

Fibrocartilage associated with human tendons and their pulleys

M. BENJAMIN, S. QIN AND J. R. RALPHS

School of Molecular and Medical Biosciences (Anatomy Unit), University of Wales College of Cardiff, Cardiff, UK

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ABSTRACT

The presence of fibrocartilage in tendons that wrap around bony or fibrous pulleys is well known. It is an adaptation to resisting compression or shear, but the extent to which the structure of most human tendons is modified where they contact pulleys is less clear, for there has been no single comprehensive survey of a large number of sites. Less is known of the structure of the corresponding pulleys. In the present study, 38 regions of tendons that wrap around bony pulleys or pass beneath fibrous retinacula have been studied in routine histology sections taken from each of 2 or 3 elderly dissecting room cadavers. Most of the corresponding pulleys have also been examined. Fibrocartilage was present in 22 of the 38 tendon sites and it was most conspicuous where the tendons pressed predominantly against bone rather than retinacula and where they showed a large change in direction. Fibrocartilage was more characteristic of tendons at the ankle than the wrist, probably because the long axis of the foot is at right angles to that of the leg. There was considerable variation in the structure of tendon fibrocartilage. The most fibrocartilaginous tendons had oval or round cells embedded in a highly metachromatic matrix with interwoven or spiralling collagen fibres. At other sites, fibrocartilage cells were arranged in rows between parallel collagen fibres. The differences probably relate to differences in development. A single tendon could be modified at successive points along its length and fibrocartilage could be present in the endotenon and epitenon as well as in the tendon itself. Pathological changes seen in 'wrap around' tendons were fragmentation and partial delamination of the compressed surface, chondrocyte clustering, fatty infiltration and bone formation. Three types of pulleys were described for tendons—bony prominences and grooves, fibrous retinacula and synovial joints. The extent of cartilaginous differentiation on the periosteum of bony pulleys frequently mirrored that in the corresponding tendon. The cartilage or fibrocartilage prevents the tendon from 'sawing' through the bone. Some of the best known retinacula were largely fibrous, though the inferior peroneal retinaculum and the trochlea for the superior oblique were cartilaginous. The results underline the considerable regional heterogeneity in different tendons and their pulleys. They show that one tendon is not like another and that tendons may need to be carefully selected for particular surgical transfers or joint reconstructions.

Key words: Retinacula; periosteum; cartilage.

INTRODUCTION

Recent studies have challenged the traditional view that one tendon or ligament is much like another in its structure and biochemical composition (e.g. Amiel et al. 1984; Harwood & Amiel, 1992; Vogel et al. 1993). An important clinical implication is that tendons and ligaments may need to be carefully selected for particular surgical transfers and joint reconstructions. It is also clear that tendons can vary regionally along

their length. Many tendons pass around bony pulleys or beneath fibrous retinacula in order to change the direction of muscle pull (see review by Benjamin & Ralphs, 1995). Such regions of tendons can be fibrocartilaginous (Merrilees & Flint, 1980; Vogel & Koob, 1989; Benjamin & Ralphs, 1995). The fibrocartilage enables the tendons to resist compression because it contains large proteoglycans typical of cartilage (Vogel & Koob, 1989; Vogel et al. 1993, 1994; Robbins & Vogel, 1994). However, the extent to

Table. Distribution of fibrocartilage in tendons and their corresponding pulleys

Tendon	Pulley	Fibrocartilage in tendon	Fibrocartilage in pulley
Hand			
Flexor carpi radialis	Trapezium	*	**
Flexor digitorum superficialis	Flexor retinaculum	—	—
Flexor pollicis longus	Flexor retinaculum	—	—
Abductor pollicis longus	Flexor retinaculum	—	*
¹ Extensor pollicis longus	Radius/extensor retinaculum	—	— and *
¹ Extensor pollicis brevis	Radius/extensor retinaculum	—	— and —
Extensor carpi ulnaris	Head of ulna	—	*
Extensor carpi ulnaris	Triquetral	—	*
¹ Extensor carpi radialis brevis	Radius/extensor retinaculum	—	* and —
Extensor carpi radialis brevis	3rd metacarpal (near attachment)	**	Unknown
¹ Extensor carpi radialis longus	Radius/extensor retinaculum	—	* and —
Extensor digitorum	Extensor retinaculum	—	—
Extensor digitorum	Metacarpophalangeal joint	***	AC
Extensor digitorum	Proximal interphalangeal joint	***	AC
Extensor digitorum	Distal interphalangeal joint	**	AC
² Flexor digitorum superficialis	² Flexor digitorum profundus	**	**
Elbow			
Biceps brachii	Radial tuberosity	**	***
Foot			
¹ Peroneus brevis	Peroneal tubercle/IPR	**	— and ***
¹ Peroneus brevis	Lateral malleolus/SPR	**	** and —
¹ Peroneus longus	Lateral malleolus/SPR	**	** and —
¹ Peroneus longus	Cuboid/retinaculum	***	*** and **
Flexor hallucis longus	Sustentaculum tali	*	**
Flexor hallucis longus	Talus	**	**
Tibialis posterior	Medial malleolus	**	**
Tibialis posterior	Plantar calcaneonavicular ligament	***	***
Tibialis anterior	Superior extensor retinaculum	—	—
Extensor hallucis longus	Superior extensor retinaculum	—	—
Extensor hallucis longus	Inferior extensor retinaculum	—	*
Extensor digitorum longus	Superior extensor retinaculum	—	—
Knee			
Popliteus	Femoral groove on femur	*	*
Lateral head of gastrocnemius	Lateral condyle of femur	*	*
Hip			
Gluteus maximus	Greater trochanter	*	**
² Gluteus maximus	² Vastus lateralis	*	—
Obturator internus	Ischium	**	Not known
Head			
Tensor veli palatini	Hook of hamulus	*	—
Superior oblique	Trochlea	—	***

—, absent; *, present; **, conspicuous; ***, highly conspicuous. ¹ Tendons where both the bony pulley and the associated retinaculum were examined. The presence or absence of fibrocartilage is recorded at both sites in the last column. ² Tendons that press against each other. AC, articular cartilage; IPR, inferior peroneal retinaculum; SPR, superior peroneal retinaculum.

which all human tendons are modified as they pass around bony or fibrous pulleys is unknown, for there has been no single comprehensive study of a wide range of 'wrap-around' tendons—only isolated reports exist. Tillmann (1992) and Koch & Tillmann (1994) found fibrocartilage in the distal tendon of biceps brachii, in supraspinatus and in peroneus longus. The proximal tendon of biceps is fibrocartilaginous as it curves over the head of the humerus (Tillmann & Kolts, 1993), but not as it runs through the intertubercular sulcus (Benjamin et al. 1993a). Tibialis posterior is fibrocartilaginous where it passes

around the medial malleolus (Vogel et al. 1993) and the extensor tendons of the fingers are similarly modified where they cross the proximal interphalangeal joints (Benjamin et al. 1993b; Ralphs & Benjamin, 1994; Ralphs et al. 1995). Even less attention has been paid to the pulleys that contact the tendons, although they too can be fibrocartilaginous (Stilwell & Gray, 1954; Balogh & Földes, 1955; Rufai et al. 1992). Pulley tissue is responsive to mechanical demands, for periosteal fibrocartilage lining a bony groove can disappear when the associated tendon is ruptured (Benjamin et al. 1993a) and fibrocartilage

(as indicated by increased quantities of type II collagen) can appear in the flexor retinaculum in patients with the carpal tunnel syndrome (Weiss et al. 1994).

The purpose of the present study was to determine whether fibrocartilage differentiation is a feature of all tendons that press on bony or fibrous pulleys, and the extent to which the pulleys themselves are modified. We addressed these points in an extensive histological survey of material from elderly dissecting room cadavers. The results underline the considerable regional heterogeneity in different tendons and their pulleys. It cannot be assumed that one wrap-around tendon or its pulley is like another.

MATERIALS AND METHODS

Thirty-eight regions of tendons that wrap around bony pulleys or pass beneath fibrous retinacula were examined in formalin-fixed dissecting room cadavers (both sexes; age 69–89 y; see Table). Two or three specimens of each tendon (each containing compressed and adjacent noncompressed regions) and the associated pulley were examined in different cadavers in order to confirm the presence or absence of fibrocartilage at a particular site. After further fixation in 10% neutral buffered formol saline, specimens were decalcified where necessary in 2% nitric acid, dehydrated in graded alcohols, cleared and embedded in paraffin wax for routine histology. Two longitudinal sections (8 µm thick) were collected at 1 mm intervals throughout each block and stained with toluidine blue (for metachromasia) or Masson's trichrome. This ensured that the contact area with the pulley was sampled. The bony pulleys were cut in a direction that corresponded to the long axis of the associated tendon so that the full thickness of the periosteum in contact with the tendon could be studied. The fibrous retinacula were generally cut in cross-section. Sections were collected at 1 mm intervals as above.

RESULTS

The distribution of fibrocartilage in the tendons and their corresponding pulleys is summarised in the Table.

Tendons

Fibrocartilage was present in 22 of the 38 sites examined in tendons. It was less conspicuous where tendons pressed predominantly against fibrous rather than bony pulleys. There was a continuous gradation

of fibrocartilage differentiation, as suggested by the intensity of metachromasia, cell shape and collagen fibre arrangement. In some tendons, there was a slight increase in metachromasia of the extracellular matrix (ECM), but the cells were fibroblasts typical of the tensional regions of tendons (Fig. 1). The most fibrocartilaginous tendons had oval or round cells irregularly arranged in an intensely metachromatic ECM with an interwoven or spiralling network of collagen fibres (e.g. peroneus longus where it grooves the cuboid; Figs 2, 3). At other sites, there were rows of rounded or oval cells that were surrounded by a metachromatic pericellular ECM and separated by parallel arrays of collagen fibres (e.g. flexor hallucis longus grooving the sustentaculum tali; Fig. 5). In addition, fibrocartilage cells could be present in the connective tissue sheaths of the tendon, i.e. the epitenon (e.g. tibialis posterior near the medial malleolus; Fig. 4) and endotenon (e.g. flexor hallucis longus near the talus; Fig. 6).

A single tendon could be modified in successive regions along its length and fibrocartilage was more conspicuous in some parts than others. Thus peroneus longus presses against 3 bony pulleys (the lateral malleolus, peroneal tubercle and cuboid) en route to its insertion on the medial side of the foot and was fibrocartilaginous in all sites. However, in all bodies it was most fibrocartilaginous where it grooved the cuboid (Fig. 2). Extensor digitorum, which has 4 pulleys (at the wrist, the metacarpophalangeal joint and the proximal and distal interphalangeal joints), was most fibrocartilaginous where it crossed the metacarpophalangeal joint.

Some tendon fibrocartilages showed degenerative change. The most typical finding was fragmentation and partial delamination of tissue from the compressed surface (Fig. 8). This was sometimes accompanied by the formation of clusters of fibrocartilage cells (Fig. 9). Structural alterations were occasionally seen in the deeper parts of tendons. These included fatty infiltration and hypercellularity of the endotenon in one tendon of peroneus brevis near the lateral malleolus, and an extensive fatty and vascular infiltration of extensor hallucis longus that totally disrupted its normal structure (Fig. 7). Intra-tendinous endochondral ossification was seen in one specimen of flexor digitorum profundus.

Pulleys

Three types of pulley were noted that allow tendons to change direction—bony grooves or prominences, fibrous retinacula and synovial joints (Fig. 10*a*). In

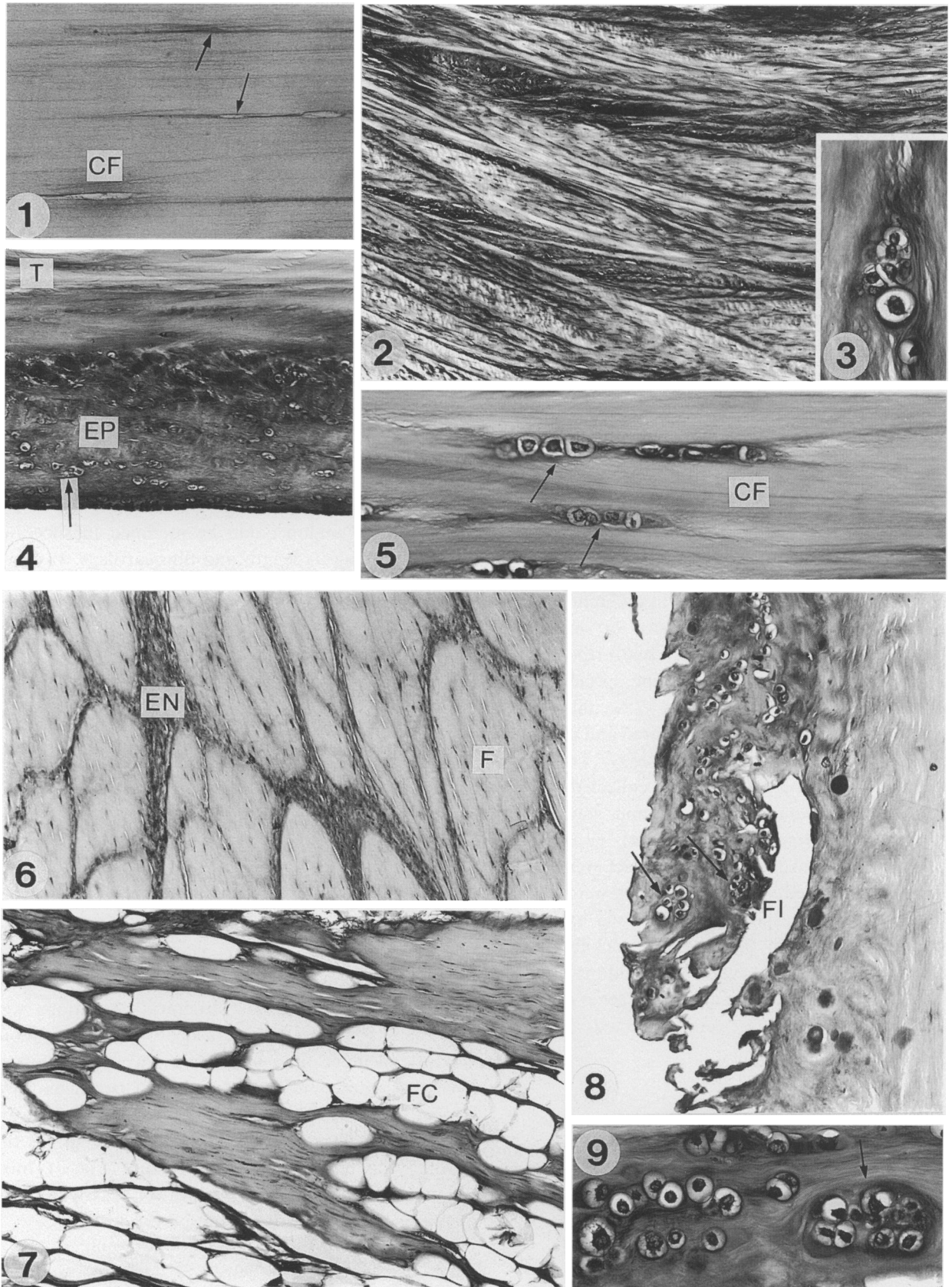


Fig. 1. Sparse fibroblasts (arrows) lying in rows between parallel collagen fibres (CF) in the tensional region of the tendon of tibialis posterior (proximal to the medial malleolus). Toluidine blue. $\times 300$.

Fig. 2. A highly fibrocartilaginous region of peroneus longus where the tendon lies in the groove on the cuboid. Note the interweaving bundles of collagen fibres and the dark staining associated with the intense metachromasia of the ECM. Toluidine blue. $\times 38$.

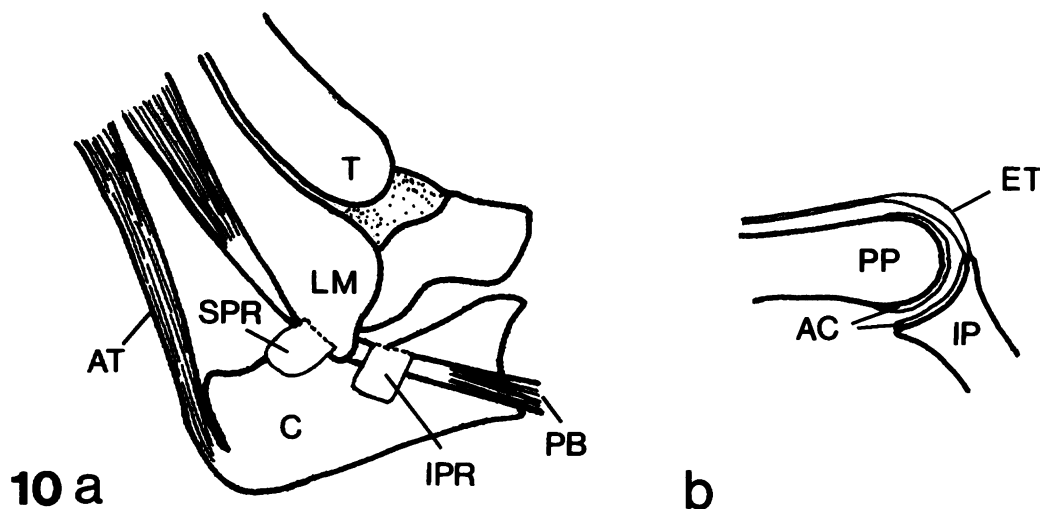


Fig. 10. Diagrammatic representation of the 3 types of pulleys that can change the direction of tendons—bony prominences and fibrous retinacula (a) and a synovial joint (b). (a) The tendon of peroneus brevis (PB) passes around a bony pulley created by the lateral malleolus (LM). It is held in position by the superior peroneal retinaculum (SPR). It then passes through an additional fibrous loop, the inferior peroneal retinaculum (IPR) which prevents it bowstringing when the foot is everted. (b) The central slip of the extensor tendon (ET) wraps around the proximal phalanx (PP) when the finger is flexed. AC, articular cartilage; AT, Achilles tendon; C, calcaneus; IP, intermediate phalanx; T, tibia.

some joints, the tendon is an integral part of the capsule and wraps around a pulley formed by the articular cartilage covering one of the bones. A good example is the central slip of the extensor tendon passing over the proximal interphalangeal joint of the finger (Fig. 10b).

The periosteum of bony grooves or prominences was frequently modified to form a fibrocartilaginous or even cartilaginous covering (Figs 11–13), although a few periosteae were purely fibrous (e.g. the groove for extensor pollicis longus on the radius; Fig. 16). At many sites, the extent of periosteal differentiation mirrored that in the associated tendon. For example, there was marked cartilaginous differentiation of the periosteum lining the groove on the cuboid (Fig. 12). This was in contact with the most fibrocartilaginous region of peroneus longus (see above). The tissue formed a thick white lining that was clearly visible to

the naked eye and in histological sections was hyaline cartilage. The other bony pulleys associated with peroneus longus were covered with fibrocartilage, correlating with slightly less conspicuous fibrocartilage in the corresponding parts of the tendon. At the lateral malleolus, the deep part of the periosteum was strongly metachromatic and fibrocartilaginous, but the superficial part was more fibrous (Fig. 11). A cartilaginous periosteum lined the popliteal groove near the tendon–bone junction of popliteus (Fig. 13).

Some of the best known retinacula were largely fibrous, e.g. the flexor and extensor retinacula of the wrist. Fibrocartilage was best developed in the inferior peroneal retinaculum (Figs 14, 15) and the pulley formed by the trochlea for the superior oblique muscle of the eye was strikingly cartilaginous (Figs 17, 18). Indeed, at both sites, the pulleys were more cartilaginous than their associated tendons.

Fig. 3. Detail of the fibrocartilage cells in Figure 2. Toluidine blue. $\times 300$.

Fig. 4. Fibrocartilage cells (arrow) in the epitenon (EP) of tibialis posterior where it presses against the medial malleolus. T, tendon. Toluidine blue. $\times 120$.

Fig. 5. Rows of fibrocartilage cells (arrows) separated by parallel bundles of collagen fibres (CF) in the tendon of flexor hallucis longus where it presses against the sustentaculum tali. Toluidine blue. $\times 300$.

Fig. 6. Prominent metachromasia associated with fibrocartilage differentiation in the endotenon (EN) between tendon fascicles (F) in flexor hallucis longus where it grooves the posterior surface of the talus. Round or oval fibrocartilage cells are present in the endotenon similar to those illustrated in Figures 3 and 5. Toluidine blue. $\times 48$.

Fig. 7. Numerous fat cells (FC) infiltrating the tendon of extensor hallucis longus as it passes beneath the superior extensor retinaculum. Toluidine blue. $\times 120$.

Fig. 8. Pathology of fibrocartilage in the epitenon of flexor hallucis longus where it grooves the posterior surface of the talus. Note the deep fissure (FI) and the clusters of fibrocartilage cells (arrows). Toluidine blue. $\times 120$.

Fig. 9. Detail of chondrocyte clusters (arrow) shown in Figure 8. Toluidine blue. $\times 300$.

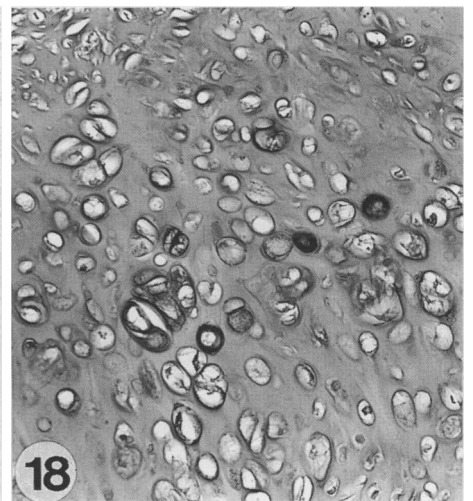
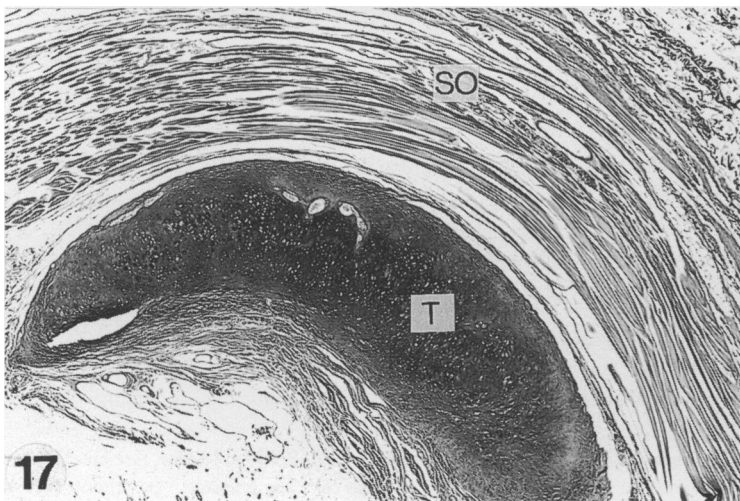
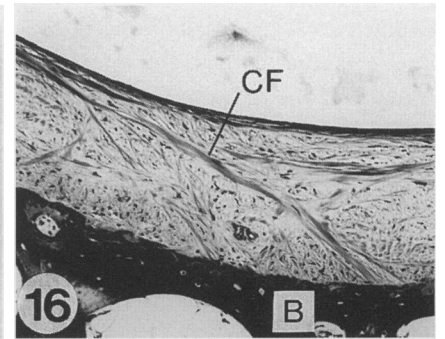
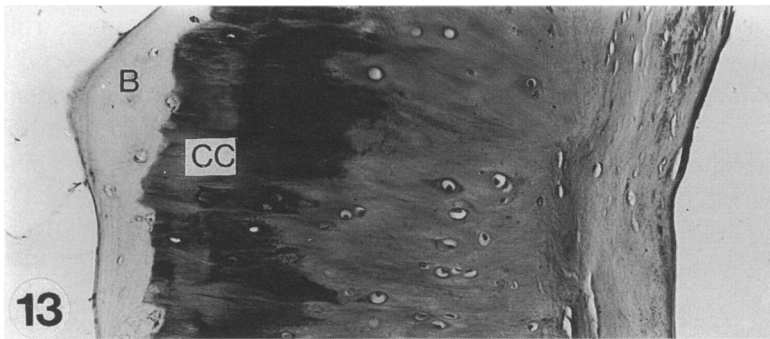
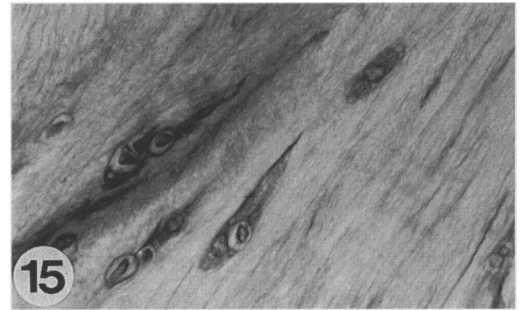
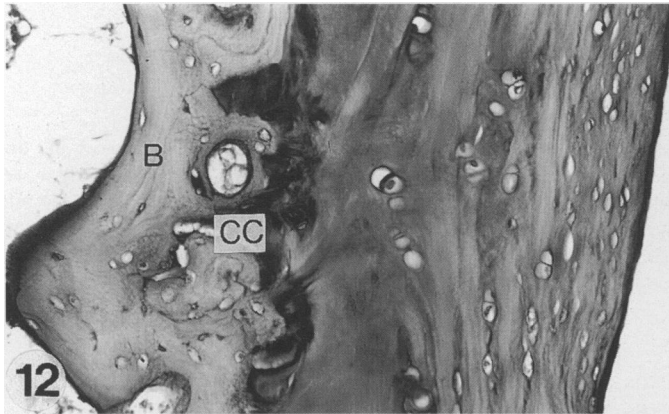
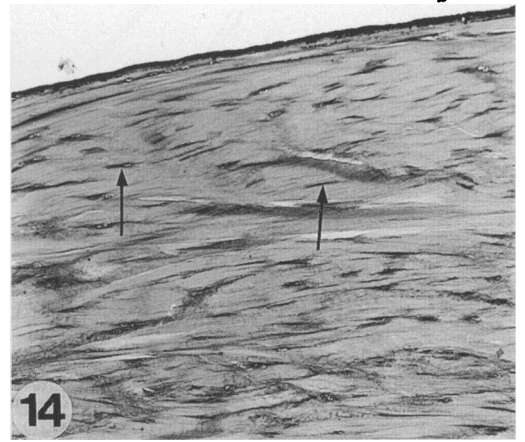
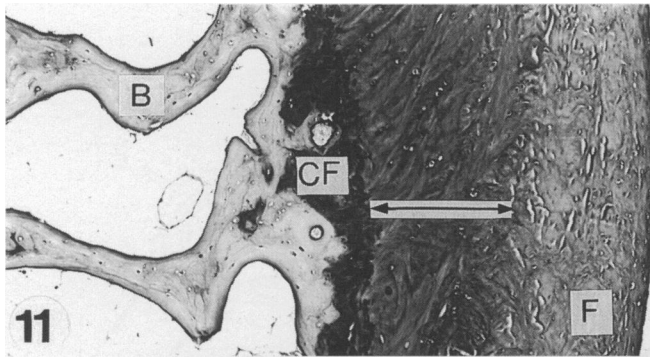


Fig. 11. The periosteum on the lateral malleolus where it contacts the peroneal tendons. The deep part of the periosteum (between the arrows) is more metachromatic and fibrocartilaginous, and the superficial part is more fibrous (F). B, bone; CF, calcified fibrocartilage. Toluidine blue. $\times 48$.

Fig. 12. Cartilaginous differentiation of the periosteum lining the groove of the cuboid where it contacts the tendon of peroneus longus. B, bone; CC, calcified cartilage. Toluidine blue. $\times 120$.

DISCUSSION

The results show that the extent of fibrocartilage differentiation in compressed regions of human tendons varies according to site and depends on the nature of the pulley. Although the work is based on tendons from elderly people, whose medical history is unknown and whose tendons could be less heavily loaded than those of younger persons, comparisons within a body are still valid. Fibrocartilage is most conspicuous in tendons that press against bony pulleys, and is usually absent where they press largely against retinacula. It should be noted that there is a distinction between a retinaculum that serves primarily to provide a fibrous pulley for a tendon and one which serves largely to retain a tendon in position against a bony pulley. In the latter, the tendon may be highly fibrocartilaginous, but this is probably associated with its mechanical loading on the bone rather than the retinaculum.

Where a tendon fibrocartilage has rows of rounded fibrocartilage cells that lie between parallel arrays of collagen fibres, it must have formed by metaplasia of tendon fibroblasts (Rufai et al. 1992; Benjamin & Ralphs, 1995). This is consistent with experimental work where tendons placed under increased compressive loading upregulate the synthesis of large proteoglycans (Gillard et al. 1979; Koob et al. 1992). Functionally, such fibrocartilages occur in tendons with moderate changes in angle around their pulleys (e.g. flexor hallucis longus grooving the sustentaculum tali). The origin of the most highly developed tendon fibrocartilage (e.g. peroneus longus in the groove of the cuboid) was less clear. It is difficult to imagine a tendon with sparse cells in a large ECM, completely reorganising the arrangement of its collagen fibres in response to increased load. This would suggest that such fibre organisation must be established early in development. This has been demonstrated in certain animal fibrocartilages (Evanko & Vogel, 1990; Ralphs et al. 1992), although different fibrocartilages may have different ways of forming such a structure. In the rat quadriceps tendon (Ralphs et al. 1992), fibrocartilage above the patella develops from a population

of cells on the deep surface and not from the tendon itself (Ralphs et al., 1992; Benjamin & Ralphs, 1995). In the annulus fibrosus of the developing intervertebral disc, the highly ordered lattice-like arrangement of collagen fibres of the lamellae is preceded by a similar arrangement of cell sheets (e.g. Rufai et al. 1995). The same may occur in certain developing tendon fibrocartilages.

Functionally, the significance of interweaving collagen fibres in fibrocartilaginous regions of adult tendons is unclear. It could be purely mechanical, preventing the tendon from splaying apart when it is under compression against a pulley—like the twisted strands of a rope. In addition, the network of collagen fibres could be organised to control the swelling of large proteoglycans in the creation of a pressure-tolerant structure. Tendons with this fibrocartilage organisation include those which most commonly contain sesamoid bones (peroneus longus and tibialis posterior; Jones, 1949; Williams et al. 1989). It seems that such extensive fibrocartilaginous modification may predispose to endochondral ossification.

The presence of fibrocartilage cells in the epitenon has been reported previously in developing bovine deep flexor tendon and in the chick digital flexor tendon (Greenlee et al. 1975; Evanko & Vogel, 1990). Here, we confirm this finding in human tendons and also describe the presence of fibrocartilage in the endotenon. The significance of these findings is unclear. The increased glycosaminoglycan content could protect blood vessels in the endotenon from compression, although compressed regions of tendons are frequently hypovascular (see Benjamin & Ralphs, 1995, for review).

There are significant differences in the way that fibrocartilage is distributed in the upper and lower limbs. Fibrocartilage differentiation was much more pronounced in tendons at the ankle than the wrist. This relates to anatomical factors which result in mechanical differences. Because the long axis of the foot is at right angles to that of the leg, tendons at the ankle are permanently bent around the bony malleoli and thus constantly subject to compression and/or shear. However, in the wrist, there is little or no

Fig. 13. Cartilaginous differentiation of the periosteum lining the popliteal groove of the femur in contact with the tendon of popliteus. B, bone; CC, calcified cartilage. Toluidine blue. $\times 120$.

Fig. 14. Fibrocartilage in the inferior peroneal retinaculum where it contacts the peroneal tendons. Note the fibrocartilage cells surrounded by metachromatic pericellular matrix (arrows). Toluidine blue. $\times 75$.

Fig. 15. Detail of the fibrocartilage cells shown in Figure 14. Toluidine blue. $\times 300$.

Fig. 16. A thick fibrous periosteum with conspicuous bundles of collagen fibres (CF) lining the groove for extensor pollicis longus near the dorsal tubercle of the radius. No fibrocartilage cells were present. B, bone. Masson's trichrome. $\times 20$.

Fig. 17. The cartilaginous trochlea (T) for the tendon of the superior oblique (SO) muscle of the eye. Toluidine blue. $\times 20$.

Fig. 18. Detail of cartilage cells in the trochlea featured in Figure 17. Toluidine blue. $\times 150$.

change in tendon direction when the hand is in the anatomical position. In flexion and extension, tendons contact retacula and bone alternately but the loading is less than in the ankle as body weight is not being supported. All these factors mean that less compressive load is placed on tendons at the wrist.

Fibrocartilaginous regions of tendons that wrap around bony pulleys are inevitably subject to wear and tear. The damage particularly affects the surface of the tendons and the fissuring and cell clusters in the epitenon are reminiscent of the fibrillation that occurs in articular cartilage early in osteoarthritis (Brandt & Mankin, 1993). Similarities between the repair response of tendon fibrocartilage and articular cartilage have been reported previously in the human Achilles tendon (Rufai et al. 1995). Extensive infiltration of tendons with fat cells has been described by Kannus & Józsa (1991) and called 'tendolipomatosis'.

The results highlight a clear link between compressive fibrocartilage in tendons and periosteal fibrocartilage on bony pulleys. Wherever the former is present in a tendon, the latter is always a feature of the bone, unless that bone is already covered with articular cartilage as part of a synovial joint. Furthermore, the most fibrocartilaginous tendon (peroneus longus) was associated with the most cartilaginous bone surface (the cuboid). Previous studies (see Beresford, 1981, for review; Rufai et al. 1992) have shown that periosteal fibrocartilage develops as a secondary cartilage in response to the mechanical action of the tendon on the bone. Stilwell & Gray (1954) examined 15 sites at which tendons contact bone and found periosteal fibrocartilage at 5 of those sites. In the present study, we describe periosteal fibrocartilage in the overwhelming majority of sites. The reason for the different findings is that we have largely chosen sites where the tendon changes direction around a bony pulley, whereas Stilwell & Gray (1954) were purely interested in sites of tendon-bone contact, only some of which were pulleys. However, where these authors did find fibrocartilage on a pulley, its structure was the same as that which we describe in several sites here—i.e. a deep fibrocartilaginous and a superficial fibrous part of the periosteum. Surprisingly, Stilwell & Gray (1954) felt unable to comment on the functional significance of periosteal fibrocartilage. In our opinion, it serves along with the associated tendon fibrocartilage to prevent tendons and their pulleys from being damaged by the 'sawing' action of the tendon.

Retacula (and the tendons in contact with them) generally showed little fibrocartilaginous differentiation. This probably relates to flexibility of the

pulley. The only substantially (fibro)cartilaginous retacula were the inferior peroneal retinaculum and the trochlea for the superior oblique muscle of the eye. The tendon of the superior oblique changes direction markedly as it passes through the trochlea and thus it could be subject to a compressive force which is relatively large for such a small tendon. It is curious that the tendon itself is not fibrocartilaginous. This could be because its pulley is highly flexible and the tendon has a large excursion through it. The compressive load may thus be spread along a considerable length of the tendon. It seems therefore that the compressive forces generated where a tendon presses against a bony or fibrous pulley may lead to modification in the tendon, the pulley or both.

REFERENCES

- AMIEL D, FRANK C, HARWOOD F, FRONEK J, AKESON W (1984) Tendons and ligaments: a morphological and biochemical comparison. *Journal of Orthopaedic Research* **1**, 257–265.
- BALOGH G, FÖLDES I (1955) Die funktionelle Gewebestruktur der Sehnenfurchen. *Acta Morphologica Academiae Scientiarum Hungaricae* **5**, 355–368.
- BENJAMIN M, RALPHS JR, NEWELL RLM, EVANS EJ (1993a) Loss of the fibrocartilaginous lining of the intertubercular sulcus associated with rupture of the tendon of the long head of biceps brachii. *Journal of Anatomy* **182**, 281–285.
- BENJAMIN M, RALPHS JR, SHIBU M, IRWIN M (1993b) Capsular tissues of the proximal interphalangeal joint: normal composition and effects of Dupuytren's disease and rheumatoid arthritis. *Journal of Hand Surgery* **18B**, 371–376.
- BENJAMIN M, RALPHS JR (1995) The developmental and functional anatomy of tendons and ligaments. In *Repetitive Motion Disorders of the Upper Extremity* (ed. S. Gordon). Park Ridge, Illinois: NIH/AAOR, in press.
- BERESFORD WA (1981) *Chondroid Bone, Secondary Cartilage and Metaplasia*. Baltimore–Munich: Urban & Schwarzenberg.
- BRANDT KD, MANKIN HJ (1993) Pathogenesis of osteoarthritis. In *Textbook of Rheumatology*, vol. 2 (ed. W. N. Kelley, E. D. Harris, S. Ruddy & C. B. Sledge), pp. 1355–1373. Philadelphia: Saunders.
- EVANKO SP, VOGEL KG (1990) Ultrastructure and proteoglycan composition in the developing fibrocartilaginous region of bovine tendon. *Matrix* **10**, 420–436.
- GILLARD GC, REILLY HC, BELL-BOOTH PG, FLINT MH (1979) The influence of mechanical forces on the glycosaminoglycan content of the rabbit flexor digitorum profundus tendon. *Connective Tissue Research* **7**, 37–46.
- GREENLEE TK, BECKHAM C, PIKE D (1975) A fine structural study of the development of the chick flexor digital tendon: a model for synovial sheathed tendon healing. *Journal of Anatomy* **143**, 303–314.
- HARWOOD FL, AMIEL D (1992) Differential metabolic responses of periarticular ligaments and tendon to joint immobilization. *Journal of Applied Physiology* **72**, 1687–1691.
- JONES FW (1949) *Structure and Function as Seen in the Foot*. London: Baillière, Tindall and Cox.
- KANNUS P, JÓZSA L (1991) Histopathological changes preceding spontaneous rupture of a tendon. *Journal of Bone and Joint Surgery* **73A**, 1507–1525.
- KOCH S, TILLMANN B (1994) Vergleichende Untersuchungen der Struktur von Gleitsehnen im Hinblick auf die Inzidenz von Sehnenrupturen. *Annals of Anatomy* **176** (Suppl.) 44.

- KOOB TJ, CLARK PE, HERNANDEZ D, THURMOND FA, VOGEL KG (1992) Compression loading in vitro regulates proteoglycan synthesis by tendon fibrocartilage. *Archives of Biochemistry and Biophysics* **298**, 303–312.
- MERRILEES MJ, FLINT MH (1980) Ultrastructural study of tension and pressure zones in a rabbit flexor tendon. *American Journal of Anatomy* **157**, 87–106.
- RALPHS JR, TYERS RNS, BENJAMIN M (1992) Development of functionally distinct fibrocartilages at two sites in the quadriceps tendon of the rat: the suprapatella and the attachment to the patella. *Anatomy and Embryology* **185**, 181–187.
- RALPHS JR, BENJAMIN M (1994) The joint capsule: structure, composition, ageing and disease. *Journal of Anatomy* **184**, 503–509.
- RALPHS JR, BENJAMIN M, KNEAFSEY B, LEWIS AR (1995) Fibrocartilages in the capsule of the proximal interphalangeal joint of human fingers in health and disease. *Transactions of the Orthopaedic Research Society* **20**, 246.
- ROBBINS JR, VOGEL KG (1994) Regional expression of mRNA for proteoglycans and collagen in tendon. *European Journal of Cell Biology* **64**, 264–270.
- RUFAL A, BENJAMIN M, RALPHS JR (1992) Development and ageing of phenotypically distinct fibrocartilages associated with the rat Achilles tendon. *Anatomy and Embryology* **186**, 611–618.
- RUFAL A, BENJAMIN M, RALPHS JR (1995) The development of fibrocartilage in the rat intervertebral disc. *Anatomy and Embryology*, in press.
- STILWELL DL, GRAY DJ (1954) The structures of bony surfaces in contact with tendons. *Anatomical Record* **118**, 358–359.
- TILLMANN B (1992) Rotatorenmanschettenrupturen. Desinsertion der Supraspinatussehne Naht der Supraspinatussehne Spaltung des Ligamentum coracoacromiale. *Operative Orthopädie und Traumatologie* **4**, 181–184.
- TILLMANN B, KOLTS I (1993) Ruptur der Ursprungssehne des Caput longum musculi bicipitis brachii. *Operative Orthopädie und Traumatologie* **5**, 107–111.
- VOGEL KG, KOOB TJ (1989) Structural specialization in tendons under compression. *International Review of Cytology* **115**, 267–293.
- VOGEL KG, ÖRDÖG A, POGANY G, OLAH J (1993) Proteoglycans in the compressed region of human tibialis posterior tendon and in ligaments. *Journal of Orthopaedic Research* **11**, 68–77.
- VOGEL KG, SANDY JD, POGANY G, ROBBINS JR (1994) Aggrecan in bovine tendon. *Matrix Biology* **14**, 171–179.
- WEISS A-PC, KRAMER AA, BARRACH H-J, AKELMAN E (1994) Variations in the quantity of type II collagen in carpal tunnel syndrome. *Transactions of the Orthopaedic Research Society* **19**, 389.
- WILLIAMS PL, WARWICK R, DYSON M, BANNISTER LH (1989) *Gray's Anatomy*, 37th edn. Edinburgh: Churchill Livingstone.