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A unique ballistosporic hypogeous sequestrate *Lactarius* from California

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Abstract: *Lactarius rubriviridis* sp. nov., characterized by hypogeous, sequestrate basidiomes with red latex, green stains, and forcibly discharged, reticulate basidiospores is described and illustrated. During the Spring, the new species forms basidiomes associated with conifers at 1400–1800 m elevation in the Sierra Nevada, and is known from two specimens collected 19 yr apart. Comparisons with the putatively polyphyletic genera *Arcangeliella* and *Zelleromyces*, and an accounting of all known members of these genera are provided.

Key Words: *Arcangeliella*, astrogastraceous series, Russulales, *Zelleromyces*

INTRODUCTION

In June 1982, an unusual and exciting new species of hypogeous sequestrate fungi was collected by Mrs. Dorothy Zediker at Foresta Campground in Yosemite National Park, California. Fresh material was obtained by Dr. Harry Thiers and Herb Saylor (then a student of Dr. Thiers) at San Francisco State University where they immediately recognized the material (*HS 921*) as representing a new species belonging to the astrogastraceous series of Russulales. Dr. Thiers and Mr. Saylor intended to publish the new species as ''Zelleromyces rubriviridis'' (currently a nom. herb.), and they submitted a formal description in a manuscript to Mycologia in 1986. Favorable reviews were received, but there were unresolved discussions regarding subgeneric classification. The new species name was never validly published, and the single specimen languished in SFSU. Recently, fresh material of the species (*DED 7312*) was collected from a similar habitat at a similar elevation during the same time of year, but from a site approx 130 miles farther north in the Sierra Nevada. The new material provided further details on macromorphology, distribution, and ecology, and for the first time displayed convincingly the ballistosporic nature of the gastroid basidiomes, a feature that is unusual among hypogeous Russulales. The new species is described below and accepted in the genus *Lactarius* subgenus *Dapetes*. Color terms and notations are from Kornerup and Wanscher (1978).

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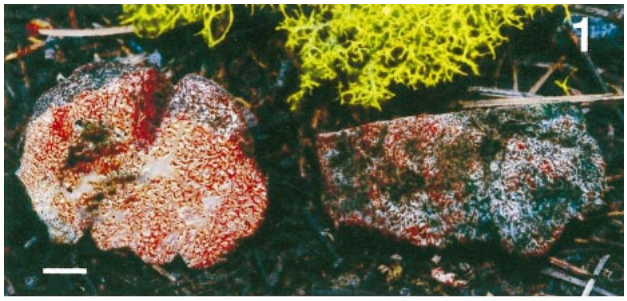
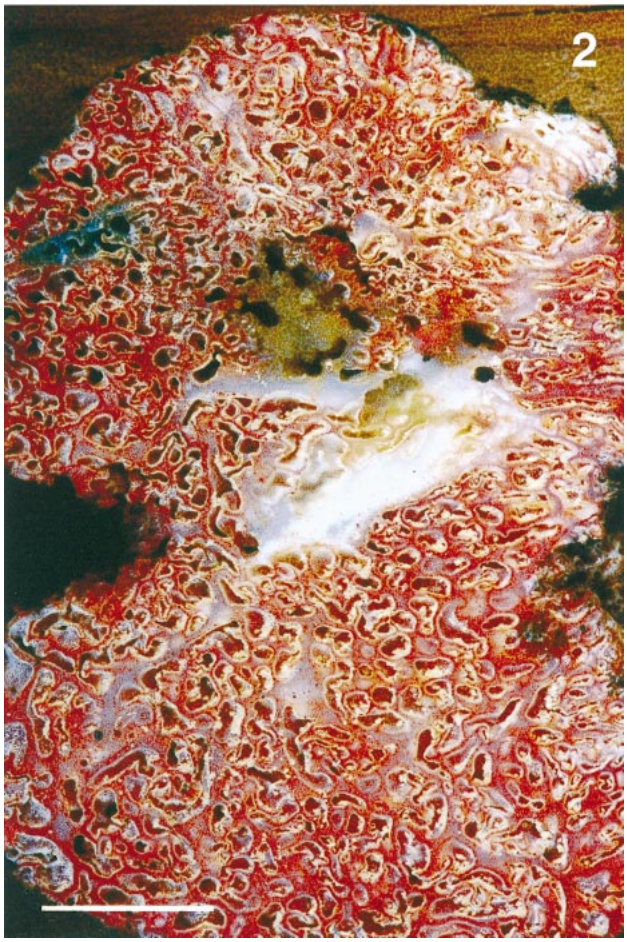
Lactarius rubriviridis Desjardin, Saylor et Thiers, sp. nov. FIGS. 1–4

Gastrocarpia 25–60 mm diametro, 20–45 mm alta, irregulatim globosa vel ellipsoidia, fusca vel rubrofusca, tactu viridescens, alveolata. Peridium nullum maturitate. Gleba lacunosa, subflavida, tactu viridescens. Contextus viridescens ubi contusus. Latex parcus, laete ruber. Stipe-columella nulla. Columella praesens, conspicua. Odor et sapor haud distinctus. Basidiosporae (8–) 8.5–11 × (7–) 7.5–8.5 μm, ellipsoideae, reticulatae vel partiale reticulatae, ballistosporae, amyloideae. Trama hymenophoris hyphis filamentosis, sphaerocystis nullus. Peridiopellis nullus. In solo subter arboribus coniferis. Holotypus hic designatus: *DED 7312* (SFSU), legit D. E. Desjardin, 14 June 2001, prope Cold Creek Campground, Sierra Co., California, USA.

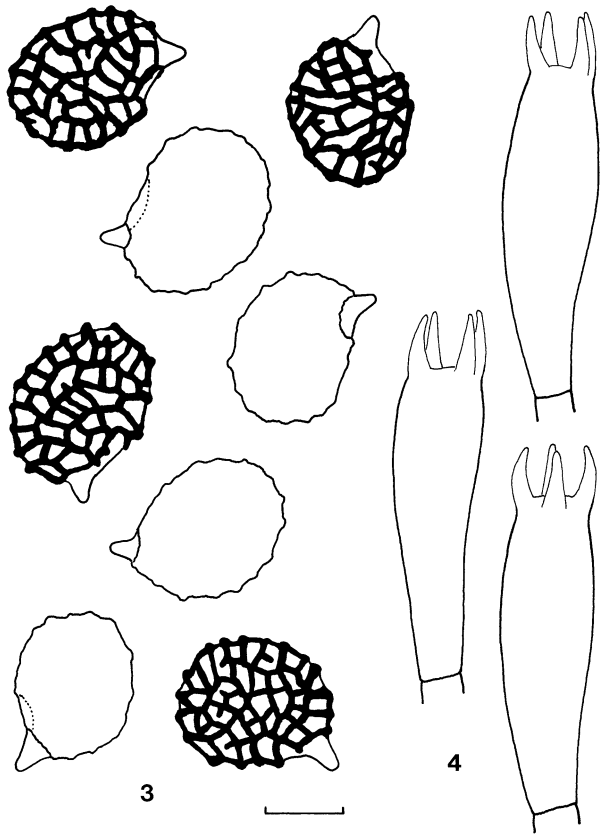
Basidiomes (FIGS. 1–2) hypogeous, 25–60 mm long × 20–45 mm broad × 15–30 mm thick, irregularly globose to ovoid or ellipsoid, sometimes lobed. *Peridium* absent, exterior surface alveolate to ridged and pitted from exposed locules and hymenophoral tramal tissue; ridges reddish brown to dark brown (8–9E–F5–7), staining deep greenish grey to bluish green or dark green (25–27F5–7) where bruised. *Gleba* loculate; locules irregular in shape, often elongate, 1–5 mm × 0.5–1.5 mm, filled with yellowish white to orangish white (4–5A2) or cream-colored (4A3) basidiospores at maturity; *hymenophoral tramal tissue* firm, waxy, white to yellowish white (4A2), but becoming reddish brown (9D7–8) when cut from exuded latex; *columella* rudimentary to well-developed, composed of radiating dendritic veins arising from a central main vein 1–4 mm diam, initially white, but staining greenish white (27A2–3) to greyish green (26C6–7) over time when cut. *Latex* scant, deep red (9B–C7–8), discoloring tramal tissue to dark brownish red (11–12E7–8). *Odor* not distinctive or sweet. *Taste* mild. *Spores* forcibly discharged, leaving an orangish white (5A2) to yellowish white (4A2) or cream (4A3) deposit.

Basidiospores (FIG. 3) (8–) 8.5–11 × (7–) 7.5–8.5 μm ($\bar{x}$ = 9.8 ± 0.7 × 7.8 ± 0.4 μm, Q = 1.1–1.4, $\bar{Q}$ = 1.26 ± 0.06, n = 25 spores per 2 specimens), ovoid





FIGS. 1–2. Basidiomes of *Lactarius rubriviridis* (DED 7312, HOLOTYPE). Note the green stains on the outer surface of the basidiome on the right in FIG. 1. Note the red latex and green stains on the hymenophoral tissues in FIG. 2. Scale bars = 10 mm.



FIGS. 3–4. Micromorphological features of *Lactarius rubriviridis* (DED 7312, HOLOTYPE). 3. Basidiospores. 4. Basidia. Scale bars: 3 = 5 μm; 4 = 10 μm.

to ellipsoid, inequilateral in profile with an eccentric hilar appendix, densely ornamented with a complete to partial reticulum; with a small, smooth to weakly ornamented suprahilar plage; ornamentation 0.5–1.0 μm tall, deeply amyloid; hilar appendix inamyloid; hyaline in H_2O and KOH. *Basidia* (FIG. 4) 40–60 × 11–13.5 μm, clavate, 4-spored, unclamped, ballistosporic; sterigmata curved, up to 6.5 μm long. *Basidioles* cylindrical to clavate. *Hymenial macrocystidia* absent; *pseudocystidia* scattered, cylindrical with a tapered apex, projecting slightly beyond the basidia, hyaline or with orange globular contents. *Subhymenium* only slightly differentiated, of short-celled hyphae. *Hymenophoral trama* of densely compact, agglutinated hyphae, 3–10 μm diam, cylindrical to subcellular, hyaline in H_2O and KOH, red (dextrinoid) in Melzer's reagent; lactiferous hyphae abundant, contorted to strangulate, 3–5 (–10) mm diam, refractive, yellowish orange to tawny in KOH. *Columella* tissues similar to the hymenophoral trama. *Sphaerocysts* absent in all tissues. *Peridium* absent. *Clamp connections* absent.

Habit, habitat and distribution. Solitary to scattered, hypogeous, buried under needle duff of conifers (*Abies* spp., *Pinus* spp.). June. Sierra Nevada, California.

Specimens examined.—USA. California. Mariposa Co., Yosemite National Park, Foresta Campground, scattered in soil under conifers, elev. ca 1400 m, *HS 921,* coll. by Mrs. Dorothy Zediker, 4 June 1982 (SFSU); Sierra Co., Cold Creek Campground off Hwy. 89, solitary in soil under *Abies* and *Pinus*, elev. ca 1800 m, *DED 7312,* coll. by D. E. Desjardin, 14 June 2001 (HOLOTYPE SFSU).

Etymology. rubri—(Latin) red; *viridis*—(Latin) green; referring to the red latex and green stains.

Commentary. The secotioid and sequestrate representatives of the Russulales (Astrogastraceous Series *pro parte*) have received considerable attention over the past seventy years. Malençon (1931) and Zeller and Dodge (1935, 1936) were the first to intensively study these fungi. Secotioid and gastroid taxa that are currently recognized as belonging in the Russulales were accepted by Zeller and Dodge (1936) in the genera *Arcangeliella*, *Elasmomyces*, and *Macowanites*. Generic distinctions were based on whether the basidiomes were large and stipitate (*Macowanites*), or whether the basidiomes were smaller with a gleba that pulled away from the stipe-columella at maturity (*Elasmomyces*), or whether the basidiomes had ''lactiferous ducts'' (and presumably latex) in the trama, peridium and columella (*Arcangeliella*). Singer and Smith (1960) redefined the group based on analyses of specimens in Zeller's herbarium (NY) and from data on abundant fresh material collected by Smith. They accepted *Arcangeliella*, *Elasmomyces*, and *Macowanites*, resurrected two older genera, *Gymnomyces* and *Martellia*, and they established two new genera, *Cystangium* and *Zelleromyces* (Singer and Smith 1960). Generic distinctions were based primarily on various combinations of the presence or absence of a stipe-columella, latex, and sphaerocysts in the hymenophoral trama. Pegler and Young (1979) revised the classification once again, based on data from an ultrastructural investigation of basidiospore morphology. They recognized two families within the Russulales: the Russulaceae Lotsy and the Elasmomycetaceae Locquin ex Pegler and Young (1979). The Russulaceae comprised ballistosporic taxa with agaricoid to gastroid and stipitate basidiomes (*Lactarius*, *Arcangeliella*, *Russula*, *Cystangium*, *Macowanites*), whereas the Elasmomycetaceae comprised statismosporic taxa with gastroid basidiomes that are stipitate or sessile (*Elasmomyces*, *Gymnomyces*, *Martellia*, *Zelleromyces*). Within these families, the generic circumscriptions followed those of Singer and Smith (1960). Beaton et al (1984) redefined the generic delimitations further, placing more emphasis on hymenophoral trama anatomy, stipe-columella development, and spore morphology, and placing less emphasis on the presence or absence of latex. Zhang and Yu (1990) redefined the generic circumscriptions of the hypogeous sequestrate genera (*Gymnomyces*, *Martellia*, *Zelleromyces*), placing primary emphasis on basidiospore ornamentation and hymenophoral trama anatomy. They recognized limited taxonomic significance to latex development and for the first time included latex-producing species in *Gymnomyces* and *Martellia* (Zhang and Yu 1990; these species have been subsequently transferred to *Zelleromyces* by Trappe et al 2002). Recently, Lebel and Trappe (2000) analyzed the type specimens of the type species for all seven sequestrate genera and concluded that peridiopellis anatomy was a more stable character than others used previously to define genera. Based on their type studies, Lebel and Trappe (2000) synonymized *Elasmomyces* with *Macowanites*, synonymized *Martellia* with *Gymnomyces*, and restricted *Cystangium* to taxa with an epithelial peridiopellis. The taxonomic boundary between *Arcangeliella* and *Zelleromyces* was left for future reconsideration (Lebel and Trappe 2000). Additional type studies of sequestrate russuloid genera leading to numerous nomenclatural changes have been published recently by Lebel and Castellano (2002) and by Trappe et al (2002). Clearly, the morphological and physiological variability displayed by known secotioid and sequestrate Russulales makes it difficult to assign species to appropriate genera with certainty. The new species described herein demonstrates this problem and offers a potential taxonomic solution.

Diagnostic features of *Lactarius rubriviridis* include a gastroid, hypogeous basidiome that lacks a peridium, and has red latex, green-stained tissues, a well-developed dendritic columella, and reticulate basidiospores. When basidiomes were cut and placed in a petri plate, an orangish white to cream-colored spore deposit was produced from basidiospores that were forcibly discharged. Moreover, the basidiospores have an eccentric hilar appendix and a rudimentary suprahilar plage, and the basidia form curved sterigmata, further indicating that the basidiospores are ballistosporic (fide Pegler and Young 1979).

Morphological features of *Lactarius rubriviridis* indicate that it could be accepted in several genera. The lactiferous, gastroid-loculate, hypogeous basidiomes with dendritic columella and reticulate basidiospores suggest that an appropriate taxonomic placement would be in the genus *Zelleromyces*. However, as redefined by Pegler and Young (1979), only statismosporic species are accepted in *Zelleromyces*. It should be noted that recently, Fogel and States (2001) described a new species of *Zelleromyces* (*Z. rogersonii*) with putatively ballistosporic spores (although the ability to form a spore deposit was not indicated) and with an evanescent peridium. Currently, 27 species are recognized in *Zelleromyces* (TABLE I). If the new species described herein were accepted in *Zelleromyces*, it would represent the only known species of the genus with red latex (see TABLE I). In addition, only one other species, *Z. rogersonii*, has been described with forcibly discharged basidiospores and poorly developed (or absent) peridium. The latter species differs from *L. rubriviridis* in lacking red latex, green-stained tissues and a columella, and differs in forming smaller basidiospores (8–9 ×

TABLE I. Latex-producing hypogeous sequestrate Russulales published to date

Species and citation	Distribution	Plant associates	Latex[a]
ZELLEROMYCES:			
albellus (Singer & A.H. Sm.) Trappe, T. Lebel & Castellano (2002)	Argentina	*Nothofagus*	absent
alveolatus (Singer & A.H. Sm.) Trappe, T. Lebel & Castellano (2002)	Oregon, USA	*Quercus*	absent
australiensis (Berk.) Pegler & T.W.K. Young (1979)	Australia	*Eucalyptus*	hyaline
cinnabarinus Singer & A.H. Sm. [Type species]: see *Z. ravenelii*			
daucinus G.W. Beaton, Pegler & T.W.K. Young (1984)	Australia	*Eucalyptus*	color not reported
gardneri (Zeller & C.W. Dodge) Singer & A.H. Sm. (1960)	W United States	*Lithocarpus, Quercus*	white
giennensis Moreno-Arroyo, J. Gomez & Calonge (1998a)	Spain	*Pinus*	white
gilkeyae Singer & A.H. Sm. (1960)	W United States	*Acer, Alnus, Picea, Tsuga*	white
glabrellus (Zeller & C.W. Dodge) Singer & A.H. Sm. (1960)	Australia, Tasmania	unspecified	not reported
hispanicus Calonge & Pegler (1998)	Spain	*Pinus*	white
josserandii Malençon (1975)	N Africa	mixed forests	white
lactifer (B.-C. Zhang & Y.-N. Yu) Trappe, T. Lebel & Castellano (2002)	China	*Castanopsis, Lithocarpus*	white
majus (J.W. Cribb) A.H. Sm. (1962)	Australia	*Eucalyptus*	absent
malaiensis (Corner & Hawker) A.H. Sm. (1962)	Australia, India, Malaysia	*Eucalyptus*	not reported
meridionalis Calonge, Moreno-Arroyo & J. Gomez (in Moreno-Arroyo, J. Gomez & Calonge, 1998b)	Spain	*Quercus*	not reported
oregonensis Singer & A.H. Sm. (1960)	W United States	*Calocedrus*, mixed conifers	white
papyraceus (Singer & A.H. Sm.) Trappe, T. Lebel & Castellano (2002)	California, USA	*Sequoia*	cream
pterosporus (E. Horak) Trappe, T. Lebel & Castellano (2002)	Chile	*Nothofagus*	absent
ramispinus (B.-C. Zhang & Y.-N. Yu) Trappe, T. Lebel & Castellano (2002)	China	hardwood forest	white
ravenelii (Berk. & M.A. Curtis) Singer & A.H. Sm. (1960) = *cinnabarinus* Singer & A.H. Sm. (1960) sensu Miller & Lebel (1999), Lebel & Trappe (2000)	SE United States	*Pinus*	white
rogersonii Fogel & States (2001)	Nevada, USA	*Pinus*	color not reported
scissilis (Zeller & C.W. Dodge) Trappe, T. Lebel & Castellano (2002)	California, USA	conifers	absent
sculptisporus S. Miller (in Miller & Lebel, 1999)	E United States	*Pinus*	white
sinensis B. Liu, K. Tao & Ming C. Chang (in Tao, Chang & Liu, 1993)	China	*Lonicera*	white
soehneri (Zeller & C.W. Dodge) Trappe, T. Lebel & Castellano (2002)	Germany	pine forest	absent
stephensii (Berk.) A.H. Sm. (1962) ≡ *Martellia stephensii* (Berk.) K. Mader & A. Mader (1992) ≡ *Arcangeliella stephensii* (Berk.) Zeller & C.W. Dodge sensu Krieglsteiner (1991)	Britain, Europe	mixed forests	white
striatus G.W. Beaton, Pegler & T.W.K. Young (1984)	Australia	*Eucalyptus*	color not reported
versicaulis S. Miller (in Miller & Lebel, 1999)	SE United States	*Quercus*	white

[a] For all taxa where latex was absent or not reported or where latex color was not reported, the gleba was described as ranging from white to pale orange or orange when fresh, lacking any red pigmentation or red exudates

6–7 μm; $\bar{x}$ = 8.4 × 6.7 μm; Fogel and States 2001). Recent molecular data from Miller et al (2001) indicate that *Zelleromyces* as currently delimited is polyphyletic, with *Z. daucinus* and *Z. striatus* allied with *Lactarius subdulcis* (Fr.) Gray of subgenus *Russularia*, whereas *Z. sculptisporus* is allied with *L. scrobiculatus* var. *pubescens* A.H. Sm. of subgenus *Piperites*. Likewise, Peter et al (2001) demonstrated that *Zelleromyces* is polyphyletic, with *Z. hispanicus* allied with members of *Lactarius* sect. *Russularia*, and with *Z. giennensis* in an unresolved position outside the Russularia clade. It should be noted that their works included only white latex-producing species of *Zelleromyces*, and did not include the type species *Z. ravenelii* (= *Z. cinnabarinus*; Miller et al 2001, Peter et al 2001). Because I infer from morphology that *L. rubriviridis* is allied with *Lactarius* subgenus *Dapetes*, to accept the red latex-producing species in *Zelleromyces* would promulgate polyphylly. Hence, placement in *Zelleromyces* is unwarranted.

Alternatively, the non-agaricoid basidiomes with forcibly discharged basidiospores produced by the new species could warrant acceptance in the genus *Arcangeliella* (fide Pegler and Young 1979). Fifty-three epithets have been established in *Arcangeliella* to date (TABLE II). Zeller and Dodge (1936) originally accepted both stipitate-secotioid and sessile-sequestrate taxa in *Arcangeliella*. Of the 31 taxa included by them (Zeller and Dodge 1936) in *Arcangeliella* (TABLE II), 8 taxa are insufficiently known for accurate taxonomic placement, 22 taxa have been transferred to other genera, and only one species, *A. borziana*, the type species, is currently accepted in *Arcangeliella*. Since 1936, the circumscription of *Arcangeliella* has changed to include only taxa with a stipe or a well-developed percurrent columella, and ballistosporic basidiospores (sensu Pegler and Young 1979) although a spore deposit may not be obtainable. Currently, only 13 taxa are unequivocably recognized in *Arcangeliella* (TABLE II). If the new species described herein was accepted in *Arcangeliella*, it would represent the only known species of the genus that lacks a well-developed stipe, lacks a peridium, and produces red latex (see TABLE II). Furthermore, although no molecular data are currently available to support this contention, it could be argued that *Arcangeliella* as currently delimited may be polyphyletic. The type species, *A. borziana*, and a few other species (*A. densa* and *A. texta*) form basidiospores ornamented with isolated spines and rods (similar to those of *Lactarius deceptivus* Peck, sect. *Albati*), whereas all other currently recognized species of *Arcangeliella* form basidiospores ornamented with a complete or broken reticulum or with concentric ridges (similar to *Lactarius* species belonging to other sections of the genus). To accept the hypogeous-gastroid, astipitate, red latex-producing *L. rubriviridis* in *Arcangeliella*, a genus represented currently by stipitate-secotioid, white latex-producing taxa, would be counterintuitive to delimiting a monophyletic *Arcangeliella*. Hence, placement in *Arcangeliella* is unwarranted.

Another alternative would be to establish a new genus for *L. rubriviridis*. The data, however, suggest that such a decision is also unwarranted. The new species described herein is undoubtedly allied with members of *Lactarius* subgenus *Dapetes*, particularly with *L. rubrilacteus* Hesler & A.H. Sm., *L. barrowsii* Hesler & A.H. Sm., *L. subpurpureus* Peck, and *L. paradoxus* Beardslee & Burl. The latter four species are all green-staining, lamellate, epigeous species with red latex, and all form basidiospores ornamented with a partial to nearly complete reticulum. Furthermore, all four species are ectotrophically associated with conifers (primarily pines), and *L. rubrilacteus* grows in the same montane habitat in California as *L. rubriviridis*. Rather than promulgate the polyphyletic genus *Zelleromyces*, or introduce an erroneous taxon into the possibly polyphyletic genus *Arcangeliella*, or establish a monotypic genus delimited by a combination of features shared in part by *Lactarius*, *Zelleromyces* and *Arcangeliella*, I accept the new species in *Lactarius* subgenus *Dapetes*. If one accepts members of *Lactarius* subgenus *Dapetes* in the genus *Lactarius*, then the new species must belong there as well. Otherwise, establishment of a distinct genus for *L. rubriviridis* would make the "Dapetes lineage" paraphyletic. The red latex, green stains, forcibly discharged basidiospores, and pine association of *L. rubriviridis* suggest that the species is relatively recently derived from an epigeous agaricoid ancestor allied with *L. rubrilacteus*. Furthermore, the existence of *L. rubriviridis* suggests that there have been at least three independent origins of the hypogeous, loculate, gastroid body form (i.e., *Zelleromyces*) within *Lactarius*.

I agree with Miller et al (2001) that the gastroid genera *Arcangeliella* and *Zelleromyces* have been derived from within *Lactarius*, and that synonymy of these genera with *Lactarius* is a viable option. An analogous example was presented by Kretzer and Bruns (1997) where they reduced the polyphyletic secotioid-gastroid genus *Gastrosuillus* to synonymy with the boletoid genus *Suillus*. Another example is the recent synonymy of the morphologically diverse secotioid genus *Thaxterogaster* (54 spp.) with *Cortinarius* (Peintner et al 2002), supported by molecular evidence (Peintner et al 2001). Based on morphology alone, it has been known for years that *Thaxterogaster* species were phenetically similar to species belonging

TABLE II. Latex-producing epigeous secotioid Russulales published to date

Species and citation	Distribution	Plant associates	Latex[a]
ARCANGELIELLA:			
borziana Cavara (1900) [Type species] ≡ *stephensii* var. *borziana* (Cavara) Krieglst. (1991)[b]	Europe	*Abies*	white
crassa Singer & A.H. Sm. (1960)	W United States	*Abies*	white/yellow
crichtonii (G.W. Beaton, Pegler & T.W.K. Young) T. Lebel & Castellano (2002)	Australia	*Eucalyptus*	not observed
densa (Heim) Singer & A.H. Smith (1960)	Thailand	*Dipterocarpus*	white/yellow
desjardinii Thiers (1984)	California	*Pseudotsuga*	white
dolichocaulis Pegler (1982)	Africa	*Brachystegia*	white
hepaticus (G.W. Beaton, Pegler & T.W.K. Young) T. Lebel & Castellano (2002)	Australia	*Eucalyptus*	absent
parva Thiers (1984)	California	*Abies, Pinus*	white/yellow
saylorii Thiers (1984)	California	*Abies, Pinus*	white
tenax A.H. Smith & Wiebe (in Smith 1963)	W United States	conifer forest	white
texta (Cribb) Pegler & T.W.K. Young (1979)	Australia	*Eucalyptus*	not reported
variegata Thiers (1979)	California	conifer forest	white
volemoides K. Mader & A. Mader (1992)	Austria	*Picea*	white
ARCANGELIELLA spp. Insufficiently Known:			
asterosperma var. *depauperata* (Tulasne) Zeller & C.W. Dodge (1935)	France	*Quercus*	not reported
asterosperma var. *hololeuca* (Hesse) Zeller & C.W. Dodge (1935)	Germany	unspecified	not reported
camphorata (Singer & A.H. Sm.) Pegler & T.W.K. Young (1979) (= *Elasmomyces* sensu Thiers 1984)	Washington	conifer forest	not reported
curtisii Zeller & C.W. Dodge (1936)	SE United States	unspecified	not reported
ellipsoidea Zeller & C.W. Dodge (1936) (=*Macowanites krjukowensis* (Buchholz) Singer & A.H. Sm. 1960	Tasmania	unspecified	not reported
lactarioides Zeller (1947) (=*nomen dubium* sensu Thiers 1984)	California	*Abies*	color not reported
occidentalis (Harkness) Zeller & C.W. Dodge (1936) (non sensu Thiers 1984 = *Martellia occidentalis* Singer & A.H. Smith)	California	unspecified	not reported
vulvaria (Petri) Zeller & C.W. Dodge (1935)	Borneo	unspecified	not reported

ARCANGELIELLA spp. Accepted in Other Genera:

africana (Lloyd) Zeller & C.W. Dodge ≡ *Octaviania africana* Lloyd sensu Bottomley (1948)
alveolata (Cooke & Massee) Zeller & C.W. Dodge = *Zelleromyces australiensis* (Berk. & Broome) Pegler & T.W.K. Young sensu Beaton et al (1984); Lebel and Castellano (2002)
ambigua Zeller & C.W. Dodge = *Chamonixia* sp. sensu Thiers (1984)
asterosperma (Vittad.) Zeller & C.W. Dodge ≡ *Octavianina asterosperma* (Vittad.) O. Kuntze sensu Pegler and Young (1979)
australiensis (Berk. & Broome) C.W. Dodge ≡ *Zelleromyces australiensis* (Berk. & Broome) Pegler & T.W.K. Young sensu Beaton et al. (1984); Lebel and Castellano (2002)
beccarii (Petri) Zeller & C.W. Dodge ≡ *Octaviania beccarii* (Petch) J.W. Cribb = *Melanogaster* sp. sensu May and Wood (1997)
behrii var. *behrii* (Harkness) Zeller & C.W. Dodge = *Chamonixia* sp. sensu Thiers (1984)
behrii var. *caudata* Zeller & C.W. Dodge = *Chamonixia* sp. sensu Thiers (1984)
brunneola (Harkness) Zeller & C.W. Dodge = *Gymnomyces seminudus* Massee & Rodway sensu Zeller and Dodge (*ut A. seminuda* 1936)
campbelliae Zeller & C.W. Dodge ≡ *Thaxterogaster campbelliae* (Zeller & C.W. Dodge) Beaton, Pegler & T.W.K. Young sensu Beaton et al. (1985a)
caudata Zeller & C.W. Dodge ≡ *Arcangeliella behrii* var. *caudata* Zeller & C.W. Dodge = *Chamonixia* sp. sensu Thiers (1984)

TABLE II. Continued

cremea Zeller & C.W. Dodge ≡ *Martellia cremea* (Zeller & C.W. Dodge) Singer & A.H. Sm. sensu Singer and Smith (1960); Thiers (1984); ≡ *Gymnomyces cremeus* (Zeller & C.W. Dodge) Trappe, T. Lebel & Castellano sensu Trappe et al. (2002)
gardneri (Zeller & C.W. Dodge) Zeller & C.W. Dodge ≡ *Zelleromyces gardneri* (Zeller & C.W. Dodge) Singer & A.H. Sm. sensu Singer and Smith (1960)
glabrella Zeller & C.W. Dodge ≡ *Zelleromyces glabrellus* (Zeller & C.W. Dodge) Singer & A.H. Sm. sensu Singer and Smith (1960)
krjukowensis (Buchholtz) Zeller & C.W. Dodge (1936) ≡ *Macowanites krjukowensis* (Buchholtz) Singer & A.H. Sm. sensu Singer and Smith (1960)
krjukowensis var. *michailowskjana* (Buchholtz) Zeller & C.W. Dodge (1936) ≡ *Macowanites krjukowensis* (Buchholtz) Singer & A.H. Sm. sensu Trappe et al. (2002)
laevis (R. Hesse) C.W. Dodge ≡ *Hydnangium laeve* (R. Hesse) Zeller & C.W. Dodge sensu Zeller and Dodge (1935)
luteocarnea (Bres.) Lloyd ≡ *Sclerogaster luteocarneus* (Bres.) Zeller & C.W. Dodge sensu Zeller and Dodge (1935)
magna (Parks in Zeller & C.W. Dodge) Zeller ≡ *Macowanites magnus* Parks in Zeller & C.W. Dodge sensu Singer and Smith (1960); Thiers (1984)
malaiensis Corner & Hawker ≡ *Zelleromyces malaiensis* (Corner & Hawker) A.H. Sm. sensu Smith (1962); ≡ *Octaviania malaiensis* (Corner & Hawker) Trappe, T. Lebel & Castellano sensu Trappe et al. (2002)
mitsueae Imai (1957) = *Octaviania* sp. sensu Desjardin (this paper)
nana (Massee & Rodway) Zeller & C.W. Dodge ≡ *Hymenogaster nanus* Massee & Rodway sensu Beaton et al. (1985a)
pilosa Zeller & C.W. Dodge ≡ *Elasmomyces pilosus* (Zeller & C.W. Dodge) Singer & A.H. Sm. sensu Singer and Smith (1960); Thiers (1984); ≡ *Macowanites pilosus* (Zeller & C.W. Dodge) Trappe, T. Lebel & Castellano sensu Trappe et al. (2002)
ravenelii (Berk. & M.A. Curtis) C.W. Dodge ≡ *Zelleromyces ravenelii* (Berk. & M.A. Curtis) Singer & A.H. Sm. sensu Singer and Smith (1960)
rosea (Harkness) Zeller & C.W. Dodge ≡ *Hydnangium roseum* (Harkness) Singer & A.H. Sm. sensu Singer and Smith (1960); Thiers (1984)
scissilis Zeller & C.W. Dodge ≡ *Martellia scissilis* (Zeller & C.W. Dodge) Singer & A.H. Sm. sensu Singer and Smith (1960); Thiers (1984); ≡ *Zelleromyces scissilis* (Zeller & C.W. Dodge) Trappe, T. Lebel & Castellano sensu Trappe et al (2002)
seminuda (Massee & Rodway) Zeller & C.W. Dodge ≡ *Gymnomyces seminudus* Massee & Rodway sensu Beaton et al. (1984); Thiers (1984); ≡ *Cystangium seminudum* (Massee & Rodway) T. Lebel & Castellano sensu Lebel and Castellano (2002)
socialis (Harkness) Zeller & C.W. Dodge ≡ *Gymnomyces socialis* (Harkness) Singer & A.H. Sm. sensu Singer and Smith (1960); Thiers (1984); = *Hydnangium carneum* Wallr. in Dietrich sensu Lebel and Castellano (2002)
soderstroemii (Lagerh.) Zeller & C.W. Dodge = *Hydnangium carneum* Wallr. in Dietrich sensu May and Wood (1997)
stephensii (Berk.) Zeller & C.W. Dodge ≡ *Zelleromyces stephensii* (Berk.) A.H. Sm. sensu Smith (1962)
tasmanica (Kalchbr.) Zeller & C.W. Dodge ≡ *Octavianina tasmanica* (Kalchbr.) Pegler & T.W.K. Young sensu Pegler and Young (1979); Beaton et al (1985b)
violacea (Massee & Rodway) Zeller & C.W. Dodge ≡ *Hymenogaster violaceus* Massee & Rodway sensu Beaton et al. (1985a)

[a] For all taxa where latex was absent or not reported or where latex color was not reported, the gleba was described as ranging from white to pale orange, clay-colored, tawny-olive, cinnamon-buff or greyish ochraceous when fresh or in alcohol, lacking any red pigmentation or red exudates.

[b] *Arcangeliella borziana* is the type species of *Arcangeliella*. *A. stephensii* is considered to belong in *Zelleromyces* by most authorities (cf. Smith 1962; Pegler and Young 1979; Miller and Miller 1986; Pegler et al. 1993). If *Arcangeliella borziana, A. stephensii* and *Z. ravenelii* (=*Z. cinnabarinus*, type species of *Zelleromyces*) are considered congeneric, then *Zelleromyces* (Singer and Smith 1960) becomes a synonym of *Arcangeliella* (Cavara 1900).

to different subgenera of *Cortinarius* (pers obs; Horak pers comm). The molecular phylogenetic studies by Peintner et al (2002) confirm these inferences. As more molecular data become available, it may result that *Lactarius* must be divided into a number of genera, wherein subgenus *Dapetes* (or some portion of it, including *L. rubriviridis*) may represent a distinct genus in need of a new name (none is currently available for this lineage). It is premature for me to preemptively propose a new generic name to accommodate *L. rubriviridis* and its epigeous, lamellate cohorts. In this scenario, *Arcangeliella* and *Zelleromyces* may remain as viable taxonomic entities in a much-restricted sense for lamellate and secotioid/gastroid species allied with *A. borziana* and *Z. ravenelii*, respectively. Other *Arcangeliella* and *Zelleromyces* species will undoubtedly require taxonomic placement elsewhere within the *Lactarius* sensu lato clade.

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