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# Incisal orientation and biting efficiency

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**Abstract**

Broad-edged 'spatulate' upper and lower incisors are distinctive of catarrhines and platyrrhines who use them in various ways to peel fruits, remove bark, and strip leaves from branches. The incisors of modern humans not only control the bite size of foods during ingestion, but often grip items in a number of non-food related tasks. Such uses have long been implicated for Neandertals as well. Despite the evolutionary importance of incision and the fact that the incisors feature prominently in clinical dentistry (via orthodontic practices designed both to correct incisal misalignments and adjust their orientation), little is known about what affects their functional efficiency. Few mechanical analyses of incisal action have been published and none that seem to take note of the mechanisms of both fracture and friction at the tooth-food interface. Here, we modeled the incisal tip as a wedge, finding that the efficiency of biting foods that fracture elastically is strongly dependent on both the apex angle of the incisor and the coefficient of friction. Based on apex angle measurements from a small sample of human central incisors, the overall efficiency of upper central incisors is predicted to be greatest when the angle between the apex bisector and the direction of applied force is zero. However, this is complicated greatly by friction, particularly for the lower incisors. The analysis probably applies not only to the use of incisors by humans, but also to some extent to frugivorous primates. This model should clarify the mechanics behind incision and can provide a basic foundation upon which more advanced models can be built on in the future.


*Keywords:* Incisor teeth; Tooth shape; Fracture efficiency; Friction; Ingestion; Toughness

## Introduction

The main function of mammalian teeth is to break down food particles prior to digestion. This increases the available food surface on which gut enzymes can work after food is swallowed, thereby increasing the rate of chemical breakdown and subsequent energy intake (Lucas, 2004). However, before any mastication can take place in the mouth, food has to be placed in the oral cavity, and this step is often achieved in humans by first taking a bite out of a piece of food with the incisors. The incisors thus control bite size and thus serve a very important role in the food intake process.

Anthropoid upper and lower incisors, including those of humans, have a broad edge on their working surfaces (Swindler, 2002). This 'spatulate' incisal shape distinguishes these primates from other mammals. However, the width of spatulate incisors varies greatly between species. Many leaf-eating primates have relatively small incisors (Hylander, 1975), probably linked to the fact that they use their teeth to grip leaf foods rather than to fracture them directly with their incisal tips (Ungar, 1994, 1996). Such grip relies on friction, which, if Amontons' laws (Ringlein and Robbins, 2004) apply, would probably not be improved by making them larger. If incisors are only used for grip, with any fracture in the potential food being remote from the incisal surfaces, then widening them confers no benefit. A large variety of incisal uses is described by Osborn et al. (1986) and Ungar (1992, 1994), which can be grouped very largely into 'friction' and 'fracture' categories (Lucas, 2004).

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Fruit-eating primates have wider incisors than those of leaf-eating forms. As arboreal tropical mammals, primate fruit-eaters are probably important in the seed dispersal of some fruits (Corlett and Lucas, 1990; Lambert, 1999). A broad distinction in the types of fleshy fruits in tropical forests distinguishes those with skins from fruits with much thicker protective coverings (Janson, 1983; Leighton, 1993). Only primates seem to take many of these 'protected' fruits, suggesting that the original evolution of spatulate incisors might be correlated with such fruit coverings (Lucas, 2004). The mechanical explanation of the difficulty that other frugivores experience in peeling fruits seems to depend on controlling the crack such that it remains on the interface between the outer rind and the flesh, rather than diverting into the rind. In peeling tests on materials, such control can be difficult to achieve (Kendall, 2001), requiring a carefully directed force and a minimized work input.

Primates vary not just in incisal form, but also in whether the upper incisors bite in front of or behind the lowers (a common feature of malocclusions in human dentitions, but the norm in some primate species—Swindler, 2002), and also in their angulation with respect to the occlusal plane (the plane in which the teeth meet). An anteriorly tilted incisal orientation is called 'proclination' in the dental literature or 'procumbency' in comparative studies. A characteristic feature of humans and some other extinct hominins is their more vertical incisal orientation, at least when first erupted, compared to apes (McHenry, 2002). However, this is variable in hominins. Neandertals may have had more procumbent incisors at eruption than seen in populations of modern *Homo sapiens* (Ungar et al., 1997), and their incisal angulation also seems to vary with age. Studies of human populations show that wear plays a key role in such a change of angle (Lysell, 1958; Hylander, 1977), and despite initial great procumbency in great apes, the incisors can be almost vertical in old age (Dean et al., 1992).

A final variable in primate incisors to consider here is their bulkiness when viewed in labiolingual view. For example, the upper incisors of chimpanzees are much larger in this respect than those of hominins, something that has recently allowed the recognition of the first fossil chimpanzee (McBrearty and Jablonski, 2005).

The aim of this paper is to analyze the most efficient orientation of the incisors for fracturing food. There have been several attempts recently to understand tooth form in terms of the loading of foods (Osborn et al., 1986; Spears and Crompton, 1996; Freeman and Weins, 1997; Agrawal and Lucas, 2003; Evans and Sanson, 2003). However, except for the experiments of Freeman and Weins, and Agrawal and Lucas, these have excluded the effects of loading patterns on fracture, examining the stresses that loading imparts instead. It is, however, now recognized generally that fracture is the result of the release of elastic strain energy, i.e., energy that is accumulated and stored within a solid as a result of loading (Atkins and Mai, 1985; Lawn, 1993; Kendall, 2001). The stresses within that solid are merely a manifestation of the loading and do not control whether it fractures or not. The rate of release of energy from within the solid into new surfaces is actually what controls fracture. This property is called toughness and is defined as the energy required to produce a unit area of crack surface. In a material where the principal cost of fracture is the release of stored elastic strain energy, it can be denoted by the symbol $G$. For any food of given toughness, we attempt to show here how the forces needed to fracture a food particle with incisors depend on the form of the incisal tip, its orientation to the food surface, and the friction between them. The theoretical approach that we use in this paper requires the geometry of the tip to be modeled in some way. We assume here that it can be approximated as a wedge. We also assume that natural selection will act to make incision efficient and define optimal efficiency as minimizing the work done during food fracture. However, there are other possible definitions of efficiency, e.g., minimizing bite forces, and it is always possible that selection does not act in the way that we suggest.

## Modeling incisal form

Incision can be visualized as the creation of new surfaces from originally unexposed matter (i.e., as fracture). That process requires energy, the amount depending on the toughness of the food object being fractured and the presence of energy-dissipating mechanisms such as friction or plastic deformation (Atkins and Mai, 1985). Natural selection would probably favor the evolution of incisors in frugivores that are efficient at fracture. To be so, incisal crowns should adapt to minimize the effects of energy-dissipating mechanisms, thus reducing the amount of work that the animal has to do and also, very often, reducing the forces that it needs to apply. The efficiency of incision has been investigated by Osborn et al. (1986), who suggested that an incisor has maximum efficiency when driven into an object in a direction parallel to its long axis (the straight line joining the root apex to incisal edge). They based their argument on pressure (stress) considerations, finding that pressure exerted on the food piece by an incisor is maximized when the direction of the bite force coincides with the long axis of the incisor. Such an argument would imply that a food particle fails and fractures primarily due to compressive stress.

The incisal tip in humans (Fig. 1A) is formed by the juncture of the labial and lingual surfaces of the incisor. If the slight curvature of the incisal edge, clear in any accurate drawing of incisors (e.g., Gabriel, 1965), is ignored, then the incisal tip can be approximated as a wedge, with the labial and lingual incisal surfaces forming the sides of the wedge, and the incisal edge represented by its apex (Fig. 1C). The angle enclosed by the sides of the wedge (Fig. 1B) would then be the apex angle, $\alpha$. With this approximation, it is possible to apply and amplify existing results of studies on wedging to an investigation of incision.

Theoretical and experimental studies by Atkins and Vincent (1984) and Williams (1998) show that a wedge-shaped object can cut into an object most efficiently when the axis bisecting the apex of the wedge (the apex bisector) forms a certain small