MATHEMATICAL MODELLING FOR UNDERSTANDING THE REGULATION OF MATRIX METALLOPROTEINASES (MMPs) BY TISSUE INHIBITORS

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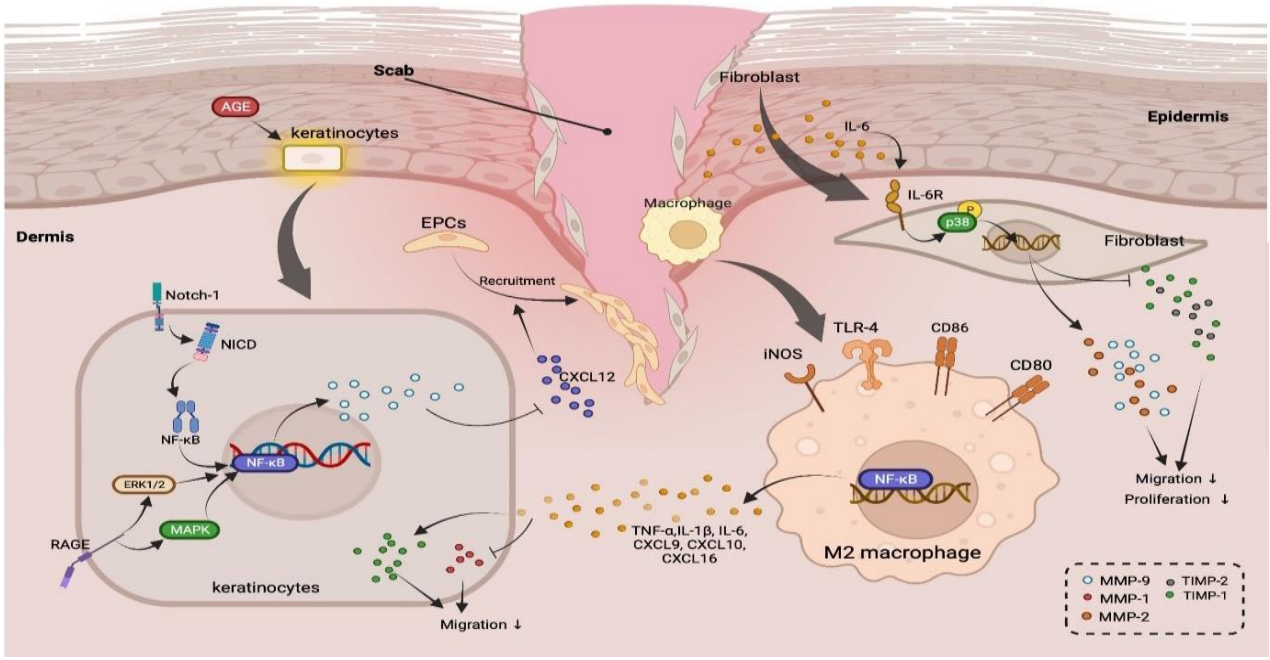
GRAPHICAL ABSTRACT:*The wound–healing process is a highly coordinated and intricated biological mechanism that restores tissue integrity. This process involves numerous cell types and proteins, including matrix metalloproteinases (MMP). In humans, 23 MMPs have been discovered, many of which are detectable in both acute and chronic wounds. Each MMP targets specific substrates and plays distinct roles at every stage of wound healing. As proteinases, MMPs can cleave both extracellular matrix (ECM) and non–ECM components. This activity regulates growth factor activation, maintains ECM homeostasis, and facilitates communications between cells and their surrounding environment, such as other cells and the ECM. During wound healing, the timely expression and activation of MMPs are critical for successful recovery, whereas imbalances in MMP activity, either excessive or insufficient, impair healing. For example, aberrant MMP expression and activity are characteristic of chronic wounds, such as diabetic foot ulcers (DFUs). In these conditions, the resulting excessive proteolysis disrupts tissue repair. Proper control of MMP expression and activity offers the potential for improving wound closure in both DFUs, underscoring their therapeutic value. Achieving this goal requires a deep and extensive understanding of the roles and molecular mechanisms of MMPs in wound healing, and knowledge in this area remains limited. This review explores the structural and functional characteristics of MMPs and their role in regulating wound healing under normal and pathological conditions, focusing on their effects in DFUs.*

Schematic of Cross–Sectional Study of Targeting Matrix Metalloproteinases (MMPs) as a Predictor of Wound Healing in Diabetic



Foot Ulcers and Their Inhibitors for Therapeutic Intervention.

Keywords: Wound Healing; Matrix Metalloproteinases (MMPs); Extracellular Matrix; Diabetic Foot Ulcers,

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1. INTRODUCTION

Wounds occur frequently throughout a person's life, with approximately 3 to 4 out of every 1000 people reporting one or more wounds [1]. Skin injuries present a significant challenge to global healthcare systems, resulting in substantial economic and social burdens [2]. While wound healing rates are often overestimated, reported as high as 90%, data from actual randomized controlled studies reveal a healing rate of

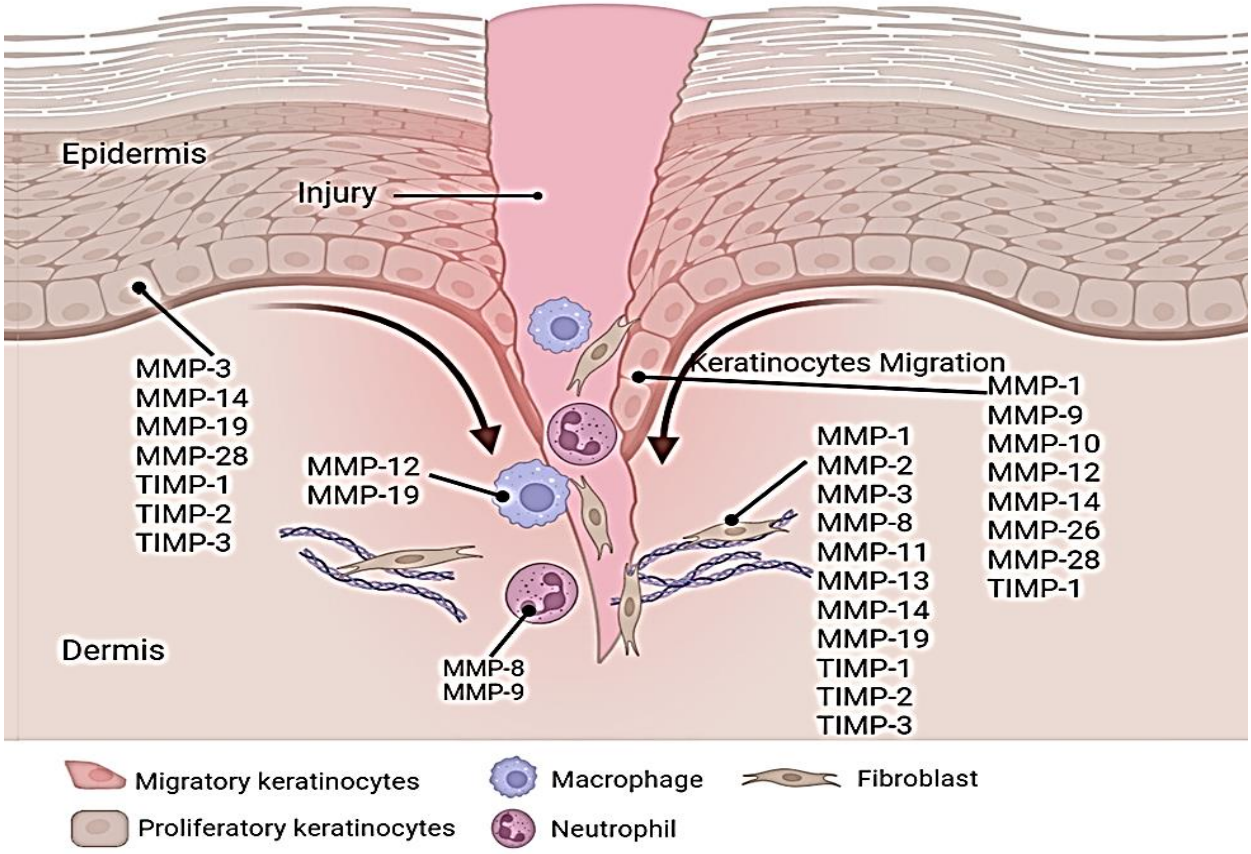
only 40% [3]. Wounds can arise from various causes, including trauma, infection, surgery, external factors (such as high pressure, heat, etc.), or pathological conditions (such as diabetes).

During wound healing, virtually all cell types surrounding the wound site express different MMPs, contributing to wound healing. MMPs participate in several critical aspects of wound healing, including re–epithelialization, neo–angiogenesis, inflammation, scar formation, and tissue remodelling. However, their overactivation often hinders wound healing [4]. Various MMPs have been detected in both acute and chronic wound exudates, with chronic wounds typically exhibiting higher levels [5].

Targeting MMPs has potential as a therapy to promote wound healing. For example, (R)–ND–336 selectively inhibits MMP9 and promotes the healing of diabetic wounds in mice [6], suggesting a potential new treatment avenue for diabetic foot ulcers (DFUs). Therefore, there is an urgent need for in–depth research on the regulatory roles of MMPs in wound healing. These studies can provide new insights into the understanding and management of wound repair and lay the foundation for developing advanced treatments as well.

2. Mechanisms of Skin Healing

Wound healing is one of the skin's key functions. This complex process requires the coordinated response of various resident and recruited cells, such as keratinocytes, fibroblasts, dermal adipocytes, and endothelial and inflammatory cells [7]. These cells work in coordination to repair damaged tissue, regenerate lost structure, and restore the integrity of the epithelial layer, with MMPs playing a crucial role (Fig.1). MMPs, particularly those secreted by cells, act on both the cells that produce them and nearby cells. They promote keratinocyte migration from the basal layer to the injury site by breaking down collagen and laminin [8], which enables keratinocytes to form a covering over the developing granulation tissue and subsequently restore skin integrity, a process known as re–epithelialization [9]. MMPs cleave chemokines to facilitate immune cell recruitment and migration and modulate their activity [10,11]. Furthermore, MMPs promote fibroblast migration into the injury site, where they fill defects and generate new ECM [12]. MMPs further stimulate the formation of an action network in fibroblasts, contributing to their differentiation into myofibroblasts and enhancing wound contraction [13].



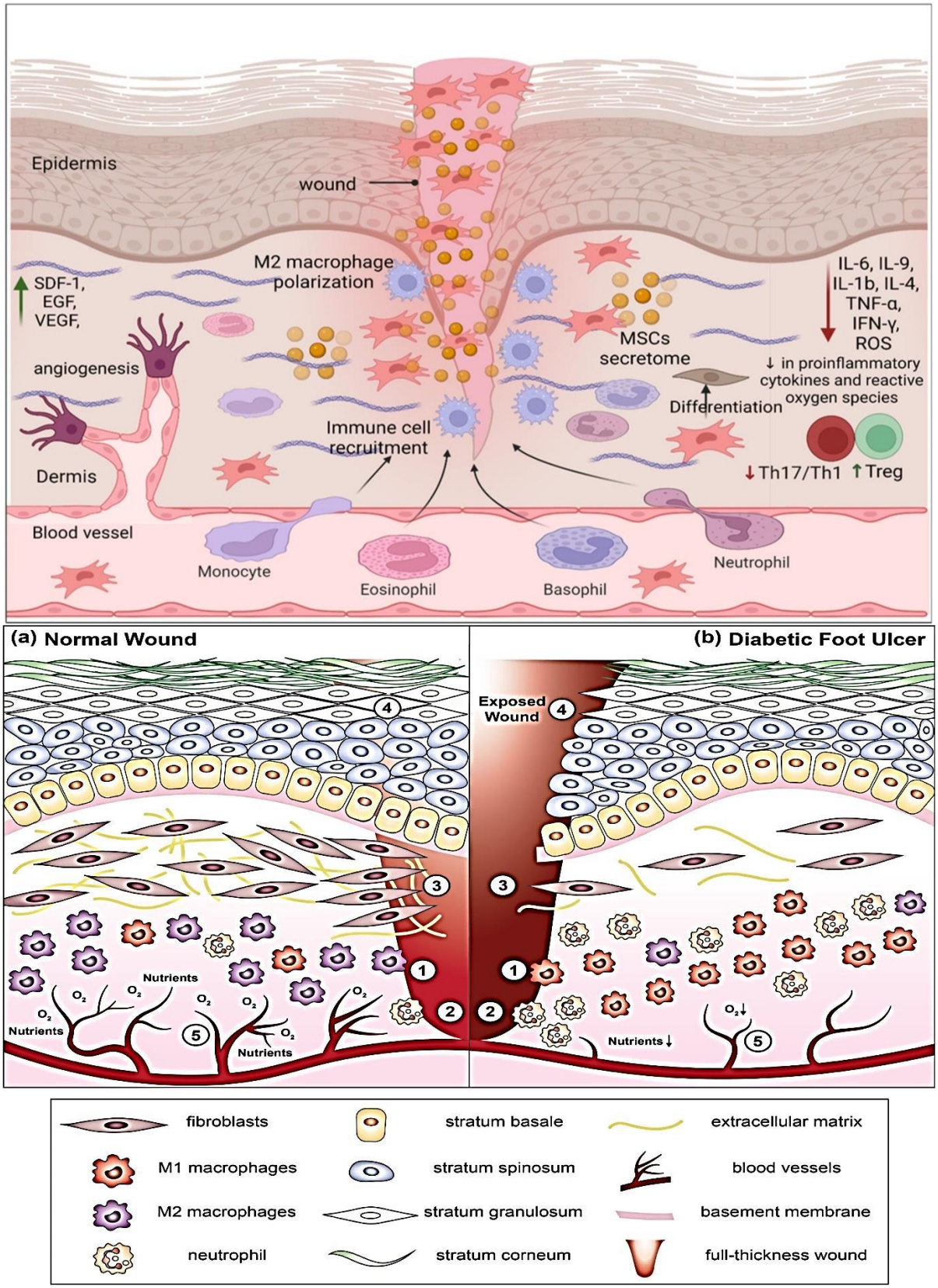
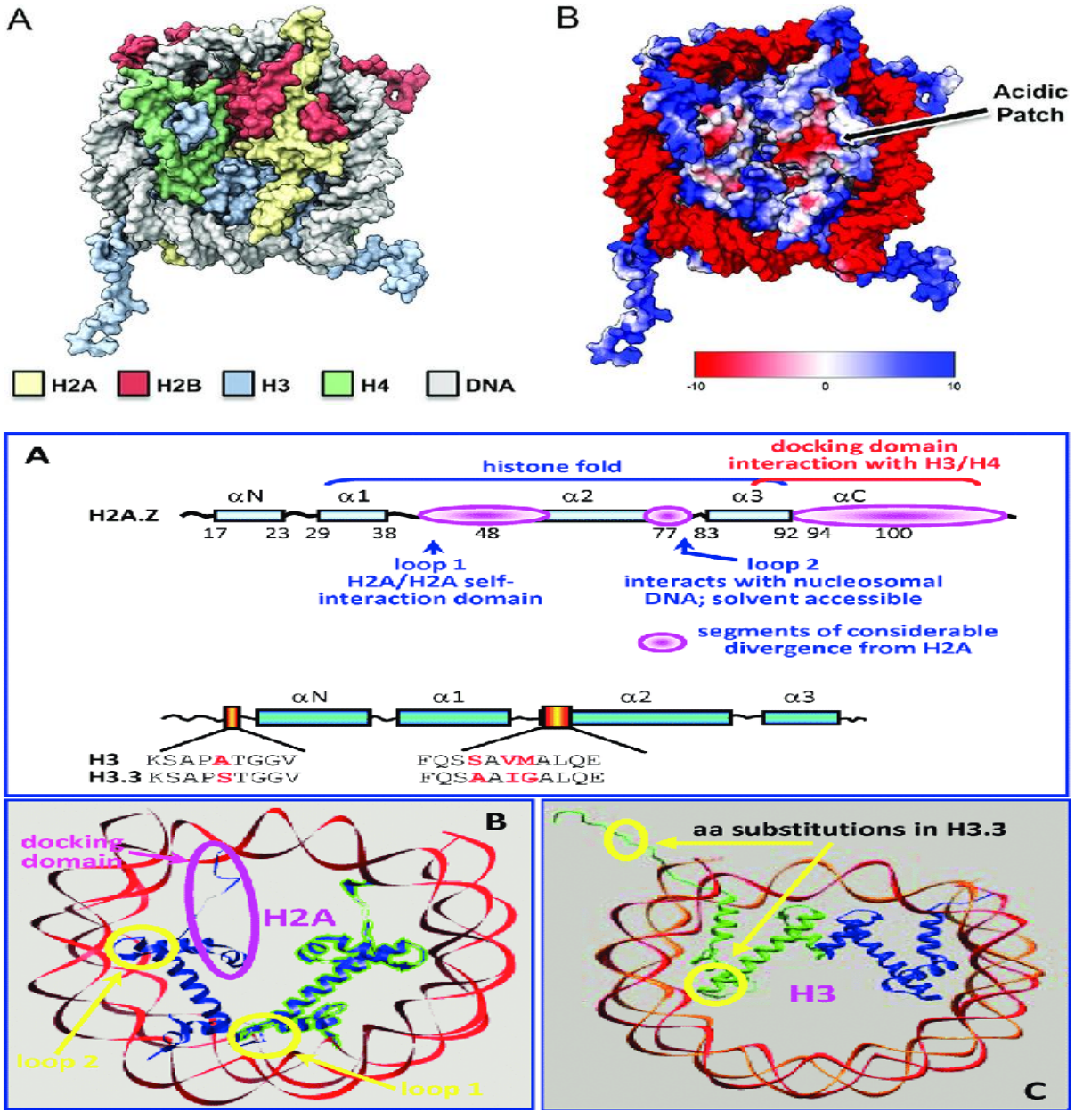
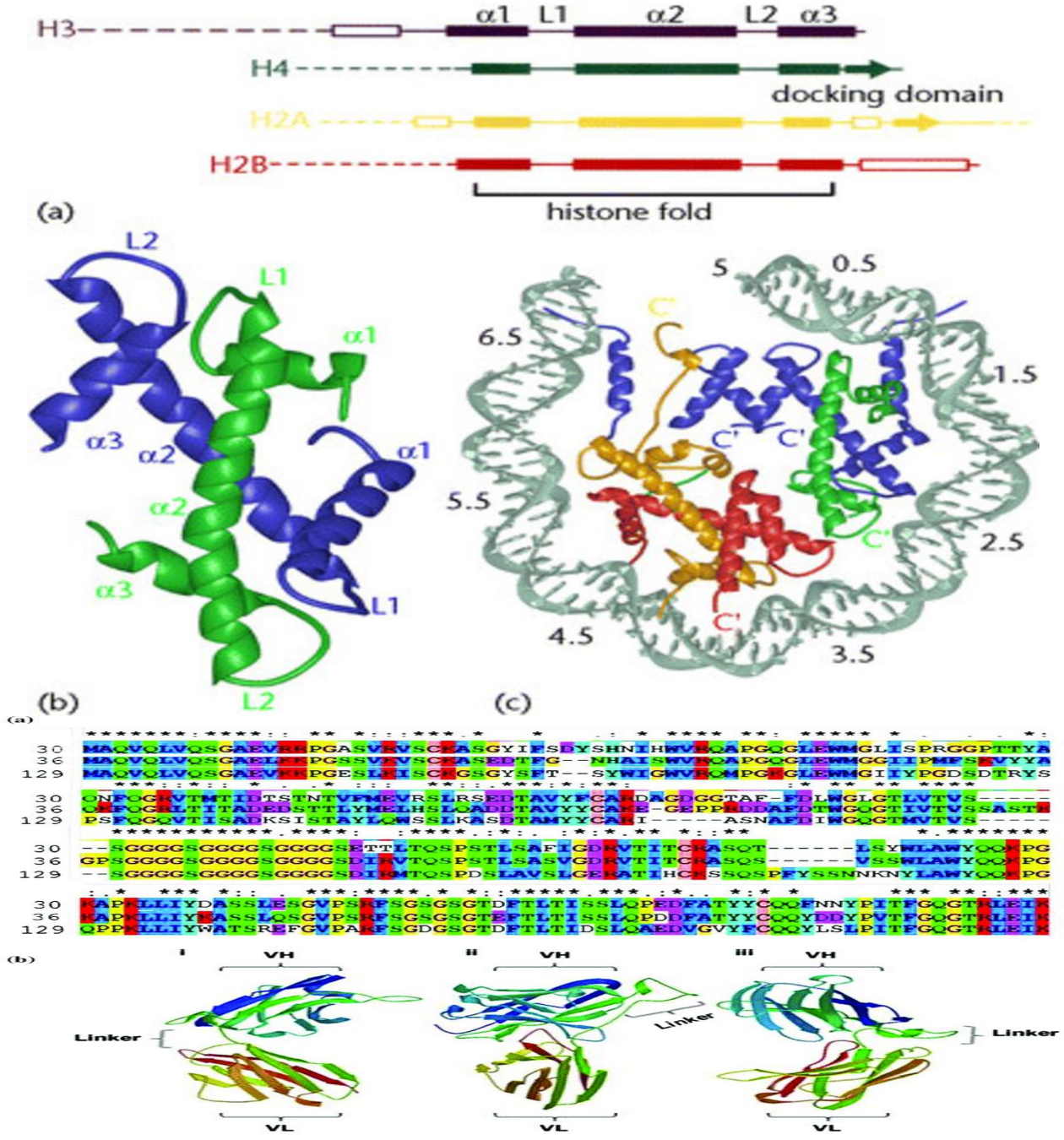


Figure 1. Expression patterns of MMPs and tissue inhibitors of metalloproteinases (TIMPs) in skin wounds. MMPs and TIPMs are mainly detected in migrating and basal keratinocytes, fibroblasts, neutrophils, macrophages, etc., at and/or around the injury site, regulating wound healing. Created with BioRender.

3. Overview of MMPs

MMPs were first identified as zinc–dependent endopeptidases in tadpoles. Data from the complete Human Genome Project reveal over 23 different types of MMPs in humans. MMPs are multidomain, zinc (Zn2+)–containing metalloproteinases. Based on substrate specificity and structural domains, they are typically classified into collagenases, gelatinases, stromelysins, matrilysins, membrane–type (MT), and other MMPs [14]. The sequence homology among different MMPs varies significantly. For example, human MMP3 and human MMP10 exhibit approximately 78% homology, while human MMP16 and human MMP24 share approximately 66% homology. In contrast, human MMP21 and human MMP23 display the lowest homology with other human MMPs (Fig. 2). Similarly, mouse MMP3 and mouse MMP10 display the highest homology at approximately 72%, followed by mouse MMP16 and mouse MMP24 at approximately 67%, while mouse MMP21 and mouse MMP23 have the lowest homology with another mouse MMPs (Fig. 2 and S1). Despite these differences, all MMPs contain a Zn2+ binding site (HEXXHXXGXXH) within their catalytic domain. Additionally, all MMPs, except MMP23, have a conserved cysteine switch sequence (PRCGXPD) (Fig. S1).





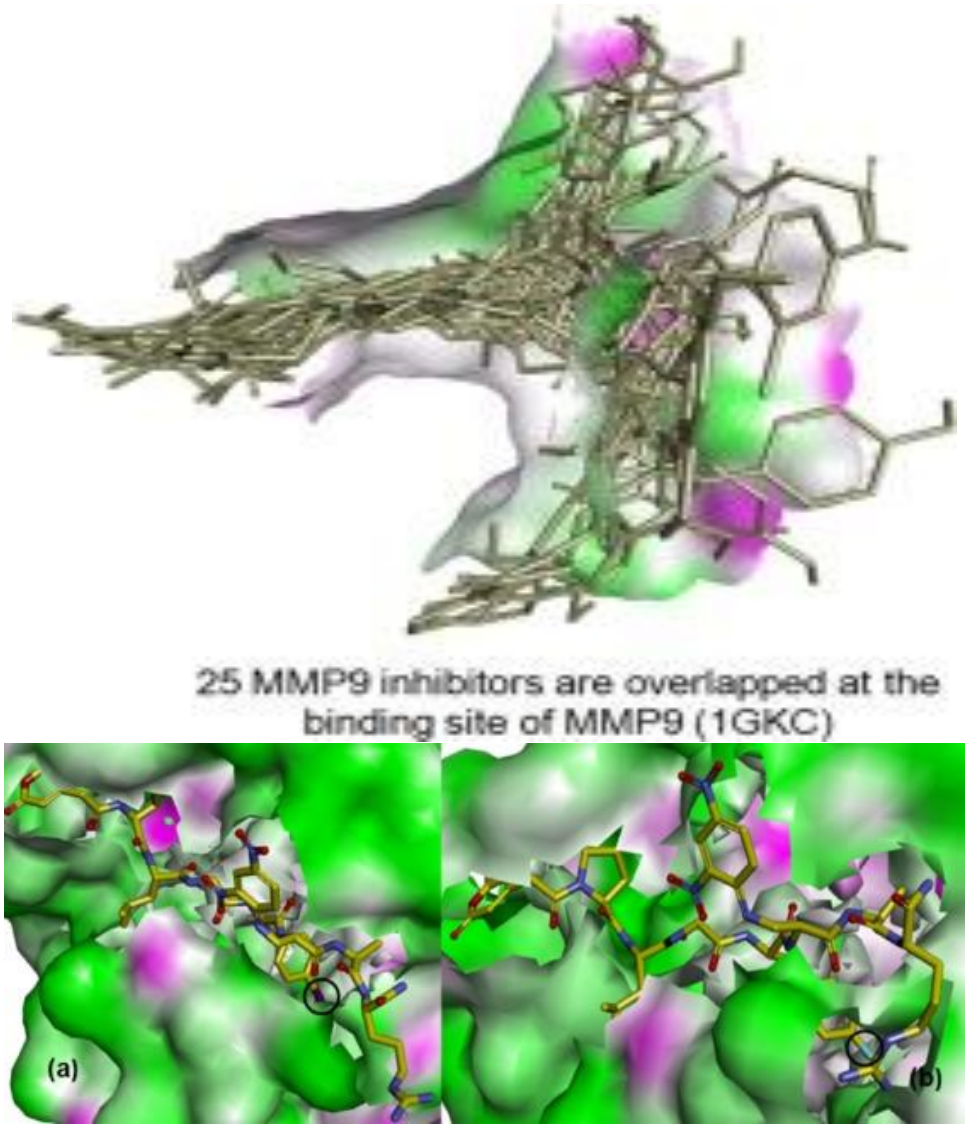
(D)

Figure 2. Sequence comparison and phylogenetic tree of the MMP family. Alignment was conducted using Clustal Omega multiple sequence alignmen. (A) Heatmap of the percentage of amino acid sequence homology among human MMPs. MMP1: sp|P03956.3; MMP2: sp|P08253.2; MMP3: sp|P08254.2; MMP7: sp|P09237.1; MMP8: sp|P22894.1: MMP9: sp|P14780.3; MMP10: sp|P09238.1; MMP11: sp|P24347.3; MMP12: sp|P39900.1; MMP13: sp|P45452.1; MMP14: sp|P50281.3; MMP15: sp|P51511.1; MMP16: sp|P51512.2; MMP17: sp|Q9ULZ9.4; MMP19: sp|Q99542.1; MMP20: sp|O60882.3: MMP21: sp|Q8N119.2; MMP23: sp|O75900.2; MMP24: sp|Q9Y5R2.1; MMP25: sp|Q9NPA2.1; MMP26: sp|Q9NRE1.2; MMP27: sp|Q9H306.2; MMP28: sp|Q9H239.2. (B) Phylogenetic tree of the human MMP family. The branch length is displayed in the branch diagram. Its actual length is indicated by the number beside each MMP. (C) Heatmap of the percentage of sequence homolog among mouse MMPs. MMP1a: sp|Q9EPL5.1; MMP1b: sp|Q9EPL6.1;MMP2: sp|P33434.1; MMP3: sp|P28862.2;MMP7: sp|Q10738.1; MMP8: sp|O70138.2: MMP9: sp|P41245.2; MMP10: sp|O55123.1; MMP11: sp|Q02853.2; MMP12: sp|P34960.3; MMP13: sp|P33435.1; MMP14: sp|P53690.3; MMP15: sp|O54732.1; MMP16: sp|Q9WTR0.3; MMP17: sp|Q9R0S3.3; MMP19: sp|Q9JHI0.1; MMP20: sp|P57748.1: MMP21: sp|Q8K3F2.1; MMP23: sp|O88676.1; MMP24: sp|Q9R0S2.2; MMP25: sp|Q3U435.1; MMP27: NP_001297646.1; MMP28: AAI45050.1. (D) Phylogenetic tree of the mouse MMPs family. The branch length is displayed in the branch diagram. Its actual length is indicated by the number beside each MMP.

Despite their diversity, MMP family members share a common core structure. A typical MMP contains multiple conserved functional domains, including a signal peptide (SP), a pro–domain (~80 amino acids), a catalytic domain (~170 amino acids), a hinge region (~14 to 69 amino acids), and a hemopexin domain (HPX, ~210 amino acids) [15] (Fig. 3). The N–terminal signal peptide varies in length and typically guides MMPs to the endoplasmic reticulum (ER) [16]. The pro–domain contains a conserved cysteine switch sequence (PRCGXPD). This switch binds Zn2+ in the catalytic site, sequestering enzymatic activity and maintaining the enzyme in its zymogen form [17].

The catalytic domain possesses a highly conserved Zn2+ binding site (HEXXHXXGXXH) featuring a pocket for Zn2+ and a shallow cleft for substrate binding. Structurally, the domain comprises five β–sheets, three α–helices, and eight connecting loops (Fig.4) [18]. It accommodates two Zn2+ ions: one participates in forming the catalytic site, while the other coordinates with three Ca2+ to maintain the protein conformational stability [19]. The high structural similarity of the catalytic domain across MMPs results in significant overlap in substrate preferences. The catalytic domain of gelatinases is distinguished by the presence of three type II fibronectin repeats. These repeats, which are less conserved than other regions, facilitate interactions with gelatin and collagen [19,20].

The hinge region, also referred as the linker peptide, varies in length and is rich in proline. It connects the catalytic domain to the C–terminal HPX, providing flexibility between the two structures [16]. HPX displays a pseudo–four–fold symmetric β–propeller topology and participates in protein–protein and protein–substrate interactions [21], thus contributing to substrate recognition and determining the functional diversity of different MMPs.



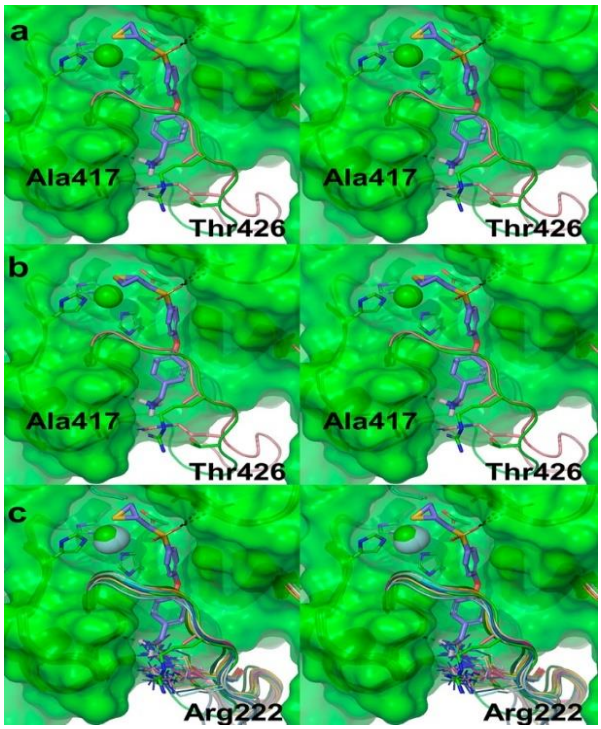
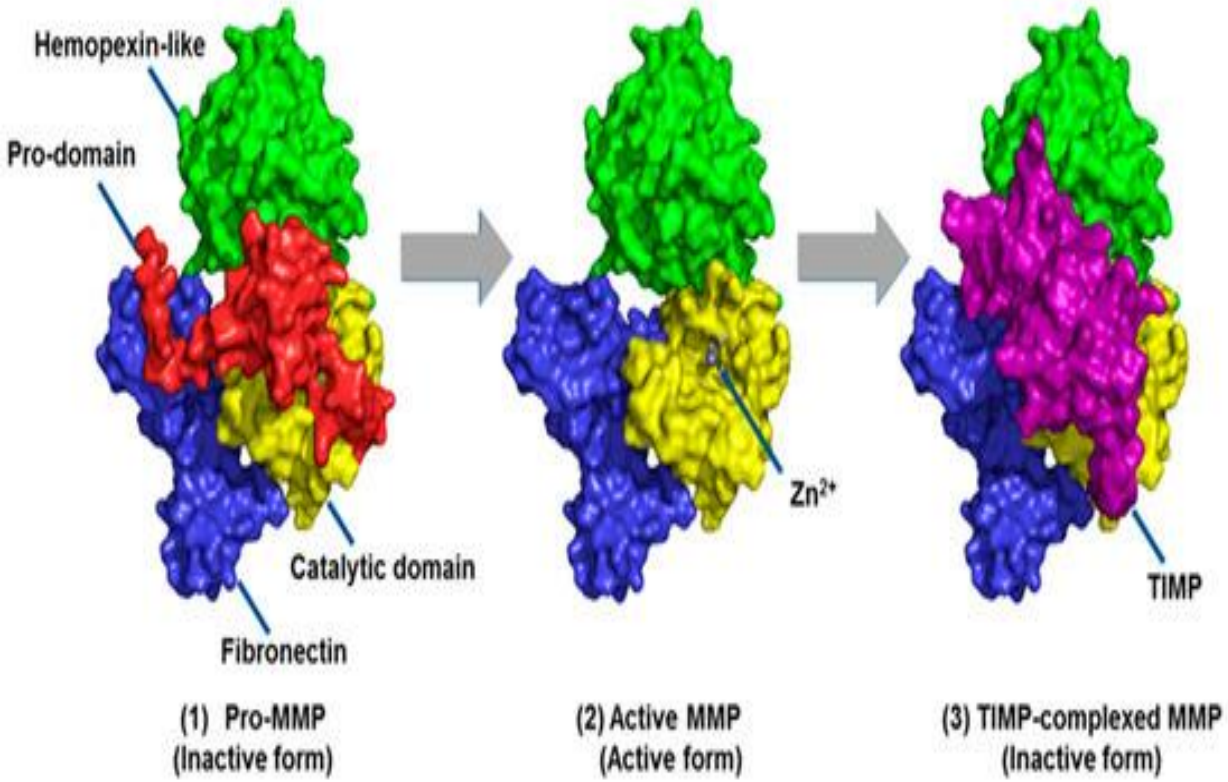


Figure 3. Schematic of MMPs. MMPs generally contain a signal peptide (SP), a pro–domain (PRO), a catalytic domain (CAT), a hinge region, and a hemopexin domain (HPX). Gelatinases contain three type II fibronectin repeats in the CAT, while the hinge region and HPX are absent in matrilysins. MMP–11, –21, and –28 have a Furin–like protease recognition sequence at the C–terminal end of the pro–domain. MMP14, MMP15, MMP16 and MMP24 possess a transmembrane domain and a cytoplasmic region, while MMP17 and MMP25 contain a glycosylphosphatidylinositol (GPI) anchor. MMP–23 does not contain the conserved cysteine switch (PRCGXPD) but contains a cysteine–rich domain (Cys) and an immunoglobulin–like (Ig) domain. Created with BioRender.



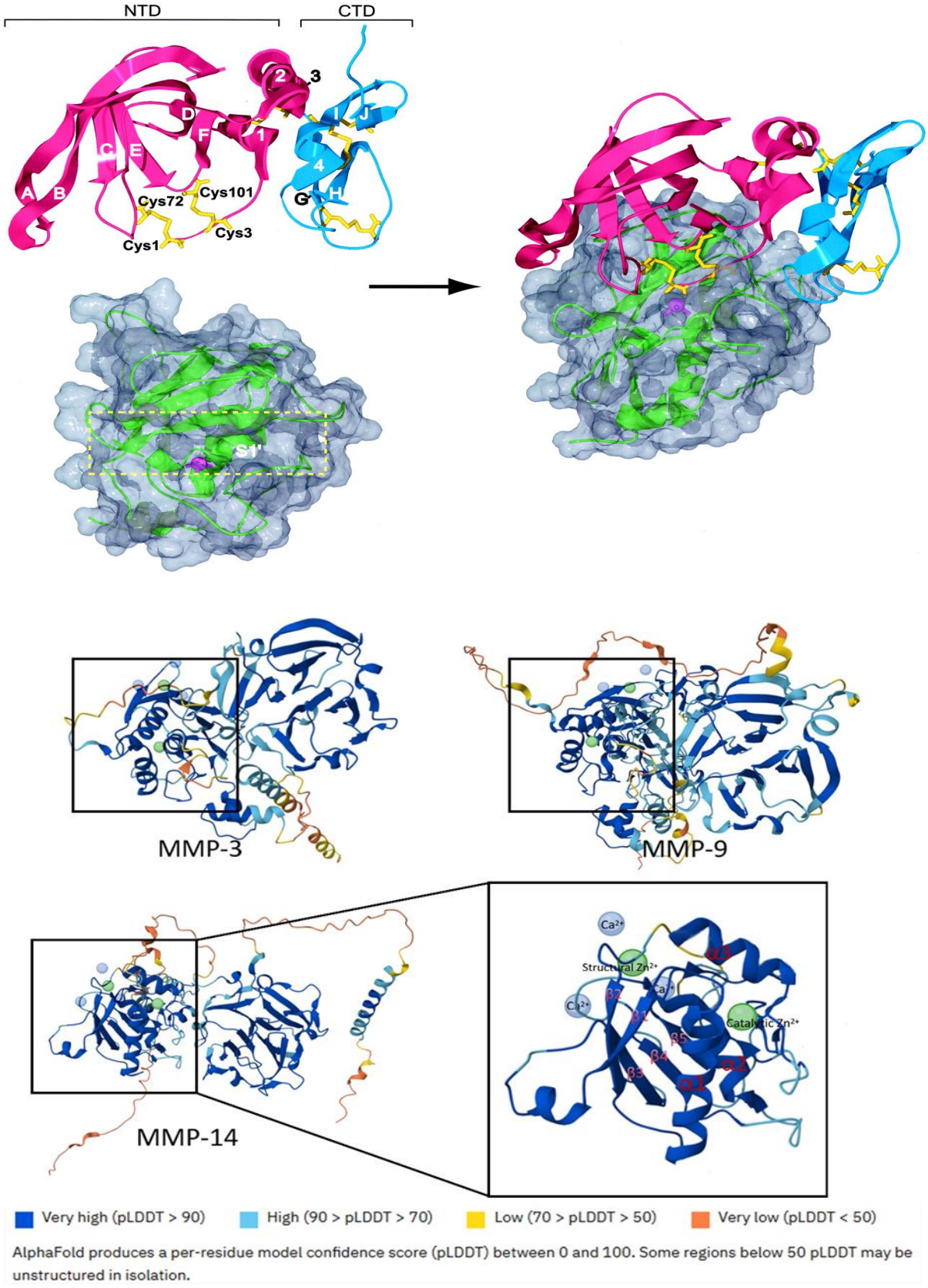


Figure 4. The structure of the catalytic domain (CAT). MMP–3, –9, and –14 exhibit a high similarity in CAT structure. They all comprise three α helices, five β folds, and 8 linking rings. They also contain two Zn2+: one participates in the formation of catalytic sites, while the other coordinates with three Ca2+ to maintain protein stability (Zn2+ in green, Ca2+ in gray). These images are adapted from AlphaFold.

4. MMPs in Normal Wound Healing

Wound healing is tightly regulated in healthy individuals. It typically occurs in four overlapping yet distinct phases: hemostasis (lasting minutes to hours after a skin injury, inflammation (1–3 days,) proliferation and repair (days to a month), and eventual wound remodelling (months to years) [9]. MMPs are vitally important for all four stages of normal wound repair. Under normal circumstances, MMP expression in the skin is minimal but increases significantly following injury, contributing directly or indirectly to the healing process [22]. During wound healing, ongoing proteolysis and protein production within the ECM are closely associated with MMP activity [23]. Additionally, MMPs release and/or activate cytokines and growth factors [24], which regulate cellular communication with surrounding cells and matrix to promote wound healing [25].

MMPs participate actively in each stage of wound healing (See Table 1 for further details).

(1) Hemostasis Phase: This phase is initiated immediately after injury, activated platelets secrete MMP1 and MMP2, which bind the αIIbβ3 integrin on the platelet surface, enhancing platelet aggregation and adhesion [26,27].

(2) Inflammatory Phase: MMPs cleave damaged epithelial cells and stimulate chemokines, such as CXCL and CCL, facilitating the recruitment of inflammatory cells into the injury site [28]. These cells, such as neutrophils and macrophages recruited by chemokines and platelets, also release MMPs to further promote healing. For example, neutrophils produce MMP8, which is believed to be the predominant collagenase in early wound healing, helping clear damaged collagens and wound debris [29].

(3) Proliferative Phase: MMPs promote angiogenesis by degrading the vascular basement membrane and remodelling the ECM [30]. They also aid in re–epithelialization in the damaged areas by promoting keratinocyte migration and proliferation [13]. MMPs also modify the wound matrix to enable tissue remodelling and cell migration and dissolve hemidesmosomes (the attachment points between keratinocytes and the ECM), thereby facilitating keratinocyte migration [31]. Additionally, MMP1 and MMP13 degrade the ECM to expose binding sites for fibroblasts and subsequently enhance fibroblast adhesion [32].

(4) Remodelling phase: MMPs are crucial in collagen remodelling by cross–linking existing collagen fibres to form new collagen fibres [33], and promoting the transition from type III collagen (COLIII, predominant in granulation tissue) to type I collagen (COLI, the primary structural component of the dermis) [34]. Additionally, MMPs promote differentiation of fibroblasts into myofibroblasts [35]. These myofibroblasts contribute to wound and scar tissue contraction through their high contractility [36].

Successful wound healing requires that all four stages occur in the correct sequence and within an appropriate time frame. Chronic wounds result from disruptions in the normal healing process, leading to an inability to heal appropriately or stagnation at a particular stage. These conditions trigger a prolonged pathological inflammatory response [37], leading to elevated levels of proteases, particularly MMPs. While MMPs are critical for normal wound healing, their sustained high expression compromises ECM proteins, receptors, and growth factors required for effective tissue repair [4,23]. Studies analysing fluid collected from wounds have shown that compared to acute wound samples, chronic wound fluid displays approximately 30–fold higher total MMP activity [38]. This excessive MMP activity severely disrupts normal wound healing in chronic wounds, including DFUs [5].

Table 1. Substrates, expression patterns, and roles in normal and chronic wound repair of MMPs.

Member	*Substrates*	*Role in wound healing*	*Role in DFUs*	*cell types*	*Ref.*
Collagenases					
MMP1 (collagenase–1)	aggrecan, COLI, COLII, COLIII, COLVII, COLX, gelatin, serpins, α2–macroglobulin, nidogen, tenascin, IGF–BPs, pro–TNF–α, IL–1β, α1–proteinase inhibitor	Promotes keratinocyte migration Participates in matrix remodeling by breaking down fibrin–rich matrices	upregulated than normal wound and promoted DFU healing	Keratinocytes and fibroblasts	[39] [40]
MMP8 (collagenase–2)	aggrecan, COLI, COLII, COLIII, α2–macroglobulin, pro–MMP–8	Regulates inflammatory cells Promotes keratinocyte migration predominant collagenase in healing wounds	upregulated than normal wound and promoted DFU healing	Neutrophils, keratinocytes and fibroblasts	[41] [42] [43]
MMP13 (collagenase–3)	aggrecan, COLI, COLII, COLIII, COLIV, COLIX, COLX, COLXIV, fibrillin, fibronectin, gelatin, tenascin, casein, laminin, proMMP2, proMMP9, and proMMP13	Has gelatinase activity to participate in matrix remodeling Promotes angiogenesis Affects wound contraction and subsequently promotes re–epithelialization	upregulated than normal wound	Fibroblasts	[44] [45] [13]
Gelatinases					
MMP2 (gelatinase A)	Gelatin, COLI, COLIII, COLIV, COLV, COLVII, COLX, COLXI, aggrecan, laminin, vitronectin, fibronectin, tenascin, elastin,	Promotes and inhibits angiogenesis	Upregulated than normal wound but inhibited DFU	Fibroblasts	[46,47]

	nidogen, IL–1β, proMMP9, proMMP13, pro–TGFβ, CCL7	Promotes keratinocyte migration	healing		[48]
MMP9 (gelatinase B)	Gelatin, COLIV, COLV, COLXI, COLXIV, laminin, aggrecan, fibrillin, elastin, plasminogen, IL–1β, pro–TNFα, CXCL8	Has both promoting and inhibiting effects of angiogenesis Overexpression inhibits angiogenesis Promote neutrophil infiltration Promotes cell migration and re–epithelialization Overexpression inhibits wound repair	Upregulated than normal wound but inhibited DFU healing	Keratinocytes, fibroblasts, neutrophils and macrophages	[47] [49] [50] [51] [6,42]
Stromelysins					
MMP3 (stromelysin −1)	Aggrecan, COLIII, COLIV, COLV, COLIX, COLX, COLXI, gelatin, fibronectin, fibrillin, elastin, E–cadherin, laminin, nidogen, vitronectin, α1–proteinase inhibitor, IL–1β, casein, proMMP1, proMMP18, proMMP19, proMMP13, and pro–TNFα	Detected in basal keratinocytes at the margin of the injury site Modulates wound contraction Enhances angiogenesis	Similar to normal wounds	Basal keratinocytes and fibroblasts	[52] [53] [54]
MMP10 (stromelysin–2)	COLIII, COLIV, COLV, aggrecan, laminin, elastin, gelatin, nidogen, fibronectin	Detected in migrating keratinocytes near the wound leading edge Promotes keratinocyte migration	Lower than normal wounds	Migrating keratinocytes	[52] [55]
MMP11 (stromelysin–3)	COLIV, α1–proteinase inhibitor, IGF–BPs, casein, laminin	Participates in organizational remodeling Involved in vascular intima formation	unclear	Fibroblasts	[56] [57]
Matrilysins					
MMP7	COLIV, COLX, α1–proteinase inhibitor, gelatin, laminin, tenascin, fibronectin, elastin, nidogen, E–cadherin, casein, pro–TNFα, plasminogen, syndecan–1	Essential for re–epithelialization of mucosal wounds	Unclear	Ductal cells in hair follicles and glands	[58]
MMP–26 (endometase)	COLIV, insulin–like growth factor–binding protein 1, gelatin, α1 antitrypsin, α2 macroglobulin, fibronectin, fibrinogen, and vitronectin	Promotes cell migration Promotes angiogenesis Enhances re–epithelialization by decomposing fibronectin	Unclear		[59] [60] [61]
Membrane–type MMPs					
MMP14 (MT1–MMP)	Gelatin, COLI, COLII, COLIII, fibronectin, laminin, vitronectin, aggrecan, tenascin, nidogen, perlecan, fibrillin, fibrin, α1–proteinase inhibitor, α2–macroglobulin, syndecan–1, CD44, αvβ3 integrin, pro–TNFα, CXCL8, CCL7, proMMP2 and proMMP13	Stimulates cell migration Promotes angiogenesis Regulates inflammation	Lower than normal wounds	Basal keratinocytes, fibroblasts and endotheliocyte	[62] [63] [64]
MMP15 (MT2–MMP)	COLI, perlecan, laminin, fibronectin, aggrecan, tenascin, nidogen, proMMP2, and proMMP13	Unclear	Unclear		
MMP16 (MT3–MMP)	COLIII, laminin, casein, fibronectin, and proMMP2	Unclear	Unclear		
MMP17 (MT4–MMP)	Fibrin, fibrinogen, gelatin, pro–TNFα	Unclear	Unclear		
MMP24 (MT5–MMP)	Gelatin, pro–MMP–2	Unclear	Unclear		
MMP25 (MT6–MMP)	Collagen IV, gelatin, fibrin, fibronectin, proteoglycan, α1–proteinase inhibitor	Unclear	Unclear		
Other MMPs					
MMP12 (metalloelastase)	COLIV, plasminogen, gelatin, fibrillin, fibronectin, laminin; elastin, and α1–proteinase inhibitor	Involved in cytoskeletal rearrangement and re–epithelialization of migratory keratinocytes	Unclear	Macrophages, keratinocytes	[65]

MMP–19 (RASI–1)	Aggrecan, COLI, COLIV, laminin, tenascin, fibronectin, nidogen, casein, and gelatin	Promotes keratinocyte migration Promotes macrophages migration	Similar to normal wounds	Keratinocytes, fibroblasts, macrophages and endothelial cells	[66] [67]
MMP20 (enamelysin)	COMP, amelogenin, and aggrecan	Unclear	Unclear	Tooth	
MMP21	α1–proteinase inhibitor	Unclear	Unclear		
MMP22	Gelatin	Unclear	Unclear	Heart	
MMP23 (cysteine array –MMP)	Gelatin	Affects wound healing by interfering with collagen deposition	Unclear		[68]
MMP27	Casein, gelatin		Unclear		
MMP28 (epilysin)	Casein	Reorganizes the newly formed basement membrane Promotes keratinocyte migration	Unclear	Keratinocytes	[69] [70]

CCL–7, monocyte chemoattractant protein–3; COL, collagen; COMP, cartilage oligomeric matrix protein; CXCL8, interleukin–8; TNF–α, tumor necrosis factor–α; IL, interleukin; RASI–1, rheumatoid arthritis synovium inflamed–1; and IGF–BP, insulin–like growth factor–binding protein.

5. Mechanisms of MMPs in Wound Healing

5.1. Collagenases

In humans, collagenases are divided into three main types: collagenase–1/MMP1, collagenase–2 /MMP8, and collagenase–3/MMP13. MMP1 is primarily produced by keratinocytes and fibroblasts [71], whereas MMP8 is mainly synthesized by neutrophils [43]. MMP–13, on the other hand, is abundantly expressed in fibroblasts [72]. These enzymes are unique in their ability to degrade the triple–helical structure in fibrillar collagen, making them essential proteases for cleaving type I, II, and III collagen [73]. One of their defining characteristics is to cleave fibrillar collagen at specific sites within the N–terminal region [15]. Despite their shared collagen–degrading capabilities, MMP1, MMP8, and MMP13 serve distinct regulatory and functional roles in wound healing. Specifically, MMP1 contributes significantly to re–epithelialization, MMP8 positively regulates inflammation, and MMP13 facilitates remodelling the collagen matrix [29,39,74].

MMP1 plays a pivotal role in the early stages of wound healing. Following tissue injury, basal keratinocytes begin expressing MMP–1 when they interact with native COLI through α2β1 integrin receptors to migrate from the basal layer to the wound site [8]. When keratinocytes encounter laminin–1 during basement membrane remodelling, MMP1 expression decreases. Migrating keratinocytes essentially cease producing MMP1 once re–epithelialization is complete [75].

In normal wounds, MMP8 is the most prevalent MMP. It is primarily produced by neutrophils [61]. MMP8 stimulates the release of proinflammatory signal molecules, recruiting inflammatory cells to the wound site [41]. Meanwhile, it also exerts anti–inflammatory effects by reducing neutrophil numbers through apoptosis [29]. This dual action helps balance the inflammatory reaction and remove cells from the wound site. Mmp8 deficient mice display persistent inflammation, delayed neutrophil infiltration, and impaired re–epithelialization, leading to prolonged wound healing [10]. Therefore, maintaining balanced MMP8 levels is crucial for effective wound healing.

MMP13 cleaves COLI and COLIII, with the resulting cleavage products participating in matrix remodelling [44]. It also possesses stronger gelatinase activity than both MMP1 and MMP8 [72]. However, the basal level of MMP13 in the skin is typically low, and Mmp13 knockout mice do not show significant impairments in cutaneous wound healing [76]. Therefore, MMP13 is generally not considered crucial for normal wound healing.

5.2. Gelatinases

Gelatinases are classified into two types: gelatinase A (MMP2) and gelatinase B (MMP9). MMP9 is secreted by various cells, such as macrophages, neutrophils, fibroblasts, and keratinocytes, while MMP2 is predominantly expressed by fibroblasts in the dermis. Gelatinases degrade ECM components and thus play a key role in wound healing [77]. They are also a crucial regulator of angiogenesis, contributing to blood vessel formation by cleaving type IV collagen [78]. This cleavage exposes hidden αvβ3 integrin–binding sites, which promotes endothelial cell migration and enhances angiogenesis [78]. Furthermore, gelatinases activate TNF–α and VEGF, which are active pro–angiogenic factors, further facilitating angiogenesis [79]. However, gelatinases have a double–edged sword role in angiogenesis. When they cleave type IV collagen, they also release hidden bioactive fragments [80], such as arresten and canstatin, which bind to integrins and effectively inhibit endothelial cell migration and proliferation, suppressing neovascularization [81]. Additionally, gelatinase can cleave plasminogen to generate angiostatin [82], and MMP9 processes COLXVIII to produce endostatin [79], both of which reduce endothelial cell proliferation. Consequently, excessive gelatinase activity hinders angiogenesis.

Gelatinases also cleave specific chemokines with CC and CXC motifs, which can either increase or decrease leukocyte infiltration and migration [84]. For example, MMP9 cleaves CXCL8 (IL–8), significantly amplifying its activity and enhancing neutrophil attraction by 10 to 30 times [85]. CXCL8, in turn, triggers the rapid secretion of MMP9 from neutrophil granules, establishing a positive feedback loop [86]. On the other hand, MMP2 processes CCL7, generating fragments that not only lose chemoattractant activity but also

act as antagonists to its receptor [87] (Fig.5). Consequently, excessive gelatinase activity can lead to prolonged inflammation, ultimately hindering wound healing.

5.3. Stromelysins

The stromelysins subfamily includes stromelysin–1 (MMP3), stromelysin–2 (MMP10), and stromelysin–3 (MMP11) [88]. MMP3 and MMP10 are closely related. Similar to gelatinase, MMP3 and MMP10 cleave collagen and non–collagen connective tissue macromolecules, contributing to ECM remodelling. Although both MMP3 and MMP10 share similar substrate specificities, MMP3 is generally a more efficient proteinase [89]. Due to their extensive range of substrates, these two stromelysins play significant roles in ECM degradation, regulating collagenolytic activity and facilitating wound remodelling. Unlike other MMPs, the mature form of MMP11 does not degrade major ECM components, but its active catalytic domain enables it to cleave alpha–1–antitrypsin, laminin, casein, and COLIV [57].

During wound healing, MMP3 and MMP10 are secreted by different groups of keratinocytes, while MMP11 is primarily produced by fibroblasts [90]. MMP10 is exclusively produced by migrating keratinocytes near the anterior margin of wounds [6]. MMP3 is detected in basal keratinocytes near the wound margin, specifically within the proliferative epidermis, where it participates in remodelling the basement membrane [91]. However, MMP3 is absent in the leading edge of migrating keratinocytes [52]. Additionally, MMP3 is prominently expressed in dermal fibroblasts [53] and is crucial for initiating wound contraction [92]. In Mmp3 knockout mice, the deficiency of this organized actin network results in impaired wound contraction due to a lack of actin–rich myofibroblasts, the primary cells responsible for contraction [53,91]. As a result, Mmp3 deficiency impairs the ability of fibroblasts to contract wounds and consequently delays wound healing.

In normal, uninjured skin, MMP10 mRNA is barely detectable but shows two distinct peaks of expression post–injury, on days 1 and 5 [93]. This delayed expression of MMP10 suggests that its upregulation is driven by inflammation and cytokines rather than direct interactions between the dermal matrix and keratinocytes [94]. MMP10 also enhances keratinocyte migration by cleaving LN–5 [95]. However, transgenic mice overexpressing active MMP10 mutants exhibit disorganized migratory epithelium, partial loss of cell–to–cell contact among migrating keratinocytes, and degradation of newly formed matrices, including LN–5[55].

MMP11 plays a beneficial role in tissue remodelling. In Mmp11 knockout mice, neointimal formation following vascular injury is markedly increased, underscoring its regulatory role in preventing neointimal thickening [57]. Despite these findings, the potential roles and mechanisms of MMP11 in wound healing remain unclear.

5.4. Matrilysins

Matrilysins consist of only two MMPs: MMP7 and MMP26. Matrilysins have a significantly lower molecular weight than other MMPs and contain only a signal peptide, a pro–domain, and a catalytic domain, which are the core structure of the MMP family. MMP7 is involved in the degradation and processing of various ECM proteins, contributing to diverse biological processes [96]. It participates in the re–epithelialization of mucosal wounds [97], but its contribution to cutaneous wound healing remains unclear.

MMP26 expression is spatially regulated during normal wound healing. The protein is detected in LN–5–positive migratory keratinocytes, where it co–localizes with LN–5[61], a marker of keratinocyte migration. However, unlike MMP2 and MMP14, MMP26 cannot cleave LN–5 to expose the site for epithelial cell migration [60]. Additionally, MMP26 participates in neovascularization and angiogenesis through cleaving fibrinogen, a process that facilitates both fibrin formation and degradation [60].

5.5. Membrane–Type (MT) MMPs

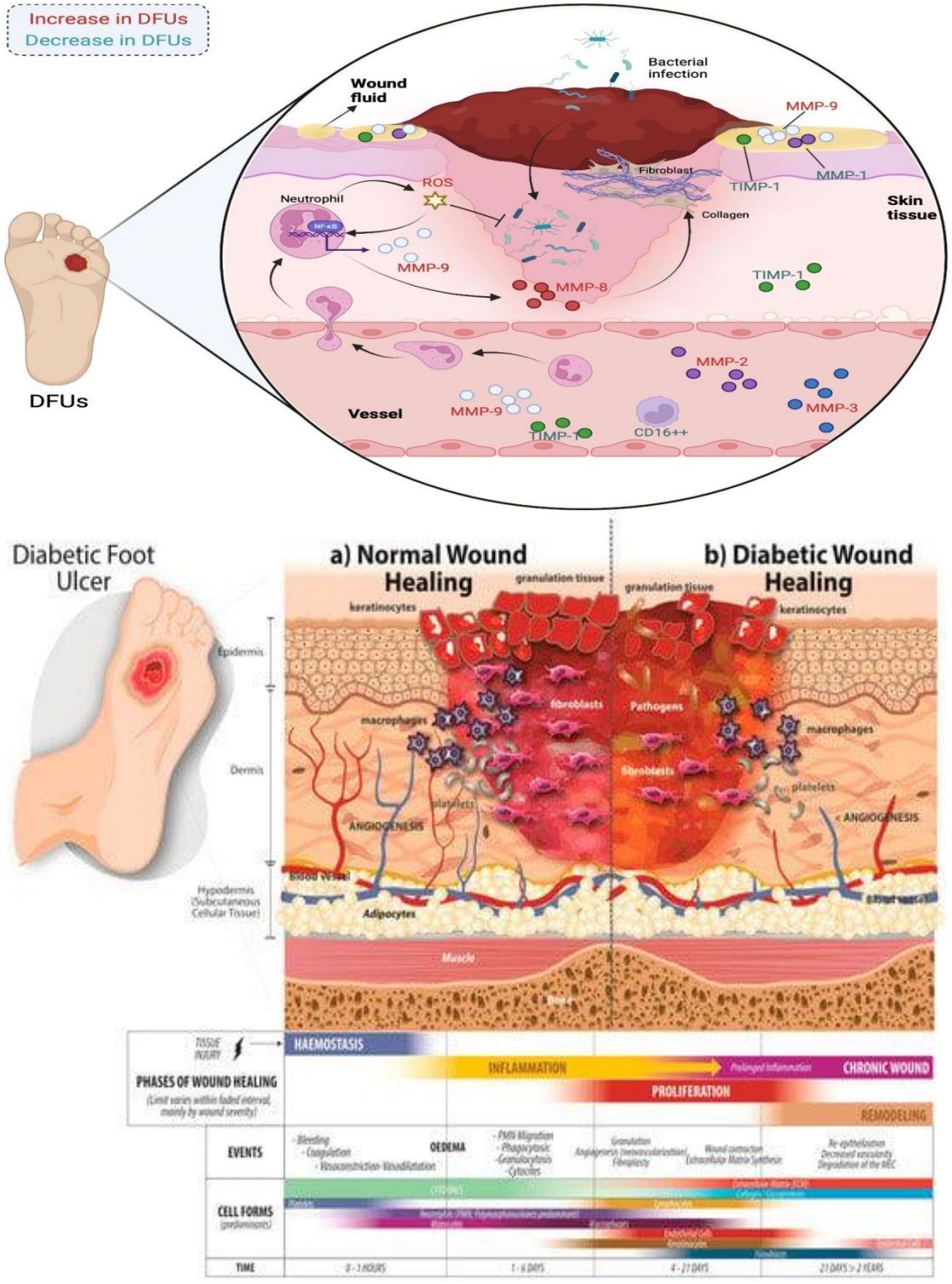
MT–MMPs comprise six members, MMP14, MMP15, MMP16, MMP17, MMP24, and MMP25. Unlike secretory MMPs, which are found in the extracellular milieu, MT–MMPs are anchored on cell membranes. Four of these (MMP14/MT1–MMP, MMP15/MT2–MMP, MMP16/MT3–MMP, and MMP24/MT4–MMP) are type–I transmembrane proteins, while MMP17/MT5–MMP and MMP25/MT6–MMP are associated with cell membranes via a glycosylphosphatidylinositol (GPI)–anchor. MMP14 is the most extensively studied MT–MMP. MMP14 promotes cell migration, as well as cancer metastasis and invasion [98]. Remarkably, of all Mmp knockout mice studied to date, Mmp14 knockout mice exhibit the most severe developmental and growth defects. Mmp14 constitutive global knockout mice typically die shortly after birth, and inducible knockout of Mmp14 in adult mice causes arthritis [99]. These observations highlight the critical role of MMP14 in both development and adult tissue homeostasis.

MMP14–mediated proMMP2 activation requires TIMP2, which binds to proMMP2 and subsequently interacts with one molecule of homodimerized MMP14 on the cell membrane [100,101]. Within the MMP14 homodimer, the molecule not bound to TIMP2 removes the pro–domain from proMMP2, generating active MMP2. This activation initiates a cascade that includes the activation of proMMP9. Specifically, active MMP2 cleaves the pro–domain of proMMP9, which is complexed with TIMP1 and ADAM10, activating MMP9 [102,103]. This dual activation of gelatinases (MMP2 and MMP9) amplifies proteolytic activity and contributes to ECM remodelling.

MMP14 accelerates cell migration by cleaving COLI, CD44, and LN–5. As a plasma membrane–anchored enzyme, MMP14 cleaves and remodels pericellular tissues enriched in COLI. Overexpression of MMP14 significantly enhances cellular invasion into COLI matrix, while fibroblasts deficient in MMP14 lose the ability to degrade fibrillar COLI or activate proMMP2 [104]. Furthermore, MMP14–mediated cleavage of LN–5, either directly or indirectly via activation of proMMP2 [105], releases an EGF–like repeat–containing fragment from LN–5, which stimulates keratinocyte migration and re–epithelialization [98]. MMP14 also interacts with CD44 (the standard form) on the cell surface, which links MMP14 to the actin cytoskeleton and directs it to the leading margin of migrating cells [106]. The polarization of MMP14 at the migration front process establishes a large proteolytic hub, facilitating cell migration.

Additionally, MMP14 plays a dual role in inflammation. It enhances inflammation by removing the first 5 residues of

CXCL8, thereby increasing its activity [107]. On the other hand, MMP14 can inhibit the proinflammatory response through two distinct mechanisms: activating the PI3/Akt3/GSK3 signaling pathway [108] or cleaving macrophage–derived CCL7 to generate a peptide that antagonizes the CCL7 receptor [109] (Fig.5). This dual function allows MMP14 to act as a brake on the proinflammatory response, helping shift inflammatory cells from a defensive state to the resolution phase.



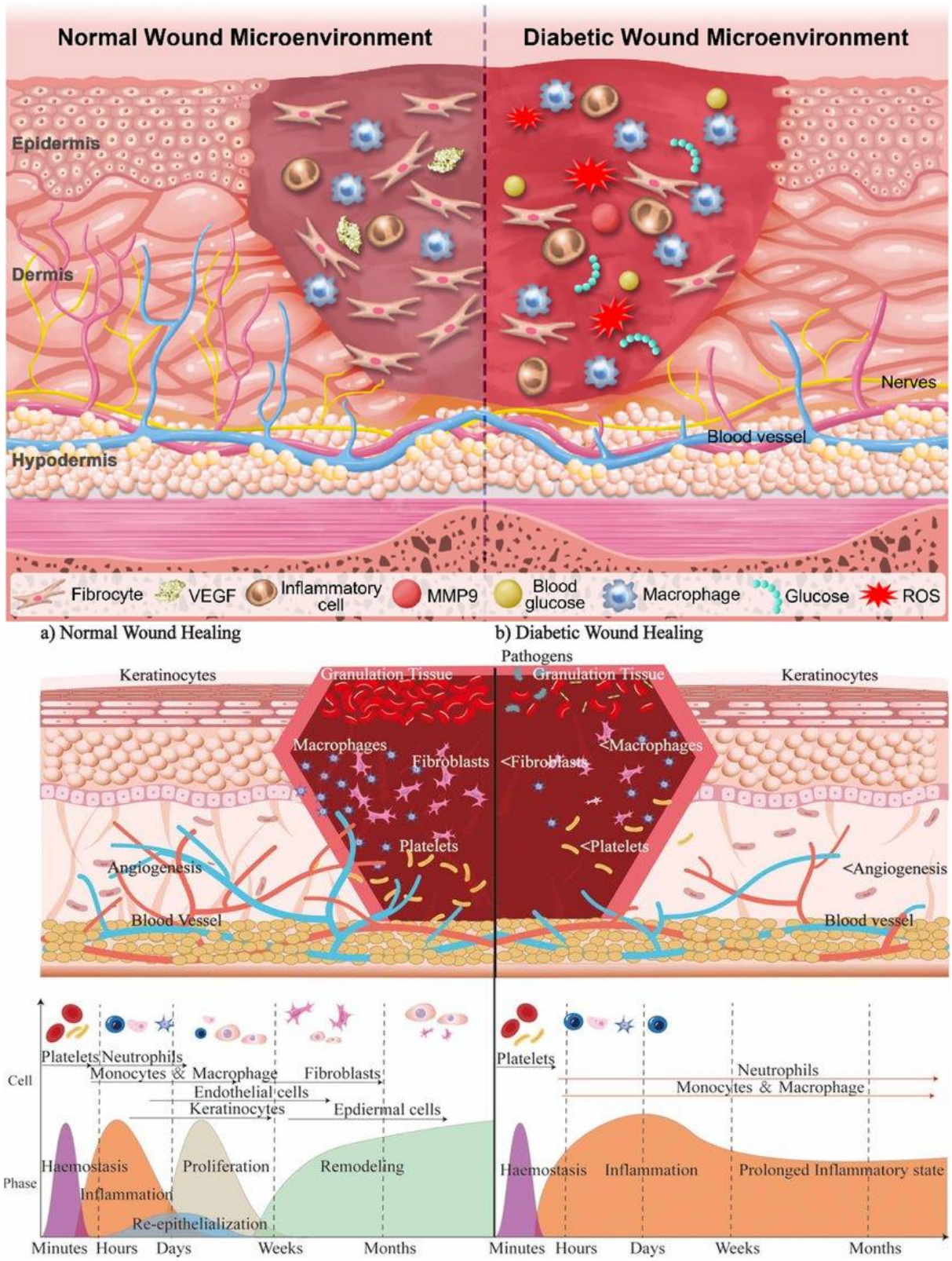


Figure 5. TIMPs mediate the cascade activation of gelatinases. TIMP2 and TIMP1 can sequentially activate gelatinases through MMP14 and ADAM10. Initially, TIMP2 interacts with pro–MMP2 and then binds it to one MMP14 within a MMP14 homodimer. This binding exposes the pro–domain of proMMP2 to the free MMP14 in the homodimer, which cleaves the pro–domain to generate active MMP2. The activated MMP2 then cleaves the pro–domain of pro–MMP9 that forms a complex with TIMP1 and ADAM–10 to produce active MMP9, resulting in dual gelatinase activity. Additionally, both MMP9 and MMP14 can cleave CXCL–8, enhancing its activity and subsequently inducing the rapid release of MMP9 from neutrophil granules, creating a positive feedback loop. Furthermore, MMP2 and MMP14 cleave CCL–7, inactivating it and producing cleaved fragments that act as antagonists to the CCL–7 receptor. Created with BioRender.

The roles of MT–MMPs besides MMP14 in wound healing remain largely unclear, underscoring the need for further research. MMP15/MT2–MMP is detected in the sebaceous gland and fibroblast–1 cells of the skin [110]. Global Mmp15 knockout mice are viable but exhibit defects in the ductal development of mammary glands [111]. According to Protein Atlas data, MMP16/MT3–MMP is substantially expressed in outer root sheath cells, fibroblast 1 and 2, endothelial cells, and mast cells in the skin. Similar to MMP14, MMP16 can activate pro–MMP2[112]. MMP17/MT4–MMP cleaves only limited ECM components and demonstrates weak hydrolytic activity against fibrinogen, fibrin and gelatin [113].

MMP24 has been shown to modulate cellular interactions between mast cells and nociceptive neurites. In the peripheral nervous system, MMP24 can activate the ERK pathway via inflammatory mediators, such as IL–1β and TNF–α, triggering pain [114]. Given the importance of effective pain management in wound healing [115], MMP24 may indirectly influence the wound healing process. MMP25/MT6–MMP, also referred to as leukolysin. Originally cloned from human peripheral blood leukocytes [116], MMP25 is primarily expressed in leukocytes, particularly neutrophils [117]. MMP25 degrades various ECM components and cytokines, its ability to degrade ECM proteins aids in the extravasation of neutrophils [118]. Neutrophils are recruited to wounds to remove microorganisms and tissue debris [119]. MMP–25 likely contributes to wound healing through these mechanisms.

5.6. Other MMPs

Other MMPs differ sufficiently in structure and function from other types and are therefore excluded from classical MMP categories. These include MMP12, MMP19 to 23, MMP27, and MMP28. MMP12, also known as metalloelastase, is particularly effective at cleaving elastin, making it the most active MMP for elastin degradation [120]. MMP12 is expressed by keratinocytes and is upregulated after skin injury, reaching its highest levels once re–epithelialization is complete [121]. Moreover, MMP12 is involved in cytoskeletal rearrangements in migrating keratinocytes, which aids in repairing adverse mechanical stress and promotes wound healing [65].

During wound repair, MMP19 (RASI–1) is detectable in macrophages, proliferating epithelial cells, fibroblasts, and capillary endothelial cells [10]. In macrophages, MMP19 cleaves COLI and gelatin, consequently promoting cell migration [11]. Additionally, MMP19 cleaves laminin–5 and IGF–binding protein–3, thereby releasing IGFs to promote cell migration, proliferation, and adhesion [122,123]. MMP20 (enamelysin) is primarily expressed in odontoblasts and the dentin matrix of teeth and plays a key role in tooth development and dentin–pulp regeneration [124]. While MMP–20 cleaves various ECM proteins, such as laminin–1, casein, gelatin, aggrecan, fibronectin, COL IV, COLV, and COLXVIII, it does not cleave COLI and COLII [125]. Although MMP21 is undetectable in adult skin, it has been identified in cultured keratinocytes, where its expression is increased by TGF–β [126].

MMP23A is a pseudogene containing a partial copy of the MMP23B gene. MMP23B, denoted as MMP23, is a unique type II membrane–anchored matrix metalloproteinase. Downregulation of MMP23 substantially enhances the formation of collagen fibres and promotes neovascularization, accelerating wound healing [68]. The known substrates for MMP27 include casein and gelatin, although it remains unclear whether MMP27 cleaves other ECM components. In adults, MMP27 is highly expressed in B cells [127], as well as in bones and kidneys, with low expression observed in the heart [128]. Considering that B cells, which express high levels of MMP27, are actively involved in wound healing [127,129], it is plausible that MMP–27 may contribute to wound healing. MMP28(epilysin) is produced by basal keratinocytes located distal to the wound margin\, where it may contribute to epithelial cell proliferation and the reorganization of newly formed basement membranes [69,70]. Additionally, MMP28 is found in migrating keratinocytes at the wound margin, where it degrades cell adhesion proteins between keratinocytes, facilitating the formation of new cells at the migration front [70].

5.7. TIMPs

TIMPs are secreted proteins that specifically inhibit metalloproteinases. TIMPs contain four members, TIMP1, 2, 3 and 4, which are tightly regulated in a temporal–spatial manner. In effectively healed wounds, TIMP1 is produced by the proliferating epithelial cells between days 3 and 5, TIMP2 is expressed in the transitional epithelium, and TIMP3 is detected in proliferating keratinocytes [130]. In contrast, TIMP4 is generally absent in normal wounds but may appear sporadically in the matrix of chronic ulcers [130]. Although all four TIMPs act as broad–spectrum inhibitors of MMPs, their inhibitory properties differ.

Compared to TIMP2 and TIMP3, TIMP1 is more effective against MMP3 and MMP7 [84]. It also preferentially inhibits MMP1 and can form a specific complex with proMMP9, contributing to the activation of this zymogen [131]. However, in chronic wounds, TIMP1 is undetectable in the epidermis and instead is expressed in basal keratocytes located distal to the wound site [132].

TIMP2 is ubiquitously expressed and maintains consistent expression levels even in various disease states [133]. In the wound environment, TIMP2 is essential for regulating the activity of gelatinases, as significant amounts of MMP2 are often found in proximity to TIMP2–positive regions [130], and TIMP2 mediates MMP2 activation. TIMP–2 binds tightly to proMMP2 and forms a complex with MMP14, making proMMP2 available for MMP14–mediated cleavage and activation [102].

TIMP3 has a broader range of substrates than other TIMPs, effectively inhibiting all ADAMTS, ADMs, and MMPs [134]. TIMP3 is expressed in both normal healing and chronic traumatic matrices, with its expression closely linked to the vascular system [130]. TIMP–3 regulates the wound–healing process through modulating local MMP activity and regulating the VEGF signaling pathway [135].

TIMP4 shares the most similarity with TIMP–2 and inhibits most MMPs [84]. Among TIMPs, TIMP4 exhibits the most restricted tissue expression [133], being primarily localized in vascular tissues of the heart. It is undetectable in acute wounds [136].

Appropriate and effective wound healing relies on maintaining a delicate balance between MMP and TIMP activity. For instance, elevated TIMP1 expression in epidermal tissues results in inactivation of MMPs, leading to fibrotic changes in wounds and the formation of hypertrophic scars [137]. Conversely, reduced levels of TIMP1, TIMP2, and TIMP3 in epidermal tissue are correlated to the development of chronic wounds [130]. Therefore, the TIMP/MMP ratio can serve as a more precise predictive indicator of wound healing outcome than the individual levels of MMPs or TIMPs.

5.8. MMPs and TIMPs in DFUs

DFUs are wounds that develop on the feet of patients with type 1 or 2 diabetes. Impaired healing in diabetic patients has been attributed to various factors, such as an elevated MMP levels, hyperglycemic environment, fibroblast dysfunction, blood hypercoagulability, increased advanced glycation end products (AGEs) and ROS, impaired angiogenesis and neovascularization, compromised host immunity, and peripheral neuropathy [138]. Importantly, one leading cause of poor healing in DFUs is the persistently high activity of certain MMPs, coupled with low levels of their inhibitors [139].

High collagenase activity is commonly observed in DFUs. MMP1 concentrations are reported to be 65–fold higher in DFU compared with acute lesions in non–diabetic patients. Additionally, MMP8 levels are increased 2–fold [140], while MMP13 is elevated approximately 40–fold in DFUs [141]. Selective inhibition of MMP8 markedly delays diabetic wound healing [142], suggesting a beneficial role for this enzyme.

MMP2 increases approximately 5–fold [143], while MMP9 levels rise 14–fold in DFUs [140]. Overactivation of these gelatinases prolongs inflammation in wounds, inhibits angiogenesis, and prevents reattachment of migrating keratinocytes, thus impeding wound healing [49]. Numerous studies have consistently shown that MMP–9 adversely impacts wound healing in DFUs. Diabetic wound healing may be accelerated by selective inhibition of MMP–9 [142].

Among the stromelysins, MMP11 expression in DFUs is unknown, while MMP3 expression in DFU is not significantly altered compared to healthy skin [136]. MMP10 is downregulated in DFUs [136], and since it promotes keratinocyte migration [136], its reduced expression may contribute to the impaired healing of these ulcers.

Among the two matrilysins, MMP7 is not detected in DFU wounds [144]. Conversely, MMP26 is expressed below the basal region but not in deep granulation tissue [61]. This pattern suggests the potential contribution of MMP26 to basement membrane remodelling and cell migration

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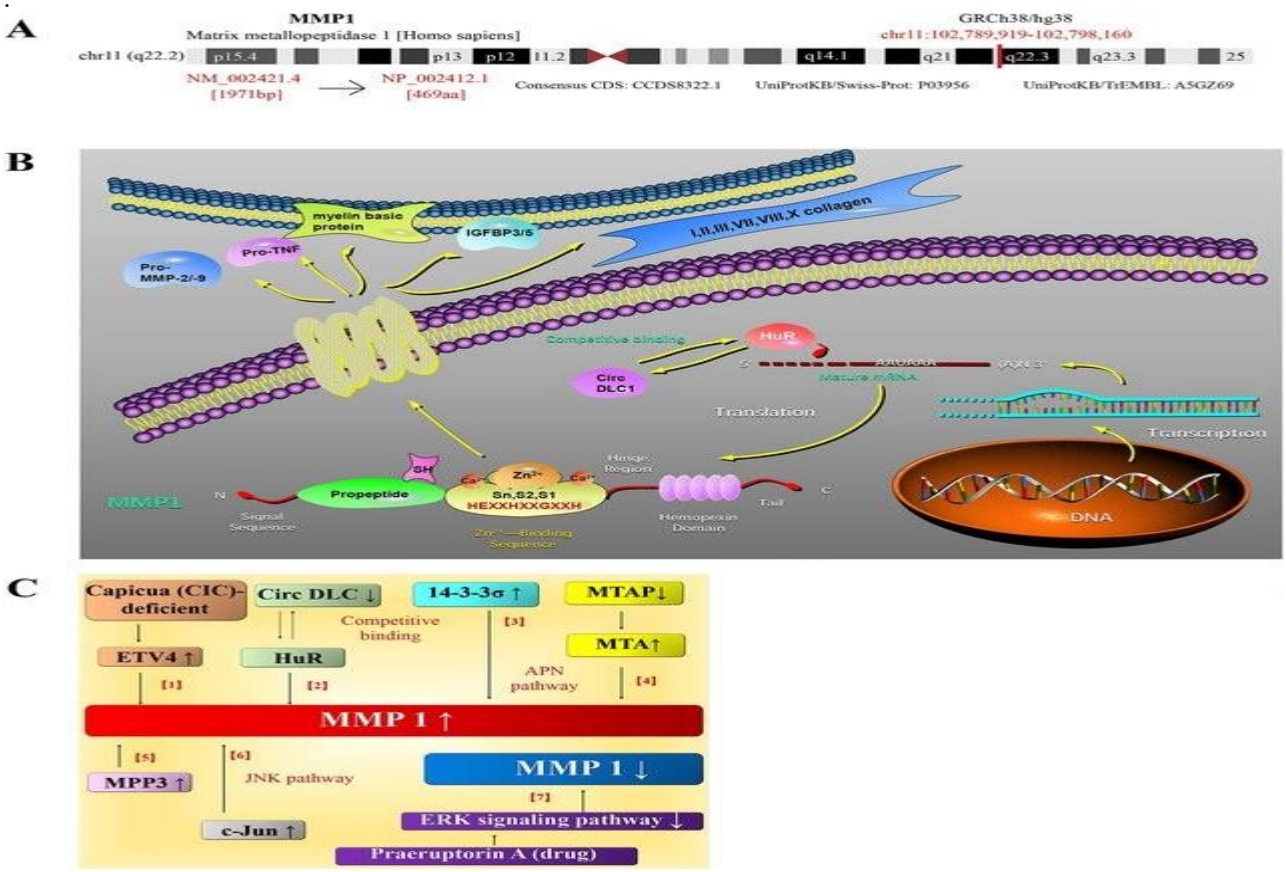

Figure 6. Alignments of human and mouse MMP1. (A) Heatmap of the percentage of MMP1 homologous protein sequences. (B) Phylogenetic tree of the human MMP family. The branch length is displayed in the branch diagram. Its actual length is indicated by the number beside each MMP. (C) Comparison of MMP–1. Alignment was performed using the Clustal Omega multi–sequence alignment. Percent Identity Matrix–created by Clustal2.1.

MMP14 is the only MT–MMP detected in DFU reported in the literature to date. The overall MMP14 levels are markedly higher in patients with DFUs than in non–DFU diabetic individuals [145]. The expression and roles of another MT–MMPs, such as MMP15, MMP16, MMP17, MMP24, and MMP25, as well as other MMPs like MMP12, MMP20, MMP21, MMP22, MMP23, MMP27, and MMP28, remain unclear in the context of DFUs.

Low TIMP1 levels and high MMP9 activity are detected in DFU wound exudates [146], contributing to excessive proteolysis and impaired wound healing. In general, DFU wounds possess higher MMP levels and lower TIMP levels compared to wound healing in non–diabetic individuals [140]. This imbalance creates an excessive protein–degrading environment, which is a significant factor in the failure of DFU wound repair. Although MMPs are essential for tissue remodelling and regeneration during wound repair, their overexpression or a disruption in the MMPs/TIMPs balance impedes DFU healing. In conclusion, achieving and maintaining an appropriate balance between MMPs and their inhibitors is crucial for effective wound healing [141–677].

6. CONCLUSIONS

In summary, this review provides an overview of the structure, classification and function of the MMP family, emphasizing their critical roles in each step of wound healing. This evidence lays a strong foundation for further exploration, particularly in the treatment of chronic wounds (e.g. DFUs), for which effective therapies are currently lacking.

A novel selective MMP9 inhibitor has demonstrated potential in treating DFUs, sparking significant interest in targeting MMPs for therapeutic applications. However, the specific roles of different MMPs in normal and pathological wound healing processes remain inadequately defined. Therefore, developing drugs that target MMPs and their associated signals or pathways is crucial for accelerating and improving wound healing outcomes. Future research should focus on the following aspects.

(1) Investigation of mechanisms regulating the expression of MMPs. MMPs display high redundancy in substrate specificity and expression, often allowing one MMP to compensate for the loss of another. For example, MMP9 levels are elevated in Mmp8 knockout mice [10]. This redundancy complicates efforts to target specific MMPs for clinical interventions. A deeper understanding of the mechanisms regulating MMP expression may reveal novel therapeutic targets. Unfortunately, studies on the mechanisms governing the expression of MMPs remain limited. One example is the inflammation, which drives the expression of various MMPs, though detailed underlying mechanisms remain elusive.

(2) Differences in MMP roles between species. Many studies on the role of MMPs in wound healing have been conducted using animal models, such as mice and rats. Notably, the expression patterns of certain MMPs differ between rodents and humans. For example, mice express MMP1a and MMP1b, neither of which is an exact homolog of human MMP1 [147,148]. MMP1a exhibits only 58% amino acid identity with human MMP1 (Fig. 6). In contrast, the amino acid identities between rabbit and human MMP1, as well as between pig MMP1 and human MMP1 are 86%, and 84% respectively. These discrepancies limit the ability to investigate the physiological roles of MMP1 in animal models and hinder the translation of findings from animal studies to human contexts.

(3) Challenges in developing specific MMP inhibitors. Due to the highly conserved catalytic domain among MMPs, all clinical trials of MMP14 inhibitors targeting the catalytic domain have failed. However, MMPs possess several distinct functional domains, with regions outside the catalytic core being less conserved. For example, inhibitors designed to target the hemopexin region of MMP13 and MMP14 have demonstrated high selectivity [148,149]. Our recent research has identified the MT–Loop in MMP14 as essential for MMP14–mediated shedding of low–density lipoprotein receptor [150], indicating the possibility of substrate–specificity targeting.

7. Conflicts of Interest

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

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