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Diversity of Magnetotactic Bacteria from a French Pristine Mediterranean Area

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Abstract Magnetotactic bacteria synthesize intracellular magnetite and/or greigite magnetosome crystals. They play a significant role in both iron and sulfur cycles in sedimentary aquatic environments. To get insight into the biogeochemical contribution of MTB, more studies concerning their ecology and their distribution in diverse habitats are necessary. The MTB community of an oil-industry polluted area of the French Mediterranean coast has been previously investigated. Here, we investigate the MTB community from coastal sediments of a Mediterranean pristine area using optical and transmission electron microscopy and phylogenetic analysis based on 16S rRNA gene sequences. A particularly high diversity of MTB was observed, with cocci phylogenetically distributed across the order Magnetococcales, including a novel cluster with sequences from the Mediterranean Sea designated as "Med group", and novel morphotypes.

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Introduction

Magnetotactic bacteria (MTB) have the ability to mineralize nano-sized magnetite (Fe_3O_4) or greigite (Fe_3S_4) crystals within cells. Their occurrence has been reported world-wide in aquatic environments (from freshwater to marine sediments). MTB identified so far are phylogenetically associated with the Alpha-, Delta-, and Gammaproteobacteria classes, the *Nitrospirae* phylum, and the candidate division OP3 [8]. Among them, magnetotactic cocci of the Alphaproteobacteria seem to be the dominant population in marine environments [8].

Studies of MTB ecology have been essentially performed on samples from China Sea, Brazilian and Pacific lagoons, North Sea, coastal salt ponds, lakes and rivers in Asian, European and American continents [5, 11, 14, 19, 21, 28]. In addition, a recent study performed in an oil-industry submitted Mediterranean area in France has suggested that some MTB are particularly well adapted to polluted marine environment [20]. From these studies, specific geographic distribution of MTB species originating from freshwater or marine areas has been established at local, continental, and Earth scales [8, 11]. As seen from magnetofossil records, magnetotactic bacteria seem to have colonized European lakes simultaneously after the last glacier retreat [18]. Thus, environmental factors and physical sediment properties rather than geographic

distance may be decisive for MTB distribution. Temperature, salinity, sulfate concentration, total iron concentration, and strength of the Earth's magnetic field may be factors of importance constraining MTB communities [8].

MTB are assumed to play important roles in microbial ecology in sediment layers, particularly in both iron and sulfur cycles [10, 16, 21, 23]. Ferrous and ferric ions are actively taken up and accumulated by MTB during the formation of magnetosomes [8]. A recent study in a pelagic carbonate sediment has shown that magnetofossils contain 30–60 % of all secondary iron phases, meaning that >30 % of the Fe cycle was certainly driven by these bacteria [12]. MTB are microaerophiles or anaerobes and are therefore found at the oxic–anoxic interface transition zone (OATZ) of the sediments. A recent report of MTB from pelagic red clays has shown that MTB might be found also in oxic settings decoupled from the occurrence of an OATZ [25].

Among the microaerophiles, such as MTB of the Magnetococcales order, some are capable of sulfide oxidation. Among those which are anaerobes, some are capable of sulfate reduction and produce iron oxide and/or iron sulfides [7, 26]. When MTB die, magnetosomes are dissolved or preserved in sediment as magnetofossils.

Despite their remarkable magnetic navigation capability and proposed ecological functions [11, 13, 26, 29], our understanding of MTB geographic distribution is still insufficient and their diversity across heterogeneous habitats remains unclear. In particular, the effect of pollution on magnetotactic bacteria abundance and diversity is poorly known. In this study, we investigate the diversity of MTB in a pristine French Mediterranean coastal area, classified as a natural zone of ecological interest ("Natura 2000" site of an ASPIM), in order to give insight on the MTB communities of the Mediterranean coast.

Materials and Methods

Sediment Sampling and Collection of Magnetotactic Bacteria

Samples were collected at Six-Fours-les-Plages (43°06′03″N; 5°49′20″E) in March 2013, in one site of a Specially Protected Area of Mediterranean Importance (SPAMI, United Nations Environment Programme), and classified as "Natura 2000" area (European ecological network; http://inpn.mnhn.fr/site/natura2000/FR9302001/tab/habitats) (Suppl data 1). The samples were taken below the tidal zone of the sandy beach of a lagoon (1.5 m water depth). The top 5-cm depth sediments until the suboxic zone, just below the OATZ, were collected (Suppl data 2). Sediments (150 mL) and marine water (300 mL) were sampled in eight 500 mL plastic bottles containing 10 % (v/v) air phase. Magnetotactic bacteria were magnetically collected the same day in the laboratory from eight bottles after homogenisation of the samples by placing the south pole of 0.4 T permanent magnets against the outer surface of the bottles [4]. After 30 min, bacteria in the brown-blackish spots underneath the magnets were collected with a pipette, counted and inspected using the hanging-drop approach [4], and magnetically purified by the race-track method using 0.4 T permanent magnets, as previously described [24]. Purified MTB were used for microscope observations and DGGE analyses.

Light and Transmission Electron Microscopy

Bacteria were observed under an optical Nikon Eclipse E600 phase-contrast microscope. The average number of bacteria was estimated by direct cell counting, using a Thoma chamber. MTB were counted after magnetic collection by hanging-drop assay [4]. Average numbers were calculated from three separate cell counts. Samples for electron microscopy observations were adsorbed on formvar-carbon copper grids (200 mesh) and examined with a Zeiss EM912 electron microscope operating at 100 kV. Photographs were taken with a Gatan Bioscan 792 camera. The size of the MTB and of their magnetosomes was measured using the GIMP 2.8 software (http://www.gimp.org/). Length and width averages were made on all of the MTB morphotypes observed by transmission electron microscopy. Thirty crystals were measured to compute a mean magnetosome length.

Physico-chemical Measurements in the Sediments

For the geochemical analysis, the top 5-cm depth sediments were sieved through 2 mm, 500 and 250 µm meshes, washed with freshwater, and dried overnight at 30 °C. The fractions were weighed and examined through a magnifying glass binocular microscope. All the measurements were performed to the top of the OATZ (Suppl data 2). Oxygen concentration, pH, and temperature were measured in situ using the SevenGo (Duo) pro™/OptiOx™ meters according to the manufacturer's instructions (*METTLER-TOLEDO*, Switzerland). For oxygen measurement, signal was in air saturation percentage, twenty-one percent oxygen (air composition) representing 100 % of the saturation scale and corresponding to 9 mg/L [O_2]. The total salinity was measured using a hand refractometer (ATAGO, Japan). Redox potential was determined using a *METTLER TOLEDO* probe (*InPro® 3253 SG*) calibrated with a buffer solution (*METTLER TOLEDO*, 427 mV at 25 °C). Values are given in mV versus reference electrode H^+/H_2. Solubilized sulfide compounds (HS^-/S^{2-}) concentrations were measured using the turbidimetric Cord-Ruwisch assay [2].

A scaled-up version of the ferrozine assay was used to determine Fe(II) and Fe(III) concentrations, as previously described [20]. Nitrate and sulfate concentrations were determined using the ionic chromatograph Metrohm 761 Compact IC and the MetrosepA Supp 1 column. The values in the text are the mean of three independent measures.

DGGE Analysis

DNAs of magnetically purified cells from eight bottles were obtained by boiling the cells in 200 µL water at 100 °C for 15 min and then centrifuged. Primers used for 16S rRNA gene amplification were 341F-GC (5′-CC TAC GGG AGG CAG CAG-3′) to which a 40 bp GC-clamp was added at the 5′ end and 907R (5′-CCG TCA ATT CMT TTG AGT TT-3′) [17]. The 50 µL PCR reaction mix contained 10 µL Taq-& LOAD^{TM} Mastermix 5xC (MP Biomedicals Europe), 0.5 µL of each primer at 25 µM, 37 µL of sterile water, and 2 µL of extracted DNA as template. PCR reactions were performed in the T100^{TM} Thermal Cycler (BIO-RAD). The cycling conditions were 5 min at 94 °C for initial denaturation; 35 cycles of 1 min at 94 °C, 1 min at 55 °C, and 1 min at 72 °C; and a final extension of 5 min at 72 °C.

Denaturing gradient gel electrophoresis (DGGE) was performed using the DCode System (BioRad), using 40 µL of each PCR product, as described previously [17]. PCR fragments were separated in a 1-mm thick polyacrylamide gel (6 %, w/v) with a 30–70 % denaturant gradient and 1X TAE electrophoresis buffer at 60 °C. After 5 h electrophoresis at a constant voltage of 200 V, the gel was stained with a 1X SYBR Gold solution (Invitrogen) during 15 min. DNA bands were excised and eluted in 50 µL water overnight at 4 °C. About 2 µL of eluates were amplified with 341F and 907R primers, and PCR products were subsequently sequenced by the GATC Biotech Company (Constance, Germany). Nucleotide sequences were deposited in the GenBank/EMBL/DDBJ databases under the accession numbers KF207829 to KF207840.

Phylogenetic Analysis

The partial 16S rRNA gene sequences were compared to the Genbank databases using the BLASTN algorithm. They were then aligned with their closest relatives retrieved from Genbank database using the MUSCLE program [3]. A phylogenetic tree was subsequently constructed using the Neighbor-Joining algorithm and Jukes and Cantor correction, with the MEGA program [3]. The robustness of tree topologies was verified by 500 bootstrap samplings.

Results

Physico-chemical Characteristics and Investigation of MTB at Sampling Site

Sediment from Six-Fours-les-Plages is a poorly sorted, medium-grained sand (Suppl data 2). Angular grains suggest a hydrodynamically quiet environment, as expected for a lagoon area. Grain size varied from 250 µm to more than 2 mm, thus belonging to the arenites granulometric class. It was composed in majority of grains of quartz, feldspar, biotite, mica-schist, shells, fragment of gastropods (Turritellidae), and spicules of sea urchins. The pH was 7.6, and the temperature was 12 °C at 5-cm depth sediments. The total salinity was at 39 (±1) g L^{-1}, dissolved oxygen concentration at 10 (±1) % atm, redox potential at 325 (±30) mV, and no sulfide was detected. The absence of sulfide corresponded with the positive redox potential and the presence of oxygen. Nitrate concentration was 2.5 (±0.2) mM and sulfate was 30 (±3.0) mM, which is consistent with concentrations frequently found in marine environments. The Fe(III) concentration was 0.40 (±0.05) mmol L^{-1}, and Fe(II) has not been detected, which corresponded with redox and pH measurements.

Community structure of MTB was investigated by optical microscopy after magnetic collection. MTB were found to be present at 10^5–10^6 per mL. As reported in other studies, the collected MTB displayed cocci as the major cell morphology (Suppl data 3). Multicellular magnetotactic prokaryotes (MMPs) displayed a pineapple-like form, with a diameter of 7.9 ± 0.6 µm, as revealed by light microscopy analysis. Their density was estimated to 10–100 per mL. Their morphology was similar to that from the Yellow Sea [30]. Several other forms of MTB were observed in minority, such as vibrios, spirilla, rods, and mulberry-like multicellular forms (diameter of 5.1 ± 0.6 µm).

Morphological Characterization of MTB and their Magnetosomes

Based on the form and the size of the cells, the number of magnetosomes chains, and the crystal type, at least 10 morphotypes were observed by transmission electron microscopy (Fig. 1). As expected from the light microscope observations, the majority of MTB from Six-Fours-les-Plages were cocci (>95 % of the MTB population). The majority was 1.4 × 1.2 (±0.2) µm in size (Fig. 1a); others were 2.1 (±0.2) µm in diameter (Fig. 1b); and a third group was 2.7 × 2.4 (± 0.2) µm in size (Fig. 1c, d). Moreover, we observed at least 2 rods (Fig. 1e, f); two vibrios (Fig. 1g, h); and two spirilla morphotypes (Fig. 1i, j).

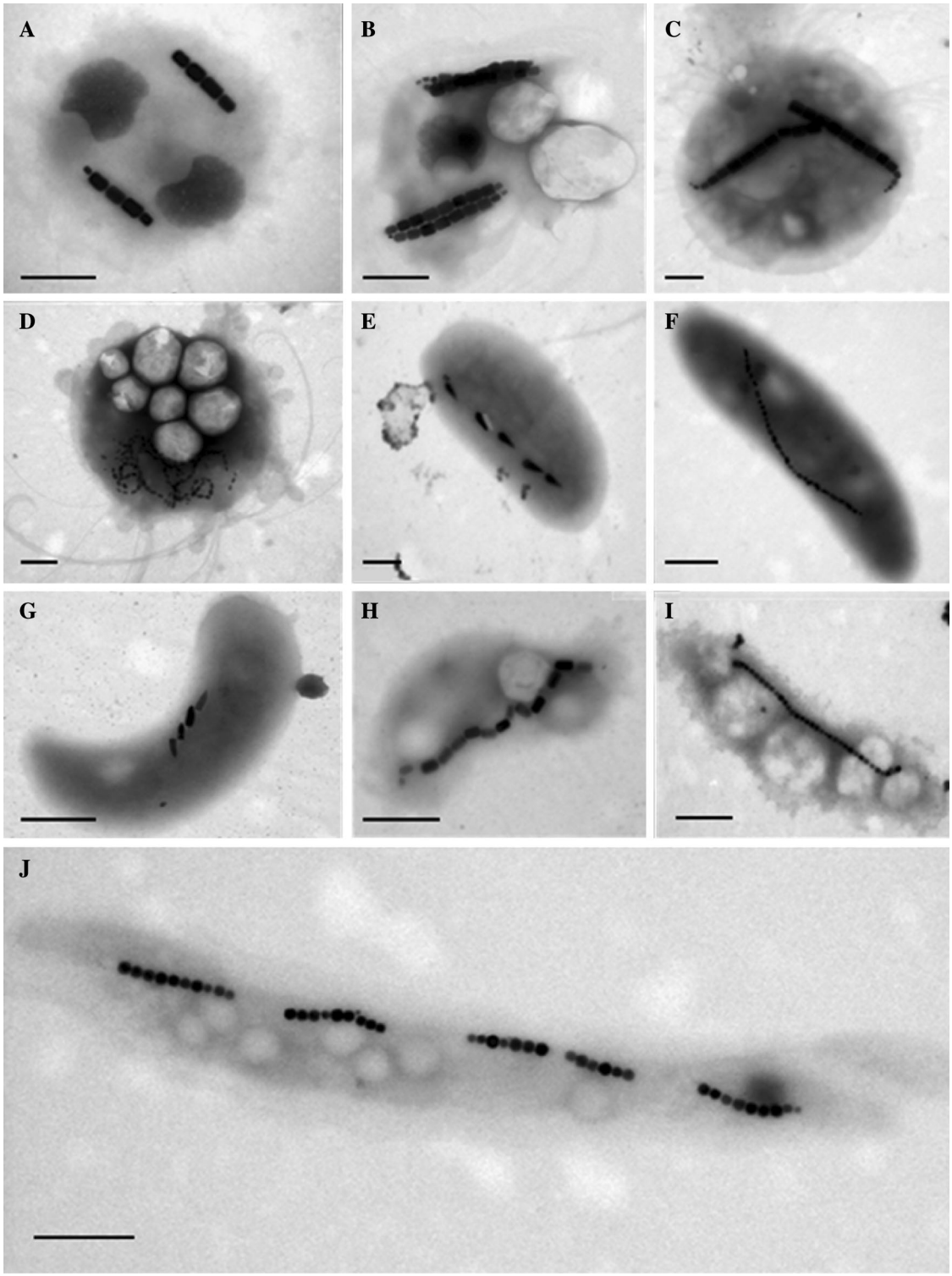

Fig. 1 Characteristics of diverse MTB collected from the Six-Fours-les-Plages lagoon determined by electron micrographs. *Scale bars* 0.5 μm

Most magnetosomes were aligned in one or two straight linear chains, but four or more chains with circular or curved distributions or unorganized crystals were also observed (Fig. 2). Crystal shapes included all the forms previously described in MTB, such as bullet- (Fig. 2a, 102 (±14) nm in length) or tooth-shaped (Fig. 2b, 146 (±15) nm in length), prismatic (Fig. 2c, 81 (±9) nm in size), rectangular (Fig. 2d, 81 (±9) nm in length), and cubo-

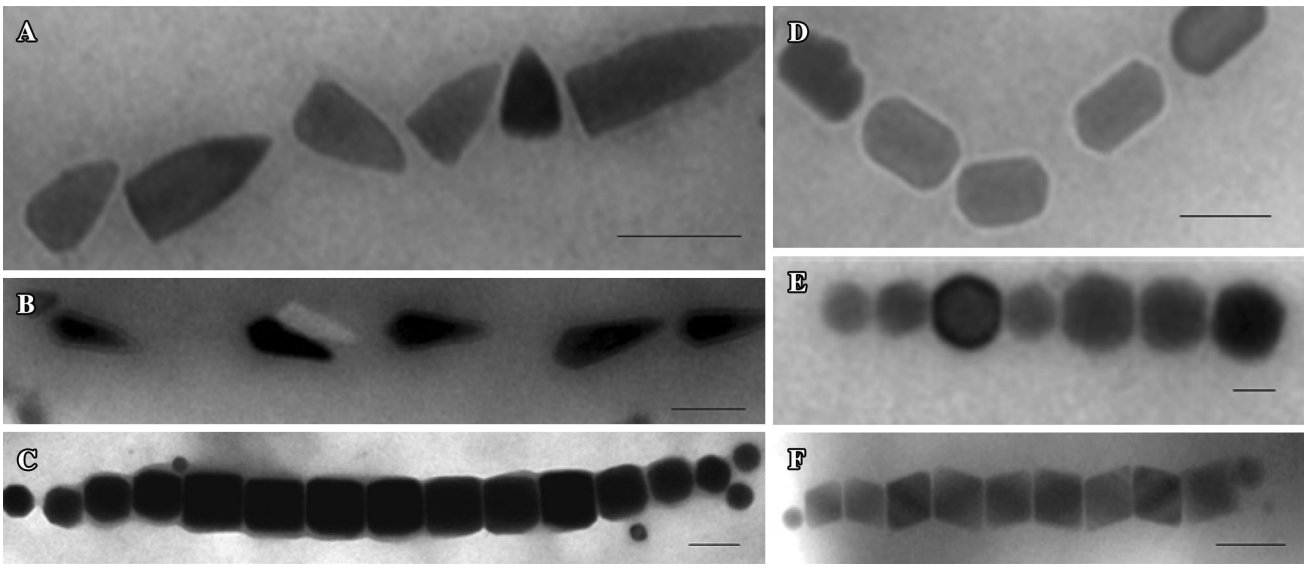

Fig. 2 Diverse crystal morphologies of magnetosomes in different MTB determined by electron micrographs. **a**, **b** Bullet- or tooth-shaped, **c** prismatic, **d** rectangular, **e** cubo-octahedral, **f** octahedral. *Scale bars* 100 nm

octahedral (Fig. 2e, 52 (±6) nm in size). In addition, a less frequently found {111} octahedral crystal structure was observed, organized in one magnetosomes chain (Fig. 2f, 114 (±8) nm in size).

DGGE and Phylogenetic Analysis

16S rRNA gene sequences amplified from DNA extracted from magnetically purified MTB were assessed by DGGE. In order to compare the MTB of Six-Fours-les-Plages to that previously obtained from other areas in the world, a phylogenetic tree was constructed, with the 16S rRNA gene sequences of 12 major bands and the closest publicly available sequences (Fig. 3). The phylogenetic tree showed that the sequences obtained in this study presented a wide distribution among the order Magnetococcales (class Alphaproteobacteria). The most closely related MTB sequences originate from diverse areas in the world (China, Brazil, USA, Germany, and France).

The closest cultivated strains are the two marine magnetotactic cocci today available, *Magnetococcus marinus* MC-1 isolated from Pettaquamscutt Estuary, Rhode Island, USA [15], and MO-1, isolated from the bay of Marseille, France [6]. However, all the sequences obtained in this study presented ≤97 % sequence identity to the sequences of these two strains. Moreover, 11 of 12 sequences obtained in this study presented ≤97 % sequence identity with the all Genbank database sequences. Thus, they might correspond to new species and genera. Only MF48 presented 99 % identity with the sequence of the clone XSE-4 of the Huiquan bay, Qingdao, China [19]. MF38, MF70, MF78, and MF98 clustered with MTB sequences of diverse origins (Itaipu lagoon in Brazil, Huiquan and Jiaozhou bays in China, and Wadden Sea in Germany). On the other hand, MF99 and MF114 clustered with sequences of the Fos^{s}/Mer area, Mediterranean Sea, France (Fig. 3). This cluster containing specifically sequences from the Mediterranean Sea was designated as "Med group".

Discussion

In this study, we investigated the MTB diversity of a pristine Mediterranean area to improve the understanding of the MTB communities. Our work highlights the most important diversity of MTB until now observed in the Mediterranean Sea, particularly within the recently characterized Magnetococcales order, among Alphaproteobacteria. The MTB observed were cocci in majority, as reported in other studies world wide [11]. However, the site of Six-Fours-les-Plages is remarkable regarding the diversity of the morphotypes and crystal forms of MTB. Some MTB were morphologically or phylogenetically close to MTB described from distant areas, such as the coccus morphotype of the Fig. 1a, which has been described in the Miyun Lake and the Huiquan bay in China [9, 19], and in the Itaipu lagoon in Brazil [22]. The morphotype of Fig. 1c has been described in China [9, 19], in the North Sea in Germany [5], and in the oil-industry polluted area of Fos^{s}/Mer, Mediterranean Sea, France [20]. Moreover, an infrequent {111} octahedral crystal structure has been observed (Fig. 2f), previously reported in a Brazilian freshwater sample [1].

In addition, a new "Med group" cluster has been designated for 16S rRNA gene sequences specifically found in

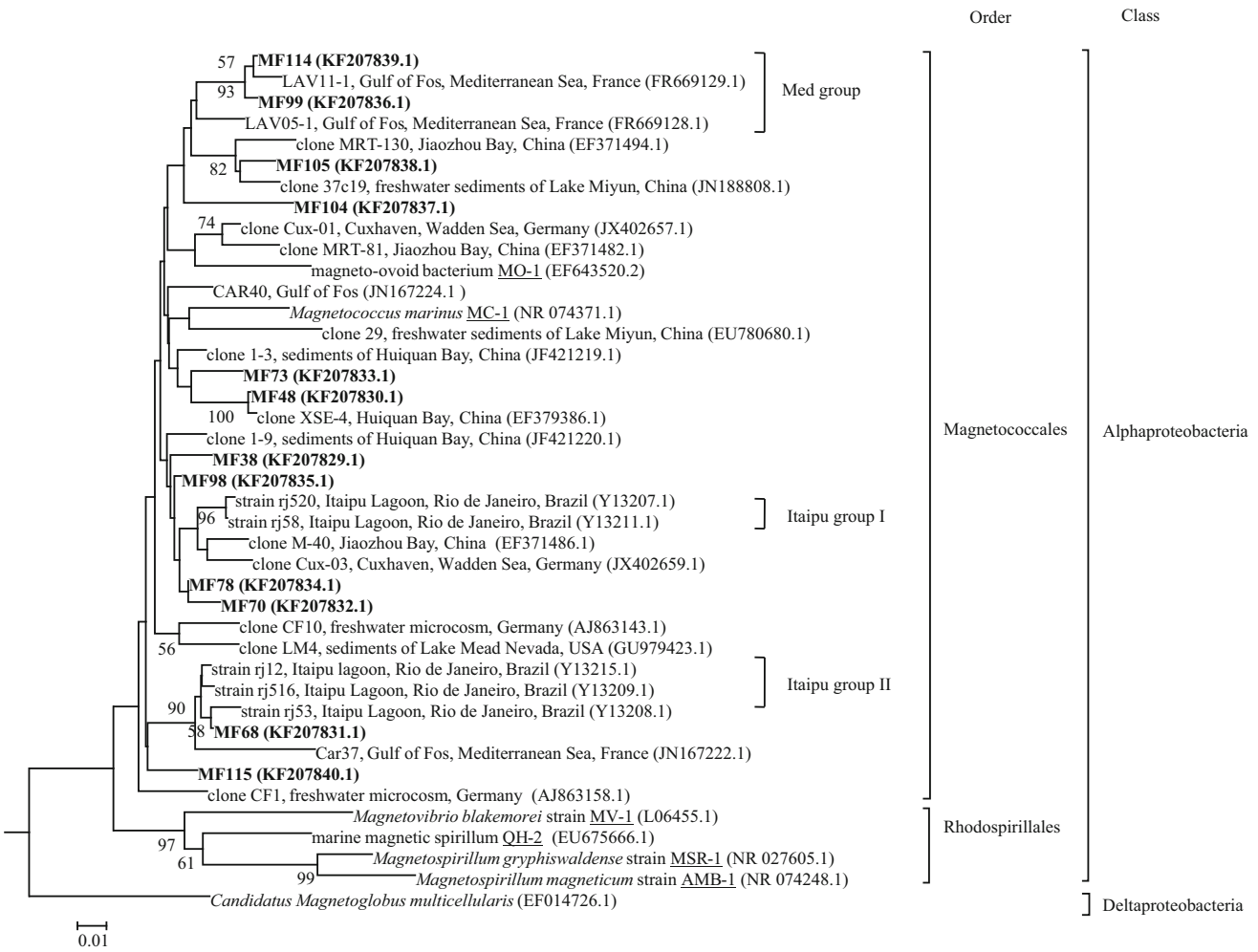

Fig. 3 Phylogenetic tree showing the relationships between the MTB of Six-Fours-les-Plages and related MTB. The tree was generated using the Neighbor-Joining method, and bootstrap values were calculated using 500 replicates. MTB sequences from this study are shown in *bold*. *Underlined* sequences correspond to cultivated MTB strains. Genbank accession numbers are indicated in *parentheses*. *Scale bar* 0.01 substitution per nucleotide position

the Mediterranean Sea, related to *Magnetococcus* sp. environmental sequences. Other sequences closely related to those of magnetotactic cocci identified in the Yellow Sea in China (99 % identity between MF48 and clone XSE-4) supports the hypothesis that magnetotactic cocci belonging to a same species could present a wide geographic distribution [27]. On the other hand, this work highlights the evidence of singular species in the Six-Fours-les-Plages pristine area (at least 11 sequences which presented $\leq$97 % sequence identity with the Genbank database sequence). These data increase the view of Magnetococcales as a major and diversified order of magnetotactic bacteria in marine environments.

MF114 was the sequence which is most closely related to those obtained from the Mediterranean polluted area of Fos ^{s}/Mer, with 97 % identity with the Lav05-1 sequence. The Fos ^{s}/Mer area is exposed to intensive oil industrial activities and is located at 100-km to the West of Six-Fours-les-Plages. The study performed in Fos ^{s}/Mer has revealed a more restricted and distinct MTB community by comparison to the present study [20]. Among the physico-chemical parameters investigated, differences between the two areas occurred mainly at the iron and hydrocarbons concentration levels. The Fos ^{s}/Mer area displayed an iron concentration around 50 times higher than in Six-Fours-les-Plages (39.5 vs 0.4 mM), and the presence of hydrocarbons was detected at the Fos s/Mer area (up to 260 mg kg^{-1}) but was not detected at Six-Fours-les-Plages. No clear differences were established between the two areas regarding salinity, redox potential, oxygen, H_2S, sulfate, nitrate, and type of sediment.

Overall, the role of pollutants (i.e. hydrocarbons and metals) rather than geographic distance and natural environmental backgrounds may influence more drastically

MTB distribution. Further studies on new industrial impacted and more preserved sites, and analyses of environmental parameters such as hydrocarbons, metals, and organic matter contents will be necessary to determine which particular conditions determine the phylogenetic discrepancy of the MTB communities. The comparison of the data obtained during this work with those of future world-wide ecological studies will allow deepening the bio-geographical knowledge of the MTB.

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