

Modeling the Mammalian Jaw Mechanism: a Comprehensive Synthesis

THE MAMMALIAN JAW: A MECHANICAL ANALYSIS. By **Walter S. Greaves,**
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At a time when continuum mechanics proposes a unified model for rigid bodies, deformable solids, and fluids using sophisticated mathematical descriptions, it is a courageous intellectual challenge to advance a classic Newtonian approach to explain the mechanics of the mammalian jaw. The Greek mathematician Archimedes (c.287 BC–c.212 BC) proposed the principle of the lever, a mechanism of force transfer with a stiff beam acting across a rotation point, or fulcrum, that may enhance either force or speed at the end of the beam. The study of the masticatory mechanics and morphology of the temporomandibular joint allow assessment of the overall capacity of the masticatory apparatus as a lever system. Jaws work as a third class lever system, with the input force acting between the pivot and output force. The temporomandibular joint acts as a pivot, the masticatory muscles provide the input force, and the output force is produced by the teeth acting on food. In a series of articles written over forty years, Walter Stalker Greaves further refined this basic model in the context of the diverse designs of mammalian jaws. However, a

chronological reading of these papers would require, as Greaves himself notes, the integration of a great amount of unordered information. Fortunately, Greaves has done this work for us in his excellent book *The Mammalian Jaw: a Mechanical Analysis*, published recently by Cambridge University Press, which integrates and organizes the information provided and concepts developed in his articles. In this neat bit of work, Greaves presents in four chapters his understanding of the mammalian jaw mechanism in a logical linear sequence, beginning with a basic geometrical mechanical model that increases in complexity as the chapters progress.

The first chapter deals with the basic two-dimensional lever system and “the one third rule,” one of Greave’s more interesting proposals. Through analysis of the bite forces on teeth, the reaction forces on the joint, and the sum of bite forces along the jaw, the model estimates the location of the line of action of the resultant force from the three masticatory muscles acting together. It also explains why biting is restricted to locations where the joint forces are compressive and, consequently, why teeth must always be positioned anterior to the muscle resultant.

In the second chapter the jaw is viewed as a three-dimensional lever. In this model the resultant force is located within a triangular region defined by the two joints and the biting point. Although more abstract, this model’s explanatory potential is promising. Three regions are described: Region I, extending from the incisors to the premolars; Region II, the location of the molars; and Region III, edentulous and extending from the joint to the last molar. The application of this more complex model provides explanations for the contour of the dental arcade, the location of the carnassial teeth, the mediolateral position of the tooth row, and the length-to-width ratio of the jaw.

The third chapter reviews the mechanical consequences of vector resultant inclination (anterior to posterior), and the mechanical and functional consequences of different heights

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of the temporomandibular joint above the tooth row. Based on the “one third rule” (more accurately, the 3:7 ratio of the perpendicular distances from the resultant vector force to the fulcrum and the anterior end of the jaw, respectively) and minimizing a pair of distances, Greaves models the jaw mechanism using four points: the anterior end of the jaw; just behind the third molar; the fulcrum; and a point on the line of action of the vector force. This model explains why certain morphologies result in an almost vertical resultant vector force (as in primates), whereas others result in a posteriorly directed vector (as in suids). The model is also refined to include those groups with an anteriorly directed vector and a long diastema (such as antelope, deer, rodents, and rabbits), and the bizarre entelodonts and glyptodonts, in which the jaw joint lies at the same level as (in the former) or extremely dorsal to the tooth row (in the latter).

The fourth chapter is a welcome “bonus track.” In the preceding three chapters the jaw is the main focus, but in this last part of the book Greaves shifts attention to the skull, and the torsional forces that it may resist during unilateral chewing. The inclusion of such broader (and generally neglected) aspects into the analyses of the jaw mechanism is highly desirable, for it places the mechanism within the context of the entire skull (of which, of course, it is an integral part); and this allows the possibility of considering selective forces other than those related exclusively to mastication in explaining overall form. Two cases are highlighted: that of selenodont artiodactyls during the mastication phase and carnivores during canine biting.

Certainly, this book does not make for light reading. Greave’s models rely heavily on concepts of shape, size, and relative position of components to explain the masticatory apparatus as a biological form. Consequently, the reader must have a considerable understanding of the language of geometry to fully grasp the physical basis and applications of Greave’s models. To this end, the author endeavors to introduce the reader to the complexity of this language and provides reinforcement when required. Explanations are often accompanied by excellent illustrations, mostly sketches and graphs at a reader-friendly size, a meritorious decision of Cambridge University Press.

In summary, *The Mammalian Jaw: a Mechanical Analysis* is a comprehensive synthesis of Greave’s understanding of the jaw mechanism as a geometric apparatus. The concepts and ideas, developed initially in articles written since the 1970s, are gathered together and presented in a logical and linear sequence that facilitates tracing the evolution of form and function of the mammalian jaw mechanism. Although the mammalian masticatory apparatus is extremely diverse, Greaves provides a general mechanical explanation of jaw function by imposing a few restrictions to the models and focusing on its basic structure (i.e., joint at the rear, teeth at the front, and muscles in between).

Although some of the concepts presented require abstract thinking, Walter Stalker Greaves has succeeded in simultaneously providing an introductory and sophisticated mechanical synthesis that serves as inspiration to those of us devoted to the study of the mammalian mastication.