Free Body Analysis, Beam Mechanics, and Finite Element Modeling of the Mandible of *Alligator mississippiensis*

Laura B. Porro,1* Casey M. Holliday,2 Fred Anapol,3 Lupita C. Ontiveros,4 Lolita T. Ontiveros,4 and Callum F. Ross1

1Department of Organismal Biology and Anatomy, University of Chicago, Chicago, Illinois 60637
2Department of Pathology and Anatomical Sciences, University of Missouri School of Medicine, Columbia, Missouri 65212
3Department of Anthropology, University of Wisconsin, Milwaukee, Wisconsin 53201
4Department of Biological Sciences, University of Wisconsin, Milwaukee, Wisconsin 53201

**ABSTRACT** The mechanical behavior of mammalian mandibles is well-studied, but a comprehensive biomechanical analysis (incorporating detailed muscle architecture, accurate material properties, and three-dimensional mechanical behavior) of an extant archosaur mandible has never been carried out. This makes it unclear how closely models of extant and extinct archosaur mandibles reflect reality and prevents comparisons of structure–function relationships in mammalian and archosaur mandibles. We tested hypotheses regarding the mechanical behavior of the mandible of *Alligator mississippiensis* by analyzing reaction forces and bending, shear, and torsional stress regimes in six models of varying complexity. Models included free body analysis using basic lever arm mechanics, 2D and 3D beam models, and three high-resolution finite element models of the *Alligator* mandible, incorporating, respectively, isotropic bone without sutures, anisotropic bone with sutures, and anisotropic bone with sutures and contact between the mandible and the pterygoid flange. Compared with the beam models, the *Alligator* finite element models exhibited less spatial variability in dorsoventral bending and sagittal shear stress, as well as lower peak values for these stresses, suggesting that *Alligator* mandibular morphology is in part designed to reduce these stresses during biting. However, the *Alligator* models exhibited greater variability in the distribution of mediolateral and torsional stresses than the beam models. Incorporating anisotropic bone material properties and sutures into the model reduced dorsoventral and torsional stresses within the mandible, but led to elevated mediolateral stresses. These mediolateral stresses were mitigated by the addition of a pterygoid-mandibular contact, suggesting important contributions from, and trade-offs between, material properties and external constraints in *Alligator* mandible design. Our results suggest that beam modeling does not accurately represent the mechanical behavior of the *Alligator* mandible, including important performance metrics such as magnitude and orientation of reaction forces, and mediolateral bending and torsional stress distributions.

**INTRODUCTION**

In both aquatic and terrestrial vertebrates, the jaws are important in transmitting muscle force to the external environment. Likewise, external forces, such as those generated at the bite point or by struggling prey or opponents, are transferred to the organism through the jaws. Thus, jaws are used by vertebrates to interact with their environment, these interactions are expected to exert selective pressure on jaw morphology, and this morphology may be optimized for performance in these interactions. The morphology of the cranium reflects a compromise between multiple functions: feeding, protecting the brain, housing sense organs, respiration, and communication. The mandible, in contrast, has feeding as its primary function, suggesting that morphological adaptations for applying and resisting feeding forces should be more obvious in the mandible than elsewhere in the skull. The biomechanics of mammalian mandibles (particularly stem mammals, primates, and carnivorans) are relatively well-studied. In contrast, the mandibles of archosaurs (crocodilians, birds, and their fossil relatives) have received substantially less attention, making it difficult to compare mandibular structure–function relationships between mammals and other vertebrates. This article begins to rectify this bias by presenting and

KEY WORDS: archosaurs; crocodilians; biomechanics; beam theory; bone stress

© 2011 WILEY-LISS, INC.
testing hypotheses regarding stress regimes in an archosaur mandible during feeding using free body analysis, beam theory, and finite element analysis (FEA).

In a series of articles, Hylander used free body analysis and in vivo bone strain to predict loading and stress regimes in primate mandibles during biting and mastication (Hylander, 1977, 1979a,b, 1981, 1984, 1985). (The term loading regime refers to a specific combination of external forces; stress regime refers to a specific combination of internal stresses.) Hylander hypothesized that the working side mandibular corpus experiences twisting about its long axis, shearing perpendicular to its long axis, and bending in sagittal planes, whereas the balancing side corpus experiences sagittal bending and long-axis twisting. Hylander also predicted that the mandibular symphysis is doroventrally sheared, twisted about a transverse axis, and bent in a transverse plane due lateral transverse bending (i.e., wishboning) of the corpora. Hylander’s work prompted subsequent studies relating variation in mammalian mandibular morphology to hypothesized loading regimes, although some aspects of mandibular morphology are apparently not optimized to resist feeding forces (Daegling, 1993).

The degree to which these results apply to mandibles of nonmammals remains to be evaluated because mandibular biomechanics of archosaurs are poorly understood. Bock’s detailed free body analysis of external forces acting on the bird bill (Bock, 1966), and his theoretical and photoelastic studies of the internal stresses in the mandible of the crow (Bock and Kummer, 1968), suggested to him that mandibular shape reflects loading regime: under dorsoventral bending, the mandible is argued to function like an I-beam, with the thickened dorsal and ventral cortices resisting tension and compression, respectively, and the lateral and medial cortices resisting shear. The region of the mandibular fenestra, present in most archosaurs, was argued to be an area of low stress, making it possible for bone to be absent. Bock and Kummer (1968) suggested that the mediolateral narrowness of the mandible permits flexibility and that “this flexibility is especially important in birds which have an intramandibular hinge such as the pelicans, herons, gulls, and numerous other groups.” Birds requiring more rigid mandibles were suggested to have rounder cross sections.

Similarly, free body analysis of the mandible of Caiman crocodilus, including integration (sensu Dullemeijer, 1974) of the effects of several different kinds of loading patterns, was also said to support the hypothesis that the transverse cross-sectional shape of the mandible is appropriate for resisting these loading patterns. As in the crow, the mandibular fenestra was argued to be an area of low stress, allowing bone to be absent in this area (Dullemeijer, 1974; van Drongelen and Dullemeijer, 1982).

These analyses suggest that archosaur mandibular morphology reflects loading and stress regimes, providing support for attempts to reconstruct feeding behavior in fossil archosaurs. Lever arm mechanics have been used to estimate the efficiency of the feeding apparatus, including the mandible, and to differentiate between feeding strategies, i.e., jaws adapted for powerful rather than fast jaw closure (Ostrom, 1961; Mazzetta et al., 1998; Desojo and Vizcaíno, 2009). Molnar (1998) used free body and space frame analyses to predict tensile and compressive stress trajectories in the mandible of Tyrannosaurus. His analyses suggested that the anterior portion of the mandible (dentry) in Tyrannosaurus behaves as a cantilevered beam; posteriorly, tensile and compressive stresses were concentrated at the dorsal and ventral margins of the mandible. This was argued to be consistent with mandibular cross-sectional morphology, in that the anterior mandible is a doroventrally elongated ellipse, whereas the posterior mandible features thickened dorsal and ventral margins supporting a thin vertical plate of bone. The great depth of the dentary in Tyrannosaurus was suggested to be an adaptation to resist sagittal bending. Therrien (2005) applied beam analysis to the mandibles of several theropod dinosaurs and assumed that bite force applied at any point along the mandible would be proportional to the geometry of that section. Furthermore, he assumed that doroventrally deep mandibular corpora were adapted to resist sagittal bending, whereas corpora that were mediolaterally expanded were adapted to resist torsional stresses. On the basis of mandibular morphology, he divided theropods into five feeding categories, including large prey hunters, small prey specialists, and bone crushers. Using FEA, Rayfield (2001) examined deformation, stress, and strain in the skull of the theropod Allosaurus; her work demonstrated that the lower jaw functioned as a beam in three-point sagittal bending. However, because the lower jaw was attached to the cranium at the quadratoarticual joint, each hemimandible was also bent in the mediolateral plane due to condylar reaction force. A similar study was carried out on the isolated mandible of the theropod Carnotaurus (Mazzetta et al., 2004). Bell et al. (2009) compared finite element models (FEMs) of ceratopsian and hadrosaur mandibles that were constrained at the jaw joint and loaded at two different bite points; muscle forces were not applied. Their loading of the ceratopsian mandible resulted primarily in sagittal bending stresses; in contrast, the hadrosaur mandible experienced high degrees of torsion in the postdental bones.

These hypotheses regarding the biomechanics of archosaur mandibles remain untested because
in vivo data on mandible function are lacking and comprehensive biomechanical analyses of extant archosaur mandibles have yet to be performed; in contrast, several studies have examined the mechanics of the crocodilian cranium (Daniel and McHenry, 2001; Metzger et al., 2005; McHenry et al., 2006; Rayfield et al., 2007 Pierce et al., 2008; Rayfield and Milner, 2008). Furthermore, several features present in archosaurs (such as patent mandibular sutures) are absent in mammals, and their effects on mandibular mechanics are unknown.

HYPOTHESES

The aims of this study are: 1) to calculate the external forces acting on the mandible resulting from muscle architecture (cross-sectional area, pin- nation, and sarcomere length), muscle orientation, and insertion sites; 2) to estimate and compare reaction forces on the mandible using lever arm mechanics, beam modeling, and FEA; 3) to estimate shear, bending, and torsional stresses in the Alligator mandible and their relative importance using beam modeling and FEA; and, 4) to compare reaction forces and stress regimes in a simple beam FEM to a high-resolution FEM of the Alligator mandible.

This study will address the following questions: 1) Does mandibular morphology in this archosaur minimize stress while minimizing bony material better than would a similarly loaded simple beam? 2) How do the material properties of the archosaur mandible affect its mechanical behavior? 3) How does the enlarged pterygoid flange of archosaurs affect mandibular stress patterns?

Bending Stresses

The mandibles of alligators and other archosaurs must be subjected to bending stresses during biting because the mandible is much longer than it is deep; thus, we expect that bending stresses should be larger than stresses due to sagittal (zy) or transverse (xz) shear. Bending stresses (σ) in a cross section through a beam-like member are directly proportional to the magnitude of the external bending moment about that cross section (M), and inversely proportional to the second moment of area of the cross section (I). These stress magnitudes vary in proportion to their distance (y) from the neutral axis of bending, and are either compressive or tensile.

The resultant bending moment acting on a cross section is the sum of the individual bending moments acting on that section. These bending moments will vary along the length of the mandible, as well as with variations in bite point.

If cross-sectional geometry (and therefore, second moment of area) varies along the Alligator mandible to minimize stress (thus minimizing the likelihood of failure or maximizing possible loading) while minimizing material, then stress due to bending will remain relatively constant. To quantify this effect in this article, bending stress magnitudes along the length of a simple prismatic beam (in which cross-sectional geometry is constant along its length) is compared with bending stress magnitudes along the length of the Alligator mandible. If Alligator mandible cross-sectional properties are optimized to maintain strength while minimizing material, stress magnitudes should vary less along the length of the Alligator mandible than they do along the simple, prismatic beam. (We emphasize that we view optimization as a process that minimizes stress relative to the amount of bone material, not an endpoint characterized by specific values.)

Transverse and Sagittal Shear Stresses

The mandibles of alligators and other archosaurs must also be subjected to sagittal (zy), coronal (xy), and transverse (xz) shear stresses because the muscle, bite, and joint reaction force vectors are not coincident. Here, we concentrate on the shear stresses in sagittal and transverse planes caused by vertical and horizontal components of bite, joint reaction and muscle forces. These shear stresses will vary along the length of the mandible, depending on the position of the cross section relative to the external shearing forces; they also vary with changes in bite point. Because the ultimate strength of bone is greater in tension or compression than in shear (Reilly and Burstein, 1975), and because the Alligator mandible approximates a long beam in its morphology, we hypothesize that bending stresses will be larger than sagittal or transverse shear stresses. This predicts that mandibular morphology is unlikely to minimize sagittal and transverse shear stresses. However, in areas of the mandible where shear stresses predominate [e.g., between bite point and jaw elevator muscles (during posterior biting) or at the symphysis], shear stress may be an important determinant of mandibular morphology; this could be reflected by morphological changes such as increased dorsoventral mandibular height.

Shear stress in a beam section is directly proportional to the magnitude of the external shearing forces and inversely proportional to the cross-sectional area of the section. In hollow beams with walls of uniform thickness shearing stresses are uniformly distributed, unless the section warps under load. In hollow beams with walls of nonuniform thickness, shear flow can result in accumulations of high stresses in thin-walled areas (Hibbeler, 2000). These considerations suggest that there may be significant differences in shear stress magnitudes between a simple prismatic beam and
the *Alligator* mandible. If sagittal and transverse shear stresses are more uniformly distributed in the *Alligator* mandible than in the prismatic beam, this will support the hypothesis that *Alligator* mandible morphology minimizes these shear stresses while minimizing material.

### Torsional Shear Stresses

The *Alligator* mandible, and those of other archosaurs, must experience torsional stresses if the external forces acting on the mandible do not pass through the centroidal axis of the mandible. In a solid beam with a circular cross section, the shear stress due to torsion ($\tau_T$) at a point in the cross section is a function of the external torque ($T$) acting on the beam and the distance of the point of interest from the twisting axis. $\tau_T$ is inversely related to the polar moment of inertia (or torsion constant), $J$, which reflects the resistance of the beam to torsion (Roark, 1965; Roark and Young, 1975; Hylander, 1979b; Turner and Burr, 1993).

The simple torsion formula cannot be applied to noncircular, hollow cross sections, such as mandibles, and other methods must be used (Daegling, 1989, 2002, 2007a,b; Daegling and Hylander, 1998). Various formulae can be used to account for eccentricity of the ellipse and wall thickness (Roark and Young, 1975), but all these formulae are approximations (Daegling and Hylander, 1998; Daegling, 2007a; Ameen, 2008). Indeed, the applicability of elliptical models is not supported by empirical observation (Daegling, 1989) and even elliptical models with nonuniform wall thicknesses (Biknevicius and Ruff, 1992) “impose a geometric regularity to (mandibular) corpus shape that is rarely observed in nature” (Daegling and Hylander, 1998). Values of $J$ can be calculated from digitized images of cross sections, providing the most direct estimate of resistance to torsion (Turner and Burr, 1993; Daegling, 2002); however, even these estimates fail to capture important aspects of the behavior of a bony cross section when subjected to a load, such as shear flow and warping of the section (Hibbeler, 2000). FEA remains “the preferred solution for modeling torsion (Hermann, 1965)” (Turner and Burr, 1993; Daegling, 2002). These considerations suggest that in order to determine whether the *Alligator* mandible functions to reduce torsional stress, comparisons between FEMs of the *Alligator* mandible and a simple beam of elliptical cross section would be useful.

### MATERIAL AND METHODS

To calculate the stresses acting within the *Alligator* mandible as accurately as possible, we estimated the external muscle forces acting on the mandible, predicted the resulting external reaction forces using lever arm mechanics, and mapped these forces onto a free body diagram of the mandible. External muscle forces and constraints were applied to a hollow, elliptical beam with a constant cross section using 2D stress analysis software, our own calculations in Excel, as well as a 3D FEM of the simple beam. To determine the extent to which *Alligator* mandible morphology acts to minimize shear and bending stresses, these forces and constraints were also applied to a high-resolution FEM of the *Alligator* mandible, and the resulting stresses in the mandible model were compared with those in the beams.

**Alligator Mandible Free Body Diagram**

A preserved head of *Alligator mississippiensis* was CT scanned (June 2005) at Stony Brook University Medical Center using a GE LightSpeed 16 CT scanner at 100 kV/70 mA. The individual had been acquired when ~1 m long and was kept in captivity for 6 months. Basal skull length (anterior rostrum—occipital condyle) of the scanned specimen was 160 mm; mandibular length (anterior tip—retroarticular process) was 189 mm. A total of 645 coronal slices (DICOM image format) was produced with a slice spacing of 0.31 mm; scan resolution was 0.25 mm/pixel. Segmentation of the CT data, as well as construction and analysis of the finite element model, were carried out at the University of Chicago from 2009 to 2010. CT data were processed using Amira 5.2.2 (Visage Imaging GmbH, Berlin, Germany). The scans were segmented to exclude soft tissues and separate the bones, sutures, teeth, and tooth sockets of the lower jaw (detailed procedures for segmentation are described by Lemberg et al., 2009); the cranium, including all bones and teeth, was segmented as a single part (Fig. 1A). Sutures and periodontal ligament (PDL) were identified as low-density areas...
between bones or between bones and teeth. Sutural morphology and thickness varies throughout the mandible, although they are continuous between bone surfaces (i.e., at no point do two adjacent bones contact each other).

The surface model generated in Amira was meshed in the finite element (FE) software package Strand7 2.4.1 (Strand7 Pty Ltd, Sydney, Australia). Muscle attachment sites on the cranium and mandible (and the nodes closest to their centroids) were mapped onto the FEM (Fig. 1B) based on dissections of the jaw muscles of Alligator and other crocodilians (Holliday and Witmer, 2007). Muscles accounted for in this study include: M. adductor mandibulae externus superficialis (mAMES), medialis (mAMEM), and profundus (mAMEP); M. adductor mandibulae internus (composed of M. pterygoideus dorsalis (mPTd) and ventralis (mPTv), and M. pseudotemporalis superficialis (mPSTs) and profundus (mPSTp)); M. adductor mandibulae posterior (mAMP); M. depressor mandibulae (mDM); and M. intramandibularis (mIM). The small muscle comprising M. constrictor internus dorsalis was excluded. (We prefer the term jaw elevator muscles to refer to the jaw “adductors,” but retain “adductor” in the proper names of these muscles for continuity with prior work.)

The 3D model and the centroids of muscle attachment sites were imported into the computer-aided design software SolidWorks 2006 (Dassault Systemes SolidWorks, Concord, MA) and the orientation and moment arm of each muscle were determined (see Discussion section below for calculation of muscle force magnitude). Lever arm mechanics were used to predict the magnitude and orientation of reaction forces at the jaw joint, bite point (working side), and symphysis (balancing side). Final images of the free body diagram (Fig. 2) were created using Adobe Illustrator and Photoshop CS (Adobe Systems Incorporated, San Jose, CA), with the length of the force vectors indicating their relative magnitude. For all models, the mediolateral/transverse axis is set as the y axis; the dorsoventral as the x axis; and the anteroposterior/longitudinal as the z axis (Fig. 1B). Mesh refinement is constant across all parts of the model (bones, teeth, sutures, PDL; Fig. 1C).

The cartilago transiliens presents a challenge in modeling jaw elevator muscle forces in Alligator. The cartilago transiliens consists of two cartilaginous discs in a bag of connective tissue onto which several muscles insert (Schumacher, 1973; Van Drongelen and Dullemeijer, 1982). The cartilago transiliens lies between the mandible (surangular-coronoid contact) and the thickened, cartilage-covered lateral edge of the pterygoid flange (torus transiliens; Iordansky, 1964, 1973). Some authors suggest that the cartilago transiliens attaches to the coronoid bone of the lower jaw via a short tendon (Iordansky, 1973; Van Drongelen and Dullemeijer, 1982); our dissections demonstrated that the cartilago transiliens is not attached to the upper jaw, and there is only a weak connection between the cartilago transiliens and the coronoid bone. This observation is supported by Holliday and Witmer (2007), who describe the cartilago transiliens as an intramuscular fibrocartilage sesamoid joining mPSTs and mIM. Thus, we have resolved the forces of mPSTs and mIM into a single force (acting on the cranium at the origin of mPSTs and acting on the mandible at the insertion of mIM) directed toward the location of the cartilago transiliens.

Muscle Force Calculations

The external muscle forces acting on the mandible were estimated from morphological measurements of the jaw elevator muscles (Table 1). The force generated by individual jaw muscles of Alligator during biting is a function of muscle fiber recruitment, frequency of motor unit action potentials, muscle contraction velocity, and physiological cross-sectional area (PCSA) taking into account sarcomere lengths at different gaps. In this study, muscle fiber recruitment was assumed to be maximal, action potential rate was assumed to be optimal, contraction velocity was assumed to be zero (i.e., static bites were modeled), and sarcomere length at the selected gape (30°) was estimated using modeled length–tension curves.

The physiological cross-sectional area of each muscle in a female Alligator (mandibular length of 206 mm; 1.33-m total body length) was calculated from measures of muscle architecture following methods detailed elsewhere (Anapol and Barry, 1996; Anapol and Gray, 2003; Anapol et al., 2004, 2008), but summarized here.

In dissected specimens, muscle fiber length and pinnation angle from up to six fibers were calculated and averaged within each muscle. Normalized fiber length was then calculated correcting for sarcomere contraction using an optimum sarcomere length of 2.5 μm. Physiological cross-sectional area was then calculated using the equation:
The lower end of the plateau was set at a sarcomere length of:

\[
(2\times1.1\,\mu m) + 1.6\,\mu m + 0.1\,\mu m = 3.9\,\mu m
\]

Standardizing these by \(l_0\) yields relative sarcomere lengths \((l/l_0)\) of 0.508, 0.68, 0.92, 1.0, and 1.56 at these points and relative force magnitudes of 0, 84, 100, 100, and 0%, respectively (Fig. 3). Linear interpolation was then used to estimate the force generated at a gape angle of 30° for the jaw elevator muscles using estimates of muscle stretch derived from the Alligator FEM (Fig. 1B). This was done by comparing muscle length on the FEM with the jaws at minimum gape and rotated open to 30° (Table 2). The proportion of cross-sectional area available at this gape was multiplied by muscle stress to yield the \(F_{p30}\) for each muscle at 30° (Table 3):

\[
F_{p30} = \frac{\gamma F_{\text{pmax}}}{100}
\]

To estimate the force components acting in sagittal, coronal, and transverse planes, the muscle forces and their moment arms were resolved into components acting about the \(x\), \(y\), and \(z\) axes (Table 4). The resulting forces were applied to the FEMs. Muscle contraction was assumed to be simultaneous and symmetrical. For the beam models, forces acting on the right mandible were applied to models representing both the working side and balancing side. In the Alligator FEMs, biting occurred on the right dentary; thus, the left mandible is the balancing side. The models created in Beam 2D (see below) were not subjected to anteroposterior muscle/reaction forces because this software package can only create in Beam 2D (see below) were not subjected to anteroposterior muscle/reaction forces because this software package can only

### Calculation of Shear and Bending Stress Using Beam 2D

The stress analysis software Beam 2D (ORAND Systems, Mississauga, ON, Canada) was used to calculate reaction forces.

### TABLE 1. Muscle architecture data from Alligator mississippiensis

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Proximal tendon length (mm)</th>
<th>Distal tendon length (mm)</th>
<th>Muscle belly length (mm)</th>
<th>Fascicle length (mm)</th>
<th>Percent sarcomere contraction at minimum gape</th>
</tr>
</thead>
<tbody>
<tr>
<td>mAMES and mAMEM</td>
<td>3.70</td>
<td>0.00</td>
<td>30.00</td>
<td>20.80</td>
<td>19.77</td>
</tr>
<tr>
<td>mAMEP</td>
<td>1.74</td>
<td>0.00</td>
<td>31.60</td>
<td>28.50</td>
<td>18.55</td>
</tr>
<tr>
<td>mAMP</td>
<td>11.04</td>
<td>12.27</td>
<td>49.00</td>
<td>14.30</td>
<td>19.61</td>
</tr>
<tr>
<td>mPSTs and mPSTp</td>
<td>2.81</td>
<td>0.00</td>
<td>5.18</td>
<td>34.00</td>
<td>15.93</td>
</tr>
<tr>
<td>mPtd Ia</td>
<td>13.06</td>
<td>0.00</td>
<td>8.82</td>
<td>54.00</td>
<td>19.70</td>
</tr>
<tr>
<td>mPtd Ib</td>
<td>18.92</td>
<td>0.00</td>
<td>11.87</td>
<td>75.00</td>
<td>20.07</td>
</tr>
<tr>
<td>mPTv</td>
<td>35.41</td>
<td>0.00</td>
<td>18.18</td>
<td>77.40</td>
<td>18.84</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Muscle weight (g)</th>
<th>Pinnation angle</th>
<th>Adjusted fascicle length (cm)</th>
<th>Cos θ</th>
<th>PCSA (cm²/force length)</th>
<th>Adjusted fascicle length (mm)</th>
<th>Adjusted muscle belly length (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>mAMES and mAMEM</td>
<td>3.70</td>
<td>0.00</td>
<td>2.70</td>
<td>1.00</td>
<td>1.30/32.42</td>
<td>77.40</td>
<td>18.84</td>
</tr>
<tr>
<td>mAMEP</td>
<td>1.74</td>
<td>0.00</td>
<td>3.87</td>
<td>1.00</td>
<td>0.43/16.63</td>
<td>38.74</td>
<td>23.45</td>
</tr>
<tr>
<td>mAMP</td>
<td>11.04</td>
<td>39.59</td>
<td>1.84</td>
<td>0.95</td>
<td>5.45/136.20</td>
<td>18.38</td>
<td>38.44</td>
</tr>
<tr>
<td>mPSTs and mPSTp</td>
<td>12.44</td>
<td>25.58</td>
<td>2.06</td>
<td>0.98</td>
<td>1.26/31.51</td>
<td>20.61</td>
<td>26.63</td>
</tr>
<tr>
<td>mPtd Ia</td>
<td>13.04</td>
<td>29.87</td>
<td>2.46</td>
<td>1.00</td>
<td>5.02/125.51</td>
<td>24.59</td>
<td>43.17</td>
</tr>
<tr>
<td>mPtd Ib</td>
<td>8.50</td>
<td>34.21</td>
<td>2.60</td>
<td>0.99</td>
<td>6.80/170.12</td>
<td>26.03</td>
<td>60.23</td>
</tr>
<tr>
<td>mPTv</td>
<td>16.87</td>
<td>27.79</td>
<td>6.20</td>
<td>0.96</td>
<td>5.17/129.25</td>
<td>62.04</td>
<td>58.32</td>
</tr>
</tbody>
</table>

Note that at minimum gape all of the muscles are contracted to ~80% of their assumed optimal sarcomere length.

Muscle architecture data obtained for two separate portions of mPtd; combined PCSA of these portions and identical values (0.80) for percent sarcomere contraction at minimum gape used to determine force available at minimum gape.

\[
\text{PCSA} = \frac{M_{\text{muscle}} \cos \theta}{L_r \times 1.0564}
\]

(1)

with \(M_{\text{muscle}}\) as muscle weight, \(\theta\) as pinnation angle, \(L_r\) as normalized fiber length, and 1.0564 as the specific gravity of the muscle. Maximum possible force production \((F_{\text{pmax}})\) was calculated by multiplying PCSA by 25 N/cm² (250 kN/m²), the specific tension of mammalian muscle (Hertzog, 2007):

\[
F_{\text{pmax}} = \text{PCSA} \times 25 \text{ N/cm}^2
\]

(2)

Ideally, length–tension curves for the elevator muscles of Alligator would be used to estimate maximum possible force generation potential for each muscle at our selected gape of 30° \((F_{\text{p30}})\) (Nordstrom et al., 1974; Nordstrom and Yemm, 1974; Weijs and van der Wielen-Drent, 1985). At present, length–tension curves are not available for Alligator muscle; instead, we constructed length–tension curves for the individual elevator muscles (Hertzog, 2007) assuming an optimal sarcomere length \((l_0)\) of 2.5 μm. Assuming a thick filament length of 1.6 μm (Walker and Schrodt, 1974), H-zone length of 0.2 μm and Z-disk length of 0.1 μm, a thin filament length of 1.1 μm yields an \(l_0\) of 2.5 μm:

\[
l_0 = (2\times1.1\,\mu m) + 0.1\,\mu m + 0.2\,\mu m = 2.5\,\mu m
\]

(3)

Using data obtained for frog (Gordon et al., 1966), the length–tension curve was anchored at a minimum sarcomere length of 1.27 μm and the point of inflection on the ascending limb of the curve was estimated to be at a sarcomere length of:

\[
1.6\,\mu m + 0.1\,\mu m = 1.7\,\mu m
\]

(4)

The lower end of the plateau was set at a sarcomere length of:

\[
(2\times1.1\,\mu m) + 0.1\,\mu m = 2.3\,\mu m
\]

(5)

Optimal sarcomere length \((l_0, \text{Eq. 3})\) was at the right end of the plateau and the maximum sarcomere length is equal to:

Journal of Morphology
and stress due to shear and bending along the mandible assuming a simple beam geometry. The beam was given a length of 189 mm, corresponding to the length of the mandible (Fig. 4A–D). The cross-sectional geometry of the beam (a hollow, dorso-ventrally elongated ellipse) was constructed, based on measurements from CT scans of the right Alligator mandible under the 19th dentary tooth (Table 5). This cross section was assumed to be constant along the length of the beam. Young’s modulus was set at 15 GPa, the approximate mean elastic modulus of Alligator mandibular cortical bone from Zapata et al. (2010).

The muscle forces acting on the mandible were applied along the beam model at positions matching the \( z \)-coordinates of their centroids in the Alligator FEM. The beam was modeled in both lateral and dorsal views (Fig. 4A–D). For lateral views, the vertical (\( y \)) components of each muscle were applied to the beam. Additionally, for mPTd and mPTv, an anteriorly directed moment generating a counter-clockwise (positive) torque about the jaw joint was applied; this was done in consideration of the large cross-sectional area and anterior orientation of the pterygoideus muscles. For dorsal views, the horizontal (\( x \)) component of each muscle was applied to the beam.

The balancing side beam was supported at the jaw joint and symphysis in lateral view, generating vertical reaction forces at both points (Fig. 4A). The constraint at the symphysis represents the working side fixed at the bite point. The working side beam was supported at the jaw joint and bite point in lateral view, and a force equal but opposite the symphysial reaction force recorded on the balancing side beam model was applied to the symphysis of the working side (Fig. 4B). This symphysial force represents the forces exerted by the balancing side musculature on the working side mandible. In dorsal view, the balancing side was supported at the jaw joint and symphysis; the working side was supported at the jaw joint, bite point, and symphysis. A preliminary set of trials included an additional support representing the pterygoid flange–mandibular contact for both the balancing side and working side in dorsal view; this support was subsequently removed to examine the effect of its presence (see more below).

**Calculation of Torques and Torsional Stresses**

To calculate torques and torsional stresses (about the \( z \) axis), vertical and horizontal muscle and reaction forces (the latter extracted from Beam 2D) were used to calculate the external torques acting along the length of the beam in Excel. Maximum shear stress due to torsion (\( \tau_{r\text{-max}} \)) in each cross section through the theoretical, hollow, elliptical beam was then calculated using Roark’s formula 13 (Young, 1989; Table 20):

\[
\tau_{r\text{-max}} = \frac{T}{2\pi(a - \frac{a}{2})}\left(\frac{b}{2}\right)
\]

where \( t \) is wall thickness, \( a \) is maximum height of the cross section and \( b \) is maximum width (see Table 5).

**Finite Element Modeling—Beam Model**

The cross section described above (Table 5) was used to create a 3D FEM of the beam (Fig. 4E). The beam FEM is 189 mm in length, is composed of 64,071 solid hexahedral elements, and was given the same elastic modulus (15 GPa) as the Beam 2D model. Values for density (1772.6 kg/m^3) and Poisson’s ratio (0.29) corresponding to the averages obtained for Alligator mandibular cortical bone (Zapata et al., 2010) were applied. Material properties were assumed to be isotropic. Muscle forces (\( x \), \( y \), and \( z \) components) and constraints were placed at the same \( z \)-coordinates as in the Beam 2D models; each muscle (and, for the working side, symphysial) force was evenly distributed over...
TABLE 2. Muscle length (centroid of origin to centroid of attachment) measured from the FE model at minimum gape and at 30° gape

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Muscle length at minimum gape (mm)</th>
<th>Muscle length at 30° gape (mm)</th>
<th>% Change</th>
</tr>
</thead>
<tbody>
<tr>
<td>Right mAMES</td>
<td>21.52</td>
<td>32.68</td>
<td>51.89</td>
</tr>
<tr>
<td>Right mAMEM</td>
<td>28.22</td>
<td>39.26</td>
<td>39.12</td>
</tr>
<tr>
<td>Right mAMEP</td>
<td>79.48</td>
<td>94.41</td>
<td>18.78</td>
</tr>
<tr>
<td>Right mAMP</td>
<td>41.24</td>
<td>52.13</td>
<td>26.42</td>
</tr>
<tr>
<td>Right mPSTd</td>
<td>39.80</td>
<td>55.87</td>
<td>40.37</td>
</tr>
<tr>
<td>Right mIM</td>
<td>24.66</td>
<td>24.66</td>
<td>0.00</td>
</tr>
<tr>
<td>Right mPSTp</td>
<td>38.88</td>
<td>56.75</td>
<td>45.97</td>
</tr>
<tr>
<td>Right mPTd</td>
<td>49.62</td>
<td>54.86</td>
<td>10.31</td>
</tr>
<tr>
<td>Right mPTv</td>
<td>47.37</td>
<td>52.20</td>
<td>11.40</td>
</tr>
<tr>
<td>Right mDM</td>
<td>24.77</td>
<td>21.00</td>
<td>-15.24</td>
</tr>
</tbody>
</table>

TABLE 3. Calculation of \( F_p \) available at 30° gape in Alligator mississippiensis

<table>
<thead>
<tr>
<th>Muscle</th>
<th>( l/l_0 ) at minimum gape</th>
<th>Interpolated ( F_p ) at 30° gape (N)</th>
<th>% of total muscle force ( b )</th>
</tr>
</thead>
<tbody>
<tr>
<td>mAMES</td>
<td>0.79</td>
<td>1.10</td>
<td>13.30</td>
</tr>
<tr>
<td>mAMEM</td>
<td>0.79</td>
<td>1.10</td>
<td>13.30</td>
</tr>
<tr>
<td>mAMEP</td>
<td>0.74</td>
<td>0.88</td>
<td>11.36</td>
</tr>
<tr>
<td>mAMP</td>
<td>0.78</td>
<td>1.04</td>
<td>125.59</td>
</tr>
<tr>
<td>mPSTd</td>
<td>0.78</td>
<td>1.15</td>
<td>11.61</td>
</tr>
<tr>
<td>mPSTp</td>
<td>0.78</td>
<td>1.15</td>
<td>11.61</td>
</tr>
<tr>
<td>mPTd</td>
<td>0.80</td>
<td>0.90</td>
<td>291.17</td>
</tr>
<tr>
<td>mPTv</td>
<td>0.75</td>
<td>0.86</td>
<td>124.03</td>
</tr>
<tr>
<td>mDM</td>
<td>—</td>
<td>—</td>
<td>15.90</td>
</tr>
</tbody>
</table>

\( a \)Equivalent to % contraction of sarcomeres at minimum gape.
\( b \)Percentage each muscle contributes to total muscle force (650 N, the sum of \( F_p \) at 30° for all muscles) produced on one side of the head.

Finite Element Modeling—Alligator Model

The FEM of the Alligator skull contains 1,001,484 linear tetrahedral elements (cranial: 360,399; mandible: 641,085). Muscle forces were evenly distributed onto origins/insertions mapped onto the skull (Fig. 1B) using the Visual Basic program BoneLoad (Grosse et al., 2007), which accounts for tensile, tangential, and normal traction loads due to muscles wrapped around curved bone surfaces. This is an important consideration for Alligator because, for example, mPTV wraps around the ventral margin of the mandible to insert on the lateral surface of the retroarticular process.

Three nodes aligned mediolaterally across the joint surfaces of each quadrato and articular were constrained against displacement (Fig. 4F), creating an axis around which the cranium and mandible rotated when muscle forces were applied. These constraints prevented rigid body motion and generated reaction forces at the jaw joints. The tip of a single dentary tooth was constrained to generate bite force; five load cases were analyzed (corresponding to the five bite point locations used in both the Beam 2D and beam FEM). For each case, the tip of the closest opposing maxillary/premaxillary tooth was also constrained. These constraints are similar to the "Strait method" used in some mammalian FEMs (Dumont et al., 2005; Ross et al., 2005; Strait et al., 2005). Constraining a single node at the bite point results in artificially high stress/strain values; however, this effect is highly localized (Grosse et al., 2007).

Three FEMs of the Alligator mandible were analyzed: two models differ in their material properties, and are referred to as simple and suture. Simple used the same homogeneous and isotropic material properties as the beam FEM. Suture reflects our current best estimate of the material properties of all the components of the Alligator mandible (Table 6). Anisotropic bone material properties are from an individual of similar size to the specimen used to construct the FEM (Zapata et al., 2010).

There is no published information on the material properties of crocodilian teeth, sutures, or PDL, so the teeth were assigned the material properties of bovine dentine (Gilmore et al., 1989), which has been applied to other archosaur FEMs (Rayfield et al., 2001). Density and Poisson’s ratio for sutures were averages of values reported in the literature (Currey, 2002; Kupczik et al., 2007). Elastic modulus for mammalian cranial sutures reported in the literature varies considerably, ranging from 1.16 GPa to 12.1 GPa (Margulies and Thibault, 2000; Radhakrishnan and Mao, 2004; Kupczik et al., 2007). Preliminary trials using the Alligator FEM found that suture elastic modulus strongly influenced stain magnitude and orientation in the suture and the immediate surrounding bone. For our suture model we assigned sutures an elastic modulus of 90 MPa, which is approximately two orders of magnitude lower than the lowest elastic modulus we used for Alligator bone and falls within the range of values recorded in other taxa. Mammalian PDL is far more compliant than sutures (Rees and Jacobsen, 1997; Yoshida et al., 2001). Unlike mammals, in which the teeth are attached to the alveolar bone socket via PDL (gomphosis), most reptiles have teeth ankylosed directly to the jawbone. Crocodilian PDL appears to be structurally intermediate between mineral-free mammalian PDL and mineralized attachment in lizards (McIntosh et al., 2002). For the suture model, PDL was assigned the same material properties as sutures.

The elongate pterygoid flanges of crocodilians have been suggested to act as braces resisting medial translation (inverse...
wish-boning) of the mandibles during jaw closure (Busbey, 1995; Iordansky, 1964). The third model, Pterygoid (PT) flange, evaluates this hypothesis by using the same material properties as the suture model, but differing in constraining a single node on the medial surface of each mandible, opposite its contact with the pterygoid flange at 30° of gape, to restrict medial movement (along the x axis) of each mandibular ramus.

### Table 4. Resultant and resolved muscle forces, moment arms, and moments for each side of the Alligator mandible

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Total force (N)</th>
<th>X force (N)</th>
<th>Y force (N)</th>
<th>Z force (N)</th>
<th>Total moment arm (m)</th>
<th>X moment arm (m)</th>
<th>Y moment arm (m)</th>
<th>Z moment arm (m)</th>
<th>Total moment (N m)</th>
<th>Moment about X (N m)</th>
<th>Moment about Y (N m)</th>
<th>Moment about Z (N m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>mAMES</td>
<td>13.30</td>
<td>8.19</td>
<td>10.33</td>
<td>-1.74</td>
<td>0.0242</td>
<td>0.0005</td>
<td>0.0044</td>
<td>0.0237</td>
<td>0.3212</td>
<td>0.2530</td>
<td>0.1989</td>
<td>-0.0584</td>
</tr>
<tr>
<td>mAMEM</td>
<td>13.30</td>
<td>10.66</td>
<td>6.92</td>
<td>-3.93</td>
<td>0.0313</td>
<td>0.0091</td>
<td>0.0028</td>
<td>0.0298</td>
<td>0.4159</td>
<td>0.2379</td>
<td>0.3537</td>
<td>-0.1215</td>
</tr>
<tr>
<td>mAMEP</td>
<td>10.36</td>
<td>7.42</td>
<td>6.38</td>
<td>-3.40</td>
<td>0.0411</td>
<td>0.0120</td>
<td>0.0068</td>
<td>0.0388</td>
<td>0.4260</td>
<td>0.2843</td>
<td>0.3312</td>
<td>-0.1344</td>
</tr>
<tr>
<td>mAMP</td>
<td>125.59</td>
<td>55.68</td>
<td>111.79</td>
<td>-13.67</td>
<td>0.0238</td>
<td>0.0069</td>
<td>0.0007</td>
<td>0.0227</td>
<td>2.9865</td>
<td>2.5611</td>
<td>1.3602</td>
<td>0.8705</td>
</tr>
<tr>
<td>mPSTs</td>
<td>11.61</td>
<td>-0.66</td>
<td>10.83</td>
<td>-4.13</td>
<td>0.0405</td>
<td>0.0035</td>
<td>0.0142</td>
<td>0.0374</td>
<td>0.4704</td>
<td>0.4635</td>
<td>-0.1571</td>
<td>-0.1588</td>
</tr>
<tr>
<td>mMI</td>
<td>33.18</td>
<td>-1.89</td>
<td>30.94</td>
<td>-11.81</td>
<td>0.0405</td>
<td>0.0035</td>
<td>0.0142</td>
<td>0.0374</td>
<td>1.3444</td>
<td>1.3247</td>
<td>-0.4491</td>
<td>-0.4537</td>
</tr>
<tr>
<td>mPSTp</td>
<td>11.61</td>
<td>-0.24</td>
<td>8.56</td>
<td>7.84</td>
<td>0.0335</td>
<td>0.0005</td>
<td>0.0226</td>
<td>0.0247</td>
<td>0.3888</td>
<td>0.3887</td>
<td>0.1937</td>
<td>0.1938</td>
</tr>
<tr>
<td>mPTd</td>
<td>291.17</td>
<td>186.17</td>
<td>70.96</td>
<td>212.35</td>
<td>0.0135</td>
<td>0.0034</td>
<td>0.0130</td>
<td>0.0014</td>
<td>3.9424</td>
<td>2.9361</td>
<td>-1.0321</td>
<td>2.6839</td>
</tr>
<tr>
<td>mPTv</td>
<td>124.03</td>
<td>95.86</td>
<td>9.53</td>
<td>78.13</td>
<td>0.0155</td>
<td>0.0050</td>
<td>0.0146</td>
<td>0.0005</td>
<td>1.9200</td>
<td>1.1530</td>
<td>-0.6204</td>
<td>1.4900</td>
</tr>
<tr>
<td>mDM</td>
<td>15.90</td>
<td>5.17</td>
<td>9.38</td>
<td>11.75</td>
<td>0.0106</td>
<td>0.0003</td>
<td>0.0051</td>
<td>0.0008</td>
<td>0.1679</td>
<td>-0.1280</td>
<td>-0.1187</td>
<td>-0.0864</td>
</tr>
</tbody>
</table>

Sign values given apply to the right (working) side ramus within the coordinate system discussed in the text—x axis is mediolateral (positive is towards the left), y axis is dorsoventral (positive is dorsally directed), and z axis is anteroposterior (positive is anteriorly directed).
My estimates of maximum shear stress due to torsion (T) is less variable than that in a simple beam, the following estimates of maximum compressive and tensile stress due to bending (σ_s) were calculated and compared:

- Maximum bending stress (σ_max) along a theoretical, hollow, elliptical beam using
  \[ \sigma_{\text{max}} = \frac{M y}{I} \]  
  \[ (10) \]
- the magnitude of σ_max along a ventral transect of the beam FEM;
- the magnitude of σ_max along a ventral transect of the Alligator mandible FEM without and with sutures, and a pterygoid flange contact.

To quantify the effect of Alligator mandibular geometry on sagittal and transverse shear stresses, the following estimates of maximum shear stress (τ_max) were calculated and compared in sagittal and transverse planes:

- τ_max in each cross section through the theoretical, hollow, elliptical beam using
  \[ \tau_{\text{max}} = \frac{F_y}{A} \]  
  \[ (11) \]

where \( F_y \) is shearing force (the sum of all shearing forces acting to one side of the cross section) and \( A \) is the area of the cross section;

- τ_max in each cross section through the beam FEM;
- τ_max in each cross section through the Alligator mandible FEM without and with sutures, and a pterygoid flange contact.

To determine whether torsional stress in the Alligator mandible is less variable than that in a simple beam, the following estimates of maximum shear stress due to torsion (τ_T) were calculated and compared:

- τ_T along the theoretical, hollow, elliptical beam using Roark’s formula 13 from (Young, 1989) [our Eq. (8)];
- τ_T in the beam FEM;
- τ_T in the Alligator mandible FEM without and with sutures, and a pterygoid flange contact.

### RESULTS

**External Forces and Free Body Analysis**

At minimum gape, all of the measured Alligator jaw elevator muscles are contracted to ~80% of their optimal sarcomere length, whereas at 30° of gape mAMP is on the plateau, three (mPST and mAMES/mAMEP) are on their descending (right) limb, and three (mPTd, mPTv, and mAMEP) are on the ascending limbs of their length–tension curves (Fig. 5). M. pterygoideus dorsalis shows the greatest change in length with change in gape, mPTv shows the least, and neither reaches the plateau of its length–tension curve at 30° of gape.

The resultant muscle force on the lower jaw (Table 4) is directed upward and medially at approximately −53° relative to the y-axis in anterior view, and forward at approximately −45° from the y-axis in right lateral view (by convention, negative values are clockwise). Muscle forces acting on the working side and balancing side are the same since symmetrical muscle activity was assumed. In lateral view (Fig. 2A,B) the mandible is subjected to muscle forces with orientations that range from antero-dorsal (mPTv, mPTd, mPSTp) to postero-dorsal (mAME, mAMP, mAMEP). Most muscles act between the jaw joint and the posterior end of the toothrow; mPTv and mPTd attach to the mandible posterior and ventral to the jaw joint, while mDM attaches posterior to and level with the jaw joint. Lever arm mechanics were used to predict vertical reaction forces at the jaw joints, biting tooth, and symphysis (Table 7). As expected, bite force is calculated to increase with more posterior bites; as a result, reaction force on the working side jaw joint is predicted to decrease with more posterior bites. Reaction force at the balancing side jaw joint is calculated to always be higher than that on the working side and is predicted to be unchanged by changes in bite point on the working side. As a result, total reaction force at the balancing side jaw joint should be more vertically oriented and larger in magnitude than reaction force on the working side.

### TABLE 5. Cross-sectional geometry of beam used in Beam2D and finite element model, taken from CT scans under 19th dentary tooth

<table>
<thead>
<tr>
<th>Maximum external height (a) (mm)</th>
<th>19.15</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum external width (b) (mm)</td>
<td>14.48</td>
</tr>
<tr>
<td>Average wall thickness (t) (mm)</td>
<td>2.94</td>
</tr>
<tr>
<td>Cross-sectional area (mm²)</td>
<td>129.32</td>
</tr>
<tr>
<td>Torsional inertia constant (J) (m⁴)</td>
<td>5.77865E−09</td>
</tr>
</tbody>
</table>

Cross section shown at right.

Results from the Alligator mandible FEMs were extracted and analyzed in the same manner as for the beam FEM; however, only bones were included in transects (i.e., sutures, periodontal ligament and teeth were not sampled). Because the balancing side is a left mandible in the Alligator FEMs (they are modeled as right mandibles in the beam models), plots of mediolateral (zx) shear stress and torsional stress for the balancing side of all Alligator FEMs were inverted for easier comparison with results from beam models.

### Hypothesis Testing

To determine whether bending stress magnitudes vary less along the length of the Alligator mandible than they do along the simple beam, the following estimates of maximum compressive and tensile stress due to bending (σ_max) were calculated and compared:

- Maximum bending stress (σ_max) along a theoretical, hollow, elliptical beam using
  \[ \sigma_{\text{max}} = \frac{M y}{I} \]  
  \[ (10) \]
- the magnitude of σ_max along a ventral transect of the beam FEM;
- the magnitude of σ_max along a ventral transect of the Alligator mandible FEM without and with sutures, and a pterygoid flange contact.

To quantify the effect of Alligator mandibular geometry on sagittal and transverse shear stresses, the following estimates of maximum shear stress (τ_max) were calculated and compared in sagittal and transverse planes:

- τ_max in each cross section through the theoretical, hollow, elliptical beam using
  \[ \tau_{\text{max}} = \frac{F_y}{A} \]  
  \[ (11) \]

where \( F_y \) is shearing force (the sum of all shearing forces acting to one side of the cross section) and \( A \) is the area of the cross section;

- τ_max in each cross section through the beam FEM;
- τ_max in each cross section through the Alligator mandible FEM without and with sutures, and a pterygoid flange contact.

To determine whether torsional stress in the Alligator mandible is less variable than that in a simple beam, the following estimates of maximum shear stress due to torsion (τ_T) were calculated and compared:

- τ_T along the theoretical, hollow, elliptical beam using Roark’s formula 13 from (Young, 1989) [our Eq. (8)];
- τ_T in the beam FEM;
- τ_T in the Alligator mandible FEM without and with sutures, and a pterygoid flange contact.
The medially directed components of all the jaw muscles (except mIM) are evident in dorsal view (Fig. 2C). Laterally directed reaction forces are generated at the jaw joints, at the contact with the pterygoid flange (Busbey, 1995), and at the bite point on the working side. Because mPTd and mPTv are large (Table 4) compared with the remaining elevator muscles, are strongly inclined medially, and attach posterior to the jaw joint, the lever arm calculations predict that the majority of the laterally directed reaction force will occur at the jaw joints, with only small reaction forces predicted at the bite point and pterygoid flange-mandibular contact. The symphysis is calculated to be in mediolaterally oriented tension.

The jaw elevators and mDM attach to the dorsal or ventral margins of the mandible, so their medially directed components generate torques about the long (z) axis (Fig. 2D,E). Because mPTd, mPTv, and mAMP attach to the ventral margin of the mandible, these powerful muscles are calculated to produce a positive (counterclockwise in anterior view) torque on the right side mandible (clockwise or negative torque on the left side). The pterygoid flange does not restrict anteroposterior motion of the mandible. Furthermore, it was assumed that the bite point does not experience anteroposterior reaction forces. Thus, a longitudinal reaction force equal but opposite to that generated by the jaw muscles is calculated to occur at the jaw joints (Table 7).

**Beam Analyses**

In describing our results, shearing and bending stresses are described as occurring within anatomical planes. Specifically, dorsoventrally directed muscle, symphyseal, bite and joint reaction forces produce shearing and bending stresses within sagittal (yz) planes. Mediolaterally directed muscle, bite, and joint reaction forces produce shearing and bending stresses within transverse planes (xz). Torsion is described as occurring around the long axis of the *Alligator* mandible and the long (z) axis of the beam models, generating shear stresses both in planes tangent to the surface of the cross section, as well as between adjacent cross sections.

**Reaction forces.** In the Beam 2D model, vertical reaction forces generated at the bite points and balancing side jaw joint are very similar to those predicted by lever arm mechanics and vertical
### TABLE 7. Reaction forces generated by each model and in other studies

<table>
<thead>
<tr>
<th>Model</th>
<th>Bite position</th>
<th>Bite force (N)</th>
<th>Jaw joint (N)</th>
<th>Total bite force/total joint rxn force</th>
<th>Joint rxn force angle (°, anterior view)</th>
<th>Joint rxn force angle (°, lateral view)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>X       Y    Z</td>
<td>X       Y    Z</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lever arm mech.</td>
<td>Balancing</td>
<td>—       —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Anterior</td>
<td>0       —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.25</td>
<td>—66.83</td>
</tr>
<tr>
<td></td>
<td>Anterior-middle</td>
<td>0     —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.28</td>
<td>—68.92</td>
</tr>
<tr>
<td></td>
<td>Middle</td>
<td>0       —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.33</td>
<td>—71.57</td>
</tr>
<tr>
<td></td>
<td>Posterior-middle</td>
<td>0  —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.38</td>
<td>—76.84</td>
</tr>
<tr>
<td></td>
<td>Posterior</td>
<td>0       —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.47</td>
<td>—80.42</td>
</tr>
<tr>
<td>Beam 2D</td>
<td>Balancing</td>
<td>—       —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Anterior</td>
<td>32.06   —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.29</td>
<td>—60.15</td>
</tr>
<tr>
<td></td>
<td>Anterior-middle</td>
<td>13.5  —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.32</td>
<td>—62.12</td>
</tr>
<tr>
<td></td>
<td>Middle</td>
<td>10.4     —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.38</td>
<td>—64.84</td>
</tr>
<tr>
<td></td>
<td>Posterior-middle</td>
<td>9.7   —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.47</td>
<td>—68.79</td>
</tr>
<tr>
<td></td>
<td>Posterior</td>
<td>10.43   —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.62</td>
<td>—76.05</td>
</tr>
<tr>
<td>Beam FEM (XYZ)</td>
<td>Balancing</td>
<td>—       —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Anterior</td>
<td>5.2     —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.55</td>
<td>—60.83</td>
</tr>
<tr>
<td></td>
<td>Anterior-middle</td>
<td>5.7   —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.52</td>
<td>—63.01</td>
</tr>
<tr>
<td></td>
<td>Middle</td>
<td>6.4     —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.50</td>
<td>—65.85</td>
</tr>
<tr>
<td></td>
<td>Posterior-middle</td>
<td>7.3   —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.52</td>
<td>—69.94</td>
</tr>
<tr>
<td></td>
<td>Posterior</td>
<td>9.249.6 —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.61</td>
<td>—77.70</td>
</tr>
<tr>
<td>Alligator</td>
<td>Balancing, anterior</td>
<td>—    —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>FEM (simple)</td>
<td>Balancing, ant-mid</td>
<td>—    —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Balancing, middle</td>
<td>—    —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Balancing, post-mid</td>
<td>—    —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Balancing, post</td>
<td>—       —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Anterior</td>
<td>25.5     —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.21</td>
<td>—42.36</td>
</tr>
<tr>
<td></td>
<td>Anterior-middle</td>
<td>31.1   —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.23</td>
<td>—44.14</td>
</tr>
<tr>
<td></td>
<td>Middle</td>
<td>29.1     —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.27</td>
<td>—46.14</td>
</tr>
<tr>
<td></td>
<td>Posterior-middle</td>
<td>25.3   —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.31</td>
<td>—47.55</td>
</tr>
<tr>
<td></td>
<td>Posterior</td>
<td>2.2    —    170.6</td>
<td>—       —    —</td>
<td>—</td>
<td>0.46</td>
<td>—50.67</td>
</tr>
<tr>
<td>Alligator</td>
<td>Balancing, anterior</td>
<td>—    —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>FEM (suture)</td>
<td>Balancing, ant-mid</td>
<td>—    —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Balancing, middle</td>
<td>—    —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Balancing, post-mid</td>
<td>—    —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Balancing, post</td>
<td>—       —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Anterior</td>
<td>17.2     —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.18</td>
<td>—41.66</td>
</tr>
<tr>
<td></td>
<td>Anterior-middle</td>
<td>22.5   —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.16</td>
<td>—43.20</td>
</tr>
<tr>
<td></td>
<td>Middle</td>
<td>21.5     —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.20</td>
<td>—44.36</td>
</tr>
<tr>
<td></td>
<td>Posterior-middle</td>
<td>18.1   —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.22</td>
<td>—45.03</td>
</tr>
<tr>
<td></td>
<td>Posterior</td>
<td>0.6    —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.30</td>
<td>—45.75</td>
</tr>
<tr>
<td>Alligator</td>
<td>Balancing, anterior</td>
<td>—    —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>FE model (PT flange)</td>
<td>Balancing, ant-mid</td>
<td>—    —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Balancing, middle</td>
<td>—    —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Balancing, post-mid</td>
<td>—    —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Balancing, post</td>
<td>—       —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Anterior</td>
<td>14.9     —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.17</td>
<td>—37.98</td>
</tr>
<tr>
<td></td>
<td>Anterior-middle</td>
<td>21.5    —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.17</td>
<td>—39.15</td>
</tr>
<tr>
<td></td>
<td>Middle</td>
<td>22.0     —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.20</td>
<td>—40.24</td>
</tr>
<tr>
<td></td>
<td>Posterior-middle</td>
<td>17.1   —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>0.23</td>
<td>—41.41</td>
</tr>
<tr>
<td></td>
<td>Posterior</td>
<td>3.2    —    115.5</td>
<td>—       —    —</td>
<td>—</td>
<td>0.31</td>
<td>—43.89</td>
</tr>
<tr>
<td>Erickson et al., 2003</td>
<td>Middle (11th maxillary tooth)</td>
<td>—    —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Sinclair and Alexander, 1987</td>
<td>Posterior</td>
<td>—    —    —</td>
<td>—       —    —</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

Sign values given apply to the right side mandible within the coordinate system discussed in the text—x axis is mediolateral (positive is toward the left), y axis is dorsoventral (positive is dorsally directed), and z axis is anteroposterior (positive is anteriorly directed). Joint reaction force angles are relative to the y axis for a right side mandible; by convention, negative values are clockwise from the y axis.

*aEstimated total bite force for 1 meter (total body length) Alligator from regression curve based on bite forces obtained in vivo during a “high-force snapping bite.”

*bEstimated bite force (assumed vertical) for a ~0.64 m Caiman. Bite force obtained for working side (37 N) doubled to account for the contribution of the balancing side jaw elevator muscles.

*cEstimated bite force (assumed ~130° from tooth row) for 0.65 m Caiman. Bite force obtained for the working side doubled to account for the contribution of the balancing side jaw elevator muscles.
reaction forces on the working side jaw joint are only slightly higher (Table 7). The beam FEM experiences higher vertical and lower horizontal reaction force at the biting tooth, and lower vertical reaction force at the working side jaw joint than the Beam 2D model at each bite position. Vertical reaction force on the balancing side jaw joint and lateral reaction forces at both jaw joints are similar in both the beam FEM and Beam 2D (Table 7).

In dorsal view, laterally directed reaction force in the Beam 2D model is similar for the balancing side and working side jaw joints, and is slightly higher than predicted by lever arm mechanics. A preliminary set of Beam 2D trials included a support at the pterygoid-mandibular contact; reaction forces generated at this support were very low (< 1 N) and tensile. Thus, this support was removed from most FEM models; however, it was included in the PT flange Alligator FEM. The beam FEM predicts a large posteriorly directed reaction force at the biting tooth, which is highest in magnitude during anterior bites and decreases at posterior bite positions. Posteriorly directed reaction force on the working side jaw joint is highest in magnitude during posterior biting. Posteriorly directed force on the balancing side jaw joint is identical to that predicted by lever arm mechanics.

**Internal stresses—Bending stress in sagittal planes.** Peak dorsoventral bending stress is higher than any other stress experienced by the beams. In both beams, muscle forces cause the beam (between the jaw joint and anterior muscle insertions) to deform dorsally (negative bending), resulting in compression along the ventral surface (Fig. 6) and tension dorsally. This negative bending stress peaks dorsal and ventral to the position corresponding to the area of insertion of several large muscles and the mandibular fenestra in the mandible. The entire balancing side experiences negative bending (Fig. 6H), with bending stress gradually decreasing to zero at the symphysis. In contrast, there is an inflection point in the working side beams (Fig. 6C–G) reflecting positive bending of the anterior mandible due to bite reaction force; this inflection point is located posterior to the bite point, and bending stress due to bite reaction force peaks at the bite point itself and decreases to zero at the symphysis. As the bite point moves anteriorly, the bending regime approaches that exhibited by the balancing side. Except during posterior biting, peak bending stress is a result of negative bending produced by muscle forces, and is highest on the balancing side and during anterior biting. Peak dorsoventral bending stress during posterior biting is a result of positive bending about the bite point. Peak bending stress is higher in the beam FEM than in the Beam 2D models but only because of irregularities due to localized high stress near the muscle insertions (Fig. 6).

**Internal stresses—Shear stress in sagittal planes.** Sagittal shear stresses are lower than the torsional shear stresses discussed below and more than an order of magnitude lower than dorsoventral bending stresses discussed above. The effects of variation in bite point on the patterns of shear stress in the beams are illustrated in Figure 7. The highest shear stresses generated in sagittal planes occur between the posterior bite point and the muscle insertions. As the bite point moves anteriorly, the magnitude of the shear stresses act-

![Fig. 6. Dorsoventral bending stress in the beam models. A: Lateral view of Alligator working side mandible with muscle force vectors (solid arrows) and reaction force vectors (broken arrows). B: Vertical forces (black arrows) and supports (black triangles) applied to Beam 2D model representing working side; black arrow at symphysis represents contribution from balancing side muscle force. C–H: Compressive bending stresses (MPa) and location relative to neutral axis indicated in gray box (Beam 2D estimate). Black line indicates stress magnitude and type (positive is tensile, negative is compressive) recorded along the ventral transect of the beam FEM. C–G: Working side, with location of bite point indicated by black triangle. H: Balancing side. Key indicates scale and conventions for positive and negative bending. Numbers to right of figures indicate maximum bending stress estimated using Beam 2D (gray) and beam FEM (black).]

Journal of Morphology
ing in the beam between the bite point and muscle insertions decreases. Sagittal shear stress in the beam between the muscle insertions and the jaw joint peaks on the balancing side and during anterior bites, and decreases as the bite point moves posteriorly. Peak sagittal shear stress magnitudes are higher in the beam FEM than in the Beam 2D calculations for each load case but only marginally (Fig. 7).

**Internal stresses—Bending and shear stress in transverse planes.** Bending and shear stresses in transverse planes predicted by Beam 2D are similar for the balancing side and working side (regardless of bite point) because horizontal reaction forces at the jaw joints are similar across all trials and horizontal reaction forces at the symphysis and bite point are very small. Powerful muscles pull medially on the beam both posterior (mPTd and mPTv) and anterior (mAMP and mAME) to the jaw joint. As a result, both bending and shear stresses peak at the jaw joint (Fig. 8) and the beam is laterally bowed (i.e., experiences positive bending), placing the pterygoid flange contact in “tension.” The mandible experiences medial (negative) bending anterior to the insertion of mAMP, decreasing to zero at the symphysis. Mediolateral bending stresses are lower than dorsoventral bending stresses; however, shear in the transverse plane is higher than that recorded in sagittal planes in Beam 2D.

![Fig. 7. Sagittal shear stress in the beam models. A: Lateral view of Alligator working side mandible with muscle force vectors (solid arrows) and reaction force vectors (broken arrows). B: Vertical forces (black arrows) and supports (black triangles) applied to Beam 2D model representing working side; black arrow at symphysis represents contribution from balancing side muscle force. C–H: Shear stresses (MPa) and location relative to the neutral axis indicated in gray box (Beam 2D estimate). Black line indicates stress magnitude recorded in xy sections of the beam FEM. Location of bite point on the working side trials (C–G) is indicated by a small black triangle. H: Balancing side. The standard conventions are shown at the bottom of the figure.](image)

![Fig. 8. Mediolateral stresses and moments in beam models. A: Dorsal view of Alligator working side mandible with muscle force vectors (solid arrows) and reaction force vectors (broken arrows). B: Horizontal muscle forces (black arrows) and supports (black triangles) applied to working side Beam 2D model. All stresses and moments were similar regardless of bite point; only those calculated for the posterior bite are shown. C: Calculated bending moments in the beam model shown in (B). Standard conventions for positive and negative moments are illustrated at left. D: Compressive and tensile bending stresses for Beam 2D model indicated in gray box; tensile stresses for beam FEM (lateral transect) indicated by black line. E: Shear forces (N) and shear stress (in N/m²) for Beam 2D model indicated in gray box; tensile shear stresses for beam FEM indicated by black line. Standard conventions shown at left.](image)
The working side beam FEMs experience strong but localized positive (lateral) bending at the bite point, whereas the balancing side experiences weak negative (medial) bending at the symphysis. Peak mediolateral bending stress is highest at the jaw joint, and was slightly lower than that recorded in Beam 2D. Transverse shear stress predicted by the beam FEM is identical on the working side and balancing side (regardless of bite point) and peaks at the jaw joint (Figs. 8 and 13). Peak transverse shear stress in the beam FEM is lower in magnitude than that predicted by Beam 2D.

**Torsional stresses.** Figure 9 illustrates estimated torsional stresses along the working side and balancing side beams. Torsional stresses derived from Excel calculations predict that the working side beam below and adjacent to the jaw joint experiences strong counterclockwise (positive) torque, whereas the portion between the muscle insertions and the bite point experiences clockwise (negative) torque. Calculations for the balancing side suggest that the entire beam experiences positive torque. These results support predictions derived from the free body diagram that the powerful jaw elevators (mAMP, mPT) tend to rotate the ventral margin of the lower jaws medially relative to the tooth rows. Twisting of the mandible on both sides must be resisted at the jaw joint and symphysis, and at the biting tooth of the working side. The working side and balancing side of the beam FEM model also experience counterclockwise torque between the jaw joint and the anterior muscle insertions due to the actions of mPT and mAMP (see videos in Supporting Information); however, torsional stress rapidly decreases anteriorly. Additionally, the beam FEM also experiences clockwise torque posterior to the jaw joint due to the action of mDM. For all beam models, torsional stress is highest near the jaw joint and is higher on the balancing side than the working side.

**Simple Alligator FEM**

**Reaction forces.** Vertical bite forces in the *Simple Alligator* FEM are more than 30% lower than at corresponding bite positions in the beam models (Table 7). Vertical reaction force at the working side jaw joint is greater in magnitude at all bite positions in the *Simple Alligator* FEM than in the beam models. Vertical reaction force at the balancing side jaw joint is more than 80 N higher than that predicted by the beam models and remains nearly constant with changes in bite position on the working side. The *Simple Alligator* FEM predicts higher medially directed forces at the bite point than the beam models (Table 7). Laterally directed reaction forces at the jaw joints are lower than those generated in the beam models.

Posteriorly directed reaction forces at the bite point of the *Simple Alligator* FEM are much lower than those in the beam FEM, whereas posteriorly directed forces on the working side jaw joint are generally higher, peaking during middle bites. Unlike lever arm mechanics or the beam models, in which the balancing side and working side were modeled independently, the two sides of the mandible were modeled together in the *Alligator* FEMs, and changes in bite point on the working side cause changes in the mechanical behavior of the balancing side. Posteriorly directed reaction force on the balancing side jaw joint of the *Simple Alligator* FEM is much lower than those predicted...
by lever arm mechanics or beam models, and increases during posterior bites.

**Internal stresses—Bending stress in sagittal planes.** Like the beams, the balancing side of the simple Alligator FEM undergoes negative bending (dorsal deformation) along most of its length (Fig. 10F–J). Peak dorsoventral bending stress on the balancing side is highest during posterior biting (on the working side), occurs midway along the length of the mandible (Fig. 10F), and is substantially lower on the balancing side of the simple Alligator FEM than in the beam FEM.

As in the beam models, the posterior working side mandible of the simple Alligator FEM experiences negative bending, whereas the anterior mandible undergoes positive bending (Fig. 10A–E). During anterior to posterior-middle bites, peak dorsoventral bending stress occurs near application of muscles forces and is lower than that recorded in the beam FEM. During posterior bites, peak bending stress occurs near the bite point. Dorsoventral bending stress varies less along the simple Alligator FEM than along the beam FEM; this is particularly evident during anterior bites and on the balancing side, but is true at all bite positions (Fig. 10).

**Internal stresses—Shear stress in sagittal planes.** Plots of sagittal shear stress in the simple Alligator FEM resemble those generated by the beam models (Fig. 11), except that shear stress decreases abruptly at the symphysis (on both the working side and balancing side). Peak sagittal shear stress is lower on the working side (but higher on the balancing side) of the simple Alligator FEM than the beam FEM. Overall, peak dorsoventral shear stress is very low compared with bending stress.

**Internal stresses—Bending and shear stress in transverse planes.** Mediolateral bending stress is more variable in the simple Alligator FEM than along the beam models (Fig. 12). The working side and balancing side of the simple Alligator FEM experience positive (lateral) bending at the jaw joint, negative (medial) bending in the area of the elevator muscle insertions, negative bending at the bite point (working side) and positive bending at the symphysis. In both sides, peak bending stress is due to medial bending and is highest during posterior bites; on the balancing side, peak mediolateral bending stress occurs in the area of the muscle insertions while on the working side it occurs at the bite point. Peak mediolateral bending stresses are higher on the balancing side than on the working side, are higher in the simple Alligator FEM than in the beam FEM, and are nearly as high as peak stresses generated by dorsoventral bending.

The working side simple Alligator FEM experiences transverse shear stresses similar to those in the beam FEM (Fig. 13). The balancing side of the simple Alligator FEM experiences positive transverse shear anterior to the muscle insertions. Transverse shear stresses are generally lower in the simple Alligator FEM than in the beam FEM.

**Torsional stresses.** The working side of the simple Alligator FEM experiences positive (counterclockwise) torsion from the jaw joint to the anterior muscle insertions, indicating that the posterior margin of the working side is being inverted (Fig. 14). Torsional stress decreases between the muscle insertions and bite point; the mandible between the bite point and the symphysis experiences high positive torques, again indicating that the tooth row is being everted. This is evident in deformation videos (see Supporting Information and Discussion).

In contrast, the balancing side of the simple model exhibits predominantly negative (clockwise) torsional stress, indicating the ventral margin of the lower jaw is being everted. Again, videos of deformation confirm this. The only exception to this pattern is the posterior balancing side during anterior bites, which experiences positive torsion and is inverted. Peak torsional stress on the balancing side occurs near the jaw joint and at the symphysis, and is higher than peak torsional stresses on the working side.

On both the working side and balancing side, torsional stress peaks posterior to the symphysis (unlike the beam FEM in which torsional stress peaks at the jaw joint and decreases to zero anteriorly), is highest during posterior bites, and is generally higher than those recorded in the beam FEM (but lower than values recorded in Beam 2D models).

**Suture Alligator FEM**

**Reaction forces.** Vertical bite forces are lower in the suture Alligator FEM than in the simple Alligator FEM (Table 7), whereas vertical reaction forces at the working side jaw joint are higher. Medial reaction force at the bite point and lateral reaction force at the working side jaw joint are lower than those recorded in the simple Alligator FEM, whereas lateral reaction force on the balancing side jaw joint was higher (Table 7). Like the simple Alligator FEM, the suture Alligator model experiences posteriorly directed force at the jaw joints; these are higher on the balancing side and lower on the working side than those recorded in the simple Alligator FEM.

**Internal stresses—Bending stress in sagittal planes.** Plots of dorsoventral bending stress for the suture Alligator FEM are similar to those of the simple Alligator FEM and the beam FEM (Fig. 10); however, peak dorsoventral bending stress magnitudes are lower in both the working and balancing side of the suture model than in the simple Alligator or beam FEMs, particularly during posterior bites.
Fig. 10. Dorsoventral bending stresses in the FEMs. A–J: Bending ($\sigma_{zz}$) stresses taken along the ventral transect of the four models (color identified in legend) on the working side (A–E) and the balancing side (F–J). Closed triangles indicate bite point on working side; open triangles are used in plots of the balancing side. Maximum dorsoventral bending stress displayed next to each plot. K: Color contour plot of the simple Alligator FEM in ventral view, showing $\sigma_{zz}$ stress during posterior biting. L: Color contour plot of the suture Alligator FEM in ventral view, showing $\sigma_{zz}$ stress during posterior biting. “WS” denotes working side, “BS” denotes balancing side.
Internal stresses—Shear stress in sagittal planes. Plots of sagittal shear stress for the suture Alligator FEM strongly resemble those from the beam and simple Alligator FEMs (Fig. 11). Peak sagittal shear stresses are generally lower with the addition of sutures (compared with the solid model), particularly anterior to the bite point (on the working side) and in the anterior portion of the balancing side.

Internal stresses—Bending and shear stress in transverse planes. Plots of mediolateral bending stress in both the working side and
balancing side suture Alligator mandibles are similar those generated by the simple Alligator FEM (Fig. 12), although peak mediolateral bending stresses are higher in the suture model than in the simple model on the working side. Plots of transverse shear stress in the suture model resemble those generated by the simple model (Fig. 13), although transverse shear stress is lower in the anterior balancing side mandible of the suture Alligator FEM.

Fig. 12. Mediolateral bending stress in the FEMs. A–J: Bending (zz) stresses taken along the lateral transect of the four models (color identified in legend) on the working side (A–E) and the balancing side (F–J). Closed triangles indicate bite point on working side; open triangles are used in plots of the balancing side. Maximum mediolateral bending stress displayed next to each plot. K–N: Color contour plots of the working (K, L) and balancing (M, N) sides of the sutures (K, M) and PTflange (L, N) Alligator FEMs in lateral view during a posterior bite, showing zz stress.
**Torsional stresses.** Torsional stress plots (Fig. 14) of the working side mandible of the suture Alligator FEM differ from those of the simple model in that stress magnitudes are substantially lower in the anterior mandible, particularly, during middle to posterior bites. The balancing side suture Alligator model also experiences lower negative torsional stresses in the anterior mandible than the simple model. Additionally, the posterior balancing side of the suture model experiences positive torque at all bite points, suggesting inversion of the ventral margin of the posterior mandible relative to the tooth row, whereas the anterior mandible continues to undergo negative torsion. This is confirmed by deformation videos (see Supporting Information). Torsional stresses on both sides peak during middle bites.

**Pterygoid Flange Alligator FEM**

**Reaction forces.** Vertical bite and jaw joint reaction forces in the PT flange Alligator FEM, as well as medial forces on the biting tooth, are similar to those in the suture model (Table 7); however, laterally directed reaction force on both jaw joints decrease substantially compared to the suture model. Unlike the suture model, the balancing side jaw joint of the PT flange model does not experience high lateral or posteriorly directed forces during biting on the posterior tooth. Laterally directed
forces occur at the contact with the pterygoid flange on the working side and balancing side mandibles at all bite positions; the magnitude of these forces range from 30 to 70 N. This force is greatest on the balancing side during posterior bites.

**Internal stresses—Bending stress in sagittal planes.** The *PT flange* Alligator model strongly resembles the *suture* model in the distribution of dorsoventral bending stresses (Fig. 10) and in peak dorsoventral bending stress magnitudes.

**Internal stresses—Shear stress in sagittal planes.** Plots of sagittal shear in the *PT flange* FEM are virtually identical to those generated by the *suture* model (Fig. 11), as are peak sagittal shear stresses.

**Internal stresses—Bending and shear stress in transverse planes.** Unlike the *simple* and *suture* Alligator FEMs, which experience medial bending in the area of the muscle insertions, the *PT flange* model experiences lateral bending in this region (Fig. 12) due to the presence of the pterygoid flange. Mediolateral bending stresses are lower in both the working side and balancing side of the *PT flange* model compared with the *suture* model, particularly during posterior bites. Peak mediolateral bending stress in the *suture* model increases as the bite point moves posteriorly; in contrast, in the *PT flange* model it peaks during anterior bites.

Unlike the *simple* and *suture* Alligator models, peak transverse shear stress in the *PT flange* model...
model does not change with changes in bite position (Fig. 13). Transverse shear stresses are lower than those in the simple and suture models, particularly, during posterior bites. Transverse shear stress occurs at the contact with the pterygoid flange.

Torsional stresses. Plots of torsional stresses in the PT flange Alligator model resemble those generated by the suture model (Fig. 14); however, peak torsional stresses are somewhat higher in both sides.

DISCUSSION

The aims of this study were several fold. Data on muscle architecture (cross-sectional area, pin,
nation, sarcomere length) and muscle orientation were obtained and used to estimate the external muscle forces acting on the Alligator mississippiensis mandible at 30° of gape. These data were then used to estimate, using beam modeling and FEA, the bite and joint reaction forces acting on, and the shear, bending and torsional stresses acting in the Alligator mandible, as well as its general patterns of deformation. By comparing the reaction forces and stress regimes in the simple beam models with the high-resolution FEMs of the Alligator mandible, we sought to address a number of questions. Does mandibular morphology in this archosaur minimize stress while minimizing bony material better than would a similarly loaded simple beam? How do the material properties of the archosaur mandible affect its mechanical behavior? How does the enlarged pterygoid flange of archosaurs affect mandibular stress patterns?

Muscle architecture and Length–Tension Curves

We found sarcomere lengths at minimum gape ranging between 1.88 and 2.01 μm; Busbey (1989) reported sarcomere lengths of 1.99–2.38 μm in Alligator elevator muscles at 0° gape. Failure to correct muscle fascicle lengths for sarcomere length at muscle fixation can result in errors in calculation of muscle PCSA. In this study, a resting, or optimal, sarcomere length of 2.5 μm was assumed, a value larger than that measured in frog (2.0–2.2) but similar to that estimated for the upper end of the plateaus for cat and lower end of the plateau region of humans (Herzog, 2007). The length–tension curves presented here will need to be recalculated as thin filament lengths and/or length tension curves for A. mississippiensis become available. These changes should not significantly alter the relative PCSA magnitudes of the muscle modeled here, although they might result in changes in absolute stress and strain magnitudes.

In Alligator, some jaw elevator muscles (mAME, mPST) reach the inflection point of the ascending limb of their length–tension curves at minimum gape, suggesting that these muscle groups are more effective (in terms of optimal sarcomere length) at low gape angles (see also Busbey, 1989). In contrast, mPTd and mPTv are below the plateau even at gape angles of 30°, suggesting these muscles are most effective at wide gapes.

Iordansky (1964) observed that mPST and mAME are enlarged relative to mPT in long-snouted crocodilians, which feed primarily on fish; the lines of actions of these vertically oriented muscles make them mechanically advantageous at small gape angles. In contrast, the pterygoid muscles are well developed in short-snouted crocodilians with generalized diets (including large animals), and their highly oblique lines of action make them mechanically advantageous at high gape angles needed to capture large prey. Additionally, EMG studies have demonstrated that activity in mPT ceases shortly after closing, whereas mAME remains active during holding and crushing at minimum gape (Busbey, 1989). Thus, optimal sarcomere length, mechanical advantage, and muscle activity patterns all suggest that mAME and mPST are adapted for closing the jaws at small gapes, while the pterygoids are better suited for closing the jaws at large gapes (Stern, 1974).

External Reaction Forces—Orientations and Magnitudes

Bite force and joint reaction force are important performance metrics. Previous studies have used reaction forces as measures of jaw efficiency and to infer changes in feeding behavior or diet among different taxa (Van der Meij and Bout, 2004; Wroe et al., 2005; Christiansen and Wroe, 2007) or during ontogeny (Thomason et al., 1990; Herrel and O’Reilly, 2006). For these reasons, it is critical to understand how differences in modeling method and model complexity affect both the absolute and relative magnitudes of the reaction forces generated.

Some general patterns are observed in all models of the Alligator mandible. Both jaw joints are in compression in all models at all bite points, with joint reaction force always directed ventrally, laterally, and posteriorly (Table 7). Additionally, vertical bite force increases as the bite point moves posteriorly, whereas vertical force at the working side jaw joint decreases. The similarity of these results across models is due to the fact that the relative magnitudes of joint and bite reaction forces are determined by the geometry, magnitude, and orientation of the external forces acting on the mandible and its overall external geometry, not by the internal shape of the mandible or its material properties. Similarly, all models experience laterally directed forces at the jaw joints, probably because the muscle forces were all applied near
the joint, or its equivalent position in the beam models. Thus, modeling technique might be expected to have little influence on the orientations and relative magnitudes of external reaction forces.

However, despite general similarities between models, substantial differences in reaction forces are observed between the Alligator FEMs and the beam models. Bite forces in the beam models (and those predicted using lever arm mechanics) are higher than those generated in the Alligator FEMs, while vertical reaction forces at the jaw joints are lower. This suggests that the morphology of the Alligator mandible makes it less efficient at transferring force from the elevator muscles to the bite point than a simple beam. Additionally, the beam models and Alligator FEMs experience substantial medial (and in the FEMs, posterior) bite reaction force components, suggesting that the common assumption made in lever arm analysis of living and fossil taxa (i.e., that bite force is vertical) is probably incorrect. Reaction force on the balancing side jaw joint was assumed to remain constant in the lever arm calculations and beam models, but varies with bite position in the Alligator FEMs; thus, beam models that consider the balancing side and working side separately do not accurately predict reaction forces experienced by the balancing side, particularly longitudinal reaction forces. Finally, the beam models predicted low, medially directed reaction forces at the pterygoid–mandibular contact; however, the PT flange model demonstrates that high laterally directed forces occur at this contact.

These differences between the results of beam and FE modeling suggest that the use of beam models to estimate bite and joint reaction force magnitudes and orientations in fossil archosaurs may yield inaccurate results. In addition, differences in reaction forces between the three Alligator FEMs suggest that failure to accurately model material properties may also yield inaccurate estimates of bite and joint reaction forces, even if geometry is precisely modeled using FEA. The addition of anisotropy/sutures/PDL to our simple mandible model resulted in lower bite forces in the sutures FEM. Furthermore, when the pterygoid flange–mandibular contact is added to the model, laterally directed reaction forces at the jaw joints are reduced, resulting in more vertically oriented joint reaction forces in anterior view than the other Alligator FEMs.

Cleuren et al. (1995) suggested that the orientation of joint reaction forces in Caiman would be aligned with the quadrate, which forms the jaw joint; the reaction forces experienced by the Alligator FEMs (but not the beam models) provide some support for this observation. The quadrate of this specimen is oriented ~38° from the y-axis (in anterior view) and ~47° from the y-axis (in lateral view). The reaction forces experienced by the Alligator FEMs average ~43° in anterior view, and ~31° in lateral view. Thus, joint reaction forces predicted by FEA more closely align with the quadrate in anterior view than lateral view.

Erickson et al. (2003) measured changes in bite force during ontogeny in Alligator; their work predicts a bite force of ~230 N in an animal with a total body length of 1 meter, the approximate size of the animal we used to build the FEM. This is similar to bite reaction forces predicted by our beam models (118.6–249.6 N) and lever arm mechanics (119.6–214.1 N; Table 7), although higher than maximum bite forces obtained from the Alligator FEMs (170.6 N). Other studies have used lever arm mechanics (Sinclair and Alexander, 1987; Cleuren et al., 1995) to estimate bite and joint reaction forces in Caiman; their results predict lower bite forces (for smaller animals) but higher bite/joint force ratios than our Alligator FEMs.

The discrepancy between bite force values calculated by our Alligator FEMs and those predicted from in vivo measurements (Erickson et al., 2003) may have a number of causes. One possibility is that the individual from which the muscles were taken (a wild female from Rockefeller Wildlife Refuge, 1.3-m body length, 0.21-m head length) may have had unusually small muscles, leading us to underestimate force produced by the elevator muscles. Additionally, muscle PCSA was multiplied by a specific muscle tension of 25 N/cm² in this study; other workers have used muscle stresses of >30 N/cm² when modeling reptilian muscles (Johnston and Gleeson, 1984; Sinclair and Alexander, 1987). Although increasing muscle tension would not change relative muscle forces or the overall mechanical behavior of our models, it would result in a 20% increase in reaction force magnitude, and presumably increase stress magnitudes and model deformation. These possibilities will be explored further in future sensitivity analyses by increasing muscle force. In addition, our estimates of material properties of sutures and PDL (which were not based on data from Alligator) may be inaccurate since the simple Alligator FEM, which does not incorporate sutures or PDL, experiences higher bite reaction forces than the suture and PT flange models. At present, we are confident that the relative magnitudes of the calculated muscle forces are correct, as well as the deformation regime and relative bite and joint reaction forces.

Internal Forces—Bending, Shearing, and Torsion

Our hypothesis, that bending stresses would be higher in the Alligator mandible than stresses due to shear or torsion is corroborated. In all models,
peak bending stresses are an order of magnitude higher than peak shear stresses. Peak stress due to torsion is always lower than peak bending stress and higher than peak shear stress. It is important to note that high shear stresses at the jaw joint and in the area of the jaw elevator muscles, as well as high torsional stress at the symphysis, suggest that shear and torsion may be important determinants of morphology in these areas.

The suture and PT flange Alligator FEMs generally experience lower, more evenly distributed dorsoventral bending and shear stress than the simple model, suggesting that the combination of anisotropic bone [stiffer along the long axis of the mandible (Zapata et al., 2010)], sutures, and PDL reduces dorsoventral bending stress in Alligator mandibles. However, the suture model exhibits higher mediolateral stresses (specifically mediolateral bending stress on the working side and transverse shear stress on the balancing side); these mediolateral stresses are reduced in the PT flange model. Anisotropy/sutures/PDL also result in lower peak torsional stress in the suture model compared to the simple model. Thus, our results indicate: 1) that sutures/anisotropy/PDL in the Alligator mandible reduce dorsoventral bending, sagittal shear stresses, and torsional stress; and 2) that the pterygoid–mandibular contact reduces high mediolateral stresses in the sutured Alligator mandible.

**Model Deformation**

The impact of sutures, bone anisotropy, PDL, and the pterygoid flange on the behavior of the Alligator mandible are evident when comparing overall deformation regimes (see Supporting Information). In the absence of sutures/anisotropy/PDL (simple model), bending of the mandible was primarily dorsoventral; in particular, the balancing side of the simple model is bent strongly upward and the tooth row is inverted (i.e., it experiences negative torsion). In all Alligator models, the anterior working side is bent dorsoventrally during posterior bites; dorsoventral bending is far less pronounced on the working side during anterior bites. In the suture model, which lacks a pterygoid–mandibular contact, mediolateral bending of the mandibles (particularly the balancing side during posterior bites) is more pronounced, resulting in higher mediolateral bending stress and transverse shear stresses in this model. Furthermore, the addition of sutures/anisotropy/PDL results in decreased torsional stress and the posterior balancing side experiences positive torsion, whereas the anterior balancing side continues to undergo negative torsion. The addition of the pterygoid flange to the model, yielding our “best guess” hypothesis regarding mandibular deformation in Alligator, results in decreased dorsoventral and mediolateral bending; instead the primary deformation of this model is twisting of the mandibles, with the ventral margin of the working side and posteroventral margin of the balancing side being inverted relative to the tooth rows. In all models, bending is more pronounced during posterior bites, whereas twisting about the long axis is the predominant deformation regime during anterior bites.

Although these verbal descriptors accurately describe deformation of the Alligator mandible, we emphasize that such descriptors are necessarily imprecise. Rather, as noted elsewhere (Chalk et al., 2010; Ross et al., 2011), the finite element model, including its specific geometry and material properties, and the resulting loading, stress, and deformation regimes, is our hypothesis regarding the mechanical behavior of the Alligator mandible during biting. The model itself should be referred to for further details.

**Form and Function of the Alligator Mandible**

The lower magnitude and less variable dorsoventral bending and sagittal shear stresses in the Alligator mandible FEMs suggest that, compared with a simple beam, the mandible of Alligator is better optimized to reduce these stresses during biting. We hypothesize that these results primarily reflect improved resistance to dorsoventral bending, and that this is an important design criterion in Alligator mandibles. Dorsoventral shear stress magnitudes are very low in all FEMs, suggesting that the improved resistance of the mandible to dorsoventral shearing forces is likely to be a secondary effect of changes in design to resist dorsoventral bending. Similarly, the low values of mediolateral shearing and torsional stresses suggest that these parameters are unlikely to exert a significant effect on Alligator mandible design.

The material properties of the Alligator mandible appear to also reflect design criteria, especially in interaction with the pterygoid flange constraint. Alligator mandibular bone is stiffer along the long axis of the mandible (Zapata et al., 2010). Our analyses show that incorporation of this anisotropic bone (as well as sutures and PDL) in the Alligator FEM reduces dorsoventral bending and torsional stresses. However, this comes at the expense of increased mediolateral bending and shear stresses, and lowered bite reaction force, due to strong mediolateral deformation of the mandible (compared with a homogeneous, isotropic mandible).

The presence of the pterygoid flange ameliorates the increased mediolateral stresses but does nothing to improve the poor efficiency suggested by the low bite to joint reaction force ratios in Alligator. The results presented here reveal that in the Alligator FEM, the addition of a contact between the mandible and pterygoid flange reduces: mediolat-
eral deformation of the mandible, reaction forces at the balancing side jaw joint, mediolateral bending stress in the working side mandible and transverse shear stress in the balancing side mandible. Lack of compressive reaction forces at the contact in the beam 2D model and lack of strong mediolateral deformation in simple Alligator FEM, however, suggest this function of the pterygoid flange may be necessitated by increased mediolateral deformation due to anisotropic bone and/or sutures found in Alligator mandibles. Future sensitivity analyses will parse out the relative importance of these two input parameters.

Finally, our results demonstrate that the symphysis is an area of high torsional stress in the Alligator mandible compared with the beam models. Computed tomography imaging reveals that the symphysis (dentary–dentary contact) in the subadult Alligator is strongly interdigitated in the coronal plane; it is possible that the morphology of this contact (as well as its material properties) is important in mitigating torsional stresses.

Limitations of the Model

The FE model of the Alligator mandible presented here incorporates the most detailed geometry, accurate bone material properties, and comprehensive information on muscle architecture and contractile properties of any model of an archosaur skull yet published. Results derived from this model are still dependent on a number of assumptions. Our model only tests the mechanical behavior of the mandible during simple, unilateral biting; however, living crocodilians load their mandibles in a number of ways: they can lift or throw prey out of the water, shake the head, and engage in “twist-feeding.” These behaviors would undoubtedly induce higher torsional and mediolateral forces on the mandible. Because we cannot at present validate the mechanical behavior of the mandible resulting from such activities, and because such activities result in more complicated loading regimes better suited for dynamic analyses, we chose not to load our model in such a manner. The loading regime applied to the model assumes that all muscles (and all portions of individual muscles) fire simultaneously and maximally; incomplete EMG data (Busbey, 1989; Cleuren et al., 1995) demonstrated that the jaw muscles of crocodilians do not behave in this manner. The model presented in this article is tested at only one gape angle (30°); future analyses will investigate changes in mechanical behavior with changes in gape angle in Alligator. Future analyses will investigate changes in mechanical behavior with changes in gape angle in Alligator. Likewise, our model is of a subadult Alligator; a study in progress examines changes in mandibular mechanical behavior within an ontogenetic series of Alligator. Finally, information on the material properties of crocodilian teeth, sutures and PDL, as well as information on the histological and material properties of the cartilago transiliens, is not currently available; as these data become available, we hope to refine our model accordingly.

CONCLUSIONS

Lever arm calculations and beam models have been used extensively to evaluate the mechanical behavior and morphology of archosaur crania and mandibles (Sinclair and Alexander, 1987; Busbey, 1995; Cleuren et al., 1995; Mazzetta et al., 1998; Henderson, 2002; Therrien, 2005; Desojo and Vizcaïno, 2009; Tanoue et al., 2009). The results presented here suggest that these calculations provide approximate estimates of the general orientation of bite or joint reaction forces, and the general distribution of dorsoventral bending stresses, and sagittal and transverse shear stresses in the mandible. However, they perform poorly in predicting absolute or relative reaction force magnitudes, precise reaction force orientation, and mediolateral bending and torsional stress distribution within the mandible. Although the beam models experienced dorsoventral bending and sagittal and transverse shear stress patterns similar to the Alligator FEMs, stress magnitudes were substantially different. One of the most notable differences between the beam models and the Alligator FEMs was the behavior of the balancing side, which varied with changes in bite position in the Alligator FEMs, suggesting that the behavior of the balancing side is poorly represented in simple beam models in which the working side and balancing side are modeled separately. Overall, beam models do not accurately represent the mechanical behavior of the archosaur mandible, despite its superficial resemblance to a beam.

It has been suggested that the morphology of the Alligator mandible reduces stress during biting while minimizing bony material (van Drongelen and Dullemeijer, 1982); we tested this hypothesis by evaluating whether stress is more evenly distributed in the Alligator mandible than in a structure with uniform geometry and material properties throughout: i.e., a simple beam. Compared with the beam models, dorsoventral stresses were more evenly distributed in the Alligator FEMs, corroborating van Drongelen, and Dullemeijer’s analyses. However, the Alligator mandible does not appear optimized to reduce mediolateral and torsional stresses, compared with a simple beam.

Most studies using FEA assume isotropic material properties for bone. Additionally, while several studies have focused on the mechanical significance of cranial sutures in Alligator and other archosaurs (Busbey, 1989; Rayfield, 2004, 2005), the sutures of the mandible have received far less attention. Results from the Alligator FEMs demon-
strate that bone anisotropy/sutures/PDL reduce dorsoventral stresses and torsional stresses, but make the mandible susceptible to mediolateral deformation. These results suggest that sutures/anisotropy/PDL must be considered when attempting to address questions about mechanical behavior in the mandibles of extinct archosaurs; this is especially important in modeling archosaurs, such as many therocephalians, which possess patent mandibular sutures or a possible intramandibular joint.

The elongate pterygoid flanges of crocodilians have been hypothesized to act as braces against medial deformation of the mandible in platyrostral forms, due to more medially inclined jaw elevators (Busbey, 1995; Jordansky, 1964). Our results corroborate this hypothesis. The development of the pterygoid flange varies among crocodilians and other archosaurs. Differences in cranial morphology among taxa that possess elongate pterygoid flanges (such as platyrostral crocodilians and ornithischian ornithopod dinosaurs) suggest that the presence of this feature may be related to mandibular morphology, sutural morphology, or jaw mechanism.

Both similarities and differences were observed between the mechanical behavior of our *Alligator* model and the behavior of mammalian (specifically primate) mandibles (see Introduction). Both jaw joints are in compression in the *Alligator* model despite changes in bite point; this contrasts with mammals, in which recruitment levels of working side and balancing side muscles must be modulated to prevent the working side jaw joint from being put under tension during posterior bites (Greaves, 1978, 1982; Spencer, 1995, 1998, 1999; Thomason et al., 1990). This difference is attributable to the more anterior position of the *Alligator* toothrow relative to mammals.

Our results demonstrated that bending stress was higher than either shear or torsional stress in the *Alligator* mandible. As the relative importance of bending, shear, and torsional stresses in primate mandibles has not yet been quantified, results from the *Alligator* model cannot be compared with primates at this time. However, we predict that bending stresses are more important in *Alligator* mandibles than in the relatively shorter mandibles of most primates.

Like the deformation regimes hypothesized by Hylander (1977, 1979a,b, 1981, 1984) to occur in primate mandibles, the *PT flange Alligator* model experiences twisting about its long axis and dorsoventral bending, with bending being predominant during posterior bites and twisting being larger in magnitude during anterior bites. Unlike primate mandibles, which experience lateral transverse bending of the corpora (i.e., “wishboning”) during mastication due to the action of the masseter, the mandibles of *Alligator* experience medial transverse bending, being pulled inward by the powerful, medially inclined pterygoideus muscles. This deformation is strongly reduced by the addition of the pterygoid flange contact. Finally, our results demonstrated that the mandibular symphysis of *Alligator* experiences dorsoventral shearing, twisting about the transverse axis (leading to elevated torsional stress) and bending in the transverse plane (due to “inverse wishboning”); similar deformation is reported in the primate mandible although transverse bending is due to lateral “wishboning.” We note that these are preliminary comparisons, based on a single archosaur taxon, and much work is still required to better understand the similarities and differences of the loading environment between mammalian and reptilian mandibles.

**ACKNOWLEDGMENTS**

The authors thank Hauke Bartsch (Visage Imaging) and Christian Wietholt (Department of Radiology, University of Chicago) for assistance with Amira. Anne Delvaux (Beaufort Analysis) provided technical support for Strand7. Ruth Elsey at the Rockefeller Wildlife Refuge generously provided specimens for study. David Reed, Justin Lemberg, and Keith Metzger as well as two anonymous reviewers provided valuable comments on the article.

**LITERATURE CITED**


