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ORIGINAL PAPER

The temporomandibular joint disc of Asian elephant (*Elephas maximus*) and African elephant (*Loxodonta africana*)

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Abstract The temporomandibular joint (TMJ) is a synovial articulation between the mandibular head of the condylar process of the mandible and the mandibular fossa of the squamous temporal bone. Extensions of the fibrous capsule into the joint space form a biconcave disc that functions as an articulating surface and divides the joint into dorsal and ventral compartments. The TMJ disc plays a crucial role in normal functioning of the joint, and differences in cranial morphology, mastication patterns, and diet are reflected in the material and biochemical properties of the disc. The purpose of the present case study was to compare the regional histologic differences between two elephant genera and quantify the biochemical and biomechanical properties of the African elephant disc. This study provides a unique insight into the elephant TMJ disc and also provides a comparison between the African and the Asian elephant genera. The results demonstrate several remarkable findings. First, structure–function relationships exist within the elephant TMJ disc. Second, regional variations exist in the elephant TMJ disc, and these are likely to correlate with its functional requirement. Additionally, it is apparent that some properties of the disc vary with the specific anatomy, diet requirement, and jaw motion. Finally, in comparison with the TMJ disc of other species, it is clear that, although the elephant disc is unique, it has properties that transcend and are preserved among the species.

Keywords Elephant · Temporomandibular joint · Disc · Jaws

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Introduction

The temporomandibular joint (TMJ) is a synovial articulation between the mandibular head of the condylar process and the mandibular fossa of the squamous temporal bone (Constantinescu et al. 2007; Ten Cate 2003). The capsule of the joint consists of a dense collagenous membrane that provides passive stability as well as active stability from proprioceptive nerve endings in the capsule (Ten Cate 2003). In addition, extensions of the fibrous capsule into the joint space form a biconcave disc that functions as an articulating surface and divides the joint into proximal and distal compartments (Ten Cate 2003).

In load bearing tissues, there is typically an intimate link between the structural and functional properties of the tissue; this relationship has been shown to exist in the TMJ disc (Allen and Athanasiou 2005; Kalpakci et al. 2011). The TMJ disc plays a crucial role in the normal functioning of the joint, and differences in cranial morphology, mastication patterns and diet are reflected in the material

and biochemical properties of the disc (Kalpakci et al. 2011). Perhaps the most important function of the TMJ disc is the dissipation and distribution of masticatory loads (Tanaka and van Eijden 2003). These functional characteristics of the TMJ disc are translated to the structural properties of the disc as evidenced by the biconcave shape, circumferential collagen orientation in the outer portions, and the higher glycosaminoglycan (GAG) content of the inner portions which aid in the dissipation and distribution of the compressive loads present during mastication (Kalpakci et al. 2011). TMJ anatomy and mechanics vary considerably among mammals, depending on the masticatory requirements and pattern (Ten Cate 2003). In carnivores, for example, the movement is restricted to a simple hinge motion by the presence of rostral and caudal bony projections that clasp the mandibular condylar process (Constantinescu et al. 2007; Ten Cate 2003). In omnivores such as humans, the masticatory process demands that the mandible be capable of opening and closing movements as well as simultaneous protrusive, intrusive, and lateral movements (Ten Cate 2003). However, in herbivores, such as, elephants, the chewing behavior is such that during mastication, the mandible moves in rostral and caudal motion rather than side to side or in circles as seen in ruminants (Eltringham 1982a; van der Merwe et al. 1995). The grinding movement of the molar teeth during this pattern of mastication ultimately wears out the tooth lamellae and leaves the last set of molars perfectly smooth (Eltringham 1982a, b). This impairs the efficiency of masticating rough foods, forcing the elephant to seek soft food and luscious vegetation usually found in banks of rivers and lakes. This is where the old elephants with worn molar teeth remain most of the time in order to survive and eventually they die there (Eltringham 1982a). If soft vegetation is not available due to drought, the elephants with worn molars usually die of malnutrition because of the inability to chew dry feedstuffs.

In an effort toward better understanding of the similarities and differences between African and Asian elephant TMJ discs, the regional histologic differences between the discs of two specimens were compared, and the biochemical and biomechanical properties of the African elephant disc were quantified.

Materials and methods

Specimen procurement

Tissue specimens were procured from two adult female elephants that were euthanized for reasons unrelated to this study: one disc from a 70-year-old Asian elephant (*Elephas maximus*) and two discs from a 50-year-old African elephant (*Loxodonta africana*). Both elephants were raised and kept in captivity. The African elephant discs were washed in 0.01 M phosphate-buffered saline (PBS), then wrapped in gauze soaked with PBS containing protease inhibitors (10 mM*N*-ethylmaleimide and 1 mM phenylmethylsulfonyl fluoride, Sigma, St. Louis, MO) and frozen at −20°C until testing. The Asian elephant disc was obtained already fixed in 10% buffered formalin. All TMJ discs were carefully dissected from their attachments and verified to be grossly normal.

Biochemical analysis

For quantitative biochemistry, the left disc of the African elephant was thawed in PBS at room temperature for 4 h, and then sectioned into five pieces as depicted in Fig. 1. All specimens were blotted to remove excess moisture, weighed to obtain a wet weight, and then lyophilized for 48 h. Digestion of the samples was completed in 1.5 mL of 125 mg/mL papain (Sigma, St. Louis, MO) solution overnight at 60°C. The DNA content of the samples was measured by reaction of DNA with Picrogreen reagent (Invitrogen, Carlsbad, CA). The total amount of sulfated GAG was measured using a dimethylmethylene blue colorimetric assay kit (Biocolor, Newtownabbey, UK). The total collagen content was determined using a hydroxyproline assay, as described previously (Almarza et al. 2006).

Histology

For topographical histology, the one disc from each species was divided into five regions as shown in Fig. 1. Disc samples were fixed in 10% buffered formalin and embedded in paraffin blocks. The tissue samples were fixed en bloc in 10% neutral buffered formalin for a minimum of 48 h, transverse sections cut in the rostrocaudal direction

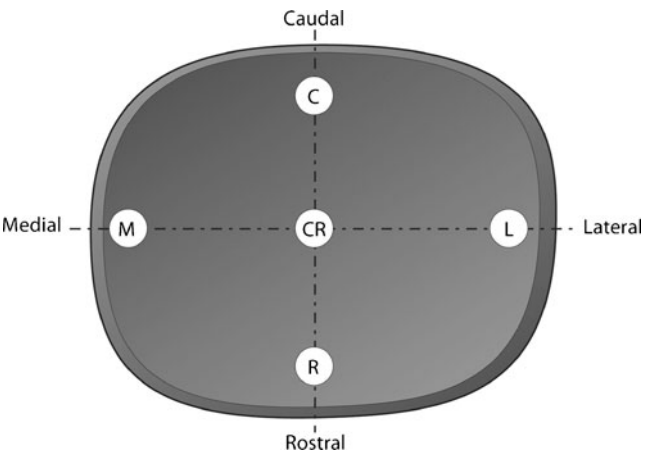

Fig. 1 Diagram illustrating the regions of the TMJ disc used for biochemical, histological, and mechanical testing: (*R*) rostral, (*C*) caudal, (*L*) lateral, (*M*) medial, and (*CR*) central zone

and were embedded in paraffin. Then, 5-μm sections were cut, mounted, and stained with hematoxylin and eosin (H&E), according to standard protocols. Qualitative analysis of sulfated GAG was conducted using alcian blue (pH 1.0). In addition, qualitative analysis of elastin was conducted using Verhoeff's Van Gieson staining using standard protocol.

Immunohistochemistry

Immunohistochemistry was performed on 4-μm serial sections using a routine streptavidin–biotin horseradish peroxidase (HRP) detection system as previously described (Norris et al. 2005). Briefly, the slides were deparaffinized, gradually hydrated to 70% ethanol and then immersed in 0.3% hydrogen peroxide in methanol for 30 min in order to block endogenous peroxidase activity. Individual slides were then pretreated with an antigen retrieval dependent on the specific collagen I and collagen II. Sections stained with the rabbit anti-collagen I antibody (1:200 Novocastra #NCL-Coll-I) were heat pretreated in citrate buffer (Dako #1699) for 20 min at 98°C. The remaining sections stained with the Mab to collagen II (1:30 Neomarkers clone 2B1.5) were pretreated with 0.4% Pepsin (Sigma #P7012) in acidulated water pH 3.3 for 20 min at 37°C. After pretreating, nonspecific antibody interactions were then blocked with immersion in 10% normal horse serum for 20 min. Slides were drained and primary antibodies were applied for 60 min at room temperature. Biotinylated secondary antibodies and streptavidin (HRP) were applied according to kit instructions (Biocare Medical, Concord, CA, USA). Positive staining was visualized using 3-amino-9-ethycarbazole (Invitrogen, San Francisco, CA) as the chromogen. Slides were counter-stained with Mayer's hematoxylin (Sigma Chemical Co., St. Louis, MO). Negative controls were prepared by omitting the primary antibody and substituting an IgG correlate for each experiment. Relevant positive controls were used for each collagen stain (e.g., articular cartilage and tendon for collagen II and I, respectively).

Tensile sample preparation and testing procedure

Discs from the African elephant were thawed and cut into two regions in either rostrocaudal or mediolateral direction. Full-thickness samples were removed and cut into a "dog bone" shape with a 1-mm width. Tests were conducted on a materials testing machine (Instron 5565, Canton, MA, USA) in an isotonic saline bath at room temperature. A 0.02-N tare load was applied to the samples followed by preconditioning with ten cycles of 5% strain at a rate of 1% strain/s. After preconditioning, the samples were pulled to failure at a constant strain rate of 1% strain/s. Data were retained only from samples that failed away from the grips. This testing enabled determination of the Young's modulus, obtained from the slope of the linear region of the stress–strain curve, and the ultimate tensile strength, defined as the maximum stress to failure, of the disc samples.

Compression sample preparation and testing procedure

Cylindrical tissue plugs were obtained from the five regions, previously described (Fig. 1) of the African elephant disc and sectioned using a cryotome blade such that the dorsal and ventral surfaces were parallel. Unconfined compression testing was performed on the materials testing machine in a saline bath at room temperature. A 0.02-N tare load was applied to the sample, followed by preconditioning with 5% strain for 15 cycles at a strain rate of 1% per second. During the test, two 10%-step strains were applied, with 10-min intervals between steps to allow for stress relaxation. Values for instantaneous modulus, relaxation modulus, and coefficient of viscosity were obtained by fitting data to a viscoelastic solution for a Kelvin solid, as described previously (Allen and Athanasiou 2005).

Results

Gross morphology

Gross morphology and measured dimensions of the discs from the two elephant genera are presented in Fig. 2. Both elephant genera were found to be slightly different in both mediolateral and rostrocaudal dimensions. More specifically, the African elephant disc was smaller and more rounded, and the Asian elephant disc was more elongated in a mediolateral direction. The discs exhibited a general pattern of concavity at the intermediate zone (e.g., at the temporal articulation dorsally and at the condylar articulation ventrally). In both discs, the caudal band was the thickest, followed by the rostral, medial, and lateral bends.

Histology and immunohistochemistry

At the rostral aspect of the TMJ disc, the collagen fibers were compact and oriented in a rostrocaudal plane. The majority of the fibers were oriented parallel to one other, and the nuclei of the fibrocytes were oval to fusiform with condensed chromatin and indistinct nucleoli, equally spaced and randomly distributed between the matrical collagen bundles. Occasionally, there were linear nuclear aggregates spanning areas of up to 400–500 μm. In these aggregates, the nuclei formed parallel rows to one another. Occasional longitudinal clefts were present between collagen fibers that may represent processing artifacts. The collagen bundles adjacent to the nuclear aggregates were slightly lighter in color than the

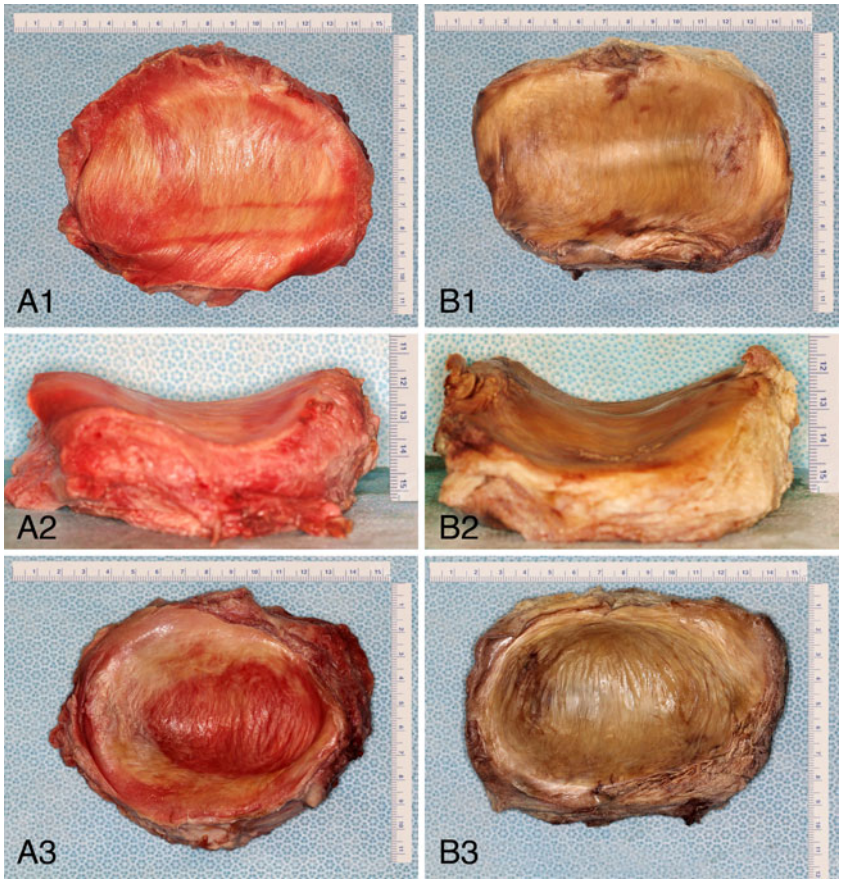

Fig. 2 Gross morphology of the African (*A1–3*) and Asian (*B1–3*) elephants TMJ discs. The discs exhibit a general pattern of concavity, demonstrated in the temporal view (*A1*, *B1*), lateral view (*A2*, *B2*) and condylar view (*A3*, *B3*). Both elephant discs were elongated in mediolateral direction with the Asian elephant disc being larger than the African

bundles in less dense cellular areas. Nuclear density was slightly higher at the margin of the examined section where collagen fibers were predominately organized circumferentially. In the disc of the Asian elephant, small caliber blood vessels were randomly distributed and present throughout the section (Fig. 3). The blood vessels were oriented perpendicular and parallel to the collagen fibers.

In the medial and lateral sections, the collagen fibers exhibited the same characteristics as in the rostral area and were directed in a rostrocaudal plane. Occasional areas of nuclear aggregates and miniature capillaries were observed. However, in the disc of the Asian elephant, distinct small to medium caliber blood vessels were present between the large collagen bundles. The blood vessels were oriented parallel or perpendicular to the collagen fibers.

At the caudal aspect, the fibers were oriented rostrocaudally in the center of the section; however, the orientation changed to mediolateral at the margin of the African elephant's disc. In the Asian elephant's disc, the large bundles of collagen intersected each other and ran in seemingly random directions, including rostrocaudal, mediolateral, and oblique. As in other portions of the Asian disc, there were variably sized vessels distributed randomly.

In the central portions of the African (Fig. 4) and Asian elephant discs, about 90% of the collagen fibers were oriented in a rostrocaudal direction. This portion of the disc was relatively avascular and contained occasional thread-like longitudinally oriented areas of increased basophilia (e.g., possible mineralization), which ran parallel to the regular collagen fibers.

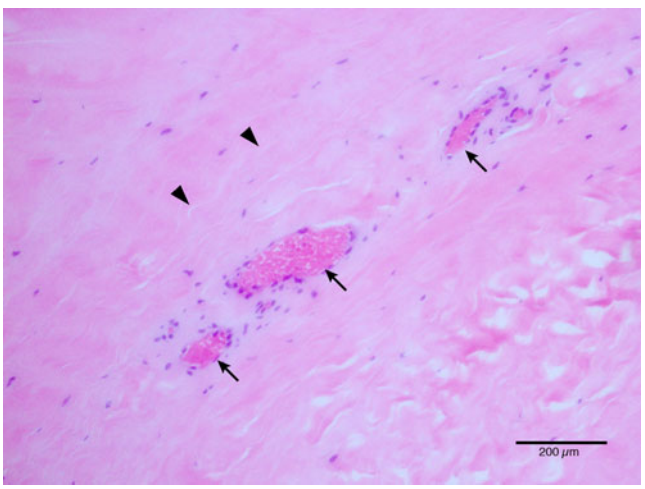

Fig. 3 Histologic section of the Asian elephant disc obtained from the rostral zone, small caliber blood vessels were randomly distributed and present throughout the section (*arrows*). The blood vessels were oriented perpendicular and parallel to the collagen fibers (*arrow heads*). (H & E×200, *bar*=200 µm)

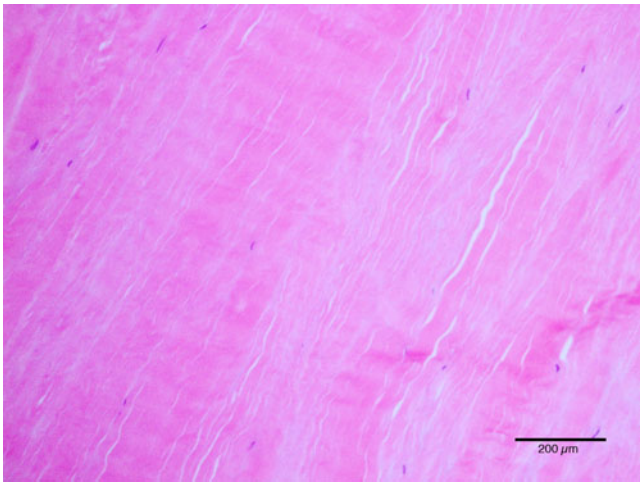

Fig. 4 Histologic section of the central portion of the African elephant disc. About 90% of the collagen fibers were oriented in rostrocaudal direction. Note the lack of vascularization (H & E×200, *bar*=200 µm)

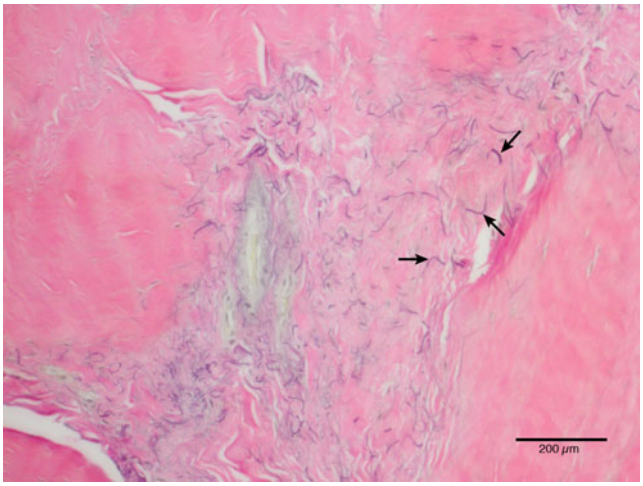

Fig. 6 Histologic section of the rostral portion of the Asian elephant disc stained with Verhoeff's Van Gieson for the detection of elastin fibers (*arrows*). In the Asian elephant, elastin was detected in higher amount then in the African disc. (VVG×200, *bar*=200 µm)

In summary, in both elephant discs, the collagen fibers forming the main bulk of the TMJ disc were oriented in a rostrocaudal direction. In the Asian elephant, vascularization was a prominent feature but was not observed in the TMJ disc of the African elephant. Positive alcian blue staining for sulfated GAGs was mostly visible at the central sections of both African and Asian elephant discs (Fig. 5). Minimal positive Van Gieson staining for elastin was present at the rostral section of the African elephant. In the TMJ disc of the Asian elephant, elastin was detected in a higher amount than in the African disc in all sections (Fig. 6). In both discs, elastin was aligned along, in between, and parallel with the collagen fibers.

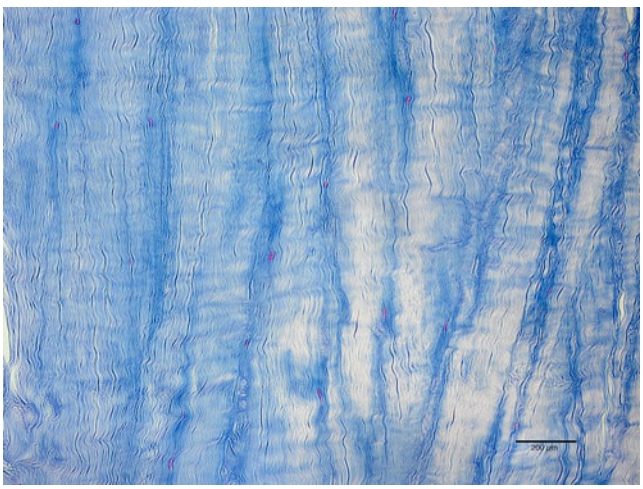

Fig. 5 Histologic section of the central portion of the African elephant disc stained with alcian blue (pH 1.0) for sulfated GAGs. Positive staining was visible mostly at the central sections of both elephant discs (alcian blue×200, *bar*=200 µm)

Immunohistochemistry of all sections from all regions were uniformly positive for collagen type I (Fig. 7) and uniformly negative for collagen type II.

Biochemical analysis

Quantitative biochemical results for the African elephant are displayed in Table 1. The biochemical analyses generally supported the histological results and were in the range of previously reported biochemical results (Kalpakci et al. 2011). Water content of the various regions of the elephant TMJ disc was similar and ranged from 73.16% to 74.49%. The collagen content normalized to dry

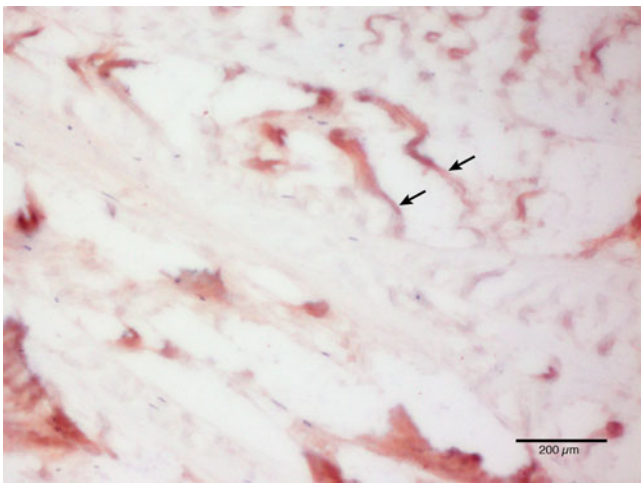

Fig. 7 Histologic section obtained from the medial portion of the African elephant TMJ disc and immunolabeled for collagen type I. Immunohistochemistry of all sections from all regions were uniformly positive for collagen type I (*arrows*) and uniformly negative for collagen type II (Col I×200, *bar*=200 µm)

Table 1 Quantitative biochemical content of the African elephant TMJ disc

Sample	Water content (%)	DNA/DW (%)	sGAG/DW (%)	Collagen/ DW (%)
C	73.16	0.058	1.10	92.58
M	74.49	0.029	1.34	86.61
CR	73.28	0.011	1.41	78.45
L	73.44	0.056	1.39	89.04
R	73.64	0.056	1.18	84.40

C caudal, *M* medial, *CR* central zone, *L* lateral, *R* rostral

weight (dw) was found to vary between 78.5% and 92.6% for all regions tested. Samples obtained from the caudal region possessed the highest collagen content while the central region had the lowest collagen content. DNA/dw ranged from 0.011% and 0.058%, thus, demonstrating a large topographical variation. The caudal, lateral, and rostral regions all possessed relatively high cellularity while the central region had low cellularity, and the medial region had intermediate cellularity. The sulfated GAG/dw content was found to vary between 1.1% and 1.41% for all samples tested. While differences in GAG/dw were only slight, the central region was found to have the highest GAG content; whereas, the caudal region had the lowest.

Tension

The Young's modulus and ultimate tensile strength (UTS) for the African elephant disc are presented in Table 2. When pulling the disc in the rostrocaudal or mediolateral direction, the Young's modulus and UTS were found to be 7.73 and 3.68 MPa, respectively. Similar to other species, the elephant disc was found to be >7 times stiffer in the rostrocaudal direction than it is in the mediolateral direction. Specifically, in the rostrocaudal direction the Young's modulus and UTS were 56.5 and 16.41 MPa, respectively.

Compression

The viscoelastic compressive properties for the African elephant disc at 10% and 20% strain are shown in Table 3.

Table 2 The Young's modulus and UTS for the African elephant disc

Sample	Young's modulus (MPa)	Ultimate tensile strength (MPa)
M–L	7.73	3.68
C–R	56.50	16.41

Similar to other species, the elephant disc was found to be more than seven times stiffer in the rostrocaudal direction than it is in the mediolateral direction

M medial, *L* lateral, *C* caudal, *R* rostral

All five regions of the disc were found to exhibit strain stiffening with higher moduli under increasing strain. Regionally, the rostral and lateral regions of the disc had by far the greatest instantaneous modulus, which was at least two times higher than any other region. The coefficient of viscosity was found to mirror the instantaneous modulus, with the rostral and lateral regions showing a more than twofold increase in resistance to fluid flow under compression. The relaxation modulus was also found to be highest in the lateral region, although the increase relative to other regions was less dramatic. The central region of the intermediate zone was the weakest region under compression, possessing the lowest moduli and coefficient of viscosity.

Discussion

Previous studies of the TMJ disc in several species, including humans, demonstrated regional histologic variation as well as biochemical and biomechanical variations (Kalpakci et al. 2011; Minarelli et al. 1997). However, to our knowledge, the elephant TMJ disc is an important structure that had not been described previously. Although we were able to study TMJ discs from only two elephants of different genera, the present report elucidated multiple characteristics of African and Asian TMJ discs and contributes to the knowledge of the masticatory apparatus in these endangered (Asian elephant) and vulnerable (African elephant) species.

Gross morphologically, the shape of both discs corresponded to the shape of the mandibular head of the condylar process of the mandible and the mandibular fossa of the squamous temporal bone. The pattern of concavity at both articulating surfaces is designed to match the corresponding articulating bone (e.g., temporal or mandibular head). Specifically, the mandibular head of the condylar process of the African elephant is smaller and more round than the Asian elephant. In the Asian elephant, the mandibular head is more elongated in a mediolateral direction.

The histologic arrangement of the collagen fibers in the African and Asian elephants was similar. The collagen fibers were arranged predominantly in a rostrocaudal direction in a parallel fashion with branching in the intermediate zone. In the intermediate zone, the collagen fibers were also predominantly aligned in a rostrocaudal direction, but orientation was also noted in mediolateral and oblique directions. These findings are consistent with the collagen fibers' arrangement in other species (Detamore and Athanasiou 2003a, b; Kalpakci et al. 2011; Minarelli et al. 1997; Nagy and Daniel 1991; Scapino et al. 1996). It is therefore remarkable that the collagen fiber architecture is conserved among species despite the differences in size,

Table 3 The viscoelastic compressive properties for the African elephant disc at 10% and 20% strain

Sample	10% Strain			20% Strain		
	Relaxation modulus (kPa)	Instantaneous modulus (kPa)	Coefficient of viscosity (kPa s)	Relaxation modulus (kPa)	Instantaneous modulus (kPa)	Coefficient of viscosity (kPa s)
C	20.86	43.50	448.93	32.19	186.31	1,982.81
M	12.98	36.50	381.06	25.57	112.82	1,933.13
CR	9.53	23.78	179.67	16.21	93.91	1,243.79
L	22.42	79.92	778.16	57.29	571.38	3,984.46
R	18.22	75.48	418.39	41.04	521.39	2,097.98

Note that the five regions of the disc were found to be strain stiffening with higher moduli under increasing strain

C caudal, *M* medial, *CR* central zone, *L* lateral, *R* rostral

weight, evolutionary origin, and chewing behavior. However, a striking difference between the elephant TMJ disc and other species examined (e.g., rabbit, cow, goat, pig, and human) is the presence of vasculature within the disc. The presence of large numbers of variable caliber blood vessels in the Asian elephant disc could be due to the large size of the disc as perfusion from the synovial fluid may not be sufficient to provide nutrients to the disc; thus, direct blood supply is needed. Nevertheless, it may also be indicative of degeneration (Leonardi et al. 2010). In summary, the collagen fibers of the elephant TMJ disc appear wavy and aligned primarily in a rostrocaudal direction in all of the examined zones. At the center of the disc (intermediate zone) this pattern is also prominent but is disrupted by oblique and mediolaterally arranged collagen fibers.

Collagen type is useful in the classification of tissue type. For example, skin and tendon contain predominantly collagen type I, articular cartilages contain predominantly collagen type II and the stifle meniscus contain both types (Detamore and Athanasiou 2003a). We have found that in the elephant TMJ disc collagen type I is uniformly present throughout the disc with remarkable absence of collagen type II. These findings are not consistent among the species. In baboons and macaques both collagen type I and II were found to be present (Mills et al. 1994). In addition, collagen type II was also found in small amounts in the bovine TMJ disc (Landesberg R et al. 1996). In summary, we have found that the elephant TMJ disc is a fibrous structure composed predominantly of collagen type I with a complete absence of collagen type II.

Proteoglycans and their associated glycosaminoglycan (GAG) chains are important constituents of cartilaginous tissue and contribute to its compressive mechanical properties (Detamore and Athanasiou 2003a). Moreover, the GAG content of the TMJ disc in general lies between that of the hyaline cartilage and tendon and is more similar to that of fibrocartilages such as the stifle meniscus (Axelsson et al. 1992). Using histology, we have found that sulfated GAGs were mostly present at the central portion of the elephant discs. It seems that GAG distribution is not homogeneous among the species (Detamore and Athanasiou 2003a). However, there is evidence that the most prominent GAGs in the TMJ disc are dermatan sulfate and chondroitin sulfate, and both are preferentially located in the center of the disc (Nakano and Scott 1989a; Nakano and Scott 1989b; Scott et al. 1989). In addition, it is possible that due to the old age of the examined elephants, there has been age-related changes in the GAG content of the discs (Nakano and Scott 1996). These changes were documented in bovine discs and include a decrease in hyaluronic acid and dermatan sulfate content and increase in chondroitin sulfate and keratin sulfate content (Nakano and Scott 1996). Since younger elephant discs were not examined in this study, these changes could not be verified in the present study.

Elastic fibers (elastin) are of minor importance in the TMJ disc and are not likely to contribute to its tensile strength and load-bearing properties (Detamore and Athanasiou 2003a; Mills et al. 1994). These fibers provide little resistance to elongation and are probably more important in restoring and retaining the resting disc form and position after loading (Mills et al. 1994; Scapino et al. 1996). Indeed, we observed small amounts of elastin at the rostral sections of the African elephant and higher amounts in the Asian disc. As described in other studies, elastin generally aligned along, in between, and parallel to the collagen fibers of the disc (Minarelli and Liberti 1997; Nagy and Daniel 1991). In addition, due to the old age of the examined discs, it is possible that the number of elastin fibers has decreased with age (Minarelli AM and Liberti EA 1997) although others have found that elastin quantity actually increases with age (Nagy NB and Daniel JC 1991). Nevertheless, it appears that due to its small quantity in the elephant TMJ disc, elastin may not contribute to the mechanical strength and may only contribute to restoring the disc to its native form.

In the present study, the biochemical composition was performed only on the African elephant disc as it was fresh frozen tissue available for biochemical evaluation (Allen and Athanasiou 2005). With regard to the water content, we have found that the elephant TMJ disc contains 73.16% to 74.49% water, which is in accordance with the range of 66% to 80% as observed in the bovine and porcine species (Nakano and Scott 1989a, 1996). However, one study observed that water content tend to decrease with age (Nakano and Scott 1996). With regard to the DNA/dw content, we have found that the lowest DNA content is present in the center of the disc. This finding was also observed in several other species (Almarza et al. 2006; Kalpakci et al. 2011). However, the overall DNA/dw content for each region of the disc was found to be lower than the porcine disc (Almarza et al. 2006). It is possible that the number of cells and hence the DNA content also decreases with age. In addition to the histologic evaluation of the presence of GAG within the disc, we have found that sulfated GAGs are present in small amounts within all regions of the disc. Moreover, as the histologic findings demonstrated, the highest amount of sulfated GAG is present in the center of the disc. These findings are also in agreement with the quantities (0.6% to 10% per dry wet) and distribution of GAGs in the disc of other species (Almarza et al. 2006; Almarza and Athanasiou 2004; Kalpakci et al. 2011; Nakano and Scott 1989a, 1996). Finally, the total collagen content was also found to have regional variation with the highest content observed in the caudal area of the disc. The overall collagen content detected in each region was found to be similar to other species (Detamore and Athanasiou 2003a; Kalpakci et al. 2011) and, as was found in our histologic evaluations, composed predominantly of collagen type I aligning mostly in rostrocaudal direction.

The TMJ disc is a viscoelastic material and its mechanical behavior is dependent on its strain history and characterized by hysteresis, stress relaxation, and creep (Detamore and Athanasiou 2003b; Kuboki et al. 1997). In the present study we could only examine the African elephant disc as the Asian elephant disc obtained had already been fixed in formalin. Nevertheless, taking into account the histologic and morphologic similarities, it is plausible that the mechanical properties are similar between the genera. We have found that the tensile strength and stiffness experience regional variation and relate with collagen fiber orientation. More specifically, the Young's modulus (stiffness) and ultimate strength values for the rostrocaudal direction were dramatically higher than for the mediolateral direction. These findings appear to be consistent between the species (Detamore and Athanasiou 2003b; Kalpakci et al. 2011). In addition, we have found that the compressive properties varied topographically with the lowest relaxation modulus in the center of the disc. Moreover, the center of the disc also exhibited the lowest coefficient of viscosity.

In conclusion, the present study provides an insight into the elephant TMJ disc and provides a preliminary comparison between the African and the Asian elephant genera. Our findings demonstrate several interesting findings. First, a structure–function relationship exists within the elephant TMJ disc. Second, regional variations exist in the elephant TMJ disc, and these are likely to correlate with its functional requirement. Additionally, some properties of the disc may vary as a function of the specific anatomy, diet requirements, and jaw motion. Finally, in comparison with the TMJ disc of other species, it is clear that although the elephant disc is unique, it has properties that transcend and are preserved among species. Elephants are an endangered (Asian elephant) and vulnerable (African elephant) species, and it is important to make efforts to study their anatomy, function, and behavior to provide them with adequate care and condition. We hope that the present study will provide a platform for further studies of the elephant TMJ.

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