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Editorial: Emergence of dynamic membranes – role of terpenoids in the evolution of membrane organization and regulation

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Editorial on the Research Topic
Emergence of dynamic membranes – role of terpenoids in the evolution of membrane organization and regulation

This Research Topic addresses the role of terpenoids in the evolution of biological membranes from a variety of perspectives. The study topics range from genetic analysis of bacterial terpenoid synthesis and the origins of sedimentary terpanes (i.e. fossilized terpenoids) to reviews on the possible roles of terpenoids in primitive membranes before the divergence of the three domains of life – Archaea, Bacteria, and Eukarya – and on the evolution of membrane dynamics in individual domains.

The review on Terpenoids and membrane dynamics evolution by Hoshino provides a comprehensive overview of the functional and structural diversification of terpenoids in the three domains, as presented in the 'membrane tree of life' (Figure 1), and the impact of terpenoid-membrane interactions on the evolutionary trajectory of membrane dynamics and resulting ecological fitness for host organisms. A key feature of the membrane tree of life is the so-called ´lipid divide´ – a fundamental bifurcation of membrane types between archaea and bacteria/eukaryotes. While archaea have exclusively terpenoid phospholipids, the other two domains have dominantly fatty acyl phospholipids and, additionally, polycyclic terpenoid regulators (hopanoids and steroids; Figure 1). From an evolutionary perspective, an interesting inference from phylogenetic terpenoid distributions is the proposition that the last universal common ancestor (LUCA) of all extant life likely contained terpenoids. Accordingly, terpenoids may have been key ingredients in a primitive pre-LUCA world. The role of terpenoids as key players in membrane evolution—as highlighted in the review article—illuminates the importance of improving our understanding of the developmental history of terpenoids as a unique tool to elucidate the evolutionary trajectory of life.

The role of terpenoids in membrane evolution is further elucidated by King and Wang in their review on the Putative roles of terpenoids in primitive membranes. Like in extant cells, terpenoids may have played an important role in primitive membranes that formed

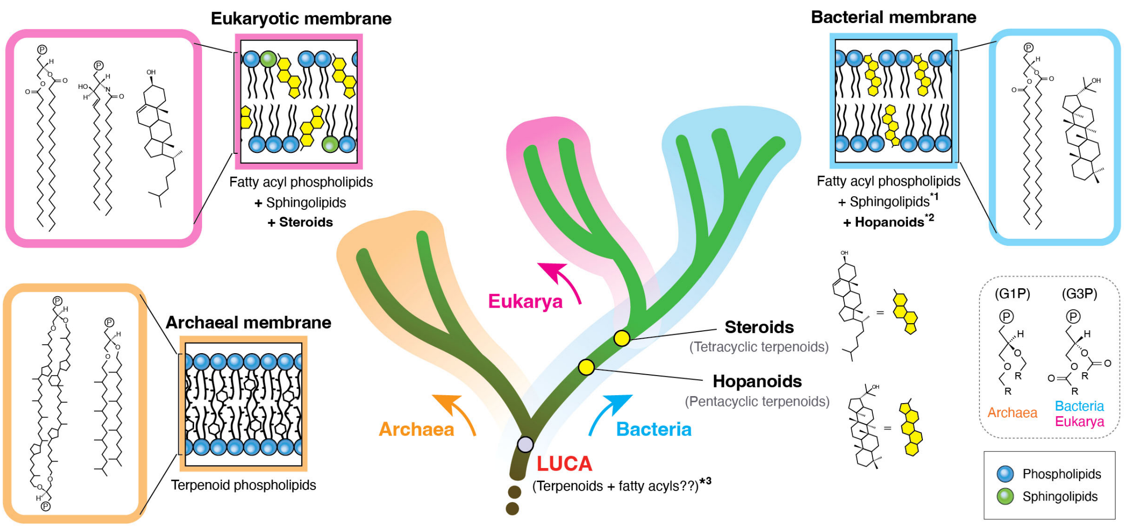

FIGURE 1
Membrane tree of life. The bifurcation of the archaeal and bacterial membranes represents the 'lipid divide' (from Hoshino, 2024 in this Research Topic). LUCA represents the last universal common ancestor of all life on earth. The antiquity of terpenoid biosynthesis that is preserved in all extant organisms suggests that LUCA and some of its ancestors may already have produced terpenoids that, from theoretical and experimental considerations, might have been key ingredients in early membrane evolution and possibly protocells.

from prebiotically available components. By discussing principles of membrane formation and reviewing the potential role that terpenoids played in the function of primitive membranes, King and Wang shed light on promising lines of investigation for future protocell research. An important principle for protocell formation and its functionality is that membrane self-assembly and fulfilment of physical protocell requirements must have been achieved without evolutionary-advanced biochemistry, such as proteins. King and Wang point out that, instead, a variety of structural terpenoid motifs could have fulfilled such functions in protocells. They note that lipid bilayers formed by single-chained molecules are more plausible configurations for prebiotic membranes than those with more complex double-tailed lipids and that single-chain terpenoids are able to form lipid bilayers on their own or in combination with various fatty acids. Terpenoids allow for enhanced membrane fluidity at lower temperatures and might prevent ion dissipation across primitive membranes. Similar to the role cholesterol plays today in animal cells, simple terpenoids could have increased ecological fitness of primitive cells—particularly for coping with environmental changes. Accordingly, King and Wang discuss the prebiotic synthesis of terpenoids and the ability of terpenoids to modify key properties of primitive membranes such as permeability, fluidity, and stability to environmental fluctuations as promising future research directions.

Marshall et al. illuminate the bacterial side of the lipid divide (Figure 1) in their study: Evolutionary flexibility and rigidity in the bacterial methylerythritol phosphate (MEP) pathway. The methylerythritol-phosphate pathway is one of the two extant pathways to generate precursor molecules for all terpenoids in bacteria, along with the mevalonate (MVA) pathway, which is mostly distributed in eukaryotes and archaea. An initial bottle neck to carbon flux in the MEP pathway that is employed for terpene biosynthesis in most bacteria is provided by 1-deoxy-D-xylulose-5-phosphate synthase (Dxs), the first enzyme in the pathway. Marshall et al. conducted comparative genomic analyses of a database comprising 4,400 diverse bacterial species and found that some bacteria evolved alternatives to Dxs, pointing to evolutionary flexibility. In contrast, no alternatives were identified for iron-sulfur cluster-containing enzymes IspG (which becomes rate limiting when Dxs is overexpressed) and IspH, indicating that these enzymes are evolutionarily rigid. According to Marshall et al., differences between species tree and MEP protein trees indicate that horizontal gene transfer may have influenced the evolution of the MEP pathway. The study highlights that the continual expansion of genomic databases provides metabolic engineers with beneficial information that is critical for identifying and implementing alternative metabolic pathway solutions. The line of research followed by Marshall et al. has the potential to improve artificial terpenoid production for industrial applications but also enhances our understanding of the evolution of terpenoid biosynthetic pathways at the heart of the Research Topic.

Killops et al. focus on Sedimentary diterpane origins—inferences from oils of varying source depositional environment and age. While diterpenes are not typical membrane constituents, they have a variety of functions in plants, including protection against microbes or herbivores, and may permeate freely through plant membranes. Therefore, diterpene evolution is likely inter-connected with the evolution of dynamic (plant) membranes. Elucidating the timeline of diterpene evolution to which Killops et al. contribute thus helps to pinpoint key evolutionary events for the evolution of modern membrane systems in plants. As pointed out by Killops et al., fossilized diterpenes (diterpanes) in the geological record further help to aid the interpretation of organic matter sources and depositional environments, which is in turn important for palaeoecological reconstructions and associated evolutionary inferences. Some diterpanes that are typically found in crude oils and rock extracts, such as C_{19} and C_{20} cheilanthanes, may represent geological transformation products of larger terpenoid precursors that may have been the actual membrane constituents of specific source organisms. Thus, the study of Killops et al. exemplifies how analyses of molecular fossils of terpenoids in the geological record could provide crucial information about the evolutionary trajectory of terpenoids, associated membrane systems, and, ultimately, past ecosystems.

Together, the contributions to this Research Topic include a variety of research directions, ranging from biophysics and synthetic biology to genetics, microbiology, and organic geochemistry. This highlights the importance of interdisciplinary approaches towards a holistic understanding of the role of terpenoids in membrane evolution and its influence on the evolutionary landscape of host organisms.

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Author contributions

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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