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Xerocomellus (*Boletaceae*) in western North America

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Abstract: Understanding diversity in the genus *Xerocomellus* in western North America has been obscured by morphological variability, widespread use of species epithets typified by specimens from Europe and eastern North America, misunderstood phylogenetic relationships, and species complexes. We collected extensively and used genetic and morphological data to establish the occurrence of ten *Xerocomellus* species in western North America. We generated ITS sequences from five type collections and from vouchered representative collections to clarify our understanding of existing species concepts. We describe three new species (*Xerocomellus atropurpureus, X. diffractus*, and *X. salicicola*) and propose two new combinations (*X. amylosporus* and *X. mendocinensis)*, transfer *Boletus coccyginus* to *Hortiboletus*, and provide a dichotomous key to species of *Xerocomellus* in western North America.

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INTRODUCTION

Historically, the genus *Boletus* (*Boletaceae*) encompassed a wide range of basidiomycete species with poroid, fleshy basidiomata. Recent molecular work has shown that *Boletus s.l.* is polyphyletic, with numerous genera erected to accommodate the phylogenetic diversity represented by the broad morphological concept of the boletes; and that in addition to typical stipitate poroid morphology and epigeous habit, there are lamellate, gastroid and hypogeous species nested throughout the *Boletaceae* (Binder & Hibbett 2006, Dentinger *et al*. 2010, Nuhn *et al*. 2013, Arora & Frank 2014, Wu *et al*. 2014).

In the process of phylogenetic separations and recombinations, Klofac & Krisai-Greilhuber (1992) placed many boletes with dry, velvety pilei in the genus *Xerocomus*, typified by *X. subtomentosus.* However, even this new genus was shown to be polyphyletic. Šutara (2008) established *Xerocomellus* to accommodate *X. chrysenteron* and its relatives, often referred to as "cracked-cap boletes" because of their tendency to develop areolate pileus surfaces. Several multi-gene analyses support the integrity of *Xerocomellus*: Nuhn *et al.* (2013) using *TEF1*, *RPB1*, and LSU, Gelardi *et al*. (2015) using ITS and LSU, and Wu *et al.* (2016a, b) using LSU, *TEF1*, *RPB1*, and *RPB2*.

While European *Xerocomellus* species are relatively well understood (Peintner *et al.* 2003, Ladurner & Simonini 2003, Ariyawansa *et al.* 2015, Crous *et al*. 2016, Simonini *et al.* 2016), the diversity of North American *Xerocomellus* has remained unclear. This is in part due to the use of European names for North American collections, a lack of robust species concepts, a high degree of morphological variability and overlapping suites of traits in the basidiomata of species in this genus.

Thiers' 1975 monograph of California boletes has been the primary resource for these species concepts in California and the western USA. His infrageneric grouping *Boletus* section *Subtomentosi* subsection *Subtomentosi* includes four species that we recognize today as belonging to *Xerocomellus* (*viz*. *B. chrysenteron*, *B. dryophilus*, *B. mendocinensis* and *B. zelleri*), as well as four non-xerocomelloid species: *B. spadiceus* and *B. subtomentosus* (in *Xerocomus*), *B. rubripes* (in *Caloboletus*), and one still in need of generic classification, *B. smithii*. Three other species in Thiers' section *Subtomentosi* were distributed among three additional subsections: *B. coccyginus* (subsection *Fraterni*), *B. mirabilis* (subsection *Mirabilis*) and *B. flaviporus* (subsection *Versicolores*); the first we show to be in *Hortiboletus* (sister to *Xerocomellus*) while the latter two have been placed more distantly in *Aureoboletus*. Thiers (1975) placed *B. truncatus* from western North America in section *Truncati*.

The need to clarify the *Xerocomellus* boletes of western North America has grown increasingly acute. At the time of this study, DNA sequences representing a single species have been deposited in GenBank under as many as four different species epithets, making it nearly impossible for researchers to identify collections, environmental samples and mycorrhizas based on ITS barcodes. The specific epithet "*chrysenteron*" has been the most commonly misapplied name, and has often served as the default name for any *Xerocomellus* with an areolate pileus; the

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specific epithet "*truncatus*" has been misapplied in western North America to those basidiomata with rapid and deeply colored staining on the pores or with truncate spores, while the specific epithet "*zelleri*" has been applied to most *Xerocomellus* exhibiting a non-areolate, dark reddish purple to purple-black pileus surface.

Here we focus on the epigeous species of *Xerocomellus* in western North America. We collected extensively and sequenced collections of *Xerocomellus* and *Xerocomellus*-like boletes from the Pacific Northwest and California. We sequenced type collections of *Ceriomyces zelleri*, *Boletus rainisiae*, *Boletus mendocinensis*, *Porphyrellus amylosporus*, *Gastroboletus xerocomoides*, and vouchered collections of *Xerocomellus truncatus* from eastern North America to confirm species identifications. We investigated the placement of *Porphyrellus amylosporus*, *Gastroboletus xerocomoides*, and *Boletus coccyginus* to determine inclusion within or generic placement outside *Xerocomellus*. We also examined collections identified as *Xerocomus spadiceus* and *X. subtomentosus* from western North America to determine whether they represented taxa in *Xerocomellus*.

Using ITS and LSU nrDNA sequence data in addition to morphological analyses, our goals were to (1) ascertain species-level diversity within the genus, (2) assess morphological variability within species, and (3) establish morphological identification criteria.

MATERIALS AND METHODS

Field work and fungarium collections

We collected and examined fresh and dried material of *Xerocomellus* and closely related species. For each, we evaluated basidioma characters including coloration, surface ornamentation of the pileus and stipe, and staining reactions after bruising and cutting. We examined herbarium specimens from San Francisco State University (SFSU), The New York Botanical Garden (NYBG), and University of California Santa Cruz (UCSC) including type collections for *Ceriomyces (Boletus) zelleri*, *Porphyrellus amylosporus*, and *Gastroboletus xerocomoides*. Additional specimens were contributed by other mycologists and members of online amateur mycological communities and citizen science biodiversity portals (www.inaturalist.org and www.mushroomobserver.org). Data from these sources helped to establish geographic ranges and morphological variability of the various taxa. Microscopic details of the pileipellis, hymenial cystidia, and spore morphology were examined with Leica DMLB and Leica DM300 compound microscopes and photographed with a SPOT insight electronic camera. For spore sizes, 50 spores (from 2–3 collections) were measured at 1 000× magnification, from dried material in 5 % KOH, and reported as range, with exceptionally large or small dimensions in parentheses, average and the average quotient (avQ). Amyloid reactions were determined in Melzer's reagent. Vouchered specimens were deposited in OSC, SOC, SFSU, UCSC and NYBG [herbarium abbreviations follow Thiers (2020)].

Molecular methods

DNA was purified from fresh or dry tissue using a modified CTAB-chloroform extraction method. Briefly, tissue samples were stored in buffer (0.1M Tris, 0.3 M NaCl, 0.04 M EDTA) at 4 °C, extracted in 2 % cetyltrimethyl ammonium bromide (CTAB) with chloroform. DNA was amplified in polymerase chain reactions (PCR) with fungal specific primer ITS1F (5'-ggtcatttagaggaagtaa-3') and universal eukaryote primer TW13 (5'- ggtccgtgtttcaagacg -3') (White *et al.* 1990, Gardes & Bruns 1993, 1996); 20 µL PCR reactions were performed using 0.6 units GoTaq and 4 µL 5x colorless buffer (Promega), 200 µM each dNTP, 0.3 µM each primer, 2.5 mM $MgCl_2$ and 2 µL undiluted DNA template. An initial 3 min at 93 °C was followed by 30 cycles of 30 s at 95 °C, 2 min at 54 °C, and 3 min at 72 °C, with a final cycle for 10 min at 72 °C. When necessary, shorter fragments from older herbarium specimens were amplified with all of the following primer pairs: ITS1F and ITS4 (5'-tcctccgcttattgatatgc-3'), ITS1 and ITS2, and ITS3 and ITS4. Four new reverse primers were designed (by JLF) using the Operon Primer Design tool (http://www.lifetechnologies.com) to amplify the *X. zelleri* species complex in a region of ITS1 approximately 180 bp downstream from the ITS1F primer site, in order to amplify a shorter fragment that would include several diagnostic single nucleotide polymorphisms (SNP): XzR1 (5' gtgtgatgatgaaaacatag 3'), XzR2 (5'- tgatgatgaaaacatagatc-3'), XzR3 (5' tgtgagagtaagagaaaggtc 3'), XzR4 (5' gtgagagtaagagaaaggtc 3'). These new primers were paired with ITS1F and used to amplify DNA extracted from the type collection for *X. zelleri*, dating from 1911. For these PCR conditions, the extension time was reduced to 60 s. All PCR products were electrophoresed on 1.5 % agarose gels, stained with GelRed nucleic acid stain (1 mg/mL) (Biotium), and visualized using a Kodak EDAS 290 UV transilluminator.

PCR products were purified with QIAquick PCR Purification kits (Qiagen, Valencia, CA), prepared with BigDye Terminator Ready Reaction Mix v. 3.1 and sequenced with an ABI 310 Genetic Analyzer (Applied Biosystems, Foster City, CA) in the Biotechnology Center at Southern Oregon University. Molecular data were obtained by sequencing the internal transcribed spacer (ITS) region, including ITS1, the 5.8S ribosomal DNA gene and ITS2, and part of the 28S ribosomal DNA gene, with forward primers ITS1F, ITS1 (5'-tccgtaggtgaacctgcgg-3'), ITS3 (5'-gcatcgatgaagaacgcagc-3') and ITS4r (5'-gcaatatcaataagcggagga-3'), and reverse primers ITS2 (5'- gctgcgttcttcatcgatgc-3'), ITS4 and TW13.

Sequences were edited with Chromas v. 1.45 (McCarthy 1998); contiguous sequences were assembled in Sequencher v. 4.7 (Gene Codes Corp. Ann Arbor, MI) and compared to fungal sequences in GenBank with BLAST (Altschul *et al.* 1990). MAFFT and ClustalX were used to generate and visually assess multiple sequence alignments (Thompson *et al.* 1997, Katoh *et al*. 2002). Alignments were edited manually using Mesquite v 3.40 (Maddison & Maddison 2011). Sequence data have been deposited in GenBank.

We aligned our ITS data with 50 additional ITS sequences from GenBank and UNITE, selecting up to four good quality sequences available to represent extralimital species. The ITS region was initially analyzed using the entire data set for the ITS, subsequent ITS trees were generated after removing the 150 bp sequence for the *X. zelleri* type, and shorter sequences that lacked large portions of ITS1 or ITS2. We aligned our LSU data with an additional 46 LSU sequences from GenBank. Alignments have been deposited in TreeBASE, available at http://purl.org/phylo/treebase/phylows/study/TB2:S22732.

Phylogenetic trees using parsimony with 1 000 bootstrap replicates and 1 000 jack-knife replicates were generated

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using PAUP v. 4.0b10 (Swofford 2002). Consensus trees with 50 % majority-rule were generated using a tree-bisection-reconnection branch-swapping algorithm. All characters were given equal weight; gaps were treated as missing. Consensus trees were examined to confirm branch positions. Maximum likelihood trees with 1 000 bootstrap replicates were generated using PhyML through the phylogeny.fr portal using the substitution model HKY85 (Dereeper *et al*. 2008) and using RAxML v. 8 on XSEDE with the GTRCAT model through the CIPRES Science Gateway: www.phylo.org/portal2/home.action (Stamatakis 2006). In addition to mid-point rooting, *Hortiboletus* spp. and *Phylloporus arenicola* were used as outgroups for ITS and LSU phylogenetic analyses respectively. Labels for GenBank submissions include quotation marks to indicate when nomenclatural inconsistencies were detected.

RESULTS

We collected and examined fresh and dried material from over 100 collections of *Xerocomellus* and closely related species. A total of 84 ITS and 16 LSU rDNA sequences were generated from 10 species of *Xerocomellus* and an additional 14 ITS and 6 LSU sequences were generated from closely related taxa in the genera *Hortiboletus* and *Xerocomus* (GenBank accessions: KM213635–KM213667, KU144741–KU144820, KU160180, KX534074–KX534079, KY659587–KY659593 and MH168533–MH168538) (Table 1).

Our ITS analysis shows a core clade around *X. chrysenteron* including the western North American taxa *X. dryophilus*, *X. rainisiae, X. macmurphyi, X. behrii, X. amylosporus* (the latter subsuming *Gastroboletus xerocomoides*), *X. mendocinensis* (including *X. truncatus sensu* Thiers), and *X. truncatus* from eastern North America; this arrangement is also supported by our LSU analyses (Figs 1, 2). North American collections previously labeled *X. chrysenteron* fall primarily into two species: one common in western North America described here as *X. diffractus,* and at least one undescribed species from eastern North America. These are not conspecific with the European *X. chrysenteron*, but rather appear more closely related to each other and to the European *X. cisalpinus* (Fig. 1). Sequences from all the eastern North American "*chrysenteron*" share a 16 bp deletion in the ITS1 approximately 200 bp downstream from the beginning of ITS1 (approximately 30 bp upstream from the beginning of the 5.8S nrDNA gene), and two 10 bp insertions near the end of ITS2. Even when discounting these deletions/insertions, the eastern North American *"chrysenteron"* taxon consistently differs from *X. diffractus* by > 5 % in the ITS region.

Only a short fragment of sequence data (<150 bp) from the type collection of *X. zelleri* was obtained (KU144803), generated from PCR amplification using ITS1F and XzR2 primer pair, and using ITS1 as sequencing primer. After confirming the identity of *X. zelleri sensu stricto*, by comparing the informative base positions, sequence data for this type collection was removed from the final phylogenetic analysis.

Both ITS and LSU phylogenetic trees support the monophyly of *Xerocomellus*, with *Hortiboletus* as sister (Figs 1, 2). *Boletus coccyginus* was found to belong in *Hortiboletus.* The Japanese truffle *Heliogaster columellifer* was recovered within *Xerocomellus*. The two xerocomelloid truffles *X. behrii* (not illustrated) and *X. macmurphyi* are treated briefly; for more detail see Smith *et al.* (2018). Based on ITS data from GenBank and UNITE, our analyses show that the European species *Rheubarbariboletus armeniacus* and *R. persicolor* appear to belong in *Xerocomellus* (Fig. 1). However, one LSU sequence labeled as *"Xerocomellus armeniacus"* (KF030295) was recovered within *Hortiboletus* (Fig. 2). We confirmed that collections of *Xerocomus subtomentosus* and *X. spadiceus* from western North America represent two different species, neither of which belongs in *Xerocomellus*.

We do not attempt to resolve all ambiguities in GenBank submitted by other researchers, as some sequences in GenBank are clearly misidentified and some do not include location information.

Taxonomy

Xerocomellus amylosporus (A.H. Sm.) J.L. Frank & N. Siegel, ***comb. nov.*** MycoBank MB821027. Figs 3A–B, 5A, 6A.
Basionym: *Porphyrellus amylosporus* A.H. Sm., *Mycopath. Mycol. appl*. **25**: 397. 1965.
Synonyms: *Tylopilus amylosporus* (A.H. Sm.) A.H. Sm., Non-Gilled Fleshy Fungi: 179. 1973 (invalid; basionym not cited).
Boletus amylosporus (A.H. Sm.) Wolfe*, Nova Hedwigia* **43**: 518. 1986.
Gastroboletus xerocomoides Trappe & Thiers, *Brittonia* **21**: 247. 1969.

Description: (typical poroid form; see discussion for gastroid form): *Pileus* 4–10 cm wide, bun-shaped at first, becoming convex to plane, dark olive brown to grayish brown, to vinaceous brown; surface dry, finely velvety to matted-tomentose, lacking cracks when young, becoming areolate around the margin, to extensively areolate in age; context in cracks dull whitish to yellow, becoming pinkish in age. *Hymenophore* (tube layer) slightly sunken around stipe; pores 1–2 per mm, slightly angular or irregular, yellow to golden yellow at first, becoming olive yellow, bruising inky blue to dark blue somewhat quickly. *Stipe* 4–10 × 1–2 cm, cylindrical to clavate, reddish or with red longitudinal striations over a yellowish base when young, soon becoming brownish to reddish brown over much of the stipe to extensively brown with a red band at apex. *Context* in pileus firm to soft, light yellow, erratically bruising blue. *Odor* indistinct. *Taste* mild. *Spore deposit* olive brown to dark reddish olive. *Spores* (11.4–)13–16.2(–18.1) × 5.2–6.5(–7.1) µm, av. 14.8 × 5.9 µm, avQ = 2.5, fusoid to subcylindrical, inequilateral, most with truncate apex, smooth, weakly to distinctly amyloid. *Basidia* 27.3–35.7 × 9.9–12.9 µm, clavate, hyaline, (2–)4-spored. *Hymenial cystidia* 28.9–73.5 × 2.9–8.1 µm narrowly ventricose with elongated apices. *Pileipellis* a trichoderm made up of elongated cells 8–10 µm wide, with brown incrustations and pigment; terminal cells conical. *Clamp connections* absent.

Distribution and ecology: USA and Canada – Pacific Northwest, north to at least to Vancouver Island, British Columbia, Canada, south into California, east to the Northern Rocky Mountains. Solitary or scattered in troops under conifers, especially *Picea sitchensis*. The type collection was described as "gregarious under *Alnus rubra*" and while *Alnus* has been present at some sites, it has not been present at all sites. Uncommon, but rather widespread.

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Table 1. Collection data for species of *Xerocomellus*.

Species	Collection No.	Fungarium	Collector	Date	County	ITS	LSU
X. amylosporus	AHS70936*	SFSU	A.H. Smith	9 Sep. 1964	Bonner Co., ID	KU144741	–
	JLF3012	OSC162184	J.L. Frank	17 Oct. 2013	Marion Co., OR	KM213635	KU144742
	JLF3498	OSC162185/NYBG/SOC	J.L. Frank	7 Oct. 2014	Lewis Co., WA	KU144743	–
	NS111112	UCSC	N. Siegel	11 Nov. 2012	Humboldt Co., CA	KM213636	–
	HDT13163**	SFSU	H.D. Thiers	14 Sep. 1965	Sierra Co., CA	KU144744	–
	JLF4665	OSC162186/SOC	J.L. Frank	12 Nov. 2016	Jackson Co., OR	KY659587	–
X. atropurpureus	JLF2379	OSC162187	J.L. Frank	30 Nov. 2011	Marion Co., OR	KM213637	–
	JLF2795	UCSC	P. Laughlin	13 Jan. 2013	Monterey Co., CA	KM213638	KM213639
	JLF3196	UCSC	J.L. Frank	21 Jan. 2014	Marin Co., CA	KM213640	–
	NS120712	UCSC	N. Siegel	7 Dec. 2012	Mendocino Co., CA	KM213641	KM213642
	JLF3379	UCSC	D. Arora	11 Nov. 2014	Nevada Co., CA	KM213643	–
	JLF2995	OSC162188	J.L. Frank	11 Oct. 2013	Lane Co., OR	KU144745	–
	JLF3018	OSC162189	J.L. Frank	18 Oct. 2013	Marion Co. OR	KU144746	–
	JLF3502	OSC162190	J.L. Frank	8 Oct. 2014	Lewis Co., WA	KU144747	–
	JLF3545	OSC162191	J.L. Frank	13 Oct. 2014	Lewis Co., WA	KU144748	–
	JLF3620*	OSC162192/NYBG/SFSU/SOC	J.L. Frank	7 Nov. 2014	Klamath Co., OR	KU144749	KU144750
	JLF3624	OSC162193/SOC	J.L. Frank	7 Nov. 2014	Klamath Co., OR	KU144751	–
	JLF3654	OSC162194	J.L. Frank	24 Nov. 2014	Jackson Co., OR	KU144752	–
	JLF3656	OSC162195	J.L. Frank	24 Nov. 2014	Jackson Co., OR	KU144753	–
	JLF3695	OSC162196	J.L. Frank	8 Dec. 2014	Douglas Co., OR	KU144754	–
	JLF3806	OSC162197	J.L. Frank	21 Apr. 2015	Lane Co., OR	KU160180	–
	NS1251	UCSC	N. Siegel	21 Oct. 2014	Humboldt Co., CA	KU144755	–
	NS1269	UCSC	N. Siegel	23 Oct. 2014	Humboldt Co., CA	KU144756	–
	NS1276	UCSC	N. Siegel	24 Oct. 2014	Kittitas Co., WA	KU144757	–
	NS1288	UCSC	N. Siegel	28 Oct. 2014	Clallum Co., WA	KU144758	–
	NS1296	UCSC	N. Siegel	1 Nov. 2014	Lane Co., OR	KU144759	–
	NS1297	UCSC	N. Siegel	1 Nov. 2014	Lane Co., OR	KU144760	–
	NS1346	UCSC	N. Siegel	13 Dec. 2014	Nevada Co., CA	KU144761	–
	NS1393	UCSC	N. Siegel	19 Nov. 2014	Humboldt Co., CA	KU144762	–
	NS1432	UCSC	N. Siegel	14 Jun. 2015	Plumas Co., CA	KU144763	–
	NS1442	UCSC	N. Siegel	14 Dec. 2015	Lassen Co., CA	KU144764	–
	MO194036	UCSC	T. Chesney & C. Hodge	22 Dec. 2014	El Dorado Co., CA	KU144765	–
	JLF4238	UCSC	A. Moore	2 Apr. 2016	Lane Co., OR	KY659588	–

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Table 1. (Continued).

Species	Collection No.	Fungarium	Collector	Date	County	ITS	LSU
	JLF4664	UCSC	J.L. Frank	12 Nov. 2016	Jackson Co., OR	KY659589	–
X. cf. chrysenteron	JLF5684	NYBG	J.L. Frank	22 Sep. 2017	Worcester Co., MA	MH168533	–
X. diffractus	JLF2644	UCSC	J.L. Frank	29 Oct. 2012	Jackson Co., OR	KM213647	–
	JLF3195	UCSC	J.L. Frank	16 Jan. 2014	Marin Co., CA	KM213648	–
	NS111012	UCSC	N. Siegel	10 Nov. 2012	Humboldt Co., CA	KM213649	–
	NS120612	UCSC	N. Siegel	6 Dec. 2012	Mendocino Co., CA	KM213650	KM213651
	JLF3528	UCSC	J.L. Frank	9 Oct. 2014	Lewis Co., WA	KU144766	–
	JLF3532	UCSC	J.L. Frank	10 Oct. 2014	Lewis Co., WA	KU144767	–
	JLF3535	OSC162198	N. Siegel	11 Oct. 2014	Lewis Co., WA	KU144768	–
	JLF3554	OSC162199	J.L. Frank	14 Oct. 2014	Lewis Co., WA	KU144769	KU144770
	JLF3555	OSC162200	J.L. Frank	14 Oct. 2014	Lewis Co., WA	KU144771	–
	JLF3559	OSC162201	J.L. Frank	14 Oct. 2014	Lewis Co., WA	KU144772	–
	JLF3585	OSC162202	J.L. Frank	27 Oct. 2014	Lane Co., OR	KU144773	–
	NS1230	UCSC	N. Siegel	29 Sep. 2014	Park Co., WY	KU144774	–
	NS1246	UCSC	N. Siegel	20 Oct. 2014	Humboldt Co., CA	KU144775	–
	NS1298	UCSC	N. Siegel	3 Nov. 2014	Lincoln Co., OR	KU144776	–
	NS1334	UCSC	N. Siegel	10 Nov. 2014	Trinity Co., CA	KU144777	–
	NS1366	UCSC	N. Siegel	14 Nov. 2014	Mendocino Co., CA	KU144778	–
	NS1369	UCSC	N. Siegel	14 Nov. 2014	Mendocino Co., CA	KU144779	–
	NS1371	UCSC	N. Siegel	14 Nov. 2014	Mendocino Co., CA	KU144780	–
	NS1376	UCSC	N. Siegel	15 Nov. 2014	Mendocino Co., CA	KU144781	–
	NS1378	UCSC	N. Siegel	15 Nov. 2014	Mendocino Co., CA	KU144782	–
	NS1438	UCSC	N. Siegel	14 Dec. 2014	Nevada Co., CA	KU144783	–
	JLF4239	UCSC	J.L. Frank	3 Apr. 2016	Lane Co., OR	KY659590	–
	JLF5745*	OSC162203/NYBG/SFSU/SOC	J.L. Frank	8 Oct. 2017	Jackson Co., OR	MH168534	–
	JLF5915	OSC162204	J.L. Frank	30 Oct. 2017	Jackson Co., OR	MH168535	–
	JLF5930	SOC	J.L. Frank	30 Oct. 2017	Jackson Co., OR	MH168536	–
	JLF6546	SOC/GILB	J.L. Frank	12 Aug. 2018	Graham Co., AZ	MK552409	–
X. dryophilus	CFS3Nov11-1	UCSC	C.F. Schwarz	3 Nov. 2011	Santa Cruz Co., CA	KM213644	–
	CFS3Nov11-2	UCSC	C.F. Schwarz	3 Nov. 2011	Santa Cruz Co., CA	KM213645	KX534074
	CSZVM-SCI-77	UCSC	C.F. Schwarz	29 Dec. 2012	Santa Barbara Co., CA	KM213646	–
	HDT18557*	SFSU	H.D. Thiers	28 Jan. 1967	Santa Barbara Co., CA	KU144784	–
	JLF3996	SOC	J.L. Frank	3 Jan. 2016	Santa Cruz Co., CA	KX534075	–
	JLF4134	OSC162205/NYBG/SOC	J.L. Frank	28 Feb. 2016	Santa Barbara Co., CA	KX534076	KY659593

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Table 1. (Continued).

Species	Collection No.	Fungarium	Collector	Date	County	ITS	LSU
X. mendocinensis	JLF2298	SOC	J.L. Frank	10 Nov. 2011	Marion Co., OR	KM213652	–
	JLF2775	UCSC	J.L. Frank	16 Dec. 2012	Santa Cruz Co., CA	KM213653	KM213654
	HDT18392*	SFSU	H.D. Thiers	8 Jan. 1967	Mendocino Co., CA	KM213655	–
	CFS1Nov11_1	UCSC	C.F. Schwarz	1 Nov. 2011	Santa Cruz Co., CA	KM213656	KM213657
	CFS1Nov11_2	UCSC	C.F. Schwarz	1 Nov. 2011	Santa Cruz Co., CA	KM213658	–
	CFS10Nov2012_1	UCSC	C.F. Schwarz	10 Nov. 2012	Humboldt Co., CA	KM213659	KM213660
	NS110511	OSC162206	N. Siegel	5 Nov. 2011	Curry Co., OR	KM213661	–
	JLF3558	OSC162207/SOC	J.L. Frank	14 Oct. 2014	Lewis Co., WA	KU144785	KU144786
	NS1333	UCSC	N. Siegel	10 Nov. 2014	Trinity Co., CA	KU144787	–
	NS1367	UCSC	N. Siegel	14 Nov. 2014	Mendocino Co., CA	KU144788	–
	JLF4821	UCSC	J.L. Frank	16 Dec. 2016	Santa Barbara Co, CA	KY659591	–
	JLF4835	UCSC	J.L. Frank	16 Dec. 2016	Santa Barbara Co, CA	KY659592	–
	JLF5926	OSC162208	J.L. Frank	30 Oct. 2017	Jackson Co., OR	MH168537	–
X. rainisiae	JLF2154	OSC162209	J.L. Frank	13 Aug. 2011	Marion Co., OR	KM213662	–
	JLF3523	OSC162210/SOC	J.L. Frank	9 Oct. 2014	Lewis Co., WA	KU144789	KU144790
	NS101013	OSC162211	N. Siegel	10 Oct. 2013	Kittitas Co., WA	KM213663	–
	OKM25915*	NYBG	A. & A. Bessette	14 Oct. 1993	Clallum Co., WA	KM213664	–
X. salicicola	CS_5Mar2014-1	UCSC	C.F. Schwarz	5 Mar. 2014	Santa Cruz Co., CA	KU144791	KU144792
	UCSC-F-1028	UCSC	C.F. Schwarz	16 Sep. 2014	Santa Cruz Co., CA	KU144793	KU144794
	UCSC-F-1721	UCSC	A. Searcy	17 Jun. 2017	Santa Barbara Co., CA	MK583671	–
	UCSC-F-1720*	UCSC/NYBG	C.F. Schwarz	21 Aug. 2018	Santa Cruz Co., CA	MK552408	–
X. truncatus	Halling6878	NYBG	R. Halling	31 Jul. 1992	Westchester Co., NY	KU144795	–
	Halling6932	NYBG	R. Halling	23 Aug. 1992	Macon Co., NC	KM213665	–
	HDT22426	SFSU	H.D. Thiers	25 Jul. 1968	Emmet Co., MI	KU144796	–
	HDT22440	SFSU	H.D. Thiers	27 Jul. 1968	Mackinac Co., MI	KU144797	–
	HDT22590	SFSU	H.D. Thiers	31 Jul. 1968	Emmet Co., MI	KU144798	–
X. zelleri	JLF2977	OSC162212	J.L. Frank	10 Oct. 2013	Lane Co., OR	KM213666	KU144799
	NS102711	UCSC	N. Siegel	27 Oct. 2011	Clallum Co., WA	KM213667	–
	NS1284	OSC162213	N. Siegel	28 Oct. 2014	Clallum Co., WA	KU144800	–
	NS1285	UCSC	N. Siegel	28 Oct. 2014	Clallum Co., WA	KU144801	–
	NS1375	UCSC	N. Siegel	15 Nov. 2014	Mendocino Co., CA	KU144802	–
	W.A. Murrill 105*	NYBG	W. A. Murrill	20 Oct. 1910	King Co., WA	KU144803	–

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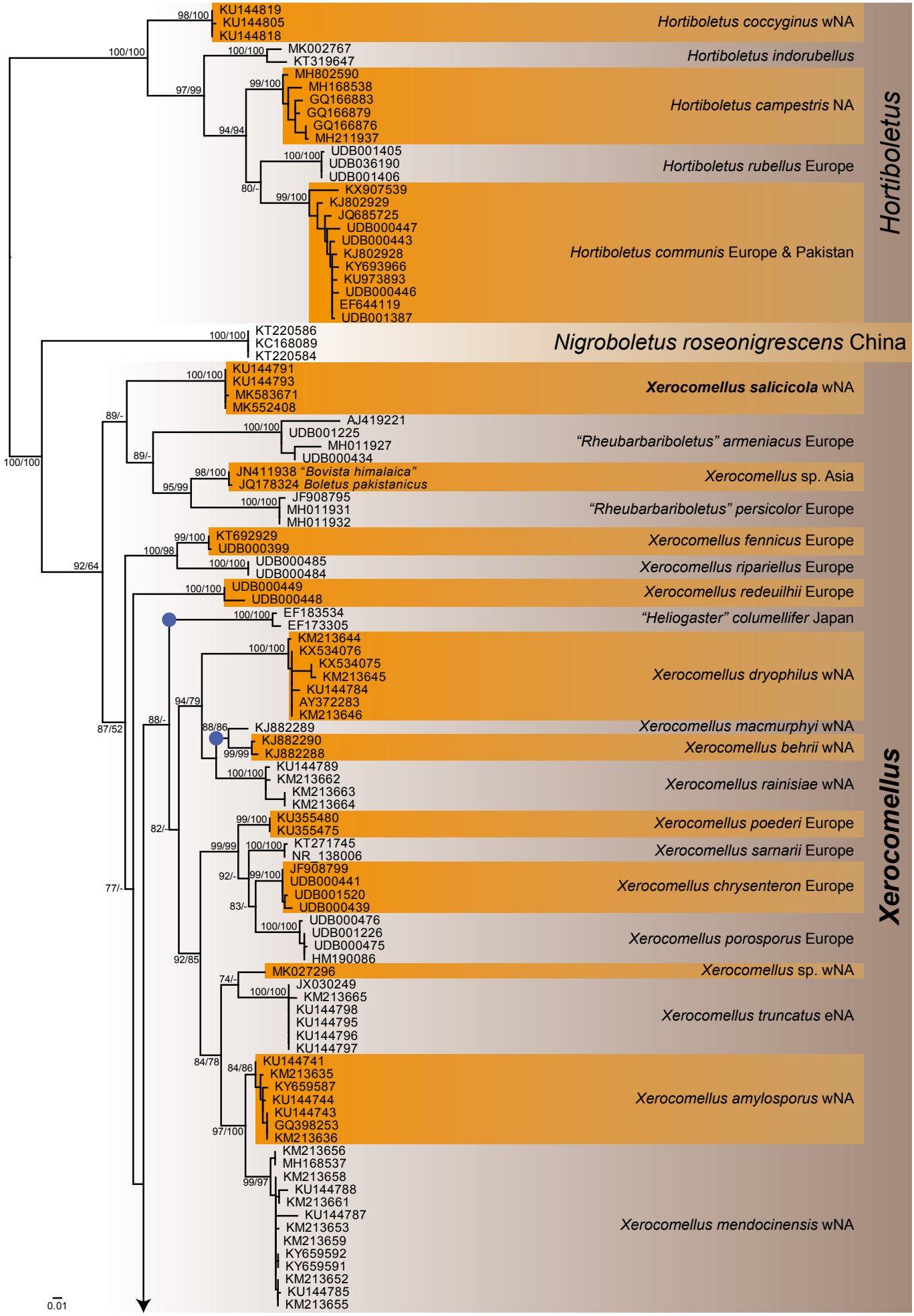
Table 1. (Continued).

Species	Collection No.	Fungarium	Collector	Date	County	ITS	LSU
OTHERS							
Hortiboletus coccyginus comb nov.	JLF3093	SOC	J.L. Frank	27 Oct. 2013	King Co., WA	KU144805	–
	CFS111711	UCSC	C.F. Schwarz	17 Nov. 2011	Santa Cruz Co., CA	KU144818	–
	NS110511	UCSC	N. Siegel	5 Nov. 2011	Curry Co., OR	KU144819	–
Hortiboletus campestris	DD614	SOC	D. Deshazer	30 Nov. 2006	Sonoma Co., CA	MH168538	MH203598
Hortiboletus sp.	DW101414	SOC	D. Winkler	14 Oct. 2014	King Co., WA		KU144804
Xerocomus "subtomentosus" sensu PNW	JLF2777	UCSC	R. Lebeuf	16 Dec. 2012	Santa Cruz Co. CA	KU144806	KU144807
	JLF2784	OSC162214	J.L. Frank	11 Jan. 2013	Santa Clara Co. CA	KU144808	KU144809
	CFS112712	UCSC	C.F. Schwarz	27 Nov. 2012	Santa Cruz Co. CA	KU144816	–
	NS120712	UCSC	N. Siegel	7 Dec. 2012	Santa Cruz Co. CA	KU144817	–
	JLF4012	UCSC/SOC	J.L. Frank	3 Jan. 2016	Santa Cruz Co, CA	KX534078	–
	JLF4060	UCSC/SOC	J.L. Frank	18 Jan. 2016	Santa Barbara Co. CA	KX534079	–
Xerocomus cf. spadiceus	JLF2961	OSC162215	J.L. Frank	9 Oct. 2013	Lane Co., OR	KU144810	–
	JLF3700	OSC162216/SOC	J.L. Frank	12 Sep. 2014	Jackson Co., OR	KU144811	–
	NS102812	UCSC	N. Siegel	28 Oct. 2012	Lane Co., OR	KU144812	KU144813
	NS111112	UCSC	N. Siegel	11 Nov. 2012	Humboldt Co., CA	KU144814	KU144815

*Denotes type collection.

**Denotes type of *Gastroboletus xerocomoides*.



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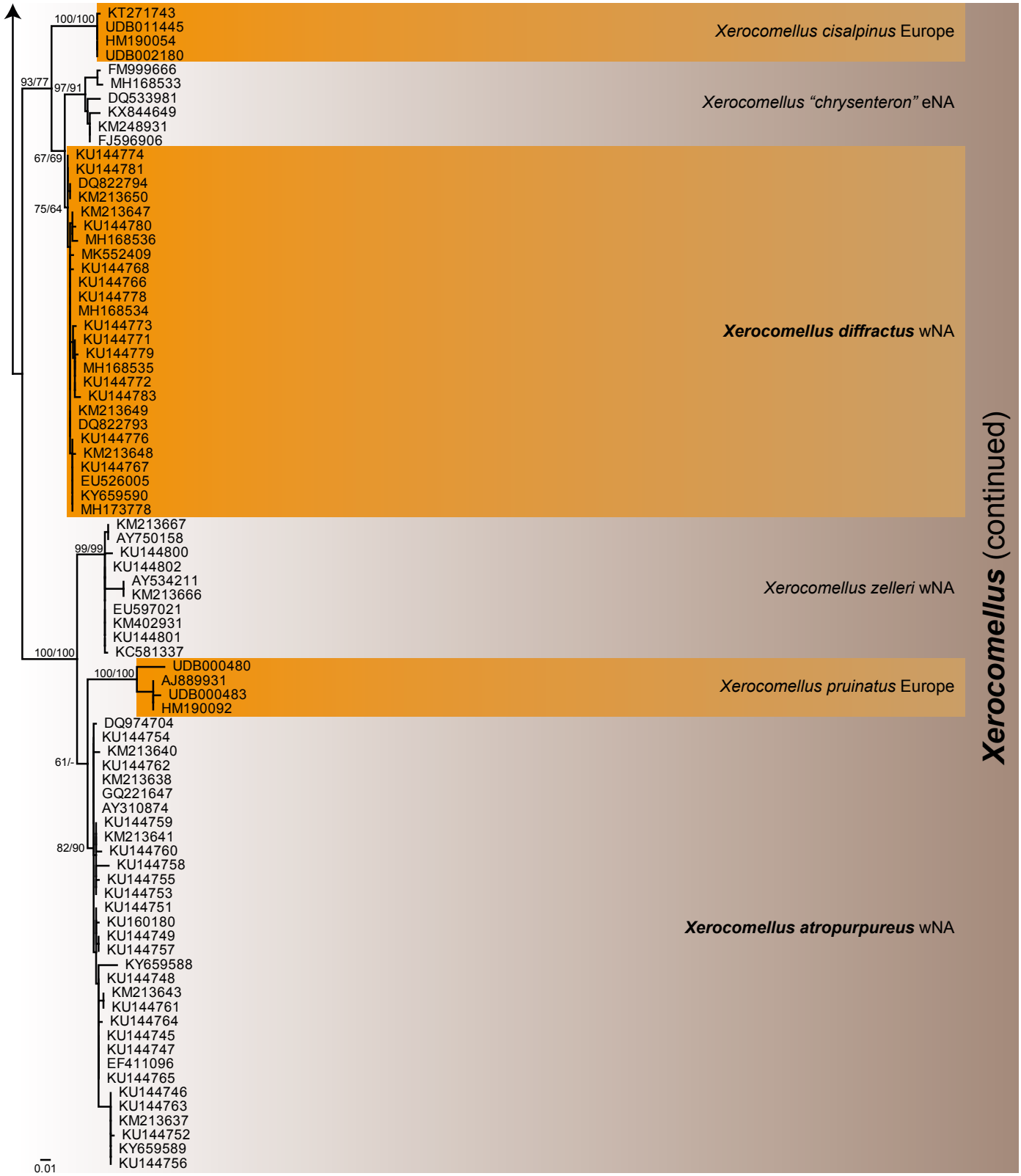

Fig. 1. (Continued).

Fig. 1. Phylogenetic tree obtained from a maximum likelihood analysis of ITS alignment using PHyML. Bootstrap support values >50 from 1 000 replicates for both ML/MP are indicated above the branches, or nearby. ● indicates the evolution of hypogeous fruiting habit. Species with names in bold are new species described in this paper. NA = North America, eNA = eastern North America, wNA = western North America.

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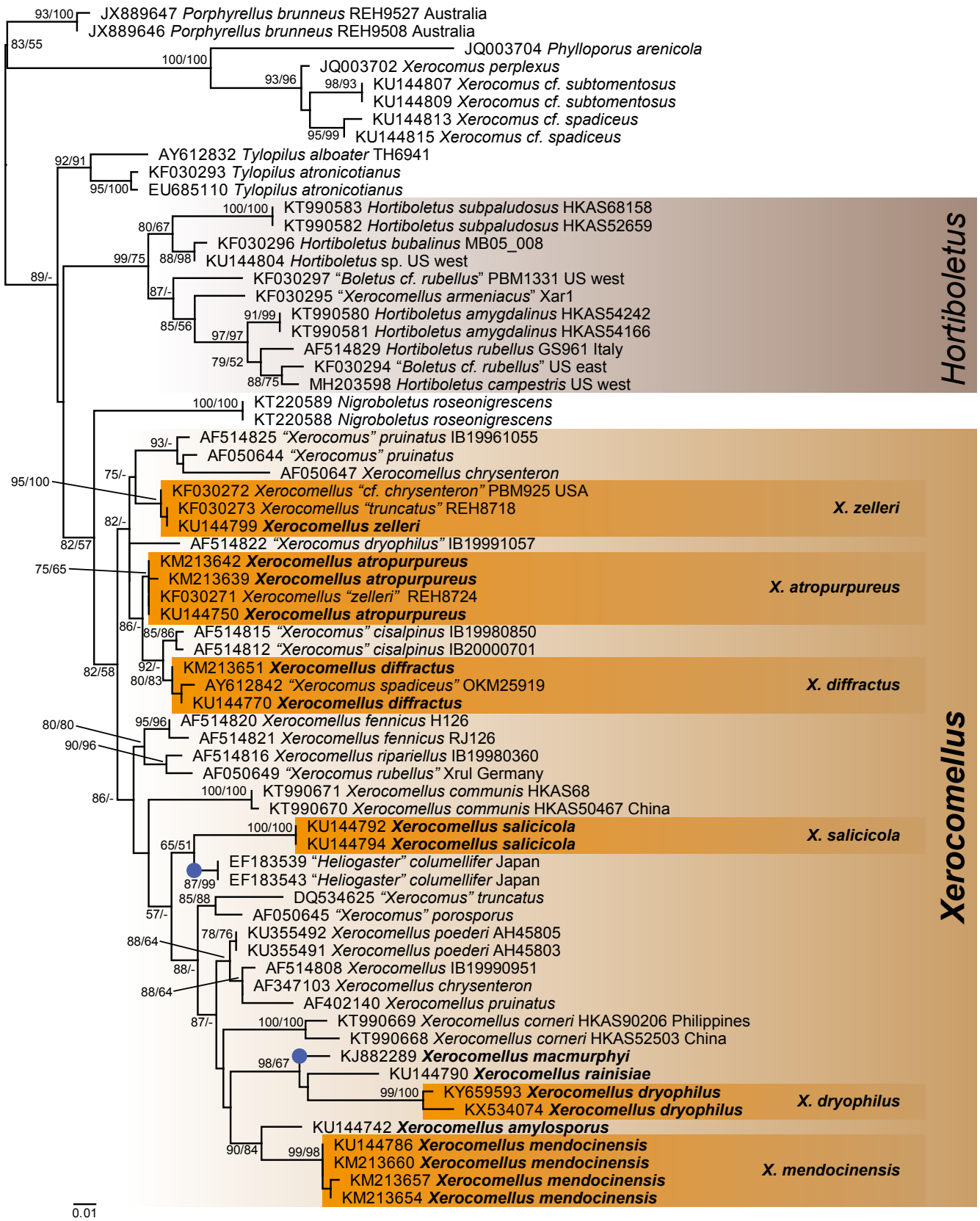

Fig. 2. Phylogenetic tree obtained from a maximum likelihood analysis of LSU alignment using PHyML. Bootstrap support values >50 from 1 000 replicates for both ML/MP are indicated above the branches, or nearby. Epithets in quotation marks are names as deposited in Genbank. ● indicates the evolution of hypogeous fruiting habit. Species with names in bold are those that occur in western North America.

Fig. 3. *Xerocomellus* basidiomata *in situ*. **A.** *X. amylosporus* (NS111112) **B.** *X. amylosporus* (JLF3012) **C.** *X. atropurpureus* (JLF3624) **D.** *X. atropurpureus* (NS1442) **E.** *X. diffractus* (JLF5745) **F.** *X. diffractus* (JLF3554) **G.** *X. dryophilus* (CSZVM-SCI-77) **H.** *X. dryophilus* (JLF4134).

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Materials examined: **USA**, California, Humboldt Co., Big Lagoon, 11 Nov. 2012, *N. Siegel* NS111112 (UCSC); Sierra Co., Yuba Pass (Type of *Gastroboletus xerocomoides*), 14 Sep. 1965, *H.D. Thiers* HDT13163 (SFSU); *Idaho*, Bonner Co., Kaniksu National Forest, Reeder Bay area, Priest Lake, 29 Sep. 1964, *A.H. Smith* AHS70936 (Type) (SFSU); Oregon, Jackson Co., Cascade-Siskiyou National Monument, 12 Nov. 2016, *J.L. Frank* JLF4665 (OSC162186); Marion Co., near French Creek, 17 Oct. 2013, *J.L. Frank* JLF3012 (OSC162184); Washington, Lewis Co., Iron Creek Campground, 7 Oct. 2014, *J.L. Frank* JLF3498 (OSC162185).

Notes: Smith (1965) described this species from Idaho as having "dark 'wood brown' spores," and placed it in the genus *Porphyrellus* based on spore color. Spore deposits we observed were olive brown to dark reddish olive, with darkness depending on the thickness and humidity of the deposited spore mass. The amyloid reaction of the spores may fade over time or may be weak in some collections. This species, or a very close relative, has recently been reported from the sky islands of southeastern Arizona (JLF unpubl. data). Collections in dry habitats tend to form gastroid basidiomata, and many Sierra Nevada collections are deformed. The ITS sequence of the type of *Gastroboletus xerocomoides* (HDT13163 GenBank KU144744) is identical to that of the type of *X. amylosporus* (Fig. 1). Gastroid morphological variation also occurs in *X. atropurpureus* in high-elevation arid habitats in the southern Cascade Range and the Sierra Nevada.

Xerocomellus atropurpureus J.L. Frank, N. Siegel & C.F. Schwarz, ***sp. nov.*** MycoBank MB821024. Figs 3C, D, 5B, 6B.
Misapplied names: *Boletus zelleri* (Murrill) Murrill *sensu* Thiers, California Mushrooms: 1975.
Xerocomellus zelleri (Murrill) Klofac *sensu* western North American authors.

Etymology: *atro-* (from *ater*, L.) = black, dark; *purpureus* (L.) = purple, referring to the color of the pileus.

Diagnosis: Basidiomata medium-sized to large, pileus (3–)5–10(–14) cm broad, with a glabrous, rugulose, blackish purple to dark reddish purple surface, yellow tubes and red stipe; pileus context whitish to yellow and typically remaining unchanged when cut, or sometimes staining blue erratically. Spores narrowly ellipsoid to subfusiform, 12.2–15.9 × 4.8–5.8 µm. Pileipellis a trichoderm made up of cylindrical cells with the terminal cells of same width or slightly wider than underlying cells. Fruiting from fall through spring (summer at higher elevations), typically under conifers, sometimes with *Quercus* and other hardwoods. Distinguished from other *Xerocomellus* (except *X. zelleri*) by the glabrous to finely pruinose, rugulose pileus surface, and contrasting coloration of the dark pileus, yellow pores, and evenly red stipe. Differs from the smaller and more slender *X. zelleri*, which has a trichoderm of subglobose to ellipsoid cells, with narrow awl-shaped terminal cells.

Typus: **USA**, Oregon, Douglas Co., Rogue River National Forest, Hamaker Campground, under *Pseudotsuga menziesii* and *Tsuga heterophylla*, 7 Nov. 2014, *J.L. Frank* 3620 (**holotype** OSC162192; **isotype** SFSU; **isotype** NYBG; **isotype** SOC); GenBank Accessions: ITS KU144749, LSU KU144750.

Description: *Pileus* (3–)5–10(–14) cm broad, rounded, bun-shaped to broadly convex at first, becoming plane, occasionally slightly wavy in age, dark blackish purple, deep reddish purple to dark wine-red or reddish brown, sometimes paler red, rarely with extensive olivaceous tones; surface dry to moist, usually glabrous or with a faint pale bloom, sometimes finely pruinose, rugulose to extensively bumpy-wrinkled, occasionally smoother; irregular cracking can occur in age or under dry conditions. *Hymenophore* (tube layer) pale yellow to yellow; pores and tubes usually concolorous; pores moderately small (2–4 per mm), round when young to slightly angular and wider in maturity, pale dull yellow to dingy greenish-yellow in age, occasionally bruising blue, occasionally reddish-blushed, or rarely extensively reddish. *Stipe* 4–12 × 0.8–3 cm, equal or with enlarged base; surface extensively red over a yellowish background, often with red punctations aggregated into blurry chevrons and streaks, rarely staining blue; base often white. *Context* in pileus firm, pale yellow to creamy white, typically not staining, sometimes erratically staining bluish; context in stipe fibrous, light yellow to creamy whitish, occasionally bluing, more often in base. *Odor* indistinct. *Taste* mild to lemony. *Spore deposit* dull olive brown. Spores (11–)12.2–15.9(–16.6) × (4.6–)4.8–5.8(–6.2) µm, av. 13.8 × 5.3 µm, avQ = 2.5, subfusoid to subcylindrical, inequilateral, smooth, inamyloid. *Basidia* 19.6–29.9 × 7.4–11.8(–13) µm, narrowly to broadly clavate, hyaline, 4-spored. *Hymenial cystidia* 40–60 × 8–12 µm, ventricose, hyaline, rare. *Pileipellis* a trichoderm with cylindrical to elongated cells with brown walls; some terminal cells clavate, slightly wider than underlying cells, some narrow with dark incrustations. *Clamp connections* absent.

Distribution and ecology: USA and Canada – From British Columbia south at least to Monterey County, California along the coast, inland to the Sierra Nevada and Cascade Range; common over most of its distribution area. Solitary or scattered in small groups, sometimes cespitose, in mixed forests, typically with conifers, especially *Pseudotsuga menziesii*, *Pinus radiata, P. muricata*, *Tsuga heterophylla,* and *Picea sitchensis*; occasionally emerging from well-rotted wood. Fruiting from late fall into early spring, and at high elevations in summer.

Additional materials examined: **USA**, California, El Dorado Co., 22 Dec. 2014 *T. Chesney & C. Hodge* MO194036 (UCSC); Humboldt Co., 21 Oct. 2014, *N. Siegel* NS1251 (UCSC); Big Lagoon, 23 Oct. 2014, *N. Siegel* NS1269 (UCSC); Elk Head, Trinidad Beach State Park, 19 Nov. 2014, *N. Siegel* NS1393 (UCSC); Lassen Co., 14 Dec. 2015, *N. Siegel* NS1442 (UCSC); Mendocino Co., 7 Dec. 2012, *N. Siegel* NS120712 (UCSC); Monterey Co., 13 Jan. 2013, *P. Laughlin* JLF2795 (UCSC); Marin Co., 21 Jan. 2014, *J.L. Frank* JLF3196 (SFSU); Nevada Co., 11 Nov. 2014, *D. Arora* JLF3379 (UCSC); North San Juan, 13 Dec. 2014, *N. Siegel* NS1346 (UCSC); Plumas Co., Lassen National Forest, Grizzly Creek Ridge, 14 Jun. 2015, *N. Siegel* NS1432 (UCSC); Oregon, Douglas Co., Rogue River National Forest, Hamaker Campground, 7 Nov. 2014, *J.L. Frank* JLF3624 (OSC162193); west of Sutherlin near the Umpqua River, 8 Dec. 2014, *J.L. Frank* JLF3695 (OSC162196); Jackson Co., near Butte Falls, 24 Nov. 2014, *J.L. Frank* JLF3654 (OSC162194); JLF3656 (OSC162195); 12 Nov. 2016, *J.L. Frank* JLF4664 (UCSC); Lane Co., near Florence, 11 Oct. 2013, *J.L. Frank* JLF2995 (OSC162188); 21 Apr. 2015, *J.L. Frank* JLF3806 (OSC162197); 1 Nov. 2014, *N. Siegel* NS1296 (UCSC); NS1297 (UCSC); 2 Apr. 2016, *A. Moore* JLF4238 (UCSC); Marion Co., near French Creek, 30 Nov. 2011, *J.L. Frank* JLF2379 (OSC162187); Humbug Campground, 18 Oct. 2013, *J.L. Frank* JLF3018 (OSC162189); Washington, Clallum Co., 28 Oct. 2014, *N. Siegel* NS1288 (UCSC); Kittitas Co. 24 Oct. 2014, *N. Siegel* NS1276 (UCSC); Lewis Co., Mount Rainier National Park, Ohanapecosh Campground, 8 Oct. 2014, *J.L. Frank* JLF3502 (OSC162190); 13 Oct.

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Fig. 4. *Xerocomellus* basidiomata *in situ*. **A.** *X. mendocinensis* (NS110511) **B.** *X. mendocinensis* (CFS10Nov2012_1) **C.** *X. rainisiae* (NS1952) **D.** *X. rainisiae* (JLF3523) **E.** *X. salicicola* (UCSC-F-1720) **F.** *X. salicicola* (UCSC-F-1721) **G.** *X. zelleri* (NS1955) **H.** *X. zelleri* (NS102711)

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2014, *J.L. Frank* JLF3545 (OSC162191); Iron Creek Campground, near Randle, 16 Oct. 2019, *N. Siegel* NS4565 (private herbarium).

Notes: *Xerocomellus atropurpureus* is distinguished from other *Xerocomellus* species by the glabrous to finely pruinose, rugulose pileus surface, and contrasting coloration of the dark pileus, yellow pores, and evenly red stipe. It is most similar in appearance to *X. zelleri sensu stricto*, and indeed, our phylogenetic analyses found that this species was one of two lineages within the existing concept of *X. zelleri*. Interestingly, *X. atropurpureus* appears to be the more common bolete to which the epithet *zelleri* has been applied. Our sampling suggests that *X. zelleri* described by Murrill in 1912 from the Seattle area is less common and likely restricted to the coastal Pacific Northwest and northern California where it is rare.

Morphological criteria to distinguish these two species are subtle – *X. atropurpureus* more often has a reddish purple to wine purple pileus rather than the dark vinaceous black, dark olivaceous black to brownish black or olive brown to gray pileus of *X. zelleri*. Additionally, *X. atropurpureus* has a glabrous to finely pruinose surface rather than the slightly velvety surface of *X. zelleri*. *Xerocomellus zelleri* almost always shows a narrow, pale band around the pileus margin, whereas this feature is more variable in *X. atropurpureus. Xerocomellus zelleri* is less likely to show blue staining, but this is complicated by the variation in blue staining reactions of *X. atropurpureus*. Microscopically, *X. atropurpureus* spores are slightly smaller on average than those of *X. zelleri;* 13.8 × 5.3 µm for *X. atropurpureus versus* 14.2 × 5.4 µm for *X. zelleri.* The trichodermal pileipellis of *X. atropurpureus* is made up of cylindrical cells with the terminal cells of same width or slightly wider than underlying cells; the cells making up the trichoderm of *X. zelleri* are globose to ellipsoid, with often narrow awl-shaped terminal cells (Fig. 6H). Geography may prove useful in identification, since *X. zelleri* appears to have a more northerly, coastal distribution.

Some collections of *X. atropurpureus* from dry, mixed-conifer forest, notably NS1432 from Lassen National Forest, exhibit semi-sequestrate, secotioid basidiomata.

Xerocomellus pruinatus is the European counterpart of these two western North American species (Fig. 1), and is likewise characterized by a dark pileus surface that either does not crack or occasionally develops small areolate patches showing pale context in age.

Dark forms of *X. mendocinensis* have been mistaken for *X. atropurpureus* or *X. zelleri*; however, *X. mendocinensis* rapidly stains dark blue, and is typically associated with hardwoods; it also shows more distinct punctations on the stipe.

Xerocomellus behrii (Harkn.) Castellano, M.E. Sm. & J.L. Frank, *Mycologia* **110**: 612. 2018.
Basionym: *Splanchnomyces behrii* Harkn., *Bull. Cal. Acad. Sci*. **1**: 30. 1884.
Synonyms: *Hymenogaster behrii* (Harkn.) DeToni, *Syll. Fung*. **7**: 174. 1888.
Arcangeliella behrii (Harkn.) Zeller & C.W. Dodge, *Ann. Missouri Bot. Gard*. **22**: 366. 1935.

Notes: One of two hypogeous (truffle-morphology) species in *Xerocomellus* from western North America that are mycorrhizally associated with *Quercus* in California and Oregon; *X. behrii* differs from *X. macmurphyi* by its smaller spores and by spore ornamentation; for more details on the xerocomelloid truffles see Smith *et al*. (2018).

Xerocomellus diffractus N. Siegel, C.F. Schwarz, & J.L. Frank, ***sp. nov.*** MycoBank MB821025. Figs 3E, F, 5C, 6C.
Misapplied names: Boletus chrysenteron Bull. *sensu* Thiers, California Mushrooms: 79–81. 1975.
Xerocomellus chrysenteron (Bull.) Quél. *sensu* western North American authors.

Etymology: From *diffringere* (L.) – "to break", referring to the extensively cracking pileus surface.

Diagnosis: Basidiomata medium-sized with a cracking olive to olive gray or dull brownish pileus, yellow pores that slowly stain blue, and yellowish stipe streaked with red, becoming more extensively red from the base up in age; context whitish to yellow, staining slowly to moderately or erratically blue when cut and exposed. Spores 12.9–16.2 × 5.1–6.2 µm, subfusoid to subcylindrical. Occurring under both conifers and hardwoods from southern California into British Columbia, Canada, east into the northern Rocky Mountains, and south to Arizona. Distinguished from other *Xerocomellus* species by its geographical location, ecology, and ITS sequences.

Typus: **USA**, Oregon, Jackson Co., Rogue River Siskiyou National Forest, 5 miles NE of Howard Prairie Lake, in mixed conifer forest, 8 Oct. 2017, *J.L. Frank* 5745 (**holotype** OSC162203, **isotype** SFSU, **isotype** NYBG, **isotype** SOC); GenBank Accession: ITS MH168534.

Description: *Pileus:* 3–10(–14) cm broad, rounded, bun-shaped to broadly convex at first, becoming flat, occasionally slightly wavy in age, olive, olive gray to leather brown or tan, becoming paler in age, more rarely reddish to pinkish brown; surface dry, finely velvety, becoming cracked, at first showing whitish to pale yellow flesh in these cracks, becoming pinkish in age. *Hymenophore* (tube layer) sunken around stipe, 0.5–1.5 cm long. *Pores* small and round at first, enlarging and becoming slightly angular, 1–3(–4) per mm; pale yellow to dingy greenish yellow in age, staining blue to bluish gray, slowly to moderately when bruised. *Stipe* 4–10 × 0.8–2 cm, equal or with an enlarged base, yellow to golden, streaked with fine red punctations with red pigment more concentrated toward base, often sparse or absent entirely towards apex, in age becoming more red upward. *Context* firm when young, becoming soft, whitish to pale yellow in pileus, yellow in stipe, bluing slowly to moderately or erratically. *Odor* indistinct. *Taste* mild. *Spore deposit* dull olive brown. *Spores* (12.5–)12.9–16.2 × (4.7–)5.1–6.2 µm, av. 14.3 × 5.5 µm, avQ= 2.6, subfusoid to subcylindrical, inequilateral to cylindrical in side view, inamyloid. *Basidia* 18.5–27.2 × 7.5–11.5 µm, clavate, hyaline, 4-spored. *Hymenial cystidia* 38.9–49.5 ×

Fig. 5. *Xerocomellus* basidiospores. **A.** *X. amylosporus* (JLF3012) **B.** *X. atropurpureus* (JLF3620) **C.** *X. diffractus* (JLF5745) **D.** *X. dryophilus* (JLF4791) **E.** *X. mendocinensis* (JLF2775) **F.** *X. rainisiae* (JLF3523). **G.** *X. salicicola* (UCSC-F-1720) **H.** *X. zelleri* (JLF2977). Scale bar = 10 µm. Arrows indicate truncate spores.

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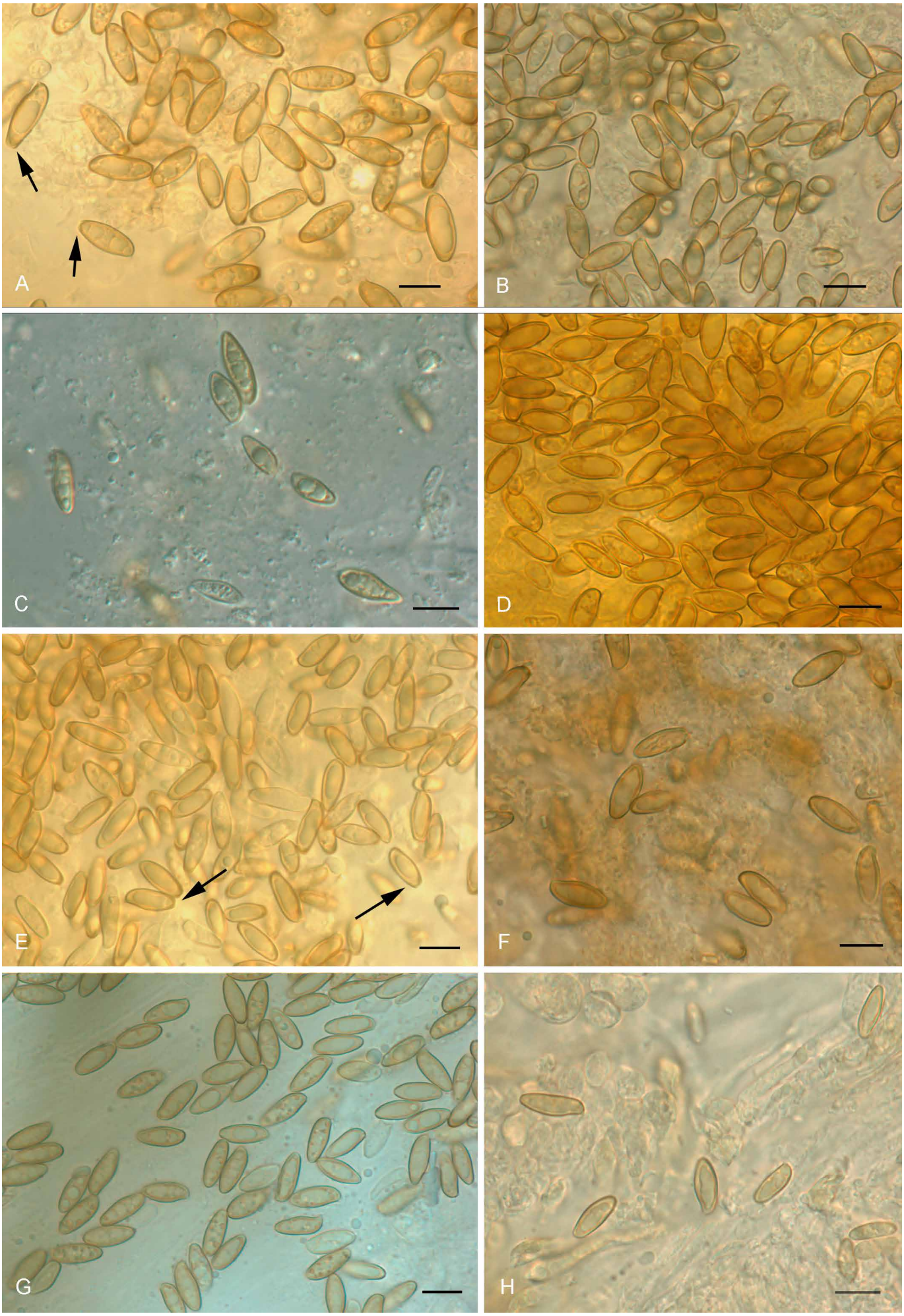

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11.6–11.9 µm, ventricose to subclavate, infrequent. *Pileipellis* a trichoderm made up of cylindrical to elongated cells; terminal cells 5–7 µm wide, often narrower than those lower down; pigment brown, parietal and incrusting, but light to absent in many terminal cells. *Clamp connections* absent.

Distribution and ecology: USA and Canada – from central California, through the Pacific Northwest into British Columbia, Canada, east to the Rocky Mountains of Wyoming, and south into Arizona. Solitary or scattered in troops under both conifers and hardwoods; common. Fruiting in fall and early winter, or occasionally in spring on the California and Oregon coast, and summer in the Southwest, and at higher elevations.

Additional materials examined: **USA**, Arizona, Graham Co., Mt Graham, 12 Aug. 2018, *J.L. Frank* JLF6546 (SOC, GILB); California, Humboldt Co., near Trinidad, 10 Nov. 2012, *N. Siegel* NS111012 (UCSC); 20 Oct. 2014, *N. Siegel* NS1246 (UCSC); Marin Co., 16 Jan. 2014, *J.L. Frank* JLF3195 (UCSC); Mendocino Co., Angelo Coast Range Reserve, 6 Dec. 2012, *N. Siegel* NS120612 (UCSC); near Caspar, 14 Nov. 2014, *N. Siegel* NS1366 (UCSC); NS1369 (UCSC); NS1371 (UCSC); Jackson State Demonstration Forest, 15 Nov. 2014, *N. Siegel* NS1376 (UCSC); NS1378 (UCSC); Nevada Co., North San Juan, 14 Dec. 2014, *N. Siegel* NS1438 (UCSC); Trinity Co., east of Willow Creek, 10 Nov. 2014, *N. Siegel* NS1344 (UCSC); Oregon, Jackson Co., near Ashland Creek, 29 Oct. 2012, *J.L. Frank* JLF2644 (UCSC); Butte Falls, 30 Oct. 2017, *J.L. Frank* JLF5915 (OSC162204); JLF5930 (OSC162205); Lane Co., near Florence, 27 Oct. 2014, *J.L. Frank* JLF3585 (OSC162202); near Eugene, 3 Apr. 2016, *J.L. Frank* JLF4239 (UCSC); Lincoln Co., near Newport, 3 Nov. 2014, *N. Siegel* NS1298 (UCSC); Washington: Lewis Co., Camp Arnold, 9 Oct. 2014, *J.L. Frank* JLF3528 (UCSC); 10 Oct. 2014, *J.L. Frank* JLF3532 (UCSC); Rocky Point, 11 Oct. 2014, *N. Siegel* JLF3535 (OSC162198); La Wis Wis Campground, 14 Oct. 2014, *J.L. Frank* JLF3554 (OSC162199); JLF3555 (OSC162200); JLF3559 (OSC162201); Wyoming: Park Co., Yellowstone National Park, 29 Sep. 2014, *N. Siegel* NS1230 (UCSC).

Notes: This morphologically variable western North American species has commonly been called *X. chrysenteron* (Thiers 1975, Arora 1986, Desjardin *et al.* 2015). Our data show that *X. diffractus* is more closely related to *X. atropurpureus* and *X. zelleri* than to the European *X. chrysenteron sensu stricto* (Figs 1, 2). Molecular data show an eastern North American *X. chrysenteron*-like species as sister to *X. diffractus* (Fig. 1), while the true *X. chrysenteron* from Europe appears to be more distantly related within *Xerocomellus*.

Xerocomellus amylosporus has a darker pileus with more scattered and irregular cracks, a stipe that develops brownish tones, pores that bruise darker (inky) blue, a spore deposit that is more reddish brown in color, and larger, distinctly truncate spores. *Xerocomellus salicicola* has a light brown to reddish pileus developing extensive cracking, an obscurely reticulate stipe that is extensively red or retains a red band near the apex, and grows with *Salix* and *Betula*. *Xerocomellus mendocinensis* has quickly blue-staining pores and a coarsely punctate stipe that is often extensively red or with a distinct red belt near the apex, and smaller truncate spores. *Xerocomellus dryophilus* has a more rosy red to pinkish brown pileus, stains blue more quickly and deeply, and grows with *Quercus,* but in dry conditions basidiomata can be hard to distinguish from *X. diffractus.*

Xerocomellus dryophilus (Thiers) N. Siegel, C.F. Schwarz & J.L. Frank*, Index Fungorum* **179**: 1. 2014. Figs 3G, H, 5D, 6D.
Basionym: *Boletus dryophilus* Thiers, California mushrooms: 82. 1975.
Synonym: *Xerocomus dryophilus* (Thiers) Singer, *Agaric. mod. Tax.*, Edn **4**: 763. 1986.
Excluding *Xerocomellus dryophilus sensu* European authors (= *X. redeuilhii).*

Description: *Pileus* 3–8(–11) cm broad, hemispheric or bun-shaped to broadly convex and then plane in age, rosy red to vinaceous red, rosy red or brick-red when fresh, becoming dull tan-brown with pinkish or reddish tones in dry weather, occasionally with olive tones to extensively olive; surface dry, velvety-floccose and usually extensively cracked into plaques or scales; context in cracks pallid yellowish white, often with some pink tones. *Hymenophore* (tube layer) sunken around stipe; pores large, slightly angular or irregularly shaped, pale yellow to dingy yellow or lemon-yellow, bruising blue quickly when damaged. *Stipe* 3–12 × 1–4 cm, cylindrical, straight or slightly curved (sometimes slightly sinuous), enlarged or clavate at base, often tapered and sometimes slightly rooting at extreme base, lemon yellow or dull yellow over upper half, red to wine red near base; reddish pigment sometimes appearing finely punctate over surface; basal tomentum yellowish. *Context* pale to bright yellow, bruising blue rapidly. *Odor* indistinct. *Taste* mild. *Spore deposit* dull olive brown. *Spores* (11.1–)12–15.7(–16.1) × (5.3–)5.8–6.9(–7.9) µm, av. 13.6 × 6.2 µm, avQ = 2.2, subellipsoid to subfusoid, smooth, inamyloid. *Hymenial cystidia* of two types: i) 23–29.8 × 6.5–8.6 µm, scattered to abundant, often fasciculate, narrowly clavate, and ii) 30.2–42.9 × 10.1–12.6 µm, scattered, clavate. *Pileipellis* a trichoderm made up of elongated cells, 8–10 µm wide; terminal cells not differentiated; pigment brown, coarsely encrusting in lower elements, finely encrusting in terminal cells. *Clamp connections* absent.

Distribution and ecology: USA and Mexico – from northern Baja California, Mexico, and California, USA**.** Common in *Quercus agrifolia* forests throughout the California Floristic Province including Channel Islands, uncommon north of the San Francisco Bay Area, where it is more often found away from the immediate coast in drier, warmer, more exposed groves of *Q. agrifolia* and possibly other *Quercus* spp.*;* frequently parasitized by *Hypomyces* sp.*,* sometimes affecting a high percentage of basidiomata and preventing sporulation (Douhan & Rizzo 2003).

Materials examined: **USA**, California, Santa Barbara Co., 28 Jan. 1967, *H.D. Thiers* HDT18557 Type (SFSU); Santa Cruz Island, 29 Dec. 2012, *C.F. Schwarz* CSZVM-SCI-77 (UCSC); Los Padres National Forest, Paradise Rd, 28 Feb. 2016, *J.L. Frank* JLF4134 (UCSC); Santa Cruz Co., Quail Hollow Ranch, 3 Nov. 2011, *C.F. Schwarz* CFS3Nov11-1 (UCSC); CFS3Nov11-2 (UCSC); 3 Jan. 2016, *J.L. Frank* JLF3996 (SFSU).

Fig. 6. *Xerocomellus* pileipellis. **A.** *X. amylosporus* (JLF3498) **B.** *X. atropurpureus* (JLF3620) **C.** *X. diffractus* (JLF5745) **D.** *X. dryophilus* (JLF4881) **E.** *X. mendocinensis* (JLF4835) **F.** *X. rainisiae* (JLF3523). **G.** *X. salicicola* (UCSC-F-1720) **H.** *X. zelleri* (NS1284). Scale bar = 10 µm.

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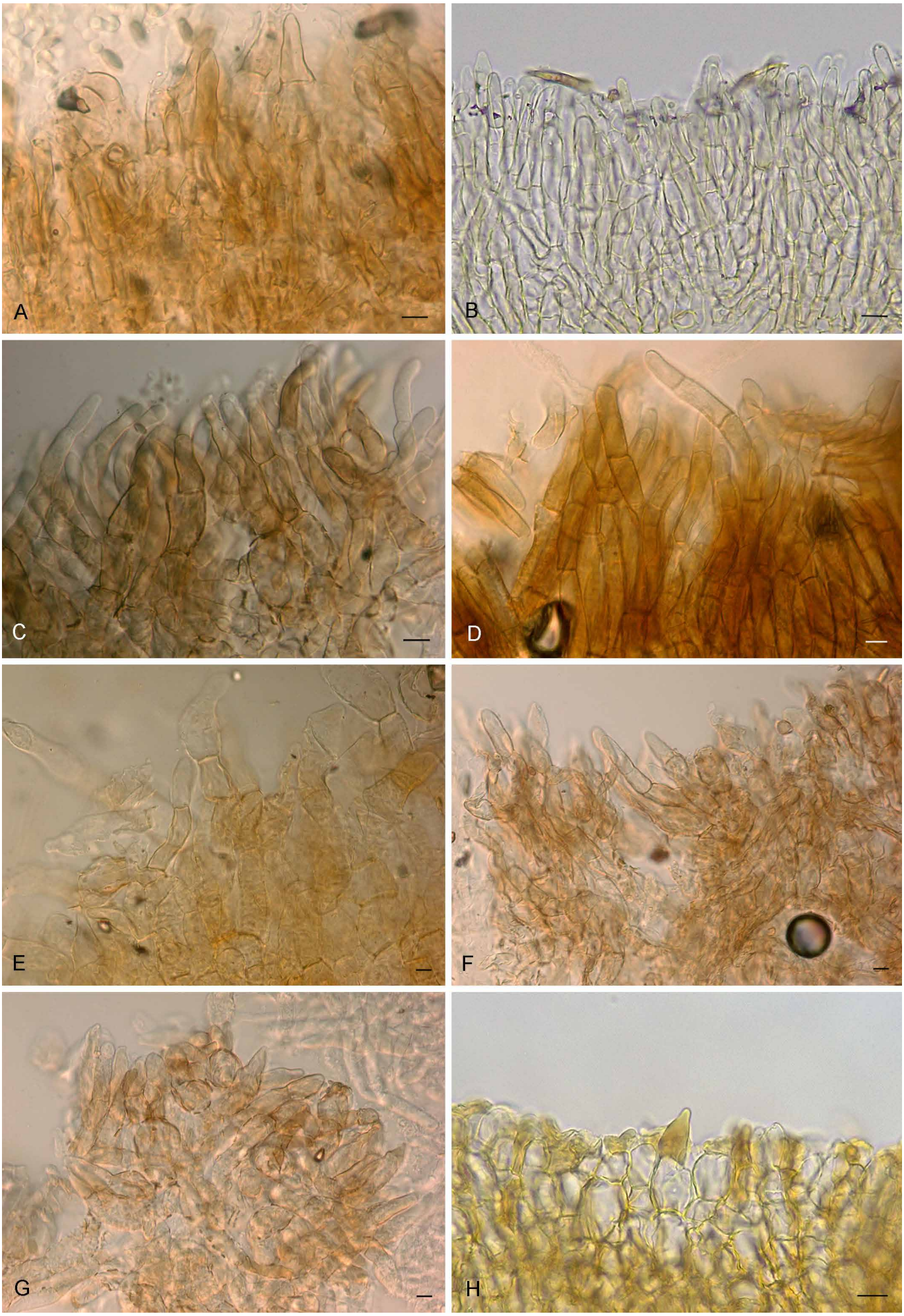

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Notes: Basidiomata of this species can be distinguished by distinctly reddish to pinkish brick colored, extensively cracked pilei, bicolored aspect of the stipe (red at base, yellow over upper half), and growth with *Quercus*. Basidiomata of *X. zelleri* and *X. atropurpureus* have smoother, darker wine red to nearly blackish-purple pilei that rarely become areolate in age, and lack the distinctly blue staining pores of *X. dryophilus*. Older or faded specimens of *X. dryophilus* might be mistaken for *X. diffractus* or *X. mendocinensis*, which have darker blackish or light gray tan, medium gray brown, or dark gray olive pilei, either lacking pinkish or reddish tones, or these restricted to cracks and damaged areas of the pileus flesh. The more extensively red and punctate stipe of *X. mendocinensis* is another good distinguishing feature, as this is the species which most commonly grows intermixed with *X. dryophilus.* A European species, to which this North American epithet had been applied was recently described as *X. redeuilhii* (Simonini *et al*. 2016).

Xerocomellus macmurphyi (Zeller & C.W. Dodge) Castellano, Saylor, M.E. Sm., & J.L. Frank, *Mycologia* **110**: 610. 2018.
Basionym: *Hymenogaster macmurphyi* Zeller & C.W. Dodge, *Ann. Missouri Bot. Gard*. **21**: 658. 1934.

Notes: Fruiting with *Quercus* spp. in California and Oregon from January to April, and forming a light brown smooth to finely tomentose peridium, with an interior of frosted brown locules, this otherwise nondescript little brown truffle was initially placed in the hypogeous catch-all genus *Hymenogaster* because its spores can appear ornamented with ridges. More recent collections were identified as *Octaviania* or *Octavianina* due to observed spore ornamentation of coarse spiny warts that appear to form underneath an outer membrane that appears as ridged (Frank 2005). For images and more details, see Smith *et al.* (2018). Additional images can also be viewed at: https://www.inaturalist.org/observations/18266184

Xerocomellus mendocinensis (Thiers) N. Siegel, C.F. Schwarz & J.L. Frank, ***comb. nov.*** MycoBank MB821028. Figs 4A, B, 5E, 6E.
Basionym: *Boletus mendocinensis* Thiers, California Mushrooms: 84. 1975.
Misapplied names: *Boletus truncatus* (Singer *et al.*) Pouzar *sensu* Thiers, California Mushrooms: 106–107. 1975.
Boletus pulverulentus Opat. *sensu* Thiers, California mushrooms: 66–67. 1975 (*pro parte*).

Description: *Pileus* 3–10 cm broad, hemispherical to bun-shaped when young, eventually broadly convex, nearly plane, sometimes wavy, most often dark olive brown when young, sometimes cool gray or nearly blackish, soon olive tan or medium brown, sometimes medium gray in age; surface dry, finely velvety, usually cracking over outer quartile of pileus radius, sometimes becoming extensively cracked over most of surface (usually in age or dry weather), rarely not cracking at all; context between pileus cracks dull tan brown to strongly pinkish or dull red. *Hymenophore* (tube layer) sunken around stipe; pores round and more densely packed when young, somewhat angular in age, pallid yellow at first, soon bright yellow, then dull yellow with orange-brown tones, occasionally orange-red to red, quickly and intensely bruising strongly blue when damaged. *Stipe* 4–10 × 1–2.5 cm, cylindrical, equal to clavate, extensively red to rose red with red punctation over a yellow ground color; uppermost part of stipe often with strongest red hues, sometimes appearing as a red band near apex, staining dark blue when handled. *Context* in pileus pale whitish yellow, moderately to strongly bluing when exposed, stipe fibrous, pale whitish yellow, with darker yellow to red in base, staining blue when cut. *Odor* indistinct. *Taste* mild. *Spore deposit* olive brown. *Spores* (9.7–)11.7–15.1(–16.7) × 4.3–5.4(–5.8) µm, av. 13.2 × 4.9 µm, avQ = 2.7, subfusoid to subcylindrical, inequilateral, roughly half with truncate apex, smooth, inamyloid. *Hymenial cystidia* 31.6–54.1 × 9.9–13.6 µm, cylindrical or ventricose with elongated apex, infrequent. *Pileipellis* a trichoderm with elongated cells and erect irregular to clavate to conical or hardly differentiated terminal cells; pigment brown, coarsely encrusting in lower elements, light brown and parietal in terminal cells. *Clamp connections* absent.

Distribution and ecology: USA – California, Oregon and Washington, at least as far south as San Diego county, likely also occurring in northwestern Mexico, and expected into southern British Columbia, Canada. Solitary, in small groups or scattered in troops, typically not clustered. Found in a wide variety of forest types; commonly in California under *Quercus agrifolia* and *Notholithocarpus densiflorus*, sometimes with *Chrysolepis chrysophylla*, and with conifers in the Pacific Northwest. Fruiting from mid-fall into mid-winter, and occasionally in spring.

Materials examined: **USA**, California, Mendocino Co., 8 Jan. 1967, H.D. Thiers HDT18392 **holotype** (SFSU); 14 Nov. 2014, *N. Siegel* NS1367 (UCSC); Santa Barbara Co., Los Padres National Forest, 16 Dec. 2016, *J.L. Frank* JLF4821 (UCSC); JLF4835 (UCSC); Santa Cruz Co., 1 Nov. 2011, *C.F. Schwarz* CFS1Nov11-1 (UCSC); CFS1Nov11-2 (UCSC); 10 Nov. 2012, *C.F. Schwarz* CFS10Nov2012-1 (UCSC); 16 Dec. 2012, *J.L. Frank* JLF2775 (UCSC); Trinity Co., east of Willow Creek, 10 Nov. 2014, *N. Siegel* NS1333 (UCSC); Oregon, Curry Co., Gold Beach, 5 Nov. 2011, *N. Siegel* NS110511 (OSC162206); Jackson Co., Butte Falls, 30 Oct. 2017, *J.L. Frank* JLF5926 (OSC162208); Marion Co., near Detroit, 10 Nov. 2011, *J.L. Frank* JLF2298 (UCSC); Washington: Lewis Co., Gifford Pinchot National Forest, La Wis Wis Campground, 14 Oct. 2014, *J.L. Frank* JLF3558 (OSC162207).

Notes: Because the ITS sequence of the type collection of *X. mendocinensis* is identical to the bulk of western North American collections labeled as "*truncatus*," we broaden the concept of *X. mendocinensis* to include *X. truncatus sensu* western North American authors (Thiers 1975, Arora 1986, Desjardin *et al.* 2015). In the majority of collections examined, the spore apex shape varies from truncate to convex, with typically about half the spores truncate. However, Thiers noted unusually large spore dimensions, "15–21(–27) × 4–5(–6) µm" and we confirmed that this collection (HDT18392) has anomalously large spores up to 27 µm with Q > 4 and a convex, non-truncate apex. For these reasons to confirm the identity of the type collection, we re-extracted DNA from the type collection and sequenced the ITS region for a second time. The stipe of *X. diffractus* is less red overall (more yellow), with red tones concentrated towards the base of the stipe and typically lacking strong red punctations. In addition, the blue staining of both *X. diffractus* and *X. amylosporus* is slower and less pronounced than in *X. mendocinensis*. The darker, rarely cracking pilei that more often show purple-red tones, more evenly smooth and non-punctate stipes, and typical lack of blue bruising in basidiomata of *X. zelleri* and *X. atropurpureus* are helpful features for distinguishing those species from *X. mendocinensis*.

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Xerocomellus rainisiae (Bessette & O.K. Mill.) N. Siegel, C.F. Schwarz & J.L. Frank [as "*rainisii*"], *Index Fungorum* **179**: 1. 2014. Figs 4C, D, 5F, 6F.
Basionym: *Boletus rainisiae* Bessette & O.K. Mill. [as *"rainisii"*], in Bessette *et al*., North American Boletes: 145. 2000.
Synonym: *Cyanoboletus rainisiae* (Bessette & O.K. Mill.) Gelardi *et al.* [as *"rainisii"*], *Index Fungorum* **176**: 1. 2014.
Misapplied name: *Boletus pulverulentus* Opat. *sensu* Thiers, California mushrooms: 66–67. 1975 (pro parte).

Description: *Pileus* 4–12 cm broad, rounded to convex when young, becoming broadly convex to nearly plane; margin downturned, becoming even, occasionally uplifted in age; surface dry, velvety to velvety-tomentose when young, more appressed-tomentose and conspicuously areolate in age, dark olive, olive-brown to blackish brown when young, becoming paler olive-brown, olive gray to yellowish brown with yellowish context showing between cracks in age, instantly staining greenish black when damaged. *Hymenophore* (tube layer) broadly attached, or with a narrow notch at stipe, 0.5–1.5 cm long; pores tiny (2–3 per mm), round to angular, yellow to golden yellow when young, becoming dark golden yellow to yellow-olive, and often developing a reddish blush with age, quickly staining dark blue-green when bruised, then slowly brownish. *Stipe* 3–9 × 1–3.5 cm, enlarged lower when young, becoming more equal with age, with a pinched base; surface dry, smooth, at base with white mycelium, bright yellow to golden yellow, often tinged with reddish longitudinally streaks, and red blotches near base, staining dark blue-green to dark teal-blue to greenish black when handled. *Context* in pileus moderately thick, firm, yellow with red in stipe base and around larva tunnels, staining blue when cut. *Odor* and *taste* indistinct. *Spore deposit* olive brown. *Spores* (11.4–)13.3–16.4(–18.5) × 5–6.5(–7.1) µm, av. 14.7 × 5.8 µm, avQ = 2.5, subellipsoid to subcylindrical, inequilateral in side view, smooth, inamyloid. *Basidia* 24.6–38.3 × 9.5–13.6 µm, clavate, hyaline, 4-spored. *Hymenial cystidia* 39.9–68.1 × 9–11.1 µm, with 2.8–4.7 µm broad necks, scattered, ventricose-rostrate to fusoid-ventricose. *Pileipellis* a trichoderm with narrowly clavate to fusiform terminal cells, wider than underlying cells; pigment brown, coarsely encrusting in lower elements, hardly present in terminal cells. *Clamp connections* absent.

Distribution and ecology: USA and Canada – Pacific Northwest, from Vancouver Island, British Columbia, Canada, south into Oregon. Solitary, scattered in troops or small clusters, in conifer forests, both along the coast and in the foothills and drier eastern slopes of the Cascade Range. Known only from a handful of locations. Typical sites are forested with mixed conifers including *Picea sitchensis*, *Abies grandis, A. concolor, Pseudotsuga menziesii,* and *Tsuga heterophylla*. Fruiting along the coast from mid to late fall into winter, typically later than other *Xerocomellus*, and at higher elevations in summer and fall.

Materials examined: **USA**, Oregon, Marion Co., north of Detroit, 13 Aug. 2011, *J.L. Frank* JLF2154 (OSC162209); Washington: Clallam Co., 14 Oct. 1993, *A. & A. Bessette* OKM25915 Type (NYBG); Kittitas Co., Little Lake Kachess, 10 Oct. 2013, *N. Siegel* NS101013 (OSC162211); Lewis Co., Gifford Pinchot National Forest, 9 Oct. 2014, *J.L. Frank* JLF3523 (OSC162210).

Notes: *Xerocomellus rainisiae* is most likely to be confused with *X. mendocinensis* and *X. diffractus,* but it can be distinguished by the thick, velvety pileipellis, the deep greenish black to bluish black staining on the lower stipe, and the lack of extensive red pigmentation or red punctations on the stipe. It also has a more northwesterly distribution than the other two. The name *Boletus pulverulentus* has been misapplied to Pacific Northwest collections of both *X. rainisiae* and *X. mendocinensis.*

Xerocomellus salicicola C.F. Schwarz, N. Siegel & J.L Frank, ***sp. nov.*** MycoBank MB821026. Figs 4E, F, 5G, 6G.

Etymology: From genus of willow (*Salix*), and *cola:* Latin "inhabitant of," referring to the dominant tree in the habitat where it is most commonly encountered.

Diagnosis: Basidiomata small to medium-sized, pileus 3–10 cm broad, surface dull red, tan to brown, becoming extensively cracked at maturity, pores dull yellow staining dingy blue, stipe nearly entirely red, often with obscure coarse reticulum at apex, spores 12–14.2 × 4.4–6 µm, elongate to ellipsoid. Occurring from San Diego Co., California north into Oregon. Distinguished from other *Xerocomellus* because of its association with *Salix, Betula* or *Populus*, smaller smooth spores, and clavate cystidia.

Typus: **USA**, California, Santa Cruz Co., Santa Cruz, in a watered lawn under planted *Betula pendula*, 21 Aug. 2018, *C.F. Schwarz*, UCSC-F-1720 (**holotype** UCSC; **isotype** NYBG); GenBank Accession: ITS MK552408.

Description: *Pileus* 3–10 cm broad, bun-shaped at first, becoming convex to plane, dull red, tan to brown, dry, slightly tomentose or suede-like when young; surface soon extensively cracked, in age this areolate pattern extending over entire surface with many brown plaques revealing pinkish yellow tones between. *Hymenophore* (tube layer) slightly sunken around stipe; pores relatively large at maturity, slightly angular or irregular; pale yellow to dingy yellow or lemon yellow, bruising dark dingy blue fairly quickly and strongly. *Stipe* 3–5 × 1–4 cm, cylindrical, or with a pinched and tapered base, reddish overall or yellowish with red streaks and a reddish band near the apex; upper portion coarsely reticulate, sometimes becoming diffuse and obscure. *Context* in pileus fleshy, light yellow; stipe fibrous, solid, light creamy yellow, bruising blue throughout; KOH turning the tissues yellow. *Odor* not distinctive. *Taste* mild. *Spore deposit* dull olive brown. *Spores* (10.5–)12–14.2(–14.5) × 4.6–6 µm, av. 12.8 × 5.3 µm, avQ = 2.4, subellipsoid to subfusoid. *Basidia* 27.3–37.1 × 10.2–12.3 µm clavate, hyaline, 4-spored. *Hymenial cystidia* 32.8–46.1 × 11.8–14.5 µm, scattered, clavate or ventricose with acute to obtuse apex. *Pileipellis* a trichoderm made up of cylindrical to ellipsoid up to 15 µm wide cells, with conical or cylindrical terminal cells; pigment brown, incrusting, but terminal cell walls often colorless.

Distribution and ecology: USA – California and Oregon, fruiting in spring, summer, and fall, in small groups of 1–4 basidiomata, sometimes clustered, often from wet, muddy or hard-packed soil in riparian areas, typically associated with *Salix* spp., and in one case with *Populus trichocarpa*, occasionally in landscaped areas under *Betula pendula*.

Additional materials examined: **USA**, California, Santa Cruz Co., Watsonville Slough, Ramsey Park, in mud near *Salix* spp., 5 Mar. 2014, *C.F. Schwarz* CFS-5Mar2014-1 (UCSC); Neary Lagoon, 16 Sep. 2014, *C.F.*

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Schwarz UCSC1028 (UCSC); Ventura Co., near the mouth of the Ventura River, in *Salix*-dominated riparian habitat, 17 Jun. 2017, *A. Searcy* UCSC-F-1721 (UCSC).

Notes: The combination of phenology, association with *Salix*, *Betula* or *Populus*, smaller spores, and clavate cystidia help distinguish *X. salicicola* from *X. diffractus* and *X. dryophilus. Xerocomellus diffractus* can share dull pileus coloration and an extensively cracked pileus surface, but differs by habitat preference, and larger spores. Faded *X. dryophilus* could cause confusion, but *X. dryophilus* usually has a more evenly pinkish red pileus, a two-toned stipe, with a yellow upper half and red base, and larger spores. Additionally, the occasionally coarsely reticulate, and reddish upper stipe of *X. salicicola* helps to distinguish it from *X. dryophilus* and *X. diffractus.* The European *X. ripariellus* also fruits in association with *Salix*, and differs by having a bright red to reddish brown pileus and striate spores; it has been introduced to New Zealand, but has not been detected in North America.

Xerocomellus zelleri (Murrill) Klofac, *Öst. Z. Pilzk*. **20**: 39. 2011. Figs 4G, H, 5H, 6H.
Basionym: *Ceriomyces zelleri* Murrill, *Mycologia* **4**: 99. 1912.
Synonyms: *Boletus zelleri* (Murrill) Murrill, *Mycologia* **4**: 217. 1912.
Xerocomus zelleri (Murrill) Snell, *Lloydia* **7**: 43. 1944.
Boletellus zelleri (Murrill) Singer *et al.*, *Mycologia* **51**: 575. 1960 [1959].
Excluding: *Boletus zelleri sensu* California authors [= *Xerocomellus atropurpureus*].

Description: *Pileus* 2–6(–9) cm broad, convex to plane, occasionally uplifted and wavy in age, dark vinaceous black, occasionally dark olivaceous black to brownish black or olive brown to gray, rarely deep reddish black, at all times with a paler, whitish beige to yellowish tan band around the extreme margin; surface smooth or finely roughened, wrinkled or pitted, finely, densely velvety when young, becoming matted to glabrous in age. *Hymenophore* (tube layer) sunken around stipe to slightly decurrent, short to moderately long; pores small, 2–4 per mm, round to slightly angular or irregular, pale creamy yellow to dingy yellow, or pale yellowish olive when young, becoming dingy yellow to dingy yellow olive, occasionally developing reddish blushes in age, not bruising blue, or occasionally erratically so in older, waterlogged specimens. *Stipe* 2–7 × 0.5–2 cm, cylindrical, or with a tapered base, with yellow base color, covered extensively with fine rosy red punctuations when young, becoming evenly rosy red to dark red in age. *Context* in pileus thin, firm, light creamy yellow, not bruising blue, or slightly so in older or waterlogged specimens, stipe fibrous, light dingy yellow, reddish at base in age. *Odor* indistinct. *Taste* mild to lemony. *Spore deposit* dull olive brown. *Spores* (11.4–)12.2–16.7(–18.4) × 4.6–6.2(–7.2) µm, av. 14.2 × 5.4 µm, avQ = 2.5, subfusoid to subcylindrical, inequilateral, inamyloid, smooth. *Basidia* 35.3–47.9 × 9.3–12.8 µm, narrowly clavate, hyaline, 4-spored. *Hymenial cystidia* 25–50 × 6–11 µm, ventricose to subcylindrical, hyaline, rare. *Pileipellis* a trichoderm with subglobose to ellipsoid underlying cells and clavate to cylindrical awl-shaped terminal cells, often narrower than lower cells; pigment brown, heavily encrusting in lower cells, parietal in terminal cells. *Clamp connections* absent.

Distribution and ecology: USA and Canada – Pacific Northwest, from southern British Columbia, Canada, south to the northern California coast. Solitary or scattered in moss or on and around moss covered stumps and logs, in mature and old growth conifer forest. Locally common in mature forests on the Olympic Peninsula in Washington, rare across the rest of its range. Despite extensive collecting over a six-year period in, we encountered this species only five times. We studied all observations of *X. zelleri* on Mushroom Observer (mushroomobserver.org) and concluded that all but one observation from California represent *X. atropurpureus.* Additional GenBank data were from Washington and British Columbia.

Materials examined: **USA**, California, Mendocino Co., 15 Nov. 2014, *N. Siegel* NS1375 (UCSC); Oregon, Lane Co., near Florence, 10 Oct. 2013, JLF2977 (OSC162212); Washington, Clallam Co., Olympic National Park, 27 Oct. 2011, *N. Siegel* NS102711 (OSC162213); 28 Oct. 2014, *N. Siegel* NS1284 (UCSC); NS1285 (UCSC); King Co., Seattle, 20 Oct. 1911, W.A. *Murrill* 105 Type (NYBG).

Notes: The dark pileus with a velvety bloom and a pale band around the margin, pallid yellow pores that rarely bruise blue (only in age), a slender red stipe with crowded punctations when young (bleeding together to yield a contiguous red color in age) and relatively small size distinguish *X. zelleri* from all other *Xerocomellus* species except. *Xerocomellus atropurpureus. Xerocomellus atropurpureus* has a variable pileus color, but usually is more purple, reddish, or vinaceous, stockier in stature, and is more common and widespread. *Xerocomellus atropurpureus* spores are slightly smaller on average than those of *X. zelleri;* 13.8 × 5.3 µm for *X. atropurpureus versus* 14.2 × 5.4 µm for *X. zelleri.* The pileipellis of *X. zelleri* is made up of subglobose to ellipsoid elements, whereas in *X. atropurpureus* the elements of the trichoderm are elongate (Fig. 6B).

The following notes accompany the type collection: W.A. Murrill, Oct. 20-Nov-1911 (NY): "So dark difficult to see, looks black, velvety in appearance, tubes pale yellow, stem bulbous purple (or "apple") red, retic-ridged on streaked flesh pale yellow, not changing. Mostly in moist virgin forests of *Pseudotsuga, Thuja, Abies, Tsuga, Acer, Alnus etc*., a few in peat bogs, some on rather dry coniferous slopes, and others in open fields and lawns." Murrill (1912) included collections from the states of Washington and California in his description of *Ceriomyces zelleri*, likely representing both *X. zelleri* and *X. atropurpureus*.

The North American *Boletus coccyginus* was found to fall in *Hortiboletus* (Figs 1, 2) and here we propose the new combination:

Hortiboletus coccyginus (Thiers) C.F. Schwarz, N. Siegel & J.L. Frank, ***comb. nov.*** MycoBank MB821029. Figs 7A–D.
Basionym: *Boletus coccyginus* Thiers, California Mushrooms: 72. 1975.

Description: *Pileus* 2–6(–8) cm broad, rounded-convex to broadly convex when young, to nearly plane or irregular or wavy in age; surface dry to moist, pubescent when young, becoming smooth, rosy red, red, pinkish red to pinkish. *Hymenophore* (tube layer) sunken around stipe and rather short at margin; pores small and irregular at first, expanding in age; dull yellow at first, to yellow or greenish yellow, becoming olive yellow in age, not staining blue on younger specimens, occasionally bruising bluish green in

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Fig. 7. *Hortiboletus coccyginus*. **A–C.** Basidiomata *in situ*: **A.** (UCSC-F-1722) **B.** (NS110213) **C.** (CFS111711) **D.** Basidiospores (NS110511). Scale bar = 10 µm.

age. *Stipe* 1.5–7 × 0.5–2(–3) cm, equal, peg-like, tapering toward base to irregular; surface dry, often streaked with longitudinal striations to appressed-fibrillose, finely punctate at apex, to smooth; pinkish red to pale reddish brown over yellow. *Context* firm, moderately thick to thin in pileus, pale yellow or yellowish brown in stipe base, not staining when cut. *Odor* indistinct. *Taste* mild. *KOH reaction* dingy olive-green flash, quickly becoming golden orange on pileus, dingy orange-brown on tubes, yellowish on stipe, no reaction on context. *Spore deposit* olive-brown. *Spores* 11–17.5 × 5–7 µm, cylindrical, ovoid to elliptical in face view; often somewhat variable in shape and size, smooth, moderately thick walled, ocher in KOH. *Basidia* 23–28 × 7–10 µm, narrowly clavate, 1- to 4-spored, hyaline. *Hymenial cystidia* absent. *Pileipellis* a tangled trichodermium of hyphae 5–7 µm wide, staining dark yellow in KOH. *Clamp connections* absent.

Distribution and ecology: USA – Pacific Northwest from northern Washington, south into central California along the coast and east into the Sierra Nevada, solitary or in small clusters under *Notholithocarpus densiflorus, Pseudotsuga menziesii*, *Alnus rubra,* and *Quercus agrifolia* on the California coast, often in stands of *Populus trichocarpa* in the Pacific Northwest, and in mixed forest with *Abies concolor, A. magnifica, Pinus contorta,* and *Populus tremuloides* in the Sierra Nevada, fruiting in late summer and fall.

Materials examined: **USA**, California, Santa Cruz Co., near Aptos, 17 Nov. 2011, *C. Schwarz* CFS111711 (UCSC); Oregon, Curry Co., near Gold Beach, 5 Nov. 2011, *N. Siegel* NS110511 (UCSC); *Washington* King Co., near Seattle, 27 Oct. 2013, *J.L. Frank* JLF3093 (OSC162211); 14 Oct. 2014, *D. Winkler* DW101414 (UCSC).

Note: *Hortiboletus coccyginus* is distinguished from *Xerocomellus* species by a rosy red to pink pileus that typically does not crack, and context that does not stain blue.

DISCUSSION

Here we examine the generic limits of the widespread and morphologically variable genus *Xerocomellus*, establish species-level diversity of the genus in western North America, and provide a framework for other researchers to confirm and update survey data and nomenclature of this group. Our analyses agree with Nuhn *et al.* (2013), who showed several secotioid and gastroid species in their phylogeny of the *Boletineae* and included *Heliogaster* (as *Octaviania columellifera*) in *Xerocomellus*. Likewise, our LSU analysis does not support the monotypic *Heliogaster* (Orihara *et al*. 2010) as a separate genus, nor does it support the recent transfers of *Xerocomellus armeniacus* and *Xerocomus persicolor* to *Rheubarbariboletus,* which was recognized as a separate genus characterized by congophilous plaques in the pileipellis and a dark

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green reaction with iron sulphate on the pileus surface (Vizzini 2015). *Nigroboletus* remains a separate monotypic clade in our analysis; differing from *Xerocomellus* in the dull grayish to blackish discoloration of the basidiomata tissues when damaged (Gelardi *et al.* 2015). While some taxonomists may consider including *Nigroboletus* within *Xerocomellus*, more data from other closely related species and possibly other genes will be required to confirm, or contest, its monophyletic status. As in other recent studies (*e.g.*, Nguyen *et al.* 2016, Trudell *et al.* 2017) sequencing of type collections, here, especially of *X. zelleri*, was essential for the delimitation of some taxa and the linking of names and morphology.

Our molecular data and analyses show that at least two *Xerocomellus* species occur in the eastern North America. In addition to *X. truncatus*, there are chrysenteron-like collections reported from Massachussetts, Tennessee (as "*Boletus chrysenteron*"), and Quebec (as "*Boletellus chrysenteroides"*) that our data place within *Xerocomellus*, near *X. diffractus* (Fig. 1). While this manuscript was being prepared, two additional species of *Xerocomellus* were reported from the sky islands of southeastern Arizona; these appear to be undescribed and possibly rare (JLF unpubl. data). It appears that *Xerocomellus* species richness is greater in western North America than in eastern North America, and no *Xerocomellus* species are presently known to occur across the entire North American continent.

Evolution of sequestrate morphology appears to have occurred at least twice in this genus; but unlike in some other genera where this phenomenon occurs, *e.g. Chlorophyllum (Endoptychum), Cortinarius* (*Thaxterogaster*), *Pholiota* (*Nivatogastrium*), *Lactarius* (*Arcangeliella, Zelleromyces)*, *Russula* (*Gymnomyces, Macowanites*) where spore morphology and other microscopic characters offered clues as to generic placement prior to molecular data, spores of the xerocomelloid truffles are dramatically ornamented, and distinctly different from their nearest relatives which form epigeous basidiomata with typical boletoid (smooth or nearly smooth, fusoid) spores. This is unusual even in the *Boletaceae*, where *Gastroboletus ruber* (= *Truncocolumella rubra*) and *Gastroboletus truncatus* var. *flammeus* form spores that are smooth and fusoid to ellipsoid, similar to their nearest epigeous relatives in *Neoboletus* and *Suillellus*. *Gymnogaster boletoides*, while in a monotypic genus, has smooth amygdaliform spores not unlike many epigeous bolete species. In contrast, while spores of *Xerocomellus macmurphyi* and *X. behrii* are ellipsoid and spores of *Heliogaster columellifer* are spherical, all are dramatically ornamented with wide pyramidal spines. An additional point of contrast is that unlike the basidiomata of related epigeous taxa, these hypogeous *Xerocomellus* species exhibit no blue staining when bruised or damaged. The truffle *X. macmurphyi* was originally placed in *Hymenogaster*, and more recently reported as *Octavianina* (Frank 2005) and *Octaviania* (Frank *et al.* 2006, Smith *et al.* 2007).

Epigeous taxa of *Xerocomellus* in western North America can generally be recognized by their tri-toned color scheme (dark or dull caps, yellow pores, and variably reddish stipes), tendency to develop areolate cap surfaces, and some degree of blue staining reaction when cut or bruised. Basidiomata of *X. zelleri* typically do not show any staining reactions, and the two hypogeous species *X. macmurphyi* and *X. behrii* (Smith *et al.* 2018) are entirely unstaining. Basidiomata of the epigeous members of this genus vary in size from very small to large, but never reach the enormous sizes of some taxa in the *Boletaceae*. A truncate spore apex is present in multiple species in the genus, *X. amylosporus, X. mendocinensis, X. truncatus, X. fennicus and X. porosporus;* and this character appears to have evolved multiple times (Fig. 1).

Environmental conditions, such as drought and rain, and the age of the basidiomata, can all dramatically change the colors and structure of the pileus surface of *Xerocomellus* species. Identification is often not easy; the best characters for species recognition are the colors of the stipe and the speed and intensity of the bluing reactions. Microscopic characters such as spore shape and pileipellis structure can help in some cases.

As with all taxa, accurate species-level identification is necessary for monitoring distribution, and population dynamics, as and thus for evaluating rare or endangered status. By defining and clarifying species concepts with vouchered collections and sequences of barcode genes, we hope to enable identification of environmental samples, mycorrhizal morphotypes, and basidiomata for ecological studies, and for forest management goals in western North America.

Dichotomous key for the epigeous species of *Xerocomellus* in western North America

1. Pileus typically deep purple-black, dark wine-colored, or ruby red, sometimes more grayish, olive, or brownish; pileus surface glabrous or very finely velvety, sometimes strongly wrinkled, typically not cracking; pores and flesh typically not staining or occasionally bluing slightly; stipe surface typically extensively red 2

1' Pileus colors ranging from light gray to dark brown, vinaceous brown, pinkish or red; or if blackish purple, pores readily staining blue; surface usually cracking at least around margin at maturity (often more extensively), nearly glabrous to finely tomentose 3

2. Pileus blackish purple to reddish brown, sometimes ruby red, glabrous, often densely wrinkled; basidiomata often stocky; pileipellis cells elongate; widespread along the coast from central California to British Columbia, also in the Sierra Nevada and Cascade Range ..... *X. atropurpureus*

2' Pileus dark vinaceous black, occasionally dark olivaceous black, brownish black, olive-brown to gray, rarely deep reddish black, typically with a contrasting pale tan to dingy yellowish band around the margin, surface smooth or finely roughened, velvety when young, becoming matted to glabrous; basidiomata typically slender; pileipellis cells globose to ellipsoid with elongate to awl-shaped terminal cells; mostly found in the Pacific Northwest, rare in coastal Northern California ..... *X. zelleri*

3. Some to most spores with a truncate apex 4

3' Spores with a rounded apex 5

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4. Stipe extensively red with red punctation, pileus gray to olive-brown or dark brown; surface typically cracking around outer margin; pores staining dark blue quickly; spores not amyloid, roughly half of the spores truncate; under *Quercus*, *Notholithocarpus*, and conifers, in California and the PNW ..... *X. mendocinensis*

4' Stipe yellow to reddish with red striations, typically browning in age, but retaining a reddish band at apex; pileus dark vinaceous brown, olive brown to grayish brown; surface lacking cracks when young, becoming areolate around the margin or sometimes extensively cracked in age; pores staining dark blue moderately quickly; spores weakly to distinctly amyloid, most with truncate apex ..... *X. amylosporus*

5. Pileus ruby red, reddish to pink, at least when young 6

5' Pileus brown, olive to gray, pink tones typically restricted to exposed contex 8

6. Growing near *Salix, Betula* or *Populus*, often in riparian areas; red tones on stipe often extending to uppermost part; stipe apex with variably distinct to obscure coarse reticulation; pileus reddish pink when very young, soon dull tan to brown or with slight pinkish tones, moderately to extensively cracking; spores av. 12.8 x 5.2 µm ..... *X. salicicola*

6' Found primarily under *Quercus* or conifers; red restricted to lower stipe, stipe lacking reticulation; spore av. >13 µm 7

7. Found primarily under *Quercus agrifolia*; stipe red at base, yellow at apex; pileus often ruby red when young, in age often browner but with at least some pinkish tones; pores staining dark blue quickly; spores av. 13.6 x 6.2 µm; common in central and southern California, uncommon north of San Francisco Bay ..... *X. dryophilus*

7' Under conifers and *Quercus*; stipe blushed reddish at base, darkening slightly and extending upward in age; pileus reddish, grayish to brown, exposed context pink; pores staining sky blue to grayish blue, slowly to moderately quickly; spores av. 14.3 x 5.5 µm; common and widespread in western North America ..... *X. diffractus*

8. Pores not staining blue, or slowly staining light grayish blue 9

8' Pores distinctly staining blue 11

9. Pores slowly staining dull grayish blue; stipe yellow with reddish near base only; pileus olive, olive-gray to leather-brown or tan, extensively cracked ..... *X. diffractus*

9' Pores not staining blue 10

10. Basidiomata stocky; pileus typically evenly colored, often developing cracks; pileipellis cells elongate; montane ..... *X. atropurpureus* "Sierra Form"

10' Basidiomata slender; pileus typically with a paler margin, not cracking; pileipellis cells globose to ellipsoid with elongate to awl-shaped terminal cells; coastal ..... *X. zelleri*

11. Stipe with a red apex, to extensively red 12

11' Stipe with a yellow apex, base reddish blushed to red 13

12. Mostly under *Quercus* or *Notholithocarpus*, with conifers in the PNW; stipe extensively red with red punctation; pileus gray to olive brown or dark brown; surface typically cracking around outer margin; spores av. 13.2 x 4.9 µm, typically about half with truncate apex ..... *X. mendocinensis*

12' Growing near *Salix, Betula* or *Populus*, often in riparian areas; stipe apex with variably distinct to obscure, coarse reticulation; pileus reddish pink when very young, soon dull tan to brown or with slight pinkish tones, moderately to extensively cracking; spores av. 12.8 x 5.2 µm, apex convex ..... *X. salicicola*

13. Stipe for the most part yellow; pores and stipe readily staining deep, dark blue green; pileus brown to olive brown; surface velvety-tomentose, smooth when young but often extensively cracking with age; growing with conifers, in PNW ..... *X. rainisiae*

13' Stipe yellow, streaked red and/or with fine red punctations, more concentrated toward stipe base; pileus olive, olive gray, or gray to leather brown or tan, becoming paler in age; surface typically extensively cracked at maturity; pores staining sky blue to grayish blue slowly to moderately quickly; widespread in western North America, with conifers, *Quercus* and *Notholithocarpus* ..... *X. diffractus*

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REFERENCES

Altschul SF, Gish W, Miller W, *et al.* (1990). Basic local alignment search tool. *Journal of Molecular Biology* **215**: 403–410.

Ariyawansa HA, Hyde KD, Jayasiri SC, *et al.* (2015). Fungal diversity notes 111–252—taxonomic and phylogenetic contributions to fungal taxa. *Fungal Diversity* **75**: 27–274.

Arora D (1986). *Mushrooms demystified* (2nd ed.). Berkeley, CA: Ten Speed Press.

Arora D, Frank JL (2014). Clarifying the butter Boletes: a new genus, *Butyriboletus*, is established to accommodate *Boletus* sect. *Appendiculati*, and six new species are described. *Mycologia* **106**: 464–480.

Binder M, Hibbett DS (2006). Molecular systematics and biological diversification of *Boletales*. *Mycologia* **98**: 971–981.

Crous PW, Wingfield MJ, Richardson DM, *et al.* (2016). Fungal Planet description sheets: 400–468. *Persoonia* **36**: 316–458

Dentinger BT, Ammirati JF, Both EE, *et al.* (2010). Molecular phylogenetics of porcini mushrooms (*Boletus* section *Boletus*). *Molecular Phylogenetics and Evolution* **57**: 1276–1292.

Dereeper A, Guignon V, Blanc G, *et al.* (2008). Phylogeny.fr: robust phylogenetic analysis for the non-specialist. *Nucleic Acids Research* 2008 Jul 1; 36 (Web Server issue): W465-9.

Desjardin DE, Wood MG, Stevens FA (2015). *California Mushrooms. The comprehensive identification guide*. Portland: Timber Press.

Douhan GW, Rizzo DM (2003). Host-parasite relationships among bolete infecting *Hypomyces* species. *Mycological Research* **107**: 1342–1349.

Frank JL (2005). *Complex mutualism in an Oregon White Oak woodland: Hypogeous fungi, mycorrhizas and small mammal mycophagy associated with* Quercus garryana. MSc thesis, Department of Biology, Southern Oregon University, Ashland, OR, USA.

Frank JL, Barry S, Southworth D (2006). Mammal mycophagy and dispersal of mycorrhizal inoculum in Oregon White Oak Woodlands. *Northwest Science* **80**: 264–273.

Gardes M, Bruns T (1993). ITS primers with enhanced specificity for basidiomycetes – application to the identification of mycorrhizae and roots. *Molecular Ecology* **2**: 113–118.

Gardes M, Bruns T (1996). Community structure of ectomycorrhizal fungi in a *Pinus muricata* forest: above- and below-ground views. *Canadian Journal of Botany* **74**: 1572–1583.

Gelardi M, Vizzini A, Ercole E, *et al.* (2015). Circumscription and taxonomic arrangement of *Nigroboletus roseonigrescens gen. et sp. nov.*, a new member of *Boletaceae* from tropical South-Eastern China. *PLoS ONE* **10**: e0134295.

Katoh K, Misawa K, Kuma K, *et al.* (2002). MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* **30**: 3059–3066.

Klofac W, Krisai-Greilhuber I (1992). *Xerocomus chrysenteron* und ähnlich aussehende Röhrlinge. *Österreichische Zeitschrift für Pilzkunde* **1**: 19–59.

Ladurner H, Simonini G (2003). *Xerocomus s.l. Fungi Europaei 8*. Alassio: Edizioni Candusso. Italy.

Maddison WP, Maddison DR (2011). Mesquite: a modular system for evolutionary analysis. Version 2.75. Online at http://mesquiteproject.org.

McCarthy C (1998). Chromas 1.45. Southport, Queensland, Australia: Griffith University.

Nguyen NH, Vellinga EC, Bruns TD *et al.* (2016). Phylogenetic assessment of global *Suillus* ITS sequences supports morphologically defined species and reveals synonymous and undescribed taxa. *Mycologia* **108**: 1216–1228.

Nuhn ME, Binder M, Taylor AFS, *et al.* (2013). Phylogenetic overview of the *Boletineae*. *Fungal Biology* **117**: 479–511.

Orihara T, Sawada F, Ikeda S, *et al.* (2010). Taxonomic reconsideration of a sequestrate fungus, *Octaviania columellifera*, with the proposal of a new genus, *Heliogaster*, and its phylogenetic relationships in the *Boletales*. *Mycologia* **102**: 108–121.

Peintner U, Ladurner H, Simonini G (2003). *Xerocomus cisalpinus sp. nov.*, and the delimitation of species in the *X. chrysenteron* complex based on morphology and rDNA-LSU sequences. *Mycological Research* **107**: 659–679.

Siegel N, Schwarz CF (2016). *Mushrooms of the Redwood Coast*. Berkeley: Ten Speed Press.

Simonini G, Gelardi M, Vizzini A (2016). *Xerocomellus redeuilhii sp. nov. Rivista di Micologia* **59**: **123**–127.

Smith AH (1965). New and unusual basidiomycetes with comments on hyphal and spore wall reactions with Melzer's solution. *Mycopathologia et Mycologia Applicata* **26**: 385–402.

Smith ME, Castellano MA, Frank JL (2018). *Hymenogaster macmurphyi* and *Splanchnomyces behrii* are sequestrate species of *Xerocomellus* from the western United States. *Mycologia* **110**: 605–617.

Smith ME, Douhan GW, Rizzo DM (2007). Ectomycorrhizal community structure in a xeric *Quercus* woodland based on rDNA sequence analysis of sporocarps and pooled roots. *New Phytologist* **174**: 847–863.

Stamatakis A (2006). RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22**: 2688–2690.

Šutara J (2008). *Xerocomus s.l.* in the light of the present state of knowledge. *Czech Mycology* **60**: 29–62.

Swofford DL (2002). PAUP*: *Phylogenetic analysis using parsimony and other methods, 4.0*, 10th ed. Sunderland, MA: Sinauer Associates.

Thiers B (ed.) (2020). *Index Herbariorum*. http://sweetgum.nybg.org/science/ih/ [accessed 20 May 2020]

Thiers HD (1975). *California Mushrooms: A field guide to the boletes*. New York: Hafner Press.

Thompson JD, Gibson TJ, Plewniak F, *et al.* (1997). The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* **24**: 4876–4882.

Trudell SA, Xu J, Saar I, *et al.* (2017). North American matsutake: names clarified and a new species described. *Mycologia* **109**: 379–390.

Vizzini A (2015). Nomenclatural novelties. *Index Fungorum* **244**: 1.

White TJ, Bruns T, Lee S, *et al.* (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: *PCR Protocols: A Guide to Methods and Applications* (MA Innis, DH Gelfand, JJ Sninsky *et al.*, eds): 315–322 Academic Press, New York.

Wu G, Feng B, Xu J, *et al.* (2014). Molecular phylogenetic analyses redefine seven major clades and reveal 22 new generic clades in the fungal family *Boletaceae*. *Fungal Diversity* **69**: 93–115.

Wu G, Li YC, Zhu XT, *et al.* (2016a). One hundred noteworthy boletes from China. *Fungal Diversity* **81**: 25–188.

Wu G, Zhao K, Li YC, *et al.* (2016b). Four new genera of the fungal family *Boletaceae*. *Fungal Diversity* **81**: 1–24.

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