BRIEF COMMUNICATIONS

A pneumo-hydrostatic skeleton in land crabs

A sophisticated dual support system enables a crab to stay mobile immediately after moulting.

Like their aquatic counterparts, terrestrial crabs repeatedly shed their rigid exoskeleton during moulting. But in the case of land crabs, little water is available to provide a temporary hydrostatic skeleton before the new skeleton hardens, and air does not provide the buoyancy necessary to support the animal. Here we show that whenever its exoskeleton is shed, the blackback land crab *Gecarcinus lateralis* relies on an unconventional type of hydrostatic skeleton that uses both gas and liquid (a 'pneumo-hydrostat'). To our knowledge, this is the first experimental evidence for a locomotor skeleton that depends on a gas. It establishes a new category of hydrostatic skeletal support and possibly a critical adaptation to life on land for the Crustacea.

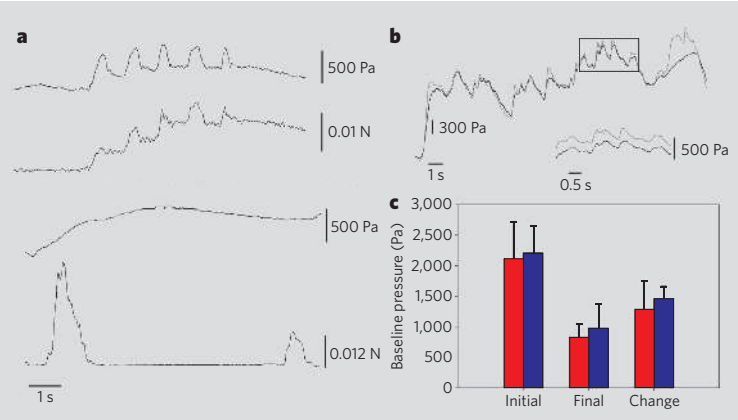

Figure 1 | Haemolymph and gut-gas pressures and movement forces in land crabs after shedding of the exoskeleton. a, Recordings made 12 h (no exoskeleton; top two traces) and 7 d (with new exoskeleton; bottom two traces) after moulting. Pressure correlates with force in the soft but not in the hard crab. For each pair of traces, the upper shows pressure (Pa, pascals) and the lower shows force (N, newtons). **b,** Pressure inside the cheliped (claw; black trace) and gut (grey trace) of a soft, newly moulted crab. Pressure peaks in the gut and baseline pressure correlate with those in the cheliped. Inset, expanded view of boxed trace. **c,** Average pressure in the cheliped (blue bars) and gut (red bars) before (initial pressure) and after (final pressure) removal of air from the gut. Error bars represent standard error.

Arthropods grow by moulting: they secrete a new exoskeleton beneath the old, shed the old skeleton, inflate to a larger size, and wait for the new skeleton to harden[1–3]. Aquatic crustaceans inflate to a larger size by using water; however, like many insects[4–7], the land crab *G. lateralis* inflates its foregut with gas[8,9]. Recently moulted crabs remain soft for several days before the new skeleton hardens sufficiently to support the forces of muscle contraction. Nevertheless, neither aquatic nor terrestrial crabs are incapacitated during this period.

The aquatic blue crab *Callinectes sapidus* maintains mobility by switching to a hydrostatic skeleton[10] — a fluid-based skeleton that is common in soft-bodied invertebrates[11]. Hydrostatic skeletons are arranged so that the force of muscle contraction is transmitted by an essentially incompressible aqueous fluid[11–13]. Muscle contraction increases the pressure in the fluid, causing the deformations or stiffening required for support, movement and locomotion.

We investigated the possibility that the water and air used by *G. lateralis* for inflation might both provide a form of hydrostatic skeletal support, a pneumo-hydrostat, following moulting. First, we simultaneously measured the pressure inside the cheliped (claw) and the force of cheliped flexure. We observed a strong correlation between force and pressure in soft, newly moulted crabs but not in hardened crabs, consistent with hydrostatic skeletal support after moulting (Fig. 1a).

We then simultaneously measured the pressure inside the cheliped and gut during cheliped flexure. (For methods, see supplementary information.) In newly moulted crabs, there was a strong correlation between the pressure in the cheliped and gut during cheliped flexure (Fig. 1b). The average baseline pressures were not significantly different (cheliped: 3,792 pascals (Pa), s.d. = 1,029 Pa, $n = 7$; gut: 2,737 Pa, s.d. = 1,329 Pa, $n = 7$; t-test, $P = 0.12$). The average maximum pressures during cheliped flexion were not significantly different either (cheliped: 808 Pa, s.d. = 563 Pa, $n = 14$; gut: 1,088 Pa, s.d. = 510 Pa, $n = 14$; t-test, $P = 0.18$). These results were as expected, because the body is not compartmentalized and therefore local muscle contraction increases the pressure of the haemolymph throughout the body of the crab. As the gut wall is flexible, this results in increased pressure in the gut as well.

We also examined the contribution of gut pressure to the turgidity of the animal. Removing air from the gut causes a decrease in pressure in both the gut and the cheliped (Fig. 1c). The average baseline pressure in the gut decreased from 2,113 Pa (s.d. = 1,343 Pa, $n = 8$) to 828 Pa (s.d. = 434 Pa, $n = 8$), whereas in the cheliped it decreased from 2,213 Pa (s.d. = 1318 Pa, $n = 8$) to 981 Pa (s.d. = 736 Pa, $n = 8$). The pressures within the cheliped and gut are not significantly different either before or after the withdrawal of air (initial: $P = 0.89$, s.d. = 1,330; final: $P = 0.64$, s.d. = 604; t-test, $n = 7$). These results support the idea that air in the gut provides skeletal support in crabs, after they have moulted, by increasing their body turgor.

We have shown that a land crab can use a compressible gas in conjunction with an incompressible liquid to provide skeletal support. This gas–liquid skeleton represents a new category of hydrostatic skeleton. The reliance on gas by a terrestrial arthropod may be more than an adaptation resulting from low water availability: it may also be a biomechanical adaptation to the greater gravitational forces associated with life on land.

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