Nellymymes megaceros gen. et sp. nov. — a new aquatic phycomycete related to Aqualinderella and Araiospora

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SITE AND TIME OF APPEARANCE

In connection with several years investigations on the aquatic fungi of Poland, I collected this year from early spring material on the territory of the Kampinos National Park near Warsaw. My attention was directed in this period particularly to fungi of the ecological group of phytosaprophytes but little known so far on the territory of Poland. Therefore I collected on various sites twigs of trees and shrubs which had fallen into water, and also male inflorescences of the alder (Alnus glutinosa Gaertn.), the birch (Betula verrucosa Ehrh. and B. pubescens Ehrh.), the hazel (Corylus avellana L.) and the poplar (Populus alba L., P. tremula L. and P. nigra L.). Moreover, I used small apples and onions as bait, which were set in some dozen places in the Park in intermittent and perennial water bodies.

The winter of 1969/1970 abounded exceptionally in snow. The early spring and spring of 1970 were also characterized by exceptionally abundant precipitation which not only compensated the acute water deficit of the last years and raised the previously low level of ground water, but filled the almost completely dried up small perennial water bodies and streamlets and formed in depressions of the terrain intermittent water pools. The sites chosen for investigation included water bodies and streams of various type such as natural flood waters in alder forest (Curici-elongatae Alnetum) in high peat (Sphagnetum medii), meadows and flood meadows (Salico-Populetum or Fraxino-Ulmetum), streams, melioration and roadside ditches, ponds and pools in villages and settlements adjacent to the Park. In spite of the marked retardation in the development of the higher plants vegetation this year, the Phycomycetes flora colonizing the above named substrata was abundant and diversified, and appeared as early as the first days of April. A characteristic feature of this spring's fungus aspect as compared with the preceding years was a high contribution of imperfect fungi (Deuteromycetes) and members of the order Leptomitales; these fungi were particularly abundant and
were represented by a number of species as numerous as that of *Saprolegniales* which up till now prevailed absolutely in these biotopes. Another peculiar feature was the general and profuse appearance of two species of *Monoblepharis* (*M. polymorpha* Cornu and *M. macandra* Woronin). All these fungi formed on the surface of plant remnants immersed in water exuberant tufts which subsisted this year exceptionally long — from the beginning of April to the second half of June. The changing specific composition of the microflora described was extremely rich over this entire period, so that each inspection of the sites resulted in the detection of 12—15 species dominating at the given moment. A discussion in detail of the results of taxonomic elaboration of these fungi will be the subject of a separate publication, whereas in the present paper only one fungus is described, no doubt the most interesting one of all. Since it represents the order *Leptomitusales* and has appeared against a background of particularly exuberant development of members of this order, the other species belonging to this order found at the same time in the Kampinos National Park will be also briefly discussed.

As early as the first ten days of April there appeared, almost on all sites investigated, on branches of various trees and their male inflorescences which had dropped into the water, *Apodachiya pyrifera* Zopf and *Sapromyces elongatus* (Cornu) Coker. The delicate hyphae of these fungi were intermixed in mats with thick hyphae of fungi of the family *Saprolegniaceae*, mainly with *Achlyla hypogyna* Cooker et Pemberton and *A. colorata* Pringsheim. Communities of this type persisted till mid May when they were substituted by colonies composed of other species of *Saprolegniaceae* [i.a. *Isoachlyla torulosa* (de Bary) Cejp] and the gradually multiplying *Monoblepharis polymorpha*. At this time, on the apples set as bait in April, there appeared at most sites numerous pustules of *Rhidiadium interruptum* Cornu, a fungus rather common on this area. On an apple immersed in flood water on Sierakowskie meadows pustules of *R. americanum* Thaxter, a rare fungus so far not reported from Poland, were observed.

One of the sites included in the observation was a permanently flooded alder forest in the nearest vicinity of the Field Station of the Institute of Ecology, Polish Academy of Sciences at Diekanów Leśny. It is one of the areas on which the Institute conducts investigations, surrounded with a fence, and access is prohibited to unauthorized persons. Installations facilitating observation are available on the area such as a gallery up in the tree crowns, stands for meteorological observations and footbridges for crossing over the pools to drier parts of the forest.

It is just near to one of the footbridges that I found the first specimens of the fungus here described. At this place the terrain forms a long rather narrow gutter separating the sandy dunes with an artificial pine stand
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from the lower lying but not immersed parts of the oak-hornbeam forest (Querco-Carpinetum). The depression through which these footbridges run is overgrown with a rather typical alder forest, the trees forming a hummock structure, however, since it occupies but a small area it is of transitional and mosaic character and contains small patches of vegetation resembling that of the oak-hornbeam forest. The water level in this area undergoes in the course of the year wide variations, but generally the free water surface persists in the lowest parts of the floodland the year round. The two preceding years were an exception in this respect since owing to long lasting drought the water had dried up completely at the beginning of June. In the spring months the spaces between the alder hummocks are flooded every year to a depth of about 50 cm, and marsh flora and fauna develop here. From among flower plants there appear here in this period Caltha palustris L., Silus latifolium L., Oenanthe aquatica (L.) Poir., Puccinellia palustris (L.) Moench., Hottonia palustris L., Lysimachia nummularia L. and L. vulgari, L., Solanum dulcamara L., Lycopus europaeus L., Sagittaria sagittifolia L., Alisma plantago-aquatica L., Iris pseudacorus L., Scirpus silvaticus L. and others. Algae develop generally in the spring period very abundantly in the neuston composed mainly of Chrysomonoadaeae, and a rich flora of epiphytic diatoms and Chlorophyceae [Characium sp. div., Chaetophora pisciformis (Roth) Agardh]. Among the filamentous algae forming macroscopically noticeable colonies conjugates prevail of the order Zygnemales and Draparnaldia glomerata (Vauch.) Agardh. The fauna of invertebrates is also very abundant, among them, beside mosquito larvae, water beetles and Heteroptera, worth noting are rarer animals living in clear water such as sessile ciliates (Campanella umbellaria L., Epistylis sp. and others), sessile rotifers (Megabotrocha sp.) or crustaceans. (Chirocephalus grubii Dybowski). The vegetation above described does not form in the depression between the hummocks uniform patches, so that a great part of the bottom is not overgrown. It is covered with a dozen or so centimeters thick humus layer and fallen tree branches, mainly of Alnus glutinosa, less of Betula verrucosa, Populus tremula, Carpinus betulus, Sorbus aucuparia and Padus avium.

April inspection of the water microflora covering the bark of the immersed branches revealed the presence of the same species which were found in this period at other sites in the Park, for instance in the Sieraków and Łoś reservations, near the Palmiry cemetery and village, etc. From among Saprolegniaceae, Achlya hypogyna predominated here, and the lower layer of the tufts was formed by Apodachlyla pyrijera and Monoblepharis polymorpha. In May, owing to the good light conditions at the bottom, there developed more and more abundantly on the bark of the immersed branches epiphytic algae, in the first place Chaetophora
pisiformis, diatoms and Characium sp. They overgrew not only the surface of the bark, but the hyphae of aquatic fungi, making their observation difficult and impeding their development. At this time the composition of the fungal tufts changed visibly, *Isochyia torulosa* and *Monoblepharis polymorpha* now began to predominate. In the course of one inspection of the site in May dr T. Majewski called my attention to a thick alder branch on which the bark was covered with fungi of a different macroscopic appearance. Between the tufts of the above named fungi one could see with the naked eye very short (2 mm) white "pins" with a distinct head as if stuck vertically singly or by several into the bark. Immediate microscopic examination revealed that the pins were arbuscular thalli of a fungus of the order *Leptomitales*, family *Rhipidiaceae*. In the course of May this fungus rapidly spread to the entire flooded area infesting all the immersed alder branches and forming with *Isochyia torulosa*, *Monoblepharis polymorpha* and *Chaetophora pisiformis* characteristic communities. This made possible the collection of profuse material and examination in detail of the morphology of this fungus. This resulted in the conclusion that the fungus is a member of the family *Rhipidiaceae* and exhibits traits characteristic for several genera of the above named family. The fungus persisted at the type locality up to mid June. In other alder forests of the Kampinos National Park, however, I did not find it, although the remaining above listed phycomyces species abounded there. In view of the combination of traits of the fungus so far not noted in members of the family *Rhipidiaceae*, I decided to establish for it a new genus — *Nellymyces* gen. nov. The new genus is named in honor of dr Nelly Jarowaja, my wife and colleague.

*Nellymyces* gen. nov.


Vegetative thallus unicellular, bipolar, comprising a system of branched, intramatrical, tubular holdfasts with rounded ends and an extramatrical body ("basal cell") that may be unbranched, cylindrical or somewhat clavate but is often apically or subapically branched; bran-
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Bases usually tubular without constrictions or cellulin plugs. True hyphal branches (i.e. thin-walled and more or less regularly constricted) usually lacking or rare. Zoosporangia smooth or spiny, dimorphic, stipitate. Oogonia smooth or spiny, monosporous, stipitate, content differentiated to peri- and ooplasm. Both zoosporangia and oogonia formed on thick-walled and usually cellulin-plugged pedicels either directly on the unbranched basal cell or on its branches. Zoospores fully formed within zoosporangium, laterally biflagellate. Oospore aplerotic, without cellular or alveolar envelope. Aquatic fungi.

Type of the genus: *N. megaceros* sp. nov.

The new genus differs from the genera *Sapromyces* Fritsch, *Rhipidium* Cornu and *Araiiospora* Thaxter by the sporangia and oogonia arising directly from the basal cell and by the lack of true hyphal branches. In this respect it resembles the genera *Mindeniella* Kanouse and *Aqualinderella* Emerson and Weston. From the *Mindeniella* the genus *Nellymyces* differs by facultative ramification of the basal cell and by aplerotic oospores, and from *Aqualinderella* — by stipitate sporangia and oogonia. Zoosporangial dimorphism distinguishes my fungus from both the above mentioned genera. It also differs from the genus *Araiiospora*, closely similar in habitus, by the absence of the alveolar envelope on the oospores.

To sum up, the taxonomic position of the new genus in the family *Rhipidiaceae* may be described by the following key.

**KEY TO THE GENERA OF RHIPIDIACEAE**

1(6) Basal cell usually giving rise to true hyphal branches, more or less regularly constricted, thin-walled, bearing the reproductive organs; antheridia usually present, oospores formed (except in *Rhipidium parthenosporum*).

2(3) Basal cell slender, usually poorly defined; hyphal branches long, with many constrictions; sporangia smooth-walled; oospore with undulate wall ................. *Sapromyces*

3(2) Basal cell stout and well defined, hyphal branches tubular, with few constrictions (often only at apex); sporangia smooth and/or spiny; oospore with reticulate outer wall or with alveolar (cellular) envelope.

4(5) Oospore wall reticulate, alveolar envelope lacking; zoosporangia smooth ................. *Rhipidium*

5(4) Alveolar envelope present, zoosporangia smooth and/or spiny .......... *Araiiospora*

6(1) Basal cell unbranched or branched, but branches thick-walled, without constrictions or cellulin plugs; true hyphal branches lacking; reproductive organs arising directly from the basal cell; antheridia lacking, parthenospores formed.
7(8) Basal cell unbranched, only sometimes slightly lobed; parthenosporocysts plerotic (i.e., more or less filling its container) ... Mindeniella
8(7) Basal cell may be branched, branches long, tubular; parthenosporocysts aplerotic (not filling oogonium).
9(10) Zoosporangia and oogonia sessile, more or less smooth-walled ......... Aqualinderella
10(9) Zoosporangia dimorphic, smooth or spiny, oogonia smooth or spiny, both oogonia and zoosporangia stipitate, pedicels considerably long, thick-walled, cellulose-plugged .......... Nellymyces

Nellymyces meghoros sp. nov.

Etym.: μέγας — large, κέρας — horn (Greek)

Species easdem quas genus proprietates habet. Cellula basalis cylindrica, 750—1600 μm crassa, saepe apice ramosa ramisquae ad 2500 μm longis; rhizoidea usque ad 1300 μm longa, apice circa 5—8 μm crassa. Zoosporangia laevia ellipsidea vel obovoidea, 50—135 μm longa et 30—54 μm crassa. Zoosporae subsparsae, 9.3—11.2 μm in diametro. Zoosporangia spinosa elipsidea vel ovoidea, 110—175 μm longa et 69—90 μm crassa, membrana paene incassata, apice cum 3, varius 4 vel 5 spinis erectis ad 100 μm longis et ad 10.5 μm crassis, sub apice cum corona ex 5—9 similibus sed transverse vel retrorsum directis spinis formata. Oogonia variabilia, sphaerica, pyriformia, versus ovoidea, elipsidea vel oblonga, laevia vel 1—4 erectis spinis ad 45 μm longis et ad 9.5 μm crassis ornata. Antheridia non sunt inventa. Oosporae (parthenosporae) sphaericae, apleroticae, 24—43.5 μm in diametro, singulares, fuscae aurantiaco colorae suffusae, epispório ad 3.6 μm crasso cum papillis numerosis minutis co- operatae. Habitat in ramis caducis Alni glutinosae Gaertn. in aquis submersis in pago Dziekanów Leśny prope Varsaviam in Polonia.

Basal cell cylindrical, 750—1600 μm long and 60—110 μm thick, or branched in upper part (if so, then 2500 μm long), without constrictions and cellulose plugs, passing at base into a system of multiply branched tubular holdfasts 5—8 μm thick in end segments, rounded at end, overall length 800—1300 μm and more. Zoosporangia dimorphic: (a) smooth zoosporangia oval or obovoid, frequently greatly elongated, 50—135 μm (average ca. 100 μm) long and 30—54 μm (average ca. 42 μm wide), relative width (in % of length) 26—60 percent (average ca. 42%), thin-walled, they open through a pore on tip. They grow on cylindrical or slightly constricted thick-walled, 20—33 μm long and 6—9 μm thick pedicels stopped with cellulose plugs, directly from an unbranched basal cell or else from
its apical branch, they are usually intermixed with oogonia formed on the same plant, but not with spiny zoosporangia; (b) spiny zoosporangia oval or ovoid, 110–175 μm (average ca. 153 μm) long and 65–90 μm (average ca. 75 μm) wide, of relative width ca. 40–59% (average ca. 50%), rather thick-walled (wall 2.5–4.3 μm thick), slightly flattened at tip with two crowns of large spines up to 100 μm long, 4.3–10.5 μm thick at base and tapering to ca. 3.2 μm at tips; the upper crown generally consists of 3 (less frequently 4–5) straight erect spines surrounding the sporangium pore, the subapical crown is formed of 5–9 generally longer and thicker, frequently slightly bent spines directed to the sides or backward towards the sporangium base; pedicels of spiny zoosporangia 15–25 μm long and up to 25 μm thick, cylindrical, plugged with cellulose, the spiny zoosporangia are generally agglomerated in an apical head on a separate plant with cylindrical unbranched basal cell, they are seldom intermixed with smooth zoosporangia and oogonia formed on the same plant. Zoosporangia from smooth zoosporangia almost spherical, 9.3–11.2 μm in diameter, with two laterally inserted and oppositely directed flagella, develop and ripen inside the sporangium. Their emergence unknown. Zoosporangia from spiny zoosporangia unknown. Oogonia of various shapes from completely spherical to narrow cylindrical, but mostly widely pyriform, obovoid or subspherical and then 45.5–62.5 μm long and 31–53 μm wide with wall 0.9–3.6 μm (usually ca. 2.5 μm) thick, smooth or with 1–4 straight spines up to 45 μm long or longer and 9.5 μm thick at base, on cylindrical or constricted pedicels up to 35 μm long and 13.5 μm thick, thick-walled and generally cellulose plugged; sometimes oogonia are intercalary or morphologically undifferentiated, not separated from basal cell by constriction; since antheridia are lacking the oogonia function as parthenosporangia: when young, the plasma is distributed along the wall and surrounds the central vacuole, then it is translocated to the centre where it forms the granular dark ooplasm with an irregular stellate contour surrounded by a lighter strongly vacuolated periplasm. Subsequently the ooplasm surrounds itself by a wall transforming to a parthenosporangia. Parthenospores single, spherical, 24–43.5 μm in diameter, golden-brown, episporium 0.8–3.6 μm (usually ca. 1.3 μm) thick, densely covered with numerous minute cylindrical papillae 1.8–3.1 μm long (average 2.7 μm) and 0.3–0.5 μm thick. Parthenosporangia germination was not observed.

Aquatic saprophytic fungus on fallen alder (Alnus glutinosa Gaertn.) branches and twigs immersed in water.

Type: Fig. 1a.

Paratypes: Figs. 1 b, c; 2 a—e, 3 a—f, 4 a—i and preserved material deposited in the herbarium of the University of Warsaw, Institute of Botany, Warsaw, Poland.
Type locality: alder forest (*Carici elongatae-Alnetum*) in Kampinos National Park near Warsaw, in close vicinity of Field Station of Institute of Ecology, Polish Academy of Sciences in Dziekanów Leśny.

MORPHOLOGICAL AND TAXONOMICAL CONSIDERATIONS

The investigated *Nellymyces megaceros* population exhibited a characteristic high morphological variability both gradual any by leaps, manifested in the dimorphism of zoosporangia and of entire thalli. Particularly variable elements were: the basal cell and the parthenosporangia, somewhat less — the smooth zoosporangia. Relatively stable as regards shape and dimensions were the spiny zoosporangia, but also in this case the number of spines and their size varied widely.

The morphological variability of the basal cell concerned mainly its branching or lack of ramifications; the shape of the particular elements remaining as a rule rather regularly cylindrical. The thalli with unbranched basal cell (Fig. 1a, b) bore on the apical part an agglomeration of zoosporangia or oogonia growing densely next to each other on the basal cell surface. Such a distribution of generative organs is a characteristic trait of the genus *Minidiella* (Kanouse 1927; Sparrow 1960). Sometimes the sporangia and oogonia were distributed less densely on the thalli on the sides of the apical part of the basal cell (Fig. 2b). They then gave the whole thallus a characteristic appearance as if of a telegraphic pole with insulators. At the tip of such a “pole” generally a sharp spine is visible or a large smooth zoosporangium markedly larger than the lateral ones. Owing to the existence of these large apical zoosporangia, the size ranges of smooth and spiny sporangia overlap masking their dimorphism.

The pedicels of zoosporangia and oogonia may be considered as greatly reduced and specialised homologues of the hyphal branches occurring in fungi of the genera *Rhipidium*, *Aratuspora* and others. These pedicels, namely, reach sometimes rather large lengths and may be constricted either at the base or under the sporangium or oogonium (Fig. 3f, 4a, d). The walls of the pedicels are much thicker than those of the basal cell, moreover in *N. megaceros* cellulin plugs are only found in the pedicels. On the other hand, the large cylindrical apical branches of the thalli with

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Fig. 1 — Thalli of *Nellymyces megaceros* gen. et sp. nov.

a — plant bearing spiny sporangia, part of the holdfast system removed; b — small unramified plant bearing parthenosporangia which arise directly from basal cell surface, holdfast removed; c — whole plant bearing parthenosporangia and two smooth zoosporangia (z) on four apical branches (iz — iconotype).
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branched basal cell (Fig. 1c, 2c) do not differ from the main stem of the thallus in wall thickness, and they are not separated from it by constrictions or cellulin plugs, therefore they cannot be considered as homologues of the hyphal branches of Rhipidium and Araiospora. Similar cylindrical branches of the basal cell, forming its integral part, and those nonhomologous to the hyphal branches have been described by Emerson and Weston (1967) in their Aqualinderella fermentans. In this respect Nellymyces megaceros is very similar to the latter fungus and forms with it and the species of Mindieniella a distinct group within the family Rhipidiaceae. It should be mentioned, however, that owing to its considerable variability, Nellymyces megaceros forms rare and rather nontypical structures as for instance greatly elongated pedicels bearing two zoosporangia (Fig. 2d, right side). In this case the sporangia do not arise directly from the basal cell, but at the tip of a greatly reduced hyphal branch, a feature not found either in Mindieniella sp. div. or in Aqualinderella fermentans. Thus, owing to the wide range of morphological variability of Nellymyces megaceros, it constitutes a link between two different groups of genera in the family Rhipidiaceae: those which have hyphal branches (Rhipidium, Araiospora, Sapromycés), and those which never form them (Mindieniella, Aqualinderella). N. megaceros tends rather towards the latter group.

Emerson and Weston (1967) contested the division of the order Leptomitales into the family Leptomitaceae and Rhipidiaceae, because almost all the genera of this order, beginning with Leptomitus Agardh have more or less arbuscular thalli with a morphologically distinct basal cell and holdfasts, they may, moreover, be arranged in the order of gradually increasing differentiation of the basal cell and more and more reduced hyphal branches. The above mentioned variability of the Nellymyces megaceros thallus supplies additional material supporting this thesis. The new fungus fills the gap in Emerson and Weston's series (it would fit between Fig. 30E and F in their paper). I believe, however, that this points rather to a necessity of critical analysis of the

Fig. 2 — Thallus structure of Nellymyces megaceros gen. et. sp. nov.

a — tip of branch showing some developmental abnormalities; formation of small parthenosporae in an intercalary parthenosporangium and within branch, near the base of an abortive sporangium, producing a bizarre cellulin deposit on the inner surface of the branch wall (c); b — apical part of small plant bearing several sporangia arranged directly on the surface of the basal cell; note very big apical smooth zoosporangium and three free-swimming zoospores above; c — view from above of three-spined parthenosporangium; d — upper part of plant of rare mixed type; note coexistence of all three types of sporangia, one spiny sporangium in apical view, smooth zoosporangia arise both from the surface of the basal cell as well as from the hyphal branches; e — upper half of young plant bearing primordia of smooth zoosporangia and parthenosporangia. Scale A — for a, b, c; scale B — for d and e.
Fig. 3 — Morphology of the spiny zoosporangia of Nettymyces megaceros.

a – e — short-stalked zoosporangia from the apical head of plant bearing spiny zoosporangia only; f — somewhat smaller spiny zoosporangium produced singly by plant of mixed type (i.e. as shown in the Fig. 2d); note free space within one of the spines.
Fig. 4 — Parthenosporangia and parthenosporangia morphology of Nellymyces megaceros.
parthenosporangia c and i in surface view, the remaining ones in optical section, all parthenosporangia except i in side view, i — in view from above.
diagnostic characteristics of the families *Leptomitaceae* and *Rhipidiaceae*, but does not prove that the distinction between these families is purposeless.

The variability of vegetative thalli of *Nellonymyces megaceros* concerns also their dimensions; their length varies from 500 μm in the case of small unbranched thalli bearing but a few sporangia, to ca. 2.5 mm in the case of large arborescent ramified thalli with many tens or even hundreds of sporangia and oogonia.

The greatest differentiation of the thalli of *N. megaceros* result, however, from the dimorphism of the zoosporangia. As already mentioned, the spiny sporangia usually are formed on separate, mostly unbranched plants, and form at their tip a spherical head. The spines of the particular zoosporangia surround this agglomeration by a net, in the meshes of which plant detritus is soon deposited, and epiphytic diatoms and green algae settle. As a result of this, the whole has the appearance of a compact club, quite unlike the fan-shaped rather widespread thallus of the large plants bearing smooth zoosporangia and oogonia. This difference in habitus is so suggestive that at first after finding the new fungus I thought I was reeling with two different species, and only the detection of several rare cases of joint occurrence of all the three types of sporangia on one and the same plant (Fig. 2d) helped me out of this error.

Very characteristic is also the shape and ornamentation of the parthenosporangia in the fungus described. The nine sporangia shown in figure 4, chosen from among the shapes most frequently found, show a wide variability of shape, dimensions and of the number of spines. Beside this, parthenosporangia of completely atypical structure are quite frequently seen — cylindrically elongated, intercalary or even morphologically completely undifferentiated simple segments of the vegetative thallus in which parthenospores are formed (Fig. 2a). The dimensions of the parthenospores also vary widely. Much less variable are, on the other hand, such features as monosporousness of the parthenosporangia, the structure and colour of their episporium, and the distribution of spines on the spiny parthenosporangia (although their number and dimensions vary widely).

Characteristic is also the structure of the constricted pedicels of all the sporangia and of their spines. Both pedicels and spines are as a rule constricted fragments of the tubular branched fungal thallus, and the constriction of the thallus diameter is associated with a considerable thickening of its walls. This leads finally to the occlusion of the pedicel or spine lumen, and their filling with celluline substance. In the *N. megaceros* population examined I found all possible degrees of development of these plugs: pedicels of some parthenosporangia were not plugged, and even only slightly constricted, others were plugged on all their length,
still others were plugged at some points. The same is true of the spines of the parthenosporangia and spiny zoosporangia: empty or tubular spines may be seen, or filled with a hyaline plug only partly, or else completely on all their length. It is characteristic that there is no correlation between the length of the spine or pedicel, and the degree of its plugging with celluline.

This striking conformity in the structure and way of formation of the constricted pedicel and the spine gives reason to believe that they are homologous structures; spines are as if pedicels on which sporangia did not develop. If we lead further this argumentation we will come to the conclusion that all nonconstricted parts formed distally from the constriction arise owing to the further normal growth of the skeletal elements after passing through the developmental phase of constriction. If this reasoning is true, then the skeletal elements of all three types of sporangia are homologous to one another. The correctness of this argumentation is confirmed by the existence of intercalary resting sporangia (Fig. 2a). The pedicel of the next sporangium the one arising from the intercalary sporangium would be in this case a spine which atavistically resumed growth after formation, and produced a swelling at the apex.

From this aspect the thallus of *N. megaceros* is composed of as few as three categories of elements: constricted (pedicels and spines), swollen peripheral (all types of sporangia), and an axial system (basal cell with holdfasts). This argument leads, although by a different way to the thesis formulated above concerning the nonhomology of the main branchings of the *N. megaceros* thallus with the hyphal branches of *Rhipidium* and *Araiospora* (p. 259, 261).

**PHYLOGENY**

The axial system of the thallus of *Nellymyces megaceros* may be considered, owing to the high variability of its structure, as distinctly less specialised than that of fungi of the genera *Rhipidium* and *Araiospora*, on the one hand, and *Mindenella*, on the other. It is indicated on page 261 what position the new fungus should hold in the developmental series of *Emerson* and *Weston* as far as the morphology of the vegetative thallus is concerned. In their comment to this series the authors, however, say: "Very possibly we are dealing here more with radiation from a common ancestor than with a sequence". This remark seems to be quite true, and my fungus, as well as to a certain degree also *Aqualinderella fermentans* are to a certain extent relict forms closely related to the above quoted common ancestor. An additional primitive trait of *N. megaceros* would be, in the light of the foregoing considerations, the facultative presence of spines on the parthenosporangia; the morpho-
genetic processes leading to the formation of sporangia seem to be inhibited in this fungus at various moments, either immediately after the formation of the bulge — the future oogonium, or as if with some delay, after the fungus, has resumed thallus extension and begun to form the next pedicel. Sometimes the inhibition is still more delayed, and instead of a spine, the pedicel of the next oogonium is formed (Fig. 2a). In Min- deniella spinospora Kanouse forming spiny zoosporangia and parthenosporangia, this inhibition of the processes of development of the sporangium has a definite place in morphogenesis and always falls to the moment at which the spines have already formed. In the smooth-sporangial fungi of the family under discussion (e.g. members of the genus Rhipidium), the moment of inhibition of sporangial morphogenesis is also fixed, but at an earlier period, and spines do not form at all. In Aqualinderella fermentans, the process of formation of the constricted and plugged elements has been completely eliminated from the morphogenesis of the fungus: not only spines are lacking, but also pedicels, the zoosporangia and oogonia are sessile. If we consider, moreover, that the pedicels of the parthenosporangia of N. megaceros have a highly variable internal structure, that all stages of development of celline plugs may be found here, from their complete absence to full plugging of the pedicel lumen on all its length, it appears that the extreme lability and instability of the structure is here the consequence of the great lability of morphogenetic processes, and evidence of the developmental primitivism of this fungus.

The structure of the zoosporangia in this fungus seems more specialised. The moment of morphogenesis inhibition discussed above has a definite place in the sequence of developmental processes and occurs either before the resumption of elongation growth (smooth zoosporangia) or after it, thus, after the formation of the characteristic horns (spiny sporangia). These two eventualities are, however, correlated with other morphogenetic processes, and in connection with this we are dealing here with dimorphism of the zoosporangia, and not with continuous variability as in the case of parthenosporangia. Both forms of zoosporangia exhibit a much greater stability of structure than the parthenosporangia, this proving also a higher degree of specialisation of these organs. The degree of this specialisation is similar to that observed in members of Araliaopora.

Thus, as regards morphology, N. megaceros seems to be a rather primitive relict fungus, developmentally very labile, exhibiting a variability of traits of generic rank not met within the family Rhipidiaceae.

Fungi of the order Leptomitaes form distinct developmental series or spectra of diversity, resulting from adaptive radiation not only as regards morphology, but also their physiology, in the first place in the relation between the ability of aerobic respiration and the ability of fer-
mentative metabolism in anaerobic conditions (Gleason 1968; Gleason and Unestam 1968). This series begins with forms exhibiting high oxygen requirements (Supromyces) incapable of decomposing carbohydrates and producing acid (Leptomitus) over Mindeniella which utilises exclusively carbohydrates and produces large amounts of acid, up to Aqualinderella fermentans, completely deprived of the ability of aerobic respiration and obligatorily fermentative (cf. Emerson and Held 1969; Held 1970). The place of Nellymyces megaceros in this series cannot of course be established until a pure culture of this fungus is obtained, and the necessary tests can be performed. The ecological situation, however, in which this fungus was found at the type locality seems to indicate that it is closer to Supromyces as regards oxygen requirement than to Mindeniella or Aqualinderella. Indeed obligatorily or facultatively fermentative fungi like Rhipidium and Aqualinderella from the order Leptomitaes or Blastocladia from the Blastocladiales (Held et al. 1969) occur usually together with bacteria of lactic acid fermentation on media rich in mono- and disaccharides as for instance fruits. Such microsnyusiæ not only form in a poorly oxygenated environment with a high CO₂ concentration, but they themselves produce such conditions in their nearest vicinity. The microsnyusin in which Nellymyces megaceros occurred included, on the contrary, numerous autotrophic organisms (diatoms and Chlorophyceae), and the other phycomycetes occurring with them, particularly Monoblepharis polymorpha and M. macandra are characterised by a rather high oxygen requirement. If physiological investigations will confirm these suppositions, my fungus will be a wonderful example of independent evolution of various groups of traits in the same organism. Closely related morphologically to the complex Mindeniella-Aralospora, it may prove diametrically opposed to them as regards physiology, and closer to Supromyces, a genus including fungi differing widely as regards morphology. The reaction of Nellymyces megaceros to treatment of laboratory gross cultures (washing, cooling, aeration) seems to indicate that this supposition is correct.

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**Nellymyces megaceros** gen. et sp. nov. — nowy grzyb wodny z rzędu *Leptomitales* zблиżony do przedstawicieli rodzajów *Aqualinderella* i *Araiospora*

**Streszczenie**