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Amanita alpinicola sp. nov., associated with *Pinus albicaulis,* a western 5-needle pine

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Abstract—A new species, *Amanita alpinicola*, is proposed for specimens fruiting under high elevation pines in Montana, conspecific with specimens from Idaho previously described under the invalid name, "*Amanita alpina* A.H. Sm., nom. prov." Montana specimens originated from five-needle whitebark pine (*Pinus albicaulis*) forests where they fruit in late spring to early summer soon after snow melt; sporocarps are found mostly half-buried in soil. The pileus is cream to pale yellow with innate patches of volval tissue, the annulus is sporadic, and the volva is present as a tidy cup situated below ragged tissue on the stipe. Analysis of the ITS region places the new species in *A.* sect *Amanita* and separates it from *A. gemmata, A. pantherina, A. aprica,* and the *A. muscaria* group; it is closest to the *A. muscaria* group.

Key words—*Amanitaceae,* ectomycorrhizal, ITS sequences, stone pine, taxonomy

Introduction

In 1954, mycologist Alexander H. Smith informally described an *Amanita* species from the mountains of western Idaho [see Addendum on p. 676]. He gave it the provisional name *Amanita "alpina",* and this name has been used by subsequent collectors of this fungus in Washington, Idaho, and Montana. The taxon is included in Tulloss's key (2008) as "*Amanita alpina* A.H. Sm. *nom. prov.*", and more informally in a key to *Amanita* in the Pacific Northwest (Lindgren 2014). We examined Smith's notes (1954) and exsiccati for herbarium collections A.H. Smith 45357 and 44902 in MICH (Thiers 2014). In these notes, Smith described a pale yellow to whitish *Amanita* that fruits almost entirely

under the duff. The collection information states that it was associated with "*Pinus flexicaulis*" at high elevations; however this is not a valid name for a tree species. He most likely meant *P. albicaulis* Engelm. (whitebark pine) and not *P. flexilis* James (limber pine), because *P. albicaulis* occurs at high elevations in the Seven Devils Mountains (Arno 2001), the original location of one Smith collection. Both pine species are in *P.* subsect. *Strobus* (Hao et al. 2015), and they host some of the same species of ectomycorrhizal fungi (Mohatt et al. 2008, Cripps & Antibus 2011).

Recent collections of a pale yellow *Amanita* found under *P. albicaulis* at high elevations (2500–3000 m asl) in Montana fit Smith's description morphologically and ecologically. Similarly to Smith's fungus, basidiocarps of the Montana fungus also occur almost totally below the soil surface, and as Smith remarked, the fungus appears to "shed its spores while completely subterranean." In addition, the presence of a thin, fragile ring is sporadic or as stated by Smith "the annulus does not form in about half of the basidiocarps." While there have been other reports of this taxon from Washington and Idaho, most do not appear to have been vouchered, photographed, or described while fresh, so we are limiting our observations to those specimens with complete information. Typically such collections have been called "*A. alpina*" or relegated to the *A. gemmata* sensu lato group because of the slight yellowish coloration of the pileus.

The epithet "*alpina*" cannot be validated for this species, because it is now occupied for one of the white alpine amanitas (Cripps & Horak 2010), *Amanita alpina* Contu (Contu 1997), occurring with dwarf *Salix* from the European Alps and neotypified by a P.-G. Jamoni specimen (CAG, Jamoni 702/90). Therefore we formally propose the western North American taxon as *Amanita alpinicola*, combining Smith's provisional name epithet with its treeline-dwelling nature.

Materials & methods

Specimens from Montana were described and photographed while fresh from the field. Vouchers were dried on a dehydrator and deposited in MONT (Thiers 2014). Smith specimens from MICH were examined in the dried state and his herbarium description used for comparison with Montana collections.

The methods for microscopic observations follow those of Tulloss et al. (1992) and Tulloss & Lindgren (2005) where appropriate. In general, the length and width of 25 spores per one basidiocarp in each collection were measured and ranges determined for both spore length and width; averages were calculated for spore length and width. The length/width (Q) ratio was determined for each spore and the ratio range and average (Q_{av}) computed. All measurements were made in 3% KOH at 1000× and drawings were done using a Leica DMSL microscope.

DNA was extracted from ground, dried sporocarp tissue using the DNeasy Plant Mini Kit (Qiagen) following the manufacturer's instructions. PCR amplification of the ITS region was performed using primers ITS1-F and ITS4 (White et al. 1990, Gardes & Bruns 1993) (Integrated DNA technologies). The PCR reaction mix consisted of 9.5 µL sterile double distilled H_2O, 1 µL ITS1-F (10µM), 1 µL ITS4 (10 µM), 12.5 µL REDtaq ReadyMix (Sigma-Aldrich), and 1 µL template DNA. The thermocycler program used was 94°C for 2 min., followed by 30 cycles of 94°C for 30 sec., 55°C for 1 min., and 72°C for 1 min.; followed by a final elongation step of 72°C for 5 min. PCR products were purified using the QIAquick PCR Purification Kit (Qiagen) following the manufacturer's instructions. PCR products were sequenced on both strands with the same primers used in PCR. DNA sequencing was performed at the Berkeley Sequencing Facility (http://mcb.berkeley.edu/barker/dnaseq/home). Consensus sequences of forward and reverse primed sequences were generated using SeqTrace v 0.8.1 (Stucky 2012).

ITS sequences from taxa of *Amanita* sections of interest were obtained from the *Amanitaceae* genetic sequence collection at Amanitaceae.org (http://www.amanitaceae.org/?Amanitaceae+genetic+sequence+collection) which provides links to reliably identified sequences housed on GenBank (some of the taxon names presented on Amanitaceae.org differ from those reported on GenBank). Most sequences of interest that could not be obtained through this site were found in Oda et al. (2002, 2004), Geml et al. (2008), or were obtained from the UNITE database (Kõljalg et al. 2013). Furthermore, the ITS sequence of *A. alpinicola* (CLC 2376, holotype) was subjected to BLAST queries on GenBank and UNITE to check for identical or similar sequences; greater than 97% similar sequences and the closest matching sequence (identified as *A. gemmata* (Fr.) Bertill. from North America) were downloaded. *Amanita pseudoporphyria* Hongo (*A.* sect. *Phalloideae*) was selected as outgroup as in Oda et al. (2004). GenBank accessions for sequences are provided (Table 1).

Multiple sequence alignment was performed using MUSCLE (Edgar 2004) under default settings and the alignment was manually edited using SeAl: Sequence Alignment Editor (Rambaut 1995). Phylogenetic analysis was carried out using PAUP* 4.0b10 (Swofford 2001) under the maximum parsimony (MP) criterion using heuristic searches including 100 random addition sequence replicates, and tree bisection reconnection branch swapping. Clade support was assessed with 1000 bootstrap replicates using heuristic searches, tree bisection reconnection branch swapping, and one random addition sequence per replicate. One representative most-parsimonious tree was randomly selected and the program TreeGraph 2 (Stöver & Müller 2010) was used to draw and edit the resulting tree.

Results

The phylogenetic analysis included 27 taxa with an ITS alignment length of 714 characters; 74 characters were excluded for a final alignment length of 640 characters, of which 495 were constant, 90 were variable but parsimony-uninformative, and 55 were parsimony-informative. The MP analysis resulted in 4001 most-parsimonious trees of 189 steps, consistency index

Table 1. *Amanita* specimens and GenBank/UNITE accession numbers of nrDNA ITS sequences used in the phylogenetic analysis

(newly generated sequences in bold)

Taxon	Voucher	Location	ITS sequence
A. alpinicola	CLC 2376 (MONT) HT	Montana, USA	**KR152655**
	CLC 2355 (MONT)	Montana, USA	**KR152656**
A. aprica *	RET 128-5 (RET) IT	Washington, USA	KF561972
	RET 534-7 (RET) IT	California, USA	KF561973
A. gemmata	F19752 (UBC)	B.C., Canada	HQ604823
	JV96-288 (C)	Denmark	UDB002326
	C29013 (C)	Denmark	UDB002325
A. ibotengutake	FB-30968 (CBM) PT	Japan	AB080987
	FB-30969 (CBM)	Japan	AB080988
A. muscaria *	RET 143-5 (RET)	Russia	EU071915
	RET 152-6 (RET)	Germany	EU071897
	GAL 4810 (ALA)	Alaska, USA	EU071937
A. muscaria subsp. *flavivolvata* *	CMP 3143 (RET)	Arizona, USA	EU071889
	CMP 1345 (RET)	Arizona, USA	EU071902
A. muscaria var. *alba*	HDT49100 (SFSU)	Idaho, USA	AB080793
A. muscaria var. *formosa*	HDT45060 (SFSU)	California, USA	AB080795
	HDT44761 (SFSU)	California, USA	AB080794
A. muscaria var. *guessowii* *	RET 124-2 (RET)	Massachusetts, USA	EU071896
	RET 271-2 (RET)	New Jersey, USA	EU071899
A. muscaria var. *persicina* *	RET 112-5 (RET) PT	Mississippi, USA	EU071887
	RET 151-4 (RET) PT	Alabama, USA	EU071892
A. pantherina	M-61495 (K)	England, UK	AB096046
	M-31408 (K)	England, UK	AB080774
A. pseudoporphyria (outgroup)	FB-30951 (CBM)	Japan	AB015702
A. regalis *	506 (O)	Norway	AB080780
	1539 (O)	Norway	AB080781
Environmental sample	—	California, USA	AY702732

Herbarium acronyms follow Thiers (2014), except for RET (Herbarium Amanitarum Rooseveltensis, New Jersey, U.S.A.)

*Accessed via the *Amanitaceae* genetic sequence collection at http://www.amanitaceae.org/ [2015]; some taxon names differ from those reported on GenBank.

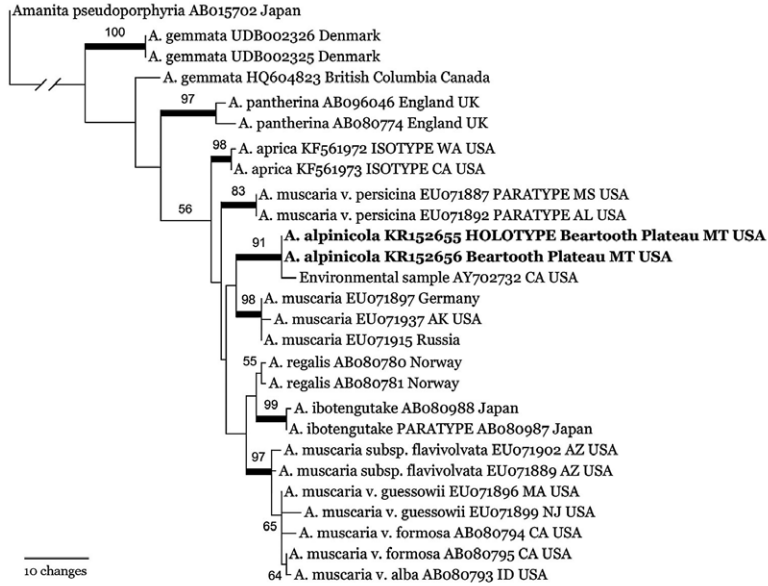

Fig. 1. One most-parsimonious tree of nrDNA ITS sequence data. Bootstrap values are indicated above or below branches leading to clades receiving ≥50% support. Thickened branches lead to clades receiving ≥75% support. Collections of *A. alpinicola* are indicated in bold type.

(CI) = 0.8571, retention index (RI) = 0.8457 and rescaled consistency index (RC) = 0.7249. Morphological and ITS sequence similarity between *Amanita alpinicola* and representative samples of *A.* sect. *Amanita* (*A. pantherina* (DC.) Krombh., *A. gemmata, A. aprica* J. Lindgr. & Tulloss, *A. regalis* (Fr.) Michael, *A. ibotengutake* T. Oda et al., and the *A. muscaria* group) suggest *A. alpinicola* belongs to *A.* sect. *Amanita* Corner and Bas.

Phylogenetically, it is clearly separated from other taxa (Fig. 1) and is described here as a new species; sequences are deposited in GenBank (KR152655, KR152656). Amplification of the ITS region was unsuccessful for Smith's collections.

Taxonomy

Amanita alpinicola C. Cripps & J. Lindgr., **sp. nov.** Figs 2, 3

MycoBank MB 812991

Differs from *Amanita muscaria, A. muscaria* var. *persicina, A. muscaria* var. *guessowii*, and *A. muscaria* var. *formosa* by its thin, fragile annulus (often ephemeral and sometimes absent) and its thick, rimmed cupulate volva.

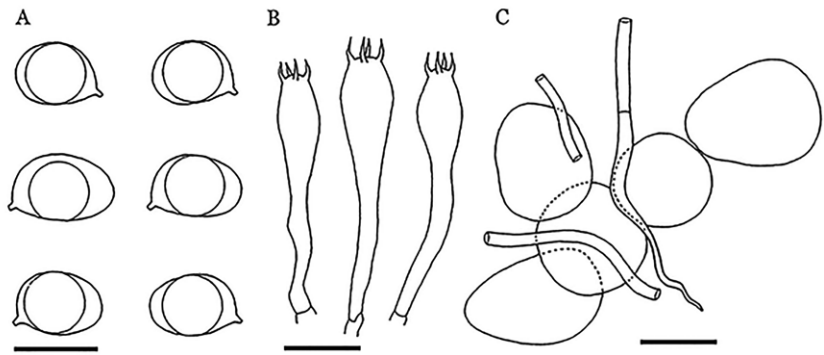

Fig. 2. *Amanita alpinicola* (holotype, CLC 2376). A. basidiospores; B. basidia; C. elements of universal veil from pileus. Scale bars: A = 10 µm; B, C = 20 µm. Drawings by E.G. Barge.

Type: USA. Montana. Carbon County: near Red Lodge, Beartooth Pass overlook, ca 2500 m asl, under *Pinus albicaulis* Engelm., 8.VIII.2008, leg. C. Cripps CLC 2376 (**Holotype,** MONT; GenBank KR152655).

Etymology: *alpinicola,* for Smith's original provisional epithet and the high elevation habitat.

Pileus 4–9 cm in diameter, convex, broadly convex, expanding to almost plane, dingy white to very pale yellow but more buff when dry, greasy or thinly viscid, covered with fine, raised dingy white to whitish tan warts from the universal veil that are somewhat integrated into the pileipellis; warts in a polygonal pattern or scattered, completely covering the pileus at first, then thinning as weathered; surface often dirty with adhering soil; margin turned down or not, indistinctly striate for a few mm or not; Lamellae free, crowded (N ≈200 or more), well separated with a few short lamellulae or not, rounded out, rather broad, white to cream, sticky; edges floccose, white; Annulus white, thin, fragile, often as a band of tissue, easily disappearing or none (exannulate form), often with torn/ragged tissue in zones on lower stipe; Stipe 5–10(–18) × 1–3 cm, equal, narrower in the middle or gradually enlarging towards base, rounding out and then often with a point at very base, white, floccose above and fibrillose below, often with torn tissue; Volva as a tidy cup, rather thick, rimmed (or with several

Fig. 3. *Amanita alpinicola.* Habit: A (CLC 2118), B (holotype, CLC 2376), C (CLC 2255). Showing subterranean fruiting habit in *Pinus albicaulis* forests: D (CLC 1994). Photos by C. Cripps.


A
B
C
D

'rims' in layers), dirty white, persistent, tough, often covered with adhering soil; Context white, stem partially stuffed; Odor indistinct or unpleasant to slightly fruity; Exsiccati colors pale orange pileus, pale (but darker than pileus) orange lamellae, and dingy cream stipe; context dingy cream with some pale orange; volva darker and covered with soil.

Universal veil on pileus consisting of plentiful inflated cells (in some areas with only inflated cells); inflated cells integrated into subtending filamentous hyphae of pileipellis; inflated cells globose, slightly elliptical or clavate, (35–)50–75(–100) µm diam.; walls thin to somewhat thickened, hyaline. Volva tissue also consisting of inflated cells, but typically more clavate than globose and also containing pale (yellowish) oleiferous hyphae ≤12 µm diam. No clamps observed; Pileipellis in cross-section, without gelatinous layer, a cutis of tightly interwoven filamentous cells, 7–10 µm diam., some with diffuse yellow pigment or yellow refractive material; some hyphae slightly swollen and existing as elliptical cells ≤24 µm wide; lower hyphal layer more parallel. No clamps observed; Partial veil a mix of filamentous and clavate cells, 4–8(–10) µm diam., sometimes with a few clavate cells connected in succession, in areas with yellow pigment; walls thin, smooth; oleiferous hyphae scattered, ≤7–20 µm diam. No clamps observed; Lamellar trama divergent, of inflated hyphae. Sub-hymenium a basement layer several cells thick of cellular thin-walled cells, irregular-squarrose, 10–15(–20) µm diam. Basidia 49–70 × 7–14 µm, clavate, 4-spored; sterigmata ≤7 × 1.5 µm; clamps infrequent; Basidiospores (holotype, CLC 2376) white in deposit, 9–12 × 7–8 µm, average 10.5 × 7.8 µm, Q range 1.25–1.5, Q_{av} = 1.4, hyaline, thin-walled, ellipsoid, smooth, non-amyloid, 1-guttulate; apiculus sublateral.

Habit, habitat & distribution—In subalpine to tree-line zones with five-needle pines. Reported from Montana, Idaho, and known from a few places in the Pacific Northwest. Phylogenetic placement of the ITS sequence isolated from a root tip in a conifer forest in the Sierra Nevada of California also suggests its presence there (Izzo et al. 2005). The fully opened fruiting bodies are often found buried in the soil in these high, dry habitats. Ectomycorrhizal with five-needle western pines including at least *Pinus albicaulis* and possibly *P. monticola*, and also with three-needle *P. jeffreyi*. Fruiting can begin 'early' in the season shortly after the snowbank fungi decline, but 'early' is a relative term and typically ranges from July to mid-August at these high elevations (2500–3000 m), and it can also be found later in the year. It also occurs in May in Washington and Idaho.

Additional specimens examined—**UNITED STATES**. **Idaho**. **Valley County**: Upper Payette Lake, Twenty mile Creek, reported with lodgepole pine [but *P. albicaulis* is in the vicinity], 13.VII.1954, leg. A.H. Smith AHS44902 (MICH); **Idaho County**: Seven Devils Mts., Heaven's Gate, scattered under "*Pinus flexicaulis*" at high elevations, 26.VII.1954, leg. Bigelow & Smith AHS45357 (MICH). **Montana**. **Park County**: near Cooke City, Fisher Creek drainage, ca 3000 m asl, under *Pinus albicaulis*, 1.VII.2004, leg. C. Cripps CLC 1994 (MONT); 12.VII.2005, CLC 2118 (MONT); 20.VII.2005, leg. C. Cripps CLC 2169 (MONT); Miller Creek drainage, ca 3000 m asl, under *P. albicaulis*, 7.VIII.2009, leg. C. Cripps CLC 2456 (MONT); **Carbon County**: near Red Lodge, Beartooth Pass overlook, ca 2500 m asl, under *P. albicaulis*, 24.VII.2008, leg. C. Cripps CLC 2355 (MONT; GenBank KR152656); **Gallatin County**: Bear Canyon, near Fridley burn, in pure unburned *P. albicaulis*, 22.VI.2006, leg. C. Cripps CLC 2235b (MONT); Sacajawea Saddle, 2700 m asl, under *P. albicaulis*, 16.VIII.2005, leg. K. Mohatt KRM 002 (MONT).

Discussion

The name *Amanita gemmata* has been used to delineate what appears to be a group of yellow *Amanita* species in *A.* sect. *Amanita* in western North America, more particularly in the Pacific Northwest, Idaho, Montana, and Canada. The use of this European name for North American collections is considered a misapplication (Tulloss et al. 1995, Lindgren 2014, Zhang et al. 2004, Tulloss 2010) and this leaves some of our taxa unnamed. In comparison with *A. alpinicola*, the pileus of *A. gemmata* is deeper yellow, the universal veil tissue on the pileus is easily removed and not innate, the habit is not subterranean, and it is not reported with five-needle pines. *Amanita aprica* has been formally separated out of the *A. gemmata* group (Tulloss & Lindgren 2005). It is a bright orange-yellow spring species reported from Washington, Oregon, northern California, and British Columbia, primarily with Douglas fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*).

The status of the yellow *Amanita muscaria* var. *formosa* Pers. and *A. muscaria* var. *guessowii* Veselý is less clear. But a yellow taxon that has gone under these names does occur in at least Montana, Idaho, Washington, and Oregon. Like *A. muscaria* (L.) Lam. var. *muscaria*, it has the quintessential rings of volval tissue at the base of the stipe and yellow color under the pileipellis. The bright red *A. muscaria* subsp. *flavivolvata* Singer occurs in Alaska south throughout the Pacific Northwest, and again in the southern Rocky Mountains, but is apparently absent from Alberta, Montana, and Idaho where the yellow variety appears with conifers and aspen. *Amanita alpinicola* is separated from these taxa by both morphological and molecular differences. In addition, the ecology is different and *A. alpinicola* appears to be specific for five-needle pines, primarily whitebark pine (*P. albicaulis*), often fruiting just below the soil surface in the open understory.

The Montana collections clearly match Smith's provisional taxon in macro- and micromorphology, although the lamellae in the Smith exsiccati are darker orange as is typical for older specimens. Smith suggested that his species might be a "satellite" species to *A. muscaria* and the molecular analysis does suggest the placement of this new species in *A.* sect. *Amanita*. Studies of this group have suggested that the presence or absence of clamps at the base of the basidia may be an important micro-morphological feature (Tulloss, pers. comm.) and here we report rare, thin clamps at the base of the basidia of *A. alpinicola*.

A mycorrhizal specificity for five-needle pines is likely for this *Amanita* species, and several *Suillus* share this ecology in western North America (Mohatt et al. 2008, Cripps & Antibus 2011). Other amanitas with a near subterranean habit appear in Australia in sandy soil under dry climatic conditions (Miller 1991), but they are in sections other than *A.* sect. *Amanita*. There is one report of poisoning for *A. alpinicola* (Beug 2016) and it is closely related to other amanitas, such as *A. muscaria*, which contain ibotenic acid and muscimol. Thus, it is likely that *A. alpinicola* is toxic and future assays may reveal the presence of these compounds.

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Addendum—Smith's original description for *Amanita* "*alpina*" (A.H. Smith 44902 and 45357) "Pileus 3–9 cm broad, convex expanding to plane or nearly so, surface thinly viscid beneath poorly formed floccose warts which collapse in age, warts somewhat conic when well-formed and white, cap margin even or rarely short-striate in extreme age, ground color pale yellow to cream color but in age often whitish finally discoloring to brownish; flesh white, unchanging, odor not distinctive, no color changes when bruised. Lamellae white or in age with a creamy tone, broad, close to subdistant. Attached narrowly to the stipe, breaking away in age, not staining when bruised. Stipe 3–9 cm long, 1–2.5 cm thick at apex, with a rounded bulb at the base, a free-margined volva which is not inrolled, above this often occur interrupted zones of partial veil tissue or a true median or superior annulus, or all remains of a partial veil obliterated (about half the specimens). Spores 9–12 × 6–7.5 μm, ellipsoid, smooth, non-amyloid. Basidia 4-spored. Clamp connections present. Scattered under *Pinus flexicaulis* at high elevations, Seven Devils Mts. Idaho, July 26, 1954, Bigelow & Smith 45357.

"Observations. The basidiocarps of this species often do not break through the duff but actually shed their spores while completely subterranean. The annulus does not form in about half the basidiocarps. The species appears to be a satellite to *A. muscaria* – which is an extremely variable species in the Idaho mountains."