

A new systematic arrangement of the genus *Oudemansiella* s. str. (Physalacriaceae, Agaricales)

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Abstract: The genus *Oudemansiella* s. str. has been revised and circumscribed as an assemblage of taxa excluding the genus *Xerula* s. str. A new systematic arrangement with four sections, i.e., *Oudemansiella*, *Mucidula*, *Dactylosporina* and *Radicatae*, is proposed. Section *Oudemansiella* is comprised of tropical to south temperate species, e.g., *O. platensis*, *O. australis*, *O. canarii* and *O. crassifolia*, with an ixotrichoderm pileipellis composed of filamentous hyphae that, in many cases, are intermixed with inflated cells often occurring in chains, while section *Mucidula* encompasses north temperate and subtropical taxa such as *O. mucida*, *O. venosolamellata* and *O. submucida* that have an ixohymeniderm-trichoderm pileipellis composed of more or less clavate terminal cells. Sections *Oudemansiella* and *Mucidula* share similar habitats and forms of basidiomata, i.e., with or without a (rudimentary) annulus on the stipe and growing on exposed rotten wood. Section *Dactylosporina* accommodates species from South and Central America with basidiospores that have finger-like ornamentation. Section *Radicatae*, represented by *O. radicata* and its allies, is the largest section and includes the remaining species of the genus in its restricted sense. *Oudemansiella americana*, *O. caussei* and *O. hongoi*, previously treated in *O.* sect. *Albotomentosae* or *Xerula* sect. *Hyalosetae*, are excluded from *Oudemansiella* in this treatment because preliminary data indicate that they represent a segregate genus. Section *Mucidula*, 32 combinations and 1 name are newly proposed.

Key words: Basidiomycetes, new combinations, new name, nomenclature, systematics, taxonomy

狭义小奥德蘑属（膨瑚菌科，蘑菇目）的一个新系统

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摘要: 本文对狭义小奥德蘑属 *Oudemansiella* s. str. 的概念做了修订, 在修订后的属中, 狭义干蘑属 *Xerula* s. str. 的物种不纳入其中。在狭义小奥德蘑属下, 提出了一个包含 4 个组 *O. sect. Oudemansiella*、*Mucidula*、*Dactylosporina* 和 *Radicatae* 的新系统。小奥德蘑组 *sect. Oudemansiella* 包括热带至南温带的一些物种, 如新热带小奥德蘑 *O. platensis*、澳洲小奥德蘑 *O. australis*、旧热带小奥德蘑 *O. canarii* 和宽褶小奥德蘑 *O. crassifolia*, 这些物种的菌盖表皮为粘栅栏型, 由菌丝组成, 但其中常夹杂有链状排列的膨大细胞。粘蘑组 *sect. Mucidula* 包含北半球温带至亚热带的一些物种, 如粘小奥德蘑 *O. mucida*、网褶小奥德蘑 *O. venosolamellata* 和近粘小奥德蘑 *O. submucida*, 其菌盖表皮为粘子实层-栅栏型, 由近棒状的顶端膨大细胞组成。小奥德蘑组和粘蘑组的物种, 在外形和小生境上有相似之处, 其担子果皆生于地表外的腐木上, 菌柄上有或无菌环。刺孢组 *sect. Dactylosporina* 包含中南美洲那些孢子表面有指状凸起的物种。长根组 *sect. Radicatae* 由长根小奥德蘑 *O. radicata* 及其近缘种为代表, 是该属中最大的组, 包括该属其他三组之外的所有种。北美的 *O. americana*、欧洲的 *O. causei* 和东亚的 *O. hongoi* 曾被置于小奥德蘑属中的白毛组 *O. sect. Albotomentosae* 或干蘑属的亮毛组 *X. sect. Hyalosetae*, 在本系统中它们没有纳入小奥德蘑属, 因为它们可能代表一个单独的属。本文还提出了 1 新等级、32 个新组合和 1 个新名称。

关键词: 担子菌, 新组合, 新名称, 命名法, 系统学, 分类学

INTRODUCTION

The genus *Oudemansiella* Speg. was proposed by Spegazzini (1881) based on the Neotropical *Agaricus platensis* Speg. *Mucidula* Pat. (1887) initially included only *A. mucidus* Schrad.: Fr. from Europe. Boursier (1924) emended *Mucidula* to include *A. longipes* Bull. and *A. radicans* Relhan. The genus *Xerula* Maire was proposed by Maire (1933) based on *A. longipes*.

Moser (1955) merged *Xerula* and *Mucidula* into *Oudemansiella*. Singer (1962a, 1962b, 1964, 1986) adapted Moser's treatment, yet regarded *Xerula* as a subgenus within the genus *Oudemansiella*. Cléménçon (1979) provided a classification of *Oudemansiella* and treated *Xerula* as one of five subgenera within *Oudemansiella* based on a computer-aided study of 16 morphological characters, while Pegler & Young (1987) divided *Oudemansiella* into five sections under two subgenera, *Oudemansiella* and *Xerula*. The treatment of Pegler & Young (1987) was adopted by Rexer & Kost (1989a, b), Yang & Zang (1993), Yang (2000) and Mizuta (2006).

Some mycologists retained *Oudemansiella* and *Xerula* as two separate genera (Dörfelt 1979; Boekhout & Bas 1986; Redhead *et al.* 1987; Petersen & Halling 1993; Petersen & Methven 1994; Corner 1994, 1996; Boekhout 1999; Halling & Mueller 1999; Contu 2000;

Petersen 2000; Mueller *et al.* 2001; Petersen & Hughes 2005; Horak 2005; Petersen & Nagasawa 2006; Petersen & Baroni 2007; Petersen 2008a, 2008b, 2008c). Among the contributions to the study of *Oudemansiella*-*Xerula*, Dörfelt's work has had great influence. He greatly emended the genus *Xerula* by transferring sections *Albotomentosae* Cléménçon, *Protoxerula* Cléménçon and *Radicatae* Cléménçon from *Oudemansiella* to *Xerula*, and restricting *Oudemansiella* only to species with a (rudimentary) annulus, such as *O. mucida* and *O. canarii* (Dörfelt 1979, 1980a, 1980b, 1981, 1983, 1984). His concept was followed by other authors, and many species have subsequently been transferred from *Oudemansiella* to, or newly described in, *Xerula*. Several section names, *e.g.*, *Albotomentosae* (Cléménçon) Dörfelt, *Hyalosetae* Dörfelt, *Radicatae* and *Xerula* have been erected in *Xerula* which has been divided into three subgenera, *viz.* *Xerula*, *Radicatae* Dörfelt and *Ixoflammula* Contu (Dörfelt 1980b; Contu 2000).

Recent molecular phylogenetic analyses place *Oudemansiella* and *Xerula* in the Physalacriaceae clade (Moncalvo *et al.* 2002; Wilson & Desjardin 2005; Matheny *et al.* 2007), and document that taxa of *Oudemansiella* and *Xerula* are resolved into two separate monophyletic clades (Zhang *et al.* 2003; Binder *et al.* 2006; Zhang 2006). Petersen (2008c) stated that *Xerula* in his definition is not monophyletic. Wang *et al.* (2008)

treated *Xerula* as a distinct genus, but in a restricted sense that includes only hispid species such as *X. pudens* (Pers.) Singer and its close allies that have a collybioid basidioma with dry surfaces of the pileus and the stipe covered with erect, lanceolate, yellow to brown, thick-walled setae, subacrose basidioles in the hymenium and a fertile lamellar edge, while *Oudemansiella sensu stricto* accommodates non-hispid species that have sterile lamellar edges with crowded cheilocystidia and clavate to narrowly basidioles in the hymenium. Based on morphology and the molecular phylogenetic analyses of Zhang *et al.* (2003) and Zhang (2006), a new systematic arrangement for *Oudemansiella* s. str. is proposed.

1 MATERIAL AND METHODS

Over 150 collections of *Oudemansiella* and *Xerula* from Asia, Europe, Australia, and North and Central America were examined, but only specimens from which illustrations in the present paper were made are listed below.

Oudemansiella canarii (Jungh.) Höhn. – China. Wild Elephant Valley, Jinghong County, Yunnan Prov., alt. 650m, 1 September 2004, X.H. Wang 1820 (HKAS 5021).

O. aff. crassifolia Corner – China. Longdao, Ruili County, Yunnan Prov., alt. 1200m, 2 August 2003, P.C. Liu 87 (HKAS 43500).

O. mucida (Schrad.: Fr.) Höhn. – Germany. Oberjoch, Allgäu, Bayern, 1 October 1997, Z.L. Yang 2111 (HKAS 31558).

O. platensis (Speg.) Speg. – Colombia. Estación Científica de la Universidad Nacional, Mpio de Leticia, Dpto de Amazonas, 4 May 1992, A.E. Franco-Molano 810 (HKAS 45442, duplicate of NY 34703).

O. venosolamellata (Imazeki & Toki) Imazeki & Hongo – Japan. Mt. Hayachine, Kawai, Iwate Prefecture, 8 August 1988, H. Neda s.n. (TFM-M-A843).

O. steffanii (Rick) Singer – Brazil. São Leopoldo, Rio Grande do sul, 1932, J. Rick s.n. [FH, holotype of *Oudemansiella echinosperma* Singer, which is usually treated as a synonym of *O. steffanii* by Singer (1964) and other authors].

O. submucida Corner – China. Mengxiu, Ruili County, Yunnan Prov., alt. 1190m, 28 July 2003, P.C. Liu

45 (HKAS 43457).

O. aff. submucida Corner – China. Mt. Changbai, Antu County, Jilin Prov., alt. 840m, 15 August 2004, L.F. Zhang 497 (HKAS 7622).

Macromorphological characters were described based on fresh material, colored photos, and/or field-notes. For micromorphological studies, sections were cut with a razor blade from basidioma and mounted on slides in 5% KOH, and then observed, measured and illustrated under a compound microscope (Zeiss Axioskop 40, Germany). Herbaria are abbreviated according to Holmgren *et al.* (1990) with one exception: HKAS = Herbarium of Cryptogams, Kunming Institute of Botany of the Chinese Academy of Sciences, which is not listed in the index or related publications.

2 RESULTS AND DISCUSSIONS

Morphological studies document that the structure of the pileipellis of *O. canarii-O. platensis* is much more diverse and complicated than in *O. mucida-O. venosolamellata*. In specimens of *O. canarii-O. platensis*, the pileipellis is an ixotrichoderm composed of both inflated cells and branching filamentous hyphae, sometimes dominantly of filamentous hyphae with few inflated elements (Figs. 1, 3, 4; see also figures 4, 7 in Corner 1994 and figure 8 in Baroni & Ortiz 2002, and Petersen *et al.* 2008), while the pileipellis in the *O. mucida-O. venosolamellata* complex, is usually a regular ixohymeniderm or an ixohymeniderm-trichoderm composed of broadly clavate, clavate to narrowly clavate cells in a layer of 1-2(3) cells (Figs. 6-8). The pileipellis of *O. mucida* is somewhat special because it made up of clavate to subcylindric to irregularly or coralloidly branched terminal cells (Fig. 5; also see Petersen *et al.* 2008). In addition, there are often flecks or warts on the pileal surface in specimens of *O. canarii-O. platensis* (Fig. 2) but not in the *O. mucida-O. venosolamellata* complex. The pileipellis of *O. radicata* complex is usually a regular ixohymeniderm composed of broadly clavate, clavate to narrowly clavate cells. A few species of this complex have no pileocystidia (Fig. 13a of Rexer & Kost 1989a), somewhat similar to those of *O. mucida-O. venosolamellata* complex, but most possess pileocystidia (Figs. 5-6 of Yang 2000; Fig. 11 of Yang & Zhang 2003). The pileipellis of *O. steffanii* (Fig. 9) is

very similar to those of *O. radicata* complex but without pileocystidia.

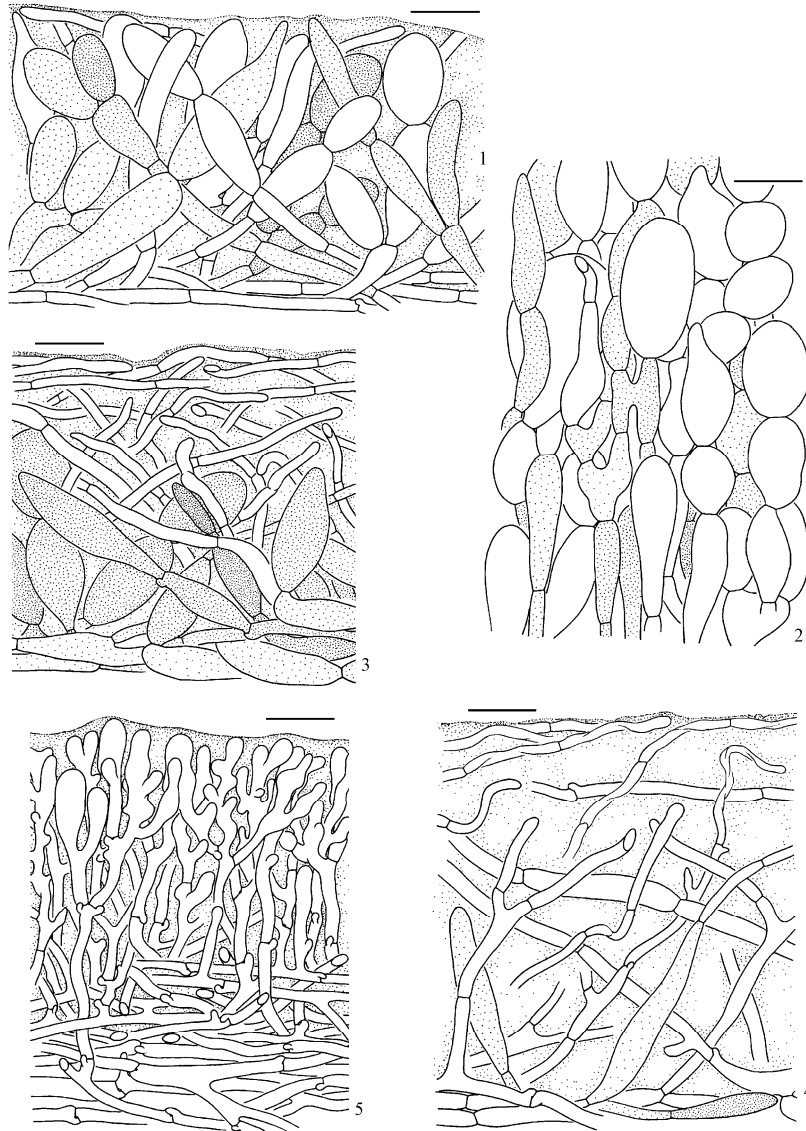


Fig. 1 Radial section of pileipellis from median between pileal centre and margin of *O. platensis* (HKAS 45442); Fig. 2 Vertical section of a wart on the pileal surface of *O. platensis* (HKAS 45442); Fig. 3 Radial section of pileipellis from median between pileal centre and margin of *O. canarii* (HKAS 5021); Fig. 4 Radial section of pileipellis from median between pileal centre and margin of *O. aff. crassifolia* (HKAS 43500); Fig. 5 Radial section of pileipellis from median between pileal centre and margin of *O. mucida* (HKAS 31558). Scale bar = 20µm.

3 TAXONOMY

The structure of the pileipellis in *Oudemansiella* is very diverse and useful for the establishment of infrageneric delimitations. Four groups can be recognized based on the pileipellis structure. These groups correspond to the following four sections.

Oudemansiella Speg., Anal. Soc. Cient. Argent. 12: 24

(1881).

Syn.: *Oudemansia* Speg., Anal. Soc. Cient. Argent. 10: 280 (1880).

Mucidula Pat., Hymén. Eur.: 95 (1887).

Phaeolimacium Henn., in Warburg, Monsunia 1: 14 (1899).

Basidioma armillarioid, tricholomatoid, collybioid to marasmiod. Surface of pileus usually viscid to gelatinous.

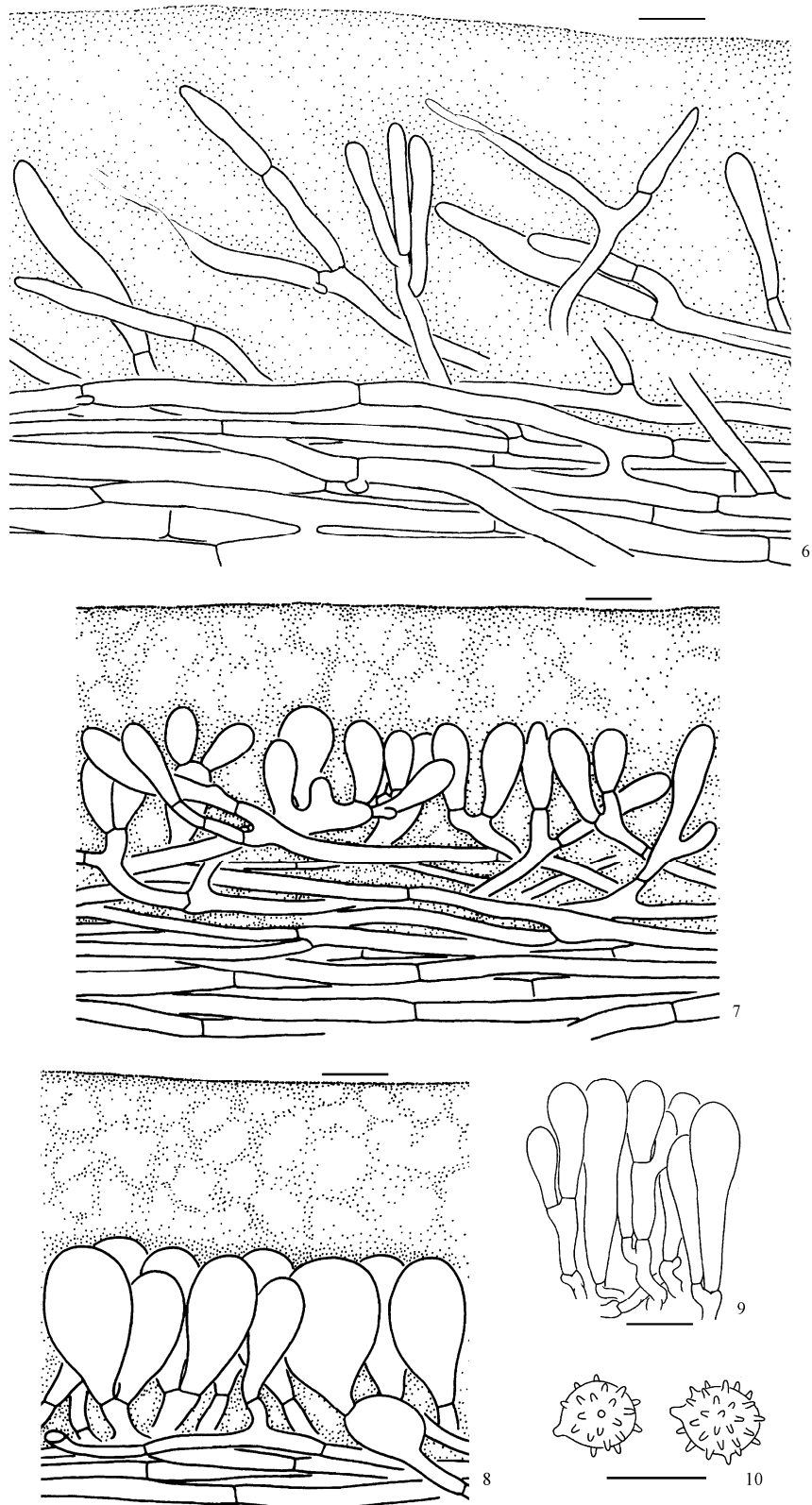


Fig. 6 Radial section of pileipellis from median between pileal centre and margin of *O. venosolamellata* (TFM-M-A843); Fig. 7 Radial section of pileipellis from median between pileal centre and margin of *O. aff. submucida* (HKAS 7622); Fig. 8 Radial section of pileipellis from median between pileal centre and margin of *O. submucida* (HKAS 43457); Figs. 9-10 Pileipellis of *O. steffanii* from median between pileal centre and margin, and basidiospores *O. steffanii* (FH, holotype of *O. echinosperma*). Scale bar = 20 μ m.

Lamellae adnexed to adnate, often with short decurrent teeth, thick, subdistant to distant. Stipe central to eccentric, annulate or exannulate, with or without a pseudorhiza. Spore print white to cream-coloured. Pileipellis more or less an ixohymeniderm, ixotrichohymeniderm or ixotrichoderm composed of inflated cells and/or filamentous hyphae. Warts or flecks on pileal surface, when present, composed of more or less vertically arranged moniliform to subglobose inflated cells intermixed with filamentous hyphae. Pileocystidia (hairs) present or absent, usually unicellular. Basidia mostly clavate to broadly clavate, sometimes suburniform, often with a distinctly narrowed base; basidioles in the hymenium usually clavate and with a broadly rounded apex, rarely subacrose. Basidiospores smooth to very delicately puckered or punctulate, sometimes with digitate ornamentation, colorless and hyaline, non-amyloid, non-dextrinoid, acyanophilic. Cheilocystidia crowded and forming a sterile lamellar edge. Clamp connections usually present and common, but for 2-spored taxa usually absent.

Type species: *O. platensis*.

Section 1 *Oudemansiella*

= *Phaeolimaecium* Henn., in Warburg, *Monsunia* 1: 14 (1899).

Basidioma armillarioid, tricholomatoid to marasmiod. Stipe with a rudimentary or fugacious annulus, often without pseudorhiza. Pileipellis an ixotrichoderm, but often stretched and extensively distorted and, thus, irregularly arranged due to the expansion of the pileus, composed of moniliform, fusiform to ellipsoid to subglobose inflated and filamentous hyphae (Figs. 1, 3 and 4). When basidioma is fully or over mature, pileipellis often distorted and cutis-like. Flecks or warts on pileal surface, when present, composed of more or less vertically arranged moniliform to subglobose inflated cells intermixed with filamentous hyphae or mainly with filamentous hyphae (Fig. 2). Basidiospores globose to subglobose, without digitate ornamentation. Tropical, subtropical to the south temperate.

Type species: *O. platensis*.

Additional species: *O. canarii*, *O. australis* G. Stev. & G.M. Taylor, *O. crassifolia*, *O. fibrillosa* T.J. Baroni & B. Ortiz, *O. lianicola* Corner.

Section 2 *Mucidula* (Pat.) Zhu L. Yang, Li F. Zhang, G.M. Muell., G. Kost & Rexer, stat. nov.

Basionym: *Mucidula* Pat., *Hymén. Eur.*: 95 (1887).

Mycobank No. MB 512737

Basidioma tricholomatoid to armillarioid. Stipe often without a pseudorhiza, but with a permanent, ephemeral, or fugacious annulus. Pileipellis a continuous and regular ixotrichohymeniderm or ixohymeniderm composed of clavate, narrowly clavate to broadly clavate, often branched sometimes coralloid terminal cells (Figs. 5-8). Flecks or patches on pileal surface absent. Basidiospores globose to subglobose, sometimes broadly ellipsoid or subamygdaliform to limoniform, without digitate ornamentation. In north temperate and subtropical regions, sometimes also in tropical mountains.

Type species: *O. mucida*.

Additional species: *O. submucida*, *O. yunnanensis* Zhu L. Yang & M. Zang, *O. venosolamellata*.

Section 3 *Radicatae* Cléménçon, *Sydowia* 32: 78 (1979).

= *Oudemansiella* sect. *Pseudoradicatae* Cléménçon, *Sydowia* 32: 77 (1979).

= *Oudemansiella* sect. *Hygrophoroides* Cléménçon, *Sydowia* 32: 78 (1979).

≡ *Xerula* sect. *Radicatae* (Cléménçon) Dörfelt, *Feddes Repert.* 91: 433 (1980).

Basidioma collybioid. stipe without annulus, often but not always with a pseudorhiza. Pileipellis a continuous and regular ixohymeniderm composed of narrowly clavate, clavate to broadly clavate to sphaeropedunculate terminal cells, with or without pileocystidia. Basidiospores globose, ovoid, broadly ellipsoid to ellipsoid or amygdaliform, without digitate ornamentation. Widely distributed.

Type species: *O. radicata* (Relhan: Fr.) Singer (≡ *Agaricus radicans* Relhan: Fr.)

Additional taxa: *O. bispora* (Natarajan & Purush.) Zhu L. Yang & Li F. Zhang, *O. japonica* (Dörfelt) Pegler & Young, *O. orientalis* Zhu L. Yang, *O. raphanipes* (Berk.) Pegler & T.W.K. Young, and the following taxa.

Oudemansiella africana (Dörfelt) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Xerula radicata* var. *africana* Dörfelt, *Feddes Repert.* 95: 195, Abb. 2, Taf. 23/10-12 (1984).

≡ *Xerula africana* (Dörfelt) R.H. Petersen, *Fungal Diversity* 30: 122 (2008).

≡ *Oudemansiella radicata* var. *africana* (Dörfelt) Pegler & T.W.K. Young, Trans. Brit. Mycol. Soc. 87: 598 (1987).

MycoBank No. MB 512738

Oudemansiella alveolata (Kalchbr.) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Agaricus alveolatus* Kalchbr., Grevillea 9: 110 (1881).

≡ *Collybia alveolata* (Kalchbr.) Sacc., Syll. Fung. 5: 202 (1887).

≡ *Xerula alveolata* (Kalchbr.) R.H. Petersen, Fungal Diversity 30: 125, figs. 7-11 (2008).

MycoBank No. MB 512739

Oudemansiella amygdaliformis* var. *bispora (R.H. Petersen & Nagas.) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Xerula amygdaliformis* var. *bispora* R.H. Petersen & Nagas., Rep. Tottori Mycol. Inst. 43: 12, figs. 6-8 (2006).

MycoBank No. MB 512741

Oudemansiella atrocaerulea (R.H. Petersen & Bougher) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Xerula atrocaerulea* R.H. Petersen & Bougher, Nova Hedwigia 87: 5, figs. 1, 2, 5-10 (2008).

MycoBank No. MB 512743

Oudemansiella aureocystidiata (R.H. Petersen & Nagas.) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Xerula aureocystidiata* R.H. Petersen & Nagas., Rep. Tottori Mycol. Inst. 43: 14, figs. 9-14 (2006).

MycoBank No. MB 512746

Oudemansiella caulovillosa (R.H. Petersen) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Xerula caulovillosa* R.H. Petersen, Mycoscience 49: 26, figs. 53-64 (2008).

MycoBank No. MB 512783

Oudemansiella chiangmaiae (R.H. Petersen & Nagas.) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Xerula chiangmaiae* R.H. Petersen & Nagas., Rep. Tottori Mycol. Inst. 43: 17, figs. 15-20 (2006).

MycoBank No. MB 512748

Oudemansiella colensoi (Dörfelt) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Xerula japonica* var. *colensoi* Dörfelt, Feddes Reper. 95: 193 (1984).

≡ *Oudemansiella japonica* var. *colensoi* (Dörfelt) Pegler & T.W.K. Young, Trans. Brit. Mycol. Soc. 87: 596, figs. 11, 52 (1987).

≡ *Xerula colensoi* (Dörfelt) R.H. Petersen, Nova Hedwigia 87: 9, figs. 11-16 (2008).

MycoBank No. MB 512749

Oudemansiella crassibasidiata (R.H. Petersen) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Xerula crassibasidiata* R.H. Petersen, Fungal Diversity 30: 128, figs. 12-17 (2008).

MycoBank No. MB 512750

Oudemansiella eradicata (Kalchbr.) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Agaricus (Collybia) eradicatus* Kalchbr., Grevillea 8: 151 (1880).

≡ *Collybia eradicata* (Kalchbr.) Sacc., Syll. Fung. 5: 202 (1887).

≡ *Xerula eradicata* (Kalchbr.) R.H. Petersen, Nova Hedwigia 87: 15, figs. 17-22 (2008)

= *Agaricus (Collybia) olivaceo-albus* Cooke & Masee, Grevillea 15: 93 (1887); *Collybia olivaceo-albus* (Cooke & Masee) Sacc. Syll. Fung. 9: 28 (1891). (fide Petersen 2008).

MycoBank No. MB 512751

Oudemansiella flavo-olivacea (R.H. Petersen & Halling) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Xerula flavo-olivacea* R.H. Petersen & Halling, Nova Hedwigia 87: 19, figs. 23-30 (2008).

MycoBank No. MB 512752

Oudemansiella flavo-olivacea* var. *kimberleyana (R.H. Petersen & M.D. Barrett) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Xerula flavo-olivacea* var. *kimberleyana* H. Petersen & M.D. Barrett, Nova Hedwigia 87: 23, figs. 31-38 (2008).

MycoBank No. MB 512753

Oudemansiella furfuracea (Peck) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Collybia radicata* var. *furfuracea* Peck, Report. N. Y. State Mus. 45 (Bot. Ed.): 31 (Mus. Ed. P. 91) (1892).

≡ *Oudemansiella radicata* var. *furfuracea* (Peck) Pegler & T.W.K. Young, Trans. Brit. Mycol. Soc. 87: 598 (1987).

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

MycoBank No. MB 512754

Oudemansiella gigaspora (Cooke & Masee) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Hygrophorus (Camarophyllus) gigasporus* Cook & Masee, Grevillea 16: 31 (1887).

≡ *Xerula gigasporus* (Cook & Masee) H. Petersen, Nova Hedwigia 87: 27, figs. 41-43 (2008).

= *Xerula radicata* var. *australis* Dörfelt, Feddes Repert. 95: 195, Taf. 23/9, 13-14 (1984), non *Oudemansiella australis* G. Stev. & G.M. Taylor, Kew Bull. 19: 33 (1964); *Oudemansiella radicata* var. *australis* (Dörfelt) Pegler and T.W.K. Young, Trans. Brit. Mycol. Soc. 87: 598 (1987); *Xerula australis* (Dörfelt) R.H. Petersen, Can. J. Bot. 72: 1152 (1994).

MycoBank No. MB 512755

Oudemansiella globospora (R.H. Petersen & Nagas.) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Xerula globospora* R.H. Petersen & Nagas., Rep. Tottori Mycol. Inst. 43: 25, figs. 28-34 (2006).

MycoBank No. MB 512757

Oudemansiella incognita (Methven & R.H. Petersen) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Xerula incognita* Methven & R.H. Petersen, Can. J. Bot. 72: 1154, figs. 5-9 (1994).

MycoBank No. MB 512758

Oudemansiella kenyae (R.H. Petersen) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Xerula kenyae* R.H. Petersen, Fungal Diversity 30: 132, figs. 18-23 (2008).

MycoBank No. MB 512759

Oudemansiella limonispora (R.H. Petersen) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Xerula limonispora* R.H. Petersen, Bull. Soc. Mycol. France 120: 38 (2005).

MycoBank No. MB 512760

Oudemansiella mammicystis (R.H. Petersen) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Xerula mammicystis* R.H. Petersen, Fungal Diversity 30: 135, figs. 24-29 (2008).

MycoBank No. MB 512761

Oudemansiella megalospora (Clem.) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Clitocybe megalospora* Clem., Bot. Survey Nebraska 4: 18 (1896).

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

MycoBank No. MB 512762

Oudemansiella mundroola (Grgur.) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Xerula radicata* var. *mundroola* Grgur., Larger Fungi of South Australia (Adelaide): 253 (1997).

≡ *Xerula mundroola* (Grgur.) R.H. Petersen, Nova Hedwigia 87: 43, figs. 39,40, 44-46 (2008).

MycoBank No. MB 512763

Oudemansiella orientiradicata Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **nom. nov.**

Basionym: *Xerula orientalis* R.H. Petersen & Nagas., Rep. Tottori Mycol. Inst. 43: 36, figs. 46-52 (2006); non *Oudemansiella orientalis* Zhu L. Yang, Mycotaxon 74: 357 (2000).

MycoBank No. MB 512765

Oudemansiella orientiradicata* var. *margaritella (R.H. Petersen & Nagas.) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Xerula orientalis* var. *margaritella* R.H. Petersen & Nagas., Rep. Tottori Mycol. Inst. 43: 39, fig. 53 (2006).

MycoBank No. MB 512767

Oudemansiella radicata* var. *bispora (Redhead, Ginns & Shoemaker) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Xerula radicata* var. *bispora* Redhead, Ginns & Shoemaker, Mycotaxon 30: 398, figs. 14, 20 (1987).

MycoBank No. MB 512768

Oudemansiella rubrobrunnescens (Redhead, Ginns & Shoemaker) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Xerula rubrobrunnescens* Redhead, Ginns & Shoemaker, Mycotaxon 30: 384, figs.4-5, 40-51 (1987).

MycoBank No. MB 512769

Oudemansiella rugosoceps (G.F. Atk.) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Collybia rugosiceps* G. F. Atk. Journ. Mycol. 8: 112 (1902)

≡ *Gymnopus rugosoceps* (G.F. Atk.) Murrill, N. Amer. Fl. (New York) 9: 360 (1916).

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

MycoBank No. MB 512770

Oudemansiella semiglabripes (R.H. Petersen) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Xerula semiglabripes* R.H. Petersen, Fungal Diversity 30: 138, figs. 30-35 (2008).

MycoBank No. MB 512771

Oudemansiella superbiens (Berk.) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Agaricus radicans* var. *superbiens* Berk., Hooker's Lond. J. Bot. 4: 43 (1845).

≡ *Collybia radicata* var. *superbiens* (Berk.) Sacc., Syll. Fung. 5: 201 (1887).

≡ *Oudemansiella radicata* var. *superbiens* (Berk.) Pegler & T.W.K. Young, Trans. Br. mycol. Soc. 87(4): 598 (1987).

≡ *Xerula radicata* var. *superbiens* (Berk.) Dörfelt, Feddes Repert. 94: 559 (1983).

≡ *Xerula superbiens* (Berk.) R. H. Petersen, Nova Hedwigia 87: 50, figs. 53, 55-60 (2008).

MycoBank No. MB 512773

Oudemansiella tetrasperma (R.H. Petersen) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Xerula tetrasperma* R.H. Petersen, Fungal Diversity 30: 141, figs. 36-40 (2008).

MycoBank No. MB 512774

Oudemansiella tetrasperma* f. *marginata (R.H. Petersen) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Xerula tetrasperma* f. *marginata* R.H. Petersen, Fungal Diversity 30: 143 (2008).

Key to the sections

1. Basidiomata armillarioid or tricholomatoid, growing directly on wood above the ground, often with ephemeral or persistent annulus; pileipellis an ixotrichoderm, ixotrichohymeniderm or ixohymeniderm with both inflated and branched filamentous hyphae or clavate terminal elements but can become cutis-like when fully mature.....2
1. Basidiomata collybioid, growing on buried wood, without annulus, usually with distinct pseudorhiza; pileipellis a continuous and regular ixohymeniderm.....3
2. Pileipellis an ixotrichoderm, or when fully mature completely distorted and cutis-like, consisting of both filamentous hyphae and inflated cells, sometimes primarily composed of filamentous hyphae; pileal surface often with flecks or patches; basidiospores globose to subglobose; tropical, subtropical to south temperate..... *O. sect. Oudemansiella*
2. Pileipellis a regular ixohymeniderm or an ixotrichohymeniderm composed of more or less clavate terminal cells; pileal surface without flecks or patches; basidiospores globose to subglobose, sometimes broadly ellipsoid or subamygdaliform to limoniform; north temperate and subtropical or in tropical mountains..... *O. sect. Mucidula*

MycoBank No. MB 512775

Oudemansiella trichofera (R.H. Petersen) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Xerula trichofera* R.H. Petersen, Nova Hedwigia 87: 54, figs. 54, 61-67 (2008).

MycoBank No. MB 512776

Oudemansiella variabilis (R.H. Petersen) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Xerula variabilis* R.H. Petersen, Nova Hedwigia 87: 59, figs. 68-73 (2008).

MycoBank No. MB 512777

Oudemansiella vinocontusa (R.H. Petersen & Nagas.) Zhu L. Yang, G.M. Muell., G. Kost & Rexer, **comb. nov.**

Basionym: *Xerula vinocontusa* R.H. Petersen & Nagas., Rep. Tottori Mycol. Inst. 43: 44, figs. 60-64 (2006).

MycoBank No. MB 512779

Section 4 *Dactylosporina* (Cléménçon) Pegler & T.W.K. Young, Trans. Br. Mycol. Soc. 87: 598 (1987).

Basionym: *Oudemansiella* subgen. *Dactylosporina* Cléménçon, Sydowia 32: 77 (1979).

≡ *Dactylosporina* (Cléménçon) Dörfelt, Feddes Repert. 96: 236 (1985).

Basidioma collybioid. Stipe without an annulus, but usually with a pseudorhiza. Pileipellis a continuous and regular hymenoderm composed of clavate, narrowly clavate to broadly clavate or sphaeropedunculate terminal cells, without pileocystidia (Fig. 9). Basidiospores with obtusely echinate ornamentation (Fig. 10). In South and Central America.

Type species: *O. steffenii*.

Additional species: *O. macracantha* Singer.

3. Basidiospores subglobose, ellipsoid or amygdaliform, generally smooth, without finger-like ornamentation; widely distributed, temperate to tropical..... *O. sect. Radicatae*
3. Basidiospores subglobose, with prominent finger-like ornamentation; Central and South America..... *O. sect. Dactylosporina*

4 DISCUSSION

4.1 Significance of development and hyphal system of basidioma in relation to systematics of the genus

The manner of basidioma development has widely been used as a trait in the delimitation of *Oudemansiella* and *Xerula* (Dörfelt 1981; Boekhout & Bas 1986; Pegler & Young 1987). However, various authors, or even the same author at different times, differ in their interpretation of basidioma development in *Oudemansiella*. For example, Dörfelt (1981, 1982) stated that the development of *O. mucida* and *O. canarii* is hemiangiocarpic (bivelangiocarpic), while the development of *O. radicata* is gymnocarpic. Corner (1934) regarded *Collybia apalosarca* (= *O. canarii*) as hemiangiocarpic, but sixty years later he (Corner 1994) redefined *Oudemansiella* as being gymnocarpic with or without a marginal veil. Our molecular analyses (data not showed) indicate that sections *Mucidula* and *Oudemansiella* have different ancestors. Thus, even though species in both sections share similar development patterns, our data suggest that development in the tropical, subtropical and south temperate section *Oudemansiella* and the north temperate sect. *Mucidula* is convergent. One explanation for the strikingly convergent morphologies in the two sections is that these are structural adaptations to exposed rotten wood, rather than buried wood as in sections *Radicatae* and *Dactylosporina*. Consequently, “hemiangiocarpic (bivelangiocarpic) development” or the formation of a “marginal veil”, i.e., an annulus, may be an adaptive feature to the environment (Pegler & Young 1987; Rexer & Kost 1989a).

Some authors used the presence of monomitic or sarcodimitic structures in the stipititrama (and partially also in lamellar trama) of *Oudemansiella* and *Xerula* as a criterion for the delimitation of subgenera, genera, or even family (Boekhout & Bas 1986; Redhead 1987; Contu 2000). However, whether a stipititrama of *Oudemansiella* and *Xerula* is monomitic or sarcodimitic appears largely dependant on the judgment and/or

interpretation of the author. For example, Rexer & Kost (1989a) stated that both *O. mucida* and *O. radicata* are sarcodimitic, while Boekhout & Bas (1986) noted *O. mucida* is monomitic and *O. radicata* is sarcodimitic. Redhead *et al.* (1987) stated that both *O. mucida* and *O. canarii* form a tissue somewhat intermediate between monomitic and sarcodimitic, but that all seven North American species of *Xerula sensu* Dörfelt (*O. sect. Radicatae* in the present sense) have sarcodimitic stipititramas. In the view point of Corner (1994, 1996), *Oudemansiella* is monomitic. As a matter of fact, there are frequently branched narrow hyphae (“connective hyphae”) among longitudinally arranged, long-celled, inflated hyphae (“sarcoskeletons” termed by Boekhout & Bas, 1986) in the stipititramas of both genera *Oudemansiella* and *Xerula*. However, such “connective hyphae” are largely restricted to the bulbillate or ventricose part of the pseudorhiza of species having a radicating stipe, a similar phenomenon as observed by Redhead (1987). For the species without a radicating stipe base, viz. *O. mucida*, *O. canarii*, *O. orientalis* (Yang 2000), such “connective hyphae” are largely restricted to the bulbillate or discoid basal part of the stipe, a portion with only a limited elongation during the development of the basidioma and the interwoven arrangement of filamentous or somewhat inflated hyphae in the disc (Corner 1934) or in the secondary nodulus (Cléménçon 2004) can be traced to certain extent even when basidioma is mature. In this study, hyphal system of the stipititrama was not used as a criterion for the delimitation of genera *Oudemansiella* and *Xerula*, or sections of *Oudemansiella*.

4.2 Variation of the pileipellis in sections *Oudemansiella* and *Mucidula*

Horak (1968) and Boekhout & Bas (1986) interpreted the pileipellis of *O. platensis* and *O. canarii* as a cutis. However, Baroni & Ortiz (2002) stated that the structure of the pileipellis of *O. canarii* needs further clarification and illustration. Petersen *et al.* (2008) described and illustrated the structures of the pileipellis

and warts or flecks on the pileus of these two species, besides *O. mucida*, in detail.

Our examinations document that the structure of the pileipellis of *O. canarii*-*O. platensis* complex can significantly vary at different stages of development as suggested by Dörfelt (1981). In young basidioma of *O. canarii* and *O. platensis*, the pileipellis is an even ixotrichoderm of vertically arranged elements. But with the expansion of the pileus, the structure of pileipellis in the pileal centre often differs from the pileal margin. In a mature basidioma of *O. canarii*-*O. platensis*, the pileipellis in the pileal centre remains a ixotrichoderm with more or less vertically arranged elements (see Figs. 1, 3, and 4) while near the pileal margin it is composed of nearly repent elements. In fully mature or weathered basidioma, the pileipellis is often stretched and it becomes extensively distorted, disrupted, or even collapsed, in part due to gelatinization. At this stage it looks like a cutis (Dörfelt 1981). A similar phenomenon was observed in *O. venosolamellata* (Fig. 6) of sect. *Mucidula*. The flecks or warts on the pileus are persistent (in *O. platensis*, Fig. 2) or can easily be washed off by the rain (in *O. canarii*).

4.3 Excluded groups

Agaricus platyphyllus Pers.: Fr. was placed in the genus *Oudemansiella* by Moser (1955) and others. Knecht (1967), Dörfelt (1981), Lindsey (1986) and Rexer & Kost (1989a) showed that there are fundamental differences between *Agaricus platyphyllus* and others species of *Oudemansiella* or *Xerula*, and should be regarded as a separate genus, *Megacollybia*, as proposed by Kotlaba & Pouzar (1972) and accepted by Pegler & Young (1987), Redhead (1987), Petersen & Gordon (1994), and many others.

Pegler & Young (1987) regarded section *Albotomentosae* Cléménçon as distinct in their system, which includes *O. causei* (Maire) M.M. Moser apud Cléménçon, *O. nigra* Dörfelt, *O. renati* Cléménçon and *O. xeruloides* Bon with *O. nigra* as the type. The former three are conspecific according to Boekhout & Bas (1986), Boekhout (1999) and Contu (2000). In the same work, they (Pegler & Young 1987) treated *Xerula* sect. *Hyalosetae* Dörfelt, the type of which is *X. americana* Dörfelt, as a synonym of *O.* sect. *Xerula* Cléménçon typified by *Agaricus longipes*. Species of *Oudemansiella*

sect. *Albotomentosae* and *Xerula* sect. *Hyalosetae*, such as *O. causei* and *O. hongoi* (Dörfelt) Zhu L. Yang, and *X. americana*, are not included in *Oudemansiella* s. str. as they may form a distinct genus according to our preliminary molecular phylogenetic analysis. The unique ultra-structure of the spore wall of *O. nigra* and *O. xeruloides*, the epitunica forming an interrupted and often discontinuous layer (Pegler & Young 1987), provides additional sound evidence for the exclusion of these taxa from *Oudemansiella*.

In our opinion, the eleven taxa of *Xerula*, with very detailed and accurate descriptions and illustrations, reported from Australia and New Zealand by Petersen (2008c) should belong to *O.* sect. *Radicatae*, a section with diverse taxa widely distributed in many parts of the world, rather than sect. *Albotomentosae* as delimited by Petersen (2008c).

4.4 Taxa of placement uncertainty

Oudemansiella mediterranea (Pacioni & Lalli) E. Horak (1988) was initially placed in the genus *Hydropus* by Pacioni & Lalli (1985) and then in *Flammulina* by Bas & Robich (1988). Quadraccia & Lunghini (1990) transferred this species to *Xerula* as *X. mediterranea*, on which *Xerula* subgen. *Ixoflammula* was based (Contu 2000).

Mycenella kuehneri Romagn., having ornamented basidiospores, was once placed in *Oudemansiella* by Singer (1962b) and, then transferred to the genus *Xerula* by Boekhout (1985), Boekhout & Bas (1986) and Boekhout (1999), but it was retained in the genus *Mycenella* by Dörfelt (1985), and Pegler & Young (1987) based on its overall soft-putrescent habit with a dry pileus, the non-lignicolous substratum and the absence of any pseudorhiza. However, Redhead *et al.* (1987) stated that the correlated presence of a monomitic stipititrama and nodose, cyanophylic basidiospores in *M. kuehneri* suggests generic distinction.

Molecular phylogenetic data are not available for either of these taxa. However, the European distribution of *M. kuehneri* may suggest that it has no close relationship with *O. steffenii*-complex in Central and South America. Horak (1988) supposed that *O. mediterranea* may have affinity with *O. causei* and *O. xeruloides*, and later treated it as a taxonomic synonym of *O. xeruloides* (Horak 2005). Because *O. causei* and

O. xeruloides have been excluded from the genus *Oudemansiella* in the present paper, the placement of *H. mediterranea* Pacioni & Lalli in *Oudemansiella* is questionable.

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