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PECULIARITIES OF BACILLI ONTOGENESIS DURING CYCLE FROM A SPORE TO A VEGETATIVE CELL

In the review, on the example of aerobic spore-forming bacteria, the problems of the development and ontogenesis of the bacterial cell are considered along with the possibilities of influencing the course of these processes. The characteristics of the main concepts «growth», «differentiation», and «development» as independent processes with their dynamic interrelation are presented. Attention is focused on the analysis of literature data on the peculiarities of vegetative cell development, starting from a spore in a dormant state and finishing with vegetative form formation. In particular, the mechanisms that maintain the spore dormant state and subsequent processes of activation, initiation, outgrowth, and vegetative cell formation are described. There are emphasized certain problems with research on the ontogenesis of bacterial cells due to the deficiency of appropriate methods, as well as the lack of a single opinion regarding individual stages of the development and vegetative form formation. It was concluded that the study of individual stages of the development of prokaryotes, which differ in spore-forming and non-spore-forming microorganisms, is still relevant. Knowledge of these processes will help scientists to develop mechanisms of influence on the ontogenesis of microorganisms.

Keywords: *spore-forming bacteria, growth, differentiation, development, ontogenesis, vegetative cells, spore.*

The problems of microbial cell growth and its ontogenesis attract attention of researchers who are trying to understand the fundamental phenomena of biology — growth, development, differentiation of cells, and the possibility of influencing their course. Taking into consideration the exceptional complexity of the issue and the

imperfection of methodological approaches, most scientists have studied the processes of microorganism development more often at the level of populations, sometimes at the level of individual cells, as well as passing into subcellular and molecular biological studies. The most numerous peculiarities of the growth and differ-

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entiation of bacterial cells have been established in the study of aerobic spore-forming bacteria (Gould & Hurst, 1969; Gould, 1971; Smirnov et al., 1993; Galperin et al., 2022; Setlow, 2006; Khanna et al., 2020; Eichenberger et al., 2004; Meeske et al., 2016; Zheng et al., 2016).

When analyzing the current data in the literature, attention was focused on two issues: the peculiarities of vegetative cell growth and sporulation processes. Let's focus on the most convincing and debatable issues of microorganism growth.

Interpretation of the main conceptions of «growth», «differentiation», and «development». When characterizing the processes of microorganism growth, some researchers employ far ambiguous terms, such as «growth», «differentiation», «ontogenesis», «development», and others. These terms are also widely used by representatives of various sciences and professions, but their essence does not always provide an objective assessment of the obtained experimental materials.

«Growth» is considered a well-ordered increase in all components of a bacterial cell (Javets et al., 1982). Reproduction is the ability of bacteria to self-reproduce. Reproduction is a consequence of growth.

The philosophical definition of the concept of «development» as generalizing is suitable for microbiological objects. It considers any development, regardless of its content, as a number of different stages of development, related to each other, in such a way that each of them negates the other (Danilyan & Dzoban, 2020).

The term «development» in biology implies the process of formation of an organism or its parts. Individual development, or ontogenesis, and historical development, or phylogeny, are distinguished. The term «development», in a broader sense, is closely related to growth and differentiation, implies the process of transition from one state to another, more perfect (Kalakutsky & Agre, 1977).

The terms «growth», «development», and «differentiation» are closely related. Growth, as

a coordinated replication of all structures, organelles, and cell components, is naturally accompanied by differentiation, that is, the formation of morphologically and functionally different structures and forms, which, in general, are characterized as a process of development.

The concepts of «growth», «development», and «differentiation» should be considered as independent processes with a dynamic relationship. Analysis of them in terms of methodology made it possible to define «development» as a process of transition from one state to another, but necessarily to a more perfect one (Fig 1).

In the process of the periodic growth of a microbial population, changes occur in those morphological and, mainly, physiological properties of the cell, which are the most important characteristics of the growth, reproduction, and viability of organisms (DNA, RNA, protein content, enhancement of genetic exchange), which leads to their differentiation (Javets et al., 1982).

In the modern interpretation, the term «ontogeny» means a complex of consecutive morphological, physiological, and biochemical metamorphosis in an organism, starting from its birth and ending with its death. This definition of ontogenesis gained more and more justification and recognition concerning the development of an individual microbial cell, although it needed new facts and evidences. For example, how to be in those cases when a complex of the same successive changes in the same microbial cell is repeated under continuation of its viability?

In the process of individual development of prokaryotes, the fate of single cells is relatively easy to assess when it becomes possible to detect certain elements of their differentiation. There is less chance to find out the individual fate of those prokaryotes that reproduce by dividing cells in half (Kalakutsky & Agre, 1977). This is due to the lack of adequate methods, the search for which becomes an urgent task of researchers when studying the ontogenesis of a microbial cell.

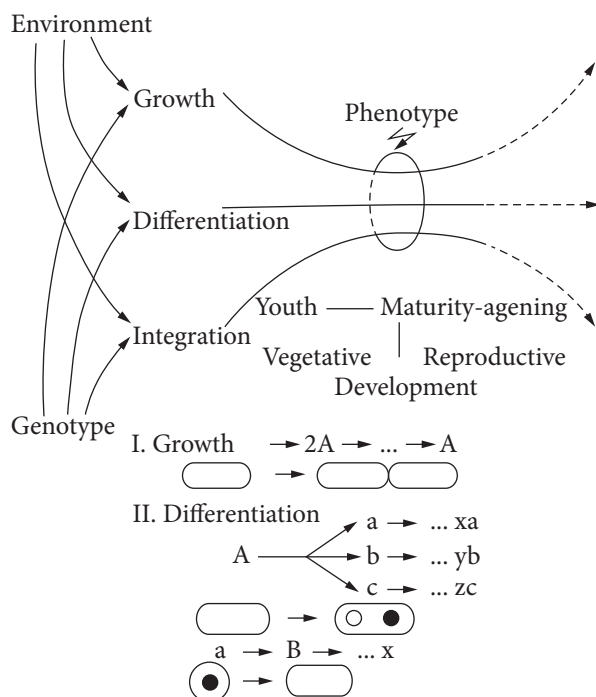


Fig. 1. «Growth», «development», and «differentiation» of cells in a schematic sketch (Kalakutsky & Agre, 1977).

Objectively evaluating the literature data on peculiarities of individual cells development, there is a difficult task of clarification the level of «perfection» in description of separate stages, their coverage by microbiological literature, which once again convinces of the need to manage the above-mentioned philosophical definition of the concept of «development».

The start position in the study of ontogeny of vegetative cells was a spore form of bacteria. The process of spore transformation into a primary vegetative cell is being studied in many scientific laboratories of highly developed countries of the world (USA, UK, France, Japan, etc.) (Secaira-Morocho et al., 2020; Galperin et al., 2022; Qin & Driks, 2013; Boone et al., 2018; Paredes-Sabja et al., 2011; Subirana & Messeguer, 2021; Maayer et al., 2019).

The metabolically active cell is formed after awakening spores and includes three consecutive stages: activation, initiation, and growth, which

are characterized by certain morphological, physiological, and biochemical features (Paul et al., 2019; Suitso et al., 2010; Wells-Bennik et al., 2016; Nicholson et al., 2000; Setlow, 2014; Zebrowska et al., 2022). The appearance of the next stage depends on the course of the previous one, which differs in its essence and mechanism of development (Gould & Hurst, 1969; Łubkowska et al., 2021; Barlass et al., 2002; Harry, 2001).

Dormant stage of the bacterial cell. A dormant stage is characteristic of almost all cells of any microorganism. A stage of rest, or a dormant state, is considered a temporary break in the development of an organism. For spore-forming microorganisms, the dormant state is a spore. But even among non-spore-forming microorganisms, there is a biological heterogeneity of forms that are in the dormant state (Keynan, 1973). Among spore-forming bacteria, it has been established that, in addition to endospores, bacilli are capable of forming alternative morphological types of dormant forms, such as anabiotic cyst-like refractory cells and proliferative «stationary cells» in the resting stage that remain intact and viable for a long time. Spore can be either activated or in the initiation state. To characterize spore-forming bacteria, a state of the so-called constitutive spore rest is distinguished, which is characterized by cytological, physicochemical, functional, and other differences from a vegetative cell (Paredes-Sabja et al., 2008a; Setlow, 2006; Gladka et al., 2015; Yu et al., 2023; Korza et al., 2023).

Endospores in the dormant stage are characterized by a high index of light refraction, low permeability of basic dyes and fixatives, extreme resistance to heat, drying, ultraviolet and radioactive radiation, to chemical compounds, and other factors (Krawczyk et al., 2017; Wang et al., 2011; Berendsen et al., 2016a; Berendsen et al., 2016b; Berendsen et al., 2015a; Berendsen et al., 2015b; den Besten et al., 2018). The reasons for such features have not been fully elucidated. It is known that the stability of spores depends on the number of cross-links in peptidoglycan,

the production of stress proteins (or heat shock proteins), proteins of the α/β type which protect spore DNA, the degree of spore dehydration, etc (Nicholson et al., 2000; Melly & Setlow, 2001; Popham et al., 1999a; Paredes-Sabja et al., 2008a).

Regarding the mechanism of the formation and preservation of the dormant state of bacterial spores, there is currently no consensus, and individual explanations, although substantiated by scientific facts, remain largely hypothetical. The dormant state of spores is most often associated with the presence of numerous coats (especially with such a specific structure as the cortex), which ensure reduced selective permeability of the spore and dehydration of its core. In the process of spore formation, the cortex becomes compacted, resulting in dehydration of core spores (Melly & Setlow, 2001; Popham et al., 1999a).

Such a specific substance as dipicolic acid is important for the maintenance of the dormant state of endospores. Perhaps, the chelated complexes of this acid with Ca^{2+} ions, sulfur-containing amino acids, and peptides act as «auto-inhibitors» of metabolic enzymes. The dormant state of bacterial cell is also maintained by other specific components and structures such as a coat protein rich in cysteine and others (Popham et al., 1999b). A very small number of spore cells in the population of bacterial spores can be very stable. Such spores are characterized by a special response to the influence of factors that cause activation and initiation of spores.

The state of spore activation. Mature spores are able to turn into vegetative cells again. However, the germination process is relatively slow, even under optimal conditions. Old spores, that is, those that have been stored for a long time, with reduced viability, germinate noticeably faster (Keynan, 1973), and young spores germinate almost simultaneously and quickly enough only after exposure to certain physical and chemical factors. Such an influence that does not cause the initiation of spore by itself but promotes its rapid and complete germination is called activation

(Gould & Hurst, 1969; Gould & Ordal, 1968; Keynan & Evenchik, 1969; Keynan et al., 1964).

Spore activation is a reversible process, unlike senescence. An activated spore can be returned to its original dormant state, whereas senescence does not restore the previous dormant level. It is considered that the mechanisms responsible for the reversibility of spore activation are disrupted during senescence. In our opinion, not all germination mechanisms take part in activation. Activated spores are able to restore their previous properties, in particular during storage. The «activation — deactivation» cycle can be repeated many times. There is a relationship between the rate of deactivation and the level of temperature decrease, particularly for *B. cereus* spores (Yu et al., 2023; Krawczyk et al., 2017).

Spore activation after the dormant stage can be caused by the following physical and chemical factors: heat (Gould & Hurst, 1969), γ -radiation (Keynan et al., 1964; Yu et al., 2023; Keynan & Evenchik, 1969), water vapour (Keynan et al., 1964; Krawczyk et al., 2017), hydrostatic pressure (Wanget et al., 2011; Berendsen et al., 2016a; Berendsen et al., 2016b), certain pH of the medium (Berendsen et al., 2015a), mercaptoethanol, dimethylsulfoxide, Ca/DPA (dipicolinic acid with Ca^{2+} ions) solutions, and other factors (Gould & Hurst, 1969; Krut' et al., 2014; Berendsen et al., 2015a; Berendsen et al., 2015b). Often, to activate spores and also different substances, heating at 60—90 °C for several minutes is used (Balko et al., 2019).

The thermal activation of spore forms of bacteria when determining the optimal regime has a clear individual character and depends on the species, their age, and nutrient environment. Spore activation was different in response to the action of factors depending on the hereditary characteristics of representatives of the bacterial population (den Besten et al., 2018; Nicholson et al., 2000; Olgún-Araneda et al., 2015; Xiao et al., 2011).

In the process of activation, spores acquire new properties, in particular, the ability to ger-

minate faster and more synchronously in the same or changed conditions, to oxidize glucose. In spores, the activity of proteases and some other enzymes increases (Gould & Hurst, 1969), the permeability rises, and dipicolinic acid (DPA) secretion begins (Melly & Setlow, 2001). However, as before, the spores remain resistant to external influences, retain their refractoriness, and are poorly stained with basic dyes. Studies of the ultrastructure of spores activated by physical and chemical agents have revealed layering and porosity in their coverings (Popham et al., 1999a).

Thus, in the current literature, spore activation is considered as a complex physicochemical process of cell development, the nature of which is not fully understood and therefore requires additional study. There is no evidence that the activation is metabolically mediated, not inhibited by metabolites, but can be interrupted by cations (Popham et al., 1999b). It is assumed that disulfide bonds in proteins of surface structures are destroyed under the influence of the activation factors in spores. In turn, this causes a conformational rearrangement of the tertiary structure of proteins. Apparently, such changes in the spore coats provide better conditions for the penetration of ions and macromolecules, thereby promoting accelerated transition of the activated spore to its next phase of development — the initiation stage.

Spore initiation is an irreversible stage of bacterial development. Activated spores, under the influence of certain germination inducers, turn into active vegetative cells within a short time. Spore initiation is the transition of activated spores into metabolically active cells, resulting in irreversible hydrolytic changes: spore stability decreases, the depolymerisation and secretion of a number of substances (mainly DPA, calcium, magnesium, peptidoglycan components) take place, as well as the destruction of coats and cortex, and spores lose refractivity (Nicholson et al., 2000; Setlow, 2014; Zebrowska et al., 2022; Berendsen et al., 2015a).

Kalakutsky L. V. proposed to combine all factors of initiation into three groups: 1) physiological initiators — normal cell metabolites (carbohydrates, amino acids, ribosides, metal ions); 2) chemical initiators (surfactants, peroxides, and others), the role of which in exchange processes has not been clarified; 3) physical initiators, for example, mechanical processing (Kalakutsky & Agre, 1977).

The most convincing data were obtained in the study of *B. subtilis*. The studies of Paidhungat M. and co-workers showed that the germination of *B. subtilis* spores was actively triggered by special germinates — D-alanine and spores of *B. anthracis* — by a mixture of adenosine, L-alanine, and D-, L-tyrosine (Paidhungat et al., 2001). The initiation of spores when they were treated with L-alanine, adenosine, and glucose occurred as quickly as when spores were transferred to a complete nutrient medium. The inhibitory effect on L-alanine initiation was executed by such amino acids as D-alanine, glycine, valine, cysteine, and methionine, which independently or in certain ratios caused the initiation (Keynan et al., 1964).

Subsequently, the idea that the classic L-alanine system is the main initiator of spores significantly changed. The conditions of germination of spores of different species and genera and even strains of the same bacterial species are significantly different. In particular, for some *B. megaterium*, initiative factors are glucose and metal ions, and for the spores of clostridiums — D- and L-lactate, various inorganic and organic salts (Olguín-Araneda et al., 2015; Xiao et al., 2011; Bhattacharjee et al., 2016). *B. fastidiosus* spores germinated in the presence of uric acid, phosphates, and allantoin and, conversely, none of the previously known stimulants of spore germination for this culture was effective (Troiano et al., 2015).

When substantiating the mechanism of action of germination inhibitors, some authors (Bhattacharjee et al., 2016; Troiano et al., 2015) considered this phenomenon associated with the penetration of metals into the corresponding areas of spore coats, assisted by complex organic

substances. However, the initiation of spores can be caused not only by various organic agents but also by mechanical processing. Shaking spores together with small glass beads, rubbing, or applying hydrostatic pressure (Wanget et al., 2011; Berendsen et al., 2016a; Warda et al., 2017) cause the so-called mechanical germination of spores. Many other factors, especially the mode of preliminary activation, temperature, pH of the medium, and aeration also promote the germination of spores (Qin & Driks, 2013).

Under the influence of initiating factors, physiological, chemical, and cytological transformations successively occurred in spores at the germination stage (Łubkowska et al., 2021; Barlass et al., 2002; Harry, 2001; Keynan, 1973). Of the currently known signs of spore germination, the earliest is a decrease in the temperature resistance. Following this, an increase in the sensitivity to ultraviolet rays is observed, however, in some mutants of *B. subtilis*, this sensitivity, on the contrary, decreases, especially at the beginning of germination (Barlass et al., 2002; Brunt et al., 2016). The resistance to ionizing radiation, pressure, chemical compounds, and other factors gradually decreases.

In the process of spore initiation, calcium, magnesium, potassium, and other metal ions were excreted, as well as DPA, amino acids, and peptides that were formed during the depolymerisation of the murein cortex under the action of lytic enzymes (Wang et al., 2015; Alberto et al., 2003; Varbanets et al., 2014; Brunt et al., 2014; Plowman & Peck, 2002). In general, a spore loses up to 30% of its dry weight during germination.

A number of cytological changes that occur in the spore coats and in its core under the influence of initiating factors have been noted, in particular the detachment of the outer covering, swelling or changes in the cortex structure (fibrous, granular, and even its disappearance). During the period of germination, a rapid darkening of spore peripheral layers is observed under a phase-contrast microscope, while the

core remains transparent. Later, the inner layer degrades with the formation of gaps. The core swells, the ribosomal and nuclear zones become clearly visible in it, the beginning of the cell wall thickens, and the spore takes on a dark appearance (Banawas et al., 2013; Paredes-Sabja et al., 2008b; Setlow, 2013; Qin & Driks, 2013). The next phase of spore darkening is longer. The least changes concern the exosporium. Such structural changes increase spore permeability to dyes.

The period of individual spore germination is staged. Thus, the first phase — «microlag» lasts from the beginning of contact with the growth medium until the appearance of the first signs of darkening, and the second phase — «microgermination» — until the complete darkening of the spore. Perhaps, the heterogeneity of the properties of individual spores explains the difference in the onset time and rate of both phases of germination. Different concentrations of germinates are required for spore germination, and some of them are unable to germinate even under optimal conditions for most ones (Paidhungat et al., 2001; Francis et al., 2013; Yu et al., 2023).

The process of germination of endospores depends on the metabolism of bacterial cells, which is evidence of their complete loss of the cryptobiotic state. Metabolic processes, especially in the early stages of initiation, are realized by enzymes of spores that were in the dormant stage (Paidhungat et al., 2001). RNA synthesis begins a few minutes before protein synthesis and is controlled by transcription.

During the germination of *B. megaterium* spores, two stages of protein synthesis have been described (Gould & Hurst, 1969; Setlow & Setlow, 1996). At the first stage (75 min), due to spore proteolysis, amino acids are excreted, which are partially used by the cell for protein synthesis, and the rest undergo catabolic transformations. Thus, protein synthesis in the early stages completely depends on the base of those amino acids that were resulted from the destruction of its own protein material by enzymes kept

in the inactive spore (Keynan, 1972; Setlow et al., 2003). The second stage is accompanied by the synthesis of all amino acids, and external sources of nitrogen are used for protein synthesis.

It is considered that the mechanism of spore germination is unique and designed to stop cryptobiosis (Keynan, 1972; Setlow et al., 2003), to create metabolically active forms and is not part of the metabolic process of a vegetative cell. There is no unequivocal interpretation of the essence of initiation, but there is an assumption that one spore has several mechanisms that induce the dormant state interruption. This hypothesis is based on the presence of different germinates effective for one or more spores.

Spore germination is a multistage developmental process based on a trigger reaction mediated by enzymes. The lytic enzyme activated at this stage destroys a significant part of the cortex and is excreted into the environment. The starter reaction of spore germination has an enzymatic nature and is confirmed by the fact that the germination can be stopped by specific antagonists of inducers or some metabolites (Vanek & Winter, 1977; Moriyama et al., 1999; Vepachedu & Setlow, 2007). Inducers are also destroyed by spore enzymes during the germination stage, and in the absence of appropriate enzymes, spore germination either does not occur or proceeds partially (Vanek & Winter, 1977).

In a generalized form, the available facts and versions of spore germination can be presented as follows. The chemical initiator triggers a series of metabolic reactions, as a result of which DPA is secreted with the formation of chelated cations, responsible for the dormant state of the cytoplasm. Spore enzymes that destroy the peptidoglycan of the cortex are also activated. DPA chelates and products of peptidoglycan dissociation are excreted, and the spore permeability increases significantly. However, triggering mechanisms of germination and, especially, the nature of the initial impulse in the development of spore-forming bacteria remain mysterious.

Outgrowth of the primary vegetative cell.

The processes of spore activation and initiation described above terminate its cryptobiotic state. As a result of germination, a vegetative cell is formed, which keeps some properties of the spore, for example, the typical shape of coats and enzymes. However, the cell acquires some new properties, in particular, the resistance to the influence of environmental factors decreases, its refractivity disappears, and cell is easily dyed by simple methods. In a medium with water and necessary nutrients, the cell intensively absorbs them and begins to grow.

The outgrowth process includes the transformation of an initiated spore into a typical vegetative cell and is characterized by the active synthesis of new macromolecules, especially RNA and protein, and the formation of a cell wall and other new structures that ensure the morphological and physiological independence of the primary vegetative cell (Gould & Hurst, 1969; Setlow, 2006; Paredes-Sabjaet et al., 2008a; Chebotarev et al., 2013; Yu et al., 2023).

It is possible to distinguish the stages of germination and outgrowth of a spore by its early morphological feature — swelling. As a result of intensive hydration of the core, the volume of the cell increases by 2—3 times compared to the size of the spore at the dormant state. Swelling is inhibited by specific inhibitors that do not affect germination and outgrowth.

On the example of *B. subtilis*, it was established that swelling of spores occurred after 30 minutes from the beginning of cultivation in a nutrient medium (Setlow et al., 2003; Vepachedu & Setlow, 2007). During this period, cracks appeared in the spore coats, the cortex decreased, and the cell wall began to thicken around the core. The spore coats degraded, and the swollen core later filled the cortex area (Wanget et al., 2011; Berendsen et al., 2015a; Berendsen et al., 2016a; Berendsen et al., 2016b; Krawczyk et al., 2017; Korza et al., 2023).

In the process of spore germination, a large part of the peptidoglycan of the cortex is destroyed

and released into the medium, and the rest is located between the cytoplasm and spore coats. When studying the fate of the cortex marked by radioactive carbon, it was established that the products of the breakdown of murein are used for the synthesis of a new cell wall, the formation of which begins at the stage of swelling (Popham et al., 1999a; Nicholson et al., 2000; Melly & Setlow, 2001; Berendsen et al., 2015b; den Besten et al., 2018). During the next 40 min, a functionally active cell wall is formed, which stabilizes the spore cytoplasm. As a result of the core swelling, the inner and outer coats of the spore are destroyed with the subsequent release of vegetative cell. This is how a primary vegetative cell is born. Under these circumstances, the exosporium does not create obstacles for the exit of the vegetative cell (Alberto et al., 2003; Paredes-Sabja et al., 2008c; Paredes-Sabja et al., 2011; Clauwers et al., 2016).

In other bacteria (*B. asidoaltarius*), the process of outgrowth of a vegetative cell from a spore proceeds in the following way: a limited narrow gap appears in the inner coat of the spore, to which the cytoplasm approaches. After the enzymatic melting of the inner and then the outer spore coats, the appearance of the vegetative cell occurs (Handley & Knight, 1975).

Under optimal conditions for growth within 50–60 min, the cell leaving occurs with the next stage of external growth — its elongation. Depending on microorganism species, the spore coats can either remain or be absorbed by the cell during outgrowth. Parts of the spore coats remain attached to the cell for a long time. In the early stages of external growth, fragments of the spore coat perform a protective function, for example, they prevent the blockade of cell wall synthesis by antibiotics. In motile forms, the formation of flagella was already observed after about 1 h. During cell outgrowth and elongation, the division of chromatin bodies is observed, and after another 1.5–2.5 h, the division and reproduction of the cell itself occurs. The synthesis of RNA and protein, as before, precedes

the synthesis of DNA, the appearance of which can be registered only about 60 min later the start of outgrowth. Sequential and orderly protein synthesis is controlled by transcription with the appearance of various types of i-RNA (Balko, 2019). It is assumed that transcription is controlled by changes in RNA polymerase, which is in the spore at the dormant stage and functions during its outgrowth (Keynan, 1973; Thackray et al., 2001; Weedmark et al., 2015).

Thus, the transformation of a spore from the dormant state into a primary vegetative cell involves 3 consecutive stages: activation, initiation, and outgrowth. The last of them, in turn, consists of the following successive stages: swelling, cell outcoming, and its elongation to the size of a typical vegetative cell, which ends at the moment of division. According to Keynan A., the first two stages correspond to the end of the cryptobiotic state of spores, followed by the activation of reactions that give rise to the processes of cell development and differentiation, and outgrowth is the process of their differentiation (Keynan, 1973).

After germination, the spore acquires wide opportunities for differentiation and, under suitable conditions, can give offspring of vegetative cells capable of turning into new spores or forming cyst-like cells.

The process of bacterial division, which is one of the most complex functions of the cell, is covered in detail in experimental works and many special reviews of the literature (Gould & Hurst, 1969; Javets et al., 1982; Balko et al., 2018; Lazarenko et al., 2023). However, in this review, it is important to analyze the process of Bacillus transformation from spore to vegetative cell. This is because the life cycle of the cell development of spore-forming bacteria ends with spore formation. In addition, a spore is a product of spore formation and is the beginning of a new cycle of bacterial development. It is important to find out the place and importance of the spore and process of its formation in the fate of microorganisms. The possibility of transforming a primary

vegetative cell into a spore remains the most debatable question. Therefore, we consider it advisable to analyze materials about the formation of spores in the conditions of macrocyclic and microcyclic development of spore-forming bacteria.

Conclusions. It was shown that the study of individual stages of development of prokary-

otes, which differ in spore-forming and non-spore-forming microorganisms, is still relevant. Knowledge of these processes will help scientists develop mechanisms of influence on the ontogenesis of microorganisms.

Conflict of interest. The authors declare that there are no conflicts of interest.

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ОСОБЛИВОСТІ ОНТОГЕНЕЗУ БАЦИЛ ВПРОДОВЖ РОЗВИТКУ ВІД СПОРИ ДО ВЕГЕТАТИВНОЇ КЛІТИНИ

В огляді на прикладі аеробних спороутворюючих бактерій розглянуто проблеми розвитку та онтогенезу бактеріальної клітини, а також описано можливості впливу на перебіг цих процесів. Представлено характеристику основних понять «ріст», «диференціація», «розвиток» як самостійних процесів з динамічним взаємозв'язком. Зосереджено увагу на аналізі даних літератури щодо особливостей розвитку вегетативної клітини, починаючи від спори в стані спокою і завершуючи утворенням вегетативної форми. Зокрема, описано механізми, які забезпечують стан спокою спори та наступних процесів активації, ініціації, проростання і формування вегетативної клітини. Наголошено на існуванні певних проблем із проведенням досліджень онтогенезу бактеріальної клітини через відсутність належних методів, а також відсутність єдиної думки щодо окремих етапів розвитку та утворення вегетативної форми. Зроблено висновок про те, що й досі залишається актуальним дослідження окремих стадій розвитку прокаріот, що відрізняються у спороутворюючих і неспороутворюючих мікроорганізмів. Знання цих процесів допоможе вченим розробляти механізми впливу на онтогенез мікроорганізмів.

Ключові слова: спороутворюючі бактерії, ріст, диференціація, розвиток, онтогенез, вегетативні клітини, спора.