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COMPARATIVE FEATURES OF DIFFERENT TYPES OF MUSCLE TISSUE

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Abstract. Muscle tissues are widespread in the human organism. Since their main feature is ability to contractility, their sarcoplasm (cytoplasm) contains a well-developed contractile apparatus, which can have its specific characteristics in different muscle tissues. Muscle tissues differ from each other not only in their localization and structural characteristics, but also in their origin, as well as their ability to regenerate. There are two main classifications of muscle tissues: morphological one taking into account the peculiarities of the structure of the contractile apparatus, and histogenetic one taking into account the origin of tissue. According to the morphofunctional classification, muscle tissues are divided into striated (cross-striated) and smooth. In turn, striated tissues are divided into skeletal and cardiac. The main tissue element of skeletal muscle tissue is myosymplast, which is formed during embryogenesis as a result of the fusion of myoblast cells. The main tissue element of cardiac muscle tissue are cells — cardiomyocytes, which during embryogenesis connect with each other to form fibers. The main tissue element of smooth muscle tissue are cells — smooth myocytes, which during embryonic development can migrate from different rudiments. Muscle tissue of internal organs and vessels has a mesenchymal origin, the muscles of the iris of the eyeball are neural, myoepithelial cells of glands are ectodermal. Despite the fact that the structure and origin of the muscle tissues are well studied, in recent years a lot of information has appeared from the field of molecular biology concerning their development in embryogenesis. In addition the issues of regenerative capabilities of different types of muscle tissues remain debatable. Skeletal muscle tissue shows the greatest regenerative abilities. Its regeneration is provided by satellite cells (myosatellitocytes), which isolate themselves on the surface of skeletal muscle fiber during intrauterine development, without fusing with it and preserving regenerative abilities due to the protein Pax7 expressed by myoblasts that are the precursors of myosatellitocytes. Until now, there is no unambiguous data on the regenerative capabilities of cardiomyocytes. There is controversial information in the literature about the possible role of cells c-kit+ as cardiac stem cells. However, they cannot provide full-fleged regeneration due to their small quantity in the myocardium. Smooth myocytes of blood vessels and internal organs are capable of reparative regeneration, which is provided by cells entering mitosis when smooth muscle tissue is damaged. But the question remains not fully clarified, which cells are capable of performing this function. Clarification of issues related to the regeneration of various types of muscle tissue may be of great importance for practical medicine.

Keywords: muscle tissues, structural and functional unit, the unit of contractility, muscle contraction, ultrastructural features, the motor unit, regenerative ability, histogenetic classification

СРАВНИТЕЛЬНЫЕ ОСОБЕННОСТИ РАЗЛИЧНЫХ ВИДОВ МЫШЕЧНЫХ ТКАНЕЙ

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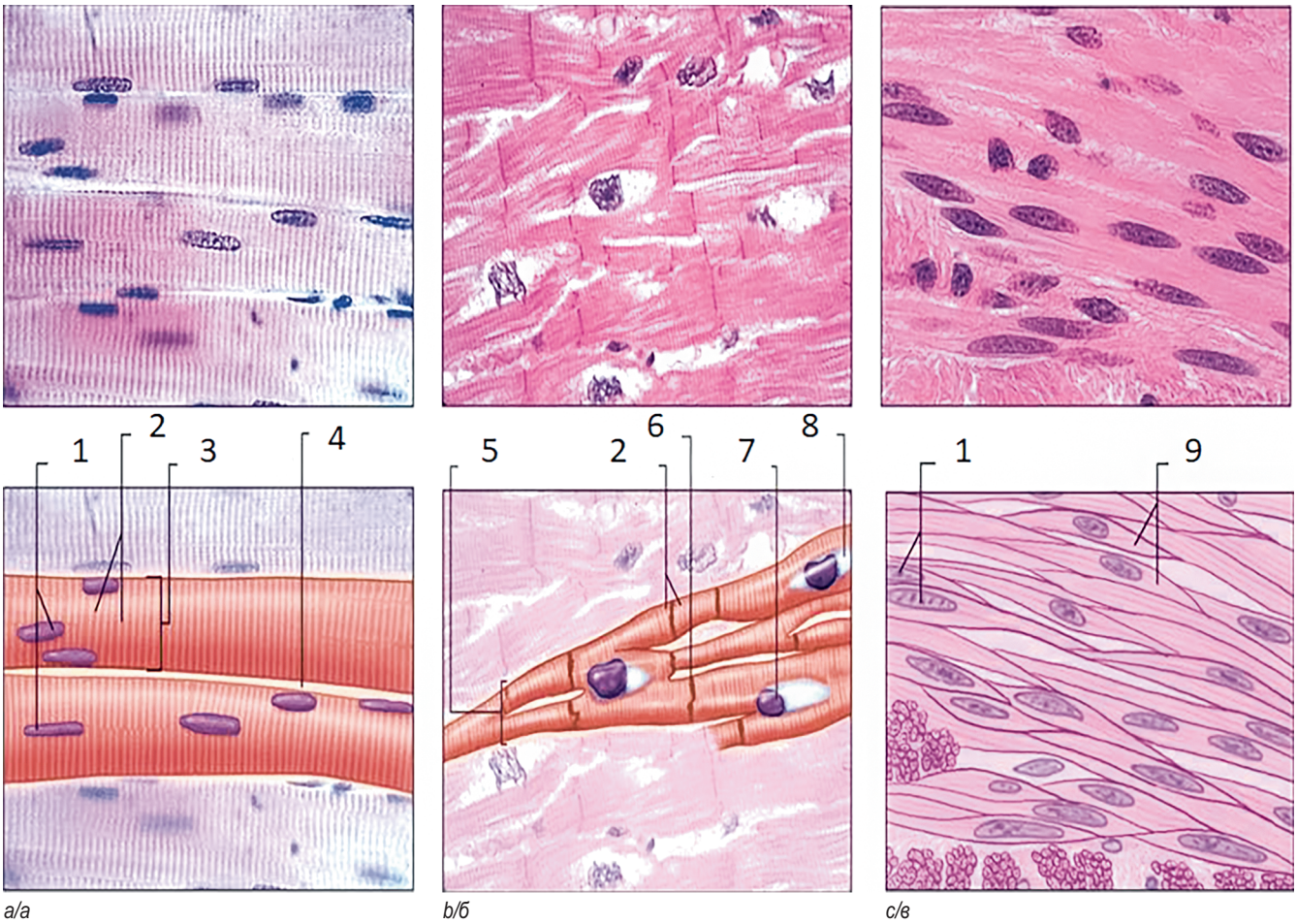
Резюме. Мышечные ткани широко распространены в организме человека. Поскольку главной их особенностью является способность к сократимости, в их саркоплазме (цитоплазме) находится хорошо развитый сократительный аппарат, который в разных мышечных тканях может иметь свои особенности. Мышечные ткани отличаются друг от друга не только своей локализацией и морфологическими характеристиками, но и происхождением, а также способностью к регенерации. Существуют две основные классификации мышечных тканей: морфологическая, учитывающая особенности строения сократительного аппарата, и гистогенетическая, учитывающая происхождение. В соответствии с морфофункциональной классификацией мышечные ткани делятся на исчерченные (поперечно-полосатые) и гладкие. В свою очередь, исчерченные подразделяются на скелетную и сердечную. Главным тканевым элементом скелетной мышечной ткани является миосимпласт, который в ходе эмбриогенеза образуется в результате слияния клеток миобластов. Главным тканевым элементом сердечной мышечной ткани являются клетки — кардиомиоциты, в ходе эмбриогенеза соединяющиеся друг с другом с формированием волокон. Главным тканевым элементом гладкой мышечной ткани являются клетки — гладкие миоциты, которые в ходе эмбрионального развития могут выселяться из разных зачатков. Мышечная ткань внутренних органов и сосудов имеет мезенхимальное происхождение, мышцы радужной оболочки глазного яблока — нейральное, миоэпителиальные клетки желез — эктодермальное. Несмотря на то что строение и происхождение мышечных тканей хорошо изучено, в последние годы появилось много информации в области молекулярной биологии, касающейся их развития именно в эмбриогенезе. Кроме того, дискутабельными остаются вопросы регенеративных возможностей различных видов мышечных тканей. Наибольшие регенеративные способности проявляет скелетная мышечная ткань. Регенерацию ее обеспечивают клетки-сателлиты (миосателлитоциты), которые обособляются на поверхности скелетного мышечного волокна в процессе внутриутробного развития, не сливаясь с ним и сохраняя регенеративный потенциал за счет белка Pax7, экспрессируемого миобластами — предшественниками миосателлитоцитов. До настоящего времени не имеется однозначных данных о регенеративных возможностях кардиомиоцитов. В литературе имеется спорная информация о возможной роли клеток c-kit+ в качестве кардиальных стволовых клеток. Однако они не могут обеспечить полноценную регенерацию, вследствие их незначительного количества в миокарде. Гладкие миоциты сосудов и внутренних органов способны к репаративной регенерации, которая обеспечивается клетками, вступающими в митоз при повреждении гладкой мышечной ткани. Но остается не до конца выясненным вопрос, какие именно клетки способны выполнять эту функцию. Уточнение вопросов, связанных с регенерацией различных видов мышечных тканей, может иметь большое значение для практической медицины.

Ключевые слова: мышечные ткани, структурно-функциональная единица, единица сократимости, мышечное сокращение, ультраструктурные особенности, двигательная единица, регенеративная способность, гистогенетическая классификация

INTRODUCTION

Muscle tissues are united by a common function — the ability to contract and the associated morphological feature (the presence of certain organelles in the cytoplasm that ensure contractility). At the same time, muscle tissues differ in the features of their contractile apparatus, origin and ability to regenerate (Fig. 1).

According to the morphofunctional classification, muscle tissues are divided into striated and smooth. Striated muscule tissues include skeletal and cardiac muscle tissues. Smooth tissues include muscle tissues of internal organs and blood vessels, muscles of the iris of the eyeball and myoepithelial cells of a number of exocrine glands.



a/а *b/б* *c/в*

Fig. 1. **The three types of muscle tissue: *a* — skeletal muscle tissue; *b* — cardiac muscle tissue; *c* — smooth muscle tissue. 1 — nuclei; 2 — striations; 3 — muscle fiber; 4 — connective tissue; 5 — anastomosis; 6 — intercalated disc; 7 — nucleus; 8 — glycogen; 9 — muscle cells [18]**

Рис. 1. **Три типа мышечных тканей: *а* — скелетная мышечная ткань; *б* — сердечная мышечная ткань; *в* — гладкая мышечная ткань. 1 — ядра; 2 — поперечная исчерченность; 3 — мышечное волокно; 4 — соединительная ткань; 5 — анастомоз; 6 — вставочный диск; 7 — ядро; 8 — гликоген; 9 — мышечные клетки [18]**

SKELETAL MUSCLE TISSUE

Such tissue is widespread in the human body, not only muscles attached to bones, but also some organs such as the esophagus, pharynx and tongue. According to the histogenetic classification, such tissue belongs to the somatic type.

Development

The source of development of this muscle tissue is the myotomes of somites. Myotome cells migrate to the sites of skeletal muscle formation. Such cells express molecular markers Pax3 and Pax7, characteristic of myoblasts and myosatellite cells [3, 7]. Migration is controlled by the genes Pax3, Met. Then myogenic cells actively proliferate under the influence of growth factors. At this stage, myogenesis is blocked by the myogenesis repressor MyoR [17].

From the 5th week of intrauterine development, myoblasts fuse to form muscle tubes, in which myofilaments are formed, from which myofibrils are assembled. After the fusion of myoblasts, DNA synthesis and nuclear division cease. Myosymplasts grow by adding new myoblasts [7]. The nuclei are initially located in the center of the muscle tube, but as the number of myofibrils increases, they shift to the periphery. In this way, relatively mature muscle fibers are formed (Fig. 2).

This occurs from the 20th week of intrauterine development. Myoblasts are isolated on the surface of muscle fibers at the G1 stage. These are myosatellite cells. *In vivo* studies on mice it has shown that the survival and proliferation of myosatellite cells is encoded by the Pax7 protein. It also prevents their fusion into muscle fiber, preserving regenerative potential [9]. *In vitro* studies also confirm the important role of this protein in myoblast survival processes [21, 22].

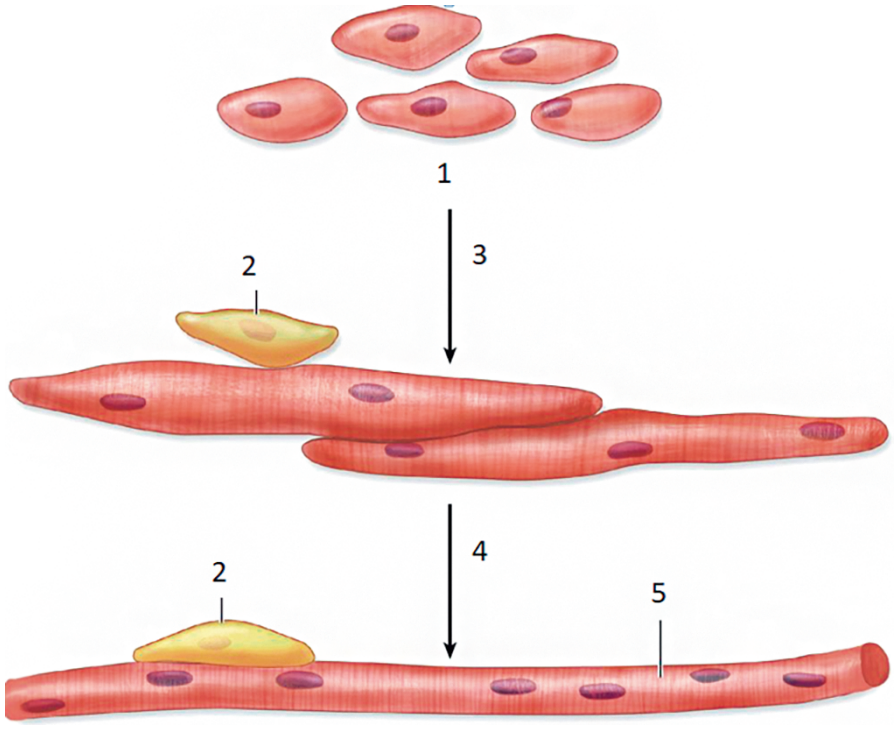
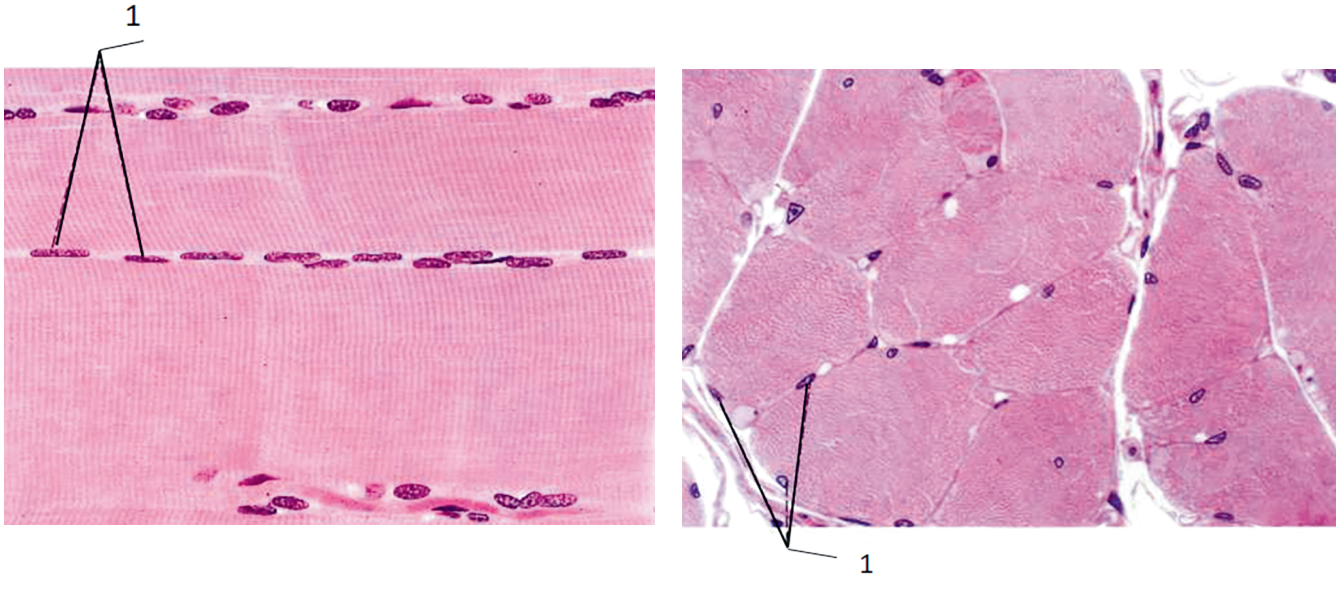


Fig. 2. **Development of skeletal muscle tissue: 1 — myoblasts; 2 — myosatellitocyte; 3 — myoblast fusion to form myotubules; 4 — differentiation; 5 — muscle fiber [24]**

Рис. 2. **Развитие скелетной мышечной ткани: 1 — миобласты; 2 — миосателлитоцит; 3 — слияние миобластов с образованием миотубул; 4 — дифференцировка; 5 — мышечное волокно [24]**



a/а *b/б*

Fig. 3. **Sceletal muscle tissue at longitudinal (*a*) and cross (*b*) section. 1 — nuclei [4]**

Рис. 3. **Скелетная мышечная ткань в продольном (*а*) и поперечном (*б*) разрезе. 1 — ядра [4]**

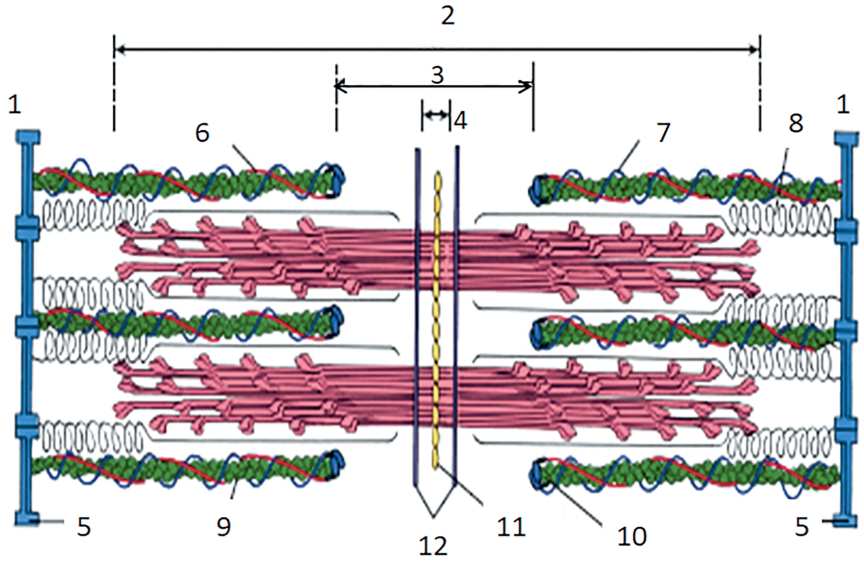


Fig. 4. **Molecular structure of a sarcomere: 1 — Z-line; 2 — A-band; 3 — H-band; 4 — M-line; 5 — α-actinin; 6 — tropomyosin; 7 — nebulin; 8 — titin; 9 — actin; 10 — tropomodulin; 11 — myomesin; 12 — C-protein [23]**

Рис. 4. **Молекулярная структура саркомера: 1 — Z-линия; 2 — A-диск; 3 — H-полоска; 4 — M-линия; 5 — α-актинин; 6 — тропомиозин; 7 — небулин; 8 — титин; 9 — актин; 10 — тропомодулин; 11 — миомезин; 12 — C-белок [23]**

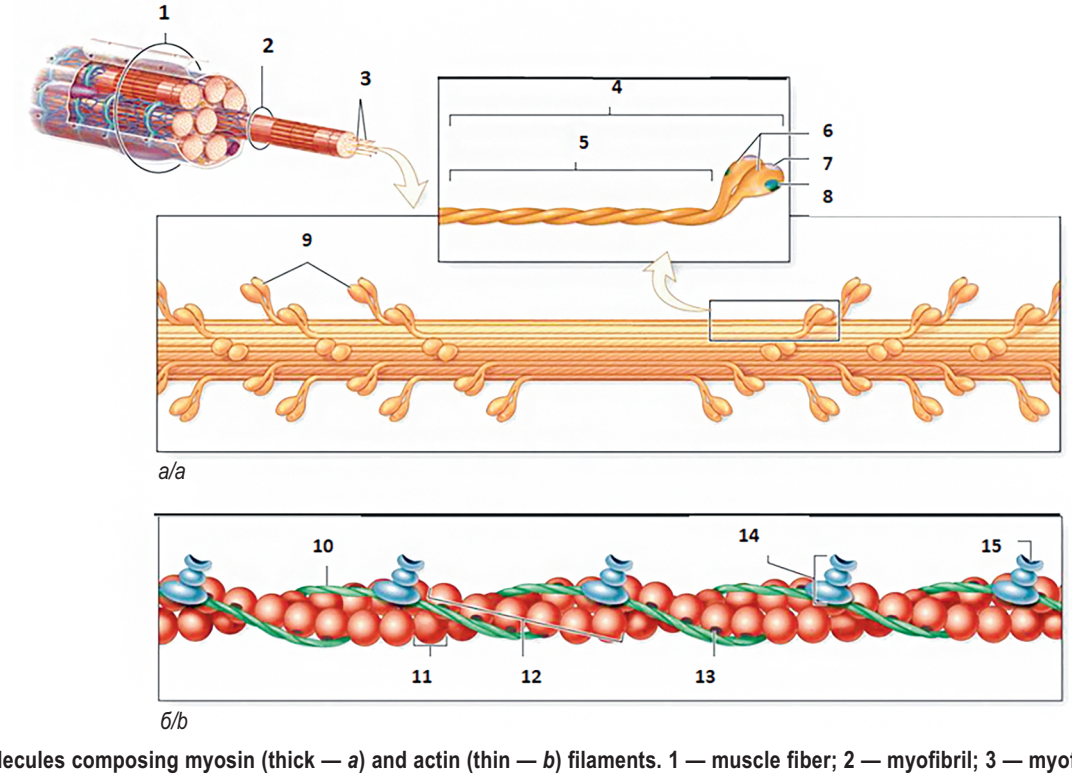


Fig. 5. **Molecules composing myosin (thick — *a*) and actin (thin — *b*) filaments. 1 — muscle fiber; 2 — myofibril; 3 — myofilaments; 4 — myosin molecule; 5 — tail; 6 — heads; 7 — actin-binding site; 8 — ATPase-binding site; 9 — myosin heads; 10 — tropomyosin; 11 — G-actin; 12 — F-actin; 13 — myosin-binding site; 14 — troponin; 15 — Ca^{2+}-binding site [18]**

Рис. 5. **Молекулы, образующие миозиновые (толстые — *а*) и актиновые (тонкие — *б*) филаменты. 1 — мышечное волокно; 2 — миофибрилла; 3 — миофиламенты; 4 — молекула миозина; 5 — хвост; 6 — головки; 7 — актинсвязывающий участок; 8 — АТФ-связывающий участок; 9 — миозиновые головки; 10 — тропомиозин; 11 — G-актин; 12 — F-актин; 13 — миозинсвязывающий сайт; 14 — тропонин; 15 — Ca^{2+}-связывающий участок [18]**

Myotubules are formed by myoblasts at the G0 stage, which have irreversibly left the cell cycle [17].

The development of skeletal muscle tissue is associated with the development of nervous tissue. During ontogenesis, it is not individual muscle fibers that develop, but motor units, represented by a motor neuron and the muscle fibers innervated by it. Thus, the development of muscle fibers is associated with the development of motor neurons [15].

Features of the structure of skeletal muscle tissue

The structural and functional unit of such tissue is the myosymplast. The cytoplasm of muscle fibers is called sarcoplasm, the plasmalemma is called sarcolemma. Each skeletal muscle fiber is represented by a myosymplast and is surrounded by a basal membrane. Between the basal membrane and the sarcolemma are myosatellite cells (Fig. 3).

The sarcoplasm of the myosymplast is characterized by a well-developed contractile apparatus. It is represented by myofibrils consisting of orderly arranged actin and myosin myofilaments. The myofibrils are located very close to each other. Each one is characterized by transverse striation associated with the alternation of isotropic (I) and anisotropic (A) disks. The disks of each myofibril are localized strictly opposite the same disks of neighboring myofibrils, due to which transverse striation of the entire muscle fiber is revealed. Anisotropic disks are represented by myosin filaments and, in an uncontracted muscle fiber, by small fragments of actin filaments. During contraction, actin filaments penetrate deeper into the spaces between the myosin filaments. Isotropic disks are represented by free fragments of actin filaments. Actin filaments consist of F-actin chains, which are two helical polymers of G-actin, resembling a twisted pearl necklace. Each groove of the F-actin helix contains tightly adjacent thread-like molecules of tropomyosin. Each tropomyosin molecule is associated with troponin, a polypeptide consisting of three subunits: troponin T, troponin I, and troponin C. Troponin I, when bound to actin, inhibits the zone in it through which actin interacts with myosin [5, 10]. In the middle of each isotropic disk is a Z-line (telophragm), which contains proteins, desmin and vimentin. The space between two telophragms is called a sarcomere. The sarcomere is considered a unit of contractility, since its length changes during muscle contraction (Fig. 4). Actin filaments are attached to the telophragm by α-actinin and nebulin. The free end of the actin filaments is coated with the protein tropomodulin.

Myosin filaments consist of 200–300 mirror-image myosin molecules. In such a molecule, heavy and light meromyosin (heavy and light parts) are distinguished. Heavy meromyosin includes two fragments: S1, represented by globular heads, and S2, represented by a linear elastic component. The S1 fragment has ATPase activity, which requires contact between the myosin heads and the active centers of the actin filaments. The terminal part of the myosin tail filament is formed by light meromyosin. Myosin has two hinge regions that allow the molecule to change conformation. One hinge region is located at the border of heavy and light meromyosins, the other is in the neck region, near the head. Light meromyosin provides aggregation of myosin molecules, while heavy meromyosin has actin-binding regions and has ATPase activity [1, 25]. Myosin molecules are assembled into aggregates in such a way that half of the heads face one end and half face the other. Myosin filaments are attached to the Z-lines by the elastic protein titin. The M-line runs through the middle of the anisotropic disk, in which the myosin filaments are linked to each other by myomesin and C-protein (Fig. 4, 5).

In addition to myofibrils, mitochondria and sarcoplasmic reticulum are well developed in the sarcoplasm.

The sarcoplasmic reticulum is a modified smooth endoplasmic reticulum that stores calcium due to the presence of the calcium-binding protein calsequestrin. The membrane of the sarcoplasmic reticulum contains integral proteins that act as calcium pumps. It surrounds each sarcomere. The sarcoplasmic reticulum is represented by anastomosing membrane tubules ending in terminal cisterns located next to the T-tubules. T-tubules are invaginations of the sarcolemma located between two terminal cisterns. Together they form a triad. Depolarization waves pass through the T-tubules to the myofibrils. Dihydropyridine receptors of T-tubules register changes in membrane potential and activate ryanodine receptors of the sarcoplasmic reticulum, followed by the release of calcium ions from the sarcoplasmic reticulum into the sarcoplasm [17].

Muscle contraction mechanism

Muscle contraction is described by the sliding filament theory. Calcium ions released from the sarcoplasmic reticulum cisterns into the sarcoplasm bind to troponin C, which causes conformational changes in the troponin-tropomyosin complex, resulting in the opening of active zones (myosin-binding zones) on actin molecules. Myosin heads attach to these zones, then the myosin heads deflect and pull actin filaments along with them, which penetrate deeper into the spaces between the myosin filaments. During this process, ATP bound to the S1 fragment of the myosin molecule is hydrolyzed. Relaxation of the muscle fiber occurs when the calcium pump pumps calcium ions from the cytosol into the sarcoplasmic reticulum system. A decrease in the calcium concentration in the cytoplasm stimulates the return of troponin C to its previous conformational state, and the tropomyosin molecule itself to its original position, closing the active center of the actin molecule [5].

Muscle fibers are characterized by different contraction speeds. This may be related to their ultrastructural features, in particular, the number of mitochondria, the density of blood capillaries, and the amount of myoglobin. Myoglobin is an oxygen-binding protein that gives muscle fibers a reddish tint, so muscle fibers containing a large amount of myoglobin are called red. Red fibers are capable of remaining in a contracted state for a long time. During prolonged muscle contraction, the lumen of blood vessels may be compressed and the transport of oxygen from the blood may be disrupted. In this case, the oxygen bound by myoglobin is consumed. Fibers containing significantly less myoglobin are called white. They exhibit the ability to contract quickly. In addition, there are intermediate fibers that have the characteristics of red and white muscle fibers.

Red muscle fibers, in addition to a large amount of myoglobin, are characterized by a large number of mitochondria and a low glycogen content. White muscle fibers are characterized by a low myoglobin content, fewer mitochondria and a high glycogen content. Intermediate fibers are characterized by a large amount of myoglobin and mitochondria and an average glycogen content [14]. Each muscle has its own unique ratio of muscle fibers.

Regeneration

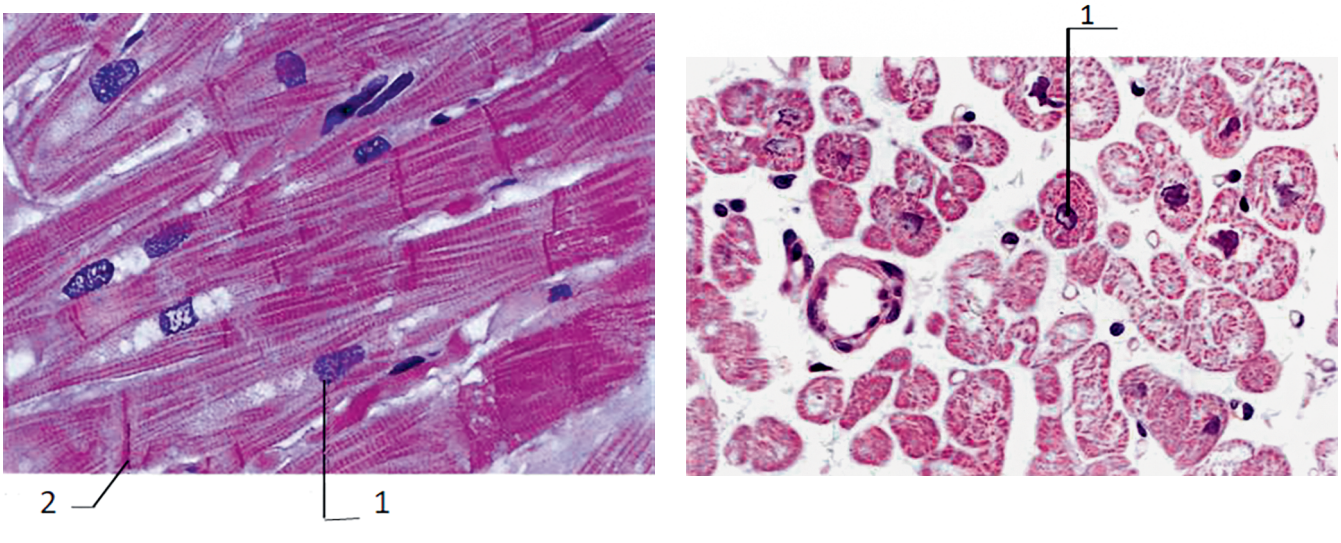
Regeneration of skeletal muscle tissue is carried out by satellite cells. The amount of transferrin increases significantly in regenerating skeletal muscle. It is assumed that transferrin and transferrin-dependent growth factor activate the proliferation of myosatellite cells. There is evidence that satellite cells themselves are capable of secreting insulin-like growth factor [7]. Animal experiments have shown that the basic fibroblast growth factor, AB and BB isoforms of platelet-derived growth factor, and beta-transforming growth factor enhance the mitotic activity of satellite cells, and insulin-like growth factors stimulate not only proliferation, but also their differentiation. The action of growth factors in various combinations is a potential mechanism for regulating the activity of myosatellite cells and can be used in medical practice [7].

CARDIAC MUSCLE TISSUE

According to histogenetic classification, it belongs to the coelomic type.

Development

Myocardial precursor cells are detected in the epiblast on the 16th day of intrauterine development. They are localized in the cranial end of the primitive streak as part of the presumptive material of the mesoderm. From there, they migrate to the middle leaflet and are subsequently located in the visceral leaflet of the splanchnotome, where they form the myoepicardial plate. It consists of two cell clusters: the primary heart field (PHF), which gives rise to the myocardium of the atria, left ventricle and part of the right ventricle, and the secondary heart field (SHF), which forms part of the right ventricle, the cardiac conus and the arterial trunk. The transcription factor NKX2.5 is key to heart development. Expression of the NKX2.5 gene is stimulated by bone



a/а *b/б*

Fig. 6. Cardiac muscle tissue. Longitudinal (*a*) and cross (*b*) section of myocardium. 1 — nucleus; 2 — intercalated disc [4]

Рис 6. Сердечная мышечная ткань. Мышечные волокна на продольном (*а*) и поперечном (*б*) разрезе. 1 — ядро; 2 — вставочный диск [4]

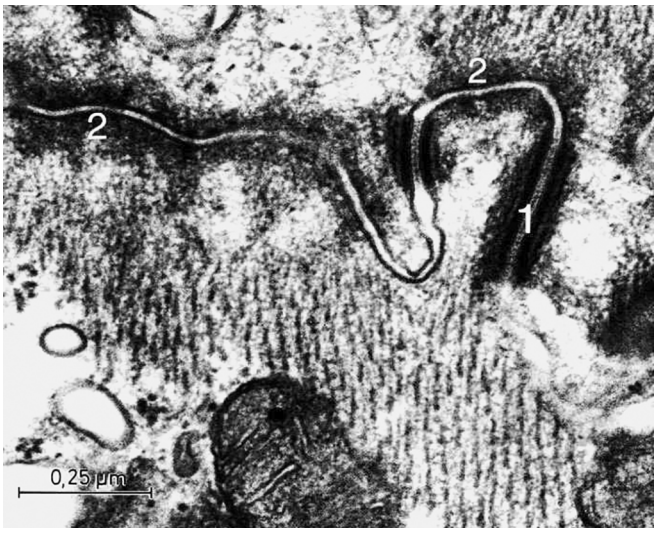


Fig. 7. Intercalated disc at high magnification (1:40 000): 1 — *macula adherens* (desmosome); 2 — *zonula adherens* [4]

Рис. 7. Вставочный диск при большом увеличении (1:40 000): 1 — десмосомы; 2 — опоясывающие десмосомы [4]

morphogenetic proteins BMP2 and BMP4 (produced in adjacent endoderm cells and acting in a paracrine manner). In addition, these morphogenetic proteins stimulate the production of fibroblast growth factor FGF8, which, in turn, is important for the expression of genes for specific cardiac proteins [11]

Features of the structure of cardiac muscle tissue

The cardiomyocyte acts as a structural and functional unit of cardiac muscle tissue. Cardiomyocytes are connected to each other, forming fibers. Unlike skeletal muscle tissue, there is a division into cells inside the cardiac muscle fiber (Fig. 6).

The contact sites between adjacent cardiomyocytes are called intercalated discs. Electron micrographs show that the intercalated disc area is uneven, because cardiomyocytes form numerous interdigitations connected by connections such as desmosomes, encircling desmosomes, and gap junctions (Fig. 7). The latter provide ionic communication between cells, thereby facilitating their combined contraction. Cardiac muscle fibers actively branch and anastomose.

There are different types of cardiomyocytes — contractile, atypical, secretory. In this lecture we will talk only about contractile cardiomyocytes. Typical (contractile) cardiomyocytes are cylindrical cells of different sizes, depending on their localization (atrial or ventricular); binuclear ones are often found among them. The nucleus, unlike skeletal muscle fibers, occupies a central position. Cardiomyocytes are covered with a basal membrane located on top of the sarcolemma.

The contractile apparatus and the mechanism of muscle contraction are similar to those in skeletal muscle fibers, but the transverse striation in cardiac muscle fibers is less pronounced than in skeletal ones, which is due to the presence of intercellular boundaries within the cardiac muscle fiber and interdigitations of cardiomyocytes, due to which isotropic and anisotropic disks of neighboring cells can shift relative to each other. The sarcoplasmic reticulum is less developed than in skeletal muscle fiber, and it deposits calcium ions less actively. T-tubules are well developed in ventricular cardiomyocytes and poorly developed in atrial cardiomyocytes.

There are differences between atrial and ventricular cardiomyocytes. Ventricular ones are thicker and longer, they have more mitochondria and myofibrils, the sarcoplasmic reticulum and T-tubules are better developed. In atrial cardiomyocytes, T-tubules are less pronounced, and in some cells, caveolae (small invaginations of the sarcolemma) are found instead of them. But gap junctions are more common between atrial cardiomyocytes.

Regeneration

The proliferative capacity of cardiomyocytes is expressed only during the period of intrauterine development and in the first days after birth. Experiments on rats have shown that in the first 4 days of postnatal life, a considerable part of cardiomyocytes divides by mitosis — 60%, during the next few days — only 6-7% [6]. In vivo studies have shown that in the first 3 days after birth, the number of cardiomyocytes increases by 68%, but then this figure drops sharply [6]. Some authors believe that mitosis slows down in the G0-G1 phase, others — in the G2-M phase [6]. For a long time, it was believed that cardiac muscle tissue is completely devoid of the ability to regenerate. Later, it was established that local progenitor cells are present in all tissues, including the myocardium. However, information on the existence and functioning of stem cells in the organs of the cardiovascular system is still limited [18, 19, 21]. Recent data indicate the presence of a cellular regenerative pool in the myocardium. One type of such cells are undifferentiated stem cells c-kit+. Committed GATA-4+ cells show an early cardiomyogenic orientation and belong to the cardiomyoblastic cellular form [24]. However, there is also an opposite point of view, where the cardiomyogenic role of these cells is questioned, since they were found in granulation tissue, which was subsequently transformed into scar tissue [20]. But even if we consider c-kit+ cells as regional cardiac stem cells, they cannot ensure full myocardial regeneration, since their content in the myocardium is insignificant and cannot cover the deficit of lost cardiomyocytes after injury [12].

SMOOTH MUSCLE

Such tissue may have different origins depending on its localization: smooth muscle tissue of vessels and internal organs differentiates from mesenchyme and, according to histogenetic classification, belongs to the visceral type. Myoepitheliocytes of glands have an ectodermal origin, this muscle tissue belongs to the epidermal type. Muscle tissue of the iris of the eyeball belongs to the neural type, since it differentiates from cells of the neural rudiment (neural crests).

Visceral muscle tissue

Development

The source of development of visceral smooth muscle tissue is the mesenchyme emanating from the visceral leaf of the splanchnotome. In the dynamics of specific differentiation, smooth myocytes (leiomyocytes) go through the stages of premyoblast, myoblast, differentiating and differentiated myocytes. In the process of differentiation, the contractile apparatus develops: the volume density of filaments and dense bodies increases, the number of vesicles, while the total volume occupied by the components of the contractile apparatus increases due to a decrease in the volume occupied by other organelles. In addition, intercellular communications and neuromuscular connections develop. The processes of specific differentiation do not block DNA synthesis and cell proliferation for a long time. In the embryonic period, there is practically no growth of smooth myocytes, which is explained by their high proliferative activity. At the postnatal stage of histogenesis, the processes of reproduction and differentiation become incompatible under conditions of increasing functional load, which leads to the exit of the overwhelming majority of leiomyocytes from the reproductive cycle [8].

Structural features

The smooth myocyte acts as a structural and functional unit of smooth muscle tissue. Smooth myocytes are spindle-shaped cells with an oval, relatively large nucleus, located almost close to each other; between them there are various connections, the most common of which are gap junctions, which ensure the transfer of excitation between cells and their combined contraction. Smooth myocytes can vary in size: the smallest are located in the walls of small vessels, the largest form the myometrium. Each smooth myocyte is surrounded by a sarcolemma and a basal membrane (Fig. 8).

There are two types of smooth myocytes: secretory and contractile. The main function of secretory myocytes is protein synthesis, which is why their cytoplasm has well-developed synthesis organelles (rough endoplasmic reticulum, Golgi apparatus), while their contractile apparatus is poorly developed. Contractile smooth myocytes specialize in the contractility function and therefore have a well-developed contractile apparatus and numerous mitochondria. Unlike striated muscle fibers, the contractile apparatus here is represented by actin and myosin myofilaments that do not form myofibrils. Actin filaments are located mainly along the long axis of the cell, but can also be located obliquely. Their ends are fastened to each other and to the sarcolemma by dense bodies — cross-linking proteins and contain α-actinin. The same protein is located at the junction of actin filaments with the telophragm in skeletal muscle fibers. Actin filaments consist of smooth muscle α-actin and tropomyosin. Unlike striated muscle fibers, they do not contain troponin. Myosin in a relaxed smooth myocyte is in a monomeric form. When a smooth myocyte is stimulated by a nerve impulse or by the action of neurotransmitters, hormones and some bioactive substances, calcium channels open and the concentration of calcium ions in the cytoplasm increases. The result is the binding of calcium to calmodulin, the resulting complex activates myosin light chain kinase, an enzyme that catalyzes the phosphorylation of myosin light chains and the subsequent assembly of myosin filaments, which is a trigger for the formation of bonds between actin and myosin filaments [8].

The sarcoplasmic reticulum is expressed here less strongly than in striated muscle fibers and is represented by narrow tubes. The sarcolemma forms small invaginations, caveolae, as analogs of T-tubes. The flow of calcium ions into the sarcolemma from the sarcoplasmic reticulum entails both the polymerization of myosin and its interaction with actin, which is ensured by the same mechanisms as in

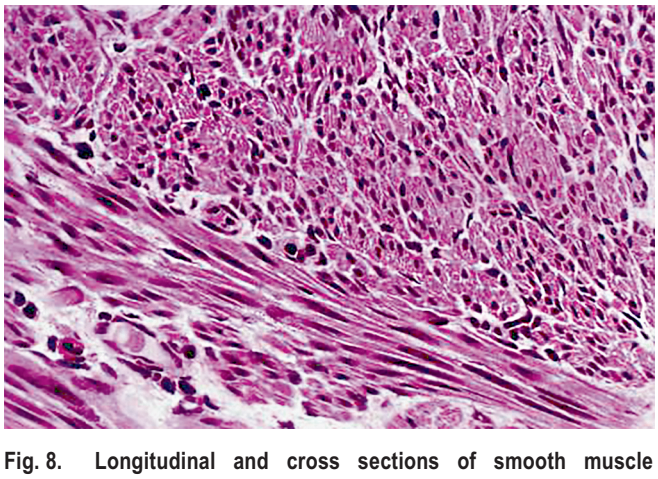


Fig. 8. Longitudinal and cross sections of smooth muscle tissue [4]

Рис. 8. Продольный и поперечный срезы гладкой мышечной ткани [4]

a/а *b/б*

Fig. 9. Smooth muscle cell relaxed (*a*) and constructed (*b*) [23]

Рис. 9. Гладкий миоцит в расслабленном (*а*) и в сокращенном состоянии (*б*) [23]

striated muscle fibers (the formation of contacts between myosin heads and active centers). Then the actin filaments are drawn in between the myosin ones, the dense bodies come together, the force is transmitted to the plasma membrane, the cell shortens and twists in a spiral, the areas of the sarcolemma to which the actin filaments are attached are drawn in, and the areas located between them bulge, so the surface of the contracted smooth myocyte is uneven (Fig. 9). Muscle relaxation occurs when the initial calcium concentration inside the cell is restored by its removal by calcium pumps. Myosin light chain kinase is inactivated by detaching from calmodulin, and myosin is dephosphorylated.

Regeneration

Smooth myocytes are rarely found in the intact definitive muscle tissue of vessels and internal organs during the division process. Proliferative activity of smooth muscle tissue is manifested in the case of its damage or with an increase in the functional load. The mechanism of regeneration of muscle tissue of vessels and internal organs has not been fully elucidated. There is evidence that these tissues contain poorly differentiated cells that can differentiate into cells capable of entering the mitotic cycle. In addition, in the case of stimulation, for example as a result of injury, cambial elements capable of entering the mitotic cycle are activated. Under the influence of damaging factors, myocytes can transform from a contractile to a synthetic (secretory) phenotype [2].

Muscle tissue of the epidermal type

This tissue is represented by myoepithelial cells, which are found in the terminal sections and small excretory ducts of the salivary, sweat and mammary glands. The cells have processes that cover the secretory cells. The contractile apparatus of myoepithelial cells is similar to that of the smooth myocyte system of the visceral type. Contraction of myoepithelial cells promotes the release of secretion from the terminal section into the excretory duct. Numerous studies have shown that myoepithelial cells develop from the same rudiment (ectoderm) as the epithelium of the glands in which they are found [13, 16]. There is no unambiguous data in the literature regarding the regeneration of myoepithelial cells. It is possible that it is carried out due to poorly differentiated epithelial cells of the terminal sections of the glands.

Muscle tissue of the neural type

The structural and functional unit of this muscle tissue is a smooth myocyte, which has a similar structure to a leiomyocyte. A feature of neural myocytes is the inclusion of melanin in the sarcoplasm. The source of the development of contractile elements of the muscle that constricts and dilates the pupil of the eye of mammals and humans are cells emanating from the edges of the optic cup. A few studies have shown low regenerative activity of this muscle tissue or its absence [7].

CONCLUSION

The tissue type of muscle tissues is distinguished by a functional feature — they are specialized in contractile function. At the same time, representatives of this type have different origins, are represented by different tissue elements, have a number of differences in structure and different regeneration abilities. Despite the fact that muscle tissues have been well studied, controversial issues still remain unresolved, primarily concerning their ability to regenerate. Actively developing molecular biology will help shed light on the solution of these issues. Knowledge of the sources of development, structural features and functioning of muscle tissues, as well as the processes of their proliferation and differentiation is of great importance for making a correct diagnosis and choosing the right treatment tactics.

ADDITIONAL INFORMATION

Author contribution. Thereby, all authors made a substantial contribution to the conception of the study, acquisition, analysis, interpretation of data for the work, drafting and revising the article, final approval of the version to be published and agree to be accountable for all aspects of the study.

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