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## Contributions from the Cryptogamic Laboratory of Harvard University. XXII.

### Observations on the genus Naegelia of Reinsch.

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WITH PLATE V.

In his paper entitled "Beobachtungen über einige neue Saprolegnieæ, etc.," published in Pringsheim's Jahrbücher about fifteen years since,[1] Reinsch has described and figured a peculiar fungus to which he gave the name *Naegelia* including under it two supposed species which he referred to in the text as "species I" and "species II" respectively, without further specific designation. The genus, which like Leptomitus and its allies is characterized by the division of its hyphæ into segments through the presence of successive constrictions, was based on its peculiar habit, any given hyphal segment producing distally whorls of sporangia and branching in a characteristic fashion. Although this habit is clearly indicated by the original figures and description, Cornu[2], in the year following Reinsch's publication, referred the genus unreservedly to his own *Rhipidium interruptum*, a form characterized by an extreme differentiation between a monstrously developed basal cell and the numerous branches arising from it, the habit of which, if published data may be relied upon, is quite different from that of the form under consideration. Nevertheless according to Cornu, single detached branches of *R. interruptum* are alone responsible for the creation of "Naegelia," a name, as he points out, inadmissable from its previous use in at least two instances. With this exception

[1] 11: 298. 1878.
[2] Bull. Bot. Soc. de France 1879. 226.

few references to Reinsch's genus are discoverable. Fischer in his recent work[3] retains the name *Naegelia* Reinsch, without further designation of the species, placing it under the insufficiently know genera included by him in the sub-family "APODYEÆ," with the remark that it cannot be considered identical with Rhipidium. Still more recently Schröter[4], without reference to the opinions of Cornu, assumes its distinctness and places it among the "LEPTOMITACEÆ," proposing as a substitute for the preoccupied Naegelia the modification *Naegeliella*, with one species, *N. Reinschii* n. g. et n. s., equivalent to the "species I" of Reinsch. Lastly Fritsch[5] calls attention to the preoccupation of Naegeliella for a genus of fresh water algæ and proposes a third name *Sapromyces* nov. gen. distinguishing two species, *S. Reinschii* (Schröter) Fritsch and *S. dubius* nov. sp., the last an equivalent for "Naegelia species II."

The last three references, for the most recent of which the writer is indebted to the kindness of Prof. Farlow, appear to be based wholly on the original account of Reinsch, the genus not having been observed since its first discovery. In view of the fact that this account has been discredited by the criticisms referred to, and is moreover defective in important points, the following observations may be of interest, based as they are on the examination of fresh material obtained during the past season.

The plant in question was first met with by the writer in the vicinity of York, Me., where it was found growing on a pine cone that had fallen into a wood pool of clear cold water. On this substratum the sporangiferous hyphæ were luxuriantly developed, forming a layer around it nearly a centimeter thick, but not very conspicuous from its transparency. The discharge of zoospores was repeatedly observed in this material; but no indication was seen of the presence of any form of sexual reproduction. Later in the season (September) the pool was again visited and additional specimens secured growing upon submerged fragments of branches, one of which furnished fine examples of the curious oogonia and antheridia. An examination of this material has afforded the data for the following account, but unfortunately no observations could be made

[3] Phycomycetes in Rabenh. Kryptogamenfl. (Pilze) **1**: pt. 4. 377. 1892.
[4] Engler and Prantl. Naturl, Pflanzenf. **1**: 103.
[5] Œsterr. bot. Zeitschr. **43**: 420. 1893.

at the time either on the germination of the oospores or the details connected with the process of fertilization.

*Hyphæ.*—The hyphæ, as has been already stated, consist of successive segments connected by constricted portions, which may be plugged by a deposit of cellulin, or, more commonly, are without any such pseudo-septum, the contents of successive segments being, as a rule, in direct communication with one another. The primary axis originates as a single basal cell or segment which is attached by its roughened surface directly to the substratum, without rhizoidal outgrowths. It is often more or less bent and distorted but otherwise undifferentiated, except that its protoplasmic contents may be separated into isolated masses (fig. 9), through the partial obliteration of its cavity by deposits of cellulin. Above this basal segment the habit of growth characteristic of the plant begins directly. The primary axis may be continued by several successive segments, but more frequently it divides almost immediately into two or more secondary axes. This successive and more or less irregular multiplication of axes is continued from the base to the summit of the plant, any given segment producing distally one to several similar segments, the whole resulting in a copiously branched and spreading structure. In addition to the new segment or segments which may arise from the distal end of any given segment, reproductive organs, whether zoosporangia, oogonia or antheridia, are usually produced either singly or more commonly in whorls of from two to (rarely) six, zoosporangia being often associated in the same whorl with oogonia or with antheridia. Each of the organs just mentioned is separated from its parent segment by the characteristic constriction which in the case of the zoosporangia and oogonia is furnished with a cellulin plug.

*Zoosporangia.*—The zoosporangia, which may be terminal as well as lateral, are very variable in size and shape, usually sub-cylindrical, often elongate but sometimes oval or elliptical. The more stunted forms with short and stout sporangia (fig. 3), corresponding to Reinsch's "species II" are, as has been suggested by Fischer, merely conditions of the more typical form, resulting apparently from the lack of nutrient material in the dead twigs on which this type occurred. The sporangia are very frequently attacked by chytridiaceous parasites, and in such cases often become considerably distorted

or otherwise modified, and although no resting spores were observed in any of the sporangia thus attacked, the thick walled spherical "oospores" described by Reinsch[6] as occurring, several in an "oogonium," are undoubtedly of this nature. At maturity the dense granular protoplasm within the sporangium divides into a large number of zoospores.

*Zoospores.* — The zoospores make their escape directly through a terminal pore without any interval of rest, swarming immediately after emergence and even while still within the partly emptied sporangium (fig. 2). They are sub-reniform in shape, biciliate and apparently monoplanetic, although this character was not definitely determined. In several instances when the discharge was observed directly, there was no indication of any process similar to that described by Cornu in Rhipidium, where the contents of the sporangium is said to be discharged simultaneously as a mass of zoospores which are then set free by the rupture of a thin surrounding membrane.

*Antheridia.*—The branches which terminate in antheridia arise like the zoosporangia terminally or more often laterally in whorls of several members and although often associated with zoosporangia do not occur in any of the specimens examined, on plants which produce oogonia. They are much more slender than the ordinary hyphæ, with few constrictions, often very elongate, flexuous, or often more or less irregularly spirally twisted especially just below the terminal antheridium. They may be several times branched, and are slightly constricted at such points, while the free tips, finding their way to the oogonia, become rather abruptly swollen into the antheridium proper. The antheridia are irregularly cylindrical, sometimes divided by a septum (fig. 5), and adhere closely to the oogonium, often winding partly round it, before reaching its receptive apex through which an entrance is effected by means of a beak-like process, which, pressing the wall of the oogonium inwards, perforates it at the bottom of the depression thus formed. Two antheridia (fig. 8), or even three, may be applied to a single oogonium invariably at its apex, their pollinodia penetrating side by side to the oosphere. After penetration there seems to be open communication between the oosphere and antheridium (fig. 5), but whether any interchange of contents takes place between them could not be determined from the material examined. As the oospore

[6] l. c. 11: *pl. 15. f. 4–5.* 1878.

matures the beak-like pollinodium becomes closed, its walls are greatly thickened, and its cavity sometimes wholly obliterated, so that even in old oogonia it is very sharply defined, the old antheridium also persisting and becoming somewhat thicker walled.

*Oogonia.*— The oogonia are either terminal or more frequently, like the sporangia with which they are often associated (fig. 4, *x*), borne laterally either singly or in whorls from the distal ends of the hyphal segments. They are nearly spherical or in the majority of cases piriform in shape, becoming covered with a brown flaky incrustation disposed transversely, and are separated from the segment which bears them by the usual constriction, which is always plugged (fig. 6) by a deposit of cellulin. Antheridia and pollinodia were present on every oogonium in the material obtained, even in the youngest specimens. In the latter the contents entirely fills the oogonium and consists of numerous large masses of refractive fatty protoplasm embedded in a more finely granular matrix. As this mass contracts to form the oospore a small amount of residual protoplasm remains unused outside it (fig. 5).

*Oospores.*—The oospores are always solitary in the oogonia, spherical, with very thick translucent walls which are slightly yellowish. The exospore, though slightly irregular in outline, shows no signs of any characteristic modification. Their germination was not observed.

From the above account it is manifest that the genus Sapromyces is very closely related to Rhipidium as far as can be determined from the fragmentary descriptions of this genus which are available. It is left quite uncertain by Cornu's account how much importance should be attached to the differentiation between the basal cell of Rhipidium and its branches, but if this character is as strikingly pronounced in the three remaining species as it is in *R. interruptum*, it would seem to constitute alone a sufficient basis for generic separation. Whether the differences existing in the method by which the zoospores are discharged in either case should also be considered of generic value can hardly be determined without further comparative observations. The characteristic branching and the verticillate arrangement of sporangia, relied upon by Reinsch as a basis for his genus, would seem, however, to be of comparatively slight importance.

In connection with the general habit of Sapromyces it may be noted that Reinsch in his first description,[7] where his subsequent "Naegelia species II" is described and figured as "Hyphomycetarum nov. gen." represents the sporangiferous hyphæ as arising at intervals from a "stroma ex filis tenuioribus elongatis subramosis inter muscos aquaticos intricatis formatum," but no reference to this mode of growth is made in his second paper; and since no such habit was observed by the writer, the account just quoted is presumably of doubtful accuracy.

That the species under consideration is not identical with *R. interruptum*, as asserted by Cornu, seems sufficiently manifest, since it lacks the highly differentiated basal cell, its sporangia are verticillate and its oospores are nearly smooth; while the receptive portion of the oogonium is always terminal, not "vers la base."[8] The close resemblances between the sexual organs and their action in the two genera is certainly striking: yet until further data are obtained concerning these phenomena in other genera of the sub-family, it seems not unreasonable to assume that they may have a more than generic significance.[9]

The form may be briefly characterized as follows:

### Sapromyces Reinschii (Schröt.) Fritsch.

Fritsch, Œsterr. bot. Zeitschr. **43:** 420. Dec. 1893.

*Hyphomycetarum* nov. gen. Reinsch, Contrib. ad Algol. et Fungol. 99 (Chloroph.) *pl. 14 f. 1. a–d.* 1875.

*Naegelia species* I et *species* II, Reinsch, Pringsheim's Jahrbücher, **11:** 298. *pl. 15. f. 1–11.* 1878. Fischer, Phycomycetes in Rabh. Kryptogamenfl. Pilze **1:** pt. 4. 377. 1892.

*Naegeliella Reinschii* Schröter, Engler and Prantl, Die Natürl. Pflanzenf. **1:** 103.

*Sapromyces dubius* Fritsch, l. c.

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[7] Contrib. ad Algol. et Fungol. 99 (Chlorph.) *pl. 14. f. 1. a–d.* 1875.

[8] Cornu, Ann des Sci. Nat. V. **15:** 30. 1872.

[9] The phenomena described by Prof. Humphrey (Saprolegniaceæ of the U. S., etc.,) in connection with the singular form described by him as *Apodachlya? completa*, do not, in the writer's opinion, afford sufficiently definite information on this point, in view of the uncertainty which exists as to their true significance. Both Rhipidium and "Naegelia Reinsch" appear to be excluded from the Leptomiteæ of Humphrey, yet it seems best on the whole, in the absence of further information, to assume the near relationship of those two genera with Leptomitus and Apodachlya, in conformity with the views of Fischer and Schroeter in the papers already cited. In this connection the close resemblance may be noted between the so-called chlamydospores of Apodachlya and the oospores of Sapromytces.

Hyphæ composed of numerous successive nearly cylindrical segments, arising one to several from undifferentiated basal segments attached to the substratum, each segment producing distally one to several similar segments, as a rule, bearing distally whorls of zoosporangia, oogonia and antheridial branches, the sexual organs on separate plants, but often associated with zoosporangia in the same whorl. Sporangia one to six in a whorl, slender sub-cylindrical to sub-clavate or stout and oval to elliptical or oblong. Oogonia sub-spherical to piriform becoming covered at maturity by a brown flaky incrustation disposed transversely, and containing a single spherical nearly smooth thick-walled oospore. Antheridia irregularly cylindrical, abruptly distinguished from the antheridial branch, sometimes divided by a septum, penetrating the oogonium always at its apex by a beak-like pollinodium. Hyphæ 7–30$\mu$ in diameter, the segments (larger) 450 × 10–15$\mu$. Zoosporangia 22–25 × 35–200$\mu$. Oogonia 26–40 × 32–55$\mu$. Oospores 20–30$\mu$.

On Viscum stems and algæ, Germany (Reinsch). On cones and twigs of Pinus in a spring, York, Maine.

*Cambridge, Mass.*

EXPLANATION OF PLATE V.

*Sapromyces Reinschii* (Schröt.) Fritsch.

Fig. 1. General habit of sporangiferous hyphæ.—Fig. 2. Whorl of three sporangia, one empty, the next before and the third during the discharge of zoospores, the axis segment turned to the right.—Fig. 3. Portion of hypha bearing stouter sporangia (Naegelia species II) before the discharge of zoospores.—Fig. 4. Hypha bearing oogonia, one of which is terminal. Also portions of two hyphæ producing antheridial branches, one of them also a zoosporangium, *x*.—Fig. 5. Oogonia and septate antheridium, a small collection of periplasm near the base and apex of the oosphere.—Fig. 6. Terminal oogonium with non-septate antheridium showing flaky incrustation of oogonium wall, a cellulin plug filling its constricted base.—Fig. 7. Empty thick walled sporangium.—Fig. 8. Oogonium showing oosphere with two antheridia attached.—Fig. 9. Three basal cells scraped from substratum, their cavities partly obliterated, that on the left giving rise to a sporangium and segments bearing oogonia and sporangia.

Fig. 1. Zeiss A, oc. 2. Figs. 2–4, 9. D, oc. 2. Figs. 5–8. D, oc. 4. Photo-reduced from ink drawings.