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Biomechanics

How do morphological sharpness measures relate to puncture performance in viperid snake fangs?

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It makes intuitive sense that you need a sharp tool to puncture through a tough material. The typical approach to evaluating sharpness in biological puncturing tools is to treat morphological measurements as a proxy for puncture ability. However, there are multiple approaches to measuring sharpness, and the relative influence of morphology on function remains unclear. Our goal is to determine what aspects of tip morphology have the greatest impact on puncture ability, using (*a*) viper fangs and (*b*) engineered punches to isolate the effects of different sharpness measures. Our results indicate that tip included angle is the strongest predictor of puncture performance in both viper fangs and engineered punches. For puncture tools with small included angles, sharpness index (based on the radius of curvature) also affects puncture ability. Finally, we found that punches serve as good predictors of fang performance at small angles and sharpness index values.

1. Introduction

Many animals that prey on vertebrates face the problem of puncturing dermal integument—while not very stiff, vertebrate skin is incredibly tough [1–3]. Intuitively, we consider puncture tools effective at breaking through this integument to be 'sharp'; however, it remains unclear what aspect of morphology determines functional 'sharpness'. The literature on biological cutting/puncturing tools defines morphological sharpness measures in multiple ways: radius of curvature or tip diameter [4–9], tip included angle [4,6,7], volume or surface area [7,10], or taper and aspect ratio [9,11]. Measurements of puncture performance typically either measure the performance of models [7,8,11,12] or test the puncturing performance of teeth correlated to a single measure of morphology [4,13]. The only one of these studies to compare the performance of multiple measures of sharpness is Evans & Sanson [7], who performed tests using man-made punches. Our goal here is to quantify functional sharpness in a set of biological puncture tools—using several metrics to measure shape, and physical puncture tests to determine which metric most accurately predicts puncture performance. Our null hypothesis, based on the range of measures in the literature and findings from previous work comparing measures, is that these metrics will be equally correlated with puncture ability.

Viper fangs present an accessible case study for quantifying functional sharpness in biological puncture tools. The evolution and development of colubrid snakes and their venom injection apparatus is well studied [14–18], as are

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venom properties [18–22], and strike kinematics of a wide range of species [23–29]. However, the specific puncture mechanics of snake fangs have yet to be experimentally tested. The Viperidae, in particular, typically have long, tubular fangs that allow them to inject venom deeply into their target, quickly incapacitating their prey, and aiding in digestion [14,30,31]. A wealth of literature, coupled with a wide range of fang lengths, makes the viperids a highly tractable and relevant system for testing biological puncture tools.

2. Material and methods

(a) Viper fangs

We obtained 29 specimens, from 10 genera and 19 species, on loan from the Field Museum of Natural History (FMNH; Chicago, IL; see electronic supplementary material, table S1 for specimen numbers and measurements). Our sample included individuals from a number of species, including the New World pit vipers and other Crotalinae species, Eurasian vipers and other Viperinae species [32]. To quantify fang tip geometry, we examined orthogonal (lateral–lingual and rostral–caudal) ESEM images (FEI Quanta FEG 450 ESEM; FEI Company), taking three measurements for each view: radius of curvature, fang thickness and included angle (figure 1). Orthogonal radii of curvature were measured from environmental scanning electron microscopy (ESEM) images at 100 µm resolution via the ImageJ [33] fit circle function, using points placed along the terminal edge of the tooth. These measures were used to calculate the sharpness index for each fang (equation (2.1)) [8].

$$\text{sharpness index} = \frac{1}{\sqrt[3]{(1/R' + 1/R'')}}. \tag{2.1}$$

We used paired measurements of fang thickness at 1 µm to estimate an ellipsoid fang tip surface area (equation (2.2)). Surface area has been previously measured in the puncture literature; however, here we model the tooth tip at a smaller scale and as an ellipsoid rather than a paraboloid [7].

$$\text{Approximate tip surface area} = 2\pi\left[\frac{(a^p b^p + a^p c^p + b^p c^p)}{3}\right]^{1/p}, \tag{2.2}$$

a = lingual–lateral 1 µm thickness; b = rostral–caudal 1 µm thickness; $c = 1$ µm; $p = 1.6075$.

Finally, from the two orthogonal included angles, taken for the terminal 0.1 mm of the fang, we calculated an average included angle for each fang tip.

We measured the amount of force required to drive each fang into a cube of ballistics gel (Vyse Professional Grade Ballistic & Ordnance Gelatin, Custom Collagen, Addison, IL, USA), chosen for its homogeneous nature, semi-reproducible material properties and extensive use in projectile mechanics literature [34,35]. To minimize target variation, all fangs were tested on a single batch of gel, and each fang was tested on two separate cubes. Fangs were fixed in place in a custom-built holder attached to a 500 N load cell on an Instron 5944 (Norwood, MA, USA). The fangs were positioned with the terminal portion normal to the surface of the ballistics gel, touching but exerting no force, and lowered at a rate of 30 mm min^{-1} until they had travelled 30% of the tool length, as measured from the base of the fang to the tip (electronic supplementary material, figure S1a). All fangs produced fracture before reaching this 30% tool length depth. The force at initial fracture (F_I) was easily detectable as a localized drop of at least 10% in the measured force (electronic supplementary material, figure S1b). We tested each fang 18 times and excluded the two highest and two lowest measurements from our analysis for $n = 14$ per fang.

Initial tests showed *Bitis gabonica* as an outlier in terms of F_I, so to determine if the single specimen was representative of the species, we obtained an additional fang (courtesy of Bill Ryerson, Saint Anselm College, NH). We collected morphological data and tested puncture ability as above. For comparison, we retested our first *B. gabonica* fang and a subset of other specimens to represent a range of included angles and sharpness index values using a new batch of ballistics gel and testing each fang 10 times, excluding the highest and lowest measurements for $n = 8$ (electronic supplementary material, table S1).

Data were analysed with R version 2.15.3 (2013-03-01—'Security Blanket') [36]. We compared average values for F_I against the tool length, sharpness index, approximate tip surface area and average tip angle for each individual fang via a multiple regression and used a type III ANOVA to determine which relationships were significant.

(b) Engineered punch puncturing

Using the viper fang measurements as a guide, we made tungsten punches to isolate the effects of tip shape in a standardized experiment. Conical tips with different included angles (narrow, moderate and wide) were shaped via electrical discharge machining, variation in sharpness index was achieved by blunting the tips with 3000 grit sandpaper (table 1; electronic supplementary material, figure S2), and punches were electrochemically etched to smooth the working surface. This range of tip morphologies encompasses the included angles measured in viperid fangs, and all but the lowest sharpness index values (figure 2). Mechanical restrictions prevented us from mimicking the lowest sharpness index values. We used a 5 N load cell on an Instron E1000 Test Instrument (Electro PlusTM E1000; Norwood, MA, USA) to measure the force each punch required to initiate the fracture in cubes of ballistics gel from a single batch. Punches were lowered at a rate of 0.1 mm s^{-1} until fracture occurred, as indicated by a sudden and significant drop in the force measurement, with each punch tested six to nine times. Data were analysed as above, comparing F_I against included angle and sharpness index.

3. Results

When comparing F_I, we found that only the single *B. gabonica* fang was significantly different from all other fangs tested (electronic supplementary material, figure S3). When comparing the effect of tooth tip morphology on F_I, the included angle was the only morphological measurement to have a significant influence (F-value = 25.15, $p \ll 0.01$, adjusted $R^2 = 0.6496$; sharpness index: F-value = 0.0886, $p = 0.7685$; surface area: F-value = 0.5020, $p = 0.4854$) (figure 2*a–c*).

Because it behaved as an outlier, we re-ran our tests excluding the *B. gabonica* fang, with similar results; included angle remained the most significant influence on F_I (F-value = 13.92, $p = 0.0011$, adjusted $R^2 = 0.5725$), but the influence of the sharpness index increased (F-value = 2.566, $p = 0.1228$; surface area: F-value = 0.1381, $p = 0.7135$). For the second round of testing, F_I values followed the same overall pattern, though values varied (electronic supplementary material, figure S4a). As expected, the two *B. gabonica* fangs, with similar included angles, had significantly higher F_I values than the other retested fangs (F-value = 166.8, $p \ll 0.01$; electronic supplementary material, figure S4b).

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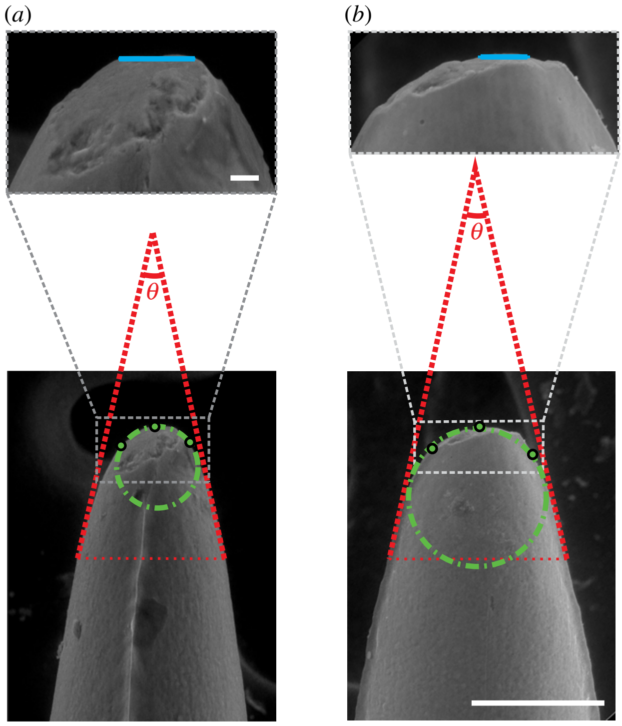

Figure 1. ESEMs of *Bitis arietans* (FMNH22258) fangs and measurements in (*a*) rostro-caudal and (*b*) lateral views. Radius of curvature was measured by fitting a circle (green dot-dash line) to points (green circles) placed along the tip of the fang. Included angle (θ) was measured starting 0.1 mm from the tip of the fang (base of the red dashed-line triangle). Surface area of the fang tip was calculated from widths measured 1 µm from the tip of the fang (enlarged panels; solid blue lines). Scale bars: 100 µm in main panels; 10 µm in enlarged panels. (Online version in colour.)

We also tested a set of tungsten punches to separately explore the influence of included angle and sharpness index on puncture initiation. Both included angle (F-value = 167.6, $p \ll 0.01$) and sharpness index (F-value = 11.93, p = 0.0008) have a significant effect on the F_I required by the punches, with included angle having the greater influence. The relationship between sharpness index and F_I varies between punches with different included angles (figure 2*d–f*). For the narrow (adjusted $R^2 = 0.5587$, $p \ll 0.01$) and the moderate punches (adjusted $R^2 = 0.5535$, $p \ll 0.01$), F_I increases with sharpness index. By contrast, there is no significant relationship between sharpness index and F_I for the wide punches (adjusted $R^2 = 0.0621$, $p = 0.0612$).

4. Discussion

These results indicate that when quantifying puncturing tool sharpness, it is important to account for both included angle and sharpness index, but the importance of the latter wanes as included angle increases. These results are in keeping with similar work on steel punches used to puncture beetles [7]. For organisms that depend on functional puncturing tools, this is of practical importance since sharpness index will increase with wear, but included angle less so.

The punches serve as good predictors of fang function at smaller included angles and low sharpness index values. However, viper fangs with larger included angles required less force to puncture than would be predicted by the punch tests, even when sharpness index was relatively low, which may be due to other shape differences not measured here. Punches were round in cross-section, in contrast to viper fangs (figure 1), which have a more oblong cross-section. Additionally, viper fangs have blade-like edges running along the length of the tooth, which can extend to the tip of the tooth, or can be worn to the point where no functional edge remains [37]. While it is tempting to suggest that these bladed edges and the non-circular cross-sections might explain this discrepancy [12], the extent to which either would affect fang morphology at the scale at which fracture initiation occurs is unclear. The surface structure of fangs and punches are also different: chemically smoothed tungsten versus enamel. However, if this were the cause of the discrepancies, we would expect to see equivalent differences for all included angles.

The data presented here suggest that the included angle is the strongest predictor of F_I. Sharpness index is also an important predictor, though the strength of this relationship decreases at larger included angles. The relative impact of included angle versus sharpness index will be important for vipers, as it will mitigate the effects of wear on the fang tip, especially in smaller fangs [7,38]. Vipers tend to have stouter bodies than other snakes [31], which may result in more force during strikes, allowing for greater fang included angles, such as those we found in the *B. gabonica* fangs. Future work on biological puncturing tools should help to determine if the same patterns hold true, detect variations in morphology that may account for the disconnect between the engineered tools and fangs and may lead to improved bioinspired needle designs [39,40].

It is unclear how much the relationship between included angle, sharpness index and F_I seen in these viperid fangs is applicable to other biological puncture systems. Puncture tool shape, the speed of the puncture event, angle of the puncture tool during the puncture event and the material properties of the puncture target will all affect F_I [39,41,42]. The fangs tested here have evolved to puncture a range of different tissues, varying with prey type, which may be more deformable than the ballistics gel used in our experiment. Such a target will interact with a greater portion of

Table 1. Tungsten punch measurements.

punch	included angle (°)	sharpness index
narrow	27.1	0.198
	34.3	0.303
	25.1	0.407
	33.7	0.420
moderate	45.4	0.223
	46.1	0.319
	45.5	0.407
	48.4	0.474
wide	64.7	0.310
	67.2	0.349
	66.5	0.430
	68.4	0.492

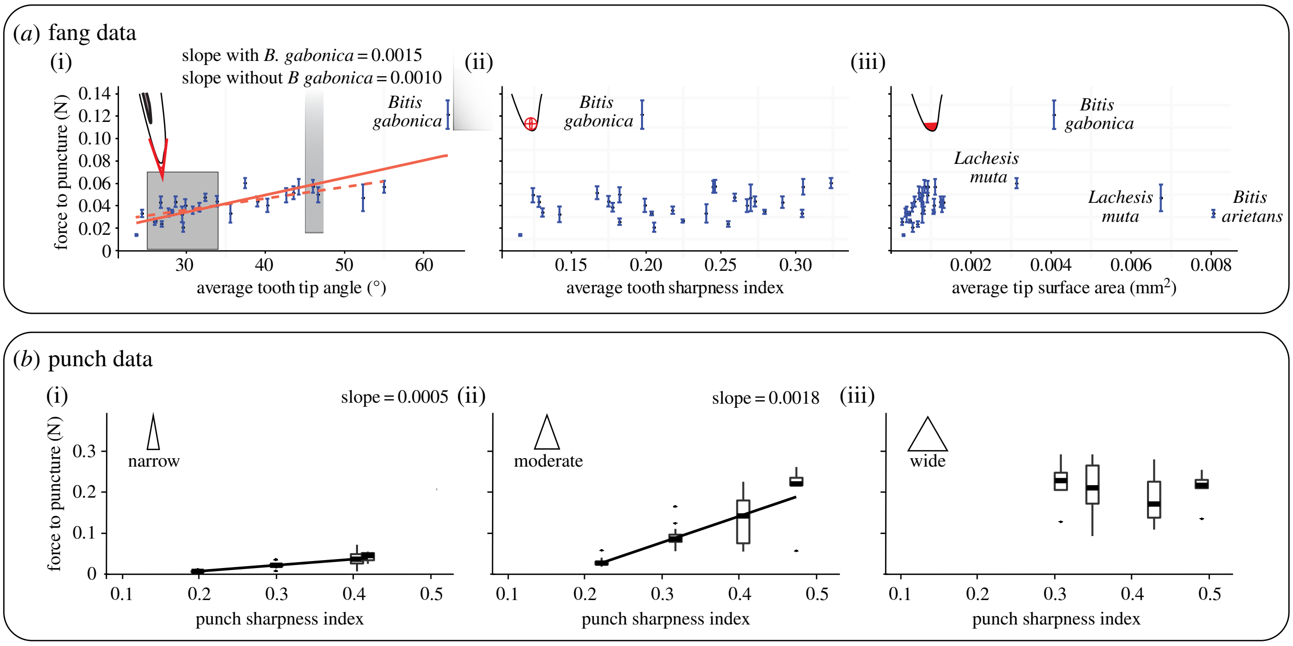

Figure 2. Results from fang and punch experiments. (*a*) F_I (N) for viper fangs plotted against (i) average tip angle (°) with *B. gabonica* (solid line) and without (dashed line), (ii) average sharpness index and (iii) average tip surface area (mm^2). (*b*) F_I (N) for punches plotted against sharpness index, with (i) narrow, (ii) moderate and (iii) wide tungsten punches. Grey rectangles in (*a*(i)) indicate the range of angles used in the narrow, moderate and wide punches and range of F_I measured. (Online version in colour.)

the tool before puncture occurs, and the overall morphology of the puncturing tool will be of greater importance [43]. Moreover, the speed at which force is applied will affect the energy being imparted to the system, as well as the material properties of the target, both of which are relevant to the puncture mechanics [34,39]. Determining the relationship between morphological measures of sharpness and actual puncture performance, whether in synthetic punches [7] or the biological tools tested here, is merely one aspect of puncture [39]. However, our results illustrate how different aspects of tip shape can have a strong influence on the mechanics required to puncture successfully.

Ethics. No live animals were used or harmed for this project. Fangs were obtained from museum collections, and one shed fang from a colleague's laboratory.

Data accessibility. Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.sn314pt [44].

Authors' contributions. S.B.C. helped design the study, carried out morphology data collection, experimental testing of fang function, and data analysis, and drafted the manuscript; Y.L. constructed tungsten punches, carried out punch data collection and provided feedback on the manuscript; Y.H. helped design the study and provided feedback on the manuscript; P.S.L.A. conceived and designed the study and helped draft the manuscript. All authors have approved the final version of this manuscript and agree to be accountable for all aspects of the work.

Competing interests. We declare we have no competing interests.

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