The genus *Schroeteria* WINTER (Ustilaginales)

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Abstract. — After a short historical review regarding the genus *Schroeteria*, the characters of this genus and its five species are presented: *S. banatica*, *S. bornmuelleri*, *S. bremeri*, *S. decaisneana* and *S. delastrina*. *S. banatica* on *Veronica austriaca* is described as a new species.

Introduction

The species of *Schroeteria* form a natural, well delimited genus within the Ustilaginales. They parasitise species of *Veronica* (Scrophulariaceae), producing teliospores in the seeds. The biology, the spore formation, the spore morphology and the type of the spore germination show close relationships, and delimit the genus against other genera.

Many studies exist in literature regarding one or a few aspects of one or more *Schroeteria* species, partly with contradictory results, which make a critical revision of this genus necessary.

History

SCHRÖTER (1869) erected the new genus *Geminella* for *Thecaphora delastrina* TULASNE (1847), based on the spore morphology (spores in pairs), and on the peculiar kind of spore germination. The name of *Geminella* was, however, already used by TURPIN (1828) for an algal genus. WINTER (1881) therefore changed it to *Schroeteria*, in honour of the German mycologist JOSEPH SCHRÖTER (1837—1895). WINTER (1876) studied the vegetative mycelium, the spore formation and the germination of *Geminella* (= *Schroeteria*) *delastrina* on *Veronica arvensis*. He found the vegetative mycelium in the medullary parenchyma of the whole host plant, from the root to the top. This mycelium grows through the floral pedicel, placenta and funiculus into the seed where the spores are formed. WINTER illustrated also the germination of a single spore by a relatively short, branched, septate promycelium with 3 ovoid sporidia on the top of the longer branch. SCHRÖTER (1877) described in detail the spore germination of the smut on *V. arvensis* (*S. delastrina*) and on *V. hederifolia* (*S. decaisneana*), both called by him *Geminella decaisneana*. In

S. delastrina he found long, septate promycelia, often with short lateral branches, carrying apically ovoidal sporidia. *S. decaisneana* germinated by short, bottle-shaped, unseptate promycelia with apical, globose sporidia, often arranged in chains.

During this period confusion existed regarding the names and delimitations of the genera *Schizonella*, *Mycosyrinx*, *Geminella* (= *Schroeteria*), for which the sole common character is that the spores are usually in pairs. *Schizonella melanogramma* (DC.) SCHRÖTER was included in the genus *Geminella* by P. MAGNUS (1875). *Mycosyrinx cissi* (DC.) BECK was described by SCHRÖTER (1876) under the name *Geminella exotica* and by HENNINGS (1893) as *Schroeteria arabica*. DE TONI (1888) also transferred *Mycosyrinx cissi* to *Schroeteria*.

BREFELD (1883) studied and illustrated the spore germination in water of *Geminella delastrina*. Like SCHRÖTER, he found two kinds of promycelia: short, bottle-shaped, unseptate, and long, septate. Both types produced apically globose sporidia in chains. In nutrient solution the result was ramified mycelium without any formation of sporidia. Thickenings which divided and gave rise to filaments appeared in time on the mycelium. These filaments interwoved and produced sclerotium-like bodies, without fructifications. On this basis LINDAU (1912) doubted that the genus *Schroeteria* belonged to the Ustilaginales. In his opinion it could be an Ascomycete, it could also be placed in Hyphomycetes, but he still kept it among the Ustilaginales, „da man sie hier zu suchen gewöhnt ist" (because we are used to looking for it here).

The second species of *Schroeteria* on *Veronica* was described by BOUDIER (1887) as *Geminella decaisneana*, on *V. hederifolia*. COCCONI (1898) investigated the smut in the seeds of *Veronica ?praecox* and described it as a new variety: *S. delastrina* var. *reticulata*, having reticulate spores of 16—20 μm in diameter. The "reticulate" spores must be an inaccuracy in the description of the verrucose and ribbed spore surface, usual in this genus. The large spore measurements could either be an inaccuracy or could represent a different taxon. It is worth noting that DE TONI (1888) also gives *S. delastrina* such large spore measurements as 8—12 × 15—23 μm, not normal for this species. On decoction of the host plant COCCONI obtained good germination, resulting in simple or forked, unseptate promycelia, bearing apical, globose sporidia in chains. This fact proves that this variety is a true *Schroeteria*. ZUNDEL (1953) treated var. *reticulata* as a synonym of *S. delastrina*. The taxonomic position of this variety can only be solved with certainity by studying the type.

MAGNUS (1911) described a new species, *S. bornmuelleri*, in the seeds of *V. biloba* from Lebanon. FERDINANDSEN & WINGE (1914) as a rule found in the young spores of *S. decaisneana* two nuclei, in

10% three, and in c. 30% only one nucleus. LIRO (1938) listed all literature dates concerning *S. decaisneana* and *S. delastina* and also treated some of the biological and nomenclatorial aspects. PETRAK (1953) described *S. bremeri* on *Veronica ?triphyllos* from Turkey. VÁNKY (1964) studied, germinated and illustrated a *Schroeteria* sp. on *V. jaquinii*, reported at that time as *S. bornmuelleri*. THIRUMALACHAR (1966; pl. 2, fig. 2) unexpectedly obtained a typical *Ustilago* — like germination in *S. delastrina* on *V. praecox*, illustrated by 2—4-celled promycelia bearing lateral and terminal ovoidal sporidia. He concluded therefore that "All indications show that BREFELD's material which had formed chains of conidia had an endophytic Hyphomycete". Later THIRUMALACHAR & WHITEHEAD (1968) considered the globose sporidia in chains on the apex of promycelium as „beaded cells" produced by inadequate conditions. So far we do not know yet the reason for this kind of germination presented by THIRUMALACHAR. On the basis of this germination and the fact that the spores are often in pairs, THIRUMALACHAR & WHITEHEAD transferred *Schroeteria* to the genus *Schizonella*, with *S. melanogramma* (DC.) SCHRÖTER as type species (on leaves of different *Carex*). In connection with this transfer, I would like to cite SCHRÖTER (in COHN, 1877: 361) when he talked about *Geminella* (= *Schizonella*) *melanogramma*: „Durch die Sporenbildung sowohl als durch die Art der Keimung unterscheidet sich diese Ustilaginee so merklich von *Geminella* DELASTR., dass es unthunlich ist, sie mit dieser in dieselbe Gattung zu stellen; sie bietet ein deutliches Beispiel dafür, dass man auf die einseitige Kenntniss morphologischer Merkmale hin die systematische Stellung eines Brandpilzes nicht sicher bezeichnen kann." (We can add that there are also great differences in the sorus characteristics as well as in the spore morphology between these two genera which also motivate treating them separately).

Schroeteria WINTER 1881
in RABENHORST, Krypt. Fl. 1: 117

Geminella SCHRÖTER [1869: 5 (nom. praeocc., non TURPIN 1828: 329, q. e. Clorophyta-Ulotrichaceae)].

Type species: *S. delastrina* (TUL.) WINTER.

Sori in the seeds of Scrophulariaceae (*Veronica* spp.) forming a grey, greyish-blue or greyish-black, powdery spore mass. Infection systemic. Infected plants do not differ in appearance from healthy ones. Spores in pairs, in threes or single, formed by division of the spore mother cell, often easily separating into single spores. Germination of intermediate type and also variable, by bottle-shaped, short, one-celled promycelium, or by long, septate, often shortly ramified promycelium, apically and successively producing globose sporidia.

Key to the species of *Schroeteria*

1. Mature spores mostly in pairs or threes 2
1*. Mature spores mostly single 3
2. Spores coarsely verruculose and ribbed, 8—11(—13.5) µm long, often in pairs ..... (5) *S. delastrina*
2*. Spores finely verruculose and ribbed, 10—16 µm long, in pairs, in threes or in fours ..... (3) *S. bremeri*
3. Spore wall 1—2 µm thick, covered by coarse warts and polyangular, flat thickenings, spores 9—20 µm long .. (1) *S. banatica*
3*. Spore wall 0.5—1 µm thick, finely wrinkled, ribbed or verruculose, spores 7—16 µm long 4
4. Spores finely wrinkled or verruculose, light olivaceous-brown, 8—16 µm long. On *Veronica biloba* ..... (2) *S. bornmuelleri*
4*. Spores ribbed or finely verruculose, light yellowish-brown, 7—13 µm long. On *Veronica hederifolia.* ..... (4) *S. decaisneana*

1. *Schroeteria banatica* VÁNKY, sp. nov. — Fig. 1 A; fig. 3 A.

Typus: Matrix: *Veronica austriaca* L. subsp. *austriaca* (= *V. jacquinii* BAUMG.). — Romania: Banat: Mt. Domogled, pr. Băile Herculane (Herkules-fürdő), alt. 1100 m. s. m., 22. VII. 1962, leg. VÁNKY (BP, holotypus; HUV, Herb. Ustil. VÁNKY, isotypus).

Sori pulverulenti, in seminibus. Infectio matricis systemica. Sporae singulares, raro geminae, forma et magnitudine variae, globosae, ovoideae irregulariter rotundato-polygonales usque elongatae (globosae vel subglobosae 9—16 µm diam., elongatae usque ad 20 µm longae), hyalinae (parum flavotinctae) vel lenissime flavobrunneae; paris sporarum 1—2 µm cr., verrucis irregularibus et incrassationibus depressis polygonalibus magnitudine variis dense verrucosus. Germinatio regulariter per promycelia 5—9 µm longa, aseptata, lagunculiformia, apicaliter basidiosporas plures (8—22), globosas, parvas (2,8—3,1 µm), hyalinas ferentia.

Sori in the capsules replacing the seeds with a grey, powdery spore mass, liberated when the capsules split up. Infection systemic and usually all capsules of a host plant are infected.

Spores (Fig. 1, A, B) single, rarely in pairs, variable in form and size, globose, ovoid, rounded polyangularly irregular to elongated, 9—16 µm in diameter (when globose or subglobose), elongated spores up to 20 µm long, yellow tinted hyaline to very light yellowish-brown. Spore wall 1—2 µm thick, coarsely verruculose by irregular warts and polyangular, flat thickenings of variable size. At room temperature fresh spores germinate abundantly, after a week in water (Fig. 3A). Promycelium short, 5—9 µm, unseptate, bottle-shaped, or short, unseptate and in its distal part shortly branched, or seldom moderately elongated, septate. Sometimes one spore developed two promycelia

of the same or different kinds. Sporidia globose, small (2.8—3.1 μm), hyaline, numerous (8—22), produced successively on the top of the branches or the bottle-shaped promycelia, arranged in chains or in groups. Known from the type locality only.

2. *Schroeteria bornmuelleri* P. MAGNUS 1911. — Fig. 1, C, D.
Mitth. Thüring. Bot. Ver., N. S., 28: 64.

Schizonella bornmuelleri (P. MAGNUS) THIRUMALACHAR & WHITEHEAD 1968: 186.

Type on *Veronica biloba* L. — Syria (Lebanon): Mt. Dschebel Baruk, 1800 m, 15. VI. 1910, J. BORNMÜLLER (11208).

Sori in the seeds transforming them into a greyish-brown, powdery spore mass.

Spores (Fig. 1, C, D) single or sometimes in pairs, variable in form and size, globose, ovoid, pyriform or irregular, when in pairs flattened on the contact side. Globose or subglobose spores 8—14.5 μm in diameter, elongated ones up to 16 μm long, light olivaceous-brown. Spore wall 0.7—1 μm thick, finely verruculose or finely, densely, irregularly or parallelly wrinkled. Germination not studied. Known from the type locality and its vicinity: Syria: above Bscherre, 1925—2000 m, 3.—5. VII. 1910, J. & F. BORNMÜLLER (11234; !).

3. *Schroeteria bremeri* PETRAK 1953. — Fig. 2, A, B, C.
Sydowia 7: 14.

Type on *Veronica ?triphyllos* L. — Turkey: Harköyü, Elâziğ, 25. V. 1949, G. KAREL 109/49 (W; !).

Sori in the capsules destroying the seeds. Spore mass powdery, greyish-brown, liberated by the opening of the capsules.

Spores (Fig. 2, A, B) in twos or in threes, sometimes in fours, globose, hemispherical to irregular, flattened on the contact sides, 8—15×10—16 μm, light to medium olivaceous-brown. Spore wall about 1 μm thick, finely and densely verruculose or ribbed, often giving the spore surface a wrinkled aspect. Spore formation (Fig. 2C) in a relatively early stage was observed by us on the type material. Transversal walls appear in the hyaline, sporogenous hyphae of 6—7 μm diameter, which run parallel. The spore mother cells formed, become somewhat swollen (ab. 10 μm), the ends rounded and the walls thickened and ornamented. New transversal walls appear in each spore mother cell in a number of 1—3, and the young groups of 2—4 spores are separated easily by manipulation. The spore wall at this stage is the thickest with evident, irregular warts and ribs. During maturation the spores increase in diameter, the wall becomes yellow

to light brown and the spore wall and ornamentation thinner and finer. Germination unknown. Found in the type locality only.

Regarding spore measurements and spore ornamentation this species resembles *S. bornmuelleri*. It differs, however, by the fact that the spores are in groups of 2—4(—5), which does not seem to be a product of the grade of maturity. I prefer to keep it as a separate species.

4. *Schroeteria decaisneana* (Boudier) de Toni 1888. — Fig. 1, E, F; fig. 3 B.

in Saccardo, Syll. Fung. 7: 501.

Thecaphora decaisneana Boudier, 1886: 167 (nom. nudum).
Geminella decaisneana Boudier, 1887: 150.
Schizonella decaisneana (Boud.) Thirumalachar & Whitehead, 1968: 186.

Type on *Veronica hederifolia* L. — France: Dépt. Seine-et-Oise, Versailles, 1868, E. Decaisne (sel. by B. Lindeberg 1959: 59).

Sori in the seeds. At first the sporogenous hyphae appear in the placenta and hylum as a white mass which is later transformed into the light to dark grey, powdery mass of spores, replacing the placenta, endosperm emergence and almost the whole endosperm. The pericarp often remains intact. The seeds are attacked successively from the base of the shoots toward the apex, while the apparently healthy host produces new flowers. Usually all capsules of the host contain infected or destroyed seeds but sometimes one or more shoots may be healthy.

Spores (Fig. 1, E, F) usually produced in pairs within the sporogenous hyphae and often separating when mature, globose to slightly irregular, flattened on the contact side, 7—11×7—12 (—13) µm, light yellowish-brown to light olivaceous-brown. Spore wall thin (0.5—0.8 µm), finely verruculose or ribbed, provided with sparsely to moderate densely situated, irregular thickenings of different diameter, or elongated, sometimes forked ridges; this ornamentation structure runs more or less parallel to the long axis of the couples of spores. Abundant germination (Fig. 3B) of fresh spores (in tapwater, at room temperature, after 1—2 weeks) developed mostly short (5—10 µm), bottle-shaped promycelia with one or two short apical sterigmata on which the globose sporidia were produced successively in chains or in groups in a number of 4—16. Sometimes the promycelium was longer (15—20 µm), with or without lateral branch and transversal septa. One spore seldom produced two promycelia. Sporidia globose, 2.5—3.5 µm in diameter, hyaline, at first connected by a thin, short, hyaline bridge which disintegrated easily. On *Veronica hederifolia* L., Europe. Rather common but easily overlooked.

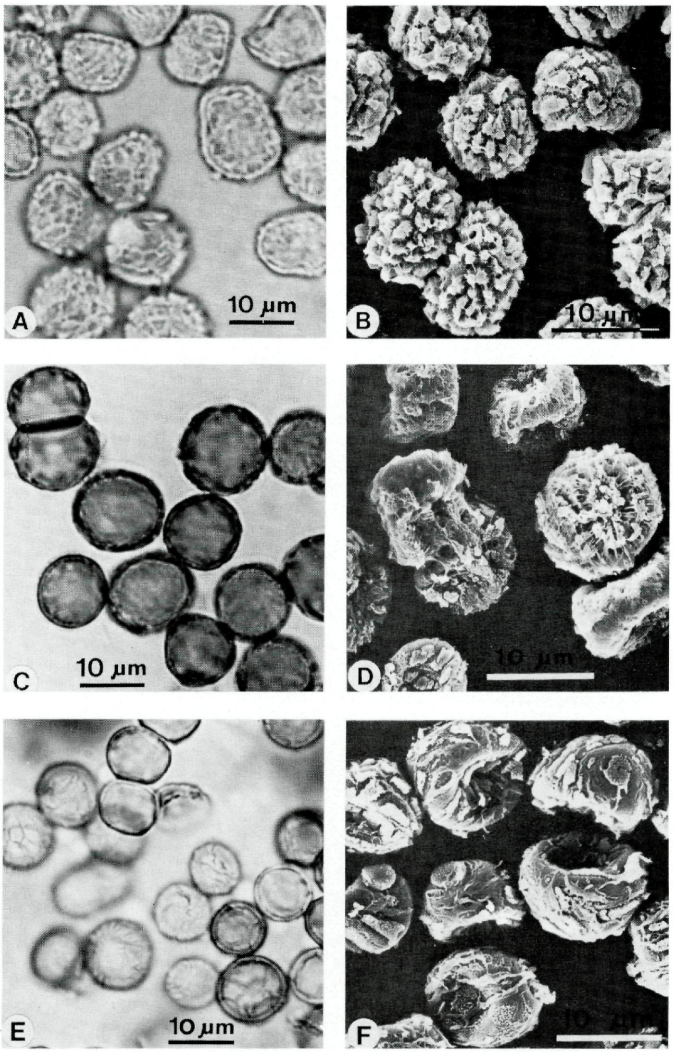

Fig. 1. A. Spores of *Schroeteria banatica* on *Veronica austriaca* (type) by LM, and B. by SEM. — C. Spores of *S. bornmuelleri* on *Veronica biloba* (Syria, Bscherre, 3.—5. VII. 1910, J. & F. Bornmüller) by LM, and D. by SEM. — E. Spores of *S. decaisneana* on *Veronica hederifolia* (Vánky, Ust. 227) by LM, and F. by SEM

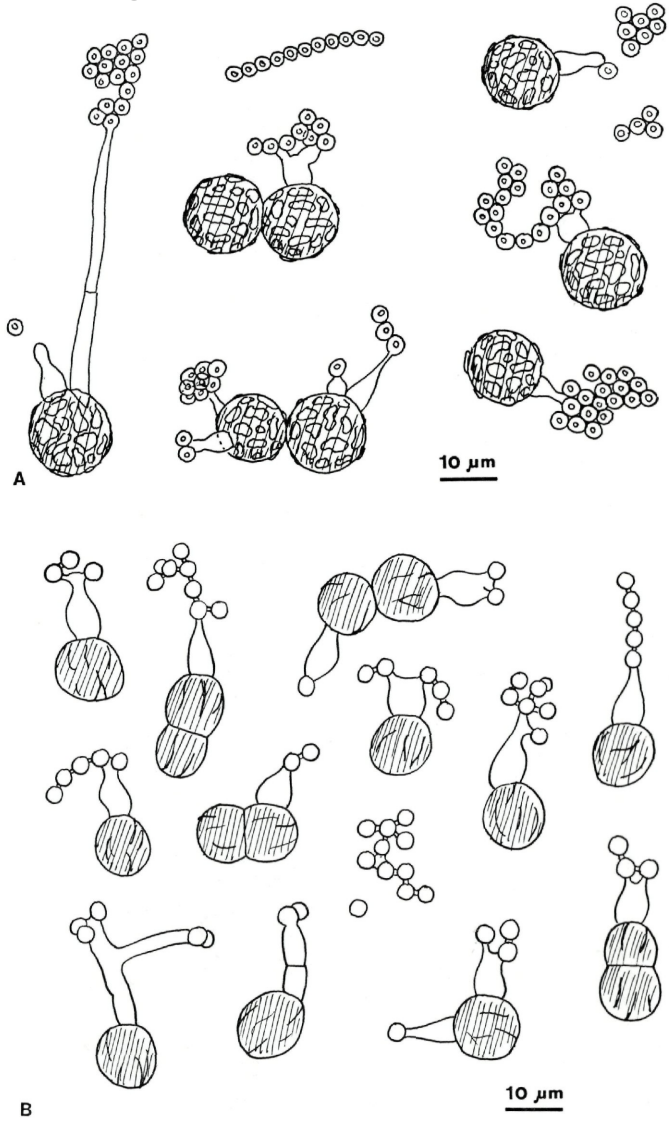

Fig. 3. Spore germination: A. *Schroeteria banatica* on *Veronica austriaca* (type). — B. *S. decaisneana* on *V. hederifolia* (VÁNKY, Ust. 27)

5. *Schroeteria delastrina* (TULASNE) WINTER 1881. — Fig. 2, D, E; fig. 4

in RABENHORST, Krypt. Fl. 1: 117.

Thecaphora delastrina TULASNE, 1847: 108.
Geminella delastrina (TUL.) SCHRÖTER, 1869: 5.
Schizonella delastrina (TUL.) THIRUMALACHAR & WHITEHEAD, 1968: 168

Type on *Veronica praecox* ALL. — France: Dépt. Vienne, Poitiers ("Pictavia"), DELASTRE.

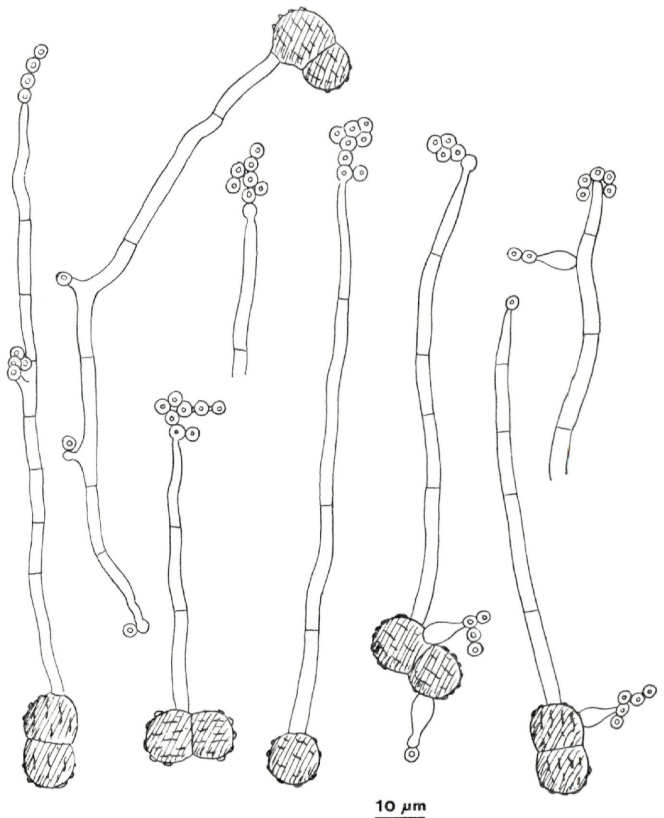

Fig. 4. Germinated spores of *Schroeteria delastrina* on *Veronica arvensis* (VÁNKY, Ust. 9)

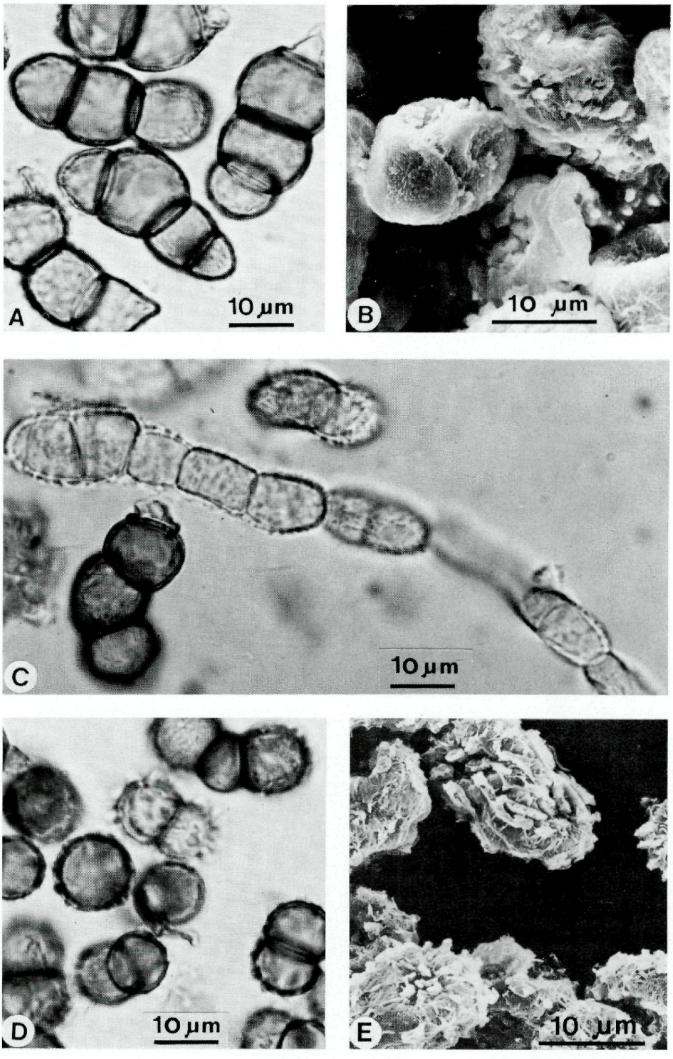

Fig. 2. A. Spores of *Schroeteria bremeri* on *Veronica ?triphyllos* (type) by LM, and B. by SEM. — C. Spore formation: sporogenous hypha with spore mother cells, each containing 2—3 young spores. — D. Spores of *S. delastrina* on *Veronica arvensis* (VÁNKY, Ust. 9) by LM, and E. by SEM

Sori in the seeds, destroying them completely and filling the capsules with a greyish-brown, powdery spore mass. Spores (Fig. 2, D, E) usually in pairs, sometimes in threes or single, globose, subglobose to irregular, flattened on the contact sides, 8—11(—13)× 8—11(—13,5) µm, light olivaceous-brown. Spore wall 0.5—1 µm thick, coarsely verruculose and ribbed, usually arranged in rows, provided with irregular warts or long ridges, running more or less parallel with the long axis of the former sporogenous mycelium. Fresh spores germinated abundantly (Fig. 4) (after a week, in tapwater, at room temperature), giving rise to 30—180 µm long, about 2,8 µm wide, multiseptate (2—9 celled) promycelia, often with short, lateral branches. Sometimes the promycelia were short, unseptate, bottle-shaped. Sporidia globose, about 3 µm wide, hyaline, born successively on the tops of the promycelia and branches in a number of 2—12. On different species of *Veronica*: *V. acinifolia* L., *V. agrestis* L., *V. arvensis* L., *V. praecox* All., *V. triphyllos* L. and *V. verna* L., in Europe, Asia and N. Africa. Not rare but easily overlooked.

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