

## COMMENTARY

# The biomechanics of burrowing and boring

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## ABSTRACT

Burrowers and borers are ecosystem engineers that alter their physical environments through bioturbation, bioirrigation and bioerosion. The mechanisms of moving through solid substrata by burrowing or boring depend on the mechanical properties of the medium and the size and morphology of the organism. For burrowing animals, mud differs mechanically from sand; in mud, sediment grains are suspended in an organic matrix that fails by fracture. Macrofauna extend burrows through this elastic mud by fracture. Sand is granular and non-cohesive, enabling grains to more easily move relative to each other, and macrofaunal burrowers use fluidization or plastic rearrangement of grains. In both sand and mud, peristaltic movements apply normal forces and reduce shear. Excavation and localized grain compaction are mechanisms that plastically deform sediments and are effective in both mud and sand, with bulk excavation being used by larger organisms and localized compaction by smaller organisms. Mechanical boring of hard substrata is an extreme form of excavation in which no compaction of burrow walls occurs and grains are abraded with rigid, hard structures. Chemical boring involves secretion to dissolve or soften generally carbonate substrata. Despite substantial differences in the mechanics of the media, similar burrowing behaviors are effective in mud and sand.

**KEY WORDS:** Fracture, Fluidization, Granular media, Hydrostatic skeleton, Sediment mechanics, Invertebrate locomotion

## Introduction

Burrowing animals inhabit soils and sediments that cover the majority of Earth's surface. They include representatives from most animal phyla and span orders of magnitude in body size. Burrowers are ecosystem engineers that modify their physical and chemical environments (Jones et al., 1997). Evidence of burrowing first appears in the fossil record near the end of the Precambrian, and the disruption of stable, microbial mat-dominated sediments by early burrowers likely contributed to the subsequent decrease in sessile invertebrates in soft sediments and the diversification of burrowing animals (Meysman et al., 2006; Thayer, 1979). Bioturbation of marine sediments alters geochemical gradients and consequently microbial communities and activities, increases nutrient regeneration, and gates the burial of organic carbon and pollutants in sediments (Meysman et al., 2006).

Boring animals in harder substrata such as rocks, wood, hard-packed clay, coral and bone are also ecosystem engineers, creating habitat for themselves and other organisms. Bioerosion by borers such as sponges, mollusks and annelids (including sipunculans) alters coral reef morphology and causes long-term damage, yet is important in the long-term cycling of materials (Hutchings, 1986).

Similarly, pholad and mytilid bivalves erode mudstone and sandstone rocks (Warne and Marshall, 1969). The bivalve *Teredo*, commonly known as the shipworm, is notorious for its damage to wooden docks, bridges and, of course, ships. In addition to causing economic damage, shipworms have had a significant role in maritime history – over half of the ships in the Spanish Armada sank during storms, and salvaged wood from the sunken ships contained enough burrow holes of shipworms to implicate these bivalves, perhaps with an even greater role than the British navy, in the defeat of the armada (Denny and Nelson, 2006).

Burrowers and borers are united in moving through and creating space within solid materials. Solids are distinguished from fluids in that stresses applied by the animals result in strains, or discrete deformations – the greater the deformation, the greater the force required. Stresses applied in fluids result instead in a strain rate, or flow, with faster flow rates requiring more force (Vogel, 1994). Whereas drag forces resist forward movement and slow the speed of a swimming animal, movement through a solid is limited to a very short distance and is completely reversible without some type of what engineers call 'material failure', which happens when enough force or stress is applied to exceed the strength of the material (Gordon, 1991). Most solid media through which animals move are heterogeneous composites of multiple materials, and failure occurs in the weakest component. Muds comprise mineral grains in a gel-like, polymeric matrix of organic material. Failure of that organic material results in the rearrangement of mineral grains. Failure of wood composites depends strongly on the orientation of the grain; splitting wood is much easier with than against the grain, and, unsurprisingly, shipworms tend to follow the grain (Board, 1970). Sands, which are granular materials, exhibit solid behavior when undisturbed but can flow under shear or gravitational forcing or be fluidized by an increase in pressure of the pore fluid sufficient to suspend the particles (Jaeger and Nagel, 1992). Fluidization – suspension of grains in a fluid medium – is used by numerous burrowers in sands, and here I distinguish burrowing as moving through solid substratum that may be locally or partially but not completely fluidized (Trueman, 1966) from swimming through a completely fluidized medium (Maladen et al., 2009).

The distinction between burrowing and boring depends in large part on the mechanical properties of the medium. Borers penetrate hard materials such as rock and wood using abrasion or chemical secretion, whereas burrowers move through softer substrata. Hardness is a broad term, encompassing the resistance to permanent yielding such as deformation, indentation or scratching. For borers, material resistance to scratching or indentation is more relevant as rocks and wood deform very minimally to small forces applied by animals. In softer materials, stiffness, the amount of force required for a given deformation, and cohesion or fracture toughness, the energy required to extend a crack, determine the mechanical failure (Dorgan et al., 2006). Fracture toughness is high in organic muds, and clean sands do not fracture. Whereas burrowers deform surrounding sediments, often forming cylindrical compacted regions around the burrow wall, bore holes are excavated without compaction.

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## Glossary

### Boring

Creating an opening in hard substrata by mechanical or chemical means; results in minimal impact to material around the burrow.

### Burrowing

Moving through soft substrata and displacing grains; generally alters material structure around the burrow, e.g. through compaction.

### Burying

Covering with a thin layer of soft, surficial sediments.

### Excavating

Creating a burrow by displacing bulk sediment and moving it towards the burrow opening, often completely out of the burrow opening.

### Fluidizing

Increasing the pressure and flow of interstitial fluids until they balance the gravitational force on grains so that grains are suspended in the fluid medium.

### Interstitial locomotion

Moving through pore spaces in sediment with minimal displacement of grains.

### Plastic granular rearrangement

Inelastic displacement of sediment grains relative to each other to alter the bulk structure of the sediment.

### Strain

Deformation normalized to original length (dimensionless).

### Stress

Force per unit area, can be pressure (perpendicular to the surface) or shear (parallel to the surface).

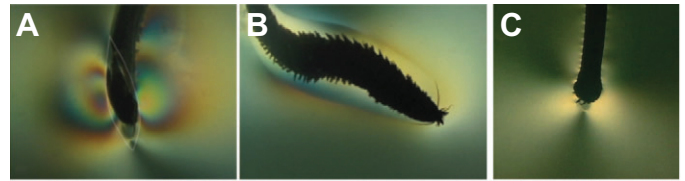
In this Commentary, I explore the relative importance of the substratum, organism morphology and behavior, and body size in different mechanisms of penetrating and moving through solid materials. Consideration of body size is important for understanding all modes of locomotion, as the relevant physics are size dependent. In heterogeneous granular materials, the size of the animal relative to the grain size determines whether bulk properties or individual grains are more important. I exclude animals small enough to move interstitially (among grains), limiting ‘burrowing’ to animals that displace grains. This review focuses primarily on marine environments.

## Locomotion through cohesive muds

### Burrow extension by crack propagation

Marine muds are elastic solids through which worms extend burrows by crack propagation (Dorgan et al., 2005; Johnson et al., 2002). The initial burrow is not cylindrical; rather, it is more tongue-depressor shaped, with the burrow extending laterally and anteriorly toward a pointed crack tip and the worm dorsoventrally compressed in the burrow (Fig. 1). To extend a burrow by fracture, worms apply dorsoventral forces to the burrow walls. The elastic walls of the burrow separate farther, and elastic energy is stored in the mud. Stress along the burrow wall is amplified at the tip of the burrow, and when enough stress builds up at the tip to exceed the fracture toughness of the material, the burrow extends by fracture, releasing stored elastic energy and creating a new burrow wall surface (Dorgan et al., 2006). This elastic behavior results from adhesion and cohesion of a matrix of organic material that fills the pore spaces around the sediment grains.

The burrowing cycle of the peristaltic burrower *Cirriformia moorei* is typical of that of many burrowing worms (Fig. 2). The worm moves forward to the tip of the crack (Fig. 2B,C, phase i),



**Fig. 1. The polychaete *Alitta virens*, burrowing in gelatin.** Burrow shape is shown from (A) anterior, (B) dorsal and (C) lateral views. Images were taken through crossed polarizers; light regions (C) indicate stress in the gelatin from forces applied by the worm, and fringes or light–dark transitions (A) show lines of constant stress. Reproduced from Dorgan et al. (Dorgan et al., 2005), with permission.

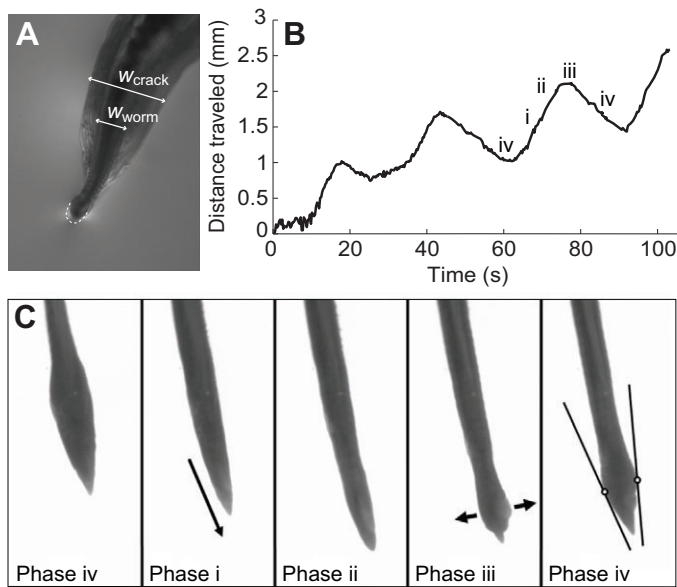
then extends the crack anteriorly (phase ii) and thickens the body, widening the crack laterally (phase iii). Then, a peristaltic wave travels along the body, moving the body wall forward as the anterior tip slips backward (phase iv) (Che and Dorgan, 2010). In most cases, anterior crack extension occurs simultaneously with forward movement, and the crack does not extend far in front of the worm (Che and Dorgan, 2010; Dorgan et al., 2007) [but see Dorgan et al. (Dorgan et al., 2008) for an exception]. In other words, the worm uses its anterior as a wedge to drive the crack. The largest component of work is to extend the burrow by fracture (Fig. 2B,C, phases ii and iii) (Dorgan et al., 2011). The other major component of work is to expand the burrow against the elastic burrow walls to create space for the animal (Fig. 2B,C, phases ii and iii) (Dorgan et al., 2011). Friction is a third component (Fig. 2B,C, phases i and iv), but because peristaltic movements involve some segments that are stationary and dilated while narrower segments move forward, friction between the narrow segments and the burrow wall is likely quite small (Dorgan et al., 2006).

Both the work of fracture and the elastic work to expand the burrow depend on the mechanical properties of the mud as well as on the size of the worm (Dorgan et al., 2008). Worms can expand the burrow dorsoventrally to an extent determined at least somewhat by their size, specifically their body thickness ( $h$ ), measured from the lateral view [although some worms can change shape quite dramatically (see Kier, 2012)]. The amount of stress that the worm must apply, and consequently the work to expand the burrow, depends on the stiffness, or elastic modulus ( $E$ ), of the sediment. In a stiffer (or more compacted) sediment, more stress is required for the worm to expand to a given body thickness. To extend the burrow by fracture, the worm needs to apply enough stress along the burrow walls to exceed the fracture toughness ( $G_c$ ) of the mud. The work of fracture ( $W_{\text{fracture}}$ ) is directly proportional to  $G_c$ . The mechanics of burrowing depend more on the ratio of  $W_{\text{fracture}}$  and the elastic work to expand the burrow ( $W_{\text{elastic}}$ ) than on their individual values. This ratio can be expressed as a dimensionless wedge number,  $Wg$ :

$$Wg = \frac{W_{\text{fracture}}}{W_{\text{elastic}}} = \frac{G_c}{Eh} \times \frac{w_{\text{crack}}}{w_{\text{worm}}}, \quad (1)$$

where  $w_{\text{crack}}$  is the width of the crack and  $w_{\text{worm}}$  is the width of the worm (dorsal view) (Dorgan et al., 2008).

Burrowing behaviors differ both among analog materials with different  $G_c/E$  (Dorgan et al., 2008) and among worms of different body sizes and therefore different thicknesses (Che and Dorgan, 2010) (Fig. 3). In a tougher material (higher  $G_c$  and higher  $Wg$ ), worms have thicker bodies and blunter anteriors to apply more stress to the burrow walls, facilitating burrow extension by fracture. In a stiffer material (higher  $E$  and lower  $Wg$ ), worms actively extend the crack laterally, which increases the width of the crack relative to

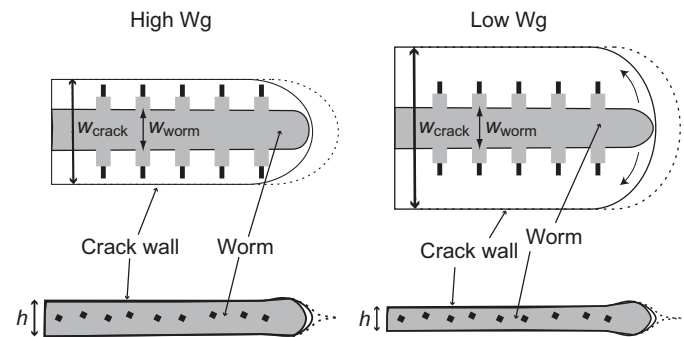


**Fig. 2. The burrowing cycle of the polychaete *Cirriformia moorei*.**

(A) Dorsal view showing the width of the worm ( $w_{worm}$ ), the crack width ( $w_{crack}$ ), and the next step of crack extension (dashed line). (B) Burrowing cycles are distinguished as periodic forward and backward movements, with the worm moving forward to the crack tip (i), extending the crack anteriorly (ii), expanding the anterior laterally (iii), then slipping backward as the peristaltic wave progresses and moves the rest of the body forward (iv). (C) Lateral view of the burrowing worm with arrows indicating forward movement (i) and force applied to the walls of the burrow (iii). Lines with circles (iv) show the slope of the burrow wall at the anterior-most position that the worm is applying force. Modified from fig. 3 of Che and Dorgan (Che and Dorgan, 2010) and fig. 7 of Dorgan et al. (Dorgan et al., 2011).

worm width ( $w_{crack}/w_{worm}$ ), reducing the elastic force compressing the worm (Dorgan et al., 2008). Small worms (with a small  $h$ ) have a large Wg and behave like worms in tougher materials (Che and Dorgan, 2010).

This mechanism of burrowing by fracture is used by worms with varying morphologies and is consistent with descriptions in the literature of burrowing by animals from diverse phyla. Trueman (Trueman, 1968) describes burrowing by bivalves as alternation between a terminal (foot) and penetration (shell) anchor, with the dilated foot anchoring while the shell is pulled down into the sediment, then the shell anchoring during probing and extension of the foot (Fig. 4). This dual-anchor system describes the behavior of many soft-bodied burrowers as well (Trueman, 1975). I have suggested that these expansions may serve a primary function of applying forces to burrow walls that are amplified at the tip of the burrow, which extends by fracture, and that anchoring may be a secondary function (Dorgan et al., 2006). Among worms, *Alitta virens* uses an eversible pharynx to apply dorsoventral forces (Dorgan et al., 2007), but force distribution along the burrow walls is similar for *Hemipodus simplex*, which has a much longer, eversible proboscis (Murphy and Dorgan, 2011). The tip of the long proboscis is more expandable and applies a focused force near the tip of the crack. Worms with non-muscular or non-eversible mouthparts can apply dorsoventral forces by expanding their anteriors using their hydrostatic skeletons (Che and Dorgan, 2010). Pointed anterior ends focus stress applied by the wider body to extend a narrow crack that is then expanded laterally by a peristaltic wave (Che and Dorgan, 2010). During and immediately following anterior crack extension, *Leitoscoloplos pugettensis* twists about its



**Fig. 3. Schematic diagram of burrowing by *A. virens* at high and low wedge number (Wg).** Dorsal (upper) and lateral (lower) views are shown. At high Wg, worms are thicker and blunter than at lower Wg to apply larger forces near the crack tip to extend the burrow by fracture (extended crack shown as a dashed line). At low Wg, worms actively extend the crack laterally (e.g. with side-to-side head movement, shown as black arrows) to increase the crack width ( $w_{crack}$ ).  $w_{worm}$ , worm width (dorsal view);  $h$ , body thickness.

longitudinal axis, orienting its width, which exceeds its dorsoventral thickness, orthogonal to the crack edge (Francoeur and Dorgan, 2014). Twisting thus increases forces to extend the crack both anteriorly and laterally. These different behaviors show remarkable similarity in applying crack-orthogonal forces focused near the crack tip to extend the burrow anteriorly and laterally.

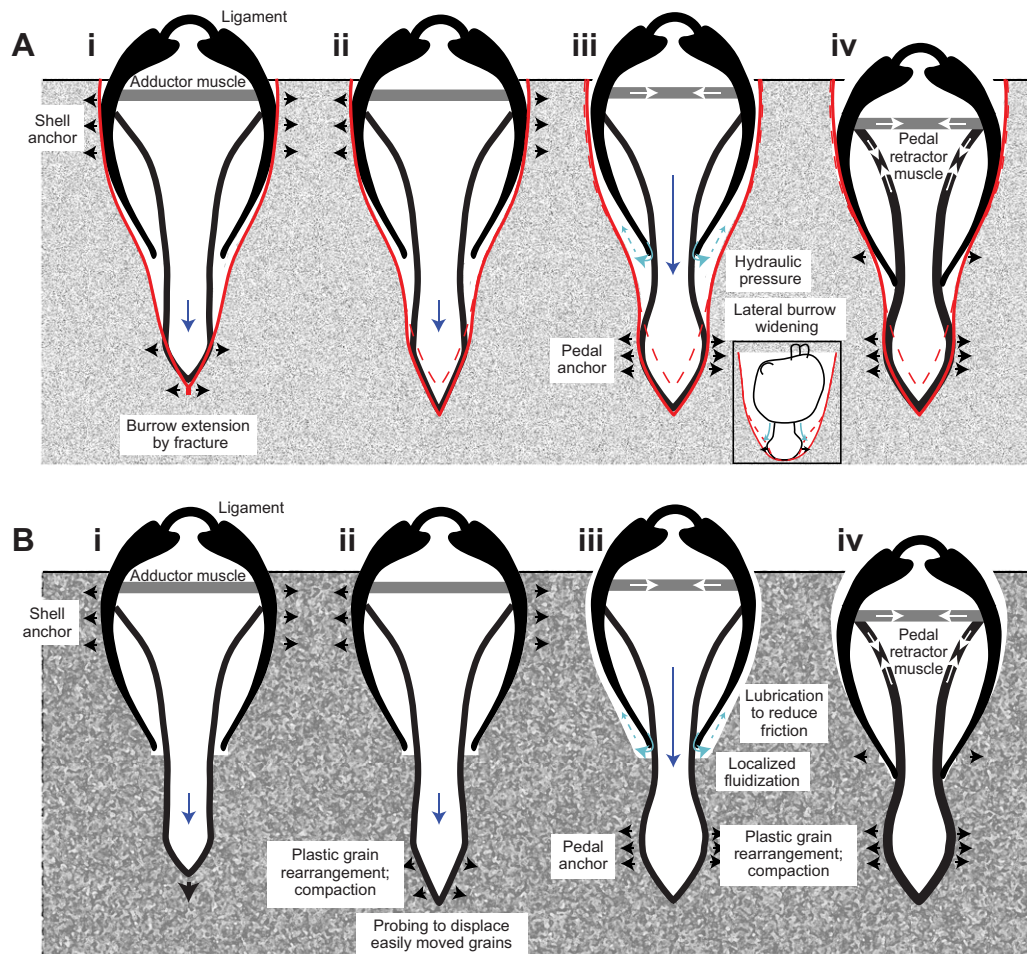
#### Other mechanisms of burrowing in mud

The body-size dependence of the mechanism of burrowing by fracture suggests both an upper and a lower bound in body size for this mechanism (Che and Dorgan, 2010). At a minimum size, exerting enough stress to the burrow walls to extend a fracture becomes difficult. At a maximum size, the force required to compress the burrow walls elastically or plastically to make space for the animal's body may make this mechanism either physiologically difficult or less efficient than other mechanisms.

Burrowing shrimp inhabit a broad range of sediments, excavating elaborate burrow structures to depths  $>3$  m (Pemberton et al., 1976). Fiddler crabs also excavate mud from burrows, which they leave as compacted balls on the sediment surface. Crabs excavate burrows in a sideways position, using their legs to scoop sediment and carry excavated sediment out of the burrow (Bellwood, 2002). This compaction works well during low tide when sediments are more likely to remain stuck together. Huang et al. (Huang et al., 2007) modeled bioturbation by fiddler crabs in mud and found that their model in which sediment was partially compacted into burrow walls and partially excavated fitted field data better than a model in which all sediment was excavated.

On the smaller end of the size spectrum, the polychaete *Armandia brevis* (~1 cm long) undulates both to burrow and to swim, and it lacks both muscular, eversible mouthparts and an expansible anterior end consistent with burrowing by fracture. Instead, its undulatory movements displace mud aggregates and plastically rearrange the sediment to create a loosely packed burrow (Dorgan et al., 2013) (Fig. 5). Worms do not fluidize grains, but rather move through a solid medium. This mechanism of burrowing is consistent with the distribution and lifestyle of the species. *Armandia brevis* is found in a range of muddy to sandy sediments that may comprise larger mineral grains or aggregates of small grains. It is relatively small and is generally found in the surface 2–3 cm, where mud is less compacted and more likely to behave as discrete particles rather than





**Fig. 4. Schematic diagram of the dual anchor system of burrowing by bivalves.** The figure shows the alternating shell (penetration) anchor and pedal (terminal) anchor, modified from Trueman (Trueman, 1968) to distinguish the mechanisms of burrowing in mud (A) and sand (B). (A) Burrowing cycles follow the same general pattern as described for worms, with (i) forward movement of the foot leading to (ii) extension of the burrow by fracture in the direction of locomotion. Next, contraction of the adductor muscle (iii) closes the shell and drives additional internal fluid (blue arrow) into the foot as well as fluid out from the mantle cavity (cyan arrow). Expansion of the foot likely widens the burrow by fracture [visible in the shell view (crack face) in the inset]; then, contraction of the pedal retractor muscle (iv) pulls the shell down toward the foot, resulting in downward movement of the body. The red line indicates the edge of the burrow, and the dashed line shows the original burrow shape (in frame i). (B) A similar pattern of movement occurs in sand but the lack of cohesion prevents fracture; rather, forces applied at both the pedal and shell anchor (black arrows) likely compact sand grains. Shell closure expels fluid from the mantle cavity (cyan arrows), and localized fluidization in front of the shell facilitates downward movement by creating space for the shell (iii). Fluid from the mantle cavity likely also moves upward between the shell and surrounding fluid, reducing frictional resistance to downward movement (iv). Modified from fig. 6 of Trueman (Trueman, 1968).

a consolidated, elastic solid. Size alone does not account for the difference in burrowing mechanism. Worms of comparable size to *A. brevis* that burrow by peristalsis are able to burrow by fracture. Whether other small worms living near the sediment surface use a similar mechanism in their natural environments, and whether a minimum size limit for burrowing by fracture exists, has yet to be explored.

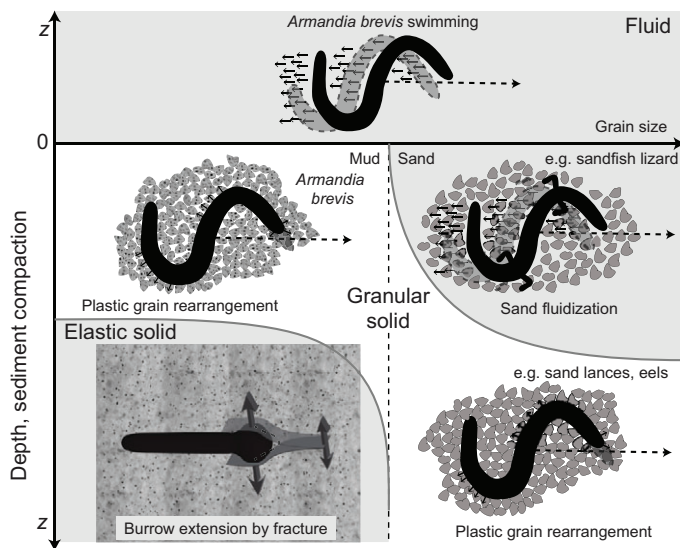
That less consolidated surface muds behave differently from elastic, subsurface sediments is supported by observations of larger organisms burrowing into sediments. Fuss (Fuss, 1964) describes pink shrimp burrowing behavior as initially grasping the substratum with pereopods and then using the pleopods to create a current to scour a furrow that the shrimp then settles into and then ‘plows ahead into the anterior end of the depression, using the walking legs to force itself further into the sediment’. Crabs burrow sideways when excavating but bury in surface sediments backwards, either loosening the sediment with pereopods or just pushing back into the sediment (Bellwood, 2002). They then cover the body either with a

‘body slam’, resuspending sediment that falls back down to cover the crab, or by scooping sediment over the carapace with chelae (Bellwood, 2002).

Although not burrowers themselves, larger animals such as rays, whales and walrus that feed on burrowing animals illustrate bulk fluidization of mud under larger forces. Gray whales suction feed for amphipods, creating feeding pits that in the Bering Sea shelf are typically 10 cm deep and over 1 m in diameter (Nelson et al., 1987). Walrus and rays create even deeper feeding pits by resuspending sediments to feed on clams (Nelson et al., 1987; Smith and Merriner, 1985).

#### Locomotion through granular sands

Beach sands are non-cohesive granular materials in which elastic fracture does not occur, yet many animals live both in mud and sand, and descriptions of burrowing behaviors are generally similar. Trueman’s (Trueman, 1968) description of bivalve burrowing using alternating terminal (pedal) and penetrating (shell) anchors applies



**Fig. 5. Scheme distinguishing swimming through fluid media and burrowing through granular and elastic solids.** Animals are shown in black, with dashed lines outlining the animal position (lighter shading) at a later time (dashed arrows indicate the direction of locomotion). Depth in sediment affects the mechanical behavior of mud and sand differently, but body size, burrowing behavior and variation in material properties are likely important as well. Swimming by the polychaete *Armandia brevis* and the sandfish lizard involves bulk transport of fluid or fluidized sand (upper shaded panel) in the direction opposite to locomotion (horizontal black arrows), in contrast to burrowing through a solid, in which forces applied by the animal (shorter arrows orthogonal to the animal) result in solid displacement but not bulk flow, and no backward slipping occurs. Both mud and sand can be granular solids (unshaded panels) in which plastic grain rearrangement can occur, although the mechanisms freeing grains likely differ. In surficial muds, the 'grains' that are mechanically relevant are likely aggregates of organic material and minerals (shown here as the same size as sand grains). Burrow extension by fracture occurs in cohesive muds (elastic solids). The crack surface is shown in gray with arrows indicating force applied by the anterior of the worm and resulting tensile stress at the crack tip. Reproduced from Dorgan et al. (Dorgan et al., 2013), with permission.

not only to mud-burrowing bivalves but also to the surf clam *Donax denticulatus* that burrows rapidly in the swash zone of sandy beaches (Trueman, 1971). In this environment, these expansions or 'anchors' are clearly not used in burrow extension by fracture, yet the behaviors are remarkably similar to those of mud-burrowing bivalves.

There are several potential mechanisms of burrowing in a granular material such as beach sand. In sands with low organic content, adhesion and cohesion of grains are much less important than in muds. Dominant forces holding grains together are instead gravitational, and these forces are transmitted between grains, forming lines of contacts or stress chains (Geng et al., 2001). On small scales, forces required to displace grains vary considerably, with some grains easily moved and others holding a disproportionate amount of the overlying weight. Consistent with intuition, deeper grains are harder to displace because they bear more overlying weight.

The mole crab, *Emerita*, burrows in the swash zone of sandy beaches very quickly, about 4 times faster than the most rapid bivalve (Trueman, 1970). *Emerita* burrows backward, using its posterior-most thoracic legs and uropods to excavate grains while the other three pairs of legs move in a rowing motion to drive the mole crab into the sand (Trueman, 1970). The legs move much faster than the forward velocity of the body, indicating that the

recently excavated sand through which the legs are moving is fluidized and that the movement, though rapid, is fairly inefficient (Trueman, 1970).

Sandfish lizards also move rapidly through fluidized sand, using undulatory body movements while holding their legs stationary against the body (Maladen et al., 2009). Backward slipping of the body accompanies bulk transport of the fluidized sand as the lizard swims (Fig. 5). Both mole crabs and sandfish lizards are relatively large animals that limit their locomotion to surface sands. Bulk fluidization becomes increasingly difficult with overlying sediment depth (Dorgan et al., 2006), and is limited by the rapid settlement of large sand grains to animals moving even more rapidly than those settling speeds.

The isopod *Tylos granulatus* lives above the driftline on sandy beaches where it can burrow to depths of a meter or more. When burrowing, the first three pairs of pereopods dig, the next three compact a bolus of sand, and the seventh pair pushes the bolus of sand behind the animal (Brown and Trueman, 1996). It also uses its flattened, shovel-shaped anterior to pack the walls of the burrow and to initiate burrowing into the sand by pushing grains aside. Fiddler crabs in mud also excavate boluses of sediment, although the mechanisms of removing grains from the matrix have not been explored in detail in either medium and likely differ. Isopods cannot burrow in completely dry sand, as the burrows collapse behind them (Brown and Trueman, 1996).

Crustacean appendages have relatively fine motor control to manipulate grains, specifically to scrape and pull grains away from the sediment matrix. For burrowers that lack appendages capable of scraping and rely on a hydrostatic skeleton, e.g. worms and bivalves, applying focused tensile forces is not feasible, making excavation considerably more challenging [although the high ingestion rates of the deposit-feeding sand-burrower *Thoracophelia mucronata* may be one solution (McConnaughey and Fox, 1949)]. These animals rely on compressive forces applied through transmission of internal pressure to the environment.

The polychaete *T. mucronata* burrows in beach sands by peristalsis, movements used by many worms that burrow in muds by fracture, e.g. *C. moorei* (Che and Dorgan, 2010). In muds, peristaltic movements in which stationary, dilated segments alternate with forward-moving narrower segments allow animals to apply normal forces to the burrow walls to burrow by fracture and also to restrict friction by moving only the narrower segments (Dorgan et al., 2006). I have recently shown that *T. mucronata* applies normal forces when burrowing in sand, and have suggested that peristalsis is effective in sand because it compacts sand, and more importantly minimizes friction (K.M.D., unpublished observations). Friction in sand causes dilatancy, or the expansion of sand (and increase in pore space) as grains slide past each other (Jaeger and Nagel, 1992). Expansion of the surrounding sand is clearly undesirable when creating a burrow.

Hydraulic pumping leading to localized fluidization is another solution to displacing sand grains without rigid appendages for excavating. In Trueman's (Trueman, 1968) description of the dual-anchor system of burrowing used by bivalves, closure of the valves forces fluid from the pericardial cavity into the foot, dilating the foot to form an anchor (Trueman, 1966) (Fig. 4). At the same time, water from the mantle cavity is ejected and liquefies the sand around the shell, facilitating movement as the shell is pulled toward the foot. Fluidization around the shell of *Ensis directus* was recently shown by Winter et al. (Winter et al., 2012), although their conclusion that valve closure caused grain collapse and pore-water flow toward the animal is clearly refuted by Trueman's (Trueman, 1967) data

showing an increase in pore-water pressure around *Ensis arcuatus* corresponding with valve closure. Ejection of water from the mantle cavity has been shown for many different bivalves burrowing both in sands and in muds (Trueman, 1968), and is consistent with localized fluidization in sands and hydraulic fracture in muds (Fig. 4). Reduction of friction by *T. mucronata* through peristalsis (K.M.D., unpublished observations) suggests a similar function for ejection of water by bivalves – water not only locally fluidizes sands but also may lubricate shell movement to reduce friction. Given that the burrow is initially extended and expanded by the foot, it seems plausible (but is yet untested) that lubrication to reduce friction may be more important than fluidization to create space for the shell (Fig. 4B).

These mechanisms of burrowing in sands – bulk fluidization, excavation, localized fluidization, and grain rearrangement and compaction – depend on body size, depth in sediments and morphology. The limited space created by localized fluidization and grain rearrangement and compaction limits this mechanism to fairly small animals. Larger animals use bulk processes like fluidization and excavation, with bulk fluidization being more depth limited. Excavation requires application of tensile stresses, e.g. by appendages or mouthparts, whereas compaction is easier for animals with a hydrostatic skeleton.

#### Locomotion through heterogeneous sediments

So far, I have focused on the two extremes of granular material – muds that are dominated by cohesion of the organic matrix and sands that lack cohesion and are dominated by gravitational forces. Most sediments fall in between these two extremes and likely exhibit more complex mechanical responses that depend on spatial scale and magnitude of forces. Lugworms, for example, construct J-shaped burrows in sediments that range from muddy to coarse sands. Behavioral patterns of irrigation, burrowing and defecation are similar for lugworms in different sediments, although pore-water pressures and advection vary substantially, from fairly even flow of pore water through permeable sands to plumes of pore water emerging from the sediment–water interface, likely resulting from hydraulic fracture of low-permeability sediments (Volkenborn et al., 2010).

#### Boring into hard substrata

Although boring lifestyles have evolved in numerous taxa, including sponges, gastropods, annelids (including sipunculans), shrimp and barnacles, I will focus primarily on bivalves here, as they exhibit considerable diversity in boring mechanisms and allow direct comparison with burrowing. Even within Bivalvia, boring has evolved numerous times from both infaunal and epifaunal ancestors, with groups exhibiting varying levels of behavioral and morphological specialization (Ansell and Nair, 1969).

On one extreme of specialization, shipworms have highly modified vermiform morphologies with reduced shells. Instead of opening and closing at one hinge, the shell articulates on opposite sides, enabling a rocking movement that rasps wood (Denny and Nelson, 2006). At the other extreme, Ansell (1970) describes the facultative borer *Petricola pholadiformis* as using a very similar cycle of movements and pressure fluctuations when burrowing in sand and boring in compacted clay and chalk (Ansell, 1970). When boring in consolidated substrata, downward movement of the shell abrades the burrow walls, whereas most burrowing bivalves close the shell before movement to reduce friction (Trueman, 1968). Although boring and burrowing bivalves both exhibit periodic mantle cavity pressure fluctuations corresponding with shell opening

and closing and both move forward in discrete steps, the movement patterns differ to apply versus avoid friction to burrow walls. Borers open their shells while moving forward to scrape the burrow wall, whereas a closed shell reduces friction for burrowers.

Mechanical boring relies on abrasion, and most boring bivalves have ridges and rasping structures on their shells for this purpose. The patterns of movement and muscles driving these movements vary considerably among taxa, however. For *P. pholadiformis*, abrasion is achieved by antero-posterior rocking; the pholad *Zirphaea* uses similar movements but the rocking stage is followed by rotation to increase abrasion (Ansell and Nair, 1969). Ansell and Nair (Ansell and Nair, 1969) suggest that borers that evolved from infaunal burrowers use adductor muscles whereas borers with epifaunal ancestors use their more powerful byssal retractor muscles to move the shell along the long axis of the burrow. This evolutionary convergence highlights the functional importance of powerful muscles in applying abrasive forces.

Although borers have traditionally been characterized as using either chemical or mechanical means, new data indicate that many taxa use both. Early studies based characterization on morphological features – soft-bodied animals that lack any obvious hard scraping device most likely are using a chemical mechanism. Species found only in carbonate substrata and not in rocks, clay or wood are likely to be chemical borers, as acid secretion dissolves carbonate. Similarly, animals such as the mytilid *Adula* that are limited to softer clay and chalk are likely mechanical borers (Owada, 2007). Increasingly, however, new evidence is suggesting that animals presumed to be mechanical borers, e.g. *Petricola*, have pallial glands consistent with chemical boring (Morton and Scott, 1988) and that those presumed to be primarily chemical borers, e.g. the mytilid *Lithophaga* spp., at least have representatives that use mechanical means (Fang and Shen, 1988).

Pallial glands, which have secretory granules and are located along the edge of the mantle of chemically boring bivalves, do not secrete acid. Instead a calcium-binding mucoprotein is used to bore chemically into carbonate rock (Jaccarini et al., 1968). Acid secretion both by the gastropod *Nucella lamellosa* to bore through bivalve shells and by the polychaete boneworms *Osedax* sp. is achieved using vascular H<sup>+</sup>-ATPase proton pumps that secrete protons produced from hydration of metabolic CO<sub>2</sub> by the enzyme carbonate anhydrase (Clelland and Saleuddin, 2000; Tresguerras et al., 2013).

#### Perspectives and conclusions

Mechanisms of burrowing and boring, or the mode of failure of the solid, depend primarily on the mechanical properties of the medium (Fig. 5; Table 1). Boring is distinguished from burrowing by the hardness of the substratum. Elastic muds fail by fracture, but on small scales especially, surface muds are loose aggregates that can be rearranged or compacted enough for small animals to move through without fracture. Excavation of mud involves pulling grains or aggregates away from the matrix, and while data are lacking, it seems likely that crack branching during fracture of the organic matrix frees particles that can then be excavated. Excavation of sand requires overcoming gravitational resistance, and cohesion is low enough that burrow collapse can be problematic. Fluidization is limited to granular materials with high permeability and low cohesiveness.

Many burrowing behaviors, however, are effective in multiple materials that fail by different mechanisms and appear to depend more strongly on body size and morphology. Small animals displace grains plastically in both sand and surficial aggregates of mud with movements such as body undulations (Fig. 5). Wedge-shaped and



Table 1. Summary of key features of different mechanisms of burrowing and boring

Mechanism of burrowing/boring	Dominant mechanical behavior	Material	Body size	Depth limitation	Morphology/behavior	Organism
Fracture	Elastic	Mud	Medium	Weak, increased work (elastic and fracture)	Wedge-shaped, expandable anterior	Worms, bivalves, gastropods, e.g. <i>Nereids</i> <sup>1</sup>
Bulk fluidization	Granular	Clean sand; sand/mud	Large	Strong, weight of overlying sand, increased pressure with depth	Fast-moving; mechanism to move fluid	Sandfish <sup>2</sup> , large predators, e.g. gray whales <sup>3,4</sup>
Localized fluidization with compaction	Granular	Sand	Medium	Weak, increased work (due to increased compaction)	Wedge-shaped, expandable anterior, mechanism to move fluid	Bivalves, e.g. <i>Ensis</i> <sup>4</sup>
Fluidization with excavation	Granular	Sand	Medium	Strong, weight and settling of sand	Fast-moving	<i>Emerita</i> <sup>5</sup>
Excavation	Plastic	Sand, mud	Medium-large	Weak, increased work to transport sediment	Appendages to pull and manipulate grains (including mouthparts for bulk feeding)	Crustaceans, e.g. burrowing shrimp <sup>6</sup> , isopods <sup>7</sup>
Localized grain rearrangement and compaction	Plastic	Sand, mud	Small-medium	Strong, overlying weight in sand; compaction in mud	Varied	Likely varied, e.g. <i>Armandia</i> <sup>8</sup> , <i>Thoracophelia</i> <sup>9</sup>
Mechanical boring	Plastic, hard	Rock, clay, wood, carbonate	Varied	Very weak or none	Ridges, hard structures for scraping; modified musculature for rotation/rasping	Bivalves, e.g. pholads <sup>10</sup>
Chemical boring	Hard	Carbonate	Varied	Very weak or none	Glands to secrete Ca <sup>2+</sup> -binding mucopolymer; proton pump for secreting acid	Bivalves, gastropods, sponges, polychaetes, e.g. <i>Osedax</i> <sup>11</sup>

Depth limitation is considered strong if mechanisms operate only near the sediment-water interface and weak if the mechanism is used at a range of depths even though the work to burrow increases with depth. \*Not a true burrower; <sup>1</sup>(Dorgan et al., 2005); <sup>2</sup>(Maladen et al., 2009); <sup>3</sup>(Nelson et al., 1987); <sup>4</sup>(Trueman, 1970); <sup>5</sup>(Trueman, 1967); <sup>6</sup>(Brown and Trueman, 1996); <sup>7</sup>(Dorgan et al., 2013); <sup>8</sup>(K.M.D., unpublished observations); <sup>9</sup>(Ansell and Nair, 1969); <sup>10</sup>(Tresgueres et al., 2013).

expandable anteriors are effective both in extending burrows by fracture in mud and in localized grain rearrangement and compaction of sand, and peristalsis effectively reduces friction in both sand and mud (Fig. 4). Excavation works in both sand and mud, and is theoretically feasible for animals of all sizes, although for smaller animals in softer sediments, compaction rather than removal of sediment is likely more efficient. Mechanical borers, which excavate a hard material in which compaction is not feasible, vary considerably in size. That excavating shrimp are among the deepest burrowers as well as being relatively large is consistent with the generality of this mechanism across substrata (mud and sand of varying depths) and body sizes.

Excavation requires some mechanism to pull or scrape grains, whereas fracture and compaction are achieved with compressive forces. Most excavators in sediments are crustaceans with exoskeletons that apply tension to loosen grains with rigid, jointed legs. In contrast, animals with hydrostatic skeletons transmit internal pressures to apply compressive stresses to burrow walls, facilitating burrow wall compaction and burrow extension by fracture. Exoskeletons can, however, be used to apply compressive stresses; for example, by using legs to push the dorsal or anterior surface into the burrow wall. Additionally, animals with hydrostatic skeletons can apply tensile stresses to dislodge particles through hydraulic pumping and localized fluidization or with mouthparts while deposit feeding. Compressive stresses applied to crack walls create tension at the crack tip, and microcracking may release particles from the matrix.

There are of course exceptions to the generalization that body size and morphology determine behavior and that burrowing behaviors are effective both in sand and in mud. For example, the holothuroid *Leptosynapta* uses tentacles to lift and move sand grains when burrowing (K.M.D., unpublished observation), a behavior unlikely to be effective in mud. Local fluidization by *Eupolymnia* and tube ratcheting by *Owenia* (Nowell et al., 1989) are likely also limited to sand (P. A. Jumars, personal communication), and there are undoubtedly many other interesting exceptions as well.

The generalization presented here relies extensively on theory for idealized solids (elastic, granular, plastic) and experiments conducted in simplified analog materials (e.g. gelatin). Natural sediments and soils exhibit more complex mechanical behavior, however, and many burrowing organisms inhabit a range of substrata. New methods of testing the mechanical properties of sediments on scales relevant to burrowers are needed to understand how grain size, organic content and quality contribute to how sediments respond to burrowers. Mechanical failure of solid substrata means success for burrowers and borers, and characterizing the various mechanisms of failure in these natural substrata is critical to developing a mechanistic understanding of bioerosion, bioturbation of sediments and feedback driving animal-sediment interactions.

Acknowledgements

This Commentary, as well as much of the work contained, benefited from insightful discussions with Pete Jumars. I thank Pete Jumars and Susann Grill for helpful comments on the manuscript.

Competing interests

The author declares no competing financial interests.

Funding

This work was supported by funds from the Dauphin Island Sea Lab.

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