Notes on *Scoliciosporum intrusum*

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Abstract: The lichen species commonly called *Carbonea intrusa* (Th.Fr.) Rambold & Triebel in modern floras, is recognized as belonging to *Scoliciosporum* A.Massal. Information on the species is compiled and the new combination *Scoliciosporum intrusum* (Th.Fr.) Hafellner is introduced. *Carbonea halacsyi* sensu Hafellner & Sancho is not a synonym of *Scoliciosporum intrusum*, but a different species with superficially similar appearance.

Zusammenfassung: Die Flechtenart, die in modernen Florenwerken als *Carbonea intrusa* (Th.Fr.) Rambold & Triebel aufscheint, wird als zu *Scoliciosporum* A.Massal. gehörig erkannt. Informationen über die Art werden zusammengestellt und die neue Kombination *Scoliciosporum intrusum* (Th.Fr.) Hafellner wird vorgeschlagen. *Carbonea halacsyi* sensu Hafellner & Sancho ist kein Synonym von *Scoliciosporum intrusum* sondern eine andere Art mit oberflächlich ähnlichem Aussehen.

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1. Introduction

The lichen genus *Scoliciosporum* A.Massal. was described in the middle of the 19th century, when better light microscopes became available (MASSALONGO 1852). Although accepted by the more critical lichenologists (e.g. Arnold, Th. Fries, Körber), it was more often reduced to the synonymy of *Bacidia* De Not. *Scoliciosporum* was resurrected by VĚZDA (1978), who accepted the genus because of constant differences in exciple texture, peculiarities of the paraphyses, and the shape of ascomata. He compares it with *Micarea* Fr. rather than *Bacidia* and supposes a closer relationship with that genus (VĚZDA 1978: 412). Although this relationship to *Micarea* could not be proven (e.g., HAFELLNER 1984, ANDERSEN & EKMAN 2004), the genus *Scoliciosporum* is now generally accepted.

Usually hyaline, transseptate, elongated ascospores are associated with the genus *Scoliciosporum*. For instance, when VĚZDA (1978) resurrected the genus, he included only phragmosporous taxa with more or less worm- to needle-shaped ascospores, which are mostly +/- coiled in the ascus. In *Scoliciosporum*, such spores are typical for the type species, *S. holomelaenum* (= *S. umbrinum*), and some other species.

In the course of extensive determination work on crustose lichens from Europe, it became evident that the species commonly named *Carbonea intrusa* (Th.Fr.) Rambold & Triebel does not belong to *Carbonea* but is a species of *Scoliciosporum* with unusual spore characters.

2. Material und Methods

The present study is based on the dried herbarium specimens cited below. 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 a 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 after treatment with Lugol's reagent (= IKI; MERCK 9261). Sections and squash preparations were not pretreated with KOH, unless otherwise stated. Measurements refer to dimensions in tap water. So far, no crystalline lichen compounds have been detected in the genus. Hymenial pigments are classified following MEYER & PRINTZEN (2000). Abbreviations for institutional herbaria follow HOLMGREN et al. (1990). Abbreviations of taxonomic authorities are taken from BRUMMITT & POWELL (1992).

The following material has been used for comparison:

Scoliciosporum umbrinum (Ach.) Arnold: **AUSTRIA, Steiermark,** Niedere Tauern, Wölzer Tauern, Planneralpe [NE oberhalb von Donnersbach], am Steig vom Plannerknot zum Rotbühel, Plannereck, ca. 1900 m, [47°24’35’’N / 14°13’10’’E], GF 8551/3, N-exponierte Gneisschrofen, 20. VII. 1988, leg. J. Hafellner 20459 (GZU). - Steirisches Randgebirge, Gleinalpe, [nördliche] Abhänge der Mugel gegen Niklasdorf, ca. 5 km E von Leoben, Niklasdorfgraben unter dem Ghf Loser, [47°22’55’’N / 15°10’50’’E], ca. 700 m, GF 8657/1; W-exponierte, niedere Silikatausbisse an der Wegböschung; 11. IV. 1977, leg. J. Hafellner 2172 (GZU). - [Gleinalpe], Murtal, Kirchkogel über Kirchdorf bei Pernegg, ca. 700 m, GF 8657, SE-exponierte Serpentinfelsrippe, 15. VI. 1990, leg. H. Mayrhofer 9197 (GZU). - **Kärnten,** Karnische Alpen, Maglern W von Arnoldstein, Geländerücken E des Ortes, ca. 640 m, GF 9447/4; S-exponiert auf bodennahen, metamorphen Silikatschrofen; 6. V. 1992, leg. J. Hafellner 29410 (GZU).

Carbonea atronivea (Arnold) Hertel: **AUSTRIA, Tirol,** Nordtirol, Nördliche Kalkalpen, Lechtaler Alpen, S-exponierte Schrofenhänge N und W der Augsburger Hütte über Grins, NW Landeck, ca. 2200–2400 m; Kalk und Mergelkalk, 9. VII. 1982, leg. J. Hafellner 9967 (herb. Hafellner). - Osttirol, Hohe Tauern, Granatspitzgruppe, E-seitige Hänge und Rücken des Nussing-Kogel, 2200–2530 m, GF 8941, Kalkschieferschrofen, 30. VIII. 1988, leg. J. Poelt (GZU). - **Kärnten,** Nationalpark Hohe Tauern, Glockner-Gruppe, NW-Grat des Großen Magrötzen Kopfs W ober dem Hochtor, knapp SW unter dem Grat, ca. 2620 m, GF 8943/1; Granatglimmerschiefer, auf SW-exponierten Schrofen und Blöcken, 30. VIII. 1996, leg. J. Hafellner 40055 (herb. Hafellner). - Nationalpark Nockberge, kleine Anhöhe ca. 600 m NW vom Mallnock, ca. 1980–2020 m, GF 9148/2, verkieselte Dolomitblöcke, 11. VII. 1990, leg J. Poelt, W. Obermayer & W. Petutschnig (GZU). – **SPAIN, Prov. Gérona,** Pyrenäen, Nuria N von Ribas de Freser, NW-Hänge SE oberhalb des Klosters, ca. 2300 m, NW-exponierte Abbrüche aus Kieselkalk und Kalkschiefer, 27. V. 1983, leg. J. Poelt (GZU).

Carbonea halacsyi sensu Hafellner & Sancho: **AUSTRIA**, **Steiermark,** 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, auf *Rhizocarpon geographicum*, 29. X. 2000, leg. J. Hafellner 53177 & A. Hafellner (GZU).

3. Results

***Scoliciosporum intrusum* (Th.Fr.) Hafellner comb. nov.**
Bas.: *Lecidea intrusa* Th.Fr., Bot. Notiser 1867: 152 (?1868).

≡ *Carbonea intrusa* (Th.Fr.) Rambold & Triebel [in Aptroot et. al.], Biblioth. Lichenol. 64: 47 (1997). - *Catillaria intrusa* (Th.Fr.) Th.Fr., Lichenographia Scandinavica, vol 1, pars 2: 579 (1874). - *Micarea intrusa* (Th.Fr.) Coppins & H.Kilias, in Coppins, Bull. Brit. Mus. (Nat. Hist.), Bot. Ser. 11(2): 138 (1983). - *Lecideopsis intrusa* (Th.Fr.) Zopf, Hedwigia 35: 338 (1896).- *Conida intrusa* (Th.Fr.) Sacc. & D.Sacc., Syll. Fung. 18: 187 (1906). - *Lecidea contrusa* Vain., Medd. Soc. Fauna Flora Fenn. 10: 29 (1883). Nom. illegit., superfluous name (ICBN Art. 63).

Typus: Finland, Tavastia australis, Mustiala, on *Amygdalaria panaeola*, 1867, leg. A. Kullhem (UPS-holotype, fide COPPINS 1983: 138). Not seen.

= *Lecidea aphanoides* Nyl., Flora, Regensburg 51: 476 (1868). (fide COPPINS 1983: 138 and SANTESSON et al. 2004: 75).

Typus: Scotland: Braemar, "supra saxa calcarea", leg. Crombie (cited from protologue, specimen not seen).

= *Lecidea melaphana* Nyl., Flora, Regensburg 52: 83 (1869). (fide COPPINS 1983: 138 and SANTESSON et al. 2004: 75).

Typus: Scotland: "socia *Lecanorae fuscatae* f. *sinopicae*, ad saxa granitosa", leg. Crombie (cited from protologue, specimen not seen).

For supposed further synonyms see below!

Icon: Fig. 1 (ascus, paraphyses, ascospores)

Exs.: ---

Description: **Thallus** black but often with brownish tinge, areolate, areolae developing between areolae of other lichens (see below) or laterally affixed to alien areolae, with uneven to granular surface, consisting of several to many dense thallus particles, bearing apothecia or not. **Photobiont** a coccal green alga, algal cells mostly 10–18 µm in diam., only autospores may be smaller; reactions: thallus K-, C-, Pd-, medulla not tested. **Apothecia** blackish, often somewhat glossy, one to several per areole, adnate, convex from the beginning, with indistinct margin or later margin excluded and apothecia virtually immarginate. **Exciple** in longitudinal section pale to brownish, darker towards the outer edge, composed of radiating hyphae; excipular hyphae branched and anastomosing, the lumina c. 1–2 µm wide. **Hypothecium** up to 200 µm high, hyaline to slightly olivaceous, in the upper part often some scattered hyphal cells with orange content, which reacts K+ purple (Intrusa-yellow). **Hymenium** hyaline, not inspersed, ca. 40–50 µm high, the upper part (epihymenium) olive to aeruginose to bluish; K+ green intensifying, N+ red to purplish to pale violet, hymenial gel IKI- but gel and outer layer of empty ascal walls IKI+ blue which may provoke the impression that the entire hymenium gives such a reaction. **Paraphyses** numerous, branched and anastomosing, c. 1,5 µm wide, with only slightly enlarged tips, with "Pigmenthauben" (sec. KILIAS 1981) which are embedded in the hymenial gel. **Asci** clavate to broadly cylindrical, mature asci 35–45 x 14–18 µm, 8-spored, ascal wall lecanoralean, strongly thickened at the apex and forming a tholus, with a broad ocular chamber (possibly indiscernible in mature asci); ascal gel: IKI+ blue, only slightly diffusing into the hymenium, outermost layer of the ascal wall: IKI+ blue, tholus IKI+ blue, with a non-reactive, broad, +/- cylindrical axial body; ascus dehiscence rostrate (Lecanora-type); apported asci and ascospores sometimes containing the substance Intrusa-yellow. **Ascospores** ellipsoid to fusiform, at least a few per preparation slightly

asymmetric to somewhat curved, simple at first, later frequently with one septum, 12–17(–19) x 4–5,5(–6) µm, old spores sometimes with up to 3 transsepta and brownish walls. **Pycnidia** not observed. **Chemistry**: For Intrusa-yellow see below.

Biology and ecology: *Scoliciosporum intrusum* grows in close associations with other crustose lichens, either on these lichens or directly on siliceous rocks but always in close contact with other species. COPPINS (1983: 138, fig. 55) has observed, that the algal cells in the *S. intrusum* thallus are penetrated by haustoria of the mycobiont which underlines the parasitic capability of the species. According to WIRTH (1995: 250), the species grows preferably in the Pertusario-Ophioparmetum.

Host spectrum: mostly on and between *Rhizocarpon geographicum*, *Lecidea lapicida* coll., *Lecidea* spec.; other hosts given in the lichenological literature include *Calvitimela melaleuca*, *Amygdalaria panaeola* (SANTESSON et al. 2004: 75); *Schaereria fuscocinerea* (MAGNUSSON 1945: 314); *Lecidea atrobrunnea* (RAMBOLD & TRIEBEL 1992: 103); *Aspicilia cinerea*, *Calvitimela aglaea* (DEGELIUS 1982: 59); *Rhizocarpon lecanorinum* (HITCH 1996: 43); *Euopsis* cf. *granatina* (APTROOT et al. 1997: 48); *Pertusaria lactea* (BERGER 2000: 70).

Distribution: Europe (Austria, Finland, France, Germany, Norway [incl. Svalbard], Sweden, United Kingdom); Asia (New Guinea); North America (U.S.A. [Maine, Arizona]).

Earlier records (published under various names, mostly the nomenclatural synonyms *Lecidea intrusa*, *Catillaria i*., or *Carbonea i.*): APTROOT et al. 1997: 47–48 (New Guinea); BOOM et al. 1996: 640 (Austria); COPPINS 1983: 138–140 (southern Scandinavia, Norway, Scotland); COPPINS 1992: 384 (Scotland); DEGELIUS 1956: 357 (Norway); DEGELIUS 1982: 59 (Norway); ELVEBAKK & HERTEL 1997: 296 (Svalbard); FRIES 1868: 152–153 (Finland); FRIES 1874: 579 (Norway, Sweden, Finland); HAFELLNER 1997: 10 (Austria); HAFELLNER 2002a: 97 (Austria); HARMAND 1899: 97 (France); HERTEL 1991: 300 (Svalbard); HINDS et al. 2002: 138–139 (U.S.A.: Maine); HITCH 1996: 43 (United Kingdom: Scotland); KILIAS 1981: 392 (Finland); KNOPH et al. 2004: 54 (U.S.A.: Arizona); KULLHEM 1871: 275 (Finland); MAGNUSSON 1945: 314 (Sweden); MAGNUSSON 1952: 140 (Sweden); POELT & TÜRK 1984: 433 (Austria); SANTESSON et al. 2004: 75–76 (Sweden, Norway, Finland); TRIEBEL 1989: 227–228 (Finland); VAINIO 1883: 29, sub *Lecidea contrusa* (Finland); VAINIO 1934: 454–455 (Finland); VOUAUX 1914: 156–157 (Norway, Sweden, Finland); WIRTH 1973: 186–187 (Germany, France); WIRTH 1974: 373 (France); WIRTH 1975: 475 (Germany); WIRTH 1989: 612 (Germany); WIRTH 1995: 248–250 (Germany).

The species is also listed for Italy in NIMIS & MARTELLOS (2003), but the only Italian record is one of the supposed synonym *Carbonea halacsyi* sensu Hafellner & Sancho (see also remark below) from Northern Italy (TRETIACH & HAFELLNER 2000). This record refers to a different taxon, a true *Carbonea*, and *Scoliciosporum intrusum* has evidently not been found in Italy so far. Furthermore, the species has been reported from Iceland, growing on *Pertusaria lactea* (BERGER 2000: 70). Because also a true *Carbonea* species is known from this host, the record will remain uncertain as long as the specimen has not been re-examined.

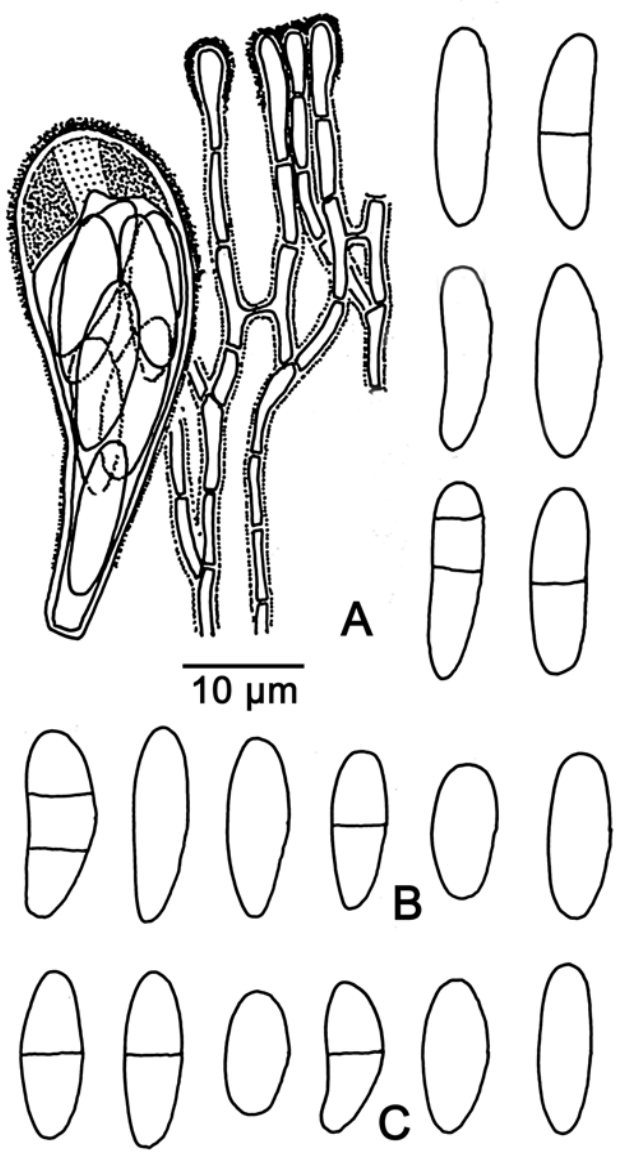

Fig. 1. *Scoliciosporum intrusum.* A: Ascus (after treatment with IKI), paraphyses and ascospores (Poelt 12419). B: Ascospores (Poelt Sc 92/478). C: Ascospores (Magnusson 22230).

Remarks: SANTESSON et al. (2004: 75) give the year of publication of the journal "Botaniska Notiser för ar 1867", in which the species *Lecidea intrusa* was published, as 1868. The title page of this volume bears the year 1867. The entire volume was not available for us, therefore it remains unclear if the volume was either delayed or published in issues.

The placement of the species in several not closely related genera (*Catillaria*, *Micarea*, *Carbonea*) within a relatively short period of time shows impressively the helplessness in finding the correct genus for this species. Only COPPINS (1983), when combining the species into *Micarea*, expressed his hesitation in doing so, mainly because of its unusual habitat for a *Micarea* and the non-micareoid photobiont cells he had observed. COPPINS (l.c.) also pointed out that the species is very similar to *Scoliciosporum umbrinum* in its external appearance and that "*Micarea*" *intrusa* should be included in any future revision of *Scoliciosporum*. COPPINS (1992) even indicated that "*Micarea intrusa*" is often mistaken for *Scoliciosporum umbrinum*. Recently also HINDS et al. (2003) emphasised the similar shape and colour of apothecia of *C*. *intrusa* and *S*. *umbrinum*, but these authors did not comment on that in more detail.

MAGNUSSON (1952: 140) already pointed to a characteristic feature of *Scoliciosporum intrusum*, i.e., the presence of both non-septate and one-septate ascospores, obviously one of the reasons why it was so difficult to accommodate the species in an appropriate genus.

Several modern, relatively complete generic descriptions of *Scoliciosporum* have been published (e.g. VĚZDA 1978, PURVIS 1992, EKMAN & TØNSBERG 2004). The transfer of *Scoliciosporum intrusum* makes it necessary to amend this description in the way that the ascospores may now be non-septate to phragmosporous with up to 7 transsepta, and their shape can be fusiform to ovate, or lunulate, or bacilliform to acicular. The ascus features of *Scoliciosporum* have first been depicted by HAFELLNER (1984). A good description of the ascal features is given by EKMAN & TØNSBERG (2004). Asci of *Scoliciosporum* and its supposed relative *Strangospora* are broadly clavate to cylindrical, 8-spored to multispored, have a thick ascal wall with the typical lecanoralean layering. The asci are apically provided with an amyloid tholus with a distinct non-amyloid central body. A conical ocular chamber is best developed as long as the ascospores are immature. Ascus dehiscence is rostrate.

The pigment colouring the epihymenium is, according to the terminology of MEYER & PRINTZEN (2000), Cinereorufa-green, which is the same as "Lecidea-Grün" (BACHMANN 1890) or pigment A (COPPINS 1983). However, MEYER & PRINTZEN (2000) omitted *Scoliciosporum intrusum* from the list of taxa, which should have this pigment, although it is mentioned by COPPINS (1983: 87). On the other hand, MEYER & PRINTZEN (2000: 575, 582) describe another insoluble apothecial pigment in "*Carbonea intrusa*", called Intrusa-yellow. According to these authors, it is identical with Pigment H characterized by COPPINS (1983). Intrusa-yellow is not a cell wall pigment nor is it deposited in the hymenial gel. It is located inside mycobiont cells, i.e., in the cytoplasm of scattered (possibly damaged) ascogenous hyphae, asci, and ascospores. This fact was not mentioned by MEYER & PRINTZEN (l.c.) but explicitely annotated by COPPINS (l.c.). This yellow to orange pigment evidently is a chinoid substance, as it reacts K+ purple and N-. It remains unclear whether it has any taxonomic importance.

Both RAMBOLD & TRIEBEL (1992: 103) and SANTESSON et al. (2004: 75) list also *Carbonea halacsyi* (J.Steiner) Hafellner & Sancho among the synonyms of *Carbonea intrusa*. However, we always applied this name to a lichenicolous discomycete entirely different from *S*. *intrusum* and confined to yellow *Rhizocarpon* species (e.g. HAFELLNER & SANCHO 1990, see also below). In the early 1990s, some of the specimens of *Carbonea halacsyi* sensu Hafellner & Sancho preserved in GZU have been revised by

Knoph et al. as *Carbonea intrusa*, which is definitely wrong. Knoph, Rambold & Triebel are announced as authors of a still unpublished *Carbonea* monograph ever since (cfr. HERTEL 1991). Evidently these authors could not distinguish true *Scoliciosporum intrusum* and the lichenicolous *Carbonea* when one of these fungi inhabited a yellow *Rhizocarpon*. Perhaps this confusion is the reason why *Lecidea intrusa* Th.Fr. was transferred to *Carbonea* by RAMBOLD & TRIEBEL (in APTROOT & al. 1992). Unfortunately also some more recent descriptions (e.g., in KNOPH et al. 2004) are rather useless due to these mixtures of *Scoliciosporum* and *Carbonea* characters. See also the note on *Lecidea intrudens* H.Magn. and chapter 4.3. below.

SANTESSON et al. (2004: 75) also mention *Lecidea intrudens* H.Magn. (MAGNUSSON 1946: 53) as a synonym of "*Carbonea*" *intrusa*. HERTEL (1970: 424) has restudied the type but not commented on the possible identity of *Lecidea intrudens* and *Scoliciosporum intrusum*. The characters mentioned in the protologue "apothecia…pauca congesta, hypothecium fuscum" (MAGNUSSON, l.c.) and in the emended description by Hertel "Befallsherde sind geschwärzte Zonen von bis 3 mm Durchmesser, Apothecium kohlig schwarz und dicht gedrängt, Hypothecium dunkelbraun, Excipulum kohlig, Paraphysen selten verzweigt" (HERTEL, l.c. [word order re-arranged by the author]) do not fit with *Scoliciosporum intrusum*, for which larger infections, non-agglomerated apothecia, a pale hypothecium, a non-carbonized exciple, and frequently branched and anastomosing paraphyses are characteristic. Magnusson compared his new species with "*Catillaria intrusa*" and regarded the hypothecium and ascospore characters as diagnostic. HERTEL (1970: 408) has also published a drawing of a longitudinal section of the apothecium, which looks perfectly like a drawing of *Carbonea halacsyi* sensu Hafellner & Sancho, thus the identity of or a close relationship between *Lecidea intrudens* and *Carbonea halacsyi* sensu Hafellner & Sancho is possible. As *Carbonea* is outside the scope of this study the problem is not addressed here in further detail.

It is worth mentioning that Magnusson has described both a *Lecidea intrudens* (see above) and a *Lecanora intrudens*. The two original names refer to two different taxa. When describing *Lecanora intrudens* H.Magn. (MAGNUSSON 1942), now *Miriquidica intrudens* (H.Magn.) Hertel et Rambold, the author compares that species in its external aspect and biological behaviour with *Scoliciosporum intrusum*, *Rimularia furvella*, and *Scoliciosporum umbrinum*. Similar observations have been published by POELT (1958: 304).

RAMBOLD & TRIEBEL (1992: 103, 140 sub *Carbonea intrusa*) give further synonyms and mention additional hosts, including *Aspicilia candida* and *Pertusaria lactea*. The specimens where these data refer to need further comparative investigation.

In the synoptic revisions of lichenicolous fungi by VOUAUX (1914) and KEISSLER (1930) the species was thought to be arthonialean and placed in *Conida*. The proposal to do so dates back to SACCARDO & SACCARDO (1906) but turned out to be completely wrong.

Specimens investigated:

AUSTRIA, **Kärnten,** Hohe Tauern, Kreuzeck-Gruppe, Grakofel, Südseite, ca. 2500 m, auf Diorit-Gestein, auf *Lecidea* spec., 13. VII. 1987, leg. W. Petutschnig (GZU). - Nationalpark Hohe Tauern, Schober-Gruppe, Graden Tal W von Döllach-Putschall, Außer Kretschitz S des Fleckenkopfs, ca. 1950 m, 9042/2, Gneisblöcke, teilweise Fe-hältig, auf *Rhizocarpon geographicum*, 22. IV. 1988, leg. J. Hafellner 20612 & M. Walther (herb. Hafellner). - **Salzburg,** Lungau, Schladminger Tauern, Lessachtal, Weg von der Lasshofer Hütte zum Landschitzsee, 9. IX. 1981, leg. J. Poelt (GZU). - Niedere Tauern, Schladminger Tauern, W-facing base of Kampspitze, path from Ursprungalm to Preneggsattel, 400 m SE above Ursprungalm, 47°17'40''N / 13°37'40''E, c. 1700 m, MTB 8747/2; subalpine *Picea-Larix* forest over siliceous rocks, on schist with Quartz veins, on and between *Rhizocarpon geographicum*; 27. VIII. 2001, leg. R. Türk, W. Mayer & O. E. Lange (GZU). - **Steiermark,** Niedere Tauern, [Seckauer Tauern], Rücken N des Geierkogel über Hohentauern, N-seitige Abbrüche bei 1900 - 1950 m, auf *Lecidea* spec., VIII. 1975, leg. J. Poelt (GZU). - Zentralalpen, Murberge, Gstoder ca. 14 km WNW von Murau, im oberen Teil des E-Rückens W ober der Gstoderhütte, 47°08'40''N / 13°59'45''E, ca. 2050 m, GF 8849/4; Blockwerk und niedere Schrofen in Blockwerk und Schrofen in Windheiden, auf N-exponierten Schrägflächen, auf *Rhizocarpon geographicum*, 26. VIII. 2000, leg. J. Hafellner 53568 (herb. Hafellner). - Gurktaler Alpen, Frauenalm S von Murau, S-exponierte Abbrüche zwischen Oberberg und Frauenalm, ca. 1830 m, auf *Rhizocarpon* spec., 18. VI. 1978, leg. H. Mayrhofer (GZU). - [Steirisches Randgebirge], Koralpe, freistehende Felsen auf der Handalpe N über der Weineben, 1750 - 1850 m, zwischen *Rhizocarpon geographicum*, 13. VI. 1972, leg. J. Poelt (GZU). - Koralpe, freie Felsgruppe auf dem Kamm ESE der Glitzfelsen, N über der Glitzalm bei Schwanberg, 1750 - 1760 m, auf *Rhizocarpon geographicum*, 16. X. 1977, leg. J. Poelt & J. Wetz (GZU). - Stubalpe, Rücken zwischen Speikkogel und Weißenstein, 2020–2030 m, Gneisfelsen und Blöcke, auf und zwischen *Rhizocarpon geographicum*, 26. V. 1985, leg. K. Kalb & J. Poelt (GZU). – **FINLAND,** Schärenhof von Turku, Korppo, Lohm, VIII. 1965, leg. J. Poelt (GZU). – **FRANCE, Elsaß,** Vogesen, Hohneck, Granitfelsen der Spitzköpfe, ca. 1250–1300 m, auf *Rhizocarpon geographicum*, VII. 1969, leg. V. Wirth 1865 (GZU). – **SLOVAKIA,** Vysoké Tatry (Hohe Tatra), Bielovodske dolina, 900–1300 m, auf Granitfelsen, auf *Rhizocarpon geographicum*, 4. VII. 1993, leg. I. Pisút & J. Poelt 93-551 (GZU). – **SWEDEN, Torne Lappmark,** Umgebung von Abisko, kurz über dem Torneträsk, unterhalb der Naturvitensk. Station Abisko, ca. 360 m, erzhaltiger Schieferblock, on *Rhizocarpon geographicum*, 19. VII. 1967, leg. J. Poelt (GZU, as accompanying species on specimen of *Miriquidica nigroleprosa*). - **Bohuslän,** Norum, St. Askerön, N of Danestan, on and between *Aspicilia* spec., together with *Scoliciosporum umbrinum* var. *compactum* (!), 12. VIII. 1950, leg. A. H. Magnusson 22230 (GZU). – **UNITED KINGDOM, Scotland,** Westerness (V.C. 97), Ariundle Wood National Nature Reserve, ca. 7 km NE of Strontian, disused mine NW of Ariundle Wood, 240–260 m, on *Rhizocarpon geographicum*, 18. VI. 1992, leg. B. Coppins, P. W. James & J. Poelt Sc92/478 (GZU).

4. Discussion

4.1. Which characters indicate that *Lecidea intrusa* Th.Fr. belongs to *Scoliciosporum*?

As already mentioned by COPPINS (1983) and HINDS et al. (2002), the habit of *Scoliciosporum intrusum* apothecia is exactly like in other *Scoliciosporum* species. Also the anatomical features of the apothecia fit perfectly with *Scoliciosporum*, i.e., the poorly developed, not carbonized exciple composed of intricate hyphae, the hyaline to weakly pigmented hypothecium, the richly branched and anastomosing paraphyses, the shape of the asci, and the construction of the ascal wall. Unusual are the unicellular ascospores which may become one-septate with age. A certain tendency of the ascospores to be asymmetric indicates that the ascospores can be regarded as an extreme within the intrageneric continuum of *Scoliciosporum*.

When SÉRUSIAUX (1993) discovered and described *S. curvatum* Sérus., it became evident that *Scoliciosporum* species do not necessarily have bacilliform to acicular ascospores, as demanded in the generic descriptions by MASSALONGO (1852) or VĚZDA (1978). The ascospores may also be fusiform to lunulate, and non- or one-

septate. Therefore the ascospore characters of *S. intrusum* are definitely within the intrageneric range.

4.2. Which characters indicate that *Lecidea intrusa* Th.Fr. does not belong to *Carbonea*?

The genus *Carbonea* (Hertel) Hertel is typified with *Carbonea atronivea* (Arnold) Hertel. According to the description given by HERTEL (1983), the diagnostic features of the genus are black, marginate apothecia, an intensely pigmented exciple lacking algal cells, *Lecanora*-type asci with non-septate ascospores, unbranched conglutinated paraphyses, and filiform pycnospores. The generic concept applied by Knoph et al. (2004) seems much wider. However, it is difficult to decide which of the generic characters have been broadened, mainly because of the inclusion of the alien *Scoliciosporum intrusum* in *Carbonea*.

If we apply the generic concept of HERTEL (1983) and also consider the characters of other *Carbonea* species, it is clear that *Lecidea intrusa* Th.Fr. does not fit into *Carbonea*, especially because of its non-carbonised exciple composed of intricate hyphae, the hardly pigmented hypothecium, and the ramified and anastomosing paraphyses,.

4.3. How can *Scoliciosporum intrusum* be distinguished from *Carbonea halacsyi* sensu Hafellner & Sancho?

As the holotype of *Lecidea halacsyi* Steiner has not been available for study, it is not sure if the species called *Carbonea halacsyi* by HAFELLNER & SANCHO (1990) and the taxon represented by the type are identical. Nevertheless it is evident that *Carbonea halacsyi* sensu Hafellner & Sancho is not conspecific with *Scoliciosporum intrusum* but a different lichenicolous fungus, which definitely belongs to *Carbonea*.

The protologue of *Lecidea halacsyi* J.Steiner (STEINER 1894) does not allow a clear decision to which taxon it refers. Some of the characters mentioned in the protologue of *Lecidea halacsyi* do not agree with *Scoliciosporum intrusum* but with a lichenicolous *Carbonea*, which is not rare in Central Europe (and a third similar lichenicolous discomycete which regularly attacks *Rhizocarpon geographicum* is not known so far). Therefore we saw a good chance that the species we had found in the Alps and in the mountains of central Spain is identical with Steiner's species (HAFELLNER & SANCHO 1990). However, Steiner (l.c.) compared *Lecidea halacsyi* with *Lecidea supersparsa* (now *Carbonea supersparsa*), a species with +/- flat apothecia growing on *Lecanora* species. The species we used to call *Carbonea halacsyi* is closer to *Carbonea aggregantula*, a species not mentioned by Steiner in his discussion.

Carbonea halacsyi sensu Hafellner & Sancho has a much narrower host spectrum than *Scoliciosporum intrusum*. Until now it is confined to yellow *Rhizocarpon* species. Although it is most frequently found on the polymorphic *Rhizocarpon geographicum*, also other yellow *Rhizocarpon* species are attacked, e.g., *Rhizocarpon alpicola*. For the host spectrum of *Scoliciosporum intrusum* see above. The infections of *Carbonea halacsyi* sensu Hafellner & Sancho remain dot-like and therefore always smaller than those of *Scoliciosporum intrusum*. In *Carbonea halacsyi* sensu Hafellner & Sancho a lichenized thallus is not discernible, usually the thallus is only visible as a prothallus line between host and parasite. Already at a very early stage, entirely black, strongly convex apothecia are developed in the infected areas. Other than in *Scoliciosporum intrusum*, sterile thalli are unknown, at least they are not discernible on the host thallus, which has a well developed black prothallus itself.

4.4. Lichenicolous growth in *Scoliciosporum*

So far, only two obligatorily lichenicolous *Scoliciosporum* species are known, *S. vouauxii* (de Lesd.) Hafellner (HAFELLNER 2002b) and *S. intrusum*. While *S. intrusum* grows on a range of saxicolous crustose lichens inhabiting siliceous rocks, *S. vouauxii* has so far been found only on *Ramalina*.

Beside these obligatorily lichenicolous *Scoliciosporum* species, the genus comprises also two facultative inhabitants of other lichen thalli. The type species, *S. umbrinum*, commonly grows on other substrates, but it is occasionally found on other lichens in different ecological niches, including saxicolous crusts (*Aspicilia caesiocinerea*, *A. cinerea*, *Lecanora rupicola*, *Lecanora sulphurea*, *Orphniospora mosigii*, *Pertusaria lactea*, *Pertusaria monogona*, *Rinodina badiella*), as well as both corticolous (*Evernia prunastri*) and terricolous (*Peltigera aphthosa*) macrolichens (e.g. BERGER 2000, CLAUZADE & RONDON 1960, HAFELLNER 2002b, POELT 1958, RAMBOLD & TRIEBEL 1992, TRETIACH & HAFELLNER 2000). Another species which is rarely found growing on lichens is *S. chlorococcum*. It has been reported on *Platismatia glauca* (HAFELLNER 2002b).

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