

# THE ECOLOGY OF PHOTOPERIODISM IN THE ANT MYRMICA RUBRA (HYMENOPTERA, FORMICIDAE).

## 1. SEASONAL CHANGES IN THE PHOTOPERIODIC REACTION

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The results of research on the principle parameters of the photoperiodic reaction (PPR) in the ant Myrmica rubra have been examined in detail in a previous series of papers (Kipyatkov, 1972; 1974a, b; 1976; 1977a, b). It has been established that colonies of these ants have a long-day PPR with a threshold day length between 16 and 17 h in the middle of the summer. When day length is below the threshold value the diapause occurs in larvae of instar III (the last), queens and workers after a definite interval (the latent period of the PPR, which reduces as the day shortens). The external expression of this is the cessation of pupation of the larvae and of egg laying by queens and workers. The pupae remaining in the colony develop into imagines, while eggs and earlier instar larvae develop to larvae of instar III, and then diapause. After this all development of individuals in the colony ceases, and its composition corresponds entirely to that of colonies overwintering under natural conditions: diapausing workers, queens and larvae of instar III.

This stage of an overwintering colony may quite justifiably be regarded as diapause at the colonial level, since it is due to an intricate system of regulatory interactions between workers, larvae and queens and does not reduce to the separate influence of the photoperiod on these groups of individuals (Kipyatkov, 1976).

Such a PPR is to be noted at the optimum temperatures for the development of M. rubra, 20-25°C. At lower temperatures the PPR is less clearly manifested: the diapause also occurs under long-day conditions, but considerably later than under short-day conditions (Kipyatkov, 1977a). In general, a decline in temperature intensifies the effect of the short day, accelerating the onset of the diapause (Kipyatkov, 1977a), as is usual and as is to be noted in insects with a long-day PPR (Danilevskiy, 1961).

The mechanism of the PPR should undoubtedly also operate under natural conditions, emerging as the main synchronizer of the seasonal development cycle of M. rubra. In the "Les na Vorskle" reservation (Belgorod Province), where this species lives in oak woods, pupation and oviposition cease in the colonies in the middle of August. Preliminary calculations allowing for the seasonal dynamics of day length and temperature within the forest in 1973 have shown that the data of laboratory experiments are well able to explain the time at which the development of M. rubra ceased noted in that year. This confirms that the mechanism of the PPR functions under natural conditions.

However, a more detailed explanation of the summer phenology of this species has still to be given. For it we need additional laboratory research and field studies, which must include a study of the microclimate of nests and nesting localities.

An ant colony does not lose its photoperiodic sensitivity with the onset of the diapause: a long day leads to rapid reactivation and to the resumption of egg laying by queens on the 4th-6th day and pupation by larvae on the 10th-12th day (at 23-25°C). A reduction in temperature slows down photoperiodic reactivation (Kipyatkov, 1977b). The PPR curves coincide completely in reactivation and in induction of the diapause and have identical thresholds (Kipyatkov, 1977b).

The retention of sensitivity to the photoperiod among diapausing ants naturally prompts the question of whether the renewal of development in the spring is governed by the mechanism of photoperiodic reactivation, or whether it is controlled by other factors. Under the conditions in the "Les na Vorskde" reservation the development of larvae and oviposition by queens commence in overwintered *M. rubra* colonies during the early days of May or even at the end of April. At this time of year the absolute length of the day on the latitude of the reservation is 14-14.5 h and does not exceed 15 h even when allowance is made for twilight in its legal definition (Sharonov, 1945). Active development is impossible at such a day length (Kipyatkov, 1974a) and photoperiodic reactivation does not occur (Kipyatkov, 1977b). It follows that the mechanism of photoperiodic reactivation is probably not operative under natural conditions in the spring. The research described below sets out to answer the question of the factors that govern the spring resumption of development in *M. rubra*.

## MATERIAL AND METHODS

The experiments were conducted in the "Les na Vorskde" reservation in summer 1973. Small plaster of paris live containers painted with nitrocellulose varnish, a considerable improvement on those described by Brian (1951a), were used to house the ants. The formicaria included a darkened nesting part, in which increased humidity was created, and an "arena", in which food was placed - *Drosophila melanogaster* imagines, 20% honey solution and water. A suction device was used to collect the material; ants and their progeny were sucked out of an open nest into a glass jar. In forming experimental groups of ants using the suction device particular attention was paid to obtaining groups of the same qualitative composition, since workers are divided into several polythetic age groups (Weir, 1958). When making examinations and counts we used CO<sub>2</sub> for 1-2 minutes as an anaesthetic; this has practically no effect on the activity of ants. In the rest of the paper larvae of instar III will be referred to simply as larvae without indicating the instar.

## COLD REACTIVATION AND SPRINGTIME DEVELOPMENT

The effect of photoperiodic and temperature conditions on the development of *M. rubra* in the spring was studied in several experiments described in this section.

**Larval development.** The material was collected on May 10-15. We used groups of 300 workers, which were given 30 large overwintered larvae (average weight 1.8-1.9 mg) or 50 small larvae (average weight 0.3-0.4 mg). There were two queens in each group with small larvae; no queens were placed in the groups with large larvae, in order to exclude their influence on the development of sexual individuals from the larvae (see Brian, 1968). The experiments were conducted at 25, 20 and 17°C and a day length of 18 and 12 h (two groups with larvae of each size in each version).

The duration of larval development and the rate of pupation exhibited the usual dependence on temperature; the photoperiod had no effect on these indicators (Tables 1, 2). Most of the larvae (65-85%) pupated in all the experiments; there was no correlation between the numbers of pupated larvae and either temperature or photoperiodic conditions. About 50% of the large larvae developed into winged females in all versions (Table 1), which shows that the process of caste differentiation is independent of temperature and photoperiodic conditions.

Some of the small larvae had not pupated even after 10 weeks; there were more such larvae in the experiments at low temperature, but not more than 10% (Table 2). Consequently, the photoperiod does not affect the development of springtime larvae and a reduction of temperature only slightly increases the number of diapausing larvae.

As has already been noted, the photoperiod and temperature have a very strong influence on larval development in the summer, as has been demonstrated in one of the previous papers (Kipyatkov, 1977a). It suffices to compare the results of experiments conducted with small larvae on the same pattern in the spring and the summer: a short day and a reduction of temperature in the summer result in a very heavy increase in the number of diapausing larvae (Kipyatkov, 1977a). In the spring, however, larval development

Table 1

Effect of Temperature and Photoperiod on the Springtime Development of Large Overwintered *Myrmica rubra* Larvae in the Absence of Queens

Temperature	Day length (h)	Weeks								Pupated (%)	Mortality (%)	Number of individuals of different castes (%)		
		1	2	3	4	5	6	7	52			53	57	
		number of larvae to pupate in the week												
25°	18	4*	43	1	0	0	0	0	48	80	25	21	53	3
25°	12	4*	42	0	0	0	0	0	46	71	23	22	53	12
20°	18	0	8*	24	13	0	0	0	45	75	23	23	45	12
20°	12	0	8*	21	12	0	0	0	41	69	24	13	49	7
17°	12	0	0	5*	7	26	4	0	44	70	30	13	53	4

Note. Data for two groups of 30 larvae each have been summed for each version; an asterisk denotes weeks in which only worker larvae pupated.

Table 2

Effect of Temperature and Photoperiod on the Springtime Development of Small Overwintered *Myrmica rubra* Larvae in the Presence of Queens

Temperature	Day length (h)	Weeks								Pupated (%)	Not pupated (%)	Mortality (%)
		1	2	3	4	5	6	7	8			
		number of larvae to pupate in the week										
25°	18	0	23	37	4	0	0	0	64	64	3	33
25°	12	0	43	41	3	0	0	0	87	87	0	13
20°	18	0	1	23	13	14	6	6	63	63	5	32
20°	12	0	2	22	25	12	6	0	67	67	8	25
17°	18	0	0	4	51	18	0	1	74	74	9	15
17°	12	0	0	3	45	14	2	0	64	64	10	26

Note. Data for two groups of 50 larvae were summed in each version.

is not dependent on day length, and a reduction of temperature increases the percentage of diapause only slightly (Table 1).

**Oviposition by queens.** The experiments to be described in the next section show that the oviposition of spring queens commences and increases irrespective of the photoperiodic conditions under which colonies are kept; an increase of temperature promotes a more rapid rise in the rate of egg laying and earlier attainment of the maximum productivity (Fig. 3a). Consequently, the renewal of oviposition in the spring is governed solely by temperature conditions.

**Oviposition by workers.** Groups of 300 spring workers were kept with larvae, but without queens at 17, 20 and 25°C and a day length of 18 and 12 h (two groups in each version). The accumulation of eggs laid by workers was observed in all versions of the experiment. It began in the 3rd week at 25°C, in the 4th-5th week at 20°C and the 5th-6th week at 17°C.

As has earlier been demonstrated (Kipyatkov, 1976), a short day causes summer workers to cease egg laying, i.e. it induces the diapause in them. The results of the experiments to be described suggest that spring workers lack such sensitivity to the photoperiod.

Table 3

Results of the Tending of Spring and Autumn *Myrmica rubra* Larvae Under Short-Day Conditions (12 h) by Spring or Autumn Workers

Workers	Larvae	N	Pupated (%)	Failed to pupate (%)	Mortality (%)
Spring	Spring	1	21	4	75
		2	37	3	60
	Autumn	3	31	5	64
		4	35	6	59
Autumn	Spring	5	0	37	63
		6	0	51	49
	Autumn	7	0	72	28
		8	0	68	32

Note. 100 small larvae used in each version; results after 6 weeks of experiment.

**Comparison of the physiological state of spring and autumn workers.** The spring material was collected at the start of May and kept to the middle of August in darkness at 0-5°C; in the middle of August wild colonies whose development had ceased were taken. We used groups of 200 spring or autumn workers without queens; 100 small spring or autumn larvae were placed in each group. The experiments were conducted under short-day conditions (12 h) at a temperature of 23-24°C.

The larvae tended by the spring workers began to pupate in the 2nd week; about 30% of the spring and the autumn larvae had pupated by 6 weeks. Only isolated larvae failed to pupate (Table 3). The very high mortality of spring larvae (up to 75%) should probably be related to the lengthy period spent by them in the refrigerator. It is also possible that spring workers kept for a long time in the refrigerator were less capable of tending the larvae, since their own viability was reduced, as may be assessed from the high mortality of these workers. Confirmation is provided by the fact that the mortality of the autumn larvae tended by autumn workers was less than half that of larvae tended by spring workers (Table 3).

None of the larvae tended by the autumn workers pupated, and except for those that perished, all diapaused (Table 3).

Consequently, the physiological state of the workers is the decisive factor governing the development of larvae. This conclusion had previously been reached from the results of special experiments described in the previous papers (Kipyatkov, 1974b, 1976).

Here we should note the appreciable physiological difference between spring and autumn workers: the former are capable of inducing active development of spring larvae and reactivating diapausing autumn larvae even under short-day conditions; the latter are incapable. Furthermore, spring workers are photoperiodically neutral, since they do not change their physiological state under short-day conditions, whereas summer and autumn workers have a PPR.

**Conclusions.** The results of the experiments described in this section point to the total absence of photoperiodic sensitivity in ant colonies after overwintering. Consequently, we are concerned in this instance with a phenomenon that occurs widely among insects, that of the loss of sensitivity to the photoperiod following cold reactivation occurring during overwintering (Danilevskiy, 1950, 1961; Danilevskiy and Shel'deshova, 1968). The resumption of development in the spring is not governed by the PPR.

We did not carry out special experiments to study the cold reactivation of *M. rubra*, since its main features are elucidated in the analysis of the experiments described above.

The process of cold reactivation undoubtedly affects both the progeny and the adult ants. The workers lose their sensitivity to the photoperiod and become capable of inducing

larval metamorphosis; imaginal diapause is replaced in them by a state of physiological activity. The diapause of workers may be lifted by a long day, as has previously been shown (Kipyatkov, 1977b), but the PPR is retained, whereas it disappears following cold reactivation.

Exposure to cold is not essential for termination of the diapause of larvae: they are reactivated by spring workers (see above), and also by long-day workers or workers reactivated by a long day (Kipyatkov, 1974b). The larvae do not have their own PPR (Kipyatkov, 1974b). In addition, it is clear from the experiment described above that spring larvae, i.e., larvae exposed to cold, do not develop when tended by autumn workers. This indicates that the diapause may be secondarily induced in them.

However, it does not follow that cold reactivation does not occur in larvae and that their development is entirely determined by the workers: when larvae are exposed to cold their physiological state is appreciably modified, as is shown by the change in the standard reaction to temperature. In fact, almost all summer larvae diapause when temperature is reduced to 17°C (Kipyatkov, 1972 etc.), whereas spring larvae almost all pupate at this temperature (Tables 1, 2). Consequently, although the influence of workers is decisive in regulating larval development (Kipyatkov, 1974b), the larvae nevertheless have their own mechanism of cold reactivation. Exposure of larvae to cold renders them capable of developing actively at considerably lower temperatures than those required for the development of summer larvae. In addition, only cooled larvae are capable of developing into alate females (Brian, 1965).

Cold reactivation undoubtedly also affects diapausing queens. In the experiments described spring queens did not exhibit the sensitivity to the photoperiod that they possess in the summer (the existence of independent perception of the photoperiod in queens has been demonstrated in previously described experiments - Kipyatkov, 1976). Consequently, exposure to cold eliminates the diapause of queens and causes them to lose photoperiodic sensitivity.

#### ALTERATION IN THE REACTION TO THE PHOTOPERIOD IN THE COURSE OF THE SUMMER

The absence of photoperiodic sensitivity in spring ant colonies raises an inescapable question, namely how and when this sensitivity appears in the course of the summer. Our investigation of this question is far from complete; nevertheless, the available experimental data do permit a tentative answer.

Induction of the diapause in larvae at different times in the year. This series of experiments was conducted at 20°C and with a day length of 18 and 12 h. The material was collected on May 15, June 1, July 12 and August 1. Four colonies were formed on each occasion (2 at each photoperiod). The colonies consisted of 300 workers, several queens and a few of all categories of progeny. Only eggs collected from ant nests in the open were placed in the colonies on the first date.

In the experiments commenced on May 15 and June 1 development of the colonies proceeded identically for the first 6-7 weeks at both photoperiods, after which pupation ceased under the short-day conditions (Figs. 1, 2a), i.e., a PPR was manifested. In the experiments commenced on July 12 and August 1 a distinct PPR was observed immediately (Fig. 2b, c). Consequently, the period required for a reaction to a short day (the latent period of the PPR) reduces gradually in the course of the summer (Table 4). A similar phenomenon has also been observed previously (Kipyatkov, 1972).

Consequently, metamorphosis ceases in the spring and early summer only following the lengthy action of a short day, but this cannot be explained by the impossibility of inducing the diapause in overwintered larvae. As has been shown in the previous section, secondary diapause occurs in spring larvae if they are tended by autumn workers (Table 3). Consequently, it is the workers in spring colonies that are insensitive to the photoperiod, and it is this that permits metamorphosis under short-day conditions.

The gradual reduction in the rate of pupation observed under long-day conditions (Figs. 1, 2), which led to the total cessation of metamorphosis, is worthy of attention. The

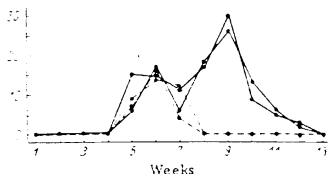


Fig. 1. Development of the progeny of *Myrmica rubra* from the first spring egg batches under long-day (18 h) and short-day (12 h) conditions at 20°C. Unbroken line) long day; dashed line) short day; the number of larvae to pupate in a week is plotted on the Y-axis. Experiment commenced on May 15. Each line presents the data for one colony. Other explanations in text.

Table 4  
Average Period (in Weeks) of the Cessation of Metamorphosis in *Myrmica rubra* in Colonies at 20°C in Experiments Begun at Different Times

Date of commencement of experiment	Day length	
	12 h	18 h
May 15	7	12
June 1	5-6	11-12
July 12	3-4	11
August 1	3	—

percentage of pupating large larvae (coefficient of metamorphosis, Cm) reduced gradually from 100% at the start of pupation to a few percent immediately before the end of pupation. The impossibility of indefinitely protracted metamorphosis at 20°C, and also the phenomenon of the accumulation of large diapausing larvae, which leads to a reduction in Cm under long-day conditions, have already been discussed in detail in one of the previous papers devoted to the effect of temperature on the PPR (Kipyatkov, 1977a).

What remains unclear is why the period of cessation of metamorphosis under long-day conditions is practically the same in all experiments begun at different times, whereas under short-day conditions a distinct reduction was observed (Table 4). There is a need for special investigation of this question.

Induction of the diapause in spring and summer queens. Experiments were begun on two dates, May 17 and July 19. On each date 12 groups, each containing 300 workers and 2 queens, were formed from natural colonies and placed under long-day (18 h) or short-day (12 h) conditions at 17, 20 and 24°C (two groups in each version).

As already noted above, the spring queens began to lay eggs and their productivity rose under long-day and short-day conditions (Fig. 3a). Temperature had a perceptible effect: an increase in temperature accelerated the increase in the productivity of the queens and the attainment of maximum oviposition; the maximum productivity of the queens was similar at 24 and 20°C, but noticeably less at 17°C. The influence of photoperiodic conditions did not become apparent for 6-8 weeks: productivity began to decline more rapidly under short-day than under long-day conditions. However, complete formation of the diapause occurred considerably later in the queens under short-day conditions (after 15-17 weeks). Under long-day conditions onset of the diapause occurred in queens only at 17°C (after 18 weeks).

From the very beginning the productivity of summer queens (Fig. 3b) was found to be heavily dependent on photoperiod and temperature, as has already been examined previously (Kipyatkov, 1977a). The short day produced a very sharp decline in productivity and onset of the diapause in the queens. A reduction of temperature accelerated this process.

If we compare the productivity dynamics of spring and summer queens (Fig. 3) we find that induction of the diapause by a short day took considerably longer in spring queens, and that the diapause occurred on average even at a slightly earlier date in summer than in spring queens, although the latter had been subjected to the effect of a short day for considerably longer. At 17°C with a long day the diapause also commenced earlier in summer queens than in spring queens. However, the diapause occurred considerably faster in spring queens at 24°C with a short day.

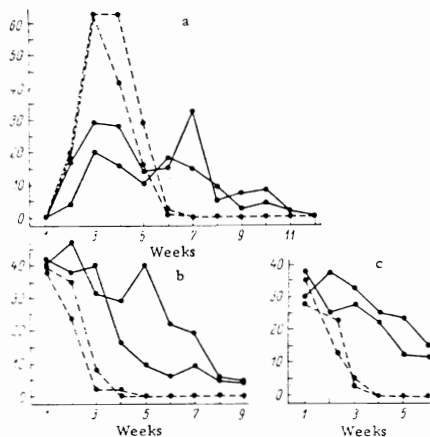


Fig. 2. Seasonal variability of the PPR in *Myrmica rubra*: dynamics of metamorphosis under long-day (18 h) and short-day (12 h) conditions at 20°C in experiments begun on different dates.

Continuous line) long-day conditions; dashed line) short-day conditions. Each line sets out the data for one colony. Start of experiments: a) June 1; b) July 12; c) August 1. The number of larvae to pupate in one colony in a week is plotted on the Y-axis.

## DISCUSSION

The experimental data indicate considerable seasonal variability of the PPR in *M. rubra*. Sensitivity to the photoperiod disappears after cold reactivation, and spring colonies completely lack a PPR. The ability to perceive the photoperiod is restored during the active season, and the PPR is already well expressed by the middle of July.

Similar facts relating to the alteration of the PPR in the course of the season have been established for other insects and acarines, and it has been shown that such changes are of an endogenous nature, although they may be modified by temperature and lighting conditions (Lees, 1960; Dubynina, 1965; Rzaumova, 1967; Geyspits, 1968; Geyspits, Simonenko, 1970; Geyspits et al., 1971). It is logical to assume that seasonal changes in the extent to which the PPR is expressed in *M. rubra* are also of an endogenous nature, although they must undoubtedly be controlled by external conditions. However, the available experimental data do not as yet enable us to establish precisely which factors influence the variability of the PPR in the season.

Lees (1960) has shown that manifestation of the PPR in the course of the season in the aphid *Megoura viciae* is not related to the number of individual generations, but is governed solely by a definite length of time, which reduces as temperature rises. Geyspits (1968) arrived at a similar conclusion from a study of the seasonal variability of the PPR in the acarine *Tetranychus urticae*.

It is probable that an increase in temperature also accelerates manifestation of the PPR in *M. rubra*. Thus, for example, in the experiments described above the diapause

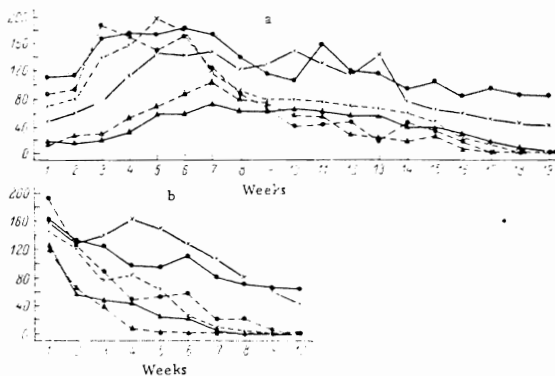


Fig. 3. Seasonal variability of the PPR in *Myrmica rubra*: effect of photoperiodic and temperature conditions on the oviposition of spring (a) and summer (b) queens.

Unbroken line) long-day conditions (15 h); dashed line) short-day conditions (12 h); number of eggs laid by a single queen in a week plotted on Y-axis, Circles at 24°C; crosses at 20°C; triangles at 17°C. Each line is a mean for two groups of two two queens. Start of experiments: a) May 17; b) July 19.

occurred more rapidly in spring than in summer queens kept under short-day conditions at 24°C (Fig. 3), which may possibly indicate accelerated manifestation of the PPR in spring queens kept at a higher temperature (24°C) than in queens experiencing natural temperatures in the wild at this time. Furthermore, it was noted in the experiments with spring queens under short-day conditions (Fig. 3a) that the onset of the diapause was later at 20°C than at 24°C, possibly in connection with more retarded manifestation of the PPR at 20° than at 24°C. The earlier induction of the diapause in spring queens at 17° than at 24° is probably explained by a strong increase in the tendency to diapause at 17°, which conceals retardation in the manifestation of the PPR. However, this complicated question is in need of special investigation.

Consequently, the seasonal variability of the PPR in *M. rubra* is most probably due to an endogenous process of the restoration of photoperiodic sensitivity in overwintered ant colonies in the course of the summer. What differs this phenomenon appreciably from known examples of the seasonal variability of the PPR is that restoration of the capacity to perceive the photoperiod does not take place through a series of successive generations, but in the same insects, workers and queens, that are insensitive to the photoperiod following cold reactivation, but acquire such sensitivity in the course of time.

We know (Brian, 1951, 1972) that *M. rubra* workers live for up to two years, queens for at least 5-6 years. Consequently, the same individual may pass through the following cycle several times: induction of diapause, cold reactivation, restoration of photoperiodic sensitivity and further induction of diapause, and so on. Such a situation may perhaps be unique for insects.

The seasonal variability of the PPR in ants undoubtedly needs more detailed investigation, since it is impossible to explain the regulation of seasonal development under natural conditions unless it is taken into account. Thus, in order to establish the part played by photoperiodism in the induction of the diapause and in the formation of the wintering state at the end of the summer we must firstly know when precisely the PPR appears in the course of the summer and which factors affect the time at which it appears. Subsequent papers will be devoted to the elucidation of all these questions.



## SUMMARY

1. Colonies of the ant Myrmica rubra. Completely lose photoperiodic sensitivity in the course of the winter. Active development is possible in the spring under any photoperiodic conditions and is governed solely by temperature; the photoperiod does not affect oviposition by queens and workers, nor the development of overwintered larvae, nor the processes of caste differentiation. Consequently, the resumption of development in the spring is determined not by photoperiodic reactivation, but by cold reactivation occurring during overwintering.

2. Cold reactivation results in a modification of the physiological state of workers, queens and larvae of the third (final) instar. Spring workers induce active development of spring, summer and autumn larvae, whatever the photoperiod. Spring larvae tended by spring workers develop actively even at 17°C, whereas almost all summer and autumn larvae diapause at this temperature even with a long day. Nevertheless, autumn workers once again induce diapause in spring larvae and prevent their active development.

3. Gradual restoration of photoperiodic sensitivity occurs in ant colonies during the spring and summer, and the photoperiodic reaction is already clearly expressed in the middle of the summer. Its appearance is apparently due to an endogenous process of the restoration of sensitivity to the photoperiod in workers and queens, but one dependent on environmental conditions.

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