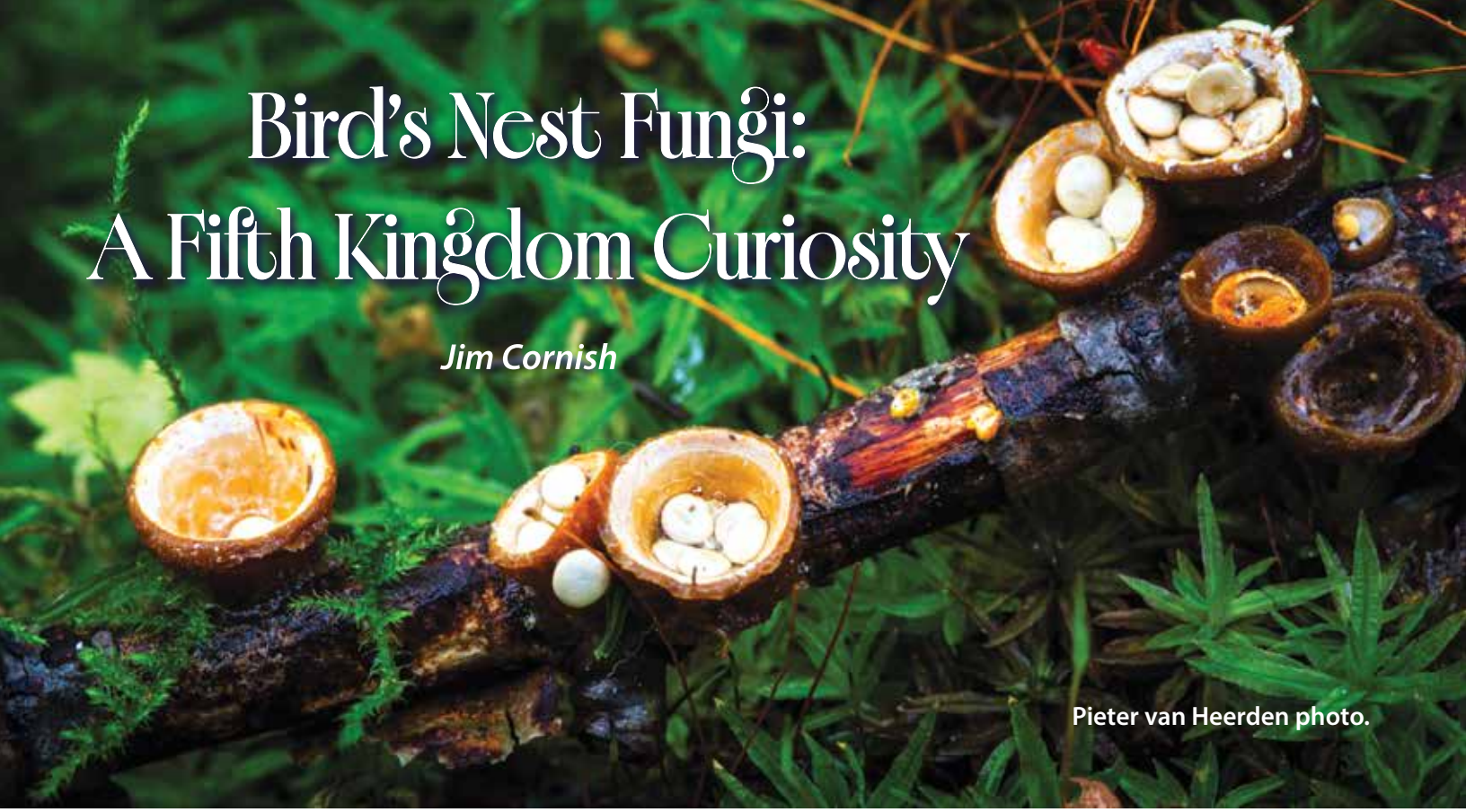
Bird's Nest Fungi: A Fifth Kingdom Curiosity

Jim Cornish



Pieter van Heerden photo.

Resembling miniature nests filled with eggs, bird's nest fungi (BNF) are described as the oddest, cutest, prettiest, most intriguing, and charismatic of mushrooms. Accolades like these make BNF one of the most sought-after mushrooms by mycophiles, amateur and professional alike.

According to Canadian mycologist Harold Brodie (1907–1989), BNF are often found serendipitously and in the strangest of places (Brodie, 1975). But today's increased use of wood in compost and mulch provide ideal substrates making these thimble-sized mushrooms more abundant and widespread and likely easier to find. Hopefully, this article will help readers who are eager to locate and cross these Fifth Kingdom curiosities off a bucket list of must-find species.

Figure 1. A cluster of *Cyathus striatus* showing different stages of development from young nests with lids intact, to egg-filled adult nests, to nests empty of their eggs. Renée Lebeuf photo.

Early Opinions and Classification

Early studies of BNF are "vague" and confusing (Lloyd, 1906). They were first mentioned in *Rariorum plantarum historia* by Flemish botanist Carolus Clusius (1601) who described them as seed-bearing fungi, a notion that sparked controversy among period naturalists. While some naturalists supported Clusius' notion, others argued that since only true plants produce seeds, BNF should be removed from Fungi altogether. This taxonomic state of confusion lasted until egg planting experiments over the decades that followed failed to produce nests.

Carolus Linnaeus settled the disagreement in 1753 when he correctly placed BNF with Fungi (White, 1902). Although Linnaeus showed more interest in flowers and animals than in mushrooms, he managed to name some BNF but mistakenly assigned them to *Peziza*, a genus of ascomycetes well known for their cup-shaped ascocarps.

The first "correct" BNF genus was erected by Irish botanist Patrick Browne

(1756) who assigned the name *Cyathia*, a spelling, or maybe a misspelling, that was changed to *Cyathus* by Swiss biologist Albrecht von Haller (1768) and accepted by Christiaan Persoon (1801). Notable advances in fungi taxonomy were made by Linnaeus's countryman Elias Magnus Fries who added numerous species to *Cyathus*, erected the suborder Nidulariaceae (family Nidulariaceae; Dumortier, 1822) within the now abandoned class Gasteromycetes and circumscribed the genus *Nidularia* (1823). Fries and his contemporaries added eight BNF genera, all of which were dropped by the end of the nineteenth century.

The greatest strides in understanding BNF taxonomy and biology soon followed largely in the works of French mycologist Louis Tulasne and his talented illustrator and brother Charles (1844). Tulasne erected the genus *Crucibulum*, divided *Cyathus* into two sections, accurately described and illustrated the finer structures of BNF eggs and wrote the first monograph on Nidulariaceae (Lloyd, 1906).

The twentieth century saw a remarkable increase in the number of new BNF taxa and significant rearrangement of many species previously but erroneously ranked. American mycologists Violetta Susan White added the genus *Nidula* (1902) while Curtis Gates Lloyd named new species and wrote a short summary of Nidulariaceae (1906). Later in the century, John T. Palmer separated *Mycocalia* from *Nidularia* (1961). Canadian mycologist Harold Brodie also added many news species, further divided *Cyathus*, clarified the mechanisms of egg dispersal and published his "magnum opus" *Bird's Nest Fungi* in 1975.

KEW's Catalogue of Life currently lists 135 accepted species of BNF worldwide. Other indices and older publications list over 300 species, a difference due to the many synonyms in BNF taxonomy or as Brodie jokingly characterized it, "rediscoveries of the same species." Recent molecular studies support the long accepted and related five genera or clades, namely *Cyathus* (107 species), *Crucibulum* (7 species) *Nidula* (7 species), *Nidularia* (9 species), *Mycocalia* (5 species) (KEW, 2026). In 2022, 2 species were moved from *Mycocalia* and placed in the new genus *Retiperidiolia.* Recent studies also show that BNF form a monophyletic group but phylogenetic relationships among genera and their placement remain unclear (Kraisitudomsook et al., 2022). New BNF are being discovered in underexplored parts of cold deserts, mountain habitats, and tropical and temperate forests almost yearly. Some additional species will likely be found hidden in existing species complexes.

In his 1975 book Brodie suggested that BNF were related to the agarics. That notion was supported in 1995 when molecular studies revealed BNF were related to gilled mushroom, puffballs and earthstars. As a result, Nidulariaceae was moved to the Order Agaricales where they are now placed in the suborder Agaricineae, close to Psathyrellaceae (Hyde et al., 2024). The order Nidulariales and class Gasteromycetes are now considered obsolete and no longer used in formal fungal classification (Hibbett et al., 1997).

The Nest and Eggs

Considered modified stems, BNF nests or peridia (Fig. 1) have 1 to 3 layers of tough but flexible hyphae shaped like cups, goblets, or vases. Immature nests often resemble miniature cupcakes or drums covered in tufts of "hair." With age, the nests increase in height while narrowing at the base to create their final vessel-like shape. At maturity, nests typically measure 5–15 mm in diameter and 4–10 mm in height. External nest walls are either bare or hairy and vary in color and shagginess depending on the species. Internal nest walls are either bare, smooth or fluted in texture, shiny or dull in luster, and buff or slate grey in color. Nest rims are bare or trimmed by minute or conspicuous bristles or marginal hairs (Fig. 3) (Brodie, 1975). All of these characteristics are important

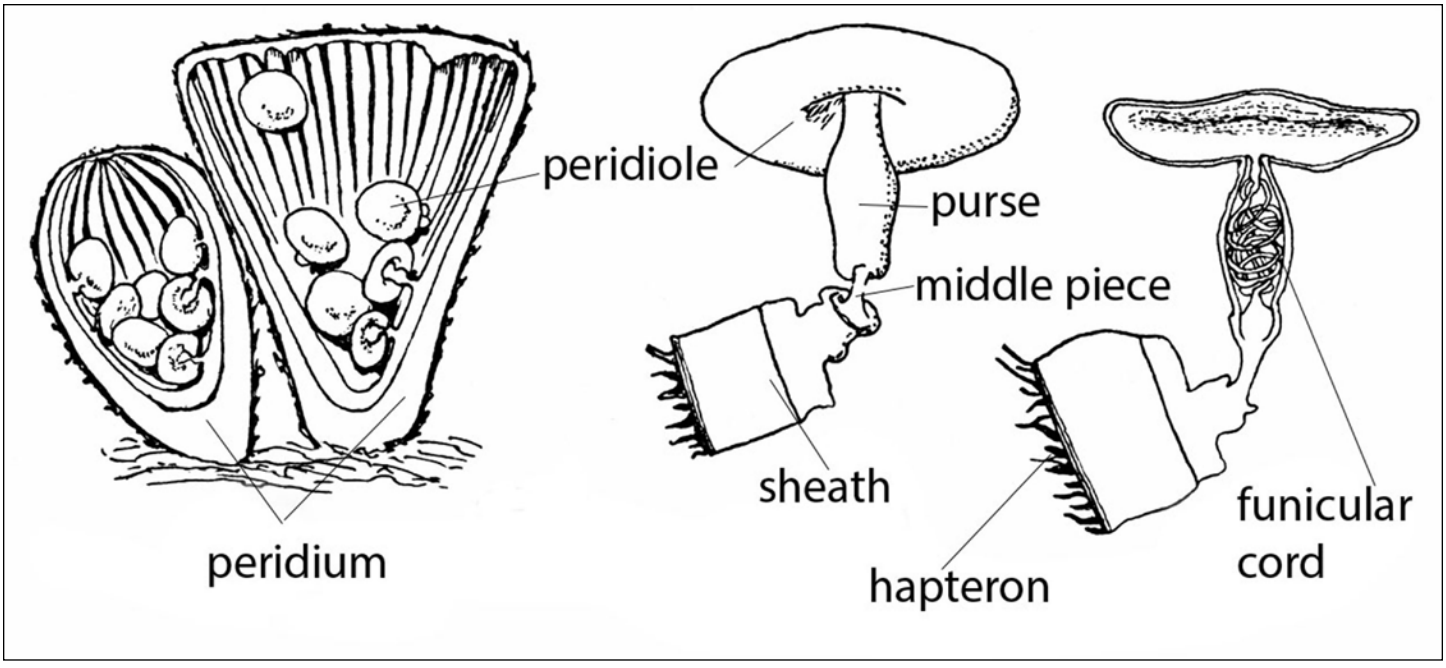


Figure 2. Anatomy of typical bird's nest fungi illustrating nest structure and the specific parts of the peridiole in some species. Source: Wikipedia Creative Commons.

Figure 3. A pair of immature *Nidula candida* showing characteristic external nest features and lids that protect the developing eggs. Renée Lebeuf photo.

considerations in identifying species.

The openings of young nests in *Nidula*, *Crucibulum* and *Cyathus* are covered by a veil-like membrane called the epiphragm that often matches the exterior nest walls in texture and color (Fig. 3). These lids act like veils and protect immature eggs from mycophages and from being prematurely ejected from the nests. With time, the hairs disappear leaving the membranes white and the BNF temporarily more visible. As the nests' mouths widen, the epiphragms rupture and disappear revealing the mature eggs below (Fig. 1) (Brodie, 1975).

Variations within any given fungal species are common and BNF are no exception. Years ago, some variants were mistakenly named as new species. Today, they are recognized simply as intraspecific differences caused by genetics or by environmental factors such as light and moisture that can vary from habitat to habitat (Brodie, 1975). Common intraspecific differences include the color, size and shape of nests and the number of eggs.

When identifying species, it helps to use descriptions that include ranges for these features. Nest "irregularities" are common too. One irregularity in *C. laeve*, for example, is "twinning" which occurs when two adjacent nests share a section of wall or basal stem (Fig. 4). Brodie suggests that twinning happens at the primordia stage when "knots" on a mycelia merge. Another irregularity is "regeneration" in which a new fruiting body grows within the remains of an old nest (Brodie, 1975). While not diagnostically important in distinguishing species, these curiosities add interest to the study of the mushrooms.

Bird's Nest Fungi eggs or peridioles (Fig. 4) are lentil-shaped, although they may appear somewhat angular in crowded nests. Individually, they measure 5 mm or less in diameter and have a thin leathery, or gelatinous outer layer. Egg color varies from colorless to creamy, black, gray, or brown depending on the species (Fig. 4 and Figs. 6–10). Mature eggs contain a gleba, a complex inner mass of spores and basidia intermingled with sterile hyphae typical of gasteroid fungi like puffballs and stinkhorns. The eggs are often neatly arranged in a single layer or multiple layers. Most *Crucibulum* and *Cyathus* nests have between 5 and 8 eggs but 15 or more are not unusual. In *Nidularia*, which have large globose nests, eggs can number around a hundred. The eggs develop at different rates depending on the species. In *Crucibulum*, they mature simultaneously. In *Cyathus striatus*, they mature gradually from the top down while in *Cyathus olla* they mature from the bottom up. A single egg can contain around thirty million spores. Once dispersed from the nests, the eggs are not replaced, so empty nests are common finds at season's end (Brodie, 1975; Hassett, et al., 2015).

Some BNF genera have unique features at the base of each egg. In *Cyathus* and *Crucibulum*, each peridiole bears a short stalk called the purse, which attaches firmly to the inner wall of the egg (Fig. 2). The purse connects to a second stalk,

Figure 4. A pair of *Crucibulum laeve* showing twinning, eight tawny eggs and smooth inner walls characteristic of the species. Jonathon Marks photo.

the sheath, which is anchored to the nest wall. A stretchy middle piece links purse and sheath, and together these three structures form the funiculus. Coiled under pressure inside the purse and attached to the egg is a cable-like cord composed of hundreds of strands of solid hyphae 2–12 cm long. Near the end of the cord is a clump of sticky hyphae called the hapteron. Species within the remaining genera lack these structures altogether (Brodie, 1975).

Spore Dispersal

Although the work of the French botanists Étienne and Edmund Tulasne uncovered the complex structure of BNF eggs, the brothers stopped short of explaining how the dispersal mechanism worked (Brodie, 1975). A role for water in egg dispersal was first mentioned by English naturalist John Ray in 1686, but never explicitly explained until 1927 when American mycologist George Willard Martin found BNF eggs adhering to corn stalks and deduced that they were propelled there by the impact of raindrops on nests clustered on the

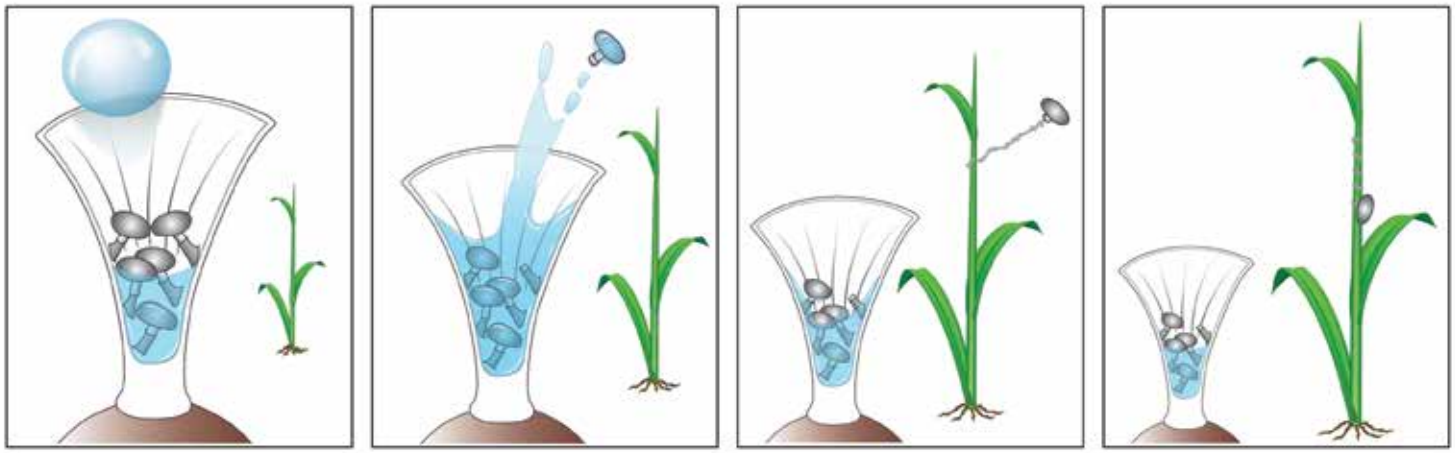


Figure 5. Stages (A, B, C, D) in egg dispersal in bird's nest fungi. Image supplied by Professor Nicholas Money, Miami University, Oxford, Ohio as found in Hassett et al., 2013; https://www.sciencedirect.com/science/article/pii/S1878614613001165.

ground below (Martin, 1927). Although Martin's follow-up lab experiments proved his deductions, his research was largely ignored. It was not until the early 1940s and the experimental work of American mycologist Arthur Buller and later by Harold Brodie that questions around BNF egg dispersal mechanism were finally answered (Brodie 1975; Hassett et al., 2013).

In Buller's explanation, the nests are called "splash cups," a label used in some bryophytes that rely on water for sperm and gemma dispersal and indicative of the importance nest shape plays in spore dispersal (Brodie, 1975). As Brodie explains and Money's diagram illustrates, the process begins when a raindrop, or a waterdrop falling from overhead vegetation, strikes the rim of a mature nest (Fig: 5A). The cup's funnel shape directs the drop and a proportion of its kinetic energy toward the nesting eggs. This energy and the resulting backsplash combine to dislodge one or more eggs from the nest. This forceful action separates the egg's purse from the sheath and the middle piece from the nest wall. Now free, the egg travels in a parabolic trajectory a meter or two away from the nest (Fig. 5B). During the flight, the funicular cord either remains coiled within the purse or uncoils and trails the ejected egg. If a stem, leaf, or other plant debris lies in the path of the egg's trajectory, the sticky hapteron snags it (Fig. 5C). The egg's forward momentum then swings it around the plant like a tetherball to firmly hold the egg in place. If the momentum is insufficient, the snagged egg might simply dangle like a pendant from the plant (Fig. 5D). Species that lack a funicular cord (namely those of *Mycocalia, Nidula*, and *Nidularia*), have eggs covered in mucilage that holds them fast to impacted surfaces (Brodie 1975; Hassett et al., 2013). If you find a nest with missing eggs, you are likely to find the eggs stuck to or hanging from nearby vegetation or other nearby standing objects.

Given that the entire egg ejection takes less than a second, it was not until the use of high-speed photography in the late 1950s that the egg process could be seen and Buller's and Brodie's explanation confirmed (Hassett et al., 2013). A high-speed video capturing the process was filmed by Maribeth Hassett and Mark Fischer in Nicholas Money's lab at Miami University of Ohio in 2011. It can be viewed on YouTube (https://www.youtube.com/watch?v=EGlaQhDi5ts). (Alert—make sure your speaker volume is turned down!)

Spore Dispersal and Germination

Spore dispersal via splash cups and domestic animal vectors are mostly local to regional in scale. Long-range dispersal likely occurs via migrating birds, nests on rafting wood, and anthropogenic activity. In a 2021 sequencing study, *Cyathus* specimens collected from North America, Europe, and New Zealand were deemed to be genetically alike, something the authors considered unusual given the distances between sample sites. This genetic likeness, they explained, was likely due to the agricultural and horticultural practices of shipping exotic plants, mulch, and soil that contain BNF eggs, spores, or living mycelium internationally (Kraisitudomsook et al., 2021).

Once the eggs are ejected from a nest, the spores must be freed and deposited in an appropriate habitat if they are to have any chance of germinating. In many cases, eggs stuck to vegetation are eaten by grazing animals. In dung-loving species like *C. stercoreus*, the eggs require temperatures around 40°C to germinate and take advantage of the warm digestive tracts of animals, and later the animals' feces as substrates, to "sprout" and produce new nests.

Although *C. stercoreus* is commonly seen in domestic animal pastures and manured soils used in gardens, this incubated germination likely occurs in fields and forests grazed by wild herbivores too. Eggs that do not require grazing to germinate likely dry out where they hang. As the eggs' coverings split, escaping spores are picked up by passing air currents and carried aloft to settle and possibly germinate further afield (Dickinson and Lucas 1979; Hassett et al., 2013).

Habits and Habitat

Bird's nest fungi grow alone, in clusters or crowded colonies on wood, dung, mulch, manured soil, and plant-based detritus in moist and shaded locations or open areas. Their mycelial cords or rhizomorphs quickly invade substrates and aggressively travel through soil. BNF are also geotropic, i.e. they use their sense of gravity to tilt their cup openings upward to catch the waterdrops essential for spore dispersal. Wild habitats include surfaces along the margins of tree canopy openings where raindrops and water drips from leaves can easily strike the

Figure 6. A cluster of *Crucibulum laeve* showing various stages of BNF development. Renée Lebeuf photo.

nests on the ground below (Brodie, 1975).

Geographical Distribution

Bird's nest fungi are cosmopolitan and grow on all continents except Antarctica. Their distribution is limited to specific climatic and biological zones and habitats where environmental characteristics such as sufficient water and light are optimal. Some species are believed to be endemic, which means they have evolved in isolation and occur nowhere else in the world. Of the species featured here, *Crucibulum laeve, C. striatus,* and *C. olla* are circumpolar and abundant in temperate zones but rare in the tropics. *Cyathus stercoreus* has a cosmopolitan distribution and is common in North America, but rare in similar habitats in Europe where, in several countries, it is considered an endangered species (Brodie, 1975; Patel, 2018; Kraisitudomsook et al., 2021).

Toxicity and Edibility

While BNF contain bioactive secondary metabolites that might be poisonous to some insects, they are harmless to living plants, animals, or humans, so controls on their growth are unnecessary. They are helpful in gardens where they can control bacteria and fungal pathogens and contribute to decomposition and nutrient cycling in the soil. Given their miniature size and tough walls, BNF are not edible although there are reports of them being used in indigenous ceremonies (Elkhateeb and Daba, 2021) .

Evolution of BNF

Studying the origins and diversification of fungi is often difficult due to morphological simplicity and a scanty fungal fossil record (Hibbett et al., 1997). Our current understanding of BNF evolution is based on Cenozoic aged Dominican and Baltic amber fossils dating back at least 30–45 million years (Poinar, 2014).

Recent DNA sequencing suggests that bird's nest fungi evolution involved a "high degree of developmental integration and a large number of differentiated tissues" that likely evolved "by elaboration from simpler Gasteromycetes morphologies" that

Figure 7. A cluster of *Cyathus striatus* showing distinctive striate inner wall. Stephen Mudge photo.

involved ancestors that changed their stem morphology into "nests" and spore-bearing gills into lintel shaped "eggs" (Hibbett et al., 1997).

The first study dedicated to resolving the phylogenetic relationship among BNF and estimating the ancestral states of the Nidulariaceae was conducted in 2024 (Kraisitudomsook et al., 2024). Trait evolution studies suggest that the ancestor of extant species was likely a gasteroid fungus with a peridium similar to what is found in the genera *Nidularia*, *Mycocalia*, and *Retiperidiolia* today. Interestingly, Brodie asserted that these complex changes are "irreversible" and unlike some other fungi features, could have evolved only once (Brodie, 1975).

Species Profiles

Crucibulum laeve (common or white bird's nest fungus)

Crucibulum was the third BNF genus to be described but it was incorrectly placed in *Peziza*, an ascomycete genus known for its cup-like ascocarps. *Crucibulum* comes from the medieval Latin word *crucibulum*, meaning "an earthen pot used to melt metals." *Laeve* comes from Latin and means "smooth," referring to the nest interior wall.

Nest Exterior: Size: Up to 10 mm in height and diameter. Shape: globose becoming broadly cup- or goblet-like. Layers: 2. Texture: velvety, no setae. Color: often shiny. Tawny yellow becoming darker with age. Texture: bald to slightly velvety. Epiphragm: membranous, velvety with coarse yellow to orange hairs turning white with age and then disappearing. Nest Interior: Color: White or pale grey. Texture: bald and smooth. Eggs: 5–8 or more per nest, 1–2 mm in diameter, ellipsoidal, tan or buff, and smooth to slightly wrinkled. Habit: Saprobic. Alone, scattered, or clustered in colonies. Habitat: old matting, dung, decaying woody debris, nut shells. Never on soil. Distribution: circumpolar in temperate-zones (Brodie, 1975; Barron, 1999).

Cyathus striatus (fluted bird's nest)

Cyathus was the first genus to be described and placed in Nidulariaceae. It is the largest and most diverse genus with 94 accepted species grouped according to some obvious similarities. The *striatus* group has distinct furrows on the interior wall of the nest. *Cyathus* comes from ancient Greek and means "a small ladle." *Striatus* comes from Latin and means "streaked or grooved" and refers to the texture of the nest interior.

Figure 8. A cluster of *Cyathus stercoreus* showing smooth buff inner wall. Renée Lebeuf photo.

Nest Exterior: Shape: Vase (slender base flaring upwards), rim margin with short but distinct setae. Size: up to 20 mm tall and up to 10 mm wide, Layers: 3. Texture: upward and downward pointing irregular shaggy or woolly hairs. Color: grey-brown to orange-brown. Epiphragm: covered in pointed hairs, becoming bald and white with age. Nest Interior: Color: pale grey to greyish brown, shiny. Texture: grooved and bald. Eggs: 2 mm, roughly triangular, white to grey, smooth. Habit: saprobic, scattered, or clustered. Habitat: softwood mulch, bark, and fallen branches, in open forest and trail margins. Distribution: widespread in temperate zones (Brodie, 1975; Barron 1999).

Cyathus stercoreus (dung-loving bird's nest)

Cyathus stercoreus is distinguished by its shaggy outer wall and black eggs that lack an outer coating. *Cyathus* comes from ancient Greek and means "ladle." *Stercoreus* comes from Latin and means "of dung" on which it commonly grows.

Nest Exterior: Shape: inverted cone. Size: up to 15 mm tall. Layers: 3. Texture: shaggy, sometimes with a tufted untidy appearance. Color: buff to yellow-brown, becoming black with age. Epiphragm: conspicuous, shaggy, red-brown, disappears with age. Nest Interior: Color: buffy brown. Texture: very smooth, lacks a tunica. Eggs: 4–8 mm wide, lead grey to blue-black. Habit: saprobic; solitary or mostly clustered. Habitat: pastures, parks and gardens on dung and heavily manured soils. Distribution: worldwide (Brodie 1975; Barron 1999).

Cyathus olla (gray bird's nest)

Cyathus olla is one of the largest BNF and distinguished by wide flaring nest openings, large eggs, smooth textures, and fine hairs on the outer next walls. It was first included in the genus *Peziza* but moved to *Cyathus* by Peerson in 1801. The specific epithet *olla* means "a squat rounded pot."

Nest Exterior: Size: large, up to 18 mm tall and 12 mm wide. Shape: flaring inverted cone, wavy margins. Layers: 3, thick. Texture: smooth, covered in appressed fine hairs, not shaggy. Color: cream to buff brown. Epiphragm: buff brown turning white with age. Nest Interior: Color: lead grey to blue-black fading to pale gray. Texture: very smooth, transverse ridges. Eggs: 8–10 in number, up to 3.5 mm wide, initially silver grey and covered in transparent outer coating. Habit: saprobic, clustered. Habitat: fallen dead twigs, rotting

Figure 9. A cluster of *Cyathus olla*. Notice how growing so close together distorts the nest shape. Renée Lebeuf photo.

timber, manured soil, and coastal dunes. Distribution: worldwide (Barron 1999; Emberger, 2022).

Nidula candida (jellied bird's nest fungi)

Nidula candida is the most common bird's nest fungus in the Pacific Northwest extending from Alaska to California. *Candida* is from Latin meaning "white or bright."

Nest Exterior: Size: 10 to 15 mm tall, 0.3–0.8 cm across. Shape: cylindric or cushion-shaped becoming mug-shaped or flowerpot-shaped when mature, recurved rim at maturity. Layers: tough and persistent. Texture: whitish beneath a gray to brown or dull cinnamon scurfy or shaggy layer. Color: grey to dark buff. Epiphragm: tufted, yellow-brown. Nest Interior: Color: white to yellowish or brown. Texture: smooth. Eggs: 1.5–2 mm wide, light grey-brown, and smooth. Habit: Gregarious to clustered. Habitat: branches, stumps, and woody debris. Distribution: primarily a North American species confined to Pacific Northwest south to California (Petersons et al., 2026).

Acknowledgments:

Canadian mycologist Harold J. Brodie wrote a very readable book on BNF that is available at some online bookstores for around $30.

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Figure 10. A cluster of *Nidula candida* with its distinct nest features. Renée Lebeuf photo.

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