

True morels (*Morchella*, Pezizales) of Europe and North America: evolutionary relationships inferred from multilocus data and a unified taxonomy

Franck Richard¹

Jean-Michel Bellanger

UMR 5175 CEFÉ, INSERM, Campus CNRS, 1919
Route de Mende, F-34293 Montpellier, France

Philippe Clowez

56 place des Tilleuls, F-60400 Pont-l'Évêque, France

Karen Hansen

Swedish Museum of Natural History, Department of
Botany, P.O. Box 50007, SE-104 05 Stockholm,
Sweden

Kerry O'Donnell

Bacterial Foodborne Pathogens and Mycology Research
Unit, National Center for Agricultural Utilization
Research, US Department of Agriculture, Agricultural
Research Service, 1815 North University Street, Peoria,
Illinois 61604

Alexander Urban

University of Vienna, Faculty of Life Sciences,
Department of Botany and Biodiversity Research,
Division of Systematic and Evolutionary Botany,
Rennweg 14, A-1030 Wien, Austria

Mathieu Sauve

UMR 5175 CEFÉ, Université de Montpellier, Campus
CNRS, 1919 Route de Mende, F-34293 Montpellier,
France

Régis Courtecuisse

Pierre-Arthur Moreau

Département des Sciences végétales et fongiques, faculté
des sciences pharmaceutiques et biologiques, Univ Lille
Nord de France, F-59000 Lille, France, and EA 4483,
UFR Pharmacie, F-59000 Lille, France

Abstract: Applying early names, with or without original material, to genealogical species is challenging. For morels this task is especially difficult because of high morphological stasis and high plasticity of apothecium color and shape. Here we propose a nomenclatural revision of true morels (*Morchella*, Pezizales) from Europe and North America, based on molecular phylogenetic analyses of portions of the genes for RNA polymerase II largest subunit (*RPB1*) and second largest subunit (*RPB2*), translation elongation factor-1 α (*TEF1*), the nuc rDNA region encompassing the internal transcribed spacers 1 and 2, along with the 5.8S rDNA (ITS), and partial nuc

28S rDNA D1-D2 domains (28S). The 107 newly sequenced collections were from both continents, including 48 types, together with previously published sequences. Names are applied to 30 of the 65 currently recognized genealogical species. Results of the present study revealed that the number of *Morchella* species in Europe ($n = 21$) is nearly identical to that in North America ($n = 22$). Only seven species were found on both continents, consistent with previous reports of high continental endemism within the genus. Presently it is not possible to tell whether the transoceanic disjunctions were due to human activities, migration across a Bering land bridge or long-distance dispersal. In an effort to stabilize the taxonomy, due in part to the recent publication of synonyms for 11 of the species, accepted names are presented together with their corresponding later synonyms. A new subclade that includes holotypes of *M. castanea* and *M. brunneorosea* is identified in sect. *Morchella* (Esculenta Clade). Lectotypes for *Morchella deliciosa*, *M. eximia* and *M. tridentina* are designated here, as well as epitypes for *M. dunalii*, *M. eximia*, *M. purpurascens* and *M. vulgaris*. *Morchella conica* was determined to be illegitimate, and further research is required to determine the identity of *M. elata* and *M. inamoena*.

Key words: Ascomycota, Morchellaceae, nomenclature, Pezizomycetes, taxonomy

INTRODUCTION

True morels (*Morchella*) comprise one of the most intensively collected groups of macrofungi worldwide, but their systematics remains in flux. A series of recent multilocus molecular phylogenetic analyses (Taşkın et al. 2010, 2012; O'Donnell et al. 2011; Du et al. 2012a, b) employing genealogical concordance phylogenetic species recognition (GCPSR, Taylor et al. 2000), showed that morphological species recognition (MSR) within this iconic genus frequently fails to delimit species, due to widespread cryptic speciation. The dearth of phenotypically informative macro- and micromorphological characters within this genus greatly reduces the utility of MSR in the absence of critical molecular phylogenetic data. As a result, MSR-based taxonomic treatments have produced conflicting estimates of species diversity. Some taxonomic treatments have recognized a few, highly variable taxa (e.g. Dennis 1978: three species in Britain; Weber 1995: three species in North America;

Submitted 25 Jun 2014; accepted for publication 10 Nov 2014.

¹Corresponding author. E-mail: franck.richard@cefe.cnrs.fr

Dissing 2000: eight species in the Nordic countries), while others accepted many species, varieties and forms (Krombholz 1834: 11 species; Boudier 1897: 20 species; Jacquetant 1984: 30 species; Clowez 2012: 52 species). The aforementioned GCPSR studies laid the foundation for a taxonomic revision of *Morchella* in North America (Kuo et al. 2012).

The molecular phylogenetic studies revealed that *Morchella* comprises three clades (O'Donnell et al. 2011), including an early diverging basal lineage (section *Rufobrunnea* sensu Clowez 2012) estimated to have evolved in the late Jurassic. This clade is represented by two extant species, *M. rufobrunnea*, which has been grown commercially (Ower et al. 1986), and *M. anatolica* (İşiloğlu et al. 2010, Taşkın et al. 2012). The origin of the later-diverging sister clades, Elata (black morels, section *Distantes* sensu Clowez 2012) and Esculenta (yellow morels, section *Morchella* sensu Clowez 2012) was dated to the early Cretaceous, approximately 125 Mya. These clades comprise at least 27 and 36 phylogenetically distinct species respectively (O'Donnell et al. 2011; Du et al. 2012a, b; Voitek et al. 2014). Because binomials could be applied to only four species with confidence, phylopecies within these two clades were informally named using *Mes* (for Esculenta Clade) or *Mel* (for Elata Clade) codes followed by a unique Arabic number. Although epithets based on European collections are typically used in taxonomic treatments of morels from Asia (Imazeki et al. 1988) and North America (Arora 1986, Weber 1995), the phylogenetic results indicate that these names might be misapplied, given that the majority of morels appear to exhibit high continental endemism and provincialism in the northern hemisphere, consistent with their proposed evolutionary origin in Laurasia (O'Donnell et al. 2011).

Uncertainty over what epithet to accept, especially for North American taxa, was complicated significantly by the recent publication of independent morphological (Clowez 2012) and molecular and morphological systematic treatments of the genus (Kuo et al. 2012). Because the epithets proposed by Clowez (2012) have priority over those applied to conspecifics in Kuo et al. (2012), the primary objective of the present study was to assess what taxa in the latter study represent nomenclatural synonyms of taxa validly published by Clowez (2012). To accomplish this objective, we attempted to obtain phylogenetically informative DNA sequence data from the holotypes and paratypes available for European species, especially those described by Clowez (2012), to determine what names should be accepted for the morels sampled. Finally, the present study sought to provide a comprehensive overview of the distribution and diversity of true morels within Europe and North America.

MATERIALS AND METHODS

Taxon sampling.—Most of the collections analyzed in the present study represent types included in Clowez (2012) that were deposited in LIP. Also, some additional collections of Pierre Collin and Pierre-Arthur Moreau, as well as recent collections deposited by P. Clowez (LIP), together with collections from LUG, O and S (Thiers B [continuously updated]) were included (SUPPLEMENTARY TABLE I). Duplicates of all material from LIP used for DNA analyses are kept in the fungal herbarium of the CEFE-CNRS (1919 route de Mende, F – 34293 Montpellier, France). Collections cited in Clowez (2012) for which DNA sequence data could not be generated are not mentioned below.

Nomenclature and typifications.—To support several early lectotypes (i.e. illustrations or material where DNA sequences could not be obtained), epitypes were selected using the following criteria: i. the collection came from the original continent and biogeographical region as indicated in the protologue; ii. a good photograph and if possible a full description from a freshly collected epitype is available; and iii. DNA sequence data was obtained from at least three loci, including the ITS, which has been recently proposed as a universal DNA barcode marker for Fungi (Schoch et al. 2012). When two names of equal priority (i.e. published simultaneously in a same paper) were treated as synonyms (McNeill et al. 2012, Art. 11.5), the choice was made in favor of the best-documented name (i.e. original material/type in good condition and documented by DNA sequence data from the most loci). The dates of effective publication were 16 Apr 2012 for Clowez (2012) and 29 Aug 2012 for Kuo et al. (2012). Although a preliminary version of the latter was published online on 11 Apr 2012, this does not qualify as effective publication (McNeill et al. 2012, Art. 30.2).

DNA extraction, amplification and sequencing.—DNA extraction and PCR amplification were conducted with the REDEExtract-N-Amp™ Plant PCR Kit (Sigma-Aldrich, St Louis, Missouri), following the manufacturer's instructions. Efforts were made to PCR amplify portions of five genetic loci with the following primer pairs: the nuc rDNA region encompassing the internal transcribed spacer and 5.8S rDNA (ITS) with ITS-1F/ITS-4 (Gardes and Bruns 1993), the partial nuc 28S rDNA D1-D2 domains (28S) with LR0R/LR7 (Vilgalys and Hester 1990), the translation elongation factor 1- α gene (*TEF1*) with EF526F/EF3AR (Rehner and Buckley 2005), the RNA polymerase II largest subunit gene (*RPB1*) with gRPB1A/aRPB1C (Matheny et al. 2002) and the RNA polymerase II second largest subunit gene (*RPB2*) with 9F/3R (Liu et al. 1999). PCR amplifications were performed in a total volume of 20 μ L, including 1 μ L genomic DNA, in a master cycler gradient thermocycler (Eppendorf AG, Hamburg, Germany). The cycling parameters were as follows: 94 C for 3 min, 35 cycles of 94 C for 30 s, 53 C for 30 s, 72 C for 1–2 min, followed by 72 C for 7 min. Amplicons were purified and sequenced at Genoscope, Evry, France, or at Biofidal, Lyon, France. Raw sequence data were edited and assembled with Codon Code Aligner 4.1.1 (CodonCode Corp., Centerville, Massachusetts) and have been deposited in GenBank (SUPPLEMENTARY TABLES I, II).

Phylogenetic analyses.—Because ITS is insufficient to fully resolve all *Morchella* species (Du et al. 2012b), phylogenetic analyses (combining ITS, *RPB1*, *RPB2* and *TEF1* sequence data) were performed when necessary to assign newly sequenced collections to a known or putatively novel phylogenetic species. Analyses were conducted online at www.phylogeny.lirmm.fr (Dereeper et al. 2008). Multiple sequence alignment was carried out with MUSCLE 3.7 (Edgar 2004) using full processing mode and 16 iterations. Alignments were edited with Gblocks 0.91b (Castresana 2000), set to the lowest stringency parameters. The three alignments and trees (FIGS. 1–3 are available from TreeBASE as accession number 16395. Maximum likelihood phylogenetic analyses were performed with PhyML 3.0 aLRT (Zwickl 2006), using the GTR + I + Γ model of evolution. Branch support was assessed using the non-parametric version of the approximate likelihood-ratio test, implemented in PhyML (SH-aLRT; Anisimova and Gascuel 2006). SH-aLRT yields values comparable with those computed by standard bootstrapping or the RAxML rapid bootstrapping method (Anisimova and Gascuel 2011). Only branch support above 70% is indicated (FIGS. 1–3) because this threshold has been considered as statistically significant in previous *Morchella* phylogenies (O'Donnell et al. 2011; Du et al. 2012a, b; Taskin et al. 2012). Trees were annotated using TreeDyn 198.3 (Chevenet et al. 2006; FIGS. 1–3).

TAXONOMY

The species treated hereafter are illustrated by: i. a selection of 19 pictures depicting the material studied (FIG. 4a–o and SUPPLEMENTARY FIG. 1a–d), and ii. a diagram depicting the geographic distribution of each species (FIG. 5). Species are presented in alphabetic order within the following three sections/clades: *Morchella*/Esculenta Clade, *Distantes*/Elata Clade and *Rufobrunnea*/Rufobrunnea Clade following Clowez (2012) and O'Donnell et al. (2011). Taxonomic synonyms accepted on the basis of type studies are cited for each species (TABLE I).

Morchella Dill. ex Pers.:Fr. in Persoon, Neues Mag Bot (Römer) 1:116 (1794).

Lectotype (Korf, 1972: 973): *Phallus esculentus* L.:Fr. (syn. *Morchella esculenta*).

= *Boletus* Tourn. ex Adans., Fam Pl 2:9. 1763 (nom. illegit., non *Boletus* L.:Fr.).

= *Phalloboletus* P. Micheli ex Adans., Fam Pl. 2:9. 1763.

= *Eromitra* Lév. in Orbigny, Dict Univ Hist Nat 8:490. 1846.

= *Mitrophora* Lév., Annls Sci Nat, Bot, sér. 3 5:249. 1846.

= *Morchella* sect. *Mitrophora* («*Mitrophorae*») (Lév.) S. Imai, Bot Mag, Tokyo 46:174. 1932.

= *Morilla* Quél., Enchir Fung. (Paris): 270. 1886.

Section *Morchella*

= Section *Adnatae* Boud., Bull Soc Mycol France 13:132. 1897.

Notes. This section (FIG. 1) corresponds to the Esculenta Clade (O'Donnell et al. 2011).

Morchella americana Clowez & C. Matherly in Clowez, Bull Soc Mycol France 126:243. 2012. FIG. 4g

= *Morchella americana* var. *elongata* Clowez, Bull Soc Mycol France 126:246. 2012.

= *Morchella californica* Clowez & D. Viess in Clowez, Bull Soc Mycol France 126: 246. 2012.

= *Morchella claviformis* Clowez, Bull Soc Mycol France 126:275. 2012.

= *Morchella populina* Clowez & R. Lebeuf in Clowez, Bull Soc Mycol France 126:246. 2012.

= *Morchella esculentoides* M. Kuo et al. in Kuo et al., Mycologia 104:1163. 2012.

Specimens examined. FRANCE. CÔTE-D'OR: Is-sur-Tille, under *Buxus sempervirens*, 1994, R. Rousseaux, PhC59 (as “*M. umbrina*”, LIP 0900096). HAUT-RHIN: Kuhneim, canal d'Alsace, under *Populus canadensis*, 15 Apr 2013, J.-C. Müller, PhC227 (CEFE-CNRS, Montpellier); Khembs, under *Populus canadensis*, 9 May 2013, J. Grandhay, PhC235 (CEFE-CNRS, Montpellier). USA. CALIFORNIA: Chico, Bidwell park, under *Fraxinus depilata*, 21 Mar 2010, D. Viess, PhC73 (holotype of *Morchella californica*, LIP 0900107); Yuba City, Wheatland, 2012, H. and S. Smith, PhC162 (LIP 0900025). MICHIGAN: locality not specified, under *Fraxinus americana*, 2009, H. and S. Smith, PhC51 (holotype of *Morchella americana*, LIP 0900091). Locality unknown, under *Acer* sp., C. Matherly, PhC133 (holotype of *Morchella claviformis*, LIP 0900161). CANADA. QUÉBEC: under *Ulmus americana*, 2010, R. Lebeuf, PhC65 (holotype of *Morchella americana* var. *elongata*, LIP 0900102); Laval, under *Populus deltoides*, 19 May 2011, R. Lebeuf 0672, PhC125 (LIP 0900153); *ibid.*, R. Lebeuf, PhC128 (LIP 0900156); Pierrefonds, under *Zanthoxylum americanum*, 19 May 2011, R. Lebeuf 0671, PhC126 (LIP 0900154).

Notes. This is *Mes-4* (O'Donnell et al. 2011; Du et al. 2012a, b). Four of the species from North America with yellow, elongate ascocaps (FIG. 4g) described by Clowez (2012) are considered here as conspecific; they are *M. americana* and *M. californica* collected under *Fraxinus*, *M. claviformis* under *Acer*, and *M. populina* under *Populus* (FIG. 1). Clowez (2012) proposed the old European name *M. rigida* (Krombh.) Boudier for European collections PhC227 and PhC235 that we found were conspecific with *M. americana*. The name *M. rigida* is not retained here because no original material exists and its application is still uncertain. Also this name has only rarely been used in taxonomic treatments of morels in Europe. Among the simultaneously published names by Clowez (2012), *M. americana* is retained against *M. californica* and *M. claviformis* because it seems most appropriate for the most common yellow morel in North America. *Morchella americana* (*Mes-4*) is found in central Europe where it has been identified as *M. esculenta* by several authors (e.g. Kellner et al. 2005; see notes

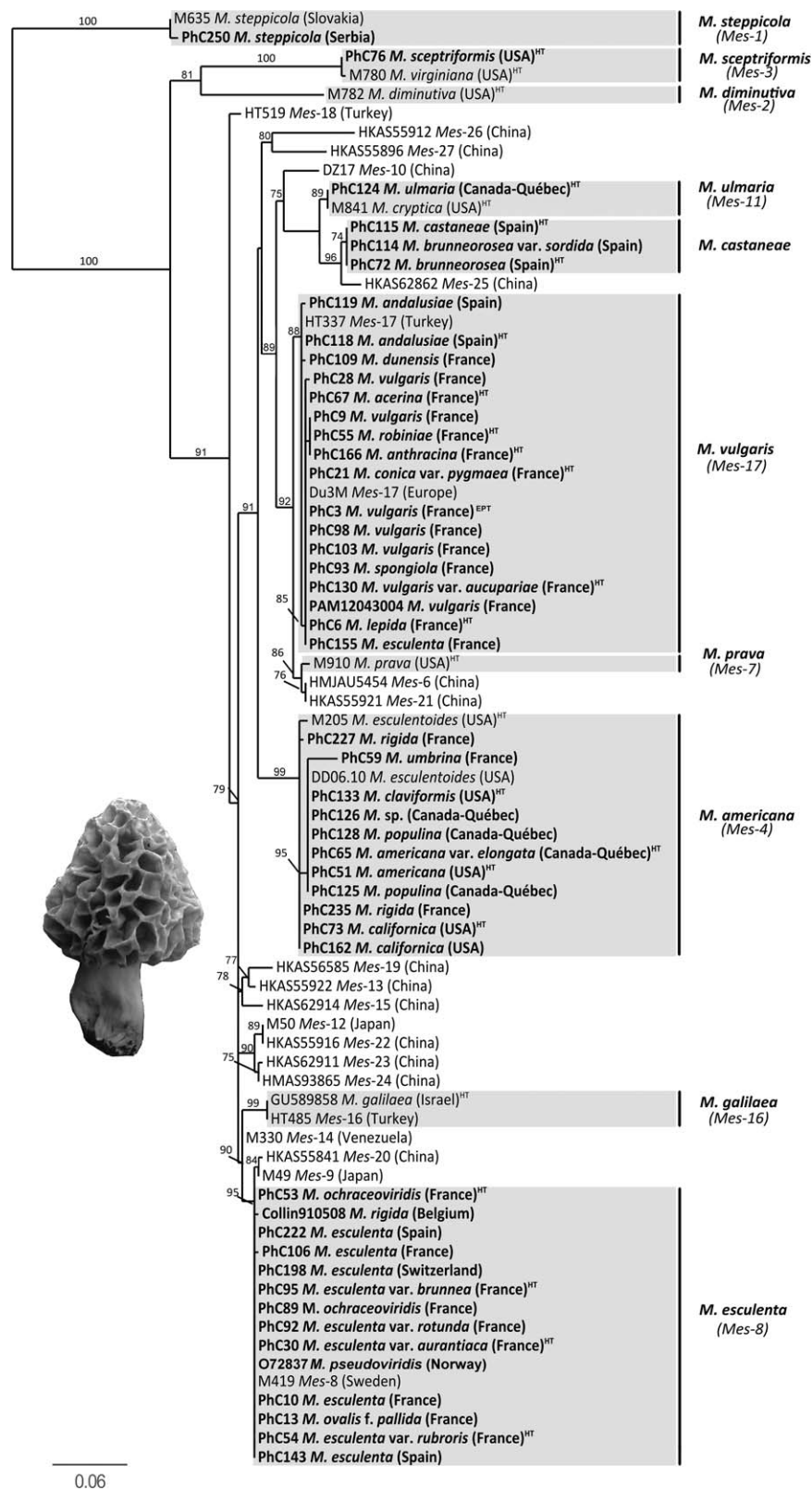


FIG. 1. Maximum likelihood (ML) phylogeny of *Morchella* sect. *Morchella* (Esculenta Clade) inferred from 77 ITS sequences, rooted on sequences of the earliest diverging lineage within this clade, *M. steppicola*. The ML analysis was run in PhyML 3.0aLRT using the GTR+I+Γ model of molecular evolution. Numbers by nodes represent branch support above 70%, as assessed by the SH-aLRT statistical test (MATERIALS AND METHODS). Gray highlight is used to identify the 10 species found in

under this name). This interpretation is not accepted here, because *M. americana* appears to be native to North America and absent from Scandinavia and Italy, the two areas within which the original observations of *M. esculenta* were made (Micheli 1729, Fries 1822). We suggest that *M. americana* was only recently introduced to Europe. This hypothesis is supported by the observation that most European collections of this species are from sites with discernible anthropogenic impact, especially hybrid poplar plantations (*PhC227*, *PhC235*, and unpublished data from Spain).

Morchella castaneae L. Romero & Clowez in Clowez, Bull Soc Mycol France 126:251. 2012. FIG. 4e

= *Morchella brunneorosea* Clowez & Ant. Rodr. in Clowez, Bull Soc Mycol France 126(3-4):250. 2012.

= *Morchella brunneorosea* var. *sordida* Becerra Parra & Clowez in Clowez, Bull Soc Mycol France 126(3-4):251. 2012.

Specimens examined. SPAIN. ANDALUSIA: Aracena, under *Castanea sativa*, 6 Apr 2011, L. Romero de la Osa, *PhC114* (holotype of *Morchella castaneae*, LIP 0900143); *ibid.*, under *Fraxinus angustifolia* and *Populus nigra*, 2011, L. Romero de la Osa, *PhC115* (LIP 0900144). BURGOS: under *Fraxinus angustifolia*, 2010, A. Rodríguez, *PhC72* (holotype of *Morchella brunneorosea*, LIP 0900106). MÁLAGA: Ronda, riparian forest under *Fraxinus angustifolia* and *Populus nigra*, 7 Apr 2009, M. Becerra Parra, *PhC88* (holotype of *Morchella brunneorosea* var. *sordida*, LIP 0900007).

Notes. This recently discovered species is currently only known from Spain (FIG. 1) and it was not included in previous molecular phylogenetic analyses. The name *M. castaneae* is retained here over *M. brunneorosea*, which was described simultaneously (Clowez 2012). Synonymy of *M. brunneorosea* var. *sordida* (*PhC88*) with *M. castaneae* was established by molecular phylogenetic analyses of *RPB2* and *TEF1*, since ITS sequence could not be obtained for *PhC88* (results not shown, see SUPPLEMENTARY TABLE I).

Morchella esculenta (L.:Fr.) Pers., Tent Disp Meth Fung:36. 1797. FIG. 4d

Basionym: *Phallus esculentus* L.:Fr. in Linné, Sp Pl:1128. 1753.

Typification: Micheli, Gen Pl: pl 85, FIG 2. 1729 (lectotype, designated by Clowez 2012). FRANCE. OISE: Béhéricourt, under *Fraxinus excelsior*, 2009, P. Clowez *PhC10* (**epitype** designated here, LIP 0900051,

MycoBank MBT 177737, cited by Clowez 2012 as “*Morchella esculenta*”). Isoepitypes S (F254891), CEFE-CNRS.

= *Morchella esculenta* var. *aurantiaca* Clowez, Bull Soc Mycol France 126:230. 2012.

= *Morchella esculenta* var. *rubroris* Clowez & L. Martin in Clowez, Bull Soc Mycol France 126:236. 2012.

= *Morchella ochraceoviridis* Clowez, Bull Soc Mycol France 126:239. 2012.

= *Morchella ovalis* var. *minor* Clowez & L. Martin in Clowez, Bull Soc Mycol France 126:242. 2012.

[= *Morchella pseudoumbrina* Jacquet., Les Morilles:103. 1984 (nom. inval., Art. 40.1); in Jacquetant & Bon, Doc Mycol 56:1. 1985(1984')] (nom. inval., Art. 33.1, 41.5)

[= *Morchella pseudoviridis* Jacquet., Les Morilles:103. 1984 (nom. inval., Art. 40.1); in Jacquetant & Bon, Doc Mycol 56:1. 1985('1984')] (nom. inval., Art. 33.1, 41.5)

Specimens examined. BELGIUM. Locality unknown, 8 May 1991, P. Collin, 910508 (LIP). FRANCE. ISÈRE: Saint-Sébastien, under *Fraxinus excelsior* subsp. *oxycarpa*, Apr 2010, L. Martin, *PhC54* (holotype of *M. esculenta* var. *rubroris*, LIP 0900092). NORMANDY: under *Malus sylvestris*, Apr 2011, P. Moinet, *PhC92* (LIP 0900120). OISE: Fleurines, under *Fraxinus excelsior* and *Aesculus hippocastanum*, Apr 2010, F. Petit, *PhC30* (holotype of *M. esculenta* var. *aurantiaca*, LIP 0900069); *ibid.*, under *Ulmus minor*, Mar 2011, F. Petit, *PhC89* (LIP 0900117); *ibid.*, under *Fraxinus excelsior*, Apr 2011, F. Petit, *PhC106* (LIP 0900135); Saint-Maximin, under *Fraxinus excelsior* on wet ground, Apr 2011, F. Petit, *PhC95* (LIP 0900122); *ibid.*, under *Ulmus minor*, Mar 2010, R. Chartier, *PhC53* (holotype of *M. ochraceoviridis*, LIP 0900010). VAR : Siou Blanc, under *Quercus ilex*, 2010, L. Martin, *PhC13* (LIP 0900054). NORWAY. ØSTFOLD: Fredrikstad, Kråkerøy, under *Ulmus* sp., 21 May 1981, R. Kristiansen, Jacquetant 150476 (as “holotype of *M. pseudoviridis*”, O 72837). SPAIN. ARAGÓN: Huesca, Arguis, under *Populus* sp., 2009, L. Ballester, *PhC143* (LIP 0900171); Belsué, under *Populus canadensis*, 19 Apr 2013, P. Clowez, *PhC222* (CEFE-CNRS, Montpellier). SWITZERLAND. GENEVA: Malval, along the Allondon river, 6 May 2004, O. Rölli, *PhC198* (CEFE-CNRS, Montpellier).

Notes. *Morchella esculenta* is the type species of *Morchella* and one of the most commonly used names. We adopt here the name for *Mes-8* (O'Donnell et al. 2011; Du et al. 2012a, b) following Clowez (2012), and based on this being one of the most common and widely distributed yellow morels in Europe (FIG. 1, 4d). It was reported as *Mes-8* from France, Sweden, Germany, Turkey, Czech Republic and China (O'Donnell et al. 2011; Du et al. 2012a, b;

←

Europe and/or North America, which are reported in the righthand column together with the *Mes* (Esculenta Clade) number (O'Donnell et al. 2011). Isolates in bold were sequenced in the present study, and all but two of these were included in Clowez (2012, *PhC* = Philippe Clowez) under the binomial as listed in the gray highlight. Sequences of 25 holotypes (HT) and 3 epitypes (EPT) were included in the analysis.

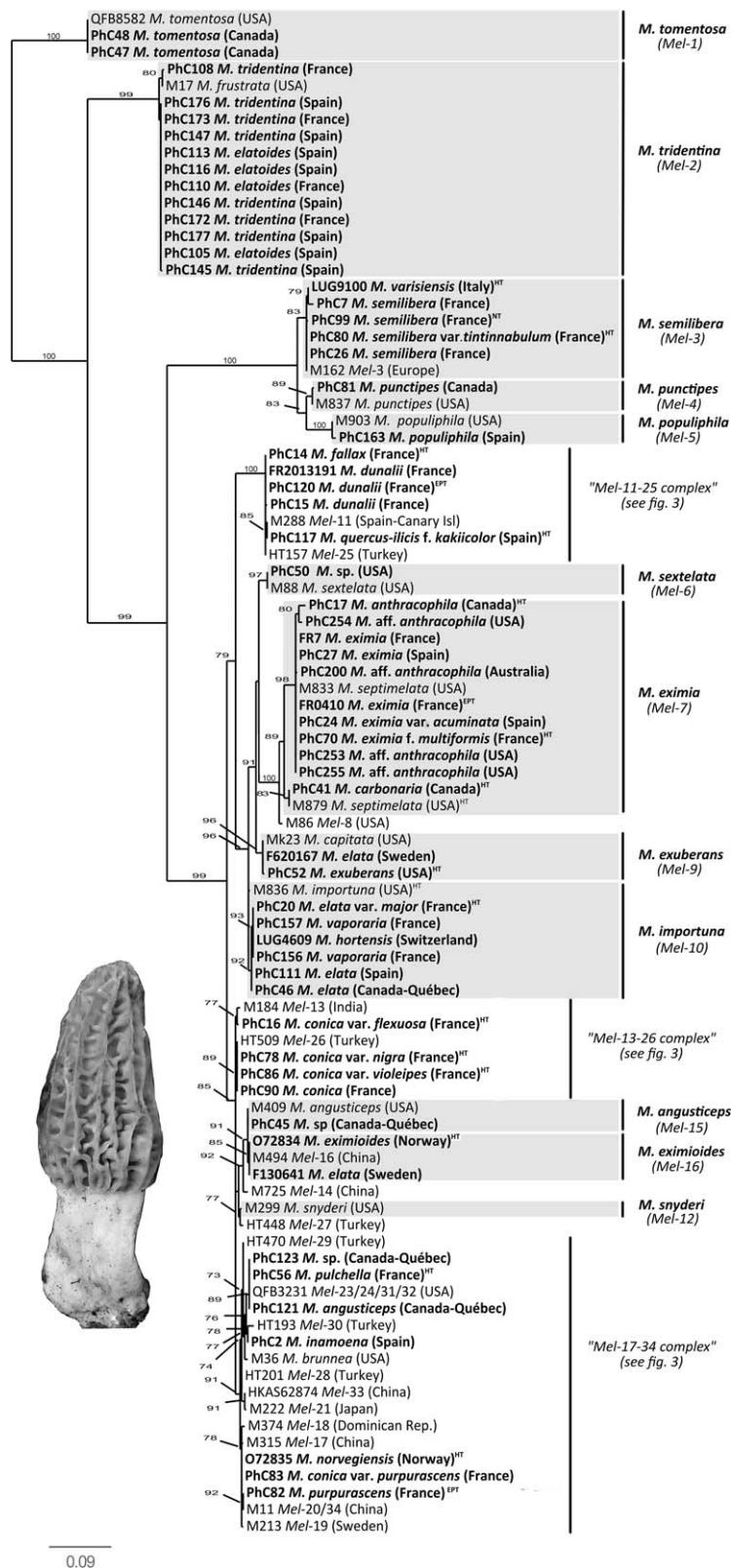


FIG. 2. ML phylogeny of *Morchella* sect. *Distantes* (Elata Clade) inferred from 91 ITS sequences, including 22 types (HT = holotype, NT = neotype, EPT = epitype). The phylogram was rooted on sequences of *M. tomentosa*, the basal most member of the Elata Clade, based on more inclusive analyses (Stefani et al. 2010; O'Donnell et al. 2011; Du et al. 2012a, b). Species present in Europe and/or North America are indicated by gray highlight, and the 60 collections sequenced in the present

Taşkın et al. 2012), as well as Norway, Spain and Switzerland (this study). Our ITS sequence analysis of *M. ovalis* var. *minor* and *M. ochraceoviridis* indicates these species are conspecific with *M. esculenta*. These taxa were previously recognized based on divergent colors and putative host specific associations with *Quercus* sp. and *Ulmus* sp. respectively (Clowez 2012). In addition, an ITS sequence of a collection identified by P. Clowez (*PhC92*) as “*M. esculenta* var. *rotunda*”, a taxon often recognized as an independent species in European literature, was found to be identical to other *Mes*-8 ITS sequences. Also, ITS sequences of *M. pseudoumbrina* and *M. pseudoviridis*, two species (invalidly published) placed in sect. *Pseudoadnatae* by Jacquetant (1984) because of a conspicuous sulcus, and collected in Norway by R. Kristiansen (original material of *M. pseudoviridis* deposited at O, and additional material in Kristiansen’s personal herbarium, cited by Kristiansen 1982:72 as “*Morchella* sp.” 10 and 11), revealed these were identical to *M. esculenta* (*Mes*-8). Large specimens of *M. esculenta* with a thick stipe are often reported as *M. crassipes*, a solid tradition in North American (McKnight and McKnight 1987, Volk and Leonard 1989) and central European (Buscot et al. 1996, Wipf et al. 1999, Kellner et al. 2005, Degreef et al. 2009; authors of the former two studies applied the name *M. esculenta* to another taxon, see notes under *M. americana*) literature. Although collections under *Quercus* sp. in Spain were morphologically distinct from typical *M. esculenta*, in that they possessed a long, slender stipe and ovoid pileus, they were nested phylogenetically within *M. esculenta* (FIG. 1).

Morchella galilaea Masaphy & Clowez in Clowez, Bull Soc Mycol France 126 (3-4): 238. 2012.

Notes. Based on an ITS sequence provided by S. Masaphy from the holotype (MS1-52, Applied Microbiology and Mycology Department, MIGAL, Kiryat Shmona and Tel Hai Academic College, Upper Galilee, Israel) and available in GenBank as “*Morchella crassipes*” (No. GU589858, cited in the protolog; Clowez 2012), *M. galilaea* was determined to correspond to *Mes*-16 (FIG. 1). It is a well characterized species, illustrated from a greenhouse in Turkey by Taşkın et al. (2012:448, FIG. 2C). The cosmopolitan distribution of *M. galilaea*, for example Hawaii (GenBank Nos. M308-M310), India (AJ539479, GQ228462 etc.), New Zealand (JF423317), Java

(M685), China (HKAS55839) and Africa (EU701000) (O’Donnell et al. 2011, Du et al. 2012b) is likely due to anthropogenic activities.

Morchella sceptriformis Clowez & C. Matherly in Clowez, Bull Soc Mycol France 126:289. 2012. FIG. 4m
= *Morchella virginiana* O’Donnell & S.A. Rehner in Kuo et al., Mycologia 104(5):1161. 2012.

Specimens examined. USA. NEW JERSEY: locality unknown, under *Liriodendron virginiana*, 2011, C. Michaud, *PhC76* (holotype of *Morchella sceptriformis*, LIP 0900110).

Notes. This eastern North American endemic is conspecific with *Morchella virginiana* and corresponds to *Mes*-3. It was collected under *Liriodendron tulipifera* in Clowez (2012) and Kuo et al. (2012).

Morchella steppicola Zerova, J Bot Acad Sci Ukraine, 2(1):155. 1941.

Specimens examined. SERBIA. Beogradi, Titelski, in grasslands, 17 Apr 2012, S. Radić, *PhC250* (LIP).

Notes. This morphologically distinct species corresponds to *Mes*-1 (FIG. 1) and represents the earliest diverging lineage within the *Esculenta* Clade (O’Donnell et al. 2011). It is known from steppic meadows of eastern Europe where it may represent a relict lineage of morels adapted to dry continental meadows.

Morchella ulmaria Clowez, Bull Soc Mycol France 126:254 (2012). FIG. 4c
= *Morchella cryptica* M. Kuo & J.D. Moore in Kuo et al., Mycologia 104(5):1166. 2012.

Specimens examined. CANADA. QUÉBEC: under *Ulmus americana*, 2011, R. Lebeuf, *PhC124*, LIP 0900152, holotype of *Morchella ulmaria*.

Notes. *Morchella cryptica* is shown to be a later synonym of *M. ulmaria* (FIG. 4c) and corresponds to *Mes*-11 (O’Donnell et al. 2011, Kuo et al. 2012). It is an eastern North American endemic that forms a monophyletic group with the European (Spanish) *M. castanea* and the Asian *Mes*-10 and *Mes*-25 (FIG. 1). The holotype was collected under a dying elm tree, but other collections were made under *Fraxinus americana*, *Liriodendron tulipifera* (tulip poplar) and *Acer* sp. (Kuo et al. 2012).

Morchella vulgaris (Pers.:Fr.) Gray, Arrangem Brit Pl 1:662. 1821. FIG. 4a

Basionym: *Morchella esculenta* β *vulgaris* Pers., Syn Meth Fung:619. 1801.

←

study are listed in boldface. Fifty-one of these collections were included in Clowez (2012, *PhC* voucher numbers). Accepted names are listed in the righthand column together with the informal *Mel* (Elata Clade) number (O’Donnell et al. 2011). Numbers by nodes represent branch support above 70%, as assessed by the SH-aLRT statistical test (MATERIALS AND METHODS).

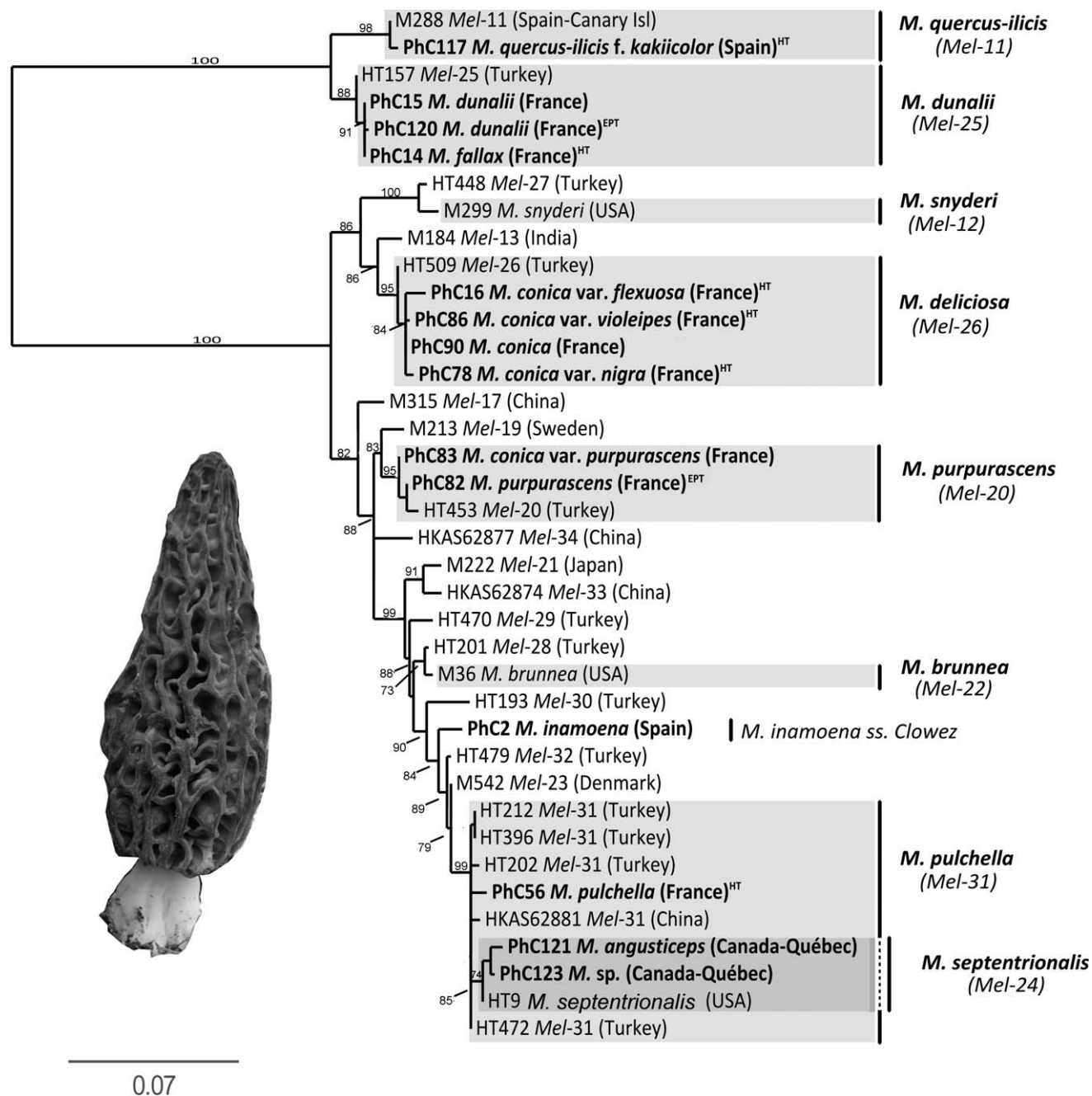


FIG. 3. ML phylogeny of terminal taxa (Elata subclade sensu O'Donnell et al. 2011) within *Morchella* sect. *Distantes* (Elata Clade) inferred from combined analysis of ITS, *RPB1*, *RPB2* and *TEF1* sequences from 38 collections. Sequences of *M. quercus-ilicis* f. *kakiicolor* and *M. dunalii* were used to root the phylogeny. Species that are known to be present in Europe and/or North America are identified by gray highlight. Darker gray highlight is used to point out that *M. septentrionalis* appears to be nested within *M. pulchella*, and to emphasize that further work is needed to assess whether they are phylogenetically distinct. The 14 collections in bold font were reported in Clowez (2012), and include nine types (HT = holotype, EPT = epitype). Accepted names are listed in the righthand column together with the informal *Mel* (Elata Clade) numbers (Du et al. 2012a, b). Numbers by nodes represent branch support above 70%, as assessed by the SH-aLRT statistical test (MATERIALS AND METHODS).

Typification: Sowerby 1797, Col fig Engl Fung 1, pl. 51, right fig. (lectotype, designated by Clowez, 2012). FRANCE. OISE: Béhéricourt, under *Fraxinus excelsior* with *Ranunculus ficaria*, 18 Apr 2010, P.

Clowez PhC3 (epitype designated here, LIP 0900044, MycoBank MBT 177738, cited by Clowez 2012 as “*Morchella vulgaris*”). Isoepitypes S (F254892), CEFÉ-CNRS.

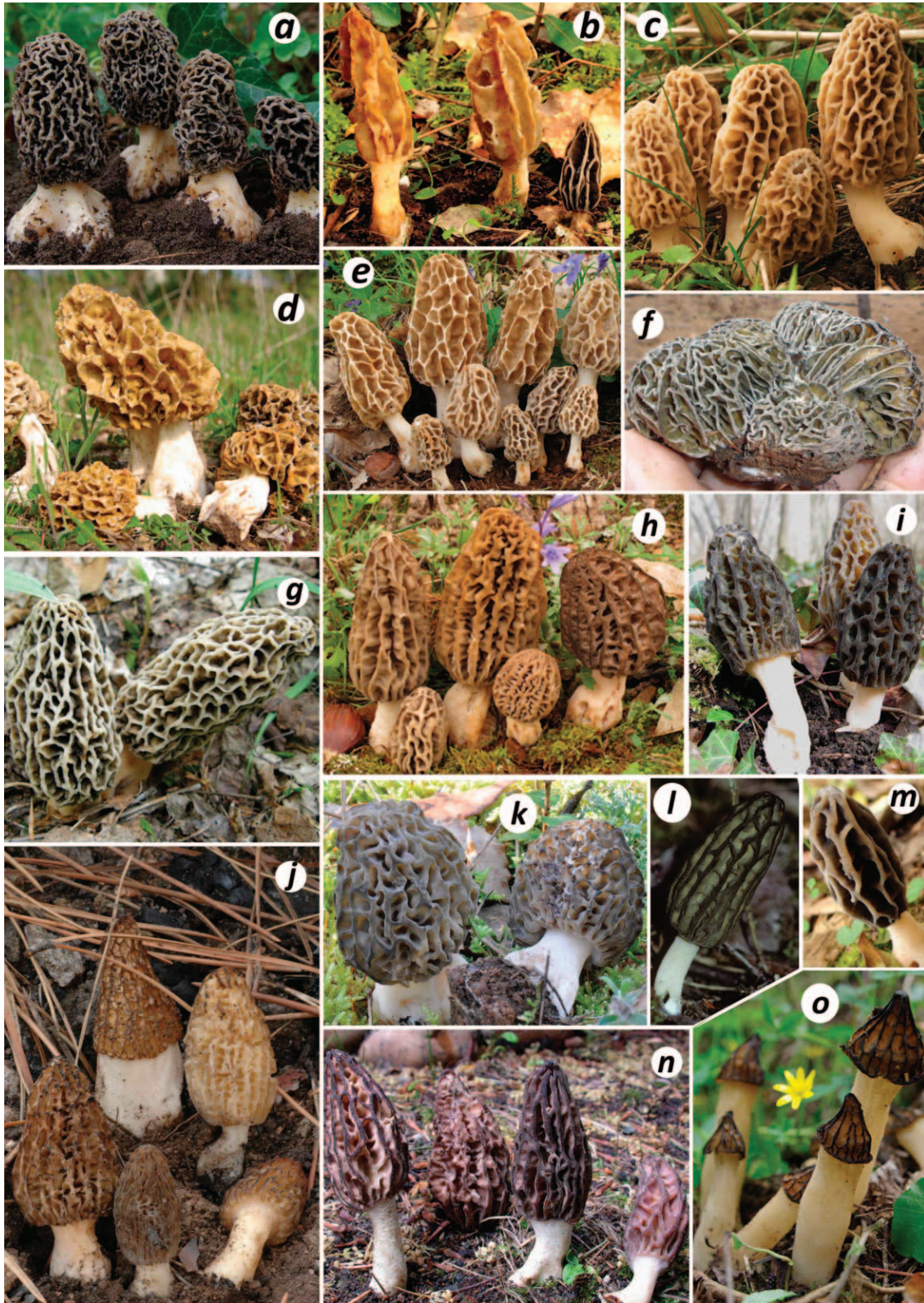


FIG. 4. *Morchella* species. a. *M. vulgaris* (epitype). b. *M. anatolica* (PhC233). c. *M. ulmaria* (holotype). d. *M. esculenta* (epitype). e. *M. castaneae* (holotype). f. *M. exuberans* (holotype). g. *M. americana* (holotype). h. *M. quercus-ilicis* f. *kakiicolor* (holotype). i. *M. deliciosa* (PhC90). j. *M. eximia* (epitype). k. *M. dunalii* (epitype). l. *M. pulchella* (holotype). m. *M. sceptriformis* (holotype). n. *M. purpurascens* (epitype). o. *M. semilibera* (neotype).

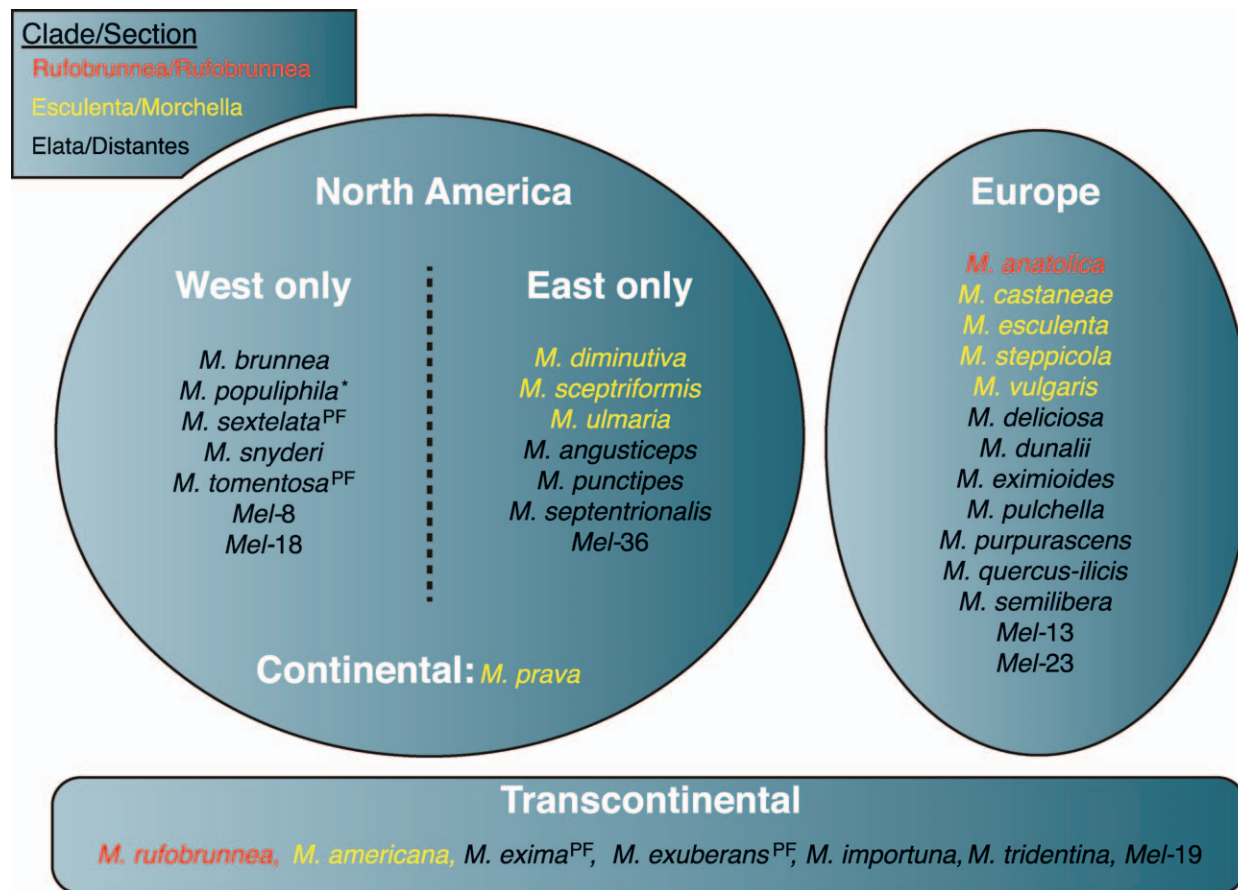


FIG. 5. Geographic distribution of *Morchella* species in Europe and North America. Font shades (print image) or colors (online image) identify clade/section. PF, post fire species. * = one report from Spain, probably introduced.

= *Morchella acerina* Clowez & C. Boulanger in Clowez, Bull Soc Mycol France 126:274. 2012.

= *Morchella andalusiae* Clowez & L. Romero in Clowez, Bull Soc Mycol France 126:255. 2012.

= *Morchella anthracina* Clowez et Vanhille in Clowez, Bull. Soc. Mycol. France 126:258. 2012.

= *Morchella conica* var. *pygmaea* Clowez & Delaunoy in Clowez, Bull Soc Mycol France 126:310. 2012.

= *Morchella lepida* Clowez & Petit in Clowez, Bull Soc Mycol France 126:259. 2012.

= *Morchella robiniae* Clowez, Bull Soc Mycol France 126:287. 2012.

= *Morchella vulgaris* var. *aucupariae* Clowez & Moingeon in Clowez, Bull Soc Mycol France 126:270. 2012.

Specimens examined. FRANCE. CHARENTES-MARITIMES: Royan, white dune with *Ammophila arenaria*, 2011, L. Martin, PhC109 (LIP 0900138). OISE: Caisnes, under *Fraxinus excelsior* with *Hedera helix*, Apr 2011, P. Clowez, PhC98 (LIP 0900125); Chiry-Ourscamp, under *Robinia pseudoacacia*, 2010, G. Deguise, PhC55 (holotype of *Morchella robiniae*, LIP 0900093); Fleurines, under *Crataegus oxyacantha*, 20 Apr 2009, F. Petit, PhC6 (holotype of *Morchella lepida*, LIP 0900047); *ibid.*, under *Sorbus aucuparia*, Apr 2011, F. Petit, PhC130 (LIP 0900158); Nampcel, under *Fraxinus excelsior*, Apr 2012, P. Clowez,

PhC155 (LIP 0900180); Suzoy, under *Fraxinus excelsior*, Apr 2009, P. Clowez, PhC9 (LIP 0900050); *ibid.*, under *Fraxinus excelsior* with *Ranunculus ficaria*, Apr 2010, P. Clowez, PhC28 (LIP 0900067); *ibid.*, under *Ulmus laevis* and *U. minor*, Apr 2011, P. Clowez, PhC93 (LIP 0900121); *ibid.*, under *Fraxinus excelsior* and *Hedera helix*, Mar 2011, P. Clowez, PhC103 (LIP 0900132); Neuilly-en-Thelle, under *Ribes nigrum*, Apr 2010, F. Vanhille, PhC166 (holotype of *Morchella anthracina*, LIP 0900181). PAS-DE-CALAIS: Marck, les Hemmes, under a young *Abies concolor* in a garden on sand dune, 30 Apr 2012, P.-A. Moreau, PAM12043004 (LIP); Wissant, Mont-de-Couple, under *Acer pseudoplatanus*, Apr 2009, C. Boulanger & D. Huart, PhC67 (holotype of *Morchella acerina*, LIP 0900013). ÎLE-DE-FRANCE: locality not specified, under *Fraxinus excelsior*, Apr 2010, M.-A. Delaunoy, PhC21 (holotype of *Morchella conica* var. *pygmaea*, LIP 0900061). SPAIN. ANDALUCÍA: Aracena, under *Fraxinus angustifolia*, 2011, L. Romero de la Osa, PhC118 (holotype of *Morchella andalusiae*, LIP 0900147); *ibid.*, under *Castanea sativa* and *Populus nigra*, 2011, L. Romero de la Osa, PhC119 (LIP 0900148).

Notes. This widespread polymorphic European endemic (FIGS. 1, 4a) was reported as *Morchella spongiosa* Boud. (Boudier 1897) in previous molecular

systematic (Buscot et al. 1996; Wipf et al. 1997, 1999; Kellner et al. 2005) and morphological studies (Clowez 2012); it corresponds to *Mes*-17 (O'Donnell et al. 2011). However, Clowez (2012) also used the name *M. vulgaris* for collections that are nested within *Mes*-17 and this name has priority over *M. spongiola*. Furthermore results of our phylogenetic analysis (FIG. 1) indicated that the following species described and/or accepted by Clowez (2012) based on putative host tree and ascomata morphology, represent taxonomic synonyms of *M. vulgaris*: *M. dunensis* (Castañera & G. Moreno) Clowez in sand dunes, *M. acerina* with *Acer pseudoplatanus*, *M. andalusiae* with *Fraxinus angustifolia*, *M. anthracina* with *Ribes nigrum*, *M. lepida* with *Crataegus* spp., *M. robiniae* with *Robinia pseudoacacia* and *M. spongiola* with *Ulmus* spp. We accept *M. vulgaris* here as lectotypified by Clowez (2012), and designate a recent collection as epitype with a color photograph and ITS, LSU, *RPB2* and *TEF1* sequences, to stabilize the name.

Section *Distantes* Boud., Bull Soc Mycol France 13:133. 1897.

= *Morchella* sect. *Mitrophora* “*Mitrophorae*” (Lév.) S. Imai, Bot Mag (Tokyo) 46:174. 1932.

Notes. This section (FIGS. 2–3) based on *Morchella distans* Fr. (Boudier 1897:143) corresponds to the Elata Clade (O'Donnell et al. 2011).

Morchella angusticeps Peck, Ann Rept N Y St Mus, 32:44. 1879.

Specimens examined. CANADA. QUÉBEC: Québec, under *Populus grandidentata*, 2010, R. Lebeuf, PhC45 (LIP 0900084).

Notes. *Morchella angusticeps* corresponds to *Mel*-15 (O'Donnell et al. 2011). It appears to be endemic to eastern North America (FIG. 2), frequently producing ascomata near *Populus* spp. or *Liriodendron tulipifera*. Kuo et al. (2012) epitypified this species. According to our molecular data, the collection PhC121, published as *M. angusticeps* by Clowez (2012), is *M. septentrionalis* (FIG. 3). Collection PhC45, reported here as *M. angusticeps*, was not published previously.

Morchella deliciosa Fr.:Fr. in Fries, Syst Mycol (Lundae) 2:8. 1822. FIG. 4i

= *Morilla deliciosa* (Fr.:Fr.) Quél., Compt-Rend Assoc Franç Avancem Sci 20:465. 1892.

Lectotype designated here: color plate by Weinmann (1739, pl. 523 fig. h, as “*Fungus cavernosus*, Mousseron”), showing one specimen, cited mistakenly

by Fries (1822:8) as “pl. 533, f. 1”. MycoBank MBT 177739.

= *Morchella conica* var. *flexuosa* Clowez & Luc Martin in Clowez, Bull Soc Mycol France 126:306. 2012.

= *Morchella conica* var. *nigra* Clowez & Moyne in Clowez, Bull Soc Mycol France 126:307. 2012.

= *Morchella conica* var. *violeipes* Clowez & Mourgues in Clowez, Bull Soc Mycol France 126:311. 2012.

Specimens examined. FRANCE. DRÔME. Lus-la-Croix-Haute, under *Picea abies* close to *Buxus sempervirens*, 2007, L. Martin, PhC16 (holotype of *Morchella conica* var. *flexuosa*, LIP 0900057). DOUBS: Bonnevaux, under old spruce (*Picea abies*), 2011, G. Moyne, PhC78 (holotype of *Morchella conica* var. *nigra*, LIP 0900111). HAUTES-ALPES: Saint-André-d'Embrun, col de la Coche, under *Larix decidua*, 2007, Y. Mourgues, PhC86 (holotype of *Morchella conica* var. *violeipes*, LIP 0900019). OISE: Uilly-Saint-Georges, under *Fraxinus excelsior*, 20 Mar 2011, P. Clowez, PhC90 (LIP 0900118).

Notes. *Morchella deliciosa* (FIG. 3; applied to *Mel*-26) is a name frequently used in European literature (Marchand 1971:192, pl. 87, as “*M. conica* var. *deliciosa*”; Jacquetant 1984: 60; Dissing 2000), although not retained by Clowez (2012), who listed the material studied here under “*Morchella conica*” and varieties (see *M. conica* under *Doubtful names* below). All of the collections we analyzed are morphologically similar: small, dark ascomata with an acute apex, frequently with bluish or purplish shades at first, colors fading little with age (FIG. 4i). As pointed out by Marchand (1971:192), a curved pileus apex was observed in most of the collections studied.

All European authors recognizing the name *M. deliciosa* have a similar concept of this taxon, that is a small, dark and early fruiting morel with longitudinal crests (e.g. Breitenbach and Kränzlin 1984:45; Marchand 1971:192; Jacquetant 1984:60; Medardi 2006:138). When Fries (1822:8) described *M. deliciosa*, he referred to the plate by Weinmann (1739) and fresh specimens collected in grassy hardwoods in Sweden. A half-tone plate by Mentzel (1682:pl. 6, as “*Fungus porosus pyramidalis et in metam fastigiatus quadruplex*, March, Br.”), illustrating five specimens, is cited by Fries (1822:6) under “*M. esculenta*”, but a part is also cited under *M. deliciosa* (Fries 1822:8; “*etiam accedit Mentzel. var. 2*”, referring to Mentzel's description “*apice pyramidali & angusto*”; Mentzel 1682:126).

Fries' description applies to a small fungus (“1–2 ½ inches”, i.e. 2.5–6.4 cm) with deep linear, oblong pits. Weinmann's (1739:pl. 523) water coloring is not very informative but compatible in showing a single, slender dark gray ascomata with conspicuous irregular longitudinal crests. No color is mentioned by Fries. Our observations suggest that the ascomata is originally pale gray with pinkish tones, usually turning dark ash-gray when ageing, with possible olivaceous

TABLE I. Correspondence between species designations in Du et al. (2012a, b), Clowez (2012), Kuo et al. (2012) and the present study

Clade/section	Du et al. (2012a, b)	Clowez (2012)	Kuo et al. (2012)	Richard et al. (this study)
Rufobrunnea/ Rufobrunnea Elata/Distantes	Mrb	<i>M. rufobrunnea</i>	<i>M. rufobrunnea</i>	<i>M. rufobrunnea</i>
	nc	<i>M. lanceolata ad int.</i>	nc	<i>M. anatolica</i> ^{HT}
	Mel-1	<i>M. tomentosa</i>	<i>M. tomentosa</i>	<i>M. tomentosa</i> ^{HT}
	Mel-2	<i>M. elatoides</i>	<i>M. frustrata</i>	<i>M. tridentina</i> ^{OM}
		<i>M. elatoides</i> var. <i>elegans</i>		
	Mel-3	<i>M. gigas</i>	<i>M. semilibera</i>	<i>M. semilibera</i> ^{NT}
		<i>M. gigas</i> var. <i>tintinnabulum</i>		
	Mel-4	<i>M. punctipes</i>	<i>M. punctipes</i>	<i>M. punctipes</i> ^{ET}
	Mel-5	nc	<i>M. populiphila</i>	<i>M. populiphila</i> ^{HT}
	Mel-6	nc	<i>M. sextelata</i>	<i>M. sextelata</i> ^{HT}
	Mel-7	<i>M. eximia</i>	<i>M. septimelataza</i>	<i>M. eximia</i> ^{ET}
		<i>M. eximia</i> f. <i>acuminata</i>		
		<i>M. eximia</i> f. <i>multiformis</i>		
		<i>M. anthracophila</i>		
		<i>M. carbonaria</i>		
	Mel-8	nc	nc	nc
	Mel-9	<i>M. exuberans</i>	<i>M. capitata</i>	<i>M. exuberans</i> ^{HT}
	Mel-10	<i>M. elata</i> ^a	<i>M. importuna</i>	<i>M. importuna</i> ^{HT}
		<i>M. vaporaria</i>		
	Mel-11	<i>M. quercus-ilicis</i>	nc	<i>M. quercus-ilicis</i> ^b
		<i>M. quercus-ilicis</i> f. <i>kakiicolor</i>		
	Mel-12	nc	<i>M. snyderi</i>	<i>M. snyderi</i> ^{HT}
	Mel-13	nc	nc	nc
	Mel-14	nc	nc	nc
	Mel-15	nc	<i>M. angusticeps</i>	<i>M. angusticeps</i> ^{ET}
	Mel-16	nc	nc	<i>M. eximoides</i> ^{HT}
	Mel-17	nc	nc	nc
	Mel-18	nc	nc	nc
	Mel-19	nc	nc	nc ^c
	Mel-20	<i>M. conica</i> var. <i>crassa</i>	nc	<i>M. purpurascens</i> ^{ET}
		<i>M. conica</i> var. <i>purpurascens</i> ^d		
	Mel-21	nc	nc	nc
	Mel-22	nc	<i>M. brunnea</i>	<i>M. brunnea</i> ^{HT}
	Mel-23	nc	nc	nc
	Mel-24	nc	<i>M. septentrionalis</i>	<i>M. septentrionalis</i> ^e ^{HT}
	Mel-25	<i>M. dunalii</i>	nc	<i>M. dunalii</i> ^{ET}
		<i>M. fallax</i>		
		<i>M. rielana</i>		
	Mel-26	<i>M. conica</i> var. <i>conica</i> ^f	nc	<i>M. deliciosa</i> ^{ET}
		<i>M. conica</i> var. <i>flexuosa</i>		
		<i>M. conica</i> var. <i>nigra</i>		
		<i>M. conica</i> var. <i>violeipes</i>		
	Mel-27	nc	nc	nc
	Mel-28	nc	nc	nc
	Mel-29	nc	nc	nc
	Mel-30	nc	nc	nc
	Mel-31	<i>M. pulchella</i>	nc	<i>M. pulchella</i> ^e ^{HT}
	Mel-32	nc	nc	nc
	Mel-33	nc	nc	nc
	Mel-34	nc	nc	nc
	Mel-35	nc	nc	nc
	Mel-36	nc	nc	nc ^g
Esculenta/Morchella	Mes-1	<i>M. steppicola</i>	<i>M. steppicola</i>	<i>M. steppicola</i>
	Mes-2	nc	<i>M. diminutiva</i>	<i>M. diminutiva</i> ^{HT}

TABLE I. Continued

Clade/section	Du et al. (2012a, b)	Clowez (2012)	Kuo et al. (2012)	Richard et al. (this study)
	<i>Mes-3</i>	<i>M. sceptriformis</i>	<i>M. virginiana</i>	<i>M. sceptriformis</i> ^{HT}
	<i>Mes-4</i>	<i>M. rigida</i>	<i>M. esculentoides</i>	<i>M. americana</i> ^{HT}
		<i>M. americana</i>		
		<i>M. americana</i> var. <i>elongata</i>		
		<i>M. californica</i>		
		<i>M. claviformis</i>		
		<i>M. populina</i>		
		<i>M. umbrina</i>		
	<i>Mes-5^h</i>	nc	nc	nc
	<i>Mes-6</i>	nc	nc	nc
	<i>Mes-7</i>	nc	<i>M. prava</i>	<i>M. prava</i> ^{HT}
	<i>Mes-8</i>	<i>M. esculenta</i>	nc	<i>M. esculenta</i> ^{ET}
		<i>M. esculenta</i> var. <i>aurantiaca</i>		
		<i>M. esculenta</i> var. <i>brunnea</i>		
		<i>M. esculenta</i> var. <i>rotunda</i>		
		<i>M. esculenta</i> var. <i>rubroris</i>		
		<i>M. esculenta</i> var. <i>theobromichroa</i>		
		<i>M. ochraceoviridis</i>		
		<i>M. ovalis</i>		
		<i>M. ovalis</i> var. <i>minor</i>		
	<i>Mes-9</i>	nc	nc	nc
	<i>Mes-10</i>	nc	nc	nc
	<i>Mes-11</i>	<i>M. ulmaria</i>	<i>M. cryptica</i>	<i>M. ulmaria</i> ^{HT}
	<i>Mes-12</i>	nc	nc	nc
	<i>Mes-13</i>	nc	nc	nc
	<i>Mes-14</i>	nc	nc	nc
	<i>Mes-15</i>	nc	nc	nc
	<i>Mes-16</i>	<i>M. galilaea</i>	nc	<i>M. galilaea</i> ^{HT}
	<i>Mes-17</i>	<i>M. acerina</i>	nc	<i>M. vulgaris</i> ^{ET}
		<i>M. andalusiae</i>		
		<i>M. anthracina</i>		
		<i>M. conica</i> var. <i>pygmaea</i>		
		<i>M. dunensis</i>		
		<i>M. lepida</i>		
		<i>M. robiniae</i>		
		<i>M. spongiola</i>		
		<i>M. vulgaris</i>		
		<i>M. vulgaris</i> var. <i>aucupariae</i>		
		<i>M. vulgaris</i> var. <i>parvipila</i>		
	<i>Mes-18</i>	nc	nc	nc
	<i>Mes-19</i>	nc	nc	nc
	<i>Mes-20</i>	nc	nc	nc
	<i>Mes-21</i>	nc	nc	nc
	<i>Mes-22</i>	nc	nc	nc
	<i>Mes-23</i>	nc	nc	nc
	<i>Mes-24</i>	nc	nc	nc
	<i>Mes-25</i>	nc	nc	nc
	<i>Mes-26</i>	nc	nc	nc
	<i>Mes-27</i>	nc	nc	nc
	nc	<i>M. castaneae</i>	nc	<i>M. castaneae</i> ^{HT}
		<i>M. brunneorosea</i>		
		<i>M. brunneorosea</i> var. <i>sordida</i>		

TABLE I. Continued

nc: Not cited in the corresponding reference. Abbreviations indicate the nomenclatural source on which the proposals are based: HT, NT, ET and OM designate holotype, neotype, epitype, original material, respectively. Note: Species names in boldface relate to taxa that are published or documented by type material in the corresponding source.

^aSee notes on *M. elata*.

^bType lost, see notes on *M. quercus-ilicis*.

^cFor a description see Beug and O'Donnell (2014).

^dSee notes on *M. conica*.

^eSee notes on *M. inamoena* and *M. pulchella*.

^fSee notes on *M. conica*.

^gFor a description see Voitek and Voitek (2014), Voitek et al. (2014).

^h*Mes-5*: The ITS rDNA region of the three collections from Europe (M216 = UME 29687 from Sweden, M454 = Museum Bot. Hauniense from Denmark and M508 = DSM 10471 from France) on which *Mes-5* was based (O'Donnell et al. 2011) could not be sequenced. Therefore, additional study is needed to critically assess whether *Mes-5* and *Mes-17* are phylogenetically distinct.

shades in the pits. Some faded collections are possibly referred to as *M. deliciosa* var. *carnea* Bres. (illustrated by Medardi 2006:139), others are initially dark gray to anthracite black and were described as *M. conica* var. *nigra* by Clowez (2012). It seems likely that the latter collections were named "*M. conica*" or "*M. intermedia*" by some authors, for example Boudier (1909), Jacquetant (1984).

ITS sequence analysis was unable to distinguish our collections of *M. deliciosa* (*Mel-26*) from *Mel-13* (FIG. 2), as previously established (Du et al. 2012b). However, the multilocus phylogenetic analysis revealed that the collections cited above correspond to *Mel-26* (FIG. 3). Previously sequences of *M. deliciosa* (as *Mel-26*) were only known from Turkey (Taşkın et al. 2012). Here we add sequences from France, confirming by molecular data the broader distribution of this species.

An epitype of *M. deliciosa* should be selected from one of the countries of origin (preferable from Sweden or from Germany in Weinmann's collecting area around Regensburg). Because we lack *Mel-26* collections from these areas, we postpone epitypification of *M. deliciosa* until such material becomes available and assigned to species through multilocus phylogenetic analysis.

Morchella dunalii Boud., Bull Soc Mycol France 3:95. 1887. FIG. 4k

Typification: original water coloring by Dunal (MPU), pl. 2 FIG. 3 (lectotype designated and reproduced by Moreau et al. 2011:269, as FIG. 2D). FRANCE. VAR: Lorgues, under *Quercus ilex*, 9 Mar 2011, L. Martin PhC120 (LIP 0900128) (**epitype** designated here, MycoBank MBT 177741, cited by Clowez 2012 as "*M. dunalii*"). Isoepitypes S (F254894), CEFÉ-CNRS.

= *Morchella fallax* Clowez & L. Martin in Clowez, Bull Soc Mycol France 126(3–4):318. 2012.

Misinterpretation: *Morchella rielana* Boud. sensu Clowez (2012: 321).

Specimens examined. FRANCE. CORSE DU SUD: Bonifacio, open forest close to *Quercus ilex* and *Olea europaea*, May 2013, P. Geniez and B. Schatz, FR2013191 (herb. CEFÉ-CNRS, Montpellier); VAR: Lorgues, under *Fraxinus excelsior* or *angustifolia* close to *Quercus ilex*, 2010, L. Martin, PhC14 (holotype of *Morchella fallax*, LIP); locality not specified, under *Pinus* sp. and *Quercus ilex*, 2009, L. Martin, PhC15 (LIP 0900056, as "*M. rielana*").

Notes. Multilocus phylogenetic analysis led us to apply the name *Morchella dunalii* to *Mel-25* (FIG. 3). *Morchella dunalii* was the first species of *Morchella* described by Boudier (1887), based on a water coloring of a Mediterranean collection from the Montpellier area (published by Moreau et al. 2011). Boudier emphasized the contrast between the dark crests and pale pits, a common feature in the collections studied here (FIG. 4k). In France and Spain, this species appears to occur typically under *Quercus ilex* on calcareous soils. But it was reported from Turkey under *Pinus* spp. (Taşkın et al. 2012, as *Mel-25*). On the basis of paler colors, Clowez (2012) distinguished *M. fallax* from *M. dunalii*. However, multilocus phylogenetic analysis of the holotype of *M. fallax* does not support it as distinct from *M. dunalii* (FIG. 3). The collection PhC15, cited as "*Morchella rielana*" by Clowez (2012:321), is also conspecific to *M. dunalii*. The identity of *M. rielana*, originally described from a non-Mediterranean area (Boudier 1909), remains to be determined.

Morchella eximia Boud., Icon Mycol, expl pl. 6, pl. 208. 1909. FIG. 4j

Typification: Holotype not located (PC). Water color painting by Boudier, "*Icones Mycologicae*" No. 532, 3 ascomata, spores and hymenium, from J.-B. Barla (Nice, F) on a post-fire site in April, collections of the National Museum of Natural History, Paris; published by Boudier 1909: pl. 208

(lectotype designated here, MycoBank MBT 177742). FRANCE. HAUTE-CORSE: Tattone, burnt forest of *Pinus nigra* subsp. *laricio*, *Pinus pinaster* and *Arbutus unedo*, 30 Apr 2008, F. Richard and P.-A. Moreau, FR0410 (epitype designated here, LIP 0900129, MycoBank MBT 177743, cited and illustrated by Clowez 2012 as “*M. eximia*”). Isoepitypes S (F254895), CEFÉ-CNRS.

= *Morchella eximia* f. *multiformis* Clowez, Bull Soc Mycol France 126(3–4):327. 2012.

= *Morchella anthracophila* Clowez & Winkler in Clowez, Bull Soc Mycol France 126(3–4):322. 2012.

= *Morchella carbonaria* Clowez & Chesnaux in Clowez, Bull Soc Mycol France 126(3–4):326. 2012

= *Morchella septimelata* M. Kuo in Kuo et al., Mycologia 104(5):1171. 2012.

- *Morchella eximia* f. *acuminata* (J.Kickx f.) Clowez Bull Soc Mycol France 126(3–4):329. 2012 (sensu Clowez, 2012).

Specimens examined. AUSTRALIA. SOUTH WEST: North-cliff, burnt forest of *Eucalyptus diversicolor*, 19 Aug 2012, P. Donecker, PhC200 (CEFÉ-CNRS, Montpellier). CANADA. BRITISH COLUMBIA: burnt ground under *Pinaceae*, 2010, R. Chesnaux, PhC17 (holotype of *Morchella anthracophila*, LIP 0900058); *ibid.*, burnt forest under *Thuja plicata*, R. Chesnaux, 2010, PhC41 (holotype of *Morchella carbonaria*, LIP 0900080). FRANCE. HAUTE-CORSE: Tattone, burnt forest of *Pinus nigra* subsp. *laricio*, *Pinus pinaster* and *Arbutus unedo*, 30 Apr 2008, F. Richard and P.-A. Moreau FR7 (CEFÉ-CNRS, Montpellier). VAR: Saint-Cyr-sur-Mer, on rubble, plaster etc., 2010, J.-C. Hermitte, PhC70 (holotype of *Morchella eximia* f. *multiformis*, LIP 0900015). SPAIN. CASTILE-LEÓN: Avila, burnt ground under *Pinus pinaster*, 2010, F. Hidalgo and J. Undagoitia, PhC27 (LIP 0900066). Locality unknown, purchased at the Rungis market (France), Apr 2011, P. Clowez, PhC24 (LIP 0900063). USA. WASHINGTON: Klickitat, highway 141, under *Pseudotsuga menziesii* after a major fire, elev. 1000 m, 5 Apr 2013, M. Beug, PhC253 (CEFÉ-CNRS, Montpellier); *ibid.*, M. Beug, PhC254 (CEFÉ-CNRS, Montpellier); 24 May 2013, M. Beug, PhC255 (CEFÉ-CNRS, Montpellier).

Notes. This widespread post-fire morel sometimes fruits extensively in burnt forests as well as on rubble. Clowez (2012) also reported this species as *M. eximia*, but accepted several forms. Collections of these forms, however, share identical sequences with collections of *M. eximia* (FIG. 2). The name *M. acuminata* could be considered, but we regard it as a doubtful name because it is poorly documented, without original material (Kickx 1867), and because this species has been interpreted in the past as a form of *M. elata* (Marchand 1973). Therefore we adopt the unambiguous name *M. eximia*, based on the detailed illustration and complete description by Boudier (1909). All collections from Europe, Turkey and North America (as *Mel-7* or *Morchella septimelata*) share an identical ITS sequence, except for the holotypes of *M. septimelata* and *M. carbonaria* that

possess slightly divergent alleles (FIG. 2). The present and previous multilocus phylogenetic analyses have resolved all these collections as a single genealogically exclusive lineage (O'Donnell et al. 2011; Du et al. 2012a, b).

Morchella eximioides Jacquet. ex R. Kristiansen, Agarica 10/11(19/20):10. 1990. SUPPLEMENTARY FIG. 1c

Specimens examined. NORWAY. FREDRIKSTAD Ø: Nabbetorp, near Glomma, Østfold, under *Salix* and other deciduous trees, 17 May 1981, R. Kristiansen, Jacquetant 290579 (holotype of *M. eximioides*, O 72834). SWEDEN. UPPLAND, Hållnäs, Slada, 14 May 1989, S. Ryman 8667 (as “*Morchella elata*”, UPS F-130641).

Descriptions and illustrations. Kristiansen (1982:72 and FIG. 7, as “9. *Morchella* sp.”); Jacquetant (1984:100–101, as “*M. conicopapyracea*”); Kristiansen (1990:10, as “*M. conicopapyracea*”).

Notes. Based on DNA sequence analysis of the holotype (FIG. 2), this species is interpreted as *Mel-16* from Europe and China (O'Donnell et al. 2011). The holotype kept at Oslo is represented by half of a well-preserved ascoma. It is obvious from our study of the specimens from the Oslo herbarium that an error was made in Jacquetant (1984:100–101): the description and watercoloring of “*M. conicopapyracea* Jacquet.” clearly applies to the half-specimen found in the herbarium envelope Jacquetant 290579, invalidly designated (without a direct reference to the page with the latin diagnosis, McNeill et al. 2012, Art. 33.1, 38.13) as “holotype” of *M. eximioides* by Jacquetant & Bon (1985) and labelled as such in the Oslo herbarium (see SUPPLEMENTARY FIG. 1c). Conversely, the “holotype” specimens of *M. conicopapyracea* Jacquet., Jacquetant 260581 (O), was described and illustrated as “*M. eximioides*” in Jacquetant (1984). An earlier publication by Kristiansen (1982:70–72), citing localities and dates of his collections that were described as *M. norvegiensis*, *M. conicopapyracea* and *M. eximioides* (as 5., 7., and 9. *Morchella* sp., respectively) suggests that the error originates from either an inversion of the labels of the duplicates sent to Jacquetant, or from Jacquetant himself. The error was replicated at the point of valid publication of the names by Kristiansen (1990:10), who reproduced the watercolorings (Jacquetant 1984:101), diagnoses (op. cit.:104) and “holotype designations” (Jacquetant and Bon 1985:1). Since names are inextricably linked to the designated holotypes, even if they bear no relation to the descriptions, we follow here the type designations (McNeill et al. 2012, Art. 9.1). *Morchella eximioides* was not included by Clowez (2012) and Kuo et al. (2012). It is a closely related sister species to the North American *M. angusticeps* (Du et al. 2012a, b).

Morchella exuberans Clowez, Hugh Sm. & Sandi Sm. in Clowez, Bull Soc Mycol France 126:330. 2012.

FIG. 4f

= *Morchella capitata* M. Kuo & M.C. Carter in Kuo et al., Mycologia 104(5):1171. 2012.

Specimens examined. SWEDEN. Lule Lappmark, Jokkmokk, Muddus National Park, burnt ground (burn 2006), 3 Sept 2007, S. Kuoljok 0720 (as “*Morchella elata*”, UPS F-620167). USA. CALIFORNIA: Emigrant Gap, burnt ground under Pinaceae, 2010, H. and S. Smith, PhC52 (holotype of *Morchella exuberans*, LIP 0900012).

Notes. This post-fire morel is distinctive because it frequently is greenish (FIG. 4f). *Morchella exuberans* (= *Mel-9*) has priority over the taxonomic synonym *M. capitata*. Its known distribution includes Western North America (O'Donnell et al. 2011) and Sweden (Taşkın et al. 2012).

Morchella importuna M. Kuo, O'Donnell & T.J. Volk in Kuo et al., Mycologia 104:1172. 2012.

- *Morchella elata* Fr.:Fr. in Fries, Syst Mycol 2:8. 1822 (sensu Clowez, 2012)

- *Morchella vaporaria* Bartayrès ex Brond., Cryptog Agenais 3 :33. 1830 (sensu Clowez, 2012)

Specimens examined. CANADA. QUÉBEC: on bark, 2010, R. Lebeuf, LIP PhC46 (LIP 0900085). FRANCE. OISE: Liancourt, under *Pyrus*, 2012, B. Sanguillaux, PhC156 (LIP 0900038); Ville, under *Malus*, 2012, S. Tourel, PhC157 (LIP 0900036). TERRITOIRE DE BELFORT: Belfort, on ground in a cellar, May 1994, C. Bouvet, PhC20 (holotype of *Morchella elata* var. *major*, LIP 090002). SPAIN. CÓRDOBA, Zagrilla, under *Cydonia oblonga*, 2011, M. Becerra Parra, PhC111 (LIP 0900140). SWITZERLAND. VALAIS: 15 May 1986, M. Ferber, (LUG 4609, as “*M. hortensis*”).

Notes. *Morchella importuna* (*Mel-10*, FIG. 2) is a widespread and genetically variable species that may have been introduced to Europe (O'Donnell et al. 2011). Clowez (2012) used the name *M. elata* Fr.:Fr. for this species, but see *Doubtful names* below. *Morchella vaporaria* Bartayrès ex Brond. (1830), described from a greenhouse with a detailed plate, or *M. hortensis* Boud. (1897), are other possible names for this species. However, because no exsiccatum is likely to exist for these two taxa, and because of the pending interpretation of the name *M. elata*, we provisionally retain the recent name *M. importuna*, documented by the sequenced type collection. The name *M. costata* (Vent.) Pers., which is often used in European literature, is an illegitimate synonym of *M. elata* (see below, *Doubtful names*). *Morchella importuna* is thought to be saprobic given that it fruits on mulch and woodchips (Kuo et al. 2012, Mann and Mann 2014).

Morchella populiphila M. Kuo, M.C. Carter & J.D. Moore in Kuo et al., Mycologia 104:1168. 2012.

Specimens examined. SPAIN. GRANADA: Arenas de Rey, under *Populus x canadensis* plantations along a river, 840 m, 21 Apr 2012, M. Becerra Parra, VG3052390 (part in CEF-CNRS, Montpellier).

Notes. This species was reported by O'Donnell et al. (2011) as *Mel-5* from western North America (FIG. 2); it was not included in Clowez (2012). This is the first report of this species in Europe (Spain), represented by a 2012 collection under introduced *Populus* cultivars originating from North America. ITS sequences of the Spanish specimen and collections from Oregon and California are identical. Altogether this suggests a possible introduction of *M. populiphila* from North America to Europe.

Morchella pulchella Clowez & Petit in Clowez, Bull Soc Mycol France 126:314. 2012. FIG. 4l

Specimens examined. FRANCE. OISE: Saint-Maximin, under *Buddleja davidii*, Mar 2010, F. Petit, PhC56 (holotype of *Morchella pulchella*, LIP 0900011).

Notes. Multilocus phylogenetic analysis of the holotype specimen of *M. pulchella* from France assigned this species to *Mel-31* (FIG. 3), which was previously only known from Turkey and China. Our analysis does not support reciprocal monophyly of *M. pulchella* (*Mel-31*) and *M. septentrionalis* (*Mel-24*); *Mel-24* renders *Mel-31* paraphyletic. Previous studies are equivocal about the phylogenetic exclusivity of *Mel-24* and *Mel-31* (see Du et al. 2012a, FIG. 4, and Taskin et al. 2012, FIG. 5). However, because morels have been shown to display high continentalism (O'Donnell et al. 2011) and their distributions are allopatric, we provisionally maintain these as two putative species. Our results emphasize the need for additional studies to assess whether there is ongoing gene flow between *Mel-31* and *Mel-24*, to more critically evaluate their taxonomic status.

Morchella punctipes Peck, Bull Torrey Bot Cl, 30:99. 1903.

Specimens examined. CANADA. QUÉBEC: under *Populus grandidentata*, 2010, R. Lebeuf, PhC81 (LIP 0900017).

Notes. This eastern North American endemic (*Mel-4*) was revised and epitypified by Kuo et al. (2012). It forms a strongly supported clade with the North American *M. populiphila* and the European *M. semilibera* (FIG. 2). A unique character, the half-free apothecial margin, supports this clade; all other morels having a margin fully attached to the stipe. *Morchella punctipes* is distinct within this clade by possessing darkening granules on the stipe.

Morchella purpurascens (Boud.) Jacquet. in Jacquetant & Bon, Doc Mycol 56:1. 1985 ('1984'). FIG. 4n

Basionym: *Morchella elata* var. *purpurascens* Boud., Bull Soc Mycol France 13:148. 1897.

Typification: Plate by Krombholz (1834, plate 16 fig. 24), cited by Boudier (1897:148) (lectotype, designated by Jacquetant & Bon 1985:1). FRANCE. ALPES DE HAUTE-PROVENCE, Seyne-les-Alpes, under *Pinaceae*, *P. Collombon* and *N. Van Vooren*, 2010, *PhC82* (**epitype** designated here, LIP 0900018, MycoBank MBT 177745). Isoepitypes S (F255984) and CEF-CNR.

Specimens examined. FRANCE. ALPES DE HAUTE-PROVENCE, Auzet, under *Pinaceae*, 2010, *P. Collombon* and *N. Van Vooren*, *PhC83* (LIP 0900113, as “*M. conica* var. *purpurascens*”).

Notes. Multilocus phylogenetic analysis of the two specimens examined by us assigns them to *Me120*, a phylogenetic species first discovered in Central Anatolia (Taşkın et al. 2010; FIG. 3). This species and *M. deliciosa* as adopted here, were collectively treated by Clowez (2012) under the name “*Morchella conica*”. Our results, however, clearly show that these collections represent distinct species (FIG. 3). The name *M. purpurascens* is proposed here as the oldest unambiguous name available for this apparently common species with a short stipe and elongate, somewhat obtuse pileus whose distribution ranges from Sweden to Turkey (Taşkın et al. 2012). We epitypify it with the representative collection *PhC82*, omitted by Clowez (2012) but found on the same locality as *PhC83* (cited by Clowez, loc.cit.:310, as “*M. conica* var. *purpurascens*”) by the same collectors. Members of this clade are characterized by ascomata with purplish or pinkish colors that do not turn dark grey or black with age. See also notes under *M. norvegiensis*.

Morchella quercus-ilicis Clowez, Ballester & L. Romero in Clowez, Bull Soc Mycol France 126:318. 2012.

FIG. 4h

= *Morchella quercus-ilicis* f. *kakiicolor* Clowez & L. Romero in Clowez, Bull Soc Mycol France 126(3–4):319. 2012.

Specimens examined. SPAIN. ANDALUCÍA: Aracena, under *Castanea sativa*, 2011, *L. Romero de la Osa*, *PhC117* (holotype of *Morchella quercus-ilicis* f. *kakiicolor*, LIP 0900146).

Notes. The holotype collection of *M. quercus-ilicis* (*PhC148*) is lost. However, multilocus phylogenetic analysis of the type of *M. quercus-ilicis* f. *kakiicolor* shows this form correspond to *Me11* from the Canary Islands (FIG. 3). The genetic identity of *M. quercus-ilicis* f. *quercus-ilicis* remains questionable until the type material is found or a neotype is designated, which is the object of a separate study (Loizides et al. pers comm). Note that multilocus phylogenetic analysis is required to resolve *M.*

quercus-ilicis from its sister species, *M. dunalii* (FIGS. 2, 3). The two species form a distinct clade within sect. *Distantes*/Elata Clade (Du et al. 2012b).

Morchella semilibera DC.:Fr. in Lamarck & Candolle 1805, Fl Fr éd 3, 2:212 (1805), *nom. cons. prop.*

FIG. 4o

Basionym: *Morilla semilibera* (DC.:Fr.) Quél., Enchir Fung (Paris):271. 1886.

= *Mitrophora semilibera* (DC.:Fr.) Lév., Ann Sci Nat, Bot 5:250. 1846.

= *Morchella patula* var. *semilibera* (DC.:Fr.) S.Imai, Sci Rep Yokohama Natl Univ 3:15. 1954.

Neotype (Moreau et al. 2014): *PhC99* (LIP 0900126). Isoneotypes S (F254893), CEF-CNR.

= *Phallus gigas* Batsch:Fr. in Batsch, Elench Fung:131. 1783.

= *Morchella gigas* (Batsch:Fr.) Pers., Syn Meth Fung:619. 1801.

= *Eromitra gigas* (Batsch:Fr.) Lév., Iconogr Champ Paulet:106. 1855.

= *Ptychoverpa gigas* (Batsch:Fr.) Boud., Hist Class Discom Europe:33. 1907.

= *Phallus undosus* Batsch:Fr. in Batsch, Elench Fung:131. 1783.

= *Morchella undosa* (Batsch:Fr.) Pers., Syn Meth Fung:620. 1801.

= *Phallus crassipes* Vent.:Fr. in Ventenat, Mém Inst Nat Sci Arts, Sci Math Phys 1:509. 1798.

= *Morchella crassipes* (Vent.:Fr.) Pers., Syn Meth Fung:621. 1801.

= *Morchella esculenta* var. *crassipes* (Vent.:Fr.) Krombh., Naturgetr Abbild Schw 3:6. 1834.

= *Mitrophora hybrida* var. *crassipes* (Vent.:Fr.) Boud., Hist Class Discom Europe:33. 1907.

= *Helvella hybrida* Sowerby, Col Fig English Fungi 2:99. 1799.

= *Morchella hybrida* (Sowerby) Pers., Syn Meth Fung:620. 1801.

= *Mitrophora hybrida* (Sowerby) Boud., Bull Soc Mycol France 13:151. 1897.

= *Morchella varisiensis* Ruini, Riv Micol 43(1):17. 2000.

= *Morchella gigas* var. *tintinnabulum* Clowez & Moinet in Clowez, Bull Soc Mycol France 126 (3–4):339. 2012.

Specimens examined. FRANCE. OISE: Bailly, under *Fraxinus excelsior*, Apr 2009, *F. Petit*, *PhC7* (LIP 0900048); Béhéricourt, under *Fraxinus excelsior* with *Ranunculus ficaria*, Apr 2010, *P. Clowez*, *PhC26* (LIP 0900065); Saint-Maximin, under *Fraxinus excelsior*, 14 Apr 2011, *F. Petit*, *PhC99* (neotype of *M. semilibera*, LIP 0900126; isoneotypes S (F254893), CEF-CNR). ORNE: Lonrai, under *Malus sylvestris*, Apr 2010, *P. Moinet*, *PhC80* (holotype of *Morchella gigas* var. *tintinnabulum*, LIP 0900008). ITALY. VARESE: Capolago, 14 Apr 1998, *S. Murin* (holotype of *M. varisiensis*, LUG 9100).

Notes. Clowez (2012) concluded that the name *M. gigas*, which was adopted by Kellner et al. (2005), has

priority for this species. However, the well-known name *M. semilibera* (*Me*13, FIG. 2) has been proposed for conservation over the earlier names, *M. gigas* and *M. undosa* (Moreau et al. 2014).

Morchella septentrionalis M. Kuo, J.D. Moore & Zordani in Kuo et al., *Mycologia* 104:1175. 2012.

Specimens examined. CANADA. QUÉBEC: Québec, under *Populus grandidentata*, 2011, R. Lebeuf, *PhC121* (LIP 0900149, as “*M. angusticeps*”); *ibid.*, under *Fraxinus americana*, Apr 2011, R. Lebeuf, *PhC123* (LIP 0900151, as “*M. sp.*”).

Notes. This is *Me*24. The paraphyletic relationships between this species and *M. pulchella* (*Me*31) are discussed under *M. pulchella* (see above). Clowez (2012) interpreted one of the collections from Québec (*PhC121*) as “*M. angusticeps*”. As epitopified by Kuo et al. (2012), *M. angusticeps* represents a distinct species (*Me*15) (see *M. angusticeps* above). Also see notes on *M. inamoena* (see *Doubtful names* below).

Morchella sextelata M. Kuo in Kuo et al., *Mycologia* 104:1170. 2012.

Specimens examined. USA. Locality unknown, burnt ground under *Pinaceae*, 17 Jun 2007, D. Winkler, *PhC50* (LIP 0900090, as “*Morchella sp.*”).

Notes. This post-fire morel corresponds to *Me*6 (O'Donnell et al. 2011). It was not included in Clowez (2012), but a collection of this species at LIP was studied by us. This species has been collected in Western North America, Mexico and Yunnan, China (Du et al. 2012a).

Morchella tomentosa Kuo, *Mycotaxon* 105:442. 2008.

Specimens examined. CANADA. BRITISH COLUMBIA: burnt ground under *Pinaceae*, 2010, R. Chesnaux, *PhC47* (LIP 0900087). Origin unknown, purchased at the Rungis market (France), May 2010, P. Clowez, *PhC48* (LIP 0900088).

Notes. This distinctive post-fire morel, which was informally designated as *Me*1 by O'Donnell et al. (2011), has only been reported from Western North America.

Morchella tridentina Bres., *Fungi Tridentini* 2:65. 1898.

SUPPLEMENTARY FIG. 1a

Typification: ITALY. TRENTINO: “in silva Tectilogii junta rivulus, acquadotta”, 10 May 1882, G. Bresadola (lectotype designated here, S F9101, MycoBank MBT178121, original material of *Morchella tridentina*).

= *Morchella frustrata* M. Kuo in Kuo et al., *Mycologia* 104:1167. 2012.

[= *Morchella elatoides* Jacquet., Les Morilles:103. 1984 (nom. inval., Art. 40.1); in Jacquetant & Bon, *Doc Mycol* 56:1. 1985(‘1984’)] (nom. inval., Art. 33.1, 41.5) (sensu Clowez, 2012).

[= *Morchella elatoides* var. *elegans* Jacquet., Les Morilles: 103. 1984 (nom. inval., Art. 40.1); in Jacquetant & Bon, *Doc Mycol* 56:1. 1985(‘1984’)] (nom. inval., Art. 33.1, 41.5) (sensu Clowez, 2012).

Specimens examined. FRANCE. HAUTE-SAVOIE: Excevenex, under *Buxus sempervirens* and *Pinaceae*, end of Apr 1999, A. Anthoine, *PhC172* (O. Röllin, part in LIP 0900023); *ibid.* *PhC173* (O. Röllin, part in LIP 0900021). VAR: Siou Blanc, under *Pinus sp.*, 7 Apr 2011, L. Martin, *PhC108* (LIP 0900137); *ibid.*, under *Quercus ilex*, 7 Apr 2011, L. Martin, *PhC110* (LIP 0900139). ITALY. TRENTINO: “Bosco confiero di Tertoly”, May 1881, G. Bresadola (original material of *Morchella tridentina*, S F9099). SPAIN. ANDALUSIA: Aracena, under *Quercus ilex*, 2011, L. Romero de la Osa, *PhC116* (LIP 0900145). MÁLAGA, Cortes de la Frontera, Sierra de Libar, under *Quercus ilex*, 2011, M. Becerra Parra, *PhC113* (LIP 0900142). CASTILE-LEÓN: Valladolid, Montemayor de Pillila, under *Quercus ilex*, 4 May 2011, A. Garcia Blanco, *PhC105* (LIP 0900134). ARAGN: Canfranc, under *Pinus sylvestris*, 18 May 2012, L. Ballester, *PhC176* (CEFE-CNRS, Montpellier); Huesca, Loarre, under *Pinus sylvestris*, 2008, L. Ballester, *PhC145* (LIP 0900173); Orol, under *Abies alba*, 2004, L. Ballester, *PhC147* (LIP 0900175). LA RIOJA: Pradillo, under *Corylus avellana*, 2010, L. Ballester, *PhC146* (LIP 0900174); *ibid.*, 12 May 2012, L. Ballester, *PhC177* (CEFE-CNRS, Montpellier).

Notes. Clowez (2012) reported French and Spanish collections as *M. elatoides*, based on exsiccata and pictures, following Jacquetant's (1984) description and watercolor. Abundant fresh specimens were collected by P. Clowez in Spain in spring 2013 that matched the protologue of *M. tridentina* (Bresadola 1898) with a detailed plate showing splitting crests with age. This character was observed in all of the Spanish collections. Pyrenean collections and some closer to Bresadola's original locality in the Southwestern Alps, identified as *M. tridentina* (Röllin and Anthoine 2001), have ITS sequences that are identical to the Spanish collections. In addition, studies of two original collections from Bresadola kept at S, one of them well preserved and in excellent condition (F9101, designated above as lectotype), supports the interpretation proposed here. Because no material from Bresadola's original area in Trentino was available to us, and Bresadola indicated on the labels that the two collections deposited at S possessed green tones, which have not been observed on any recent collection cited, an epitype is not proposed here. As noted in the description of *M. frustrata* (*Me*2, Kuo et al. 2012), *M. tridentina* displays characters of both sect. *Morchella* (dark ascomata that turn ochraceous to pinkish with age) and sect. *Distantes* (broad sulcus and conical shape).

Doubtful names in sect. *Distantes*

Morchella conica Pers.:Fr., Persoon, Tr. Champ. comest.:256. 1819.

≡ *Morchella esculenta* δ *conica* (Pers.:Fr.) Fr., Syst Mycol 2:7. 1822.

≡ *Morilla conica* (Pers.:Fr.) Quél., Enchir Fung:271. 1886.

Notes. This universally used name in old and recent literature is illegitimate at the rank of species. *Morchella continua* Tratt. (Trattinnick 1805:11) was cited in the protologue of *M. conica*, and it was explicitly included in *M. conica* by Persoon (1818). Therefore, according to the present Code (McNeill et al. 2012), *M. conica* was published as a superfluous name for *M. continua*. Fries' sanctioning (1822:7) applies only at the subgeneric level. Many authors have interpreted *M. conica* as a darkly pigmented species with longitudinal crests. But Trattinnick's plate represents an umber-brown ascoma with 4- to 6-sided polygonal pits and it lacks a sulcus. As such, it does not correspond to any taxon within sect. *Distantes* and we suggest it belongs to sect. *Morchella*. Fries (1822) interpreted it as such when sanctioning it as a variant of *M. esculenta* (at an undefined rank). So did Krombholz (1834) in describing *M. conica* var. *rigida* as a member of the *M. esculenta* group. Boudier (1909) was the first to apply the name *M. conica* to a species within *Distantes*.

Following a long tradition, Clowez (2012) applied the name *M. conica* to typical collections of sect. *Distantes*. Some of the collections we analyzed (cited as var. *conica*, var. *flexuosa*, var. *nigra*, and var. *violeipes*) corresponded to *Me*26, for which the name *M. deliciosa* is used here (FIG. 3). Others corresponded to *Me*20, here named *M. purpurascens* (cited as var. *crassa* and var. *purpurascens*) (FIG. 3); to *M. vulgaris* (*Mes*-17) (cited as var. *pygmaea*); and to *M. tridentina* (*Me*2) (cited as var. *pseudoeximia* Clowez, from Chile) (not shown, see SUPPLEMENTARY TABLE I). Given the confusion concerning the name *M. conica*, a proposal to conserve the name together with one to reject *M. continua*, will be challenging.

Morchella conicopapyracea Jacquet. ex R. Kristiansen, Agarica 10/11:0. 1990. SUPPLEMENTARY FIG. 1b
Specimens examined. NORWAY. ØSTFOLD: Fredrikstad, Torp Bruk towards Glomma, 26 Apr 1981, R. Kristiansen, Jacquetant 260581 (holotype of *M. conicopapyracea*, O 72834).

Descriptions and illustrations. Kristiansen (1982:71 and FIG. 5, as “7. *Morchella* sp.”); Jacquetant (1984:100–101, as “*M. eximioides*”); Kristiansen (1990:10, as “*M. eximioides*”).

Notes. The ITS sequence from the holotype (Kristiansen 1990; see notes about *M. eximioides*

above) places *M. conicopapyracea* in a complex of phylogenetic species (*Me*17-19-20-34) that cannot be resolved by this single locus (Du et al. 2012b). Unfortunately, several attempts at amplifying other loci from this Norwegian collection failed. More recent collections from Scandinavia are required before the name *M. conicopapyracea* can be validated and applied unambiguously to a phylogenetic species. See also *M. norvegiensis* below.

Morchella elata Fr.:Fr. in Fries, Syst Mycol 2:8. 1822.

Lectotype (Clowez, 2012): line drawing published by Micheli (1729), pl. 85 FIG. 3, not validly designated (see Notes).

≡ *Morilla esculenta* var. *elata* (Fr.:Fr.) Quélet, Enchir Fung:271. 1886.

≡ *Phallus anastomosis* Batsch, Elench Fung, cont prim:131. 1783.

≡ *Phallus costatus* Vent., Dissert. *Phallus* 1:510. 1798.

≡ *Morchella costata* (Vent.) Pers., Syn Meth Fung:620. 1801.

≡ *Morchella elata* f. *costata* (Vent.) Quél., Mém Soc Émul Montbéliard II, 5:388. 1873.

≡ *Morchella elata* var. *costata* (Vent.) Kreisel, Boletus, 1:29. 1984.

Notes. Application of the name *M. elata* is postponed because it is still uncertain what species it represents. All collections cited under this name by Clowez (2012), as well as those identified as “*M. vaporaria*” and “*M. hortensis*” in the herbaria LIP and LUG, refer to *M. importuna* (= *Me*10) based on ITS sequence data. This interpretation of *M. elata* was based on the ascoma with typically parallel and straight longitudinal crests with transverse anastomoses, as illustrated in the plate by Micheli (1729:pl. 85 FIG. 3), the only iconographic reference cited by Fries (1822). However, Fries (loc. cit.) also based *M. elata* on living material from Sweden (“*v.v.*”), and possibly original material is present in UPS. Clowez (2012:331) failed to designate Micheli's plate as a lectotype in omitting to state “designated here” or equivalent (McNeill et al. 2012, Art. 7.10). Therefore Fries' collection could be selected as a lectotype if it can be interpreted as original (as per Art. 9.12, for lectotype designation, specimens (isotype & syntypes) have preference over illustrations). Unfortunately, DNA sequence data could not be obtained from this two-century-old material (O'Donnell 2014). Currently no collection of *Me*10 is known from Scandinavia and it would be unfortunate to epitypify *M. elata* with a taxon that may not occur in Sweden. We sequenced eight additional recent collections from Sweden from the *Elata* Clade, but none of them correspond to *Me*10 (TABLE I). Typification has therefore been deferred until additional studies of the *Elata* Clade/sect.

Distantes in Europe are completed. Thus, the name *M. importuna* is retained provisionally for *Mel*-10.

Morchella inamoena Boudier, Bull Soc Mycol France 13:149. 1897

Specimens examined. SPAIN. ANDALUSIA: Granada, under *Populus*, 2010, J. Bleda, *PhC2* (LIP 0900043).

Notes. This species was interpreted by Clowez (2012:311) using a water coloring published by Boudier (1909:pl. 213) from the original collection by J.-B. Barla from Southern France (Nice). The collection cited by Clowez (*PhC2*) belongs to a complex of species (i.e. *Mel*-22-23-24-28-29-30-31-32) that cannot be resolved by ITS sequence data (Du et al. 2012b). Also multilocus phylogenetic analysis of *PhC2* failed to unambiguously assign this collection to one of the known phylopecies within the complex (FIG. 3). Additional Southern European collections will be required to determine the identity of *M. inamoena*.

Morchella norvegiensis Jacquet. ex R. Kristiansen, Agarica 10/11:9. 1990. SUPPLEMENTARY FIG. 1d

Specimens examined. NORWAY. ØSTFOLD: Fredrikstad, Torp Bruks towards Glomma, 23 Apr 1981, R. Kristiansen, Jacquetant 230581 (holotype of *M. norvegiensis*, O 72835).

Descriptions and illustrations. Kristiansen (1982:70 and FIG. 3, as “5. *Morchella* sp.”); Jacquetant (1984:100–101); Kristiansen (1990:9).

Notes. The ITS and LSU rDNA sequences from the holotype of *M. norvegiensis* places it in a complex of phylogenetic species (*Mel*-17-19-20-34) (FIG. 2, SUPPLEMENTARY FIG. 1d). The ITS sequence is identical to that generated from the holotype of *M. conicopapyracea*, which was collected on the same site three days later. Thus, *M. norvegiensis* and *M. conicopapyracea* are likely conspecific, although this needs to be confirmed using DNA sequence analyses from other loci (*RPB1*, *RPB2* and *TEF1*) (Du et al. 2012b).

Morchella section Rufobrunnea Clowez & Courtec., Bull Soc Mycol France 126(3–4):219. 2012.

Notes. The holotypes of *Morchella anatolica* (K(M)157099) and *M. rufobrunnea* (XAL 31565) have been analyzed phylogenetically (O’Donnell et al. 2011, Taşkın et al. 2012).

Morchella anatolica Işıloğlu et al., Mycologia 102:455. 2010. FIG. 4b

[= *Morchella lanceolata* Clowez & Illescas in Clowez, Bull Soc Mycol France 126(3–4):282. 2012, nom. inval. (“*ad int.*”, no diagnosis, no type designated)]

Specimens examined. SPAIN. CÓRDOBA: Hornachuelos, pasada de la Agciras, under *Phyllirea latifolia* and *Nerium*

oleander, close to *Fraxinus* sp. and *Quercus* sp., Apr 2013, T. Illescas, *PhC233* (CEFE-CNRS, Montpellier, as “*M. lanceolata*”).

Notes. Before the discovery of this distinctive species in Spain in Apr 2013, it was only known from the type locality in Turkey (Işıloğlu et al. 2010). *Morchella anatolica* is sister to *M. rufobrunnea*, and together they represent the earliest diverging clade of true morels (Taşkın et al. 2012). The provisional name *Morchella lanceolata* was previously used for the Spanish collection (Clowez 2012). The known distribution of *M. anatolica* suggests that it might be present in other Mediterranean areas. In contrast to the description and picture published by Işıloğlu et al. (2010), the material collected by T. Illescas lacked purplish tinges (FIG. 4b).

Morchella rufobrunnea Guzmán et F. Tapia, Mycologia, 90:706. 1998.

Specimens examined. AUSTRALIA. Locality unknown, under olive trees on pine woodchips, 2011, P. Donecker, *PhC96* (LIP 0900123).

Notes. This basal species has only been collected from disturbed sites in Mexico (Guzmán and Tapia 1998), California, Michigan and Oregon (Kuo 2008), Australia (Elliott et al. 2014), Israel (Masaphy et al. 2010) and Cyprus (Loizides 2012). Following the initial report of its culture on a mulch substrate in the laboratory as *M. esculenta* (Ower 1982), it was grown commercially in Michigan and Alabama (Ower et al. 1986). Its current transcontinental distribution appears to be due to recent human activities. The specimens studied here represent the third collection of this species from Australia (Elliott et al. 2014).

DISCUSSION

Results of the present study provide the most detailed taxonomic assessment and nomenclatural treatment of true morels (*Morchella*) to date in Europe and North America. In response to the recent publication of a morphology-based taxonomic treatment of true morels in Europe and North America (Clowez 2012), followed shortly thereafter by a molecular phylogenetic and morphology-based revision of *Morchella* in North America (Kuo et al. 2012), the current study was initiated to determine whether any of the taxa reported in these two studies are synonyms. Forty-seven *Esculenta* and 60 *Elata* Clade collections, mostly from Clowez (2012), were sequenced and analyzed phylogenetically together with morel sequences downloaded from GenBank (FIGS. 1–3). These analyses revealed that at least six of the 13 species described in Kuo et al. (2012) are later synonyms of ones published in Clowez (2012). For example, *M.*

esculentoides, the most common Esculenta Clade yellow morel in North America (O'Donnell et al. 2011), was shown to be a synonym of *M. americana*. Our type studies also revealed that 12 new species names introduced in Clowez (2012) are synonyms, including one name in *M. esculenta*, three names in *M. americana* and six in *M. vulgaris* (TABLE I). While progress was made towards stabilizing the taxonomy of *Morchella* by designating lectotypes or epitypes for nine taxa, and determining that *M. conica* is illegitimate at the rank of species, the taxonomic position of *M. elata* requires further study. Even if Elias Fries deposited authentic material of *M. elata* in UPS, his two-century old specimens are unlikely to yield any useful DNA sequence data. Nevertheless, Fries' collections may help identify the type locality so that the identity of this iconic species can be determined by analyzing multiple contemporary collections.

Contrary to reports of low species diversity in Europe based on limited sampling (O'Donnell et al. 2011, Taşkın et al. 2012), we discovered that Europe and North America possess similar numbers of *Morchella* spp. by analyzing the rich collections included in Clowez (2012). Only three of the *Morchella* species phylogenetically identified in Europe (i.e. *Mel*-19, *Mel*-23 and *Mes*-5) and North America (i.e. *Mel*-8, *Mel*-19 and *Mel*-36) are now unnamed (TABLE I), and preliminary descriptions of the latter two taxa have been made, though not formally published (Beug and O'Donnell 2014; Voitek and Voitek 2014; Voitek et al. 2014). However, because most early names of *Morchella* were described from Europe (roughly 77 valid European names were available prior to Clowez (2012), excluding many subspecific epithets; see Index Fungorum <http://www.indexfungorum.org/>), and because many of the species in Asia ($n = 21$) and Turkey ($n = 6$) are thought to be endemic, these are still left unnamed (Taşkın et al. 2010, 2012; Du et al. 2012a, b). It should be pointed out that the European names published by Jacquetant are invalid (Jacquetant 1984, Jacquetant and Bon 1985), because none of the publications included, or made reference to, both the description, Latin diagnosis and type material (see notes about *M. eximoides* above).

To reflect the taxonomic advances reported herein, we have updated the NCBI GenBank and *Morchella* MLST databases, and ARS (NRRL) and CBS-KNAW Culture Collection databases, with the names accepted here. The sequence data generated in the present study, in which roughly half of the sequences are derived from type specimens, will serve as invaluable reference points for future systematic, ecological and evolutionary studies on *Morchella*. Future studies can

also benefit significantly from the discovery of additional phylogenetically informative genes once they are mined from several morel whole genome sequences (e.g. <http://genome.jgi.doe.gov/programs/fungi/1000fungalgenomes>). Once discovered, these genes should provide invaluable markers for assessing the endemic area of widespread species (Pringle et al. 2009), such as *M. rufobrunnea* and *M. galilaea*, which we speculate may have been introduced inadvertently into exotic areas by the global trade of plants (Vellinga et al. 2009). Lastly, because the present and previous molecular phylogenetic studies have revealed that the majority of *Morchella* species are restricted geographically to a continent, results of the present study will be invaluable in formulating policies that promote the conservation genetics of these charismatic fungi (Hibbett and Donoghue 1996).

ACKNOWLEDGMENTS

We are especially grateful for the help of the curators of the herbaria who kindly allowed us to generate DNA sequences from exsiccata kept at O (Katriina Bendiksen, Oslo) and LUG (Neria Röhmer, Lugano), to colleagues who contributed DNA sequences from their own material: Segula Masaphy (Israel), Mustapha İşiloğlu and Hayrunisa Bas Sermenli (Turkey), and by providing bibliographic and unpublished data: Philippe Callac (INRA, Bordeaux), Christophe Lécure (LIP, Lille), Michael Loizides (Cyprus), Anne Molia (Oslo) and Nicolas Van Vooren (Lyon), to Roy Kristiansen (Fredrikstad) for detailed information about his collections and correspondences with Émile Jacquetant, to Francesco Bellù (Bolzano) for the translation of Bresadola's handwritten labels on collections of *M. tridentina* kept at Stockholm, and to David Hawksworth and Scott Redhead for pointing out the invalidity of Jacquetant's names and their expert assistance in resolving the mix-up of the original material of *M. eximoides* and *M. conicopapyracea*. P. Clowez especially thanks all professional and amateur mycologists who sent him exsiccata and photographs of morels cited above (see SUPPLEMENTARY TABLE I). Photo credits for FIGS. 4 and SUPPLEMENTARY FIGS. 1, 2 are: Philippe Clowez (4a, 4d, 4i, 4l and 4o), Tomás Illescas (4b), Renée Lebeuf (4c), Luis Romero de la Osa (4e, 4h), Hugh and Sandi Smith (4f), Chris Matherly (4g), Pierre-Arthur Moreau (4j, S1b, S1c and S1d), Luc Martin (4k), Claudine Michaud (4m), Nicolas Van Vooren (4n), Ramona Ubral Hedenberg (S1a) and Roy Kristiansen (S2a-m). DNA sequences were generated at the Service of Genetic Markers of UMR CEFE 5175. We thank Stacy Sink (ARS-USDA, Peoria, Illinois) and Xianghua Wang (SMNH, Stockholm) for generating some of the DNA sequence data and Nathane Orwig (ARS-USDA, Peoria, Illinois) for running them in the NCAUR DNA Core Facility, and Béatrice Boury (Univ. Lille 2) for assistance in the computerized management of LIP. The mention of firm names or trade products does not imply

that they are endorsed or recommended by the US Department of Agriculture over other firms or similar products not mentioned. The USDA is an equal opportunity provider and employer. This project was supported by the the grant “Diversité des champignons mycorhiziens des plantes” (DivMyc, to Marc-André Selosse) from the network Bibliothèque Du Vivant (BDV) funded by the CNRS, the Muséum National d’Histoire Naturelle de Paris, the INRA and the CEA (Centre National de Séquençage). We are grateful to Marie-Pierre Dubois, Finn Kjellberg and Jean-Yves Rasplus for their support from the BDV program.

LITERATURE CITED

- Anisimova M, Gascuel O. 2006. Approximate likelihood-ratio test for branches: A fast, accurate, and powerful alternative. *Syst Biol* 55:539–552, doi:10.1080/10635150600755453
- , Gil M, Dufayard J-F, Dessimoz C, Gascuel O. 2011. Survey of branch support methods demonstrates accuracy, power, and robustness of fast likelihood-based approximation schemes. *Syst Biol* 60:1–15, doi:10.1093/sysbio/syr041
- Arora D. 1986. Mushrooms demystified: a comprehensive guide to the fleshy fungi. Berkeley: Ten Speed Press. 959 p.
- Beug M, O’Donnell K. 2014. Morel species Mel-19—preliminary report. *Omphalina* 5:3–4.
- Boudier J-LE. 1887. Notice sur les discomycètes figurés dans les dessins inédits de Dunal conservés à la Faculté de Montpellier. *Bull Soc Mycol Fr* 3:88–96, pl. 8.
- . 1897. Révision analytique des Morilles de France. *Bull Soc Mycol Fr* 13:129–153.
- . 1909. Icones mycologicae ou iconographie des champignons de France principalement discomycètes avec texte descriptif. Tome II, pl. 194–421. Librairie des Sciences Naturelles, Paris.
- Breitenbach J, Kränzlin F. 1991. Champignons de Suisse, tome 1. Mykologia, Lucern.
- Bresadola G. 1898. Fungi tridentini novi, vel nondum delineati, descripti, et iconibus illustrati. Vol. 2. J. Zippel, Trento.
- Brondeau ALG, (Jegun de Marans, dit L de). 1830, Recueil de plantes cryptogames de l’Agenais, omises dans la Flore Agenaise, décrites et dessinées par M. L. de Brondeau. Fascicule III. P. Noubel, Agen.
- Buscot F, Wipf D, Di Battista C, Munch JC, Botton B, Martin F. 1996. DNA polymorphisms in morels I: PCR/RFLP analysis of the ribosomal DNA spacers and microsatellite primed PCR. *Mycol Res* 100:63–71, doi:10.1016/S0953-7562(96)80101-8
- Castresana J. 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Mol Biol Evol* 17:540–552, doi:10.1093/oxfordjournals.molbev.a026334
- Chevenet F, Brun C, Bañuls AL, Jacq B, Christen R. 2006. TreeDyn: towards dynamic graphics and annotations for analyses of trees. *BMC Bioinform* 7:439, doi:10.1186/1471-2105-7-439
- Clowez P. 2012(‘2010’). Les morilles. Une nouvelle approche mondiale du genre *Morchella*. *Bull Soc Mycol Fr* 126:199–376.
- Degreef J, Fischer E, Sharp C, Raspé O. 2009. African *Morchella crassipes* (Ascomycota, Pezizales) revealed by analysis of nrDNA ITS. *Nova Hedwigia* 88:11–22, doi:10.1127/0029-5035/2009/0088-0011
- Dennis RWG. 1978. British Ascomycetes. J. Cramer, Vaduz.
- Dereeper A, Guignon V, Blanc G, Audic S, Buffet S, Chevenet F, Dufayard JF, Guindon S, Lefort V, Lescot M, Claverie JM, Gascuel O. 2008. Phylogeny.fr: robust phylogenetic analysis for the non-specialist. *Nuc Acids Res* 36(Web Server issue):W465–469, doi:10.1093/nar/gkn180
- Dissing H. 2000. Pezizales Bessey. In: Hansen L, Knudsen H, eds., Nordic Macromycetes. Vol. 1. Ascomycetes, 55–127. Nordsvamp, Copenhagen.
- Du X-H, Zhao Q, O’Donnell K, Rooney AP, Yang ZL. 2012a. Multigene molecular phylogenetics reveals true morels (*Morchella*) are especially species-rich in China. *Fungal Genet Biol* 49:455–469, doi:10.1016/j.fgb.2012.03.006
- , Yang ZL, Hansen K, Taşkın H, Büyükalaca S, Dewsbury D, Moncalvo J-M, Douhan GW, Robert VARG, Crous PW, Rehner SA, Rooney AP, Sink S, O’Donnell K. 2012b. How well do ITS rDNA sequences differentiate species of true morels (*Morchella*)? *Mycologia* 104:1351–1368, doi:10.3852/12-056
- Edgar RC. 2004. MUSCLE: a multiple sequence alignment method with reduced time and space complexity. *BioMed Cen Bioinform* 5:113, doi:10.1186/1471-2105-5-113
- Elliott TF, Bougher NL, O’Donnell K, Trappe JM. 2014. *Morchella australiana* sp. nov., an apparent Australian endemic from New South Wales and Victoria. *Mycologia* 106:113–118, doi:10.3852/13-065
- Fries EM. 1822. Systema Mycologicum II (1). Lundae.
- Gardes M, Bruns TD. 1993. ITS primers with enhanced specificity for basidiomycetes – application to the identification of mycorrhizae and rusts. *Mol Ecol* 2: 113–118, doi:10.1111/j.1365-294X.1993.tb00005.x
- Guzmán G, Tapia F. 1998. The known morels in Mexico, a description of a new blushing species, *Morchella rufobrunnea*, and new data on *M. guatemalensis*. *Mycologia* 90:705–714, doi:10.2307/3761230
- Hibbett D, Donoghue MJ. 1996. Implications of phylogenetic studies for conservation of genetic diversity in shiitake mushrooms. *Conser Biol* 10:1321–1327, doi:10.1046/j.1523-1739.1996.10051321.x
- Imazeki R, Otani Y, Hongo T. 1988. Fungi of Japan. Yama-Kei Publishers Co., Ltd., Tokyo (in Japanese). 623 p.
- Işiloğlu M, Alli H, Spooner BM, Solak MH. 2010. *Morchella anatolica* (Ascomycota), a new species from southwestern Anatolia, Turkey. *Mycologia* 102:455–458, doi:10.3852/09-186
- Jacquetant E. 1984. Les morilles. Lausanne, Piantanida.
- , Bon M. 1985(‘1984’). Typifications et mises au point nomenclaturales dans l’ouvrage “Les morilles” (de E. Jacquetant), Nature-Piantanida 1984. *Doc Mycol* 14:1.
- Kanwal HK, Acharya K, Ramesh G, Reddy MS. 2011. Molecular characterization of *Morchella* species from

- the western Himalayan region of India. *Curr Microbiol* 62:1245–1252, doi:10.1007/s00284-010-9849-1
- Kellner H, Renker C, Buscot F. 2005. Species diversity within the *Morchella esculenta* group (Ascomycota: Morchellaceae) in Germany and France. *Org Diver Evol* 5:101–107, doi:10.1016/j.ode.2004.07.001
- Kickx J. 1867. Flore cryptogamique des Flandres. Tome Premier. Gent, H. Hoste.
- Korf RP. 1972. Synoptic key to the genera of the Pezizales. *Mycologia* 64:937–994, doi:10.2307/3758070
- Kristiansen R. 1982. Bidrag til Østfolds Ascomycetflora I. *Agarica* 3:65–72.
- . 1990. Nye arter for vitenskapen, originalbeskrevet fra Østfold. *Agarica* 10/11:6–12.
- Krombholz JV von. 1834. Naturgetreue Abbildungen und Beschreibungen der essbaren, schädlichen und verdächtigen Schwämme, Heft 3. G. Calve, Praha J, 36 p., pl. XV–XXII.
- Kuo M. 2008. *Morchella tomentosa*, a new species from western North America, and notes on *M. rufobrunnea*. *Mycotaxon* 105:441–446.
- , Dewsbury DR, O'Donnell K, Carter MC, Rehner SA, Moore JD, Moncalvo JM, Canfield SA, Stephenson SL, Methven A, Volk TJ. 2012. Taxonomic revision of true morels (*Morchella*) in Canada and the United States. *Mycologia* 104:1159–1177, doi:10.3852/11-375
- Liu YJ, Whelen S, Hall BD. 1999. Phylogenetic relationships among ascomycetes: evidence from an RNA polymerase II subunit. *Mol Biol Evol* 16:1799–1808, doi:10.1093/oxfordjournals.molbev.a026092
- Loizides M. 2012. *Morchella rufobrunnea*. *Μυκητολόγος* 5: 10–13.
- Mann H, Mann P. 2014. *Morchella importuna*. The Pasadena mulch morel. *Omphalina* 5:11–12.
- Marchand A. 1971. Les champignons du Nord et du Midi. Tome 1. Perpignan.
- . 1973. Les champignons du Nord et du Midi. Tome 2. Perpignan.
- Masaphy S, Zabari L, Goldberg D, Jander-Shagug G. 2010. The complexity of *Morchella* systematics: a case of the yellow morel from Israel. *Fungi* 3:14–18.
- Matheny PB, Liu YJ, Ammirati JF, Hall BD. 2002. Using *RPB1* sequences to improve phylogenetic inference among mushrooms (*Inocybe*, Agaricales). *Am J Bot* 89: 688–698, doi:10.3732/ajb.89.4.688
- McKnight KH, McKnight VB. 1987. A field guide to mushrooms in North America. Petersons Field Guides. New York, Houghton Mifflin Co. 429 p.
- McNeill J, Barrie FR, Buck WR, Demoulin V, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Marhold K, Prado J, Prud'homme Van Reine WF, Smith GF, Wiersema JH, Turland NJ. 2012. International Code of Nomenclature for algae, fungi, and plants (Melbourne Code). *Regnum Vegetabile* 154. Koeltz Scientific Books, Königstein.
- Medardi G. 2006. Atlante fotografico degli Ascomiceti d'Italia. AMB Trento.
- Mentzel G. 1682. *Index nominum plantarum multilinguis*. Berlin.
- Micheli PA. 1729. *Nova plantarum genera juxta Tournefortii methodum disposita*. Florence.
- Moreau P-A, Bellanger J-M, Clowez P, Courtecuisse R, Hansen K, Knudsen H, O'Donnell K, Richard F. 2014. (2289) Proposal to conserve the name *Morchella semilibera* against *Phallus crassipes*, *P. gigas* and *P. undosus* (Ascomycota). *Taxon* 63:677–678, doi:10.12705/633.20
- , Hériveau P, Bourgade V, Bellanger J-M, Courtecuisse R, Fons F, Rapior S. 2011. Redécouverte et typification des champignons de la région de Montpellier illustrés par Michel-Félix Dunal et Alire Raffeneau-Delile. *Cryptog Mycol* 32:255–276, doi:10.7872/crym.v32.iss3.2011.255
- O'Donnell K. 2014. A preliminary assessment of the true morels (*Morchella*) in Newfoundland and Labrador. *Omphalina* 5:3–6.
- , Rooney AP, Mills GL, Kuo M, Weber NS, Rehner SA. 2011. Phylogeny and historical biogeography of true morels (*Morchella*) reveals an early Cretaceous origin and high continental endemism and provincialism in the Holarctic. *Fungal Genet Biol* 48:252–265, doi:10.1016/j.fgb.2010.09.006
- Ower R. 1982. Notes on the development of the morel ascocarp: *Morchella esculenta*. *Mycologia* 74:142–144, doi:10.2307/3792639
- , Mills GL, Malachowski JA. 1986. Cultivation of *Morchella*. US patent 4594809.
- Persoon CH. 1818. *Traité sur les champignons comestibles*. Paris, Belin-Leprieur.
- Pringle A, Adams RI, Cross HB, Bruns TD. 2009. The ectomycorrhizal fungus *Amanita phalloides* was introduced and is expanding its range on the west coast of North America. *Mol Ecol* 18:817–833, doi:10.1111/j.1365-294X.2008.04030.x
- Rehner SA, 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, doi:10.3852/mycologia.97.1.84
- Röllin O, Anthoine A. 2001. Les morilles noires du Chablais savoyard genre *Morchella*, section Distantes. 1 - Remarques préliminaires et présentation de *Morchella elata* Fr. et *Morchella tridentina* Bres. *Bull trimestriel Féd mycol Dauphiné-Savoie* 161:7–12.
- Schoch CL, Seifert KA, Huhndorf S, Robert V, Spouge JL, Levesque CA, Chen W, Fungal Barcoding Consortium. 2012. Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for Fungi. *Proc Natl Acad Sci USA* 109:6241–6246, doi:10.1073/pnas.1117018109
- Stefani FOP, Sokolski S, Wurtz TL, Piché Y, Hamelin RC, Fortin JA, Bérubé JA. 2010. *Morchella tomentosa*: a unique belowground structure and a new clade of morels. *Mycologia* 102:1082–1088, doi:10.3852/09-294
- Taşkın H, Büyükalaca S, Doğan HH, Rehner SA, O'Donnell K. 2010. A multigene molecular phylogenetic assessment of true morels (*Morchella*) in Turkey. *Fungal Genet Biol* 47:672–682, doi:10.1016/j.fgb.2010.05.004
- , ———, Hansen K, O'Donnell K. 2012. Multilocus phylogenetic analysis of true morels (*Morchella*) reveals

- high levels of endemics in Turkey relative to other regions of Europe. *Mycologia* 104:446–461, doi:[10.3852/11-180](https://doi.org/10.3852/11-180)
- Taylor JW, Jacobsen DJ, Kroken S, Kasuga T, Geiser DM, Hibbett DS, Fisher MC. 2000. Phylogenetic species recognition and species concepts in fungi. *Fungal Genet Biol* 31:21–32, doi:[10.1006/fgbi.2000.1228](https://doi.org/10.1006/fgbi.2000.1228)
- Thiers B. [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/>).
- Trattinnick L. 1805. *Fungi austriaci ad specimina viva cera expressi, descriptiones ac historiam naturalem complect.* Wien: J. Geistinger.
- Vellinga EC, Wolfe BE, Pringle A. 2009. Global patterns of ectomycorrhizal introductions. *New Phytol* 181:960–973, doi:[10.1111/j.1469-8137.2008.02728.x](https://doi.org/10.1111/j.1469-8137.2008.02728.x)
- Vilgalys R, Hester M. 1990. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *J Bacteriol* 172:4238–4246.
- Voitk A, Burzynski M, O'Donnell K, Voitk M, Marceau A. 2014. Mel-36 – preliminary description of a new morel species. *Omphalina* 5:7–10.
- , Voitk M. 2014. The effects of weather on the color of Mel-36. *Omphalina* 5:16–21.
- Volk TJ, Leonard TJ. 1989. Physiological and environmental studies of sclerotium formation and maturation in isolates of *Morchella crassipes*. *Appl Environ Microbiol* 55:3095–3100.
- Weber NS. 1995. *A morel hunter's companion: a guide to the true and false morels.* Lansing, MI: Thunder Bay Press. 209 p.
- Weinmann JG. 1739. *Phytanthozoa-Iconographia, sive Conspectus aliquot millium, tam indigenarum quam exoticarum, ex quatuor mundi partibus, longâ annorum ferie indesessoque studio.* Vol. II. C.D.E.F. Ratisbonae: H. Lenzium. p 1–516, pl. 276–525.
- Wipf D, Clowez P, Bedell JP, Kochinsky S, Botton B, Buscot F. 1997. Recent advances in ecology and systematics of morels. *Cryptogamie Mycol* 18:95–109.
- , Fribourg A, Munch JC, Botton B, Buscot F. 1999. Diversity of the internal transcribed spacer of rDNA in morels. *Can J Microbiol* 45:769–778, doi:[10.1139/w99-070](https://doi.org/10.1139/w99-070)
- Zwickl DJ. 2006. Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. Ph.D. Dissertation. The University of Texas at Austin.