

First record of the parasitic aquatic oomycete *Ducellieria chodatii* from Pirin Mts (Bulgaria) with notes on its taxonomy, life cycle and ecology

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The present paper provides data on the new record of the interesting organism, transferred from algae to oomycotic stramenopilous fungi, *Ducellieria chodatii*, from south-eastern Europe (Bulgaria), which is also its first record for the region of Pirin Mts in the country. Additionally, discussion on the taxonomy, life cycle and ecology of the species is provided.

Keywords: aquatic parasitic stramenopiles, taxonomy, life cycle, *Coelastrum* stage, pollen.

The oomycetes in general sense are a ubiquitous group of fungal-like heterokont zoosporic organisms, referred also as non-photosynthetic stramenopiles (in the sense of Patterson 1989), and commonly known as water molds and downy mildews. The rank of the group ranged from class to phylum, therefore we want to stress that the name Oomycetes (Winter 1880) and its associated formal name Oomycota (Arx 1967) are used in the present paper following Lévesque (2011), while the alternative group name, the Peronosporomycetes formally proposed by Dick (2001) is considered a synonym, as in the last edition of the Dictionary of fungi (Kirk *et al.* 2008). There, oomycetes are defined as a class within the kingdom Chromista and the more formal kingdom name Straminipila given by Dick (2001) is not accepted. Currently Lévesque (2011) suggested again the usage of the kingdom name Straminipilia, outlining the opportunities which this clarifying could create for future studies of the group and for the oomycete research community. Beakes *et al.* (2012) accept fungal-like oomycetes and hy-

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phochytrids, together with the marine flagellates *Pirsonia* (parasite on marine diatoms) and *Developayella* (free-living bacteriotroph), as part of the clade defined by Cavalier-Smith & Chao (2006) as the phylum “Pseudo-fungi”, which is a sister to the photosynthetic chromistan algae (phylum Ochrophyta). Together both clades constitute the Chromalveolate “super-kingdom” clade.

The evolutionary roots of oomycetes are in marine environments, from which they migrated to land with host organisms early in the evolution of eukaryotes (Beakes & Sekimoto 2009, Lara & Belbahri 2011, Beakes *et al.* 2012) but nowadays these zoosporic organisms are found all over the world as aquatic (marine, brackish and freshwater) and terrestrial saprotrophs or parasites, most of which behave as opportunistic pathogens of plants and animals and few are symbiotic (Cook *et al.* 2001, Hudspeth *et al.* 2003, Soanes *et al.* 2007, Wurzbacher *et al.* 2010, Lara & Belbahri 2011, Thomas *et al.* 2011, Beakes *et al.* 2012 among the many others). Many freshwater molds grow in well-aerated water bodies and within these habitats they are most common in shallow waters near the bank or shore (Alexopoulos *et al.* 1996).

During the last three decades the phylum Oomycota was enriched by the freshwater genus *Ducellieria*, accepted previously as an algal genus (Kusel-Fetzmann & Nouak 1981, Kusel-Fetzmann & Carniel 1984, Hesse *et al.* 1989) and this resulted in establishment of a new family – Ducellieriaceae Dick 2001 in the order Leptomitales (Dick 2001, Kirk *et al.* 2008, Moore *et al.* 2011). The proposal to transfer *Ducellieria* from algae to fungal-like protists was based on detailed studies on the ultrastructure and life cycle of the species *Ducellieria chodatii* (F. Ducell.) Teiling 1957 in cultures (Kusel-Fetzmann & Nouak 1981, Kusel-Fetzmann & Carniel 1984, Hesse *et al.* 1989). However, *Ducellieria* remained in the list of green or yellow-green (heterokont) algae in some commonly used manuals and floras, and in some scientific papers (e.g. Komárek & Fott 1983, Couté 1984, Dillard 1989, Ott & Oldham-Ott 2003). At present it is pointed as an entity that is currently accepted taxonomically in the most used database for algae – AlgaeBase (Guiry & Guiry 2012). The genus *Ducellieria* is not even mentioned in the modern reviews on the “oomycete fungi” (Lévesque 2011, Beakes *et al.* 2012). Irrespectively of the fact – was it assumed as alga or as an aquatic fungus – this organism was relatively rarely reported from field studies after its first description as *Coelastrum chodatii* by Ducellier (1915) and its later taxonomical designation as the basionym of the type species *Ducellieria chodatii* Teiling of the genus *Ducellieria* by Loeblich (1967). The present paper provides data on the new record of *D. chodatii* from south-eastern Europe (Bulgaria), which is also its first record for the region of Pirin Mts in the country. Additionally, discussion is provided on the taxonomy, life cycle and ecology of this species.

Materials and methods

During an algological investigation of the alpine zone in the northern part of Pirin Mts 52 samples from different habitats and ecological groups (e.g. phytoplankton, metaphyton, phytobenthos) have been collected. The material described in this study was found in one of these samples, which was taken from a water surface film nearby the shore at the outflow of the lake “Popovo Ezero 2” (IWB 0447 in Michev & Stoyneva 2007), situated at ca. 2252 m a.s.l. The water temperature was 13.9 °C, pH 8.2 and conductivity 9 µS.

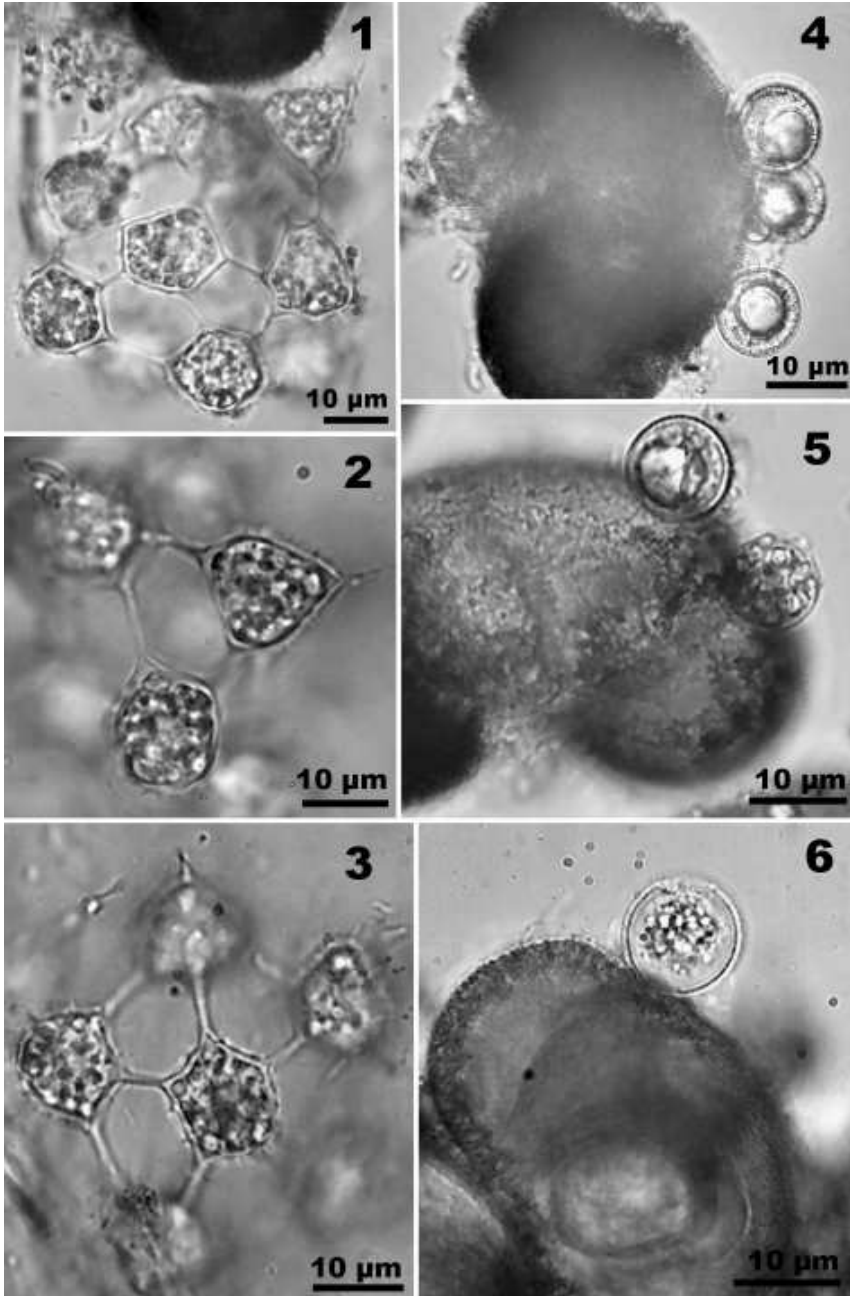
The algal sample was collected in a plastic tube and fixed immediately with 4 % formaline final concentration. The material was checked in the lab on non-permanent slides by means of light microscopy (LM) on microscope Motic BA 400 equipped with immersion and phase contrast objectives. The photos were taken by camera Moticom 2000 and images have been processed by special program Motic Images Plus 2.0.

Results and discussion

The first determination of *Ducellieria chodatii* in our material was done according to the algological literature (Bourrelly 1968, Ettl 1978) due to its typical coenobial outfit (Ducellier 1915, Rayss 1915, Teiling 1957) (Figs. 1–3). The cells were (7)10–13(15) µm in diameter, the hollow spines were (5)7–11(13) µm in length and the diameter of the “coenobium” was up to 65–70 µm. The further checking of references lead us to the profound investigations of this species, done by Kusel-Fetzmann & Nouak (1981), Kusel-Fetzmann & Carniel (1984), Hesse *et al.* (1989). These authors demonstrated that the yellow-green alga *Ducellieria chodatii* (formerly known as the green alga *Coelastrum chodatii* Ducell.) should be transferred to the group of oomycetes in general sense.

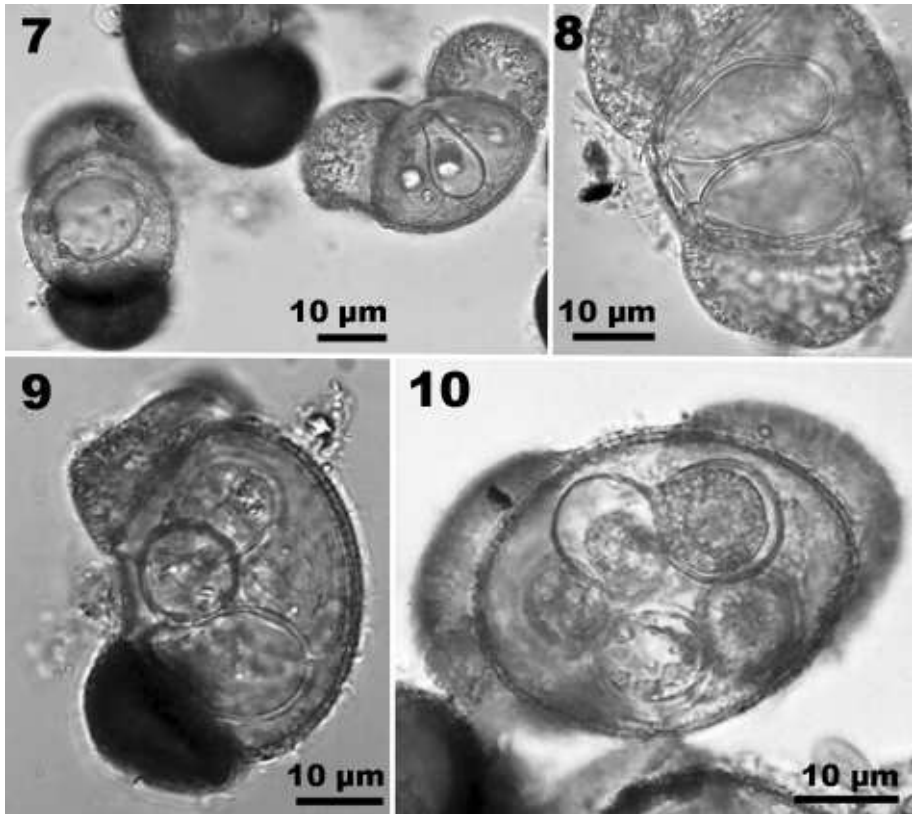
Further detailed and purposeful investigations of the collected material by light microscope revealed almost all stages of the life cycle of *Ducellieria* related with pollen grains, as they were described by Hesse *et al.* (1989), except the stages depicted in part C of their figure 10 (see also Fig. 21 in this paper):

- Empty secondary cysts on the pollen exine (ca. 10–12 µm), which remained after settling and encystment of the zoospores and which, according to Hesse *et al.* (1989), could persist outside the pollen grain for more than 24 hours in living material (Fig. 4).
- Holocarpic saccate (bottle-shaped) thalli/zoosporangia inside the pollen grains (“intramatrical zoosporangia” in the terminology by Hesse *et al.* 1989) in different number – from one to five, ca. 8–10 × 20–22 µm (Figs. 7–10).
- Cyst aggregates (“primary zoosporangial aggregates” according to Hesse *et al.* 1989, “*Coelastrum* stage” or also “pseudo-*Achlya* like spore ball” according to Dick 2001, formerly known as algal coenobia of *Ducellieria*



Figs. 1–6. *Ducellieria chodatii*. 1–3. Free floating ‘Coelastrum stage’; 4–6. Secondary cysts and specific globular encystment stages of zoospores on the pollen exine (proximal side of the corpus region).

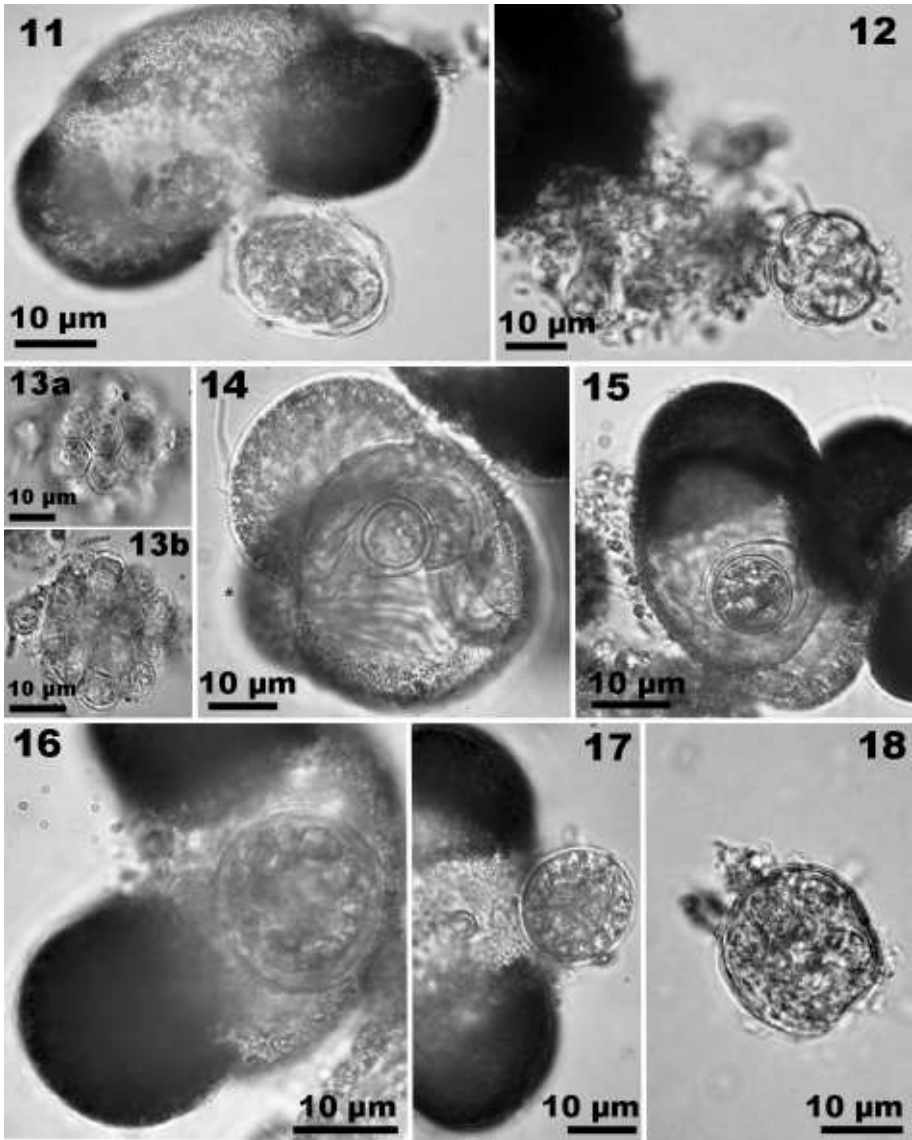
chodatii), in different stages of their release from the pollen (with a “nose-like discharge tube” and “mucilagenous court” in a “morula-like agglomeration” of “plasmaportions, i.e. individual spores” in the terminology of Hesse *et al.* 1989) and free-floating hollow spheres or irregular aggregates of individual cysts connected with hollow spines outside the pollen grains (Figs. 1–3, 11–13 a, b).



Figs. 7–10. *Duceillieria chodatii*. Holocarpic thalli inside the pollen grains in different numbers: 7. One and three thalli; 8. Two thalli; 9. Four thalli; 10. Five thalli.

- Oosporangia with globular oospores (also “resting spores” in the terminology of Hesse *et al.* 1989 and Dick 1981; one oospore per oosporangium), (10)20–30 µm in diameter, with a thick smooth cell wall, inside the pollen grains (Fig. 14).

All these stages fit well to the descriptions of Hesse *et al.* (1989, depicted on their figures 1, 4, 5 and 10) and afterwards concisely reported by Dick (2001) in his book on straminipilous fungi. Additionally to the structures and stages, which have been already described, we found some structures which

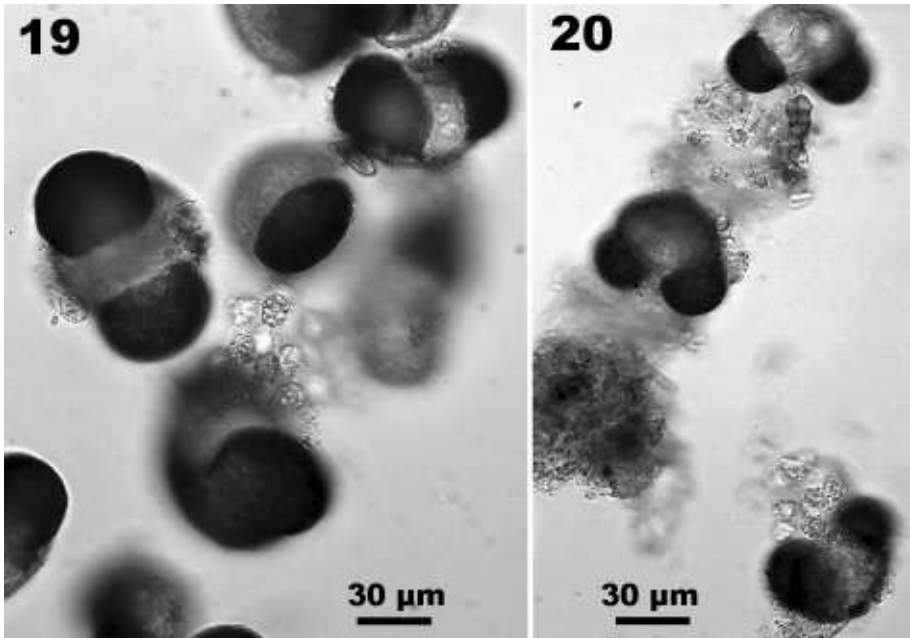


Figs. 11–18. *Ducellieria chodatii*. 11–13. Release of the “morula-like agglomerations” from pollen grains: 11. Morula-like agglomeration in a ‘bubble’; 12–13. Free-floating morula-like agglomerations, which will develop in typical ‘*Coelastrum stage*’; 13 a and 13 b represent the same “morula” in different focus. 14. Plerotic oospore in the oosporangium inside the pollen grain. 15–18. “Morula-like agglomeration” covered with a thick wall inside the oosporangium (15–16) and free-floating outside the grain (17–18).

have not been mentioned in the literature but are obviously related with the complicated life cycle of this aquatic fungus. These findings allowed us to suppose more possibilities for the development of the zoospores and to emend the descriptions of the formation of the peculiar for the species cyst aggregation (the *Coelastrum* stage) (Fig. 21). Relatively large globules, up to 15(20) μm in diameter (rare - vase-shaped forms, $13 \times 16 \mu\text{m}$ with up to 3 μm wide opening) with thick structured (?sculptured) wall were observed as situated mainly on the upper (proximal) side of the corpus region of the pollen grains (Figs. 4–6). It is possible to suppose that they represent specific encystment stages of zoospores, which could not enter the pollen grain (most probably because of its hard crested character) or did not penetrate it due to other, unknown reasons. Afterwards, by means of multiple protoplast division, they develop into cysts (zoosporangia) which are aggregated in the same *Coelastrum*-like structures (generally containing 8–16 cysts, each 3–4 μm in diameter) like the cysts (primary zoosporangia) released from the holocarpic thalli, formed inside the pollen grains (Figs. 5, 6, 12, 13). According to the photos and descriptions provided by Hesse *et al.* (1989: figure 5) the size of the cysts in the pre-aggregates (“morula-like agglomerations”, released in mucilaginous “bubbles” in the terminology of these authors) coming out from the pollen coincides with the size of the cysts in the free-floating *Coelastrum*-like aggregates. However, the observations from our material clearly show the enlargement of the pre-aggregates with significant changes of the size until they form the typical “*Coelastrum* stage” (Figs. 12, 13). The lack of data on these globular and vase-shaped structures in previous papers could be easily explained if the generalization provided by Dick (2001, p. 235) is taken into account: “in attenuated cultures ... the “*coelastrum*” stage is omitted”.

Although the investigated material was abundant, we did not see any gametangial fusion. By contrast, many oosporangia, each with a single oospore with a thick smooth cell wall (Fig. 14), were observed. Therefore, it is possible to suppose with a high probability that in the life cycle of *Ducellieria* a parthenogenetic reproduction (oospore formation) is involved. The possibilities for the appearance of such a reproduction type in Oomycota were already outlined by Cherepanova (1981). Doubtless, the clearing of the sexual process in this species should continue, since Hesse *et al.* (1989: p. 6–8) mentioned that “the fusion of gametangial thalli may occur inside the pollen grain, but could not be observed directly” and Dick (2001: p. 236) described the sexual reproduction as “apparently plerotic”.

Inside the pollen grains and inside the oosporangia we saw globular structures with a thick cell wall and divided protoplast, resembling the morula-like agglomeration, and the same structures (10–20 μm in diam.) were seen as released out of the cells (Figs. 15–18). By contrast to the pre-aggregates released from the intramatrical zoosporangia, these morula-like aggregations from the beginning are covered by a thick wall, which remains during their floating outside (Figs. 17, 18). We could only suppose that these



Figs. 19–20. *Ducellieria chodatii*. General view of ‘Coelastrum stages’ between the pollen grains in the collected sample.

are future *Coelastrum*-like cyst aggregates, which in this stage could survive unfavorable, harsh environmental conditions. The probability for the existence of such a pathway for zoospore formation from oospores in nature was suggested by Hesse *et al.* (1989), but was not observed in their experiments.

Taking into account all the observations of our field material, we could enrich the schematic representation of the life cycle of *Ducellieria chodatii*, proposed by Hesse *et al.* (1989: fig. 10) in the way depicted in Fig. 21.

The ecological requirements of *Ducellieria chodatii*, drawn from the published data on its habitats (e.g. Komárek & Fott 1983, Ott & Oldham-Ott 2003), are in conformity with the generalization made by Alexopoulos *et al.* (1996) for most of the aquatic oomycetes, which develop in calm waters near the shores of the water bodies. In the special case of *Ducellieria*, it has to be pointed out that it is related with the abundant appearance of pollen grains (in thick yellowish films on the water surface or on the surface of submerged leaves, twigs, etc.) and therefore it is to be expected in water bodies various in shape and size and surrounded by or in a close vicinity of coniferous trees, while the findings in the pelagial phytoplankton of large clear lakes (for details see Teiling 1957) are obviously occasional. This explains the rare findings of the species in the phytoplankton samples and the significance of presence of “pollen substrate” for its development, pointed out by Kusel-Fetzmann & Nouak (1981). This habitat description is absolutely relevant for the

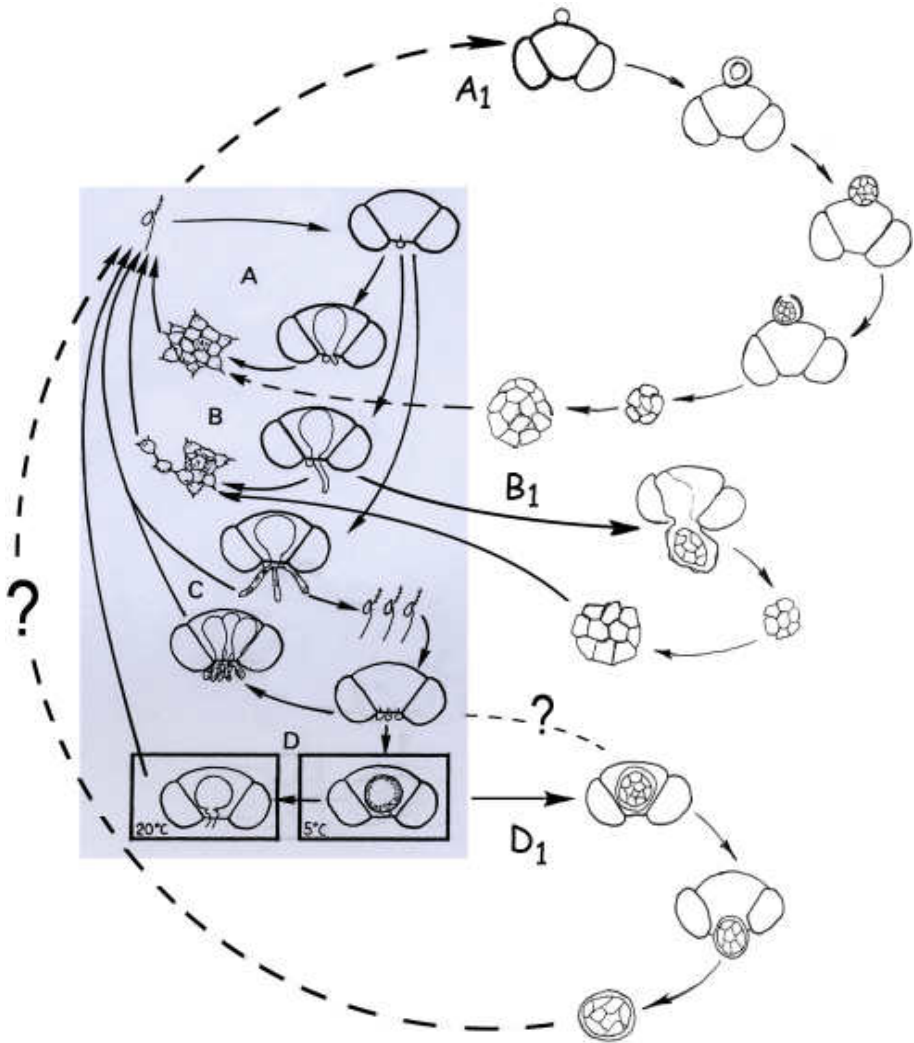


Fig. 21. Life cycle of *Ducellieria chodatii* (details described in the text): **A-D**. Original figures of Hesse *et al.* (1989); **A₁** additional way of zoospore development from encystment on the pollen exine until new zoospore release from primary zoosporangia; **B₁** more detailed depiction of the stages in the cycle part B of Hesse *et al.* (1989); **D₁** – additional way of oospore development into zoosporangia through morula-like agglomeration in a thick wall.

species distribution in Bulgaria. Until now it was reported altogether four times (as *Coelastrum chodatii*) for mountain water bodies of different types and size, surrounded by conifers: (1) a small swamp among *Picea abies* and *Pinus mugo* near the rivulet Urdina Reka and (2) peat bogs near the rivulet Marinovitsa in Rila Mts (Wodenitscharov 1960 a, b, 1962), (3) mountain lakes

Smolyansko Ezero and (4) Chairski Ezera in Rodopi Mts (Kiriakov 1981). On the basis of the first data the species was included in the Bulgarian algal flora as known from Rila Mts (Vodenicharov *et al.* 1971). In our material from Pirin Mts *Ducellieria chodatii* appeared in the calm-side waters of the alpine lake outflow among the pollen film (Figs. 19, 20) on the surface of the water and on the fallen and submerged leaves of *Veratrum album* near to a group of *Pinus mugo* needles, aggregated by wind.

The taxonomic history of *Ducellieria* was described in detail by Hesse *et al.* (1989). We have to note that in addition to both species mentioned by them (and by almost all other authors) – *D. chodatii* and *D. tricuspидata* (Borge) Teiling 1957 (basionym: *Coelastrum tricuspидatum* Borge 1936), there is one more variety – *D. chodatii* var. *armata* (Skuja) Teiling 1957 (basionym: *Coelastrum augustae* var. *armatum* Skuja 1934), and one more species – *D. corcontica* Matula 1980, which have not been discussed and were not included in Kirk *et al.* (2008) obviously because of lack of confirming records up to now. Moore *et al.* (2011) only mention the inclusion of the genus *Ducellieria* among Leptomitales, but did not provide information on species. Dick (2001) did not accept the transfer of *C. tricuspидatum* and *C. augustae* var. *armatum* to the genus, writing only about the discrepancy of the illustration of the last variety in Teiling (1957) with the hollow nature of spines, typical in his opinion for the new family Ducellieriaceae. In our opinion, figure 11 in Teiling (1957) could be treated more like a schematic representation of the contact of each two spines by their ends, rather than representing septa in one spine. This is obvious, if figures 2 d and 3 b of Kusel-Fetzmann & Nouack (1981) and figure 6 from planche I of Couté (1984) are considered, and sometimes in our material such joining points were seen by immersion on high magnifications of the light microscope. Couté (1984) especially raised the question about the taxonomic importance of the difference in joining of two spines, writing that figures 9–11 in Teiling (1957) show the diversity of these connections, and that in *D. corcontica* the two spines join side by side. Therefore, we could suppose that these taxa should not be taken away from *Ducellieria* until their thorough investigation is done and for the moment they should be included in the genus at least in *incertae sedis* status.

In conclusion, our observations justify the considerations of Kusel-Fetzmann & Nouak (1981), Kusel-Fetzmann & Carniel (1984), Hesse *et al.* (1989) and according to the current state-of-art we accept the opinion of Dick (2001), Kirk *et al.* (2008) and Moore *et al.* (2011) for the taxonomic position of *Ducellieria chodatii* among Oomycota.

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