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STRUCTURAL HETEROGENEITY OF THE PLASMALEMMA OF THE YEAST, *SCHWANNIOMYCES OCCIDENTALIS*, INDUCED BY SUBSTRATE

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The growth of the yeast *Schwanniomyces occidentalis* on hydrocarbons (C_{12}–C_{20}) is followed by the formation of spherical invaginations. They are inwardly directed and border the 'canals' of the cell wall forming with them a single complex. The invaginations differ from the rest (smooth) part of the plasmalemma in the density of intramembrane particles. There is also a significant difference in the distribution of intramembrane particles in the plasmalemma of *S. occidentalis* grown on hydrocarbons and glucose. Invaginations and 'canals' are considered as a manifestation of the structural heterogeneity of the yeast cell envelope induced by a hydrocarbon substrate and, evidently, conditioned by adaptive processes.

The growth of a number of yeasts (*Schwanniomyces occidentalis* IBPhM-Y-395, *Candida tropicalis* IBPhM-Y-303, *Candida mesenterica* IBPhM-Y-65, *Torulopsis candida* IBPhM-Y-451, etc.) on hydrocarbons is followed by the appearance of numerous (up to 100 per cell) characteristic zones in the cell wall. These zones or 'canals' have a high affinity for osmium and a high catalase activity [1–4]. The formation of 'canals' is also induced by cultivation of the above mentioned yeasts on other carbon sources (fatty acids, higher alcohols) [3] and is paralleled by the enhancement of β-glucosidase, β-glucanase and α-mannosidase activities which are capable of degrading cell wall polysaccharides [5]. The cytochemical reaction for polysaccharides confirms the participation of these hydrolases in the cell wall modification resulting in the 'canal' formation [5]. It was the purpose of the given work to elucidate whether the 'canal' formation affects also the plasmalemma and whether the structural cell wall heterogeneity extends for the entire yeast cell envelope.

The ultrastructural freeze-fracture [6] of *S. occidentalis* grown on C_{12}–C_{20} showed the formation, already during the first hours of cultivation, of inwardly directed invaginations in the regions of the plasmalemma contacting 'canals'. These were spherical invaginations 150 nm in diameter and about 30 nm in height (Fig. 1a, b). Their number

TABLE I

DENSITY OF INTRAMEMBRANE PARTICLES (NUMBER PER 1 μm^2) ON EF AND PF SURFACES OF THE PLASMALEMMA OF *S. OCCIDENTALIS* DEPENDING ON THE CARBON SOURCE (ALL VALUES ARE GIVEN AS MEAN ± S.E.)

	Substrate	Density of particles	
		Smooth surface	Spherical invaginations [a]
EF surface	Hydrocarbons	1345 ± 180	712 ± 105
	Glucose	706 ± 131	
PF surface	Hydrocarbons	3119 ± 185	3488 ± 137
	Glucose	4435 ± 263	

[a] With regard to the surface curvature.

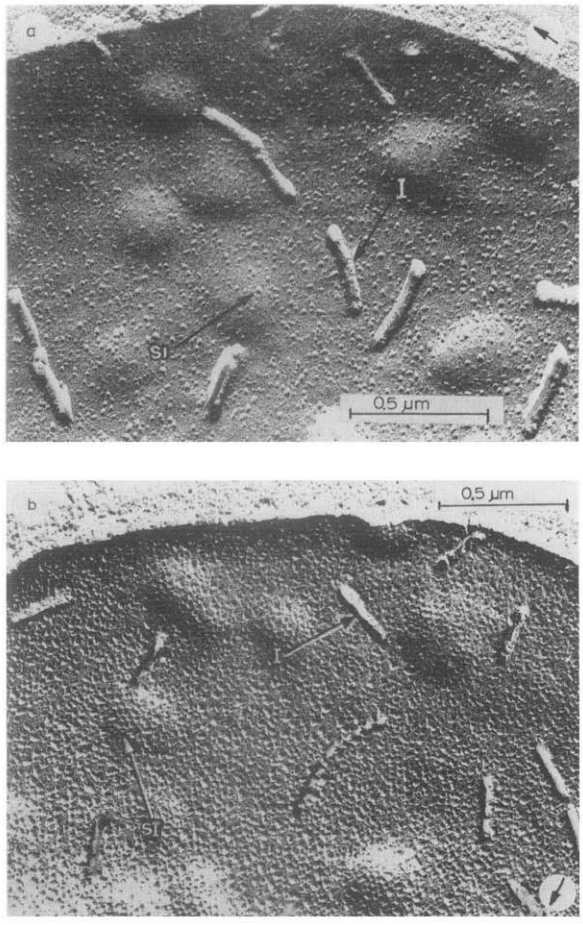

Fig. 1. Periplasmic (EF) (a) and cytoplasmic (PF) (b) surfaces of the plasmalemma hydrophobic zone of the yeast *S. occidentalis* grown on hydrocarbons. I, invagination, SI, spherical invagination.

was maximal (40 per cell) at the logarithmic growth stage. These spherical formations differed drastically from ordinary invaginations of the plasmalemma and had never been described earlier in yeasts. Spherical invaginations were not found only in a small number of cells (no more than 5%).

To elucidate the dependence of the formation of spherical invaginations on the supramolecular structure of the plasmalemma, we analysed the distribution of intramembrane particles in various parts of the membrane of *S. occidentalis* grown on hydrocarbons. As seen from Table I, their density on the periplasmic surface (EF) was less almost by half compared to the rest of the plasmalemma and somewhat more (by about 12%) on the cytoplasmic surface (PF).

In cells grown on hydrocarbons, intramembrane particles were more abundant in the periplasm than in the cytoplasm as compared to cells grown on glucose (Fig. 2a, b) and sampled at the same growth phase (Table I). These distinctions were more pronounced in regions without invaginations.

The asymmetric distribution of intramembrane particles between EF and PF surfaces of the plasmalemma reflects the functional differences between the outside and inside of the cytoplasmic membrane [7]. The displacement of particles in the membrane points evidently to the increase in the biochemical activity of the periplasmic part of the plasmalemma of *S. occidentalis* grown on hydrocarbons. On the other hand, in the course of

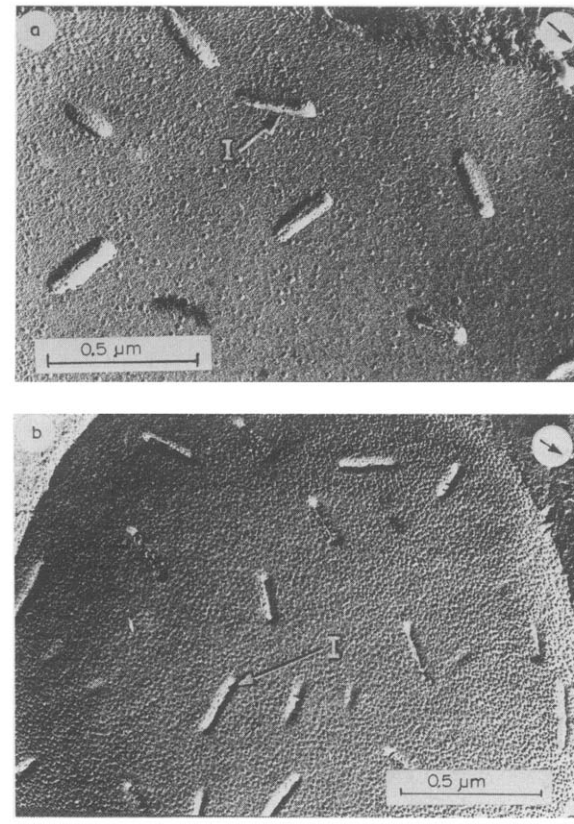

Fig. 2. Periplasmic (EF) (a) and cytoplasmic (PF) (b) surfaces of the hydrophobic zone of the yeast *S. occidentalis* grown on glucose (a, b). I, invaginations.

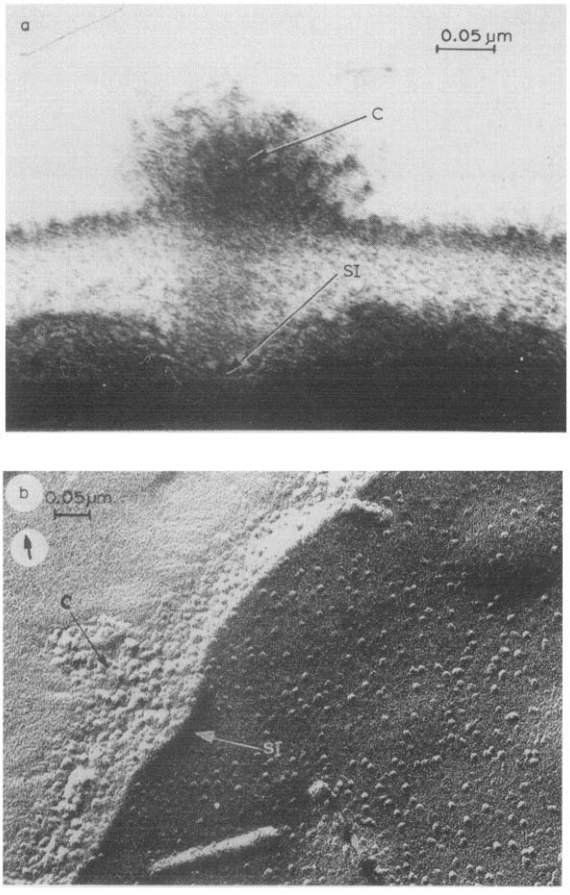

Fig. 3. Cross section of the envelope of *S. occidentalis* grown on hydrocarbons (a); cross freeze-fracture of the envelope of *S. occidentalis* grown on hydrocarbons (b). C, 'canals' in the cell wall; SI, spherical invaginations of the plasmalemma.

adaptation to hydrocarbons, the yeast cell plasmalemma undergoes quantitative and qualitative changes in the intramembrane protein and lipids [8]. Reasoning from the possible protein nature of particles [7], all the above said indicates evidently that the localization of the plasmalemma intramembrane protein in the form of intramembrane particles changes simultaneously with the modification of proteins themselves when yeast cells are grown on hydrocarbons. The total density of particles on EF and PF surfaces of cells grown on hydrocarbons decreases by 18% in regions of spherical invaginations and by 13% in the rest of the membrane as compared to cells grown on glucose. This results probably from the decrease in the intramembrane protein of the plasmalemma of cells grown on hydrocarbons or the transmembrane migration of particles from the hydrophobic region of the membrane.

The structural heterogeneity of the plasmalemma of *S. occidentalis* reproduced on the cell division (distribution and density of intramembrane particles, and surface curvature) probably reflects significant functional distinctions between spherical invaginations and the rest (smooth) part of the membrane.

The described spherical invaginations of the plasmalemma and rearrangements of intramembrane particles are a unique manifestation of the trophic adaptation of cells to some hydrophobic carbon substrates, hydrocarbons in this case. The cause of the plasmalemma heterogeneity and its effect on the utilization of hydrocarbons are unclear yet. However, it is felt that the existing anatomic association between structurally modified regions of the plasmalemma and the cell wall is a convincing indication of their functional interrelation. From this point of view, the described spherical invaginations and adjacent 'canals' should be considered as a single complex structure of the yeast envelope which plays an important part in the trophic adaptation of yeasts to the above mentioned substrates.

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