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MORPHOLOGICAL CHARACTERISTICS OF THE CULTURE *CLATHRUS ARCHERI* (PHALLACEAE, BASIDIOMYCOTA)

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Abstract

This article touches upon the morphological and growth characteristics of the gasteroid mushroom *Clathrus archeri* from the *IBK* Mushroom Culture Collection (Ukraine). For fungus identification *in vitro*, the micromorphological properties of vegetative mycelium have been specified by light and scanning electron microscopy. The presence and structure of crystals, vesicular cells, septum swelling, and mycelial cords have been described. Experimental data on fungi growth rate were obtained on five agar nutrient media at different temperatures ranging from 4ºC to 28ºC. The temperature of 26ºC has been determined as optimal for mycelium incubation, and 39ºC – as critical for culture viability. The morphological characteristics of the fungi on various agar media have been reported. According to the radial growth rate within 0.1–2.9 mm/day, the investigated species belongs to the slow-growing fungi. Nutrient media such as wort agar and compost agar have appeared to be the most favorable for the vegetative growth of *C. archeri* mycelium.

Introduction

The studies on various aspects of biology and systematics of macromycetes traditionally involve the macroscopic and microscopic characteristics of fruit bodies for species identification. At the same in modern *in vitro* experimental studies; macromycetes at the vegetative stage of develop-

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ment. Unfortunately, gasteroid saprotrophic macromycetes are studied insufficiently *in vitro*. It is due to the difficulties associated with pure culture isolation and deposition. The crucial criteria used for taxon characterization at the vegetative stage of development and culture identification remain ambiguous. One such inadequately investigated species at the vegetative stage of development is *Clathrus archeri* (Berk.) Dring (1980), (synonyms: *Anthurus archeri* (Berk.) E. Fisch., *Anthurus sepioides* McAlpine, *Aserophallus archeri* (Berk.) Kuntze, *Lysurus* archeri Berk, *Pseudocolus archeri* (Berk.) Lloyd, *Schizmaturus archeri* (Berk.) Locq.). Due to the unusual appearance of the fruit bodies, *Clathrus archeri* has several common names, such as "devil's fingers", "octopus stinkhorn", and "squidward mushroom". According to the Dictionary of Fungi, the *Clathrus* genus (Phallaceae, Phallales) comprises 16 species (SPECIES FUNGORUM 2021, *Catalogue of life* 2021) mainly found in subtropical and tropical regions. *C. archeri* undergoes two phases in the sporomic stage: a mycoegg phase and a receptacle phase (PIETRAS et al. 2016). This species is a saprotrophic gasteroid fungus belonging to ephemeral macromycetes with primary subtropical and tropical distribution. The fungi occur mainly in the southern hemisphere regions – in New Zealand, Australia, Tasmania, South America, Southern, and Eastern Africa, Mauritius, St Elena Islands (DRING 1980). The first findings of this species are dated back to 1914 in Europe on the territory of France. It is believed that the mycelium and spores of *C. archeri* may have been transferred from Australia and New Zealand to Europe with military fodder or wool for the textile industry (DRING 1980, ZYKOVA 2007). The following findings of the fungi were described on the territory of northeastern France in the 1920s–1930s (PARENT et al. 2000). Over the next few decades, *C. archeri* began spreading rapidly throughout Europe (from Spain to Scandinavia). The mechanism of that fast spread across Europe is not fully understood. Nevertheless, some scientists report on the specific odor of mature fruit bodies of fungus that attracts insects that spread the spores over a considerable distance (KRIEGLSTEINER 1992, JOHNSON and JÜRGENS 2010). In Ukraine, *C. archeri* was first registered in August 1977 near Onokovtsi village located in Uzhorod district of Zakarpattia region (HELUTA and ZYKOVA 2018). After that, there were no reports on new findings of this fungus in Ukraine. Given the low frequency of *C. archeri* occurrence, the third edition of the Red Data Book of Ukraine listed it as an endangered species with a disjunctive range (DUDKA 2009). In recent years, however, researchers have begun to record the mass formation of *C. archeri* fruit bodies in the anthropogenically modified Carpathian plant associations and adjacent areas. There are detailed literature reviews on this species spreading in Europe

and Ukraine presented in the publications by Ukrainian mycologists (Zykova 2007, Heluta and Zykova 2018). The vast majority of the published works are devoted to the systematics, ecology, distribution, and conservation status of this species in nature (Arora et al. 1982, Stengl-Rejthar and Wojewoda 1985, Hosaka et al. 2006, Zykova 2007, Desprez-Loustau 2009, Bîrsan et al. 2014, Stebel 2015, Pietras et al. 2016, Heluta and Zykova 2018, Matus et al. 2018). However, the biological features of this fungus *in vitro* are almost unknown. According to the World Federation of Cultural Collections (WFCC), five strains of this species are maintained in the following official collections: Filamentous fungi and Yeast Collection in the Netherlands, Belgian Coordinated Collection of Microorganism (BCCM), Culture Collection of Basidiomycetes (CCBAS) of Institute of Microbiology in the Czech Republic, Culture Collection of Basidiomycetes of the Komarov Botanical Institute (LE BIN), All-Russian Collection of Microorganisms (WKM) both in Russian Federation, International Collection of Microorganisms from Plants (ICMP) in New Zealand. Dikaryotic strain *C. archeri* 2405, isolated from mycological material, gathered on the territory of Ukraine, is deposited in the *IBK* mushroom culture collection of M.G. Kholodny Institute of Botany, NAS of Ukraine (Lomberg et al. 2015, Bisko et al. 2018). Given the limited knowledge of the cultural and morphological characteristics of *C. archeri*, our work aimed to determine the morphological and growth properties of the strain *C. archeri* 2405 on solid growth media of different compositions and to find out the optimal conditions for its deposition in the culture collection.

Materials and Methods

Pure culture isolation

The object of the study was *C. archeri* 2405 from the Collection of pileate fungi (*IBK*) (Bisko et al. 2021). Mycological material for *C. archeri* pure culture isolation was gathered during the expedition to Hutsulshchyna National Nature Park (15th October 2015). Young fungal fruits of *C. archeri* (in myco-egg phase) were collected in the Ivano-Frankivsk region, in the Shtefantsi mountain area located in Babyn village, Kosiv district, Hutsulshchyna National Nature Park (meadows, grazing). 48°16'02.4" N, 25°02'38.3" E.

Mycelial culture of *C. archeri* was obtained from the young fruit body of the fungi (Figure 1). In this development stage (myco-egg phase) fungal fruits have pear- or egg-like forms, are surrounded by a slime layer, and

are covered with white dense peridium. The inoculum (pieces of gleba) was placed in the plates with wort agar (WA) media using sterile lancet. The inoculated plates were incubated at 25°C in a thermostat. Nutrient media were supplemented with penicillin (200 IU/ml) for bacterial growth inhibition.

Fig. 1. *Clathrus archeri* – the source of the strain *IBK* 2405
Source: photo by M.O. Zykova

The plates were incubated in the thermostat until the appearance of the colonies with a well-developed mycelium. The pure culture of fungi was maintained in the test tubes with WA media for culture deposition and follow-up studies. The absence of foreign microflora, morphological properties of colonies and vegetative mycelium were controlled visually and using a microscope.

Cultural and morphological investigations

For further characterization, cultures were inoculated onto different agar media with a pH adjusted to 6.0 in Petri dishes (diameter 90 mm, 20 mL per dish): malt extract agar (MEA, Merck, Germany); potato dextrose agar (PDA, DIFCO, USA); wort agar (8°Balling) (WA), wort agar supplemented with wheat straw (1%) (WAS), and glucose-peptone-yeast-agar (GPYA) consisted of (g/l): glucose – 25.0; peptone – 5.0; yeast extract – 3.0;

KH_2PO_4 –1.0; K_2HPO_4 – 1.0; $MgSO_4$ – 0.25; agar-agar – 20.0. Compost agar (CA) was prepared according to the method described by PRYDIUK and LOMBERG (2021). For CA, GPYA, WA, and WAS media preparation we gently mixed 1 L liquid and 20 g agar. All media were sterilized by autoclaving at 121°C for 30 min.

Surface cultivation was conducted at temperatures of 4±0.1, 18±0.1, 22±0.1, 26±0.1, and 28±0.1°C. Culture viability was checked by incubation on WA medium at 30–40°C in increments of 1±0.1°C. The presence or absence of mycelium growth was checked after ten days of incubation. The survival or viability loss of culture mycelium was examined by further cultivation at 26±0.1°C.

Growth rate and morphology study

The inoculum was prepared by cultivating *C. archeri IBK* 2405 mycelium on WA in darkness at 26°C for 14 days. 5 mm agar plugs were cut out from the actively growing part of a colony using a cork borer and placed into a center of the Petri dishes with a fresh medium (three cultures per isolate). The growth parameters of mycelia were analyzed weekly for up to a month according to a previously described method (LOMBERG and SOLOMKO 2012). The average radial growth rate (G_R) of mycelial colonies was determined by the formula:

$$G_R \text{ (mm/day)} = (R_2 - R_1)/(T_2 - T_1),$$

where R_2 and R_1 were the radii of the colonies (in mm) on the day of the beginning of growth (T_1) and the day of the last measurement of growth (T_2).

Microscopic investigations

Micro- and marcomorphological characteristics of the mycelium were examined on the 4-weeks old colonies by means of Stalpers scales (STALPERS 1978). Macromorphological features included a description of colony type, color and density, mycelium odor, the color of the reversum and the presence or absence of concentric circles. Micromorphological properties involved a description of hyphae system features, and occurrence of clamps and anamorphs on the mycelium. Microstructures of the vegetative mycelium of *C. archeri* were observed using optical microscope MBI-15 (Russia) and scanning electron microscope JSM-6060 LA 4 nm (JEOL, Japan) according to the modified method by Quattlebaum E. and Carner G. (BUCHALO et al. 2009).

Statistical analysis

The statistical analysis of obtained results was performed by standard methods using Student t-criteria by means of Microsoft Excel software and StatSoft Statistica 6.0. The values of standard deviations (SD), coefficients of variation, confidence intervals were calculated. Experimental data were expressed from quintuple measurements as mean ± SD. The values at $P < 0.05$ were considered significant.

Results and Discussion

Cultural and morphological examination of *C. archeri IBK* 2405 on standard agar growth media of different compositions – WA, MEA, PDA, GPYA, CA showed the variability of the morphological features of mycelial colonies depending on the compounds of the nutrient medium. On WA, PDA, CA media the strain formed dense colonies with numerous radial silky cords, white-colored at the early stage of growth, and pink shaded over time, with the zones of high tangled hyphae. The colony rim was uneven and raised over the substrate, the reverse matched the color of the substrate (Figure 2*a*). On GPYA medium the culture formed dense, velvety colonies with a noticeable concentric zonal sequence and a few short aerial hyphae along the rim of the colony. The mycelium acquired a pink-cream color with age, the rim was uneven and raised, the reversum matched the color of the substrate (Figure 2b).

The least cultivatable media for *C. archeri IBK* 2405 was MEA with very slow growth observed. Even on the 30th day of cultivation, the diameter of the colony did not exceed 20 mm. The culture formed white, dense, woolly colonies that acquired pink color with age, and had drops of exudate appeared. The colony rim was uneven, the reversum matched the substrate color (Figure 2c).

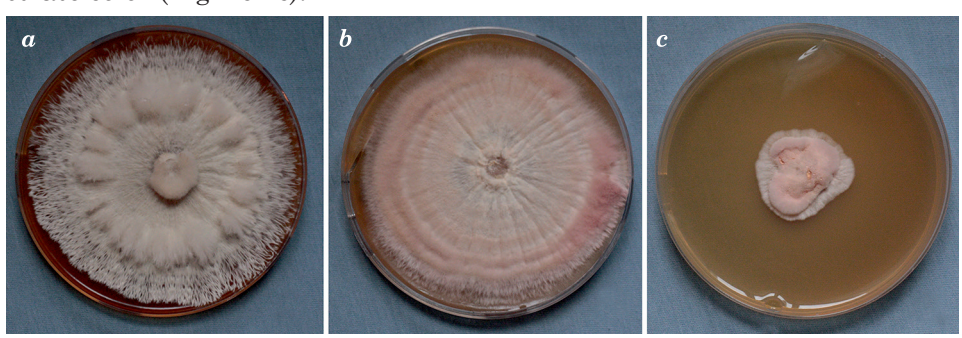

Fig. 2. Mycelial colonies of *Clathrus archeri IBK* 2405 on solid media: *a* – WA; *b* – GPYA; *c* – MEA at incubation temperature 26±0.1°C (30th day of cultivation)

We have examined the effect of various incubation temperatures on the radial growth rate and the morphology of the colonies of *C. archeri* 2405. The optimum temperature for growth was 26°C (Table 1). Based on the results of a study of *C. archeri* 2405 growth on agar growth media of different compositions, *C. archeri* 2405 can be attributed to the group of slowly growing fungi evidenced by its radial growth rate (Table 1).

Table 1

Radial growth rate (G_R, mm/day) of vegetative mycelium of *Clathrus archeri IBK* 2405 on agar nutrient media at different incubation temperature

Incubation temperature [°C]	G_R, mm/day on different agar nutrient media				
	WA	MEA	GPYA	PDA	CA
18±0.1	2.2±0.1	0.1±0.2	1.1±0.2	0.5±0.2	2.4±0.2
22±0.1	2.4±0.1	0.3±0.1	1.3±0.1	0.8±0.1	2.5±0.2
26±0.1	2.6±0.1	0.4±0.2	1.8±0.2	1.1±0.2	2.9±0.1
28±0.1	2.5±0.2	0.1±0.2	1.4±0.1	1.0±0.1	2.6±0.2

The effects of critical temperatures on the viability of *C. archeri* 2405 were investigated. For culture viability examination, the strain was incubated on CA medium at 30–40°C in increments of 1°C. After the third day of incubation, the presence or absence of mycelium growth was taken into account. The survival or viability loss of the plant mycelium was tested by the following incubation at 26±0.1°C. The critical temperature for *C. archeri* 2405 strain was 39±0.1°C.

Using SEM, we have obtained new data on the micromorphology of *C. archeri in vitro*. Vegetative mycelium consists mainly of thin-walled, moderately branched, regularly separated, unvarnished generative hyphae with a diameter of (2.94)3.81–4.63(5.17) µm (Figures 3–5).

Based on literature sources, the red and orange colors of fungal mature fruit bodies are imparted by the presence of carotenes, for the most part, lycopene, and *β*-carotene. While *β*-carotene is peculiar to Phallaceae species *Mutinus caninus*, *M. ravenelii*, and *M. elegans*, lycopene is present in the closely related fungus *C. archeri* (FIASSON and PETERSEN 1973).

According to M. Nobles (NOBLES 1971), the strains of the same species may vary in the texture and color of mycelial colonies. More stable taxonomic features are micromorphological properties of the hyphae system, growth rate, optimal growth temperature. As revealed by literature data, both the composition of the growth media and the incubation temperature has a strong impact on the culture growth rate (LOMBERG and SOLOMKO 2012). Information about the growth characteristics of *C. archeri* on agar media is available only in the article by PASAILIUK et al. (2018). Fungi

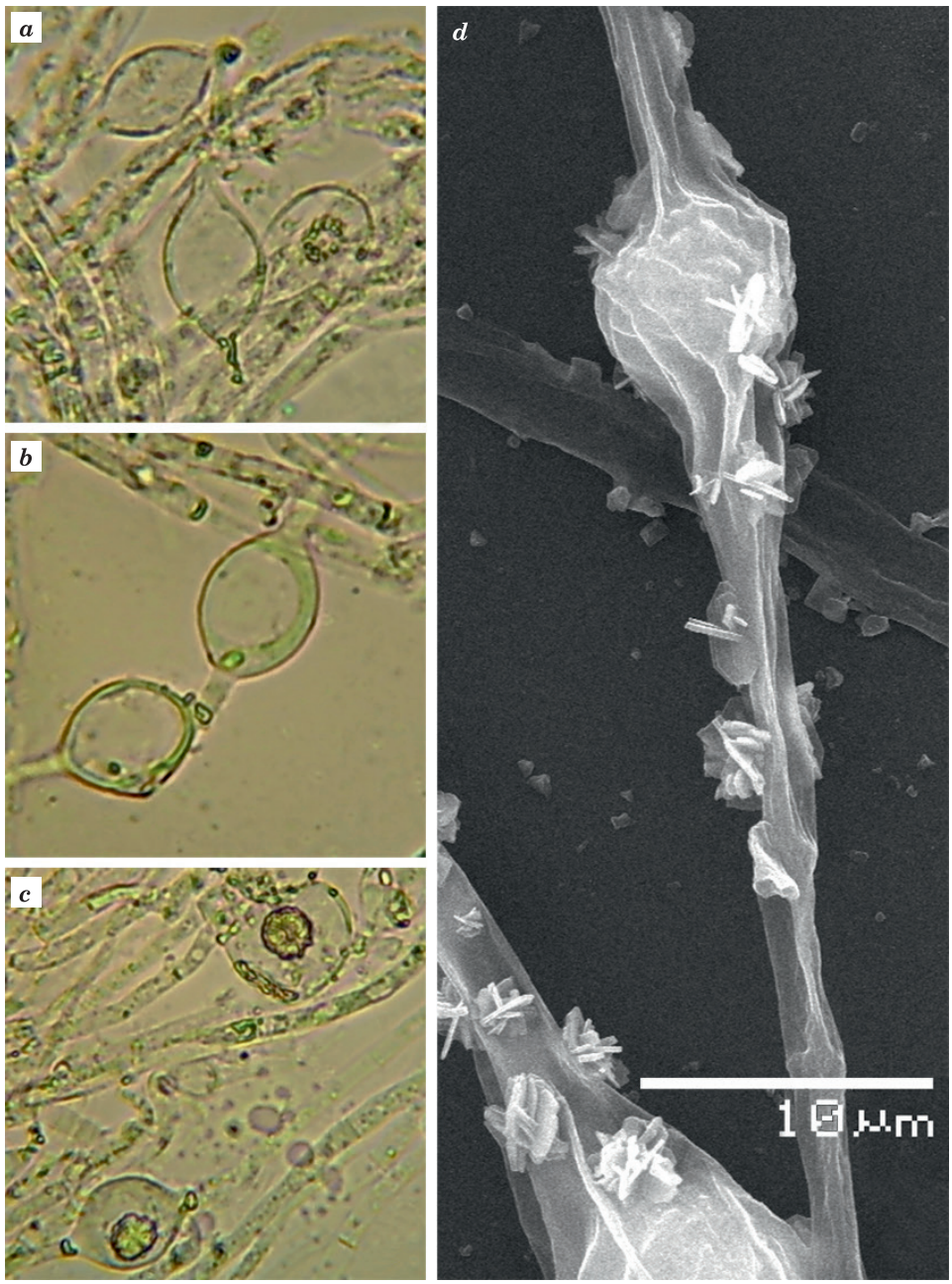

Fig. 3. *Clathrus archeri* IBK 2405: (*a–c*) vesicular cells (× 40); *c* – cells with oil droplets inside (× 40); *d* – crystals on hyphae; hyphae with irregular swelling in septum (SEM × 2200)

mycelium develops under natural and artificial conditions exclusively within a certain temperature range. The identification of this substantial environmental factor is needed to provide the optimal condition for the cultivation and deposition of fungi cultures. The effect of temperature on the growth and development of *C. archeri* has been studied fragmentarily. The majority of the published material on this topic is devoted to the observations of the appearance and development of *C. archeri* fruit bodies in the wild.

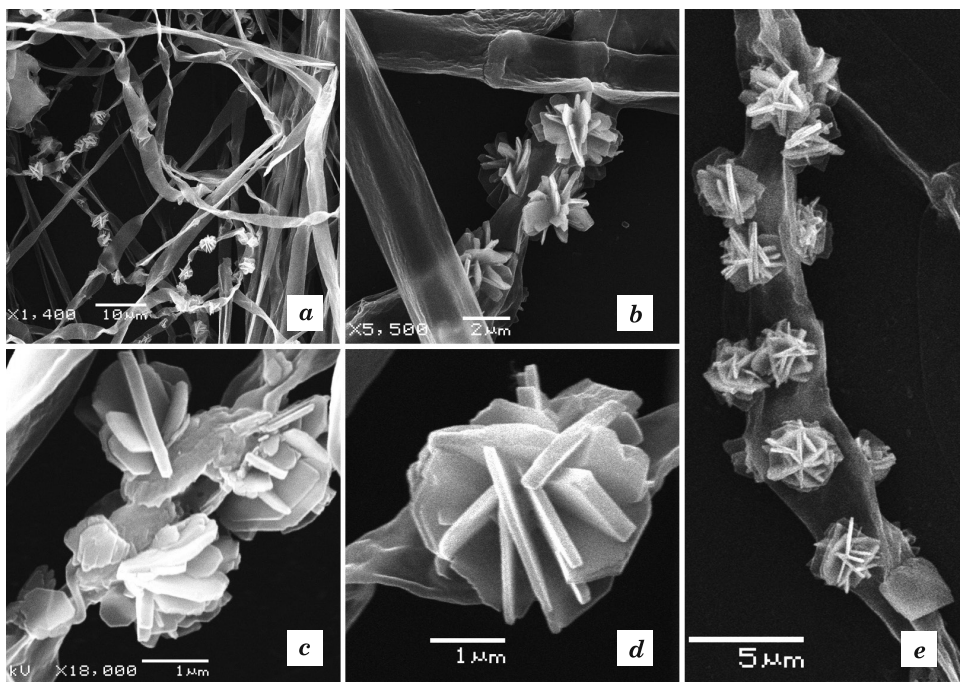

Fig. 4. *Clathrus archeri IBK* 2405: *a–e* – crystals on hyphae; *a*, *b* – septa without clamp cells

This species characterizes by the formation of rounded large vesicular cell of width (7.32)12.96–14.95(16.48) and length (19.26)25.49–27.74(30.92) µm. We observed large vacuoles and oil droplets in the middle of these cells (Figure 3). The presence of such cells was previously reported for *Phallus impudicus L.*, *Ph. hadrianii*, *Lycoperdon perlatum* Pers. (BUCHALO et al. 2009, DYAKOV et al. 2010, BUKO et al. 2019). One of the most requisite taxonomic features when identifying basidium macromycetes in the culture is the presence of clamps, formed on the hyphae of the dikaryotic mycelium of many members of this group of fungi (STALPERS 1978, BUCHALO et al. 2009). Different species feature specific differences in the position of the clamps on the hyphae, their location frequency, shape, size,

etc. (BUCHALO et al. 2009). However, in our study, we haven't observed any clamps formation in *C. archeri IBK* 2405. There was mainly clampless vegetative mycelium (Fig. 5). According to the reports, clamps are not also present in species of the genus *Armillaria, Lycoperdon perlatum Pers., L. pyriforme* Schaeff.

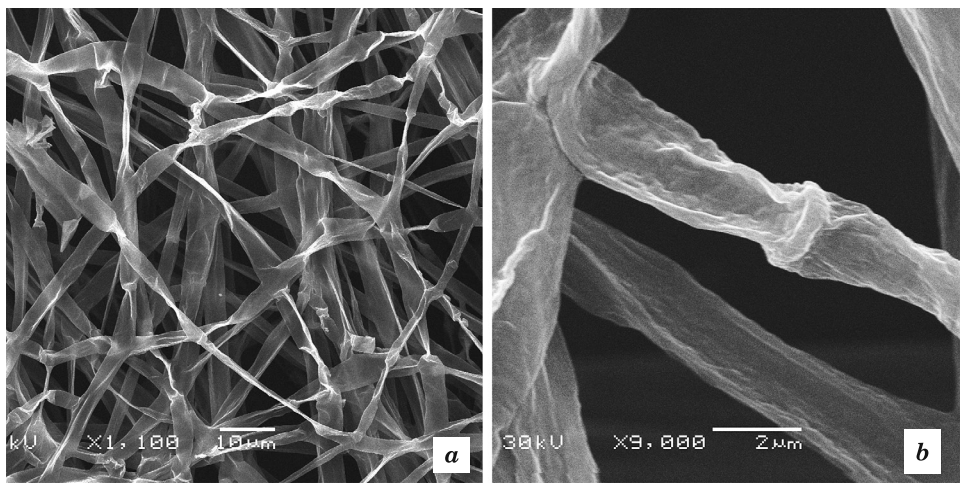

Fig. 5. Micromorphological structures in *Clathrus archeri IBK* 2405: *a* – clampless mycelia; *b* – anastomose and a septum inside the collapsed hypha

The morphological markings of secretory activity such as secretory hyphae and crystal deposition were observed in *C. archeri IBK* 2405 culture on the 20th day of cultivation. Numerous plate-like calcium oxalate crystals formed on the surface of hyphae, collected in bundles and resembled a flower (Figures 3, 4). *In vitro* crystal formation is described for fungi of different environmental groups (ARNOTT 1995, AROCENA et al. 2001, BUCHALO et al. 2009, TUASON and AROCENA 2009, BADALYAN and BORHANI 2019). The density of the crystals on the surface of hyphae may vary. They grow inside the cell and exit it perpendicularly or at an angle to its surface. As a rule, the formed crystals remain on the surface of the cell wall and are rarely removed from it. As a result of hyphae lysis, crystals can occur in the environment. Some researchers suggest that the inlay of calcium oxalate in hyphae provides a hydrophobic protective layer on the surface of the fungus hyphae. It reduces the propensity of the hyphae when exposed to various microorganisms (SNETSELAAR and WHITHNEY 1990, ARNOTT 1995). In a natural environment, the ability of fungi to form calcium oxalate crystals on the surface of the hyphae and secrete them into the substrate affects the biochemical processes in soils (GADD et al. 2014). Mycelium acts as a place for calcium pooling, thereby changing the

pH of the soil and the availability of phosphorus for plants (CROMACK et al. 1979, TUASON and AROCENA 2009). Based on the experimental data, it was concluded that oxalic acid dominates among other organic acids secreted by fungi in natural biogeocenoses. Oxalic acid performs different functions. Its geochemical value consists of metal cations binding and secondary mineral formation, as well as the dissolution of certain minerals and the conversion of some elements into forms accessible to fungi and plants. The acid can inhibit the growth of other microorganisms in the communities and can be a factor in allelopathy. The secretion of oxalic acid (the strongest organic acid) causes a rapid acidification of the external environment that may activate acidic hydrolases in the cell walls of plants, contributing to their destruction and penetration of fungi into plant tissues (FRANCESCHI and LOEWUS 1995, TUASON and AROCENA 2009). In addition, oxalic acid secreted by mycorrhizal fungi contributes to the establishment of a trophic relationship between plant roots and fungi hyphae.

Culture collections should ensure the security of intact biomaterial storage, relevant characterization, and information support of samples in modern databases. That is why the priority task of the macromycetes culture collections is the preservation of fungi strains *in vitro*, namely to support their purity, genetic stability, viability, and biological activity (PEARCE et al. 2020). In world culture collections, various nutrient media are used for maintaining macromycetes in an active physiological state. According to reports, *C. archeri* strains are stored in the collections on standard nutrient media, such as WA (WKM, LE BIN), MEA (CCBAS), PDA, and Norkrans modified media (BCCM). When selecting the composition of the nutrient medium, we took into account the ecological suitability of *C. archeri* to natural substrates. In nature, the mass fruiting of *C. archeri* is associated with disturbed ecosystems that have noticeable anthropogenic impacts (tree felling, roads, grazing of livestock, landfills, etc.), are rich in organics – wood chips, sawdust, branches, leaves, dry grass, dead wood, and presumably have a high degree of substrate nitrification (HELUTA and ZYKOVA 2018). For this reason, we propose to use simultaneously three nutrient media for the storage of *C. archeri* strains: wart agar (WA), compost agar (CA), wart agar supplemented with wheat straw (1%) (WAS). CA and WAS have been successfully used in *IBK* for the storage and cultivation of *Agaricus bisporus* (JE Lange) Imbach, *Lepista nuda* (Bull.) Cooke, *Macrolepiota procera* (Scop.) Singer, *Phallus impudicus* L., *Lycoperdon perlatum* which like *C. archeri* belong to the environmental group of saprotrophic macromycetes.

In recent times, there were a few reports on the possibility of repeated reproduction of *Anthurus archeri* in the territory of the Hutsulshchyna

National Nature Park by applying the *re-situ* methodology (PASAILIUK et al. 2018). As a result of renaturalization actions, started in 2012, the annual fruiting of the fungus was obtained at the three mycological-reproductive sites. However, given that *C. archeri* is a species belonging to the alien mycobiota that aggressively exploits natural and man-made phytocenosis, its active spread constitutes a threat to natural phytocenosis. This species intensively inhabits azotized, affected areas: landfills, fellings, where its density reaches more than 10 copies per 100 m^2. The species occurs near settlements, avoiding natural cenosis, which indicates the signs of its adventisation. With this in mind, any introduction of these macromycetes into the ecosystems of Ukraine is wrong. From the standpoint of Ukrainian mycologists (HELUTA and ZYKOVA 2018), it is necessary to give up the idea of enriching the biodiversity of botanical gardens, dendrological parks, and other objects of the natural preservation fund with the macromycetes, including invasive ones. It is due to the fact that such contamination of mycobiota in Ukraine may become hazardous, resulting in unexpectedly severe and uncontrollable consequences. Considering the significant occurrence frequencyof this species in natural plant formations, *C. archeri* should be excluded from the Red Data Book of Ukraine as an alien and invasive species (HELUTA and ZYKOVA 2018).

Conclusions

The paper addresses the data on the growth and the morphology of *C. archeri IBK* 2405 culture on agar nutrient media of various compositions at different incubation temperatures. According to the growth rate, the strain belongs to the group of slow-growing fungi. The critical temperature for the viability of *C. archeri IBK* 2405 mycelium is 39±0.1°C.

The key micromorphological features of *C. archeri IBK* 2405 vegetative mycelium have been examined *in vitro* by means of scanning electron microscopy (SEM). This species is distinguished by a formation of roundish vesicular cells with large vacuoles and droplets of oil inside, along with numerous crystals.

The defined micro- and macromorphological properties of mycelium on the specific media and culture growth rate can be regarded as additional taxonomical characteristics of *C. archeri* at the vegetative stage of development. With ecological and biological peculiarities of *C. archeri* in mind, we have selected the composition of agar nutrient media for strain cultivation and preservation in the proper physiological state *in vitro*.

The specified biological characteristics are essential for establishing reliable means of pure culture maintenance in an artificial environment. It will contribute not only to the protection and genetic conservation of the fungi but their practical application as well.

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