1.2

General Anatomy of the Muscle Fasciae

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CHAPTER CONTENTS

INTRODUCTION

The soft connective tissues associated with muscle tissue can be referred to as muscle fasciae (MF). A description of MF structure and function in skeletal muscle (Purslow 2014) lists 17 previous reviews in addition to a great deal of original source material, and the reader is referred to these substantial sources for detailed information. Here we shall summarize the main features of their structure, composition, and functional properties. There is a tendency in previous literature to call MF "tubes" or "sheaths" that surround each fiber or fasciculus. The concept of muscle fasciae as continuous connective tissue networks provides a better understanding of the functional anatomy of these structures. MFs form a three-dimensional matrix that is continuous throughout the entire organ, providing connections between fibers and fascicles rather than separating them.

GENERAL STRUCTURE AND COMPOSITION OF MUSCLE FASCIAE

The following description of the general structure of fasciae associated with striated muscles summarizes the consensus of several sources and is schematically shown in Fig. 1.2.1.

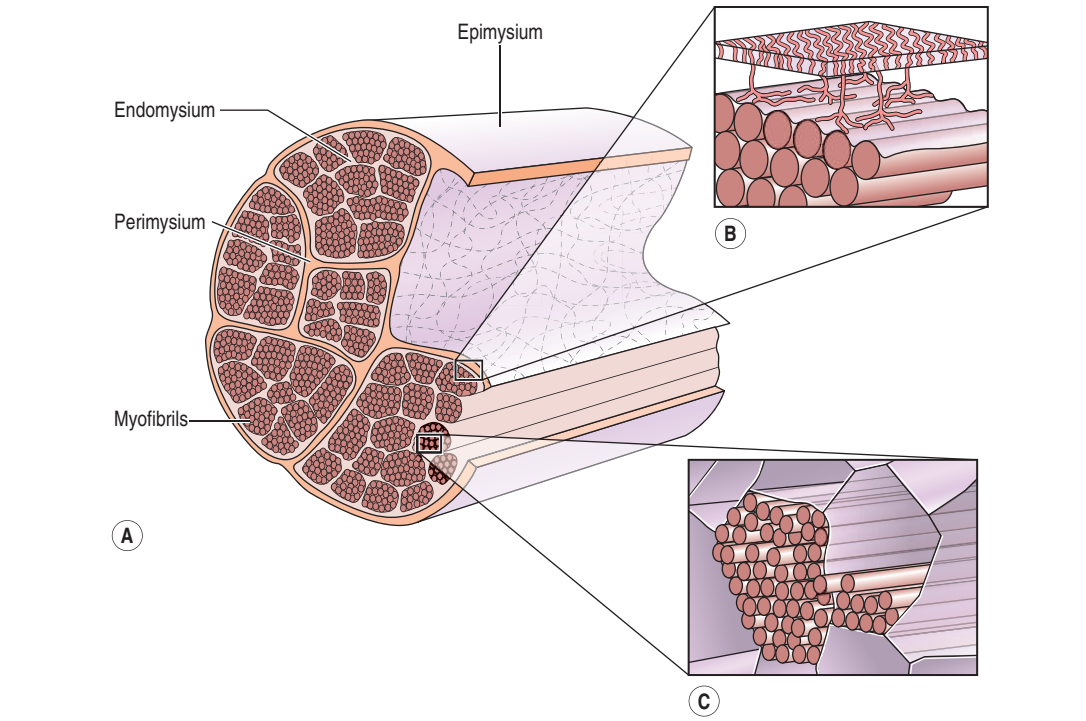
Each individual muscle is surrounded by the **epimysium,** a connective tissue layer that is continuous, with the tendons attaching the muscle to the bones. The **perimysium** is a continuous network of connective tissue that divides the muscle up into fascicles or muscle fiber bundles.

KEY POINT

The division of each muscle into fascicles by the perimysium allows flexible movement between the fascicles as the muscle contracts and changes shape. Great variability in the size, shape, and number of muscle fascicles exists between functionally different muscles.

The perimysial network merges into the tendons and into the epimysium at the surface of the muscle and is mechanically connected to them. Within each fascicle or muscle fiber bundle, the **endomysium** is a continuous network of connective tissue that separates individual muscle fibers.

Generally speaking, these connective tissue layers are composed of collagen fibers (and occasionally also elastin fibers) in an amorphous matrix of hydrated proteoglycans (PGs), which mechanically links the



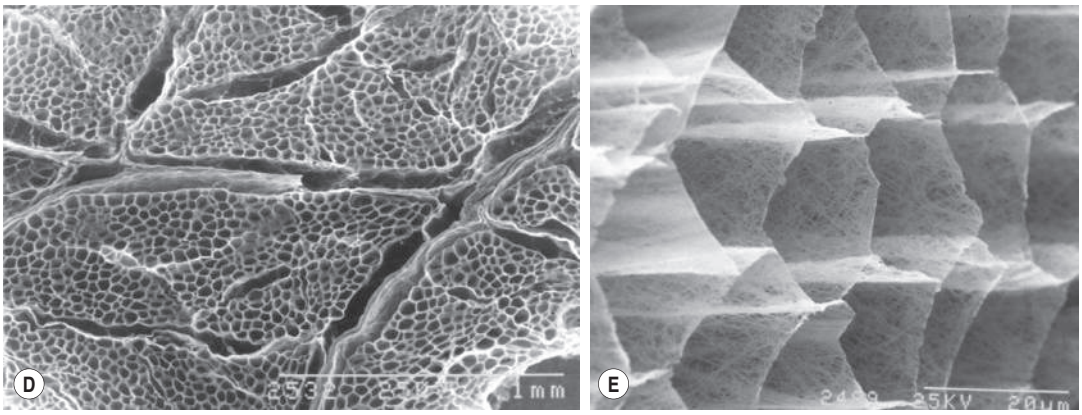


Fig. 1.2.1 General Anatomy of the Fasciae Associated With a Skeletal Muscle. (A) Schematic view of the general arrangement of the epimysium, perimysium, and endomysium within muscle. (B) Schematic depiction of junction zones between the thick perimysium and the endomysium of muscle fibers in the surface layer of the fascicle. Although a gap is shown between the perimysium and endomysium to illustrate the connections, no gap occurs in living muscle. (Separation of the endomysium from the perimysium is seen in some fixed tissue due to shrinkage artefacts; see Fig. 1.2.2). (C) Schematic depiction of myofibrils of an individual muscle cell residing in the honeycomb network of the endomysium. (D&E) Micrographs of IMCT structures in muscle treated with NaOH to digest away myofibrillar proteins and PGs. (D) The spatial arrangement of the thicker perimysium surrounding the honeycombed endomysial network within a fascicle. (E) A higher magnification view of the endomysial network. Abbreviations: IMCT, intramuscular connective tissue; PGs, proteoglycans. Figure reproduced with permission from Purslow, P. P., 2014. New developments on the role of intramuscular connective tissue in meat toughness. Annual Review of Food Science and Technology 5, 133–153.

collagen fiber networks in these structures. Listrat and colleagues (Listrat et al. 1999; Listrat et al. 2000) and Passerieux et al. (2006) identified seven molecular types of collagen in muscle (types I, III, IV, V, VI, XII, and XIV). Types I, III, and V are fibrillar collagens (fiber-forming types). Types I and III are the most prevalent in mammalian striated muscle. Light et al. (1985) found that type III collagen (containing intermolecular disulphide cross-links) comprised approximately 40% of the total of type I and III collagens in a range of bovine muscles. Types XII and XIV are thought to act as molecular bridges connecting the fibrillar collagens to other components in the amorphous matrix. The basement membrane layer of the muscle fibers contains nonfibrous type IV collagen, together with proteoglycan components such as laminin and fibronectin and heparin sulfate–containing PGs, and forms the boundary between the phospholipid cell membrane and the collagen fiber networks of the "reticular layer" of the endomysium.

Collagen fibers are mechanically stabilized by the formation of covalent crosslinks (Eyre and Wu 2005). The formation of crosslinks is essential for the mechanical strength and stiffness of collagen fibers, as without them the collagen molecules slide past each other under load and the fibers have no strength. Throughout gestation and during postnatal maturation there are substantial changes in the types and amounts of covalent crosslinks that mechanically stabilize the collagen molecules in muscle fasciae. The subject of cross-link formation during maturation and aging of connective tissues is reviewed in excellent detail by Avery and Bailey (2008). Here we shall just note that muscle fasciae are rich in covalent crosslinks, that these crosslinks are known to undergo maturation changes in both endomysial and perimysial connective tissue, and that compounds promoting glycation crosslinks can be incorporated into the body from dietary sources and from tobacco smoke. Thus diet and lifestyle may conceivably affect the mechanical properties of some connective tissues, including muscle fasciae, via crosslinking of collagens.

The amounts and composition of muscle fasciae vary among different muscles in the body. A comparison of transverse sections through different muscles from the same species (Purslow 2005; Fig. 1.2.2) shows that the continuous perimysial network surrounds or separates fascicles of very different sizes and shapes in different muscles. This difference also results in different thicknesses of perimysial connective tissue. These variations, especially in the amount and spatial organization of the perimysium, have long been attributed to variations in mechanical roles of different anatomical muscles. If this is correct, then the muscle fasciae must play strong roles in the normal physiological functioning of each muscle. Some possible explanations of these roles are emerging but are far from complete.

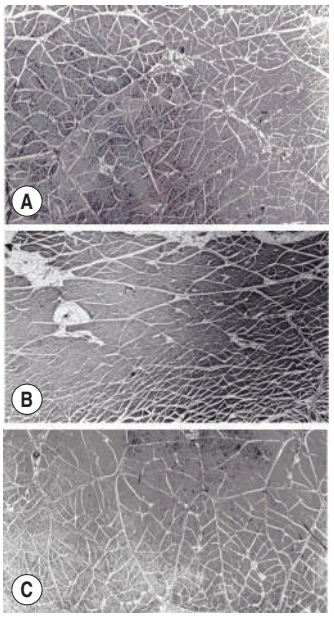


Fig. 1.2.2 Comparison of the fascicular architecture in cross-sections of three muscles from the same (bovine) animal: rhomboideus cervicus (A), sternocephalicus (B), and pectoralis profundus (C). Clear differences in fascicle size, shape, and perimysial thickness can be seen among them and within each muscle. The white gaps between fascicles (separating perimysium from the endomysium of surface muscle fibers) are shrinkage artefacts produced by fixation. Reproduced with permission from Purslow, P.P., 2005. Intramuscular connective tissue and its role in meat quality. Meat Sci. 70, 435–447.

FUNCTIONAL ANATOMY OF THE ENDOMYSIUM

There are three distinct structures separating the surface of one muscle fiber (cell) from its adjacent neighboring fiber:

1. At the surface of the fiber is the plasma membrane (plasmalemma) of the muscle cell, which is approximately 9-nm thick.

2. Outside the plasma membrane is the endomysial basement membrane. It is approximately 50 to 70 nm thick and is composed of two layers: the lamina lucida (or lamina rara) next to the plasma membrane and an outer lamina densa.

KEY POINT

The endomysium forms a continuous network binding together all the muscle fibers in a muscle fascicle.

Load sharing by shear through the endomysium coordinates deformations between muscle fibers and can transmit contractile forces.

Each muscle fiber has its own plasmalemma and basement membrane surrounding it. Filling the space between the basement membranes of two adjacent muscle fibers is the third layer:

3. The collagen fiber network (or reticular) layer, comprised of a network of collagen fibrils and fibers in a proteoglycan matrix. Schmalbruch (1974) reported reticular layer thicknesses of 0.2 to1.0 μm in frog sartorius muscle.

As shown by classical transmission electron microscopy images of longitudinal muscle sections (Trotter and Purslow 1992), the thickness of the endomysium varies with muscle length, becoming thicker at short muscle lengths and thinner as the muscle is extended. The fibrous reticular layer is a common structure shared between adjacent muscle cells and forms a continuous network that runs across the whole muscle fascicle. Muscle cells (with their individual plasma membranes and basement membranes) occupy the polygonal "holes" in the endomysial network, as shown in Fig. 1.2.1(D & E).

The reticular region of the endomysium is often described as a random or quasirandom network of irregularly wavy fine collagen fibers, which lie in the plane parallel to the muscle fiber surface. The network is not truly random. There is a preferred direction in the wide distribution of collagen fiber orientations, and this preferred orientation changes with muscle length (Purslow and Trotter 1994).

A large number of muscles in animals from many phyla contain intrafascicularly terminating muscle fibers, i.e., muscle fibers that are not continuous along the entire length of fascicles and do not run from tendon to tendon. Trotter (1993) lists 28 studies on a wide range of muscles from humans, amphibians, mammals and birds, showing series-fibered architecture. Muscle fibers in series-fibered muscles are relatively short compared with the length of the fascicle, particularly so in avian species where individual fibers can be as short as 0.4 to 2.6 cm. The endomysium is the only structure that links these muscle fibers together in the fascicle. Transmission of tension generated in intrafascicularly terminating fibers to the tendons at the ends of the fascicles necessitates transmission of force through the endomysial network, as this is the only structure continuously linking the fibers. The endomysium is very compliant to tensile forces acting within the plane of the network and so can easily deform to follow the length and diameter changes of muscle fibers in contracting and relaxing muscles. However, the transmission of force between adjacent muscle fibers by shear through the thickness of the endomysium (translaminar shear), as first described by Street (1983), is an efficient force transduction pathway (Purslow and Trotter 1994; Trotter and Purslow 1992; Trotter et al. 1995). Any linkage that transmits force from intrafascicularly terminating muscle fibers to tendinous attachments must not deform too much in order to be efficient. Particularly in isometric muscle contractions, any significant stretching in the length of the fascicle due to stretchy connections would result in a very poor transmission of contractile force. Purslow (2002) showed that transmission of force by translaminar shear of the endomysium fulfils this criterion; the displacements along the long axis of the muscle due to translaminar shearing of the endomysium are insignificant. The functional significance of this is that the endomysium provides a shear linkage of force from one muscle cell to its neighbors, which is highly efficient while still being able to deform easily in the plane of the network so as to allow the muscle fibers to change length and diameter as they contract and relax.

The architecture of the endomysium linking adjacent muscle fibers in continuous fibered muscles appears identical to that of endomysium in series-fibered muscles. The obvious inference is that load sharing between adjacent muscle cells is a common function in both continuous-fibered and series-fibered striated muscles and even cardiac muscle (Purslow 2008). The endomysium, therefore, forms a continuous three-dimensional connecting matrix that tightly shear-links adjacent fibers together to coordinate force transmission in a fascicle and keep fibers in uniform register.

FUNCTIONAL ANATOMY OF THE PERIMYSIUM

The amounts and spatial distribution of perimysium vary much more between muscles in the body than do those of endomysium (Purslow 1999). Using two pennate muscles from the cow and the rat, Passerieux et al. (2007) showed that the perimysium is a well-ordered structure that lies throughout the muscles. Thick amounts of perimysium enclosing large fascicles of myofibers form tubes in a honeycomb arrangement in the direction of myofibers, the walls of the tubes in continuity with tendons at their ends and in continuity with epimysium at the outer surface of the muscle. The walls of the tubes are made of two (or even more) flat layers of long wavy collagen fibers running in the same direction in each layer. The direction of collagen fibers from each layer crosses the direction of myofibers at ±55° at muscle rest length. Long, flattened bundles of collagen fibers can overlap between adjacent walls of tubes so that the assembly of tubes is a very coherent structure. Many of the wide flat cables of collagen fibers diverge into secondary sheets of perimysium, dividing the primary fascicles into secondary fascicles of myofibers, then separate successively as thinner cables separating smaller fascicles. (This is possible in the case of the muscle of the cow because the collagen fibers are up to 5 cm in length.) At the end of the process, small cables join the surface of the myofibers so that the small cables form a rather regular network of long collagen fibers (Passerieux et al. 2007) and rather regular numerous contacts with each myofiber.

The perimysial layers separating two fascicles are comprised of two or more crossed-plies of wavy collagen fibers in a proteoglycan matrix. The long axis of each set of collagen fibers lies at ±55° to the longitudinal axis of the fascicle when the muscle is at its relaxed (resting) length. This angle increases as muscle shortens and decreases if it is passively stretched out (Purslow 1989). The waviness of the collagen fiber bundles also changes with muscle length, being maximal at the resting length of relaxed muscle. Perimysium is easily deformed in tension and does not exhibit a high tensile stiffness until it has been stretched far enough that the collagen fibers have become aligned along the stretching direction and the waviness in the fibers pulled out straight (Lewis and Purslow 1989). Thus the perimysium can show a high tensile stiffness and carry large loads in tension, but only at very large extensions well beyond the range of working lengths in living muscle.

The tensile properties of the perimysium are therefore similar in nature to the endomysium, and it is tempting to suppose that the perimysium could also act to transmit the forces generated in fascicles to their adjacent neighbors by translaminar shear. Although it is undoubtedly the case that force transmission by such a mechanism can be invoked in extreme circumstances of muscle damage or surgical disconnection of the tendinous attachments to some fascicles, there are two considerations that weigh against this mechanism under normal working conditions in living muscle. First, an analysis shows that simply because perimysium is so much thicker than endomysium, deformations caused by shear through its thickness would be of orders of magnitude greater than in the endomysium, and so perimysium would represent a rather sloppy and inefficient force transmission pathway at physiologically relevant muscle lengths (Purslow 2002). Second, why should perimysial content and architecture vary so much more than the endomysium if it is fulfilling the same kind of functional role?

Schmalbruch (1985) cites an old model by Feneis (1935) supposing that perimysial structures provide "neutral" connections between muscle fascicles that allow muscle the fascicles to slide past each other, as the geometry of a muscle changes upon contraction. Measurements of "borders" between fascicles in ultrasonic images of human muscles in clinical and sports studies and their rotation on contraction allow these shear strains to be estimated. Using the values in the literature from seven such clinical studies (Purslow 2002), it is possible to show that shear strains within actively contracting human muscles are substantial and vary considerably between quadriceps, vastus lateralis, gastrocnemius, and tibialis muscles. The theory that division of muscle into fascicles facilitates shear deformations explains why fascicle shape and size vary so much from muscle to muscle. However, until detailed quantitative assessment of any relationship between perimysial architecture, fascicle size, and the distributions of shear strains in working muscles has been carried out, this theory remains just an interesting possibility. Using supersonic shear imaging (SSI), Lacourpaille et al. (2012) measured the shear modulus of 9 muscles in 30 human subjects, reporting values of shear modulus in the range 2.99 to 4.50 kPa. A review of in-vivo measurements using the same SSI techniques

(Lima et al. 2018) reported nonlinear shear modulus values in the range 15 to 70 kPa. The longitudinal modulus of the muscles increased as the degree of contraction increased, but values at maximal contractions of 258 kPa (tibialis anterior), 225 kPa (gastrocnemius medialis), and 55 kPa (soleus) were reported. So, in general, the shear stiffness of human muscles in vivo appears to be up to almost one order of magnitude lower than the maximum longitudinal stiffness of contracting muscle. This again argues that, although transmission of force by shear in the perimysium may be possible, it provides a rather flexible connection between adjacent fascicles.

PERIMYSIAL–ENDOMYSIAL JUNCTION ZONES

The endomysium surrounding muscle fibers is connected to the perimysium by intermittent perimysial junctional plates (PJPs), described by Passerieux et al. (2006).

KEY POINT

Perimysial–endomysial junction zones: the perimysium is only sporadically connected to the endomysium at the surface of a muscle fascicle by sparse junction zones. These junctions are infrequent, which may limit their ability to efficiently transmit contractile forces of the muscle, but they probably act as sites of mechanotransduction (input of mechanical signals into the muscle cells).

If, like the endomysial network, the perimysium principally acts to transmit muscle force, then the perimysial–endomysial junction must necessarily be mechanically strong and noncompliant. Alternatively, if the perimysium has only a limited role in myofascial force transmission under normal physiological conditions but is more involved in relieving shear displacements between fascicles during muscle contractions, then the connections could be expected to be more tenuous.

PJPs are staggered at the surface of each myofiber and separated by a distance of approximately 300 μm. They are made of a set of branches of collagen fibers at the end of cables (Fig. 1.2.3) that arise from the tubes separating fascicles. The branches cross the perimysial layer of myofibers and reach their surface on the top and between costameric structures, with attachments on the reticular work of perimysium and the basement membrane of myofibers.

Fracture procedures (as seen in Fig. 1.2.3) show that the perimysium remains present only in the regions where perimysial plexi are attached to myofibers, which leads to the conclusion that these points of attachment between perimysium and myofibers are rather strong and therefore allow transmission of contractile force in synergy with the endomysium. However, the long dimensions of these collagen fibers suggest that the perimysium is stressed after the endomysium and acts under large intramuscular displacements or eccentric contractions produced during downhill exercises. Measurement

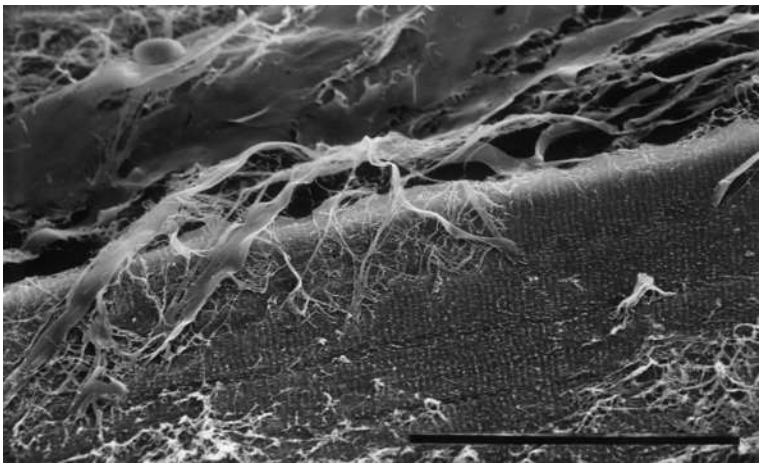


Fig. 1.2.3 View of One PJP (Junction of Terminal Branches of a Perimysial Cable on the Top with the Surface of One Myofiber at the Sarcomeric Level). Note the presence of some endomysium at the bottom of the myofiber. Bovine muscle; scanning electron microscopy; bar = 100 μm. Abbreviation: PJP, perimysial junctional plates.

of the strength of intramuscular connective tissue networks perpendicular to the muscle fiber direction showed that the force required to separate these structures connecting the perimysium and endomysium was low compared with the strength of the perimysial layer (Lewis and Purslow 1990).

PERIMYSIUM AND INTRACELLULAR SUBDOMAINS

Among the main cytoplasmic components of myofibers, nuclei and mitochondria are of importance because they control, respectively, metabolism and energetic production of myofibers, and it can be considered that their position in myofibers is of particular interest. Regarding nuclei, it was thought that they are distributed at the same distance along the myofibers, each of them at the control of a surrounding "myonuclear domain." However, Roy et al. (1999) found that nuclei have a clustered distribution along the myofibers and the number of nuclei in clusters varies with exercise. The case of mitochondria is somewhat different: they are distributed with a great regularity at the level of sarcomeres except for large subsarcolemmal accumulations. Nuclei and subsarcolemmal accumulations of mitochondria are linked to the cytoskeleton in regions where myofibers are crossed by capillaries (Ralston et al. 2006) that are embedded into the perimysium, and Passerieux et al. (2006) found that they are statistically colocalized with PJPs (Fig. 1.2.4).

In addition, the lack of the collagen VI component of perimysium is associated with apoptosis of nuclei and mitochondria of myofibers (Irwin et al. 2003), so it can be expected that the terminal branches of perimysial cables play an important role in mechanotransduction when they are stressed under myofiber contraction.

CONCLUSIONS

Muscle fasciae are important to the functioning of muscle tissues. Load transmission between tightly linked adjacent muscle fibers within fascicles allows for coordination of forces and protection of damaged areas of fibers against overextension, and, in series-fibered muscle at the very least, is a major pathway for the transmission of contractile force. Substantial evidence exists to show that perimysium and epimysium can also act as pathways for myofascial force transmission.

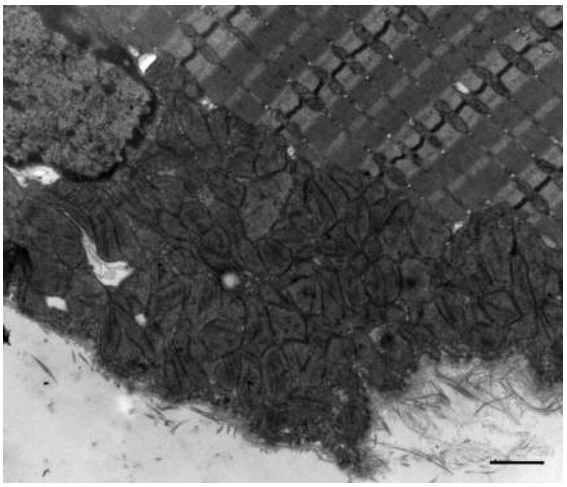


Fig. 1.2.4 View of a PJP-Associated Intracellular Subdomain. Perimysium as thin filaments at the borders of the myofiber is in the vicinity of a nucleus and a large subsarcolemmal accumulation of mitochondria. Rat muscle; transmission electron microscopy; bar = 1 μm. Abbreviation: PJP, perimysial junctional plates.

However, definition of boundaries between muscle fascicles by the perimysium may also have a role in allowing the whole tissue to accommodate large shear displacements. As detailed elsewhere in this book, muscle fasciae are in a continuous dynamic balance between synthesis and remodeling so as to be continually adapted for their mechanical roles in working muscles.

Summary

Each individual muscle is an organ, surrounded and defined by its external fascia, the epimysium. Internally, the muscle is divided into fascicles by another fascia, the perimysium, which forms a continuous network across the muscle and is joined to the epimysium. The division of the muscle into fascicles allows shape changes to occur as the muscle contracts. Within each fascicle a continuous network (the endomysium) integrates and coordinates the forces and deformations of individual muscle cells. There are sporadic junctions between the endomysium and perimysium at the surface of the fascicles that may possibly serve as pathways for force transmission but probably act as pathways for mechanotransduction, i.e., for external mechanical signals to be passed into the muscle cells to affect their expression.

REFERENCES

Avery, N.C., Bailey, A.J., 2008. Restraining cross-links responsible for the mechanical properties of collagen fibers; natural and artificial. In: Fratzl, P. (Ed.), Collagen: Structure and Mechanics. Springer, New York, pp. 81–110 (Chapter 4).

Eyre, D.R., Wu, J.J., 2005. Collagen cross-links. Top. Curr. Chem. 247, 207–229.

Feneis, H., 1935. Uber die Anordnung und die Bedentung des Bindegewebes für die Mechanik der Skelettmuskulatur. Morph Jb 76, 161–202.

Irwin, W.A., Bergamin, N., Sabatelli, P., et al., 2003. Mitochondrial dysfunction and apoptosis in myopathic mice with collagen VI deficiency. Nat. Genet. 35, 367–371.

Lacourpaille, L., Hug, F., Bouillard, K., Hogrel, J.Y., Nordez, A., 2012. Supersonic shear imaging provides a reliable measurement of resting muscle shear elastic modulus. Physiol. Meas. 33 (3), N19–N28.

Lewis, G.J., Purslow, P.P., 1989. The strength and stiffness of perimysial connective-tissue isolated from cooked beef muscle. Meat Sci. 26, 255–269.

Lewis, G.J., Purslow, P.P., 1990. Connective tissue differences in the strength of cooked meat across the muscle fibre direction due to test specimen size. Meat Sci. 28 (3), 183–194.

Light, N., Champion, A.E., Voyle, C., Bailey, A.J., 1985. The role of epimysial, perimysial and endomysial collagen in determining texture in six bovine muscles. Meat Sci. 13 (3), 137–149.

Lima, K.M.M.E, Júnior, J.F.S.C., de Albuquerque Pereira, W.C., de Oliveira, L.F., 2018. Assessment of the mechanical properties of the muscle-tendon unit by supersonic shear wave imaging elastography: a review. Ultrasonography 37, 3–15.

Listrat, A., Picard, B., Geay, Y., 1999. Age-related changes and location of type I, III, IV, V and VI collagens during development of four foetal skeletal muscles of double muscles and normal bovine muscles. Tissue Cell 31, 17–27.

Listrat, A., Lethias, C., Hocquette, J.F., et al., 2000. Age related changes and location of types I, III, XII and XIV collagen during development of skeletal muscles from genetically different animals. Histochem. J. 32, 349–356.

Passerieux, E., Rossignol, R., Chopard, A., et al., 2006. Structural organisation of the perimysium in bovine skeletal muscle: junctional plates and associated intracellular subdomains. J. Struct. Biol. 154, 206–216.

Passerieux, E., Rossignol, R., Letellier, T., Delage, J.P., 2007. Physical continuity of the perimysium from myofibres to tendons: involvement in lateral force transmission in skeletal muscle. J. Struct. Biol 159, 19–28.

Purslow, P.P., 1989. Strain-induced reorientation of an intramuscularconnective tissue network: Implications for passive muscle elasticity. J. Biomechanics. 22, 21–31.

Purslow, P.P., 1999. The intramuscular connective tissue matrix and cell/matrix interactions in relation meat toughness. In: Proc. 45th Intl. Cong. Meat Sci. Technol., 1999 (Yokohama, Japan), Available from: <http://icomst-proceedings.helsinki.fi/papers/1999_04_01.pdf>.

Purslow, P.P., 2002. The structure and functional significance of variations in the connective tissue within muscle. Comp. Biochem. Physiol. A Mol. Integr. Physiol. 133, 947–966.

Purslow, P.P., 2005. Intramuscular connective tissue and its role in meat quality. Meat Sci. 70, 435–447.

Purslow, P.P., 2008. The extracellular matrix of skeletal and cardiac muscle. In: Fratzl, P. (Ed.), Collagen: Structure and Mechanics. Springer, New York, pp. 325–358 (Chapter 12).

Purslow, P. P. (2014). New developments on the role of intramuscular connective tissue in meat toughness. Annu. Rev. Food. Sci. Technol. 5, 133–153.

Purslow, P.P., Trotter, J.A., 1994. The morphology and mechanical properties of endomysium in series- fibred muscles; variations with muscle length. J. Muscle Res. Cell Motil. 15, 299–304.

Ralston, E., Lu, Z., Biscocho, N., et al., 2006. Blood vessels and desmin control the positioning of nuclei in skeletal muscle fibers. J. Cell. Physiol. 209, 874–882.

Roy, R.R., Monke, S.R., Allen, D.L., Edgerton, V.R., 1999. Modulation of myonuclear number in functionally overloaded and exercised rat plantaris fibers. J. Appl. Physiol. 87, 634–642.

Schmalbruch, H., 1974. The sarcolemma of skeletal muscle fibres as demonstrated by a replica technique. Cell Tissue Res. 150, 377–387.

Schmalbruch, H., 1985. Skeletal Muscle. Springer, Berlin, pp 20–21.

Street, S. F.,1983. Lateral transmission of tension in frog myofibers: a myofibrillar network and transverse cytoskeletal connections are possible transmitters. J. Cell. Physiol. 114, 346–364.

Trotter, J.A., 1993. Functional morphology of force transmission in skeletal muscle. Acta Anat. (Basel) 146, 205–222.

Trotter, J.A., Purslow, P.P., 1992. Functional morphology of the endomysium in series fibered muscles. J. Morphol. 212, 109–122.

Trotter, J.A., Richmond, F.J.R., Purslow, P.P., 1995. Functional morphology and motor control of series fibred muscles. In: Holloszy, J.O. (Ed.), Exercise and Sports Sciences Reviews, vol. 23. Williams & Watkins, Baltimore, pp. 167–213.

1.3

Somatic Fascia

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CHAPTER CONTENTS

GLOBAL ORGANIZATION OF FASCIA IN THE BODY

Overview of the Organization of Somatic Fascia in the Body

When we think about the somatic portion of the body, images of skeletal muscle, bones, and joints usually come to mind. However, none of these structures can suffer much direct contact without developing significant pathology. For protective reasons, most of the somatic structures are embedded in a matrix of soft connective tissue termed fascia—the bandage or packing substance of the body. Muscles develop in a matrix of connective tissue such that the adult organ is surrounded by an epimysium; bone arises in a matrix of embryonic fascia termed mesenchyme, which in the adult form becomes the periosteum; and joint capsules consolidate out of a thickening in mesenchyme (Gardner 1963) that ultimately forms a fascial covering over the dense layers of the capsule. In each case, the fascial sheet embracing the somatic structure protects it from direct abrasion by surrounding structures while also providing a conduit through which neurovascular bundles can easily penetrate. By surrounding the components of the somatic system, fascia creates complex and continuous planes or sheets of connective tissue that unite all portions of the body and present continuous planes along which anatomists tend to dissect (Huber 1930).

The functions of fascia tend to dictate its structure. Fascia must be capable of significant distortion in multiple planes of direction and return rapidly to its native shape. This type of action is best met by constructing fascia out of irregular connective tissue where the fibrous component is interwoven; thus proper fascia is defined as connective tissue with an irregular distribution of fibrous elements as opposed to those tissues containing parallel or well-oriented arrays such as are seen in tendons, ligaments, aponeuroses, and some joint capsules (Clemente 1985; Standring 2008). The irregular weave of the fibrous component allows for easy movement and resistance in all directions but is master of none. Thus tearing fascia apart can be difficult in all planes of dissection. Conversely, because of the highly regular arrangement of collagen fibers in a tendon, ligament, or aponeurosis, these structures can provide maximal resistance of stretch in one or a limited number of directions but can easily be shredded with fingertips when stressed in orthogonal planes.

The density of the fibrous component of fascia will vary tremendously with is location and function. Thus fascia underlying the skin must be very movable and therefore has a lower density of collagenous fibers; this is often given the term *superficial fascia* (Clemente 1985;

Singer 1935; Standring 2008; Stecco 2015). Alternatively, the fascia that invests muscle, ligament, tendon, or joint capsule is providing a stronger support role and is often termed *investing fascia* or *deep fascia,* the density of its collagen fibers being considerably higher; however, they are still irregular in weave (Clemente 1985; Singer 1935; Standring 2008, Stecco 2015).

Finally, unlike the highly differentiated structures of the somatic system—muscle, tendon, ligament, and aponeurosis—fascial planes tend to lack precise borders. Muscles have fairly recognizable origins and attachments, and where they joint with tendons a precise line can be seen even in the microstructure. Attachments of muscle-tendon complexes to bone are definitive, forming an enthesis. However, the lack of precise borders seen in the fascial tissue facilitates the formation of long planes spanning multiple organ systems or compartments surrounding multiple muscles. When entering fascial compartments, neurovascular bundles—which themselves are surrounded by irregular, dense, connective tissue fascial wrappings called an adventitia—course along or through fascial planes that would otherwise represent obstacles if composed of highly organized, regularly arranged fibrous elements such as seen in an aponeurosis, tendon, ligament, or most joint capsules. Lymphatic flow, which would be quickly interrupted if forced through tissue with precise boundaries, can flow easily through lymphatic vessels distributed in the irregular tissue of the fascial plane. From this discussion it is evident that the function of fascia in the somatic body is closely associated with its structure.

A recently discovered function of fascia focuses on its role in guiding the development of limb muscles (Kardon et al. 2003). The myogenic mesenchymal cells migrate from the somites located along the lateral margins of the neural tube. Some of the migrating cells differentiate into myoblasts and give rise to myocytes, whereas others form the fascial matrix into which the myoblasts develop. Evidence supports the concept that the muscle connective tissue is required for the normal development of the muscle.

This chapter divides the fascial system of the body into four primary layers, emphasizing the somatic component, and then describe our initial understanding of the role played by somatic fascia in the development of the musculoskeletal system.

KEY POINT

Fascia is distinct from the more specialized connective tissue such as tendons, ligaments, aponeuroses, bone cartilage, and blood by its irregular organization and its function as a universal support tissue. It is also apparent that the cells of primitive fascial tissues play a significant role in guiding the initial development of more specialized tissues such as skeletal muscle.

ARCHITECTURE OF FASCIA—THE FOUR PRIMARY LAYERS

General Approach

Several attempts at characterizing the fascia system of the body have been published (Benjamin 2009; Gallaudet 1931; Singer 1935; Stecco 2015). This chapter focuses on irregular connective tissue or "proper fascia" and will describe a system of four primary layers that cover the axial portion of the body. These layers are arranged as a series of "tubes within tubes." Modification of this fundamental plan will allow accommodation of the limbs.

The four primary layers in the torso are arranged as a series of concentric tubes (Fig. 1.3.1). Starting with the outermost layer of fascia, it is best termed the **panniculus** or panniculus adiposus, a term used by Singer (1935) in his treatise on fascia and strongly recommended for general usage by Last (1978) in his textbook of anatomy. Deep to the pannicular layer is the **axial fascia** of the torso (deep fascia described in Stecco 2015). This layer gives rise to the investing fascia or epimysium of the axial muscles; peridentium and periligamentum of tendons, ligaments, and aponeuroses; and the periosteum of bone and perichondrium of cartilage. The axial layer of fascia is continuous with the **appendicular** (deep or investing) **fascia** in the extremity at the shoulders and the hips. As with the pannicular layer, the axial layer can be subdivided; however, again, in this chapter it will be treated as a primary layer. Internal to the axial fascia are two additional layers: the first surrounds the neural structures and can be termed **meningeal fascia,** and the second surrounds all body cavities and is best termed **visceral** (**splanchnic**) **fascia**. In considering the limbs, the pannicular layer extends outward covering the entire surface of the limb. Under the pannicular layer, a fascial layer of similar composition to the axial fascia is present, surrounding the muscles of the extremity, and can be termed

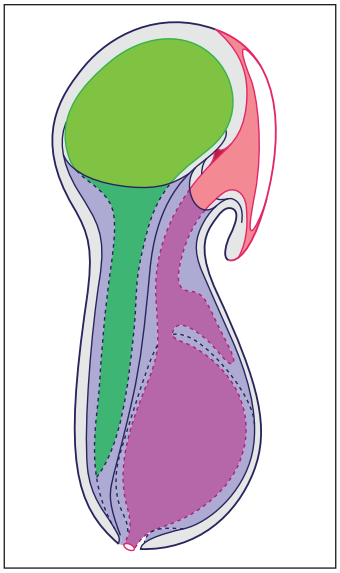

Fig. 1.3.1 The "Fascunculus". This is a schematic diagram of the fascial layers of the human. The whole diagram is covered by a panniculus of fascia (pale gray layer). The axial fascia covers the torso of the body (blue layer) but does not extend to the head. Visceral fascia extends from the naso-oro-pharyngeal region to the aboral (anal) region (red layer). Meningeal fascia surrounds the brain and spinal cord (green layer). Finally, a thin black line in the center of the body represents the notochord separating the meningeal fascia from visceral fascia. In the adult, the notochord would be replaced by portions of the vertebral column. From the Willard/Carreiro Collection, with permission.

appendicular fascia. It lies deep to the pannicular fascia and invests the appendicular muscles. Regional names often relate the fascia to a specific muscle, i.e., deltoid fascia, pectoral fascia, etc. Internal to the appendicular fascia is the intramuscular septum housing the neurovascular bundles; this septal layer is most likely to be derived from the axial fascia at the base of the limb.

KEY POINT

The fascial systems create a series of "tubes within tubes" that define the construction of the body. The outermost tube is the pannicular or superficial fascia within which is a complex tube of axial investing fascia in the torso and appendicular investing fascia in the extremities. Central to the axial fascia are two tubes separated by the notochord in the embryo and the vertebral column in the adult. These latter tubes represent the meningeal fascia posteriorly and the visceral fascia anteriorly.

Four Primary Layers of Fascia

Pannicular Fascia

The outermost layer is the pannicular fascia (Singer 1935) and is often termed superficial fascia (Clemente 1985; Standring 2008). This layer can be subdivided into several sublayers. The pannicular layer is derived from the somatic mesenchyme and surrounds the entire body, with the exception of its orifices, such as the orbits, nasal passages, and the oral and aboral openings. It is composed of irregular connective tissue with marked regional variation in collagen fiber density as well as variation in adipose cell density (Fig. 1.3.2). Whereas the outermost portion of this layer is typically invaded by much adipose tissue, the inner portion is more membranous in nature and generally very adherent to the outer portion, except over the abdomen where the two can be easily separated by blunt dissection. The thickness of the pannicular layer is highly variable in the human population. In the region of the head and neck, humans have several thin muscles embedded in the pannicular fascia; these are the platysma and associated facial muscles innervated by the facial nerve. Pannicular fascia covers both the axial and appendicular body.

Axial Fascia

The second layer is the axial or investing fascia (deep fascia, as described in Clemente [1985], Standring [2008], and Stecco [2015]). Axial fascia is fused to the panniculus peripherally and extends deep into the body, surrounding the hypaxial and epaxial muscles. This layer, like the pannicular layer, is derived from mesenchyme and forms the primitive matrix in which skeletal muscles, tendons, ligaments, aponeuroses, and joints develop. The mesenchymal matrix then contributes to the epimysium of skeletal muscle, the periosteum of bone, the peritendon of the tendons, and the investing layer surrounding the joint capsule. The peritendon subdivides into an epitenon, which grasps the regular collagenous fiber bundles of the tendon, and a paratenon, which surrounds the entire tendon; both layers form the peritendon and are constructed of irregular collagenous bundles (Jozsa and Kannus 1997). The arrangement of fascia around an aponeurosis is similar to that of a tendon or ligament; however, the terminology used has created some confusion. In the older literature, two terms exist: "aponeuroses of

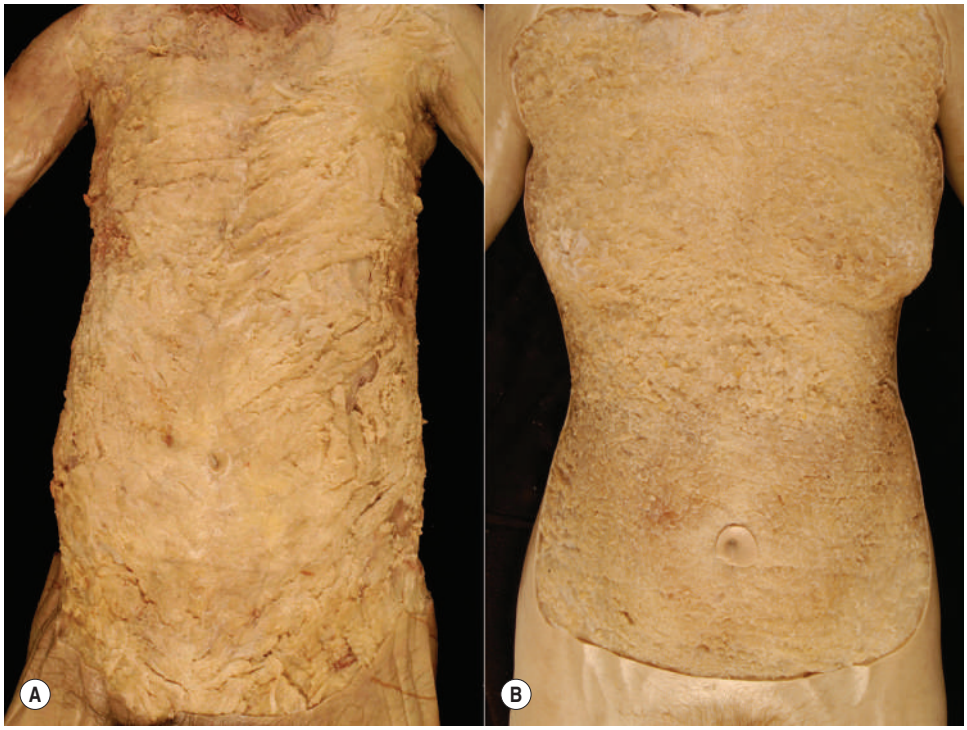

Fig. 1.3.2 The Pannicular Layer of Fascia. This is an anterior view of the thorax and abdomen of a male and female cadaver. The body on the left (A) is that of a 54-year-old male and on the right (B) a 54-year-old female. Both specimens have had the dermis removed to reveal the pannicular layer of fat and fascia. From the Willard/Carreiro Collection, with permission.

attachment" and "aponeuroses of investment" (Singer 1935). Aponeuroses of attachment referred to the well-organized bands of dense connective tissue that made up the true aponeuroses that attached the muscle to its target, whereas those "of investment" made up the irregular connective tissue composing the investing or axial fascia surrounding the true aponeuroses.

The axial fascia can be described as being composed of two, parallel, connective tissue tubes and course anterior and posterior to the vertebral column (Fig. 1.3.3A–C). Developmentally, these two tubes would be separated by the notochord, which is approximated by the vertebral column in the adult. The anterior tube surrounds the hypaxial muscles and attaches to the vertebral column at the transverse process. The hypaxial muscles include the longus and scalene muscles in the cervical region, the intercostal muscles in the thoracic region, and the oblique and rectus muscles in the abdominal region. The posterior tube of the axial fascia surrounds the epaxial muscles and is attached to the transverse processes. The spinous process of each vertebra divides the epaxial fascial tube into two "half-tubes" (Fig. 1.3.3C). The paraspinal muscles of the back are contained in the "half-tubes" of the epaxial fascia.

Complex fascial relationships exist where the extremities meet the axial portion of the body. Axial fascia extends into the extremities as the intermuscular septum and the appendicular fascia investing individual muscles (Fig. 1.3.4). The fascial sheath that surrounds the neurovascular bundles such as the brachial plexus and lumbosacral plexus extends outward to form the intermuscular septum, in which branches of the neurovascular bundle will course as they progress distally in the extremity. In the upper extremity, the axial fascia surrounding the brachial plexus is regionally termed the axillary sheath; however, it represents an extension of the axial fascia—specifically, it extends from a portion of the axial fascia regionally termed the "prevertebral