

# Biomechanical Tissue Characterization of the Superior Joint Space of the Porcine Temporomandibular Joint

KYOUNG-WON KIM,<sup>1,2</sup> MARK E. WONG,<sup>1,2</sup> JOHN F. HELFRICK,<sup>2</sup> JAMES B. THOMAS,<sup>1</sup>  
and KYRIACOS A. ATHANASIOU<sup>1,2</sup>

<sup>1</sup>Department of Bioengineering, Rice University, Houston, TX and <sup>2</sup>Department of Oral and Maxillofacial Surgery,  
The University of Texas Houston Health Science Center, Dental Branch, Houston, TX

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**Abstract**—The objective of this study was to characterize the biomechanical properties of articular cartilage in the superior joint space of the porcine temporomandibular joint (TMJ). These properties and thickness of the disk and fossa cartilage were obtained from eight joints using creep indentation. Five sites per surface were tested to obtain the aggregate modulus, Poisson's ratio, permeability, creep, recovery percentage, and cartilage thickness. Histology was also performed to characterize the orientation of the collagen fibers and the proteoglycan content. It was found that the temporal fossa cartilage was 57% thinner and 50% stiffer than the disk. The aggregate modulus of the porcine TMJ disk and fossa was much smaller, but the permeability of the TMJ disk and fossa was much higher than those of articular cartilage in other joints. It was also noted that the TMJ disk did not fully recover following indentation testing unlike the articular cartilage in other joints. The biomechanical properties of the TMJ disk and temporal fossa obtained in this study are significantly different from those of cartilage present in other diarthrodial joints. This suggests that the function of the fibrocartilage in the superior TMJ space is substantially different from that of hyaline cartilage in other joints. © 2003 Biomedical Engineering Society. [DOI: 10.1114/1.1591190]

**Keywords**—TMJ, Fibrocartilage, Indentation, Articular cartilage.

## INTRODUCTION

The temporomandibular joint (TMJ) is a ginglymus diarthrodial joint,<sup>15</sup> which allows both rotational and translatory movement. The TMJ is the only bilateral diarthrodial joint in the human body because left and right sides of the TMJ must function together with mandibular movement.

There are three types of joints in the human body: synarthrosis, amphiarthrosis, and diarthrosis.<sup>21</sup> A synarthrosis (fibrosis) joint is an immovable union of connective tissue, such as the coronal suture of the skull, and has no relative motion. An amphiarthrosis (cartilaginous)

joint such as the vertebral body—intervertebral disk—vertebral body joint, allows limited mobility. A diarthrodial joint such as the knee and the shoulder, is characterized by a large degree of motion, in support of body movement and locomotion. Under normal conditions, a diarthrodial joint is an amazingly efficient load bearing system capable of providing nearly frictionless performance with little wear for the entire life span of the individual.

Although their individual anatomical forms and material properties vary considerably, all diarthrodial joints contain synovial fluid and connective tissues. Connective tissues include articular cartilage, meniscus, ligaments, and tendons. The two main functions of articular cartilage are to decrease contact stresses in the joint and to allow motion of the opposing surfaces with minimum friction and wear.<sup>6,21</sup> Articular cartilage is a multiphasic, nonlinearly permeable, viscoelastic material consisting of two principal phases: a solid organic matrix composed predominately of collagen fibrils and proteoglycan macromolecules, and a predominately water, movable, interstitial fluid phase.<sup>1,21</sup> Almost all articular cartilage in human diarthrodial joints is composed of hyaline cartilage. However, the articulating surfaces of the TMJ are covered with fibrocartilage rather than hyaline cartilage.<sup>8</sup> The presence of a fibrous articular surface is one of the specialized features that distinguishes the TMJ from most other synovial diarthrodial joints.

The TMJ disk is also composed of fibrocartilage and divides the joint into an upper (superior) compartment, and a lower (inferior) compartment. The functions of the TMJ disk are to improve congruity between two bony articulating surfaces, to provide stability during mandibular movements (both rotational and translatory movements), to distribute forces over a large area, and to facilitate the spread of synovial fluid.<sup>10</sup> Anatomical studies of the TMJ disk demonstrate that collagen fibers run in the anteroposterior direction within the superficial layers, whereas small fibers in the central region are

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Address correspondence to Kyriacos Athanasiou, PhD, PE, Rice University, Department of Bioengineering – MS 142, P.O. Box 1892, Houston, TX 77251-1892. Electronic mail: athanasiou@rice.edu

oriented in a random fashion.<sup>24,27</sup> This orientation gives the TMJ disk the ability to resist forces in two directions, tensile forces are borne by superficial layers in the anteroposterior direction, and compressive loading by a three-dimensional network in the central region.<sup>28</sup>

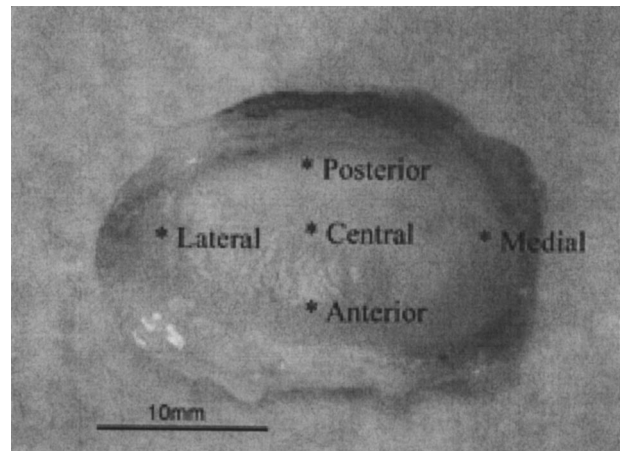
The TMJ disk is composed of water, collagen fibers, proteoglycans, and elastin.<sup>10,28</sup> The elastin component affords the TMJ articular tissues the resiliency of hyaline cartilage present in most synovial joints.<sup>10,23</sup> There have been numerous investigations on the TMJ which describe its morphology, disk position, histologic characteristics, ultrastructure, and biochemistry. However, there are few accounts concerning the biomechanical properties of the articular cartilage of the TMJ.

Temporomandibular disorders (TMDs) constitute one of the major topics in dentistry. There have been numerous studies on TMD, that suggest that structural and positional changes of TMJ components are leading causes of TMD. To further understand the etiology of TMD, it is important to identify the normal biomechanical properties, behavior, and histomorphometric characteristics of the TMJ disk and articulating surfaces of the condyle head and temporal fossa. While the orthopedic literature is replete with descriptions of the biomechanical properties of other human and animal diarthrodial joints, little work has been performed on the TMJ.<sup>1,3,6,16</sup>

To correct this deficiency, several studies have been initiated in our laboratory to study the biomechanical properties, thickness, and histomorphometric characteristics of the TMJ. We chose to separate the superior and inferior joint spaces because of the different types of motion which predominate in these areas: translation in the superior space and rotation in the inferior space. This paper focuses on the superior compartment of the TMJ, using a porcine model. The results from our experiments have been compared with those of other joint articulating cartilages reported in previous experiments.

## MATERIALS AND METHODS

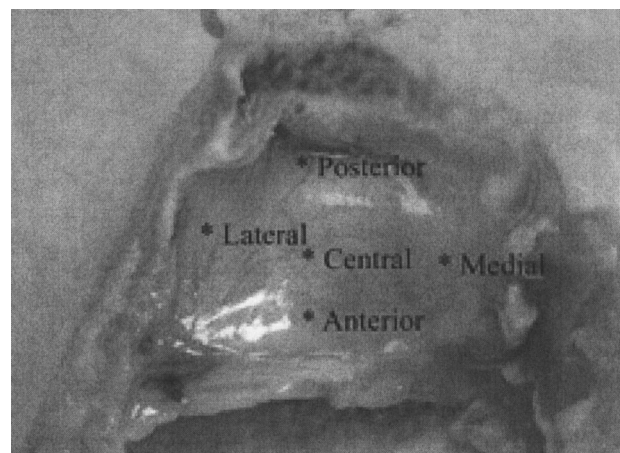
Eight fresh porcine TMJs were used for this study. The joints were collected from young adult pigs, weighing about 60 kg, within 24 h of euthanasia. To prepare each specimen, peripheral soft tissue was removed and the joint disarticulated. The disk, temporal fossa, and condyle head of each porcine TMJ were harvested and discarded if gross abnormalities were present. At the time of dissection, each TMJ disk was sectioned mediolaterally into three pieces comprising a medial region, a middle region (including anterior, central, and posterior test sites), and a lateral region. India ink was used to mark five test sites (anterior, central, lateral, medial, and posterior test sites) on the superior surface of the porcine TMJ disk (Fig. 1). Corresponding test sites (anterior, central, lateral, medial, and posterior test sites) were also



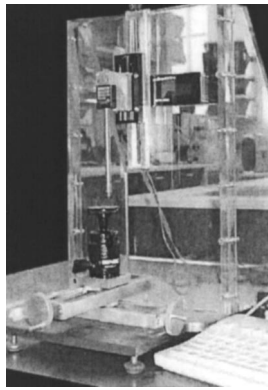
**FIGURE 1.** Superior surface of the porcine temporomandibular joint (TMJ) disk and five test sites are indicated.

marked on the temporal fossa (Fig. 2). Specimens were then wrapped in gauze soaked in a normal saline solution with protease inhibitors (N-ethylmaleimide, 10 mM; benzamidine HCl, 5 mM; EDTA, 2 mM; and phenylmethylsulfonyl fluoride, 1 mM) and stored at  $-20^{\circ}\text{C}$  until mechanical testing.

Before testing, each specimen was thawed to  $20\text{--}22^{\circ}\text{C}$  (room temperature) for 1 h in normal saline with protease inhibitors. An automated indentation apparatus was used to determine the creep behavior of the TMJ disk and articulating cartilage of temporal fossa (Fig. 3). Each specimen was attached to a sample holder using cyanoacrylate glue and submerged in the saline solution with protease inhibitors. The sample holder was attached to the base of the creep indentation apparatus using a spherical joint. The specimen was positioned under the loading shaft of the apparatus so that each test



**FIGURE 2.** Articular surface of porcine temporal fossa and five test sites are indicated.



**FIGURE 3.** Automated indentation apparatus used for the biomechanical characterization of specimen.

site of the superior surface of the disk, or the articulating surface of the temporal fossa, was perpendicular to the indenter tip.

The TMJ disk and the temporal fossa specimens were automatically loaded using a computer-controlled, closed-loop system. A tare load of 4.9 mN (0.5 g) was applied using a 2.0 mm diam rigid, flattened, porous indenter tip. Each specimen was allowed to reach tare creep equilibrium, defined as a deformation of less than  $1 \times 10^{-6}$  mm/s. When tare equilibrium was reached, a step force of 18.6 mN (1.9 g) was applied. Displacement was measured using a linear variable differential transformer with a  $0.25 \mu\text{m}$  computer resolution. Data were collected for each  $2.5 \mu\text{m}$  of surface displacement or every 50 s using a computer-based acquisition system. The creep responses of the disk and the articular cartilage of the temporal fossa were monitored until equilibrium was reached. The step load was then removed and the recovery displacement of each specimen was again recorded until equilibrium giving a recovery percentage. This methodology, which uses a creep indentation solution with a corresponding numerical algorithm,<sup>18,20</sup> has been employed in numerous studies to obtain the intrinsic material properties of articular cartilage.<sup>2,3,5,6,17,25</sup> The tissue's material properties determined using the linear biphasic theory, were the aggregate modulus ( $H_A$ ), Poisson's ratio ( $\nu$ ), and permeability ( $k$ ).<sup>22</sup> The aggregate modulus is the tissue's compressive stiffness, the Poisson's ratio represents the tissue's apparent compressibility, and permeability is indicative of the tissue's interstitial fluid flow inside the pores of articular cartilage.

For specimen thickness measurements, a computer-controlled, instrumented needle was used. The thickness measurements were made 15 min after the creep relaxation experiment to allow for tissue recovery after indentation. The needle was inserted at the test site perpendicularly to the specimen surface. The needle was advanced into the specimen at a constant rate ( $9 \mu\text{m/s}$ )

**TABLE 1.** The thickness and recovery (mean  $\pm$  standard deviation) of the superior surface of the disk and the articular cartilage of temporal fossa of the porcine temporomandibular joint ( $n=8$ ).

Test site		$h^a$ (mm)	Recovery (%)
Disk	Anterior	$1.438 \pm 0.144$	$49.050 \pm 6.570$
	Central	$0.797 \pm 0.234$	$49.400 \pm 9.110$
	Lateral	$0.853 \pm 0.259$	$58.288 \pm 11.148$
	Medial	$0.841 \pm 0.235$	$59.150 \pm 16.790$
	Posterior	$1.322 \pm 0.141$	$57.050 \pm 10.176$
Fossa	Anterior	$0.493 \pm 0.065$	$82.450 \pm 10.980$
	Central	$0.398 \pm 0.098$	$85.263 \pm 7.774$
	Lateral	$0.490 \pm 0.113$	$83.288 \pm 14.520$
	Medial	$0.572 \pm 0.089$	$77.600 \pm 11.877$
	Posterior	$0.286 \pm 0.062$	$95.100 \pm 5.692$

<sup>a</sup> $h$ =thickness.

while the force and displacement were measured. When the force reached 6.37 N (650 g), the test was stopped. The specimen thickness was determined using the force displacement curve. A change in slope identified the point where the needle had perforated through the disk and reached the sample holder plate. In the case of the articular cartilage of the temporal fossa, a change in slope indicated the point where the needle contacted the bone of the temporal fossa.

Standard hematoxylin and eosin (H and E) staining and Fast Green/Safranin O special staining of sections corresponding to each test site provided a histomorphologic description of the disc and the articular cartilage of temporal fossa of porcine TMJ.

Analysis of the effects of independent variables on dependent variables was accomplished with the use of analysis of variance (ANOVA). Independent variables included type (superior surface of disk, articular cartilage of temporal fossa) and test sites (anterior, central, lateral, medial, and posterior test site). Dependent variables included aggregate modulus, Poisson's ratio, permeability, thickness, and recovery percentage. The Fisher's least significant difference multiple comparisons test of the means was applied when the F-test in the analysis of variance was significant. Statistical significance level was set at  $p < 0.05$  for all tests.

## RESULTS

Mean and standard deviation values of the thickness (mm) and recovery (%) of the superior surface of the porcine TMJ disk and articular cartilage of the temporal fossa in the test sites are shown in Table 1. Significant differences in the thickness were observed between the disk and the articular cartilage of the temporal fossa. Overall, the disk thickness is about two times greater than that of the articular cartilage of the temporal fossa. The anterior region of the disk is the thickest ( $1.438$



**TABLE 2. Intrinsic material properties (mean±standard deviation) of the superior surface of the disk and articular cartilage of temporal fossa of the porcine temporomandibular joint (n=8).**

Test site		$H_A^a$ (kPa)	$\nu$	$k \times 10^{15}$ (m <sup>4</sup> /N s)
Disk	Anterior	18.8±4.7	0.014±0.003	26.7±8.3
	Central	18.6±5.2	0.059±0.064	22.8±9.8
	Lateral	16.3±2.1	0.066±0.046	29.3±14.0
	Medial	28.9±12.3	0.068±0.067	15.4±7.0
	Posterior	22.1±6.5	0.020±0.013	26.4±6.3
Fossa	Anterior	35.0±8.3	0.022±0.019	10.1±2.4
	Central	36.5±13.3	0.063±0.061	16.8±11.5
	Lateral	36.3±13.8	0.064±0.060	21.7±20.4
	Medial	42.6±18.9	0.020±0.013	8.8±2.4
	Posterior	58.9±18.1	0.132±0.110	67.3±34.9

<sup>a</sup> $H_A$ =aggregate modulus;  $\nu$ =Poisson's ratio;  $k$ =permeability.

±0.144 mm), whereas the posterior region of the temporal fossa is the thinnest (0.286±0.062 mm). The anterior and posterior regions of the disk are thicker than the lateral, medial, and central regions of the disk. In the temporal fossa, the medial region is the thickest (0.572±0.089 mm), and the posterior region of the temporal fossa is the thinnest (0.286±0.062 mm).

Significant differences in the recovery percentage were observed between the superior surface of the disk and the articular cartilage of the temporal fossa. The recovery percentages of each test site of the articular cartilage of the temporal fossa are significantly greater than those of corresponding test sites of the superior surface of the disk. The recovery percentage of the articular cartilage of the temporal fossa is 60% greater than that of the superior surface of the disk.

Mean and standard deviation values of the intrinsic biomechanical material properties (aggregate modulus or  $H_A$ , Poisson's ratio or  $\nu$ , and permeability or  $k$ ) of the superior surface of the porcine TMJ disk and the articular cartilage of the temporal fossa, as a function of test sites, are shown in Table 2. Significant differences in the aggregate modulus were observed in the superior joint space of the porcine TMJ between the superior surface of the disk and the articular cartilage of the temporal fossa. The aggregate modulus of the articular cartilage of the temporal fossa is about two times greater than that of the superior surface of disk. Thus, the articular cartilage of the temporal fossa is significantly stiffer than the superior surface of TMJ disk. The aggregate modulus of the posterior region of the temporal fossa is the largest (58.9±18.1 kPa). In the superior surface of the TMJ disk, the medial region has the largest aggregate modulus (28.9±12.3 kPa). There are no significant differences in aggregate modulus among four test sites (anterior, central, lateral, and posterior test sites) of the porcine TMJ disk, except for the medial test site, which is signifi-

cantly stiffer. Similarly, on the fossa, the posterior site is also the stiffest.

The largest Poisson's ratio is seen in the posterior region of the temporal fossa (0.132±0.110), and the lowest is found in the anterior region of the disk (0.014±0.003). No significant differences in Poisson's ratio are found in the superior surface of the disk or the temporal fossa except for the posterior region of the temporal fossa.

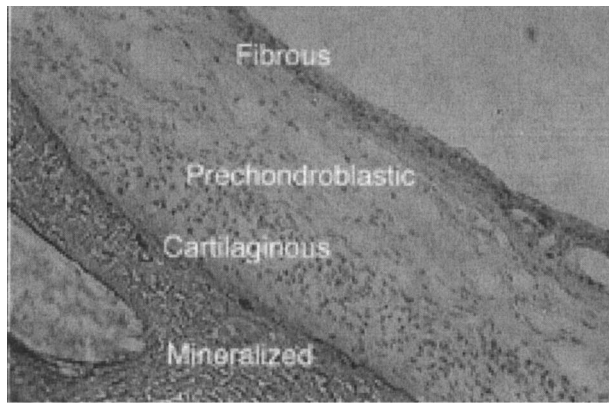
The posterior region of the temporal fossa was found to be the most permeable (67.3±34.9×10<sup>-15</sup> m<sup>4</sup>/N s), whereas the medial region of the temporal fossa is the least permeable (8.8±2.4×10<sup>-15</sup> m<sup>4</sup>/N s). The medial region of the superior surface of the disk is the least permeable (15.4±7.0×10<sup>-15</sup> m<sup>4</sup>/N s), and the medial region is the least permeable among the five test sites of the temporal fossa. In general, the permeability of the superior surface of the disk is greater than that of corresponding test sites of the temporal fossa except for the posterior region.

Histology revealed that the temporal fossa is covered with dense connective tissue (Fig. 4). The TMJ disk is also composed of dense fibrous connective tissue. Distinct collagen fibers ran in the anteroposterior direction in the middle portion (including the anterior, central, and posterior test sites) of the disk (Fig. 5). However, in the medial portion collagen fibers were noted to be oriented in a random pattern (Fig. 6); the pattern of collagen fibers was found not to be particularly directional in the lateral test site portion. These findings might support that the medial region was stiffer (higher aggregate modulus value) than other regions in the superior TMJ disk.

## DISCUSSION

When researching the TMJ, it is first important to select a proper animal model. We believe that a porcine model is the best model for TMJ studies. Studies have shown that the pig was the best experimental model of the TMJ after comparison to sheep, cows, dogs, cats, rabbits, rats, and goats.<sup>7,9</sup> In particular, selection of the pig was attributed to similar size of TMJ structures, the shape of the disk, and omnivorous diet. In addition, the pig and human TMJs have been shown to have similar gross morphology and structure, including the disk and its attachments.<sup>12,26</sup> Moreover, the pig has been supported as a model of the human TMJ for its similar range of motion.<sup>12</sup> Therefore, one can conclude that the pig is an optimal animal model for TMJ research after one considers the characteristics of similar anatomy, relative size, omnivorous diet, cost, and ethical acceptance, in addition to morphological and functional similarities.

Mechanical factors, such as normal load bearing, play an important role in the maintenance of normal articular cartilage.<sup>6</sup> A direct correlation can be seen between the



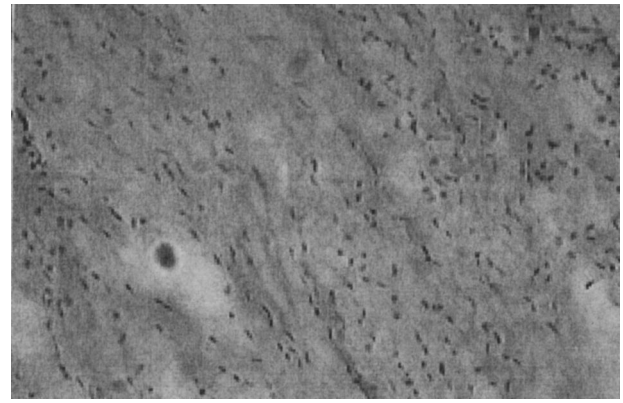
(a)



(b)

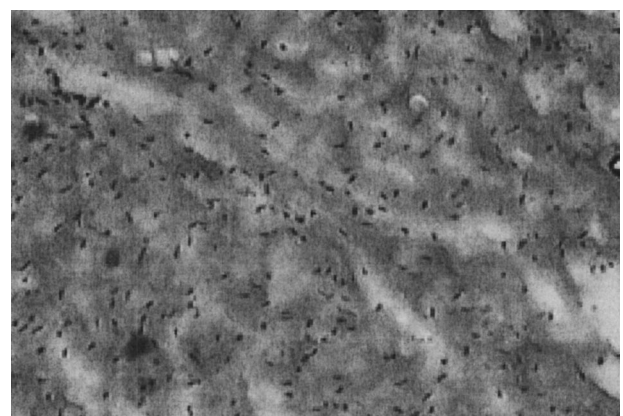
**FIGURE 4.** (a) and (b) Histologic section showing sagittal view of the anterior portion of the porcine temporal fossa. The articular cartilage could be divided into four zones; the fibrous layer, the prechondroblastic zone, the cartilaginous zone, and the zone of mineralization (hematoxylin and eosin stain,  $\times 100$ ).

mechanical properties of articular cartilage and its biochemical composition. The mechanical properties of articular cartilage are controlled by both the intrinsic mechanical properties of the components of the tissue and the interactions of these components during deformation.<sup>1,2</sup> Many previous investigations of the mechanical characteristics of articular cartilage have used indentation tests.<sup>11,13,16</sup> A biphasic model for articular cartilage has been developed that considers cartilage a mixture of two interacting materials; a porous, permeable, elastic, solid matrix, and an incompressible fluid that occupies the matrix pores.<sup>18,20–22</sup> According to Armstrong *et al.*,<sup>1</sup> the visual, or histological appearance of a cartilage specimen may be a poor indicator of its ability to function as the load bearing material in the intact joint. A more reliable indicator of the functional properties of a specimen can be obtained either by direct mechanical testing, or by biochemical analysis of its composition.



**FIGURE 5.** Histologic section of the sagittal view of the central portion of the porcine TMJ disk. The collagen fibers run in the anteroposterior direction (hematoxylin and eosin stain,  $\times 200$ ).

The intrinsic biomechanical material properties measured in this study are substantially different than other diarthrodial joints previously published. The differences may be due to the fundamental differences between hyaline cartilage of other joints and fibrocartilage of the TMJ. Athanasiou *et al.*<sup>2</sup> reported that cartilage in the human hip joint is twice as stiff, less permeable, and half as thick when compared with cartilage in the human knee. In that study, human acetabular and femoral head cartilage ( $n=140$ ) was found to have the following values: aggregate modulus of  $1207 \pm 606$  kPa, Poisson's ratio of  $0.045 \pm 0.060$ , permeability of  $0.895 \pm 0.537 \times 10^{-15} \text{ m}^4/\text{N s}$ , and a test site tissue thickness of  $1.34 \pm 0.38$  mm. For cartilage of the human knee ( $n=14$ ), the corresponding values were  $604 \pm 154$  kPa,  $0.060 \pm 0.074$ ,  $1.446 \pm 0.609 \times 10^{-15} \text{ m}^4/\text{N s}$ , and  $2.631 \pm 1.04$  mm.



**FIGURE 6.** Histologic section of the sagittal view of the medial portion of the porcine TMJ disk. The collagen fibers are oriented in a random pattern (hematoxylin and eosin stain,  $\times 200$ ).

Although we obtained data on the porcine TMJ and not the human TMJ, direct comparisons can be made on their mechanical properties. In this study, we found the aggregate modulus of the superior surface of the porcine TMJ disk to be  $20.9 \pm 8.0$  kPa (about 1/60 of human hip joint cartilage and about 1/30 of human knee joint cartilage). Also, we found the aggregate modulus of the articular cartilage of the temporal fossa to be  $41.9 \pm 16.8$  kPa (about 1/30 of human hip joint and about 1/15 of human knee joint). Thus, the aggregate modulus of the porcine disk and temporal fossa is much smaller than that of the human knee and hip joint cartilage. The finding that the articulating cartilage of the porcine TMJ is 15–60 times softer than that of hyaline cartilage of the human hip and knee joints suggests that the biomechanical environment of the TMJ is substantially different from that in the hip and knee.

The values of the Poisson's ratio of the superior surface of the disk and the temporal fossas are  $0.045 \pm 0.050$  and  $0.060 \pm 0.073$ , respectively. There are no significant differences in the Poisson's ratio between the porcine TMJ and the human hip and knee joints.

The permeability values of the superior surface of the disk and temporal fossa are  $24.1 \pm 10.2 \times 10^{-15}$  and  $25.0 \pm 28.3 \times 10^{-15}$  m<sup>4</sup>/Ns, respectively. The permeability of the superior space of the porcine TMJ is about 30 times larger than that of the human hip joint, and about 20 times larger than that of the human knee joint.

The porcine TMJ disk is  $1.050 \pm 0.340$  mm thick, and the temporal fossa is  $0.448 \pm 0.129$  mm thick. The articular cartilage thickness of the temporal fossa is about 1/3 that of the human hip joint and 1/6 that of the human knee joint. Thus, we can state that the porcine TMJ disk cartilage is dramatically soft, permeable, and thin, when compared to human hyaline cartilage. However, further studies elucidating interspecies differences in TMJ cartilage properties are needed.

The intrinsic equilibrium modulus and the permeability are highly correlated with the water content of the tissue. As water content increases, the matrix of the tissue becomes softer and more permeable.<sup>1</sup> Maroudas *et al.*<sup>19</sup> showed that tissue permeability is inversely related to the proteoglycan content of the tissue. The intrinsic material properties of cartilage have been shown to be directly related to its biochemical composition.<sup>3</sup> The compressive stiffness of articular cartilage is proportional to the tissue's total proteoglycan content,<sup>14</sup> but varies inversely with its water content.<sup>1</sup> Athanasiou *et al.*<sup>6</sup> suggested that low-weight-bearing areas of articular cartilage have a higher collagen content and lower proteoglycan content, and high-weight-bearing areas have a higher proteoglycan content and lower collagen content. Because a high proteoglycan content suggests a high compressive modulus, a low-weight-bearing area is expected to have a compressive modulus that is smaller

than that of a high-weight-bearing area.<sup>4,5</sup> This suggests that the superior porcine TMJ is most likely a low-weight-bearing joint, and experiences relatively little biomechanical stress.

The water content of articular cartilage of the porcine TMJ is most likely high based on our biomechanical results. However, proteoglycan content is probably low. A histomorphologic examination revealed a low proteoglycan content through safranin O staining. Further studies are required for detailed biochemical analysis of the TMJ. In this study, the medial and posterior region of the superior surface of disk and temporal fossa were found to be relatively stiffer than other regions. Thus, the medial and posterior region of the porcine TMJ disk and temporal fossa may be relatively high-load-bearing areas during mandibular functioning.

The tensile stiffness is proportional to the collagen content. Permeability is proportional to the water content, and varies inversely with the proteoglycan content and collagen content.<sup>1,3</sup> It has been suggested that the Poisson's ratio may depend on the density and strength of the interactions between proteoglycans and collagen fibers.<sup>3</sup> A small Poisson's ratio indicates a higher apparent compressibility of the tissues and, hence, a propensity for enhanced fluid transport; whereas a large permeability indicates greater ease of fluid movement through the solid matrix.<sup>6</sup> Therefore, a combination of low Poisson's ratio and high permeability means rapid fluid transport under the applied load, which is conducive to greater stress relaxation and better distribution of applied load.<sup>4,6</sup>

This study's most salient finding is that the biomechanical properties of the superior surface of the disk and the temporal fossa of the porcine TMJ are dramatically different than cartilage from other diarthrodial joints. It appears that during normal translation of the joint, little mechanical stress is expected. Increases in load may occur when the condylar head moves forward during opening and moves laterally during excursions towards the contralateral side. In this position, the space between the superior and inferior articulating surfaces is narrowed secondary to the anatomy of the joint, i.e., the presence of an articulating eminence. To counter the increased loading when the joint translates forward, the medial and posterior regions of the disk are stiffer and more resilient than other parts. Maintenance of loading patterns within physiological limits is aided by joint components which are more permeable and capable of greater load distribution.

These findings suggest that significant differences in biomechanical properties exist in various regions of the superior surface of the disk. The regions' separation by small distances lends credence to the belief that relatively minor displacements of the disk may produce unfavorable biomechanical loading patterns which hasten



the deterioration of joint structures. Pathological processes, such as softening of the disk or auricular cartilage from inflammation, loss of tension in the capsule and ligaments responsible for joint stability, and prolonged, excessive translation, may all contribute to the malpositioning of articular structures. The superior surface of the disc would then be unable to tolerate even physiological loads.

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