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Woody desert puffballs of the Pacific Northwest 1: *Chlamydopus meyenianus*

Lorelei L. Norvell¹, Joseph F. Ammirati² & Scott A. Redhead³

¹Pacific Northwest Mycology Service, 6720 NW Skyline Boulevard, Portland, OR 97229-1309 USA.

²Department of Biology, 235 Johnson Hall, University of Washington, Seattle, WA 98195-5235 USA

³Biodiversity (Mycology & Botany), Agriculture & Agri-Food Canada, Ottawa, ON K1A 0C6 CANADA

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Corresponding author: L.L. Norvell, lnorvell@pnw-ms.com. Accepted for publication March 3, 2008.
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Abstract: Observation of a population of *Chlamydopus meyenianus* over a fifteen-year period provides insights into the development of an infrequently collected woody stalked gasteromycete. Color photographs of *Chlamydopus* collections from an Oregon site along Interstate Highway 84 from 1993–2008 illustrate for the first time its complete development from late spring emergence (with all external tissues intact) to the more commonly encountered ‘bones’ of specimens dried in situ during the summer. Other desert puffballs are also briefly discussed.

Key words: *Basidiomycota*, *Phelloriniaceae*, *Tulostomatales*, *Agaricales*, *Artemisia tridentata*, sagebrush, Washington.

Introduction: In North America’s Pacific Northwest, woody desert puffballs inhabit the high-plains desert and arid regions, characteristically in the interior away from the temperate rainforests and humid areas along the Pacific coast. These basidiomycetes survive low

moisture regimes and generally fruit rapidly after early and late summer rainstorms. The basidiospores, which are protected from heat and low humidity by one to several peridial layers, generally develop underground. After emergence above ground, the basidiomes lose

their exoperidia and are rapidly dried by sun and wind. Spores escape through peristomes or ribs torn in the endoperidium (inner spore case). Genera collected from sandy regions along the Columbia and Snake rivers in Washington, Oregon, and Idaho include *Abstoma*, *Agaricus* (*Gyrophragmium*, *Longula*), *Battarrea*, *Chlamydomus*, *Chlorophyllum* (*Endoptychum*), *Disciseda*, *Itajahya*, *Montagnea*, *Phellorinia*, *Podaxis*, and *Tulostoma*. Except for Trueblood (1975a, 1975b) and Oliver and Hosford (1979), little has been published on woody desert fungi in Washington and Oregon despite their avid collection by Pacific Northwest university students and mushroom aficionados.

The 1993 discovery of an unusually large stalked puffball, *Battarrea phalloides* (Dicks.) Pers., in the University of Washington herbarium (Susan Libonati-Barnes s.n.) triggered our current interest in woody desert puffballs. That spring and summer we made several Washington collections from sand dunes along the Columbia River near Vantage, dunes further east in Pot Holes State Park, and sagebrush lands to the east (near Kennewick) and northeast (near Tonasket, ~30 km south of the Canadian border). In mid-summer, the senior author collected more specimens to the south on the Oregon bank of the Columbia River. Species collected during 1993 included *Battarrea phalloides*, *Calvatia cyathiformis* (Bosc) Morgan, *Chlamydomus meyenianus* (Klotzsch) Lloyd, at least two different *Disciseda* species, *Gyrophragmium delilei* Mont., *Itajahya rosea* (Delile) E. Fisch., *Montagnea arenaria* (DC) Zeller, and several *Tulostoma* species. This represents the first in a projected series of papers devoted to the taxonomy, development, and ecology of woody puffballs in Oregon and Washington.

***Chlamydomus meyenianus*:** Over a century ago, Lloyd (1903) reported the presence of *Chlamydomus meyenianus* for the first time from south central Washington, noting that the only previous North American report of the

gasteromycete (originally described from Peru in 1843) was from New Mexico. In transferring Klotzsch's '*Tylostoma*' to Spegazzini's new genus, *Chlamydomus* (now regarded as monotypic, cf. Kirk et al. 2001), Lloyd quoted Piper, the collector who sent Lloyd the Washington specimens in 1899:

"The plant is by no means rare in the drifting heaps of sand in the vicinity of Pasco. As it usually grows, nothing but the peridium is exposed, all the remaining part being subterranean. This point, however, varies with the looseness of the sand, in some cases the wind exposing nearly the entire plant. Where, however, the sand is fairly firm, the whole stipe is underground. The length seems to vary wholly with the amount of loose sand through which it must grow to reach the surface." (Lloyd 1903)

Long & Stouffer (1946), who have provided the most thorough documentation of *Chlamydomus meyenianus* in North America to date, reported its occurrence in desert regions of North America (Arizona, California, New Mexico, Washington; see also Lloyd 1903, 1905, 1906; Coker & Couch 1928, States 1990), South America (Argentina, Peru; see also Spegazzini 1898, Farr 1973, Dios et al. 2004), North Africa, and Australia (see also Lloyd 1905, Cleland 1935, Grgurinovic 1997). The genus has additionally been reported from Oregon and Idaho (Scates 1973, Trueblood 1975ab, Bailey & Bailey 1985, Arora 1986), Bolivia (Lunghini 2001), Costa Rica (Calonge et al. 2005), Mexico (Mahú 1980, Moreno et al. 1995, Martín et al. 2000), South Africa (Bottomley 1948), southeastern Europe and north-central Asia (Sosin 1973), and India (Dring 1973).

Although Long & Stouffer (1946) described *Chlamydomus* as producing a basidiome enclosed within a 'double' peridium, they maintained that the basidiomes lacked a 'true' exoperidium and instead referred to a universal veil that they characterized as:

Six *Chlamydopus meyenianus* collections were found from 1993–2008 lying or growing in loose sand near the sagebrush plant at center. The northern Oregon site overlooks railroad tracks (far left), an abandoned roadbed, and Hwy I-84 (upper right) directly south of the Columbia River and Washington state.

“bizonate, dehiscence circumscissile along the equator, upper portion of volva or volva-cap thin, membranous, very fragile and brittle, verrucose, warts coarse, usually 2×2 mm, thick, quadrangular, normally deciduous in pieces as the stipe elongates, but sometimes this verrucose cap remaining on the endoperidium as a false exoperidium...” (Long & Stouffer 1946)

Given the differential retention of the outer pellis as a membranous pileus cover and volva after basidiome expansion, it would seem that the term ‘universal veil’ is more appropriate. However, as Lloyd (1903), Smith & Smith (1973), Smith et al. (1981), Bailey & Bailey (1985), Arora (1986), and Miller & Miller (1988) all refer to the outermost

tissue as an exo- (or outer) peridium, we do likewise.

Spegazzini (1899) initially described and illustrated (pl. 4) the genus based upon two volvate species, *Chlamydopus clavatus* Speg. and *C. amblaiensis* Speg., with the former lacking an annulus and the latter possessing one. These two have been synonymized with *C. meyenianus*, as the annulus is thought merely to represent the residual universal veil. Based upon a limited taxon sampling and ITS rDNA comparison, Martín et al. (2000) suggest that *C. meyenianus*, previously referred to the *Tulostomataceae*, belongs with *Phellorinia* and *Dictyocephalos* in the *Phelloriniaceae* (*Agaricales*). Cannon & Kirk

(2007), however, note that further molecular studies are needed to support the transfer of the morphologically distinct *Chlamydopus* to the *Phelloriniaceae*.

The chlamydopus from Interstate 84: Since Lloyd's first mention of Piper's Pasco collection in 1903, *Chlamydopus meyenianus* has only rarely been reported from the Pacific Northwest region, even though the stalked puffball inhabits the same barren terrains as the more commonly found woody desert puffballs. One small but productive study site is located along US Interstate 84 at the eastern edge of the Columbia Gorge, approximately three miles east of Arlington, Oregon. It consists of two embankments on either side of the westbound highway lanes between mileposts 140 and 141; the westbound highway is flanked by a northern embankment rising ~7 m before sloping steeply down to the south bank of the Columbia River and a south embankment that rises steeply ~20 m and serves as a median strip separating the upper eastbound lanes. Both areas are covered by shrubby vegetation (primarily Great Basin sage brush — *Artemisia tridentata* — amidst scattered miner's lettuce, lupine, and grasses) covering dry, hard gravelly ground interrupted by the sandy patches where desert puffballs are most likely to occur.

The senior author collected several desert puffballs from this small area over a period of fifteen years. From 1993–1999, the site yielded several *Chlamydopus meyenianus* and *Disciseda* collections as well as 16 *Tulostoma* specimens

thought to represent more than one species. No fungi were found at the site during the next three years, and sometime during the summer of 2002, a small wildfire burned over a portion of the southern embankment. The next year, however, *Chlamydopus* and *Gyrophragmium delilei* were collected during two different visits. A solitary specimen found growing under sagebrush on the unburned portion of the northern embankment on May 10, 2003, was first mistaken for a young *Amanita malheurensis* Trueblood, O.K. Mill. & D.T. Jenkins. When the heavily heavily warted cap and thick white volva were sliced open, however, the specimen was not lamellate, possessing instead the rusty gleba characteristic of *Chlamydopus*.

To our knowledge, no photographs have ever been published showing *Chlamydopus meyenianus* in a fresh state just after emergence with all tissues intact. Plates 1D & 2B–C show the white, soft young basidiome with a relatively thick verrucose exoperidium completely covering the pileus and a short thick stipe emerging from a thick basal volva. The fresh exoperidium was not a 'thin, hyphal sand case [that] breaks up and falls away' as suggested by Miller & Miller (1988); instead, the microscope shows the sand resting only loosely on the surface hyphae (Plate 5H). Likewise, although loose and somewhat friable, the exoperidium was not quite as thin as suggested elsewhere in the literature (*e.g.*, Dring 1973); its ephemeral state appears better explained by erosion caused by wind and sand. Long & Stouffer (1946: 621 & 623) did publish photographs of

PLATE 1—*Chlamydopus meyenianus* specimens from Interstate 84 (*right*). A–C. 'Bones' are typically found in sandy sagebrush areas weeks to months after spring rains trigger fruiting. A&B. [LLN1990521-2]: A—Broken stipe and sand-covered pseudorhiza imply early subterranean development but give no trace of an outer peridium. B—Detail of ruptured endoperidium surrounding the rust-colored gleba in 1-A. C. [LLN1970525] —A single collection containing a bare stipe topped only by a few spores and endoperidial remnants (extreme left), another (center) with intact endoperidial sac, a third (extreme right) with intact sac plus sand-covered basal volva, a fourth (left center) shorter stipe separated from basal volva but with warty exoperidium still covering spore sac, and a fifth (right center) with the shortest stipe, partially exposed gleba, and exoperidium connected to pileus and basal volva. D. [LLN2030511] —The 'definitive' fresh basidiome collected two days after a rain and initially mistaken for a rare desert amanita. (All scales in millimeters.)

dried specimens retaining a warty ‘universal veil’ and ruptured basal volva that illustrate the ‘footed cloak’ of the generic epithet. Virtually all other authors (Lloyd 1903: pl. 10, 1905: Fig. 6; Vasil’kov 1955: 52; Sosin 1973: 129; Mahú 1980: 421; Smith et al. 1981: 253; Arora 1986: 721; Miller & Miller 1988: 55; Moreno et al. 1995: 103; Lunghini 2001: 23–24) have been able to publish only illustrations of ‘bones’ — defined here as dried hard basidiome remnants with or without smooth endoperidial spore cases topping long

fluted stipes. Such bones have long been regarded as the typical form because most specimens are collected well after erosion and disappearance of the exoperidium by sun, wind, and blowing sand.

Previous authors (Dring 1973, Moreno et al. 1995) have cited the fasciculate habit of basidia (present even in well aged bones) as a key character. Our microscopical examinations of the gleba of the fresh basidiome (Plates 4 & 5) confirm that even in young specimens, basidia

PLATE 2—Retention of *Chlamydopus meyenianus* exoperidium as seen in specimens dried *in situ*. The left basidiome (LLN1990521-1) still bears an intact heavily warted exoperidium on the pileus, while the exoperidium is partially detached from the pileus of the right specimen. (LLN1990521-2).

2A—The exoperidium on the shorter specimen extends from pileus to volva, with the endoperidium ruptured to expose the rust colored gleba. Volva of taller specimen (detached from stipe when found) not shown. 2B—Rotation of the shorter specimen shows the exposed smooth endoperidium encasing the spore sac. (Scales in millimeters.)

PLATE 3—*Chlamydopus meyenianus* basidiomes prior to stipe elongation. A—With only pileus disc visible above the sand when collected, this tiny specimen apparently dried before it could elongate. The thinning exoperidium that covers the cap also forms the flaring volva at the stipe base. (LLN1990521-1; scale in millimeters). B. & C. [LLN2030511]—Fresh young basidiome with intact thick exoperidium. B—The white amanita-like ‘mushroom’ with warty pileus, fleshy stipe, and thick flaring volva. (Scale in millimeters.) C—A longitudinal section reveals a powdery rusty-brown gleba containing already mature *Chlamydopus* basidiospores.

PLATE 4—*Chlamydopus meyenianus* [LLN2030511]. A—Exoperidial warts (top) over the endoperidium conceal both immature (whitish) & mature (rust-colored) gleba. B—Although the immature pileus readily separated from the stipe, the stipe and endoperidial base tissues are clearly confluent (arrow). C—Basidial fascicle on thick-walled capillitium. D–F—Thick-walled capillitial threads bear frequent clamp connections. (Scales: A & B = 1 mm; C–F = 10 μm)

PLATE 5—*Chlamydopus meyenianus* [LLN2030511]. A–G—Basidia and basidiospores (A & F mounted in Melzer's solution; the remainder rehydrated in 6% KOH aqueous solution). A—Young barrel-shaped basidia congregate in clusters. B—Thick-walled developing basidiospores atop sterigmata on 4-spored basidium (arrow). C—Immature basidiospore bud and young sterigma (arrow). D—Row of mature 4-spored basidia bearing young basidiospores in one basidial fascicle. E—Immature basidiospores (single at lower left; two on center basidium) in basidial fascicle. F—4-spored basidium bearing thick-walled, compressed, verrucose basidiospores (center). G—Mature verrucose thick-walled subglobose basidiospores ($6.8\text{--}9 \times 7.1\text{--}9.4 \mu\text{m}$; verrucae $\leq 1 \mu\text{m}$) surround a thick-walled capillitium in crowded fascicle; H—Thin-walled exoperidial hyphae inflate to $12\text{--}17.5 \mu\text{m}$ diam from $2\text{--}6 \mu\text{m}$ diam septa. Variably shaped loose hyphal ends are frequent throughout the exoperidial tissue. (All scales = $10 \mu\text{m}$)

and basidioles arise in fascicles along the thick-walled, clamped capillitia, (Plate 4C–F). We also establish that the barrel-shaped to subglobose basidia are primarily 4-spored (Plate 5A, 5C–E).

While the 2003 Oregon basidiome is significant because it was collected fresh with the verrucose exoperidium present in its entirety, dried specimens with exoperidia partially attached had previously been found scattered under sage on the same sandy slope. Four years earlier an immature basidiome bearing a full exoperidium with volva that had obviously dried immediately after barely emerging from the sand (LLN1990521-1, Plate 3A) was collected along with a fully extended bone broken into two pieces (LLN1990521-2, Plate 1A&B). A 1997 collection of seven specimens (LLN 1970525) contained one slightly elongated basidiome with ruptured exoperidium still attached to both pileus and basal volva and another with a warty exoperidium still attached to the pileus but with a missing volva reclaimed only after excavation (Plates 1c & 2). The remaining five specimens resembled the more typically encountered *Chlamydomys* bones with most smooth endoperidial cases intact except for central apical tears exposing the rusty gleba within; one bone was extricated from the sand with the volva still attached (Plate 1c). The loose bone (Plate 6B) found in 2008 on the sand near the sagebrush where the first was collected 15 years earlier gives hope that the population will survive for some time to come.

Collections examined: OREGON, Gillium Co., N of I-84 between mp 140 & 141— LLN1930801-3, LLN1970525-1, LLN1990521-1&2, LLN2030510, LLN2080619. [Norvell (LLN) collection numbers incorporate YYYYMMSS date-based codes (i.e., 2030510 = May 10, 2003). The specimens are currently held in the Pacific Northwest Mycology Service Herbarium.]

Dedication: The authors affectionately dedicate this paper to the indomitable West Virginian transplanted to eastern Washington's Palouse, Jack Rogers.

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PLATE 6—*Chlamydopus meyenianus* continues to fruit in 2008. A—A fencepost flags the *Artemesia tridentata* obscuring the sandy chlamydopus site. B—A solitary bone fragment (LLN2080619) lies on top of the sand imprinted with faint animal tracks. C—Only a few specimens have been found rooting *in situ*; most are found lying on loose sand, scattered by wild animals or the heavy winds characteristic of the east gateway to the Columbia River Gorge.

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