A new *Dangeardia* which invades motile Chlamydomonadaceous monads

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INTRODUCTION

In a cool, but sunny, period in the first days of November 1967 the author collected a sample of dirty-greenish foam blown by the wind into a pool intensively contaminated with organic substances, on the sandy beach along the Vistula bank in Warsaw (Poland). The intensive insolation together with the low temperature of the water at this period were favourable for the blooming of algae in small water bodies, whereas the perfect aeration of the material in the foam provided conditions favourable for the development of zoosporic fungi parasitizing on algae, thus the author expected to find in such samples an abundant material for studies on zoosporic fungi of Poland. This anticipation found full confirmation in the course of a preliminary inspection of the collected material: the fluid which collected at the bottom of the vessel when the foam fell was dark green and contained a swarm of plankton organisms. Diatoms of the genera *Cyclotella, Navicula, Nitschia* and others, as well as green algae of the order *Volvocales* were most abundant among the phytoplankters. Moreover the material contained a considerable number of cells of *Cryptomonas* sp., *Euglena* sp. div. and *Scenedésmus* sp. div. as well small fragments of a very young coenobium of *Hydrodictyon reticulatum* (L.) Lagerh. In the zooplankter population ciliates predominated, and among them *Paramaecium bursaria* (Ehrenb.) with numerous symbiotic zoochlorellae in the ectoplasm were very abundant. Besides, a profusion of various *amoeba nuda* and *Heliozoa* was present.

Volvocales were represented by *Eudorina elegans* Ehrenb., *Pandorina morum* Bory, *Gonium pectorale* Müll., *G. sociale* Warm., *Phacotus subglobosus* Pasch., *Chlamydomonas angulosa* Dill., *Ch. reinhardi* Dang. (?) and *Sphaerellopsis aulata* (Pascher) Gerloff, the latter species being most abundant.

The presence of several species of zoosporic fungi parasitizing on

algae was also revealed in the course of the preliminary inspection of the freshly collected material: sporangia of an epibiotic monocentric member of *Chytridiales* were found on several cells of *Navicula* sp. and *Nitschia* sp. as well as on monads of *Chlamydomonas angulosa*, whereas more than half of the monads of *Sphaerellopsis aulata* exhibited symptoms of infection with a parasitic fungus forming sporangia and resting spores, epibiotically in respect to the host's protoplast, but lying under the outer cellulose-pectinic wall. The parasites of diatoms and *Chlamydomonas angulosa* were relatively few, thus the author did not succeed in a more detailed study of their development and morphology. On the other hand, the fungus parasitizing on *Sphaerellopsis aulata* was abundantly represented in the sample not only at the moment of its collection, but in the course of ten days in the laboratory it multiplied so intensively that finally it selectively exterminated the representatives of the host present in the sample. This made possible a detailed study of the structure of both the parasite and its host which was found to be a little known species, presenting several interesting taxonomic and nomenclature problems. In view of this the description of the fungus will be preceded by the information on the results of observation of its host.

THE HOST

The mature monads of *Sphaerellopsis aulata* are characterized by a loose position of the pyriform protoplast in the considerably larger and generally almost spherical outer wall (Fig. 1, 11). The stable position of the protoplast in respect to the outer wall indicated that the space between them is filled with a rigid, gelatinous substance and not with fluid. The body proper of the monad is about 26×21 μm. The monad's chromatophore has the shape of a bowl with a thick bottom and walls thick at the base and strongly tapering towards their top; the chromatophore's surface is covered with delicate streaks arranged more or less meridionally; a large pyrenoid covered with amylum grains lies at the bottom of the chromatophore bowl. A spherical translucent nucleus is observed in the relatively small internal space of the protoplast free of the chromatophore; two contractile vacuoles adhering to each other are visible in the anterior part of the protoplast containing blepharoplasts of the flagella. Since these vacuoles function alternately, generally only one, that in the diastole phase, is readily visible. The dark red stigma with a circular outline and somewhat convex profile is invariably well visible on the surface of the protoplast at about mid length of the monad's body. The two thin flagella, well visible even
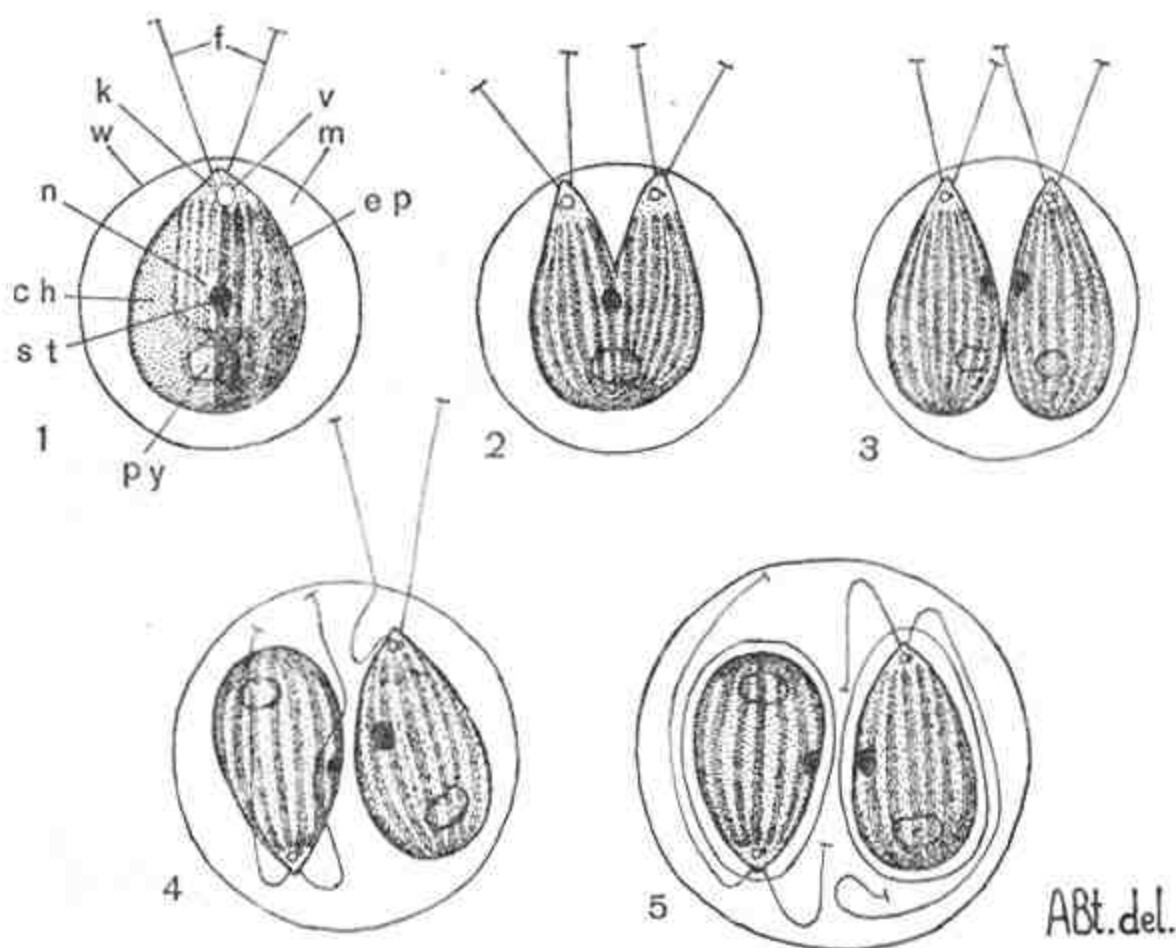
Figs. 1—5. Thallus structure and asexual reproduction of *Vitreochlamys aulata* (Pascher) comb. nov. Fig. 1. — mature monad, left — optical section, right — surface view: *f* — flagella, *w* — metaplasmatic wall, *m* — gelatinous layer, *ep* — euplasmatic membrane, *ch* — superficially striated protoplast, *py* — pyrenoid, *st* — stigma, *n* — nucleus, *v* — contractile vacuoles, *k* — kinetoplast. Fig. 2 — splitting of the kinetoplast and the anterior pole of the monad's protoplast. Fig. 3 — two already separated zoospores with flagella still protruding through the maternal monad's wall. Fig. 4 — right — successive threading of the zoospore flagella through the pores in the zoosporangium wall, left — zoospore with both flagella already inside the zoosporangium. Fig. 5 — two young monads already covered with their own metaplasmatic walls (i.e. — differentiated) in the swollen, gradually dissolving zoosporangium.

(Free-hand drawing of the material sampled in Warsaw: Figs. 2—5 in surface view, all figures somewhat schematized).

without employing contrast phase microscopy are over twice the length
of the monad's protoplast and about 1.5 times longer than the entire
cell together with its outer wall.

Most of the monads of *Sphaerellopsis aulata* observed in the freshly
collected material were in the phase of vegetative growth; only about
20 per cent of the total number of monads were in the course of asexual
reproduction. Only completely mature, large monads, with protoplast
length exceeding 22 μm started division at this period. To the author's
knowledge the division of monads of this species has not hitherto been
the subject of published observations. In view of this and of the im-
portance of this process for the establishment of the taxonomic posi-
tion of the alga studied, the process of division will be discussed in
detail.

The earliest phase of division observed (Fig. 2) was characterized
by the splitting of the kinetoplast, i.e. the anterior pole of the monad's
protoplast containing the bases of the flagella with blepharoplasts (in-
visible in vivo) and the contractile vacuoles. Since in all the cases
observed both daughter kinetoplasts formed in this process contained
a full set of organelles, i.e. two flagella and two vacuoles, it is probable
that the partial cleavage of the kinetoplasts is preceded by duplication
of these organelles. It seems, however, that this process occurs directly
before the division starts and lasts a very short time since the author
did not succed in observing it "in flagranti", though Ettl (1963) detected
a considerable number of monads with four contractile vacuoles in the
S. aulata population studied.

Ettl does not mention the possible connection between this symptom
and the preparation of the monad for division. At any rate, in the
monads collected in Warsaw the duplication of the set of the kineto-
plast's organelles seems to have occurred rather before the beginning of
the division than after the formation of the furrow. This, according
to Z a k h v a t k i n's (1949) terminology qualifies this type of di-
vision to paratomy. At this phase both sets of flagella protrude
through four separate pores in the monad's outer wall. Owing to this, at
first sight under low magnification these monads had the appearance of
four-flagellate individuals and exhibited a motility normal for vegetative
monads.

The further process of longitudinal fission of the monads occurs very
rapidly, in the course of a dozen or so minutes. The author observed
this process only several times, and in view of the great motility of the
dividing monads, the behavior of the cell nucleus and pyrenoid during
this process could not be established. It is probable that karyokinesis
started in the monads soon after, or almost simultaneously but not
earlier than the splitting of the kinetoplast, since a single nucleus was

rather well visible in the monads exhibiting a shallow furrow. Soon after this the nucleus became invisible *in vivo*, and only after completion of plasmotomy did nuclei appear in the daughter protoplasts. On this basis, the conclusion may be advanced, that the paratomy of the alga studied exhibits the following two characteristics: 1) it does not start by the prophase of the nucleus, but by the duplication of the kinetoplast's organelles, 2) the processes connected with the preparation of the cell for division do not precede the formation of the furrow but occur simulataneously, taking place successively in various organelles from the anterior towards the posterior pole. In all the cases observed the gradually deepening furrow ran through the stigma, which split, and for a short period lost its regular circular outline.

Still before the final separation of the daughter protoplasts, the segments of flagella visible externally undergo a marked shortening since they are partially drawn into the maternal cell. The two separated daughter monads perform several energetic oscillatory movements with their anterior body ends threading successively one and then the second flagellum through the pores in the outer wall of the maternal cell (Fig. 4). Owing to this the cell is deprived of its motility and transforms into a zoosporangium containing two zoospores. Moreover, the zoospores in the fresh material from Warsaw almost immediately underwent a final differentiation into young monads, consisting in the formation of their own outer cellulose-pectic walls (Fig. 5). The young monads of *S. aulata* enclosed in the zoosporangium differed from the free-swimming monads of this alga in the first place in that their outer wall closely adhered to the protoplast, this resulting in an oval outline. During the several-hour presence of young monads within the zoosporangium the outer wall of the latter gradually became thinner and thinner and less visible in transmitted light; simultaneously the diameter of the sporangium increased distinctly and this suggests that at this period it is distenned by internal pressure and gradually dissolved. In this period the young monads exhibited a constant moderate motility; their appearance changed somewhat owing to the gradual formation of a layer of gelatinous matrix under their own outer wall. The final formation of this layer and the characteristic rounded outline occurred, however, only after the disruption of the weakened sporangium wall and emergence into the external environment.

The transformation of the dividing monad into a zoosporangium is accompanied by significant changes in the gelatinous matrix lining the internal side of the outer wall: the mobility of zoospores and young monads in the zoosporangium as well as Brown's movements of casual contaminations of the sporangium content e.g. remnants of the dead

zoospore, indicate that this matrix transforms into a fluid of very low viscosity.

The further development of monads which abandoned the zoosporangium consists in an about twofold increment of the protoplast's volume and multiple increment of the entire monad by the rapid secretion of the gelations substance mentioned above.

The mode of the cell division of the Polish *Sphaerellopsis aulata* strain does not exhaust the developmental abilities of this alga. In a number of cases the author observed within the sporangia four, instead of two, young monads. The number of individuals exhibiting such a mode of division was practically null in the fresh material brought to the laboratory and stored for 3 days at low temperature (about 10°C), but as the population grew older, and particularly after its transfer to higher temperatures (16—18°C) this number increased. At the same time the author observed the characteristic phenomenon of dwarfing of the *S. aulata* population, since even monads with a protoplast not exceeding 18—20 µm started to divide. Owing to this and the division into four instead of two parts, the size of the monads emering from the sporangia was not 12—14.5 µm as originally but only 8—10.5 µm.

The initial phase of this type of division exhibited an identical course as in the former type. The difference appeared only after the transformation of the material cell into a zoosporangium. Namely, at this period the zoospores did not form their pectocellulose wall, but immediately underwent a repeated longitudinal division in a "naked" state. Except for this the course of division was identical as in the former type. The four zoospores thus formed underwent further differentiation into young monads, i.e. they developed their own outer walls. Their further development was identical as in the first type of division.

According to the classification of modes of division in *Protista* proposed by Z a k h v a t k i n (1949) the first type of division of *Sphaerellopsis aulata* monads may be considered as m o n o t o m y i n d i f f e r e n t i a t e d s t a t e, since the cell undergoes division into two tomites without any previous dedifferentiation, i.e. it loses neither its flagellum nor other organelles characteristic of mature monads. According to Zakhvatkin this type of division is rather rarely observed in lower *Chlorophyceae*. It has been observed in *Polyblepharidaceae* cells deprived of the separate metaplasmatic wall (an outer wall separate from the protoplast membrane) and enclosed only in an euplasmatic membrane (a thin, elastic membrane — integral part of the living protoplast). According to the same author, the monads of *Chlamydomonadaceae*, the protoplasts of which have both metaplasmatic walls and euplasmatic membranes, generally undergo division in the d e d i f f e r e n t i a t e d s t a t e, i.e. at least after losing the flagellum, or even in the h y p e r-

d e d i f f e r e n t i a t e d s t a t e, when only the internal part of the protoplast containing the nucleus and chromatophore undergoes division while the thin peripheral protoplast layer adjacent to the metaplasmatic wall together with the entire kinetoplast, flagella, contractile vacuoles and stigma does not take part in the division and after the conclusion of this process is rejected and does not become the component of any of the daughter monads. Moreover, in both cases the *Chlamydomonadaceae* monads undergo repeated divisions in rapid succession without differentiation and without growing in the intervals between divisions, thus the final number of tomites is generally 4, 8, 16 etc. up to 128 in some cases (when spermatozoids are produced in oogamic species). In Zakhvatkin's classification this type of division is termed p a l i n - t o m y. In view of this the monotomy of *Sphaerellopsis aulata* taking place in the differentiated state (the rejection of the metaplasmatic wall cannot be actually treated as dedifferentiation) significantly distinguishes this alga from other representatives of the family *Chlamydomonadaceae* known in this respect, and particularly from the *Chlamydomonas* species, and indicates that this species should be classified between lower *Volvocales* (*Polyblepharidaceae*) and *Chlamydomonadaceae* proper. The second mode of division of *S. aulata* cells can be regarded as a rather simple case of palintomy in the differentiated state, thus this alga must be classified to *Chlamydomonadaceae*, though in the range of this family it occupies one of the most primitive positions.

The considerations on the taxonomic significance of the cell division processes in *Sphaerellopsis aulata* are included in view of the controversy as to the purposefulness of establishing this genus. Many investigators and among them the author of the genus *Sphaerellopsis* himself later included this genus in the *Chlamydomonas* claiming that *Sphaerellopsis* is at the utmost a subgenus. Other authors, such as G e r l o f f, S k u j a, B o u r e l l y and E t t l (see E t t l, 1963) claim that the genus *Sphaerellopsis* should remain a separate genus and stress that the morpho-anatomic bases of this genus are no less taxonomically significant than those of many other *Chlamydomonadaceae* genera, such as *Chlorogonium* Ehrenb., *Gloeomonas* Klebs or *Thorakomonas* Korschikoff (see also G e r l o f f 1940). The distinct differences as regards the development of *Sphaerellopsis aulata* as compared with the species of *Chlamydomonas* s. str. quoted in this paper seem to confirm the opinion of Gerloff and Ettl, and I myself believe it to be correct. It should be stressed, however, that the species discussed in the present paper is not the type-species of the genus *Sphaerellopsis* Korschikoff, and only a more detailed study of the division processes in the type-species,

i.e. in *Sphaerellopsis fluviatilis* Pascher (syn.: *S. crassicauda* Korschikoff) may supply convincing evidence to support this concept.

Though the preliminary identification of the alga discussed collected in Warsaw was relatively easy and it was identified as *Sphaerellopsis aulata* (Pascher) Gerloff [described as *Chlamydomonas aulata* Pascher (1927) on the basis of the material collected in Ukraine by Korschikoff], it should be remembered that it differed from the type-strain from Ukraine by the following features: the metaplasmatic wall of the alga studied had an ideally even outline and was deprived of any convex papilla at the site at which the flagella protrude, whereas the dimensions of the protoplast distinctly exceeded those given by P a s c h e r ($15-22 \times 10-17 \mu m$). E t t l (1963) described a form of *S. aulata* from Slovakia more similar to that observed by the present author; namely it was also deprived of the papilla, whereas its dimensions coincided both with the results of P a s c h e r and mine ($15-38 \times 7.5-30 \mu m$) [*]. On the other hand, the strain from Slovakia differed from those from Ukraine and Warsaw by the fact that a part of the monads exhibited four contractile vacuoles functioning in pairs. As mentioned above Ettl gives no evidence to prove whether this phenomenon has any connection with the preparation of cells for division. In view of this the differences occurring between the three strains of *Sphaerellopsis aulata* are in my opinion symptoms of geographical or clonal variability and I classify the alga from Warsaw as *Sphaerellopsis aulata* stressing its morphological similarity to the strain observed by Ettl in Slovakia.

Independently of the taxonomic problems certain nomenclature questions arise in connection with this alga, since the generic name *Sphaerellopsis* Korschikoff (1926) is a later homonym of the generic name *Sphaerellopsis* Cooke (1883) given to a genus of ascomycetous fungi. The name *Sphaerellopsis* Cooke is not only formally valid and this automatically invalidates the name *Sphaerellopsis* Korschikoff in view of the Art. 64 of the International Code of Botanical Nomenclature (L a n j o u w et al. 1961, further referred to as the "Code"), but it is used contemporarily. Moreover, its taxonomic sense has been recently more precisely defined by P e t r a k (1968). This state excludes the use of the generic name *Sphaerellopsis* Korschikoff and renders impossible the proposal of its maintenance according to Art. 14 of the Code. In view of this I propose its substitution by a new name and the formation of new combinations for the type species of this genus and for the one discussed in the present paper:

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[*] The similar strain has been recently found in Romania by L. Peterfi, Nova Hedwigia 16 (1—2): 215—250. 1968.

Vitreochlamys nom. nov.

= *Sphaerellopsis* Korschikoff, Arch. Russ. Protistol. 5: 1926, nom. praeocc. (homo-
nym prius: *Sphaerellopsis* Cooke, Grevillea 12: 23, 1883).
Typus generis: *V. fluviatilis* (Stein) comb. nov.

Vitreochlamys fluviatilis (Stein) comb. nov.

Basonym: *Chlamydococcus fluviatilis* Stein, Der Organismus der Infusionstiere.
II. Abtlg., I. Hälfte. Der Organismus der Flagellaten, I. Hälfte, Leipzig. 1878.
= *Sphaerellopsis fluviatilis* (Stein) Pascher, Süsswass. Fl. 4: 324, fig. 292. 1927.
= *Sphaerellopsis crassicauda* Korschikoff, Arch. Russ. Protistol. 4: 1926.

Vitreochlamys aulata (Pascher) comb. nov.

Basonym: *Chlamydomonas aulata* Pascher, Susswass.-Fl. 4: 225. 1927.
= *Sphaerellopsis aulata* (Pascher) Gerloff, Arch. Protistenk. 94: 482. 1940.
= *Chlamydomonas gloeocystiformis* Dill sensu Korschikoff in Pascher, l. c.: 225, 1927.

THE STRUCTURE AND DEVELOPMENT OF THE PARASITE THALLUS

The vegetative monads as well as the zoospores and young monads of *Vitreochlamys aulata* hidden in the sporangium are motile at any stage of their development. Owing to this the entire development of the fungus parasitizing on this alga takes place under rather specific conditions. This circumstance affects particularly the initial developmental stages of the fungus, namely the phase of infection and initial period of the phase of thallus growth.

Phase of infection. The either spherical or somewhat elongated fungal zoospores provided with a long backward directed flagellum move rather rapidly. Their movements are fluent and not "hopping" as it is observed in many other *Chytridiales* species parasitizing on algae. A grain intensively refracting light is readily visible in the zoospores, particularly in those which recently abandoned the sporangia. In the material studied a single drop of suspension placed in a microscopic preparation generally contained at least several mature fungal zoosporangia. Therefore soon after illumination of the preparation with a strong light under the microscope the number of zoospores liberated from these zoosporangia became so numerous that they could be seen in almost every field of vision. The initially rapid and fluent movement of the zoospores remains undisturbed even when they pass close to the alga cells. This state, however, lasts but 15—30 min. After this period distinct changes occur in the behaviour of the zoospores: the several-second periods of rapid movements alternate more and more frequently with longer — even several-minute periods in which the zoospores remain immobile on the cover slip surface. It seems that this phenomenon may be partly ascribed to the rapid changes of physical and chemical coniditions occurring in the small intensively illuminated

and heated water volume inhabited by the dense alga population. After a period of intensive mobility the *Volvocales* monads present in the preparation generally settle on the lower surface of the cover slip, but rarely changing their position.

The seemingly chaotic movement of the fungal zoospores in the sample is at this period already distinctly influenced by the host. Under a small magnification the author generally observed a higher density of zoospores near sessile *Vitreochlamys aulata* cells than near other algae present in the preparation.

At this period, i.e. a dozen to thirty minutes after abandoning the zoosporangium, the fungal zoospores come into a direct contact with the host. They settle on the host's metaplasmatic wall directly with their body, while their flagella are directed either backward or sideward

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EXPLANATIONS FOR FIGS 6—20 IN PAGE 417

Fig. 6 — nearly mature zoosporangium of the fungus attached by a bunch of rhizoids to the contracted remnant of the killed *Vitreochlamys aulata* monad; simple apiculus of the parasite pierces host's metaplasmatic wall. Fig. 7 — early phase of infection of a small monad of *V. aulata*; parasite thallus consists of a stalked cystospore and a primary rhizoid. Fig. 8 — infection of the host's zoosporangium containing two young monads; the parasite thallus consists of a stalked cystospore, external appressorium, "doll"-shaped body and the primary rhizoid. Fig. 9 — as Fig. 8 but the parasite thalli consist of cystospores and germ tubes. Fig. 10 — as Fig. 6. Fig. 11 — motile *V. aulata* monad with the parasite zoospore attached by the end of its flagellum to the surface of the host's metaplasmatic wall. Fig. 12 — Resting spore of *Dangeardia echinulata* attached by a bunch of rhizoids to the reddish remnant of the host's body and piercing by its simple apiculus the host's metaplasmatic wall. Fig. 13 — one of the later phases of infection of the motile *V. aulata* monad; note a changed outline of the attacked monad's body due to the influence of a growing pear-shaped thallus of the parasite ended by a compound apiculus. Fig. 14 — early phase of zoosporogenesis in the zoosporangium of *D. echinulata*, note fine granulation of the protoplasmatic content of sporangium and the vitreous plug in the apiculus. Fig. 15 — mature resting spore of *D. echinulata*. Fig. 16 — infection of two young *V. aulata* monads in the zoosporagium by five young thalli of the parasite, note bending and folding of three germ tubes due to the motility of the attacked monads (apical view). Fig. 17 — evacuation of the parasite zoospores from the zoosporangium. Fig. 18 — monad of *V. aulata* (apical view) attacked by one zoospore, one cystospore with a short germ tube and two "doll"-shaped thalli of the parasite. Fig. 19 — young monad of *V. aulata* under the metaplasmatic wall of the zoosporangium attacked by the parasite; young thallus of the latter consists of a sessile cystospore, the proximal segment of the intramatrical part of the germ tube, internal appressorium, the distal segment of the intramatrical part of the germ tube and primary rhizoid (comp. Fig. 24). Fig. 20 — Four *D. echinulata* thalli developing on one *V. aulata* monad, below — two young resting spores, left above — normally maturating zoosporangium, right above — dwarf zoosporangium. (Drawn with camera lucida, magnifications: Figs. 6, 7, 8, 9, 11, 12, 13, 14, 17, 20 — × 770, Fig. 10 — × 1200, Figs. 15, 16, 18, 19 — × 1620).

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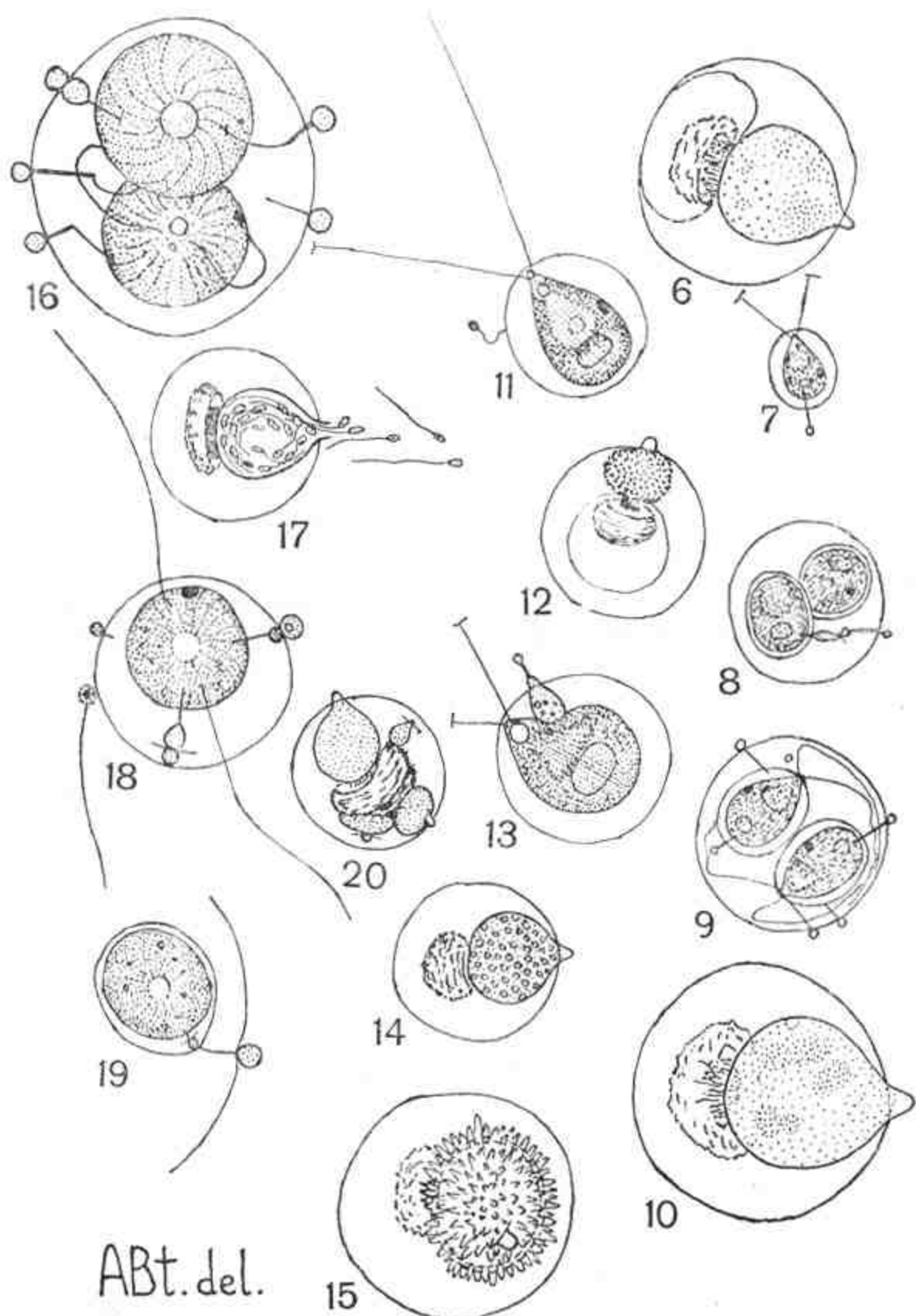
Figs 6—20. *Dangeardia echinulata* sp. nov. (type figures). (Explications of figures
see p. 416)

(Fig. 18). Frequent cases were also observed in which the zoospores were attached to the host by means of their flagella (Fig. 11). This occurred mostly when the zoospore attacked an actively moving monad and not a sessile monad on the glass. It seems that this mode of attack less frequently observed in the microscopic preparation is the main mode under natural conditions, since in the fresh material thus attacked monads were more frequent than those infected by zoospores directly settled on the host's surface contrary to the situation in the preparation.

Soon after settling on the host the zoospore loses its flagellum and transforms into a cystospore. It seems that the loss of the flagellum is mainly due to its retraction and not rejection. At any rate the zoospores which were initially attached to the host by the end of their flagellum gradually came nearer to the surface of the host's wall in the course of encystation but only rarely did they finally setle on it. The zoospores which settled directly on the host's wall generally later trans- formed into sessile cystospores, whereas those which were attached to the host by means of their flagellum transformed into stalked cysto- spores, though it seems that there are exceptions to this rule (see below).

The cystospore enclosed in a thin but distinct wall is spherical 1.8—2.5 µm in diameter (Fig. 16, 18). Directly after the encystation the fungus starts to develop a very thin, elastic germ tube. This was observed in cases of collision of the freshly infected host with various obstacles in the preparation. In stalked cystospores (Fig. 7) the germ tube de- velops in the form of a direct prolongation of the stalk, whereas in sessile cystospores it grows at the point of junction of the cystospore and the host's wall. The rapidly growing germ tube perforates the host's metaplasmatic wall and penetrates into the cell. In some cases the growth of the germ tube developing from a sessile cystospore was so rapid that the tube not only penetrated through the host's envelope but also lifted the sessile cystospore from its substrate transforming it into a stalked one. In many cases, particularly when large monads or zoosporangia with thick metaplasmatic walls were infected, the stalked cystospores formed small appressoria (Fig. 8) at the point of junction of their germ tubes and the substrate. These appressoria com- pactly adhered to the host's wall, whereas the infection tubes proper grew from them penetrating the metaplasmatic wall of the alga. The three schemes in Fig. 21—23 illustrate the space relations between the cystospore of the parasite and the metaplasmatic wall of the host.

After the perforation of the host's metaplasmatic wall the elongation growth of the germ tube is extraordinarily rapid, thus in the course of 10—15 min. the tube penetrates through the thick metaplasmatic gel layer i.e. the layer formed by the protoplast, but not being its component or through the fluid filling the zoosporangium.

In the first case the tip of the germ tube reaches the „naked" surface of the monad's prostoplast i.e. the surface covered only by the thin euplasmatic membrane, perforates it and forms a hardly visible primary rhizoid within the protoplast. In the second case the tip of the germ tube once more encounters the metaplasmatic wall of a daughter monad and sometimes develops an appressorium, then it penetrates through the membrane and through the thin gel layer into the protoplast of the daughter monad in the form of a primary rhizoid. In this case the intramatrical part of the germ tube joins two rather stiff pectocellulose walls, the wall of the sporangium and the outer wall of the daughter monad, which are mobile in respect to one other. Owing to this the author frequently observed cases of bending or even folding of the germ tubes, but this did not interrupt the development of the fungus (Fig. 16).

Thus, in the most complex cases of infection the following elements were distinguishable in the fungal thallus at this developmental stage (Fig. 24): the cystospore (a), the extramatrical part of the germ tube (b), the proximal or external appressorium (c), the proximal segment of the intramatrical part of the germ tube (d), the distal or internal appressorium (e), the distal segment of the intramatrical part of the germ tube (f), and the primary rhizoid (g).

Such a complex structure of the parasite's young thallus was observed, however, only in several cases, generally the course of infection was far more simple. In the freshly collected material large vegetative monads of *Vitreochlamys aulata* prevailed. Probably the fungus attacked them in motion, thus its thallus consisted of cystospores, the extramatrical part of the germ tube, the proximal appressorium, the intramatrical part of the germ tube and the primary rhizoid (elements a, b, c, d and g in Fig. 24). At the period when smaller thin-walled monads undergoing more frequent cell divisions prevailed in the V. *aulata* population, the fungus attacked more frequently the zoosporangia and then its thallus generally consisted of the elements a, d, f and g (lack of appresoria, Fig. 9). In the entire period of observation there occurred frequent cases in which the infection took place according to the most simple scheme, i.e. the fungal thallus consisted of the elements a, d and g (Fig. 18).

Vegetative growth phase. After the establishment of the fungal thallus the proximal fragment of the intramatrical part of the germ tube started to increase distinctly in thickness beginning from the outer surface of the substrate, i.e. directly from the point of junction with the cystospore or with the external appressorium. This growth continued gradually in the distal direction and after a certain period the fungal thallus acquired a characteristic shape of a "doll" stuck on

a stalk formed by the distal part of the germ tube (Fig. 16, 18, 25, 26). The "doll's head" — i.e. either the cystospore or the appressorium protruded from the surface of the monad's wall in the form of an apiculus. In this developmental phase the young thallus contained vitreous plasma with one or several intensively light refracting relatively large grains, while the apiculus contained a small vacuole.

The second stage of this developmental phase started by an intensive thickening of the hitherto thin stalk of the thallus. Owing to this the latter lost its doll-like shape and acquired a wide pear-shape settling with its wider base on the host's protoplast (Fig. 13, 27). At this period additional thin rhizoids forming a delicate poorly visible bundle grew from the wide surface of junction between the zoosporangium and the monad's body.

The protoplasmatic content of the developing zoosporangium under-went the following characteristic changes: at the end of its growth the dense, fine-grained plasma of the pear-shaped thallus was filled with clod-like agglomerations, and its wall slightly thickened (Fig. 6, 10). The processes were inhibited at the moment when the zoosporangium reached the size characteristic of the mature state, i.e. when the maxi-mum thickness of the zoosporangium is 85—95 per cent of its entire length.

It should be stressed that in the initial developmental phases of the parasite the infected V. *aulata* monads exhibit a characteristic increased motility. Owing to this the characteristic thalli apiculi consisting of cystospores and short fragments of the germ tube protruding in some cases from the host's walls were frequently broken off, thus they could but rarely be observed on the apexes of mature sporangia, though they were frequently found on the apexes of young thalli. In the literature the cystospore remnants protruding from the sporangium apex are known as apiculi (e.g. S p a r o w, 1936, 1960). G e i t l e r (1963) indicated that this term is inaccurate and ambiguous. He suggested for the apiculus formed from a sessile cystospore (Fig. 25) the name "sporapiculus", and for that consisting of a cystospore and a part of the germ tube (in our case frequently also of an appressorium, Fig. 26) — the name "appendix". In view of the larger popularity of Sparrow's terminology I will use the term a p i c u l u s in this paper, and for distinguishing the sessile apiculi, they will be additionally denoted as s i m p l e and the stalked ones — as c o m p o u n d.

It should be stressed that in the cases when the apiculus is broken off from the developing sporangium, the neck of the latter consisting of the outmost fragment of the germ tube and of the appressorium remains in the monad's wall.

The zoospore cleavage lasted rather long: in three zoosporangia the

development of which was observed in a hanging drop this process lasted 2.5—3 hr. After a certain period, the cloddines mentioned above disappeared, the protoplasm once more became uniform and fine-granulated (Fig. 20) and then again dense areas, though smaller and less frequent, appeared. A single grain was readily visible in the center of each clod (Fig. 14). Gradually the individual clods moved more and more apart and transformed into zoospores. No vacuolization of the sporangium content such as observed in other *Chytridiales* was found.
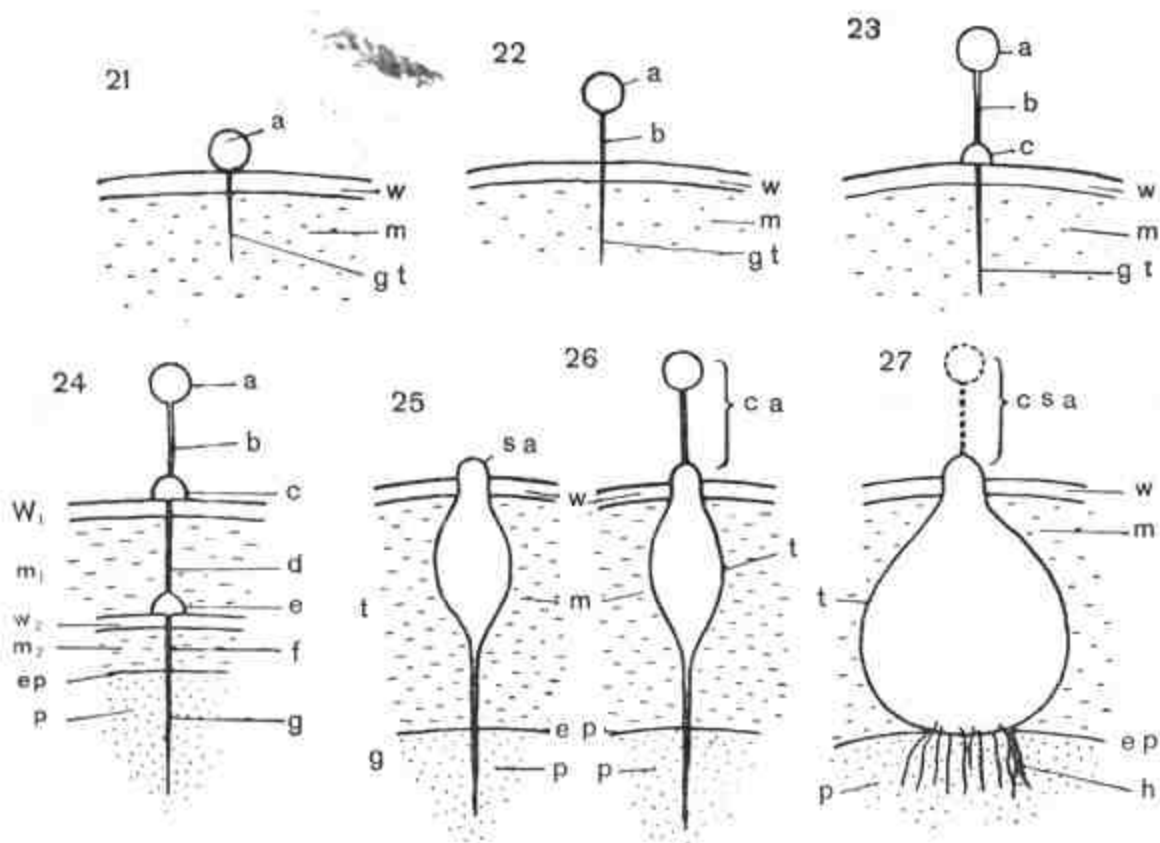
Figs. 21—27. Scheme of space relationships between the host's and parasite's thalli. Fig. 21 — sessile cystospore (a) on the surface of host's metaplasmatic wall (w) with germ tube (gt) immersed in host's gelatinous matrix (m). Fig. 22 and 23 — two stalked cystospores, the second one with an appressorium (c). Fig. 24 — elements of the young parasite thallus developing on host's zoosporangium containing young differentiated monads: a — cystospore, b — extramatrical part of the germ tube, c — proximal or external appressorium, d — proximal segment of the intramatrical part of the germ tube, e — distal or internal appressorium, f — distal segment of the intramatrical part of the germ tube, g — primary rhizoid, w_1 — the host's sporangium metaplasmatic wall, m_1 — liquid filling this sporangium, w_2 — the host's young monad metaplasmatic wall, m_2 — gelatinous layer of young monad ep — monad's euplasmatic membrane, p — monad's cytoplasm. Figs. 25 and 26 — parasite thalli in the "doll"-phase of development, one with simple (sa), the second — with compound (ca) apiculus, t — future sporangium body. Fig. 27 — mature pear-shaped parasite's zoosporangial thallus with secondary rhizoids (h) and compound or simple (csa) apiculus.

The zoospores in a number generally exceeding 100 completed their development within the zoosporangium. At a certain moment the entire mass of zoospores enclosed in the zoosporangium started to rotate at first slowly and then more and more rapidly around the transversal axis. This rotation lasted five to ten minutes and the zoospores flowed past the base of the sporangium neck without penetrating into the latter. The apex of the apiculus opened for a fraction of a second in the form of a pore and the zoospores successively separated from the rotating mass and fell out through the pore, rapidly moving away (Fig. 17). Only some of them stopped for several seconds near the zoosporangium though not in its direct vicinity and then moved further away. As the zoosporangium emptied the movement of the remaining zoospores became less regular, somewhat chaotic, nevertheless the zoospores further, rather regularly abandoned the zoosporangium. The latter was completely evacuated after 30—60 sec. The empty zoosporangia neither perished nor collapsed. Such zoosporangia freed of decomposed remnants of the host's cells were observed in the material studied.

In the first phases (i.e. the phase of infection and the initial period of the phase of vegetative growth) the development of resting spores was identical as that of zoosporangia. Only at the period when the doll-like thallus acquired the pyriform shape, the resting spores thalli began to differ from the zoosporangia. These thalli were distinctly shorter and wider (Fig. 20, below) and gradually acquired the characteristic shape of a transversal ellipsoid i.e. an ellipsoid produced by the rotation of the ellipse around its shorter axis. In contrast to the zoosporangia, the young resting spores were practically deprived of the neck, and the apiculus protruded from the center of the almost flat or slightly convex upper surface (Fig. 12). Soon after the final stabilization of the resting zoosporangium shape, its wall thickened intensively and became covered with minute spines. The vacuole disappeared from within the apiculus and a vitreous plug consisting of an intensively light refracting substance appeared instead (Fig. 15). The colorless content of the spore was poorly visible through its spined walls. None of the cases observed allowed to establish that the development of resting spores in this fungus was preceded by a sexual process.

The pathogenicity of the fungus for *V. aulata* differed in various cases and depended on both the size of the host's monad and the intensiveness of infection, i.e. on the number of thalli of the parasite developing on a given monad. A single fungal thallus parasitizing on a large monad produced no visible damage, frequently it even did not deprive the monad of its motility. On the other hand, smaller, up to

20 µm long monads generally perished even in cases of infection by a single thallus, whereas 2—3 thalli killed even large host cells. The host's death occurred rather late at about the end of the period of vegetative growth. The mature zoosporangia and resting spores generally lay on a contracted reddish remnant of the host's protoplast attached to it by a bunch of delicate rhizoids (Fig. 6, 10, 12, 14, 17). If the host died earlier, as it occurred in cases when a single cell of the alga was infected by 4—10 fungal thalli, the development of the fungus occurred normally only up to the "doll" phase. Cases were observed in which up to ten young thalli parasitized on a single host, but more than three mature zoosporangia or resting spores were never found on a single *V. aulata* monad.

TAXONOMIC POSITION OF THE PARASITE

The monocentric members of *Chytridiales* discussed in this paper forms zoosporangia opening by a pore, epibiotic in respect to the host's protoplast but penetrating into its metaplasmatic products (cellulose--pectinic wall and gelatine substance). These characteristics allow to classify this fungus to the family *Phlyctidiaceae* sensu Sparrow (1960). It is most similar to the following species belonging to this family: *Dangeardia mamillata* Schröder (1898), *Entophlyctis apiculata* (Braun) Fischer (1892) and *Scherffeliomyces appendiculatus* (Zopf) Sparrow (1936).

Dangeardia mamillata parasitizes on coenobia of *Pandorina morum* Bory at the stage of asexual reproduction and on coenobia of *Eudorina elegans* Ehrenb. in Germany (S c h r ö d e r 1898), in the U.S.A. (S p a r r o w 1960) and in Great Britain (C a n t e r 1946 and 1951, G r i f i t h s 1925, I n g o l d 1940). This fungus forms zoosporangia from the intramatrical part of the germ tube, which begins to widen from the point of junction with the cystospore and gradually acquires the shape of a stalked cylinder. Then the lower part of the stalk begings to grow and sessile flask-shaped zoosporangia with a bunch of thin rhizoids and a straight extramatrical apiculus develop. The zoospores of *D. mamillata* develop within the zoosporangium. Before abandoning the latter, the zoospores rotate within it and fall out singly. Despite the wide developmental and morphologic differences which prove that we are dealing with separate fungal species, the characteristics given above point to a similarity of the fungus discussed to the type-species of the genus *Dangeardia*.

Entophlyctis apiculata parasitizes on members of the family *Chlamydomonadaceae*. Contrary to the other species of the genus *Entophlyctis* the sporangia of which lie within the host's protoplast, the sporangia of *E. apiculata* lie under the outer metaplasmatic wall of the

alga cell but on the protoplast's surface. In this respect *E. apiculata* is similar to the fungus described in the present paper. When Fischer (1892) established the genus *Entophlyctis*, he classified the following three species to this genus: *E. bulligera* (Zopf) Fischer, *E. vaucheriae* (Fisch) Fischer and *E. apiculata*. Neither Fischer nor Sparrow (1960) designated the type-species of the genus *Entophlyctis*. According to the recommendations of Art. 7 of the Code (L a n j o u w 1961) and to the "Instructions for the determination of types" included in this Code, a lectotype should be designated for the genus. Among the three species mentioned by Fischer, *E. apiculata* differs from the others by the situation of the sporangium, thus it is a feature which is generally assumed as an intergeneric difference. On the other hand, *E. vaucheriae* is according to S p a r r o w (1960) a critical species "doubtfully distinct from *Entophlyctis confervae-glomeratae* (Cienkowski) Sparrow", whereas according to M i n d e n (1915) — a synonym of *E. rhizina* (Schenk) Minden. In this situation I propose to designate *E. bulligera* parasitizing on filiform green algae as the lectotype of the genus *Entophlyctis* Fischer. In view of the recent opinions on the systematics of *Phlycti-diaceae*, however, this solution excludes *E. apiculata* from the genus *Entophlyctis*, since the outer metaplasmatic wall of the *Chlamydomo-nadaceae* cells, similarly as the gelatinous substance of the coenobia of *Volvocaceae* is a product and not a component of the cell (Z a k h-v a t k i n 1949). Moreover, both these structures are chemically and developmentally similar, e.g. the gelatinous matrix of the coenobia of *Pandorina* or *Eudorina* is the product of sliming of the wall of the maternal cell of the coenobium and contains both cellulose and pectins. Thus, the difference in the situation of the zoosporangia in *Dangeardia mamillata* and *Entophlyctis apiculata* can be hardly considered as significant from the taxonomic standpoint. Moreover, the parasite of *Vitreo-chlamys aulata* described in this paper represents an intermediate case since its host is covered with both a gelatinous layer of mucilage and the superposed stiffer metaplasmatic wall. Thus, the fungal zoosporangium lies beneath the host's cell wall like in *Entophlyctis apiculata*, but it is also embedded in the gelatinous matrix similarly as in the case of *Dangeardia mamillata*. In this situation it seems that the zoosporangia of all three fungi mentioned above should be considered as extracellular according to S p a r r o w's (1960) terminology, i.e. "embedded in material of the host as, for example, in a gelatinous sheet, but resting on the cytoplasm (*Dangeardia*, etc.)".

Although the similarity of the fungus studied to *E. apiculata* has been stressed above, it should be borne in mind that there also exist wide differences such as the different shape and size of the zoosporangia, the size and number of zoospores. Moreover, recent studies on the

development of *E. apiculata* (G e i t l e r 1962 a) proved that the evacuation tube of its zoosporangium does not develop from the apiculus which perishes earlier, but is formed independently. This approximates this species to *Dangeardina eudorinae* Valkanov (1964) parasitizing on *Eudorina* and distinguishes it from *Dangeardia mamillata*.

Let us now consider the relation of the fungus described to *Scherffeliomyces appendiculatus* and the entire genus *Scherffeliomyces* Sparrow. The original diagnosis of this genus includes the following data: "zoospores lying free in the water, upon germination producing narrow tube, the tip of which upon coming into contact with the host cell becomes anchored to the latter ... extramatrical tip of the germ tube expanding and becoming the sporangium, to which is attached the empty cyst of zoospores ... resting spores extramatrical, ... with a single appendicular cell..." (S p a r r o w 1936 p. 446). Of the two species originally classified by S p a r r o w (1936, 1960) to this genus *S. parasitans* forms typically epibiotical zoosporangia on the surface of *Euglena* sp. cysts, whereas *S. appendiculatus* (Zopf) Sparrow parasitizing on the palmelloidal stage of *Chlamydomonas* sp. exhibits sporangia embedded in the gelatinous substance of palmelli but epibiotic to the host's protoplast. This indicates that the original conception of the genus *Scherffeliomyces* is mainly based on the presence of a compound, stalked apiculus on the the apex of the sporangium, independently of its position in respect to the substrate (epibiotic or extracellular).

A great diversity in the modes of infection by the fungus described was observed. In dependence on the ecological factors this fungus forms sporangia provided with either simple, sessile or compound, stalked apiculi. This would qualify it to the genus *Dangeardia*, but also to the genus *Scherffeliomyces*. Moreover the simple apiculus of this fungus may develop from the cystospore residue, i.e. as in *Dangeardia mamillata*, of from the basal part of the compound stalked apiculus after the cystospore residue and the thin connective are broken off. In this situation and in view of the higher stability of the feature common to both this fungus and *D. mamillata* as well as in view of the lability of the feature characteristic of the genus *Scherffeliomyces*, it seems justified to classify the fungus parasitizing on *Vitreochlamys aulata* to the genus *Dangeardia* and to describe it as a new species — *D. echinulata* sp. nov.

Dangeardia echinulata sp. nov.

Etymol.: *echinulatus*, -*a*, -*um* (lat.) — echinulate. The name stresses the characteristic appearance of the resting spore.

Zoosporangium pyriforme, in massa gelatinosa infra membranam metaplasmaticam hospitis immersum, in superficie hospitis protoplasmae

sessile, ex tubo germinali formatum, 19.5—27.3 μm longum et 18.2—22.1 μm crassum, apice brevi (ca 2,6 μm) apiculo, simplici (ex cystoporae formatum) vel compositi (ex appressorio cystosporaque fictum) ornatum, membrana laevi, hyalina, perenni. Rhizoideis multis, tenuibus. Zoosporae sphaericae, ca 2.5 μm diametro, vel paene oblongae, 1.8—2.6 μm longae et 1.3—1.5 μm crassae, in zoosporangio maturantes (supra 100 in uno sporangio), singulatim emergentes; flagellum unum in tergum directum, 10—12 μm longum. Sporae durantes sub membrana hospitis immersae, transversae-ellipsoideae, hyalinae, 9—10 μm longae et ca 12 μm crassae, dense echinulatae, apice cum brevi apiculo, composito vel simplico. Parasitus algarum Vitreochlamydis aulatae (Pascher) comb. nov.

Localitas typica: Varsovia (Polonia).
Typus: figurae 6—20.

Zoosporangium pyriform, 19.5—27.3 × 18.2—22.1 μm, sessile on the protoplast of the alga and embedded in the gelatinous matrix under the outer cellulose-pectinic host cell wall, with small apiculus (ca 2.6 μm long) piercing this wall; sporangium wal smooth, hyaline, somewhat rigid, after emergence of the zoospores not collapsing; rhizoids numerous, thin, scarcely visible. Apiculus sometimes compound, with stalked appendix (cystospore residue on the short and thin fragment of the germ tube). Zoospores spherical, about 2.5 μm in diam., or ovoid, sometimes even somewhat constricted in the middle of the length, 1.8—2.6 μm long and 1.3—1.5 μm wide, with one colourless small refractive globule in the cytoplasm and one trailing flagellum 10—12 μm long, maturate in the sporangium in a number usually exceeding 100, before the emergence whirl around the transverse sporangial axis, emerge singly, squeezing out to small opening formed by the deliquescence of the sporangial apex. After a period of intensive, rather fluent movement in the water zoospores attack both the motile vegetative and immobile dividing host monads attaching itself to their outer wall and then encysting. Cystospore spherical, small, colourless, sessile on the alga wall or stipitate, attached to the host by a short extramatrical piece of the germ tube. Germ tube penetrates the outer host's wall and underlying layer of the gelatine (occasionally — the second outer wall and second gelatinous matrix) and goes deep into the host's protoplasm. Sometimes the germ tube passing through the walls forms appressoria. After implantation the germ tube swells from the cystospore or appressorium successively, proximally to distally until the thallus is of the characteristic "doll" shape. The base continues to swell and the whole becomes a pyriform sporangium, which is embedded in the gelatinous host matrix and apiculus piercing the outer host's wall and protruding outwards. Resting spore asexually formed, borne like the zoosporangium, transverse ellipsoidal, 9—10 μm long and about 12 μm in diameter, with the simple or compound apiculus of the same structure and appearance as in the zoosporangium; wall of the resting spore thick, hyaline, covered with numerous, dense, conical spines up to 1.6 μm long. Germination not observed. Parasite of the motile monads and zoosporangia of the *Vitreochlamys aulata* (Pascher) comb. nov.

TAXONOMIC RELATIONSHIPS WITH ALLIED FORMS

Of the members of *Phlyctidiaceae* not only the species of *Dangeardia*, *Scherffeliomyces* and *Entophlyctis* mentioned above, but also some species

of the genera *Rhizophydium* Schenk, *Phlyctidium* (Braun) Rabenhorst etc. develop on the substrates enveloped in a thicker layer of meta-plasmatic secretions. The development of these fungi invariably starts by the encystation of a zoospore on the surface of either the gelatinous substance or the metaplasmatic wall of the host, or even at a certain distance from this surface when the cystospore germinates with a long germ tube which perforates the metaplasmatic structures and penetrates into the host's protoplast. The course of the further de-velopmental phases varies in dependence on the species. Two main developmental types may be distinguished here:

1. The zoosporangium develops from the intramatrical part of the germ tube (*Dangeardia* type),

2. The zoosporangium develops from the cystospore (*Rhizophydium* type).

A number of *Rhizophydium* species such as *R. sphaerocystidis* Canter, *R. agile* (Zopf) Fischer, *R. brauni* (Dangeard) Fischer, *R. simplex* (Dan-geard) Fischer and *R. fulgens* Canter (see S p a r r o w 1960), the zoo-sporangia of which lie on the surface of the metaplasmatic layer or only partly embedded in the latter, belong to the second type. The sinking of originally superficial zoosporangia in the mucilage in the course of maturation is rather frequently observed, and according to the opinion of many authors, is attributable to an intensified mucilage secretion by the host or even to the shortening of the distal part of the germ tube contacting the zoosporangium with the endobiotic rhizoids (a similar process was observed also in fungi developing according to the *Dangeardia* type, see e.g. G e i t l e r 1963 and P a t e r s o n 1958). In some cases this process of sinking may be so intensive that the result of the development will be identical to that of *Dangeardia*, therefore forms with zoosporangia embedded in the gelatinous layer like *Rhizo-phydium anomalum* Canter (1950) and *R. hyalothecae* (S c h e r f f e l 1926) are also observed among the *Rhizophydium* species.

The first developmental group, beside the species classified by their authors to the genus *Dangeardia*, comprises also single species belonging to other *Phlyctidiaceae* genera such as e.g.: *Phlyctidium eudorinae* Gimesi (Sparrow 1960), *Scherffeliomyces appendiculatus* (Zopf) Sparrow (Zopf 1884), *S. leptorrhizus* Johns (1956), *Dangeardiana eudorinae* Valkanov (1964) and also *Entophlyctis apiculata* (Braun) Fischer. In this connec-tion I transfer the latter species to the genus *Dangeardia*. Beside *Dan-geardiana eudorinae* all the other species mentioned belong to genera, the type-species of which develop according to modes completely dif-ferent from that of *Dangeardia*, since they form either epibiotic zoo-sporangia not surrounded by the host's mucous secretions (*Phlyctidium*, *Scherffeliomyces*) or endobiotic zoosporangia in the strict sense of the

word (*Entophlyctis*). In these cases the inclusion of the given species to a definite genus depends on the solution of the problem of taxonomic significance ascribed to individual features, e.g. whether a higher rank is ascribed to the endobiotic structure of the vegetative part of the thallus (in the case of *Phlyctidium*) or to the presence of the apiculus (in the case of *Scherffeliomyces*) than to that ascribed to the developmental features (i.e. the mode of development of the zoosporangium). In view of the lack of objective criteria the solution of these problems is rather difficult, thus the propositions of various authors are invariably subjective. It seems that the taxonomic procedure can be relatively more objective when the species analyzed is compared as a whole with the type-species of individual genera and the greatest general similarities are sought without any a priori arguments establishing a hierarchy of individual features.

S p a r r o w (1960) included two species to the genus *Dangeardia*: the type-species *D. mamillata* and *D. laevis* Sparrow et Barr (1955). In later years two further species were described: *D. ovata* Paterson (1958) and *D. sporapiculata* Geitler (1963); but the latter species should be rather qualified to the later described genus *Dangeardiana* Valkanov (1964) owing to the origin and subapical position of the evacuation tube.

Phlyctidium eudorinae exhibits a great similarity to *Dangeardia mamillata* as regards its development (H o v a s s e 1936, S p a r r o w 1960) but it differs from the type of the genus *Dangeardia* by the structure of the vegetative system since it forms a single small, spherical, vesicular haustorium without rhizoids almost identical to that of *P. anatropum* (Braun) Rabenhorst (1868). In my opinion a high taxonomic rank should be ascribed to this feature since it serves for differentiating two large genera: *Phlyctidium* and *Rhizophydium*. Therefore the eventual transfer of *P. eudorinae* to the genus *Dangeardia* should rather be abandoned.

The genus *Scherffeliomyces*, as mentioned above (page 425), has been established for the epibiotic species *S. parasitans* Sparrow (1934) parasitizing on *Euglena* sp. cysts. After establishing this genus S p a r- r o w transferred the fungus *Rhizidium appendiculatum* Zopf (1884) to this genus. This fungus parasitizes on the palmelloidal stage of *Chlamydomonas* sp., developing according to the *Dangeardia* type and forming intramatrical epibiotic sporangia. Moreover, G e i t l e r (1963) indicated that S p a r r o w had disregarded the fact that *R. appendiculatum* exhibits a certain developmental plasticity, namely, the zoospore of this fungus may be encysted both on the palmellal gel surface or at a certain distance from it, thus the apiculus may be either simple or compound (according to the terminology applied in this

work; sporapiculus or appendix according to Geitler's terminology). In the light of these data, the similarity of *R. appendiculatum* to *Dangeardia* species, and particularly to the newly described *D. echinulata*, becomes obvious, therefore I propose the following new combination for this species:

Dangeardia appendiculata (Zopf) comb. nov.

Basonym: *Rhizidium appendiculatum* Zopf, Nova Acta Acad. Caes. Leop.-Carol. 47: 203, pl. 20, figs. 17—27. 1884.
= *Rhizophydium appendiculatum* (Zopf) Fischer, Rabenhorst's Kryptogamen-Fl. 1 (4): 101. 1892.
= *Scherffeliomyces appendiculatus* (Zopf) Sparrow, Jour. Linnean Soc. London (Bot.) 50: 449. 1936.

The last species hitherto classified to the genus *Scherffeliomyces* — *S. leptorrhizus* Johns (1956) parasitizes on *Zygnema* sp. Johns explains the qualification of this species to the genus *Scherffeliomyces* as follows: "In this organism the sporangium is produced from an expansion of the epibiotic portion of the germ tube formed by the encysted zoospore, the zoospore cyst and a segment of the germ tube persisting as in appendage on the developing and mature sporangium". The same paper indicates, however, that the zoospore of this fungus is encysted on the surface of the mucilage surrounding the *Zygnema* filament and not at a certain distance from this surface, thus the zoosporangium ends is a simple, and not compound apiculus. This opinion is confirmed also by illustrations given in Johns' paper (1956, Figs. 1—5) demonstrating that the development of this fungus approximates much more closely that of *Dangeardia mamillata* than that of *Scherffeliomyces parasitans*. Thus the qualification of this fungus to the genus *Scherffeliomyces* seems unjustified.

A new problem arises, however, together with the question of the taxonomic position of *Scherffeliomyces leptorrhizus*. Namely the zoosporangia of this fungus open in the form of a pore which develops on the tip of a special evacuation papilla growing subapically from the zoosporangium. In this case the apiculus does not function as the evacuation papilla as in *D. mamillata* and other representatives of this genus. Geitler detected a similar mechanism of evacuation of the sporangium in observations on the development of *Entophlyctis apiculata* (Braun) Fischer (Geitler 1962 a). In his later paper (1963) describing *Dangeardia sporapiculata* parasitizing on the palmelloidal stage of *Chlamydomonas* sp., Geitler stressed that also this fungus forms subapical evacuation papillae. In this connection he provisionally classifies this species to the genus *Dangeardia* pointing to the necessity of a future establishment of a separate genus for this and similar species. Such a genus, called *Dangeardiana*, has been proposed by V a l-

k a n o v (1964) for a new fungal species parasitizing on *Eudorina ele-
gans*. The type-species of this genus — *D. eudorinae* Valkanov (1964)
initially develops according to the classical *Dangeardia* scheme, but the
long evacuation tube of the sporangium grows subapically (later it shifts
to the apical position). V a l k a n o v stressed the similarity of this
genus to *Dangeardia* by the name proposed, and claimed that the forma-
tion of the special evacuation tube is the only taxonomically significant
difference between these genera. In view of this, it seems justified
to also include *Entophlyctis apiculata*, *Scherffeliomyces leptorrhizus* and
Dangeardia sporapiculata to the genus *Dangeardiana*. V a l k a n o v
published the diagnosis of the genus *Dangeardiana* and the type species
D. eudorinae only in German. In view of Art. 43 of the Code this
renders impossible the qualification of any new taxa to this genus until
the validation of its name. Under these circumstances I give below short
diagnoses in Latin for both taxa, compiled on the basis of Valkanov's
paper and I propose suitable new combinations:

Dangeardiana Valkanov, Arch. Mikrobiol. 48:245—246. 1964.

   *Thallus eucarpicus, monocentricus, intramatricalis, extracellularis.
Sporangium modo intercalari evolvens, cum apice cystospora extrama-
tricall, in maturitate zoosporas opistoconthas per subapicalem tubum
liberans. Sporae perdurantes simili modo quam zoosporangia, ex femineo
thallo conjugatione cum masculina cystospora peracta, creantur.*

   Typus generis: D. eudorinae Valkanov.

Dangeardiana eudorinae Valkanov, Arch. Mikrobiol. 48: 246, figs. 1—11.
   1964.

   Sporangium ad 35 µm *longum et ad* 18 µm *crassum. Evacuationis tubus*
20—130 µm *longus. Sporae perdurantes ad* 16 µm *in diametro, membrana
crassa, laevi, hyalina. Parasitus oosporarum Eudorinae elegantis.*

Dangeardiana leptorrhiza (Johns) comb. nov.

Basonym: *Scherffeliomyces leptorrhizus* Johns, Mycologia 48: 433, figs. 1—12. 1956.

Dangeardiana sporapiculata (Geitler) comb. nov.

Basonym: *Dangeardia sporapiculata* Geitler, Sydowia 16: 330, figs. 1, 2. (1962). 1963.

Dangeardiana apiculata (Braun) comb. nov.

Basonym: *Chytridium apiculatum* Braun, Monatsber. Berlin Akad.: 383. 1855;
   Abhandl. Berlin Akad.: 57, pl. 5, figs. 5—20. 1856.
= *Olpidium apiculatum* (Braun) Rabenhorst, Flora Europaea Algarum, 3: 283. 1868.
= *Rhizidium apiculatum* (Braun) Zopf, Nova Acta Acad. Caes. Leop.-Carol. 47:
   207, pl. 21, figs. 21—31. 1884.
= *Entophlyctis apiculata* (Braun) Fischer, Rabenhorst's Kryptogamen.-Fl. 1 (4):
   117. 1892.

   The taxonomic relationships between the fungi mentioned above
and *Dangeardia echinulata* sp. nov. are given below in the form of a key.

Moreover, two Phlyctidiaceae species, i.e. *Coralliochytrium scherffelii* Domján (1936) and *Scherffeliomycopsis coleochaetis* Geitler (1926 b) exhibiting a morphology and life history similar to the new species have been included in this key.

A KEY TO THE SPECIES OF *DANGEARDIA* AND RELATED FORMS

I The epibiotic zoosporangium irregularly pyriform, 17.6—23.8 µm high and 15.4—23.8 µm wide, with a simple spherical apiculus opens by pores at the tips of 2—5 protruding lateral evacuation papillae; the vegetative system consist of a cylindrical endoapophysis and a short, thin, unramified rhizoid ending in an irregular broadly lobed haustorium. Parasite of *Zygnema* sp.

Coralliochytrium scherffelii Domján (1936).

II The zoosporangium opens by a single evacuation pore.

   1. Apiculus mostly compound, in the form of the cystospore residue based on the apex of the zoosporangium by means of a short segment of the germ tube, persisting, visible on most mature zoosporangia and resting spores.

      A. Zoosporangium internally proliferating (primary one invariably with compound apiculus, secondary one — without), irregular, wide pyriform, 25—38 µm wide and 10—15 µm high (if measured without papilla). Evacuation pore and papilla apical. Secondary zoosporangia smaller. Zoospores ameboidal, without flagella. Parasite of *Coleochaete* sp. div.

Scheffeliomycopsis coleochaetis Geitler (1962 b).

      B. Zoosporangium unproliferating, when mature almost spherical, 17—22 µm in diameter, opening by a wide apical pore, without evacuation papilla. Zoospores numerous, with a single flagellum, spherical, 2—3 µm in diameter, abandoning the zoosporangium in the form of a dense mass, then dispersing. Resting spore spherical or ovoid, smooth, brown, epibiotic, with compound apiculus. Parasite of *Euglena* sp. div. cysts.

Scherffeliomyces parasitans Sparrow (1934).

   2. Apiculus mostly simple, developing from the cystospore residue inserted directly on the zoosporangium; in some species also compound apiculi develop paralelly to simple ones, but generally they are evanescent and rarely visible on mature zoosporangia or resting spores.

      A. Zoosporangium opens through the apiculus, by a pore developing on their tip or in consequence of their destruction; the apiculus either functions as an evacuation papilla or disappears.

         a. Endobiotic vegetative part of the thallus in the form of a well visible spherical haustorium. Zoosporangium pyriform or oval, embedded in the host's gelatinous envelope, 10—18 × 4—10 µm, apiculus extramatrical. Zoospores 3.5 × 2.6 µm. Parasite of *Eudorina* sp. div.

Phlyctidium eudorinae Gimesi (1924).

         b. Endobiotic part of the thallus in the form of filamentous rhizoids.

           aa. Zoospores relatively few (a dozen or so in the zoosporangium), rather big (over 3 µm in diameter); resting spores smooth.

              α. Zoosporangium oviform, when mature completly embedded in the host's gelatinous envelope, 9—14.5 × 6.5—10.5 µm, without distinct neck, apiculus evanescent. Zoospores abandon

singly the zoosporangium. Parasite of *Sphaerocystis schroeteri* Chod.

Dangeardia ovata Paterson (1958).

β. Zoosporangium flask-shaped, with a distinct neck and a somewhat rounded simple apiculus, 22—38 × 8—16 μm. Zoospores initially abandon the sporangium agglomerated in a ball then singly. Parasite of *Glenodinium* sp. (?).

Dangeardia laevis Sparrow et Barr (1955).

bb. Zoospores numerous (several dozens or over 100 in one zoosporangium), small (up to 2.5 μm in diameter, occasionally their length somewhat exceeds this dimension). Resting spores mostly covered with spines or sculptured.

α. Parasite of cenobial *Volvocales* (*Pandorina morum, Eudorina elegans*), zoosporangium embedded in the common gelatinous coenobial matrix, but sessile on the surface of the metaplasmatic proper wall of the monads, flask-shaped or pyriform, with a simple apiculus, 10—30 × 7—20 μm. Resting spores develop from the female thallus, spherical or oval, with long necks, granular, papillate or spined, male thallus smaller, flask-shaped.

Dangeardia mamillata Schröder (1898).

β. Parasite of unicellular *Chlamydomonadaceae* (*Vitreochlamys aulata*). Zoosporangium embedded in gelatinous matrix under the metaplasmatic wall of the infected monad, sessile directly on the monad's protoplast, wide pyriform, 19.5—27.3 × 18.2—22.1 μm, with a simple or compound apiculus. Resting spores develop asexually, similarly as the zoosporangium, transversally ellipsoidal, 9—10 μm high, about 12 μm in diameter, spined, with small short neck.

Dangeardia echinulata sp. nov.

B. Zoosporangium opens by a pore developing on the tip of a special evacuation tube growing subapically from the zoosporangium, the apiculus takes no part in the evacuation of zoospores (*Dangeardiana* Valkanov 1964).

a. Zoosporangium opens by a pore at the tip of a long (20—130 μm) evacuation tube protruding high above the host's gelatinous matrix. Apiculus simple, separated from the sporangium by a deep constriction. Resting spores form in the female thallus, which initially develops as the zoosporangium, after conjugation with the male thallus reduced to a sporocyst which settles on the apiculus of the female thallus. Parasite of oospores of *Eudorina elegans*.

Dangeardiana eudorinae Valkanov (1964).

b. Zoosporangium opens by a short evacuation papilla.

aa. Zoosporangium embedded in the mucilage or gelatinous matrix covering the outer surface of the host's metaplasmatic wall and settled on the surface of the latter. Apiculus simple, persistent.

α. Mature zoosporangium generally deep embedded in the mucilage surrounding the host's cell, wide pyriform, 20 × × 16 μm. Parasite of the palmelloidal stage of *Chlamydomonas* sp.

Dangeardiana sporapiculata (Geitler) comb. nov.

β. Mature zoosporangium only partly (to 50—75% of its height) embedded in the rather thin layer of mucilage covering the host's thallus, wide pyriform, 18—27 × 15—26 μm. Parasite of *Zygnema* sp.

Dangeardiana leptorrhiza (Johns) comb. nov.

bb. Zoosporangium under the host's metaplasmatic wall, sessile directly on the protoplast, wide pyriform, 11—13 μm in diameter, apiculus simple, initially extramatrical, disappearing in the course of development (it is built into the sporangium wall). Parasite of motile *Chlamydomonas* sp. div. monads.

Dangeardiana apiculata (Braun) comb. nov.

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Nowy gatunek *Dangeardia* pasożytujący na ruchliwych monadach zielenicy z rodziny *Chlamydomonadaceae*

Streszczenie

Autor opisuje nowy gatunek grzyba z rodziny *Phlyctidiaceae* (*Chytridiales*) pasożytujący zarówno na ruchliwych, jak i znieruchomiałych na czas podziału monadach zielenicy z rodziny *Chlamydomonadaceae*. Grzyb został znaleziony w kałuży na piaszczystej nadwiślańskiej plaży w Warszawie. Żywiciela oznaczono jako *Sphaerellopsis aulata* (Pascher) Gerloff. Po stwierdzeniu, że nazwa rodzajowa *Sphaerellopsis* Korschikoff (1925) jest nazwą zajętą, nomen praeoccupatum (homonym prius: *Sphaerellopsis* Cooke 1883), autor nadał rodzajowi nową nazwę *Vitreochlamys* i utworzył nowe kombinacje *V. aulata* (Pascher) comb. nov., *V. fluviatilis* (Stein) comb. nov. Glon znaleziony w Warszawie różnił się nieco od glonu opisanego przez Paschera; został zidentyfikowany dokładniej jako forma opisana przez E t t l a (1963).

Pasożytujący na *V. aulata* monocentryczny przedstawiciel *Phlyctidiaceae* tworzył zoosporangia typu bezwieczkowego ukryte pod zewnętrzną (metaplazmatyczną) błoną żywiciela i pogrążone w żelatynowatej substancji wypełniającej przestrzeń między tą błoną a protoplastem żywiciela. Spośród wszystkich grzybów z omawianej rodziny odznaczających się podobną lokalizacją zarodni i podobnym jej rozwojem, najbliższą do opisywanego gatunku okazała się *Dangeardia mamillata* Schröder (1898), gatunek-typ rodzaju *Dangeardia*. W związku z tym pasożyta *Vitreochlamys aulata* zaliczono do rodzaju *Dangeardia* i nadano mu nazwę D. *echinulata* sp. nov.

Ponadto w pracy dokonano krytycznej analizy systematyki jeszcze dziewięciu innych gatunków *Phlyctidiaceae* odznaczających się podobnym rozwojem i lokalizacją zarodni. W wyniku przytoczono diagnozy łacińskie rodzaju *Dangeardiana* Valkanov i gatunku *D. eudorinae* Valkanov (1964) dla ich uprawomocnienia oraz utworzono następujące nowe kombinacje: *Dangeardiana apiculata* (Braun) comb. nov., D. *leptorrhiza* (Johns) comb. nov. i D. *sporapiculata* (Geitler) comb. nov. (str. 430) oraz *Dangeardia appendiculata* (Zopf) comb. nov. (str. 429). Opracowano klucz do oznaczania gatunków *Dangeardia* i *Dangeardiana* oraz pokrewnych im form, do którego włączono oprócz wyżej wymienionych grzybów *Scherffeliomyces*

parasitans Sparrow (1934), *Phlyctidium eudorinae* Gimesi (1924), *Dangeardia ovata*
Paterson (1958), *Dangeardia laevis* Sparrow et Barr oraz *Coralliochytrium scherffelii*
Domján (1936).

BIBLIOGRAPHY

B r a u n A., 1855, Ueber *Chytridium*, eine Gattung einzelner Schmarotzergewachse
    auf Algen und Infusorien, Monatsber. Berlin Akad., 1855: 378—384.
C a n t e r H. M., 1946, Studies on British chytrids. I. *Dangeardia mamillata* Schrö-
    der, Trans. Br. mycol. Soc. 29: 128—134.
C a n t e r H. M., 1950, Studies on British chytrids. VIII. On *Rhizophydium anoma-*
    lum n. sp., New Phytologist 49: 98—102.
C a n t e r H. M., 1951, Studies on British chytrids. XII. Fungal parasites of the
    phytoplankton. II. Ann. Bot. (N. S.) 15: 129—156.
C o o k e M. C., 1883, New American Fungi. Grevillea 12: 22—23.
E t t l H., 1963, Über zwei *Sphaerellopsis*-Arten, Nova Hedwigia 5 (1—2): 255—261.
F i s c h e r A., 1892, Die Pilze Deutschlands, Oesterreich und der Schweiz. IV. Ab-
    teilung: *Phycomycetes*, in Rabenhorst's Kryptogamen-Fl., 1.
G e i t l e r L., 1962 a, Entwicklungsgeschichte der Chytridiale *Entophlyctis apicu-*
    lata auf der Protococcale *Hypnomonas lobata*, Österr. Bot. Zeitschr. 109:
    138—149.
G e i t l e r L., 1962 b, Entwicklung und Beziehung zum Wirt der Chytriadiale
    Scherffeliomycopsis coleochaetis n. gen., n. spec., Österr. Bot. Zeitschr. 109:
    250—275.
G e i t l e r L., (1962)) 1963, *Dangeardia sporapiculata* n. sp., der Begriff „Apikulus"
    und die Gattungsabgrenzung bei einigen Chytridialen, Sydowia 16: 324—330.
G e r l o f f J., 1940, Beitrage zur Kenntnis der Variabilität und Systematik der
    Gattung *Chlamydomonas*, Arch. Protistenk. 94: 311—502.
G i m e s i N., 1924, Hydrobiologiai Tanulmányok. *Phlyctidium eudorinae* Gim.,
    n. sp. (Adatok A Phycomycesék Ismerethez), Növénytani Szakosztályának: 1—5.
    Németül 6—8.
G r i f f i t h s B. M., 1925, Studies in the phytoplankton of the lowland waters
    of Great Britain. No. III. The phytoplankton of Shropsire, Cheshire, and Staf-
    forshire, Jour. Linn. Soc. London (Bot.) 47: 75—98.
H o v a s s e R., 1936, *Rhizophidium beauchampi* sp. nov., Chytridinée parasite
    de la Volvocinée *Eudorina* (*Pleodorina*) *illinoisensis* (Kofoid), Ann. Protistol.
    5: 73—81.
I n g o l d C. T., 1940, *Endocenobium eudorinae*, gen. et sp. nov., a chytridiaceous
    fungus parasitizing *Eudorina elegans* Ehrenb., New Phytologist 39: 97—103.
J o h n s R. M., 1956, Addition to the phycomycete flora of the Douglas Lake
    region. III. A new species of *Scherffeliomyces*, Mycologia 48: 433—438.
K o r s c h i k o f f A., 1926, Beiträge zur Morphologie und Systematik der Volvo-
    cales, Russ, Arch. Protistenk. 4.
K o r s c h i k o f f A., 1938 a, Visnatschnik prisnovodnikh vodorosley. IV — *Vol-*
    vocinae, Kiyev.
K o r s c h i k o f f A., 1938 b, Materialy k florie vodorosley Gorkovskogo kraya.
    I. Utschenye Zapiski Charkovskogo Universitieta, 14, Trudy Instituta Botaniki 3:
    1—21.
L a n j o u w J., ed., 1961, International Code of Botanical Nomenclature, Reg.
    Veget. 1.

Minden von, M., 1911, *Chyrtridiinae*, in: Kryptogamenfl. Mark Brandenburg, 5. Pt. 3: 353—496.

Pascher A., 1927, Die Süsswasser Flora Deutschlands, Österreich und der Schweiz. 4. *Volvocales* = *Phytomonadineae*. Jena.

Paterson R. A., 1958, Parasitic and saprophytic *Phycomycetes* which invade planktonic organisms. II. A new species of *Dangeardia* with notes on other lacustrine fungi, Mycologia 50: 453—468.

Paterson R. A., 1962, Lacustrine Chytridiaceous Fungi from Maryland, Mycologia 54: 694—703.

Petrak F., (1966) 1968, Über die Gattung *Sphaerellopsis* Cooke, Sydowia 20: 200—202.

Rabenhorst L., 1868, *Flora Europaea Algarum* .... 3. Leipzig.

Scherffel A., 1926, Einiges über neue oder ungenugend bekannte Chytridineen (Der Beiträge zur Kentniss der Chytridinee, Teil II), Arch. Protistenk. 54: 167—260.

Schröder B., 1898, *Dangeardia*, ein neues Chytridineen Genus auf *Pandorina morum* Bory, Ber. deutsch. botan. Ges. 16: 314—321.

Sparrow F. K., Jr., 1933, New chytridiaceous fungi, Trans. Br. mycol. Soc. 18: 215—217.

Sparrow F. K., Jr., 1934, *Scherffeliomyces*, Mycologia 26: 377.

Sparrow F. K., 1936, A contribution to our knowledge of the aquatic *Phycomycetes* of Great Britain, Jour. Linn. Soc. London (Bot.) 50: 417—474.

Sparrow F. K., Jr., 1960, Aquatic *Phycomycetes*, Ann. Arbor, 2-nd ed.

Sparrow F. K., Jr., and M. E. Barr, 1955, Addition to the Phycomycete flora of the Douglas Lake region. I. New taxa and records, Mycologia 47: 546—556.

Valkanov A., 1964, *Dangeardiana eudorinae* n. g. n. sp. — ein neuer Vertreter der Algenpilze, Arch. Mikrobiol. 48: 239—246.

Zopf W., 1884, Zur Kenntnis der Phycomyceten. I. Zur Morphologie und Biologie der Ancylisteen und Chytridiaceen, Nova Acta Acad. Caes. Leop.-Carol. 47: 143—236.

Zakhvatkin A., 1949, Embryologiya nisschikh biespozvonotschnykh, Moskwa.