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Diversity of myxobacteria isolated from Weizhou Island, Guangxi, and their potential biological activities

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Abstract: This study investigated the diversity of cultivable marine myxobacteria from Weizhou Island in the Beibu Gulf of Guangxi, with a particular focus on strains exhibiting potential antibacterial activity and associated enzyme production. The *Escherichia coli* entrapment method and filter paper methods were employed for separation, followed by purification using sequential conversion techniques. Myxobacteria were identified through morphology characterization and 16S rRNA gene sequence analyses. The antibacterial activity against porcine pathogens was assessed using the plate confrontation method, and enzyme activity was evaluated through the plate assay method. From 13 island samples, 28 myxobacteria cultures were isolated, representing 13 species across 8 genera, predominantly *Myxococcus*. The antibacterial test showed remarkable activity in 9 myxobacteria strains. *Cystobacter fuscus* (GXIMD 01665c) and *Myxococcus virescens* (GXIMD 01661b) produced inhibition zones of 54.4±0.18 mm and 57.33±0.09 mm against *E. coli* L2 and *E. coli* 10, respectively. The enzyme activity experiment revealed that all 9 strains of myxobacteria could produce protease and cellulase, with 7 strains specifically producing chitinase, 6 strains producing amylase, and 4 producing lipase. These findings highlight the diverse antibacterial properties and enzymatic potential of myxobacteria from Weizhou Island. Strains GXIMD 01665c and GXIMD 01661b emerged as valuable microbial resources, holding great promise for further research and development.

Keywords: Myxobacteria, *Cystobacter fuscus*, *Myxococcus virescens*, antibacterial activity, multidrug resistance, Weizhou Island

INTRODUCTION

Despite advancements in antibiotics, widespread use has led to multidrug-resistant (MDR) bacteria and superbugs, making antibiotic resistance a critical global issue. A report [2] emphasized that antibiotic resistance is the third leading cause of death globally. In 2019, about 4.95 million deaths were linked to antibiotic-resistant infections, with 1.27 million directly attributable to this resistance. Overusing antibiotics accelerates the evolution of resistance genes, resulting in fast-developing, drug-resistant bacterial strains. The 2020 national bacterial resistance monitoring report by the China Antimicrobial Resistance Surveillance System (CARSS) noted a yearly increase in resistant strains, including *Escherichia coli* and *Klebsiella pneumoniae*, among 10 common bacterial strains [4,5]. This signifies a troubling trend in bacterial resistance. In the livestock industry, particularly pig farming, the rampant overuse of antibiotics has raised alarming concerns. Pigs can often serve as hosts for various pathogens, including *E. coli*, *Salmonella enterica*, and *Staphylococcus aureus*, due to their intestines and waste. These microscopic invaders lurk silently, posing a constant threat. This is a ticking time bomb that complicates disease control efforts in profound ways. For instance, the porcine epidemic diarrhea virus (PEDV) and porcine reproductive and respiratory syndrome virus (PRRSV) create a complex web of infections that can be hard to untangle. Consequently, there is an urgent need to expedite the discovery of new antimicrobial drugs to combat this threat.

Myxobacteria, classified as Gram-negative bacteria in the phylum Proteobacteria, subclass δ-proteobacteria,

demonstrate intricate multicellular behaviors and gliding motility, as recognized in the updated taxonomy [6,7]. Myxobacteria are renowned for their capacity to produce a wide range of secondary metabolites, rendering them a valuable source of bioactive compounds [8,9]. These metabolites exhibit various biological activities, including antiviral, antibacterial, anticancer, and antiparasitic properties [10]. The novel natural product corramycin, isolated from the myxobacterium *Corallococcus coralloides*, does not exhibit cross-resistance with commonly used clinical antibiotics [11]. This discovery underscores the potential of myxobacteria as an important source of new antibacterial agents, given their production of a diverse array of secondary metabolites and their significant contribution as a source of various enzymes [12]. Myxobacteria are remarkable for their impressive capacity to release a wide array of extracellular enzymes, such as lipases [13], cellulases [14], phosphatases [15], among others, showcasing their exceptional biological capabilities. The *Corallococcus* sp. strain EGB produces an outer membrane β-1,6-glucanase (GluM). This enzyme effectively degrades the cell walls of the plant pathogen *Magnaporthe oryzae*, making it a vital tool for predation [16]. *C.* sp. EGB produces enzymes capable of breaking down the cell walls of oomycetes *Phytophthora* [17]; it also secretes a thiaminase, CcThi1, which inhibits the growth of *P. sojae* [18]. These findings confirm the potential of myxobacteria to secrete a diverse range of microbial enzymes, rendering them well-suited for industrial applications.

Marine islands are characterized as land masses surrounded by the ocean, creating a distinctive geographical setting that nurtures abundant microbial resources [19]. Island communities in the ocean have different microbial diversity compared to continental communities [20]. Islands harbor rich microbial communities due to their extreme conditions, representing crucial patches of microbial resources essential for ecosystem functioning. The study of islands explains their ability to separate microbial communities [21]. Weizhou Island is the largest island in the Guangxi Beibu Gulf. It is located in a tropical area with a climate conducive to a vibrant coral reef ecosystem, which supports the abundance of marine resources in the Guangxi Beibu Gulf. The complex and rich marine ecological environment likely harbors a wealth of marine myxobacterial resources [23].

This study aimed to isolate and purify myxobacteria from samples of plant rhizosphere soil, moss, soil, and sediments of Weizhou Island. Strain identification was conducted through morphological assessment and 16S rRNA gene sequencing. Antibacterial activity against porcine pathogens was assessed using the plate confrontation method, while enzyme activity was evaluated by the plate assay method. This work expands on the resources of myxobacteria and lays the groundwork for further investigation into the active mechanisms of fermented extracts from these strains. It has also created possibilities for exploring valuable enzymes derived from these myxobacteria.

MATERIALS AND METHODS

Sample collection and preparation

Samples were collected from Weizhou Island, Beihai City, Guangxi Province, China, in October 2022. To isolate myxobacteria, each sample was air-dried individually in a dry environment before the enrichment procedure to reduce the contamination of other bacteria and fungi [24]. Thirty g of ground air-dried sample were mixed with cycloheximide solution (100 $\mu g \cdot mL^{-1}$), soaked in a sterile Petri dish overnight, filtered, and set aside for further analysis [25]. The specific sampling profile locations are detailed in Supplementary Table S1.

Isolation of myxobacteria strains

Myxobacteria were isolated according to separation methods [24,26]. *E. coli* was activated, and a bacterial suspension was prepared. WCX basal medium (0.15% $CaCl_2 \cdot 2H_2O$, 25 $\mu g \cdot mL^{-1}$ cycloheximide, and 1.5% agar) was spotted with the *E coli* suspension. All cultures were incubated at 30°C. Another isolation method was used [27,28], in which 2 cm^2 sterilized filter paper was covered with CNST medium (0.05% KNO_3, 0.084% $Na_2HPO_4 \cdot 12H_2O$, 0.1% $MgSO_4 \cdot 7H_2O$, 0.0018% $FeCl_3 \cdot 7H_2O$, 2% agar, 0.1% yeast solution (20 $mg \cdot mL^{-1}$), and 0.1% trace elements), and a small sample was sprinkled evenly and cultured at 30°C. Seven experiments were performed for each sample. After 7 days of incubation, myxobacterial fruiting body structures were detected under a dissecting microscope and observed for 15-20 days. New fruiting bodies were aseptically

picked using the tip of a syringe and transferred to fresh VY/2 medium (1% baker's yeast, 0.05% $CaCl_2 \cdot 2H_2O$, 0.05% $MgSO_4 \cdot 7H_2O$, 0.5 mg·mL^{-1}, and 1.5% agar) for cultivation. The isolates were transferred from the colony edge onto VY/2 medium every 4 days.

PCR amplification of 16S rDNA segment and phylogenetic analysis

The DNA of 29 strains was extracted using BT Chelex® 100 Resin. According to the method of Chelex [29], PCR amplification of the 16S rDNA segment utilized the primers 27F (5'-AGAGTTTGATCCTGGCTCAG-3') and 1492R (5'-CGGTTACCTTGTTACGACTT3'). The amplified products were observed on a 1% agar-gel electrophoresis using a gel imager. Upon confirmation of band quality, the sequencing was commissioned by using the EzBioCloud homologous comparison (https://www.ezbiocloud.net/). The 16S rRNA phylogenetic tree was constructed utilizing the neighbor-joining method in MEGA-X software.

Analysis of antibacterial activity of myxobacteria

The antibacterial activity of myxobacteria was evaluated using a lawn predation method [30,31], with few modifications. Briefly, 9 strains of porcine pathogens as prey organisms (Supplementary Table S2) were shaken and grown in beef extract peptone broth (0.3% beef extract, 1% peptone, 0.5% NaCl, 1.5% agar) at 37°C for 12-16 h. Following centrifugation at 1706 ×g for 30 min, the pelleted cells were resuspended in beef extract peptone broth to yield a dense culture with an OD_{600} of about 0.5. A 25 μL aliquot of the prey bacteria suspensions was pipetted onto a 9-cm diameter beef extract peptone agar plate, spread evenly to form a uniform lawn, and allowed to dry. The lawn served as a shared nutrient source for the myxobacteria and their prey strains. Myxobacterial isolates were cultured on VY/2 plates at 30°C for 4-5 days. Subsequently, 6-mm diameter colonies were excised and placed upside down onto predation assay plates [32]. The plates were incubated at 37°C for 3 days, after which the diameter of the inhibition zones was measured. All tests were performed at least three times, with controls including predator-free setups and positive controls containing 1 mg·mL^{-1} of either ampicillin sodium or ciprofloxacin.

Qualitative verification of enzyme production in myxobacteria

Five enzyme activity identification media for cellulase, amylase, protease, chitinase, and lipase were prepared. Myxobacterial cells were collected using a syringe tip from the colored edge of the culture, where many active cells are located. These plates were incubated at 30°C and examined after three days. The cellulase activity identification plate was stained with 1 mg·mL ^{1} Congo Red and washed with 1 M NaCl, resulting in a clear, transparent circle around the colony. The enzymatic activity was quantitatively evaluated as the ratio of halo diameter (D) to colony diameter (d), with a higher ratio indicating increased enzyme activity.

Statistical analysis

Antibacterial activity experiments were performed in triplicate and statistically evaluated using IBM SPSS Statistics 27 software and reported as the mean±SEM (standard error of mean). The differences between the means were statistically analyzed using one-way ANOVA. $P<0.05$ was considered statistically significant.

RESULTS

Myxobacteria isolates from Weizhou Island

Twenty-eight pure strains were successfully isolated from 13 different samples collected from Weizhou Island in the Guangxi Beibu Gulf, based on their distinct morphologies and 16S rRNA gene sequence analysis. All isolated strains showed fruiting body formation and swarming behavior on the surface of the VY/2 agar medium. Preliminary identification of these pure strains was carried out based on the taxonomic criteria described in Bergey's Manual of Systematic Bacteriology (2005) and The Prokaryotes (2nd ed. 1992) [28,34]. The strains were categorized into eight genera: *Cystobacter*, *Corallococcus*, *Myxococcus*, *Archangium*, *Melittangium*, *Vitiosangium*, *Pyxidicoccus*, and *Nannocystis*. *Myxococcus* was the most prevalent genus, accounting for 12 of the identified strains. The accession numbers of 28 strains of myxobacteria are shown in Supplementary Table S3.

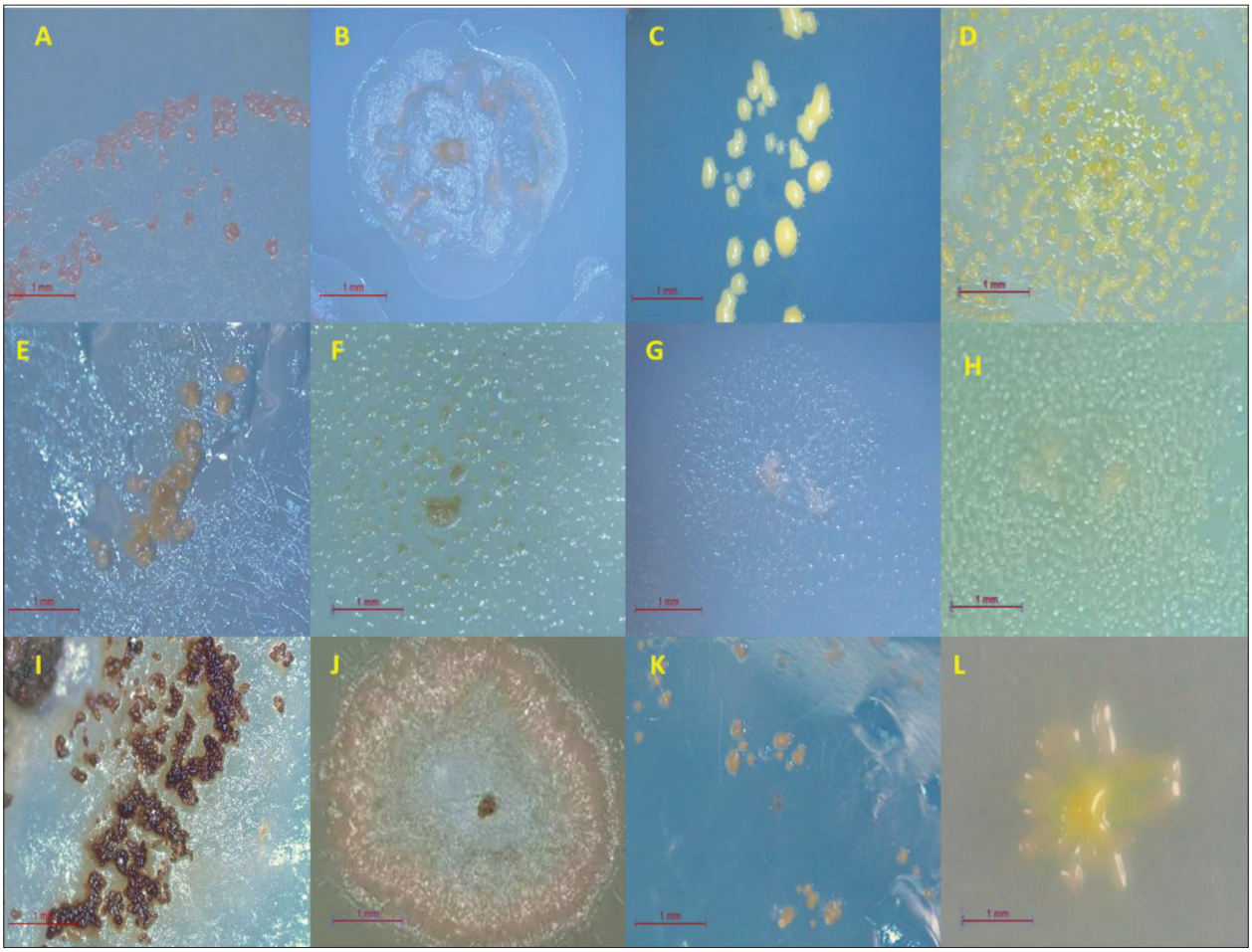

Fig. 1. Map of myxobacteria fruiting body and colony morphology. **A**, **B** – *Nannocystis exedens*, *Nannocystis* fruiting bodies and their colonies; **C**, **D** – *Myxococcus fulvus*, *Myxococcus* fruiting bodies and their colonies; **E**, **F** – *Cystobacter fuscus*, *Cystobacter* fruiting bodies and their colonies; **G**, **H** – *Corallococcus interemptor*, *Corallococcus* fruiting bodies and their colonies; **I**, **J** – *Archangium violaceum*, *Archangium* fruiting bodies and their colonies; **K**, **L** – *Melittangium boletus, Melittangium* fruiting bodies and their colonies.

The distinctive morphological characteristics of the fruiting bodies and colonies of the isolated myxobacteria are shown in Fig. 1. The rare species *Nannocystis exedens* (GXIMD 01668) produces solitary, smooth, spherical cysts that are light red. On a VY/2 plate, its colony appears rounded. As nutrients in the VY/2 medium deplete, the agar erodes, creating deep holes and furrows. In contrast, the *Melittangium boletus* strain GXIMD 01658 has round, yellowish-brown fruiting bodies with a rough surface. It grows radially on the VY/2 plate and has a sticky texture. The strain *Vitiosangium cumulatum* (GXIMD 01657) is another rare species that forms a halo around colonies on yeast agar whose fruiting bodies are light pink, elliptic, and smooth. The fruiting bodies of the strain *Pyxidicoccus fallax* (GXIMD 01669) are wave-shaped, grouped, white, and have a mucous texture.

Phylogenetic analysis of 16S rRNA in myxobacterial strains

A total of 28 myxobacterial strains were obtained from the samples through molecular identification using 16S rRNA sequencing. These strains were identified as belonging to 13 species based on sequence alignment. Phylogenetic analysis was conducted using the neighbor-joining (NJ) and maximum likelihood (ML) methods. A phylogenetic tree was constructed for these 14 representative strains based on their 16S rRNA sequences (Fig. 2). The resulting phylogenetic

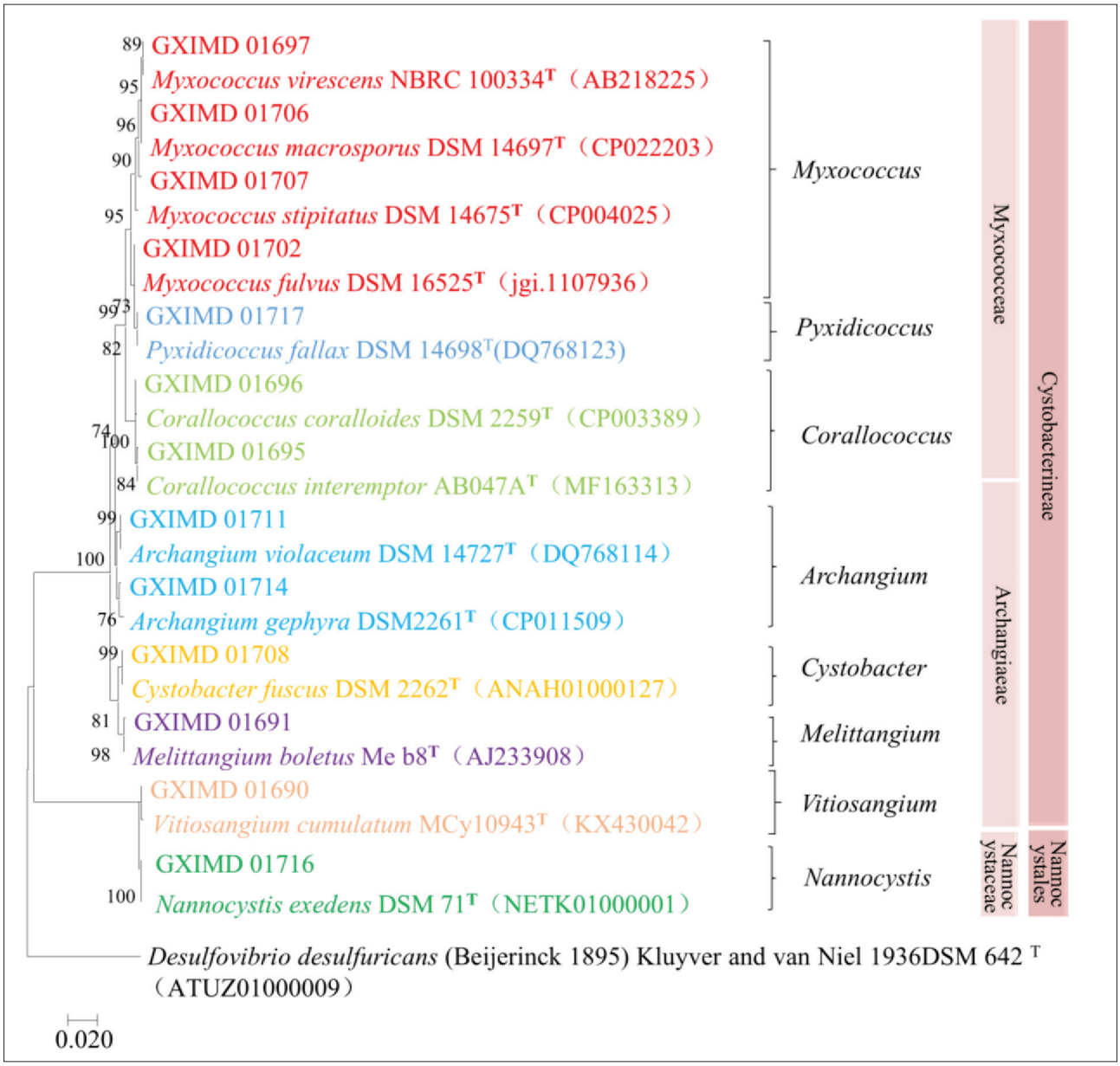

Fig. 2. Phylogenetic tree of myxobacteria based on the 16S rRNA sequence. The accession numbers in parentheses represent GenBank accession numbers of the 16S rRNA sequences for each strain. The numerical values on the clades indicate the results of 1000 bootstrap analyses; the scale of 0.020 represents the evolutionary distance.

tree revealed that the strains clustered into 8 major clades. The strains with the highest similarity were type strains. The results of the similarity comparison for the 28 myxobacterial strains are shown in Table 1.

Antimicrobial activity of myxobacteria

Twenty-four myxobacterial strains were screened for their antibacterial activity against 9 pathogenic bacteria associated with swine diseases using a plate confrontation test. After 4 days of incubation, the efficacy of the strains was evaluated based on the diameters of the inhibition zones. *Cystobacter fuscus* (GXIMD 01665c),

Table 1. Results of isolation and identification of 28 strains of myxobacteria pure culture based on 16S rRNA homology analysis

Sample Accession number	Related type strain (Accession number)	Entry number	Similarity to Type strain (%)	Sequence length (bp)	Sources
GXIMD 01657	*Vitiosangium cumulatum* MCy10943(T)	KX430042	98.66	585	Plant rhizosphere soil
GXIMD 01658	*Melittangium boletus* Me b8(T)	AJ233908	99.86	721	Plant rhizosphere soil
GXIMD 01659a	*Corallococcus interemptor* AB047A(T)	MF163313	99.86	721	Rock wall moss rhizosphere sediments
GXIMD 01659b	*Corallococcus interemptor* AB047A(T)	MF163313	100	721	Plant rhizosphere soil
GXIMD 01659c	*Corallococcus interemptor* AB047A(T)	MF163313	99.86	721	Soil sediment
GXIMD 01659d	*Corallococcus interemptor* AB047A(T)	MF163313	99.96	721	Interrhizosphere soil of alterniflora in Xijiaogou river
GXIMD 01660	*Corallococcus coralloides* DSM 2259(T)	CP003389	99.86	838	Bitter rhizosphere soil
GXIMD 01661a	*Myxococcus virescens* NBRC 100334(T)	AB218225	100	721	Rock wall moss rhizosphere sediments
GXIMD 01661b	*Myxococcus virescens* NBRC 100334(T)	AB218225	100	1395	Inter-rhizosphere soil of alterniflora in Xijiaogou river
GXIMD 01662a	*Myxococcus fulvus* DSM 16525(T)	jgi.1107936	99.86	1399	Rock wall moss rhizosphere sediments
GXIMD 01662b	*Myxococcus fulvus* DSM 16525(T)	jgi.1107936	99.86	1391	Soil sediment
GXIMD 01662c	*Myxococcus fulvus* DSM 16525(T)	jgi.1107936	99.86	721	Bitter rhizosphere soil
GXIMD 01662d	*Myxococcus fulvus* DSM 16525(T)	jgi.1107936	99.86	721	Limestone surface sandy soil
GXIMD 01662e	*Myxococcus fulvus* DSM 16525(T) DSM 16525T	jgi.1107936	99.86	721	Inter-rhizosphere soil of alterniflora in Xijiaogou river
GXIMD 01662f	*Myxococcus fulvus* contaminant ex DSM 436	CP012109	98.89	721	Inter-rhizosphere soil of alterniflora in Xijiaogou river
GXIMD 01662g	*Myxococcus fulvus* DSM 16525(T)	jgi.1107936	99.86	721	Limestone surface sandy soil
GXIMD 01663	*Myxococcus macrosporus* DSM 14697(T)	CP022203	100	721	Limestone surface sandy soil
GXIMD 01664	*Myxococcus stipitatus* DSM 14675(T)	CP004025	99.86	721	Plant rhizosphere soil
GXIMD 01665a	*Cystobacter fuscus* DSM 2262(T)	ANAH01000127	99.86	1394	Limestone surface sandy soil
GXIMD 01665b	*Cystobacter fuscus* DSM 2262(T)	ANAH01000127	99.58	721	Plant rhizosphere soil
GXIMD 01665c	*Cystobacter fuscus* DSM 2262(T)	ANAH01000127	99.86	720	Soil sediment
GXIMD 01666a	*Archangium violaceum* DSM 14727(T)	DQ768114	100	721	Plant rhizosphere soil
GXIMD 01666b	*Archangium violaceum* DSM 14727(T)	DQ768114	98.92	1387	Inter-rhizosphere soil of alterniflora in Xijiaogou river
GXIMD 01667a	*Archangium gephyra* Cb G35	MPOI01000017	100	721	Plant rhizosphere soil
GXIMD 01667b	*Archangium gephyra* DSM2261(T)	CP011509	99.20	1386	Bitter rhizosphere soil
GXIMD 01667c	*Archangium gephyra* DSM 2261(T)	CP011509	99.17	721	Inter-rhizosphere soil of alterniflora in Xijiaogou river
GXIMD 01668	*Nannocystis exedens* DSM 71 (T)	NETK01000001	99.85	1367	Water floating plant moss
GXIMD 01669	*Pyxidicoccus fallax* DSM 14698(T)	DQ768123	98.89	721	Inter-rhizosphere soil of alterniflora in Xijiaogou river

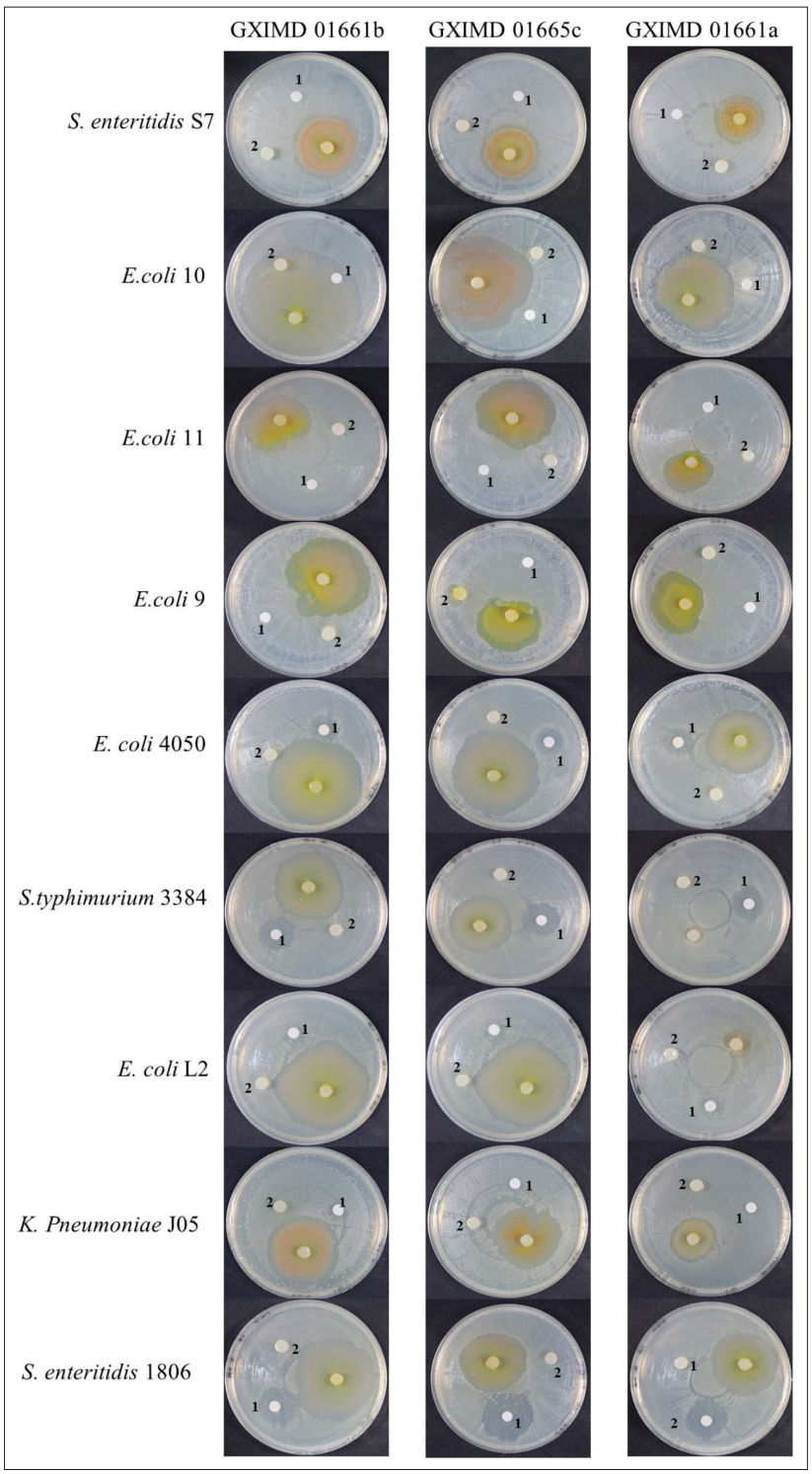

Fig. 3. Antibacterial effect of some myxobacteria strains. "Marker 1" indicates a positive control, and "marker 2" a blank control. The plate diameter is 90mm.

and *Myxococcus virescens* (GXIMD 01661a, and GXIMD 01661b) demonstrated significant antibacterial activity, producing larger inhibition zones than those of the conventional antibiotics, ampicillin, and ciprofloxacin, suggesting a broad-spectrum antibacterial effect (Fig. 3). Strain GXIMD 01661b showed the best antibacterial effect against *E. Coli* 10, reaching an inhibition zone diameter of 57.33 mm (Table 2). The results indicated that *S. enterica* S7, *E. coli* 10, *E. coli* 11, and *E. coli* 9 were the resistant strains with ineffective effects on positive controls, ampicillin sodium, and ciprofloxacin. The strains GXIMD 01661b and 01665c revealed their potential for development into effective treatments against resistant bacterial strains, inhibiting *E. coli* 9, *E. coli* 10, and *E. coli* 11 with inhibition zones above 41 mm.

Verification of enzyme production by myxobacteria

The enzyme production capabilities of 28 strains of myxobacteria were evaluated using the plate clearance method for 5 types of enzymes, protease, cellulase, diastase, chitinase, and lipase. The presence of a degradation halo around a single colony was indicative of a strain's ability to produce the respective enzyme. The enzyme production capacity was quantified using the ratio of the colony diameter to the diameter of the transparent zone (D/d). Of the 28 tested strains, 9 exhibited the ability to produce one or more enzymes (Fig. 4). All 9 strains demonstrated significant protease and cellulase activities. The enzyme activity results for 5 types of enzymes are summarized in Table 3, detailing the diameter sizes of the transparent

Table 2. Antibacterial activity of myxobacteria strains against different indicator strains, mean±SEM

Species	Strain number	Inhibition zone diameter X±SEM (mm)								
		***S. enteritidis* S7**	***E. coli* 10**	***E. coli* 11**	***E. coli* 9**	***S. typhimurium* 3384**	***E. Coli* L2**	***E. coli* 4050**	***K. Pneumoniae* J05**	***S. enteritidis* 1806**
Cystobacter fuscus	GXIMD 01665c	28.53±0.27	53.45±0.16	50.29±4.22	31.13±0.13	41.87±0.13	54.4±0.18	48.21±0.11	24.58±0.04	37.12±0.28
Myxococcus virescens	GXIMD 01661b	34.24±0.12	57.33±0.09	34.45±0.29	41.12±0.12	41.2±0.20	51.24±0.14	48.29±0.15	28.93±0.34	36.67±0.09
	GXIMD 01661a	19.27±0.15	47.46±0.18	25.50±0.50	28.07±0.07	-	-	36.77±0.07	23.67±0.36	30.63±0.08
Myxococcus fulvus	GXIMD 01662f	9.91±0.31	14.12±0.06	13.29±0.15	12.33±1.33	9.25±0.25	10.21±0.11	11.97±0.31	-	-
Myxococcus macrosporus	GXIMD 01663	17.26±0.13	-	-	8.12±0.12	-	-	-	9.11±0.42	-
Myxococcus fulvus	GXIMD 01662b	-	10.07±0.07	-	-	-		-	8.07±0.07	-
	GXIMD 01662g	-	-	-	-	-	9.63±0.04	-	-	-
	GXIMD 01662a	-	-	-	-	-	-	8.08±0.08	-	-
Myxococcus stipitatus	GXIMD 01664	-	-	-	-	-	-	18.25±0.25	-	-
Ampicillin sodium (1 mg·mL^{-1})	-	-	-	-	-	25.31±0.17	13.37±0.17	19.11±0.11	-	-
Ciprofloxacin (1 mg·mL^{-1})	-	-	-	-	-	-	-	-	10.17±0.09	-
Ampicillin sodium (100 mg·mL^{-1})	-	-	-	-	-	39.48±0.29	29.05±0.05	35.89±0.43	-	40.76±0.09
Ciprofloxacin (100 mg·mL^{-1})						-	-	-	25.59±0.01	-
Blank control	-	-	-	-	-	-	-	-	-	-

- – no antibacterial activity

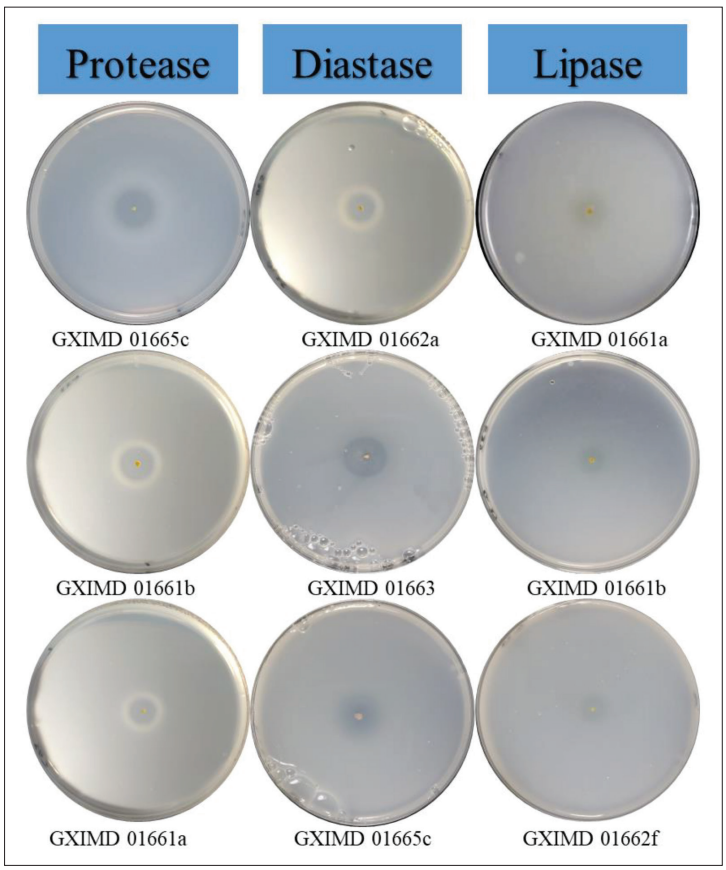

Fig. 4. Results of enzyme activity detection of some myxobacteria strains. The plate diameter is 90mm.

Table 3. Enzyme activity of 9 myxobacteria strains on 5 enzyme activity identification plates

Strain number	Enzyme species				
	Protease	Cellulase	Diastase	Chitinase	Lipase
GXIMD 01665c	+++	+	++	+	-
GXIMD 01662a	+	+	++	+	+
GXIMD 01662f	+	+	+	+	++
GXIMD 01664	+	+	-	-	-
GXIMD 01661b	++	+	+	+	++
GXIMD 01661a	++	+	+	+	++
GXIMD 01663	++	+	++	+	-
GXIMD 01662b	+	+	-	-	-
GXIMD 01662g	+	+	-	+	-

0-5: +, 5-10: ++, >10: +++
- – no corresponding enzyme activity

zones for each strain on the respective enzyme identification agar plates. *Cystobacter fuscus* (GXIMD 01665c) showed the strongest protease activity, with a D/d ratio exceeding 10 mm (Fig. 4). Among the enzymes studied, lipase production was observed in the fewest number of strains. Only *Myxococcus fulvus* (GXIMD 01662a, and GXIMD 01662f), and *M. virescens* (GXIMD 01661a, and GXIMD 01661b) could produce lipase, with D/d ratios of 2.79 mm, 6.47 mm, 7.3 mm, and 7.38 mm, respectively. *M. stipitatus* (GXIMD 01664), and *M. fulvus* (GXIMD 01662b) exhibited protease and cellulase production activities, with D/d ratios of 2.67 mm, 1.15 mm, 2.01 mm, and 1.04 mm, respectively. *M. fulvus* (GXIMD 01662g) produced protease, cellulase, and chitinase, with D/d ratios of 2.01mm, 1.04 mm, and 1.27 mm, respectively.

DISCUSSION

Our initial studies indicate that sediment samples from Weizhou Island in the Beibu Gulf region show a pH range between 7.45 and 7.89 and salinity levels from 13.20 g kg^{-1} to 14.10 g kg^{-1} [23]. The myxobacterial strains from Beibu Gulf marine habitats grow in seawater with a salt concentration >2%. Several halophilic myxobacteria, such as *Haliangium* spp. [35], *Enhygromyxa salina* [35], and *Plesiocystis pacifica* [36] were isolated from diverse marine environments. We successfully isolated 28 strains of myxobacteria pure cultures from Weizhou Island and conducted a systematic classification based on morphological features and 16S rRNA gene sequence analysis. These strains were classified into eight genera: *Cystobacter*, *Corallococcus*, *Myxococcus*, *Archangium*, *Melittangium*, *Vitiosangium*, *Pyxidicoccus*, and *Nannocystis*, with the genus *Myxococcus* predominating, demonstrating a significant presence of halotolerant myxobacteria.

Myxobacteria genomes contain numerous orphan biosynthetic pathways [36] that produce secondary metabolites with strong antibacterial properties, including polyketides, non-ribosomal peptides, terpenoids, phenylpropanoids, and alkaloids. This suggests a potential for discovering new natural products [37,38].

These metabolites are effective against both Gram-positive and Gram-negative bacteria [36,39], with unique mechanisms that make their antibacterial action different from traditional antibiotics, such as disrupting bacterial RNA polymerase, inhibiting key enzymes like acetyl-CoA carboxylase, and interfering with cell wall synthesis [37,40,41]. The study identified 9 myxobacterial strains exhibiting antimicrobial activity against 9 porcine pathogens, with *Cystobacter. fuscus* (GXIMD 01665c) and *Myxococcus. virescens* (GXIMD 01661b) inhibiting all tested pathogens. These broad-spectrum and potent antibacterial properties suggest bioactive metabolites may underlie their efficacy. The results revealed that *Salmonella enteritidis* S7 and *E. coli* strains (9,10, and 11) became resistant to the antibiotic used as a positive control. However, the myxobacteria strains GXIMD 01665c, 01661b, 01661a, 01662f, 01663, and 01662b remained effective against these resistant pathogens. This indicates that slime molds might overcome current drug-resistance mechanisms and may hold promise as candidates for novel antibiotic therapies. Myxobacterial and their compounds target biological pathways that current antibiotics cannot.

This study preliminarily explored the enzyme-producing activities of myxobacteria. Five antimicrobial myxobacterial strains, *Cystobacter fuscus* (GXIMD 01665c), *Myxococcus fulvus* (GXIMD 01662a, GXIMD 01662f), and *M. virescens* (GXIMD 01661a, GXIMD 01661b), showed an ability to produce all 5 tested enzymes. This indicates a potential link between their predatory characteristics and these enzymatic functions. Myxobacteria produce enzymes like cellulases, isoamylases, amylases, proteases, chitinases, lipases, and lysozymes to break down organic matter for nutrients. This supports their feeding and promotes material cycling and energy flow in ecosystems. For example, cellulase allows myxobacteria to consume biological macromolecules and prey on fungi and bacteria, increasing the availability of organic matter in the soil [37]. This improvement in soil structure is essential in enhancing fertility and supporting healthy plant growth. Furthermore, myxobacteria demonstrate predatory behavior and enzymatic activity, which influence the diversity and functionality of microbial communities. By decomposing organic matter, they release nutrients and hinder pathogenic microbes [44]. The *Corallococcus.* sp. strain EGB combats cucumber *Fusarium wilt* by altering the soil microbial community around plant roots, showcasing its potential as a biological control agent [45]. Myxobacteria naturally produce antimicrobials that balance microbial ecosystems.

CONCLUSIONS

Our study investigated the diversity of cultivable marine halotolerant myxobacteria from Weizhou Island, Beibu Gulf, Guangxi, focusing on strains with potential antibacterial activity and enzyme production. From 13 island samples, 28 pure cultures of myxobacteria were isolated, representing 13 species across 8 genera, with *Myxococcus* emerging as the dominant genus. The antibacterial test against porcine pathogens showed significant activity in 9 strains of myxobacteria, resulting in a positivity rate of 37.5%. *Cystobacter fuscus* (GXIMD 01665c) and *Myxococcus virescens* (GXIMD 01661b) showed broad and significant antagonistic activity against swine pathogens, indicating their potential for research and development. In the enzyme activity assays, all 9 myxobacterial strains produced protease and cellulase. Strain GXIMD 01665c is a myxobacterium that produces significant amounts of protease and cellulase, while strain GXIMD 01663 (*M. macrosporus*) was identified as a high chitosanase-producing myxobacterium. Strain GXIMD 01662a (*M. fulvus*) exhibited high amylase production, and strain GXIMD 01661a (*M. virescens*) high lipase production. These findings reveal the varied antibacterial properties and enzymatic potential of myxobacteria. Strains GXIMD 01665c and GXIMD 01661b represent valuable microbial resources with significant potential for advancing research and development initiatives.

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Author contributions: KM and WJ contributed equally to this manuscript. KM, HC, ZY, and YY participated in experiments and data collection. KM and WJ performed data analysis and drafted the manuscript. WJ and HC provided software technical support. ZS participated in the conception and design of the study and revision of the manuscript. ZS and ZY provided funding support. All authors have read and agreed to the published version of the manuscript.

Conflict of interest disclosure: The authors declare that they have no competing interests.

Data availability: All 16S rRNA sequences of myxobacteria have been deposited in the GenBank database (National Center for Biotechnology Information) under accession numbers PV168447-PV168474. The data are accessible at https://www.ncbi.nlm.nih.gov/nuccore/.

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SUPPLEMENTARY MATERIALS

Supplementary Table S1. Basic information on sample and sampling sites

Soil sample	Sample name	Latitude and longitude	Soil type
186T	Plant rhizosphere soil	109°8'30.43"E, 21°3'30.20"N	Fertile soil
187T	Plant rhizosphere soil	109°7'57.34"E, 21°3'58.91"N	Fertile soil
188T	Rock wall moss	109°7'41.38"E, 21°0'59.93"N	Vegetative soil
189T	Reef moss	109°7'39.65"E, 21°0'57.99"N	Vegetative soil
190T	Plant rhizosphere soil	109°5'52.60"E, 21°0'59.92"N	Fertile soil
191T	Soil sediment	109°5'32.70"E, 21°4'14.95"N	Sandy soil
192T	Riparian soil of Xijiaogou	109°6'9.22"E, 21°3'27.02"N	Fertile soil
193T	Reef moss	109°5'52.60"E, 21°0'59.92"N	Vegetative soil
194T	Water floating plant moss	109°7'41.38"E, 21°0'59.93"N	Vegetative soil
195T	Bitter rhizosphere soil	109°8'30.43"E, 21°3'30.20"N	Sandy soil
196T	Rhizosphere soil	109°6'33.46"E, 21°3'46.08"N	Fertile soil
197T	Limestone surface sandy soil	109°7'51.75"E, 21°1'11.89"N	Sandy soil
198T	Interrhizosphere soil of alterniflora in Xijiaogou river	109°7'57.34"E,21°3'58.91"N	Fertile soil

Supplementary Table S2. Information on nine prey bacteria

Pathogenic microorganisms	Type	Source of information
Salmonella enteritidis S7	Gram-negative bacteria	Guangxi Wuming Jiashen ecological Technology Co., LTD
Salmonella typhimurium 3384	Gram-negative bacteria	Chinese Culture Preservation Center
Salmonella enteritidis 1806	Gram-negative bacteria	Chinese Culture Preservation Center
Escherichia coli 9	Gram-negative bacteria	Guangxi Beihai Canine Cat
Escherichia coli 10	Gram-negative bacteria	Guangxi Nanning Pig Source
Escherichia coli 11	Gram-negative bacteria	Chinese Culture Preservation Center
Escherichia coli L2 (CGMCC 1.12875)	Gram-negative bacteria	Guangxi Jingxi Pig source
Escherichia coli 4050	Gram-negative bacteria	Chinese Culture Preservation Center
Klebsiella Pneumoniae J05	Gram-negative bacteria	Guangxi Wuming Pig Source

Supplementary Table S3. Accession numbers of 28 strains of myxobacteria

Strain number	Species	Accession numbers
GXIMD01660	*Corallococcus coralloides*	PV168447
GXIMD01661b	*Myxococcus virescens*	PV168448
GXIMD01666b	*Archangium violaceum*	PV168449
GXIMD01663	*Myxococcus macrosporus*	PV168450
GXIMD01668	*Nannocystis exedens*	PV168451
GXIMD01659b	*Corallococcus interemptor*	PV168452
GXIMD01664	*Myxococcus stipitatus*	PV168453
GXIMD01662d	*Myxococcus fulvus*	PV168454
GXIMD01669	*Pyxidicoccus fallax*	PV168455
GXIMD01665c	*Cystobacter fuscus*	PV168456
GXIMD01658	*Melittangium boletus*	PV168457
GXIMD01657	*Vitiosangium cumulatum*	PV168458
GXIMD01667a	*Archangium gephyra*	PV168459
GXIMD01662e	*Myxococcus fulvus*	PV168460
GXIMD01662f	*Myxococcus fulvus*	PV168461
GXIMD01659a	*Corallococcus interemptor*	PV168462
GXIMD01661a	*Myxococcus virescens*	PV168463
GXIMD01662a	*Myxococcus fulvus*	PV168464
GXIMD01662b	*Myxococcus fulvus*	PV168465
GXIMD01659c	*Corallococcus interemptor*	PV168466
GXIMD01665a	*Cystobacter fuscus*	PV168467
GXIMD01666a	*Archangium violaceum*	PV168468
GXIMD01665b	*Cystobacter fuscus*	PV168469
GXIMD01662c	*Myxococcus fulvus*	PV168470
GXIMD01667b	*Archangium gephyra*	PV168471
GXIMD01667c	*Archangium gephyra*	PV168472
GXIMD01659d	*Corallococcus interemptor*	PV168473
GXIMD01662g	*Myxococcus fulvus*	PV168474