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Review

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The many faces of *Raoultella* spp.

Różne oblicza *Raoultella* spp.

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Summary

Raoultella genus consists of Gram-negative, aerobic, encapsulated and non-motile rods. The name of the genus derives from the name of the French bacteriologist Raoul. Currently, four species belong to the genus: *R. planticola, R. ornithinolytica, R. terrigena* and *R. electrica.* The standard biochemical test used to identify *Raoultella* genus should be supplemented with additional tests, because of the close relationship between the genera *Raoultella* and *Klebsiella*. In 2001 *Klebsiella planticola, K. ornithinolytica* and *K. terrigena* were re-classified to new genus *Raoultella*. Re-classification was based on 16S rRNA sequence and *rpo*B, *gyr*A and *gyr*B genes. An alternative to phenotypic identification may be mass spectrometry or genetic methods (16s rRNA). These bacteria are commonly associated with natural environments (plants, water, soil). *Raoultella* spp. rods are not a highly virulent pathogen. Their virulence factors include polysaccharide capsule, fimbriae, siderophores, toxins and ability to form a biofilm. It has been shown that *Raoultella* spp. may colonize the gastrointestinal and upper respiratory tract in humans and cause cholangitis and lung infections. The literature also includes works on the antimicrobial activity of *Raoultella* rods and the possibility of using them in the environment protection. This review summarizes the current knowledge of *Raoultella* species identification, virulence and the possibility of using them in the protection of the environment.

Keywords: **identification • *Raoultella* genus • taxonomy • virulence**

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INTRODUCTION

Raoultella spp. are Gram-negative, encapsulated, short rods of the *Enterobacteriaceae* family. *Raoultella* spp. belongs to non-motile and non-spore forming bacteria, primarily isolated from the natural environment [14, 23, 31, 44]. They are catalase-positive and oxidase-negative. All *Raoultella* spp. strains ferment glucose and lactose. Most strains ferment glucose forming acid and gas. The main product of glucose fermentation is 2,3-butanodiol. Those bacteria, like other *Enterobacteriaceae,* reduce nitrates to nitrites. *Raoultella* spp. are facultative anaerobes capable of growing at the temperature range from 4°C to 40°C. They have low nutritional requirements and can grow on simple media. Most *Raoultella* spp. strains grow on solid media in the form of mucous colonies, which is related to the forming of polysaccharide capsules [44] (Fig. 1).

Since the time of their discovery, *Raoultella* spp. have been regarded as an environmental infection-causing bacteria, which has rarely been isolated from patients. Although they do not belong to well-recognized human pathogens, *Raoultella* spp. receive much attention from microbiologists because they increasingly more often cause bacteremia, cholangitis and pneumonia [49]. The best-described species is *R. planticola*, which is also most frequently isolated from infections in humans. The growing interest in *Raoultella* is not only connected with the increasing frequency of isolation from clinical specimens, but also from the introduction of new diagnostic methods that enable reliable identification of those bacteria with respect to genus and species. Reports published concern the biology of these bacteria, their occurrence in water, food and their potential use in environmental protection.

HISTORY, CLASSIFICATION AND IDENTIFICATION OF *RAOULTELLA*

The history of *Raoultella* genus is very complex. In 1977, Gavini et al. [19] suggested that *Klebsiella* strains isolated from the natural environment belonging to J, K, L and M groups should be described with the common name "*Klebsiella*-like organisms". In the 1980s, the species names *K. planticola* [3], *K. terrigena* [22] and *K. ornithinolytica* [48] were introduced for these bacteria. In 1983, Ferragut et al. [14] discovered the fourth species – *K. trevisanii.* Three years later, Freney et al. [18] included the latter into the species – *K. planticola*, based on homology to the species *K. planticola* and *K. trevisanii.* In 2014 Kimura et al. [25] published an article about a new species *R. electrica*.

In 2001, Drancourt et al. [12] re-classified *Klebsiella* species isolated from the natural environment to a new genus *Raoultella*. Re-classification was based on 16S rRNA sequence and *rpo*B, *gyr*A and *gyr*B genes.

Biochemical identification remains the most frequently used method for bacteria identification in many microbiological laboratories. Because of the close relationship between the genera *Raoultella* and *Klebsiella,* biochemical tests normally used in microbiological laboratories often do not allow them to be distinguished. Therefore, differentiation of those genera is largely based on biochemical reactions unavailable in commercial diagnostic tests. *Raoultella* spp. use histamine and 3-DL-beta-hydroxybutyric acid as the only source of carbon in the medium, whereas *Klebsiella* spp. use ethanolamine. The use of 3-DL-beta-hydroxybutyric acid as the only source of carbon is also characteristic of *K. pneumoniae* and *K. rhinoscleromatis* strains. Studies of various authors [21, 30, 56] confirm that additional biochemical reactions,

Fig. 1. *R. ornithinolytica* culture on MacConkey Agar

i.e. the use of histamine, ethanolamine and 3-DL-beta-hydroxybutyric acid as the only source of carbon in the medium, enables identification of *Raoultella* rods at genus, and sometimes at species level. *Raoultella* spp. strains can grow at 10°C, similarly to *K. oxytoca* strains. Unlike rods from *Klebsiella* genus, *Raoultella* grow at 4°C and do not produce gas from lactose at the temperature of 44.5°C [13, 56]. The differentiation of *Raoultella* spp. is based mostly on the use of D-melezitose as the only source of carbon in the medium by *R. terrigena* strains, the ability to grow at 42°C for *R. planticola* and *R. ornithinolytica* and production of ornithine decarboxylase by the strains of *R. ornithinolytica*. As shown in Table 1, the three species within the genus may be distinguished based on their characteristic biochemical profiles.

Identifying *Raoultella* rods concerning both genus and species is very difficult. Liu et al. [29] claim that strains earlier identified as *K. oxytoca* may belong to the species *R. planticola*. This was based on a PCR analysis of beta-lactamases genes and beta-lactamases isoelectric points values.

Genetic methods, based on the analysis of 16S rRNA, *rpo*B gene or *hdc* gene may be an alternative to the biochemical identification of *Raoultella* spp. [12, 20, 37, 45, 55], as well as mass spectrometry [10, 33, 45, 46], analysing the unique protein profile of the bacteria, referred as a molecular "fingerprint". Risch et al. [46] identified *Raoultella* by mass spectrometry and confirmed identification by 16SrRNA sequencing. Ponce-Alonso et al. [45] correctly identified 11 *Raoultella* species by MALDI-TOF (score 2.35-2.50) and *rpo*B sequencing, whereas 16S rRNA provided inconclusive results. The authors in the MALDI-TOF MS method obtained identification score ≥ 2.35 for all *R. ornithinolytica* and *R. planticola* strains. In turn, de Alegria Puig et al. [9] identified 97 *Raoultella* strains by mass spectrometry: Vitek MS and Bruker Bio-

Table 1. Biochemical profiles of *Raoultella* species

Biochemical profile	*R. planticola*	*R. ornithinolytica*	*R. terrigena*
Voges-Proskauer test	+	+	+
Lysine decarboxylase	+	+	+
Histidine decarboxylase	V	+	–
Phenylalanine deaminase	–	–	–
β-galactosidase	+	+	+
b-glucosidase	+	+	+
5-Keto-D-gluconate	+	+	+
Indole production	V	+	–
Citrate utilization	+	+	+
Malonate utilization	+	+	+
Fermentation of D-glucose at 44.5°C	–	–	–
Fermentation of D-turanose	V	V	V
Fermentation of β-gentiobiose	+	V	+
Fermentation of L-sorbose	+	+	V
Fermentation of L-rhamnose	+	+	+
Fermentation of L-fucose	+	+	+
Lipase (corn oil) activity	–	–	–
Gelatin hydrolysis (22°C)	–	–	–
Gas formation from lactose at 44.5°C	–	–	–
Utilization of hydroxy-L-proline	+	+	V
Growth in KCN presence	+	+	+
H_2S production	–	–	–
Urea hydrolysis	+	+	–
Pectate degradation	–	–	–
Methyl red test	V	+	+
Utilization of m-hydroxybenzoate	–	–	+

Characteristics were compiled from several references [3, 13, 30, 44, 48] V – Variable reaction result.

typer. The authors obtained sensitivity 98.9 and 57.9%, and specificity 98.9 and 37.0%, respectively. Earlier studies confirm the effectiveness of the MALDI TOF method in the identification of *Raoultella* in terms of the genus and species [10, 46, 49]. In turn, Ponce-Alonso et al. [45] suggested sequencing specific genes: bla_{ORN} in *R. ornithinolytica* strains and bla_{PLA} in *R. planticola* strains as reference method for identification of *Raoultella* strains. The authors detected bla_{ORN} gene in all of analyzed *R. ornithinolytica* strains and bla_{PLA} gene in *R. planticola* strains.

VIRULENCE FACTORS OF *RAOULTELLA* SPP.

Raoultella genus is not a highly virulent pathogen. The virulence factors of these bacteria are similar to *Klebsiella* rods (Table 2). Like other Gram-negative bacteria, *Raoultella* have a lipopolysaccharide (LPS) localized in the outer membrane. LPS is responsible for the biological activity of endotoxins, which are of key importance in the systemic infections [44]. LPS consists of three parts: the somatic antigen (O-antigen), the core and lipid A. O antigen are built out of repeating saccharide chains. This is the most immunogenic factor, determining the O serotype of the bacteria [44]. Leone et al. [27] detected a characteristic linear tetrasaccharide containing cyclic aceto-pyruvic acid in *R. terrigena*. Pillon et al. [39], analysing the composition of exopolysaccharide in *R. terrigena,* detected a pentasaccharide composed of repeating subunits of galactose, glucose, mannose and glucuronic acid in a ratio of 1:2:1:1.

Like in the case of *Klebsiella* spp., the polysaccharide capsule is the essential virulence factor of bacteria from *Raoultella* genus. It protects the bacteria from phagocytosis [41]. *Raoultella* spp. typing based on capsular antigen was conducted by Podschun et al. [41, 42]. They detected this antigen in 96% strains of *R. planticola*. According to the cited authors, the most often identified antigens were: K14 (13.0%), K2 (9.0%) and K70 (9.0%). Antigen K70 it is common for *R. planticola* species. No work was found in the currently available literature where the authors would detect this (K70) serotype in strains of the genus *Klebsiella*. Strains with antigen K2 is regarded as more virulent than strains with the other serotypes [43]. The study of Podschun et al. [43] concerning *R. planticola* strains isolated from water indicate that highly virulent strains of K2 serotype can also be isolated from the natural environment.

The ability to form biofilm is also likely to be of vital importance in the infections caused by *Raoultella* spp. [35]. Participation in forming multispecies biofilm was confirmed for strains of *R. planticola* and *R. terrigena*. It was proven that these bacteria could produce large amounts of an exopolysaccharide, essential for the bacteria survival in the biofilm structure [35]. The biofilm is formed by adjoining cells of the microorganism surrounded by the extracellular matrix. One of the stages of biofilm production is the adhesion, which involves fimbriae. Podschun et al. [43] list fimbriae as one of the virulent factors. These are structures responsible for the adhesion of bacterial cells to the host cells. They allow adhesion, which facilitates the colonization of the host mucous membranes, often enabling the development of the infection. According to Podschun et al. [41], mannose-sensitive type 1 fimbriae occur in 83.0% of *R. planticola* strains, mannose-resistant type 3 in 69.0%, and 4.3% of the strains do not have fimbriae. Type 1 and 3 fimbriae are crucial for adhesion to the epithelial cells of the urinary, respiratory and digestive tracts.

Bacterial ability to survive in the host tissues is limited not only by the host defensive mechanisms but also by the limited availability of iron, which is necessary for bacterial growth. The ability to form siderophores, structures which enable bacteria to take up iron, necessary for life processes, was detected in strains of *R. planticola*. *R. planticola* can produce two types of siderophores: enterobactin (100% strains) or aerobactin (only 2.2% of strains) [43]. The ability to produce siderophores was also confirmed for 81.8% strains of *R. ornithinolytica* [2].

Many of the Gram-negative bacteria strains are sensitive to the bactericidal effect of human serum, whereas pathogenic strains often exhibit serum resistance properties [36]. Podschun et al. [42] also reported the resist-

Table 2. Virulence factors of *Raoultella* species

Virulence factor	Species
LPS, O-antigen	*R. planticola, R. terrigena, R. ornithinolytica*
Serum resistance	*R. planticola, R. terrigena*
Polisaccharide capsule, K antigen	*R. planticola*
Adhesins (type 1 fimbriae, type 3 fimbriae)	*R. planticola, R. terrigena*
Siderophores (enterobactin, aerobactin)	*R. planticola, R. terrigena, R. ornithinolytica*
Ability to form biofilm	*R. planticola, R. terrigena*
Toxins, tetrodotoxin	*R. terrigena*
Bacteriocins, raoultellin L	*R. terrigena, R. ornithinolytica*

Virulence factors were compiled from several references [2, 13, 27, 30, 35, 43, 44].

ance of *R. planticola* strains to the bactericidal effect of serum. They indicated that there is a relationship between the strain isolate and this property. Interestingly, this property seems to be more expressed in clinical strains than in those isolated from the natural environment. Of the 92 clinical strains, 30.4% were resistant to serum, whereas, among the strains cultured from water, only less than 4% showed this trait [43].

Little is known about toxins synthesized by *Raoultella*. Yu et al. [59] described the ability to produce tetrodotoxin by *R. terrigena* strains. Poisoning appeared after consumption of the pufferfish. This toxin is one of the most fatal neurotoxins. Bacteria producing tetrodotoxin were isolated from different marine organisms, mostly from fish *Takifugu* and *Fugu*. Tetrodotoxin can be accumulated in different organs of the fish, mostly in the skin, intestine, liver and ovaries. The ability to synthesize this toxin was also confirmed in other bacteria, e.g., *Pseudomonas*, *Vibrio*, *Aeromonas, Shewanella, Bacillus, Lysinibacillus* genera [59].

Fish poisoning with scombrotoxin is the main cause of seafood poisoning. Studies by Bjornsdottir-Butler et al. [5, 6] assessed the number of histamine-producing bacteria in fish. One of the most common species of histamine-producing bacteria are *R. planticola* [5] and *R. ornithinolytica* [26]. Histamine-producing bacteria ussually have bla_{HDC} gene. Sabry et al. [47] reported that hdc-positive strains exhibit higher levels of histamine that hdc-negative.

Besides toxins, bacteriocins are of importance in bacterial pathogenicity of *Raoultella* spp. Fleming et al. [17] isolated from a strain of *R. terrigena* a substance with antimicrobial activity, which inhibited the growth of the following strains isolated from food samples *E. coli*, *Klebsiella* spp., *Enterobacter* spp. and *Salmonella* spp. The obtained bacteriocin was called raoultellin L, and it was proposed to be used as a biological weapon against food contaminating microorganisms. The ability to produce bacteriocins was also detected in *R. ornithinolytica* strains isolated from clinical specimens [44].

Additionally, Yu et al. [59] suggested that one of the essential virulence factors in *Raoultella* may be located at a pathogenicity island, similar to the reported in *Yersinia* spp. strains.

Further studies on *Raoultella* spp. morphology and biological properties are needed. Broadening the knowledge of and studying *Raoultella* spp. may help us to understand the pathomechanism of the infections they couse.

USE OF *RAOULTELLA* SPP. IN ENVIRONMENTAL PROTECTION

Taking into account the common occurrence of *Raoultella* strains in the natural environment, attention was paid to the possibility of using them for environment protection [7, 8, 34]. Sugimori et al. [53] used *R. planticola* 232-2 strain to decompose various fatty compounds, e.g. vegetable oil, beef tallow, oleic acid, lard. They proved that the degree of this degradation depends on the experimental conditions. The highest effectiveness was obtained at 35°C and pH 4.0. Further research needs to confirm whether the properties of *Raoultella* strains in the degradation of wastes derived from restaurants or sewage can be used in the future. Lipolytic activity of *R. planticola* and *R. ornithinolytica* strains was also confirmed by results from studies by Peil et al. [38]. They suggest the potential usefulness of these strains in different industry branches for biodegradation of lipidscontaining compounds.

Bidja-Abena et al. [4] isolated the *R. ornithinolyitca* PS strain, which decomposed to 83.5% of crude oil. This strain was more effective than *Bacillus subtilis* BJ11 (81.1%), *Acinetobacter lwoffii* BJ10 (75.8%), *A. pittii* BJ6 (74.9%) and *Serratia marcescens* PL (70.0%). All five strains degraded over 94% of crude oil after 10 days of incubation. In addition, these strains degraded straight alkanes, branched alkanes and aromatic hydrocarbons. The authors suggested the large potential of these strains in the remediation of an environment contaminated with crude oil.

The study by Alegbeleye et al. [1] showed that *R. ornithinolytica* degraded acenaphthene and fluorine (polycyclic aromatic hydrocarbon compounds). Among polycyclic aromatic hydrocarbon degrading bacteria *R. ornithinolytica* degraded fluorene most efficiently (99.90%). In turn, degradation of acenaphthene was 97.5% and *R. ornithinolytica* was the second species, after *Aeromonas hydrophila* in term of degradation efficiency. Alegbeleye et al. [1] suggested that *R. ornithinolytica* can be used on a larger scale to restore polluted aquatic ecosystems.

De Lima Brossi et al. [11] described the enzymatic activity of *R. terrigena* strains. The studied strains have strong cellulolytic and xylanolytic activity, crucial for biopolymers degradation. In turn, Muňoz et al. [32] also investigated the ability of different strains to decompose paper. The authors have shown that *R. ornithinolytica* promotes cell wall degradation of microalgae through cellulolytic action at low temperatures, resulting in increased biogas production. Kim et al. [24] described *R. ornithinolytica* B6 strain that was able to use lignocellulose biomass for the production of 2,3-butanediol. *R. ornithinolytica* strains appeared to be the most effective in this field, which suggests the potential usefulness of these bacteria for paper decomposition.

The natural environment is contaminated by different toxic substances. In literature, there are available works about the degradation of trinitrotoluene by *Raoultella* spp. strains. The study by Thijs et al. [54] showed that *R. ornithinolytica* strain release nitrite from trinitrotoluene. The nitrite then can be used by plants for their growth. The analysed strain was isolated from forest soil at a military site in Belgium. In turn, Claus et al. [8] used the strain of *R. terrigena* for removing 2,4,6-trinitrotoluene from polluted environments, such as water.

2,4,6-trinitrotoluene is used for explosive material production. Its residues are toxic and mutagenic for the natural environment. The use of bacterial strains, e.g. *R. terrigena,* for degrading noxious substances may be useful in the protection of the natural environment [8, 34].

In turn, Skłodowska et al. [52] isolated the *Raoutella* strain, which reduced iron and precipitated uranium in sediments of the closed down uranium mine in Kowary (Poland). This strain was capable of dissimilatory reduction of iron (III) and uranium (VI) in the presence of citrate as an electron donor. The authors suggest that this may be useful in the bioremediation of uranium contaminated waters and sediments. The possibility of using *Raoultella* for disintegrating or mineralizing pollutants into less harmful or non-toxic compounds was also investigated by other authors [39, 58]. Ping et al. [40] described the high potential of *R. planticola* strain for bioremediation of the soil contaminated with aromatic polycyclic hydrocarbons.

Shin et al. [51] and Kim et al. [24] described the potential advantages of 2,3-butanediol production using *R. ornithinolytica* strains. The important characteristic of this strain is the possibility of using different saccharides as the only carbon source (glucose, fructose, galactose, galactose and xylose). 2,3-butanediol is an important substance for pesticides and drugs production. However, from the economic point of views, the common usage of these properties of bacterial strains in the massive scale industry is not possible.

Xu et al. [57] reported *Raoultella* spp. strain cadmium resistant. Cadmium is of the most concern in soils due to its high toxicity. The authors suggested that *Raoultella* spp. X13 strain is an effective treatment for potential application in cadmium remediation.

PRODUCTION OF ANTIMICROBIALS BY *RAOULTELLA* SPP.

The literature also includes works on the antimicrobial activity of *Raoultella* rods. Fiołka et al. [16] isolated from the *Dendrobena veneta* earthworm gut the *R. ornithinolytica* strain with antimicrobial activity against four species of fast-growing mycobacteria: *Mycobacterium butiricum*, *M. jucho*, *M. smegmatis* and *M. phlei*. Further research confirmed that the protein with a molecular mass above 100kDa is responsible for the anti-bacilli activity.

Also, Fiołka et al. [15] isolated the polysaccharide-protein complex, which is a metabolite of *R. ornithinolytica* with activity against *Candida albicans* fungi from the *Dendrobena veneta* earthworm gut. These authors noticed that the action of the complex disturbed metabolic activity and damaged the fungal cell wall. Researchers suggest the potential use of the complex as a fungicide component. These authors also observed the induction of tumour cell death by apoptosis and necrosis in the presence of the above complex. However, it was cytotoxic to human fibroblasts. Hence, there is a need for further research on its possible use in anti-cancer therapy.

Li et al. [28] discovered the nematicidal activity of *R. terrigena* against *Meliodogyne incognito*. It is a parasite of crops. Studies have confirmed that treating the cultivated plants with only *R. terrigena* suspension, and in combination with fresh wasabi extract, effectively combats *Meliodogyne incognito* on tomatoes.

In recent years, more studies have been published describing the virulence factors, diagnostics, biological properties and the possibility of using *Raoultella* strains in environmental protection, but some questions remain unanswered. Further studies will allow us to broaden the knowledge of *Raoultella* spp., explaining their virulence potential.

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