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## Epsilonproteobacteria dominate bacterial diversity at a natural tar seep

Florence Lormières<sup>a,b</sup>, Phil M. Oger<sup>b,c,\*</sup>

<sup>a</sup> Département de biologie, ENS de Lyon, 69364 Lyon, France

<sup>b</sup> Université de Lyon, ENS de Lyon, CNRS UMR 5276, 69364 Lyon, France

<sup>c</sup> Université de Lyon, INSA Lyon, UCBL, CNRS, UMR5240, 69621 Villeurbanne, France

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### ABSTRACT

The bacterial diversity of a naturally seeping bitumen source was investigated by 16S rRNA gene cloning and sequencing. *Epsilonproteobacteria* were shown to dominate the bacterial diversity in the underground water and within the bitumen, representing ca. 75% of the total bacterial diversity. These *Epsilonproteobacteria* were dominated by *Sulfurimonas* OTUs, while *Sulfurovum* and *Arcobacter* OTUs completed the remaining diversity. *Epsilonproteobacteria* are sulfur-oxidizer, nitrate-reducing chemo-lithoautotrophic bacteria, unable to use most organics for growth but capable of CO<sub>2</sub> fixation. Thus, reduced sulfur species, but not the complex organic matter of the tar, are utilized for growth by bacterial communities at the Puy-de-la-Poix. The large prevalence of populations of *Epsilonproteobacteria* is a clear indication that crude oil offers a competitive ecological niche for these organisms.

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### R É S U M É

Nous avons caractérisé la diversité bactérienne au niveau d'une source naturelle de bitume altéré par séquençage d'une librairie de gènes *ribosomiques 16S* clonés. Nous avons observé que la diversité bactérienne est largement dominée par des Epsilonprotéobactéries dans le bitume et dans l'eau souterraine. Ces Epsilonprotéobactéries représentent 75 % de la diversité bactérienne totale. Cette diversité est dominée avant tout par les OTU de *Sulfurimonas*, que complètent des OTU de *Sulfurovum* et *Arcobacter*. Les Epsilonprotéobactéries sont des bactéries chimiolithotrophes, oxydant les sulfures et réduisant les nitrates, incapables d'assimiler les molécules organiques, mais capables de fixer le carbone des carbonates dissouts. Ainsi, les composés soufrés, et non la matière organique complexe du bitume, seraient dégradés par les communautés bactériennes du Puy-de-la-Poix. La présence massive d'Epsilonprotéobactéries indique que l'interface eau hydrothermale/bitume offre une niche écologique favorable à ces microorganismes.

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\* Corresponding author at: Adaptation in Extreme Environments, UMR 5240 CNRS Microbiology, Adaptation and Pathogenicity, INSA de Lyon, bâtiment Pasteur, 11, avenue Jean-Capelle, 69621 Villeurbanne cedex, France.

E-mail address: [philippe.oger@insa-lyon.fr](mailto:philippe.oger@insa-lyon.fr) (P.M. Oger).

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## 1. Introduction

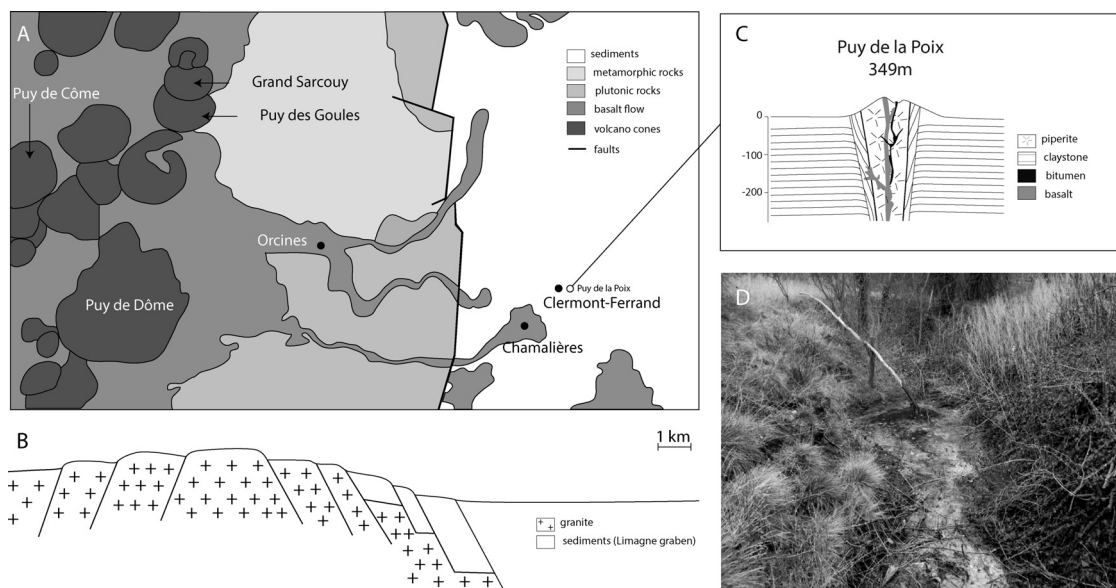
There is growing evidence that crude oil is degraded *in situ* by anaerobic prokaryotes. Heavy oils, tar and gas are the legacy of this microbial degradation over geological times. Petroleum reservoirs are important habitats within the deep biosphere, in which microbial consortia live at the oil–water interface, despite the drastic physicochemical conditions in the reservoirs, e.g., temperatures up to 190 °C in the Elgin–Franklin fields, North Sea [1], salinities up to 400 g/l in the Verkhnechona field, Russia [2], or the lack of oxygen. Many anaerobic prokaryotes have been retrieved both by molecular and cultural approaches from such ecosystems [3]. The microbial mineralization of OM relies on the cooperation of different groups of anaerobic microorganisms in sequence: fermenters, syntrophs, and methanogens [3]. This microflora is composed of genera belonging to the bacterial phyla *Firmicutes*, *Bacteroidetes*, and *Proteobacteria* and methanogenic archaea, such as *Methanomicrobiales*, *Methanosarcinales*, and *Methanobacteriales* [4]. The bacterial diversity in oil reservoirs often presents large populations of *Epsilonproteobacteria* [5,6]. *Epsilonproteobacteria* are major sulfur-oxidizers, nitrate reducers autotrophs and mixotrophs, whose contribution to the sulfur cycle is essential in different environments, such as deep-sea hydrothermal vents and sediments [7], sulfidic cave springs [8], or episymbiotic associations [9]. In these environments, the diversity of *Epsilonproteobacteria* is often dominated by a single genus: *Sulfurovorum* in sulfidic biofilms, *Sulfurimonas* in the Colleville oil field, *Arcobacter* in the Pelican Lake oil field or *Sulfuricum* in the Athabasca oil sand reservoir. Although *Epsilonproteobacteria* are frequent, or dominate the bacterial diversity in different oil environments, it is unlikely that they partake in the breakdown of the organic matter of the oil, but more

likely oxidize the fraction of sulfur compounds of the oil [5,6].

In the absence of the appropriate geologic structure to form a reservoir, crude oil and gas formed in the depth naturally seep out at the surface. These oils are often heavily degraded as a result of microbial activity before or during the migration to the surface, which raises questions about whether the oil-degrading prokaryotes migrate to the surface along with the oil, and whether petroleum degradation persists at the surface. To address this question, we investigated the microbial populations at the Puy-de-la-Poix, a small, naturally flowing seep of heavily degraded oil, or bitumen, in the Limagne region (France). We show here that as observed in other degraded-oil environments, the bacterial diversity at the Puy-de-la-Poix was characterized by a large majority of *Epsilonproteobacteria* of the *Sulfurimonas* genus.

## 2. Methods

**Sampling:** The “Puy-de-la-Poix” is a naturally flowing tar source located near the airport of Clermont-Ferrand (France, 45.7822 N 3.14642 E, 340 m, Fig. 1). The source appears as a small pool of ca. 3 m by 2 m, which may be covered by rain fall water according to the season, and overflows into the adjacent agricultural fields. At the time of sampling, the air temperature was 6 °C. The tar formed a thick mass on top of the source and the water covering the tar was ca. 2–5 cm deep. The water above the tar was sampled aseptically using sterile syringes (100 ml, surface water samples, SW). The remaining surface water was removed to avoid cross contamination with waters below the tar. Underground waters (UW, 100 ml) were sampled below the tar using sterile tubing punched through the tar. The chemical composition of the underground water can



**Fig. 1.** Geographical and geological characteristics of the Puy-de-la-Poix. Panel A: Geologic map close up of the Clermont-Ferrand area. The Puy-de-la-Poix is located east of the city, next to the airport. Panel B: Corresponding cross section. Panel C: detailed geologic structure at the Puy-de-la-Poix Panel D: The seep flows from the top of the ancient volcano into the nearby agricultural fields.

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