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EXPERIMENTAL ARTICLES

Ultrastructure of Cyanobacterium *Nostoc* sp. f. *Blasia* Cell Forms in Persisting Populations

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Abstract—Cell clusters formed in persistent populations of *Nostoc* sp. f. *Blasia*, a cyanobacterium capable of cell differentiation, under prolonged storage in the dark at low temperatures were studied for the first time. Cell reorganization was observed, including changes in the ultrastructure of thylakoids, the cell wall peptidoglycan layer, and carboxysomes. Subcellular structures involved in intercellular communication within the clusters were revealed (structures similar to microplasmodesms and contact pores, secretory vesicles, etc.) Persistence of cyanobacterial populations was concluded to result from formation not only of specialized dormant cells (akinetes), but also L-forms, as well as from the modification changes of the clustered vegetative cells. A cluster containing the vegetative cells and L-like forms within a common intercellular matrix is considered a structural unit at the supracellular level, which is responsible for survival of cyanobacterial populations when mass akinete formation does not occur.

Key words: cyanobacteria, persistence, ultrastructure, modification changes, thylakoids, carboxysomes, intercellular interactions, cell clusters, L-forms, symbiosis.

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For many filamentous cyanobacteria (subsections IV and V of the phylum *Cyanobacteria*), the dormant cells (akinetes) are the most widespread and well-studied cell type responsible for persistence of the populations. Akinetes are differentiated cells with a number of specific ultrastructural characteristics, including the thickened peptidoglycan layer of the cell wall, an additional multilayered envelope, and high content of storage polymers. Akinete formation results from a limitation of sources of energy and certain nutrients, as well as temperature changes in natural environments and in the in vitro cultures. However, formation of such cells is probably not the only mechanism to ensure persistence of cyanobacterial populations. Investigations in our Department [1–3] revealed that these organisms are capable of L-transformation, a process common to a number of bacteria, which ensures persistence under environmental changes. Abundant evidence was obtained of induction of L-transformation in cyanobacteria forming natural or experimental symbioses with plants [4–9]. The recent research on epizoic microbial communities hydropolyps *Dynamena pumila* (L., 1758), including detection of cyanobacterial cells with degraded cell walls [10], suggest that cyanobacterial L-forms may exist in symbioses with lower invertebrates. Existence in cyanobacteria of persistence mechanisms and persistent forms other than akinetes is, however, presently poorly studied. Recently, our understanding of the diversity of the processes and cell types, which are involved in survival and adaptation of microbial populations to unfavorable conditions, improved significantly [11]. Knowledge of the potential diversity of persistence strategies in cyanobacteria and of their realization mechanisms is essential for further investigation of the behavior of cyanobacterial populations under changing conditions, including formation of symbioses with other organisms. In our research, the cultures of filamentous symbiotic cyanobacteria were used, which have a range of mechanisms for cell modification; they are capable of differentiation with formation of various cell types (akinetes, heterocysts, hormogonia, and L-like forms) [12].

The goal of the present work was the description and analysis of the ultrastructure of the cell forms developing in persistent populations of symbiotic cyanobacteria under prolonged storage in the dark at low temperature.

MATERIALS AND METHODS

Subjects of research were axenic cultures of the cyanobacterium *Nostoc* sp. f. *Blasia* isolated from a natural symbiosis with the liverwort *Blasia pusilla* [5]. The procedure for cyanobacterial isolation and obtaining laboratory cultures was described previously, as well as the cultivation conditions [6].

Two lines of cyanobacterial cultures were investigated, which were isolated in 1990 from the symbiotic cavities of the different samples of liverwort thallus. The cultivation was carried out in liquid media, nitrogen-free

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$BG\text{-}11_0$ [13] (line I) and nitrogen-containing Kratz and Myers medium [14] (line II). The cultures were then transferred to agarized media of the same composition, incubated for a week in a lumenostat (1500 lx) at 20–26°C, and subsequently stored in a refrigerator for 5 months at 4°C in the dark. The viability of *Nostoc* sp. f. *Blasia* persistent populations was determined by their growth after transfer into nitrogen-containing liquid BG-11 medium [13] supplemented with fructose (5 g/l) and subsequent incubation in a lumenostat (750–1000 lx) at 20–26°C.

Electron microscopy. For transmission electron microscopy under JEM-100B and JEM-1011 electron microscopes (JEOL, Japan), cyanobacterial samples were treated as described previously [15]. For scanning electron microscopy, the samples were fixed, dehydrated, critical-point dried in a Dryer HCP-2 (Hitachi, Japan), sprayed with gold and palladium on an IB-3 Ion Coater (Eiko, Japan), and examined under S-405A (Hitachi, Japan) and JSM-6380LA (JEOL, Japan) scanning electron microscopes.

RESULTS AND DISCUSSION

Colony organization. The colonies of two lines of *Nostoc* sp. f. *Blasia* stored for a long time in a refrigerator were usually formed by a number of cell clusters joined by mucous bands or conglomerates (Fig. 1a, b). The clusters are groups of vegetative and differentiated cells, single or in trichomes, which are united by a joint mucous matrix. The matrix may be homogeneous in structure and density or consist of more or less pronounced layers. Individual clusters differ in shape and size, as well as in the ultrastructure of their component cells (Fig. 1c–e).

In the culture of line I, the clusters were mostly large, with a homogeneous or lamellar matrix. In this culture, two groups of clusters were observed, drastically different in the ultrastructure of the component cells. In the clusters of the first group, coiled trichomes of vegetative cells with heterocysts predominated, while in the second group, unicellular vegetative forms with a defective cell wall (FDCW) predominated (Fig. 1c, d). Both cell forms were surrounded by proprietary sheaths, which join with the junctional matrix in the periphery.

The clusters of line II were organized differently (Fig. 1e). The mucous matrix combined the coiled, closely located trichomes and the polymorphic FDCW. The matrix was characterized by the presence of an electron-dense layer with aggregations of loosely packed fibrillar matter on its surface.

Analysis of the population structure of the clustered cells of both lines revealed that mass formation of akinetes (typical persisting forms) did not occur under the conditions of storage. The lines exhibited significant differences in the thin structure of the vegetative forms and in the presence of heterocysts. The latter were revealed in the population of line I cells. Since heterocysts are differentiated cells responsible for dinitrogen fixation in cyanobacteria, their presence in the culture maintained in nitrogen-free medium was understandable. On nitrogen-containing medium (line II), heterocysts were not revealed.

Structural basis for cell communication within the clusters. A significant portion of the heterocysts remain structurally intact. The ultrastructure of the contact between a heterocyst and a vegetative cell (the zone of the heterocyst pore) suggests the possibility of active metabolite exchange between these cell forms. This implies not only the characteristic mutual location of the components of the cell wall of two cells, but also the presence of porelike structures in the peptidoglycan of the septum; these structures are revealed as electron-transparent channels (Fig. 2a). On some sections, the cords of electron-dense matter can be seen passing through the channels and contacting with the cytoplasmic membrane (CM). Such structures in cyanobacteria are believed to be microplasmodesms [16–18]. Their internal organization, however, remains poorly understood. The role of CM in their formation was not strictly confirmed. Similar porelike structures were present in the septa between the vegetative cells in the trichomes within the clusters of both lines (Fig. 2b). According to our observations and literature data [18], microplasmodesm-like structures between the cells in a trichome are found, though extremely rarely, in other filamentous cyanobacteria.

Apart from the microplasmodesm-like structures, transverse, uniform electron-transparent channels approx. 15 nm in diameter were found in the walls of line II vegetative cells (Fig. 3a). Their localization, regular mutual position, and size resemble those of the junctional pores described in gliding cyanobacteria [19]. These organelles are known to participate in secretion of polysaccharide mucus during trichome gliding. Fig. 3a demonstrates that conglomerates of finely granular material penetrated by fibrils are located close to the cell wall crossed by numerous channels. The particles of this material are found close to the channel's opening. This picture suggests production of a mucous material forming the intercellular matrix of the clusters.

Secretion of the components of the intracellular matrix in line II clusters is also possible by formation of vesicles from the outer cell wall membrane of the vegetative cells. This is mostly typically for the polymorphic forms with altered peptidoglycan structure, i.e., for FDCW. Vesicle formation was observed simultaneously with the surface extrusions of the outer membrane, which limited the aggregates of electron-dense matter merging with the peptidoglycan. Secretion of various high-molecular weight compounds by vesicle formation involving the outer membrane is known in a number of gram-negative bacteria [20]. In line II cultures, FDCW exhibited local ruptures of the pepti-

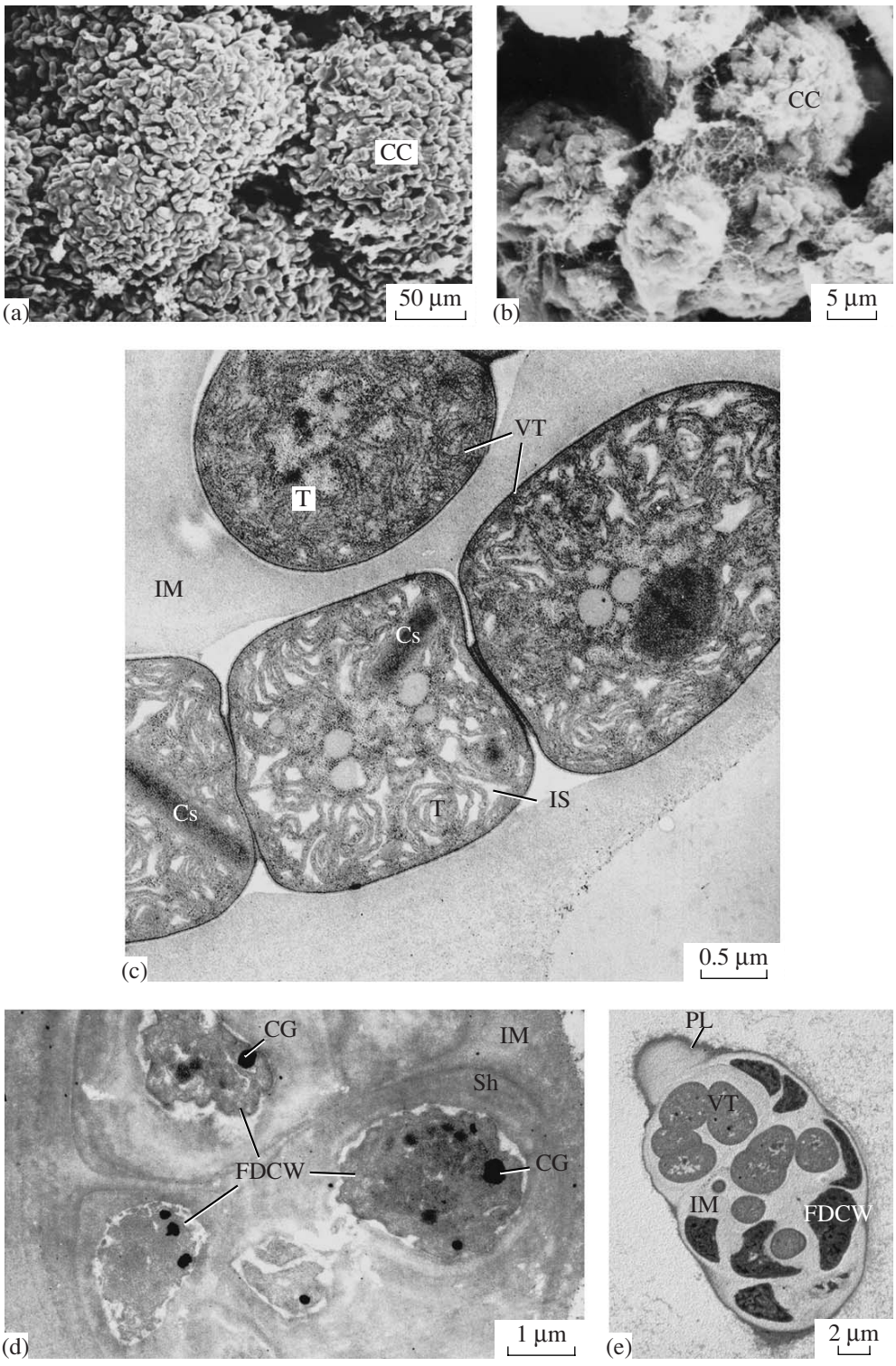

Fig. 1. Cell clusters of *Nostoc* sp. f. *Blasia* in the cultures of two lines: aspect of line I clusters (a); aspect of line II clusters (II); fragment of line I cluster (c); fragment of line II cluster (d); section of line II cluster (e). Designations: IS, intrathylakoid space; VT, trichome of vegetative cells; CC, cell cluster; Cs, carboxysome; IM, intercellular mucous matrix; PL, peripheral layer of the matrix; T, thylakoids; FDCW, forms with a deficient cell wall; CG, cyanophycin granule; Sh, sheath.

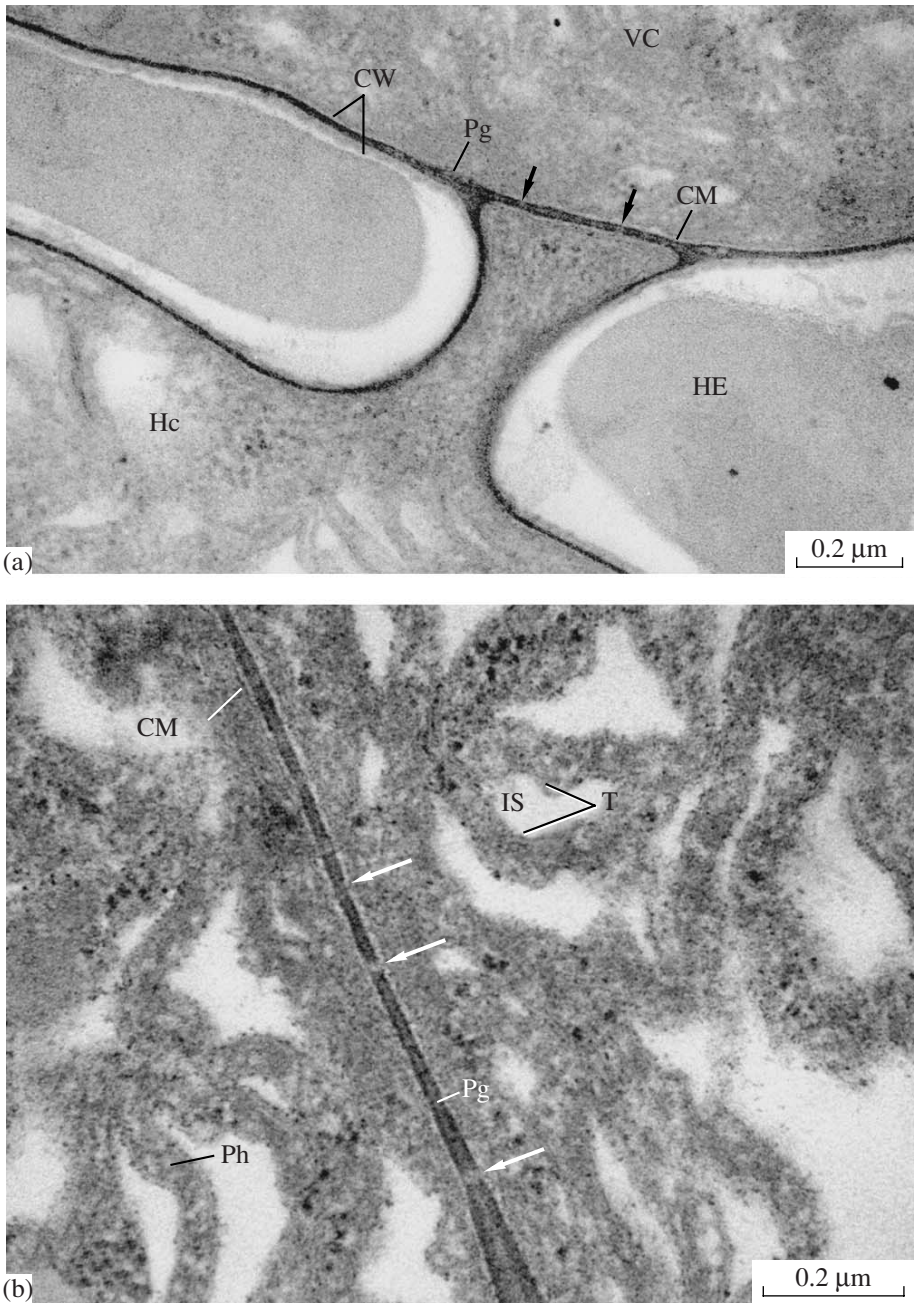

Fig. 2. Ultrastructure of the zone of intercellular contact in line I *Nostoc* sp. f. *Blasia* trichomes: between a vegetative cell and a heterocyst (a) and between vegetative cells (b). Designations: IS, intrathylakoid space; VC, vegetative cell; Hc, heterocyst; CW, cell wall; HC, heterocyst envelope; Pg, peptidoglycan; Ph, phycobilisomes; T, thylakoid; CM, cytoplasmic membrane. Arrows indicate the microplasmodesm-like structures.

doglycan layer associated with excretion from the enlarged periplasmic space (Fig. 3b).

Vegetative cell forms. In the clusters of different lines, the vegetative cells without visible damage to the cell wall exhibit peculiarities in the ultrastructural organization of the cytoplasmic content, i.e., the thylakoid system and inclusions of storage polymers. In line I, the intrathylakoid space is significantly enlarged, which is a structural manifestation of thylakoid swelling (Figs. 1c, 2b). On the outer surface of these organelles, complexes of light-harvesting pigments (phycobilisomes) remain visible; therefore, destruction of the photosynthetic apparatus possibly does not occur. A previous investigation, including research on cyanobacteria persisting in the dark for a long time, suggests that thylakoid swelling is an indication of a shutdown of the respiratory and photosynthetic electron-transport chain in the thylakoid membranes [21]. The respiratory function is probably carried out by

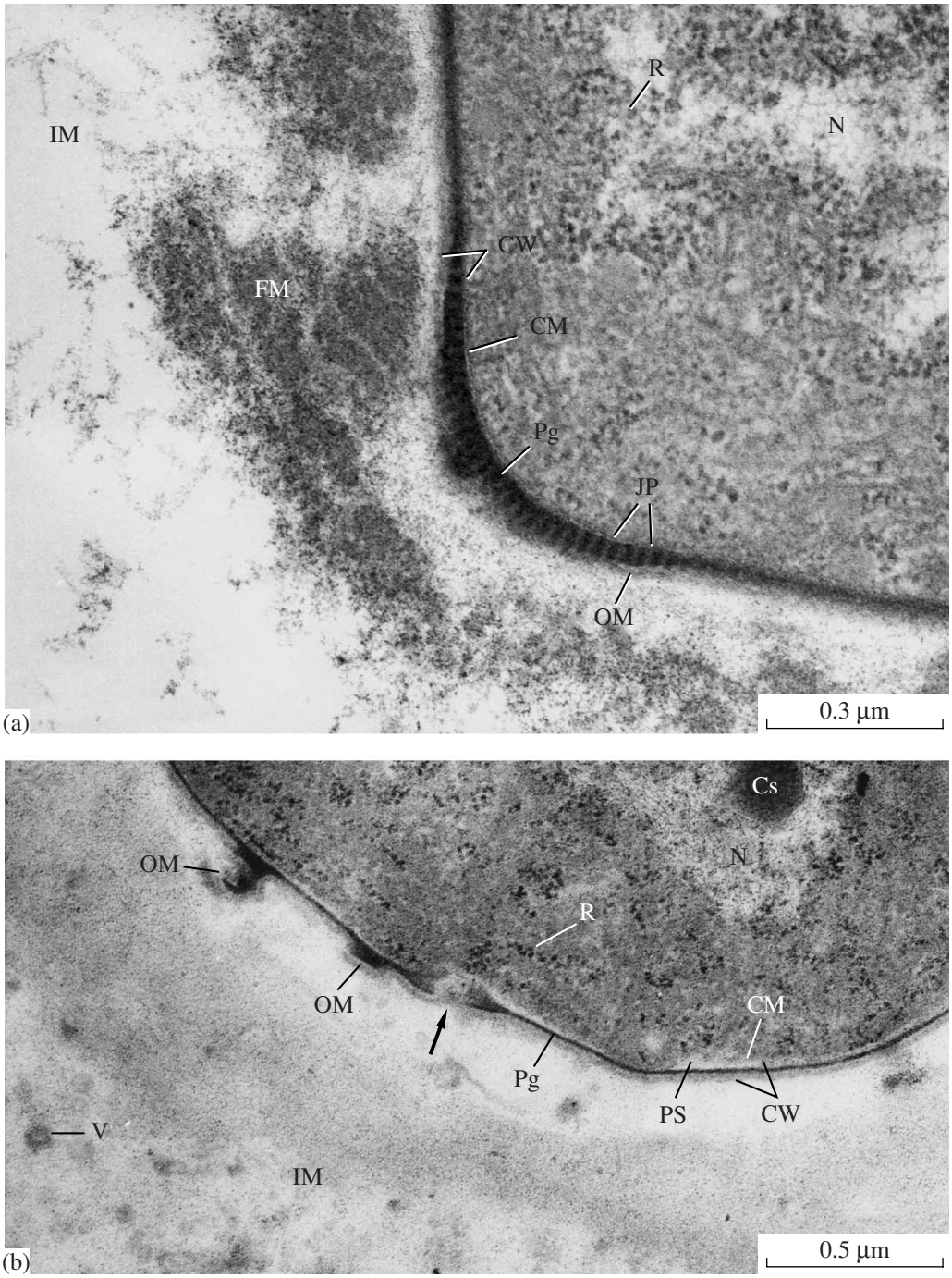

Fig. 3. Ultrastructural organization of the cell surface of line II *Nostoc* sp. f. *Blasia* vegetative cells: fragment of a vegetative cell with the structures resembling junctional pores (a) and FDCW fragment (b). Designations: V, vesicle; FM, fine-grained matter; JP, junctional pores; CW, cell wall; Cs, carboxysome; IM, intercellular mucous matrix; N, nucleoid; Pg, peptidoglycan; PS, periplasmic space; R, ribosomes; OM, outer membrane; CM, cytoplasmic membrane. The arrow indicates a rupture in the peptidoglycan layer.

the CM alone. Cyanobacterial survival in the dark is known to depend on the utilization of endogenous storage compounds, especially the polyglucoside glycogen. Catabolism of glucose from glycogen is carried out via the oxidative pentose phosphate cycle, which is coupled to the electron-transport chain via NADP. However, in line I cells glycogen was not revealed as α-granules, while the globules resembling lipids and occasional poly-β-hydroxybutyrate granules were observed. The last two types of compounds may probably be considered as potential substrates for both energy and constructive metabolism. The nitrogen-containing storage com-

pound cyanophycin (a multi-L-arginyl-poly-L-aspartate peptide) was not present. These cells had carboxysomes of different configurations. These inclusions are usually the macromolecular complexes of ribulose bisphosphate carboxylase/oxygenase packed as polyhedral bodies. In the cells of line I, apart from the typical cyanobacterial ones, large rod-shaped carboxysomes were present (Figs. 1c, 4a, b). Such carboxysomes are extremely rare in cyanobacteria. They have been reported for unicellular cyanobacteria *Synechococcus* in wild type cells under stress conditions [22, 23] and in some mutants [24]. Considering the biogenesis of anomalous carboxysomes, Orús et al., suggested that formation of such hypertrophied inclusions resulted from the imbalance in precursor synthesis and carboxysome assembly, rather than from damage of the cyanobacterial genome [24]. This is probably true for the line I cells, since geometrically different carboxysome sections (hexagonal and rhombic, elongated rectangular and trapezoid) were revealed on ultrathin sections, as well as the unusual lamellar packaging of the subunits of macromolecular complexes (Fig. 4b). In general, this structural organization suggests metabolic inactivity in this cell type.

In the cells of line II, the thylakoid ultrastructure is similar to that of the *Nostoc* sp. f. *Blasia* laboratory cultures grown under illumination [6]. Unlike line I cells, no significant increase of the intrathylakoid space occurred; the membranes were therefore in an energized state (Fig. 4c). The respiratory electron-transport chain was therefore possibly functioning in the thylakoids. The pool of carbon-containing compounds for the metabolic processes was represented mainly by poly-β-hydroxybutyrate inclusions. No significant amount of glycogen was found in the samples. Cyanophycin granules were rare. No intracytoplasmic anomalies were observed which could have indicated metabolic imbalance. The ultrastructural organization of the system of protein synthesis (ribosomes and nucleoid) was typical of cyanobacteria (Figs. 3a, 4c). Some of the cells in chains were at the division stage.

Among the vegetative FDCWs in the clusters of both lines, the spheroplast-type forms with a reduced cell wall (FRCW) predominated, while the protoplasts were rare. In the line I culture, FRCW exhibited signs of destruction of the outer membranes, thylakoids, and other cytoplasmic content, except for the unexpectedly large cyanophycin granules (Figs. 1d, 5a). Cyanophycin accumulation in a culture grown in a nitrogen-free medium may result from high intensity of dinitrogen fixation and/or cyanophycinase inhibition. In our experiment (culture storage in the dark without exogenous sources of combined nitrogen and carbon), cyanophycin accumulation certainly occurred at the stage of preincubation in the light; it was then not consumed in the dark for constructive and energy metabolism. The absence of cyanophycin assimilation, together with destructive changes in the cell components, indicates decreased activity or complete inhibition of the metabolic processes in line I FRCWs.

In contrast, line II FRCWs have minimal destructive features. Moreover, on some ultrathin sections, apparently dividing FRCW were found (Fig. 5b). Some of them form short chains. Most of the spheroplasts and protoplasts have an amoeboid shape due to peptidoglycan reduction; pseudopodia-like protrusions are often formed, which penetrate between the cells with intact cell walls (Fig. 1e). Capacity for division, and thus the viability of the protoplasts is confirmed by the ultrastructural integrity of these cell forms. Their hyaloplasm exhibits no signs of autolysis; compact nucleoid zones with peripheral aggregates of ribosomes are observed, as well as numerous regularly positioned thylakoids formed by closely located membranes of the typical three-layer profile (Figs. 5b, c). In some zones of the cell, the neighboring thylakoids lay close together; this was an indication of the absence of phycobilisomes on their cytoplasmic surface. Carboxysomes, as a rule, had usual morphology. Cyanophycin and α-granules glycogen were not revealed. Membrane vesicles, segregating into the intercellular space were formed on the FRCW surface. The ultrastructural analysis of line II FRCWs demonstrates that the metabolic processes promoting their viability occurred within these cells.

Diversity of cell forms and the viability of the population. Preservation of the viability of *Nostoc* sp. f. *Blasia* persistent populations was confirmed by their growth after transfer of the largest green colonies into a BG-11 medium with fructose with subsequent incubation in the light. Growth of line I cyanobacteria commenced after a prolonged lag phase (3–4 weeks) in one of the three repeats. Inoculates from the line II cultures were viable in all repeats; lag phase duration did not exceed two weeks. Since in the cultures of both lines akinetes were formed in single instances, differentiated cells of this type are not the only ones responsible for the population persistence. Comparison of the viability data and the ultrastructural organization of cell types in the clusters suggest a conclusion that modification changes of the vegetative cell forms are probably to some extent responsible for persistence of the populations of both lines. In the case of line I, these changes did not result in the abnormalities of the cell wall visible on ultrathin sections; they rather affected the thylakoids and the structure of the septal peptidoglycan. In the septal peptidoglycan, the structures resembling microplasmodesms or pores were often revealed. According to our observations, such structures occur in large amounts in the trichomes of cyanobacteria of the genes *Anabaena* and *Nostoc* incubated under suboptimal and extremely unfavorable conditions, resulting in the degradation changes of peptidoglycan [15; Gorelova, unpublished data]. Detection of such structures in the septa between vegetative cells becomes possible as a result of potentially reversible degradation processes in stored cultures. On the other hand, these structures may remain intact and participate in the intercellular transport of molecules, i.e., support the vital activity of

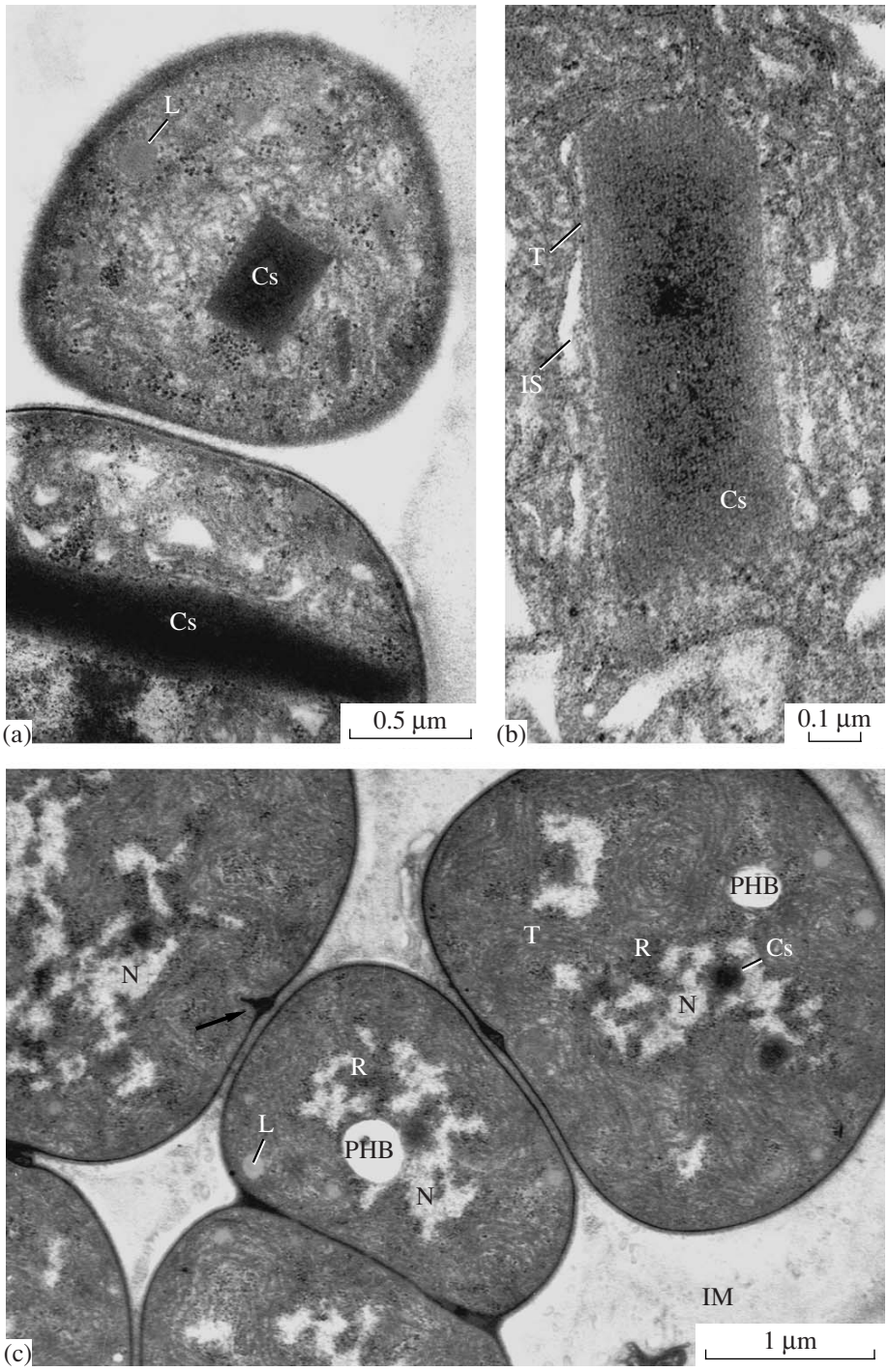

Fig. 4. Ultrastructure of *Nostoc* sp. f. *Blasia* vegetative cells: line I culture (a, b) and line II culture (c). Designations: IS, intrathylakoid space; Cs, carboxysome; L, lipids; PHB, poly-β-hydroxybutyrate; IM, intercellular mucous matrix; N, nucleoid; R, ribosomes; T, thylakoids. The arrow indicates a forming septum.

persisting cells. The changes in the photosynthetic apparatus (thylakoid swelling) are in principle also reversible. This possibility has been previously demonstrated for *Anabaena variabilis* CALU 458 persisting in the dark and retaining endogenous carbon-containing inclusions [25].

In the population of line II, modification changes of the vegetative cell forms included, apart from visualization of the intercellular channels, active production of the mucous matter of the cluster and formation of structurally integral FDCW, including dividing FRCW. The latter are probably L-forms, which are usual for *Nostoc* sp. f. *Blasia* in symbioses and newly isolated cultures [5, 6]. Secretion of the material of the intracellular matrix is joined to the formation of cell clusters of het-

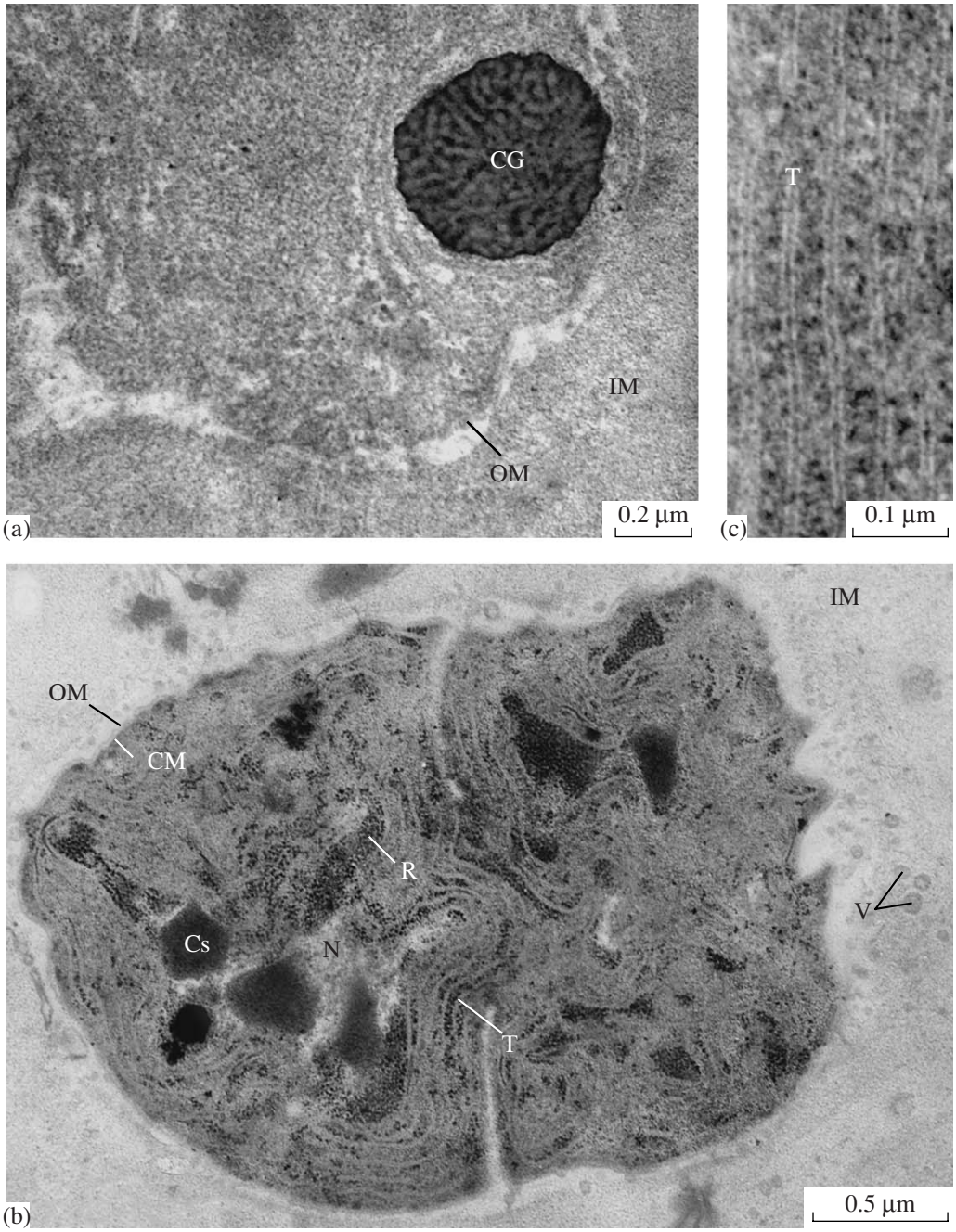

Fig. 5. Ultrastructure of *Nostoc* sp. f. *Blasia* FRCW: in line I culture (a) and in line II culture (b, c) (c is the FRCW fragment with thylakoids). Designations: V, vesicle; Cs, carboxysome; IM, intercellular mucous matrix; N, nucleoid; OM, outer membrane; R, ribosomes; T, thylakoids, CG, cyanophycin granule; CM, cytoplasmic membrane.

erogeneous composition surrounded by a dense peripheral envelope. In the limited space of the cluster, cells of various types exist; they probably communicate both via the septal channels and the common periplasmic space and via the intercellular matrix by diffusion and vesicular transport. Analysis of the organization of line II clusters makes it possible to consider them a structural persisting unit of a supercellular level.

Thus, the study of the ultrastructure of the cell forms of two lines of symbiotic cyanobacteria *Nostoc* sp. f. *Blasia* under prolonged storage in the dark at low temperatures demonstrated that persistence of the popula-

tions is possible ensured by formation of not only akinetes, but also of L-forms, as well as by modification changes in the vegetative cells within the clusters.

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