



PHYTOTAXA

180

Molecular phylogeny and phylogeography of Holarctic species of *Pluteus* section *Pluteus* (Agaricales: Pluteaceae), with description of twelve new species

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Magnolia Press
Auckland, New Zealand

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Pluteaceae), with description of twelve new species**
(*Phytotaxa* 180)

85 pp.; 30 cm.

24 Sept 2014

ISBN 978-1-77557-495-8 (paperback)

ISBN 978-1-77557-496-5 (Online edition)

FIRST PUBLISHED IN 2014 BY

Magnolia Press

P.O. Box 41-383

Auckland 1346

New Zealand

e-mail: magnolia@mapress.com

<http://www.mapress.com/phytotaxa/>

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ISSN 1179-3155 (Print edition)

ISSN 1179-3163 (Online edition)

Table of contents

Abstract	3
Introduction	3
Material and Methods	4
Results	5
Taxonomic Part	15
I. cervinus clade	19
II. pouzarianus clade	34
III. brunneidiscus clade	46
IV. petasatus clade	52
V. salicinus clade	60
VI. atromarginatus clade	69
Discussion	75
Identification keys	78
Acknowledgements	81
References	82

Abstract

The taxonomy and phylogeography of *Pluteus* section *Pluteus* in the Holarctic region was investigated using morphological and molecular data. Over 300 specimens spanning the major areas of boreal and temperate forests of the Northern Hemisphere were studied and nrITS and *tef1* were obtained for phylogenetic analyses. In order to stabilize the taxonomy of the group all available type collections were studied and, if possible, sequenced. A total of 26 species occurring in Eurasia and North America were recovered in the phylogenetic analyses. Twelve species are described as new (*Pluteus rangifer*, *P. elaphinus*, *P. hibbettii*, *P. eos*, *P. orestes*, *P. methvenii*, *P. shikae*, *P. kovalenkoi*, *P. leucoborealis*, *P. sepiicolor*, *P. oreibatus*, *P. atrofibrillosus*), one is provisionally named (*P. parilis*) and one variety is raised to species rank (*P. americanus*). In many cases separation of the species based on morphology alone is challenging. In general, *tef1* distinguishes the species better than nrITS. Structured infraspecific genetic variation was detected in the nrITS phylogenies for five species (*P. atromarginatus*, *P. hibbettii*, *P. orestes*, *P. primus* and *P. shikae*) and in the *tef1* phylogenies for *P. cervinus*. Phylogeographic patterns are strikingly different among the species in this group and include widespread Holarctic species, exclusively Palearctic, putative disjuncts and endemics in each Holarctic subregion (Eastern/Western Palearctic and Nearctic). Identification keys are provided for each subregion.

Introduction

The taxonomy of the genus *Pluteus* Fr. has recently been revised using molecular phylogenies, which essentially upheld the morphologically recognized sections (*Pluteus*, *Celluloderma* Fayod and *Hispidoderma* Fayod) with minor rearrangements (Justo *et al.* 2011a, 2011b). Section *Pluteus* Fr. accommodates the species with metuloid hymenial cystidia and a pileipellis organized as a cutis, and includes the type species of the genus, *Pluteus cervinus* (Schaeffer) Kummer (1874: 138) or “deer mushroom”. *Pluteus cervinus* is commonly depicted in popular field guides (e.g. Bessette *et al.* 1997; Phillips 2010) and websites (e.g. <http://mushroomobserver.org/>; http://www.mushroomexpert.com/pluteus_cervinus.html) although it has been suspected for a long time to be a complex of several species (Singer 1956).

The questions about the actual number of species in section *Pluteus* that occur in the Northern Hemisphere, the morphological characters that might be used to separate them and the correct names that should be applied to these taxa have baffled mycologists for decades. Studies on section *Pluteus* in Europe (Kühner & Romagnesi 1953; Singer 1956; Orton 1986; Bonnard 1986, 1987, 2001; Vellinga 1990) have recognized around thirteen species, with numbers varying depending on taxonomic opinion, and with as many as seven described in the last three decades (Singer 1984; Bonnard 1986, 1987, 1991, 2001; Deparis 2003; Justo & Castro 2007a,b). In North America, section *Pluteus* has received considerable attention (Murill 1917; Singer 1956; Smith & Stuntz 1958; Banerjee & Sundberg 1993, 1995). A total of 18 species have been reported, again with discrepancies depending on the taxonomic concepts of the different authors. Furthermore, many species names based on European material (*P. atromarginatus*, *P. cervinus*, *P. pellitus*, *P. patricius*, *P. petasatus*, *P. pouzarianus*, *P. salicinus*) have been applied to North American collections (Banerjee & Sundberg 1995; Rodríguez 2013).

to DSH. U.S. Forest Service funds contributed to this work. The study of Russian collections was supported by the Russian Foundation for Basic Research (projects № 12-04-33018 and № 13-04-00838).

References

- Banerjee, P. & Sundberg, W.J. (1993) Three new species and a new variety of *Pluteus* from the United States. *Mycotaxon* 47: 389–394.
- Banerjee, P. & Sundberg, W.J. (1995) The genus *Pluteus* section *Pluteus* (Pluteaceae, Agaricales) in the midwestern United States. *Mycotaxon* 53: 189–246.
- Batsch, A.J.G.K. (1786) *Elenchus fungorum. Continuatio prima*. Joannem J. Gebauer, Halae Magdeburgicae, 280 pp.
- Beatty, G.E. & Provan, J. (2013) Post-glacial dispersal, rather than in situ glacial survival, best explains the disjunct distribution of the Lusitanian plant species *Daboecia cantabrica* (Ericaceae). *Journal of Biogeography* 40: 335–344.
<http://dx.doi.org/10.1111/j.1365-2699.2012.02789.x>
- Benson, D.A., Karsch-Mizrachi, I., Lipman, D.J., Ostell, J. & Sayers, E.W. (2011) GenBank. *Nucleic Acids Research* 39: D32–D327.
<http://dx.doi.org/10.1093/nar/gkr1202>
- Berkeley, M.J. (1845) Decades of fungi. Decades VIII–X. Australian and North American fungi. *London Journal of Botany* 4: 298–315.
- Berkeley, M.J. & Broome, C.E. (1871) The fungi of Ceylon (Hymenomycetes from *Agaricus* to *Cantharellus*). *The Journal of the Linnean Society Botany* 11: 494–567.
- Berkeley, M.J. & Curtis M.A. (1849) Decades of fungi. Decades XXI–XXII. North and South Carolina Fungi. *Hooker's Journal of Botany and Kew Garden Miscellany* 1: 97–104.
- Bessette, A.E., Bessette A.R. & Fischer, D.W. (1997) *Mushrooms of Northeastern North America*. Syracuse University Press, 582 pp.
- Bonnard, J. (1986) *Pluteus lidipocystis* sp. nov. *Mycologia Helvetica* 2: 35–42.
- Bonnard, J. (1987) *Pluteus brunneoradiatus* sp. nov. *Mycologia Helvetica* 2: 141–154.
- Bonnard, J. (1988) Les cystides de la section *Pluteus* (Agaricales). *Mycologia Helvetica* 3: 53–72.
- Bonnard, J. (1991) *Pluteus primus* sp. nov. (Agaricales, Basidiomycetes) *Mycologia Helvetica* 4: 169–178.
- Bonnard, J. (1993) Clé provisoire des Plutées européens à boucles. *Mycologia Helvetica* 6: 203–205.
- Bonnard, J. (1995) *Pluteus pellitus* désignation d'un néotype (Section *Pluteus*, Agaricales, Basidiomycetes). *Mycologia Helvetica* 7: 97–103.
- Bonnard, J. (2001) *Pluteus albineus* sp. nov. (Agaricales, Basidiomycetes). *Mycologia Helvetica* 11: 131–136.
- Boudier, J.L.E. (1905) *Icones Mycologicae, ou Iconographie des champignons de France principalement Discomycetes avec texte descriptif*. P. Klincksieck, Paris, 193 pp.
- Buyck, B. & Hofstetter, V. (2011) The contribution of *tef-1* sequences to species delimitation in the *Cantharellus cibarius* complex in the southeastern USA. *Fungal Diversity* 49: 35–46.
<http://dx.doi.org/10.1007/s13225-011-0095-z>
- Carlson, A., Justo, A. & Hibbett, D.S. (2014) Species delimitation in *Trametes*: a comparison of ITS, RPB1, RPB2 and *TEF1* gene phylogenies. *Mycologia* (in press).
<http://dx.doi.org/10.3852/13-275>
- Contu, M. (2001) Studi sulle Pluteaceae della Sardegna – II una nuova specie di *Pluteus* con giunti a fibbia. [Studies on the Pluteaceae of Sardinia II: a new species of *Pluteus* with clamp-connections.] *Mycologia Helvetica* 11: 137–144.
- Crous, P.W., Gams, W., Stalpers, J.A., Robert, V. & Stegehuis, G. (2004) MycoBank: an online initiative to launch mycology into the 21st century. *Studies in Mycology* 50: 19–22.
- Deparis, L. (2003) Description de *Pluteus alniphilus*, nouvelle espèce de la section *Pluteus*. *Bulletin Trimestriel de la Fédération Mycologique Dauphiné-Savoie* 169: 5–15.
- Favre, J. (1948) *Matériaux pour la flore cryptogamique suisse*. Böhler & Cie, Berne, 228 pp.
- Fayod, M.V. (1849) Prodrome d'une histoire naturelle des Agaricinés. *Annales des Sciences Naturelles Botanique* 9: 181–411.
- Fries, E.M. (1821) *Systema Mycologicum* vol. 1. Lund, 520 pp.
- Fries, E.M. (1836) *Epicrasis systematis mycologici seu synopsis Hymenomycetum*. Upsaliae, 612 pp.
- Gardes, M. & Bruns, T.D. (1993) ITS primers with enhanced specificity for basidiomycetes application to the identification of mycorrhizae and rusts. *Molecular Ecology* 2: 132–118.
<http://dx.doi.org/10.1111/j.1365-294x.1993.tb00005.x>
- Gazis, R., Rehner, S. & Chaverri, P. (2011) Species delimitation in fungal endophyte diversity studies and its implications in ecological and biogeographic inferences. *Molecular Ecology* 20: 3001–3013.
<http://dx.doi.org/10.1111/j.1365-294X.2011.05110.x>
- Gillet, C.C. (1876) *Les Hyménomycètes ou Description de tous les Champignons qui Croissent en France*. Ch. Thomas, Alençon, 560 pp.
- Harder, C.B., Læssøe, T., Frøslev, T.G., Ekelund, F., Rosendahl, S. & Kjoller, R. (2013) A three-gene phylogeny of the *Mycena*

- pura* complex reveals 11 phylogenetic species and shows ITS to be unreliable for species identification. *Fungal Biology* 117: 764–775.
<http://dx.doi.org/10.1016/j.funbio.2013.09.004>
- Horak, E. (1964) Fungi austroamerici II. *Pluteus* Fr. *Nova Hedwigia* 8:163–199.
- Horak, E. (2008) Agaricales of New Zealand 1: Pluteaceae-Entolomataceae. Fungal Diversity Press, Hong Kong, 305 pp.
- Hughes, K., Petersen, R.H. & Lickley, E.B. (2009) Using heterozygosity to estimate percentage DNA sequence similarity for environmental species delimitation across basidiomycete fungi. *New Phytologist* 182: 795–798.
<http://dx.doi.org/10.1111/j.1469-8137.2009.02802.x>
- Justo, A. & Castro, M.L. (2007a) Observations in *Pluteus* section *Pluteus* in Spain: Two new records for Europe. *Mycotaxon* 102: 209–220.
- Justo, A. & Castro, M.L. (2007b) *Pluteus nothopellitus* sp. nov. and a review of white species of *Pluteus* section *Pluteus*. *Mycotaxon* 102: 221–230.
- Justo, A. & Castro, M.L. (2007c) An annotated checklist of *Pluteus* in the Iberian Peninsula and Balearic Islands. *Mycotaxon* 102: 231–234.
- Justo, A. & Hibbett, D.S. (2011). Phylogenetic classification of *Trametes* (Basidiomycota, Polyporales) based on a five-marker dataset. *Taxon* 60: 1567–1583.
- Justo, A., Castro, M.L., Rodríguez-Ramos, N. & Infante, F. (2006) Neotipificación de *Pluteus sandalioticus*. *Cryptogamie Mycologie* 27: 197–200.
- Justo, A., Minnis, A.M., Ghignone, S., Menolli, Jr. N., Capelari, M., Rodríguez, O., Malysheva, E., Contu, M. & Vizzini, A. (2011a) Species recognition in *Pluteus* and *Volvopluteus* (Pluteaceae, Agaricales): morphology, geography and phylogeny. *Mycological Progress* 10: 453–479.
<http://dx.doi.org/10.1007/s11557-010-0716-z>
- Justo, A., Vizzini, A., Minnis, A.M., Menolli, Jr. N., Capelari, M., Rodríguez, O., Malysheva, E., Contu, M., Ghignone, S. & Hibbett, D.S. (2011b) Phylogeny of the Pluteaceae (Agaricales, Basidiomycota): Taxonomy and Character Evolution. *Fungal Biology* 115: 1–20.
<http://dx.doi.org/10.1016/j.funbio.2010.09.012>
- Kalchbrenner, C. (1874) *Icones selectae Hymenomycetum Hungariae, vol. 2*. Typys Athenaei, Budapest, 36 pp.
- Katoh, K. & Toh, H. (2008) Recent developments in the MAFFT multiple sequence alignment program. *Briefings in Bioinformatics* 9: 286–298.
<http://dx.doi.org/10.1093/bib/bbn013>
- Kreft, H. & Jetz, W. (2010) A framework for delineating biogeographical regions based on species distributions. *Journal of Biogeography* 37: 2029–2053.
<http://dx.doi.org/10.1111/j.1365-2699.2010.02375.x>
- Kühner, R. (1935) Deux espèces rares d'agarics à revêtement piléique celluleux. *Bulletin Mensuel de la Société Linnéenne de Lyon* 4: 50–51.
- Kühner, R. & Romagnesi, H. (1953) *Flore analytique des champignons supérieurs*. Masson, Paris, 556 pp.
- Kummer, P. (1871) *Der Führer in die Pilzkunde*. C. Luppe, Zerbst, 146 pp.
- Lasch, W.G. (1828) Enumeratio Agaricorum Marchiae Brandenburgicae, nondum in floris nostratibus nominatorum, cum observationibus in cognitos et novorum descriptionibus. *Linnaea* 3: 153–162.
- Maddison, D.R. & Maddison, W.P. (2002) MacClade4: analysis of phylogeny and character evolution. Sinauer Associates, Sunderland.
- McClatchie, A.J. (1897) Seedless plants of southern California. *Proceedings of the Southern California Academy of Sciences* 1: 338–395.
- McNeill, J., Barrie, F.R., Buck, W.R., Demoulin, V., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Marhold, K., Prado, J., Prud'Homme Van Reine, W.F., Smith, G.F., Wiersema, J.H. & Turland, N.J. (2012) International Code of Nomenclature for algae, fungi, and plants (Melbourne Code): adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011. *Regnum Vegetabile* 154.
- Menolli Jr., N., Asai, T., Capelari, M. (2010) Records and new species of *Pluteus* from Brazil based on morphological and molecular data. *Mycology* 1: 130–153.
<http://dx.doi.org/10.1080/21501203.2010.493531>
- Merényi, Z., Varga, T., Geml, J., Orczán, Á.K., Chevalier, G., & Bratek, Z. (2014) Phylogeny and phylogeography of the *Tuber brumale* aggr. *Mycorrhiza* 24: S101–S113.
<http://dx.doi.org/10.1007/s00572-014-0566-7>
- Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) *Creating the CIPRES Science Gateway for inference of large phylogenetic trees*. Proceedings of the Gateway Computing Environments Workshop (GCE). New Orleans, USA: GCE, pp. 1–8.
- Montagne, J.F.C. (1856) *Sylloge generum specierumque plantarum cryptogamarum*. Paris, 498 pp.
- Moser, M.M & Stangl, J. (1963) Ein neuer *Pluteus* aus Süddeutschland: *Pluteus pseudo-roberti* Mos et Stangl. *Zeitschrift für Pilzkunde* 29: 36–39.
- Munsell, C. (Ed.) (2009) *Munsell Soil Color Charts*. Grand Rapids, Michigan (USA).
- Murat, C., Díez, J., Luis, P., Delaruelle, C., Dupré, C., Chevalier, G., Bonfante, P. & Martin, F. (2004) Polymorphism at the ribosomal DNA ITS and its relation to postglacial re-colonization routes of the Perigord truffle *Tuber melanosporum*. *New*

- Phytologist* 164: 401–411.
<http://dx.doi.org/10.1111/j.1469-8137.2004.01189.x>
- Murrill, W.A. (1917) *Pluteus*. *North American Flora* 10(2): 127–139.
- Murrill, W.A. (1945) New Florida Fungi. *Proceedings of the Florida Academy of Sciences* 7: 107–127.
- Orton, P.D. (1960) New check list of British Agarics and Boleti, part III (keys to *Crepidotus*, *Deconica*, *Flocculina*, *Hygrophorus*, *Naucoria*, *Pluteus* and *Volvaria*). *Transactions of the British Mycological Society* 43: 159–439.
- Orton, P.D. (1986) *British Fungus Flora*. Agarics and Boleti 4: Pluteaceae: *Pluteus* and *Volvariella*. Royal Botanic Garden, Edinburgh, 99 pp.
- Pegler, D.N. (1983) Agaric Flora of the Lesser Antilles. *Kew Bulletin* 9: 1–695.
- Pegler, D.N. (1986) Agaric Flora of Sri Lanka. *Kew Bulletin* 12: 1–519.
- Persoon, C.H. (1798) *Icones et Descriptiones Fungorum Minus Cognitorum*. Breitkopf-Haertel, Leipzig, 26 pp.
- Persoon, C.H. (1801) *Synopsis methodica fungorum*. Göttingen, 706 pp.
- Phillips, R. (2010) *Mushrooms and Other Fungi of North America*. Firefly Books, Buffalo, 384 pp.
- Pradeep, C.K., Vrinda, K.B. & Abraham, T.K. (2002) *Pluteus* section *Pluteus* from Kerala State, India. *Mycotaxon* 83: 59–66.
- Rehner, S.A. & Buckley, E. (2005) A *Beauveria* phylogeny inferred from nuclear ITS and EF1- α sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. *Mycologia* 97: 84–98.
- Rodríguez, O. (2013) El género *Pluteus* (Agaricales, Pluteaceae) en México. *Revista Mexicana de Biodiversidad* 84: 128–151.
- Rodríguez, O., Vargas, O. & Guzmán-Dávalos, L. (1997) New reports of the genus *Pluteus* (Agaricales) from Mexico. *Mycotaxon* 56: 473–480.
- Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.
- Saccardo, P.A. (1887) *Sylloge fungorum omnium hucusque cognitorum*, vol. 5. Patavii, 1146 pp.
- Saccardo, P.A. (1891) *Sylloge fungorum omnium hucusque cognitorum*, vol. 9. Patavii, 1141 pp.
- Saccardo, P.A. (1895) *Sylloge fungorum omnium hucusque cognitorum*, vol. 11. Patavii, 753 pp.
- Schaeffer, J.C. (1774). *Fungorum qui in Bavaria et Palatinatu circa Ratisbonam nascuntur Icones*. Regensburg, 136 pp.
- Schoch, C.L., Seifert, K.A., Huhndorf, S., Robert, V., Spouge, J.L., Levesque, C.A., Chen, W. & Fungal Barcoding Consortium. (2012) Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for Fungi. *Proceedings of the National Academy of Sciences (USA)* 109: 6241–6246.
<http://dx.doi.org/10.1073/pnas.1117018109>.
- Schulz, R. (1912) Studie über Pilze des Riesengebirges I. Teil. *Verhandlungen des Botanischen Vereins der Provinz Brandenburg und die angrenzenden Länder* 54: 102.
- Schumacher, H.C.F. (1803) *Enumeratio Plantarum, in Partibus Saellandiae Septentrionalis et Orientalis Crescentium*. F. Brummer, København, 489 pp.
- Secretan, L. (1833) *Mycographie Suisse, ou Description des Champignons, qui Croissent en Suisse, Particulièrement dans le Canton de Vaud, aux Environs de Lausanne*. P.A. Bonnant, Geneve, 592 pp.
- Singer, R. (1925) Pflanzengeographische Beobachtungen an oberbayerischen und oberpfälzischen Hymenomyceten. 3. Reihe. *Zeitschrift für Pilzkunde* 4: 37–44.
- Singer, R. (1952) The agarics of the Argentine sector of Tierra del Fuego and limitrophous regions of the Magallanes area. *Sydowia* 6: 165–226.
- Singer, R. (1956) Contributions towards a monograph of the genus *Pluteus*. *Transactions of the British Mycological Society* 39: 145–232.
- Singer, R. (1958) Monographs of South American Basidiomycetes, especially those of the East Slope of the Andes and Brazil 1: The Genus *Pluteus* in South America. *Lloydia* 21: 195–299.
- Singer, R. (1961a) Monographs of South American Basidiomycetes, specially those of the east slope of the Andes and Brazil. 4. *Inocybe* in Amazone region with a supplement to part 1 (*Pluteus* in South America). *Sydowia* 15: 112–132.
- Singer, R. (1961b) *Pluteus lilacinus*. *Mycologia* 52: 337–338.
- Singer, R. (1973) Diagnoses fungorum novorum Agaricalium III. *Beihefte zur Sydowia* 7: 1–106.
- Singer, R. (1984) Weiss-und rosasporige Agaricales (Tricholomatales und Pluteaceae) aus Österreich. *Sydowia* 36: 277–287.
- Singer, R. (1986) *The Agaricales in modern taxonomy*, 4th edition. Koeltz Scientific Books, Koenigstein, 981 pp.
- Singer, R. (1989) New taxa and new combinations of Agaricales (Diagnoses fungorum novorum Agaricalium IV). *Fieldiana Botany, new series* 21: 1–133.
- Singer, R. & Clémencez, H. (1972) Notes on some leucosporous and rhodosporous European agarics. *Nova Hedwigia* 23: 305–351.
- Singer, R. & Digilio, A.P.L. (1952) Pródromo de la Flora Agaricina Argentina. *Lilloa* 25: 5–461.
- Smith, A.H. & Bartelli, I. (1965) A previously undescribed species of *Pluteus* from Michigan. *Michigan Botanist* 4: 60–61.
- Smith, A.H. & Stuntz, D.E. (1958) Studies on the genus *Pluteus* I. Redescriptions of American species based on a study of type specimens. *Lloydia* 21: 115–136.
- Stamatakis, A., Hoover, P. & Rougemont, J. (2008) A Rapid Bootstrap Algorithm for the RAxML Web-Servers. *Systematic Biology* 75: 758–771.
- Stevenson, G. (1962) The Agaricales of New Zealand. II. Amanitaceae. *Kew Bulletin* 16: 65–74.
- Swofford, D.L. (2002) PAUP*: phylogenetic analysis using parsimony (and other methods) 4.0 Beta. Sinauer Associates,

Sunderland.

- Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. (2011) MEGA5: Molecular Evolutionary Genetics Analysis using Maximum Likelihood, Evolutionary Distance, and Maximum Parsimony Methods. *Molecular Biology and Evolution* 28: 2731–2739.
<http://dx.doi.org/10.1093/molbev/msr121>
- Thiers, B. (2014) (continuously updated) Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/ih/>
- Velenovský, J. (1939) *Novitates mycologicae*. Praha, 211 pp.
- Vellinga, E.C. (1987) White plutei. *Beiträge zur Kenntnis der Pilze Mitteleuropas* 3: 173–180.
- Vellinga, E.C. (1988) Glossary. In: Bas C., Kuyper, Th.W., Noordeloos, M.E. & Vellinga, E.C. (Eds.) *Flora Agaricina Neerlandica, vol. 1*. A.A. Balkema, Rotterdam, pp. 54–64.
- Vellinga, E.C. (1990) *Pluteus*. In: Bas, C., Kuyper, Th.W., Noordeloos, M.E. & Vellinga, E.C. (Eds.) *Flora Agaricina Neerlandica, vol 2*. A.A. Balkema, Rotterdam, pp. 31–55.
- Vellinga, E.C. & Schreurs, J. (1985) *Notulae ad floram agaricinam Neerlandicum*–8. *Pluteus* Fr. in West Europe. *Persoonia* 12: 337–373.
- White, T.J., Bruns, T., Lee, S.S. & Taylor, J. (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis, M.A., Gelfand, D.H., Sninsky, J.J. & White, T.J. (Eds.) *PCR Protocols: A Guide to Methods and Applications*. Academic Press, New York, pp. 315–322.