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A three dimensional free body analysis describing variation in the musculoskeletal configuration of the cynodont lower jaw

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SUMMARY The evolution of the middle ear from the cynodont craniomandibular bones is one of the key mammalian innovations, and the mechanics underlying this anatomical transformation represents an intriguing paradox. Because the jaw joint of nonmammalian cynodonts was functionally coupled to the inner ear, auditory performance would favor low joint reaction forces. However, this could not be achieved at the expense of feeding performance, favoring high bite forces. The balance of these two seemingly incompatible performance criteria in the context of the morphological diversity of the cynodont lower jaw is poorly understood. Here we derive a series of equations using three dimensional free body analysis that describe the relationship between the orientation and position of the jaw elevator muscles, the position of the jaw articulation relative to the bite point, the joint reaction forces and the bite force in the lower jaw of the nonmammalian cynodont *Probainognathus*. These equations permit the effects of variation in each variable to be tested independently, yielding three terms that act to limit joint reaction forces without substantially impacting bite force: the reorientation of the resultant muscle force more vertically, shifting the position of the bite point medial to the jaw articulation, and elevating the jaw articulation above the level with the tooth row only when the muscles are oriented principally in the anterior direction. The predictions from our equations provide insights for functional interpretations of patterns of morphological diversity in the cynodont fossil record. They also illustrate that the musculoskeletal configuration of the cynodont lower jaw can be evolutionarily labile without negatively impacting the dual performance criteria of the auditory and feeding system.

INTRODUCTION

The emergence of mammals from nonmammalian cynodonts involved a dramatic reorganization of the bones and muscles of the lower jaw. The postdentary bones reduced in size and translated posteromedially, the dentary expanded posteriorly and took over as the primary site of jaw articulation, and new musculature emerged altering the direction of the elevator forces on the jaw (Crompton 1963; Hopson 1966; Barghusen 1968; Barghusen and Hopson 1970; Barghusen 1972; Crompton and Jenkins Jr 1973; Kemp 1982; Hopson 1987; Allin and Hopson 1992; Luo and Crompton 1994; Sidor 2003). These musculoskeletal modifications in the lower jaw, in conjunction with modifications of the quadrate-quadratojugal complex in the skull (Anthwal et al. 2013), were advantageous in that their connection to the middle ear improved high frequency auditory performance (Allin 1975; Sidor 2003). However, this transition did not occur in a step-wise progression of increasingly optimal configurations. Homoplasy in the mammalian fossil record suggests that selection experimented with the configuration of the auditory and feeding systems (Luo 2011).

The variation resulting from this experimentation occurred within the bounds of dual, overlapping, performance criteria. To maintain auditory function, it is hypothesized that reaction forces at the jaw joint remained low (Barghusen and Hopson 1970; Allin 1975; Crompton and Hylander 1986; Crompton 1995). However, selection for feeding performance required that this be accomplished without substantial decreases in bite force. Several authors have noted that the jaw elevator musculature in therapsids actually increase in mass as the post-dentary bones forming the jaw joint decrease in size. The mechanics of this paradoxical anatomical transformation has been addressed by several authors (Crompton and Parkyn 1963; Bramble 1978; Crompton and Hylander 1986). Using simple two-dimensional mechanical models, it has been shown that the musculoskeletal configuration of several different cynodont taxa can yield low vertical compressive joint reaction forces on the balancing side, low vertical tensile joint reaction forces on the working side, and a high bite force during biting on the post-canine dentition.

A limitation of analyses of this nature is that calculations based on individual taxa represent a very narrow sample of the diversity in cynodont lower jaws. Modeling has the advantage of placing musculoskeletal variation, informed by the diversity of the clade, in the context of specific performance criteria. Taking this approach, Greaves (1978) proposed the ‘triangle of support’ model demonstrating that joint reaction forces and bite force are geometrically related to the position of the resultant force describing the jaw elevator musculature (Spencer 1998; 1999 for discussion). This model illustrates the bite and joint reaction forces depend on two important factors as follows: (i) the position and orientation of the elevator musculature on the jaw and (ii) the position of the jaw articulation relative to the tooth row/bite point. There is substantial variation in each of these factors accompanying the anatomical transformations taking place within the lower jaws of cynodonts and stem mammaliaformes.

The jaw elevator musculature in early cynodonts was dominated by the posteriorly directed temporalis (Bramble 1978). The effect of the temporalis on the rotation and translation of the mandible can be altered by changing the height of its site of attachment on the coronoid process (DeMar and Barghusen 1972). An elevated coronoid process has evolved independently in several clades (Gould 1970). In advanced cynodonts, there is a pattern of gradual posterior displacement of the coronoid process (DeMar and Barghusen 1972; Bramble 1978).

The masseter emerges in early cynodonts such as *Thrinaxodon* (Barghusen 1968). Initially, the masseter is small and the muscle fibers are oriented in the posterior direction. In advanced cynodonts such as *Trirachodon* and *Probainognathus*, the masseter divides into superficial and deep components (Barghusen 1972; Crompton and Parker 1978). The superficial component is oriented in the vertical or anterior direction while the deep component is oriented in the posterior direction. The elevator mass of the jaw is further increased in advanced cynodonts by the emergence of the medial pterygoid (DeMar and Barghusen 1972; Bramble 1978), which is hypothesized to improve the motor control and occlusal dynamics of the feeding system (Crompton and Parker 1978). The effect of the masseter on mandibular movement can be altered by shifting either the angular process on the inferior border of the mandible or the position of the muscular insertion on the zygomatic arch. In most advanced cynodonts, the angular process is located between the jaw articulation and the posterior most tooth (Fig. 1). In stem and crown mammaliaformes, the angular process is more variable, expanding posteriorly and inferiorly in some groups.

There is also substantial variation in the geometric relationship of the jaw articulation to the tooth row across the clade. Two dimensional models have demonstrated that changes in both the mediolateral (Greaves 1988) and in the vertical (Maynard Smith and Savage 1959; Scapino 1972; Greaves 1974) position of the of the jaw articulation relative to the bite point will impact joint reaction forces and bite force. The mediolateral position of the jaw articulation relative to the bite point is particularly important in cynodonts because of the morphological patterns underlying the emergence of the secondary jaw joint. The jaw articulation of all non-mammals and stem cynodonts is between the articular bone on the jaw and the quadrate bone on the skull. As the dentary expands and the post-dentary bones of the jaw reduce in size in more advanced cynodonts, a dual, secondary jaw articulation forms. In all cynodonts, the secondary load bearing joint surface forms lateral to the primary, quadrato-articular joint surface (Crompton 1995; Anthwal et al. 2013). Changes in the shape of the lower jaw and the mediolateral position of the jaw articulation may have also occurred in early cynodonts, shifting the posterior-most cheek teeth medial of the jaw articulation (Fig. 1; Greaves 1988).

There is less variation in the vertical relationship of the jaw articulation to the tooth row. Nearly all nonmammalian cynodonts have jaw articulations at or below the level of the tooth row (Sidor 2003; in what follows “tooth row“ will refer to the level of the occlusal surface of the mandibular cheek teeth). This is true for all trophic niches filled by cynodonts, including the two herbivorous groups Traversodontidae and Tritylodontidae (Kemp 1982; Crompton and Attridge 1986; Crompton 1995). The taxa of Tritylodontidae show the largest amount of variation in the height of the jaw articulation amongst cynodonts (Fig. 1). Extant eutherian mammals show considerably more variation in the height of the jaw articulation relative to the tooth row (Maynard Smith and Savage 1959; Scapino 1972; Noble 1973; Greaves 1974). Herbivores tend to have a highly elevated jaw articulation whereas carnivores tend to have have a low jaw articulation (Maynard Smith and Savage 1959; Scapino 1972; Greaves 1974; Greaves 1980; Crompton et al. 2006). The elevated jaw articulation of eutherian herbivores is hypothesized to be adaptively significant for several reasons, including increasing bite force (Scapino 1972), producing a more even force at the occlusal surface (Ward and Molnar 1980), improving occlusal mechanics (Becht 1953; Crompton et al. 2006; Rak and Hylander 2008), and facilitating translation of the mandibular condyle (Crompton et al. 2006).

Thus, the anatomical transformations taking place within the lower jaws of cynodonts and stem mammaliaformes include not only the reorientation of jaw elevator musculature more vertically but also variation in the geometric relationship of the jaw articulation to the tooth row in both the vertical and mediolateral direction. How this variation manifests itself with respect to the dual performance criteria of minimizing joint reaction forces while maximizing bite force has yet to be resolved. This is due in part to the inability of two dimensional approaches to simultaneously solve variables reflecting three dimensional variation. Here we perform a three dimensional free body analysis that yields equations describing the relationship between the orientation of the jaw elevator

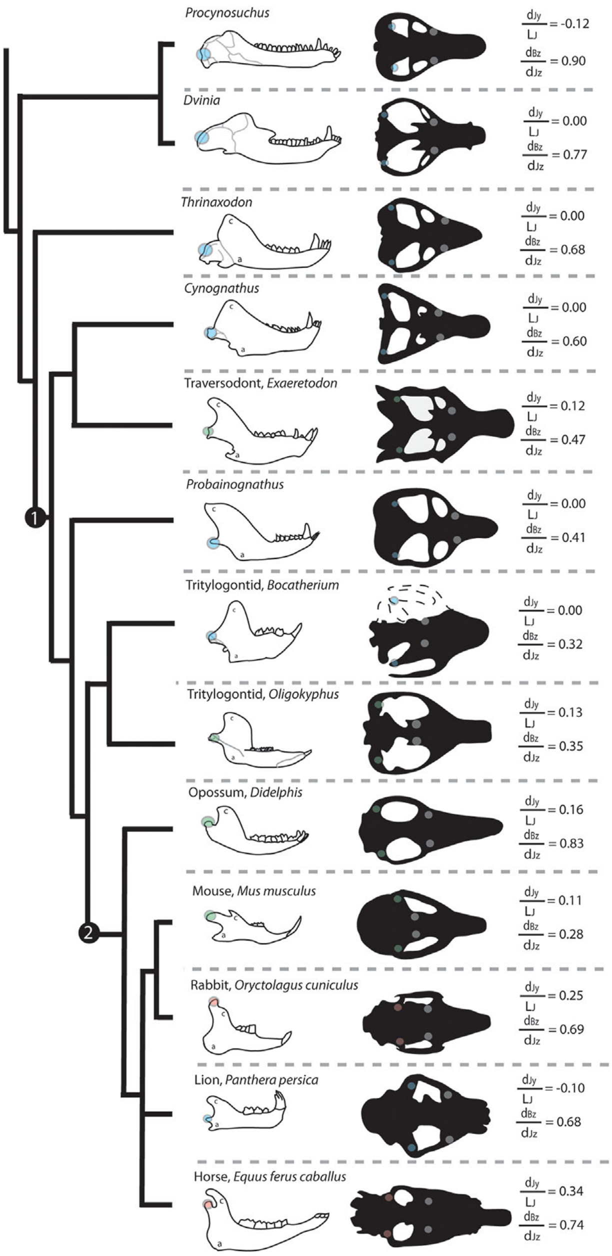

Fig. 1. Phylogeny of cynodont lower jaws illustrating the position of the jaw articulation relative to the tooth row. The vertical position of the jaw articulation is indicated on sagittal diagrams of the lower jaw with a circle. Blue circles designate a jaw articulation level with the tooth row, green circles designate a jaw articulation slightly elevated above the tooth row, and red circles designate a jaw articulation highly elevated above the tooth row. Elevation values are also reported with the d_{Jy}/L_j ratio. d_{jy} is defined as the height of the jaw articulation above the occlusal surface of the tooth row measured from the superior most point on the jaw articulation to the superior most point on the posterior most tooth. L_j is defined as the length of the mandible measured from the posterior most point on the jaw articulation to the anterior most point of the lower jaw excluding the teeth. The mediolateral position of the jaw articulation relative to the tooth row is indicated on the black outline of the skull in ventral view. The position of the jaw articulation is indicated with the colored circles. The position of the most posterior tooth is indicated by the white circles. Mediolateral values are reported with the d_{Bz}/d_{Jz} ratio. d_{Bz} is defined as the mediolateral position of the posterior most tooth relative to the midline of the skull. d_{Jz} is defined as the mediolateral position of the jaw articulation relative to the midline of the skull. Phylogeny adapted from Ruta et al. (2013). Node 1 on the phylogeny indicates the clade Cynognathia. Node 2 indicates the clade Mammalia. All measurements from fossil taxa taken from referenced sources. Lower jaws of *Procynosuchus* and *Dvinia* are adapted from Kemp (1982), *Thrinaxodon* and *Bocatherium* from Sidor (2003), *Probainognathus* from Crompton and Hylander (1986), *Cynognathus* from Kermack et al. (1973), *Exaeretodon* from Chatterjee (1982), and *Oligokyphus* from Crompton and Parkyn (1963). All skull reconstructions are adapted from Kemp (1982) except *Bocatherium* adapted from Clark and Hopson (1985) and *Exaeretodon* adapted from Liu (2007).

muscles, the position of the jaw articulation relative to the bite point, the joint reaction forces and the bite force. We use a reconstruction of the lower jaw of *Probainognathus* from Crompton and Hylander (1986) as the reference taxon for our analysis. *Probainognathus* is ideally suited for such a reference as it sits in a phylogenetically informative position (Fig. 1), and possesses a suite of characters pertinent to our free body analysis of a hypothetically basal condition including muscles directed principally in the posterior direction, a tooth row located medial to the jaw articulation, and a jaw articulation vertically level with the tooth row. We then evaluate the effects of variation in the musculoskeletal configuration in a manner representative of changes that occurred in early mammals and their ancestors and solve for joint reaction forces and bite force.

METHODS

Free body analysis

Any system of forces acting on a rigid body in equilibrium can be reduced to a single resultant force and a couple moment that maintain the equivalent translation and rotation of the original system of forces (Hibbeler 2004). The system of forces used in our analysis is taken from a reconstruction of the lower jaw of *Probainognathus* with jaw elevator forces scaled to a mandibular length of 10 a.u. (artibtrary units; Crompton and Hylander 1986). The resultant muscle force (F_M) from each hemi-mandible is calculated by summing the components of each muscle force in each direction (F_{Mx}, F_{My}). The magnitude of F_M for the system of forces describing the lower jaw of *Probainognathus* is 46 a.u. This value is used as a constant in our analysis. The couple moment of the force system is calculated by summing the product of the muscle force and the distance of each muscle from the jaw joint for each jaw elevator. The couple moment from the system of forces describing the *Probainognathus* lower jaw is 197.03 a.u. (Fig. 2a).

For a free body analysis, the system of forces must be in static equilibrium, where the sum of all of the forces acting on the lower jaw equals zero. Therefore, the resultant muscle force (F_M) is considered together with the biting force (F_B) and the reaction forces at the working- and balancing-side jaw joints (F_{WS} and F_{BS}, respectively). The equations describing this relationship are written as:

$$\sum F_x = 0 = F_{Mx} + F_{WSx} + F_{BSx} + \cancel{F_{Bx}} \tag{1}$$

$$\sum F_y = 0 = F_{My} + F_{WSy} + F_{BSy} + F_{By} \tag{2}$$

$$\sum F_z = 0 = \cancel{F_{Mz}} + F_{WSz} + F_{BSz} + \cancel{F_{Bz}} \tag{3}$$

where the subscripts *x*, *y* and *z* correspond to the horizontal, vertical, and lateral component of the forces, respectively (Fig. 2b).

Several of these terms can be zeroed with the appropriate assumptions. Zeroed terms are represented here by crossed out terms in the equations. We assume that the working and balancing side forces along the *z* axis will be equal and opposite since the muscles of the working and balancing side are contracting symmetrically. Furthermore, we assume that the bite point only has a vertical component, zeroing out F_{Bz} and F_{Bx}. The *x* and *y* component of the resultant muscle force (F_M) are known, and the *z* component of the muscle force is zero. This leaves five unknowns. To solve for these variables, we need to sum the moment for these forces about point *m* which we placed at the mediolateral midpoint between the two jaw joints to simplify the calculations:

$$\sum M_x = 0 = M_{Mx} + M_{WSx} + M_{BSx} + M_{Bx} \tag{4}$$

$$\sum M_y = 0 = M_{My} + M_{WSy} + M_{BSy} + M_{By} \tag{5}$$

$$\sum M_z = 0 = M_{Mz} + M_{WSz} + M_{BSz} + M_{Bz}$$

Equations 4–6 with zeroed terms per our assumptions can be written as:

$$\begin{aligned}\sum M_x &= 0\\ &= M_{Mx} + \left[\left(F_{WSz} * \cancel{d_{wsy}}\right) - \left(F_{WSy} * d_{WSz}\right)\right]\\ &\quad + \left[\left(F_{BSz} * \cancel{d_{BSy}}\right) - \left(F_{BSy} * d_{BSz}\right)\right]\\ &\quad + \left[\left(\cancel{F_{Bz}} * d_{By}\right) - \left(F_{By} * d_{bz}\right)\right]\end{aligned}$$

$$\begin{aligned}\sum M_y &= 0\\ &= M_{My} + [(F_{WSx} * d_{wsz}) - (F_{WSz} * \cancel{d_{WSx}})]\\ &\quad + [(F_{BSx} * d_{BSz}) - (F_{BSz} * \cancel{d_{BSx}})]\\ &\quad + [(\cancel{F_{Bx}} * d_{Bz}) - (\cancel{F_{Bz}} * d_{bx})]\end{aligned}$$

$$\begin{aligned}\sum M_z &= 0\\ &= M_{Mz} + \left[\left(F_{WSy} * \cancel{d_{WSx}}\right) - \left(F_{WSx} * \cancel{d_{wsy}}\right)\right]\\ &\quad + \left[\left(F_{BSy} * \cancel{d_{BSx}}\right) - \left(F_{BSx} * \cancel{d_{BSy}}\right)\right]\\ &\quad + \left[\left(F_{By} * d_{Bx}\right) - \left(\cancel{F_{Bx}} * d_{By}\right)\right]\end{aligned}$$

where *d*, corresponds to the distance of a force with respect to the point *m*.

Together, equations 1–6 reduce to:

$$F_{By} = -\frac{M_{Mz}}{d_{Bx}} \tag{7}$$

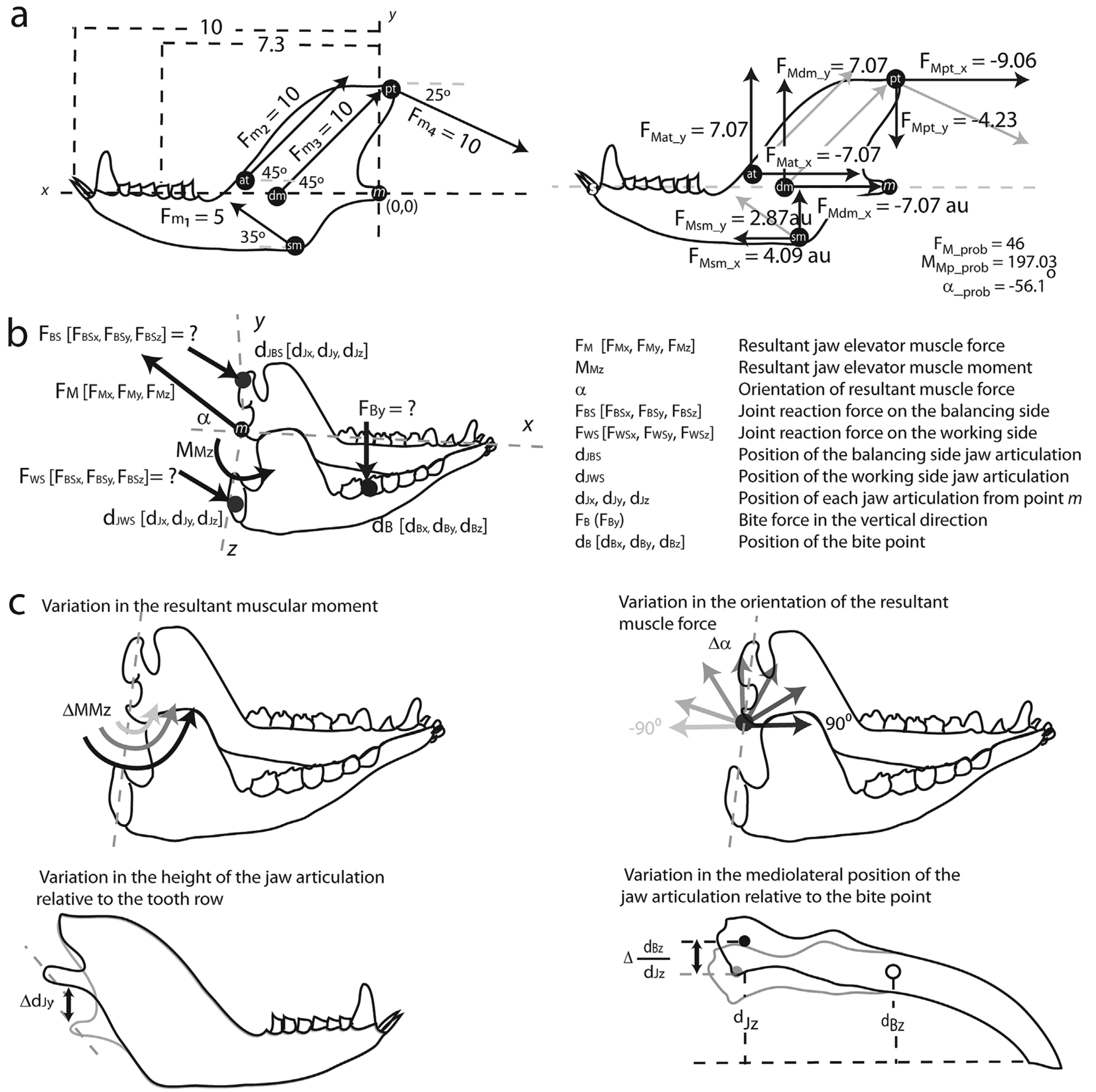

Fig. 2. Diagram illustrating the reduction of the elevator muscles in *Probainognathus* to an equivalent system of forces, and the variation in the resultant muscle orientation, resultant muscular moment, height of the jaw articulation relative to the tooth row, and position of the jaw joint relative to the tooth row. a. Diagram of the lower jaw of *Probainognathus* in sagittal view modified from Crompton and Hylander (1986) with muscle forces scaled to a jaw length of 10 a.u. representing the deep masseter (dm), superficial masseter (sm), anterior temporalis (at), and posterior temporalis (pt; left), and jaw elevator muscle forces that have been decomposed into *x* and *y* values (right). From these values, the magnitude and orientation of the resultant muscle force and the resultant muscle moment are calculated. b. Three-dimensional reconstruction of the *Probainognathus* lower jaw showing the dependent and independent variables of our model. The muscle forces from both the working and balancing side have been reduced to a single vector (F_M) and a couple moment (M_{Mz}). The orientation of F_M in the coordinate system of the lower jaw is indicated by α. The reaction forces at the bite point (F_B) and the jaw joints (F_{WS} and F_{BS}) are unknowns. All variables used in the manuscript are defined on the right c. diagrams of the *Probainognathus* lower jaw illustrating how variation is introduced into the free body analysis, including variation in the magnitude of the resultant muscle moment (upper left), orientation of the resultant muscle force (upper right), elevation of the jaw joint relative to the tooth row (lower left), and mediolateral position of the jaw joint relative to the bite point (lower right).

$$
\begin{aligned}
F_{WSy} &= -\left[\frac{F_{By}}{2} * \left(\frac{d_{Bz}}{d_{Jz}} + 1\right)\right] - \left(\frac{F_{My}}{2}\right) + \left(\frac{\cancel{M_{Mx}}}{2 * \cancel{d_{Jz}}}\right) \\
&= -\left[\frac{F_{By}}{2} * \left(\frac{d_{Bz}}{d_{Jz}} + 1\right)\right] - \left(\frac{F_M \sin\alpha}{2}\right)
\end{aligned}
\tag{8}
$$

$$
\begin{aligned}
F_{BSy} &= \left[\frac{F_{By}}{2} * \left(\frac{d_{Bz}}{d_{Jz}} - 1\right)\right] - \left(\frac{F_{My}}{2}\right) - \left(\frac{\cancel{M_{Mx}}}{2 * d_{Jz}}\right) \\
&= \left[\frac{F_{By}}{2} * \left(\frac{d_{Bz}}{d_{Jz}} - 1\right)\right] - \left(\frac{F_M \sin\alpha}{2}\right)
\end{aligned}
\tag{9}
$$

$$
F_{WSx} = -\frac{F_{Mx}}{2} = -\frac{F_M \cos\alpha}{2} \tag{10}
$$

$$
F_{BSx} = -\frac{F_{Mx}}{2} = -\frac{F_M \cos\alpha}{2} \tag{11}
$$

where F_M and α are the magnitude and the direction of the resultant muscle force. It must be noted that M_{Mx} and M_{My} are zero only in the case of bilaterally symmetrical muscle activation patterns. If the magnitudes of working and balancing side jaw elevator muscle forces are unequal (fire asynchronously), several addition terms must be added to eq. 7-11 (Spencer 1999). Bilaterally unequal muscle forces have played an important role in the evolution of the mammalian masticatory apparatus (Weijs 1994; Williams et al. 2011), and warrant consideration if making comparisons between mammals and non-mammals, particularly with respect to unilateral occlusion. Unfortunately, this point is beyond the scope of what can be addressed in this paper.

Together, equations 7–11 represent the relationship between an equivalent force system describing the musculoskeletal configuration of the lower jaw to joint reaction forces and bite force. These equations can be used for calculating joint reaction forces and bite force from a single taxon with known input variables or to map the effects of variation in the input variables on joint reaction forces (F_{WS} and F_{BS}) and bite force (F_B). Here we map the effects of variation in the input variables relative to values calculated from *Probainognathus*. We first introduce variation in the resultant muscular moment (M_{Mz}). The magnitude of the resultant muscle force (F_M) is constant. The magnitude of M_{Mz} can be changed by either shifting the position of F_M along the x axis or changing the orientation of the resultant muscle force (α). This is because M_{Mz} and α are coupled variables expressed by the equation:

$$
\begin{aligned}
M_{Mz} &= \left(F_{My} * d_{Mx}\right) - \left(F_{Mx} * d_{My}\right) \\
&= F * (\sin\alpha * d_{Mx} - \cos\alpha * d_{My})
\end{aligned}
\tag{12}
$$

Variation in M_{Mz} can be introduced into equations 7–11 by changing either α or the position of F_M along the x axis (Fig. 2c).

Equations 7–11 also allow us to test for the effect of variation in mandibular geometry on joint reaction forces and bite force when all other variables are held equal. Equations 8 and 9 illustrate that the ratio describing the lateral distance from biting point to jaw articulation (d_{Bz}/d_{Jz}) impacts joint reaction forces. This ratio was calculated following the mandibular geometry of *Probainognathus* estimated from Luo (2011) and Kemp (1982) to be 0.41, with both hemi-mandibles forming a triangular shape in ventral view (Fig. 1). The ratio describing the mediolateral geometry of *Probainognathus* is found to be lower than that of basal cynodonts such as *Thrinaxodon* with a d_{Bz}/d_{Jz} ratio of 0.68. Here we calculated joint reaction forces and bite force using two different d_{Bz}/d_{Jz} ratios, representing both the *Thrinaxodon* and *Probainognathus* configurations (Fig. 2c).

To explore the effect of a vertical shift in the location of the jaw articulation with respect to the tooth row, we must add an additional moment to M_{Mz} because the distance of F_M to the axis of rotation has changed. This new moment, that we will call the total moment (M_T), can be calculated by adding the moment produced by the resultant muscle force about the z axis (M_{Mz}) to a moment produced by those forces about a new axis shifted only in the vertical direction (M_{shift}):

$$
M_T = M_{Mz} + M_{\text{shift}}
$$

Since the jaw joint is only translating in the vertical direction (d_{My_shift}), the equation for M_{shift} is:

$$
M_{\text{shift}} = F_{My} * d_{Mx} - F_{Mx} * d_{My\_\text{shift}}
$$

The new total moment (M_T) can then be applied to eq. 7 in place of M_{Mz} to solve for the three reaction forces as (i) the orientation of the resultant muscle force is varied and (ii) the position of the jaw articulation is varied relative to the bite point.

RESULTS

The equations derived from this three dimensional free body analysis are used here to address questions regarding the evolution of the cynodont lower jaw. It should be noted that these equations can be applied to any musculoskeletal configuration of the lower jaw, regardless of taxonomic group, provided that the assumptions of the model are not violated. Our model illustrates how variation in (i) the orientation of the resultant muscle force and (ii) the position of the jaw articulation relative to the bite point impacts bite force (F_B) and joint reaction forces (F_{WS} and F_{BS}). Because this is a three-dimensional free body analysis, we have simultaneously solved for all of the variables in equations 7–11. As a result, the relationships between these variables are complex. We will explore them using contour plots (Fig. 3).

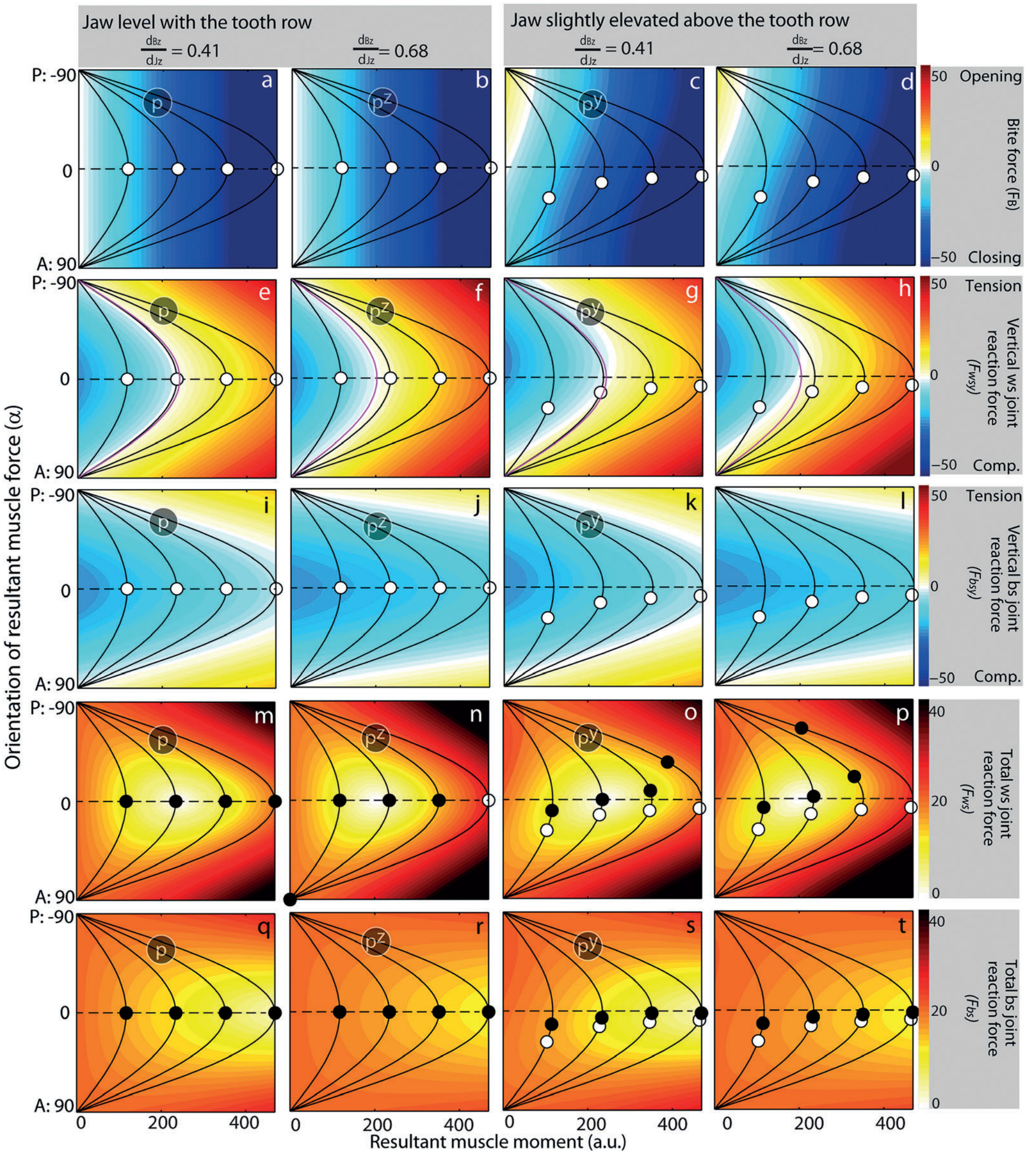

Fig. 3. Contour plots illustrating the effect of variation in the orientation of the resultant muscle force, the position of the jaw articulation relative to the tooth row, and the resultant muscle moment on joint reaction forces and bite force. Variation in the orientation of the resultant muscle forces (α) is graphed on the y axis. Negative values represent a posteriorly directed resultant force. Positive values represent an anteriorly directed resultant force. Values of zero represent vertical forces. The resultant muscular moment (M_{MZ}) is plotted on the x axis. It can be changed by either shifting the resultant muscle force along the x axis or changing the orientation of the resultant force at any given position. Changes in the moment arm of the resultant muscle force are represented by the black isolines, corresponding to positions at 25%, 50%, 75%, and 100% of mandibular length. Tracing an isoline from the top of the graph to the bottom of the graph illustrates how changes in muscle orientation will impact the resultant moment when all variables are held equal. These contour plots are superimposed over the dependent variables of our analysis. a-d illustrates variation in bite force, e-h illustrates variation in the vertical component of the working side joint reaction force, i-l illustrates variation in the vertical component of the balancing side joint reaction force, m-p illustrates variation in the total reaction force on the working side joint, and q-t illustrates variation in the total reaction force on the balancing side joint. For e-f, the magenta line indicates the position where the vertical working side joint reaction force is zero. For g-h, the magenta line is a reference line corresponding to the position in e and f respectively. Maximum bite forces are indicated with white circles and minimum joint reaction forces are indicated with black circles. Note that black circles overlay the white circles in some cases. Each column represents variation in the position of the jaw articulation relative to the tooth row. A jaw level with the tooth row indicates a d_{Jy}/L_y ratio of 0.00 and a jaw slightly elevated above the tooth row indicates a d_{Jy}/L_y ratio of 0.13. d_{Bz}/d_{Jz} ratios indicate the mediolateral position of the jaw articulation relative to the tooth row. Point p represents the musculoskeletal configuration of *Probainognathus*. Point p^z represents a musculoskeletal configuration identical to point p in all ways except that the d_{Bz}/d_{Jz} ratio is 0.68. Point p^y represents a musculoskeletal configuration identical to point p in all ways except that the d_{Jy}/L_y ratio is 0.13.

In general, the contour plots are organized as follows. Variation in the resultant muscle moment (M_{Mz}) is expressed on the x axis of each graph. Variation in the orientation of the resultant muscle force (α) is expressed on the y axis of each graph, with horizontal forces in the anterior/rostral direction at 90°, vertical forces at 0°, and horizontal forces in the posterior/caudal direction at -90°. Since M_{Mz} and α are coupled variables, their relationship is illustrated with black isolines superimposed over each contour plot.

The impact of variation in the orientation of the resultant muscle force and the position of the jaw articulation on bite force

Bite force is determined by two variables, the resultant muscle moment (M_{Mz}) and the position of the bite point along the x axis (d_{Bx}; Eq. 7). The reaction forces at several bite points on the lower jaw were calculated. While the magnitude of the output variables was found to change with the position of the bite point, the patterns describing how these variables change with variation in the resultant muscle orientation and moment were only marginally affected. As such, we have limited the results to a single bite point. Variation in F_B changes proportionately with M_{Mz}. When all other variables are equal, the reorientation of the resultant muscle force (α) in the vertical direction increases F_B by increasing the moment about the z axis. M_{Mz} can also be increased by shifting F_M away from the jaw articulation along the x axis, independent of α (Figs. 3a and 4a–c).

When all else is equal, changes in the vertical, but not mediolateral, position of the jaw articulation relative to the tooth row will alter bite force (Fig. 3b). When the jaw articulation is elevated relative to the tooth row, asymmetry in the relationship between F_B and muscle force orientation is introduced into the contour plots (Fig. 3a and c, respectively). This asymmetry is the result of an additional moment about the z axis, following eq. 15. An anteriorly directed resultant muscle force will produce an extra moment that will elevate the jaw, while a posteriorly directed resultant muscle force will produce an extra moment that will depress the jaw. The hot colors located in the upper left corner of Figure 3c and d represent a positive force at the bite point (i.e., the jaw is opening). This is the result of posteriorly directed forces, when approaching $-90°$ on the vertical axis, producing a moment about the jaw joint greater than and opposite the input moment (M_{Mz}). This region of the graph represents a functionally unusable configuration of forces and can be considered a functional constraint on the system. Conversely, values of F_B are darker in the lower right hand corner (i.e., the bite force is higher).

Based on these equations, we can also estimate a muscle orientation that optimizes for bite force magnitude. When the jaw joint is at the level of the tooth row, F_B will be maximal when F_M is oriented vertically (white dots on Fig. 3a,b). As the jaw joint is elevated above the tooth row, musculoskeletal configurations with anteriorly directed muscle forces produce maximal bite force magnitudes (Figs. 3c, d and 4a–c).

The impact of variation in the orientation of the resultant muscle force on joint reaction forces

The vertical component of the joint reaction forces is dependent on the vertical component of the resultant muscle force (F_{My} or $F_M{}^* \sin(\alpha)$), the reaction force at the bite point (F_B), and the mediolateral position of the bite point relative to the jaw joint (d_{Bz}/d_{Jz}; Eq. 8 and 9). When the jaw articulation is level with the tooth row, F_B increases proportionately with M_{Mz}. However, the vertical component of F_M changes as a function of α, so reaction forces at the jaw joints (F_{WS} and F_{BS}) change as a function of both α and M_{Mz} (Figs. 3e–f, i–j, m–n, q–r, and 4d–i).

On the working side jaw joint, there is an M_{Mz} that produces zero joint reaction forces (Fig. 3e–h). This region of the graph corresponds to a neutral axis that occurs when the muscle force is applied at a position corresponding to the anterior limit of Greaves' triangle of support (Greaves 1982) defined by the equation $d_{Mx} = d_{Bx}/[(d_{Bx}/d_{Jz})+1]$. This position is defined geometrically and occurs independently of the magnitude of F_M and F_B. In contrast, geometric and anatomical constraints on the position of the jaw elevator muscles prevent the balancing side jaw joint from ever having a neutral vertical joint reaction force (Figs. 3i–j and 4g–i).

Total joint reaction force includes both vertical and horizontal components. Since the magnitude of the x component of the reaction force (F_{BSx} & F_{WSx}) will always be half of F_M (Eq. 10 and 11), total joint reaction force can only be zero when F_M is completely vertical. The vertical component of the joint reaction force can equal zero on the working side joint but not the balancing side. Therefore, when α nears a vertical orientation, both the vertical and horizontal components of the joint reaction force can approach zero on the working side (F_{WS}; Figs. 3m and 4d–f). On the balancing side, total joint reaction force (F_{BS}) decreases as α nears a vertical orientation because the horizontal component of F_M approaches zero (Figs. 3q and 4g–i).

The impact of variation in the ratio of d_{Bz}/d_{Jz} on joint reaction forces

Following equations 8 and 9, variation in the ratio of d_{Bz}/d_{Jz} will impact vertical joint reactions forces when all other variables are held equal. On the working side, increasing the d_{Bz}/d_{Jz} ratio either makes F_{WSJ} less compressive at low values of M_{Mz} (Fig. 4d) or more tensile at high values of M_{Mz} (Fig. 4e–f). On the balancing side, increasing the d_{Bz}/d_{Jz} ratio always makes the vertical joint reaction forces less compressive (Fig. 4g–i).

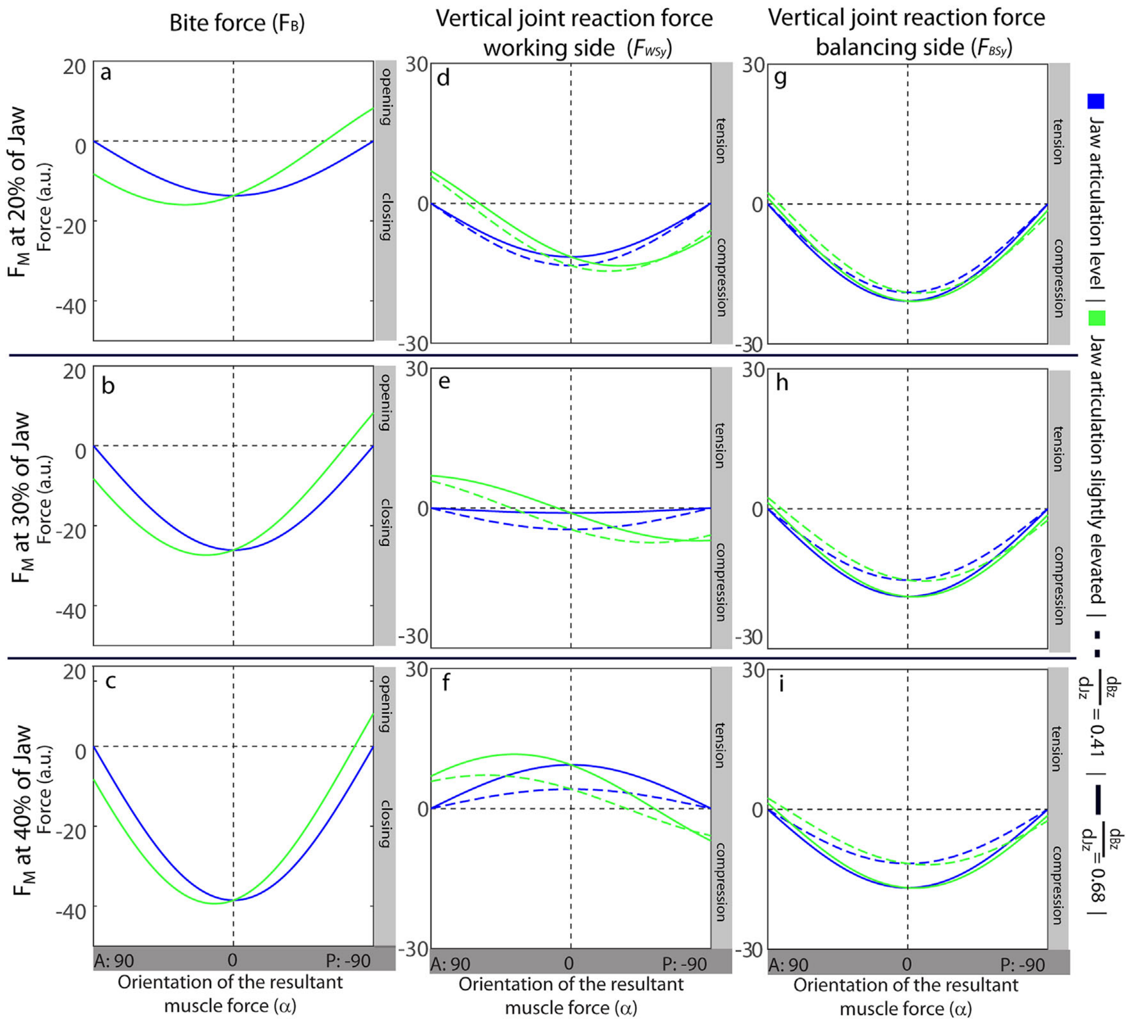

Fig. 4. Line graph illustrating the effect of variation in muscle orientation and jaw position relative to the tooth row on bite force and joint reaction forces when all other variables are held constant. The orientation of the resultant muscle force (α) varies along the *x* axis. Anteriorly directed forces are on the left, vertical forces in the middle, and posteriorly directed forces on the right. Each row represents values calculated at different moment arms. The left column illustrates variation in bite force, the middle column illustrates variation in the vertical component of joint reaction force on the working side, and the right column illustrates variation in the vertical component of joint reaction force on the balancing side. For the leftmost column, negative values indicate jaw closing while positive values indicate jaw opening. For the middle and right column, positive values indicate tension and negative values indicate compression. Values from a jaw articulation at the level of the tooth row are plotted in blue corresponding to a d_{Jy}/L_j ratio of 0.00, from a jaw articulation slightly elevated above the tooth row are in green corresponding to a d_{Jy}/L_j ratio of 0.13. Dotted lines indicate values from a d_{Bz}/d_{Jz} ratio of 0.41 and solid line indicate values from a d_{Bz}/d_{Jz} ratio of 0.68.

The impact of variation in the vertical position of the jaw articulation relative to the tooth row on joint reaction forces

Elevating the position of the jaw articulation relative to the bite point adds an additional moment (M_{shift}) to the total moment of the system (M_T). As a result, the neutral axis describing the transition from compression to tension shifts toward the region of the graph representing α values approaching −90° (Fig. 3g, k). This asymmetry in the contour plots illustrates how an elevated jaw articulation could be advantageous for joint reaction forces in certain musculoskeletal configurations. On the working side, the vertical position of the jaw articulation does not impact F_{WSy} when F_M is vertically oriented (Fig. 4d–f). When values of M_{Mz} are low, an F_M with a slight anterior orientation will produce lower compressive values of F_{WSy} (Fig. 4d). When M_{Mz} if high, an F_M with a slight posterior orientation will produce lower tensile values of F_{WSy} (Fig. 4f). The effect of an elevated jaw articulation on the balancing side joint reaction force (F_{BSy}) is negligible (Fig. 4g–i).

The rate of change in F_{WS} per unit α is also affected by the height of the jaw articulation. A higher jaw articulation results in a greater change in joint reaction force per unit α (i.e., the slope of the curve is greater). Therefore, when all other variables are held equal, the reaction force on the working side jaw articulation changes more quickly as the muscles are reoriented when the jaw articulation is elevated.

The case of Probainognathus

Following the reconstruction of *Probainognathus* from Crompton and Hylander (1986), we calculate an $M_{Mz} = 197.03$ and an $\alpha = -56.1°$. This point is plotted on the contour plots as point p (Fig. 3a, e, i, m). Our model estimates that *Probainognathus* has a bite force of -27.18 a.u. when the bite point is at 72.5% of the jaw length. The vertical working side joint reaction force is 6.33 a.u. of tension (Fig. 3b), and the vertical balancing side joint reaction force is -4.80 a.u. of compression (Fig. 3c) or 17.8% of the bite force. As expected, our values are slightly different from those calculated by Crompton and Hylander (1986). We attribute the difference to our model being three-dimensional rather than two-dimensional, and this being a free body analysis rather than a summation of moments. However, the loading conditions and approximate magnitudes on each joint are in agreement.

We can now use point p as a reference as we explore the variation introduced into the model. All else being equal, the reorientation of the resultant muscle force vertically will have the effect of increasing the resultant muscle moment and bite force (Fig. 3a), increasing the vertical tensile reaction forces on the working side (Fig. 3e), increasing the vertical compressive forces on the balancing side (Fig. 3i), and lowering the total joint reaction forces on both sides (Fig. 3m, q).

Point p^z in the second column represents a theoretical morphology identical to *Probainognathus* in every way except that the ratio of d_{Bz}/d_{Jz} has been increased along the z axis. This is a condition more similar to the configuration of basal cynodonts like *Trinaxodon* (Fig. 1). When all else is equal, increasing the d_{Bz}/d_{Jz} ratio from 0.41 to 0.68 has no effect on bite force (Fig. 3b), increases the vertical tensile joint reaction forces on the working side to 10.52 a.u. (Fig. 3f), increases the vertical compressive joint reaction forces on the balancing side to -8.48 a.u. or 31% of the bite force (Fig. 3j), and increases the total joint reaction forces on both sides (Fig. 3n, r).

Point p^y in the third column represents a theoretical morphology identical to *Probainognathus* in every way except that the position of the jaw articulation has been elevated slighted above the tooth row along the y axis similar to the conditions of *Exaeretodon* and *Baocatherium*. This has the effect of decreasing bite force to 20.33 a.u. (Fig. 3c), decreasing the vertical tensile joint reaction force on the working side to 1.51 a.u. (Fig. 3g), and increasing the vertical compressive joint reaction force on the balancing side to -6.8 a.u. or 33.6% of the bite force (Fig. 3k).

DISCUSSION

The cynodont lower jaw is a morphological diverse structure with a complex system of forces acting on it. The complexity of this musculoskeletal system makes it difficult to interpret patterns of morphological diversity in the context of the dual performance criteria of low joint reaction forces and high bite force. Free body analysis yields equations that are a powerful tool for exploring this relationship because they reduce a complex system of forces to a single equivalent resultant force and couple moment, and permit the effects of variation in each variable to be tested independently. Using this approach, we have identified three musculoskeletal terms that can independently lower joint reaction forces without substantially impacting bite force: (i) the reorientation of the resultant muscle force more vertically moderately increases the vertical joint reaction force, decreases total joint reaction force, and improves bite force when all variables are equal (ii) decreasing the d_{Bz}/d_{Jz} ratio decreases joint reaction forces independent of all other variables, and (iii) increasing the height of the jaw articulation relative to the tooth row increases the joint reaction force and decreases bite force when the resultant muscle force is posteriorly directed but decreases the joint reaction force and increases bite force when the resultant muscle force is anteriorly directed.

The effect of these three musculoskeletal terms on joint reaction forces and bite force is best illustrated by first examining our reference taxa of *Probainognathus* in more detail. When the bite point is located on the distal post-canine dentition, the reconstruction of *Probainognathus* used in this analysis produces a balancing side joint that is in compression and a working side jaw joint that is in tension. The tensile force on the working side jaw joint is largely an effect of the distal nature of the bite point. Crompton and Hylander (1986) propose that the *Probainognathus* jaw joint is not well suited to resist tensile loads, and hypothesize that the post-canine dentition was not extensively used for food reduction. Our model is in agreement with their hypothesis. A more anterior bite point will have the effect of decreasing bite force, pushing the working side joint reaction force into compression, and decreasing the compressive joint reaction force on the balancing side.

The critical principle illustrated by this relationship is that there is a combination of bite point (d_{Bx}) and resultant muscular moment (M_{Mz}) that produces a vertical force of zero on the working side jaw joint. The musculoskeletal configuration producing this reaction force is defined geometrically and corresponds to the anterior limit of the Greaves' triangle of support (Fig. 3e; Greaves 1982). It is important to note that even in this loading condition, neither of the jaw joints are in equilibrium. A resultant muscle force directed posteriorly along the *x* axis, as is the case in *Probainognathus*, will always produce a reaction force at the jaw joint equal and opposite to this resultant muscle force (Eqs. 10 and 11; Fig. 3m). Posteriorly directed forces are hypothesized to be important for prehensile behaviors (DeMar and Barghusen 1972); however, the impact of these forces in reference to auditory performance in cynodonts and the evolution of the middle ear is an unresolved issue. In contrast, the vertical component of the balancing side joint reaction force can never approach zero. Since this joint will always be in compression regardless of the bite point, resultant muscle orientation, or resultant muscle moment (Eq. 9; Fig. 3i, q), it is important to understand how the musculoskeletal system can be modified to limit reaction forces on the balancing side jaw joint.

The total joint reaction force on both the working and balancing side can be lowered by reorienting the resultant muscle force vertically when the jaw articulation is low. The differentiation and reorientation of the masseter complex is hypothesized to have been a critical step toward this end (Crompton 1963; DeMar and Barghusen 1972; Bramble 1978; Crompton and Parker 1978). The attachment site of the superficial masseter on the dentary is between the most posterior tooth and the jaw articulation. This facilitates a more vertical orientation in the case of *Thrinaxodon*, or a slightly anterior orientation in the case of other cynodonts such as *Trircachodon* (Crompton and Parker 1978). The anterior inclination of the superficial masseter works antagonistically against the posterior line of action of the temporalis. Therefore, the orientation of the resultant muscle force can be shifted vertically/anteriorly by a decrease in the relative contribution of the temporalis, an increase in the relative contribution of the masseter complex and/or a re-orientation of the masseter to have an anterior line of action (adapted from Bramble 1978). Any of these three alterations change not only the resultant muscle force but also the associated moment. Our analysis demonstrates that the optimal bite force/total reaction force ratio occurs when the resultant muscle force is vertical, independent of the resultant muscle moment (Fig. 3m, q).

The vertical component of the balancing side joint reaction force can be limited by the geometric ratio describing the mediolateral position of the jaw joint and the bite point relative to the midline of the skull (i.e., d_{Bz}/d_{Jz} ratio). If d_{Bz} equals d_{Jz} and the ratio is one, the compressive force on the balancing side jaw joint will approach half of the vertical component of the resultant muscle force (Fig. 3i–j and q–r). Lowering the d_{Bz}/d_{Jz} ratio has no effect on bite force, but will decrease the compressive forces acting on the balancing side jaw joint. Thus, the d_{Bz}/d_{Jz} ratio may prove to be an important functional metric for interpreting patterns of morphological diversity in the cynodont lower jaw. Preliminary measurements support this hypothesis. Basal cynodonts including *Dvinia*, *Procynosuchus*, *Thinaxodon*, *Cynognathus* appear to have higher d_{Bz}/d_{Jz} ratio than more advanced cynodonts such as *Exaeretodon*, *Bocatherium*, *Oligokyphus*, and *Probainognathus* (Fig. 1). However, the d_{Bz}/d_{Jz} ratios of several therocephalians, including *Moschorhinus*, *Theriognathus*, and *Scaloposaurus*, are nearly as low as those from the advanced cynodonts, underscoring the importance of considering this measure in a robust phylogenetic context.

There are a number of ways that the morphology of the lower jaw can be modified to decrease the d_{Bz}/d_{Jz} ratio. Greaves (1988) and Druzinsky and Greaves (1979) proposed that this is achieved by changing the geometric configuration of the lower jaw in ventral view from pentagonal in basal therapsids to triangular in mammals, shifting the distal most post-canine tooth medially. When the lower jaw has a more triangular configuration, the d_{Bz}/d_{Jz} ratio can be further decreased by increasing the lateral position of the site of jaw articulation relative to jaw length. The morphological patterns underlying the emergence of the secondary jaw joint may have influenced the d_{Bz}/d_{Jz} ratio in this way. The secondary jaw articulation emerged in all cases lateral to the site of primary articulation on the quadrato-articular joint surface. Bramble (1978) notes that the dentary–postdentary interface is hypothesized to have the capacity for progressive kinesis, possibly shielding the postdentary bones from the full impact of the joint reaction forces. An additional consequence of this kinesis is that the joint reaction forces would shift to the laterally positioned dentary, the rigid body on which the elevator musculature attaches.

Variation in the vertical position of the jaw articulation relative to the tooth row is less pronounced in most nonmammalian cynodonts. Two herbivorous taxa, *Exaeretodon* and *Oligokyphus*, slightly elevated the jaw articulation, but this elevation is moderate when compared to extant herbivorous eutherians such as *Equus*, *Bos*, or *Lepus* (Fig. 1). The cheek teeth of *Exaeretodon* and *Oligokyphus* have morphologically complex occlusal patterns, and patterns of wear indicative of propalinal jaw movements. Taken together with fossil reconstructions, the resultant muscle forces are hypothesized to be posteriorly directed (Chatterjee 1982; Kemp 1982; Kermack and Kermack 1984; Crompton and Attridge 1986). Our model illustrates that when the resultant muscle force is posteriorly directed, elevation of the jaw articulation relative to the tooth row will decreases bite force and increase joint reaction forces (Fig. 4). Conversely, a resultant muscle force oriented in the anterior direction, as is the case in *Equus*, *Bos*, and *Lepus* (Weijs and Dantuma 1980; Radinsky 1985; Greaves 1991) and most herbivores with few exceptions (Turnbull 1970; Greaves 1991), increases bite force and lowers joint reactions forces when all else is equal (Fig. 4). Because of the posterior inclination of the resultant muscle force in nonmammalian cynodonts, a jaw articulation level with the tooth row is the musculoskeletal configuration that produces the best ratio of bite force to joint reaction forces.

The equations derived from this free body analysis illustrate that there are mathematical and geometric conditions that drive the relationship between the orientation of the resultant muscle force, the position of jaw articulation relative to the bite point, the joint reaction forces, and the bite force. Understanding how the patterns of morphological diversity in the cynodont lower jaw reduce to an equivalent system of forces and relate to these mathematical and geometric relationships is an important next step. Because systems of forces with different individual components can still reduce to similar equivalent systems, it may be the case that all of the musculoskeletal diversity in the cynodont lower jaw reduces to an equivalent system of forces similar to that of *Probainognathus*. However, our model illustrates that dissimilarity from this equivalent force system can still produce low joint reaction forces and a high bite force, supporting the inference from the fossil record that the musculoskeletal configuration of the cynodont lower jaw can be evolutionarily labile without violating the dual performance criteria of the auditory and feeding system.

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