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# Advances in Molecular Function and Recombinant Expression of Human Collagen

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**Abstract:** Collagen is the main protein found in skin, bone, cartilage, ligaments, tendons and connective tissue, and it can exhibit properties ranging from compliant to rigid or form gradients between these states. The collagen family comprises 28 members, each containing at least one triple-helical domain. These proteins play critical roles in maintaining mechanical characteristics, tissue organization, and structural integrity. Collagens regulate cellular processes such as proliferation, migration, and differentiation through interactions with cell surface receptors. Fibrillar collagens, the most abundant extracellular matrix (ECM) proteins, provide organs and tissues with structural stability and connectivity. In the mammalian myocardial interstitium, types I and III collagens are predominant: collagen I is found in organs, tendons, and bones; collagen II is found in cartilage; collagen III is found in reticular fibers; collagen IV is found in basement membranes; and collagen V is found in nails and hair. Recombinant human collagens, particularly in sponge-like porous formats combined with bone morphogenetic proteins, serve as effective scaffolds for bone repair. Due to their biocompatibility and low immunogenicity, collagens are pivotal in tissue engineering applications for skin, bone, and wound regeneration. Recombinant technology enables the production of triple-helical collagens with amino acid sequences identical to human tissue-derived collagens. This review summarizes recent advances in the molecular functions and recombinant expression of human collagens, with a focus on their biomedical applications.

**Keywords:** biological properties; collagen structure; extracellular matrix; molecular function; recombinant collagen

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## 1. Introduction

Collagens derived from animal tissues pose risks of allergic reactions, immunogenicity, and pathogen transmission [1]. In contrast, recombinant human collagens offer advantages such as high purity, non-animal sourcing, and elimination of viral or prion contamination risks [2–4]. Skin defects caused by trauma or pathology often lead to infections, inflammation, chronic wounds, and scarring [5,6]. As a major ECM component in skin, collagen is essential for maintaining structural integrity and physiological function [7]. Fibroblasts and collagen collectively regulate dermal physiology, including wound healing and tissue remodeling [7–10]. Patrawalla et al. [11] demonstrated that collagen interacts with glycoproteins, glycosaminoglycans, and proteoglycans to form a complex ECM, which underpins tissue diversity and mechanical resilience.

Collagen's low antigenicity, biocompatibility, and ability to promote cell attachment and migration make it a cornerstone of wound-healing biomaterials [10,11]. Additionally, collagen interacts with host-defense proteins (e.g., C1q collectins and macrophage scavenger receptors) and forms a network of interconnected fiber bundles. These bundles, composed of fibrous protein assemblies, provide skin with tensile strength, elasticity, and mechanical stability [12].

Humans produce at least 28 collagen types, categorized into fibril-forming collagens (e.g., types I, II, III, V, and XI) and nonfibrillar collagens [13,14]. Collagen I, the primary ECM component in human skin, is widely used in dermatological and cosmetic applications due to its role in maintaining tissue biomechanics [15–17].

Recombinant human collagen was firstly modified with methacrylate anhydride (MA) to synthesize the derived collagen hydrogels RHCMA, and MI-RHCMA hydrogel could induce the regeneration of damaged corneal stroma in vivo [18]. Collagen fibril length and angle do not significantly change with region, age, or vitreoretinal adhesive strength, and collagen fibrils in the vitreous cortex have been proved to penetrate the inner limiting membrane of the retina at the vitreous base [19–21]. The preparation process of the novel recombinant human collagen hydrogel (RHCH) is low-cost and simple, as RHCH can be effective in migration of cells essential for wound healing, as well as positively influencing this process in in vitro trials [22]. A combination of different bioceramics and collagen has been found to be more effective in enhancing the amount of bone formation, as collagen-based scaffolds usually present from low osteoconductive capacity in comparison with bioceramic materials [21,22]. The goal of this manuscript is to survey and study the recent findings in recombinant expression and molecular function of human collagen. This review also discusses biosynthesis, structure, isolation techniques, sources, and characterization of the physicochemical properties of different collagens. Important information on various collagens of animal by-products and extraction methods of collagens are shown in Table 1. The collagen protein family and associated disorders are shown in Table 2.

**Table 1.** Important information on different collagens of animal by-products and extraction methods of collagens.

| Animal by-Products Collagen | Collagen Types | Location of Collagen | Collagen Extraction Methods |
|---|---|---|---|
| Fish bones and skin | Type I | Skin, bone, scales, and body | Acid extraction procedure; pepsin-aided acetic acid extraction procedure |
| | Types I and V | Mantle | Acid extraction procedure; pepsin-aided acetic acid extraction procedure |
| | Type IV | Tissues | Acid extraction procedure; pepsin-aided acetic acid extraction procedure |
| | Types I, II, and III | Bell and oral arms | Acid extraction procedure; Pepsin-aided acetic acid extraction procedure |
| Bovine tendons, body, organs, and skin | Type I and type V | Body | Treatment with a defatting agent at soft temperature; treatment with soft acid and pepsin at low temperature; treatment with acid/alkali or high temperature; treatment with enzymes to break down polypeptide chains collagen; treatment with enzymes followed by isolation of certain bioactive peptides |
| | Type II | Elastic cartilage | treatment with a defatting agent at soft temperature; treatment with soft acid and pepsin at low temperature; treatment with acid/alkali or high temperature; treatment with enzymes to break down polypeptide chains collagen; treatment with enzymes followed by isolation of certain bioactive peptides |
| | Type III | Muscles, organs, and arteries | Treatment with a defatting agent at soft temperature; treatment with soft acid and pepsin at low temperature; treatment with acid/alkali or high temperature |
| | Type IV | The Layer of skin | Treatment with acid/alkali or high temperature; treatment with enzymes to break down polypeptide chains collagen; treatment with enzymes followed by isolation of certain bioactive peptides |

**Table 1.** *Cont.*

| Animal by-Products Collagen | Collagen Types | Location of Collagen | Collagen Extraction Methods |
|---|---|---|---|
| Porcine skins | Types I, II, and III | Skin | Treatment with a defatting agent at soft temperature; treatment with soft acid and pepsin at low temperature; treatment with acid/alkali or high temperature |
| Poultry cartilages, skin, and bone | Types I and III | Skin | Enzyme hydrolysis extraction for skin; acid-soluble extraction for bone; alkali-soluble extraction for bone |
| | Type II | Cartilage | Enzyme hydrolysis extraction for skin; acid-soluble extraction for bone; alkali-soluble extraction for bone |
| | Types I and II | Bone | Enzyme hydrolysis extraction for skin; acid-soluble extraction for bone; alkali-soluble extraction for bone |

**Table 2.** The collagen proteins family and associated disorders.

| Collagens | Type | Location |
|---|---|---|
| Fibrillar collagens | Collagens I | Bone, skin, cornea, tendon, vascular ligature, and organs |
| | Collagens II | Vitreous body, cartilage, and gristle |
| | Collagens III | Reticulate, commonly found together with collagen type I skin, vessels, intestine, and uterus |
| | Collagens V | Skin, cell surfaces, cornea, placenta, skin, and hair |
| | Collagens XI | Intervertebral disc, and gristle |
| | Collagens XIV | Gristle, skin, tendons, bones, eye, nerves, and vessels |
| | Collagens XXVII | Gristle |
| Nonfibrillar collagens | Collagens IV | Forms basal lamina, the epithelium-secreted layer of the basement membrane, and capillaries |
| | Collagens VII | Umbilical cord, amniotic fluid, skin, bladder, and mucous membranes |
| | Collagens VI, XXVIII, and XXIX | Collagen VI can be found in cornea, gristle, vessels, bones, and skin<br>Collagen XXVIII can be found in nervous system cells.<br>Collagen XXIX can be found in skin. |
| | Collagens VIII, X | Collagen VIII can be found in gristle, vessels, bones, brain, kidneys, skin, and heart.<br>Collagen V can be found in gristle. |
| | Collagens XIII, XVII, XXIII, and XXV | Collagen XIII can be found in skin, endothelial cells, heart, eye, and skeletal muscles.<br>Collagen XVII can be found in skin.<br>Collagen XXIII can be found in metastatic carcinogenic cells.<br>Collagen XXV can be found in testicles, brain, heart, and eye. |
| | Collagens IX, XII, XIV, XVI, XIX, XX, XXI, XXII, XXVI, and XXIV | Collagen IX can be found in the gristle, vitreous body, and cornea.<br>Collagen XII can be found in the tendons, skin, and gristle.<br>Collagen XVI can be found in the kidneys, smooth muscle, heart, and skin.<br>Collagen XIV can be found in gristle, skin, tendons, bones, eye, nerves, and vessels.<br>Collagen XIX can be found in the prostate gland, placenta, spleen, kidneys, liver, and skin.<br>Collagen XX can be found in corneal epithelium.<br>Collagen XXI can be found in vessels, skeletal muscles, placenta, kidneys, heart, and stomach.<br>Collagen XXII can be found in tissue connections.<br>Collagen XXVI can be found in ovaries and testicles.<br>Collagen XXIV can be found in cornea and bones. |
| | Collagens XV and XVIII | Collagen XV can be found in placenta, kidneys, testicles, skin, ovaries, heart, and capillary vessels.<br>Collagen XVIII can be found in lungs, liver, and kidneys. |

## 2. Classification and Function of Human Collagen

Collagens present a common structural basis known as the abundance of repeating Gly-C-Y amino acid triplets, where Y and X are usually represented by 4-Hyp and Pro, respectively [23–25]. In some researches, it is noted that collagen from human bone has a specific amino acid sequence from which it is possible to assess the C/N ratio, as the C/N ratio is applied to evaluate availability of collagen derived from bone for isotope measurement [26]. It is also discovered that collagen and human amniotic membrane (hAM) are usually applied biomaterials in regenerative tissue repair, such as peripheral nerve regeneration, and hAM nerve wraps are an important biomaterial which is effectual for enhancing results of peripheral nerve regeneration. Moreover, compared to collagen nerve wraps, hAM nerve wraps may lead to better functional recovery and superior nerve regeneration [27]. Rosu et al. [28] found that three-dimensional biopolymers with collagen

are important models for extracellular matrix researches, and human apolipoprotein A-I (apoA-I) bound less to matrices with heparin and collagen than to those with only collagen. Human-like collagen (HLC) is bio-safe, biomimetic, and hydrophilic, and HLC self-assembles loaded on the oxidized-modified hyaluronic acid (oxi-HA) showed higher biological activity characteristics than hyaluronic acid, which proves its importance as a new component of multifunctional HA-based wound-healing generation [29]. Voziyan et al. [30] mentioned that the advanced glycation end products (AGEs) play an important function in pathogenesis of diabetic complications, and the map may improve evaluation of pathogenic mechanisms involving collagen I and AGEs. The high amount of secondary amino acids and Gly in these triplets can induce stabilization of the $3_{10}$-helical conformation of individual collagen chains and promote the assembly of triple helices [31].

Collagen peptides are effective in decreasing excessive hair shedding and thinning associated with patterned hair loss or aging [32]. Compared to tubes made of collagen hydrogels, collagen filaments have increased mechanical characteristics, and endothelial cells (ECs) cultured within the hollow fibers under perfused conditions indicate obvious cell−cell contacts, high cell viability, and remodeling of the underlying matrix [33]. The lipid extraction may not be a necessary stage of bone collagen isolation, especially for non-marine diet populations. Although the collagen-based scaffold plays the appropriate biological roles in tissue engineering, there are still some limitations because of its rapid degradation rate and poor mechanical strength [34–36].

Recombinant human collagen (RHC) has high resistance to gastrointestinal digestion, and RHC digestates can reduce reactive oxygen species (ROS) levels by increasing antioxidant enzyme activities, improve the synthesis and inhibition the degradation of ECM and have higher protective impact on fibroblasts than animal collagens [37]. The mechanical behavior of human periodontal ligament (PDL) follows the trend of hyperelastic materials and noticeably relies on the spatial angles of internal collagen fibers. This model could significantly show the hyperelastic characteristics of human PDL [38]. On the basis of electron microscopic analyses and fibrillation kinetics, it is reported that lutein does not interfere with the fibrillation procedure of collagen. However, it increases the lateral fusion of collagen fibrils, leading to the formation of compact bundles of thick fibrils under physiological conditions [39]. This demonstrates the interaction between carotenoid and collagen, indicating the unique property of lutein in bundling collagen fibrils and its potential in application in tissue engineering [39]. Ben et al. [40] described that the recombinant human collagen gel is considered to be an appropriate alternative for the heterologous/homologous skin disorders. Type VII collagen (COL7) can be encoded by COL7A1, and its mutations may cause recessive dystrophic epidermolysis bullosa (RDEB) that is a severe skin fragility disease. COL7 can reduce anchoring, repair defects and enhance skin integrity in RDEB patients [41]. Fischer et al. [42] concluded that the collagen fiber arrangement is important for constitutive description of anisotropic mechanical reaction of the arterial wall. Guo et al. [43] designed a novel recombinant human collagen (rhCol), and on the basis of RT-qPCR and immunofluorescence staining, it was proved that rhCol/basic fibroblast growth factor (bFGF) can promote expression of bone-related proteins, which shows its importance as a suitable scaffold in clinic applications.

Studies showed that collagen hydrogel has important biocompatibility and considerable capacity to increase expression and cell viability of stemness-associated genes, including SRY-box transcription factor 2 (SOX2), Nanog homeobox (Nanog), and organic cation/carnitine transporter4 (Oct-4) of human umbilical cord mesenchymal stem cells (uMSCs) [44]. The primary human intestinal myofibroblast (HIMF)-derived ECM in inflammatory bowel disease (IBD) binds a remarkably increased number of T cells which is dependent on integrin $\alpha v\beta 1$ and collagen VI, and the expression of Collagen VI is a risk

parameter for the future complicated Crohn's disease (CD) course [45]. Members of the microRNA-29 (miR-29) gene family could inhibit proliferation and induce apoptosis in human fetal scleral fibroblasts (HFSFs), with important role in scleral remodeling, and it could also downregulate heat shock protein 47 (Hsp47), COL1A1 and Smad3 in HFSFs [46]. Kaviani et al. [47] found that the reconstruction of the destructed matrix with collagen microspheres and alginate hydrogels can be useful to increase the culture of the islets through TUNEL positive cells and the reduction of activated caspase-3. It is discovered that the newly synthesized collagen/poly(3-hydroxybutyrate) (COL/P3HB) scaffold increased the colon anastomosis healing [48]. Collagen types V and I fibrils have important functions in the structural backbone of bone [49,50], collagen types XI and II usually contribute to the fibrillar matrix of articular cartilage [49], and collagen types XIV, XII, and IX have an important function in regulating the diameter of collagen fibrils [51]. In collagen types X, VIII, VII, VI, and IV, non-collagenous domains have significant functions in network formation and aggregation [52], types XI and V collagens are formed as heterotrimers of three different $\alpha$-chains ($\alpha$1,$\alpha$2,$\alpha$3), and types XIV and XII collagens are structurally associated with short-chain collagens [52].

Fibrillar collagens are collagen I which can be found in bone, skin, cornea, tendon, vascular ligature, and organs; collagen II which can be observed in vitreous body, cartilage, and gristle; collagen III that can be observed in reticulate, commonly found together with collagen type I in skin, vessels, intestine, and uterus; collagen V in skin, cell surfaces, cornea, placenta, skin, and hair; collagen XI in intervertebral disc and gristle; collagen XIV which can be found in gristle, skin, tendons, bones, eye, nerves, and vessels; and collagen XXVII in gristle.

Nonfibrillar collagens are the collagens as follows. Collagen IV can form basal lamina, the epithelium-secreted layer of the basement membrane, and capillaries. Collagen VII can be found in umbilical cord, amniotic fluid, skin, bladder, and mucous membranes. Collagen VI is in cornea, gristle, vessels, bones, and skin. Collagen XXVIII is in nervous system cells, and collagen XXIX can be observed in skin. Collagen VIII can be found in gristle, vessels, bones, brain, kidneys, skin, and heart; collagen V can be observed in gristle; collagen XIII can be found in skin, endothelial cells, heart, eye, and skeletal muscles; collagen XVII can be observed in skin; collagen XXIII can be observed in metastatic carcinogenic cells. Collagen XXV can be discovered in testicles, brain, heart and eye; collagen IX can be found in the gristle, vitreous body, and cornea; collagen XII can be discovered in the tendons, skin, and gristle. Collagen XVI is in the kidneys, muscle, heart, and skin; collagen XIV is in gristle, skin, tendons, bones, eye, nerves, and vessels; collagen XIX can be found in the prostate gland, placenta, spleen, kidneys, liver, and skin; collagen XX is in corneal epithelium; collagen XXI is in vessels, skeletal muscles, placenta, kidneys, heart, and stomach. Collagen XXII can be found in tissue connections; collagen XXVI is in ovaries and testicles; collagen XXIV is in cornea and bones; collagen XV is in placenta, kidneys, testicles, skin, ovaries, heart, and capillary vessels; and collagen XVIII can be found in lungs, liver, and kidneys. The collagen protein family and their locations are presented in Figure 1.

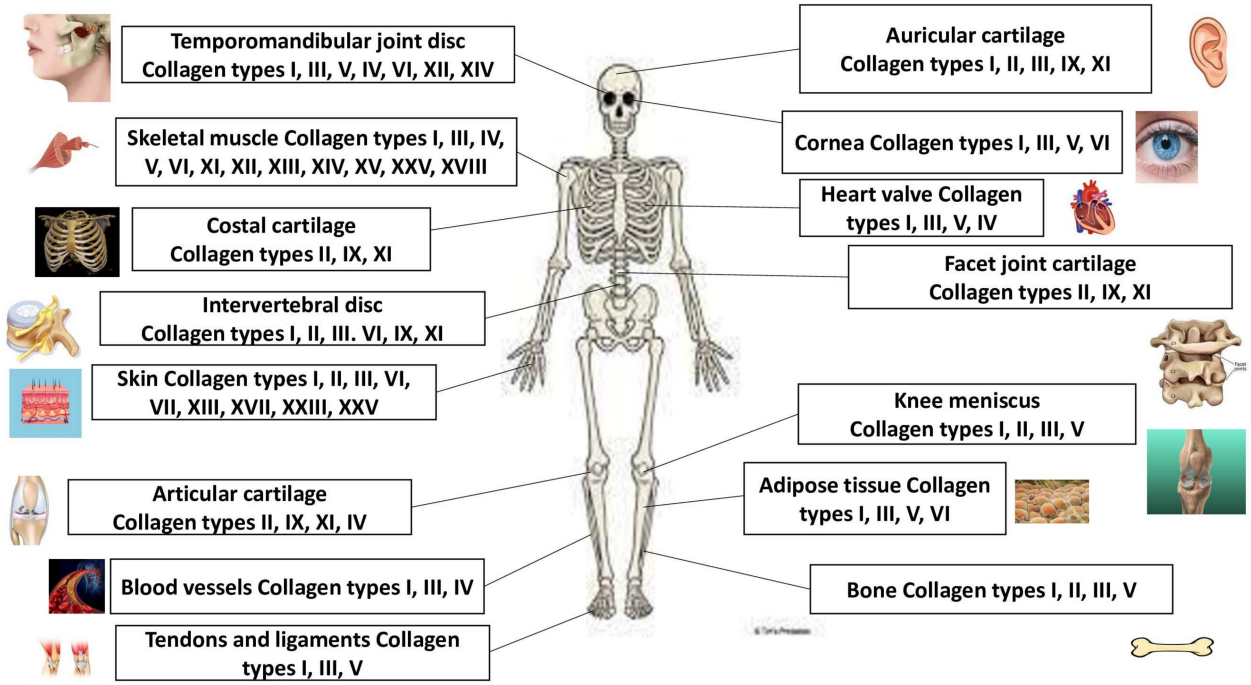



**Figure 1.** The collagen protein family and their main locations.

## 3. Collagen I

The most abundant protein in the body, especially in the connective tissues, is type I collagen [53], and it is the main component of the extracellular matrix [53], which is found in tissues tendon, bone, and skin [54]. It forms a heterotrimer consisting of two α1(I) chains and a genetically distinct α2(I) chain. The α111(I) homotrimer has been also found in different limited situations in vivo such as cancer tissues, fibrotic, osteoarthritis, and fetal [55]. It is considered as the gold standard biomaterial for the manufacturing of medical devices used in healthcare [55], and collagen type I from equine tendon preserves its native fibrillar conformation [54,55]. Taga et al. [56] found that the most suitable method which can clearly detect the rare form of type I collagen is LC-MS method.

The most abundant collagen in long-lived extracellular matrix proteins is type I collagen, as they can accumulate higher levels of advanced glycation end products (AGEs) and glycoxidation of collagen I. Glycation, together with other proteins of bone ECM, has been proved to contribute to the diabetes-related increase in bone fragility [57]. Voziyan et al. [57] showed levels and sequence positions of main AGEs in human bone collagen I, and molecular modeling revealed the effects of AGEs on collagen structure in diabetic bone. Wu et al. [58] reported the introduced recombinant human collagen I in fabricating a new hydrogel loaded with human umbilical cord mesenchymal stem cell (hUCMSC)-derived exosomes, which can significantly promote skin regeneration and wound closure, showing high potential in severe skin wound healing treatment. Collagen I can inhibit the accumulation of damaged mitochondria in ultraviolet B (UVB)-treated cells, and precoating culture plates with collagen I can reduce UVB-induced HaCaT cell apoptosis [59–63]. Hu et al. [61] reported that the transplantation of the menstrual blood mesenchymal stem cell (MBMSC)-loaded collagen scaffold (CS) reduced collagen I and enhanced the CK 18 significantly, and according to the findings of immunoblotting results, the upregulation of CK 18 and downregulation of collagen I were proved. Marin et al. [64] found that treatment of older and young adult human skin cells with sacubitril and valsartan may induce a five-fold boost in collagen type I production in the young cells and a four-fold increase in collagen type I in older adult cells.

It is noted that the length and density of collagen I fibers in triple-negative breast cancer make an important contribution to patient prognosis and tumor size, and it may allow

breast cancer cells to metastasize to the lungs [65,66]. Its matrices have been applied both as three-dimensional environments and tissue engineering for biological research [67–69]. Stromal collagen type I may predict chemotherapy response, and protein expression and low stromal collagen type I mRNA are associated with unfavorable tumor characteristics in breast cancer [70,71]. Zhang et al. [72] reported that collagen type I has a relatively stable quality while completely resistant to digestion due to its complex triple helix structure. It inhibits autophagy by upregulating the YAP-mTOR pathway, and it can improve lipid metabolism and glucose through the YAP-autophagy axis [73–75]. Collagen type I proteolysis by matrix metalloproteinase (MMP)-2 activates focal adhesion kinase (FAK) in aortas and induces vascular smooth muscle cell (VSMC) proliferation and hypertrophic remodeling [75]. Collagen type I produced by pancreatic cancer cells is the oncogenic homotrimer variant, and it may enrich T cells and promote a beneficial tumor microbiome [74,75]. Preston et al. [75] also reported that collagen type I plays an important role in treatment of breast cancer. It may present challenges as a bioink [76]. Tumor-associated collagen I contributes to aberrant transcriptional activity. This promotes intracellular signaling that induces mechanotransduction-associated procedures which may give rise to chemoresistance [77].

## 4. Collagen II

Collagen type II is a main structural protein of cartilaginous tissues [78], which is first synthesized as procollagen [79–82]. As one of the basic components of the cartilage matrix, it can improve bone health and promote chondrocyte differentiation, especially for rheumatoid arthritis [83,84]. Collagen II type is heterotypically associated with type XI and type IX collagens [85]. It is the main constituent of cartilage tissue, and its devices in cartilage engineering are linked with suboptimal functional therapeutic outcomes [86]. It is usually isolated from the cartilages of terrestrial animals such as bovine and swine [87]. As collagen type II is a fibrillar collagen, it includes 95% of the collagen and nearly 60% of the dry weight of cartilage [88,89]. In fact, collagen is a polymer which exists as a triple helix with chains connected by hydrogen bonds [90], and types II and I collagens are different in amino acid [91,92]. Type I collagen is more effective in increasing surimi gel properties than type II [93], and the expression of collagen type II is regulated by the Sox trio of transcription factors [94,95]. Its strength and stability can provide the tissue with resiliency and integrity to stress [96,97], and the amount of collagen type II is higher in the tissue around the calcium deposit [98,99]. During skeletal development, type II collagen plays an important role in the embryonic cartilaginous skeleton [100,101]. Type II collagen could be induced to strengthen a weakened cornea [101], and degradation of type II collagen caused by pro-inflammatory cytokines is one of the main pathological traits of osteoarthritis (OA) [102,103]. A type II collagen-specific neoepitope is the first technically robust serological biomarker assay related to osteoarthritis cohorts, which proves its role as a translational biomarker for cartilage degradation [104,105]. The metabolic disorder and degradation of collagen type II in human cartilage can influence the development of osteoporosis and osteoarthritis [106].

## 5. Collagen III

Collagen III can be found in the endometrium and consists of a main portion of the extracellular matrix [107]. It possesses the ability to influence cell proliferation, adhesion and migration and bind to integrins [107]. As the second most abundant collagen, type III collagen is extensively distributed in various connective tissues, such as the vascular system and internal organs [108]. It is found that both collagen III and collagen I play significant roles in fibroblast activation [108]. It is reported that it plays important roles in normal cardiovascular development in humans and wound healing [109]. Both types I and III collagens are main ingredients in tissue regeneration and wound healing [110,111].

Recombinant human collagen III is synthesized via a re-optimized gene sequence design according to the primary functional domains and the features of human collagen [112]. Type III and type I collagens bind to collagen receptors, perform various biological roles, such as a supportive function in cell migration, differentiation, and adhesion as well as M2 macrophage polarization, and promote ECM, platelet aggregation, and angiogenesis [111,112]. Li et al. [112] found that recombinant human collagen (rhCOL)-derived material with high cell adhesion characteristic can promote migration, HULF adhesion, and ECM synthesis, regulate the metabolism of human uterosacral ligament fibroblast (HULFs), influence the focal adhesion kinase (FAK)/RhoA/ROCK signaling pathway, improve pelvic floor function in pelvic floor dysfunction rats and reduce remodeling effects. The collagen α1(III) chain (COL3A1) is considered as an important structural protein on the surface of human skin [113]. Human collagen type III (hCOL3A1) associates to the fibril-forming collagens, which is distributed in an extensive connective tissue-like vascular system with important roles in collagen fibrillogenesis and wound healing [114]. It is reported that a human type III collagen (hCOLIII)-based ECM-mimetic coating can be used as a tailored blood-contacting component for cardiovascular stents, as it suppressed inflammatory response, increased endothelialization and inhibited the excessive neointimal hyperplasia [114–116]. As one of the main structural proteins, collagen III is classified as one of the main fibrillar collagens [116], and it can influence the occurrence of incisional hernia and play a considerable role in maintaining tissue tensility and elasticity [117,118]. Both types I and III collagens are the major components of the interstitial matrix [119,120]. It plays a notable role in different inflammation-associated pathologies such as arthropathies, lung injury, kidney fibrosis, liver disease, vascular disorders, and hernia [121,122]. Collagen type III promotes migration and cell viability of endometrial stromal cells [123,124]. Both collagen types III and I can reduce aged skin [125], and their accumulation can be found in fibrotic diseases. They can also regulate type I collagen fibril formation [126–128]. Type III collagen is less abundant in women with diastasis recti than in those without the condition [129,130], and it can influence the aggrecan network compression possibly via mediating collagen network integration and the aggrecan [131]. It can serve as a potential treatment method for breast cancer patients to improve prognosis of patients [132] and reduce deposition in metastatic prostate cancer [133]. Collagen type III promotes the proliferation of myoblasts, and it has the capability to inhibit the differentiation of myoblasts [134,135]. Collagen type III can be considered as an anti-osteoarthritic candidate [136], and it can regulate myofibroblast differentiation and scar formation after cutaneous injury [137,138].

## 6. Collagen V

Collagen V is a fibrillar collagen which is needed for the normal formation of collagen III and I fibrils by determining and initiating their properties and diameters [139]. It can contribute to the corneal stroma, bone matrix, and the interstitial matrix of liver, muscles, placenta, and lungs [140]. Elhers−Danlos syndromes (EDS) are the main cause of collagen V mutations [140], and collagen V can regulate collagen fiber assembly and geometry and link stromal and strength of collagen to the basement membrane [141]. The most common collagen V isoform is $\alpha1(V)_2$ α2(V) found in cornea, but other isoforms include the [α1(V)α2(V)α3(V)] form, an $\alpha1(V)_3$ homotrimer, and hybrid type V/XI forms [142]. The deficiency of collagen V can enhance scar size after acute heart injury [143–145], and increases in collagen V are associated with an increased number of TGF-β1, fibroblasts. These changes are more pronounced in chronic, long-standing persistent atrial fibrillation (cAF) patients than those in paroxysmal AF (pAF) patients, which proves that AF is significantly associated with increased expression levels of TGF-β1 and collagen V, showing its

important function in the pathogenesis of atrial fibrosis [146]. Collagen V most probably acts as fibril diameter regulators as they can keep a bulky amino-terminal portion linked to the triple helix after their final extracellular processing [145,146]. It has a significant function in connective tissue contraction, especially during tissue regeneration and wound healing [146]. Reduction of collagen type V can decrease aberrant cell clustering and cell density in both hyaline and fibrous layers, and its loss may lead to reduced $\beta$-catenin expression and cell proliferation in the fibrous layer [147]. Collagen V plays an important role in the formation of human islet organoids which harbor all main pancreatic endocrine cell types, and it can augment the generation of endocrine which secretes glucagon and glucose level-regulated insulin [148]. It can induce a specific transcriptional signature in murine splenic B cells as well as rapid production of anti-collagen V antibodies [148]. Collagen type V turnover may be significantly important in the pathogenesis of ankylosing spondylitis [147,148]. It can influence migration, adhesion, viability, and metastatic potential of pancreatic cancer cells, and its downstream pathway exerts possible therapeutic targets in pancreatic ductal adenocarcinoma (PDAC) [149]. It also has a significant function in modifying cell behavior during remodeling and development when very soft tissues are present [150]. Pre-treatment by intravenous injection of collagen V may inhibit bleomycin-induced pulmonary fibrosis by suppressing IL-6 and IL-17 production [151].

## 7. Collagen IV

Nonfibrillar collagens arise from disruptions in the Gly-X-Y repeats of the alpha chains [152–157]. Instead of forming fibrils, these nonfibrillar collagens form mesh-like networks in the ECM, such as collagen IV found in basement membranes [158–172]. They are expressed in smaller amounts [173–180] and influence the shape and fiber thickness of type I collagen or anchor the groups of fibers to each other and surrounding tissues [181–190]. They are rich in proline, glycine, and hydroxyproline and form triple-helical units [191–210]; however, the helical region is short or interrupted [211–225]. The nonfibrillar collagens form basement membranes, anchors, and microfibrils [226–240]. The N- and C-terminal regions of the triple helices are not cleaved off, as in fibrous collagens, nor are they cross-linked by oxidized lysine residues [241–258]. The main cross-links found in types IV, VII, and XVII collagens are mediated by cysteine disulfide bonding, mostly within their C-terminal regions [259–266].

Collagen IV is an important constituent of the glomerular basement membrane (GBM), and its synthesis starts with the transcription of genes encoding the alpha chains into messenger RNA within the cell nucleus [152]. It can be found in several tissues such as vascular endothelial and skeletal muscles [153]; moreover, the main ingredient of the basement membrane in epithelial tissues is collagen IV [154]. Its two important functions are to enhance development of architecture tissues and structural stability [155]. In fact, it includes three $\alpha$-chains of primarily repeating Gly-Xaa-Yaa triplets, which induces each $\alpha$-chain to adopt a left-handed poly-pro-II helix [154–157]. As the major collagen ingredient of the basement membrane [173] and a heterotrimeric molecule, it has the globular C-terminal NC1 domain, a central triple-helical domain, and the N-terminal 7S [174]. It is a network-forming collagen which underlies endothelial and epithelial cells and acts as a barrier between tissue components [175]. It has six highly homologous polypeptide chains, namely $\alpha$1(IV) to $\alpha$6(IV) with each including the carboxy-terminal, triple-helical, and amino-terminal domains [176]. Transforming growth factor (TGF) beta can regulate type IV collagen production in stromal corneal fibroblasts [177]. It is also reported that collagen IV is the main backbone of the basement membrane [178,179]. It has capability to downregulate ERK which may induce Mucin 5AC (MUC5AC) secretion [180], and it can be useful in treatment of breast cancer [179,180]. It is an appropriate indicator of basement membrane damage in workers occupationally exposed

to volatile organic compounds [181], and it is reported as an important agent for treatment of non-small cell lung cancer cells [182,183]. It has also an important function for treatment of tumor-initiating cells in oral cancer [184,185]. Collagen IV could shape organs and cells by exerting a mechanical constricting tension [185]. It can influence the invasive behavior of trophoblast cells at the implantation site and also represents a structural protein providing tissue integrity [186]. It has a dynamic contractile activity in reaction to electrical pulse stimulation which proves its role in the design of myoblast-based therapies [187]. Collagen IV could predict the presence of advanced fibrosis in non-alcoholic fatty liver disease (NAFLD) patients [188], and it has also shown effective function relevance to ocular diseases [189].

## 8. Collagen VI

Collagen VI is an important component of the extracellular matrix in all connective tissues [190], which can be found at the interface between the interstitial matrix and basement membrane [191]. It is both a signaling and a structural protein [191], which can be found in tendon, bone, cartilage, cornea, and muscles [192]. The major collagen type VI genes are *COL6A3*, *COL6A2*, and *COL6A1*, which are expressed by interstitial muscle [193]. These genes are primarily found in close connection with basement membranes with important functions in progenitor cell attachment and matrix conformation [192,193]. The incorporation of collagen type VI in immunoisolated human islets supports survival of human pancreatic islets and in vitro viability [194], and collagen VI in hippocampal slices could decrease glutamate release, which leads to a decline in neuronal excitability [195]. Collagen VI deposition is associated with higher T cell density in prostate cancer patients, and it can directly influence lung epithelial cell phenotype in vitro [196]. It is also reported that it has an important function in the preterm chronic lung diseases, including Bronchopulmonary Dysplasia (BPD) [197].

## 9. Collagen VII

As the major component of anchoring fibrils, collagen type VII is important for skin integrity [156,157], and it is also vital for linking various skin layers together [158]. It includes a central collagenous triple-helical domain flanked by two non-collagenous domains, namely NC2 and NC1 [157,158]. Functional defects in type VII collagen are accountable for recessive dystrophic epidermolysis bullosa (RDEB) and severe autosomal recessive kinds of the skin blistering disease [158]. It is important for stability and function of the ECM as it is an anchoring fibril collagen [198], and it is basically synthesized by fibroblasts and keratinocytes [199]. It is involved in systemic sclerosis, chronic obstructive pulmonary disease, and Crohn's disease [189,199]. Type VII collagen has a positive effect on treatment of brittle bone disease known as osteogenesis imperfecta (OI), and the initial synthesize of collagen VII is via basal keratinocytes and dermal fibroblasts [199,200]. It is originally known because of its unusually lone and an extended molecule [199,200]. The lack of type VII collagen disrupts cellular proteostasis and acts as a scaffold to load Transport and Golgi Organization-1 (TANGO1)-mediated COPII carriers by binding both the coat protein II complex (COPII) and TANGO1 cargo [201]. It is important for the stability of the skin and other epithelial organs [200,201], and its genetic loss may cause dystrophic epidermolysis bullosa, which can manifest with fibrosis and chronic skin fragility [202]. It has been identified via resistance to pepsin, sensitivity to purified collagenase, and its immunoreactivity with several antibodies [203]. It shows an unusual corkscrew distribution pattern related to the dentin enamel interface [204]. As a single structural protein, it has intra- and extra-cellular consequences, resulting in inflammatory processes which can promote keratinocyte-driven tissue destabilization and progressive fibrosis [205].

## 10. Collagen VIII

It is a nonfibrillar, a short-chain collagen, and the main components of Descemet's membrane [206], which is basically synthesized by endothelial cells, and can be found in cartilage, muscles, lung, liver, brain, and heart [207]. It was first discovered as an extracellular protein in bovine aortic endothelial cell cultures which is composed of α1 and α2 collagen chains [206,207]. It can be found in large fibrotic vessels of angiomas and proliferating vessels of brain tumors with signaling and structural properties [207,208]. Its signaling properties originate from vastatin, which is a non-collagenous C-terminal globular NC1 [207,208]; moreover, it is an important component of blood vessels [209]. It has important functions in treatment of systemic sclerosis, angina pectoris, chronic obstructive lung disease, and different cancers [210]. It can negatively regulate elastin, and it can also increase the content in carotid arteries and elastin synthesis [211]. It is significantly upregulated in different cancer types [210,211], with important function in glial scar formation during the repair process by astrocytes [212]. Collagen VII is important for the maintenance of vessel wall elasticity and integrity [213,214].

## 11. Collagen X

Collagen type X is strongly expressed in hypertrophic chondrocytes, and it is a short-chain collagen [161]. It is expressed particularly in the growth plate of long bones [161]. Metaphyseal chondrodysplasia type Schmid (MCDS) is caused by mutations in the human collagen X gene [162]. It is a network-forming collagen which is basically expressed in hypertrophic chondrocytes in the cartilage of the hypertrophic zone of the growth plate [215]. It is active in human lumbar intervertebral discs, and it is produced by hypertrophic cartilage undergoing endochondral ossification [216]. Its biomarkers are shown to be elevated in rheumatological disorders influencing cartilage and bone, and of course, in cancer treatment [215,216]. It appears in the matrix of the hypertrophic zone [215–218].

## 12. Collagen XI

It is a minor fibrillar collagen which is extensively distributed in the lung, placenta, skeletal muscle, trabecular bone, tendon, trachea, testis, articular cartilage, and the neuroepithelium of the brain [219]. It can regulate fibrillogenesis by keeping the spacing and diameter of type II collagen fibrils [220]. It can also work as a nucleator for the fibrillogenesis of types II and I collagens [219,220], and it has various isoforms such as α1(XI)α2(XI)α3(XI), as well as XI and V hybrids such as $[\alpha1(XI)]_2\alpha2(V)$ [219,220]. COL11A1, COL11A2, and COL2A1 can encode different three α-chains of collagen type XI, namely α1(XI), α2(XI), and α3(II), respectively [221], and this collagen type plays an important role in skeletal morphogenesis and fibril formation [222]. Mutations in type XI collagen are linked with Marshall syndrome, Stickler syndrome, Weissenbacher−Zweymuller syndrome, otospondylomegaepiphyseal dysplasia deafness, and fibrochondrogenesis [221,222]. It is also significantly linked with cancer-associated fibroblasts and cancer progression [223], and it can also bind dermatan sulfate, heparan sulfate, and heparin [224]. The α1 chain of a minor human collagen, type XI, is not discovered in normal stroma, but it is overexpressed in some tumor stroma, and its detection may need appropriate probes [159]. Lorenzo-Gomez et al. [160] found that the detection of the α1 chain of human collagen XI was possible in cell lysates, which was also admitted by aptacyfluorescence. Its biomarkers have shown high capability as prognostic and diagnostic markers in cancer diseases [225], and it can regulate mechanical properties and acquisition of fibrillar structure [224,225]. As the ECM component, it shows high activity in increasing the inhibiting and reducing the degradation of the cartilage matrix [224,225]. It can regulate the stroma surrounding breast cancer, and it may help predict which women are at risk of having lymph node metastases [226]. It is

present in the nucleus pulposus and fibrosus of intervertebral discs [226,227]. Stromal collagen is associated with invasive recurrence in the breast ductal carcinoma in situ (DCIS) and is an important marker to predict the response to radiotherapy [228], and type XI collagen genes can be considered as important markers for chondrogenic tumors [229,230]. It can be considered as a locus for fibrochondrogenesis and reveal the possible phenotypic manifestations among carriers [231]. In addition, it can increase the potential of distinguishing the cancer-associated desmoplastic stroma which is linked with misplaced adenomatous mucosa [232]. It is important for the development and integrity of the skeleton because of mutations in the genes [233].

Unlike type II collagen, the structure of collagen type XI has been of interest because the proteolytic processing of the amino-terminal domain is very slow and sometime after processing is completed, and some portion of the domain is retained [163]. Collagen type XI plays a role in the control of fibril diameter [164], and sometimes, mutations in its genes have been reported to cause multiple epiphyseal dysplasia (MED) [163–166]. It can also interact with type IX and type II collagens to form the meshwork of collagen fibrils, which gives cartilage its notable tensile strength [167]. It is also reported that type XI and type V collagens are not separate collagen types but are part of a larger collagen family in which chains of both collagens participate in the formation of different native molecules [166,167]. The specific locations of type XI and V collagens in cartilaginous tissue can play different functional roles for these two components in the tissue [166,167].

## 13. Collagen IX

Collagen IX is synthesized as short and long forms which lack or contain, respectively, a 27 kDa non-collagenous (NC) 4 domains at the N-terminus of the α1(IX) chain of the molecules [168,234,235], it is an important structural component of the extracellular matrix of connective tissues [169]. Moreover, it is important for the normal structural integrity of the tissue [170]. It is a fibril-associated collagen with interrupted triple helices [233]. It is present in adult articular cartilage, chondrocytes of growth-plate cartilage, the inner ear, and intervertebral discs [234]. It can contribute to the stabilization of the fibrillar collagen network in the cartilage matrix [234,235]. Its absence may lead to early developmental, biomechanical, and structural changes in the spine, which lay the ground for disc degeneration in aged mice [235], and it is an important part of the articular cartilage [236,237]. Its mutations may induce abnormal integrity of collagen fibers in the tectorial membrane [237], and it plays an important role in the tectorial membrane in the auditory system [238]. The interaction between biglycan and collagen IX can be considered as the weak link in the cartilage collagen architecture [238].

## 14. Collagen XII

Type XIII collagen molecules are believed to be composed of four non-collagenous domains (NC1-4) and three collagenous domains (COL1−3), with two located at the N- and C-terminal ends of the polypeptide and two of them separating the collagenous domains [161,241]. It is a fibril-associated collagen with interrupted triple helices [239], and it consists of alpha chains which are nearly 90 kDa larger than the 200 kDa alpha chain [240]. It can be found in the interstitial matrix and is an ingredient of human skeletal muscle [241]. It is important to stabilize the joint extracellular matrix in humans and mice [242], and it can interact with tenascin, fibromodulin, COMP, and decorin [243]. It has function in regulating corneal stromal transforming growth factor (TGF)-β activation and latency [244]. It can prevent the formation of atherosclerotic lesions, and it can also stabilize the vascular structure [243,244]. Collagens XIV and XII are both associated with muscle metabolism [243,244], and this association occurs regardless of breeds [245]. It is important

to attain wound closure and scar maturation [246], and it is a key element which can control growth factor availability, improve the orchestration of a proper skin matrix structure and regulate cellular function and composition [246,247]. Type XIV and XII collagens produced by tenocytes represent minor collagenous components of the tendon [247–249].

## 15. Collagen XIII

Collagen XIII is a nonfibrillar, type II transmembrane collagen which belongs to a subgroup of collagens called membrane-associated collagen with interrupted triple helices [250]. It includes a short N-terminal cytosolic domain, a largely collagenous ectodomain, a transmembrane domain, and exists as a soluble form because of its ectodomain shedding [251]. It can bind to proteins like α1β1 integrin, type IV collagen, nidogen-2, vitronectin, perlecan, and fibronectin, and its expression decreases toward adulthood and becomes more pronounced during postnatal and development growth [250,251]. The complete primary structure of the mouse type XIII collagen chain was shown by cDNA cloning [252], and it is significantly expressed in cells producing connective tissue, during corneal wound healing, with higher expression in certain tumors and renal fibrosis [253]. It is important for the normal function and structure of neuromuscular synapses [253,254], and its loss may influence maturation of both the pre- and postsynaptic specialization of the neuromuscular junctions [254–256]. Its overexpression can induce the development of massive bone overgrowth because of an increased osteoblast differentiation capacity [257,258]. It is also reported that the most important collagen ectodomain which is in triple helical conformation is type XIII collagen [259].

## 16. Collagen XIV

Collagen XIV belongs to the subclass of fibril-associated collagens with interrupted triple helices [169,170], and it is strongly present in the native human bone marrow, as shown by immunofluorescence staining and immunoblotting with an affinity-purified antibody [171]. Both collagens XIV and XII localize near the surface of banded collagen fibrils [172]. Collagen XIV is a fibril-associated collagen with interrupted triple helices which can be found mainly in articular cartilage, cornea, tendon, and the skin [260], and it can adhere to fibrillar collagen to regulate fibrillogenesis by limiting the collagen fibril diameter [261]. It can prevent the lateral fusion of adjacent fibrils [261,262], and it can bind to the dermatan sulfate chain of decorin and to the heparan sulfate chain of perlecan [263]. Its expression is highest during development, but it is also co-distributed with type I collagen in adult tissues [264–266]. It consists of three α1(XIV) chains [264], and each α1(XIV) chain is composed of two collagenous domains, namely COL2 and COL, with three non-collagenous NC1-NC3 domains [264]. It is present in tissue areas with high mechanical stress, showing that it provides important mechanical characteristics to tissues [265]. It is reported that increased type XIV collagen expression has been indicated in the progression of lung fibrosis and metastatic colon cancer [265]. It plays a significant regulatory role in early stages of collagen fibrillogenesis with tissue differences [266], and it has an important function in corneal development with an important role in the adult cornea [265,266].

## 17. Collagen XV

Human collagen XV is a homotrimer with α chains consisting of 1363 amino acid residues, including a highly interrupted collagenous domain of 577 amino acids. It shares structural homology with collagen XVIII, with the highest similarity in the C-terminal non-collagenous domain, known as the endostatin domain [267]. It is a nonfibrillar basement membrane-associated collagen [268]. It is produced mainly by endothelial cells, muscle cells, and fibroblasts, and it is basically located in the basement membrane zones of cardiac,

microvessels, and skeletal myocytes [269]. Collagens XVIII and XV are very similar, and both are the members of the multiplexin collagen family [269]. The maximum level of sequence homology between types XVIII and XV is located in the NC1 domain [269]. It is reported that collagen XV may have important function in the invasiveness of tumors due to its ductal carcinomas and adenocarcinomas, and it may inhibit the migration and adhesion of fibrosarcoma cells when available in fibronectin-containing matrices [270]. Its expression is widespread in the basement membrane zones of various internal organs, such as testis, ovary, skeletal, heart, kidney, adrenal gland, and placenta [271], and the human gene for the α1 chain of type XV collagen is around 145 kilobases in size with around 42 exons. The NC1 domains of both types are organized into an N-terminal trimerization domain [272]. The high stability, solubility, expression level, and its small size of its trimerization domain make it appropriate for engineering homotrimeric antibodies for cancer therapy and detection [273,274]. It has notable functions in the neuromuscular and cardiovascular systems [274]. It can enhance adhesion of cells to collagen L, and its gene and its human counterpart can be found in the chromosomal segments with conserved syntenies [274,275].

## 18. Collagen XVI

Nonfibrillar collagens such as XXV, XVII, and XIII appear to localize at the cell surface, and they have transmembrane domains [276]. It is part of the family of fibril-associated collagens with interrupted triple helices [277]. It is synthesized by different cell types such as myofibroblasts, chondrocytes, smooth muscle cells, keratinocytes, dendrocytes, and fibroblasts [277]. It is observed that the collagen type XVI is regulated by TGF-β and bFGF in a manner very similar to the regulation of collagen I in arterial smooth muscle cells and human dermal fibroblasts [278]. Collagen XVI can also act as a substrate for invasion and adhesion of connective tissue tumor cells, altering the cell−matrix interaction and induce a proliferative tumor phenotype by increasing an early S-phase entry [279]. It is expressed in different tissues such as kidney, arterial walls, lung, intestine, heart, cartilage, and skin [280]. Its major functions are anchoring microfibrils to the basement membrane, organize the extracellular matrix by focal adhesions and collagen fibrils and mediate intracellular signaling which can influence cell invasiveness, proliferation, adhesion, and the formation of focal adhesions [281]. It is integrated into particular fibrillin-rich microfibrils in skin which lacks an amorphous elastin core [282], and it is a component of small heterotypic D-banded fibrils, basically found in the territorial matrix of chondrocytes in cartilage [282]. Collagen XVI may show collagenous constituents in the extracellular matrix and may play an important role in the structural integrity of different tissues [283], and it is a transmembrane protein which mediates skin homeostasis [283].

## 19. Collagen XVII

It is a hemidesmosomal anchorage molecule of basal keratinocytes which increases stable epidermal−dermal adhesion [284], and it has function in epithelial hemidesmosomes of colonic mucosa, skin, brain, cornea, placenta, and kidney with different binding partners [285]. COL15 is the largest collagenous domain of type XVII, which has been reported as a cell adhesion domain [284,285], and it keeps the linkage between extracellular and intracellular structures [286]. Its ectodomain, part of its transmembrane molecule, includes a series of collagen-like repeats which is related to homotrimeric structures [286], and the intracellular domain binds to bullous pemphigoid antigen, integrin α6β4, and plectin [287]. As a structural transmembrane component of the hemidesmosomes, collagen XVII keeps stable dermis−epidermis adhesion and is traditionally linked with the pathogenesis of blistering skin disease [288]. It is abundant in the epidermis, which is an ectodermal deriva-

tive [289], and it consists of three 180 kDa α1 (XVII) chains, each containing an intracellular N-terminal domain with a short transmembrane stretch [289]. One of the main characteristics of collagen XVII is the constitutive release of its collagenous ectodomain from the cell surface [290]. Collagen XVII directly binds to collagen IV at the basement membrane zone in both oral mucosa and skin [291]. As it is a transmembrane hemidesmosomal protein of basal keratinocytes, the changed expression of collagen XVII is linked with melanoma progression [292]. Mutations in type XVII collagen can induce epithelial recurrent erosion dystrophy disease with recurrent corneal erosions and junctional epidermolysis bullosa with skin blistering [293], and collagen XVII plays a role in various cancers in relations to proliferation, migration, and overall survival of the patients [293,294]. It is an autoantigen in bullous pemphigoid, a blistering skin disease [293,294], and it is discovered to be linked with the maintenance of EMT phenotypes and metastasis capability in lung cancer stem cells [295]. Its integrin-β1 activity can increase contact following collective invasion and is localized to the intercellular site in a cancer cell population [296]. In addition, COL17A1 is highly expressed in hair follicle stem cells and involved in hair-follicle-associated pluripotent (HAP) stem cell differentiation [297].

## 20. Collagen XVIII

Collagen XVIII is in the regression of vasa hyaloidea propria, while collagen XV plays an important role in the tunica vasculosa lentis regression procedure [298]. On the basis of reports on fragments, collagens XVIII and XV have a similar binding repertoire for extracellular matrix proteins, but they have differences in basement membrane zones and the immunohistological localization in vessel walls [298]. It is known by three variants N termini, a C-terminal antiangiogenic domain known as endostatin, and an interrupted collagenous domain [299]. It is reported that mutations in human collagen XVIII may induce occipital encephalocele in Knobloch syndrome, macular abnormalities, and vitreoretinal degeneration [300]. Collagen type XVIII was found to be a ubiquitous basement membrane ingredient, occurring prominently at epithelial and vascular basement membranes throughout the body [300,301]. It possesses features of proteoglycans and collagens which are localized in different basement membrane zones, and it can inhibit tumor growth and angiogenesis [302]. Its absence may cause distinct ultrastructural defects of nephrons [302,303]. Collagen XVIII isoforms have various spatial and temporal expression patterns during renal development [303,304], and its isoforms vary in their N-terminal domains; however, they have a common C-terminal anti-angiogenic endostatin domain [305]. The long isoform is available in the liver, and the short isoform is available in epithelial and vascular basement membrane structures [305]. It plays an important role in maintaining basement membrane integrity and has positive function in eye development [306]. It is abundant in basal laminae of epidermis, retina, cardiac, pia, striated muscle, lung, blood vessels, and kidney [306], and it can influence the skin structural characteristics, resulting in decreased wrinkles, increased surface homogeneity, and improved skin elasticity [307].

## 21. Collagen XIX

Collagen type XIX is a collagen which is linked with the basement membrane zone [300,301], and it can bind to αvβ3 integrin, reducing the phosphorylation of proteins which are active in the FAK/PI3K/Akt/mTOR pathway [301]. It is a member of the fibril-associated collagens with the interrupted triple helices (FACIT) family [308]. It can organize the ECM through its ability to manage as a cross-bridge between other ECM molecules and fibrils [309]. It is a homotrimer composed of three α1 chains and is expressed in mesenchymal, neuronal, vascular, and epithelial basement membrane zones in spleen, skin, skeletal muscle, prostate, placenta, liver, kidney, colon, and breast [310]. It is also

active in the development of muscle tissue of the heart and esophagus as well as the brain [310].

## 22. Collagen XX

It is assigned to the fibril-associated collagens with the interrupted triple helices collagen subfamily because of its similarities with type XIV and XII collagens [311]. It consists of a von Willebrand factor A domain, six fibronectin type III repeat domains, two triple-helical domains, and a laminin G-like domain [312].

## 23. Collagen XXI

It belongs to the family of fibril-associated collagens with interrupted triple helices [313], and it serves as a molecular bridge between different extracellular matrix proteins and collagen fibrils [314]. It is expressed in lymph nodes, pancreas, lung, kidney, skeletal muscle, jejunum, stomach, placenta, and heart [314].

## 24. Collagen XXII

As the minor collagen, it belongs to the family of fibril-associated collagens with interrupted triple helices [315], and it is usually expressed at the basement membrane zones of tissue junctions in cartilage, heart, skin, and muscle [316]. It helps stabilize the junctions by binding to integrins $\alpha 11\beta 1$ and $\alpha 2\beta 1$ [317]. It plays an important role in cancer treatment, keeping vascular stability, and supporting tissue development [316,317].

## 25. Collagen XXIII

It is a type II transmembrane collagen [318], which can be identified in mouse tissues and healthy human tissues of tendon, skin, cornea, and lung [318]. It plays an important role in the polarization of epithelial cells and keeps the formation of cell−cell contacts [319]. It plays an important role in diagnosis of certain kinds of cancer [320].

## 26. Collagen XXV

Collagen XXV belongs to the membrane collagen subgroup, and it is basically expressed in the neurons of the brain, different tissues of the eye testis, and the heart [321]. Collagen XXV is vital during early muscle and brain development.

## 27. Collagen XXVI

Collagen XXVI includes a collagenous domain in its structure; however, it does not fit squarely within any of the collagen family subgroups [322]. It has a connection with modeling and generation of tissue, and its primers are mainly formed from the intermolecular disulfide bonds between NC1 regions [322]. No mutations or biomarkers have been found so far for this protein [322].

## 28. Collagen XXIV

Collagens XXVI, XXIV, XXVII, XXVIII, and XXIX are fibril-associated collagens with interrupted triple helices (FACIT), which associate with the surface of the collagen fibrils, and modify their interactive characteristics [323]. Collagens support soft tissues and cardiovascular components [324]. Collagen XXIV is a fibrillar collagen including three non-collagenous domains and two collagenous domains [325]. It is commonly expressed in the formation of bone, as well as the ovary, testis, lung, liver, spleen, kidneys, muscle, and brain [326]. It can be as a marker of osteoblast differentiation [327], and it consists of a long triple helical domain flanked by typical propeptide-like sequences [328]. It is also

suggested that collagen XXIV, as an ancient molecule, may play an important role in the regulation of type I collagen fibrillogenesis [329].

## 29. Collagen XXVII

It is reported that collagens XXVII and XXIV are likely to form distinct homotrimers [324,330]. Collagen XXVIII is commonly found in low levels in healthy lung tissue; however, its expression is enhanced in a bleomycin-induced lung injury model, and it plays an important role in damage repair [331]. It is a fibrillar collagen, which has a different molecular structure than other fibrillar collagens [332,333]. In its structure, it has no N-terminal telopeptide-like region and has a minor triple-helical domain [334]. Steel syndrome is a disease that is definitively connected to mutations in the type XXVII collagen gene [335,336]. Collagen type XXVII has significant function during the calcification of cartilage and during the transition from cartilage to bone [336].

## 30. Collagen XXVIII

It is reported that collagens XXVII and XXIV are likely to form distinct homotrimers [324,330]. Collagen XXVIII is commonly found in low levels in healthy lung tissue; however, its expression is enhanced in a bleomycin-induced lung injury model, and it plays an important role in damage repair [331]. Its structure is similar to collagen type VI [337]. It is located in dorsal root ganglia and in peripheral nerves surrounding most non-myelinating glial cells [337]. It can be found in skin calvaria, and it is also located in murine lungs related to basement membranes [338].

## 31. Collagen XXIX

Collagen XXIX belongs to the group of collagens consisting of von Willebrand factor type A domains [339], and it plays a significant role in protein−ligand interactions for the organization of cell adhesion and tissue architecture [340].

## 32. The Main System of Recombinant Collagen Expression and Its Expression Research Status

The application of recombinant human collagens in medicine and research, as well as cosmetic, food, and drug industries, offers a promising alternative to the application of collagen materials. Due to its considerable structure, collagen has exceptional degradability, hemostasis, and biocompatibility characteristics, which is widely applied tissue repair in cartilage, bone, teeth, skin, cornea, neurons, and different other aspects [341]. It stands as the predominant protein in vertebrates and includes around 25% of the total proteins of vertebrates [342], which is also characterized by its fibrous structure, and its capability to break down in an environmentally friendly manner [341–346]. The advantage of collagen synthesis has been shown by different studies, and researchers have reported less joint pain perception after collagen peptide application in patients with osteoarthritis [347–349]. Collagen peptides have been found to show significant physiological functions with a positive effect on health, and various studies have shown the recovery of lost cartilage tissue, an improvement in skin elasticity, strengthened tendons and ligaments, reduced activity-related joint pain, increased bone mineral density in postmenopausal women, and enhanced lean body mass in premenopausal women and elderly men [350–352]. Important types of recombinant human-like collagen and natural collagen are allergenicity, affinity, production technology, biological activity, security, and purity. The expression systems of recombinant collagen usually fall into the following groups: microbial expression systems including *E. coli* (prokaryotic), eukaryotic expression systems, animals, and plant expression systems [347–350]. *E. coli* expression currently stands as the foremost prokaryotic cell

expression system utilized in the production of recombinant proteins, and its advantages include a well-defined genetic background, an exhaustive range of commercial vectors and strains, an intricate regulatory mechanism, cost-effectiveness, a short growth cycle, and exceptional expression effectiveness. However, there are also some deficiencies related to the *E. coli* expression system, such as the inability to glycosylate proteins, low biological activity, formation of insoluble inclusion bodies because of insufficient secretion capacity, and the arduous task of eradicating endotoxins it generates [350–364]. The yeast expression system shows different benefits including the absence of endotoxin, the ability for large-scale high-density culture, simplicity in operation, and cost-effectiveness [351–353]. Animal and plant expression systems commonly use host cells including insect cells, mammalian mouse cells, and silkworm cells for animal expression systems, and the advantage of the insect expression system is that the recombinant collagen retains its complete protein structure and biological activity, can accept the insertion of large fragments of foreign genes and enables extracellular protein expression. However, the disadvantages are also considerable such as glycosylation which is different from that of mammals, high cost, and limited protein expression [353–355].

Some examples of experimental protein replacement techniques with the application of recombinant collagens are collagen VII for dystrophic epidermolysis bullosa in which intravenous or intradermal delivery of recombinant collagen VII into mice was checked [353,354], and systemic delivery for collagen IV for Alport syndrome [354]. Although significant progress has been made to produce and design recombinant collagens with collagen-derived constructs and native structures, the proteins have not advanced very well in the clinical marketplace, as there is no clear consensus on a system for large-scale recombinant collagen production that meets the regulatory factors responsible for approval in commercial clinical applications. Additionally, there is no consensus on the most related forms of recombinant collagens needed in the market, and there is still no recognizable leading product which could attract the attention of the market. While tissue engineering is still a promising application for recombinant collagen variants, its potential has not been fully realized in novel recombinant collagen-based materials in different ways [353,354]. In tissue engineering applications, recombinant collagen biomaterials have been widely studied for skin regeneration because of their natural abundance of collagen in the dermis, as collagen hydrogels promote wound healing by stimulating cell proliferation, migration, angiogenesis, and collagen deposition [351–354].

Various tissue engineering techniques for recombinant human collagens focus on stroma regeneration, which can promote skin regeneration, support cell differentiation, and proliferation. It can be used to construct different tissue scaffolds for wound treatment, which can provide unique biocompatibility and cell adhesion and increase wound healing; for 3D printing which has potential to create personalized implants and can create complex and patient-specific structures. In orthopedics, it is appropriate for immune response, stimulating bone growth, is applied for bone tissue techniques and offers high bioresorbability and biocompatibility [352]. Important points of physicochemical identifications of recombinant collagens are shown in Table 3. Important points of recombinant human-like collagens and natural collagens are shown in Table 4. Various tissue engineering techniques for recombinant human collagens are shown in Table 5.

Bio-production of recombinant collagens still suffer from high cost and low yield, and the products are unable to obtain the same post-translational changes seen in native collagens, which makes current recombinant collagens both non-biological and expensive. Therefore, new and trustable bio-manufacturing techniques are needed to make economical large-scale manufacturing of recombinant collagens suitable for future studies [353]. It is also important to study and design a versatile platform to analyze tissue-specific cellular

interactions by applying collagen type I scaffolds with highly tunable biophysical characteristics, as the kinetics of collagen fibrillogenesis are stimulated via a combination of varied pH and shear rate during neutralization to obtain a broad range of fibril diameter, porosity, anisotropy, and storage modulus. The function of each of these properties in guiding vascular, bone, and muscle cell types is well recognized and evaluated in vitro during the generation of various distinct musculoskeletal engineered constructs.

**Table 3.** Survey on physicochemical identifications of recombinant collagens.

| Physiochemical Items | Identified Methods | Requirements |
|---|---|---|
| Visible foreign substance | Light inspection | No obvious foreign substance |
| Appearance | Visual identification | White/like-white powder or sponges in the solid state; white/yellow or transparent liquids or gels |
| Moisture content | Thermogravimetry analysis | Meeting the technical requirement |
| Solubility | Visual identification | The solubility should be elaborated and characterized. |
| pH | pH meter | Meeting the technical requirements |
| Residue on ignition | High-temperature burning | Meeting the technical requirements |
| Quantity | - | Meeting the technical requirements |
| Thermal stability | Differential scanning calorimetry | No gelation of visible floc |
| Dynamic viscosity | Rotational viscometer method | Meeting the technical requirements |

**Table 4.** Important points of recombinant human-like collagens and natural collagens.

| Types | Recombinant Human-like Collagen | Natural Collagen |
|---|---|---|
| Allergenicity | Low allergy risk | High allergy risk |
| Affinity | High | Weak |
| Production technology | Bio-fabrication | Chemical extraction |
| Biological activity | High | Low |
| Security | Virus-free | Vulnerable to animal viruses |
| Purity | Single collagen, fixed composition, and $\leq$ 95% purity | Mixed collagen and complex composition |

**Table 5.** Various tissue engineering techniques for recombinant human collagens [352].

| Application | Challenges | Advantages |
|---|---|---|
| Stroma regeneration | Control over mechanical characteristics can be challenging.<br>Possible immunogenicity | It promotes skin regeneration<br>It can be used to construct different tissue scaffolds.<br>It can support cell differentiation and proliferation. |
| Wound treatment | Cost of purification and production can be high.<br>Potential for immune response | It can be fabricated into different forms.<br>It can provide unique biocompatibility and cell adhesion.<br>It can enhance wound healing. |
| 3D printing | It needs a specialized 3D printing process.<br>It can control over mechanical characteristics. | It has potential to create personalized implants.<br>It can be combined with various materials to enhance its properties.<br>It can create complex and patient-specific structures. |
| Orthopedics | It is appropriate for immune response.<br>Mechanical strength can be less than some synthetic materials. | It can stimulate bone growth.<br>It can offer high bioresorbability and biocompatibility.<br>It can be applied for bone tissue techniques. |

## 33. Necessary Factors for the Formation of Collagen Structure: Proline Hydroxylation and Glycosylation

The major common factor of all collagens is their noticeable structural element which is the collagen triple helix [354], also known as a triple-helical domain [354]. The tiple-helical domain of type I collagen has a semi-rigid rod-like structure of about 1.5 nm width and 300 nm length [354]. It is important to consider the dual functions of collagens in the ECM, acting as both signaling molecules in matricellular communications and structural components [354,355]. Its defining characteristic is an elegant structural motif in which three parallel polypeptide strands, in a left-handed, polyproline II-type helical conformation, coil about each other with a one-residue stagger to form a right-handed triple helix.

The post-translational modifications of a collagen single chain start with hydroxylation or proline and lysine residues, which thermally stabilizes the triple helix [355], and after that, some of the formed hydroxylysine (Hyl) residues are glycosylated. Then, the unique glycosylation of collagen includes linking β-D-galactopyranose via β-linkage to Hyl and

adding glucopyranose to the C2 position of galactopyranose by α-linkage [356]. It is also reported that collagen glycosylation was associated with autoimmune diseases like systemic sclerosis, rheumatoid arthritis, and cancer [356].

Higher stability of the collagen structure can be related to the capability of new dimethyl sulfoxide (DMSO) to simultaneously change both resin components and biological components within the hybrid layer [357]. Proline hydroxylation is extensively found post-translational modification with collagen being the pre-eminent sample [356,357], and the hydroxylation of proline is commonly discovered in conotoxins which are the main component of many samples [358–360]. The position of glycosylated hydroxylysine, which is clarified by comprehensive liquid chromatography (LC)/MS analysis, can provide clear insights into the physiological function of the various modifications. The lysine (Lys) hydroxylation pattern of collagen type I produced by fibroblasts is domain-specific within the collagen molecule, which is an appropriate method to characterize the cell phenotypes in pathological/normal connective tissues [357–360]. The new sustainable technique for solubilizing collagen provides a direct method for preparing active and essential low-molecular-weight collagen peptides directly from collagen in a single step, which can enable the sustainable dissolution of collagen, exposing aromatic amino acid residues with obvious antibacterial activity [360,361]. Collagen gradient membranes showed a dense outer layer and a loose inner layer, as membranes had good porosity, strong mechanical properties, and hydrophilicity [360,361]. In another experiment, N-hydroxysuccinimide-activated suberic acid (NHS-SA)-crosslinked assembled collagen fibers (NACFs) implant showed promising results in collagen regeneration, which present its importance in advancing skin rejuvenation therapies. The structure of collagen may regulate affinity and the extent of the binding under flow of plasma constituents such as the Willebrand factor. Mutations can also influence collagen fiber structure, formation, as well as function, which can result in different bone pathologies, highlighting the significance of collagen in maintaining healthy bone tissue.

It is believed that fibril formation happens more readily on more hydrophobic surfaces, which is attributed to a higher mobility of individual molecules adsorbed on more hydrophobic substances [359–361]. The rate of fibrillogenesis of the collagen−DNA complex associates to the DNA structure, and the spatial distribution of collagen and DNA in the complexes shows that the characteristic collagen−DNA interaction relates to the DNA forms [361,362]. It is also confirmed that collagen undergoes conformational alterations related to pH changes during disease as it is the main component of the extracellular matrix, and more research on this topic can help to better understand how pH changes can be modulated to restore healthy collagen characteristics [360–362]. Post-translational modifications of collagen, namely *N*-glycosylation, the *O*-glycosylation of Hyl, lysine and proline hydroxylation, the oxidative deamination of Hyl and Lys residues in the telopeptide domains, and following inter- and intramolecular covalent cross-linking are important characteristics of collagen are important characteristics of collagen [360–362]. Moreover, the hydroxylation of proline in positions 3 and 4 is essential for the stability of the triple-helical structure, while the hydroxylation of lysine residues is needed for subsequent glycosylation [361–364].

## 34. Conclusions

Collagens are divided into two groups: fibrillar collagens, such as collagens I, II, III, V, XI, XIV, and XXVII, and non-fibrillar collagens, such as collagens IV, VII, VI, XXVIII, XXIX, VIII, X, XIII, XVII, XXIII, XXV, IX, XII, XIV, XVI, XIX, XX, XXI, XXII, XXVI, XV, and XVIII. The most abundant structural protein in vertebrates is collagen type I, which is a heterotrimeric molecule composed of one α1 chains and one α2 chain, forming a long uninterrupted triple helical structure with short non-triple helical telopeptides at both the C- and N-termini. The

most ubiquitous and abundant collagen macroaggregates are the highly ordered banded fibrils made of fibrillar collagen, namely collagens XI, V, I, II, and III, which share a common structure, i.e., a long triple helical domain. The significance of collagen types XVIII, XV, and XIII, known solely on the grounds of their repetitive Gly-X-Y sequence, can be only evaluated from a genetic analysis of mutations in the respective genes. The location of collagen I is in vascular ligature, cornea, tendon, bone, and skin; collagen II is in vitreous body, cartilage, and gristle; collagen III is available in reticulate, intestine, uterus, skin, and vessels; collagen V is in hair, cornea, placenta, skin, bones, and cell surfaces; collagen IV is in capillaries and forms basal lamina; collagen VI is in cornea, gristle, vessels, bones, and skin; collagen VII is in amniotic fluid, skin, bladder, and mucous membranes; collagen VIII is in gristle, vessels, bones, brain, kidneys, skin, and heart; collagen X is in gristle; collagen XI is in intervertebral disc and gristle; collagen IX is in gristle, vitreous body, and cornea; collagen XII is in tendons, skin, and gristle; collagen XIII is in skin, endothelial cells, heart, eye, and skeletal muscles; collagen XIV is in gristle, skin, tendons, bones, eye, nerves, and vessels; collagen XV is in placenta, kidneys, testicles, skin, ovaries, heart, and capillary vessels; collagen XVI is in kidneys, smooth muscle, heart, and skin; collagen XVII is in skin; collagen XVIII is in lungs, liver, and kidney; collagen XIX is in prostate gland, placenta, spleen, kidneys, liver, and skin; collagen XX is in corneal epithelium; collagen XXI is in vessels, skeletal muscles, placenta, kidneys, heart, and stomach; collagen XXII is in tissue connections; collagen XXIII is in metastatic carcinogenic cells; collagen XXV is in testicles, brain, heart, and eye; collagen XXVI is in ovaries and testicles; collagen XXIV is in cornea and bones; collagen XXVII is in gristle; collagen XXVIII is in nervous system cells; and collagen XXIX is in skin. The most widespread and abundant family of collagens is presented by fibril-forming collagens, while types V and I collagen fibrils play important roles in the structural backbone of bone, types XI and II collagens usually contribute to the fibrillar matrix of articular cartilage, and type IV collagens with their significant flexible triple helix assemble into mesh-works blocked to basement membranes. Fibril-associated collagens such as collagens XIV, XII, and IX apparently have a function in regulating the diameter of collagen fibrils, and type X and VIII collagens from hexagonal networks. It is important to consider the point that all features of collagens are a triple helical conformation composed of repeats of the G-X-Y motif, in which proline and lysine usually occur at the y and x positions. During translation in the endoplasmic reticulum, selected lysine and proline residues are hydroxylated by dedicated hydroxylases, therefore yielding hydroxylysine and hydroxyproline. The formation of hydroxyproline is important to stabilize the collagen triple helix and confer its thermal stability at body temperature. Lysyl hydroxylation is active in the formation of covalent inter- and intra-molecular crosslinks, contributing to fibril formation and condensation. Hydroxylysine also acts as an acceptor for the attachment of collagen specific glycans. Microbes' expression system has a clear genetic background, strong operability, and low cost and is suitable for large-scale production; animal expression system is suitable for the expression of complete macromolecular proteins, which can be secreted and expressed, exhibit high protein activity and undergo correct advanced structure and protein modification such as glycosylation and hydroxylation; the plant expression system has a wide range of host sources and low cost with high security. It is obvious that with technological and scientific progresses, recombinant collagens will play a significant role in the large-scale collagen production, and on the basis of findings, recombinant collagens have special potential for various applications. However, more research is needed for recombinant collagens or combining the recombinant collagen with new biological materials and information to make them effective in a broad spectrum of biological fields.

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