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# Feeding mechanics and bite force modelling of the skull of *Dunkleosteus terrelli*, an ancient apex predator

Philip S. L. Anderson<sup>1,\*</sup> and Mark W. Westneat<sup>2</sup>

<sup>1</sup>Department of Geophysical Sciences, University of Chicago, 5734 S Ellis Avenue, Chicago, IL 60637, USA

<sup>2</sup>Department of Zoology, Field Museum of Natural History, Chicago, IL 60605, USA

\*Author for correspondence (andersps@uchicago.edu).

Placoderms are a diverse group of armoured fishes that dominated the aquatic ecosystems of the Devonian Period, 415–360 million years ago. The bladed jaws of predators such as *Dunkleosteus* suggest that these animals were the first vertebrates to use rapid mouth opening and a powerful bite to capture and fragment evasive prey items prior to ingestion. Here, we develop a biomechanical model of force and motion during feeding in *Dunkleosteus terrelli* that reveals a highly kinetic skull driven by a unique four-bar linkage mechanism. The linkage system has a high-speed transmission for jaw opening, producing a rapid expansion phase similar to modern fishes that use suction during prey capture. Jaw closing muscles power an extraordinarily strong bite, with an estimated maximal bite force of over 4400 N at the jaw tip and more than 5300 N at the rear dental plates, for a large individual (6 m in total length). This bite force capability is the greatest of all living or fossil fishes and is among the most powerful bites in animals.

**Keywords:** placoderms; bite force; *Dunkleosteus*; biomechanics

## 1. INTRODUCTION

The structure and function of placoderm skulls are important aspects of the evolutionary history of vertebrate feeding, because these ancient predators are considered to be the sister group to the rest of jawed vertebrates (Goujet & Young 2004). This phylogenetic placement, coupled with remarkable morphological variation in the feeding system, makes placoderms one of the earliest examples of jaw diversification among vertebrates (Carr 1995). The largest of the placoderms were voracious predators, such as the arthrodire *Dunkleosteus terrelli* (figure 1), that were equipped with powerful, bladed jaws that conferred the novel ability to fragment prey items prior to ingestion (Miles 1969). Modern sharks possess a set of well-known jaw mechanisms which also accomplish this task (Dean *et al.* 2005; Wilga 2005). However, the earliest definitive examples of shearing, bladed teeth in elasmobranchs did not develop until the Mesozoic, 100 Myr

after *Dunkleosteus* was a top predator of the Devonian seas (Janvier 1996).

Biomechanical models based on engineering theory are often used to test ideas regarding fish skull function (reviewed by Westneat 2006). Models of living fishes can accurately represent the mechanics of skull function, and studies have shown that skull mechanisms are correlated with natural diet. Biomechanical models have also been employed in surveys of fossil forms to examine jaw mechanics in extinct herbivores (Bellwood 2003) and predatory gars (Kammerer *et al.* 2006). Here, we take advantage of the exquisite three-dimensional preservation of placoderms to conduct a biomechanical analysis of cranial kinesis in one of the largest aquatic predators ever to have lived. Our goals are to develop a biomechanical model of *D. terrelli* that involves a novel four-bar linkage mechanism, and to use reconstructions of the mass, volume and force trajectories of the jaw muscles to simulate the speed, angular rotations and bite forces of *Dunkleosteus*.

## 2. MATERIAL AND METHODS

The feeding mechanism of *D. terrelli* was modelled as a four-bar linkage, using techniques similar to previous skull modelling (Westneat 2006). Five specimens of *D. terrelli* from the Cleveland Museum of Natural History (CM5768, CM6090, CM7054, CM7424 and CM6194) were used to develop this model. For the largest specimen (CM5768), muscle casts were made to fit muscle cavities, from which we measured muscle length, volume and cross-sectional area. For muscle simulations, a range of average muscle contraction speeds from 2.3 to 5.0 muscle lengths  $s^{-1}$  (Josephson 1993) and a peak muscle stress of 200 kPa were used.

The four-bar linkage mechanism in *D. terrelli* is unique due to the connections of the skull, thoracic shield, jaw depressor muscle and inferognathal (lower jaw), which are joined by kinetic joints (figure 1). The cranio-thoracic articulation (nuchal joint) connects the back of the skull to the thoracic shield, allowing the skull to rotate dorsally during contraction of epaxial (EP) muscles. The jaw depressor muscle (coracomandibularis, CM) originates on the scapulocoracoid and inserts on the anteroventral portion of the inferognathal (Johanson 2003). The thoracic shield forms a framework for three movable elements: the skull, the inferognathal, and the depressor muscle. This structure is a classical four-bar linkage from mechanical engineering (figure 1c), involving a fixed link (thoracic shield) and three rotational links. As the skull is rotated dorsally by the action of the EP, the jaw joint is pulled forward and the inferognathal rotates due to its connection with the thoracic shield (figure 1b,c).

A computer model was developed to simulate skull motions and bite forces by shortening four cranial muscles (figure 1b). These include the EP muscles that rotate the skull dorsally (figure 2a, EPv2), and open the four-bar linkage at the jaw joint (figure 2a, EPv3), and the CM muscle which rotates the inferognathal ventrally. Owing to tension in the CM, EP force is transmitted to the jaw (figure 2a, EPv4). For jaw closing, the cranial depressor (CD) muscle rotates the skull downward and pushes the jaw joint rearward (figure 2b, CDv2). The adductor mandibulae (AM) jaw muscle rotates the jaw and forces the jaw joint rearward (figure 2b, AMv2). Thus, the bite force from the upper jaw (figure 2b, BF1 and BF3) comprises CD force exerted by the skull lever and AMv2 force that is transmitted by the four-bar linkage. Lower jaw bite force (figure 2b, BF2 and BF4) is generated by the powerful lever advantage of the AM muscles.

We simulated a 10% contraction of the opening muscles in increments of 0.5%, then reversed this pattern, closing the system with the CD and jaw closers. These simulations focused on linkage motion, assuming that the skull closes without encountering a prey item. Important variables include mechanical advantages of muscles on rotational levers (computed as inlever distance divided by outlever distance) and the kinematic transmission coefficient (KT) of the linkage, calculated as output rotation of the mandible divided by the input rotation of the skull (see electronic supplementary material for specific variables). Bite forces were calculated in a separate set of simulations at each stage of jaw closing by assuming that a prey item was caught between the jaws at that position (figure 2). We used the physiological cross-sectional area of the CD and AM to calculate the force that was transmitted through the four-bar linkage as bite force.

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2006.0569> or via <http://www.journals.royalsoc.ac.uk>.

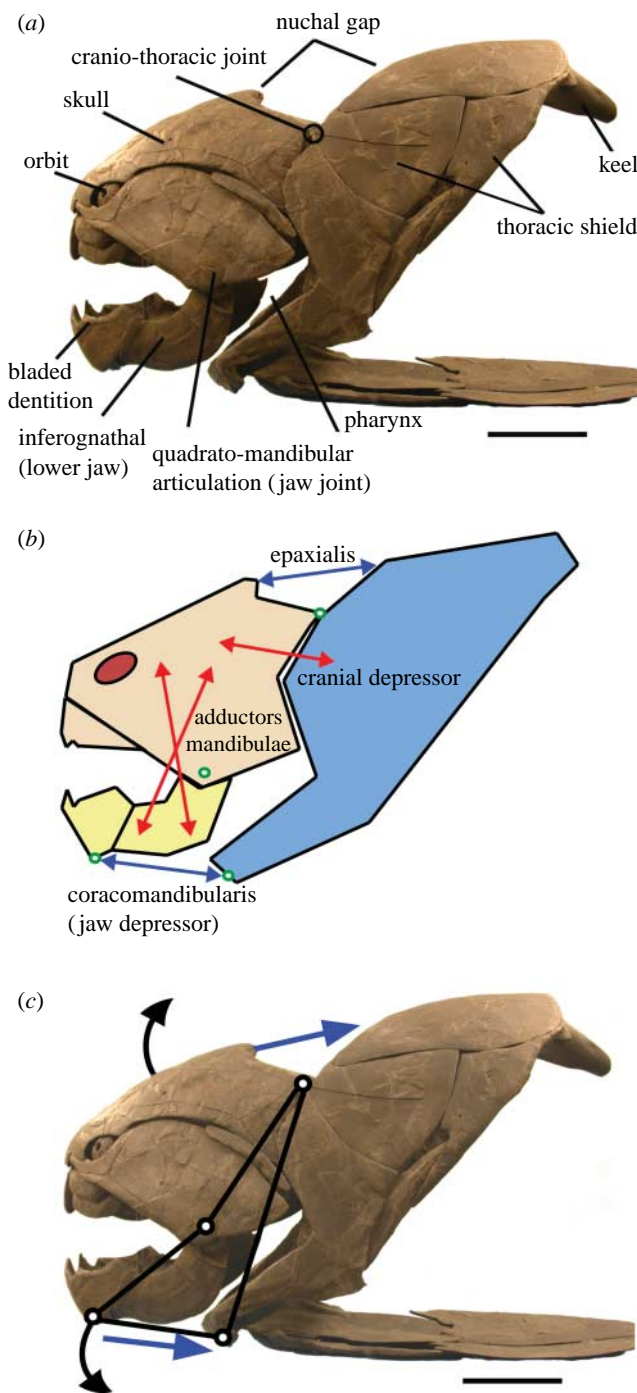


Figure 1. Anatomy and biomechanical model of the skull and thoracic region of *Dunkleosteus terrelli*. (a) Anatomy of *Dunkleosteus terrelli*, highlighting the cranio-thoracic joint and quadrato-mandibular joints involved in skull mechanics. (b) Drawing showing the four rotational joints (green) forming the four-bar linkage that mediates skull and mandibular rotation. The lines of action of four muscles are shown, including epaxialis and coracomandibularis in blue and cranial depressor and adductor mandibulae in red. (c) Four-bar linkage motion during opening. Scale bar, 20 cm. Specimen no. CM6090, Cleveland Museum of Natural History.

### 3. RESULTS AND DISCUSSION

The anatomical configuration of the skull, thoracic shield, mandible and jaw depressor muscle in placoderms may be accurately modelled as a four-bar linkage mechanism. The cranio-thoracic articulation, which is a key component of this linkage design, is

found only in the placoderms (Janvier 1996). The central result of this study is that *D. terrelli* used this unique four-bar linkage in the skull to achieve high speeds during jaw opening and transmit extremely high bite forces to its prey during jaw closing. *Dunkleosteus* appears to have had a rapid gape expansion, going from closed jaws to peak gape in as little as 20 ms and completing the feeding cycle in 50–60 ms, using an average muscle speed estimate of 5 muscle lengths  $s^{-1}$  (figure 2c–e). This rapid gape expansion is comparable to that of modern fishes, which use suction feeding to assist in prey capture (Westneat 2006). Simulations using slower muscle velocities (such as shark muscle at 2.3 or 3.8 muscle lengths  $s^{-1}$ ) resulted in longer duration feeding strikes of up to 130 ms, slower than teleost suction feeding but similar to the duration of suction feeding in nurse sharks (Motta *et al.* 2002). Previous research (Miles 1969) had speculated that *Dunkleosteus* had a powerful but slow jaw system; however, the average opening KT for *Dunkleosteus* is 3.0 (see table 1 of electronic supplementary material), indicating that the lower jaw rotates at three times the speed of the cranial rotation that drives it. This KT is twice as high as the highest values calculated for a different type of oral jaw linkage in modern groups (Wainwright *et al.* 2004). This high KT is augmented by CM contraction that pulls the lower jaw downward, providing *Dunkleosteus* with a two-muscle opening system that had the ability to rapidly achieve high gape. We conclude that the *Dunkleosteus* skull is an early example of a complex, kinetic feeding mechanism that may have utilized an early form of suction feeding.

*Dunkleosteus* also had one of the most powerful bites in vertebrate history. Simulations showed that a large specimen was able to generate maximum bite forces of 4414 N on the anterior fang and 5363 N on the posterior part of the blade. Simulation of an alternative muscle reconstruction (AM1, figure 2f) resulted in slightly lower bite forces, from 4004 N anteriorly to 4469 N posteriorly. These bite forces greatly exceed the bite forces collected for all other fish species that have been reported (Huber *et al.* 2005) and those for most modern mammalian predators, including the spotted hyaena (Binder & Van Valkenburgh 2000), which is known to crack bones with its jaws. The *Dunkleosteus* specimen on which these estimates are based is large (estimated to be 6 m long and 1000 kg) and the bite forces conform to a recently compiled scaling trend of increasing bite force with body mass (Huber *et al.* 2005). The only reports of higher bite forces are those found in some extremely large alligators and dinosaurs (Erickson *et al.* 2003). The biomechanical source of high bite forces in *Dunkleosteus* is a combination of large adductor muscles, the efficient force transmission characteristics of a four-bar linkage (figure 2), and high mechanical advantage of the jaw closing lever (see table 1 of electronic supplementary material).

The bladed dentition of *Dunkleosteus* provided for extremely high local bite stress (force/area) because the bite force was focused into a small area, the fang tip (147 million  $N m^{-2}$ ) or the blade edge (107 million  $N m^{-2}$ ). High bite stress enabled

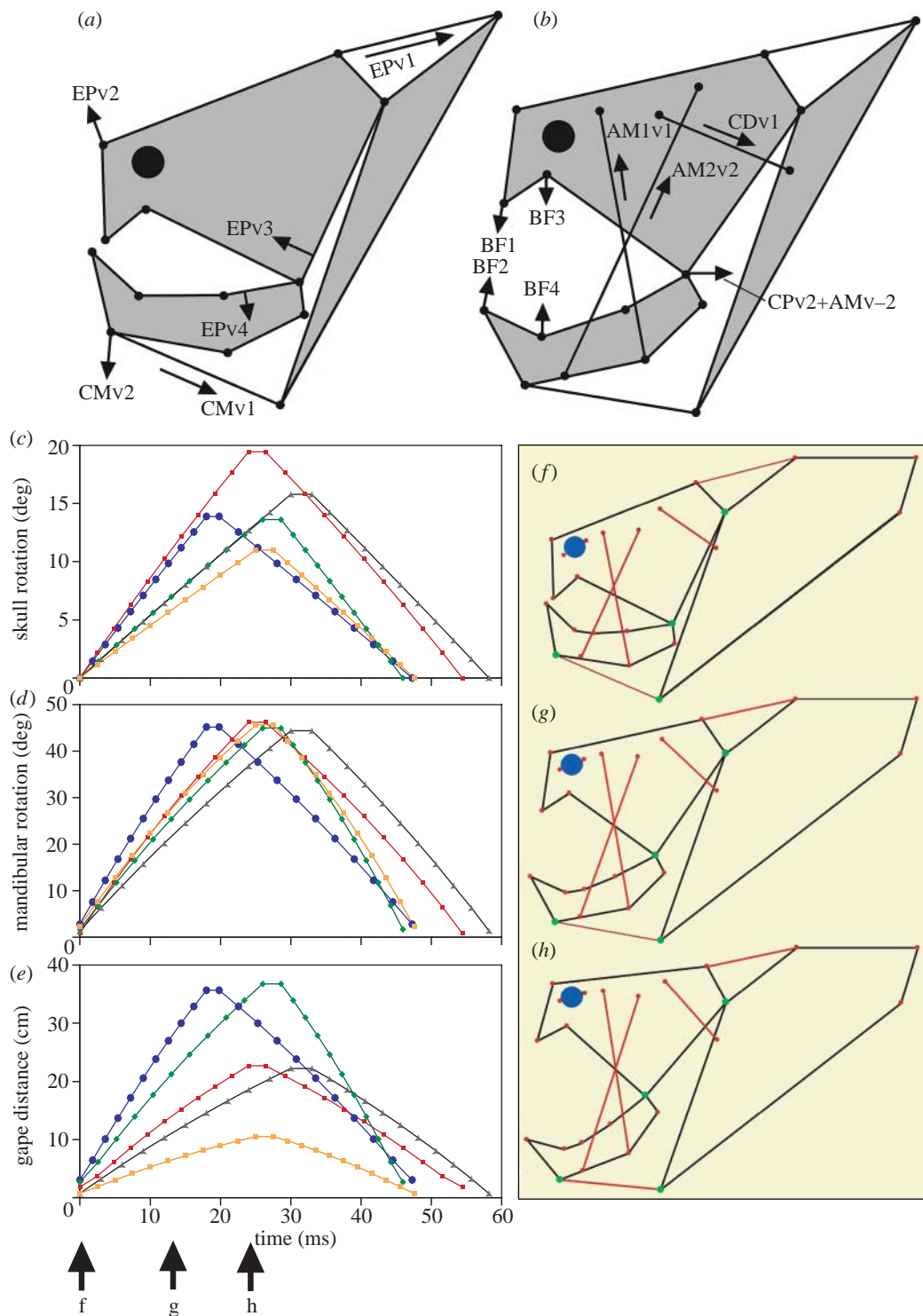


Figure 2. Biomechanics of feeding in *Dunkleosteus terrelli*, under a muscle contraction speed of 5 muscle lengths  $s^{-1}$ . (a) During jaw opening, epaxialis vector 1 (EPv1) and coracomandibularis vector 1 (CMv1) cause cranial elevation (EPv2) and jaw depression (EPv3 and EPv4). (b) Jaw closing mechanics is driven by force vectors of the cranial depressor (CDv1) and adductor mandibulae, reconstructed in two configurations (AM1v1 and AM2v1). Bite force is exerted by both lever and linkage force vectors (BF1 and BF2) or between the rear dental blades (BF3 and BF4). Simulated kinematics in five specimens of *Dunkleosteus terrelli* include (c) skull rotation, (d) mandibular rotation and (e) change in gape during feeding. The simulated positions of skeletal elements are shown in (f) closed, (g) intermediate and (h) open positions, with their corresponding points shown (black arrows) on the kinematic plots.

*Dunkleosteus* to puncture and fragment hard materials, such as cuticle or dermal bone. The Cleveland Shale is known primarily for its placoderms, but also contains selachian sharks, arthropods and ammonoids. These were all free-swimming organisms that shared the presence of a hard armour (cuticle, calcium carbonate or dermal bone), which

must be punctured prior to consuming the flesh underneath. These mobile and often hard prey would require both high capture speed and high bite force to consume, for which the feeding system of *Dunkleosteus*, with its high forces and high KT values, appears well suited. The combination of power and speed seen in *Dunkleosteus* would have

allowed it to consume virtually all other aquatic species in the fauna, making it one of the first true apex predators seen in the vertebrate fossil record.

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