



Review

Incomplete sterols and hopanoids pathways in ciliates: Gene loss and acquisition during evolution as a source of biosynthetic genes



Mariela L. Tomazic^a, Tomas J. Poklepovich^b, Clara B. Nudel^b, Alejandro D. Nusblat^{b,*}

^a Instituto de Patobiología, Centro de Investigaciones en Ciencias Agrarias y Veterinarias (CICVyA), INTA-Castelar, Argentina

^b Cátedra de Biotecnología y Microbiología Industrial, Facultad de Farmacia y Bioquímica, Universidad de Buenos Aires, Junín 956, C1113AAD Buenos Aires, Argentina

ARTICLE INFO

Article history:

Received 19 August 2013

Revised 16 December 2013

Accepted 27 January 2014

Available online 10 February 2014

Keywords:

Ciliates

Sterols

Hopanoids

HGT

Tetrahymena

Paramecium

ABSTRACT

Polycyclic triterpenoids, such as sterols and hopanoids, are essential components of plasmatic membrane in eukaryotic organisms. Although it is generally assumed that ciliates do not synthesize sterols, and many of them are indeed auxotrophic, a large set of annotated genomic sequences and experimental data from recently studied organisms indicate that they can carry putative genes and respond to the presence/absence of precursors in various ways. The pre-squalene pathway, for instance, is largely present in all sequenced ciliates except in *Ichthyophthirius multifiliis*; although *Paramecium tetraurelia* lacks the squalene synthase and *Oxytricha trifallax* the squalene hopene synthase, in addition to the former. On the other hand, the post-squalene pathway, requiring oxygen in several steps, is mostly incomplete in all ciliates analyzed. Nevertheless, a number of predicted genes, with high sequence similarity to C-4 methyl oxidase/s, C-14 demethylase, C-5 and C-7 desaturases and C-24 reductase of sterols are found in *Tetrahymena* and *Paramecium*, and scattered in other Stichotrichia ciliates. Moreover, several of these sequences are present in multiples paralogs, like the C-7 desaturase in *Paramecium*, that carries six versions of the only one present in *Tetrahymena*.

The phylogenetic analyses suggest a mixed origin for the genes involved in the biosynthesis of sterols and surrogates in this phylum; while the genes encoding enzymes of the pre-squalene pathway are most likely of bacterial origin, those involved in the post-squalene pathway, including the processing of sterols obtained from the environment, may have been partially retained or acquired indistinctly from lower eukaryotes or prokaryotes. This particular combination of diverse gene/s acquisition patterns allows for survival in conditions of poor oxygen availability, in which tetrahymanol and other hopanoids may be advantageous, but also conditions of excess oxygen availability and abundant sterols, in which the latter are preferentially phagocyte, and/or transformed. Furthermore, the possibility that some of the genes involved in sterol metabolism may have another biological function in the most studied ciliate *T. thermophila*, was also explored.

© 2014 Elsevier Inc. All rights reserved.

Contents

1. Introduction	123
1.1. Sterols and hopanoids	123
1.2. Ciliates and polycyclic triterpenoids	125
2. Phylogenomics of tetrahymanol synthesis in ciliates	125
2.1. Bacterial origin for tetrahymanol biosynthetic enzymes	127
2.2. Gene expression analysis	127
3. Phylogenomics of sterol pathway in ciliates	129
3.1. The role of sterols in the regulation of tetrahymanol	129
3.2. Sterol modifying enzymes	129
3.3. Genes identified in ciliates	131

* Corresponding author. Fax: +54 11 4964 8200.

E-mail address: anusblat@ffyb.uba.ar (A.D. Nusblat).

3.4. Biological roles of putative genes.	132
4. Conclusions.	132
Acknowledgments	132
Appendix A. Supplementary material.	133
References	133

1. Introduction

1.1. Sterols and hopanoids

Sterols and hopanoids are polycyclic triterpenoids that derive from the cyclization of squalene or oxidosqualene by evolutionary related cyclases (Fig. 1). There is a large diversity in the distribution of pentacyclic triterpenoids in nature; as a rule of thumb, sterols are mostly found in eukaryotes, whereas hopanoids are found in prokaryotes (Volkman, 2005).

It is well known that sterols have essential functions in eukaryotic cells: (i) are the major non-polar lipids of cell membranes and, in association with phospholipids, modulate and refine membrane properties forming a liquid-ordered phase (Van Meer et al., 2008), (ii) serve as precursors of bile salts and a number of different steroid hormones implicated in growth, cell cycle and development in mammals, of brassinosteroids in plants (Benveniste, 2004), of antheridiol and oogoniol in aquatic fungi (Brunt and Silver, 1991), of ecdysteroids in arthropods (Gilbert et al., 2002) and of daphacronic acids in nematodes (Motola

et al., 2006); (iii) cholesterol is actively involved in the formation of specialized microdomains, termed lipid rafts, which form platforms that function in signaling and trafficking (Hancock, 2006). It is assumed that hopanoids play similar roles in organisms that are not able to synthesize sterols; for instance, they control fluidity in bacterial membranes (Ourisson et al., 1987; Sáenz et al., 2012). However, other distinctly functions were also shown, such as tolerance towards high temperatures and low pH, and a role in the protection of a nitrogenase-complex against oxygen, in nitrogen fixing bacteria (Berry et al., 1993).

Hopanoids and sterols are derived from isopentenyl diphosphate (IPP), a universal precursor which is present and synthesized in the three domains of life (albeit by different pathways) with a clear preference for the 2-C-methyl-D-erythritol 4-phosphate (MEP) pathway in bacteria, the classical mevalonate pathway (MVA) in eukaryotes and the alternative MVA pathway in archaea (Fig. 1).

However, exceptions to this rule are also known. For instance some bacteria make use of the MVA pathway, a trait that has been commonly explained by the occurrence of genes likely acquired by

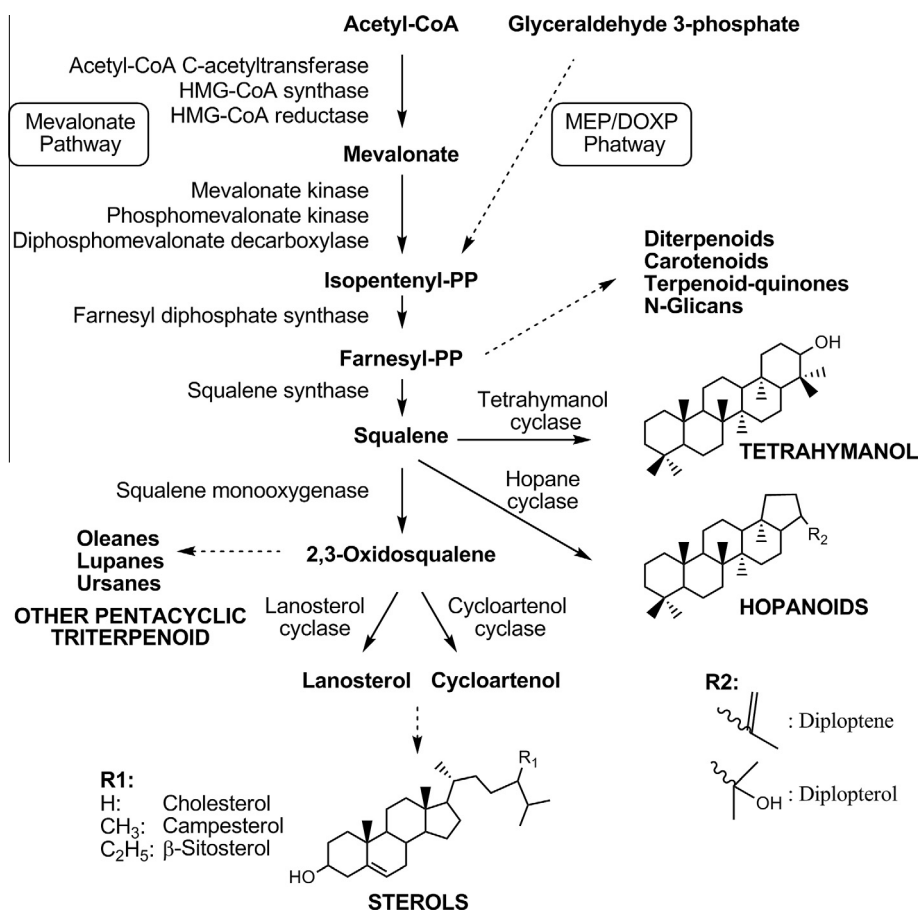


Fig. 1. Canonical polycyclic triterpenoid pathway, leading to hopanoids in bacteria, tetrahymanol in ciliates, sterols in most eukaryotic organism and oleanes, lupanes and ursanes in plants. The biosynthesis of Isopentenyl-PP is shown via mevalonate pathway found in eukaryotes and archaea; and via MEP/DOXP pathway found in bacteria and several photosynthetic eukaryotes.

Download English Version:

<https://daneshyari.com/en/article/2833853>

Download Persian Version:

<https://daneshyari.com/article/2833853>

[Daneshyari.com](https://daneshyari.com)