MAXILLOMANDIBULAR CAM ARTICULATION DISCOVERED IN NORTH ATLANTIC MINKE WHALE

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Cranial anatomy of baleen whales was examined in order to identify evolutionary morphological novelties. Complex surfaces of the mandibles and craniums of 4 minke whales (Balaenoptera acutorostrata) were plotted in 3 dimensions by close-range photogrammetry. Photogrammetric data sets representing naturally opposed borders of the mandible and maxilla were used to determine 3-dimensional (3D) conformal coordinate transformations. These allowed the creation of precise 3D computer models of the skulls in which the strongly bowed mandibles were closely opposed along their entire length to the curved lateral borders of the rostrum. This simulated mouth closure. Subsequent internal measurements demonstrated a biomechanical specialization heretofore unknown in the class Mammalia—a maxillomandibular cam articulation. This novel articulation would operate as an adjunct to the temporomandibular joint in the final stage of mouth closure. Our functional interpretation is that it is at least a mechanism by which the energy cost of carrying a gigantic, expandable mouth at speed through an aqueous medium could be kept to a minimum. This articulation also may be part of a critically important trigger mechanism needed for precisely timed deployment of the feeding apparatus while it is under high hydrodynamic loads. We suggest that this evolutionary innovation was the root enabling cause of the adaptive radiation of rorquals (Balaenopteridae).

Key words: anatomy, Balaenopteridae, Cetacea, key evolutionary innovation, rorqual

Adaptation to the marine environment has led to striking modifications of the musculoskeletal system in members of the Cetacea, including elimination of parts rendered useless in a buoyant medium, and extreme remodeling of those that have remained functional. Among the latter, extraordinary changes in the cetacean skull traditionally have been grouped under the term telescoping (Gaskin 1982; Miller 1923; Sanderson and Wassersug 1993; Werth 2000). This process constitutes structural divergence from a generalized original mammalian form associated with modification of contact relationships of individual cranial elements, not just their size or shape. Two types of telescoping generally are recognized on the basis of new relationships taken by the maxillary bone. In members of the Odontoceti, the proximal portion of the maxillary passes up over the frontal toward the dorsum of the skull, approaching or meeting the supraoccipital. In members of the Mysticeti, the proximal maxillary passes underneath the frontal to form a distinct suborbital plate (Gaskin 1982; Miller 1923).

A peculiar feature of the maxillary suborbital plate (SP) found in mysticetes is that it projects freely as a thin shelf of bone into the soft tissue beneath the orbit (Miller 1923). In prepared skulls, the posterior edge of the SP also may appear irregular in outline, whereas its ventral surface contains numerous vacuities (Miller 1923). In view of these features, Miller (1923) noted that the SP could not contribute strength to the bony connection between the rostrum and cranium, and argued that it is in an advanced state of evolutionary degeneration. A more recent postulate, in contrast, holds that the SP might provide a thin shelf of bone at the back of the mouth against which the tongue could work in feeding (Gaskin 1982).

Investigations of anatomical relations pertinent to this unsettled controversy have been conducted on the head of a minke whale (Balaenoptera acutorostrata) and that of a humpback whale (Megaptera novaeangliae) that stranded on the coast of New England, and on the heads of fin whales (B physalus) and sei whales (B. borealis) landed in whaling operations (Lambertsen 1983, 2001; Lambertsen and Hintz 2001; Lambertsen et al. 1995). In addition, prepared skulls of baleen whales have been examined in various museums, as were defleshed skulls of bowhead whales (Balaena mysticetus) taken by Inupiat whale hunters (Kreiton et al. 1990; Lambertsen et al. 1990). This research confirmed that the SP is a freely projecting
posterior extension of the maxilla in Balaena, Megaptera, and Balaenoptera. As Gaskin (1982) understood, this contributes a skeletal member from which the oropharyngeal portion of the baleen apparatus is suspended. In addition, vacuities in the surface of the SP typically were found to harbor blood vessels supplying the germinal epithelium of the baleen. These findings rejected the claim that the SP is in a state of evolutionary degeneration.

Moreover, in the balaenopterids examined, an array of anatomical features was noted that suggested a radically novel function for the SP (Lambertsen 2001; Lambertsen and Hintz 2001). In both Megaptera and Balaenoptera, the peculiar, straplike tendon of origin of the superficial masseter muscle was found to originate not on the small jugal bone or the aponeurosis of the optic canal, as originally claimed (Carte and MacAlister 1868), but more deeply (Beauregard 1882), on a distinct bony process that forms the posterolateral terminus of the SP. When carefully traced inward, this tendon was always found to envelope, and in a sense cap, the free posterior edge of the SP. Thus, in situ, the free posterior edge or rim of the SP took the form of a smooth and regular gliding surface composed of dense white connective tissue. The sometimes irregular calcified border of the maxilla lay internal to this collagenic tissue. Furthermore, the large, laterally deviated coronoid process found on the mandible in balaenopterids appeared perfectly positioned to interact with the SP in a biomechanically interesting cam-follower mechanism (Figs. 1A–C).

More particularly, we predicted that, during the final stage of mouth closure in balaenopterids, contraction of the superficial masseter muscle might entrain the coronoid process (Fig. 1C), forcing it to slide along the superficial masseter tendon onto the rim of the SP. In this way, a novel maxillo-mandibular articulation might be established, creating an intermittently operating cam-follower mechanism that works in conjunction with the temporo-mandibular joint. In a cam-follower mechanism, the shape of 1 mechanical element (the cam) controls the action of a 2nd element (the follower). The cam of the novel articulation hypothesized would be the maxilla, whereas the follower would be the mandible. The fibroelastic temporomandibular joint of balaenopterids (Beauregard 1882; Hunter 1787; Lambertsen et al. 1995), in combination with their flexible mandibular symphyses (Lambertsen et al. 1995; Lillie 1915; Pivorunas 1977), would facilitate the cam action predicted, because these are highly mobile articulations that allow rotation of the mandibles around 3 spatial axes, with rostrocaudal and mediolateral condylar displacements (Lambertsen et al. 1995). However, such a cam articulation could not exist in any other taxonomic family of Cetacea, because in this mammalian order only members of the Balaenopteridae (rorquals) have a distinct coronoid process (Miller 1923; Ridgway and Harrison 1985). Furthermore, no other species of mammals could have an articulation of this configuration because, in this vertebrate class, only baleen whales have a SP (Miller 1923).

We hypothesized that a maxillo-mandibular cam articulation exists in balaenopterid whales. To test this hypothesis, we conducted computer-based simulation experiments with 3-dimensional (3D) models of skulls of North Atlantic minke whales (B. acutorostrata). This species was chosen because sequencing of the mitochondrial DNA control region in all extant mysticetes indicates that this smallest of the rorquals probably is genetically the least differentiated (Armason et al. 1993), a finding that has since been confirmed by complete mitogenomic analyses (U. Armason, pers. comm.). The present paper gives the results of these biomechanical experiments. This study indicates that the craniomandibular system of at least 1 species of Balaenoptera is far more complex than previously thought, because it features a maxillo- as well as a temporomandibular articulation.
MATERIALS AND METHODS

We employed a Nikon F3 35-mm camera equipped with a 25-mm f2.8 Nikkor lens (Nikon Inc., Melville, New York) for stereophotography and 3D model development. Stereopaired images were collected separately from the right side of the ventral surface of 4 prepared skulls from minke whales and the dorsolateral surface of corresponding right mandibles (specimens 55-8201 and 55-8202, Swedish Museum of Natural History; specimen 571236, United States National Museum of Natural History; and specimen CN16xx, University of Copenhagen Museum of Zoology). A metric scale was included with the specimens photographed. By using the resultant stereopaired images with a Kern Swiss DSR 11 stereoplotter (Leica Geosystems A. G., Heinrich Wild Strasse, Heerbrugg, St. Gallen, Switzerland), we plotted the x, y, and z Cartesian coordinates of the dorsal border of the mandible, condyle of the mandible, insertion of the superficial masseter muscle, origin of the superficial masseter muscle, outline of the maxillary, ventral surface of the frontal above the rim of the SP, outline of the squamous temporal, and articular surface (glenoid fossa) of the squamous temporal (Fig. 2).

Outlining of selected bones and anatomical surfaces was achieved by linear bridging of serial spot elevations plotted along discrete anatomical borders. Nonuniform rational B-splined surfaces were fit to these outlines, most notably between the origin and insertion of the superficial masseter muscle.

FIG. 2.—Three-dimensional model in which principal elements of maxillomandibular cam articulation of *Balaenoptera acutorostrata* are reconstructed. Illustration is based on close-range photogrammetry of museum specimen 55-8201. Outline of selected bones was achieved by linear bridging of serial spot elevations plotted along discrete anatomical borders. Nonuniform rational B-splined surfaces were fit to these outlines, most notably between the origin and insertion of the superficial masseter muscle.
ensuing mathematical transformations. The extent of forward placement of the distal end of the mandibular submodel from the posterior surface of the occipital condyles along the midsagittal plane was defined as a proportion of the length of the skull (Table 2). The length of the skull was measured from the posterior surface of the occipital condyle to the rostral tip of the premaxilla.

Coarse longitudinal alignment introduced the initial approximation for determination of a standard 3D conformal coordinate transformation (Wolf and DeWitt 2000). All computations used to satisfy simultaneously the multiple nonlinear equations of this transformation employed only the 3D data points defining the dorsal border of the mandible and the labial border of the maxilla (see Fig. 2). This mathematical approach formalized an anatomically based premise that these 2 data sets approximately describe a single surface when the mouth is tightly closed. We considered this a biologically reasonable simulation of mouth closure because the osteological borders identified are naturally opposed in situ and would need to be in close proximity along their entire lengths to seal the mouth and streamline the head. Moreover, the aforementioned dissections indicated that in rorquals these osteological borders are covered by only thin layers of soft tissue.

The 3D conformal coordinate transformation specified all rotations and translations of the mandibular data set needed to minimize the sum of the squares of the distances between the 2 coordinate sets after rotation and transformation (cf. Wolf and DeWitt 2000). The only exception to the standard 3D coordinate transformation was with regard to scale. The ratio of the scales of the mandibular and cranial coordinate sets was specified a priori as 1:1, because the metric scale in the stereoimages allowed uniform calibration of scale in the 2 coordinate systems. The 3D root mean square residual error of the transformation (Table 2) then quantified the average error in what can be called a 3D least squares fit of the 2 anatomical surfaces, with a particular trial being defined by the initial coarse alignment.

Further, this same computational approach allowed us to bring together in computer space for quantitative investigation all the photogrammetric data describing the craniomandibular system of a given specimen. Consistent with the above procedure, all photogrammetric data sets collected from the mandible were rotated and translated in accordance with the results of the 3D coordinate transformation. The transformed mandibular data sets were then imported to a 3D visualization and measurement program (Surfer Access System, Golden Software, Inc., Golden, California) along with the cranial data to complete a half model for each specimen. Internal measurements subsequently were made with this program on the 3D half models visualized from various angles. These measurements determined critical anatomical relationships after simulated mouth closure (Table 2). In addition, chiral (mirror image) transformations of the right craniomandibular data sets with respect to the midsagittal plane were used to plot bilaterally symmetrical images with a mechanical printer (Figs. 2 and 3).

**Table 1.**—Reproducibility of spot elevations obtained with 35-mm photogrammetric technique. Data give repeat plots of a single point marked with a dot on the cranium of a minke whale.

<table>
<thead>
<tr>
<th>Observation</th>
<th>x</th>
<th>y</th>
<th>z</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>4.327</td>
<td>6.990</td>
<td>0.322</td>
</tr>
<tr>
<td>2</td>
<td>4.305</td>
<td>7.034</td>
<td>0.257</td>
</tr>
<tr>
<td>3</td>
<td>4.331</td>
<td>7.032</td>
<td>0.279</td>
</tr>
<tr>
<td>4</td>
<td>4.325</td>
<td>6.985</td>
<td>0.173</td>
</tr>
<tr>
<td>5</td>
<td>4.309</td>
<td>7.021</td>
<td>0.200</td>
</tr>
<tr>
<td>Variation</td>
<td>0.026</td>
<td>0.049</td>
<td>0.149</td>
</tr>
</tbody>
</table>

**RESULTS**

A striking agreement existed between the anatomically based prediction and the 3D observations made by close-range photogrammetry. In the simulated mouth-closed position, the 4 skulls studied all took on a highly streamlined appearance, as well as the prognathous condition normally seen in swimming rorquals (Fig. 3). And despite a close fit between the dorsal border of the mandible and labial border of the maxilla, as indicated by 3D root mean square residual errors ranging from 0.8 to 1.2 cm, no substantial interference was found between any element of the mandible and the cranium (Table 2). Furthermore, z-coordinates consistently showed the origin of the superficial masseter muscle to rest ventral to the crest of the coronoid process, and that the insertion of this muscle was more ventral. In addition, the anterior terminus of the crest of the coronoid process (point CC) lay immediately adjacent to the rim of the SP in the xy plane (Fig. 3), or if not (trial 1 for specimen 55-8202; Table 2), could be made to do so by the 3D conformal coordinate transformation method after slightly different initial coarse longitudinal alignment of the mandible (Trial 2 for 55-8202; Table 2; Fig. 3). Last, consistently positive differences between z-coordinates for point CC and the closest point on the maxilla showed that the crest of the coronoid process always fell dorsal to the rim of the SP (Table 2). These observations indicated that when the mouth is closed the tendon of a contracted superficial masseter muscle would be situated spatially to control the mandible by virtue of having entrained the coronoid process. They also indicated that in the mouth-closed position the coronoid process of the mandible in *B. acutorostrata* is positioned to articulate with the maxilla. The hooklike configuration of the well-developed, laterally deviated coronoid process allows it to engage the rim of the SP, to glide along it. As such, the lateral surface of the coronoid process just below its crest would provide the primary articulating segment of the mandible. It also is apparent (Fig. 2C) that the sloped anterior border of the coronoid process may contribute an extension of this articulating surface, given the elevating pull of the temporalis muscle on the coronoid (cf. Lambertsen et al. 1995). As described elsewhere (Lambertsen et al. 1995), this surface is characterized by dense white connective tissue intimately attached to the bone.

**DISCUSSION**

The biomechanics and evolutionary significance of the maxillomandibular articulation discovered warrant further research. Our functional interpretation is that this articulation is at least a mechanism by which the energy cost of carrying a gigantic, expandable mouth at speed through an aqueous medium could be kept to a minimum. This is because this cam system probably serves in part to close the mouth tightly and streamline the head. Given the anatomy of this system (Figs. 1–3), the principal mechanical advantage achieved would be equivalent to that of the screw.

During the final stages of mouth closure, forceful apposition of the lips thus evidently would be achieved in critical aspects by contraction of the small superficial masseter muscle, despite
both the mass of the jaw and the known passive tendency of the mandibles to rotate outward around their longitudinal axes (Lillie 1915; Lamberty et al. 1995). This forceful apposition presumably would enable the establishment of a hydrostatic oral seal in a craniodistal mandibular system otherwise adapted (or preadapted) for engulfment feeding. Negative oral pressure relative to ambient then probably could serve to maintain mouth closure with no requirement for continuous contraction of other cranial muscles, such as the massive temporalis–deep masseter complex.

In fact, given the relatively flat rostrum characterizing rorquals (Ridgway and Harrison 1985; True 1904), negative oral pressure generated by asymmetrical flow of water over the head could result in a virtually self-tending system to maintain mouth closure. If this asymmetrical flow established a mere superficial masseter in this system would be to counter torques, a consequence of increased tension in the wall of the ventral surface of the head. These torques, a consequence of increased tension in the wall of the ventral pouch, would tend to rotate the bowed mandibles outward around their longitudinal, or α-axes (Lamberty et al. 1995).

Hence, one major physiological benefit of a maxillomandibular cam articulation would be enhanced craniodistal stability in the face of the flow asymmetries and drag forces inevitably associated with normal swimming and surfacing. In addition, such a stabilizing mechanism has important evolutionary implications. With it, the newly adapted lineage probably could evolve rather broad rostrums—a distinguishing characteristic of all modern rorquals (Kellogg 1928; True 1904). By the same token, the absence of such a stabilizing mechanism in both right whales (Balaenidae) and gray whales (Eschrichtiidae) probably explains their remarkably narrow rostrums. In comparative terms, the narrow rostrums of right and gray whales (Kellogg 1928) reduce the horizontal area of the mouth over which hydrodynamic pressures act. In this light, examination of our data suggests that the laterally compressed configuration of the rostrums of both balaenids

| Table 2.—Spatial relationships between cranium and mandible in the North Atlantic minke whale (Balaenoptera acutorostrata) after mathematical simulation of mouth closure. All data are in centimeters. See Fig. 3 for dorsal view of corresponding 3-dimensional models. “Fit” indicates that simulation brought coronoid process of mandible into direct juxtaposition with rim of suborbital plate of maxilla without causing substantial interference between mandible and cranium. Juxtaposition of anterior end of crest of coronoid process (point CC) and rim of suborbital plate (SP) in xy plane is indicated by delta x and delta y values approximately equal to zero for “CC-SPmin,” the minimum distance between point CC and the suborbital plate. Positive delta z values for CC-SPmin further indicate that crest of coronoid process consistently fell dorsal to the rim of the SP, as required for articulation of the mandible and maxilla. “No fit” indicates that a 3-dimensional fit was not evident in a particular trial because of finding of substantial spatial interference between bones; however, see data for trial 2 for same specimen, 55-8202 (2), which indicate satisfactory fit after slightly different initial longitudinal alignment of mandible. “NP” designates a measurement that was not possible because of the perspective of stereorimages used for 3-dimensional data capture from mandible of specimen 571236.

<table>
<thead>
<tr>
<th>Specimen number (trial number)</th>
<th>55-8201 (2)</th>
<th>571236 (3)</th>
<th>55-8202 (1)</th>
<th>55-8202 (2)</th>
<th>CN16xx (2)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Length of skull (L)</strong></td>
<td>180.3b</td>
<td>115.7b</td>
<td>149.4</td>
<td>149.4</td>
<td>164.7</td>
</tr>
<tr>
<td><strong>Width of skull</strong></td>
<td>104.3</td>
<td>56.9</td>
<td>90.6</td>
<td>90.6</td>
<td>85.6</td>
</tr>
<tr>
<td><strong>Forward placement of mandibular data set with respect to cranial data set</strong></td>
<td>1.04 L</td>
<td>1.04 L</td>
<td>1.04 L</td>
<td>1.09 L</td>
<td>1.015 L</td>
</tr>
<tr>
<td><strong>Three-dimensional root mean square residual error</strong></td>
<td>1.1</td>
<td>0.9</td>
<td>1.1</td>
<td>1.2</td>
<td>0.8</td>
</tr>
<tr>
<td><strong>Minimum distance between glenoid fossa and mandibular condyle</strong></td>
<td>2.7</td>
<td>8.2</td>
<td>3.0</td>
<td>5.4</td>
<td>7.2</td>
</tr>
<tr>
<td><strong>CC-SPmin</strong></td>
<td>3.8</td>
<td>3.1</td>
<td>7.7</td>
<td>6.0</td>
<td>2.5</td>
</tr>
<tr>
<td>Delta x</td>
<td>-0.5b</td>
<td>-1.8b</td>
<td>-1.7b</td>
<td>-0.2b</td>
<td>-1.8b</td>
</tr>
<tr>
<td>Delta y</td>
<td>-0.1b</td>
<td>2.4</td>
<td>4.9b</td>
<td>0.4</td>
<td>-0.3b</td>
</tr>
<tr>
<td>Delta z</td>
<td>3.8</td>
<td>0.7</td>
<td>5.6</td>
<td>6.0</td>
<td>1.7</td>
</tr>
<tr>
<td><strong>Elevations (z)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Closest point on frontal bone from crest of coronoid process</td>
<td>981.7d</td>
<td>991.7</td>
<td>983.7c</td>
<td>978.5</td>
<td>984.1d</td>
</tr>
<tr>
<td>Crest of coronoid process</td>
<td>981.0d</td>
<td>993.5</td>
<td>981.3c</td>
<td>980.8</td>
<td>984.0d</td>
</tr>
<tr>
<td>Masseteric process (origin of superficial masseter muscle)</td>
<td>985.4</td>
<td>994.6</td>
<td>988.0</td>
<td>987.8</td>
<td>987.4</td>
</tr>
<tr>
<td>Maximum elevation of insertion of superficial masseter muscle</td>
<td>1,000.8</td>
<td>NP</td>
<td>994.8</td>
<td>993.6</td>
<td>997.6</td>
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<tr>
<td><strong>Summary result</strong></td>
<td>Fit</td>
<td>Fit</td>
<td>No fit</td>
<td>Fit</td>
<td>Fit</td>
</tr>
</tbody>
</table>

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\* Measurement is an underestimate because of minor breakage of tip of premaxillary bone.

\* Designates trivial degree of spatial interference between coronoid process of mandible and suborbital plate of maxilla, direction of which is accounted for by absence of labial soft tissue.

\* Data indicating lack of fit in this trial.

\* Designates trivial degree of spatial interference between mandibular coronoid process and frontal bone, direction of which is accounted for by absence of labial soft tissue.

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esrichtiids is a primitive locomotor adaptation. Like the maxillomandibular cam articulation discovered, the skull configuration of balaenids and esrichtiids would enhance craniomandibular stability, as required for effective forward movement.

Going one step further, the biophysical problem of maintaining craniomandibular stability at speed in a dense fluid medium also may have given way to a qualitative change in function. That is, the cam articulation of *B. acutorostrata* likely permits high amplitude rotations of the bowed mandibles around their longitudinal, or α-axes, rotations that appear critical for engulfment feeding. Biomechanical experiments have demonstrated that during feeding these rotations would involve an automatic outward (negative) α-rotation of the mandibles at low gape angles that is partly reversed at high gape angles due to the operation of an internal stay apparatus (Lambertsen et al. 1995). In this way, the mass of prey-laden water engulfed can be caught before bouncing back out of the mouth (prey included). Moreover, the phenomenon of bounce, or mass rebound, thereby can be used to help drive the massive jaw closed, so as to project the water mass engulfed, as a jet, through the baleen (Lambertsen et al. 1995). In contrast, the skim-feeding right whales and bottom-feeding gray whales make no known use of mass-rebound, or bounce phenomena. The former is a slow, continuous filtration process, whereas the latter uses suction to power prey acquisition (Berta and Sumich 1999; Lambertsen 1983; Nerini 1984; Pivorunas 1979; Werth 2000).

However, the near certainty of a hydrostatic oral seal in rorquals also points to the critical biomechanical problem of opening the mouth at speed. In particular, analysis thus far indicates a critical need for a trigger mechanism (sensu Lotka 1945) to enable precisely timed deployments of the rorqual’s mandibular apparatus and ventral pouch in response to sensory stimuli. This is particularly so because anticipatory modification of the shape of the mental region, so as to dynamically preload the mandibular apparatus, is a likely means to ensure rapid depression of the lower jaw during engulfment, with minimization of a prey-scattering bow wave (Lambertsen et al. 1995). Anticipatory change in head shape to take advantage of hydrodynamic phenomena presumably would involve forward displacement of the massive tongue inside the mouth by contraction of the genioglossus muscle (cf. Lambertsen 1983). The resultant increased convexity of the mental region would be expected to increase both flow asymmetry and negative lift acting on the lower jaw. Supporting this notion, unusually high tissue stress in the mental region is suggested by the finding of Pivorunas (1977) of a fibrocartilaginous skeleton within the wall of the ventral pouch just posterior to the mandibular symphysis. This Y-shaped structure extends caudally from the fibrocartilage of the symphysis, reinforcing the ventral pouch.

Consequently, the question now demanding further research is whether the novel articulation discovered also serves as a key part of a trigger mechanism for deployment, at speed, of the rorqual’s remarkable feeding apparatus. Our results provide no data on how a hydrostatically sealed, dynamically loaded craniomandibular system could be opened in a rapidly swimming whale. One can only conjecture that the huge sternomandibularis muscle of rorquals, which pulls posteriorly on the mandibular apparatus (Shulte 1916), is somehow involved.

Even so, there can be little doubt that those whales possessing the cam articulation discovered did enter a new adaptive zone previously unavailable to vertebrates. Defined by a novel ability to carry a gigantic, expandable mouth at high speed, this “rorqual adaptive zone” would be characterized biophysically by unsurpassed phenotypic scope for action and the use of mass-rebound or bounce phenomena in feeding. If also equipped with a trigger-release mechanism for precisely timed mandibular deployments, the newly adapted (= balaenopterid) lineage then could reap the huge dietary gains brought to it by positive feedback. That is, the larger and faster its members became, the more they could engulf and filter, because feeding power in rorquals is derived principally from the kinetic energy of the moving body (Lambertsen et al. 1995). This could have allowed nektom such as squid and gregarious fish—in aggregate probably strong primordial competition for planktonic resources—to be exploited efficiently as prey. In this light, it is more than...
noteworthy that neither balaenids nor eschrichtiids are known to feed on nekton. The only reported exception is an occasional small fish found in the stomachs of bowhead whales (B. mysticetus), thought to have been ingested incidentally with planktonic prey (Lowry and Burns 1980). This contrasts with a diet in most balaenopterid species that does include significant quantities of fish, although zooplankton such as krill (Euphausiidae) may be preferred (Gaskin 1976, 1982).

Consuming one’s competitors efficiently is probably an effective part-time evolutionary strategy. Moreover, as 1 element of a broader feeding repertoire, it can be pursued opportunistically when preferred prey items are either scarce or distant. On this and the above bases, we suggest that the novel articulation discovered probably accounts for the adaptive radiation of Balaenopteridae, which includes the blue whale (Balaenoptera musculus), the most powerful nontechnological animal ever to exist. Balaenopteridae, notably, is the only mysticete family to have undergone adaptive radiation (Whitmore 1994).

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LITERATURE CITED


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