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Exploring the Multifaceted Genus Acinetobacter: The Facts, the Concerns and the Opportunities

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Remiero

Exploring the Multifaceted Genus *Acinetobacter*: The Facts, the Concerns and the Opportunities

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Abstract: In recent years, the research community has been interested in members of the *Acinetobacter* genus mainly because of their role as causative agents of nosocomial infections. However, this rich-in-species genus has been proven to play a significant role in different biotechnological processes, such as bioremediation and fermented foods production. To partially fill the lack of information on *Acinetobacter's* dualistic nature, in this review, based on literature data, we attempt to summarize the available information on the different roles the members of the genus play by considering their genetic constitution and metabolic properties. We found pieces of evidence of genetic divergence between the pathogenic and non-pathogenic species and strains, which can be explained by their high adaptability to the different ecological niches. In turn, this adaptability could result from intrinsic genetic variability due to mechanisms of horizontal genetic transfer, as well as high mutability determined by the expression of error-prone DNA polymerases. Yet, further studies are needed, especially whole-genome sequencing of non-pathogenic isolates, which for the moment are relatively scarce.

Keywords: *Acinetobacter* genus; pathogenic and non-pathogenic species and strains; genetic divergence

1. Introduction

The genus *Acinetobacter* is a part of the family *Moraxellaceae*, order *Pseudomonadales*, and represents a group of Gram-negative, typically aerobic, non-motile, nonfastidious, catalase-positive, oxidase-negative bacteria [1]. They are widely distributed in various environments, including fertile and non-fertile soil, fresh and sea water, solid wastes, fruits and vegetables, and foods with animal origins – meat, fish, honey and dairy products [2–4]. Their presence on the human skin and gut microbiome is notable, as is their existence in other animals - cattle, pigs, honeybees, and more [5,6]. These bacteria are distinguished for their metabolic versatility and adaptability to these diverse ecological niches. Such qualities of the genus can be benefited from, as various strains can produce a number of economically valuable secondary metabolites, including hydrolase enzymes, bioemulsifiers and a range of biopolymers [7]. That would suggest their possible biotechnological application, which relies on their ability to biodegrade oil, xenobiotics and halogens, remove phosphate and heavy metals in wastewaters, and potentially produce industrially important bioproducts [8].

In recent years, *Acinetobacter* species have garnered significant attention due to their peculiar role in both public health and food technology. They affect the middle ground of the two concepts as well. Evidence suggests that the presence of those bacteria in raw food such as vegetables and fruits and in dairy products might cause the consumer to have a foodborne disease, among others, typically

diarrheal. Their ability to do so is not very well determined, as many associate the disorder's origin with the usual foodborne pathogens, such as *Staphylococcus aureus* or *Escherichia coli* [9]. Certain species are implicated in severe healthcare-associated infections, characterized by their remarkable ability to acquire resistance to multiple antibiotics [10,11]. The common antimicrobial resistance genes present in the genus include class D oxacillinases like OXA-23, OXA-24/40, OXA-58, and the inherent OXA-51 in *Acinetobacter baumannii*, which are responsible for hydrolyzing β-lactam antibiotics, including carbapenems. Multiple drug resistance efflux pumps (AdeABC, AdeIJK, and AdeFGH), aminoglycoside-modifying enzymes (aph(3')-VIa, AAC(6')I-ad, and ArmA) and colistin resistance genes (mutations in *pmrA* and *pmrB*) are all present to a notable extent in various strains, with the pathogenic ones being most relevant [12]. Due to the immense ecological spread of the genus *Acinetobacter* members, these bacteria have the potential to further escalate the growth of antimicrobial resistance genes throughout the environment [13–15].

Contrarily, in parallel to the genus's pathogenic nature, some non-pathogenic species could play beneficial roles in the fermentation of foods, contributing to flavor development and preservation. A study reported high proteolytic activity from *Acinetobacter*, detected in 13 samples from Koozeh cheese, traditional for west Azarbaijan, from the 15 taken [4]. An examination of some types of French cheese made explicitly from raw goat's milk concluded that *A. baumannii* accounted for 3.2% of the total isolated strains from the milk and rind during ripening [16]. *Acinetobacter johnsonii*, along with another unidentified representative of the genus, were noticed in French Livarot cheese both on its surface and core [17]. The same species were predominant in the ripening of Grana-like hard cheese, made from raw cow's milk, in the Piedmont region in northwest Italy [18]. These observations could raise speculations that the presence of these bacteria in foods, especially in fermented ones, is a result of poor hygiene and lack of sanitary regulations in their production, therefore implying that detection of *Acinetobacter* is not recommended for the finished stock. While that might be an explanation, recent findings suggest that the genus might possess certain characteristics that could positively impact the result [4,19].

2. The Dualistic Nature of the Genus Acinetobacter

Genus *Acinetobacter* was first described in 1954 by Brisou and Prévot, who recognized the distinct characteristics that separated these organisms from other Gram-negative bacteria [20]. Initially, the genus included only a few species, but subsequent advances in molecular biology techniques, particularly DNA-DNA hybridization and 16S rRNA gene sequencing, have further expanded the understanding and classification of this group [21]. As of today, the genus *Acinetobacter* contains over 80 recognized species [22]. These bacteria have a DNA G+C content of between 39 and 47% [23,24] and are divided into several complexes and subgroups based on their genetic, biochemical, and phenotypic characteristics. These complexes include the *Acinetobacter calcoaceticus* – *A. baumannii* complex, which is the most clinically significant group [25]. Other common ones are the *Acinetobacter lwoffii* and *A. johnsonii* complexes, which are less associated with pathogenicity and more with their presence in the environment, in various foods, and in the natural microflora of humans and animals [21].

Acinetobacter species typically appear in pairs under a microscope and are known for their distinctive coccobacillary morphology, especially on non-selective agar media [1]. The cells of these bacteria differ in size and arrangement, usually 0.9 to 1.6 μ m in diameter and 1.5 to 2.5 μ m in length in the exponential growth phase. They can use different carbon sources for growth. When grown on solid media, *Acinetobacter* species usually form smooth or mucoid colonies ranging from white to pale yellow or light grey [26].

One of the genus's representatives, *A. baumannii*, is infamous for its involvement in nosocomial infections, such as hospital-acquired pneumonia, bloodstream infections, and wound contaminations. They often affect patients with compromised immune systems, as well as elderly persons and young children [27]. The ability of *A. baumannii* to survive on various surfaces for prolonged periods and its rapid acquisition of antibiotic resistance mechanisms have provided considerable challenges for pathogenic control and effective treatment [11].

Acinetobacter haemolyticus is another reported pathogen known for its ability to cause hemolysis. It has been suspected to cause bloody diarrhea in a case where no other enteropathogenic bacteria were detected [28]. The same species has been isolated from an 86-year-old patient diagnosed with recurrent bronchiectasis.

Other opportunistic pathogens such as *A. iwoffi, A. johnsonii* and *Acinetobacter junii* have been associated with secondary meningitis and bacteremia, among others, although not as frequently as *A. baumanii* [29,30]. The highly adaptive nature of the genus indicates the need for more data from investigating the potential pathogenicity of non-baumanii species.

On the contrary, research into the environmental and beneficial aspects of *Acinetobacter* spp. has revealed their role in biodegradation and bioremediation processes, as well as their presence in fermented foods. These bacteria are capable of producing a range of enzymes, such as lipases, proteases, and esterases, which are crucial in breaking down complex food substrates into more pure, flavorful compounds [31]. For instance, two *Acinetobacter* strains (*Acinetobacter sp.* 1H8 and *Acinetobacter indicus* 3B2) were inoculated in cigar tobacco leaves, where they not only increased the degradation of macromolecules, produced aldehydes and ketones and increased the content of more flavorful agents, but also promoted the growth of other functional bacteria, such as some *Bacillus* species [32]. *Acinetobacter* also made up the fourth most abundant genera overall in differently sourced da-jiang samples, a traditional soybean fermented food from China, suggesting a high possibility of their active involvement in the product's processing [33].

Despite those positives, however, researchers argue that consuming food with the presence of *Acinetobacter* may lead to colonization of the bacteria in the digestive tract and further the spread of multidrug-resistant species (Figure 1) [34].

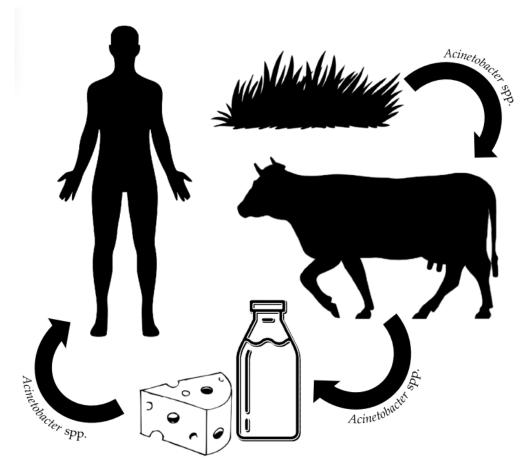


Figure 1. The possible pathway of spreading multidrug-resistant *Acinetobacter* to humans through consuming contaminated food.

3. Virulence and Pathogenicity Genetic Determinants

3.1. Antibiotic Resistance Genes

What makes a pathogen a pathogen is a crucial topic for many investigations, primarily those dealing with the nature of microorganisms. A plethora of genetic determinants mainly drives the pathogenicity of *Acinetobacter*, each contributing to the genus' unique ability to adapt to stress and cause diseases. The most well-known—factor is the presence of various antibiotic-resistance genes in their genome, possibly acquired by horizontal transfer of plasmids and transposons from other already resistant microorganisms [35]. Non-pathogenic *Acinetobacter* are significantly more susceptible to antibiotics than their pathogenic counterparts [36]. Therefore, the genome of opportunistic pathogens such as *A. baumannii* has a higher content of mobile genetic elements, which promotes the acquisition and the further spread of novel antibiotic-resistance genes [37].

3.2. Error-Prone DNA Polymerases

Additionally, investigations have shown the existence of many error-prone DNA polymerases (EPPs). Within the *Acinetobacter* genus, they may result in point mutations that aid survival, thus furthering their resistance to antibiotics and toxins [21], especially the UmuD'₂C polymerase (also known in *Escherichia coli* as pol V) [38], associated with a process known as SOS mutagenesis [39]. Interestingly, the SOS response in *Acinetobacter* does not rely on LexA protein, which has been proven to be absent within the genus [40]. Most probably, because the expression of the UmuD'₂C polymerase depends on the unique for the genus non-homologous to LexA proteins UmuDAb and DdR [40,41], the SOS mutagenesis process is more robust, resulting in gaining resistance to antimicrobial agents under DNA damaging stress caused. Within the clinical environment this stress can be caused by antibiotics, UV light and desiccation – practices used in patients' treatment and desinfection [42].

3.3. Biofilm Formation

Acinetobacter representatives such as A. baumannii, Acinetobacter nosocomialis and Acinetobacter pittii possess a couple of strategies for successful biofilm formation, which ensures bacterial survival due to the encasing of the colonies with a protective extracellular matrix [43]. They can form on various surfaces in clinical settings and in the human body, thus providing a protective environment against antibiotics, cleaning agents and the host immune system. The csuA/BABCDE operon encodes components of a chaperone-usher pili assembly system, which is essential for initial attachment and biofilm development. The biofilm-associated protein (Bap) is crucial for biofilm formation on abiotic surfaces. The control of biofilm formation and virulence gene expression is regulated by quorum sensing (QS) systems in response to population density [44]. The ability of Acinetobacter, particularly A. baumannii, to form such biofilms is one of the leading causes of their infamous pathogenic nature.

3.4. Other Outer Membrane Proteins

The existence of outer membrane proteins plays a crucial role in bacterial adherence, invasion and immune evasion. The outer membrane protein A (OmpA), a significant meditator of biofilm formation, is one of the most investigated virulence factors of *A. baumannii*, as its overproduction is closely associated with the mortality rate of the nosocomial infections caused by the bacterium [45]. Notably, the initial contact between the pathogen and the epithelial host cell is the binding of OmpA to fibronectin [46]. The protein also modulates the secretion of outer membrane vesicles such as Omp33-36, which also play an important role in the pathogenicity of *A. baumannii* [47]. The porin is the result of the expression of the *mapA* gene. It instigates apoptosis in infected immune and connective cells by activating caspases and blocking autophagy, thus allowing the bacteria to persist inside autophagosomes [48]. Other distinguished OMPs, possessed by pathogenic *Acinetobacter* are CarO, carbapenem susceptibility porin, and OprD, an orthologous protein with a role in drug resistance [49].

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3.5. Toxins Secretion

Protein secretion systems are detrimental to the possible interactions of bacteria with the environment and host cells. Type II secretion (T2SS) is common in Gram-negative pathogens as it secretes multiple effector proteins such as lipases and proteases, some of which require membrane-bound chaperons to be correctly produced. It has been found that the presence of human serum slightly increased the expression of T2SS in *A. baumannii*, which suggests that environmental factors may positively or negatively influence the virulence of a strain [50]. A clear correlation between the T2SS function and the colonization and infection of mice with *Acinetobacter* has been determined. However, the specific virulence-promoting mechanisms of the secretion system have yet to be pointed out [51]. Type VI secretion (T6SS) is a complex mechanism for injecting toxins directly into contact with competing bacteria, ensuring a possible pathogenic dominance. The genes encoding T6SS in *Acinetobacter* are conservative and are found on a single chromosomal locus. Notably, a non-clinical strain of *A. baumannii*, DSM30011, could eliminate *E. coli*, *Kleibsiella pneumoniae*, *Pseudomonas aeruginosa*, and a clinical isolate of *A. baumannii* with a fully active T6SS [52]. Those results hint that while useful in bacterial competition, fully functional T6SS might not be absolutely necessary in pathogenic strains.

3.6. Siderophores

Another distinguished virulence determinant is the presence of iron acquisition systems. It is well known that iron is essential for bacterial growth and metabolism [53]. *A. baumannii* produces acinetobactin and baumannoferrin, which are siderophores, used to sequester iron from host cells with their high affinity. Their production is mediated by a ferric uptake regulator (Fur), a protein that controls the expression of iron acquisition genes in a metabolic response [54]. Such strategies are crucial for the survival of *Acinetobacter* pathogens inside the animal and human bodies, as they are iron-limited environments [55].

Acinetobacter species possess a wide range of virulence factors that enable them to adhere to host cells, form biofilms, and evade immune responses. They provide insights into the complex mechanisms that cause their pathogenicity, which could aid potential disease control strategies. The variety of determinants and genetic differences differentiates a pathogen from a non-pathogen Acinetobacter species. Below is a comparison of the genomes between the pathogen A. baumannii and the environmental Acinetobacter baylyi (Table 1).

Table 1. A comparison of the genomes of *Acinetobacter baumannii* and *Acinetobacter baylyi* in different categories.

	A. baumannii	A. baylyi	Source
Size of genome	Approximately	Approximately	
	3.4 to 4.2 Mb	3.5 Mb	[56,57]
Malaila ann tion al ann an ta	Plasmids, transposons, More stab	More stable	[57,58]
Mobile genetic elements	Insertion sequences	genome	
Antibiotic resistance	A Plethora of genes such as	Lack of many	[12,57]
	blaOXA-51 and pmrA, efflux	determinants,	
	pumps such as AdeABC,	more	
	aminoglycoside-modifying	susceptible to	
	enzymes	antibiotics	

Virulence factors

Various factors, such as

6

	OmpA, CarO, T2SS and T6SS Significantly		[40 57]
	components	less or none	[49,57]
Metabolic adaptability	Equipment for survival in	More adaptive	[57 50]
	hostile environments	and versatile	[57,59]
	Bap, csu operon, quorum	Less developed	[42,60]
Biofilm formation	sensing system	strategies	[43,60]
	Ferric uptake regulator,	Lack of	
Iron acquisition system	siderophores - acinetobactin	advanced	[55,57]
	and baumannoferrin	system	

4. Acinetobacter in the Environment

Acinetobacter species possess the capacity to spread on numerous diverse ecological niches, as they have been assessed as microbial weeds [61]. An attempt to explore the distribution of Acinetobacter in nature determined that the genus was present in 28 of the 30 unique soil samples and 29 of the 30 unique water samples taken from a vast area along the coast of central California [62]. Aside from being present in differently sourced soil, water, foods and animals, they are also a part of the basic commensal microflora of healthy humans [63]. The genus's omnipresence, coupled with its representatives' high adaptability, proposes studying these bacteria as model organisms for environmental, biotechnological and industrial microbiological investigations. For example, A. baylyi ADP51 - a soil-inhabiting strain, has been found to have the highest research opportunity due to its high transformation and recombination competency, genome plasticity, versatile metabolic abilities, and fast and easy cultivation [64].

4.1. Soil

Members of the genus inhabit a plethora of soil environments. Studies generally focus on their presence in agricultural fields due to both their role in nutrient cycling, specifically in nitrogen fixation and degradation of complex organic elements, and their ability to carry antibiotic resistance genes and virulence-related traits, which in turn could harm the consumers of the eventually produced crops [65]. Acinetobacter has been found to be among the dominant genera in the rhizosphere soil of wheat and maize in Turkey. Interestingly, the same investigation concluded that inoculating wheat (Triticum aestivum) with Acinetobacter sp. WR922, one of the isolated strains, increased the phosphorus content of the plant by 27% at 15 days after the emergence, and the dry matter by 15% at 30th day. These results are attributable to the strain's phosphorus-solubilizing ability without the need for pyrroloquinoline quinone - like many other phosphate-solubilizing bacteria [66]. Strains of Acinetobacter guillouiae and A. calcoaceticus were used as bioinoculants in combination with chemical fertilizers to induce growth of onion (Allium cepa), which in turn grew in length biomass and had a higher availability of valuable compounds, demonstrating Acinetobacter representatives as plant growth promoting microbes [67]. Thus, it is suggested that these bacteria contribute to the growth of plants by providing nutrient compounds. Recent findings also demonstrate that Acinetobacter could play a role in soil bioremediation through hydrocarbon and phenol biodegradation [26,68].

4.2. Waters

Acinetobacter strains are present in both fresh and marine waters as free-living organisms or as biofilms on various surfaces. Such biofilms have been noted in drinking water distribution systems, as they are much less susceptible to antiseptics than planktonic Acinetobacter species. The genus is

found to be the prevalent isolate from chlorinated distributional systems, making up more than 5% of all identified microorganisms [63]. This could result from high resistance to chlorine, the most commonly used water disinfectant, with *A. baumannii* being able to persist in 0.2 to 4 ppm of free chlorine exposure, thus raising concerns for causing potential water-borne diseases [69]. *Acinetobacter* spp. has been identified in 38 % of untreated groundwater supplies and 16% of the water supplies, with no total coliforms detected in northern Preston County. Researchers find no notable difference in slime production, a virulence factor for *A. calcoaceticus*, in drinking water strains and clinical isolates while also highlighting that *Acinetobacter* might mask the presence of total coliforms in water, which poses a significant threat to the safety of the consumers [70]. Furthermore, the drug-resistant *A. baumannii* ST219 caused an outbreak in Tokai University Hospital's emergency intensive care unit due to the strain's colonization of the water systems, therefore spreading the infection by tap water [71]. Another concern for the genera's presence in tap water is the dissemination of antibiotic resistance to other species [72].

On the contrary, some strains could be a promising alternative to cleaning oil spills and reducing the toxicity of pollutants in wastewater [7]. *Acinetobacter sp.* SCYY-5 has been proven to reduce total petroleum hydrocarbon contamination by 69.17% in 10 days and under optimal degradation conditions by 79.94% in the same period [73]. Another study proposes that *A. junii* strain b2w is highly suitable for chromium bioremediation in contaminated waters since the bacterium could accumulate the heavy toxin effectively without disrupting cell integrity [74]. The positive environmental impact of several *Acinetobacter* strains in waters could be an excellent tool for industrial and biotechnological advancements and thus should be explored further.

4.3. Acinetobacter as an Animal Skin Commensal

Acinetobacter is considered to be a part of the common commensal skin microflora of humans and animals. They have been isolated from multiple animals, including dogs, cats, horses, pigs, and birds [75]. Investigations, mainly relevant to veterinary medicine, argue that Acinetobacter might become an opportunistic animal pathogen and should be given more attention due to the genus's high affinity for antimicrobial resistance [76,77]. For instance, a carbapenem-resistant A. pittii isolate was detected in a cat skin sample [78]. A. baumannii caused necrotizing fasciitis, an infection of the deep layers of the skin and fascia, with septic shock in a domestic shorthair cat, which ended in cardiac arrest [79]. The same has been detected in various animal infection sites, such as chronic eczema and open wounds in dogs [75]. While the presence of pathogenic strains on the skin of domestic animals is alarming, their detection in livestock appears to be a broader question. A study examined the possible existence of drug-resistant A. baumannii in 422 cattle, containing 280 dairy cows, 59 beef cattle, and 83 calves over 14 months. A total of 15.6% of the diverse samples were positive, with dairy cows being the prevalent group with 21.1%, followed by beef cattle (6.8%) and calves (2.4%) [80]. Different farms in Lebanon have been similarly investigated through fecal samples taken from cattle, pigs and hens. Four isolates were inhibited with A. baumannii, resistant to a wide range of antibiotics [81]. Tigecycline-resistant Acinetobacter towneri has been identified in 684 fecal and environmental isolates from six livestock farms, as Acinetobacter species appear to be the leading carrier of tigecycline-resistant tet(X) genes. Notably, the most tet(X)-positive isolates seem to be associated with livestock [58]. Such results pose a multitude of speculations about a possible contamination of animal foods with virulent Acinetobacter, considering that the genus has already been identified in a plethora of such products [2,34]. Research into the presence of non-pathogenic strains in animals is severely limited, due to the higher urgency of virulence.

5. Acinetobacter in Fermented Foods

From balancing the gut microflora and reducing blood pressure to vitamin increase and reduction of inflammation, the numerous health benefits of fermented foods and their content have been extensively researched and promoted; hence, the consumption of fermented products has gained significant popularity over the years. These qualities are attributed to the bioactive compounds, including vitamins, peptides and polysaccharides, produced by the microbial

communities responsible for the fermentation process [82]. Certain *Acinetobacter* representatives have been detected in metagenomic analyses of various fermented foods (Figure 2). The reasons behind the latter, however, could not be only a result of contamination of the processing environment or the raw material, as consistently mentioned, but also due to the metabolic capacities of the genus that play a practical role during food fermentation. Nonetheless, the strains found in food and those in clinical environments have substantial differences in their genotypes and, therefore, variable metabolic properties [83]. This could possibly impact the finished product in a different way.

5.1. Presence in Fermented Non-Dairy Foods

A study exploring the dynamic microflora of surimi, a protein extract from fish meat during fermentation, concluded that Acinetobacter was the second most abundant genera, making up 19.75% and 7.34% of the total bacterial diversity after 36 and 48h, respectively. Interestingly, at 0 h, its abundance accounted for 2.02%, then at 12h - for only 0.99%, before it grew to 12.44% at 24h. Although the microbiome of the raw ingredient, marine fish, appears to be inhabited mainly by gramnegative microorganisms, including Acinetobacter, the growth of the bacteria in the process could suggest a possible practical activity, even though the problem is left unspecified [84]. Acinetobacter has been revealed to be a dominant genus in Daqu, a cereal starter culture needed to produce Baijiu, a Chinese distilled spirit, as it produces esterases, pectinases and lipases, among others, and oxidizes glucose to produce acetic acid. All those components are essential for making the flavorful Baijiu [31]. Similarly, the predominance of the genus was observed in another Chinese product, red sufu, traditional soybean food, where it has been suggested that the bacteria could have a microflora stabilizing property [85]. A. baumannii TU04 has been isolated from Tapai Ubi, a Malaysian traditional cassava-fermented food, from which researchers identified an SPSFQ gene, a determinant of the production of extracellular serine protease that can degrade a variety of tissue-associated protein substrates [86]. A. lwoffii has also been identified as the dominant species (4.60%) in fermented rice Bhaati Jaanr, a product with proven antitumor activity [87]. Other fermented foods in which the species have been noticed are chicha, a rice-based fermented beverage; pulque, an alcoholic drink from the Agave plant; chikwangue, a starchy cassava product; koko, fermented maize porridge; and kenkey, steamed dumplings made from a steeping maze in water [88]. The possible functionality of Acinetobacter in those foods is scarcely explored, as many attribute its presence to an unsanitary environment.

5.2. Presence in Fermented Dairy Foods

Acinetobacter strains had a significant abundance in the maturation of two Camembert cheeses, with more than half of the strains presenting lipolytic activities on butterfat and tributyrin agar. Notably, NaCl enhanced the lipase production. No proteolytic strains were detected. In one sample, A. calcoaceticus was the most abundant species, apart from lactic acid bacteria. Furthermore, significant growth of Acinetobacter was only noticed after the growth of the yeast Debaryomyces hansenii [19]. Another study proposed that the genus could possess a secondary activity in the maturation of Istrian cheese [89]. A. baumannii has been identified as one of the species with relative abundance >1% in 92 different spontaneously fermented dairy products, such as shubat, yogurt, butter, sour cream and cottage cheese, all from different regions in Northeast Asia [90]. The same was present in 3.3% of overall samples of Domiati cheese, which is attributed to possible inefficient heat treatment or improper handling. In Kareish cheese, another Egyptian product, A. baumannii, was detected in 10% of the samples, along with a 3.3% presence of A. calcoaceticus, possibly due to the raw milk production process. The latter study also identified A. baumannii and A. haemolyticus in 13.3% of all cream samples. All of the strains from Domiati and Kareish cheese and three-fourths of those in cream presented positive lipolytic activity, which is argued to potentially reduce the shelf life of the milk products due to a possible production of ropy milk, which is a particular characteristic of the bacteria, although rarely encountered [91,92]. A. baumannii and A. pittii have been isolated from raw cheese samples in Lebanon [93]. Furthermore, A. calcoaceticus, Acinetobacter guillouiae, A. johnsonii and unidentified Acinetobacter were all present during the ripening of May bryndza cheese but were

absent in the finished product [94]. Similarly to the non-dairy foods, knowledge of the activity of the genus in dairy fermented foods is limited, besides their aforementioned lipolytic and proteolytic ability, which appears to be a characteristic, not all strains possess [4,91]. It appears that the strains that are present in various products are highly specific, therefore inducing a lack of perceivable trends and broader investigations.



Figure 2. A visual representation of the presence of *Acinetobacter* in fermented foods, all varying in type and origin.

5. Conclusions

Acinetobacter is a fascinating, highly heterogeneous genus that includes pathogens, biodegradators, stabilizers, model organisms and flavor enhancers. While their virulence is being thoroughly explored, broader and more specific investigations are needed to determine the reason behind their significant presence in a plethora of fermented food products. So, future studies are needed. One way to fill the existing information gap on the genetic bases for biotechnological applications is whole-genome sequencing of non-pathogenic, environmental and fermented foods *Acinetobacter* isolates.

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Appendix A

The appendix is an optional section that can contain details and data supplemental to the main text—for example, explanations of experimental details that would disrupt the flow of the main text but nonetheless remain crucial to understanding and reproducing the research shown; figures of replicates for experiments of which representative data is shown in the main text can be added here if brief, or as Supplementary data. Mathematical proofs of results not central to the paper can be added as an appendix.

Appendix B

All appendix sections must be cited in the main text. In the appendices, Figures, Tables, etc. should be labeled starting with "A" —e.g., Figure A1, Figure A2, etc.

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