STRUCTURE-STRENGTH RELATIONS IN

MAMMALIAN TENDON

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ABSTRACT The stress-strain relations in mammalian tendon are analyzed in terms of the structure and mechanics of its constituents. The model considers the tensile and bending strength of the collagen fibers, the tensile strength of the elastin fibers, and the interaction between the matrix and the collagen fibers. The stress-strain relations are solved through variational considerations by assuming that the fibermaxtrix interactions can be modeled as beam on elastic foundation. The tissue thus modeled is a hyperelastic material. It is further shown that on the basis of the model, the dominant parameters to the tendon's behavior can be evaluated from simple tensile tests.

INTRODUCTION

The role of the tendon is to transmit mechanical force. The load-bearing elements in the tendon are collagen fibers. Its efficiency as a force transmission element is exemplified by the very low extensions (1-2%) it undergoes under physiological conditions. Skin on the other hand, undergoes very large physiological deformations (stretch ratio of up to 2.0), whereas its collagen consistency is similar to that of a tendon (Crisp, 1972). The most important reason for this difference is the structure of the collagen fibers in these two tissues: in the tendon they are parallel, nearly straight, and aligned in the direction of applied loads; in the skin they are structured in a three-dimensional wavy array. Hence, the effect of collagen structure on the tissue's function is most important. A most comprehensive review of the structure and function of tendon is given by Elliot (1965) and Crisp (1972). The present work is confined to specific aspects of structure and structure-function relations, namely those which affect the stress-strain relations.

The geometry of the collagen fibers in the tendon was described as helical by Lerch (1950), Verzar (1964), Cruise (1958), and Barbenel et al. (1971). Rigby et al. (1959), and more recently, Yannas and Huang (1972) and Diamant et al. (1972) in a most detailed study, determined that the fibers in rat tail tendon are planar and sinusoidally shaped. Evans and Barbenel (1974) suggest that the collagen geometry may be sinusoidal in tail tendon and helical in others.

Stress-strain relations in tendons are reversible if strain does not exceed levels of 2-4% (Rigby et al., 1959; Abrahams, 1967; Partington and Wood, 1963). In the reversible range, tendons show marked nonlinear behavior. It is customary to divide the curve into three ranges: the primary range of low strain in which the curve has a

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small slope; the secondary range of gradually increasing slope; and the tertiary range of constant, high slope. Gibson and Kenedi (1968) show that the final slope at the tertiary range corresponds to the slope of stress-strain curve of a straight collagen fiber (Morgan, 1960). This is the case with skin and ligamentum flavum as well. From this work and the works of Rigby et al. (1959), Vidiik and Ekholm (1968), Diamant et al. (1972), and Millington et al. (1971), it can be concluded that, at the secondary range, the behavior corresponds to the gradual straightening of the collagen fibers until they are fully straight at the tertiary range.

Several models have been proposed for the stress-strain relation of tendons. Two classes seem to be predominant. One is the class of macroscopic, phenomenological models that attempt to approximate experimental results. Thus, Frisen et al. (1969) presented a model consisting of springs, dashpots, and dry friction elements. Hartung (1972) adopted the linear theory of locking materials to nonlinear cases. Haut and Little (1972) used Fung's (1972) quasi-linear viscoelastic concept for rat tail collagen fibers and proposed a simple power law for stress-strain relations under constant rate of stretch.

Another class of models are those based on structural considerations. Lerch (1950) proposed a ropelike configuration of the collagen fibers in tendons but did not develop a workable model for stress-strain relations. Diamant et al. (1972) propose a model for stress-strain relations based on their investigations of the structure of the collagen fibers in the tendon. The tendon strength is associated with the bending rigidity of the collagen fibers. The contribution of elastic fibers and matrix-fiber interaction are ignored. The fibers are modeled as zigzag-shaped inflexible hinges. The stress-strain relation is obtained by using the theory of elastica.

Their theory agrees with experimental stress-strain data only if the diameter is thick ($\sim 500 \text{ nm}$) compared to the observed amplitude and wavelength ($\sim 200 \text{ nm}$). Under these conditions the theory of elastica used in the model does not apply.

Dale et al. (1972) observed the changes of the collagen fiber geometry during strain. By comparing results to theoretical prediction, they concluded that the fiber's shape is a planar sine wave.

In a recent report Comninou and Yannas (1976) developed a stress-strain equation for a single, sinusoidally shaped collagen fiber as well as for bundles of fibers embedded in a matrix. The single fiber model results from linearization of Reissner's (1972) one-dimensional finite-strain beam theory. The bundles of fibers in the tendon are modeled as alternating, parallel fibers and matrix layers glued together. It is assumed that initial waviness is small and that the elastic modulus of the matrix is much smaller than that of the fibers. Under these assumptions Bolotin's (1966) analysis of composite material of similar geometry is used to derive the stress-strain law for the tendon. The results are not compared quantitatively to data, but show similarity to experimental curves. Their model of the single fiber corresponds well with morphological evidence. The layered model of fibers and matrix, however, does not agree with observations.

Another model in this class is the one proposed by Beskos and Jenkins (1975).

The tendon is modeled as an incompressible fiber-reinforced composite with continuously distributed inextensible fibers of helical shape embedded in a hollow right circular cylinder. They solve the stress-strain relations of such a system by using the theory of internal constraints which was developed by Ericksen and Rivlin (1954). Since the collagen fibers extensibility is not taken into consideration, the model predicts infinite strength at high strain, which is not the case.

In the present work a model for the tendon structure and structure-function relationship is developed. The fiber's geometry and mechanics as well as the interactions between the fibers and the matrix is taken into consideration. Attention is paid to the following questions: (a) How is the observed structure of collagen fibers maintained under equilibrium? (b) What is the function and interplay between various tissue constituents under stretch? (c) What is the effect of the fiber mechanics and geometry on the tendon's stress-strain relations? (d) What are the key parameters dominating the tissue's behavior? (e) How can these parameters be evaluated from simple mechanical tests?

THE PRESENT MODEL

Following the works of Diamant et al. (1972), Dale et al (1972), Vidiik (1968), and Yannas and Huang (1972), we shall assume that the collagen fibers in mammalian tendons are parallel, planar, and sinusoidally shaped. It will be further assumed that this observed configuration represents the state of minimum energetic level of this system, which contains the collagen fibers themselves, the matrix in which they are embedded (ground substance), and the elastin fibers. Upon stretching, the energy of the system changes due to the tensile and bending strength of the collagen fibers, the matrix-fiber interaction, and the tensile strength of the elastin fibers. A simple workable model of one section of this system is shown in Fig. 1.

Although the role of elastin in undulating the tendon's collagen fibers has not yet been proved, it has been shown by Daly (1969) that in the skin (which resembles the tendon in many ways), and by Wood (1954, Fig. 2) for ligamentum nuchae, the role of elastin is predominant on the mechanical behavior at low ranges of strain. Similar results were obtained for arteries (Roach and Burton, 1957).

Consider an element of the collagen fiber (Fig. 2). In equilibrium its shape is given by:

$$Y_0 = A_0 \sin \beta X, \tag{1}$$

where the x-axis coincides with the length of the fiber and $\beta = 2\pi/\lambda$. A_0 is the



FIGURE 1 A simple model for the basic functional unit of the collagen-elastin system.



FIGURE 2 Free body diagram of an infinitesimal section of the collagen fiber. F, axial load; Q, shear load; M, moments; q_y , intensity of lateral matrix reaction; m, intensity of matrix reactive moments.

initial amplitude and λ is the wavelength. Upon stretching, the length changes from ds to ds (1 + e) where e is the tensile strain of the collagen fibers. The additional internal forces in the fiber (F, M, and Q) and the additional reactions of the matrix on the wire $(q_y \text{ and } m)$ are shown in Fig. 2. Comminou and Yannas (1976) analyzed the behavior of a single fiber in a similar manner, but excluded the reactions of the matrix $(q_v \text{ and } m)$. By assuming that the horizontal force in each element of the fiber is constant throughout its length, they formulated equilibrium conditions in the form of a nonlinear second-order differential equation of the angle ϕ (the angle between the tangent to the collagen fiber at a point and the horizontal x-axis) in terms of the length s. They solve the load-strain relations of the fiber by several approximations based on the fact that the strain e is very small compared to unity. Herrmann et al. (1967) also used this approach in their analysis of the response of reinforcing wires to compressive state of stress. The reaction of the matrix was introduced by considering the wire as a "beam on elastic foundation" where the reaction of the foundation is characterized by foundation constants. It was assumed that the wires' shape remains sinusoidal upon deformation. Since $e \ll 1$ they further assumed that the wavelength of the wires is constant and only its amplitude changes with the deformation. Lanir and Fung (1972) showed that under these assumptions the load-strain relations of the wire can be readily obtained from variational considerations. The variational approach will be used in the present work due to its simplicity compared to detailed equilibrium analysis.

If a horizontal stretching load F is applied, the system of Fig. 1 will change its length λ . If the change of length $\Delta\lambda$ is very small compared with λ , then the effect of this change on the geometry of the system can be neglected. Nevertheless, the value of $\Delta\lambda$, however small, must be considered in evaluating the overall strain and the magnitude of the external work applied on the system. These assumptions are common in cases in which the principle of virtual works is used. In the tendon, the overall strain D is very low ($\sim 1-2\%$). We shall thus adopt the above approach.

Thus, the fiber (considered now as a beam on elastic foundation) with original shape given by Eq. (1), changes upon stretch to:

$$Y = A \sin \beta X \quad \beta = 2\pi/\lambda, \tag{2}$$

where it is assumed that λ is unaltered due to the smallness of e.

The following further assumptions are made: (a) The fiber obeys Hooke's law: (b) The combined effect of matrix-fiber and fiber-fiber interaction under small strain can be characterized by foundation constants. This assumption is reasonable since the collagen fibers, although closely packed, are parallel to each other and change uniformly upon stretch (Diamant et al., 1972; Dale et al., 1972).

The matrix exerts on the fiber a force in the y direction (q_y) and a moment (m) given by:

$$q_{y} = K_{y}(Y_{0} - Y) = K_{y}(A_{0} - A)\sin\beta X, \qquad (3)$$

$$m = -K_m \cdot \mathrm{d}(Y_0 - Y)/\mathrm{d}X = -K_m\beta(A_0 - A)\cos\beta X, \qquad (4)$$

where K_y and K_m are foundation constants.

Hence the corresponding strain energies stored in a section of length λ of the matrix in the deformed state are:

$$W_1 = \int_0^\lambda K_y (Y_0 - Y)^2 dX/2, \qquad (5)$$

$$W_2 = \int_0^{\lambda} K_m (d(Y_0 - Y)/dX)^2 dX/2.$$
 (6)

By using Eqs. 1 and 2 we get:

$$W_1 = K_y (A_0 - A)^2 \lambda / 4, \tag{7}$$

$$W_2 = K_m \cdot \beta^2 (A_0 - A)^2 \cdot \lambda/4.$$
 (8)

Evaluation of the foundation constants can be done in certain cases as was shown by Lanir and Fung (1972) and Herrmann et al. (1967), (Appendix I).

The strain energy stored in the fiber due to its bending is:

$$W_3 = \int_0^\lambda E_c I[(d^2(Y_0 - Y)/dX^2)^2] dX/2, \qquad (9)$$

where E_c and I are the Young modulus and the moment of inertia of the fiber, respectively.

By inserting Eqs. 1 and 2 into Eq. 9, we get:

$$W_3 = E_c I \beta^4 (A_0 - A)^2 \lambda / 4.$$
 (10)

The shortening of one wavelength of the fiber ($\Delta\lambda$) is (Appendix III):

$$\Delta \lambda = \int_0^{\lambda} \left[(dY_0/dX)^2 - (dY/dX)^2 \right] dX/2,$$
(11)

or

$$\Delta \lambda = \lambda \beta^2 (A_0^2 - A^2)/4. \tag{12}$$

The stretch load applied on the collagen fibers will be denoted F'_c . The load applied on the elastin fiber is F_e . Hence the total load is (Fig. 1):

$$F = F_c + F_e, \tag{13}$$

where F_c is the horizontal component of F'_c . The external work exerted on the system is W_4 .

The variational equation of equilibrium is:

$$(\partial W_4/\partial A)dA = (\partial W_1/\partial A)dA + (\partial W_2/\partial A)dA + (\partial W_3/\partial A)dA, \quad (14)$$

where $(\partial W_4/\partial A) dA = F_c(\partial (\Delta \lambda)/\partial A) dA$.

By using Eqs. 7, 8, 10, and 12 we get from Eq. 14:

$$F_c = (K_y/\beta^2 + K_m + E_c I\beta^2) (A_0 - A)/A.$$
(15)

The amplitude ratio δ can be evaluated in terms of F_c as:

$$\delta = A/A_0 = [1 + F_c/(K_y/\beta^2 + K_m + E_c I\beta^2)]^{-1}.$$
 (16)

The overall strain of the collagen fiber has two components: the geometrical strain, D_G , which results from the configurational change of the fiber during the stretching, and the elastic strain, D_c , related to the extension of the fiber itself under the stretching load.

The amplitude A of the collagen in the tendon is small compared with the wavelength λ . Hence the elastic strain D_c can be approximated by:

$$F_c = D_c E_c \cdot S_c = D_c \cdot K_c, \tag{17}$$

where S_c is the cross-sectional area of the collagen fiber and K_c is the "spring" constant of this fiber.

By introducing Eq. 17 to Eq. 16 we get:

$$\delta = (1 + \alpha D_c)^{-1}, \tag{18}$$

where

$$\alpha = E_c S_c / (K_y / \beta^2 + K_m + E_c I \beta^2).$$
(19)

The "geometric" strain of the fiber is given by $D_G = \Delta \lambda / \lambda$. By using Eq. 12 we get for D_G :

$$D_G = \beta^2 (A_0^2 - A^2)/4.$$
 (20)

The total strain will be

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$$D = D_c + D_G = D_c + (\beta A_0/2)^2 (1 - \delta^2) = D_c + \gamma (1 - \delta^2), \quad (21)$$

where $\gamma = (\beta A_0/2)^2$.

By using Eq. 18 we get:

$$D = D_c + \gamma \cdot \Delta(\Delta + 2)/(1 + \Delta)^2, \qquad (22)$$

where $\Delta = \alpha \cdot D_c$.

The elastin fiber obeys Hooke's law. Hence:

$$F_{\boldsymbol{e}} = E_{\boldsymbol{e}} \cdot S_{\boldsymbol{e}} \cdot D = K_{\boldsymbol{e}} \cdot D, \qquad (23)$$

where E_e , S_e are respectively the Young modulus and cross-sectional area of the elastin fiber, and K_e is a spring constant which incorporates the two of them.

By combining Eqs. 13, 17, and 23 we get:

$$F = F_c \cdot D_c + K_e \cdot D. \tag{24}$$

Eqs. 18, 21, and 24 are three parametric equations of D_c , from which the relations F = F(D) can be readily calculated.

The slope \overline{K} of the F(D) curve can be evaluated as follows:

$$\overline{K} = dF/dD = (dF/dD_c)(dD_c/dD), \qquad (25)$$

and by using Eqs. 18, 21, and 24 we get:

$$\overline{K} = K_c [1 + 2\gamma \alpha (1 + \alpha D_c)^{-3}]^{-1} + K_e.$$
(26)

From the above analysis it is apparent that four overall parameters specify the behavior of the tendon: The spring constants K_e and K_c , the geometrical parameter γ , and the mixed mechanical geometrical parameter α (Eq. 19).

The effects of these parameters on the normalized load-strain relations are shown in



FIGURE 3 The effect of the ratio K_e/K_c on the normalized load-strain relations: ---, $K_e/K_c = 0$; o, $K_e/K_c = 1/30$; ×, $K_e/K_c = 1/10$. $\alpha = 160$ and $\gamma = 0.033$.



FIGURE 4 The effect of the parameter α (Eq. 19) on the normalized load-strain relations: —, $\alpha = 50$; \circ , $\alpha = 160$; \times , $\alpha = 500$. $K_e/K_c = 1/30$ and $\gamma = 0.033$.

Figs. 3–5. The levels chosen for the parameters are around the physiological ones (Diamant et al., 1972). The resulting curves resemble experimental data.

Eq. 22 is identical to the one obtained by Comninou and Yannas (1976). In the present work the model is generalized to include the effect of the matrix-fiber interactions and the role of the elastin fibers is taken into consideration.

THE STRAIN ENERGY FUNCTION

A strain energy function can be derived for the tendon. The load under adiabatic or isothermal conditions can then be derived from this strain energy function W as F = dW/dD. The tendon can thus be regarded as hyperelastic.



FIGURE 5 The effect of the parameter $\gamma (= \beta^2 A_0^2/4)$ on the normalized load-strain relations: —, $\gamma = 0.025$; $o, \gamma = 0.033$; $\times, \gamma = 0.045$. $\alpha = 160$, and $K_e/K_c = 1/30$.

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FIGURE 6 Comparison between the model's prediction and experimental data of Abrahams (1967, Fig. 5). The obtained values of the parameters are: $K_c = 2.95 \times 10^5$, $K_e = 1.15 \times 10^2$; $\alpha = 1607.8$; $\gamma = 1.22 \times 10^{-2}$.

It is difficult to derive W as an explicit function of the overall strain D since the relationship F = F(D) are implicit. It is possible, however, to express W as a function of D and the elastic strain of the collagen fiber, D_c , in the following manner:

$$W = K_e D^2/2 + (K_c/\alpha) [\Delta^2/2\alpha - \gamma(2\Delta + 1)/(1 + \Delta)^2], \qquad (27)$$

where $\Delta = \alpha \cdot D_c$ and from Eq. 22 we have:

$$D = \Delta/\alpha + \gamma \Delta(\Delta + 2)/(1 + \Delta)^2.$$
(28)

Upon derivation with respect to D we get:

$$dW/dD = K_e D + (K_c/\alpha)(\partial/\partial\Delta)[\Delta^2/2\alpha - \gamma(2\Delta + 1)/((1 + \Delta)^2)/(dD/d\Delta).$$
(29)

By using Eq. 28 we get:

$$dW/dD = K_e D + K_c D_c.$$
(30)

By comparing Eq. 30 to Eq. 24 we conclude that F = dW/dD. The tendon is therefore hyperelastic.

THE INVERSE PROBLEM

In the inverse problem we wish to obtain information on the mechanics and structure of the tissue constituents from simple mechanical tests.

In the tendon we can evaluate the key parameters K_e , K_c , α , and γ which dominate its mechanical response by fitting the set of the three parametric Eqs. 18, 21, and 24 to experimental data. The value of the above parameters can be obtained by nonlinear least-square procedure. The success of this approach depends primarily on the closeness of the initial guess of the parameters to their "true" levels. One way of obtaining a close initial guess is the following: At high strain the slope \overline{K} approaches asymptotically to $K_e + K_c$. Since $K_c/K_e \gg 1$ (order of 100) we can evaluate K_c manually from the slope at this region. Furthermore, by using Eq. 21, we have for the asymptotic line ($\delta = 0$):

$$D = D_c + \gamma, \tag{31}$$

and its equation in the F(D) plane:

$$F = D(K_e + K_c) - K_c \gamma.$$
(32)

This asymtotic line crosses the D-axis at:

$$D^{1} = \gamma \cdot K_{c}/(K_{e} + K_{c}) \simeq \gamma.$$
(33)

The approximate levels of the K_e and α can be obtained by solving the following equations (Appendix II):

$$(\delta^{1})^{2} - 1/(3 - 2\delta^{1}) + A^{1} = 0, \qquad (34)$$

$$\alpha = (1 - \delta^1) / [\gamma(\delta^1)^3], \qquad (35)$$

$$K_{e} = F^{1}/\gamma - K_{c}(\delta^{1})^{2}, \qquad (36)$$

where 1 denotes the value at $D = D^1$ and

$$A^{1} = [\bar{K}^{1} - F^{1}/\gamma]/K_{c}.$$
 (37)

We can now proceed to obtain improved evaluations of the four parameters $(K_c, K_e, \alpha, and \gamma)$ with one of several available nonlinear computer codes. An example of the results obtained by this method is shown in Fig. 6, where the original data is compared with the model's predictions.

CONCLUSIONS

A mechanical model for the tendon is developed. The model considers a system of undulated planar collagen fiber attached at numerous points along its length to straight elastin fiber. Both are embedded in a matrix of ground substance. Upon stretch, the elastin fibers' length increases, whereas the collagen fiber gradually becomes straight. Its lateral displacement invokes a reaction of the matrix.

If these tissue constituents are considered as linearily elastic then the interaction between the collagen fiber and the matrix can be modeled as a beam on elastic foundation. Load-strain relation can then be solved by means of variational considerations. It is shown that the tissue is hyperelastic and its behavior is dominated by four parameters: K_e , K_c ,—the spring constants of the elastin and collagen respectively; α , a parameter defined in Eq. 19; and $\gamma = \beta^2 A_0^2/4$, $\beta = 2\pi/\lambda$, where λ is the wavelength and A_0 is the initial amplitude of the collagen fiber. Finally it is shown that the value of these parameters can be determined from simple tensile tests.

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APPENDIX I

Evaluation of the Foundation Constants K_{y} and K_{m}

Evaluation of the foundation constants K_y and K_m was done for cases in which a fiber of circular cross-section is embedded in a matrix, and both fiber and matrix obey Hooke's law. Fiber-fiber interactions are neglected.

By solving exactly the elastic problem of a sinusoidally shaped fiber in this system, Herrmann et al. (1967) obtained the following values for K_{ν} and K_{m} :

$$K_{y} = 2\pi R G_{M}[\beta C_{1}K_{1}(\beta R)/2 + C_{2}\beta R K_{2}(\beta R) - C_{3}\beta^{2}K_{1}(\beta R)/2], \quad (I-1)$$

and

$$K_m = 2\pi R^2 G_M \{ C_1[K_1(\beta R)/2R - \beta K_2(\beta R)] - C_2[\beta R K_1(\beta R) + (3 - 2\nu_M) K_2(\beta R)] - C_3 \beta K_1(\beta R)/2R \},$$
(1-2)

where R is the fiber's radius, G_M and ν_M are the matrix shear modulus and Poisson's ratio, respectively, K_1 is the modified Bessel function of the second kind and C_1 , C_2 , C_3 are constants whose values are functions of β , R, ν_M , G_M , ν_F , and G_F and can be determined by solving a set of three complicated algebraic equations. Another approach was used by Herrmann et al. (1967) and by Lanir and Fung (1972). Here an assumption is made that the sinusoidally shaped, thin fiber exerts on the matrix a sinusoidally varying force. By integration of Kelvin's solution for a point force case one obtains the value of K_y . Herrmann et al. (1967) obtained for K_y :

$$K_{y} = \frac{16 \pi G_{M}(1 - \nu_{M})}{[2(3 - 4\nu_{M}) K_{0}(\beta R) + \beta R K_{1}(\beta R)]}; \quad (I-3)$$

Lanir and Fung (1972) showed that the actual value of K_y varies around the fiber circumference between the following values:

$$K_{\nu \min} = \frac{8\pi G_M (1 - \nu_M)}{[(3 - 4\nu_M) K_0(\beta R) + \beta R K_1(\beta R)]}, \quad (I-4)$$

$$K_{\nu \max} = \frac{8\pi G_M (1 - \nu_M)}{[(3 - 4\nu_M) K_0(\beta R)]}, \quad (I-5)$$

where K_0 is a modified Bessel function of the second kind.

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APPENDIX II

Derivation of Eqs. 34-36

For $D = D^1 = \gamma$ we have from Eqs. 18 and 21:

$$(\delta^1)^2 = D_c^1/\gamma, \qquad (\text{II-1})$$

$$D_c^1 = (1 - \delta^1)/(\alpha \delta^1). \qquad (II-2)$$

Hence:

$$\alpha(\delta^1)^3\gamma = 1 - \delta^1. \tag{II-3}$$

From Eqs. 18 and 26 we have:

$$K_{e}/K_{c} = \overline{K}^{1}/K_{c} - [1 + 2\alpha\gamma(\delta^{1})^{3}]^{-1}.$$
 (II-4)

By inserting Eq. II-3 to II-4 we get:

$$K_e/K_c = \overline{K}^1/K_c - 1/(3 - 2\delta^1).$$
 (II-5)

From Eqs. 24 and II-1 we have for $D = D^1 = \gamma$:

$$K_e/K_c = F^1/(\gamma K_c) - (\delta^1)^2.$$
 (II-6)

By comparing Eqs. II-5 and II-6 we get:

$$(\delta^{1})^{2} - 1/(3 - 2\delta^{1}) + A^{1} = 0,$$
 (II-7)

where

$$A^{1} = (\bar{K}^{1} - F^{1}/\gamma)/K_{c}.$$
 (II-8)

Hence δ^1 can be evaluated by solving Eq. II-7. The parameters α and K_e can now be evaluated.

From Eq. II-3 we have:

$$\alpha = (1 - \delta^1) / [\gamma(\delta^1)^3]$$
(II-9)

From Eq. II-6 we get:

$$K_e = F^1/\gamma - K_c \cdot (\delta^1)^2. \tag{II-10}$$

APPENDIX III

Derivation of Eq. 11

The infinitesimal arc length ds is given by:

$$ds = (dX^{2} + dY^{2})^{1/2} = dX[1 + (dY/dX)^{2}]^{1/2}.$$
 (III-1)

In the collagen fibers of the tendon, the amplitude is small compared with the wavelength λ . Hence $(dY/dX)^2 \ll 1$ and the above equation can be expanded as a Taylor series as follows:

$$ds = dX[1 + (dY/dX)^2/2 - (dY/dX)^4/4 + \cdots].$$
(III-2)

Due to the "flatness" of the fiber, the shortening of this infinitesimal section, $d(\Delta \lambda)$ can be approximated by:

$$d(\Delta \lambda) = ds_0 - ds.$$
 (III-3)

Eq. III-3 can be integrated and we get:

$$\Delta \lambda = \int_0^{\lambda} [(dY_0/dX)^2 - (dY/dX)^2] dX/2, \qquad (III-4)$$

where terms of higher order of (dY/dX) are neglected.