REVIEW

Making a point: shared mechanics underlying the diversity of biological puncture

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ABSTRACT

A viper injecting venom into a target, a mantis shrimp harpooning a fish, a cactus dispersing itself via spines attaching to passing mammals; all these are examples of biological puncture. Although disparate in terms of materials, kinematics and phylogeny, all three examples must adhere to the same set of fundamental physical laws that govern puncture mechanics. The diversity of biological puncture systems is a good case study for how physical laws can be used as a baseline for comparing disparate biological systems. In this Review, I explore the diversity of biological puncture and identify key variables that influence these systems. First, I explore recent work on biological puncture in a diversity of organisms, based on their hypothesized objectives: gripping, injection, damage and defence. Variation within each category is discussed, such as the differences between gripping for prey capture, gripping for dispersal of materials or gripping during reproduction. The second half of the Review is focused on specific physical parameters that influence puncture mechanics, such as material properties, stress, energy, speed and the medium within which puncture occurs. I focus on how these parameters have been examined in biology, and how they influence the evolution of biological systems. The ultimate objective of this Review is to outline an initial framework for examining the mechanics and evolution of puncture systems across biology. This framework will not only allow for broad biological comparisons, but also create a baseline for bioinspired design of both tools that puncture efficiently and materials that can resist puncture.

KEY WORDS: Puncture, Diversity, Materials, Energy, Morphology, Impact

Introduction

Puncture, defined as using a sharpened tool to penetrate a target, is widespread in the biological realm. Examples of biological puncture mechanisms can be found in numerous phyla and span several orders of magnitude in size (from the beaks of great blue heron to the stinging cells on jellyfish) and a range of speeds (from passive puncturing in cacti to the ultrafast puncturing in mantis shrimp). This diversity of puncture mechanics has drawn the attention of engineers looking to design better puncture tools (Ramasubramanian, et al., 2008; Oppegard et al., 2009; Frasson et al., 2012), as well as materials that can resist penetration (Chintapalli et al., 2014). In many cases, nature still outperforms our technology: in order to pierce human skin, ultra-sharp artificial microneedles require three times the force needed by a mosquito (Kong and Wu, 2009). The inferred commonality of puncture mechanics underlying these biological

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systems offers an opportunity to explore how disparate organisms varying in scale, materials, morphologies and kinematics have evolved to overcome common mechanical challenges, while giving insights into the physical laws that underlie those challenges.

Although puncture appears to be a relatively simple event, it is mechanically complex. Puncture events are influenced by several factors, including tool shape, the properties of the target material, the relative scale between the tool and target, the dynamics of their interaction and the medium within which the event occurs (Fig. 1). In order to understand the evolution and diversity of biological puncture systems, it is necessary to build a framework outlining how these variables interact during puncture. Such a framework must draw from fields including fracture mechanics, impact dynamics and material sciences. An increase over the last decade in the accessibility of methods such as scanning electron microscopy, tomographic visualization, high-speed videography and multi-level material characterization makes it a perfect time to explore the biology and physics of this widespread mechanical behavior.

In this Review, I will first examine the diversity of biological puncture systems in the context of their hypothesized roles (e.g. prey capture, injection, defence, etc.). I then outline the fundamental physical parameters associated with puncture (e.g. stress, energy, etc.) and how their influence has been examined in biological systems. The ultimate objective is to construct a framework for evaluating the mechanics and evolution of puncture systems that will both allow for broad comparisons across biology and form a baseline for bioinspired designs involving both puncture and puncture resistance.

Diversity of biological puncture structures and functions

Puncture occurs when a tool is used to create a fracture in a target material, followed by penetration of the tool into the material (Fig. 1). Note that both the creation of a fracture and the insertion of the tool are necessary for puncture to occur. This definition of puncture is in sharp (pun intended) contrast with the crushing/ cutting mechanics associated with mastication that have been the focus of work on vertebrate dentitions (Lucas, 2004). The goal of mastication is to create numerous smaller pieces from one large piece, allowing for easier digestion. Puncture requires the target to remain coherent, so the tool can be inserted within it. This definition is mechanistic, but when discussing biological puncture, we must address the functional context. Organisms puncture for a reason, and these objectives will influence both the morphology of the tool and the behavior during puncture. Below, I discuss the potential functions of biological puncture and the morphologies of the tools involved.

Gripping/capture

Many organisms utilize puncture behaviors to capture prey (Fig. 2). In this case, the main objective of puncture is to restrain the target by anchoring the tool within it. A common way to keep the puncture



Glossary

Impulse

The change in momentum of an object when it is acted upon by a force over an interval of time.

Included angle

The angle between two sides of a triangle. Included angle can be used as a measure of sharpness in puncture tools. It refers to the angle between two sides of a sharpened tool that tapers to a point. The sides should be oriented 180 deg from each other around the circumference of the tool. The more acute this angle, the sharper the tool.

Kinetic energy

Energy in a body as a result of being in motion. Can be calculated as onehalf mass times velocity squared $(1/2mv^2)$.

Material properties

Properties that define how a material behaves under various conditions. Includes properties such as Young's modulus and strength.

Momentum

Mass times velocity of a moving body.

Radius of curvature

A measure of curvature quantified as the radius of a circular arc that best approximates the curve at a given point. It is often used to describe the sharpness of puncture tools by fitting the circular arc to the curve at the tip of the tool. The smaller the radius, the sharper the tool.

Reynolds number

Dimensionless number that represents the ratio of inertial to viscous forces in a fluid flow. In terms of biology, Reynolds number is used to signify what types of fluid dynamics a particular organism must adapt to. Reynolds number is influenced by fluid density and viscosity, the size of the organism in question and the speed of the flow around the organism. Large animals in dynamic flows will show higher Reynolds numbers influenced by inertial forces, while small animals in calmer, less dynamic flows will be under more viscous forces.

Strain

Deformation in a material or structure caused by a load (stress).

Strain rate

The rate at which a material or structure is deformed. Strain rate can influence how materials react to loads (stress).

Strength

The critical stress at which a material will fail.

Stress

The force applied to a material or structure divided by the contact area over which it is applied. Stress is important to fracture creation.

Work

A measure of energy defined as force applied over a distance. Work is required for both fracture creation and inserting puncture tools into open fractures.

Young's modulus

A measure of the stiffness of a material, calculated as the amount of stress required to create a set amount of strain.

tool lodged in the target is via the use of multiple tools aligned in opposition to each other, such as the puncturing teeth of many vertebrates. When punctured by multiple tools from different directions, a struggling prey animal cannot shake itself off of one tool without being further embedded on the other. Examples include clutching teeth in sharks (Cappetta, 1987; Ramsay and Wilga, 2007; Whitenack and Motta, 2010; Galloway et al., 2015), felid canines used for throat gripping (Eaton, 1970; Schaller, 1972; Ewer, 1973; Leyhausen, 1979; Van Valkenburgh and Ruff, 1987) and the opposing mandibles found in a number of arthropods (Schofield et al., 2016). These behaviors all involve the application of continuous pressure to keep the puncture tools embedded.

It is also possible to capture prey using a single puncture tool, as demonstrated by humans harpooning whales or sharks. Several clades of mantis shrimp capture prey via a high-speed spearing action involving an elongate raptorial claw. Once caught, prey is



Fig. 1. Schematics defining puncture. (A) Components of a puncture event including the structure used to puncture (tool), the material being punctured (target), the relative movement of the tool and the target (action), and where the event occurs (medium). (B) The four phases of a puncture event: the initiation of contact between the tool and the target, the deformation of the target under load, the initiation of fracture and the penetration of the tool into the target after fracture.

pulled close to the body, where it can be controlled and consumed (Dingle and Caldwell, 1978; deVries et al., 2012). These puncture tools sport hooked barbs that prevent potential prey from slipping off the end of the tool before it can be retained (Caldwell and Dingle, 1976) (Fig. 2B). Similar ornamentation for anchoring the puncture tool within a target has evolved multiple times, including in mammals (Cho et al., 2012), insects (Zhao et al., 2015) and even plants (Mauseth, 2006).

Puncture used to maintain a grip is not exclusive to prey capture. Spine structures protruding from male genitalia are found in a wide range of animals and have been hypothesized to play a role in sexual antagonism (Waage, 1979; Crudgington and Siva-Jothy, 2000; Ronn et al., 2007; Brennan et al., 2010; Friesen et al., 2014; Orr and Brennan, 2016). Although the nature of this mechanism is debated, empirical evidence exists for puncture playing a role in maintaining the male genitalia's grip within the female organ (Friesen et al., 2014, 2016; Dougherty et al., 2017).

Special case in plants: dispersal

Puncture can also be used as a form of dispersal where, as with prey capture, the objective is for the tool to remain embedded in the target material. However, here the puncture tool and adjoining tissue separate from the main body of the puncturing organism and remain in the target (Bobich and Nobel, 2001; Rebman and Pinkava, 2001; Mauseth, 2006). In several cacti groups (including members of the genera *Consolea* and *Opuntia*), spine-covered cladodes (flat photosynthetic segments that comprise the cactus shoot system) and fruits break off of the main plant easily when their spines embed in the tissue of passing animals (Bobich and Nobel, 2001).

These spines often have surface ornamentation that help the tool remain lodged in the target (Schill et al., 1973; Robinson, 1974; Schlegel, 2009) (Fig. 2C). This ornamentation shows convergence in surface structures with several animal groups such as porcupines (Cho et al., 2012). The convergence between cactus spines and animal spines is a potentially fruitful area of future research, especially as the tools are made of very different materials.

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Fig. 2. Examples of organisms that use puncture to anchor their tools in the target. (A) *Carcharhinus limbatus* (blacktip shark; photo credit: L. Whitenack, Allegheny College) and *Strumigenys baldaria* (trap-jaw ant; photo credit: www.antweb.org) both use rows of puncture tools in opposition to each other to grip prey. (B) *Lysiosquillina maculata* (mantis shrimp; photo credit: R. Caldwell, University of California, Berkeley) use hook-like ornamentation on their appendages to harpoon prey [scanning electron microscopy (SEM) image of *Lysiosquillina glabriuscula*; SEM credit: Patek lab, Duke University]. (C) Cacti such as *Cylindropuntia fulgida* (jumping cholla; photo credit: John N. Trager, Huntington Botanical Garden; SEM credit: Anderson lab, University of Illinois at Urbana-Champaign) use their barbed spines for dispersal. Red boxes show magnified views of the structures indicated by the arrows.

Injection/removal

Many animals utilize puncture tools to inject toxic substances (such as venom) into a target (Fig. 3A). This can be done either to subdue prey or as a defensive mechanism. Regardless of the purpose, injection has a specific requirement for puncture: the tool must be inserted far enough and long enough to deliver the venom before removal. However, unlike the harpooning examples given above, this may not require the tool to be inside the target for long.

Snakes from the viperid (mambas, asps, etc.) and elapid (cobras, etc.) clades are known for extremely dynamic puncture (Kardong and Bels, 1998; Herrel et al., 2010; Young, 2010). These snakes strike fast and release quickly, leaving the fangs embedded in the target only briefly (Kardong and Bels, 1998). The fangs of these snakes tend to be smooth, with a tube running through them akin to a hypodermic needle; they deliver a bolus of pressurized venom and are easily removed (Kardong and Bels, 1998; Young et al., 2001; Jackson, 2002, 2007) (Fig. 3A). Snakes from the family Colubridae

(e.g. the mangrove and banded snakes) have grooved fangs located near the back of their jaws. Unlike vipers, these snakes leave their fangs embedded as their venom works its way down the groove and into the wound (Young et al., 2011). However, colubrid fangs also lack ornamentation (their grip is maintained through muscle action), as they still must be removed after injection.

Certain injection tools do have ornamentation, particularly if the goal is to leave the tool behind in the target, similar to cactus spines. Honey bee stingers have barbs that anchor within the target, causing them to be torn from the abdomen of the bee after puncture (Haydak, 1951; Zhao et al., 2015). Leaving a puncture tool behind can also occur in situations where the tool is replaceable, such as seen in cnidarians (Holstein and Tardent, 1984; Godknecht and Tardent, 1988). Jellyfish and other cnidarians possess cells called nematocytes (or stinging cells) that contain capsular organelles called nematocysts. These nematocysts have harpoon-like stylets that are used for venom injection (Holstein and Tardent, 1984). When triggered by a combination of chemical and mechanical cues (Pantin, 1942; Lubbock, 1979; Arai, 1997), the stylets are discharged at incredible speeds, likely driven by a combination of osmotic pressure and mechanical energy storage in the capsule walls (although the precise mechanisms are still debated) (Godknecht and Tardent, 1988; Nüchter et al., 2006; Oppegard et al., 2009). These harpoon-like structures are barbed and expendable once they have delivered their sting.

Some injecting tools double as harpoons, to allow for easy retrieval of prey after injection. Cone snails utilize a barbed, ballistic tooth to harpoon and restrain prey while injecting toxins (Schulz et al., 2004; Stewart and Gilly, 2005) (Fig. 3A). In several clades of hermaphroditic molluscs, reproduction is aided by the use of structures called 'love darts' (Zizzari et al., 2014; Reyes-Tur et al., 2015). These darts are used to puncture the body wall of the partner, anchoring the individuals together and allowing sperm exchange (Lind, 1973; Jeppesen, 1976; Chung, 1987; Adamo and Chase, 1988; Landolfa, 2002). The darts themselves inject glandular products that aid in sperm survival (Chase and Blanchard, 2006; Kimura et al., 2014). In some taxa, the dart is left behind after puncture (Adamo and Chase, 1988), whereas others show repeated puncture events using the same tool (Webb, 1942; Koene, 2006; Koene and Chiba, 2006; Reyes-Tur and Koene, 2007; Kimura and Chiba, 2013).

Several members of the braconid and ichneumonid parasitoid wasps inject eggs through their elongate ovipositors (Quicke, 2015) (Fig. 3B). Parasitoids deposit these eggs in many different materials, including fruits (Kundanati and Gundiah, 2014), animal larvae (Le Ralec et al., 1996) and wood (Vincent and King, 1995; Le Lannic and Nénon, 1999). The mechanics of these puncture tools are complex (Quicke et al., 2000), involving sliding actions that allow the wasps to steer their tool through the target and simultaneously control movement of the egg through the ovipositor (Quicke and Fitton, 1995; Quicke et al., 1995; Boring et al., 2009; Ko et al., 2011; Frasson et al., 2012; Quicke, 2015). This process is aided by ornamentation that allows gripping of the target substrate (Le Ralec et al., 1996; Kundanati and Gundiah, 2014) (Fig. 3B).

Puncturing can also be used to extract material, such as a mosquito drawing blood (Gordon and Lumsden, 1939; Hudson, 1970; Jones, 1978). These tools must stay embedded in the target for an extended period of time during extraction. Furthermore, mosquitoes must remain undiscovered by prey during the extraction of blood, so the puncture should be as painless as possible. To grapple with these challenges, mosquito proboscises are composed of multiple piercing tools (Fig. 3C), some of which vibrate and act as micro-saws to aid in fracture creation, allowing for a relatively painless initial puncture at A Copperhead 2 mm Fig. 3. Examples of organisms that inject or extract materials during puncture. (A) Both vipers (Agkistrodon contortrix; photo credit: W. Ryerson, Saint Anselem College; fang SEM of Lachesis muta, FMNH31147, courtesy of Anderson lab, University of Illinois at Urbana-Champaign) and cone snails (Conus striatus; photos and SEM credit: J.-P. Bingham and J. Milisen, University of Hawaii, Manoa) use puncture to inject toxins into their prey. (B) Parasitoid wasps (such as this Xorides species; photo credit: ©Alex Wild, used by permission) inject eggs into a variety of substrates using specialized ovipositors (SEM of Gambrus extrematis, INHS206.789, courtesy of Anderson lab). (C) Mosquitoes such as this Anopheles species (photo credit: insectsunlocked.org) use a highly modified proboscis (SEM of Aedes vexans, INHS832.490, courtesy of Anderson lab) to extract fluids from prey after puncture. Red boxes show magnifications of the indicated structures.

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extremely low forces (Aoyagi et al., 2008; Ramasubramanian et al., 2008; Kong and Wu, 2009; Ma and Wu, 2017).

Damage

In all puncture events, the target sustains tissue damage, but for some puncturing organisms damage itself is the goal. The initial bite of a shark involves puncture, but is often followed by a head-shake movement that utilizes cutting behavior to increase damage to the prey (Frazzetta and Prange, 1987; Whitenack and Motta, 2010). A similar behavior is seen in animals that use their claws for hunting, such as felids (Gonyea and Ashworth, 1975; Bryant et al., 1996). This behavior can involve simply 'hooking' their claws into the prey, as seen in cheetahs (Russell and Bryant, 2001), or inflicting debilitating damage such as disemboweling (Bryant et al., 1996) (Fig. 4A). Much like in the sharks, piercing is used as a prelude to a cutting/tearing action.

Hunting by prehistoric (and modern) humans relies heavily on puncture tools (spears, arrows or bullets) whose main purpose is to cause sufficient internal damage to the target, resulting in a killing blow (Fackler, 1988; Churchill, 1993; Hughes, 1998; Churchill and Rhodes, 2009; Kneubuehl and Sellier, 2011; Wilkins et al., 2014). How the shape of man-made projectiles creates sufficient damage has been a focus of archeological studies, particularly those interested in the evolution of projectile technology (Churchill, 1993; Hughes, 1998; Brown et al., 2012; Sahle et al., 2013). This has led to several attempts to quantify how tool shape relates to puncture damage (Sisk and Shea, 2011; Newman and Moore, 2013; Wilkins et al., 2014).

Birds use their beaks to create damage for a variety of reasons. Woodpeckers use their beaks to create openings in trees in order to access invertebrates that live in the wood (Spring, 1965; Wang et al., 2011) (Fig. 4A). This behavior entails repeated puncture events as the woodpeckers chip away at the wood to create as large an opening as possible. Another avian example comes from the hosts of brood parasites. Brood parasites, such as the brown-headed cowbird and the common cuckoo, leave their eggs in the nests of other birds to be



Fig. 4. Examples of organisms that use puncture for damage or defense.

(A) Damage: woodpeckers such as Melanerpes erythrocephalus (photo credit: S. Lawson, University of Illinois at Urbana-Champaign) use repeated strikes with their beaks to create fractures in wood, while predatory cats (such as Caracal caracal; photo credit: G. Slater, University of Chicago) use their claws to puncture and tear at prey. (B) Defense: lionfish (Pterois volitans; photo credit: public domain) have elongate spines that transmit toxins, while many gardeners have run afoul of the thorns on rose stems (photo credit: Anderson lab, University of Illinois at Urbana-Champaign).

raised (Davies, 2000). The host birds can reduce or eliminate the costs of raising foreign offspring by removing parasitic eggs from the nest. They accomplish this by piercing the shells of parasitic eggs and grasping them by the fractured surface (Brooker and Brooker, 1991; Marchetti, 2000; Henger and Hauber, 2014).

Passive defence

A final category of puncture behaviors is passive defense, where the movement of the puncture event comes from the target, not the tool (Fig. 4B). Defensive spines, found on organisms as varied as plants (Mauseth, 2006), invertebrates (Williamson et al., 1996), fish (Hoogland et al., 1956; Forbes, 1989; Bosher et al., 2006) and mammals (Cho et al., 2012), will only puncture if a target pushes themselves onto the spines. For puncture to occur in this situation, the tip of the tool must be extremely sharp, as the puncturing organism has little control over the speed or force of the event. In order for puncture to be an effective defense mechanism, the puncture event must deter the target and make it leave the vicinity. In some cases, this may involve mechanisms similar to other puncture behaviors: lionfish have venom that diffuses into the wounds caused by their spines (Saunders and Taylor, 1959; Morris et al., 2008) (Fig. 4B). Although defensive in nature, this venom can cause cardiovascular, neuromuscular and cytolytic effects, including potential paralysis (Kizer et al., 1985; Cohen and Olek, 1989). In other cases, simply the act of puncture itself is painful enough to deter the target (as the author knows from personal experience with cacti).

The act of puncture may be incidental to defense in these groups. In many cases, fish spines may simply make the animal too big to fit in a predator's mouth (Hoogland et al., 1956; Forbes, 1989; Bosher et al., 2006; Price et al., 2015). Any predator who tried to eat the fish would potentially incur puncture wounds in their mouth, but more importantly would not be able to swallow the fish. Experimental work has shown that the presence of a predator can induce spine growth, and that predators selectively attack prey with smaller spines (Moodie, 1972; Gross, 1978; Januszkiewicz and Robinson, 2007; Weber et al., 2012).

A final note on the evolution of puncture systems

From the discussion of defensive spines, it is clear that we should be cautious in assigning puncture ability as the primary evolutionary driver to all elongate, sharp structures. Like the fish spine examples, several seemingly 'obvious' puncture tools may have actually evolved for different purposes. While some woodpeckers break open wood with their beaks, others use the pecking action to create sound for communication, a behavior that does not require any puncture to occur (Spring, 1965; Wang et al., 2011). Recent work has shown that cactus spines have many functions outside of stabbing herbivores (e.g. acting as shading, water absorption mechanisms and secretory glands; Mauseth, 2006).

Parameterizing puncture

The preceding section, while not exhaustive, outlined the vast diversity of puncture in biology. Although biological puncture comes at many scales and from many phylogenetically and structurally distinct organisms, all these organisms must overcome the same mechanical challenges involved in puncture. This commonality provides an opportunity for exploring what specific morphological, material or kinematic parameters are important in influencing puncture. Once these variables are identified, we can compare the relative influence of each, giving insights into selective pressures controlling the evolution of these systems.

Puncture basics

A puncture event can be broken down into four phases: (1) the tool initiates contact with the target, (2) the target deforms under the load from the tool, (3) fracture occurs in the target and (4) the tool

penetrates the target while propagating the fracture (Fig. 1B). The material properties (see Glossary) of the target determine how the material deforms in response to the load applied by the tool. This load is best described as a stress (see Glossary; force over an area). Creating a fracture and propagating it during insertion requires applying enough energy to the system (via a stress) to break the atomic bonds within a material (Anderson, 2005). The mechanics of a puncture event are also influenced by the rate at which it occurs and the environment (air versus water) in which it occurs. These fundamental parameters (energy, stress, material properties, speed and medium) represent a good starting point for examining puncture mechanics in biology.

Material properties

Material properties describe how a material behaves under given conditions (Callister, 2004). These properties include Young's modulus, toughness, strength (see Glossary) and a myriad of others (Callister, 2004; Thompson et al., 2014). It is often unclear which of these properties are most useful when addressing specific biological functions (Berthaume, 2016). Therefore, I will focus this section on examining the behavior of biological materials during the initiation and propagation of fracture during puncture.

When a load is applied to a material, the material deforms. The nature of this deformation, called strain (see Glossary), can dictate how materials fracture. Brittle materials, such as mollusk shells or ceramics, store energy when deformed. When fracture initiates, this stored energy is released, causing the fractures to propagate explosively, shattering the material (Callister, 2004). Ductile materials, such as vertebrate integument, dissipate energy when they deform. When a fracture is initiated, there is no stored energy available to propagate the fracture. Instead, energy must be constantly applied to the fracture via a focused load (Callister, 2004). In general, fracturing a ductile material requires the use of a sharpened tool such as a razor or a needle to apply constant load to the tip of the fracture. As most puncture events occur in ductile material (the surface integument of the target), puncture tools tend to be elongate, allowing them to apply this continuous, focused load.

Biological puncture behavior is further complicated by the nature of biological tissues, which often defy simple categorization. As an example, vertebrate integument (a common puncture target), is a fiber-reinforced composite composed of multiple layers with varying properties (Finlay, 1970; Lanir and Fung, 1974; Wainwright et al., 1978; Grear et al., 2018). Although the properties of mammalian integument have been characterized in several taxa (Billingham and Medawar, 1952; Belkoff and Haut, 1991; Diridollou et al., 2000; Shergold et al., 2006; Pailler-Mattei et al., 2008), these studies often ignore variation between layers (Grear et al., 2018). Arthropod cuticle, another common puncture target (Evans and Sanson, 1998), is just as complex, comprising chitin layers in varying orientations that can be either ductile or brittle (Strait and Vincent, 1998; Vincent, 2002; Vincent and Wegst, 2004). Notably, both skin and cuticle have been used as target materials for testing the shape of biological puncture tools (Evans and Sanson, 1998; Freeman and Lemen, 2006, 2007), although the nature of the target material is not directly investigated. Studies on medical needle design have gone into more depth (van Gerwen et al., 2012), although it is still rare to find studies looking at the effect of puncture through layered materials (Carra and Avila-Vilchis, 2010).

The material properties of the tool itself will also influence puncture mechanics. In order for puncture to occur, sufficient force/energy must be applied to the target. However, the ability of a structure to transfer force/energy is reliant on its stiffness (Bendsøe, 1989, 1995; Bendsøe

and Kikuchi, 1988; Dumont et al., 2009). The bending/buckling behavior of several biological puncture tools has been examined (Freeman and Lemen, 2007; Amini et al., 2014; Bar-On et al., 2014; Habegger et al., 2015; van der Meijden and Kleinteich, 2017) and, in all of these cases, there is a potential trade-off between the ability to puncture and the resistance of the tool itself to failure (Freeman and Lemen, 2007). Some animals have gotten around this by altering their behavior during puncture. Bees and wasps puncture at angles to the surface (Zhao et al., 2015), altering the forces felt by both the target and tool (Bao et al., 2016). Mosquitoes utilize lateral supports to greatly increase the resistance of their proboscis to buckling during penetration (Ramasubramanian et al., 2008).

Stress

The load applied to create fracture is best considered as a stress: force over area. In the field of biology, the force component of stress has received most of the attention, as bite force is a staple functional metric in numerous studies (e.g. van der Meij and Bout, 2004; Huber et al., 2005; Wroe et al., 2005; Davis et al., 2010). While a useful metric for understanding food processing, bite force is not the only factor that influences stress and fracture initiation.

Small forces can create high stresses provided that the area over which the force is applied is small. In a puncture event, this area is determined by the morphology of the puncture tool, particularly its sharpness, i.e. the contact area between the tool and the target material. The sharper the tool, the smaller the contact area and the greater the stress. The sharpness of biological puncture tools has been quantified by several groups (Frazzetta, 1988; Popowics and Fortelius, 1997; Evans et al., 2005; Jones et al., 2012), and experimental tests have indicated that it can be an accurate predictor of puncture efficiency in biological systems (Freeman and Weins, 1997; Evans and Sanson, 1998; Freeman and Lemen, 2007; Whitenack and Motta, 2010).

The best way to characterize sharpness in biological puncture tools is not straightforward (Fig. 5). Sharpness of cutting edges has been described as: (1) the radius of curvature (see Glossary; also called tool tip radius), (2) the included angle (see Glossary) of the tip or (3) the width of the tool an arbitrary distance from the tip (usually <1 mm) (Fig. 5A–C; Atkins, 2009). Radius of curvature is a primary metric for sharpness often used when testing resistance to fracture in orthogonal cutting tests (Atkins, 2009; Blackman et al., 2013). However, both radius of curvature and included angle have been shown to influence puncture (Evans and Sanson, 1998; Shergold and Fleck, 2005) and have been used to characterize biological tools (Lucas, 1982; Freeman, 1992; Evans and Sanson, 2003; Jones et al., 2012). Recently, a survey of arthropod puncture tools proposed the



Fig. 5. Different definitions of sharpness. (A) Radius of curvature: the radius of the circular arc that best fits the tip of the tool. (B) Tip angle: the included angle formed by the tapering of the tool. (C) Width of the tool at 1 mm distance from tip. (D) Cross-sectional area/perimeter of the tool at 1 mm from the tip.

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perimeter of the cross-section of the tool as a metric (Fig. 5D; Schofield et al., 2016). Both tip cross-sectional perimeter and tip cross-sectional area have been used by archeologists to categorize prehistoric weaponry (Hughes, 1998; Shea, 2006; Riede, 2009; Sisk and Shea, 2009, 2011). Archeologists measure cross-sectional perimeter and area at the widest part of the tool tip, while Schofield et al. (2016) measure them 1 mm from the tip of the tool.

These sharpness measures are scale dependent. The effects of scale on radius of curvature has been examined in mammalian dentitions with mixed results (Popowics and Fortelius, 1997; Evans et al., 2005). Across many scales, there is no significant relationship between size and sharpness (Evans et al., 2005). However, when the very smallest mammalian dentitions are included, an isometric relationship between size and sharpness emerges (Popowics and Fortelius, 1997; Evans et al., 2005). Beyond these trends in mammals, little empirical data have been collected regarding size and sharpness. We can hypothesize that smaller tools should be sharper, because smaller animals have less musculature, so sharper tools can compensate for lower forces, keeping stress high. Conversely, larger animals with higher bite forces can use blunter tools without reducing the stress applied.

Energy

The stress that a tool applies to a target is driven by mechanical energy described as work (see Glossary): force times distance. When applied to a material, this work can deform the material, create a fracture or be converted into other forms of energy (such as heat) (Atkins, 2009). In this way, energy defines the central conflict between organisms during puncture: puncturing organisms aim to convert as much mechanical work into fracture as possible, while the target tries to avoid fracture by dissipating energy via deformation. Research on bladed dentitions has shown that structures that restrict a target's ability to deform reduce the energy required to cut (Lucas, 2004; Anderson and LaBarbera, 2008; Anderson, 2009; Anderson and Rayfield, 2012). Natural selection should push biological puncture systems to maximize the energy that goes into creating new fractures, while minimizing energy lost to deformation and other factors.

The need for energy efficiency influences the shape of puncture tools, most of which are sharp, narrow and elongate. Sharp tools with small cross-sections require less fracture surface to be inserted into the target, reducing the energy required. Sharp tools also reduce the volume of material being interacted with, which can prevent large-scale deformations that would blunt fracture growth (Atkins, 2009). The elongate aspects of the tool are important for applying continuous energy to the growing fracture in ductile materials (Lucas, 2004). There is a trade-off, however: elongate tools require more displacement to insert, which will increase the work required. How much this trade-off matters will depend on how deep the tool must penetrate to accomplish its job.

Many biological puncture tools have raised features along the sides that can reduce contact area during penetration, reducing the energy lost overcoming friction (Figs 2B,C and 3A,B). These sharpened ridges also act as cutting tools, focusing mechanical energy to the edges (Frazzetta, 1988; Abler, 1992). Experimental studies have shown that sharpened ridges on biological tools allow for more efficient puncture than tools lacking such ridges (Freeman and Lemen, 2006; Cho et al., 2012). Recent work has identified helically oriented barbs on honey bee stingers that aid in puncture when coupled with a rotating motion during insertion (Wu et al., 2014). Work on porcupine spines and hymenopteran stingers has shown that barbs can act as stress concentrators during insertion (Cho et al., 2012; Zhao et al., 2015).

Puncture energetics will be influenced by the overall scale of the system. The energy required for a successful puncture event correlates with the area of fracture surface required to insert the tool, which is related to both tool size and how far the tool needs to penetrate to achieve its objective. In active puncturing systems, the energy available to meet this requirement comes from the work applied by the puncturing organism. This energy can be generated by muscles, elastic storage systems (tendons, springs, etc.) or even hydrodynamic pressures (e.g. nematocytes). Large organisms can achieve sufficient energy from muscle alone, but smaller animals may need to rely on alternative systems to achieve sufficient energy for fracture, such as the use of a sharper tool. As noted above, the energy dissipated by a material is directly related to the volume of material being deformed (Vogel, 2013). The sharper the tool at a given size, the smaller the volume of material deformed, meaning less energy is dissipated and more is available for fracture creation.

Speed

All of the discussion so far has assumed that puncture is occurring under quasi-static conditions (i.e. steady, slow speed). However, biological puncture often occurs at high velocities, with many cases occurring at impact speeds (i.e. $>1 \text{ m s}^{-1}$). The intersection of fracture mechanics and impact dynamics is an area of focus in engineering beyond the scope of this Review (Anderson, 2005). However, I can examine how velocity can modify the parameters I have already discussed.

Most biological tissues are viscoelastic, meaning that their response to applied stresses is dependent on the rate of application (strain rate; see Glossary) (Burstein and Frankel, 1968; Kunzek et al., 1999; Vogel, 2013). Most of what we know about rate dependency in biological tissues has come from an interest in human injury as a result of impact trauma (Champion et al., 2003; Chatelin et al., 2010; Karunaratne, 2016; Zhu et al., 2017), with most of the experimental work performed on various bovine and porcine tissues (McElhaney, 1966; Van Sligtenhorst et al., 2006; Shergold et al., 2009; Nie et al., 2009; Pervin and Chen, 2009; Pervin et al., 2009; Nie et al., 2011; Comley and Fleck, 2012; Rashid et al., 2013; Farid et al., 2017). This is just a small sample of the literature; however, little empirical data exist for strain rate effects on biological tissues outside of mammalian model taxa.

Although detailed biological data are lacking, a general rule of thumb for materials is that when strain rate increases, materials become more resistant to deformation, essentially becoming stiffer (Anderson, 2005; Karunaratne et al., 2018). This rate-induced stiffening means the materials cannot dissipate energy through deformation as well, allowing more mechanical energy for fracture creation. This has been demonstrated in high-speed puncture tests on ballistics gelatin: the volume of material deformed is inversely proportional to the speed of the tool (Anderson et al., 2016). Imagine a viper fang impacting mammalian skin at different strain rates. At low strain rates, the skin (a ductile material) will deform a great deal, dissipating energy and requiring more work to create the required puncture for injection. At high strain rates, the material will act stiffer, dissipating less energy through deformation, requiring less energy for puncture to occur. A trade-off becomes apparent: the amount of energy saved by impacting at high speeds versus the energy that is required to attain those speeds.

These changes in material behavior at high strain rates may be related to the propagation of stress waves through the material (Kolsky, 1963; Anderson, 2005). Stress waves can be thought of as waves of deformation traveling through an object after impact. The speed and pattern of these waves are dependent on the speed of the

	Tool	Action	Target	Medium
Energy	Sharpness; ornamentation	Work; kinetic energy	Work to fracture; deformation	Drag forces
Stress	Sharpness	Force; momentum	Critical stress	Drag profile
Materials	Stiffness; buckling resistance	Strain rate; stress waves	Stiffness; toughness	Relative density
Scale	Depth required; length	Mass	Microstructure	Reynolds number
Velocity	Shape; hydrodynamics	Impact dynamics	Strain rate effects	Reynolds number

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Each cell represents how basic mechanical variables (rows) are incorporated into the components of puncture (columns; see Fig. 1). As an example: the sharpness and ornamentation on the tool will directly influence the energy required for puncture. Note that scale and velocity act as modifiers to the other variables: strain rate effects, arising from high velocity will alter how the target reacts to puncture.

projectile and the properties of the material, but their effects can be generalized. Stress wave dynamics influence the inertial response of the target; an object will not react to being impacted until the stress waves caused by the impact have accelerated its entire volume (Atkins, 2009). This is how farmers cut unrestrained stalks of wheat with a single bladed scythe: the scythe moves so fast that it cuts through the thickness of the stalk before the end of the stalk is accelerated to the speed of the blade (Persson, 1987; Atkins, 2009).

In quasi-static situations, energy applied is evaluated as work: force times displacement. However, tools traveling at high speeds will have a certain amount of kinetic energy $(0.5mv^2; \text{ see Glossary})$ associated with them, determined by their size (mass) and speed. Previous experimental work has shown a strong correlation between kinetic energy and puncture depth (a proxy for the amount of fracture created) in ballistics gelatin (Anderson et al., 2016). These experimental results suggest that the kinetic energy of the tool in flight is directly connected to the energy used to create fracture surfaces in a target. This leads to a scaling issue: organisms with low mass will have less kinetic energy available and, at small enough sizes, may not even have enough to create sufficient fracture surface. The energy available for puncture (based on mass/volume) will scale down faster than energy required (based on surface area created). Small organisms can offset this by increasing velocity. Not surprisingly, the fastest puncturing systems tend to be some of the smallest (Patek et al., 2006; Nüchter et al., 2006; Seid et al., 2008).

Finally, the stress available for puncture is modified by velocity via momentum (see Glossary): mass times velocity. When a projectile hits a target, it transfers momentum to the target. The momentum transferred by the projectile after impact (called impulse; see Glossary) is equal to the impact force of the projectile multiplied by the time over which the force is applied. A high-speed projectile hitting a target will undergo a drop in momentum over a short period of time, resulting in higher impact forces. This is intuitive: faster projectiles hit with more force than slower ones. This can be a useful strategy for small animals with low absolute muscle mass and low static force generation. Animals with power-amplified systems, such as mantis shrimp (deVries et al., 2012), trap-jaw ants (Patek et al., 2006) and jellyfish (Nüchter et al., 2006), can achieve high impact forces and high stresses by increasing the speed of their system.

Medium

Much like velocity, the density and viscosity of the medium within which the puncture occurs (air versus water) will modify the system. Underwater, puncturing organisms lose energy simply by moving the tool through a denser medium. We might expect for puncture tools underwater to have more hydrodynamic shapes, so as to reduce the energy lost to drag. However, making the tool hydrodynamic may alter the shape in ways that reduces its ability to create stress upon impact. This potential trade-off between hydrodynamics and stress production has not been explored in biology, although a similar trade-off has been identified in the evolution of man-made weapons (Hughes, 1998).

The medium also plays a major role at small scales. At small Reynolds numbers, viscous forces become important, fluid movement becomes reversible and actually moving through the fluid at all becomes problematic (Vogel, 2013). One effect of this is that when an organism tries to approach another object, it is likely that the object will be pushed away from it by viscous forces. How can puncture occur when the target is moved away by fluid forces every time it is approached? It is possible that if the animal can generate high enough speeds, it can actually increase the Reynold's number (see Glossary) of the event, allowing for inertial forces to dominate and puncture to occur. This may explain some of the extreme speeds seen in aquatic animals (Patek et al., 2004; Nüchter et al., 2006).

Putting it all together

How do these physical parameters relate to the diversity of puncture systems seen in biology? Research into the mechanics of biological puncture is currently too thin to offer much in the way of full synthesis. However, we can evaluate the various components of a biological puncture system using the parameters discussed (Table 1). To explore the potential of this framework, let us briefly compare the puncture systems of three taxa: a pit viper (snake), a spearing mantis shrimp (crustacean) and the jumping cholla (cactus). All three taxa have puncturing tools, although they vary in their use: the fangs of the viper inject venom, the mantis shrimp uses its raptorial appendages to harpoon prey, and the spines of the jumping cholla allow it to disperse itself via cloning. Although very different in functional role, the puncture tools of these groups can be directly compared using the above parameters.

Each of the three taxa must apply a sufficient stress to the target material for fracture to occur. The viper and mantis shrimp can increase stresses via impact forces that are related to the velocity with which they puncture their target (Herrel et al., 2010; deVries et al., 2012). The cholla is a passive system and has to increase stress another way, perhaps by having a sharper tool. The viper and mantis shrimp differ in scale (cm versus mm length scales) and medium (air versus water). Being larger, the viper has more mass available for kinetic energy, and loses less of this energy to drag forces compared with the mantis shrimp. The mantis shrimp has a faster strike that will help generate kinetic energy and impact forces while loading the target at higher strain rates, allowing more energy to go into the creation of a fracture surface. Both the mantis shrimp and the cholla have surface ornamentation that help anchor the target. This ornamentation extends all the way to the tip of the tool, meaning that their tools do not have to penetrate far before they snag the target material, further reducing the energy required for 'success'. The viper, by contrast, must create sufficient fracture for the venom to be injected (Fig. 3A).

The material properties of both the tools and the targets in these systems will be important as well. All three taxa have tools made from different materials (enamel/dentine, cuticle and cellulose/ lignin in the viper, mantis shrimp and cactus, respectively). Each of these tools must be able to withstand the loads required to puncture without buckling. This behavior is reliant on the properties of the target materials. The viper and cactus most likely puncture the integument and muscle tissue of vertebrates, while the mantis shrimp often captures crustaceans and occasionally fish. Both the snake and the mantis shrimp puncture at high strain rates, altering the deformation response of the target materials. For puncture to be successful, the target material must fracture before the tool does. There is a caveat to this: the tools need not escape undamaged. Both the viper and the mantis shrimp replace their puncture systems periodically, so they can afford some damage to the tool. Cholla spines are disposable; they are meant to break off after puncture, so they need not be as robust.

Final thoughts

Puncture mechanics are widespread in biology, found within most major phyla and used for a wide variety of objectives from defense to prey capture and even reproduction. Underlying this diversity are the physical principles that control puncture, to which all of these systems must conform. The framework established here is only a starting point, offering a set of parameters to examine when evaluating puncture systems across biology. Much more data are needed in order to fully synthesize these ideas. Particular avenues of inquiry include: (1) how does strain rate affect biological tissues other than mammalian muscle/skin; (2) how do stress waves behave within biological tissues; (3) how do different sharpness measures relate to fracture creation; (4) how is energy transferred from tool to target during impact puncture; and (5) what are the various tradeoffs between size, speed and shape in relation to the medium within which puncture occurs?

Addressing these questions will move us closer to identifying the fundamental principles of puncture mechanics and understanding how these principles influence biological diversity. Once identified, these principles can be incorporated into phylogenetic comparative analyses to examine evolutionary processes within puncturefocused clades such as vipers or hymenopterans. The principles can also be used as a point of comparison between disparate clades, such as for the snake, shrimp and cactus examples discussed above. Identifying these principles will improve our understanding of puncture mechanics from a biomimetics perspective as well: medical needle design already looks to nature for inspiration, but relies on examining single taxa in isolation. By exploring how biological systems have evolved to address the mechanical challenges of puncture across a wide range of sizes, structures and environments, we can exploit a broader source of biological inspiration (Patek, 2014).

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