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The CRISPR-Cas, pAgo, and CBASS Mediated Abortive Infection and Its Potential Application

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Abstract. Throughout a long evolutionary history, prokaryotes have co-evolved with bacteriophages. To resist phage invasion, prokaryotes have developed a diverse range of prokaryotic immunity. The prokaryotic immune system primarily operates through four mechanisms: inhibiting phage adsorption, blocking phage nucleic acid injection, degrading phage nucleic acids, and mediating abortive infection of phages. Among the numerous mechanisms of anti-phage defense systems, some immune systems based on the abortive infection mechanism, such as certain subtypes of the CRISPR-Cas system, the prokaryotic Argonaute immune system (pAgo), and cyclic-oligonucleotide-based anti-phage signaling systems (CBASS), have garnered significant attention in academia due to their high potential application value. This paper summarizes certain prokaryotic immune systems based on abortive infection mechanisms and provides a brief review of their potential application progress.

Keywords: Prokaryotic immunity, Anti-phage defense mechanism, Gene editing, Nucleic acid testing

1. Introduction

The prokaryotic immune system mainly operates through four types of mechanisms. The first mechanism inhibits phage adsorption, whereby bacteria alter, eliminate, or block surface receptors, thereby limiting successful attachment and entry of phages [1]. The second mechanism blocks phage nucleic acid injection; the peptidoglycan of the bacterial cell wall provides some resistance to phage nucleic acids. Additionally, superinfection exclusion (Sie) also falls under this mechanism. For example, when a bacterial cell is infected by T-even coliphage, it effectively blocks the infection by other closely related phages [2]. The third mechanism involves the degradation of phage nucleic acids, such as through restriction-modification (R-M) and CRISPR-Cas systems. The fourth mechanism is abortive infection (Abi), where the infected cell undergoes suicide before the phage completes its replication cycle (Figure 1), preventing the spread of phages to surrounding bacteria, thereby effectively protecting the bacterial population [3].

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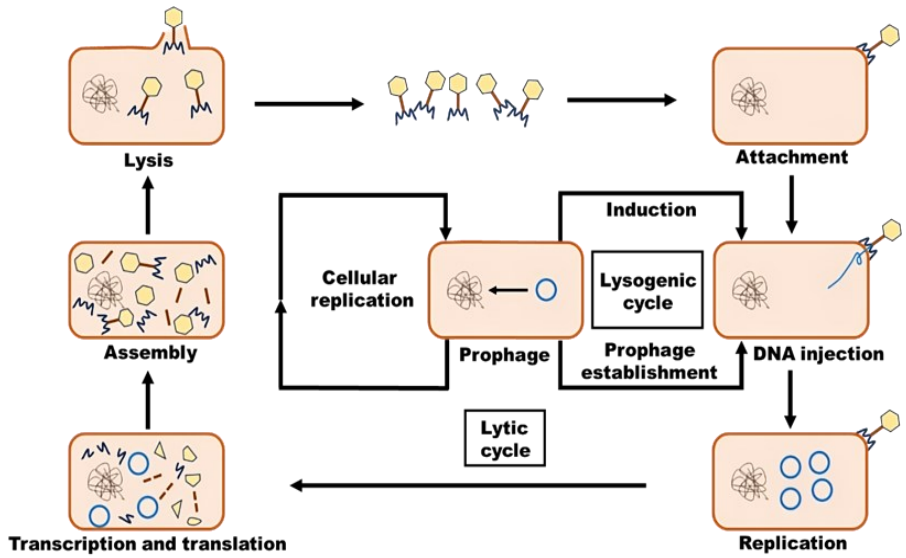

Figure 1. Lysogenic Cycle and Lytic Cycle of Bacteriophage Infection in Bacteria.

The process of bacteriophage infection in bacteria can be categorized into two types based on the kind of bacteriophage involved. The infection by lytic bacteriophages primarily involves the following six steps: The first step is adsorption, where the bacteriophage binds to the bacterial surface through protein interactions. The second step is invasion, where the bacteriophage uses its tail spike to penetrate the bacterial surface and then injects its genetic information into the bacterium via its tail. The third step is replication, in which the DNA of the bacteriophage is copied using the injected nucleic acids as a template. The fourth step is transcription and translation, where the DNA from the third step serves as a template for synthesizing bacteriophage proteins. The fifth step is assembly, where the bacteriophage proteins combine with the bacteriophage nucleic acids to form new bacteriophages. The sixth step is release, during which the bacterium lyses and the bacteriophages are released . The infection process of temperate bacteriophages differs slightly; after the second step, the bacteriophage DNA sequence integrates into the bacterial DNA (referred to as prophage) or exists freely within the bacterium, replicating alongside the bacterium and being evenly distributed to new bacterial cells. Lytic induction occurs only under UV or other stimulating conditions. In this process, the temperate bacteriophage transitions into a lytic bacteriophage, and the prophage sequence is excised from the bacterial genome. New bacteriophage-related proteins and nucleic acid components replicate and assemble, producing progeny bacteriophages that are then released .

2. CRISPR-Cas Systems Following the Abortive Infection Mechanism

The CRISPR-Cas system is an adaptive immune mechanism found in prokaryotes, first discovered in a special repetitive sequence structure at the 3' end of Escherichia coli [4]. A typical CRISPR-Cas system consists of CRISPR loci and Cas proteins, functioning through three stages. In the adaptation phase, a unique complex of Cas proteins typically binds to the target DNA after recognizing a specific short sequence known as the protospacer adjacent motif (PAM) and cleaves a portion of the target DNA, referred to as the protospacer. Following the $5'$ end repeats of the CRISPR array, the adaptation complex inserts the protospacer DNA into the array, creating a new spacer region. In the expression phase, the CRISPR array is usually transcribed into a single transcript—CRISPR pre-RNA (pre-crRNA)—which is then processed into mature CRISPR RNA (crRNA) with the involvement of tracrRNA and RNase III [5]. In the interference phase, the complex bound to crRNA recognizes the protospacer sequence (or a very similar sequence) in the invading viral or plasmid genome, recruiting Cas nucleases for cleavage, thus rendering it inactive [6]. Some CRISPR-Cas systems possess ancillary effectors that can also perform functions such as collateral nucleic acid cleavage [7].

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3. pAgo Abortive Infection System

The discovery of the Argonaute (Ago) gene originated from studies on leaf curling in Arabidopsis thaliana [8]. It plays a crucial role in various biological activities. Previous research has shown that Argonaute proteins (Agos) are essential components of the defense mechanisms in both prokaryotes and eukaryotes [9]. In eukaryotes, eukaryotic Argonaute proteins (eAgos) are key players in RNA interference (RNAi), a mechanism in which dsRNA precursors are processed by RNase III-like domains (Dicer and Drosha) to produce 5' phosphorylated short dsRNA molecules (small interfering RNAs, siRNAs). The passenger strand of the siRNAs is removed while the guide strand is loaded onto eAgos. The guide strand directs eAgos to bind to complementary mRNA fragments, extending towards the 3' end of the guide strand. The 3' end of the guide strand is released from eAgos, leading to conformational changes in eAgos and resulting in cleavage of the target strand. Once cleavage is completed, the target strand is released, allowing eAgos to engage with the next target [10]. Furthermore, eAgos play a significant role in the repression of target gene expression by microRNAs (miRNAs), wherein the mature miRNA binds to a member of the Ago protein family to form the RNA-induced silencing complex (RISC), a process known as RISC loading [11]. In prokaryotes, Prokaryotic Argonautes (pAgos) serve as nucleic acid-guided defense systems, protecting prokaryotes from the invasion of mobile genetic elements and activating various toxic effectors to kill infected cells, thereby preventing the spread of invaders [7].

In prokaryotes, pAgos are typically represented by Thermus thermophilus (TtAgo) and Rhodobacter sphaeroides (RsAgo). TtAgo mediates DNA-guided DNA interference, associating with small interfering DNA (siDNA) guides derived from plasmid DNA. Upon recognizing invading DNA, it cleaves cognate DNA targets. This guide is produced by TtAgo's catalytic site using a mechanism known as "chopping." Additionally, two TtAgo–siDNA complexes with complementary siDNA guides can mediate dsDNA breaks[12-13]. RsAgo mediates RNA-guided DNA interference, associating with small interfering RNA (siRNA) guides that originate from the degradation of mRNA transcribed from invading DNA. The gene encoding RsAgo is clustered with a gene that encodes a putative DNA nuclease, which degrades the invading DNA upon recognition by RsAgo. Similar to RsAgo, many pAgos are associated with putative nucleases, helicases, and DNA-binding proteins [14].

4. CBASS Abortive Infection System

CBASS (Cyclic oligonucleotide-based antiphage signaling systems) is a widely prevalent anti-phage defense mechanism found in bacteria and archaea, closely associated with the mammalian cGAS-STING pathway [15]. First proposed in 2019, this discovery revealed that cGAS/DncV-like nucleotidyltransferase (CD-NTase) enzymes produce Cyclic GMP-AMP (cGAMP) molecules upon sensing cell infection, activating phospholipases that degrade the bacterial inner membrane, leading to cell death before the phage replication cycle is completed [16] (Figure 2). The specific mechanism by which bacterial cyclases detect phage infection is still unclear. Currently, only one CBASS-activating bacteriophage RNA (cabRNA) has been demonstrated, which binds to a positively charged surface of the CdnE03 cyclase, promoting the synthesis of the cyclic dinucleotide cGAMP to activate the CBASS immune response [17].

The CBASS system typically consists of three types of components. The first is the oligonucleotide cyclase, which generates signaling cyclic oligonucleotides during phage infection [18]. In addition to cGAMP, the oligonucleotide cyclase can also produce Cyclic AMP-UMP, Cyclic UMP-UMP, Cyclic AMP-AMP-GMP, Cyclic AMP-AMP-AMP, and Cyclic AMP-AMP-AMP-AMP cyclic oligonucleotides [18-21]. The second component is the effector protein, which, upon activation by cyclic oligonucleotides, can induce cell death to prevent phage replication and spread. Effectors also serve as the basis for classifying various CRISPR subtypes. In addition to phospholipases, endonucleases can act as effectors to non-specifically degrade genomic DNA [19][22]. TM-effector proteins can also disrupt the inner membrane through raft-like aggregation, initiating the abortive infection process to inhibit phage replication [23]. Additionally, rare effector types include Toll/interleukin-1 receptor (TIR) domains, the Phosphorylase/nucleosidase superfamily, and Peptidases. The third component is ancillary

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genes, which encode additional protein structural domains related to the function of the CBASS system, mainly belonging to the Cap protein family.

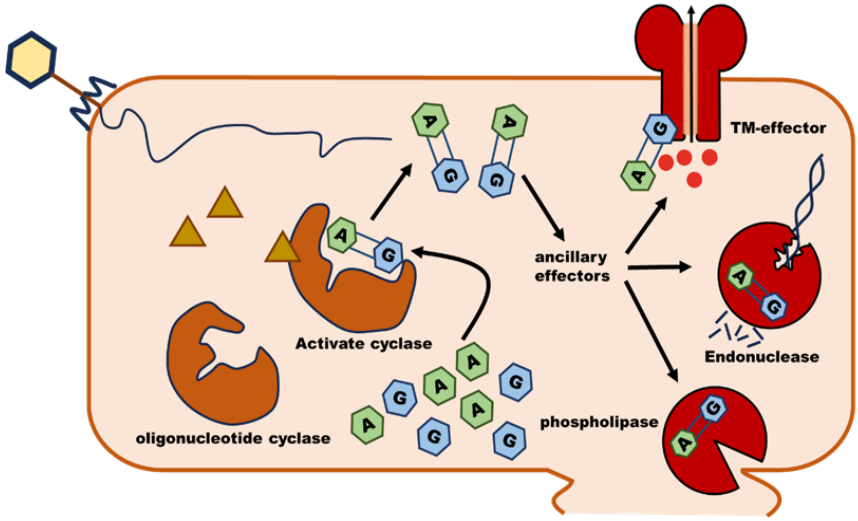

Figure 2. The Mechanism of the CBASS Abortive Infection System.

In this system, the oligonucleotide cyclase synthesizes various circular oligonucleotides in response to stimulation from phage components. These circular oligonucleotides activate multiple ancillary effectors. Currently, three types of ancillary effectors have been identified: TM-effector, endonuclease, and phospholipase. These effectors execute the abortive infection mechanism through different mechanisms.

5. Connections Among CRISPR-Cas, pAgo, and CBASS Systems Following the Abortive Infection Mechanism

Table 1. Immune Mechanisms of CRISPR-Cas System, pAgo System, and CBASS System That Follow the Abortive Infection Mechanism.

Immune system	Type	subtype	core protein	Guide type	Recogni-zed target	associated / ancillary effectors	Action
CRISP R-Cas	Type III	Type III-A	Cas10	RNA	RNA	Nuclease, protease	Collateral ssDNA cleavage, synthesis of cyclic oligoadenylates (cOA), target RNA, ssDNA cleavage
		Type III-E	Cas7-11-Csx29	RNA	RNA	Csx30	target RNA cleavage, cell growth arrest
	Type V	Type V-A2	Cas12a2	RNA	RNA	-	Collateral RNA, ssDNA, dsDNA cleavage
		Type V-G	Cas12g	RNA	RNA	-	target RNA, ssDNA cleavage, Collateral RNA, ssDNA cleavage
	Type VI	Type VI-A	Cas13a	RNA	RNA	-	Collateral RNA cleavage
		Type VI-B	Cas13b	RNA	RNA	Csx27, Csx28	Collateral RNA cleavage, membrane depolarization
pAgo	Long	long-A	Ago with four domain (MID, PIWI, PAZ, N)	DNA	DNA	nuclease, helicase, DNA-binding protein	target ssDNA cleavage

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Table 1. (continued).

		long-B	Ago with four domain (MID, PIWI, PAZ, N)	RNA	DNA (ssDNA)	nuclease, trans membrane protein	collateral dsDNA cleavage
	short		Ago with two domain (MID, PIWI)	RNA	DNA (ssDNA)	NAD(P)ase	NAD+ depletion
						nuclease	collateral dsDNA and RNA cleavage
CBASS	Type I	Type I-A	oligonucleotide cyclase	-	-	phospholipase	degrade the phospholipids of the inner cell membrane
		Type I-B	oligonucleotide cyclase	-	-	TM	forming pores in the cell membrane
		Type I-C	oligonucleotide cyclase	-	-	Endonuclease	collateral dsDNA cleavage
		Type I-D	oligonucleotide cyclase	-	-	TIR	-
		Type I-F	oligonucleotide cyclase	-	-	Peptidase	cleavage essential cellular proteins
	Type II	Type II-A	oligonucleotide cyclase	-	-	phospholipase	degrade the phospholipids of the inner cell membrane
		Type II-C	oligonucleotide cyclase	-	-	Endonuclease	collateral dsDNA cleavage
		Type II-D	oligonucleotide cyclase	-	-	TIR	-
	Type III	Type III-C	oligonucleotide cyclase	-	-	Endonuclease	collateral dsDNA cleavage
		Type III-D	oligonucleotide cyclase	-	-	TIR	-
		Type III-E	oligonucleotide cyclase	-	-	Phosphorylase/nucleosidase superfamily	-
	Type IV	Type IV-B	oligonucleotide cyclase	-	-	TM	forming pores in the cell membrane

Note: Each system is subdivided according to its type and subtype [19][22][24]. The table lists the core protein, associated/ancillary effectors, and the action of each effector corresponding to each subtype. CRISPR-Cas and pAgo can complementarily pair with exogenous invading nucleic acids, with additional details on guide types and recognized target types. The CBASS system does not possess this mechanism, so it is not listed in the table. The subtypes of CRISPR-Cas and pAgo mentioned in the table are all supported by literature. Among the subtypes of CBASS, only Type I-B, Type II-A, Type II-C, and Type III-C have been referenced in previous literature, while the others are predicted results from bioinformatic analysis.

There is a certain relationship among the CRISPR-Cas, pAgo, and CBASS systems that follow the abortive infection mechanism. First, there are two major shared steps in the processes from detecting foreign phage nucleic acid invasion to executing cell suicide: Identification of infection and Activation of the ancillary effectors. These two steps correspond to the two components of the abortive infection system: the element sensing phage invasion and the element that kills the cell and shuts down metabolic pathways upon detecting the invasion [25] (Figure 3). Information about the core proteins, ancillary effectors, and various types and subtypes of the three systems is summarized in Table 1. During the Identification of infection phase, CRISPR-Cas acts as an adaptive immune system. Its encoded Cas1-Cas2 complex selects a portion of the foreign DNA and integrates it into the host's CRISPR array, a step known as adaptation. Next, the CRISPR array is transcribed into a long pre-crRNA that is further processed by Cas proteins or cellular RNases, a process referred to as crRNA biogenesis. The mature

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crRNA then serves as a guide, combining with Cas proteins to pair complementarily with the target in subsequent steps [26-28]. In this phase, both the pAgo system and CRISPR-Cas load guide nucleic acid fragments, but the sources of the guides differ. Fragments of invader DNA or its mRNA integrate into the Ago protein, providing the system with the ability to specifically recognize the target [12-13]. In the CBASS system, the oligonucleotide cyclase is activated by a component of the invading phage [3]. After the Identification of infection phase, the core proteins in the system serve as effectors to perform their functions. For example, Cas10 and Cas12g mediate target RNA and ssDNA cleavage upon binding to the target [29-32]. Long-A pAgos can mediate ssDNA cleavage upon binding to target DNA [24]. The activated oligonucleotide cyclase generates second messenger cyclic oligonucleotides to transmit information about phage invasion within the cell [18]. Some core proteins directly mediate the abortive infection mechanism; for example, Cas12a2 nonspecifically mediates collateral cleavage of RNA, ssDNA, and dsDNA. However, in most cases, abortive infection is mediated by ancillary effectors rather than core proteins. These effectors are encoded by gene operons adjacent to the core protein gene operons [7][14][26]. In the CRISPR-Cas system, ancillary effectors that mediate abortive infection are typically nucleases that cleave collateral DNA or RNA [33-38]. Additionally, effectors such as Csx28 can create membrane pores, leading to membrane depolarization [7]. Long-B pAgo mediates collateral dsDNA cleavage through associated nucleases [39]. Short pAgo associates with two types of ancillary effectors, NAD(P)ase and nuclease, leading to cell suicide through NAD+ depletion and collateral dsDNA and RNA cleavage [40-42]. In the CBASS system, the ancillary effector phospholipase mediates abortive infection by damaging cell membrane structures [16]. Endonucleases mediate abortive infection through collateral dsDNA cleavage [19][22]. TM effectors act as membrane channel proteins, mediating membrane depolarization that leads to cell suicide [41]. Peptidases cleave essential cellular proteins, disrupting normal cellular activities and mediating abortive infection. In summary, the CRISPR-Cas and pAgo systems have very similar target recognition mechanisms, with all three systems activating ancillary effectors in response to the stimulus of foreign nucleic acid invasion, leading to cell death through different mechanisms and mediating abortive infection.

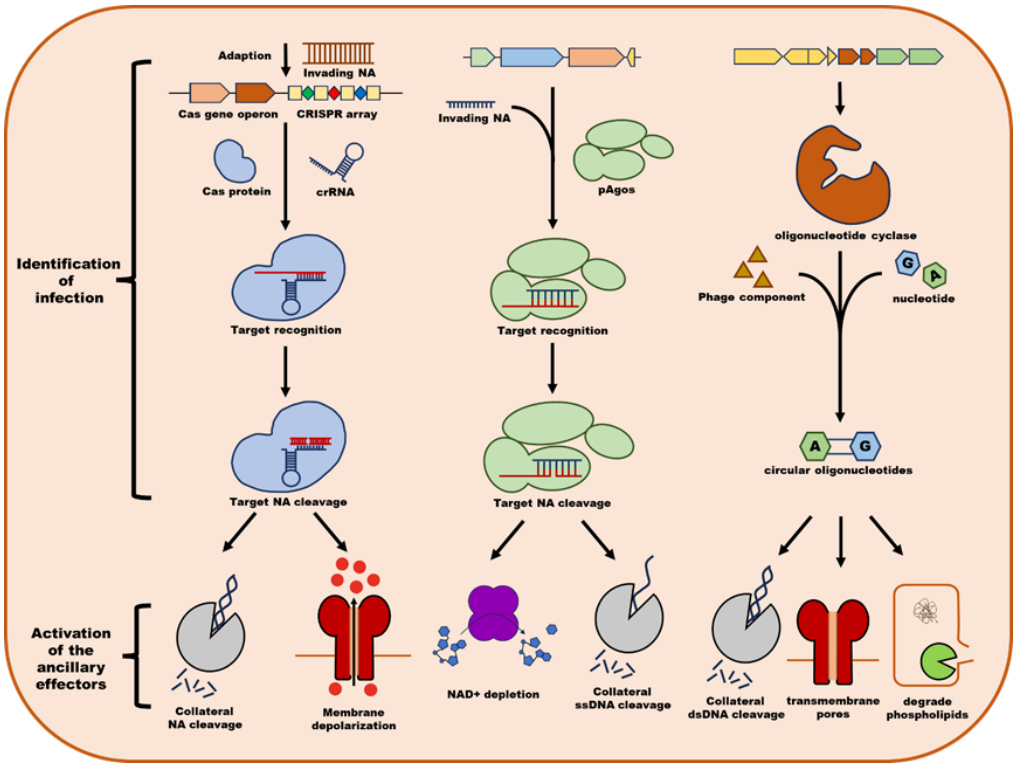

Figure 3. Immune Responses Mediated by CRISPR-Cas, pAgo, and CBASS That Follow the Abortive Infection Mechanism.

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During the identification of infection stage, CRISPR-Cas acquires the exogenous invading nucleic acids and stores them in the spacers of the CRISPR array. These sequences are then transcribed into crRNA, which mediates target recognition and specifically facilitates double-stranded nucleic acid cleavage. pAgos directly acquire guides from the invading nucleic acids, generally mediating single-stranded nucleic acid cleavage. In CBASS, the oligonucleotide cyclase synthesizes circular oligonucleotides upon stimulation by certain phage components. After recognizing the invasion of exogenous nucleic acids, various ancillary effectors, which closely interact with the core proteins of the three systems, come into play to mediate the abortive infection mechanism that leads to cell suicide.

6. Potential of Technologies Exploration Based on the pAgo and CBASS Systems That Follow the Abortive Infection Mechanism

Compared to the CRISPR-Cas systems that follow the abortive infection mechanism, the practical application range of pAgo and CBASS is relatively small. Compared to common systems such as CRISPR-Cas9, CRISPR-Cas12, and CRISPR-Cas13, the siDNA carried by pAgos has advantages, including being relatively cheap to synthesize, having shorter DNA guides compared to the RNA guides of the CRISPR-Cas system, and being theoretically designed to specifically target any desired location [43]. This makes the pAgo system promising for broader applications in gene editing and nucleic acid detection [44]. However, due to the lack of helicase activity, the conditions for pAgos to achieve target dsDNA cleavage are quite stringent. Currently, successful dsDNA cutting has only been achieved under high-temperature conditions in thermophiles [45-46]. Additionally, changes in temperature can affect the specificity of target recognition and cleavage by pAgos [47]. Therefore, finding pAgos capable of producing dsDNA cleavage under milder conditions is the next direction for researchers. Regarding the CBASS system, since some of its mechanisms remain unknown, further research should focus on the biogenesis, structure, function, and molecular interactions of phage components, such as RNA that activates bacterial cyclases, in order to explore more potential applications of this system [18]. Furthermore, due to the similarities between the CBASS system in prokaryotes and the cGAS-STING pathway in mammals [15], an in-depth study of the CBASS system can enhance our understanding of the evolutionary process from prokaryotic anti-phage defense to animal immunity, explaining the fundamental rules that remain unchanged [15]. This will provide valuable materials for studying the evolution of immune systems from prokaryotes to eukaryotes.

7. Conclusion

Among the three systems, the CRISPR-Cas system that follows the abortive infection mechanism has been extensively applied in gene editing, nucleic acid detection, and transcriptional regulation, expanding and optimizing the application scenarios of CRISPR-Cas tools based on CRISPR-Cas9. The side effects generated by ancillary effectors in the CRISPR-Cas12 and CRISPR-Cas13 need to be further overcome. Although pAgo and CBASS have not been widely applied, they possess unique advantages that require further elucidation of unknown mechanisms, exploration of more relevant resources, and the search for materials that can function under milder conditions to provide more tools for biological research.

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