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Observations on Chytridiaceous Parasites of Phanerogams

XVI. Notes on Physoderma from Scirpeae*

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With 15 Figures in the Text

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Members of the Tribe *Scirpeae* Kunth of the *Cyperaceae* have had a variety of fungi described from its members. Phycomycetous parasites, however, are not common and in *Physoderma* of the *Chytridiales*, 3 species have been described thus far, namely, *P. heleocharidis* (Fuckel) Schroeter on *Eleocharis*, *P. schroeteri* Krieger on *Scirpus*, and *P. dulichii* Johns on *Dulichium*.

In this paper are recorded miscellaneous notes on fungi referable to *Physoderma* which occur on species of *Eleocharis*. A subsequent paper will deal with *P. dulichii*. Thus far, we have not encountered the parasite of *Scirpus* in our area and hence can contribute nothing new concerning it. A few notes[1] and comments derived from a study of herbarium material are appended. A considerable number of collections were examined and a good conception of variability of host symptoms and resting spore characters was obtained. Furthermore, ample material of the types of *Physoderma heleocharidis* and *P. schroeteri* was available for examination.

1. Physoderma on Eleocharis compressa Sulliv.

Material of *Eleocharis compressa* collected in a shallow pool at Sedge Point on Douglas Lake at the University of Michigan Biological Station in northern Lower Michigan showed evidence of fungus infection. Both culms and basal sheaths bore dark flecks or raised spots. Most commonly these occurred on the upper part of the culm just beneath the spikelet and were rounded and $^1/_4$—3 mm in diameter, or elongate and 1—4 × 2—8 mm, with irregular margins. On the sheaths infected areas were less regular in shape and more numerous. Young areas of infection were dark purple to purplish-black with a yellowish halo, whereas fully mature spots were

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** Deceased, 1963.

[1] Thanks are expressed to the Curators of the following herbaria for the loan of specimens for examination: University of Copenhagen; Institute Botanici Universitatis Wratislaviensis; Botanisches Museum Berlin-Dahlem; Farlow Herbarium; New York Botanical Gardens; Conservatoire et Jardin Botanique, Geneva; Royal Botanic Garden, Kew; Commonwealth Mycological Institute; National Fungus Collection Beltville; Bernice P. Bishop Museum, Honolulu; University of Michigan.

black. Anthocyanin production by host cells in infected areas was sometimes so great as to render microscopic examination of the endobiotic fungus very difficult.

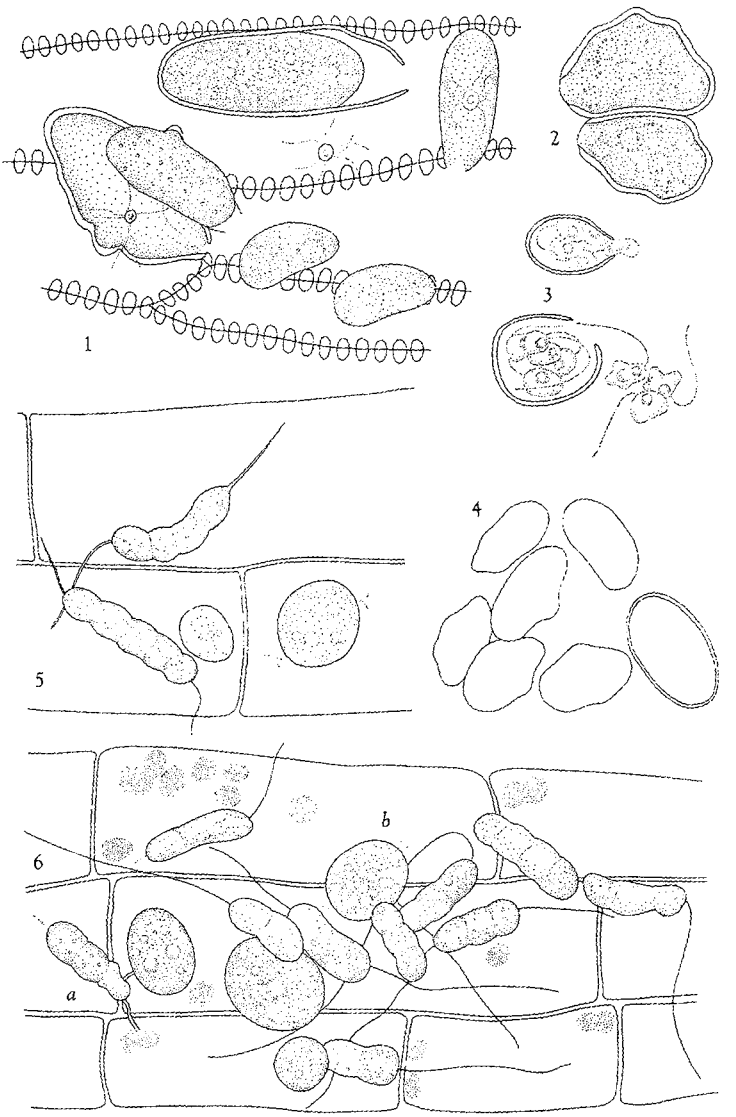
Infected areas, when examined microscopically, were seen to contain great numbers of brownish resting spores of a *Physoderma*, readily recognizable by their characteristic ellipsoidal outline and striking disposition of their contents.

It will be recalled that most species of *Physoderma* produce two distinct and independent thalli in their life history (1) an epibiotic, thin-walled sporangial stage with rhizoidal system confined to one host cell and (2) an endobiotic, extensive rhizoidal thallus ramifying from cell to cell in the host and bearing at intervals peculiar, usually septate, "turbinate cells", and, as outgrowths from these, relatively enormous, dark-colored, thick-walled resting spores. The second stage is visible macroscopically, in contrast to the first. It is not usual to find both simultaneously in field collections.

Epibiotic, thin-walled sporangia of a *Physoderma* type were found on the outermost bud sheath of young unemerged culms. Unusually heavy concentrations of these were found at the apices of such sheaths. Uprooted *Eleocharis* plants left under submerged conditions in the laboratory for several weeks continued to have epibiotic stages formed on them. These sporangia were colorless, had surprisingly stout walls (Figs. 1—3), were ovate in top view, blunt-ended, and occasionally had a somewhat undulate outline (Fig. 4). They rested with their long axis parallel with the surface of the host. Viewed from the side they were irregularly humped, and some bore a hemispherical apiculus 4—7 μ in diameter, which was probably an unenlarged portion of the original zoospore cyst. In the course of zoospore maturation they underwent the same sequence of changes noted in other species (SPARROW, GRIFFIN, and JOHNS 1961). At maturity they bore a varying number (up to approximately 30) of colorless, regularly-spaced globules of uniform size and, at one end, a blunt discharge papilla. They were 20—49 μ long by 13—20 μ broad and up to 38 μ high.

Within the host epidermal cells each sporangium bore a centrally-placed very short penetration tube, usually surrounded by a ring of callus material of host origin, which terminated in a tuft of 6—8 delicate somewhat undulating, occasionally branched rhizoids (Fig. 1). These radiated for a short distance into the host cell lumen.

At sporangial discharge (Fig. 3) the papilla deliquesced, and through the resultant pore the zoospores emerged singly and amoeboidly. Outside, after a brief period of quiescence, they became nearly spherical, were 4.5—5.5 μ in diameter, bore a colorless refractive globule 2.5 μ in diameter and an anterior nuclear cap (Fig. 3). A posterior flagellum propelled them at a lively rate through the water.



Figs. 1—6. × 825. *Physoderma heleocharidis*, in *Eleocharis compressa*. Fig. 1. Portion of surface of host showing epibiotic sporangia in various stages of development. The endobiotic ring of host callus material around the axis of the rhizoidal system is shown; in one instance the sporangium has fallen off, leaving the callus ring and rhizoids. — Fig. 2. Two sporangia showing thick undulating walls and discharge papillae; the contents are in the "ring stage". — Fig. 3. Two sporangia discharging their zoospores. — Fig. 4. Outlines of group of sporangia to show shapes. — Fig. 5. Portion of endobiotic system to show shape and septation of turbinate cells; two immature resting spores also in section. — Fig. 6. Portion of host tissue bearing turbinate cells, rhizoids and developing resting spores. At (*a*) is shown a resting spore developing at the tip of a laterally-produced tube from a segment of a turbinate cell. At (*b*) an immature resting spore bears a few antler-like projections

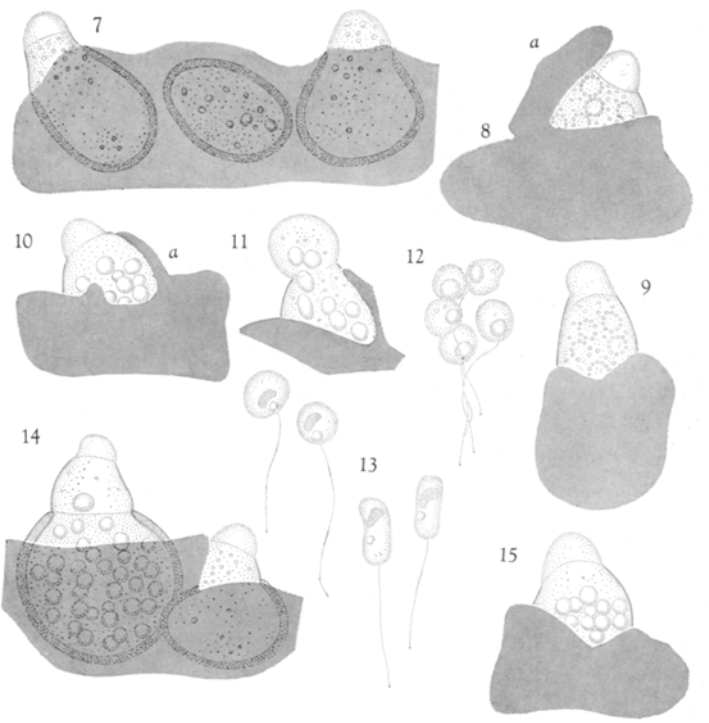
The polycentric endobiotic system, except for the resting spores, was observed in living material with difficulty because of crowding and residue within the host cells. It was almost never found in the epidermis. A striking feature was the formation at intervals along the seemingly unbranched rhizoids of long septate turbinate organs (Figs. 5, 6). These were usually cylindrical with rounded apices and were divided transversely by cross-walls into 2—3 or even 5 cells. Both in their exceptional length (17—30 μ × 5—8 μ) and particularly in their degree of septation they exceeded all other species seen by us, except *Physoderma maydis* (unpublished). The resting spore originated as a spherical swelling at the tip of a short tubular projection from (usually) an end cell of a turbinate organ (Fig. 6a). A few antler-like outgrowths were occasionally visible from its body (Fig. 6b). As maturation of the resting spore rudiment proceeded this structure became broadly ellipsoidal and bore numerous refractive bodies in its contents.

At maturity the spore was invested with a golden wall 1.5 μ thick. Its contents were disposed in typical *Physoderma*-like fashion, i.e., a large central vacuole surrounded by one or more layers of small spherical fatty globules. One to several spores were found in a single cell and were usually surrounded by a dark residuum of host material so dense as to obscure the wall and hence shape of the spore. Those in elongate parenchyma cells nearly filled the cell and conformed to its shape, whereas in broader cells they were larger and more typically ellipsoidal. The resting spores varied from 20.8—31 μ, long axis, by 13—20.8 μ, short axis, averaging 23.4 μ × 14.9 μ.

Considerable difficulty was experienced in obtaining germination of resting spores and, after repeated efforts, this was finally accomplished in the spring of 1964. Spores collected at Sedge Point, 21 May 1964, on culms which had overwintered in the bottom of the pond, were placed in distilled, charcoal-treated water. After 2 days germination was initiated (Fig. 7). The sequence of events at germination did not differ materially from that already described in detail in other papers. This involved formation of a broad, tapering, finger-like endosporangium (Figs. 8—10, 14, 15) usually about 15 μ high by 15 μ broad at the base tapering to 10 μ at the apex, surmounted by a prominent discharge papilla 10 μ broad by 5 μ high. Owing to the dense dark material which enveloped the resting spores within the host tissue it was at first thought that no operculum was dehisced at germination. Prolonged probing, however, revealed that there was, indeed, a lid, but because of the debris it was usually obscured (Figs. 8a, 10a) and after discharge even flapped back into place on the spore. Rarely, unobscured spores showed it clearly. Such accumulation of debris is also characteristic of *P. menyanthis* and *P. dulichii* and may

account for the fact that these species are the only ones said to germinate without dehiscence of a lid.

The zoospores from resting spores were discharged from the endosporangium coincident with the swelling up and quick dissolution of the prominent apical discharge papilla (Fig. 11). These zoospores were almost



Figs. 7—15. × 825. *Physoderma heleocharidis, in Eleocharis compressa.* — Fig. 7. Three resting spores buried in adherent host debris. — Fig. 8. Germinating resting spore with endosporangium bearing discharge papilla; its contents in "ring stage". The cap dehisced at germination is at (*a*) and is totally obscured by host debris. — Fig. 9. Same stage as previous one; cap not visible. — Figs. 10—11. Stages in discharge of zoospores. — Fig. 12. Cluster of recently discharged resting spore zoospores. — Fig. 13. Resting spore zoospores from Ann Arbor No. 1 strain. Note smaller globule and conspicuous nuclear cap. — Figs. 14—15. Other resting spores germinating

globular even when in motion, nearly 9 μ in diameter with a 3—4 μ in diameter centrally or basally placed colorless globule and anterior to this 1—3 small refractive bodies (Fig. 12). Occasionally a nuclear cap could also be detected. The posterior flagellum was approximately 30 μ long. Thus, these zoospores were distinctly larger than those produced by the epibiotic sporangia (4.5—5.5 μ).

Since the original Sedge Point collections of 1957, *Physoderma* has been found at a number of sites in the vicinity of the Biological Station

on *Eleocharis smallii*, *E. elliptica*, and *E. compressa*, and an examination of material in the herbarium of the Biological Station indicated infected plants from other nearby sites on the above hosts, as well as on *E. (Scirpus) pauciflorus*.

2. Physoderma on Eleocharis sp. from Ann Arbor

This material was found by MARILYN L. SHAW in great profusion in a stand of *Eleocharis* sp. (growing in a tub at the University Botanical Gardens) and originally collected in a marshy spot along the Huron River in October 1963 by SPARROW and GRIFFIN. The fungus produced dark-brown, slightly raised pustules, often with a surrounding discolored yellowish area, 2—6 mm long by 0.5—2 mm wide, sometimes becoming confluent. These were either on the basal sheath or lower part of the culm, or on both. No great differences from the Sedge Point fungus in size of resting spores was noted, these being 23.66×16.7 μ. They had, however, a thinner golden wall. They occupied parenchyma cells where they were surrounded by reddish- to dark-brown host residue. The endobiotic system bore, as did that in *E. compressa*, once or twice septate turbinate organs up to 35 μ long by 5—7 μ in diameter.

Unlike the Sedge Point fungus, these resting spores germinated readily and apparently after little rest period. The most remarkable feature was the percentage of germination, which was often 90—95%, and, in addition, was simultaneous rather than sequential within a population. Indeed, of the many Physodermas collected by us, this has yielded the highest percentage of resting spore germination. This has made it favorable material for a study of ultrastructure and such work has been initiated.

Free-swimming zoospores from resting spores were slightly bent and asymmetrically cylindrical when in motion (Fig. 13, below). At rest the body became nearly spherical and 8—9 μ in diameter (Fig. 13, above). Within the body was a laterally—and somewhat basally—borne refractive globule 2.5—3 μ in diameter, often seen to be associated with material of less refractivity. Anterior to this was a very conspicuous nuclear cap. The posterior flagellum was 2—2.5 times the length of the body. Occasionally, refractive anterior granules were seen, but not so constantly as in the Sedge Point fungus. Furthermore, the globule was distinctly smaller than in the last-named material.

The epibiotic stage, produced here in the laboratory, does not differ significantly from that found in the field in Sedge Point material.

Morphologically, therefore, we find these two fungi to be essentially alike in both epi- and endobiotic stages except that the resting spore wall of the Ann Arbor fungus is thinner and the globule of its resting spore zoospore smaller.

3. Physoderma on Eleocharis smallii Britt.

This material was first found in 1957 in a swale in Section 23, Hebron Township, Cheboygan Co., Mich., on *E. smallii*, in association with *Physoderma*-infected plants of *Sium suave*, *Mimulus ringens*, and *Lycopus americanus*. An identical fungus has

been collected in Trout Lake in the Huron Mountain Club holdings bordering Lake Superior, in Marquette Co., Mich., June, 1965. On *Eleocharis* it formed beneath the spikelet and along the upper culm small, round, brown, slightly raised pustules. Resting spores were $24.4 \times 15.6\ \mu$. No further data have as yet been collected.

On infected *Eleocharis smallii* collected by DEAM (No. 25920) near Cass City, Michigan, in 1918, there has been found another type of symptom. This fungus produced conspicuous, elongate, gray, raised pustules beneath the spikelet and along the culm. The resting spores were (average) $24.6 \times 13.4\ \mu$, i.e., not significantly different from the averages of the others heretofore discussed.

4. Physoderma on Eleocharis obtusa (Willd.) Schultes and E. palustris (L.) R. et S. from Hawaii

Physoderma on *E. obtusa* was collected in the Hawaiian Islands by the senior author (1965). Pustules were confined to the sheath and were slightly raised, dark brown, ovoid or elongate, and up to 2 mm in length. Although the material was very mature when collected, the endobiotic system and a few once-septate turbinate organs were found. No instances of resting spore germination or of the epibiotic stage were observed.

Identical material was found on Mauai along the Olinda Pipeline Trail, Makawao Forest Reserve, on the NE slope of Haleakala Volcano (4000′), 20 April 1963, and in a pool on Parker Ranch, N. Hamakua District, SE of Kamuela on Hawaii, 14 April 1963. In both collections the resting spores were approximately alike in size, $28.7 \times 19\ \mu$.

A survey of considerable material in the herbarium of the Bernice P. Bishop Museum by the senior author, of *Eleocharis* collected throughout Polynesia, yielded only two other sites for *Physoderma*. A large collection of *Eleocharis palustris* collected by FORBES (No. 2360.0) in 1916 in the Kaimuki district of Honolulu (on 9th Ave.), Oahu, bore brownish pustules up to 2 mm long by 1 mm wide on the sheaths. The resting spores were $27.5 \times 24.8\ \mu$, and slightly rounder than those on *E. obtusa*. Another collection of *E. obtusa* from the Kohala Mountains on Hawaii by CRANDELL, SKOTTSBERG, et al. in 1938 (Hawaiian Bog Survey No. 3445), bore pustules up to 1 mm long, again confined to the sheath. Resting spores were $28.53 \times 20.13\ \mu$, thus, not differing significantly from the other Hawaiian collections.

5. Notes from Herbarium Material

A. Of first importance among the many collections existing in herbaria is the material from which the original *Physoderma* was described on *Eleocharis*, namely, by FUCKEL 1866, as *Protomyces heleocharidis*.

A goodly amount remains in the Geneva Herbarium over and above that widely distributed as No. 1610 of FUCKEL's "Fungi rhenani". It is contained in a packet, together with a few sketches, bearing a woodcut-printed label, "No. 1610, Nassau's Flora", and was collected in marshy ground near Budenheim in the autumn. This material, said to be very rare, was formally described and distributed and identical descriptions given in Hedwigia **5**, 29 (1866), and Jahrb. Nassau Ver. Naturk. **23**, 75 (1869), ("Symbolae Mycologicae"). In the latter description the locality is given as between Budenheim and the Ludwigshöhe.

All FUCKEL's material we have seen indicates a fungus on the culms (no sheaths were included) which produces flecks or low pustules 3—4 × 1—1.5 mm with dark brown or purple-black context and light colored irregular margin, most often in loose groups scattered along the culm. Microscopic examination of the pustules has revealed the typical ellipsoidal *Physoderma* resting spores, pale amber-colored, flattened on one face and moderately thick-walled. In narrowly elongate host cells they are up to 6 and uniseriate, whereas in more irregularly-shaped ones they are haphazardly placed. Several show a well-defined circumcissile line of cleavage on one face. As in the Sedge Point material, nearly all are imbedded in a dark residue of host material. Size ranges are shown in Table 1, where other data on resting spores are assembled.

B. In 1885 SCHROETER transferred *Protomyces heleocharidis* to *Physoderma* as *P. heleocharidis* (Fckl.) Schroeter and gave an expanded description based upon specimens, now in the Univ. Wratislav. Herbarium, from several sites near Liegnitz and Breslau on "*Scirpus palustris*". Representatives of this important material, including that from several of the sites listed in "Kryptogamenflora Schlesiens", have been examined and compared with the type. Spore sizes are included in Table 1. SCHROETER's material as now available was collected by GERHARDT in the vicinity of Liegnitz and all appears to parasitize *Eleocharis*, not *Scirpus*. Notes on the symptomology follow. Further details are given in Table 1.

a) Pfaffendorf. 5.11.83. Sterile host plant.

Symptomology. Culms brown; the small clusters of brown pustules not caused by *Physoderma* (Ascomycete?). Lesions caused by *Physoderma* blackish, elliptical, 5—6 mm × 1—1½ mm, raised. Resting spores one-several in cell, much host debris around them. Irregular, or ± ellipsoidal.

b) Sophienthal. 10.1871.

Symptomology. As in (a). Resting spores as (a).

c) "Liegnitz" Ex Herb. de Thumen 10.71. Undoubtedly from (a) above, on sheath, lesion 1 mm, blackish, ellipsoidal. Resting spores as above.

d) Breslau. Weidendamm — mentioned in "Kryptogamenfl. Schles." but no specimens found.

In addition to these, Schroeter's collection includes a small brown paper packet labeled in his script "*Physoderma heleocharidis a H. ovata*". There are 4 more words which are illegible. The notation "694 Flora . . ." and possibly "26.10.87" then follows.

Symptomology. Great numbers of small black or rich brown (immature?) specks ± 1 mm long and 0.25 mm wide, on culm. Resting spores appear identical with Gerhardt collections.

C. Sydow, "Mycotheca Marihica" No. 2207, *Physoderma heleocharidis* on *Eleocharis palustris*, collected at "Steglitz b. Berlin" in August 1888.

Symptomology. Large erumpent pustules, black, up to 6×2 mm, some completely surrounding whole culm; some confluent; scattered smaller ones. This is the most striking infection of the "Liegnitz-type". Resting spores are as in Liegnitz (a).

D. KRIEGER, "Fungi saxonici" No. 682, *Physoderma heleocharidis* from near Königstein, collected in 1891. "Fungi saxonici" No. 540, "*Microphlyctis polyspora* Schroeter n. sp.", on *Eleocharis palustris*, from near Königstein and collected in 1889, also has a *Physoderma* on it showing as small blackish areas. The resting spores are heavily obscured by host debris.

E. RABENHORST-WINTER-PAZSCHKE, "Fungi europaei" No. 3875 was also collected by KRIEGER, probably from the same Königstein site, but in September 1891.

All KRIEGER's collections near Königstein are alike in having large, blackish or leadcolored, ellipsoidal areas of fungus infection. A collection from "Pirna i/Sachs." 4.7.92, differs in having very much smaller and greater concentrations of leadcolored pustules. The resting spores are mostly one in a cell, and obscured by dense dark red host material.

All resting spore sizes of the above collections can be found in Table 1.

None of the Liegnitz infections resembles very closely in symptomology the rich red-brown scattered small pustules of the type specimens. FUCKEL's material also seems to have more regularly rounded, lighter and thinner-walled spores. How significant these differences are we cannot say now.

One further KRIEGER collection should be mentioned. In Schroeter's herbarium is a packet labeled "*Physoderma sp.*" on *Eleocharis palustris*, collected 20 July 1887. A notation by him states this fungus does not agree with *P. heleocharidis*, there being a great many, small, resting spores in the cells. He asks for an explanation from SCHROETER. We do not know what the latter replied but we have found in abundance the structures alluded to by KRIEGER. They possibly relate to a plasmodiophoraceous organism, not a *Physoderma*.

6. Physoderma on Scirpus maritimus L. (P. schroeteri Krieger)

As earlier indicated we have not succeeded in locating, as yet, any *Physoderma* on the common species of *Scirpus* (*S. acutus*, *S. validus*, *S. americanus*, *S. fluviatilis*, *S. hudsonianus*, *S. atrovirens*, etc.) in our flora. No doubt such will eventually be found.

KRIEGER, in 1896, described a *Physoderma* from *Scirpus maritimus* in Germany as *P. schroeteri* and distributed it as No. 546 of "Fungi saxonici". He stated that this very rare fungus appeared on the host either as black rounded spots $^1/_3$—1 mm in diameter or as black lines up to

2 mm long. The elliptical resting spores were 1—4 in the parenchyma cells and had a light yellow to brownish color and a thick brown wall. In the material of No. 546 examined by us they were $23.5 \times 32\ \mu$.

In the Supplement to "Fungi saxonici" No. 546-b is a series of excellent specimens collected (1900, 1901) at the same site as No. 546, which was, KRIEGER said, soon to be destroyed. Furthermore, material of this species distributed by VESTERGREN ("Micro. rar. selecti" No. 1094) and SYDOW ("Phyco. et Proto." No. 179) seem all to have been collected at the same locality by KRIEGER.

Only four other collections of *Physoderma* on *Scirpus* are known to us. These are JAAP, "Fungi sel. exsic." No. 3 from Schleswig-Holstein (1897), VESTERGREN "Micro. rar. selecti" No. 1610 from France, and material presumed to be (and probably is) *Scirpus* from Portugal, intercepted 6 March 1955 at Mobile, Alabama, by the U.S.D.A., and identified by STEVENSON and WATSON. The material on *Scirpus supinus* from India, Ind. Agric. Res. Inst. New Delhi No. 652 in our hands failed to yield *Physoderma* spores, and No. 2064 of the same Institution was an undoubted rust. On the other hand, BUTLER's collection on this same host from India, C.M.I. No. 27861, is a *Physoderma*. Indian material (New Delhi No. 22132) on *Cyperus compressus*, a genus not considered here, bears a *Physoderma*, and is referred by its collector to *P. schroeteri*, as is the fungus on *C. rotundus* L. from the Sudan, C.M.I. No. 27865.

No great differences in size or other resting spore characteristics were noted in the *P. schroeteri* material cited above, certainly no more than were represented in KRIEGER's several collections at the same site.

Whether *Physoderma heleocharidis* and *P. schroeteri* are distinct species is debatable. On the label of "Krypto. exsicc." No. 1940, said to be *P. schroeteri* (det. MOESZ, coll. FILARSZKY) on *Eleocharis palustris*, but indistinguishable to us from *P. heleocharidis* (see Table), KEISSLER comments that *P. schroeteri* seems hardly more than a form of *P. heleocharidis* which produces smaller spots on the host and bears somewhat larger resting spores. No one seems to have tried cross-inoculation work, the results of which might give a decisive answer to the authenticity of *P. schroeteri*. We do note, however, that on the basis of herbarium material alone, in *P. schroeteri* the resting spores are 20—23% larger than the *Eleocharis* parasite. Less important distinctions are, that in *P. schroeteri* the residue around the spores is chestnut brown, whereas in *P. heleocharidis* it is always deep purplish-black; and that a fair number of spores are found in the epidermal cells of *Scirpus*, whereas almost never are these seen in this tissue in *Eleocharis*.

We have tried several times to infect *Scirpus acutus* with the Ann Arbor No. 1 strain from *Eleocharis* and have succeeded in one instance, the fungus producing resting spores identical with those of the inoculum. They ranged from $19.2—28 \times 14—26.2\ \mu$, average being $24.3 \times 18.6\ \mu$ (cf. 23.6×16.7).

Table. *Collection and Resting Spore Size Data (50 spores) Physoderma heleocharidis*

Collection	Date	Country	Host	Sizes (long axis × short axis)	
				Extremes μ	Mean μ
FUCKEL, "Fungi rhenani" No. 1610	1866	Germany	*E. palustris*	21—31.5 × 14—28	26.04 × 20.37
SPARROW and JOHNS, Sedge Point	1957	U.S.	*E. compressa*	20.8—31.2 × 13—20.8	23.4 × 14.9
SHAW, Ann Arbor, No. 1	1964	U.S.	*Eleocharis* sp.	19.25—28 × 12.25—22.75	23.6 × 16.7
SPARROW and JOHNS	1957	U.S.	*E. smallii*	18.2—31.2 × 10.4—23.4	24.4 × 15.6
DEAM, No. 25920	1918	U.S.	*E. smallii*	15.75—31.5 × 8.75—19.25	24.1 × 13.3
SPARROW, Hawaii and Maui	1963	U.S.	*E. obtusa*	16—36.8 × 12.8—27.2	28.7 × 19.0
FORBES, Oahu	1916	U.S.	*E. palustris*	22.4—32.0 × 16,0—30.4	27.5 × 24.8
CRANDELL, SKOTTSBERG et al., Bog Survey No. 3445	1938	U.S.	*E. obtusa*	21.0—38.5 × 12.25—24.5	26.56 × 17.11
SCHROETER (GERHARDT) "Pilze Schlesiens" No. 280, Liegnitz Sophienthal	1871	Poland	*E. palustris*	17.5—31.5 × 10.5—21	24.6 × 15.4
SCHROETER, do. Liegnitz, Pfaffendorf	1883	Poland	*E. palustris*	21.0—31.5 × 8.75—22.75	24.15 × 15.36
SYDOW, "Phyco. et Proto." No. 46	1895	Poland	*E. palustris*	21—28 × 10.5—22.75	24.92 × 18.23
SYDOW, "Mycotheca marihica" No. 2207	1888	Germany	*E. palustris*	19.25—31.5 × 14.0—22.75	24.95 × 17.15
KRIEGER, "Fungi saxonici" No. 682	1891	Germany	*E. palustris*	18.2—33.8 × 10.4—20.8	26.6 × 14.7
KRIEGER, "Fungi saxonici" No. 540 (with *Microphlyctis*)	1889	Germany	*E. palustris*	24.5—36.75 × 14.0—24.5	24.97 × 19.81
KRIEGER, "Pirna i. Sachs."	1892	Germany	*E. palustris*	21—36.7 × 14—28	28.3 × 20.5
MAGNUS, Berlin	1896	Germany	*E. palustris*	21—35 × 10.5—22.75	25.86 × 16.13
LUDWIG, "Fl. ostfriesisch. Inseln"	1938	Germany	*E. palustris*	24.5—42 × 14—28	33.53 × 19.98
FILARSZKY, "Kryptogam. exsicc." No. 1940 (as *P. schroeteri*)	?	Hungary	*E. palustris*	15.6—26 × 10.4—23.4	23 × 15
ANZI, "Erb. Critt. Ital." Ser. II, No. 1275	?	Italy	*E. palustris*	21—33.25 × 15.75—28	27.16 × 20.26
DAVIDSSON, No. 1445	1900	Greenland	*E. palustris*	25—34.4 × 15.6—31.2	29.63 × 23.13
STEENSGAARD	1877	Denmark	*E. palustris*	17.5—33.25 × 10.5—24.5	25.23 × 14.31
BRENCKLE, "Fungi dakotensis" No. 39	1908	U.S.	*E. palustris*	21—35 × 10.5—21	27.82 × 15.26
ELLIS and EVERHART, "Fungi colombiani" No. 1613 (Suksdorf)	1901	U.S.	*E. palustris*	19.25—28 × 10.5—21	24.25 × 14.7
BOYD, Ayrshire	1907	Scotland	*E. palustris*	21—31.5 × 14—24.5	26.14 × 18.72
MOSS, Cambridgeshire	1916	England	*Eleocharis* sp.	21—31.5 × 12.25—24.5	25.16 × 18.51
VESTERGREN "Micro. rar. selecti" No. 1605 (Hariot)	1912	France	*E. palustris*	17.5—28 × 10.5—17.5	22.47 × 14.7

Until more evidence from cross-inoculation work is forthcoming, we will maintain the two as distinct, but with considerable reservation. Similar evidence will be needed for the *Physoderma* on *Carex nigra* (C.M.I. No. 76822) from England called *P. eleocharidis*.

The following table summarizes resting spore sizes in the collections of *P. heleocharidis* examined by us. With respect to host symptoms, we find such a variety on individuals of the same collection and reoccurrence of the same types on different collections that no generalizations can be made. There is noticeable in some collections, however, a preponderance of infection on sheaths rather than culms, but this difference can probably be explained by the relation of the stage of host development to water level and to the presence of infective agents.

Inasmuch as there were no essential major differences of a morphological nature in the Sedge Point and Ann Arbor fungi, especially in turbinate organs and epibiotic sporangia, they are considered the same. It must be pointed out, however, that they possibly represent different taxa, considering the marked differences in behavior of resting spores at germination, their slightly thinner wall and size of resting spore zoospore globule. We cannot now, of course, equate our fungi with any certainty with FUCKEL's, available only to us in century-old dead material of the resting spore stage. Enough similarity is seen, however, in all these fungi on *Eleocharis*, to justify fitting them into a single taxon under the binomial *P. heleocharidis* (Fuckel) Schroeter. The following diagnosis is sufficiently broad to embrace them all. Future work will no doubt necessitate a different treatment.

Physoderma heleocharidis (Fuckel) Schroeter, amend.
Kryptogamenfl. v. Schlesien 3 (1): 194. 1886
Syn. *Protomyces heleocharidis* Fuckel. Hedwigia 5, 29. 1866

Epibiotic sporangium elongate-ovate, somewhat gibbose, with a 4—7 μ in diameter apiculus in mid-region, wall stout, with a broad discharge papilla at one end, the long axis parallel with the host wall surface, contents colorless, 20—49 $\times$ 13—20 μ, up to 38 μ high; rhizoidal system a tuft of 6—8 delicate, elongate, somewhat undulating, occasionally branched rhizoids arising from a very short centrally-placed axis, which is usually surrounded by a ring of callus material; internally proliferous; zoospores sub-spherical, 4.5—5.5 μ in diameter, slightly elongate when in motion, with a colorless 2.5 μ globule, an anterior nuclear cap, and posterior flagellum; endobiotic system composed of seemingly unbranched rhizoids, 2—5-celled cylindrical turbinate organs 17—30 $\times$ 5—8 μ, and resting spores; the latter originating at the tip of a delicate lateral protuberance of a cell of a turbinate organ, sometimes bearing a few antler-like outgrowths, at maturity broadly ellipsoidal when not

crowded, sometimes irregular or conforming to host cell shape, with a golden to brownish unpitted wall 1.5 μ thick, often covered with reddish-black host cell residue, upon germination dehiscing by an often obscured lid, the subsequently developed protruding endosporangium broadly conical, $15 \times 15\,\mu$, tapering to a prominent $10\,\mu$ in diameter, apical discharge papilla, the zoospores nearly globular, $9\,\mu$ in diameter, somewhat cylindrical when in motion, with a $2.5-4\,\mu$ in diameter, colorless, centrally or basally placed colorless globule, 1—3 anterior granules and posterior flagellum.

Parasitic; forming scattered, sometimes confluent, reddish-brown, black, grayish-brown, or lead-gray, often margined pustules up to 6 mm long by up to 2 mm wide on sheaths and culms of *Eleocharis* spp.

Summary

A study of the morphology and life cycle of two *Physoderma* taxa occurring on *Eleocharis* spp. in Michigan is presented in detail. Both fungi possess almost identical endobiotic and epibiotic stages. They differ significantly with respect to the ease of germination of the resting spores, those on *E. compressa* being difficult to germinate whereas those from *Eleocharis sp.* from the vicinity of Ann Arbor do so readily.

Resting spore stages of other collections, American, Polynesian and European, including the type of *Physoderma heleocharidis* (Fuckel) Schroeter, when compared, do not differ significantly from one another. *P. schroeteri* Krieger described from *Scirpus* is hardly distinguishable from *P. heleocharidis* on resting spore stage alone. Furthermore, we have successfully produced mature thalli and resting spores of the *Physoderma* on *Eleocharis* from Ann Arbor on *Scirpus actus*. Other such successful cross inoculations will be needed before we will say with certainty *P. schroeteri* is not distinct from *P. heleocharidis*.

Enough similarity is to be found in all the fungi on *Eleocharis* to place them for now, at least, in a single taxon, *Physoderma heleocharidis*. Future work with living material will no doubt necessitate a different treatment. An expanded technical diagnosis of *P. heleocharidis* based on our studies is included.

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