A CONTRIBUTION ON THE NERVE TERMINATIONS IN NEURO-TENDINOUS END-ORGANS.

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With Plates XIII to XVIII.

Some years ago, the writers undertook a series of researches on the innervation of muscular tissues in the belief that many of the points still in dispute concerning the termination of the nerve fibers and their relation to the elements of the tissue might receive further elucidation, if, in such investigation, the nerve fibers were stained differentially by means of a method or methods which would admit of the making of thin sections of the tissues to be studied. The method selected was the intra-vitam methylen blue method, using ammonium picrate and ammonium molybdate as fixatives. We have thus far presented observations on the motor endings in voluntary muscle, heart muscle and involuntary muscle, sensory ending in the neuro-muscular spindles, sensory ending in the extrinsic eye muscles of the rabbit, and sensory endings in the tendons of the extrinsic eye muscles of the cat.

In the present contribution it is our aim to give the results of extended observations on the ending of nerves in the neuro-tendinous end-organs which, both from an anatomic and physiologic standpoint, must be and are regarded as end-organs associated functionally with muscular tissues. This investigation embraces observations made on neuro-tendinous end-organs of the frog, tortoise, bird, rat, rabbit, cat and dog. Our mode of procedure was in each case as follows:

A 1 % solution of methylen blue in normal salt was injected into the artery supplying the region in which the neuro-tendinous end-organs to be studied were situated, until the part assumed a distinctly blue color. Some thirty minutes to one hour after the injection, the muscles and tendons to be studied were quickly exposed and removed to a slide moistened with normal salt and were then placed in one or the other of the fixatives mentioned, as soon as the nerve terminations were clearly seen under the microscope. Many end-organs from each of the above mentioned vertebrates were, after staining in methylen blue, fixed in ammonium picrate and cleared in glycerine-ammonium-picrate; the ending was then carefully teased out under the dissecting microscope and mounted in the glycerine-picrate solution.

By this method, preparations are obtained, in which the general structure of the nerve-ending, its relation to the tendon fasciculi and muscle fibers and the general distribution of the nerve fiber or fibers terminating in the ending, as also the configuration of the ultimate ending of the nerves, may be readily made out. Other neuro-tendinous end-organs were, after staining, fixed in ammonium molybdate, dehydrated, embedded in paraffin and sectioned, transversely or longitudinally, the sections were then fixed to the slide or cover glass and counter-stained in alum carmine. In such preparations, the relation of the ultimate ending of the nerve-fibers to the other structural elements of the end-organs is clearly brought out. Some few end-organs, after staining and fixing in ammonium molybdate and after dehydration, were cleared in xylol, teased, and mounted in balsam.

The literature bearing on nerve terminations in tendinous tissue may appropriately be divided into observations antedating and those following a communication on this subject, which we have from the pen of Golgi, to whom must be given the credit of first recognizing in tendon a special nerve end-organ.

Rollet, as early as 1876, drew attention to a nerve plexus and a nerve network in the musculus sterno-radialis of the frog. After describing in detail the procedure used for exposing and removing the muscle and the methods employed in bringing to view the nerve fibers and endings (dilute hydrochloric acid, nitric acid, osmic acid and gold chloride), the author describes a plexus of medullated fibers and a termination which he designated as "*Nervenschollen.*" These endings, he states, are in the substance of the tendon and have many points of resemblance with the end-plates of striped muscle fibers. That Rollet had before him the neuro-tendinous endings of the frog, can hardly be questioned from his description and from the figures given. The methods employed by him revealed, however, little else than the medullated portions of the nerve fibers going to this ending.

Contemporaneously with the above communication, appeared one by Sachs, who, at the instigation of Kühne, in whose laboratory the research was carried on, examined tendons of the frog, salamander, sparrow, rat and cat. In the frog, nerve fibers were found in the musculus sterno-radialis and musculus semi-tendinosus. In the salamander, nerve fibers were found in several tendons; in the sparrow, the leg and wing tendons were examined with negative results. In the mouse, nerve fibers were readily demonstrated in the long tendons of the tail, near the insertion of the muscle fibers into these tendons, and also in the diaphragm; in the cat also in the tendons of the tail and a few in the patellar tendons. In these tendons, cleared in dilute mineral acids, the nerve fibers could be traced until they lost their medullary sheaths and the figures given by Sachs show that he recognized the branching of medullated fibers in the nerve-ending in question.

With the gold chloride method, this investigator obtained a number of preparations, especially from the salamander and frog, which he interpreted as showing the ultimate ending of the nerves in tendon. Several types of endings are mentioned: one in which the medullated nerves end in an interlacing network of fine fibers, ("Die markhaltigen Endzweige der Faser lösen sich in ein wirres Gestrüpp markloser Aestchen auf, die nach allen Richtungen sich myceliumartig verfilzen ").

Another form of ending to which Sachs assigns a secondary position was found in the tendons of the frog. As the description given by him approached one which may now be given of these endings as found in the frog, we give it in his own words: "Es finden sich nämlich einzelne Fasern, namentlich in Froschsehnen, welche pinsel-förmig in eine Anzahl sehr feiner, blasser Aestchen ausstrahlen. Die letzteren sind mit wenigen spindleförmigen Kernen versehen, und verlaufen über grössere Strecken des Präparates ohne sich weiter zu verästeln. Sie endigen wahrscheinlich Spitz."

To the nerves terminating in tendon, Sachs ascribes a sensory function, believing that they subserve the muscle sense.

Gemt's investigations on nerve-endings in connective tissue did not materially further our knowledge concerning this question. His investigations on the nerve endings in tendons of mammalia gave negative results. Concerning the nerve endings in tendons of frogs and lizards, he says: "From the several medullated branches of the nerves going to tendon, there proceed varicose fibers of variable size, which branch often and now and then anastomose; these end free in the tissues without any terminal enlargement."

Golgi's observations on this subject were much more comprehensive and must be regarded as fundamental to our more accurate knowledge of the special sensory end-organs in tendon, especially with reference to those found among the higher vertebrates. His own summary of the literature preceding his publication may be here inserted, as it states comprehensively the status of the question under consideration at the time he began his work. He says: We may say, therefore, that while we possess a fairly detailed knowledge concerning the nerves ending in the tendons of lower vertebrates (frog and lizard), concerning the problem of the connection of the nerves with the tendons of higher vertebrates in general and man in particular, our knowlege has not been materially advanced since Kölliker stated that he had observed in the tendons of small bats, numerous nerves spreading out superficially. In larger tendons of man, tendo Achillis, tendon of quadriceps extensor and central tendon of diaphragm, the nerves enter with the blood vessels. In fascias, tendinous sheaths, and synovial sheaths, he had discovered no nerves.

Golgi's observations extended over those made on the tendons of man and several other mammals (rabbit, dog, cat and mouse), birds (sparling, finch and swallow), amphibia (frog) and reptilia (lizard). For reasons above given, they will be considered somewhat fully.

In the lizard, tendon endings were found by Golgi in muscles of the anterior and posterior extremity and in several small tendons belonging to muscles of the vertebral column and tail. The endings were found near the muscular end of the tendon. The nerve fibers terminating in tendon could usually be distinguished from the motor fibers; the former could usually be traced for long distances in one direction, branches being given off at relatively long intervals, often at right angles. When the nerve fibers reach the transition zone between muscle fibers and tendon, they send off branches at quite regular intervals, which may, after a short course, lose their medullary sheath, and terminate in the ending or may divide into secondary and tertiary branches before losing the medullary sheath, each branch presenting its own ending. The end-apparatus is described as follows: The axis cylinder, after losing its medullary sheath, divides into two, three or four branches; each of these branches gives off in various directions numerous other fibrils, which again divide into branches of utmost fineness, which anastomose and intertwine forming a network with irregular meshes, at the nodal points of which thickenings are found. Such an end-apparatus measures 60-110 μ in length and 40-50 μ in breadth and is not only spread out over the surface of the tendon, but extends to some depth embracing several tendon fasciculi. Oval nuclei were now and then found on the fibrils of the network, especially on the primary branches.

The endings found in the tendons of the frog were essentially as above described for the lizard, except that the end-apparatus was somewhat larger and its fibrils finer. The endings in the lizard and frog are not surrounded by a special sheath, being distingushed in this respect from endings found in birds and mammals. (*Vide infra*).

In the tendons of man and other mammals Golgi found two distinct types of end-organs. The one type, which resembles closely the corpuscles found in the conjunctiva and glands, will here receive no further mention, as they are foreign to the present contribution.

The other type to which he gives the name nervous musculo-tendinous end-organs (" *nervöse musculo-tendinöse Endorgane* ") is deserving of further consideration.

This organ is of spindle form and varies in size from such as are 70-80 μ broad and 300-400 μ long to such as have a diameter of 100-120 μ and a length of 800 μ or even longer. One end of the spindle is always attached to a muscle bundle, while the other, which may be unbranched or double, becomes continuous with tendon fasciculi.

The line of demarcation between spindle and surrounding tendon fasciculi is usually quite distinct, the boundary of the spindle being often marked by a glistening line, along which nuclei are seen. The presence of a capsule does not seem indicated by this glistening line, although in silver nitrate preparations it would appear that there was present a superficial endothelial covering.

Golgi states that often only one medullated nerve goes to a spindle: not seldom, however, spindles to which two, three or four medullated nerve fibers go, may be seen. The medullated fibers, after entering the spindle, divide into primary, secondary and tertiary branches, these still retaining their medullary sheaths and diverging as they approach the periphery of the spindle. After the medullated branches have lost their myelin, they divide into several diverging branches. Golgi's account of the ending of these non-medullated branches is as follows: "Wenn sie da angekommen sind" (when the non-medullated branches reach the periphery of the spindle) "bilden sie durch noch feinere und häufigere Zertheilungen in kurzen

Zwischenräumen zahlreiche umschriebene, längliche, netzartige Geflechte, welche der Oberfläche parallel liegen." He draws especial attention to the similarity in the structure of the nerve endings found in the tendons of man and other mammals and those found in lizards, and to the resemblance of the nerve ending in tendon to that observed in the muscle plates.

Golgi found the "musculo-tendinous end-organs" very widely distributed, "if not in all, yet in nearly all muscles of the body," the eye-muscles forming an exception. He stated that they are most easily found in the rabbit, in which animal they are more numerous in the posterior than in the anterior extremity, being especially numerous in the deep tendinous lamina of the gastrocnemius and in the deep tendinous expansion of the back muscles. Similar observations were made in the mouse, dog and cat; in these animals, however, the endings are more difficult to find. In the bird, the greatest number of these end-organs was found in the wings and in the deep tendinous expansion of the large thoracic muscles.

Victor Marchi, soon after the appearance of the above communication of Golgi, investigated the tendons of the extrinsic eye-muscles with reference to the presence or absence of terminal end-organs in them. The Golgi tendon spindles were found by him in the tendons of the eye-muscles of cattle, swine, dogs, cats, rabbits and men. These observations were of especial interest in so far as they showed the presence of the nerve endings in the tendons of the eye-muscles, denied by Golgi. They added, however, little to the then existing knowledge of the manner of termination of the nerve fibers known to terminate therein.

In 1888, appeared a communication from Pansini on the nerve endings in the tendons of vertebrates. In his investigations he made use of the method suggested by Paladino, which consists in immersing small pieces of tissue, previously macerated in formic or arsenic acid, in a weak solution of palladium chloride; afterward he fixes the tissue in sodium or potassium iodide and teases and mounts the preparations in acidulated glycerine. By means of this method Pansini studied the nerve endings in the tendons of the hippocamp (sea horse), torpedo, frog, lizard, tortoise, bird and mammal.

In the hippocamp he finds free endings, composed of branched or unbranched axis cylinders, having many small nuclei, some of these being mere granules and others large, round or oval nuclei. According to the number of nuclei, the length of the pedicles and the length of the axis cylinders, the whole plaque resembles a bush, a tuft, or rarely a star-like small plaque. Pansini considers these morphologically equivalent to motor endings.

For the torpedo, he describes a rich plexus with large, irregular meshes, in which are found plaques consisting of medullated fibers, which branch and rebranch and finally become non-medullated and have many round or oval nuclei attached, some small and granular, others larger and having nucleoli. Three classes of endings are described—one free; one larger and surrounded by a thin membrane; the third surrounded by a definite capsule.

In the frog and lizard, he used the tendo Achillis and the tendons of the small muscles of the foot. The nerve ending consists of a fine delicate reticulum at the nodal points of which are granular nuclei, some showing nucleoli. The endings are free in the frog and generally in the lizard, but in some cases in the lizard, the sheath of Henle of the nerve innervating the organ forms a sort of investing capsule. In the lizard, also, the network is more complicated, the plaques larger and the nuclei more numerous, with more of those that have nucleoli. In the tendo Achillis of the turtle are found the beginnings of true neuro-tendinous organs of Golgi. Two to five plaques like those described for the frog and the lizard, are grouped into a quite definite organ, surrounded by one or several layers of connective tissue—elementary neuro-tendinous organs. These plaques are arranged on tendon fasciculi, whose elements are smaller and more numerous than those of the surrounding tendon. The fusiform enlargements found in connection with the nerves supplying tendon, and mentioned by Golgi, Cattaneo and Marchi are considered by the author as nerve endings like those of Pacini and Krause, but less developed.

In the aponeurosis of the pectoral muscles of the dove, he finds neuro-tendinous end-organs more numerous and more elongated than in the turtle, but containing plaques similar to those described above.

In mammalia (dog, rabbit and man), the plaques are the same as in the lizard, but the nuclei are larger, more granular and more abundant and more plaques are grouped together within one connective tissue sheath to form the neuro-tendinons organ.

Opposing the idea of Golgi that these organs are always muscular at one extremity and tendinous at the other, which gave to them the name "musculo-tendinous end-organs," Pansini states that he has found neuro-tendinous end-organs frequently, in mammalia as well as in the lower vertebrates, which were tendinous at both extremities. Besides these organs, he also finds in tendon, corpuscles resembling those of Pacini, Meissner and Krause. From Pansini's descriptions and from his figures, compared with the corresponding figures of Ciaccio and with our own, we are led to conclude that in his preparations, the ultimate terminations of the non-medullated fibers were very imperfectly stained.

Contemporaneously with Pansini, Cattaneo published the results of his investigations with the double chloride of gold method, applied to tissues previously made transparent by immersion in arsenic acid and fixed in osmic acid. His studies were confined to neuro-tendinous end-organs of guinea pigs, rabbits, cats and dogs. Cattaneo's minute description of the general structure of the organ does not differ materially from that given by Golgi. He demonstrates, however, a distinct capsule for the spindle, consisting of one or several layers of fine, interlacing connective tissue fibers, which, in his silver nitrate preparations, are seen to be covered by a layer of large, polygonal endothelial cells with round or oval nuclei, resembling those described by Ranvier for the sheath of Henle; the author concludes from this, that the sheath of Henle of the nerve fiber terminating in the spindle constitutes the investment.

Cattaneo also mentions a collar or ring, surrounding one extremity of the spindle, which, he thinks, may be due to the action of the acids, or may consist of circular or spiral fibers surrounding the spindle or may be regarded as the termination of the capsule.

He emphasizes the fact that the spindles vary with the age of the animal, being smaller, less prominent and with more numerous nuclei in the young than in the adult of the same species; also that they vary with the species, being smaller and less distinct in the guinea pig than in the rabbit, while in the dog, the spindles are still larger, approaching those of man, in whom are found very large and complicated end-organs.

The nervous structure he describes as follows: Generally but one nerve fiber innervates the organ, rarely two; oftener one fiber divides and supplies two or more organs. This nerve fiber generally divides before entering the spindle, loses its sheath of Henle as it enters, which becomes continuous with the investing capsule; these medullated fibers then divide and redivide, always approaching the periphery of the spindle, either suddenly or gradually becoming non-medullated. Finally the pale fibers reach the periphery, where, by finer and closer ramifications, they form numerous, circumscribed reticular networks, like small tufts, sometimes well isolated, sometimes closely crowded together, which cease at some distance from the periphery. "These networks" he says, "show from time to time nodosities which may be due to the action of the arsenic acid on the nerve termination."

The blood supply of these organs comes from the neighboring vessels, which send generally two, but sometimes only one branch to supply the spindle. These run along on either side of the spindle and send off side branches at intervals which anastomose with those from the opposite side, thus forming a long-meshed plexus somewhat resembling that of muscle.

The author discusses at some length the relation of these organs to other sensory corpuscles, such as neuro-muscular spindles, Pacinian corpuscles, corpuscles of Krause, etc., deciding that, while these different forms of nerve endings are often found very near together and while he even occasionally finds Pacinian corpuscles incorporated in the substance of the tendon spindle, yet the nerve supply is always distinct and he believes that the relation is accidental.

In order to decide the question of the function of the neuro-tendinous spindles, Cattaneo undertook a brief series of degeneration experiments. In the first set of experiments, he sectioned the posterior roots, causing an ataxic gait, but no degeneration of the neuro-tendinous spindles was found and he considered these experiments as negative.

In the second set, he sectioned the anterior roots, causing paralysis of the posterior extremities and degeneration of the muscle fibers and nerves supplying them, while the neuro-tendinous spindles and their nerves were unaltered. In the third set of experiments he sectioned the sciatic nerves and found that the intrafusal tendon fibers were reduced in size and otherwise altered, a long time after the operation, while the nerve supplying the spindle showed the usual degeneration phenomena soon after section of the nerve, the termination of the non-medullated fibers in the spindle being still more radically and quickly altered. From these facts and from their position in the boundary zone between muscle and tendon, the author concludes that these organs are sensory and probably organs of muscle sense.

Apropos of Cattaneo's degeneration experiments, it may not be amiss to mention briefly Brazzola's investigations on tabes dorsalis, in which he examined for pathological lesions, not only the central nervous system, but also some peripheral nerve endings—among them the neuro-tendinous end-organs. He finds the ultimate portion of the nerve fiber going to the plaque altered and also the ramifications of the axis cylinder. Only the "bush-like terminations in ring or spiral" of Ciaccio remain, very much atrophied and these too finally disappear.

In the fifth edition of his Handbuch der Gewebelehre, Kölliker mentions having observed nerves in the tendons of the bat. The details concerning their mode of ending seem, however, to have escaped this observer at that time. In the sixth edition of this well known work, Kölliker considers these endings much more fully. His later observations may be summarized as follows: He corroborates Golgi's statement that in lizards the nerves terminating in tendon end in a dense network of non-medullated nerve branches, with here and there free endings and occasional enlargements, but adds that "*diese sensiblen Endblatten,*" as he terms these endings, consist, as do the motor endings, of non-medullated fibers, surrounded by a nucleated sheath of Schwann. Concerning the "*Golgi'schen Sehnenspindeln*" as he terms the "*Organi nervosi terminali musculo-tendinei,*" in honor of their discoverer, he makes the following comment: In one individual seven years old, the Golgi tendon spindles were 1.28 mm. to 1.42 mm. long and 0.17 mm. to 0.25 mm. broad at the muscular end. In the rabbit, they were 0.24 mm. to 0.79 mm. long and 0.02 mm. to 0.11 mm. broad. The Golgi tendon spindles are surrounded by a well developed fibrous tissue capsule, which is continuous with the sheaths of the contiguous tendon fasciculi. This capsule, he believes with Cattaneo, possesses an endothelial lining. Within the capsule, there are found two, three, and sometimes more tendon fasciculi, at other times, as it would seem, a less differentiated mass of tendon substance (eine mehr zusammenhängende Masse von Sehnensubstanz). One, two, three or four medium sized medullated nerves go to each spindle, which they reach, usually in the equatorial region, but not infrequently at one end of the spindle. These nerves divide into a number of medullated branches and are distributed through their non-medullated terminal branches, over the greater part of the thicker portion of the spindle. Kölliker's observations on the ultimate ending of the spindle nerves are in accord with those given by Golgi and Cattaneo and will therefore need no farther mention.

In a summary of observations on sensory nerve endings, Kerschner mentions briefly his own observations and those of other investigators on the nerve endings in tendon, giving, however, no figures to elucidate his text. In amphibia, he was not able to add to the results obtained by Rollet and Gemt. The end-organs obtained by Golgi, he regards as modifications of Rollet's "*Endschollen,*" to be distinguished from the latter largely by the fact that they are partially separated from the contiguous tendon fasciculi by a sheath lined by endothelium which he regards as a continuation of Henle's sheath of the nerve terminating in the end-organ. Kerschner regards the term "*organi musculo-tendinei*" as inappropriate, as these structures are not always found near the muscular end of the tendon. The tendon nerves, Kerschner states, do not end, as Golgi and Cattaneo had stated, in a network of anastomosing terminal fibrils, but in freely dividing and intercrossing branches, which do not anastomose and often terminate in end-knobs, which now and then appear to be in connection with cells found by him within the end-organs.

In 1888, 1889 and 1891, articles appeared from the pen of Ciaccio, describing the results of his investigations with the double chloride of gold method of Fischer and Löwit on the nerve endings in tendons of mammalia, birds, reptilia, amphibia and fish. His researches are the most exhaustive and his diagrams and descriptions are the most accurate and minute that have appeared up to the present time, especially since, by means of longitudinal and transverse sections of the tendon corpuscle, he has observed and pictured the minute internal structure of the organ, the details of the nerve ending and its relation to the intrafusal tendon fibers in a way which is impossible from mere surface preparations. For these reasons we desire to give a somewhat more extended account of this author's work.

He finds these nerve plaques (either encapsulated or not) which he designates "plaques tendineuses avec terminaison buissonneuse des nerfs à anneaux ou à spirale," in the tendons of all vertebrates studied except the *Batraciens anoures* (frog, toad and tree-toad), in which the nerve ending is free on the primary tendon bundles and is of such form that he designates it "buisson nerveux final."

Ciaccio describes three peculiarities of the neuro-tendinous organs of mammalia, not noticed by previous writers: (1) spindles, found in the eye-muscles of man, in which both extremities are tendinous; (2) compound spindles, united together along their whole length, but each part having an independent nerve supply; (3) neuro-tendinous end-organs into which some of the muscle fibers are prolonged into the organ to the margin and even to the middle of the nerve plaque.

His description of the nerve ending is as follows: The numerous ramifications of the axis cylinders, which compose the nerve plaque in the neuro-tendinous end-organ show along their course certain enlargements of different form and size, described by most writers as nuclei, but really, he believes, masses of one of the two substances of which the axis cylinder is composed (neuroplasm). Most of these ramifications are plates with one or several transverse projections or "crêtes d'empreinte." These ramifications are arranged in different planes, thus producing the plexus-like appearance described by Golgi and others who viewed the corpuscles only in surface preparations. Sections—cross and longitudinal—showed that "the branches of the axis cylinder run across the loose connective tissue which binds the primary tendon bundles together, then penetrate these latter and continue to ramify in a bush-like manner; each branch surrounds in spiral or ring, in several parts of their length, one or several of the small bundles of dense fibrillar connective tissue of which each primary tendon bundle is composed."

This description of nerve ending applies also to the ending of the nerves in the neuro-tendinous end-organs of birds.

In reptilia, however, in which he has studied the tendons of the interspinous muscles of the *Coluber natrix* and of the gastrocnemius of the *Lacerta agilis*, no encapsulated organs are found. The nerve plaques are distributed along the medullated nerves which divide repeatedly and end in the depths of the tendon in a confused intercrossing of very fine fibers, thread-like or ribbon-like, beset with projections of different form and size. These fibers also surround the primary tendon bundles in ring or spiral before their final termination.

In amphibia, however, he finds no plaque as above described, but a plexus of fine fibers which end in a bush-like expansion of small varicose nerves ("*touffe nerveuse finale*") of which the greater number penetrate the primary tendon group and probably end free without surrounding the bundles.

In the fish, which only he and Pansini have studied, he has examined the tail and fin tendons of the ray, the tench and the carassin. He finds medullated nerves ending free, more or less deeply in the tendon, in peculiar plaques, simple or compound, formed of axis cylinders in the form of turns of ribbon ending in a "*ligne en relief*" or "*crete d'empreinte*," which is more deeply stained in gold chloride than the rest of the ending. Each turn of the ribbon corresponds to a turn of the axis cylinder which surrounds one or several of the small secondary tendon bundles.

Concerning the function of the neuro-tendinous end-organs, the author considers the sensory nature proven both by the microscopic anatomy and by physiological experiment. The special function being, however, still unsettled, the author advances the view that it is "to proportion the amount of distension and resistance of the tendon to the amount of contraction of the corresponding muscle," supporting his view by the fact that the most frequent site of these organs is in the tendons of the most active and efficient muscles.

In 1890, Mazzoni described and figured certain forms of terminal nerve organs found in the tendons of man. Similar organs had been mentioned by Golgi and Ciaccio and were afterwards noted by Ruffini, the two latter finding them in the tendons of other mammalia than man. These are often found in more or less intimate connection with the neuro-tendinous end-organs and may therefore be mentioned in this connection. In their simplest form, where a single nerve fiber enters and passes unbranched through the encapsulated granular substance, ending in a terminal enlargement, they closely resemble small Pacinian corpuscles. In the more complicated forms, however, where a single branched nerve or several independent nerves enter the granular substance and break up into many branches, forming a twisted, network-like mass, each filament ending in a terminal enlargement, the resemblance to the Pacinian corpuscles is lost and it is to these especially that the name "Golgi-Mazzoni organs" is sometimes applied.

In 1893, Ruffini, in a brief note, described the results of some investigations, by means of Fischer's gold chloride method, on the neuro-tendinous end-organs of the cat.

In this communication, waiving the questions of the structure of the organ and the form and relations of the nerve ending therein, he emphasizes the fact, already discovered by Cattaneo, that Pacinian corpuscles are found, not only near the neuro-tendinous end-organs, but even within their capsules. In two later communications, of which we have seen only the reviews, he again dwells upon this relation, which he, disagreeing with Cattaneo, considers important in the consideration of the structure of the neuro-tendinous end-organs of the cat. He says that in this animal, from one to five Pacianian corpuscles are found in each neuro-tendinous end-organ. In the rabbit, although they are found, there are not so many nor is the relation so close.

He also, in all these communications, describes a reticulum ("*réticule nerveux*") which is sometimes found on the neuro-tendinous end-organs of the cat.

The nerve fiber forming this network may be a branch of the nerve supplying the tendon organ or may be independent of it. This nerve becomes non-medullated, divides and subdivides, the resultant branches twining themselves about the neuro-tendinous end-organs, not anastomosing, and finally ending in a small ball-like enlargement on the striated muscle, either near the neuro-tendinous organ or at some distance from it.

The author speaks also of the "*bandelette*" of connective or elastic tissue surrounding the organ at one of its extremities and mentioned by Cattaneo and Ciaccio. In none of these communications, has Ruffini added anything to our knowledge of the structure and nerve terminations of the end-organ.

In a recent article, Ruffini describes a new nerve ending found in the sub-cutaneous connective tissue of the human finger. He used Fischer's gold chloride method upon material taken from the fingers of a girl of eleven years. The ending is spindle-shaped and consists of bundles of white fibrous and yellow elastic connective tissue fibers surrounded by a capsule largely of yellow elastic tissue. The author thus distinguishes this spindle, which may bear his name, from the neuro-tendinous end-organs of Golgi.

(1) In the neuro-tendinous organ, the medullated fiber runs a nearly straight course to the point where it becomes non-medullated, while in the Ruffini spindle, the nerve makes long and tortuous turns in the interior of the spindle before becoming non-medullated.

(2) In the neuro-tendinous organ, the non-medullated nerve breaks up rapidly into short, ribbon-like branches in the form of arborizations, while in the Ruffini organ, the divisions are irregular and the branches long, tortuous and varicose.

(3) The plaque-like distribution met in the neuro-tendinous organ is never found in the author's spindle.

(4) The Golgi organs, in transverse section, show a rather regular arrangement of the turns of non-medullated fibers in spiral or in ring around the small tendons of the organ, the intertwining never completely occupying the cross section. In the Ruffini organ, the twinings are very regular and occupy the whole cross section, so that nearly all the serial sections show about the same figure.

(5) The Ruffini organ is composed of connective and elastic tissue, while the Golgi organ consists of tendon fasciculi.

We have given somewhat fully Ruffini's account of the nerve end-organ found by him in the connective tissue of the hand, since by doing so, we have been able to give, in an indirect way, Ruffini's observations on the terminations of nerves in the neuro-tendinous end-organs.

In 1893, Smirnow published some observations on the terminations of nerves in the frog and toad, having used a modification of Ehrlich's *intra-vitam* methylen-blue method. He finds, in the musculus sterno-radialis and musculus semi-tendinosus, special tendon nerves and nerve endings which extend to the muscular extremity of the tendon. These tendon nerves, in the frog and toad, end in the shape of groups of tufts of fine varicose fibrillae, situated between the tendon fibers. The number of tufts depends on the number of medullated fibers entering the tendon, this in turn depending on the size of the animal and therefore the size of the tendon. These nerve endings are situated at different depths in the tendon. His figures agree in the main with those given by us.

In the same year, appeared a communication from Ivanhoff, in which among nerve endings in other connective tissues, he describes the sensory nerve endings in the fascia lumbo-dorsalis and fascia transversalis and the fascias of the anterior and posterior extremities of the rabbit, cat and dog. The method used by Ivanhoff also, was the *intra-vitam* methylen-blue method of Ehrlich. He describes three types of endings: (1) those in the form of a tassel; (2) some in the form of a bush; and (3) others in globular form. The terminal filaments may end abruptly or in an enlargement or in a more or less complicated ending resembling a snare. These endings have no capsule and are identical, according to Ivanhoff, with the nerve endings in tendon. While some of the figures given by Ivanhoff resemble somewhat the nerve plaques found in the simpler tendon end-organs, we do not think, either from his description or his figures, that these endings can be considered identical with the endings found in the neuro-tendinous end-organs of the animals he has studied.

In turning now to our own observations, we may again call attention to the methods used by us. As may have been observed, all investigators, with the exception of Smirnow and Ivanhoff, who have studied nerve end-organs in tendon, have employed one or the other of the gold chloride methods, or platinum chloride, for staining the nerve terminations. And while it is not our purpose to reflect in any way on the results obtained with these methods, and while we are ready to accord all observers who have used them due credit for the many valuable observations which they have made, we can but feel that the methylen-blue method, as used by us, and especially in the end-organs under discussion, gives results which should be given consideration whenever they are at variance with the results obtained by the older methods.

We shall discuss our own observations *seriatim*, beginning with the amphibia.

Amphibia.

Of the results obtained by numerous observers who have studied the terminations of nerves in the tendons of amphibia, those obtained by Ciaccio and Smirnow were such that we find it unnecessary to add materially to the account given by them. A corroborative statement may, however, not be wanting in value.

Rollet, who first described the termination of nerves in the tendon of the frog, designates the endings in them as "*Nervenschollen*" and finds two parts, the one consisting of a short internodal segment, ending in a sharp point, the other of small cellular plates with round nuclei or of grains arranged in undulating lines and separated by spaces of the same form. Sachs and Gemt described non-medullated fibers in the endings; Golgi described a network of small non-medullated fibers; this Kölliker corroborated, adding that the nerve branches of the ending were invested with a nucleated sheath of Schwann. Ciaccio, after describing the arrangement of the nerve in plexus, says that it ends in a peculiar nerve plaque which he designates as "touffe nerveuse finale." These tufts, he says, are oblong in shape, larger in the middle than at the extremities, and composed of a bush-like mass of fine varicose fibers, which penetrate the primary tendon groups and end in free endings. He thus disagrees with Gemt and Golgi, who affirm that the nerve ending in the frog is the same as in reptilia.

Smirnow also describes nerves ending in tufts of fine varicose fibrillæ, situated between the tendon fibers. The figures given by Smirnow, who, it may be remembered, used the methylen-blue method in his investigations, are very similar to the ones we give for the nerve ending in the tendon of the frog, although it would appear to us that our endings were more fully stained or that we were dealing with much larger endings.

In the frog, in many thin, flat, fascia-like tendons, into which the muscle fibers are inserted, notably in the tendon of the *tibialis posticus* from which many of our preparations were taken, we have found numerous terminal arborizations of nerve fibers.

Often we have been able to trace medullated nerve fibers for some distance, which, at each node of Ranvier, send off a medullated branch, which passes out for a considerable but variable distance from the parent trunk and then breaks up into a a large number of fine non-medullated nerves, all extending in the same general direction and sometimes branching again and appearing as ordinary varicose fibers. The varicosities are all round or oval in shape, vary but little in size and are connected by very fine thread-like fibrillæ. There are usually no side branches and no projections along the course of the non-medullated nerves, but the nerve fibers differ in length and the whole tuft looks not unlike a small tree-like bush with long, slender nearly parallel branches, tapering toward the top, on which the buds are somewhat swollen, but which are unadorned with flowers, fruit or foliage.

Occasionally at the end of some of the terminal branches, may be seen a round or oval enlargement somewhat larger than the varicosities found along the non-medullated fiber. At other times, the fiber seems to stop quite abruptly as if it were broken off, or it may terminate in a sharp point. This description of terminal nerve tufts applies equally well to all the plaques seen in the frog. Whatever variation is seen in the ending is due therefore to the arrangement of these plaques and their relation to each other and to the medullated nerve. At times, the medullated nerve divides into two main branches at right angles to the stem, each of which quickly breaks up into a tuft similar to the one just described. The whole appearance is then not unlike what might be presented were two such bushes as above described, cut off just below the point of branching and placed base to base. Occasionally we see a tuft from one nerve fiber extending out and meeting one from another nerve fiber, the whole forming a spindle-shaped ending with medullated fibers at each extremity such as may be seen in the central tuft of Fig. 1, Plate XIII.

Sometimes a nerve fiber approaches an end-tuft from a direction at right angles to its length ; but before reaching it, divides into three or four branches, each of which ends in a typical end-bush, but all so massed and mingled together as to produce a most complex picture. At other times, the main nerve, as it nears its extremity, shows very short internodal segments, and at each of the nodes, a short medullated nerve, branching and rebranching and ending in a typical tuft, is given off, the whole producing the effect of one very large ending, spread out over a considerable space. In Plate XIII, Fig. 2, we have represented such an ending, in which the main nerve divides into seven or eight branches, each subdividing a number of times, and each subdivision terminating in a tuft of varicose fibrils and producing the tree-like ending seen in the figure, with its large bushy spreading top. In Plate XIII, Fig. 1, we have represented a very large ending, arising from the terminal branching of a large medullated fiber. This fiber first divides into two branches, one of which soon redivides into two secondary branches, at right angles to the main stem, which soon end in the tuft of varicose fibrils. The other primary branch extends for some distance before dividing into two secondary branches, one of which divides into tertiary branches at right angles to itself and all terminate in end-tufts. One of the latter tufts passes back and meets the top of the tuft coming from the first branch, forming the spindle-like ending seen in the center of the figure and previously described. We have found endings of the most varied size and complexity, depending on the number of branches given off at each division and entering into the formation of the end-organ. It has not been unusual to observe twelve to fifteen end-tufts of different size and shape, formed by the division of a single nerve fiber.

Longitudinal sections of the frog's tendon, as represented in Plate XIII, Fig. 3, show that these end-brushes are found, not in the zone of passage from muscle to tendon, but deeply embedded in the tendon. They show also that these endings are spread out on peculiar bundles of tendon fasciculi, which are sharply differentiated from the surrounding tendon fasciculi by reason of the fact that they are smaller, stain much more deeply with alum carmine and show large numbers of round, oval or oblong nuclei, which also stain deeply red in alum carmine, even in preparations in which the ordinary tendon nuclei are not at all stained. The tendon on which the nerve ending is found partakes, in other words, of the character of embryonic tendon. We see also in longitudinal sections that the varicose fibers described either lie on the surface of the tendon fasciculi in long, undulating lines, or twine about or between them in long serpentine windings, while the cross sections show especially well that the fibers penetrate these fasciculi and terminate, usually with no enlargement, on the smaller bundles of which the primary fasciculi are composed. We see also in cross sections as in Plate XIII, Fig. 4, that, sharply as the tendon bundles are differentiated from surrounding tendon and compact and complicated as the whole ending often appears, there seems to us to be no indication of a connective tissue capsule surrounding the fasciculi and holding them together. The nerve ending in frog's tendon is, as has been stated by Cattaneo, Ciaccio, Smirnow and others, a free ending.

As stated in the introduction, many of our preparations, after staining in methylen-blue, were fixed in ammonium picrate and cleared, teased and mounted in glycerine ammonium picrate. This fixative softens somewhat the tendon and connective tissue and the whole ending is readily flattened out. While this, it seems to us, is an advantage in studying the final terminations of the nerve fibers, their size, shape and relation to the main nerve fibers, yet it sometimes gives a rather false idea of the end-organ and the relation of the nerve ending to the tendon fasciculi of the organ, unless this idea is corrected by comparison with preparations fixed in ammonium molybdate and either cleared and teased in xylol and mounted in balsam, or sectioned longitudinally. This fact can be readily substantiated by a comparison of Figs. 1 and 2 of Plate XIII, which are surface preparations, teased out of the glycerine-ammonium picrate solution, with Fig. 4 of Plate XIII. which gives more nearly the natural size of the organ.

Reptilia.

Our own observations on the termination of nerves in the neuro-tendinous organs in reptilia agree more closely with those made by Ciaccio than with those recorded by Golgi and Pansini, who described a network of fine nerve branches, at the nodal points of which thickenings are found. Ciaccio investigated under reptilia the tendons of the interspinous muscles of *Coluber natrix* and the tendon of the gastrocnemius of *Lacerta agilis*. He found in these no true Golgi neuro-tendinous end-organs, but nerve plaques situated in small tendinous groups, primary as well as secondary. "The plaques," he says, "consist of a confused intercrossing of very fine fibers, some filamentous and some ribbon-like, arranged in two planes and beset with projections of different form and size." In cross sections, he showed that the fibers, near their termination, penetrate the primary tendon bundle and surround one or several of the secondary tendon bundles composing it. In our investigations, we have used almost exclusively the tendons of the posterior extremity of *Emys meleagaris*, especially the flat tendinous aponeuroses of the quadriceps extensor and the tendon of the gastrocnemius. In this animal as in the frog, we have frequently been able to trace large medullated nerves with rather short internodal segments, for considerable distances, which, at each node of Ranvier, give off a medullated branch and sometimes more than one. This, after a longer or shorter course, terminates in a more or less complex end-arborization. In some cases the medullated nerve divides into four or five finer medullated nerves, some of which break up at once into a number of non-medullated fibers ; others extend for considerable distances along the tendon and toward its extremities, giving off at intervals side branches, which either are or soon become non-medullated or divide into numerous non-medullated nerves. Thus, along such an ending, very large numbers of such tufts may be seen. After losing the medullary sheath, the fibers proceed for a variable distance along the tendon fasciculi, some as simple varicose fibrils, like those described for the frog, but most of them beset by round, oval, or oftener very irregular enlargements, either resting directly on the fiber or supported by a longer or shorter pedicle. These enlargements, which so sharply distinguish this end-plaque from that of the frog, vary markedly in size and form. Sometimes a fine branch serves as a pedicle for one or several granular enlargements, pear shaped, irregularly quadrangular or polygonal or leaf-like or resembling a large plate beset on several sides by sharp thorns or triangular or quadrangular or oval bud-like projections. Sometimes the non-medullated nerve fiber itself enlarges and is beset with secondary enlargements of the most varied size and shape. Sometimes a single enlargement rests on a rather long stem ; at other times, the pedicle itself is adorned with other sessile or pedunculated enlargements, or may divide at its extremity into two or three branches, each supporting one or more of the enlargements. Thus the plaque may be quite simple or much more complex. Sometimes the nerve enters the ending, the branches with their terminal tufts spreading in opposite directions. Sometimes it enters at one extremity, all the branches extending in the same direction, more closely resembling a bush whose branches are adorned with the most fantastic foliage. Sometimes the main nerve fiber breaks up near its extremity into a large number of fine branches, coming off at different closely approximated nodes, each branching repeatedly and ending in the characteristic end-plaque, the whole somewhat resembling in general appearance, though not in the minuter structure, the large, bushy ending described and figured for the frog.

In Plate XIV, Fig. 5, we have represented one of the simpler endings, which has been very much flattened out, so that the form and relative size of the final tufts and their relation to the nerve fiber are very well shown, with no attempt to represent the relation to the tendon fasciculi. The medullated nerve sends off two medullated branches from neighboring nodes, each ending in a short, simple tuft. The nerve finally divides dichotomously, one of the resultant branches terminating quickly, while the other gives rise to two sets of tufts, before breaking up into its final arborization.

Longitudinal sections, as represented in Plate XIV, Figs. 7 and 8, show that in the turtle, as in the frog, the tendons on which these nerve endings are arranged, have not the characteristics of ordinary tendon, but have smaller tendon fasciculi and many more nuclei, both fasciculi and nuclei staining more deeply than the surrounding tendon. The endings are usually found deeply embedded in the tendon and may even be nearer its superficial surface than its muscular face. In some cases, however, as in Plate XIV, Fig. 7, they are found just at the boundary of muscle and tendon. We see also that the terminal fibers have a somewhat undulating, serpentine course, winding about or between the tendon fasciculi, while the terminal plates may enclasp or partially surround the smaller bundles of tendon fibers. Neither the spirals nor the rings, however, which are so strongly emphasized by Ciaccio in both his figures and his descriptions as a most characteristic feature of the terminal plaque, seem, in our preparations and figures, so definite and strongly marked a feature of the ending as his figures would seem to indicate. This fact, which we note in all our preparations from all species of vertebrates studied, may, it seems to us, be due to the fact that, while the gold chloride stains, not only nerve fibers, but also tendon fasciculi, connective tissue, tendon cells and nuclei, or may precipitate in the lymph spaces or semi-fluid ground substance, so that the appearance is often deceptive, the methylen-blue far more sharply differentiates the nerve structures from all other tissue elements of the end-organ. In many preparations which we believe to have been perfectly stained and in which only the nerve fibers and their terminal ramifications were blue, we have found no rings, such as Ciaccio finds in all his preparations, except those from the amphibia, and no spirals, the rings being reduced to a clamp-like partial encircling of the tendon by the terminal disks, and the spiral to an occasional loose winding of the fine terminal fibers in and out between the bundles of tendon.

In cross sections, as represented in Plate XIV, Figs, 9, 10 and 11, we note the small size of the tendon fasciculi and the large number of nuclei and that the non-medullated nerve fibers penetrate the tendon fasciculi, while the terminal plate-like enlargements are found clasping one or more of the smaller bundles of connective tissue fibers of which the fasciculi are composed.

Golgi and Ciaccio, from the various reptilia which they examined, concluded that in this type of vertebrates, as in the amphibia, the nerve endings were free and that no encapsulated endings were found, as in the higher vertebrates. Pansini, however, while he finds the endings in the lizard either free or surrounded by an imperfect sheath, finds in the turtle the beginning of true Golgi neuro-tendinous organs, surrounded by a distinct capsule of connective tissue. In the majority of our preparations, the absence of a connective tissue sheath is easily noted, the peculiar tendon fasciculi, on which the nerve ends, fading off gradually into the ordinary tendon. But in some of our preparations, we have been able to demonstrate a more or less distinct capsule of connective tissue fibers, surrounding a spindle-shaped group of fasciculi, on which a more or less complex nerve ending was found. This capsule has been especially well shown in transverse sections of the tendon, one of which is shown in Plate XIV, Fig. 11. It may be added that we have usually found the encapsulated organs in the zone of passage from muscle to tendon, while the non-encapsulated or free endings were found deeper in the tendon and showing no relation to the muscle. There seems, however, to be no particular tendon or part of the body in which encapsulated forms are especially prevalent, but they are often found in the same tendon with non-capsulated endings. The nerve endings in the encapsulated forms seem generally more complex than those in the free ending.

Bird.

Golgi and Pansini describe, for the bird, endings like those which they described for the lizard—networks of fine fibers at the nodal points of which thickenings or nuclei are found. Our results, however, are more in accord with those of Ciaccio, who, investigating with the gold chloride method the nerve endings in the tendons of the wing muscles of the sparrow, the sparling and the swallow, found the nerve plaques always in the neuro-tendinous end-organs of Golgi, surrounded by a connective tissue sheath and an endothelial investment. He finds that usually only one nerve fiber innervates the organ ; this may divide, either before or after entering, into two primary branches each passing toward an opposite extremity of the organ. They divide and subdivide into many non-medullated nerves, which form the plaques, appearing as a multitude of small pieces of axis cylinders, differently formed and grouped in masses ("groupés en amas"). His cross sections show that the nerves pass between the small bundles of fibrillar connective tissue of which the tendon fasciculi are composed, embracing one or several of them before ending.

Ciaccio's results regarding the general structure of the organ in birds have been in most particulars corroborated by our observations with the *intra-vitam* methylen-blue method, on the tendons of the wing muscles of doves. Although in most cases the ending has been surrounded by a distinct investment of connective tissue and endothelium, we have been able to see endings, which like most of those in the turtle, possessed no capsule, but were distributed free on the primary or secondary tendon groups. While the usual encapsulated form was always found at the musculo-tendinous junction, these free endings were usually found embedded somewhat more deeply in the tendinous tissue. In these, however, as well as in the encapsulated forms, the tendon fasciculi differed from the ordinary tendon fasciculi in the same way as has been described for the frog and the turtle, staining more deeply and possessing more numerous and more deeply staining nuclei.

The form and size of the neuro-tendinous end-organs in birds vary according to the number of nerves which supply them and the part of the organ where the nerves pierce the capsule. Sometimes a medullated nerve passes along the muscle or tendon and, without changing its direction, branches into two or three primary medullated branches, each of which sooner or later re-divides and ends in one or several non-medullated fibers. Side branches are also given off, which, after a very short course, divide into two or three non-medullated fibers, which usually run nearly parallel to the main nerve of the ending. In the bird, as in the turtle, the characteristic appearance of the end-tuft is produced by peculiar, fantastic enlargements, granular in appearance and of the most varied size and shape, which beset all the non-medullated fibers. Sometimes they are quite regularly round or oval, but oftener they are very irregular, plate-like, with prominent projections, which may be pointed, blunt or round, or they may resemble long leaves somewhat twisted. These enlargements are in general longer and more complex than those that we find in the turtle, the form which seems to predominate being that in which the non-medullated fiber itself enlarges, widens out into a large, irregular granular plate, other granular plates, round, oval, rectangular, club-shaped or spike-like, being added on, now at the side and now at the end, and still others, until we have a long, irregular string of such granular masses, at no point showing a return to the normal size of the non-medullated fiber.

The complexity of the ending may be varied by the number of times that the non-medullated fiber branches before thus spreading out into this terminal enlargement, and by the number, size and shape of the granular plates that are thus pieced on to the simple terminal enlargement. In addition to these widenings of the main stem, we have also numerous varicosities, which may rest directly on the main stem before its final enlargement, or may be separated from it by a slender pedicle.

The medullated nerves are usully quite straight throughout their length, but the non-medullated fibers wind in long, sinuous waves, now for some distance on the one surface of the tendon fasciculus, now partly surrounding it and now coiling from one fasciculus to another, finally entering one of the peripheral fasciculi and passing between the secondary bundles of tendon fibers composing it, while the side and terminal enlargements enclasp the bundles of tendon fibers, partly encircling them. The fibers and terminations passing in the same general direction while the enlargements are long and generally slender, the side projections being rarely lifted far from the parent stem, gives a rather cylindrical shape to the entire ending, a form which we have not found unusual for the bird, although Ciaccio mentions that he has found it quite rare. In all the endings observed in the bird, we have found terminal plaques similar to those described above, but there are variations in the length of the terminal plaque and also in the number of plaques taking part in the formation of the neuro-tendinous end-organ. Sometimes the varicosities are so small and closely packed together and the fibril so straight that it resembles somewhat a sprig of mignonette, with its straight slender stem and small, closely packed pedicled flowers surrounding the stem on all sides. The length, thickness and compactness of the terminal plaque differ in the different end-organs and also their number and arrangement and hence the form of the entire end-organ.

Often one or several medullated nerves enter the organ, either at the extremity or in the equatorial region, breaking up near the center into three or four medullated fibers, which spread out, re-divide, become non-medullated, each branch terminating in the characteristic varicose end-plaques. Such a spindle is shown in Plate XV, Fig. 13. The spindle is rather short, broad at the center and tapering at the two extremities. Or we may have organs like that represented in Plate XV, Fig. 15, where the spindle broadens out at the center, tapering at one extremity, and, at the other, dividing into two parts into each of which the terminal plaques extend. In plate XV, Fig. 12, is represented a rather simple ending, which has been so flattened out that the one medullullated nerve, with its two primary branches and their seven or eight terminal plaques are spread out all in nearly the same plane and their relation to the tendon fasciculi is not shown. In this end-organ, there was no capsule, or at most, a very imperfect one. While this preparation gives us no idea of the structure of the end-organ, it shows more clearly than any other preparation the character of the terminal plaque. In Plate XV, Fig. 14, is a rather simple ending, consisting of one medullated nerve which branches little and shows only a few terminal plaques.

Longitudinal sections, stained in methylen-blue and counter-stained in alum carmine, as represented in Plate XV, Figs. 16 and 17, show that the few large tendon fasciculi, which enter the spindle, break up into smaller fasciculi and these still farer divide and then re-unite at the distal extremity of the spindle; that the intrafusal tendons have very numerous nuclei, oval or elliptical; that the non-medullated fibers have a sinuous course, now on and now between the tendon bundles, while the terminal plates are granular and seem to pass between the bundles of fibrillar connective tissue. In some cross sections, as shown in Plate XV, Figs. 18 and 19, we see a thin connective tissue capsule, which is seen to be wanting in others. We see also that the medullated nerves pass in the connective tissue surrounding the fasciculi while the non-medullated fibers, as Ciaccio has mentioned, penetrate the fasciculus and end on the small groups of fibrillar connective tissue of which the fasciculus is composed.

Mammalia.

Concerning the general structure of the neuro-tendinous end-organs in the different forms of mammalia studied, our observations have not differed materially from those of Golgi, Cattaneo and Ciaccio. Concerning the form of the end-organs, we may say that the true spindle-shape is not quite uniform, the amount of enlargement in the equatorial region varying so much that at times we find the spindles reduced to long, slender cylinders, having nearly the same dimensions throughout their length, but usually tapering slightly at the ends. This cylindrical form seems especially common in the dog. The length of the organ, according to Cattaneo, varies from 80 μ to 800 μ, the width, from 50 μ to 400 μ. These figures seem to us not correctly given in the text cited and do not correspond with the proportions of those end-organs figured by Cattaneo. Kölliker gives his measurements of the human spindle as 1.28 mm. to 1.42 mm. long and 0.17 mm. to 0.25 mm. wide at the muscular end, while in the rabbit, the end-organs were 0.24 to 0.79 mm. long and 0.02 to 0.11 mm. broad, while Golgi gives them as varying in length from 300 μ to 800 μ and in breadth from 80 μ to 120 μ. Ciaccio mentions a neuro-tendinous organ found in a woman, which was 2 to 3 mm. long and 1-10 to 1-5 mm. wide. As our own observations have to do largely with the termination of the nerve in the neuro-tendinous end-organ, we have made no measurements of the end-organs studied by us, but have added here some measurements given by other observers; this to call attention to the great size of this end-organ, especially in man. In preparations stained in methylen-blue and fixed in ammonium picrate, cleared and teased and mounted in glycerine ammonium picrate, the end-organs are usually, as we have stated, somewhat flattened; we have therefore felt that our measurements would not be wholly accurate; in longitudinal sections it is somewhat difficult to obtain a section of the entire end-organ in one preparation.

Compound spindles, as mentioned by Ciaccio, have been not infrequently noticed by us, and we have represented (Plate XVII, Fig. 23) a triple one taken from the rat.

We have found neuro-tendinous end-organs in the tendons of practically all muscles studied, but they are especially numerous, or at least more easily found, in connection with certain muscles, as for instance in the large fascia of the back muscles and in the tendons of the interossei of the foot of the rabbit and in the tendons of the gastrocnemius, tibialis posticus and extensor longus digitorum of the cat. Something of the number and relative position of these organs may be seen from a figure given by Golgi and reproduced by Barker in his Textbook of the Nervous System, of the back muscles of the rabbit. Preparations similar to that reproduced by Golgi, we have often made.

The position of the neuro-tendinous end-organ is, in nearly all cases, in the transition zone between muscle and tendon, and one extremity is attached to muscle, while the other becomes continuous with tendon fasciculi. But Ciaccio notes that in the tendon of the superior rectus (eye) in man, he has found certain end-organs which are tendinous at both extremities and we have observed the same fact in a few cases.

In all the mammalia we have studied, we have found no neuro-tendinous end-organs which were not encapsulated. Ciaccio, however, mentions the peculiar fact that in the bat, he finds the spindles in the anterior extremity non-encapsulated, while those in the posterior extremity always possess a distinct investing sheath. While we have observed no such marked variation in the end-organs of the mammalia which we have studied, we do find a marked difference in the thickness and density of the capsule, it being at times so thin that our most careful manipulations failed to preserve it intact; at others, so dense that it held the intrafusal tendon bundles in place in spite of much more violent treatment. Cross sections also show a marked difference in the thickness of the capsule, at times showing only one or two layers of connective tissue fibers with a few nuclei, at others, several layers arranged rather densely around the spindle and surrounded by still other layers of looser connective tissue. This variation was noticed, not only in different muscles of the same animal, as observed by Ciaccio, but even in different parts of the same muscle.

The capsule consists of from one to several layers of white fibrous connective tissue, in which we have been unable to demonstrate any yellow elastic fibers, either by Unna's orcein stain for elastic tissue or by the methylen-blue, which often stains yellow elastic fibers a pale blue. Between the bundles of white fibrous connective tissue in the capsule, are connective tissue cells. Both Golgi and Cattaneo have demonstrated, by means of silver nitrate, that this capsule is enveloped by a layer of large polygonal endothelial cells.

In the axial space, we find a varying number of tendon fasciculi, the intrafusal tendons, which differ from ordinary tendon in having a greater number of nuclei, the fasciculi being smaller, both nuclei and fasciculi staining more readily and more intensely so that they are readily differentiated from the surrounding tendon. We now and then find in certain regions of the intrafusal tendon fasciculi what Kölliker has described as a "mehr zusammenhängende Masse von Sehnensubstanz." In such regions, the tendon looks even more like embryonic connective tissue than in places where the fasciculi are smaller, stain more deeply and possess more nuclei. Cattaneo has noted that the neuro-tendinous end-organs vary in size and in the complexity of the nerve ending with the different species of animals studied, being larger in the rabbit than in the guinea pig and larger than either in the dog, whose spindles approach in size and complexity those found in man. That they also vary with the age of the animal, Cattaneo mentions, being smaller and less complex, the younger the animal. This fact we have observed, especially with regard to the cat, having investigated the end-organs in numerous young kittens, in which they were uniformly much shorter, the capsule thinner and the nerve ending simpler than in the adult cat.

Concerning the blood supply of these organs, we have nothing to add to the observations of Cattaneo.

Nerve Structure.—As Golgi stated, the nerve destined to supply these organs can be readily distinguished from ordinary motor nerves as it passes through the muscle, the fiber being large, rarely branching and the internodal segments shorter than those of the motor nerve, as it approaches its termination.

Although in general, we agree with the writers quoted that the neuro-tendinous end-organ is usually supplied by one nerve, which divides at a variable distance from the organ, yet we hardly think it so unusual for two or more independent nerves to innervate one spindle as we are led to believe from the emphasis placed upon this fact by Cattaneo and others. The nerve fibers, as said before, may divide first after entering the spindle, or may divide at variable distances from the organ, into two or more medullated fibers, which, as they enter the spindle, lose their sheath of Henle, which becomes continuous with the capsule of the spindle, but retain their medullary sheath for a time. The nerve usually enters the end-organ near its center, more rarely toward its muscular extremity.

The nerves which innervate the neuro-tendinous end-organ usually approach it from the muscular side, often turning sharply at right angles to their course and entering the spindle from a direction at right angles to its long axis. At other times, the branches turn back to spindles behind their point of branching, forming a long curve not unlike what Cattaneo likens to the branches of the weeping willow. At other times, the nerve approaches the spindle from the same direction as its long axis, when it either enters at the extremity or passes along beside the organ to near the center and then turns sharply and enters the end-organ. In nearly all cases in which the nerve enters the the end-organ near its center, it at once divides into two primary medullated branches, which turn toward the the two extremities of the organ. These fibers may extend with shorter and shorter internodal segments and with few side branches to near the extremities of the organ, before breaking up into a number of finer branches, each of which redivides, the resultant tertiary branches soon becoming non-medullated and terminating as we shall describe later. The few side branches given off nearer the center are either non-medullated or quickly become so and soon terminate in the typical end-arborization. This massing of the end-brushes at the two extremities of the spindle, the center being comparatively free, gives a peculiar appearance, although it is not at all uncommon, especially in the cat. Such a spindle is represented in Plate XVI, Fig. 21. At other times, and this may perhaps be considered a more typical form of the ending, the nerve fiber divides at once on entering the end-organ, the branches turning toward the extremities of the spindle, but the primary medullated branches are very short and soon divide into a number of secondary branches, some passing back toward the center and some on toward the extremities and all quickly dividing into a number of non-medullated fibers which soon form the characteristic plaque. In this form, the equatorial region of the organ is occupied by a dense and confused mass of terminal ramifications, mingled with the large but short medullated fibers, the whole mass gradually diminishing in size as it approaches the poles. In other end-organs, the nerve branches before entering the organ, or two or more independent nerves enter the organ so that three or four large medullated fibers enter near the center, divide into secondary and tertiary branches, which soon become non-medullated and terminate, the whole ending resembling a bush or low tree whose trunk is at right angles to the long axis of the organ. In still other organs, less frequently found, the nerve enters near the extremity and either branches at once or runs for some distance before branching, sending off at intervals side branches with their terminal plaques and finally breaking up into a large number of non-medullated fibers and ending in the typical end-arborization. This gives a more distinctly tree-like appearance than any of the other forms seen. These are the four principal types of end-organs seen by us in the mammalia studied and they may, any or all of them and many modifications of them, be seen in any of the species examined. They may even all be seen at times in different parts of the same tendon, so that none of them can be said to be distinctive of any species of mammalia nor of any special part of the same animal, the form of the ending depending largely on the accidental arrangement of the medullated nerves and their relation to the ending.

In addition to the nerves found ramifying in the end-organ, nerves may sometimes be seen running through the sheath or capsule of the organ and sometimes fine varicose fibers crossing the organ, whose ending we have not observed, but which seem to be quite independent of the nerve supplying the end-organ, and which may be a part of the "*réticule nerveux*" described by Ruffini as occurring occasionally about the neuro-tendinous end-organs of the cat, and terminating on the striated muscle either near the organ or at some distance from it. If so, its occurrence does not seem to be confined to the end-organs of the cat. In the dog, a peculiar long cylindrical form of end-organ seems to predominate, in which the large medullated nerves enter the organ more or less obliquely, divide into two or three medullated branches, which pass nearly unbranched in various directions through much of the length of the organ, giving off at intervals side branches which are either non-medullated or quickly become so and there is very little branching of either medullated or non-medullated nerves, so that the typical arborization effect is nearly lost. We have observed this type of end-organ in none of the other animals studied.

While the general structure of the neuro-tendinous end organs and the general arrangement of nerves in the organ are the same for all mammalia studied by us, the terminal nerve apparatus differs somewhat in the different animals and is quite characteristic for each species. We will therefore describe the nerve end-plaque for the different forms somewhat in detail.

In the dog, as stated above, long medullated nerves pass through the organ almost unbranched, lose their sheath of myelin, but as still rather large and nearly unbranched axis cylinders pass toward the extremity of the organ and either end unbranched in a terminal granular enlargement, round or pear-shaped, or irregular expansions of the axis cylinders, or branch into a number of varicose fibers, fine axis cylinders, on which are seen numerous round, oval, pear-shaped, irregularly polygonal or leaf-like enlargements, which may rest directly on the fine nerve fiber or may be raised from it by a very fine nerve filament in which case it resembles still more a leaf or flower attached to a stem by a long, slender pedicle. At the extremity of each non-medullated branch, as at the end of the main nerve fiber, the axis cylinder widens out into the peculiar granular enlargement characteristic of this ending in all its forms. This terminal enlargement may be a simple round or oval ball or the whole fiber may broaden out for a considerable length, having thorn- or leaf- or plate-like masses attached to it, at the sides, at the ends, in an irregular confused way, wherever room can be found for one to lodge. The whole non-medullated nerve may twine about and between the fasciculi in a serpentine manner, penetrating the fasciculi, while the characteristic enlargements clasp the bundles of tendon fibers composing the fasciculi. In addition to the terminal arborization, all along the long, large non-medullated fiber, short fine side branches are given off, which end as do the parent fibers. Besides these, many processes are given off from the main stem, of different shapes, all granular, some with slender, short pedicles, supporting the most varied form of enlargement, some broad and ungainly, resting directly on the nerve trunk, sometimes simply rectangular processes, but oftener other bits or masses of granular matter, sharp and pointed or oval or irregular, are attached to it in all conceivable ways and places, making an indescribably irregular ending. Some of these side processes twine themselves about or enclasp the fasciculus, while others are simply spread out upon it, the whole ending resembling somewhat a long, climbing vine, with broad, strong tendrils, enclasping the fasciculus against which the vine rests, and bearing leaves and flowers of the most fantastic patterns to adorn its surface. We have represented in Plate XVI, Fig. 20, a typical end-organ taken from a dog, which had been injected with methylen-blue, the tissues fixed in ammonium molybdate, dehydrated, and cleared and teased in xylol and mounted in balsam. In this method, there is no softening of tissues and all the parts bear their normal relation to each other.

In the neuro-tendinous end-organ of the cat, the main stem of the nerve usually forms a much less prominent part of the picture, the finer medullated branches, with their still finer non-medullated divisions and the terminations with their graceful curves and fanciful twining tend to cover and conceal the straight rude, ungraceful outline of the large trunk, which in the end-organ just described, formed such a prominent part of the ending. In Plate XVI, Fig. 21, is shown, however, an end-organ from the cat, in which the large medullated nerve, nearly unbranched, occupied the greater part of the equatorial region of the organ. Usually the large nerve branches and rebranches, bush-like, the branches becoming finer and finer, finally losing their sheath of myelin, and as axis cylinders, further divide and twine in long, graceful curves, and become beset with enlargements of the most varied size and form; some in long strings, like strings of beads, the enlargements small, granular and mostly round or oval and connected by the fine axis cylinders, these simply lying on the surface of the tendon fasciculus or twining in undulating curves about it or between adjacent fasciculi and sometimes sending off larger processes which partially encircle the tendon bundles, thus realizing to a very limited extent the truth of Ciaccio's description "*a anneaux ou à spirale.*" Sometimes the non-medullated nerves run for some distance and then widen out at the extremity into large, granular, flower-like masses. As a rule, however, in the cat the terminal processes are rather short and simple, compared with those of the rabbit and dog and the enlargements rather small, often sessile or with very short stems, and quite irregular, often leaf-like. The endings are quite distinct, being rather small and well separated, the one from the other. In the young kitten, a characteristic end-organ from which is shown in Plate XVII, Fig. 24, the entire ending is shorter and simpler. While the medullated nerve branches quite as much as in the typical end-organ of the adult, the terminal axis cylinders are short and but slightly branched, often bearing at their extremities a single oval or pear-shaped or clover-leaf granular enlargement, sometimes having a few enlargements along their length, the larger ones enclasping the tendon bundles and the whole spray twining slightly about the fasciculus. The difference in complexity, then, which has been mentioned, seems to depend entirely upon the difference in the length and branching of the non-medullated fiber and the difference in number and size of the peculiar granular enlargements which characterize this ending.

In the rabbit, the form of neuro-tendinous end-organ, which we have observed most frequently, is distinctly fusiform, the nerve or nerves entering in the equatorial region and soon branching into two or three or more secondary branches, terminating by dividing into two or more non-medullated nerves, which extend unbranched for considerable distances, bearing at very short intervals enlargements of varied form and size, round, oval, club-shaped, or very irregular masses, most of them supported by a short pedicle. These are so closely packed and so regularly placed about the fiber that the whole tuft has a peculiar, long, cylindrical shape, but curves slightly in long, sinuous lines, through the organ, while the side processes partially encircle one or more of the small tendon bundles. This form of terminal plaque is repeated with some variations at each branching of the nerve fiber. Often numerous such endings lie close together and uniformly parallel to each other, the whole resembling somewhat a poplar with its long, slender, leafy, nearly parallel branches, or rather two such trees placed base to base, with their tops extending toward the extremities of the spindle. A not infrequent form of end-organ met in the rabbit, has one or more large medullated nerves enter the organ at the muscular extremity, extend unbranched through about one-third the length of the organ and then break up suddenly into numbers of these long, slender, densely packed, non-medullated nerves. At times, mingled with the more characteristic tufts, we see a single nerve rise from the medullated trunk, pass out unbranched and terminate in a rather large, club-shaped enlargement. In other spindles, we see endings more closely resembling those in the cat, being shorter, wider and less compact and spread out more over the surface of the tendon than those we have described. The end-organ shown in Plate XVI, Fig. 22, represents a rabbit's spindle in which three medullated nerves enter the organ, each, after repeated subdivision, breaking up into the end-arborization, the final non-medullated fibers, with their lateral and terminal varicosities being shorter and simpler than those found in many of the end-organs of the rabbit. But in all the end-organs studied, whatever their form, we find the characteristic plate-like enlargements, besetting the varicose fibers, larger and more complex and more closely packed together than those in the cat, resembling more in complexity and in the long, slender cylindrical plaques, the end-organ of the dog.

In the rat, the terminal tuft is comparatively simple. In the triple end-organ, represented in Plate XVII, Fig. 23, we have three large medullated nerves entering the organ, each dividing into two or three secondary branches, one of which passes to one division of the organ and one to another, so that there is a somewhat intricate intercrossing of nerves. The termination of each nerve is, however, comparatively simple, having few side branches. The non-medullated fibers twine slightly about and between the fasciculi and are beset with broad, irregular, leaf-like enlargements, which encircle the bundles of connective tissue making up the tendon fasciculi of the end-organ. The terminal enlargements remind us slightly of those found in the simpler ending of the turtle, a characteristic form consisting of a broadening and flattening out of the whole axis cylinder, which becomes granular and is fantastically adorned on all sides by other granular masses of different shapes and sizes.

In addition to these endings, we see an occasional varicose fibril, winding through the connective tissue and showing none of the terminal enlargements. This simple, varicose fibril, which seems not connected with the proper ending of the end-organ, we have observed occasionally in end-organs from other species of mammalia studied, and it seems to us to have no important relation to the end-organ or the nerve ending therein, but to be perhaps analogous to the fine nerve fibers which Ruffini has described in the end-organs of the cat as forming a "*réticule nerveux*" and ending on the striated muscle. It has occurred to us, however, that they may be vaso-motor fibers of the arterioles of the end-organs, only partly stained.

Longitudinal sections of the neuro-tendinous end-organs of mammalia, as sketched in Plate XVIII, Figs. 27 and 28, show that the varicose fibrils, while slightly undulating, often lie upon the tendon fasciculus, and may seem to pass between two adjacent bundles, but never seem to form a complete spiral. The terminal plates are seen to pass between the tendon bundles. The character of the ending appears the same as in surface preparations.

In cross sections, as illustrated in Plate XVII, Figs. 25 and 26, we see a thin connective tissue capsule, enclosing a variable number of tendon fasciculi, which stain readily and show nuclei more frequently than the adjacent tendon. In other cross sections of the series, the fasciculi seem broken up into smaller tendon bundles, which may or may not be surrounded by loose connective tissue. As Ciaccio has said, and as our sections show, the nerve branches run in the connective tissue binding the small bundles of tendon fibers together, finally penetrating the fasciculus and partially surrounding the smaller bundles. The ring described by Ciaccio seems to us rather like a clamp, partially surrounding the tendon, while the spiral is neither uniform nor well marked. The nerve plaque seems in each case to surround fasciculi near the superficial surface of the end-organ, and never or seldom those in the interior, while the larger medullated fibers are found mostly in the deeper parts and their secondary and tertiary branches approach the surface, finally ending in the plaques above described on the smaller tendon bundles of the fasciculi nearest the surface of the end-organ.

In all these neuro-tendinous end-organs, with all their variations in size and complexity, the same characteristics are noted: Medullated fibers, branching and rebranching, becoming non-medullated, the non-medullated fibers being beset by larger or smaller granular enlargements of varied form; these granular masses were interpreted as nuclei by the older writers, but we believe with Ciaccio that they are accumulations of neuroplasm. The complexity of the organ depends largely on the number of medullated branches, while the complexity of the nerve plaque depends rather on the length and number of the non-medullated fibers and the number and size of the characteristic granular enlargements besetting them. In the amphibia only, have we observed no characteristic granular enlargements on the varicose fibrils constituting the plaque. In amphibia, the ultimate branches of the nerves ending in the neuro-tendinous end-organs are not unlike the ultimate branches of the nerves ending in the neuro-muscular end-organs of these vertebrates as described by Smirnow and the writers, which also differ markedly from the nerve terminations in the neuro-muscular end-organs of other vertebrates.

The nerve endings in the tendons of the eye-muscles, concerning which Ciaccio speaks especially, saying that in man they are found either in the neuro-tendinous end-organs of Golgi, or free on the primary tendon bundles, while in other mammalia, they are only in the neuro-tendinous end-organs, have been fully described for the cat by one of us in another communication.

Relation to other sensory endings.—Golgi and Cattaneo both mentioned the intimate relation existing sometimes between the neuro-tendinous end-organs and certain small sensory endings resembling small rudimentary Pacinian corpuscles and usually spoken of as Golgi-Mazzoni organs. Ciaccio also refers briefly to this fact and Ruffini has dwelt upon it with considerable emphasis in each of the series of three papers before alluded to. In our preparations, we have observed neuro-tendinous end-organs in close proximity to large Pacinian corpuscles, to small Pacinian or Golgi-Mazzoni organs, to Krause's cylindrical and spherical end-bulbs, and to neuro-muscular spindles. Some of these preparations deserve a little fuller mention. In one preparation, two medullated nerves separated themselves from the main trunk and ran together for a considerable distance. One of these finally left the other and divided into two branches, one of which bore at its extremity a large spherical end-bulb of Krause. The other branch divided, each subdivision innervating a cylindrical end-bulb of Krause, in close proximity to a large neuro-tendinous end-organ, which was supplied by the nerve which had accompanied that supplying the three Krause end-bulbs. In the same preparation and almost in the same field of the microscope was a neuro-muscular spindle, having an independent nerve supply.

We have often seen neuro-tendinous end-organs and neuro-muscular spindles in close proximity, sometimes lying side by side, oftener end to end, and often enclosed in the same connective tissue capsule. In most cases noted, however, the two end-organs have had an independent nerve supply no matter how closely related they might seem to be; or if the nerve supply has not been independent, it has been difficult to demonstrate the contrary fact. In one particularly fortunate preparation, however, we were able to see a neuro-muscular spindle and a neuro-tendinous end-organ, lying end to end, in the same capsule, where it seemed to us that one medullated nerve fiber ran along beside them sending off fibers at right angles to itself to innervate the neuro-muscular spindle and then at the other extremity of the capsule, a nerve was given off which supplied the neuro-tendinous end-organ and ended therein in the characteristic arborization and end-plaques.

We have, also, observed in a few cases, the fact mentioned by Cattaneo and emphasized by Ruffini, that the so-called Golgi-Mazzoni organs are found sometimes in and sometimes under the capsule of the neuro-tendinous end-organs. Our observations, however, even with the most perfectly stained preparations, have not led us to conclude that this relation is so constant, even in the end-organs of the cat, as Ruffini's descriptions would seem to indicate. We have found many end-organs perfectly stained, in which no trace of a Pacinian or Golgi-Mazzoni organ was to be seen. In other preparations, these organs were found in or under the capsules. The fact that this is a region where sensory nerves and sensory endings seem to abound; that sensory endings of many kinds are found here, sometimes in relation with the neuro-tendinous end-organs and sometimes not; and that the nerve supply, as Cattaneo has stated, is usually independent, would lead us to conclude, as did Cattaneo for the neuro-muscular spindle, that the relation is purely accidental.

As to the encapsulation of the neuro-tendinous end-organs, different opinions are expressed by the different authors who have worked on this subject. Golgi and later Cattaneo, finding that the nerve endings in tendon, in the lower types of vertebrates (amphibia and reptilia) were free, while those in the higher types (birds and mammalia) possessed a distinct capsule, drew the natural conclusion that the capsule was the result of a higher development of the organ; that the end-organ in mammalia was but the result of a condensation of connective tissue about the tendon fasciculi and a number of the free endings thereon, in the amphibia. Ciaccio, however, having observed the fact, already cited, that in the bat, the end-organs of the anterior extremity were free, while those of the posterior extremity were encapsulated, decides that Golgi and Cattaneo were wrong and that the capsule is not the result of such development and condensation.

As noted before, we have found the tendon nerve endings free in the frog, generally free but occasionally encapsulated in the turtle, generally encapsulated but occasionally free in the bird and always encapsulated in the mammal; that in the young kitten, the capsule is thinner and more imperfect than in the adult cat and that end-organs taken from different parts of the same body may differ in the thickness of the capsule; and that, whether free or encapsulated, the nerve invariably ends on tendon fasciculi having the same characteristics and differing in the same way from ordinary tendon. There seems to be here a gradual transition corresponding to the development of the animal. We think it true also in general that those end-organs which have the most perfect capsule are the most complex and well developed as regards their nervous structure. Since end-organs of different degrees of complexity of nerve endings are often found in the same animal as well as of different degrees of perfection of the capsular envelope, we can not agree with Ciaccio that his finding is a logical argument against the idea that the encapsulated neuro-tendinous end-organs of the higher types of vertebrates are developed from the free endings in the lower forms and that the capsule is one indication of that development.

Function.—All those who have investigated the neuro-tendinous end-organs seem agreed that they are sensory in their nature. The resemblance of general structure to that of other known sensory organs, the fact that the nerve supplying this organ resembles in character those supplying other sensory organs and can often be traced from the same nerve bundle, and still more conclusive, the fact that we have observed the same nerve fiber supplying this organ which supplies a neuro-muscular spindle, proved sensory by Sherrington's physiological experiments, all seem to make the conclusion fairly certain, while, if any doubt remained, the experiments of Cattaneo, showing the degeneration of the nerves and endings in the end-organs, after section of the peripheral nerve trunk, while they remained unaltered after section of the anterior roots, should set them at rest.

As to the special function of the neuro-tendinous end-organs, there are many differences of opinion. Sachs believed that they regulated the distension of tendons in the contraction of the corresponding muscles. Golgi regarded them as instruments of special nerve reverberation of tendon to muscle and was supported by Erb, Westphal, Schultze and Fürbringer. Cattaneo regarded them as organs of muscle sense, while Ciaccio believed that they proportioned the amount of distension and resistance of the tendon to the amount of contraction of the corresponding muscle. We will not venture to add one more to this list of conflicting opinions, none of which are supported by proofs, but will merely say that Ciaccio's opinion seems to us reasonable. As to the manner of producing this effect, their general structure, the peculiar clamp-like endings surrounding the peripheral bundles of the organ seem to render it probable that they, like the neuro-muscular spindles, are peculiarly adapted to respond to impulses mechanical in their nature.

Conclusion and Summary.

From the results of our investigations on the four classes of vertebrates studied, we think we are warranted in the following conclusions:

I. In the four classes of vertebrates studied, the tendons are supplied with a special nerve end-organ consisting of several tendon fasciculi, embryonic in nature, which in birds and mammalia are generally surrounded by a connective tissue capsule, while they are usually not so surrounded in reptilia and never in amphibia.

II. These end-organs have an independent blood supply as shown by Cattaneo and an independent nerve supply.

III. They are usually innervated by a single nerve fiber, which may branch before reaching the organ or after penetrating the capsule. There may, however, be two or more independent nerves.

IV. These nerves, after repeated branching, end in a manner which, in its minuter details, differs for the different types observed, but in general consists of one or many tufts of non-medullated fibers which, in all the forms studied, except the frog, are beset with large, irregular, sessile or pedunculated granular end-disks, not resembling the varicoseties on ordinary non-medulated fibers, but still consisting of accumulations of neuroplasm. These terminations are either applied to the surface of the tendon fasciculus or enclasp it or a part of it in a clamp-like manner and end on the smaller bundles of fibrillar connective tissue composing the tendon fasciculi. In the frog, the ending consists of groups of tufts of simple varicose fibers.

V. The neuro-tendinous end-organ is sensory in function, but its special function is not yet decided.

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DESCRIPTION OF FIGURES.

All figures were sketched, at the level of the table, with the aid of the camera lucida and are from preparations stained in methylen-blue. All figures giving surface views of neuro-tendinous end-organs, unless otherwise stated, were drawn from preparations fixed in a saturated solution of ammonium picrate, cleared, teased and mounted in ammonium-picrate-glycerine.

REFERENCE LETTERS.

c.—capsule of neuro-tendinous end-organs.
m.—striated muscle fibers.
mn.—medullated nerve fibers.
nR.—nodes of Ranvier.
t.—tendon.

PLATE XIII. *Amphibia.*

Figs. 1 and 2.—Terminations of nerve fibers in neuro-tendinous end-organs of frog, from *tibialis posticus.* Only the nerve fiber and its terminal branches reproduced. Leitz No. 7 objective ; No. 2 eye-piece. Figure 1, reduced to ¼ original size ; figure 2, ⅓ original size.

Fig. 3.—A portion of longitudinal section of neuro-tendinous end-organ of frog, stained in methylen blue, fixed in ammonium molybdate, sectioned and counterstained in alum carmine. Leitz 1-12 oil immersion ; No. 2 eye-piece. Reduced to ¾.

Fig. 4.—Cross section of neuro-tendinous end-organ of frog. Prepared as in Fig. 3. Leitz 1-12 oil immersion ; No. 2 eye-piece. Reduced to ¾.

PLATE XIV. *Reptilia* (Emys meleagaris).

Fig. 5.—Nerve fiber with terminal branch and irregular end-disks from tendon taken from posterior extremity of turtle. Preparation was compressed before sketching to bring out more clearly the general distribution of the nerve branches and their terminations. Leitz No. 7 objective ; No. 2 eye-piece. Reduced in figure to ⅓ the size of drawing.

Fig. 6.—Nerve termination from neuro-tendinous end-organ of turtle, from preparation fixed in ammonium molybdate, teased and mounted in balsam. Leitz No. 7 objective; No. 2 eye-piece; reduced in figure to ⅓ the size of drawing.

Fig. 7.—Longitudinal section of neuro-tendinous end-organ in fascia-like tendon. Shows relative position of nerve ending in tendon. Tissue fixed in ammonium molybdate, sectioned and counterstained in alum carmine. Leitz No. 7 objective; No. 2 eye-piece. Figure reduced to 2-5 of the size of drawing.

Fig. 8. Preparation made as in Fig. 7. Leitz No. 7 objective; No. 2 eye-piece. Figure reduced to ½ the size of the drawing.

Figs. 9, 10 and 11.—Cross sections of neuro-tendinous end-organs of turtle. Tissue fixed in ammonium molybdate, sectioned and counterstained in alum carmine. Fig. 11 shows an imperfectly encapsulated neuro-tendinous end-organ. Leitz 1-12 oil immersion; No. 2 eye-piece. All reduced to ¾ of size of drawing.

PLATE XV. *Bird* (Dove).

Figures in Plate XV are from neuro-tendinous end-organs obtained from the tendons of the wings of doves.

Fig. 12.—Small neuro-tendinous end-organ, with no, or imperfectly developed capsule, compressed under cover-glass to bring out more clearly the general arrangement of nerve branches and terminations. Leitz No, 7 objective; No. 2 eye-piece. Figure ½ the size of drawing.

Figs. 13, 14 and 15.—Neuro-tendinous end-organs of dove, showing difference in size and shape and complexity of nerve terminations. Leitz No. 7 objective; No. 2 eye-piece. Figure 13 reduced to ⅓, Figs. 14 and 15 to ½ the size of drawings.

Figs. 16 and 17.—Longitudinal sections of neuro-tendinous end-organs of dove; from sections made by fixing tissue in ammonium molybdate, sectioning and staining in alum carmine. Show relation of end-organs to the tendon and muscular fibers. Leitz No. 7 objective; No. 2 eye piece. Figures reduced to ⅓ the size of drawings.

Figs. 18 and 19.—Cross sections of neuro-tendinous end-organs of doves. Sections prepared as for figures 16 and 17. Leitz 1-12 oil immersion; No. 2 eye-piece. Figures ½ the the size of drawings.

PLATE XVI. *Mammalia.*

Fig. 20.—Neuro-tendinous end-organs from interossei muscles of posterior extremity of a dog. From preparation fixed in ammonium molybdate, teased and mounted in balsam. In this figure, the shape and general structure of this end-organ, as found in the dog, are well reproduced. Leitz No. 7 objective; No. 2 eye-piece. Figure reduced to ⅓ the size of drawing.

Fig. 21,—Neuro tendinous end-organ of cat. Leitz No. 7 objective; No. 2 eye-piece. Figure reduced to ⅓ the size of drawing.

Fig. 22.—Neuro-tendinous end-organ of rabbit. Leitz No. 7 objective; No. 2 eye-piece. Figure reduced to ⅓ size of drawing.

PLATE XVII. *Mammalia.*

Fig. 23.—Compound neuro-tendinous end-organ from fascia of back muscles of white rat. Leitz No. 7 objective; No. 2 eye-piece. Figure reduced to ⅓ of size of drawing.

Fig. 24.—Longitudinal section, cut parallel to the surface of the tendon of one of the leg (posterior extremity) muscles of kitten about one month old. Attention is called to the simple terminations as compared with other figures given. Tissue was fixed in ammonium molybdate sectioned and counterstained in alum carmine. Leitz 1-12 oil imm.; No. 2 eye-piece. Figure ⅓ size of drawing.

Figs. 25 and 26.—Cross sections of neuro-tendinous end-organs of rabbit from tissue fixed in ammonium molybdate, sectioned and counterstained in alum carmine. Leitz 1-12 oil imm.; No 2 eye-piece. Figures reduced to ½ size of drawings.

PLATE XVIII. *Mammalia.*

Fig. 27.—Longitudinal section of neuro tendinous end-organ of cat, from tissue fixed in ammonium molybdate, sectioned and mounted in balsam. Section not counterstained. For this reason, the nuclei are not shown in the figure. Leitz No. 7 objective; No. 2 eye-piece. Figure reduced to ½ the size of drawing.

Fig. 28.—Longitudinal section of neuro-tendinous end-organ of rabbit. Specimen prepared as in figure 27. Leitz No. 7 objective; No. 2 eye-piece. Figure reduced to ½ size of drawing.

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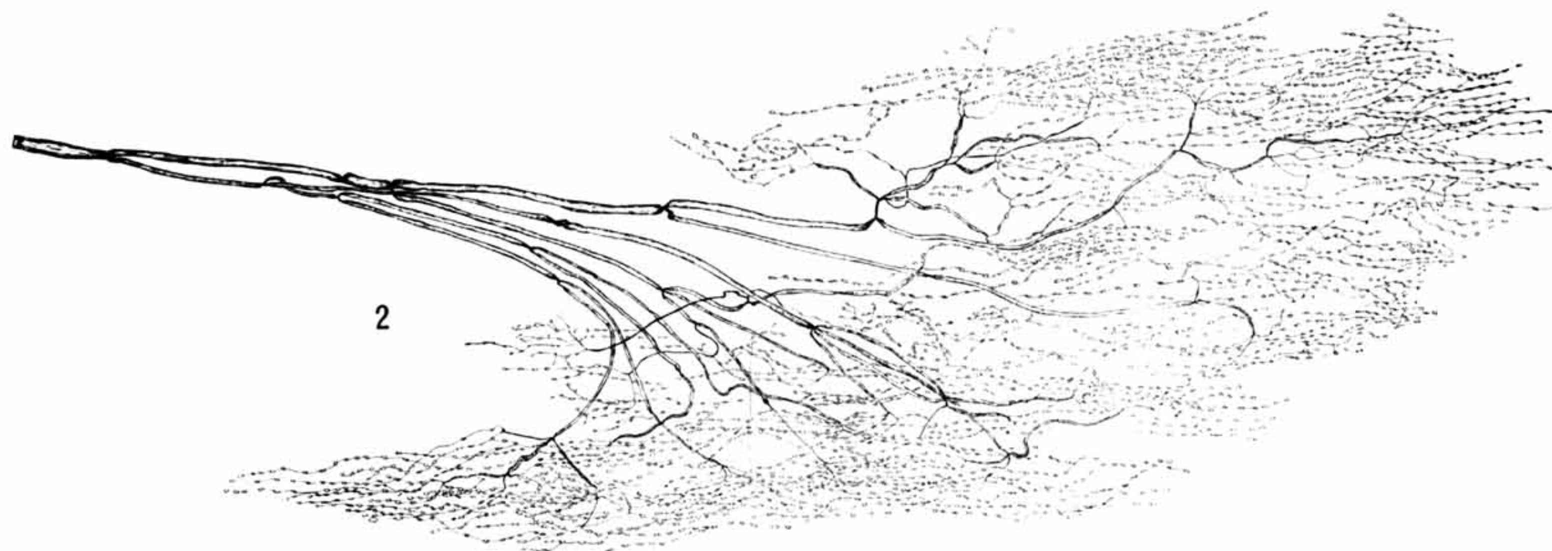

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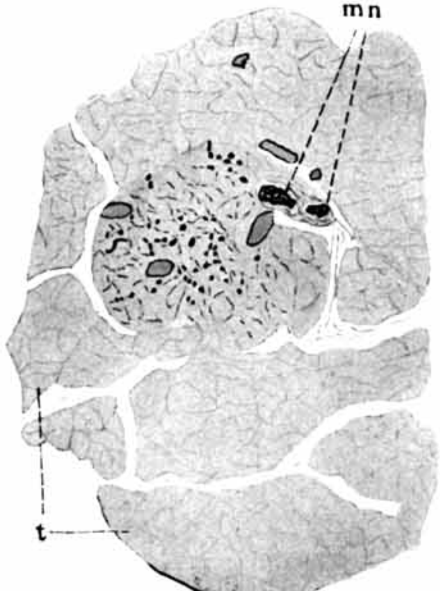

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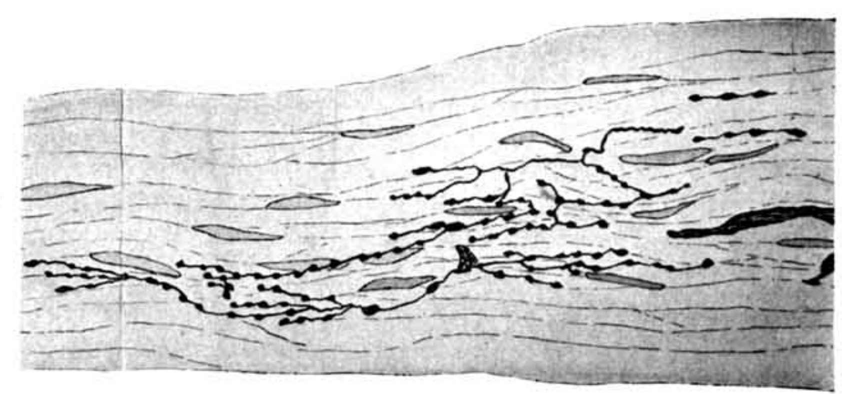

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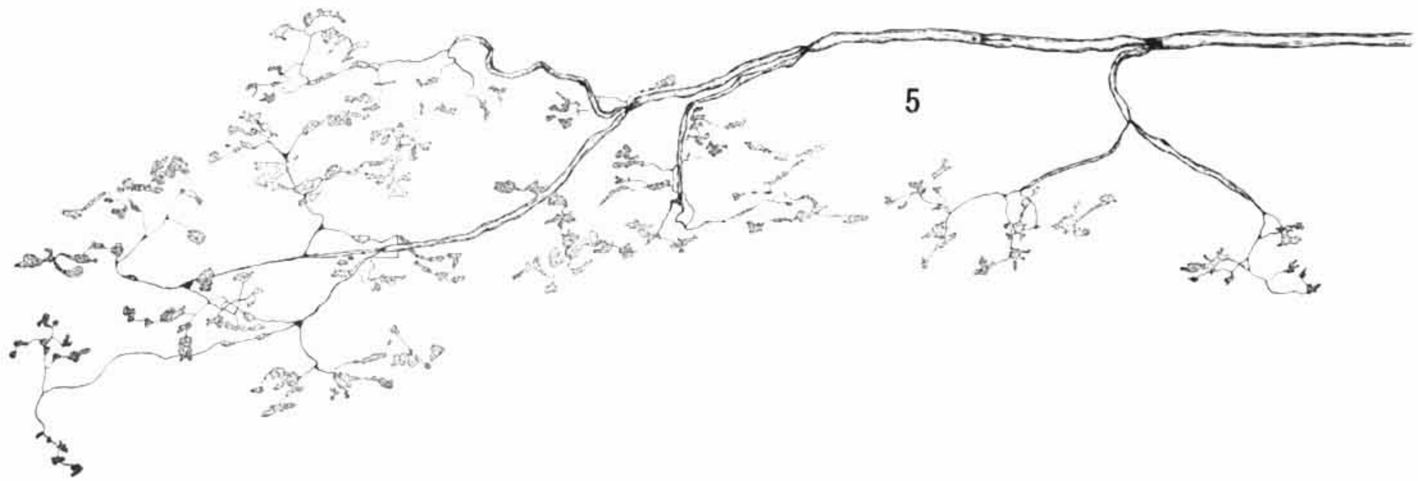

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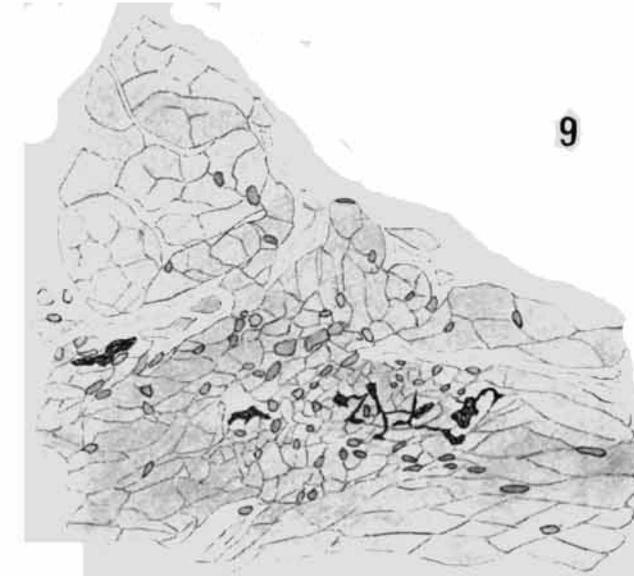

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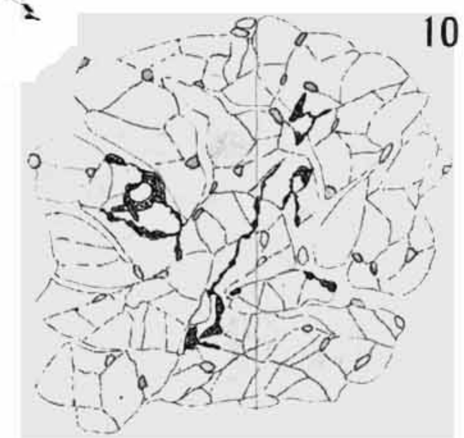

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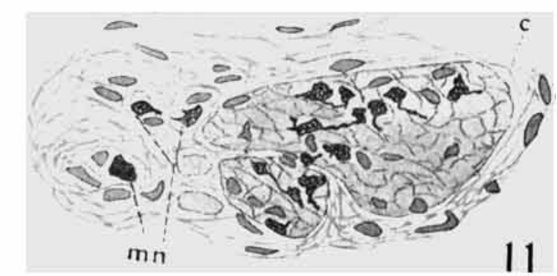

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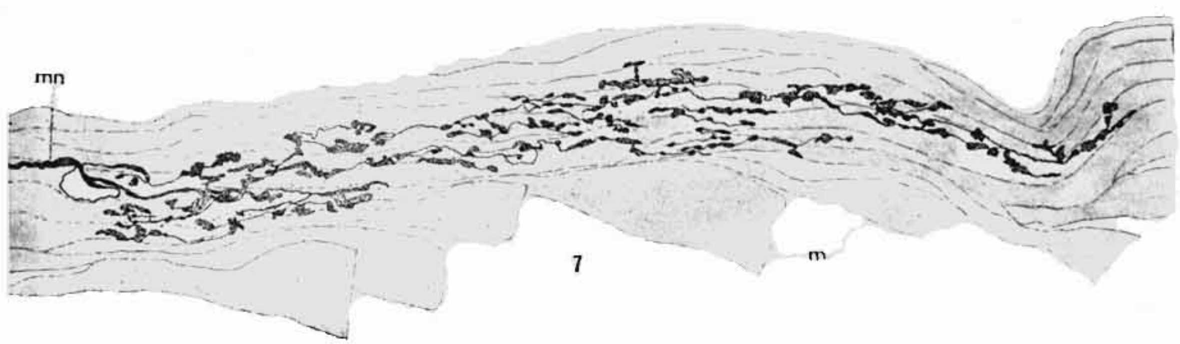

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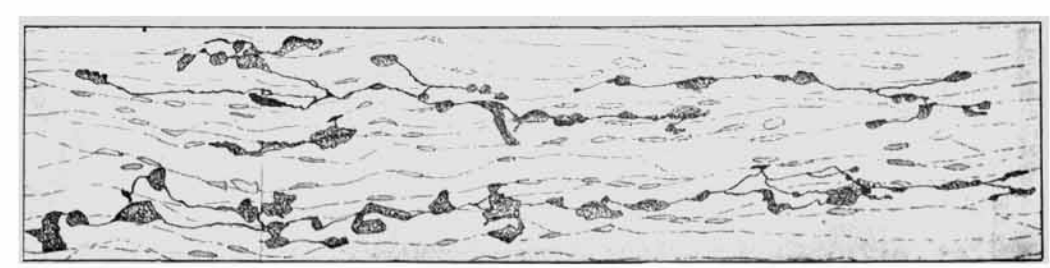

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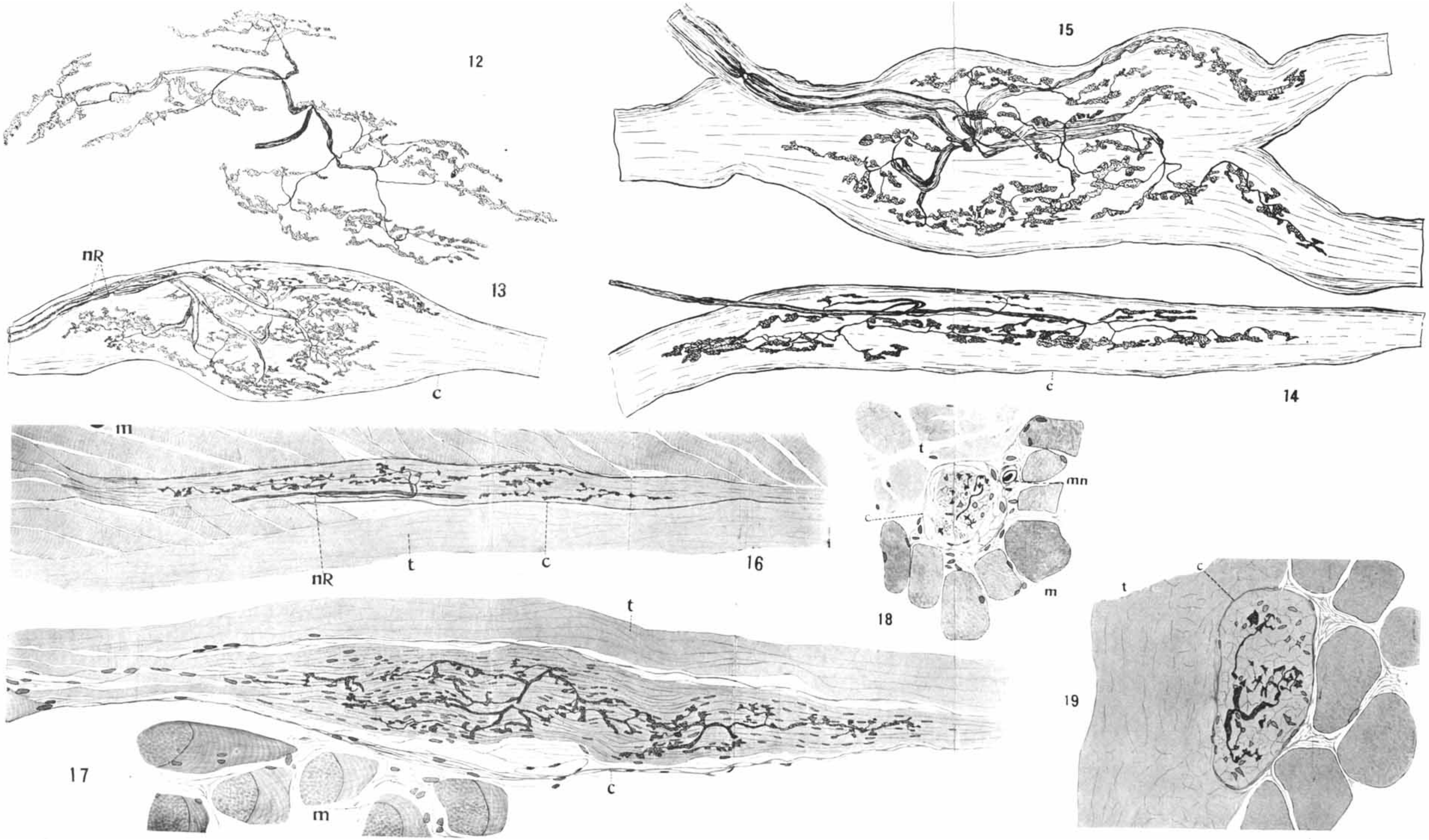

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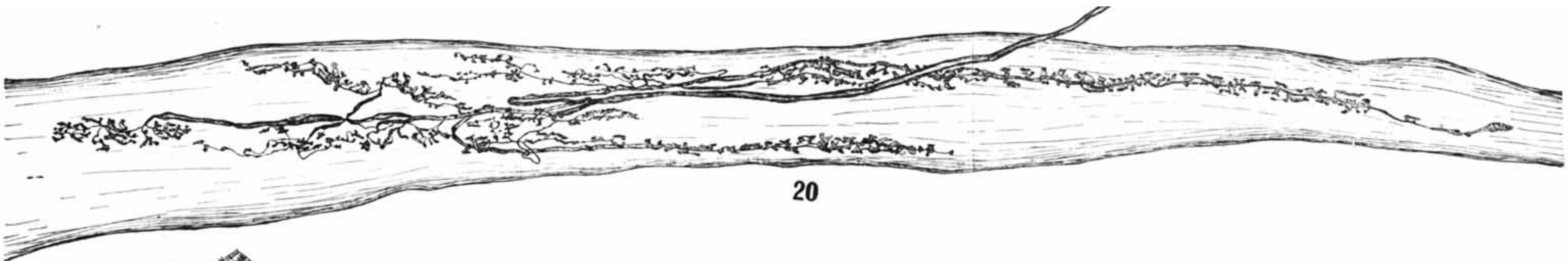

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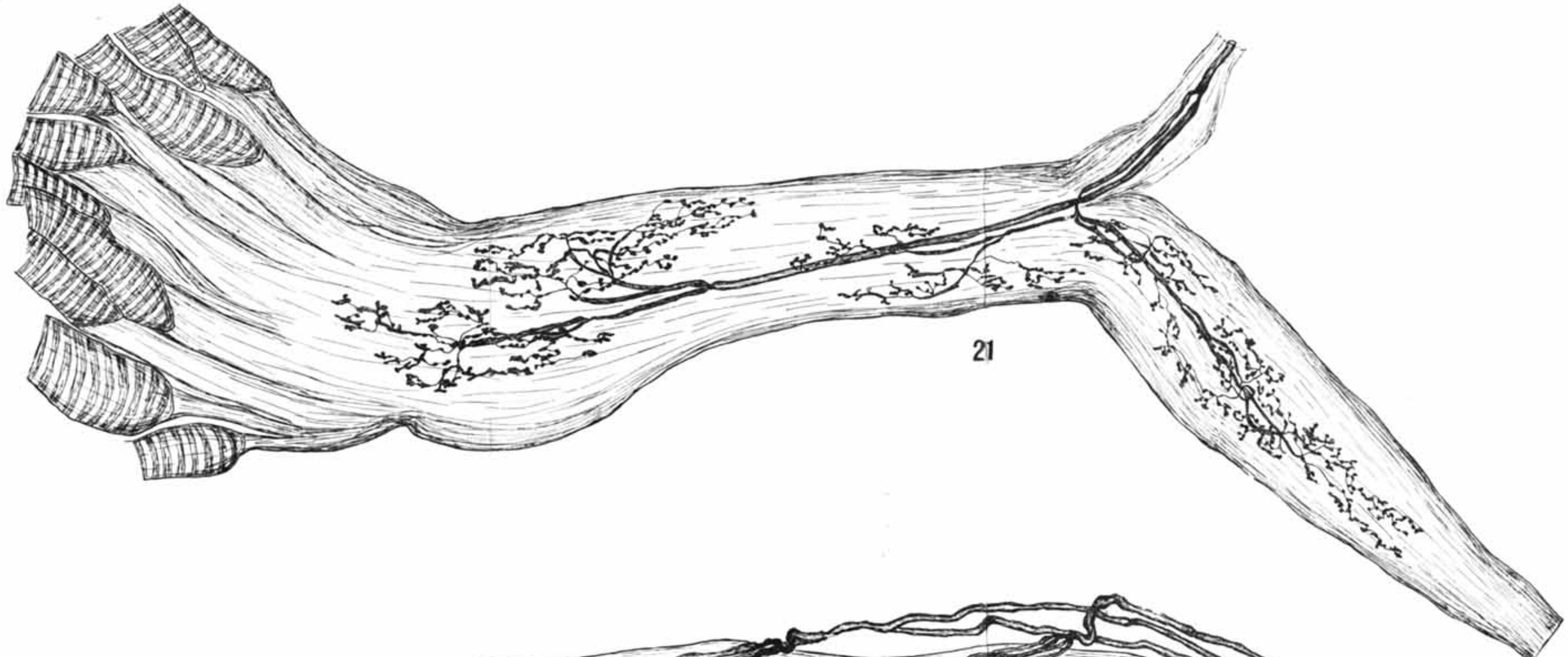

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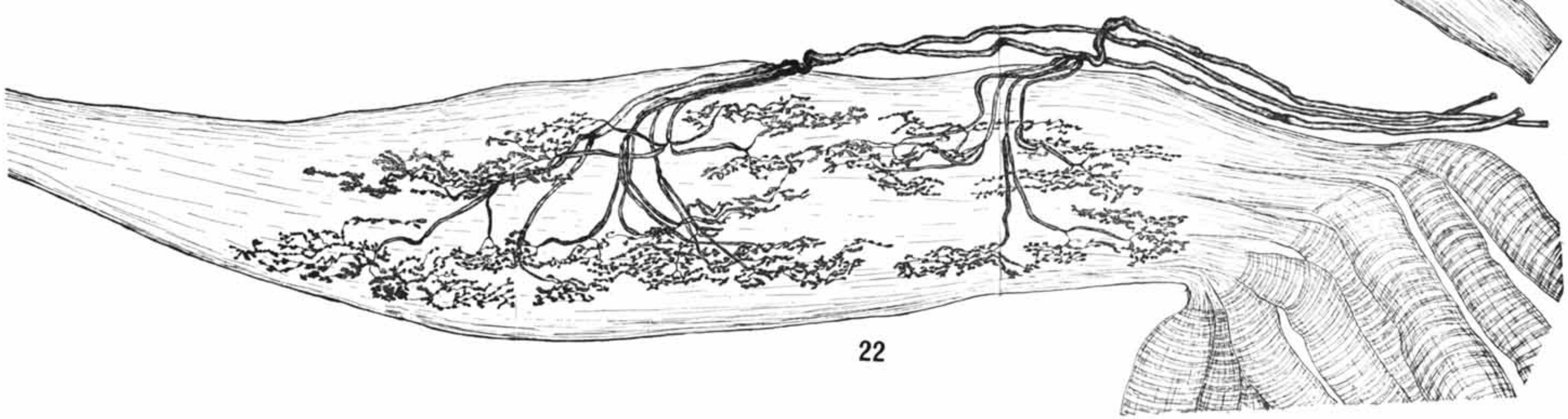

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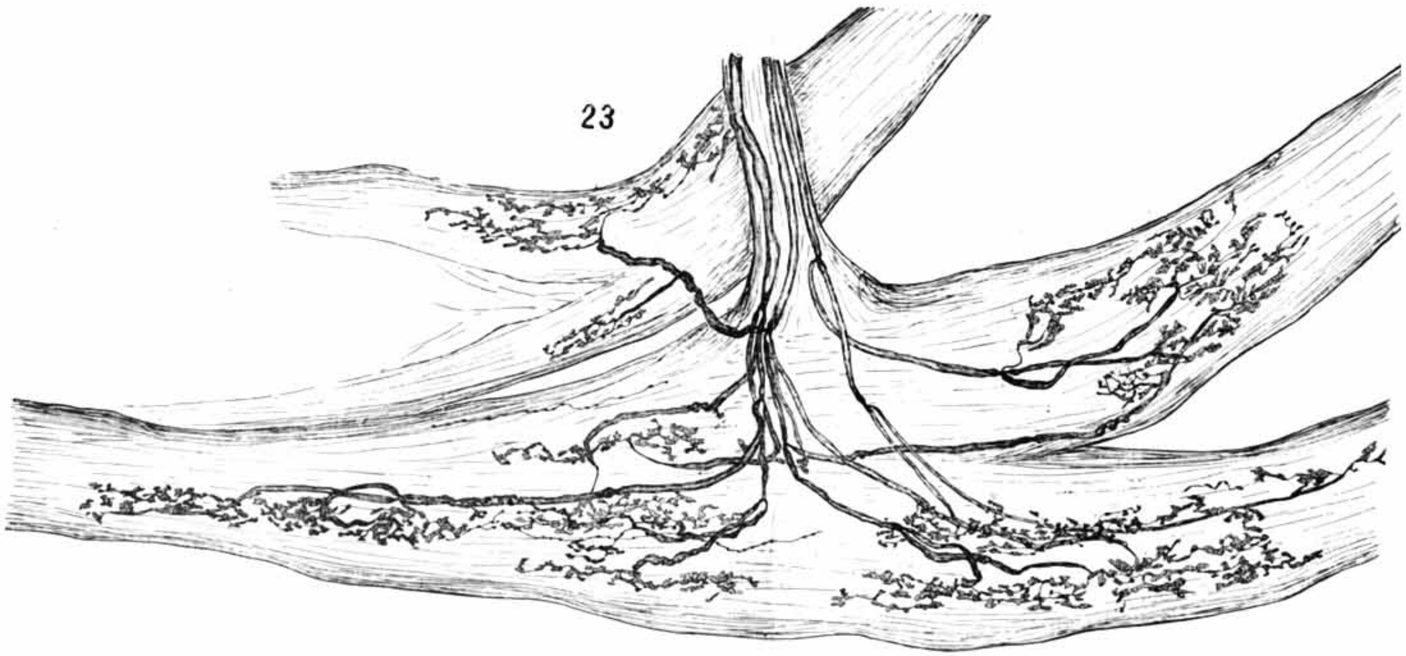

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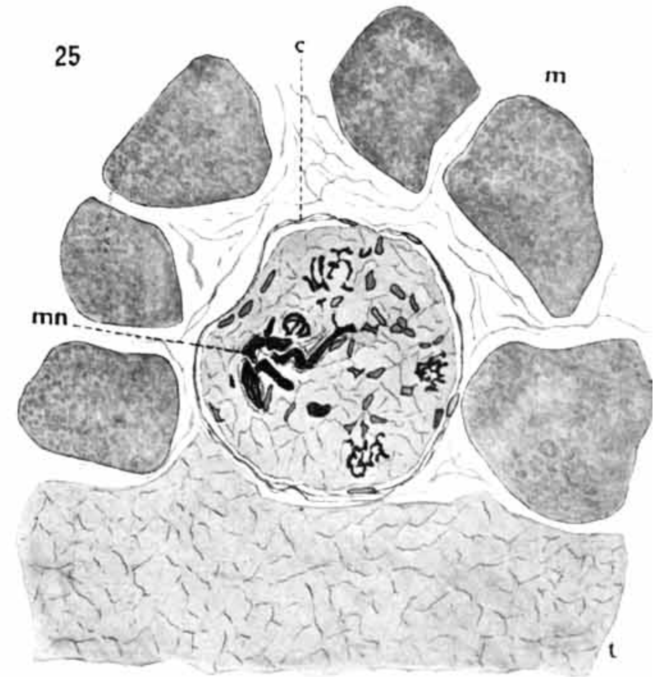

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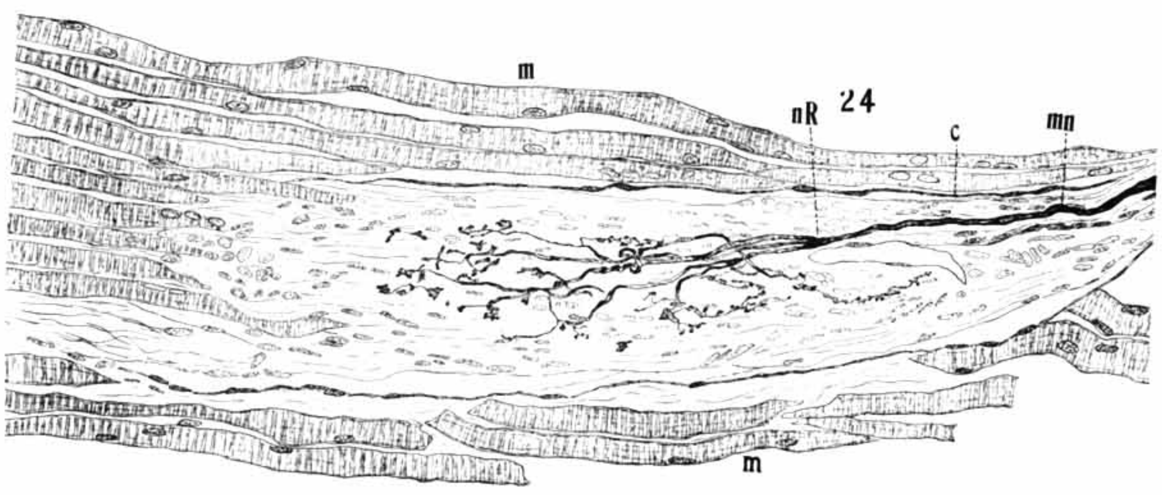

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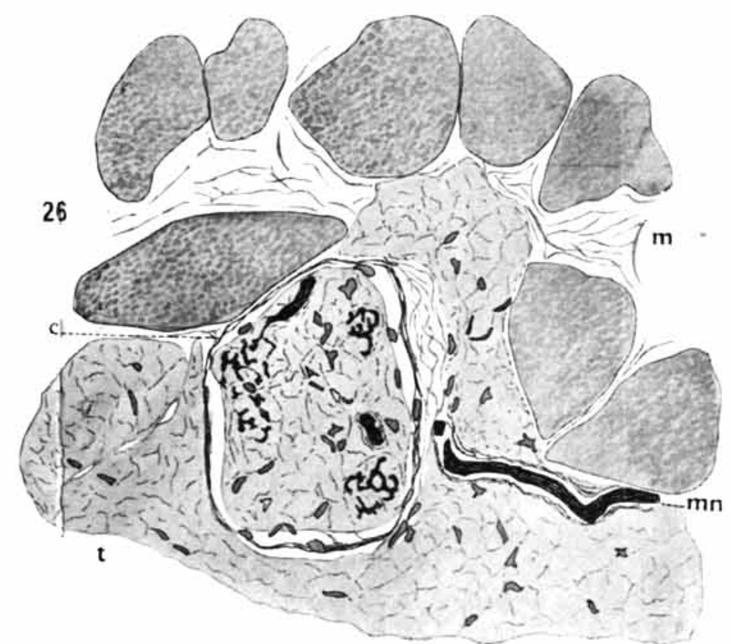

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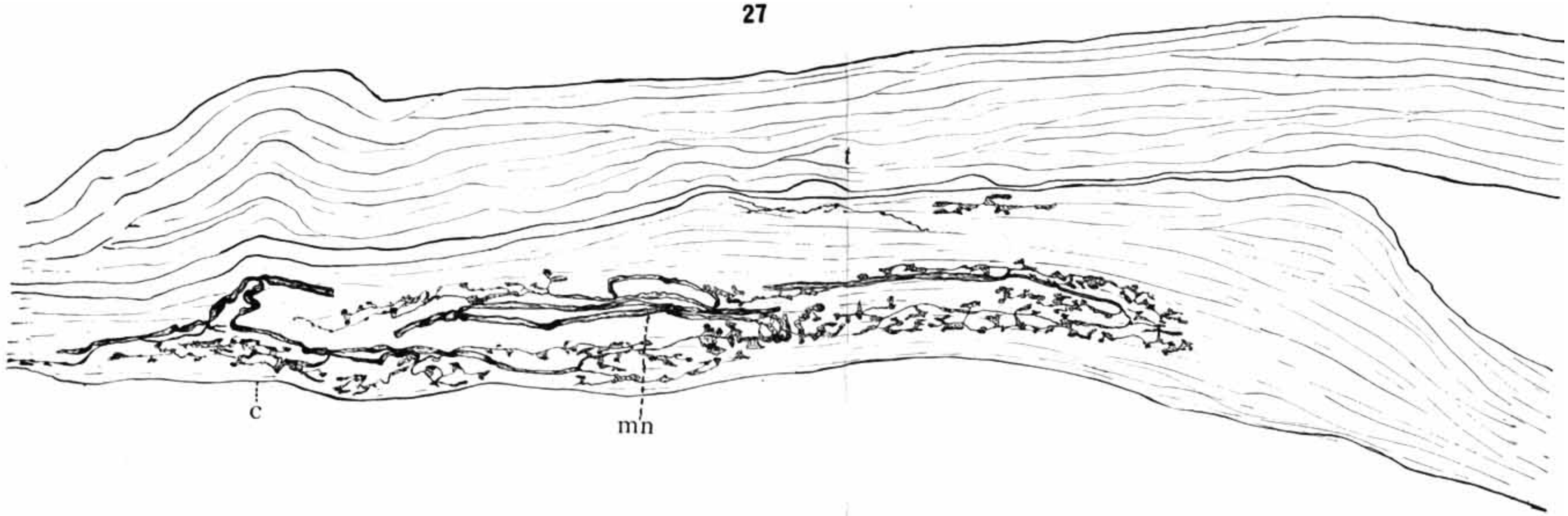

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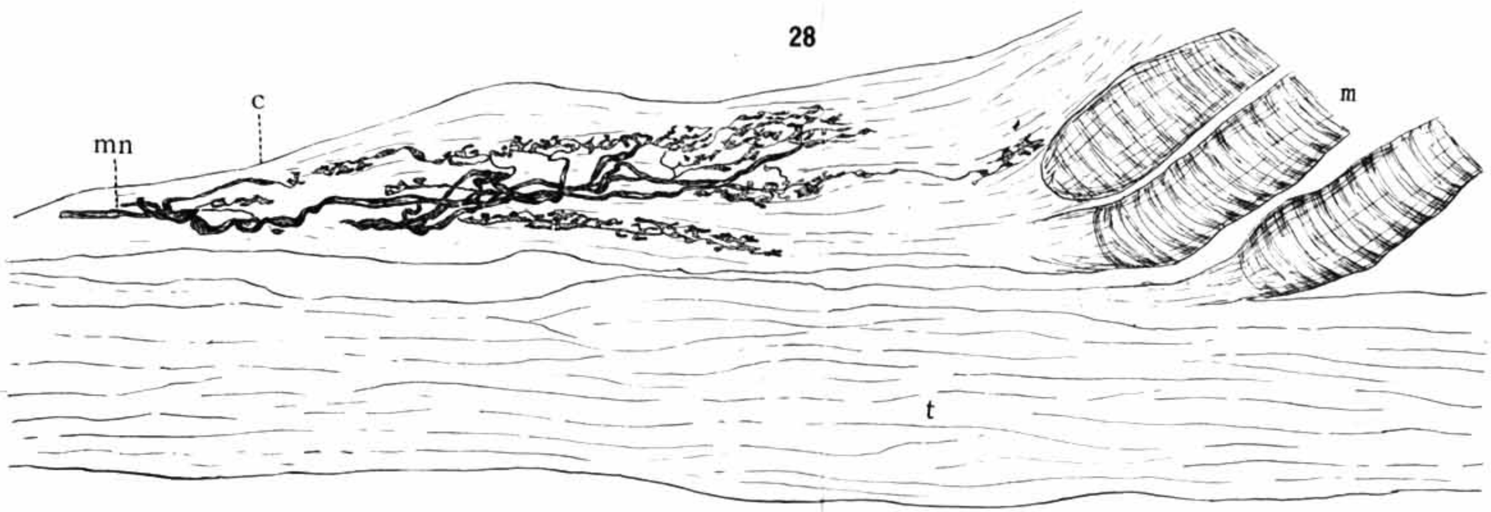

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