RESEARCH ARTICLE

Bone-Breaking Bite Force of *Basilosaurus isis* (Mammalia, Cetacea) from the Late Eocene of Egypt Estimated by Finite Element Analysis

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Abstract

Bite marks suggest that the late Eocene archaeocete whale *Basilosaurus isis* (Birket Qarun Formation, Egypt) fed upon juveniles of the contemporary basilosaurid *Dorudon atrox*. Finite element analysis (FEA) of a nearly complete adult cranium of *B. isis* enables estimates of its bite force and tests the animal’s capabilities for crushing bone. Two loadcases reflect different biting scenarios: 1) an initial closing phase, with all adductors active and a full condylar reaction force; and 2) a shearing phase, with the posterior temporalis active and minimized condylar force. The latter is considered probable when the jaws were nearly closed because the preserved jaws do not articulate as the molariform teeth come into occlusion. Reaction forces with all muscles active indicate that *B. isis* maintained relatively greater bite force anteriorly than seen in large crocodilians, and exerted a maximum bite force of at least 16,400 N at its upper P³. Under the shearing scenario with minimized condylar forces, tooth reaction forces could exceed 20,000 N despite lower magnitudes of muscle force. These bite forces at the teeth are consistent with bone indentations on *Dorudon* crania, retract-and-shear hypotheses of *Basilosaurus* bite function, and seizure of prey by anterior teeth as proposed for other archaeocetes. The whale’s bite forces match those estimated for pliosaurus when skull lengths are equalized, suggesting similar tradeoffs of bite function and hydrodynamics. Reaction forces in *B. isis* were lower than maxima estimated for large crocodylians and carnivorous dinosaurs. However, comparison of force estimates from FEA and regression data indicate that *B. isis* exerted the largest bite forces yet estimated for any mammal, and greater force than expected from its skull width. Cephalic feeding biomechanics of *Basilosaurus isis* are thus consistent with habitual predation.
Introduction
Cetacean Evolution

Modern cetaceans (Odontoceti and Mysticeti) emerged from archaeocete whales in the latest Eocene or earliest Oligocene, ca. 34 m.y.a. [1], [2], [3], [4]. Archaeocetes originated from terrestrial artiodactyls around the Paleocene-Eocene boundary, ca. 54 m.y.a. [3], [5], [6], with the earliest representatives of archaeocete whales appearing in the early Eocene [4].

The transition from life on land to life in the sea took place within archaeocetes throughout the Eocene, as is documented by various semiaquatic (protocetids, ambulocetids, andremingtonocetids) and fully-aquatic forms (basilosaurids) in the middle and late Eocene, respectively (for reviews see, e.g., [3], [4]). This transition brought about morphological and functional changes that affected not only the locomotor apparatus, sensory and reproductive organs, but also feeding and diet [3], [7], [8], [9], [10], [11], [12], [13]. Isotopic and morphological studies [14], [15], [16] show that the transition to a marine environment happened relatively fast, and that semiaquatic forms were likely already marine.

Feeding and Diet

Primitive terrestrial artiodactyls had bunodont teeth, and were most likely herbivorous and chewed their food [13]. Modern whales, on the other hand, do not masticate. Mysticetes filter-feed, while odontocetes capture their prey and swallow it whole or in large pieces. Suction feeding is also widespread in both groups [17], [18], [19].

Shearing facets on the cheek teeth of archaeocete whales indicate that archaeocetes chewed their food. Pakicetids and protocetids had a protocone on their molars, indicating that some grinding function was retained. The cheek teeth of basilosaurids were mediolaterally compressed and lacked grinding surfaces [13], [20]. Fahlke et al. [21] observed tooth wear and bite marks suggesting that the basilosaurid Basilosaurus isis used a single, orthal-retractional occlusal movement to puncture, crush, and shear its food.

Stomach contents of the basilosaurids Basilosaurus cetoides and Dorudon atrox consist of different teleost fish and, in the case of B. cetoides, sharks of up to 50 cm in length [10], [22]. Microwear analysis suggests that archaeocetes generally had quite a mixed diet including crustaceans and mollusks besides fish. In some species, e.g., Basilosaurus isis, tooth wear indicates the consumption of large hard objects such as vertebrate bones [23]. Very destructive tooth wear in B. isis and the protocetid Babiacetus has been interpreted as evidence of forceful crushing of large, hard objects, such as mammal bones, thus indicating the consumption of meat [13], [21]. Fahlke [24] matched morphology and positions of bite marks on skulls of juvenile D. atrox to the dentition of an adult Basilosaurus isis, suggesting that B. isis, like the modern killer whale (Orcinus orca), included other cetaceans in its diet.

Estimating bite force in Basilosaurus isis

Some carnivorous vertebrates exert high bite forces to comminute bone, and bite marks and tooth wear [21], [23], [24] strongly suggest that Basilosaurus isis applied such forces on its prey. Estimating bite forces of B. isis enables us to test its attribution as the animal that left bite traces on juvenile Dorudon, to determine relative forces at different teeth, and hence to infer aspects of its feeding behavior. Many authors have estimated bite force by using Thomason’s [25] dry skull method to approximate muscle force [26], and Finite Element Analysis (FEA) to obtain reaction forces at the teeth and jaw joint. In mammals and other synapsids, including B. isis, the zygomatic arches and braincase delimit anatomical cross-sectional areas (ACSA) of jaw muscles [25], [27]. Multiplying ACSA by a specific tension (force/area) gives an estimate of adductor
muscle force. This initial estimate can be corrected for muscle pennation angles [25], other aspects of muscle function [28], and refined specific tensions [29], and checked against experimental results for living animals [30], [31]. Muscle forces are then applied to FEA models, which are constrained at the jaw joint and bite points to obtain food and joint reaction forces.

Modelling Basilosaurus bite force with tooth constraints alone can assess the effectiveness of hypothesized orhthal retractional shear on the food, as the teeth near occlusion. Bite force modelling with FEA usually assumes maximal force with all adductors active, and the upper and lower jaws in full articulation. With a retractive, food-shearing component to jaw closure evident from Basilosaurus bite marks [21], joint reaction forces would be minimized [32], [33], [34] and food reaction forces maximized. In such a bite scenario, the mandible would behave temporarily as a direct link between the cranium and the food, rather than a lever actuated about centers of rotation at the jaw joints [32], [33], [34]. Physical manipulation of the original B. isis mandible relative to the cranium confirms that the articular condyle of B. isis shifts anteriorly out of the cotyle as large molariform teeth occlude; these kinematics and morphology are currently under study for more extensive treatment. The animal’s application of tooth reaction forces hence would be more versatile than in carnivorous animals with tightly articulating jaws, such as felids, mustelids, and crocodylians. FEA enables virtual activation of only those adductor muscles that would cause the hypothesized shearing orhthal retraction of the lower jaw.

We combine the dry-skull method with FEA to model and estimate bite force for Basilosaurus isis as a primarily vertical, crushing bite with all adductor muscles activated, and with a shearing load case powered by the posterior temporalis alone. Because B. isis tooth wear and bite marks on Dorudon atrox indicate preferential bite positions, it is possible to localize estimates of bite force to functionally critical locations. Such bites by B. isis would be analogous to those alligators exert with their molariform teeth to break turtle shells [30], and jaguars biting with their canines into the crania of peccaries [35]. Bite force estimates for B. isis can facilitate comparisons of function and absolute bite force between predatory aquatic tetrapods with skulls in the 0.8–2 meter range, including the pliosaurs Kronosaurus and Pliosaurus [36], [37], large crocodilians [30], [36], [38], and more recent cetaceans. These analyses of Basilosaurus can anchor future comparative evolutionary studies of bite force in archaeocetes during their land-sea transition, and of bite force in more derived whales [39].

With its enormous skull and body size, Basilosaurus is an outlier among carnivorous mammals for which bite force data are available. Thus, we compare our modeled bite force with estimates for other mammals [26], [29] to test whether B. isis had a particularly forceful bite for a mammal with its skull dimensions. Previous bite force estimates are based on diverse methods, including the dry skull method [25] and FEA, and comparisons among these modeled estimates warrant caution. Notably, dry skull mammal studies present a comprehensive and rigorous database of bite force estimates, and these estimates are only slightly lower than FEA results, which have muscle forces distributed across attachments [27], [36], [37] rather than between estimated centers of pull [25], [26], [29]. The current study’s bite force comparisons between B. isis and other mammals will therefore be worthwhile and testable by applying FEA [28], [30], [31] to more carnivorous mammals in Wroe and colleagues’ original results [26]. We construct a simple lever model of B. isis (Fig. 1) to check correspondence between simplified dry skull and 3D FEA approaches.

FEA approach: testing bite force with plate element and solid models from surface scans

Normally in FEA of vertebrate skulls, a virtual surface derived from CT data is meshed volumetrically, creating a solid mesh of internal brick elements. Although such a volumetric FE
Fig 1. Jaw muscles of *Basilosaurus isis* and constraints for FEA. A. Jaw muscles of *B. isis* and muscle vector and moment arms for leverage-based force calculation. B. Adductors (red arrows) mapped onto a CT-based finite element model of the cranium of *Basilosaurus isis* WH-74, including the dentaries. C. Constraints for finite element analyses. In the all-muscles active analysis, the cranium was fully constrained at the left and right temporomandibular joints (TMJ), and tooth constraints were applied in respective bite analyses. In the posterior shear analysis, the only active muscles are the posterior temporalis, and only P₃ is constrained.

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mesh is necessary to resolve internal stresses, simpler models can be used to test hypotheses of bite force and other aspects of structural behavior [31], [40], [41], [42], [43], [44]. We introduce two surface-based models of *Basilosaurus isis* derived from a CT scan of a cast reconstructed from separate but perfectly articulating original bones, to explore the precision of different FE models for obtaining bite reaction forces. The original fossils could not be safely assembled and scanned together, and the skull’s internal structure is currently being described. However, our bite force estimates based on surface data can be tested in the future against models that include internal CT data of individual bones.

To estimate bite force in *Basilosaurus isis*, our FE models respectively use thickened plate elements [45] and a cavity-filling solid mesh to approximate 3D cranial geometry, bracketing the complex internal anatomy (with braincase and sinus cavities) with hollow and fully solid structures. For structures consisting mostly of discrete walls (such as a vertebrate cranium) whose width is 10% or less than the whole object’s dimensions, plate elements have advantages over a solid internal mesh of those walls. Plate elements are computationally time-efficient, enabling large meshes, and testing with many loadcases and resolutions to estimate peak stresses (see S1 Text). Because plate elements can vary in thickness, they enable us to explore possible stress and strain distribution in hollow structures modeled with external surface scans from fossil CT scans with suboptimal internal resolution, and of skulls reconstructed from CT scans of individual bones as in the current study.

Element type and thickness of plate elements theoretically have little effect on interpretations of theoretical feeding forces if the cranium deforms little. To compare the effects of a solid mesh versus plate (and modeled bone) thickness on resulting reaction forces, we ran a sensitivity analysis by varying model type—a solid volume and three different plate thicknesses—with muscle forces held constant. We predicted that stress and strain values would decrease linearly with increasing plate thickness, but that theoretical food and jaw joint reaction forces would remain consistent regardless of plate thickness.

**Materials and Methods**

**Specimen and Manual Preparation**

WH-74 (WH for Wadi Al-Hitan) is a virtually complete skeleton of an adult individual of *Basilosaurus isis* with a total body length of ca. 16 m. It was excavated in the shallow-marine deposits of the late Eocene (Priabonian) Birket Qarun Formation of Wadi Al-Hitan, Fayum Province, Egypt (ca. 150 km southwest of Cairo), in 1989 and 2005. For more geographical, geological, and paleoenvironmental information on Wadi Al-Hitan, consult Gingerich [46] and Peters et al. [47].

WH-74 is currently housed in trust at the University of Michigan Museum of Paleontology (UMMP), Ann Arbor, Michigan, USA. The cranial elements and dentaries were found disarticulated in the field. The individual cranial elements included the left premaxilla and maxilla (disarticulated), the right premaxillae and maxilla (articulated), the frontal shield (frontals, parietals, and nasal bones in articulation), the articulated braincase/basicranium, both isolated squamosals, and left and right bullae. No taphonomic deformation was noted except for a slight mediolateral flattening of the right dentary. After preparation, the individual cranial elements of WH-74 were molded and casted, and the casts reassembled into a whole skull at the UMMP. Our skull length estimate for the entire skull of WH-74 is 113 cm.

All elements of the reconstructed skull belong to WH-74, and no other individual was used for the digital reconstruction. At least one disarticulated jugal and both pterygoid bones were confirmed after our reconstruction, and confirmed the accuracy of the reconstructed skull and cast. The completeness of these remains, their individual taphonomic integrity and perfect re-
articulation with each other, and similarity to other taphonomically intact *Basilosaurus* skulls engender confidence in the cast skull for biomechanical study.

**Digital Preparation**

Cranial parts, dentaries, and the composite cast of the cranium of WH-74 were scanned using computed tomography (CT) at the University of Michigan Department of Radiology (scanner GE HD-750). In-plane resolution was 0.879 mm, and slice thickness was 0.625 mm. Three-dimensional (3D) surfaces were extracted from image stacks using Amira 5.0 and post-processed in Materialise Magics 14. Slight taphonomic flattening of the right dentary was removed in Autodesk 3ds Max 2010 with reference to the undistorted left dentary and other specimens by bending the surface manually to allow for best-fit occlusal articulation of the upper and lower tooth rows. The dentaries were aligned with the cranium using Materialise 3-Matic 4.4, following the best possible dental occlusion.

**FE model geometry and material properties**

For the plate element models, the cranium and dentary surfaces were exported from Materialise Magics as .stl files (binary, little endian) into Autodesk Simulation. The complete model is available as S1 Dataset, under Supporting Information. Element type was set to plate elements. To assess the sensitivity of bite force and stress to plate thickness, four models were constructed with respective thicknesses of 0.5, 1, 1.5, and 2 cm, in the range found for posterior dentary bone of *Basilosaurus isis* [12]. Thicknesses of 1–2 cm ensured that the teeth and sagittal and nuchal crests would be solid, and that the braincase and airways would be hollow. However, CT scans reveal that the frontal and parietals are thicker than 2 cm between their external surfaces and the endocranial cavity.

For the solid mesh model, we imported the surface into Materialise Mimics for solid meshing in Nastran format (.nas). This model was a simplified representation of the cranium because all internal cavities were meshed solid. Autodesk Simulation did not accept the model, so we imported the mesh into Strand7 for solving. We subdivided the mesh in Strand7 to produce a model with 1,256 million four-node tetrahedral elements. All material properties, constraints, and muscle forces were applied in Strand7 exactly as for the plate models in Autodesk Simulation. Autodesk Simulation and Strand7 both use standard Nastran-related mathematical code in their FE solvers, and their results are precisely the same with identical models.

In the absence of data on material properties of archaeocete cranial tissues, we initially assigned isotropic properties to the entire model in an overlapping range for mammalian compact bone and dentine (elastic modulus $E = 17.4$ GPa, Poisson’s ratio = 0.34 [48]). The enamel on the teeth of *Basilosaurus is* very thin, so to preliminarily examine stresses in within the teeth we considered properties of dentine to be appropriate, especially where the enamel has worn down. Because whales are cetartiodactyls, we further ran an analysis using properties of bovid Haversian bone ($E = 10$ GPa, Poisson’s ratio = 0.4 [40]). The lower stiffness (stress/strain) of Haversian bone will give unrealistically high strain readings for the teeth, but may be more realistic for the cranial bone. Because material properties were considered isotropic (independent of direction), Autodesk Simulation and Strand7 estimated shear modulus from $E$ and Poisson’s ratio.

**Muscle force estimates**

In order to estimate the bite forces generated by *Basilosaurus isis* during the occlusal movement of the lower jaw, the position, magnitude and direction of pull of the elevator muscles of WH-74 were reconstructed in Autodesk Simulation. Muscles exert isometric force when velocity is
0 m/sec, as might occur when teeth of a biting animal encounter resistant food. This force will equal a cross-sectional area of the muscle times a specific tension $ST$ (force/area). Isometric specific tension in vertebrates is often set at 30 N/cm$^2$ \cite{25, 49}. Complexities of muscle geometry, including pennation and varying fiber lengths, can increase this specific tension for a given anatomical cross sectional area (ACSA), by increasing the physiological cross sectional area (PCSA: \cite{50}; dramatically in some reptiles: \cite{51}, \cite{52}). We apply two specific tensions to \textit{B. isis} simulations: 30 N/cm$^2$ assuming simple geometry, and 37 N/cm$^2$ to account for realistic pennation of mammalian jaw adductors \cite{25}, \cite{29}, \cite{53}.

Cross-sectional areas of the musculus (m.) temporalis were estimated with the dry-skull method \cite{25}. A 3D, stl surface model of the articulated \textit{Basilosaurus isis} cranium and dentaries was exported from Materialize Magics into Autodesk Simulation. A posterodorsal-view screen capture of the model, with scale and without perspective distortion, imaged the area of m. temporalis between the braincase and zygomatic arches.

Anatomical cross-sectional areas (ACSA) were estimated using two methods. First, measurements of major and minor radii enabled approximation of the areas as ellipses, using the equation $ACSA = \pi \times r_m r_{min}$. Second, the image was imported into ImageJ (National Institutes of Health of the United States: rsb.info.nih.gov/ij/), its scale set to the original fossil’s size, and ACSA calculated within anatomical regions traced manually with the pen tool.

Estimating ACSA for the masseter was more difficult than for the well-delineated temporalis. The zygomatic arches and origin areas for m. masseter are slender in \textit{Basilosaurus isis}, and the masseteric fossa is shallow. As a starting point for forces of m. masseter, we assumed that its ACSA was 10% that of m. temporalis. This area is reasonable considering the length of the masseter’s origin, but may be an overestimate considering the large ACSA of the temporalis. Varying the area would multiply ad hoc assumptions with minimal realistic effects on overall bite force, and we suspect that the masseter assisted the medial pterygoid in laterally positioning the lower jaws (see below).

Origins of temporal and masseter muscles were positioned on the model cranium of WH-74 based on osteological correlates, i.e., recognizable attachment surfaces, on the cranium and dentaries. Vectors were distributed homogeneously to nodes of the FE model on these surfaces. Force directions were estimated by measuring distances from the centroids of muscle origination to their insertion surfaces on the dentaries (\textit{Table 1, Table 2}), which were digitally aligned to the cranium with the mouth slightly opened. From these dimensions, $x$, $y$, and $z$ force components were calculated trigonometrically. Muscle force magnitudes were divided equally among divisions of the temporalis and masseter. Origins for the temporalis include the nuchal crest, the temporal region anteroventral to the nuchal crest, and anterior, middle, and posterior regions of the sagittal crest. We found that attachment surfaces of the masseter group represent superior and inferior m. masseter, and m. zygomaticomandibularis (Fig. 1A), in contrast to Uhen’s \cite{10} results for \textit{Dorudon atrox}, but in agreement with the results of Carpenter and White \cite{54} for another basilosaurid, \textit{Zygorhiza kochii}. Magnitude for each temporalis division was therefore 1/5 of the overall magnitude calculated for the muscle, and for the masseter 1/3 of its full force magnitude was applied to each of its divisions.

No forces were estimated for the pterygoid muscles, because their attachments are ambiguous and the function of these muscles in mammals is inconsistent with powerful adduction. The lateral pterygoid protracts and opens the lower jaw \cite{55}, and ensures proper position and function of the temporomandibular joint meniscus. Inclusion of the medial pterygoid (m. pterygoideus internus) would increase estimated adductor force, indicating an underestimate in our values. However, the pterygoid bones are partially broken and were reconstructed in the composite cast of WH-74, and no unambiguous muscle attachment surfaces could be identified on the original bones. Thus we could not confidently reconstruct the position and extent of the
origin m. pterygoideus internus, although the muscle’s overall morphology probably resembled that of other mammals (Fig. 1A). Divisions of m. pterygoideus internus normally insert onto the posteromedial surface of the dentary, which is a thin flange of bone in Basilosaurus isis (Fig. 1C) without clear demarcations of muscle scars. These divisions are highly active and effective during lateral grinding in pigs [56], [57], [58]. All of these factors suggest low adductor force of any one division of m. pterygoideus internus, and little contribution to adduction force compared with the temporalis muscles.

Table 1. Inputs and results for estimating adductor muscle forces in Basilosaurus isis, assuming 30 N/cm² baseline isometric specific tension (ST).

| Left side | Temporalis Muscle Area (cm²) | Muscle Force 30 N/cm² F_{temporalis} | Origin to insertion (mm) |
|-----------|-----------------------------|--------------------------------------|------------------------|
| 896       | 26889                       |                                       |                        |
| Division  | F_{division} = F_{temporalis}/5 | x         | y       | z     | F_{x} | F_{y} | F_{z} |
| m. temporalis |                         |                        |                        |
| temporal  | 5378                        | 148                   | 47                   | 12    | 5105  | 1641  | 412   |
| nuchal    | 5378                        | 171                   | 73                   | -91   | 4446  | 1890  | -2363 |
| sag. crest p | 5378                      | 63                    | 166                  | -115  | 1607  | 4227  | -2910 |
| sag. crest m | 5378                      | -50                   | 173                  | -126  | -1221 | 4225  | -3095 |
| sag. crest a | 5378                      | -3                    | 115                  | -136  | -87   | 3472  | -4106 |
| m. masseter |                            |                        |                        |
| F_{masseter} |                     |                        |                        |
| Division  | F_{division} = F_{masseter}/3 | X         | y       | z     | F_{x} | F_{y} | F_{z} |
| Superior  | 896                         | -399                 | 13                   | -215  | -789  | 26    | -425  |
| Inferior  | 896                         | -181                 | 5                    | -169  | -655  | 17    | -612  |
| zygomat. | 896                         | 49                   | -77                  | -123  | 286   | -449  | -721  |

| Right side | Temporalis Muscle Area (cm²) | Muscle Force 30 N/cm² F_{temporalis} | Origin to insertion (mm) |
|------------|-------------------------------|--------------------------------------|------------------------|
| 760        | 22806                         |                                       |                        |
| Division   | F_{division} = F_{temporalis}/5 | x         | y       | z     | F_{x} | F_{y} | F_{z} |
| m. temporalis |                         |                        |                        |
| temporal   | 4561                         | 156                   | -63                  | 16    | 4207  | -1709 | 433   |
| nuchal     | 4561                         | 170                   | -113                 | -108  | 3595  | -2239 | -2123 |
| sag. crest p | 4561                      | 69                    | -185                 | -107  | 1406  | -3755 | -2174 |
| sag. crest m | 4561                      | -61                   | -165                 | -109  | -1335 | -3644 | -2397 |
| sag. crest a | 4561                      | -6                    | -127                 | -147  | -149  | -2981 | -3449 |
| m. masseter |                            |                        |                        |
| F_{masseter} |                      |                        |                        |
| Division   | F_{division} = F_{masseter}/3 | X         | y       | z     | F_{x} | F_{y} | F_{z} |
| superior   | 760                         | -423                 | -46                  | -207  | -680  | -74   | -332  |
| inferior   | 760                         | -216                 | -3                   | -152  | -621  | -110  | -438  |
| zygomat. | 760                         | 20                   | 88                   | -79   | 128   | 559   | -499  |

Areas are estimated in ImageJ, and multiplied by ST to calculate overall m. temporalis force F_{temporalis}. Total m. masseter F_{masseter} were assumed to be 10% of temporalis forces. Forces applied in FEA to origination areas of these muscles were calculated by dividing their total force by the number of divisions (5 for m. temporalis, 3 for m. masseter). Distances from origin to insertion centroids of the muscle divisions were used to calculate their F_{xyz} directional components. Abbreviations: sag. crest p = sagittal crest posterior; sag. crest m = sagittal crest middle; sag. crest a = sagittal crest anterior; zygomat = m. zygomaticomandibularis.

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We applied two loading and constraint regimes to the modeled cranium of *Basilosaurus* to determine reaction force at P3, a tooth inferred strongly as indenting specimens of *Dorudon* cranial [24].

1. One load assumed that all tested adductors were fully active. Constraints at P3 and the left and right articular condyles gave respective tooth and jaw reaction forces. This would more likely occur at relatively high gape angles, as the teeth would be in contact with a large food item. Although a crushing bite at this gape angle may not be realistic, it enables

### Table 2. Adductor muscle forces in *Basilosaurus isis*.

| Side   | Temporals Muscle Area (cm²) | Muscle Force 37 N/cm² $F_{temporalis}$ | Origin to insertion (mm) |
|--------|-----------------------------|----------------------------------------|--------------------------|
|        |                             |                                        | X  | y  | z  | $Fx$ | $Fy$ | $Fz$ |
| **Left side** |                                |                                        |    |    |    |       |      |      |
| Division | $F_{division} = F_{temporalis}/5$ |                                        |    |    |    |       |      |      |
| m. temporalis |                   |                                        |    |    |    |       |      |      |
| temporal     | 6633                      | 148                                   | 47 | 12 | 6296 | 2024 | 508  |
| nuchal       | 6633                      | 171                                   | 73 | -91| 5483 | 2331 | -2914|
| sag. crest p | 6633                      | 63                                    | 166| -115| 1981 | 5214 | -3590|
| sag. crest m | 6633                      | -50                                   | 173| -126| -1506| 5211 | -3817|
| sag. crest a | 6633                      | -3                                    | 115| -136| -108 | 4283 | -5064|
| m. masseter  | 3316                      |                                        |    |    |    |       |      |      |
| Division | $F_{division} = F_{masseter}/3$ |                                        |    |    |    |       |      |      |
| superior    | 1105                      | -399                                  | 13 | -215| -973 | 32   | -524 |
| inferior    | 1105                      | -181                                  | 5  | -169| -808 | 21   | -754 |
| zygomat.    | 1105                      | 49                                    | -77| -123| 353  | -554 | -889 |

| **Right side** |                                |                                        |    |    |    |       |      |      |
| Division | $F_{division} = F_{masseter}/3$ |                                        |    |    |    |       |      |      |
| m. temporalis |                   |                                        |    |    |    |       |      |      |
| temporal     | 5625                      | 156                                   | -63| 16 | 5188 | -2108| 534  |
| nuchal       | 5625                      | 170                                   | -113| -108| 4143 | -2761| -2619|
| sag. crest p | 5625                      | 69                                    | -185| -107| 1734 | -4631| -2681|
| sag. crest m | 5625                      | -61                                   | -165| -109| -1647| -4494| -2956|
| sag. crest a | 5625                      | -6                                    | -127| -147| -184 | -3676| -4254|
| m. masseter  | 2813                      |                                        |    |    |    |       |      |      |
| Division | $F_{division} = F_{masseter}/3$ |                                        |    |    |    |       |      |      |
| superior    | 938                       | -423                                  | -46| -207| -839 | -91  | -409 |
| inferior    | 938                       | -216                                  | -3 | -152| -766 | -12  | -540 |
| zygomat.    | 938                       | 20                                    | 88 | -79 | 158  | 689  | -616 |

Inputs and results for estimating adductor muscle forces $F_{realistic ST}$ in *B. isis*, assuming 37 N/cm² isometric specific tension (ST), a realistic value incorporating pennation. Areas are estimated in ImageJ, and multiplied by ST to calculate overall m. temporalis force $F_{temporalis}$. Total m. masseter $F_{masseter}$ were assumed to be 10% of temporalis forces. Forces applied in FEA to origination areas of these muscles were calculated by dividing their total force by the number of divisions (5 for m. temporalis, 3 for m. masseter). Abbreviations: sag. crest. p. = sagittal crest posterior; sag. crest. m. = sagittal crest middle; sag. crest. a. = sagittal crest anterior; zygomat. = m. zygomaticotemporalis.

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### Load cases and constraints for bite force at P3

We applied two loading and constraint regimes to the modeled cranium of *Basilosaurus* to determine reaction force at P3, a tooth inferred strongly as indenting specimens of *Dorudon* cranial [24].

1. One load assumed that all tested adductors were fully active. Constraints at P3 and the left and right articular condyles gave respective tooth and jaw reaction forces. This would more likely occur at relatively high gape angles, as the teeth would be in contact with a large food item. Although a crushing bite at this gape angle may not be realistic, it enables
us to compare forces with those of large-headed reptiles that apply such bites, such as *Alligator* feeding on turtles.

2) Another load assumed orthal retractional occlusion, with only the posterior temporalis active acting to retract the jaws, and masseter active for slight adduction. Under these conditions, the only constraint was at P³ where it would meet the food. Force magnitude of the posterior temporalis was its proportion of the total adductor force.

Regression and FEA for comparing bite forces of *Basilosaurus* and other carnivorous mammals

Using data from Wroe et al. [26] on carnivorous mammals (Table 3), we log-10 transformed basal skull length and skull width across the zygomatic arches (both in cm), and linearly regressed these quantities against log-10 of canine bite force (N [26]). Wroe et al. [26] used the dry skull method to estimate force for both extant and extinct mammalian carnivores, instead of estimating extinct forces using a modern-specimen regression. Our regressions thus avoid double-counting the influence of bite force in the extinct forms, a danger if their forces were estimated statistically. Regression equations gave us expected bite forces for *Basilosaurus isis* at the position of the canines in other carnivorous mammals (more anterior than the canine in *B. isis*). These regression-based force estimates are highly tentative, because the skull of *B. isis* is over three times longer and wider than the largest specimens in Wroe et al.’s [26] sample. As an additional check, we estimated bite force of *B. isis* with a lever model (Fig. 1), assuming (1) a vertical force through the centroid of ACSA, and (2) multiplying this by the sin of the angle between this vertical force and the sagittal crest, where most of the adductor muscles attach.

We compared regression estimates of *Basilosaurus isis* bite force with reaction forces from FE simulations. We used FEA to estimate forces at the canine and the caniniform I² in *B. isis* (at a similar position to the canine in other mammals: [26]), by constraining these teeth in simulations of unilateral bites. In these analyses all muscle forces were active (as in P³ bite simulation 1), with the FE model set to 2 cm plate thickness, E = 17.4 GPa, and Poisson’s ratio = 0.34.

Testing the precision of bite force results with different plate element models

We used FEA primarily to calculate bite forces. However, we also compared von Mises stresses between models of different plate thickness, to examine the sensitivity of bite reaction forces to both plate thickness and to stress magnitudes. Von Mises stresses represent the entire stress tensor as a scalar, enabling comparison of distortional stresses and risk of failure in ductile materials [48], such as bone under low strains. Von Mises stress is proportional to strain energy density, and values above yield or ultimate stress are good predictors of material and structural failure. We would expect higher stress (force/area) in thinner-plate models. If tooth reaction force is consistent regardless of plate element thickness and stress, we can conclude that plate element modelling is useful for estimating bite forces. Conversely, we can reject the current application of the plate FE method if tooth reaction forces vary greatly between thick and thin plate models, indicating high sensitivity to plate thickness and von Mises stress.

Results

Muscle and reaction forces

Anatomical CSA and inferred muscle forces of the temporal and masseter muscles are asymmetrical between the left and right sides for *Basilosaurus isis* (Table 1, Table 2). Areas measured
in ImageJ are 896 cm² on the left side and 760 cm² on the right, for respective m. temporalis force magnitudes of 33,163 N and 28,127 N, assuming 37 N/cm². This discrepancy is unsurprising, considering the asymmetry of Basilosaurus and other whales’ skulls [12]. Total adductor forces at this specific tension are 61,291 N (Table 2). Anatomical CSA and forces based on

### Table 3. Reaction forces and von Mises stresses with unilateral bites in *Basilosaurus isis*.

| Loadcase 1: Full adduction (all adductors active) |  |
|---|---|
| Plate thickness (mm) | $F_{\text{resultant}}$ | $P^2$ | $F_Z$ | $P^2$ | $\sigma_{\text{VM}}$ | $P^2$ | $F_{\text{resultant}}$ JA LEFT | $\sigma_{\text{VM}}$ JA LEFT | $F_{\text{resultant}}$ JA RIGHT | $\sigma_{\text{VM}}$ JA RIGHT |
| 5 | 16453 | -16128 | 399 | 9256 | 300 | 12854 | 386 |
| 10 | 16448 | -16041 | 162 | 9233 | 94 | 12558 | 129 |
| 15 | 16458 | -15975 | 94 | 9317 | 49 | 12400 | 65 |
| 20 | 16483 | -15921 | 63 | 9384 | 33 | 12282 | 40 |
| Average $F$ | 16461 | -16016 | 9298 | 12523 |  |

| Loadcase 2: Orthal retraction (posterior temporalis and masseter active) |  |
|---|---|
| Plate Thickness (mm) | $F_{\text{resultant}}$ | $P^2$ | $F_Z$ | $P^2$ | $\sigma_{\text{VM}}$ | $P^2$ | n/a | n/a | n/a | n/a |
| 20 | 20427 | 19107 | 283 |  |

Shown are reaction forces (N) and von Mises stresses ($\sigma_{\text{VM}}$; MPa) with unilateral bites in *B. isis* at $P^2$ and the left and right jaw articulations (JA). Muscle specific tension is 37 N/cm². Results for Loadcase 1 (with all tested adductors active) are for models with four different thicknesses of plate elements. In addition to resultant forces ($F_{\text{resultant}}$), vertical reaction force ($F_Z$) is reported at $P^2$. Results for Loadcase 2 (orthal retraction with only the posterior temporalis and masseter activated) include the x-axis component of the reaction force. The high magnitude of $F_X$ indicates high shear force.

Fig 2. Sensitivity of $P^3$ von Mises stresses and reaction forces to plate element thickness and a solid volume mesh. Note that bite force estimates at the third premolar ($F_{P3}$, black bars, right scale) are consistent (16,453 N-16,483 N) regardless of plate element thickness. By contrast, peak von Mises stresses (red bars, left scale) vary widely with varying plate thickness, from 399 MPa at 5 mm plate thickness to only 160 MPa at 10 mm thickness, and 64 MPa at a realistic 20 mm. These results indicate that plate element FEA is precise and useful for estimating bite forces, but not recommended for estimating stress magnitudes unless element thickness matches that of the original structure, $F_{P3}$ for the volume mesh is 16,541 N and peak stress is 51 Pa.

Fig 2: Sensitivity of $P^3$ von Mises stresses and reaction forces to plate element thickness and a solid volume mesh. Note that bite force estimates at the third premolar ($F_{P3}$, black bars, right scale) are consistent (16,453 N-16,483 N) regardless of plate element thickness. By contrast, peak von Mises stresses (red bars, left scale) vary widely with varying plate thickness, from 399 MPa at 5 mm plate thickness to only 160 MPa at 10 mm thickness, and 64 MPa at a realistic 20 mm. These results indicate that plate element FEA is precise and useful for estimating bite forces, but not recommended for estimating stress magnitudes unless element thickness matches that of the original structure, $F_{P3}$ for the volume mesh is 16,541 N and peak stress is 51 Pa.

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ellipse dimensions were 67% of values from ImageJ, suggesting that areas approximated as ellipses will underestimate forces.

Under the load case with full muscle activation and constraints at P3 and both jaw joints, all reaction forces scaled linearly with specific tension. With the realistic ST of 37 N/cm² [29], the average theoretical food reaction force at P3 was 16,461 N (Table 3). The joint reaction force was greater on the right side at 12,523 N, versus 9,298 N on the left, despite greater muscle force and a bite point both on the left side (Table 3). Reaction forces were insensitive to element thickness or type and hence to von Mises stress (Fig. 2), with a magnitude at P3 of 16,483 N for elements of 2 cm thickness, only 0.18% greater than 16,453 N for 0.5 cm thickness (Fig. 2). Vertical (z-axis) bite reaction force was more variable, with relative forces reversed at 1.28% greater for the model at 0.5 cm thickness than at 2 cm. Stress magnitudes (Fig. 2) do not affect hypothetical distributions of stress (Fig. 3) in tests with models of different plate thickness.

Under the load case with only the posterior temporalis and masseter active and constrained only at P3, reaction force magnitude at the left P3 was 20,487 N (Table 3). This magnitude was substantially greater than P3 experienced under the load case with all muscles active, and with constraints at the tooth and both jaw joints. The reaction force was anteriorly directed, indicating that the tooth would impose posteriorly-directed shearing force on the food.

### Bite force magnitudes compared with other mammals

Fig. 4 shows regressions for mammalian terrestrial carnivores from data in Table 4, and Table 5 compares regression estimates of *Basilosaurus* bite force with results of FE analyses. FE-estimated forces for *B. isis* are close to those expected from its skull width at both the caniniform I² and at its more posterior, actual canine (9.6% and 15.7% greater, respectively, than the expected 9,614 N). However, *B. isis*’s FEA-estimated canine-position force is 32.5% lower than expected for its skull length and its canine force is 28.8% lower. The FEA-derived forces for *B. isis* are within the 95% (and even 85%) confidence intervals of the regression (Fig. 4), whereas residuals for many mammals in the initial regressions fall outside these bounds. The simulated forces for *B. isis* thus are not exceptionally high or low compared with predicted values. The skull width/bite force regression is tighter (R² = 0.938) than the regression for length/force (R² = 0.808).

Based on the lever model, reaction forces at I² and the canine were 9,219 N and 12,655 N with the assumption of 30 N/cm² specific muscle tension, compared with the 10,536 N and 11,122 N values from the FEA model. These results suggest that the methods give adequately similar results for gross comparisons of forces derived from FEA and extrapolated from regression of lever models. However, using a single vertical resultant force (as with this lever model) gave unpredictably different results (+/- 10%) compared with our asymmetrical FE model with 3D component and reaction forces.

### Discussion

This study of *Basilosaurus isis* reveals the utility of simple FE representations of skeletal geometry (plate and solid-filled models) for obtaining reaction forces. As photogrammetry and other surface-modelling methods proliferate [59], [60], [61], [62], FE models based on this surface data alone can be useful for estimating reaction forces associated with biting and locomotion [58]. However, stress magnitudes and distribution require traditional, continuously advancing CT-based volumetric models [63], [64], [65]. Plate [41], [66], [67], structurally abstracted [68], and cavity-filled models are recommended primarily for broad comparisons of stress distribution. Encouragingly, both types of simplified models are biologically informative for estimating absolute reaction forces, as shown here for *Basilosaurus* biting (Fig. 2).
Ability of *Basilosaurus isis* to crush bone

With all muscles active, unilateral estimated tooth reaction forces for this specimen of *Basilosaurus isis*, at a realistic 37 N/cm² [29], were about 16,400 N at P³ regardless of model plate thickness and von Mises stress (Fig. 2). Including the medial pterygoid muscles would likely increase this force. This magnitude greatly exceeds forces necessary to crush or comminute bone with blunt-edged or rounded conical teeth [69], [70], [71], [72]. Captive spotted hyenas exert about 3,500 N [72] and wild hyenas perhaps double this value [73]. Indentation of a *Triceratops* ilium by a *Tyrannosaurus rex* tooth required 6,410 N [69], and *Basilosaurus* forces at P³ exceed that study’s extrapolated value (13,400 N) for the *T. rex’s* posterior teeth [69]. Finite element-modeled anterior bite forces in *B. isis* (10,536–13,716 N, depending on tooth position and specific tension: Table 5) are also sufficient to indent bone.
Fig 4. Regressions of canine bite force against skull width and basal skull length in carnivorous mammals. (A) Regressions of log10-transformed canine bite forces against log10 skull width and (B) regressions of log10-transformed canine bite forces against log10 basal skull length, in carnivorous mammals. Canine bite force values are compiled from Wroe et al. (2005), and listed in Table 3. Isometric specific tension is 30 N/cm². *Basilosaurus isis* (blue diamond) has a slightly greater FEA-estimated bite force.
Under the orthal retraction load case, anteriorly-directed food reaction forces of about 20,000 N (Table 3), on the small area of tooth-food contact, would likely exceed the ultimate (breaking) shear stress of bone tissue. These high reaction forces are consistent with the heavy macroscopic tooth wear seen in WH 74, as well as the suggested consumption of large hard objects such as mammal bones [23]. Because muscle force of a unilateral bite would induce a moment about the tooth and retract the contralateral side, we suggest that Basilosaurus isis would moderate the muscle forces it applied during such behaviors. The von Mises stress at the tooth under the orthal retraction load case (>200 MPa; Table 3) greatly exceeds shear stress of bone or dentine. This suggests deficiency of the plate element model, but also that the animal might moderate forces to below the maximum theoretical value. Reaction forces would be lower with more teeth in contact with the food, and still exceed shear strength of prey tissues. Traditional FEA with a continuous-solid model is necessary to test the plate models’ results for stress magnitude and distribution (Figs. 2 and 3); we predict grossly similar distribution but lower magnitudes of von Mises stress, because the specimen’s cranial bone is often very thick.

Implications of bite force in Basilosaurus isis for predation and scavenging

Fahlke [24] considered Basilosaurus isis as a likely predator that included juvenile Dorudon atrox in its diet. Distribution of bite marks indicates that B. isis bit D. atrox calves across the head from a lateral position, and sometimes adjusted prey in the mouth prior to a more powerful bite that penetrated the bone. High bite forces that break bone enable efficient carcass processing, whether an animal kills prey or is scavenging [71], [74].

We interpret high bite forces in Basilosaurus isis as indicating capability for habitual predation, rather than exclusive scavenging. Fahlke [24] did not rule out scavenging for B. isis, and scavenging occurs among large marine carnivores. Shark bite marks on fossils [75], [76] and forensics on modern animals indicate that sharks both scavenge and prey upon marine mammals [77], and did so upon mosasaurs during the Cretaceous [75]. However, pure scavenging among endotherms is known only in energy-efficient soaring birds [78], [79], including turkey vultures (Cathartes aura), which have weak bites and pedal grips compared with other carnivorous birds (ES, pers. obs.). In contrast with scavenging birds, the greatest bite forces known are from extant carnivores observed killing prey (crocodilians and white sharks: [80]), or extinct forms that broke bones of live prey which escaped, and whose bones healed (e.g. Tyrannosaurus rex: [81], [82], and giant sharks: [76], [80]). B. isis had comparable bite forces to these predators (Table 6). Healed bite marks in Dorudon could confirm predaceous habits for B. isis, but the cause(s) of the few healed injuries that are known in Dorudon [10] could not be identified unequivocally.

Basilosaurus isis bite force compared with other large-headed carnivores and smaller mammals

The great diversity of methods for estimating bite forces (Table 6) warrants caution when comparing our results for Basilosaurus isis with forces for other animals. Imperfections of our method likely underestimate bite force in B. isis. These include omission of the medial pterygoid for its primary role in jaw lateral movements in mammals, and posteriorly-originating

**Basilosaurus isis** bite force compared with other large-headed carnivores and smaller mammals

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Table 4. Regression of canine bite force against basal skull length and skull width.

| Species                  | log-10 BSL (cm) | log-10 SW (cm) | log-10 CB (N) |
|--------------------------|-----------------|----------------|---------------|
| Alopex lagopus           | 1.142           | 0.906          | 2.250         |
| Canis alpinus            | 1.248           | 1.033          | 2.497         |
| Canis aureus             | 1.131           | 0.910          | 2.217         |
| Canis lupus dingo        | 1.256           | 0.999          | 2.496         |
| Canis lupus hallstromi   | 1.203           | 0.974          | 2.371         |
| Lycaon pictus            | 1.268           | 1.139          | 2.631         |
| Vulpes vulpes            | 1.140           | 0.866          | 2.215         |
| Ursocyon cinereargentus  | 1.076           | 0.788          | 2.057         |
| Canis latrans            | 1.275           | 0.994          | 2.439         |
| Canis lupus lupus        | 1.360           | 1.121          | 2.773         |
| Canis dirus              | 1.418           | 1.245          | 2.951         |
| Ursus americanus         | 1.387           | 1.236          | 2.733         |
| Ursus arctos             | 1.431           | 1.212          | 2.876         |
| Ursus thibetanus         | 1.321           | 1.044          | 2.494         |
| Meles meles              | 1.090           | 0.906          | 2.387         |
| Gennetta tigrinus        | 1.039           | 0.715          | 1.863         |
| Crocuta crocuta          | 1.374           | 1.223          | 2.888         |
| Hyaena hyaena            | 1.301           | 1.181          | 2.736         |
| Proteles cristatus       | 1.096           | 0.859          | 2.179         |
| Panthera onca            | 1.347           | 1.270          | 3.006         |
| Panthera tigris          | 1.460           | 1.357          | 3.183         |
| Acinonyx jubatus         | 1.202           | 1.090          | 2.674         |
| Felis yagouaroundi       | 1.004           | 0.841          | 2.104         |
| Lynx rufus               | 0.880           | 0.773          | 1.991         |
| Felis concolor           | 1.225           | 1.111          | 2.674         |
| Felis lybys              | 0.876           | 0.732          | 1.748         |
| Neofelis nebulosa        | 1.224           | 1.075          | 2.775         |
| Panthera leo             | 1.524           | 1.395          | 3.247         |
| Panthera pardus          | 1.256           | 1.115          | 2.669         |
| Smilodon fatalis         | 1.470           | 1.291          | 2.989         |
| Dasyurus maculates       | 1.004           | 0.779          | 2.185         |
| Dasyurus viverrinus      | 0.862           | 0.618          | 1.813         |
| Sarcophilus harrisii     | 1.145           | 1.048          | 2.621         |
| Nimbacinus dicksoni      | 1.122           | 0.907          | 2.427         |
| Thylacinus cynocephalus  | 1.399           | 1.171          | 2.907         |
| Priscileo rosellyae      | 0.921           | 0.802          | 2.265         |
| Wakaileo vanderleuei     | 1.268           | 1.100          | 2.828         |
| Thylacoleo carnifex      | 1.381           | 1.304          | 3.228         |
| Thylacosmilus atrox      | 1.411           | 1.145          | 2.548         |
| *Basilosaurus isis*      | 2.053           | 1.785          | -             |

Data for regressions of log-10 canine bite force (CB) against log-10 of basal skull length (BSL) and skull width (SW) in carnivorous mammals from Wroe et al. [26]. Forces assume a specific tension of 30 N/cm². Log-10 BSL and SW measurements are given for *Basilosaurus isis*.

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muscles that cause only jaw reaction forces, rather than taking advantage of the moment arm of the coronoid process. Underestimating masseter cross-section would also underestimate the total bite force. Applying the dynamics-based methods of Bates and Falkingham [52] to B. *isis* would allow surer comparisons of *B. isis* forces with their results for large reptiles, particularly for impact bite force.

Despite these caveats, bite force estimates for *Basilosaurus isis* appear to be comparable to those of very large white sharks [80], although relatively lower than those of some large-headed

### Table 5. Regression-predicted and FE-reaction “canine” bite forces in *Basilosaurus isis*.

|                     | Canine | Canine |
|---------------------|--------|--------|
| **Predicted forces (N)** |  log 10 | Absolute | log 10 | Absolute |
| Skull length regression | 4.194  | 15617  |        |        |
| Skull width regression | 3.983  | 9614   |        |        |
| 2D lever model       | 9219   |        |        |        |
| **FEA forces (N)**   |        |        |        |        |
| ST = 30 N/cm²        | 4.023  | 10536  | 4.046  | 11122  |
| ST = 37 N/cm²        | 4.114  | 12995  | 4.137  | 13716  |

Predicted forces are from regressions of force at the canine position (i² in *Basilosaurus*) against skull measurements in carnivorous mammals. The FEA results are bite reaction forces at i² and, for comparison, at the true canine. Results in boldface all assume 30 N/cm² specific tension of jaw muscles, as in Wroe et al. (2005); note similarity between the finite element and skull width-predicted forces.

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### Table 6. *Basilosaurus isis* bite force estimates (N) compared with other long-skulled carnivores, including skull length and method.

| Method                              | Skull length (m) | Posterior F 37 N/cm² max 30N/cm² | Anterior F 37 N/cm² max 30N/cm² |
|-------------------------------------|------------------|-----------------------------------|---------------------------------|
| **Basilosaurus isis** jaws articulated | FEA              | 1.13                              | 16461|20020 12994–13717| 16026–16918 |
| **Basilosaurus isis** orthal retraction | FEA              | 1.13                              | 20487|24844 (ant. shear) n/a |
| **Kronosaurus queenslandicus**       | FEA              | 1.8                               | 27716 15169 |
| **Pliosaurus kevani**               | FEA              | 2                                 | 27865–48278 11865–20884 |
| **Crocodylus porosus**              | force transducer | 0.65                              | 16414 11216 |
| **Crocodylus porosus**              | extrapolated transducer | -                                 | 27531–34424 - |
| **Deinosuchus riograndensis**       | extrapolated transducer | 1.3–2                             | 102803 - |
| **Tyrannosaurus rex**               | dynamics         | 1.3                               | 35640–57158 18065–31086 |
| **Tyrannosaurus rex**               | indentation      | -                                 | 13400 6410 |
| **Tyrannosaurus rex**               | extrapolated dynamics | 1.3                              | 105732 53593 |
| **Dunkleosteus terrelli**           | dynamics         | 0.8                               | 7495 5625 |
| **Carcharodon crocarias**           | FEA              | -                                 | 18216 9320 |
| **Carcharodon / Carcharocles megalodon** | extrapolated FEA | 108514                            | 55522 |

Ranges are cited when available. Tooth reaction forces of *B. isis* are given for 37 N/cm² muscle specific tensions, and the maxima (max) calculated from common 1.5X underestimates of mammalian bite force at a specific tension of 30 N/cm². Anterior bite forces for *B. isis* vary with tooth position. Note that *B. isis* bite forces are lower than in large-headed reptiles (especially crocodylians and *Tyrannosaurus rex*). However, considering its shorter skull, forces in *B. isis* are comparable to estimates for the marine pliosaurs *Kronosaurus* and *Pliosaurus*. Sources: [36], [37], [30], [28], [69], [52], [89], [80].

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reptilian predators of similar skull length (Table 6). Reptiles have a laterally unconstrained, multi-aponeurosis m. pterygoideus posterior/ventralis that loops around the lower jaw, and pennate temporal muscles with greater forces per ACSA than the 30–37 N/cm² specific tension (ST) values for mammals [25, 29]. (When isometric ST for Tyrannosaurus [28] is scaled to ST of the tuatara Sphenodon [52], the tyrannosaur’s posterior bite forces reach the 100,000 N values estimated through structural mechanics [83], and calculated for giant crocodilians [30].) Forces remain lower in B. isis even with greater estimates of specific tension in mammalian jaw muscles. Thomason found that the dry skull method can underestimate mammalian bite forces at 30 N/cm² by 1.3–1.5 [25]. Scaling up to these values to assume 39–45 N/cm² of specific tension, maximum estimates for mandible elevation in B. isis (load case 1) would therefore be 17,350–20,020 N using our method. These reaction forces are still lower than estimated for the largest Crocodylus porosus [30] (Table 6).

Despite relatively lower forces than in crocodylians and one dinosaur, our bite force estimates for Basilosaurus isis are similar to estimates for marine pliosaurs Kronosaurus queenslandicus and Pliosaurus kevani [36], [37], when considering the longer skulls of these reptiles. Assuming that muscle force is proportional to the square of linear increases in size, a B. isis with a 2 m skull would be expected to have a bite force of about 50,000 N: (2m/1.13m)² = 3.13; 3.13 x 16,451 N = 51,523 N. This value is in the range of 48,000 N estimated for Pliosaurus kevani with a 2 m skull, and may suggest similar trade-offs of hydrodynamics and bite force in these large marine carnivores [36], [37].

More directly instructive for Basilosaurus bite force and feeding style, the ratios of anterior/posterior bite forces that we estimate for B. isis (Table 6) are 15–22% greater than the ratio recorded in Crocodylus porosus [30]. This suggests that B. isis applied relatively greater anterior bite forces than crocodilians for the same posterior forces (about 16,000 N in both B. isis and a 4.6 m C. porosus), and maintained effective bone-crushing abilities at all tooth positions. High anterior bite force in B. isis would also enable it to capture and hold large prey with its widely-spaced anterior teeth, possibly prior to processing it, a predation technique Uhen [10] suggested for Dorudon atrox.

Our conservative modeled bite force estimates for Basilosaurus isis are the largest known for any mammal, and are much greater than in bone-breakers like spotted hyenas. With comparable specific tensions of 30 N/cm², the anterior caniniform (I²) bite force of B. isis (10,536 N: Table 5) is over twice the canine force estimated for the giant ursid Agriotherium africanum (4,566 N: [84]). Basilosaurus isis had somewhat greater estimated bite force than expected from regressions of bite force versus skull width in carnivorous mammals (Table 3, Fig. 4), and lower force than expected for its skull length. Its elongated rostrum probably accounts for the lower-than-expected values from the length regression, and its relatively narrow braincase may have given B. isis relatively more muscle cross-sectional area and force than in mammals with broader braincases compared with their overall skull width. However, FEA and lever model results are not dramatically different from those expected from regressions, falling well within confidence intervals. Comparisons with terrestrial mammals such as the huge Megistotherium [85] and mesonychid Andrewsarchus [86], and cetartiodactyls of the land-water transition, will place B. isis bite force in productive comparative biomechanical and evolutionary context.

For example, comparing Basilosaurus with other whales will be informative about predatory ecomorphology, both at the time of their Eocene radiation and in adaptation to certain prey. Basilosaurus was certainly specialized among the aquatic archaeocetes, as is implied not only by its destructive tooth wear but also by its unusually elongate vertebrae and consequently serpentine body shape (cf. [87], [88]). From the evolutionary aspect, it would therefore also be interesting to conduct a bite force analysis for the more generalized dorudontine basilosaurids. Finally, our understanding of the ecological role of B. isis would benefit from comparisons of
its bite force with forces estimated for modern aquatic mammals that have a similar range of
prey items, e.g., the killer whale (*Orcinus orca*).

**Summary and Conclusions**

Bite force of the middle-to-late Eocene archaeocete *Basilosaurus isis* from Egypt was estimated
using FEA modeling. Bite reaction forces varied negligibly with FE element formulation. Re-
sulting maximum bite forces for *B. isis* are conservative, yet are the highest ever estimated or re-
corded for a mammal, and are comparable with or only moderately lower than many bite
forces recorded or estimated for large reptiles (e.g. *Crocodylus porosus*, pliosaurs, and *Tyranno-
saurus rex*) and white sharks. Bone crushing was definitely possible for *B. isis*, potentially even
when it was using its anterior teeth, and estimated bite force in the anterior teeth is relatively
higher than in reptiles, suggesting *B. isis* was capable of manipulating large prey using its ca-
nines and incisors. Very high bite forces at P\(^3\) and farther anteriorly are consistent with *B. isis*
being an active predator rather than a scavenger. *B. isis* was probably a specialist among archae-
ocetes, and comparing its bite force with those of other extinct and extant cetartiodactyls will
place our results into evolutionary and ecological context more comprehensively.

**Supporting Information**

S1 Dataset. Autodesk Multiphysics finite element model of *Basilosaurus isis*.
(FEM)

S1 Text. Use of plate elements for vertebrate FEA. Elaborates on the use of plate elements for
vertebrate FEA.
(DOCX)

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**Author Contributions**

Conceived and designed the experiments: ES JF. Performed the experiments: ES JF. Analyzed
the data: ES JF RW. Contributed reagents/materials/analysis tools: ES RW. Wrote the paper:
ES JF.

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