

NORTH AMERICAN DESERT TRUFFLES: THE GENUS *CARBOMYCES*
(ASCOMYCOTA, CARBOMYCETACEAE)

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Abstract. The genus *Carbomyces* was erected by Gilkey to accommodate two species of North American desert truffles, *C. emergens* and *C. longii*. These differ from other hypogeous Ascomycetes in having nonamyloid, brown asci and a gleba of large, thin-walled hyphae, both of which dry in the desiccating desert conditions and disintegrate at maturity to form a powdery spore mass. At maturity the ascomata emerge and are blown about, the spore powder being released as the dried peridium abrades away or breaks. Younger ascomata are eaten by rodents. Because these novel features do not otherwise occur in the Pezizaceae, Trappe erected the monotypic family Carbomycetaceae. Weber discovered that a species assigned to the Gasteromycete genus *Abstoma* by Zeller, *A. longii*, was in fact an Ascomycete. In this paper *A. longii* is transferred to *Carbomyces*, but as the epithet *longii* is already in use in the genus, we assign a new epithet to it, *C. gilbertsonii*, in honor of Dr. Robert Gilbertson, who has devoted much of his mycological interest to fungi of the southwestern deserts.

Keywords: *Abstoma*, Ascomycota, Carbomycetaceae, *Carbomyces*, desert truffles, North America.

The genus *Carbomyces* is endemic to desert habitats in the southwestern United States, principally the Chihuahuan, Sonoran and Mojave deserts. Gilkey (1954a) described the genus to accommodate two new species, *C. emergens* and *C. longii*, characterized by having a two-layered peridium which, when dry, has a "texture somewhat that of carbonized wood" and evanescent brown asci. She placed the genus in the Terfeziaceae, distinguished at that time from other described families of hypogeous Ascomycetes by having a solid gleba with "nest-like areas containing asci" separated by sterile veins. Trappe (1971) erected the monotypic family *Carbomycetaceae* because no other members of the Terfeziaceae had the friable, brown-walled asci or sterile veins of greatly inflated hyphae markedly differentiated from the other ascomatal tissues.

In studies of the Gasteromycetes, one of us (NSW) examined types of species in the genus *Abstoma*. Intact asci containing spores typical of the species were scattered in the insect-grazed, powdery spore mass of the holotype of *A. longii* Zeller (1944). Accordingly, we transfer this species to *Carbomyces*, but the epithet

longii is already occupied, so we propose the name *C. gilbertsonii* in honor of Dr. Robert L. Gilbertson of the University of Arizona for his keen interest in fungi of the southwestern deserts. The most widely distributed species is *C. emergens*. *C. longii* and *C. gilbertsonii* are known only from the holotypes.

Little is known of the ecology of *Carbomyces* species. Most specimens have been found lying loose and dry where wind-blown in places in the desert such as arroyos. Bob Gilbertson found a specimen of *C. emergens* caught in a brush pile in his back yard in Tucson, Arizona (see "Collections Examined" under *C. emergens*). Such specimens evidently emerge as they mature and dry in the desert sun and air. The thin-wall, inflated glebal cells disintegrate with drying to form a powdery mass of cell fragments, asci and spores. As specimens blow about, the peridium ruptures and the spores are released.

Species of *Carbomyces* also have a second strategy for spore dispersal: animal mycophagy. Zak and Whitford (1986) report that fresh ascomata are excavated by rodents, probably the spotted ground squirrel (*Spermophilus spilsoma*).

We thank personnel of these mycological herbaria for loan of collections: U. S. Department of Agriculture, Agricultural Research Service, Beltsville, MD (BPI); New York Botanical Garden, Bronx (NY); Oregon State University, Corvallis (OSC); University of Arizona, Tucson (ARIZ). The junior author wishes to specially thank Dr. Robert Shaffer, former Director, The University of Michigan Herbarium, for use of facilities and help in arranging loans, and Drs. Peggie Hollingsworth and Wilber Bigelow (deceased) of the Scanning Electron Microscope-Electron Probe Analytical Laboratory of the University of Michigan, who made possible the SEM work. Her initial studies of *C. gilbertsonii* were supported by a National Science Foundation grant to Dr. Alexander H. Smith (deceased). These studies were also supported in part by National Science Foundation Grant DEB 9400545 and the U. S. Forest Service, Pacific Northwest Research Station.

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They found ascomata of *C. emergens* *in situ* in and around recent rodent excavations in interdune areas between dunes vegetated with thickets of *Atriplex canescens*, *Prosopis glandulosa* and herbaceous annuals.

Other species of desert truffles form mycorrhizae with annual or perennial plants (Dexheimer et al., 1985; Alsheikh, 1994). Zak and Whitford (1986), however, found ascomata of *C. emergens* *in situ* under *Prosopis glandulosa*, a member of the Mimosaceae. *P. glandulosa* so far has only been reported as arbuscular mycorrhizal (Staffeldt and Vogt, 1975). The Mimosaceae does include genera such as *Acacia* that can have both arbuscular and ectomycorrhizae (Warcup, 1980). Although direct evidence is not yet available, we concur with Zak and Whitford that *Carbomyces* species probably form mycorrhizae with desert shrubs or trees.

MATERIALS AND METHODS

W. H. Long (Zeller, 1944; Gilkey, 1954a) and Zak and Whitford (1986) reported fresh characters for species in the genus. We have translated Long's Ridgway color terminology to the ISCC-NBS standard terminology (Kelly and Judd, 1965). Most other collections had already dried in the field when collected. Terminology on macroscopic structures follows Weber et al. (1997). Dimensions of ascomata are given height first and breadth second.

Free hand sections were cut with a razor blade and mounted for microscopic study in water, 3% KOH and Melzer's reagent, respectively. For scanning electron microscopy, samples of asci and ascospores were pulse-coated for 6 min in a glow-discharge coater with about 300 µm of gold and examined with a JEOL-U3 SEM at 15 or 25 KV. Spores were measured in water mounts from spores naturally released from asci; measurements exclude surface ornamentation. Other structures were measured in KOH mounts.

Names of herbaria containing collections of

Carbomyces spp. are abbreviated according to Holmgren et al. (1990) in the "Collections Examined" sections under each species and listed acknowledgements.

TAXONOMY

Carbomyces Gilkey, N. Amer. Flora Ser. 2, 1: 27, 1954.

Ascomata regular to compressed or bilateral stereothecia, hypogeous, often emerging and detaching at maturity, 2–4 cm in diam., smooth, firm, white to dull yellow or brown, glabrous. *Peridium* with a two-layered ectal excipulum: outer layer a narrow textura intricata of thin, periclinal hyphae; inner layer a textura intricata of periclinal hyphae with cells in the underlying layer often inflated and globose to rectangular. *Gleba* solid, of brown fertile pockets separated by white to olive veins. *Asci* with brown walls, subglobose to globose, with 8 clustered spores, nonamyloid, indehiscent but disintegrating at maturity, randomly embedded in tissue of fertile glebal pockets. *Spores* globose or ellipsoid, hyaline to pale brownish pink, smooth or ornamented with sinuous rods and spines.

Etymology: Latin, *carbo* (carbon) and Greek *-myces* (fungus), the "carbonized fungus" in reference to the dried peridium that has a "texture somewhat that of carbonized wood" (Gilkey, 1954a).

Remarks: the ascomata of *Carbomyces* spp. are solid in fresh specimens and hence are stereothecia (Weber et al., 1997). In ascomata that have dried and blown about the desert, the thin-walled, inflated cells of the gleba and the asci may disintegrate to form a powdery mass of spores and cell fragments similar to that of pulverothecia. However, a true pulverothecium develops as a hollow ascoma which becomes stuffed with loosely arranged ascogenous cells and asci that by maturity disintegrate to leave a powdery spore mass; species of *Elaphomyces* form pulverothecia (Weber et al., 1997).

KEY TO SPECIES OF *CARBOMYCES*

- 1a. Spores ellipsoid *C. longii*
 1b. Spores globose to subglobose 2
 2a. Spores smooth or minutely roughened *C. emergens*
 2b. Spores distinctly spiny *C. gilbertsonii*

Carbomyces emergens Gilkey, N. Amer. Flora Ser. 2, 1: 27, 1954. TYPE: UNITED STATES. New Mexico: Eddy Co., Carlsbad, 2 November 1916, W. H. Long 7840, Gilkey 403b (Holotype: OSC; Isotype: BPI). Fig. 1, A–B.

Illustrations: Gilkey (1954b), p. 786, figs. 6–9; Zak and Whitford (1986), p. 841, fig. 1.

Ascomata hypogeous, single or in clusters, regular to compressed or turbinate stereothecia, 5–30 x 8–40 mm, white to cream color, yellow

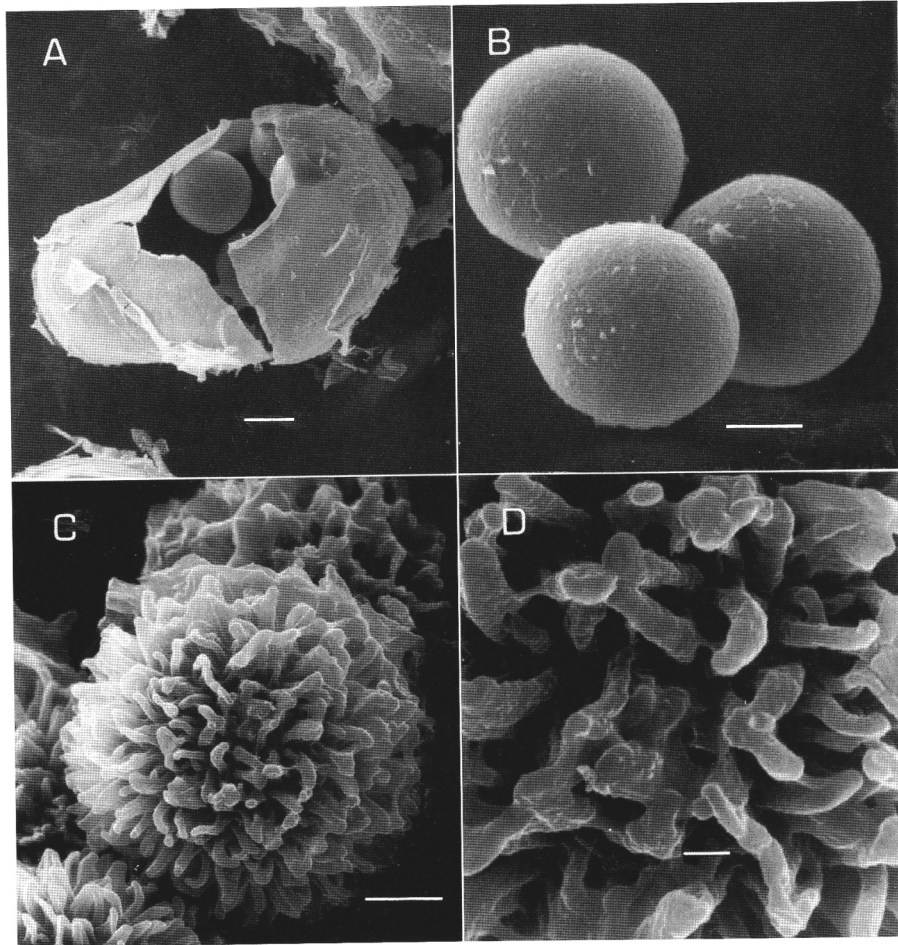


FIGURE 1. A–B. *Carbotomyces emergens*: A, SEM of ascus with spores, Bar = 10 μ m; B, SEM of spores showing minutely roughened surface that appears smooth with light microscopy, Bar = 5 μ m. C–D, *Carbotomyces gilbertsonii*: C, SEM of spore, Bar = 5 μ m; D, SEM of spore ornamentation, Bar = 1 μ m.

or brownish orange, the surface sometimes cracked. Gleba white in youth, at maturity with yellowish brown to moderate olive brown fertile pockets separated by white to grayish yellow tramal veins that tinge yellow when exposed, when mature and dry the fertile pockets becoming powdery. Taste and odor not recorded. *Peridium* with a two-layered ectal excipulum: outer layer a poorly rehydrating textura intricata 30–50 μ m thick, of periclinal, hyaline, somewhat amorphous hyphae 2–4 μ m in diam.; inner layer up to 2000 μ m thick, a textura intricata of periclinal hyphae 10–25 μ m in

diam., the cells often inflated and globose to rectangular, in youth the walls thin and hyaline but by maturity often thickening up to 2 μ m and brown; hyphae in Melzer's reagent light orange. Glebal tissue of light brown hyphae 10–25 μ m in diam. with walls thin to 2 μ m thick, in Melzer's reagent dull brown. *Asci* subglobose to occasionally ellipsoid, ovoid or pyriform, astipitate, subglobose to broadly ellipsoid, 48–69 x 42–57 μ m, 8-spored; walls friable, dark brown, up to 1 μ m thick, overlain by a rugulose to roughened, mucilagenous outer layer 0.25–1 μ m thick, by maturity disin-

tegrating to release spores when dry, in Melzer's reagent pale brown and more or less smooth on the surface. *Spores* globose, 9.5–19 μm in diam., appearing smooth by light microscopy but roughened by SEM, pale brown, the walls \pm 1–1.5 (–2) μm thick and 2-layered: outer layer < 2 μm thick and hyaline, inner layer 1–1.5 μm thick and faintly greenish tinged; spore contents amorphous. No distinctive reaction to Melzer's reagent.

Etymology: Latin, *emergens* (emerging), in reference to the tendency of ascomata to emerge from below ground to the surface as they mature.

Distribution, habitat and season: New Mexico to southern California in the Chihuahuan, Sonoran and Mohave Deserts, in sandy soil and sand hills with *Artemisia*, *Atriplex*, *Prosopis*, and various herbaceous species, often lying loose on soil and where windblown into arroyos, brush patches, etc.; September through April, probably strongly dependant on rainfall patterns.

Additional specimens examined: UNITED STATES. ARIZONA. Pima Co.: Tucson, Santa Catalina foothills, Camino Padre Isidoro, 27 January 1980, *R. L. Gilbertson 12289* (ARIZ, OSC). CALIFORNIA. Imperial Co.: Mohave Desert, Red Rock Canyon, 16 October 1939, *W. H. Long 8689* (BPI, OSC). NEW MEXICO. Bernalillo Co.: Albuquerque, just S. of airport grounds, 1 September 1941, *W. H. Long 9489* (BPI, OSC); near Albuquerque, 4 mi. S. of Belen Ridge, 6 December 1941, *W. H. Long and A. J. Stouffer, Long 9928* (BPI, OSC) and 18 September 1941, *Long 9683* (BPI, OSC); Albuquerque, N. of airport garbage dump, 28 November 1941, *W. H. Long 9914* (BPI, OSC). Chaves Co.: 8 mi. E. of Hagerman, 6 February 1973, *Dan Holland, Trueblood 5320* (OSC); Haystack Mountain, 25 April 1974, *Dan Holland, Trappe 4518*, and 25 April 1975, *Trappe 4519* (OSC); near Roswell, 10 February 1975, *Dan Holland, Trappe 4520* (OSC). Dona Ana Co.: Jornada Experimental Range Headquarters, 8 September 1941, *W. H. Long and A. J. Stouffer, Long 9599* (BPI, OSC); Jornada Experimental Range sandhill area, 7 September 1941, *W. H. Long and A. J. Stouffer, Long 9584* (BPI); Jornada Experimental Range entrance, 13 March 1985, *J. Zak and W. G. Whitford* (OSC); New Mexico State College Ranch, 10 April 85, *J. Zak and W. G. Whitford* (OSC). Eddy Co.: Carlsbad, October 1920, *W. H. Long 6172* (OSC). Luna Co.: 10 mi. W. of

Deming, 9 September 1941, *W. H. Long, A. J. Stouffer and Brigham, Long 9711* (BPI, OSC).

Remarks: *Carbomyces emergens* appears to be the most common and widely distributed member of the genus. It differs from the other two species of the genus in having nearly smooth spores. *Carbomyces longii* and *C. gilbertsonii* are known only from the rather scanty type collections, so at present other differences cannot be noted in any detail.

Carbomyces gilbertsonii N. S. Weber & J. M. Trappe, *nom. nov.* TYPE: UNITED STATES. New Mexico: Dona Ana Co.: Jornada Experimental Range, 11 November 1918, *W. H. Long 8310* (Holotype: NY; Isotype: OSC). Fig. 1, C–D.

Synonym: *Abstoma longii* Zeller, *Mycologia* 36: 628. 1944.

Ascomata up to 2 cm in diam., regular to compressed stereothecia, dark brown, glossy in some places, the peridium with sand inclusions and fragile but mostly persisting. *Gleba* at first soft, by maturity dark brown and flocculent-powdery. *Asci* subglobose, 8-spored, up to 100 μm in diam., with friable, thin, light brown walls, by maturity drying and disintegrating to release spores. No distinctive reaction to Melzer's reagent. *Spores* globose, 20–27 μm in diam. excluding the ornamentation of crowded, sinuous, sometimes forked spines 3–4 μm tall that often adhere together in small clumps; spore walls 1–1.5 μm thick and hyaline in youth, by maturity moderate brown; contents amorphous. No distinctive reaction to Melzer's reagent.

Etymology: in honor of Dr. Robert L. Gilbertson of the University of Arizona, internationally recognized authority on taxonomy of wood-decay fungi and avid collector of desert fungi in the southwestern United States.

Distribution, habitat and season: known only from the type collection from New Mexico, in open sandy dunes with *Prosopis glandulosa*; November.

Remarks: Zeller (1944) described this species as the gasteromycete *Abstoma longii*, because its gleba was filled with a mass of loose, powdery spores. In studying the type collection 34 years later, which by then consisted of broken fragments, however, the junior author discovered a few intact asci. Zeller described the gleba as "at first soft, then dark sepia and flocculent." The gleba of *Carbomyces* is initially solid, a stereothecium, and the asci are

brown. Accordingly we reassign this species to *Carbomyces*. The name *C. longii* already exists, so a new epithet is required.

With its spore ornamentation of prominent spines, *Carbomyces gilbertsonii* is readily distinguished from the other globose-spored species, *C. emergens*, which has smooth or minutely roughened spores.

Carbomyces longii Gilkey, N. Amer. Flora Ser. 2, 1: 27, 1954. TYPE: U. S. A. New Mexico: Lincoln Co.: Oscura area, 18 April 1942, W. H. Long 10103, Gilkey 798 (Holotype: OSC; Isotype: BPI). Fig. 2, A–C.

Illustrations: Gilkey (1954b), p. 786, fig. 10.

Ascomata hypogeous, 2–3 cm in diam., at first white, later becoming pale yellow to pale

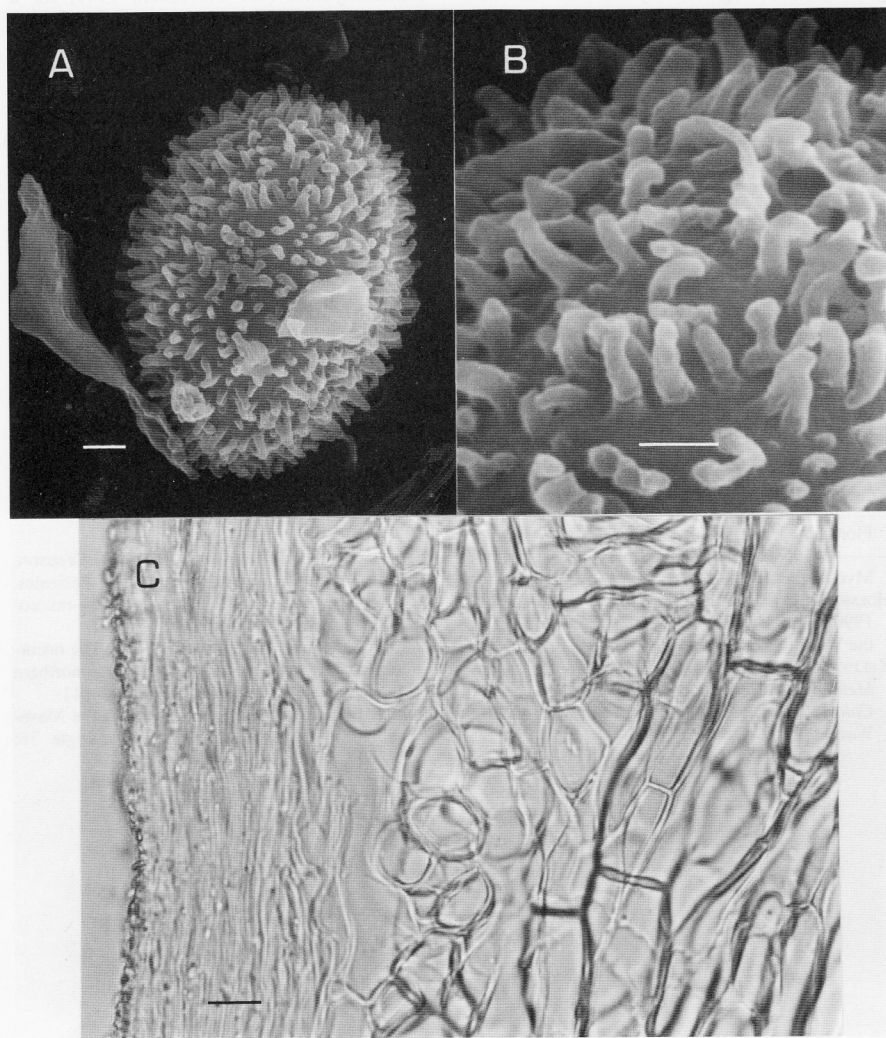


FIGURE 2. A–C. *Carbomyces longii*: A, SEM of spore, Bar = 2 µm; B, SEM of spore ornamentation, Bar = 1 µm; D, light microscopy of peridium in cross section, the narrow outer layer of ectal excipulum to the left, the broad inner layer to the right, Bar = 10 µm.

brown. *Gleba* with brown pockets of fertile tissue separated by moderate olive brown veins, by maturity becoming powdery. *Peridium* with a two-layered ectal excipulum: outer layer a textura intricata 40–50 μm thick, of periclinal, hyaline, thin-walled hyphae 2–4 μm in diam.; inner layer a textura intricata of periclinal hyphae 7–20 μm in diam., the cells often inflated and globose to rectangular, in youth the walls thin and hyaline but by maturity often thickening up to 2 μm , hyaline near the peridium grading to dark brown in the veins between pockets of fertile tissue; no distinctive reaction in Melzer's reagent. *Asci* globose, astipitate, 8-spored; walls friable, brown, smooth, $\pm 1 \mu\text{m}$ thick, by maturity drying and disintegrating to release spores, in Melzer's reagent the walls pale brown. *Spores* ellipsoid, 17–19 x 11–14 μm excluding

the ornamentation of crowded, tapered spines 0.5–1 x 0.25–0.75 μm ; spore walls 1 μm thick, light brown, in Melzer's reagent pale brown, often with fragments of asci clinging to the spines; spore contents with 1–4 guttules.

Etymology: in honor of the southwestern mycologist, William H. Long, collector of the holotype and pioneer in study of southwestern Gasteromycetes (see Stevensen, 1949, for a brief biography of Long).

Distribution, habitat and season: known only from the type collection from New Mexico; April.

Remarks: *Carbomyces longii* is readily distinguished from the other two species of the genus by its ellipsoid spores. Meaningful ascus measurements were not possible, because all asci were fragmented.

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