Observations on the musculoskeletal anatomy of the head of a neonate gray whale (*Eschrichtius robustus*)

CASSIE JOHNSTON

Biology Department,
San Diego State University,
San Diego, California 92182, U.S.A.
E-mail: cjjohnston@cox.net

THOMAS A. DEMÉRÉ

Department of Paleontology,
San Diego Natural History Museum,
San Diego, California 92112, U.S.A.

ANNALISA BERTA

JOSHUA YONAS

Biology Department,
San Diego State University,
San Diego, California 92182, U.S.A.

JUDY ST. LEGER

SeaWorld of California,
500 SeaWorld Drive,
San Diego, California 92109, U.S.A.

In the late 1800s and early 1900s, a number of studies reported on anatomical observations of selected species of living cetaceans. For mysticetes, most accounts focused on rorquals (Balaenopteridae), although several studies of right whales (Balaenidae) were also published. One notable study (Andrews 1914) provided a detailed account of the natural history, external morphology, and skeletal anatomy of the gray whale (*Eschrichtius robustus*). However, this study did not examine the myology of *E. robustus*. Unfortunately, this paucity of musculoskeletal information for the gray whale has remained to the present day. This lack of basic anatomical information is especially frustrating given the current view that gray whales occupy a unique ecological position as the only suction-feeding baleen whales (Pivorunas 1979, Werth 2001). A recent dissection (February 2008) of a young male gray whale (LACM 95548, stranded 7 February 2008 at Huntington Beach, Orange County, California) measuring 517 cm in total body length provided the opportunity to examine some poorly known or undescribed anatomical features relevant to understanding the evolution and specialized feeding strategy of *E. robustus*. Based on total length data in Sumich (1986) this gray whale was approximately 2 mo old at the time of death and therefore represents a neonate.

Eschrichtius robustus is considered a benthic suction feeder, which reportedly dives to the ocean floor, rolls on one side, and uses oral suction to draw amphipod- and

cumacean-rich sediment into its mouth (Ray and Schevill 1974, Pivorunas 1979, Werth 2001). Gray whales are also reported to suction feed within the water column on dense clouds of mysids near rocky outcrops (Darling *et al*. 1998). Phylogenetically, the gray whale is positioned as sister to the engulfment-feeding balaenopterids, together comprising the balaenopteroid clade (Deméré *et al*. 2005, 2008). In this light, it is not unexpected that gray whales and rorquals share several morphological characteristics associated with feeding, such as short baleen with coarse fringe and relatively deep interdigitation of cranial and rostral bones (Bouetel 2005). Interestingly, the gray whale also shares a number of characters with skim-feeding balaenids, including a subrostral gap between the anterior terminations of the baleen racks, a small coronoid process on the dentary, a more dorsally oriented mandibular condyle, and a narrow rostrum and arched palate (Bouetel 2005). Below we discuss unreported morphological features revealed during our dissection, including musculoskeletal features of the temporomandibular joint, the mandibular symphysis, and the gular region.

Temporomandibular Joint

   The typical mammalian condition for this joint is a synovial articulation. In mysticetes, this generalized type of temporomandibular articulation occurs in balaenids (Eschricht and Reinhardt 1866, Lambertsen *et al*. 1989). In balaenopterids, however, the temporomandibular articulation is neomorphic and has been described as nonsynovial and fibrocartilaginous (Hunter 1787, Carté and MacAlister 1868, Schulté 1916, Pivorunas 1977, Lambertsen *et al*. 1995). Instead of possessing a discrete joint capsule, balaenopterids have a fibrocartilaginous interarticular "cushion" consisting of a mass of fibrocartilage tapering from an expansive origin in the glenoid fossa of the squamosal to envelop the entire mandibular condyle of the dentary. Lambertsen *et al*. (1995) noted structural complexities within the fibrocartilaginous mass, consisting of dense connective tissue with irregular, inelastic white fibers dorsolaterally and a more loosely fibrous oil-rich articular cushion with yellow elastic fibers dorsomedially. This structure facilitates the unusual kinematics of the balaenopterid mandibular arch (Lambertsen *et al*. 1995), in which the dentaries are able to rotate along three axes: longitudinal (Alpha), vertical (Omega), and transverse (Delta). Thus, the balaenopterid mandibular arch is capable of a wide range of movements, two of which would approach a condition of subluxation in more generalized mammals (*e.g.*, subluxation of the mandibular symphysis during Alpha rotation and subluxation of the temporomandibular joint during Omega rotation).
   As noted by Lambertsen *et al*. (1995), the temporomandibular joints of gray whales and pygmy right whales (*Caperea marginata*) have not been previously described, which has limited our ability to ask certain questions about character evolution and development of the diverse feeding strategies seen in crown mysticetes. However, our dissection of LACM 95548 revealed a nonsynovial temporomandibular joint in *E. robustus* similar to that described in balaenopterids (Fig. 1). In LACM 95548, a large mass of fibrocartilage was observed to invest the entire glenoid fossa of the squamosal and to extend across the temporomandibular joint, enveloping the
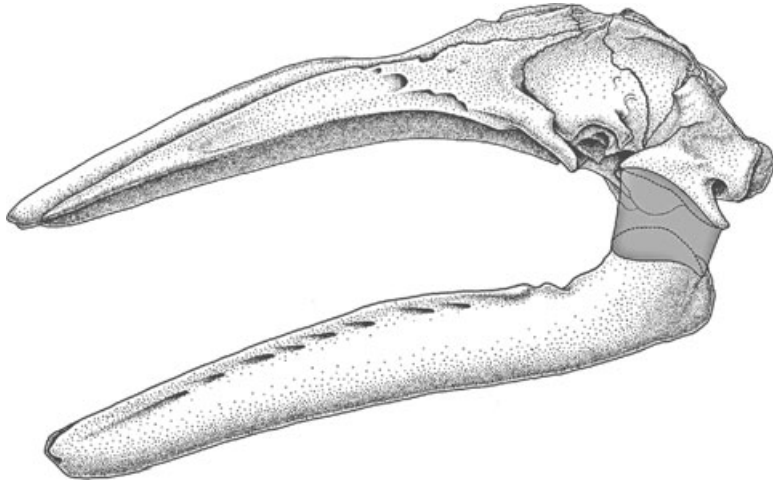
Figure 1. Lateral aspect of skull of *Eschrichtius robustus*. Gray shaded area indicates approximate extent of fibrocartilaginous tissues of the temporomandibular joint.

entire mandibular condyle (Fig. 1). No trace of synovial compartments or a fibrous meniscus was observed. Unfortunately, due to decomposition of tissues, it was not possible to determine if differences in fiber type also existed between portions of the fibrocartilaginous mass as documented in balaenopterids (Lambertsen *et al.* 1995). We propose that the fibrocartilaginous jaw articulation observed in *E. robustus* is homologous with the balaenopterid condition and represents a shared derived feature that evolved in their common ancestor. To what extent this similarity in gross anatomy of the balaenopteroid temporomandibular joint has evolved to accommodate the functional differences exhibited by balaenopterids and eschrichtiids is unclear and requires additional study. It is likely that Alpha rotation, as allowed by a fibrocartilaginous temporomandibular joint, plays an important role in gray whale suction feeding as the dentaries alternately roll laterally and medially to occlude the lower lips against the upper lips during pumping of water into and out of the sides of the mouth.

Mandibular Symphysis

Unlike the rigid and sometimes fused (synostotic) mandibular symphysis of more generalized mammals, mysticete cetaceans possess a flexible and almost elastic symphysis permitting a remarkable degree of independent interdentary movement. As described by Lillie (1915), Pivorunas (1977), and Lambertsen *et al.* (1995), the balaenopterid mandibular symphysis consists of a fibrocartilage articulation connecting the distal ends of the dentaries. This interdentary connection is constructed as a dense, cylindrical fibrocartilage annulus with a mucoid fluid-filled center (Lillie 1915). Pivorunas (1977) provided a more detailed description of balaenopterid symphyseal anatomy in which the fibrocartilage annulus is continuous posteriorly with a
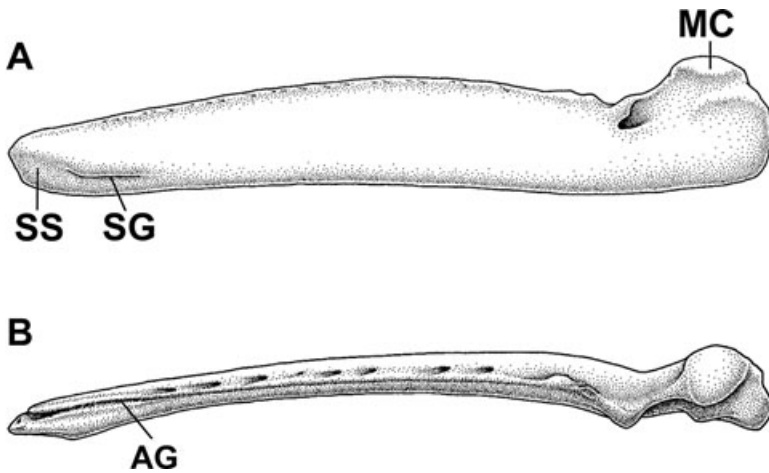
Figure 2. Dentary of *Eschrichtius robustus*. (A) Medial aspect of right dentary. (B) Dorsal aspect of right dentary. AG = alveolar groove, MC = mandibular condyle, SG = symphyseal groove, SS = symphyseal surface.

fibrous arcade (Schulté 1916) constructed of dense fibrocartilage. This fibrous arcade has the form of a "Y" with the stem grading anteriorly into the mandibular symphysis and the distal, posterolaterally diverging arms oriented parallel to and medial to the right and left dentaries (Pivorunas 1977). This fibrocartilage skeleton is closely associated with the musculature of the ventral throat pouch and has been implicated in reinforcement of this unique feeding apparatus (Pivorunas 1977).

Osteologically, the extreme anteromedial portion of the mysticete dentary can be divided into an anterior roughly planar symphyseal surface and a posterior longitudinal symphyseal groove (Fig. 2A). The fibrocartilage annulus in balaenopterids occupies the planar anterior symphyseal surface, while a thickened portion of the periosteum occupies the posterior symphyseal groove (this study).

Although all extant mysticetes possess a kinetic interdentary connection (Pivorunas 1977), the structure of the symphysis in balaenids and eschrichtiids has not been previously described in detail. During our dissection of the neonate gray whale (LACM 95548) we discovered a large, globular fibrocartilage mass between the symphyseal surfaces of the dentaries (Fig. 3). Like the balaenopterid interdentary connection, this globular mass consists of dense connective tissue forming an annulus with a mucoid fluid-filled center. Unlike the balaenopterid condition, however, no fibrous arcade was observed extending posteriorly into the ventral musculature of the gular region. Unfortunately, because of decomposition, it is not possible to unequivocally report the absence of a fibrous arcade in *E. robustus*.

Functionally, the fibrocartilage annulus forming the mandibular symphysis of gray whales accommodates, as in balaenopterids, both Alpha and Delta rotation during feeding. We speculate, however, that the degree of Alpha rotation is smaller in gray whales than in balaenopterids and is correlated with the taller, fleshy lower lips and much straighter dentaries in the former compared to the shorter, lower lips and more
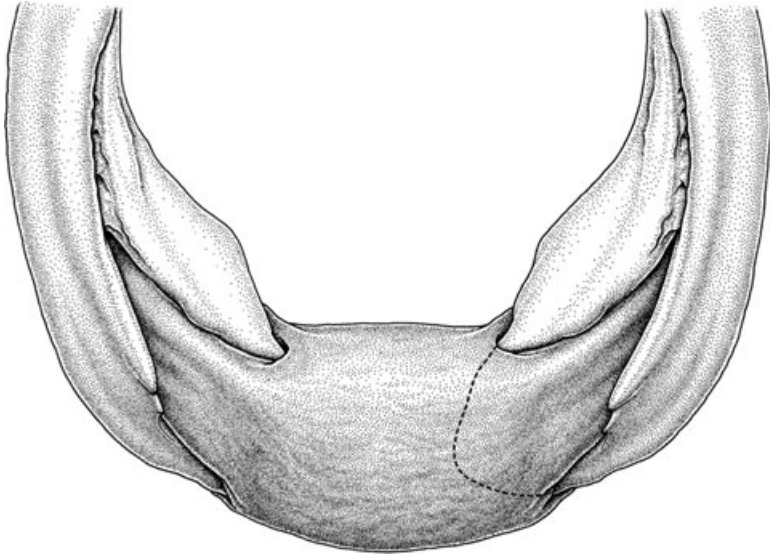
Figure 3. Mandibular symphysis of *Eschrichtius robustus* in slightly oblique anterodorsal aspect. Dashed line indicates the anterior extent of the left dentary and the heavily stippled area indicates symphyseal fibrocartilage mass. Note the "chin-strap" emerging from the alveolar groove.

broadly bowed dentaries in the latter. Thus, the arch traversed by the rorqual lower lip during Alpha rotation is much longer than it is for the gray whale, and results in a larger initial opening of the ventral throat pouch during engulfment feeding. In contrast, the shorter arch traversed by the gray whale lower lip may be implicated in more precise control of the lower lip, as well as in providing a more planar profile to the side of the face during benthic suction feeding.

In the neonate gray whale the anterior terminations of each dentary were seen to fit into the anterolateral corners of the fibrocartilage mass. Posteriorly, the fibrocartilage is in intimate contact with the symphyseal surfaces of both dentaries. Although functionally the fibrocartilage annulus allows each dentary to move independently during Alpha and Omega rotation (Lambertsen *et al*. 1995), it is unclear to what extent the annulus functions in preventing subluxation of the symphyseal joint. Instead, another new structure observed during dissection of LACM 95548 is more likely involved in maintaining articulation of the unfused mandibular symphysis. This new feature is a strap-like structure (here termed the "chin-strap") that connects the tips of the dentaries by merging medially with the anterolateral portions of the fibrocartilage mass (Fig. 3, 4), occupying the mandibular symphysis. This "chin-strap" emerges from the anterior opening of the prominent bony canal (Fig. 3, 4), homologous with the alveolar groove in toothed mammals (Ridewood 1922), on the anterodorsal portion of the dentary (Fig. 2B). The fleshy "chin strap" completely fills the distal opening of the canal and is continuous with the soft tissues located posteriorly within the internal portions of the canal. Histological analysis (JSL)
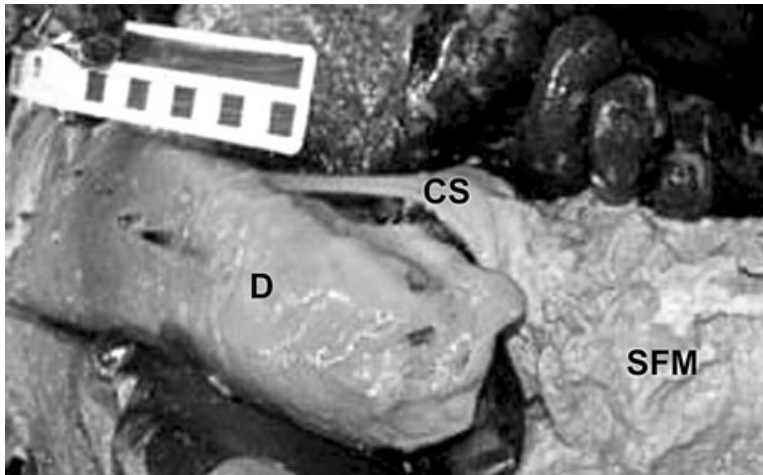
Figure 4. Photograph of partially dissected mandibular symphysis of neonate gray whale (LACM 95548) showing anterior portion of right dentary with "chin-strap" tissue partially removed from alveolar groove and merging with the symphyseal fibrocartilage mass. D = dentary, CS = "chin-strap," SFM = symphyseal fibrocartilage mass.

revealed a mixed composition of skeletal muscle and fibroelastic collagen fiber, as well as a peripheral nerve (thought to be the mandibular nerve). A variation of this "chin-strap" was noted during a dissection conducted in June 2008 by Dr. T. K. Yamada at the National Museum of Nature and Science, Tokyo, Japan, of a young minke whale (*Balaenoptera acutorostrata*, NSMT M32713). Interestingly, in the minke whale the "chin-strap" was not an isolated structure as in the neonate gray whale, but instead was fused dorsally with the mandibular periosteum. We propose this "chin-strap" may serve to help hold the dentaries together, thereby strengthening the symphysis to counteract the lateral forces exerted on the mandibular arch during Alpha and Omega rotation and feeding.

The soft anatomy associated with the symphyseal groove is less clear in mysticetes. Although this feature has been referred to as a ligamental groove by some workers (Sanders and Barnes 2002), our dissection of the neonate gray whale, as well as the dissection of the minke whale conducted by Dr. Yamada and another dissection conducted by us of a neonate fin whale (*B. physalus*, SDSU S970), found no ligament associated with this groove. Instead, a thickened portion of the mandibular periosteum was seen to form an invagination that filled the symphyseal groove in both the minke and fin whale specimens. A slight variation was seen in the gray whale specimen, where a shallow longitudinal groove is present on the dentary instead of a deep groove, and a thickened portion of the mandibular periosteum filled this symphyseal sulcus. We hypothesize that the soft tissues associated with the mysticete symphyseal groove/sulcus may also contribute to strengthening the symphysis, thus counteracting the lateral forces exerted on the mandibular arch resulting from increasing the volume of the oral cavity while feeding.

Suction Feeding

Our dissection of LACM 95548 also confirmed several previously reported features attributed to suction feeding in odontocetes. One such feature is the presence of ventral throat grooves (Werth 1992, Heyning and Mead 1996). We found the gray whale to have two large grooves (one right and one left) 635 and 620 mm long, respectively, and 20–30 mm deep. A smaller, third groove, 100 mm lateral to the right groove, was only 91 mm long and 1–2 mm deep (Fig. 5). These integumentary grooves are confined to the throat region, unlike the condition in balaenopterids where the much more numerous ventral grooves extend essentially from the chin to the umbilicus. In rorquals, the heavily pleated ventral integument accommodates the extreme oral expansion of the *cavum ventrale* that occurs during engulfment feeding (Pivorunas 1977). In the gray whale, the more reduced throat grooves are implicated in gular expansion during suction feeding (Werth 1992, Heyning and Mead 1996). Other observed features probably related to suction feeding included a very large, muscular tongue, as well as a nonankylosed hyoid complex, which is a result of the specimen's young age. During our dissection we also attempted to examine the gular musculature; however, due to the advanced decomposed condition of the specimen, the muscles were in suboptimal condition, making identification of individual muscles very difficult. This was also the case for the area of the head in which the frontomandibular stay of balaenopterids (Lambertsen *et al.* 1995) was described; however, there was no evidence of such structure in the gray whale.

Figure 5. Photograph of ventral region of neonate gray whale head (LACM 95548) showing prominent throat grooves.

Overall, our recent dissection work has provided information on several morphological features including two that have not been previously reported for the gray whale. The gray whale temporomandibular joint has hitherto remained unknown or unreported, but is now known to be a nonsynovial, fibrocartilaginous articulation homologous to the condition in balaenopterids. Also, the difference seen in the structure of the symphyseal "chin-strap" in the mandibular arch of the gray whale and minke whale has raised functional questions and warrants further comparative investigations among all mysticete species. Other features noted during the dissection (specifically the throat grooves and large, muscular tongue) are functionally related to the gray whale's ability to suction feed, as these features are also common in suction-feeding odontocetes (Werth 1992, Heyning and Mead 1996). Further study of these features, as well as other morphological characters associated with suction feeding, is being conducted to examine the evolutionary history of suction feeding in cetaceans.

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