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Puncturing Ability of Bat Canine Teeth: The Tip

Patricia W. Freeman and William N. Weins

Abstract

Casts of upper canine teeth of 15 species of microchiropteran bats were fixed securely into a testing machine and made to puncture the bloom side of an apple. The force necessary to break through the surface of the apple was regressed against both shape of the tip of the canine and the size of the animal. Sharper tips require less force to puncture than blunt ones. Results were also verified using giant two-dimensional models of Plexiglas™ with sharp and blunt tips that were loaded onto a Plexiglas™ beam. Fringes, or stress lines, are more highly concentrated at the point of contact for a smaller radius than for a larger radius under the same loading conditions, indicating that stress in the beam is higher and more concentrated at the sharper tip. Ours is some of the first experimental work to quantify apical sharpness of a tooth and performance as it punctures a substance.

INTRODUCTION

That small heels of high-heeled shoes exert more force on the floor than do the broader heels of an Oxford is a well-known phenomenon called the principle of stress concentration. For all the description and emphasis placed on the form of mammalian teeth, little experimentation has been done to correlate dental form with dental function. Our objective in this study was simply to demonstrate that the principle of stress concentration could be applied to sharp and blunt canine teeth of some of the smallest mammals—bats. Seeing the actual patterns of stress at the tooth–food interface, however, was impossible given the small size of the teeth and the simple nature of our equipment. We verified that patterns of stress at the tooth-food interface are different by using oversized plastic models with sharp and blunt tips and photoelasticity, a technique borrowed from engineering.

Canine teeth are among the simplest teeth in the mammalian toothrow and are ideal for detailed study precisely because they are relatively simple. Methods devised to study function in canines could be used ultimately to study function in more complex teeth. Cross-sectional shapes of microchiropteran upper canine teeth are diverse (Freeman, 1992). The shanks of the canines have a variety of acute and obtuse edges that run the length of the tooth that are different from the round or oval shanks found in carnivorans. How swiftly and effectively a tooth penetrates a substance and how cracks radiate or propagate from that penetration through the substance could be important to animals that fly and capture prey. Forelimbs of bats are occupied with flying, and although the wings and tail membrane may be used as temporary scoops to bring food to the mouth, canines and other teeth must do the initial immobilizing and processing of food. Here we present data on how easily the tip of the canine of a bat punctures a surface, which is the first step in examining what is happening at the interface between tooth and food.

Quantification of canines as tools involves at least two aspects: first, the morphology of the tip and the force that the tip exerts to penetrate a substance; and second, the morphology of the shank, the force of continued penetration, and the potential pattern of food breakup. It is the tip that is the subject of this study. The force necessary for puncturing a food item with

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the tip can be precisely described and measured with a uniaxial compression tester.

Much has been written about the mechanical properties of teeth including hardness, biomechanics, and structure (Halstead, 1974; Waters, 1980). Still more has been written about the functioning of the jaws, mastication, occlusion, and wear facets (Maynard Smith and Savage, 1959; Mills, 1967; Hiiemae, 1967; Crompton and Hiiemae, 1969, 1970; Turnbull, 1970; Kay, 1975; Hiiemae, 1978). Little has been written about the shapes of teeth and how that shape may affect chewing efficiency or food breakup. Studies by Lucas (1979, 1980, 1982) are notable exceptions where he first describes the theoretical framework for how shapes of molars may be breaking up different foods, then examines the cusps on premolars and molars of humans experimentally for bluntness and ability to fracture food items. Another exception is a study by Osborn et al. (1988), who examined the spatulate incisors of higher primates and concluded the incisors are tilted forward for maximum efficiency for cutting food rather than for any other purpose. This paper is one of the few actually to test teeth experimentally. Cinefilm was used to analyze upper teeth as subjects bit into apples. Van Valkenburgh and Ruff (1987) describe the strength of canines of large carnivorous mammals and how changes in shape among different kinds of carnivorans are probably correlated with strength and the animal's biting behavior. No experimental work was done. Most studies concerning mechanical properties of teeth or patterns of movements of teeth are studies of premolars and molars. Canines are only cursorily considered, if at all, in the above studies, and variation in shape of canines has not been systematically examined.

Microchiropteran bats are ideal for study because they are a monophyletic group with remarkable dietary diversity. In addition, 1) there is high diversity in canine cross-section among species; 2) their teeth are the primary tools for gathering and consuming prey; and 3) the jaws of bats exhibit a tightly constrained system of centric occlusion and isognathy or near isognathy so that differences in canine shape may have substantial functional significance (Freeman, 1992).

The New World family Phyllostomidae exhibits the greatest diversity in diet and contains species that are insectivorous, carnivorous, frugivorous, nectarivorous, and omnivorous. The families Molossidae, Mystacinidae, Vespertilionidae (the most speciose family), and Natalidae are primarily insectivorous as are Rhinopomatidae, Emballonuridae, Mormoopidae, Rhinolophidae, and Nycteridae. Noctilionids exhibit both insectivory and piscivory, desmodontids are sanguivorous, and megadermatids are insectivorous and carnivorous. However, regardless of food habit, bat teeth are small—teeth in this study range in size from 2.0 to 8.5 mm above the gum line—and prohibit anything but simple analysis without more sophisticated techniques or equipment.

To mimic activity at the actual tooth–food interface of bats, we conducted similar compression tests with oversized two-dimensional Plexigas™ models that were wedge-shaped but had tips of different radii. Not only did large models help us see interactions better, we could also test the efficacy of using plastic to quantify differences made by different tips when loaded into a plastic material. The birefringent qualities of plastic when stressed produce patterns that can be viewed and quantified under a polariscope using an engineering technique called photoelasticity.

MATERIALS AND METHODS

We cast replicas of upper canine teeth of single male specimens of each of 15 species from six microchiropteran families (*Megaderma lyra, Hipposideros commersoni, Hipposideros pratti, Noctilio leporinus, Vampyrum spectrum, Chrotopterus auritus, Phyllostomus hastatus, Trachops cirrhosus, Artibeus lituratus, Centurio senex, Cheiromeles torquatus, Eumops perotis, Scotophilus heathi, Lasiurus cinereus*, and *Eptesicus fuscus*). Plastic-resin casts of the teeth were produced following procedures from vertebrate paleontology, but modified for our purposes (Goodwin and Chaney, 1994; G.W. Brown, pers. comm.). Casts were made with the following materials: 1) molds: General Electric RTV 700 Silastic with Beta 1 catalyst, a silicon rubber; 2) casts: standard casting epoxy-resin of medium hardness, TAPOX 4 : 1 formula.

We glued the replica of the tooth to a 6.5 mm diameter wooden pedestal about 50 mm long and inserted it into a chuck on an Instron uniaxial compression tester (Model TTCL, Instron, USA). Right and left replicate canine of each cast were separated and tested separately to get a cleaner puncture without obstruction from the other canine. Three punctures were made with each replica.

After experimentation with artificial materials, we found that apples were an excellent test-surface for several reasons. There is a large literature of tests on apples (Hamann, 1969; Hanna and Mohsenin, 1972; Mohsenin, 1977; Osborn et al., 1988), and a spherical object like an apple can be turned for better orientation and angle of attack. Punctures to the surface were made with as perpendicular an angle to the tip as possible. Finally, the surface of an apple is covered with a skin through which the tooth has to break. It is this penetration of the skin that gives clearcut results from the Instron compression testing. Artificial surfaces without a "skin" gave indistinct results (e.g., urethane and styrofoam). There is a bloom side (facing the sun) and non-bloom side to the apple that may affect results. Care was taken to stay within a small test area on the bloom side of a single apple for all punctures in this study. The loading rate was 20 mm min^{-1} with a maximum load scale of 4.91 N. The depth of deformation can also be recorded from the Instron; this is the distance traveled by the tooth from the point of contact to the point of breaking through the skin on the apple.

We quantified morphology of the tip of the canines using Hertzian theory, a materials science approach, that utilizes two orthogonal radii and produces a sharpness index (Mohsenin, 1986; Fig. 1). These radii were measured by mounting the skull of the bat on a right-angle stand under a Wild M5 dissecting microscope with camera lucida and drawing the tip from anterior and lateral (90° turn) views. Quantification was done by fitting circles from an engineering template. The sharpness-quantity is a reciprocal so that smaller numbers indicate sharper tips (Fig. 1). The size characteristic (SIZE) in Fig. 2 is one that the first author has used in several previous papers and is the sum of the natural logs of condylocanine length, zygomatic breadth, and temporal height (Freeman, 1984, 1988, 1992). Using a polariscope, we quantified stress patterns (fringes) created by models with different radii as they were loaded onto a photoelastic beam (a beam of Plexiglas™). The oversized "teeth" were two-dimensional Plexiglas™ points with radii of 12.7 mm, 5.1 mm, and 1.6 mm, and were loaded to 13.34 N and 22.27 N. Three trials were performed with each load using each point. The beam itself was 6.22 mm thick by 171.45 mm by 25.4 mm, and after calibration, three locations within the beam were selected for quantification. These were the point of contact, 25.4 mm from the side of contact, and the point opposite contact on the inferior surface of the beam. The fringes at all three points were counted by observation through a polariscope, and the stress represented by the fringes were quantified by a null balance compensator.

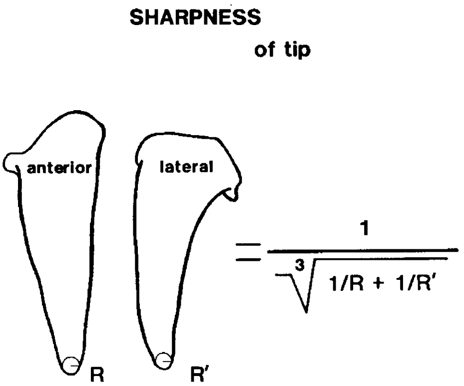

Fig. 1. Sharpness of tip depends on quantifying orthogonal radii of the tip and is used as an index. The smaller the number, the sharper the tip. Details are found in Materials and Methods.

RESULTS

Uniaxial compression tests performed on the Instron produced highly repeatable measurements of the force needed for a canine to puncture a material. Repeated measures of the force needed for a single tooth to penetrate a surface produced a coefficient of variation of only 9%. In an ANOVA, the variance in force was partitioned among replicate punctures of a single

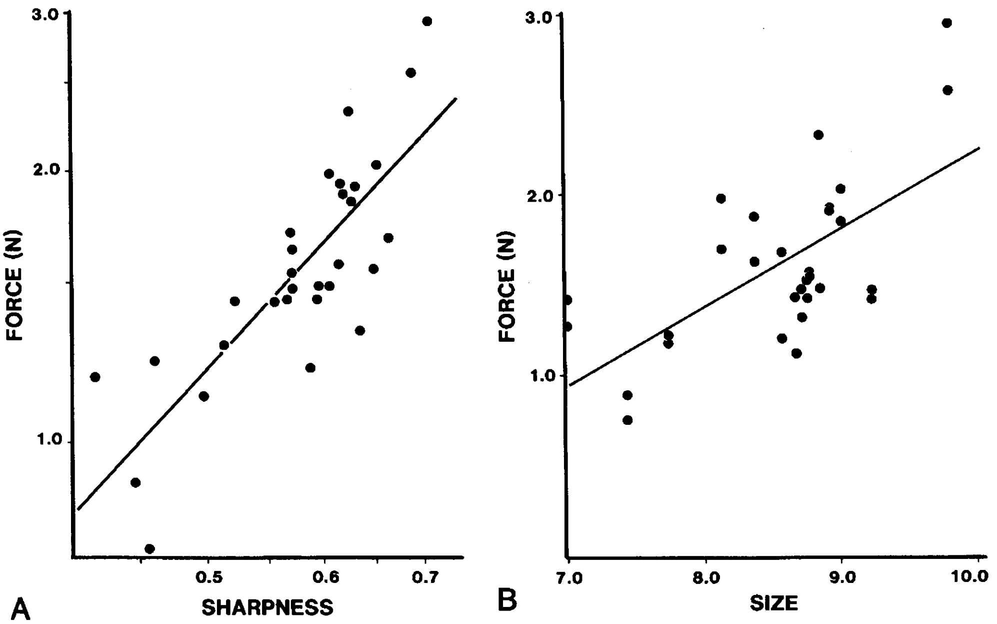

Fig. 2. Uniaxial compression tests showing the amount of force in Newtons (N) necessary for tips of varying sharpness (A, r = 0.79, b = 1.802, a = 1.446; b and a are logged values) and for animals of different size (B, r = 0.70, b = 0.441, a = -2.126) to penetrate an apple. Both are significant ($p < 0.0001$). Sharpness of tooth and size of animal are defined in Materials and Methods. Less force is required for sharp teeth, which have the smallest numbers and are found in small bats. In A, the vertical axis is in Newtons, but has been plotted on a logarithmic scale. Sharpness on the horizontal axis is also on a logarithmic scale.

tooth, different canines of the same species, and canines of different species. The significant variance in force among teeth of the same species was 13 times greater than the variance among replicate punctures of a single canine. There was also a highly significant effect by different species. The variance in force among species was 107 times greater than the variance among replicates of a single canine. Using a correlation analysis, we found that the sharpness of a canine (as measured by orthogonal radii of a canine apex, Hertz theory; Mohsenin, 1986; Fig. 2) explained 63% ($p < .0001$) of the variation in force required to puncture the material.

In general, the sharper the tip, the smaller the force required for penetration, and smaller bats use less force to penetrate an item than larger bats (Fig. 2). Big bats have absolutely duller teeth (but not necessarily relatively, i.e., within its size class) that take greater amounts of force to break through a surface. But size is not the reason more force is necessary. More force is necessary because the big bat lacks a sharp tip. Sharpness of the tip explains most of the variation in force. In Fig. 2, a regression line has been drawn to indicate how canines of differently-sized individuals vary. Actual heights of canine range from 2.0 mm to 8.5 mm. The depth at which the tooth punctures the surface of the apple, depth of deformation, occurs at about 10% of the length of the canine (a range from 8 to 13%). Results for the model "teeth" show that stress at points away from the contact point is constant regardless of the size of the radius (Fig. 3). As expected, stresses at the point of contact are higher for smaller radii. However, even though stress at the point of contact is less for larger radii, the stresses present at points that are a distance away from the tip (> 2.54 cm) are equal. That is, fringes are more spread out and less concentrated for larger radii.

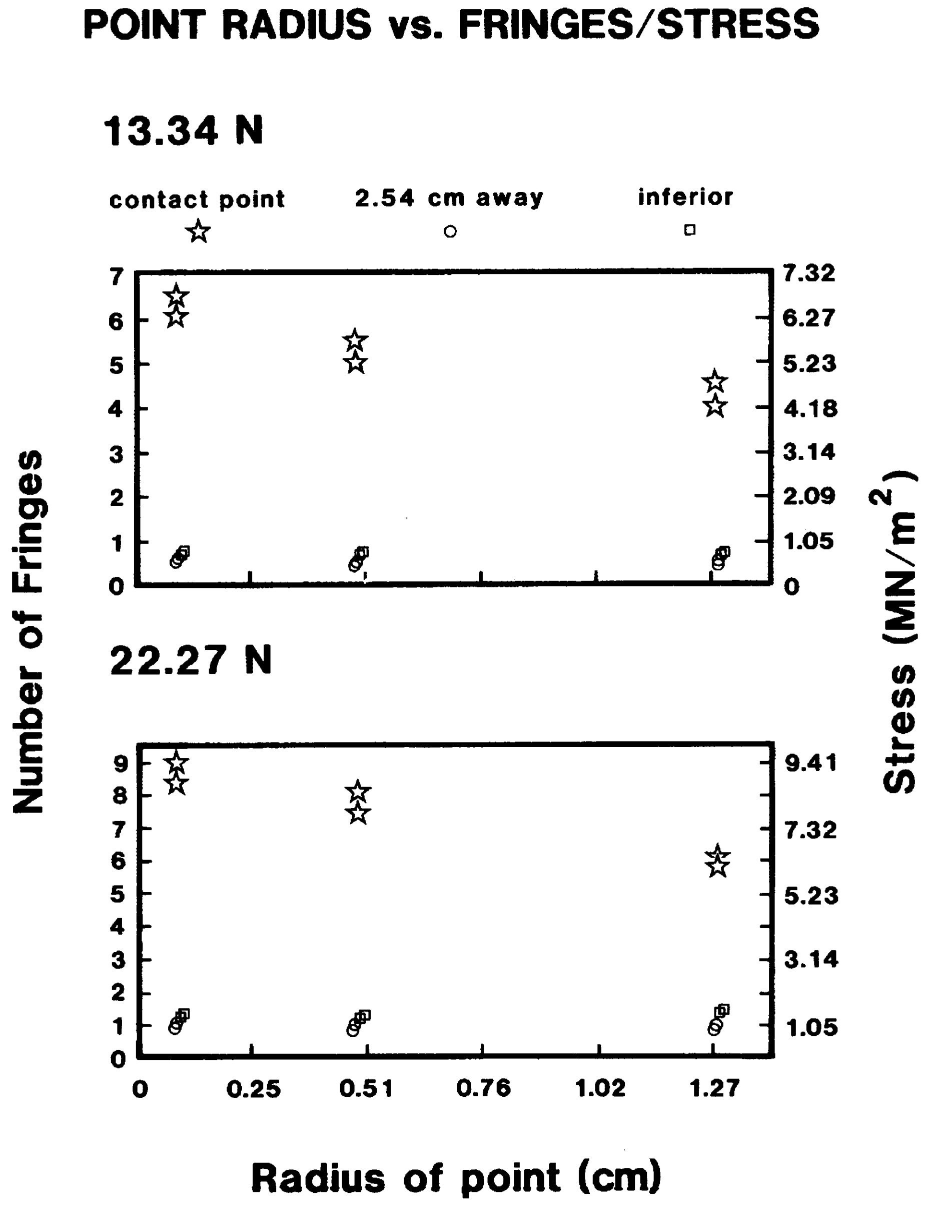

Fig. 3. Giant two-dimensional Plexiglas™ model "teeth" of different radii at the tip loaded onto a photoelastic beam under a 13.34 N and 22.27 N load regime. The points with the smallest radii produced the greatest number of fringes, or stress lines, at the point of contact, indicating higher stress and greater stress concentration.

DISCUSSION

This work is some of the first experimental work actually to quantify apical sharpness of a tooth and performance as the tooth punctures a substance. Lucas (1980, 1982) experimented with pressing items against cusps of molars and, because of the bluntness of the cusps, suggested that cheek teeth in humans were adapted to a diet of hard, brittle foods. In an earlier paper, Lucas (1979) proposed that shapes and configurations of mammalian teeth are largely an evolutionary response to kinds and textures of foods eaten.

Smaller teeth can puncture with greater ease because they concentrate the force in a smaller area (creating greater stress in that area). It is not surprising that the principle of stress concentration applies to small teeth, but it is a first step in matching canine form with canine function. Quantifying force and stress produced by different points under different loads makes possible future experiments that examine stresses created by the shank of the tooth rather than just the tip. Indeed, recent work has proven this as a viable technique (Freeman and Weins, 1994; Freeman, In Press).

What occurs at the interface between tooth and food is difficult information to obtain considering variation in both teeth and food. Some bats are not physically able to take certain hard prey items (Goldman and Henson, 1977), canine teeth can be worn or broken, and some insects can be tougher than others, depending on the amount of chitin in the exoskeleton. There must also be compromises between toughness and nutritional value of different foods, not to mention size of prey. Canines are on the "front line" of action for a bat and may be the most readily changed for dietary requirements. Maier (1984:304) suggests the same thing for primates, and states "that anterior teeth are more directly correlated with the gross structure of food and they may more directly reflect ecological adaptations of a species."

The final shape of the canine in flying predators like bats must be a compromise between sharpness, the ability to penetrate foods swiftly, and wear and breakage, which are blunting features that would impede swift penetration. Wear and breakage is a problem among terrestrial predators, even in hyaenas that have strong, blunt, and conical teeth (Van Valkenburgh and Ruff, 1987). Freeman (1992) thinks bats can afford to have longer, more slender canines because their prey lack hard, brittle, and potentially tooth-breaking substances. Once food is penetrated, how the shank may direct cracks in the food to other teeth could have significant functional implications for an animal that captures prey while flying. Indeed, there is now evidence that enlarged geometric models, mimicking the edged and non-edged cross-sectional nature of canine teeth in bats, produce different patterns of stress in photoelastic plastic (Freeman and Weins, 1994; Freeman, In Press). There is a concentration of stress in the substance being penetrated at the edge of a pyramid-shaped "tooth" that is not present in the conical, non-edged "tooth" that should make penetration easier. However, the initiation of the puncture and the resulting cracks that may radiate from it, no matter what the food may be, is the function of the tips of the canine teeth in bats. Sharp or blunt canines are features we can actually test.

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