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Evolutionary and ontogenetic transformations of contractile cells: Adaptive and regulatory mechanisms

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The appearance of muscle tissue is an important step in the evolution of animals, as it enabled them to disperse, escape, hunt, and explore new habitats. Modern contractile cells of animals form an evolutionary continuum - from the unspecialized contractile epithelium of placozoans, through the epithelium with supracellular actomyosin bundles, which are characteristic of modern sponges, to the epitheliomuscular tissues of sea anemones. The final link in this continuum was specialized muscle tissue, which has lost most or all of its epithelial properties and is represented in ctenophores, jellyfish, and bilaterians. The ontogeny of muscle tissue reflects the main stages of its phylogenetic evolution. In the course of evolution, animal muscle tissue was formed under the influence of a fundamental physiological limitation: the faster a muscle fiber contracts, the less economically it uses energy and the faster it tires. Therefore, a continuous functional series of striated fibers was formed in animals: type I → type IIa → type IIx → type IIb, which reflects a gradual transition from energy economy to maximum contraction speed. Different types of muscle fibers are not just histological variants of tissue, but different evolutionary strategies for using energy for movement. The diversity of muscle fiber types reflects a fundamental evolutionary compromise between the speed of contraction and the energy efficiency of muscle work. Within the framework of this compromise, a functional gradient of fibers from slow oxidative to maximally fast glycolytic fibers has formed, which ensures the implementation of different locomotion strategies in animals. During the evolutionary process, a general pattern of the functioning of the muscular system was formed: with an increase in the body weight of the animal, the maximum speed of muscle fiber contraction decreases. In contrast, in smaller rodents and predators, the fastest glycolytic IIb fibers dominated, providing a high frequency of movements, fast reactions to short distances of movement. Therefore, the diversity of muscle fiber types is determined not only by metabolism, but also by the allometry of the body and the mechanics of movement.

Keywords: muscle tissue; evolution; ontogenesis; types of contractile cells; adaptive mechanisms; regulatory mechanisms.

Introduction

Muscle-based locomotion is a hallmark of animal biology, but the evolutionary origin of myocytes is unknown. Muscles are present in all metazoans except sponges and placozoans. Their appearance marks an important step in evolution, as it allows organisms to disperse, escape, hunt, and explore new habitats (Jahnel et al., 2014; Shankar & Mahadevan, 2024). Cell motility is a vital feature for every biological aspect of life. For example, even before a baby is born, sperm swims in the mother's reproductive tract in search of an egg. Embryonic development of the embryo depends on the coordinated movement of layers and individual cells. The speed of leukocyte movement affects resistance to disease.Leukocytes rush to the site of injury, track down pathogens, and neutralize them. The wave-like movements of epithelial cell cilia help clear the airways. Even death can result from the movement of pathogens or the migration of metastatic cancer cells. Cell movement is divided into two main categories: flagellar motility and actin-dependent cell migration (Fritz-Laylin, 2020). It is known that some species of bacteria can move by pulling on their own cell using molecular mechanisms that function as grappling hooks (Denise et al., 2019).

Over the past five years, the problem of evolutionary and ontogenetic transformations of muscle tissue, mechanisms of its functioning and adaptive specialization has been studied in the following areas: the mechanism of regulation of contraction and relaxation (Shankar & Mahadevan, 2024); remodeling of muscle tissue (Kuibida, et al., 2021, 2022); pathways of formation of new cell types (Cole et al., 2023); origin of muscles (Zullo et al., 2020); evolutionary role of multinucleation of muscle fibers (Millay, 2022); actin-dependent cell migration (Fritz-Laylin, 2020); expression of fast and slow myosin heavy chains in *Ephydatia muelleri* (Colgren & Nichols, 2022), *Nematostella vectensis* (Cole et al., 2023), *Clytia hemisphaerica* (Chari et al., 2021), *Hydra vulgaris* (Garg et al., 2023); evolutionary and ontogenetic development and features of muscle tissue in Porifera (Colgren & Nichols, 2022), *Octopus vulgaris* (Gilly et al., 2020), *Caenorhabditis elegans* (Wang et al., 2020; Özcan & Tursun, 2023), *Drosophila melanogaster* (Boukhatmi, 2021); evolutionary specialization of pericytes (Shimizu & Kanda, 2020; Eltanahy et al., 2021), myoepithelial (Shams, 2022; Nakashima et al.,2023), myofibroblast-like (Tai et al., 2021), smooth cells (Chevalier et al., 2024; Wang et al., 2025; Fu et al., 2026), cardiac (Guo & Pu, 2020; Litviňuková et al., 2020), fast and slow striated fibers (Nuzzo, 2024; Hu et al., 2024), etc.

To date, no review has provided a comprehensive integrated treatment of the evolutionary and ontogenetic transformations of contractile cells, their diversity, specialization pathways, adaptive and regulatory adaptations. Therefore, the chosen topic of the review article is relevant because it has theoretical and practical significance. The goal is to clarify the evolutionary and ontogenetic transformations of muscle tissue, their adaptive and regulatory mechanisms. The literature search was carried out based on the above-mentioned keywords in the electronic database PubMed and others.

Cells with contractile functions are found in almost all multicellular animals. Despite their structural similarities, the origin of muscles is considered to be the result of a process of convergent evolution (Zullo et al., 2020), however, the mechanisms underlying the emergence of new cell types remain unclear (Cole et al., 2023).

Evolution and adaptive capabilities of contractile function in the process of phylogenetic development

Early in evolution, epithelia served as sealing, sensing, and contractile functions. The division of functions initiated and led to the formation of specialized epithelial, sensory, nerve, and muscle cells (Rieger & Ladurner, 2003). Eukaryotic cells use a variety of mechanisms to swim in fluids or crawl on solid surfaces. Flagellar swimming and actin-dependent cell migration are used by animal cells and unicellu-

lar eukaryotes. Both forms of movement involve myosin II (Fritz-Laylin, 2020). The spatial and temporal coordination of the assembly and activity of actomyosin networks in multiple cells was the first key innovation. The emergence of muscle cells and the evolution of completely new genes (titin, troponin, and myoD) in bilateral striated muscles is the second (Steinmetz et al., 2012; Brunet, 2023).

The split between visceral smooth myocytes and somatic striated myocytes was the result of a long process of individuation that began before the emergence of the last common protostome/deuterostome ancestor. Fast- and slow-twitch cells expressing different variants of the myosin II heavy chain (ST-MHC vs. SM-MHC) gradually acquired increasingly contrasting molecular profiles, and this process of divergence continues to this day in separate bilateral types. Blurring this pattern of divergence, co-optation events led to the random replacement of the slow-twitch module by the fast-twitch module, leading to the transformation of smooth myocytes into striated ones (Brunet et al., 2016).

Premetazoan functions of the actin+myosin complex existed in unicellular eukaryotes, long before the emergence of multicellular organisms. The last common ancestor of eukaryotes already had a complex cell with some genomic and cellular features, including: motility, spliceosomal introns, mitochondria, cytoskeleton and several intracellular transport systems. Myosins of the common ancestor of eukaryotes differed significantly from myosins of modern eukaryotes, but a unified picture of their evolution has not yet been formed. Contractile actomyosin networks depend on the interaction of F-actin and myosin II. Myosin II is part of a large class of myosin molecular motors that are present in all eukaryotes and are currently classified into 79 families (Kollmar & Mühlhausen 2017). Most myosin families are monomeric and do not form filaments. They mediate the anchoring or transport of vesicles or organelles on the F-actin cytoskeleton. Myosin II and its close relative myosin V are able to form dimers with two motor heads. Myosin II is unique in that it can assemble into bipolar filaments that are capable of contracting actomyosin networks. The assembly of myosin II into filaments and its contractile activity are modulated by phosphorylation, as has been reported in all amorphous organisms studied (Hartman & Spudich 2012; Levayer & Lecuit 2012). In protists, myosin II provides the final stage of cell division, during which one cell physically divides into two daughter cells (Brunet, 2023). The transformation of actomyosin into a multicellular contractile apparatus was not a simple matter of “scaling up.” Prerequisites for each origin of multicellularity were the evolution of mechanisms for stable cell-to-cell adhesion or attachment (Abedin & King, 2010) and the evolution of intercellular communication to coordinate contractions in space and time through mechanically driven cell deformation cycling (Bailles et al., 2019) or serotonin signaling (Karki et al., 2023).

Choanoflagellates are considered an evolutionary bridge between unicellular organisms and multicellular animals. Apical and basal contractile poles in choanoflagellates were probably present in their last common ancestor with animals. In animals, the apical contractile field evolved into actomyosin, as well as a medioapical actomyosin network, which together contribute to epithelial cohesion and collective apical constriction. Basal contractile fibers containing either NM/SM-MyHC or ST-MyHC expanded into myonemes, giving rise to epithelial muscle cells. A subset of these cells eventually lost their epithelial features and transformed into muscle cells. In some cases, the cells developed striation. Both transitions probably occurred several times independently in different lineages (Brunet, 2023).

Based on the analysis of literature sources, we expanded the list of cells proposed (Brunet, 2023) and identified some new groups of living organisms and cells that express the fast/striated and slow / smooth myosin heavy chain (Table 1).

Porifera sponges are capable of coordinated whole-body contractions when they clear their internal water channels of debris (the "sneeze" reflex). The contractile module of sponge tissues consists of actin, striated muscle myosin II, and transgelin, and contractions are regulated by the release of internal Ca^{2+} stores. The module shares elements of homology with contractile tissues of other animals, including muscle, indicating their origin from a common, multifunctional tissue in the animal stem lineage (Imperadore & Fiorito, 2018; Colgren & Nichols, 2022). Typical sets of basic muscle proteins are present even in unicellular or early divergent organisms such as sponges, which lack "true" muscles. In contrast, cnidarians have muscle-like cells, but they lack almost all the molecular features of bilaterally striated muscles, suggesting the evolution of cells with an ancient contractile apparatus (Steinmetz et al., 2012).

Sponges and placozoans lack recognizable muscle cells. They undergo deformations by contractions of the epithelial cells that line their bodies (Armon et al., 2018). Animal locomotion is accomplished by the coordinated activity of two cell types: myocytes (contractile cells of the muscular system) and neurons (signaling cells of the nervous system) (Colgren & Nichols, 2022). Myocytes enable movement only within the sponge, but these animals generally remain sedentary. Myocytes are spindle-shaped cells that resemble smooth muscle, containing microtubules and arranged parallel to peripheral microfilaments. They contract like muscle cells due to a non-muscle myosin type II with high homology to that found in bilaterians and vertebrates. Myocytes enable the ability to change shape and eject deposits into sponges even without a nervous system. Myocyte contraction is completely regulated at the cellular level by changes in calcium Ca^{2+} concentration (Lorenz et al., 1996). Calcium and calcium channels perform dual functions in the cell. They can depolarize the membrane potential of electrical excitability and activate transient cytoplasmic Ca^{2+} signals during muscle contraction (Senatore & Raiss, 2016).

Cnidaria (hydras, jellyfish, corals, sea anemones), sister group to Bilateria, are an extremely diverse group of animals in terms of morphology, life cycle, ecology and development (Zapata et al., 2015). They are represented by a great variety of muscle types and organizations that participate in many important physiological functions such as feeding, locomotion or defense (Leclere & Rottinger, 2016). Although this group of marine invertebrates lacks a significant part of the molecular features of striated muscles, jellyfish do have some ultrastructural and functional features such as striated myonemes, thick and thin myofilaments, desmosomes, and a mechanism of excitation-contraction coupling based on intracellular calcium an store, which resembles the structure and function of striated muscles (Helm et al., 2015).

Three main types of cells of the muscular system of the sea anemone *Nematostella vectensis* have been identified. The first type is an epitheliomuscular cell with a nucleus, connected to neighboring cells by apical intercellular junctions, which ensures complete integration into the epithelial-cellular complex of the circular muscle cells of the column and tentacles. Epitheliomuscular cell type 2 resembles the previous type 1, but its apical-basal axis is extremely elongated. The apical and basal parts of this cell are connected only by an elongated and very thin cytoplasmic bridge. Basiepithelial myocytes of the epidermis of the tentacles form the 3rd type of cells of the muscular system. The second and third types are specialized muscle cells that underlie different pathways of muscle development. Type 1 and 2 muscle cells are classical epitheliomuscular cells. Type 3 muscle cells have lost their apical integration and have become basioepithelial myocytes (Jahnel et al., 2014).

Striated muscles are found in bilateral animals (vertebrates, insects, etc.) and some non-bilateral eumetazoans (cnidaria and ctenophores). The significant ultrastructural similarity of striated muscles between these groups of animals reflects their common evolutionary origin. The core muscle protein complex, including the type II motor protein heavy chain (MyHC), characteristic of striated muscles in vertebrates, was already present in unicellular organisms before the emergence of multicellular animals. In addition, the orthologs of "non-muscle cells" and "striated muscle" MyHC are differentially expressed in the two sponges. This appears to be consistent with functional diversification prior to the emergence of true muscles and the subsequent use of striated muscle MyHC in fast-twitch smooth and striated muscles. Phasic smooth muscles contract faster than tonic smooth muscles, but are significantly slower than striated muscles. Cnidarians and ctenophores have striated muscle orthologs of MyHC, but lack key components of bilateral striated muscles, such as the ge-

nes encoding titin and the troponin complex. These findings suggest convergent evolution of striated muscles. Consistently, the jellyfish orthologs of the shared set of Z-disc proteins are not associated with striated muscle, but are expressed elsewhere or ubiquitously. The independent evolution of eumetazoan striated muscle by the addition of new proteins to an existing ancestral contractile apparatus may serve as a model for the evolution of complex animal cell types. Phylogenomic comparisons between bilaterians and cnidarians have shown that striated muscle arose independently in both groups, suggesting that close structural similarity does not necessarily indicate homology of muscle cell types. Striated cardiac and non-cardiac muscles may have arisen independently in different groups of bilaterians (Steinmetz et al., 2012; Razy-Krajka & Stolfi, 2019).

Table 1
Cells expressing different types of myosin heavy chains in some taxonomic groups of animals

Type, species	Cells expressing fast/striated myosin heavy chain	Cells expressing slow/smooth myosin heavy chain	Source
Type Porifera			
Spongilla lacustris (Linnaeus, 1759)	Exopinacocytes, endopinacocytes, lophocytes	Myopeptidocytes, endopinacocytes, basopinacocytes	Musser et al., 2021
Ephydatia muelleri (Lieberkühn, 1856)	Pinacocytes and myopeptidocytes. Express a single non-muscle myosin II heavy chain, which in myopeptidocytes functions in a relatively fast contractile mode, providing the "sneeze" effect	Pinacocytes and myopeptidocytes of sponges. In pinacocytes, the myosin II heavy chain functions predominantly in the slow tonic mode. In contrast, the genetically distinct fast and slow NMHC II are absent in sponges.	Colgren & Nichols, 2022
Tethya wilhelma (Schmidt, 1862)	Reticuloapopilocytes (cells that close the exit from the choanocyte chambers)	Pinacocytes	Steinmetz et al., 2012
Type Placozoa			
Trichoplax adhaerens (Schulze, 1883)	Epithelial cells	Fibrous cells	Sebé-Pedrós et al. 2018a)
Type Ctenophora			
Pleurobrachia pileus (Müller, 1776)	MHCIIb1: all muscle cells MHCIIb2: nerve plexus of tentacles, oocytes, some epithelial cells	Probable stem and progenitor cells	Dayraud et al., 2012
Type Cnidaria			
Nematostella vectensis (Stephenson, 1935)	Ectodermal tentacle retractors, mesenteric retractors	Gastrodermal circular muscles, parietal muscles	Steinmetz et al., 2012; Sebé-Pedrós et al., 2018b; Cole et al., 2023
Nematostella vectensis (Stephenson, 1935)	Epithelial muscle cells types 1, 2, basal epithelial myocytes of columnar and tentacle cells; myosin type not specified	Epithelial muscle cells types 1, 2, basal epithelial myocytes of columnar and tentacle cells; myosin type not specified	Jahnel et al., 2014
Clytia hemisphaerica (Linnaeus, 1767)	Striated circular muscles of the olfactory and subumbrella layers, longitudinal smooth muscles of the tentacles and ectoderm of the oral tube	Smooth muscles of the gastrointestinal system	Steinmetz et al., 2012; Chari et al., 2021
Hydra vulgaris (Pallas, 1766)	Ectodermal longitudinal muscles	Gastrodermal circular muscles	Siebert et al., 2019
Hydra vulgaris (Pallas, 1766)	HyNMII in cnidocytes, it is a non-muscle variant of myosin II, therefore it belongs to neither the fast (striated) nor the slow (smooth) type of muscle myosin		Garg et al., 2023
Type Annelida			
Platynereis dumerilii (Audouin & Milne-Edwards, 1834)	Somatic muscles and foregut muscles of a marine polychaete worm	Muscles of the intestine (except for the foregut) of a marine polychaete worm	Brunet et al. 2016
Type *Arthropoda*			
Drosophila melanogaster (Meigen, 1830)	Somatic and visceral muscle cells	Absent (except for general expression of non-muscle myosin II in all cells)	Hooper and, Thuma, 2005; Hooper et al., 2008
Type Nematoda			
Caenorhabditis elegans (Maupas, 1900)	Somatic and visceral muscle cells	Absent (except for general expression of non-muscle myosin II in all cells)	Hooper & Thuma, 2005; Hooper et al., 2008
Type Vertebrata			
Homo sapiens Linnaeus, 1758	Somatic muscles, cardiac muscle	Visceral muscles	Marib & Hen, 2018

Coleoid cephalopods (octopuses, squid, and cuttlefish) are active, resourceful predators with a rich behavioral repertoire. They have the largest nervous system among invertebrates and exhibit other striking morphological innovations, including chambered eyes, prehensile arms, highly developed early embryogenesis, and an extremely complex adaptive coloration system (Albertin et al., 2015). Squid use eight arms and two slender tentacles to capture prey. The muscular stalks of the tentacles extend by 80% in 20–40 ms toward the prey, which adheres to the terminal clubs by means of sucker arrays (van Leeuwen & Kier, 2023). Their limbs consist of a densely packed three-dimensional array of muscle fibers controlled by a complex peripheral nervous system (Zullo et al., 2019).

Cephalopod actins form a single cluster and are distinct from their bivalve counterparts. The modeled tertiary structure of squid actin closely resembles that of rabbit actin (Ochiai, 2013). Fast-twitch tentacle fibers have an almost tenfold advantage in sodium conductance over arm fibers. Unlike arm fibers, tentacle muscle fibers generate action potentials. During a rapid tentacle strike, several closely spaced action potentials result in maximal activation of the transverse tentacle muscle. Activation of the slower transverse muscle fibers in the arms requires the summation of postsynaptic potentials over a longer time, which allows precise regulation of the force required to support slower hand movements (Gilly et al., 2020).

Octopus vulgaris muscle cells are cholinergically innervated at acetylcholine receptor sites, which resembles the neuromuscular junctions of vertebrates. Membrane depolarization due to the movement of sodium and calcium ions leads to the appearance of a postsynaptic current and the opening of Ca^{2+} channels (Nesher et al., 2019). Unlike typical skeletal muscles, cephalopod arm muscle cells lack a proper T-tubule system, but have smaller sarcoplasmic structures. These structures are called terminal cisternae and contact the invaginations of the plasma membrane and form a “dyad” at the level of the Z-discs. Unlike muscle cells in other invertebrates, they are isopotential. Thus, each synaptic signal can control the membrane potential of the entire muscle cell (Kier, 2016). In the freshwater planarian *Dendrocoelum lacteum*, muscle cells combine features common to skeletal and smooth muscles. It has two main muscle systems: somatic and pharyngeal, which differ in the isoforms of the myosin heavy chain, func-

tion and location, possibly due to their different biological functions. The planarian muscle system is generally considered smooth, rather than striated in the classical sense, as in vertebrates. Therefore, the division into "fast" and "slow" myosin heavy chains, characteristic of striated muscles of vertebrates, does not apply here (Cebria, 2016). It was later demonstrated that in planarians, muscles perform a signaling and structural function. They provide the formation of the spatial structure necessary for regeneration and coordinate tissue repair and regrowth after injury (Scimone et al., 2017; Cote et al., 2019).

The composition of muscle tissue in the parasitic flatworm *Schistosoma mansoni* has been revealed, which helps to clarify the stages of its evolution. Thus, in most animals, striated muscles move the body, and smooth muscles move internal organs. In both types of muscles, contraction is the result of the interaction between myosin and actin filaments. It was traditionally believed that smooth and striated muscles have different protein components and filament structures. However, based on the study of the ultrastructure of the muscles of *Schistosoma mansoni*, it was found that this point of view is not confirmed. This human parasite has only smooth muscle. However, its myosin sequence and filament structure are identical to those in striated muscle, but the actin filaments resemble smooth muscle. Such "hybrid" muscles may be common in other invertebrates. This discovery challenges the paradigm that smooth and striated muscles always have different components (Sulbarán et al., 2015).

The free-living soil nematode *Caenorhabditis elegans* has a generation period of about three days. During this period, it completes its embryonic development by hatching. Early embryonic cells show plasticity: muscle cells usually originate from the MS blastomere, and some other mesodermal or even endodermal progenitor cells can convert into muscle when developmental signals change (Özcan & Tursun, 2023). The muscle cells of the body wall of these nematodes are spindle-shaped mononuclear cells with several sarcomeres per cell and oblique striation. They form muscles that run along the length of the nematode body beneath the epidermis (Corsi et al., 2015). During egg laying in *Caenorhabditis elegans*, the vulva muscles relax and contract to expel the eggs. Unlike skeletal muscles, vulva muscles do not have visible sarcomere bands (Wang et al., 2020). The general structure of the muscle sarcomere is conserved from nematodes to humans. In nematodes, the molecules involved in sarcomere assembly, maintenance, and regulation are also largely conserved. Unlike most other animals, their innervation is unusual in that nerves do not branch into muscles. Instead, muscle cells extend their branches into the nerve cord where they form synapses with motor neurons along their axons (Gieseler et al., 2017).

Three types of muscles can be recognized in the larval and adult arthropod *Drosophila melanogaster*. Most skeletal muscles of adults are tubular with characteristic transverse striations and a nucleus in the center and are classified as the first type. They belong to the synchronous muscles, since each nerve impulse causes the release of calcium from internal stores, which triggers mechanical contraction of the muscle, as in the skeletal muscles of vertebrates. The second type is the indirect flight muscles, or "fibrillar" muscles of adults. These are transversely striated and asynchronous muscles, which contract as a result of the action of calcium ions after a nerve impulse and as a result of stretching-activation of the cuticle of the thorax. In them, regeneration processes are triggered by damage resulting from physical or pathological trauma, as well as damage associated with aging. Given the lifespan of flies, these events occur less frequently. From an evolutionary perspective, they should exert little pressure to establish a true regenerative mechanism in adult muscles. The third type consists of hypercontractile striated visceral and cardiac muscles, as well as the muscles of the larval body wall. They can contract over a distance of about 50% of their resting length (Josephson et al., 2000; Zullo et al., 2020). *Drosophila* cardiac and visceral muscle progenitors are populations of mesodermal-derived cells that are committed to myogenic differentiation but are not yet mature cardiomyocytes or visceral smooth muscle cells. They are generated from precursor cells by compartmentalization in segmental regions (Chaturvedi et al., 2017). In some cases, larval muscles are used as templates for the formation of adult muscles. In other cases, peripheral nerve fibers and the space between larval muscle fibers stimulate the development and differentiation of adult muscle fibers. They originate from precursors, adult muscle stem cells, which undergo proliferation, differentiation, and fusion. The fusion of myocytes results in the formation of myotubes, and subsequently mature muscle fibers. Only a small number of progenitor stem cells remain associated with the differentiated fibers of adult indirect flight muscles. Stem cell progenitors resemble mammalian satellite cells, which are associated with adult skeletal muscle fibers and retain the capacity to proliferate and differentiate into myoblasts. This occurs after stimulation by skeletal muscle fiber injury. Fly satellite cells undergo a proliferation/differentiation program that results in the formation of myoblasts that fuse with the injured indirect flight muscle fiber (Postigo et al., 1999; Boukhatmi, 2021).

In the echinoderms of the phylum Echinodermata, two main groups of muscle fibers have been identified, the first (and most common), in which individual bundles consist of spindle-shaped myocytes and resemble smooth muscle fibers of vertebrates. These fibers are embedded in an extracellular matrix of connective tissue, consisting of a network of thick striated (collagenous) and thin smooth muscle fibers and an amorphous component. This component contains fibroblasts, nerve cells and various coelomocytes (immune effector cells of sea urchins). The second type of muscle is typical of crinoid arms. They consist of obliquely striated fibers, and each muscle bundle consists of 8–20 myocytes and is surrounded by a basal lamina (Zullo et al., 2020).

A typical larva of the ascidian – Ascidiacea bears two bands of mononuclear muscle cells in the tail, one on each side of the chord. The myofibrils of each cell are connected by intercellular junctions, similar to vertebrate cardiomyocytes. Each row of cells behaves like a syncytium, enabling swimming movements. The myocytes are arranged in a striated pattern and express the myosin heavy chain. After metamorphosis, the sarcomerically organized musculature is reabsorbed with the tail. The musculature of the formed zooid usually consists of longitudinal and annular multinucleated fibers that run along the entire mantle along the body and around the two siphons. Although ultrastructural studies show a non-striated morphology, the adult body musculature has characteristics intermediate between vertebrate smooth and striated muscles (Meedel et al., 2007). The focus has been on the development and cellular structure of the heart of the ascidian Ciona in comparison with other chordates, mainly vertebrates. It has been found that postmetamorphic muscles use a troponin-tropomyosin complex similar to vertebrate striated muscles. Their myocytes are specified by transcription factors that generally control vertebrate skeletal muscle development, and lack the specification of smooth muscle (Anderson & Christiaen, 2016).

In Pisces, skeletal, cardiac, and smooth muscle cells are similar in structure and function to those of other vertebrates, but have some features specific to their aquatic lifestyle. In particular, the skeletal muscle of *Danio rerio* is a heterogeneous tissue composed of slow, fast, and intermediate muscle cells. However, unlike the mixed muscle bundles of mammals, the trunk has spatially separated slow and fast muscle fibers, and the slow myocytes are embryonically mononuclear (Lai et al., 2017).

Mammals and humans retain some capacity for cardiomyocyte renewal throughout postnatal life. However, after trauma, such as acute myocardial infarction, *Danio rerio* efficiently regenerates lost cardiac muscle. Cardiac muscle regenerates to normal after resection injury, primarily through activation and expansion of cardiomyocyte populations (Kikuchi et al., 2010).

Mature mammalian skeletal muscle plays an important role in locomotion, respiration, body temperature maintenance, and organ protection.

Its biological functions are mainly manifested in contraction, thermogenesis, and myokine secretion (Brooks et al., 2023). In vertebrates, smooth and non-muscle cells express one family of myosin II heavy chains (smooth/non-muscle myosin II heavy chain or SM/NM-MyHC), while striated muscle cells express another family (striated myosin II or ST-MyHC) (Steinmetz et al., 2012). In vertebrates, striated myocytes are found in voluntary skeletal muscles, as well as in the anterior and posterior ends of the digestive tract (anterior esopha-

geal muscles and external anal sphincter), and in the myocardium of the heart. Smooth myocytes are found in involuntary visceral muscles, which provide slow, long-range deformation of internal organs. This includes the posterior part of the esophagus and the rest of the intestine, as well as blood vessels and most of the genitourinary system (Brunet et al., 2016).

Based on the results of the study of planarians (Cebria, 2016), myoepithelial cells of mammalian mammary glands (Moumen et al., 2011) and myoepithelial cells of human sweat glands, which contract and participate in sweat transport (Nakashima et al., 2023), it was concluded that these hybrid cells can participate in the regeneration process through biochemical signals independent of contraction (Zullo et al., 2020). Skeletal muscles contain two types of cells: fibrous, which make up the contractile muscle mass and contain hundreds of myonuclei, and satellite cells, i.e. myogenic mononuclear stem cells located at the periphery of the fibers and responsible for muscle growth and repair (Cisterna & Malatesta, 2024).

Ontogenesis, types of adaptive strategies, specialization, regulatory mechanisms of contractile cells

We attempted to compare the historical development of muscle tissue with embryonic development and noted that, in general, the phylogenesis of muscle tissue demonstrates parallelism with ontogenesis. In particular, at the first stage of ontogenesis, contractile cells of the non-muscle type appear. Cells that are not yet muscle but already contain contractile filaments appear from the ectoderm and mesenchyme. These include early pericytes (Shimizu & Kanda, 2020; Eltanahy et al., 2021), myoepithelial (Shams, 2022; Nakashima et al., 2023) and myofibroblast-like (Beffagna, 2019; Tai et al., 2021) hybrid cells. In addition to the contractile function, hybrid cells retain the properties of epithelial or connective tissue. In addition to the contractile function, hybrid cells retain the properties of epithelial or connective tissue. The first contractile cells do not belong to true muscles and are only an ontogenetic analogue of the epithelial-muscle cells of cnidarians.

In the second stage, the mesoderm is formed and smooth muscle cells are laid down. During this period, smooth muscle cells of the vessels, intestine, bronchi and genitourinary system differentiate (Wang et al., 2015). These are the first true muscle cells in ontogenesis. The parallelism of ontogenesis with phylogenesis is confirmed by vascular remodeling of muscle cells after endothelial dysfunction or damage. In this process, contractile smooth muscle cells of the vessels acquire the properties of secretory-type cells (Wang et al., 2015; Fu et al., 2026), and smooth muscle of the lungs of adult mammals is transformed into different phenotypes (Goodwin et al., 2023).

In the third stage, cardiomyocytes develop in parallel or with a slight time shift. In particular, the heart begins to contract on days 22–23 of human embryogenesis. In ontogenesis, as in phylogenesis, cardiac muscles represent an early stage of specialization of striated muscles (Guo & Pu, 2020).

At the fourth stage, the process of differentiation of striated fibers in the muscles of the trunk, limbs and partly the head occurs. Skeletal muscles are the latest type of true muscle cells in ontogenesis and phylogenesis. The results of the comparison of the stages of development of muscle cells in ontogenesis and phylogenesis are presented below (Table 2).

Table 2
Comparative characteristics of muscle cell development in ontogenetic and phylogenetic development

Phylogeny	Ontogenesis
Protozoa - lack tissues; move with the help of a cytoskeleton	Early embryonic tissues - no muscle cells; only general cellular contractility
Cnidaria - emergence of early hybrid epithelial-muscle cells	Emergence of hybrid myoepithelial cells and pericytes; true muscle tissue absent
Early bilaterians - formation of the first smooth muscle cells and mesoderm (the first true muscles)	Differentiation of smooth muscle cells from mesenchyme
Primary chordates - emergence of cardiac muscle tissue; intensification of the process of specialization of striated muscles	Formation of cardiomyocytes; onset of cardiac contractility
Arthropods, chordates - development of skeletal striated muscles	Differentiation of skeletal muscle from somites
Parallel at different stages of phylogenesis - functioning of hybrid muscle cells (myoepithelial, myofibroblasts, pericytes)	Formation of hybrid cells from different germinal sources throughout ontogenesis

Thus, the ontogenesis of human muscle tissue reflects the main stages of its phylogenetic evolution: from early contractile hybrid cells through the formation of smooth muscles to cardiac and striated muscles, with the parallel development of hybrid muscles. In ontogenesis, there is no direct copy of the epithelial-muscle cell of cnidarians, but there is a functional analogue.

Striated muscle fiber is a unique cellular structure called multinucleated syncytium. It is formed as a result of the fusion of numerous myoblasts during embryonic development. This result of formation and organization provided these cells with significant adaptive advantages and fundamentally new opportunities for the evolutionary specialization of muscle tissue. The presence of dozens and even hundreds of nuclei within one muscle fiber significantly increased its plasticity and created the prerequisites for rapid morphofunctional restructuring. This enabled rapid changes in the intensity of contractile protein synthesis and the increase in muscle fiber mass, strength, and power in response to changes in the nature of the functional load. Multinucleation actually ensured the functioning of a large number of copies of genetic information that control the synthesis of the main myofibril proteins - actin, myosin, troponin, and other components of the contractile apparatus (Millay, 2022).

At the same time, evolutionary adaptations were implemented not only by increasing muscle mass, but also by improving their signaling and enzymatic apparatus. If the conditions of existence required significant strength, speed and endurance, without a significant increase in body weight, adaptive changes occurred mainly at the level of energy metabolism enzymes. In such cases, the synthesis of fast energy-supplying enzymes was enhanced – primarily myosin adenosine triphosphatases, creatine phosphokinases and glycolysis enzymes, which ensure rapid and voluminous formation and use of ATP during intensive muscle work.

The above evolutionary prerequisites are characteristic of biotopes with limited visibility – dense shrubs, forests, tall grass or rugged terrain, where short-term predator-prey interactions often occur over short distances. In such conditions, predators are forced to use a strategy of sudden attack or short pursuit, while prey survive due to instantaneous acceleration and the fastest possible escape.

The sprint type of locomotion caused further specialization of contractile structures of muscle fibers. As a result, fast glycolytic fibers of intermediate type IIx and maximally fast glycolytic fibers of intermediate type IIb were formed. They are characterized by a high contraction speed, significant activity of myosin ATPase, dominance of anaerobic creatine phosphokinase and glycolytic energy supply. At the same time, corresponding fast neuromuscular units were formed, features of neuromuscular transmission and regulation, which ensured the implementation of short-term but extremely powerful motor acts.

During intense work, fast muscle fibers with anaerobic energy supply adapted to develop very high contraction power, but they quickly tired. In the process of their activity, a significant oxygen debt is formed, anaerobic metabolism products accumulate, in particular lactate and other metabolites, which cause a decrease in the pH of the internal environment and accelerate the development of fatigue. Such fibers are innervated by large motor neurons with thick axons and are part of large neuromuscular motor units, in which one motor neuron regulates a significant number of muscle fibers. These adaptations

provide rapid and powerful muscle contraction. The sarcoplasm of fast-twitch fibers contains significant amounts of glycogen and creatine phosphate, which provides explosive energy production under anaerobic conditions.

The number of mitochondria in such fibers is relatively small, while the T-tubule system and sarcoplasmic reticulum are well developed, which contributes to the rapid spread of excitation and intense release of calcium ions during contraction. These fibers are characterized by high activity of myosin ATPase and high excitability of the sarcolemma to the action of acetylcholine, which ensures rapid occurrence of action potentials and powerful contraction (Nuzzo, 2024).

One of the determining factors of survival for animals inhabiting open spaces, as well as for migratory species and migratory birds, was the ability to move for a long time. Under such conditions, natural selection contributed to the formation of specialized morphofunctional properties of striated muscles, which provide long-term work without rapid exhaustion and fatigue. In the course of evolution and in the process of individual development, striated muscle fibers of these animals differentiated into slow oxidative fibers of type I and fast oxidative-glycolytic fibers of type IIa, which function as part of slow neuromuscular units. The specified organization of contractile activity provided an optimal combination of moderate contraction speed with high endurance. These muscle fibers are characterized by a high degree of capillarization, intensive mitochondrial biogenesis, dominance of aerobic energy supply, significant myoglobin content and high activity of oxidative metabolism enzymes. The combination of these structural and functional features ensured efficient use of oxygen and stable energy formation for a long time, which is a necessary condition for long migrations, long running or flying.

Unlike the previous group, slow muscle fibers have acquired adaptive specialization for prolonged work and are characterized by high resistance to fatigue. Their energy supply occurs mainly by aerobic oxidation of glucose and fatty acids. In the process of this metabolism, mainly non-toxic products are formed - water and carbon dioxide, and the reaction of the internal environment remains relatively stable. Slow fibers are innervated by smaller motor neurons and are part of small motor units, which provides more precise regulation of the force of contraction. They are characterized by a developed capillary network, a high content of myoglobin and a large number of mitochondria, which ensures efficient use of oxygen and long-term energy production in the process of cellular respiration. The sarcoplasmic reticulum system in these fibers is less developed, the activity of myosin ATPase is lower, which causes a slower contraction speed, but more economical use of energy resources. The combination of these properties ensures long-term muscle work without rapid fatigue (Hu et al., 2024). Thus, in the course of evolution, two contrasting types of muscle fibers have formed, reflecting different strategies of motor adaptation: fast glycolytic fibers adapted to short-term powerful work, and slow oxidative fibers specialized for long-term and energy-efficient contraction.

Between the extreme adaptive strategies, an intermediate type of skeletal muscle organization has been formed in the process of evolution, providing an optimal combination of speed and endurance. This strategy is characteristic of many animals that are forced to move over considerable distances, but at the same time retain the ability to make quick jerks during the pursuit of prey or escape from predators. In these species, the composition of striated muscles is dominated by fast oxidative-glycolytic fibers of type IIa and partially fast glycolytic fibers of type IIx, which function as part of fast neuromuscular units. Such fibers are characterized by a relatively high contraction speed, significant strength, and moderate resistance to fatigue.

In terms of their structural and metabolic properties, they occupy an intermediate position between slow oxidative fibers of type I and maximally fast glycolytic fibers of type IIb. They are characterized by a combination of a sufficiently developed capillary network, a moderate content of mitochondria and myoglobin with high activity of enzymes of glycolytic metabolism and myosin adenosine triphosphatase. Such an organization provides the possibility of effective use of both aerobic and anaerobic energy supply mechanisms, which allows animals to implement a variety of motor activity strategies - from long movements to short high-speed jerks. It is these integral properties of the locomotor system that are characteristic of many species of ungulates, medium-sized predatory mammals, and species that combine endurance with the ability to accelerate rapidly.

The ratio of muscle fiber types in the body depends on the species of animal, muscle group, sex, age, nature of innervation, body weight, nature of physical activity or its absence. The nature of motor activity and the above factors cause various switching of muscle fiber types and changes in their ratio. In particular, the following transformations of muscle fiber types can occur: type I (slow oxidative endurance) → 2a (fast oxidative glycolytic) → 2 IIx (fast glycolytic intermediate) → 2b (maximally fast glycolytic) (Schiaffino & Reggiani, 2011; Hudson et al., 2012; West et al., 2013).

In our opinion, the above-mentioned direction of the vector of adaptive plasticity is inherent in such animal species (Table 3).

Table 3

The influence of the nature of running specialization and body mass on the structure of animal muscle tissue

Evolutionary strategy/adaptive vector of muscle fiber switching↓	Kind of animals	Travel speed, km/h	Body weight, kg	Movement time
Long-term movement I (slow oxidative endurance)	*Canis lupus* (Linnaeus, 1758)	60	30–50	3–6 hour
Fast running of medium duration IIa (fast oxidative glycolytic)	*Lepus europaeus* (Pallas, 1778)	70	3–6	2–5 min
Fast bursts – a combination of Iia (fast oxidative glycolytic) and Iix (fast glycolytic intermediate)	*Panthera leo* (Linnaeus, 1758)	60–80	150–250	20–40 sec
Ultrafast IIb (maximal fast glycolytic)	*Acinonyx jubatus* (Schreber, 1775)	110–120	40–65	20–30 sec

Along with the advantages, striated muscles have received some disadvantages of high specialization. The large number of nuclei makes it impossible for them to divide and regenerate, which is characteristic of poorly specialized contractile cells. Mature muscle fibers have lost the ability to divide, because it has become difficult to evenly distribute chromosomes between daughter cells. However, muscle fibers contain dormant embryonic myocytes, which provide regeneration after damage. In this way, the advantages of high specialization were used and the ability to regenerate, which is characteristic of single-nucleated contractile cells, was restored.

Each of the listed types of muscle fibers is mainly served by a certain energy supply system: aerobic mitochondrial and glycolytic, anaerobic creatine phosphate and glycolytic. The sequence of switching between different types of muscle fibers and the ratio between the methods of energy supply are always different.

Therefore, the multinucleation of skeletal muscle fibers can be considered as a key evolutionary mechanism that ensured the plasticity and functional differentiation of the muscular system of vertebrates, and rapid adaptation to any physical load.

By the nature of contractile activity, smooth muscles are divided into phasic and tonic functional types. This differentiation reflects the evolutionarily formed adaptation of smooth muscles to perform their physiological functions. Phasic smooth muscles are specialized in ensuring the movement and evacuation of contents by peristalsis of the stomach, intestine, ureters, bile and lymphatic ducts, uterus, and fallopian tubes. They are characterized by a response to nervous and humoral signals and wave-like and rapid contraction and relaxation. In contrast, tonic smooth muscles contract very slowly and can maintain tension for a long time. This evolutionary adaptation is important for maintaining stable blood vessel pressure, bronchial and bronchiole tone, sphincters of the digestive system, urinary bladder, and iris. Smooth muscle tissue is characterized by a number of morphological and functional features. Its cells are uninucleate, do not have transverse striations, are not attached to bones, contract spontaneously, and

almost do not tire. Compared to striated muscle tissue, smooth muscle contraction occurs more slowly because not every muscle cell is approached by a nerve ending, and the transmission of the nerve impulse is carried out through tight contacts between neighboring myocytes (Huizinga, 2019; Chevalier et al., 2024; Wang et al., 2025).

The structural and functional unit of cardiac muscle tissue is the cardiomyocyte – a specialized cell, the evolutionary organization of which ensures the continuous and rhythmic work of the heart as the central organ of blood circulation. In the course of vertebrate evolution, a unique architectonics of the myocardium was formed. Cardiomyocytes are interconnected by end sections, forming branched chains and numerous anastomoses, which form a three-dimensional mesh structure of the tissue. Such an organization ensured the mechanical integrity of the myocardium and enabled the spread of electrical excitation between cells, which is an important prerequisite for the synchronization of heart contractions. Between the muscle fibers is a loose connective tissue containing a dense network of blood vessels, nerve fibers, and intercellular matrix. It performs support, trophic, and signaling functions and ensures intensive metabolism of cardiomyocytes. They are characterized by a high mitochondrial density and significant energy requirements (Litviňuková et al., 2020).

Cardiomyocytes in different layers of the myocardium are oriented in different directions - longitudinal, transverse and oblique, and form ring-shaped structures around large vessels. Such a complex spatial organization of fibers is the result of evolutionary optimization of the pumping function of the heart and ensures the efficient conversion of muscle cell contraction into directed blood flow. Specialized cells of the cardiac conduction system generate electrical impulses. The rhythm of heart contractions is formed by its own pacemaker, while the central nervous system and humoral factors play a mainly modulating role. Autonomic regulation is an important evolutionary adaptation that ensures the stability of cardiac functioning regardless of external conditions (Monfredi et al., 2010).

Cardiac muscle cells are connected to each other by intercalated discs, which contain several types of intercellular contacts: desmosomes and adhesive contacts, which provide mechanical strength of the tissue, as well as gap junctions, through which the rapid propagation of ions and electrical impulses between cells occurs. Thanks to this system of intercellular interactions, the myocardium functions as a single functional syncytium, this ensures the synchrony of cardiac muscle contraction (Vermij et al., 2017). Cardiomyocytes usually have one, rarely two nuclei, which are located in the center, a well-developed contractile apparatus and a large number of mitochondria, which reflects their specialization for prolonged, energy-intensive work.

Several specialized types of cardiomyocytes are distinguished in the myocardium, including: contractile, pacemaker (impulse generators), conductive and secretory cells. This spectrum of cells was formed during evolution as an adaptive mechanism that ensures an effective combination of mechanical, electrical and humoral regulation of the heart. Contractile cardiomyocytes constitute the bulk of the myocardium and structurally resemble striated muscle fibers. They contain a large number of myofibrils organized into sarcomeres, which ensures their ability to rhythmically contract and the mechanical force necessary to push blood out of the heart chambers. (Litviňuková et al., 2020).

Pacemaker cells are localized mainly in the sinoatrial node. They are capable of spontaneous membrane depolarization and generation of electrical impulses that determine the rhythm of cardiac contractions and maintain the ability to contract. These cardiomyocytes have the properties of functional hybrids, combining the characteristics of nerve and muscle cells (Monfredi et al., 2010).

Conducting cardiomyocytes form the conduction system of the heart (atrioventricular node, atrioventricular node, bundle of His, Purkinje fibers) and ensure the rapid propagation of electrical excitation throughout the myocardium. They are characterized by a smaller number of contractile elements, but a high ability to conduct electrical impulses, which ensures the synchronization of contractions of different parts of the heart (Vermij et al., 2017). Secretory cardiomyocytes are localized mainly in the atria and perform an endocrine function. These cells regulate the production of two polypeptide hormones: atrial natriuretic peptide (ANP) and B-type natriuretic peptide (BNP), which are involved in the regulation of water-salt balance, blood pressure, and diuresis. The combination of contractile and secretory properties of these cells reflects the complex functional integration of the heart in the system of neurohumoral regulation of the body (Goetze et al., 2020; Nyberg et al., 2023).

Cardiomyocyte energy metabolism is predominantly aerobic. About 60–70% of the energy required for cardiac muscle contraction is generated by the oxidation of fatty acids. Glucose, amino acids, and ketones play a supporting role. This metabolic strategy is an important evolutionary adaptation that ensures a high level of energy efficiency and continuity of cardiac function (Lopaschuk et al., 2021). Unlike skeletal muscle, the myocardium has virtually no reserve satellite cells that provide muscle tissue regeneration after damage. The mammalian heart in the early neonatal period has a remarkable regenerative capacity, which is mediated by the proliferation of endogenous cardiomyocytes and is lost when cardiomyocytes stop dividing shortly after birth (Cardoso et al., 2020). In newborn mice, there is a short period of time during which the heart retains full regenerative capacity after injury, which is also potentially relevant to the neonatal human heart (Costa et al., 2022).

Conclusions

The evolution of animal contractile tissue involved two main types of key morphofunctional specialization. First, it is the acquisition of the ability to coordinate and integrate actomyosin assemblies between multiple cells, which ensured tissue integrity, coordinated morphogenesis and movement at the organismal level. Second, it is the evolution of specialized types of contractile cells adapted to slow or fast, short-term or long-term movements of the adult individual. The outcome of muscle specialization is determined by a number of factors, and primarily by the expression of fast (striated type) and slow (smooth/non-muscle) myosin II paralogs.

Modern animal contractile cells form an evolutionary continuum, from the unspecialized contractile epithelium that underlies the behavior of modern placozoans, through epithelium with supracellular actomyosin bundles that extend across several cells and are characteristic of modern sponges, to epitheliomuscular tissues in which supracellular actomyosin fibers are concentrated in the basal processes of sea anemones. The final link in this continuum is specialized muscle tissue that has lost most or all of its epithelial properties and is present in ctenophores, jellyfish, and bilaterians.

The ontogeny of human muscle cells reflects the main stages of their phylogenetic evolution: from early contractile hybrid cells through the formation of smooth muscles to cardiac and striated muscles, with the parallel development of hybrid muscles. In the course of evolution, the muscular system of animals was formed under the influence of a fundamental physiological limitation: the faster a muscle fiber contracts, the less economically it uses energy and the faster it tires. Therefore, a continuous functional series of fibers was formed in animals: type I → type IIa → type IIx → type IIb, which reflects a gradual transition from energy economy to maximum contraction speed.

Different types of muscle fibers are not just histological variants of tissue, but different evolutionary strategies for using energy for movement. The diversity of muscle fiber types reflects a fundamental evolutionary compromise between the speed of contraction and the energy efficiency of muscle work. Within the framework of this compromise, a functional gradient of fibers from slow oxidative to maximally fast glycolytic fibers has formed, which ensures the implementation of different locomotion strategies in animals.

There is a general pattern in the process of evolution: with an increase in the body mass of an animal, the maximum speed of contraction of muscle fibers decreases. This phenomenon is associated with the allometry of movement and the biomechanics of locomotion. Large animals have a greater body mass and inertia of the limbs, a longer step cycle and a lower frequency of movements, longer muscle fibers and a longer time of neuromuscular activation. Therefore, they

are dominated by I, IIa, IIx fibers, while IIb is either absent or very rare. Humans also lack typical IIb fibers. With these parameters, extremely fast contractions become energetically disadvantageous and biomechanically inefficient. Therefore, natural selection shifts the functional balance of muscles towards more economical and more durable fibers. In contrast, small rodents and predators have the fastest glycolytic IIb fibers, which provide a high frequency of movements and quick reactions over short distances.

The authors declare they have no conflict of interest.

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