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Marine actinomycetes: a hidden treasure trove for antibacterial discovery

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Oceans boast a substantial microbial diversity, which is widely prevalent in seawater, marine sediments, and marine organisms. In contrast to terrestrial resources explored in traditional natural product research, the habitats of marine microorganisms are distinctly unique. Actinomycetes serve as a vital source of secondary metabolites, including antibiotics and other potent natural products like streptomycin and tetracycline. They have played a pivotal role in clinical treatments for significant diseases such as pathogenic bacterial infections. Nevertheless, the extensive use of antibiotics has led to a sharp increase in the variety and number of drug-resistant bacteria, notably multidrug-resistant (MDR) and extensively drug-resistant (XDR) bacteria, in clinical settings, posing a grave threat to human survival. Consequently, there is an immediate need to discover structurally novel antibacterial natural products and develop new antibiotics. This mini review summarizes a total of 45 novel antibacterial natural products derived from marine actinomycetes, published in 2024. These products, including polyketides, alkaloids, macrolactams, and peptides, are highlighted in terms of their structures and biological activities. The objective of this article is to provide valuable insights for the research and development of novel antibiotics.

KEYWORDS

marine actinomycetes, antibacterial activity, polyketides, alkaloids, macrolactams

1 Introduction

In recent years, the emergence of multidrug-resistant (MDR) and extensively drug-resistant (XDR) bacteria has become a significant threat to global public health due to the overuse of antibiotics (Chin et al., 2018; Hu et al., 2019; Lin et al., 2019; Cui et al., 2020; Wang X. et al., 2020; Ding Q. et al., 2021; Wei et al., 2021; Zhu et al., 2021; Rasheed et al., 2024). The Lancet journal published a comprehensive analysis of the global impact of antimicrobial resistance (Murray et al., 2022). Analysis of data from 204 countries and regions revealed that antimicrobial resistance has become a major cause of death worldwide. In 2019, infections caused by antimicrobial resistance directly resulted in

1.27 million deaths and indirectly led to 4.95 million deaths, surpassing those from AIDS or malaria (Murray et al., 2022).

On the other hand, since the late 1990s, with the continuous exploitation of natural resources, discovering new bioactive natural products has become increasingly challenging (Demain, 2009; Spížek et al., 2010). Traditional strategies for the isolation and identification of natural products have led to the repeated isolation of numerous known compounds, making it increasingly difficult to discover new bioactive natural products. Over the past two decades, the number of antibiotics discovered by pharmaceutical companies has been declining (Zhang et al., 2022; Brüssow, 2024). There is an urgent need for humans to search for new natural products with novel structures, unique bioactivities, and mechanisms of action as lead compounds for new drug development (Cui et al., 2019; Ding et al., 2019; Li et al., 2019; Afrin et al., 2020; Zhang J. et al., 2020; Chen et al., 2024; Muhammad et al., 2024).

Compared to terrestrial biological resources, marine organisms inhabit vastly different environments (Liu et al., 2019; Zhong et al., 2020; Otero et al., 2023). The drastic differences in survival conditions (such as high pressure, high salinity, oligotrophic environments, lack of light, lack of oxygen, etc.) determine that marine organisms exhibit significant characteristics in metabolism, survival strategies, information transmission, and adaptation mechanisms (Surendhiran et al., 2021; Hamadou et al., 2023; Iqbal et al., 2024). Actinomycetes in marine organisms, as an important component, have always been one of the hotspots in natural product research (Jagannathan et al., 2021; Ryu et al., 2023). Eravacycline (Xerava®), a novel fluorocycline antibacterial agent, is a semisynthetic derivative of tetracycline from *Streptomyces*, which functions by inhibiting bacterial protein synthesis (Huang P. Y. et al., 2024). In 2018, it was approved by the U.S.A. FDA and exhibits potent *in vitro* activity against Gram-positive and -negative strains expressing certain common tetracycline-specific acquired resistance mechanisms. *In vitro*, eravacycline demonstrates potent activity against a broad spectrum of clinically relevant Gram-positive and -negative aerobic and anaerobic bacteria.

The actinomycetes genome typically contains a rich repertoire of biosynthetic gene clusters for secondary metabolites (Scherlach and Hertweck, 2021; Wen et al., 2024). The number of compounds we have discovered so far is far less than the number of compounds that microorganisms can produce, and a large number of potential secondary metabolites remain undiscovered (Zhang X. et al., 2020; Tianqiao et al., 2021; Zhang et al., 2021). Searching for potential novel secondary metabolites and exploring lead molecules with significant pharmacological activities, marine actinomycete secondary metabolites, as important sources of new drug precursors, are gradually demonstrating significant research value and application potential (Donald et al., 2022; Gomez-Banderas, 2022; Ngamcharungchit et al., 2023; Zhang et al., 2024).

Based on data from PubMed, Elsevier, the American Chemical Society, and Google Scholar, this review comprehensively summarizes the sources, structures, and bioactivity progress of 45 novel antibacterial active natural products isolated from marine actinomycetes in 2024. According to their structural characteristics, these natural products are classified into four major categories, including polyketides (57.8%, 26/45), alkaloids (26.7%, 12/45), macrolactams (8.9%, 4/45), and peptides (6.7%, 3/45) (Figure 1A). These secondary metabolites are primarily isolated from actinomycetes across 6 different sources, including China (60%, 9/15), Korea (13.3%, 2/15), Thailand (6.7%, 1/15), United States (6.7%, 1/15), Japan (6.7%, 1/15) and Indian Ocean (6.7%, 1/15) (Figure 1B). Among these biological samples, 12 belong to the genus *Streptomyces*, accounting for 80%, highlighting the significance of *Streptomyces* in the discovery of novel antibacterial natural products (Figure 1C). Of particular note are the remarkable findings by Professor Jongheon Shin and Kibong Oh, researchers at Seoul National University, who discovered corynetoxin U17a (32). This compound demonstrated potent antibacterial activity against *Staphylococcus aureus*, with a minimum inhibitory concentration (MIC) of 0.06 μg/mL (Lee et al., 2024). Table 1 outlines the names, sources of isolation, species, and MIC values of the antibacterial compounds identified.

2 Polyketides

Among the secondary metabolites produced by microorganisms, polyketide compounds typically constitute the majority in statistical analysis due to their large quantity and diverse types of activities (Yang et al., 2020; Li et al., 2021; Yixuan et al., 2021). They primarily originate from the condensation of short-chain fatty acids by microorganisms. Additionally, the biosynthesis of polyketides can also involve modifications of the carbon chain produced at each step through processes such as oxidation and hydroxylation, leading to the generation of numerous distinct structures and a wide range of activities.

Four unique compounds (1-4), characterized by the presence of an $_{L}$-rhodinose and spiroketal moiety, and featuring unusual continuous hydroxy groups within their macrolide structure, were isolated from a marine-derived *Micromonospora* sp. FIMYZ51 (Figure 1D) (Zhao W. et al., 2024). These compounds demonstrated strong antifungal properties against *A. niger*, with MIC values ranging from 0.5 to 2 μg/mL. Additionally, they exhibited varying levels of inhibitory activity against the pathogenic bacterium *M. luteus*, with MIC values from 0.0625 μg/mL to 1 μg/mL (Table 1). Separately, two heronamides (5 and 6) were isolated from a deep-sea *Streptomyces* sp. OUCT16-38 (Zhao Y. et al., 2024). When tested for antibacterial activity, both 5 and 6 showed significant growth inhibition against multidrug-resistant pathogens *E. faecium* and *E. faecalis*, with MIC values of 3.1 μg/mL (Table 1).

Metabolomic fingerprinting analysis, utilizing mass spectrometry (MS) and nuclear magnetic resonance (NMR), of the marine-derived actinomycete *Streptomyces* sp. FXY-T5 resulted in the identification of five novel oligomycins: 24-lumooligomycin B (7), 4-lumooligomycin B (8), 6-lumooligomycin B (9), 40-homooligomycin B (10), and 15-hydroxy-oligomycin B (11) (Figure 1D) (Feng et al., 2024). Notably, 40-homooligomycin B (10) exhibited antifungal activity that was either stronger or comparable to that of positive controls, suggesting its potential as a biocontrol agent against plant pathogens such as *C. musae* and *C. coccodes* (Table 1). In a separate study, Xiaofei Huang and

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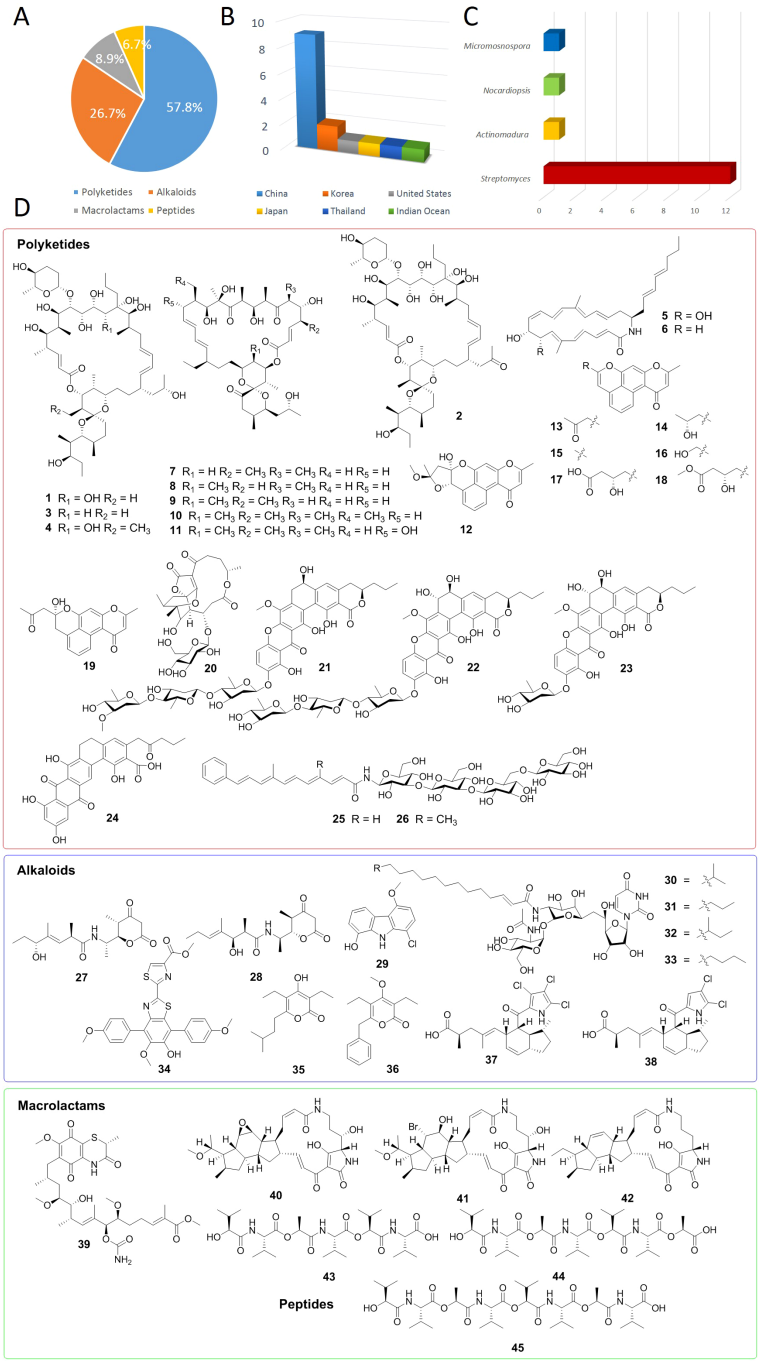

FIGURE 1
(A) Antibacterial compounds derived from marine actinomycetes according to structure types. **(B)** The different sources of marine actinomycetes. **(C)** The different genus of marine actinomycetes. **(D)** Chemical structures of compounds 1-45.

colleagues reported the discovery of eight new aromatic polyketides, naphpyrones A-H (12-19), from the heterologous expression strain *Streptomyces coelicolor* (Huang X. et al., 2024). Evaluation of their bioactivity showed that compounds 12 and 13 possessed antibacterial activity against *S. aureus*, with MIC values of 1 μg/mL and 4 μg/mL, respectively.

Glycoabyssomicin A (20), a novel abyssomicin variant incorporating a sugar moiety, was isolated from the deep-sea *Streptomyces koyangensis* SCSIO5802 through LC-MS-guided analysis (Zhu et al., 2024). When tested against a panel of Gram-positive and Gram-negative bacteria (including *M. luteus*, *S. aureus*, MRSA, and *E. coli*), it exhibited no antibacterial activity at a concentration of 10 μg per filter paper disc. During a screening of actinomycetes from mangrove rhizosphere sediment samples, a strain of *Streptomyces* sp. SCSIO 40068 demonstrated robust antibacterial activity. Further purification of its extract led to the

TABLE 1 Antibacterial compounds from marine actinomycetes.

Compounds	Source	Species	Activities (MIC, μg/mL)	Ref
Polyketides				
IB96212 (**1**)	China	*Micromonospora* sp. FIMYZ51	*M.luteus* 1; *A.niger* 1; *C.albicans* 4	(Zhao W. et al., 2024)
43-Oxy-IB96212 (**2**)			*M.luteus* 1; *A.niger* 0.5; *C.albicans* 2	
11-Dehydroxy-IB96212 (**3**)			*M.luteus* 0.0625; *A.niger* 1; *C.albicans* 4	
46-Methy-IB96212 (**4**)			*M.luteus* 0.5; *A.niger* 1-2; *C.albicans* 4	
Heronamide C (**5**)	Indian Ocean	*Streptomyces* sp. OUCT16-38	*S. aureus* 12.5; *E. faecium* 3.1; *E. faecalis* 3.1	(Zhao Y. et al., 2024)
8-Deoxyheronamide C (**6**)			*S. aureus* >50; *E. faecium* 3.1; *E. faecalis* 3.1	
24-Lumooligomycin B (**7**)	China	*Streptomyces* sp. FXY-T5	*C. musae* 0.42 mm[a]; *C. coccodes* 0.57 mm[a]	(Feng et al., 2024)
4-Lumooligomycin B (**8**)			*C. coccodes* 0.60 mm[a]	
6-Lumooligomycin B (**9**)			Inactive	
40-Homooligomycin B (**10**)			*C. musae* 0.94 mm[a]; *C. coccodes* 0.73 mm[a]	
15-Hydroxy-oligomycin B (**11**)			Inactive	
Naphpyrone A (**12**)	China	*Streptomyces coelicolor*	MRCNS[b] 64; MRSA[c] 64; *S. aureus* 1	(Huang X. et al., 2024)
Naphpyrone B (**13**)			MRCNS[b] 32; *S. aureus* 4	
Naphpyrone C (**14**)			MRCNS[b] 16; MRSA[c] 32	
Naphpyrone D (**15**)			Inactive	
Naphpyrone E (**16**)			Inactive	
Naphpyrone F (**17**)			Inactive	
Naphpyrone G (**18**)			Inactive	
Naphpyrone H (**19**)			Inactive	
Glycoabyssomicin A (**20**)	China	*Streptomyces koyangensis* SCSIO 5802	Inactive	(Zhu et al., 2024)
Kebanmycin A (**21**)	China	*Streptomyces* sp. SCSIO 40068	*S. aureus* 0.125; MRSA[c] 0.125	(Zhao M. et al., 2024)
Kebanmycin B (**22**)			*S. aureus* 2; *B. subtilis* 1	
Kebanmycin C (**23**)			*S. aureus* 0.5; *B. subtilis* 4	
Kebanmycin D (**24**)			*S. aureus* 32	
Maduraflavacin A (**25**)	China	*Actinomadura glauciflava*	*S. aureus*; 4 mm[a], 0.5 mg/mL	(Zou et al., 2024)
Maduraflavacin B (**26**)		NA03286	*M. luteus*; 3 mm[a], 0.5 mg/mL	
Alkaloids				
Alpiniamide H (**27**)	China	*Streptomyces* sp. ZS-A65	Inactive	(Pu et al., 2024)
Alpiniamide I (**28**)			*P. aeruginosa* 87.5 μM	
1-Chloro-4-methoxy-9H-carbazol-8-ol (**29**)	Thailand	*Streptomyces* sp. OUCMDZ-5511	*C. violaceum* 100	(Liu et al., 2024)
Tunicamycin VII (**30**)	Korea	*Streptomyces* sp. MBTG32	*S. aureus* 0.13; *E. faecalis* 2; *E. faecium* 2	(Lee et al., 2024)
Tunicamycin VIII (**31**)			*S. aureus* 0.13; *E. faecalis* 2; *E. faecium* 2	
Corynetoxin U17a (**32**)			*S. aureus* 0.06; *E. faecalis* 1; *E. faecium* 2	
Tunicamycin IX (**33**)			*S. aureus* 0.25; *E. faecalis* 4; *E. faecium* 8	
Nocarterphenyl I (**34**)	China	*Nocardiopsis* sp. HDN154086	*B. subtilis* 0.8; *E. coli* 0.8 μM	(Zhou et al., 2024)

(Continued)

TABLE 1 Continued

Compounds	Source	Species	Activities (MIC, μg/mL)	Ref
Alkaloids				
Nocardiopyrone D (**35**)			Inactive	
Nocardiopyrone E (**36**)			MRSA[c] 12.5; *B. subtilis* 50 μM	
Indanopyrrole A (**37**)	United States	*Streptomyces* sp. CNY-716	MRSA[c] 2; VRE[d] 2; *E. coli* 4	(Sweeney et al., 2024)
Indanopyrrole B (**38**)			Inactive	
Macrolactams				
Seco-geldanamycin B (**39**)	China	*Streptomyces* sp. ZYX-F-97	*S. aureus* 64; *B. subtilis* 64	(Yi et al., 2024)
Hydroxycapsimycin (**40**)	Japan	*Streptomyces* sp. KKMA-0239	*M. intracellulare* 50	(Shigeno et al., 2024)
Brokamycin (**41**)			*M. avium* 50; *M. intracellulare* 12.5	
Ikarugamycin (**42**)			*M. avium* 25; *M. intracellulare* 25; *B. subtilis* 3.13	
Peptides				
Homiamide A (**43**)	Korea	*Streptomyces* sp. ROA-065	*B. subtilis* 32; *S. aureus* 32; *E. coli* 64	(Ding et al., 2023)
Homiamide B (**44**)			*B. subtilis* 64; *S. aureus* 32; *E. coli* 32	
Homiamide C (**45**)			*B. subtilis* 32; *S. aureus* 64; *E. coli* 64	

[a]Zones of inhibition (mm).
[b]MRCNS, methicillin-resistant coagulase negative *Staphylococci.*
[c]MRSA, methicillin-resistant *Staphylococcus aureus.*
[d]VRE, vancomycin-resistant *Enterococcus faecium.*

identification of four new compounds, kebanmycins A-D (21-24) (Figure 1D) (Zhao M. et al., 2024). Among them, kebanmycin A (21) stood out for its potent antibacterial activity against *S. aureus* and MRSA, with an MIC value of 0.125 μg/mL, which is generally lower than that of the positive control vancomycin (MIC 1 μg/mL). Kebanmycin A's (21) notable anti-MRSA efficacy makes it a promising candidate for further drug development targeting MRSA. Additionally, two new phenyl polyene metabolites, maduraflavacins A and B (25, 26), were isolated from a rare marine-derived actinomycete strain, *Actinomadura glauciflava* NA03286 (Figure 1D) (Zou et al., 2024). These compounds displayed weak antibacterial activity against the Gram-positive bacteria *S. aureus* and *M. luteus*, respectively (Table 1).

3 Alkaloids

Alkaloids are a class of nitrogen-containing alkaline organic compounds with complex and diverse chemical structures, occupying an important position among secondary metabolites (Liu et al., 2020; Sun et al., 2020; Zhang C. et al., 2020; Wang et al., 2022; Xia et al., 2022). Alkaloids exhibit abundant physiological activities and pharmacological effects, such as antibacterial, anti-inflammatory, and antitumor activities, making them a crucial resource for drug development and possessing potential value for the research and development of new drugs (Liu et al., 2021; Bhatti et al., 2022; Waseem et al., 2022; Mei et al., 2023; Yu et al., 2023).

During an investigation of *Streptomyces* sp. ZS-A65, which was isolated from marine sediments, two novel alpiniamide-type alkaloids were discovered: alpiniamides H and I (27, 28) (Figure 1D) (Pu et al., 2024). When tested for antibacterial activity against *P. aeruginosa*, compound 28 demonstrated robust antibiofilm activity, with an MIC of 87.5 μM (Table 1). Additionally, a new 9H-carbazole derivative, compound 29, was isolated from a solid fermented medium of the mangrove-derived *Streptomyces* strain OUCMDZ-5511, collected in Thailand, which was grown under fluoride stress conditions (Figure 1D) (Liu et al., 2024). Compound 29 exhibited antiquorum sensing activity against *C. violaceum* by reducing violacein production and inhibiting biofilm formation in a concentration-dependent manner, suggesting its potential as a novel quorum sensing inhibitor (Table 1). Furthermore, four tunicamycin class compounds, tunicamycin VII (30), tunicamycin VIII (31), corynetoxin U17a (32), and tunicamycin IX (33), were isolated from the culture broth of the marine-derived *Streptomyces* sp. MBTG32 (Figure 1D) (Lee et al., 2024). These compounds displayed potent antibacterial activity against Gram-positive bacteria, particularly *S. aureus*, with MIC values ranging from 0.06 to 0.25 μg/mL (Table 1). The research also supported the notion that tunicamycins exert their antibacterial effects by inhibiting the MraY enzyme activity in *S. aureus*.

Utilizing the OSMAC strategy, researchers isolated and characterized one novel *p*-terphenyl and two new α-pyrone derivatives, specifically nocarterphenyl I (34) and nocardiopyrone D-E (35, 36), from the marine sediment-derived actinomycete *Nocardiopsis* sp. HDN154086 (Figure 1D) (Zhou et al., 2024). Notably, compound 34 features a rare 2,2'-bithiazole structure among natural products and exhibited promising antibacterial activity against *B. subtilis* and *E. coli*, with MIC values of 0.8 μM. 36 displayed notable antibacterial activity against MRSA when compared to the positive control ciprofloxacin (Table 1). In another study, Douglas Sweeney and colleagues employed

pattern-based genome mining to explore the biosynthetic potential of the marine-derived actinomycete *Streptomyces* sp. CNY-716. This led to the discovery of the first halogenated pyrroloketoindane natural products, indanopyrrole A (37) and B (38) (Figure 1D) (Sweeney et al., 2024). Indanopyrrole A (37) demonstrated potent broad-spectrum antibiotic activity against clinically relevant pathogens, including *E. coli* (MIC = 4 μg/mL), MRSA (MIC = 2 μg/mL), and VRE (MIC = 2 μg/mL) (Table 1).

4 Macrolactams

Macrolactams are a class of large molecular cyclic compounds produced by microorganisms through secondary metabolic pathways, containing amide bonds and multiple ring structures (Hong et al., 2018; Wang P. et al., 2020; Ding L. et al., 2021). Macrolactams generally exhibit pharmacological activities such as antibacterial and antitumor effects, making them an important resource for drug development.

The ansamycin derivative, seco-geldanamycin B (39), was obtained through solid fermentation of the marine-derived actinomycete *Streptomyces* sp. ZYX-F-97 (Figure 1D) (Yi et al., 2024). This compound displayed moderate inhibitory effects against *S. aureus* and *B. subtilis*, with MIC values of 64 μg/mL (Table 1). Additionally, two novel polycyclic tetramate macrolactams (PTMs), hydroxycapsimycin (40) and brokamycin (41), were isolated alongside the known PTM ikarugamycin (42) from the culture broth of marine-derived *Streptomyces* sp. KKMA-0239 (Figure 1D) (Shigeno et al., 2024). Compound 40 showed weak activity against *M. intracellulare*, with an MIC of 50μg/mL. Compound 41 exhibited moderate activity against both *M. intracellulare* and drug-resistant *M. avium*, with MICs of 12.5 and 50 μg/ml, respectively. In comparison, ikarugamycin (42) demonstrated more potent antimicrobial activity than both 40 and 41 (Table 1).

5 Peptides

Peptides are primarily synthesized by microorganisms through non-ribosomal peptide synthetase (NRPS) pathways, and these compounds typically possess complex structures and diverse biological activities (Xu et al., 2023). Peptides occupy an important position among microbial secondary metabolites, not only in terms of their large quantity but also their rich variety. They often exhibit pharmacological activities such as antibacterial, antitumor, and immunoregulatory effects, holding tremendous potential value and application prospects for new drug development (Xu et al., 2020; Liang et al., 2018; Zhang et al., 2019; Wen et al., 2020; Wong et al., 2020; Chai et al., 2021).

From a marine sediment-derived strain of *Streptomyces* sp. ROA-065 (Figure 1D), researchers isolated three novel depsipeptides named homiamides A-C (43-45) (Ding et al., 2023). These compounds displayed weak antibacterial activities against both Gram-positive (*B. subtilis*, *S. aureus*) and Gram-negative (*E. coli*) bacteria, with MIC values ranging from 32 to 64 μg/mL (Table 1).

6 Conclusion

The escalating problem of global drug resistance has spurred intensive searches for novel antibacterial agents. Marine natural products have proven pivotal in drug discovery, forming the foundation for the early stages of generic drug development (Cao et al., 2016; Hussain et al., 2021; Shams Ul Hassan et al., 2021; Hassan et al., 2022; Carroll et al., 2024; Hassan et al., 2024). This review delves into 45 compounds reported in 2024 to possess antibacterial activity, sourced from marine actinomycetes. These compounds encompass polyketides, alkaloids, macrolactams, and peptides (Figure 1D; Table 1). The review outlines the origins, chemical structures, and biological activities of these compounds. In essence, the persistent emergence of drug-resistant bacteria poses a grave risk to human health. Marine microbial secondary metabolites present a promising avenue for discovering natural antibacterial agents characterized by unique structures, robust activities, and specific modes of action. Thus, the pursuit of novel antibacterial drugs from marine actinomycetes warrants particular focus.

Author contributions

CP: Data curation, Methodology, Writing – review & editing. SH: Conceptualization, Software, Writing – review & editing. MI: Formal analysis, Resources, Writing – review & editing. SY: Validation, Writing – review & editing, Project administration. HJ: Investigation, Writing – review & editing, Project administration, Validation, Supervision.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

Publisher's note

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