

ON THE FORM AND ARRANGEMENT IN FASCICULI OF STRIATED VOLUNTARY MUSCLE FIBERS

A PRELIMINARY REPORT

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FOUR FIGURES

In the last few decades, relatively little special attention has been given to the form of striated voluntary muscle fibers and to their arrangement in the fasciculi. In the anatomic literature of this period, consideration is given mainly to the structure of the myofibrils, to the relation of the connective tissue of the muscle to the fibers, to the development of muscle fibers and the development of the musculature as a whole. One studying current texts is impressed with the unanimity of expressed views concerning the form of muscle fibers and the question is treated as having received satisfactory solution.

Heidanhain¹ in 'Plasma und Zelle' treats of the form and length of voluntary muscle fibers as follows:

Da der Gegenstand allgemein bekannt ist, können wir uns kurz fassen. Es handelt sich um lange faserförmige Gebilde, welche in kleinen Muskeln von einem Sehnenende bis zum anderen hindurchlaufen und an diesem immer abgestumpft enden, im Inneren sehr grosser Muskeln hingegen auch frei und zwar unter allmählicher Verschmälung mit spitzen Enden auslaufen. Sie werden bei geringer Breite (9-60 μ) bis zu 12 cm. lang und daher findet man nur in Muskeln, welche, parallel der Faserung gemessen, die Ausdehnung von 12 cm. überschreiten, die erwähnten freien Endigungen.

This quotation expresses fairly well, I believe, the current views of the form and mode of ending of striated voluntary muscle fibers.

¹ Heidanhain, M., Plasma und Zelle. Fischer, Jean, 1911, p. 529.

Bardeen,² as a result of a study of teased preparations made from the external oblique of certain mammals, deviates from the current views and gives a much more correct statement as concerns the form and relations of striated voluntary muscle fibers; indeed his brief statement is one of the most accurate I have found and is here given in full. His words read as follows:

The individual muscle-fibres either run from one tendon to another or they may end at one extremity or at both within the muscle fasciculi which extend from tendon to tendon. We may therefore distinguish two modes of ending of individual muscle-fibres: the '*intratendinous*', where the tip of the fibre terminates within a definite extension of a well marked tendon; and the '*intrafascicular*,' where the muscle-fibre terminates in the midst of a bundle of other muscle fibres which have a different region of termination. In the former case the muscle-fibre has a rounded or cone-shaped termination, often swollen in isolated specimens. In the intrafascicular mode of ending the muscle-fibre gradually becomes more and more narrow until it terminates in a thread-like extremity.

In Bardeen's figures 2 and 4, types of these modes of ending and of the form of muscle-fibers are given, figure 4 including spindle-shaped fibers. Bardeen's statement of the form and mode of ending of muscle fibers, however, is antedated by the account given by v. Kölliker in his *Handbuch der Gewebelehre des Menschen*, which may be added to the references here given. Kölliker's³ account reads as follows:

Ueber die Gestalt der Muskelfasern haben besonders die Untersuchungen von Herzig und Biesiadecki, dann von mir, W. Krause, Weismann, Aeby und Kühne Aufschluss gegeben. Nach diesen Erfahrungen kann es wohl als Regel bezeichnet werden, dass die Muskelfasern im Innern grösserer Muskeln spindelförmig sind, die an den Enden dagegen ein inneres spitzes und ein in die Sehne übergehendes breites Ende besitzen, welches entweder abgerundet ist oder in einige stumpfe Spitzen ausläuft oder auch wie treppenförmige Absätze darbietet. Ausser spindelförmigen Fasern kommen im Innern der Muskel noch manche andere Formen vor, am gewöhnlichsten an dem einen oder an beiden Enden stumpfe Fasern.

² Bardeen, C. R., Variations in the internal architecture of the m. Obliquus Abdominis Externus in certain mammals. *Anat. Anz.*, vol. 23, 1903.

³ v. Kölliker, A., *Handbuch der Gewebelehre des Menschen*. Erster Band. Engelmann, Leipzig, 1889, p. 371.

Kölliker quotes E. H. Weber (the original I have been unable to find) as regarding spindle-shaped fibers as the prevalent form of striated voluntary muscle fibers.

It is not my purpose at the present time to enter upon a more extended discussion of the literature dealing with the form and arrangement in fasciculi of striated voluntary muscle fibers. It is hoped that the quotations given may suffice to orient the results here to be presented. In the course of this brief report other pertinent literature will be considered as occasion demands.

My own studies on the form of striated muscle fibers have been made largely on teased preparations. The muscular tissue was obtained largely from adult rabbits. The maceration preparatory to teasing was by the hydrochloric acid method developed in this laboratory.⁴ The method as used for the maceration of muscular tissue may be given here in detail in the hope that other workers may feel tempted to make use of it in a further analysis of this tissue, since a correct understanding of the form and arrangement of muscle fibers in fasciculi, as also their length, is of importance in valuating certain fundamental conceptions concerning the functions of muscles. For instance, according to E. Weber's law of the working capacity of a muscle we are taught that the lifting power of a muscle is proportionate to the cross section of its fibers or fasciculi when arranged parallel, while the extent of elevation is proportionate to the length of its fibers.

The method as used is as follows:

After freely bleeding an adult rabbit a cannula was inserted into one of the iliacs central to the inguinal ligament or into the subclavian before it passes under the clavicle and firmly secured by ligature. A 75 per cent solution of hydrochloric acid was then quickly injected at a pressure of 25 to 30 pounds. The apparatus used in obtaining and maintaining pressure was described by the author in the *Am. Jour. Anat.*, vol. 6.⁵ It is desirable to have the acid injected enter the tissues as quickly and as freely as possible. The pressure is maintained for several minutes. Some 15 to 20 minutes after the injection is com-

⁴ Huber, G. Carl, A method for isolating the renal tubules of mammals. *Anat. Rec.*, vol. 5, 1911.

⁵ Huber, G. Carl, The arteriolar rectae of the mammalian kidney. *Am. Jour. Anat.*, vol. 6, 1907.

pleted, the muscles are exposed and separated and removed and placed in a 75 per cent solution of hydrochloric acid. In removing a muscle care should be taken to remove the entire muscle, at least portions extending from tendon to tendon and great care should be taken not to crush the muscle during removal. The muscle pieces or entire muscles remain in the hydrochloric acid for about 3 hours, the period varying a little, depending on the thoroughness of the preliminary injection. After thorough maceration is obtained, the acid is carefully poured off and distilled water slowly added. The water is renewed at frequent intervals until it is practically free from acid. In the distilled water the muscle pieces remain about 24 hours, though a stay of 4 to 6 days is not harmful. After thorough washing in distilled water the larger pieces are usually readily broken up into smaller bundles of fasciculi. Small bundles of fasciculi are now transferred to a hemalum solution diluted to one half with distilled water. The transfer from the distilled water to the hemalum solution should be executed with care if one wishes to obtain fasciculi through their entire length. The transfer is best made with a glass rod, lifting the small bundle carefully as it leaves the water. In the hematoxylin solution the small bundles remain about 24 hours. This interrupts the maceration and stains the fibers. They may be kept indefinitely in the hematoxylin solution and are best stored in this solution for future use. In this solution the muscle bundles become quite hard and brittle and contract to about two-thirds or even to one-half of their former length. The preliminary teasing I have carried on in Esmarch dishes under the stereoscopic binocular and in a 0.5 per cent solution of ammonia water. In the ammonia water the stain attains a purple-blue color and the hard and brittle bundles become soft and pliable. A stay of one half hour to one hour in the ammonia water prepares the bundles for preliminary teasing. In the Esmarch dishes the bundles of fasciculi are with care separated into separate fasciculi. It should be stated, however, that a fasciculus is not a unit of muscle structure. For a distance all of the fasciculi of a bundle are readily separated. However, at one or several points small bundles of fibers or single fibers pass from one fasciculus to contiguous fasciculi. Great care is thus necessary and very careful teasing to completely separate what is known as a fasciculus. Bardeen² has noted the fact that muscle fasciculi are joined by fibers. After the preliminary teasing resulting in the separation of a single fasciculus, the final teasing is undertaken on a large slide or lantern slide cover prepared as follows. The slide is thoroughly cleaned in acids and alcohol and wiped dry. Narrow strips of wax plates (the plates used in wax reconstructions) 2 mm. thick are cut and placed near the borders of the slide in the form of an oblong and pressed to the slide. The slide is then gently heated until the wax strips adhere. The slide on cooling is ready for use. The shallow well thus formed is filled with ammonia water and an isolated muscle fasciculus transferred to it. The final teasing may then be undertaken. It has repeatedly been possible to separate completely all or nearly all of the muscle fibers of a given fasciculus, even with fasciculi having a length of about 6 cm. The teased fibers may then be arranged in their approximate positions. Only when this has been accomplished can a muscle fasciculus be considered as having been teased. A worker should not attempt this unless he has at his disposal some 3 to 4 uninterrupted hours, and ought to bear in mind that the best results are obtained by 'making haste slowly.' The mounting of such preparations presents many difficulties and discouragements. My procedure

is as follows: A fasciculus is teased until nearly all its fibers have been separated. The ammonia water is then very slowly and carefully withdrawn by means of a small dropper with point drawn to a capillary tube. This is undertaken under the binocular, observing the effects of currents. The water is withdrawn until only a thin layer remains, only sufficient to enable moving the fibers on the slide. The final teasing and arranging of fibers may now be undertaken. As the ammonia water evaporates, the muscle fibers begin to adhere to the slide. The wax wall may now be removed and a large cover glass, on the under side of which a thin layer of glycerin has been spread, is gently lowered over the preparation from one edge. It is necessary to obtain the right degree of drying in order to gain successfully mounted preparations. If not sufficiently adherent to the slide the muscle fibers will move, float and break. If allowed to dry too much the muscle fibers, although fixed in place, will appear fragmented. Such preparations are not valueless since the fragments of the fibers are not displaced laterally. Thus a single fiber may readily be traced throughout its whole length.

By this method of preparation the muscle fibers show only faint cross striations, though they present a blue color. The nuclei are not evident. Neither has it been possible to locate the place of entrance of the nerve fibers. The sarcolemma seems very resistant to the acid, the neurolemma less so. In the ammonia water the muscle fasciculi appear to regain the length they had prior to staining in the hematoxylin solution. The exact relation existing between the lengths as presented by teased fibers and living muscle fibers I am unable to determine definitely.

The drawings here presented were made from preparations of muscle fasciculi teased completely, and arranged on the slide in their approximate positions, approximate with reference to the ends of the fasciculus teased. The drawings were made with the aid of the camera lucida at a magnification of 50 diameters, and are reduced 10 times in reproduction. The length of the respective fibers is accurately given. The thickness of the fibers is correctly given as pertains to the thicker portions of the fibers. At the attenuated ends the ink lines follow the outer border of the pencil outlines.

The results of these observations may be briefly recorded as follows:

It is usually stated that in muscles having relatively short fasciculi the muscle fibers extend from tendon to tendon. This is of course not determined by the size and length of the muscle as a whole since in semipinnate, pinnate and compound pinnate muscles and in muscles where distal and proximal tendons overlap the lengths of the respective fasciculi of a given muscle are much shorter than the length of the muscle as a whole.

In figure 1 are presented some muscle fibers teased from fasciculi taken from the gastrocnemius of an adult rabbit. The fibers in group A, drawn from a completely teased fasciculus taken from the proximal portion of this muscle have an actual length of 1 cm. (these and all measurements given are obtained by dividing the length of the respective fiber as measured in

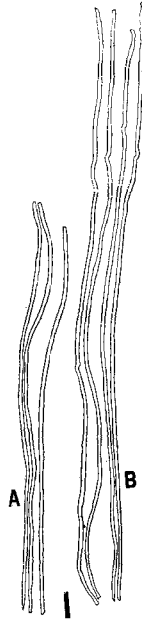


Fig. 1 Muscle fibers from the gastrocnemius of an adult rabbit. Group A, actual length 1 cm., from fasciculus taken from the more proximal portion of the muscle. Group B, actual length 1.5 cm., from fasciculus taken from the more distal portion of the muscle. $\times 5$.

the drawing by 50, the drawing having been made at a magnification of 50 diameters). The fibers in group B have an actual length of 1.5 cm. and are from a completely teased fasciculus taken from the more distal part of the same muscle. In all of the fasciculi from this muscle completely teased, the great majority of the muscle fibers extend from end to end or from tendinous insertion to tendinous insertion. In material prepared as above described, at the place of termination of a muscle fiber

in tendon, the end of the muscle fiber stains more deeply in hematoxylin than does the same fiber in close proximity. The true end of the fiber differs in appearance from the end of a broken fiber. The tendon ends of various fibers vary slightly in shape. They may appear as if cut at right angle to the fiber, as slightly beveled, as slightly rounded, tapering a little or having the form of a blunt cone and now and then as slightly expanded, though this may be due to a slight flattening of the end of the fiber. Now and then tendon ends of muscle fibers are met with that give the impression as though the sarcolemma did not enclose the end but terminated ring-shaped at the extreme tendon end of the respective fiber, but the limitations of the method used are such that this question could not be conclusively decided. In this connection it is of interest to note the observations of O. Schultze,⁶ who believes that muscle fibrils and tendon fibrils are parts of a single structure but this observer adds that the behavior of the sarcolemma at the ends of the fibers deserves further study. Also the studies of Baldwin,⁷ who regards the sarcolemma as covering the tendon ends of muscle fibers and denies the continuity of muscle fibrillae and tendon fibrillae, and discusses two types of terminations of muscle fibers in tendon; one type in which the long axis of muscle and tendon fibers coincide, the other type in which they meet at an angle. In the former the tendon fibrils are attached to cone shaped processes of the sarcolemma dovetailed into the tendon ends; in the latter type the sarcolemma end is considerably thickened and presents a number of projections into the muscle substance. Digitations or branchings of muscle ends or step formations have not been observed by me in my teased preparations. It should be understood, however, that in successfully macerated preparations the collagenous connective tissue is so completely removed that it is not evident on teasing. Out of quite a number of fasciculi with fibers of type B, of figure 1,

⁶ Schultze, O., Über den direkten Zusammenhang von Muskelfibrillen und Sehnenfibrillen. *Arch. f. Mik. Anat.*, vol. 79, 1912.

⁷ Baldwin, W. M., The relation of muscle fibrillae to tendon fibrillae in voluntary striped muscle of vertebrates. *Morph. Jahrb.*, vol. 45, 1913.

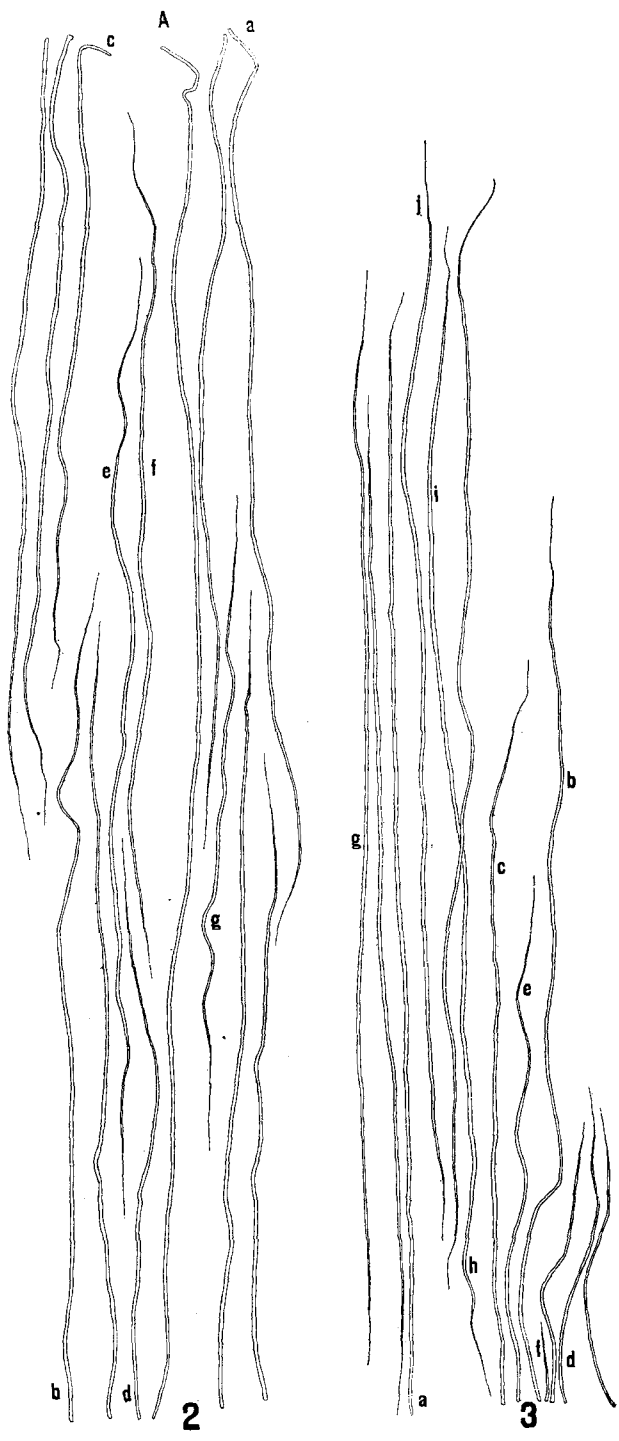
successfully and completely teased, in only two and in each only one fiber was found which did not extend from tendon end to tendon end. In both of these fibers one end reached the tendon, terminating as adjacent fibers, while the other end reached to about the middle of the fasciculus ending in a fine tapering filament. The fibers in a number of fasciculi having muscle fibers of the length of type B were counted and averaged about 20 fibers to a fasciculus.

What length a muscle fasciculus of an adult rabbit may attain and still have the great majority of its fibers reach from end to end is a question I am at present unable to answer definitely. Of the muscles teased, none in which the contained fasciculi reached a length of a little over 2.5 cm. did I find such in which the majority of the muscle fibers reached from end to end. However, samples have not been taken from nearly all of the muscles and it may be that in certain of them fasciculi having a length of over 2.5 cm. in which the majority of the fibers extend from end to end, may be found.

In figure 2 are presented type fibers obtained from a completely teased and successfully mounted fasciculus, taken from one of the adductor muscles of the thigh of an adult rabbit. In this fasciculus a single muscle fiber (A) extends from end to end or from tendon insertion to tendon insertion; both extremities showing the characteristic staining and appearance of the tendinous end of a muscle fiber. This fiber has an actual length of 3.64 cm., a length which is regarded as the length of the fasciculus. After final teasing and after withdrawing the ammonia water

Fig. 2 Muscle fibers from the thigh adductor of an adult rabbit. Teased fasciculus had a length of about 3.5 cm. The completely teased fibers are in the drawing placed with reference to the ends of the fasciculus. Fiber A, has actual length of 3.64 cm.; a, 2.1 cm.; b, 1.8 cm.; c, 1.5 cm.; d, 1.3 cm.; e, 2.1 cm.; f, 1.9 cm.; g, 1.7 cm. $\times 5$.

Fig. 3 Types of muscle fibers teased from a single muscle fasciculus, having a length of a little over 4 cm., taken from one of the larger thigh muscles of a rabbit. This fasciculus contained 37 fibers. The fibers are arranged with reference to an imaginary line, bottom of figure. The tendon ends of fibers ending intrafascicular are brought to this line. Certain of the fibers sketched have an actual length as follows: a, 2.9 cm.; b, 2.4 cm.; c, 1.92 cm.; d, 0.9 cm.; e, 1.4 cm.; f, 0.14 cm.; g, 2.9 cm.; h, 3.04 cm.; i and j, 2.9 cm. $\times 5$.



from the well on the slide, as explained in the detailing of the method used, I was able to arrange the teased fibers so as to have the tendon ends of the teased fibers reach imaginary lines drawn at right angles to the ends of the single muscle fiber which extends from end to end in this fasciculus. The spindle-shaped fibers hold approximately the same relative position with reference to the ends of the fasciculus as before teasing as was determined at the time of teasing. This fasciculus, completely teased, contains 26 muscle fibers, of which as stated one passes from end to end, 10 others reach one tendon end, 12 the other tendon end and 3 are spindle shaped fibers reaching neither tendon end. Of the 26 fibers, 15 type fibers are given in figure 2. This bundle of fibers completely teased is here spoken of as a fasciculus. I have above stated that fasciculi are not units of structure, but that from each small bundles of fibers or single fibers pass from one fasciculus to contiguous fasciculi. A single 'fasciculus' completely separated constitutes thus an artificially separated bundle of muscle fibers. Thoma⁸ has also appreciated the fact that a muscle fasciculus is not a unit of structure. In serial cross sections of the gastrocnemius of the frog, in which, with the aid of the camera lucida, the outlines of the muscle fibers were sketched serially he noted single muscle fibers passing from one muscle fasciculus to another, concluding as follows: "Die einzelnen Muskelfaserbündel hängen somit vielfach durch Muskelfasern zusammen, welche bald mit dem einen, bald mit dem anderen Bündel sehr innig verbunden sind, und die ganze Muskelmasse bildet ein stark in die Länge gezogenes Netzwerk von Muskelfasern." The fasciculus above referred to as containing 26 fibers is to be considered in this light. In the figure as drawn, at each end 5 fibers begin with blunt ends showing by form, structure and staining that they are muscle fibers ending in tendon. Each of the fibers extends into the fasciculus for a distance which varies for the several fibers, becoming attenuated and finally terminates in a thread like filament having a thickness of 3μ to 4μ . It requires very

⁸ Thoma, R., Über die netzförmige Anordnung der quergestreiften Muskelfasern. Virchow's Archiv, vol. 191, 1908.

thorough maceration to enable one to separate completely these fine, intrafascicular terminations of the muscle fibers. The length of the muscle fibers having one tendon end at the end of the fasciculus, the other ending in an intrafascicular filamentous termination varies as follows; fiber a, 2.1 cm.; fiber b, 1.8 cm.; fiber c, 1.5 cm.; fiber d, 1.3 cm. The other fibers of this type sketched are intermediate in length between fibers a and d. The three spindle shaped intrafascicular fibers with both extremities attenuated and neither end reaching the tendon ends of the fasciculus measure as follows, fiber e, 2.1 cm.; fiber f, 1.9 cm.; and fiber g, 1.7 cm. The extent of overlapping of fibers beginning at the tendon end of the fasciculus and ending intrafascicular in fine, attenuated ends may be noted in this figure (2). Their exact relation cannot be readily seen in a completely teased preparation, with fibers separated and arranged on the slide. To gain their relationship actual teasing is necessary. While teasing the details of the arrangement of the muscle fibers becomes evident and it is observed that the fine filamentous intrafascicular ends are applied usually to the thicker portions of other fibers, usually not near a filamentous end of another fiber. The same is true of the ends of the spindle-shaped fibers reaching neither fascicular end. This figure (2) I regard as representative of the form and arrangement of the striated voluntary muscle fibers in the fasciculi of rabbit muscles having a fascicular length of from about 3 cm. to about 5 cm. Probably the same is true of voluntary muscle of other vertebrates, though my observations have not been extensive outside of rabbits and birds (rooster).

In muscle with longer fasciculi the length of the muscle fibers having blunt tendon ends and filamentous intrafascicular terminations varies more than indicated by the measurements above given, and the spindle shaped fibers with intrafascicular position may lie nearer one end or the other of the respective fasciculus or occupy a more middle position. This variation in the length of the muscle fibers I have indicated in figure 3, giving type fibers from a fasciculus having a length of somewhat over 4 cm., and taken from one of the thigh muscles. Un-

fortunately the specific muscle could not be determined after the maceration. This fasciculus was also completely teased and successfully mounted. It contains 37 fibers of which 8 are spindle shaped and have an intrafascicular position. In it one fiber extends from end to end, through the length of the fasciculus. The fibers could readily have been sketched in approximate relative position with reference to the ends of the fasciculus, but the resulting figure, at the magnification used, would have been too long to admit of publication in the pages of this Journal. The arrangement of the fibers, however, is not unlike that presented in figure 2. For figure 3, type fibers were selected. The single fiber extending from end to end could not be included by reason of its length. The fibers having a tendon end are arranged with reference to an imaginary line, at the bottom of the figure; the tendon end being brought to this line. Of certain of the fibers with tendon ends and intrafascicular filamentous terminations the actual lengths are as follows, fiber a, 2.9 cm.; b, 2.4 cm.; c, 1.92 cm.; d, 0.9 cm.; e, 1.4 cm.; f, 0.14 cm. The spindle shaped fibers sketched with both ends terminating intrafascicular with filamentous endings present the following measurements, fiber g. 2.9 cm.; h, 3.04 cm.; i and j, 2.9 cm. The single fiber extending through the entire fasciculus presents a length of almost 4.5 cm.

For rabbit muscle fasciculi having a length of more than 4.5 cm. to about 5 cm., so far as my observations go, there are no muscle fibers that extend the whole length of a respective fasciculus. In some of the longer fasciculi taken from the latissimus dorsi, the pectoralis major and the extensor cruris almost complete teasing was obtained. Many muscle fibers were completely isolated, though never all of the fibers of a given fasciculus. In some of the most successfully macerated fasciculi, their distal ends were slightly crushed during removal, so that not all of the fibers could be traced to their tendinous ends. For final teasing of these longer fasciculi, lantern slide covers answer the purpose of slides very well. In the longer fasciculi, having a length of 6 cm. to about 6.5 cm., in which many fibers were completely isolated, no fibers were found

reaching from end to end. Fibers with blunt tendon ends and filamentous intrafascicular terminations, these, severally of varying lengths, and spindle shaped fibers with intrafascicular position, with ends terminating in hair like processes, constituted the types of fibers isolated. In these longer fasciculi one end of certain of the spindle shaped fibers reaches nearly to one or the other tendinous end of the respective fasciculus while others of the spindle shaped fibers have a more nearly central position, with reference to the length of the fasciculus. In the longer and longest fasciculi teased, no muscle fibers having a length of more than about 3.5 cm. were observed.

Felix⁹ is quoted as having isolated striated muscle fibers approaching a length of about 12 cm. In his account stress is laid on the fact that in the macerating fluids used, acids mainly, the muscular tissue contracts by one-third to two-thirds of the original length. In his own material he sought to obviate this contraction by maintaining the original length through tension. I have noted the fact that in the method used, hydrochloric acid is injected into the living muscle while under extension, that during immersion in the hydrochloric acid and in the hematoxylin stain, a contraction of the muscle fasciculi to about two-thirds to one-half of their original length is obtained, but also that in the ammonia water fasciculi of muscle taken from the hematoxylin solution extend in length so as to approach very nearly their length in fresh muscle. Exact measurements I am unable to give since, obviously, it would be necessary to isolate at least small bundles of fasciculi from fresh muscle, and trace them through the various steps, making measurements at various stages. Of the longest fibers isolated by Felix, one from the gracilis of man measured 11.5 cm. and one from the sartorius of man 12.3 cm.; the latter fiber having a broken end. Division of fibers was not seldom found. A figure of a single fiber with branchings is reproduced natural size. This fiber in the figure measures approximately 12 cm. Concerning this fiber the text speaks as follows: "Die Faser theilt sich, lässt

⁹ Felix, W., Die Länge der Muskelfaser bei dem Menschen und einigen Säugethieren. Festschrift, Albert von Kölliker, Englemann, Leipzig, 1887.

Spalträume erkennen, steht mit anderen Fasern in Verbindung, kurz um, das Bild wird durch vielfach abgehende Fasern ein so complicirtes, dass man ein Gewirr von mehreren Fasern vor sich zu haben glaubt, bis eine genaue mikroskopische Untersuchung ihre Zusammengehörigkeit nachweist." Felix teased unstained tissue. I have not teased human muscle. However, the figure presented by Felix is not unfamiliar to me. In incompletely macerated tissue such 'fibers' are now and then obtained. However, they are interpreted by me as representing an incompletely teased fiber complex. The fine hair like intrafascicular ends of muscle fibers are so closely applied to the sides of other fibers that the cross diameter of the thicker fiber is scarcely increased. Such a misinterpretation, I can conceive, may readily be made in incompletely macerated and teased muscle tissue. Felix gives data concerning the length of muscle fibers in the rabbit, a tissue with which I am familiar. This observer isolated fibers from the pectoralis, sartorius, latissimus dorsi and extensor cruris of the rabbit. His own words concerning them read as follows: "Hier waren fast sämtliche Fasern mindestens 5 cm. lang, doch waren unter 6 cm. nur wenige zu erzielen. Die meisten Fasern schwankten zwischen 6.0 und 7.5 cm. Die Fasern zeichneten sich sämtlich durch ihre Stärke aus. Die längste Faser isolierte ich aus dem extensor cruris, der am Thiere selbst nur 8 cm. mass, von 8 cm. Länge. Die Dicke war ungemein schwankend, dickere und dünnere Stellen wechselten ab, die dünnste Stelle mass nur 0.0109 mm., während dickere Stellen 0.111 mm. gemessen wurden. Offenbar sind hier verschiedene Wirkungen der Salpetersäure zur Geltung gekommen. Theilung konnte ich häufig beobachten."

An analysis of this statement from Felix in the light of my own investigations leads me to conclude that this observer did not obtain completely teased muscle fibers. Many hundreds of muscle fibers of the rabbit have been completely isolated and in no instance have I observed branching of fibers. Often have I seen apparent branching, but on careful teasing such structures have been separated into several fibers. The variation in thickness of the long fibers referred to in the above quotation, I be-

lieve, is explained by a linking in chain of several fibers. Even granting that the fasciculi teased by me after a stay in ammonia water, some attaining a length of about 6.5 cm., had not attained their full, original length, the difference in the length of muscle fibers of the rabbit teased by Felix and by myself is not accounted for. Felix found few attenuated ends of fibers with intrafascicular terminations, while, as my own figures show, these are numerous. In the light of these studies I am inclined to regard the measurements of the length of striated voluntary muscle fibers as given by Felix as inaccurate and as made on incompletely teased muscle tissue, and to regard the figures given by earlier observers as more accurate. These, to quote freely from Felix, are for the medium length of muscle fibers of man 2 cm. to 3.5 cm., Krause giving as the longest of the fibers of the sartorius 4 cm.

Striated voluntary muscle fibers of other mammals and other vertebrates have thus far been only incidentally teased by me. Bardeen's² figure 4, b, gives a flat band of fibers dissected from the external oblique of a dog, having a length of approximately 15 cm. (figure one-half natural size) with figures of completely isolated fibers; spindle shaped fibers having a length of approximately 8 cm. and fibers with blunt tendon ends and attenuated intrafascicular terminations, varying in length from approximately 4 cm. to 6 cm. The general shape of these fibers appears to me as correctly drawn. Since I have not teased muscle fasciculi of the dog I am unable to verify the accuracy of the measurements given. For the dogs muscle fibers Felix gives 3 cm. to 4.5 cm. as common measurements and 5.5 cm. to 6.5 cm. as long fibers.

Opportunity presented itself to tease muscle fibers of an adult rooster (*Gallus domestica*), injected with hydrochloric acid for other purposes. In one specimen, the thigh muscles were well macerated. In figure 4 are shown four completely teased spindle shaped fibers taken from these muscles. These fibers, some of which are among the longest completely teased, present the following measurements: fiber a, 3.2 cm.; b, 3 cm.; c, 3.2 cm. and d, 2 cm. Several spindle shaped fibers with intra-

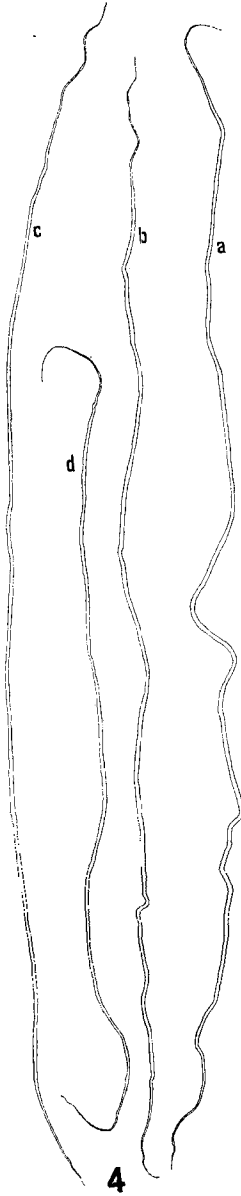


Fig. 4 Spindle shaped muscle fibers teased from the thigh muscles of an adult rooster (*Gallus domestica*). Actual length of fibers, a, 3.2 cm.; b, 3 cm.; c, 3.2 cm.; d, 2 cm. $\times 5$.

fascicular position, with undoubted branching were observed. The division extended to about the middle of the respective fibers, the two parts terminated in attenuated, hair like fibers. Muscle fibers with blunt tendon ends and filamentous intra-fascicular terminations were also observed.

It is the purpose, as opportunity presents, to include in this study fibers from different types of muscles from the different classes of vertebrates and to extend the investigation so as to include several different mammals with types of muscle from each.

Schiefferdecker¹⁰ and certain of his pupils have spent infinite pains in determining, among other things, the relative thickness of muscle fibers. The thickness and form of muscle fibers these workers have determined largely in cross sections of various muscles. Each muscle is said to be composed of muscle fibers having specific size and form (cross section) with specific arrangement of connective tissue and elastic fibers. It is recognized that in each muscle, muscle fibers of varying sizes are found. In many muscles this difference in size of fibers is said to be considerable, in others less so. This difference in size of fibers may be ascribed, according to Schiefferdecker, to two possibilities: 1, the muscle may be composed of fibers which in reality differ in size; 2, the smaller and smallest cross cut fibers of a given cross section may represent cross sections of the ends of fibers terminating in the muscle. In considering the structure of muscle, he adds, the second possibility plays only an unimportant rôle, and only as concerns the smallest fibers. The fibers sketched in figures 2 and 3 may serve to show that such contention is difficult to support in the light of this work. Except for muscles in which the fibers of the respective fasciculi extend from end to end, or in which the majority of the fibers do this, the variation in the size of the fibers in a given cross section is largely dependent on the fact that many of the fibers of a given fasciculus do terminate intrafascicularly. In order to make the numerous measurements of Schiefferdecker and his pupils of real value, or of similar investigations, it would be necessary to ascertain by means of teasing and complete isola-

¹⁰ Schiefferdecker, P., *Muskeln und Muskelkerne*. Barth, Leipzig, 1909.

tion of fibers, the arrangement of the fibers in the fasciculi of muscles, the fibers of which are measured in cross sections.

MacCallum's¹¹ investigations led him to conclude, as a result of counting the fibers of the sartorius muscle in man at various ages that the muscle fibers cease to multiply in the fetuses from 13 cm. to 17 cm. in length, and that after that period muscles increase in size by increase in size of individual fibers. This statement, it would seem to me, needs verification and could only be verified by study of muscles in which all of the fibers of the fasciculi extended from end to end or by very careful and painstaking teasing, of fasciculi, covering the several periods in which the muscle fibers are counted.

Myofibrils are usually regarded as extending from end to end in a given muscle fiber. In muscle fibers having filamentous intrafascicular terminations, and this includes the majority in the longer fasciculi, this is obviously not the case. Concerning the relations of the ends of myofibrils not reaching the ends of the respective muscle fibers, my teased preparations give no evidence. The festooning of the sarcolemma, described by certain authors, may perhaps be brought in relation with the ends of myofibrils which do not extend the entire length of the muscle fiber.

In this communication the expression "completely teased and isolated muscle fibers" has been repeatedly used. Therefore it will no doubt seem paradoxical, for me to express in this concluding paragraph, even tentatively, the view that striated voluntary muscle is syncytial in character.

From the arrangement of muscle fibers in the fasciculi of striated voluntary muscle; from the fact that muscle fasciculi are not units of structure; from the further fact that in teasing muscle fibers there are always found points of contact where the fibers are ultimately separated with great difficulty, I am led to tentatively express the view that striated voluntary muscle tissue presents syncytial character even in its fully developed state, as does involuntary muscle and cardiac muscle, though

¹¹ MacCallum, J. B., On the histogenesis of striated muscle fibers and the growth of the human sartorius muscle. Johns Hopkins Bull., 1898.

not to the same degree as the last named. This question cannot be finally decided by teasing. It is not my purpose at the present time to enter upon the mooted question of the histogenesis of voluntary muscle tissue, nor to consider the extensive literature involved. The problem of the syncytial character of voluntary muscle is one of histogenesis. Embryological evidence at hand indicates that the histogenesis of voluntary muscle lends support to the view that striated voluntary muscle is syncytial in origin. Material is being collected to determine this question if possible. One of Schiefferdecker's¹⁰ general conclusions reads as follows: "Muskelnetze fanden sich in den untersuchten Muskeln so vielfach, dass man sie wohl als eine allgemein verbreitete Erscheinung ansehen kann." Thoma⁸ finds frequent anastomoses between fibers. Reference, however, is not had to anastomoses between fibers such as described by Thoma. This observer finds intimate contact between adjacent fibers, so that for a distance only a single layer of sarcolemma appears to separate them. Myofibrils are not thought to pass from one fiber to another. It has seemed to me that this may be verified in teased preparations. Now and then two fibers adhere together, for a short distance, so closely, that separation, even in well macerated tissue, is impossible; this very generally in thicker portions of fibers. Involuntary muscle, if successfully macerated in potassium hydrate or by the hydrochloric acid method here detailed is readily teased so as to present spindle shaped cells, although as shown by McGill¹² this muscle develops from mesenchyme, retaining its syncytial character. The mere arrangement of striated, voluntary muscle fibers in a fasciculus possessing fibers with attenuated intrafascicular terminations, is such as to suggest the syncytial character of this tissue. In partially teased, though well macerated tissue, a mesh work of fibers, with long meshes is now and then evident. It is usually possible to tease the fibers having intrafascicular termination, quite readily, so far as concerns the thicker portions of these fibers and to isolate them to near their thread like terminations

¹² McGill, Caroline, The histogenesis of smooth muscle in the alimentary and respiratory tract of the pig. *Monatschrift Anat. u. Phys.*, vol. 24, 1907.

on other fibers. Near their intrafascicular ends they adhere very tenaciously to adjacent fibers. In ammonia water the macerated and stained fibers become quite pliable and present an elasticity and a tensile strength which is often surprising. Yet, often the finer ends are broken before they can be detached from adjacent fibers. It is evident that the relations of the intrafascicular ends of muscle fibers to adjacent fibers is different at their attenuated terminations than in course. Their exact relation I am unable to determine in teased preparations, though even the finest ends often present the appearance of a torn sarcolemma which does not extend to the extreme tip. I am unable to state whether the myofibrils extend from the attenuated ends to fibers on which they appear to end. In a number of preparations of rabbit embryos of the tenth day, cut serially in the sagittal plane, sections having a thickness of $2\ \mu$ and $3\ \mu$, stained in iron-lac-hematoxylin, the syncytial character of the cells from which the voluntary muscle tissue is developing is evident. Conclusive preparations, from embryos varying in ages, have thus far not been obtained. This question shall form the subject of a further study now under way. It may be recalled here that Godlewski¹³ considers striated muscle as presenting a syncytial character, basing his deductions on a study of the histogenesis of skeletal and heart muscle.

It is impossible at the present time to do more than suggest that striated voluntary muscle, like involuntary and cardiac muscle, presents a syncytial character, evidence of which is seen in its full development.

¹³ Godlewski, E., Die Entwicklung des Skelet- und Herzmuskelgewebes der Säugethiere. Arch. f. Mik. Anat., vol. 60, 1902.