Burrow extension by crack propagation

A worm minimizes its energy expenditure as it forges a path through mud sediment.

Until now, the analysis of burrowing mechanics has neglected the mechanical properties of impeding, muddy, cohesive sediments, which behave like elastic solids[1]. Here we show that burrowers can progress through such sediments by using a mechanically efficient, previously unsuspected mechanism — crack propagation[1,2] — in which an alternating 'anchor' system of burrowing serves as a wedge to extend the crack-shaped burrow. The force required to propagate cracks through sediment[1,2] in this way is relatively small: we find that the force exerted by the annelid worm *Nereis virens* in making and moving into such a burrow amounts to less than one-tenth of the force it needs to use against rigid aquarium walls[3].

Using gelatin as an analogue for sediment (on the basis of its similar mechanical properties)[1,2,4] and polarized light to visualize the burrow around *N. virens*, we investigated whether these worms burrow by crack propagation. Gelatin is birefringent, which enables its stress to be analysed[5] during burrowing.

We found that the edges of the burrow were visible and that they showed evidence of a discoidal crack, which was held open by the dorsal and ventral surfaces of the animal (Fig. 1a, b). The arc of the crack extends laterally beyond the setae and anteriorly to the tips of the antennae. Visualization of stress fields by photoelastic stress analysis (for methods, see supplementary information) reveals a force exerted dorsoventrally by eversion of the animal's pharynx against the relatively flat wall of the crack (Fig. 1c).

According to linear elastic fracture mechanics, the stress intensifies at the crack tip, propagating it when the critical stress intensity is reached[1,6]. Here, the everted pharynx acts as a wedge, with the radial force intensified at the tip of the crack, which propagates, allowing the animal to move forward (Fig. 2). The crack's aspect ratio (T/W in Fig. 2) is a function of the material properties of the sediment (the critical stress intensity and Young's modulus). Expansion of a subterminal body portion has previously been considered as an anchor[7]; we infer instead that a terminal or subterminal lateral expansion acts as a wedge in elastic mud.

We measured the maximum force required to propagate a crack as 0.023 ± 0.002 newtons (mean ± s.e.m.; $n = 5$), which is less than 10% of the 'radial' force of 0.6 N that is exerted by a worm against an aquarium wall[3]. Sediment behaves like an elastic solid that deforms under stress, as evidenced by acoustic[8] and bubble-growth experiments[1]. The relatively small forces exerted by growing bubbles in sediment are well predicted by linear elastic fracture mechanics from the mechanical properties of the medium[1]. According to the theory of elasticity, a closer, rigid boundary necessitates greater force for a given displacement, resulting in substantial effects of nearby rigid walls on burrowers.

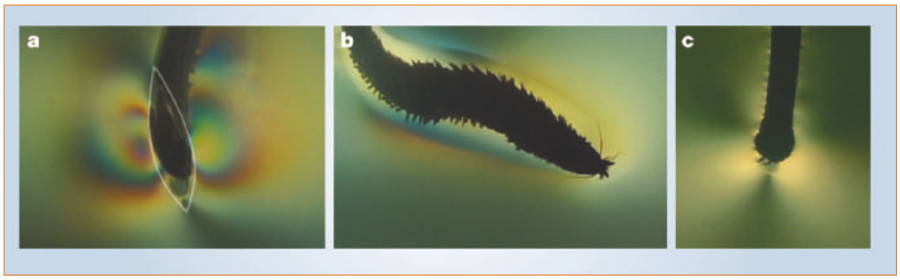

Figure 1 The crack-shaped burrow around the annelid worm *Nereis virens* in polarized light. **a,** Anterior view in crosspolarized light, showing the longer axis of the discoidal crack, which is parallel to the setae, and showing the dorsal and ventral surfaces against the gelatin substrate; the shape of the burrow follows the line encircling the crack. **b,** Dorsal view in crosspolarized light, showing the shape of the burrow around the animal. **c,** Side view in circularly polarized light, showing the stress field dorsal and ventral to the worm, and the crack extending anteriorly.

Crack propagation may also be a likely mechanism of movement for burrowers from several other marine phyla. For example, clams and echinoids, which are both found in muddy sediments, could exploit their wedge-like shape — and some echinoids have been reported to push directly into the frontal sediment, rather than excavating it, and to move through the sediment by means of a repeated rocking motion, unlike more globular, excavating echinoids living in sands[9]. Gammarid amphipods could exploit their resemblance to oblate bubbles[1,2], and subterminal expansions in earthworms indicate that they may burrow, and roots grow[10], by an analogous mechanism.

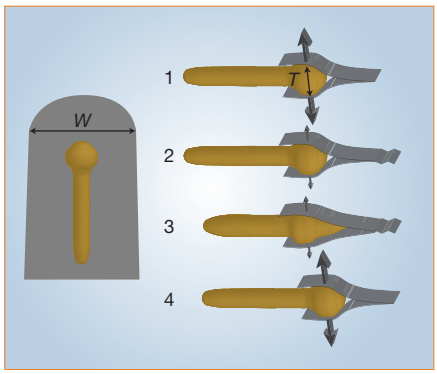

Figure 2 Scheme showing dorsal view of crack shape and lateral oblique views of crack propagation during burrowing. Arrows extending vertically from the crack indicate forces. The worm everts its pharynx and exerts a force normal to the direction of movement (1), which causes the crack to propagate, releasing energy (2). The worm then retracts the pharynx and moves forward into the crack (3) before repeating the cycle (4). *W* is the longer axis of the discoidal crack; *T*, the shorter.

Burrowing by crack propagation also bears on bioturbation, the movement of sediment grains and fluids by living organisms. Bioturbation models have generally ignored the polymeric matrix that leads to elastic behaviour and that keeps sediment grains in the same relative position to each other, instead considering particles as separate, "randomly wandering" elements[11]. But cracks open new surfaces from which animals can feed, leading to unsteady release and uptake of solutes. Crack propagation focuses stresses at the propagating crack tip. These stresses are probably the highest experienced by sediments after their deposition and bear on issues such as the permanence of clay–grain associations and the mechanical protection of organic material from decay.

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