Underwater Bipedal Locomotion by Octopuses in Disguise

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As described in Steinbeck's *Cannery Row* (*1*), "the creeping murderer, the octopus… pretending now to be a bit of weed, now a rock… runs lightly on the tips of its arms." Far from the California tide pools in this book, we have observed octopuses that do indeed walk. Individuals of *Octopus marginatus* (from Indonesia) and *Octopus* (*Abdopus*) *aculeatus* (from Australia) move bipedally along sand using a rolling gait. This locomotion differs from their normal crawling, which usually involves several arms sprawling around the body, using the suckers to push and pull the animal along (*2*).

Underwater video allowed kinematic analyses of the strides (*3*). (A stride is defined as two steps or a complete cycle of leg movements in which a leg returns to its initial relative position.) While crawling quickly, *O. marginatus* draws six arms around its body and moves backward on the backmost (ventral) arm pair (Fig. 1A and movie S1). The animal is pushed back as each arm tip alternates rolling along the oral face (sucker edge) of approximately its distal half. The phase is variable (Fig. 1B), sometimes with short periods during which no arm is on the bottom. On average, each arm is on the sand for more than half the stride, which kinematically qualifies these strides as walking (duty factor 0.56, SD 0.08, $n = 4$ strides, two each from two animals). Two individual *O. marginatus*, both ~55 mm in mantle (or body sac) length (ML), moved bipedally at 1.2 and 2.6 ML per s, corresponding to ~0.06 and ~0.14 m/s, respectively. These speeds are slightly faster than the average speed calculated for the same octopuses crawling with several arms (1.1 ML per s, SD 0.36, or 0.06 m/s, SD 0.02; $n = 4$ strides, two each from two animals).

O. aculeatus moves bipedally in a slightly different manner. Walking is preceded by a cryptic display in which the octopus coils and raises the two front (dorsal) arms above its head and generally sits on the other six (this is named the "flamboyant display") (*4*). *O. aculeatus* may then raise the four lateral arms and walk backward using the ventral arms (Fig. 1D and movie S2). Relative to mantle length, *O. aculeatus* has longer arms than *O. marginatus*, and this is evident in their stride. The distal ~75% of the walking arm rolls under the body, sometimes completing more than a full wheel (Fig. 1D, frame 4). The octopus rolls along the sand as if on alternating conveyer belts. The phase of this stride is also variable, but at least one of the two arms is always on the bottom (duty factor: right arm, 0.69; left arm, 0.91) (Fig. 1C), kinematically qualifying this movement as walking.

Bipedal locomotion has been thought to require the opposition of muscle against a rigid skeleton (*5*). Instead, transverse, longitudinal, and oblique bands of muscle in the arms allow octopuses exceptional flexibility, while their internal volume remains constant and provides support (*6*). Bends propagate down single arms from base to tip in a relatively stereotyped wavelike fashion (*7*) that appears to underlie bipedal locomotion in these animals. This motion has been elicited in severed arms, without direct control from the brain (*7*, *8*), and we hypothesize that it allows the octopuses described here to move bipedally with minimal neural feedback.

Crypsis is the primary defense of most octopuses, yet camouflage requires cephalopods to remain still or move only very slowly (*9*). When an octopus moves quickly, it becomes visually conspicuous and must employ unique behaviors to evade its predator's search image (*9*). By walking, both *O. marginatus* and *O. aculeatus* are able to move quickly while using six of their arms to remain disguised: *O. marginatus* perhaps as a rolling coconut and *O. aculeatus* as a clump of algae tiptoeing away.

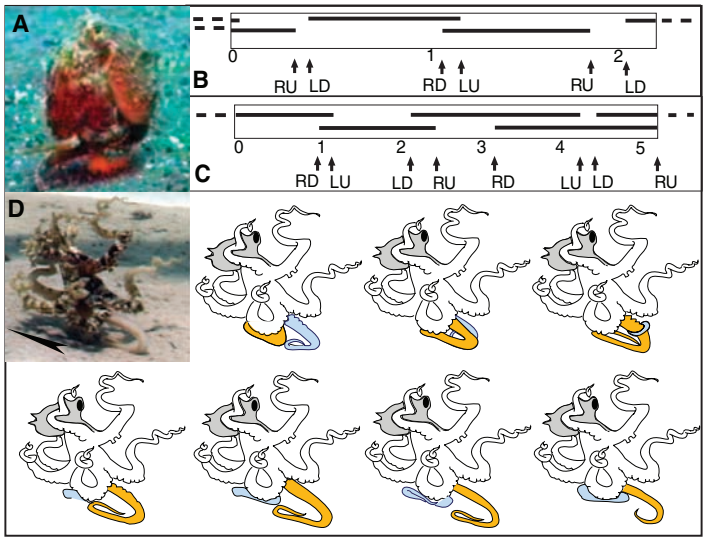

Fig. 1. Kinematics of bipedal movements in octopuses. (**A**) Video frame of *O. marginatus* walking bipedally. (**B**) Phase diagram of *O. marginatus*. L, left arm; R, right arm; U, arm lifted from the bottom; D, arm placed on the bottom. (**C**) Phase diagram of *O. aculeatus*. (**D**) Gait diagram of *O. aculeatus* drawn from video (7/60-s lapse between each panel). The arrowhead in the first frame indicates the direction of walking. Six arms (white) coil, raise off the bottom, and obscure the head and mantle (gray). The right arm (orange) pushes the animal backward throughout the sequence. The left arm (blue) is lifted from the bottom in frame 4 and replaced on the bottom in frame 5. At least one arm is in contact with the bottom at all times. (Video courtesy of Sea Studios, Inc.)

References and Notes

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10. Supported by an American Malacological Society Student Research Grant to C.L.H. and by NSF Frontiers in Integrative Biological Research grant no. 0425878 to R.J.F. Video of *O. marginatus* is provided by Sea Studios, Inc., Monterey, CA, USA (cameraman, Bob Cranston).

Supporting Online Material
www.sciencemag.org/cgi/content/full/307/5717/1927/DC1
Materials and Methods
Movies S1 and S2

11 January 2005; accepted 14 February 2005
10.1126/science.1109616

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