This Week's Citation Classic®

Ourisson G, Albrecht P & Rohmer M. The hopanoids: palaeochemistry and biochemistry of a group of natural products. *Pure Appl. Chem.* 51:709-29, 1979.
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Fossil triterpenes, the "geohopanoids," ubiquitous and abundant in sediments, are useful in petroleum exploration. Their precursors, the "biohopanoids," are cholesterol surrogates stabilizing bacterial membranes, a role played in all living organisms by polyterpenoids. Biohopanoids form a phylogenetic series and may have played an important role in prebiotic chemistry. [The *SCI*® indicates that this paper has been cited in over 155 publications.]

Fossil Triterpenes Reveal Unrecognized Microbial Lipids

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February 25, 1990

Representatives of one triterpene family, the previously rarely found hopane derivatives, are *always* present in sediments and are very varied. Their ubiquity[1] makes them probably the most abundant organic substances on Earth. Their varied structures (> 200 so far), linked to conditions of deposition and extent of maturation, provide criteria widely used in industry as an adjunct to classical methods of oil exploration (evaluation of maturation, source-rock/oil correlations).[2] "Geohopanoids" derive from a previously unrecognized family of quite varied bacterial lipids, the highly amphiphilic "biohopanoids."[3]

We have postulated,[4] and it has been demonstrated, that biohopanoids are surrogates of cholesterol as reinforcers of biomembranes in many bacteria; more noble roles are probable, but not demonstrated, e.g., for hopane-peptide derivatives, or for an extraordinary C-adenosylhopane.[3] We have also postulated, and it has been demonstrated *in vitro* and *in vivo*, that, in microorganisms lacking hopanoids and cholesterol, other families of polyterpenoids play a similar role in stabilizing biomembranes by being included as rigid, well-adapted and oriented inserts in the fluid matrix of the phospholipids. These include bacterial carotenoids; archaebacterial polyterpenic ether lipids; cycloartenol, which we had shown to be the biosynthetic precursor of sterols in plants;[4,5] probably tricyclopolyprenols, the molecular fossils of which are present in many sediments; and possibly isoarborinol, a plant triterpene also found in several sediments. These substances can be arranged in a plausible phylogenetic sequence requiring the successive recruitment of new enzymatic reactions or progressive minor changes in similar enzymes.[6]

We have even postulated a prebiotic origin for polyterpenoid phospholipids susceptible to form spontaneously vesicles, i.e., protocells.

Research continues on various fronts: the molecular constitution of the insoluble part of sedimentary organic matter—the kerogen, also rich in hopanoids and other terpenoids; the mechanisms of maturation of organic matter in soils and sediments; the identification of the organisms responsible for the huge accumulation of terpenoids in sediments, determined by microscopic studies or by isotopic enrichment; the study of the nonclassical biosynthetic pathways used by microorganisms to produce biohopanoids; the identification of the microbial lipids of protozoa and other little-studied phyla; the interpretation of the presence of "microbial" hopanoids in ferns; the biophysical study of postulated "primitive" polyterpenoids on model membranes; the abiotic formation of polyterpenic protocells; and so on. Other laboratories, with which we cooperate, study the enzymes involved in the biosynthesis of these polyterpenes.

Our work, helped by Institut Français du Pétrole, the ELF and Chevron oil companies, CNRS, and others, has been very widely presented in invited lectures and has been generously rewarded, in particular by the Roussel Prize, the Heinrich Wieland Prize, the Alfred Treibs Prize, the Alexander von Humboldt Research Prize, several French prizes and, for the senior author (Ourisson), by his election to eight academies of sciences. However, on the whole, we feel that we have not generated the attention this field deserves, and this probably explains why most of our papers have not been widely cited: Petroleum companies do use "hopanograms" but do not publish, and microbial chemistry is not really fashionable any longer.

The *Citation Classic* paper is a short review. It is now superseded by references 3 and 6.

1. **Van Dorsselaer A, Ensminger A, Spyckerelle C, Dastillung M, Sieskind O, Arpino P, Albrecht P, Ourisson G, Brooks P W, Gaskell S J, Kimble B J, Philp R P, Maxwell J R & Eglinton E.** Degraded and extended hopane derivatives as ubiquitous geochemical markers. *Tetrahedron Lett.* 1974:1349-52. (Cited 55 times.)
2. **Ourisson G, Albrecht P & Rohmer M.** The microbial origin of fossil fuels. *Sci. Amer.* 251:44-51, 1984. (Cited 35 times.)
3. **Ourisson G, Rohmer M & Poralla K.** Prokaryotic hopanoids and other polyterpenoid sterol surrogates. *Annu. Rev. Microbiol.* 41:301-33, 1987. (Cited 15 times.)
4. **Benveniste P, Hirth L & Ourisson G.** La biosynthèse des stérols dans les tissus de tabac cultivés *in vitro*. 1. Isolement de stérols et de triterpenes (Biosynthesis of sterols in tobacco tissue cultures. 1. Isolation of sterols and triterpenes). *Phytochemistry* 5:31-44, 1966. (Cited 135 times.)
5. ————. La biosynthèse des stérols dans les tissus de tabac cultivés *in vitro*. 2. Particularités de la biosynthèse des phytostérols des tissus de tabac cultivés *in vitro*. (Biosynthesis of sterols in tobacco tissue cultures. 2. Aspects of the biosynthesis of phytosterols in tobacco tissue culture). *Phytochemistry* 5:45-58, 1966. (Cited 85 times.)
6. **Ourisson G.** The evolution of terpines to sterols. *Pure Appl. Chem.* 61:345-8, 1989.

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