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Degenerative temporomandibular joint disease in a lioness (*Panthera leo*)

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ABSTRACT

The temporomandibular joint (TMJ) is a synovial joint that consists of two articulating surfaces, the mandibular head on the condylar process ventrally and the mandibular fossa of the squamous temporal bone dorsally, with a thin fibrocartilage disc that separates the joint into two non-communicating compartments. Degenerative joint disease (DJD) of the TMJ has been evaluated in other carnivorous species; however, it has not previously been described in the lion (*Panthera leo*). This study characterized the histological, biomechanical and biochemical properties of the TMJ in health and disease in a lioness. The components of the articulating surface and general features of the disc of the TMJ were comparable to other carnivorous species described previously. Spontaneous DJD was observed unilaterally, revealing comparable features with other carnivores. Tensile strength and stiffness differed substantially between the diseased and healthy disc, with the diseased disc having altered direction-dependent mechanical properties. Biochemically, the disc exhibited a similar pattern of collagen and glycosaminoglycan composition to other carnivores. The role of DJD of the TMJ in potential pain or disability is not well understood in these species, and this report offers a glimpse into these disorders.

1. Introduction

The temporomandibular joint (TMJ) is a mammal specific adaptation appearing relatively late in evolutionary development [1]. This articulation is consistent in mammals and plays a role in the survival of species through its major role in mastication. The TMJ is a synovial joint characterized by articulation ventrally by the condylar process of the mandible and dorsally by the mandibular fossa of the squamous temporal bone [2]. Between the two articulating surfaces lies an intra-articular, fibrocartilaginous, biconcave disc surrounded by a fibrous joint capsule. However, there is demonstrable variation in the anatomy and morphology between species [3,4]. The vast differences in masticatory function and dietary mode across mammalian species are thought to be responsible for the observed variations in the TMJ [5]. Differences are seen in areas such as load capacity and movement, and manifest as changes in the size of the articular surface and the orientation of the joint [3,6]. In carnivorous species specifically, the TMJ is generally highly congruent with the joint's motion, being mainly limited to opening and closing (sliding movements), and sustains higher loading compared to primates for example [3,6].

The disc of the TMJ has a strong structure–function relationship [7–10]. The TMJ disc is composed of mainly type 1 collagen with minimal amounts of glycosaminoglycan (GAG) and is considered to have low cellularity [2,5,11–13]. The overall composition of the disc is consistent across mammalian species; however, regional variations in the biochemical and biomechanical properties of the disc are present and are thought to relate to the functional needs of the specific species [7]. Across species, the fibre organization of the disc is largely consistent, with the central region having a rostrocaudal (RC) alignment while the periphery has a circumferential (ring-like) alignment. The orientation of collagen imparts a greater effect on the tensile strength than the total collagen content and is demonstrated by the central region's superior tensile strength when tested rostrocaudally compared to mediolaterally [7,10,14–16]. Robust descriptions related to the functional capacity of the TMJ disc in the face of pathological changes are lacking in non-domestic carnivore species, especially as it relates to changes in the disc's key load distribution function.

Degenerative changes in the TMJ (TMJ DJD) have been described in several species including in carnivores [2,17–19]. In fact, studies show that up to 50% of domestic dogs have demonstrable degenerative changes of the TMJ when examining the articulating surface and the disc [2,20]. In a comparison study, variations in the incidence of TMJ

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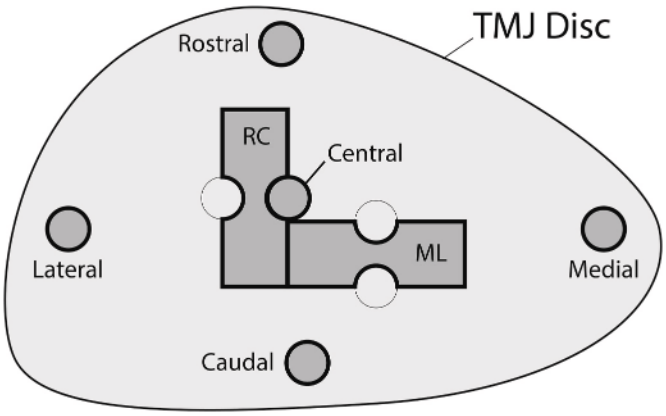

Fig. 1. Right temporomandibular joint disc, schematic for biochemical and tensile testing segments. Biochemical specimens obtained in five individual disc regions: caudal, rostral, lateral, medial and central. Tensile testing was performed on two specimens in the central region in two directional axes: mediolateral (ML) and rostrocaudal (RC). Same samples were obtained from the left disc.

degeneration in other carnivore species are apparent. The California bobcat (*Lynx rufus*) had an incidence of bony changes consistent with TMJ DJD of 0%, whereas the California sea lion (*Zalophus californianus*) demonstrated an incidence of up to 85% [18].

The TMJ and disc of the lion (*Panthera leo*) in health or disease have not been previously described and characterized; specifically, degenerative changes in the TMJ have not been reported in this species. The present study is aimed at a comparative characterization of the TMJ and its disc in a lioness through biomechanical, biochemical and histological analysis.

2. Materials and methods

2.1. Specimen procurement

TMJs were procured from a 22-year-old female spayed African lioness that was euthanized for reasons unrelated to this study. On entering the joint capsule, each TMJ disc was dissected from the bony joint components (condylar process, temporal bone) using a scalpel and periosteal elevator and processed for characterization. Periodic irrigation with phosphate buffered saline (PBS) prevented the disc specimen from dehydration. The discs were wrapped in gauze soaked with PBS-containing protease inhibitors, 10 mmol/L N-ethylmaleimide and 1 mmol/L phenylmethylsufonyl fluoride (Sigma Aldrich, www.sigmaaldrich.com), and frozen at 20 °C until processing and analysis could be completed [21]. Each disc (left and right) was then thawed and processed for histology, biochemistry and mechanical characterization. Biochemical samples were collected from the following regions: caudal, rostral, medial, lateral and central (Fig. 1).

2.2. Histology

Due to a grossly observed partial defect in the left disc, the histological samples were obtained from two regions of the left disc. One

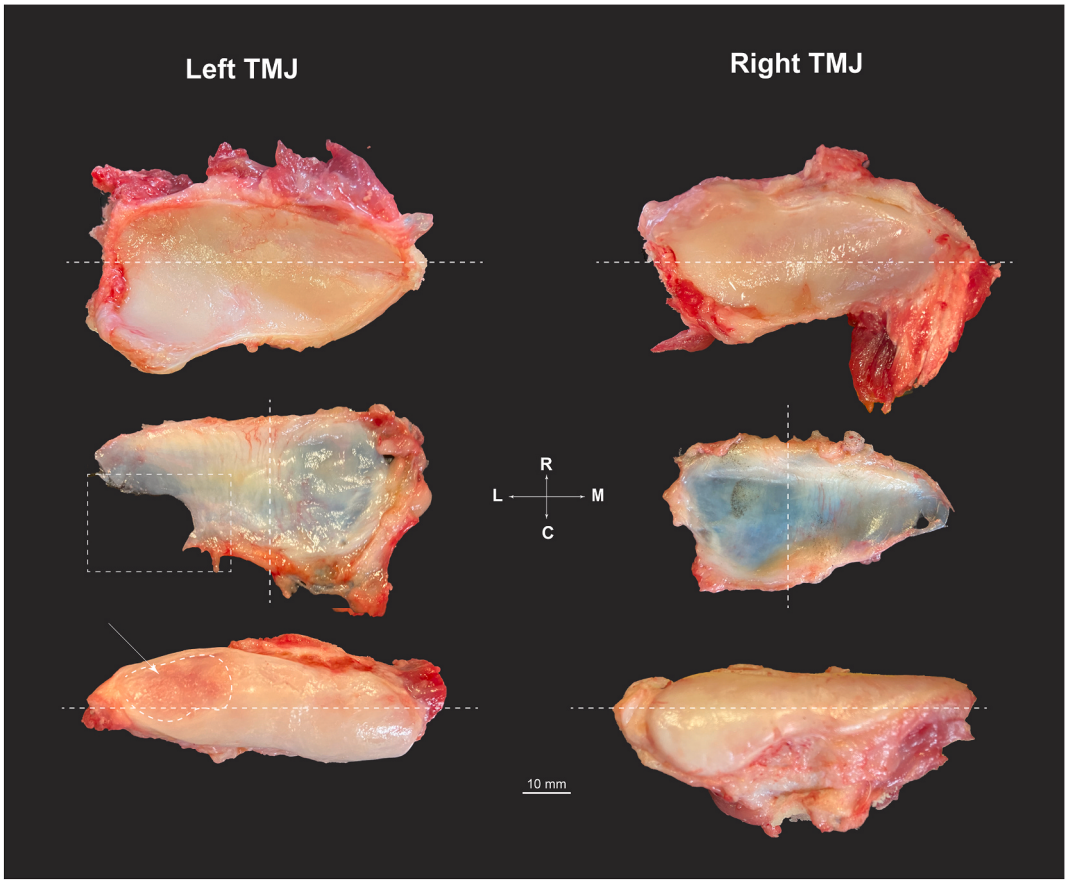

Fig. 2. Right and left temporomandibular joint (TMJ) components (top row: fossa; middle row: disc; bottom row: mandibular head). Note the relatively smooth coverage of the articulating surfaces of the fossa and the mandibular head by fibrocartilage on the right side. Note the severe erosion of the articular surface on the lateral aspect of the left mandibular head. The left TMJ disc is partially missing on the lateral aspect, with the smooth outline of the remaining disc with slightly tattered edges posteriorly. R, rostral; C, caudal; L, lateral; M, medial. Dashed lines and dashed rectangle represent sections that were examined histologically.

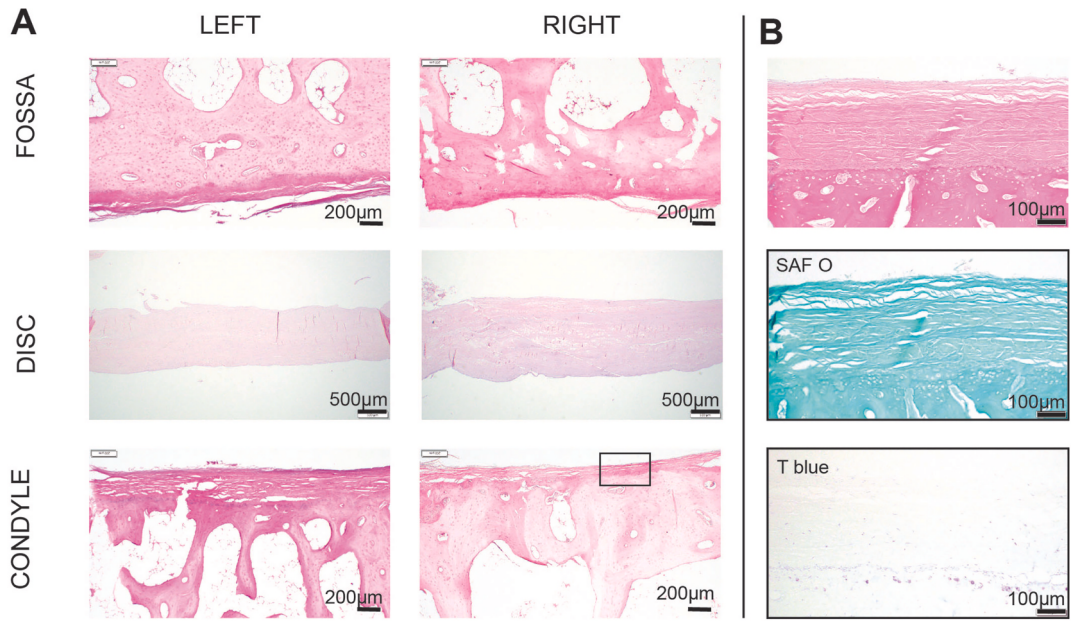

Fig. 3. Histological sections, right and left temporomandibular joint components. (**A**) Low magnification of the right and left fossa, mandibular heads, and discs. Note the uniform eosinophilic staining of the articulating surfaces, indicative of low glycosaminoglycan content. Disc fibres are tightly packed and arranged parallel to each other in the rostrocaudal orientation. HE. Bar, 200 μm. (**B**) Higher magnification of area enclosed in black rectangle in **A** (right condylar head articular surface) stained with HE, Safranin O and Toluidine blue stains. These three images of the same anatomical location highlight the low GAG content and indicate the fibrous nature of the articular surfaces lining the condylar head. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

section was acquired in a craniocaudal direction and one in the horizontal plain (parallel to the disc plain) to encompass the defect. One craniocaudal section was obtained from the right disc (Fig. 2). The temporomandibular fossae and mandibular heads were fixed in 10% buffered formalin-saline for 48 h and then underwent decalcification using 10% formic acid until they could be sectioned in a lateromedial direction prior to processing through graded alcohols and embedding in paraffin wax. Sections (5 μm) from formalin-fixed, paraffin wax-embedded tissues were stained with haematoxylin and eosin (HE) and assessed histologically. In addition, 5 μm sections were stained with Safranin O with fast green counterstain and Toluidine blue to highlight glucosamine matrix, as per standard procedures.

2.3. Biochemistry

Samples from five regions of the TMJ disc were obtained from each specimen and analysed for biochemical content (Fig. 1). Samples were weighed before and after 48 h lyophilization, and digested in 125 μg/ml papain (Sigma Aldrich) in 100 nM phosphate buffer (pH 6.5) containing 5 mM N-acetyl cysteine (Sigma Aldrich) and 5 mM EDTA for 18 h at 60°C. After digestion, no residual tissue remained. GAG content was quantified with Blyscan Glycosaminoglycan Assay (Bicolor, www.bicolor.co.uk), based on 1,9-dimethylmethyl blue binding, according to the manufacturer's instructions. Total collagen was quantified after hydrolyzing samples with 2 N NaOH for 20 min at 110°C using a chloramine-T hydroxyproline assay with Sircol collagen standards (Bicolor). Cellularity was quantified using Quant-iT PicroGreen dsDNA Assay Kit (Invitrogen, www.thermofisher.com) following the manufacturer's instructions. The GAG, collagen and cellularity analyses were performed in triplicate.

2.4. Mechanical testing

Tensile testing was performed on the discs' central region in two directions, RC and mediolateral (ML), using a single specimen cut from each region (Fig. 1). Specimens were stamp-cut using parallel razor blades with an 8 mm separation and 25 mm in length. A 3 mm diameter biopsy punch was used to cut two circular notches at mid-length to create the necked region of a nominal 4 mm width. Specimens were photographed in two perpendicular views with a calibration ruler in the field of view to allow for length and width measurements to be made using Fiji software (https://imagej.net) [22]. Tensile testing was conducted using an Instron 5965 (Instron, www.instron.com). Specimens were tested according to the ASTM D638 standard test method in pneumatic grips with a 400-grit sandpaper surface. The exact gauge length, nominally 4 mm, was captured as the initial grip-to-grip separation for each sample. Samples were elongated at a rate of 1% strain per second. The load, elongation and specimen geometry data was loaded into a custom software program (Matlab R2024; MathWorks, www.mathworks.com) to generate stress-strain plots. The linear region of the curve between 25% and 75% maximum stress was used to calculate the elastic stiffness (Young's modulus [E]) and ultimate tensile strength (UTS) was captured.

3. Results

3.1. Gross morphology and histology

The right TMJ morphology was within normal limits with no evidence of cartilage defects on either the mandibular head or the mandibular fossa. The disc was roughly triangular and intact. The left TMJ articulating surface of the mandibular fossa was within normal limits and had continuous and even cartilage coverage. However, the lateral aspect of the left mandibular head had a focally extensive cartilage irregularity spanning approximately 20 mm × 10 mm of the lateral aspect. The corresponding area to this cartilage defect in the left lateral area of the TMJ disc segment was missing, outlined by tattered disc edges. The morphology of the remaining disc was smooth with no additional defects (Fig. 2). Histologically, the tissues covering the articulating surfaces of the left and right TMJs were fibrocartilaginous, composed of compact collagen fibres facing the joint space subtended by a thin layer of hyaline cartilage transitioning into mineralized cartilage

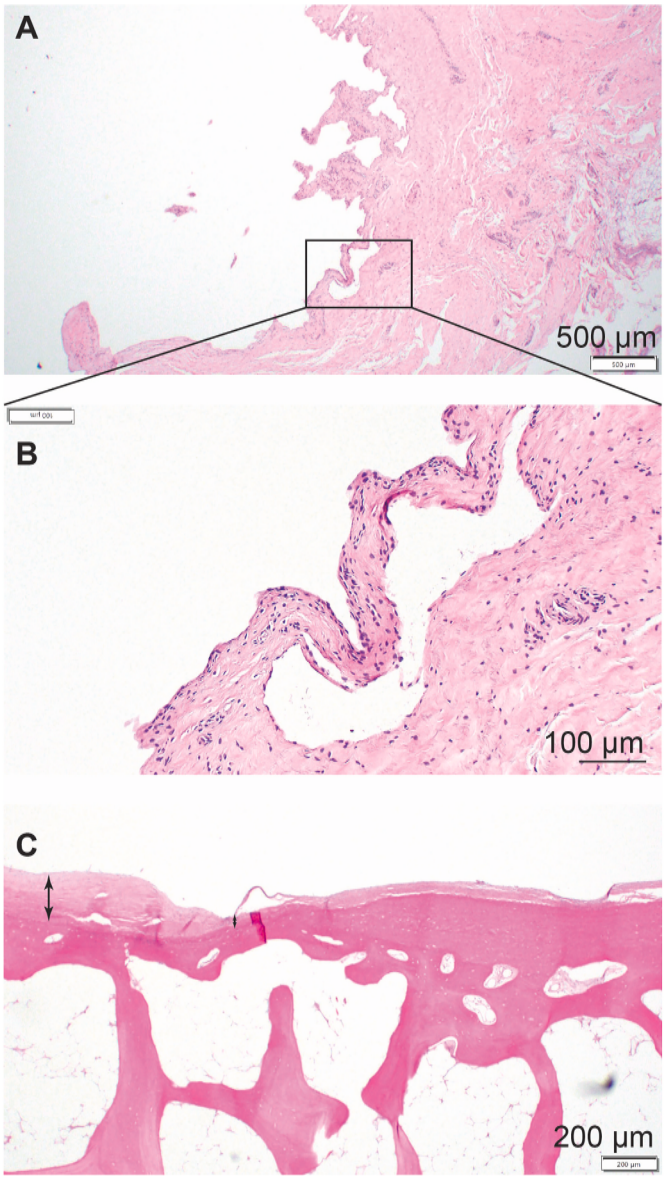

Fig. 4. Damaged left temporomandibular joint disc. (**A**) Lower magnification of disc defect is shown. Note tattered fibres and irregular outline of defect. HE. Bar, 500 µm. (**B**) Higher magnification of area enclosed in black rectangle in **A**. Note disjoined disc fibres are lined by mixture of spindle and round cells resembling synoviocyte types B and A, respectively (synoviocyte-like cells). HE. Bar, 100 µm. (**C**) Higher magnification of left condyle where lateral aspect contains an eroded cartilage area. Note thinning (erosion) of cartilage of thin area compared with thickness of intact adjacent cartilage (double-head arrows). HE. Bar, 200 µm.

followed by subchondral bone (Fig. 3A and B). The GAG content in the extracellular matrix of the hyaline cartilage was low based on the pale basophilic staining with HE (Fig. 3B). Histologically, the defective left TMJ disc had an increased number of vascular channels and synoviocyte-like cells lining the frayed disc fibres (Fig. 4A and B). Synoviocyte-like cells are comprised of spindle cells with a small amount of cytoplasm and fusiform nuclei admixed with round cells with indistinct cytoplasmic borders and round nuclei with condensed chromatin. A similar cell population is observed in non-reactive synovium, where cells are classified as type A and type B synoviocytes. However, without definitive immunohistochemical markers, this classification is suggestive only. Therefore, we cautiously use the term synoviocyte-like cells. The lateral aspect of the left mandibular head where the cartilage defect was observed grossly corresponded to an area of cartilage thinning (erosion) (Fig. 4C). No inflammatory cell infiltration was observed in any of the examined sections of the disc, fossa or condyles.

3.2. *Mechanical properties*

The mechanical properties were characterized under tension in the disc's central region in two directions (RC and ML). The tensile stiffness, characterized by Young's modulus, was greatest in the left disc in both the RC (9.0 MPa) and ML (31.2 MPa) axes compared to the RC (8.3 MPa) and ML (6.5 MPa) axes of the right disc (Fig. 5A). The UTS demonstrated disc variation with the greatest strength being the left disc in the ML axis (13.9 MPa) and the weakest being the right disc in the ML axis (2.4 MPa) (Fig. 5B). The UTS in the RC axis showed less variation, with the left disc demonstrating a UTS of 8.1 MPa and the right demonstrating a UTS of 9.7 MPa.

3.3. *Biochemical content*

The biochemical content of both discs was evaluated in five regions for water content, cellularity, GAG content and collagen (Table 1). Water content of the disc demonstrated a non-regional-dependent variation with an overall range of 69.5–81.0%. Cellularity, as measured by DNA content, varied between regions and discs, but demonstrated a low cellularity with DNA content between 0.042% and 0.26% by dry weight (DW). The mean cellularity was lowest in the right disc (0.11%) compared to the left disc (0.14%) on a DW basis. The GAG content by DW demonstrated mild variation between region and disc and represented a small proportion of the DW, ranging between 1.13% and 5.57%. The left disc had a lower average GAG content of 2.11% compared to 2.92% in the right disc. The left disc demonstrated a higher percentage collagen content on average compared to the right disc; 91.1% and 85.8%, respectively.

4. Discussion

To the authors' knowledge, this study is the first to characterize the histological, biomechanical and biochemical properties of the TMJ of a lion. Our findings demonstrate several clinically relevant features of the lioness TMJ in health and disease. First, we demonstrated that the general features of the TMJ in this species are similar to those of other carnivores. Second, DJD occurs spontaneously in this species with gross and histological features similar to other carnivore species. In addition, with the limitation of a single animal, we noted substantial differences in the tensile stiffness and strength between the affected and unaffected TMJ discs. Lastly, the biochemical composition of both discs was consistent with previous reports in carnivores.

This study demonstrated several features of the lioness TMJ that are shared with other species. Like other mammals, the articulating surfaces are covered with fibrocartilage as opposed to the hyaline cartilage present in other synovial joints [5,14,23]. The hyaline component is reduced to a single layer of cells supported by GAG-poor extracellular matrix (Fig. 3A). This structural difference is typically reflective of the type of force the TMJ experiences, as the joint is mainly subjected to load bearing and tension during high-stress, multidirectional forces during mastication rather than the mostly compressive weight-bearing forces experienced by appendicular joints [24,25]. The features of the disc fibres were also consistent with the findings in other carnivores. The fibres were oriented parallel to each other in the RC direction, which is thought to contribute to the direction-dependent mechanical properties of the disc in other carnivores [2,15].

This report also describes spontaneous DJD in a lioness as demonstrated by the presence of several features characteristic of degenerative changes in the left TMJ. A focally extensive cartilage irregularity was present, with histological evidence of erosion and a distinct gross defect observed in the affected disc, which corresponded to a visible loss of disc

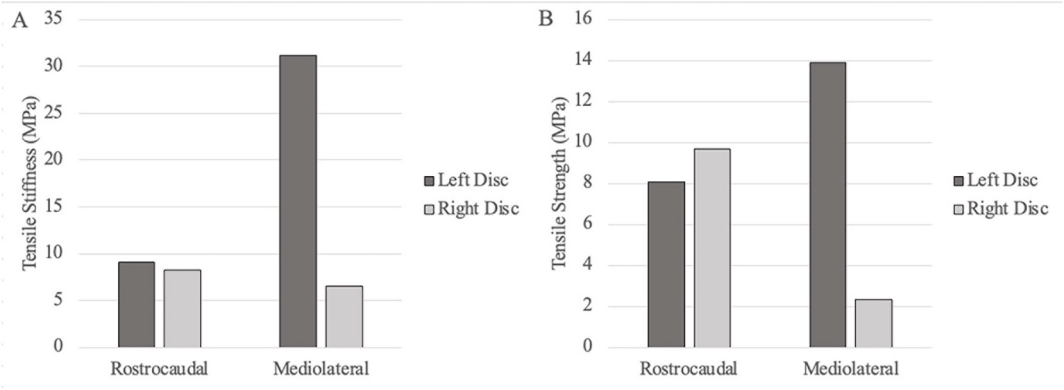

Fig. 5. Temporomandibular joint disc, tensile properties. The disc was mechanically tested in tension with segments in both rostrocaudal and mediolateral orientations of the disc (see Fig. 1). The left disc demonstrated largest tensile stiffness (**A**) and strength (**B**) overall in the mediolateral direction.

Table 1
Biochemical properties of the temporomandibular joint disc. The DNA, glycosaminoglycan (GAG) and collagen are reported on a per dry weight basis.

	Disc region	% Water	% DNA	% GAG	% Collagen
Left disc	Central	70.62	0.057 (± 0.0012)	1.89 (± 0.0030)	96.18 (± 0.85)
	Rostral	80.78	0.17 (± 0.0076)	1.96 (± 0.0077)	75.17 (± 1.7)
	Caudal	76.48	0.12 (± 0.0062)	1.15 (± 0.0042)	124.46 (± 2.5)
	Lateral	68.55	0.069 (± 0.0038)	2.52 (± 0.0015)	84.92 (± 2.4)
	Medial	81.01	0.26 (± 0.012)	3.05 (± 0.0051)	74.88 (± 1.9)
Right disc	Central	77.29	0.062 (± 0.0023)	3.34 (± 0.0024)	106.47 (± 3.7)
	Rostral	78.26	0.092 (± 0.0023)	2.0 (± 0.0054)	68.94 (± 3.6)
	Caudal	79.53	0.042 (± 0.0026)	5.57 (± 0.013)	86.9 (± 2.4)
	Lateral	69.48	0.2 (± 0.0081)	1.13 (± 0.0051)	66.47 (± 2.8)
	Medial	79.35	0.17 (± 0.0059)	2.55 (± 0.0027)	100 (± 5.9)
		Average % water	**Average % DNA**	**Average % GAG**	**Average % collogen**
Left disc		75.49	0.14	2.11	91.122
Right disc		76.78	0.11	2.92	85.756

material in that region. The presence of increased numbers of vascular channels and synoviocyte-like cells lining the frayed disc fibres support previously reported changes in chronic degenerative remodelling of the TMJ disc [26–28]. The increase in vascularization without associated inflammation is most consistent with the reparative fibrovascular remodelling commonly associated with chronic mechanical stress and degeneration in fibrocartilaginous tissue [29]. Spontaneous DJD of the TMJ has also been documented in other carnivores, such as the domestic dog (*Canis lupus familiaris*), the grey wolf (*Canis lupus*) and the Siberian (*Panthera tigris altaica*) and Bengal (*Panthera tigris tigris*) tiger, and with similar features [2,15,19,20]. A comparison of the spontaneous occurrences in wild and domestic carnivores is an essential step toward understanding the clinical relevance of TMJ disease in those species. The patterns of disc degeneration were consistent with other carnivore species, although the more severe bony changes that have been reported were not appreciated in this study [2,9,15,19]. The loss of disc material that was identified has been demonstrated in other animal species as well as in humans [2,30,31]. The significance of this finding remains unclear as it relates to dysfunction of the joint and manifestation of pain [23,31]. In addition, the relationship between the changes associated with DJD and pain is difficult to assess in wildlife as exhibition and documentation of subtle behavioural signs of pain are often not observed easily [32].

Assessment of the discs mechanical strength and stiffness revealed several noteworthy characteristics. Direction-dependent mechanical properties (anisotropy) are commonly observed in other carnivore species [2,6,15,19]. In the present study, this anisotropy was appreciated in the healthy disc demonstrating superior strength when tested in the RC direction. In other reports, loss of anisotropic behaviours with degenerative changes can be observed, representing changes to the organization in the fibre structure of the disc [15]. Severe degenerative changes reported in the Siberian tiger resulted in decreased strength and stiffness in the RC direction of >70% when compared with a healthy disc of a Bengal tiger [15]. This pattern was not appreciated to the same extent here as the difference in strength and stiffness was 18%; however, there was a substantial increase in these values in the ML direction. This shift may suggest an altered collagen fibre organization or increased fibrous tissues deposition in response to a chronic increase in mechanical loading.

Examination of both discs biochemically demonstrated a comparable pattern to that of previously reported values in other species, with collagen making up a substantial portion of the disc. Collagen constituted 91% of the left disc and 85% of the right disc, a result that is slightly higher than the 80% typically reported in other species [2,9,33]. The average GAG content was 2.11% in the left disc and 2.92% in the right disc, which is similar to values demonstrated in canids [2]. While only a single comparison, higher average collagen and lower GAG content in the left disc are again consistent with a pattern of degenerative remodelling and may reflect the myxoid degeneration and early fibrous tissue deposition observed in DJD [33]. How these values relate to the compressive properties of the disc remain unclear and further investigation is warranted [34,35].

5. Conclusion

This present study provides the first gross, histological, biomechanical and biochemical characterization of the TMJ in the lion. We demonstrated several important features such as similarities of the joint to other carnivore species in health and disease. Additionally, considerable changes to the biomechanical strength and stiffness were noted in the diseased disc. Finally, this study indicated that the biochemical composition remains similar in both the diseased and healthy disc as well as being consistent with other carnivore species. Collectively, although studied on a single lioness, these findings provide a comprehensive evaluation of the TMJ of the lion in health and disease and further develop the knowledge of TMJ DJD in carnivore species.

Statement of author contributions

Nicole Cox: Study methodology; Analysis; Visualization; Writing of manuscript. **Natalia Vapniarsky:** Study concept and design; Obtaining study material; Funding; Analysis; Writing of manuscript; Supervision. **Iris Rivas:** Study methodology and analysis; Review of manuscript for important intellectual input. **Tanya Garcia:** Study methodology; Analysis; Data curation; Review of manuscript for important intellectual input. **Boaz Arzi:** Study concept and design; Obtaining study material; Funding; Review of manuscript for important intellectual input; Supervision.

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Declaration of competing interest

The authors declared no conflicts of interest in relation to the research, authorship and publication of this article.

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