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Studies on pigments of the myxomycete *Physarum nudum*

I. Absorption spectra of the crude extracts of pigments from plasmodia cultured in continuous light and in darkness

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Abstract:

1. Method for extraction and crude separation of the plasmodial pigments of the myxomycete *Physarum nudum* cultured in light and in darkness were elaborated.

2. By the use of various solvents in the procedure of extraction three pigment fractions were obtained from plasmodia cultured in the dark and four fractions from those grown under continuous light.

3. The absorption spectra of the particular fractions within the UV and visible range were determined.

INTRODUCTION

Light exerts an essential influence on the metabolism of the Myxomycetes and its effect can be manifested more or less drastically in at least three ways, e.g. in phototaxis, sporulation, and a change in the plasmodial pigment.

Baranetzki (1876) observed negative phototaxis in *Myxomycetes*. However, investigations on the behaviour of the plasmodia of the myxomycete *Physarum nudum* in the light gradient revealed a varying reaction to light depending on the age of the culture (Rakoczy, 1962). Negative phototaxis was demonstrated only in young (2–4-day-old) plasmodia of this species, while the older ones migrated to the illuminated places (positive phototaxis).

Many authors have proved that in a number of species the sporulation process is affected by light (Table 1). The indispensability of light for this process has been ascertained above all for the slime moulds characterized by coloured plasmodia. Recent reports of a similar necessity of light for sporulation in the species with colourless or white plasmodia have not been verified by studies on pigments. Even a negligible, imperceptible amount of one or more pigments may suffice to absorb radiation which in turn stimulates sporulation. In all likelihood, this should explain

Table 1

Sporulation induced by light (literature data)

Author, year	Species	Plasmodial pigmentation
Skupieński, 1928	*Didymium difforme*	grey
Gray, 1938	*Physarum polycephalum*	yellow
,, ,,	*Physarum tenerum*	,,
,, ,,	*Fuligo septica*	,,
,, ,,	*Leocarpus fragilis*	orange-yellow
Gray, 1949	*Physarella oblonga*	yellow
Sobels and van der Brugge, 1950	*Physarum polycephalum*	,,
,, ,, ,,	*Badhamia utricularis*	orange-yellow
Gehenio and Luyet, 1951	*Physarella oblonga*	yellow'
Straub, 1954	*Didymium nigripes*	brown
Lieth, 1956	,, ,,	,,
Gray, 1961	*Physarum flavicomum*	yellow
McManus, 1961	*Stemonitis fusca*	white
Daniel and Rusch, 1962	*Physarum polycephalum*	yellow
Rakoczy, 1962	*Physarum nudum*	yellow
Solis, 1962	*Physarum nicaraguense*	white or cream
Fergus and Schein, 1963	*Physarum gyrosum*	white
Koevenig, 1963	,, ,,	,,
Nair and Zabka, 1965	,, ,,	,,
,, ,,	*Physarum polycephalum*	yellow
,, ,,	*Didymium iridis*	brown
Ling, 1968	,, ,,	,,

the requirement of light for sporulation of some myxomycete species with "white" plasmodia.

That light participates in sporulation is also evidenced by the dependence of this process on light intensity. The higher the intensity the shorter is the period of sporulation and the higher the per cent of sporulating cultures (Gray, 1938; Daniel and Rusch, 1962; Rakoczy, 1962; and others). This dependence is correlated with the age of plasmodia (Rakoczy, 1962; Ling, 1968). The older the plasmodia the smaller dose of light (intensity × exposure period) is required to induce sporulation. Daniel and Rusch (1962), and Rakoczy (1962) have demonstrated that light is indispensable for the stimulation of sporulation, while further processes connected with the formation of the sporangia and the spores can take place in darkness. It was found for most species under investigation that near UV and blue as well as red (near red) light is active in the sporulation process (Straub, 1954; Gray, 1941; 1953; Rakoczy, 1963, 1965; Nair and Zabka, 1965). The action spectrum obtained for the sporulation of the myxomycete *Physarum nudum* (Rakoczy, 1965) shows the highest influence of near UV and blue light; it declines with increase of the wave-length. A much weaker stimulating effect on sporulation is exerted by

red radiation. The green part of the spectrum not only fails to induce this process, but inhibits it. Similar observations have been made by Lieth (1956) for *Didymium nigripes*. Nair and Zabka (1965) found that near red reverses the inhibition of sporulation imposed by far red light in *Didymium iridis*.

Moreover, light induces a change of plasmodial pigmentation. Baranetzki (1876), Gray (1938), and Rakoczy (unpublished data) observed a change of plasmodial pigments in *Fuligo septica* from yellow to cream. *Physarum nudum* changes its colour under the effect of white light (Rakoczy, 1962) and of monochromatic radiation (Rakoczy, 1965) in the range of the visible part of the spectrum (417–520 nm); the longer the wave the more intense radiation is necessary in a definite period of exposure to alter the colour of the pigment from yellow to brown (Rakoczy, 1962, 1965). No change in the plasmodial pigments of this species of myxomycete was observed under UV or red light. Koevenig (1963) and Nair and Zabka (1965) reported a change in the plasmodial pigment of *Physarum gyrosum* (from white to yellow) induced by white light. Besides, the latter authors found that this slime mould turns yellow in blue light and changes from white to brown in red light.

All these observations of both change of pigmentation and induction of sporulation are undoubtedly only a final results of the effect of the light absorbed in a photoreceptor on metabolism. The data concerning the metabolic changes evoked by light are scanty. Daniel (1966) demonstrated an essential change in the metabolism of the myxomycete *Physraum polycephalum* under the influence of light (photometabolism). The alteration affected the content of macromolecular components (protein, RNA, DNA, polysaccharide), as well as the plasmodial ATP level. Moreover, the light inhibited respiration and light-dependent oxidation-reduction reactions were noted.

It is a basic law of photochemistry that if light affects some process, it must have been absorbed. The effect of visible light on the sporulation or a change in the plasmodial pigment indicates that some colour substance (or substances) absorbs radiation. This does not exclude the possibility of maximum absorption attained by this substance in UV.

The light effect on phototaxis, sporulation or a change in the plasmodial pigment points to the existence in the plasmodia of a photoreceptor, or rather some of them, responsible for the absorption of radiation, which in turn influences these processes. These photoreceptors, and especially the one responsible for reproduction in the slime moulds, were sought in the investigations on the pigments of these organisms. Unfortunately, the results of research on pigments, carried out so far, demonstrate a wide divergence even within the same species of the myxomycete, as can be seen from the data listed in Table 2.

These data show that up till now no investigator has managed to characterize the photoreceptor responsible for absorption of the radiation participating in sporulation, moreover there are no reliable data on the chemical nature of the pigments for at least one species of slime mould. Neither can the data on the absorption of pigments isolated from a plasmodium be associated with the action spectrum of sporulation. Therefore, further studies on pigments seem indispensable.

Table 2

Literature data on slime moulds pigments

Author, year	Species	Chemical nature of the pigments
Seifriz and Zetzmann, 1935	*Physarum polycephalum*	flavones
Gray, 1953, 1955	,, ,,	riboflavin
Sobels, 1954	*Badhamia utricularis* strain II	flavones
Wolf, 1959	*Physarum polycephalum*	pteridine
Dresden, 1959	,, ,,	peptide-type pigments
Kuraishi et al. 1961	,, ,,	neither pteridine nor peptide-type
Brewer, 1965	,, ,,	conjugated polyenes containing nitrogen and a carboxyl group
Nair and Zabka, 1966	,, ,,	phenolic compounds
Daniel, 1966	,, ,,	conjugated polyenes with a carbonyl group as the essential part of the chromophore
Kuraishi (personal communication to Nair and Zabka, 1966)	,, ,,	xanthophyll?
Nair and Zabka, 1966	*Physarum gyrosüm*	flavones
,, ,, ,, ,,	*Didymium iridis*	phenolic compounds

In this situation an attempt was made to investigate the pigments of the myxomycete *Physarum nudum*. This species seems most suitable for this kind of studies because a good deal has been learnt about its reactions to light, the action spectrum of sporulation of this species has been determined, and the radiation range evoking an alteration in the plasmodial pigment from yellow to brown has been defined.

The object of the investigations was to examine the pigments of the myxomycete *Physarum nudum* in relation to exogenous conditions (mainly light and darkness) and to the phase of vegetative growth of the plasmodium as well as to determine their physiological role in the process of sporulation.

In the first part of the study the author tried to elaborate extraction method which would make possible a comparison of the spectral curves of crude extracts of pigments of plasmodia cultured in light and in darkness.

MATERIAL AND METHODS

The investigations were carried out on the slime-mould *Physarum nudum* Macbride. The standard cultures were grown similarly as in the previous studies (Rakoczy 1962, 1965) in darkness, on oat flakes agar according to Howard (1931),

on Petri dishes 8 cm in diameter, at 21°C. Plasmodia cultured for 7 days following their transplantation on the oat flakes agar at 21°C in conditions of continuous darkness or light, were used as experimental material. The thermostate was illuminated with six 25 W white light fluorescent tubes. The light intensity at the level of the cultures was about 2,000 lux. The experimental plasmodia were transferred onto freshly prepared pure agar and after they had spread over the surface of the agar (in approximately 3 to 4 hours), they were collected with a plastic spatula. The earlier transfer of the plasmodium to pure agar allowed to eliminate all contaminations of the plasmodium with the nutrient agar. 1,000 mg of fresh weight of plasmodia was used for extraction.

In the preliminary experiments various extraction solvents were employed. Fresh plsmodia were submerged in the test solution, then trituated in a mortar and filtered through a Schott filter G 5. The colour of the filtrate and sediment were determined in a visual (non-photometric) way.

The aim of the investigations was to elaborate a proper method that would ensure complete extraction. It was assumed that the same method could, as a rule, be adopted for the extraction of pigments from plasmodia grown in light and in the dark.

Absorption of plasmodia from darkness and light were measured first to compare a plasmodial pigmentation of the two kinds of the cultures.

In these case the flat cells 0.01 mm thick and spectrophotometer Specord UV-Vis in which the cells could be placed near a photomultiplayer were used.

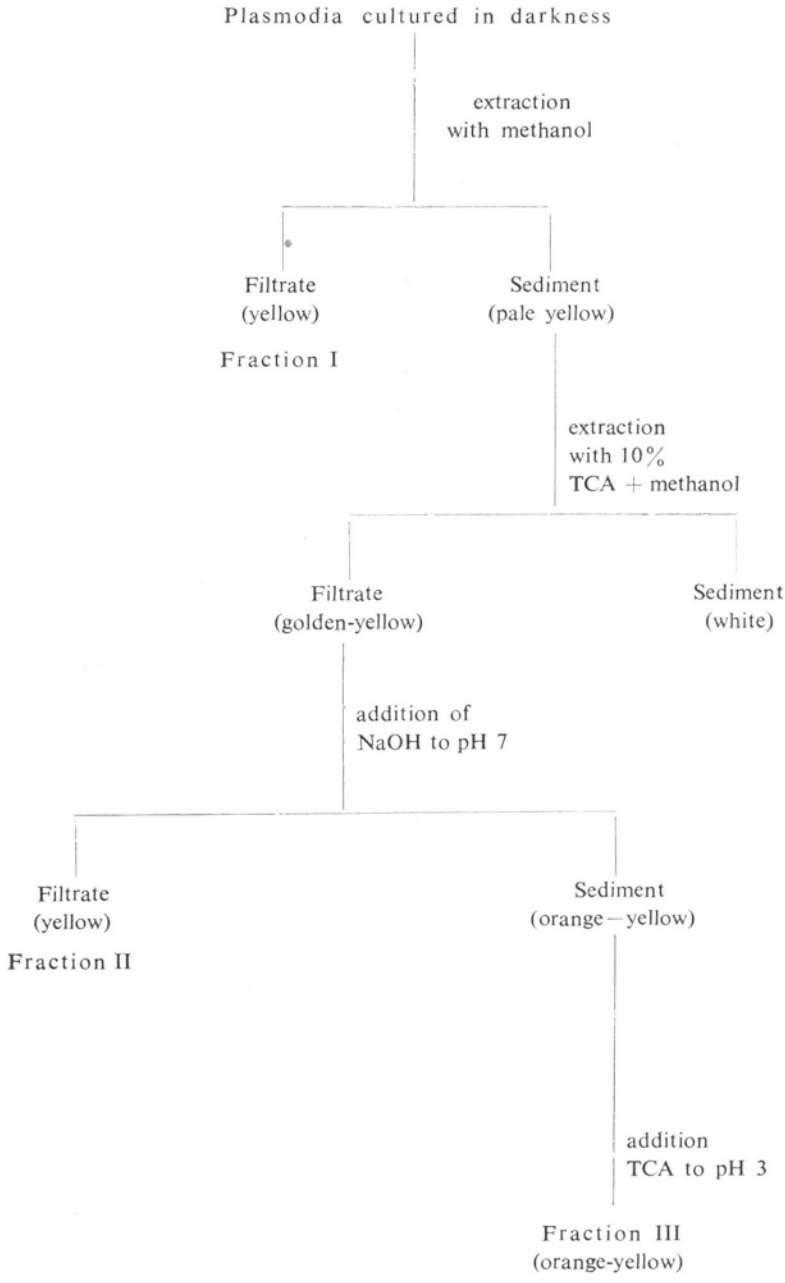
The absorption of extracts obtained by the worked out method was measured within the range of 250–600 nm by means of a recording spectrophotometer Unicam SP 500 B, cells 1 cm thick being used. The results of extraction by this method were repeated several times, the obtained fractions manifesting invariably a similar character of spectral absorption. The diagrams in Figures 2–8 are typical examples of the absorption curves.

RESULTS

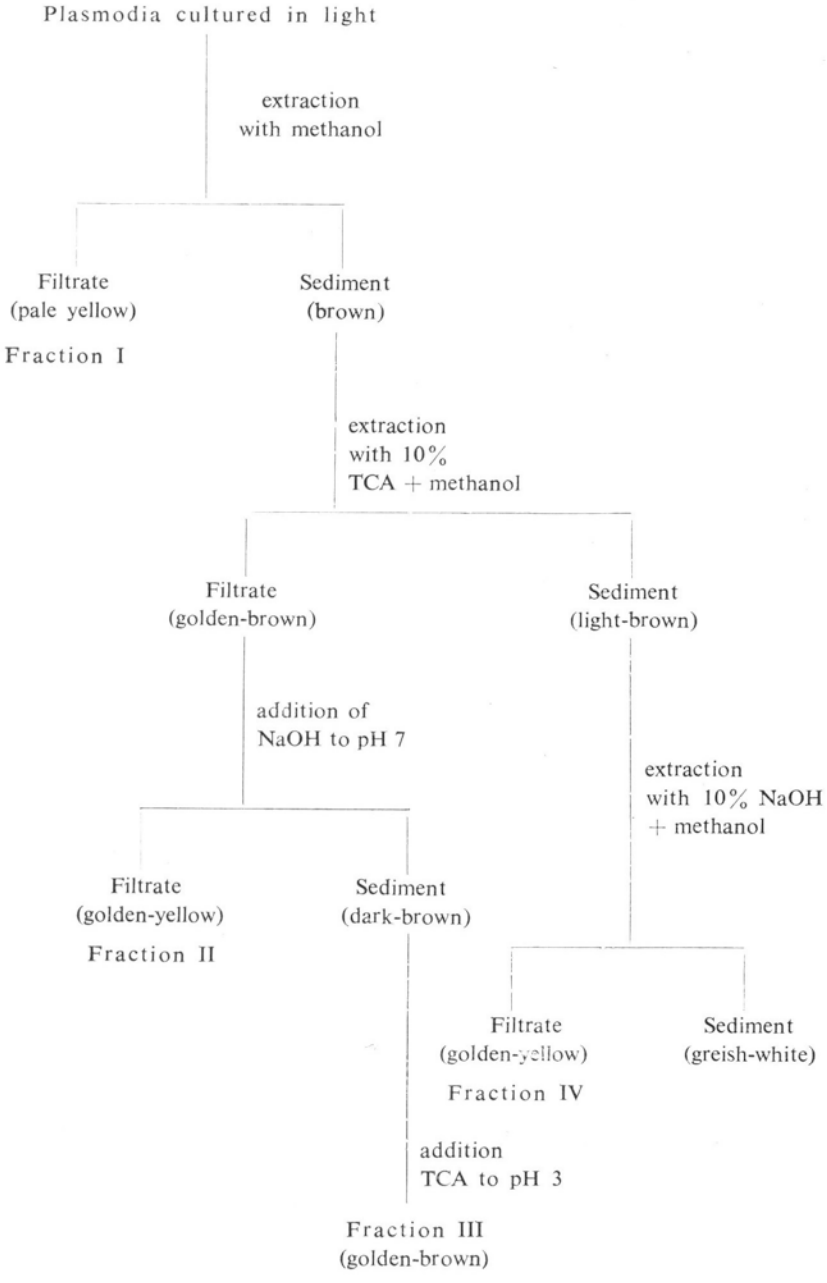
The plasmodia cultured in light and in darkness differ in their pigmentation (Rakoczy, 1962, 1965). Those grown in the dark for 7 days are yellow, while the colour of the plasmodia grown in light is brown. The change of the plasmodial pigment in light conditions depends on the intensity of illumination and deepens with longer exposure to light. The 7 day-old plasmodia, just before the stage of sporulation manifest a wide divergences in pigmentation as compared with those of the same age but cultured in darkness (Fig. 1).

Furthermore, the difference between the material exposed to light and that cultured in darkness concerns the facility of pigment extraction. It was found in the preliminary tests that elution of the pigments with the most extraction solvents employed were much more easy from the plasmodia kept in darkness than from the

DIAGRAM OF EXTRACTION AND CRUDE



SEPARATION OF THE PLASMODIAL PIGMENTS



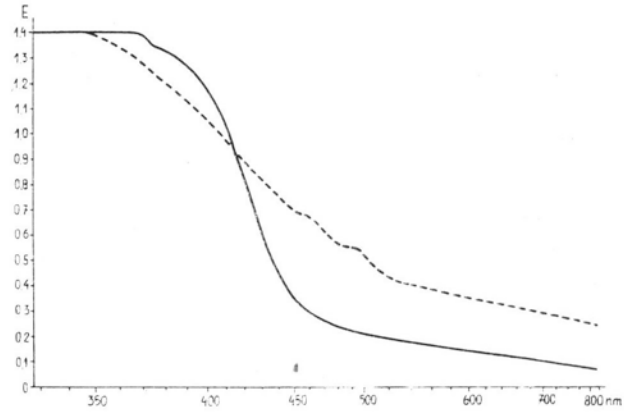


Fig. 1. Absorption spectra of the whole plasmodium of the myxomycete *Physarum nudum*
Plasmodia from darkness: ———; plasmodia from light: — — — —

material exposed to light. Table 3 gives the results of extraction obtained in the experiments.

As follows from the above examples for the plasmodium cultured in darkness, the use of methanol as extraction solvent causes elution of most pigments, with the

Table 3

Some examples of comparison of the results of pigments extraction from the slime mould *Physarum nudum*

Plasmodia kept in darkness			Plasmodia kept under light	
Extraction solvents	Results of extraction	Colour of sediment	Results of extraction	Colour of sediment
Buffer solutions (M/15 phosphate buffer):				
pH 2.1 (with HCL)	XXX	pale yellow	XXX	light brown
pH 4.7	XX	,, ,,	X	brown
pH 6.5	XX	,, ,,	X	,,
pH 7,0	XX	,, ,,	X	,,
pH 8.0	XXX	,, ,,	XXX	light brown
pH 11.2	XXX	nearly white	XXX	,, ,,
Ethanol	XXX	pale yellow	XX	brown
Methanol	XXX	,, ,,	XX	,,
Acetone	XXX	,, ,,	XX	,,
Methanol + 10% TCA	XXXX	white	XXX	light brown
Methanol + 10% NaOH	XXX	pale yellow	XXX	,, ,,

X–XXXX – degree of extraction from partial to complete.

pale yellow sediment left over. The insignificant amount of the pigments retained in the plasmodium is completely eluated after denaturation of the plasmodial proteins with trichloro-acetic acid (TCA). On the other hand, none of the employed extracting mixtures gave entirely white sediments from plasmodia cultured under light.

The final version of the extraction method consists of several stages and permits to obtain a few fractions of pigments. It has been adopted as the best since it enables a complete pigment extraction from both the "dark" and "light" plasmodia. The stages of the procedure allow, on the one hand, to obtain fractions the overall analysis of which yields some information on the effect of light on the complex of pigments, and, on the other, such a procedure permits the employment of identical steps in the extraction of the material both in light and dark conditions, at least in the first stages. The schematic diagram of the above course of extraction is given above.

Figures 2–8 present the absorption curves for the particular fractions obtained with the material grown in darkness (Figs. 2, 3 and 4) and in light (Figs. 5, 6, 7

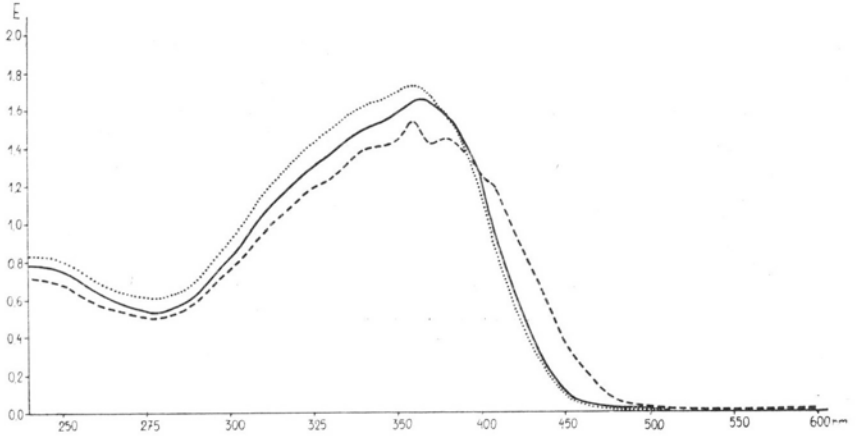


Fig. 2. Absorption spectra of the fraction I of the pigments from plasmodia cultured in darkness
The curves present the extinction values for the concentration of pigments obtained from 1,000 mg of the fresh weight of plasmodia and diluted to 200 ml of methanol. ———: pB 7; — — — —: pH 3; .....: pH 11.

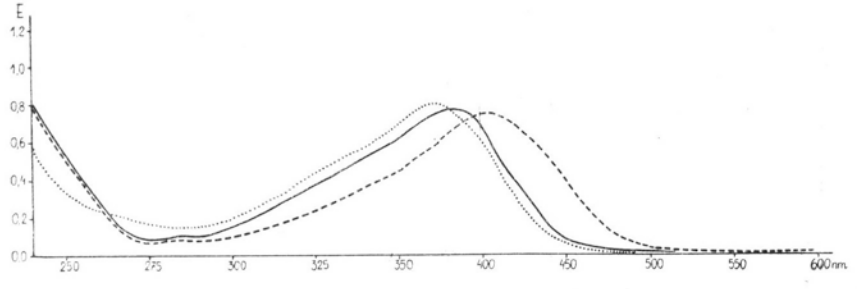


Fig. 3. Absorption spectra of the fraction II (from darkness).
———: pH 7; — — — —: pH 3; .....: pH 11. Extinction values are 10 times higher than the real ones.

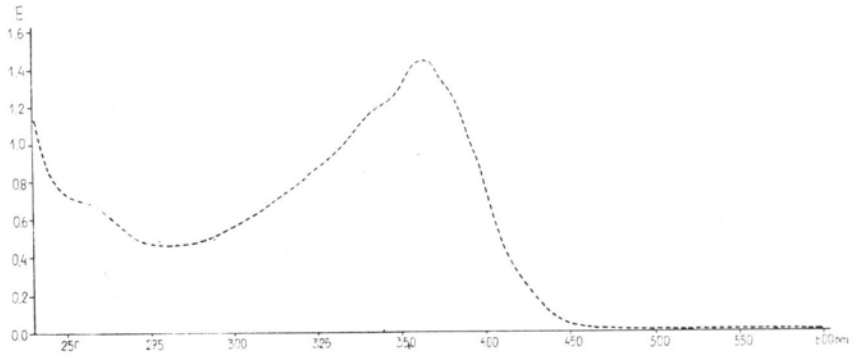


Fig. 4. Absorption spectrum of the fraction III of the pigments (from darkness) in acid solution (pH 3). Extinction value at the maximum is 20 times higher than real one.

and 8). Absorption spectra of the fractions I and II from plasmodia cultured in darkness (Figs. 2 and 4) and absorption of fractions I, II and IV from illuminated cultures (Figs. 5, 6, 8) are presented in neutral, acid and alkaline solutions. Absorption of the III fraction from "dark" and the III from "light" (Figs. 3 and 7 respectively) were drawn in acid solution only, because in neutral and alkaline solution sedimentation of these fractions took place (sediment from "dark" was orange yellow, and from "light" — dark brown). The concentration of the individual fraction of pigments extracted from 1,000 mg of the fresh weight of the plasmodia cultured in darkness or under light and diluted to 200 ml of methanol was taken as the

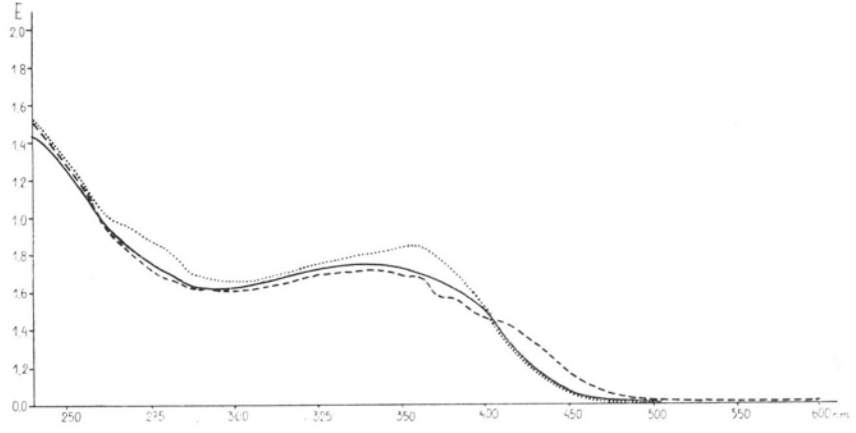


Fig. 5. Absorption spectra of the fraction I of the pigments from plasmodia cultured under light. ———: pH 7; — — — —: pH 3; . . . . .: pH 11. The curves present the extinction values at the maxima 4 times higher than the real ones.

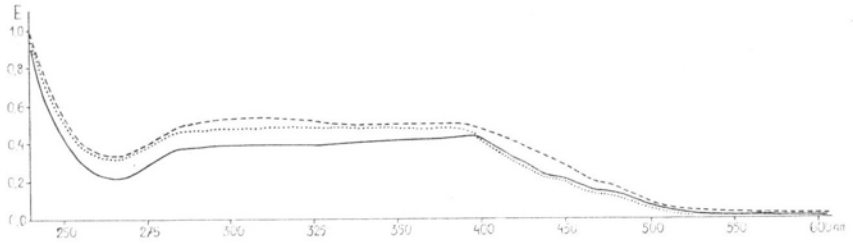


Fig. 6. Absorption spectra of the fraction II of the plasmodial pigments (from light). ———: pH 7; — — — —: pH 3; .....: pH 11. The extinction values afre 4 times higher than real ones.

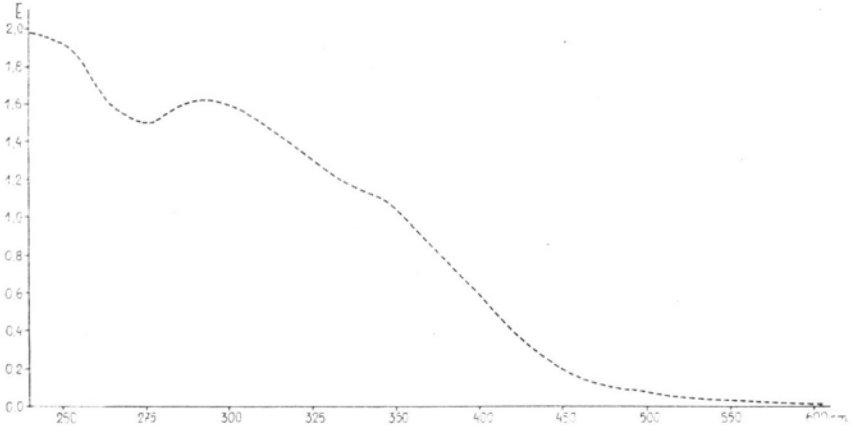


Fig. 7. Absorption spectrum of the III fraction of pigments from light in acid solution (pH 3). Extinction value at maximum is 4 times higher than real one.

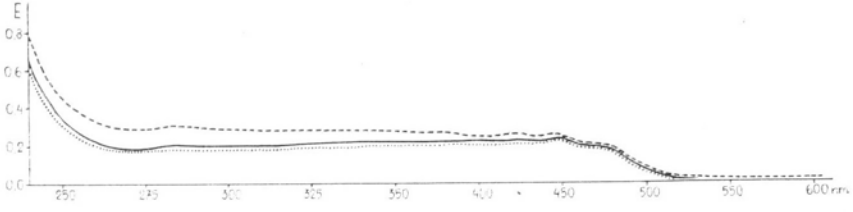


Fig. 8. Absorption spectra of the IV fraction of pigments in: neutral (———); acid (— — —), and alkaline (.....) solution. Extinction values are 20 times higher than real one.

standard concentration of the pigment solution. The extinction values attained for such concentration of pigments represented a real extinction of the individual fraction of pigments.

DISCUSSION

The method of graded (stage) extraction employed in the present investigations made it possible to isolate three fractions of pigments from the plasmodia cultured in darkness and four fractions from those kept under light. The particular fractions are not solution of one pigment. They constitute a mixture of pigments as was demonstrated by preliminary tests of their chromatographic separation. By means of thin-layer chromatography it is possible to distinguish, e.g. from the methanol fraction (from plasmodia cultured in darkness) 12 pigment bands. Although fractionation does not ensure a complete isolation of individual pigments, the results of extraction allow some conclusions as to the effect of light on the pigment system of plasmodia. A comparison of the absorption curves for the fractions from darkness and light shows clear differences in the pigment composition of each fraction as well as in the relative proportion of the pigments present therein. The total amount of the pigments obtainable from the plasmodia exposed to light is much smaller than from the plasmodia cultured in darkness. Most pigments in the latter plasmodia are extracted with methanol, while in the former this can be achieved only after protein denaturation with trichloric-acetic acid (TCA). This encourages the assumption that light can cause not only the disappearance of part of the pigments, but also the binding of the rest of them with proteins. That the proportions in the pigment composition in both cases change is also testified by the appearance of fraction IV in the "light" plasmodium alone.

Comparison of the results obtained with the available scanty literature data on pigments of slime moulds is difficult. Most of these studies deal with other species of myxomycetes (*Physarum polycephalum*: Seifriz and Zetzmann, 1935, Gray, 1953, Allman, 1955, Wolf, 1959, Dresden, 1959, Brewer, 1965, Daniel, 1966; *Physarum gyrosum*: Nair and Zabka, 1966) or different genera (*Didymium nigripes*: Lieth, 1954, yellow variant of *Didymium nigripes*: Kerr and Waxlax, 1968; *Didymium iridis*, *Didymium squamulosum*, *Physarella oblonga*: Nair and Zabka, 1966; *Badhamia utricularis*: Sobels, 1954).

In most cases the pigments from plasmodia grown in darkness were extracted. Only Wolf (1959) statesdthat he used material growing in the laboratory "under normal conditions of alternating light and darkness". However, he repeated his experiments on cultures grown in darkness and merely mentioned that the results were not "grossly different from those which characterize light-grown cultures", while he did not give any absorption spectra of the pigments obtained from the dark-grown cultures. Daniel (1966) observed that "during the photoinduction period considerable amount of pigment is bleached to unidentified products". All three components obtained by him on paper chromatography "undergo photobleaching during the

illumination period". Nevertheless, the author does not enumerate any more definite characteristics of these pigments.

The extraction methods applied by various investigators were also different. Thus, e.g. Gray (1953) extracted pigments from the plasmodia of *Physarum polycephalum* with cold acetone, Allman (1955) and Wolf (1959) with acetone or ethanol, and Nair and Zabka (1966) with boiling methanol or 95% ethanol. Lieth (1954) extracted pigments from *Didymium nigripes* with hot (75°C) 5% NaOH in alcohol solution.

The results obtained in the present study for *Physarum nudum* can be to some extent compared with those for *Physarum polycephalum*. The absorption maxima for the latter species in acid solution are attained at 380–390 nm, and in alkaline solution at 415 nm (Daniel 1966). The methanol extract (Fraction I) of the *Physarum nudum* pigments displays in acid solution two major peaks at 340 and 360 nm and marked shoulders at 380 and 410 nm. Unfortunately, Daniel (1966) did not give a complete absorption curve of the pigments isolated from the plasmodia of *Physarum polycephalum* only the maxima of absorption of these pigments; therefore, a more precise comparison of the results obtained in his experiments and of those for *Physarum nudum* is not possible. Nair and Zabka (1966) give a more detailed description of the characteristics of absorption of crude extracts of *Physarum polycephalum*. They report the occurrence of a major peak at 380 nm and minor peaks at 335 and 400–405 nm for the methanol solution of the pigments of this slime mould species. They do not, however, provide any spectral characteristic of these pigments in acid solution which also makes it difficult to compare their results with those obtained in the present investigation. To be sure, the absorption of crude extracts of the pigments in methanol from the myxomycete *Physarum nudum* cultured in darkness exhibits a maximum at 360–364 nm, but the peak is very broad and the extinction values do not differ much within the range of 340–400 nm.

On the other hand, the absorption curves for the fraction II (Fig. 3) of the slime mould *Physarum nudum* from darkness manifest a similar character as the absorption curves for *Physarum polycephalum* obtained by Wolf (1959) for component 1. Maximum absorption is at 380 nm in neutral solution and bathochromic shift occurs in acid solution.

The present study reports the preliminary results of the investigation on pigments of the myxomycete *Physarum nudum*. The work is continued and the author hopes the results will permit of a more detailed characteristic of the pigments of this slime mold and, perhaps, will enable the determination of the role of light in the process of sporulation of this myxomycete.

I wish to thank warmly Professor J. Zurzycki for his permanent interest in the investigated problem and for his unflinching belief in the successful results of this research.

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Badania nad barwnikami śluzowca Physarum nudum

I. Widma absorpcji barwników plazmodiów hodowanych w warunkach światła i w ciemności

Streszczenie

Praca zawiera wstępne wyniki badań nad barwnikami śluzowca *Physarum nudum*. Opracowano metodę ekstrakcji pozwalającą na całkowitą eluację barwników z plazmodiów naświetlanych i hodowanych w ciemności oraz na uzyskanie kilku frakcji barwników. Widma absorpcyjne poszczególnych frakcji barwników wykazują, że światło wywiera wyraźny wpływ na barwniki badanego gatunku śluzowca. W kulturach plazmodiów prowadzonych w warunkach światła zachodzą duże zmiany ilościowe i jakościowe barwników wywołane działaniem światła na plazmodia w porównaniu z barwnikami plazmodiów hodowanych w warunkach ciemności.