

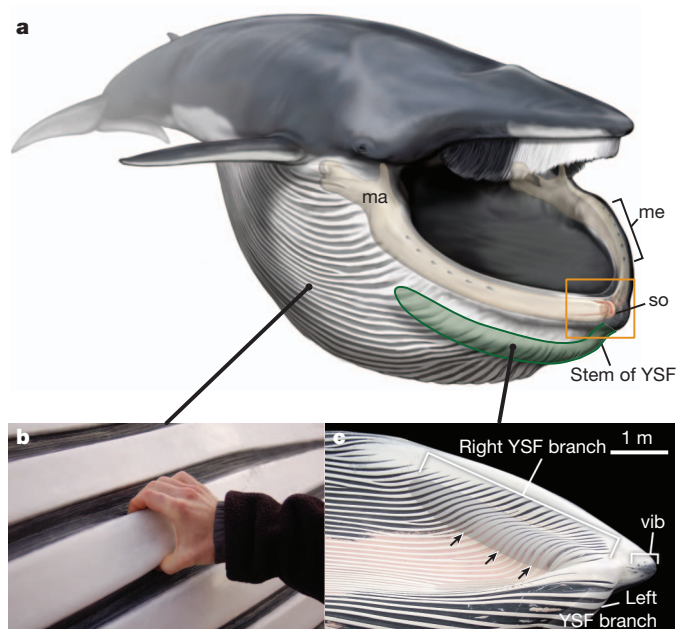
# Discovery of a sensory organ that coordinates lunge feeding in rorqual whales

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Top ocean predators have evolved multiple solutions to the challenges of feeding in the water<sup>1–3</sup>. At the largest scale, rorqual whales (*Balaenopteridae*) engulf and filter prey-laden water by lunge feeding<sup>4</sup>, a strategy that is unique among vertebrates<sup>1</sup>. Lunge feeding is facilitated by several morphological specializations, including bilaterally separate jaws that loosely articulate with the skull<sup>5,6</sup>, hyper-expandable throat pleats, or ventral groove blubber<sup>7</sup>, and a rigid y-shaped fibrocartilage structure branching from the chin into the ventral groove blubber<sup>8</sup>. The linkages and functional coordination among these features, however, remain poorly understood. Here we report the discovery of a sensory organ embedded within the fibrous symphysis between the unfused jaws that is present in several rorqual species, at both fetal and adult stages. Vascular and nervous tissue derived from the ancestral, anterior-most tooth socket insert into this organ, which contains connective tissue and papillae suspended in a gel-like matrix. These papillae show the hallmarks of a mechanoreceptor, containing nerves and encapsulated nerve termini. Histological, anatomical and kinematic evidence indicate that this sensory organ responds to both the dynamic rotation of the jaws during mouth opening and closure, and ventral groove blubber<sup>7</sup> expansion through direct mechanical linkage with the y-shaped fibrocartilage structure. Along with vibrissae on the chin<sup>9</sup>, providing tactile prey sensation, this organ provides the necessary input to the brain for coordinating the initiation, modulation and end stages of engulfment, a paradigm that is consistent with unsteady hydrodynamic models and tag data from lunge-feeding rorquals<sup>10–13</sup>. Despite the antiquity of unfused jaws in baleen whales since the late Oligocene<sup>14</sup> (~23–28 million years ago), this organ represents an evolutionary novelty for rorquals, based on its absence in all other lineages of extant baleen whales. This innovation has a fundamental role in one of the most extreme feeding methods in aquatic vertebrates, which facilitated the evolution of the largest vertebrates ever.

Large marine suspension feeders have evolved many times over the past 200 million years (Myr)<sup>1–3</sup>. These vertebrates, which include extinct bony fish, chondrichthyans and baleen whales (Mysticeti), all show similar morphological specializations for feeding in water while maintaining large body sizes<sup>2,3</sup>. For those vertebrates with solely aquatic ancestries, such as bony fish and chondrichthyans, feeding modes mostly consist of variations on unidirectional ram filter feeding, using gill rakers<sup>1</sup>. By contrast, baleen whales are secondarily adapted to marine environments from a terrestrial ancestry<sup>3</sup>. Their feeding specializations thus reflect a trade-off between evolutionary innovations (for example, baleen) and fundamental constraints from a mammalian body plan (such as air breathing)<sup>3</sup>. The origin of suspension feeding in mysticetes represents an evolutionary novelty with no parallel in any other mammalian or known synapsid lineage<sup>15</sup>. Moreover, the innovation of baleen preceded the origin of extremely large body sizes in mysticetes<sup>16</sup>, which rank among the largest vertebrates ever.

Although mysticetes use several different modes of filter feeding<sup>3</sup>, rorquals exclusively engulf large volumes of prey-laden water in a single, rapid gulp<sup>4</sup>. In fin whales (*Balaenoptera physalus*), for example, the entire process of a lunge occurs in a short time span (~6 s), during which approximately 60–80 m<sup>3</sup> of water and prey are engulfed, a volume equal to or greater than that of the individual rorqual itself<sup>17</sup> (Fig. 1). During a lunge, rorquals accelerate to high speed and open their jaws in a complex sequence of rotation around three orthogonal axes<sup>6</sup>, including an overall gape angle that approaches 90 degrees at the peak of the lunge<sup>5</sup>. Dynamic pressure imposed on the floor of the mouth forces inversion of the tongue<sup>18</sup> and expansion of the ventral groove blubber (VGB) to accommodate the engulfed water<sup>5,7</sup>. Hydro-mechanical models suggest that the expansion of the oropharyngeal cavity (or ventral pouch<sup>8</sup>) requires active resistance, in a highly coordinated fashion, by eccentric action from musculature associated with the VGB<sup>10–13</sup>. The lunge sequence ends once the mandibles close around the volume of engulfed water, with the VGB and the oropharyngeal cavity slowly returning to its original size, allowing the baleen plates to filter the captured prey from the engulfed water<sup>3</sup>.



**Figure 1 | Key jaw anatomy of a rorqual lunge, shown in a fin whale (*B. physalus*).** **a**, Jaw in oblique view. **b**, Laterally extensible, accordion-like VGB. **c**, YSF embedded in the VGB of an adult fin whale, demarcated by arrows and digitally enhanced with a low opacity mask. **ma**, mandibles; **me**, mental foramina; **so**, sensory organ; **vib**, vibrissae. Art by C. Buell.

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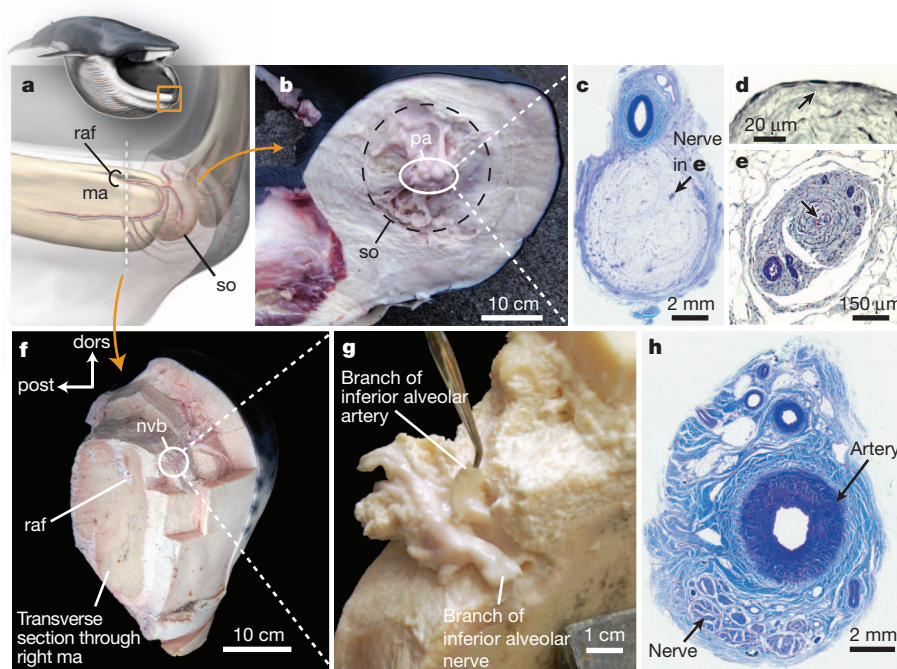
In addition to the accordion-like VGB, lunge feeding is facilitated by a suite of bony and soft tissue morphological adaptations<sup>5–9</sup> (Fig. 1). The lower jaw consists of two mandibles unfused at the symphysis and flexibly anchored to the skull by fibrous joints<sup>5,6</sup>. These atypical fibrous temporomandibular joints<sup>5</sup> increase kinetic freedom and resist shear forces during the rapid excursions of a lunge. The mandibular symphysis has a direct mechanical linkage to the VGB<sup>7</sup> through the y-shaped fibrocartilage (YSF) structure<sup>8</sup>, which has a raised stem that emerges from the symphysis and extends posteriorly in two branches, parallel to the jaws and embedded within the VGB<sup>8</sup>. How these structures are integrated into the engulfment apparatus has remained enigmatic, although hydro-mechanical models and kinematic data from tagged rorquals suggest that lunge feeding is a highly coordinated process<sup>10–13</sup>. Here, we identify a novel sensory organ that is mechanically linked to both bony and soft tissues, and can provide the brain with mechanosensory information for coordinating the rapid and marked expansion of the oral cavity during a lunge.

We analysed the functional morphology of the mandibular symphysis in small, medium and large balaenopterid species, including both adult and fetal specimens (see Supplementary Information). Midline sagittal cuts along the mandibular symphysis showed that the sensory organ is mostly located on the dorsal half of the region between the symphyseal surfaces of the mandibles, and occupies a roughly spheroidal cavity. The organ is bound on all sides by dense connective tissue; the inner surface of the cavity is lined by a discontinuous squamous layer of cells and filled with a viscous gel-like matrix. The gel-like matrix supports numerous small connective tissue papillae that extend from the inner surface and sometimes cluster in irregular numbers within the cavity. Notably, the papillae contain nerves and encapsulated nerve termini (Fig. 2).

We also analysed the three-dimensional soft-tissue anatomy of an adult fin whale mandibular symphysis before dissection, using both magnetic resonance imaging (MRI) and X-ray computed tomography (XRCT) scanning (Fig. 3). Our analyses showed that the organ receives neurovascular bundles that emerge from vestigial alveolar foramina of

the mandibles, a structure that is homologous with the lower first incisor tooth socket of fossil ‘toothed’ mysticetes<sup>14–16</sup>. The presence and identity of these neurovascular bundles, which contain branches of the mandibular division of the trigeminal nerve, were confirmed by subsequent dissection of the same specimen. They were also present in fetal specimens of the same species (see Supplementary Information). Three-dimensional renderings also indicated that these bundles are asymmetrically arranged, with a single bundle extending medially from one mandible. We verified that this asymmetry fluctuates in dominance, with 60% from the left in fin whales ( $n = 10$ ). In minke whales (*Balaenoptera acutorostrata*), we observed bundle dominance from both the left and right ( $n = 2$ ). XRCT and MRI scans showed the precise anatomical geometry of the organ relative to the distal ends of the mandibles (Fig. 3), with XRCT indicating that the organ directly overlies the anterior termination of the YSF stem along the anterior margin of the throat pouch. This configuration provides the mechanical linkages that connect this organ to both bony and soft tissues (that is, the rotation of the bony mandibles<sup>6</sup> and the expansion of the throat pleats<sup>7</sup>) during the course of a single lunge (Fig. 1).

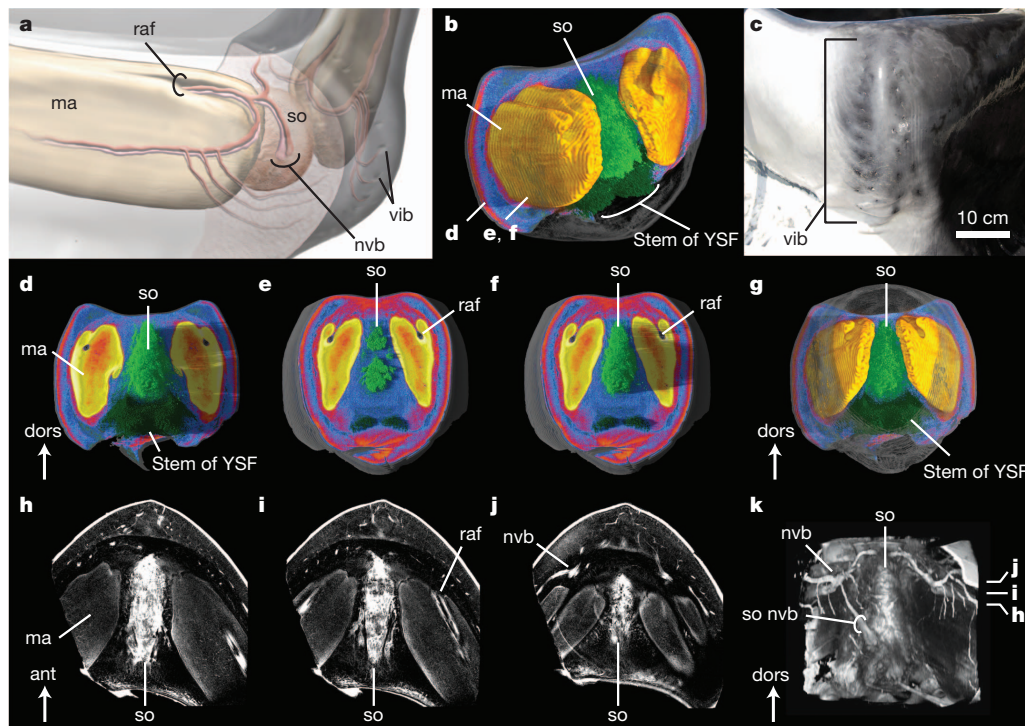
Following initial observations<sup>8</sup>, it was suggested that the mandibular symphysis in fin whales contained a synovial cavity<sup>19</sup>. Our results show that the symphysis is unlike a typical synovial joint with cartilage. Instead, it is bridged by very dense connective tissue, with cruciate fibres, but without true or patent ligaments that originate from the symphyseal groove. In addition, our anatomical and histological analyses indicate that its overall geometry and specialized tissues satisfy the criteria of a sensory organ. Specifically, we argue that the organ responds to localized changes in jaw configuration during lunge feeding, in which the rotation of the bowed jaws will cause deformation of the symphysis, similar to an intervertebral joint<sup>20</sup>. This action provides the mechanical input to the sensory organ, which the brain receives through the mandibular branch of the trigeminal nerve (Fig. 3). The organ’s asymmetric vascularization and innervation is the first such fluctuating asymmetry reported in the soft tissue of mysticetes, although asymmetric morphology is not unprecedented in toothed



**Figure 2 | Anatomy and histology of the rorqual mandibular symphysis, shown in fin whales (*B. physalus*).** **a, b**, Mandibular symphysis in sagittal section, showing bony and soft tissue around the sensory organ (so) and papillae (pa) within it. raf, relictual alveolar foramen. **c–e**, Luxol fast blue histological stains showing neurovascular bundles (nvb) and cell layers within

the sensory organ, with arrows pointing to discontinuous squamous cell layer in **d** and nerve termini in **e**. **f, g**, Dissection showing neurovascular bundles in close association with the alveolar groove. dors, dorsal; post, posterior. **h**, Histological section of the tissue shown in **g**. Art by C. Buell.





**Figure 3 | Digital imaging of the rostral chin, shown in fin whales (*B. physalus*).** **a**, Mandibular symphysis showing bony and neurovascular tissue around the sensory organ (so). **b**, Three-dimensional XRCT rendering of **a**, showing the mandibles (ma), sensory organ and YSF and location of slices **d–f**. **c**, Chin of an adult fin whale. **d–g**, Transverse XRCT slices through the chin

(**g**) showing the sensory organ (light green) in different thicknesses. **h–j**, Coronal MRI slices through the chin. **k**, Asymmetric neurovascular bundles (nvb), with mandibles digitally removed for clarity, and location of MRI slices **j–h**. Ant, anterior. Art by C. Buell.

whales, for both bony tissue (for example, tusks in narwhals (*Monodon monoceros*<sup>21</sup>)) and soft tissue (for example, nasal sacs and bursae<sup>22</sup>). The asymmetry associated with this sensory organ may reflect lateralized feeding behaviours (for example, rolling, side gulping) that have individual side biases for several rorqual species<sup>23,24</sup>.

The new rorqual morphology described here provides yet another example of how aquatic<sup>25</sup> and marine mammals<sup>26</sup> have evolved unique sensory systems to navigate, communicate and feed in the water<sup>27</sup>. Mechanoreceptors embedded within fibrous mandibular symphyses have been observed in other terrestrial mammals<sup>28</sup>, but rorquals alone possess clear mechanoreceptors suspended within a gel-like cavity between a completely unfused symphysis. In terms of lunge-feeding kinematics, anatomical and histological evidence suggest that the organ's mechanosensors assist in controlling and providing neurological information about the configuration of the jaws during rapid lunges. We propose a three-step lunge-feeding model to explain the organ's role during a lunge: (1) using vibrissae present on the external surface of the chin<sup>9</sup>, rorquals register prey fields of sufficient density; (2) the jaws disengage and rotate<sup>6</sup>, thereby compressing and shearing the organ; and (3) the oropharyngeal cavity reaches full expansion, with drag forces acting on the inside of the mouth<sup>17,18</sup> transmitted to the organ through the YSF<sup>8</sup> (Fig. 2). According to dynamic modelling studies<sup>10–13</sup>, rorquals must actively control the rate of mouth opening and throat-pouch expansion to effectively maximize volume captured; we propose that the sensory organ has a key role in coordinating this movement.

The discovery of this organ raises questions about its role in the evolution of lunge feeding in whales. The ancestral mandibular condition of modern cetaceans was probably a fused (or strong sutural) symphysis<sup>28</sup> with an elongate surface<sup>14</sup>, as seen in nearly all basilosaurids, and a fused symphysis persists in modern toothed whales. By contrast, all living mysticetes possess unfused symphyses<sup>3,14–16</sup>. Recently described fossil evidence from *Janjucetus hunderi*, a stem 'toothed' mysticete, demonstrates that the transition from fused to unfused

mandibles occurred early in baleen whale evolution, with unfused symphyses in mysticetes having a late Oligocene antiquity (~23–28 Myr ago)<sup>14</sup>. Our investigations of the mandibular symphyses in living mysticetes show that bowhead, right and pygmy right whales (*Balaena mysticetus*, *Eubalaena* spp. and *Caperea marginata*, respectively) do not possess a gel-like cavity in their mandibular symphysis, although small papillae intruding into the connective-tissue matrix in this area are patent among adult and immature specimens (see Supplementary Information). The condition of the mandibular symphysis in grey whales (*Eschrichtius robustus*) has only been reported for a decayed neonatal specimen<sup>29</sup>, although the suggestion of a mucoid centre is broadly similar with the morphology of the organ described here. On the basis of this equivocal evidence, we propose that the organ evolved either at the node of Balaenopteroidae (grey whales and rorquals), or along the stem to crown Balaenopteridae (rorquals)<sup>15</sup>. If the former, the organ is a pre-adaptation for lunge feeding; if the latter, the organ evolved in tandem with VGB and specializations of the mandible morphology, such as a laterally deflected coronoid process<sup>6</sup> and flexible temporomandibular joints<sup>5</sup>, which exhibit a degree of mandible rotation and oropharyngeal cavity expansion far greater than that of grey whales<sup>29</sup>. Regardless of evolutionary sequence, we argue that multiple lines of evidence indicate that the sensory organ has a key role in lunge feeding by registering the rotation of the mandibles during a lunge and the expansion of the throat pouch through the YSF, all of which evolved before the extremely large body sizes observed in today's rorquals. Despite the opportunity to observe the adult morphology of large rorquals during decades of sustained hunting<sup>30</sup>, these findings demonstrate how poorly we understand the basic functional morphology of these ecologically important ocean predators.

## METHODS SUMMARY

**Fieldwork.** We recorded macroscopic observations and collected tissue samples from fresh fin whale carcasses that were collected as part of commercial catch operations in Hvalfjörður, Iceland, in 2009 and 2010, as well as carcasses of minke

whales collected by Hrefnuveiðimenn ehf in 2010. For both species, intact carcasses belonged to adult individuals and had been dead for less than 24 h. We directly observed the sensory organ in all of the specimens in which we dissected the mandibular symphysis (see Supplementary Information). All tissue samples from Iceland were transferred and imported to Canada under Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) permits.

**Imaging and histology.** XRCT scanning was conducted on frozen specimens of *B. physalus* and *B. acutorostrata* at the CT Imaging Centre at the FPIInnovations Wood Products Division, using a 4 MeV linear accelerator X-ray source with 0.4 mm spatial resolution, and with a large (1 m) scanning envelope. CT images were rendered using VGStudioMax 2.0 software. MRI scans were conducted on a 1.5 Tesla General Electric superconducting magnetic resonance system at the UBC MRI facility. MRI volume-rendered images were produced at the Cleveland Clinic Lerner College of Medicine of Case Western Reserve University, with a volume-rendering technique using the Inspace application on a Siemens Multimodality Work Place with VE36A software and Fujitsu hardware. Tissues were fixed in standard buffered formalin for histology. Sections were stained using either a generalized haematoxylin and eosin stain or a myelin stain (Luxol fast blue), following protocols devised at Wax-it Histology Services.

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**Supplementary Information** is linked to the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

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