Topic Introduction

Analyzing and Understanding Lipids of Yeast: A Challenging Endeavor

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Lipids are essential biomolecules with diverse biological functions, ranging from building blocks for all biological membranes to energy substrates, signaling molecules, and protein modifiers. Despite advances in lipid analytics by mass spectrometry, the extraction and quantitative analysis of the diverse classes of lipids are still an experimental challenge. Yeast is a model organism that provides several advantages for studying lipid metabolism, because most biosynthetic pathways are well described and a great deal of information is available on the regulatory mechanisms that control lipid homeostasis. In addition, the composition of yeast lipids is much less complex than that of mammalian lipids, making yeast an excellent reference system for studying lipid-associated cell functions.

INTRODUCTION

Lipid research has gained great momentum in recent years, fueled not only by the pandemic dimensions of lipid-associated disorders in humans, but also by the potential for exploiting single-cell lipids as a source for biofuel (“biodiesel”). In addition, a major limitation in lipid research—the analytical part—has recently been overcome by the implementation of mass spectrometry techniques that provide high-resolution insight into lipid molecular species content and metabolism in cells and tissues. The yeast *Saccharomyces cerevisiae* represents an excellent experimental reference organism to study physiological and pathophysiological roles of lipids at the cellular level. Lipid metabolic pathways have been well elucidated and a great deal of information is available about the regulatory processes controlling lipid homeostasis in yeast (Nohturfft and Zhang 2009; Carman and Han 2011; Henry et al. 2012; Kohlwein et al. 2013). Most metabolic pathways are conserved, and also the regulatory circuitry that links lipid metabolism to energy homeostasis, cell growth, and development shares several levels of homology with mammalian cells (Nohturfft and Zhang 2009; Natter and Kohlwein 2013). Despite this remarkable level of functional conservation, yeast lipid composition is rather simple compared to that of mammalian cells (Ejsing et al. 2009; Shui et al. 2010; Klose et al. 2012), facilitating experimental setups and interpretation of the complex dynamic processes that govern lipid homeostasis.

Nevertheless, work with lipids is still a challenging task. First, lipids have highly diverse chemical structures, although they all have a rather hydrophobic or amphipathic nature and are defined by their “solubility in organic solvents.” Second, various lipid classes differ dramatically in their abundance, ranging from “bulk” lipids such as storage triacylglycerols and membrane phospholipids to less abundant sphingolipids, which are lipid-signaling molecules present only in trace amounts. Third, despite the relative simple lipid composition in yeast (see below), there is a great deal of combinatorial chemistry in

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terms of variations in acyl chain composition in various phospholipid classes, giving rise to a quite complex set of lipid molecular species even in the “simple” yeast cell (Guan and Wenk 2006; Ejsing et al. 2009; Shui et al. 2010; Knittelfelder et al. 2014; Casanovas et al. 2015). Fourth, lipid metabolism is a highly dynamic process, which correlates with cell growth, nutritional supply, and even the cell cycle (Kurat et al. 2006, 2009; Zanghellini et al. 2008; Klose et al. 2012; Chauhan et al. 2015). Thus, comparing lipid data between cells grown under different conditions or between mutants can be very misleading, making functional and mechanistic conclusions from lipidomic data typically quite difficult.

LIPIDS OF YEAST: COMPOSITION, METABOLISM, AND CELLULAR FUNCTION

The lipid composition of yeast is rather simple and comprises some 150 distinct molecular species that have been identified to date (Guan and Wenk 2006; Ejsing et al. 2009; Guan et al. 2010; Klose et al. 2012; Casanovas et al. 2015). Table 1 summarizes the total lipid composition of various yeast wild-type strains grown in minimal medium supplemented with inositol (Daum et al. 1999).

Fatty Acids

Fatty acids (FAs) are the essential building blocks of all glycerolipids and sphingolipids (see below) and they are either synthesized de novo from acetyl-CoA units that are assembled in a cyclic series of

TABLE 1. Lipid composition of various yeast wild-type strains: (A) phospholipid content; (B) sterol and triacylglycerol content; and (C) fatty acid (FA) content and ratios of C16 to C18 and unsaturated to saturated FAs

A									
		Percentage of total phospholipids							
Yeast strain	PL*	PA	PS	PE	PC	PI	CL	PDME	Lyso
JL 20	31.5	4.0	5.0	24.5	40.6	18.9	2.1	2.3	2.3
YJ3C 366	28.0	2.7	6.9	21.0	41.8	21.6	1.9	3.3	0.6
JS91.13-23	30.2	7.4	3.3	13.6	45.9	23.1	3.1	2.5	1.1
W303-1A	26.4	1.9	5.5	21.0	46.2	18.9	3.1	2.7	0.9
FY1679	31.5	2.0	9.2	20.4	40.0	19.1	2.9	4.0	2.0
CEN.PK2-1C	31.4	2.2	5.4	19.0	49.4	16.7	2.9	2.3	0.6
B									
		Sterol and triacylglycerol content							
Yeast strain	Ergosterol*	SE*	TS*	E (%)	L (%)	Sq (%)	TAG*		
JL 20	5.7	9.1	14.9	76.5	6.2	16.8	4.7		
YJ3C 366	4.7	7.8	12.5	94.1	3.9	2.0	8.1		
JS91.13-23	6.0	8.7	14.8	73.8	17.5	8.7	10.0		
W303-1A	4.1	14.1	18.2	85.4	9.7	4.9	7.8		
FY1679	6.0	2.6	8.5	75.3	17.0	7.7	2.4		
CEN.PK2-1C	4.0	16.0	20.0	78.9	14.3	6.8	15.2		
C									
		Percentage of total fatty acids							
Yeast strain	C16:0	C16:1	C18:0	C18:1	Ratios C16/C18	Unsat/Sat			
JL 20	12.0	42.7	5.3	40.0	1.2	4.8			
YJ3C 366	6.3	38.3	3.6	51.8	0.8	9.1			
W303-1A	6.1	24.6	5.8	63.5	0.44	7.4			
FY1679	20.8	45.1	4.8	27.1	2.1	2.8			
CEN.PK2-1C	4.5	40.0	2.7	52.0	0.8	12.8			

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Note that values are quite comparable between wild-type strains, with some marked differences in sterol and triacylglycerol as well as FA composition, which may be the result of different growth characteristics. Asterisks indicate values are milligrams lipid per gram cell dry weight.

PL, total phospholipids; PA, phosphatidic acid; PS, phosphatidylserine; PE, phosphatidylethanolamine; PC, phosphatidylcholine; PI, phosphatidylinositol; CL, cardiolipin; PDME, phosphatidylmethylethanolamine; Lyso, lysophospholipids; SE, steryl esters; TS, total sterol; E, ergosterol; L, lanosterol; Sq, squalene; TAG, triacylglycerol; C16:0, palmitic acid; C16:1, palmitoleic acid; 18:0, stearic acid; C18:1, oleic acid.

reactions by the fatty acid synthase complex, or they may be taken up by yeast cells if they are supplied in the culture medium (Tehlivets et al. 2007). In yeast, *de novo* synthesis delivers CoA-activated FAs (acyl-CoAs), whereas exogenously added FAs require activation with CoA before their incorporation into lipids, or further modification, such as elongation or desaturation (Black and DiRusso 2007). Yeast contains mostly FAs with 16 or 18 carbon atoms, which are saturated (~20%) or mono-unsaturated (~80%) (see Table 1). Minor FA species are C14 and very long chain FAs, up to C26, which are mostly present in sphingolipids and glycosylphosphatidylinositol anchors (Tehlivets et al. 2007; Ejlsing et al. 2009). In contrast to mammalian cells, yeast contains only mono-unsaturated FAs harboring a double bond between C9 and C10, which drastically reduces the combinatorial acyl-chain complexity in the yeast lipids; the double bond is introduced into the acyl chain by the essential Ole1 $\Delta 9$ FA desaturase (Martin et al. 2007).

FA analysis is typically performed by gas–liquid chromatography after transmethylation of lipid-bound FAs to their respective volatile methylesters. Since yeast does not contain polyunsaturated FAs, which are susceptible to (per)oxidation during the isolation procedure, no specific precautions need to be taken.

Glycerophospholipids

Glycerolipids are the most abundant class of lipids in yeast. They are derived from glycerol and harbor one, two, or three acyl chains esterified to the hydroxyl groups of the glycerol moiety. In triacylglycerols (triglycerides; TAG), all three hydroxyl groups are esterified with an FA, and these molecules are “neutral lipids,” which are uncharged and have a highly apolar structure. TAG are typically stored in cytosolic lipid droplets and provide a most efficient means to store FAs, which may serve as a source of energy by β -oxidation on demand, for example, in the absence of other carbon sources. In addition, FAs released by lipolysis may also serve as precursors for membrane lipids. *sn*-1,2-diacylglycerol (DAG) is only a minor neutral lipid intermediate and is a precursor for the synthesis of TAG or glycerophospholipids. In addition, DAG is generated in the course of signaling processes (e.g., degradation of phosphatidylinositol phosphates) and may activate protein kinase C in the plasma membrane. The main route of DAG synthesis is via the dephosphorylation of phosphatidic acid (PA), which is also the central precursor for all glycerophospholipids. PA (also a minor lipid class) harbors two acyl chains in positions *sn*-1 and *sn*-2 and a phosphate group at position *sn*-3, which is negatively charged at intracellular pH. In addition to its metabolic role as a key intermediate in DAG, TAG, and phospholipid synthesis, PA also has signaling function, which operates through its specific interaction with the transcriptional repressor Opi1. This binding of Opi1 to PA regulates the subcellular distribution of the repressor and hence its nuclear repressing activity (Loewen et al. 2004; Henry et al. 2012; Hofbauer et al. 2014).

PA is synthesized by two sequential acylation reactions of glycerol-3-phosphate, each of which is catalyzed by two redundant acyl-CoA-dependent acyltransferases. Subsequently, in *de novo* phospholipid synthesis, PA is activated with CTP to CDP-DAG (a very minor lipid class), which is the substrate for several transesterification reactions: (i) CDP-DAG and inositol give rise to phosphatidylinositol (PI); (ii) CDP-DAG and glycerol-3-phosphate are precursors of phosphatidylglycerol phosphate (PGP), which is further processed to the mitochondria-specific lipid, cardiolipin (CL); and (iii) transesterification of CDP-DAG with serine generates phosphatidylserine (PS). PGP, CL, PI, and PS are all negatively charged phospholipids. PS is converted by decarboxylation to phosphatidylethanolamine (PE), which is methylated in a three-step reaction to phosphatidylcholine (PC), the major glycerophospholipid in yeast. In an alternative pathway, PE and PC can be generated by transesterification of CDP-ethanolamine or CDP-choline, and DAG, respectively (Henry et al. 2012). This so-called CDP-choline or Kennedy pathway is essential in the absence of the *de novo* methylation pathway (i.e., in respective mutants) and requires supplementation of cells with choline. However, this pathway is also highly active in the absence of exogenous ethanolamine or choline to recycle precursors derived from lipid turnover. PE and PC both carry positive and negative charges at cellular pH, but appear overall as neutral. Intermediates of glycerophospholipids during synthesis or degradation are so-called lysophospholipids (i.e., with the structure *sn*-1-acyl-glycerol-3-phosphate),

which are typically present only in very low amounts, and may have detrimental, detergent-like effects on cell membranes. The observation of elevated lysolipids in cellular extracts indicates some level of degradation during the isolation procedure.

All glycerophospholipids have an amphipathic structure, which is the basis for their spontaneous assembly into bilayers in which the hydrophobic acyl chains interact with each other to exclude water (the hydrophobic effect) and the highly polar, charged, or uncharged head groups are oriented toward the aqueous phase, where they interact with ions (to balance the charges), proteins, and metabolites. Most biosynthetic pathways of glycerolipid synthesis are associated with the endoplasmic reticulum, but some reactions take place in the cytosol or mitochondria. The occurrence of specific lipid profiles in subcellular membranes (Schneider et al. 1999) requires extensive lipid trafficking and remodeling, and also implies that various subcellular lipid (precursor) pools must exist, dependent on the localization and activity of the anabolic or catabolic enzymes. Nevertheless, mutant analyses have shown that yeast cells are able to tolerate dramatic alterations in their FA and lipid composition (Henry et al. 2012; Klose et al. 2012).

It should also be noted that lateral movement of lipid molecules and proteins is a highly dynamic process, whereas transversal movement of lipids (flip-flop) from one monolayer to the opposite side is kinetically extremely unfavored and requires enzymes for catalysis. As a consequence, lipid composition of both leaflets of the membrane is typically asymmetric, which has profound biological consequences for membrane function. These subcellular differences have to be taken into account for the interpretation of lipidomics data, when analyzing total lipid extracts!

Sphingolipids

In addition to glycerophospholipids, yeast cells contain a second class of phospholipids termed sphingolipids (Schneider 1999; Guan and Wenk 2006; Dickson 2010). These lipids are derived from sphingosine or phytosphingosine, which are produced in a condensation reaction between serine and palmitoyl-CoA. Further addition of a very long chain FA (up to C26) in an amide linkage generates ceramide. Ceramide is modified with inositol phosphate (PI is the inositol phosphate donor), giving rise to the essential inositol phosphoryl ceramide (IPC), which is further modified with sugar (mannose) to form mannosyl inositol phosphoryl ceramide (MIPC) and with one additional inositol phosphate to form mannosyl di-inositol phosphate ceramide (M[IP]₂C). These complex sphingolipids are not essential under normal growth conditions, but lack of these lipids renders cells highly temperature and ion (e.g., calcium) sensitive. Sphingolipids are enriched in the plasma membrane and contribute to membrane stability; they also serve as membrane anchors for proteins.

Sterols

Sterols are chemically and structurally quite distinct from other classes of lipids. They are membrane-active compounds, but do not form bilayers on their own. The main yeast sterol is ergosterol, which is synthesized in a complex series of condensation, cyclization, and redox reactions from C5 (isoprene) building blocks (Espenshade and Hughes 2007). Fungal sterol biosynthesis follows steps similar to mammalian cholesterol synthesis, with some distinct differences, which make sterol biosynthesis (an essential pathway) a prime target for antifungal drugs (Lupetti et al. 2002). Free sterols modulate membrane fluidity and are enriched in the yeast plasma membrane, where their content is regulated not only by the activity of key biosynthetic enzymes, but also by their partial sequestration by acylation and storage as steryl esters, together with TAG, in cytosolic lipid droplets (Czabany et al. 2007; Kohlwein et al. 2013).

Minor Lipid Components in Yeast

In addition to lipid intermediates, such as lysolipids, PA, CDP-DAG, and DAG, numerous other classes of lipids are present only in minor amounts in yeast lipid extracts: These include phosphatidylinositol phosphate (PIP) and its higher phosphorylated derivatives, PI(3)P, PI(4)P, PI(3,5)P₂, and

PI(4,5)P₂, and sphingosine derivatives, some of which are present only in trace amounts, but nevertheless play essential roles as signaling molecules.

YEAST LIPID ANALYTICS

Advances in lipid mass spectrometry have significantly facilitated lipid analysis in yeast and other cell types and have unveiled unprecedented insight into the molecular species composition of yeast lipids (Guan and Wenk 2006; Ejsing et al. 2009; Guan et al. 2010; Shui et al. 2010; Klose et al. 2012; Casanovas et al. 2015). Because lipid molecular masses are typically <1000 Da, they are excellent targets for mass spectrometry approaches. Despite the relatively simple composition of the yeast lipidome, major differences in chemical nature and abundance make a total lipid analysis from yeast cells a challenging task, starting with cell breakage and extraction, and various levels of qualitative and quantitative analysis. It should be noted that not all lipids are extracted with the same efficacy in a given solvent system; thus, depending on the type of lipid under analysis, alternative extraction procedures may need to be considered (e.g., for sphingolipids or PIPs). For a standard protocol for the isolation of lipids from yeast, see Protocol: **Lipid Extraction from Yeast Cells** (Knittelfelder and Kohlwein 2015a). For protocols describing the quantification of FAs, the major glycerophospholipids, and sterols/steryl esters from yeast, see Protocol: **Thin-Layer Chromatography to Separate Phospholipids and Neutral Lipids from Yeast** (Knittelfelder and Kohlwein 2015b), Protocol: **Derivatization and Gas Chromatography of Fatty Acids from Yeast** (Knittelfelder and Kohlwein 2015c), and Protocol: **Quantitative Analysis of Yeast Phospholipids and Sterols by High-Performance Liquid Chromatography—Evaporative Light-Scattering Detection** (Knittelfelder and Kohlwein 2015d).

ACKNOWLEDGMENTS

I would like to thank the members of my laboratory for helpful suggestions. Research in my laboratory is supported by the PhD program “Molecular Enzymology” (W901-B05) and project F3005-B12 (SFB LIPOTOX), which are funded by the Austrian Science Funds (FWF). Additional support NAWI Graz and BioTechMed Graz is gratefully acknowledged.

REFERENCES

- Black PN, DiRusso CC. 2007. Yeast acyl-CoA synthetases at the crossroads of fatty acid metabolism and regulation. *Biochim Biophys Acta* 1771: 286–298.
- Carman GM, Han GS. 2011. Regulation of phospholipid synthesis in the yeast *Saccharomyces cerevisiae*. *Annu Rev Biochem* 80: 859–883.
- Casanovas A, Sprenger RR, Trarasov K, Ruckerbauer DE, Hannibal-Bach HK, Zanghellini J, Jensen ON, Ejsing CS. 2015. Quantitative analysis of proteome and lipidome dynamics reveals functional regulation of global lipid metabolism. *Chem Biol* 22: 412–425.
- Chauhan N, Visram M, Cristobal-Sarramian A, Sarkleti F, Kohlwein SD. 2015. Morphogenesis checkpoint kinase Swel is the executor of lipolysis-dependent cell-cycle progression. *Proc Natl Acad Sci* 112: E1077–E1085.
- Czabany T, Athenstaedt K, Daum G. 2007. Synthesis, storage and degradation of neutral lipids in yeast. *Biochim Biophys Acta* 1771: 299–309.
- Daum G, Tuller G, Nemec T, Hrastnik C, Balliano G, Cattel L, Milla P, Rocco F, Conzelmann A, Vionnet C, et al. 1999. Systematic analysis of yeast strains with possible defects in lipid metabolism. *Yeast* 15: 601–614.
- Dickson RC. 2010. Roles for sphingolipids in *Saccharomyces cerevisiae*. In *Advances in experimental medicine and biology* (eds. Chalfant C, Del Poeta M), pp. 217–231. Kluwer Academic, New York.
- Ejsing CS, Sampaio JL, Surendranath V, Duchoslav E, Ekroos K, Klemm RW, Simons K, Shevchenko A. 2009. Global analysis of the yeast lipidome by quantitative shotgun mass spectrometry. *Proc Natl Acad Sci* 106: 2136–2141.
- Espenshade PJ, Hughes AL. 2007. Regulation of sterol synthesis in eukaryotes. *Annu Rev Genetics* 41: 401–427.
- Guan XL, Wenk MR. 2006. Mass spectrometry-based profiling of phospholipids and sphingolipids in extracts from *Saccharomyces cerevisiae*. *Yeast* 23: 465–477.
- Guan XL, Riezman I, Wenk MR, Riezman H. 2010. Yeast lipid analysis and quantification by mass spectrometry. *Methods Enzymol* 470: 369–391.
- Henry SA, Kohlwein SD, Carman GM. 2012. Metabolism and regulation of glycerolipids in the yeast *Saccharomyces cerevisiae*. *Genetics* 190: 317–349.
- Hofbauer HF, Schopf FH, Schleifer H, Knittelfelder OL, Pieber B, Rechberger GN, Wolinski H, Gaspar ML, Kappe CO, Stadlmann J, et al. 2014. Regulation of gene expression through a transcriptional repressor that senses acyl-chain length in membrane phospholipids. *Dev Cell* 29: 729–739.
- Klose C, Surma MA, Gerl MJ, Meyenhofer F, Shevchenko A, Simons K. 2012. Flexibility of a eukaryotic lipidome—Insights from yeast lipidomics. *PLoS One* 7: e35063.
- Knittelfelder OL, Kohlwein SD. 2015a. Lipid extraction from yeast cells. *Cold Spring Harb Protoc* doi: 10.1101/pdb.prot085449.
- Knittelfelder OL, Kohlwein SD. 2015b. Thin-layer chromatography to separate phospholipids and neutral lipids from yeast. *Cold Spring Harb Protoc* doi: 10.1101/pdb.prot085456.

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- Knittelfelder OL, Kohlwein SD. 2015c. Derivatization and gas chromatography of fatty acids from yeast. *Cold Spring Harb Protoc* doi: 10.1101/pdb.prot085464.
- Knittelfelder OL, Kohlwein SD. 2015d. Quantitative analysis of yeast phospholipids and sterols by high-performance liquid chromatography—Evaporative light-scattering detection. *Cold Spring Harb Protoc* doi: 10.1101/pdb.prot085472.
- Knittelfelder OL, Weberhofer BP, Eichmann TO, Kohlwein SD, Rechberger GN. 2014. A versatile ultra-high performance LC-MS method for lipid profiling. *J Chromatogr B Analyt Technol Biomed Life Sci* 951–952: 119–128.
- Kohlwein SD, Veenhuis M, van der Klei IJ. 2013. Lipid droplets and peroxisomes: Key players in cellular lipid homeostasis or a matter of fat—Store 'em up or burn 'em down. *Genetics* 193: 1–50.
- Kurat CF, Natter K, Petschnigg J, Wolinski H, Scheuringer K, Scholz H, Zimmermann R, Leber R, Zechner R, Kohlwein SD. 2006. Obese yeast: Triglyceride lipolysis is functionally conserved from mammals to yeast. *J Biol Chem* 281: 491–500.
- Kurat CF, Wolinski H, Petschnigg J, Kaluarachchi S, Andrews B, Natter K, Kohlwein SD. 2009. Cdk1/Cdc28-dependent activation of the major triacylglycerol lipase Tgl4 in yeast links lipolysis to cell-cycle progression. *Mol Cell* 33: 53–63.
- Loewen CJ, Gaspar ML, Jesch SA, Delon C, Ktistakis NT, Henry SA, Levine TP. 2004. Phospholipid metabolism regulated by a transcription factor sensing phosphatidic acid. *Science* 304: 1644–1647.
- Lupetti A, Danesi R, Campa M, Del Tacca M, Kelly S. 2002. Molecular basis of resistance to azole antifungals. *Trends Mol Med* 8: 76–81.
- Martin CE, Oh CS, Jiang Y. 2007. Regulation of long chain unsaturated fatty acid synthesis in yeast. *Biochim Biophys Acta* 1771: 271–285.
- Natter K, Kohlwein SD. 2013. Yeast and cancer cells—Common principles in lipid metabolism. *Biochim Biophys Acta* 1831: 314–326.
- Nohturfft A, Zhang SC. 2009. Coordination of lipid metabolism in membrane biogenesis. *Annu Rev Cell Dev Biol* 25: 539–566.
- Schneider R. 1999. Brave little yeast, please guide us to Thebes: Sphingolipid function in *S. cerevisiae*. *BioEssays* 21: 1004–1010.
- Schneider R, Brugger B, Sandhoff R, Zellnig G, Leber A, Lampl M, Athenstaedt K, Hrastnik C, Eder S, Daum G, et al. 1999. Electrospray ionization tandem mass spectrometry (ESI-MS/MS) analysis of the lipid molecular species composition of yeast subcellular membranes reveals acyl chain-based sorting/remodeling of distinct molecular species en route to the plasma membrane. *J Cell Biol* 146: 741–754.
- Shui G, Guan XL, Low CP, Chua GH, Goh JS, Yang H, Wenk MR. 2010. Toward one step analysis of cellular lipidomes using liquid chromatography coupled with mass spectrometry: Application to *Saccharomyces cerevisiae* and *Schizosaccharomyces pombe* lipidomics. *Mol Biosyst* 6: 1008–1017.
- Tehlivets O, Scheuringer K, Kohlwein SD. 2007. Fatty acid synthesis and elongation in yeast. *Biochim Biophys Acta* 1771: 255–270.
- Zanghellini J, Natter K, Jungreuthmayer C, Thalhammer A, Kurat CF, Gogg-Fassolter G, Kohlwein SD, Von Grünberg HH. 2008. Quantitative modeling of triacylglycerol homeostasis in yeast—Metabolic requirement for lipolysis to promote membrane lipid synthesis and cellular growth. *FEBS J* 275: 5552–5563.

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