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Mycosyrinx and other pair-spored Ustilaginales

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The revision of the genus *Mycosyrinx* resulted in the recognition of three species, all on Vitaceae: *M. cissi* (type on *Cissus sicyoides*), *M. arabica* (type on *Cissus quadrangularis*), and *M. microspora* (type on *Cissus afzelii*), and in the description of a new genus. After a short historical review, the genus *Mycosyrinx* is characterized and descriptions, synonyms, illustrations, and a key are given for the three recognized *Mycosyrinx* species. *Mycosyrinx globosa* (nomen nudum, on *Cissus* sp.) is considered to be immature *M. microspora*. Lectotype is selected for *Schizonella colemani* (= *M. arabica*). A short characterization is given for the genera *Schizonella* and *Ustacystis* and they are compared with *Mycosyrinx* and *Schroeteria*. For *M. nonveilleri* (type on *Triplochiton scleroxylon*, Sterculiaceae) a new genus, *Geminago*, is proposed. A key to the pair-spored genera of Ustilaginales is given. *Mycosyrinx osmundae* (type on *Osmunda regalis*, Pteridophyta, Osmundaceae) and its var. *cinnamomae* are excluded from *Mycosyrinx*.

Key Words——*Geminago*; *Geminago nonveilleri*; *Mycosyrinx*; taxonomy; Ustilaginales.

The genus *Mycosyrinx* was erected by Beck (1894; as "*Mykosyrinx*") for *Uredo cissi* DC., a smut fungus possessing spores in pairs. Two further genera with paired spores are: *Schroeteria* G. Winter (*Geminella* Schröter, not Turpin) and *Schizonella* Schröter, genera to which *Uredo cissi* was earlier attributed. Beck (1894), describing his new genus, demonstrated that the spore formation as well as the sorus structure of *Uredo cissi* are different from those of *Schroeteria* and *Schizonella*. Spore germination in these three genera is markedly different, but in Beck's time spore germination was only known for *Schroeteria* and *Schizonella*. The spore germination of *Schizonella melanogramma* (DC.) Schröter, the type of the genus, is of *Ustilago*-type (Brefeld, 1895; Ingold, 1992). The spore germination of *Schroeteria* is peculiar, not typical of Ustilaginales (comp. Vánky, 1968, 1981). The reason: *Schroeteria* is the anamorph of an ascomycete (Nagler et al., 1989; Vánky, 1994). Until recently, germination was known only for *M. nonveilleri* Zambettakis & Foko (Zambettakis and Foko, 1971; Ofong, 1978). The germination of *Mycosyrinx cissi* (DC.) G. Beck is unique (Piepenbring and Bauer, 1995) and completely different from that of *M. nonveilleri*. In the past, several new taxa were described under different specific and generic names, e.g., *Puccinia incarcerata* Léveillé (1845), *Geminella exotica* Schröter (1876), *Mycosyrinx osmundae* (Peck) Peck (1912), *Schroeteria cissi* var. *arabica* Hennings (1891), *Schizonella colemani* Iyengar & Narasimhan (1922), *Mycosyrinx microspora* Cantournet (1948). Viennot-Bourgin (1952) studied the genus *Mycosyrinx*. He recognized three species (*M. cissi*, *M. microspora*, *M. arabica*) and published (invalidly) an additional one, *M. globosa*. Zambettakis and Foko (1971) described *Mycosyrinx nonveilleri*, a highly interesting fungus, from the flowers of a tree, *Triplochiton scleroxylon*. These taxa were variously treated and synonymized by different authors, which is the reason why I have studied this group of fungi.

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Materials and Methods

For microscopical studies dried specimens were used. Light microscope (LM) with an oil immersion lens, at a magnification of 1000x was used for measurements and studies of spore morphology. For this purpose dried spores were soaked in lactophenol by gentle heating to the boiling point.

For studies of soral and ultrastructural characters, dried sori were rehydrated, fixed in 2% glutaraldehyde in 0.1 M Na-cacodylate buffer at pH 7.2 for several days. After six transfers in 0.1 M Na-cacodylate buffer, the material was postfixed in 1% osmium tetroxide in the same buffer for 1 h in the dark, washed in distilled water, and stained in 1% aqueous uranyl acetate for 1 h in the dark. After five washes in distilled water, the material was dehydrated in acetone series, embedded in Spurr's plastic and sectioned with a diamond knife. For studies of the sorus structure, 0.5 μm thick sections were prepared and stained with new fuchsin–crystal violet, mounted in "Entellan" and studied under a light microscope. For transmission electronmicroscopic (TEM) studies, ultra-thin sections were mounted on copper slot grids, post-stained with lead citrate for 5 min, and examined in a TEM at 80 kV.

For scanning electron microscopic (SEM) studies, dried spores were dusted on double-sided adhesive tape, mounted on specimen stub, sputter-coated with gold-palladium, ca. 20 nm, and examined in a SEM at 10 kV.

For the study of germination, freshly collected, completely mature spores were spread thinly on water agar (WA) in Petri dishes kept at room temperature (ca. 22°C) and at 30°C. When basidiospores were produced (after ca. 4 d), a suitable piece of medium (about 10 mm square) was cut out, transferred to a slide and covered with a coverglass. A small droplet of lactophenol with cotton blue added to the side of the square of medium, fixed and stained the basidiospores.

Results and Discussion

Studies of the sorus structure, spore morphology, spore germination and ultrastructure of species of *Mycosyrinx*, completed with data from the literature, resulted in the recognition of three species of *Mycosyrinx*, all on *Cissus* spp. (Vitaceae). The species are described and illustrated, and a key is constructed. *Mycosyrinx nonveilleri* (type on *Triplochiton scleroxylon* K. Schum., Sterculiaceae) shows several characters markedly different from those of *Mycosyrinx*, and a new genus, *Geminago* K. Vánky & R. Bauer, is proposed for it. *Mycosyrinx osmundae* (type on *Osmunda regalis* L., Pteridophyta, Osmundaceae) and its var. *cinnamomae* Peck are excluded from the genus *Mycosyrinx*. Work is going on to elucidate their generic position.

Mycosyrinx G. Beck, Ann. K. K. Naturhist. Hofmus. **9**: 123+Pls. II-III. 1894 (as "*Mykosyrinx*").

Sori in strongly deformed, ramified host tissues forming witches' brooms. Spores powdery, dark colored, in pairs, more or less hemispherical, connected on their flattened sides. Spore germination of *Mycosyrinx*-type. Mycelia intercellular. Septal pore structure is of *Ustilago*-type. Typus generis: *M. cissi* (DC.) G. Beck.

Three species of *Mycosyrinx* are recognized, all on *Cissus* species (Vitaceae).

Mycosyrinx cissi (DC.) G. Beck, Ann. K. K. Naturhist. Hofmus. **9**: 123+Pls. II-III. 1894.

Uredo cissi De Candolle, in Poiret, 1808 (as "*cyssi*"). — *Ustilago? cissi* (DC.) L.-R. Tulasne & C. Tulasne, 1847. — *Schroeteria cissi* (DC.) de Toni, in Saccardo, 1888. — *Geminella exotica* var. *de candollei* Fischer v. Waldheim, 1877a (nomen novum illegit.). — Type on *Cissus sicyoides* L., Island of Saint Dominique (Dominican Republic), coll. P. A. Poiteau.

Puccinia incarcerata Léveillé, 1845.—Type on *Cissus* sp., Guyana, coll. P. A. Poiteau.

Geminella exotica Schröter, 1876. — Type on *Cissus sicyoides* L., Brazil, Parà Prov., collected in September by C. F. Ph. von Martius (M!).

Sori (Fig. 1) in the distal, cylindrical, swollen part of the branches of up to 1 m or longer, hanging, repeatedly branching witches' brooms. Single sori cylindrical, 1-2×5-30 mm, first green, later brown, composed of an outer layer of host tissues and an inner, whitish layer of hyphae producing paired spores which fill the interior of the tubes (Fig. 2). At maturity, the sori split longitudinally disclosing the black, powdery mass of spores. Spores (Figs. 3, 4) in pairs arising from the division of the spore mother cell, connected on the middle of their flattened or, in rehydrated spores, slightly conical sides. Single spores in side view subhemispherical or subhemiellipsoidal, 7-8.5(-9)μm wide, in face view rounded or elliptical, 9.5-12.5×10.5-13.5 μm, dark reddish brown; wall ca. 1 μm thick, free surface minutely and densely punctate-verruculose, facing surface smooth. In LM, the two surfaces are delimited by a sharp, often slightly protruding line. Sectioned spores in TEM (Fig. 5) show an electron dense area of the median part of the facing walls, at the place where the spore pairs are connected. At the transition between the flattened and hemispherical part of the spore wall, a narrow, electron-transparent channel is seen, the sectioned germ ring. The parasitic hyphae are intercellular, septate (Fig. 6). The septal pore (Fig. 7) is of *Ustilago*-type; a septum with a moreorless closed, micropore-like channel. Spore germination (Fig. 8; on WA, at room temp., in 4 d) results in up to four (rarely 5 or 6), peculiar and unique, bent basidiospores produced successively on very short, pedicel-like basidia or directly from the spores (comp. also Piepenbring, 1994; Piepenbring and Bauer, 1995). The spores split at the line between the flat and hemispherical side and up to 20 μm long basidiospore initials grow out. The distal part of the basidiospore initials swells up (2.5 μm), bends strongly back and their tip becomes subacute. In this stage, the young basidiospores look like the neck and head of a swan. During maturation, the proximal part of the basidiospores becomes thinner and may detach from the spores, leaving behind a short pedicel (=? basidium) or not, or the basidiospores may remain attached to the spores. The mature basidiospores are more or less strongly bent with an evidently swollen, asymmetrical part and two subacute ends, measuring 1.5-2.5×14-20 μm. Rarely, concomitantly with production of typical basidiospores, long hyphae may result from spore germination.

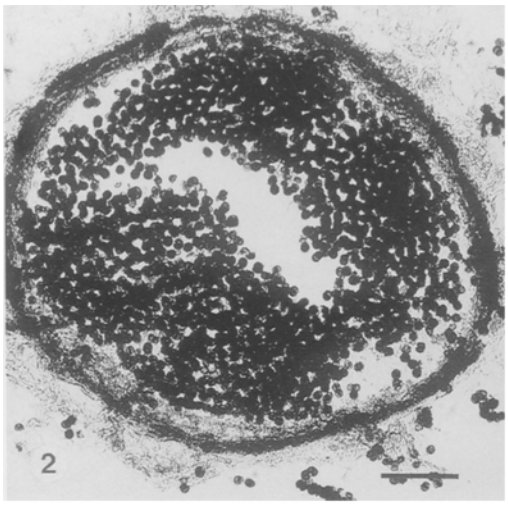
On Vitaceae: *Cissus acida* L., *C. erosa* Rich., *C. rhombifolia* Vahl., *C. sicyoides* L., *C. trifoliata* L., *Cissus* sp., southern North America, Central and South America, Africa (?).

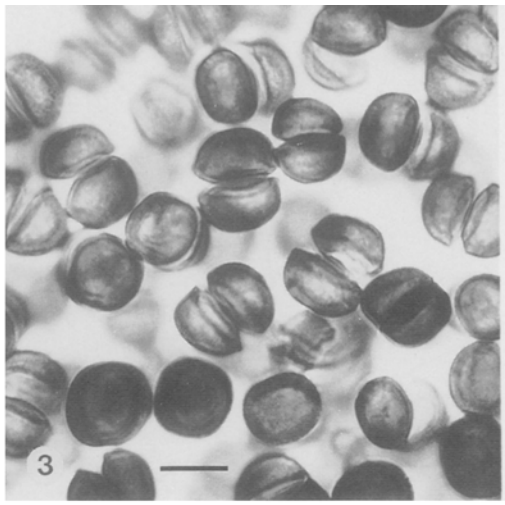
Schröter (1876), in the short description of his *Geminella exotica* n. sp., mentions as host plant *Cissus sicyoides*, collected in Brazil by Martius, preserved in M as *Puccinia*. In M there are three collection of this fungus made by Martius in Brazil. One of these is provided with a hand-written label of Schröter mentioning that it is no *Puccinia* but *Ustilago* (*Geminella*). This collection from Brazil, State of Pará, collected in September, is considered to be the type of *Geminella exotica*.

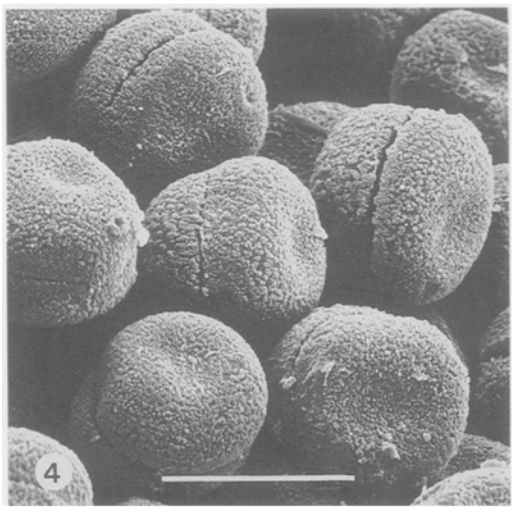
There is no consensus about the origin of the host plant tissues in which the sori develop. Léveillé (1845) and Cornu (1883) considered the sori to be localized in deformed leaf petioles, probably because some specimens (e.g. in the type of *Geminella exotica*, seen by me)

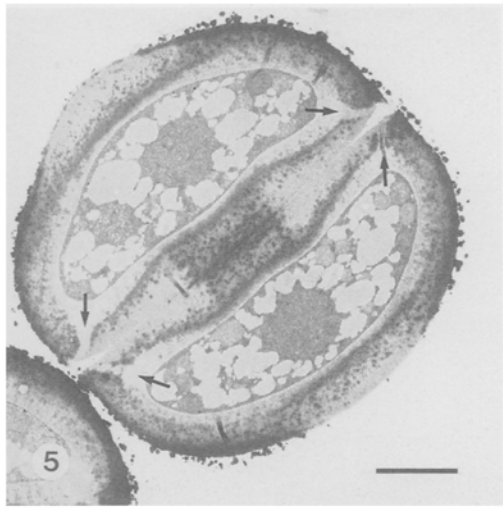
Fig. 1. *Mycosyrinx cissi* (DC.) G. Beck on *Cissus sicyoides* L. Healthy plant and a small part of a ca. 1 m long, repeatedly ramifying witches' broom, with tubular sori on short pedicels (Vánky, Ust. exs. No. 835). Bar = 1 cm.

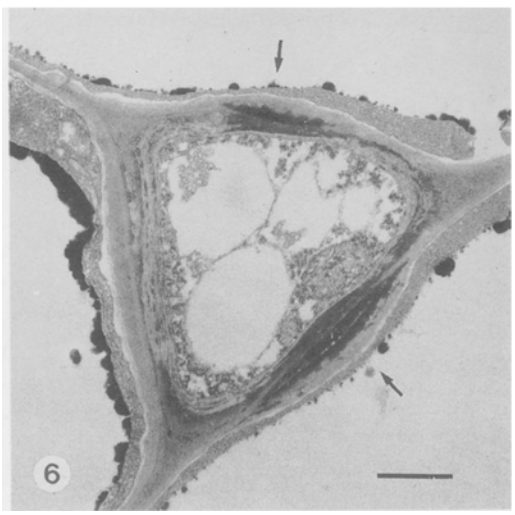
have rudimentary leaves on the top of soral branches. Sori were attributed to fruits by Fischer v. Waldheim (1877b) and by Poiret (quoted by L.-R. and C. Tulasne, 1847). According to Beck (1894) and Vánky (1987), the sori are modified, deformed floral pedicels. Viennot-Bourgin (1952), from the literature and his own research, concluded that witches' brooms produced by *M. cissi* are strongly modified inflorescences, whereas the witches' brooms produced by *M. arabica* originate from vegetative tissues (shoots) of the host plant. Viennot-Bourgin (1952) had seen an infected *Cissus producta* Afzel, from Ivory Coast, showing sori not only in the shape of an

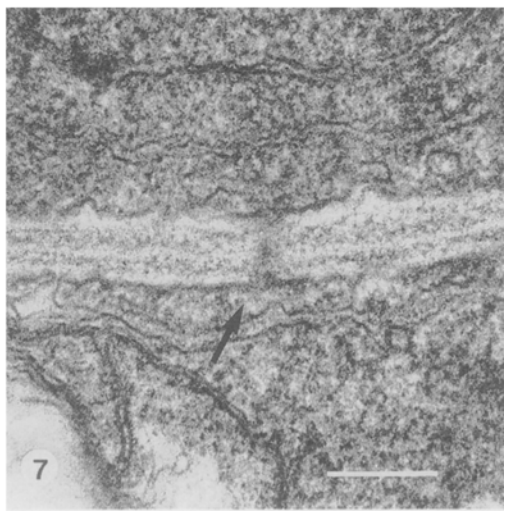












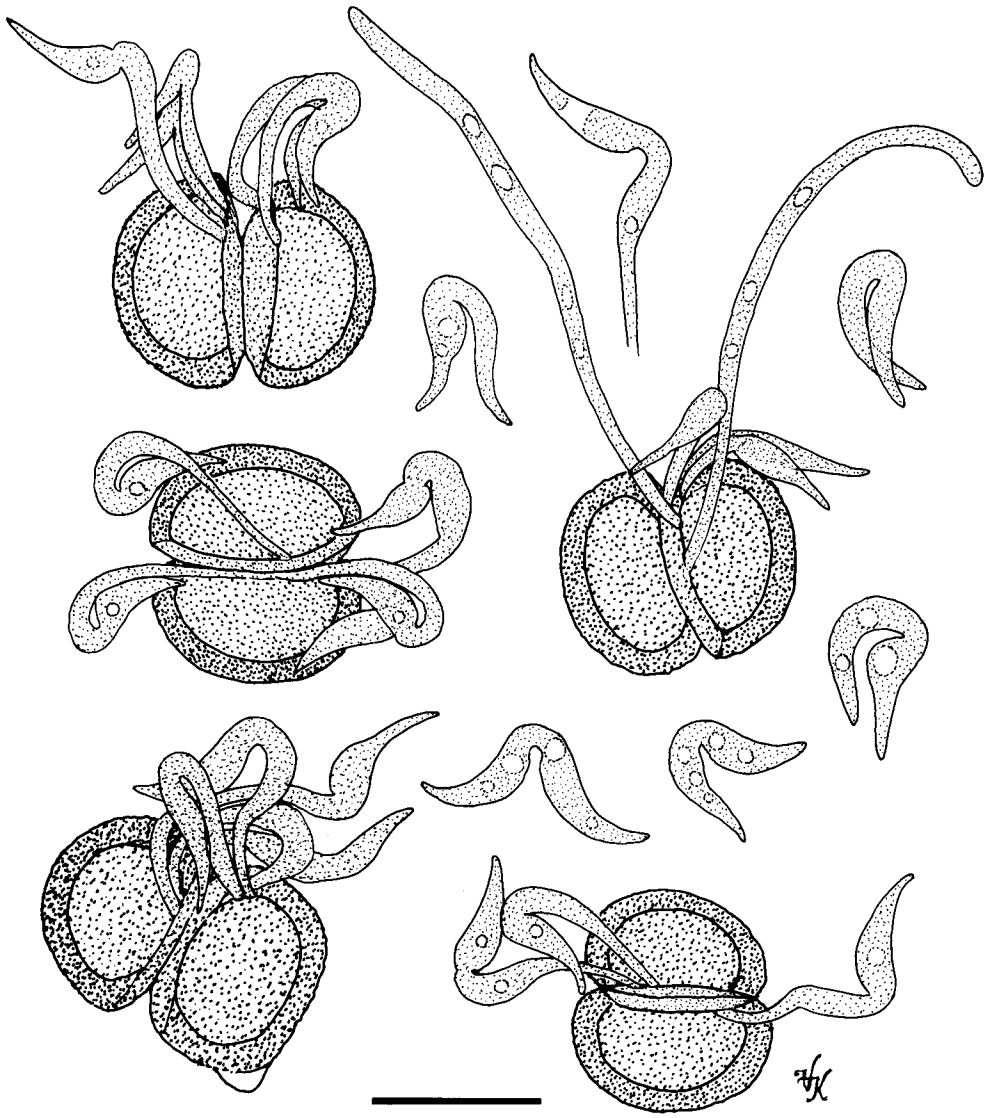


Fig. 8. Germinating spores of *Mycosyrinx cissi* (DC.) G. Beck on *Cissus sicyoides* L. (Costa Rica, Cartago Prov., near Monumento Nacional Guayabo, 2.I.1994, coll. M. Piepenbring 1017, germinated by R. Bauer; HUV 16014). Bar = 10 μm.

inflorescence but also with some rudimentary flowers. In the opinion of Piepenbring (1994), the witches' brooms of *M. cissi* are modified vegetative shoots. These conflicting reports suggest that host organ specificity may be low and the fungus may invade buds of both shoots and inflorescences, producing witches' brooms and sori in either.

According to Beck (1894), the parasitic hyphae are septate, with short, one- to several-celled, simple haustoria. The spores are formed either on the top and on short, lateral branches of the sporogenous hyphae, or the cells of the sporogenous hyphae are transformed into a chain of spore pairs. The presence of haustoria could not be confirmed (Dr. R. Bauer, pers. comm.). Piepenbr-

Fig. 2. Transverse section of a mature sorus of *Mycosyrinx cissi* (DC.) G. Beck on *Cissus sicyoides* L. (USA, Florida, Okeechobee Co., N. of Fort Drum, 19.II.1950, coll. D. Blake, det. E. West; HUV 1445) showing the (dark colored) ring of host tissue and the internal space filled by spore mass. Bar = 100 μm.

Figs. 3, 4. *Mycosyrinx cissi* (DC.) G. Beck on *Cissus* sp. Spores in LM and in SEM, showing the spores in pairs connected on their flattened sides (Crypt. exs. Vindob. No. 11; HUV 1441). Bars = 10 μm.

Figs. 5–7. *Mycosyrinx cissi* (DC.) G. Beck on *Cissus sicyoides* L. in TEM (Vánky, Ust. exs. No. 835; HUV 15194).

5. Sectioned pair of spores connected on the median part of their contact walls, where the wall is electron-dense. Note the sectioned germ ring (arrows) at the transitional area between the contact and free part of the spore wall. Bar = 2 μm.

6. Transverse section of an intercellular hypha between three host cells. In two places (arrows) evident traces of interaction between the parasitic hypha and the host cells can be seen. Bar = 1 μm.

7. Septal pore is of *Ustilago*-type: septum with a more or less closed micropore-like channel (arrow). Bar = 0.2 μm.

ing (1994) and Beck (1894) provide conflicting descriptions and illustrations of spore building. According to Piepenbring, sporogenous hyphae produce small spore initials separated by and embedded in a gelatinous matrix. These spore initials may divide several times into smaller pieces and are pushed toward the center of the sorus. The middle or one side of these elongated pieces swells up, and a transversal wall divides the piece into two cells, each with one or two short appendages which later disappear. The paired spore initials enlarge, become pigmented and develop into spore pairs.

Only one of several *Mycosyrinx* collections from Cos-

Fig. 9. Sori of *Mycosyrinx arabica* (Hennings) Penzig on *Cissus quadrangularis* L. (Type of *Schizonella colemani*; reproduced from Iyengar and Narasimhan, 1922).

ta Rica germinated. This sample of fully mature spores was taken from *Cissus* branches with most sori opened and partly emptied. Spores germinated equally well whether they were kept at room temperature or at 30°C. Spores were viable and still germinated after 14 mo.

As a curiosity, it can be mentioned that samples of *Cissus sicyoides* L. infected by *Mycosyrinx* were described in 1831 as a new genus and species of Onagraceae under the name of *Spondylantha aphylla* K. B. Presl (as "*Sphondylantha*").

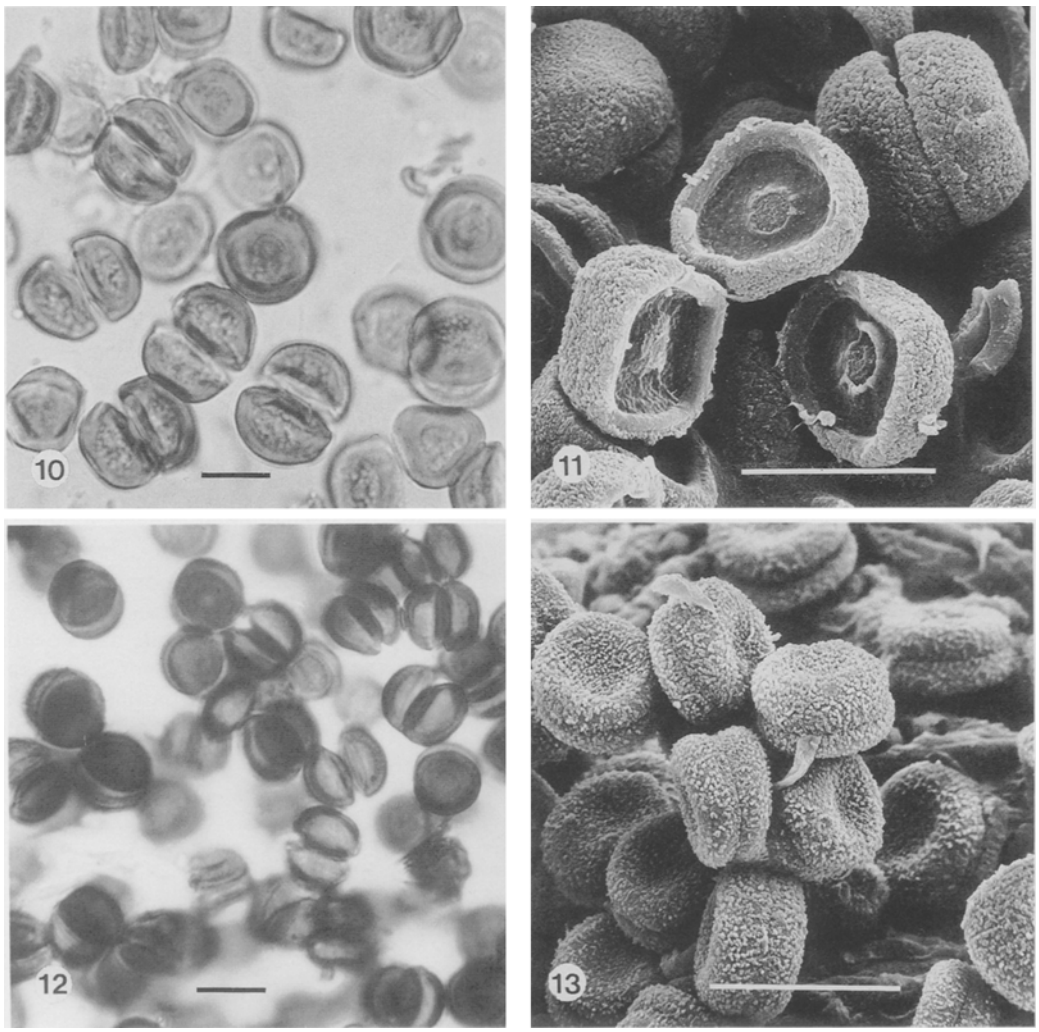
Hennings (in Engler, 1895) described *Schroeteria cissi* (DC.) de Toni var. *usambarensis* Hennings on *Cissus* sp. from tropical Africa (as "tropical America"). According to Hennings, the variety differs from *Schroeteria cissi* by having much thicker branches of the witches' brooms and somewhat larger spores. Probably it belongs to *Mycosyrinx cissi*, but a final conclusion can be drawn only after examination of the type material.

Mycosyrinx arabica (Hennings) Penzig, Malpighia **13**: 530. 1899.

Schroeteria cissi (DC.) de Toni var. *arabica* Hennings, 1891.—*Schroeteria arabica* (Henn.) Hennings, 1893.—Type on *Cissus quadrangularis* L., Arabia, Yemen, near Uossil, alt. 1400 m, 1889, G. Schweinfurth.

Schizonella colemani Iyengar & Narasimhan, 1922.—Lectotype on *Vitis quadrangularis* (L.) Wall. (=*Cissus quadrangularis* L.), India, near Madras (selected here) Vandalur, coll. M. O. P. Iyengar and M. N. Narasimhan (BPI189952!).

Sori (Fig. 9) in more or less globoid witches' brooms at the nodes of the host plant, as a result of repeatedly, irregularly branching host tissues (modified shoots?) which do not resemble any part of the healthy host plant. On the branches shorter or longer, bullate pustules contain the blackish-brown, powdery mass of spores. The pustules partly or completely surround branches which are pale green in color with a reddish tinge towards the end of the branches. Spores (Figs. 10, 11) borne in pairs, connected by a short bridge. Spores separate if



Figs. 10, 11. Spores of *Mycosyrinx arabica* (Hennings) Penzig on *Cissus quadrangularis* L. in LM and in SEM (type of *Schizonella colemani*; BPI189952). Bars=10 μm.

Figs. 12, 13. Spores of *Mycosyrinx microspora* Cantournet on *Cissus afzelii* G. & Br. in LM and in SEM (isotype; HUV 14982). Bars=10 μm.

the bridge ruptures. Spores in side view hemispherical or elongate, 7.5-10 μm wide, in face view rounded or elliptical to slightly irregular, 11.5-14.5 × 12.5-15(-16) μm, yellowish brown; wall 1.5-3 μm thick, in LM smooth to very finely and densely punctate. Germination unknown.

On Vitaceae: *Cissus quadrangularis* L. (*Vitis quadrangularis* (L.) Wall.), Arabia (Yemen) and India.

Mycosyrinx microspora Cantournet, Bull. Soc. Mycol. France **64**: 167. 1948.

Type on *Cissus afzelii* G. & Br., Central African Rep., Oubangui, Yalinga, without date, coll. G. M. P. C. le Testu, Mission scientifique Africaine No. 2977 (PC, isotype HUV 14982!).

Sori, spore mass and spores (Figs. 12, 13) as in *M. cissi*, differing only in the spore measurements, which for single spores of *M. microspora* are: in side view 5-7 μm wide, in face view 8-10.5 × 8-12 μm. Germination unknown.

On Vitaceae: *Cissus afzelii* G. & Br., *C. diffusiflora* Planche, *C. producta* Afzel, and *Cissus* sp., Central Africa, S. America (?).

Mycosyrinx globosa Viennot-Bourgin, Rev. Int. Bot. Appl. Agric. Trop. **33**: 264. 1952.

Mycosyrinx globosa was invalidly published (ICBN 36.1, nomen nudum, without Latin description). I have seen the specimen, mentioned by Viennot-Bourgin in his description, on *Cissus* sp., France Congo, 13.IX.1902, A. Chevalier, Mission Chari, Lac Tchad (PC!). The spore pairs are more or less globoid and sole spores are 9-11 μm long, finely and densely verruculose. In my opinion, this specimen, and some additional specimens, considered by Viennot-Bourgin to be *M. globosa*, are in fact somewhat immature spores of *M. microspora*, in which the spore pairs are still connected on the whole surface of their flattened sides. I also observed this phenomenon in some immature samples of *M. cissi*. On the other hand, a few spore pairs in the above-mentioned specimen of *M. globosa* were less closely connected, typical for *M. microspora*.

Key to the recognized *Mycosyrinx* species

1. Sori as tubes on the distal part of ramified branches. Spores dark brown 2
— Sori as pustules on ramified branches. Spores yellowish-brown ..... *M. arabica*
2. Single spores 10.5-13.5 μm long. ..... *M. cissi*
— Single spores 8-12 μm long ..... *M. microspora*

The paired spores of *Mycosyrinx* resemble (superficially) the paired spores of *Schroeteria* Winter, *Schizonella* Schröter, and somewhat also those of *Ustacystis* Zundel. On the basis of this resemblance, several fungi were placed by earlier mycologists in one or another of these genera. This morphological resemblance, however, does not reflect a relationship between these genera, as can be demonstrated, i.a., by the spore germination. This is so different that there is no doubt that there are four distinct genera. Moreover, it was demonstrated that *Schroeteria delastrina* (L.-R. & C. Tul.) Winter and *S. poeltii* K. Vánky are ascomycetes (Nagler et al., 1989), and the genus *Schroeteria* with its six known species was excluded from the smut fungi by Vánky (1994).

The genus *Schizonella* Schröter (in Cohn, 1877) is characterized by sori in the leaves and stems of Cyperaceae, forming black, short or long, sometimes confluent, pustulate, intraepidermal streaks with agglutinated to semiagglutinated spore masses. Spores in pairs, arising by internal division of a spore mother cell, sometimes separating into single spores, sometimes (in *S. cocconii* (Morini) Liro) agglutinated into larger, irregular balls. Germination of *Ustilago*-type. Typus generis: *S. melanogramma* (DC.) Schröter, lectotype on *Carex digitata* L., France, Jura, coll. J. F. de Chaillet. Four species of *Schizonella* are known.

The genus *Ustacystis* Zundel (1945a, b) is characterized by swollen sori in the leaf-veins of Rosaceae. At maturity, these split longitudinally, exposing the semiagglutinated to powdery, blackish-brown spore mass. Spores single, in pairs or in indefinite, loose, few-spored balls. Germination of *Ustacystis*-type: two-celled basidia produce large, dikaryotic basidiospores, dikaryotic hyphae, or both. Usually either one basidiospore or one hypha is produced per basidial cell, either lateral or one lateral and one terminal. Typus generis: *U. wal-*

Table 1. The main differenciating characters of the genera *Mycosyrinx*, *Schizonella* and *Ustacystis*.

	Mycosyrinx	*Schizonella*	*Ustacystis*
Sori	in cavities	intraepidermal	intratracheal
Spore mass	powdery	semi-agglutinated	semi-agglutinated to powdery
Spores	in pairs	in pairs (or in groups)	single, in pairs or in small groups
Germination	*Mycosyrinx*-type	*Ustilago*-type	*Ustacystis*-type
Septal pore	*Ustilago*-type	*Ustilago*-type	*Urocystis*-type
Host plants	Dicot: Vitaceae	Monocot: Cyperaceae	Dicot: Rosaceae

dsteiniae (Peck) Zundel, type on *Waldsteinia fragarioides* (Michx.) Tratt., USA, New York, Albany Co., Alcove, VI.1892, C. L. Shear. *Ustacystis* is a monotypic genus.

The main characters of and differences between *Mycosyrinx*, *Schizonella* and *Ustacystis* are presented in Table 1.

A peculiar fungus was collected in Cameroon by the entomologist G. Nonveiller, looking for insect galls in the deformed flowers of *Triplochiton scleroxylon* K. Schum. (Sterculiaceae or Triplochitonaceae), a large tree, rather frequent in deciduous forests of Central Africa. The samples were studied by Zambettakis and Foko (1971) and described as *Mycosyrinx nonveilleri*. The fungus infects the flowers producing considerable hypertrophy and deformation of all floral elements. The spores are in pairs. They develop in small cavities superficially embedded in the host tissues. These characters, the hypertrophy of the host tissues, and paired spores which develop within the host tissues, are good characters for a *Mycosyrinx* species. However, the spore germination results in a septate, ramified "promycelium" (basidium) composed of a variable number of cells on which lateral chains or groups of ovoid or elongated, brown "sporidia" (basidiospores) are produced (Zambettakis and Foko, 1971; Ofong, 1978). This *Ustilago*-type of germination excludes *M. nonveilleri* from the genus *Mycosyrinx*, which seems to be restricted to host plants belonging to the Vitaceae family. Brown colored basidiospores are not typical for Ustilaginales and I suspected that *M. nonveilleri* could belong to another major group of fungi. The study of the ultrastructure of the type specimen revealed the presence of many-layered hyphal walls, typical for basidiomycetes (Dr. R. Bauer). Because this fungus cannot be included in any known genus, a new genus is

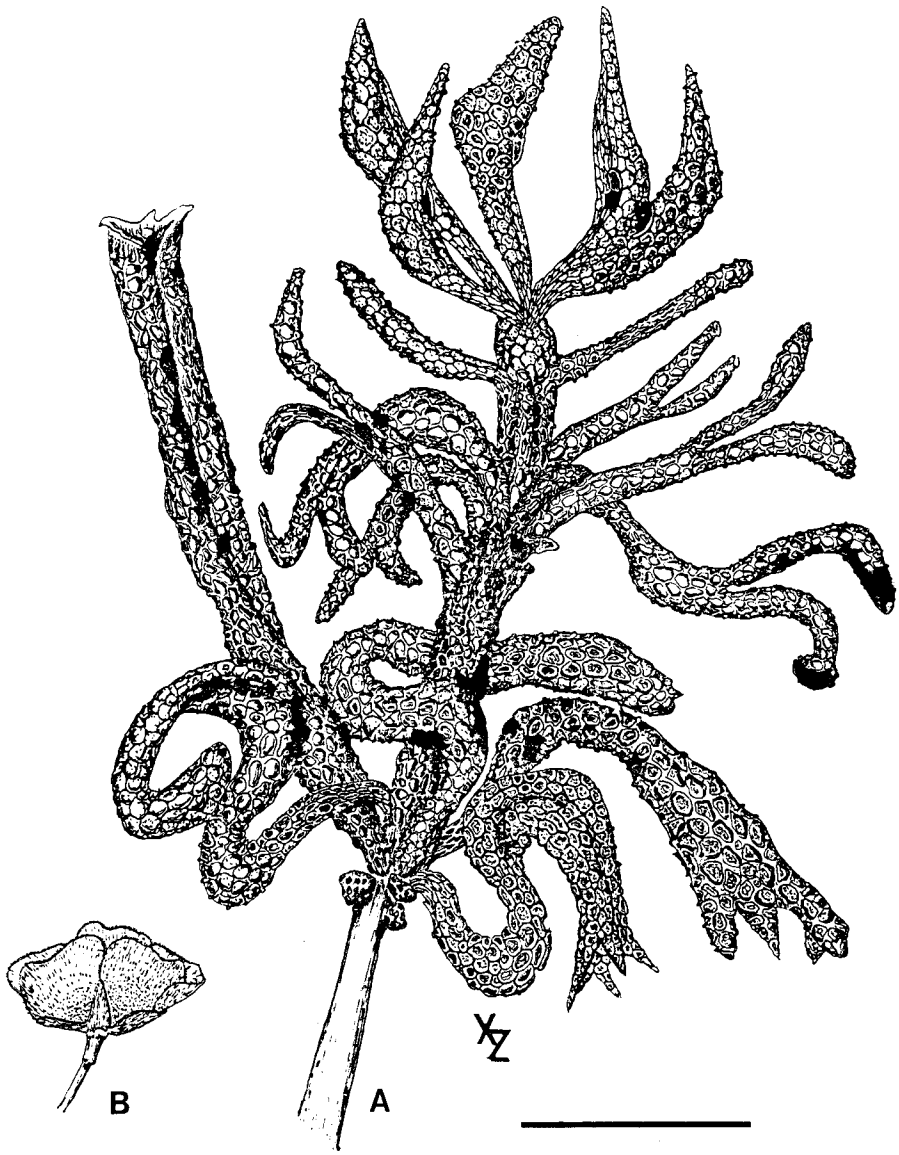
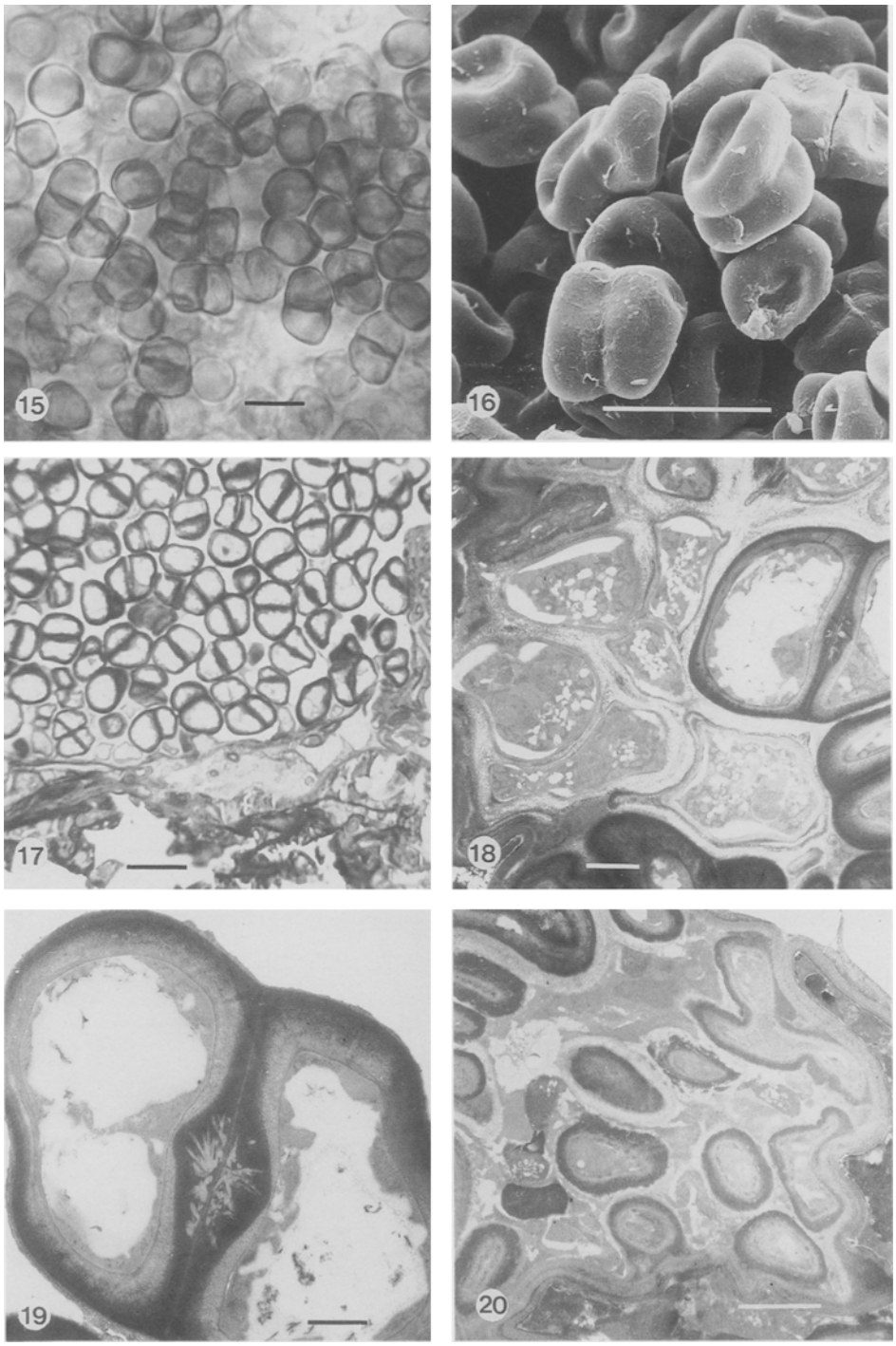


Fig. 14. A. Sori of *Geminago nonveilleri* (Zambettakis & Foko) K. Vánky & R. Bauer in a hypertrophied and strongly deformed flower of *Triplochiton scleroxylon* K. Schum. B. A healthy flower (type; reproduced from Zambettakis and Foko, 1971, by zerox on the author's responsibility). Bar = 5 cm.

proposed for it:

Geminago K. Vánky & R. Bauer, gen. nov.

Sori in cavis telarum matricis per hypertrophiam tumefactarum. Massa sporarum atra, pulverea. Sporae binae, coloratae. Germinatio sporarum et struc-



Figs. 15-20. *Geminago nonveilleri* (Zambettakis & Foko) K. Vánky & R. Bauer (isotype; HUV 1449).
15, 16. Spores in LM and in SEM. Bars = 10 μm.
17, 18. Transverse section through the basal part of a sorus in LM and in TEM with pairs of spores in different developmental stages. Bars = 10 μm and 2 μm.
19. Ultrathin section of pair of spores. The outer, electron-dense layer of the spore walls is considerably thickened towards the center of the adhering surface and shows a peculiar, irregular, radial pattern of medium electron density. Bar = 1 μm.
20. Intracellular hyphae in TEM. Bar = 2 μm.

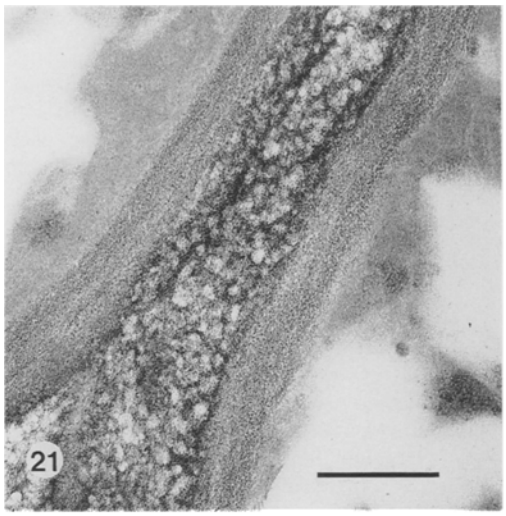
tura pori septorum secundum "*Ustilago*-typum."

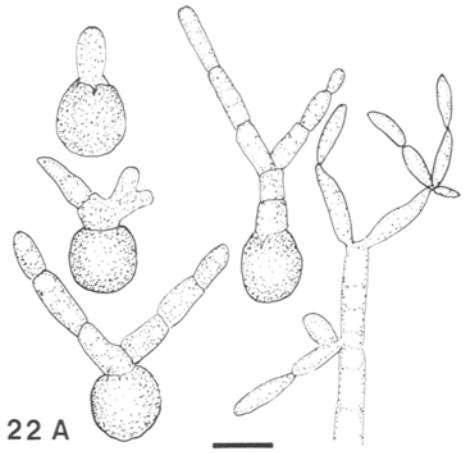
Sori in cavities of hypertrophied host tissues. Spore mass dark, powdery. Spores in pairs, pigmented. Spore germination and septal pore structure of *Ustilago*-type. Typus generis: *Geminago nonveilleri* (Zambettakis & Foko) K. Vánky & R. Bauer.

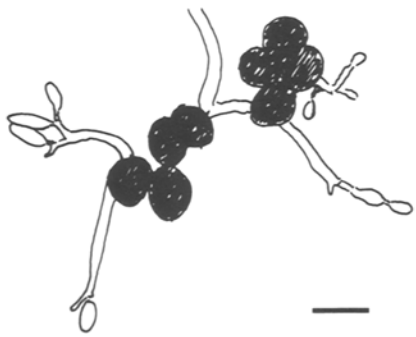
Geminago nonveilleri (Zambettakis & Foko) K. Vánky & R. Bauer, comb. nov.

Basionym: *Mycosyrinx nonveilleri* Zambettakis & Foko, Rev. Mycol. (Paris) **35**: 304. 1971.—Type on *Triplochiton scleroxylon* K. Schum., Central Africa, Cameroon, Yaoundé, 1970, G. Nonveiller (PC, isotype in HUV 1449!).

Sori (Fig. 14) in all floral parts which are considerably hypertrophied and deformed, with dark brown, semi-powdery spore masses produced centripetally in globoid, ovoid or irregular cavities of 1–2 × 1.5–4 mm, more or less superficially embedded in the host tissue which later ruptures disclosing the spores. With maturation the sorus surface becomes spotted, first by a few, scattered, blackish brown dots, the opened cavities. These are lined by sporogenous hyphae and filled by spores. Later the spots increase in number giving the sorus surface a peculiar, alveolar pattern, resembling an irregular honeycomb. The floral bud is susceptible to direct infection (Zambettakis and Foko, 1971). Spores (Figs. 15–19) in pairs, adhering side by side on the whole flattened surface of the spores, later they may separate partially or completely. Single spores in side view hemispherical or somewhat irregular with a flattened side, 5–7(–8) μm wide, in face view rounded or slightly irregular, 7–9.5 × 7–10.5 μm, olivaceous-brown; wall uneven, 1–2 μm thick, smooth. In TEM (Figs. 17–19) the paired spores are tightly adhering. The outer, electron-dense layer of the spore wall is considerably thickened towards the centre of the adhering surface and shows a peculiar, irregular, radial pattern of medium electron density. The







22 B

Fig. 21. *Geminago nonveilleri* (Zambettakis & Foko) K. Vánky & R. Bauer (isotype; HUV 1449). Part of two hyphae with finely layered, fibrillar wall structure, typical for basidiomycetes. The space between the hyphae is filled with a mucous substance of foamy structure. Bar = 1 μm.

Figs. 22. A, B. Germinating spores of *Geminago nonveilleri* (A. after Zambettakis and Foko, 1971; B. after Ofong, 1978). Bars = 10 μm.

hyphae are intracellular (Fig. 20). The hyphal wall has a finely layered, fibrillar structure (Fig. 21) indicating also that the fungus is a basidiomycete. Spore germination (Figs. 22 A, B) results in septate, ramified "promycelia" (basidia) composed of variable numbers of cells. On the basidia, ovoid, elongate, fusiform, brown "sporidia" (basidiospores) are produced in chains or in groups, laterally or terminally (Zambettakis and Foko, 1971; Ofong, 1978). In cultures short-celled hyphae were observed producing "sporidia" at the edge of colonies and large, thick-walled, dark brown chlamydospores in chains towards the center of the colonies (Ofong and Okafo, 1980).

On Sterculiaceae: *Triplochiton scleroxylon* K. Schum., Central Africa (Cameroon, Ivory Coast, Nigeria). Probably more widespread and locally may be rather common "causing poor fruiting of the trees" (Ofong and Okafo, 1980).

Key to the pair-spored smut genera

1. Spore germination of *Mycosyrinx*-type. On Vitaceae ..... *Mycosyrinx*
— Spore germination of *Ustilago*-type. Not on Vitaceae 2
2. Sori hypertrophied. Spores produced in cavities. Basidiospores brown. On Sterculiaceae ..... *Geminago*
— Sori not hypertrophied. Spores produced intraepidermally. Basidiospores hyaline. On Cyperaceae ... *Schizonella*

Excluded species and variety

Mycosyrinx osmundae (Peck) Peck, New York State Mus. Bull. **157**: 43. 1912.

Ustilago osmundae Peck, Bot. Gaz. (Crawfordsville) **6**: 276. 1881. — Type on *Osmunda regalis* L. (Pteridophyta, Osmundaceae), USA, Vermont State, 27.VIII.1880, C. G. Pringle (1541; NY!).

The fungus produces a yellowish brown or cinnamon-brown cover on the surface of pinnules of the fern *Osmunda regalis* L. and its var. *spectabilis* (Willd.) A. Gray, which are deformed and contracted into tufts. The spores are variable in shape and size, globose, subglobose, ellipsoidal, ovoid or slightly irregular, 9–17.5 × 10–18(–21) μm, globose spores are 10–17 μm in diam, light to medium dark yellowish red. The spores may be solitary or adhering in few-spored groups; wall 1–2 μm thick, provided with small, irregularly, rather sparsely situated warts.

The spores and the morphology of the sori of this species are not typical for *Mycosyrinx*. Clinton (1904) excluded *Ustilago osmundae* Peck from the North American smut fungi, considering it to be a hyphomycete (?). The study of the ultrastructure (hyphal wall, septal pore structure) revealed that this fungus is a basidiomycete (Dr. R. Bauer, pers. comm.). Work to elucidate its generic position continues.

Mycosyrinx osmundae (Peck) Peck var. *cinnamomae* Peck, Now York State Mus. Bull. **157**: 43. 1912.

Type on *Osmunda cinnamomea* L., USA, Washington Co., Cambridge, 17.VI.1911, coll. S. H. Burnham (NY!). Differs from *M. osmundae* in the paler brown color of the spore mass and the even surface of the spores.

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