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

Franck Richard
Jean-Michel Bellanger
UMR 5175 CEFE, INSERM, Campus CNRS, 1919 Route de Mende, F-34293 Montpellier, France

Philippe Clowez
56 place des Tilleuls, F-60400 Pont-l’Eveêque, 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 CEFE, Université de Montpellier, Campus CNRS, 1919 Route de Mende, F-34293 Montpellier, France

Régis Courtecuisse
Pierre-Arthur Moreau
Département des Sciences végétales et fungiques, 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-Ia (TEFa), 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 (Taskin 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;
Dissing 2000: eight species in the Nordic countries), while others accepted many species, varieties and forms (Krombholz 1834: 11 species; Boudier 1897: 20 species; Jacquemant 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* (İsıloglu 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; Voit et al. 2014). Because binomials could be applied to only four species with confidence, phyllospecies 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 REDExtract-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/EFS3AR (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 μL, including 1 μL genomic DNA, in a master cycler gradient thermos-cycler (Eppendorf AG, Hamburg, Germany). The cycling parameters were as follows: 94 C for 3 min, 35 cycles of 94 C for 30 s, 55 C for 30 s, 72 C for 1–2 min, followed by 72 C for 7 min. Ambiplos 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 (Codon Code 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 approximate likelihood-ratio test, implemented in PhyML support was assessed using the non-parametric version of the approximate likelihood-ratio test, implemented in PhyML (SHaLRT; 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 Rufobrunneae/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).


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


Section *Morchella*


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


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. stepicola*. The ML analysis was run in PhyML 3.0aLRT using the GTR+$\Gamma$+$\Phi$ 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


**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 RPB and TEF1, since ITS sequence could not be obtained for *PhC88* (results not shown, see SUPPLEMENTARY TABLE 1).

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

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


SWITZERLAND. GENEVA: Malval, along the Allondon river, 6 May 2004, O. Röllin, *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;
FIG. 2. ML phylogeny of *Morchella* sect. *Distantes* (Elatia 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 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...
M. esculenta within and ovoid pileus, they were nested phylogenetically. 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. Pseudoaphanatae 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).


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.


Specimens examined. USA. NEW JERSEY: locality unknown, under Liriodendron virginiana, 2011, C. Michaud, PhC76 (holotype of Morchella sceptri-formis, 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).


Specimens examined. SERBIA. Beograd, Titelisky, 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.


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).


Fig. 4a Basionym: Morchella esculenta β vulgaris Pers., Syn Meth Fung:619. 1801.

Notes. Accepted voucher numbers). Accepted 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).
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), CEFE-CNRS.

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).

Specimens examined. FRANCE. CHARENTES-MARITIMES: Royan, white dune with Ammophila arenaria, 2011, L. Martin, PhC109 (LIP 0900138). OISE: Cainses, 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); Fleuryes, 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 Rumunculus 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); Neully-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 0900015). ILE-DE-FRANCE: locality not specified, under Fraxinus excelsior, Apr 2010, M.-A. Delaunoy, PhC21 (holotype of Morchella conica var. pygmaea, LIP 0900061). SPAIN. ANDALUCIA: 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 spongiola 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. spongiosa. 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. spongiosa with Ulmus spp. We accept M. vulgaris here as lectotyphified 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.


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. septentri- nalis (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


Notes. Morchella deliciosa (Fig. 3; applied to Mel26) 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 Kraenzlin 1984:45; Marchand 1971:192; 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).

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.


Notes. Morchella conica (Clowez, Bull Soc Mycol France 126:306. 2012) 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 Kraenzlin 1984:45; Marchand 1971:192; 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.
TABLE I. Correspondence between species designations in Du et al. (2012a, b), Clowez (2012), Kuo et al. (2012) and the present study

<table>
<thead>
<tr>
<th>Clade/section</th>
<th>Du et al. (2012a, b)</th>
<th>Clowez (2012)</th>
<th>Kuo et al. (2012)</th>
<th>Richard et al. (this study)</th>
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<td><strong>Rufobrunnea</strong></td>
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370 Mycologia myco-107-02-10.3d 4/3/15 09:56:48 370 Cust # 14-166
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**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.

*See notes on *M. elata*.
*See notes on *M. quercus-ilicis*.
*For a description see Beug and O’Donnell (2014).
*See notes on *M. conica*.
*See notes on *M. inamoena* and *M. pulchella*.
*See notes on *M. conica*.
*For a description see Voit and Voitk (2014), Voitk et al. (2014).
*M. deliciosa*: 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 M5 was based (O’Donnell et al. 2011) could not be sequenced. Therefore, additional study is needed to critically assess whether M5 and M17 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* (*Mel25*) from *Mel13* (Fig. 2), as previously established (Du et al. 2012b). However, the multilocus phylogenetic analysis revealed that the collections cited above correspond to *Mel26* (Fig. 3). Previously sequences of *M. deliciosa* (as *Mel26*) were only known from Turkey (Taskin 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 Weimann’s collecting area around Regensburg). Because we lack *Mel26* collections from these areas, we postpone epitypification of *M. deliciosa* until such material becomes available and assigned to species through multilocus phylogenetic analysis.


**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* and *Olea europaea*, May 2009, L. Martin PhC15, (locity 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 *Mel25* (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. (Taskin et al. 2012, as *Mel25*). 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.

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

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 **M**<sub>el</sub>-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).


Notes. This species has been assigned 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.


Specimens examined. CANADA. QUEBEC: under Populus grandidentata, 10 May 2011, 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.


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 CEFE-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.

**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 *Pinus sylvestris*, 2010, PhC82 (epitype designated here, LIP 0900019, MycoBank MBT 177745). Isoepitypices S (F255984) and CEFE-CNRS.

**Specimens examined.** FRANCE. ALPES DE HAUTE-PROVENCE, Auzet, under *Pinus sylvestris*, 2010, PhC83 (LIP 0900115, as ‘*M. conica var. purpurascens*’).

**Notes.** Multilocus phylogenetic analysis of the two specimens examined by us assigns them to *M* &20, a phylogenetic species first discovered in Central Anatolia (Taşkin et al. 2010; Fig. 3). This species and *M. deliciosa* as adopted here, were collectively treated by Clowez (2012) under the name ‘*M. conica var. purpurascens*’. 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 (Taşkin 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. norvegicensis*.


**Fig. 4h**


**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 *M* &11 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. duvalii* (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


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

Specimens examined. CANADA. QUEBEC: Quebec, under Populus grandidentata, 2011, R. Lebeuf, PhC121 (LIP 09000149, as “M. angusticeps”); ibid., under Fraxinus americana, Apr 2011, R. Lebeuf, PhC123 (LIP 0900151, as “M. sp.”). 

Notes. This is Mel24. The paraphyletic relationships between this species and M. pulchella (Mel31) are discussed under M. pulchella (see below). Clowez (2012) interpreted one of the collections from Quebec (PhC121) as “M. angusticeps”. As epityped by Kuo et al. (2012), M. angusticeps represents a distinct species (Mel15) (see M. angusticeps above). Also see notes on M. inamoena (see Doubtful names below).


Specimens examined. USA. Locality unknown, burnt ground under Pinusaceae, 17 Jun 2007, D. Winkler, PhC350 (LIP 09000990, as “Morchella sp.”).

Notes. This post-fire morel corresponds to Mel6 (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. Cheema, PhC47 (LIP 09000087). Origin unknown, purchased at the Rungis market (France), May 2010, P. Clowez, PhC48 (LIP 09000088).

Notes. This distinctive post-fire morel, which was informally designated as Mel1 by O’Donnell et al. (2011), has only been reported from Western North America.


Supplementary fig. 1a. Typification: ITALY. TREVINO: “in silva Tectiologicum junta rivulos, acquadotta”, 10 May 1882, G. Bresadola (lectotype designated here, S F9101, MycoBank MBT178121, original material of Morchella tridentina).

Doubtful names in sect. **Distantes**

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


**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. **Tratt.** (Trattinnick 1805:11) was published as a superfluous name in sect. **Distantes** and we suggest it belongs to sect. **Tratt.** (Trattinnick 1805:11) was cited in the protologue of *M. continua* by Persoon (1818). Therefore, according to the present Code (McNeill et al. 2012), *M. continua* was published as a superfluous name for *M. conica*. 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 will be challenging. 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. *violacea*) corresponded to *Mel*-26, for which the name *M. delicosa* is used here (Fig. 3). Others corresponded to *Mel*-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* (Mes-2) (cited as var. *pseudoeximia* Clowez, from Chile) (not shown, see Supplementary Table 1). 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**


**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 (*Mel*-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.


**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* (= *Mel*-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 *Mel*-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 *Mel*-10 (Table 1). 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

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 phyllospecies 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


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, SUPPLEMENTARYFIG. 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 (RPBI, RPB2 and TEF1) (Du et al. 2012b).


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

Specimens examined. SPAIN. CORDOBA: Hornachuelos, pasada de la Algeciras, under Phylirea 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 (Isılogoğlu et al. 2010). Morchella anatolica is sister to M. rufobrunnea, and together they represent the earliest diverging clade of true morels (Taskin 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 Isılogoğlu et al. (2010), the material collected by T. Illescas lacked purplish tinges (Fig. 4b).

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.
Morchella 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, Taskin 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*-9 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; Voitk and Voitk 2014; Voitk 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 (Taskin 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. esculioides* 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).

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