Characterization of the temporomandibular joint of the harbour porpoise (Phocoena phocoena) and Risso’s dolphin (Grampus griseus)

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A R T I C L E   I N F O

Article history:
Accepted 2 January 2015

Keywords:
Temporomandibular joint
Temporomandibular disc
Cetacea
Odontocete
Harbour porpoise
Risso’s dolphin

A B S T R A C T

Objectives: The temporomandibular joint (TMJ) in cetaceans is largely uncharacterized. This study aims to describe the macroscopic, microscopic, biochemical and biomechanical features of the TMJ of two species of the suborder Odontoceti: the harbour porpoise (Phocoena phocoena) and Risso’s dolphin (Grampus griseus). Furthermore, we aim to elucidate the structure–function relationship of their TMJs and their possible role in echolocation.

Design: The TMJs from fresh cadaver heads of harbour porpoise (n = 4) and Risso’s dolphin (n = 2) acquired from stranding were examined. Following macroscopic evaluation, the TMJs were investigated for their histological, mechanical and biochemical properties.

Results: The TMJs of the studied odontocetes were found to be fundamentally different from other mammals. Macroscopically, the TMJ lacks the typical joint cavity found in most mammals and is essentially a syndesmosis. Histological and microstructural analysis revealed that the TMJ discs were composed of haphazardly intersecting fibrous-connective tissue bundles separated by adipose tissue globules and various calibre blood vessels and nerve fibres. The collagen fibre composition was primarily collagen type I with lesser amounts of collagen type II. Sulphated glycosaminoglycan (sGAG) content was lower compared to other studied mammals. Finally, mechanical testing demonstrated the disc was stronger and stiffer in the dorsoventral direction than in the mediolateral direction.

Conclusion: The spatial position of the TMJ, the absence of an articulating synovial joint, and the properties of the TMJ discs all reflect the unique suction-feeding mechanism adopted by the harbour porpoise and Risso’s dolphin for underwater foraging. In addition, the presence of unique adipose globules, blood vessels and nerves throughout the discs may indicate a

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http://dx.doi.org/10.1016/j.archoralbio.2015.01.005
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functional need beyond food apprehension. Instead, the disc may play a role in neurological sensory functions such as echolocation.

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1. Introduction

The typical mammalian temporomandibular joint (TMJ) is a bilateral, diarthrodial synovial joint with an important role in mastication and communication.\(^1,2\) While its anatomy is variable in mammals, it shares a close relationship among cranial morphology, masticatory patterns and dietary requirements.\(^1,3–5\)

In Odontoceti, a suborder of Cetacea that is comprised of toothed whales, dolphins and porpoises, the TMJ and its associated structures are largely uncharacterized. In fact, more than two centuries have passed since John Hunter first described the articulation in balaenopterids, a family in the suborder Mysticeti.\(^5\) Since then, only a few anecdotal investigations have reported on the TMJ, all with a focus on baleen whales. Together, these reports found that in contrast to terrestrial mammals the TMJ articulation in studied cetaceans is non-synovial, lacks a joint capsule and is composed of a thick, fibrous, oily tissue spanning from the mandibular head of the condylar process to the mandibular fossa of the squamous bone.\(^7\) The bowhead whale (Balaena mysticetus), by exception, is reported to have a synovial articulation.\(^14,15\) A non-synovial morphology was found in two odontocetes: the bottlenose dolphin (Tursiops truncatus) and the Pacific white-sided dolphin (Lagenorhynchus acutus) with the distinguishing presence of a dense fibrous capsule surrounding the joint.\(^7\) Apart from this short description in a more than century-old report, however, the articulation in other species of Odontoceti has not been described. Furthermore, a robust biochemical, histological and mechanical analysis of the joint in any cetacean has not been previously reported.

One of the most specialized and sophisticated land-to-water adaptations adopted by species in both Odontoceti and Mysticeti is the ability to perceive sounds underwater. Odontocetes sense their environment and forage for food using echolocation: the production of sound pulses and the subsequent information processing from the reverberations of the sound waves off of objects.\(^16,17\) Echo conduction and reception pathways have been studied extensively in the last 60 years. While novel theories on auditory reception and processing have been proposed,\(^18\) the predominating model is Norris’s “jaw hearing” hypothesis, supported by a number of experimental studies.\(^19,20\) In this model, sound waves returning from objects travel through low-impedance acoustic mandibular fat bodies before being sent to the tympanoperiosteal complex for auditory processing.\(^21,22,23\) In addition, odontocetes have developed specialized systems for acoustic isolation during diving including an accessory sinus system.\(^22,23–25\) Despite the body of knowledge on sound reception in odontocetes, the TMJ has never been implicated as a participant in echolocation. Based on its close proximity to both the tympanoperiosteal complex and the mandibular fat body, and its association with the middle sinus of the pterygoid air sinus,\(^26\) we hypothesize that the TMJ may have a neurological function that contributes to sensory physiology of odontocetes.

This study aims to describe the macroscopic, microscopic, biochemical and biomechanical features of the TMJ of two species of Odontoceti: the harbour porpoise (Phocoena phocoena) and Risso’s dolphin (Grampus griseus). Furthermore, we aim to elucidate the structure-function relationship of their TMJ and its possible role in echolocation.

2. Materials and methods

2.1. Specimens

The TMJs of four stranded harbour porpoises and two stranded Risso’s dolphins were obtained with the approval of the United States Department of Commerce, National Oceanic and Atmospheric, National Marine Fisheries Services (Administrative File: 151408SWR2013PR000037). The freshly stranded specimens were collected by The Marine Mammal Center, Sausalito, California, and were stored at \(-20\,^\circ\mathrm{C}\) for 1–5 months prior to dissection. Each head was labelled with catalogue number, sex, age and collection date. The specimens were skeletally mature adults with fully erupted adult dentition. Prior to dissection, the heads were thawed at \(-20\,^\circ\mathrm{C}\) for 18–24 h. Remaining specimens are currently being stored at \(-20\,^\circ\mathrm{C}\) at the University of California, Davis.

2.2. Gross evaluation

Gross evaluation and description of the anatomical features were performed and aided by the use of computed tomographic (CT) images of the skulls of Risso’s dolphin and harbour porpoise. Transverse collimated images were obtained at a slice thickness of 0.6 mm. Evaluation of osseous structures was performed with a window width of 2500 Hounsfield units and window level of 480 Hounsfield units. All CT images were processed using Invivo5 software (Anatomy, San Jose, CA) and evaluated on a medical-grade flat-screen monitor. Three-dimensional reconstructive images were generated to assess the spatial relationship of the bones of the TMJ.

2.3. Microscopic evaluation

Tissue samples were obtained from the bones of the TMJ and the discs. Whole joints, which included the mandibular head
of the condylar process, the disc and the squamosal,\textsuperscript{32} were obtained from one harbour porpoise and one Risso's dolphin. Half of the disc samples were randomly selected, fixed in formalin and paraffin-embedded. Bony samples underwent decalcification in 15% formic acid prior to routine tissue processing. Five-micron sections from formalin-fixed paraffin-embedded tissues were stained with haematoxylin and eosin (HE) and assessed histologically by a veterinary pathologist (NVA). Special stainings were performed according to standard protocols and consisted of picrosirius red for collagen content and organization, safranin-O and alcin blue for glycosaminoglycan content and Bielschowsky silver for nerve fibres.\textsuperscript{33} Additional samples were formalin-fixed, frozen and sectioned at four microns for oil Red O staining for lipoproteins.

2.4. Immunohistochemistry evaluation

Immunohistochemistry for CD31, factor VIII and neurofilament 200 was performed on five micron thick, formalin-fixed, paraffin-embedded tissue sections, mounted on charged slides and air-dried overnight at 37 °C.\textsuperscript{34–36} Sections were deparaffinized, treated with 0.3% hydrogen peroxide in 100% methanol and then rehydrated. Heat-induced antigen retrieval was performed for mouse anti-CD31 (Dako, Carpinteria, CA) and mouse anti-neurofilament 200 (Leica Biosystems, Buffalo Grove, IL) labelling, whereas proteinase K digestion (Dako) was performed for mouse anti-factor VIII (Dako) labelling. Following antigen retrieval, the slides were blocked in 10% normal horse serum then incubated with primary antibody for 1 h prior to being treated with detection antibody (Biocare Medical, Concord, CA). Labelled slides were then incubated with streptavidin-HRP (Biocare Medical) for 20 min. Slides were developed using Vector NovaRed Chromogen (Vector Labs, Burlingame, CA) and counterstained with haematoxylin.

Immunohistochemistry for collagens type I and type II was performed on frozen sections as previously described.\textsuperscript{37} Briefly, the sections were fixed in chilled acetone and then submerged in 3% H\textsubscript{2}O\textsubscript{2} to block endogenous peroxidase. Samples were subsequently blocked with horse or goat serum (Vectastain ABC Kit, Vector Labs) and incubated with either mouse anti-collagen type I (Fitzgerald Industries International, Acton, MA) or rabbit anti-collagen type II (Cedar Lane Labs, Burlington, NC) antibodies. Secondary antibodies, Vectastain ABC and DAB solutions were applied as instructed by the Vectastain ABC Kit (Vector Labs). The slides were counterstained with haematoxylin.

2.5. Immunofluorescence evaluation

Disc samples were immersed in optimal cutting temperature compound (OCT) and frozen before being sectioned into 10-micron cryosections and stored at −80 °C. Before IF, sections were fixed in 4% paraformaldehyde and subsequently blocked in a 5% normal goat serum in PBS containing 0.2% Triton-X-100. Samples were incubated at 4 °C overnight with rabbit anti-beta III tubulin (Covance Inc.) and mouse anti-NF200 (Leica Biosystems) primary antibodies, followed by corresponding fluorescent conjugated secondary antibodies at room temperature for 1 h before being mounted using Vectashield HardSet mounting medium (Vector Labs, Burlingame, CA) and visualized utilizing an EVOS fluorescent microscope (Life Technologies).\textsuperscript{38}

2.6. Scanning electron microscopy

Fresh samples were fixed in 3% glutaraldehyde for 48 h at 4 °C and then dehydrated in ascending series of ethanol. Samples were subsequently critical point-dried and sputter-coated with gold prior to imaging on a Phenom Pro Desktop SEM (PhenomWorld, Eindhoven, the Netherlands). Quantification of collagen fibre and bundle diameter was performed using ImageJ image analysis software (National Institutes of Health, Bethesda, MD).

2.7. Biochemical characterization

Tissue samples for biochemical tissue evaluation were collected from each specimen in the central region of the TMJ disc.\textsuperscript{39} Tissue samples were massed prior to and following 48 h lyophilization. Samples were then digested in 125 μg/mL papain (Sigma, St. Louis, MO) in phosphate buffer (pH 6.5) containing 2 mM N-acetyl cysteine (Sigma) and 2 mM ethylenediaminetetraacetic acid for 18 h at 60 °C. Glycosaminoglycan content was quantified by Blyscan GAG assay (Biocolor, Westbury, NY), based on 1,9-dimethylmethanol blue binding. 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\textsuperscript{TM} collagen standards (Biocolor).

2.8. Mechanical characterization

Tensile testing was conducted using an Instron 5565 (Instron, Norwood, MA) test equipment designed to evaluate mechanical properties of materials and tissues.\textsuperscript{39} Following American Standardized Testing Materials (ASTM) Standard D3939, rectangular samples of the soft-tissue disc were collected in the dorsoventral and mediolateral directions. Samples were approximately 9–11 mm in length, 2.8 ± 0.6 mm in width and 2.3 ± 0.7 mm in thickness. Samples were placed between two grips and elongated at a rate of 1% of the length between the two grips per second. The length between the two grips was 3.0 ± 2.4 mm. The cross-sectional area of the samples was measured using ImageJ (NIH). Stress-strain curves were developed from the load–displacement curve. Young's modulus (E\textsubscript{v}, tensile stiffness) and ultimate tensile strength (UTS) were quantified.

3. Results

3.1. Gross evaluation

The bony structures of the TMJs of the Risso’s dolphin and harbour porpoise are illustrated in Fig. 1. Gross and CT evaluation indicated that in contrast to terrestrial mammals, the mandibular rami extended caudally and ventrally so that the condylar process was positioned ventral to the occlusal plane (Fig. 2). Upon dissection, a dense, fibrous capsule
enveloped the joint in both the harbour porpoise and the Risso’s dolphin. When the capsule was removed, neither fluid nor cavities (i.e., compartments) were observed near the condylar process of the mandible, the disc or the mandibular fossa of the squamosal. This morphology is in line with other cetaceans, except the bowhead whale, but differs from most other mammals that contain both dorsal and ventral cavities filled with synovial fluid. Instead, the space was filled with a fibrous, pink-coloured, disc-shaped tissue as depicted in Fig. 3. The disc adhered tightly to both articular surfaces and was not easily separated. Once exposed, the condylar processes exhibited a fusiform-shaped rough surface. A similar rough facet was noted when the disc was removed from the mandibular fossa of the temporal bone. The longest extensions of the fusiform-shaped articular facets were oriented in a ventrolateral to dorsomedial direction, while the flattened articular facets were oriented in a nearly transverse plane (Fig. 2).

The disc itself displayed even thickness in both species. For the Risso’s dolphin, disc dimensions were 54.9 ± 2.4 mm in the dorsoventral direction and 36.2 ± 1.0 mm in the mediolateral direction. The harbour porpoise disc was smaller measuring 22.4 ± 0.4 mm in the dorsoventral direction and 13.8 ± 0.8 mm in the mediolateral direction (Fig. 3).

3.2. Histology and immunohistochemistry evaluation

As was observed grossly, there was no histological evidence of joint compartments or synovial lining on the condylar process of the mandible, the squamosal or surrounding the disc itself. Instead, the bony portions of the joint transitioned directly into the fibrous discs. The central portion of the discs was composed of haphazardly intersecting fibrous connective tissue bundles separated by adipose tissue globules and various calibre blood vessels and nerve fibres (Figs. 4–7). The fibrous bundles averaged 9.61 ± 4.37 μM in diameter, while individual fibres averaged 0.23 ± 0.06 μM in diameter. In the dorsal and ventral portions of the discs transitioning into the bone, the collagen fibres were densely packed, oriented primarily dorsoventrally with no evidence of adipose tissue amongst the fibres. Immunohistochemical analysis revealed that the collagen fibre composition was primarily collagen type I with small amounts of collagen type II (Fig. 4). Oil red O staining highlighted the adipose globules amidst the collagen fibres. Small amounts of sulphated glycosaminoglycans (sGAG) were evident via alcian blue staining around the blood vessels and nerves (Figs. 4 and 5). Immunohistochemistry for CD31 and factor VIII antigens confirmed the presence of endothelium-lined blood vessels (Figs. 6 and 7). The blood vessels varied in calibre from medium-sized arteries and veins to small calibre capillaries, distributed randomly throughout the disc, including in the collagen dense areas. The presence of nerve fibres was confirmed via immunohistochemistry and immunofluorescence for neurofilament 200 and beta-III tubulin antigens (Fig. 7).

3.3. Biochemical content

Biochemical content of the discs is reported in Fig. 8. Hydration of the discs ranged between 58 and 78% dry weight and averaged 77.3 ± 1.28% per dry weight for the Risso’s dolphin and 70.15 ± 10.23% per dry weight for the harbour porpoise. Sulphated GAG content averaged 0.62 ± 0.3% per dry weight for all discs. Collagen content in the discs ranged from 64 to 89% per dry weight and averaged 80.75 ± 2.67% per dry weight for the Risso’s dolphin and 76.14 ± 10.96% per dry weight for the harbour porpoise.

3.4. Mechanical characterization

Tensile properties of the TMJ discs were evaluated in the Risso’s dolphin and harbour porpoise. Tensile stiffness is reflected in Fig. 9 for each population in the dorsoventral and mediolateral directions. Young’s modulus for the Risso’s dolphin and harbour porpoise averaged 6.58 ± 6.6 and 1.01 ± 0.83 MPa in the mediolateral direction, respectively, and 8.95 ± 6.78 and 2.71 ± 3.03 MPa in the dorsoventral direction, respectively. The tensile strength of each species
Lateral view (left), ventral view (right). The condylar process of the mandible (blue arrows) is positioned ventral to the occlusal plane (indicated by the green, dotted line). Note the orientation of the articular facets in a transversal plane (indicated by the blue dotted line). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

in the two directions is reflected in Fig. 9. Ultimate tensile strength for the Risso’s dolphin and harbour porpoise averaged 2.82 ± 1.99 and 0.72 ± 0.56 MPa in the mediolateral direction, respectively, and 3.57 ± 4.10 and 1.25 ± 0.96 MPa in the dorsoventral direction, respectively.

4. Discussion

This first comprehensive study on the TMJ of two species of Odontoceti demonstrates that the joint exhibits critical structure–function relationships likely adapted for life below water. The spatial position of the TMJ, the absence of an articulating synovial joint and the composition features of the TMJ discs all reflect the unique suction-feeding mechanism adopted by the harbour porpoise and Risso’s dolphin for underwater foraging. In addition, the presence of unique adipose globules, blood vessels and nerves throughout the discs may indicate a functional need beyond food apprehension. Instead, the disc may play a role in neurological sensory functions such as echolocation.

Grossly, the configuration of the TMJ in the studied species is fundamentally different than other mammalian TMJs. The loss of a synovial membrane and the absence of dorsal and ventral compartments suggest that the joint is a syndesmosis. Traditionally, the TMJ is load-bearing with anatomical structure–function relationships adapted for mastication and feeding. Many odontocete species, including the harbour porpoise and likely the Risso’s dolphin, however, use suction feeding—a non-masticatory method of capturing and swallowing prey, whereby negative pressures in the oral and pharyngeal cavities simultaneously draw in prey and water. In the harbour porpoise, as in several Odontoceti species, the upper and lower teeth interdigitate, but do not occlude for the purpose of mastication. Investigations on dental patterns in both raptorial and suction-feeding odontocetes have revealed dental wear on the lateral margins of the teeth likely owing to repeated tooth contact during the more common vertical movement of the jaws and especially when the jaws are closed, as well as apical wear for which less common lateral and circular jaw movements are responsible.
Furthermore, use of teeth during aggressive male–male behaviours has been attributed to dental wear.\textsuperscript{52,53} This suggests that teeth are important for food acquisition and behaviour, but have limited function in food processing, even in species that do not suction-feed.\textsuperscript{48,50,54}

A number of adaptations have occurred to account for suction-feeding method in those species that employ it including the development of a robust hyoid apparatus,\textsuperscript{55,56} reduced masticatory muscles and their bony attachments,\textsuperscript{57} a large, muscular, caudally positioned tongue,\textsuperscript{58} and a reduction or, in some species, complete loss of teeth.\textsuperscript{46,48} In fact, there is a complete absence of teeth in the upper jaw of the Risso’s dolphin.\textsuperscript{46} In addition to these adaptations, we demonstrate that the TMJ articulation in the studied odontocetes is positioned lower than the occlusal plane and may render it less functional for the purpose of bearing load during mastication. This is further supported by the presence of predominantly collagen type I, found in non-load-bearing tissues such as tendons and skin, and a minimal amount of collagen type II, traditionally found in load-bearing tissues such as hyaline cartilage.\textsuperscript{40,59} In addition, biochemical analysis of sulphated glycosaminoglycans, polysaccharides that normally provide compressive stiffness to the disc,\textsuperscript{60} showed values that were slightly lower than averages reported for other species,\textsuperscript{60,61} providing further support that the TMJ disc in these species is a non-load-bearing structure. However, the hydration and collagen content of the discs were in ranges previously reported for other mammals.\textsuperscript{51} Finally, mechanical analysis demonstrated that the discs were both stronger and stiffer in the dorsoventral direction than in the mediolateral direction, which reflects the typical vertical mandibular movement of these species and presumably allows more freedom of movement in the dorsoventral direction to accommodate size variation of prey.

The presence of adipose globules throughout the TMJ discs in the studied odontocetes has not been reported in other mammals. While the function of this adipose globules remains elusive, grossly the globules appear to be an extension of the internal mandibular fat channel in Norris’s “jaw hearing” hypothesis.\textsuperscript{24} To elucidate its function, biochemical analysis on the specific nature of these globules

Fig. 3 - Gross morphology of the TMJ of (A and C) Risso’s dolphin and (D and F) harbour porpoise show a fibrous disc located between the bony structures. No compartments were observed. The interface between the condylar process of the mandible and the squamosal in the (B) Risso’s dolphin and (E) harbour porpoise shows the transition from bone to fibrous disc (syndesmosis), and the lack of compartments (H&E 2× magnification; (E) contains a processing artefact). For orientation: CP: condylar process, D: disc, SQ: squamosal bone. (For interpretation of the references to color in text, the reader is referred to the web version of this article.)
Fig. 4 – Histological and microstructural analyses of the TMJ disc of a Risso’s dolphin. (A) Haphazardly arranged connective tissue bundles (H&E, 20× magnification) are primarily composed of (B) collagen type I fibres (IHC, 20× magnification) with lesser amounts of (C) collagen type II fibres (IHC, 20× magnification). (D) Safranin-O staining and (E) alcian blue staining revealed only small amounts of sGAG (20× magnification). (F and G) Scanning electron microscopy of the disc demonstrated haphazard fibre arrangement, as well as bundles ensheathed by connective tissue.

Fig. 5 – Histological and microstructural analysis of the TMJ disc of harbour porpoise. (A) Adipose globules (black arrows, H&E, 20× magnification) are stained with (B) oil-Red-O (20× magnification).

Fig. 6 – Blood vessels in the TMJ disc of a Risso’s dolphin. (A) Endothelial marker CD31 (IHC, 20× magnification) is shown lining a blood vessel in transverse (arrowhead) and sagittal sections (arrow). (B) Factor VIII-related antigen IHC (20× magnification) and (C) SEM confirms the presence of blood vessels (980× magnification).
must be conducted and compared to the “acoustic fat” of the mandible found in previous studies.65,66
The TMJ disc of the studied odontocetes is a vascular and innervated structure, which is uniquely distinguished from other mammalian species. Blood vessels have been reported in an Asian elephant with two possible explanations: that the large size of the disc warranted a nutrient supply above and beyond the synovial capsule67 or instead was a result of degeneration.68 In addition, blood vessels in porcine TMJ have been reported, but only on the periphery of the disc near attachment sites.69 Similarly, nerves in human and animal TMJ studies have only been reported in and around the joint capsule and periarticular tissues,66–68 although one anecdotal report found free nerve endings in the anterior and posterior bands of the disc parenchyma in human TMJ.69 On its own, the presence of nerves in the disc does not directly imply a neurological function in echolocation. However, we suggest that taken together with the presence of potential acoustic fat and blood vessels within the disc, as well as the position of the disc as an extention of the the “jaw hearing” mandible, these nerves may participate in the sound reception pathway. Interestingly, the mandibular branch of the trigeminal nerve runs through these fats and is closely associated with the joint.69 In addition, the pterygoid air sinus, one of a handful

**Fig. 7** – Nerve bundles were present throughout the discs as demonstrated by (A) Bielschowsky’s silver stain and IHC for (B) neurofilament marker NF200 (Risso’s dolphin, 20× magnification). Furthermore, (C1) immunofluorescence staining shows two nerve fibre foci (harbour porpoise, 10× magnification) containing (C2) nuclei-marker DAPI, and neuron-specific markers (C3) beta-III tubulin and (C4) NF200 (harbour porpoise, 40× magnification). (C5) shows a merged image of all three markers (40× magnification).

**Fig. 8** – Biochemical composition of the discs of the harbour porpoise and Risso’s dolphin. Hydration of the discs averaged 77.3 ± 1.28% per dry weight for the Risso’s dolphin and 70.15 ± 10.23% per dry weight for the harbour porpoise. Sulphated GAG content averaged 0.62 ± 0.3% per dry weight for all discs. Collagen content averaged 80.75 ± 2.67% per dry weight for the Risso’s dolphin and 76.14 ± 10.96% per dry weight for the harbour porpoise.
Young’s Modulus  
Ultimate Tensile Strength

Fig. 9 – Mechanical analysis demonstrates Young’s modulus for the Risso’s dolphin and harbour porpoise averaged 6.58 ± 6.6 and 1.01 ± 0.83 MPa in the mediolateral direction, respectively, and 8.95 ± 6.78 and 2.71 ± 3.03 MPa in the ventrodorsal direction, respectively. UTS for the Risso’s dolphin and harbour porpoise averaged 2.82 ± 1.99 and 0.72 ± 0.56 MPa in the mediolateral direction, respectively, and 3.57 ± 4.10 and 1.25 ± 0.96 MPa in the ventrodorsal direction, respectively.

extracranial air sinuses that help isolate sound27,30 also envelops the TMJ and the middle and inner ears.29 Additional studies to elucidate the complex anatomical relationship of these structures should also be considered.

In conclusion, the present study is the first to characterize the unique structure of the TMJ of two species of Odontoceti: the harbour porpoise and Risso’s dolphin. Our findings demonstrate interesting structure-function relationships that may have evolved in some species of odontocetes, as previously proposed, in their evolution from land to water beginning 60 million years ago.70 First, our findings demonstrate the joint, a syndesmosis, is likely non-load-bearing—a feature that corresponds with the suction-feeding method used by these species. Second, our findings suggest that the TMJ could be a participant in echolocation and communication based on the presence of possible acoustic fat, nerves and blood vessels within the disc. However, this hypothesis requires further mechanistic studies. We hope this study will provide a platform for further studies of the cetacean TMJ in an effort to elucidate its role in feeding and potentially in sensory functions.

Ethical approval
Not required.

Acknowledgement

The authors would like to thank Christine Fontaine, as well as the volunteers and staff of the Marine Mammal Center, Sausalito, California, for making its stranded harbour porpoises and Risso’s dolphins available for this study and John Doval for the help with the images. We also would like to thank Kurt Takahashi for his instrumental support with the technical aspects of the histopathology and S. Jason Peters and Rich F. Larson for the computed tomography support. Finally, we would like to thank Dr. Kyriacos A. Athanasiou for the generous use of his laboratory for a part of this study.

Funding

This work was supported by an Academic Senate Research Grant, University of California, Davis. Financial support was provided by the Students Training in Advanced Research (STAR) program, University of California, Davis. This specimens for this study were obtained with approval of the United States Department of Commerce, National Oceanic and Atmospheric, National Marine Fisheries Services (Administrative File: 151408SWR2013PR000037).

Competing interests

The authors do not have any conflicts of interest to report with any of the materials described in the manuscript.

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