Blue Biotechnology

REVIEW

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Degradation from hydrocarbons to synthetic plastics: the roles and biotechnological potential of the versatile *Alcanivorax* in the marine blue circular economy

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Abstract

Alcanivorax bacteria are among the most important hydrocarbon degraders in the ocean. Previous studies have focused mainly on the degradation processes of hydrocarbons and assessments of their roles and contributions to marine hydrocarbon and carbon cycles. Recently, studies on their involvement in the degradation of synthetic plastics are constantly emerging. Therefore, on the basis of a brief review of the research progress on the phylogeny, classification, ecology and hydrocarbon degradation of *Alcanivorax*, this review focuses on their participation in the degradation of synthetic plastics in marine environments, including their occurrence among plastispheres and the degradation characteristics of various plastics caused by themselves and their enzymes. In addition, the application potential of esterases derived from *Alcanivorax* for recycling bio-based polyester plastic waste, such as PLA and PHB, is also discussed. Given the currently known excellent hydrolysing ability of esterases derived from *Alcanivorax* on bio-based polyester plastic, as well as the existence of a wide variety of understudied esterases in their genomes, it is reasonable to assume that *Alcanivorax* and its enzymes are expected to play important roles in the future recycling of bio-based polyester plastic waste. Overall, this review provides a reference for evaluating the biotechnological potential of *Alcanivorax* and its enzymes in the marine blue circular economy and their roles in promoting sustainable management and protection of the marine environment.

Keywords *Alcanivorax*, Hydrocarbon, Biodegradation, Plastic recycling, Marine circular economy

Introduction

Hydrocarbon is a type of high-energy organic matter widely present in the ocean and is also the raw material for the synthesis of petroleum-based plastics. Anthropogenic activities, marine biosynthesis and natural seeps are the main sources [1]. Although it has long been known that photosynthetic organisms in the upper ocean are capable of synthesising hydrocarbons [2], the sources and fates of hydrocarbons in the ocean have long been focused mainly on petroleum hydrocarbons imported into the ocean by anthropogenic activities or release as natural seeps. However, it is estimated that between 0.47 and 8.3 million tons of petroleum hydrocarbons are

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discharged into the ocean every year [3]. More recently, studies have shown that the amount of annual hydrocarbons synthesised only by cyanobacteria [4] in the global ocean is approximately 100–500 times the total amount of petroleum hydrocarbons discharged by anthropogenic activities [5], that is, 308–771 million tons per year [6]. Interestingly, there is no significant hydrocarbon accumulation in the ocean, mainly due to the presence of many kinds of microorganisms capable of metabolising hydrocarbons. On this basis, a "cryptic hydrocarbon cycle" is thought to exist in the upper ocean [3], and the hydrocarbons at the core of this cycle may sustain the population of hydrocarbon-metabolising microorganisms [7]. Among them, *Alcanivorax* is one of the most widely distributed and abundant groups [8]. Therefore, they are highly important for both the marine hydrocarbon and carbon cycles.

In the past decade, an increasing number of studies have shown that *Alcanivorax* bacteria are also involved in the degradation of emerging marine contaminants, such as synthetic plastics. After all, many plastics (especially fossil-based plastics) have a C–C structural skeleton similar to that of hydrocarbons, but the former possess a greater degree of polymerisation. Considering the wide distribution of these *Alcanivorax* bacteria in the ocean, their ability to transform and degrade plastics will help maintain the healthy operation and sustainable management of marine ecosystems. In this review, recent advances in the phylogeny, taxonomy, ecology and hydrocarbon degradation of *Alcanivorax* are briefly reviewed. Research progress on their participation in the degradation of synthetic plastics in the ocean, including their distribution characteristics in plastispheres and their degradation properties for various plastics, was subsequently summarised. Moreover, the ability of their esterases to degrade bio-based polyester plastics was emphasised. Overall, this review provides a reference for evaluating the biotechnological potential of *Alcanivorax* and its enzymes in the recycling of bio-based polyester plastic waste and in the marine blue circular economy.

Phylogeny, taxonomy, ecology and hydrocarbon degradation of *Alcanivorax*

Considering the importance of hydrocarbons to marine ecosystems, the study of hydrocarbon metabolism in *Alcanivorax* has been one of the hotspots in the field of marine environmental microorganisms. Recently, numerous studies on the diversity, taxonomy, evolution, ecological distribution and hydrocarbon metabolism mechanism of *Alcanivorax* have been reported, which have greatly improved the understanding of its ecological functions and environmental effects in marine environments.

Phylogeny and taxonomy

Alcanivorax bacteria are highly diverse. They are a group of marine bacteria belonging to the order *Oceanospirillales* of *Gammaproteobacteria* within the phylum *Pseudomonadota*. In 1998, their first type species, *A. borkumensis* SK2^T, was isolated and reported [9]. In 2023, on the basis of whole-genome phylogenetic analysis, Rai et al. first retained the genus *Alcanivorax* and then transferred the remaining species to two other new genera, *Alloalcanivorax* and *Isoalcanivorax* [10]. To date, the *Alcanivorax* group consists of 3 genera and 19 species (Fig. 1, https://lpsn.dsmz.de/genus/alcanivorax) [11]. They are mainly isolated from various marine habitats (Table 1), including coastal seawater [9, 12–14], coastal

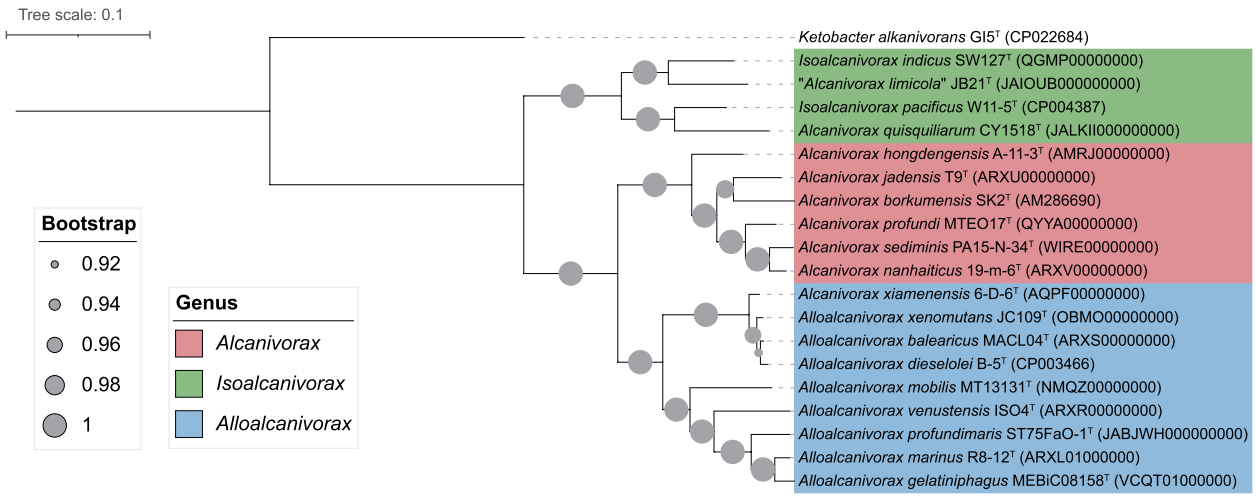

Fig. 1 Phylogenomic tree of the species within the *Alcanivorax* group

Table 1 Information on published species within the *Alcanivorax* group

Genus	Species[#]	Strain	Isolation sources (water depth, m)	Source categories	References
Alcanivorax	*A. borkumensis*	SK2^T	tetradecane-enriched consortium from seawater/sediment of Borkum island in North Sea, (na.)	coastal seawater/sediment	[9]
	A. jadensis	T9^T	Hexadecane-enriched consortium from intertidal sediment of the North Sea in German, (0)	coastal sediment	[15]
	A. hongdengensis	A-11-3^T	oil-enriched consortium from the surface seawater of the Straits of Malacca, (0)	coastal seawater	[13]
	A. nanhaiticus	19-m-6^T	oil-enriched consortium from deep-sea sediment of the South China Sea, (-2150)	deep-sea sediment	[23]
	A. profundi	MTEO17^T	deep seawater from the Mariana Trench, (-1000)	deep-sea water	[20]
	A. sediminis	PA15-N-34^T	deep-sea sediment from the eastern Pacific Ocean, (-5335)	deep-sea sediment	[24]
Alloalcanivorax	*Alloa. venustensis*	ISO4^T	offshore Atlantic ocean mesopelagic seawater from the coast of Spain, (-200)	ocean upper seawater	[18]
	Alloa. dieselolei	B-5^T	oil-enriched consortium from surface water of the Bohai Sea in China, (0)	coastal seawater	[12]
	Alloa. balearicus	MACL04^T	surface water of the saline Lake Martel in Spain, (0.1 m)	saline lake water	[27]
	Alloa. marinus	R8-12^T	oil-enriched consortium from the deep-sea water of the Indian Ocean, (-668)	deep-sea water	[21]
	Alloa. xenomutans	JC109^T	Sediment sample collected from a shrimp cultivation pond in India, (na.)	aquaculture pond sediment	[17]
	Alloa. gelatiniphagus	MEBiC 08158^T	oil-enriched consortium from coastal sediment from an oil spill site in Korea, (na.)	coastal sediment	[16]
	Alloa. mobilis	MT13131^T	oil-enriched consortium from deep-sea sediment of the Indian Ocean, (-2792)	deep-sea sediment	[25]
	Alloa. profundimaris	ST75FaO-1^T	mesopelagic seawater of the South China Sea, (-75)	ocean upper seawater	[19]
	A. xiamenensis	6-D-6^T	oil-enriched consortium from surface seawater of Xiamen island in China, (0)	coastal seawater	[14]
Isoalcanivorax	*Isoa. pacificus*	W11-5^T	pyrene-enriched consortium from deep-sea sediment of western Pacific Ocean, (-2682)	deep-sea sediment	[26]
	Isoa. indicus	SW127^T	deep seawater collected from the Indian Ocean, (-1500)	deep-sea water	[22]
	"A. limicola"	JB21^T	soda alkali-saline soil in the northeast China, (na.)	alkali-saline soil	[28]
	A. quisquiliarum	CY-1518^T	anaerobic fermentation liquid of food waste in China, (na.)	waste water	[29]

#: A., *Alcanivorax*; Iso., *Isoalcanivorax*; Alloa., *Alloalcanivorax*; na., data not available

sediment [15, 16], coastal aquaculture farm sediment [17], ocean upper layer seawater [18, 19], deep-sea seawater [20–22] and deep-sea sediment [23–26]. Recently, they have also been isolated from terrestrial high-salt habitats, such as salt lake water [27], saline–alkali soil [28] and urban fermented food wastewater [29]. Notably, 52.6% (10/19) of these species were isolated from the hydrocarbon-enriched consortia of a variety of environmental samples (Table 1), indicating once again that *Alcanivorax* is closely related to hydrocarbon metabolism in the ocean.

In addition, comparative genomic analysis of the *Alcanivorax* bacteria isolated in our laboratory from various marine habitats around the world with those of 19 known species revealed that they belong to at least 38 different species. This means that there are at least 19 potential novel species (unpublished data) within the *Alcanivorax* group, which further indicates that *Alcanivorax* species are quite diverse.

Ecology and biogeography

In natural marine habitats

Alcanivorax is a group of ubiquitous bacteria. Based on 16S rRNA gene survey and strain isolation, they were successively detected from various marine habitats, such as crude oil-contaminated seawater, beaches and sediments. Notably, they have even been detected from uncontaminated surfaces, mesopelagic and deep seawater, hydrothermal vents, mud volcanoes, gray whale carcasses, corals, sponges and dinoflagellates [30]. Recent

studies have expanded the diversity of their habitats, including the surface water of the Antarctic [31], the sediment of the Haima cold seep in the South China Sea [32], the core microbiome of laboratory-cultured flagellates [33], the coastal saline-alkaline soil [34], the surface waters of the Yellow and Bohai Seas in China [35], and the hydrothermal plumes of the South Pacific [36].

In marine plastispheres

Synthetic plastics are currently one of the most vastly widespread solid wastes in the ocean. In the past two decades, global plastic production has repeatedly reached new levels, rapidly increasing from 275 million tons in 2010 [37] to 400.3 million tons in 2022 [38]. That is, the total plastic production increased by nearly 71%. In 2022, the produced plastics were mainly composed of polypropylene (PP, 18.9%), low- and linear low-density polyethylene (LD- and LLDPE, 14.1%), polyvinyl chloride (PVC, 12.7%), high- and medium-density polyethylene (HD- and MDPE, 12.2%), polyethylene terephthalate (PET, 6.2%), polyurethane (PU, 5.3%), polystyrene (PS, 5.2%), and others (25.4%) [38]. Unfortunately, owing to improper use and management, a significant proportion of these pollutants are discharged into the ocean, estimated at approximately 4.8 to 12.7 million tons in 2010 alone [37]. According to the latest assessment of the United Nations Environment Programme (UNEP), up to 23 to 37 million tons of plastic waste annually will be discharged into the ocean by 2040 [39].

Plastics and their degradation products, micronano plastics (MNPs), have invaded almost all types of marine habitats [40]. They not only are widely distributed in coastal areas and estuaries [41, 42] but also have been detected in other particular marine habitats, such as coral reefs [43], cold seeps [44], ocean gyres [45, 46], deep seas [47], hadal trenches [48] and polar regions [49–51]. The average abundances of plastics and MNPs in global ocean water and sediments are estimated to be 0.1–1 and 10^3–10^4 particles/m^3, respectively [52]. So many plastics are present in the ocean, providing a new habitat for marine microorganisms called the plastisphere [53, 54]. An integrated analysis of 16S rRNA high-throughput sequencing and metadata from 2229 different marine and terrestrial sampling sites revealed that the abundance of hydrocarbon-degrading bacteria, including the *Alcanivorax* found at marine sites, in the microbial communities of the plastisphere was consistently significantly higher than that of non-plastic controls [55].

Previous studies have shown that hydrocarbon-degrading bacteria such as *Alcanivorax* are the early key colonisers of the plastisphere and play an important role in community formation of the plastisphere [56–58]. As shown in Table 2, *Alcanivorax* usually occurs in two different types of plastispheres. The first is the in situ plastisphere (hereafter called ISP), which naturally forms on various plastics in an in situ marine environment. The second one is the ex situ plastisphere (ESP), which is obtained when environmental samples are enriched under controlled conditions in the laboratory using various kinds of plastics as sole carbon and energy sources. Notably, the abundance of *Alcanivorax* was significantly lower in ISP ($p < 0.01$) than in ESP (Fig. 2 and Table 2), and this difference was probably caused by the distinct supply of nutrients such as nitrogen and phosphorus. Moreover, the abovementioned ISPs and ESPs mainly originated from coastal areas and laboratories, while those from the deep sea or open ocean are still scarce. This may be due to sampling obstacles and high costs from deep sea or ocean environments.

In ISPs, the plastic types of the plastisphere containing *Alcanivorax* vary, such as PET, PE, PP, PA, PU and PS etc.. However, the abundance of *Alcanivorax* in the microbial community of these plastispheres is generally low (approximately 1% or less, Fig. 2 and Table 2). For example, Oberbeckmann et al. analysed the microbial community succession on the PET plastisphere obtained from three buoys in the North Sea in different seasons. The results showed that *Alcanivorax* colonised the PET plastic surface more specifically than it colonised the glass surface and in situ seawater, but its relative abundance in the PET plastisphere was lower, especially in summer [59]. Similarly, Delacuvellerie et al. analysed the microbial community structure in plastispheres collected from Calvi Bay in the Mediterranean Sea and reported that the proportion of *Alcanivorax* was less than 0.2% [60]. Subsequently, Delacuvellerie et al. used metagenomic and macroproteomic methods to further analyse the microbial structure and function of PE and PP plastispheres collected from Calvi Bay. Although *Alcanivorax* was detected in the metagenome, no proteins that might be involved in plastic degradation were detected in the metaproteome, suggesting that *Alcanivorax* may not participate in the biodegradation of PE and PP plastics under the conditions of this study [63]. Another possibility is that *Alcanivorax* is indeed involved in the degradation of PE and PP in situ. However, the target proteins involved in degradation are redundant or generic hydrocarbon degradation-related enzymes, such as oxygenases and carboxylases. Moreover, the detection limit of the metaproteome is not as good as that of a single bacterial proteome. Together, these factors may result in negative feedback of the metaproteome. In addition, Hou et al. studied the succession of microbial communities on PET, PE and PP plastic surfaces in an offshore aquaculture farm in China and reported that

Table 2 Occurrence of different *Alcanivorax* spp. in marine plastispheres

Plastisphere types	Plastics	Habitats	Source category	Source details	Temp (°C)	Closest neighbour	Proportion in plastsphere	References
in situ plastisphere (ISP)	PET	Coastal sea	plastics debris	Biofilm of PET drinking water bottles attached on SmartBuoys in North Sea off the U.K. coast	7.4–18.3	*Alcanivoracaceae*	a small proportion, no precise data	[59]
	LDPE	Coastal sea	plastics debris	Macroplastics (> 5 cm) collected from Calvi Bay of northern Corsica in the Mediterranean Sea	20 and 30	*A.borkumensis*	< 0.2% of the bacterial community from nature original plastics	[60]
	HDPE, PS	Coastal sea	plastics debris	Plastic debris collected from coastal areas of Maxwell Bay in King George Island in the Antarctica	nd	*Alcanivorax* spp.	1.24% in the clone library of the HDPE plastisphere	[61]
	PE,PE cling film	Coastal sea	plastics debris	Macroplastics (4–5 mm) incubated in a large yellow croaker cage in Xiangshan harbour in the East China Sea	summer	*Alcanivorax* spp.	> 1% in the bacterial clone library from the PE cling film	[62]
	PE, PP	Coastal sea	plastics debris	Macroplastics were collected from the Oscellucia beach of Calvi Bay in Corsica of the Mediterranean Sea	17.8	*Alcanivorax* spp.	detected in metagenomes but not in metaproteomics	[63]
	PA, PU, PE, PS	Coastal sea	plastics debris	Floating plastics collected at ten stations along the continental shelf off the coast of South Brazil	nd	*Alcanivorax* spp.	detected, but not the top10 most abundant bacterial OTUs in the floating plastisphere	[64]

Table 2 (continued)

Plastisphere types	Plastics	Habitats	Source category	Source details	Temp (°C)	Closest neighbour	Proportion in plastsphere	References
ex situ plastisphere (ESP)	PET film	Coastal sea	coastal seawater &sediment	Seawater and sediment samples collected from the site Torre Faro located at the Messina Strait	RT	*Alcanivorax* spp.	> 12.6% in the PET-enriched bacterial community	[65]
	PET	Coastal sea	plastics debris	Bulk marine plastic debris collected from Porthcawl beach in Wales, UK	30	*Alcanivorax* spp.	> 15.06% at later stage in the amorphous PET films enriched consortia	[66]
	PET	Deep-sea	deepsea sediment	Deep-sea surface sediment collected from the eastern central Pacific Ocean	RT	*Alloa. xenomutans*	51% in PET-enriched consortia	[67]
	PE, PHBV	Lab Aquarium	coastal seawater	Seawater directly pumped at 30 m from the coast and 4 m depth in Banyuls bay of NW Mediterranean Sea, France	12.5–13.5	*Alcanivorax* spp.	10% at early stage of plastisphere formation on PE power and films	[56]
	LDPE	Coastal sea	plastics debris	Macroplastics (> 5 cm) collected from Calvi Bay of Northern Corsica in the Mediterranean Sea	20 and 30	*A.borkumensis*	> 60% of the bacterial community after 2 months of culture in plastic-associated biofilm	[60]
	HDPE	Lab Aquarium	seawater	HDPE microbeads incubated in a lab aquarium after 108 h at room temperature	RT	*Alcanivorax* spp.	Top 6 most abundant bacterial OTUs in the enriched consortia	[57]
	PE, PS, PLA, PHBV, PCL	Lab Aquarium	coastal seawater	Seawater directly pumped at 30 m from the coast and 4 m depth in Banyuls bay of NW Mediterranean Sea	12.5–19.5	*Alcanivorax* spp.	17% of the order *Oceanospirillales* (*Alcanivorax* as one of major members) in all plastic biofilms	[68]
	PE, PLA	Lab flasks	coastal seawater	Coastal seawater collected from Qingdao in the Eastern China	37	*Alcanivorax* spp.	55% and 20% in PE and PLA biofilm, respectively	[69]
	EPS	Coastal sea	plastic debris	Expanded polystyrene waste samples obtained from epilittoral zone of a mangrove in Zhangzhou, China,	28	*Alloa. xenomutans*	Top 5 most abundant bacterial OTUs in the enriched consortia	[70]

PET polyethylene terephthalate, *PE* polyethylene, *LDPE* low-density polyethylene, *HDPE* high-density polyethylene, *PS* polystyrene, *PP* polypropylene, *PU* polyurethane, *PHBV* poly(-3-hydroxybutyrate-co-3-hydroxyvalerate), *PLA* polylactic acid, *PCL* polycaprolactone, *EPS* expanded polystyrene, *nd*. no data, *RT* room temperature

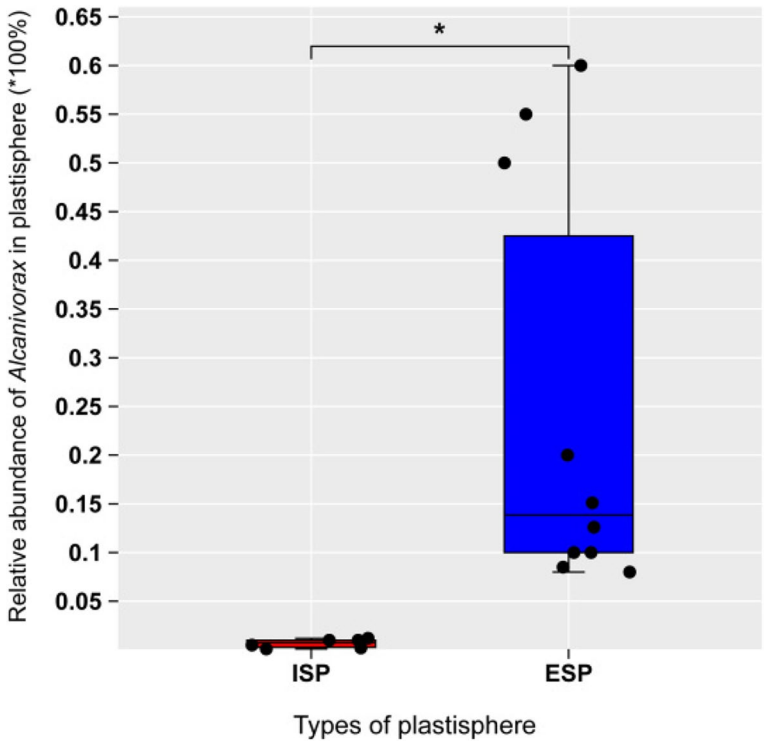

Fig. 2 Relative abundance of *Alcanivorax* spp. in the plastisphere. ISP, in situ plastisphere; ESP, ex situ plastisphere

Alcanivorax preferentially colonised the PE surface and accounted for more than 1% of the PE plastisphere [62]. Lacerda et al. carried out qualitative and quantitative analyses of microorganisms in floating plastispheres collected from 10 stations along the southern coast of Brazil. Although *Alcanivorax* was detected, its abundance was very low, which resulted in it not being one of the top ten dominant groups in these plastispheres [64]. Cappello et al. conducted 16S rRNA gene clone library sequencing analysis on the microbial communities of HDPE plastispheres collected from Antarctica. The results revealed that the proportion of *Alcanivorax* was only approximately 1.24% [61].

Like those of ISPs, in ESPs, the plastic types of plastispheres containing *Alcanivorax* also vary and are mainly fossil-based plastics, including PET, PE, PS and PCL. Moreover, some plastisphere-originated bio-based plastics, such as PHBV and PLA, have also been reported. For example, three different types of PET plastic-degrading consortia were obtained after enrichment at 30 °C in the laboratory using plastic debris collected from Porthcawl Beach in the UK as inoculants. The results revealed that *Alcanivorax* became the dominant group in the later stage of the enriched consortium with the amorphous PET film, with a maximum abundance of 15.06% [66]. Similarly, several other PET-degrading consortia were obtained from seawater and sediments of the Messina Channel in Italy. Subsequent analysis revealed that the abundance of *Alcanivorax* reached 12.6% [65].

In the PE-enriched consortia, the abundance of *Alcanivorax* further increased. For example, Delacuvellerie et al. collected floating plastics and sediments from Calvi Bay in the Mediterranean Sea and enriched them with LDPE for 2 months at 30 °C. The proportion of *Alcanivorax* in the consortia reached 60%, while its abundance in the original plastisphere was less than 0.2% [60]. Girard et al. placed HDPE in a laboratory aquarium and cultured it at room temperature for 108 h. After that, they reported that *Alcanivorax*-related OTUs were among the six dominant OTUs in the enriched consortia [57]. Chu et al. studied the effects of metal ions on microbial communities in coastal seawater plastispheres. The results revealed that the abundance of *Alcanivorax* in the PE and PLA plastispheres reached 55% and 20%, respectively. Furthermore, the addition of Zn^{2+} significantly promoted their abundance in the PE plastisphere, but their abundance in the PLA plastisphere was significantly reduced [69]. To evaluate the degradation of non-biodegradable and biodegradable plastics in seawater, Ghiglione et al. immersed different types of plastics in an aquarium while maintaining seawater exchange with in situ seawater pumped from the Mediterranean Sea to maintain

the temperature at 13.5 °C. In the first short-term 45-day experiment, *Alcanivorax* bacteria were the key colonisers (up to 10% in abundance) at the beginning of PE plastisphere biofilm formation, but strangely, they did not colonise the PHBV surface [56]. In the subsequent 7-month long-term experiment, regardless of the type of plastic (such as the non-biodegradable plastics PE and PS and the biodegradable plastics PLA, PHBV and PCL), in the early stages of biofilm formation (3–10 days), *Alcanivorax* bacteria were always the dominant group [68]. In addition, Liu et al. used EPS plastic debris collected from mangroves as inoculants and subjected them to 3 rounds of enrichment at 28 °C with PS as the sole carbon and energy source. Finally, they reported that *Alcanivorax* became the 5th dominant group in the enriched consortium [70].

Notably, Zhao et al. first investigated the diversity of PET-degrading bacteria in deep-sea sediments. They collected deep-sea surface sediments from the eastern Pacific Ocean and enriched them at room temperature for two years using PET as the sole carbon and energy source. Subsequently, *Alcanivorax* was found to be the most dominant group in the enriched consortia, with a maximum abundance of 51% [67]. However, there was no evidence in this study to prove that *Alcanivorax* degrades PET. Overall, this study is perhaps the only one to report the detection of large amounts of *Alcanivorax* in the plastisphere originating from the deep sea.

Collectively, bacteria of *Alcanivorax* are widely distributed in marine plastispheres around the world (Fig. 3), and they are more likely to occur in the plastispheres of fossil-based plastics (Table 2). This could be explained by the following reasons. First, fossil-based plastics continue to release additives. Second, they also dissociate low-molecular-weight (LMW) aliphatic polymers due to physical, chemical or biological factors. Coincidentally, these two substances are analogues of the primary hydrocarbon substrates of *Alcanivorax*.

Degradation of hydrocarbons

As a typical representative of aliphatic hydrocarbons, alkanes have always been a common substrate for the study of hydrocarbon metabolism in *Alcanivorax*. Currently, the alkane metabolism mechanism of *Alcanivorax* is relatively clear. Specifically, terminal or subterminal oxidation is the key initiating step for *Alcanivorax* to degrade alkanes of different chain lengths. This key step converts alkanes to primary or secondary alcohols and significantly improves the bioavailability of hydrophobic hydrocarbons. These resulting alcohols are further oxidised to the corresponding aldehyde or ketone and finally converted into fatty acids. Finally, fatty acids are oxidised to CO_2 via beta-oxidation [71, 72]. According to the type of protein family, alkane hydroxylases can be divided into several different types, such as AlkB, AlmA, LadA and cytochrome P450 oxidase. Notably, *Alcanivorax* often employs several different types of alkane hydroxylase to metabolise alkanes.

Recently, studies on the alkane metabolic mechanisms of *Alcanivorax* other than the initial hydroxylation of

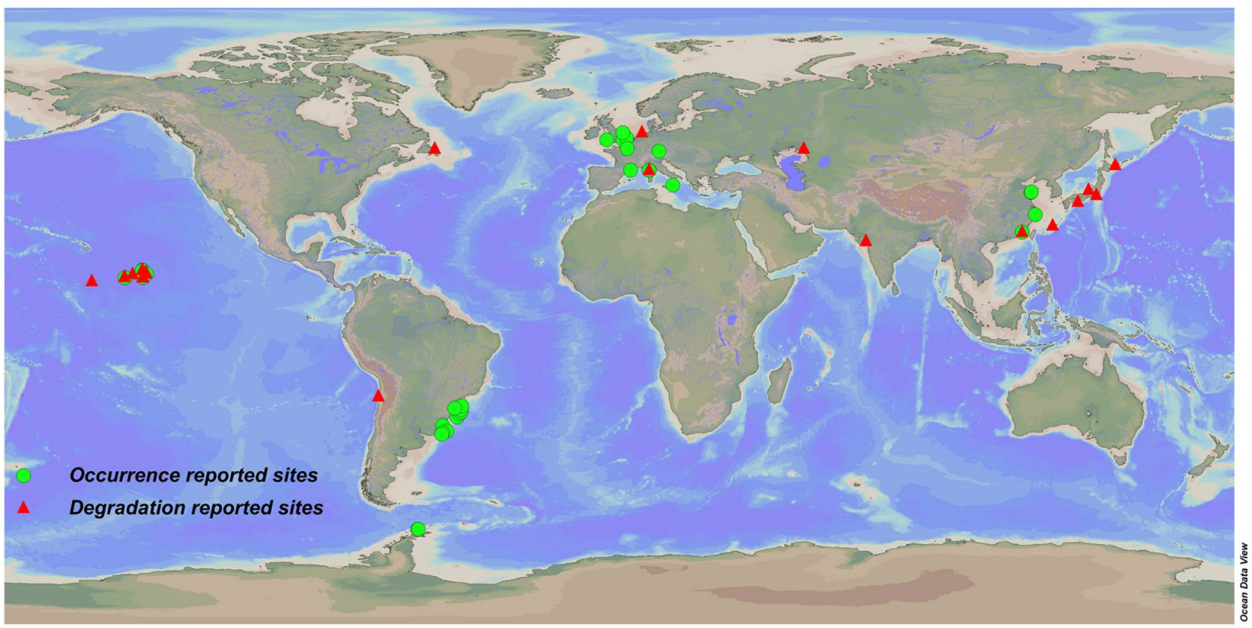

Fig. 3 Known sites for *Alcanivorax* occurring in a plastisphere or being reported to degrade plastics

alkanes have emerged. (i) Small RNA (sRNA) regulation during hydrocarbon metabolism. Wei et al. identified 549 candidate sRNAs from the transcriptome of strain *A. dieselolei* B-5 after alkane induction and nonalkane induction. These sRNAs came from almost any position in the genome of strain B-5 and were also widely present in other *Alcanivorax* bacteria. In addition, several core sRNAs, including 6S RNA, M1 RNA and tmRNA, were found to be involved in metabolic regulation during alkane degradation [73]. (ii) Hydrocarbon metabolism mechanism based on AlkB protein structure analysis. In 2023, two research groups successively decoded the 3D structures of the AlkB protein based on cryo-electron microscopy analysis and reported that the catalytic active center of AlkB has an unexpected diiron center configuration. Finally, they deduced that one of the iron atoms, after interacting with O_2, produced a highly oxidising Fe(V) oxo complex, which completed the initial oxidation of the hydrocarbon terminal. Moreover, molecular determinants for the substrate selectivity of AlkB have also been identified in detail [74, 75]. These results are consistent with previous studies on key amino acid residue base mutations in AlkB substrate channels in other hydrocarbon-degrading bacteria [76]. These studies further enhance the understanding of the mechanism of initial hydroxylation and substrate selection of AlkB. (iii) In addition, a breakthrough has been made in the analysis of the role and mechanism of biofilms in hydrocarbon degradation using biophysical methods. During the consumption of hydrocarbons, *Alcanivorax* often forms biofilms on the surface of hydrophobic hydrocarbon droplets. However, the role of biofilms during degradation is unclear. Prasad et al. revealed the relationship between biofilms formed by *A. borkumensis* SK2 and hydrocarbon degradation using a microfluidic observation system combined with high-resolution confocal microscopy. Specifically, SK2 reshapes oil droplets by forming a dendritic biofilm, which speeds up the consumption rate of hydrocarbon droplets [77–79]. This study deepens the understanding of the hydrocarbon metabolism mechanism and provides implications for how to use marine bacterial communities to enhance the remediation of environments polluted with oil.

In summary, the abovementioned studies on the hydrocarbon-degrading mechanism of *Alcanivorax* provide useful information for the analysis and understanding of the degradation process of synthetic plastics, especially fossil-based aliphatic plastics.

Degradation of synthetic plastics

Considering that plastic and MNPs pollution has become a public concern of global marine pollution, the UN has called for effective solutions to be found as soon as possible [80]. According to the abovementioned UNEP technical report, plastic waste is currently the most abundant, harmful and persistent component of marine litter, accounting for at least 85% of all marine litter [39]. Although the total amount of plastic currently entering the ocean is increasing, plastic recycling, as one of the means of controlling plastic pollution, still needs to be strengthened. Plastics Europe estimated that only 9.5% of total plastic production was recycled in 2022 [38]. That is, most plastic ends up in landfills, and 32% of it enters the ocean [60].

Compared with large pieces of recyclable plastic, less evident MNPs pose a more serious threat to marine ecological environments and human health, and the need for their treatment is more urgent. When large pieces of plastics are discharged into the ocean, they are further decomposed into smaller microplastics (< 5 mm) and nanoplastics (< 1 μm) under physical and chemical conditions (such as UV, mechanical force and high hydrostatic pressure) [53] and biological action [81, 82]. Previous studies have shown that only approximately 1% of plastic floats on the ocean surface, with the remaining 99% entering the water column or seafloor sediments [83, 84]. After being ingested and accumulated by marine organisms, plastics pass through the food chain, endangering the entire marine ecosystem and human health. With increasing global MNPs pollution, almost all types of MNPs particles have been detected in human organs, increasing the potential risk of people suffering from non-communicable diseases [85]. The most recent example is that PE and PVC MPNs were detected in carotid plaque specimens from 59.5% of patients who participated in the study. The presence of these MPNs was demonstrated to increase the risk of cardiovascular disease [86, 87].

Recently, physicochemical methods have been developed to address MNPs pollution in the environment. Although these methods are very efficient, secondary pollutants, such as chemical reagents [88] and safety-unknown nanomaterials [89], are inevitably introduced. In contrast, the biodegradation of MNPs, although slow, may be the main or even the only way to remove MNPs in many particular marine environments. For example, plastics floating in ocean garbage patches [90] appear to be recoverable by direct fishing. However, the high cost of recycling may be prohibitive because these ocean garbage patches are thus far from land. Therefore, these floating plastics and their disintegrating MNPs will eventually sink into the ocean [91]. Their ultimate fate is likely to be degraded by various microorganisms. Although this biodegradation process is very slow, it is ongoing. On the other hand, the presence of these MNPs is also a continuous evolutionary driver for marine microbes.

Currently, many marine microorganisms participate in the biodegradation of plastics in many different ways under aerobic or anaerobic conditions [92, 93]. It is foreseeable that the in-depth study of highly active plastic-degrading microorganisms and their enzymes will promote their application in plastic recycling and contribute to the development of a marine blue biological circular economy and sustainable management of the marine ecological environment.

Degradation of fossil-based plastics

It is believed that the fossil-based aliphatic plastics represented by PE and PP are non-biodegradable, but recent studies have shown that there are microorganisms that can transform or degrade these plastics on land or in marine environments. *Alcanivorax* is one such member.

The degradation of fossil-based plastics by *Alcanivorax* is one of the current research hotspots of marine microorganisms. This is mainly because the world's largest production of several common plastics, such as PP, PE, PVC, PET, PUR, and PS, are fossil-based [38]. Generally, most of the reported plastic-degrading *Alcanivorax* originated from coastal environments, and few studies have been conducted in the deep sea (Table 3). Moreover, current studies have focused mainly on the degradation characteristics of *Alcanivorax* against different types of plastics, and research on the degradation mechanism is still limited.

In coastal areas

Alcanivorax bacteria isolated from coastal areas are thought to degrade fossil-based plastics, although whether they can degrade PE or PP is still controversial.

At present, many studies have reported the degradation of PE plastics by *Alcanivorax* (Table 3). For example, an *A. borkumensis* strain isolated from a plastic-enriched consortium was able to form biofilms on the surfaces of LDPE, PET, and PS in artificial seawater media containing small amounts of hexadecane. The biomass of the LDPE biofilm was much higher than that of the PET and PS biofilms. Furthermore, when the strain was cultured with LDPE film at 30 °C for 80 days, the weight loss ratio of the LDPE film reached 3.5 ± 0.34%. In addition, ATR-FTIR spectra also confirmed that obvious oxidation peaks were observed on the surface of the LDPE films [60]. Zadjelovic et al. collected plastic debris from coastal beaches in Chile and enriched plastic-degrading bacteria with PHB as the sole carbon and energy source. The strain *Alcanivorax* sp. 24 was subsequently isolated. This strain could cause the weight loss of LDPE films to reach 0.9% in 34 days at 30 °C and reduce the molecular weight of LDPE films. Further proteomic analysis revealed that many metabolic pathways related to aliphatic compound degradation were upregulated in strain 24. Therefore, combined with the oxidation phenomenon on the surface of the LDPE film and the increased concentration of superoxide in the culture system, these authors suggested that the initial degradation of the LDPE membrane by strain 24 was achieved through the production of extracellular reactive oxygen species [96]. To the best of our knowledge, this study is the first to report the PE degradation mechanism of *Alcanivorax*. In addition, Zhang et al. identified a cold-tolerant strain, *Alcanivorax* sp. N3-2A, which was isolated from petroleum hydrocarbon-polluted coastal seawater in southeastern Canada and could degrade LDPE at 4, 15 and 22 °C by quantifying the total bacterial protein in the culture using LDPE film as the sole carbon source [81]. Khandare et al. screened 4 strains with good degradation ability for LDPE membranes from 216 marine bacterial strains and reported that the strain *Alcanivorax* sp. H-265 could reduce the weight of LDPE membranes by 0.46% and 0.97% in 30 and 90 days, respectively [95].

Although the abovementioned studies have all claimed that *Alcanivorax* can degrade LDPE to some extent, studies using more precise detection methods have indicated that *Alcanivorax* may not be able to degrade LDPE on its own in the absence of other simple carbon sources. For example, Rose et al. established a method using gas chromatography to determine CO_2 release and then quantitatively analysed the ability of microorganisms to degrade plastics. They measured the amount of CO_2 released in culture systems with or without LDPE as the sole carbon and energy source and demonstrated that *A. borkumensis* SK2 does not degrade LDPE [94]. Coincidentally, there have been calls for more robust and accurate methods, such as isotopic labelling, to assess the ability of microbes to degrade plastics [105].

PP is the most produced plastic in 2022, accounting for 18.9% of the total plastics. Although it is a highly polymerised plastic and has strong resistance to biodegradation, a recent study by Koike et al. revealed that *Alcanivorax* can degrade liquid PP (PP oligomers) [97]. Specifically, mesopelagic seawater (at a water depth of -374 m) collected from the coastal sea of Japan was enriched with liquid PP at 10 °C, after which the sw2 strain was isolated from the enriched consortium with 100% sequence identity with the strain *A. borkumensis* SK2. Strain sw2 could not grow with liquid PP as the sole carbon and energy source. However, liquid PP can be degraded by this strain in the presence of other simple carbon sources, such as hexadecane and sodium pyruvate. Furthermore, degradation intermediates such as pentamers and hexadecamers were detected by GC–MS, indicating that the degradation of PP did occur. Finally, they deduced that the degradation mechanism

Table 3 Degradation of synthetic plastics by different *Alcanivorax* spp

Plastics	Habitats	Source category	Source details	Temp. (°C)	Closest neighbour	Strain	Evidence of the degradation	References
Fossil-based								
LDPE	Coastal sea	plastic debris	Macroplastics (> 5 cm) collected from Calvi Bay in Northern Corsica of the Mediterranean Sea	30	*A. borkumensis*	nd	Confirmed by LDPE film weight loss (3.5% ± 0.34) and observed oxidative peaks in ATR-FTIR spectra	[60]
LDPE	Coastal sea	seawater and sediment	Seawater/sediment collected near the isle of Borkum in the North Sea	30	*A. borkumensis*	SK2	Does not seem to utilise LDPE as a substrate confirmed by CO2 produce based on GC analysis	[94]
LDPE	Unknown	nd	Marine bacteria but no isolation information	30	*Alcanivorax* sp.	H-265	Dry weight loss of LDPE films after 30 and 90 days of incubation were 0.46% and 0.97%, respectively	[95]
LDPE	Coastal sea	plastic debris	Plastic debris collected from the high intertidal zone at La Rinconada beach, Antofagasta, Chile	30	*Alcanivorax* sp.	24	Confirmed by weight loss 0.9% within 34 days and the molecular weight reduction of LDPE film	[96]
LDPE	Coastal sea	seawater	Oil-contaminated coastal seawater collected from southeast coast of Newfoundland Canada	4, 15, 22	*Alcanivorax* sp.	N3-2A	Confirmed by strain growth using total protein quantify	[81]
PP	Coastal sea	seawater	Mesopelagic water collected from the coastal area of Muroto, Kochi, Japan	10	*A. borkumensis*	sw2	Liquid PP-degradation identified by GC–MS	[97]
EPS	Coastal sea	plastic debris	EPS waste samples obtained from epilittoral zone of a mangrove in Zhangzhou, China	28	*Alloa. xenomutans*	ZN12A4	Confirmed by the changes in physical properties of PS surface, ATR-FTIR data, and weight loss etc	[70]
PCL	Deep-sea	deep seawater	Deep-sea water collected from three locations in Japan	4, 10, 25	*Alloa. xenomutans*	KCL01	Breaking strength of the PCL fibres decreased to 81% after treating with strain KCL01	[98]
PET	Deep-sea	deep-sea sediment	Deep-sea surface sediment of the eastern central Pacific Ocean	28	*Alloa. xenomutans*	A02-7	Confirmed by strain growth and metabolites detection using UPLC–MS	[99]
EPS	Deep-sea	deep-sea sediment	Deep-sea surface sediment of the eastern central Pacific Ocean	28	*Alloa. xenomutans*	MCCC1A17309	Confirmed by strain growth, biofilm observation, FTIR spectra and water contact angle analysis	[82]
Bio-based								
PLA	Coastal sea	seawater and sediment	Seawater/sediment collected near the isle of Borkum in the North Sea	28	*A.borkumensis*	SK2	40% solid PLA10 was degraded within 1 h by the cloned carboxylesterases (ABO2449) from strain SK2	[100]
PHB	Coastal sea	seawater	Seawater collected form coastal sea of Taura, Wajima and Ishikawa in Japan	30	*Alcanivorax* sp.	NBRC102022	Observed clear zone with radius larger than 5 mm on PHB-contained plate for 1 week at 30°C	[101, 102]
PHB	Coastal sea	plastic debris	Plastic debris collected from the high intertidal zone at La Rinconada beach, Antofagasta, Chile	30	*Alcanivorax* sp.	24	Declared the degradation but not provided the evidence	[103]
PHB	Coastal sea	seawater	Oil-contaminated coastal seawater collected from southeast coast of Newfoundland Canada	28	*Alcanivorax* sp.	N3-2A	360 µg/mL total bacterial protein contents after cultivated with PHB in 10 days	[104]

Fossil-based plastics: *PCL* polycaprolactone, *PET* polyethylene terephthalate, *EPS* expanded polystyrene, *LDPE* low-density polyethylene, *PP* polypropylene

Bio-based plastics: *PLA* polylactic acid, *PHB* polyhydroxybutyrate

of liquid PP by strain sw2 is similar to that of branched alkanes and that *Alcanivorax* is an important PP degrader in mesopelagic environments [97].

Recently, *Alcanivorax* has also been reported to be involved in the biodegradation of PS. Liu et al. sampled EPS plastic debris from mangroves and enriched them with PS as the sole carbon and energy source at 28 °C for 3 cycles. After enrichment, bacteria of the genus *Alloalcanivorax* were the most dominant group among the enriched consortia and the representative strain *Alloa. xenomutans* ZN12A4 was isolated. Finally, the degradation characteristics of this strain against PS were identified using several analysis methods, such as SEM, ATR-FTIR and weight loss [70].

In the deep-sea

Compared with coastal areas, there are still fewer studies on plastic degradation by deep-sea originating *Alcanivorax* (Table 3, Fig. 3). In 2011, Sekiguchi et al. analysed the degradation of so-called degradable fossil-based aliphatic polyester plastics (PCL, PBS, etc.) in deep-sea water. Subsequently, the strain *Alloa. venustensis* KCL01 was isolated from the tested deep-sea water. Compared with that of the control, the breaking strength of the PCL fibres after treatment with this strain was reduced by 19%. Moreover, the surface of the PCL fibres was rough due to the obvious changes observed by SEM. Therefore, the ability of this strain to degrade PCL was preliminarily demonstrated [98]. In 2024, Liu et al. studied the diversity of PET-degrading bacteria in deep-sea surface sediments collected from the eastern Pacific Ocean. They reported that the abundance of *Alcanivoracaceae*-related OTUs in the enriched consortia reached 65.8%. The representative *Alcanivorax* strain A02-7 was subsequently obtained and could grow with PET as the sole carbon and energy source. Moreover, the degradation intermediate (mono-(2-hydroxyethyl) terephthalate, MHET) of PET was also detected using UPLC-MS, confirming the ability of the strain to degrade PET [99]. In addition, Lv et al. studied the PS degradation characteristics of the strain *Alloa. venustensis* MCCC 1A17309, which was also isolated from the deep-sea sediment of the eastern Pacific Ocean. The ability of this strain to degrade PS was determined by various methods. Moreover, this report also revealed that 1.3% of the initial PS membrane was released into the culture as MNPs, whereas only 4.5% of the PS membrane was mineralised by this strain [82]. This highlights the negative impact of plastic biodegradation caused by bacteria, which can lead to the continued release of large quantities of MNPs, resulting in significant secondary pollution in marine ecosystems.

Degradation of bio-based plastics

Since fossil-based plastics are traditionally considered non-biodegradable, a large number of so-called biodegradable bioplastics (BBPs) and biodegradable fossil-based plastics (BFPs) are emerging. However, in 2019, Napper et al. warned that BBPs are also recalcitrant in the marine environment and likewise represent an emerging contaminant [106]. The aforementioned UNEP technical report also warned against the use of single-use plastic products or other damaging plastic alternatives, such as BBPs. The main reason for this warning is that these degradable plastics pose similar chemical threats to the environment as conventional fossil-based plastics do [39]. Therefore, the degradation of bio-based plastics in the environment is receiving increasing attention. For example, the Natural Environment Research Council (NERC) of the UK is providing funding of 2.6 million pounds [107] to support the BIO-PLASTIC-RISK (2020–2024) project, whose main research objectives are to determine the fate of BBPs in the environment and their impact on biological and ecosystem functions [108].

Although *Alcanivorax* tends to occur in fossil-based plastispheres (Table 2 and Fig. 2) and the current studies on their characteristics and mechanisms of plastic degradation are focused mostly on fossil-based plastics, there are still many reports on their ability to degrade BBPs. The enzymes found in BBPs degradation studies have been shown to play important roles in plastic recycling.

Polylactic acid (PLA) is a type of BBPs that is widely used at present, and it is also one of the main materials used to replace disposable fossil-based plastic straw in restaurants. Owing to the rapid growth of global PLA production, there is an urgent need to develop efficient recycling technology to realise the recycling of PLA waste plastics. To this end, as early as 2016, Hajighasemi et al. obtained the carboxylesterase ABO_2449 from 90 microorganisms by screening the α/β-hydrolase activities. This carboxylesterase originated from strain *A. borkumensis* SK2 and could hydrolyse 40% of solid PLA10 (average molecular weight M_w $1.0–1.8\times10^4$) plastic into lactic acid monomers, dimers and larger oligomers within 1 h, suggesting that strain SK2 and its carboxylesterase ABO_2449 have good application potential in PLA plastic recycling [100].

Polyhydroxybutyrate (PHB) is another emerging BBP that may occupy the future plastic market. Therefore, PHB plastic waste enzymolysis is also an important way to realise the recycling economy of plastics. In 2017, the strain *Alcanivorax* sp. NBRC 102022 was isolated from coastal seawater in Japan. After 1 week of cultivation at 30 °C on a PHB medium plate, a clear hydrolysis cycle occurred ($\Phi > 5$ mm), indicating that this strain is a potential PHB degrader [101]. Another

strain, *Alcanivorax* sp.24, which was isolated from plastic debris collected from a beach in Chile, was found to possess large amounts of esterases, peroxidases, and predicted laccases in its genome, suggesting that this strain may play a role in the biodegradation of BBPs [103]. Through heterogeneous expression, Zadjelovic et al. subsequently confirmed the high hydrolysis activities of strain 24 toward the bio-based polyester plastics PHB and PHBV, as well as toward the fossil-based polyester plastics PBS, PES (polyethersulfone) and PCL. Finally, they also demonstrated that esterase ALC24_4107 was responsible for the abovementioned hydrolysis ability. These results suggest that strain 24 and its esterase ALC24_4107 have high biotechnological potential in the recycling of polyester plastics [109]. In addition, Cao et al. confirmed the PHB degradation ability of the strain *Alcanivorax* sp. N3-2A, which was isolated from oil-polluted coastal seawater from southeastern Canada, through culture experiments using PHB plastic as the sole carbon and energy source and the determination of extracellular enzyme activity induced by PHB [104].

Biotechnological potential of *Alcanivorax*-derived enzymes in plastic recycling

The continuous growth of global plastic production has led to increasingly critical marine plastic pollution and subsequent negative environmental effects. The enzymatic depolymerisation of synthetic plastics is an effective and sustainable way to recycle plastic waste. Currently, studies on the degradation of bio-based polyester plastics by esterases derived from *Alcanivorax* are relatively in depth. These enzymes mainly include alpha/beta hydrolase fold esterase (α/βHFE) and PHB-depolymerase family esterase (PHBdfe). They have shown very promising application potential in the recycling of PLA and PHB/PHBV plastics. In contrast, studies on the *Alcanivorax*-derived enzymes involved in the degradation of fossil-based plastics are still limited. A few studies have shown that *Alcanivorax* also uses esterases to depolymerise PET plastic. However, for fossil-based aliphatic plastics such as PE and PP, the current main deduction is that *Alcanivorax* first produces extracellular reactive oxygen species to partially degrade fossil-based plastics, then transports low molecular weight intermediates (LMWIs) into the cell, and finally activates hydrocarbon degradation enzymes to achieve complete degradation of LMWIs.

α/βHFE

α/βHFEs are potential candidate enzymes for the enzymatic hydrolysis recycling of PLA plastic waste. For example, to discover new polyester hydrolases from low-temperature marine habitats, five highly active polyester hydrolases were screened from three marine metagenomic libraries. The amino acid sequences of two enzymes (ABO_1197 and ABO_1251) were identical to those of putative carboxyl esterases of the strain *A. borkumensis* SK2. Subsequent tests revealed that these enzymes exhibited high activity not only toward model esterase substrates but also toward PLA2 (M_w 0.2×10^4) at room temperature or low temperature (5 °C). In particular, ABO_1197 can also hydrolyse several other types of polyester plastics, such as PCL10 (M_w 1.0×10^4), PCL45 (M_w 4.5×10^4), PCL70 (M_w $7.0–9.0\times10^4$), PBSA (polybutylene succinate adipate) 3001 (M_w undefinable) and PBSA3020 (M_w undefinable) [110]. Similarly, Hajighasemi et al. screened the enzyme activity of α/βHFE from 90 marine microorganisms. Two unknown proteins, ABO_2449 and RPA1511, with high hydrolytic activity toward PLA were obtained from the strains *A. borkumensis* SK2 and *Rhodopseudomonas palustris* CGA009, respectively. They can catalyse the complete or extensive hydrolysis of solid PLA and produce lactic monomers, dimers and larger oligomers. In particular, ABO_2449 showed 30%, 36%, 75%, and 90% degradation rates for solid PLA10 within 1, 3, 18, and 36 h, respectively [100]. Hajighasemi et al. subsequently cloned, expressed and screened 213 hydrolases from environmental metagenomes and strain genomes. Ten of these hydrolases showed high hydrolytic activity for the synthesis of polyesters. Among them, the metagenomic-derived α/βHFE GEN0105 had 45.7% amino acid sequence identity with an α/βHFE (WP_055099617) of *Alloa. xenomutans* KS-293. Phylogenetic analysis confirmed that these genes belong to the same esterase family. Further tests revealed that GEN0105 could hydrolyse PLA, PCL and bis(benzoyloxyethyl) terephthalate (3PET, a model substrate of PET). In particular, the ability of GEN0105 to hydrolyse PLA is particularly outstanding. It can hydrolyse 70% of solid PLA within 18 h. Hydrolysate is a mixture of lactate monomers, dimers and oligomers, and lactate monomers account for approximately 50% of the total hydrolysate [111].

The high hydrolytic activity of the abovementioned α/βHFEs toward PLA is a common feature, indicating their great potential as attractive biocatalase preparations for the depolymerisation and recycling of polyester plastics. Notably, when the amino acid sequence of the abovementioned ABO_2449 gene was used as a query for BLASTP analysis, the first 82 hit α/βHFEs (identity 55.7–99.7%) were all from different genera within the *Alcanivorax* group. Further phylogenetic analysis revealed that these α/βHFEs were evolutionarily specific, i.e., the α/βHFEs derived from different genera tended to cluster in separate branches (Fig. 4).

Considering the wide distribution of these α/βHFEs in *Alcanivorax* and their excellent hydrolytic activity toward PLA, it is highly desirable to continue mining more highly active α/βHFEs from *Alcanivorax* bacteria and apply them to the recycling of PLA waste.

PHBdfe

PHB is another important class of bio-based polyester plastics. Recent studies have shown that *Alcanivorax*, especially those within the genus *Alloalcanivorax*, has remarkable hydrolysing activity toward PHB plastics.

As mentioned above, Zadjelovic et al. confirmed that the strain *Alcanivorax* sp. 24 exhibited distinguished hydrolytic activities against PHB and PHBV, as did fossil-based polyester plastics such as PBS, PES and PCL [109]. The PHBdfe ALC24_4107 (WP_133493510) of strain 24 was subsequently confirmed to be responsible for its hydrolysis ability. These results indicate that ALC24_4107, similar to α/βHFEs, may have good biotechnological potential for the recycling of polyester plastic waste. Notably, in strain 24, the esterase most closely related to the α/βHFE ABO_2449 of strain SK2 was not ALC24_4107 but ALC24_2069. However, transcriptomic and proteomic data have shown that ALC24_2069 does not respond to the induction of many types of polyesters, such as PHB, PHBV, and PES [109]. These results suggest that *Alcanivorax* possesses a variety of substrate-specific polyester plastic hydrolytic esterases, which extends the application of *Alcanivorax* in plastic recycling to a certain extent. Interestingly, when the amino acid sequence of ALC24_4107 was used as a query for BLASTP analysis, 35 hit PHBdfes (identity 70.0–99.7%) among the first 38 hits were all retrieved from the genus *Alloalcanivorax* but were scattered among different species (Fig. 5). Compared with the abovementioned PLA-degrading α/βHFEs (Fig. 4), these PHBdfes are more species- and genus specific.

In addition, phylogenetic analyses (Fig. 5) based on amino acid sequences revealed that the esterase PhaZ (WP_089031498) of *Alcanivorax* sp. N3-2A, another strain with strong hydrolytic activity toward PHB [104], was most similar (99.5%) to the esterase WP_101674902 of the type strain *Alloa. mobilis* MT13131^{T}. Coincidentally, the BLASTP results for PhaZ were similar to those for the abovementioned ALC24_4107. Among the first 68 PHBdfes (61.0–99.5% identity) with the highest homology, 38 of them (68.4–99.5%) were also all originated from the genus *Alloalcanivorax* (Fig. 5). Furthermore, the closest related esterase of PhaZ in the abovementioned strain 24 was WP_205655668 but not WP_133493510 (ALC24_4107). These results suggest that many different PHBdfes co-occur in different species of the genus *Alloalcanivorax* and further highlight the potential application of *Alloalcanivorax* in the recycling of PHB plastic waste.

PETase

In 2016, when the PET degradation mechanism [113] of a new PET-degrading bacterium, *Ideonella sakaiensis* 201-F6^{T} [114], and the molecular mechanism of PET degradation catalysed by IsPETase [115, 116] were reported, research on PET waste enzymatic hydrolysis recovery set off a new climax. Notably, amino acid sequence and crystal structure analysis indicated that the IsPETase found in strain 201-F6^{T} also belongs to the α/βHFE family. It is homologous to known cutinases found in many bacteria but exhibits a more open active-site cleft than homologous cutinases do [116].

In contrast, to the best of our knowledge, PET has not been reported to be hydrolysed by enzymes derived from *Alcanivorax*. However, Hajighasemi et al. screened more than 200 macrogenomic and strain genome-derived hydrolases and reported that four esterases of the strain *A. borkumensis* SK2 exhibited high hydrolytic activity toward 3PET (a model substrate of PET plastic) [111]. The four esterases were ABO_1197 (carboxylic ester hydrolase), ABO_1251 (carboxylesterase), ABO_1895 (phospholipase/carboxylesterase) and ABO_2449 (α/βHFE). In addition to the four esterases, another esterase, GEN0105 (AKJ87216), which is closely related to the α/βHFEs (WP_055099617) of strain *Alloa. xenomutans* KS-293, was also detected. The esterase GEN0105 also has high hydrolytic activity against 3PET [111].

In short, considering that α/βHFE family esterases are widely present in *Alcanivorax* (Fig. 4), there should be enzymes that can directly hydrolyse PET, but more research is needed to clarify these enzymes in the future.

Candidate enzymes for depolymerisation of other fossil-based plastics

Bacteria of *Alcanivorax* occur frequently in various types of fossil-based plastispheres from many different marine habitats (Table 2, [56, 57, 60–64, 68–70]), and there are numerous reports of these bacteria degrading different fossil-based plastics (Table 3, [60, 70, 82, 94–98]). However, to the best of our knowledge, the enzymes of *Alcanivorax* that can directly depolymerise PE, PP, PS and other fossil-based plastics have not been reported.

In fact, in the 1970s, Albertsson et al. co-cultured ^{14}C-labelled PE and soil microorganisms and demonstrated that microorganisms can degrade < 1000 Da LMW components in PE plastics. Therefore, they speculated that this degradation process was similar to that of alkane degradation [117, 118]. Coincidentally, through numerical simulation, Kawai et al. speculated

Fig. 4 Phylogenetic tree of alpha/beta hydrolase fold esterases retrieved from *Alcanivorax* spp. The esterase ABO_2449 (WP_011589723.1) of *A. borkumensis* SK2 was used as the query during the NCBI BLASTP analysis. The phylogenetic tree was generated by IQ-TREE 2 (v.2.0) [112] using the maximum likelihood method. The grey dots on the nodes correspond to the percent recovery from 1000 bootstraps. The scale indicates the number of amino acid substitutions per site. GenBank accession numbers are shown in front of each protein ID

that the molecular weight limit of PE plastics that can be degraded by microorganisms is approximately 2000 Da [119, 120]. Recently, Koike et al. reported that the strain *A. borkumensis* sw2 isolated from mesopelagic seawater was able to degrade liquid LMW PP at 10 °C in the presence of other simple carbon sources. Considering that the molecular structure of liquid LMW PP is similar to that of branched alkanes, they suggested that strain sw2 should achieve initial degradation of liquid LMW PP through monooxygenases such as AlkB and P450 [97]. As early as 2012, AlkBs from soil-originating *Pseudomonas* were shown to degrade LMW PEs [121–123]. Furthermore, a recent quantum mechanism study also suggested that monooxygenases such as P450 could catalyse the cleavage of C–C bonds in polyolefin plastics (such as PE and PS) [124].

The above studies suggested that LMW intermediates, originating from PE, PP and other fossil-based plastics after degradation by photo-, chemical- and thermal-oxidation in marine environments, can be mineralised by *Alcanivorax*. Finally, the abiotic and biological joint degradation of fossil-based plastics can be achieved in

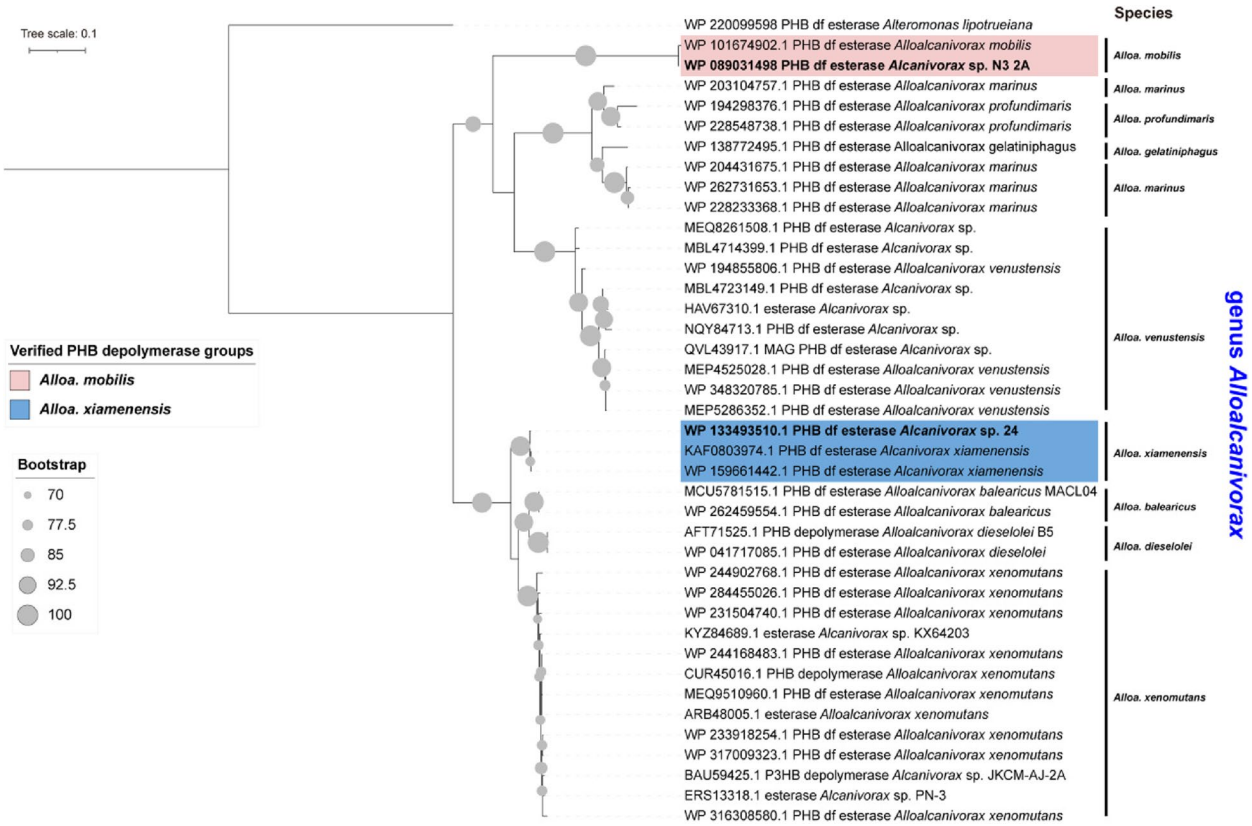

Fig. 5 Phylogenetic tree of PHB depolymerase family esterases in the genus *Alloalcanivorax*. The PHB depolymerases were retrieved by NCBI BLASTP analysis using the functionally verified esterases WP_133493510 (*Alcanivorax* sp. 24) and WP_089031498 (*Alcanivorax* sp. N3-2A) as query sequences. The phylogenetic tree was generated by IQ-TREE 2 (v.2.0) [112] using the maximum likelihood method. The grey dots on the nodes correspond to the percent recovery from 1000 bootstraps. The scale indicates the number of amino acid substitutions per site. GenBank accession numbers are shown in front of each protein ID. "PHB df" in each protein ID indicates the PHB depolymerase family. A PHB depolymerase family esterase from *Alteromonas lipotrueiana* (WP_220099598) was used as the outgroup

marine environments. Considering that large amounts of monooxygenases exist in *Alcanivorax* [125], we believe that they are involved in the degradation of fossil-based plastics such as PE and PP in the ocean to a certain extent. However, the biochemical functions of these monooxygenases need to be further characterised to help reveal the plastic-degrading pathway of *Alcanivorax* accurately and evaluate their potential for use in the recycling of fossil-based plastics.

Conclusions and prospective

As one of the predominant hydrocarbon-degrading bacteria in the ocean, *Alcanivorax* plays important roles not only in the marine hydrocarbon and carbon cycles but also in the biodegradation and transformation of synthetic plastic waste (Fig. 6). However, the latter role has been substantively underestimated due to a lack of extensive studies.

Although *Alcanivorax* occur widely in marine plastispheres, especially fossil-based plastispheres, they are likely attracted by LMW hydrocarbon analogues released from fossil-based plastics. In a certain sense, *Alcanivorax* may not be able to directly or independently trigger the initial or complete degradation of fossil-based plastics, which should greatly limit its application in the recycling of these plastics. In contrast, although there are few reports about *Alcanivorax* in bio-based plastispheres, studies on its degradation characteristics and mechanisms against bio-based plastics are far more in-depth and extensive than those of fossil-based plastics. Moreover, their ability to degrade bio-based plastics is far better than that of fossil-based plastics. Therefore, *Alcanivorax* and its enzymes have shown great application potential in the recycling of bio-based polyester plastics, thereby contributing to the development of the marine blue circular economy.

Conceivably, significant work remains before *Alcanivorax* and its enzymes can be used on a large scale for commercial recycling of polyester plastics (such as PLA and PHB/V). This includes, but is not limited to, the following:

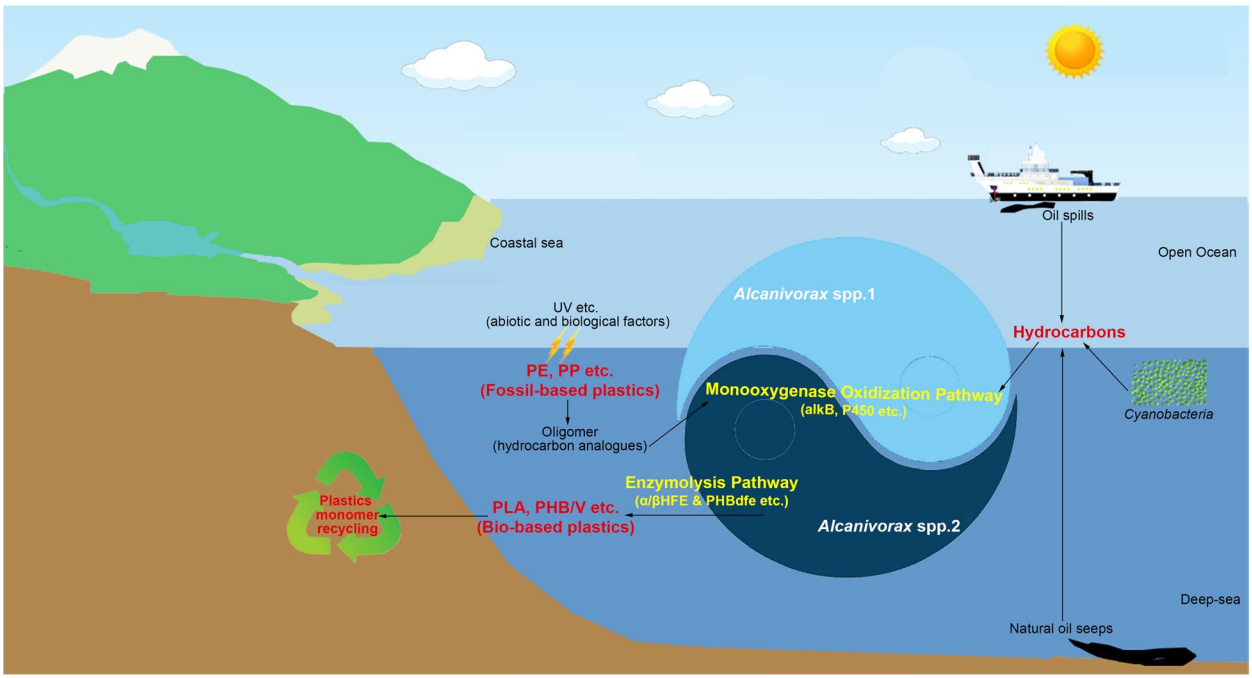

Fig. 6 Schematic diagram of the versatile *Alcanivorax* involved in the marine hydrocarbon cycle and plastic depolymerisation and recycling

(1) In-depth mining of various esterases from *Alcanivorax* and construction of an esterase database. With the rapid development and application of artificial intelligence (AI), the use of AI to quickly and efficiently screen and discover novel esterases with high activity on polyester plastics will be an important research direction in the future.
(2) In-depth decoding of esterase degradation characteristics and mechanisms against polyester plastics. In-depth studies of the catalytic mechanisms of plastic-degrading enzymes and the constraints that affect their activities are essential for their application in the biodegradation and recycling of bio-based plastic waste.
(3) Directed modification or evolution of active esterases. Compared with fossil-based plastics, many types of polyester plastics have lower glass transition temperatures (GTTs). For example, the GTTs of PLA and PET are only 60 °C and 70 °C, respectively. Since plastics under glass transition conditions are more susceptible to enzymolysis, improving the optimal temperature and thermal stability of esterases is highly desirable. In addition, further improving the hydrolytic activity of esterases on polyester plastics is another important research direction.
(4) Construction of heat-resistant engineered strains for polyester plastic enzymolysis. With the help of synthetic biology, highly active polyester hydrolases from *Alcanivorax* can be "transformed" into other marine thermophiles to complete engineered bacterial construction. Then, the modified engineered bacteria and polyester plastic waste could be co-cultured at high temperatures to achieve more convenient and efficient depolymerisation of polyester plastics and recycling of high-value intermediates.
(5) Establishing more robust and precise methods to assess the ability of microorganisms and their enzymes to degrade plastics accurately. Understandably, more robust and precise methods will help to identify *Alcanivorax* strains and their enzymes with the best plastic degradation activity, laying the foundation for large-scale commercial recycling of plastics.

In summary, there is still a long way to go before enzymes can be used to recycle plastic waste at scale. Therefore, the most important goal at present is to control the total production of plastics to improve the health of marine ecosystems and achieve sustainable management and protection of marine environments.

Acknowledgements
We appreciate the efforts of Dr. Ruolin Cheng to maintain the bioinformation analysis server.

Authors' contributions
ZZS supervised the study. CMD conceived the structure of this review and drafted the original manuscript. CMD, ZZS and ZSW revised the manuscript. All authors reviewed and approved the manuscript.

Funding
This work was financially supported by the National Natural Science Foundation of China (41976107, 91851203 and 42030412), the Natural Science Foundation of Fujian Province, China (2021J01508) and the Scientific Research Foundation of the Third Institute of Oceanography, MNR (2020009, 2019021).

Availability of data and materials
No datasets were generated or analysed during the current study.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

Received: 11 July 2024 Accepted: 14 September 2024
Published online: 20 November 2024

References

1. Wilkes H, Schwarzbauer J. Hydrocarbons: An introduction to structure, physico-chemical properties and natural occurrence. In: Timmis KN, editor. Handbook of hydrocarbon and lipid microbiology. Berlin, Heidelberg: Springer Berlin Heidelberg; 2010. p. 1–48.
2. Blumer M, Guillard RRL, Chase T. Hydrocarbons of marine phytoplankton. Mar Biol. 1971;8(3):183–9.
3. McGenity TJ, McKew BA, Lea-Smith DJ. Cryptic microbial hydrocarbon cycling. Nat Microbiol. 2021;6(4):419–20.
4. Schirmer A, Rude MA, Li X, Popova E, del Cardayre SB. Microbial biosynthesis of alkanes. Science (New York, NY). 2010;329(5991):559–62.
5. Love CR, Arrington EC, Gosselin KM, Reddy CM, Van Mooy BAS, Nelson RK, Valentine DL. Microbial production and consumption of hydrocarbons in the global ocean. Nat Microbiol. 2021;6:489–98.
6. Lea-Smith DJ, Biller SJ, Davey MP, Cotton CA, Perez Sepulveda BM, Turchyn AV, Scanlan DJ, Smith AG, Chisholm SW, Howe CJ. Contribution of cyanobacterial alkane production to the ocean hydrocarbon cycle. Proc Natl Acad Sci USA. 2015;112(44):13591–6.
7. Vigneron A, Cruaud P, Lovejoy C, Vincent WF. Genomic insights into cryptic cycles of microbial hydrocarbon production and degradation in contiguous freshwater and marine microbiomes. Microbiome. 2023;11(1):104.
8. Yakimov MM, Bargiela R, Golyshin PN. Calm and Frenzy: marine obligate hydrocarbonoclastic bacteria sustain ocean wellness. Curr Opin Biotechnol. 2022;73:337–45.
9. Yakimov MM, Golyshin PN, Lang S, Moore ER, Abraham WR, Lunsdorf H, Timmis KN. Alcanivorax borkumensis gen. nov., sp. nov., a new, hydrocarbon-degrading and surfactant-producing marine bacterium. Int J Syst Bacteriol. 1998;48(Pt 2):339–48.
10. Rai A, Suresh G, Ria B, L V, PK S, Ipsita S, Sasikala C, Venkata Ramana C: Phylogenomic analysis of the genus Alcanivorax: proposal for division of this genus into the emended genus Alcanivorax and two novel genera Alloalcanivorax gen. nov. and Isoalcanivorax gen. nov. Int J Syst Evol Microbiol 2023;73(1). https://doi.org/10.1099/ijsem.0.005672.
11. Parte AC, Sardà Carbasse J, Meier-Kolthoff JP, Reimer LC, Göker M. List of Prokaryotic names with Standing in Nomenclature (LPSN) moves to the DSMZ. Int J Syst Evol Microbiol. 2020;70(11):5607–12.
12. Liu C, Shao Z. Alcanivorax dieselolei sp. nov., a novel alkane-degrading bacterium isolated from sea water and deep-sea sediment. Int J Syst Evol Microbiol. 2005;55(3):1181–6.
13. Wu Y, Lai Q, Zhou Z, Qiao N, Liu C, Shao Z. Alcanivorax hongdengensis sp nov, an alkane-degrading bacterium isolated from surface seawater of the straits of Malacca and Singapore, producing a lipopeptide as its biosurfactant. Int J Syst Evol Microbiol. 2009;59(6):1474–9.
14. Lai Q, Fu X, Wang J, Dong C, Wang L, Wang W, Shao Z: Alcanivorax xiamenensis sp. nov., a novel marine hydrocarbonoclastic bacterium isolated from surface seawater. Int J Syst Evol Microbiol 2023;73(3). https://doi.org/10.1099/ijsem.0.005798.
15. Bruns A, Berthe-Corti L. Fundibacter jadensis gen nov., sp. nov., a new slightly halophilic bacterium, isolated from intertidal sediment. Int J Syst Bacteriol. 1999;49(Pt 2):441–8.
16. Kyoung Kwon K, Hye OhJ, Yang SH, Seo HS, Lee JH. Alcanivorax gelatiniphagus sp. nov., a marine bacterium isolated from tidal flat sediments enriched with crude oil. Int J Syst Evol Microbiol. 2015;65(7):2204–8.
17. Rahul K, Sasikala C, Tushar L, Debadrita R, Ramana ChV. Alcanivorax xenomutans sp. nov., a hydrocarbonoclastic bacterium isolated from a shrimp cultivation pond. Int J Syst Evol Microbiol. 2014;64(Pt 10):3553–8.
18. Fernandez-Martinez J, Pujalte MJ, Garcia-Martinez J, Mata M, Garay E, Rodriguez-Valeral F. Description of Alcanivorax venustensis sp. nov. and reclassification of Fundibacter jadensis DSM 1 21 78T (Bruns and Berthe-Corti 1999) as Alcanivorax jadensis comb nov., members of the emended genus Alcanivorax. Int J Syst Evol Microbiol. 2003;53(Pt 1):331–8.
19. Dong C, Lai Q, Liu X, Gu L, Zhang Y, Xie Z, Wang D, Shao Z. Alcanivorax profundimaris sp. nov., a Novel Marine Hydrocarbonoclastic bacterium isolated from seawater and deep-sea sediment. Curr Microbiol. 2021;78(3):1053–60.
20. Liu J, Ren Q, Zhang Y, Li Y, Tian X, Wu Y, Tian J, Zhang XH. Alcanivorax profundi sp. nov., isolated from deep seawater of the Mariana Trench. Int J Syst Evol Microbiol. 2018;69:371.
21. Lai Q, Wang J, Gu L, Zheng T, Shao Z. Alcanivorax marinus sp. nov., isolated from deep-sea water. Int J Syst Evol Microbiol. 2013;63(Pt 12):4428–32.
22. Song L, Liu H, Cai S, Huang Y, Dai X, Zhou Y. Alcanivorax indicus sp. nov., isolated from seawater. Int J Syst Evol Microbiol. 2018;68(12):3785–9.
23. Lai Q, Zhou Z, Li G, Li G, Shao Z. Alcanivorax nanhaiticus sp. nov., isolated from deep sea sediment. Int J Syst Evol Microbiol. 2016;66(9):3651–5.
24. Liao X, Lai Q, Yang J, Dong C, Li D, Shao Z. Alcanivorax sediminis sp. nov., isolated from deep-sea sediment of the Pacific Ocean. Int J Syst Evol Microbiol. 2020;70:4280.
25. Yang S, Li M, Lai Q, Li G, Shao Z. Alcanivorax mobilis sp. nov., a new hydrocarbon-degrading bacterium isolated from deep-sea sediment. Int J Syst Evol Microbiol. 2018;68(5):1639–43.
26. Lai Q, Wang L, Liu Y, Fu Y, Zhong H, Wang B, Chen L, Wang J, Sun F, Shao Z. Alcanivorax pacificus sp. nov., isolated from a deep-sea pyrene-degrading consortium. Int J Syst Evol Microbiol. 2011;61(Pt 6):1370–4.
27. Rivas R, Garcia-Fraile P, Peix A, Mateos PF, Martinez-Molina E, Velazquez E. Alcanivorax balearicus sp. nov., isolated from Lake Martel. Int J Syst Evol Microbiol. 2007;57(Pt 6):1331–5.
28. Zhu L, Wang Y, Ding Y, Luo K, Yang B, Yang S, Liu S, Cui H, Wei W. Alcanivorax limicola sp. nov., isolated from a soda alkali-saline soil. Arch Microbiol. 2021;204(1):106.
29. An MM, Shen L, Liang RN, Lu YJ, Zhao GZ: Alcanivorax quisquiliarum sp. nov., isolated from anaerobic fermentation liquid of food waste by high-throughput cultivation. Int J Syst Evol Microbiol 2023;73(4). https://doi.org/10.1099/ijsem.0.005764.
30. Cappello S, Yakimov MM. Alcanivorax. In: Timmis KN, editor. Handbook of hydrocarbon and lipid microbiology. Berlin, Heidelberg: Springer Berlin Heidelberg; 2010. p. 1737–48.

31. Cappello S, Corsi I, Patania S, Bergami E, Azzaro M, Mancuso M, Genovese M, Lunetta A, Caruso G. Characterization of five psychrotolerant Alcanivorax spp. Strains Isolated from Antarctica. Microorganisms. 2022;11(1):58.
32. Lyu L, Li J, Chen Y, Mai Z, Wang L, Li Q, Zhang S. Degradation potential of alkanes by diverse oil-degrading bacteria from deep-sea sediments of Haima cold seep areas. South China Sea Front Microbiol. 2022;13:920067.
33. Deng Y, Wang K, Hu Z, Hu Q, Tang YZ. Identification and implications of a core bacterial microbiome in 19 clonal cultures laboratory-reared for months to years of the cosmopolitan dinoflagellate Karlodinium veneficum. Front Microbiol. 2022;13: 967610.
34. Sajid S, de Dios VR, Zveushe OK, Nabi F, Shen S, Kang Q, Zhou L, Ma L, Zhang W, Zhao Y, et al. Newly isolated halotolerant Aspergillus sp showed high diesel degradation efficiency under high salinity environment aided with hematite. J Hazard Mat. 2023;443(Pt B):130324.
35. Shi H, Gao W, Zheng Y, Yang L, Han B, Zhang Y, Zheng L. Distribution and abundance of oil-degrading bacteria in seawater of the Yellow Sea and Bohai Sea, China. Sci Total Environ. 2023;902:166038.
36. Dede B, Priest T, Bach W, Walter M, Amann R, Meyerdierks A. High abundance of hydrocarbon-degrading Alcanivorax in plumes of hydrothermally active volcanoes in the South Pacific Ocean. ISME J. 2023;17(4):600–10.
37. Jambeck JR, Geyer R, Wilcox C, Siegler TR, Perryman M, Andrady A, Narayan R, Law KL. Marine pollution Plastic waste inputs from land into the ocean. Science (New York, NY). 2015;347(6223):768–71.
38. Plastics–the fast Facts 2023 [https://plasticseurope.org/knowledge-hub/]
39. McGlade J, Fahim I, Green D, Landrigan P, Andrady A, Costa M, Geyer R, Gomes R, Hwai A, Jambeck J et al. From Pollution to Solution: A Global Assessment of Marine Litter and Plastic Pollution. In.: Nairobi: United Nations Environment Programme; 2021.
40. Allen D, Allen S, Abbasi S, Baker A, Bergmann M, Brahney J, Butler T, Duce RA, Eckhardt S, Evangeliou N, et al. Microplastics and nanoplastics in the marine-atmosphere environment. Nature Rev Earth Environ. 2022;3(6):393–405.
41. Belli IM, Cavali M, Garbossa LHP, Franco D, Bayard R, de Castilhos Junior AB. A review of plastic debris in the South American Atlantic Ocean coast - Distribution, characteristics, policies and legal aspects. Sci Total Environ. 2024;938:173197.
42. Jiang Y, Yang F, Hassan Kazmi SSU, Zhao Y, Chen M, Wang J. A review of microplastic pollution in seawater, sediments and organisms of the Chinese coastal and marginal seas. Chemosphere. 2022;286(Pt 1): 131677.
43. Pinheiro HT, MacDonald C, Santos RG, Ali R, Bobat A, Cresswell BJ, Francini-Filho R, Freitas R, Galbraith GF, Musembi P, et al. Plastic pollution on the world's coral reefs. Nature. 2023;619(7969):311–6.
44. Feng J, Li C, Tang L, Wu X, Wang Y, Yang Z, Yuan W, Sun L, Hu W, Zhang S. Tracing the century-long evolution of microplastics deposition in a cold seep. Adv Sci. 2023;10(10):e2206120.
45. Rynek R, Tekman MB, Rummel C, Bergmann M, Wagner S, Jahnke A, Reemtsma T. Hotspots of floating plastic particles across the North Pacific Ocean. Environ Sci Technol. 2024;58(9):4302–13.
46. Chong F, Spencer M, Maximenko N, Hafner J, McWhirter AC, Helm RR. High concentrations of floating neustonic life in the plastic-rich North Pacific Garbage Patch. PLoS Biol. 2023;21(5): e3001646.
47. Sanganyado E, Chingono KE, Gwenzi W, Chaukura N, Liu W. Organic pollutants in deep sea: Occurrence, fate, and ecological implications. Water Res. 2021;205: 117658.
48. Xie J, Chen C, Luo M, Peng X, Lin T, Chen D. Hidden dangers: High levels of organic pollutants in hadal trenches. Water Res. 2024;251: 121126.
49. Mishra AK, Singh J, Mishra PP. Microplastics in polar regions: An early warning to the world's pristine ecosystem. Sci Total Environ. 2021;784:147149.
50. Kim SK, Kim JS, Kim SY, Song NS, La HS, Yang EJ. Arctic Ocean sediments as important current and future sinks for marine microplastics missing in the global microplastic budget. Sci adv. 2023;9(27):2348.
51. Waller CL, Griffiths HJ, Waluda CM, Thorpe SE, Loaiza I, Moreno B, Pacherres CO, Hughes KA. Microplastics in the Antarctic marine system: an emerging area of research. Sci Total Environ. 2017;598:220–7.
52. Erni-Cassola G, Zadjelovic V, Gibson MI, Christie-Oleza JA. Distribution of plastic polymer types in the marine environment. Meta-analysis J Hazard Mat. 2019;369:691–8.
53. Amaral-Zettler LA, Zettler ER, Mincer TJ. Ecology of the plastisphere. Nat Rev Microbiol. 2020;18(3):139–51.
54. Wright RJ, Erni-Cassola G, Zadjelovic V, Latva M, Christie-Oleza JA. Marine plastic debris: a new surface for microbial colonization. Environ Sci Technol. 2020;54(19):11657–72.
55. Wright RJ, Langille MGI, Walker TR. Food or just a free ride? A meta-analysis reveals the global diversity of the Plastisphere. ISME J. 2021;15(3):789–806.
56. Dussud C, Hudec C, George M, Fabre P, Higgs P, Bruzaud S, Delort AM, Eyheraguibel B, Meistertzheim AL, Jacquin J, et al. Colonization of non-biodegradable and biodegradable plastics by marine microorganisms. Front Microbiol. 2018;9:1571.
57. Girard EB, Kaliwoda M, Schmahl WW, Wörheide G, Orsi WD. Biodegradation of textile waste by marine bacterial communities enhanced by light. Environ Microbiol Rep. 2020;12(4):406–18.
58. Erni-Cassola G, Wright RJ, Gibson MI, Christie-Oleza JA. Early colonization of weathered polyethylene by distinct bacteria in marine coastal seawater. Microb Ecol. 2020;79(3):517–26.
59. Oberbeckmann S, Osborn AM, Duhaime MB. Microbes on a bottle: substrate, season and geography influence community composition of microbes colonizing marine plastic debris. PLoS One. 2016;11(8):e0159289.
60. Delacuvellerie A, Cyriaque V, Gobert S, Benali S, Wattiez R. The plastisphere in marine ecosystem hosts potential specific microbial degraders including Alcanivorax borkumensis as a key player for the low-density polyethylene degradation. J Hazard Mater. 2019;380: 120899.
61. Cappello S, Caruso G, Bergami E, Macrì A, Venuti V, Majolino D, Corsi I. New insights into the structure and function of the prokaryotic communities colonizing plastic debris collected in King George Island (Antarctica): Preliminary observations from two plastic fragments. J Hazard Mater. 2021;414: 125586.
62. Hou D, Hong M, Wang K, Yan H, Wang Y, Dong P, Li D, Liu K, Zhou Z, Zhang D. Prokaryotic community succession and assembly on different types of microplastics in a mariculture cage. Environ Pollut (Barking, Essex : 1987). 2021;268(Pt A):115756.
63. Delacuvellerie A, Géron A, Gobert S, Wattiez R. New insights into the functioning and structure of the PE and PP plastispheres from the Mediterranean Sea. Environ Pollut. 2022;295:118678.
64. Lacerda A, Taylor JD, Rodrigues LDS, Kessler F, Secchi E, Proietti MC. Floating plastics and their associated biota in the Western South Atlantic. Sci Total Environ. 2022;805:150186.
65. Denaro R, Aulenta F, Crisafi F, Di Pippo F, Cruz Viggi C, Matturro B, Tomei P, Smedile F, Martinelli A, Di Lisio V, et al. Marine hydrocarbon-degrading bacteria breakdown poly(ethylene terephthalate) (PET). Sci Total Environ. 2020;749:141608.
66. Wright RJ, Bosch R, Langille MGI, Gibson MI, Christie-Oleza JA. A multi-OMIC characterisation of biodegradation and microbial community succession within the PET plastisphere. Microbiome. 2021;9(1):141.
67. Zhao S, Liu R, Wang J, Lv S, Zhang B, Dong C, Shao Z. Biodegradation of polyethylene terephthalate (PET) by diverse marine bacteria in deep-sea sediments. Environ Microbiol. 2023;25(12):2719–31.
68. Odobel C, Dussud C, Philip L, Derippe G, Lauters M, Eyheraguibel B, Burgaud G, Ter Halle A, Meistertzheim AL, Bruzaud S, et al. Bacterial abundance, diversity and activity during long-term colonization of non-biodegradable and Biodegradable plastics in seawater. Front Microbiol. 2021;12:734782.
69. Chu WC, Gao YY, Wu YX, Liu FF. Biofilm of petroleum-based and bio-based microplastics in seawater in response to Zn(II): Biofilm formation, community structure, and microbial function. Sci Total Environ. 2024;928:172397.
70. Liu R, Zhao S, Zhang B, Li G, Fu X, Yan P, Shao Z. Biodegradation of polystyrene (PS) by marine bacteria in mangrove ecosystem. J Hazard Mater. 2023;442: 130056.
71. Hara A, Baik SH, Syutsubo K, Misawa N, Smits TH, van Beilen JB, Harayama S. Cloning and functional analysis of alkB genes in Alcanivorax borkumensis SK2. Environ Microbiol. 2004;6(3):191–7.

72. Singh SN, Kumari B, Mishra S. Microbial degradation of alkanes. In: Singh SN, editor. Microbial degradation of xenobiotics. Berlin, Heidelberg: Springer Berlin Heidelberg; 2012. p. 439–69.
73. Wei G, Li S, Ye S, Wang Z, Zarringhalam K, He J, Wang W, Shao Z. High-resolution small RNAs landscape provides insights into alkane adaptation in the Marine Alkane-Degrader Alcanivorax dieselolei B-5. Int J Mol Sci. 2022;23(24):15995.
74. Guo X, Zhang J, Han L, Lee J, Williams SC, Forsberg A, Xu Y, Austin RN, Feng L. Structure and mechanism of the alkane-oxidizing enzyme AlkB. Nat Commun. 2023;14(1):2180.
75. Groves JT, Feng L, Austin RN. Structure and function of Alkane Monooxygenase (AlkB). Acc Chem Res. 2023;56(24):3665–75.
76. Williams SC, Forsberg AP, Lee J, Vizcarra CL, Lopatkin AJ, Austin RN. Investigation of the prevalence and catalytic activity of rubredoxin-fused alkane monooxygenases (AlkBs). J Inorg Biochem. 2021;219: 111409.
77. Prasad M, Obana N, Lin SZ, Zhao S, Sakai K, Blanch-Mercader C, Prost J, Nomura N, Rupprecht JF, Fattaccioli J, et al. Alcanivorax borkumensis biofilms enhance oil degradation by interfacial tubulation. Science (New York, NY). 2023;381(6659):748–53.
78. McGenity TJ, Laissue PP. Bacteria stretch and bend oil to feed their appetite. Science (New York, NY). 2023;381(6659):728–9.
79. Taglialegna A. Feasting on hydrocarbons via dendritic biofilms. Nat Rev Microbiol. 2023;21(11):703.
80. Plastic pollution on course to double by 2030 [https://news.un.org/en/story/2021/10/1103692]
81. Zhang Y, Cao Y, Chen B, Dong G, Zhao Y, Zhang B. Marine biodegradation of plastic films by Alcanivorax under various ambient temperatures: Bacterial enrichment, morphology alteration, and release of degradation products. Sci Total Environ. 2024;917:170527.
82. Lv S, Cui K, Zhao S, Li Y, Liu R, Hu R, Zhi B, Gu L, Wang L, Wang Q, et al. Continuous generation and release of microplastics and nanoplastics from polystyrene by plastic-degrading marine bacteria. J Hazard Mater. 2024;465: 133339.
83. Oberbeckmann S, Labrenz M. Marine microbial assemblages on microplastics: diversity, adaptation, and role in degradation. Ann Rev Mar Sci. 2020;12:209–32.
84. Sebille E, Wilcox C, Lebreton L, Maximenko N, Hardesty B, Van Franeker J, Eriksen M, Siegel D, Galgani F, Law K. A global inventory of small floating plastic debris. Environ Res Lett. 2015;10:124006.
85. Krause S, Ouellet V, Allen D, Allen S, Moss K, Nel HA, Manaseki-Holland S, Lynch I. The potential of micro- and nanoplastics to exacerbate the health impacts and global burden of non-communicable diseases. Cell Rep Med. 2024;5(6):101581.
86. Marfella R, Prattichizzo F, Sardu C, Fulgenzi G, Graciotti L, Spadoni T, D'Onofrio N, Scisciola L, La Grotta R, Frigé C, et al. Microplastics and nanoplastics in Atheromas and cardiovascular events. N Engl J Med. 2024;390(10):900–10.
87. Landmark study links microplastics to serious health problems [https://www.nature.com/articles/d41586-024-00650-3]
88. Zhou T, Song S, Min R, Liu X, Zhang G. Advances in chemical removal and degradation technologies for microplastics in the aquatic environment: A review. Mar Pollut Bull. 2024;201: 116202.
89. Goh PS, Kang HS, Ismail AF, Khor WH, Quen LK, Higgins D. Nanomaterials for microplastic remediation from aquatic environment: Why nano matters? Chemosphere. 2022;299: 134418.
90. Lebreton L. The status and fate of oceanic garbage patches. Nat Rev Earth Environ. 2022;3(11):730–2.
91. Egger M, Sulu-Gambari F, Lebreton L. First evidence of plastic fallout from the North Pacific Garbage Patch. Sci Rep. 2020;10(1):7495.
92. Li S, Yang Y, Yang S, Zheng H, Zheng Y. M J, Nagarajan D, Varjani S, Chang JS: Recent advances in biodegradation of emerging contaminants - microplastics (MPs): Feasibility, mechanism, and future prospects. Chemosphere. 2023;331: 138776.
93. Miri S, Saini R, Davoodi SM, Pulicharla R, Brar SK, Magdouli S. Biodegradation of microplastics: Better late than never. Chemosphere. 2022;286(Pt 1): 131670.
94. Rose RS, Richardson KH, Latvanen EJ, Hanson CA, Resmini M, Sanders IA. Microbial degradation of plastic in aqueous solutions demonstrated by CO(2) evolution and quantification. Int J Mol Sci. 2020;21(4):1176.
95. Khandare SD, Chaudhary DR, Jha B. Marine bacterial biodegradation of low-density polyethylene (LDPE) plastic. Biodegradation. 2021;32(2):127–43.
96. Zadjelovic V, Erni-Cassola G, Obrador-Viel T, Lester D, Eley Y, Gibson MI, Dorador C, Golyshin PN, Black S, Wellington EMH, et al. A mechanistic understanding of polyethylene biodegradation by the marine bacterium Alcanivorax. J Hazard Mater. 2022;436: 129278.
97. Koike H, Miyamoto K, Teramoto M. Alcanivorax bacteria as important polypropylene degraders in mesopelagic environments. Appl Environ Microbiol. 2023;89(12): e0136523.
98. Sekiguchi T, Saika A, Nomura K, Watanabe T, Watanabe T, Fujimoto Y, Enoki M, Sato T, Kato C, Kanehiro H. Biodegradation of aliphatic polyesters soaked in deep seawaters and isolation of poly(***ε***-caprolactone)-degrading bacteria. Polym Degrad Stab. 2011;96(7):1397–403.
99. Liu R, Xu H, Zhao S, Dong C, Li J, Wei G, Li G, Gong L, Yan P, Shao Z. Polyethylene terephthalate (PET)-degrading bacteria in the pelagic deep-sea sediments of the Pacific Ocean. Environ Pollut. 2024;352:124131.
100. Hajighasemi M, Nocek BP, Tchigvintsev A, Brown G, Flick R, Xu X, Cui H, Hai T, Joachimiak A, Golyshin PN, et al. Biochemical and structural insights into enzymatic depolymerization of polylactic acid and other polyesters by microbial carboxylesterases. Biomacromol. 2016;17(6):2027–39.
101. Suzuki M, Tachibana Y. Kazahaya J-i, Takizawa R, Muroi F, Kasuya K-i: Difference in environmental degradability between poly(ethylene succinate) and poly(3-hydroxybutyrate). J Polym Res. 2017;24(12):217.
102. Syutsubo K, Kishira H, Harayama S. Development of specific oligonucleotide probes for the identification and in situ detection of hydrocarbon-degrading Alcanivorax strains. Environ Microbiol. 2001;3(6):371–9.
103. Zadjelovic V, Gibson MI, Dorador C, Christie-Oleza JA. Genome of Alcanivorax sp 24: A hydrocarbon degrading bacterium isolated from marine plastic debris. Marine Genomics. 2020;49:100686.
104. Cao Y, Zhang B, Cai Q, Zhu Z, Liu B, Dong G, Greer CW, Lee K, Chen B. Responses of Alcanivorax species to marine alkanes and polyhydroxybutyrate plastic pollution: Importance of the ocean hydrocarbon cycles. Environ Pollut (Barking, Essex : 1987). 2022;313:120177.
105. Obrador-Viel T, Zadjelovic V, Nogales B, Bosch R, Christie-Oleza JA. Assessing microbial plastic degradation requires robust methods. Microb Biotechnol. 2024;17(4): e14457.
106. Napper IE, Thompson RC. Environmental deterioration of biodegradable, oxo-biodegradable, compostable, and conventional plastic carrier bags in the sea, soil, and open-air over a 3-year period. Environ Sci Technol. 2019;53(9):4775–83.
107. Scientists awarded £2.6 million to examine environmental impacts of biodegradable plastics [https://www.plymouth.ac.uk/news/scientists-awarded-_26million-to-examine-environmental-impacts-of-biodegradable-plastics]
108. BIO-PLASTIC-RISK: biodegradable bioplastics–assessing environmental risk [https://www.plymouth.ac.uk/research/marine-litter/bio-plastic-risk]
109. Zadjelovic V, Chhun A, Quareshy M, Silvano E, Hernandez-Fernaud JR, Aguilo-Ferretjans MM, Bosch R, Dorador C, Gibson MI, Christie-Oleza JA. Beyond oil degradation: enzymatic potential of Alcanivorax to degrade natural and synthetic polyesters. Environ Microbiol. 2020;22(4):1356–69.
110. Tchigvintsev A, Tran H, Popovic A, Kovacic F, Brown G, Flick R, Hajighasemi M, Egorova O, Somody JC, Tchigvintsev D, et al. The environment shapes microbial enzymes: five cold-active and salt-resistant carboxylesterases from marine metagenomes. Appl Microbiol Biotechnol. 2015;99(5):2165–78.
111. Hajighasemi M, Tchigvintsev A, Nocek B, Flick R, Popovic A, Hai T, Khusnutdinova AN, Brown G, Xu X, Cui H, et al. Screening and characterization of novel polyesterases from environmental metagenomes with high hydrolytic activity against synthetic polyesters. Environ Sci Technol. 2018;52(21):12388–401.
112. Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, von Haeseler A, Lanfear R. IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. Mol Biol Evol. 2020;37(5):1530–4.
113. Yoshida S, Hiraga K, Takehana T, Taniguchi I, Yamaji H, Maeda Y, Toyohara K, Miyamoto K, Kimura Y, Oda K. A bacterium that degrades and assimilates poly(ethylene terephthalate). Science (New York, NY). 2016;351(6278):1196.

114. Tanasupawat S, Takehana T, Yoshida S, Hiraga K, Oda K. Ideonella sakaiensis sp. nov., isolated from a microbial consortium that degrades poly (ethylene terephthalate). Int J Syst Evol Microbiol. 2016;66(8):2813–8.
115. Joo S, Cho IJ, Seo H, Son HF, Sagong HY, Shin TJ, Choi SY, Lee SY, Kim KJ. Structural insight into molecular mechanism of poly(ethylene terephthalate) degradation. Nat Commun. 2018;9(1):382.
116. Austin HP, Allen MD, Donohoe BS, Rorrer NA, Kearns FL, Silveira RL, Pollard BC, Dominick G, Duman R, El Omari K, et al. Characterization and engineering of a plastic-degrading aromatic polyesterase. Proc Natl Acad Sci USA. 2018;115(19):E4350-e4357.
117. Albertsson A-C. Biodegradation of synthetic polymers. II. A limited microbial conversion of 14C in polyethylene to 14CO2 by some soil fungi. J Appl Polymer Sci. 1978;22(12):3419–33.
118. Albertsson A-C, Bánhidi ZG. Microbial and oxidative effects in degradation of polyethene. J Appl Polym Sci. 1980;25(8):1655–71.
119. Kawai F, Watanabe M, Shibata M, Yokoyama S, Sudate Y. Experimental analysis and numerical simulation for biodegradability of polyethylene. Polym Degrad Stab. 2002;76(1):129–35.
120. Watanabe M, Kawai F, Shibata M, Yokoyama S, Sudate Y. Computational method for analysis of polyethylene biodegradation. J Comput Appl Math. 2003;161(1):133–44.
121. Yoon M, Jeon H. Biodegradation of polyethylene by a soil bacterium and AlkB cloned recombinant cell. J Bioremed Biodegrad. 2012;03:1.
122. Jeon HJ, Kim MN. Functional analysis of alkane hydroxylase system derived from Pseudomonas aeruginosa E7 for low molecular weight polyethylene biodegradation. Int Biodet Biodegrad. 2015;103:141–6.
123. Jeon HJ, Kim MN. Comparison of the functional characterization between alkane monooxygenases for low-molecular-weight polyethylene biodegradation. Int Biodeter Biodegrad. 2016;114:202–8.
124. Xu J, Cui Z, Nie K, Cao H, Jiang M, Xu H, Tan T, Liu L. A quantum mechanism study of the C-C bond cleavage to predict the bio-catalytic polyethylene degradation. Front Microbiol. 2019;10:489.
125. Liu C, Wang W, Wu Y, Zhou Z, Lai Q, Shao Z. Multiple alkane hydroxylase systems in a marine alkane degrader, Alcanivorax dieselolei B-5. Environ Microbiol. 2011;13(5):1168–78.

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