

Rigid-body analysis of a lizard skull: Modelling the skull of *Uromastix hardwickii*

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Accepted 17 January 2008

Abstract

Lizard skulls vary greatly in their detailed morphology. Theoretical models and practical studies have posited a definite relationship between skull morphology and bite performance, but this can be difficult to demonstrate *in vivo*. Computer modelling provides an alternative approach, as long as hard and soft tissue components can be integrated and the model can be validated. An anatomically accurate three-dimensional computer model of an *Uromastix hardwickii* skull was developed for rigid-body dynamic analysis. The *Uromastix* jaw was first opened under motion control, and then muscle forces were applied to produce biting simulations where bite forces and joint forces were calculated. Bite forces comparable to those reported in the literature were predicted, and detailed muscular force information was produced along with additional information on the stabilizing role of temporal ligaments in late jaw closing.

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Keywords: Bite force; Muscle force; Temporal ligament; Multibody dynamics analysis; Lizards

1. Introduction

Lizards, snakes and their relatives (Squamata) comprise the largest and most successful group of living reptiles. They are distinguished from crocodiles and turtles by a variable degree of intracranial mobility (e.g. Metzger, 2002), most notably streptostyly. In the latter movement, the quadrate bone is able to pivot fore-and-aft due to a relaxation of its bony contacts with the rest of the skull, allowing the mandible to move forwards during mouth opening. These movements are constrained dorsally and ventrally by ligamentous attachments, the precise role of which is debated (Iordansky, 1996; Herrel et al., 1998a, b). Furthermore, although squamate skulls show a number of common characteristics (e.g. Estes et al., 1988; Evans, 2003), they differ markedly in overall shape, in the details

of their joint morphology, in bone density, and in the structure and implantation of the teeth. These structural and shape differences must be linked to differences in feeding strategy (e.g. Herrel et al., 2001; Erickson et al., 2003; Metzger and Herrel, 2005). However, developing an understanding of the evolutionary selective factors influencing craniofacial geometry is a daunting task, as it requires knowledge of the interactions between bone form and function, ligament arrangement, muscle forces, joint forces and bite forces.

Unravelling the effects of these different components *in vivo* is difficult, precisely because they are closely integrated, but computer modelling techniques provide an opportunity to explore in detail the biomechanical characteristics of different skulls and to examine the development, adaptation and influence of specific features. The relatively new technique of multibody dynamics analysis (MDA) allows us to simulate rigid-body motion and to model the external forces and internal musculature responsible for skull loading (Langenbach et al., 2002; Sellers and Crompton, 2004). This, in turn, enables biting simulations to be performed, and the resulting information

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can then be applied to finite element analysis (FEA) studies to calculate stresses and strains, where the internal and external bone structure is widely believed to be influenced by the loading.

Although computational simulation is a relatively new approach in the study of cranial functional morphology, a growing body of work demonstrates both its potential and its validity. Validation is always an area of concern, but there is suitable bite force data available in the literature for comparison (e.g. Hylander, 1979; Dumont and Herrel, 2003). In a preliminary study, Langenbach and Hannam (1999) developed a three-dimensional (3D) dynamic model of the human jaw to assess the role of passive muscle tension. More recently, Langenbach et al. (2002, 2006) were able to demonstrate the accuracy of computational simulations with a computer model of a pig jaw that agreed well with recorded *in vivo* data. Sellers and Crompton (2004) used MDA in a study of the sensitivity of muscle force application, and this helped validate their computational model into the prediction of bite force in the human skull. Koolstra and Van Eijden (2005, 2006) were among the first to use a combined rigid-body and finite element method to study the musculoskeletal system, developing a model of the human jaw joint with the help of MADYMO (TNO Automotive, The Netherlands). Most recently, Peck and Hannam (2007) modelled the human jaw, and de Zee et al. (2007) performed a validation study that compared the results of *in vivo* experiments on the human mandible with those from musculoskeletal models. The potential applications to extinct taxa were illustrated by Konakanchi (2005) who used AnyBody musculoskeletal modelling software to predict the bite force of a saber-toothed cat (*Smilodon fatalis*), and by Del Signor (2005) who integrated a Graphical-User-Interface (GUI) of MATLAB into MSC VisualNastran4D, again to estimate the bite force of an extinct cat.

The present work is part of a larger study into the evolution of reptilian skull architecture. The goal was to develop an anatomically accurate computational model of a lizard skull (*Uromastix hardwickii*), in which biting simulations are conducted by applying varying muscle loads to predict ligament, joint and bite reaction forces. The extensive data produced from this research will improve the accuracy of future FEA studies, in which questions directed towards mechanical loading and facial morphology can begin to be answered.

2. Materials and methods

2.1. Model construction

Micro-CT data of an *Uromastix hardwickii* skull (skull length ~44 mm; skull width ~41 mm) were supplied by the University of Texas, Austin, in the form of a tiff image data set. The data set was imported into AMIRA image segmentation software (Berlin, Germany), which was used to extract the bony geometries through a segmentation process and to create accurate surface models of the upper skull (cranium), lower jaws (mandibles), and the quadrates. Separation of the quadrates allowed

them to move independently. The mandible was divided into left and right sections. The surface models were exported from AMIRA in a wavefront format (.obj) and imported into MSC ADAMS motion simulation software (Santa Ana, US) as rigid-bodies for MDA.

Definition of the mass properties of all moving parts, constraints on their motion, and the forces or motions applied to them must be defined when carrying out multibody dynamic modelling. The mass of the jaw and quadrates was calculated directly from ADAMS using the geometry of the rigid-bodies and assuming a standard tissue density of 1050 kg/m³ (Sellers and Crompton, 2004). A mass of 1.54 and 0.27 g was produced for the jaw and quadrates, respectively. Gravity was also applied in the model, with a constant value of 9.81 m/s². The cranium was fixed throughout all testing and the quadrates were attached to the cranium at one end (quadrato-squamosal joint—specified as joint 1) and the mandible at the other (quadrato-mandibular joint—specified as joint 2) via hinge joints. The mandible was imported as two separate parts that were rigidly connected via the coupler tool in ADAMS.

2.2. Muscle, ligament and food bolus development

The attachment locations of the masticatory muscles and the temporal ligament were defined in accordance with the anatomical data described by Haas (1973) and Throckmorton (1976). Since we were interested in jaw closing/biting only the adductor muscles were represented: these were the adductor mandibulae externus superficialis anterior (MAMESA), adductor mandibulae externus superficialis posterior (MAMESP), adductor mandibulae externus medialis (MAMEM), adductor mandibulae externus profundus (MAMEP), pterygoideus externus (MPTE), pterygoideus medialis (MPTM) and the pseudotemporalis superficialis (MPST). To cover the broad attachment areas the MPTE and MPTM muscle groups were divided into 3 sections and fanned out accordingly. All other muscle groups were divided into two sections (see Fig. 1). Muscle pennation could not be taken into account as fibre lengths and orientations vary throughout each muscle.

The muscles were modelled according to van Ruijven and Weijjs (1990) (see Eq. (1)), which in turn are based on the Hill-type muscle model (Hill, 1938). An additional feature was included into the muscle model such that if the working length of the muscle became less than its resting length then that muscle would not exert a force:

$$F_{\text{muscle}} = F_{\text{max}} \times (F_A \times F_V \times F_Q + F_P), \quad (1)$$

where F_{max} is the maximal tetanic force, i.e. physiological cross-sectional area (PCSA) \times 30 N/cm² (van Ruijven and Weijjs, 1990), F_A is a force/length factor, F_V is a force/velocity factor, F_Q is an activation factor and F_P a passive muscle element. The PCSA values used to calculate F_{max} were based on scaled PCSA data reported by Herrel et al. (1998a, b).

The force length factor (F_A) was estimated by a second order polynomial, as defined in Eq. (2) (Epstein and Herzog, 1998):

$$F_A = -6.25(L/L_0)^2 + 12.5(L/L_0) - 5.25, \quad (2)$$

where L is the current muscle length and L_0 is optimal muscle length at which the muscle can apply its maximum force. For the purpose of this study an optimum gape of 15° was chosen (Herrel, personal communication; Turkawski and van Eijden, 2001) and then the corresponding muscle length (i.e. L_0) for each individual muscle was calculated. The force velocity relation (F_V) was specified separately for shortening and lengthening according to the model of Otten (1987) which again was based on Hill's equations (Hill, 1938) (Eq. (3)).

$$F_V = \begin{cases} (1 - V/V_{\text{max}})/(1 + V/k \times V_{\text{max}}), & V \geq 0, \\ 1.8 - 0.8(1 + V/V_{\text{max}})/(1 - 7.56V/k \times V_{\text{max}}), & V < 0, \end{cases} \quad (3)$$

where V_{max} is the maximum contraction velocity, which is dependent on the length of muscle. Here we scaled muscle fibre lengths published by Herrel et al. (1998a, b) according to the skull length of our model, and multiplied this by a value of 14.6 \times muscle length/s, as reported by Marsh and Bennett (1985) (see Table 1). k (= 0.25) is a constant calculated by Close (1964) assuming that jaw muscles consist mainly of fast fibres

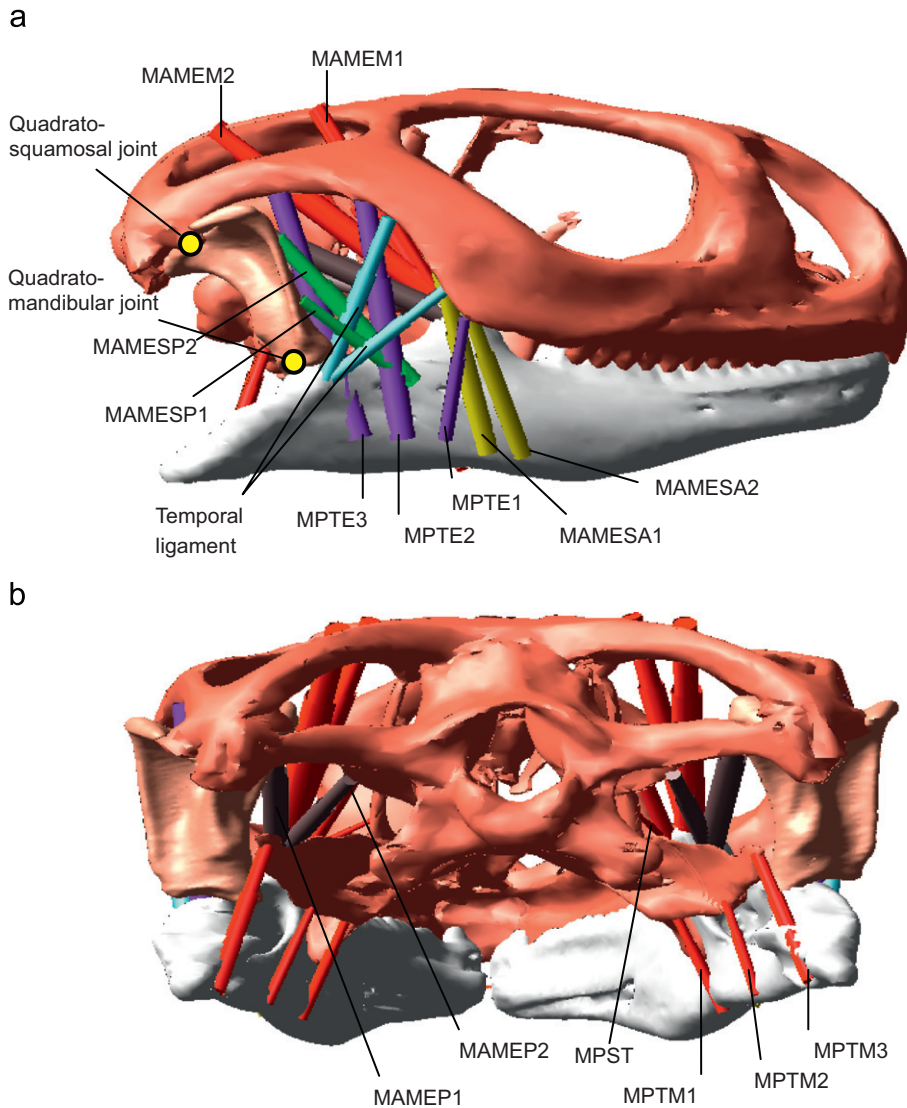


Fig. 1. (a) Lateral and (b) dorsal view of the *Uromastyx* model showing all muscle and ligament structures. The MPST is an internal muscle and its second section is not visible in this figure.

(van Eijden and Turkawski, 2001). A summary of the muscle PCSA, force and contraction velocity data is presented in Table 1.

The effect of the passive element was estimated according to Eq. (4) (Weijs et al., 1989):

$$F_p = 0.0014e^{6(L-L_0)/L_0} \tag{4}$$

The temporal ligament was divided into anterior and posterior sections (identified as *lig1* and *lig2*, respectively), and modelled as tension only springs (i.e. no compressive resistance), as defined by Eq. (5). A default stiffness value of 50 N/mm was assigned to each section of the ligament (*lig 1* and *lig 2*). This stiffness value was later varied in the stiffness sensitivity study (see Fig. 5). To the best of our knowledge no data are available on the stiffness of the lizard ligament, thus a value of 100 N/mm (sum of *lig 1* and *lig 2*) was chosen in accordance with other data in the literature (e.g. Noyes and Grood, 1976; Trent et al., 1976; Woo et al., 1991; Momersteeg et al., 1995; Kucuk, 2006).

$$F_{\text{ligament}} = \begin{cases} K \times (L - L_i), & L \geq L_i, \\ 0, & L < L_i, \end{cases} \tag{5}$$

where K is the stiffness of the ligament and L_i is the initial resting ligament length (i.e. at a gape of zero—see Fig. 1).

It was necessary to define a food particle for the biting simulations and this was represented by a resisting spring located between the teeth and defined by

$$F_{\text{bite}} = B \times (L - L_0) + C \times V, \tag{6}$$

where B ($= 50 \text{ N/mm}$) is the stiffness of the food and C ($= 9 \text{ Ns/mm}$) the damping ratio.

2.3. Simulations

Using realistic data for the *Uromastyx* specimens (e.g. Throckmorton, 1980; Herrel et al., 1998a, b) a motion driven analysis lasting 0.32 s was performed to open the jaw (jaw opening phase). A 50° rotation at the quadrato-mandibular joint (joint 1) and a 15° rotation at the quadrato-squamosal joint (joint 2) was applied during the opening phase, resulting in a gape angle of 35° [gape angle = joint 1–joint 2], as illustrated in Fig. 2; these movements agree with the literature (e.g. Throckmorton, 1976). The open jaw position was the start point for the forward dynamic simulations (biting simulations), in which a food bolus was in direct contact with the teeth (Moazen et al., 2007).

Muscle lengths $[L]$ (i.e. the distance between the muscle attachment on the cranium and the muscle attachment of the mandible) directly influence muscle forces as defined in Eq. (2). These muscle lengths along with their rate of change, or velocity (V) are measured by ADAMS and used to solve

Table 1
Muscle data used in the MDA modelling

Muscle group	Scaled PCSA (cm ²)	F_{max} (N/cm ²)	Scaled fibre length (cm)	V_{max} (mm/s)
MAMEM	0.353		0.120	17.520
MAMEM1	0.176	5.295		
MAMEM2	0.176	5.295		
MAMESP	0.274		0.144	21.024
MAMESP1	0.137	4.110		
MAMESP2	0.137	4.110		
MAMESA	0.230		0.064	9.344
MAMESA1	0.115	3.450		
MAMESA2	0.115	3.450		
MAMEP	0.187		0.096	14.016
MAMEP1	0.093	2.805		
MAMEP2	0.093	2.805		
MPTE	0.531		0.351	51.246
MPTE1	0.177	5.310		
MPTE2	0.177	5.310		
MPTE3	0.177	5.310		
MPTM	0.442		0.175	25.550
MPTM1	0.147	4.410		
MPTM2	0.147	4.410		
MPTM3	0.147	4.410		
MPST	0.051		0.032	4.672
MPST1	0.025	0.765		
MPST2	0.025	0.765		

the muscle force equations needed for the forward dynamic simulations in which ligament, joint and bite forces are calculated. An assumption in the muscle model is the optimum muscle length (L_0), which in the present research was defined as the length of the muscle fibres when the jaw was at a gape of 15° (through a combination of quadrato-squamosal and quadrato-mandibular joint rotations).

Dynamic simulations were performed during the jaw-closing phase, which assumed 100% muscle activation (i.e. $F_Q = 1$) and formed the biting simulations, during which two variables were assessed. First, the food particle was positioned between different teeth to investigate the effects on bite force and joint force, by moving it from the front of the mouth (incisiform tooth) to the back of the mouth (posterior teeth). The front, middle 1, middle 2 and back bite points were 2, 5, 13 and 18 mm from the tip of the mandible, respectively. Second, the temporal ligament stiffness was varied ($K = 10, 60$ and 100 N/mm) to help qualify its role and to assess the sensitivity of the model in relation to this parameter.

3. Results

Fig. 3 shows sample muscle forces applied during the jaw opening and closing phases. It was assumed that the jaw adductor muscles only became active during the jaw-closing phase of the simulations, thus force was only generated in the muscles after 0.32 s (after the jaw opening phase). During the jaw opening phase some sections of pterygoideus externus and pterygoideus medialis (MPTE 3 and MPTM 2 & 3) were compressed, and therefore assumed slack (i.e. no force generated), which meant that they were inactive during jaw closing.

Biting at the back of the mouth produced bite forces 72% larger than those at the front, while the quadrato-squamosal joint force (joint 1) decreased by 17% and quadrato-mandibular joint force (joint 2) decreased by 10% (see Fig. 4). In addition, shifting the bite point posteriorly in the mouth resulted in lower strain in the

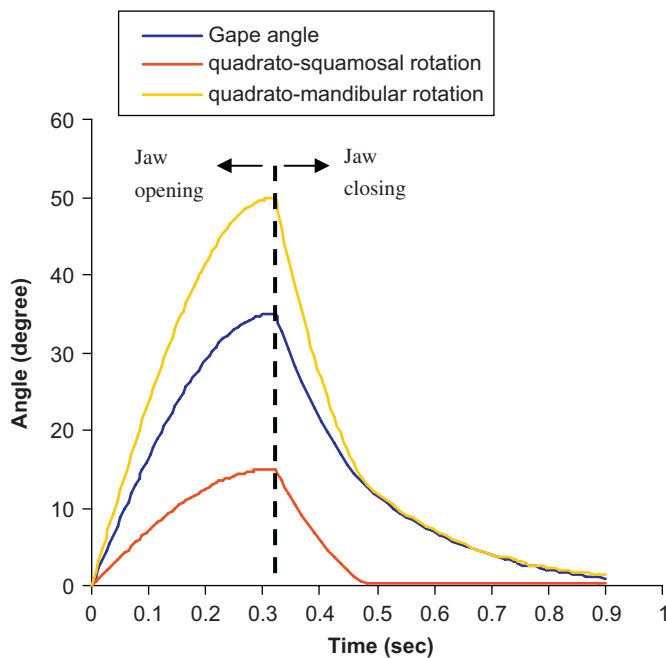


Fig. 2. Quadrato-squamosal, quadrato-mandibular and gape angles during one cycle of mastication.

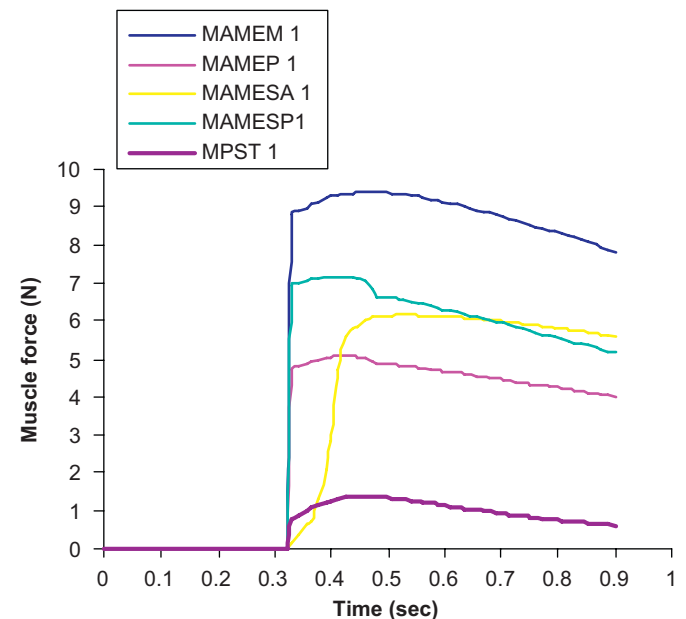


Fig. 3. Muscle force data versus time for selected adductor muscle sections. The muscles contract at maximum gape (time = 0.32 s, gape = 35°) and continue until the jaw closes (time = 0.9 s).

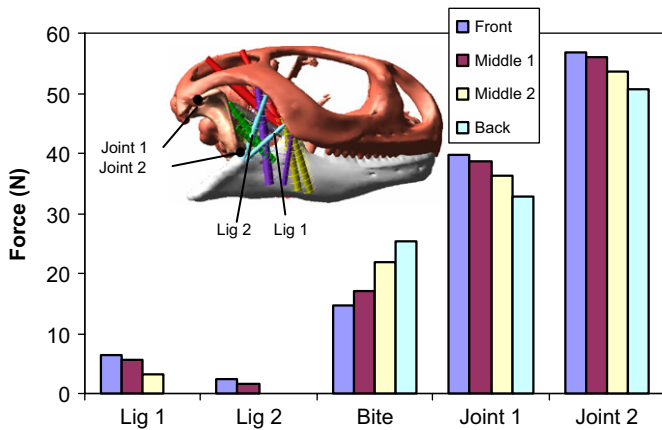


Fig. 4. Variation in the bite force, joint force and ligament force as a result of moving the bite point from the front of the mouth to the back. All values are taken at a gape of 10° and reported for the right hand side of the model.

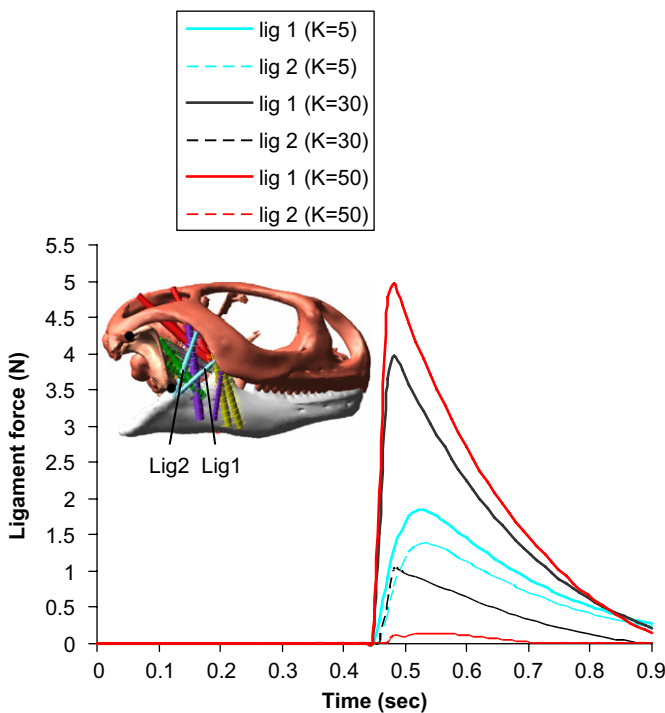


Fig. 5. Effect of varying ligament stiffness on the forces generated in the anterior (lig1) and posterior (lig2) portions of the temporal ligament during biting.

temporal ligament. Excluding the temporal ligament completely in the model caused the jaw to reach an unstable state at low gape angles. A temporal ligament stiffness of 10 N/mm added stability to the model at low gapes, where maximum forces of approximately 3.2 N were recorded within the temporal ligament. Increasing the stiffness of the temporal ligament to 60 and 100 N/mm did not alter the motions of the jaw during biting, but the maximum force generated within the ligament increased to approximately 5.0 and 5.1 N for the 60 and 100 N/mm stiffnesses, respectively (see Fig. 5). However, as the

stiffness of the ligament tissue was increased, the loading of the anterior and posterior sections varied. At a ligament stiffness of 10 N/mm both the anterior and posterior ligament sections were loaded similarly ($1.6 \pm 0.3 \text{ N}$), but at a stiffness of 60 N/mm the anterior portion carried 80% of the load, with this value increasing to 98% at a stiffness of 100 N/mm . In no bite position did the quadrates rotate forward rather than backwards (Herrel et al., 1998a, b).

4. Discussion

The aim of the present research was to perform an MDA on a lizard skull, in which biting simulations are conducted by applying varying muscle loads to predict ligament, joint and bite reaction forces. Past biomechanical models of the masticatory apparatus, such as those developed by Koolstra et al. (1988), Cleuren et al. (1995), Herrel et al. (1998a, b) and Sellers and Crompton (2004) have tended to represent muscle forces as a single working line based on the muscles' PCSA. In addition, researchers have traditionally applied the maximum muscle force at all gape angles (or never actually assumed a specific gape) even though normal force/length relationships of muscle fibres indicate that muscle forces will vary with gape. In the present study we developed a model applying new methods of muscle force application, where broad anatomical muscle attachment areas have been recreated by dividing muscle groups into multiple sections, where the number of sections depended on the size of the muscle. All muscles were divided into at least two sections, allowing the forces across the muscle to be assessed. This development has demonstrated that the forces throughout the muscle are not constant, and that some areas of the muscle may even be slack while others were stretched. During the jaw opening phase the MPTE 3 and MPTM 2 & 3 muscle sections were slack in our model, which meant that during the biting simulations the maximum muscle force was only applied to the active regions of the muscle (i.e. MPTE 1 & 2 and MPTM 1). Varying force within individual muscle groups is something that has been noted experimentally (e.g. Turkawski and van Eijden, 2001).

Inevitably there are approximations and simplifications in the model. Muscle wrapping was applicable around the mandible but not the cranium, and based on the work by Curtis et al. (2007) the difference in fibre length extensions during jaw movements between the wrapping and non wrapping fibres would be minimal. For this reason muscle wrapping was not simulated. The joints were defined as simple hinges, and if these hinge constraints were removed there would undoubtedly be increased instability in the model. Solving this instability would require the addition of extra soft tissue structures to limit joint motions, which may then influence the load carried by the temporal ligaments. This will be investigated in future MDA studies, allowing the effect of joint geometry to be assessed in more detail, with an interposed cartilage layer to dampen joint forces.

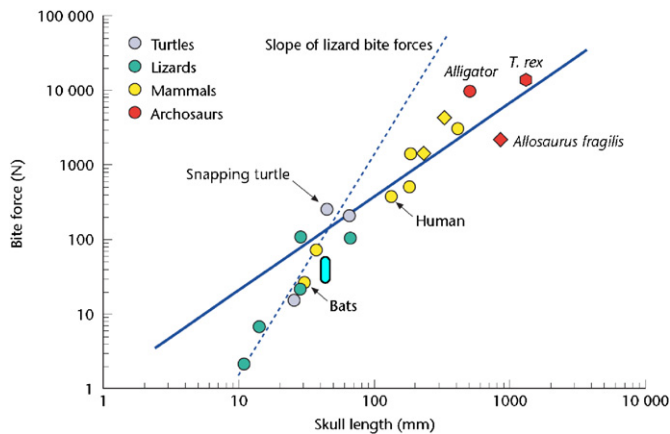


Fig. 6. Comparison of our bite force prediction (oval) and the force data taken from *in vivo* studies (circles), modelling studies (diamonds) and indentation studies (hexagons) for skulls of varying size (adapted from Herrel and Aerts, 2003). The oval shape represents bite forces at the front, middle 1, middle 2 and back positions of the mouth (see text).

For the *Uromastyx hardwickii* skull with a length of approximately 40 mm, the bite forces predicted using the MDA model (51 N) were comparable to those reported in the literature (Herrel and Aerts, 2003) (see Fig. 6). This is particularly encouraging since it has been shown here and by others (Sellers and Crompton, 2004) that bite forces are sensitive to location and direction of the food bolus. Validation is difficult, but the agreement between the motion and bite force data predicted by the MDA model and the values reported in the literature (Throckmorton, 1976; Herrel and Aerts, 2003) suggest that the model is reasonable. Since all the reaction forces (i.e. bite forces and joint forces) are calculated in direct response to the applied muscle loading, a state of equilibrium is reached in the MDA model. This is an added benefit when the data are used in subsequent finite element simulations, since zero reaction forces will be generated at the models' constraints.

Amongst lizard biologists the role and function of the temporal ligament has received increased attention over the last few decades (e.g. Frazzetta, 1962; Throckmorton, 1976; Iordansky, 1996; Herrel et al., 1998a, b; Wu, 2003). Modelling the temporal ligament and varying its stiffness allowed us to evaluate its function more closely. Data on the ligaments of lizards are limited; hence a sensitivity study was undertaken to assess the effect of ligament stiffness on the model's behaviour. We found that the total ligament loading was similar irrespective of the ligament stiffness (when the stiffness assessed ranged from 10 to 100 N/mm). It is clear that the temporal ligament plays an important stabilising role during biting, particularly at low gape angles. The absence of the ligament produced an unstable joint, and therefore our work agrees with others who state that the temporal ligament provides stability to the quadrates (e.g. Herrel et al., 1998a, b; Wu, 2003), while allowing some freedom of movement. Throckmorton (1976) noted that the ligament constrained posterior movement of the quadrate, and this was observed in our

model. However, according to Herrel et al. (1998a, b), food reaction forces may occasionally be directed forward rather than backwards in *Uromastyx*. Under those rare circumstances, the temporal ligament would be ineffective and the moments about the quadrate would tend to rotate it forward rather than backward during strong biting. None of our simulations induced this condition.

The advantages of using MDA in the study of the masticatory apparatus are clear, with detailed predictions of the varying loading environment, including muscle, ligament, bite and joint forces. Improving the realism in such models, for example, by adding more complex muscle activation data, will further refine the loading results and help in our understanding of skull function and development. In addition, the calculated loading conditions can be applied directly to finite element models, allowing detailed stress and strain distributions and their variations to be found at any point during that loading cycle.

Conflict of interest

The authors confirm that there is no conflict of interest in this manuscript.

Acknowledgments

The authors thank Mehrdad Moazen, Catherine Dobson and Anthony Herrel for their advice, and Jessie Maisano, University of Texas, Austin, Digimorph Laboratory, for the micro-CT data of the *Uromastyx*. We also gratefully acknowledge the financial support of BBSRC.

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