Schroeteria Decaisneana, S. Poeltii, and Ciboria Ploettneriana (Sclerotiniaceae, Helotiales, Ascomycota), Three Parasites on Veronica Seeds: First Report of Teleomorphs in Schroeteria

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Abstract

Three little known, morphologically similar species of *Sclerotiniaceae* which form their apothecia on fallen stromatized *Veronica* seeds are described and illustrated in detail based on fresh collections or moist chamber cultures of infected seeds: *Ciboria ploettneriana*, *Schroeteria decaisneana*, and *Schroeteria poeltii*. The former two were found on *Veronica hederifolia* agg. at different sites of temperate central Europe, the latter on *V. cymbalaria* in a mediterranean region of Spain. The latter two are anamorph-typified and here reported for the first time with their teleomorph.

Ciboria ploettneriana was described by Kirschstein as *Sclerotiniaploettneriana* on seeds of *V. hederifolia* agg. but is currently treated in *Ciboria*. Based on the reexamination of four syntype specimens in B it became evident that Kirschstein confused the two species on *V. hederifolia*. A lectotype is therefore designated for *S. ploettneriana*.

Members of *Schroeteria* are specific plant parasites infecting fruits of different *Veronica* spp. *Schroeteria* has earlier been referred to the *Ustilaginales* (*Basidiomycota*) based on its smut-like chlamydospores, but later light-microscopic and ultrastructural studies suggested that it represents a false smut fungus belonging to the *Sclerotiniaceae* (*Helotiales*).

rDNA sequences were obtained from chlamydospores of *Schroeteria bornmuelleri* (on *V. rubrifolia*), *S. delastrina* (generic type, on *Veronica arvensis*), *S. decaisneana*, and *S. poeltii*, and from apothecia on *V. hederifolia* agg. and *V. cymbalaria* seeds. As a result, the anamorph-teleomorph connection could be verified for *Schroeteria decaisneana* and *S. poeltii* based on a 100% ITS similarity between both morphs, whereas *Ciboria ploettneriana* in the here redefined sense could not be connected to an anamorph.

Our phylogenetic analyses show that *Ciboria ploettneriana* belongs in the relationship of *Sclerotinia*, *Stromatinia*, and *Grovesinia* rather than *Ciboria*, but its placement was not supported. Also *Schroeteria poeltii* clustered unresolved in this relationship but has a much higher molecular distance to those. The remaining three *Schroeteria* spp. formed a supported monophyletic group, the *Schroeteria* core clade, which clustered with medium to low support distantly to a member of the *Monilinia alpina* group of section *Disjunctoriae* (*M. jezoensis*). ITS distances of 5–6.3% were found among members of the *Schroeteria* core clade, and 13.8–14.7% between the core clade and *S. poeltii*. The high distance of *S. poeltii* reflects its deviating chlamydospore morphology.

Despite the high heterogeneity in the available ITS and LSU data, *Schroeteria* is accepted here under inclusion of *S. poeltii* as a genus distinct from *Monilinia*, particularly because of its very special anamorphs. A similar heterogeneity in rDNA analyses was observed in *Monilinia* and other genera of *Sclerotiniaceae*. Protein-coding genes should be investigated in order to obtain a more natural phylogeny within the *Sclerotiniaceae*.

Introduction

The family *Sclerotiniaceae* comprises about 150 mainly plant parasitic species in 28 accepted genera (Baral 2016). Most of these genera are pleomorphic, producing apothecia (teleomorph, sexual) and a conidial state (anamorph, asexual), but some are still without a known teleomorph. *Sclerotiniaceae* are thought to be a relatively recently evolved lineage of primarily necrotrophic but often biotrophic (parasitic) host generalists or specialists (Andrew et al. 2012). Species of the family are generally hygrobionts, i.e., they form their apothecia and conidial states on fallen, permanently moist remnants of various mono- and dicotyledonous plants: on herbaceous stems, leaves, flowers, fruits and seeds, also on wood and bark, rarely on dung (Whetzel 1945, Schumacher & Kohn 1985, Spooner 1987, Palmer 1991, Baral 2016). Three xerobiotic, apparently necrotrophic species on air-exposed branches, previously included in the heterogeneous subfamily *Encoelioideae* of *Helotiaceae*, have recently been transferred to *Sclerotiniaceae* and placed in the new genus *Sclerencoelia* Pärtel & Baral (Pärtel et al. 2016), which raises the number of accepted genera to 29.

A main characteristic of the *Sclerotiniaceae* and the closely related, paraphyletic, necrotrophic to parasitic *Rutstroemiaceae* is the amyloid ascus apical ring of the *Sclerotinia*-type (Baral 1987, Verkley 1993). Members of both families have usually brownish coloured apothecia, and their stipe base is often blackish. Apothecia of *Sclerotiniaceae* emerge from a black sclerotium (sclerotial stroma) or, similar as in *Rutstroemiaceae*, from stromatized host tissue (substratal stroma). Species of *Sclerencoelia* deviate from the remaining genera of the family in persistent, drought-tolerant apothecia and in asci with a more or less reduced apical ring. *Sclerotiniaceae* generally have at their flanks of the receptacle an ectal excipulum of textura globulosa which often includes rhomboid crystals, whereas *Rutstroemiaceae* mostly have a textura prismatica without crystals (Baral 2016).

Hyphomycetous or sometimes sporodochial, acervular, or pycnidial anamorphs are typical of the family (for references see Baral 2016). Various members form characteristic macroconidial anamorphs, the most familiar being *Botrytis* P. Micheli ex Pers. and *Monilia* Bonord.,

which are important plant pathogens and also known for their teleomorph-typified names *Botryotinia* Whetzel and *Monilinia* Honey. Most members of *Sclerotiniaceae* possess phialidic microconidial synanamorphs which are either formed directly from ascospores or on short germ tubes (Schumacher & Kohn 1985).

The genus *Schroeteria* G. Winter, a group of false smut fungi, which over a long time has been misplaced in *Ustilaginales* (now *Ustilaginomycetes*), is extraordinary in forming sori of pigmented mitosporic diaspores, which are classified as chlamydospores, in fruits of different *Veronica* spp. They form a powdery spore mass which at maturity often completely fills the capsules of their host. The chlamydospores are roundish, warted, somewhat thick-walled, and show light yellowish- to reddish- or greyish-brown colours under transmitted light.but appear macroscopically dark brown to blackish. *Schroeteria* also possesses a phialidic microconidial synanamorph that develops on the chlamydospores, for which it was assumed to represent a member of *Sclerotiniaceae* (Brefeld 1883, 1912, Vánky 1982, Nagler et al. 1989). The mycelium of *Schroeteria* spp. destroys the interior (seeds and/or funiculi and placenta) of the capsules of living plants without forming a dark stroma.

During 1986–2019, two morphologically similar sclerotiniaceous discomycetes have been collected on fallen previous year's seeds of *Veronica hederifolia* agg. (ivy-leaved speedwell) at different sites of central Europe. In the first collection made in 1986 by P. Blank near Schaffhausen (Switzerland), the substrate was misinterpreted as gall of a gall wasp, therefore, the species was compared with gall-inhabiting *Sclerotiniaceae* (Baral 1986, Palmer 1991). Further collections were made in 2003–2004 by G. Hensel, M., W. & E. Huth, and P. Rönsch in Sachsen-Anhalt (Germany), during which the substrate was correctly identified as *Veronica* seeds, owing to

At that time it became evident that one of the two discomycetes must be *Ciboria ploettneriana* (Kirschst. in Rehm) N.F. Buchw. This rarely reported species was described by Kirschstein (1906) on seeds of *V. hederifolia* agg. from collections made in 1899 and 1905 near Brandenburg a. d. Havel, and distributed by him in Ascom. exsicc. (Rehm 1905). Only a few later reports under this name are known to us (all from Germany): Benkert (2005) presented a sample made in 1992 in Berlin-Baumschulenweg, Kreisel (2011) published another sample made in 2008 by D. Benkert in the park of castle Liebenberg in Brandenburg, and Huth (2009: 103, pl. 36 fig. 104) reported three samples made by G. Hensel, M. & W. Huth, and P. Rönsch in April–May 2003–2004 near Merseburg and Freyburg in Sachsen-Anhalt.

In 2019 we started our bibliographic and molecular investigations on the genus *Schroeteria*, based on M. Bemmann's suspicion that this genus could represent the anamorph of the two discomycetes. In fact, chlamydospores of *S.decaisneana* (Boud.) De Toni could subsequently be detected in May 2019 by H. & U. Richter at the Zeuchfeld site on mature non-stromatized seeds in the capsules of living plants. As a result from rDNA sequences obtained by A. Urban and J. Kruse, *Ciboria ploettneriana* is closely related to *Sclerotinia* but not to *Schroeteria*, whereas the other discomycete on *V. hederifolia* agg. is conspecific with *Schroeteria decaisneana*. Apothecia of a third species, which was detected by F.J. Valencia in January 2017 on seeds of *V.cymbalaria* in a mediterranean area of southern Spain and which morphologically only slightly differs from *S. decaisneana*, turned out to belong to *S. poeltii* Vánky. Accordingly, we here adopt *Schroeteria* as the correct name for the holomorphs of *S. decaisneana* and *S. poeltii*, and retain the name *Ciboria ploettneriana* for the time being.

Usually, apothecia of each of the two species on *V. hederifolia* agg. were collected at different sites in Sachsen-Anhalt, but at one of these sites (Zeuchfeld near Freyburg) both species occurred sympatric in the same habitat, though in different months. Their growth on the same substrate at the same site could speak for some kind of hyperparasitism, based on comparable hypotheses which have earlier been proposed in other genera of *Sclerotiniaceae*, in which two different species emerge from sclerotia formed on the same host plant, but any observations that would support this hypothesis are lacking.

Materials And Methods

Used abbreviations: LBs = KOH-inert oil drops (lipid bodies); VBs = KOH-sensitive refractive vacuolar bodies; SCBs = KOH-sensitive cytoplasmic bodies; OCI = relative oil content index (0 = without oil drops, 5 = maximum lipid content); * = observation of living cells, † = observation of dead cells; MTB = Messtischblatt (German topographic map), IVV = www.in-vivo-veritas.de (link to drawings and photographs); sin. doc. = without macro- or microscopic documentation, ø = unpreserved, sq. = sequence in GenBank.

Pure cultures from ascospores were tried on MEA (Malt Extract Agar) and MMN (Modified Melin Norkrans Medium) (A.U.). In order to induce the formation of microconidia from ascospores, apothecia were placed for 3–4 days in a moist chamber at 10–20°C. The formation of apothecia from seeds was achieved by picking up infected, blackened seeds in June and placing them at the same day in a garden.

Veronica species were identified using Jäger (2017) and Parolly & Rohwer (2019), for *V. cymbalaria* Jahn & Schönfelder (1995), and for *V. campylopoda* Hong & Fischer (1998). Current plant names were established using The Plant List (2020).

Molecular methods. Sequences of ITS and LSU rDNA were obtained by A. Urban from apothecia of two samples of *Schroeteria decaisneana* (Zeuchfeld near Freyburg, Germany) and one of *Ciboria ploettneriana* (Alte Göhle near Freyburg). Further sequences of ITS and LSU rDNA were obtained by J. Kruse and S. Ploch from anamorph sori of *Schroeteria decaisneana* (Zeuchfeld, Sachsen-Anhalt), *S. delastrina* (Tul. & C. Tul.) G. Winter (Kyffhäuser and Hainleite, Thüringen), *S. bornmuelleri* P. Magnus (Mahhad, Iran), and *S. poeltii* Vánky (Rhodos, Greece), and from apothecia of *S. poeltii* (Ronda, Spain). These sequences comprise the entire ITS region and the LSU D1–D2 domain. Three of the sori extracts were 2–3× sequenced. For verifying the macroscopically identified *V. cymbalaria* the plant ITS was sequenced.

Methods used by J. Kruse and S. Ploch: About 2–10 mg of spore mass was taken from infected seeds of the fungarium samples J.K. S1346 (GLM-F129032), S1304, B2278, V. K. P1652-23, -26, -27, H.U.V. 750 ex TUB and C.V.L.040117 (GLM-F29000). The material was placed in 2 mL plastic reaction tubes and homogenized in a mixer mill (MM2, Retsch) using a combination of five to eight 1 mm and three 3 mm metal beads at 25 Hz for 5 min. Genomic DNA was extracted using the E.Z.N.A Plant DNA Mini Kit (VWR).The incubation time was extended to one hour. The complete nrITS of all DNA extracts were amplified using the primer pair ITS1F and ITS4 (White et al. 1990, Gardes & Bruns 1993) at 56 °C annealing temperature. The cycling reaction was performed in a thermocycler (Eppendorf Mastercycler 96 vapo protect; Eppendorf, Hamburg) with an initial denaturation at 95 °C for 4 min, 36 PCR cycles of denaturation at 95 °C for 40 s, annealing at 56 °C for 40 s and elongation at 72 °C for 60 s, followed by a final elongation at 72 °C for 4 min. The LSU rDNA was amplified using the primer pair LR0R and LR5 (Vilgalys 1988) with the condition mentioned in Vilgalys & Hester (1990). The resulting amplicons were sequenced at the Biodiversity and Climate Research Centre (BiK-F) laboratory using the abovementioned PCR primers. Sequences were deposited in GenBank (https://www.ncbi.nlm.nih.gov/genbank/, Tab. 1).

Alignments were done with MAFFT (https://mafft.cbrc.jp/alignment/server/). Maximum likelihood phylogenetic analyses were carried out with MEGA7 and MEGAX with the settings ‘use all sites, nearest-neighbour-interchange, weak branch swap filter’, also with IQ-tree. Branch support is given as maximum likelihood bootstrap percentages. P-distances were evaluated with MEGA6 and MEGA7 using individual alignments of species pairs. ana = anamorph, tel = teleomorph.

Table 1. Sequences included in phylogenetic analyses (new sequences in bold; tel = teleomorph, ana = anamorph, T = from type).

Species	Collection number	Country	Host	ITS	LSU	Reference
Botrytis cinerea	CBS 179.71	Netherlands	*Cichorium endivia*	MH860054	MH871836	Vu et al. 2019
***Botrytis porri* tel**	**WU 43987**	**Germany**	***Allium scorodoprasum***	**MZ048347**	**MZ048347**	**This study**
Cenangium acuum	H.B. 9325b, TAAM:198515	Germany	*Pinus sylvestris*	LT158439	KX090822	Pärtel et al. 2016
Cenangium ferruginosum	G.M. 2015-08-15.1	Luxembourg	*Pinus*	KY462796	KY462796	G. Marson unpubl.
Chlorociboria aeruginosa	UBC F19715	Canada	indet. wood	HQ604856	HQ604856	M.L. Berbee et al. unpubl.
Ciboria amentacea	A.U. 2760	Austria	*Alnus glutinosa*	KT970066	KT970066	Baral & Haelewaters 2015
Ciboria americana	CBS 117.24	?	*Castanea sativa*	MH854767	MH866271	Vu et al. 2019
Ciboria asphodeli	F142282	Spain	*Asphodelus fistulosus*	KJ941085	KJ941065	Checa et al. (Bicorn.)
Ciboria batschiana	TNS:F-44241	Japan	?	AB926056	AB926143	T. Hosoya et al. unpubl.
Ciboria betulae	1145.P	Norway	*Betula*	Z81427	Z81403	Holst Jensen et al. 1997b
Ciboria carunculoides	ms94	China	*Morus*	HQ833459	–	Hu et al. 2011
Ciboria caucus	1572.1	Norway	*Salix caprea*	Z73766	Z73740	Holst Jensen et al. 1997b
Ciboria conformata	F145906	Spain	*Alnus glutinosa*	KJ941075	KJ941057	Galán et al. (2015)
Ciboria aff. *conformata*	KL102, TAAM:137925	Greenland	*Salix glauca*	LT158414	–	Pärtel et al. 2016
***Ciboria coryli* tel**	**WU 31551**	**Austria**	***Corylus avellana***	**XXXXXXX**	**XXXXXXX**	**This study**
Ciboria shiraiana	KUS-F52447	Korea	*Morus australis*	JN033430	JN086733	Han et al. 2014
Ciboria shiraiana	ms93	China	*Morus*	HQ833458	–	Hu et al. 2011
Ciboria viridifusca	KL212, TAAM:165962	Estonia	*Alnus*	LT158429	KX090812	Pärtel et al. 2016
Ciborinia erythronii	CBS 300.31 T	USA	*Erythronium americanum*	MH855221	MH866671	Vu et al. 2019
Ciborinia erythronii	1838.P	Canada	*Erythronium* sp.	Z73767	Z73741	Holst Jensen et al. 1997b
Ciborinia foliicola	1932.H	Canada	*Salix*	Z80892	Z81404	Holst Jensen et al. 1997b
Ciborinia gentianae	JCM 13253 T	Japan	*Gentiana trifl.* var. *japon.*	LC228669	LC228727	G. Okada et al. unpubl.
Ciborinia whetzelii	1927.H	Canada	*Populus tremuloides*	Z73768	Z73742	Holst Jensen et

						al. 1997b
Coprotinia minutula	1916.P	Canada	*Coleoptera* dung	Z81428	Z81405	Holst Jensen et al. 1997b
Cristulariella depraedans	KUS-F25920	Korea	*Acer ginnala*	KT462571	KX098505	Cho et al. 2017
***Dumontinia tuberosa* tel**	**B.S.I. 10/20, WU 43990**	**Switzerland**	***Anemone nemorosa***	**MZ048350**	**MZ048350**	**This study**
Elliottinia kerneri	KL402, TU:104529	Switzerland	*Abies alba*	LT158475	LT158475	Pärtel et al. 2016
Gloeotinia granigena	1931.S	?Norway	*Elymus repens*	Z81432	Z81408	Holst Jensen et al. 1997b
Grovesinia moricola	KUS-F26901	Korea	*Humulus scandens*	KC460209	KX098504	Cho et al. 2013
Grovesinia moricola	1836.K, LMK38	USA	*Juglans nigra*	Z81433	Z81409/AJ226081	Holst Jensen et al. 1997b
Haradamyces foliicola	MAFF 411026 T	Japan	*Cornus florida*	AB329720	–	Masuya et al. 2009
Hymenoscyphus scutula	G.M. 2014-12-25.2	Luxembourg	indet. herb	MK674606	MK674606	G. Marson unpubl.
Kohninia linnaeicola	3200.H T?	Norway	*Linnaea borealis*	AY236422	–	Holst Jensen et al. 1997b
Lambertella corni-maris	CLX4075	USA	*Malus*	KC958562	KC964858	Wiseman et al. 2015
Lambertella pyrolae	TNS-F 40132 T	Japan	*Pyrola incarnata*	AB926081	AB926164	T. Hosoya et al. unpubl.
Martininia panamaensis	CBS 358.72, CUP 50076	France	indet. wood	MH860497	MH872212	Vu et al. 2019
Monilinia amelanchieris	1918.K	USA	*Amelanchier canadensis*	Z73769	Z73743	Holst Jensen et al. 1997b
Monilinia aucupariae	885.2	Norway	*Sorbus aucuparia*	Z73771	Z73744	Holst Jensen et al. 1997b
Monilinia azaleae	1939.S, ATCC58539	USA	*Rhododendron roseum*	AB182266	Z73745	Holst Jensen et al. 1997b
Monilinia baccarum	951.2	Norway	*Vaccinium myrtillus*	Z73773	Z73746	Holst Jensen et al. 1997b
Monilinia cassiopes	1459.S	Norway	*Cassiope tetragona*	Z73776	Z73747	Holst Jensen et al. 1997b
Monilinia fructicola	CBS 127259	Australia	*Prunus persica*	MH864497	MH875934	Vu et al. 2019
Monilinia fructicola	782.K	Canada	*Prunus persica*	Z73777	Z73748	Holst Jensen et al. 1997b
Monilinia fructigena	CBS 493.50	Netherlands	*Malus sylvestris*	MH856721	MH868240	Vu et al. 2019
Monilinia gaylussaciae	1919.P ATCC 64508	USA	*Gaylussacia baccata*	Z73782	Z73750	Holst Jensen et

						al. 1997b
Monilinia jezoensis	4222 T	Japan	*Rhododendron kaempferi*	AB182265	–	Takahashi et al. 2005
Monilinia johnsonii	1920.K	USA	*Crataegus*	Z73783	Z73751	Holst Jensen et al. 1997b
Monilinia laxa	2013/LX2	Hungary	*Prunus armeniaca*	LT615187	LT615187	A. Lantos unpubl.
Monilinia linhartiana	CBS 150.22	Germany	*Mespilus germanica*	MH854729	MH866235	Vu et al. 2019
Monilinia megalospora	619.2	Norway	*Vaccinium uliginosum*	Z73788	Z73753	Holst Jensen et al. 1997b
Monilinia mumeicola	Hirodai #3231 T?	Japan	*Prunus mume*	AB125620	–	Harada et al. 2004
Monilinia oxycocci	1087.P	Norway	*Vaccinium* cf. *oxycoccus*	Z73789	Z73754	Holst Jensen et al. 1997b
Monilinia padi	923.K	Norway	*Prunus padus*	Z73791	Z73755	Holst Jensen et al. 1997b
Monilinia polystroma	2015/PS32	Hungary	*Malus domestica*	LT615192	LT615192	A. Lantos unpubl.
Monilinia seaverii	1992.K	USA	*Prunus serotina*	Z73793	Z73757	Holst Jensen et al. 1997b
Monilinia urnula	476.1	Norway	*Vaccinium vitis-idaea*	Z73794	Z73758	Holst Jensen et al. 1997b
Monilinia vaccinii-corymbosi	CBS 172.24	N-America	*Vaccinium corymbosum*	MH854791	MH854791	Vu et al. 2019
Mycopappus alni	KUS-F27033	Korea	*Salix pierotii*	KC753529	KY696722	Park et al. 2013
Myriosclerotinia scirpicola	1435.P	Norway	*Scirpus lacustris*	Z81440	Z81414	Holst Jensen et al. 1997b
Myriosclerotinia sulcatula	CBS 303.31	Denmark	*Carex elata*	MH855222	MH866673	Vu et al. 2019
Ovulinia azaleae	1835.P	?	*Rhododendron*	Z73797	Z73760	Holst Jensen et al. 1997b
Ovulinia azaleae	CBS 680.88	Netherlands	*Rhododendron*	MH746075	MH873840	Vu et al. 2019
Piceomphale bulgarioides	KL374, TAAM:198322	Estonia	*Picea abies*	LT158469	KX090836	Pärtel et al. 2016
Pycnopeziza sejournei	KL267, J.H.P. 11.054	France	*Hedera helix*	LT158443	KX090827	Pärtel et al. 2016
Pycnopeziza sympodialis	CBS 332.39, CUP 25161	USA	*Alnus rugosa*	MH856037	MH867534	Vu et al. 2019
Rutstroemia firma	G.M. 2014-12-01.1	Luxembourg	*Quercus*	KT876987	KT876987	G. Marson unpubl.
Rutstroemia henningsiana	608.P	Norway	*Carex rostrata*	Z81442/KC533543	Z81416	Holst Jensen et al. 1997b

Rutstroemia luteovirescens	KL217, TU:104450	Estonia	*Acer platanoides*	LT158431	KX090814	Pärtel et al. 2016
***Schroeteria bommuelleri* ana**	**H.U.V. 750**	**Iran**	***Veronica rubrifolia***	**MW915653**	**–**	**This study**
***Schroeteria decaisneana* ana**	**J.K. S1346, H.B. 10206**	**Germany**	***Veronica hederifolia* s.str.**	**MW915644**	**MW915644**	**This study**
***Schroeteria decaisneana* tel**	**A.U. 2273**	**Germany**	***Veronica hederifolia* agg.**	**MZ048345**	**MZ048345**	**This study**
***Schroeteria decaisneana* tel**	**WU 43982**	**Germany**	***Veronica hederifolia* agg.**	**MZ048346**	**MZ048346**	**This study**
***Schroeteria delastrina* ana**	**V.K. P1652-23**	**Germany**	***Veronica arvensis***	**MW915652**	**–**	**This study**
***Schroeteria delastrina* ana**	**V.K. P1652-27**	**Germany**	***Veronica arvensis***	**MW915646**	**MW915646**	**This study**
***Schroeteria delastrina* ana**	**V.K. P1652-26**	**Germany**	***Veronica arvensis***	**MW915645**	**MW915645**	**This study**
***Schroeteria poeltii* ana**	**J.K. S1304**	**Greece**	***Veronica cymbalaria***	**MW915654**	**–**	**This study**
***Schroeteria poeltii* ana**	**J.K. B2278**	**Greece**	***Veronica cymbalaria***	**MW915647**	**MW915647**	**This study**
***Schroeteria poeltii* tel**	**C.V.L. 040117**	**Spain**	***Veronica cymbalaria***	**MW915648**	**MW915648**	**This study**
Sclerencoelia fascicularis	G.M. 2016-03-09.1	Luxembourg	*Populus tremula*	MH194576	MH194576	G. Marson unpubl.
Sclerencoelia fraxinicola	H.B. 9358, TAAM:198511 T	Germany	*Fraxinus excelsior*	KT876983	KT876983	Pärtel et al. 2016
Scleromitrula calthicola	1368.1	Norway	*Iris pseudacorus*	Z80887	Z81422	Holst Jensen et al. 1997b
Scleromitrula shiraiana	Hirayama062001	?	?	AY789408	AY789407	H.O. Baral unpubl.
Scleromitrula spiraeicola	1336.1	Norway	*Filipendula ulmaria*	Z81448	Z81424	Holst Jensen et al. 1997b
***Sclerotinia 'binucleata'* tel**	**B.S.I. 10/7, WU 43992**	**Switzerland**	***Ranunculus ficaria***	**MZ048348**	**MZ048348**	**This study**
Sclerotinia bulborum	CBS 297.31	USA	?	MH855218	MH866668	Vu et al. 2019
***Ciboria ploettneriana* tel**	**WU 43984**	**Germany**	***Veronica hederifolia* agg.**	**MZ048354**	**MZ048354**	**This study**
Sclerotinia sclerotiorum	1980 UF-70, ATCC 18683	USA	bean pods	CP017820	CP017820	Derbyshire et al. 2017
Seaverinia geranii	CBS 168.24	USA	*Geranium*	MH854790	MH866294	Vu et al. 2019
Septotinia podophyllina	CBS 318.37, CUP 25277 T	USA	*Podophyllum peltatum*	MH855916	MH867422	Vu et al. 2019
Septotinia populiperda	CBS 339.53	Germany	*Populus*	MH857235	MH101506	Vu et al. 2019
Stromatinia cepivora	CBS 276.93	Netherlands	*Allium*	MH862401	MH874059	Vu et al. 2019
Stromatinia	TNS:F-40103	Japan	*Cryptomeria*	AB926160	AB926160	T. Hosoya et

cryptomeriae			*japonica*			al. unpubl.
Stromatinia gladioli	CBS 265.28 T	N-America	*Gladiolus*	MH855008	MH866477	Vu et al. 2019
Stromatinia narcissi	CBS 339.33	Netherlands	*Narcissus*	MH855451	MH866916	Vu et al. 2019
Stromatinia pyrolae	1471.S	Norway	*Pyrola minor*	Z73798	Z73761	Holst Jensen et al. 1997b
Stromatinia rapulum	1243.1	Norway	*Polygonatum multiflorum*	Z73801	Z73763	Holst Jensen et al. 1997b
***Stromatinia rapulum* tel**	**A.U. Dum03**	**Germany**	***Polygonatum odoratum***	**MZ048352**	**MZ048352**	**This study**
Valdensia heterodoxa	485.2	Norway	*Vaccinium myrtillus*	Z81447	Z81423	Holst Jensen et al. 1997b

Results

Molecular results

The obtained sequences of the three *Schroeteria decaisneana* samples fully concur in the ITS region between the two apothecial isolates (teleomorph) and the sorus isolate (anamorph), except for 1 nt in the ITS1 in one of the apothecial isolates (Tab. 2). Also in the LSU D1–D2 no difference was observed between the two apothecial isolates and the sorus isolate (Tab. 2). The two *S. poeltii* sequences likewise fully concur in the ITS and LSU D1–D2 region between apothecial and sorus isolate, except for 1 nt in the LSU. Considering the interspecific distances among the *Schroeteria* species and the identity of the host species, our result proves that teleomorph and anamorph belong together.

The interspecific distances in the ITS (457–462 nt in core clade of *Schroeteria*) and LSU D1–D2 (598 nt) range at 5–6.3% / 2.5–2.7% within the core clade, but at ~14% / 8.5–9.6% between core clade and *Schroeteria poeltii*, 16.7–18% / 8.9–9.7% between core clade and *Ciboria ploettneriana*, and 9.2% / 3.7–3.9% between *Schroeteria poeltii* and *Ciboria ploettneriana*, respectively. The S1506 intron is absent in all sequences in which the 3'-end region of SSU was included (the region is missing in *Schroeteria bornmuelleri*).

Table 2. Inter- and intraspecific distance matrix of the ITS1-5.8S-ITS2 region (before slash) and LDU D1–D2 domain (after slash) for *Schroeteria* spp. in comparison with *Ciboria ploettneriana* (p-distances, transitions + tansversions, pairwise deletion).

	S. decaisneana	***S. delastrina***	***S. bornmuelleri***	***S. poeltii***	***Cib. ploettneriana***
S. decaisneana	0–0.2 / 0 %				
S. delastrina	5–5.3 / 2.5–2.7 %	0–0.4 / 0.2 %			
S. bornmuelleri	6–6.3 / – %	5.2 / – %	– / –		
S. poeltii	14–14.3 / 9.4–9.6 %	14.2–14.7 / 8.5–8.9%	13.8 / – %	0 / 0.2 %	
Cib. ploettneriana	17.2–18 / 9.7 %	17.2–17.6 / 8.9–9 %	16.7 / – %	9.2 / 3.7–3.9 %	– / –

A strongly supported *Schroeteria* core clade is formed in our combined maximum likelihood analysis of ITS+LSU (Pl. 1), but also in separate analyses of ITS and LSU (S1, S2). The clade comprised *S. decaisneana*, *S. delastrina*, and *S. bornmuelleri*, and nested in our combined analysis in an unsupported clade with various *Monilinia* spp. of section *Disjunctoriae* growing on fruits of *Ericaceae* and *Rosaceae* (Pl. 1). When separately analysing the ITS region (S1), this clade was strongly supported but included also *Ciborinia foliicola*, *C. whetzelii*, and *Ciboria betulae*, whereas when separately analysing LSU (S2) the *Schroeteria* core clade clustered with medium support with *Ciboria shiraiana* (on *Morus*), which in the other two analyses formed a supported clade with *C. carunculoides* (also on *Morus*) outside *Sclerotiniaceae* and *Rutstroemiaceae*.

The *Schroeteria* core clade clustered particularly with two *Ericaceae* inhabiting species: it formed a medium (Pl. 1, S1) or strongly (S3) supported sister clade of *M. jezoensis*, though with a rather long branch, and together with this species a less supported sister clade of *M.*

azaleae (Pl. 1, S1). Both species grow on *Rhododendron* and are members of the *Monilinia alpina* group of section *Disjunctoriae*, to which also *M. cassiopes* belongs (Batra 1991: 102), but apparently also *Stromatinia pyrolae*.

In contrast to the phylogenetic affiliation of the *Schroeteria* core clade with *Monilinia* section *Disjunctoriae*, *Schroeteria poeltii* clustered distant from *Schroeteria* s.str. It formed an unsupported (Pl. 1) or strongly supported (S3) distant sister clade to the supported clade of *Sclerotinia bulborum* and *S.* '*binucleata*' (an undescribed species of *Sclerotinia* s.l. parasitizing on *Ranunculus ficaria* and *Corydalis cava*). *Ciboria ploettneriana* clustered with comparatively short branches with these and other typical members of *Sclerotinia*, *Stromatinia*, and *Grovesinia* in an unsupported clade (Pl. 1, S1).

Morphological results

In the following, *Ciboria ploettneriana*, *Schroeteria decaisneana*, and *S. poeltii* are described in detail from their teleomorph, the latter two also from their anamorph.

Key to species of *Sclerotiniaceae* with known teleomorph growing on *Veronica* seeds

1. Ascospores mainly *12.5–16.5 × 6–7.5 µm, with several LBs 0.5–0.8 µm diam. grouped near each end, (2–)4-nucleate; living paraphyses containing ± refractive vacuolar bodies (VBs) in terminal cell; on blackened seeds of *Veronica hederifolia* agg., climate temperate humid ..... ***Ciboria ploettneriana***
2. Ascospores mainly *10–13 × 5.5–6.5 µm, with 1(–2) LBs 1.4–2.7 µm diam. near each end, uninucleate; living paraphyses without refractive vacuoles in terminal cell 2

2. Apothecial stipes 3–13 mm long; ascospores ellipsoid to fusoid, LBs subpolar, 1.4–2.7 µm diam.; on light to bright (grey-)brown seeds of *Veronica hederifolia* agg., climate temperate humid ..... ***Schroeteria decaisneana***
3. Apothecial stipes 5–25 mm long; ascospores ellipsoid, LBs more polar, 1.5–1.8 µm diam.; on blackened seeds of *Veronica cymbalaria*, climate mediterranean semihumid ..... ***Schroeteria poeltii***

Table 3. Comparison of teleomorph characteristics of *Schroeteria decaisneana*, *S. poeltii*, and *Ciboria ploettneriana*. # = data evaluated from Nagler et al. (1989).

	Schroeteria decaisneana	*Schroeteria poeltii*	*Ciboria ploettneriana*
Ascospores size [µm]	*(9.5–)11–13(–14.5) × (5–)5.5–6.5(–6.7)	*(9.5–)10–11(–11.3) × (5.3–)5.5–6(–6.3)	*(10.5–)12.5–16.5(–19) × (5.5–)6–7.5(–9)
- shape	ellipsoid to fusoid or slightly ovoid	ellipsoid to slightly ovoid	ellipsoid- to ovoid-fusoid
- LBs (living state!)	1(–2) LBs of 1.4–2.7 µm diam. and some small ones near each end	1(–2) LBs of (1–)1.5–1.8 µm diam. and some small ones at each end	1(–2) LBs of 0.5–0.8(–1) µm diam. and some small ones near each end
- nuclei in ascospores	1 nucleus, 2.8–3 µm diam.	1 nucleus, 3–3.2 µm diam.	(2–)4-nuclei, 2.2–2.9 µm diam.
Phialides [µm]	†2.5–5 × 1.5–3	8–20 × 3.5–5.8#	*6–10 × 2.6–3.5(–4)
- phialoconidia [µm]	*2.8–3.6 × 2.6–3.4	(2.7–)3–3.6(–4) × (2.7–)2.9–3.5(–3.8)#	*2.5–3.2 × 2.5–3
Asci [µm]	*(145–)157–185(–192) × 11–12.3(–13)	*145–160 × 9.5–10.5(–10.8)	*180–210 × (10–)11–12(–13)
Paraphysis terminal cells	with non-refractive vacuoles	with non-refractive vacuoles	with slightly to strongly refractive VBs
Ectal excipulum	vertically or often horizontally oriented textura globulosa(-prismatica)	vertically oriented textura globulosa(-prismatica)	vertically oriented textura globulosa-prismatica
- lower flank cells [µm]	*(16–)20–45(–70) × (12–)15–28(–35)	*20–50 × 15–30	*20–40(–58) × 15–25(–30)
- marginal cells [µm]	*38–70 × 6–10	*25–35 × 13–15	*8–15(–25) × 5–11.5
- cells in stipe [µm]	*28–46 × 3–4 textura porrecta	†25–40 × 6–9.5 textura prismatica-porrecta	*20–45 × 7–17 textura prismatica
Apoth. disc diam. [mm]	1.5–3.5	(1–)1.3–2.5(–3)	(1.2–)2–4
- stipe colour	medium grey-brown, near base blackish-brown	ochraceous, near base blackish-brown	whitish to creamish, sometimes brownish below
- stipe size [mm]	(3–)5–10(–13) × (0.2–)0.4–0.6(–0.8)	5–18 × 0.2–0.55	2–7 × (0.35–)0.5–0.8(–1)
Seed size (infected) [mm]	2–2.5	(0.9–)1.7–2.8	2–3.2
- surface	light to bright (grey-)brown	bright grey-brown to blackish	blackish-brown to black
Phenology (apothecia)	XI–V	I	IV–V
Host	*Veronica hederifolia* agg.	*Veronica cymbalaria*	*Veronica hederifolia* agg.
climate	temperate humid	meso-/supramediterranean semihumid	temperate humid

Ciboria ploettneriana (Kirschst. in Rehm) N.F. Buchw., K. Vet. Landbohøjsk., Aarsskr. 32: 165 (1949) — Pls 2–6

≡ *Sclerotinia ploettneriana* Kirschst., in Rehm, Ascom. exsicc.: no. 1603 (1905), nom. inval., Art. 38.1(a) ICN

≡ *Sclerotinia ploettneriana* Kirschst., in Rehm, Annls mycol. 3(5): 411 (1905), nom. inval., Art. 38.1(a) ICN

≡ *Sclerotinia ploettneriana* Kirschst., Verh. Bot. Ver. Prov. Brandenburg 48: 43 (1906)

Etymology: named after the collector, the German Traugott Plöttner (1853–1923), who frequently accompanied W. Kirschstein (1863–1946) on his excursions (Kummer 2010).

Lectotype (designated here, MBT 10000619): Germany, Brandenburg, Groß Behnitz, Hasellake, on black stromatized seeds of *Veronica hederifolia* agg., 27.IV.1905, W. Kirschstein (B 70 0100006).

DESCRIPTION. **Teleomorph**: **Apothecia** fresh (1.2–)2–4 mm diam., non-gelatinous, disc light to bright ochraceous-brown, slightly concave, finally flat, darker brown with age, margin thin, not protruding, smooth to very finely whitish denticulate, exterior pale to light ochraceous, smooth to slightly hairy, receptacle at base 0.7 mm thick, at margin 0.35 mm; **stipe** 2–7 × (0.35–)0.5–0.8(–1) mm, whitish to pale cream, at base often darker brown, usually somewhat hairy and with adhering particles, emerging singly (rarely also in pairs) from concave or convex side of the seed. **Asci** *180–210 {2} × (10–)11–12(–13) µm {3}, †150–173 × 8–10(–11) µm {1}, protruding *5–30 µm beyond paraphyses or (†) ± equalling the paraphyses, with 8 equal-sized spores (in overmature apothecia also unequal-sized), pars sporifera *61–73 µm long, spores obliquely (sub)biseriate, †65–83 µm, spores subbiseriate to uniseriate; **apex** (†) hemispherical to moderately truncate, apical thickening immature or mature †2–3.8 µm thick, apical ring blue in IKI {4}, euamyloid (BB), of *Sclerotinia*-type, lower ring strongly blue, upper parts less so; **base** with short and thick stalk, arising from croziers {3}. **Ascospores** *(10.5–)12.5–16.5(–19) × (5.5–)6–7.5(–9) µm {4}, †(11–)12–15(–16) × (4.5–)4.8–6 µm {5}, ellipsoid-fusoid to ellipsoid-fusiform (homopolar) or often distinctly ovoid-fusoid (heteropolar), ends obtuse to subacute, ± equilateral; containing a few minute **LBs** near each end, (0.2–)0.5–0.8(–1)((–2)) µm diam. {4}, OCI 0.5–1(–2), with ((1–))(2–)4 **nuclei** in centre {4}, without distinct **glycogen**; surrounded by a very delicate **sheath** that slips off the spore after ejection, spore wall surface CRB–; **overmature** spores 0–1(–2)-septate (septum median or sometimes eccentrical when 1-septate), *17–19 × 7.5–9 µm, without LBs; forming germ tubes and/or phialides. **Paraphyses** apically uninflated to slightly clavate or lageniform, terminal cell *(20–)42–100(–133) × (3–)4–5(–5.7) µm {3}, †2.5–4 µm wide {1}, lower cells *17–39 × 2.2–3.5 µm {2}; branched in lower and middle part; terminal cell containing hyaline, slightly to strongly refractive vacuolar bodies (**VBs**) in (11–)15–50(–70) µm long upper part {3}, VBs staining turquoise in CRB, in H_2O turning light purplish-pink with age (vital state) {2}, without SCBs; when senescent ensheathed by an ochre-brass-brown exudate along entire length. **Subhymenium** light ochre, 30 µm thick, of dense textura intricata. **Medullary excipulum** subhyaline, non-gelatinized, at base of receptacle ~200–400 µm thick, near margin 100 µm, upper part of ± loose t. intricata, individual cells *40–110 × 6–16 µm, smooth, without exudate; lower part of dense, horizontal t. porrecta, 150 µm thick at base of receptacle, sharply delimited from ectal excipulum, **in stipe** of t. porrecta. **Ectal excipulum** ± hyaline, 50–150 µm thick at lower flanks, of thin-walled (wall †0.2–0.4 µm thick), ± vertically oriented t. globulosa-prismatica, cells *20–40(–58) × 15–25(–30) µm {2}, cortex of smaller globose cells which sometimes form clavate to stalked **hair-like** protuberances of *10–21 × 8–10(–11) µm; at mid flanks 30–40 µm thick, at margin 20 µm thick, with ochre-brown exudate, marginal cells *8–15(–25) × 5–11.5 µm {2}, ellipsoid to clavate or stalked; exterior without hyphal layer, at lower flanks with hair-like, globose to clavate or stalked cells of *10–21 × 8–10(–11) µm, often containing **VBs**; **in stipe** of large-celled, subhyaline t. prismatica (cells *20–45 × 7–17 µm), covered by a thin layer of hyphoid, *3–7 µm wide elements, with scattered, indistinctly protruding, irregularly clavate to stalked, thin-walled, **hair-like** cells of *13–28 × 6–8 µm that contain **VBs**, at very base of stipe of dark red-brown t. angularis. **Rhomboid crystals** abundantly present in medullary excipulum {5}, diagonal diameter 8–22(–32) µm, small scattered crystals occurring on ectal excipulum and hymenium, crystals present also in medullary excipulum of basal part of stipe and a few in mycelial tissue within seed, sometimes forming druses 10–20 µm diam. **Amyloidity of tissue**: subhymenium {2} and outer medullary excipulum {2} pale to distinctly bluish in IKI (sometimes only visible after squashing). – **Anamorph**: **Cultural characteristics**: In pure culture on MEA the ascospores tardily germinated but did not form a mycelium. **Smut-like synanamorph** unknown. **Microconidial synanamorph** formed on ascospores germinating in senescent apothecia, producing **phialides** of *6–10 × 2.6–3.5(–4) µm that emerge terminally or laterally, either directly or on short to long germ tubes; **phialoconidia** globose to subglobose, *2.5–3.2 × 2.5–3 µm {3}, smooth, with a single eccentrical LB 1.2–2 µm diam.

Habitat: on fallen, heavily stromatized, previous year's seeds of *Veronica hederifolia* agg. {20/9}, seeds 2–3.2 mm diam., hard, surface ± rugose, entirely blackish-brown to black due to abundant, dark brown intracellular hyphae in epidermial layer and more sparse in outer parenchym cells. **Desiccation tolerance**: not tested for apothecia (probably intolerant), but surviving min. 9 months within the dry stromatized seeds. **Phenology**: IV–V. **Altitude**: 30–195 m. **Geology:** on basophilic to calcareous or more acidic soil: Muschelkalk (partly covered by loess), pleist- & holocene marl, sand & gravel, and fluviatile sediments.

Phenology of *Ciboria ploettneriana*							
	Feb-2	Mar-1	Mar-2	Apr-1	Apr-2	May-1	May-2
teleomorph	–	–	–	9	9	2	–

Specimens included (all on fallen seeds of *Veronica hederifolia* agg.).

Teleomorph: **Germany**: **Mecklenburg-Vorpommern**, 3.7 km S of Wismar, 1.2 km NE of Metelsdorf, slope at road, MTB 2134/232, 30 m, 14.IV.2019, T. Richter, vid. M. Reul (T.R., M.R. 6806). – **Berlin**, 8.5 km SE of Berlin, Treptow, Baumschulenweg, Späth-Arboretum, 37 m, MTB 3546/24, 30.IV.1992, D. Benkert, vid. V. Kummer (B 70 0009941, d.v.). – **Brandenburg**, 22.5 km NE of Brandenburg, SW of Groß Behnitz, Hasellake, 35 m, MTB 3442/123, 14.IV.1905, W. Kirschstein, vid. V. Kummer (B 70 0100005). – ibid., 27.IV.1905, W. Kirschstein, vid. V. Kummer (B 70 0100006, **lectotype**). – 1.7 km SW of Teupitz, ~1.5 km SE of Egsdorf, between Mittel-Mühle and Tornower See, ~45 m, MTB 3847/43, 27.IV.1972, D. Benkert, vid. V. Kummer (B 70 0009940, d.v.). – **Sachsen-Anhalt**, 2.2 km SE of Merseburg, WSW of Trebnitz, Werder canal, MTB 4638/31, 88 m, 20.VI.2003, G. Hensel (blackened seeds without apothecia, deposited at the same day in a box in the garden of M. Huth); 3.IV.2004, M. Huth (apothecia developed in box, M.H.). – ibid., 30.IV.2019, G. Hensel (blackened seeds without apothecia, H.B. 10210). – 4.3 km NE of Freyburg, W of Zeuchfeld, above vineyard, MTB 4736/42, 195 m, 13.IV.2009, P. & S. Rönsch (P.R., H.B. 9037). – ibid., 15. & 23.IV.2010, U. Richter. – 1.7 km ENE of Freyburg, NW-corner of Alte Göhle, Bauernholz, 185 m, MTB 4736/4, 2.V.2003, M., W. & E. Huth (W.H.). – ibid., 20.VI.2003, M. Huth & P. Rönsch (blackened seeds without apothecia, deposited at the same day in a box in the garden of M. Huth); 15. & 18.IV.2004, M. Huth & P. Rönsch (apothecia developed in box, M.H. & P.R.). – ibid., 15.IV.2007, P. & S. Rönsch (P.R., sin. doc.). – ibid., 22.IV.2010, U. Richter et al. (WU 43984, sq.: ITS/LSU MZ048354). – ibid., 23.IV.2010 U. Richter (H.B. 9271 ø). – 5.5 km WSW of Freyburg, S of Hirschroda, Hirschrodaer Graben, 185 m, MTB 4836/1, 12.IV.2004, P. Rönsch, S. Thieme, M. Huth (P.R.). – 4.3 km NW of Naumburg, 1 km WNW of Roßbach, Scherbitzberg-Schlucht, MTB 4836/2, 195 m, 8.IV.2009, W. Huth (ø). – ibid., 2.V.2019, W. Huth (W.H.).

Taxonomic remarks: *Ciboria ploettneriana* resembles *Schroeteria decaisneana* in most of its morphological traits, including various microscopic details, such as size of asci and paraphyses, size and shape of medullary and ectal excipular cells, IKI-reaction of ascus apex and medullary excipulum, and presence of crystals. The species deviates macroscopically in light-coloured, often whitish, somewhat shorter apothecial stipes with a lighter colour at the base, and seeds with a more blackish surface, causing a strong optical contrast between stipe and seed, in contrast to grey-brown seeds in *S. decaisneana*. Microscopically, *Ciboria ploettneriana* deviates from *Schroeteria decaisneana* in distinctly larger, slightly more heteropolar ascospores with often pointed, subacute ends. Under vital study, *Ciboria ploettneriana* differs in ascospores with a distinctly lower lipid content composed of much smaller LBs and (2–)4 nuclei instead of only one, and in ± strongly refractive vacuoles (VBs) in the terminal cells of paraphyses (Tab. 3). Less evident or possibly variable features of *C. ploettneriana* are slightly longer asci, slightly smaller conidia formed on longer phialides, and an ectal excipulum of vertically oriented cells in the receptacle (in *S. decaisneana* often horizontal) and wider cells in the stipe (textura prismatica vs. t. porrecta), also with much shorter cells at the margin (Tab. 3).

Variation: Ascus and spore size was rather consistent among the specimens studied. Also the size of LBs never exceeded 1 µm diam., with rare exceptions of single spores. The number of nuclei in the spores varied between two and four within all four samples in which living spores have been studied in detail (H.B. 9037 & 9271, M.R. 6806, 2.V.2019), but the tetranucleate spores were often distinctly more numerous than the binucleate spores when regarding only mature, freshly ejected spores.

Cultural studies: Microconidia were abundantly produced from the ascospores in senescent apothecia after incubation in a moist chamber. When shot on agar medium (MEA), the ascospores did not produce a mycelium even after several weeks of incubation at room temperature.

In two of the here studied samples, apothecia were obtained after incubation of blackened seeds placed in June directly . In this the apothecia developed during April of the following year.

Nomenclature and misidentifications: Hein & Gerhardt (1981) listed four voucher specimens as syntypes of *Sclerotinia ploettneriana* in B (Botanisches Museum Berlin-Dahlem): one from Rathenow (29.X.1899), two from Groß Behnitz (14. & 27.IV.1905), and one containing a mixture taken from both sites (29.X.1899 and 'April 1905'). Kirschstein's protologue mentions both sites with the dates 29.X.1899 and IV.1905 (without specifying the exact date in April). Under the latter date Kirschstein distributed the fungus as an exsiccata in Rehm: Ascom. exsicc. no. 1603. In the present study all four specimens, which now bear the herbarium numbers B 70 0100003–0100006, were examined by one of us (V. Kummer).

The first report of *Sclerotinia ploettneriana* in Rehm (1905 no. 1603, in sched.) and also the publication of this exsiccata in Annales Mycologici (Rehm 1905) is invalid, because only the collection data was provided but no description. Valid publication with description was done in Kirschstein (1906). The unillustrated protologue reports apothecia 2–3 mm diam., stipes 1–10 × 0.5 mm, emerging singly or

up to four from one seed, asci 160–180 × 10–12 µm, and oval spores of 15–18 × 6–7 µm with 1–2 small oil drops. Kirschstein emphasized the black stromatization of the seeds in contrast to the whitish uninfected seeds.

The Rathenow specimen (B 70 0100003) contains principally about ten light brown seeds of *Veronica hederifolia* agg. from which apothecia with ellipsoid spores of †9–11 × 5–6 µm emerge (Pl. 13). The light seed colour and the small spores indicate that this collection represents *Schroeteria decaisneana*, although the spores often contained more than one comparatively small oil drop in each half. A single seed without adhering apothecium appears to belong to *Ciboria ploettneriana* because of its black-brown colour. The date of this collection (end of October) coincides with the phenology of the *S. decaisneana* teleomorph which comprises autumn, winter, and spring, according to our study.

The two samples from Groß Behnitz (B 70 0100005–6, one shown on Pl. 6: 1) each contain numerous bright to dark black-brown seeds of *Veronica hederifolia* agg., and apothecia which much better fit the protologue of *Sclerotinia ploettneriana* regarding spore shape (ellipsoid to fusoid, rarely clavate) and spore size (B 70 0100005: †11–16 × 5–6 µm, B 70 0100006: †12–15 × 4.5–6 µm, examined in water). Because of the small spore size in the Rathenow collection we conclude that the protologue derives from the large-spored species alone and not from a mixture with *Schroeteria decaisneana*. Therefore, we here designate one of the two specimens from Groß Behnitz, B 70 0100006, as **lectotype** of *Sclerotinia ploettneriana*.

The examined duplicate of Rehm's exsiccata (B 70 0100004) provided a surprize: it does not contain any seeds of *Veronica*, but half a dozen of sclerotia with apothecia of an undetermined *Sclerotiniaceae*, also a few seeds of a ?*Stellaria*. The original label indicates that this exsiccata was composed of a mixture of two collections: the vast majority of the material was from Groß Behnitz (IV.1905), whereas a sparse minority came from Rathenow (29.X.1899). Other duplicates of this exsiccata might therefore actually contain seeds of *Veronica* with apothecia of *Ciboria ploettneriana*.

Ecology: *Ciboria ploettneriana* was recorded near Freyburg at three sites, in a thermophilous deciduous forest with *Ulmus minor* bordered by *Prunus spinosa* (Zeuchfeld, Pl. 12), in a thermophilous *Querco-Carpinetum* (Alte Göhle), and in a more shady *Aceri-Fraxinetum* (Hirschrodaer Graben). The site near Merseburg was a ?*Pruno-Fraxinetum* river bank forest with *Prunus padus* (Elster-Luppe-Aue), that near Naumburg a nitrophilous *Quercus-Fraxinus* forest edge (*Alliarion*, Pl. 5), and that near Wismar a narrow forest strip of *Acer*, *Aesculus* and *Tilia* between road and farmland. *Monilinia johnsonii* on *Crataegus* fruits occured together with *Ciboria ploettneriana* at the site near Naumburg.Besides the collections from Mecklenburg-Vorpommern, Brandenburg (including Berlin), and Sachsen-Anhalt as listed under Specimens included, no further unequivocal records of *Ciboria ploettneriana* came to our notice.

Schroeteria decaisneana (Boud.) De Toni, in Saccardo, Syll. fung. 7(2): 501 (1888) — Pls 7–14

≡ *Thecaphora decaisneana* Boud., Bull. Soc. mycol. Fr. 2: 167 (1886)

≡ *Geminella decaisneana* (Boud.) Boud., Bull. Soc. mycol. Fr. 3(2): 150, pl. 15 fig. 2 (1887)

≡ *Schizonella decaisneana* (Boud.) Thirum. & M.D. Whitehead, Am. J. Bot. 55: 186 (1968)

= *Schroeteria parvispora* (Bref.) Ferd. & Winge, Dansk bot. Ark. 2(1): 4 (1914)

≡ *Geminella parvispora* Bref., Unters. Gesamtgeb. Mykol. 15: 75 (1912)

Etymology: named after the French botanist Joseph Decaisne (1807–1882), who made the first record.

Type: collected in 1868 by J. Decaisne in the surroundings of Versailles, and later during several years in spring and summer by E. Boudier near Montmorency (Paris), always on "*Veronica hederacea*" (= *V. hederifolia* agg.). No lectotype appears to have been designated, and no material was ordered in this study.

DESCRIPTION. **Teleomorph**: **Apothecia** fresh 1.5–3.5 mm diam., non-gelatinous, disc light ochraceous-brown, slightly concave, finally flat to medium convex, darker brown with age, margin thin, not protruding, ± smooth, sometimes deeper red-brown, exterior pale ochraceous, finely rough, receptacle at base 0.5–0.75 mm thick, at margin 0.25–0.35 mm; **stipe** (3–)5–10(–13) × (0.2–)0.4–0.6(–0.8) mm, concolorous with receptacle or darker red-brown, especially in lower part, black-brown at base, here or also upwards with ± appressed hairs; one or sometimes 2–3(–4) stipes emerging from concave or convex side of the seed. **Asci** *(145–)157–185(–192) × 11–12.3(–13) µm {2}, †118–147 × (7.5–)8.5–10(–11.7) µm {2}, protruding *25–35 µm beyond paraphyses or †10 µm shorter up to 10 µm longer than paraphyses, containing 8 equal-sized spores, pars sporifera *(48–)52–65 µm long, spores obliquely (sub)biseriate, †48–72 µm, spores uniseriate; **apex** (†) hemispherical to subtruncate or obtuse, apical thickening †1.7–2.8 µm thick when ± mature, apical ring medium to

strongly blue in IKI {5}, euamyloid (BB), sometimes slightly hemiamyloid (rB, very dirty reddish-grey at high concentration), of *Sclerotinia*-type, all parts equally reactive or sometimes upper ring paler, upper and lower ring deep blue when KOH-pretreated; **base** with (very) short and thick stalk arising from croziers {3}. **Ascospores** *(9.5–)11–13(–14.5) × (5–)5.5–6.5(–6.7) µm {5}, †(8.5–)9–11(–12.8) × 4.7–6.2(–6.5) µm {5}, ellipsoid to fusoid (homopolar) or slightly ovoid (heteropolar), ends rounded to obtuse, rarely subacute, ± equilateral; containing two medium-sized **LBs** (1.4–)1.8–2.4(–2.7) µm diam. {4}, each surrounded by a few small LBs, OCI (2–)3, sometimes with two small **glycogen** regions staining dextrinoid (red-brown in IKI), with 1 **nucleus** of 2.8–3 µm diam. in centre {1}; surrounded by a very delicate **sheath** that slips off the spore after ejection, spore wall surface CRB–; **overmature** 0–1-septate (septum median, rarely strongly eccentrical), *10.5–12.5 × 5–6 µm, without or with only small LBs; forming germ tubes and/or phialides. **Paraphyses** apically uninflated to slightly clavate {4}, in some apothecia frequently ± strongly clavate to capitate or spathulate-lageniform to moniliform {1}, terminal cell *(32–)52–85(–93) × 4–5.5(–6.5) µm {2}, †38–55 × 2.5–4.2 µm {1}, *6–10 µm wide if inflated, lower cells *(10–)20–32(–49) × 2.7–3.5 µm {2}; branched only in lower part; terminal cell containing large non-refractive vacuoles and a few very low-refractive globose SCBs; inflated apices laterally covered by a thin, pale ochraceous exudate. **Subhymenium** light ochre-brown, 20–30 µm thick, of dense textura intricata. **Medullary excipulum** subhyaline, *indistinctly/†distinctly gelatinized, of loose to dense t. intricata, individual cells *(40–)75–115 × 7–16 µm, smooth or slightly rough by some granular, pale ochraceous exudate, at base of receptacle 270 µm thick, at margin 80 µm, of dense, horizontal t. porrecta, sharply delimited from ectal excipulum; **in stipe** of vertical t. porrecta; hyaline **stromatic tissue** inside seed only observed close to insertion of stipe. **Ectal excipulum** ± hyaline, 50–100 µm thick at lower flanks, of thin-walled († slightly gelatinized, common walls 1–2 µm thick), ± vertically or often horizontally oriented t. globulosa(-prismatica) from base of receptacle up to mid flanks, cells *(16–)20–35(–70) × (12–)15–25(–35) µm {H.B. 8687}, †15–23 × 12–18 µm {H.B. 5698}, or †30–45 × 15–28 µm {H.B. 8955}, at mid flanks 30–40 µm thick, with ochre-brown exudate, marginal cells *38–70 × 6–10 µm {1}, hyphoid but terminally ± strongly inflated; exterior covered by 1–2 layers of *5–10 µm wide hyphae, these sometimes vertically projecting as 1–2-celled, short-cylindrical, hyaline **hairs** (†10–22 × 3–5 µm); **in stipe** of subhyaline to pale ochraceous, more basally bright red-brown t. porrecta, cells *28–46 × 3–4 µm, at very base of dark red-brown t. angularis; **hairs** on stipe scattered to dense, appressed or projecting, subhyaline, †40–80(–150) × 3–5 µm, at base light brown, †9–10.5 µm wide, with 0.5–1.3 µm thick smooth wall, covered with scattered granules. **Rhomboid crystals** very scattered to abundant in or on ectal excipulum {3}, especially at margin, sometimes also in hymenium, abundant in medullary excipulum of basal part of stipe and in stromatic tissue within seed, here forming druses 15–20 µm diam. **Amyloidity of tissue**: subhymenium {2} and outer medullary excipulum {1} distinctly pale blue (but negative at high concentration), or entire tissue IKI–, even if KOH-pretreated {2}. – **Anamorph**: **Cultural characteristics**: In pure culture on MEA and MMN the ascospores did not germinate. **Sori** formed mainly on the funiculus; **conidiogenous cells** not observed; **chlamydospores** singly, only sometimes in pairs, pale greyish-brown under transmitted light, blackish-brown under reflected light, coarsly warted and with irregular ridges, individual cells †(8.2–)8.7–11(–11.8) × 7.9–10.8 µm (without ornamentation) {H.B. 10206}, wall 0.7–1 µm thick, ornamentation ~0.2–0.5 µm high; germinating by **phialides** 7–14 × 3–6.5 µm on which **microconidia** 2.5–3.5 µm diam. are formed in (basipetal) chains {Vánky 1982}. **Microconidial synanamorph** formed on ascospores germinating in senescent apothecia, producing conidia either terminally or rarely laterally, directly on spore wall (sessile), or from small **pegs** 0.5–1.5 × 0.5–1.3 µm {H.B. 8687} or lageniform **phialides** †2.5–5 × 1.5–3 µm {H.B. 5698}; **phialoconidia** globose to subglobose, exceptionally subangular, *2.8–3.6 × 2.6–3.4 µm {H.B. 8687}, †2.5–2.9 µm diam. {H.B. 5698}, surface smooth or very indistinctly rough, CRB–; containing a single eccentrical LB (0.8–)1.2–1.6(–1.8) µm diam. {H.B. 8687}.

Habitat: **Teleomorph** on fallen, present or previous year's, moderately stromatized seeds of *Veronica hederifolia* agg. {11/6}, seeds 2–2.5 mm diam., surface always rugose, light to bright grey-brown, distinctly blackened only at a small area around insertion of stipe. **Anamorph**: chlamydospores formed apparently on placentae and funiculi of non-stromatized seeds of *Veronica hederifolia* s.str. {2/1} inside the initially closed capsule of living plants. **Desiccation tolerance**: apothecia dead in all parts after 1 day in the herbarium (except for ascospores); chlamydospores not tested. **Phenology**: apothecia: X–I, III–V; anamorph: V–VI (BubÁk 1916, SĂvulescu 1957, Zogg 1985, present collections); **Altitude**: 60–530 m. **Geology**: on basophilic to calcareous or more acidic soil: Muschelkalk (partly covered by loess), Lettenkeuper (clay), pleisto- & holocene sand & gravel and fluviatile sediments.

Phenology of *Schroeteria decaisneana*												
	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
teleomorph	1	0	1	1	1	0	0	0	0	1	4	1
anamorph					7	5						

Specimens included (all on *Veronica hederifolia* agg.).

Teleomorph (on fallen seeds): **Switzerland**: **Schaffhausen**, 7 km NE of Schaffhausen, 1 km ENE of Thayngen, Flüheweg, MTB 8218/1, 530 m, ~10.I.1986, P. Blank & H.O. Baral (H.B. 2981). – **Germany**: **Brandenburg**, 25 km NW of Brandenburg, Rathenow, graveyard, 40–50 m, 29.X.1899, W. Kirschstein, vid. V. Kummer (B 70 0100003). – 3 km NE of Luckenwalde, WSW of Woltersdorf, Bürgerbusch, MTB 3845/3, 60 m, 9.V.1999, D. Benkert & V. Kummer, vid. V. Kummer (D.B., V.K., as *Ciboria ploettneriana*). – **Sachsen-Anhalt**, 5.5 km NE of Merseburg, NE of Burgliebenau, Elster-Luppe-Aue, MTB 4638/1, 85 m, 8.III.2009, G. Hensel (G.H. 080309). – Saale-Unstrutgebiet 4.3 km NE of Freyburg, 0.8 km W of Zeuchfeld, above vineyard, MTB 4736/42, 195 m, Muschelkalk (covered by Löss), 14.XI.2007, H. & U. Richter (U.R., sin. doc.). – ibid., 24.XI.2007, H. & U. Richter, P. & S. Rönsch (P.R., ex H.B. 8687, M-0276405). – ibid., 16.XI.2008, P. & S. Rönsch, U. Richter (P.R., H.B. 8955). – ibid., 29.XI.2009, U. Richter (U.R., A.U. 2273, sin. doc., sq.: ITS/LSU MZ048345). – ibid., 10.XII.2009, U. Richter (U.R., A.U. 2274, WU 43982, sin. doc., sq.: ITS/LSU MZ048346). – **Bayern, Unterfranken**, 7 km SSW of Schweinfurt, 1.5 km S of Grafenrheinfeld, near NSG Oberes Holz, Alter Main, MTB 6027/1, 200 m, 26.IV.1994, L.G. Krieglsteiner (L.K., H.B. 5698).

Anamorph (on seeds in capsules of living plants of *V. hederifolia* s.str.): **Sachsen-Anhalt**, 4.3 km NE of Freyburg, 0.8 km W of Zeuchfeld, above vineyard, MTB 4736/42, 195 m, 13.V.2019, H. & U. Richter (U.R., V.K. P1656/10, sin. doc.). – ibid., 21.V.2019, H. & U. Richter (H.B. 10206, J.K. S1346, GLM-F129032, sq.: ITS/LSU MW915644).

Taxonomic remarks: The first collection of the teleomorph of *Schroeteria decaisneana* was made in 1986 by P. Blank near Schaffhausen (Switzerland) and studied by the first author in the fresh state (Pl. 8: 1). The fungus was briefly reported by Baral (1986) as "*Ciboria*" cf. *gemmincola* Rehm, because it was erroneously believed to grow on galls of *Neuroterus albipes* (*Cynipidae*, *Hymenoptera*), a gall wasp that inhabits leaves of *Quercus* in Europe. In fact, oak galls, especially those of the related *N. numismalis*, resemble seeds of *Veronica*. In his review of *Sclerotiniaceae* on oak galls, Palmer (1991) mentioned the above collection by reproducing the first author's drawing, though without personal study. *Ciboria gemmincola* was described in Wagner (1895) on galls of *Cynips gemmae* with distinctly smaller, especially narrower spores of 8–9 × 3.5 µm.

In the following years the species was repeatedly collected in Sachsen-Anhalt (Pl. 7). At this occasion the fungus turned out to grow in fact on seeds of *Veronica hederifolia* agg. Therefore, the provisional name "*Ciboria seminis-veronicae*" was used for it, which appears also on the herbarium label of the specimen deposited in M as the intended holotype (H.B. 8687).

Variation: In all collections of *Schroeteria decaisneana*, from which detailed documentation was made, the paraphyses were cylindrical and apically scarcely inflated. Yet, in one of the large apothecia of a sample from Freyburg (Zeuchfeld, H.B. 8687) they were predominantly strongly inflated and variously shaped (Pls 7, 8: 3a, 11: 1j). The pale blue IKI-reaction of the subhymenium and outer medullary excipulum appears to be variable: it was present in the samples from Schweinfurt and Schaffhausen, but absent in those from Freyburg (no data available for the sample from Merseburg). Variation was also noted in ectal excipular cell size at the lower flanks, being much larger in the samples from Freyburg (H.B. 8687, 8955) compared to Schweinfurt (H.B. 5698) (no data available for those from Schaffhausen and Merseburg). Also the orientation of the cells varied. Finally, crystals were present in the collections from Schaffhausen and Freyburg, but they were not seen in those from Schweinfurt and Merseburg. In the Schweinfurt collection the germinating ascospores were predominantly 1-septate but also non-septate, and often they budded at both ends (Pl. 8: 2g), whereas in that from Freyburg they were always non-septate and germinated only at one conidiogenous locus (Pl. 8: 3c).

Cultural studies: Microconidia were abundantly produced from ascospores in senescent apothecia after incubation in a moist chamber. When shot on agar medium (MEA), the ascospores did not produce a mycelium even after several weeks of incubation at room temperature. According to studies by Brefeld (1912) and Vánky (1982), fresh chlamydospores germinated in tap water or strongly diluted nutrient solution at room temperature after 1–2 weeks and formed hyphae that abundantly produced phialides and microconidia. After adding concentrated nutrient solution, abundant mycelium developed instead. No attempts have been undertaken in the present study to obtain apothecia from stromatized seeds in a moist box.

Similar species: The study by the first author of a recent collection of *Ciboria polygoni-vivipari* Eckblad [Sweden, Lapland, Saxnäs, Marsfjället, 950 m, on bulbils of *Bistorta vivipara* (= *Polygonum viviparum*), 28.VII.2010, P. Perz, H.B. 9387, Baral ined., see IVV and https://svampe.databasen.org/taxon/11632] revealed some resemblance with the *S. decaisneana* teleomorph, particularly regarding the ascospores containing mostly two polar, medium-sized LBs. However, the spores were distinctly larger (*15–19 × 7.2–7.8 µm) and contained at least two nuclei, the paraphyses contained many low-refractive VBs in their apex, the ectal excipulum was of textura globulosa, and no crystals were seen. *Ciboria seminicola* (Kienholz & E.K. Cash) Hechler [including the questionable *C. betulae* (Woronin) W.L. White] on fruits of *Alnus* and *Betula* differs in somewhat longer and narrower, fusoid, warted ascospores and in asci arising from simple septa without croziers (Baral ined., H.B. 3677, 3682, 5136, 9774, see IVV).

Ecology: *Schroeteria decaisneana* was recorded near Freyburg (Zeuchfeld, Pl. 12) in a thermophilous deciduous forest with *Ulmus minor* bordered by *Prunus spinosa*, near Schweinfurt (Alter Main) in a riverbank forest (*Querco-Ulmetum*), near Merseburg (Elster-Luppe-Aue) in a riverbank forest with *Prunus padus* (?*Pruno-Fraxinetum*), and near Luckenwalde (Bürgerbusch) in a *Pruno-Fraxinetum*.The distribution of the anamorph of *S. decaisneana* comprises various countries of Europe (Scholz & Scholz 1988): Austria, former Czechoslovakia, France, Germany, Greece, Hungary, Italy, Poland, Romania, Sweden, Switzerland, and former Yugoslavia.

Schroeteria delastrina (Tul. & C. Tul.) G. Winter, Rabenh. Krypt.-Fl., Edn. 2 (Leipzig) 1.1: 117 (1881) [1884] – Pl. 15

≡ *Geminella delastrina* (Tul. & C. Tul.) J. Schröt., in Rabenh. Fungi Eur. exs. Cent. 14: no. 1376 (1870)

≡ *Schizonella delastrina* (Tul. & C. Tul.) Thirum. & M.D. Whitehead, Am. J. Bot. 55: 186 (1968)

≡ *Thecaphora delastrina* Tul. & C. Tul., Annls Sci. Nat., Bot., sér. 3 7: 108 (1847)

= *Schroeteria delastrina* var. *reticulata* Cocc., Mém. R. Accad. Sci. Ist. Bologna, Ser. 5 7: 219 (1898)

For a description see Vánky (1982).

Taxonomic remarks: A microscopic documentation of *Schroeteria delastrina* was done on the sample from Hannover (Pl. 15: 4c). Spore size was here evaluated as 7.8–11 × 7–9 µm (without ornamentation, see Tab. 4), the ornament as ~0.5–1(–2) µm high. According to Zogg (1985: 89, pl. 20B figs 1–5) the spore ornament is very different between *S. delastrina* and *S. decaisneana*, with warts and ridges up to 2 µm high in the former compared to only ~0.2 µm in the latter species.

Ecology: *Schroeteria delastrina* was reported by earlier workers on different *Veronica* species, though mainly on *Veronica arvensis*, the type substrate. Our investigated collections from Germany and Greece were all on this host plant which occurred at the collection sites in different biotops: in Germany in ruderal vegetation at the border of farmland (Kelbra), in mown meadows (Hannover, Thale), and in a Mesobromion grassland (Bad Frankenhausen, Leistadt, Sondershausen), in Greece in an annual vegetation on a raised area on the border of a summer-dry stream bed. The geology was mainly basophilically influenced, the phenology is May–June, in southern Europe March.

The distribution of the anamorph of *S. delastrina* comprises various countries of Europe (Scholz & Scholz 1988): Austria, Belgium, former Czechoslovakia, Denmark, Finland, France, Germany, Great Britain, Greece, Italy, Netherlands, Portugal, Poland, Romania, Sweden, Switzerland, former Soviet Union, and former Yugoslavia.

Specimens included (all in capsules of living plants of *Veronica arvensis*).

Anamorph: **Germany**: **Thüringen**, Kyffhäuser, 15 km SE of Nordhausen, 4 km WSW of Kelbra, between Mittelberg and Schloßberg Kleiner Heuweg, MTB 4531/44, 161 m, 28.V.2015, V. Kummer (V.K. P1652-23, sin. doc., sq.: ITS MW915652). – 0.9 km N of Bad Frankenhausen, Schlachtberg, 235 m, MTB 4632/23, 14.VI.2019, V. Kummer (V.K. P1652-26, sq.: ITS/LSU MW915645). – Hainleite, ESE of Sondershausen, N of Jecha, Panzerstraße 1, 185 m, MTB 4631/14, 14.VI.2019, V. Kummer (V.K. P1652-27, sin. doc., sq.: ITS/LSU MW915646). – **Niedersachsen**, 5.5 km ENE of Hannover, Groß Buchholz, Roderbruchmarkt, Nobelring, in front of hostel, MTB 3624/22, 55 m, 30.V.2011, J. Kruse (ex J. K. S0045, GLM-F129676). – **Rheinland-Pfalz**, N of Bad Dürkheim, Leistadt, 230 m, 13.V.2020, J. Kruse (J.K. S0969). – **Hessen**, Frankfurt/Main, SW airport, nearby Mönchhofdreieck, Flugschneise, 100 m, 24.V.2014, J. Kruse (J. K. S0239). – Darmstadt, Winkelschneise, forest sports park, ruderal area, 11.VI.2016, J. Kruse (J.K. S0604). – ~5 km SW of Darmstadt, L3097, Pfungstädter Hausschneise, 105 m, 11.VI.2016, J. Kruse (J.K. S0597) – 11 km NW of Eschwege, Frankershausen, Kripp- und Hielöcher, 270 m, 13.VI.2015, J. Kruse (J.K. S0335). – Nordrhein-Westfalen, Essen-Frohnhausen, Martin-Luther-Straße, 75 m, 31.V.2017, J. Kruse (J. K. S0956) – **Sachsen-Anhalt**, 11 km SW of Quedlinburg, Thale, Hubertusstraße, “Friedenspark”, 180 m, 9.VI.2017, J. Kruse (J.K. S0969). – L208 between Balgstädt and Hirschroda, 2,1 km WNW of Balgstädt, Balgstädter Berge, 24.V.2017, J. Kruse (J.K. S0953). – **Berlin**, 15 km SE of Berlin, Altglienicke, 50 m, 17.V.2014, V. Kummer (ø). – **Bayern**, ca. 2,4 km W Ibind, Fitzendorfer Wollgraswiesen, 340 m, 20.VI.2020, J. Kruse (ø). – Coburg, ~1 km NNW of Gemünda, Heiligenwiesen/Heiligenleite, 310 m, 21.VI.2020, J. Kruse (ø). – **Greece**: **Rhodos**, 4 km SW of Malonas, 1.8 km SSE of monastery Kamiri, entrance to zur Scoutljaris gorge, 60 m, 29.III.2011, V. Kummer (V.K. P1652-20).

Schroeteria bornmuelleri Magnus, Mitt. Thür. Bot. Ver., N.F. 28: 64 (1911)

For a description see Vánky (1982).

Specimens included (in capsules of living plants of *Veronica rubrifolia*).

Anamorph: **Iran**: **Khorasan**, 40 km NE of Mahhad, Gughghi (Gojgi), ~1250 m, 11.V.1990, D. Ershad, T. & K. Vánky (H.U.V. 750 ex TUB, sq.: ITS MW915653; BRIP H.U.V. 14892, 15006, non. vid.).

Schroeteria poeltii Vánky, Mycotaxon 18(2): 326 (1983) — Pls 16–19

Etymology: named after the Austrian lichenologist Josef Poelt (1924–1995) who sent the Hungarian smut fungi specialist Kálmán Vánky (*1930) some samples of the fungus.

Holotype: France, Alpes-Maritimes, Menton, Ste. Agnés, seeds of *Veronica cymbalaria*, 20.VI.1962, H. Teppner (BRIP H.U.V. 10800, non. vid.).

DESCRIPTION. **Teleomorph**: **Apothecia** fresh (1–)1.3–2.5(–3) mm diam., non-gelatinous, disc light ochraceous, slightly concave, finally flat, margin thin, not protruding, ± smooth, exterior pale ochraceous, very finely pubescent, receptacle at base 0.5–0.75 mm thick, at margin 0.25–0.35 mm; **stipe** 5–17 × (0.07–)0.15–0.55 mm, concolorous with receptacle in upper part, darker red-brown in lower part, black-brown at base, overall densely pubescent with rather long hairs; often gradually thinner towards base, flexuous especially in lower part, emerging singly from convex or lateral side of the seed. **Asci** *145–160 × 9.5–10.5(–10.8) µm {1}, †114–135 × 7–8.5 µm {1}, protruding *5–30 µm beyond paraphyses or (†) ± equalling the paraphyses, with 8 equal-sized spores (in overmature apothecia also unequal-sized), pars sporifera *53–63 µm long, spores obliquely subbiseriate; **apex** (†) hemispherical to moderately truncate, apical thickening immature or mature †2–3.8 µm thick, apical ring blue in IKI {2}, euamyloid (BB), of *Sclerotinia*-type, lower ring strongly blue, upper parts less so; **base** with short and thick stalk, arising from croziers {1}. **Ascospores** *(9.5–)10–11(–11.3) × (5.3–)5.5–6(–6.3) µm {1}, †(8.6–)8.8–10(–10.3) × 4.7–5(–5.3) µm {1}, ellipsoid (homopolar) or very slightly ovoid (heteropolar), ends rounded to obtuse, ± equilateral; containing 1(–2) medium-sized **LBs** close to each end, (1–)1.5–1.8 µm diam. {3}, OCI 2, **glycogen** not observed, with 1 **nucleus** 3–3.2 µm diam. in centre {1}; without **sheath**; **overmature** spores not observed. **Paraphyses** apically uninflated to slightly clavate-capitate or sublageniform {1}, terminal cell *57–70 × 3.5–4.7(–5.2) µm {1}, †3–4.1 µm wide, projecting beyond †asci by 5–10 µm; terminal cell containing large non-refractive vacuoles. **Subhymenium** light ochre-brown, 25–35 µm thick, of dense textura intricata. **Medullary excipulum** subhyaline, non-gelatinized, of dense horizontal t. intricata-porrecta, individual cells *(40–)70–130 × 6–11 µm, smooth or slightly rough by some granular, pale ochraceous exudate, 100–130 µm thick at lower flanks, sharply delimited from ectal excipulum; **in stipe** of vertical t. porrecta, cells *60–90 × 7–13 µm. **Ectal excipulum** 80–90 µm thick at lower flanks, ± hyaline, at mid flanks 25–35 µm thick, brown; of thin-walled, ± vertically oriented t. globulosa(-prismatica) from base of receptacle up to mid flanks, cells *20–50 × 15–30 µm {1}; exterior without covering hyphae but with scattered to abundant, protruding, vesiculous or cylindrical to conical, hyaline to brownish, 0–1-septate hair-like cells or hairs *25–35 × 13–15 µm, †18–25 × 3–10 µm; **in stipe** of subhyaline to pale ochraceous t. prismatica-porrecta, cells †25–40 × 6–9.5 µm; **hairs** on stipe scattered to dense, appressed or projecting, subhyaline to pale brown, †(22–)35–195(–258) × (3–)4–6(–8) µm, with 0.3–0.7 µm thick smooth wall, covered with scattered granules, sparsely septate, individual cells ~38–85(–140) µm long, usually emerging from superficial, swollen basal cells †15–32 × 11–17 µm. **Rhomboid crystals** scattered in medullary and ectal excipulum, more abundant in stipe. **Amyloidity of tissue**: subhymenium weakly pale blue (KOH-pretreated) {1}. – **Anamorph**: **Cultural characteristics**: ascospores germination not examined. **Sori** forming a reddish-brown mass of chlamydospores under reflected light which completely replace the seeds; **conidiogenous cells** not observed; **chlamydospores** cohering to form strongly curved (U-shaped) chains of (2–)4–5(–7) spores {2}, light yellowish-brown under transmitted light, ± smooth or often with distinct low warts, individual cells *10–11 × 8–10 µm {1}, †(5.5–)6.5–12 × 6.5–13 µm {type}, multiguttulate, wall 0.5–0.8 µm thick, ornamentation ~0.3–1(–2) µm high. **Microconidial synanamorph** (formed on chlamydospores, evaluated from Nagler et al. 1989) hyphoid conidiophores with **conidiogenous cells** phialidic, cylindrical to lageniform, 8–20 × 3.5–5.8 µm, **microconidia** ± globose, *(2.7–)3–3.7(–4) × (2.7–)2.9–3.5(–3.8) µm, with one eccentrical LB of 1.5–2 µm diam.

Habitat: **Teleomorph** on fallen, previous year's, moderately stromatized seeds of *Veronica cymbalaria* {1}, seeds (0.9–)1.7–2.8 mm diam., surface always rugose, light to bright grey-brown or blackish. **Anamorph**: chlamydospores formed apparently on placentae and funiculi of non-stromatized capsules of *V. cymbalaria* {3/3} by replacing the seeds inside the initially closed capsule of living plants. **Desiccation tolerance**: not tested. **Phenology**: apothecia I; anamorph III, VI. **Altitude**: 7–650 m. **Geology**: on acidic and calcareous soil.

Specimens included (all on *Veronica cymbalaria*).

Teleomorph (on fallen seeds): **Spain**: **Andalucía**, **Málaga**, 14 km S of Ronda, N of Pujerra, arroyo Bollage, 590 m, 4.I.2017, F.J. Valencia, vid. R. Tena (ex C.V.L. 040117, JA-CUSSTA 9523, GLM-F29000, sq.: ITS/LSU MW915648).

Anamorph (on seeds in capsules of living plants): **France**: **Provence-Alpes-Côte-d'Azur**, **Alpes-Maritimes**, ~4 km NW of Menton, near Ste.-Agnès, ~600 m, 20.VI.1962, H. Teppner (BRIP H.U.V. 10800, holotype, GZU 292883 & 294859 isotypes, doc. vid.). – ibid., ~650 m,

10.VI.1987, K. Vánky (BRIP H.U.V. 13121, topotype, doc. vid.). – **Greece**: **Rhodos**, 1.7 km SSW of Ialysos, 0.2 km E of Filerimos, monastery park, 212 m, 20.III.2018, J. Kruse & V. Kummer (V.K. P1675/cymbalaria 1, J.K. S1304, sq.:.ITS MW915654). – 2.7 km SSE of Masari, SW of Vagies, coastal road, 5 m, 22.III.2018, J. Kruse (J.K. B2278, sq.: ITS/LSU MW915647) – 2.5 km SE of Masari, Charaki, coastal road, former barracks area on the beach, 0 m, 21.III.2018, J. Kruse (J.K. B2279).

Taxonomic remarks: In the teleomorph, *Schroeteria poeltii* deviates from *S. decaisneana* merely by slightly smaller asci and ascospores, the latter having their LBs a bit closer to the spore ends, perhaps also in the absence of glycogen in the ascospores and in a tendency to wider excipular cells (Tab. 3). Despite these minor differences, the anamorph sharply differs by smooth, yellowish-brown chlamydospores cohering in strongly curved (U-shaped) chains of (2–)4–7 spores from the other *Schroeteria* spp. with their warted, greyish-brown chlamydospores cohering in straight chaines of 2–4 spores or detaching as single spores. The exclusive occurrence of *S. poeltii* on *V. cymbalaria* and the remarkable anamorph make any confusion with other species very unlikely.

Nagler et al. (1989) investigated the type of *Schroeteria poeltii* and a collection of *S. delastrina* on *V. arvensis* by light and electron microscopical methods. The authors observed microconidia formed endogenously in phialides which emerge either from germ tubes of the chlamydospores or directly from the chlamydospores. Besides, the authors illustrated an unusual case of endogenous maturation of microconidia inside of chlamydospores (fig. 7), which they also observed inside hyphal cells of *S. delastrina* (fig. 9). Problematic is that the scales are wrong in some of their illustrations. In order to achieve reasonable measurements, the scales in figs 6 and 9 should be around 20 µm instead of 5 µm and that in fig. 7 around 3 µm instead of 2 µm, whereas the scales in figs 12–17 appear to be correct.

In the collection from Filerimos, not all capsules of a given plant individuum were filled with chlamydospores but numerous were with seed formation. However, this varied even on a single shoot of a plant. Whether the seeds are able to germinate has not been tested. This is in contrast to our collections of *Schroeteria delastrina* on *Veronica arvensis* where all capsules of a shoot on a plant were either filled with chlamydospores or with seeds, suggesting a systemic infection.

Typification and etymology: Vánky (1983), who investigated the type of *S. poeltii*, stated that the species was only known from the type locality, where it was collected by H. Teppner in 1962. In a footnote he explained the reason for naming the species *S. poeltii*: shortly after publication of Vánky's *Schroeteria* monograph which appeared in 1982, Josef Poelt had sent him a specimen of Teppner's collection. Part of this collection then remained in GZU, whereas the holotype was stated by Vánky to have been deposited at UPS. However, according to Å. Kruys (pers. comm.) the specimen could not be found at UPS. In 1987 Vánky collected a topotype, which Nagler et al. (1989) investigated. In 2013 Vánky gave his entire herbarium to BRIP (Brisbane) where the holotype and also the topotype are listed in the online database.

Ecology: The host plant of *Schroeteria poeltii* has a (sub)mediterranean distribution and forms urn-shaped seeds similar as in *V. hederifolia* (cyathiform fide Muñoz-Centeno et al. 2006).

The French holotype collection was from a mesomediterranean semihumid site northeast of Monaco in dépt. Alpes-Maritimes. The collecting locality is not fully clear: the rough coordinates (43° 47' N, 7° 30' E) given by Vánky (1983) are in a region about 1 km north of the seaside town Menton and cover a region of about 50–200 m altitude. The given data about altitude (ca. 600 m) and site (tract Ste. Agnès, Umgebung von Ste. Agnès) in Vánky (l.c.) and on the handwritten isotype label in GZU (which lacks coordinates), suggest that the collection site was about 4 km northwest of Menton, i.e., about 3 km away from the published coordinates.

The *Schroeteria poeltii* anamorphs from thermomediterranean semihumid Greece were collected at the site Filerimos in an open grove with *Quercus coccifera* on top of a hill in the monastery park at 212 m altitude in the north of Rhodos, and near Charaki in a ruderal farmland area with *Mercurialis annua* etc., a former military area close to coastline at 7 m altitude in the middle east of Rhodos. The teleomorph from supramediterranean semihumid Spain was from an acidic floodplain forest in Málaga (Andalucía). The apothecia were found on stromatized seeds of *Veronica cymbalaria* fallen to the ground. The plants grew just above the ground on the vertical area of a schist rock. The floodplain forest consisted of *Populus alba* and *Salix alba*, and mediterranean plants such as *Quercus faginea* and *Rubia peregrina*, also *Lamium flexuosum*, *Rubus ulmifolius*, *Dorycnium rectum*, *Ranunculus ficaria*, and *Vinca difformis*. Outside of the flooded area are large *Castanea sativa* plantations, the main agricultural product of the local people.

Discussion

Circumscription of *Sclerotiniaceae*: Whetzel (1945), who erected the family *Sclerotiniaceae*, characterized it by apothecia arising from black stromata. He included, besides the above-mentioned 150 species in 28 genera, further ca. 55 more or less saprobic species in six genera, which were later separated by Holst-Jensen et al. (1997b) in the new family *Rutstroemiaceae*. In phylogenetic analyses of rDNA or

rDNA + protein-coding genes, both families formed together with the small *Piceomphale* clade the highly supported "*Sclerotiniaceae* lineage", and this lineage formed with the family *Cenangiaceae* the strongly supported "Lineage A" or "sclerotinioid clade" (Baral 2016, 2019; Pärtel et al. 2016: fig. 1; Kowalski et al. 2018; Johnston et al. 2019: figs 2, 5). In the latter analysis of 15 concatenated gene regions, this lineage included with less support also *Cordieritidaceae* and with low support *Chlorociboriaceae* and *Polydesmia*.

Holst-Jensen et al. (1997b) defined the family *Sclerotiniaceae* s.str. by determinate (sclerotial) stromata in or outside the host tissue ("sclerotial stromatal lineage"), and the *Rutstroemiaceae* by indeterminate stromata formed on the substrate ("substratal stromatal lineage"). Yet, several taxa with a black indeterminate stroma that have been included in *Rutstroemiaceae*, particularly some members placed in *Lanzia* and *Torrendiella*, turned out to belong to other families, mainly *Helotiaceae*, e.g., species related to *Hymenoscyphus fraxineus*, the causal agent of the ash dieback disease (Baral & Bemmann 2014), and species reallocated to the new genus *Hymenotorrendiella* (Johnston et al. 2014).

Phylogeny within *Sclerotiniaceae*. Different generic concepts have been developed within the *Sclerotiniaceae* in the past decades. The available phylogenetic analyses of rDNA (including our analysis in Pl. 1) and rarely protein-coding genes suggest heterogeneity of some of the classical genera, such as *Ciboria*, *Monilinia*, *Schroeteria*, and *Stromatinia*, their species clustering in different clades with often unresolved phylogenetic position. These analyses also raise doubts about the current splitting into small genera, for instance, they question the distinction between *Dumontinia*, *Grovesinia*, *Sclerotinia* s.str., and *Stromatinia* s.str., which could all be assigned to a single genus *Sclerotinia* s.l. (Pl. 1, S2).

Based on anamorph morphology, heterogeneity of *Monilinia* was observed by Honey (1936), who subdivided the genus into two sections: *Junctoriae* (*Monilinia* s.str., growing on fleshy, edible fruits of domesticated *Rosaceae*, without intercalating disjunctors of the macroconidial chains) and *Disjunctoriae* (*Monilinia* s.l., growing on stromatized fruits of *Rosaceae*, *Ericaceae*, *Empetraceae*, and *Pyrolaceae*, with intercalating disjunctors). This subdivision was followed by Batra (1988, 1991: 101), who distinguished in 1991 five different groups within *Disjunctoriae* according to the inhabited host, and Schumacher & Holst-Jensen (1998), who raised the *Disjunctoriae* to a new though never validly published genus *Franquinia* Holst-Jensen & T. Schumach.

Heterogeneity of *Monilinia* was confirmed by molecular phylogenetic analyses by Holst-Jensen et al. (1997a: fig. 9, SSU+ITS+LSU; 2004, ITS), Takahashi et al. (2005, ITS), Masuya et al. (2009, ITS), and in the present study (Pl. 1), with the conclusion that the genus represents two distinct evolutionary lineages. However, a phylogenetic analysis of three protein-coding genes (*hsp60*, *g3pdh*, *cal*) by Andrew et al. (2012) provided evidence for a supported monophyletic clade for *Monilinia* s.l., suggesting validity of the genus in the sense of Honey (1936), whereby its two sections formed supported sister clades. This analysis also suggests a broad concept of *Sclerotinia*, because members of *Dumontinia* (*D. tuberosa*, *D. ulmariae*) and *Stromatinia* s.str. (*S. rapulum*, *S. cepivora*) are included with *Sclerotinia* s.str. in a supported clade with comparatively short branches. Similar problems with generic concepts were addressed by Holst-Jensen et al. (1998), who followed a narrow concept of *Sclerotinia*: they found that the type species of *Grovesinia*, *G. pyramidalis* (= *G. moricola*), consistently contributed to the paraphyly of *Sclerotinia* in all of their ITS rDNA analyses, unless one ignores the multicellular diaspores of *Grovesinia* as a valuable morphological marker and includes *Grovesinia* in *Sclerotinia*.

Heterogeneity of *Schroeteria* in the current generic concept resulted from the distant position of *S. poeltii* (Pl. 1). Although *Veronica cymbalaria*, the host plant of *S. poeltii*, is closely related to *V. hederifolia* agg. (Muñoz-Centeno et al. 2006), the conidia of the *S. poeltii* anamorph are very different from those of other *Schroeteria* spp. This and the deviating molecular result appear to justify a separation of *S. poeltii* at some taxonomic level. In the morphology of the teleomorph, however, *S. poeltii* can hardly be separated from *S. decaisneana*, including their stromatized seeds. The specialized occurrence of *Schroetria* s.str. and *S. poeltii* on the same host genus *Veronica* suggests a common ancestor which also grew on *Veronica* seeds. This consideration makes a generic split of *Schroeteria* in our opinion premature at the moment. Multigene analyses which include protein-coding genes should be carried out to better understand the phylogenetic position of *Schroeteria* and in particular *S. poeltii*, comparable to the study by Andrew et al. (2012), which revealed for *Monilinia* a supported relationship between the two distant subgroups.

The genetically most heterogeneous genus in our analysis was *Ciboria*, an assemblage of species without a macroconidial anamorph. This heterogeneity was also seen in analyses of, e.g., Galán et al. (2015: fig. 4, LSU, fig. 5, ITS) and Pärtel et al. (2016: fig. 2, ITS). In two analyses (Pl. 1, S2), a supported core clade of *Ciboria* with two species growing on male catkins was formed, *C. caucus* (type species, on *Salicaceae*) and *C. amentacea* (on *Betulaceae*). Although morphologically very similar to those, *C. coryli* on male *Betulaceae* catkins was not associated but clustered unsupported with *Stromatinia cryptomeriae* (Pl. 1, S2). Another strongly supported clade was formed by *Ciboria americana* on *Castanea* cupules, *C. viridifusca* on *Alnus* cones, and *Coprotinia minutula* on dung, which clustered with medium (Pl. 1) or strong (S3) support sister to *Pycnopeziza sympodialis*. Various other *Ciboria* spp. clustered in different clades scattered across

the family. The molecular heterogeneity of *Ciboria* is in contrast to its high morphological homogeneity. Similar as in *Schroeteria* and *Monilinia*, the three *Ciboria* spp. on catkins are morphologically so similar that they can hardly be conceived to have evolved in two distant lineages.

With the present knowledge, the generic position of *Ciboria ploettneriana* could not satisfyingly be resolved, neither with morphological nor with molecular methods. In our combined analysis (Pl. 1) the species clustered unresolved within the *Sclerotiniaceae* though close to the type species of *Sclerotinia* (*S. sclerotiorum*), *Stromatinia* (*S. rapulum*), and *Dumontinia* (*D. tuberosa*). The distances in the ITS region and LSU D1–D2 domain to these taxa and other genera (*Myriosclerotinia*, *Botrytis*, *Kohninia*) appear to be too low in order to resolve generic limits. Multigene analyses would probably better resolve phylogenetic lineages in this group.

Because of a high similarity in the teleomorphs, a taxonomically satisfying solution which does not strictly follow monophyletic principles but also includes morphological considerations is very difficult to achieve. Despite its low molecular distance to species of *Sclerotinia* s.l. (including *Dumontinia*, *Stromatinia* s.str., and perhaps *Grovesinia*) and a characteristic motif in the ITS1 region (see below), we here use the current combination *Ciboria ploettneriana* instead of *Sclerotinia*, where it was originally placed, because *Sclerotinia* and *Dumontinia* have been characterized by freely formed sclerotia which do not incorporate remnants of host tissue (Kohn 1979: 377–378). *Stromatinia* forms an indefinite stroma comparable to *C. ploettneriana* and might be a suitable genus for this species. Nevertheless, BLAST search for the ITS region of *C. ploettneriana* yields species of *Sclerotinia* s.str. as closest match. Placement of *S. ploettneriana* in this group of genera (*Sclerotinia* s.l.) is supported by very similar ascospores which contain 2–4 nuclei associated with comparatively small LBs, perhaps also by the lack of a macroconidial state which is only known in *Grovesinia.* However, VBs in the paraphyses, which are characteristic of *Ciboria ploettneriana*, have not been seen in other members of *Sclerotinia* s.l., but are typical of *Botrytis* (= *Botryotinia*) (see IVV).

When Buchwald (1949: 165) proposed the combination *Ciboria ploettneriana*, he did not give arguments for doing so and also did not describe the fungus. Here and in his treatment of Danish *Sclerotiniaceae* (Buchwald 1947: 240, 255), he distinguished two subgroups within *Ciboria*: subgenus '*Euciboria* Boud.' for species on more or less stromatized catkins of *Betulaceae* and *Salicaceae* and subgenus '*Stromatinia* Boud.' for species on more or less stromatized seeds of *Betulaceae*, *Fagaceae*, and monocots. It must be noted that Buchwald (1947: 309) treated *Stromatinia rapulum* (type of *Stromatinia*) as a synonym of *Sclerotinia tuberosa*. Therefore, Buchwald (1949: 164) suggested to rename subgenus *Stromatinia* to subgenus *Pseudociboria* Buchw. (non *Pseudociboria* Kanouse). In his concept of subgenera, Buchwald followed Boudier (1885: 115) who considered the type of stromatization as taxonomically important and distinguished three subgenera within *Ciboria* (subgenus *Sclerotinia* with sclerotia, subgenus *Stromatinia* with a stroma, and subgenus *Ciboria* without stromatization). Buchwald accepted *Sclerotinia* as a distinct genus, and the stromatization in *C. ploettneriana* was obviously the reason why he included this species in *Ciboria* subgenus *Stromatinia* (in 1949 named *Pseudociboria*).

The genus *Ciboria* has been circumscribed by apothecia emerging from locally stromatized catkins, fruits, leaves, or wood and bark, the lack of both sclerotia and a macroconidial anamorph, an ectal excipulum of non-gelatinized textura globulosa, and by comparatively small, hyaline ascospores with a low lipid content (Spooner 1987, Baral in Baral & Krieglsteiner 1985). However, generic concepts vary among authors. Based on the first author's personal observations, *Ciboria* can hardly be distinguished by teleomorph and microconidial anamorph morphology from various other genera of *Sclerotiniaceae*, such as *Botrytis*, *Scleromitrula* (= *Ciborinia*), and *Sclerotinia* s.l.

The anamorphs of *Sclerotiniaceae*. According to Schumacher & Kohn (1985), nine teleomorph-typified genera of *Sclerotiniaceae* possess a macroconidial anamorph (*Botryotinia*, *Grovesinia*, *Monilinia*, *Ovulinia*, *Phaeosclerotinia*, *Pycnopeziza*, *Seaverinia*, *Septotinia*, *Valdensinia*). In the traditional dual nomenclature these anamorphs were treated in separately named anamorph-typified genera, such as *Botrytis* with a synchronous polyblastic conidiogenesis and *Monilia* with a monoblastic or sympodial conidiogenesis and conidia in branched acropetal chains.

Phialidic microconidial synanamorphs were observed in many genera of *Sclerotiniaceae*. They have currently been referred to the anamorph-typified genus *Myrioconium*, which is characterized by small, ± globose, hyaline, smooth or sometimes warted conidia. The three sclerotiniaceous genera *Coma*, *Microgloeum*, and *Mycopappus* have been erected for their microconidial anamorphs, but are so far without a known teleomorph.

The conidiophores in the various types of macroconidial anamorphs known in the family are short to long, often branched, hyaline or brown. Conidiogenesis is holoblastic, mono- to polyblastic, sympodial, singly or in acropetal chains. The conidia are globose to ellipsoid-fusoid, non-septate, (sub)hyaline, typically smooth (except for *Verrucobotrys* = *Seaverinia*, Seifert et al. 2011), rarely cylindrical and 1-septate (*Septotis* = *Septotinia*, *Acarosporium* with appendages = *Pycnopeziza*), or forming complex staurosporous multicellular diaspores (*Hinomyces* = *Grovesinia*, *Cristulariella* = *Nervostroma*, *Valdensia* = *Valdensinia*). It must be noted here that, although the diaspores

sharply differ between *Grovesinia* (pyramidal) and *Cristulariella* (flattened-spherical), strain CBS 737.68 was erroneously renamed in CBS and GenBank from *Cristulariella depraedans* to *Grovesiniapyramidalis* (= *G. moricola*). *Verrucobotrys* resembles *Botrytis* but its conidia are subglobose, pale brown and minutely tuberculate (Whetzel 1945, Seifert et al. 2011) and superficially resemble the thallic chlamydospores of *Schroeteria*.

In their "Recommendations on generic names competing for use", Johnston et al. (2014) proposed to use the anamorph-typified names *Botrytis* and *Valdensia* for the holomorph in replacement of *Botryotinia* and *Valdensinia*, respectively. In all the remaining pleomorphic genera the authors proposed to maintain the teleomorph-typified name, with one exception: although they gave recommendations on three of the four above-mentioned microconidial genera, they did not treat the oldest genus *Myrioconium* as a genus competing with *Myriosclerotinia*. According to Schumacher & Kohn (1985), the type species of *Myrioconium*, *M. scirpi*, is a synonym of *Myrioconiumscirpicola*, the anamorph of *Myriosclerotinia scirpicola*, which in turn is the type species of *Myriosclerotinia*. Thus, *Myrioconium* is a synonym of the younger *Myriosclerotinia* which was introduced by Buchwald (1947) at a time when different names were required for different morphs. Today *Myriosclerotinia* should be protected as it appears much more often in internet search engines than *Myrioconium*.

Remarks on the genus *Schroeteria*

Schroeteria G. Winter, Rabenh. Krypt.-Fl., Edn 2 (Leipzig) 1.1: 117 (1881) [1884]

≡ *Geminella* J. Schröt., in Rabenh. Fungi Eur. exs. Cent. 14: no. 1376 (1870), nom. illegit., Art. 53.1 (non *Geminella* Turpin 1828, *Chlorophyta*)

Etymology: *Schroeteria*: named after the German mycologist and physician Joseph Schröter (1837–1894); *Geminella*: after the frequently occurring twin spores in the type species.

Type species: *S. delastrina* (Tul. & C. Tul.) G. Winter

Circumscription of the genus. The genus *Schroeteria* represents a small group of Ascomycetes growing as biotrophic plant parasites on different *Veronica* spp. (*Plantaginaceae*, earlier placed in *Scrophulariaceae*) (Brefeld 1883, 1912; Vánky 1982, 1983, 1994). It is characterized by chlamydospores (resting spores) with an under transmitted light bluish-grey to pale yellowish- or reddish-brown, usually warted epispore. Spore formation is thallic by fragmentation of a richly branched mycelium, from which the spores are formed by division of a "spore mother cell" (Vánky 1982: 159; Scholz & Scholz 1988: 250) which may be variously curved or spirally twisted (Winter 1876: 148, pl. IV, 1881; see also Pl. 21: 6). At maturity the irregularly roundish spores often remain coherent as pairs (twin spores) or threes by showing strong constrictions between the individual spores. In contrast to the typical case, *Schroeteriapoeltii* mainly forms chlamydospore chains of 2–7 cells by showing only slight constrictions at their septa.

Schroeteria chlamydospores are formed in sori inside the capsules of the host plants where they replace either more or less entirely the seeds (e.g., *S. delastrina*, *S. poeltii*) or only placenta, funiculus and hilum by leaving the testa, endosperm and embryo unaffected (*S. decaisneana*). When the capsules finally burst, the chlamydospores appear to be spread by wind and water. During germination on agar, they form hyaline germ tubes on which phialides arise that produce globose, smooth microconidia (earlier referred to as 'sporidioles' or 'sporidia') with an eccentric oil drop (Brefeld 1883; Vánky 1982, Nagler et al. 1989). Other species earlier placed in the genus *Schroeteria* lack this kind of phialides and grow on other host genera.

According to Zundel (1953), Kochman & Majewski (1973), Vánky (1982, 1983, 1994: 456), Scholz & Scholz (1988), and Nagler et al. (1989), six *Schroeteria* spp. are now accepted, all forming their chlamydospores on seeds of *Veronica*: *S. banatica* Vánky (*Veronica austriaca*), *S. bornmuelleri* (*V. biloba*, *V. rubrifolia*), *S. bremeri* Petrak (*V.* ?*triphyllos*), *S. decaisneana* (*V. hederifolia* agg., after Terrier 1958 also *V. campylopoda*, but see below), *S. delastrina* (*V. acinifolia*, *V. agrestis*, *V. arvensis*, *V. dillenii*, *V. praecox*, *V. triphyllos*, *V. verna*), and *S. poeltii* (*V. cymbalaria*). Furthermoore, Gaponenko (1965) reported about a *S. delastrina* infection on *V. campylopoda*. Scholz & Scholz (1988) listed *S. banatica* as infecting also *V. prostrata*, based on a record from Romania which is not included in Bontea (1985), and *S.banatica* and *S. delastrina* on *V. prostrata* from Slovakia, according to a report by Vánky (1985). The report of *S. delastrina* on *V. triloba* listed in Zundel (1953) was not adopted by Vánky (1982) and Scholz & Scholz (1988).

Nomenclature. *Schroeteria* was erected by Winter (1881) as a replacement name (nom. nov.) for Schröter's illegitimate name *Geminella*. The hitherto cited original publication by Schröter (in Rabenhorst 1870: 137) represents a copy of his shortly before issued herbarium label of Rabenhorst's Fungi Europaei exsiccati, which includes a valid description of the genus including a diagnosis (Pl. 20, U. Braun & K. Bensch pers. comm.). Here, Schröter recognized in *Geminella* only one species, *G. delastrina*. *Geminella* and consequently also

Schroeteria are thus typified by *G. delastrina*. Vánky (1982) incorrectly cited "*Geminella* Schröter (1869: 5)", being unaware that 1869 was not the year of printing but refers to the reporting year of the publication to which Schröter's article was assigned.

Schröter's article finally appeared in the "Abhandlungen der schlesischen Gesellschaft für vaterländische Kultur, Abtheilung für Naturwissenschaften und Medicin 1869/72" (Schröter 1872), while Rabenhorst (1871: 8–12) gave a summary of the complete work already in the January issue of Hedwigia vol. 10. Schröter (l.c.) added *G. foliicola* (W. Hausm.) J. Schröt. to the genus (as *G. foliicola* n. sp. with the reference "*Ustilago destruens* a *foliicola* Hauskn. in herb. critt. Ital.", apparently confusing Hausmann and Hausknecht), which grows erumpent on leaves of *Carex bigelowii* subsp. *dacica* (Heuff.) T.V. Egorova, published as *C. rigida* Good. Shortly afterwards, however, Magnus (1875) excluded this species from *Geminella* when he synonymized it with *Schizonella melanogramma* (DC.) J. Schröt. (as *Uredo melanogramma*, *Ustilaginales*). As a consequence, Winter (1881) treated *Schroeteria* once again with only one species, *S. delastrina.* He mentioned four *Veronica* spp. as hosts of *S. delastrina*: *V. arvensis* (type host of *S. delastrina*, Tulasne & Tulasne 1847), *V. triphyllos*, *V. praecox*, and *V. hederifolia*. The latter indicates that Winter did not differentiate between *S. delastrina* and *S. decaisneana* as suggested later by Boudier (1887, as *Geminella*). Two species growing on *Cissus* (*Vitaceae*), described at the end of the 19th century in *Schroeteria* because of similar paired spores, were transferred to *Mycosyrinx* as *M. cissi* (DC.) Beck and *M. arabica* (Henn.) Penz. (Vánky 1982), a genus of *Urocystidales* (*Ustilaginomycetes*) according to molecular data in GenBank.

History about the phylogenetic placement of the genus *Schroeteria*.

Since its description by J. Schröter in Rabenhorst (1870) under the illegitimate name *Geminella*, the genus has been considered over more than a hundred years as belonging to the smut fungi (*Ustilaginales*, now *Ustilaginomycetes*) in the *Basidiomycota*. Therefore, its dark-coloured warted chlamydospores were often called "teliospores", whereas Brefeld (1912), who pointed out the true relationship with *Ascomycota*, called them chlamydospores because of their thallic ontogeny that represents a direct transformation of hyphal cells into spores. Vánky (1982, 1983) and Nagler et al. (1989) simply named them "spores", whereas Bauer et al. (2001) and Vánky (2008a, b) proposed to reinstate the term teliospores in a wide sense for thick-walled resting spores of plant parasites surviving unfavourable periods, mainly during winter, and not to restrict the term to dicaryotic probasidia of basidiomycetous rusts and smuts. They also redefined the term "smut fungus", i.e., from a taxonomic group to a life strategy and organization, to include non-ustilaginomycetous groups of plant parasites that develop teliospores as organs of dispersal and resistance. Other authors have used the term "false smuts" for such non-ustilaginomycetous fungi, e.g., Tanaka et al. (2008). This usage traces back to Brefeld who applied the German version "Falsche Brandpilze" (Brefeld 1908: 221).

The later ignorance of its true relationship is astonishing, since already Brefeld (1883, 1912) mentioned the strong similarity of germ tubes, phialides and microconidia in *G. delastrina* and *G. parvispora* (= *S. decaisneana*) with those of the helotialean genus *Sclerotinia*, viz. in *S.tuberosa* (Hedw.) Fuckel, *S. sclerotiorum* (Lib.) de Bary, and perhaps *S. trifoliorum* Erikss. (all under the name *Peziza*, the latter as *P. ciborioides*), compared to a high dissimilarity to hemibasidia of *Ustilaginomycetes*. Brefeld was convinced about *Schroeteria* belonging in relationship of *Sclerotinia*, e.g., because the microconidia did not germinate, which is typical of *Sclerotiniaceae* and generally interpreted as an indication that they function as spermatia. He could even verify the formation of sclerotium-like bodies in pure culture after several weeks, but did not succeed in obtaining apothecia (see also Vánky 1982, Nagler et al. 1989). Brefeld also failed to find sclerotia or apothecia at the sites where the infected plants grew (Brefeld 1912: 79). Although Brefeld's observations and conclusions have later widely been recognized, they were only sometimes accepted, particularly by Schellenberg (1911) who listed *Schroeteria delastrina* among the genera and species to be excluded from the *Ustilaginaceae*. Also Lindau (1912) accepted Brefeld's opinion by expressing doubts that *Schroeteria* belongs in the "*Ustilagineae*", but he preferred to leave it there because of the custom at that time to associate the genus with this family.

Others doubted a relationship with Ascomycota, e.g., Ferdinandsen & Winge (1914: 4). Thirumalachar & Whitehead (1968) referred *Schroeteria* in synonymy with *Schizonella* J. Schröt. (*Ustilaginales*) by misinterpreting the observations of Schröter and Brefeld as an untypical case, believing that the microconidia never separate from each other, i.e., the germ tubes convert into "beaded cells". In their studies of *S. delastrina* (l.c.: fig. 8), these authors observed instead elongate fusoid "secondary sporidia" of 6 × 2.5 µm on septate germ tubes and they concluded that this type of germination is typical of *Ustilago* spp. Also Vánky (1982), who illustrated the characteristic microconidial synanamorph of *Schroeteria* in detail and stressed its possible relationship with *Ascomycota*, still retained the genus in *Ustilaginales* and referred to the chlamydospores as "teliospores".

Nagler et al. (1989) studied *S. delastrina* and *S. poeltii* by cultural and ultrastructural methods. The authors could not obtain sclerotial structures, but they concluded that *Schroeteria* represents an anamorphic genus of *Ascomycota*, based on the absence of caryogamy and meiosis, the consistent presence of multinucleate germ tubes, the morphology of the spindle pole bodies, the presence of septal pores

with a pore plug and Woronin bodies, and the absence of layering in the cell wall. This opinion then also Vánky (1994) accepted. Nagler et al. (l.c.) doubted Thirumalachar & Whitehead's (1968) findings of spore germination in *S. delastrina* as they could never see this type of germination in their studies. Their unusual observation of endogenous maturation of microconidia inside chlamydospores of *S. poeltii* and inside germ tubes of *S. delastrina* (Nagler et al. 1989: figs 7, 9) requires further attention.

A similar fungus with warted brown spores, though not formed in pairs, is *Restilago* Vánky with one species, *R. capensis* Vánky growing in capsules of *Ischyrolepis capensis* (*Restoniaceae*, *Poales*). This was shown to be "the second genus of smut fungi of ascomycetous origin" (Vánky 2008a) because of Woronin bodies at the septal pores. Another false smut fungus is *Hapalosphaeria deformans* (Syd. & P. Syd.) Syd. It causes stamen blight of blackberry (*Rubus* ?*corylifolii* agg., as *Rubus dumetorum*) and was already stated by Diedicke & Sydow (1908) as belonging to ascomycetes, but requires further, particularly molecular investigations. Contrary to *Schroeteria* and *Restilago* it forms hyaline, smooth phialoconidia inside brown pycnidia in anthers of *Rubus*. No sequence data of these two genera are known to us. Another false smut is *Ustilaginoidea* Brefeld, which forms teliospore-like, olive-brown, subglobose, warted chlamydospores (Brefeld 1895: 194 f.). Earlier placed in *Ustilago* or *Tilletia*, the two economically important plant parasites of rice (*Ustilaginoidea oryzae* (Pat.) Bref.) and a bristle grass (*Ustilaginoidea setaria* Bref.) were shown by Brefeld to produce in culture *Claviceps*-like ascomata emerging from sclerotia (Brefeld 1896: 103, 1912: pl. III figs 1–15; see also Tanaka et al. 2008). Based on molecular methods, Bischoff et al. (2004) placed *Ustilaginoidea* in *Clavicipitales*. Finally, Tanaka et al. (2020) referred four species, which were previously placed in *Ustilago* and infect ovaries of monocot flowers of the family *Commelinaceae*, to a new genus *Commelinaceomyces* in *Clavicipitaceae* (*Sordariomycetes*).

Specific nucleotide positions in the rDNA

Within the core clade of *Sclerotiniaceae*, no specific nucleotide positions in the ITS region and LSU D1–D2 domain have been found that characterize any of the different genera, such as *Botrytis*, *Elliottinia*, *Grovesinia*, *Monilinia* s.str., *Myriosclerotinia*, *Ovulinia*, *Pycnopeziza*, *Sclerotinia* s.l., or *Valdensia*. Regarding placement of *Ciboria ploettneriana*, only one position in the middle of ITS1 gives a hint on its generic affiliation: the species shares the motif **G**GGGYCT (Y = C or T) with most species of *Sclerotinia* s.l., but also with *Grovesinia moricola*, whereas other species have mostly the motif **H**GGGCCT (H = A or C or T).The *Schroeteria* core clade shows some characteristic motifs. In the ITS region, pos. 123 of the 5.8S region is C and pos. 4 of the ITS2 region is G, whereas *S. poeltii* and other *Sclerotiniaceae* have T + T, except for *Monilinia jezoensis* which has T + G. In the LSU D1-D2 domain, *Schroeteria decaisneana* and *S. delastrina* have several extraordinary positions. Some of them occur also in *Ciborinia erythronii*, but none were observed in *Ciboria ploettneriana* and any other *Sclerotiniaceae* in GenBank.

Species delimitation within *Schroeteria*, doubtful measurements of chlamydosporesand microconidia.

Vánky (1982) treated five species in *Schroeteria*, which he distinguished by the mature chlamydospores occurring mostly in pairs or threes to fours (*S. bremeri*, *S. delastrina*) or mostly single (*S. banatica*, *S. bornmuelleri*, *S. decaisneana*). Species delimitation was further accomplished by spore wall thickness and the kind of spore ornamentation. Chlamydospore size lies in the five species within a similar range of about (7–)8–16(–20) µm diam., which makes spore measurements comparatively useless for species delimitation, considering the high infraspecific, particularly intrapopulational variability observed in each species. For instance, chlamydospore size of *S. decaisneana* varied considerably within a preparation made by us from a single sorus (Pl. 14: 2e–k). Vánky (1982) used chlamydospore size in his key, but the given measurements strongly overlap. They clearly refer to single cells, whereas in the older literature it is not always clear whether they mean single cells or twin spores. Vánky (1983) described the morphologically deviating *S. poeltii* as a sixth species within *Schroeteria*, characterized by up to 6(–7)-celled, strongly curved (horseshoe-shaped), almost smooth chlamydospores.

Boudier (1887) separated *S. decaisneana* from *S. delastrina* owing to slightly smaller, soon single, at first glaucous or bluish-grey, finally grey-black or slate-grey spores born on narrower hyphae, and a different host plant on which it merely attacks the funiculus, leaving the seed and placenta intact. Brefeld (1912: 75) was unaware of *S. decaisneana* when he proposed the name "*Geminella* (*Schroeteria*) *parvispora*" (a taxon which we here consider a synonym of *S. decaisneana*) for collections on *Veronica hederifolia* agg. The name *Geminella parvispora*, which was not listed in databases before November 2020, is mentioned several times in Brefeld's text and in his legend to tab. III fig. 16–17. When first mentioned on p. 75, he cites it as follows (translated from German): "The fungus living on *V. hederaefolia* is the small, single-spored bluish form which produces an easily dispersed spore dust and is here named *Geminella* (*Schroeteria*) *parvispora*". In our opinion, the taxon is to be considered as validly described on p. 75 under the name *Geminella parvispora*.

Two years later, the valid combination *Schroeteriaparvispora* was used by Ferdinandsen & Winge (1914: 4). In the same year also Fischer (1914) published this combination, but that paper appeared later, apparently after September 1914, whereas Ferdinandsen & Winge's appeared on 17. July 1914. Later, Liro (1938) considered *G. parvispora* as a synonym of *S. decaisneana*.

Brefeld (1912) characterized *Geminella parvispora* by small, mostly single, only slightly rough, blueviolet spores that easily get dispersed, in contrast to *S. delastrina* on *V. triphyllos* and *V. arvensis* etc. which has rough-warted, black, double-sized spores that are formed in pairs or sometimes threes. He did not indicate the origin of his samples, but it can be assumed that he collected them during his term in Münster (Nordrhein-Westfalen, Germany) where he worked as a botanist at the university and director of the botanical garden until 1898 (Brefeld 1912: 79). Thereafter he was offered a chair in Breslau where he started to go blind in the same year due to a glaucoma.

Regrettably, Brefeld did not give any measurements of conidia or other elements. When looking at his illustrations (Brefeld 1912: pl. III figs 16 & 18), it is evident that the individual cells of the chlamydospores of *Geminella parvispora* are only slightly smaller than those of *G. delastrina* and not "almost half the size" (Brefeld 1912: 75) or, a few lines later, vice versa those of *G. delastrina* not "more than double" the size of *G. parvispora*, provided that he compared the diameter of the cells and not their volume. Brefeld referred in this context to "single spores", and as he wrote that the "spores" often remain connected in pairs or threes, it appears that his remark on double-sized spores of *G. delastrina* cannot refer to the length of twin spores compared to single spores in *G. parvispora*. On the other hand, some authors used to measure chlamydospores of *Schroeteria* as an entity, e.g., in his key Ciferri (1938) gave for *S. delastrina* a spore size of 15–23 × 8–12 µm (referring to twin spores) and for *S. decaisneana* 10–12 × 8–12 µm (referring to single spores), and also Bubák (1916) measured *S. delastrina* as 20–30 × 12–17 µm regarding twin or sometimes triple spores, and *S. decaisneana* as 7.5–15 µm regarding single spores (see Tabs 4–5).

As a common usage in earlier times, Brefeld (1883: pl. XI fig. 13, pl. XII fig. 14–18; 1912: pl. III figs 16, 18) did not provide scales but only enlargement factors for his detailed illustrations, which were drawn at a 150× up to 400× magnification, according to his captions. Our reevaluation of spore size based on the printed books yields values much above the current data of the two species (Tabs 2, 3). Actually, a cell diameter above 17–18 µm appears to have never been reported for chlamydospores of *Schroeteria*, therefore, the real values of Brefeld's material were probably much lower. The actual average chlamydospore cell sizes of *Schroeteriadelastrina* and *S. decaisneana* lie in the range of 8–12 µm, which is just half of what can be evaluated from Brefeld's sketches of *S. delastrina* (Tab. 4), whereas his drawing of *G. parvispora* yields a cell size of about 1.5× larger than the current values (Tab. 5). On the other hand, Brefeld's (1883: pl. VI) illustration of *Microbotryum cardui* (as *Ustilago cardui*) yields teliospores of 16–19 µm diam., in good agreement with data given by Vánky (2012) for this species (15–20 × 14.5–19 µm).

Brefeld's observations and drawings were always made from material he cultured in nutrient media rather than from freshly collected specimens. As an example, he described the enormous swelling of the endosporium of a twin spore (Brefeld 1883: 144, pl. XII fig. 17a), which means that spore size evaluated from his drawings needs to be compared with caution with measurements of other authors who usually observed uncultured material. However, spores drawn by him without germ tubes or without emerging endosporium appear also oversized, although they should concur in size with uncultured spores because of an inelastic exosporium.

The presumed error in Brefeld's scale becomes evident when comparing microconidial size among reports of different authors. Surprizingly, also Cocconi's (1898) illustration of *S. delastrina* var. *reticulata* Cocc. yields double-sized values for chlamydospores (20–26 µm) as well as microconidia (7–8 µm), according to the stated magnification factor (Tab. 4). We thereby presume that the spore size of 16–20 µm given by Cocconi for twin spores of this variety refers to the diameter of single cells.

Without having examined the type, Ciferri (1931, 1938) raised doubts about Cocconi’s var. *reticulata*, which Cocconi (1898) distinguished by a reticulate epispore from the type variety which has a verrucose epispore. Because Cocconi’s drawing shows spores with a dense spiny ornament in contrast with the description, and the host plant was seemingly *Veronica praecox*, on which also *S. delastrina* has been reported, Ciferri concluded that *S. delastrina* var. *reticulata* is a synonym of *S. delastrina*. Also Vánky (1982) considered Cocconi’s description of reticulate spores as an inaccuracy, arguing that the spore surface in *Schroeteria* is generally verrucose and ribbed (but Vánky figured reticulate spores in *S. decaisneana*), and he also doubted Cocconi's large spore measurements.

Table 4. Measurements of chlamydospores and microconidia of *Schroeteria delastrina* (on *Veronica arvensis*) in the literature. Chlamydospore values refer to single cell diameters (without ornamentation), length of twin spores, and cell number. [t] = values reported in text; [s] = values gained based on scale or magnification factor of illustration; [§] = type of *S. delastrina* var. *reticulata*, [$] = including *S. decaisneana*. Note that Brefeld's and Cocconi's data (highlighted in italics) are about 1.5–2× higher than those of other authors and obviously erroneous.

	single cells of chlamydospores [µm]	twin spores	cell number	microconidia [µm]
Tulasne & Tulasne 1847	12–14 [t]	16–20 [t]	2 (–3)	–
	(8.5–) 10–12 × (4.5–) 6.5–11 [s]	15–20 [s]		
Winter (1876)	7–9.5 × 6–8.5 [s]	16–23 [t]	2	–
Schröter (1877)	7.7–9.5 × 6.7–8.5 [s]	12.5–16.5 [s]	(1–) 2	2.7–4.3 [s]
Fischer v. Waldheim (1877) [$]	10–13 × 8–10.5 [t]	?	?2	–
Winter (1881)	9–12 [t] × 8–11.5 [s]	?	2 (–3)	–
Brefeld (1883)	*(12.5–) 16–24 (–26)× (12.3–) 15–21*[s]	*30–40*[s]	(1–) 2	*6–7*[s]
Boudier (1887)	11–15 [t] / 7–12 × 6–11 [s]	16–18.5 [s]	(1–) 2–3	–
De Toni (1888)	8–12 [t]	15–23 [t]	2 (–3)	–
Cocconi (1898) [§]	*16–20* [t] */ 20–26 × 16.5–23*[s]	*37–45*[s]	2	*7–8*[s]
Brefeld (1912)	*16.5–26.5 × (10–) 15–22.5* [s]	*32–45* [s]	(1–) 2–3	–
Bubák (1916)	12–17 [t]	20–30 [t]	2 (–3)	–
Ciferri (1938)	8–18 × 8–12 [t]	15–23 [t]	2 (–3)	–
Liro (1938)	9–13 [t]	?	2 (–3)	–
SĂvulescu (1957)	(9–) 10–12 (–15) × (8–) 9–12 [t]	~14–21 [s]	2 (–3)	–
Vánky (1982)	8–11 (–13.5) × 8–11 (–13) [t]	18–20 [s]	(1–) 2 (–3)	2.7–3.3 [t]
	9.5–11 × 8–10 [s]			2.5–3 [s]
Zogg (1985)	(8–) 9–12 (–13) × (7–) 8–11 (–12) [t]	?	2 (–3)	–
present study (Hannover)	**7.8–11 × 7–9**	**14–17**	**2 (–3)**	**–**

Table 5. Measurements of chlamydospores and microconidia of *Schroeteria decaisneana* (on *Veronica hederifolia* agg.) in the literature. Chlamydospore values refer to single cell diameters (without ornamentation), length of twin spores, and cell number. [t] = values reported in text; [s] = values gained based on scale or magnification factor of illustration; [§] = type of *Geminella parvispora*. Note that Brefeld's values (highlighted in italics) are about 1.5–2× higher than those of other authors and obviously erroneous.

	single cells of chlamydospores [µm]	twin spores	cell number	microconidia [µm]
Boudier (1887)	10–12 × 8–12 [t] / 7–10 × 7–9.5 [s]	13.5–15 [s]	1–2	–
De Toni (1888)	10–12 × 8–12 [t]	?	2 → 1	–
Brefeld (1912) §	*14–17 × 12–15* [t] / *13.5–20 × 11.2–18.5* [s]	*24–27* [s]	1 (–2)	*6–7* [s]
Bubák (1916)	7.5–15 [t]	?	2 → 1	–
Liro (1938)	7–11 × 7–11 [t]	?	1 (–2)	–
Ciferri (1938)	10–12 × 8–12 [t]	?	2 → 1	–
SĂvulescu (1957)	9–12 (–15) × (7–) 8–11 (–12) [t]	~14–18 (–26) [s]	1–2	–
Vánky (1982)	7–12 (–13) × 7–11 [t]	17.5–21 [s]	1–2	2.7–3.3 [t]
	9–13 × 8–11 [s] / 7.5–11.2 × 6.5–10.3 [s]			2.6–3.3 [s]
Zogg (1985)	(8–) 9–11 (–11) × (7–) 8–11 (–12) [t]	?	1 (–2)	–
present study (Freyburg)	**(8.2–) 8.7–11 (–11.8) × 7.9–10.8**	**13.3–15 (–18.5)**	**1 (–2)**	***2.8–3.6 × 2.6–3.4**

Ecological remarks on *Schroeteria decaisneana* and *Ciboria ploettneriana* and their host plant Phenology and life cycle: Kirschstein (1906) collected apothecia on seeds of *Veronica hederifolia* agg. at first in October 1899 and a second time in April 1905. The first collection was reidentified by us as *Schroeteria decaisneana*, whereas we selected the second collection as lectotype of *Ciboriaploettneriana*. Under the assumption that the ascospores infect flowers of other individuals of this plant, Kirschstein was astonished about the occurrence of apothecia in October as he could not find any evidence for a second flowering period of the annual host plant, which generally blooms in central Europe during (February–)March–May(–June) and fruits during April–June.

Indeed, the two species have a different phenology: *Schroeteriadecaisneana* forms apothecia during November–January, whereas those of *Ciboria ploettneriana* are found during March–May. However, collections of mature *Schroeteriadecaisneana* apothecia from three different sites were made during March–May. The occurrence in late autumn suggests that ascospores of *S. decaisneana* do not infect the host's flowers but start their life cycle in another way. The black stroma of *C. ploettneriana* might aid in surviving the frosty wintertime in order to form apothecia next spring, whereas the greyish-brownish stroma of *S. decaisneana* could be an adaptation in surviving the warm and dry summertime in order to form apothecia next autumn.

Observations indicate that mycelia of *Schroeteria* spp. exist endophytically in the plant from where they grow up to the flowers. According to Brefeld (1912) and Vánky (1982), plants infected by *Schroeteria* anamorphs do not differ in general appearance from healthy ones. The vegetative mycelium can be found systemically in the intercellular space of the medullary parenchyma of the entire host plant (Winter 1876: 147, pl. IV fig. 15), though sometimes one or more shoots or in some cases only some flowers may remain healthy. It grows through the floral pedicel, placenta and funiculi into the young seeds where the chlamydospores are formed. In *S. decaisneana* the fungus replaces placenta, funiculus, and hilum (Boudier 1887: 150) or only the funiculus (Bubák 1916: 59) by leaving the seed unaffected although this can no longer germinate, whereas in *S. delastrina* the seeds are entirely absorbed whereas funiculi and placenta remain unaffected (Winter 1876: 148, Boudier l.c.: 151). Winter (1881: 118), who did not distinguish *S. decaisneana*, wrote that *S. delastrina* infects placentae, funiculi, and the young seeds. The produced spores form a moldy smelling, greyish-brown, greyish-blueviolet, or greyish-black powdery spore mass which in *S. decaisneana* fills the ventral cavity of each seed and in *S. delastrina* the entire capsule (Winter 1881, see also Vánky 1982). The spore mass of the infested seeds or capsules is generally called "sorus" following the custom with teliospores of ustilaginomycetous smut fungi. The capsule later tears open to release the spores passively.

Brefeld (1912: 79) was convinced that the chlamydospores do not infect flowers of other plants but germinate in the soil by forming a persistent mycelium that either infects young plants or produces apothecia that infect with their ascospores young seedlings. Brefeld could not detect apothecia associated with *Veronica* in the field, but he correctly imagined that they develop from the ovaries (Brefeld 1895: 204). He could not know, however, that during teleomorph formation the fungus transforms the seeds into a sclerotium-like stroma.

Hyperparasitism. Owing to the fact that two sclerotiniaceous species grow on the same organ of the same host plant, the possibility should be considered that one species is a hyperparasite on the stroma of the other. Yet, any such evidence is lacking. *Schroeteria*

decaisneana as hyperparasite would be in contradiction to the biology of its anamorph which, like anamorphs of other *Schroeteria* spp., is known as a direct parasite of the plant. *Ciboria ploettneriana* as hyperparasite would mean that during spring its ascospores attack plants that have been already invaded by *S. decaisneana*. But where do the ascospores of *S. decaisneana* germinate when they are ejected during late autumn and winter?

Similar hypotheses of hyperparasitism have been assumed in some other sclerotiniaceous fungi. For instance, Spooner (1987: 251) thought that *Scleromitrula shiraiana* could be a hyperparasite on stromata of *Ciboria shiraiana*, both occurring on fruits of *Morus*, and he also mentioned other examples of possible hyperparasites, viz. *Episclerotium sclerotiorum* (as *Mitrula*) on sclerotia of *Sclerotinia trifoliorum*, and *Episclerotiumsclerotipus* (as *Mitrula*) on sclerotia of *Typhula*.

Because *Ciboriaploettneriana* clustered in our phylogenetic analysis near *Sclerotinia* spp. distant from all investigated *Schroeteria* spp., it appears improbable that it possesses a *Schroeteria*-like anamorph. Yet, also *Schroeteriapoeltii* did not group with the core clade of *Schroeteria* nor with any other clade in the family, but whether its deviating anamorph is correlated with a deviating biology is unknown.

Microspecies of *V. hederifolia*. The *V. hederifolia* aggregate consists of three microspecies, the mainly southeast European, (sub)mediterranean *V. triloba* and the more temperate *V. sublobata* (= *V. hederifolia* ssp. *lucorum*) and *V. hederifolia* (ssp. *hederifolia*). *V. sublobata* is typical of floodplain forests but appears to occur also at ruderal and agricultural places, whereas *V. hederifolia* is adapted to arable weed vegetation. The latter is considered an allopolyploid (hexaploid) hybrid of the diploid *V. triloba* and tetraploid *V. sublobata* (Fischer 1974, 1985), but the morphological distinction is very difficult. For photos of the three microspecies see https://www.badvoeslau.at/de/lebenswert/umwelt/kalenderblaetter/april-2014.html.

The identification of the microspecies in the present study was complicated by the fact that *V. hederifolia* and *V. sublobata* apparently occurred at the same site. Fallen infected seeds cannot clearly be assigned because of their very similar morphology, thus we refrained from specifying the exact identity of the host plant. Also *C. ploettneriana* and *S. decaisneana* were sometimes observed at the same plot, but it appears unlikely to us that apothecia of the two species prefer different *Veronica* microspecies. The unequivocal identity of the microspecies as *V. hederifolia* s.str. was established in two anamorph collections of *S. decaisneana* from Zeuchfeld (13. & 21.V.2019, V.K. P1656-10 and H.B. 10206), yet based on morphological criteria only. It appears probable that some of the teleomorph collections were instead on *V. sublobata*.

Seed morphology and dispersal. The seeds of *Veronica hederifolia* agg. and *V. cymbalaria* are extraordinary in resembling a collapsed ball (Juan et al. 1994, Muñoz-Centeno et al. 2006). They are called cymbiform (boat-shaped) or cyathiform (urn-shaped) by showing a roundish ventral cavity. Also *V. persica* seeds have a ventral but more elongated cavity. The mature uninfected seeds usually remain inside the still closed capsules. Their cavity is finally filled with air which aids in the dehiscent capsule being transported by rain. The cavity includes also the elaiosome, a fleshy structure rich in nutrients. The elaiosome attracts ants which thereby transport the seeds with their head. In the case of *V. hederifolia* agg., the elaiosome contains sugars, proteins, Ricinoleic acid and vitamins B1 and C (Bresinsky 1963). Seeds of many other *Veronica* spp., e.g. *V. arvensis*, have more elongated, ellipsoid to flattened seeds without a cavity.

Host specificity. *Veronica* spp. on which *Schroeteria* spp. have been reported belong to six different subgenera of *Veronica*, according to Albach et al. (2004a & b) and Hassan & Khalik (2014): subgenus *Beccabunga* includes *V. acinifolia*, subgenus *ChamaedrysV. arvensis*, *V. dillenii* and *V. verna*, subgenus *CochlidiospermaV. hederifolia* and *V. cymbalaria*, subgenus *PocillaV. agrestis*, *V. biloba*, *V. campylopoda* and *V. rubrifolia*, subgenus *Pellidosperma V. praecox* and *V. triphyllos*, and subgenus *Pentasepalae V. austriaca* and *V. prostrata*.

The here reported teleomorph states of *Ciboriaploettneriana* and *Schroeteriadecaisneana* were exclusively found on seeds of *Veronica hederifolia* agg. Also the *S. decaisneana* anamorph has exclusively been reported in the literature on *V. hederifolia* agg., except for Terrier (1958) who believed to have found it on seeds of *V. campylopoda* received from Yerevan (Armenia). We have some doubts about this, because *V. campylopoda* belongs to another subgenus of *Veronica* with a clearly different seed morphology. The present reexamination of Terrier's specimen in NEU verified the host species but raised doubts about the fungus, which deviated from *S. decaisneana* by slightly larger chlamydospores of †(9.5–)10–12 µm diam. which never cohered in pairs, and with a higher ornamentation (0.3–0.5 µm) of more distinct ridges that form an incomplete net (see IVV). The few known collections of *Schroeteriapoeltii* were all on *V.cymbalaria*, including the here reported teleomorph (the host of the teleomorph being determined morphologically and by an ITS sequence). *S. delastrina* was reported from no less than eight different *Veronica* spp., though mostly from *V. arvensis*. Particularly *S. delastrina* should be investigated in the future for a possible molecular heterogeneity regarding its broad host spectrum.

Declarations

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Availability of data The sequences generated in this study are available in the NCBI GenBank (https://www.ncbi.nlm.nih.gov) under the accession numbers given in Tab. 1.

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Author's contributions: H.O. Baral made the main morphological evaluation and worked on the taxonomical conclusions, wrote text and tables, arranged most of the plates, and made the molecular analyses and illustration. P. Rönsch and U. Richter wrote a German draft about their observations on the teleomorph of *Ciboria ploettneriana* and *Schroeteria decaisneana*. H.O. Baral, P. Rönsch, and G. Hensel documented some of these collections by drawings and/or photographs. W. Huth studied and identified cultured apothecia and supplied data about the ecology of the two species. A. Urban obtained sequences from the teleomorphs of these species and some other *Sclerotiniaceae*, and J. Kruse from anamorphs of *Schroeteria* spp. and the teleomorph of *S. poeltii*. F.J. Valencia documented the teleomorph of *S. poeltii* and arranged the plate. Martin Bemmann contributed variously regarding literature reports and particularly with his hypothesis of an anamorph-teleomorph connection in *Schroeteria decaisneana*. V. Kummer reexamined and documented original material of Kirschstein's collections in B, also Terrier's anamorph specimen on *Veronica campylopoda* in NEU by verifying the identity of the host plant.

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Figures

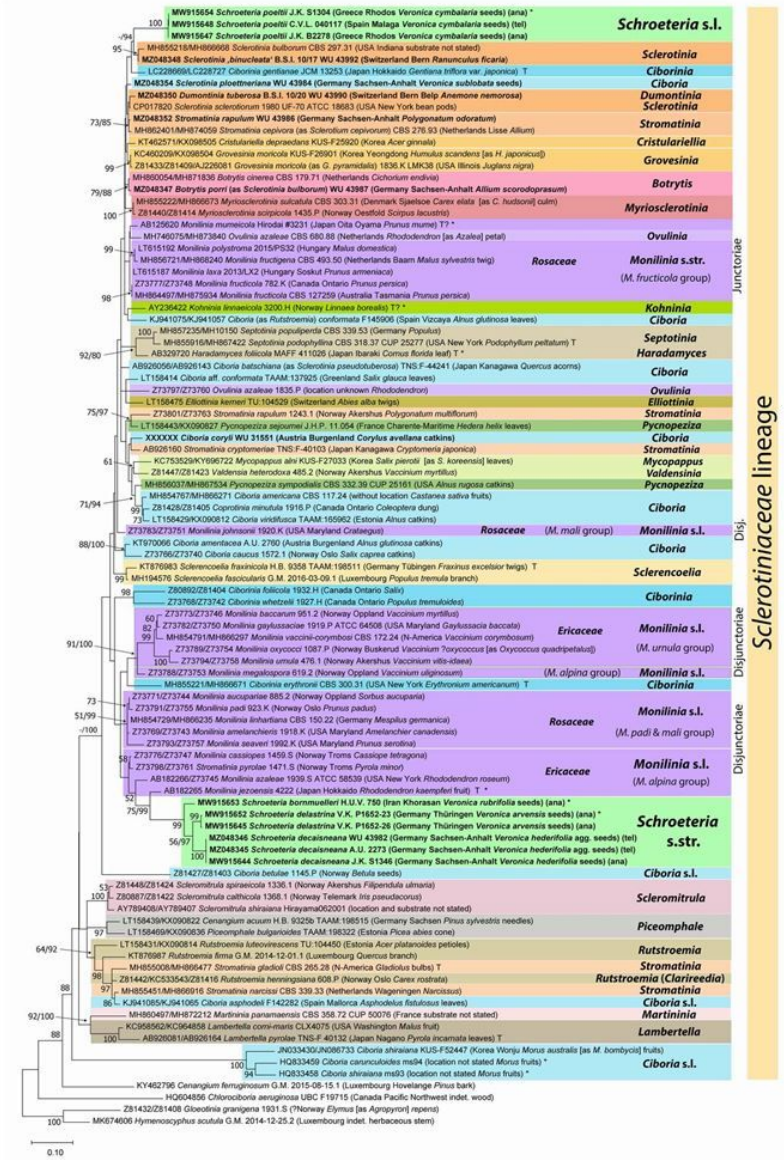


Figure 1

Combined maximum likelihood analysis of the Sclerotiniaceae lineage (including Rutstroemiaceae and Piceomphale clade), based on ITS1-5.8S-ITS2 and LSU D1–D2 rDNA, obtained with MEGAX (model GTR+G+I, 500 replicates). The outgroup comprises members of Cenangiaceae, Chlorociboriaceae, and Helotiaceae. Bootstrap values below 50 are not shown, those after the slash were obtained with IQ-tree (see S3) and are given whenever they distinctly deviated from those obtained with MEGAX. The asterisk indicates that only ITS was available. The different genera are highlighted in different colours.

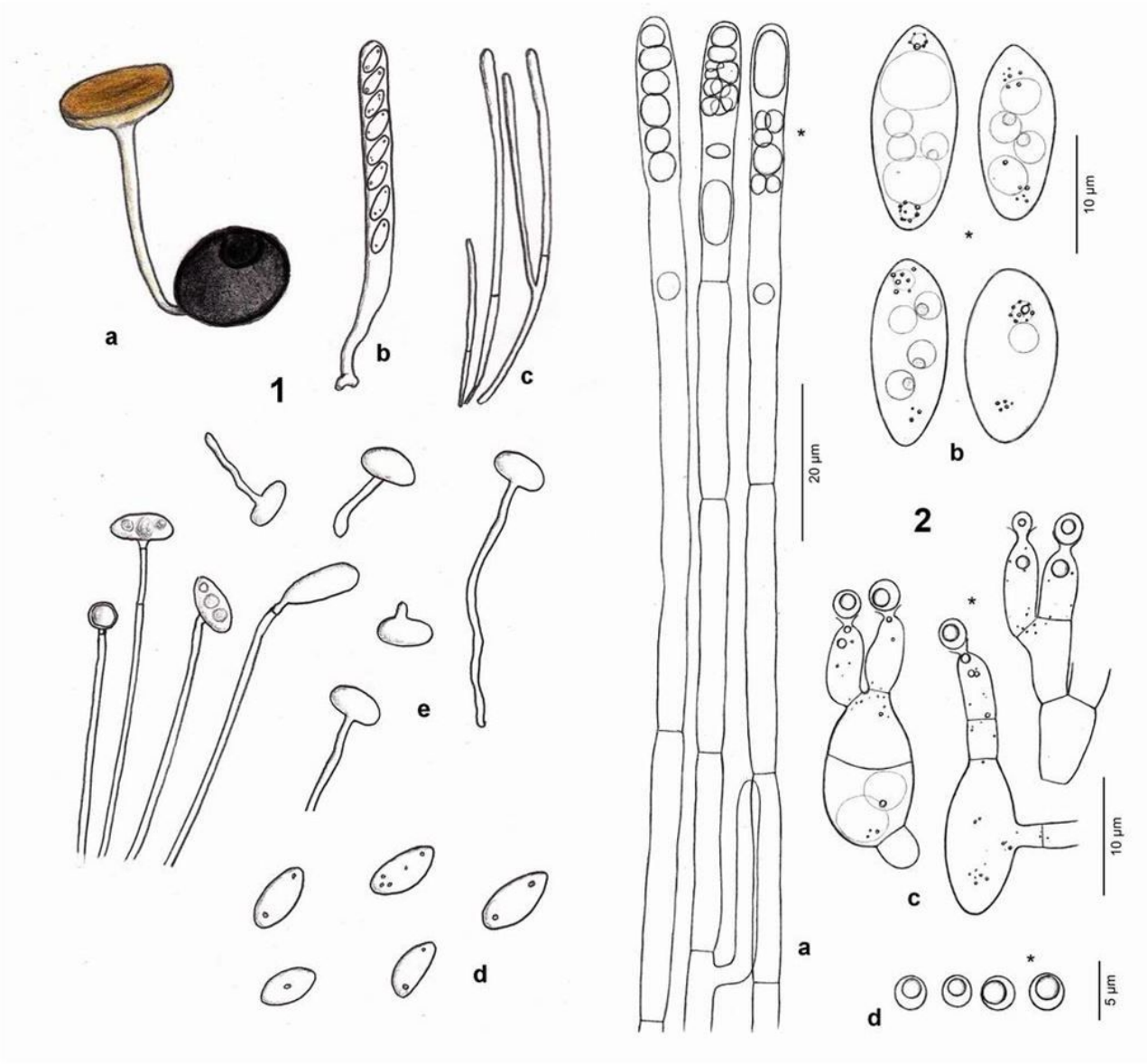


Figure 2

Ciboria ploettneriana (from Sachsen-Anhalt, Freyburg). 1a. fresh apothecium emerging from blackened seed. 1b. ascus; 1c, 2a. paraphyses, terminal cell containing hyaline VBs; 1d, 2b. mature ascospores containing some minute LBs near each end (in 2b. 2–4 central nuclei and two vacuoles visible); 1e. overmature ascospores with germ tubes (in hymenium); 2c. overmature ascospores budding conidia (in hymenium); 2d. conidia detached from ascospores, containing one large eccentrical LB. All in water, all in living state except for ascus in 1b and paraphyses in 1c. – 1. 12.IV.2004: Hirschrodaer Graben; 2. 13.IV.2009 (H.B. 9037): Zeuchfeld. – Del. 1. P. Rönsch (not drawn to scale); 2. H.O. Baral.

Figure 3

Ciboria ploettneriana (from Sachsen-Anhalt, Freyburg). 1, 2, 3a–c. fresh apothecia emerging from stromatized (blackened) seeds of Veronica hederifolia agg.; 3g–h. infected (blackened) seeds (3h. with uninfected whitish seed below); 4c. median section of infected seed; 3f, 4d–e. idem, detail of stromatized cortex of seed; 3d–e. median section of apothecial stipe base and seed tissue; 4a–b. idem, young apothecium, medullary excipulum containing crystal druses. All in fresh state. – 1. 15.IV.2004: Alte Göhle; 2. 12.IV.2004: Hirschrodaer Graben (from HUTH 2009: pl. 36 fig. 104); 3. 13.IV.2009 (H.B. 9037): Zeuchfeld; 4. 23.IV.2010 (H.B. 9271): Alte Göhle. – Phot. 1, 2, 3a. P. Rönsch; 3b–h, 4a–e. H.O. Baral.

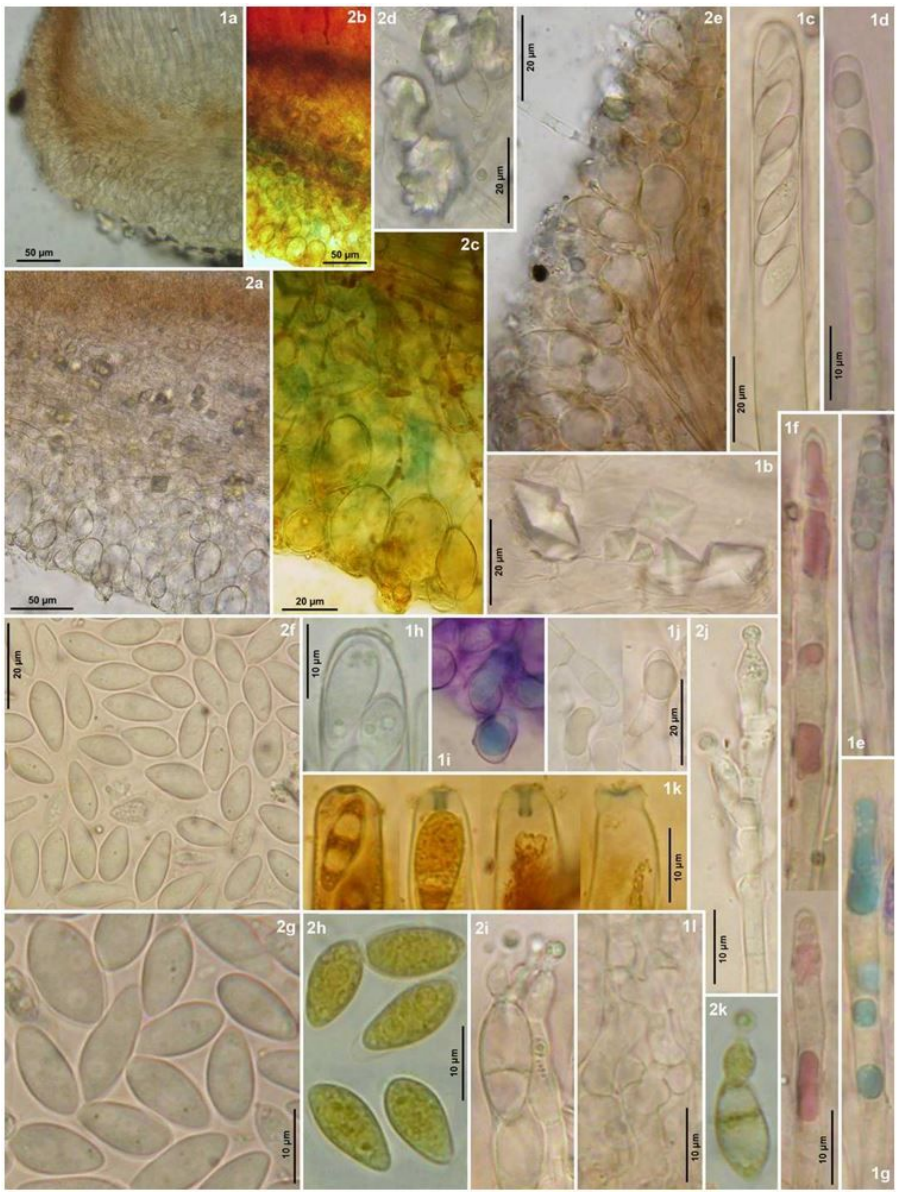


Figure 4

Ciboria ploettneriana (from Sachsen-Anhalt, Freyburg). 1a. median section of receptacle; 2a–c. idem, ectal excipulum at flanks; 2e. idem, at margin; 2d, 1b. idem, medullary excipulum with crystals; 1i–j. hair-like elements on ectal excipulum at flanks, containing refractive vacuoles (staining turquoise in CRB); 1c. ascus; 1l. ascogenous hyphae with croziers; 1h, k. apices of immature and mature asci; 1d–f. paraphyses, containing refractive vacuoles (in 1f. turning purplish with age), 1g. stained turquoise in CRB; 2f–g. mature ascospores containing a few minute LBs, 2–4 nuclei faintly visible; 2h. idem, in IKI, nuclei distinctly visible; 2i, k. overmature ascospores budding conidia from phialides; 2j. phialides formed on germ tube. Living state (in water; 2b–c, 2h, 2k. in IKI; 1f. in water, colour change in older apothecia; 1g, 1i. in CRB), dead state (1k. in IKI). – 1. H.B. 9271: Alte Göhle; 2. H.B. 9037: Zeuchfeld. – Phot. H.O. Baral.

Figure 5

Ciboria ploettneriana biotop (Germany, Sachsen-Anhalt, Naumburg, Roßbach, Scherbitzberg-Schlucht): 1. mixed oak forest (Alliarion) on calcareous soil (Muschelkalk covered by Loess), with Quercus robur, Acer campestre, Crataegus monogyna, Fraxinus excelsior; Veronica ? sublobata occurring close to the forest edge on the left; 2. view on Veronica hederifolia agg. population (apparently V. sublobata) with Alliaria petiolata, Anemone nemorosa, Convallaria majalis, Dactylis sp. (not on photo), Polygonatum multiflorum (not on photo), Stellaria holostea, young Acer campestre and Fraxinus excelsior. – Phot. W. Huth (2.V.2019).

Figure 6

Ciboria ploettneriana (from Kirschstein's and Benkert's collections). 1a, 2–3. dry apothecia on blackened seeds of Veronica hederifolia agg.; 1b. median section of seed; 1c. ascospores (in KOH); 1d. original label of lectotype written by Kirschstein. – 1a–d. 27.IV.1905 (B 70 0100006, lectotype): Brandenburg-Groß Behnitz; 2. 30.IV.1992 (B 70 0009941): Berlin-Treptow; 3. 27.IV.1972 (B 70 0009940): Teupitz-Egsdorf. – Phot. V. Kummer.

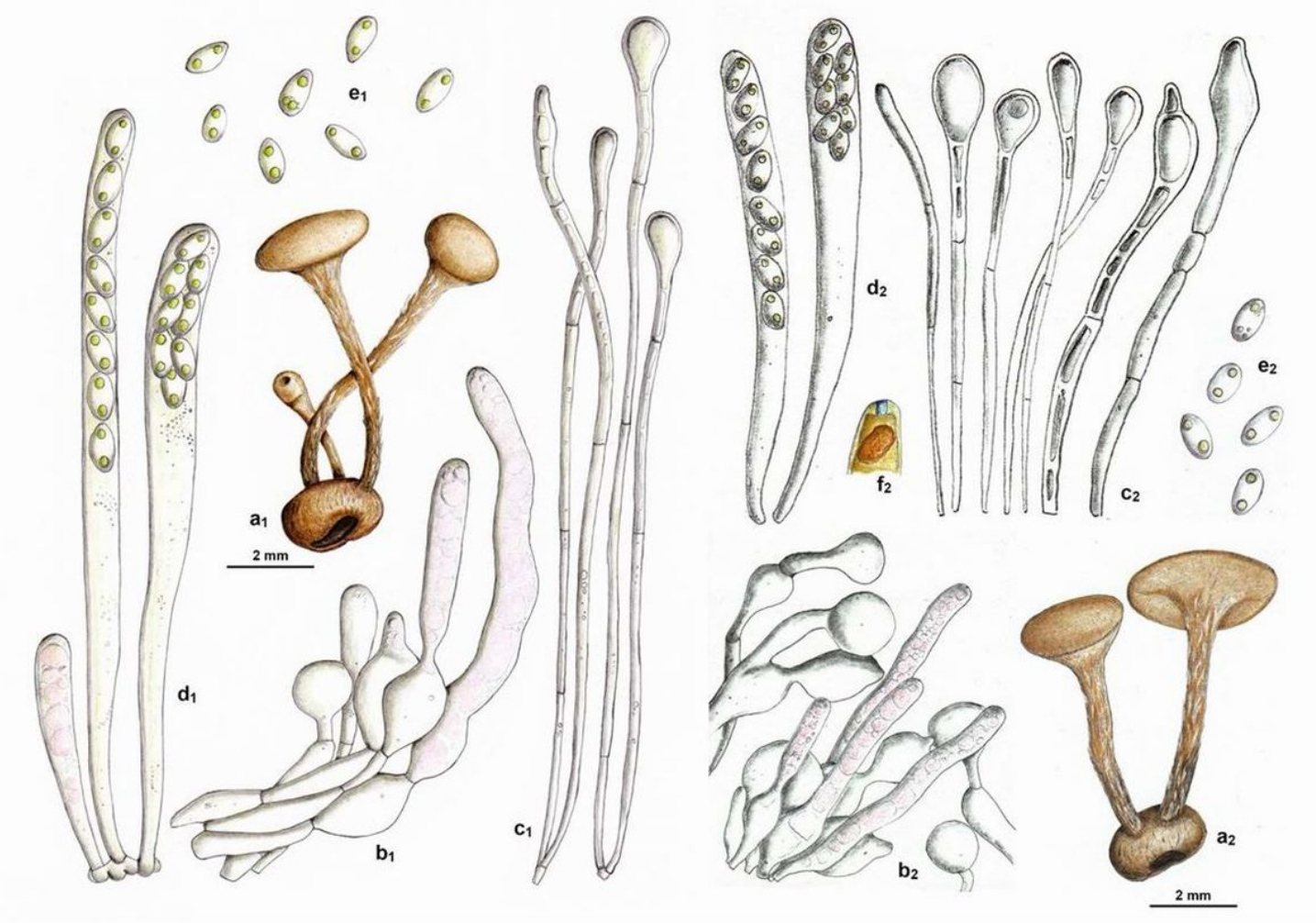


Figure 7

Schroeteria decaisneana (teleomorph, H.B. 8687: Sachsen-Anhalt, Freyburg, Zeuchfeld). a. fresh apothecia emerging from seeds of Veronica hederifolia agg.; b. marginal excipular cells; c. paraphyses; d. asci; e. ascospores; f. ascus apex in IKI. Living state, except for some cells of the paraphyses. – Del. P. Rönsch (microscopic elements not drawn to scale, numbers 1 and 2 refer to different apothecia).

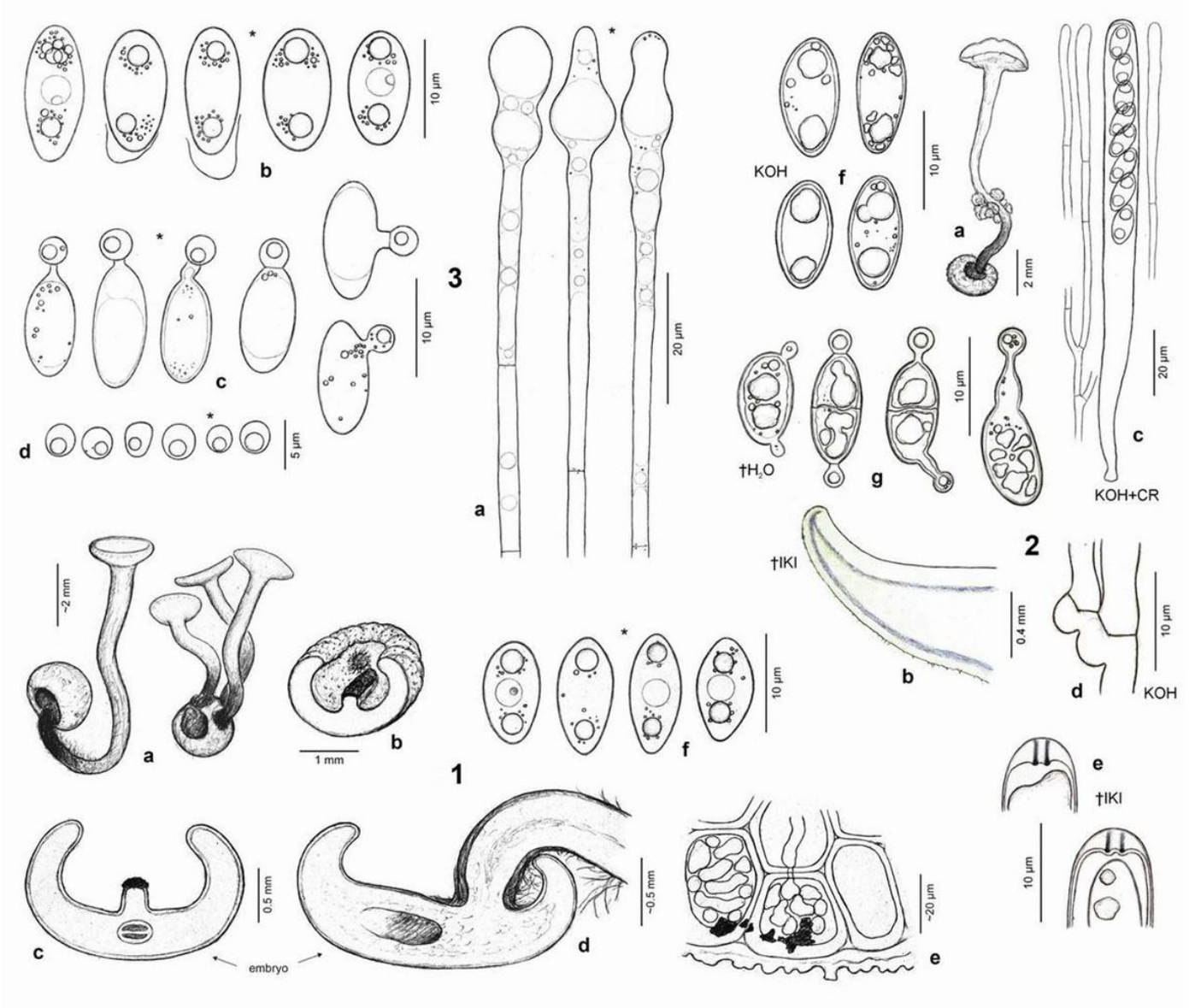


Figure 8

Schroeteria decaisneana (teleomorph). 1a. fresh apothecia emerging from seeds of Veronica hederifolia agg.; 2a. idem, rehydrated; 1b–d. median section of seed (b–c. with central hilum, c–d. with embryo, d. with insertion of apothecial stipe); 1e. hyphae inside epidermial cells of seed; 2b. median section of receptacle (with amyloid subhymenium and outer medullary excipulum); 2c. ascus and paraphyses; 2d. ascus bases with croziers; 2e. apices of immature (above) and mature (below) asci; 3a. paraphyses, terminal cell containing inconspicuous large vacuoles but no VBs; 1f, 2f, 3b. mature ascospores containing one central nucleus and one large and some minute LBs at each end); 2g, 3c. overmature ascospores budding conidia; 3d. conidia detached from ascospores, containing one large eccentrical LB. Living state (1 & 3.), dead state (2.). – 1. H.B. 2981: Schaffhausen, Thayngen, Flüheweg; 2. H.B. 5698: Unterfranken, Schweinfurt, Alter Main; 3. H.B. 8687: Sachsen-Anhalt, Freyburg, Zeuchfeld. – Del. H.O. Baral.

Figure 9

Schroeteria decaisneana (teleomorph, from Sachsen-Anhalt). 1, 2a–d, 3b–f. apothecia emerging from stromatized (partially blackened) seeds of Veronica hederifolia agg.; 3a. apothecia in situ (seeds hidden in soil under organic debris). All in fresh state. – 1. G.H. 080309: Merseburg, Burgliebenau; 2. H.B. 8687: Freyburg, Zeuchfeld; 3. H.B. 8955: ibid. – Phot. 1. G.. Hensel; 2a, 3a–f. P. Rönsch; 2b–c. H.O. Baral.

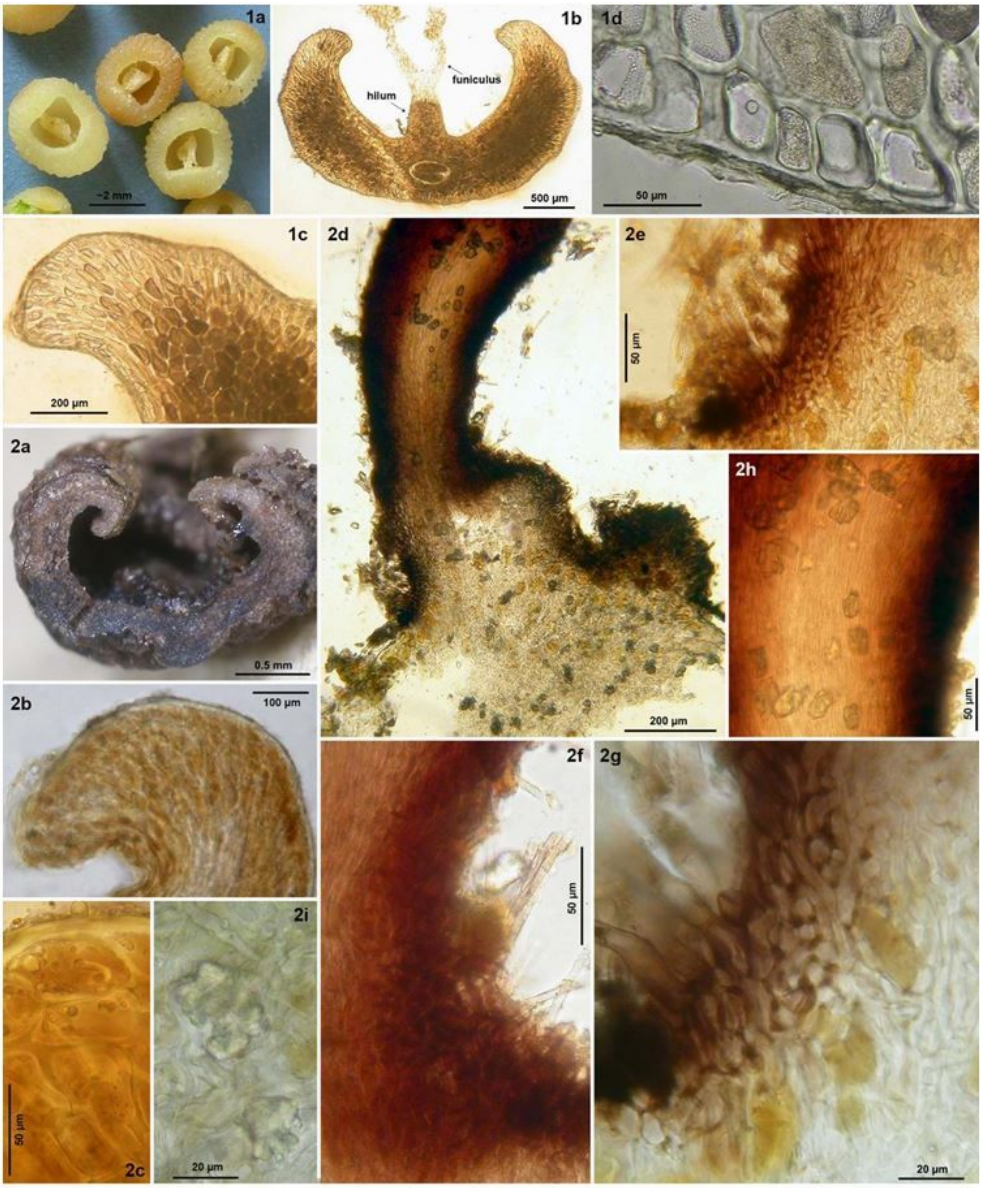


Figure 10

Uninfected seeds of Veronica hederifolia agg. (1.), Schroeteria decaisneana stromatized seed and base of apothecial stipe (2.). 1a. uninfected seeds with deep cavity and central attachment (hilum and funiculus); 1b, 2a. median section of seed (1b. showing embryo below hilum); 1c, 2b–c. idem, detail of marginal part of seed; 1d. idem, lower part of seed; 2d. median section of stromatized apothecial stipe and basal stroma; 2e–g. idem, details of stroma and stipe base (with hairs); 2h. idem, crystals in medullary excipulum of stipe; 2i. idem, crystals in medullary excipulum of basal stroma. – Mounted in water (fresh state); – 1a–d. 13.V.2008: Tübingen-Pfrondorf, Blaihofstr. 42; 2. H.B. 8687: Sachsen-Anhalt, Freyburg, Zeuchfeld. – Phot. H.O. Baral.

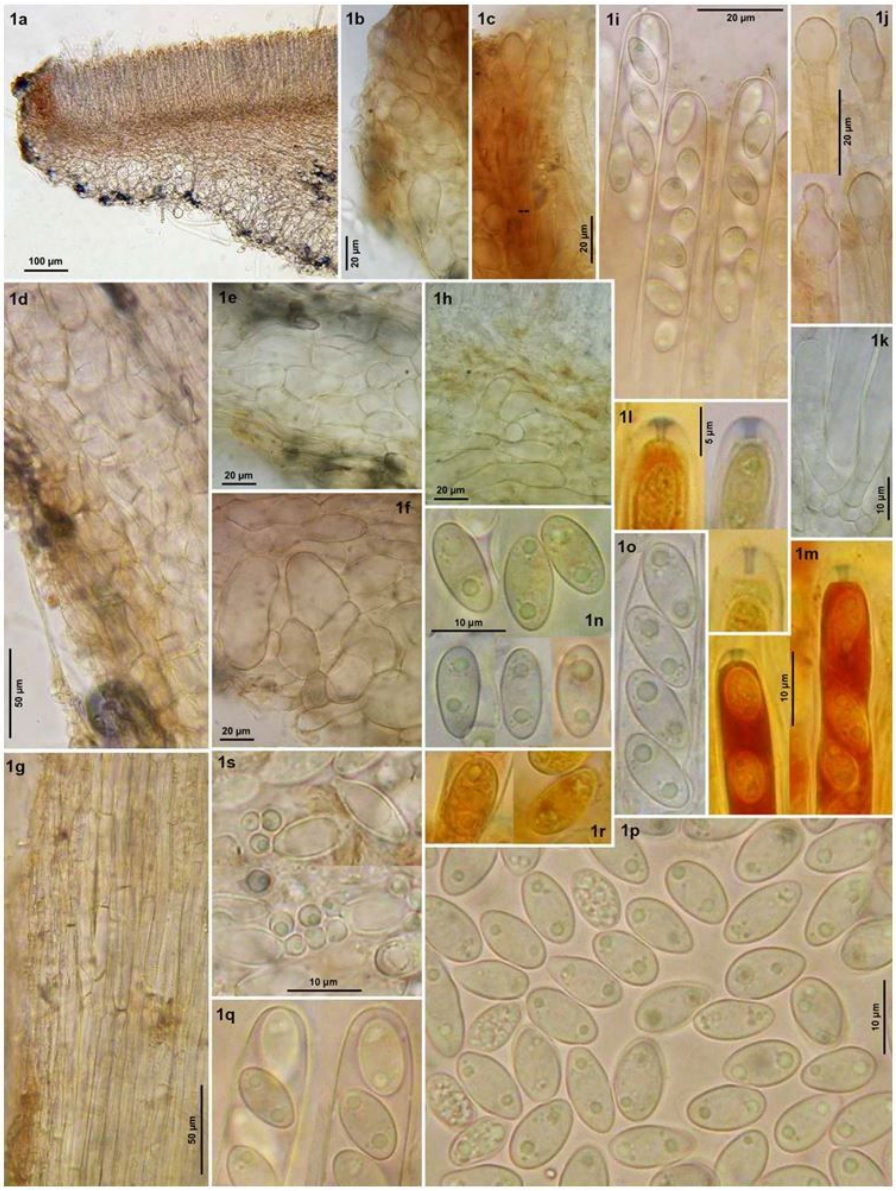


Figure 11

Schroeteria decaisneana (teleomorph, H.B. 8687, Sachsen-Anhalt, Freyburg, Zeuchfeld). 1a. median section of receptacle; 1b–c. idem, ectal excipulum at margin (1c with paraphysis-like intermediate elements); 1d–f. idem, ectal excipulum at lower flanks and junction with stipe; 1g. idem, ectal excipulum in stipe; 1h. idem, medullary excipulum and subhymenium; 1i. mature asci; 1j. paraphyses, containing large non-refractive vacuoles; 1k. ascus bases with croziers; 1l–m, o, q. apices of mature asci (l–m. with amyloid ring); 1n, p. free ascospores containing two large and some minute LBs, central nucleus faintly visible; 1r. central nucleus more clearly visible (right spore with two glycogen regions); 1s. overmature ascospores budding conidia with large eccentrical LB. Living state (in water, 1r. in IKI), except for 1l–m. (dead state in IKI), ascus in 1o., four spores in 1p. – Phot. H.O. Baral.

Figure 12

Collection site of Schroeteria decaisneana (teleomorph, from Sachsen-Anhalt, Freyburg, Zeuchfeld). 1–2. dry draining ditch in temperate humid, thermophilous forest strip between cornfield in the north and vineyard in the south, in spring (1., 21.V.2019) and late autumn (2., 16.XI.2008, H.B. 8955), with Ulmus minor, Acer campestre, Veronica hederifolia agg., S. Thieme & U. Richter; 3. vineyard south of forest strip (16.XI.2008); 4. location of forest strip in the west of Zeuchfeld (Google Earth). – Phot. 1. U. Richter, 2–3. P. Rönsch, 4. from Google Earth.

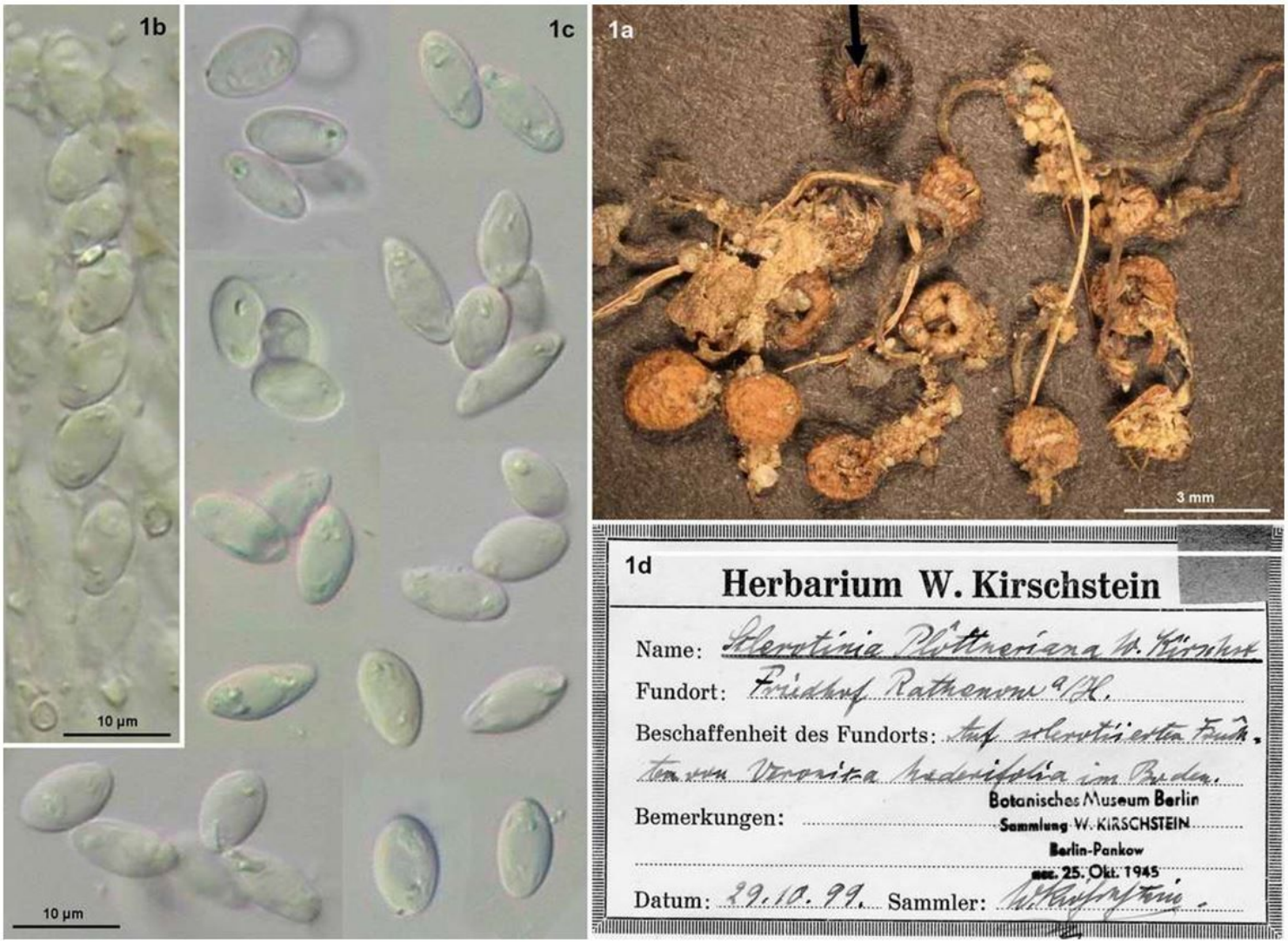


Figure 13

Schroeteria decaisneana (from Kirschstein's collection 29.X.1899 under the name Sclerotinia ploettneriana, B 70 0100003, Brandenburg, Rathenow). 1a. dry apothecia on light brown seeds of Veronica hederifolia agg. (the arrow points to one blackened seed which appears to belong to Ciboria ploettneriana); 1b. ascospores in ascus (in KOH); 1c. free ascospores (in KOH); 1d. original label written by Kirschstein. – Phot. V. Kummer.

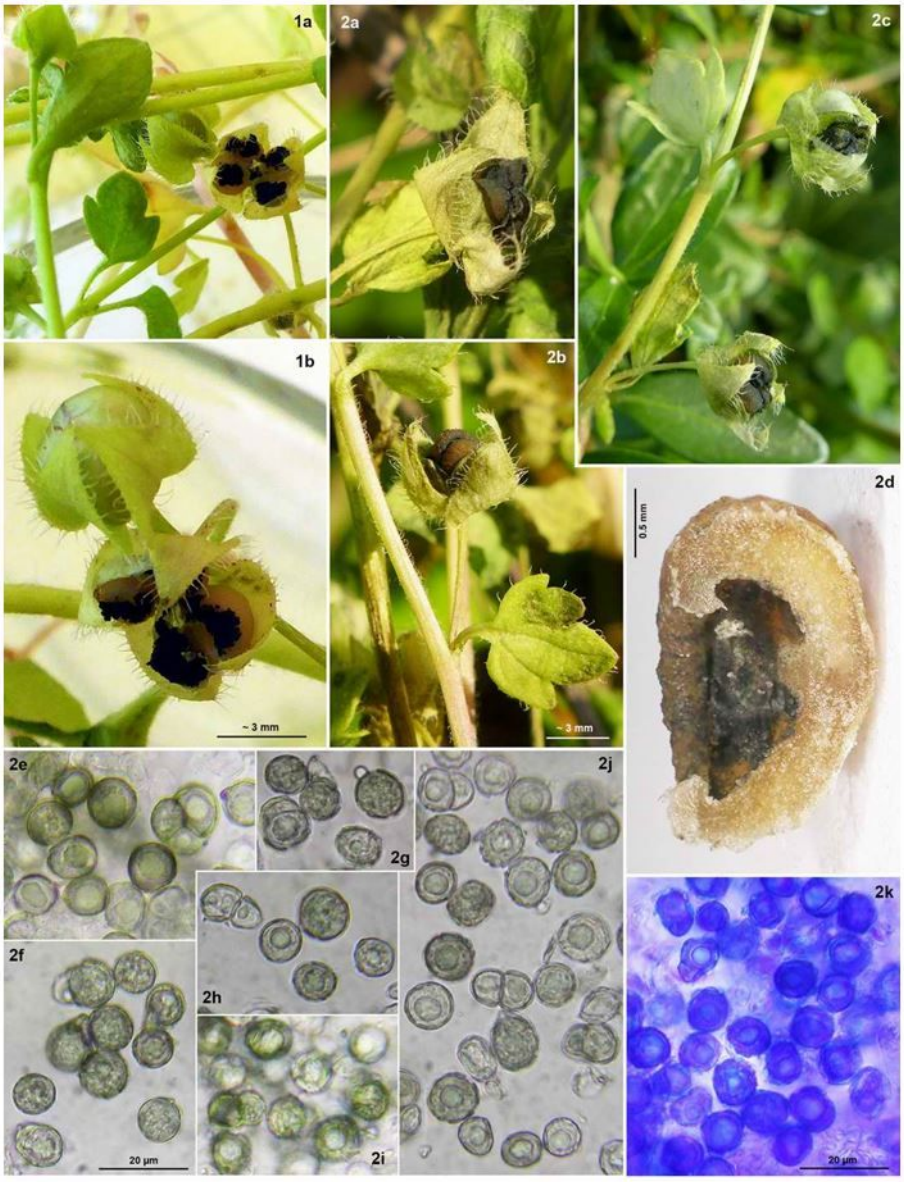


Figure 14

Schroeteria decaisneana (anamorph, from Sachsen-Anhalt, Freyburg, Zeuchfeld, on Veronica hederifolia s.str.). 1a–e. infected plant with black sori in the cavity of each seed; 2a. median section of infected seed, with chlamydospores formed on hilum/funiculus; 2b–h. chlamydospores (singly, rarely in pairs). – 1a–b. 13.V.2019 (V.K. P1656-10); 2a–k. 21.V.2019 (J.K. S1346, GLM-F129032,H.B. 10206). – Phot. 1a–b. U. Richter (fresh), 2a–c. J. Kruse (half dried); 2d–k. H.O. Baral (dead state, e–j. in water, k in CRB).

Figure 15

Schroeteria delastrina (anamorph) on Veronica arvensis. 1a–e. 9.VI.2017: Sachsen-Anhalt, Rosstrappe; 2a–b. 11.VI.2016: Hessen, Darmstadt; 3. V.K. P1652-20: Rhodos, Kamiri monastery; 4a–c. 30.V.2011: Niedersachsen, Hannover. – Phot. 1–2, 4. J. Kruse, 3. V. Kummer.

Figure 16

Schroeteria poeltii (teleomorph). 1a–c, 2a–b. apothecia emerging from stromatized seeds of Veronica cymbalaria (1 in situ); 3a–b. collection site with V. cymbalaria growing on vertical schist rock, apothecia found on seeds fallen to the ground; 4a–c. uninfected flower, fruits and leaves of V. cymbalaria; 4d. infected and uninfected mature seed. Fresh state. – 1a–c, 2a–b, 4d. 4.I.2017 (C.V.L. 040117). Spain, Andalucía, Málaga, Pujerra; 3a–b, 4a–c. 28.V.2020. ibid. – Phot. F.J. Valencia.

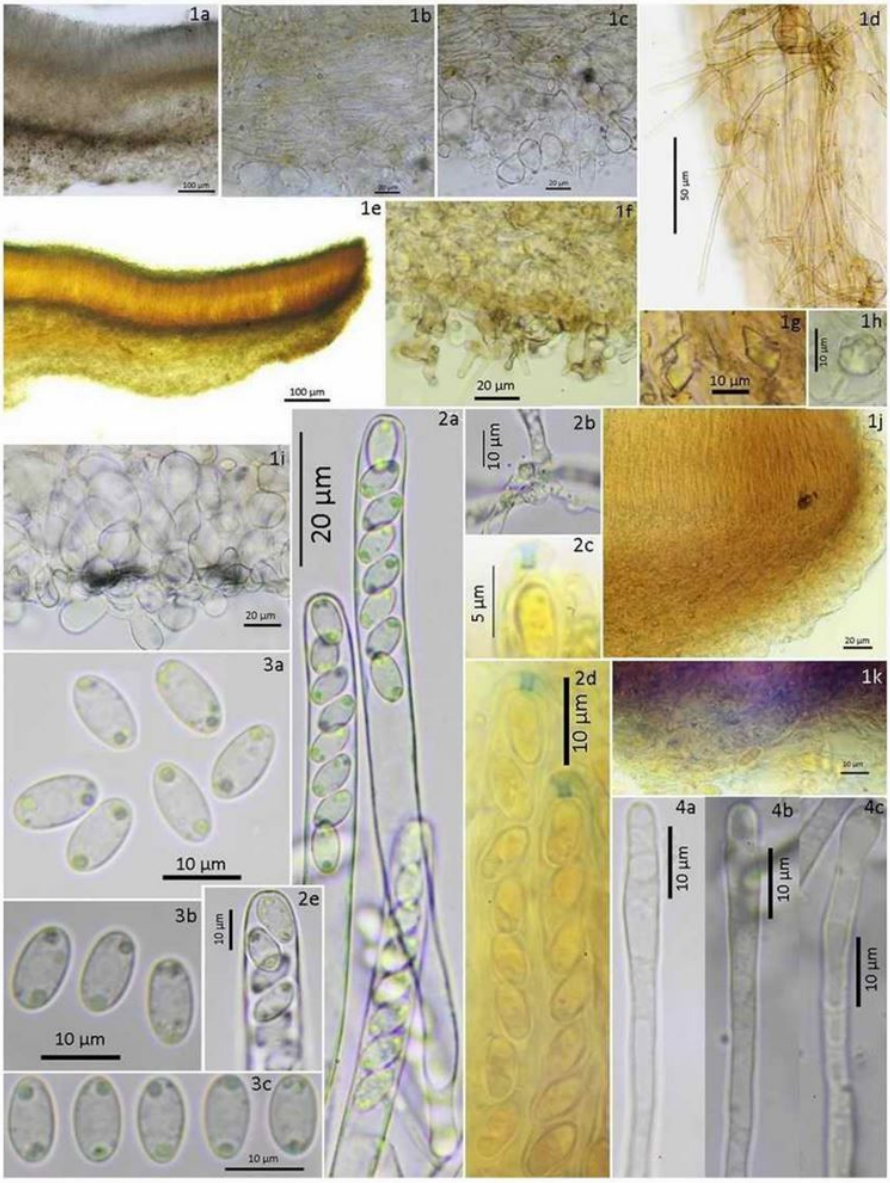


Figure 17

Schroeteria poeltii (teleomorph). 1a, e, j. Median section of apothecium (1e in IKI, 1f, j in KOH); 1b. idem, medullary excipulum; 1c, f, i. idem, ectal excipulum; 1d. Surface view on stipe showing hairs (in KOH); 1g–h. crystals in stipe and medullary excipulum, respectively (in KOH); 1k. faintly amyloid subhymenium (in IKI); 2a, e. living mature asci; 2b. ascus base with croziers; 2c–d. dead asci and spores (in IKI), with amyloid ring; 3a–c. living ascospores; 4a–c. living paraphyses. In water, if not otherwise stated. – 1–4. 4.I.2017 (C.V.L. 040117). Spain, Andalucía, Málaga, Pujerra. – Phot. F.J. Valencia.

Figure 18

Schroeteria poeltii (teleomorph, C.V.L. 040117: Spain, Andalucía, Málaga, Pujerra). 1. supramediterranean floodplain forest with Populus alba, Salix alba, Quercus faginea, Veronica cymbalaria and various other mediterranean herbs; 2. apothecia on stromatized seeds of Veronica cymbalaria. – Phot. 1. C. Borrego, 2. F.J. Valencia.

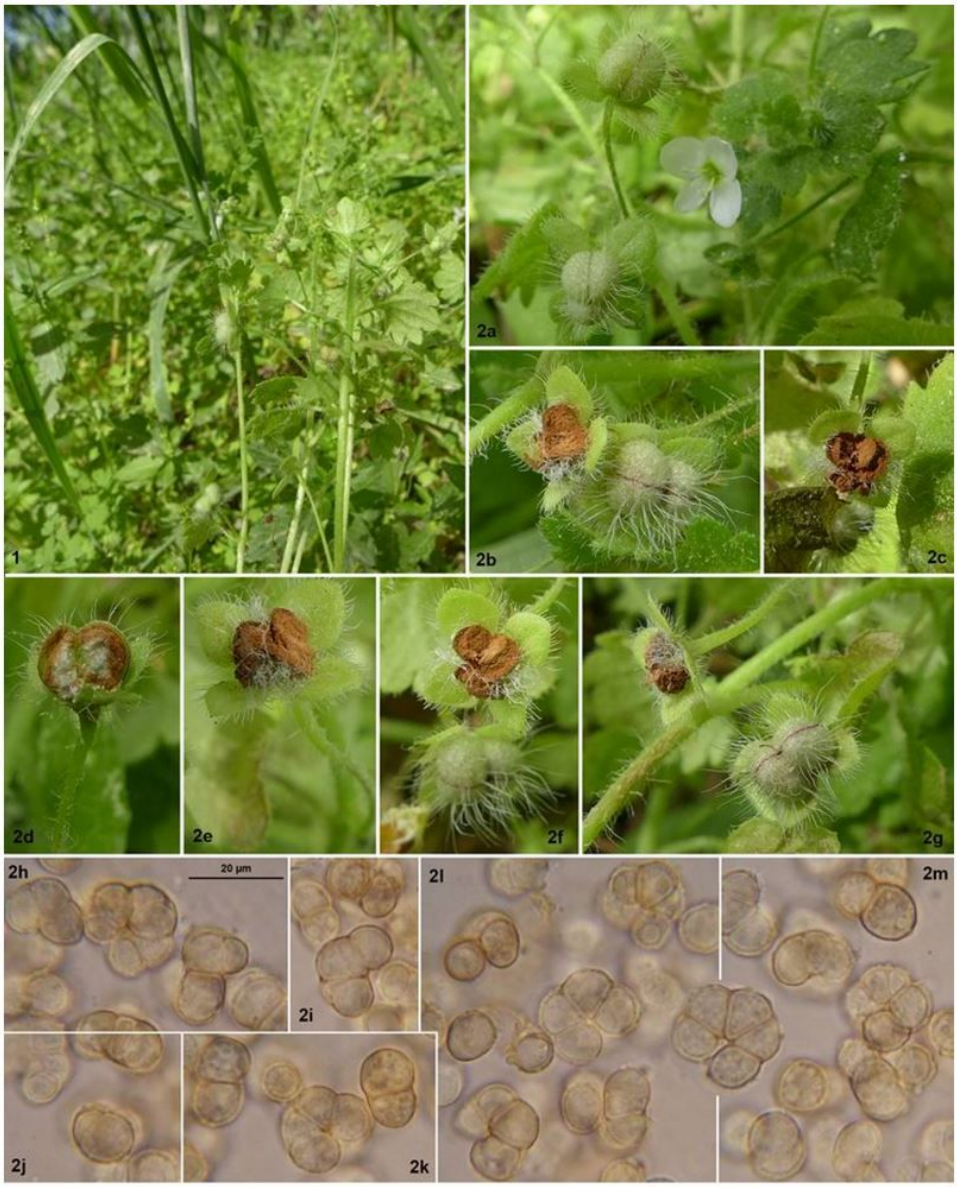
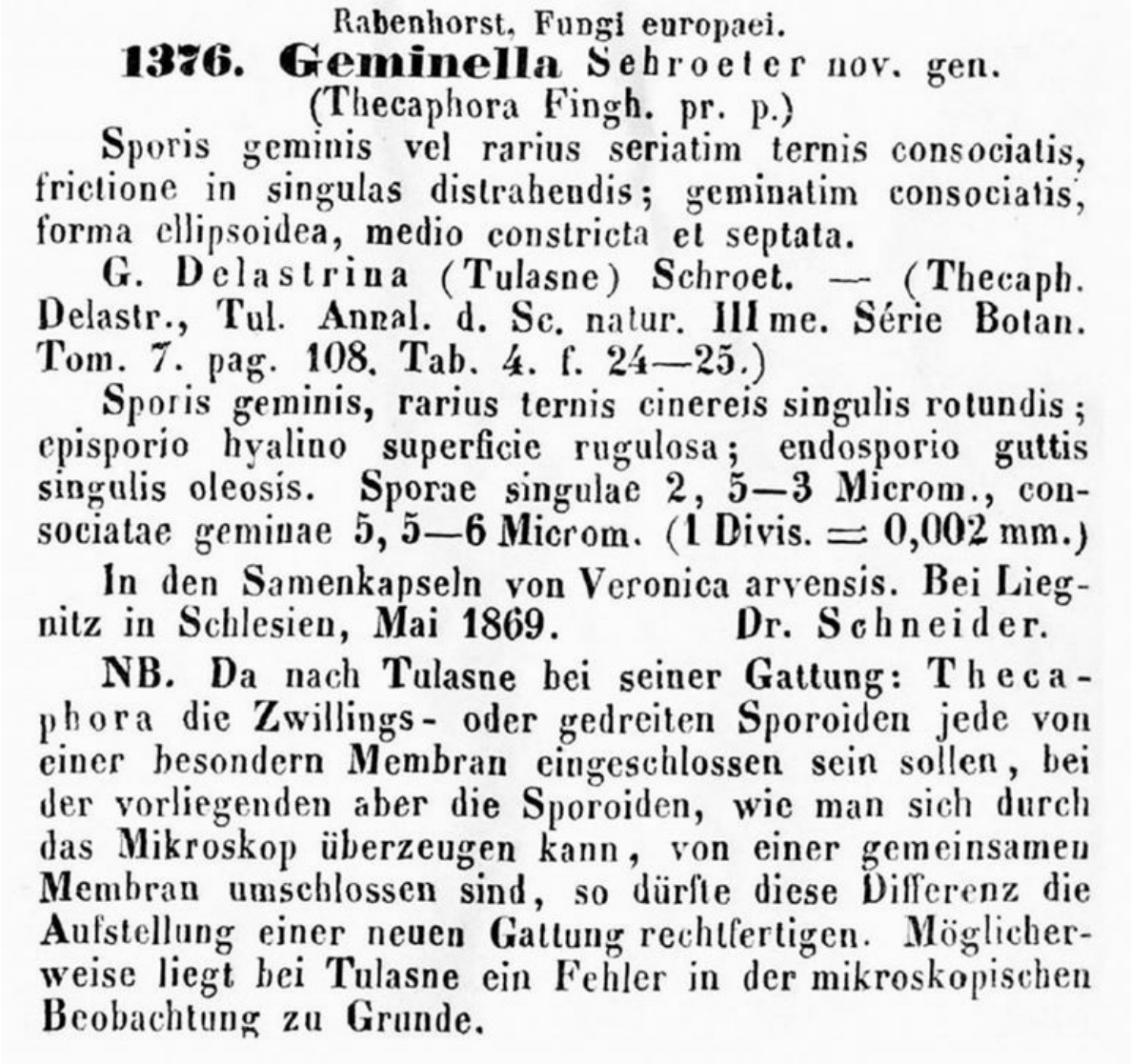


Figure 19

Schroeteria poeltii (anamorph, on Veronica cymbalaria). 1. ruderal meadow; 2a. uninfected plant; 2b–g. opened capsules exposing brown sori; 2h–m. chlamydospores (living state, in water) cohering in numbers of 2–5. – 1. 21.III.2018. Greece, Rhodos, Archangelos, Charaki; 2. 20.III.2018. ibid., Ialysos, Filerimos. – Phot. J. Kruse.



Rabenhorst, Fungi europaei.

1376. Geminella Sehroeter nov. gen.

(Thecaphora Fingh. pr. p.)

Sporis geminis vel rarius seriatim ternis consociatis, frictione in singulas distrahendis; geminatim consociatis, forma ellipsoidea, medio constricta et septata.

G. Delastrina (Tulasne) Schroet. — (Thecaph. Delastr., Tul. Annal. d. Sc. natur. IIIme. Série Botan. Tom. 7. pag. 108. Tab. 4. f. 24—25.)

Sporis geminis, rarius ternis cinereis singulis rotundis; episporio hyalino superficie rugulosa; endosporio guttis singulis oleosis. Sporae singulae 2, 5—3 Microm., consociatae geminae 5, 5—6 Microm. (1 Divis. = 0,002 mm.)

In den Samenkapseln von Veronica arvensis. Bei Liegnitz in Schlesien, Mai 1869. Dr. Schneider.

NB. Da nach Tulasne bei seiner Gattung: Thecaphora die Zwillings- oder gedreiten Sporoiden jede von einer besondern Membran eingeschlossen sein sollen, bei der vorliegenden aber die Sporoiden, wie man sich durch das Mikroskop überzeugen kann, von einer gemeinsamen Membran umschlossen sind, so dürfte diese Differenz die Aufstellung einer neuen Gattung rechtfertigen. Möglicherweise liegt bei Tulasne ein Fehler in der mikroskopischen Beobachtung zu Grunde.

Figure 20

SCHRÖTER's (1870) description of the genus Schroeteria under the illegitimate name Geminella on the herbarium label of an exsiccata of the type species G. delastrina from Silesia in Rabenhorst's Fungi Europaei exsiccati Cent. 14: no. 1376 (U. BRAUN & K. BENSCH pers. comm.).

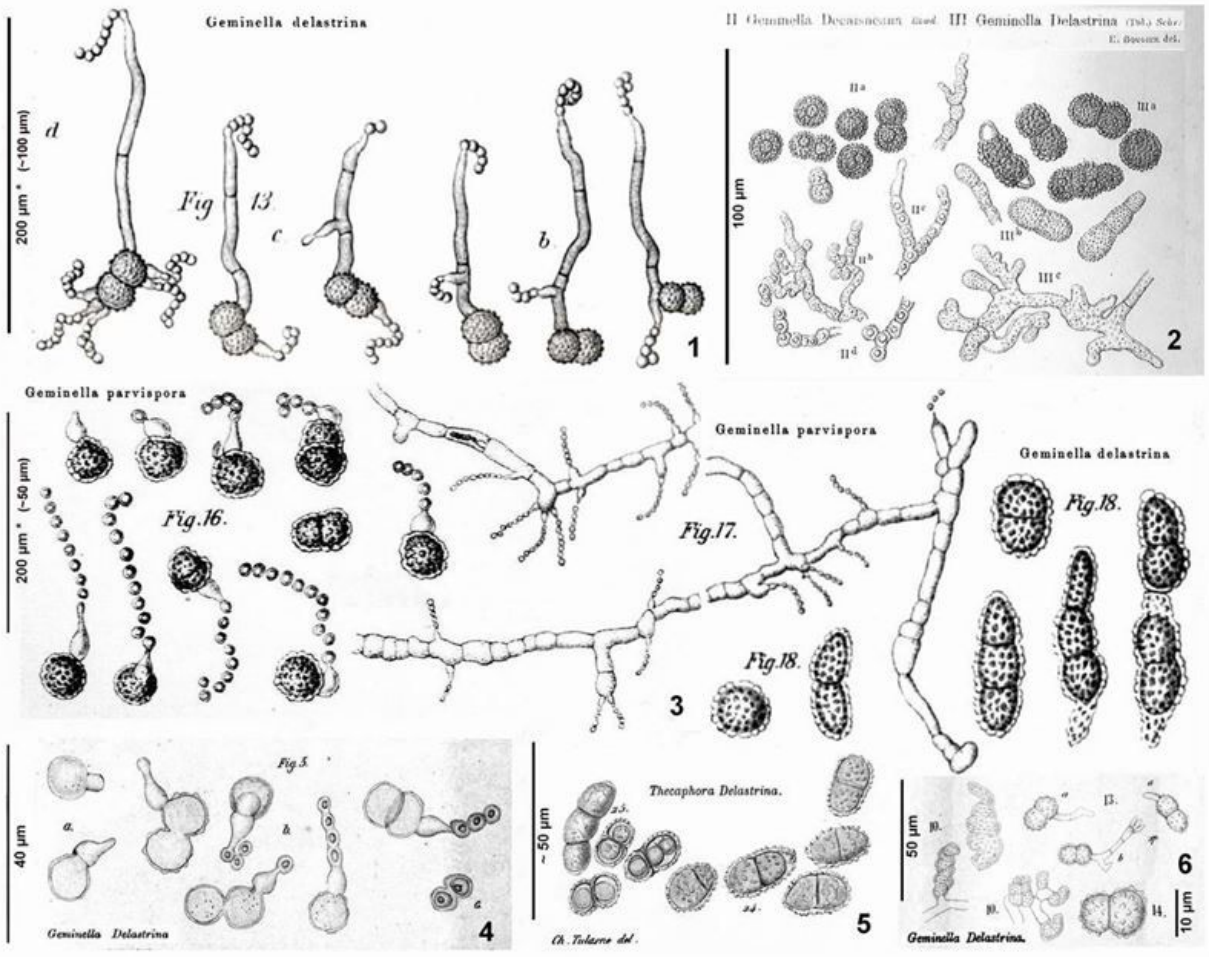


Figure 21

Chlamydospores and microconidial anamorphs in Schroeteria delastrina and S. decaisneana (= Geminella parvispora) as illustrated by different authors. 1, 3–4. chlamydospores germinating by hyphae producing phialides and microconidia; 2, 6. formation of chlamydospores from hyaline multi-branched, flexuous to helicoid hyphae. 1. BREFELD (1883: pl. XI fig. 13), 2. BOUDIER (1887: pl. XV figs II–III), 3. BREFELD (1912: pl. III figs 16–18), 4. SCHRÖTER (1877: pl. XI fig. 5), 5. TULASNE & TULASNE (1847: pl. 4 figs 24–25), 6. WINTER (1876: pl. IV figs 10, 13, 14). All scales were evaluated from the original prints based on the indicated magnification factor. Scales in Brefeld's drawings (with asterisk) were considered by us to be erroneous: in 1. the scale should be around 100 µm instead of 200 µm and in 3. around 50 µm instead of 200 µm when compared with drawings of Boudier (2.) and others (see also Tabs 4–5).

Supplementary Files

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- S1SchroeteriaITS1000MLMEGA7.pdf
- S2SchroeteriaLSU1000MLMEGA7.pdf
- S3SclerotiniaceaeIQTREEtopology.pdf