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
Ciboria ploettneriana, Schroeteria decaisneana, and S. poeltii produce morphologically very similar apothecia emerging from fallen stromatized seeds of Veronica spp., the former two on V. hederifolia agg. in temperate central Europe and S. poeltii on V. cymbalaria in mediterranean southern Europe. They are described and illustrated in detail based on fresh collections or moist chamber cultures of infected seeds. A key is provided to differentiate the three species from their teleomorphs.

For the first time, connections between two teleomorphs and two Schroeteria anamorphs are reported.

Members of the anamorph-typified genus Schroeteria are known as host-specific plant parasites that infect seeds of different Veronica spp. In earlier times, they were classified in the Ustilaginales (Basidiomycota), but since more than 30 years, they are referred to as false smut fungi producing smut-like chlamydospores, based on light microscopic and ultrastructural studies which referred them to the Sclerotiniaceae (Helotiales). During the present study, rDNA sequences were obtained for the first time from chlamydospores of Schroeteria bornmuelleri (on V. rubrifolia), S. decaisneana (on V. hederifolia), S. delastrina (generic type, on V. arvensis), and S. poeltii (on V. cymbalaria) and from apothecia of C. ploettneriana, S. decaisneana, and S. poeltii. As a result, the anamorph-teleomorph connection could be established for S. decaisneana and S. poeltii by a 100% ITS similarity, whereas C. ploettneriana could not be connected to a smut-like anamorph.

Ciboria ploettneriana in the here-redefined sense clustered in our combined phylogenetic analyses of ITS and LSU in relationship of Sclerotinia s.l., Botrytis, and Myriosclerotinia rather than Ciboria, but its placement was not supported. Its affiliation in Ciboria was retained until a better solution is found. Also Schroeteria poeltii clustered unresolved in this relationship but with a much higher molecular distance. The remaining three Schroeteria spp. formed a strongly supported monophyletic group, here referred to as “Schroeteria core clade”, which clustered with medium to high support as a sister clade of Monilinia jezoensis, a member of the Monilinia alpina group of section Disjunctoriae. We observed ITS distances of 5–6.3% among members of the Schroeteria core clade, but 13.8–14.7% between this clade and S. poeltii, which appears to be correlated with the deviating chlamydospore morphology of S. poeltii. Despite its apparent paraphyly, Schroeteria is accepted here in a wide sense as a genus distinct from Monilinia, particularly because of its very special anamorphs. A comparable heterogeneity in rDNA analyses was observed in Monilinia and other genera of Sclerotiniaceae. Such apparent heterogeneity should be met with skepticism, however, because the inclusion of protein-coding genes in phylogenetic analyses resulted in a monophyletic genus Monilinia. More sclerotiniaceous taxa should be analysed for protein-coding genes in the future, including Schroeteria. Four syntype specimens of Ciboria ploettneriana in B were reexamined in the present study, revealing a mixture of the two species growing on V. hederifolia agg. Based on its larger ascospores in comparison with S. decaisneana, a lectotype is proposed for C. ploettneriana.

Keywords Anamorph-teleomorph connection · Plant parasite · False smut fungi · Seed infection · Veronica hederifolia · Veronica cymbalaria

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Introduction

The family Sclerotiniaceae comprises about 150 mainly plant parasitic species in 28 accepted genera (Baral 2016). Members of 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 to biotrophic host generalists or specialists (Andrew et al. 2012). Species of the family are generally hygrobiotous; 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 xerobirotic, apparently necrotrophic species on air-exposed branches, previously included in the heterogeneous subfamily Enceloioideae 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 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, pseudosclerotium). Species of Sclerencoelia deviate from the remaining genera of the family by 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).

Mononematous or sometimes sporodochial, acervular, or pycnidial anamorphs are typical of the family Sclerotiniaceae (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 the family 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 Ustilaginaceae (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. They are either formed singly or cohere in pairs or larger groups. 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 of the capsules (seeds and/or funiculi and placenta) of the 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. and E. Huth, and P. Rönsch in Sachsen-Anhalt (Germany), during which the substrate was correctly identified as gall of V. hederifolia agg. with those being stromatized. Not only fallen blackened seeds with apothecia but also blackened seeds without apothecia were collected at two localities (Trebnitz, Werder canal; Freyburg, Alte Göhle) in spring 2003 and incubated in a garden inside a plastic box with some moist earth and moss, in which apothecia developed during next spring.

At that time, it became evident that one of the two discomycetes must be Ciboria ploettneriana (Kirschst.) 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, p. 103, pl. 36 fig. 104) reported three samples collected by G. Hensel, M. and W. Huth, and P. Rönsch in April–May 2003–2004 near Merseburg and Freyburg in Sachsen-Anhalt. Apothecia of a third species were detected by F. J. Valencia in January 2017 on seeds of V. cymbalaria.
in a mediterranean area of southern Spain. Although it differs only slightly from *S. decaisneana* in its teleomorph morphology, it turned out to belong to a species of its own based on rDNA.

In 2019 we started our bibliographic and molecular investigations on the genus *Schroeteria*, based on M. Bemmman’s suspicion that this genus could represent the anamorph of the two discomycetes. Chlamydospores of *S. decaisneana* (Boud.) De Toni could subsequently be detected in May 2019 by H. and U. Richter at the Zeuchfeld site on mature non-stromatized seeds in the capsules of living plants and offered the possibility for comparative rDNA studies.

**Circumscription of Sclerotiniaceae with survey of their anamorphs**

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 *Ruststroemiacae*. In phylogenetic analyses of rDNA or rDNA + protein-coding genes, both families formed together with the small *Piceophyllum* clade the highly supported “Sclerotiniaceae lineage”, and this lineage formed with the family *Cerangicaceae* 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 *Polydesmidae*.

Holst-Jensen et al. (1997b) defined the family *Sclerotiniaceae* s.str. by determinate (sclerotial) stromata in or outside the host tissue (“sclerotal stromatal lineage”) and the *Ruststroemiacae* by indeterminate stromata formed on the substrate (“substratal stromatal lineage”). Yet, several taxa with a black indeterminate stroma that have been included in 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 *Polydesmidae*.

According to Schumacher and Kohn (1985), nine teleomorph-typified genera of *Sclerotiniaceae* possess a macroconidial anamorph (*Botryotinia, Grovesinia, Monilinia, Ovalinia, 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, and smooth or sometimes warty conidia. The three sclerotiniaceous genera *Coma, Microgloeum*, and *Mykopappus* 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, and 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, Acaespatorium* with appendages = *Pycnopeziza*), or forming complex staurosporous multicylindrical diaspores (*Hinomyces = Grovesinia, Cristulariella = Nervostruma, 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 Grovesinia pyramidalis (= G. moricola according to Johnston et al. 2014b). *Verrucobotrys* resembles *Botrytis*, but its conidia are subglobose, pale brown, and minutely tuberculare (Whetzel 1945; Seifert et al. 2011) and superficially resemble the thallial chlamydospores of *Schroeteria*.

In their “Recommendations on generic names competing for use”, Johnston et al. (2014b) 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-typied name, with one exception: although they gave recommendations on three of the four above-mentioned macroconidial genera, they did not treat the oldest genus *Myrioconium* as a genus competing with *Myriosclerotinia*. According to Schumacher and Kohn (1985), the type species of *Myrioconium, M. scirpi*, is a synonym of *Myriosclerotinia scirpicola*, 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 in Internet search engines much more often than *Myrioconium*.

**The genus Schroeteria**

*Schroeteria* G. Winter, Rabenh. Krypt.-Fl., Edn 2 (Leipzig) 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 (Plate 1).

**Circumscription of the genus.** The genus Schroeteria represents a small group of Ascomycota 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, p. 159; Scholz & Scholz 1988, p. 250) which may be variously curved or spirally twisted (Winter 1876, p. 148, pl. 4, 1881; see also Plate 1: 6). At maturity, the roundish chlamydospores often remain coherent as pairs (twin spores) or threes by showing strong constrictions between the individual spores. In contrast to the typical

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**Plate 1** Chlamydospores and microconidial anamorphs of 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. 11 fig. 13), 2 Boudier (1887: pl. 15 figs. 2–3), 3 Brefeld (1912: pl. 3 figs. 16–18), 4 Schröter (1877: pl. 11 fig. 5), 5 Tulasne & Tulasne (1847: pl. 4 figs. 24–25), 6 Winter (1876: pl. 4 figs. 10, 13, 14). All scales were evaluated from the original prints based on the indicated magnification factors. In Brefeld’s drawings, these magnification factors were considered by us to be erroneous (wrong scales marked with asterisk); in 1 the figured scale should correctly 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).
case, *Schroeteria poeltii* forms strongly curved chlamydo-sporic chains of 2–7 cells by showing only moderate con-strictions 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. delastra, Schroeteria, 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 taxa earlier placed in *Schroeteria* (*S. annulata* Ellis & Everh., *S. arabica* (Henn.) Benn., *S. cissi* (DC) De Toni) lack this kind of phialides and grow on other host genera.

According to Zundel (1953), Kochman & Majewski (1973), Vánky (1982, 1983, 1994, p. 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. *triphyllus*), *S. decaisneana* (V. *hederifolia* agg., after Terrier 1958 also *V. campylopoda*, but see below), *S. delastra* (V. acinifolia, V. agrestis, V. arvensis, *V. dillenii*, *V. praecox, V. triphyllus, V. verna*), and *S. poeltii* (V. *cymbalaria*). Furthermore, Gaponenko (1965) reported about a *S. delastra* infection on *V. campylopoda*. Scholz and 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. delastra* on *V. prostrata* from Slovakia, according to a report by Vánky (1985). The report of *S. delastra* on *V. triloba* listed in Zundel (1953) was not adopted by Vánky (1982) and Scholz and 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 1870a: 137) represents a copy of his shortly before-issued herbarium label of Fungi europaei exsiccati (Rabenhorst 1870a: no. 1376), which includes a valid description of the genus including a diagnosis (Plate 2, U. Braun & K. Bensch pers. comm.). Here, Schröter recognized only one species in *Geminella, G. delastra. Gemi-nella* and consequently also *Schroeteria* are thus typified by *G. delastra*. Vánky (1982) incorrectly cited “Geminella Schröter (1869, p. 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) 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 bigelovii* 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. delastra*. He mentioned four *Veronica* spp. as hosts of *S. delastra: V. arvensis* (type host of *S. delastra*, see Tulasne & Tulasne 1847), *V. tripityllos, V. praecox, and V. hederifolia*. The latter indicates that Winter did not differentiate between *S. delastra* and *S. decaisneana* as later Boudier (1887, as *Geminella*) did.

Two taxa growing on *Cissus* (*Vitaceae*), described at the end of the nineteenth 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 higher classification of the genus Schroeteria**

Since its valid description by J. Schröter (in Rabenhorst 1870a, b) 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 chlamydomspores were often called “teliospores”, whereas Brefeld (1912), who pointed out the true relationship with *Ascomycota*, called them chlamydomspores 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’s opinion who applied the German version “Falsche Brandpilze” (Brefeld 1908, p. 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.) F. Fuckel, *S. sclerotiorum* (Lib.) de Bary, and perhaps *S. trifoliorum* Eriks. (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. Ferdinandansen & Winge (1914, p. 4). Thirumalachar & Whitehead (1968) referred *Schroeteria* in synonymy with *Schizonella*. (Ustilaginales) by misinterpreting the observations of Schröter and Brefeld as an atypical 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* (i.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. (i.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.

**Other false smut fungi with ascomycetous relationship**

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* (Restionaceae, *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 ?corylifolius* 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, p. 194 f.). Earlier placed in *Ustilago* or *Tilletia*, the two economically important plant species...
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, p. 103; 1912, pl. 3 figs. 1–15; see also Tanaka et al. 2008). Based on molecular methods, Bischoff et al. (2004) placed *Ustilaginoidea* in *Clavicipitaceae*. 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*.

**Materials and methods**

**Morphology.** All collections were examined in the living state in tap water (see Baral 1992), using a Zeiss Standard 14 microscope with 10× Zeiss and 15× Euromex oculars and Nikon Coolpix E4500 (H.B.), a Zeiss L 421 (1939) with 7× and 10× oculars (P.R.), a Zeiss Axioscope with Nikon Coolpix E4500 and Zeiss Stemi 2000C with Canon EOS 600D (V.K.), and an Optika B-353PLi microscope with E-Plan IOS objectives and a Canon EOS 1200D reflex camera, and for macrophotographs the same camera with a Tamron SP AF 90 mm macro lens (C.V.L.). The iodine reaction was tested with Lugol’s solution (IKI = 1% I₂, 2% KI, in H₂O), without and with potassium hydroxide (KOH ca. 3%) pretreatment. Brilliant Cresyl Blue (CRB, ~1% in H₂O) added to a water mount was used for vital staining the vacuoles, also for staining spore wall surfaces for the detection of gel. All drawings were done free-hand. Kirschstein’s syntype specimens were reexamined from B (Botanisches Museum Berlin-Dahlem, Germany) and Terrier’s specimen on Veronica campylopoda from NEU (Université de Neuchâtel, Switzerland). Personal voucher specimens were deposited in the following herbaria: M (Botanische Staatsammlung München, Germany), GLM (Senckenberg Museum für Naturkunde Görlitz, Germany), and JA-CUSSTA (Junta de Andalucia, La Trufa, Zagrilla, Priego de Córdoba, Spain). Additional collections or duplicates are held in the private herbaria of H.O. Baral (H.B.), D. Benkert (D.B.), G. Hensel (G.H.), W. Huth (W.H.), L.G. Krieglsteiner (L.K.), J. Kruse (J.K.), V. Kummer (V.K.), M. Reul (M.R.), T. Richter (T.R.), U. Richter (U.R.), P. Rösch (P.R.), A. Urban (A.U.), F.J. Valencia Lopez (C.V.L.), and K. Vánky (H.U.V. = Herbarium *Ustilaginales* Vánky, since 2013 in BRIP = Queensland Plant Pathology Herbarium, Brisbane, Australia; exsiccateae see http://kalman-vanky.de/smut-host-index-1.html). Collections by Guy Marson (G.M.) are usually unpreserved. Numbers in curly brackets {} refer in the descriptions to the number of collections and under habitat after the slash to the number of collection sites.

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, 0 = 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 on damp earth covered by moss inside a not completely water-tight plastic box that was deposited on the ground under a box-wood hedge in a garden.

*Veronica* species were identified using Jäger (2017) and Parolly & Rohwer (2019), for *V. cymbalaria* Jahn & Schönheder (1995), and for *V. campylopora* Hong & Fischer (1998). *V. cymbalaria* from Spain was confirmed by an ITS sequence. Current plant names were established using The Plant List (2020), and the names of fungi generally follow Index Fungorum.

**Molecular methods.** Sequences of ITS and LSU rDNA were obtained by A. Urban from apothecia of two samples of Schroeteria decaisneana (Zeuchfeld near Freyburg in Sachsen-Anhalt, Germany) and one of Ciboria ploettneri-ana (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), *S. delastrina* (Kyffhäuser and Hainleite, Thüringen), *S. bornmei-elleri* (Mashhad, Iran), and *S. poeltii* (Rhodos, Greece), and from apothecia of *S. poeltii* (Ronda, Spain). These sequences comprise the entire ITS region and the LSU D1–D2 domain. DNA from three sori extracts was 2–3 × sequenced. For verifying the macroscopically identified *V. cymbalaria*, the plant ITS was sequenced.

Methods used by A. Urban: About a quarter to one asco-carp was processed from dry fungarium samples, depending on asco-carp size. The material was placed in 2 mL plastic reaction tubes and pulverized in a grinding mill (MM2, Retsch) using a combination of five 2 mm and two 3 mm glass beads and about at 30 Hz (maximum speed) for 15 min. If pulverization was incomplete, about 0.4 mL of coarse quartz sand was added and the grinding repeated. A modified CTAB miniprep DNA extraction protocol (Schickmann et al. 2011) was used for DNA extraction. DNA fragments spanning the whole nuclear ribosomal internal transcribed spacer region (ITS1, 5.8S, ITS2) and...
about 600 basepairs from the 5′ end of the 28 s ribosomal RNA encoding DNA were amplified using the following primer combination: ITS1F (CTTGGTACTTGGAGGAA GTAA; Gardes & Bruns 1993) and TW13 (GGTCGCTGT TTCAAGACG; http://nature.berkeley.edu/brunslab/tour/ primers.html). Sanger sequencing was performed using the PCR primers and the internal primers ITS3 (GCATCG ATGAAGAACGCAGC) and ITS4 (TCCTCCGCTTAT TGATATGC; White et al. 1990). DNA was amplified with the following thermocycling pattern: initial denaturation at 96 °C for 2 min (one cycle); denaturation at 95 °C for 30 s; annealing at 54 °C for 30 s; 72 °C for 90 s (40 cycles); and final elongation at 72 °C for 180 s; using a TGradient thermocycler (Biometra, Göttingen, Germany) and DreamTaq™ green PCR master mix (Thermo Fisher Scientific). Exo1/FastAP co-digestion (Thermo Fisher Scientific) was used to dephosphorylate unincorporated nucleotides and to digest excess primers. Sanger sequencing was performed using BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) and was analysed on an automated DNA sequencer (ABI 3730xl Genetic analyser, Applied Biosystems) after purification of cycle sequencing products using Sephadex (GE Healthcare Life Sciences) filtration.

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 was 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 (Table 1).

Alignments were done with MAFFT (https://mafft.cbrc.jp/alignment/server/). They can be found in supplementary information S4–S6. Maximum likelihood phylogenetic analyses were carried out with MEGA6 and MEGA7 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 or MEGA7 using individual alignments of species pairs, with the settings transitions + transversions and pairwise deletion.

**Morphological results**

In the following, Schroeteria decaisneana, S. poeltii, and Ciboria poeltneriana are described in detail from their teleomorph, the former two also from their anamorph. Personal notes on S. delastrina and S. bornmuelleri are also presented.

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 decaisneana (Boud.) De Toni, in Saccardo, Syll. fung. 7(2): 501 (1888) — Plates 3, 4, 5, 6, 7, 8, 9, 10.

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

≡ Geminella decaisneana (Boud.) Boud., Bull. Soc. mycol. Fr. 3(2): 150, pl. 15 figs. 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.
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      | References                      |
|------------------------------|-------------------|-------------|---------------|---------|---------|---------------------------------|
| *Botrytis cinerea*           | CBS 179.71        | Netherlands | *Cichorium divia* | MH860054 | MH871836 | Vu et al. (2019)                |
| *Botrytis porri* (tel)       | WU 43987          | Germany     | *Allium scorodopra*sum | MZ048347 | MZ048347 | This study                      |
| *Cenangium acuum*            | H.B. 9325b,      | Germany     | *Pinus sylvestris* | LT158439 | KX090822 | Pärtel et al. (2016)            |
|                             | TAAM:198515      |             |               |         |         |                                 |
| *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 | Galán et al. (2015)             |
| *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 caucas*             | 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* | MZ546198 | MZ546198 | This study                      |
| *Ciboria ploetleri-anana* (tel) | WU 43984        | Germany     | *Veronica hederifolia agg* | MZ048354 | MZ048354 | 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 viridiflora*        | KL212, TAAM:165962 | Estonia     | *Alnus*       | LT158429 | KX090812 | Pärtel et al. (2016)            |
| *Ciborinia erythronii*        | CBS 300.31T       | USA         | *Erythronium americanum* | MH855221 | MH866671 | Vu et al. (2019)                |
| *Ciborinia erythronii*        | 1838.P            | Canada      | *Erythronium sp.* | Z73767  | Z73741  | Holst-Jensen et al. (1997b)     |
| *Ciborinia folicola*          | 1932.H            | Canada      | *Salix*       | Z80892  | Z81404  | Holst-Jensen et al. (1997b)     |
| *Ciborinia gentianae*         | JCM 13253T        | Japan       | *Gentiana triflora var. japonica* | LC228669 | LC228727 | G. Okada et al., unpubl.        |
| *Ciborinia whetselii*         | 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 depresdans*   | 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 kernerii*        | KL402, TU:104529  | Switzerland | *Abies alba* | LT158475 | LT158475 | Pärtel et al. (2016)            |
| *Gloeotinia grandigena*       | 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) |
Table 1 (continued)

| Species                        | Collection number | Country    | Host          | ITS          | LSU          | References                                |
|--------------------------------|-------------------|------------|---------------|--------------|-------------|-------------------------------------------|
| *Haradamyces foliicola*        | MAFF 411026T      | Japan      | *Cornus florida* | AB329720    |             | Masuya et al. (2009)                       |
| *Hymenoscyphus scutulata*      | 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 cornimaris*       | CLX4075           | USA        | Masus         | KC958562    | KC964858    | Wiseman et al. (2015)                      |
| *Lambertella pyrolae*          | TNS-F 40132T      | Japan      | *Pyrola incarnata* | AB926081    | AB926164    | T. Hosoya et al. unpubl.                   |
| *Martininia panamaensis*       | CBS 358.72, CUP   | France     | inedt. 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 syvlestris* | MH856721    | MH868240    | Vu et al. (2019)                          |
| *Monilinia gaylas-saccae*      | 1919.P ATCC64508  | USA        | *Gaylussacia baccata* | Z73782      | Z73750      | Holst-Jensen et al. (1997b)                |
| *Monilinia jezoensis*          | 4222T             | 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 poly-stroma*        | 2015/PS32         | Hungary    | *Malus domestica* | LT615192    | LT615192    | A. Lantos unpubl.                         |
| *Monilinia seaveri*            | 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 pierottii* | KC753529    | KY696722    | Park et al. (2013)                        |
| *Myriosclerotinia scirpicola*  | 1435.P            | Norway     | *Schoenoplectus lacustris* | Z81440      | Z81414      | Holst-Jensen et al. (1997b)                |
| Species                        | Collection number | Country    | Host     | ITS        | LSU        | References                      |
|-------------------------------|-------------------|------------|----------|------------|------------|---------------------------------|
| 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 bulgaroiodes      | KL374, TAAM:198322 | Estonia    | Picea abies | LT158469   | KK090836   | Pärtel et al. (2016)            |
| Pycnopeziza sejournieri       | KL267, J.H.P. 11.054 | France    | Hedera helix | LT158443   | KK090827   | Pärtel et al. (2016)            |
| Pycnopeziza sympodialis       | CBS 332.39, CUP 25161 | USA      | Alnus rugosa | MH856037   | MH867534   | Vu et al. (2019)                |
| Rutstroemia firma             | G.M. 2014-12-01.1 608.P | Luxembourg | Quercus   | KT876987   | KT876987   | G. Marson unpubl.               |
| Rutstroemia henningsiana      | KL217, TU:104450  | Estonia    | Acer platanoides | LT158431  | KT876987   | Holst-Jensen et al. (1997b)     |
| Schroeteria bornmuelleri (ana) | H.U.V. 750        | Iran       | Veronica rubrifolia | MW915653  | –          | This study                      |
| Schroeteria decaisneana (ana) | J.K. S1346, H.B. 10206 | Germany    | Veronica hederofolia s.str | MW915644   | MW915644   | This study                      |
| Schroeteria decaisneana (tel) | A.U. 2273         | Germany    | Veronica hederofolia agg | MZ048345   | MZ048345   | This study                      |
| Schroeteria delastrina (ana)  | WU 43982          | Germany    | Veronica hederofolia 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:198511T | 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 | Ficaria verna | MZ048348   | MZ048348   | This study                      |
| Sclerotinia bulborum          | CBS 297.31        | USA        | ?          | MH855218   | MH866668   | Vu et al. (2019)                |
| 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 25277T | USA      | Podophyllum petatum | MH855916   | MH867422   | Vu et al. (2019)                |
Table 1 (continued)

| Species                  | Collection number | Country   | Host        | ITS          | LSU          | References                |
|--------------------------|-------------------|-----------|-------------|--------------|--------------|---------------------------|
| Septotinia populi-perda  | CBS 339.53        | Germany   | Populus     | MH857235     | MH101506     | Vu et al. (2019)           |
| Stromatina cepivora      | CBS 276.93        | Netherlands | Allium     | MH862401     | MH874059     | Vu et al. (2019)           |
| Stromatina cryptomeriae  | TNS:F-40103       | Japan     | Cryptomeria japonica | AB926160     | AB926160     | T. Hosoya et al. unpubl.   |
| Stromatina gladioli      | CBS 265.28 T      | N-America | Gladiolus   | MH855008     | MH866477     | Vu et al. (2019)           |
| Stromatina narcissi      | CBS 339.33        | Netherlands | Narcissus  | MH855451     | MH866916     | Vu et al. (2019)           |
| Stromatina pyroleae      | 1471. S           | Norway    | Pyrola minor | Z73798       | Z73761       | Holst-Jensen et al. (1997b) |
| Stromatina rapulum       | 1243.1            | Norway    | Polygonatum multiflorum | Z73801       | Z73763       | Holst-Jensen et al. (1997b) |
| Stromatina rapulum (tel) | A.U. Dum03        | Germany   | Polygonatum odoratum | MZ048352     | MZ048352     | This study                 |
| Valdensia hetero-doxa    | 485.2             | Norway    | Vaccinium myrtillus | Z81447       | Z81423       | Holst-Jensen et al. (1997b) |

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. Ascii *(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, spars 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}, euamylloid (BB), sometimes slightly hemiamylloid (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-pre-treated; 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 eccentricial), *10.5–12.5 × 5–6 µm, without or with only small LBs; forming germ tubes and/or phialides. Paraphyses apically uninflected to slightly clavate {4}, in some apothecia frequently ± strongly clavate to capitate or spathulate-lageniform to moniliform {1}, terminal cell *(32–)52–85(–93) × 4.5–5.5(–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, coarsely warty 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 forming phialides 7–14 × 3–6.5 µm on which microconidia 2.5–3.5 µm diam. arise in (basipetal) chains {Vánky 1982}. Microconidial synanamorph formed on ascospores that have germinated 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},

Plate 3 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)
†2.5–2.9 µm diam. {H.B. 5698}, surface smooth or very indistinctly rough, CRB–; containing a single eccentric LB (0.8–1.2–1.6–1.8) µm diam. {H.B. 8687} (Plates 3, 4).

**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 capsules 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), Pleistocene and Holocene sand and gravel and fluviatile sediments.
Phenology of *Schroeteria decaisneana* (tel=teleomorph, ana=anamorph)

| Jan | Feb | Mar | Apr | May | June | July | Aug | Sept | Oct | Nov | Dec |
|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| 1   | 0   | 1   | 1   | 1   | 0   | 0   | 0   | 0   | 1   | 4   | 1   |
| tel | 1   | 0   | 1   | 1   | 0   | 0   | 0   | 0   | 1   | 4   | 1   |
| ana | 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, ~10.1.1986, P. Blank & H.O. Baral (H.B. 2981). — Germany: Brandenburg, 25 km NW of Brandenburg, Rathenow, graveyard, MTB 3339/4 (or 3340/3), 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 ploetteriana*). — 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 MZ048346). — 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 (Plate 4: 1). The fungus was briefly reported by Baral (1986) as “*Ciboria*” cf. *geminicola* 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 gemminicola* 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 (Plate 3). 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 documentations were 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 (Plates 3, 4: 3a, 7: 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 those from Brandenburg and 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 Brandenburg, Merseburg, and Schaffhausen). 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 (no data available for that from Brandenburg). In the Schweinfurt collection, the germinating ascospores were predominantly 1-septate but also non-septate, and often they budded at both ends (Plate 4: 2g), whereas in that from Freyburg, they were always non-septate and germinated only at one conidiogenous locus (Plate 4: 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, Marsfjälet, 950 m, on bulbils of *Bistorta vivipara (=Polygonum viviparum)*, 28.VII.2010, P. Perz, H.B. 9387, Baral ined., see IVV and https://svampe.databases.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 seminicolca* (Kienholz & E.K. Cash) Hechler (including the questionable *C. betulce* (Woromin) 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 cziowers (Baral ined., H.B. 3677, 3682, 5136, 9774, 9777, see IVV).

Terrier (1958) believed to have found *Schroeteria decaisneana* on *Veronica campylopoda* based on a collection received from Yerevan (Armenia). We have some doubts about this, because *V. campylopoda* belongs to *Veronica* subgenus *Pocilla* with a clearly different seed morphology. The present reexamination of Terrier's specimen in NEU verified the host species but confirmed our doubts about the fungus, which severely deviated from *S. decaisneana* by chlamydosporcs which filled the entire capsules similar as in *S. delastrina* but, unlike those, never cohered in pairs. The chlamydosporcs had a size of †(9.5–)10–12 µm diam. and an ornamentation of 0.3–0.5 µm high ridges forming an incomplete network (see IVV). The low ornamentation and the absence of cohering spores are actually reminiscent of *S. decaisneana*, except for the slightly larger spore size.

**Ecology:** Schroeteria decaisneana was recorded near Freyburg (Zeuchfeld, Plate 8) in a thermophilous deciduous forest with *Ulmus minor* bordered by *Prunus spinosa*, near Schweinfurt (Alter Main) in a riverbank forest (*Quercus-Ulmetum*), near Merseburg (Elster-Luppe-Aue) in a riverbank forest with *Prunus padus* (?*Pruno-Fraxinetum*), and near Luckenwalde (Bürgerbusch) in a *Pruno-Fraxinetum*.

**Distribution:** 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 MW915646). – 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, Rodenbruchmarkt, Nobelingen, in front of hostel, MTB 3624/22, 55 m, 30.V.2011, J. Kruse (ex J.K. S0045, GLM-F129676).
Plate 6 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: Freyburg, Zeuchfeld. Phot. H.O. Baral

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– Rheinland-Pfalz: N of Bad Dürkheim, Leistadt, 230 m, 13.V.2020, J. Kruse (J.K. S0969). – Hessen, Frankfurt/Main, SW airport, nearby Mönchhodfriedeck, 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 Häuschenstrasse, 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, Hubertusstraße, “Friedenspark”, 180 m, 9.VI.2017, J. Kruse (J.K. S0969).

Schroeteria poeltii Vánky, Mycotaxon 18(2): 326 (1983) — Plates 12, 13, 14, 15.

Etymology: named after the Austrian lichenologist Josef Poelt (1924–1995) who sent the Hungarian smut fungus specialist Kálmán Vánky (1930–2021) some samples of the fungus (Vánky 1983).

Holotype: France, Alpes-Maritimes, Menton, Ste. Agnés, in 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 ocreaceous, slightly concave, finally flat, margin thin, not protruding, ± smooth, exterior pale ocreaceous, 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, flexuose 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 (het- eropolar), 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; overma- ture 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 fasci by 5–10 µm; terminal cell containing large non-refractive vacuoles. Subhymenium light ochre-brown, 25–35 µm thick, of dense texture intricata. Med- ullary 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 ocreaceous exudate, 100–130 µm thick at lower flanks, sharply delimited from ectal excipulum; in stipe of vertical t. porrecta-correcta, 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 ori- ented t. globulosa-(prismatic) 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 ocreaceous t. prismatico-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 med- ullary and ectal excipulum, more abundant in stipe. Amy- loidity of tissue: subhymenium weakly pale blue (KOH-pretreated) *{1}. – Anamorph: Cultural characteristics: ascospores germination not examined. Sori forming a red- dished 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 chlamydos- spores, evaluated from Nagler et al. 1989) hyploid conidi- ophores with conidiogenous cells phialidic, cylindrical to lageniform, 8–20 × 3.5–5.8 µm, microconidia ± globose,
Plate 7 Schroeteria decaisneana (teleomorph, H.B. 8687, Sachsen-Anhalt, Freyburg, Zeuchfeld). 1a Median section of receptacle; 1b–e idem, ectal excipulum at margin (1e with paraphysis-like intermediate elements); 1f–i idem, ectal excipulum at lower flanks and junction with stipe; 1g idem, ectal excipulum in stipe; 1h idem, medullary excipulum and subhymenium; 1i mature ascii; 1j paraphyses, containing large non-refractive vacuoles; 1k ascus bases with croziers; 1l–m, o, q apices of mature ascii (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 ecentrical 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

*(2.7–)3–3.7(–4)×(2.7–)2.9–3.5(–3.8) µm, with one ecentrical 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 in seeds of non-stromatized capsules of V. cymbalaria (3/3) by destroying the seeds inside the initially closed capsules of living plants. Desiccation tolerance: not tested. Phenology: apothecia I; anamorph III, VI. Altitude: 5–650 m. Geology: on acidic and calcareous soil.

Specimens included (all on Veronica cymbalaria).

Teleomorph (on fallen seeds): Spain: Andalucia, Malaga, 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, JACUSSTA 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, toptype, doc. vid.). – Greece: Rhodos, 1.7 km SSW of Ialysos, 0.2 km E of Filerimos, monastery park, 212 m, 20.III.2013. J. Kruse & V. Kummer (V.K. P1675/cymbalaria 1, J.K. S1304, sq.: ITS MW915654). – 2.7 km SSE of Masari, SW of Vages, coastal road, 5 m, 22.III.2018. J. Kruse (J.K. B2278, sq.: ITS/LSU MW915647). – 2.5 km SE of Masari, Charki, coastal road, former barracks area on the beach, 7 m, 21.III.2018. J. Kruse (J.K. B2279).

Taxonomic remarks: In the teleomorph, Schroeteria poeltii deviates from S. decaisneana merely by slightly smaller ascii 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 wider marginal excipular cells (Table 2). 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 chains 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 our 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 A. Kruys (pers. comm.) the specimen could not be found at UPS. In 1987 Vánky collected a toptype, which Nagler et al. (1989) investigated. In 2013 Vánky gave his entire herbarium to BRIP (Brisbane) where the holotype and also the toptype 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 few phenological data suggest that the anamorph occurs during spring (March–June) and the teleomorph during winter (January).
The French holotype collection was from a meso-Mediterranean semihumid site northeast of Monaco in the 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, Umgung 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 cocciifera 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, Ficaria verna, and Vinca difformis. Outside of the flooded area are large Castanea sativa plantations, the main agricultural product of the local people.

**Distribution:** Schroeteria poeltii was found in France, Greece, and Spain. No further records than those listed above came to our notice.
**Ciboria ploettneriana** (Kirschst.) N.F. Buchw., K. Vet. Landbohøjsk., Aarsskr. 32: 165 (1949) — Plate 16, 17, 18, 19, 20.

≡ **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 010006).

**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* × (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)biserrate, †65–83 µm, spores subbiseriate to uniseriate; **apex** (†) hemispherical to 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

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Plate 9 *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. (in upper part with one blackened seed

1b ascospores in ascus (in KOH); 1c free ascospores (in KOH); 1d original label written by Kirschstein. Phot. V. Kummer
Plate 10  *Sclerotia decaisneana* (anamorph, from Sachsen-Anhalt, Freyburg, Zeuchfeld, on *Veronica hederifolia* s.str.), 1a–e Infected plant with black sorus in the cavity of each seed (seeds inside closed capsules also contain sori); 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).

moderately truncate, apical thickening immature or mature ±2–3.8 µm thick, apical ring blue in IKI 4), emuloid (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 eccentric 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 vacu-olary bodies (VBs) in (11–)15–50(–70) µm long upper part 3], VBs staining turquoise in CRB, in H₂O turning light purplish-pink with age (vital state) 2], without SCBs; when senescent emeshed by an ochre-brown-brushtexxonade 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, 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 anamorph* formed on ascospores that have germinated 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; *phialonidia* globose to subglobose, *2.5–3×2.5–3 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 epidermal 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), Pleistocene and Holocene marl, sand and 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, Baumschulenweg, Späth-Arboretum, 37 m, MTB 3546/24, 30.IV.1992, D. Benkert, vid. V. Kummer (B 700009941, d.v.). – Brandenburg. 22.5 km NE of Brandenburg, SW of Groß Behnitz, Haselleke, 35 m, MTB 3442/123, 14.IV.1905, W. Kirschstein, vid. V. Kummer (B 70 010005). – ibid., 27.IV.1905, W. Kirschstein, vid. V. Kummer (B 70 010006, lectotype). – 1.7 km SW of Teupitz, ~1.5 km SE of Egards, 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 (apothece 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, 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, H.B. 10210).

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**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 by 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, *C. ploettneriana* deviates from *S. decaisneana* by distinctly larger, slightly more heteropolar ascospores with often pointed, subacute ends. Under vital study, *C. 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 (Table 2). 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 prismaticata vs. t. porrecta), also with much shorter cells at the margin (Table 2).

**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 tetraneucleate 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 on damp earth in an untight plastic box that was deposited on the ground at a shady place. In this plastic box 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* by Rehm (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 19–11×5–6 µm emerge (Plate 9). 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 ploetneriana* 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 Plate 20: 1) each contain numerous bright to dark black-brown seeds of *Veronica hederifolia* agg., and apothecia which much better fit the protologue of *Sclerotinia ploetneriana* 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 ploetneriana*.

The examined duplicate of Rehm’s exsiccata (B 70 0100004) provided a surprise: 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 ploetneriana*.

**Ecology:** *Ciboria ploetneriana* was recorded near Freyburg at three sites, in a thermophilous deciduous forest with *Ulmus minor* bordered by *Prunus spinosa* (Zeuchfeld, Plate 8), 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*, Plate 19), and that near Wismar a narrow forest strip of *Acer, Aesculus* and *Tilia* between road and farmland. *Monilinia johnsonii* on *Crataegus* fruits occurred together with *Ciboria ploetneriana* at the site near Naumburg.

**Distribution:** Besides the collections from Mecklenburg-Vorpommern, Brandenburg (including Berlin), and Sachsen-Anhalt as listed under Specimens included, no further unequivocal records of *Ciboria ploetneriana* came to our notice.

**Key to the three species with a known teleomorph, based on teleomorph morphology**

(For a key to the accepted anamorphs of *Schroeteria*, see Vánky 1982)

1. Ascospores mainly *12.5–16.5 × 6–7.5 µm*, with several LBs of 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

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

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 supramediterranean semihumid

### 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 (Table 3). Also in the LSU D1–D2, no difference was observed between the two apothecial isolates and the sorus isolate (Table 3). Likewise, the two *S. poeltii* sequences fully concur in the ITS and LSU D1–D2 between apothecial and sorus isolate, except for 1 nt in the LSU. Considering the comparatively high interspecific distances among the *Schroeteria* species and the concordant host of each species, our data prove 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 *S. poeltii*, 16.7–18%/8.9–9.7% between core clade and *Ciboria ploetneriana*, and 9.2%/3.7–3.9% between *S. poeltii* and *C. ploetneriana*, respectively (Table 3). The S1506 intron is absent in all sequences in which the 3′-end region of SSU was included (the region is missing in *S. bornmuelleri*).
A strongly supported Schroeteria core clade is formed in our combined maximum likelihood analyses of ITS+LSU (Plate 21, S3) but also in separate analyses of ITS and LSU (S1, S2). The clade comprises S. decaisneana, S. delastra, and S. bornmuelleri and nested in an unsupported clade with various Monilinia spp. of section Disjunctoriae growing on fruits of Ericaceae and Rosaceae (Plate 21, S1). When separately analysing LSU (S2), the Schroeteria core clade clustered with medium support with Ciboria shiraiiana (on Morus), apparently through long branch attraction by convergent evolution when considering their placement in the other analyses.

The Schroeteria core clade clustered particularly with two Ericaceae inhabiting species: it formed a medium (Plate 21, S1) or strongly (S3) supported sister clade of M. jezoensis, for which only ITS was available, though with a rather long branch, and together with this species a less supported sister clade of M. azaleae (Plate 21, S1). Both species grow on Rhododendron and are members of the Monilinia alpina group of section Disjunctoriae, to which also M. cassinopæ belongs (Batra 1991, p. 102) and according to our analyses also Stromatinia pyroleae.

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 with long branch an unsupported (Plate 21) or strongly supported (S3) sister clade of the supported clade of Sclerotinia bulborum and S. “binucleata” (an undescribed species of Sclerotinia s.l. on Ficaria verna and Corydalis cava). Ciboria ploeotteriana clustered unsupported and with comparatively short branch with these and other typical members of Botrytis, Grovesinia, Myriosclerotinia, Sclerotinia, Stromatinia etc.

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, Elliottiogina, Grovesinia, Monilinia s.str., Myriosclerotinia, Oulinia, Pycnopeziza, Scle- rotinia s.l., or Valdensia. Regarding placement of Ciboria ploeotteriana, only one position in the middle of ITS1 gives a hint on its generic affiliation: the species shares the motif GGGGYCT (Y = C or T) with most species of Sclerotinia s.l., but also with Grovesinia moricola, whereas other species have mostly the motif HGGGCT (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. delastra have several extraordinary positions. Some of them occur also in Ciboria erythronii, but none was observed in Ciboria ploeotteriana and any other Sclerotiniaceae in GenBank (Plate 21).

Discussion

Species delimitation within Schroeteria, doubtful measurements of chlamydospores and 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. delastra) 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 (Plate 10: 2e–k). Vánky (1982) used chlamydospore size in his key, but the given measurements strongly overlap. Chlamydospore size clearly refers to single cells, whereas in the older literature, it is not always clear whether authors 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. delastra owing to slightly smaller, soon single, at first glaouous 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, p. 75) was unaware of S. decaisneana when he proposed the name “Geminella (Schroeteria) parvispora” (a taxon which we here consider as a synonym of S. decaisneana) for collections on Veronica hederiformia 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 figs. 16. When first mentioned on p. 75, he cites it as follows
The fungus living on *V. hederae-folia* 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 *Schroeteria parvispora* was used by Ferdinandsen & Winge (1914, p. 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, blue-violet 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 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, p. 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. 3 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, p. 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 Tables 4 and 5).

As a common usage in earlier times, Brefeld (1883: pl. 11 fig. 13, pl. 12 figs. 14–18; 1912: pl. 3 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 (Tables 2 and 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 *Schroeteria delastrina* 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* (Table 4), whereas his drawing of *G. parvispora* yields a cell size of about 1.5× larger than the current values (Table 5). On the other hand, Brefeld’s (1883: pl. 6) illustration of *Microbotryum cardui* (as *Ustilago cardui*) yields teliospores of 16–19 µm diam., in good

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**Plate 14** *Schroeteria poeltii* (teleomorph, C.V.L. 040117: Spain, Andalucía, Málaga, Pujerra). 1 Collection site: supramediterranean floodplain forest with *Populus alba*, *Salix alba*, *Quercus faginea*, *Veronica cymbalaria*, and various other mediterranean herbs; 2 apothecia on stromatized seeds of *V. cymbalaria*. – Phot. 1 C. Borrego, 2 F.J. Valencia
Plate 15  *Schroeteria poeltii* (anamorph, on *Veronica cymbalaria*). 1 Ruderal meadow; 2a uninfected plant; 2b–g opened capsules exposing brown sori; 2h–m chlamydosporic (living state, in water) cohering in numbers of 2–5. – 1 21.III.2018. Greece, Rhodos, Charaki; 2 20.III.2018. ibid., Ialysos, Filerimos. – Phot. J. Kruse
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, p. 144, pl. 12 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. Surprisingly, 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 (Table 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 2 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–)5.5–6.5(–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(–) LBs of 1.4–2.7 µm diam. and some small ones near each end | 1(–) LBs of (1–)1.5–1.8 µm diam. and some small ones at each end | 1(–) LBs of 0.5–0.8(–1) µm diam. and some small ones near each end |
| - Nuclei in ascospores  | 1 nucleus, 2.8–3.5 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 | Without 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-porrecta |
| 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 | Supramediterranean semihumid | Temperate humid |
Ecological remarks on *Schroeteria* spp. and *Ciboria ploettneriana* and their host plants

**Host specificity.** *Ciboria ploettneriana* and *Schroeteria decaisneana* may be considered as specific to *Veronica hederifolia* agg. since all collections of their teleomorph states and the anamorph of the latter reported here emerged from seeds of this plant. Also in the literature, the *S. decaisneana* anamorph was reported solely on *V. hederifolia* agg., with exception of Terrier (1958), who misidentified a sample on *V. campylopoda* which appears to represent a different, possibly undescribed species (see chapter “Similar species” under *S. decaisneana*). The few known collections of *S. poeltii* were all on *V. cymbalaria*, including the here-reported teleomorph. This is in strong contrast to *S. delastrina* which was reported from no less than eight different *Veronica* spp., though mostly from *V. arvensis*.

Species of *Veronica*, 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), and can be listed as follows: subgenus *Beccabunga* includes *V. acinifolia*, subgenus *Chamaedrys* *V. arvensis*, *V. dillenii* and *V. verna*, subgenus *Cochlidiosperma* *V. hederifolia* and *V. cymbalaria*, subgenus *Pocilla* *V. agrestis*, *V. biloba*, *V. campylopoda* and *V. rubrifolia*, subgenus *Pellidosperma* *V. praecox* and *V. tripilloylos*, and subgenus *Pentasepalae* *V. austriaca* and *V. prostrata*. Thus, the hosts of *S. decaisneana* and *S. poeltii* belong to subgenus *Cochlidiosperma*, whereas the host of Terrier’s fungus belongs to subgenus *Pocilla*. The broad host spectrum of *S. delastrina* encompasses four different subgenera (*Beccabunga*, *Chamaedrys*, *Pellidosperma*, *Pocilla*), and collections on these different hosts should be investigated in the future for a possible molecular heterogeneity of *S. delastrina*.

**Microspecies of *Veronica hederifolia***. The *V. hederifolia* aggregate consists of three microspecies, the mainly southeast European, (sub)mediterranean *V. triloba*, and the two more temperate *V. sublobata* (= *V. hederifolia* subsp. *lucorum*) and *V. hederifolia* (subsp. *hederifolia*). *V. sublobata* occurs in different forest types, such as floodplain...
Plate 17 *Ciboria ploettneriana* (from Sachsen-Anhalt, Freyburg). 1, 2, 3a–c Fresh apothecia emerging from stromatized (blackened) seeds of *Veronica hederifolia* agg.; 3 g–h infected (blackened) seeds (3 h 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
forests, but apparently 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). For photos of the three microspecies see, e.g. https://www.badvoeslau.at/de/lebenswelt/umwelt/kalenderblatt/2014.html.

The morphological distinction of the three microspecies is difficult. It was complicated in the present study by the fact that *V. hederifolia* and *V. sublobata* may occur at the same site. Fallen infected seeds cannot clearly be assigned because of their very similar morphology; thus, we mostly refrained from specifying the microspecies. Apothecia of *Ciboria ploettneriana* and *Schroeteria decaisneana* were sometimes observed at the same plot, but it appears unlikely to us that the two species prefer different microspecies of *Veronica hederifolia* agg. In two anamorph collections of *S. decaisneana* from Zeuchfeld (13. & 21.V.2019, V.K. P1656-10 and H.B. 10206), the identification as *V. hederifolia* s.str. was established by morphological criteria. Possibly, some of our teleomorph collections of both species were on *V. sublobata* instead of *V. hederifolia*.

**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 cavity is finally filled with air which aids in their transport by rain. The cavity includes also the elaiosome, a fleshy structure rich in nutrients. The elaiosome attracts ants which 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: tabs 3, 6–7). Seeds of many other *Veronica* spp., e.g. *V. arvensis*, have more elongated, ellipsoid to flattened seeds without a cavity.

**Phenology and life cycle.** Host infection by *Schroeteria* spp. is systemic; i.e. the mycelium grows endophytically in the plant up to the flowers (Winter 1876; Brefeld 1912, p. 75). Like in smut fungi, it produces mitospores (here called chlamydospores) only in a special organ of the host (here *Veronica* fruits). According to Brefeld (1912) and Vánky (1982), plants infected by *Schroeteria* spp. do not differ in general appearance from healthy ones. The vegetative mycelium can be found in the intercellular space of the medullary parenchyma of the entire host plant (Winter 1876, p. 147, pl. 4 fig. 15), though sometimes one or more shoots or only some fruits may remain healthy. The mycelium grows through the floral pedicel, placenta, and funiculi into the young seeds where the chlamydospores are formed. In *S. decaisneana*, mycelium and chlamydospores replace placenta, funiculus, and hilum (Boudier 1887, p. 150) or only the funiculus (Bubák 1916, p. 60) by leaving the seed morphologically unaffected although this can no longer germinate, whereas in *S. deelastrina*, the seeds are entirely absorbed by leaving placentae and funiculi unaffected (Winter 1876, p. 148, Boudier l.c.: 151, Bubák l.c.). Winter (1881, p. 118), who did not distinguish *S. decaisneana* from *S. deelastrina*, wrote that the mycelium infects placentae, funiculi, and young seeds. The produced spores form a moldy-smelling, grey-brown, greyish blue-violet, or greyish black powdery spore mass which in *S. decaisneana* fills the ventral cavity of each seed and in *S. deelastrina* the entire capsule (Winter 1881, see also Vánky 1982). The spore mass is generally called “sorus” following the custom with teliospores of ustilaginomycetous smut fungi. The capsule later usually tears open to release the spores passively.

Kirschstein (1906) based his description of *Ciboria ploettneriana* on collections from October 1899 and April 1905. Under the assumption that the ascospores infect flowers of other individuals of this plant, he 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. However, Kirschstein’s collections belonged to two different fungal species: the April collection we have selected as lectotype of *Ciboria ploettneriana* and the October collection we have reidentified as *Schroeteria decaisneana*. Indeed, the two species have a different phenomenology: apothecia of *S. decaisneana* were observed during end of October to first half of May and *S. poelitii* once in January, whereas those of *C. ploettneriana* only in April and first half of May.

Comparable to other taxa recognized in *Ciboria*, such as *C. semincola* growing on *Alnus* seeds or *C. amentacea* on male *Alnus* catkins, the infection by *C. ploettneriana* ascospores could happen via the flowers during spring. After seed formation, the infected seeds would fall to the soil and later get stromatized. In the next spring, a new generation of apothecia will be being produced from these stromatized seeds. The apparent absence of a seed-born anamorph would exclude a pleiomorphic life cycle of this fungus (the phialospore mass is generally called “sorus” following the custom with teliospores of ustilaginomycetous smut fungi). The apparent absence of a seed-born anamorph would exclude a pleiomorphic life cycle of this fungus (the phialospore mass is generally called “sorus” following the custom with teliospores of ustilaginomycetous smut fungi).
Plate 18 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; 1I ascogenous hyphae with croziers; 1h, k apices of immature and mature ascii; 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

79) was quite convinced that Schroeteria chlamydospores do not infect flowers of the host plants but germinate in the soil by producing a persistent mycelium that infects roots of young plants. Brefeld (1895, p. 204, 1912, p. 79) further correctly imagined that ovaries of the host plants might be transformed into “sclerotia”, which in turn form apothecia during the first stages of seed germination. However, Brefeld and his coworker A. Kappenberg could not detect pseudo-sclerotia in the ovaries or apothecia associated with Veronica during their field work.

The hypothetical life cycle of Schroeteria decaisneana can thus be circumscribed as follows: Infection of young winter-annual seedlings of Veronica hederifolia agg. appears to take place during late autumn, warmer stages in winter, or early spring of the following year, either via chlamydospores that have germinated by forming a mycelium in the soil or via ascospores that have germinated there or perhaps on the host plant. During the next fruiting period in late spring (May–June), the mycelium inside the infected plants produces a new generation of chlamydospores in the capsules. According to our observations, virtually all capsules of infected plants contained chlamydosporides in the seed cavities. Although such seeds superficially look healthy, Bubák (1916) found them to be incapable to germinate. We suspect, therefore, that the mycelium also enters the endosperm and/or the embryo of the seeds. We further suspect that the capsules either open in late spring to distribute their chlamydosporides, e.g. by wind or water, or the infected capsules or seeds fall down into the litter, where they successively lose their chlamydosporides. In either case, the seeds may finally get stromatized in order to produce apothecia during the next autumn, winter, or early spring. In this way, the fungus has two possibilities to infect young seedlings: (1) via chlamydosporides produced in spring and resting or producing a persistent mycelium in the soil during summer, and (2) via stromatized seeds resting in the soil during summer and producing apothecia and ascospores during the colder season.

In S. poeltii we observed that most capsules of an infected population of V. cymbalaria were filled with chlamydosporides, but some shoots of a few plants had not only capsules with chlamydosporides but also some with apparently normally developed seeds. It seems possible that these seeds are also infected and, after falling to the soil, finally get stromatized and produce apothecia during the germination time of the winter annual plant. The observation of S. poeltii apothecia in January suggests that also in this species the ascospores infect young seedlings after having germinated in the soil.

Hyperparasitism

The occurrence of two sclerotiniaceous species on the same organ of the same host plant could also mean that one species is a hyperparasite on the stroma of the other. Within Sachsen-Anhalt, apothecia of Ciboria ploettneriana and Schroeteria decaisneana were usually not collected at the same site; only at the site Zeuchfeld near Freyburg both species were found sympatric in the same habitat, though in different months. Comparable hypotheses have been proposed in other taxa of Sclerotiniaceae, in which two different species emerge from sclerotial structures formed on the same host plant. For instance, Spooner (1987, p. 251) thought that Scleromitrula shiraiiana could be a hyperparasite on stromata of Ciboria shiraiiana, both occurring on fruits of Morus, and he also mentioned other examples of possible hyperparasites, viz. Episcerotium sclerotiorum (as Mitrula) on sclerotia of Sclerotinia trifoliorum and Episcerotium sclerotipus (as Mitrula) on sclerotia of Typhula.

The hypothesis of S. decaisneana being a hyperparasite of C. ploettneriana would be in contradiction to the biology of its anamorph which, like anamorphs of other Schroeteria spp., is a direct parasite of the plant. C. ploettneriana as a hyperparasite of S. decaisneana would mean that during spring its ascospores attack plants that already have been invaded by S. decaisneana. Yet, any observation that supports this hypothesis is lacking.

Generic concepts within Sclerotiniaceae

Different generic concepts have been proposed within the Sclerotiniaceae in the past. The available phylogenetic analyses of rDNA (including our analyses) and rarely protein-coding genes suggest heterogeneity of some of the classiﬁcal 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

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could alternatively be assigned to a single genus Sclerotinia s.l.

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 and Ericaceae—including the former Empetraceae and Pyrolaceae—with intercalating disjunctors). This subdivision was followed by Batra (1988, 1991, p. 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 (Plate 21), 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 sections Junctoriae and Disjunctoriae formed supported sister clades. A similar result for a smaller dataset was achieved by Marcat-Houben et al. (2021) based on a phylogenomic analysis of numerous secreted proteins.

The analysis of Andrew et al. (2012) 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 diasporic 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 (Plate 21). Although Veronica cymbalaria, the host plant of S. poeltii, is closely related to V. hederifolia agg. (Muñoz-Centeno et al. 2006), the chlamydospore chains of the S. poeltii anamorph are very different in shape compared to those of other Schroeteria spp. This and the deviating molecular result appear to justify separation of S. poeltii at some taxonomic level. In the morphology of the teleomorph, however, S. poeltii can hardly be distinguished from S. decaisneana, including the stromatized seeds. The specialized occurrence of Schroeteria s.str. and S. poeltii on seeds of the same host genus Veronica suggests a common ancestor which also grew as a biotrophic parasite of Veronica seeds, making a scenario of polyphyletic evolution quite improbable. In the absence of conclusive evidence, we refrain from postulating non-monophyly of Schroeteria and from implying highly convergent anamorph and teleomorph morphologies, host relationships, and life cycles. From these considerations, we think that a generic split of Schroeteria is premature at the moment. Multigene analyses based on 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 monophyletic relationship between the two distant subgroups.

The genetically most heterogeneous genus in our analyses was Ciboria. Its heterogeneity was also seen in analyses of, e.g. Galán et al. (2015: fig. 4, LSU, fig. 5, ITS), Pärtel et al. (2016: fig. 2, ITS), and Navaud et al. (2017, ITS). The genus is currently 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 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 (= Cibornia), and Sclerotinia s.l.

In most of our analyses (Plate 21, S2, S3), a supported core clade of Ciboria was formed, with two species growing on male catkins: C. caucus (Rebent.) Fückel (type species, on Populus and Salix, Salicaceae) and C. amantacea (Balb.)
Fuckel (on Alnus and Corylus, Betulaceae). Surprisingly, C. coryli on male Corylus catkins (Betulaceae) was not associated with those despite its high morphological similarity, but clustered unsupported with Stromatinia cryptomeriae Kubono & Hosoya. Another strongly supported clade was formed by Ciboria americana E.J. Durand on Castanea cupules, C. viridifusca (Fuckel) Höhn. on Alnus cones, and Coprotinia minutula Whetzel on dung, which clustered with medium (Plate 21) or strong (S3) support sister to Pycnopeziza sympodialis (Bubák) W.L. White & Whetzel. 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 distinct lineages.

With the present knowledge, the generic position of Ciboria ploettneriana could not satisfactorily be resolved, neither with morphological nor with molecular methods. In our combined analyses (Plate 21, S3), the species clustered unresolved within the Sclerotiniaceae though close to the type species of Dumontinia (D. tuberosa), Sclerotinia (S. sclerotiorum), and Stromatinia (S. rapulum), but also to those of Botryis, Kohninia, and Myriosclerotinia. The distances to these taxa in the ITS region and LSU D1–D2 domain 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 above), 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, pp. 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 C. ploettneriana in 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 Botryis (see IVV).

When Buchwald (1949, p. 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, pp. 240, 255), he distinguished two subgenera within Ciboria: subgenus “Euciboria Boud.” for species on flowers and subgenus “Stromatinia Boud.” for species on fruits. It must be noted that Buchwald (1947, p. 309) treated Stromatinia rapulum (type of Stromatinia) as a synonym of Sclerotinia tuberosa. Therefore, Buchwald (1949, p. 164) suggested to rename subgenus Stromatinia to subgenus Pseudociboria Buchw. (non Pseudociboria Kanouse). In his concept of subgenera, Buchwald followed Boudier (1885, p. 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).

Because Ciboria ploettneriana clustered in our phylogenetic analysis near Sclerotinia spp. distant from all investigated Schroeteria spp. and because only one smut-like anamorph is known on Veronica hederifolia agg., it appears improbable that C. ploettneriana also possesses such an anamorph. Although S. poetii did not group with the core clade of Schroeteria nor with any other clade in the family, we assume that all species with a smut-like anamorph parasitizing Veronica seeds evolved from a common ancestor on this host genus, whereas C. ploettneriana should have derived from another lineage of sclerotiniaceous fungi.
Sclerotinia
Ciborinia
Ciboria
Dumontinia
Sclerotina
Stromatina
Cristulariella
Grovesinia
Botrytis
Mycocystis
Rosaceae
Monilinia s.str.
(M. fructicola group)

Kohninia
Ciboria
Septotinia
Haradamae
Ciboria

Elliottinia
Stromatina
Puccinia
Ciboria
Ciboria

Sclerotiniaceae

Sclerotinia s.l.
Table 3  Inter- and intraspecific distance matrix of the ITS1-5.8S-ITS2 region (before slash) and LSU D1–D2 domain (after the slash) for *Schroeteria* spp. in comparison with *Ciboria ploettneriana*. Values indicate differences in percent

|                      | *S. decaisneana* | *S. delastrina* | *S. bornmuelleri* | *S. poeltii* | *C. 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 / –       | 0 / 0.2            |              |                   |
| *S. poeltii*         | 14–14.3 / 9.4–9.6 | 14.2–14.7 / 8.5–8.9 | 13.8 / –          | 0 / 0.2     |                   |
| *C. ploettneriana*   | 17.2–18 / 9.7   | 17.2–17.6 / 8.9–9 | 16.7 / –          | 9.2 / 3.7–3.9 | – / –             |

Table 4  Measurements of chlamydospores and microconidia of *Schroeteria delastrina* (on *Veronica arvensis*) in the literature

|                      | Single spores (µm) | Twin spores (µm) | Cell number | Microconidia (µm) |
|----------------------|--------------------|-----------------|-------------|-------------------|
| Tulasne & Tulasne (1847) | 12–14¹           | 16–20¹          | 2 (–3)      | –                 |
|                       | (8.5–)10–12×(4.5–)6.5–11⁸ | 15–20⁸         | –           |                   |
| Winter (1876)         | 7–9.5×6–8.5⁴     | 16–23³          | 2           | –                 |
| Schröter (1877)       | 7.7–9.5×6.7–8.5⁴ | 12.5–16.5⁶     | (1–)2       | 2.7–4.3³         |
| Fischer v. Waldheim (1877)³ | 10–13×8–10.5³ | ?               | ?2          | –                 |
| Winter (1881)         | 9–12×8–11.5⁴     | ?               | 2 (–3)      | –                 |
| Brefeld (1883)        | (12.5–)16–24₂(12.3–)15–21³ | 30–40⁸         | (1–)2       | 6–7⁶             |
| Boudier (1887)        | 11–15¹ / 7–12×6–11³ | 16–18.5⁵      | (1–)2–3     | –                 |
| De Toni (1888)        | 8–12³            | 15–23³         | 2 (–3)      | –                 |
| Cocconi (1898)³       | 16–20² / 20–26×16.5–23³ | 37–45 s       | 2           | 7–8³             |
| Brefeld (1912)        | 16.5–26.5×(10–)15–22.5⁵ | 32–45⁵        | (1–)2–3     | –                 |
| Bubák (1916)          | 12–17¹           | 20–30³         | 2 (–3)      | –                 |
| Ciferri (1938)        | 8–18×8–12³       | 15–23³         | 2 (–3)      | –                 |
| Liro (1938)           | 9–13¹            | ?               | 2 (–3)      | –                 |
| Săvulescu (1957)      | (9–)10–12×(8–)9–12² | ~14–21¹       | 2 (–3)      | –                 |
| Vánky (1982)          | 8–11×(13.5)×8–11×(13)³ | 18–20⁸        | (1–)2–3     | 2.7–3.3³         |
| Zogg (1985)           | (8–)9–12×(13)×(7–)8–11×(12)³ | ?             | 2 (–3)      | –                 |
| Present study (Hannover) | 7.8–11×7–9      | 14–17          | 2 (–3)      | –                 |

Chlamydospore values refer to single cell diameters (without ornamentation), length of twin spores, and cell number. ¹ = values reported in text; ⁸ = values gained based on scale or magnification factor of illustration; ³ = type of *S. delastrina* var. reticulata; *⁸ = 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.
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Author contribution  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 teleomorph connection in Schroeteria decaisneana. V. Kummer reexamined and documented original material of Kirschstein’s collections in B and Terrier’s specimen on Veronica hederifolia agg. in the NCBI GenBank (https://www.ncbi.nlm.nih.gov/genbank/) under the accession numbers given in Table 1.

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Table 5  Measurements of chlamydospores and microconidia of Schroeteria decaisneana (on Veronica hederifolia agg.) in the literature

|          | Single spores (µm) | Twin spores | Cell number | Microconidia (µm) |
|----------|-------------------|-------------|-------------|-------------------|
| Boudier (1887) | 10–12×8–12 / 7–10×7–9.5 | 13.5–15 | 1–2 | – |
| De Toni (1888) | 10–12×8–12 | ? | 2 → 1 | – |
| Brefeld (1912) | 14–17×12–15 / 13.5–20×11.2–18.5 | 24–27 | 1 (–2) | 6–7 |
| Bubá (1916) | 7.5–15 | ? | 2 → 1 | – |
| Liro (1938) | 7–11×7–11 | ? | 1 (–2) | – |
| Ciferri (1938) | 10–12×8–12 | ? | 2 → 1 | – |
| Sávulescu (1957) | 9–12(–15)×(7–8)–11(–12) | ~14–18 (–26) | 1–2 | – |
| Vánky (1982) | 7–12×(13)×7–11 | 17.5–21 | 1–2 | 2.7–3.3 |
| | 9–13×8–11 / 7.5–11.2×6.5–10.3 | * | | 2.6–3.3 |
| Zogg (1985) | (8–9)–11(–11)×(7–8)–11(–12) | ? | 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 |

Chlamydospore values refer to single cell diameters (without ornamentation), length of twin spores, and cell number. 1 = values gained from scale or magnification factor of illustration; 1 = 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.

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