

On the discomycetous genera *Ascocalyx* NAUMOV and *Gremmeniella* MORELET

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Summary. – The causal agent of “*Scleroderris* canker” or “dieback” of pines, originally described as *Crumenula abietina* LAGERB., was transferred several times to other genera, partly because of differing concepts of its taxonomic position, and partly because of nomenclatural necessities. As general agreement among pathologists and mycologists on the correct fungus name and on relationships to several similar coniferous discomycetes is still lacking, a thorough comparative investigation on that group, including the genera *Ascocalyx* NAUMOV, *Gremmeniella* MORELET, and *Encoeliopsis* NANNF. is presented. In spite of morphological differences (table 1) among the involved species, these are best arranged within the genus *Ascocalyx* due to similarities of ascomal structures (asci and ascospores) and in consideration of the results of biochemical investigations. Therefore, *Ascocalyx abietina* (NAUMOV) SCHLAEFFER-BERNHARD for the pine pathogen, and *Ascocalyx laricina* (ETTL.) SCHLAEFFER-BERNHARD for the larch pathogen are accepted. Additionally, *Gremmeniella juniperina* HOLM & HOLM is transferred to *Ascocalyx*.

Zusammenfassung. – Der pilzliche Erreger des „*Scleroderris*-canker“ oder des „Triebsterbens“ der *Pinus*-Arten, ursprünglich als *Crumenula abietina* LAGERBERG beschrieben, wurde mehrmals, teils aus nomenklatorischen, teils aus taxonomischen Gründen zu anderen Gattungen gestellt. Leider fehlt heute unter den Forstpathologen und den Mykologen Übereinstimmung über den zu verwendenden Namen und über den Grad der verwandtschaftlichen Beziehungen zu anderen Coniferen parasitierenden Discomyceten. Die vergleichende Untersuchung der Gattungen *Ascocalyx* NAUMOV, *Gremmeniella* MORELET und *Encoeliopsis* NANNF. zeigt nun, dass trotz einiger auffallenden morphologischen Unterschiede der einbezogenen Arten auf Grund der Übereinstimmung in wichtigen morphologischen und biochemischen Eigenschaften eine Vereinigung in der Gattung *Ascocalyx* angezeigt ist. Als Namen für den *Pinus*-Parasiten stehen *Ascocalyx abietina* (LAGERB.) SCHLAEFFER-BERNHARD, für den *Larix*-Parasiten *Ascocalyx laricina* (ETTLINGER) SCHLAEFFER-BERNHARD zur Verfügung; für *Gremmeniella juniperina* HOLM & HOLM wird *Ascocalyx juniperina* (HOLM & HOLM) MÜLLER & DORWORTH vorgeschlagen.

Introduction

The pathogen causing pine diseases named “*Scleroderris* canker” in North America and “dieback”, “topkill”, or “bud drought” in Europe was originally described as *Crumenula abietina* by LAGERBERG (1913). Subsequently several proposals for name changes, always presented with well offered reasons, were made by

GREMME (1953; 1955: to *Scleroderma abietina* and *Scleroderma lagerbergii* respectively), by MORELET (1969: to *Gremmeniella abietina*), by SCHLAEFFER-BERNHARD (1969: to *Ascocalyx abietina*), and by REID (ap. DENNIS, 1971: to *Lagerbergia abietina*). Of course a situation with such a number of available names is not tenable, neither for the pathologist who needs a name accepted and used by all his colleagues (expressed by DORWORTH, 1981), nor for the mycologist who, additionally has to consider relationships to other organisms and who is bound to the nomenclatural rules regulating the names of fungal organisms.

As the names *Scleroderma* (PERS.) BON. and *Crumenula* de NOT. represent younger synonyms of *Godronia* MOUGEOT & LÉVEILLÉ and *Lagerbergia* REID is an obligate synonym of *Gremmeniella* MORELET, all species names combined with these names have to be rejected. The genus *Godronia*, now including *Crumenula* s. str. and *Scleroderma*, has to be applied to ascomycetes clearly distinct from *Crumenula abietina* (GROVES, 1965). In that respect all authors agree. However, there is no reason to reject also the term "Scleroderma canker" for a disease caused by that fungus; pathologists may continue to use that term. On the other hand, the genus names *Gremmeniella* and *Ascocalyx* (MORELET, 1969; SCHLAEFFER-BERN-

Table 1. Comparison among species of *Ascocalyx* and *Encoeliopsis*.

Structures	Original names	<i>Crumenula abietina</i>	<i>Ascocalyx abietis</i>	<i>Ascocalyx asiaticus</i>	<i>Ascocalyx tenuisporus</i>	<i>Crumenula laricina</i>	<i>Gremmeniella juniperina</i>	<i>Encoeliopsis rhododendri</i>
Apothecium	margo, textura exceptulum, textura	prismatica angularis	prismatica angularis	prismatica angularis porrecta	prismatica angularis	prismatica angularis	prismatica angularis	globose, globose
	hypothecium, textura number on stromata	intricata 1	intricata 1 to 3	epidermoidea 1 to 6	intricata 1 to 10	intricata 1 to 2	intricata 1	obovate
<i>Hypostroma</i>	shape	bulbous, sometimes, stipe-like not conspicuously erumpent	largely erumpent, in apical portion small loculi of anamorph	as in <i>Ascocalyx abietis</i>	as in <i>Ascocalyx abietis</i>	bulbous stipe-like erumpent	not conspicuous stipe-like	only sub
	textura	angularis epidermoidea	angularis	epidermoidea	angularis epidermoidea	angularis	angularis	
Asci	iodine reaction size µm	80-125×7.5-10.5	70-110×8.5-10.5	100-125×17-20	80-95×8-10.5	65-115×6-9	75-100×9-10	70-80
Ascospores	shape	ellipsoidic or slightly clavate	fusoid	elongated fusoid to filiform	fusoid	fusoid	clavate	ellipsoidic
	septation size µm	2 to 3 14-20 × 3.5-5	1 to 3 14-23 × 4-4.5	up to 15 65-80 × 5-6	3 to 5 30-50 × 2-3	1 to (3) 10-16 × 3-4	3 18-20 × 4	12-25
Paraphyses		filiform, hyaline, nodose	filiform slightly swollen at apex	filiform slightly swollen at apex	filiform slightly swollen at apex	filiform slightly swollen at apex	filiform slightly swollen at apex	filiform and branched
Anamorph	form genus conidiogenous cell	<i>Branchorhizia</i> phialidic	<i>Bothrodiscus</i> holoblastic sympodial	<i>Bothrodiscus</i> holoblastic sympodial	<i>Bothrodiscus</i> holoblastic sympodial	<i>Branchorhizia</i> phialidic	not named holoblastic	probable
	conidiomata	pycnidia, sometimes multi-locular	loculi in upper portion of hypostroma	as in <i>Ascocalyx abietis</i>	as in <i>Ascocalyx abietis</i>	pycnidia	on ascospores	
	conidia, shape	fusoid, curved	fusoid, curved	elongate cylindrical or fusoid	fusoid, curved	fusoid	ellipsoidic	
	septation size µm	up to 7 24-50 × 2.5-4.5	up to 5 20-39 × 3.5-4.5	3 to 4 35-65 × 3-4.5	3 to 5 20-45 × 3-4	1 to (3) 15-23 × 3-4	0 3-4 × 2	

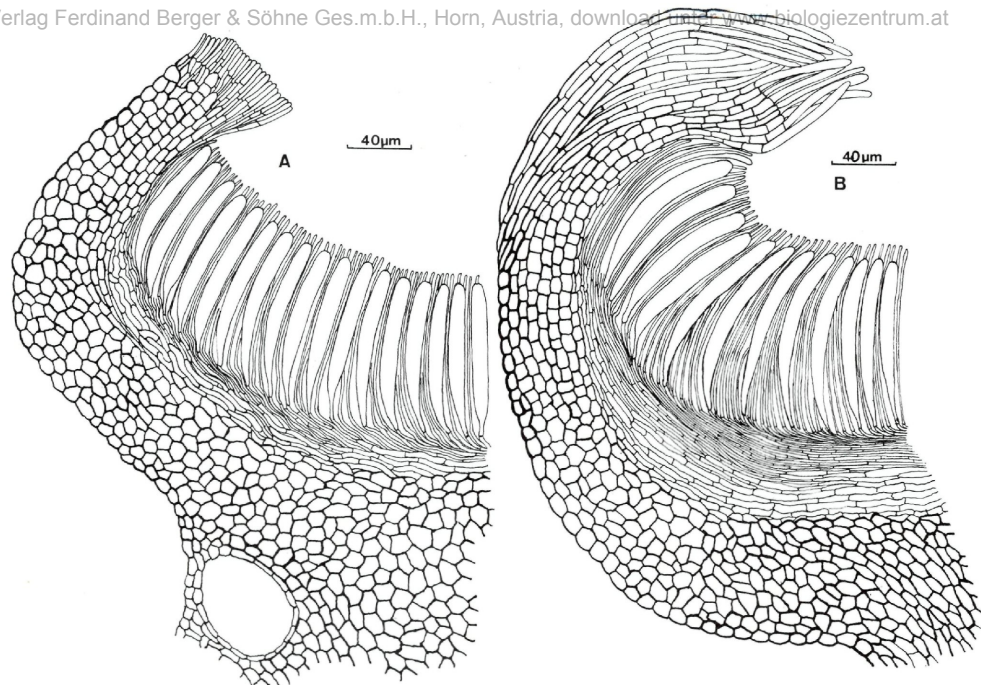


Fig. 1. Section trough a portion of the ascoma of A: *Ascocalyx abietis*; B: *Ascocalyx abietina*.

HARD, 1969) conform with the nomenclatural rules; the choice of only one of them is a taxonomic problem which centres on the question whether the pathogen is nearly related to and objectively not separable from the genus *Ascocalyx* NAUMOV (1925), or whether it requires an isolated position within the inoperculate discomycetes of the order Helotiales, and therefore, justifies the erection of a genus of its own: *Gremmeniella* MORELET.

A somewhat similar problem concerns *Crumenula laricina* ETTLINGER (1945) which is involved in a dieback of young *Larix* trees in Europe and in North America. It was transferred to *Scleroderris* by GREMMEN (1953), to *Encoeliopsis* NANNFELDT by GROVES (1965), and to *Ascocalyx* by SCHLAEFFER-BERNHARD (1969). At present pathologists prefer the name *Encoeliopsis laricina* although the fungus does not at all fit the genus *Encoeliopsis* which must be restricted to a small number of discomycetes on Ericaceae (KORF, 1973) and may even be monotypic. The type species, *Encoeliopsis rhododendri* (CES.) NANNF. forms its apothecia on a hyphal subiculum covering old fruits of *Rhododendron ferrugineum* L. No stromatic structures are formed. Furthermore the tissue of the ectal excipulum is of "textura globulosa", and the paraphyses are distinctly inflated and brown at the apex (fig. 5). *Crumenula laricina* forms a *Brunchorstia* anamorph, as does *C. abietina* and the apothecial morphology is also similar (figs. 2, 3). For SCHLAEFFER-BERNHARD (1969) the logical decision was to put *C. laricina* also into *Ascocalyx*, although it differs somewhat in that the majority of ascospores and conidia are two-celled (three- and four-celled spores are also present). Therefore, it is necessary to decide as well whether *C. laricina* belongs within *Gremmeniella* or *Ascocalyx*.

Commonly there is agreement that the perfect state (= teleomorph) represents the main base for ascomycete taxonomy. The principles of NANNFELDT (1932) demand that consideration be given as well to the diversity of structures of ascomata viz. wall (peridium, for discomycetes = excipulum), hymenium, composed of asci with ascospores and sterile structures (= paraphyses), and some other criteria (e. g. position in or on substrate, stromatic structures upon or within ascomata develop). Additionally, imperfect states (= anamorphs) may be considered. However, these should not present the main reason much less the exclusive reason for the judgement of the taxonomic position because they may be lacking or their developmental type is not fully understood. For decisions on the application of genus names, we have also to consider possible variation among species involved and a clear delimitation from related or morphologically similar genera is demanded. Furthermore, the circumscription of a genus should not impede inclusion of species not presently known.

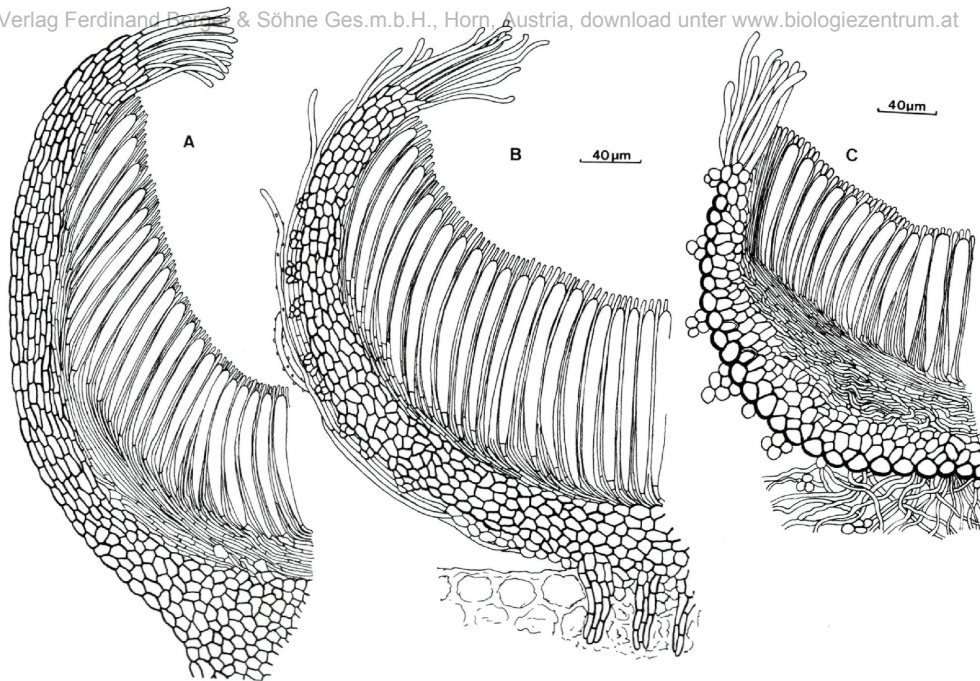


Fig. 2. Section through a portion of the ascoma of A: *Ascocalyx laricina*; B: *Ascocalyx juniperina*; C: *Encoeliopsis rhododendri*.

As to our problem the only way to reach a satisfactory solution is by comparison of all taxa involved viz. the known species of *Ascocalyx* (GROVES, 1968), *Crumenula abietina*, *Crumenula larinica*, the recently described *Gremmeniella juniperina* (HOLM, 1977), and *Encoeliopsis rhododendri* (for that discussion we use the original names). The results of that comparison are summarized in table 1. It is obvious that there is a distinct gap between *Encoeliopsis rhododendri*, with an excipulum of textura globulosa, and all the others with an excipulum of textura prismatica-angularis (figs. 1, 2, 3, 4 and 5). The iodine negative ascus apex and the ascospores (shape, colour, size and septation) vary within certain limits but represent a rather uniform complex within inoperculate discomycetes (fig. 6). Therefore, in accordance with the presently accepted rules for generic arrangement of inoperculate discomycetes (NANNFELDT, 1932; KORF, 1973), the separation of these six species into two genera does not seem justified.

However, we also have to consider the need for stability in the use of names, urgently demanded by pathologists who at present prefer "*Gremmeniella*" for the pine "*Scleroderris* canker" fungus and "*Encoeliopsis*" for the larch dieback fungus. We also have to consider MORELET'S (1981) comparison of *Crumenula abietina* and *Ascocalyx abietis* in which he provided a detailed genus description for *Gremmeniella*. According to that comparison the two species are convincingly separated based on their stromatal structures and on the anamorphs. On the other hand that separation is not demonstrated for the ascomata, asci and ascospores, which in fact reveal a near relationship. As the stromatal structures do not differ in their tissue texture but only in their size, use of this characteristic forms a weak argument. MORELET'S main reason for the separation into two genera, therefore, is based on the developmental differences of the two conidial states involved: *Brunchorstia* belonging to *Gremmeniella* forms phialidic conidia whereas *Bothrodiscus*, belonging to *Ascocalyx abietis* exhibits a holoblastic-sympodial conidiogenesis (e. g. SUTTON, 1980). However, in both cases the conidia (but not the conidiomata) are almost identical in shape, colour, and septation. According to recent investigations (e. g. COLE & SAMSON, 1979; MADELIN, 1979) the gap between phialidic and holoblastic sympodial conidiogenesis is not always of principal significance. Some genera even include taxa with both kinds such as the deuteromycetous genus *Chloridium* LINK (HAMMILL, 1972; GAMS & HOLUBOVA-JECHOVA, 1976) and the genus *Codinea* MAIRE (HUGHES & KENDRICK, 1968). At present a thorough investigation of conidiogenesis is available only for *C. abietina* (MORELET, 1981) so that no exact comparison is possible. But we have to consider KENDRICK (1981) who noted explicitly that developmental criteria among deuteromycetes cannot

form the basis of a system of classification among these fungi that is more nearly valid than that based upon characteristics of the sexual states.

Additionally, the near relationship between these two species is clearly demonstrated by the results of acrylamid gel patterns of the soluble proteins and by immunodiffusion against soluble antisera (DORWORTH, 1974). Then we also have to consider that MORELET (1981) accepted *Gremmeniella juniperina* as a component of *Gremmeniella*, but excluded *Crumenula laricina*. The former does not have a pycnidial anamorph (only conidia formed on germinating ascospores) and its hypostroma is very weakly developed; the latter has a *Brunchorstia* anamorph similar to that of *C. abietina* and a hypostroma somewhat larger and higher than in *C. abietina*. The possible restriction of the genus *Gremmeniella* to *C. abietina* would result in the exclusion of *Gremmeniella juniperina* and *Crumenula laricina* from both *Ascocalyx* and *Gremmeniella*. In that event, it probably would be necessary to place these species in new genera, a procedure

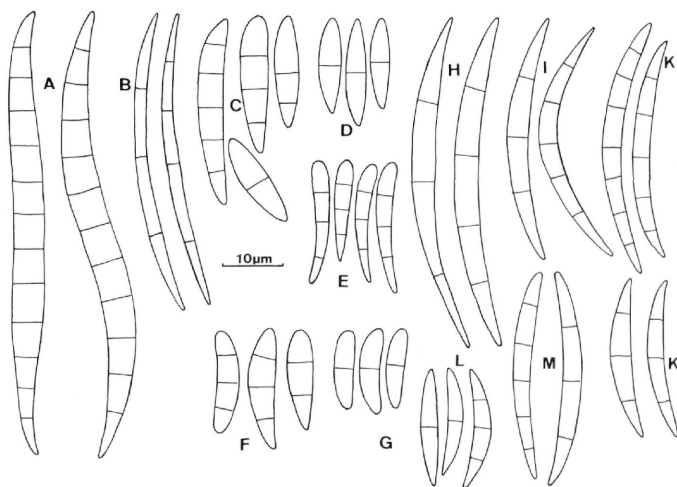


Fig. 3. Ascospores of A: *Ascocalyx asiaticus*; B: *Ascocalyx tenuisporus*; C: *Ascocalyx abietis*; D: *Ascocalyx laricina*; E: *Ascocalyx juniperina*; F: *Ascocalyx abietina*; G: *Encoeliopsis rhododendri*.

Conidia of H: *Bothrodiscus* state of *Ascocalyx asiaticus*; I: *Bothrodiscus* state of *Ascocalyx tenuisporus*; K₁: *Brunchorstia* State of *Ascocalyx abietina* (*Brunchorstia pinea* var. *cembrae*), K₂: *Brunchorstia* state of *Ascocalyx abietina* (*Brunchorstia pinea* var. *typica*); L: *Brunchorstia* state of *Ascocalyx laricina* (*Brunchorstia laricina*); M: *Bothrodiscus* state of *Ascocalyx abietis* (*Bothrodiscus berenice*).

which would confuse the situation further. For our decision we must also consider KORF (1973) who had to synonymize the two genera for his key for all discomycetous genera and DENNIS (1976) who separated them only on the basis of the differences in conidial states.

A comparison with the morphologically similar (but not nearly related) genus *Godronia* MOUG. & LÉV. (GROVES, 1965; SCHLAEFFER-BERNHARD, 1969) reveals a similar situation. It includes also species with large stromata (e. g. *G. ribis*) and those with weak or even non-existent stromatal structures. Furthermore, the known *Godronia* species form either the *Fuckelia* anamorph (e. g. *G. ribis*) or the anamorph belongs to the quite distinct genus *Topospora*. On the other hand it would be extremely difficult to divide *Godronia* convincingly into two (or more) genera on behalf of these differences.

In respect of all these facts we cannot see any demonstrable reason for existence of the genus *Gremmeniella* and we propose, therefore, to follow SCHLAEFFER-BERNHARD (1969) and KORF (1973) in the inclusion of *Crumenula laricina*, *Crumenula abietina* and in addition of *Gremmeniella juniperina* in the genus *Ascocalyx*.

Ascocalyx NAUMOV

Bolezni rast 14: 138 (1925)

Synonyms: *Gremmeniella* MORELET – Bull. Soc. Sci. archéol. Toulon, 183: 9 (1969)

Lagerbergia REID ap. DENNIS, Kew Bull. 25: 350 (1971)

Typus: *Ascocalyx abietis* NAUMOV.

Apothecia cup-like, dark brown, solitary or in groups of 2 to 10, erumpent, either on stipe-like, sometimes rather weakly developed hypostromata or on large and thick hypostromata which include loculi-like pycnidia in the apical portion; with ectal excipulum of textura prismatica to textura angularis and with margin of textura prismatica and often ending with free hyphae; medullary excipulum of textura angularis to textura epidermoidea; hypothecium colourless, of textura intricata or textura porrecta. Asci cylindrical or slightly clavate, iodine negative, accompanied by filiform, occasionally somewhat branched paraphyses, eight – spored. Ascospores hyaline, fusoid, elliptic-cylindrical or slightly clavate, often curved, 1- to pluriseptate.

Anamorphs: *Bothrodiscus* SHEAR, *Brunchorstia* ERIKSSON, occasionally with conidia on germinating ascospores.

Key to species

1. Hypostromata clearly erumpent, large, carrying one to ten cupulate apothecia, loculi-like conidiomata of *Bothrodiscus*

- formed within apical portion, empty loculi often present with apothecia 2
- 1*. Hypostromata smaller, stipe-like, carrying mostly one, rarely two apothecia, pycnidial conidiomata of the *Brunchorstia* anamorph rarely connected with apothecia, often occurring independently or lacking 4
2. Ascospores comparatively short, up to 25 µm long, 3- to 5-septate, on *Abies* spp. *Ascocalyx abietis* (1)
- 2*. Ascospores longer than 25 µm, up to 15-septate 3
3. Ascospores (55)65–80(90)×5.0–6.0(7.0) µm, up to 15-septate, on *Abies pindrow* *Ascocalyx asiaticus* (2)
- 3*. Ascospores (25)30–50(60)×2.0–3.0 µm, 3- to 5-septate, on *Abies lasiocarpa* *Ascocalyx tenuisporus* (3)
4. Apothecia distinctly hairy, hypostroma very weakly developed, ascospores clavate, 18–20×3.5–4.0 µm, on *Juniperus communis* *Ascocalyx juniperina* (4)
- 4*. Apothecia not hairy or with very few hairs, ascospores not clavate 5
5. Ascospores mainly 2-celled, 10–16×3.0–4.0 µm, on *Larix* spp. *Ascocalyx laricina* (5)
- 5*. Ascospores 2- to 4-celled, 14–20×3.5–5.0 µm, mainly on *Pinus* spp., occasionally on other coniferous hosts (e. g. *Abies*, *Larix*) *Ascocalyx abietina* (6)

Sometimes only asexual states are present; they may be keyed out in the following way:

1. Conidiogenous cells phialidic, pycnidial conidiomata not connected with perfect state stromata (= *Brunchorstia*) 2
- 1*. Conidiogenous cells holoblastic-sympodial, numerous pycnidial conidiomata integrated as small holes in the basal portion of the cup-like structures of stromata, on which apothecia later develop (= *Bothrodiscus*) 3
2. Conidia mainly 2-celled, 15–23×3.0–4.0 µm, on *Larix*, *Brunchorstia laricina* state of *Ascocalyx laricina* (5)
- 2*. Conidia up to 8-celled, 24–50×2.5–4.0 µm, on *Pinus* spp. occasionally on other coniferous hosts
..... *Brunchorstia pinea* state of *Ascocalyx abietina* (6)
3. Conidia 35–65×3.0–4.5 µm, on *Abies pindrow* (Pakistan):
..... *Bothrodiscus* state of *Ascocalyx asiaticus* (2)
- 3*. Conidia 20–45×3.0–5.0 µm, on *Abies lasiocarpus* (North America) *Bothrodiscus* state of *Ascocalyx tenuisporus* (3)
- 3** Conidia 20–39×3.5–4.5 µm, on *Abies* spp. (North America and northern Europe)
..... *Bothrodiscus berenice* state of *Ascocalyx abietis* (1)

1. *Ascocalyx abietis* NAUMOV (1925). Bolezni rast 14, 138 (Fig. 1: A; 3: C, M)
Synonym: *Godronia abietis* (NAUMOV) SEAVER (1945), Mycologia 37: 356.
Anamorph: *Bothrodiscus berenice* (BERK. & CURT.) GROVES (synonymy in GROVES, 1968).
Geographical range: northern North America, northern Europe.
2. *Ascocalyx asiaticus* GROVES (1968). Canad. J. Bot. 46: 1274 (Fig. 3: A, H.)
Anamorph: *Bothrodiscus* (not named).
Geographical range: Himalaya (Pakistan).
3. *Ascocalyx tenuisporus* GROVES (1968). Canad. J. Bot. 46: 1275 (Fig. 3: B, T.)
Anamorph: *Bothrodiscus* (not named).
Geographical range: northern North America.
4. *Ascocalyx juniperinus* (HOLM & HOLM) MÜLLER & DORWORTH comb. nov. (Fig. 2: B; 3: E)
Typonym: *Gremmeniella juniperina* HOLM & HOLM (1977). Symb. Bot. Upsal. 21 (3): 11.
Anamorph: conidia formed only on germinating ascospores.
Geographical range: northern and central Scandinavian mountains.
5. *Ascocalyx laricina* (ETTLINGER) SCHLAEFFER-BERNHARD (1969). Sydowia 22: 42 (Fig. 2: A; 3 D, L)
Synonyms: *Crumenula laricina* ETTLINGER (1945). Beitr. Krypt. Fl. Schweiz 10 (1): 53.
Scleroderris laricina (ETTLINGER) GREMMEN (1953). Acta Bot. Neerl. 2: 236.
Encoeliopsis laricina (ETTLINGER) GROVES (1969). Canad. J. Bot. 47: 1324.
Anamorph: *Brunchorstia laricina* Ettliger.
Geographical range: probably circumpolar, recorded from northern North America and Europe, including mountainous regions of both continents.
6. *Ascocalyx abietina* (LAGERBERG) SCHLAEFFER-BERNHARD (1969). Sydowia 22: 44 (Fig. 1: B; 3: F, K)
Synonyms: MORELET (1981), sub *Gremmeniella abietina*.
Anamorph: *Brunchorstia pinea* (KARST.) v. HÖHN.
Geographical range: North America, Europe, probably circumpolar.
7. *Encoeliopsis rhododendri* (CES.) NANNFELDT (1932). Nova acta reg. soc. sci. Upsal. 4 (8): 306 (Fig. 2: C; 3: G)
Synonyms: SCHLAEFFER-BERNHARD (1968).
Anamorph: none
Geographical range: Alps.

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