). - **Steiermark**: Niedere Tauern, Schladminger Tauern, E-Grat der Grobfeldspitze W oberhalb der Buckelkarseen, [47°17'15''N / 13°40'25''E], 2200 m, GF 8748/1; auf Gneisblöcken, 5. VII. 1989, leg. J. Hafellner no. 50357 (herb. Hafellner). - Niedere Tauern, Schladminger Tauern, Kleinsölk-Obertal, am Steig vom Schwarzensee zur Rettingscharte, am Fuß der S-exponierten Abbrüche des Großen Gnasen, ca. 1940 m, 47°17'50''N / 13°50'50''E, GF 8749/1; Blockschutt, auf Neigungsflächen von Gneisblöcken, 8. IX. 1993, leg. J. Hafellner no. 50139 & M. Möslinger (herb. Hafellner). - Gurktaler Alpen, Kirbisch ca. 11 km SW von Murau, oberhalb von St. Lorenzen, NE-exponierte Hänge knapp unter dem Gipfel, 47°03'05''N / 14°03'05''E, ca. 2100 m, GF 8950/1; niedere Schrofen und Blockwerk aus paläozoischen Schiefern zwischen Zwergstrauchheiden, auf Neigungsflächen der Schrofen, 24. VIII. 2003, leg. J. Hafellner no. 62306 (GZU). - Ibid., auf Überhangsflächen der Schrofen, auf *Rhizocarpon* spec., 24. VIII. 2003, leg. J. Hafellner no. 62330 (GZU). - Gurktaler Alpen, Eisenhut ESE von Turrach, SW-Rücken ober der Geißeckhütte, 46°57'05''N / 13°55'05''E, ca. 2260 m, GF 9049/2; kleine Schutthalden eines vulkanogenen, paläozoischen Schiefers in lückigen Zwergstrauchheiden, auf kleinen Schieferplatten, 28. VII. 2002, leg. J. Hafellner no. 61500 (GZU). - Steirisches Randgebirge, Koralpe, Kleiner Speikkogel, N-Hänge kurz NW unter dem Gipfel, 46°47'05''N / 14°58'40''E, ca. 2080 m, GF 9255/2, Glimmerschieferschrofen in alpinen Rasen, auf N-exponierten Neigungsflächen, 29. X. 2000, leg. J. Hafellner no. 53177 & A. Hafellner (GZU). - Steirisches Randgebirge, Stubalpe W von Köflach, Schwarzkogel, im Gipfelbereich, 47°05' 30''N / 14°52'05''E, ca. 1810 m, GF 8955/1, W-exponierte, niedere Schrofen aus Glimmerschiefer, auf Neigungsflächen, 15. VIII. 2002, leg. J. Hafellner no. 59808 (GZU). - **Italy: Piemonte, prov. Cuneo**: Alpi Cozie, crest SW above Colle dell' Agnello, 44°40'55''N / 06°58'35''E, ca. 2830 m; outcrops of calcareous schists on steep slope exposed to the SE, on banks of calcareous schist, 25. VII. 2000, leg. J. Hafellner no. 60264 (GZU). - **Trentino-Alto Adige, prov. Trento**: Southern Alps, Dolomiti, Passo di Rolle N of San Martino di Castrozza, northern slopes of the mountain Tognazza, 46°17'20–25''N / 11°47'05–15''E, ca. 2100 m; low outcrops of siliceous rocks in subalpine pastures, on inclined rock faces exposed to the N, 1. IX. 2002, leg. J. Hafellner no. 61115, 61134 (both in GZU). - **Emilia Romana, Prov. Reggio Emilia**: Apennino, Monte Ventasso S above the village Ramiseto, slopes exposed to N, SE above Lago Calamone, 44°22'55''N / 10°17'35''E, ca. 1450 m; scree of sandstone boulders, on inclined rock faces of sandstone boulders, 23. VII. 2001, leg. J. Hafellner no. 58371 (GZU).- **Makedonia**: Šar planina, Rudoka, Popova šapka W von Tetovo, Hänge W der Bergstation der Bergbahn, 1700–2300 m, 8. VII. 1977, leg. J. Hafellner no. 41469 (GZU). – **NORTH AMERICA: Greenland**: N. Greenland, area NE of Hiawatha Gletscher, 78°50'N / 67°18'W, on siliceous stones, 30. VII. 1999, leg. E. S. Hansen (separated from Lich. Groenlandici exs. 788) (GZU).

Locality data of specimens published under the name *Carbonea halacsyi* by the author at various occasions (see above) are not repeated here.

Distinguishing the *Carbonea* species and other lecanoralean fungi on yellow *Rhizocarpon* species

The three *Carbonea* species inhabiting yellow *Rhizocarpon* species are quite easy to distinguish, already under the dissecting microscope. *C. intrudens*, confined to this group of host species, forms agglomerated apothecia which are convex from the beginning and a margin is not discernable. Beside this endocapylic species also *Carbonea assimilis* and *Carbonea invadens* (H.Magn.) Andreev are sometimes reported as inhabiting *Rhizocarpon*. Both these species are lichenized and have a distinct thallus. Whereas the thallus of *C. assimilis* consists of pale-brown, convex, glossy areoles (HERTEL 1969), that of *C. invadens* is said to have greyish, flat areoles (ANDREEV 2003).

Character	*Scoliciosporum intrusum*	*"Lecidea" halacsyi*	*Carbonea intrudens*
Lichenized thallus	present in small patches, crustose, black but often with brownish tinge, fissured-areolate	absent	absent
Areolae	uneven to granular, each consisting of several to many dense thallus particles	absent	absent
Biological behaviour	autonomous, facultatively lichenicolous (?obligate youth parasite)	obligately lichenicolous (?parasymbiotic)	obligately lichenicolous (?parasymbiotic)
Shape of infection, arrangement of apothecia	small patches, sometimes fusing, apothecia scattered	apothecia +/- arranged in rows along the host areolae	apothecia in roundish agglomerations, often on the prothallus or near to host apothecia
Colour and shape of apothecia	blackish, often with greenish or brownish tinge, almost flat to medium convex	black, dull, plane to slightly convex, with thin but distinct margin	black, glossy, strongly convex from the beginning, immarginate
Colour and texture of excipulum	dull to brownish, of intricate hyphae	outer zone green-black, inner zone dark red-brown, excipular hyphae in radial arrangement	dark brown, getting more intense to carbonized towards the outside
Colour and reaction of epihymenial pigment	bluish-greenish to dull	blue-green-black, K+ dark blue-green, N+ purple-violet	dull blue-green or emerald green, K+ vividly blue-green, N+ for a short time intensely blue, then purple-violet
Colour of hypothecium	hyaline to pale-olive	pale throughout, brownish in the upper part	brown to dark brown
Paraphyses	branching and anastomosing, but hardly conglutinated	conglutinated, with few ramifications	conglutinated, with few ramifications and anastomoses
Asci	*Lecanora*-type	*Bacidia*-type	*Lecanora*-type
Ascospores	ellipsoid to fusiform, often somewhat asymmetric, non-septate with often several 1-septate intermingled, 12–17(–19) x 4–5,5(–6) µm	ellipsoid, non-sepate, 8–12 x 3–5 µm	ellipsoid to oblong, non-septate, 8–12 (–16) x 3,5–5 µm

Tab. 1: Characters distinguishing among +/- cryptothalline lecideoid fungi upon *Rhizocarpon* subgen. *Rhizocarpon*

"Lecidea" halacsyi has flat apothecia with a persisting lecideine margin visible, and the apothecia do not develop in dense agglomerations but are arranged in rows along the edges of host areolae.

Beside the two crypothalline lecideoid species, *Carbonea intrudens* and *"Lecidea" halacsyi*, four further lichens are regularly found upon *Rhizocarpon*: *Scoliciosporum intrusum*, *Rimularia furvella* and *Miriquidica intrudens*, in lower elevations also *Protoparmelia atriseda*. All these are more or less distinctly lichenized, and *Rimularia furvella* and *Miriquidica intrudens* are sorediate and usually sterile. The apothecia of *Protoparmelia atriseda* are brown and provided with a thalline margin. Thus, only *Scoliciosporum intrusum* can be called lecideoid. Apothecia of *S. intrusum* are blackish and more or less convex. An internally pale exciple, a hardly pigmented hypothecium, and anastomosing paraphyses are characteristic (HAFELLNER 2004).

Key to lecideoid lecanoralean fungi inhabiting taxa of *Rhizocarpon* subgen. *Rhizocarpon*

1 Thallus sorediate **2**
1* Thallus with apothecia **4**

2 Thallus grey, soredia blackish ..... **Miriquidica nigroleprosa**
2* Thallus brown **3**

3 Thallus granular-sorediate throughout ..... **Rimularia furvella**
3* Thallus consisting of small flat areolae provided with grayish margin ..... **Miriquidica intrudens**

4 A thallus surrounding the apothecia is present (at least distinct under the dissecting microscope!) 5
4* Thallus indistinct 7

5 Exciple in longitudinal section pale, brownish-greenish, paraphyses with anastomoses, ascospores often somewhat asymmetric ..... **Scoliciosporum intrusum**
5* Exciple in longitudinal section dark brown throughout, paraphyses hardly interconnected by anastomoses, ascospores symmetrically ellipsoid **6**

6 Areolae pale brown, convex to even subsquamulose, glossy ..... **Carbonea assimilis**
6* Areolae greyish, plane ..... **Carbonea invadens**

7 Apothecia plane to subconvex, with thin margin when young, dull, arranged in rows along fissures between host areolae ..... **"Lecidea" halacsyi**
7* Apothecia convex and immarginate from the beginning, glossy, aggregated in dense groups preferably on the prothallus or near host apothecia ..... **Carbonea intrudens**

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