

Ronald H. Petersen

Scanning electron microscope images of basidiospores of *Xerula* (Physalacriaceae, Agaricales)

Received: February 5, 2007 / Accepted: August 30, 2007

Abstract Structure and ornamentation of basidiospore walls in *Xerula* (inclusive of *Dactylosporina*) are illustrated using scanning electron microscope (SEM) images. *Oudemansiella* spores are not depicted, but all sections of *Xerula* are represented by 17 taxa. Spore wall sculpturing cannot be used as an infrageneric diagnostic character, nor to separate *Oudemansiella* and *Rhizomarasmusius* from *Xerula*. *Xerula caulovillosa* is proposed as a new species, and *Xerula radicata* f. *marginata* as a new combination.

Key words SEM · Spore wall ornamentation

Introduction

Pegler and Young (1971: 57–58 with accompanying figures and plates) used carbon replica techniques and some transmission electron microscope (TEM) images in their comprehensive treatise on basidiospore morphology in the Agaricales. This work was done in the infancy of electron microscopy and was, simultaneously, a breakthrough in described details of spore walls and their variability and an exercise in fastidious technique revealing a minimum of detail. Among a series of papers on smaller groups of agarics, Pegler and Young (1987) described in more detail the spore wall structure in *Oudemansiella* Speg., which for those authors included the taxonomic complexes of *Xerula*, *Oudemansiella*, and *Mucidula* Pat. Through great progress in electron microscopy, theretofore undescribed spore wall features were depicted. In the 1987 paper, so many taxa were considered that the paper covered a wider concept than spore wall structure, namely, generic classification. Both papers (1971, 1987) reviewed literature on spore wall complexity in basidiomycetes, and because TEM images

were included, wall structure could be described with some precision.

Almost simultaneous to the second Pegler and Young (1987) paper, Redhead et al. (1987) published a floristic survey of *Xerula* Maire (*Oudemansiella* s.s. Pegler and Young, pro parte) for Canada, with some notes on extralimital collections. Without knowledge of Pegler and Young's work and using only light microscopy, Redhead et al. (1987) observed some subtle spore wall relief, especially of spores of *X. megalospora* (Clem.) Redhead, Ginns & Shoemaker. This feature was not mentioned by Pegler and Young (1987), for the lowest resolution of their images was considerably higher than that of the illustrations offered by Redhead et al. (1987). Thus, while describing the spores of *X. megalospora* as “finely roughened,” the illustrations (their figures 23, 24, 37–39) were hardly informative on this point. All other authors, including Dörfelt (1979, 1986, and see the bibliography in the latter), were satisfied that spores in this complex were smooth. Spores have often been described as thick walled, but spores of most taxa include a single large guttule (or several smaller guttules), and it is difficult, especially using bright field light microscopy (BF), to separate the spore wall from the guttule outline. Especially the guttule is strongly light refringent, often masking the outline of the spore wall. Phase-contrast microscopy (PhC) is helpful in this regard.

As part of a larger study on the genus *Xerula* (see Petersen and Hughes 2004; Petersen and Nagasawa 2006; Petersen and Methven 1994), spore prints and/or hymenial surfaces of lamellae were used to produce scanning electron microscopy (SEM) images of basidiospores of selected taxa. Three objectives were investigated: (1) is spore wall sculpturing sufficiently different in the genus to distinguish species? (2) what is the range of variation in wall sculpturing across the genus? and (3) is the observed “dimpling” or “puckering” of spores observed by Redhead et al. (1987) an artifact or does it extend to SEM resolution images? Some of Pegler and Young's (1987: figs. 34, 35, 66) images seem to depict this obscure spore surface relief. Because the present study has not been expanded to *Oudemansiella* s.s. (sect. *Oudemansiella* in the sense of Pegler and Young

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1987), no images of spores of this group are depicted here. Pegler and Young (1987) discussed and illustrated spore ornamentation in this group.

Throughout this article, spore walls are referred to only as outer wall, middle wall, and inner wall. Some illustrations and text by Pegler and Young (1987: figs. 23, 24, 38, 45, 47, 53, 56, pp 585–586, table 1) accurately describe the complexity of the spore wall in the generic group. Two major layers, the inner coriotunica and outer myxosporium, surround the spore contents of all spores. The coriotunica is further composed of the innermost corium, the tunica, and epitunica, not all developed equally across the group. Of the myxosporium, the inner podostratum, almost always present as a differentiated layer, presents the sculpturing described in this article as the “middle wall”; the mucostratum and sporothecium are mucoid surrounding layers. For further explanations and alternative constructions, see Clemençon (2004).

Materials and methods

All images are of spores present on dried, preserved specimens (that is, no spores were shed on SEM stubs from fresh specimens) or from spore prints. For SEM observation, a small piece (ca. 2 × 2 mm) of lamella was removed from the dried specimen and mounted on an aluminum specimen stub using conductive carbon tape. For spore prints, an aluminum stub with tape was gently touched to the spore print to attach spores to the conductive tape. Just before examination, mounted samples were coated with a thin layer (ca. 10 nm) of gold using a Structure Probes Inc. (SPI) sputter coater. Samples were viewed in a LEO 1525 field emission SEM using an accelerating voltage of 3 kV and a working distance of 5 mm. Images were recorded digitally at various magnifications.

The following abbreviations are used: TFB = Tennessee field book, in which fresh collections are numbered before accession into the Tennessee Herbarium under another, unrelated number (TENN); GSMNP = Great Smoky Mountains National Park, spanning the boundary between the states of North Carolina and Tennessee. In the description of *X. caulovillosa*, colors cited alphanumerically (i.e., 4A6) are from Kornerup and Wanscher (1967): those within quotation marks (i.e., “sayal brown”) are from Ridgway (1912).

Results

The species complex here treated under the genus name *Xerula* has been sorted in different ways by several preceding authors. Spegazzini first described *Oudemansia*, but when it was discovered to be a later homonym, he revised the genus name to *Oudemansiella*. Pegler and Young (1987) briefly summarized the evolution of generic concepts. Two basic generic dispositions have developed: (1) the use of *Oudemansiella* to shelter species fruiting directly on wood,

usually exhibiting a partial veil as well as basidiomata with no partial veil and a radicating stipe (Singer 1964; Clemençon 1979; Corner 1994; Pegler and Young 1987; Yang and Zang 1993; Yang 2000, etc.); and (2) the separation of these two habits into *Oudemansiella* for the former and *Xerula* for the latter (Maire 1933; Dörfelt 1979, 1986, and intervening; Boekhout and Bas 1986; Petersen and Methven 1994; Contu 2000, etc.). The latter arrangement is followed here.

Below, taxa are taken up alphabetically under the section of *Xerula* to which they belong (i.e., *Xerula*, *Albotomentosi*, *Radicatae*; *Dactylosporina*). This scheme merely follows the plan laid out by Pegler and Young (1987) in a similar paper. Their paper, however, took on the added task of presenting a generic key to worldwide taxa, certainly not the aim of the present work.

Sect. *Xerula*

Xerula pudens (Pers.) Singer. 1951 [“1949”]. Lilloa 22: 289.

Members of *Xerula* sect. *Xerula* exhibit the same general spore wall characters as members of sects. *Albotomentosi* and *Radicatae*. *Xerula pudens* [neotype: ex herb. Persoon, no. 910.255-278 (L); annot. Dörfelt (!)] forms subglobose spores, which, when immature, are very finely roughened (Fig. 1), as is usual for the genus. Even when turgid, spores are often “dimpled,” a texture usually discernible under PhC microscopy (Figs. 2, 3). Once the outer spore wall has been removed, the middle wall is represented by closely set papillose, wart-like pillars, of which a few are significantly larger than most (Figs. 4, 5). Two specimens (TENN 59208, 29330) showed close similarity of number and arrangement of separating pillars.

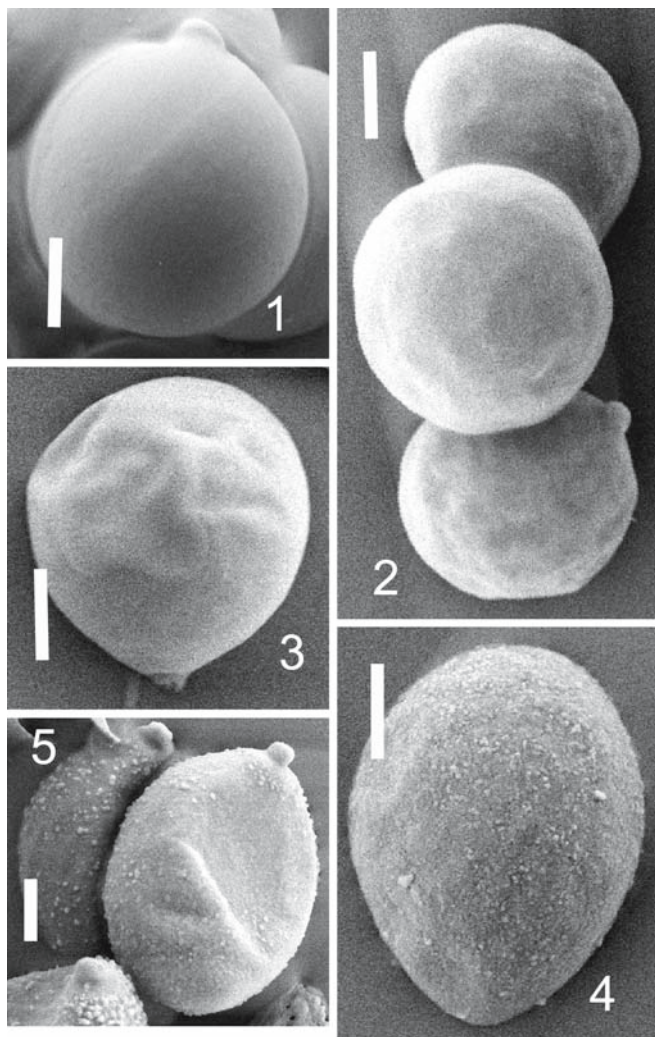
Pegler and Young (1987; figs. 33–38) illustrated spores comparable to those in Figs. 1–3 here. A TEM image of a wall section indicated little or no differentiation of corium, epitunica, or sporothecium. In our experience, rather few spores show the differentiation of middle wall depicted in Figs. 4 and 5, but the possibility of contaminant spores cannot be dismissed completely.

Material used: AUSTRIA, Lower Austria, Vienna, 23rd Dist., Mauerwald, 28.IX.2001, TFB 11469 (59330, TENN). AUSTRIA, Lower Austria, Vienna, riverine forest, vic. Wolfsthal, 23.IX.2001, coll. H. Voglmayr, TFB 11432 (59208, TENN).

Sect. *Albotomentosi*

Xerula amygdaliformis (Zhu L. Yang & M. Zang) R.H. Petersen & Nagas., 2006. Rep. Tottori Mycol. Inst. 43: 8. **var. amygdaliformis**

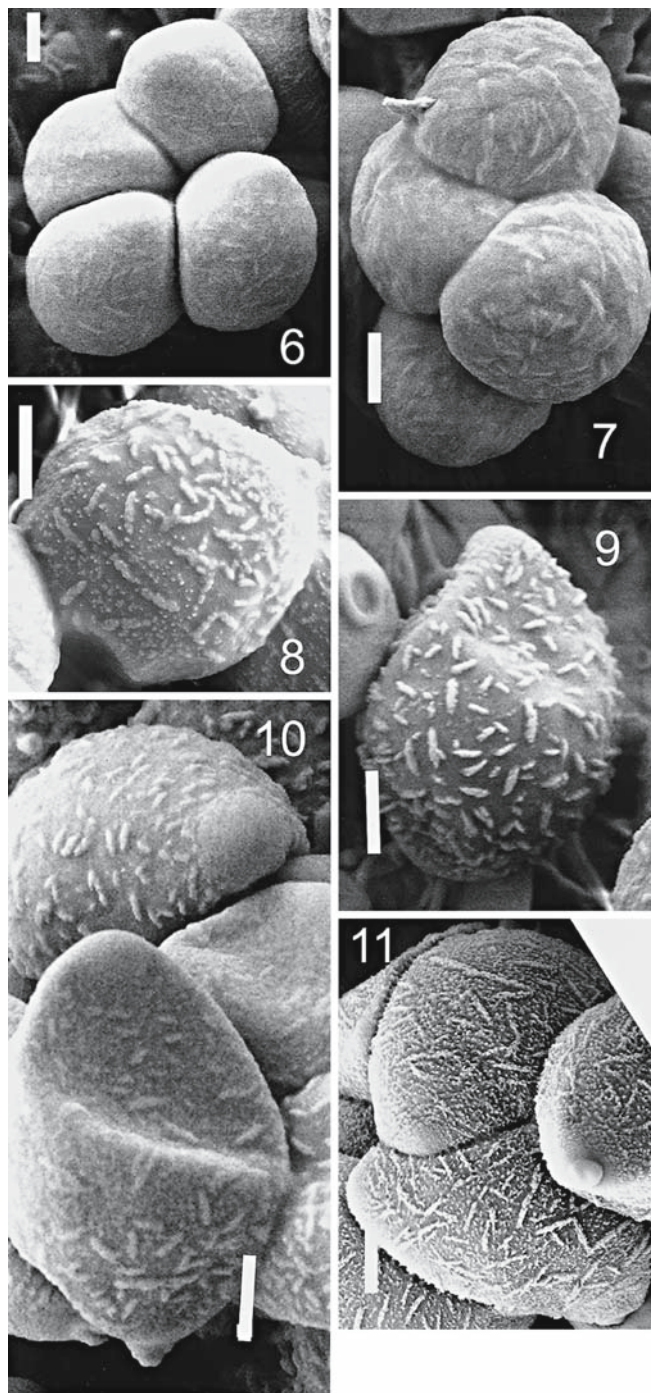
Xerula amygdaliformis spores exhibit, perhaps, the most unusual sculpturing in the genus. Young spores, with outer wall complete, show a suggestion of underlying middle wall sculpturing [Fig. 6 (TMI 18706)] and, as the outer wall is increasingly stretched [Fig. 7 (TMI 18706)], interior relief is more pronounced. Once the outer wall has been removed, the separating sculpturing between the outer and inner



Figs. 1–5. *Xerula pudens*, basidiospores. **1** TENN 59330. **2–5** TENN 69208. Bars 2 μ m

walls is clearly seen as randomly distributed bars and scattered pegs [Figs. 8–10 (TMI22231), 11 (TMI 18706)]. With two specimens used to produce these images, the density of scattering of bars and pegs differs somewhat, but the basic configuration is consistent. Moreover, this patterning is not universal over the spore wall surface. As expected, sculpturing is suppressed in the immediate neighborhood of the hilar appendix, but the abhilar or distal end of the spore also experiences decreased sculpturing to become smooth over the distal terminus itself (Figs. 9–11). In these areas (distal apex, vicinity of hilar appendix), spore walls may undergo a minimum of stretching during spore maturation, leaving the middle wall essentially intact.

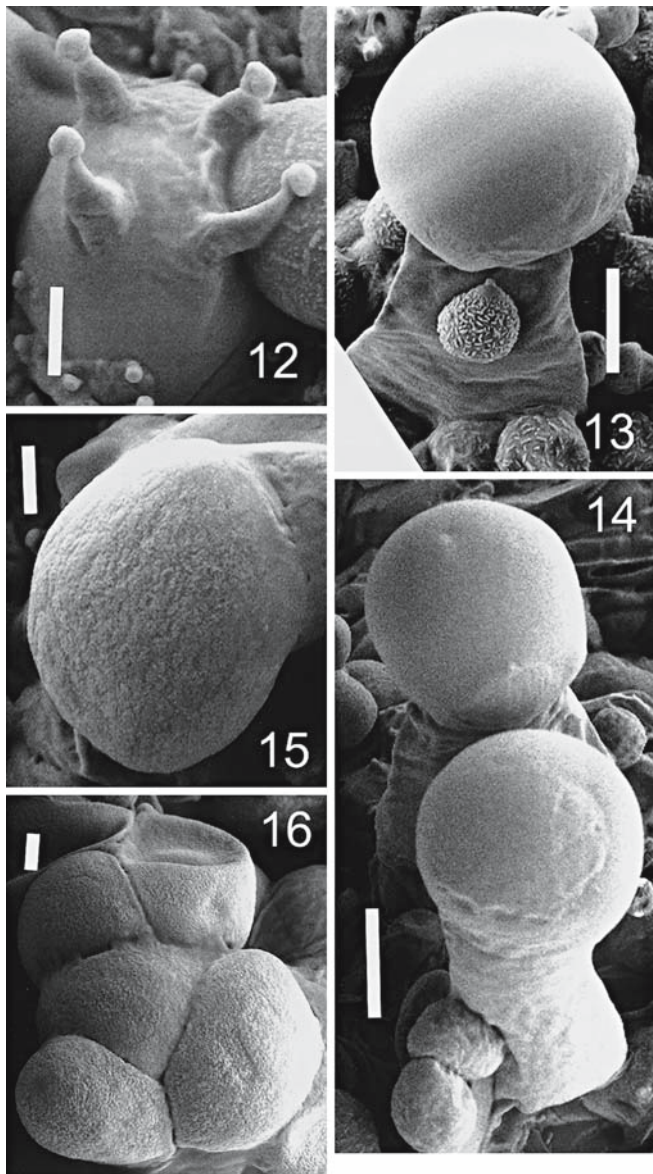
Basidia in the typical variety (var. *amygdaliformis*) are four spored [Fig. 12 (TMI 22231)], and, as is usual for SEM images, there is some shrinking of the wall structure to appear somewhat puckered. Likewise, pleurocystidia are unusually common in the type variety, and can be seen as a semicollapsed shaft protruding through the hymenium, with a relatively turgid or hardened capitulum [Figs. 13 (TMI 22231), 14 (TMI 18706)].



Figs. 6–11. *Xerula amygdaliformis*, basidiospores. **6, 7, 11** TMI 18706. **8–10** TMI 22231. Bars 2 μ m

The two Japanese specimens used for SEM images have been compared to the holotype of *X. amygdaliformis* [CHINA, Yunnan Prov., Mengla, Menglun, 6.XI.1989, Yang 972 (22754, HKAS (!)].

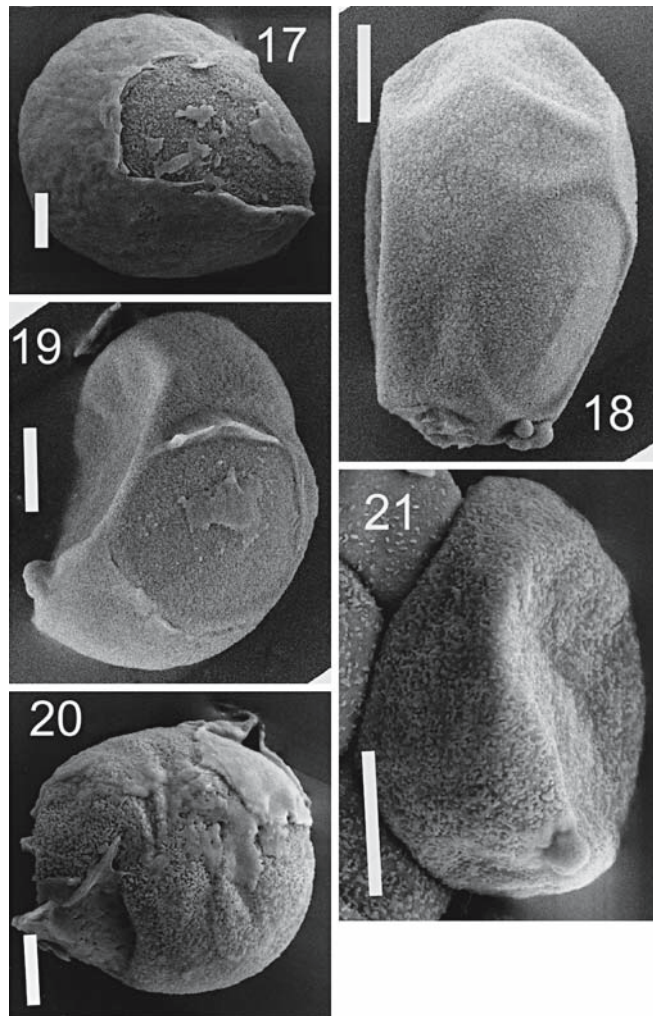
Material used: JAPAN, Tottori Pref., Tottori-shi, Kokoge, 31.VIII.1993, Nagasawa 93-92 (187096, TMI). JAPAN, Tottori Pref., Mt. Daisen, Kakamiganaru, 19. IX.1996, coll. E. Nagasawa, s.n. (22231, TMI).



Figs. 12–16. *Xerula* structures. **12–14** *X. amygdaliformis*. TMI 22231. **12** Basidium apex with four sterigmata. **13, 14** Pleurocystidial apices. **15, 16** *X. amygdaliformis* var. *bispora*, basidiospores. TMI 23351. Bars 12–14 10 μ m; 15, 16 2 μ m

Xerula amygdaliformis var. *bispora* R.H. Petersen & Nagas., 2006. Rep. Tottori Mycol. Inst. 43: 12.

Based on similarities in spore dimensions and statistics, cheilocystidial shape and size, and occurrence of a black reticulum on the pileus surface, basidiomata exhibiting these characters were proposed as a two-spored variety under *Xerula amygdaliformis*. SEM images of spores, however, show little resemblance between the typical variety and var. *bispora*. Spores of var. *amygdaliformis* show a complex ornamentation of the middle wall in coarse bars and scattered pegs, whereas the middle wall of spores of var. *bispora* exhibits a densely scattered pattern of intricate ridges (Figs. 15, 16). This discordant character might suggest that the two varieties are not as closely related as originally conjectured.



Figs. 17–21. *Xerula chiangmaiae*, basidiospores. **17, 20, 21** TENN 57273. **18, 19** TENN 49170. Bars 2 μ m

Material used: JAPAN, Honshu, Tottori Pref., Tottori-shi, Kokoge, 11.VI.1992, Nagasawa 99-22 (23351, TMI).

Xerula chiangmaiae R.H. Petersen & Nagas., 2006. Rep. Tottori Mycol. Inst. 43: 17.

Intact spores of *X. chiangmaiae* show the characteristic “dimpling” that can be seen under PhC microscopy (Fig. 17, left). Young spores appear somewhat felty (Figs. 18, 19). Subsequently, the outer spore wall peels away (Figs. 17, 19, 20), revealing intricate separating pillars extremely densely but randomly arranged (Figs. 17, 19, 21). Images of the two specimens used (TENN 49170, 57273) show close agreement in texture of the middle wall. These specimens were compared to the holotype (THAILAND, vic. Chiangmai, Doi Inthenon National Park, 26.VI.2003, TFB 11734 (59791, TENN[!])).

Material used: CHINA, Guizhou Prov., Fan Jing Shan Nature Preserve, 28.VIII.1991, TFB 4107 (57273, TENN). CHINA, Yunnan Prov. Simao Pref., vic. Simao, 6.VIII.1990, TFB 3142 (49170, TENN).

Xerula furfuracea (Peck) Redhead, Ginns & Shoemaker. 1987. Mycotaxon 30: 362.

The specimen used for SEM images was compared to the holotype [USA, New York, Sevey, VII, leg. C.H. Peck, s.n., Mycology Type Database no. 1302 (NYS!)]. Young spores of *X. furfuracea* (TENN 48028) exhibit the normal delicately felty appearance of the outer wall as well as the low undulating relief here called “dimpled” (Fig. 22). The outer wall peels or weathers away (Fig. 23), revealing the middle wall composed of intricate, minute, low ridges and warts (Figs. 23–25).

The image produced by Pegler and Young (1987, fig. 63) showed an intricate middle wall ornamentation composed of short, sinuous rods. The spores of the taxon (as *Oudemansiella radicata* var. *furfuracea* (Peck) Pegler & T.W.K. Young) were described as “ovoid to ellipsoid, adaxially applanate, with an obtusely rounded or slightly tapering apex.” In our experience, the spores of *X. furfuracea* are always obtusely rounded, and the “slightly tapering apex” might include another species such as *X. incognita* R.H. Petersen & Methven. In any case, the sculpturing shown in our images is not closely similar to that shown by Pegler and Young.

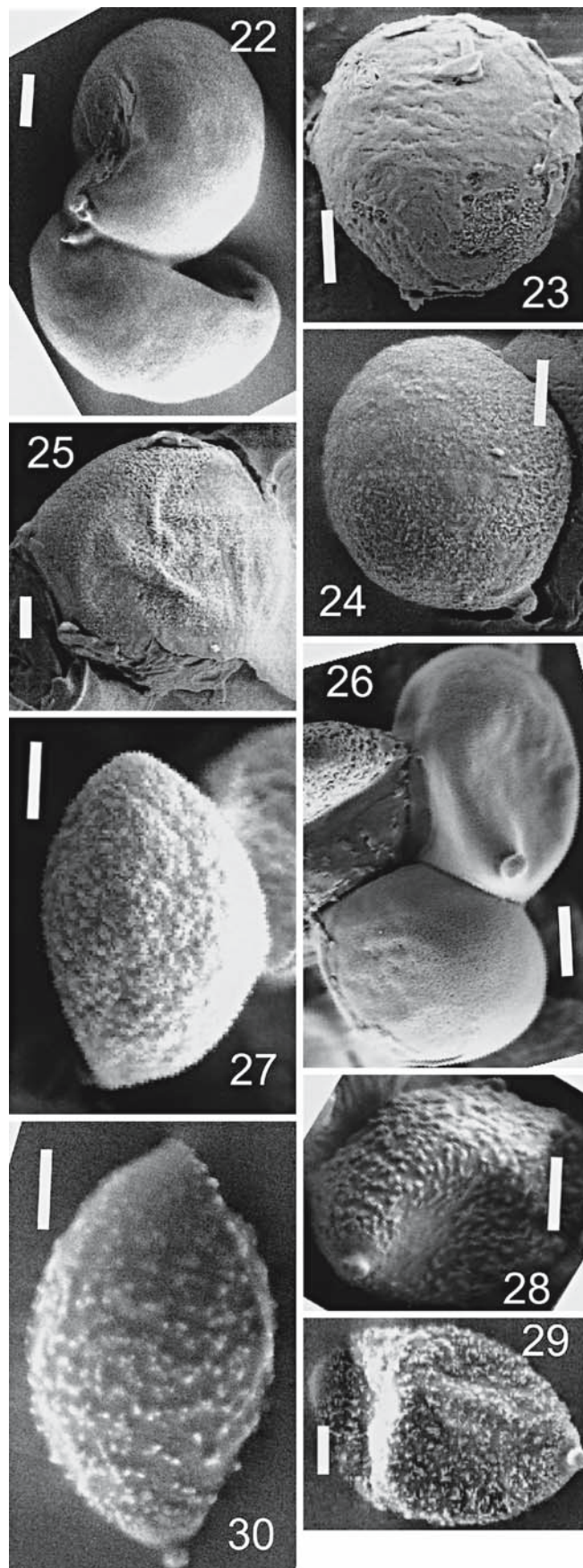
Basidiomata of *X. furfuracea* vary considerably in pileipellis construction. Most specimens exhibit scattered pileal hairs (i.e., pileocystidia extended into cylindrical or slightly tapering filaments), but often these structures cannot be demonstrated. It is necessary, therefore, to include the species under both sect. *Albotomentosi* and sect. *Radicatae*. Rarely, however, the pileal hairs are observed as thick walled, closely resembling the pileisetae defining sect. *Xerula*. As tempting as it might be to describe infraspecific taxa to accommodate these variations, until molecular data can show them to be separable, it is premature to segregate them.

Redhead et al. (1987) drew attention to the separation of *X. furfuracea* from *X. megalospora* based on spore shape and cystidial (pleuro-, cheilo-, and caulo-) shape and abundance. Comparison of the middle spore wall structure in the two species further separates them, with the ornamentation in *X. megalospora* considerably coarser.

Material used: USA, North Carolina, Macon Co., vic. Highlands, 26.IX./1988, TFB 1779 (48028, TENN).

Xerula megalospora (Clem.) Redhead, Ginns & Shoemaker. 1987. Mycotaxon 30: 374.

In *X. megalospora*, young spores are smooth and show some dimpling (Fig. 26). As the outer wall ages, it begins to appear felty (Fig. 26, lower). Once the outer wall has been removed, the middle wall sculpturing is revealed (Figs. 27–30). Although images are from two collections (TENN 48372, 50261), the configuration of the middle wall sculpturing is quite similar, composed of coarsely arranged pegs and short, sinuous bars (Figs. 27–30). All characters of these two specimens agree with those of the type (USA, Nebraska, Saltillo, 7.???. 1894 or 1895, leg. Pound & Clements, no. 4239 (slide of holotype, NY[!]; holotype lost from NEB). Together with *X. furfuracea*, these species are the most commonly collected in eastern



Figs. 22–30. *Xerula* basidiospores. 22–25 *X. furfuracea*. TENN 48028. 26–30 *X. megalospora*. 26–28. TENN 48372. 29, 30 TENN 50261. Bars 2µm

North America, as also reported by Redhead et al. (1987).

Material used: USA, Tennessee, Sevier Co., Great Smoky Mountains National Park, 28.VII.1989, coll. E. Rothberger, TFB 2034 (48372, TENN). USA, Tennessee, Blount Co., GSMNP, Spruce Flats, 25.VI.1991, TFB 4064 (50261, TENN).

Xerula raphanipes (Berk.) Dörfelt, 1983. Feddes Repert. 94: 557.

After comparison with the type specimen of *Agaricus raphanipes* (INDIA, Sikkim, Jilapahar, VI–VII, coll. J.D. Hooker, Hooker 96 [K(M) 124276!]), the binomial was used as the basionym for a two-spored organism whose characters resembled those of *X. chiangmaiae*. In both varieties (var. *chiangmaiae*, var. *raphanipes*), spores begin with a felty surface of the outer wall (Figs. 31, 32), sometimes with a suggestion of dimpling (Fig. 31). As the outer wall disintegrates (Fig. 33), the sculpturing of the middle wall is revealed as a scattering of discrete papillae (Fig. 34). The configuration of middle wall sculpturing between the two varieties, although not identical, is not significantly different. The illustration of a holotype spore by Pegler and Young (1987; fig. 55) seems similar to the configuration see in our figures.

Proposal of *Agaricus raphanipes* Berk. as basionym for an infraspecific taxon under a more recently proposed species epithet (*X. chiangmaiae*) violated the ICBN (see

Petersen and Nagasawa 2006). Rather than subordinating *X. chiangmaiae* (four spored and therefore assumed to be sexual) as an infraspecific taxon under *A. raphanipes* (two spored and therefore assumed to be asexual; see Petersen and Nagasawa 2006), I consider that a better alternative is to consider *Xerula raphanipes* (Berk.) Dörfelt at species rank (see above for citation). To do so is somewhat controversial, for asexual organisms do not qualify for inclusion under the usual articles of the ICBN, but under Art. 59, which deals with pleomorphic taxa. Technically, therefore, if *X. raphanipes* is confirmed to be asexual, it should be referred to as a “form species.”

Material used: JAPAN, Honshu, Tottori Pref. Tottori City, Kokoge, 6.X.1995, coll. Nagasawa, s.n. (20283, TMI).

Xerula rugosoceps (G.F. Atk.) Redhead, Ginns & Shoemaker. 1987. Mycotaxon 30: 386.

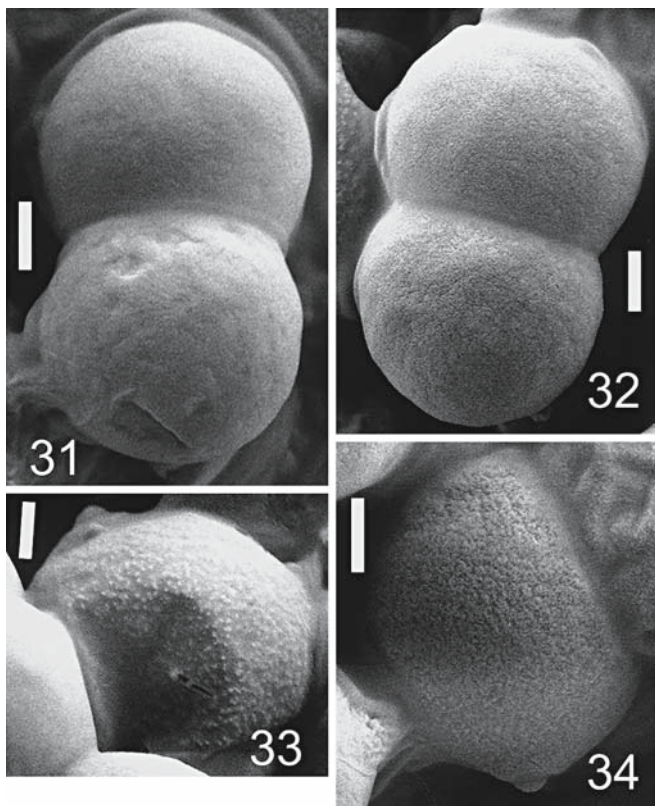
As in other species of this genus complex, basidiospores of *X. rugosoceps* (TENN 57902) are not smooth when immature, but the outer spore wall appears to be composed of closely packed units so as to appear felty (Fig. 35). Once this outer wall has been removed (Figs. 36–38), the columns that separate the outer and inner walls are revealed. In *X. rugosoceps*, these pillars take the form of randomly oriented rods (Figs. 36–38), absent only from a small areola in proximity to the hilar appendix. Apparently these pillars are easily sloughed off, revealing the outer surface of the inner wall as a somewhat pock-marked surface (Figs. 36, 37, 39). The coarse appearance of the interintegumental rods is unique for taxa in *Xerula*.

Using TENN 59563, two features were added: (1) the outer wall can be seen as both peeling off (Figs. 40, 41) and wearing through (Fig. 40); and (2) the pillars that separate the outer and inner walls are seen as considerably finer and more delicate (Figs. 42, 43). Whether this variation in middle wall sculpturing is consistent cannot be judged using only two specimens, but the species is so clearly marked morphologically that there is little doubt about the identification of the specimens. They have been compared to the holotype (USA, New York, Tompkins Co., Ithaca, South Hill Woods, coll. C.O. Smith, 27.VII.1902, no 13062 (CUP-A[!])).

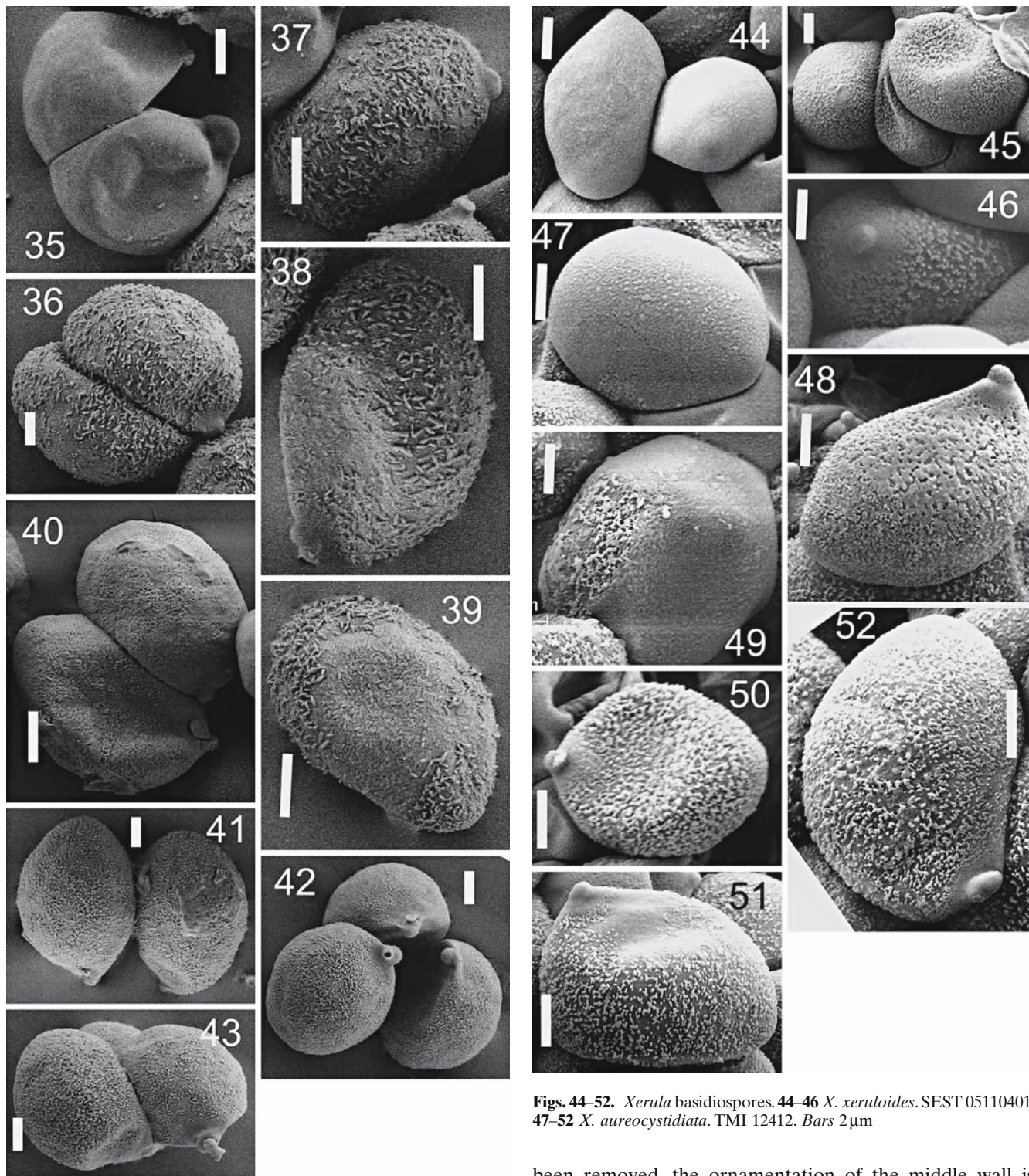
Material used: USA, North Carolina, Macon Co., Whitesides Cove Rd, 8.VII.1999, coll. RHP, TFB 10341 (57902, TENN). USA, Arkansas, Perry Co., Lake Sylvia State Park, 28.V.2003, coll. J. Justice, TFB 11080 (59563, TENN).

Xerula xeruloides (Bon) Dörfelt. 1980. Feddes Repert. 92: 216.

Pegler and Young (1987, figs. 45–49) produced several illustrations of spores of *X. xeruloides* (as *Oudemansiella*). The TEM images were instructive, clearly showing the sculpturing of the epitunica-podostratum complex. The two SEM images differed somewhat in the topographic relief distinguishable. In our study we examined the type specimen, but used a Spanish specimen (SEST-05110401) for imaging (FRANCE, Loire Atlantique, Odonne, 3.II.73, coll. & det. M. Bon, LIL 73110309) and the Laffoley speci-



Figs. 31–34. *Xerula raphanipes*, basidiospores. TMI 20283. Bars 2 µm



Figs. 35-43. *Xerula rugosoceps*, basidiospores. 35-39 TENN 57902. 40-43 TENN 59563. Bars 2 μ m

Figs. 44-52. *Xerula* basidiospores. 44-46 *X. xeruloides*. SEST 05110401. 47-52 *X. aureocystidiata*. TMI 12412. Bars 2 μ m

men used by Pegler and Young (1987), leading to a secure comparison of our images with theirs.

Spores begin (Fig. 44, right) with the normal “smooth” texture to the surface of the outer wall, which later begins to separate slightly (Fig. 44, left). Once the outer wall has

been removed, the ornamentation of the middle wall is exposed as an intricate pattern of complex pegs and meandering ridges (Figs. 45, 46). As expected, this ornamentation disappears in the neighborhood of the hilar appendix (Fig. 46), with the middle wall apparently remaining intact, perhaps an indication that the spore walls are not stretched in this region.

Material used: SPAIN, Burgos, Castrobarto, 4.XI.2005, leg. J.L. Pérez-Butrón & R.M. Pérez, no. 05110401 (SEST).

Sect. *Radicatae*

Xerula aureocystidiata R.H. Petersen & Nagas. 2006. Rep. Tottori Mycol. Inst. 43: 14.

Figure 47 shows an immature spore with a late-stage outer wall still intact, although beginning to separate. The outer wall can become punctate and slowly wear off (Fig. 48), or it can peel away (Fig. 49), in either case revealing the sculpturing of the middle wall. In the case of *X. aureocystidiata*, the configuration of the separating pillars of the middle wall is particularly intricate (Figs. 50–52), but the area surrounding the hilar appendix remains without significant sculpturing (Figs. 50–52).

The process of outer wall punctation and gradual disappearance is quite similar to that pictured by Petersen and Hughes (2004; figs. 5C,D) for *X. limonispota* R.H. Petersen. In fact, middle wall sculpturing in *X. limonispota* (Petersen and Hughes 2004; fig. 4) is quite similar to that in *X. aureocystidiata*. Both species belong in sect. *Radicatae*. The two species differ in pleurocystidial shape, spore dimensions, and geographic distribution.

Material used: JAPAN, Honshu, Tottori Pref., Mt. Daisen, 22.VII.1980, EN 80-110 (12412, TMI, holotype).

Xerula caulovillosa R.H. Petersen, sp. nov. Figs. 53–64

Basidiomata collybioidea, radicata. Pileus 15–35 cm latus, convexus, planescens, umbonatus, ferrugineus vel cinnameus (“sayal brown”), humidus vel viscidus, rugulosus, opacus; caro alba. Lamellae late adnatae, ventricosae, albae, non marginatae. Stipes 90–140 mm × 3–7 mm, striatus, aridus, sursum albus, deorsum pallide brunneus, badescens, cum tomento albo, tenui. Pseudorhiza usque ad 70 mm longa. Pileus pellucidus, viscidus hymenimorphus; pileocystidia 39–97 × 13–38 μm, clavata vel pyriformia, levia, fusca. Lamellae tramis sarcodimiticae. Pleurocystidia 85–130 × 27–45 μm, late fusiformi-capitata, levia. Cheilocystidia ventricosa, 20–95 × 6–32 μm, fusiformia. Basidia 50–66 × 12–19 μm, tetraspora, clavata, fibulata. Basidiosporae 13–17

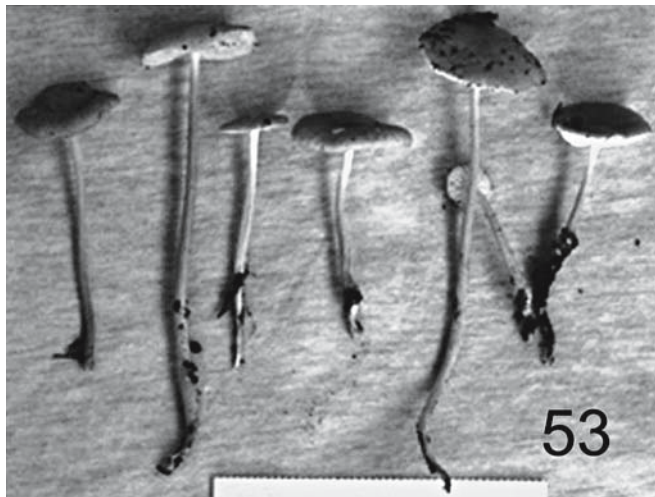


Fig. 53. *Xerula caulovillosa*, basidiomata. Holotype. Bar 50 mm

× 10–12.5 μm, late ovoideae vel ovoideae, hyalinae, uniguttulatae, inamyloideae. Hyphae fibulatae. Tomenta hyphae ad 1000 μm longa, scleroidea, fibulata, alba.

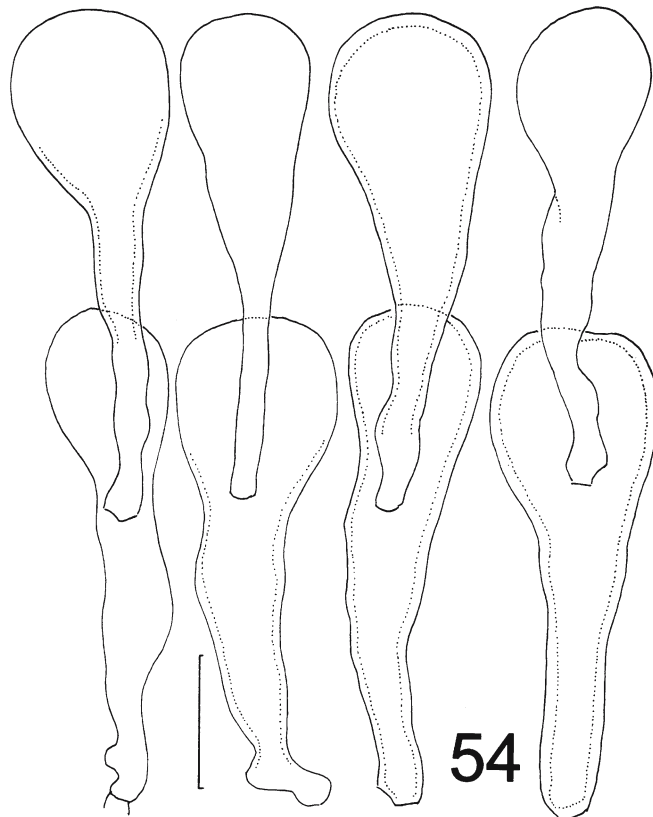


Fig. 54. *Xerula caulovillosa*, pileocystidia. Holotype. Bar 20 μm

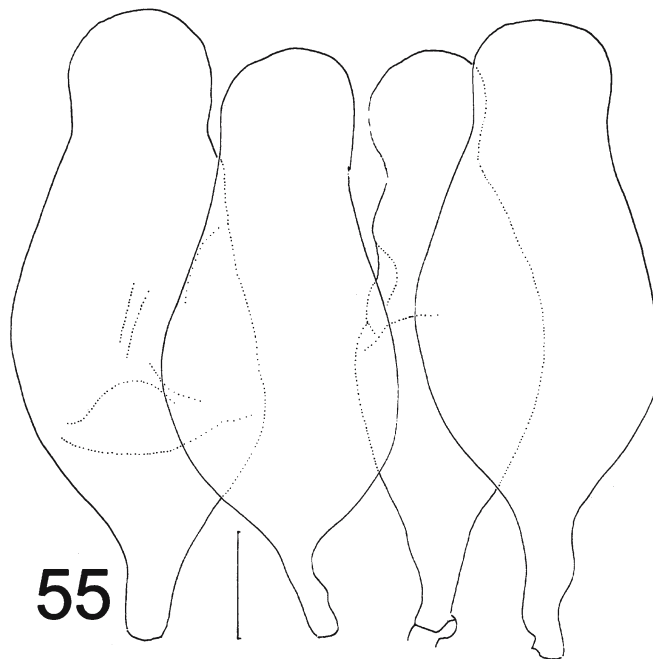


Fig. 55. *Xerula caulovillosa*, pleurocystidia. Holotype. Bar 20 μm

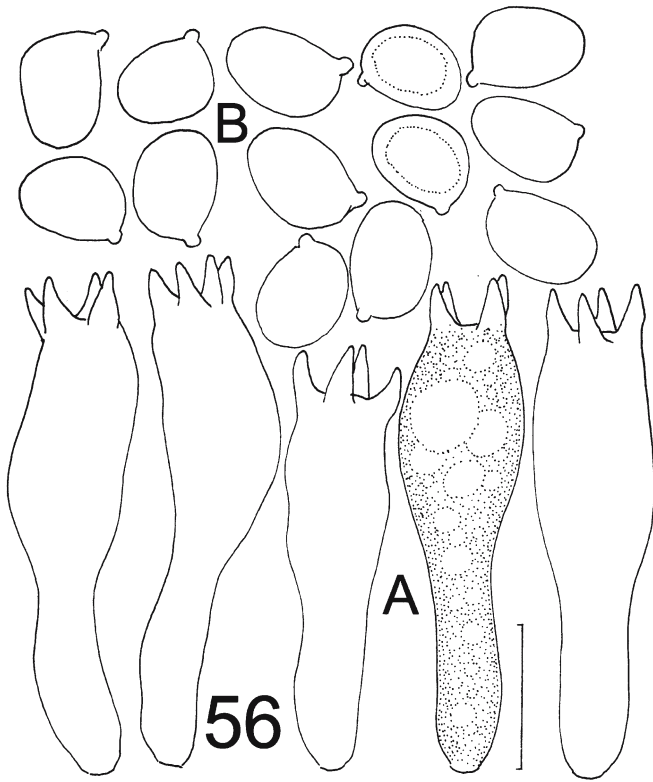


Fig. 56. *Xerula caulovillosa*, basidia and basidiospores. Holotype. **A** Basidia. **B** Basidiospores. Bar 20 μm

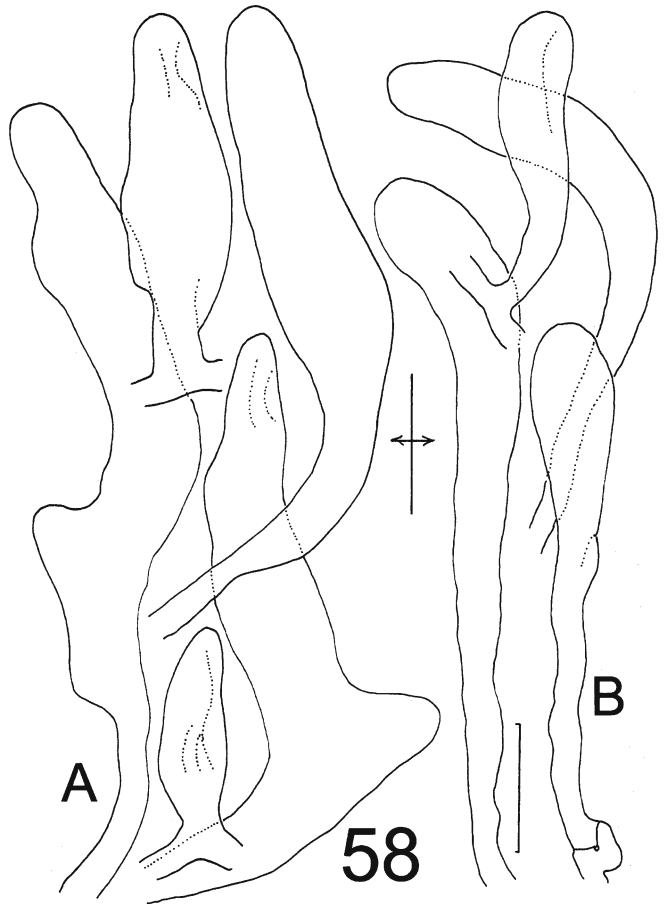


Fig. 58. *Xerula caulovillosa*, caulocystidia. Holotype. **A** Caulocystidia from stipe apex. **B** Caulocystidia from stipe midsection. Bar 20 μm

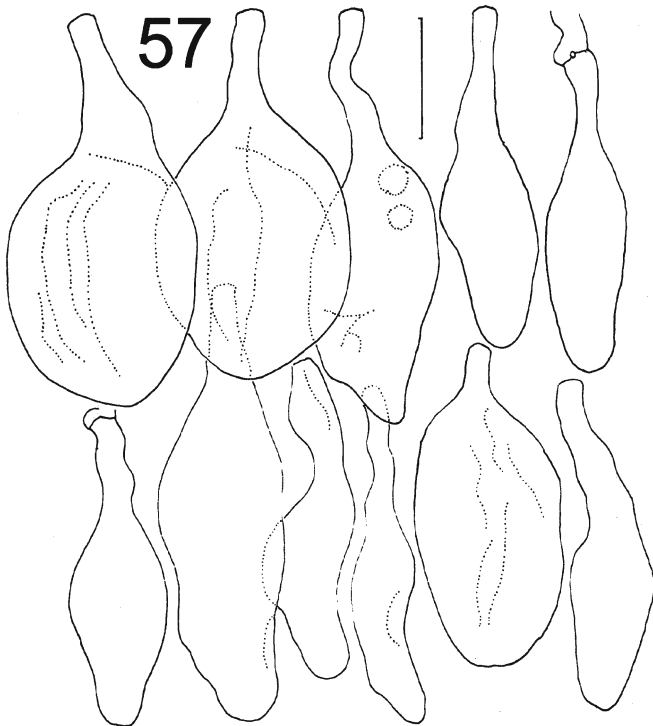


Fig. 57. *Xerula caulovillosa*, cheilocystidia. Holotype. Bar 20 μm

Holotypus: RUSSIA, Krasnodar Reg., Caucasus Mts., vic. Chosta Mt., N 43°32.942', E 39°50.938', 7.IX.1996, coll. J. Johnson & R.H. Petersen, TFB 7757 (54717, TENN).

Basidiomata (Fig. 53) usually diminutive, collybioid; pileus 15–35 mm broad, shallowly umbonate, convex to plane, near “sayal brown,” 3B2-3, 4B2-3, 3A2, 4C2, surface glutinous, viscid, or tacky, smooth to rugulose; margin entire to sulcate, straight or slightly decurved. Lamellae adnate, broad, close, unequal with four ranks, white, developing ochraceous to orange-ochre (“ochraceous buff”) necropigment; margin drying somewhat darker than lamellar face, but not marginate. Stipe 90–140 mm long, central, terete, with radicating base, white apically, downward off-white to discoloring grayish-tan where handled and on drying, near base, and over pseudorhiza apex covered with thin white tomentum; veil remnants none. Scattered on buried wood (sometimes detecting substrate was impossible). Odor not distinctive; taste mild.

Habit: Solitary to gregarious under *Fagus sylvaticus*, *Picea orientalis*, *Quercus* spp., radicate, probably attached to buried wood.

Pileipellis composed of a single element; pileocystidia (Fig. 54) 39–97 \times 13–38 μm , broadly clavate to subcapitate, hyaline to slightly pigmented, consistently long-pedicellate, clamped, thin- to (usually) thick walled (wall up to 1.5 μm

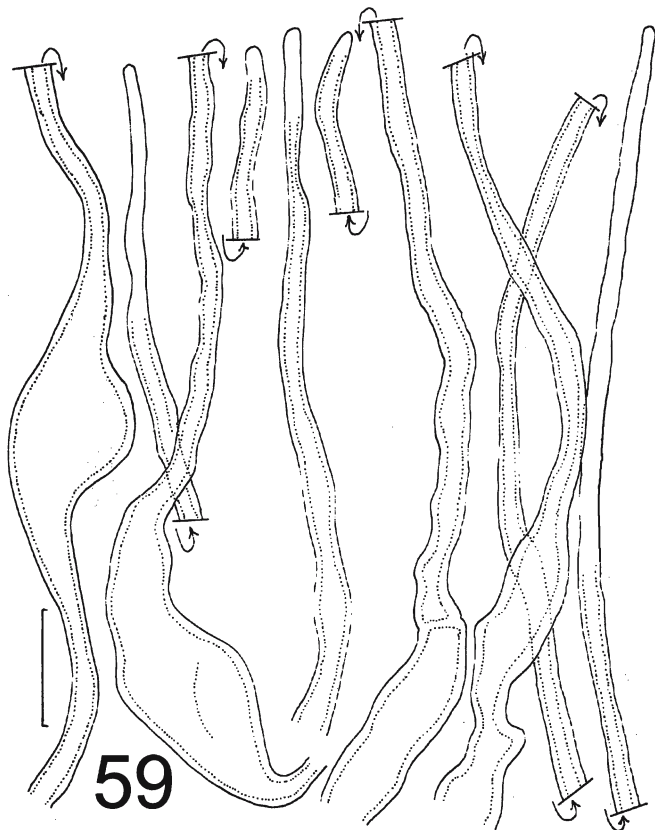
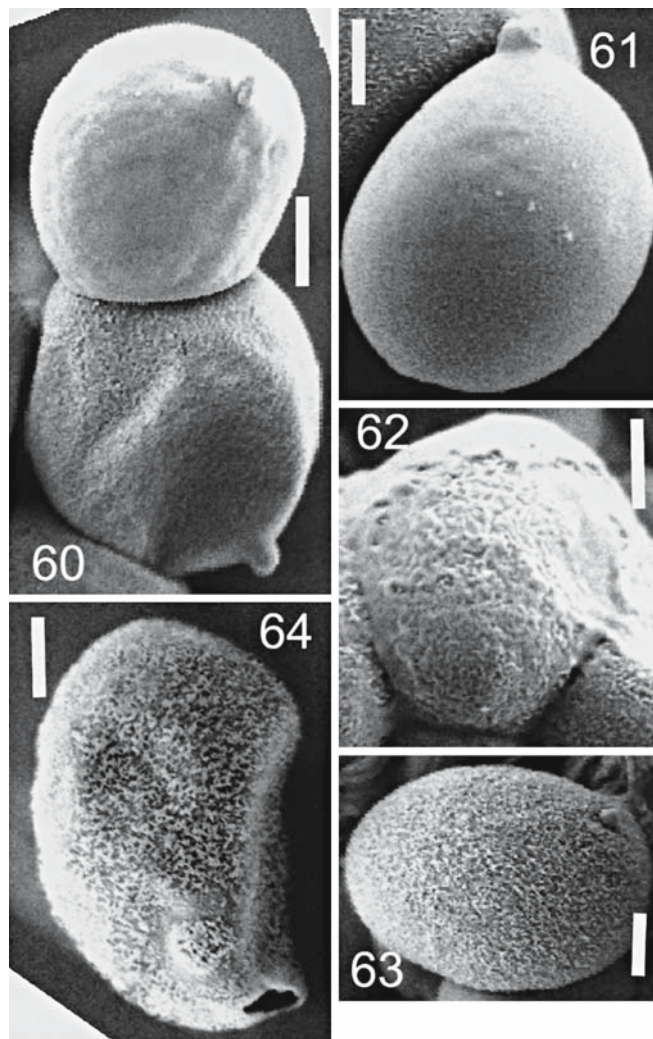


Fig. 59. *Xerula caulovillosa*, stipe tomentum hyphal apices. Holotype. Hyphal origins not shown. Arrows indicate continuation of hyphal apices. Bar 20 μm

over flanks or over entire cystidium); contents multigranular, now peripheral; thin-walled individuals easily collapsed, especially apically. Pileal hairs absent. Pleurocystidia (Fig. 55) 85–130 \times 27–45 μm , broadly ten pin-shaped, pedicellate, greatly inflated in median section, narrowing to the rounded apex, hyaline, thin walled (but capitulum usually refringent as though thick walled), sometimes with thin “halo” of granular deposit surrounding capitulum, clamped; contents homogeneous, often with a few granular deposits peripherally. Basidia (Fig. 56) 50–66 \times 12–19 μm , clavate, somewhat inflated subapically, hardly pinched at base, four spored, clamped; contents multiguttulate when mature, usually with 1–3 major guttules plus ancillary smaller guttules. Basidiospores (Fig. 56) 13–17 \times 10–12.5 μm ($E = 1.08$ –1.54; $E_m = 1.32$; $L_m = 15.05 \mu\text{m}$), broadly ovoid to ovoid to narrowly ovoid, smooth, thin walled; contents uniguttulate when mature, refringent and apparently multiguttulate when immature. Lamellar margin sterile, a solid palisade of cheilocystidia. Cheilocystidia (Fig. 57) (15–) 20–95 \times 6–32 μm , ranging from short, digitate-capitate side branches to fusiform or broadly fusiform (shaped like a sweet potato), sometimes sphaeropedunculate, thin walled, clamped, hyaline. Stipe apex covered with a pruina of white caulocystidia. Apical caulocystidia (Fig. 58) 32–<250 \times 10–20 μm , arising from slender (2.5–3.5 μm diameter), thick-walled stipe surface hyphae and extending outward as a side lobe, to elongate-fusiform, often with a significant proximal spur,



Figs. 60–64. *Xerula caulovillosa*, basidiospores. Holotype. Bars 2 μm

to extremely inflated (up to 62 μm broad) and sphaeropedunculate, hyaline, thin walled over inflated area, thick walled (wall up to 1 μm thick) over stalk, clamped (but only at a long distance from the inflated portion), easily collapsed and only partially reviving in KOH. Midstipe caulocystidia very sparse, arising from slender, superficial hyphae, 45–<130 \times 10–20 μm , curled-clavate, thick walled over stalk area, thin walled over inflated area, hyaline. Tomentum of stipe base (Fig. 59) and pseudorhiza surface a tangle of gnarled sclerified hyphae, 4.5–15 μm diameter, hyaline, thick walled (wall often up to 2 μm thick), obscurely clamped. From this tomentum arise stiff hairs as extensions of inflated, sclerified cells; hairs up to 450 μm , thick walled (wall decreasing from 2 μm thick to <0.7 μm thick at hair apex), tapering gradually (1.5–2.5 μm broad at apex).

Commentary: Pleurocystidia are certainly not shaped like those of typical *X. radicata* (i.e., broadly utriform), and cheilocystidia are more variable than those of *X. radicata*. Apical caulocystidia are well developed in size and quantity (nearly absent in *X. radicata*). The spur near the base is so formidable that the caulocystidium could be term branched.

Midstipe caulocystidia are sparse, but this may be specimen specific.

Several basidiomata bear the white tomentum over the stipe base and pseudorhizal apex, unlike any specimen of *X. radicata* I have seen.

Basidiomata of *X. caulovillosa* seem to dry somewhat lighter in color than those of *X. radicata*, so that pileus and stipe are both about "saya brown." Although these taxonomic distinctions may fall within the range of *X. radicata*, the specimens below are all consistent, and were collected within the same general biotope.

To confirm the novelty of this proposed new species, it was necessary to compare specimens of two other taxa proposed from the same general geographic region. They are cited below. Material of *X. radicata* var. *aurantiacolutesa* Melik-Chachatryan (1970. Micol. e Fitopat. 4(5): 475. HT: ARMENIA, Idzhevan-Berd, 24.VI.1968, s.n.; PT, 26.VII.1968, both in herb Univ. Erebanensis) was not available for study, and no type material is at LE. Although the basidioma of *X. radicata* var. *alba* is diminutive, other micro- and macroscopic characters differ from *X. caulovillosa*.

Specimens examined (in addition to those cited above and below): *X. caulovillosa*: RUSSIA, Krasnodar Reg., vic. Sochi, Sergei Polya, N 43°41.063', E 39°42.711', 2.IX.1996, coll. RHP, TFB 8895 (55515, TENN); Krasnodar Reg., Abkasia, Frances Patzicer, "Fungi Caucasi Exsiccati," 4. VI.1902, leg. G. Woronov (as *Collybia radicata* var. *minor*), Woronov no. 211 (756342, BPI). TURKEY, Trabzon Dist., vic. Mataraci, N 40°51.719', E 39°36.783', 26.IX.1996, coll. RHP, TFB 8987 (55647, TENN). *X. radicata* var. *alba* Melik-Chachatryan: ARMENIA, vic. Dilizhan, in carpetino, 26.VII.1968, coll. Melik-Chachatryan, in herb. Univ. Erebanensis; isotype LE! [non-*X. radicata* var. *alba* Dörfelt. 1983. Feddes Repert. 93: 61]. *X. radicata* var. *rubescens* Melik-Chachatryan: ARMENIA, Idzhevan-Berd, in carpino, 25.VI.1968, coll. Melik-Chachatryan, in herb. Erebanensis; isotype LE!

The outer spore wall in *Xerula caulovillosa* exhibits some of the "dimpling" seen under PhC microscopy (Fig. 60, above), but is basically minutely felty (Fig. 61). When the outer spore wall is peeled away (Fig. 62), the sculptured middle wall is revealed. The pattern of these pillars is somewhat dense, intricate, and low (Figs. 60, lower; 63, 64).

Material used for SEM images: RUSSIA, Krasnodar Reg., vic. Sochi, Dagomys, 22.IX.1996, coll. B Tuniyev, TFB 8975 (55635, TENN).

Xerula japonica Dörfelt. 1984. Feddes Repert. 95: 190.

The illustration by Pegler and Young (1987; fig. 50, holotype) showed an almost smooth spore. This was explained as "...differentiation of a thin, electron-lucent corium forming the innermost layer of the eusporium. The myxosporium consists of a broad mucostratum, without any formation of a podostratum." After examination of the holotype specimen (JAPAN, Honshu, Shiga Pref., Otsu, Mt. Hiei-san, 19.IX.1952, coll. T. Hongo, Hongo 572 [K(M) 124270]) by light microscopy, I am convinced that this material (TMI 14821) is conspecific.

Immature spores show the normal felty appearance of the outer wall (Fig. 65), with some dimpling often observed under PhC microscopy. As the outer wall disintegrates, the sculptured middle wall is revealed (Fig. 66). The middle wall appears extremely densely sculptured (Figs. 66, 67) but continues to undergo stretching, eventually seen as gregariously scattered papillae often fused into short, intricate ridges (Figs. 68, 69).

Material examined: JAPAN, Tottori Pref., Mt. Daisen, 2.VIII.1988, EN 88-137 (TMI 14821).

Xerula orientalis R.H. Petersen & Nagas. 2006. Rep. Tottori Mycol. Inst. 43: 36. var. *orientalis*

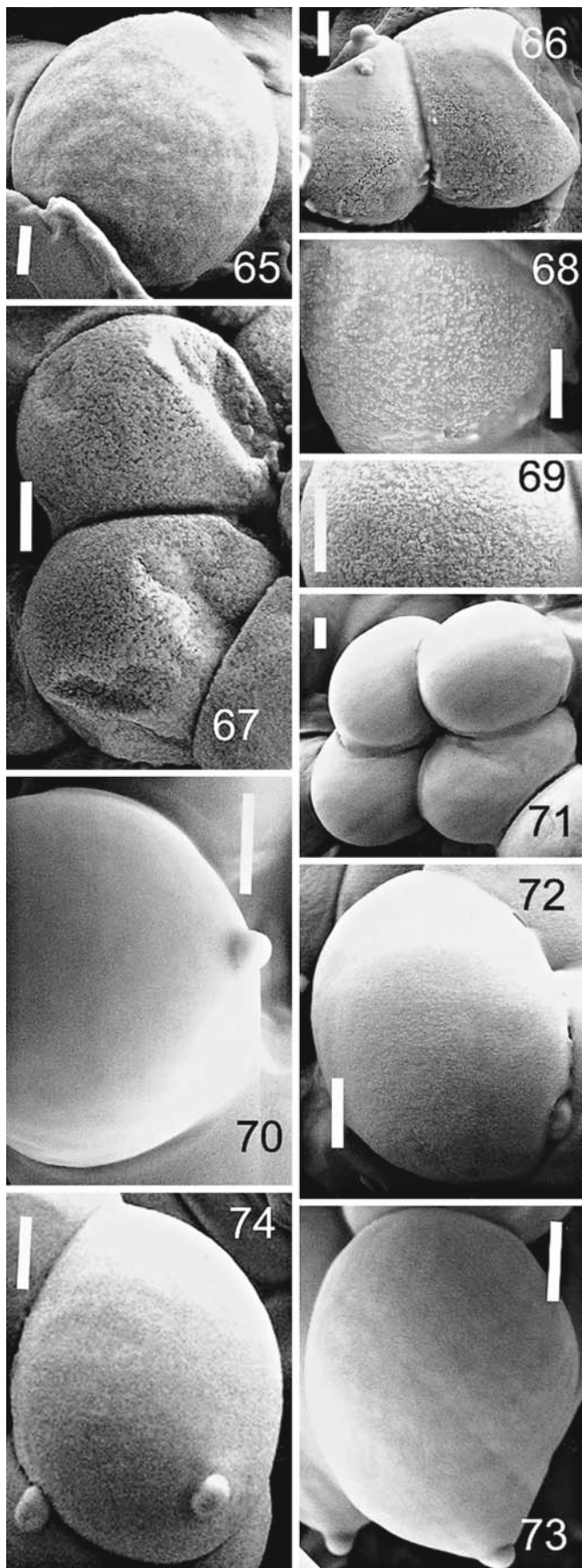
Xerula orientalis R.H. Petersen & Nagas. 2006. Rep. Tottori Mycol. Inst. 43: 39. var. *margaritella*

Xerula orientalis was proposed as a temperate Asian species in sect. *Radicatae*, and its var. *margaritella* merely for more gracile, diminutive, paler basidiomata. Spores would be expected, therefore, to be similar, if not identical. This appears to be the case, but surveying the several hundred spores depicted in SEM images, no spores were seen to exhibit the characteristic sculpturing of the middle wall. All spores were either immature and smooth (Figs. 70, 71), or showed the outer wall beginning to separate (Figs. 72, 73). Spores in Figs. 70 and 74 may show the subtle dimpling sometimes observed under PhC microscopy. Whether the consistent view of the outer wall indicates that (1) no interior sculpturing is formed, (2) the outer wall is indehiscent and perhaps tightly adherent to the inner wall, or (3) the middle wall is so compactly sculptured as to appear indistinguishable from the outer wall cannot be discerned from these images.

Material used: JAPAN, Honshu, Okayama Pref., Nishiawakura-mura, 8.X.1999, E. Nagasawa, EN 99-174 (*X. orientalis*) (26108, TMI). JAPAN, Honshu, Niigata Pref., Higashikubiki-gun, Matsunoyama-machi, Matsugushi, 26.IX.2003, EN 03-198 (*X. orientalis* var. *margaritella*) (26111, TMI).

Xerula radicata (Relhan) Dörfelt. 1975. Veröff. Mus. Gera, Naturwiss. R., 2/3: 67 f. *radicata*

Pegler and Young (1987) illustrated spore wall structure in *Xerula radicata*. Their fig. 59 closely resembles the images presented here. Their fig. 56, a TEM image of wall structure, clearly shows the ornamentation of the middle wall (for which they used the term podostratum, the innermost layer of the myxosporium). Spores appear only minutely roughened when young (Fig. 75, left; their figs. 60, 61), a condition that Pegler and Young (1987: 586) reported as follows: "...the surface of spores in sections *Albotomentosi*, and particularly *Oudemansiella* and *Radicatae* is characterized by a granular or crystalline encrustation in SEM and carbon replica preparations. This is not a true wall ornamentation as it is due to the close association of the fine, disintegrating sporothecium (or ectosporium) and the mucostratum, which are both derived from the myxosporium." Here, these layers are merely called the outer wall.



Figs. 65–74. *Xerula* basidiospores. **65–69** *X. japonica*. TMI 14821. **70, 71** *X. orientalis*. TMI 26108. **72–74** *X. orientalis* var. *margaritella*. TMI 26111. Bars 2µm

Figure 75 (left) shows the common “dimpling” often distinguishable under PhC light microscopy at high magnification. Figures 76–78 show the separating pillars of the middle wall and match fig. 59 of Pegler and Young (1987). These separating pillars are remarkably coarse for spores that appear completely smooth in bright field and PhC microscopy. These separating pillars apparently are easily removed (Fig. 75, right; Fig. 76, left), revealing the smooth to minutely pitted inner wall. Although SEM images were taken from three specimens (TENN 57276, 59223, 59314), configuration of the middle wall sculpturing is quite consistent.

In spite of Pegler and Young’s (1987) disposition of this species and its several, worldwide, putative infraspecific taxa, and the report by Redhead et al. (1987) of its occurrence in North America, my experience indicates that it is absent from all continents except Europe, where it extends from the British Isles to at least the Ural Mountains (if not farther east) and south to at least the Caucasus, and perhaps Morocco (viz. Malençon and Bertault 1975: 341; the whereabouts of these specimens is unknown).

No type specimen has been designated for *Agaricus radicans*, but Dörfelt (1983. Feddes Repert. 93: 83) cited “Tafel 48” of Sowerby as the lectotype. As Sowerby’s plate was published in 1796 and Relhan’s description of *Agaricus radicans* was published in 1786, Sowerby’s plate cannot be considered a lectotype. Technically, the binomial remains without a type to which to compare later material. Conversely, *Xerula radicata* is either the only member of sect. *Radicatae* or the most commonly collected taxon of the group in the British Isles, so there can be little controversy over identification of specimens.

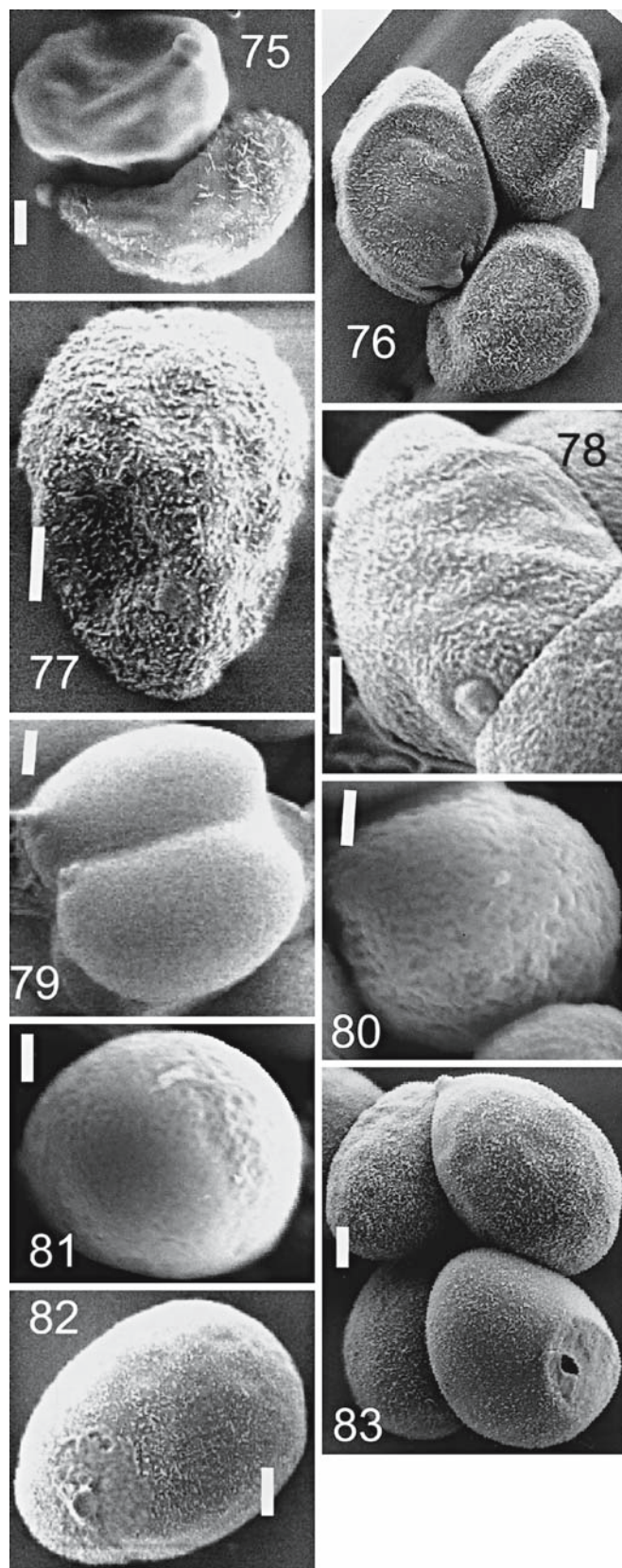
Material used: UNITED KINGDOM, Scotland, vic. Kindrogen, 9.X.1991, coll. T. Laessle, TFB 4165 (57276, TENN). FRANCE, Rhône-Alpes, Dpt. Savoie, Commun. St. Germain la Chambotte, 10.IX.2001, TFB 11339 (59223, TENN). AUSTRIA, Lower Austria, Weinviertal, Kühnring, 24.IX.2001, TFB 11453 (59314, TENN).

Xerula radicata f. *marginata* (Konrad & Maubl.) R.H. Petersen, comb. nov.

Basionym: *Mucidula radicata* f. *marginata* Konrad & Maubl. 1932. Icon. Sel. Fung. 4: 199.

Occasionally, basidiomata otherwise indistinguishable from those of *X. radicata* exhibit marginate lamellae. This morphology was noted by Konrad and Maublanc as *Mucidula radicata* f. *marginata*. Basidiospores of the two forms (f. *radicata* and f. *marginata*) do not differ significantly in dimensions or statistics. The whereabouts of a Konrad & Maublanc specimen to represent their proposed taxon is unknown, so there is no type specimen for comparison to more recent collections.

Immature spores of f. *marginata* show the normal felty appearance (Fig. 79). In this particular preparation, numerous spores showed an outer wall shrunk to some extent (Figs. 80, 81), distinguished from the sculptured separating pillars of the middle wall (Figs. 82, 83) revealed when the outer wall is peeled away (Fig. 82). In all, spore wall con-



Figs. 75–83. *Xerula* basidiospores. 75–78 *X. radicata*. 75 TENN 59314. 76 TENN 59223. 77, 78 TENN 57276. 79–83 *X. radicata* f. *marginata*. TENN 59301. Bars 2 μ m

struction and SEM appearance differ insignificantly from what is observed in f. *radicata* (q.v.).

Pegler and Young (1987) illustrated several spores showing shrunken outer walls (their figs. 22, 27, 31, 35, 40, 43, 48, 51, 55, 66, and perhaps 62). The configuration of the separating pillars of the middle wall in these taxa has yet to be observed.

Material used: AUSTRIA, Lower Austria, Dist. Gänserndorf, Stophenreuth, 23.IX.2001, TFB 11440 (59301, TENN).

Xerula rubrobrunnescens Redhead, Ginns & Shoemaker. 1987. Mycotaxon 30: 384.

In *Xerula rubrobrunnescens*, young spores present a similar felty appearance as others of the genus (Fig. 84, right). The outer spore wall can be seen peeling away (Figs. 85, 86). Once the outer spore wall is removed, the pillars that separate the outer and inner spore walls are widely scattered and rather wart-like in appearance (Fig. 84, left; Figs. 87, 88). The separating pillars can be worn off (Fig. 89), but the areola around the hilar appendix remains (Fig. 89).

Two specimens used for these images (TENN 47676, 47678) show good similarity in the density and placement of the separating pillars. The specimens compared favorably to the type (USA, Pennsylvania, Washington Co., vic. Houston, 21.IX.1940, L.K. Henry no. 4425, Carnegie Mus. No. 12515 (NY[!])).

Material used: USA, North Carolina, Blue Ridge Parkway, milepost 363, 4.VIII.1959, coll. unknown, det. S.A. Redhead, 47676 (TENN, part of TENN 23216). USA, Kentucky, Cumberland State Park, 22.X.1955, coll. T.H. Campbell, det. S.A. Redhead, 47678 (TENN, part of TENN 22196).

Xerula vinocontusa R.H. Petersen & Nagas. 2006. Rep. Tottori Mycol. Inst. 43: 44–45.

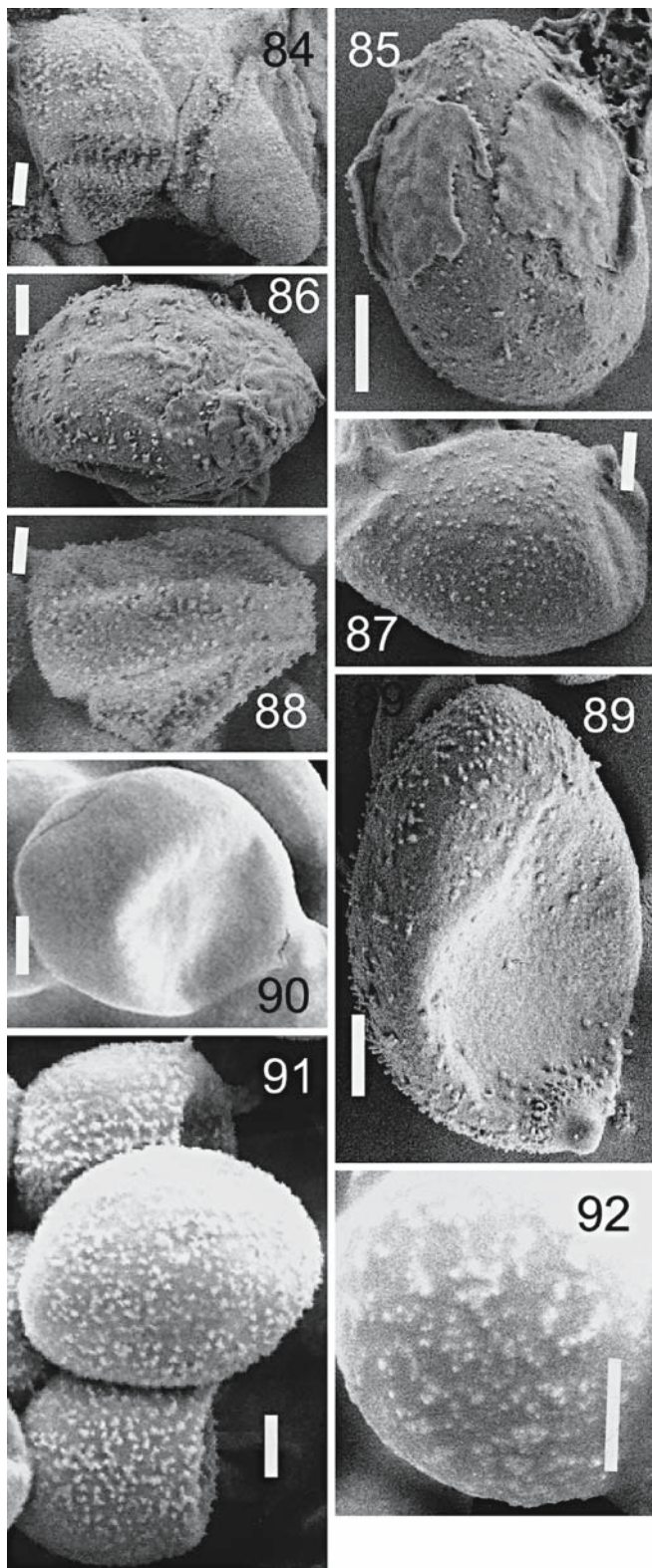
Xerula vinocontusa was proposed based on some pleurocystidial differences and a different staining reaction from *X. aureocystidiata* and *X. rubrobrunnescens*, which were considered morphologically similar. Spores of *X. vinocontusa* are felty at first (Fig. 90), but when the outer wall has been removed, sculpturing of the middle wall is revealed. In *X. vinocontusa*, the separating pillars are rather evenly scattered, peg like, and rarely form ridges (Figs. 91, 92). In this way, they are similar to the markings in *X. rubrobrunnescens* and *X. aureocystidiata*, q.v.

Material used: JAPAN, Honshu, Gifu Pref., vic. Amotoge, 4.X.1992, coll. S. Koizumi, EN 92-240 (17669, TMI, holotype).

Sect. *Dactylosporina*

Xerula macracantha (Singer) Dörfelt. 1985. Feddes Repert. 96: 237.

Presented here are images of spores of *Dactylosporina*, a segregate section from *Xerula* based on echinulate basidiospores. In *X. macracantha*, some suggestion of sculpturing of inner wall can be seen through the outer wall (Fig. 93).



Figs. 84–92. *Xerula* basidiospores. **84–89** *X. rubrobrunnescens*. **84–86**, **89** TENN 47676. **87**, **88** TENN 47678. **90–92** *X. vinocontusa*. Holotype. Bars 2 μ m

In addition (Fig. 94, 95, lower left), occasionally spines have been broken off, and there is some suggestion of inner structure within the spines. Finally, spores of *X. macracantha* seem to remain turgid in spite of the vacuum applied by the electron microscope (Figs. 93–95), while in my experience, the spores of *D. steffanii* (Rick) Dörfelt are consistently semicollapsed, assumedly by SEM preparation treatment. This would hardly seem to be a specific character, but it is consistent nonetheless.

Pegler and Young (1987; figs. 68–70) identified their specimen as *Oudemansiella* (sect. *Dactylosporina*) *steffanii* (Rick) Singer, but spores appear turgid. Singer (1964) attempted to sort basidiome and microscopic characters to segregate taxa out of *O. steffanii* but was unsuccessful. He finally concluded that the best separating character between *O. steffanii* and *O. macracantha* was the number and length of spines on basidiospores, with those of *O. macracantha* more numerous and longer than those of *O. steffanii*. I have been unable to sort specimens into two discrete entities, although the spines on spores in Figs. 93, 95, and 96 appear not to differ markedly from those figured by Pegler and Young (1987).

I have examined two specimens with two-spored basidia that otherwise match the characters of *X. steffanii* (Rick) Boekhout & Bas. One was from southern Brazil, the other from Colombia. Likewise, I have seen three two-spored specimens matching *X. macracantha* from Mexico and Argentina. These specimens confirm that two-spored states occur in all accepted sections of *Xerula* [or *Oudemansiella* s.s. Pegler and Young (1987)].

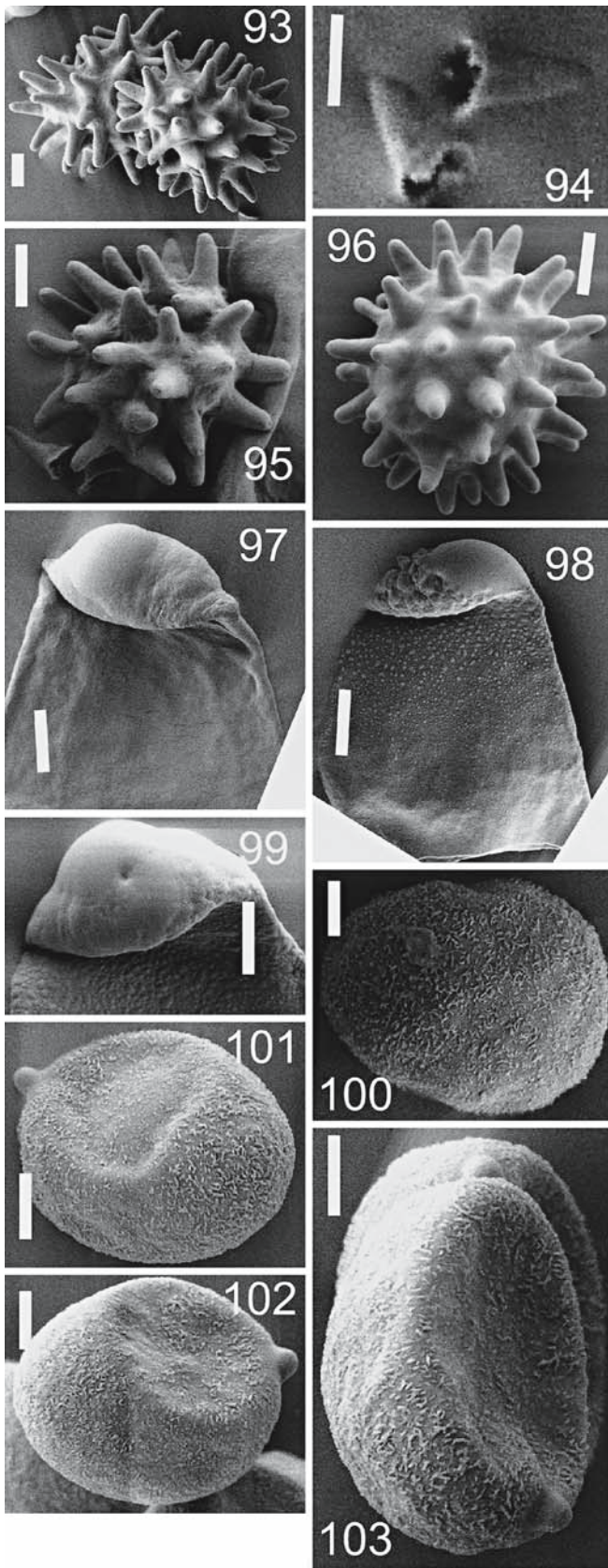
Pleurocystidia of *X. macracantha* collapse in the vacuum of the electron microscope but thereby reveal an additional character not visible in normal bright field or PhC microscopy. The tip of the pleurocystidium remains more or less smooth (Figs. 97–99), but the shaft of the pleurocystidium may be merely wrinkled (Fig. 97) or distinctly pebbled or warted (Figs. 98, 99). This distinctive ornamentation diminishes downward on the body of the pleurocystidium (Fig. 98).

Material used: ARGENTINA, Prov. Misiones, Parque Nacional Iguazu, 28.V.2001, TFB 10789 (58995, TENN). MEXICO, Est. Chiapas, vic. Cacoahatan, Mixcum, 18.X.1997, TFB 3871 (55845, TENN).

A note on *Rhizomarasmius*

Rhizomarasmius undatus (Berk.) R.H. Petersen. 2000. Mycotaxon 75: 335.

When *Rhizomarasmius* R.H. Petersen was proposed as a segregate genus from *Marasmius* (Petersen 2000), its molecular and morphological characters appeared to match those of the “Xerulaceae” (more correctly known as the Physalacriaceae). As depicted here, an outer spore wall can be peeled away (Fig. 100) to reveal an intricate pattern of thickly set, meandering, often reticulate, ridges and small warts separating the outer and inner spore walls (Figs. 100–



Figs. 93–103. Microstructures of *Xerula macracantha* and *Rhizomarasmius undatus*. 93–99 *X. macracantha*. 93, 95, 96 Basidiospores. 94 Disarticulated basidiospore spines. 97–99 Pleurocystidial apices. 93–95, 97–99 TENN 55845. 96 TENN 55995. 100–103 *R. undatus*, basidiospores. TENN 59310. Bars 93–96, 100–103 2 μ m; 97–99 10 μ m

103). This arrangement is comparable to that found in other members of the Physalacriaceae, specifically in all sections of *Xerula*. The neotype specimen of *Agaricus undatus* Berk. (UNITED KINGDOM, Batheaston, 1861, coll. C.E. Broome, K!, PRM; des. Antonín and Noordeloos; see Petersen 2000) compares well to the Austrian specimen cited here. A modern specimen (ITALY, Ravenna, Pineta san Vitale, “I Bosconi,” 14.XI.1990, coll. & det. H. Schwöbel, no. 9196 WU) has also been examined.

Material used: AUSTRIA, Lower Austria, Waldviertel, vic Dobrasperre, 24.IX.2001, TFB 11449 (59310, TENN).

Discussion

Three objectives were addressed with the data derived from this study. First: can middle spore wall sculpturing be used to distinguish species? This question is best addressed together with the second objective. Second: what is the range of variation in wall sculpturing across the genus? The middle wall of spores of *X. orientalis* (see Figs. 70, 71) and var. *margaritella* (see Figs. 72–74) are virtually smooth and thus unique in sampling used in this study. Because morphological separation of var. *margaritella* is nominal, such similarity in spore wall sculpturing is expected. Spores of most taxa of *Xerula*, however, exhibit closely scattered pillars between the outer and inner walls. These taxa include *X. pudens* (sect. *Xerula*; see Figs. 4, 5), members of sects. *Albotomentosae* and *Radicatae* including *X. amygdaliformis* var. *bispora* (see Figs. 15, 16), *X. chiangmaiae* (see Figs. 18, 21), *X. raphanipes* (see Figs. 33, 34), *X. japonica* (see Figs. 67–69), and *X. xeruloides* (see Figs. 45, 46). Exhibiting somewhat coarser sculpturing are spores of *X. furfuracea* (Figs. 23, 24), *X. caulovillosa* (Figs. 62–64), and *X. rubrorunnescens* (Figs. 86–89). Similar markings are seen on spores of *Rhizomarasmius undatus* (Figs. 100–103). *Xerula amygdaliformis* (see Figs. 8–11) produces a unique pattern of small pillars and scattered raised bars. Spores of several species show a system of coarse pillars sometimes anastomosed into short ridges. Included are *X. megalospora* (see Figs. 27–30), *X. rugosoceps* (Figs. 36–39), *X. vinocontusa* (Figs. 91, 92), *X. aureocystidiata* (Figs. 49–52), and *X. radicata* (Figs. 77, 78). Although these spore wall sculpturing patterns are relatively easily distinguished, only the coarsest could serve to distinguish separate taxa. Within the other sculpture classes, spores would be almost indistinguishable, and the character less than useful for species-level taxonomy.

Third: is the observed “dimpling” or “puckering” of spores observable at the resolution of SEM? It appears that this feature involves the outer spore wall, not the middle or inner wall. In images selected to show middle wall sculpturing, the texture of the outer wall is incidental. Nonetheless, several images suggest this character in numerous taxa, including *X. pudens* (see Figs. 2, 3), *X. chiangmaiae* (see Fig. 17), *X. furfuracea* (see Fig. 22), *X. raphanipes* (see Figs. 31, 32), *X. xeruloides* (see Fig. 44), *X. caulovillosa* (see Fig. 60), *X. japonica* (see Fig. 65), *X. radicata* (see Figs. 72, 73), and

X. vinocontusa (see Fig. 90). These images cannot discern if this wall undulation is caused by spore shrinkage in the herbarium, but not only do spores revived in KOH show this feature, but also freshly collected spores straight from nature. The results presented here show that spore wall sculpturing across not only *Xerula*, but also *Dactylosporina* (sect. or genus) and *Rhizomarasmius*, cannot be used as a diagnostic genus character. It remains to be seen if this "middle wall" ornamentation extends to other parts of the family (i.e., *Physalacria*, *Strobilurus*, *Pseudohiatula*, *Gloiocephala*, etc.).

No focused molecular phylogeny has yet been aimed at distinguishing generic concepts in this aggregate. In a paper testing intercontinental distribution of some species complexes, Mueller et al. (2001) produced two trees that indicated that *Xerula sensu stricto* (i.e., radicating basidiomata with setose, dry pileipellis; *X. pudens*, etc.) was about as related to the glutinous, non-setoid, radicating group (i.e., *X. radicata*, etc.) as was the non-radicating, annulate group (i.e., *O. mucida*, etc.). Even less germane is a phylogeny by Binder et al. (2006) in which two species of *Oudemansiella s.s.* (*O. mucida*, *O. canarii*) appeared as a sister clade to the *radicata* group (*X. furfuracea*, *X. megalospora*). Virtually the same results were reported by Moncalvo et al. (2002) in a large subunit (LSU)-based phylogeny of the euagarics. Should the distinction among these three complexes be confirmed by further molecular work, the *radicata* complex will be in need of a new genus name to complement *Oudemansiella* and *Xerula*.

Acknowledgments I am indebted to Dr. John Dunlap of the University of Tennessee Electron Microscope Facility for producing the SEM images featured here. Dr. Karen W. Hughes supplied technical assistance for publication of the images.

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