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ANTIPATHOGENIC ACTION AND ANTIBIOTIC SENSITIVITY PATTERN OF THE "BORHANI"-ASSOCIATED LACTIC ACID BACTERIUM *WEISSELLA CONFUSA* LAB-11

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ABSTRACT

Assessment of the beneficial and safety properties of food-associated microbes is inevitable since they engage in direct interactions with their host via the digestive system. In this view, we have studied the pathogen inhibitory activity and antibiotic susceptibility pattern of a newly isolated lactic acid bacterium obtained from the traditional beneficial beverage borhani. 16S rRNA gene based taxonomic and phylogenetic analysis combined with sugar fermentation tests identified the isolate as *Weissella confusa*; strain LAB-11. Antimicrobial activity of the lactic acid bacterium was examined using its culture supernatant against ten bacterial pathogens by agar diffusion technique. The isolate inhibited species of *Acinetobacter*, *Bacillus*, *Escherichia*, *Klebsiella*, *Pseudomonas*, *Salmonella*, *Shigella* and *Staphylococcus* which indicated a broad spectrum of its antimicrobial activity. Further investigation by coincubation assay revealed a prolonged effect of the antibacterial activity against the above pathogens. The inhibitory activity was found highly effective on the fungal pathogen *Candida albicans* as well. Antibiotic susceptibility assay revealed that the isolate was sensitive to most of the tested antibiotics while resistant against four antibiotics including ciprofloxacin, cloxacillin, ofloxacin, and vancomycin that might be ascribed to intrinsic resistance. The ability to inhibit a wide range of pathogens while itself being relatively safe concerning the transfer of antibiotic resistance suggests that dairy beverages like borhani which carry such beneficial lactic acid bacteria can be of particular benefits to the consumers exerting preventive effects on associated diseases.

Keywords: *Weissella confusa*, antibacterial activity, antifungal activity, antimicrobial secretion, antibiotic susceptibility, probiotic lactic acid bacteria, dairy beverage

INTRODUCTION

In the recent decades antimicrobial resistance (AMR) in pathogenic bacteria has been an issue of serious concern considering the fact that AMR severely limits treatment options for the associated infection. AMR is primarily developed by the widespread use of antibiotics in human medicine, animal practice, and agriculture **(Brinkac *et al.*, 2017; Michael *et al.*, 2014)**. Moreover, pathogens may obtain additional new resistance factors from other species making the disease management more challenging (**Bengtsson-Palme *et al.*, 2018**). Hence, pathogen inhibitory effects received from the microbes naturally present in our diet can be of high benefits upon the pathogens' attack. In this regard, fermented foods can be a good example since they generally bear beneficial microbes such as the lactic acid bacteria which, in addition to providing nutritional benefits, may stimulate the antimicrobial activity as well (**Hossain *et al.*, 2022; Mokoena *et al.*, 2016**). On the other side, the food associated microbes that would provide the host with antimicrobial activity and other beneficial effects, should itself be safe from spreading antibiotic resistance to other microbes. Objectives of the present study, therefore, are the determination of antimicrobial activity and AMR profile of a *Weissella confusa* strain that has recently been isolated from the popular dairy beverage borhani. Borhani appears to be a healthy synbiotic beverage which is widely consumed in the South Asian countries. It is often consumed after a heavy meal and is thought to stimulate metabolism. Moreover, consumption of the beverage is also believed to relieve the lack of appetite, constipation and nausea. The health benefits implicated with borhani may come from the ingredients used in its preparation incorporating several spices and vegetables. The various ingredients may include sour curd, sugar, beet salt, common salt, mustard, ginger paste, coriander paste, mint leaf paste, cumin powder, chilli powder, pepper powder, white pepper powder, tomato ketchup and water. Having a sour-sweet-spicy taste and a soothing flavor, the beverage is very popular among all people.

W. confusa has gained increasing interest in recent years as a beneficial food-associated bacterium. The species was demonstrated to be a leading taxon of lactic acid bacteria among the many species identified in fermented foods. They include chemoorganotrophic, facultative anaerobic, Gram-positive, catalase-negative, spore-forming organisms having coccoid or rod-shaped morphology (**Collins *et al.*, 1993**). *W. confusa* grow optimally between 15 °C and 37 °C but some strains also grow at higher temperatures (**Fessard and Remize, 2017**). They were isolated from diverse environments but most often found in foods and beverages such as milk and milk-products, fruit and vegetable juice, cereal-based beverage etc., and also identified in a few human specimens such as gut and vagina **(Jin *et al.*, 2019; Kumar *et al.*, 2011; Purkayastha *et al.*, 2017; Wang *et al.*, 2020)**. These bacteria possess probiotic and prebiotic properties, have demonstrated the ability to induce an oxidative attack, produced exopolysaccharides, could reduce cholesterol and was able to inhibit proliferation of pathogenic microorganisms (**Dey *et al.*, 2019**). Foods containing such beneficial species are much appreciated especially as they resist pathogens' growth in the host. However, previous studies also reported *W. confusa* strains that bear some antibiotic resistance genes thus posing the risk for their horizontal transfer to other microbes including the pathogenic ones (**Mathur and Singh, 2005**). In addition to evaluating the presence of beneficial traits such as antimicrobial activity of the food-associated microbes, therefore, assessment of the risk for AMR transfer should also be studied.

In the present work, we have investigated antibacterial effect of the borhani associated *W. confusa* isolate LAB-11 employing agar diffusion assay that was further validated using coincubation inhibitory assay against several Gram positive and negative pathogenic species. Antimicrobial activity against the fungal pathogen *Candida albicans* was also demonstrated. Antibiotic susceptibility pattern of the isolate was also determined towards fourteen common antimicrobial agents. Being a microbe normally found in natural foods and food-products, the *W. confusa* species are in direct interactions with our gastrointestinal cells. However, it cannot be considered for probiotic application until it is isolated and shown to have unique beneficial properties. Hence, the present investigation on the assessment of its antagonistic activity and antibiotic susceptibility will provide valuable insights into the beneficial and safety properties of this important species.

MATERIALS AND METHODS

Borhani samples

The borhani samples used for the isolation of bacteria were purchased from local retail outlets. Samples of five different brands, sold in 250 mL to 1L PET bottles, were bought and transported to the laboratory for analysis.

Isolation, storage and maintenance of bacteria

For the isolation of bacteria, 5 ml of each sample was mixed in a sterile conical flask and stirred at room temperature for 10 min. 100 µL of the mixture and its 5× serial dilutions up to 5^{-6} were plated on de Man, Rogosa and Sharpe (MRS) agar media (20 g/L glucose, 10 g/L peptone, 10 g/L beef extract, 5 g/L yeast extract, 2 g/L dipotassium hydrogen phosphate, 5 g/L sodium acetate trihydrate, 2 g/L triammonium citrate, 0.1 g/L magnesium sulphate heptahydrate, 0.05 g/L manganese sulphate tetrahydrate, 1 ml/L Tween-80, 18 g/L agar and water) supplemented with 5 g/L L-cysteine hydrochloride (pH 6.0) and incubated overnight at 37°C anaerobically. Samples were also spread on the MRS media without cysteine-supplementation and incubated aerobically. All colonies with unique morphological appearances were selected, picked by a sterile tooth-pick and streaked on MRS agar medium two to three times in succession to obtain pure cultures preserved as glycerol stocks at -80°C as described by **Hossain *et al*. (2011) and Hossain *et al*. (2021**). The isolates were revived in MRS broth before use, and subsequently transferred and maintained in the MRS medium at 37℃.

Amplification, sequencing and analysis of 16S rRNA gene

For taxonomic classification of the isolate, fragment of its 16S rRNA gene was sequenced as described in **Hossain *et al*. (2020)**. In brief, the 16S rRNA gene was amplified by PCR using the isolate's genomic DNA extracted by Maxwell 16 Blood DNA Purifcaton Kit (Promega) with the universal primers 27F and 1392R. After purification, the PCR product was sequenced using a BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) following manufacturer's instructions. The sequence was deposited in the NCBI GenBank database under the accession number OM980644.1.

Taxonomic study

Taxonomic assignment of the isolate was based on (1) percent identity of its 16S rRNA gene sequence to that of other bacteria in GenBank (**Hossain *et al*., 2018**) and (2) the number of hits produced against various phylotypes in BLAST result (**Hossain *et al*., 2021**). BLAST was run with default setting except that the "Max target sequences" was set to 100 (default), 250, 500, 1,000 or 5,000. Further taxonomic analysis was carried out by the Ribosomal Database Project (RDP)'s SeqMatch application using default setting but the source set to "isolates" instead of "all" (**Bacci *et al*., 2015**).

Phylogenetic analysis

Phylogenetic analysis was performed as previously described using the MEGA application, version X **(Ali *et al*., 2021; Hossain *et al*., 2020**). Strains used in the phylogenetic analysis include: *W. confusa* N17, sequence ID: CP049097.1; VTT E-133279, CP027563.1; LM1, CP080582.1; *W. cibaria* strains CBA3612, CP041193.1; SRCM103448, CP035267.1; BM2, CP027427.1; and the type strains listed in Table 1.

Morphological analysis

Colony morphology of the isolate was observed after 48 h of growth at 37°C on MRS agar. Color, shape, elevation, and surface properties of the colonies were recorded. Cell morphology was subsequently inspected under microscope using the conventional Gram-staining protocol.

Sugar fermentation tests

To distinguish whether the isolate was *W. confusa* or *W. cibaria*, its ability to ferment galactose and arabinose was performed. Preculture of the isolate was inoculated into phenol-red carbohydrate broth containing 10 g/L peptone, 5 g/L sodium chloride, 1 g/L beef extract, 10 g/L of galactose or arabinose in sterile distilled water with 18 mg/L phenol red used as pH indicator. The culture was incubated at 37 °C for 24 to 48 h. Color change of the broth from reddish orange to yellow was interpreted as an indication of acid production.

Collection of supernatant

Supernatant was collected from fresh culture reaching an optical density of ∼1.5 at 600 nm by centrifugation at 10,000×g for 20 min at 4°C. The supernatant was washed twice in sterile distilled water, sterilized using 0.22 µm syringe filter and preserved at -20°C.

Test microbes

The antimicrobial activity was examined against ten test bacteria including *Acinetobacter baumannii* ATCC 7978, *Bacillus cereus* ATCC 14574, *Bacillus subtilis* ATCC 6633, *Escherichia coli* ATCC 25922, *Klebsiella pneumonia* ATCC 13883, *Pseudomonas aeruginosa* ATCC 9027, *Salmonella abony* ATCC 14028, *Salmonella typhi* ATCC 14028, *Shigella flexneri* ATCC 9199, and *Staphylococcus aureus* ATCC 6538. The test strains were routinely maintained in Luria-Bertani (LB) or nutrient broth at 37°C unless otherwise noted. The fungal strain *Candida albicans* ATCC 10231 was used in the antifungal assay and maintained on Potato Dextrose Agar (PDA) at 25ºC.

Agar diffusion assay

Agar diffusion assay was conducted according to a previously described method (**Hossain *et al*., 2022**). Briefly, each test strain revived in LB or nutrient broth was transferred to fresh medium and adjusted to 0.5 McFarland standard. The cell suspension was subsequently added to Mueller Hinton medium, mixed and poured in petri dishes. Wells of 5 mm diameter were punched in the medium and filled with supernatant collected from the isolate. After a 3 h pre-incubation at 4°C and a 24 h incubation at 37° C, diameter of inhibition zone was measured.

Coincubation inhibition assay

The test strains were each grown in 2 mL nutrient broth added with 400 µL supernatant collected from the isolate. Density of the cell suspension was subsequently measured at 600 nm at 0 h, 2 h, 4 h, 8 h and 24 h of incubation at 37° C. Growth kinetics of the test strains was therefore obtained by plotting cell density against the incubation time. Control experiment included supernatant collected from another bacterium also isolated from borhani but without having any antimicrobial activity (**Hossain *et al*., 2022**).

Antifungal assay

The antifungal assay was performed using the poisoned food technique (**Ferdouse *et al*., 2022**). A mixture of 25-mL molten nutrient agar medium and 0.5 mL of the LAB supernatant was placed in a petri plate. After the medium was solidified, a 5 mm well was made at the center of the plate which was filled with a 5 mm fungal block. Controls were performed without any LAB supernatant in the medium. The plates were incubated at 25 ◦C for 7 days, and the diameters of the fungal colonies were measured every day. Percentage of inhibition was determined using the following formula.

$$\text{Fungal inhibition (\%)} = \frac{\text{Diameter of fungal colony in control} - \text{Diameter of fungal colony in treatment}}{\text{Diameter of fungal colony in control}} \times 100.$$

Antimicrobial susceptibility assay

Susceptibility towards antibiotics was determined following a previous report (**Ali *et al*., 2021**). Briefly, fresh culture of the isolate was adjusted to a cell density of OD_{600} 0.08 to 0.1 and streaked on MRS agar plates. Subsequently, discs of azithromycin (15 µg), amoxycillin (10 µg), chloramphenicol (30 µg), ciprofloxacin (5 µg), clindamycin (2 µg), cloxacillin (5 µg), doxycycline (10 µg), erythromycin (15 µg), gentamicin (10 µg), ofloxacin (5 µg), tetracycline (30 µg), vancomycin (30 µg) were placed on the agar and incubated at 37° C. After 18 h of incubation, zone of no-growth was measured and interpreted as per the guidelines of Clinical and Laboratory Standards Institute.

RESULTS

Taxonomy, phylogeny and morphology

The isolate was taxonomically classified as *Weissella confusa* based on the analysis of its 16S rRNA gene sequence combined with carbohydrate fermentation test results. The 16S rRNA gene was, however, highly similar to two distinct *Weissella* species: *W. confusa* and *W. cibaria*. When default setting was used in BLAST-search with "Max target sequences" set to 100, the species that appeared in the search result were all *W. confusa*; but when the target sequences were set to 250, 97% of the species were *W. confusa* and one was *W. cibaria*. Interestingly, the number of *W. cibaria* species in the BLAST results increased significantly as the target sequences was set to 1,000 or 5,000. Number of hits for the various phylotypes in BLAST result is presented in Fig. 1a which revealed 714 hits for *W. confusa* and 254 hits for *W. cibaria* when "Max target sequences" was set to 1,000; and 949 hits for *W. confusa* and 657 for *W. cibaria* when target sequences set to 5,000. Indeed, the 16S rRNA gene sequences of the two species were reported to be very similar to each other sharing over 99% sequence identity that may make it quite difficult to differentiate the two species from their 16S rRNA gene analysis only (**Björkroth *et al*., 2002**). The sequence alignment revealed more than 99% identity of the isolate's 16S rRNA gene to the *W. confusa* strains 3273, KB18-18281, YM5S2, RCB327, XT7-7 etc., and *W. cibaria* strains 5522, WC10, HBUAS53398, 2381, GI21 etc. each with 100% query coverage (Table 1). Moreover, 99.93% sequence identity was revealed between the isolate and its nearest type strain *W. confusa* JCM 1093(T) having just one mismatch (1350/1351 identity), but 99.26% identity was found with the *W. cibaria* type strain KACC 11862(T) with 10 mismatches (1341/1351 identity). A phylogenetic analysis of LAB-11 with strains of *W. confusa* and *W. cibaria* present in the database was further conducted. However, there appears to be concern whether the *Weissella* species in the database were precisely classified if it was solely based on the sequence-similarity which might not be sufficient to distinguish between these two species (**Björkroth *et al*., 2002**). Hence, 16S rRNA gene sequences for phylogenetic analysis were extracted from the respective whole genome sequences to ensure inclusion of more accurately classified *Weissella* species in the tree. The phylogenetic analysis produced two distinct clades, one each for *W. confusa* strains and *W. cibaria* strains wherein LAB-11 was placed in the former clade (Fig. 1b). The phylogenetic tree also indicated a close association of the isolate with *W. confusa* LM1 strain. Further support for the taxonomic assignment was obtained from the SeqMatch analysis as well (Fig. 1c).

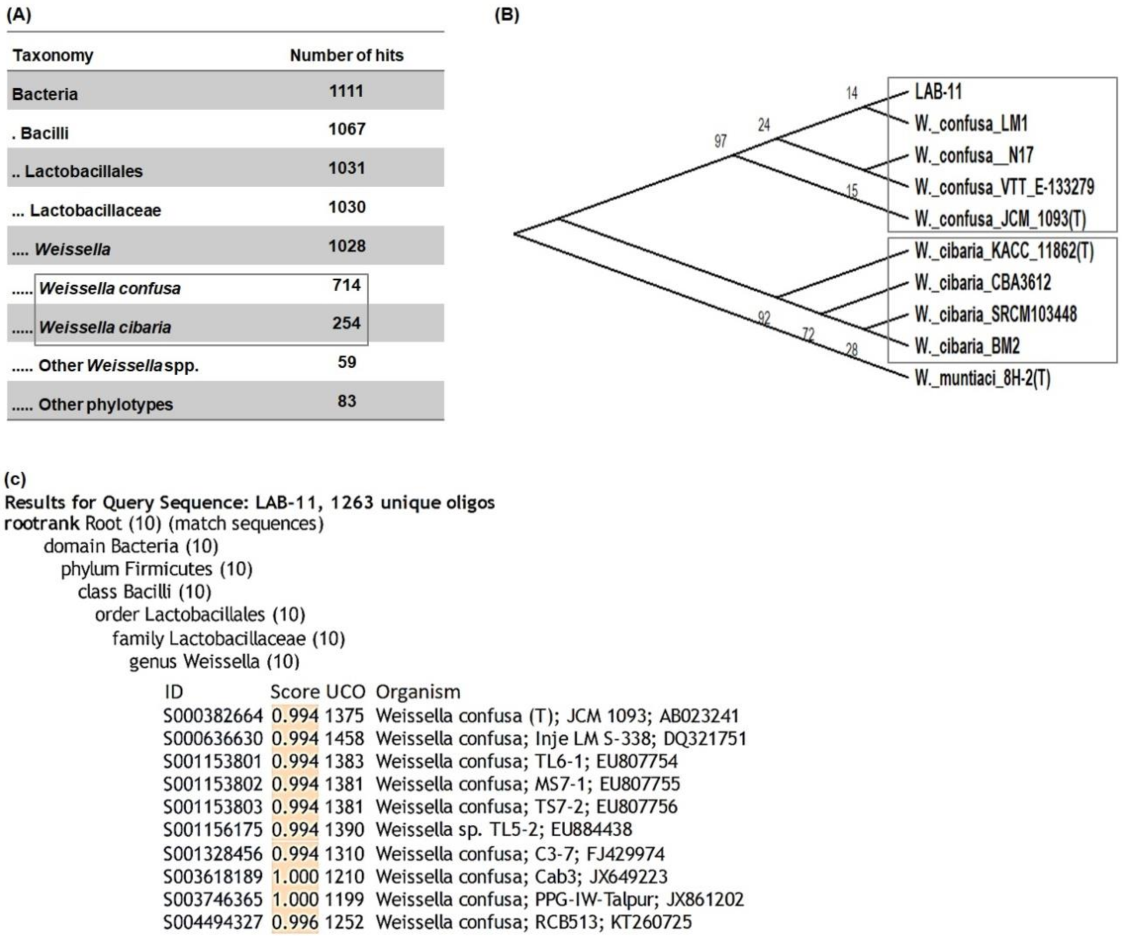

Figure 1 Taxonomic assignment of the isolate. (A) Number of hits obtained against each taxonomic group in BLAST search of the isolate's 16S rRNA gene as the "Max target sequences" was set 1,000. The "other *W. confusa* spp." or "other phylotypes" include the uncultured and/or unclassified bacteria as well. (B) Phylogenetic analysis of various *W. confusa* strains. The tree was constructed as described in Materials and Methods. The two clades of *W. confusa* strains and *W. cibaria* strains are in grey boxes. (c) Results of taxonomic affiliations by SeqMatch analysis presenting top 10 SeqMatch scores (S_ab). Similarity score was not calculated. Sequence short IDs, S_ab score, unique common oligomers (UCO) and organisms with accession numbers are shown.

Table 1 Percent identity of the 16S rRNA gene of LAB-11 to those of other *W. confusa* and *W. cibaria* strains in GenBank and to the respective type strains (T).

Strains	Score	Query Cover	E value	Per. Ident	Acc. Length	Accession
Top selected strains in BLAST result						
W. confusa 3273	2490	100	0.00	99.93	1417	MT613585.1
W. confusa KB18-18281	2490	100	0.00	99.93	1493	LC506181.1
W. confusa YM5S2	2490	100	0.00	99.93	1470	MN894020.1
W. cibaria 5522	2490	100	0.00	99.93	1487	MT510313.1
W. cibaria WC10	2488	100	0.00	99.33	1414	MK852333.1
W. cibaria HBUAS53398	2473	100	0.00	99.70	1499	MK402185.1
Top type strains in EZBiocloud 16S based ID						
W. confusa JCM 1093(T).	2490	100	0.00	99.93	1477	AB023241
W. cibaria KACC 11862(T)	2490	100	0.00	99.26	1741	AEKT01000037
W. muntiaci 8H-2(T)	2276	96	0.00	98.09	1504	MK774696

Subsequently, carbohydrate fermentation test was carried out which allowed further distinction between the two species. The isolate produced acid from galactose fermentation but did not ferment arabinose, typical characteristic previously reported for *W. confusa* (**Quattrini *et al*., 2020**). Altogether, the higher number of hits for *W. confusa* in the BLAST result, higher sequence similarity of 16S rRNA gene to the *W. confusa* type strain, phylogenetic placement within the *W. confusa* clade, and the sugar fermentation test-results suggested that the isolate was indeed a *W. confusa* strain. Consistent with this taxonomic assignment, LAB-11 showed characteristic creamy white colonies on MRS agar medium with a raised and wet surface. The cells appeared to be Gram-positive bacilli in single or short chains and were non-motile.

Inhibitory effects against pathogenic and spoilage bacteria

To test antimicrobial activity of *W. confusa* LAB-11 strain, its culture supernatant was placed in wells in the agar media spread with each test strain. Formation of the zones of no-growth surrounding the wells revealed presence of antimicrobial substances in the supernatant. Growth inhibition of all test strains including several

Gram positive and negative species suggested that the antimicrobial substances possessed a wide range of inhibitory effects. The inhibition zones were smallest for *S. flexneri* and *B. subtilis* and largest for *K. pneumoniae* (Table 2). Further insights on the inhibitory extents were obtained from the coincubation assay that allowed the test strains to grow in nutrient broths added with the supernatant of LAB-11. Measurement of growth rate from 0 to 24 h revealed a strong and prolonged antimicrobial activity of LAB-11 against the test pathogens (Fig. 2). For most isolates the antimicrobial activity lasted for at least 8 h. Thereafter, the inhibitory effects decreased to some extent which suggests a gradual depletion of the antimicrobial substances in the supernatant. However, in case of *A. baumannii*, the inhibitory effect continued to resist the growth even after 8 h. According to both agar diffusion and coincubation assays, the most affected test strains appeared to be *A. baumannii* and *K. pneumoniae*.

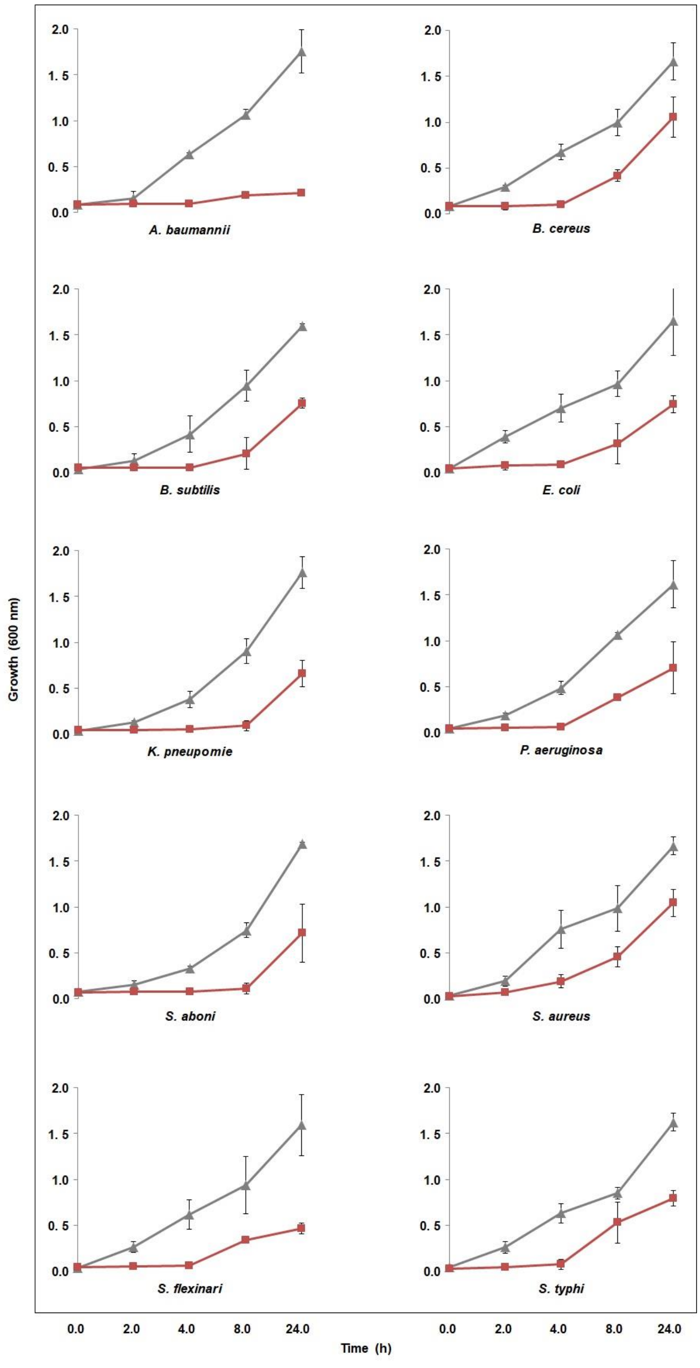

Figure 2 Antagonistic effects of LAB-11. Growth of the test strains with (red) or without (grey) supernatant added from the LAB-11 culture measured at 2, 4, 8, and 24 hours.

Antifungal activity

Inhibitory activity of LAB-11 CFS against the fungal test strain *C. albicans* was assessed by the poisoned-food method in which the isolate could effectively suppressed growth of the pathogenic strain. The inhibition (%) of the fungal mycelium was measured to be 57.83 (±4.37) as compared to that of the control.

Table 2 Diameter of inhibition zones produced by *W. confusa* LAB-11 against test strains in the agar diffusion assay.

Test strains	Inhibition zone diameter (mm)
Gram negative test strains	
A. baumannii	5.7 (±0. 6)
E. coli	5.0 (±1.7)
K. pneumoniae	6.3 (±1.5)
P. aeruginosa	5.7 (±0. 6)
S. abony	5.0 (±0.0)
S. typhi	5.3 (±0. 6)
S. flexneri	3.3 (±2.9)
Gram positive test strains	
B. cereus	4.3 (±1.2)
B. subtilis	3.7 (±3.2)
S. aureus	5.3 (±1.2)

Antimicrobial susceptibility and resistance

Antimicrobial susceptibility of LAB-11 was determined by disc diffusion assay in which the isolate was found sensitive to six (amoxicillin, ampicillin, chloramphenicol, clindamycin, erythromycin, and penicillin) of the fourteen antibiotics tested, intermediate to four antibiotics (azithromycin, doxycycline, gentamicin, and tetracycline), and resistant to four antibiotics (ciprofloxacin, cloxacillin, ofloxacin, and vancomycin). The isolate, therefore, appeared to be a multidrug resistant (MDR) strain, although the associated multiple antibiotic resistance (MAR) index was calculated as 0.29 which suggests a relatively limited level of antibiotic resistance.

DISCUSSION

Frequently isolated from a variety of foods, the *W. confusa* appears to be a species autochthonous to food components (**Fessard and Remize, 2017; Galli *et al.*, 2020**). Regular consumption of the species via food-intake implies that characterization of its "good and bad" aspects is an important issue that needs surveillance. The direct connection between the food associated species and consumers' health, therefore, incited the present investigation to understand the antagonistic effects and antibiotic resistance of the new *W. confusa* isolate which we have recovered from borhani. Borhani is a dairy based beverage very popular in the countries of Indian subcontinent. Usually consumed after a meal, the beverage is considered to be a beneficial food that stimulates digestion (**Hossain, 2022a**). Already, a number of beverages, juices, prickles and other food products have been reported as sources for *W. confusa* and other lactic acid bacteria (**Björkroth *et al.*, 2002; Hossain, 2022b**). For example, *W. confusa* strains were isolated from beverages like human milk, cow milk, camel milk, several fruit and vegetable juices etc., and foods such as dairy products, plants, spices, meat, fish etc. A detail list of the food-origin *W. confusa* can be found in Table 3 which shows that the species has been frequently reported in cereal-based foods and beverages. Besides, *W. confusa* appears to be a common member in the gut flora of human and other animals. It has been recovered from the feces of healthy human individuals and young children, from the feces of horse, panda and yak, and from the vagina of women (**Jin *et al.*, 2019; Lee, 2005; J. Liu *et al.*, 2020; Purkayastha *et al.*, 2017; W. Wang *et al.*, 2020; Xia *et al.*, 2019; Xiong *et al.*, 2019**). However, as the name implies, the correct identification of the *W. confusa* might be "confusing" for its high similarity with closely related species in morphological and metabolic features (**Medford *et al.*, 2014; Spiegelhauer *et al.*, 2020**). Moreover, the species shares 99% or more similarity of its 16S rRNA gene with *W. cibaria* (**Björkroth *et al.*, 2002**). As a result, 16S rRNA gene-based distinction between the two species might be challenging. Hence, a detailed analysis of the strain's 16S rRNA gene using BLAST search, RDP SeqMatch, phylogenetic association was performed in the present study alongside sugar fermentation tests in the efforts towards accurate identification of the strain.

Table 3 Occurrence of *W. confusa* in foods and beverages.

Food types	Name	Description	Reference
Beverages and juices:			
Milk and dairy beverages	Borhani	Traditional dairy beverage of Indian subcontinent	This study
	Human milk		(**Martín *et al.*, 2007**)
	Cow milk		(**Zambou *et al.*, 2008**)
	Camel milk		(**Mercha *et al.*, 2020**)

Continue Table 3	Water buffalo milk		(**Hameed *et al*., 2022**)
	Nunu/Nono	West African traditional yogurt beverage	(**Akabanda *et al*., 2013; Ayeni *et al*., 2011**)
	Suusac	Kenyan fermented camel milk	(**Jans *et al*., 2012**)
	Kulenaoto	Kenyan Maasai traditional fermented dairy beverage	(**Mathara *et al*., 2004**)
	Fermented zebu milk	Kenyan Maasai traditional fermented milk from Zebu cattle	(**Isono *et al*., 1994**)
Fermented cereal beverages	Bushera	Ugandan traditional fermented cereal beverage	(**Muyanja *et al*., 2003**)
	Togwa	East African fermented cereal beverage	(**Mugula *et al*., 2003**)
	Kunu-zaki	Nigerian fermented cereal beverage	(**Ogunremi *et al*., 2022**; **Oguntoyinbo *et al*., 2011**)
	Boza	Bulgarian fermented cereal-based low alcoholic beverage	(**Heperkan *et al*., 2020**)
	Borde	Ethiopian traditional fermented cereal-based alcoholic beverage	(**Abegaz, 2007**)
	Shanxi aged vinegar	Chinese traditional cereal based vinegar	(**Wu *et al*., 2012**)
	Thobwa	Malawian and Zambian fermented cereal-based beverage	(**Ng'ong'ola-Manani *et al*., 2015**)
	Fura	African millet-based spontaneously fermented beverage	(**Owusu-Kwarteng *et al*., 2012**)
	Makgeolli	Traditional Korean starchy alcoholic beverage (rice wine)	(**Jung *et al*., 2012**)
	Pozol	Mexican fermented corn dough beverage	(**Hernández-Oaxaca *et al*., 2021**)
	Gowe´	Beninese malted sorghum-based food	(**Vieira-Dalodé *et al*., 2007**)
	Banh men	Vietnamese alcoholic beverage made from rice, a variety of herbs and spices	(**Thanh and Tuan, 2008**)
	Atole agrio	Mexican traditional maize-based beverage	(**Pérez-Cataluña *et al*., 2018**)
	Chicha	Argentine traditional maize-based beverage	(**Elizaquível *et al*., 2015**)
Fruit and vegetable juices	Tomato juice		(**Di Cagno *et al*., 2009**)
	Apple juice		(**Fessard *et al*., 2017**)
	Pineapple juice		(**Fessard *et al*., 2017**)
	Coconut water		(**Seesuriyachan *et al*., 2010**)
	Carrot juice		(**Björkroth *et al*., 2002**)
Foods:			
Fermented dairy foods	Commercial yoghurts		(**Rosca *et al*., 2018**)
	Dahi	Indian traditional fermented curd	(**Patel *et al*., 2013**)
	Klila	Algerian traditional cheese product	(**Benhouna *et al*., 2019**)
	Vento d'Estate	Italian traditional cheese	(**Di Cagno *et al*., 2007**)
Cereal foods	Pasta	Consisting of dough made from durum wheat and water	(**Russo *et al*., 2010**)
	Sourdough	Bread made by the fermented dough	(**Bounaix *et al*., 2010**)
	Durum wheat semolina	Purified wheat middlings of durum wheat for pasta making	(**Fusco *et al*., 2011**)
	Spelt sourdough	Wheat flour for bread making	(**Buksa *et al*., 2021**)
	Wheat sourdough	Light and flavorful bread made with 20% whole wheat flour	(**Corsetti *et al*., 2001**)
	Rye sourdough	Made with a base of rye and spelt flour for lighter rye bread	(**Ispirli *et al*., 2018**)
	Zichi	Italian traditional sardinian sourdough bread	(**Catzeddu *et al*., 2006**)
	Yellow corn flour	Made from the whole dried kernels of yellow corn	(**Petrovici *et al*., 2018**)
	Quinoa flour	Gluten-free flour consisting of dried quinoa seeds	(**Lorusso *et al*., 2018**)
	Calugi	Brazilian traditional non-alcoholic fermented food prepared from corn, cassava and rice	(**Miguel *et al*., 2012**)
	Fermented sorghum flour	Gluten free fermented flour making bakery products	(**Falasconi *et al*., 2020**)
	Fermented batter	The batter making south Indian traditional dish "Mudakathan dosai"	(**Lakra *et al*., 2020**)
	Idli batter	South Indian fermented rice and black gram based food	(**Sharma *et al*., 2018**)
	Fermented uttapam batter	South Indian cuisine fermented with Piper betle L. leaves	(**Dubey and Jeevaratnam, 2015**)
	Dosa batter	Indian dish made by soaking and blending black gram lentils and rice to a batter	(**Kaur and Tiwari, 2016**)
	Ogi	Nigerian fermented cereal pudding	(**Schillinger *et al*., 2008**)
	Tapai	Malaysian traditional alcoholic dessert made from rice	(**Björkroth *et al*., 2002**)
	Maize bran fermentation	by-product of various corn maize processing industries	(**Decimo *et al*., 2017**)
	Fermented rice	Fermented rice of Indian subcontinent	(**Nath *et al*., 2021**)
	Nukadoko	Japanese fermented rice bran bed traditionally used for pickling vegetables	(**Ono *et al*., 2014**)
Fruits and related products	Cherry tomato		(**Álvarez *et al*., 2021**)
	Unripe green tomato		(**Pereira *et al*., 2021**)
	Papaya		(**Fessard *et al*., 2017**)
	Cherry		(**Xu *et al*., 2018**)
	Banana leaves		(**Paludan-Müller *et al*., 1999**)
	Tomato ketchup		(**Bjorkroth and Korkeala, 1997**)
	Native fruit of Ecuadorian Amazon		(**Garzon *et al*., 2017**)
Plants, vegetable and associated foods	Carrot mesh		(**Maina *et al*., 2008**)
	Cabbage		(**Fessard *et al*., 2017**)
	Deli-type pickle	Nonacidified, refrigerated cucumber pickles	(**Reina *et al*., 2005**)
	Vegetable mixture	a fermentation of a mixture of green tomatoes, carrots and cauliflower	(**Wouters *et al*., 2013**)
	Kimchi	Korean traditional side dish of salted and fermented vegetables	(**Lee, 2005**)
	Sauerkraut	German traditional fermented cabbage product	(**Plengvidhya *et al*., 2007**)
	Tempeh	Indonesian traditional food made from fermented soybeans.	(**Björkroth *et al*., 2002**)
	Doenjang	Korean fermented soybean paste	(**Kim *et al*., 2009**)
	Tuaw jaew	Thai fermented soybeans	
	Fresh tofu	Asian traditional soybean-derived food product	(**Rossi *et al*., 2016**)
	Stinky tofu	Chinese fermented tofu having strong odor	(**Chao *et al*., 2008**)

Continue Table 3	Douchi	Chinese salt-fermented and black soybean product	(**C. Liu *et al*., 2012**)
	Gari	West African creamy granular flour derived from fermented cassava roots	(**Huch *et al*., 2008**)
	Attieke	Ivorian steamed fermented semolina	(**Djeni *et al*., 2015**)
	Lafun	Nigerian fermented flour derived from cassava roots	(**Padonou *et al*., 2009**)
	Ntoba mbodi	Congolese traditional alkaline-fermented cassava food	(**Ouoba *et al*., 2010**)
	Fermented cocoa bean	Fermented seeds for making chocolate	(**Camu *et al*., 2007**)
	Miang	Southeast Asian fermented tea leaf	(**Miyashita *et al*., 2012**)
Spices	Garlic		(**Paludan-Müller *et al*., 1999**)
	Onion		(**Säde *et al*., 2016**)
	Red pepper		(**Di Cagno *et al*., 2009**)
	Yellow pepper		(**Di Cagno *et al*., 2009**)
	Chili bo	Malaysian food ingredient for many chili-based dishes	(**Leisner *et al*., 1999**)
Meat and fish	Chicken		(**Ji *et al*., 2011**)
	Dry-fermented sausages		(**X. Liu *et al*., 2020**)
	Morcilla de burgos	Spanish traditional blood sausages	(**Santos *et al*., 2005**)
	Nham	Thai fermented pork sausage	(**Wongsuphachat & Maneerat, 2010**)
	Pla-ra	Thai fermented fish product	(**Rodpai *et al*., 2021**)
	Plaa som	Thai fermented fish product	(**Deatraksa *et al*., 2018**)
	Sidra	Eastern himalayan traditional smoked and sun-dried fish product	(**Thapa *et al*., 2006**)
	Salted sea foods	Korean traditional fermented food	(**Yoon and Hwang, 2016**)

W. confusa is considered to be a promising lactic acid bacterium which can be proposed for probiotic application in food and beverages because of its various useful properties (**Teixeira *et al*., 2021**). However, as compared to the better-known lactic acid bacteria such as *Lactobacillus acidophilus*, *L. bulgaricus*, *L. plantarum*, *L. casei*, *L. rhamnosus* or *Bifidobacterium bifidium*, this species appears to be relatively less-studied. In the present work, we have demonstrated the presence of a strong and broad-spectrum antimicrobial activity in the dairy-origin *Weissella* strain. Recently, a few other strains of the species have been reported which also possessed antimicrobial activity and other beneficial effects on both food-quality and health. The strains were demonstrated to be required for fermentation in food preparation, for adding flavor and taste to food-products, and for prolonging foods' shelf life (**Ray and Sivakumar, 2009**). Among the health promoting effects, antimicrobial activity, antioxidant activity, cholesterol reduction, exopolysaccharide biosynthesis, and hydrolytic enzyme production have been described in different isolates (**Teixeira *et al*., 2021**). The LAB-11 isolate of the current study showed a large antimicrobial spectrum inhibiting a number of pathogenic or spoilage bacteria. In previous studies with *W. confusa*, the antimicrobial study was usually performed against relatively small number of test strains. Lakra *et al*. reported two promising *W. confusa* strains MD1 and MD2 which were isolated from fermented batter and inhibited the foodborne pathogens *Listeria monocytogenes, S. aureus S. enterica, E. coli* and *S. typhi* (**Lakra *et al*., 2020**). In another study, a novel bacteriocin purified from a milk associated *W. confusa* strain had antimicrobial effects against *B. cereus, E. coli, P. aeruginosa* and *Micrococcus luteus* (**Goh and Philip, 2015**). In a co-culture assay, *W. confusa* AI10 strain inhibited two clinical pathogens *E. coli* NG 502121 and *S. aureus* AY 507047 (**Shah *et al*., 2016**). Two other strains isolated from buffalo ruminal gut showed antimicrobial activity against *L. monocytogenes* and *S. aureus* (**Wali *et al*., 2021**). Strains isolated from human feces and horse feces could both inhibit the common test microbes *S. aureus* and *E. coli*. Moreover, in our study, growth of the fungal pathogen was also hindered in presence of the antimicrobial secretion from the *Weissella* isolate. In previous studies, anticandidal activity was reported in the *W. confusa* strain BTA20 from cabbage and BTA40 from lettuce (**Bamidele *et al*., 2019**). Moreover, Baek *et al*. demonstrated in situ anticandidal activity by the strain D2-96 in rice cake (**Baek *et al*., 2012**). *C. albicans* is the most common fungal pathogen of humans which can cause diseases ranging from non-lethal superficial infections of the skin to life-threatening systemic infections, the latter particularly in immunocompromised patients (**Mayer *et al*., 2013**). The bacterial test strains used in the antimicrobial assays in the present work are also known foodborne pathogens that have been implicated with various clinical conditions (**Hossain *et al*., 2022**). Moreover, previous studies have reported several multi-drug resistant strains in these pathogenic groups. Their inhibition by the food associated indigenous microbes should therefore be considered a remarkable benefit in view of the preventive effects they may provide against associated diseases.

Any microbe, be it pathogenic or probiotic, can be of serious concern if it bears genes encoding acquired or transmissible antibiotic resistance (**Clementi and Aquilanti, 2011**). For the pathogenic bacteria, the concern is that the associated illness may become difficult to treat with the antibiotic drugs; for the beneficial bacteria it is due to the risk of horizontal gene transfer to harmful microbes in the gut (**Álvarez-Cisneros and Ponce-Alquicira, 2018**). In this concern, LAB-11 isolate was tested against several typical antibiotics in which the isolate showed resistance towards ciprofloxacin, cloxacillin, ofloxacin, and vancomycin. Resistance to multiple antibiotics has been often encountered with *W. confusa* strains wherein vancomycin resistance appeared to be the most common. The vancomycin resistant strains were identified in Moroccan raw camel milk, naturally fermented Chinese cured beef, fermented batter, human knee aspirate, giant panda feces etc. (**Lakra *et al*., 2020; Medford *et al*., 2014; Mercha *et al*., 2020; Wang *et al*., 2018; Xiong *et al*., 2019**). Gentamicin and tetracycline resistance were also detected in a few strains of W. confusa (**Mercha *et al*., 2020; Quattrini *et al*., 2020; Xia *et al*., 2019**), although LAB-11 showed intermediate resistance to both of them. The MD1 and MD2 strains described above had resistance towards vancomycin, nalidixic acid and sulphonamides-trimethoprim whereas MD2 showed additional resistance to kanamycin (**Lakra *et al*., 2020**). Strains isolated from sourdough were resistant against vancomycin, kanamycin, streptomycin, and gentamycin (**Khanlari *et al*., 2021**). Another strain identified in veal cubes demonstrated resistance to nitrofurantoin, rifampin, teicoplanin and vancomycin (Akpınar Kankaya & Tuncer, 2020). Wang *et al*. reported vancomycin and kanamycin resistance in all the five strains isolated from Chinese naturally fermented cured beef (**Wang *et al*., 2018**). The resistance to vancomycin was often described in other lactic acid bacteria as well. Previously, Guo *et al*. also reported vancomycin resistance in a few food-associated lactic acid bacteria such as *L. plantarum, L. casei*, and *L. helveticus* but the responsible genes were located in the chromosome suggesting that the resistance was not transferable (**Guo *et al*., 2017**). Moreover, in an analysis including 54 *Weissella* spp. from environmental sources, all strains showed intrinsic resistance to vancomycin, kanamycin, nalidixic acid, and teicoplanin (Fhoula *et al*., 2022). In fact, lactic acid bacteria have been reported to carry natural resistance to several of the antibiotics (**Mathur and Singh, 2005**). This intrinsic non-transferable resistance can be considered a desirable trait for probiotic bacteria in the sense that it will help these beneficial microbes survive in the gut during an antibiotic course (**Ferdouse *et al*., 2022; Zommiti *et al*., 2017**) Moreover, treatment to some diseases may include both antibiotic and probiotic ingestion at the same time such as in inflammatory bowel disease or pouchitis (**Gionchetti *et al*., 2006; Gionchetti *et al*., 2015; Mack, 2011**). The resistance might also help restore normal balance of the host intestinal flora following the antibiotic treatment. Altogether, the LAB-11 isolate can be considered relatively safe with regards to the transfer of antibiotic resistance. The ability to inhibit a range of pathogens while itself being relatively safe, therefore, suggests that natural presence of the isolate in borhani, or its exogenous application in food preparation might be of particular benefit to help acquire protection from pathogenic bacteria.

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