Finite Element Analysis in Vertebrate Biomechanics

CALLUM F. ROSS[*]

Department of Organismal Biology and Anatomy, University of Chicago,
Chicago, Illinois

ABSTRACT

This special issue of *The Anatomical Record* presents a series of papers that apply the method of finite element analysis (FEA) to questions in vertebrate biomechanics. These papers are salient examples of the use of FEA to test hypotheses regarding structure-function relationships in complexly shaped biological objects such as skulls and in areas of the skeleton that are otherwise impervious to study. FEA is also a powerful tool for studying patterns of stress and strain in fossil animals and artificial constructs hypothesized to represent ancestral conditions. FEA has been used deductively, to study patterns of growth and development, and to investigate whether skull shapes can be created from amorphous blocks using an iterative approach of loading and removing elements. Several of the papers address methodological issues, such as the relative importance of loading conditions and material properties for generating an accurate model and the validation of models using in vivo strain data. Continuing improvements in model building techniques will make possible increased application of FEA to study the functional effects of variation in morphology, whether through ontogenetic or phylogenetic transformations. © 2005 Wiley-Liss, Inc.

Key words: finite-element analysis; fossils; dinosaurs; primates; skulls; bone strain; stress

Finite-element modeling (FEM) is a numerical tool for solving complex mathematical problems in order to determine patterns of stress, strain, deflections, heat transfer, fluid flow, etc., in computer models of structural components. FEM provides a method for addressing a range of questions that are otherwise intractable, or very difficult to solve (Richmond et al., 2005, this issue), and is potentially one of the most powerful tools in the methodological arsenal of vertebrate biomechanics.

One of the central aims of vertebrate biomechanics is elucidating the functional consequences attendant on the remarkable histological and morphological diversity of vertebrate skeletal tissues (Currey, 2002). This structure-function relationship is important to clinically oriented research on various disorders or diseases of the skeleton, research aimed at improving skeletal health during long-term space flight, as well as interpretation of skeletons found in the fossil and archeological records. The form-function relationships of the skeleton are therefore of concern to bioengineers, clinicians, biological anthropologists, and paleontologists, and FEM provides a method for studying them.

The availability of increasingly powerful computers at progressively more affordable prices has made FEM an accessible tool for vertebrate biomechanists. Consequently, the wide use of FEM in clinical research is now beginning to be replicated in basic science research. Those of us who are not finite-element modelers can see that FEM clearly presents opportunities, but what is it precisely, and what are its limitations?

These questions were addressed in a symposium on finite-element analysis of vertebrate skulls at the International Congress of Vertebrate Morphology in Boca Raton, Florida, in July 2004. This special issue of *The Ana-*

tomical Record presents the research papers on which those presentations were based, along with two complementary papers by researchers on the postcranium. Although this issue is not exhaustive, it presents a comprehensive overview of the burgeoning application of this method to vertebrate biomechanics (see also Huiskes and Chao, 1983; Beaupre and Carter, 1992). Several issues are highlighted by these contributions.

BUILDING THE MODELS

Richmond et al. (2005, this issue) describe the sequence of tasks in building an FEM: the geometry of the object of interest must be captured and expressed digitally in such a way that it can be turned into a mesh of finite elements that can then be loaded by external forces. Various techniques are available for capturing the geometry, including manual tracing, CT scanning, and MRI, then bringing the data into a computer-aided design (CAD) program, from which a meshable file can be exported. The various contributors to this issue use different methods, and it is clear that better methods are needed for performing these functions more quickly. Building the models can be extremely time-consuming, and only when this process is streamlined will it be possible to build the large number of models needed to study effects of variation in morphology on variation in function. In this context, one particularly productive line of work would be the development of methods for integrating geometric morphometrics (GM) with FEM. GM already has the geometric and statistical techniques for describing shape, shape variation, and shape change, as well as for comparing shapes in multidimensional space (Zelditch et al., 2004). It only seems logical to interface these tools with those of FEM to explore the functional consequences of morphological variation and change.

Another aspect of model construction is the assignment of material properties to the elements. Bone exhibits variability in its material properties, including density, elastic modulus, anisotropy, and viscoelastic behavior. The contributors to this issue assigned material properties in a number of ways. Silva et al. (2005, this issue) assumed that the cortical bone is isotropic and linearly elastic and derived an elastic modulus for their mouse model using nanondentation data. Rayfield (2005, this issue) modeled the dinosaur skull with the material properties of bovine Haversian bone. Metzger et al. (2005, this issue) first loaded an isotropic model, then adjusted the orientation of maximum stiffness to match the orientation of principal stress. Thomason et al. (2005, this issue) used published data for real hooves to build their horse hoof model. Dumont et al. (2005, this issue) select average values for elastic modulus and Poisson's ratio in mammalian bone.

Two papers in this issue directly addressed the issue of how variation in material properties affects behavior of the model. Marinescu et al. (2005, this issue) measured material properties from the same macaque mandible specimen that their model was derived from and Strait et al. (2005, this issue) measured material properties from different macaque skulls to that that was modeled. Both studies then quantified the effects on model behavior of variation in degree of isotrophy and homogeneity in the model. Both studies found that material properties matter: differences in material properties did result in different patterns of deformation in the models. Strait et al. (2005) found that the model that behaved most like the in vivo data was the one with the most detailed modeling of the bone material properties. Although material properties data are time-consuming to gather, they seem to be essential for building an accurate model.

LOADING THE MODELS

In order to obtain realistic patterns of stress and strain in FEMs, it seems that accurate data on the external forces acting on object would also be important. But how important are these data relative to data on geometry and material properties, and how are these external forces to be calculated and modeled? The loading conditions in these papers range from the highly controlled four-point bending of the murine tibia (Silva et al., 2005, this issue) to the hypothetical forces acting on the skull of the fossil dinosaur, *Allosaurus fragilis* (Rayfield, 2005, this issue).

The most detailed treatments of the sensitivity of the models to different loading conditions were carried out by Marinescu et al. and Ross et al. The former varied degrees of freedom, orientation of external forces, and number of nodal constraints on their FEM of the macaque mandible and found all to have significant effects on model behavior. Small changes in the direction of load application resulted in significant changes in predicted strains. Ross et al. studied the relative importance of various assumptions regarding relative forces exerted on the macaque skull by the chewing muscles. Using principal coordinates analysis of the variable deformations of the model to summarize overall differences in loading patterns, they conclude that information on the relative cross-sectional areas of the jaw muscles is important, whereas assumptions regarding EMG force latencies have little effect on model behavior. Whether this is generally true or specific to some group (e.g., catarrhines or anthropoids) remains to be determined.

Further sensitivity analyses are needed to determine the relative importance of material properties, geometry, constraining conditions, and external forces in finite-element analysis (FEA) (Dar et al., 2002; Marinescu et al., 2005, this issue; Ross et al., 2005, this issue; Strait et al., 2005, this issue). Only when such analyses are performed can an estimate of the robustness of the results be provided.

VALIDATING THE MODELS

Validation of an FEM entails comparing the behavior of the model with in vivo or in vitro data gathered from parts of the modeled structures. With notable exceptions (Coleman et al., 2002, 2003; Kotha et al., 2003; Srinivasan et al., 2003), few studies gather the kinds of detailed bone strain data needed to evaluate their models. This will probably always be true for most models of human skeletal structures, so construction of well-validated models of nonhuman animals is important because they provide insight into the kinds of data that are important in producing an accurate and valid model.

In vivo bone strain data are used to assess the accuracy of the macaque skull model discussed by Ross et al. and Strait et al., the alligator skull model presented by Metzger et al., and the mouse tibial bending model presented by Silva et al. Marinescu et al. evaluate their model using in vitro bone strain data gathered from the same specimen from which their CT scan and material properties data were derived.

The macaque skull FEM is the most extensively validated, with in vivo data from numerous sites across the face. The strain orientations and relative magnitudes from the model generally fall within the range of the in vivo data, although the variation in the strain patterns from the model is much less than those from the in vivo data. This is probably due to variation in gauge location between individuals and interindividual variation in behavior, anatomy, and material properties. More detailed studies of patterns of strain variation within and between experiments and individuals will shed light on these issues. Analysis of changing strain patterns within a single chewing cycle would also eliminate effects of averaging multiple loading events (cf. Coleman et al., 2003).

The FEM of the alligator skull is also validated by experimental data, but this was much less successful. Metzger et al. attribute this to the fact that, although sutures were not modeled in either the macaque or the alligator model, sutures have a greater influence on overall patterns of skull deformation in alligators than macaques. Given that alligators show indeterminate growth, this seems plausible, although data on the structure and in vivo function of sutures in primates are virtually nonexistent.

In their murine leg bending model, Silva et al. used periosteal strain data measured at the loading point to establish the relationship between applied force and strain on the periosteal surface in two strains of mice. They then built FEMs of the tibiae to quantify the ratio of peak periosteal-to-peak endocortical strain at the loading point, using this ratio to estimate the force versus endocortical strain relationships.

In vitro bone strain data are particularly valuable for validating FEMs because the in vitro environment allows control over more variables. Marinescu et al. use this approach in their sensitivity analysis of their FEM of the macaque mandible, but their in vitro strain results resemble their FEM results less closely than do the in vivo strain and FEM results from the cranium (Ross et al., 2005, this issue; Strait et al., 2005, this issue). One possible explanation is that the mandible is more difficult to model accurately because the geometry and external forces combine to make a broader range of loading regimes possible. Perhaps the geometry of the cranium highly constrains the loading patterns of the face, so that wide variation in external forces produces only minimal changes in strain patterns. If true, this has significant implications for our understanding of skull form and function. Whether skulls of nonprimate vertebrates are similarly robust against changes in loading regime remains to be determined.

STRUCTURE-FUNCTION RELATIONSHIPS OF COMPLEX SHAPES

Biological structures have diverse and complex shapes that pose problems for those seeking to understand the functional significance of shape. Standard engineering textbooks give formulae for calculating stresses, strains, and deformations of relatively simple structures, such as square, circular, elliptical, or triangular beams with hollow or solid cross-sections, usually made of homogeneous material properties, subjected to concentrated or distributed forces. Some texts include equations for shell structures. Although these equations can be used to estimate patterns of stress and strain in relatively simply shaped biological structures, such as long limb bones (Rybicki et al., 1977; Carter et al., 1981; Biewener and Dial, 1995; Demes, 1998; Blob and Biewener, 1999), curved mandibles (Hylander, 1984), or zygomatic arches (Hylander and Johnson, 1997), the complex morphology of the skull makes it difficult to say definitive things about exactly how the skull is deformed during feeding (Herring et al., 2001; Ross, 2001). For example, the question "Is the skull twisting like a cylinder?" actually needs to be broken down into two parts: "Is it twisting?" and "Is it behaving like a cylinder?" Without FEM, questions like these are very difficult to answer. Moreover, the steep strain gradients in the skulls of primates and other vertebrates during feeding suggest that skull morphology is adapted for various nonfeeding functions (Hylander et al., 1991; Rafferty and Herring, 1999; Ravosa et al., 2000; Ross, 2001; Ross and Metzger, 2004). The complex shape of the skull and the presence of these other functional units make it difficult to predict precisely the loading regimes resisted by specific features of the skull.

The paper by Dumont et al. (2005, this issue) provides a nice example of the use of FEA to compare the behavior of different-shaped skulls subjected to similar and different forces. The skulls they examined were those of bats. Because bats are volant, it is reasonable to think that bat skulls are optimized for strength with minimum material. Using FEM, Dumont et al. studied the patterns of stress and strain in the skulls of two species of fruit bats that bite hard-food objects in different ways: *Artibeus* uses unilateral biting when biting on hard fruits, whereas *Cynopterus* uses predominantly bilateral bites. The skull of *Artibeus* was strongest when loaded in a manner most similar to its natural biting behavior, whereas the skull of *Cynopterus* showed little difference in stress magnitudes between the two loading regimes. The skull of *Artibeus* appears to be more closely optimized for resisting feeding forces than that of *Cynopterus*. In addition to being an elegant test of the effects of wild biting behavior on skull morphology, this study nicely illustrates how FEM enables testing of the behavior of skulls of very small animals during feeding.

Metzger et al. (2005, this issue) also use FEA to reconstruct the loading regime in a vertebrate skull, that of *Alligator mississippiensis*. Previous workers had suggested that the alligator rostrum is bent in sagittal planes and twisted about a rostrocaudal axis during biting (Busbey, 1995). Given that the only external forces acting on the alligator snout during biting will produce bending and twisting, this hypothesis is reasonable. But what is the relative importance of these two loading regimes, how do features such as overlapping scarf joints impact these loading regimes, and what kind of strain and stress magnitudes are generated during biting? Metzger et al. tested hypotheses regarding loading regimes in the alligator snout by collecting in vivo bone strain data from the bones of the snout during biting on a bite force transducer. They compare the strains recorded in vivo with those predicted for an ellipsoid beam subjected to the same external forces, and those extracted from a finite-element model of the alligator skull. They found only rough correspondence between the in vivo strains and those extracted from either the model or the simple beam equations. They attribute the poor correspondence between in vivo and FEM data to the low resolution of the model and the absence of sutures in the model.

STRUCTURE-FUNCTION RELATIONSHIPS IN HARD-TO-REACH PLACES

One of the advantages of FEM is the ability to model the behavior of all parts of the skeleton, even very inaccessible ones. In vivo strain data can be gathered from some unusual places under unusual circumstances (e.g., Ross, 2001), and it is possible to gather strain data from humans (Fritton and Rubin, 2001), but there will always be parts of the skeleton even in larger animals that are impossible to reach. One such place is the endosteal surface of bones, which is impossible to put strain gauges on during normal activity. Consequently, most studies of the relationship between strain patterns and bone adaptation have focused on the periosteal surface. However, the marrow cavity is a rich source of mesenchymal stem cells, which can give rise to osteoblasts, so an understanding of the relationship between strain patterns and bone adaptation there is of interest. Silva et al. (2005, this issue) use FEA to estimate the strain profile on the endosteal surface of the cortical bone of the mouse tibia as part of their development of a murine model of osteoporosis. Silva et al. estimated strains on the endosteal surface of the mouse tibia under four-point bending using both FEA and a simple beam model. They found that a simple beam model performed almost as well as the FEM in estimating the ratio of endosteal to periosteal strains under simple bending, but point out that in situations where the loading regime and material properties are not well defined or controlled, simple beam models will not suffice.

Another example of this application of FEA is the study of Thomason et al. of the laminar junction of the horse hoof (Thomason et al., 2005, this issue). The laminar junction is the epidermodermal connection binding the external keratinous hoof wall to the distal phalanx. The epidermodermal junction is thrown into a series of laminae, the primary epidermal laminae (PEL), which project inward from the hoof wall. Despite being keratinous, these laminae are remodeled and Thomason et al. investigate the relationship between this remodeling of PEL and mechanical stress. FEA of nine hoof models was used to quantify circumferential and proximodistal stress distributions and relative displacement of the laminar junction. Comparison of the stress and displacement data with histological data on morphology of the PEL revealed significant correlations between laminar spacing and various displacement and stress variables, providing a concrete link between mechanical behavior of the hoof and the laminar morphology of the PEL.

STRUCTURE-FUNCTION RELATIONSHIPS IN FOSSILS

Most vertebrate species that ever existed are now extinct and are represented at best by fossils. Testing hypotheses regarding the relationship between structure and function in fossils requires an understanding of this relationship in living animals (Kay and Cartmill, 1977; Plavcan et al., 2001). However, there are also many animals for which living analogs are either not obvious or are not available for study; FEA provides a method to study structure-function relationships in these animals. Good examples of applications of FEA to fossils include studies of pterosaurs (Fastnacht et al., 2002), synapsids (Jenkins et al., 2002), dinosaurs (Rayfield et al., 2001; Snively and

Russel, 2002; Rayfield, 2004), and vertebrate skulls in general (Preuschoft and Witzel, 2002).

Rayfield's studies of dinosaur skulls exemplify the strengths and problems surrounding FEA of fossil taxa (Rayfield et al., 2001; Rayfield, 2004). In her contribution to this issue, Rayfield (2005) addresses a thorny but extremely important question: the functional significance of sutural morphology in skulls. Understanding the biomechanics of sutures is fundamental for understanding vertebrate skull function and evolution. If sutural morphology provides insight into how skulls were stressed during life (Thomson, 1995; Rafferty and Herring, 1999; Thomason et al., 2001; Rafferty et al., 2003), then sutures will provide significant insight into skull function in fossils. Rayfield investigates this question by comparing patterns of deformation at sutural boundaries in an FEM of the skull of *Allosaurus* with sutural morphology in the fossils. She finds mixed support for the notion that sutural morphology reflects loading regimes. In some sutures it does and in others it does not. Clearly, further work on this question in living animals is required.

Teeth provide a plethora of important data on behavior and ecology of fossil animals, including diet, life history, and social group structure. Macho et al. (2005, this issue) apply FEA to study the functional significance of enamel microstructure in the fossil hominin, *Australopithecus anamensis*, and the extant hominids, *Pan*, *Gorilla*, and *Homo*. Using software developed previously, blocks of enamel were constructed with the different internal geometries seen in the extant and fossil taxa and converted to FEMs with different geometries. The model was then loaded in compression and the ability of the different enamels to dissipate stress was quantified. The results suggest that the enamel microstructure of *A. anamensis* more effectively dissipates loads than other hominin species, suggesting that *A. anamensis* was better adapted at puncture-crushing and a hard, tough diet than other hominins. The future of FEA for the study of fossils is enormous. Integration of FEA of fossils with in vivo and FEA studies of the living animals that bracket them promises to greatly expand our ability to study structure-function relationships in fossils.

USING FEA TO STUDY GROWTH, DEVELOPMENT, AND EVOLUTION

One of the most exciting but underexploited potentials of FEA is its use to test hypotheses about morphological transformations through development, growth, and evolution. The pioneers in this field are Dennis Carter and his colleagues, who for many years have used FEA to test their hypotheses regarding the relationship between loading history and ossification patterns in bones (Carter, 1987; Carter and Beaupre, 2001). They hypothesize that patterns of shear, tension, and compression in the cartilaginous precursors of bones strongly influence patterns of appearance of ossifications in those bones. To test these hypotheses, Carter and his colleagues built FEMs of these cartilaginous models, assigned them the material properties of cartilage, loaded them with estimated external forces, and used the patterns of stress in the models to predict where to alter material properties for subsequent loads. This process was repeated iteratively and the patterns of ossification documented in the models were compared with those actually observed in vivo.

This approach has enormous potential. It provides a method for explicitly testing hypotheses about the relationship between bone growth and loading patterns. More sophisticated models can be envisaged, in which skull growth is modeled using complex material properties and morphology, including growing brains putting the braincase under tension, chewing muscles stimulating sutures, and nuchal muscles and occipitoatlantal reaction forces stimulating basicranial development.

The beginnings of this iterative, deductive approach to skull form are seen in the work of Preuschoft and Witzel (2002, 2005, this issue; Witzel and Preuschoft, 2005, this issue). In these studies, the authors start with nonspecific block-shaped FEMs, which are loaded at points corresponding to the positions of muscle attachment and bite points in the living animals they seek to replicate. Various loading regimes are applied, including bite forces at various places along the tooth row, inertial forces accompanying head-shaking to subdue prey, chewing and nuchal muscle forces, and the weight of the skull itself. These forces are then superimposed and the maximum stress values experienced by each element in the model are recorded. Those elements that are not stressed, or are only minimally stressed, by these activities are removed, and the model is loaded again. After several iterations, the resulting shapes are compared with the skulls of extant animals. The results are of interest, because many of the skulls produced in this manner do indeed resemble the skulls of living and fossil animals.

The application of this technique is of particular interest because there are extensive in vivo bone strain data from skulls of primates, alligators, pigs, sheep, and hyraxes demonstrating steep strain gradients in all taxa so far examined (Hylander et al., 1991; Ravosa et al., 2000; Ross, 2001; Lieberman et al., 2004; Ross and Metzger, 2004). The presence of areas of low strain in vertebrate skulls is not predicted by the approach of Preuschoft and Witzel, yet the resemblance of their synthesized skulls to living animals is remarkable. Resolution of this inconsistency between modeling and in vivo data is needed.

FEA clearly has much to offer the fields encompassed by vertebrate biomechanics. The papers in this issue cover some of the diverse approaches to which it is being applied. Any hypothesis that relates an aspect of morphology to patterns of stress and strain can be evaluated using FEA. The development of methods for rapid construction of FEMs will enable a larger number of models to be built, so that soon studies of variation and morphological changes will be possible. The work of various workers (Dumont, Grosse, Strait, and Richmond) on these methodological issues promises to expand the potential for this method in the future. Finally, it is also exciting to realize that FEA can be used to study ancestral forms that have only been estimated, not found. Hodges (2004) has developed methods for generating hypothetical ancestors based on a parsimonious interpretation of morphology quantified with CT data. One particularly exciting avenue of research would be the development of methods for integrating these reconstructions of ancestral trait combinations with FEM in order to test hypotheses regarding the functional significance of structural change and unusual trait combinations through evolution.

LITERATURE CITED

Beaupre GS, Carter DR. 1992. Finite element analysis in biomechanics. In: Biewener AA, editor. Biomechanics: structures and systems—a practical approach. Oxford: IRL Press. p 149–174.

Biewener AA, Dial KP. 1995. In-vivo strain in the humerus of pigeons (*Columba livia*) during flight. J Morphol 225:61–75.

Blob RW, Biewener AA. 1999. In vivo locomotor strain in the hindlimb bones of *Alligator mississippiensis* and *Iguana iguana*: implications for the evolution of limb bone safety factor and non-sprawling limb posture. J Exp Biol 202:1023–1046.

Busbey AB. 1995. The structural consequences of skull flattening in crocodilians. In: Thomason JJ, editor. Functional morphology in vertebrate paleontology. Cambridge: Cambridge University Press. p 173–192.

Carter DR. 1987. Mechanical loading history and skeletal biology. J Biomech 20:1095–1109.

Carter DR, Beaupre GS. 2001. Skeletal function and form. Cambridge: Cambridge University Press.

Carter DR, Harris W, Vasu R, Caler W. 1981. The mechanical and biological response of cortical bone to in vivo strain histories. In: Cowin SC, editor. Mechanical properties of bone. New York: American Society of Mechanical Engineers. p 81–92.

Coleman JC, Hart RT, Owan I, Tankano Y, Burr DB. 2002. Characterization of dynamic three-dimensional strain fields in the canine radius. J Biomech 35:1677–1683.

Coleman JC, Hart RT, Burr DB. 2003. Reconstructed bone end loads on the canine forelimb during gait. J Biomech 36:1837–1844.

Currey JD. 2002. Bones: structure and mechanics. Princeton, NJ: Princeton University Press.

Dar FH, Meakin JR, Aspden RM. 2002. Statistical methods in finite element analysis. J Biomech 35:1155–1161.

Demes B. 1998. Use of strain gauges in the study of primate locomotor biomechanics. In: Strasser E, Fleagle J, Rosenberger A, McHenry H, editors. Primate locomotion: recent advances. New York: Plenum Press. p 237–254.

Dumont ER, Piccirillo J, Grosse IR. 2005. Finite element analysis of biting behavior and bone stress in the facial skeletons of bats. Anat Rec 283A:319–330.

Fastnacht M, Hess N, Frey E, Weiser H-P. 2002. Finite element analysis in vertebrate paleontology. Senckenbergiana Lethaea 82: 195–206.

Fritton SP, Rubin CT. 2001. In vivo measurement of bone deformations using strain gauges. In: Cowin SC, editor. Bone mechanics handbook, 2nd ed. Boca Raton, FL: CRC Press. p 8:1–8.41.

Herring SW, Rafferty KL, Liu ZJ, Marshall CD. 2001. Jaw muscles and the skull in mammals: the biomechanics of mastication. Comp Biochem Physiol 131:207–219.

Hodges W. 2004. Integrating CT-scanning, 3D-morphometrics, and phylogenetics to reconstruct hypothetical ancestral morphologies of horned lizards. J Morphol 260:299.

Huiskes R, Chao EYS. 1983. A survey of finite element analysis in orthopedic biomechanics: the first decade. J Biomech 16:385–409.

Hylander WL. 1984. Stress and strain in the mandibular symphysis of primates: a test of competing hypotheses. Am J Phys Anthropol 64:1–46.

Hylander WL, Picq PG, Johnson KR. 1991. Masticatory-stress hypotheses and the supraorbital region of primates. Am J Phys Anthropol 86:1–36.

Hylander WL, Johnson KR. 1997. In vivo bone strain patterns in the zygomatic arch of macaques and the significance of these patterns for functional interpretations of craniofacial form. Am J Phys Anthropol 102:203–232.

Jenkins I, Thomason JJ, Norman DB. 2002. Primates and engineering principles: applications to craniodental mechanisms in ancient terrestrial predators. Senckenbergiana Lethaea 82:223–240.

Kay RF, Cartmill M. 1977. Cranial morphology and adaptations of *Palaechthon nacimienti* and other paromomyidae (Plesiadapoidea? Primates), with description of a new genus and species. J Hum Evol 6:19–53.

Kotha SP, Hsieh Y-F, Strigel RM, Muller R, Silva MJ. 2003. Experimental and finite element analysis of the rat ulnar loading model: correlations between strain and bone formation following fatigue loading. J Biomech 37:541–548.

Lieberman DE, Krovitz GE, Yates FW, Devlin M, St Claire M. 2004. Effects of food processing on masticatory strain and craniofacial growth in a retrognathic face. J Hum Evol 46:655–677.

Macho GA, Shimizu D, Jiang Y, Spears IR. 2005. *Australopithecus anamensis*: a finite element approach to studying the functional adaptations of extinct hominins. Anat Rec 283A:310–318.

Marinescu R, Daegling DJ, Rapoff AJ. 2005. Finite element modeling of the anthropoid mandible: the effects of altered boundary conditions. Anat Rec 283A:300–309.

Metzger KA, Daniel WJT, Ross CF. 2005. Comparison of beam theory and finite-element analysis with in vivo bone strain from the alligator cranium. Anat Rec 283A:331–348.

Plavcan JM, Kay RF, van Schaik CP, editors. 2001. Reconstructing behavior in the primate fossil record. New York: Kluwer Academic/Plenum.

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

Preuschoft H, Witzel U. 2005. The 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 S. 1999. Craniofacial sutures: morphology, growth and in vivo masticatory strains. J Morphol 242:167–179.

Rafferty KL, Herring S, Marshall CD. 2003. Biomechanics of the rostrum and the role of facial sutures. J Morphol 257:33–44.

Ravosa MJ, Noble VE, Johnson KR, Kowalski EM, Hylander WL. 2000. Masticatory stress, orbital orientation, and the evolution of primate postorbital bar. J Hum Evol 38:667–693.

Rayfield EJ. 2004. Cranial mechanics and feeding in *Tyrannosaurus rex*. Proc Royal Soc Lond B 271:1451–1459.

Rayfield EJ. 2005. Using finite element analysis to investigate suture morphology—a case study using large, carnivorous dinosaurs. Anat Rec 283A:349–365.

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. Anat Rec 283A:259–274.

Ross CF. 2001. In vivo function of the craniofacial haft: the interorbital "pillar." Am J Phys Anthropol 116:108–139.

Ross CF, Metzger KA. 2004. Bone strain gradients and optimization in tetrapod skulls. Ann Anat 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. Anat Rec 283A:288–299.

Rybicki EF, Mills EJ, Turner AS, Simonen FA. 1977. In vivo and analytical studies of forces and moments in equine long bones. J Biomech 10:701–705.

Silva MJ, Brodt MD, Hucker WJ. 2005. Finite element analysis of the mouse tibia—estimating endocortical strain during three-point bending in SAMP6 osteoporotic mice. Anat Rec 283A:380–390.

Snively E, Russel A. 2002. The tyrannosaurid metatarsus: bone strain and inferred ligament function. Senckenbergiana Lethaea 82:35–42.

Srinivasan S, Agans AC, King KA, Moy NY, Poliachik SL, Gross TS. 2003. Enabling bone formation in the aged skeleton via rest-inserted mechanical loading. Bone 33:946–955.

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? Anat Rec 283A:275–287.

Thomason JJ, Grovum LE, Deswysen AG, Bignell WW. 2001. In vivo surface strain and stereology of the frontal and maxillary bones of sheep: implications for the structural design of the mammalian skull. Anat Rec 264:325–338.

Thomason JJ, McClinchey HL, Faramarzi B, Jofriet J. 2005. Mechanical behavior and quantitative morphology of the equine laminar junction. Anat Rec 283A:366–379.

Thomson KS. 1995. Graphical analysis of dermal skull roof patterns. In: Thomason JJ, editor. Functional morphology in vertebrate paleontology. Cambridge: Cambridge University Press. p 193–204.

Witzel U, Preuschoft H. 2005. Finite element model construction for the virtual synthesis of the skulls in vertebrates: case study of *Diplodocus*. Anat Rec 283A:391–401.

Zelditch ME, Swiderski DL, Sheets DH, Fink WL. 2004. Geometric morphometrics for biologists: a primer. Amsterdam: Elsevier Academic Press.