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Splash and grab: Biomechanics of peridiole ejection and function of the funicular cord in bird's nest fungi☆

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ABSTRACT

The bird's nest fungi (Basidiomycota, Agaricales) package millions of spores into peridioles that are splashed from their basidiomata by the impact of raindrops. In this study we report new information on the discharge mechanism in *Crucibulum* and *Cyathus* species revealed with high-speed video. Peridioles were ejected at speeds of 1–5 m per second utilizing less than 2 % of the kinetic energy in falling raindrops. Raindrops that hit the rim of the basidiome were most effective at ejecting peridioles. The mean angle of ejection varied from 67 to 73° and the peridioles travelled over an estimated maximum horizontal distance of 1 m. Each peridiole carried a cord or funiculus that remained in a condensed form during flight. The cord unravelled when its adhesive surface stuck to a surrounding obstacle and acted as a brake that quickly reduced the velocity of the projectile. In nature, this elaborate mechanism tethers peridioles to vegetation in a perfect location for browsing by herbivores.

Introduction

The unusual fruit bodies of the bird's nest fungi (Basidiomycota, Agaricales) were described by Carolus Clusius in 1601 and attracted the interest of pioneering mycologists in the eighteenth and nineteenth centuries (Brodie 1975). Surprisingly, the mechanism of splash dispersal was not recognized until the 1920s, when Martin (1927) deduced that raindrops propelled peridioles from their fruit bodies and that they stuck to surrounding vegetation. Harold Brodie, who studied with A. H. R. Buller, dedicated his research career to the bird's nest fungi (Savile 1989). Brodie's experiments on peridiole discharge included studies on the relationship between basidiome morphology and the splash patterns formed by water ejected from the cups and the distance of peridiole ejection. He also looked at the structure and function of the funicular cord carried by peridioles of *Crucibulum* and *Cyathus* species (Brodie 1975).

The funicular cord is condensed within a structure called the purse that is connected to the inner surface of the

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basidiome (Fig 1). Manipulation of the peridioles with fine forceps is instructive: peridioles can be removed from their basidiomata without opening the purse; the purse ruptures when the hyphae that attach it to the wall of the basidiome are pulled, and this exposes the funicular cord which can be unravelled to a length of a few centimetres. The free end of the funicular cord is widened to form an adhesive pad called the hapteron. In nature, elongated funicular cords are seen wrapped around the stems and petioles of plants to which peridioles are tethered. From these observations, Brodie concluded that the funicular cord remains in its condensed form during the flight of the peridiole, and unravels when the peridiole hits an obstacle. In the absence of high-speed cameras, however, this hypothesis could not be tested. In the present study, we have used high-speed video to examine the details of peridiole ejection and funicular cord function in the bird's nest fungi.

Methods

Specimens

Mature basidiomata of *Crucibulum laeve*, *Cyathus olla*, *Cyathus stercoreus*, and *Cyathus striatus* were collected from landscaping mulch and wood chips on the campus of Miami University, Oxford, Ohio, USA.

Models

Models of *Crucibulum* and *Cyathus* basidiomata of various sizes were crafted by cutting plastic microfuge tubes (1.5 mL volume) with a heated scalpel to heights of 8–15 mm and mouth diameters of 5–8 mm. The base of the tubes was melted and fused to the base of inverted Petri dishes to provide a stable platform. Models resembling the more open types of fruit body produced by *Mycocalia* and *Nidularia* were made with modelling clay (ShurTech Brands, Avon, OH). Mucilage in these fruit bodies was modelled using 0.8 % agar (w/v). Peridioles were modelled with nylon spheres (3/32 inch diameter; Small Parts Manufacturing, Portland, OR); 5–6 of these plastic beads were placed in the models of *Crucibulum* and *Cyathus*; 10–15 beads were placed in the soft agar inside the models of *Mycocalia* and *Nidularia*.

High-speed video

Fresh specimens of basidiomata were pinned to squares of corkboard to maintain an upright orientation during the splash experiments. The corkboard was placed on a rack inside a glass enclosure that protected the camera and lenses from water. The same enclosure was used for experiments with the model fruit bodies. Water drops were released from a burette positioned 1.2 m above the basidiomata to simulate water drops. The diameter of these drops was 6 mm and they hit the fruit bodies with a mean velocity of 4.4 ± 0.1 m s^{-1} ($n = 41$). Most freefalling raindrops are 1–2 mm in diameter (Marshall & Palmer 1948; Lamb & Verlinde 2011). The larger drops used in our experiments are characteristic of water drops shed from wet vegetation. Because the drops were released from a height of 1.2 m they did not reach their terminal velocity (approx. 9 m s^{-1}), nor did they fall long enough to deform and fragment (Gunn & Kinzer 1949; Villermaux & Bosa 2009). In order to study the mechanics of peridiole attachment, basidiomata were surrounded by 5 cm lengths of floral wire. Video recordings of splash discharge were captured at frame rates between 3000 and 6000 frames per second (fps) and minimum shutter speed of 0.17 ms using a tripod-mounted FASTCAM 1024 PCI camera (Photron, San Diego, CA) fitted with a macro lens.

Image analysis and mathematical modelling

For analysis, video clips compiled from 70 to 200 individual image files edited from recordings of tens of thousands of images captured in a few seconds (e.g., 42 000 frames in 7 s at 6000 fps). Analysis of video clips was performed using VideoPoint v.2.5 (Lenox Softworks, Lenox, MA), Image-Pro Plus 6.2 (Media Cybernetics, Bethesda, MD), and proprietary software from Photron. For calculations of peridiole kinetic energy (½ mv^2) and trajectories after discharge, wet weight of peridioles was measured with an accuracy of 0.1 mg. Models of peridiole trajectories were created using MATHEMATICA 6 (Wolfram Research, Champaign, IL). To generate equations for the *x*- and *y*-positions of spore mass as functions of time, the software was used to integrate Newton's Second Law ($\Sigma F = ma$), where the forces were taken to be gravity (mg) in the *y*-direction and Stokes Law drag opposing motion according to the following equation:

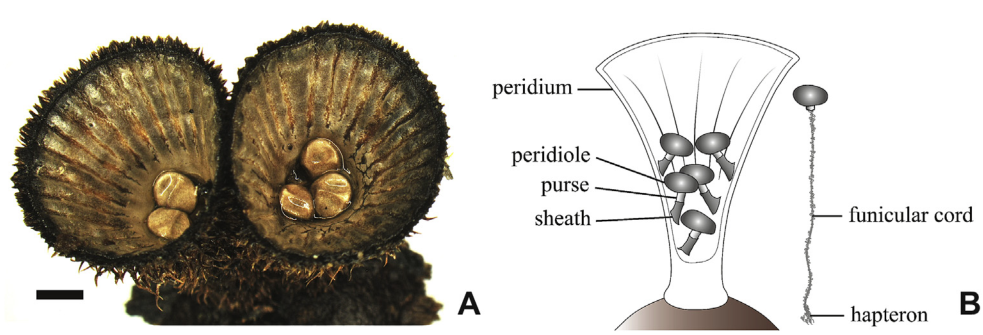

Fig 1 – Structure of the bird's nest fungus basidiome. (A) Pair of fruit bodies of *Cyathus striatus* showing peridioles glistening with surrounding fluid at the bottom of the fruit body. Scale bar, 2 mm. (B) Diagram of sectioned fruit body showing structure of peridioles before discharge and single peridiole following splash discharge. Adapted from Money *et al.* (2013).