# INVESTIGATING THE BIOMECHANICS OF A LIZARD SKULL USING ADVANCED COMPUTER MODELLING TECHNIQUES WITH EXPERIMENTAL VALIDATION

Being a Thesis submitted for the Degree of PhD

In the University of Hull

By

Mehran Moazen, BSc (Hons)

December 2008

Dedicated to my parents

# Table of contents

Abstract	
Acknowledgements	
Contents	i
Chapter 1: Introduction	1
1.1 Overview	1
1.2 Model creation: geometry	4
1.3 Biomechanical modelling	5
1.3.1 Musculoskeletal modelling	5
1.3.2 Finite element modelling	7
1.4 Experimental validation study	7
1.5 Methodology	
1.6 Goals of project	9
1.7 Chapter organization	9
Chapter 2: Lizard anatomy	
2.1 Introduction	
2.2 General comments on lizards	
2.3 Morphological evolution	
2.3.1 Temporal openings	
2.3.2 Cranial kinesis	
2.4 Uromastyx	
2.4.1 Why is <i>Uromastyx</i> interesting?	
2.4.2 Lifestyle	
2.4.3 The dentition	
2.4.4 Cranial anatomy	

2.4.5 Cranial joints	18
2.4.6 Cranial muscles and ligaments	21
2.4.6.1 Muscle	21
2.4.6.2 Ligaments	22
2.4.7 Feeding	23
2.5 Discussion	24
Chapter 3: Literature review	25
3.1 Introduction	25
3.2 Bone	25
3.2.1 Bone structure	27
3.2.2 Mechanical properties of bone	28
3.2.2.1 Cortical bone analysis	29
3.2.2.2 Cancellous bone analysis	30
3.3 Sutures	31
3.3.1 Microscopic and macroscopic morphology of sutures	32
3.3.2 Mechanical property of sutures	33
3.4 Muscles	35
3.4.1 Skeletal muscle structure	35
3.4.2 Mechanical properties of muscles	37
3.4.2.1 Active and passive length-tension	38
3.4.2.2 Force-velocity	41
3.5 Experimental electromyography, cineradiography and bite force analysis	43
3.6 Strain gauge analysis	45
3.7 Free body diagram analysis and computer modelling of mastication	50
3.7.1 Free body diagram analysis	50
3.7.2 Basic computer model	52

3.7.3 Multi-body dynamic analysis	54
3.8 Finite element analysis of skulls	
3.9 Combined dynamic and finite element analysis of mastication	66
Chapter 4: Dynamic analysis of a lizard skull	
4.1 Introduction	68
4.2 Overview of ADAMS	68
4.3 MDA modelling of a <i>Uromastyx</i> skull	69
4.3.1 Study 1: Basic model development	70
4.3.1.1 Method	70
4.3.1.2 Results	74
4.3.1.3 Discussion	79
4.3.2 Study 2: Accurate geometry model	
4.3.2.1 Method	
4.3.2.2 Results	
4.3.2.3 Discussion	
4.3.3 Study 3: Accurate muscle model	
4.3.3.1 Method	93
4.3.3.2 Results	97
4.3.3.3 Discussion	100
4.4 Discussion	101
Chapter 5: Finite element analysis of a lizard skull	
5.1 Introduction	
5.2 Overview of ANSYS	104
5.3 FEA modelling of a <i>Uromastyx</i> skull	105
5.3.1 Study 1: FEA vs. combined FEA and MDA	105
5.3.1.1 Method	

5.3.1.2 Results	
5.3.1.3 Discussion	
5.3.2 Study 2: FEA modelling of biting	112
5.3.2.1 Method	112
5.3.2.2 Results	113
5.3.2.3 Discussion	
5.3.3 Study 3: Suture modelling	
5.3.3.1 Method	
5.3.3.2 Results	
5.3.3.3 Discussion	
5.3.4 Study 4: The role of the quadrate and temporal bar	
5.3.4.1 Method	
5.3.4.2 Results	
5.3.4.3 Discussion	
5.4 Discussion	
Chapter 6: Experimental validation of the finite element	: model 149
6.1 Introduction	149
6.2 Methods	149
6.2.1 Rapid prototype model	149
6.2.2 Dynamic Mechanical Analysis	151
6.2.3 Experimental strain analysis	
6.2.4 Coordinate measurement with the MicroScribe	154
6.2.5 Finite element modelling	154
6.3 Results	
6.3.1 DMA	
6.3.2 FEA	

6.3.3 Comparison of strain gauge result with FEA	
6.4 Discussion	
Chapter 7: Discussion	
7.1 Introduction	
7.2 Uromastyx	
7.3 Literature review	
7.4 Dynamic analysis of a lizard skull	
7.5 Finite element analysis of a lizard skull	
7.6 Experimental validation of the finite element model	
Chapter 8: Conclusions and future work	
8.1 Conclusions	
8.2 Future work	
References	
Appendix A: List of publications	
Appendix B: Published papers	

### Abstract

Lizard skulls vary greatly in shape and construction, and radical changes in skull form during evolution have made this an intriguing subject of research. The mechanics of feeding have surely been affected by this change in skull form, but whether this change in feeding is the driving force behind the change in skull shape is the underlying question being addressed throughout this project.

Here the skull of *Uromastyx hardwickii*, an akinetic herbivorous lizard has been analysed using advanced computer modelling techniques. This study aimed to perform a multibody dynamics analysis (MDA) on a biting lizard skull so that bite forces, joint forces, ligament forces and muscle forces could be accurately predicted. Then, using this MDA load data stresses and strains within the skull were assessed using finite element analysis (FEA). These FE analyses were used to assess biting performance and to test hypotheses that consider biomechanical optimization of bone as the main reason behind the modification of skull shape during its evolution. Sutures were modelled and their effect on skull strains was assessed through a series of investigative studies. Finally, representative basal skull forms were examined to highlight potential implications of specific skull variations. To assist in validation of the computational modelling experimental strain gauging was conducted.

The MDA provided detailed information on cranial biomechanics and associated cranial forces in this animal. It is believed that this technique will play a pivotal role in the analysis of skulls in the future and this study has demonstrated its definite potential. Cranial kinesis was seen to be mechanically significant in reducing joint reaction forces acting upon the skull, and specific groups of sutures (i.e. the frontal-parietal suture) in the *Uromastyx* skull played a substantial role in relieving strain compared to the other sutures, raising the questions about the original role of mesokinesis in squamate evolution.

# Acknowledgements

My deepest appreciation is extended to my mother Tayebeh Sarabi, and to my father Mehdi Moazen, who I deeply miss. I would like to express my sincerest thanks to my sister and brother, Shirin Moazen and Mehrdad Moazen, and my cousins, especially Behnam Moazen, along the rest of my family for their constant emotional and financial supports during my study. Indeed without them the completion of this thesis would have had no meaning.

I am forever indebted to my supervisor, Michael Fagan, for taking me on as a student, providing the opportunity to conduct this study and teaching me the skills required to be successful as a scientist. Thank you to Neil Curtis for his continuous support throughout all stages of the study, without him the completion of this thesis would not have been possible. Thank you Michael and Neil for being great mentors, teachers and friends. I greatly appreciate the advice and assistance of Susan Evans and Paul O'Higgins, who introduced me to the world of anatomy and exposed me to the fascinations of biology. You all taught me a great deal and I look forward to our continued personal and professional relationship.

I would like to express my gratitude to committee members Callum Ross and Sam Cobb for accepting the review of this project, and Philip Rubini for chairing the *viva voce*. Also special thanks is given to the six anonymous reviewers of the research publications, as their comments directly or indirectly improved the quality of the study.

I was very fortunate to have the support, advice and comments of: Mohammad Afshar, Ali Alazmani, Irene Alférez Cañavera, Omar Altuwaijri, Hamed Ariamatin, Shobeir Bavagharian, Jason Collier, Catherine Dobson, Tayebeh Esnaashari, Simin Farazmand, Laura Fitton, Grishma Desai, Maryam Ghavidel, Flora Groning, Bahman Hashemzadeh, Anthony Herrel, Mohammad Hojjati, Masoumeh Jahani, Hamed Mortazavi, Marc Jones, Kaveh Kabir, Janaka Karunanayake, Reza Khalaj, Konelius Kupczik, Steeve Lamvohee, Jia Liu, Sanaz Manouchehrian, Foad Najafi, Charles Oxnard, Olga Panagiotopoulou, Mike Park, Devi Putra, Ali Ranjbar, Jun Fen Shi, Amit Swamy, Sue Taft, Jassen Venkaya, Peter Watson, Ulrich Witzel, Gik Hong Yeap, the Engineering Department of the University of Hull, along with others who I have forgotten.

I would take this opportunity to thank the sponsors of this project namely Mehrdad Moazen and the University of Hull. Clinical Biosciences Institute of the University of Hull and The Anatomical Society of the Great Britain and Ireland travel grants, helped me to participate at two international conferences.

# Chapter 1: Introduction 1.1 Overview

The questions surrounding the homologies and significance of skull fenestration and emargination are not new, but remain largely unresolved because of the difficulty of examining them in any objective way. Despite this, questions repeatedly resurface in this area, with an example being the on-going debate on the relationships of turtles and where they fit in phylogenetic classifications (Rieppel and De Braga, 1996; Zardoya and Meyer, 2001). With this in mind it is vital that we understand and investigate the different factors that influence key skeletal traits amongst all living taxa.

Considerations about human phylogeny, as well as primate taxonomy, and diversity of human population are based on skull morphology in the majority of cases. It is important therefore to search for reasons for morphological differences among hominoids, including the evolutionary factors that have led to human and general primate evolution. It is generally assumed that biomechanical necessities play an outstanding role among the evolutionary factors. In the case of the postcranial skeleton, we certainly know that mechanical conditions play a significant role in the development of geometry. Yet still there is yet no definite proof that skull shape is optimized to withstand the mechanical stresses that occur in fulfilling its mechanical functions, which some say is due to the lack of sufficient tools that allow us to determine the stress and strain in these exceedingly complex biological structures (e.g. Preuschoft and Witzel, 2004a).

The present research is part of a larger project which aims to develop our understanding of the complex relationship between biomechanical forces, soft tissue structures and skeletal morphology, more specifically related to the optimization of the tetrapod skull. Tetrapod skulls must balance the conflicting demands of strength and stability with flexibility, so that maximum bite forces and maximum gape angles can be achieved without damaging the enclosed brain and other sensory organs. The skulls of early amniotes (i.e. animals having embryos with amniotic membranes) were fully roofed except for the orbits and nasal openings, but they evolved fenestration in serial lineages. Patterns of fenestration now play a pivotal role in the characterisation of amniotes (Figure 1.1).



Figure 1.1 Skull diversity in amniotes (Adopted from Barghusen and Hopson, 1979).

Despite the significance of temporal fenestration, there is little data on its origins, development, or biomechanical relevance. For many years, researchers identified fenestration as a way to increase muscle attachment areas, as well as permitting jaw muscles to bulge outwards on contraction (e.g. Romer, 1956). However, we are now testing hypotheses relating to the biomechanical significance of fenestrae and emarginations. This is an alternative explanation that defines fenestration as a consequence of biomechanical optimisation (maximum strength for minimum material), whereby bone is thickened and strengthened along stress trajectories, but may be lost from less stressed regions (e.g. Carrall, 1982; Preuschoft and Witzel 2002, 2005). This optimisation of form to biomechanical loading would aid mineral conservation as well as permitting a reduction in skull weight. Findings of the present research can be related to all tetrapods as well as other living organisms that have a hard bony skeleton. In addition, understanding the complex relationship between biomechanical forces, soft tissue structures and skeletal morphology is critical, not only to general biology (since it impacts on our use of the skeleton to infer relationships and life history) but also to medicine (e.g. bone repair and remodelling, over-use injuries and osteoporosis).

The latest generation of computational technologies provides an opportunity to build three dimensional (3D) models out of multiple two dimensional (2D) images (for example from micro-CT) in order to explore in detail the biomechanical characteristics of different skulls and to examine the development, adaptation and influence of a wide variety of variables. With the help of image processing techniques we are able to construct an exportable geometry that can be used in multibody dynamics analysis (MDA), which is a relatively new computer modelling technique. MDA can be use to model the external forces and internal musculature responsible for skull loading (e.g. Sellers and Crompton, 2004). The data obtained via MDA can then be applied to finite element (FE) models to calculate stress and strain across the skull. With these we can test hypotheses that relate skull architecture to patterns of stress produced by feeding and locomotion (e.g. Ross, 2005).

# **1.2 Model creation: geometry**

Computer-aided design (CAD) is a tool that was developed for the engineering world to create accurate geometric models of current and future products. A skull has an extremely complex geometry, which would be virtually impossible to construct using simple CAD methods. However, imaging techniques such as computed tomography (CT) and magnetic resonance imaging (MRI) can provide 2D images that can be transformed into 3D models (Figure 1.2). Different image processing software exists (e.g. AMIRA [Mercury systems, Germany], ScanIP [Simpleware Ltd., UK]), which digitally extracts the appropriate information from the images and reconstructs a 3D geometry by stacking the 2D images together. The 3D models can be modified depending on their intended application, for example meshed models for FEA and shell or solid models for MDA.



Figure 1.2 An example of creation of FE mesh model (Richmond et al., 2005).

### **1.3 Biomechanical modelling**

"Biomechanics is the science that examines forces acting upon and within a biological structure and effects produced by such forces" (Hay, 1973).

There are different modelling approaches in biomechanics. The simplest are conceptual models, which are used to illustrate a point without undertaking a detailed mathematical analysis (Alexander, 2003). An example of a conceptual model can be the comparison between human walking and a rolling egg, which rolls end over end on a level surface (Margaria, 1976). The second group of models are classed as physical models, which mostly aim to explore the mechanisms observed in a biological system. An example of this kind of modelling approach is the paper models of insect wings developed by Hass and Wootton (1996) to explain two mechanisms of folding that are used by many beetles and insects. The third type of models are mathematical models, which can be grouped into two major classifications: deformable elements (FEA) and rigid body representations (MDA). The work of Koolstra and van Eijden (2006) is a good example of a mathematical model and is a combined finite element and rigid body analysis developed to predict strain in the human temporomandibular joint cartilage during jaw movement.

The research described in this thesis applies mathematical modelling, and more specifically musculoskeletal modelling and finite element modelling, which are introduced below, and described in more detail in later chapters.

#### 1.3.1 Musculoskeletal modelling

A musculoskeletal model can be defined as a "unique representation of skeletal and muscular structure of human or an animal" (Konakanchi, 2005). In general, most musculoskeletal models aim to predict muscle forces, joint forces or other parameters that are difficult to measure mathematically or experimentally. The two methods used to calculate these unknown parameters are known as forward and inverse dynamic techniques (De Zee et al., 2007). In inverse dynamic analysis, the motion and external loads on the body are assumed to be known, and the purpose of the computation is to determine internal forces (e.g. muscle and joints forces). In the forward dynamic analysis it is the muscle forces themselves that produce the motions. Musculoskeletal modelling can also be termed computational testing, and has the advantage of overcoming limitations of *in vivo* experimentation.

Recently a number of musculoskeletal modelling packages have been developed to simulate systems consisting of bones, muscles, ligaments and tendons. Some software has being designed primarily for human analysis, for example ADAMS/LifeMOD (Santa Ana, USA), Anybody (AnyBody Technology, Denmark) and SIMM (MusculoGraphics Inc., USA) (Delp and Loan, 1995), while other packages such as Vertebrate Analyzer (VA, University at Buffalo) have been developed initially to model the behaviour of extinct species. Figure 1.3 depicts a typical example of the musculoskeletal softwares listed above.



Figure 1.3 Musculoskeletal model simulation performed within LifeMOD, AnyBody, and SIMM (Adopted from http://anybody.auc.dk and www.musculographics.com).

### 1.3.2 Finite element modelling

Finite element analysis (FEA) is a numerical technique that has been used extensively in structural engineering. It uses a mathematical model to mimic a real structure to a certain degree of approximations, and following a solution procedure estimates the stresses that are generated in the structure (Huiskes and Chao, 1983). FEA was developed in the 1950's for the aerospace industry, but has now been applied to many applications. In medical and biological applications it has also been used widely, for example, to understand the stress that bones are subjected to in the body, heat transfer and temperature patterns during heating and cooling of different cells and tissues, and or blood flow in arterial vessels. Therefore, FEA has a broad range of application to a number of engineering problems.

One of the key reasons for the extensive use of FEA is its versatility. There are virtually no restrictions to the geometry, boundary conditions, applied loading or material properties that can be considered. Thus, FEA provides solutions to problems that could not be solved otherwise. With the dramatic increase in computer efficiency, power and memory over the last few decades, the technique can now be used to solve very large complex problems. Many FEA software packages are commercially available (e.g. ANSYS [ANSYS Inc., USA], ABAQUS [ABAQUS Inc., USA]), making application of these techniques even more widespread.

# 1.4 Experimental validation study

Experimental validation is essential to test the accuracy of computational models. Strain gauge analysis is the most common method and was used in the present study to validate the strain distribution across a lizard skull, as described in Chapter 6. Other techniques such as electromyography and cineradiography are also used frequently in the validation of musculoskeletal models and have been considered as future work to continue this study.

# **1.5 Methodology**

Micro-CT data of a *Uromastyx hardwickii* skull (skull length ~44mm; skull width ~41mm) was supplied by the University of Texas, Austin in the form of a tiff image dataset. The dataset was imported into image segmentation software, which was used to extract the bony geometries through a segmentation process and to create accurate surface and solid models. The surface models were imported into motion simulation software as rigid-bodies for musculoskeletal modelling, while the solid models were imported into FEA software for stress analysis. Meanwhile to validate the FE results a validation study was performed on a rapid prototype model of the *Uromastyx hardwickii* skull. Figure 1.4 shows the methodology behind this study. Validation of the musculoskeletal modelling was not thoroughly investigated due to time limitations and lack of equipmental techniques.



Figure 1.4 Schematic diagram of the main steps involved in this study.

### **1.6 Goals of project**

The overall aim of the research that is being undertaken at the University of Hull is to gain an understanding of the complex relationship between biomechanical forces, soft tissue structures and skeletal morphology, particularly as it relates to the optimization of the skull in amniotes (the group that includes birds, reptiles and mammals). The key underlying hypothesis is that of Olson (1961), which states that changes in sensory, neural and feeding anatomies, individually or in combination, affect skull biomechanics and prompt a radical change in skull architecture, whereby the skull develops holes (fenestrae) and/or emarginations.

The first goal was to develop a method of performing MDA on skulls and more specifically to accurately model and simulate the bite forces and muscle forces acting on the skull/ mandible structure of a *Uromastyx hardwickii*. Then, using the information from these simulations we aimed to investigate the strain/stress distributions related to chewing and begin to test the hypothesis that biomechanical optimization of the cranial system is the main reason behind the modification of skull shape during the evolution of amniotes. Realism is vital in the computational studies, therefore developing an anatomically accurate muscle model for dynamic analysis, and including sutures in the finite element analysis were seen as important considerations. And lastly, validation of the biomechanical models was undertaken to demonstrate that FE can reliably predict the strains measured *in vitro*, and expected *in vivo*.

# **1.7 Chapter organization**

The thesis is organized as follows:

- Chapter 2 provides a review of the anatomical aspects of the project and more specifically of the lizard species chosen for this study (*Uromastyx*). It includes a general overview of lizards and a discussion on morphological evolution.

- Chapter 3 provides a general literature review of bone, muscle and sutures in terms of their structural and mechanical properties. There is a brief review of previous electromyography, cinerdiography, strain gauge analysis and bite force measurement studies, and the chapter ends with a review of previous computational modelling studies of skulls.

- **Chapter 4** describes all the computational multibody dynamics analyses conducted during this research. A brief introduction to the software is followed by detailed methods, results and discussions of the multibody modelling investigations. These investigations are divided into three sections and describe the *Uromastyx hardwickii* model development stages.

- **Chapter 5** describes all finite element analyses conducted during this research. A brief introduction to the software is followed by detailed descriptions of the studies conducted. The finite element studies are divided into four sections: (1) comparing this modelling approach to other approaches, (2) applying a full MDA loading cycle to an FE analysis and the analysis of the results, (3) investigation into the role of sutures and (4) an investigation into the function of the temporal bar in amniotes.

- **Chapter 6** describes an experimental strain gauge investigation and consequent validation study with the finite element model of the *Uromastyx* skull.

- **Chapter 7** provides a summary discussion of the whole research project. Major findings are highlighted and discussed.

- **Chapter 8** outlines final conclusions and points to future research and development in this area.

10

# **Chapter 2: Lizard anatomy**

### **2.1 Introduction**

Tetrapods (vertebrate animals possessing four leg-like appendages), which include Synapsida (mammals and lineages ancestral to mammals) and Reptilia (by modern definition including birds) together constitute the Amniota (Evans, 2003a). All living reptiles can be classified into three groups: Chelonia (turtles, tortoises), Archosauria (crocodiles and birds), and Lepidosauria (lizards, snakes and their relatives), with Lepidosauria possessing two subgroups, Rhynchocephalia and Squamata (see Figure 2.1 for a selection of Lepidosauria). Rhynchocephalia were once represented by many species, however today there are only two remaining species of tuatara (genus Sphenodon), which are endemic to New Zealand. Living squamates include over a 7000 species of lizards, snakes, and amphisbaenians and are distributed all over the world (Schwenk, 2000; Evans, 2003a). A full review of the squamata, or more specifically lizards in phylogenetic terms, evolution, and fossil history is beyond the scope of this thesis. However, some knowledge of this area would increase interest when interpreting the results of this research. Therefore this chapter reviews some general characteristics of lizards (e.g. size, body temperature and reproduction), the evolutionary modifications that occur in the cranium of amniotes, and the anatomical, functional and behavioral points of interest of Uromastyx (the lizard assessed in this study).

# 2.2 General comments on lizards

Lizards are generally small in size, but do vary in length from a few millimetres (geckos) up to several metres (Komodo dragon). Proportionally, most lizards have a small skull, a long vertebral column, short limbs, and a long tail. Behaviour though is hugely diverse amongst lizards; there are climbers (chamaeleons, geckos), facultative

bipedal runners (the iguanian genus *Basiliscus*), gliders (the agamid genus *Draco*, "Flying Dragons"), and ground dwellers (Evans, 2003a; Benton, 2005) (see Figure 2.1 for the diversity of the lepidosauria).

Lizards adopt behavioural means to control their body temperature since they do not have a direct, internal control to do so (ectotherms). Indeed when the sun rises, they move out of their hiding places and absorb heat, until they are warm enough to be active. When the temperature becomes too high they may shelter in a dark place, and at night, as their body loses heat they become inactive. Lizards are capable of operating efficiently over a range of body temperature (4-10°C), with an ability to conserve water, allowing them to live in hot, cold and arid regions (Adolph and Porter, 1993; Benton, 2005). "Most lizards are insectivores, but a few are herbivores, omnivores or durophages and some are active predators" (Evans, 2003a).

Most lizards lay eggs, with between 1 and 60 in a clutch depending on the species. Some lizards produce live young, but this differs from the live-bearing birth in mammals in that the mother lizard retains the eggs inside until they hatch. Typically lizards have short lives and in most species, individual lizards are unlikely to survive for more than 1-2 years (Benton, 2005).



Figure Sample (A) Sphenodon punctatus, 2.1 Lepidosauria Rhynchocephalia (www.ryanphotographic.com) (B) Uromastyx hardwickii, Agamidae (www.digimorph.org) (C) Iguana iguana, Iguanidae (www.animaldiversity.ummz.umich.edu) (D) Chamaeleo deremensis, (www.forestryimages.org) Eublepharis Chamaeleonidae **(E)** macularius, Gekkota (www.hilozoo.com) (F) Draco volans, Agamidae (www.magma.nationalgeographic.com) (G) Cnemidophorus tigris, Teiidae (www.classreptilia.com) (H) Varanus komodoensis, Komodo dragon, Varanidae (www.csus.edu).

### 2.3 Morphological evolution

## 2.3.1 Temporal openings

There are many variations between the skulls of Reptilia, and the evolutionary divergences from the primitive form have been divided into seven groups by Romer (1956): "(1) a reduction, fusion, modification, or increase in individual dermal elements, (2) changes in skull proportions, (3) changes in skull openings, (4) changes in the temporal (cheek) region associated with the action of the temporal muscles, (5) modifications of the palate, (6) variations in the occipital region and (7) variations in the ossification of the braincase." As mentioned in Chapter 1, patterns of fenestration (openings in the skull) now play a pivotal role in the characterisation of amniotes, with the recognition of four skull types (see Figure 2.2) the archaic anapsid type; synapsid with a single lower fenestra (e.g. mammals); diapsid with upper and lower fenestrae (e.g. birds, crocodiles, lizards); and parapsid with a single upper fenestra (extinct marine reptiles). Despite the significance of temporal fenestration, there is little data on its origins, development, or biomechanical relevance. Hypotheses do exist to explain these modifications, with early suggestions stating that the temporal openings were there to facilitate bulging of temporal muscles during their contraction (Romer, 1956; Porter, 1972). However, current thinking is that the temporal openings represent a form of biomechanical optimization (maximum strength for minimum weight) (e.g. Carroll, 1982; Preuchoft and Witzel, 2005). One other suggestion is that the transition from a flat amphibian skull to a higher and narrower amniote skull could alter the mechanical properties or requirements of the skull. Amphibians probably forced air into the lungs by contracting the floor of the mouth (buccal breathing), therefore flattening the skull enlarges the capacity of the mouth and facilitates respiration, whereas the high, arched amniote skulls provide greater strength and were permitted by the transition to thoracic breathing (Porter, 1972).



Figure 2.2 Major lineages of cranial evolution within amniotes. Abbreviations: jugal (J), parietal (P), postorbital (Po), quadratojugal (Qj), squamosal (Sq) (From Kardong, 2002).

#### 2.3.2 Cranial kinesis

The independent movement of the bony sections of the skull is termed cranial kinesis, and is seen in some lizards but is particularly prevalent in snakes. There are four main forms of cranial kinesis: (1) Metakinesis; this involves articulation based on five primary contact points, the supraoccipital and parietal in the midline (one contact), the paroccipital processes and skull roof bilaterally (two contact points), and the basipterygoid processes and palate (pterygoids) bilaterally (two contact points). Flexion about a transverse axis is defined by the lateral articulations of the paroccipital processes with the upper temporal arches (Evans, 2003a). (2) Mesokinesis; this involves dorsoventral movement about an axis that runs between the frontal and parietal bones of the skull roof, with compensatory hinges in the palate and postorbital region. (3) Prokinesis; this involves movement about an axis that runs between the frontal (integrated with the braincase) and nasal bones. (4) Streptostyly; this involves the movement of the quadrate on its dorsal articulation with the squamosal. Strepostyly is mainly anteroposterior, but some lateral flexion

might be possible in some species (Schwenk, 2000). See Figure 2.3 for a schematic of the separation of cranial bones over the evolution of Lepidosauria and the different types of cranial kinesis. Cranial kinesis is another fascinating example of functional morphology, which has dominated discussions of squamate evolution for a long time (e.g. Frazzetta, 1962; Iordansky, 1990; Metzger, 2002).

Metzger (2002) divided the functional significances of streptostyly into three major categories: (1) providing increased mechanical advantage to components of the adductor musculature, (2) increasing the gape angle and (3) facilitating food processing. He also discussed various hypotheses regarding mesokinesis including: (1) shock absorption during biting, (2) finer control during prey prehension and (3) increase of the gape angle. However, there are some doubts surrounding the consequences of having kinetic skulls, with Herrel et al. (2007) showing that a kinetic skull can also lead to reduction in bite force.



Figure 2.3 (A) illustrating separations of cranial bones over the evolution of Lepidosauria. The epipterygoid (E) is pale grey; the quadrate (Q) in darker grey; the pterygoid (P) is uncoloured while the dark grey colour of the lowest mesokineic skull shows the antorbital maxillary segment (Adopted from Evans, 2003a). (B) Illustrating different types of cranial kinesis in squamates (Adopted from Kardong, 2002).

Temporal openings and cranial kinesis are two major patterns observed in the evolution of amniotes, and the function of streptostyly and mesokinesis are of particular interest to this project (see for example the results of studies 3 and 4 in Chapter 5).

# 2.4 Uromastyx

As discussed previously, Squamata is the group that incorporates lizards, snakes, and amphisbaenians. A subdivision of Squamata includes Iguania, which in turn houses the family of Agamidae, to which *Uromastyx* belongs (Evans, 2003a).

#### 2.4.1 Why is Uromastyx interesting?

Amongst agamids, *Uromastyx* is generally considered to be one of the two basal genera (the other being *Leiolepis*), and as such offers a good starting point for biomechanical investigations. *Uromastyx* is interesting for a number of reasons: (1) it is primarily herbivorous; (2) it has a specialised arrangement of pterygoideus muscles; (3) it has a skull that shows streptostyly; (4) it has been quiet well described in the literature (e.g. El-Toubi, 1945; Islam, 1955; Throckmorton, 1976; Herrel, 1998; Evans, 2008)' and (5) it is a good animal for studying evolutionary changes in amniote skulls, by comparing against, for example, *Sphenodon* (e.g. absence of the lower temporal bar).

### 2.4.2 Lifestyle

*Uromastyx* is a desert lizard found in rocky and sandy regions such as North Africa, the Middle East, India, Afghanistan and Pakistan. Over fifteen species are currently recognised, of which *U. aegyptius* (Egypt), *U. acanthinurus* (Morocco), and *U. hardwickii* (India, Pakistan) may be among the more familiar. They have a strong, thick body with a thick and muscular spiny tail which can be swung at an attacker,

and posess powerful claws which they use to create large spiral burrows. Adults vary in size, from a total length (including tail) of 145 mm up to 1 m. Young *Uromastyx* feed predominantly on invertebrates while adults incorporate a high degree of plant material into their diet, being almost fully herbivorous (Evans, 2003b).

### 2.4.3 The dentition

In terms of dentition *Uromastyx* has a wholly acrodont dentition, meaning that the apex of the root of each tooth is fused to the jaw bone (Robinson, 1976). The teeth occlude precisely like the blades of scissors or 'pinking shears'. The bite is particularly powerful in *Uromastyx* where the complex pterygoideus muscle is believed to make a significant contribution (Evans, 2003b).

#### 2.4.4 Cranial anatomy

The skull of *Uromastyx* shows the features of a typical agamid lizard, namely "reduced single premaxilla; strong anterior maxillary contact behind the premaxilla; single frontal and parietal with wide frontoparietal suture; strong preorbital pillar (prefrontal-palatine contact); palate palaeochoanate (i.e. without separation of the vomeronasal opening from the choana); and braincase exposed in dorsal view" (Evans, 2003b). Figure 2.4 and 2.5 describe the anatomical bones of the skull of a *Uromastyx hardwickii*, a diapsid skull.

#### 2.4.5 Cranial joints

In *Uromastyx* the cranial joints are mainly butt joints (where bones meet at a flat face perpendicular, or near perpendicular, to the long axes of the bones); scarf joints (where bones partially overlap), or recessed versions of each of these where one bone 'plugs' into another, or fits like a tongue-in-groove. These joints range from very strong articulations (e.g. along the skull roof, frontal-parietal [frontal median process

fitting into a notch in the parietal, and the bilateral frontal edges being received into recesses in the parietal], jugal-maxilla) to light contacts (e.g. postorbital-parietal, jugal-squamosal).



Figure 2.4 Lateral (A) and posterior (B) views of the skull of *Uromastyx hardwickii* illustrating the anatomical names of the skull (From Evans, 2003b).



Figure 2. 5 Dorsal (A) and ventral (B) views of the skull of *Uromastyx hardwickii* illustrating the anatomical names of the skull (From Evans, 2003b).

#### 2.4.6 Cranial muscles and ligaments

#### 2.4.6.1 Muscle

The muscle systems that produce movement of the mandible are relatively complex in *Uromastyx*. Overall they can be divided into two groups based on their function in depression or elevation of the mandible. The main depressor mandibulae muscle is situated behind the head and arises from the posterior edges of the parietal and squamosal bones and from the fascia covering the neck and the adductor muscles (Throckmorton, 1976).

The jaw adductor muscles are classified into six groups by Throckmorton (1976): (1) muscles that arise from the temporal fossa of the skull and insert into the bodenaponeurosis, a tendinous connective tissue, (MAMEM: adductor mandibulae externus medialis); (2) the superficial portion of the pterygoideus muscle (MPTE: pterygoideus externus); (3) muscles that arise from the lateral temporal fenestra and insert into the lower jaw (MAMESA: adductor mandibulae externus superficialis anterior); (4) muscles that arise from the quadrate bone and insert into the lower jaw (MAMESP: adductor mandibulae externus superficialis posterior; and MAMP: adductor mandibulae externus profundus); (5) deep portion of the pterygoideus muscle (MPTM: pterygoideus medialis); and (6) fibres that arise from the epipterygoid bone and insert into the lower jaw (MPST: pseudotemporalis superficialis). Figure 2.6 shows the main groups of jaw adductor muscles in *Uromastyx acanthinurus*, which has been labelled based on the above classification. These muscles are the ones used in the computer models developed in this research (see Chapters 4).

#### 2.4.6.2 Ligaments

There are two main ligaments that aid in stabilization of the quadrate and are involved during general mastication in *Uromastyx*. The first ligament is named the quadratopterygoid ligament and is a thick ligament connecting the dorsal part of the quadrate ramus to the pterygoid. The second ligament is named the quadratomaxillary (temporal) ligament, and is a thick triangular ligament sheet that connects the ventral half of the posterior edge of the jugal to the end of the quadrate and the lateral surface of the mandibular joint. Figure 2.7 shows these ligaments in the skull of *Uromastyx aegyptius* from a study that was conducted by Throckmorton (1976).



Figure 2.6 The jaw adductor muscles in *Uromastyx acanthinurus*. MPtext or MPTE, m. pterygoideus externus; MAMESA, MAMESP, mm. adductor mandibulae externus superficialis anterior and posterior; MAMP, m. adductor mandibulae posterior; MPsTS or MPST, m. pseudotemporalis superficialis; MAMEM, m. adductor mandibulae externus medialis; MPTmed or MPTM, m. pterygoideus medialis (Adopted from Herrel, 1998).



Figure 2.7 (A) illustrating the quadratopterygoid ligament connecting pterygoid (p) to quadrate (q). (B) illustrating the quadratomaxillary ligament (QML) connecting jugal to quadrate. Note EA, SP and EP show the anterior, posterior and superficial portion of the external adductor of the *Uromastyx aegyptius* (From Throckmorton, 1976).

### 2.4.7 Feeding

Prey capture starts by a slow jaw opening during which the tongue begins to protrude. Next, in what is commonly called the fast opening phase, the tongue is protruded completely at the same time as the depressor mandibulae and the deep portion of the pterygoideus muscle are active. This causes the gape angle to rapidly increase while the upper and lower jaws move away from each other and the quadrate moves anteriorly. Following retraction of the tongue, the next stage is named the fast closing phase, during which the jaw adductor muscles are active and gape angle decreases rapidly as the elevation of the mandible, depression of the head and posterior movement of the quadrate take place simultaneously (Throckmorton, 1976, 1980). Once the jaws touch the prey, the closing speed decreases and the slow closing/power stroke phase starts. This is a stage that is often absent during prehension cycles in *U. acanthinurus* (Herrel et al., 1999a). Thorockmorton (1976) observed a mean gape of  $31.3^{\circ}$  with a standard deviation of  $8.7^{\circ}$  and a maximum of  $25^{\circ}$  anterior rotation of the quadrate during jaw opening, and he pointed out that the gape angle is a combination of the rotation around the mandibular joint and the quadrate-squamosal joint.

### **2.5 Discussion**

The purpose of this chapter was to introduce squamates and to identify the high degree of skull variation and complexity among amniotes in general. Here we have focused on *Uromastyx* and highlighted certain features that form part of the computational modelling studies described later in this thesis. For example:

- temporal openings: Uromastyx shows upper temporal fenestration.

- cranial kinesis, and more specifically streptostyly and mesokinesis: *Uromastyx* shows streptostyly and our simulations investigate mesokinesis.

- cranial osteology and myology of *Uromastyx*: necessarily for the construction of the MDA and FEA models (Chapters 4 and 5).

A broader overview of other aspects of this project are provided in Chapter 3.

# **Chapter 3: Literature review**

# **3.1 Introduction**

This chapter reviews the key literature associated with the present research project. The main areas of investigations are structural anatomy and function, experimental studies and computational modelling studies. Computational modelling of the masticatory system is the focus of this study, and clearly therefore we must be aware of the relevant anatomy. Bone, sutures and muscles are reviewed briefly in terms of their structure, morphology and mechanical properties. Experimental studies involving electromyography, cineradiography, bite force analysis and strain gauge analysis are reviewed, and finally previous skull modelling studies are summarized, including analysis by simple free-body diagrams, more sophisticated multibody dynamic analysis (MDA) and finite element analysis (FEA). Figure 3.1 gives an overview of the structure of this chapter.

### 3.2 Bone

Bone is a hard, dense tissue that provides structural support for the body and protection for internal organs. Information on skeletal processes, microscopic structures, mechanical adaptation and failure criteria of bone is widely available in the literature, however only an introduction to general structural components and mechanical properties of bone is included here, to provide some context to the modelling of the skull.

	Bone -structure -mechanical properties a) Cortical bone b) Cancellous bone
Fundamental studies	Suture -structure -mechanical properties
	Muscle -structure -mechanical properties a) Active and passive length-tension b) Force-velocity
	Strain gauge analysis
Experimental studies	Electromyography, cineradiography and bite force analysis
	Free body diagram basic computer models and multibody dynamic analysis (MDA)
Modelling studies	Finite element analysis (FEA)
	Combined MDA and FEA


### **3.2.1 Bone structure**

Bones vary considerably in size and shape but in general four principal types exist, namely: long (e.g. bones of the leg and arm), short (e.g. bones of the wrist and ankle), flat (e.g. bones of the cranium) and irregular (bones that do not fall into any of the other three categories). Despite the variety in bone shape, the morphology of bone at the organ, tissue and cellular levels is relatively consistent. Figure 3.2 illustrates the structural components of a long bone. The ends are called epiphyses and are the regions which articulate with other bones and for this reason are protected by articular cartilage. The area between the two ends of a long bone (i.e. the shaft) is called the diaphysis, and is a hollow tube like structure surrounding the medullary cavity. The medullary cavity is used for storage of fat and is lined by a thin, cellular connective tissue membrane called the endosteum. Flat bones do not have a medullary cavity. All bones are surrounded by a periosteum, which is a tough, vascular, fibrous tissue (Nigg and Herzog, 1999).

At a gross level all bones have two basic components: cortical and cancellous bone. Cortical (or compact) bone is a dense, solid mass with microscopic channels, which forms the outer wall of bone. Cancellous (or spongy) bone is a lattice of large plates and rods known as trabeculae, found in the inner parts of some bone. It is also noteworthy that these trabeculae orient themselves in the direction of the forces applied to the bone (e.g. Townsend et al., 1975; Fung, 1993; Mittra et al., 2005). Distribution of cortical and cancellous bone varies between individual bones but approximately 80% of the skeletal mass in an adult human skeleton is cortical bone (Jee, 2001).



Figure 3.2 Illustrating important features of a typical long bone (From www.web-books.com).

## **3.2.2** Mechanical properties of bone

Bone has a basic stress-strain relationship as do all structural materials, but because bone is a living organ its strength varies with the age, sex, location, the orientation of the load, and the test condition (whether it is dry or wet). The cortical and the cancellous elements differ in strength and elastic modulus (cancellous bone has much lower strength than cortical bone (Fung, 1993)). Figure 3.3 shows a comparison between the ultimate stress of cancellous and cortical bone. This combination of stiff and soft materials makes bone a non-homogeneous and anisotropic material, meaning that its properties vary in different directions.

Different techniques have been used in the measurement of bone properties; in early studies, traditional mechanical testing such as uniaxial tensile, compressive and three-point bending were applied, whereas in more recent times techniques such as ultrasound and nanoindentation are being used increasingly because they require less material and can measure directional effects. Below is a summary of some of these techniques.



Figure 3.3 A comparison between the ultimate stress of cortical and cancellous bone (From Nigg and Herzog, 1999).

#### **3.2.2.1** Cortical bone analysis

Some of the earliest studies into the mechanical properties of cortical bone are reported by Ascenzi and Bonucci (1964, 1967, 1968, and 1972). These studies involved the extraction of cylindrical samples of single osteons from human femurs, whose deformations were recorded under incremental loading. Their results showed a variation in mechanical properties caused by the microstructure of the cortical bone. Some of the most recent research in this area has been performed by Wang et al. (2006) and Wang and Dechow (2006). These studies analysed cylindrical samples of cortical bone from monkey skulls using ultrasound techniques (see Figure 3.4), allowing the elastic properties in three dimensions to be determined. They looked at different species of monkeys to investigate their hypothesis that closely related species would have similar distributions of bone properties. Based on their results they concluded that reasonable estimates of cortical bone properties should be possible for extinct species through the study of phylogenetically related and functionally similar modern forms. They found that, in general, cortical bone exhibits anisotropic elastic properties. See Figure 3.5 for a summary of the mechanical properties of human and monkey (macaque) cortical bone.



Figure 3.4 Location of cortical specimen used in study of Wang and Dechow (2006) in lateral view (Adopted from Wang and Dechow, 2006).

	V	al	Tor		Zyg		Alv		Muz	
	Macaque	Human								
Density (mg/cm <sup>3</sup> )	1699	1805	1513	1766	1641	1753	1630	1667	1685	1785
Thickness (mm)	2.06	2.49	2.81	2.43	1.84	2.20	1.88	1.98	1.75	1.48
$E_1$ (GPa)	10.2	13.0	9.7	12.4	8.6	11.5	11.7	9.8	11.2	11.7
$E_2(GPa)$	13.3	14.3	10.4	13.8	11.2	12.0	14.0	9.0	14.0	12.2
$E_3$ (GPa)	17.0	19.9	13.7	19.2	17.5	22.0	18.6	17.7	19.0	22.0
$G_{12}(GPa)$	4.2	4.5	3.8	4.3	3.7	4.0	4.8	3.3	4.6	3.6
$G_{31}(GPa)$	5.3	4.9	4.9	4.8	4.6	4.5	6.0	3.8	5.9	4.1
$G_{23}(GPa)$	7.6	6.7	5.5	6.4	7.6	6.1	7.8	4.6	7.6	5.7
$v_{12}$	0.41	0.47	0.39	0.46	0.43	0.51	0.33	0.40	0.33	0.38
$v_{B13}$	0.27	0.22	0.19	0.20	0.29	0.17	0.24	0.32	0.22	0.31
$v_{B23}$	0.18	0.23	0.20	0.23	0.21	0.18	0.15	0.47	0.19	0.52
$E_2/E_3$	0.79	0.70	0.77	0.70	0.64	0.55	0.76	0.51	0.73	0.57

Figure 3.5 Summary of thickness and elastic properties of external cortical bones in macaque and human skull. Abbreviations: Val-Vault; Tor-Supraorbital torus; Zyg-Zygomatic arch; Alv-Alveolar area; Muz-Muzzle; E<sub>1</sub>, E<sub>2</sub>, E<sub>3</sub> relate to principal Young's modulus; G<sub>12</sub>, G<sub>31</sub>, G<sub>23</sub> relate to principal shear modulus;  $v_{B12}$ ,  $v_{B13}$ ,  $v_{B23}$  relate to principal poisson's ratio (Adopted from Wang et al., 2006).

#### **3.2.2.2 Cancellous bone analysis**

Porosity and the small dimensions of individual trabeculae within the cancellous bone makes analysis difficult, however, many studies have still been performed on bulk cancellous bone. The study by Townsend et al. (1975) is one of the earliest exploring anisotropy of cancellous bone. They performed compression testing on human patella (knee caps) samples, where cubes of bone were cut from articular and non-articular regions of the patella. The elastic modulus of the cancellous bone was measured in anterior-posterior, proximal-distal and lateral-medial directions, and from which they concluded that the anisotropy of the stiffness was related to the changing direction of the basic structural unit. Giesen et al. (2001) explored the effect of loading direction and bone density parameters on the elastic and failure properties of cancellous bone. They tested this concept on a human mandibular condyle by performing uniaxial compression tests on cylindrical samples. Their conclusions were that cancellous bone is stiffer in axial loading compared to transverse loading, and that its anisotropic mechanical properties can possibly be considered as a mechanical adaptation to the *in vivo* loading condition.

In summary, bone is anisotropic and varies throughout an individual skull. Ideally this anisotropy and spatial variation should be included in any finite element analysis of a skull. However, it is not feasible to find that information for an individual skull to a sufficient level of detail to warrant its inclusion in a finite element model, and certainly not possible for the normally very small *Uromastyx* skull. Incorporating variable property values from the work of others, such as Wang et al. (2006) is likely to introduce artefacts into the results which aren't actually there. Furthermore, in reality the properties will vary smoothly across a skull, but in a model they will have to define over discrete volumes, again resulting in a discontinuity between different regions of the model. This is mentioned further in the specification of the finite element model in Chapter 5.

# **3.3 Sutures**

There are different definitions for the term "suture". Gray's Anatomy (Goss, 1959) defines it as "an articulation in which contiguous margins of adjacent bones are united by a thin layer of fibrous tissue." Wagemans et al. (1988) refer to suture as "the entire complex of cellular and fibrous tissues lying between, and surrounding the edges of, two skull bones, and including the bony edges." Overall, sutures are connective joints that facilitate the longitudinal growth of the majority of bones in

the skull and possibly relieve part of the stress generated during biting. Below is a brief review on structure of sutures and their mechanical properties.

## **3.3.1** Microscopic and macroscopic morphology of sutures

In general the facial and cranial bones of the vertebrate skull are of intramembranous origin where growth happens by apposition and resorption at the periosteal surfaces during sutural growth. The microscopic structure of sutures, and sutural histology was reviewed by Wagemans et al. (1988), which discusses the most widely accepted theory of Pritchard et al. (1956). Pritchard et al. recognized five distinct layers of cells and fibres, two cambial and two capsular layers of the periosteum of each adjoining bone separated by a middle vascular layer (see Figure 3.6). With maturation, the cambial layer reduces to new layers of bone, the capsular layer thickness reduces, and its fibres direction become parallel to the sutural faces of the bones, while the middle layer becomes increasingly vascular (Cohen, 1993).



Figure 3.6 Diagram to illustrate the general construction of a suture (From Pritchard et al., 1956).

In terms of the macroscopic morphology of sutures, sutures initially have straight edges of bone separated by connective tissue. Interdigitations develop gradually with increasing age, becoming more irregular until fusion of opposing bony edges occurs. Very basic classifications of the shapes of the bony edges of sutures can be made, with so called end-to-end (or butt, flat, or plane) and overlapping (or beveled or squamous) forms (Wagemans et al., 1988). Herring (1972) was one of the first to propose that sutural morphology and fusion are affected by stress distribution, and therefore that different sections of the skull experience different stresses. Figure 3.7 shows an example of this classification in a fish skull. Also, a study by Kathe (1995) attempted to classify different types of sutures according to their shape and surface topology among amphibians and reptiles (see Figure 3.8).

## 3.3.2 Mechanical property of sutures

From the complexity and variety of sutural forms it is evident that it is likely to be difficult to measure their mechanical properties. However, their presence and form indicate that their inclusion in computational stress/strain modelling studies is probably important. Previous studies that have focused on the measurement of mechanical properties of sutures will be reviewed in this section.



Figure 3.7 Example of end-to-end and overlapping sutures in a fish skull (From Markey et al., 2006).



Figure 3.8 Schematic profiles of different sutural types in the dermal skull roof of Amphibia and Reptilia. A "Lamellae" and B "Basal Lamellae" are characterized by the presence of ornamentation, usually consisting of regular ribs. C "Shelf" and D "Basal Shelf" refer to subjacent areas entirely or largely lacking ornamentation. E "Steep Bevel" and F "Vertical Wall" sutures with steep bevels or vertical walls. G "Groove" occur when one bone is forming a longitudinal process along side of articulation and H "Plug-Contact" consist of a transverse process formed by one bone-element, exactly fitting into a wrap-process in the adjacent bone (From Kathe, 1995).

McLaughlin et al. (2000) measured the load-displacement characteristics of the sagittal, coronal and posterior frontal sutures in 7 day old rats, reporting Young's modulus values of 13, 14 and 2.3 MPa respectively, with a mean tensile modulus for all sutures of 10 MPa. Similarly, Radhakrishnan and Mao (2004) measured the elastic moduli of three rabbit facial sutures, the zygomaticotemporal, nasofrontal and pre-maxillomaxillary finding an average Young's modulus of 1.20, 1.16 and 1.46 MPa respectively. These studies show that structural differences exist between different cranial sutures, and that mechanical properties of sutures vary between different animals. Henderson et al. (2005) studied the effect of age on the mechanical properties of sutures, measuring the Young's modulus of the sagittal sutures of rats aged 2 to 60 days old. They also pointed out that measurement of Young's modulus is dependent on the cross-section of the structure, thus varied Young's modulus values will be obtained. They reported elastic moduli of 9.24 to 27 MPa based on the thickness of suture (only the bone) and 4.72 to 13 MPa when considering the thickness of suture and its surrounding fibrous tissue.

All the evidence suggests that sutures play an important role in skull biomechanics. However, exactly how they modify the stress distribution through the skull is not obvious, but can be explored by finite element analysis – as described later in this thesis. Suture geometry is frequently very complex, therefore some simplification was necessary before inclusion in the FE model of *Uromastyx*, as discussed in Chapter 5, the results of which provide some useful insights into the role of sutures and skull biomechanics in general.

# **3.4 Muscles**

Muscles are the structures that produce force and are responsible for the movement of the body. A description of muscle anatomy can help us understand the mechanical attributes of muscle function. Muscles are classified functionally into three groups: skeletal, cardiac and smooth. The focus of this review is on skeletal muscle.

### **3.4.1 Skeletal muscle structure**

Skeletal muscles are attached to bones (sometimes via tendinous structures) and are responsible for skeletal movements. They are predominantly made up of striated fibres but can vary greatly in size, shape and fibre arrangement, with their activation controlled by the central nervous system. Figure 3.9 shows a schematic of the structure of skeletal muscle.

Dividing the skeletal muscle into its components, we start with the whole muscle body, which itself is covered by a membranous tissue called the epimysium. The muscle body is divided into bundles of fascicles, which themselves are made up of bundles of muscle fibres that are surrounded by a sarcolemma membrane. The individual muscle fibres contain myofibrils that are about  $1\mu m$  in diameter. Myofibrils are mostly made up of the two proteins, actin and myosin, but do contain a small proportion of other proteins. At an even more basic level, myofibrils can be divided into subunits known as sarcomeres, which are the functional units of muscle contraction. Sarcomeres contain "Z Lines" (or discs) at their ends, which give support to the muscle laterally, and from the Z lines running towards the centre of the sarcomere are actin filaments; these filaments do not extend the whole length of the sarcomere. The area with only actin is known as the I band. Myosin filaments run through the middle of the sarcomere, but do not extend to the Z lines at either end, they are held in place by other proteins in the "M Band", located in the centre of the sarcomere. The area with only myosin is known as the H Band, and the area where the actin and myosin overlap is known as the A Band (Lieber, 1999).



Figure 3.9 Structural hierarchy of skeletal muscle (From http://www.uoguelph.ca).

## 3.4.2 Mechanical properties of muscles

The mechanical properties of skeletal muscle can be divided into three elements: (1) an active length-tension element, (2) a passive length-tension element and (3) a force-velocity element. The active length-tension element arises from the overlap of the actin and myosin filaments. The passive length-tension element is traditionally believed to be related to the outside of the actomyosin cross-bridge, however others (e.g. Magid and Reedy, 1980; Labeit and Kolmerer, 1995; Linke et al., 1998) have

identified a protein named "titin" within the myofibrils and state this is responsible for the passive tension. The force-velocity element can be interpreted as the muscle fibre or sarcomere force-velocity relationship. In general, the mechanical properties of muscles depend strongly on the intrinsic properties of muscle fibres and the extrinsic arrangement or architecture of the muscle groups. Muscle architecture can be described in terms of muscle mass, length, physiological cross sectional area (PCSA) of the muscle fibres and pennation angle (i.e. the angle between the line of action and the muscle fibres) (Lieber, 1999).

#### **3.4.2.1** Active and passive length-tension

Studies by Nordstrom and Yemm (1972, 1974) and Nordstrom et al. (1974) on the masseter and temporal muscles of rats are some of the earliest that aimed to explore the active length-tension properties of masticatory muscles. They employed an experimental approach in their studies, in which anaesthetized rats were placed on a frame which fixed the head while allowing the jaw to opening to a measurable angle. Stimulating electrodes were inserted into selected muscles causing jaw movement, allowing measurement of the jaw rotation angle, time course of the twitch and the twitch tension of the muscles. They concluded that the massater muscle was composed of fast-twitch fibres and that its optimum length for development of twitch tension was greater than its length when the teeth were in occlusion. In addition to this they discussed differences between the optimum working length for the masseter and temporal muscle groups.

Muhl et al. (1978) and Muhl (1982) implemented the same approach as Nordstrom and Yemm when investigating the digastric muscle in rabbits. One additional technique used by Muhl (1982) was to capture the resting and active lengths of the muscle during the length-tension experiments. Muhl et al. (1978) also investigated the effect of pennation angle within the muscle and reported a tetanic tension of 10 N for the digastric muscle, which was greater than the 5 N reported by Nordstrom and Yemm (1974) for the masseter muscle of a rat (Tetanic stimulation is a high-frequency sequence of individual stimulation of a neuron which result in tetanic tention of a muscle fibre). Their results also showed that the increase in muscle length had a linear relationship with muscle fibres, stating "...for a given length of fibre, muscle excursion is enhanced by pennation, relative to muscle in which the fibres lie in parallel to the line of muscle action." A study by Anapol and Herring (1989) is another example of length-tension measurement on masseter and digastric muscles, this time in a pig. They found that passive muscle force begins to rise in the masseter at lengths as short as 87% of optimum muscle length (in younger pigs), and is slightly longer than optimum muscle length for digastric muscles in younger pigs and shorter in older pigs (see Figure 3.10). A more recent study of the force-length characteristics of muscles can be found in the research of Turkawski and van Eijden (2001), in which they reported the average optimum gape angle of 12° in rabbits and discuss the variation of magnitude and direction of masseter muscle force. They demonstrated the variability of motor unit properties and that the gape angle-force curve of the whole muscle is broader than each of the individual motor units.



Figure 3.10 Composite length tension curves for masseter and digastric muscles in miniature pigs. A vertical dash line shows optimum muscle length, whereas short vertical solid lines represent *in situ* length (with teeth in occlusion). Light dots are active tetanic force at each muscle length and darker dots shows passive force that occurred at each consecutive stretch of the muscle (From Anapol and Herring, 1989).

#### 3.4.2.2 Force-velocity

While there is a relatively large amount of data available on the length-tension characteristics of masticatory muscles in mammals, there is little information on the masticatory muscles of reptiles, and more specifically lizards. Hence, for the force-velocity properties of muscles, we have to consider other animal and human studies. Close (1965) and Close and Hoh (1967) reported the force-velocity characteristics of mouse and kitten extensor digitorum longus and soleus muscles. They recorded the muscle contraction of anaesthetised animals, and based on the distance moved and time curves of after-loaded isotonic tetanic contractions, speed of shortening was calculated. Their experimental results showed that the relationship between the speed of shortening and the load can be approximated by the method of least squares using the Hill equation (Hill, 1938), i.e.

$$(P+a)V = b(P_0 - P)$$

where  $P_0$  = maximum isometric tetanic tension, P = load, V = speed of shortening, and a and b are constants).

The studies of Marsh and Bennett (1985, 1986) and John-Alder and Bennet (1987) investigated thermal dependency of locomotion and the muscles used in locomotion among lizards (*Dipsosaurus dorsalis, Sceloporus occidentalis,* some species belong to *Sphenomorphu* group). Their studies focused on the force-velocity characteristics of muscles where they dissected the ilio-fibularis muscle from the leg and pelvis of the lizard. Their *in vitro* study showed that the time dependent contractile properties of muscles are affected by temperature and that the force-velocity curve changed with temperature (see Figure 3.11). In terms of locomotion, a temperature-independent process is needed to modulate the effects of temperature on contractile properties of the muscles that supply the power for the locomotion. A temperature dependent form of the Hill equation for force-velocity was proposed. A

more recent study by Nelson et al. (2004) measured the force-velocity properties of the hindlimb muscles of wild turkeys. They reported a maximum unloaded shortening velocity of  $13.0\pm1.6$  L/s (where L/s = Length/sec) for the lateral gastrocnemius and  $14.8\pm1.0$  L/s for the peroneus longus.



Figure 3.11 Force-velocity relation of iliofibularis muscle of *Dipsosaurus dorsalis* recorded at different temperatures (From Marsh and Bennett, 1985).

A brief review on muscles and in particular their mechanical properties has been presented, and it is obvious that they must be modelled as precisely if the multibody model is to produce meaningful results (see Chapter 4). The incorporation of a realistic muscle model was therefore a key objective for this study and is described in detail in study 3 of Chapter 4. A Hill-type muscle model was programmed into the software, which included the active and passive force-length and force-velocity properties for the muscles.

# **3.5 Experimental electromyography,** cineradiography and bite force analysis

Electromyography (EMG) is a technique that measures changes in electrical potential across muscle fibres and provides data on the activation of muscles. Cineradiography and motion analysis are techniques that capture images or movies from a specimen while markers are tracked as movement takes place. Bite force measurement is a technique that uses force transducers to quantify the bite force. These three techniques have been used widely in studies involving the masticatory system and a selection are summarised below.

Many studies have been performed to find out the activity of different muscle groups during mastication in mammals, such as in opossum (Crompton et al., 1977), bat (Kallen and Gans, 1972), pig (Herring and Scapino, 1973), goat (de Vree and Gans, 1976), rabbit (Weijs and Dantuma, 1981), guinea pig (Byrd, 1981), rat (Weijs and Dantuma, 1975), hamster (Gorniak, 1977), cat (Gorniak and Gans, 1980), monkey (Byrd and Garthwarte, 1981; Luschei and Goodwin, 1974) and also in humans (Moller, 1966; Vitti and Basmajian, 1977). This large diversity and interest shows the importance of this type of research amongst biologists. Studies by Throckmorton (1976, 1978 and 1980) are seen as some of the earliest to use electromyography and cineradiography techniques on reptiles, where he compared food processing in two herbivore lizards (*Uromastyx* and *Iguana iguana*). His cinematography studies identified four phases during a cycle of mastication in *Uromastyx* slow opening, fast opening, closing and stationary. Electromyography activity in the depressor mandibulae, deep pterygoideus and superficial pterygoideus were recorded throughout the different phases of mastication.

Herrel et al. (1998a) and Herrel and de Vree (1999) conducted a series of experimental cineradiography and electromyography studies on *Uromastyx* 

43

*acanthinurus* to quantify the kinematics of the jaw and tongue along with the activation of jaw and hyolingual muscles. Their results did not support the functional explanation of quadrate mobility in *Uromastyx* proposed by Throckmorton (1976) (i.e. it is for cropping motions and retraction of the lower jaw to hold the food in a steady position during shearing), but they did find that the tongue plays an important role in holding and transport of food. Also in Herrel studies they did not observe quadrate mobility during slow closing or in the stationary phase of the mastication cycle. Studies by Gorniak et al. (1982) on *Sphenodon punctatus*, Gans et al. (1985) on the lizard *Trachydosaurus rugosus* and Herrel et al. (1997) on the lizard *Agama stellio* are some other examples of combined cineradiography and electromyography studies of reptiles.

Gorniak (1985) investigated the pattern of muscle activation during mastication in early and late phases of jaw opening or jaw closing in mammals. He concluded that the level of muscle activity and its timing depended on many factors such as food resistance, food size and lateral or anteroposterior jaw movement. These have been key topics of research of others, such as Thexton et al. (1980), where the effect of food consistency and bite size as a regulator of jaw movements in cats was assessed, and Lucas et al. (1986) who investigated relationships between jaw movements and food breakdown in humans. Thexton and Hiiemae (1997) followed the same methodology in their study of macaques by feeding them a variety of foods that differed in stiffness. Herrel et al. (2001) in a similar study discussed different possible masticatory regulators among lizards, where they considered the hyolingual muscles as a feedback system involved in mastication. Further information on masticatory regulator can be found in Smith (1984), Herrel et al. (1999c) and Williams et al. (2005).

There is a wide variety of literature available on the experimental measurement of bite force. This area is of particular interest to functional biologists to expand their understanding of how skulls are loaded during biting, as well as to justify the many hypothesis regarding relationships between body size and bite force. The bite force work of Hylander (1978) is amongst the earliest, with interest in this area continuing for the next 25 to 30 years with studies by, for example Herrel et al. (1999, 2001). These bite force investigations test hypotheses related to sexual head size dimorphism and relationships between head shape and bite performance in lizards, with Herrel noting that in the Xenosaurid species high-headed lizards bite harder than flat ones. The work of Erikson et al. (2001) on American alligators (Alligator mississippiensis) and McBrayer and White (2002) on Teiid lizard (Tupinambis teguixin) are other examples of experimental bite force measurements on reptiles, in which the former study confirmed the correlation between bite force and body size. Dumont and Herrel (2003) assessed the relationship between bite force, gape angle and bite point with different species of bats in an experimental analysis. They concluded that bite force decreased considerably with increasing gape and that unilateral molar biting generated the highest bite force, while unilateral canine biting produced the lowest bite force.

Validation of computational studies is very important, and some sample experimental studies have been summarised in this section to highlight possible validation options. In addition it is essential that we understand how the real animal moves and performs so that we can create realistic virtual models.

# 3.6 Strain gauge analysis

A strain gauge is a device that can determine the deformations on the surface of material, such as bone, metals and ceramics. The technique has been used widely in *in vivo* studies on bone and on the masticatory system, and is reviewed below.

In the early 1960s Banri Endo initiated a distinctive series of experimental and mathematical studies on human and gorilla skulls, of which parts were discussed by others nearly 30 years later (Picq and Hylander, 1989). In 1965, Endo performed a strain gauge analysis of human skulls that included the effect of the temporalis and masseter muscle groups in addition to forces acting on the mandibular fossa (Endo, 1965). The results of his study showed that strain in facial skeletons increased due to changes in bite point towards the foreteeth, and that strain generation in the facial skeleton was due predominantly to bending moments. A study by Endo (1966) is one of the classic studies of the skull, which posited that the human face can be modelled as a rigid frame composed of several straight elements (see Figure 3.12). He calculated the internal forces of the proposed rigid model of the face based on muscle force and bite forces and consequently evaluated the stresses throughout the frame and compared them to results of strain gauge analysis. Endo found comparable results that complemented each other and therefore he concluded that the stresses in the facial skeletal can be deduced fairly well from the stresses solved in the rigid frame.



Figure 3.12 Frontal view of rigid frame model presented by Endo (1966) for the human face (Adopted from Ross, 2001).

Buckland-Wright (1978) performed a comprehensive study on the patterns of force transmission in the cat skull (*Felis catus*), where bio-engineering techniques were compared to the structural organisation of the skull bones to explore the pattern of force transmission during jaw closing. Force distribution through the skull under loading was visualised by the cracking of a resin coating applied to the surface of the skull. From these findings areas for strain measurement were highlighted and strain gauges were attached to both an anaesthetised and a dry cat skull. In addition stereoprojection microradiography methods were applied to compare the density of the osseous structures with the strain gauge results. Buckland-Wright concluded that "the structural continuum is common to the compact and cancellous bone and comprises bony bars which are aligned in the optimum direction for transformation of force to a region in the bone or bones where it is effectively resisted."

Behrents et al. (1978) investigated the effect of muscle force on the morphology of the cranial vault in *Macaca mulatta*. Strain gauging was used to record the transmission of the tensile bone strain along the cranial vault to the parasagittal region during temporalis contraction. The study built on previous hypotheses concerning the driving force for separation and growth of the cranial bones, which included regulated increase of sutural tissue, growth of the brain and growth of the cranial cartilage. It was concluded that even with small bite forces the muscle forces that act upon the skull were sufficient to cause a separation of the sagittal suture, stating that such separation might act as a major factor in local control of osteogenesis of the sutures.

Hylander (1979) looked at mandibular strain in adult and sub-adult *Macaca fascicularis* on the neck of the condyle, when biting different types of food. The results also showed the TMJ reaction forces varied in response to the position of bite

point, with the TMJ being loaded in compression during powerful biting and bilateral molar and incisor biting.

Smith and Hylander (1985) conducted a strain gauge analysis on the lizard *Varanus exanthematicus*. Strain gauges were placed across the mesokinetic joint of the skull to investigate the extent and timing of mesokinetic movement in relation to different stages of feeding. It was found that cranial kinesis is not a mechanism to increase gape angle or to control the activity of skull movement, which contradicted other studies (e.g. Frazzetta, 1962; Benton, 2005) who believed that cranial kinesis allowed lizards to open their mouths wider and hold a food particle easier.

In long-term experimental strain gauge studies on pig skulls, Herring and colleagues (1991, 2000) investigated the loading patterns of the zygomatico-squamosal suture and general braincase during mastication. In addition, they proposed a correlation between loading patterns and the histological structure of the suture. They concluded that pig braincases act as cylindrical structures composed of adjustable plates, with flexible joints that are easily strained due to their angulation, but not twisted. However, if these were much stiffer plates twisting would be the main strain regime.

Various hypotheses exist regarding loading regimes in the primate skull (e.g. bending beam, twisting cylinder, rigid frame) and were the motivation behind a unique strain gauge study performed by Ross (2001) on an owl monkey, rhesus macaques and a galago. He concluded that the interorbital region cannot be modelled as a bending beam, but his results did support the theory that the skull is twisted during mastication, agreeing with Endo's (1966) hypothesis that the interorbital region is a rigid frame subjected to lateral bending. Ross and Metzger (2004) studied the variation of strain magnitudes across the skulls of four genera of primate to investigate hypotheses suggesting that different parts of the skull carry out different

functions. Their results showed large strain variations between the taxa and that strain was always higher in the zygomatic arch and jaw than the circumorbital and neurocranial parts of the skull. These strain variations themselves hint towards optimization of bone in response to different criteria. Also, Ross and Metzger (2004) showed that strain magnitudes are higher in alligators than in mammals, showing that alligator skulls are designed to resist higher forces than mammal skulls.

In studies by Usui et al. (2003, 2004) strain gauge analyses were performed on the mandible of a dry human skull. Fifteen rosette strain gauges were attached to the jaw while bilateral mastication was simulated with the help of the masseter, medial pterygoid and temporalis muscle groups (see Figure 3.13 for their experimental setup). They concluded that strain generated during mastication varies significantly across the mandible, particularly on the medial and lateral aspects.



Figure 3.13 Lateral view of the experimental strain gauge study of Usui et al. (2004).

A study by Markey et al. (2006) aimed to establish a relationship between suture form and function. They conducted combined strain gauge and cineradiography studies on fish skulls to evaluate whether maximum strains take place during biting or suction feeding. Their strain gauge results showed that each half of the skull rotates laterally during biting and suction, and that different muscle loading effects different types of sutures.

A brief review of previous strain gauge studies conducted on skulls is summarized here. Understanding the procedure is important since strain gauging was performed in this research as a part of a validation study (Chapter 6). So far this chapter has reviewed the properties and function of bone and muscle and assessed different experimental approaches in relation to these structures. Now mathematical and computer modelling techniques will be reviewed. They are powerful tools that have developed over the last fifty years and their application in the study of the masticatory system has become widespread.

# **3.7** Free body diagram analysis and computer modelling of mastication

Free body diagrams and static analysis have been used frequently in the area of biomechanics to answer questions surrounding form and function of different structures. This section provides a brief review on basic static analyses related to the study of the masticatory system, and more recent and more advanced computer modelling studies.

## 3.7.1 Free body diagram analysis

Weijs (1980) reviewed biomechanical models of the mammalian masticatory apparatus, criticizing the accuracy of static analyses because they do not (usually) take into account the fact that the activation of muscles depends on bite point and that the magnitude and direction of muscle forces change during the chewing cycle (see Figure 3.14). He also emphasized the estimation of muscle, joint and bite forces based on 3D, 2D or 1D static analysis, and highlighted the importance of including

jaw movement for estimation of muscle force and joint force in modelling of mastication.



Figure 3.14 Figure showing the change in direction of jaw closing muscle forces (temporalis (tem), anterior deep masseter (adm) and superficial masseter (sm)) as activation levels increase during jaw closing (phase 1-4) and masticatory power stroke (phase 5-8) in the rat (From Weijs, 1980).

van Eijden et al. (1988) used a two-dimensional mathematical model to study the variation of bite force directions and magnitudes that jaw muscles can produce during human jaw closing. Their model was developed based on static equilibrium conditions, where the magnitude and direction of muscle forces and bite point were the known variables and the equations were solved to obtain the magnitude and direction of bite force and joint force. Their calculations predicted a variety of TMJ reaction force directions and showed that each muscle produces a unique range of bite force directions. Koolstra et al. (1988) developed a three-dimensional model of human mastication to find the maximum theoretical bite force that can be generated. They used an optimization technique in which minimization of muscle activation was the objective function of the simulation. Their results predicted a maximum bite force of 693 N on the second molar perpendicular to the occlusal plane and that anteriorly positioned and medially or laterally directed bite forces yield the greatest joint forces.

The studies of Sinclair and Alexander (1987) and Cleuren et al. (1995) are examples of static analyses which aimed to predict bite force and joint force in reptiles. Sinclair and Alexander (1987) approximated the muscle force based on physical cross-sectional area (PCSA) while Cleuren et al. (1995) included EMG data into their static analysis, allowing comparison between a fully active muscle model and an EMG activated muscle model. Herrel et al. (1998b, c) also approximated muscle forces based on its PCSA, and applied these to a *Uromastyx acanthinurus* along with other related lizard species to study the function of temporal ligament and temporal arcade. Their results support the view that the temporal ligaments fulfil the role of the lower temporal arcade in stabilization of quadrate. Also the ligament attachment site (to the jaw or the quadrate) can confine the orientation of joint reaction forces to a narrower range.

## 3.7.2 Basic computer model

The work of Otten (1987) is one of the earliest studies using computer based muscle models of the masticatory system, in which he analysed a rat skull programmed directly in PASCAL. The muscle models were used to assess a variety of parameters, such as the relationship between muscle force and fibre length based on the sarcomere morphometric data, and the relationship between muscle force and muscle length based on myomorphometric data. The dynamic muscle models took into account muscle length, contraction velocity and activation rates based on the fibre type data, calcium dynamics and velocity-force relations. Otten also devised a kinematic model of the masticatory system, assessing the possible movements of the jaw in relation to the morphometrics of the bones, joints and connective tissue. The final stages of his work involved the use of a three-dimensional reconstruction package to review the analysis and display the position and movement of the system and force vectors. These models showed similar movements to those measured experimentally, concluding that the force-velocity relation of the muscles is important in stabilizing the velocities of the system.

van Ruijven and Weijs (1990) developed a similar type of muscle model to that of Otten (1987), however, they assessed the relationship between EMG data and the activation factor in their model of a rabbit skull, as well as the non-linear relationship between EMG and activation based on Otten's (1987) work. They validated their bite force values against experimental bite force data, and proposed that their model could be used to assess other more complex movements. Similar studies include those of Koolstra and van Eijden (1997a, b) who used programs written in FORTRAN. They simulated jaw opening and closing in a human skull, where the mandibular condyle was modelled as a sphere that could contact with the articular surface of the skull, which itself was modelled by a medio-laterally angulated third-order polynominal function. Biting was permitted by modelling a single point-shaped structure that could contact a flat surface coinciding with the occlusal plane of the skull. They assumed straight line muscles between origin and insertion points and included the effect of instantaneous change of sarcomere length based on the muscle length. They approximated the active and passive muscle force as well as the force-velocity relationship of the muscles. When investigating the cocontraction of the jaw-opening and jaw-closing muscles during mastication, they noted that the jaw-opening muscles produced negligible passive resistance during jaw closing, but the passive properties of the jaw-closing muscles did contribute significantly to the limitation of the jaw-opening movement.

One of the more recent studies that use computer programming to assess skulls is that of Daumas et al. (2005). Their work was aimed at designing a device using MATLAB SimMechanic toolbox to reproduce human chewing behaviour. Muscle function was approximated by six linear actuators that were attached to the skull and jaw by twelve spherical joints. Their model reproduced comparable jaw movements to that cited in the literature.

## 3.7.3 Multibody dynamic analysis

Using commercial dynamic packages to model jaw open/closing or more specifically developing a package to model the masticatory system has become ever more popular. A study by Weingartner (1998) is one of the first in this field, where a dynamic simulation of the jaw was developed for the purpose of pre-operative planning and the education of surgeons. In their work special devices were used to record three dimensional movement of the mandible. They developed realistic temporomandibular joints that permitted both rotation and sliding, and they tried to implement force-length and force-velocity characteristics into their muscles. See Figure 3.15 for an image of their model, which was developed using an in-house visualisation toolkit named KaVis.



Figure 3.15 Multibody dynamic models of human mastication developed by Weingartner (1998).

Langenbach and Hannam (1999) developed a 3D dynamic model of the human mandible (using dynamic simulation package ADAMS, Mechanical Dynamics Inc., Michigan) to predict active and passive tension of muscles involved during mastication. Their model included an artificial food bolus located between the teeth and eighteen Hill type actuators representing jaw muscles. Two positions were simulated in their modelling. Firstly, all the optimal lengths for the length-tension curves were set while the incisor teeth were 2 mm apart. Secondly, optimal lengths were defined when there was a 12 mm interincisal separation. Their results during a chewing cycle revealed that their second configuration was more comparable to human behaviour.

Langenbach et al. (2002, 2006) developed a dynamic model of pig mastication again using ADAMS. They constructed a three-dimensional model of a pig mandible with combined anatomical and functional features, which they used to investigate jaw movements. They used data from CT and MR imaging to construct the model geometry as well as recording muscle activities using bipolar intramuscular electrodes. The movements produced from their model were in good agreement with published data on the anatomical movement of a pig jaw during mastication.

Hulme et al. (2003) developed a computational toolkit called Vertebrate Analyzer, which as the name suggests, allows the biomechanical analysis of vertebrates. Their ultimate aim for developing this software was to test hypotheses related to form and function of jaws and teeth. This software enables the detailed properties of muscles to be assessed, such as active, passive and total force within the muscle and the optimum allowable length of the muscle bundles. Another example of specially developed software for the analysis of musculoskeletal systems is that of Rasmussen et al. (2003) named AnyBody (AnyBody Technology, Denmark). De Zee et al. (2007) worked with AnyBody to perform a validation study using a human mandible in a study on mandibular distraction osteogenesis. Optimization algorithms were used to calculate muscle activations, muscle forces and TMJ reaction forces for different clenching and dynamic tasks. They did not find a strong agreement with their experimental results, however this work is significant since it is rare in the fact that it assessed subject-specific models of patients.

The work of Sellers and Crompton (2004) is another example of bite force modelling studies using the ADAMS multibody dynamics package. A model of the human jaw was built and incorporated the jaw adductor muscles used during jaw closing. They performed a sensitivity analysis to predict the maximum bite force of the human mandible at each tooth position, validating their results against published experimental data. They concluded that bite force values were highly sensitive to the muscle origins, and without sensitivity analysis it would not be possible to validate this sort of biomechanical modelling.

Konakanchi (2005) modelled the extinct saber-toothed cat (*Smilodon fatalis*) to predict maximum bite force using AnyBody musculoskeletal modelling software. His findings showed that the muscle insertion and origin locations had a significant effect on the amount of force that could be produced, and as such ran an optimization routine to determine the muscle origin and insertion points (within set limits) that would produce a maximum bite force. This study shows the possible applications of dynamic analysis, in which sophisticated models of biological systems can be developed to help answer previously unanswerable questions on anatomical performance.

Some of the latest studies in this area are that of Stavness et al. (2006) and Hannam et al. (2008). These studies looked at integrated models of the human jaw and laryngeal structures and used software known as ArtiSynth. Their models

56

consisted of a fixed rigid skull, a movable mandible and a rigid planar constraint and were used to predict bite force and to assess laryngeal substructures. Their model used forty five actuated straight-line Hill type muscles and was validated by comparing model motions at different positions, such as wide jaw opening with anatomical motions reported in the literature. Figure 3.16 shows an example image of their model.



Figure 3.16 The jaw model developed by Stavness et al. (2006) showing rigid-bodies and connective tissue involve in their model.

van Lopik and Acar (2007) developed a computational model of the human head and neck using the multibody dynamic software MSC.visualNastran4D. This model was developed to study the behaviour of the human head and neck in response to impacts. Their model was comprised of nine rigid bodies that represented the head, the seven cervical vertebrae of neck and the first thoracic vertebrae. Also included in their model were non-linear viscoelastic ligaments, muscles groups that in some sections wrapped around the vertebrae and intervertebral discs elements. They validated the cervical spine motion of their model by comparing it to published experimental data for small and large static loads, finding a good agreement. Studies such as that by van Lopik and Acar (2007) show that multibody dynamic analysis can be a reliable technique when studying the biomechanics of anatomical systems.

The potential of multibody dynamic analysis (MDA) of skulls and cranial systems is obvious from the overview of the literature included here. Its application to problems in biology is still relatively rare. Certainly it is not so widely known as finite element (FE) analysis, and yet it is an obvious method to provide the detailed load data required for more accurate FE studies, as demonstrated later in this thesis.

## **3.8** Finite element analysis of skulls

Studies into the effects of skull loading (i.e. bite forces and muscle forces) have been of interest for some time. Finite element analysis (FEA) is a powerful tool that enables us to study these loading effects more closely, where stress distributions are created in response to a specific loading scenario. FEA has been used relatively widely in the modelling of skulls, and in some cases incorporate experimental EMG data and use strain gauge results for validation purposes. In this section some of the key studies of skull modelling are summarised.

In a pioneering study, Tanne et al. (1988) developed an FE model of the human skull. This was later developed by Miyasaka et al. (1994) to investigate the nature of the stress distributions in the craniofacial sutures, with the model including eighteen cranial and facial sutures, but with a mesh of less than 2000 solid elements. In this model different material properties were assigned to cortical and cancellous bone as well as the teeth. It was constrained around the foramen magnum and loaded on the canines. Their results showed that a 30° upward force on the canines produced the greatest stress on the sutural system. They concluded from this preliminary work that future studies could be used to determine an optimal force that might produce desirable sutural responses during orthopaedic maxillary protraction therapy.

Verrue et al. (2001) developed a finite element model of a dog skull using an FE package called PATRAN. This model included different material properties for the cortical bone, cancellous bone, teeth and sutures, however, the model still only included around 3600 elements with only one element through the suture thickness. Despite these two factors (which raise questions about the convergence and accuracy), the model did compare reasonably well to *in vivo* laser speckle interferometry displacement data.

Rayfield et al. (2001) carried out an FEA on the skull of a dinosaur (Allosaurus fragilis) which can be considered to be one of the earliest uses of FE in palaeontology. Different loading conditions were assessed, and clearly demonstrated that FEA has the potential for testing the mechanical behavior of fossils. Later studies by Rayfield (2005a) included the development of 2D FE models for the assessment of three different species of dinosaurs (Coelophysis, Allosaurus, Tyrannosaurus), where simple loading conditions were incorporated (e.g. fixed constraint at the back of skull and a vertical load to represent bite force) to explain morphological differences of these skulls. Rayfield concluded that morphology dictates the stress distribution to some extent such that diffrences in stress distribution may be linked to differences in cranial morphology between taxa. Figure 3.17 shows an example of this work. In addition to this, Rayfield (2005b) tried to explore the mechanical importance of sutures in skulls using the finite element method. She studied the relationship between stress intensity, cranial strength and sutural morphology in the skull of the Allosaurus fragilis dinosaur. To determine whether sutures can accommodate stress and strain patterns generated during mastication. Rayfield is prominent in this area, and her latest publication (2007) comprehensively reviews the use of FE in the biomechanics of living and fossil skulls.



Figure 3.17 An example of comparative FE approach that Rayfield implemented in a study on three phylogenetically related taxa (A, B and C). D, E, F shows the 3<sup>rd</sup> principal stress (From Rayfield, 2005a).

Witzel and Preuschoft have done extensive work in the area of functional morphology, assessing the biomechanics of reptile and mammalian skulls (e.g. Preuschoft and Witzel, 2002). The focus of their work is the deductive approach of FEA, where skull geometries are formed biomechanically to resist the loading conditions that are imposed on them. Wolff's law ("Only static usefulness and necessity or static superfluity determine the existence and location of every bony element and, consequently of the overall shape of the bone" (Wolff, 1892)) drives these deductive methods, and is applied to transform a simplistic shape (e.g. a block) into a recognisable skull shape. Boundary conditions are applied to the simple shapes (e.g. bite force and muscle force), which are then iteratively loaded and solved using finite element analysis. Elements below a specific level are removed to allow the geometry to change over time, see Figure 3.18. This technique has been

applied to skulls of Hominoidea (Preuschoft and Witzel, 2004a), human (Witzel and Preuschoft, 2002), *Diplodocus* (Witzel and Preuschoft, 2005), primates and ancestral synapsids (Preuschoft and Witzel, 2004b and 2005). Conclusions from this work are that the stress flows in skulls depend on a few factors, such as the position and shape of the dental arcade, snout, eye openings, brain size and the arrangement of muscles.



Figure 3.18 An example of the studies of Witzel and Preuschoft (2005) of a *Diplodocus* skull. (A) the skull of *Diplodocus*. (B) the original FF-model and loading condition. (C) compressive surface stress after the first model iteration. Note how the occipital, region (supraoccipital: soc; basiocbipital: boc) is highly stressed. Elements experiencing less than -0.8 N/mm<sup>2</sup> will be removed. (D) final model of successive iterations and element removal (From Rayfield, 2007).

Ross et al. (2005) developed an FE model of a *Macaca fascicularis* skull, in which they carried out a sensitivity analysis in relation to the muscle forces. Forces were varied according to the PCSA data and experimental EMG data that was obtained for different species of *Macaca* (i.e. *M. mulatta*, *M. fuscata* and *M. fascicularis*). Thirty-six different loading regimes were modelled, with four different PCSA sets and nine different scaling parameters corresponding to the EMG data. They concluded from this work that approximations of muscle force according to PSCA can predict deformation patterns in the *Macaca* skull, but for increased

accuracy the relative contribution of the recruitment levels of the masticatory muscles is essential.

Strait et al. (2005) focused on assessing the effect of including more detailed material property information in an FE model of a Macaca fascicularis skull, and comparing the findings to experimental strain gauge data. Four FE models were created: (1) with a single isotropic elastic modulus value based on human bone, (2) with a single isotropic elastic modulus based on average values from across a Macaca skull, (3) with multiple isotropic material properties based on a Macaca skull and (4) with several orthotropic material properties based on values published of Wang and Dechow (2006) for a Macaca mulatta skull. Figure 3.19 shows a comparison of their FE results to *in vivo* strain gauge data. They concluded that using more realistic bone material properties in FE models would produce more reliable results. However, they state that using isotropic material properties does derive qualitatively similar patterns of deformation. A later study by Strait et al. (2007) used FEA to assess the effect of thickening the palate of Macaca fascicularis. Their results showed that lower strains were present within a thicker palate, but this did lead to an increase in strain in other regions of the skull. Based on this finding they discussed whether some of the facial features related to chewing might have evolved in an integrated fashion.


Figure 3.19 A comparison of (A) maximum shear stress and (B) max/min principal strain ratio of different FE models with *in vivo* experimental data. Analysis types 1-4 are explained in the text (From Strait et al., 2005).

Dumont et al. (2005) and Dumont (2007) also used FEA to test hypotheses concerned with biomechanical relationships between feeding mechanisms and craniofacial morphology. In the first, FE models of two different species of bat skulls were investigated and the stress patterns during biting were compared. In their FE models muscle forces were applied at three nodes representing regions of muscle attachment, while single node constraints were modelled to represent the temporomandibular joint and bite point. Their results showed that one of the species could resist load to a greater extent, and indicated that other factors other than feeding may have had impact on craniofacial morphology. Grosse et al. (2007) focused on developing more realistic muscle models and added to the previous work of Dumont et al. (2005). Grosse et al. (2007) compared the effect of modelling muscles as simple-point loads and as more sophisticated, distributed and wrapped muscle loads. As would be expected, more accurate representation of muscle loading provided different and most likely more accurate stress distribution about some regions of the skull. However, depending on the analysis objective, simple-point load muscle modelling could be used to predict reliable patterns of stress across some regions of skull. See Figure 3.20 for an overview of the results of Grosse et al. (2007).



Figure 3.20 Right lateral view of the distribution of von Mises stress. (A) Muscle forces modelled as point-loads. (B) Muscle forces wrapped over the skull surface to include tangential-plus-normal traction force (From Grosse et al. 2007).

Daniel and McHenry (2001) used FE modelling to assess the cranium of an alligator. They built a simple FE model (2400 shell elements) of the *Alligator mississippiensis*, which had spring supports placed at the jaw and back of skull while the model was loaded by the adductor muscle. This preliminary study was later developed by McHenry et al. (2006) using the same technique to assess six species of crocodilian. From their results of beam models and FE models they concluded that flat-snouted (platyrostry) geometries that evolved in corocodilians are not in response to torsional loading, and as such could be a response to hydrodynamic loads acting on the rostrum during feeding and swimming. Metzger et al. (2005) compared the results of beam theory and FEA with *in vivo* strain gauge data for the same species examined by Daniel and McHenry (2001). Poor correspondence was found between their FEA and the *in vivo* strain data leading to the conclusion that their FE models needed to be modified by the addition of sutures.

The recent FEA works by Wroe et al. (2007a, b) are probably among the most precise in the area of skull analysis in terms of resolution and material property definition. Bone was modelled as a heterogeneous material, with material properties defined according to the density in CT images, and muscle forces were distributed over their attachment areas and modelled as beam elements attached to the cranium and mandible. Skulls of a dingo (Wroe et al., 2007a) and a chimpanzee (Wroe et al., 2007b) were modelled to compare differences between results obtained in homogenous material models and heterogenous material models. While these models do improve on earlier models in some instances, there are still many approximation and simplifications. These include the absence of sutures and muscle wrapping, limited modelling of the muscles and simple joint mechanics.

Kupczik et al. (2007) performed a comprehensive validation study to assess the mechanical function of the zygomatic region of two adult male *Macaca*  *fascicularis* skulls. Their FE models represented bone as a homogenous and isotropic material structure, where they retrieved material properties from nanoindentation studies. In the FEA the zygomatico-temporal suture was represented. Their findings highlighted the importance of craniofacial sutures in terms of their influence on the strain distribution on the skull. In addition, the subject of accurate material properties was also addressed. Figure 3.21 shows the regional strain relief that the zygomatico-temporal suture produced. Additional findings from their FE modelling study showed that the application of load vectors to nodes along the corresponding bony structures of the skull provided a more realistic result than its application across a simulated muscle mass, in this case the masseter muscle group.



Figure 3.21 Distribution of  $1^{st}$  principal strain. (A) zygomatic arch fused ( $E_{bone}=E_{suture}=7.2$  GPa) (B) zygomatico-temporal suture present ( $E_{bone}=7.2$ ,  $E_{suture}=0.0025$  GPa) (Adapted from Kupczik et al., 2007).

Unlike multibody dynamics analysis there have been many previous FEA studies of skulls. This brief review highlights important aspects of some of these earlier models, some of which have been useful in the development of the models used in this present study, which are discussed in more detail in Chapter 5.

# **3.9** Combined dynamic and finite element analysis of mastication

The work of Koolstra and van Eijden (2005, 2006) combined FEA and MDA to analyse the distribution of stresses and deformations that occur in the cartilaginous structures of the human jaw joint during mastication. They used the MADYMO, which has the capability to combine multibody dynamic and finite element analysis. Muscle activation patterns controlled the jaw motion in the multibody model, with the articular cartilage layers modelled with the help of the finite element method. Their results showed that as the muscles were activated during jaw movement, joint force and consequently the stress over the area of the articular surface increased. This stress was distributed over a wider area by the articular disc by transforming compressive stress to shear stress.

The research of Curtis et al. (2008) on a macaque skull is the latest combined FEA and MDA study to date. The MDA part of their study aimed to assess the effect of representing the muscle groups as single components, several components and several components that wrapped around the cranium. Running the multibody simulations permitted the prediction of bite forces, joints forces and muscle forces. The load step data from the MDA was then imported into the FEA. Due to the fact that the model was in equilibrium, high stresses were not observed around the constraints. The results also showed that dividing muscle each into several sections and wrapping them around the bone reduce the strains in the certain areas of the skull.

Combined multibody and finite element analyses are to date, relatively rare, as summarised above. One of the main aims of this study is to perform a combined MDA and FEA on the skull of *Uromastyx*. The following chapter describes the MDA part of this study.

# Chapter 4: Dynamic analysis of a lizard skull 4.1 Introduction

Multibody dynamics analysis (MDA) is a relatively new computer modelling technique used in engineering and has been used here to model the mechanism of chewing in a lizard. This chapter includes a brief review of the multibody simulation software used in this research, followed by details and results from the different models developed throughout this work. The chapter concludes with a general discussion and summary of all work covered.

# 4.2 Overview of ADAMS

ADAMS (Automatic Dynamic Analysis of Mechanical Systems) was developed by Mechanical Dynamics Inc. (Ann Arbor, Michigan) in the 1970s, and is a threedimensional modelling package for the simulation of dynamic mechanisms. The general structure of ADAMS is similar to other engineering packages in that it consists of a pre-processor, a simulation solver, and post-processor.

In order to formulate the equations of motion of the problem under consideration, the user represents the mechanism as a system of rigid bodies and constraints. Each part is initially considered free, possessing six degrees of freedom, which can then be subjected to constraints. The solution then provides the constraint forces. A library of predefined common constraints is available within ADAMS (i.e. revolute joint, translational joint, etc.), however, constraint relations can also be customized using FORTRAN subroutines. A graphical user interface can be used to setup a model (ADAMS/View) or the user may describe the model using commands and parameters. The user specifies the simulation time along with other integration parameters to start the simulation. The first step in this phase is to determine if the system is an indirect dynamics problem (kinematic analysis) or a direct dynamics problem (dynamic analysis). The decision is based on the Grüebler method for determination of dynamic degrees of freedom:

$$N = 6S - C$$

where N is the total number of dynamic degrees of freedom of the system, S is the number of rigid body segments, and C is the number of active constraints specified (Patton, 1993). A dynamic analysis is required if the system exhibits at least one degree of freedom. In the case of the kinematic analysis, a set of algebraic equations is obtained, and the system is solved simultaneously for each instant of time. If the system is determined to be a dynamic analysis problem, a system of non-linear differential equations is obtained. A Jacobian matrix (a matrix of partial derivatives) is created for each instant of time, and the equations are integrated. Data files are written that record the simulation. The final stage in the process is the analysis of the results. ADAMS/View provides graphic animation, charting, and processing of results where the data can also be restructured into different forms (spreadsheet files, bitmaps, etc.).

# 4.3 MDA modelling of a Uromastyx skull

All the MDA computer modelling that has been performed during this research is summarised below, and can be divided into three sections: Study 1, feasibility investigations into representing skull mechanics using ADAMS MDA software; Study 2, development of the MDA models including anatomically accurate structures in relation to the particular *Uromastyx* lizard species and Study 3, application of sophisticated muscle models to provide more realistic muscle force predictions. The subsequent FE studies used the most accurate data produced in Study 3.

### 4.3.1 Study 1: Basic model development

This study describes the construction of a preliminarily MDA model (using the ADAMS software) that was used to test the feasibility of performing biting simulations in *Uromastyx*.

#### 4.3.1.1 Method

#### **Model Construction**

Micro-CT data of an *Uromastyx hardwickii* skull (skull length ~44mm; skull width ~41mm) was supplied by the University of Texas, Austin. Image processing software (Amira V3, Berlin, Germany) was used to segment the dataset and create surface models of the skull and lower jaw. After micro-CT segmentation the surface models were imported into ADAMS motion simulation software (Santa Ana, US) as .OBJ files. A cylinder was added to represent the neck and was fixed to the upper skull. The jaw was assigned a mass of 0.04 kg (estimated from the total mass of the skull listed by Herrel et al., 1998a, b), with the centre of mass located 4 mm below in the midline and 24 mm posterior to the front of the lower jaw (automatically calculated from ADAMS). Acceleration due to gravity was included as a constant value of 9.81 m/s<sup>2</sup>.

Simplified muscle groups were represented by springs (with tensile and compressive resistance, see equation (1)) with specific muscle attachment locations defined in accordance with the anatomical data described by Haas (1973) (see Figure 4.1). The muscle groups simulated were: Adductor mandibulae externus superficialis anterior (MAMESA); adductor mandibulae externus superficialis posterior (MAMESP); adductor mandibulae externus medialis (MAMESP); adductor mandibulae externus medialis (MAMESP); depressor mandibulae externus profundus (MAMEP); pterygoideus externus (MPTE); pterygoideus medialis (MPTM); pseudotemporalis superficialis (MPST); depressor

mandibulae (MDM). The depressor mandibulae muscle, which is associated with jaw opening, was included in the model for visualisation and possible future investigations. However, in this study, which is interested only in jaw closing it was assigned a stiffness value of zero. The stiffness values of the individual muscle



Figure 4.1 (A) Lateral and (B) dorsal view of the *Uromastyx* model showing simplified muscle groups. The MPST is an internal muscle and its second section is not visible in this figure.

groups were estimated from physical cross-section area (PCSA) data from Herrel et al. (1998a, b) where a stiffness value of 1 N/mm was assigned to the MAMEP muscle, and all other stiffness values were scaled accordingly (see Table 4.1). The force produced by each muscle was then calculated from:

$$F = D\left(\frac{dl}{dt}\right) + K\left(l - l_0\right) \tag{1}$$

where F is the force generated (N), D is the damping ratio (Ns/mm), t is the

simulation time (s), *K* is the stiffness coefficient (N/mm), *l* is the calculated length of the spring (mm) and  $l_0$  is the original length of the spring (mm). In this analysis *D* was assigned a value of 0.01 Ns/mm for all muscle groups since no information was available on the viscoelastic properties of masticatory muscles (Langenbach et al., 2002).

The neck and upper skull were assumed to be fixed (i.e. fully constrained) in the model, while the lower jaw could move relative to the upper skull. Initially jaw motion was constrained by a simple hinge joint located at the point of articulation between the quadrate and articular and surangular bones (see Figure 4.2). This was later modified to include a planar joint that permitted additional anterior/ posterior translations.

Muscle group	Muscle physical cross- section area (cm <sup>2</sup> )	Stiffness (N/mm)
MAMEM	0.221	1.89
MAMESP	0.172	1.47
MAMESA	0.144	1.23
MAMEP	0.117	1
MPTE	0.333	2.85
MPTM	0.277	2.37
MPST	0.032	0.27
MDM	0.094	0.00

Table 4.1 Spring properties used for the various muscle groups in the *Uromastyx hardwickii* model along with the cross-sectional data reported by Herrel et al. (1998a, b). Adductor mandibulae externus superficialis anterior (MAMESA); adductor mandibulae externus superficialis posterior (MAMESP); adductor mandibulae externus (MPTE); pterygoideus medialis (MPTM); pseudotemporalis superficialis (MPST); depressor mandibulae (MDM).

#### Simulations

ADAMS uses a kinematic approach to calculate a specific muscle force, which can then be applied to produce muscle induced motions. The general approach included the rotation of the lower jaw by a pre-defined angle, and in doing so the muscle groups were deformed from their original positions, allowing the relative muscle forces to be estimated according to equation (1). These muscle force data were then



Figure 4.2 Bite point locations: Position  $1 \sim 16$ mm from jaw tip; Position  $2 \sim 13$ mm from jaw tip; Position  $3 \sim 10$ mm from jaw tip.

input directly into the model to simulate biting. The work by Herrel et al. (1998a, b) provided key information for this study (specifically their PCSA information on the *Uromastyx*), thus their food particle location (bite point approximately 16mm from the jaw tip) was represented. During this simulation the jaw was initially rotated by  $20^{\circ}$  to estimate the individual muscle forces and then a biting simulation was performed to evaluate both bite force and joint force. The food particle was represented by a resisting spring of high stiffness (1000 N/mm) correctly positioned on both sides of the jaw as in other computational studies (e.g. Seller and Crompton, 2004). Muscle forces were estimated and then applied to calculate bite forces and joint forces for additional gape angles (5° to 40°, in 5° increments). To allow a comparison with similar studies in the literature (e.g. Cleuren et al., 1995; Herrel et al., 1998a), where a constant muscle force was assumed at all gapes, the muscle force data retrieved for the 20° gape simulation was also applied at all other gape angles (i.e. 5° to 40°). The variation in bite and joint forces was then assessed.

Additional studies into the effect of bite point location and a more realistic articular joint were conducted. It is commonly accepted that bite point location has a significant effect on bite force (e.g. Dumont et al., 2003), and this was investigated

here by simulating three different bite points at gape angles of 10° and 20°. The bite point was moved anteriorly from the initial position (position 1) by approximately 3 mm (position 2) and 6 mm (position 3) (see Figure 4.2). To represent a more anatomically realistic articular joint, anterior/ posterior translations were also allowed, in addition to the previous rotations by assigning a planar joint to the model. The translations were set to 1 mm and 2 mm in the initial investigation to assess the sensitivity of muscle forces at gapes of 10° and 20°. As a result, the lower jaw was observed to translate posteriorly with jaw opening.

#### 4.3.1.2 Results

The relative contribution of each muscle group as the jaw opens through various gape angles was investigated. Rotation to a maximum gape angle of  $40^{\circ}$  was simulated at 5° increments (range 5° to 40°) recording the maximum force within each muscle group and also the joint force during these motions, see Table 4.2. The muscle values presented are an average of the left and right muscle groups, and the joint force is the total force (sum of both sides) on the skull.

	Gape angle (degrees)							
	5	10	15	20	25	30	35	40
MAMEM	1.47	2.95	4.43	5.89	7.33	8.75	10.11	11.44
MAMEP	0.63	1.24	1.82	2.36	2.88	3.37	3.83	4.25
MAMESA	1.25	2.47	3.65	4.79	5.88	6.93	7.92	8.86
MAMESP	0.64	1.24	1.79	2.29	2.75	3.16	3.52	3.83
MPST	0.85	0.34	0.51	0.69	0.87	1.05	1.23	1.40
MPTE	1.08	1.64	2.36	3.02	3.58	4.09	4.51	4.86
MPTM	1.08	2.15	3.20	4.23	5.23	6.35	7.13	8.02
JOINT								
FORCE	10.59	20.92	30.92	40.52	49.68	58.35	66.49	74.07

Table 4.2 Muscle force and joint force data for differing gape angle (obtained from the jaw opening phase of the modelling). Note all values are in Newtons.

To assess the effect of gape angle on bite force, two studies were conducted. In the first the muscle force data predicted by jaw opening was applied. In the second the muscle force data at 20° gape were applied at all other gape angles. Figure 4.3 and Figure 4.4 show the effect of gape angle on bite force and joint force respectively with changing muscle forces. Figure 4.5 and Figure 4.6 show the effect of gape angle on bite force and joint force with constant muscle forces at all gapes.



Figure 4.3 Bite force at varying gapes with varying muscle force values.



Figure 4.4 Joint force at varying gapes with varying muscle force values.



Figure 4.5 Bite force at varying gapes from applying a constant muscle force value.



Figure 4.6 Joint force at varying gapes from applying a constant muscle force value.

It has been reported (e.g. Dumont et al., 2003) that as the bite point moves from the front of the mouth (incisiform tooth) to the back of the mouth (posterior teeth) the bite force increases. To investigate this we simulated two additional bite points, one approximately 3 mm and one 6 mm from the original position (16 mm from the tip of the jaw position 1 in Figure 4.2) at gape angles of 10° and 20° using constant muscle force loading. The bite force and joint force results are shown in Table 4.3, Figure 4.7 and Figure 4.8.

	Bite force (N)		Joint force (N)		
	10°	20°	10°	20°	
Position 1	12.34	9.09	26.02	25.68	
Position 2	10.04	7.75	27.92	28.32	
Position 3	8.07	6.65	26.94	29.22	

Table 4.3 The effect of bite point on bite force at  $10^{\circ}$  and  $20^{\circ}$  gape angle applying constant muscle forces.



Figure 4.7 Effect of bite point on bite force at 10° and 20° applying constant muscle forces.



Figure 4.8 Effect of bite point on joint force at 10° and 20° applying constant muscle forces.

Alexander (1971) amongst others remarked that the jaw moved forwards and backwards during feeding in many lizards. Therefore, to assess the effect of this motion on the muscle forces a planar joint was created in place of the hinge joint and jaw displacements of 1 mm and 2 mm were applied to the joint during the jaw opening phase of the simulation. The average of the left and right muscle forces was recorded for gapes of 10° and 20°. Table 4.4 shows the muscle forces associated with the posterior displacement simulation, as well a comparison with the muscle forces from the simple hinge joint simulation (from Table 4.2). Figure 4.9 graphically shows the muscle force of the posterior displacement simulation at a 20° gape.

		Muscle force (N)		Change in force (N)	
	Joint displacement	Gape angle (degrees)		Gape angle (degrees)	
	(mm)	10	20	10	20
	1	2.41	5.68	-0.55	-0.21
MAMEM	2	1.62	4.91	-1.33	-0.98
	1	0.51	1.80	-0.72	-0.56
MAMEP	2	-0.31	1.02	-1.55	-1.34
	1	2.25	4.86	-0.22	0.08
MAMESA	2	1.85	4.53	-0.62	-0.26
	1	0.50	1.89	-0.74	-0.41
MAMESP	2	-0.42	1.07	-1.66	-1.23
	1	0.23	0.64	-0.10	-0.05
MPST	2	0.13	0.54	-0.21	-0.15
	1	1.64	3.69	-0.72	0.67
МРТЕ	2	1.27	3.41	-1.09	0.39
	1	3.53	6.11	0.33	1.88
МРТМ	2	4.75	7.45	2.60	3.22

Table 4.4 Muscle force data for gapes of 10° and 20° with a planar joint and the change in force when compared to the hinge joint (from Table 4.2). Negative values represent a theoretical compressive muscle force (columns 3), and a decrease in force (in columns 5 and 6).



Figure 4.9 Effect of posterior displacement of the jaw on the muscle forces at a 20° gape.

#### 4.3.1.3 Discussion

Muscle forces are traditionally approximated from the muscle's physiological cross sectional area (e.g. Weijs and Hillen, 1985; Sinclair and Alexander, 1987). Here we applied a constant stiffness coefficient to each muscle group, which was scaled relative to the PCSA of the anatomic muscle. In reality, muscles are controlled by the nervous system and possess greater complexity than is represented in this initial model. Turkawski and van Eijden (2001) showed that muscle force is dependent on sarcomere length, and that during jaw opening the force generate by the muscle depends on their instantaneous length. The methods reported here for muscle force calculation are unique in that the muscle force values varied with angle, and these muscle forces were then applied to predict joint force and bite force in the *Uromastyx* lizard.

As mentioned previously, the study of Herrel et al. (1998a, b) formed the base of the present research. Herrel et al. (1998a, b) measured the PCSA of the jaw

adductor muscles of the *Uromastyx acanthinurus* along with other lizards, and from these findings they performed a two dimensional static analysis to predict bite force and assess the effect of different food particle directions on joint reaction forces. Their muscle data was used in this work, and a comparison of bite force was made at a gape angle of 10°. Herrel et al. (1998a) reported a bite force of 9.1 N and a joint force of 25.7 N for a food reaction force of 90° (as simulated in this work-see Figure 4.2). The model described here predicted a bite force and joint reaction force of 6 N and 14 N respectively (Figure 4.3 and Figure 4.4) at a 10° gape angle. However, when a constant muscle force was applied (calculated at 20° gape) a more comparable bite force of 12 N and a joint force of 25 N were produced (Figure 4.5 and Figure 4.6). Using the muscle force from a 20° gape we see (Figure 4.5) that bite force decreases as gape angle increases (inverse of Figure 4.3), which is also true for a more anterior bite point. This is comparable with the literature (e.g. Cleuren et al., 1995).

Analysing the forces generated within the muscles gives interesting, and potentially useful information. Compressive forces were recorded in the MAMESP and MAMEP muscle groups, when a posterior joint displacement was considered which implies that these muscles do not participate in jaw opening. However, these are preliminary simulations and it may be the case that a 10° opening with a 2 mm backward movement of jaw is not a fully realistic kinematic representation for the lizard, since others have shown via EMG data that these muscles are active during jaw opening (e.g. Throckmorton, 1980).

# 4.3.2 Study 2: Accurate geometry model

This study builds on the model described in Study 1, but greater anatomical accuracy was included in the skull model, and the broad attachment areas of the muscles were represented.

#### 4.3.2.1 Method

#### **Model Construction**

There were some additional modifications to the MDA model in the second stage of development. First we included mobile quadrate bones which are able to pivot foreand-aft due to a relaxation of the bony contacts with the rest of the skull. They were segmented separately in the CT images using AMIRA and imported back into ADAMS MDA software as separate parts. In addition to this, the mandible was divided into two sections and imported as two separate parts, which were connected together at their anterior tips by a spring of high stiffness (1000 N/mm). This modification allowed separate hinges to be defined at each joint on each quadrate, allowing asymmetric biting to be modelled. The masses of the jaw and quadrates were calculated directly from ADAMS, based on the volumes of the rigid-bodies and assuming a standard tissue density of 1050 kg/m<sup>3</sup> (Sellers and Crompton, 2004). A mass of 1.54 g and 0.27 g was predicted for the jaw and each quadrate respectively. The cranium was fixed throughout all testing (hence no mass was required) 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 (Figure 4.10).

The adductor mandibulae externus superficialis anterior (MAMESA) muscle was also repositioned to represent more realistic origin and insertion areas of this muscle, while, the MPTE and MPTM muscle groups were divided into 3 sections, where the attachment of the springs represented the broad attachment areas of the actual muscles. All other muscle groups were divided into two sections (see Figure 4.10). In addition, the temporal ligament was included in this model. The temporal ligament was divided into two sections, where each section had a stiffness value of 50 N/mm (i.e. total ligament stiffness of 100 N/mm); this is comparable to ligament values reported in the literature (e.g. Noyes and Grood, 1976; Trent et al., 1976; Woo et al., 1991; Momersteeg et al., 1995; Kucuk, 2006). The ligament and muscle springs were defined as tension only elements (i.e. no compressive resistance), and again were specified with stiffness values scaled from the cross-sectional area data specified in Herrel et al. (1998a, b). A stiffness value of 1 N/mm was assigned to the muscle spring that had the smallest PCSA, and all other stiffness values were scaled accordingly (see Table 4.5). Equation (2) was defined to specify the properties of the springs:

$$F = \begin{cases} 0 & l \le l_{oB} \\ D\left(\frac{dl}{dt}\right) + K\left(l - l_0\right) & l > l_0 \end{cases}$$
(2)

where *F* is the force generated (N), *D* is the damping ratio (Ns/mm), t is the simulation time (s), *K* is the stiffness coefficient (N/mm), *l* is the calculated length of the spring (mm) and  $l_0$  is the original length (mm). In this analysis, D = 0.01 Ns/mm was assumed for all muscles.

The muscle PCSA values can also be used to define the maximum muscle force that each muscle can apply, where the theoretical maximum muscle force is calculated from equation (3) (e.g. Weijs and Hillen, 1985; Sinclair and Alexander, 1987).

$$maximum\ muscle\ force = PCSA \times maximum\ active\ stress$$
(3)

Maximum active stress (often termed specific tension) varies according to fibre types

and species, but generally has a value of  $25 \text{ N/cm}^2$  for the muscles of mastication (Nigg and Herzog, 1999). The maximum force that each muscle section could then produced is summarised in Table 4.5.





The neck and the depressor mandibulae were removed from this model. The neck was not required as no neck muscles were modelled, and the depressors were removed since jaw closing was being simulated and not jaw opening. The final modification to the MDA model was the inclusion of a spring (stiffness = 10 N/mm)

	PCSA (cm <sup>2</sup> )	Scaled PCSA (cm <sup>2</sup> )	Stiffness (N/mm)	Max muscle force(N)
MAMEM	0.221	0.353	6.921	
MAMEM1			3.460	4.412
MAMEM2			3.460	4.412
MAMESP	0.172	0.274	5.372	
MAMESP1			2.686	3.425
MAMESP2			2.686	3.425
MAMESA	0.144	0.230	4.509	
MAMESA1			2.254	2.875
MAMESA2			2.254	2.875
MAMEP	0.117	0.187	3.667	
MAMEP1			1.833	2.337
MAMEP2			1.833	2.337
MPTE	0.333	0.531	10.411	
MPTE1			3.470	6.637
MPTE2			3.470	6.637
MPTE3			3.470	
MPTM	0.277	0.442	8.667	
MPTM1			2.889	11.05
MPTM2			2.889	
MPTM3			2.889	
MPST	0.032	0.051	1	
MPST1			0.5	0.637
MPST2			0.5	0.637

located between the teeth on both sides of jaw to represent a food particle.

Table 4.5 Muscle data PCSA value are those reported by Herrel et al. (1998a, b) for *Uromastyx acanthinurus* with 28.2 mm in skull length and 26.6mm in skull width, PCSA scaling are scaled value of muscle cross section according to skull length of *Uromastyx hardwickii* with 45 mm in skull length, a stiffness of 1 N/mm assigned to smallest muscle cross section the other muscle stiffness changed accordingly, and maximum muscle force calculated from equation (3).

#### Simulations

The relative muscle and ligament forces were calculated directly from ADAMS using an inverse dynamic solution. The jaw was opened by applying a constant vertical force to the mandible, whose value was arbitrary and was varied until the jaw opened to an equilibrium state, which equated to a gape angle of approximately 21.5°. As the jaw opened the muscle and ligament groups were stretched or

compressed, and thus the relative force distribution through the muscles could be calculated.

Biting simulations were then performed in two ways, either based on forces from the PCSA values or from the inversely calculated muscle forces. At a constant gape of 21.5° single component force vectors were applied from the origin and insertion markers of the springs, which were deactivated during the biting simulations. The food bolus angle was approximately 80° (to the horizontal) during these biting simulations (see Figure 4.12).

To help understand the role of the temporal ligament, two variations were considered. Firstly, a backward mandibular force was applied to the retroarticular process (see Figure 4.11). Secondly, the angle of the bite force during biting simulations was varied (see Figure 4.12). These additional simulations were performed since the quadrate angle and muscular forces indicated that the jaw would simply collapse during biting unless there was an additional posterior force component to stabilise the model. During the assessment of the food particle direction, we discovered (through trial and error) that a minimum backward force of 4 N (2 N on each side) was necessary to prevent instability.



Figure 4.11 A biting simulation with an additional horizontal backward force applied at the back of the jaw (retroarticular process), to prevent collapse during biting.



FP angle  $\approx 40^{\circ}$ 

Figure 4.12 Variation of the loading angle of the food particle (FP), where the same tooth was used on the cranium, but a different tooth was used on the mandible.

#### 4.3.2.2 Results

Table 4.6 (column 2) presents the muscle forces calculated from the inverse dynamic simulations as the jaw reached a gape of 21.5°, which was accompanied by a 7° forward movement of the quadrate. All values are an average of the left and right muscle forces. Traditionally, researchers have applied the maximum muscle force at all gape angles, however it is reasonable to expect muscle forces vary with gape and most muscles will not act at a maximum level during all activities. Taking this into account we note that some of the inversely calculated muscle forces are significantly higher than their maximum allowable values (see column 3 of Table 4.6), while some are lower. The most significant deviation was noted in the MAMEM 2, which was

approximately two times larger than its maximum allowable value (i.e. 9.607: 4.412).

	MDA	Max allowable	Scaled muscle
	prediction (N)	muscle force	force (N)
		(N)	
MAMEM			
MAMEM 1	8.843	4.412	4.061
MAMEM 2	9.607	4.412	4.412
MAMESP			
MAMESP 1	2.344	3.425	1.076
MAMESP 2	3.327	3.425	1.527
MAMESA			
MAMESA 1	3.578	2.875	1.643
MAMESA 2	4.731	2.875	2.172
MAMEP			
MAMEP 1	4.864	2.337	2.233
MAMEP 2	3.840	2.337	1.763
MPTE			
MPTE 1	4.582	6.637	2.104
MPTE 2	0.341	6.637	0.156
MPTE 3	0		0
MPTM			
MPTM 1	3.016	11.050	1.385
MPTM 2	0		0
MPTM3	0		0
MPST			
MPST 1	1.019	0.637	0.467
MPST 2	1.193	0.637	0.547

Therefore, all muscle forces were scaled down accordingly as shown Table 4.6.

Table 4.6 Muscle force values calculated from the MDA which are then scaled down so that no force exceeds the maximum muscle force predicted from the muscle's PCSA.

Applying the scaled inversely calculated muscle forces to the model, a total bite force of approximately 24 N (12 N on each side) was predicted, however this analysis did not include the additional backward force and the simulation ended in a collapsed un-equilibrated state. Applying the maximum muscle force a total bite force of 44 N was predicted under the same test conditions.

During jaw opening the temporal ligaments are in compression (i.e. slack), similarly, when during a biting simulation (food bolus angle >  $82^{\circ}$ ) without the backward force, the temporal ligaments remain slack, resulting in an unstable model. Including the backward force balanced the model and resulted in tensile forces in the temporal ligaments. The effect of different backward forces on the temporal ligament tensions and bite forces are summarised in Figure 4.13 and Figure 4.14 respectively.



Figure 4.13 Effect of the backward force on the ligament forces (where the forces are the sum of the left and right hand sides).



Figure 4.14 Effect of backward force (where the forces are the sum of the left and right hand sides) on the bite force.

The bite force angle varies during natural chewing, which was also examined in the present study by noting the effect of the changing bite force direction during the biting simulations (Figure 4.12). Tensioned temporal ligaments reflect a stable biting model, since the ligaments restrict the motion in the horizontal plane, thus the effect of changing the bite force angle on the temporal ligament forces are summarised in Figure 4.15. It can be seen that a bite force angle in excess of 82° requires a complementary horizontal posterior force to maintain equilibrium. However, the posterior force component applied to the model by some bite force directions means that the backward force is not necessary at all bite force angles. In addition to the changing temporal ligament forces we also note that the bite force varies with varying food bolus angle (see Figure 4.16). However, note that these findings will be attributable in part to the changing bite point as well as bite force direction.



Figure 4.15 Variation of ligament force versus change of food particle direction.



Figure 4.16 Variation of bite force versus change of food particle direction.

#### 4.3.2.3 Discussion

Past biomechanical models of the masticatory apparatus, such as these developed by Koolstra et al. (1988), Cleuren et al. (1995), Herrel et al. (1998a, b), and Sellers and Crompton (2004) tend to represent muscle forces as a single working line based on the muscles PCSA. In the present study the broad anatomical muscle attachment areas have been recreated in some part 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 identified that the forces throughout the muscle are not constant, and it was even noted that one section of a muscle could be in compression (slack) while its neighbour was in tension (see Table 4.6). This finding compares well to experimental work by Turkawski and van Eijden (2001), which showed varying masseter muscle function at changing gape angles.

During the simulations, the MPTE3 and MPTM2 and MPTM3 muscle groups went into compression, thus they were assumed to be inactive. The biting simulations therefore did not include these muscle sections, and the maximum muscle force predicted from the muscles PCSA was only applied to the remaining active regions (MPTE1, MPTE2 and MPTM1). Before carrying out the biting simulations it was hypothesised that an additional horizontal force would be required to help the quadrate move back to its initial position and produce a stable model. This proved true during a biting simulation where the bite force angle was in excess of 80°. No sensory mechanisms were included in the models to regulate muscle activity, and in reality it is likely that lower muscle forces would be generated to chew food with a lower stiffness (such as the 10 N/mm stiffness in these studies). In this model of *Uromastyx*, maximum muscle forces were applied to bite a food particle with a stiffness of 10 N/mm, which could be the reason for the buckling that occurred during the biting simulations. *In vivo*, muscle activity is regulated by mechanoreceptors that can vary muscle activation according to the stiffness of food bolus (e.g. Thexton et al., 1980; Thexton and Hiiemae, 1997). In addition we cannot ignore the stabilization role of the muscles attached underneath the mandible (see Figure 4.17).

Amongst biologists the role and function of the temporal ligament has received a lot of attention over the last few decades (e.g. Frazzetta, 1962; Throckmorton, 1976; Iordansky, 1996; Herrel et al., 1998a; Wu, 2003). From this study we can conclude that the temporal ligament is inactive during jaw opening, but plays an important stabilising role during biting. As the posterior forces increase, either as a result of the muscular forces or the food bolus reaction forces, the ligament tensions increase (see Figure 4.13 and Figure 4.15), highlighting their importance in restricting excessive posterior motions of the mandible.



Figure 4.17 "Uromastix acanthinurus Jaw and hyolingual musculature. Upper left: Lateral view after removal of the skin, the m. pterygoideus externus, the quadratojugal ligament, and the m. depressor mandibulae. Lower left: Deeper lateral view, after the additional removal of the complete m. adductor mandibulae externus. Upper right: Superficial ventral view of the hyolingual muscles after removal of the skin, part of the m. intermandibularis anterior, the m. constrictor colli, and the m. omohyoideus. Lower right: Deeper dissection; after removal of the hyoid retractor and protractor muscles, the m. genioglossus medialis and the m. branchiohyoideus. CBI, ceratobranchiale I; CBII, ceratobranchiale II; CH, ceratohyale; MAMEM, m. adductor mandibulae externus medialis; MAMEP, m. adductor mandibulae externus profundus; MAMESA, MAMESP, mm. adductor mandibulae externus superficialis anterior and posterior; MAMP, m. adductor mandibulae posterior; MEM, m. epistermocieidomastoideus; MGGL, MGGM, mm. genioglossus medialis and laterlis; MHG, m. hyoglossus; MIMASP, m. intermandibularis anterior superficialis posterior; MLAO, m. levator anguli oris; MMH1, MMH2, MMH3, mm. mandibulohyoideus 1,2, and 3; MPsTS, . pseudotemporalis superficialis; MPtext, m. pterygoideus externus; MRAO, m. retractor anguli oris; MSH, m. sternohyoideus; MST, m. sternothyroideus" (Herrel et al., 1998c).

# 4.3.3 Study 3: Accurate muscle model

This study again advances on the previous models described in Studies 1 and 2. Here a sophisticated muscle model was introduced to provide more realistic muscle force predictions.

#### 4.3.3.1 Method

#### **Model Construction**

The basic model construction has been explained in detail in the previous sections, with the only modification in this analysis being the addition of a coupler to replace the stiff spring that connected the two parts of mandibles together. This coupler provided a rigid connection between the two sections and eliminated any movement at the joint.

All muscle origin and insertion points remained the same as the previous model however, the muscles were modelled according to van Ruijven and Weijs (1990) (see equation (4)) using a 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. Thus,

$$F_{muscle} = F_{max} \times \left( F_A \times F_V \times F_Q + F_P \right) \tag{4}$$

where  $F_{max}$  is the maximal tetanic force, i.e. physiological cross-sectional area (PCSA) × 30 N/cm<sup>2</sup> (van Ruijven and Weijs, 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 the scaled PCSA data reported by Herrel et al. (1998a, b) and previously described in Section 4.3.2.1.

The force length factor ( $F_A$ ) was estimated by a second order polynomial, as defined in equation (5) (Epstein and Herzog, 1998).

$$F_{A} = -6.25 \left(\frac{L}{L_{0}}\right)^{2} + 12.5 \left(\frac{L}{L_{0}}\right) - 5.25$$
(5)

where *L* is the current muscle length and  $L_0$  is the optimal muscle length at which the muscle can apply its maximum force. For the purpose of this study an optimum gape angle of 15° was chosen (Herrel, personal communication; Turkawski and van Eijden, 2001) at which point the corresponding optimal muscle length ( $L_0$ ) 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 equation (Hill, 1938) - see equation (6).

$$Fv = \begin{cases} \frac{\left(1 - \frac{V}{V_{\text{max}}}\right)}{\left(1 + \frac{V}{k \times V_{\text{max}}}\right)} & V \ge 0 \\ \frac{1.8 - 0.8\left(1 + \frac{V}{V_{\text{max}}}\right)}{\left(1 - \frac{7.56V}{k \times V_{\text{max}}}\right)} & V < 0 \end{cases}$$
(6)

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. (1998) according to the skull length of our model, and multiplied this by a value of 14.6 × muscle length/s, as reported by Marsh and Bennett (1985) (see Table 4.7). k (=0.25) is a constant calculated by Close (1964) assuming that jaw muscles consist mainly of fast fibres (van Eijden and Turkawski, 2001). A summary of the muscle PCSA, force and contraction velocity data is presented in Table 4.7.

The effect of the passive element in equation (4) was estimated by equation (7) (Weijs et al., 1989).

$$F_p = 0.0014e^{\frac{6(L-L_0)}{L_0}} \tag{7}$$

Muscle	Scaled PCSA	$F_{max}$	Scaled fibre	V <sub>max</sub>
group		(N/CIII)	length (cm)	(1111/8)
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
MAMESAI	0.115	3 4 5 0	0.004	7.54
MAMESA1	0.115	3.450		
IVIAIVIESA2	0.115	5.450		
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		
мртм	0.442		0.175	25 550
MDTM1	0.442	4.410	0.175	25.550
MDTM2	0.147	4.410		
MDTM2	0.147	4.410		
	0.14/	4.410		
MPST	0.051		0.032	4.672
MPST1	0.025	0.765		
MPST2	0.025	0.765		

Table 4.7 Muscle PCSA, force and contraction velocity data used in the third study.

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 equation (8). A default stiffness value of 50 N/mm was assigned to each section of the ligament (note a value of 100 N/mm for sum of lig1 and lig2). This stiffness value was later varied in the stiffness sensitivity study (see Section 4.3.3.2).

$$F_{ligament} = \begin{cases} K \times (L - L_i) & L \ge L_i \\ 0 & L < L_i \end{cases}$$
(8)

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 Figure 4.12).

Finally, a food particle was included in the biting simulations, represented by a resisting spring-damper located between the teeth and defined by equation (9).

$$F_{bite} = B \times (L - L_0) + C \times V \tag{9}$$

where B (= 100 N/mm) is the stiffness of the food and C (= 9 Ns/mm) is the damping ratio.

#### Simulations

Based on the experimental data for *Uromastyx* specimens reported in the literature (e.g. Throckmorton, 1980; Herrel et al., 1999a) a motion driven analysis lasting 0.32 seconds 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-squomosal joint (joint 2) was defined during opening, resulting in a gape angle of  $35^{\circ}$  [gape angle = joint 1 – joint 2], as illustrated in Figure 4.18. These movements agree with the literature (e.g. Throckmorton, 1976). The open jaw position was then the start point for the forward dynamic simulation (biting simulation) in which a food bolus was in direct contact with the teeth.

Muscle lengths [L], i.e. the distance between the muscle attachment on the cranium and the muscle attachment of the mandible, directly influence the muscle forces as defined in equation (5). These muscle lengths along with their rate of change, or velocity (V) are calculated by ADAMS and used in the muscle force equations needed for the forward dynamic simulations in which the ligament, joint and bite forces are calculated. An assumption was made for 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 quadratosquamosal and quadrato-mandibular joint rotations).



Figure 4.18 Quadrato-squamosal, quadrato-mandibular and gape angles during one cycle of biting.

The dynamic simulations of the jaw closing phase assumed 100% muscle activation (i.e.  $F_Q = 1$ ) and formed the biting simulations, during which the effects of two parameters were assessed. Firstly, the food particle was positioned between different teeth to investigate the effect of its position on bite force and joint force. It was moved 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 mm, 5 mm, 13 mm and 18 mm from the tip of the mandible respectively. Secondly, the temporal ligament stiffness was varied (K=5, 30 and 50 N/mm) to help quantify its role and to assess the sensitivity of the model to this parameter.

#### 4.3.3.2 Results

Figure 4.19 shows sample muscle forces applied during the jaw opening and closing phases. It was assumed that the jaw adductor muscles were only became active during the jaw closing phase of the simulations, thus force was only generated in the

muscles after 0.32 seconds (after the jaw opening phase). During the jaw opening phase some sections of pterygoideus externus and pterygoideus medialis (MPTE3, MPTM2 and MPTM3) were compressed and therefore assumed slack, which meant that they were inactive during jaw closing.



Figure 4.19 Muscle force data versus time for selected adductor muscle sections. The muscles start to contract at maximum gape (time=0.32 sec, gape=35°) and continue until the jaw closes (time=0.9sec).



Figure 4.20 Variation in the bite force, joint forces and ligament forces 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.
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 Figure 4.20). In addition, moving the bite point posteriorly in the mouth resulted in lower strain in the temporal ligament. Excluding the temporal ligament completely caused the jaw to become unstable at low gape angles. A temporal ligament stiffness of 5 N/mm was found to add stability to the model at low gapes, where a combined maximum force of approximately 3.2 N was recorded within the temporal ligaments. Increasing the stiffness of the temporal ligaments to 30 N/mm and 50 N/mm did not alter the motions of the jaw during biting, but the combined maximum force in the ligaments increased to approximately 5.0 N and 5.1 N for the 30 N/mm and 50 N/mm stiffnesses respectively (see Figure 4.21). However, as the stiffness of the ligament tissue was increased, the loading of the anterior and posterior sections varied. At a ligament stiffness of 5 N/mm both the anterior and posterior ligament sections were loaded similarly (1.6 N  $\pm$  0.3 N), but at a stiffness of 30 N/mm the anterior portion carried 80% of the load, with this value increasing to 98% at a stiffness of 50 N/mm.



Figure 4.21 The effect of varying ligament stiffness on the forces generated in the anterior (lig1) and posterior (lig2) portions of the temporal ligament during biting.

#### 4.3.3.3 Discussion

For the *Uromastyx hardwickii* skull with its 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 Figure 4.22). 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.



Figure 4.22 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 different bite points i.e. front, middle 1, middle 2, and back.

Modelling the temporal ligament and varying its stiffness allowed us to evaluate its function more closely. Data on the ligaments of lizards is very limited, hence a sensitivity study was undertaken to assess the effect of ligament stiffness on the model's behaviour. It was found that the total ligament loading was similar irrespective of the ligament stiffness (when the total ligament stiffness assessed ranged from 5 to 50 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; 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) 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 the simulations here induced this condition.

## **4.4 Discussion**

This chapter has outlined the development of the multibody dynamic models used to simulate biting in the *Uromastyx* lizard. The effects of parameters such as food particle location, direction and stiffness, ligament stiffness and representation of muscles as either single or multiple strands have been assessed, and despite some approximations within the models, comparable results to those reported in the literature have been produced. The MDA simulations began with a relatively simple representation of a single hinged joint with single muscle strands modelled as springs. Progression to an additional planar element in the joint permitted anterior-

posterior translations. This was then replaced by the inclusion of the quadrates and the formation of the quadrato-squamosal and quadrato-squamosal joints. Muscles were defined with appropriate relative stiffness values and divided into multiple sections to cover the broad anatomical attachment areas of some of the muscle groups, and simulations were run where muscle forces varied with gape. Later more complex force-length characteristics were implemented into the muscle models and biting simulations conducted.

As with most computational modelling studies there are simplifications and assumptions in the model. Knowing the model's limitations and understanding how the simplifications and approximations affect the results obtained is vital. The muscles that move and control the lizard jaw are complex and designed to undertake a variety of different activities. For example, chewing (bilateral and unilateral biting, grinding) and opening and closing the mouth for vocal and visual display. Using 100% activation for each muscle in the biomechanical simulations of these activities is a simple, convenient approach, but is almost certainly wrong. Muscle wrapping should be also included around the mandible of this animal but based on the work of Curtis et al. (2008), 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. If they were removed and replaced with more realistic saddle-type joints this would undoubtedly lead to 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, possibly with an interposed cartilage layer to dampen joint forces.

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.

# **Chapter 5: Finite element analysis of a lizard skull**

# **5.1 Introduction**

This chapter describes the finite element analysis (FEA) of different skull models loaded with the force data obtained from the MDA work described in Chapter 4. The first section gives a brief review of the FEA package used in this study, with the rest of the chapter divided into four main studies. Each study description includes its own aims and objectives followed by the results obtained and a brief discussion. An overarching discussion is then included at the end of the chapter.

# **5.2 Overview of ANSYS**

ANSYS (ANSYS Inc., Canonsburg, Pennsylvania USA) is a three-dimensional finite element modelling package that is widely used in industry and academia. Originally developed in the 1970's to analyse mechanical systems, ANSYS is now being increasingly used in the anatomical and biological sciences. The finite element method (FEM) provides a numerical solution to a specific problem by sub-dividing the structure in question into a finite number of elements, which are connected at their corners (and sometimes along their sides) by nodes. A variable (such as displacement or temperature) is assumed to act throughout each element in a predefined manner, so that the variable distribution through the whole body can be approximated by combining all the individual element solutions. A set of equations defining the behaviour of each element is formed from its geometry and material properties. The individual element equations are then assembled to give the system equations that describe the behaviour of the whole body, and is generally of the form:

$$[K]{U} = {F} \tag{1}$$

where [K] is known as the stiffness matrix,  $\{U\}$  is a vector of the unknown parameters (displacement or temperature) and  $\{F\}$  is a vector of the applied nodal forces (or applied heat). From a user point of view, loads, constraints and material properties are applied to a meshed model (i.e. divided into elements) and the finite element package generates and solves the system equations. More detailed descriptions of the FE method and its application are available (e.g. Burnett, 1987; Fagan, 1992; Cook, 1995).

# 5.3 FEA modelling of a Uromastyx skull

Four main FEA studies were conducted: Study 1 was a preliminary investigation to compare simplistic loading methods with more comprehensive (static) load data obtained by MDA; Study 2 applied the dynamic load data obtained from the MDA to the FE model to assess the stress and strain over a full biting cycle; Study 3 investigated the role of cranial sutures; and Study 4 assessed the effect of varying the morphology of the skull.

## 5.3.1 Study 1: FEA vs. combined FEA and MDA

In Study 1 different boundary conditions were applied to the skull and their effects on the stress and strain in the skull assessed. The specific aim of this study was to provide a qualitative comparison between the FEA results obtained using different constraint and loading methods.

## 5.3.1.1 Method

#### **Model Construction**

The three-dimensional cranium model developed for the MDA was transformed into a meshed solid geometry using AMIRA image segmentation software (Mercury Computer Systems Inc., USA). All the FE models developed in this chapter used SOLID92 tetrahedral elements (which are 10 node elements with a quadratic displacement behaviour) that are well suited for modelling irregular geometries (ANSYS Theoretical Manual, version 11). The meshed models were imported into ANSYS V11 Mechanical (ANSYS, Inc., Canonsburg, PA, USA) in preparation for the FEA. The models consisted of 207,000 elements and were assigned isotropic material properties, with a Young's modulus of 10 GPa and a Poisson's ratio of 0.3. These values are comparable to bovine haversian bone as used in other studies (e.g. Rayfield et al., 2001; Rayfield, 2005). Although bone is known to be anisotropic, previous studies (e.g. Strait et al., 2005) have shown that comparable patterns of strain across the model are generally produced assuming isotropy.

#### Simulations

To highlight the benefits of MDA, a simple study was undertaken to assess three different boundary conditions as illustrated in Figure 5.1. Model A assumed a simple loading condition in which a bite force of 30N was applied to the front teeth (which corresponds to the bite force at a gape angle of 23° obtained from the MDA simulations) and constraints were placed at three nodes at the back of the skull (occipital condyle) in all directions. Model B had constraints at the quadrato-squamosal joint in two directions (y, z) and at the bite point in one direction (z), with muscle forces applied as single force vectors for each muscle group. In Model B the muscle groups simulated were: Adductor mandibulae externus superficialis anterior (MAMESA); adductor mandibulae externus medialis (MAMEM); adductor mandibulae externus profundus (MAMEP); pterygoideus externus (MPTE); pterygoideus medialis (MPTM), and pseudotemporalis superficialis (MPST) (see Section 4.3.2.1). Muscle forces were estimated based on the equation (2) and the muscle orientations were simplified into two dimensions (y-z plane) using the data obtain via the MDA simulations.



Figure 5.1 Models A, B and C, illustrating the different loading regimes  $\blacktriangleright$  and  $\blacktriangle$  signify constraints in the horizontal and vertical directions respectively, while the vertical arrow shows the bite force location. Muscle forces were also applied at the attachment points of the muscles in models B and C (see text for further information).

(2)

where a maximum active stress of 300 KPa was used based on the study of van Ruijven and Weijs (1990) and the physical cross-sectional area (PCSA) of each muscle group was obtained from (Herrel et al., 1998a). Model C included all the load data from the MDA simulations at a load step corresponding to a gape of 23°. Here 3D muscle forces (with several strands representing each), ligaments, joint and bite forces were all included in the FEA.

Interpreting the vast amount of data produced from a finite element analysis can be difficult, with different published studies often reporting different output parameters. The most popular data plots are principal strains and stresses, maximum shear stress and von Mises stress (or strain). The full three dimensional stress field at each point in the model consists of three direct stresses in the x, y and z directions and three shear stresses (commonly known as  $\sigma_x$ ,  $\sigma_y$ ,  $\sigma_z$  and  $\tau_{xy}$ ,  $\tau_{xz}$ ,  $\tau_{zy}$  respectively). These six values can be resolved into three perpendicular principal stresses known as  $\sigma_1, \sigma_2, \sigma_3$ ; (which are the normal stresses on planes which have no corresponding shear stresses). The advantage of considering the principal stresses is that they show the variation of the 'most tensile' and 'most compressive' stresses through the structure and reveal information about its mode of loading. Also, very importantly, their directions show the load transfer paths through the structure. Of course, on the surface of the model, the normal stress must equal zero, thus only two principal stresses need to be considered. The mode of loading and load path information is not provided by the maximum shear stress or the von Mises stress (or strain) values. The maximum shear stress is simply half the difference between the minimum and maximum principal stresses. The von Mises stress combines all the stresses at a point

into a single parameter 
$$(\sigma_v = \sqrt{\frac{(\sigma_1 - \sigma_2)^2 + (\sigma_1 - \sigma_3)^2 + (\sigma_2 - \sigma_3)^2)}{2}})$$
, and is a

convenient way of expressing the state of stress at that point by a single value. Like the maximum shear stress it gives no indication of whether the material is under tension or compression. In engineering analyses, both the maximum shear stress and the von-Mises stress are used in the prediction of failure of ductile materials – called Tresca's failure criterion and the von Mises failure criterion respectively (Timoshenko, 1955). While bone is a ductile material (Nalla et al., 2003), failure is not considered in most FE models of bone, and maximum shear stresses and von Mises stresses are simply used as simple scalar measures of stress level (e.g. Dumont et al., 2005; Grosse et al., 2007; Wroe et al., 2007). After consideration von Mises stress was chosen as the representative parameter in this chapter.

### 5.3.1.2 Results

Figure 5.2 shows the von Mises stress for models A, B, and C. In Model A, high stress concentrations were observed at the back of the skull in the region of the constraints. However, in models B and C the stress in this region was negligible, even though model C was also constrained at this point. Areas of high stress were seen in models B and C at the muscle attachment points and at the quadrato-squamosal joint in model B.



Figure 5.2 Comparison of the von Mises stress in models A, B and C. Note stress values are in MPa and that grey colours indicate stresses in excess of 32 MPa (selected to give more visually interesting contour plots).

#### 5.3.1.3 Discussion

The methods of constraining and loading an FE model are known to have an effect on the output of FE analysis. Therefore different boundary conditions were investigated in this study, where three models were constrained and loaded in different ways so that the effect on the stress distributions could be assessed. There are of course other factors that can affect the results of an FEA (such as muscle activation and bone material property) and these have been discussed in more detail by others (e.g. Ross, 2005; Richmond et al., 2005; Rayfield, 2007). Model A represented the simplest model (i.e. basic constraint and applied bite force), similar in design to that employed by others (e.g. Tanne et al., 1988; Miyasaka et al., 1994; Rayfield, 2005b). This approach, despite its simplicity can still be informative in comparative studies where the properties of different skull geometries are beings investigated. However, it clearly does not represent a realistic loading condition. Model B added more complexity by including (2D) muscle forces, with the model being constrained at the joints and bite position. This results in reaction forces being produced at the constraints, and is a method applied by others (e.g. Strait et al., 2005; Dumont et al., 2005; Grosse et al., 2007). Model C was the most complex situation that applied 3D forces (muscle, ligament, joint and bite forces) and was only constrained at the occipital condyle.

Model A and model C were both constrained at the same position (occipital condyle), however there was a negligible stress concentration at this point in model C, because it was loaded from the MDA simulations, which produced a state of equilibrium between the muscle forces, ligament forces, joint forces and bite forces. The stress distributions in model B and model C seem virtually identical, even though model B was loaded with only 2D muscle forces and constrained at the joints

and at the bite point. This indicates that in this case using a simplified loading regime can produce similar findings to more complex loading.

In model B and model C stress concentrations were observed in the dorsal region of the jugal/squamosal suture due to the action of the locally-applied muscle forces, which were not present in model A. This is caused by the use of point loads rather than distributed loads (as occur *in vivo*). Recent research, by Grosse et al. (2007) has attempted to address this by distributing the muscle forces over a wide area. In our study one interesting finding was that in the ventral view stress distributions were similar in the nasal and frontal bones for both models, confirming that the stress in this region is predominately due to the bite force, as expected (see Figure 5.2).

In summary it has been shown that similar FE results can be obtained with either an MDA loaded model and a model loaded via traditional means. However, it is not known which produces the most physiologically reasonable result. We believe that since gape angle is changing during biting the MDA solution should be used or alternatively model B must be repositioned during each bite step. The effect of this variation in gape angle was considered in study 2.

## 5.3.2 Study 2: FEA modelling of biting

In study 2 the MDA load data for an entire cycle of biting was applied to an FE model so that the variation in the stress with time can be assessed. The specific aim of this study was to assess the variation of stress throughout the skull during a complete biting cycle.

### 5.3.2.1 Method

#### **Model Construction**

The model in this study was identical to that described in study 1, i.e. the same element type, number of elements and material property, with the same boundary conditions as those of model C of study 1.

#### Simulations

To investigate the variation of stress across the skull during an entire cycle of biting, fifty load steps from the MDA solution were imported into the FE model. These included muscle forces, ligament forces, bite forces and joint forces. This loading data was taken for three different bite points and represented initial biting at a gape of 32.6° until final biting at a gape of 0.9° (i.e. jaw closing as the food particle was compressed, see Section 4.3.3.1). Figure 5.3 shows the MDA model with the three bite points highlighted (i.e. front, middle, back).



Figure 5.3 Figure showing the different bite points considered in the FE model.

#### 5.3.2.2 Results

Figure 5.4 shows the von Mises stress distribution during a bilateral biting simulation at the front of the mouth (incisiform teeth), corresponding to the varying loading conditions (i.e. muscle forces, joint forces and bite forces) at gapes of 32°, 23° and 0.9°. Ten regions were also identified on the surface of the model (Figure 5.5) in which the data were examined in more detail. For example, the variation in the von Mises stress at these ten locations during the biting simulations is shown in Figure 5.6.



Figure 5.4 Ventral and lateral view of the von Mises stress during bilateral biting on the front teeth. A, B and C correspond to biting at gape angles of 32°, 23° and 0.9°. Note stress values are in MPa and that grey colours indicate stresses in excess of 32 MPa (selected to give more visually interesting contour plots).



Figure 5.5 Location of ten regions used for further more detailed results analysis. (A) is a ventral view. (B) is a lateral view. R1 and R2 are close to the upper temporal fenestra whereas R3 is positioned between the eyes. R1, R2, R3 can provide information on parietal and frontal bones. R4 is selected on the narrow region between the eye and upper temporal fenestra. R5, R6, R7 are all positioned on the jugal which is a relatively thick bone. R8 is located on the maxilla, close to the connection of the jugal, the maxilla, the prefrontal and the palatine. R9 is on the nasal region between nose and eyes. R10 was selected in the dorsal region of the skull on palatine.



Figure 5.6 Variation of von Mises stress during biting at the front of the mouth (Note the reversed X-axis labels reflecting jaw closing during biting).



Figure 5.7 Comparison of the von Mises stress in three regions of the skull for different bite points.

A comparison of the von Mises stress at three locations on the skull (R1, R3 and R7) is shown in Figure 5.7 for the three different bite positions (Figure 5.3). These three points (at the root of the left postparietal process, between the orbits, and at the root of the left postorbital bar above the end of the tooth row) were chosen to represent anterior, posterior, and lateral skull regions. The maximum variation was noted at R3, where biting at the rear of the mouth led to a reduction in stress of 81% compared to the front of the mouth (front -2.96 MPa, back -0.54 MPa). A reduction of 23% was also noted at R1 (front -11.40 MPa, back -8.81 MPa), but the stress in R7 did not vary significantly.

Figure 5.8 shows a vector plot of the stress distribution on the surface of the skull, with blue arrows representing compression and black arrows representing tension. Because of the number of elements in the model, it is impossible to see the detailed directions in this plot, but it is interesting to observe the regions where tension and compression are dominant. Figure 5.9 illustrates the third principal (most compressive) stress, where Figure 5.9A shows those elements that are negative, i.e. compressive, and Figure 5.9B shows those (few) elements that are positive, i.e. tensile (the loading data that produced the stress plots in Figure 5.9 were taken from a front bite point MDA simulation at a 0.9° gape).



Figure 5.8 Lateral and ventral views of a stress vector plot for biting in the front of the mouth at a gape of 0.9° of stress. Blue arrows represent compression and black arrows represent tension.

Figure 5.10 compares the first principal (most tensile) stress and the third principal (most compressive) stress obtained from a biting simulation in the front of the mouth (biting at gape angles of  $0.9^{\circ}$ ) and a real *Uromastyx* lizard skull in which the cranial sutures are highlighted. From this figure it appears that higher stress regions exist near the suture locations.



Figure 5.9 Third principal stress in the skull during biting in the front of mouth at a gape angle of 0.9°. (A) is a negative scale and (B) is a positive scale. Note the grey colour in (A) shows values greater than zero whereas in (B) it shows values less than zero.



Figure 5.10 (A) first principal (most tensile) stress; (B) real *Uromastyx* skull; (C) third principal (most compressive) stress. A comparison of the distribution of the stress predicted by the FE model with the location of the sutures in a real skull of an *Uromastyx hardwickii* (UCL collection) in ventral and lateral views. Note the quadrate was included in the MDA model but is not modelled in the FEA study, and hence is not shown in the FE plot. The grey colour in (A) shows values less than zero whereas in (C) it shows values greater than zero. FE plots obtained from biting at a gape angle of 0.9°at the front of the mouth. [Nomenclature: pop, postparietal process; pof, postfrontal; pob, postorbital bar-i.e. separating orbit from temporal region; aom, antorbital margin; f, frontal; pf, prefrontal j, jugal; n, nasal; oc, occipital condyle; pal, palatine; par, parietal; pm, premaxilla; q, quadrate; sq, squamosal; ep, epipterygoid; pt, pterygoid].

#### 5.3.2.3 Discussion

One of the main areas that distinguishes the present research from other previous work is the incorporation of detailed MDA load data into the FEA. Here we investigate the variation of stress during an entire biting cycle, whereas most of the previous FE studies are limited to a single loading condition. However, there are some exceptions, such as a study by Ross et al. (2005) where thirty-six different loading conditions were considered based on electromyography data (note, in the present study, 100% activity is assumed in all the muscles to estimate the maximum stresses).

From Figure 5.4 and Figure 5.6 it can be seen that stress varies throughout the skull during biting, and to different degrees in different regions of the skull. This variation in stress is due to the variation in boundary conditions at different gapes (different magnitudes and directions of the muscle forces, bite forces and joint forces as calculated by MDA). A sudden increase of stress between a gape angle of 20° and 15° was noted during the biting simulation (see Figure 5.6). This occurs as a result of the combined increased tension in the different muscle groups at this stage of jaw closure and the resultant changes in reaction at the bite point and joint 1. See for example MAMESA1 in Figure 5.11 (from study 3 of Chapter 4); note other muscle strands, not shown, follow a similar pattern of activity to MAMESA1. Whether this happens as abruptly *in vivo* is not known, but the identification of this likely cause and effect highlights the value of MDA modelling.

This work has also shown that it is important to look at several loading situations, since variation in stress values across the skull clearly will occur with varying activity. Previously (in Chapter 4) we have shown that greater bite forces were produced with a more posterior bite point (also shown by others e.g. Koolstra et al., 1988; Dumont and Herrel, 2003; Sellers and Crompton, 2004), however, the FE

analyses in this chapter show that the peak stress within different regions of the skull tends to reduce with a more posteriorly positioned food bolus, even though the bite force increases (see Figure 5.7).



Figure 5.11 Sample muscle and ligament force data plotted versus gape angle from MDA corresponding to front biting.

The vector plot in Figure 5.8 provides information on the directional flow of stress and strain, as well as highlighting regions of compression and tension. From the lateral view we see that the frontal bone and teeth are in pure compression while the epipterygoid is in tension. From this visual assessment it seems as though the metakinetic axis (between sphenoid and pterygoid, epipterygoind and pterygoid and braincase and parietal) has the potential to alleviate some of these stresses.

The studies of Preuschoft and Witzel (2002, 2004, and 2005) (discussed in Chapter 3) consider FE models of skulls developed from primitive shapes. Their studies use the 3<sup>rd</sup> principal stress as an indicator for bone remodelling, and follow Wolff's Law (Wolff, 1892) which states that if bone is not used (i.e. it is unloaded) it is not needed and is therefore removed. Figure 5.9 examines this approach by plotting the tensile and compressive zones of the 3<sup>rd</sup> principal stress. This plot shows that virtually the whole skull is in compression (grey colour), thus showing that bone is loaded throughout. There are however small regions within the model that are in

pure tension, but would almost certainly be placed under compression if more loading situations were applied to the model (i.e. unilateral biting).

Another interesting finding during these FE studies was the identification of elevated 1<sup>st</sup> principal and/or 3<sup>rd</sup> principal stress patterns around anatomical suture zones (see Figure 5.10). Most notably between the prefrontal, maxilla and palatine in the antorbital margin, the postorbitofrontals and parietal, at the junction of the nasals, the prefrontals, the frontal and premaxilla on the snout, around the junction of the frontal and parietal, and at the suture between the jugal and squamosal and jugal and postorbitofrontal. This finding suggests that sutures may be located in areas of high tension/compression, and as such could act to alleviate the stress arising from biting, as suggested by previous experimental and computational studies (Herring et al., 1996; Herring and Teng, 2000; Rafferty et al., 2003; Rayfield, 2005). Figure 5.10 plots 1<sup>st</sup> principal stress and and 3<sup>rd</sup> principal stress for a model loaded with the MDA load data corresponding to a gape of 0.9° (comparable to the von Mises plot in Figure 5.4C). This highlights the importance of selecting the appropriate output parameter, since the information important to the analysis of sutures is shown in the 1<sup>st</sup> principal stress plot but not in the von Mises plot.

There are also high levels of stress at many of the interfaces between the braincase and the dermal skull, notably in the basipterygoid processes of the basisphenoid where they meet the pterygoids, in the paroccipital processes of the opisthotic (meeting the parietal, squamosal, supratemporal and quadrate), and in the posterior processes of the parietal. These strains may reflect the tendency of the braincase to move in relation to the skull roof and palate and thus be indicative of a selective advantage for greater freedom of movement (metakinesis). Comparison of the first and third principal stress (Figure 5.10) highlights another related feature not evident in the von Mises plots, namely the high level of tension in the epipterygoids

during biting in *Uromastyx* (Figure 5.10A). In lizards, the epipterygoids are slender mobile columns. Each has a synovial ventral joint with the pterygoid (in a pit, the fossa columellae) and a ligamentous dorsal attachment to the parietal and the braincase. Where present, the epipterygoids give origin to parts of the m. pseudotemporalis. They are thought to brace the braincase against the dermal skull when (if) one moves on the other during metakinesis, and may be absent or reduced in taxa where this movement is lost (e.g. chamaeleons, snakes, some agamids, Schwenk, 2000). The high level of tensile strain seen in this model during biting may result from direct muscle action, although the m. pseudotemporalis is not generating much force at this stage of the bite. Alternatively, like the stresses noted above, the tension in the epipterygoid may reflect a tendency of the braincase to rotate on the dermal skull during biting, pushing the pterygoids apart. In the living animal, these strains in the epipterygoid would be mitigated by its mobile dorsal and ventral articulations.

## 5.3.3 Study 3: Suture modelling

Study 3 builds on the findings from the previous studies. Areas of higher stress were noted around the location of sutures, even though they were not represented in the model. In study 3 the cranial sutures were included and their role and function examined by the FEA. The specific aim of this study was to test whether sutures relieve strain in skulls, as well as facilitating their growth.

#### 5.3.3.1 Method

#### **Model Construction**

From study 2 we observed that higher stress patterns occurred around the locations of the anatomical sutures, therefore to permit further analysis more detailed FE models were created that included the cranial sutures of the *Uromastyx*. Manual

segmentation of the original micro-CT dataset was performed to create four models, named: model A (bilateral jugal-squamosal suture), B (bilateral postorbital-parietal sutures), C (frontal-parietal suture) and D; where models A, B and C only included one simplified suture each to assess their individual roles, whereas model D included <u>all</u> the cranial sutures and were represented with greater anatomical accuracy (see Figure 5.12). As in the previous studies, all models were meshed with SOLID92 tetrahedral elements. Table 5.1 summarizes the number of meshed elements in each model. Based on some preliminary work and reported values in the literature (McLaughlin et al., 2000) sutures were assigned a Young's Modulus of 10 MPa and a Poisson's ratio of 0.3 (bone had E=10 GPa and  $\nu$ =0.3). All boundary conditions were applied as in the previous study (study 2), together with the load data from an MDA set to a posterior bite point at a gape of 7° (see Figure 5.3). A posterior bite point was chosen since models A, B and C all included sutures that are located in the back of skull, thus in theory greater stresses should be experimented by them compared to values developed by a front bite point.

	Model A	Model B	Model C	Model D
No. of elements	199,830	203,458	186,849	72,894

Table 5.1 Summary of element numbers in models A to D.

#### **Simulations**

There are many experimental studies reported in the literature to assess the mechanical properties of sutures (e.g. McLaughlin et al., 2000; Henderson et al., 2005 - also see review in Chapter 3). The reported values vary considerably from 1.2 MPa by Radhakrishnan and Mao (2004) to 15.7 GPa by Kupczik et al. (2007), and for this reason a sensitivity study was conducted into the effect of varying suture

stiffness. Thus the elastic modulus of the sutures was varied as follows: 1.2 MPa, 2.3 MPa, 10 MPa, 27 MPa, 2000 MPa, 8000 MPa and 10000 MPa in model A.

Models (A-D) were then loaded and constrained as before (see study 2). In all the models, two conditions were assessed, one representing the suture as fully fused (i.e. sutures assigned the same material properties of the bone), and one representing the suture as unfused (i.e. with a Young's Modulus of 10MPa). In the fused suture state, models A to D represent an identical condition (i.e. each element in the model is assigned bone material properties), thus any minor difference in the results is likely to be attributable to the varying number of elements between models (see Table 5.1). A qualitative and quantitative comparison was made between the two suture conditions in each of the models. The ten locations identified in study 2 (see Figure 5.5) were also assessed in each model along with additional locations, as shown in Figure 5.13. These additional locations allowed local suture effects to be assessed.

#### 5.3.3.2 Results

Figures 5.14 and 5.15 show the values of the 1<sup>st</sup> principal and von Mises strain obtained from the suture stiffness sensitivity study in model A. The strain reduced in R2, R5, R6, R7 and R11 as the suture stiffness increased from 1.2 MPa to 27 MPa, whereas in all other regions the strain increased. When the modulus of the sutures was set at 2000, 8000 and 10000 MPa there was no notable difference in strain. A qualitative comparison of von Mises strain in model A for a fused and unfused suture is shown in Figure 5.16, while Figure 5.17 presents a vector plot of strain obtained from the same model, showing that the strain vectors are perpendicular to the suture.

The von Mises strain values in model B for fused and unfused sutures are shown in Figure 5.18, with von Mises plots in Figure 5.19. These findings indicate that strains are relieved locally around the suture, but elevated in other regions of



Figure 5.12 The FE models created to test individual and combined role of sutures.



Figure 5.13 The additional regions identified on the skull for quantitative assessment of role of sutures used in addition to those shown in Figure 5.5.



Figure 5.14 First principal strain obtained from variation of suture stiffness across the different regions of skull (obtained from model A).



Figure 5.15 Von Mises strain obtained from variation of suture stiffness across the different regions of skull (obtained from model A).



0 .411E-03 .828E-03 0.001244 .001660 .002077 .002493 .002909 .003326 .003742

Figure 5.16 Von Mises strain in model A. (A) suture and bone modelled with same stiffness values ( $E_{bone} = E_{suture} = 10$  GPa), (B) suture and bone modelled with different stiffness values ( $E_{bone}=10$  GPa and  $E_{suture}=10$  MPa). Note the grey colour shows values greater than 0.003742.

the skull. Similar findings were noted in model C, as shown in Figures 5.20 and 5.21.

Model D, which modelled all the cranial sutures, showed a decrease of strain in R1, R13, R14, R15, R16 and an increase in all other regions, see Figure 5.22 and Figure 5.23. This was an unexpected finding, as one might expect the overall pattern of strain to reduce. From Figure 5.23 it is difficult to judge the overall reduction or increase of strain, therefore to visually display these findings von Mises strains in model D with fused and unfused sutures were subtracted from each other to give the plot shown in Figure 5.24. The scale in Figure 5.24 was set so that red areas represented a reduction of strain due to unfused sutures, while grey areas represented an increase in strain. Note model D consisted of 72894 elements in which 15013 were assigned to the sutures. It was found that, overall, the strain reduced in only 31% of the model. Also, since the larger strain values within the sutures themselves could affect the adjoining bone elements, when those adjoining bone elements were excluded strain was reduced in 37% of the remaining 28253 elements.



Figure 5.17 Vector plot of strain obtained from model A. Blue arrows represent compression and black arrows representing tension. (A) suture and bone modelled with same stiffness ( $E_{bone} = E_{suture} = 10$  GPa), (B) suture and bone modelled with different stiffness ( $E_{bone}=10$  GPa and  $E_{suture} = 10$  MPa). Note that the ovals highlight the jugal-squamosal suture.



Figure 5.18 Numerical comparison of von Mises strain over the specified regions of the skull in model B for fused and unfused sutures.



0 .411E-03 .828E-03 .001244 .00166 .002077 .002493 .002909 .003326 .003742

Figure 5.19 Von Mises strain in model B. (A) suture and bone modelled with same stiffness values ( $E_{bone} = E_{suture} = 10$  GPa), (B) suture and bone modelled with different stiffness values ( $E_{bone}=10$  GPa and  $E_{suture}=10$  MPa). Note the grey colour shows values greater than 0.003742.



Figure 5.20 Numerical comparison of von Mises strain over the specified regions of the skull in model C for fused and unfused sutures.



0 .411E-03 .828E-03 .001244 .00166 .002077 .002493 .002909 .003326 .003742

Figure 5.21 Von Mises strain in model C. (A) suture and bone modelled with same stiffness values ( $E_{bone} = E_{suture} = 10$  GPa), (B) suture and bone modelled with different stiffness values ( $E_{bone}=10$  GPa and  $E_{suture}=10$  MPa). Note the grey colour shows values greater than 0.003742.



Figure 5.22 Numerical comparison of von Mises strain over the specified regions of the skull in model D for fused and unfused sutures.



0 .411E-03 .828E-03 .001244 .00166 .002077 .002493 .002909 .003326 .003742

Figure 5.23 Von Mises strain in model D. (A) suture and bone modelled with same stiffness values ( $E_{bone} = E_{suture} = 10$  GPa), (B) suture and bone modelled with different stiffness values ( $E_{bone}=10$  GPa and  $E_{suture}=10$  MPa). Note the grey colour shows values greater than 0.003742.



Figure 5.24 A comparison of the stress before and after including all the sutures in the model D where grey elements show increase of von Mises strain and red elements show a decrease of strain.

## 5.3.3.3 Discussion

Sutures are connective joints that facilitate the longitudinal growth of skull bones. In addition, the jaw and skull have to be able to resist forces resulting from prey capture, chewing, and general impacts, which must be absorbed by the bone or by the sutures. There have been many studies involving sutures, looking for example at their shock absorbing/ stress releasing characteristics (e.g. Smith and Hylander, 1985; Jaslow, 1990; Herring and Teng, 2000; Rafferty et al., 2003; Popowics and Herring, 2007), or general sutural morphology (Tanaka et al., 2000; Mao, 2002). The properties of sutures change with age, suggesting that sutures are adaptive structures that regulate themselves according to the mechanical stimuli in a process that can occur over both short and long periods (e.g. Wagemans et al., 1988). Some
experimental studies, such as those by Herring and Mucci (1991) and Markey et al. (2006), show that the morphology of sutures reflects the loading and consequent strain patterns applied to them.

This present study examined their biomechanical role via FEA. Potential strain relieving characteristics of sutures were assessed by modelling individual sutures in the cranium, with results showing local strain relief, but only at the expense of elevated strain in other parts of skull. This shows that sutures do work to relieve some of the strain generated within the skull during biting. To verify whether strain was reduced over the entire skull, all cranial sutures were considered in another model. The full suture model possessed a relatively coarse mesh compared to previous models, because many elements were assigned to the sutures themselves, reducing the number of elements available for the bone. Despite this situation, the FE model was still adequate for the purposes of this study. While an overall reduction of strain was expected with all sutures modelled, strain actually increased in 60%-70% of the model. This result therefore suggests that all the sutures working together do not reduce the strain pattern across the whole skull. However, it is important to bear in mind that the same stiffness was assigned to all the sutures, which is not necessarily realistic (e.g. Henderson et al., 2005; Markey et al., 2006). Different sutures in different parts of skull may possess different stiffness properties, therefore the question of whether sutures work together to reduce the strain level across the skull has not been proven unequivocally. That may not be possible without the use of experimental work.

An interesting finding was obtained from the results of model D (see Figure 5.24), where strain reduced around the frontal–parietal suture, and which highlighted the contribution of this suture in reducing strain within the skull roof in *Uromastyx*. This relates the passive kinesis (relative bone movements in response to loading), as

discussed by Rayfield (2005), who distinguished between active kinesis (as found in gekkotan lizards; Herrel et al., 2000) and passive kinesis. For the latter, strain reduction is the most obvious explanation, but the relationship between passive kinesis and the evolution of active kinesis remains uncertain. Our results here suggest that there would have been a selective advantage to increased flexibility at this joint, provided that the flexibility within the postorbital bar, upper temporal bar and palate (mesokinesis axis) were also modified to avoid creating new foci of strain. Very little is known about skull morphology in early squamates (Evans 2003a, in press) but it has been suggested that the origins of active kinesis might be found in the shockabsorptive passive kinesis of ancestral taxa (e.g. De Vree and Gans, 1987, 1989; Evans, 2008). Our results provide support for this view.

Of course there are approximations within the modelling process that may lead to some variability within the results. As already highlighted, model D had a relatively coarse mesh, which could have caused some degree of inaccuracy. Comparing all the models (A-D) with fused sutures against each other would indicate whether the coarse mesh in model D affects the strains within the bone. Model D did show some variation in the peak von Mises strains predicted compared to the other models, however these were relatively small and the general strain patterns were similar in all models. Another possible cause of error was the method of representing the sutures. Here the sutures were modelled as a less stiff material that was directly attached to the bone (modelled with solid elements), another method would be to remove the suture material and model the bony edges with contact elements.

A finite element analysis will only generate the right answer if the model is both valid and accurate. Validity depends on how accurately the physical problem is modelled, and accuracy depends on how close the model is to convergence. Clearly the answer will only converge to the solution of the computer's representation of the problem. Validation of this study is difficult but simple validation study is included in Chapter 6. Regarding the accuracy of a model, it can be improved by using smaller elements (increasing the mesh density) or by using a higher order interpolation function. Increasing the element order is limited in ANSYS and since the models already used second-order (i.e. quadratic) elements the only other possible option to improve the model would be to increase the mesh density. But at the same time there is a limitation in terms of the maximum number of elements (250,000) that can be used with this version of the FE package. Therefore, the models used in the study were the best that could be constructed. The convergence of the models can be considered by comparing the von Mises results obtained from models A to D (see Figure 5.16A, 5.19A, 5.21A and 5.23A) simulating fused sutures. They all show comparable results. However model D, predicted slightly different results although with the same overall strain pattern as models A, B and C which all had almost three times more elements.

#### 5.3.4 Study 4: The role of the quadrate and temporal bar

In study 4 the roles and functions of the quadrate and temporal bar in the lepidosaurian skull were investigated. The skull of *Uromastyx* was modified manually so that it resembled a more primitive form using image processing and analysis software. The modified skulls were then subjected to FEA. The specific aims of this study were: (1) to test whether quadrate movement reduces the joint forces acting upon the skull; and (2) to test whether the absence of a temporal bar in the lepidosaurian skull is a form of biomechanical optimization (maximum strength for minimum weight).

#### 5.3.4.1 Method

#### **Model Construction**

Differences in skull morphology are observed between *Uromastyx* and its primitive ancestors prompting the question as to whether this is caused by differences in the mechanical environment (stress and strain) in the bone. The absence of the temporal bar in *Uromastyx* is the subject of debate amongst biologists, and is investigated in this section. An artificial temporal bar was constructed on the original *Uromastyx* skull and its effect on the stress distribution investigated.

In reality and in all of the analyses performed so far in this research the quadrate can move relative to the skull of a *Uromastyx*. In this section, however, the consequences of fixing the quadrate with and without a temporal bar are investigated (see Figure 5.25). The first step in this process involved the creation of different models of adapted *Uromastyx* skulls, using AMIRA image processing and segmentation software (Mercury Computer Systems Inc, USA) which were exported as FE models. Load data was obtained as before, by MDA analyses.

Model 1 (M1) in this study was the same basic model used in the previous studies (e.g. study 2). For all the other models, the loading conditions imposed in the FEA corresponded to biting at a 7° gape angle at the back of the mouth. Three nodes were also constrained at the occipital condyle in all directions, as in the previous studies, and bone was assigned a Young's Modulus of 10 GPa and a Poisson's Ratio of 0.3 (no sutures were present in this study). The bite point, gape angle, constraints and material properties were the standard for all the investigations in this study.

In the second model (M2) the quadrate was fixed relative to the skull, so that it did not move during the biting process (Figure 5.25-M2). Load data for the FEA was obtained by fixing the quadrate in the multibody dynamic model and running the normal biting simulation (i.e. from a 35° rotation at the quadrato-mandibular joint to closure - see Chapter 4, study 3). The same MDA load data were then used in all later models in this study. Table 5.3 compares the MDA load data for the M1 and M2 analyses.

Model 3 (M3) was constructed to investigate the effect of attaching the quadrate to the pterygoid. The original micro-CT data were modified during the image segmentation process establish this attachment (see Figure 5.25). Finally models 4a and 4b (M4a and M4b) included an artificial temporal bar, which had a typical thickness of 0.3 mm in M4a and 1.0 mm in M4b, connecting the quadrate to the jugal (Figure 5.25). Table 5.2 summarizes the number of elements within each of these models.

	Model 1	Model 2	Model 3	Model 4a	Model 4b
No. of elements	207,000	219,652	219,084	217,957	216,000

 Table 5.2 Comparison of the number of elements within the models developed in study 4.





Figure 5.25 Illustration of the different models constructed in this study. In M1 the quadrate is not present whereas in M2 the quadrate is present. M3 shows the connection between the quadrate and pterygoid. M4a and M4b show an artificial thin and thick temporal bar.

	Mobile quadrate (M1)				Fixed quadrate (M2)			
	Fx	Fy	Fz	Mag	Fx	Fy	Fz	Mag
MAMEM1	-2.55	-4.88	7.32	9.16	-2.54	-4.93	7.48	9.31
MAMEM2	-1.21	-7.10	5.55	9.09	-1.22	-7.17	5.72	9.25
MAMESP1	-	-	-	-	2.27	-4.6	3.88	6.43
MAMESP2	-	-	-	-	1.77	-4.07	4.98	6.67
MAMEP1	-	-	-	-	0.16	-4.17	2.33	4.78
MAMEP2	-1.40	-4.16	1.64	4.68	-1.40	-4.21	1.78	4.78
MPTE1	3.16	1.41	7.77	8.50	3.10	1.59	7.86	8.60
MPTE2	1.46	-0.90	7.57	7.76	1.49	-0.81	7.79	7.97
MPTE3	0	0	0	0	0	0	0	0
MPTM1	-2.47	-1.12	6.87	7.38	-2.40	-0.77	6.97	7.41
MPTM2	0	0	0	0	0	0	0	0
MPTM3	0	0	0	0	0	0	0	0
MPST1	-0.91	-0.59	0.65	1.26	-0.92	-0.61	0.74	1.33
MPST2	-0.52	-0.78	0.96	1.34	-0.51	-0.78	1.00	1.37
MAMESA1	1.98	-1.09	5.69	6.12	1.95	-0.95	5.76	6.15
MAMESA2	2.40	-1.31	5.49	6.13	2.36	-1.14	5.60	6.18
Lig1	-0.16	-1.50	-1.34	2.02	-0.47	-4.32	-3.83	5.79
Lig2	0	0	0	0	-0.14	-0.68	-1.97	2.09
Bite force	0	-0.84	-21.84	21.86	0	-1.43	-21.86	21.91
Joint force 1	0.20	22.87	-26.37	34.91	-	-	-	-
Joint force 2	-	-	-	-	-3.49	39.07	-34.26	52.30

Table 5.3 A summary of the loading conditions applied in M1 and M2. Loading is obtained from one side of the MDA model. MAMESP1, 2 and MAMEP1 originate from the jaw and insert on the quadrate, and therefore do not apply any force directly on the skull. With a mobile quadrate (M1), joint force 2 (quadrato-mandibular joint force) in not applicable, and with a fixed quadrate, joint force 1 (quadratosquamosal joint) is not applicable. Force values are in Newtons. Fx, Fy, Fz represent force components and Mag represents the force magnitude. The coordinate system is defined in Figure 5.3.

#### **5.3.4.2 Results**

Plots of von Mises stress (lateral view) are shown in Figure 5.26 for models M1 to M4b. A qualitative comparison between M1 and M2 shows that the fixed quadrate is under a relatively high stress. In M3, when the quadrate is attached to the pterygoid the stress distribution across the whole skull is significantly reduced (compared to of M1 and M2). The inclusion of a temporal bar (M4a and M4b) leads to a further reduction of stress in the quadrate (compared to M3). Increasing the thickness of the temporal bar (see M4a and M4b) does not change the stress pattern notably across the skull (at least for the thicknesses considered here).



Figure 5.26 Comparison of von Mises stress in models M1 to M4b. Note the grey colour shows values greater than 30 MPa (selected to give more visually interesting contour plots).

#### 5.3.4.3 Discussion

The variation in the MDA load data between the fixed and mobile quadrate simulations is shown in Table 5.3. These results show firstly that the magnitudes of the muscle forces acting on the skull are marginally higher in the simulation with a fixed quadrate than in a mobile quadrate, presumably because of the different muscle orientations. Second, both sections of the modelled temporal ligament go into tension in the fixed quadrate simulation to prevent a posterior displacement of the jaw during biting (as predicted by Herrel et al., 1998a, b, and 2007). Third, bite force is again marginally higher and joint force is significantly higher in the fixed quadrate model compared to the mobile quadrate model. These all show that under the same biting conditions (i.e. bite position and angle) higher forces can be generated in a non-streptostylic lepidosaurian skull. This raises the question of the selective advantage of streptostyly.

One potential concern with the FEA findings of this study is differences between load data applied in M1 and M2. However, a qualitative comparison of the FEA results shows similar stress patterns in M1 and M2, alleviating this concern. An examination of the FEA results (Figure 5.26) shows that the reconstructed lower temporal bar undergoes relatively high stress, although the general pattern of stress across the whole skull is reduced when models M4a and b are compared to models M1 and M2. This implies that the reconstructed condition in M4a and b is more robust, being able to withstand higher forces. It is difficult to know whether the absence of a lower temporal bar is due to biomechanical optimization (maximum strength for minimum weight), as there are likely to be many selective advantages and disadvantages for the absence or gain of this bar among the lepidosauria. For example, the results show that having a fixed quadrate with a strong bony attachment as reconstructed in M4a and b probably allows the animal to have a more rigid skull that can withstand higher bite forces (as also predicted by Herrel et al., 2007). However, a mobile quadrate allows more flexibility and as such permits greater anterior and posterior movements of the lower jaw, facilitating shearing and cropping of food (e.g. Herrel and De Vree 1999a).

As pointed out earlier in Chapter 2, Rhynchocephalia and Squamata are both sub-groups of lepidosauria. *Sphenodon* is a member of Rhynchocephalia, and is of great interest in the study of the evolution of lizards and snakes, and it has been compared in the literature with *Uromastyx* (as a member of Squamata) (Robinson, 1976). Figure 5.27 and Figure 5.28 show a comparison of the skull of *Uromastyx* and *Sphenodon* in lateral and posterior views. The models with fixed quadrate and temporal bar developed here resemble *Sphenodon*, and this study provides a useful comparison between these two in terms of shape and form of the quadrate, pterygoid and temporal bar.

A representative connection was made in the *Uromastyx* model between the quadrate and the pterygoid to simulate the attachment in *Sphenodon*. However, an exact comparison with *Sphenodon* is difficult due to the different cranial anatomy, but the effect of this attachment in the *Uromastyx* is still interesting. Reviewing model M3 in Figure 5.26 we can see a general reduction in stress across the whole skull and more specifically in the epipterygoid when compared to M1 and M2. The role and function of the epipterygoid in the *Uromastyx* needs more investigation, but the difference between the forms of the epipterygoid in *Uromastyx* and *Sphenodon* is notable and could be linked to the altered stresses (see Figure 5.27). M3 also shows a high stress concentration at the connection between the quadrate and pterygoid. This could just be caused by the small attachment area. In reality this attachment site might be wider, as is the case in *Sphenodon* (see Figure 5.28). Additional attachment between the jugal and the quadrate (via the temporal bar) reduced the mechanical

stress on the quadrate (compare M3 to M4), while an increased temporal bar thickness reduced the stress in the temporal bar, as expected.



Figure 5.27 Lateral view of (A) *Sphenodon* and (B) *Uromastyx* skulls highlighting differences in the epipterygoid form.



Figure 5.28 Posterior view of (A) *Sphenodon* and (B) *Uromastyx* skulls highlighting differences between the pterygoid and the quadrate. Note that the pterygoid and the quadrate are attached in the *Sphenodon* whereas they are separate in the *Uromastyx*.

Some generalisations have been made in these comparative studies which show higher levels of stress in the true *Uromastyx* skull compared to the primitive representations. Assessing the results more closely reveals the mechanical significance of the moveable quadrate (streptostyly). The results show a reduction of the joint force acting on skull as a direct result of a movable quadrate. Also, some details may have been neglected during this study. Throckmorton (1976) and Metzger (2002) explored the existence of a ligament between the quadrate and the pterygoid (the quadratopterygoid ligament), which has not been included in these models. This ligament together with the temporal ligament may play a pivotal role in stabilizing the quadrate, so including this ligament in the MDA model could transfer some of the tensile forces carried by the temporal ligament to the pterygoid. In addition, possible movements of the epipterygoid could significantly reduce the stress levels in this bone and all connected bones. Lu et al. (2008) state that the jaw ligaments play an important role in balancing the jaw adductor muscle forces and preventing backward rotation of the quadrate in lizards such as *Uromastyx*. A complete lower temporal arcade together with a firm pterygoid–quadrate contact may behave in the same way as a quadrate stabilizer in *Sphenodon*. This could mean that the lower stress levels found in M2, M3 and M4 may actually be higher in reality in animals such as *Sphenodon* since not all necessary muscles have been included in this study.

### **5.4 Discussion**

This chapter has covered many aspects, investigating issues such as the effect of basic constraints on our models the importance of applying relevant loading conditions and testing hypotheses concerning the role of cranial sutures and streptostyly. It clearly demonstrates the huge potential of MDA and FEA in the study of functional morphology.

Investigating the variation of stress over a cycle of biting was the original aim of this study, and was assessed by importing many load steps from an MDA into an FEA. This study (study 2) revealed higher patterns of strain in regions where cranial sutures are located in the skull. From these findings FE analyses were performed (study 3) on skulls with sutures (individually and in a groups) to investigate their role and function more thoroughly. The results show that individual sutures relieved strain locally, but only at the expense of elevated strain in other regions of the skull. Also it was found that modelling the groups of sutures with the same stiffness could reduce the overall stress generated during a specific gape angle, across the whole volume of the skull by approximately 37%.

Study 4 focused on reconstruction of more primitive skull shapes based on the *Uromastyx* skull, and by incorporating MDA in this study, it was shown that streptostyly reduces the joint forces acting on the skull. Secondly, any attachment of the quadrate and pterygoid would play a pivotal role in reduction of overall level of stress across the skulls of lepidosauria. And thirdly, the presence of the temporal bar reduces the level of stress in the quadrate.

# **Chapter 6: Experimental validation of the finite element model**

## **6.1 Introduction**

Chapter 5 described the finite element analysis (FEA) conducted in this project and analysed the results produced. This chapter aims to confirm the validity of the FEA by comparing equivalent experiments and assessing the strain produced. Published *in vivo* studies of the pattern of strain across the skulls of lizards are limited, mainly due to the difficultly in experimenting with the small size of the lizard skull (Smith and Hylander, 1985). To address this issue the experimental validation study conducted here was performed on an enlarged replica of the *Uromastyx* skull. To measure strain experimentally there are a number of different techniques available, with the most common being strain gauging, double exposure holography and laser speckle interferometry. The resources and expertise available led to the use of the first of these to carry out a validation study of a *Uromastyx hardwickii* skull.

## 6.2 Methods

#### 6.2.1 Rapid prototype model

Rapid prototyping (RP) is a relatively new technology for the fast creation of physical models, produced from computer-assisted designs (CAD). These prototypes are usually used for design testing, as they can significantly reduce the cost and time of product development. Here we scaled the computational model created for the MDA to two times its original size, and used this to produce a physical RP model of the skull. The RP model had a skull length of approximately 90 mm.

All RP systems employ a similar process to create the model. In brief, a 3D computer model of the object is exported in an industrial format that is recognized by the RP machine (commonly an STL file). The RP machine then builds up the

physical model layer by layer, using a variety of different techniques (e.g. resin or powder; see Pham and Dimov, 2001 for more information on the different RP methods). In this project, the RP was created using a "fused deposition modelling" technique (FDM), which extrudes a heated thermoplastic through a nozzle and deposits it in a thin layer on a support platform. The process is repeated to build up the layers until the final shape of the model is complete. Figure 6.1 shows a schematic of this technique. The RP material was ABS (Acrylonitrile butadiene styrene), which is ideal for the rapid production of prototypes. ABS is generally used in applications where high impact resistance and structural strength is required. The actual mechanical properties of the ABS were measured via tensile testing, as described in the next section.



Figure 6.1 A schematic of the FDM (Adopted from http://www.promod-technologie.de).

#### **6.2.2 Dynamic Mechanical Analysis**

During the FEA validation procedure it is essential that the correct material properties are used in the FE model. To determine the properties of the ABS plastic three tensile specimens (dimensions:  $15.1 \times 2.1 \times 0.2$  mm) were tested in a dynamic mechanical analyser (DMA) [TA Instrument Q800 series, Delaware, USA]. In essence the DMA is a tensile/ compression test machine that can measure the material properties (e.g. Young's Modulus, stress relaxation, creep) of small samples. A variety of test protocols can be performed by the DMA, such as dual/single cantilever, 3-point bend, shear sandwich, compression and tension; however, for the purposes of this study only the tensile test was required. See Figure 6.2 for a photograph of the test setup. The loading was applied at a rate of 1.0 N/min, up to a maximum force of 18 N (the limit of the machin). The average Young's modulus was then calculated.



Figure 6.2 Photograph of the TA Instruments Q800 DMA and close-up view of the tension clamp.

#### **6.2.3 Experimental strain analysis**

A specialist test rig that had been built previously in-house for the purposes of loading skulls, was used in this strain gauge experiment (see Kupczik et al., 2007). The scaled rapid prototype model of the Uromastyx hardwickii skull was placed on the test rig, resting on two rubber-coated T-bars placed at the posterior teeth and the quadrates (Figure 6.3A). Six  $120 \pm 0.5 \Omega$  rosette strain gauges wired in a three-wire quarter-bridge circuit (TML FRA-1-11, Tokyo Sokki Kenkyujo, Tokyo, Japan) were placed on the postorbital, jugal, nasal and parietal regions of the skull. These six points were chosen to represent anterior, posterior, and lateral skull regions (see Figure 6.3A and B. Note that one of the gauges on the side cannot be seen in these figures). The gauges were applied according to the manufacturer's guidelines and connected to a Vishay 5100B Wheatstone bridge amplifier with an excitation voltage of 0.5 V (Vishay Micro-Measurements, USA). Loading was applied to the skull via strings at the location of the pterygoideus externus muscle, by manually placing weights on load hangers at the ends of the strings. These strings were glued to the skull and as such were attached over a small area (see Figure 6.3B). Loading was increased gradually from 1.4 N (Exp1) to 2.1 N (Exp2) and 2.8 N (Exp3) on both sides of the skull. All forces were applied vertically with the exact positions recorded by taking three-dimensional (3D) coordinates with a MicroScribe GTX digitizing system (Immersion Corporation, San Jose, CA, USA), as described in the next section. This enabled the force vectors to be determined for use in the FEA model. In addition the exact locations of the strain gauges were recorded using the same technique. However, to avoid damage to the gauges, three points around the gauge were used to determine its centre rather than pushing down onto the gauge directly with the MicroScribe.



Figure 6.3 Ventral (A) and lateral (B) view of the RP model placed on the test rig. (C) showing the experimental set up along with the MicroScribe measuring device (POL= postorbital left; POR= postorbital right; JL= jugal left; JR= jugal right).

#### 6.2.4 Coordinate measurement with the MicroScribe

A coordinate measuring machine (CMM) provides the three dimensional coordinate of a point of interest with respect to a reference point. Here, we used a MicroScribe GTX digitizing system (Immersion Corporation, San Jose, CA, USA), which can be used to record 3D coordinates as well as capturing many points on an object that can used to create a visual 3D computational model. The MicroScribe was used to determine the attachment locations of the strain gauges, the position and orientation of the applied loads and the location of the model constraints (i.e. points of contact between the test rig and the RP model). Figure 6.3C shows the MicroScribe GTX digitizing system on the test rig.

#### 6.2.5 Finite element modelling

The geometry of the FE model was created using the same micro-CT dataset of the *Uromastyx hardwickii* skull used in the production of the rapid prototype model (supplied by the University of Texas). The model was created using AMIRA image segmentation software (Mercury Computer Systems Inc, USA), and consisted of approximately 123,000 tetrahedral (second order) solid elements (SOLID92). The model was imported into ANSYS V11 Mechanical (ANSYS, Inc., Canonsburg, PA, USA) for the FEA, where an isotropic material property was assigned with a Young's modulus of 942.5 MPa, as determined by the DMA tests (see Section 6.3.1). The material's Poisson's ratio could not easily be measured, therefore its value was varied from 0.25 to 0.4 (0.05 increments) to assess its effect on the FE results. For comparison with the experimental testing a Poisson's ratio of 0.3 was used. The FEA was arranged to replicate the experimental strain gauging model as closely as possible. The model was fixed at the quadrates in the y and z directions and at the posterior teeth in the y direction (points F1 to F4 in Figure 6.4). The applied loads

were distributed over five nodes along the length of the lines indicated in Figure 6.4, corresponding to the loading regions in the experimental model (Figure 6.3) with 1.4 N (FEA1), 2.1 N (FEA2) and 2.8 N (FEA3) on both sides of the model. The strain results from the FEA and the experimental strain gauging were then compared.



Figure 6.4 Schematic of the FE model. F1 to F4 (i.e. blue dots) shows where the skull has fixed, L1 to L4 shows where the loading has applied, the black dotes indicated the attachment of the strain gauges (POL= postorbital left; POR= postorbital right; JL= jugal left; JR= jugal right).

#### **6.3 Results**

#### 6.3.1 DMA

Figure 6.5 shows the results of the DMA measurements, where stress is plotted with respect to strain. The Young's modulus of the three samples tested were calculated from the linear slope of the graph, and values of 957.3 MPa, 946.5MPa and 923.9 MPa were obtained, giving an average modulus value of 942.6 MPa for the RP material.



Figure 6.5 Experimental DMA results of the testing of the RP materials.

#### 6.3.2 FEA

The effect of varying the Poisson's ratio in the FEA is shown in Figure 6.6, which plots the first principal strain at each of the strain gauge position. The POL position showed the maximum sensitivity to Poisson's ratio (43.0 to 59.4 microstrain), with the strain at all other positions varying by a maximum of 29%. Figure 6.7 shows a sample plot of first principal strain distribution across the skull, applying the loading from FEA 1 (1.4 N on both sides of the skull).



Figure 6.6 Effect of variation of the Poisson's ratio on the first principal strains in FEA 1.



Figure 6.7 First principal strain distribution in the finite element model (FEA 1 - 1.4 N loading). Note values are in microstrain.

#### 6.3.3 Comparison of strain gauge result with FEA

Figure 6.8 compares the experimental and FEA results using Young's modulus of 942.6 MPa and Poisson's ratio of 0.3. Comparable results were noted at the Nasal, JR, POL, POR and Parietal positions but not at the JL.



Figure 6.8 Comparison of the first principal strains between the experimental strain analysis data and the FEA.

#### **6.4 Discussion**

*In vivo* strain measurements in skulls have been undertaken by a number of researchers, as briefly described in Chapter 3. However, there is very little information for lizard skulls, with one of the main obstacles being the small size of the lizard skulls, making such strain gauging very difficult. This data would have been useful for validation of the computational modelling studies conducted in this research. However, as a compromise and as a means of validating the FE procedure we conducted an experimental strain analysis on a scaled replica of the *Uromastyx* skull. The Young's modulus of the material used in the RP model was measured experimentally and the sensitivity to the Poisson's ratio was assessed in the FEA.

In general there was a good correlation between the experimental and computational strain results. There was one strain position that did not compare well (JL -Jugal region of the skull). This could be for a number of reasons: (1) excessive glue used during attachment could stiffen the plastic and reduce the measured strain, (2) a rough or curved surfaces could result in inaccuracies and (3) the gauge could have been damaged during application. The most likely cause of error in this case is thought to be excessive glue applied during attachment. Since, the gauge did not seem to be damaged and still appeared to record.

An interesting finding from this study was the pattern of first principal strain distributions across the model. Although the FEA considered a simple loading situation which was not anatomically accurate, the pattern of strain (but not the actual values) was comparable to the more complete models created in Chapter 5 (e.g. see Figure 5.10). Higher values of strain were again noted around the normal positions of the sutures. Increased strain in the nasal region was also observed caused by the bite force on the posterior teeth, whereas the high strain in the postorbital-parietal region was probably caused solely by the geometry of the skull. The epipterygoid also experienced high strain.

In summary, it has been shown that finite element analysis can reliably predict the strains in a physical model under loading. The test setup was simplified and was not aimed at producing anatomically meaningful results, but was instead designed to create an experimental and computational comparison study. This proved to be successful, with comparable strains at varying locations on the skull. Use of the producing a RP model for this validation experiment has also proved to be successful.

# **Chapter 7: Discussion**

#### 7.1 Introduction

This chapter provides an overview of all the work conducted throughout this project. Only the key results are discussed here, since detailed discussion and analysis of the earlier results has already been included in Chapters 4, 5 and 6.

## 7.2 Uromastyx

Lizard skulls have appeared in a variety of forms during their evolution and understanding why this has happened initiated this research project. The skull of *Uromastyx hardwickii* was chosen for the analysis for a variety of reasons: it is primarily an herbivore; it shows dietary specialisation in its dentition; it has a specialised arrangement of the pterygoideus muscles, and possesses streptostyly. In addition, *Uromastyx* has been the subject of many experimental and biological studies in areas concerned with: gut structure; dentition; food processing; and muscular anatomy (e.g. El Toubi and Bishai, 1959; Robinson, 1976; Thorockmorton, 1976, 1980; Herrel et al., 1998a, b, 1999b). The available anatomical and kinematic data from the literature were used to construct a detailed computational model of *Uromastyx* to investigate cranial architecture from a functional and morphological point of view. This is something that has not been conducted previously.

#### 7.3 Literature review

After the survey of the available literature on *Uromastyx*, Chapter 3 reviewed the fundamentals of bone, muscles and sutures as the key components of the masticatory system. This also revealed different methods to study skulls and the masticatory system. Following this, a comprehensive review of previous computer modelling studies of skulls was undertaken. This identified the potential of a combined

computational study using multibody dynamic analysis (MDA) and finite element analysis (FEA) to advance our understanding of the architecture of the lizard skulls and more specifically *Uromastyx*.

#### 7.4 Dynamic analysis of a lizard skull

Chapter 4 discusses the development of the multibody dynamics analysis (MDA) models used in this study. In summary, muscle and kinematic data were taken from the literature (Throckmorton, 1976, 1980; Herrel et al., 1998a, b) and applied to the computational model. The main areas of investigation were movements of the quadrate and the development and implementation of a realistic muscle model. To the best of our knowledge, no bite force data are available for Uromastyx in the literature, and as such we carried out investigations to predict bite force using MDA. These bite forces were comparable to those of other animals based on the correlation between skull size and bite force (Herrel and Aerts, 2003). In addition to this, the effect of altering the direction and location of the food particle within the mouth was assessed. This lead to some interesting conclusions, the most important of which was that additional soft tissue structures (muscles or ligaments) are required for jaw stability and certain movements, that have not previously been documented or identified as being involved during the jaw opening and closing phases. The quadratopterygoid ligament, cervical muscles, and jaw depressor muscles were not included in the MDA models, and may contribute during jaw closing (Koolstra and van Eijden, 1997b). However, the results of the standard MDA were comparable to experimental findings of bite force, and relationships between bite point and bite force agreed with the literature (e.g. Dumont and Herrel, 2003).

This research has shown that MDA can contribute to the discipline of functional morphology, where for example, hypotheses relating to the evolution of cranial kinesis in squamates can easily be tested in relation to mechanical factors such as joint forces, bite forces, and role and function of muscles and ligaments. This research differs from other MDA studies of bite modelling (e.g. Langenbach and Hannam, 1999; Sellers and Crompton, 2004; Konakanchi, 2005; Del Signore, 2005; Langenbach et al., 2002, 2006; Stavness et al., 2006; de Zee et al., 2007; van Lopik and Acar, 2007; Hannam et al., 2008) as its main purpose was to gather complex loading data to incorporate into an FEA. This link between these two powerful engineering tools to test ideas and hypotheses both in terms of dynamic and static analyses is novel and has many potential applications.

#### 7.5 Finite element analysis of a lizard skull

Chapter 5 discusses the FEA work conducted in this research. Obtaining the data from the MDA meant that all forces acting on the skull were in equilibrium, at all points during the biting cycle, and as such resulted in negligible stress concentrations about the fixation points. In other FEA studies (e.g. Tanne et al., 1988; Miyasaka et al., 1994; Rayfield, 2005a) this is not the case, with substantially higher levels of stress about the fixation points. In reality, when we bite and crush food, load will be transferred to the skull over the entire biting cycle, therefore to assess the effect of dynamic loading (loading over time) the MDA load data for a complete simulation (fifty load steps) was imported to the finite element model. This type of loading is the first of its kind in the field of functional morphology. The results showed elevated levels of stress in the regions that correspond to sutures in the actual skull (note that sutures were not modelled in the FEA at this point). This was a particularly interesting finding and lead to additional investigations into sutures.

The FEA models incorporating sutures showed that unfused sutures undergo high deformation and reduce the bone strain locally. This agrees with the published literature (e.g. Jaslow, 1989; Herring et al., 1996; Herring and Teng, 2000; Rafferty et al., 2003; Rayfield, 2005b). However, when all cranial sutures were modelled, the overall pattern of strain reduced in only approximately 30% of the skull and increased in the remaining 70%. The major strain reduction tended to occur in regions of the skull that corresponded to mesokinesis in some lizards, which was interesting since *Uromastyx* does not show mesokinesis (Thorockmorton, 1976, 1980; Herrel et al., 1999b). This finding shows a shock-absorptive function for mesokinesis and suggests that the origins of active kinesis might be found in the shock-absorptive passive kinesis of ancestral taxa (e.g. De Vree and Gans, 1987, 1989; Evans, 2008).

In study 4 of Chapter 5 the roles of streptosly and the lower temporal bar were investigated. Uromastyx does not possess a temporal bar therefore an artificial one was created to assess its possible function. These models were to test the function of primitive characteristics observed in early lizards, and were used to study the mechanics of the Uromastyx skull and answer a series of "what if" questions. While this approach carries approximations it does allow the investigation of specific skull features and suggests potential theories of evolutionary development of skulls. Results of this study showed: (1) streptostyly (quadrate movement) reduced joint forces acting on the skull, (2) fusion of the pterygoid and quadrate reduced stress levels across the whole skull and more significantly within the epiptrygoid and (3) the presence of the temporal bar (connecting quadrate to jugal) reduced stress on the quadrate. Reviewing these findings suggests that a primitive lepidosaurian skull (i.e. one with a lower temporal bar) has a higher capacity to reduce stress during biting when compared to its present day ancestors. The fact that the lower temporal bar is loaded but still becomes absent contradicts the mechanical optimization hypothesis of bone, where we assume the development of an optimum shape to withstand the stresses. Instead it suggests that there might be some other selective criteria regarding the absence or presence of the lower temporal bar in lepidosaurian skulls. As always,

we must be aware that there were some assumptions within the modelling, specifically regarding the loading of the skulls. All load data were taken from the *Uromastyx* MDA model, and is likely to be inaccurate for the primitive skulls, where muscle and ligament forces would differ. Therefore, from this study just the general effect of specific features should be considered rather than exact answers.

The absence of the connection between the pterygoid and quadrate, and quadrate and jugal (via the temporal bar) is likely to be linked to the increased mobility within lepidosaurian skulls. This provides more flexibility for the cranial system and allows anterior and posterior movements of quadrate and lower jaw that can facilitate shearing and cropping of food material (e.g. Herrel and De Vree 1999a). However, as discussed by Herrel et al. (2007) this increase of flexibility can have consequences such as reduction in bite force. In fact our results show that absence of a connection between the quadrate and pterygoid and jugal reduces the robustness of the skull. The form and function of the epipterygoid from a mechanical point of view is another interesting topic. This structure can vary significantly between lepidosauria, as is shown in the lateral view of the skull of *Sphenodon* and *Uromastyx* in Figure 5.27.

# **7.6 Experimental validation of the finite element model**

The validation of computational modelling work is important if we are to be confident in the results that are obtained. Ideally a variety of experimental techniques should be used such as bite force measurements, cineradiography, electromyography, and strain gauge analysis. However, these experimental methods would require a substantial amount of time, effort and expense to conduct plus invasive experimental animal studies are difficult to undertake, and as such were beyond the scope of this project. However, due to the availability of the testing equipment a strain gauge analysis was performed to validate the FEA. Here a rapid prototype model of the *Uromastyx* skull was created and loaded to generate small deformations that could be recorded via strain gauges.

Anatomically accurate loading was not applied as this would undoubtedly lead to additional approximations and uncertainties. Also, the aim was to directly compare the results with the computational FEA, thus the important factor in this work was to produce constraints and loading that were the same in the experimental and computational work. Chapter 6 describes the findings in detail, but in summary comparable strain measurements were noted in the experimental and computational models. This work showed that if loading is replicated accurately in the FEA then the results could be used with confidence.

# Chapter 8: Conclusions and future work 8.1 Conclusions

The main aim of this thesis was to conduct a combined multibody dynamics analysis (MDA) and finite element analysis (FEA) of a lizard skull (*Uromastyx*), complemented by an experimental strain gauge analysis. This was the first combined study of its kind at the University of Hull, which has now led to other research into reptiles and primates skulls. The ultimate aim of this work was to develop a method to predict the loading of the skull, and help increase understanding of the evolutionary changes in skull morphology. A method of combining the output of an MDA with an FEA was found and allowed investigations into the role and function of sutures, streptostyly, and the evolution of the temporal bar to be carried out (see Chapters 4 and 5). The main conclusions of the research are summarised below:

- MDA has great potential and many future applications with regards to assessing the role and function of skulls, e.g. the function of cranial kinesis among amniotes.
- Performing an MDA provides accurate and equilibrated loading conditions and improved loading data for an FEA.
- Sutures are located in regions of the skull that experience high stress (at least for the *Uromastyx* considered here).
- Sutures work in groups rather than individually, and are likely to possess different stiffnesses based on their location and shape of surroundings bones.
- The loss of the temporal bar in lizards most likely results in a mobile skull, which facilitates wider gapes and an anterior movement of the lower jaw.
- Streptostyly in amniote skulls leads to a reduction in joint forces acting on skull.

#### 8.2 Future work

Many suggestions for future developments of this work have been highlighted already through the thesis arising from conclusions and/or questions from a combination of this project results and literature knowledge. Indeed a second phase to the project has already started with the work of Curtis et al. at the University of Hull where MDA and FEA techniques are being implemented together with experimental data on basal amniotes.

To build on the preliminary findings on sutures and cranial kinesis, future studies of skulls with high mobility would be of particular interest, such as that of the gecko (coupled kinesis - streptostyly and mesokinesis). With the help of experimental data (e.g. Herrel et al., 2000) the area of mesokinesis should be investigated further. Also, validation of computational work is important, therefore experimental cineradiographic, electromyographic and bite force data are undeniably useful and should be conducted in future studies if possible. In addition, it would be beneficial to use realistic food material properties, where experimental studies could be performed to measure force/deflection characteristics of different food types to input directly into the MDA models. Some previous studies have been performed to measure food stiffnesses (e.g. Wang and Stohler, 1990; Agrawal et al., 1997; Toole et al., 2000; Williams et al., 2005), however these values may vary depending on teeth shape and should be repeated with a realistically shaped tooth model.

A limitation on the validility of the modelling work in this study arises from the lack of actual muscle data of lizards (in terms of maximum force, optimum lengths, force-velocity data, force-elongation data etc.). In addition, despite the recent measurements of anisotropic mechanical properties of bone in primates (e.g. Wang et al., 2006; Wang and Dechow, 2006) there is little if any information on bone properties of lizards. Future work could investigate these areas using techniques such as micro-MRI and micro-CT along with traditional methods.

This research has highlighted the significance of sutures and their effect on stress and strain distributions over the skull during FEA. However, our understanding of sutures is still very limited, and gathering data on individual sutural properties would advance research in this area significantly. This could be addressed by performing nano-hardness indentation, micro-CT analysis, and tension/compression testing of various cranial sutures. One other modification within the FEA could be to assess the effect of using contact elements to represent sutures between adjoining bones instead of the addition of a softer material as was modelled in this study. Overall FEA can play a major role in understanding the function of sutures and the effect of early suture fusion on the stresses around the skull can be assessed and may allow conditions such as craniosynostosis to be investigated further.

## References

Adolph SC, Porter WP, 1993. Temperature, activity and lizard life histories. American Naturalist, 142: 273-295.

Agrawal KR, Lucas PW, Prinz JF, Bruce IC, 1997. Mechanical properties of foods responsible for resisting food breakdown in the human mouth. Archives of Oral Biology, 42 (1): 1-9.

Alexander RMcN, 1971. Animal Mechanics. London: Sidgwick & Jackson.

**Alexander RMcN, 2003.** Modelling approaches in biomechanics. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 358: 1429-1435.

**Anapol F, Herring SW, 1989.** Length-tension relationships of masseter and digastric muscles of miniature swine. The Journal of Experimental Biology, 143: 1-16.

ANSYS Theoretical Manual (version 11), ANSYS, Inc., Canonsburg, PA, USA.

Ascenzi A, Bonucci E, 1964. The ultimate tensile strength of single osteons. The Anatomical Record, 58: 160-183.

Ascenzi A, Bonucci E, 1967. The tensile properties of single osteons. The Anatomical Record, 158: 375-386.

Ascenzi A, Bonucci E, 1968. The compressive properties of single osteons. The Anatomical Record, 161: 377-392.

Ascenzi A, Bonucci E, 1972. The shearing properties of single osteons. The Anatomical Record, 172: 499-510.

**Barghusen HR, Hopson A, 1979.** The endoskeleton: The comparative anatomy of the skull and visceral skeleton. In: *Hyman's Comparative Anatomy*. (ed. Wake M), pp. 265-326. Chicago: The University of Chicago Press.

Behrents RG, Carlson DS, Abdelnour T, 1978. *In vivo* analysis of bone strain about the sagittal suture in *Macaca mulatta* during masticatory movements. Journal of Dental Research, 57: 904-908.

**Benton MJ, 2005.** Sauria (lizards). In: *Encyclopaedia of Life Sciences*, Chichester: John Wiley & Sons Ltd.

**Buckland-Wright JC, 1978.** Bone structure and the patterns of force transmission in the cat skull (*Felis catus*). Journal of Morphology, 155: 35-62.

**Burnett DS, 1987.** *Finite Element Analysis – From Concepts to Applications.* Reading: Addison Wesley.

**Byrd KE, 1981.** Mandibular movement and muscle activity during mastication in the guinea pig (*Cavia porcellus*). Journal of Morphology, 170: 147-169.

**Byrd KE, Garthwaite CR, 1981.** Contour analysis of masticatory jaw movements and muscle activity in *Macaca mulatta*. American Journal of Physical Anthropology, 54: 391-399.

Carroll RL, 1982. Early evolution of reptiles. Annual Review of Ecology and Systematics, 13: 87-109.

Cleuren J, Aerts P, De Vree F, 1995. Bite and joint force analysis in *Caiman* crocodilus. Belgium Journal of Zoology, 125: 79-94.

**Close R, 1964.** Dynamic properties of fast and slow skeletal muscle of the rat during development. The Journal of Physiology, 173(1): 74-95.

Close R, 1965. Force: velocity properties of mouse muscles. Nature London, 206: 718-719.

Close R, Hoh JFY, 1967. Force: velocity properties of kitten muscles. The Journal of Physiology, 192: 815-822.

**Cohen MM, 1993.** Sutural biology and he correlates of craniosynostosis. American Journal of Medical Genetics, 47: 581-616.

Cook RD, 1995. Finite Element Modeling for Stress Analysis. New York: John Wiley & Sons.

Crompton AW, Thexton AJ, Parker P, Hiiemae K, 1977. The activity of the jaw and hyoid musculature of the Virginia oppossum, *Didelphus virginiana*. In: *The Biology of Marsupials* (eds. Stone-House B, Gilmore D), pp. 287-307. New York: Macmillan Press Ltd.

**Curtis N, Kupczik K, O'Higgins P, Moazen M, Fagan MJ, 2008.** Predicting skull loading: applying multibody dynamics analysis to a macaque skull. The Anatomical Record, 291: 491-501.

**Daniel W, McHenry C, 2001.** Bite force to skull stress correlation - modelling the skull of *Alligator mississippiensis*. In: *Crocodilian Biology and Evolution*, (eds. Grigg GC, Seebacher F, Franklin CE), pp. 135-143. Surrey: Beatty & Sons.

**Daumas B, Xu WL, Bronlund J, 2005.** Jaw mechanism modeling and simulation. Mechanism and Machine Theory, 40: 821-833.

**Delp SL, Loan JP, 1995.** A graphics-based software system to develop and analyze models of musculoskeletal structures. Computers in Biology and Medicine, 25: 21-34.

**Del Signor MJ, 2005.** A screw -theoretic framework for musculoskeletal system modeling and analysis. MSc thesis, University of New York, Buffalo.
**De Vree F, Gans C, 1976.** Mastication in pigmy goats (*Capra hircus*). Annales de la Societe Royale Zoologique de Belgique, 105: 255-306.

**De Vree F, Gans C, 1987.** Kinetic movements in the skull of adult *Trachydosaurus rugosus*. Anatomy, Histology, Embryology, 16: 206-209.

**De Vree F, Gans C, 1989.** Functional morphology of the feeding mechanisms in lower tetrapods. In: *Trends in Vertebrate Morphology*, (eds. Splechtna H, Hilgers H), pp. 115-127. Stuttgart: Gustav Fischer.

**De Zee M, Dalstra M, Cattaneo PM, Rasmussen J, Svensson P, Melsen B, 2007.** Validation of a musculo-skeletal model of the mandible and its application to mandibular distraction osteogenesis. Journal of Biomechanics, 40: 1192-1201.

**Dumont ER, 2007.** Feeding mechanisms in bats: variation within the constraints of flight. Integrative and Comparative Biology, 47: 137-146.

**Dumont ER, Herrel A, 2003.** The effect of gape angle and bite point on bite force in bats. The Journal of Experimental Biology, 206: 2117-2123.

**Dumont ER, Piccirillo J, Grosse IR, 2005.** Finite-element analysis of biting behaviour and bone stress in the facial skeletons of bats. The Anatomical Record Part A, 283A: 319-330.

**El-Toubi MR, 1945.** Notes on the cranial osteology of *Uromastyx aegyptia* (Forskål). Bulletin of the Faculty of Science Cairo Faud 1 University, 25: 1-10.

**El-Toubi MR, Bishai HM, 1959.** On the anatomy and histology of the alimentary tract of the lizard *Uromastix aegyptia* (Forskal). Bulletin of the Faculty of Science Cairo Faud 1 University, 34: 13-50.

**Endo B, 1965.** Distribution of stress and strain produced in the human facial skeleton by the masticatory force. Journal of the Anthropological Society of Nippon, 73: 123-136.

**Endo B, 1966.** Experimental studies on the mechanical significance of the form of the human facial skeleton. Journal of the Faculty of Science of the University of Tokyo [V], 3: 1-106.

**Epstein M, Herzog W, 1998.** *Theoretical Models of Skeletal Muscle Biological and Mathematical Considerations.* Chichester: John Wiley & Sons.

Erickson GM, Lappin AK, Vliet KA, 2003. The ontogeny of bite-force performance in American alligator (*Alligator mississippiensis*). The Zoological Society of London. 260, 317-327.

**Evans SE, 2003a.** At the feet of the dinosaurs: the origin, evolution and early diversification of squamate reptiles (Lepidosauria: Diapsida). Biological Reviews Cambridge, 78: 513-551.

**Evans SE, 2003b.** *Uromastyx hardwickii* (On-line), Digital Morphology. Accessed October 3, 2005 at http://digimorph.org/specimens/Uromastyx\_hardwickii/.

**Evans SE, 2008.** The skull of lizards and *Sphenodon*. In: *Biology of the Reptilia*, vol. 20 (eds. Gans C, Gaunt AS), pp. 1-347. New York: Academic Press.

Fagan MJ, 1992. Finite Element Analysis - Theory and Practice. Essex: Longmans.

**Frazzetta TH, 1962.** A functional consideration of cranial kinesis in lizards. Journal of Morphology, 111: 287-319.

Fung YC, 1993. Biomechanics: Mechanical Properties of Living Tissues, New York: Springer.

Gans C, De Vree F, Carrier D, 1985. Usage pattern of the complex masticatory muscles in the shingleback lizards, *Trachydosaurus rugosus*: a model for muscle placement. American Journal of Anatomy, 173: 219-240.

**Giesen EBW, Ding M, Dalstra M, van Eijden TMGJ, 2001.** Mechanical properties of cancellous bone in the human mandibular condyle are anisotropic. Journal of Biomechanics, 34: 799-803.

Gorniak GC, 1977. Feeding in golden hamsters, Mesocricetus auratus. Journal of Morphology, 154: 427-458.

**Gorniak GC, 1985.** Trends in the action of mammalian masticatory muscles. American Zoologist, 25: 331-337.

Gorniak GC, Gans C, 1980. Quantitative assay of electromyograms during mastication in domestic cats (*Felis catus*). Journal of Morphology, 163: 253-281.

**Gorniak GC, Rosenberg HI, Gans C, 1982.** Mastication in the tuatara, *Sphenodon punctatus* (Reptilia: Rhynchocephalia): structure and activity of the motor system. Journal of Morphology, 171: 321-353.

Goss CM, 1959. *Gray's Anathomy*. Philadelphia: Lea & Febiger.

Grosse IR, Dumont ER, Coletta C, Tolleson A, 2007. Techniques for modeling muscle-induced forces on finite element models of skeletal structures. The Anatomical Record, 290: 1069-1088.

Haas F, Wootton RJ, 1996. Two basic mechanisms in insect wing folding. Proceedings of the Royal Society B: Biological Sciences, 263: 1651-1658.

**Haas G, 1973.** Muscle of the jaws and associated structures in the Rhynchocephalia and Squamata. In: *Biology of the Reptilia*. vol. 4 (eds. Gans C, Parsons T) pp. 285-490. London: Academic Press.

Hannam AG, Stavness I, Lloyd JE, Fels S, 2008. A dynamic model of jaw and hyoid biomechanics during chewing. Journal of Biomechanics, 41(5): 1069-1076.

Hay JG, 1973. *Biomechanics of Sports Techniques*. Englewood Cliffs, NJ: Prentice Hall Inc.

Henderson JH, Chang LY, Song HM, Longaker MT, Carter DR, 2005. Agedependent properties and quasi-static strain in the rat sagittal suture. Journal of Biomechanics, 38: 2294-2301.

Herrel A, 1998. Lizard herbivory, a functional morphological approach. PhD thesis, University of Antwerp, Antwerp.

Herrel A, Aerts P, 2003. Biomechanical studies of food and diet selection. In: *Encyclopaedia of Life Sciences*, London: Nature Publishing Group.

Herrel A, Aerts P, De Vree F, 1998a. Static biting in lizards: functional morphology of the temporal ligaments. Journal of Zoology, 244: 135-143.

Herrel A, Aerts P, De Vree F, 1998b. Ecomorphology of the lizard feeding apparatus a modelling approach. Netherlands Journal of Zoology, 48: 1-25.

Herrel A, Aerts P, De Vree F, 2000. Cranial kinesis in geckoes: functional implications. The Journal of Experimental Biolology, 203: 1415-1423.

Herrel A, Cleuren J, De Vree F, 1997. Quantitative analysis of jaw and hyolingual muscle activity during feeding in the lizard *Agama stellio*. The Journal of Experimental Biology, 200: 101-115.

Herrel A, De Vree F, 1999a. Kinematics of intraoral transport and swallowing in the herbivorous lizard *Uromastix acanthinurus*. The Journal of Experimental Biology, 202(9):1127-1137.

Herrel A, Grauw ED, Lemos-Espinal JA, 2001b. Head shape and bite performance in xenosaurid lizards. Journal of Experimental Zoology, 290: 101-107.

Herrel A, Meyers JJ, Nishikawa KC, De Vree F, 2001a. The evolution of feeding motor patterns in lizards: modulatory complexity and possible constraints. American Zoologist, 41: 1311-1320.

**Herrel A, Schaerlaeken V, Meyers JJ, Metzger KA, Ross CF, 2007.** The evolution of cranial design and performance in squamates: consequences of skullbone reduction on feeding behavior. Integrative and Comparative Biology, 47: 107-117.

Herrel A, Spithoven L, Van Damme R, De Vree F, 1999b. Sexual dimorphism of head size in *Gallotia galloti*; testing the niche divergence hypothesis by functional analyses. Functional Ecology, 13(3): 289-297.

**Herrel A, Timmermans J-P, De Vree F, 1998c.** Tongue-flicking in agamid lizards: morphology, kinematics and muscle activity patterns. The Anatomical Record, 252(1): 102-116.

Herrel A, Verstappen M, De Vree F, 1999c. Modulatory complexity of the feeding repertoire in scincid lizards. Journal of Comparative Physiology A, 184: 501-518.

Herring SW, 1972. Sutures- a tool in functional cranial analysis. Acta Anatomica, 83: 222-247.

Herring SW, Mucci R J, 1991. *In vivo* strain in cranial sutures: the zygomatic arch. Journal of Morphology, 207: 225-239.

Herring SW, Scapino RP, 1973. Physiology of feeding in miniature pigs. Journal of Morphology, 141: 427-460.

Herring SW, Teng S, 2000. Strain in the braincase and its sutures during function. American Journal of Physical Anthropology, 112: 575-593.

Herring SW, Teng SY, Huang XF, Mucci RJ, Freeman J, 1996. Patterns of bone strain in the zygomatic arch. The Anatomical Record, 246: 446-457.

**Hill AV, 1938.** The heat of shortening and the dynamic constants of muscle. Proceedings of the Royal Society B: Biological Sciences, 126: 136-195.

Huiskes R, Chao EYS, 1983. A survey of finite element analysis in orthopaedic biomechanics: the first decade, Journal of Biomechanics, 16: 385-409.

**Hulme KF, Mendel FC, Chugh KP, 2003.** Development of a computational toolkit for biomechanical analysis and simulation: The vertebrate analyzer. 16<sup>th</sup> International Conference on Computer Applications in Industry and Engineering, Las Vegas, USA.

**Hylander WL, 1978.** Incisal bite force directions in humans and the functional significance of mandibular translation. American Journal of Physical Anthropology 48: 1-8.

**Hylander WL, 1979.** An experimental analysis of temporomandibular joint reaction forces in macaques. American Journal of Physical Anthropology, 51:433–456.

**Iordansky NN, 1990.** Evolution of cranial kinesis in lower tetrapods. Netherlands Journal of Zoology, 40: 32-54.

**Iordansky NN, 1996.** The temporal ligaments and their bearing on cranial kinesis in lizards. Journal of Zoology, 239: 167-175.

Islam A, 1955. The skull of *Uromastix hardwickii* Gray. Biologia (Lahore), 1: 141-196.

**Jaslow CR, 1989.** Sexual dimorphism of cranial suture complexity in wild sheep (*Ovis orientalis*). Zoological Journal of the Linnean Society, 95: 273-284.

Kallen FC, Gans C, 1972. Mastication in the little brown bat, Myotis lucifugus. Journal of Morphology, 136: 385-420.

**Kardong KV, 2002.** *Vertebrates: comparative anatomy, function.* Boston: McGraw-Hill.

Kathe W, 1995. Morphology and function of the sutures in the dermal skull roof of *Discosauriscus austriacus makowsky*, 1876 (Seymouriamorpha; Lower Permian of Moravia) and *Onichiodon labrinthicus* Geinitz, 1861 (Temnospondyli, Lower Permian of Germany). Geobios, 19: 255-261.

Konakanchi K, 2005. Musculoskeletal modelling of *Smilodon fatalis* for virtual functional performance testing. MSc thesis, University of New York, Buffalo.

Koolstra JH, van Eijden TMGJ, 1997a. Dynamics of the human masticatory muscles during a jaw open-close movement. Journal of Biomechanics, 30: 883-889.

Koolstra JH, van Eijden TMGJ, 1997b. The jaw open-close movements predicted by biomechanical modelling. Journal of Biomechanics, 30: 943-950.

Koolstra JH, van Eijden TMGJ, 2005. Combined finite-element and rigid-body analysis of human jaw joint dynamics. Journal of Biomechanics, 38: 2431-2439.

**Koolstra JH, van Eijden TMGJ, 2006.** Prediction of volumetric strain in the human temporomandibular joint cartilage during jaw movement. Journal of Anatomy, 209: 369-380.

Koolstra JH, van Eijden TMGJ, Weijs WA, Naeije N, 1988. A three-dimensional mathematical model of the human masticatory system predicting maximum possible bite forces. Journal of Biomechanics, 21: 563-576.

**Kucuk H, 2006.** The effect of modeling cartilage on predicted ligament and contact forces at the knee. Computers in Biology and Medicine, 36(4): 363-375.

**Kupczik K, Dobson CA, Fagan MJ, Crompton RH, Oxnard CE, O'Higgins P, 2007.** Assessing mechanical function of the zygomatic region in macaques: validation and sensitivity testing of finite element models. Journal of Anatomy, 210: 41-53.

Labeit S, Kolmerer B, 1995. Titins: Giant proteins in charge of muscle ultrastructure and elasticity. Science, 270: 293-296.

**Langenbach GEJ, Hannam AG, 1999.** The role of passive muscle tensions in a three-dimensional dynamic model of the human jaw. Archives of Oral Biology, 44: 557-573.

Langenbach GEJ, Zhang F, Herring SW, Hannam AG, 2002. Modelling the masticatory biomechanics of a pig. Journal of Anatomy, 201: 383-393.

Langenbach GEJ, Zhang F, Herring SW, van Eijden TMGJ, Hannam AG, 2006. Dynamic mechanics in the pig mandibular symphysis. Journal of Anatomy, 209: 69-78.

**Lieber RL, 1999.** Skeletal muscle is a biological example of a linear electro-active actuator. 6<sup>th</sup> Annual International Symposium on Smart Structures and Materials, San Diego, USA.

Linke WA, Ivemeyer M, Mundel P, Stockmeier MR, Kolmerer B, 1998. Nature of PEVK-titin elasticity in skeletal muscle. Proceedings of the National Academy of Sciences USA, 95: 8052-8057.

Lü JC, Ji SA, Dong ZM, Wu XC, 2008. An Upper Cretaceous lizard with a lower temporal arcade. Naturwissenschaften, 95: 663-669.

Lucas PW, Ow RK, Ritchie GM, Chew CL, Keng SB, 1986. Relationship between jaw movement and food breakdown in human mastication. Journal of Dental Research, 65: 400-404.

Luschei ES, Goodwin GM, 1974. Patterns of mandibular movement and jaw muscle activity during mastication in the monkey. Journal of Neurophysiology, 37: 954-966.

**Jee WS, 2001.** Integrated bone tissue physiology: anatomy and physiology. In: *Bone mechanics handbook*, (ed. Cowin SC) pp. 1-53. Boca Raton: CRC Press.

John-Alder HB, Bennett AF, 1987. Thermal adaptation in lizard muscle function. Journal of Comparative Physiology B, 157: 241-252.

**Magid A, Reedy MK, 1980.** X-ray diffraction observations of chemically skinned frog skeletal muscle processed by an improved method. Biophysical Journal, 30: 27-40.

Mao JJ, 2002. Mechanobiology of craniofacial sutures. Journal of Dental Research, 81: 810-816.

Margaria R, 1976. Biomechanics and Energetics of Muscular Exercise. Oxford: Clarendon.

**Markey MJ, Main RP, Marshall CR, 2006.** *In vivo* cranial suture function and suture morphology in the extant fish *Polypterus*: implications for inferring skull function in living and fossil fish. The Journal of Experimental Biology, 209: 2085-2102.

Marsh RL, Bennett AF, 1985. Thermal dependence of isotonic contractile properties of skeletal muscle and sprint performance of the lizard *Dipsosaurus dorsalis*. Journal of Comparative Physiology B, 155: 541-551.

**Marsh RL, Bennett AF, 1986.** Thermal dependence of contractile properties of skeletal muscle from the lizard Sceloporus occidentalis, with comments on methods for fitting and comparing force-velocity curves. The Journal of Experimental Biology, 126: 63-77.

**McBrayer LD, White TD, 2002.** Bite force, behaviour, and electromyography in the Teiid lizard *Tupinambis teguixin*. Copeia, 1: 111-119.

McHenry CR, Clausen PD, Daniel WJT, Meers MB, Pendharkar A, 2006. Biomechanics of the rostrum in crocodilians: a comparative analysis using finite element analysis. The Anatomical Record Part A, 288A: 827-849.

McLaughlin E, Zhang Y, Pashley D, Borke J, Yu J, 2000. The load-displacement characteristics of neonatal rat cranial sutures. Cleft Palate-Craniofacial Journal, 37: 590-595.

**Metzger KA, 2002.** Cranial kinesis in Lepidosaurs: skull in motion. In: *Topics in functional and ecological vertebrate morphology*. (eds. Aerts P, D'Août K, Herrel A, Van Damme R), pp. 15-46. Herzogenrath: Shaker Publishing.

Metzger KA, Daniel WJT, Ross CF, 2005. Comparison of beam theory and finiteelement analysis to *in vivo* bone strain in the alligator cranium. The Anatomical Record Part A, 283A (2): 331-348.

Mittra E, Rubin C, Qin Y-X, 2005. Interrelationship of trabecular mechanical and microstructural properties in sheep trabecular bone. Journal of Biomechanics, 38: 1229-1237.

**Miyasaka J, Tanne K, Nakamura S, 1994.** Finite element analysis for stresses in the craniofacial sutures produced by maxillary protraction forces applied at the upper canines. British Journal of Orthodontics, 21: 343-348.

**Moller E, 1966.** The chewing apparatus. An electromyographic study of the action of the muscles of mastication and its correlation to facial morphology. Acta Physiologica Scandinavica, 280: 1-229.

Momersteeg TJA, Blankevoort L, Huiskes R, Kooloos JGM, Kauer JMG, Hendriks JCM, 1995. The effect of variable relative insertion orientation of human knee bone-ligament-bone complexes on the tensile stiffness. Journal of Biomechanics, 28(6): 745-752.

**Muhl ZF, 1982.** Active length-tension relation and the effect of muscle pinnation on fiber lengthening. Journal of Morphology, 173: 285-292.

Muhl ZF, Grimm AF, Glick PL, 1978. Physiologic and histologic measurements of the rabbit digastric muscle. Archives of Oral Biology, 23: 1051-1059.

Nalla RK, Kinney JH, Ritchie RO, 2003. Mechanistic failure criteria for the failure of human cortical bone. Nature Materials, 2: 164-168.

Nelson FE, Gabaldon AM, Roberts TJ, 2004. Force-velocity properties of two avion hindlimb muscles. Comparative Biochemistry and Physiology Part A, 137: 711-721.

**Nigg BM, Herzog W, 1999.** *Biomechanics of the Musculo-Skeletal System.* Chichester: John Wiley & Sons.

Nordstrom SH, Bishop M, Yemm R, 1974. The effect of jaw opening on the sarcomer length of the masseter and temporal muscles of the rat. Archives of Oral Biology, 19: 151-155.

Nordstrom SH, Yemm R, 1972. Sarcomere length in the masseter muscle of the rat. Archives of Oral Biology, 19: 895-902.

**Nordstrom SH, Yemm R. 1974.** The relationship between jaw position and isometric active tension produced by direct stimulation of the rat masseter muscle. Archives of Oral Biology, 19: 353-359.

Noyes FR, Grood ES, 1976. The strength of the anterior cruciate ligament in humans and rhesus monkeys: age and related and species related changes. Journal of Bone and Joint Surgery-Series, 58A: 1074-1082.

**Olson EC, 1961.** Jaw mechanisms: rhipidistians, amphibians, reptiles. American Zoologist, 1: 205-215.

**Otten E, 1987.** A myocybernetic model of he jaw system of the rat. Journal of Neuroscience Methods, 21: 287-302.

**Patton JL, 1993.** Forward dynamic modelling of human locomotion. MSc thesis, Michigan State University, Michigan.

**Pham DT, Dimov SS, 2001.** *Rapid Manufacturing – The Technologies and Applications of Rapid Prototyping and Rapid Tooling*. London: Springer-Verlag.

**Picq PG, Hylander WL, 1989.** Endo's stress analysis of the primate skull and the functional significance of the supraorbital region. American Journal of Physical Anthropology, 79: 393-398.

**Popowics TE, Herring SW, 2007.** Load transmission in the nasofrontal suture of the pig, *Sus scrofa*. Journal of Biomechanics, 40: 837-844.

Porter KR, 1972. Herpetology. Philadelphia: W. B. Saunders Co.

**Preuschoft H, Witzel U, 2002.** Biomechanical investigations on the skulls of reptiles and mammals. Senckenbergiana Lethaea, 82: 207-222.

**Preuschoft H, Witzel U, 2004a.** Functional structure of the skull in hominoidea. Folia Primatologica, 75: 219-252.

**Preuschoft H, Witzel U, 2004b.** A biomechanical approach to craniofacial shape in primates, using FESA. Annals of Anatomy, 186: 397-404.

**Preuschoft H, Witzel U, 2005.** Functional shape of the skull in vertebrates: which forces determine skull morphology in lower primates and ancestral synapsids? The Anatomical Record Part A, 283A: 402-413.

Pritchard JJ, Scott JH, Girgis FG, 1956. The structure and development of cranial and facial sutures. Journal of Anatomy, 90: 73-86.

**Radhakrishnan P, Mao JJ, 2004.** Nanomechanical properties of facial sutures and sutural mineralization front. Journal of Dental Research, 83: 470-475.

**Rafferty KL, Herring SW, Marshall CD, 2003.** Biomechanics of the rostrum and the role of facial sutures. Journal of Morphology, 257: 33-44.

**Rasmussen J, Damsgaard M, Surma E, Christensen ST, de Zee M, 2003.** Designing a general software system for musculoskeletal analysis. IX International Symposium on Computer Simulation in Biomechanics, Sydney, Australia. **Rayfield EJ, 2005a.** Aspects of comparative cranial mechanics in the theropod dinosaurs Coelophysis, Allosaurus and Tyrannosaurus. Zoological Journal of the Linnean Society, 144: 309-316.

**Rayfield EJ, 2005b.** Using Finite-Element Analysis to investigate suture morphology: a case study using large carnivorous dinosaurs. The Anatomical Record Part A, 283A: 349-365.

**Rayfield EJ, 2007.** Finite element analysis and understanding the biomechanics and evolution of living and fossil organisms. The annual Review of Earth and Planetary Sciences, 35: 541-576.

**Rayfield EJ, Norman DB, Horner CC, Horner JR, Smith PM, Thomason JJ, Upchurch P, 2001.** Cranial design and function in a large theropod dinosaur. Nature, 409: 1033-1037.

Richmond BG, Wright B, Grosse IR, Dechow PC, Ross CF, Spencer MA, Strait DS, 2005. Finite Element Analysis in Functional Morphology. The Anatomical Record Part A, 283A: 259-274.

Rieppel O, De Braga M, 1996. Turtles as diapsid reptiles. Nature, 384: 453-455.

**Robinson P, 1976.** How *Sphenodon* and *Uromastyx* grow their teeth and use them. In: *Morphology and Biology of Reptiles*, vol. 3 (eds. Bellairs Ad'A, Cox C), pp. 43-64. London: Academic Press.

Romer AS, 1956. Osteology of the Reptiles. Chicago: University of Chicago Press.

**Ross CF, 2001.** *In vivo* function of the craniofacial haft: the interorbital "pillar." American Journal of Physical Anthropology, 116: 108-139.

**Ross CF, 2005.** Finite element analysis in vertebrate biomechanics. The Anatomical Record Part A, 283A: 253-258.

**Ross CF, Metzger KA, 2004.** Bone strain gradients and optimization in vertebrate skulls. Annals of Anatomy, 186: 387-396.

**Ross CF, Patel BA, Slice DE, Strait DS, Dechow PC, Richmond BG, Spencer MA, 2005.** Modeling masticatory muscle force in finite element analysis: sensitivity analysis using principal coordinates analysis. The Anatomical Record Part A, 283A: 288-299.

Schwenk K, 2000. Feeding in lepidosaurs. In: *Feeding: Form, Function and Evolution in Tetrapod Vertebrates.* (ed. Schwenk K), pp. 175-291. San Diego: Academic Press.

Sellers WI, Crompton RH, 2004. Using sensitivity analysis to validate the predictions of a biomechanical model of bite forces. Annals of Anatomy, 186: 89-95.

Sinclair AG, Alexander RMcN, 1987. Estimates of forces exerted by the jaw muscles of some reptiles. Journal of Zoology, 213: 107-115.

Smith KK, 1980. Mechanical significance of streptostyly in lizards. Nature, 283: 778-779.

Smith KK, 1984. The use of the tongue and hyoid apparatus during feeding in lizards (*Ctenosaura similis* and *Tupinambis nigropunctatus*). Journal of Zoology, 202: 115-143.

Smith KK, Hylander WL, 1985. Strain gauge measurement of mesokinetic movement in the lizard *Varanus exanthematicus*. The Journal of Experimental Biology, 114: 53-70.

**Stavness I, Hannam AG, Lloyd JE, Fels S, 2006.** An integrated dynamic jaw and laryngeal model constructed from CT data. In: *Lecture Notes in Computer Science-Biomedical Simulation*. vol. 4072 (eds. Harders M, Szekely G), pp. 169-177. Berlin: Springer-Verlag.

**Strait DS, Richmond BG, Spencer MA, Ross CF, Dechow PC, Wood BA, 2007.** Masticatory biomechanics and its relevance to early hominid phylogeny: An examination of palatal thickness using finite-element analysis. Journal of Human Evolution, 52: 585-599.

**Strait DS, Wang O, Dechow PC, Ross CF, Richmond BG, Spencer MA, Patel BA, 2005.** Modeling elastic properties in finite-element analysis: How much precision is needed to produce an accurate model? The Anatomical Record Part A, 283A: 275-287.

Tanaka E, Miyawaki Y, del Pozo K, Tanne K, 2000. Changes in the biomechanical properties of the rat interparietal suture incident to continuous tensile force application. Archives of Oral Biology, 45: 1059-1064.

**Tanne K, Miyasaka J, Yamagata Y, Sachdeva R, Tsutsumi S, Sakuda M, 1988.** Three-dimensional model of the human craniofacial skeleton: method and preliminary results using finite element analysis. Journal of Biomedical Engineering, 10: 246-252.

**Timoshenko SP, 1955.** *Strength of Materials : Part 1 : Elementary Theory and Problems*, New York: Van Nostrand.

**Thexton AJ, Hiiemae KM, 1997.** The effect of food consistency upon jaw movement in the Macaque: a cineradiographic study. Journal of Dental Research, 76: 552-560.

**Thexton AJ, Hiiemae KM, Crompton AW, 1980.** Food consistency and bite size as regulators of jaw movement during feeding in the cat. Journal of Neurophysiology, 44: 456-474.

**Throckmorton GS, 1976.** Oral food processing in two herbivorous lizards, *Iguana iguana* (Iguanidae) and *Uromastix aegyptius* (Agamidae). Journal of Morphology, 148: 363-390.

**Throckmorton GS, 1978.** Action of the pterygoideus muscle during feeding in the lizard *Uromastix aegyptius*. The Anatomical Record, 190: 217-222.

**Throckmorton GS, 1980.** The chewing cycle in the herbivorous lizard *Uromastix aegyptius* (Agamidae). Archives of Oral Biology, 25(4): 225-233.

Toole GA, Parker ML, Smith AC, Waldron KW, 2000. Mechanical properties of lettuce. Journal of Materials Science. 35: 3553-3559.

Townsend PR, Raux P, Rose RM, Miegel RE, Radin EL, 1975. The distribution and anisotropy of the stiffness of cancellous bone in the human patella. Journal of Biomechanics, 8: 363-367.

**Trent PS, Walker PS, Wolf B, 1976.** Ligament length patterns, strength, and rotational axes of the knee joint. Clinical Orthopaedics and Related Research, 117: 263-270.

**Turkawski SJJ, van Eijden TMGJ, 2001.** Mechanical properties of single motor units in the rabbit masseter muscle as a function of jaw position. Experimental Brain Research, 138: 153-162.

Usui T, Maki K, Toki Y, Shibasaki Y, Takanobu H, Takanishi A, Hatcher D, Miller A, 2003. Measurement of mechanical strain on mandibular surface with mastication robot: influence of muscle loading direction and magnitude. Orthodontics and Craniofacial Research, 6 (Suppl. 1): 163-167.

Usui T, Maki K, Toki Y, Shibasaki Y, Takanobu H, Takanishi A, Miller A, 2004. Mechanical strain on the human skull in a humanoid robotic model. American journal of orthodontics and dentofacial orthopedics. American Journal of Orthodontics and Dentofacial Orthopedics, 126: 421-431.

van Eijden TMGJ, Klok EM, Weijs WA, Koolstra JH, 1988. Mechanical capabilities of the human jaw muscles studied with a mathematical model. Archives of Oral Biology, 33: 819–826.

van Eijden TMGJ, Turkawski SJJ, 2001. Morphology and physiology of masticatory muscle motor units. Critical Reviews in Oral Biology and Medicine, 12: 76-91.

van Lopik DW, Acar M, 2007. Development of a multi-body computational model of human head and neck. Proceedings of the Institution of Mechanical Engineers, Part K: Journal of Multi-body Dynamics, 221: 175-197.

van Ruijven LJ, Weijs WA, 1990. A new model for calculating muscle forces from electromyograms. European Journal of Applied Physiology, 61: 479-485.

**Verrue V, Dermaut L, Verhegghe B, 2001.** Three-dimensional finite element modelling of a dog skull for the simulation of initial orthopaedic displacements. European Journal of Orthodontics, 23: 517-527.

Vitti M, Basmajian JV, 1977. Integrated actions of masticatory muscles: Simultaneous EMG from eight intramuscular electrodes. The Anatomical Record, 187: 173-190.

**Wagemans PAHM, van de Velde JP, Kuijpers-Jagtman AM, 1988.** Sutures and forces: a review. American Journal of Orthodontics and Dentofacial Orthopedics, 94: 129-141.

Wang JS, Stohler CS, 1990. Textural properties of food used in studies of mastication. Journal of Dental Research, 69(9): 1546-1550.

Wang Q, Dechow PC, 2006. Elastic properties of external cortical bone in the craniofacial skeleton of the rhesus monkey. American Journal of Physical Anthropology, 131: 402-415.

Wang Q, Strait DS, Dechow PC, 2006. A comparison of cortical elastic properties in the craniofacial skeletons of three primate species and its relevance to the study of human evolution. Journal of Human Evolution, 51: 375-382.

Weijs WA, 1980. Biomechanical models and the analysis of form: A Study of the mammalian masticatory apparatus. American Zoologist, 20: 707-719.

Weijs WA, Dantuma R, 1975. Electromyography and mechanics of mastication in albino rat. Journal of Morphology, 146: 1-34.

Weijs WA, Dantuma R, 1981. Functional anatomy of the masticatory apparatus in the rabbit (Oryctolagus cuniculus L). Netherlands Journal of Zoology, 31: 99-147.

Weijs WA, Hillen B, 1985. Cross-sectional area and estimated intrinsic strength of the human jaw muscles. Acta Morphology Neerlandico-Scandinavica, 23: 267-274.

Weijs WA, Korfage JAM, Langenbach GJ, 1989. The functional significance of the position and centre of rotation for jaw opening and closing in the rabbit. Journal of Anatomy, 162: 133-148.

Weingatner T, 1998. A functional 3D simulation of the mastication system. 9<sup>th</sup> International Training and Education Conference(ITEC 98), Lausanne.

Williams SH, Wright BW, Truong VD, Daubert CR, Vinyard CJ, 2005. Mechanical Properties of Foods Used in Experimental Studies of Primate Masticatory Function. American Journal of Primatology, 67: 329-346.

Witzel U, Preuschoft H, 2002. The functional shape of the human skull, as documented by three-dimensional FEM studies. Anthropologischer Anzeiger, 60: 113-35.

Witzel U, Preuschoft H, 2005. Finite-element model construction for the virtual synthesis of the skulls in vertebrates: case study of *Diplodocus*. The Anatomical Record Part A, 283: 391-401.

Wolff J, 1892. Das Gesetz der Transformation der Knochen (Transl. The law of Bone Remodelling). Berlin: Springer-Verlag.

Woo SL, Hollis JM, Adams DJ, Lyon RM, Takai S, 1991. Tensile properties of the human femur-anterior cruciate ligament-tibia complex: The effects of specimen age and orientation. American Journal of Sports Medicine, 19: 217-225.

Wroe S, Clausen P, McHenry C, Moreno K, Cunningham E, 2007a. Computer simulation of feeding behaviour in the thylacine and dingo: a novel test for convergence and niche overlap. Proceedings of the Royal Society B: Biological Sciences, 274(1627): 2819-2828.

Wroe S, Moreno K, Clausen P, McHenry C, Curnoe D, 2007b. High resolution computer simulation of hominid cranial mechanics. The Anatomical Record, 290: 1248-1255.

**Wu X-C, 2003.** Functional morphology of the temporal region in the Rhynchocephalia. Canadian Journal of Earth Sciences, 40: 589-607.

Zardoya R, Meyer A, 2001. The evolutionary position of turtles revised. Naturwissenschaften, 88: 193-200.

# **Appendix A: List of publications**

## **Published papers**

Moazen M, Curtis N, O'Higgins P, Evans SE, Fagan MJ, (to be submitted) Biomechanical assessment of evolutionary changes in the lepidosaurian skull.

Moazen M, Curtis N, O'Higgins P, Jones MEH, Evans SE, Fagan MJ, 2009. Assessment of the role of sutures in a lizard skull- a computer modelling study. Proceedings of the Royal Society, Part B, 276: 39-46.

Moazen M, Curtis N, Evans SE, O'Higgins P, Fagan MJ, 2008. Combined finite element and multibody dynamics analysis of biting in a *Uromastyx hardwickii* lizard skull. Journal of Anatomy, 213: 499-508.

Moazen M, Curtis N, Evans SE, O'Higgins P, Fagan MJ, 2008. Rigid-body analysis of a lizard skull: modelling the skull of *Uromastyx hardwickii*. Journal of Biomechanics, 41: 1274-1280.

**Curtis N, Kupczik K, O'Higgins P, Moazen M, Fagan MJ, 2008.** Predicting skull loading: applying multibody dynamics analysis to a macaque skull. The Anatomical Record, 291: 491-501.

## **Published abstracts**

Moazen M, Curtis N, Jones MEH, Evans SE, Fagan MJ, 2008. The role of cranial sutures in a lizard skull: a finite element analysis investigation. Journal of Vertebrate Paleontology, 28(3): 117A.

Moazen M, Curtis N, O'Higgins P, Evans SE, Fagan MJ, 2007. Musculoskeletal modelling and finite element analysis of lizard skulls. Journal of Morphology, 268(12): 1108.

Fagan MJ, Curtis N, Dobson CA, Karunanayake JH, Kupczik K, Moazen M, Page L, Phillips R, O'Higgins P, 2007. Voxel-based finite element analysis – working directly with microCT scan data. Journal of Morphology, 268(12): 1071.

### Conferences

**Moazen M, Curtis N, Jones MEH, Evans SE, Fagan MJ, 2008.** The role of cranial sutures in a lizard skull: a finite element analysis investigation. 68<sup>th</sup> Annual Meeting of the Society of Vertebrate Paleontology. Renaissance Cleveland Hotel. Ohio. USA. October 2008.

Moazen M, Curtis N, O'Higgins P, Evans SE, Fagan MJ, 2008. Dynamics analysis of a *Uromastyx hardwickii* skull. 26<sup>th</sup> Anniversary Meeting of the Alternative Muscle Club. University of Leeds. UK. July 2008.

Moazen M, Curtis N, O'Higgins P, Evans SE, Fagan MJ, 2007. Using musculoskeletal modelling to predict skull loading: a case study on a Uromastyx

*hardwickii*. Computer Aided Visualisation in Palaeontology. Imperial College London. UK. September 2007.

Moazen M, Curtis N, O'Higgins P, Evans SE, Fagan MJ, 2007. Musculoskeletal modelling and finite element analysis of lizard skulls. 8<sup>th</sup> International Congress of Vertebrate Morphology. Paris. France. July 2007.

Fagan MJ, Curtis N, Dobson CA, Karunanayake JH, Kupczik K, Moazen M, Page L, Phillips R, O'Higgins P, 2007. Voxel-based finite element analysisworking directly with microct scan data.8<sup>th</sup> International Congress of Vertebrate Morphology. Paris. France. July 2007.

**Fagan MJ, Curtis N, Moazen M, O'Higgins P, Evans SE, 2006.** Multibody dynamic analysis of a *Uromastyx hardwickii* (Indian Spiny-Tailed Lizard) skull sensitivity studies.7<sup>th</sup> International Symposium on Computer Methods in Biomechanics and Biomedical Engineering. Juan Les Pins. France. March 2006.

# **Appendix B: Published papers**



Journal of Biomechanics 41 (2008) 1274-1280

JOURNAL OF BIOMECHANICS

www.elsevier.com/locate/jbiomech www.JBiomech.com

## Rigid-body analysis of a lizard skull: Modelling the skull of Uromastyx hardwickii

M. Moazen<sup>a,\*</sup>, N. Curtis<sup>a</sup>, S.E. Evans<sup>c</sup>, P. O'Higgins<sup>b</sup>, M.J. Fagan<sup>a</sup>

<sup>a</sup>Centre for Medical Engineering and Technology, University of Hull, Hull, East Yorkshire HU6 7RX, UK

<sup>b</sup>Department of Biology and Hull York Medical School, University of York, York YO10 5DD, UK <sup>c</sup>Department of Anatomy and Developmental Biology, UCL, London WC1E 6BT, UK

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 *Uromastyx hardwickii* skull was developed for rigid-body dynamic analysis. The *Uromastyx* 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. © 2008 Elsevier Ltd. All rights reserved.

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

<sup>\*</sup>Corresponding author. Tel.: +441482466036; fax: +441482466664. *E-mail addresses:* m.moazen@2005.hull.ac.uk (M. Moazen),

n.curtis@hull.ac.uk (N. Curtis), ucgasue@ucl.ac.uk (S.E. Evans), paul.ohiggins@hyms.ac.uk (P. O'Higgins), m.j.fagan@hull.ac.uk (M.J. Fagan).

<sup>0021-9290/\$-</sup>see front matter © 2008 Elsevier Ltd. All rights reserved. doi:10.1016/j.jbiomech.2008.01.012

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 (*Uromastyx 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 *Uromastyx hardwickii* skull (skull length  $\sim$ 44 mm; skull width  $\sim$ 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  $1050 \text{ kg/m}^3$  (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  $9.81 \text{ m/s}^2$ . 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 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 Weijs (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:

$$F_{\text{muscle}} = F_{\text{max}} \times (F_{\text{A}} \times F_{\text{V}} \times F_{\text{Q}} + F_{\text{P}}), \tag{1}$$

where  $F_{\text{max}}$  is the maximal tetanic force, i.e. physiological cross-sectional area (PCSA) × 30 N/cm<sup>2</sup> (van Ruijven and Weijs, 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  $F_{\text{max}}$  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):

$$F_{\rm A} = -6.25(L/L_0)^2 + 12.5(L/L_0) - 5.25,$$
(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)).

$$F_{\rm V} = \begin{cases} (1 - V/V_{\rm max})/(1 + V/k \times V_{\rm max}), & V0, \\ 1.8 - 0.8(1 + V/V_{\rm max})/(1 - 7.56V/k \times V_{\rm max}), & V < 0, \end{cases}$$
(3)

where  $V_{\text{max}}$  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 × 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):

$$F_{\rm p} = 0.0014 {\rm e}^{6(L-L_0)/L_0}.$$
(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).

$$F_{\text{ligament}} = \begin{cases} K \times (L - L_{\text{i}}), & LL_{\text{i}}, \\ 0, & L < L_{\text{i}}, \end{cases}$$
(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 N/mm) is the stiffness of the food and C (= 9 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-squomosal 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 <sup>2</sup> )	$F_{\rm max}$ (N/cm <sup>2</sup> )	Scaled fibre length (cm)	V <sub>max</sub> (mm/s)	
МАМЕМ	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			



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

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. 3. Muscle force data verses time for selected adductor muscle sections. The muscles contract at maximum gape (time = 0.32 s, gape =  $35^{\circ}$ ) 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  $10^{\circ}$  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  $(1.6\pm0.3 \text{ N})$ , 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 quadrate 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 none 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.

#### References

- Cleuren, J., Aerts, P., De Vree, F., 1995. Bite and joint force analysis in *Caiman crocodilus*. Belgium Journal of Zoology 125, 79–94.
- Close, R., 1964. Dynamic properties of fast and slow skeletal muscle of the rat during development. The Journal of Physiology 173 (1), 74–95.
- Curtis, N., Kupczik, K., O'Higgins, P., Fagan, M.J., 2007. Multibody dynamics analysis of a macaque skull. Journal of Morphology 268 (12), 1063.
- Del Signor, M.J., 2005. A screw-theoretic framework for musculoskeletal system modeling and analysis. M.Sc. Thesis, University of New York, Buffalo.
- de Zee, M., Dalstra, M., Cattaneo, P.M., Rasmussen, J., Svensson, P., Melsen, B., 2007. Validation of a musculo-skeletal model of the mandible and its application to mandibular distraction osteogenesis. Journal of Biomechanics 40, 1192–1201.
- Dumont, E.R., Herrel, A., 2003. The effect of gape angle and bite point on bite force in bats. Journal of Experimental Biology 206, 2117–2123.
- Epstein, M., Herzog, W., 1998. Theoretical Models of Skeletal Muscle Biological and Mathematical Considerations. Wiley, Chichester, pp. 23–69.
- Erickson, G.M., Lappin, A.K., Vliet, K.A., 2003. The ontogeny of bite force performance in American alligator (*Alligator mississippiensis*). Journal of Zoology 260 (3), 317–327.
- Estes, R., De Queiroz, K., Gauthier, J., 1988. Phylogenetic relationships within Squamata. In: Estes, R., Pregill, G. (Eds.), Phylogenetic Relationships of the Lizard Families. Stanford University Press, Stanford, pp. 119–281.

- Evans, S.E., 2003. At the feet of the dinosaurs: the early history and radiation of lizards. Biological Reviews 78, 513–551.
- Frazzetta, T.H., 1962. A functional consideration of cranial kinesis in lizards. Journal of Morphology 111, 287–320.
- Haas, G., 1973. Muscle of the jaws and associated structures in the Rhynchocephalia and Squamata. In: Gans, C., Parsons, T. (Eds.), Biology of the Reptilia, vol. 4. Academic Press, London, pp. 285–490.
- Herrel, A., Aerts, P., 2003. Biomechanical studies of food and diet selection. In: Encyclopaedia of Life Sciences. Nature Publishing Group, London.
- Herrel, A., Aerts, P., De Vree, F., 1998a. Static biting in lizards: functional morphology of the temporal ligaments. Journal of Zoology 244, 135–143.
- Herrel, A., Aerts, P., De Vree, F., 1998b. Ecomorphology of the lizard feeding apparatus a modelling approach. Netherlands Journal of Zoology 48, 1–25.
- Herrel, A., Grauw, E.D., Lemos-Espinal, J.A., 2001. Head shape and bite performance in xenosaurid lizards. Journal of Experimental Zoology 290, 101–107.
- Hill, A.V., 1938. The heat of shortening and the dynamic constants of muscle. Proceedings of the Royal Society of London, Series B, Biological Sciences 126, 136–195.
- Hylander, W.L., 1979. An experimental analysis of temporomandibular joint reaction force in macaques. American Journal of Physical Anthropology 51, 433–456.
- Iordansky, N.N., 1996. The temporal ligaments and their bearing on cranial kinesis in lizards. Journal of Zoology, London 239, 167–175.
- Konakanchi, K., 2005. Musculoskeletal modelling of *Smilodon fatalis* for virtual functional performance testing. M.Sc. Thesis, University of New York, Buffalo.
- Koolstra, J.H., Van Eijden, T.M.G.J., 2005. Combined finite-element and rigid-body analysis of human jaw joint dynamics. Journal of Biomechanics 38, 2431–2439.
- Koolstra, J.H., Van Eijden, T.M.G.J., 2006. Prediction of volumetric strain in the human temporomandibular joint cartilage during jaw movement. Journal of Anatomy 209, 369–380.
- Koolstra, J.H., Van Eijden, T.M.G.J., Weijs, W.A., Naeije, N., 1988. A three-dimensional mathematical model of the human masticatory system predicting maximum possible bite forces. Journal of Biomechanics 21, 563–576.
- Kucuk, H., 2006. The effect of modeling cartilage on predicted ligament and contact forces at the knee. Computers in Biology and Medicine 36 (4), 363–375.
- Langenbach, G.E.J., Hannam, A.G., 1999. The role of passive muscle tensions in a three-dimensional dynamic model of the human jaw. Archives of Oral Biology 44, 557–573.
- Langenbach, G.E.J., Zhang, F., Herring, S.W., Hannam, A.G., 2002. Modelling the masticatory biomechanics of a pig. Journal of Anatomy 201, 383–393.
- Langenbach, G.E.J., Zhang, F., Herring, S.W., van Eijden, T.M.G.J., Hannam, A.G., 2006. Dynamic mechanics in the pig mandibular symphysis. Journal of Anatomy 209, 69–78.
- Marsh, R.L., Bennett, A.F., 1985. Thermal dependence of isotonic contractile properties of skeletal muscle and sprint performance of the

lizard *Dipsosaurus dorsalis*. Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology 155, 541–551.

- Metzger, K., 2002. Cranial kinesis in lepidosaurs: skulls in motion. In: Aerts, P., D'Août, K., Herrel, A., van Damme, R. (Eds.), Topics in Functional and Ecological Vertebrate Morphology. Shaker publishing, Antwerp, pp. 15–46.
- Metzger, K.A., Herrel, A., 2005. Correlation between lizard cranial shape and diet: a quantitative, phylogenetically informed analysis. Biological Journal of the Linnean Society 86, 433–466.
- Moazen, M., Curtis, N., O'Higgins, P., Evans, S.E., Fagan, M.J., 2007. Musculoskeletal modelling and finite element analysis of lizard skulls. Journal of Morphology 268 (12), 1108.
- Momersteeg, T.J.A., Blankevoort, L., Huiskes, R., Kooloos, J.G.M., Kauer, J.M.G., Hendriks, J.C.M., 1995. The effect of variable relative insertion orientation of human knee bone–ligament–bone complexes on the tensile stiffness. Journal of Biomechanics 28 (6), 745–752.
- Noyes, F.R., Grood, E.S., 1976. The strength of the anterior cruciate ligament in humans and rhesus monkeys: age and related and species related changes. Journal of Bone and Joint Surgery 58A, 1074–1082.
- Otten, E., 1987. A myocybernetic model of he jaw system of the rat. Journal of Neuroscience Methods 21, 287–302.
- Peck, C.C., Hannam, A.G., 2007. Human jaw and muscle modeling. Archives of Oral Biology 52, 300–304.
- Sellers, W.I., Crompton, R.H., 2004. Using sensitivity analysis to validate the predictions of a biomechanical model of bite forces. Annals of Anatomy 185, 89–95.
- Throckmorton, G.S., 1976. Oral food processing in two herbivorous lizards, *Iguana iguana* (Iguanidae) and *Uromastix aegyptius* (Agamidae). Journal of Morphology 148, 363–390.
- Throckmorton, G.S., 1980. The chewing cycle in the herbivorous lizard Uromastix aegyptius (Agamidae). Archives of Oral Biology 25 (4), 225–233.
- Trent, P.S., Walker, P.S., Wolf, B., 1976. Ligament length patterns, strength, and rotational axes of the knee joint. Clinical Orthopaedics and Related Research 117, 263–270.
- Turkawski, S.J.J., van Eijden, T.M.G.J., 2001. Mechanical properties of single motor units in the rabbit masseter muscle as a function of jaw position. Experimental Brain Research 138, 153–162.
- van Eijden, T.M.G.J., Turkawski, S.J.J., 2001. Morphology and physiology of masticatory muscle motor units. Critical Reviews in Oral Biology and Medicine 12, 76–91.
- van Ruijven, L.J., Weijs, W.A., 1990. A new model for calculating muscle forces from electromyograms. European Journal of Applied Physiology 61, 479–485.
- Weijs, W.A., Korfage, J.A.M., Langenbach, G.J., 1989. The functional significance of the position and centre of rotation for jaw opening and closing in the rabbit. Journal of Anatomy 162, 133–148.
- Woo, S.L., Hollis, J.M., Adams, D.J., Lyon, R.M., Takai, S., 1991. Tensile properties of the human femur-anterior cruciate ligament–tibia complex. The effects of specimen age and orientation. American Journal of Sports Medicine 19, 217–225.
- Wu, X.-C., 2003. Functional morphology of the temporal region in the Rhynchocephalia. Canadian Journal of Earth Sciences 40, 589–607.

# Combined finite element and multibody dynamics analysis of biting in a *Uromastyx hardwickii* lizard skull

Journal of Anatomy

M. Moazen,<sup>1</sup> N. Curtis,<sup>1</sup> S. E. Evans,<sup>3</sup> P. O'Higgins<sup>2</sup> and M. J. Fagan<sup>1</sup>

<sup>1</sup>Department of Engineering, University of Hull, Hull, UK <sup>2</sup>Department of Biology and Hull York Medical School, University of York, York, UK <sup>3</sup>Research Department of Cell and Developmental Biology, UCL, London, UK

#### Abstract

Lizard skulls vary greatly in shape and construction, and radical changes in skull form during evolution have made this an intriguing subject of research. The mechanics of feeding have surely been affected by this change in skull form, but whether this is the driving force behind the change is the underlying question that we are aiming to address in a programme of research. Here we have implemented a combined finite element analysis (FEA) and multibody dynamics analysis (MDA) to assess skull biomechanics during biting. A skull of *Uromastyx hardwickii* was assessed in the present study, where loading data (such as muscle force, bite force and joint reaction) for a biting cycle were obtained from an MDA and applied to load a finite element model. Fifty load steps corresponding to bilateral biting towards the front, middle and back of the dentition were implemented. Our results show the importance of performing MDA as a preliminary step to FEA, and provide an insight into the variation of stress during biting. Our findings show that higher stress occurs in regions where cranial sutures are located in functioning skulls, and as such support the hypothesis that sutures may play a pivotal role in relieving stress and producing a more uniform pattern of stress distribution across the skull. Additionally, we demonstrate how varying bite point affects stress distributions and relate stress distributions to the evolution of metakinesis in the amniote skull. **Key words:** biting; finite element analysis; multibody dynamics analysis; skull.

#### Introduction

This study addresses the mechanical function of the skull of the lizard Uromastyx hardwickii (Squamata, Agamidae) using a combined finite element analysis (FEA) and multibody dynamics analysis (MDA) approach. Uromastyx is generally considered to be one of the two basal agamid genera (the other being Leiolepis) and is interesting as (1) being primarily herbivorous, (2) having a specialized arrangement of the pterygoideus muscle whereby an additional external slip attaches to the outside of the skull, and (3) in having a skull that is said to be essentially akinetic (lacking obvious intracranial movements) but hyperstreptostylic (Throckmorton, 1976). Uromastyx is a common ground-living lizard in India, Africa and the Middle East and has therefore been quite well described in the literature (e.g. Saksena, 1942; El-Toubi, 1945; George, 1955; Islam, 1955; Throckmorton, 1976). With regard to mechanical function we are concerned to investigate the

Correspondence

Accepted for publication *30 July 2008* Article published online *14 October 2008* 

© 2008 The Authors Journal compilation © 2008 Anatomical Society of Great Britain and Ireland

relationship between sutures and stress distribution, the extent to which there is potential for metakinesis, and the effects of varying bite point on stresses.

The application of FEA and MDA has increased rapidly in the area of functional morphology, as these technologies have the potential to advance our understanding of the driving forces that shape bone, as well as more complex and specific structures such as the skull (e.g. McHenry et al. 2007; Curtis et al. 2008). The advantages of using these mechanical engineering tools is that forces acting upon the skull can be estimated and then applied to a model of it to estimate patterns of strain and stress across the skull. In conjunction with knowledge of evolutionary paths, this information can be used to develop hypotheses regarding the genetic and epigenetic factors that shape the skeleton. Both MDA and FEA warrant a brief overview.

MDA involves two or more rigid bodies whose motions can be independent of each other, or whose motions are constrained by joints or specified contact surfaces and springs. As the term rigid body implies, no deformation of the geometries occurs, and as such, deformation does not affect gross body motion. This area of dynamics can be divided into two disciplines: (1) a kinetic analysis, which is the study of motion produced under the action of forces, and (2) a kinematic analysis, which is the study of motion regardless of the masses or forces. For example, a kinetic

M. Moazen, Department of Engineering, University of Hull, Hull, HU6 7RX, UK. E: m.moazen@2005.hull.ac.uk

simulation is applied when assessing jaw motion that is driven by the masticatory muscles, and a kinematic simulation is applicable when a rotation is defined to a joint and motion is produced without concern for mass and muscle forces (e.g. Geradin & Cardona, 2001; Hannam, 2003). FEA works by dividing the geometry of the problem under investigation (e.g. a skull) into a finite number of sub-regions, called elements, which are connected together at their corners (and sometimes along their mid-sides). These points of connection are called nodes. For stress analysis, a variation in displacement (e.g. linear or quadratic) is then assumed through each element, and equations describing the behaviour of each element are derived in terms of the (initially unknown) nodal displacements. These element equations are then combined to give a set of system equations which describes the behaviour of the whole problem. After modifying the equations to account for the loading and constraints applied to the problem, these system equations are solved. The output is a list of all the nodal displacements. The element strains can then be calculated from the displacements, and the stresses from the strains. More detailed descriptions of FEA principles and its applications to craniofacial mechanics are available (e.g. Fagan, 1992; Richmond et al. 2005; Rayfield, 2007).

MDA, predominately an engineering tool, was brought to the area of biomechanics to study human movement, and more recently it is being used by those interested in functional morphology (e.g. Langenbach et al. 2002; Sellers & Crompton, 2004; de Zee et al. 2007; Curtis et al. 2008; Moazen et al. 2008). MDA can be used to estimate the loading conditions that act, for example, on the skull during biting and which, if modelled accurately, will provide more precise data for FEA. Whereas MDA is a relatively under-utilized tool in this area, FEA is widely applied, with some authors adopting inductive methods (Preuschoft & Witzel, 2002, 2005) and some deductive methods (e.g. Rayfield et al. 2001; Dumont et al. 2005; Ross et al. 2005). Recent FEA studies have become increasingly complex, with approximations in material properties of bone (e.g. Strait et al. 2005; Wang & Dechaw, 2006) and the representation of muscle loading (e.g. Grosse et al. 2007; Wroe et al. 2007) being addressed more thoroughly. However, so far there are few combined MDA and FEA studies in the literature (e.g. Koolstra & van Eijden, 2005, 2006; Curtis et al. 2008).

The aim of this present phase of our work is to evaluate the potential of an MDA approach to the loading of skulls using a finite element model of *Uromastyx*. In this paper, the resulting MDA load data are used to explore the variation of stress across the skull to consider the possible role of sutures, the potential for metakinesis and the effects of varying bite point. During each simulation, gape angle, muscle force, bite force and joint force all vary with time, with the MDA solution outputting the load data at discrete time steps. These load steps are then transferred to the FE analysis, where the variation of stress and strain over time can be examined. In this study we also compared the results of FEA models that used MDA load data with models using loading methods more widely described in the literature.

#### Materials and methods

#### Multibody dynamics analysis

The development of a multibody dynamics model and its subsequent simulations has been discussed in detail previously (Moazen et al. 2008). In brief, three-dimensional models of the cranium, mandible and guadrates of a Uromastyx hardwickii skull were constructed from microCT data and then imported into MSC ADAMS motion simulation software (Santa Ana, CA, USA) in preparation for a multibody dynamics analysis. Mass properties were assigned to the moving parts (jaw and quadrates) and soft tissue structures (i.e. muscles and ligaments) applied. The ligaments were modelled as tension-only springs (i.e. no compressive resistance) and the jaw-closing muscles [named as 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)] were defined with Hill-type muscle properties (Hill, 1938) as described by van Ruijven & Weijs (1990). A kinematic analysis was performed to open the jaw, and then muscle forces, which varied with gape, were applied to close the jaw during a forward dynamic biting simulation. Ligament, bite and joint forces were calculated, as a food particle with viscoelastic material properties (i.e. stiffness of 50 N mm<sup>-1</sup> and damping ratio of 9 Ns mm<sup>-1</sup>) was modelled in the mouth aligned perpendicular to the teeth. The food particle was placed at three positions, moving from the front of the mouth (incisiform tooth) to the back of the mouth (posterior teeth) (Fig. 2).

#### Finite element analysis

The three-dimensional model of the cranium developed for the MDA was transformed into a meshed solid geometry using AMIRA image segmentation software (Mercury Computer Systems Inc., Chelmsford, MA, USA). The model consisted of 207 000 quadratic tetrahedral elements and was imported into ANSYS11 Mechanical (ANSYS, Inc., Canonsburg, PA, USA) in preparation for FEA. Bone was modelled as an isotropic material with a Young's modulus of 10 GPa and a Poisson's ratio of 0.3. These values are comparable to bovine Haversian bone as used in other studies (e.g. Rayfield et al. 2001; Rayfield, 2005a). Although bone is known to be anisotropic, previous studies (e.g. Strait et al. 2005) have shown that comparable patterns of stress across the model are formed with an isotropic assumption.

Boundary conditions (i.e. muscle force, ligament force, bite force and joint force) were imported directly from the MDA solutions, which were divided into 50 load steps for each bite position (three bite positions in total), representing initial biting at a gape of 32.6° until final biting at a gape of 0.9° (i.e. jaw closing as the food particle was compressed). The force in each muscle or ligament strand was applied in the FEA at one node, which was chosen by finding the closest coordinate in the FE model to the muscle force application in the MDA model. In the MDA model,



**Fig. 1** Sample muscle and ligament force data plotted vs. gape angle from MDA corresponding to an anterior bite. The MPST is an internal muscle and it is not visible in this figure.



**Fig. 2** 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.

the cranium, quadrates and mandible were represented as separate bodies, allowing the bite force, quadrato-mandibular (joint 2) and quadrato-squamosal (joint 1) joint forces, and muscle and ligament forces to be calculated. In the FE model, only the cranium was represented with the relevant forces calculated by the MDA applied directly to it. Thus the quadrate was not modelled in the FEA, but its effect was included, without any loss of accuracy, by application of the calculated quadrato-squamosal joint forces. Three nodes were constrained at the back of the skull (occipital condyle); however, as the loading data came directly from the MDA models, where the muscle forces and reaction forces (bite and joint) were in equilibrium, negligible stress values were subsequently recorded at the constraints. This is one of the important advantages of using MDA before FEA. The element stress values were then automatically written into an element table for each of the loading conditions for postprocessing.

To demonstrate the effects of incorporating the load data produced by an MDA analysis, a simple FEA comparison was carried out between a model with one step of the MDA solution, and a model with very simple loading and constraint conditions. In the latter, a bite force was applied at the front of the cranium while three nodes on the occipital condyle were fully constrained (Model A); this is comparable to other similar studies (e.g. Tanne et al. 1988; Miyasaka et al. 1994; Rayfield, 2005b). A second model was similarly constrained, but loaded with the load data from an MDA solution (i.e. bite force, muscle force, ligament force and joint force) corresponding to biting at the front of the cranium with a 23° gape angle (Model B). Both models had the same applied bite force of 30 N.

#### Results

#### MDA of Model B

Sample muscle and ligament force data used in the MDA are presented in Fig. 1. Many of the muscle forces were relatively constant, despite the non-linear force–length relationships used in their definitions (see Moazen et al. 2008), whereas the force in others [for example, the posterior strand of the MAMESA 1 and ligament forces] gradually increases or decreases as the geometry of the model and moment arms of the muscles change with time. The muscle forces were applied to biting simulations on a viscoelastic food particle as described in Moazen et al. (2008), and provided joint, bite and ligament forces for three different bite positions, as shown in Fig. 2.



**Fig. 3** Comparison of von Mises stress of two FE models in dorsal and ventral view. Both Models A and B were loaded with the same bite force (biting in front) and constraints (at the occipital condyle – see text), whereas Model B also included muscle, ligament and joint forces. Note stress values are in MPa and that grey colours indicate stresses in excess of 32 MPa.

#### Comparison of FEA for Models A and B

Finite element analysis produces a vast amount of data. Interpreting those data, or even presenting it in a concise way, can be difficult, and different studies often report different output parameters. The most popular are principal stresses, maximum shear stress and von Mises stress (or strain). For example, the full three-dimensional stress field at each point in the model consists of three direct stresses in the x, y and z directions and three shear stresses. These six values can be resolved into three perpendicular principal stresses (which are the normal stresses on planes which have no corresponding shear stresses). The advantage of considering the principal stresses is that they show the variation of the 'most tensile' and 'most compressive' stress through the structure and reveal information about its mode of loading. Also, very importantly, their directions show the load transfer paths through the structure. Of course, on the surface of the model, the normal stress must equal zero, thus only two principal stresses need to be considered. The mode of loading and load path information is not provided by the maximum shear stress or the

von Mises stress (or strain) values. The maximum shear stress is simply half the difference between the minimum and maximum principal stresses. The von Mises stress combines all the stresses at a point into a single parameter, and is a convenient way of expressing the state of stress at that point by a single value. Like the maximum shear stress it gives no indication of whether the material is under tension or compression. In engineering analyses, both the maximum shear stress and the von Mises stress are used in the prediction of failure of ductile materials - called Tresca's failure criterion and the von Mises failure criterion, respectively (Timoshenko, 1955). As bone is a ductile material (Nalle et al. 2003), failure is not considered in most FE models of bone, and maximum shear stresses and von Mises stresses are simply used as simple scalar measures of stress level (e.g. Grosse et al. 2007; McHenry et al. 2007; Wroe et al. 2007; Moreno et al. 2008).

In this part of the work, von Mises stress was plotted for both Model A and Model B (as shown in Fig. 3) to get a general indication of the stress levels in the two models with an anterior bite point. In Model A high stress concentrations were observed in the basicranium in the region of

	R1	R2	R3	R4	R5	R6	R7	R8	R9	R10
Model A	8.47	6.24	1.60	3.03	4.61	2.21	2.60	7.78	3.85	12.94
Model B	11.57	14.19	3.14	17.76	19.61	8.48	5.61	17.90	5.00	14.53







**Fig. 4** Location of 10 identified regions used for quantitative representation of results. (A) Ventral and (B) lateral views.

the constraints; however, in Model B the stress in this region was negligible. Areas of high stress were seen in Model B at the points of muscle force application. Table 1 presents a quantitative comparison of von Mises stress between these two models over 10 selected regions whose locations are shown in Fig. 4.

#### FEA of Model B

Figure 5 shows the von Mises stress distribution during bilateral biting simulation at the front of the mouth (incisiform teeth), where the stress varies as the jaw closes, corresponding to the varying loading conditions (i.e. muscle force, joint force and bite force) at different gapes. Von Mises stress was again assessed at 10 selected regions across the skull during this simulation to show how peak stress in different regions of the skull can vary (see Figs 4 and 6). Figure 7 shows a comparison between the first principal (most tensile) stress and the third principal (most compressive) stress obtained from a biting simulation in the front of the mouth (biting at gape angles of 0.9°) and a real *Uromastyx* lizard skull in which cranial sutures are highlighted. The first principal stress and the third principal stress are more relevant than von Mises stress for this aspect of the research. From this analysis it was noted that higher stress regions were formed near the suture locations.

A quantitative comparison of the von Mises stress at three locations on the skull (R1, R3 and R7 see Fig. 4) was made while biting at different positions in the mouth (see Fig. 8). These three points (at the root of the left post-parietal process, between the orbits, and at the root of the left post-orbital bar above the end of the tooth row) were chosen to represent anterior, posterior, and lateral skull regions. The maximum variation was noted at R3, where biting at the back of the mouth led to a reduction in stress of 81% compared to the front of the mouth (front – 2.96 MPa, back –0.54 MPa). A reduction of 23% was also noted at R1 (front –11.40 MPa, back –8.81 MPa), but there was a small increase in stress in R7.

#### Discussion

#### Methodological approaches

Multibody dynamics analysis is a powerful tool that allows many loading scenarios to be investigated, in turn providing increased data for finite element analyses (i.e. unilateral and bilateral bite forces, varying muscle loading at different gapes, etc). The main goal of this study was to apply the previously generated load data from an MDA simulation (Moazen et al. 2008) to a finite element model. Moazen et al. (2008) developed a model of jaw open/closing in Uromastyx in which the jaw was opened by defined motion data (Throckmorton, 1980), during which a mobile quadrate moved anteriorly and resulted in a slack temporal ligament. During jaw closing, muscle forces (assuming 100% activity) were applied to close the jaw against a viscoelastic food particle. This resulted in posterior movement of the quadrate to its starting position while the temporal ligament limited this backward movement by becoming tense (see Fig. 1). Movement of a food particle from the front of the mouth (incisiform tooth) to the back of the mouth (posterior teeth) showed that biting

#### 504 FEA and MDA of biting in Uromastyx, M. Moazen et al.



**Fig. 5** Model B: ventral and lateral views showing the variation in von Mises stress durin bilateral biting at the front teeth. (A–C) Biting a gape angles of 32°, 23° and 0.9°, respectively. Note stress values are in MPa and that grey colours indicate stresses in excess of 32 MPa.

toward the back of the mouth is more effective because it leads to an increase in bite force, with a decrease in joint forces, as well as less tension in the temporal ligament (see Fig. 2).

There are currently two main methods of loading and constraining FE models of skulls in the literature. The simplest is to apply a bite force on one or more teeth on the skull, possibly with additional muscle loads, while applying rigid constraints at the occipital condyle. This ignores any reaction forces acting upon the skull via the jaw joints, and does not attempt to equilibrate the skull (e.g. Tanne et al. 1988; Miyasaka et al. 1994; Rayfield, 2005b). The second is to constrain the skull at the jaw joints and the teeth in the vertical direction while applying muscle forces directed towards their mandibular insertions (e.g. Dumont et al. 2005; Strait et al. 2005). This second method is similar to one solution step in the MDA method described above, except (1) it does not easily allow for different gape angles and changes in geometry; (2) it is time-consuming to calculate the directions of the muscle forces accurately; and (3) it is not easy to incorporate the actual physiological behaviour of the jaw joints – for example, the mobile quadrate in the *Uromastyx* described here, or the translation and rotation of the jaw joint observed in primate skulls. These affect the moment arms of the muscles and create more complex boundary conditions at the jaw joints.

Erroneous stress concentrations about constraints in the FEA were noted in the simple model (bite force only with constraints at the occipital condyle). These constraint stresses were not present in the MDA-loaded FEA model,



Fig. 6 Variation of von Mises stress during the biting cycle at 10 sample locations, with an anterior bite point (see Fig. 4 for locations of the sampling points).

as the bite and joint forces are derived in response to applied muscle forces and provide a state of equilibrium. Also, a quantitative comparison of the von Mises stress in 10 identified regions between these two models confirms that the stresses recorded from the approach that was implemented in this research are higher than in the simple model, and depending on the area of interest on the skull this can lead to significant differences (see Table 1 and Fig. 3). Stress concentrations were, however, observed in the MDA-loaded FEA model in the dorsal region of the postorbitofrontal/jugal and jugal/squamosal sutures due to the action of the muscle forces, which of course were not present in the simply loaded model. The issue of higher stresses in areas where distributed loads are applied as point loads is a common problem in all finite element analyses (because load is applied over a vanishingly small area), and has been addressed in more detail for this application by Grosse et al. (2007). An interesting finding in this study was that in the ventral view, stress distributions were similar in the nasal and frontal bones for both models, confirming that the stress in this region is predominantly due to the bite force, as expected (see Fig. 3).

#### Biting in Uromastyx

From Figs 5 and 6 it can be seen that stress varies throughout the skull during biting, to different degrees in different regions of the skull. This variation is due to the variation in muscle, joint and ligament forces and their respective moment arms at different gapes (see Figs 1 and 2). A sudden increase of stress between a gape angle of  $20^{\circ}$  and  $15^{\circ}$  was noted during the biting simulation (see Fig. 6). This occurs as a result of the combined increased tension in the different muscle groups at this stage of jaw closure and the resultant changes in reaction at the bite point and joint 1 (see Fig. 1 – MAMESA 1; note other muscle strands, not shown, follow a similar pattern to MAMESA 1). Whether this happens as abruptly *in vivo* is not known, but the identification of this likely cause and effect highlights the value of MDA modelling.

One interesting finding during these FE studies is the identification of higher areas of first principal and/or third principal stress around anatomical suture zones (see Fig. 7), most notably between the prefrontal, maxilla and palatine in the antorbital margin; between the postorbitofrontals and parietal; at the junction of the nasals, prefrontals, frontal and premaxilla on the snout; around the junction of the frontal and parietal; and at the sutures between the jugal and squamosal, and jugal and postorbitofrontal. This finding suggests that sutures are located in areas of high tension/compression, and as such could act to alleviate the stress arising from biting, which agrees with previous experimental and computational studies (Herring et al. 1996; Herring & Teng, 2000; Rafferty et al. 2003; Rayfield, 2005a). Further work is now on-going to introduce sutures into these models to see whether they do indeed reduce the level of stress in these regions.

There are also high levels of stress at many of the interfaces between the braincase and the dermal skull, notably in the basipterygoid processes of the basisphenoid where they meet the pterygoids, in the paroccipital processes of the opisthotic (meeting the parietal, squamosal, supratemporal and quadrate), and in the posterior processes of the parietal. These strains may reflect the tendency of the braincase to move in relation to the skull roof and palate and thus be indicative of a selective advantage for greater freedom of movement (metakinesis). Comparison of the first and third principal stress (Fig. 7) highlights a related feature not evident in the von Mises plots, namely the high level of tension in the epipterygoids during biting in Uromastyx (Fig. 7A). In lizards, the epipterygoids are slender mobile columns. Each has a synovial ventral joint with the pterygoid (in a pit, the fossa columellae) and a ligamentous dorsal attachment to the parietal and the braincase. Where present, the epipterygoids are the origin of parts of the m. pseudotemporalis. They are thought to brace the braincase against the dermal skull when (if) one moves against the other during metakinesis, and may be absent or reduced in taxa where this movement is lost (e.g. chamaeleons, snakes, some agamids; Schwenk, 2000). The high level of tensile strain seen in our model during biting may result from direct



Fig. 7 (A) First principal (most tensile) stress. (B) Real Uromastyx skull. (C) Third principal (most compressive) stress. A comparison of the distribution of the stress predicted by the FE model with the location of the sutures in a real skull of a Uromastyx hardwickii (UCL collection) in ventral and lateral views. Note the quadrate was included in the MDA model but is not modelled in the FEA study, and hence is not shown in the FE plot. The grey colour in (A) shows values less than zero, whereas in (C) it shows values greater than zero. FE plots obtained from biting at a gape angle of 0.9° at the front of the mouth. pop, postparietal process; pof, postfrontal; pob, postorbital bar (i.e. separating orbit from temporal region); aom, antorbital margin; f, frontal; pf, prefrontal j, jugal; n, nasal; oc, occipital condyle; pal, palatine; par, parietal; pm, premaxilla; q, quadrate; sq, squamosal; ep, epipterygoid; pt, pterygoid.



**Fig. 8** Comparison of the variation in von Mises stress in three sample regions of the skull at varying bite points in the mouth.

muscle action, although (Fig. 2) the m. pseudotemporalis does not generate much force at this stage of the bite. Alternatively, like the stresses noted above, the tension in the epipterygoid may reflect a tendency of the braincase to rotate on the dermal skull during biting, pushing the pterygoids apart. In the living animal, these strains in the epipterygoid would be mitigated by its mobile dorsal and ventral articulations.

This work has also shown the importance of considering different loading scenarios, as the variation in stress across the skull varies with different load conditions. Our results agree with others who noted greater bite forces with a more posterior bite point (e.g. Koolstra et al. 1988; Dumont & Herrel, 2003; Sellers & Crompton, 2004). However, we also found that peak stress values generally tended to reduce with more posteriorly positioned food boluses, even though the bite force increased (see Figs 2 and 8). For any lizard herbivore, the primary role of the jaws and dentition is in cropping (Schwenk, 2000). Herbivorous lizards tend to have shorter, deeper jaws than insectivores (Herrel et al. 1999), with a higher mechanical advantage, and this is the pattern seen in Uromastyx. Uromastyx uses a combination of jaw closure and anteroposterior jaw movement (streptostylic quadrate) to tear off plant food and bring it into the mouth (Throckmorton, 1976), but uses jugo-mandibular ligaments to fix the quadrate in hard biting. An anterior bite, as in cropping, would induce compressive stress in the premaxilla and up through to the frontal, which it directly abuts between the nasals, to the parietal; these bones are thick and strongly united. A posterior bite would have a different force trajectory with much of the stress passing through the jugal and along the lateral aspect of the skull. The drop in strain at R3 (frontal) and, to a lesser degree, R1 (parietal) between anterior and posterior bite positions could reflect these different trajectories, as might the slight increase in strain at R7.

#### Limitations

As with most biomechanical simulations, there are a number of simplifications and approximations in this analysis. Probably the most significant is that we have assumed 100% activation for each muscle; this is a simple, convenient approach, but is unlikely to be physiologically accurate. For our long-term goal, to understand the structure of the skull, it may be relevant because it allows us to predict the maximum possible stress that the skull could experience, and that it is perhaps ultimately constructed to withstand. However, we aim to refine this aspect of the simulation to allow us to explore the habitual stresses experienced by the skull, rather than the exceptional. Both must affect skull development but presumably in different ways. Also in real life the position of the food particle in relation to the teeth will change during the bite cycle. Here we only consider a food particle positioned perpendicular to the teeth (both in the MDA and FEA).

The assumption of isotropy in the bone properties is also known to affect the level of stress in the bone, but not the overall distribution (Strait et al. 2005). Detailed material property values were not available for the specimen examined in this study, and would be extremely difficult to obtain due to the size of the skull. Also, the use of assumed non-isotropic material properties will introduce unquantifiable artefacts into the results. Therefore we followed the usual pragmatic approach of assuming isotropic properties (Witzel & Preuschoft, 1999; Rayfield et al. 2001; Cattaneo et al. 2003; Cruz et al. 2003; Kupczik et al. 2007; Strait et al. 2007).

#### Conclusions

Despite these limitations, this work demonstrates the benefits of using MDA to estimate the biomechanical loads for application to FE models of skulls. We feel this is the best way to properly test hypotheses in functional morphology in a more objective way, where muscle data, joint data and bite data can all be obtained and then applied to calculate stress and strains throughout the skull. More work is required to improve the complexity and realism of both the MDA and FEA models, but the results shown here demonstrate the effects of different bite positions on patterns of strain in the lizard skull, suggest a selective advantage for the elaboration of joints involved in relative movements of the braincase against the dermal skull, and provide evidence of a functional role for cranial sutures. Additional loading scenarios need to be considered in the MDA, such as unilateral biting, and in the FEA the inclusion of sutures and anisotropic material properties would allow more accurate stress and strain results.

#### Acknowledgements

The authors thank Mehrdad Moazen for his support, Jessie Maisano, University of Texas, Austin, Digimorph Laboratory, for the microCT data of the *Uromastyx*, and Mike Park for photographing our specimens. We also gratefully acknowledge the financial support of BBSRC.

#### References

- Cattaneo PM, Dalstra M, Melsen B (2003) The transfer of occlusal forces through the maxillary molars: a finite-element study. *Am J Orthod Dentofacial Orthop* **123**, 367–373.
- Cruz M, Wassall T, Toledo EM, Barra LP, Lemonge AC (2003) Three-dimensional finite-element stress analysis of a cuneiformgeometry implant. Int J Oral Maxillofac Implants 18, 675– 684.
- Curtis N, Kupczik K, O'Higgins P, Moazen M, Fagan MJ (2008) Predicting skull loading: applying multibody dynamics analysis to a Macaque skull. Anat Rec 291, 491–501.
- **Dumont ER, Herrel A** (2003) The effect of gape angle and bite point on bite force in bats. *J Exp Biol* **206**, 2117–2123.
- Dumont ER, Piccirillo J, Grosse IR (2005) Finite-element analysis of biting behaviour and bone stress in the facial skeletons of bats. *Anat Rec* 283A, 319–330.
- El-Toubi MR (1945) Notes on the cranial osteology of Uromastyx aegyptia (Forskål). Bull Fac Sci Cairo Faud 1 Univ 25, 1–10.
- Fagan MJ (1992) Finite Element Analysis Theory and Practice. Harlow: Longmans.
- George JC (1955) On the cranial osteology of Uromastix hardwickii (Gray). J Anim Morphol Physiol 1, 23–29.
- Geradin M, Cardona A (2001) Flexible Multibody Dynamics: A Finite Element Approach. New York: J Wiley & Sons.
- Grosse IR, Dumont ER, Coletta C, Tolleson A (2007) Techniques for modeling muscle-induced forces on finite element models of skeletal structures. *Anat Rec* 290, 1069–1088.
- Hannam AG (2003) Dynamic modeling and jaw biomechanics. Orthod Craniofac Res 6, 59–65.

- Herrel A, Aerts P, Fret J, De Vree F. (1999). Morphology of the feeding system in agamid lizards: ecological correlates. *Anat Rec* 254, 496–507.
- Herring SW, Teng SY (2000) Strain in the braincase and its sutures during function. Am J Phys Anthropol 112, 575–593.
- Herring SW, Teng SY, Huang XF, Mucci RJ, Freeman J (1996) Patterns of bone strain in the zygomatic arch. *Anat Rec* 246, 446–457.
- Hill AV (1938) The heat of shortening and the dynamic constants of muscle. *Proc R Soc Lond B Biol Sci* **126**, 136–195.
- Islam A (1955) The skull of Uromastix hardwickii Gray. Biologia (Lahore) 1, 141–196.
- Koolstra JH, van Eijden TMGJ (2005) Combined finite-element and rigid-body analysis of human jaw joint dynamics. *J Biomech* **38**, 2431–2439.
- Koolstra JH, van Eijden TMGJ (2006) Prediction of volumetric strain in the human temporomandibular joint cartilage during jaw movement. J Anat 209, 369–380.
- Koolstra JH, van Eijden TMGJ, Weijs WA, Naejie M (1988) A three-dimensional mathematical model of the human masticatory system predicting maximum possible bite forces. J Biomech 21, 563–576.
- Kupczik K, Dobson CA, Fagan MJ, Crompton RH, Oxnard CE, O'Higgins P (2007) Assessing mechanical function of the zygomatic region in macaques: validation and sensitivity testing of finite element models. J Anat 210, 41–53.
- Langenbach GEJ, Zhang F, Herring SW, Hannam AG (2002) Modelling the masticatory biomechanics of a pig. J Anat 201, 383–393.
- McHenry C, Wroe S, Clausen P, Moreno K, Cunningham E (2007) Super-modeled sabercat, predatory behaviour in *Smilodon fatalis* revealed by high-resolution 3-D computer simulation. *Proc Natl Acad Sci U S A* **104**, 16010–16015.
- Miyasaka J, Tanne K, Nakamura S (1994) Finite element analysis for stresses in the craniofacial sutures produced by maxillary protraction forces applied at the upper canines. *Br J Orthod* 21, 343–348.
- Moazen M, Curtis N, Evans SE, O'Higgins P, Fagan MJ (2008) Rigid-body analysis of the lizard skull: modelling the skull of Uromastyx hardwickii. J Biomech 41, 1274–1280.
- Moreno K, Wroe S, Clausen P, et al. (2008) Cranial performance in the Komodo dragon (*Varanus komodoensis*) as revealed by high-resolution 3-D finite element analysis. J Anat 212, 736–746.
- Nalle RK, Kinney JH, Ritchie RO (2003) Mechanistic fracture criteria for the failure of human cortical bone. *Nat Mater* **2**, 164–168.
- Preuschoft H, Witzel U (2002) The functional shape of the human skull, as documented by three-dimensional FEM studies. Anthropol Anz 60, 113–135.
- Preuschoft H, Witzel U (2005) Functional shape of the skull in vertebrates: which forces determine skull morphology in lower primates and ancestral synapsids? Anat Rec 283A, 402–413.
- Rafferty KL, Herring SW, Marshall CD (2003) Biomechanics of the rostrum and the role of facial sutures. J Morphol 257, 33– 44.
- Rayfield EJ (2005a) Using finite-element analysis to investigate

suture morphology: a case study using large carnivorous dinosaurs. Anat Rec 283A, 349–365.

- Rayfield EJ (2005b) Aspects of comparative cranial mechanics in the theropod dinosaurs *Coelophysis*, *Allosaurus* and *Tyrannosaurus*. *Zool J Linnean Soc* **144**, 309–316.
- Rayfield EJ (2007) Finite element analysis and understanding the biomechanics of evolution of living and fossil organisms. *Annu Rev Earth Planet Sci* 35, 541–576.
- Rayfield EJ, Norman DB, Horner CC, et al. (2001) Cranial design and function in a large theropod dinosaur. *Nature* **409**, 1033–1037.
- Richmond BG, Wright BW, Grosse I, et al. (2005) Finite element analysis in functional morphology. Anat Rec 283A, 259–274.
- Ross CF, Patel BA, Slice DE, et al. (2005) Modeling masticatory muscle force in finite element analysis: sensitivity analysis using principal coordinates analysis. *Anat Rec* 283A, 288–299.
- van Ruijven LJ, Weijs WA (1990) A new model for calculating muscle forces from electromyograms. *Eur J Appl Physiol* **61**, 479–485.
- Saksena RD (1942) The bony palate of *Uromastix* Merrem. *Proc Ind Acad Sci B* **16**, 107–119.
- Schwenk K (2000) Feeding in lepidosaurs. In Feeding: Form, Function and Evolution in Tetrapod Vertebrates (ed. Schwenk K), pp. 175–291. San Diego: Academic Press.
- Sellers WI, Crompton RH (2004) Using sensitivity analysis to validate the predictions of a biomechanical model of bite forces. *Ann Anat* 185, 89–95.
- Strait DS, Wang Q, Dechow PC, et al. (2005) Modeling elastic properties in finite element analysis: How much precision is needed to produce an accurate model? *Anat Rec* 283A, 275–287.
- Strait DS, Richmond BG, Spencer MA, Ross CF, Dechow PC, Wood BA (2007) Masticatory biomechanics and its relevance to early hominid phylogeny: An examination of palatal thickness using finite-element analysis. J Hum Evol 52, 585–599.
- Tanne K, Miyasaka J, Yamagata Y, Sachdeva R., Tsutsumi S, Sakuda M (1988) Three-dimensional model of the human craniofacial skeleton: method and preliminary results using finite element analysis. J Biomed Eng 10, 246–252.
- Throckmorton GS (1976) Oral food processing in two herbivorous lizards, *Iguana iguana* (Iguanidae) and *Uromastix aegyptius* (Agamidae). J Morphol **148**, 363–390.
- Throckmorton GS (1980) The chewing cycle in the herbivorous lizard Uromastix aegyptius (Agamidae). Arch Oral Biol 25, 225–233.
- Timoshenko SP (1955) Strength of Materials: Part 1: Elementary Theory and Problems. New York: Van Nostrand.
- Wang Q, Dechow PC (2006) Elastic properties of external cortical bone in the craniofacial skeleton of the rhesus monkey. Am J Phys Anthropol 131, 402–415.
- Witzel U, Preuschoft H (1999) The bony roof of the nose in humans and other primates. Zool Anz 238, 103–115.
- Wroe S, Moreno K, Clausen P, McHenry C, Curnoe D (2007) High resolution computer simulation of hominid cranial mechanics. *Anat Rec* 290, 1248–1255.
- de Zee M, Dalstra M, Cattaneo PM, Rasmussen J, Svensson P, Melsen B (2007) Validation of a musculo-skeletal model of the mandible and its application to mandibular distraction osteogenesis. J Biomech 40, 1192–1201.



## Assessment of the role of sutures in a lizard skull: a computer modelling study

Mehran Moazen<sup>1,\*</sup>, Neil Curtis<sup>1</sup>, Paul O'Higgins<sup>2</sup>, Marc E. H. Jones<sup>3</sup>, Susan E. Evans<sup>3</sup> and Michael J. Fagan<sup>1</sup>

> <sup>1</sup>Department of Engineering, University of Hull, Hull HU6 7RX, UK
>  <sup>2</sup>The Hull York Medical School, University of York, York YO10 5DD, UK
>  <sup>3</sup>Research Department of Cell and Developmental Biology, Anatomy Building, University College London, Gower Street, London WC1E 6BT, UK

Sutures form an integral part of the functioning skull, but their role has long been debated among vertebrate morphologists and palaeontologists. Furthermore, the relationship between typical skull sutures, and those involved in cranial kinesis, is poorly understood. In a series of computational modelling studies, complex loading conditions obtained through multibody dynamics analysis were imposed on a finite element model of the skull of *Uromastyx hardwickii*, an akinetic herbivorous lizard. A finite element analysis (FEA) of a skull with no sutures revealed higher patterns of strain in regions where cranial sutures are located in the skull. From these findings, FEAs were performed on skulls with sutures (individual and groups of sutures) to investigate their role and function more thoroughly. Our results showed that individual sutures relieved strain locally, but only at the expense of elevated strain in other regions of the skull. These findings provide an insight into the behaviour of sutures and show how they are adapted to work together to distribute strain around the skull. Premature fusion of one suture could therefore lead to increased abnormal loading on other regions of the skull causing irregular bone growth and deformities. This detailed investigation also revealed that the frontal–parietal suture of the *Uromastyx* skull played a substantial role in relieving strain compared with the other sutures. This raises questions about the original role of mesokinesis in squamate evolution.

Keywords: suture; finite element analysis; Squamata; cranial kinesis

#### **1. INTRODUCTION**

In the vertebrate skull, individual bones are joined together at sutures by fibrocellular soft tissues (Herring 2008). The role of sutures in cranial biomechanics has interested vertebrate morphologists for decades (e.g. Gans 1960; Buckland-Wright 1972, 1978; Herring 1972; Bolt 1974; Wagemans & Kuijpers-Jagtman 1988; Jaslow 1989; Klembara 1994; Kathe 1995; Thomson 1995; Herring & Teng 2000; Mao 2002; Rayfield 2004, 2005; Markey et al. 2006; Markey & Marshall 2007), but there are many unanswered questions. In young animals, individual skull bones have weak contacts or they are separated by gaps, which allow post-natal enlargement of the head, with the skull bones growing by bone deposition at their margins (Mao 2002; Sun et al. 2007). The process is of particular importance in humans, where premature suture closure (craniosynostosis) can result in the skull and brain defects (Herring 2000). However, if the primary function of vertebrate cranial sutures is simply to permit skull growth, sutures should close at the end of ontogeny to form a strong protective shell. In the adult skull, cranial sutures may appear immobile but they allow small intracranial movements (Moss 1954; Buckland-Wright 1978; Jaslow 1990; Jaslow & Biewner 1995; Herring & Teng 2000; Byron et al. 2004; Rayfield 2004). Their continued patency argues for an important adult role, and this view is supported by the variation in shape, complexity and stiffness that exists both within and between skulls. The most obvious interpretation is that sutures remain open for a particular purpose—possibly for shock absorption or to allow micro-movements to dissipate forces acting on the skull (Pritchard *et al.* 1956; Jaslow 1989). Sutures would thus act as 'strain sinks' that remove stress from surrounding bones (Buckland-Wright 1972; Rafferty *et al.* 2003; Rayfield 2005).

These hypotheses have been tested experimentally by recording strain across cranial sutures (e.g. Behrents *et al.* 1978; Herring & Mucci 2000; Popowics & Herring 2007) but few studies have taken advantage of computer modelling (e.g. Rayfield 2005). Finite element analysis (FEA) and multibody dynamic analysis (MDA) are powerful tools for which applications to functional morphology are increasing rapidly. In combination, they have the potential to answer hypothetical questions in relation to animal structure and evolution (Rayfield *et al.* 2001; Dumont *et al.* 2005; Preuschoft & Witzel 2005; Ross *et al.* 2007; Gurtis *et al.* 2008).

Uromastyx hardwickii is a herbivorous agamid lizard (Iguania, Acrodonta) native to the Indian subcontinent. Its robust skull is streptostylic (mobile quadrate) but is otherwise akinetic (lacking intracranial hinges) (Throckmorton 1976). Its cranial joints are mainly butt joints (where bones meet at a flat wall perpendicular, or near perpendicular, to the external surface of the bones);

<sup>\*</sup>Author for correspondence (m.moazen@2005.hull.ac.uk).

scarf joints (where bones partially overlap) or recessed scarf joints; and joints where one bone 'plugs' into another or fits like a tongue-in-groove. These joints range from very strong articulations (e.g. along the skull roof, jugal-maxilla) to light contacts (e.g. postorbital-parietal, jugal-squamosal). A preliminary analysis (Moazen et al. 2008b) demonstrated elevated levels of strain focused on locations that correspond to cranial sutures in the functioning skull. In this current analysis, cranial sutures were modelled in detail and we applied both MDA and FEA to assess suture biomechanics in this lizard. In the FEA analyses, we focused on three sutures that are important in the skulls of kinetic lizards: (i) the frontalparietal suture (between the anterior and posterior segments of the skull roof) and the (ii) jugal-squamosal; and (iii) postorbital-parietal sutures that link the postorbital bar with the skull roof and temporal region, respectively (figure 1). These sutures were modelled independently to assess their impact on strain relief. The jugal-squamosal suture was also tested further by varying its stiffness, simulating gradual closure of the joint as might occur in aged or abnormal individuals. All these models were loaded with the mastication data obtained via MDA (Moazen et al. 2008a,b). Finally, a high-resolution finite element (FE) model of the Uromastyx skull was constructed including all the sutures of the cranium.

#### 2. MATERIAL AND METHODS

#### (a) Model construction

Three-dimensional FE models of a U. hardwickii skull (skull length approx. 44 mm, skull width approx. 41 mm) were created from micro-computed tomography (CT) data supplied by the University of Texas, Austin, in the form of a tiff image dataset. AMIRA image segmentation software (Berlin, Germany) was used to segment out the bone and sutures carefully from the two-dimensional micro-CT slice images. Four different models were developed: one that included just the bilateral jugal-squamosal sutures; one that included just the bilateral postorbital-parietal sutures; one that included just the frontal-parietal suture; and one that included all the cranial sutures in the Uromastyx skull (highly detailed model; figure 1). After image segmentation, three-dimensional surface models were created in AMIRA, which were then transformed into meshed solid geometries composed of solid tetrahedral elements (10 node elements with a quadratic displacement behaviour). The individual suture models consisted typically of 200 000 elements and the detailed full suture model consisted of over 800 000 elements. All models were imported into ANSYS v. 11 (ANSYS, Inc., Canonsburg, PA, USA) in preparation for FEA.

#### (b) Material properties

Bone was modelled as a homogeneous isotropic material with Young's modulus of 10 GPa (gigapascal) and Poisson's ratio of 0.3. These values are comparable with bovine haversian bone as used in other studies (e.g. Rayfield *et al.* 2001). Although bone is known to be anisotropic, previous studies (e.g. Strait *et al.* 2005) have shown that comparable patterns of strain are formed with an isotropic assumption. We assessed the sensitivity of the mean strain (i.e. von Mises) results by varying Young's modulus of the jugal–squamosal suture based on published experimental data (McLaughlin



Figure 1. Cranial sutures of *Uromastyx.* (a) All the sutures represented in the high-resolution full suture model and the locations of the individual model sutures, (b) a lateral view of a micro-computed tomography image showing the jugal-squamosal suture, (c) a ventral view of the postorbital-parietal suture and (d) a ventral view of the frontal-parietal suture.

*et al.* 2000; Radhakrishnan & Mao 2004; Kupczik *et al.* 2007). For all other suture modelling, Young's modulus of 10 MPa (megapascal) and Poisson's ratio of 0.3 were used.

#### (c) Boundary conditions

Imposing accurate boundary conditions is a crucial step in an FEA. Skull load data such as muscle, bite and joint forces were obtained from a previous MDA study, where a cycle of mastication was modelled for bilateral biting (Moazen et al. 2008a). Ligaments were modelled as tension-only springs, and the jaw-closing muscles (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; pseudotemporalis superficialis, MPST) were defined with Hill-type muscle properties (Hill 1938). Bite and joint force data were obtained from a bilateral biting simulation (gape angle of 7°; bite point at the back of the mouth). The MDA analysis assumed each muscle to be 100 per cent activated, which explains why the peak strains are higher than might normally be expected in bone (Fritton & Rubin 2001). However, since the same loading was applied in all models, the relative effect of the sutures will still be the same and the results still valid.

In the MDA model, the cranium, quadrates and mandible were represented as separate bodies, allowing the bite force, quadrato-mandibular and quadrato-squamosal joint forces,



Figure 2. Comparison of the mean strain distributions across the anterior, posterior and lateral skull regions, as the stiffness of the jugal–squamosal suture is varied. *E* refers to Young's modulus.

and muscle and ligament forces to be calculated. In the FE model, only the cranium was represented with the relevant forces calculated by the MDA applied directly to it. The quadrate was not modelled in the FEA, but its effect is included, without any loss of accuracy, by the calculated quadrato-squamosal joint forces. All FE models were constrained at three nodes at the back of the skull (occipital condyle); however, since the loading data came directly from the MDA models, where the muscle forces and reaction forces (bite and joint) were in equilibrium, negligible stress values would be expected at the constraints (Curtis *et al.* 2008).

#### (d) Simulations

A linear static FEA was performed in all cases. First, a sensitivity analysis was carried out to assess the effect of varying Young's modulus value applied to the jugal-squamosal suture on the overall distributions of the strain across the skull. The average strain value within each of the locations highlighted in figure 2 was taken directly from the model (average of nine nodes within each location). Based on this sensitivity analysis and average Young's modulus values reported in the literature, a value of 10 MPa was chosen for the sutures (e.g. McLaughlin et al. 2000). The roles of the postorbital-parietal and frontalparietal sutures were then assessed both in isolation and together with all other sutures. Finally, to assess the overall effect of sutures on cranial strains, element strain tables were automatically created for the high-resolution FE models for simulations with and without sutures. Relative increases and decreases in strain could be plotted to evaluate the effects of introducing the cranial sutures.

#### 3. RESULTS

The quantitative mean strain (i.e. von Mises) results obtained from the modelling of the jugal–squamosal suture (considering all other sutures within the skull as fused) are summarized in figure 2. These results show that as the jugal–squamosal suture becomes stiffer, as might occur in old individuals, it significantly raises the mean strain in the jugal, within the upper temporal bar (R11, figure 2) but, interestingly, not on the adjacent squamosal (R12, figure 2). Other regions are relatively unaffected, with a small rise in strain in the postorbital (R5, figure 2) and jugomaxillary ramus (R7, figure 2), and a slight drop elsewhere (parietal, R1, R2; frontal, R3; postorbital ramus of jugal, R6; figure 2).

Mean strain distributions for the simulations with the postorbital-parietal and frontal-parietal sutures in place are shown in figures 3 and 4, respectively. In each case, the presence of an open suture relieves strain locally, but appears to raise it somewhat in other regions, as highlighted by a circle or a box in figures 3 and 4. This agrees with previous work (Herring *et al.* 1996; Herring & Teng 2000) reporting that sutures experience high strain deformations and that they relieve strain locally. One simple and obvious conclusion from this would be that including all sutures in the model would substantially reduce strain across the whole skull. However, from the strain contour plots for individual sutures, it is difficult to get a clear understanding of the effect open sutures have on the skull.

Results of the FEA full suture analyses provide a more complete picture (figure 5a,b). Once again, they show that open sutures decrease strain in some regions and increase it in others. To identify these regions more clearly, the strain values in figure 5a were subtracted from those in figure 5b. In the resultant figure 5c, the red and grey areas show a decrease and increase in mean strain, respectively, as a result of including the sutures. Ignoring the strain in the sutures themselves, the mean strain has reduced in approximately 30 per cent of the model volume (red areas in figure 5c) as a result of including open sutures (i.e. with an assigned Young's modulus of 10 MPa). However, the strain has been reduced significantly in some areas, notably in the prefrontal, frontal and parietal bones located around the frontal-parietal suture, at the junction of the postfrontal and parietal bones on the postorbital bar and in the epipterygoid bones.

#### 4. DISCUSSION

#### (a) General principles

A thorough understanding of both biology and mechanics is required if we are to use computer modelling approaches to analyse biological systems. Greater knowledge may lead to more approximations within the computational models; however, these details may be necessary as an oversimplified model may not satisfy its purpose, as discussed by others (e.g. Alexander 2003). If we describe and understand these approximations to an acceptable level, justified conclusions can be drawn from the results. Here, we used FEA to study the role and function of sutures, a methodology that itself required two major assumptions. First, owing to the lack of data on the material properties of different cranial sutures, all sutures were modelled with the same Young's modulus value


Figure 3. Mean strain distributions considering the effect of the postorbital-parietal suture. *E* refers to Young's modulus. (*a*) Model with a fused suture ( $E_{\text{bone}} = E_{\text{suture}} = 10 \text{ GPa}$ ) and (*b*) model with an unfused suture ( $E_{\text{bone}} = 10 \text{ GPa}$ ;  $E_{\text{suture}} = 10 \text{ MPa}$ ). Note that the grey colour indicates strain larger than 0.0037. The main regions of decreased strain are highlighted by circles and the main region of increased strain is highlighted by a rectangle.



Figure 4. Mean strain distributions considering the effect of the frontal-parietal suture. *E* refers to Young's modulus. (*a*) Model with a fuse suture ( $E_{\text{bone}} = E_{\text{suture}} = 10$  GPa) and (*b*) model with an unfused suture ( $E_{\text{bone}} = 10$  GPa;  $E_{\text{suture}} = 10$  MPa). Note that the grey colour indicates strain larger than 0.0037. The main region of decreased strain is highlighted by a circle and the main regions of increased strain are highlighted by squares.

(10 MPa). We expect that, in the functioning skull, specific sutures would carry unique stiffness properties (Herring 2000; Markey *et al.* 2006). However, figure 2 shows that, with the exception of locations close to the sutures, the effect on the strain distribution of reasonable changes in suture stiffness may be marginal. Second, as the role of cervical muscles and their contribution to skull mechanics are not fully understood in lizards, we assumed the muscles applied no force to the skull during biting. In

fact, they probably do. Koolstra & van Eijden (1997), for example, suggested that muscles could have a passive effect on the skull due to passive muscle forces. With these assumptions in mind, the main conclusion of our investigation is that sutures do not play a substantial role in reducing the total strain within the skull, but probably act in various combinations to allow the skull to respond to different loading conditions by distributing strain around the skull.



Figure 5. Mean strain distributions considering the effect of all sutures. *E* refers to Young's modulus. (*a*) Model with all sutures fused ( $E_{\text{bone}} = E_{\text{suture}} = 10 \text{ GPa}$ ), (*b*) model with all sutures unfused ( $E_{\text{bone}} = 10 \text{ GPa}$ ;  $E_{\text{suture}} = 10 \text{ MPa}$ ) and (*c*) a visual comparison in which grey and red show where the mean strain has increased or decreased, respectively, in (*b*) compared with (*a*). Note that the grey colour indicates strain larger than 0.0037 in (*a*,*b*).

As observed by others (e.g. Herring 2008), individual sutures reduce strain locally, but sometimes at the expense of increased strain in other regions of the skull. The reverse is also true. Figure 6 shows a simple explanatory model. Two parallel bars (yellow) are of equal dimensions and identical Young's moduli. When force is applied in the direction of the arrows each bar will be strained equally (figure 6a). If Young's modulus in one part of the upper bar is reduced (red section, representing a suture, figure 6b), then this section will deform to a greater extent and, in turn, will reduce the deformation (strain) in the flanking yellow parts of the bar. The lower bar will now carry a greater proportion of the force and as a result will have increased strain. If Young's modulus of one part of the lower bar (blue section, figure 6c) is then reduced to match that of the red section above, the strain will once again be equal in both bars-but overall somewhat less in the yellow (bone) regions than it was at the start. This is essentially what is occurring in the skull, although in reality the situation is much more complex.

In modelling individual open sutures, we have generated a situation that does not normally occur in real life, but the marked increase of strain that results from early fusion of one or more cranial sutures could have important implications for the skull development, both normal and abnormal (Cohen 1993; Margulies & Thibault 2000). Here, we have shown the potential of FEA to predict which skull regions, in lizards or humans, are likely to be affected by premature closure of any one, or more, sutures.

## (b) Lizard skull function

Our quantitative results from modelling the jugal– squamosal suture with different levels of stiffness (figure 2) showed that the maintenance of an open jugal–squamosal suture is important to the integrity of the upper temporal bar, a region placed under severe strain during biting. This additional strain may be due partly to an unusual external slip of the pterygoideus muscle that attaches to this region in the living *Uromastyx* (and was included in the MDA analyses, Moazen *et al.* 2008*a*). The jugal–squamosal joint is a relatively weak tongue-in-groove articulation (S.



Figure 6. Explanatory model of suture biomechanics. (a) Parallel bars of equal dimensions and Young's moduli, (b) upper bar with region of reduced Young's modulus (red, representing suture) and (c) region of reduced Young's modulus (blue, representing suture) added to lower bar.

E. Evans 2008, personal observations) that probably permitted anteroventral-posterodorsal compensatory sliding between the bones in life. Similarly, an open postorbital-parietal suture (figure 3), a weak contact joint, relieves strain in the upper part of the postorbital bar. More globally (figure 5*c*), open sutures generally relieve strain in the antorbital margin (where bite forces may be concentrated, Buckland-Wright 1972), in the joints between the upper jaw and palate (maxilla-palatine, maxilla-ectopterygoid), in the skull roof, and in the epipterygoid linking the palate and skull roof.

## (c) Kinesis

In the adult vertebrate skull, most movements at cranial sutures are very small. However, when this movement becomes visible to the naked eye, it falls within the definition of cranial kinesis (Metzger 2002). Squamates (lizards, snakes and amphisbaenians) demonstrate varying levels of cranial kinesis (Herrel et al. 2000; Metzger 2002), but there is considerable debate as to the degree of movement involved, its presence or absence in different families, its evolutionary history and its function (e.g. Frazzetta 1962; Metzger 2002; Evans 2003, in press; Herrel et al. 2007). Rayfield (2005) distinguished between active kinesis (as found in gekkotan lizards; Herrel et al. 1999, 2000) and passive kinesis (relative bone movements in response to loading). For the latter, strain reduction is the most obvious explanation, but the relationship between passive kinesis and the evolution of active kinesis is uncertain.

Two main types of kinesis have been described in squamates (e.g. Frazzetta 1962), metakinesis and mesokinesis. Metakinesis remains enigmatic (Metzger 2002), but, where present, is essentially a passive movement of the braincase in relation to the skull roof and palate. Functional explanations have focused on the shock absorption and protection of the brain against feeding strains (e.g. Rieppel 1978; De Vree & Gans 1987, 1989). Interestingly, when we added open sutures between the braincase and skull to our model, it increased rather than decreased the strain on the supraoccipital and basicranium, although strains in the epipterygoid, thought to be important in bracing the skull during metakinesis (Schwenk 2000), were significantly reduced. Work on this topic is ongoing.

Mesokinesis involves a dorsoventral flexion/extension around an axis that runs transversely through the frontalparietal suture (Metzger 2002). It permits the muzzle unit (maxilla, premaxilla, prefrontals, nasals, frontal, anterior palate and usually juga) to be raised and lowered in relation to the rest of the skull, but it must be accommodated by joints within the postorbital bar and palate (hypokinetic axis-palatine/ectopterygoid/pterygoid sutures). Functional explanations have included increasing gape and improving the mechanical advantage of specific muscles (e.g. Auffenberg 1981; Metzger 2002), shock absorption (De Vree & Gans 1994) and improved prev handling (e.g. Schwenk 2000). However, the origins of mesokinesis, and even its distribution among living squamate groups, are not well understood. Although some authors (e.g. Frazzetta 1962) considered iguanian lizards, including agamids, to be mesokinetic, more recent opinion (e.g. Schwenk 2000; Metzger 2002) is that they are not. The frontal-parietal joint in Uromastyx is strong (with a frontal median process fitting into a notch in the parietal, and the bilateral frontal edges being received into recesses in the parietal; S. E. Evans 2008, personal observations) and, although it probably contained substantial soft tissue, Throckmorton (1980) was unable to observe mesokinesis in this lizard. Nonetheless, our results highlight the contribution of the frontal-parietal suture in reducing strain within the skull roof in this akinetic lizard, and this situation may be analogous to that in early squamates. There would have been a selective advantage to increasing the flexibility of this joint, provided those within the postorbital bar, upper temporal bar and palate were also modified to avoid creating new foci of strain. Very little is known of skull morphology in early squamates (Evans 2003, in press) but it has been suggested that the origins of active kinesis might be found in the shock-absorptive passive kinesis of ancestral taxa (e.g. De Vree & Gans 1994; Evans in press), and our results provide support for that view.

The authors thank Mehrdad Moazen, Catherine Dobson and Lisa Partridge for their support, and Jessie Maisano, University of Texas, Austin, Digimorph Laboratory, for the micro-CT data of the *Uromastyx*. The idea for the explanatory model in figure 6 was suggested by one of our anonymous referees, to whom we are grateful. We also gratefully acknowledge the financial support of the Biotechnology and Biological Sciences Research Council (BBSRC).

## REFERENCES

Alexander, R. McN. 2003 Modelling approaches in biomechanics. *Phil. Trans. R. Soc. B* 358, 1429–1435. (doi:10.1098/rstb.2003.1336)

- Auffenberg, W. 1981 The behavioural ecology of the Komodo Monitor, 1st edn. Gainesville, FL: University Press of Florida.
- Behrents, R. G., Carlson, D. S. & Abdelnour, T. 1978 In vivo analysis of bone strain about the sagittal suture in Macaca mulatta during masticatory movements. J. Dent. Res. 57, 904–908.
- Bolt, J. R. 1974 Evolution and functional interpretation of some suture patterns in Palaeozoic labryrinthodont amphibians and other lower tetrapods. *J. Palaeontol.* 48, 434–459.
- Buckland-Wright, J. C. 1972 The shock-absorbing effect of cranial sutures in certain mammals. J. Dent. Res. 51, 1241.
- Buckland-Wright, J. C. 1978 Bone structure and the patterns of force transmission in the cat skull (*Felis catus*). *J. Morphol.* 155, 35–62. (doi:10.1002/jmor.1051550104)
- Byron, C. D., Borke, J., Yu, J., Pashley, D., Wingard, C. J. & Hamrick, M. 2004 Effects of increased muscle mass on mouse sagittal suture morphology and mechanics. *Anat. Rec. A* 279, 676–684. (doi:10.1002/ar.a.20055)
- Cohen, M. M. 1993 Sutural biology and the correlates of craniosynostosis. Am. J. Med. Genet. 47, 581–616. (doi:10.1002/ajmg.1320470507)
- Curtis, N., Kupczik, K., O'Higgins, P., Moazen, M. & Fagan, M. J. 2008 Predicting skull loading: applying multibody dynamics analysis to a macaque skull. *Anat. Rec.* 291, 491–501. (doi:10.1002/ar.20689)
- De Vree, F. & Gans, C. 1987 Kinetic movements in the skull of adult *Trachydosaurus rugosus*. *Anat. Histol. Embryol.* **16**, 206–209.
- De Vree, F. & Gans, C. 1989 Functional morphology of the feeding mechanisms in lower tetrapods. In *Trends in vertebrate morphology* (eds H. Splechtna & H. Hilgers), pp. 115–127. Stuttgart, Germany: Gustav Fischer.
- De Vree, F. & Gans, C. 1994 Feeding in tetrapods. In Advances in comparative and environmental physiology: biomechanics of feeding in vertebrates (eds V. Bels, M. Chardon & P. Vandewalle), pp. 93–118. Berlin, Germany: Springer.
- Dumont, E. R., Piccirillo, J. & Grosse, I. R. 2005 Finiteelement analysis of biting behaviour and bone stress in the facial skeletons of bats. *Anat. Rec. A* 283, 319–330. (doi:10.1002/ar.a.20165)
- Evans, S. E. 2003 At the feet of the dinosaurs: the origin, evolution and early diversification of squamate reptiles (Lepidosauria: Diapsida). *Biol. Rev.* **78**, 513–551. (doi:10. 1017/S1464793103006134)
- Evans, S. E. In press. The skull of lizards and Tuatara. In *The skull of Lepidosauria* (eds C. Gans & A. S. Gaunt). Biology of the Reptilia, vol. 20, pp. 1–347. Ithaca, NY: Society for the Study of Amphibians and Reptiles.
- Frazzetta, T. H. 1962 A functional consideration of cranial kinesis in lizards. J. Morphol. 111, 287–320. (doi:10.1002/ jmor.1051110306)
- Fritton, S. P. & Rubin, C. T. 2001 In vivo measurement of bone deformations using strain gages. In Bone mechanics handbook (ed. S. C. Cowin), pp. 8.1–8.41. Boca Raton, FL: CRC Press.
- Gans, C. 1960 Studies on amphisbaenians (Amphisbaenia, Reptilia), I. A taxonomic revision of the Trogonophidae, and a functional interpretation of the amphisbaenid adaptive pattern. *Bull. Am. Mus. Nat. Hist.* **119**, 131–204.
- Grosse, I. R., Dumont, E. R., Coletta, C. & Tolleson, A. 2007 Techniques for modeling muscle-induced forces on finite element models of skeletal structures. *Anat. Rec. A* 290, 1069–1088. (doi:10.1002/ar.20568)
- Herrel, A., Aerts, P., Fret, J. & De Vree, F. 1999 Morphology of the feeding system in agamid lizards: ecological correlates. *Anat. Rec.* **254**, 496–507. (doi:10.1002/(SICI)1097-0185(19990401)254:4<496::AID-AR5>3.0.CO;2-Q)

- Herrel, A., Aerts, P. & De Vree, F. 2000 Cranial kinesis in geckoes: functional implications. *J. Exp. Biol.* 203, 1415–1423.
- Herrel, A., Schaerlaeken, V., Meyers, J. J., Metzger, K. A. & Ross, C. F. 2007 The evolution of cranial design and performance in squamates: consequences of skull-bone reduction on feeding behavior. *Integr. Comp. Biol.* 47, 107–117. (doi:10.1093/icb/icm014)
- Herring, S. W. 1972 Sutures—a tool in functional cranial analysis. Acta Anat. 83, 222–247. (doi:10.1159/0001 43860)
- Herring, S. W. 2000 Sutures and craniosynostosis: a comparative, functional, and evolutionary perspective. In *Craniosynostosis* (eds M. M. Cohen & R. E. MacLean), pp. 3–10. Oxford, UK: Oxford University Press.
- Herring, S. W. 2008 Mechanical influences on suture development and patency. In *Craniofacial sutures. Development, disease and treatment* (ed. D. P. Rice), pp. 41–56. Basel, Switzerland: Karger.
- Herring, S. W. & Mucci, R. J. 2000 *In vivo* strain in cranial sutures: the zygomatic arch. *J. Morphol.* 207, 225–239. (doi:10.1002/jmor.1052070302)
- Herring, S. W. & Teng, S. 2000 Strain on the braincase and its sutures during function. *Am. J. Phys. Anthropol.* **112**, 575–593. (doi:10.1002/1096-8644(200008)112:4<575:: AID-AJPA10>3.3.CO;2-S)
- Herring, S. W., Teng, S. Y., Huang, X. F., Mucci, R. J. & Freeman, J. 1996 Patterns of bone strain in the zygomatic arch. *Anat. Rec.* **246**, 446–457. (doi:10.1002/(SICI)1097-0185(199612)246:4 < 446::AID-AR4 > 3.0.CO;2-T)
- Hill, A. V. 1938 The heat of shortening and the dynamic constants of muscle. *Proc. R. Soc. B* 126, 136–195. (doi:10.1098/rspb.1938.0050)
- Jaslow, C. R. 1989 Sexual dimorphism of cranial suture complexity in wild sheep (*Ovis orientalis*). Zool. J. Linn. Soc. 95, 273–284. (doi:10.1111/j.10963642.1989.tb0 2312.x)
- Jaslow, C. R. 1990 Mechanical properties of cranial sutures. *J. Biomech.* 23, 313–321. (doi:10.1016/0021-9290(90) 90059-C)
- Jaslow, C. R. & Biewner, A. A. 1995 Strain patterns in the horncores, cranial bones and sutures of goats (*Capra hircus*) during impact loading. J. Zool. Lond. 235, 193–210.
- Kathe, W. 1995 Morphology and function of the sutures in the dermal skull roof of *Discosauriscus austriacus* Makowsky, 1876 (Seymouriamorpha; Lower Permian of Moravia) and *Onchiodon labyrinthicus* Geinitz, 1861 (Temnospondyli, Lower Permian of Germany). *Geobios* 28, 255–261. (doi:10.1016/S0016-6995(95)80123-5)
- Klembara, J. 1994 The sutural pattern of skull-roof bones in Lower Permian *Discosauriscus austriacus* from Moravia. *Lethaia* 27, 85–95. (doi:10.1111/j.1502-3931.1994.tb0 1560.x)
- Koolstra, J. H. & van Eijden, T. M. G. J. 1997 The jaw openclose movements predicted by biomechanical modelling. *J. Biomech.* 30, 943–950. (doi:10.1016/S0021-9290(97) 00058-4)
- Kupczik, K., Dobson, C. A., Fagan, M. J., Crompton, R. H., Oxnard, C. E. & O'Higgins, P. 2007 Assessing mechanical function of the zygomatic region in macaques: validation and sensitivity testing of finite element models. *J. Anat.* 210, 41–53. (doi:10.1111/j.1469-7580.2006.00662.x)
- Mao, J. J. 2002 Mechanobiology of craniofacial sutures.*J. Dent. Res.* 81, 810–816.
- Margulies, S. S. & Thibault, K. H. 2000 Infant skull and suture properties: measurements and implications for mechanisms of pediatric brain injury. *J. Biomech. Eng. Trans. ASME* 122, 364–371. (doi:10.1115/1.1287160)
- Markey, M. J. & Marshall, C. R. 2007 Terrestrial-style feeding in a very early aquatic amphibian: evidence from

experimental analysis of suture morphology. Proc. Natl Acad. Sci. USA 104, 7134–7138. (doi:10.1073/pnas. 0701706104)

- Markey, M. J., Main, R. M. & Marshall, C. R. 2006 In vivo cranial suture function and suture morphology in the extant fish *Polypterus*: implications for inferring skull function in living and fossil fish. *J. Exp. Biol.* 209, 2085–2102. (doi:10.1242/jeb.02266)
- McHenry, C., Wroe, S., Clausen, P., Moreno, K. & Cunningham, E. 2007 Super-modeled sabercat, predatory behaviour in *Smilodon fatalis* revealed by high-resolution 3-D computer simulation. *Proc. Natl Acad. Sci. USA* **104**, 16 010–16 015. (doi:10.1073/pnas.0706086104)
- McLaughlin, E., Zhang, Y., Pashley, D., Borke, J. & Yu, J. 2000 The load-displacement characteristics of neonatal rat cranial sutures. *Cleft. Palate Craniofac. J.* **37**, 590–595. (doi:10.1597/1545-1569(2000)037<0590:TLDCON> 2.0.CO;2)
- Metzger, K. 2002 Cranial kinesis in lepidosaurs: skulls in motion. In *Topics in functional and ecological vertebrate* morphology (eds P. Aerts, K. D'Août, A. Herrel & R. Van Damme), pp. 15–46. Herzogenrath, Germany: Shaker Publishing.
- Moazen, M., Curtis, N., Evans, S. E., O'Higgins, P. & Fagan,
  M. J. 2008a Rigid-body analysis of a lizard skull: modelling the skull of *Uromastyx hardwickii*. *J. Biomech.* 41, 1274–1280. (doi:10.1016/j.jbiomech.2008.01.012)
- Moazen, M., Curtis, N., Evans, S. E., O'Higgins, P. & Fagan, M. J. 2008b Combined finite element and multibody dynamics analysis of biting in a Uromastyx hardwickii lizard skull. J. Anat. 213, 499–508. (doi:10.1111/j.1469-7580. 2008.00980.x)
- Moss, M. L. 1954 Growth of the calvaria in the rat, the determination of osseous morphology. *Am. J. Morphol.* 94, 333–361. (doi:10.1002/aja.1000940302)
- Popowics, T. E. & Herring, S. W. 2007 Load transmission in the nasofrontal suture of the pig, *Sus scrofa*. *J. Biomech.* 40, 837–844. (doi:10.1016/j.jbiomech.2006.03.011)
- Preuschoft, H. & Witzel, U. 2005 Functional shape of the skull in vertebrates: which forces determine skull morphology in lower primates and ancestral synapsids? *Anat. Rec. A* 283, 402–413. (doi:10.1002/ar.a.20176)
- Pritchard, J. J., Scott, J. H. & Girgis, F. G. 1956 The structure and development of cranial and facial sutures. *J. Anat.* **90**, 73–86.
- Radhakrishnan, P. & Mao, J. J. 2004 Nanomechanical properties of facial sutures and sutural mineralization front. J. Dent. Res. 83, 470–475.
- Rafferty, K. L., Herring, S. W. & Marshall, C. D. 2003 Biomechanics of the rostrum and the facial sutures. *J. Morphol.* 257, 33–44. (doi:10.1002/jmor.10104)
- Rayfield, E. J. 2004 Cranial mechanics and feeding in *Tyrannosaurus rex. Proc. R. Soc. B* 271, 1451–1459. (doi:10.1098/rspb.2004.2755)
- Rayfield, E. J. 2005 Using finite-element analysis to investigate suture morphology: a case study using large carnivorous dinosaurs. *Anat. Rec. A* 283, 349–365. (doi:10.1002/ar.a.20168)
- Rayfield, E. J., Norman, D. B., Horner, C. C., Horner, J. R., Smith, P. M., Thomason, J. J. & Upchurch, P. 2001 Cranial design and function in a large theropod dinosaur. *Nature* 409, 1033–1037. (doi:10.1038/35059070)
- Rieppel, O. 1978 The phylogeny of cranial kinesis in lower vertebrates with special reference to the Lacertilia. N. *Jb. Geol. Palaont. Abh.* 156, 353–370.
- Ross, C. F., Patel, B. A., Slice, D. E., Strait, D. S., Dechow, P. C., Richmond, B. G. & Spencer, M. A. 2005 Modeling masticatory muscle force in finite element analysis: sensitivity analysis using principal coordinates analysis. *Anat. Rec. A* 283, 288–299. (doi:10.1002/ar.a.20170)

- Schwenk, K. 2000 Feeding in lepidosaurs. In *Feeding: form, function and evolution in tetrapod vertebrates* (ed. K. Schwenk), pp. 175–291. San Diego, CA: Academic Press.
- Strait, D. S., Wang, Q., Dechow, P. C., Ross, C. F., Richmond, B. G., Spencer, M. A. & Patel, B. A. 2005 Modeling elastic properties in finite element analysis: how much precision is needed to produce an accurate model? *Anat. Rec. A* 283, 275–287. (doi:10.1002/ar.a.20172)
- Sun, Z., Lee, E. & Herring, S. W. 2007 Cell proliferation and osteogenic differentiation of growing pig cranial sutures. *J. Anat.* 211, 280–289. (doi:10.1111/j.1469-7580.2007. 00761.x)
- Thomson, K. S. 1995 Graphical analysis of dermal skull roof patterns. In *Functional morphology in vertebrate palaeontology* (ed. J. J. Thomason), pp. 193–204. Cambridge, UK: Cambridge University Press.

- Throckmorton, G. S. 1976 Oral food processing in two herbivorous lizards, *Iguana iguana* (Iguanidae) and Uromastix aegyptius (Agamidae). J. Morphol. 148, 363–390. (doi:10.1002/jmor.1051480307)
- Throckmorton, G. S. 1980 The chewing cycle in the herbivorous lizard Uromastix aegyptius (Agamidae). Arch. Oral. Biol. 25, 225–233. (doi:10.1016/0003-9969(80) 90027-8)
- Wagemans, P. A. H. M. & Kuijpers-Jagtman, A. M. 1988
  Sutures and forces: a review. *Am. J. Orthod. Dentofacial Orthop.* 94, 129–141. (doi:10.1016/0889-5406(88) 90361-7)
- Wroe, S., Moreno, K., Clausen, P., McHenry, C. & Curnoe, D. 2007 High resolution computer simulation of hominid cranial mechanics. *Anat. Rec. A* 290, 1248–1255. (doi:10. 1002/ar.20594)