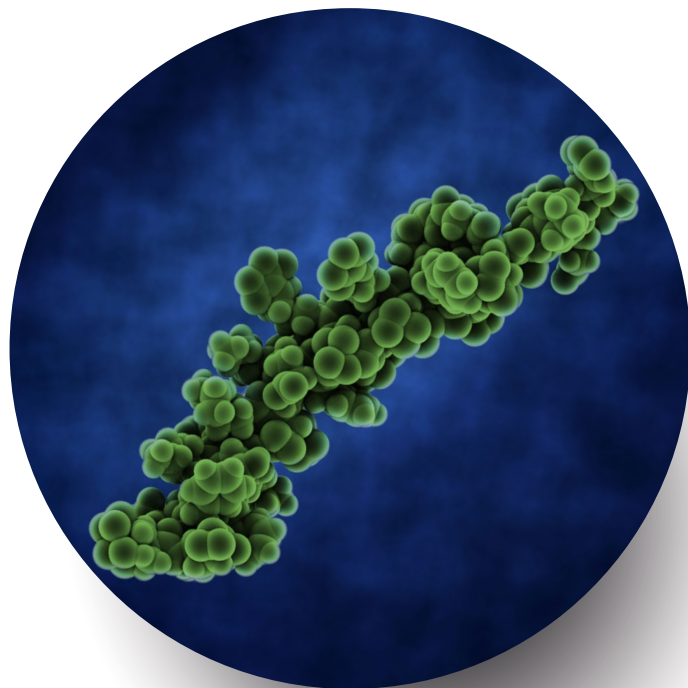


ANTIMICROBIAL PEPTIDES BACHEM

LEADING PARTNER IN TIDES



ANTI- MICROBIAL PEPTIDES OFFERED BY BACHEM

Ribosomally synthesized antimicrobial peptides (AMPs) constitute a structurally diverse group of molecules found virtually in all organisms. Most antimicrobial peptides contain less than 100 amino acid residues, have a net positive charge, and are membrane active. They are major players in the innate immune defense but can also have roles in processes as chemokine induction, chemotaxis, inflammation, and wound healing. In addition to their antimicrobial effects, many of them show antiviral and antineoplastic activities.

INTRODUCTION

AMPs are a heterogeneous group of relatively small molecules usually containing less than a hundred amino acids. They were first described in the 1960's by Zeya and Spitznagel in polymorphonuclear leukocyte lysosomes.

To date, more than 2600 AMPs have been identified and registered in databases (e.g. <http://aps.unmc.edu/AP/main.php>).

They are produced by nearly all groups of organisms, including bacteria, fungi, plants, and animals. Many vertebrate AMPs are secreted by epithelial surfaces such as the tracheal, lingual, or intestinal mucosa of mammals or the skin of amphibia. Some are expressed in neutrophils, monocytes, and macrophages.

AMPs are involved in both animal and plant immune defense systems. Constitutively expressed or induced they play a key role in the first line of defense against microbial intruders.

Structure/Classification

AMPs can be classified on the basis of their amino acid composition and structure. Two major groups of AMPs can be distinguished. The first group consists of linear molecules which either tend to adopt α -helical structure or are enriched in certain amino acids such as arginine, glycine, histidine, proline, and tryptophan. The second group consists of cysteine-containing peptides which can be divided into single or multiple disulfide structures. In many cases, the presence of disulfide bridges is required for antimicrobial activity.

Most AMPs are cationic peptides, but there are also anionic peptides such as dermcidin, an aspartic acid-rich peptide from human and maximin H5 from amphibian

skin. Other non-cationic AMPs include fragments from neuropeptide precursor molecules such as proenkephalin A, aromatic dipeptides primarily isolated from dipteran larvae, or peptides derived from oxygen-binding proteins from arthropod or annelid species.

Mode of Action

Most AMPs act by provoking an increase in plasma membrane permeability. They preferentially target microbial versus mammalian cells. Selectivity is influenced by several factors such as differences in membrane composition: membranes of many bacterial pathogens contain negatively charged lipid moieties such as phosphatidylglycerol (PG), cardiolipin, and phosphatidylserine (PS), whereas mammalian membranes, commonly enriched in phosphatidylethanolamine (PE), phosphatidylcholine (PC) and sphingomyelin, are generally neutral in net charge. The presence of sterols such as cholesterol and ergosterol within the membrane may be a further means by which AMPs can distinguish between mammalian or fungal cells and prokaryotes.

A first step in the mechanism of membrane permeabilization is the electrostatic interaction between the positively charged AMP with the negatively charged membrane surface of the microorganism. Subsequent disruption of the membrane by creation of pores within the microbial membrane ultimately results in cell death of the organism due to leakage of ions, metabolites, cessation of membrane-coupled respiration, and biosynthesis. Several models for pore formation such as the Barrel-Stack, the Toroidal or Wormhole Model, and the Carpet Model have been proposed (Fig. 1).

The Barrel-Stave Model

The Barrel-Stave model describes a mechanism in which AMPs form a barrel-like pore within the bacterial membrane with the individual AMPs or AMP complexes being the staves. Arranged in this manner, the hydrophobic regions of the AMPs point outwards towards the acyl chains of the membrane whereas the hydrophilic areas form the pore.

Another example for changing the surface net charge is the production of cationic lysine-substituted phosphatidylglycerol (L-PG) found in certain *Staphylococcus aureus* strains. In Gram-negative bacteria, addition of 4-aminoarabinose (Ara4N) to the phosphate group of the lipid A backbone or increased acylation of lipopolysaccharides (LPS) are important mechanisms of AMP resistance.

MOST AMPs ACT BY PROVOKING AN INCREASE IN PLASMA MEMBRANE PERMEABILITY

The Toroidal Pore or Wormhole Model

The pores described by this model differ from those of the Barrel-Stave model. Primarily, the outer and inner leaflet of the membrane are not intercalated in the trans-membrane channel.

The Carpet Model

A different mechanism is proposed in the Carpet model where AMPs first cover the outer surface of the membrane and then disrupt the membrane like detergents by forming micelle-like units.

Certain AMPs penetrate the bacterial membrane without channel formation. They act on intracellular targets by e.g. inhibiting nucleic acid and/or protein synthesis.

Resistance

Resistance to AMPs can either be constitutive or inducible. Inherited resistance mechanisms include altered surface charge, active efflux, production of peptidases or trapping proteins, and modification of host cellular processes. For instance, *Staphylococcus aureus* manages to reduce the overall cell surface charge by esterification of the cell wall component teichoic acid with D-alanine and thereby increases its resistance against human AMPs.

Exposure to AMPs may also induce stress responses by which microorganisms try to survive. Inducible regulatory mechanisms have been described in a variety of organisms. For instance, the PhoP/PhoQ regulon in *Salmonella* has been demonstrated to regulate transcriptional activation of surface and secretory proteins, enzymes that modify lipopolysaccharide, lipid and protein constituents of the outer membrane and proteases that likely degrade certain AMPs.

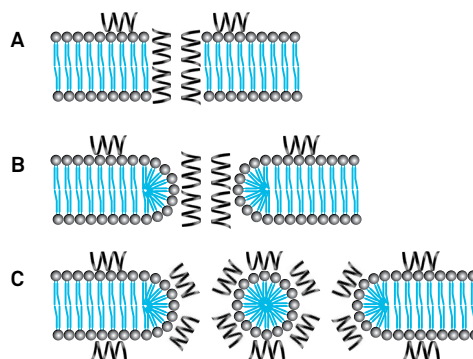


Fig. 1.
Mode of Action

- A** Barrel-Stave Model
- B** Toroidal Pore or Wormhole Model
- C** Carpet Model

| Examples | |
|---|---|
| Linear cationic α-helical peptides | Andropin from insects Bombinin from amphibians Buforin II from amphibians CAP18 from rabbits Cecropins from insects Cecropin P1 from the pig intestinal parasitic nematode, <i>Ascaris suum</i> Ceratotoxin from insects Dermaseptin from amphibians LL-37 from human Magainin from amphibians Melittin from insects Pleurocidin from <i>Pseudopleuronectes americanus</i> |
| Cationic peptides enriched for specific amino acids | |
| Glycine-containing peptides | Hymenoptaecin from honeybees |
| Glycine- and proline-containing peptides | Coleopterucin from beetles Holotricin from beetles |
| Histidine-containing peptides | Histatins from humans and some higher primates |
| Proline-containing peptides | Abaecin from honeybees |
| Proline- and arginine-containing peptides | Apidaecins from honeybees Bactenicins from cattle Drosocin from <i>Drosophila</i> PR-39 from pigs |
| Proline- and phenylalanine-containing peptides | Prophenin from pigs |
| Tryptophan-containing peptides | Indolicidin from cattle |
| Anionic and cationic peptides that contain cysteine and form disulfide bonds | |
| 1 Disulfide bond | Brevinins |
| 2 Disulfide bonds | Protegrins from pigs |
| 3 Disulfide bonds | α -Defensins from human, rabbits and rats β -Defensins from humans, cattle, mice, rats, pigs, goats and poultry θ -Defensin from the rhesus monkey Insect defensins (Defensin-A from <i>Aedes aegypti</i>) |
| 4 Disulfide bonds | Antifungal defensins from plants Drosomycin from <i>Drosophila</i> |
| Anionic peptides | |
| | Dermcidin from human skin Maximin H5 from amphibian skin |
| Anionic and cationic peptide fragments derived from precursor proteins | |
| | Antimicrobial domains from bovine α -lactalbumin, human hemoglobin, lysozyme, and ovalbumin Aromatic dipeptides from dipteran larvae Casocidin I from human casein Enkelytin from proenkaphalin A Lactoferricin from lactoferrin |

Adapted from K.A. Brogden, Nat. Rev. Microbiol. 3, 238-250 (2005)

IMPORTANT FAMILIES OF AMPs

Bombinins

Bombinins constitute a family of AMPs produced in fire-bellied toads (*Bombina* species) active against Gram-negative and Gram-positive bacteria and fungi. Bombinins, bombinin-like peptides (BLPs), and Bombinin H molecules are found in the species *Bombina bombina*, *Bombina variegata*, and *Bombina orientalis*, whereas the homologous maximins and maximin H peptides are derived from the giant fire-bellied toad *Bombina maxima*.

Bombinin H peptides contain either 17 or 20 amino acid residues and are more hydrophobic than bombinins, some of them contain D-alloisoleucine at position 2. They exhibit lower antibacterial activity than bombinins but, in contrast to them, they possess haemolytic activity.

Cathelicidins

Members of this family are amphipathic, cationic peptides with a broad-spectrum antimicrobial activity. Cathelicidins typically act by disrupting the integrity of bacterial membranes. They are characterized by an evolutionary conserved N-terminal cathelin-like domain of approximately 99-114 amino acid residues linked to a C-terminal antimicrobial domain of 12-100 residues that can be released upon proteolytic processing.

Members of this family include linear peptides amongst them a number of proline-rich AMPs that show different types of proline repeat motifs (Bac5, Bac7, PR-39, prophenins) and the tryptophan-rich indolicidin characterized by three regularly spaced proline residues.

The protegrins (PG-1 to PG-5) contain two disulfide bridges and an amidated C-terminus. Cathelicidins have been found in every mammalian species examined. In human, LL-37 (Product 4042456) is the only member of the cathelicidin family. The peptide consists of 37 amino acids and contains two leucine residues at the N-terminus. It

is proteolytically cleaved from the 18 kDa precursor protein human cathelicidin antimicrobial protein CAP-18. LL-37 is primarily produced by phagocytic leucocytes and epithelial cells, and is involved in various processes such as direct killing of microorganisms, binding and neutralizing LPS, chemotaxis and chemokine induction, regulation of inflammatory responses, and wound healing. Its production is influenced by several factors such as microbial products, host cytokines, vitamin D₃, and availability of oxygen.

LL-37 orthologues in mouse and rat are CRAMP (mouse) (Product 4056438) and CRAMP (rat), respectively.

Cecropins

Cecropins were first isolated from the giant silk moth *Hyalophora cecropia*. They can form amphipathic, α -helical structures and are structurally related to other cecropins as bactericidin, lepidopteran, and sarcotoxin. Cecropin P1 (Product 4039862), found in pig intestine, also belongs to this family. Most cecropins show broad-spectrum antibacterial activity. Cecropin A (Product 4030488) and B (Product 4030477) have also been demonstrated to possess tumoricidal activity against mammalian leukemia, lymphoma, and carcinoma cell lines.

Ceratotoxins

This family consists of cationic α -helical amphipathic peptides expressed in the female reproductive accessory glands of the Mediterranean fruit fly *Ceratitis capitata*. The production of the peptides is enhanced by mating.

Ceratotoxin A and ceratotoxin B are 29 amino acid peptides differing in two amino acids. Ceratotoxin C and D consist of 32 and 36 amino acids, respectively.

The peptides of this family are active against Gram-negative as well as Gram-positive bacteria and are supposed to act via the Barrel-Staff model. Ceratotoxin A

has been shown to be mainly antibacterial for Gram-negative organisms.

Defensins

Defensins are small cysteine-rich cationic peptides containing three or four disulfide bridges. They have been isolated from molluscs, acari, arachnids, insects, mammals, and plants. They are further divided into families on the basis of the spatial distribution of their cysteine residues.

Three families, the α -, β - and θ -defensins, can be distinguished in mammals. α - and β -defensins are characterized by antiparallel β -sheet structures stabilized by three disulfide bonds. The θ -defensins are found in rhesus monkey and some other non-human primates but not in human, chimpanzee and gorilla. They consist of two nine amino acid peptides derived from different precursor proteins joined by head-to-tail cyclization. Invertebrate and plant defensins contain three or four disulfide bridges, respectively. Insect and mammalian defensins are mainly active against bacteria while most plant defensins possess antifungal activity.

Dermaseptins

The peptides of the dermaseptin family are closely related and consist of 28-34 amino acids. They were originally isolated from skin extracts of the South American arboreal frog *Phyllomedusa sauvagei* and contain a conserved tryptophan residue at position 3. Dermaseptins exhibit broad-spectrum antimicrobial activity against Gram-positive and Gram-negative bacteria.

Histatins

Histatins are histidine-rich and mostly cationic peptides found in the saliva of humans and some higher primates. They are active against a broad-spectrum of bacteria and fungi.

The antifungal activity of the human salivary peptide histatin-5 has been extensively studied and is supposed to be due to inhibition of mitochondrial respiration and the formation of reactive oxygen species. Histatin-5 has also been shown to inhibit both host-derived and bacterial proteolytic enzymes involved in periodontal diseases. Histatin-8, a peptide from human parotid secretion, has been shown to inhibit hem-

agglutination activity of *Porphyromonas gingivalis* 381, a Gram-negative bacterium involved in certain forms of periodontal disease. The peptide may function as a binding domain for the hemagglutinins of *Porphyromonas gingivalis* during agglutination.

Magainins

Magainins constitute a family of linear amphipathic cationic AMPs discovered in the skin of *Xenopus laevis*. The two closely related members of this family, magainin I (Product 4012844) and magainin II (Product 4013706) differ merely in two positions and are 23 amino acids in length. Magainins exhibit broad-spectrum antimicrobial activity against Gram-negative and Gram-positive bacteria, fungi and protozoa and are also cytotoxic for many murine and human cancer cell lines.

CONCLUSIONS

The structures of AMPs represent a unique source for the targeted exploration of new applications in the therapy of microbial and viral infection, cancer, and sepsis. Modern synthetic methods will allow the relatively cheap and accurate production of lead compounds and peptide candidates. The achievements in peptide library generation, analytical methods as mass spectrometry, and screening and formulation technologies may contribute to solve intrinsic problems associated with the use of AMPs as therapeutic agents such as susceptibility to proteases and host toxicity. Bachem has considerable expertise and long-standing experience in peptide synthesis. With our capacity to upscale the production of simple and modified peptides, we are the partner of choice for the pharmaceutical industries.

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ANTI- MICROBIAL PEPTIDES

Antimicrobial peptides are produced by plants and most organisms throughout the animal kingdom including humans. AMPs protect against a broad range of infectious agents, as bacteria, fungi, and viruses.

CECROPINS

Cecropin A

4030488

KWKLFKKIEKVGQNIRDGIIKAGPAVAV-
VGQATQIAK-NH₂

Cecropin A (1-7)-Melittin A (2-9) amide

4042609

KWKLFKKIGAVLKVL-NH₂

Cecropin A (1-8)-Melittin (1-18) amide

4028472

KWKLFKKIGIGAVLKVLTTGLPALIS-NH₂

Cecropin B

4030477

KWKVFKKIEKMGRNIRNGIVKAGPAIAVL-
GEAKAL-NH₂

Cecropin B (free acid) **NEW**

4095745

KWKVFKKIEKMGRNIRNGIVKAGPAIAVL-
GEAKAL

Cecropin P1

4039862

SWLSKTAKKLENSAKKRISGIAIAIQG-
GPR

DEFENSINS

Defensin 5 (human) **NEW**

4102158

ATCYCRTGRCATRESLSGVCEIGRLYLCCR
(Disulfide bonds, air oxidized)

α -Defensin 6

4059148

AFTCHCRRSCYSTEYSYGTCTVMGINHRF-
CCL
(Disulfide bonds between Cys⁴ and
Cys³¹/Cys⁶ and Cys²⁰/Cys¹⁰ and Cys³⁰)

Defensin HNP-1 (human)

4025473

ACYCRIPACIAGERRYGTCTIYQGRLWAFCC
(Disulfide bonds between Cys² and
Cys³¹/Cys⁴ and Cys¹⁹/Cys⁹ and Cys²⁹)

Defensin HNP-2 (human)

4025474

CYCRIPACIAGERRYGTCTIYQGRLWAFCC
(Disulfide bonds between Cys¹ and
Cys²⁹/Cys³ and Cys¹⁸/Cys⁸ and Cys²⁸)

Defensin HNP-3 (human)

4025495

DCYCRIPACIAGERRYGTCTIYQGRLWAFCC
(Disulfide bonds between Cys² and
Cys³⁰/Cys⁴ and Cys¹⁹/Cys⁹ and Cys²⁹)

rec β -Defensin 1 (human)

4038285

β -Defensin 2 (human) **NEW**

4034693

GIGDPVTCLKSGAICHVPVFCPRRYKQI-
GTCGLPGTKCKKP
(Disulfide bonds, air oxidized)

rec β -Defensin 2 (human)

4038287

Retrocyclin-1 (RC-100)

4045698

c(GICRCICGRGICRCICGR)
(Disulfide bonds between Cys³ and
Cys¹⁶/Cys⁵ and Cys¹⁴/Cys⁷ and Cys¹²)

HEPCIDINS

Hepcidin-20 (human)

4065374

ICIFCCGCCHRSKCGMCCKT
(Disulfide bonds, air oxidized)

Hepcidin-22 (human)

4065376

FPICIFCCGCCHRSKCGMCCKT
(Disulfide bonds, air oxidized)

Hepcidin-24 (human)

4084346

THFPICIFCCGCCHRSKCGMCCKT
(Disulfide bonds, air oxidized)

Hepcidin-25 (human)

4040671

DTHFPICIFCCGCCHRSKCGMCCKT
(Disulfide bonds between Cys⁷ and
Cys²³/Cys¹⁰ and Cys¹³/Cys¹⁴ and Cys²²)

Biotinyl-Hepcidin-25 (human)

4056950

Biotinyl-DTHFPICIFCCGCCHRSK-
GMCCCKT
(Disulfide bonds between Cys⁷ and
Cys²³/Cys¹⁰ and Cys¹³/Cys¹⁴ and Cys²²)

Hepcidin-1 (mouse)

4062144

DTNFPICIFCCCKCCNNSQCGICCKT
(Disulfide bonds between Cys⁷ and
Cys²³/Cys¹⁰ and Cys²²/Cys¹¹ and Cys¹⁹/
Cys¹³ and Cys¹⁴)

LL-37 AND FRAGMENTS

LL-37

4042456

LLGDFFRKSKEKIGKEFKRIVQRIKDFL-
RNLVPRTES

LL-37 (37-1) **NEW**

4099710

SETRPVNLNRLFDKIRQVIRKFEKGIKEK-
SKRFFDGLL

Biotinyl-LL-37 **NEW**

4099715

Biotinyl-LLGDFFRKSKEKIGKE-
FKRIVQRIKDFLRNLVPRTES

5-FAM-LL-37 **NEW**

4104169

Fluorescein-5-carbonyl-LLGDFFRK-
SKEKIGKEFKRIVQRIKDFLRNLVPRTES

Tide Fluor™ 2-LL-37 **NEW**

4104170

Tide Fluor™-2-LLGDFFRKSKEKIGKEFKR
IVQRIKDFLRNLVPRTES

LL-37 (scrambled) **NEW**

4099707

GLKLRFEFSKIKGEFLKTPEVRF-
DIKLDNRISVQR

Biotinyl-εAhx-LL-37 (scrambled) **NEW**

4099709

Biotinyl-εAhx-GLKLRFEFSKIKGEFLKTP
EVRFRDIKLDNRISVQR

LL-37 amide

4046855

LLGDFFRKSKEKIGKEFKRIVQRIKDFL-
RNLVPRTES-NH₂

5-FAM-LL-37 (scrambled) **NEW**

4099708

5-FAM-GLKLRFEFSKIKGEFLKTPEVR-
FRDIKLDNRISVQR

Tide Fluor™ 2-LL-37 (scrambled) **NEW**

4104171

Tide Fluor™-2-GLKLRFEFSKIKGEFLKTP
EVRFRDIKLDNRISVQR

Tyr-LL-37 NEW
4099712
YLLGDFFRKSKEKIGKE-
FKRIVQRIKDFLRNLVPRTES

LL-37 FK-13 NEW
4099695
FKRIVQRIKDFLR

LL-37 FKR NEW
4099697
FKRIVQRIKDFLRNLVPRTES

LL-37 GKE NEW
4099696
GKEFKRIVQRIKDFLRNLVPR

LL-37 KRI NEW
4064381
KRIVQRIKDFLRNLVPRTES

LL-37 LLG NEW
4099698
LLGDFFRKSKEKIGKEFKRIV

LL-37 RKS NEW
4064380
RKSKEKIGKEFKRIVQRIKDFL-
RNLVPRTES

LL-37 SKE NEW
4099699
SKEKIGKEFKRIVQRIKDFLR

KR-12 (human)
4064798
KRIVQRIKDFLR-NH₂

Biotinyl-KR-12 (human) NEW
4099713
Biotinyl-KRIVQRIKDFLR

MAGAININS

Magainin I
4012844
GIGKFLHSAGKFGKAFVGEIMKS

Magainin II
4013706
GIGKFLHSAKKFGKAFVGEIMNS

MELITTINS

Cecropin A (1-7)-Melittin A (2-9) amide
4042609
KWKLFKKIGAVLKVL-NH₂

Cecropin A (1-8)-Melittin (1-18) amide
4028472
KWKLFKKIGIGAVLKVLTTGLPALIS-NH₂

Melittin
4030808
GIGAVLKVLTTGLPALISWIKRKRQQ-NH₂

Melittin (free acid) NEW
4061024
GIGAVLKVLTTGLPALISWIKRKRQQ

PSEUDIN PEPTIDES AND ANALOGS

Pseudin-2
4060547
GLNALKKVFQGIHEAIKLINNHVQ



HUMAN CATHELICIDIN LL-37

Human cathelicidin LL-37. Computer model showing the structure of human cathelicidin LL-37 which plays an essential role in protecting humans against infectious diseases.

(KEystone/SCIENCE PHOTO LIBRARY)

TUFTSIN AND ANALOGS

Macrophage Inhibitory Peptide

(Tuftsin (1-3))

4007532

TKP

Tuftsin

4003033

TKPR

MISCELLANEOUS

ACV

4028307

Aad(Cv)

Bis-ACV

4009950

(Aad(Cv))₂

Baceridin **NEW**

4105366

Cyclo(-D-Ala-D-allo-Ile-Val-D-Leu-Leu-Trp)

Bactenecin

4030388

RLCRIVVIRVCR
(Disulfide bond)

Beauvericin

4013628

Cyclo(-D- α -hydroxyisovaleryl-N-Me-Phe)₃

Crotalicidin **NEW**

4105369

KRFKFFKVKKSVKRLKKIFKKPM-VIGVTIPF-NH₂

Cyclo(-Leu-Pro)

4003115

c(LP)

Dermaseptin

4018008

ALWKTMLKKLGTMLHAGKAAL-GAAADTISQGTQ

Dermcidin-1L (human)

4061590

SSLLEKGLDGAKKAVGGGKLGK-DAVEDLESVGGKAVHDVKDVLDSVL

EcAMP3 **NEW**

4105368

GADRCRERCERRHRGDWQGGKQRCL-MECRRREQEED
(Disulfide bonds between Cys⁵ and Cys²⁷/Cys⁹ and Cys²³)

Endotoxin Inhibitor

4014453

KTKCKFLKCC
(Disulfide bond)

Epinecidin-1

4070287

GFIFHIIKGLFHAGKMIHGLV-NH₂

Extracellular Death Factor

4060185

NNWNN

Hispidalin **NEW**

4105367

SDYLNNNPLFPRYDIGNVELSTAYRSFAN-QKAPGRLNQNWALTADYTYR

Indolicidin

4030762

ILPWKWPWWPWRR-NH₂

Lactoferricin B (4-14) (bovine) **NEW**

4057344

RRWQWRMKKLG

Lactoferricin B25

4087382

FKCRRWQWRMKKLGAPSITCVRRAF
(Disulfide bond)

Lysozyme C (46-61) (chicken)

4044059

NTDGSTDYGILQINSR

Parasin I

4029070

KGRGKQGGKVRKAKTRSS

Penetratin

4036091

RQIKIWFQNRRMKWKK-NH₂

Polybia-MP1 NEW

4099795

IDWKKLLDAAKQIL-NH₂

Ranalexin

4025017

FLGGLIKIVPAMICAVTKKC
(Disulfide bond)

Seminalplasmin Fragment (SPF)

Analog

4025057

PKLLKTFLSKWIG

Tachyplesin I

4030734

KWCFRVCYRGICYRRCR-NH₂
(Disulfide bonds between Cys³ and
Cys¹⁶/Cys⁷ and Cys¹²)

H-Tyr-Ser-Pro-Trp-Thr-Asn-Phe-OH

(RIP (free acid))

4034200

YSPWTNF

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