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REVIEW

Has taxonomic vandalism gone too far? A case study, the rise of the pay-to-publish model and the pitfalls of *Morchella* systematics

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Abstract

The genus *Morchella* has gone through turbulent taxonomic treatments. Although significant progress in *Morchella* systematics has been achieved in the past decade, several problems remain unresolved and taxonomy in the genus is still in flux. In late 2019, a paper published in the open-access journal *Scientific Reports* raised serious concerns about the taxonomic stability of the genus, but also about the future of academic publishing. The paper, entitled “High diversity of *Morchella* and a novel lineage of the esculenta clade from the north Qinling Mountains revealed by GCPSR-based study” by Phanpadith and colleagues, suffered from gross methodological errors, included false results and artifactual phylogenies, had misapplied citations throughout, and proposed a new species name invalidly. Although the paper was eventually retracted by *Scientific Reports* in 2021, the fact that such an overtly flawed and scientifically unsound paper was published in a high-ranked Q1 journal raises alarming questions about quality controls and safekeeping procedures in scholarly publishing. Using this paper as a case study, we provide a critical review on the pitfalls of *Morchella* systematics followed by a series of recommendations for the delimitation of species, description of taxa, and ultimately for a sustainable taxonomy in *Morchella*. Problems and loopholes in the academic publishing system are also identified and discussed, and additional quality controls in the pre- and post-publication stages are proposed.

Keywords Cryptic species · Genealogical Concordance Phylogenetic Species Recognition · Integrative taxonomy · Methodology · Phylogenetics · Morels · Nomenclature · Species delimitation · Systematics

Introduction

Species of *Morchella* Dill. ex Pers. (Ascomycota, Pezizomycetes) are highly sought after and prized edible fungi, but taxonomic arrangements in the genus have been chronically unstable due to considerable morphological overlap among taxa and inherent difficulties in the delimitation of species (O’Donnell et al. 2011; Taşkin et al. 2010, 2012;

Du et al. 2012a, 2012b). Over 80 species-level lineages of *Morchella* have been inferred by molecular phylogenetics in recent years, mostly distributed in temperate latitudes of the Northern Hemisphere. So far, about 58 of these have been linked to classical or newly proposed Linnaean binomials and a number of synonymies have been established (Richard et al. 2015; Du et al. 2019b; Weholt et al. 2020; Loizides et al. 2021). However, several taxonomic issues remain to be resolved and systematic arrangements in the genus are still in flux. Much of the instability can be attributed to a number of problems, such as (i) the absence of a uniformly applied methodology in species delimitation; (ii) insufficient sampling efforts; (iii) a shortage of integrative taxonomical approaches; (iv) unresolved synonymies

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and misapplied names; (v) occasional hybridization among species; (vi) poor or inaccurate morphological descriptions of taxa; (vii) a fragmented or incomplete understanding of their distributional patterns and ecological niches; (viii) lack of molecular data from early-described taxa; and (ix) lack of a common language in descriptive terminology (Du et al. 2012b, 2019a, 2020; Loizides et al. 2015, 2016, 2021; Loizides 2017; Clowez and Moreau 2018a, 2018b; Baroni et al. 2018; Petrželová and Sochor 2019).

In December 2019, a paper entitled “High diversity of *Morchella* and a novel lineage of the esculenta clade from the north Qinling Mountains revealed by GCPSR-based study” by Phanpadith and colleagues was published in the open-access journal *Scientific Reports*. This journal was reported to be the 7th most cited in the world with 2 million viewers per month and has an impact factor (IF) of 3.998 (Journal Citation Reports, Clarivate Analytics 2020). A “rigorous, objective and constructive peer review” is promised by the journal, which claims to publish “scientifically robust, original, and of the highest quality research” (<https://www.nature.com/srep/about>). The publication by Phanpadith et al. (2019) falls profoundly short of such standards. This paper, which has been subsequently retracted by the journal, suffered from an array of methodological deficiencies and fallacious claims, presented false results and artifactual phylogenies, and introduced a new species name invalidly. Because it was published in a high-ranked Q1 journal, a post-publication review of this paper was deemed necessary to debunk the numerous errors and false claims, and prevent contamination to other studies. Indeed, by the time the present review had been completed, another paper by Lagrange and Vernoux (2020) had already cited Phanpadith et al. (2019) reproducing some of their fallacious claims. A point-by-point rebuttal of this study was therefore drafted and an open letter asking for the retraction of the paper was submitted to *Scientific Reports* for publication.

Besides this obvious urgency, the present review was initiated to also address other ongoing problems in *Morchella*, including opposing views with regard to the delimitation of species. These are, on one hand, expressed by multilocus approaches employing a “merging” method based on the concept introduced by O’Donnell et al. (2011) and, on the other hand, by approaches advocating for strict application of Genealogical Concordance Phylogenetic Species Recognition (GCPSR) with polygenic differentiation as a prerequisite, as recently proposed by Petrželová and Sochor (2019). In an effort to stabilize taxonomy within the genus, the current pitfalls in *Morchella* systematics are here further debated and a unified methodology for the circumscription of taxa, including a glossary of descriptive terminology, is proposed. A global up-to-date phylogeny and an overview of confirmed and doubtful species of *Morchella* are also included, to serve as guidelines for future studies. Following

the deeply flawed publication by Phanpadith et al. (2019), problems and loopholes in the current academic publishing system are also identified and discussed, and recommendations for additional quality controls in the pre- and post-publication stages are offered.

Methods and concepts

For the purpose of this review, “species” are broadly understood as separately evolving and potentially interbreeding populations or metapopulations isolated by irreversible reproductive barriers (following, e.g., Mayr 1942; Wiley 1978; Coyne and Orr 2004; de Queiroz 2005; Butlin and Stankowski 2020). “Cryptic species” are defined as phenotypically, ecologically, and biogeographically indistinguishable species. The term “semicryptic” is reserved for species with subtle or unstable discriminating traits and considerable phenotypic overlap with other evolutionary isolated taxa. The term “pseudocryptic” is applied to species that have at some point been regarded as “cryptic,” but have reasonably reliable diagnostic traits that had been previously overlooked (see, e.g., Sáez et al. 2003; Mann and Evans 2007; Lajus et al. 2015). An extended analysis of the inconsistencies of species concepts and species delimitation in *Morchella* is provided below. Definition of GCPSR is based on Taylor et al. (2000). A list of taxonomically resolved and unresolved lineages of *Morchella* is provided in Table 1, with brief notes on the current status and distribution for each species. A glossary of descriptive terminology, along with notes on the taxonomic significance of each morphoanatomical character, are provided in Table 2. Phylogenetic analyses in this work were based on methods described in Richard et al. (2015) and Loizides et al. (2016, 2021). A point-by-point critique of the Phanpadith et al. (2019) paper is available in [Supplemental information](#).

The Phanpadith et al. (2019) paper

A detailed analysis of the paper by Phanpadith et al. (2019) demonstrates that this study suffers from serious methodological, phylogenetic, taxonomical, nomenclatural, and conceptual problems. The phylogenetic grounds of this paper, in particular, are far from sound and include basic errors such as duplicate, poorly amplified, and erroneously aligned sequences, inappropriate use of cladograms and artifactual phylogenies. As an example, in one of the phylogenetic trees (Suppl. Figure 2, Phanpadith et al. 2019), a *Tuber* species (*T. taiyuanense* B. Liu) nests in the same clade as *Morchella* species, with no attempt by the authors to explain this outstanding anomaly. Furthermore, the name of the new species introduced in this paper is invalid, as

Table 1 Overview of phylogenetically and taxonomically resolved and unresolved phylopecies of *Morchella*, including typification details, known distribution range based on molecularly verified collections and current status for each species

Linnaean name	Phylospecies	Typification details	Phylogeography	Status
Rufobrunnea clade (section <i>Rufobrunnea</i>)				
<i>Morchella anatolica</i> = <i>M. lanceolata</i> nom. inval.	–	Described from Turkey (Işiloğlu et al. 2010); sequence attached to the isotype K(M)157099 (Taşkın et al. 2012)	Cyprus, Greece, Spain, Turkey	Resolved and uncontested
<i>Morchella rufobrunnea</i>	–	Described from Mexico (Guzmán and Tapia 1998); sequence attached to the holotype XAL 31565 (O'Donnell et al. 2011)	Australia, Cyprus, Israel, Malta, Mexico, Spain, Switzerland, USA; cultivated	Resolved and uncontested
Esculenta clade (section <i>Morchella</i>)				
<i>Morchella americana</i> = <i>M. americana</i> var. <i>elongata</i> = <i>M. californica</i> = <i>M. claviformis</i> = <i>M. esculentoides</i> = <i>M. populina</i>	Mes-4	Described from Western USA (Clowez 2012); sequence attached to the holotype LIP 0900091 (Richard et al. 2015)	Canada, Czech Republic, France, Germany, Spain, Switzerland, Turkey, USA	Not conclusively resolved because it appears to encompass two biogeographically supported clades and an earlier name probably exists for at least the European clade should the two clades be split in the future; until further clarified, the usage of the current name is provisionally recommended for the inclusive clade
<i>Morchella castaneae</i> = <i>M. brunneorosea</i> = <i>M. brunneorosea</i> var. <i>sordida</i>	–	Described from Spain (Clowez 2012); sequence attached to the holotype PhC114 (Richard et al. 2014)	Portugal, Spain	Resolved and uncontested
<i>Morchella clivicola</i>		Described from China; sequence attached to the holotype FCNU1021 (Du et al. 2019a, 2019b)	China	Resolved and uncontested
<i>Morchella diminutiva</i>	Mes-2	Described from Eastern USA; sequence attached to the holotype F 05030404 (Kuo et al. 2012)	USA	Resolved and uncontested
<i>Morchella dunensis</i> ≡ <i>M. esculenta</i> f. <i>dunensis</i> = <i>M. andalusiae</i>	Mes-17	Described from Spain as <i>M. esculenta</i> f. <i>dunensis</i> (Castañera et al. 1996) and later elevated to species by Clowez (2012); sequence attached to the isoparatype AH18336 (Loizides et al. 2016)	China, Cyprus, England, France, Italy, Norway, Pakistan, Spain, Turkey	Not conclusively resolved; displays no or weakly supported reciprocal monophyly relative to <i>M. vulgaris</i> , while recent collections from Italy (Snabl et al. 2019) and China (Du et al. 2019a, 2019b) unveiled higher levels of ITS polymorphism than previously anticipated, reducing the phylogenetic distance between <i>M. dunensis</i> and <i>M. vulgaris</i> to 2 fixed SNPs in the ITS1; based on European collections, the two species seem to display ecological and subtle morpho-anatomical apomorphies (Loizides et al. 2016), perhaps supporting some sort of (intraspecific?) autonomy; until further clarified, the usage of the two names is provisionally recommended

Table 1 (continued)

Linnaean name	Phylospecies	Typification details	Phylogeography	Status
<i>Morchella esculenta</i> ≡ <i>Phallus esculentus</i> = <i>M. esculenta</i> var. <i>aurantiaca</i> = <i>M. esculenta</i> var. <i>brunnea</i> = <i>M. esculenta</i> var. <i>ruboris</i> = <i>M. ochraceoviridis</i> = <i>M. ovalis</i> var. <i>minor</i> = <i>M. pseudoumbrina</i> nom. <i>invalida</i> = <i>M. pseudoviridis</i> nom. <i>invalida</i>	Mes-8	Described from Italy as <i>Phallus esculentus</i> (Micheli 1729; Linnaeus 1753) and transferred to <i>Morchella</i> by Persoon (1801); sequence attached to the epitype LIP 0900051 (Richard et al. 2014)	Belgium, China, Czech Republic, France, Germany, India, Netherlands, Norway, Poland, Slovakia, Spain, Sweden, Switzerland, Turkey, Ukraine	Resolved and uncontested, this is the type species of the genus
<i>Morchella fluviatilis</i>	Mes-18	Described from Spain; sequence attached to the holotype LIP 0900033 (Clowez et al. 2014)	Spain, Turkey	Resolved and uncontested
<i>Morchella galilaea</i>	Mes-16	Described from Israel; sequence attached to the holotype MS1-52 (Richard et al. 2014)	China, Egypt, France (La Reunion), India, Indonesia, Israel, Java, New Zealand, Rwanda, Spain, Turkey, USA (Hawaii)	Resolved and uncontested
<i>Morchella gracilis</i>	Mes-14	Described from the Dominican Republic; sequence attached to the holotype CORT013766 (Baroni et al. 2018)	Dominican Republic, Ecuador, Venezuela	Resolved and uncontested
<i>Morchella palazonii</i>	–	Described from Spain; sequence attached to the holotype LIP 0900177 (Clowez et al. 2015)	China, Spain	Resolved, but the Chinese collection slightly deviates from Spanish sequences; more collections and sequences of other loci from Spanish collections are needed to better assess conspecificity with the Chinese collections
<i>Morchella peruviana</i>	–	Described from Peru; sequence attached to the holotype NY02861412 (Baroni et al. 2018)	Peru	Resolved and uncontested
<i>Morchella prava</i>	Mes-7	Described from Eastern USA; sequence attached to the holotype F 05100602 (Kuo et al. 2012)	Canada, USA	Resolved and uncontested
<i>Morchella sceptriformis</i> = <i>M. virginiana</i>	Mes-3	Described from Eastern USA; sequence attached to the holotype LIP 0900110 (Richard et al. 2015)	USA	Resolved and uncontested
<i>Morchella steppicola</i>	Mes-1	Described from Ukraine (Zerova 1941); sequence attached to the epitype CWU-D0208 (Yatsiuk et al. 2016)	Croatia, Germany, Hungary, Kazakhstan, Serbia, Slovakia, Ukraine, Uzbekistan	Resolved and uncontested
<i>Morchella ulmaria</i> = <i>M. cryptica</i>	Mes-11	Described from Quebec (Canada); sequence attached to the holotype LIP 0900152 (Richard et al. 2015)	Canada, USA	Resolved and uncontested

Table 1 (continued)

Linnaean name	Phylospecies	Typification details	Phylogeography	Status
<i>Morchella vulgaris</i> ≡ <i>M. esculenta</i> β <i>vulgaris</i> = <i>M. acerina</i> = <i>M. anthracina</i> = <i>M. conica</i> var. <i>pygmaea</i> = <i>M. lepida</i> = <i>M. robiniae</i> = <i>M. spongiola</i> = <i>M. vulgaris</i> var. <i>aucupariae</i>	Probably <i>Mes-5</i>	Described from Italy as <i>M. esculenta</i> β <i>vulgaris</i> (Micheli 1729; Persoon 1801) and elevated to species by Gray (1821); sequence attached to the epitype LIP 0900044 (Richard et al. 2015)	Armenia, Czech Republic, Denmark, Estonia, France, Germany, India, Norway, Pakistan, Slovakia, Ukraine	Not conclusively resolved as it is yet unclear whether <i>M. dunensis</i> is conspecific, a distinct species, or perhaps a variant of <i>M. vulgaris</i> (see comments under <i>M. dunensis</i>); until further clarified, the usage of the two names is provisionally recommended
<i>Morchella yangii</i>	–	Described from China; sequence attached to the holotype FCNU1012 (Du et al. 2019a, 2019b)	China	Resolved and uncontested
<i>Morchella yishuica</i>	–	Described from China; sequence attached to the holotype FCNU1016 (Du et al. 2019a, 2019b)	China	Resolved and uncontested
Unnamed	<i>Mes-6</i>	Not typified; phylospecies identified in O'Donnell et al. (2011)	China	Yet to be formally described or linked to an existing binomial
Unnamed	<i>Mes-9</i>	Not typified; phylospecies identified in O'Donnell et al. (2011)	China, Japan, South Korea	Yet to be formally described or linked to an existing binomial
Unnamed	<i>Mes-10</i>	Not typified; phylospecies identified in O'Donnell et al. (2011)	China	Yet to be formally described or linked to an existing binomial
Unnamed	<i>Mes-12</i>	Not typified; phylospecies identified in O'Donnell et al. (2011)	China, Japan	Yet to be formally described or linked to an existing binomial
Unnamed	<i>Mes-13</i>	Not typified; phylospecies identified in O'Donnell et al. (2011)	China	Yet to be formally described or linked to an existing binomial
Unnamed	<i>Mes-15</i>	Not typified; phylospecies identified in O'Donnell et al. (2011)	China	Yet to be formally described or linked to an existing binomial
Unnamed	<i>Mes-19</i>	Not typified; phylospecies identified in Du et al. (2012b)	China	Yet to be formally described or linked to an existing binomial
Unnamed	<i>Mes-20</i>	Not typified; phylospecies identified in Du et al. (2012b)	China	Yet to be formally described or linked to an existing binomial
Unnamed	<i>Mes-21</i>	Not typified; phylospecies identified in Du et al. (2012b)	China	Yet to be formally described or linked to an existing binomial
Unnamed	<i>Mes-22</i>	Not typified; phylospecies identified in Du et al. (2012b)	China	Yet to be formally described or linked to an existing binomial
Unnamed	<i>Mes-23</i>	Not typified; phylospecies identified in Du et al. (2012b)	China	Yet to be formally described or linked to an existing binomial
Unnamed	<i>Mes-24</i>	Not typified; phylospecies identified in Du et al. (2012b)	China	Yet to be formally described or linked to an existing binomial
Unnamed	<i>Mes-25</i>	Not typified; phylospecies identified in Du et al. (2012b)	China	Yet to be formally described or linked to an existing binomial

Table 1 (continued)

Linnaean name	Phylospecies	Typification details	Phylogeography	Status
Unnamed	<i>Mes-26</i>	Not typified; phylospecies identified in Du et al. (2012b)	China	Yet to be formally described or linked to an existing binomial
Unnamed	<i>Mes-27</i>	Not typified; phylospecies identified in Du et al. (2012b)	China	Yet to be formally described or linked to an existing binomial
Unnamed	<i>Mes-28</i>	Not typified; phylospecies identified in Loizides et al. (2016)	Cyprus	Yet to be formally described or linked to an existing binomial
Elata clade (section <i>Distantes</i>)				
<i>Morchella angusticeps</i>	<i>Mel-15</i>	Described from Eastern USA (Peck 1879); sequence attached to the epitype F 04090601 (Kuo et al. 2012)	Canada, USA	Resolved, but its autonomy from <i>M. eximoides</i> has been contested by Petrželová and Sochor (2019), based on strictly phylogenetic grounds; integrative taxonomy, however, supports this species as closely related but distinct from <i>M. eximoides</i> , <i>M. confusa</i> , and a yet-to-be described lineage from the Czech Republic (see also “Discussion”)
<i>Morchella arbutiphila</i>	<i>Mel-30</i>	Described from Cyprus; sequence attached to the holotype LIP 0000366 (Loizides et al. 2016)	Cyprus, Turkey	Resolved and uncontested
<i>Morchella australiana</i>	<i>Mel-35</i>	Described from Australia; sequence attached to the holotype Trappe 35077 (Elliott et al. 2014)	Australia	Resolved and uncontested
<i>Morchella brunnea</i>	<i>Mel-22</i>	Described from Western USA; sequence attached to the holotype OSC 138686 (Kuo et al. 2012)	Canada, USA	Resolved and uncontested
<i>Morchella confusa</i>	–	Described from China; sequence attached to the holotype FCNU1027 (Du et al. 2019a, 2019b)	China	Resolved and uncontested

Table 1 (continued)

Linnaean name	Phylospecies	Typification details	Phylogeography	Status
<i>Morchella conifericola</i>	<i>Mel-32</i>	Described from Turkey; sequence attached to the holotype ANK Taşkın 110 (Taşkın et al. 2016)	Norway, Turkey	Not conclusively resolved; the autonomy of this species from its closest relatives, supported in part by its assumed endemism in Turkey, has recently been challenged by its occurrence in Norway (Weholt et al. 2020), and by a multilocus analysis of broad biogeographical sampling, suggesting that this species may be better merged into a wider concept including also <i>M. pulchella</i> , <i>M. septentrionalis</i> , <i>M. inamoena</i> ss Clowez and <i>Mel-23</i> (Petrželová and Sochor 2019); considering the taxonomic and nomenclatural implications of such move and the need for more conclusive data (both molecular and morpho-ecological) to support it, we recommend provisionally maintaining the usage of these names; should an inclusive clade be considered, <i>M. pulchella</i> would be the priority name, though an earlier European name probably exists
<i>Morchella deliciosa</i> = <i>M. conica</i> var. <i>flexuosa</i> = <i>M. conica</i> var. <i>nigra</i> = <i>M. conica</i> var. <i>violipes</i>	<i>Mel-26 + Mel-13</i>	Not typified by Fries (1822) but lectotypified by Richard et al. (2015) by an iconotype from Germany. No epitype designated yet, the current interpretation as <i>Mel-26</i> follows Richard et al. (2015)	Czech Republic, China, Estonia, France, Germany, India, Norway, Poland, Sweden, Turkey	Not conclusively resolved because species limits may extend beyond <i>Mel-26</i> so as to include also <i>Mel-13</i> (Du et al. 2012a, b, 2019a, b; Taskin et al. 2012; Petrželová and Sochor 2019) and because an epitype is needed for this early-described taxon; further synonyms probably exist but until further clarified, the usage of the current name is provisionally recommended for the inclusive clade
<i>Morchella disparilis</i>	–	Described from Cyprus; sequence attached to the holotype LIP 0400220 (Loizides et al. 2016)	Cyprus, Greece, Spain	Resolved and uncontested
<i>Morchella dunalii</i> = <i>M. fallax</i>	<i>Mel-25</i>	Described from France (Boudier 1887) and lectotypified by Moreau et al. (2011); sequence attached to the epitype MBT 177741 (Richard et al. 2015)	Cyprus, France, Israel, Spain, Turkey	Resolved and uncontested

Table 1 (continued)

Linnaean name	Phylospecies	Typification details	Phylogeography	Status
<i>Morchella eximia</i> = <i>M. anthracophila</i> = <i>M. carbonaria</i> ? = <i>M. septimelata</i>	<i>Mel-7</i>	Described from France (Boudier 1909); sequence attached to the epitype LIP 0900129 (Richard et al. 2015)	Argentina, Australia, Canada, China, Cyprus, France, Mexico, Spain, Portugal, Turkey, USA; cultivated	Not conclusively resolved because <i>M. septimelata</i> forms a distinct clade, warranting further investigation to confirm or reject its conspecificity with <i>M. eximia</i> ; until further clarified, the usage of the current name for the inclusive clade is provisionally recommended
<i>Morchella eximioides</i>	<i>Mel-16</i>	Invalidly described from Norway by Jacquetant (1955) but later validated by Kristiansen (1990); sequence attached to the holotype (Weholt et al. 2020)	China, Norway, Sweden	Resolved, but its autonomy from <i>M. angusticeps</i> has been contested by Petrželová and Sochor (2019); since this species is both reciprocally monophyletic and morphologically distinct from <i>M. angusticeps</i> , its proposed synonymy with the latter taxon is not endorsed here (see also comments above and in the main review)
<i>Morchella exuberans</i> = <i>M. capitata</i>	<i>Mel-9</i>	Described from Western USA; sequence attached to the holotype LIP 0900012 (Richard et al. 2015)	Canada, China, Cyprus, Norway, Spain, Sweden, Turkey, USA	Resolved and uncontested
<i>Morchella fekeensis</i>	<i>Mel-28</i>	Described from Turkey; sequence attached to the holotype ANK Taşkın 101 (Taşkın et al. 2016)	Turkey	Resolved and uncontested
<i>Morchella hispaniolensis</i>	<i>Mel-18</i>	Described from the Dominican Republic; sequence attached to the holotype NY02861410 (Baroni et al. 2018)	Dominican Republic	Resolved and uncontested
<i>Morchella iberica</i>	–	Described from Spain; sequence attached to the holotype LIP 0001675 (Clowez et al. 2020)	Spain, Turkey	Resolved and uncontested although initially overlooked and lumped in an inclusive <i>M. semilibera</i> species concept (Taşkın et al. 2012)
<i>Morchella importuna</i>	<i>Mel-10</i>	Described from Western USA; sequence attached to the holotype F 04130401 (Kuo et al. 2012)	Canada, China, Cyprus, Czech Republic, Estonia, Finland, France, Germany, Israel, Italy, Lithuania, Norway, Poland, Portugal, Spain, Switzerland, Turkey, USA; cultivated	Not conclusively resolved because most European collections belong to a clade distinct from that of the American type, suggesting two species may be involved, and because several old European names, incl. the seminal <i>M. elata</i> , are candidate priority synonyms for at least the European clade; until further clarified, the usage of the current name is provisionally recommended for the inclusive clade

Table 1 (continued)

Linnaean name	Phylospecies	Typification details	Phylogeography	Status
<i>Morchella inamoena</i> ss Clowez	–	Described from France (Boudier 1897) but type lost; not epitypified	France, Spain	Yet to be formally epitypified and linked to Boudier's species; the autonomy of this lineage within the <i>M. pulchella</i> complex is further challenged by recent multilocus analyses (Petrželová and Sochor 2019), suggesting that <i>M. conifericola</i> , <i>M. pulchella</i> , <i>M. septentrionalis</i> , <i>Mel-23</i> , and this taxon should probably be merged into a single species
<i>Morchella kaibabensis</i>	–	Described from Western USA; sequence attached to the holotype ARIZ AN043595 (Baroni et al. 2018)	USA	Resolved and uncontested
<i>Morchella kakiicolor</i> ≡ <i>M. quercus-ilicis</i> f. <i>kakiicolor</i>	<i>Mel-11</i>	Described from Spain as a form of <i>M. quercus-ilicis</i> (Clowez 2012) and later recombined as a species by Loizides et al. (2015); sequence attached to the holotype LIP 0900146 (Richard et al. 2015, as “f. <i>kakiicolor</i> ”)	Spain (incl. Canary Islands)	Resolved and uncontested, although the holotype of this taxon was at first erroneously ascribed to <i>M. quercus-ilicis</i> , the latter now a synonym of <i>M. tridentina</i> and genetically unrelated to <i>M. kakiicolor</i>
<i>Morchella laurentiana</i>	<i>Mel-36</i>	Described from Canada; sequence attached to the holotype DAOM 574925 (Voitk et al. 2016)	Canada	Resolved and uncontested
<i>Morchella magnispora</i>	<i>Mel-29</i>	Described from Turkey; sequence attached to the holotype ANK Taşkın 104 (Taşkın et al. 2016)	Turkey	Resolved and uncontested
<i>Morchella mediterraneensis</i>	<i>Mel-27</i>	Described from Turkey; sequence attached to the holotype ANK Taşkın 98 (Taşkın et al. 2016)	Turkey	Resolved and uncontested
<i>Morchella norvegiensis</i> = <i>M. eohespera</i>	<i>Mel-19</i>	Invalidly described from Norway by Jacquetant (1955) but later validated by Kristiansen (1990); sequences attached to the holotype O-72835 (Richard et al. 2015) and epitype O-255619 (Weholt et al. 2020)	Canada, China, Czech Republic, France, Netherlands, Norway, Slovakia, Sweden, Switzerland, USA	Resolved and uncontested

Table 1 (continued)

Linnaean name	Phylospecies	Typification details	Phylogeography	Status
<i>Morchella odonnellii</i>	–	Described from China; sequence attached to the holotype FCNU1024 (Du et al. 2019a, 2019b)	China	Not conclusively resolved because the phylogenetic relationships of this species to <i>M. tridentina</i> are still unclear; the latter species, as currently defined, is phylogenetically organized into distinct subclades reflecting biogeography; therefore, <i>M. odonnellii</i> may simply represent slightly divergent Chinese populations of <i>M. tridentina</i> ; the few sequence differences between <i>M. odonnellii</i> and the Eurasiatic <i>M. tridentina</i> , all restricted to the <i>rpb1</i> locus with questionable, if any, morphological differences between the two taxa, support this hypothesis and link the taxonomic status of <i>M. odonnellii</i> to that of current geographical clades within <i>M. tridentina</i> ; until this complex is further clarified, the current name is provisionally recommended for this clade
<i>Morchella oweri</i>	<i>Mel-39</i>	Described from China; sequence attached to the holotype FCNU1026 (Du et al. 2019a, 2019b)	China, Czech Republic, Germany, Norway; cultivated	Resolved and uncontested
<i>Morchella pakistanica</i>	–	Described from Pakistan; sequence attached to the holotype LAH35075 (Hernández-Restrepo et al. 2016)	Pakistan	Not conclusively resolved; poorly described from a single collection and only from the ITS locus; additional sequences are needed to confirm its status and phylogenetic position within the genus
<i>Morchella populiphila</i>	<i>Mel-5</i>	Described from Western USA; sequence attached to the holotype F 03240401 (Kuo et al. 2012)	North America, Portugal, Spain	Resolved and uncontested

Table 1 (continued)

Linnaean name	Phylospecies	Typification details	Phylogeography	Status
<i>Morchella pulchella</i>	<i>Mel-31</i>	Described from France (Clowez 2012); sequence attached to the holotype (Richard et al. 2015)	China, Czech Republic, France, Pakistan, Turkey	Not conclusively resolved because the autonomy of this species from <i>M. septentrionalis</i> has never been supported phylogenetically (Du et al. 2019a, 2019b); Taskin et al. 2012; Richard et al. 2015) and was mostly extrapolated from presumed disjunct distributions; however, a recent multilocus analysis of a broad biogeographical sampling in this complex suggests that this species may be better merged into a wider concept also including <i>M. conifericola</i> , <i>M. septentrionalis</i> , <i>M. inamoena</i> ss Clowez, and <i>Mel-23</i> (Petrželová and Sochor 2019); considering the taxonomic and nomenclatural consequences of such move and the need of additional data to support it, we recommend to maintain the usage of these names for the time being, but should the inclusive clade be considered, <i>M. pulchella</i> would be the priority name, though an earlier European name for this widespread taxon most likely exists
<i>Morchella punctipes</i>	<i>Mel-4</i>	Described from Eastern USA by Peck (1903); sequence attached to the epitype F 05020502 (Kuo et al. 2012)	Canada, USA	Resolved and uncontested

Table 1 (continued)

Linnaean name	Phylospecies	Typification details	Phylogeography	Status
<p><i>Morchella purpurascens</i> ≡ <i>M. elata</i> var. <i>purpurascens</i> = <i>M. conicopapyracea</i></p>	<i>Mel-20 + Mel-34</i>	Described from France and Bohemia (Czech Rep.) as <i>M. elata</i> var. <i>purpurascens</i> (Boudier 1897) and elevated to species by Jacquetant and Bon (1985); sequence linked to the epitype LIP 0900018 (Richard et al. (2012)	China, Czech Republic, Denmark, France, Norway, Spain (Canary Islands), Sweden, Taiwan, Turkey	Not conclusively resolved because of uncertain/poorly supported phylogenetic limits (Du et al. 2012a, 2012b, 2019a, 2019b; Taskin et al. 2012; Petrželová and Sochor 2019) and because early priority synonyms may exist (i.e., <i>M. rielana</i>); close phylogenetic vicinity and possible co-occurrence with <i>M. norvegiensis</i> and <i>Mel-38</i> necessitate careful analysis of an extended multilocus dataset to confirm species assignment of any novel collection; the autonomy of <i>Mel-34</i> from this species, initially proposed based on a single and very peculiar sequence (Du et al. 2012a, 2012b), is no longer supported by a recent multilocus analysis of a broader biogeographical sampling (Petrželová and Sochor 2019); since no description of this lone lineage is currently available and at least until additional sequences of <i>Mel-34</i> are available, the usage of <i>M. purpurascens</i> is provisionally recommended to designate the <i>Mel-20/Mel-34</i> inclusive clade
<p><i>Morchella semilibera</i> nam. cons ≡ <i>Mitrophora semilibera</i> = <i>Phallus crassipes</i> nom. rej = <i>Phallus gigas</i> nom. rej = <i>Phallus undosus</i> nom. rej = <i>Morchella hybrida</i> = <i>Morchella varisiensis</i></p>	<i>Mel-3</i>	Described from France (Lamarck and Candolle 1805); sequence attached to the neotype LIP 0900126 (Moreau et al. 2014)	Czech Republic, France, Germany, India, Italy, Japan, Kazakhstan, Netherlands, Spain, Sweden	Resolved and uncontested; conserved against earlier synonyms (Moreau et al. 2014)

Table 1 (continued)

Linnaean name	Phylospecies	Typification details	Phylogeography	Status
<i>Morchella septentrionalis</i>	<i>Mel-24</i>	Described from Eastern USA; sequence attached to the holotype F 05110405 (Kuo et al. 2012)	Canada, USA	Not conclusively resolved because the autonomy of this species from <i>M. pulchella</i> has never been properly supported (Du et al. 2012a, 2012b; Taşkın et al. 2012; Richard et al. 2015) and was hypothesized from putatively disjunct distributions; recent multilocus analyses (Petrželová and Sochor 2019) suggest this species may be better merged into a broader concept to include <i>M. conifericola</i> , <i>M. pulchella</i> , <i>M. inamoena</i> ss Clowez, and <i>Mel-23</i> (see also comments under <i>M. pulchella</i>); until fully resolved, we recommend the usage of the current name for North American collections belonging in this clade
<i>Morchella sextelata</i>	<i>Mel-6</i>	Described from Western USA; sequence attached to the holotype F 07130403 (Kuo et al. 2012)	China, Mexico, USA; cultivated	Not conclusively resolved because as currently delineated, the species encompasses two well-delimited and quite distant (19 SNPs) clades; careful examination of sequenced collections in the two groups should allow identifying diagnostic features
<i>Morchella snyderi</i>	<i>Mel-12</i>	Described from Western USA; sequence attached to the holotype OSC 139277 (Kuo et al. 2012)	China, USA	Resolved and uncontested

Table 1 (continued)

Linnaean name	Phylospecies	Typification details	Phylogeography	Status
<i>Morchella tridentina</i> = <i>M. quercus ilicis</i> = <i>M. frustrata</i> = <i>Morchella conica</i> var. <i>pseudoeximia</i> = <i>M. elatoides</i> nom. inval = <i>M. elatoides</i> var. <i>elegans</i> nam. inval	<i>Mel-2</i>	Described from Northern Italy (Bresadola 1898); repeated attempts to sequence original material have failed (Richard et al. 2015; Loizides et al. 2015). Not epitypified	Argentina, Armenia, Canada, Chile, Cyprus, France, India, Israel, Mexico, Spain, Turkey, USA	Not conclusively resolved because currently available sequences delineate distinct clades according to their geographical origins (Eurasian, North American, South American), but with no apparent morphological differences suggesting either (1) the presence of several cryptic species or (2) that subpopulations of this widespread species are phylogenetically continentalized; careful integrative analyses of collections from different continents are necessary to assign the most suitable taxonomic rank, if any, to each clade, with possible consequences on the taxonomic status of <i>M. odonellii</i> (see comments above); a sequenced epitype from Northern Italy further needs to be designated to definitively stabilize the usage of this classical name
<i>Morchella tomentosa</i>	<i>Mel-1</i>	Described from Western USA (Kuo 2008); sequence attached to the holotype MDCP 06150405 (O'Donnell et al. 2011)	Canada, USA	Resolved and uncontested
Unnamed	<i>Mel-8</i>	Not typified; phylospecies identified in O'Donnell et al. (2011)	USA	So far represented by a single sequence, yet to be formally described or linked to an existing binomial
Unnamed	<i>Mel-14</i>	Not typified; phylospecies identified in O'Donnell et al. (2011)	China	Yet to be formally described or linked to an existing binomial
Unnamed	<i>Mel-17</i>	Not typified; phylospecies identified in O'Donnell et al. (2011)	China	So far represented by a single sequence, yet to be formally described or linked to an existing binomial
Unnamed	<i>Mel-21</i>	Not typified; phylospecies identified in O'Donnell et al. (2011)	China, Japan	Yet to be formally described or linked to an existing binomial

Table 1 (continued)

Linnaean name	Phylospecies	Typification details	Phylogeography	Status
Unnamed	<i>Mel-23</i>	Not typified; phylospecies identified in O'Donnell et al. (2011)	Denmark, Norway	Yet to be formally described or linked to an existing binomial; the obscure <i>M. distans</i> , type species of the section, has been suggested as a Linnean name for this lineage (Weholt et al. 2020), but this hypothesis needs further investigation; the autonomy of this lineage within the <i>M. pulchella</i> complex is further challenged by recent multilocus analyses (Petrželová and Sochor 2019), suggesting that <i>M. conifericola</i> , <i>M. pulchella</i> , <i>M. septentrionalis</i> , <i>M. inamoena</i> ss Clowez, and <i>Mel-23</i> should probably be merged into a single species (see comments above)
Unnamed	<i>Mel-33</i>	Not typified; phylospecies identified in Du et al. (2012b)	China	Yet to be formally described or linked to an existing binomial
Unnamed	<i>Mel-37</i>	Not typified; phylospecies identified in Pildain et al. (2014)	Argentina	Yet to be formally described or linked to an existing binomial
Unnamed	<i>Mel-38</i>	Not typified; phylospecies identified in Loizides et al. (2016)	Cyprus	Yet to be formally described or linked to an existing binomial; more sequences are needed to confirm its exclusivity from <i>M. purpurascens</i> (see notes above and “Discussion”)

the authors have neglected to designate a holotype and thus failed to fulfill the criteria of Articles 40.1 and 40.6 of the International Code of Nomenclature of Algae, Fungi and Plants (Turland et al. 2018; Aime et al. 2021). Also disturbing is the fact that many citations throughout the paper have been intentionally or unintentionally misapplied, and are often unrelated to, or directly contradict the context in which they have been used. In a point-by-point analysis of the paper Phanpadith et al. (2019) (Point-by-point critique of Phanpadith et al. (2019), [Supplemental Information](#)) a total of 71 false, erroneous, or inaccurate statements have been identified, including extraordinary claims that only 315 species of fungi are recorded in fungal databases and only four species of *Morchella* have been given Latin binomials.

Considering the status and high visibility of the journal, but also the amount of misinformation disseminated and taxonomic instability brought upon the genus by potential citations of this paper (e.g., Lagrange and Vernoux 2020), a full retraction of Phanpadith et al. (2019) was deemed necessary. An open letter asking for the retraction of this paper was therefore drafted by the authors (Open Letter to the Editor of Scientific Reports, [Supplemental Information](#)) and submitted for publication to *Scientific Reports* on 5 May 2021. The journal refused to publish the letter, but eventually retracted the paper with the following note: “Several errors were discovered in the data-sets used to construct the phylogenetic trees, including duplicate sequences, incorrect accession numbers, and the inadvertent inclusion of a bacterial sequence. In addition, the *EF1- α* and *RPB2* sequences cited in Table 2 were poorly amplified and sequenced, reducing the reliability of their application in tree constructions. As a result, the phylogenetic trees reported in the paper cannot be replicated.” (<https://www.nature.com/articles/s41598-021-93655-1>). While the retraction of the paper is certainly welcome, several unanswered questions remain as to how such an outstandingly flawed paper, claiming among other things that 10–15-nm sections were made by hand, has evaded the attention of the editor-in-chief, the senior editorial board members, the section editor, and an unknown number of reviewers to be published in a Q1 journal. Concerns are also raised about quality controls and safekeeping procedures in *Scientific Reports* (and other pay-to-publish journals), but also with regard to the non-transparent retraction procedure itself, which in this case has resulted in a short editorial note not accurately conveying the enormity of malpractice that has taken place.

The system of binomial nomenclature and the *Mel/Mes* designators

The Linnaean system of binomial nomenclature (Linnaeus 1758) has been fundamental for biological sciences (Russell et al. 2007; Paterlini 2007; Polaszek 2010; Patterson

et al. 2010). Up to 2010, a great deal of confusion had persisted over the number of species present in *Morchella* and the binomials applicable to them, with some authors accepting as few as three species (Groves and Hoare 1953; Dennis 1978) and others as many as 34 (Jacquetant 1984; Clowez 2012). While molecular phylogenetics have since clarified the species richness debate, early phylogenetic assessments were faced with the daunting task of matching the numerous phylogenetic clades (phylospecies) inferred through molecular tools to the several dozens of Linnaean binomials available, many of which type material were not available for or, if it existed, were too old to yield useful DNA data. To tackle this problem, the system of informal *Mel/Mes* designators for each phylospecies was introduced by Taşkın et al. (2010) and O’Donnell et al. (2011), and widely adopted in subsequent studies (Du et al. 2012a, b; Pildain et al. 2014; Richard et al. 2015; Loizides et al. 2016; Petrželová and Sochor 2019). This system, which used the prefix “*Mel*” for the */Elata* clade and “*Mes*” for the */Esculenta* clade followed by a serial number for each species, did not intend to replace binomial nomenclature (as falsely assumed by Phanpadith et al. 2019), but was introduced as a temporary solution until the phylogenetic identity of early published binomials could be clarified. For precisely this reason, unambiguous clades such as those of *Morchella anatolica* and *Morchella rufobrunnea* were not assigned informal designators, because the phylogenetic identity of these taxa had been conclusively resolved via sequencing of original material (O’Donnell et al. 2011; Taşkın et al. 2012). Since then, the genetic identity of many classical names has also been clarified through lecto- and epitypification (Richard et al. 2015), while further synonymies have been established (Richard et al. 2015; Loizides et al. 2015; Weholt et al. 2020), and several new taxa were proposed (Clowez et al. 2014, 2015, 2020; Loizides et al. 2016; Voitk et al. 2016; Taşkın et al. 2016; Baroni et al. 2018; Du et al. 2019a). To date, 58 classical or recently proposed binomials are linked to known phylogenetic clades (see Fig. 1, Table 1).

The conceptual and methodological difficulties of linking a DNA sequence to an early-described binomial are by no means unique to morels. In the absence of DNA data from the holotype or other original material, attaching a sequence to an old binomial is challenging and essentially relies on correct interpretation of phenotypic, ecological, chorological, and other data (Ariyawansa et al. 2014; Dayarathne et al. 2016). Similar problems are in fact widespread throughout basidiomycete and ascomycete genera, not least *Caloboletus* (Loizides et al. 2019), *Cortinarius* (Limatainen et al. 2014a, 2017), *Ganoderma* (Fryssouli et al. 2020), *Gyromitra* (Miller et al. 2020), *Helvella* (Nguyen et al. 2013), *Hydnellum* (Parfitt et al. 2007; Ainsworth et al. 2010), *Hydnum* (Grebenc et al. 2009; Niskanen et al. 2018), *Inocybe* (Larsson et al. 2009; Matheny and Swenie 2018),

Lyophyllum (Bellanger et al. 2015; Bellanger 2016), or *Otidea* (Hansen and Olariaga 2015), to name a few. Although radical views to bypass some of these difficulties have occasionally been put forward, such as the controversial PhyloCode advocating for a system of rankless phylotaxonomy (de Queiroz and Gauthier 1990, 1992, 1994), or calls to abandon binomial nomenclature altogether (Money 2013), these have been widely rejected by the academic community and Linnaean binomial nomenclature continues to form the basis of scientific communication (e.g., Nixon and Carpenter 2000; Carpenter 2003; Wheeler 2004; Will et al. 2005; Korf 2005; Schoch et al. 2014; Minnis 2015; Dayarathne et al. 2016; Zamora et al. 2018). Therefore, genetic characterization of early-described taxa through sequencing of original material and/or designation of sequenced epitypes remains the most cautious, widely accepted, and least disruptive method of solving complex taxonomic problems and stabilizing taxonomy and nomenclature within critical genera (Hyde and Zhang 2008; Ariyawansa et al. 2014; Liimatainen et al. 2014b; Vesterholt et al. 2014; Borovička et al. 2015; Olariaga et al. 2015; Vizzini et al. 2016, 2020; Richard et al. 2015; Dima et al. 2016; Skrede et al. 2017; Moreau et al. 2018; Lombard et al. 2018; Turland et al. 2018; Van Vooren et al. 2019; Loizides et al. 2020; Van Vooren 2020). Powerful new technologies such as next-generation sequencing, able to produce useful DNA sequences from old and contaminated material, are expected to be decisive in decrypting the genetic identity of early-described taxa in the years to come (Wibberg et al. 2020; Bellanger et al. 2021; Bidaud et al. 2021). Against this backdrop, the persistence of Phanpadith et al. (2019), but also other recent studies (e.g., Petrželová and Sochor 2019; Lagrange and Vernoux 2020) to ignore, sideline, or dismiss phylogenetically resolved binomials in favor of a permanent *Mell/Mes* coding system is unfortunate, inexplicable, and perpetuates taxonomic and nomenclatural instability within the genus.

The pitfalls of single-method approaches in taxonomy

The view expressed by Phanpadith et al. (2019) and others that molecular phylogenetics should be used “instead of morphology to identify cryptic species” is both simplistic and misguided, because it is based on the fallacious assumptions that (1) DNA is the only valuable source of diagnostic information; (2) DNA analyses have zero failure rate in delimiting species; and (3) all so-called cryptic species are truly cryptic. For all the profound impact molecular phylogenetics have had in fungal taxonomy, Sanger sequencing of specific DNA regions is not foolproof and, much like other methods, relies on a series of simplified assumptions (Nixon and Carpenter 2000; Will et al. 2005; Carstens et al. 2013; Li et al. 2017). Considering that full genomic sequencing of each and every collection will be neither practical nor cost-effective anytime soon, the

accuracy of species delimitation by present DNA techniques inevitably rests with the choice of loci analyzed, the method of analysis, the number and quality of sequences, their correct alignment, and ultimately personal interpretation of the data (Sung et al. 2007; Philippe et al. 2011; Leliaert et al. 2014). In a recent study by Wei et al. (2016), for example, two lichenized ascomycetes with apparently distinct reproductive modes, *Hypogymnia hypotrypa* (Nyl.) Rass. and *H. flavida* McCune & Obermayer (Parmeliaceae), received strong support when analyzed by the multispecies coalescent approach (BPP) and Bayes factor delimitation, but failed to resolve in Automatic Barcode Gap Discovery (ABGD), Bayesian implementation of Poisson tree process model (bPTP), and general mixed Yule coalescent (GMYC), which delineated either one or multiple species, instead. It is in fact not uncommon for support (or lack of it) for a group of sequences to be spurious and by modifying the number of sequences, loci analyzed, or method of analysis, support values might change, sometimes drastically (Knowles and Carstens 2007; Ballenghien et al. 2017; Wilson et al. 2018; Thines et al. 2018). Other confounding factors such as horizontal gene transfer, intragenomic polymorphism of rDNA cistrons, recent diversification and incomplete lineage sorting, or hybridization and introgression may further complicate or obscure taxonomical conclusions (Philippe et al. 2011; Kiss 2012; Leliaert et al. 2014; Mailund et al. 2014; Stewart et al. 2014; Chan et al. 2020; Stadler et al. 2020).

In *Morchella*, the pitfalls of single-method approaches are exemplified by another recent study by Petrželová and Sochor (2019), focusing on molecular phylogenetics. While the authors of this study are correct to point out that many problems in the genus stem from the application of different methods of analysis and in some cases over-splitting, some of their proposals are unlikely to help. Specifically, Petrželová and Sochor (2019) advocate for the introduction of an additional prerequisite in species delimitation in *Morchella*: polygenic differentiation. This inference method, originally introduced by Taylor et al. (2000) as “GCPSR,” is useful in delimiting morphologically reduced fungi or species that permanently exhibit their asexual stages and has been widely applied in fungal systematics (Nguyen et al. 2015). However, this method is also based on the precarious assumption that all species differ *equally* (or at least *sufficiently*) in *all* loci. By strictly applying this method as the sole criterion of species delimitation in *Morchella*, therefore, two phylogenetically supported, reciprocally monophyletic, and morphologically distinct species, *M. eximoides* Jacquet. ex R. Kristiansen (supported by Bayesian posterior probability of 1 and with spores up to 24–26 μm long) and *M. angusticeps* Peck (supported by Bayesian posterior probability of 1 and with spores up to 30–34 μm long), are lumped into a single species by Petrželová and Sochor (2019) because they are separated by only two of the four loci tested. We consider this a particularly dubious



Fig. 1 Radial multilocus phylogeny of *Morchella*: genus-wide Bayesian inference analysis of a multilocus (*RPB1* + *RPB2* + *TEF1*) sequence dataset including the 81 published species and *MelMes* phylospecies, excluding *M. pakistanica*, for which only ITS sequence is available. Note that a few additional lineages have been identified

but not formally described nor been assigned a phylospecies number. Lineages not conclusively resolved or contested are marked by question bars and bracket or branching symbol, for possible lumping or splitting, respectively (see Table 1 for details)

conclusion, not just because the lack of apomorphies in two of the tested loci does not in this case conflict with the monophyly of the two species, but also because phenotypic differences between them have been entirely ignored. It is unrealistic to expect the evolutionary history of all species

to be symmetrically imprinted in all loci (Maddison 1997; O'Donnell and Cigelnik 1997; Hudson and Coyne 2002; Crous and Groenewald 2005; Knowles and Carstens 2007; Harder et al. 2013; Altermann et al. 2014; Zamora et al. 2018) and, as shown by Du et al. (2012a), the LSU, *TEF1*,

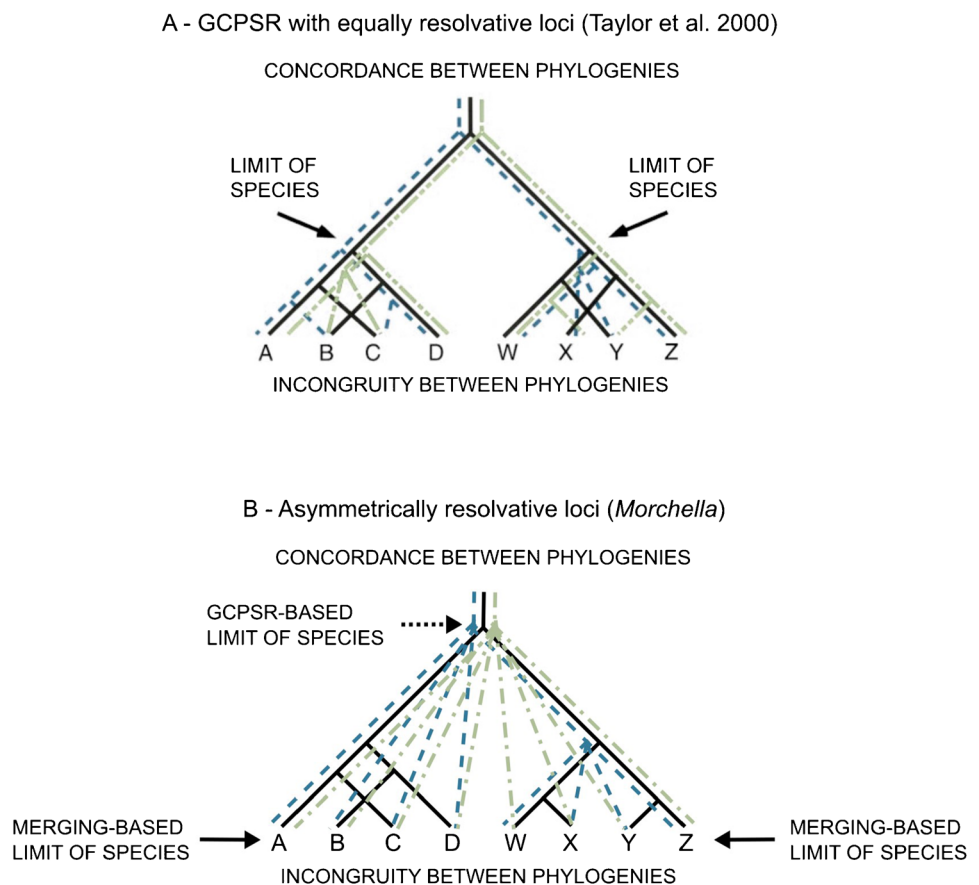
RPB1, and *RPB2* loci are indeed less variable than ITS in the majority of morels. Such radical lumping, therefore, is bound to create more problems than it solves and ultimately disqualifies genuine evolutionary units in favor of an uninformative, methodologically biased, and largely artificial taxonomical model.

Combined multigene phylogeny vs classic GCPSR

GCPSR, as originally defined by Taylor et al. (2000), is a multilocus method designed to detect cryptic speciation by identifying the transition from concordance to incongruity between phylogenies inferred from several loci, which evolve at their own pace (lineage sorting, genetic drift). This concordance is then interpreted as reflecting reproductive barriers to gene flow between populations, which ultimately lead to speciation (Taylor et al. 2000). Although generally regarded as a powerful method of species delimitation, GCPSR still assumes vertical heredity, which makes it unsuitable for representing, for instance, reticulate evolution. Moreover, GCPSR does not take into account incomplete lineage sorting and may be just as limited as other phylogenetic approaches in resolving recently evolved species (Liu et al. 2016). Being sensitive to sampling, GCPSR will

convey different messages depending on the quality of the dataset. In an ideal scenario (such as the one depicted in Taylor et al. 2000, reproduced in Fig. 2A), phylogenetic markers are all sufficiently and equally polymorphic to resolve all terminal clades. But what if this is not the case? Strictly applying the principles underlying GCPSR in such cases of asymmetric phylogenies would lead to define species limits at the deepest node in the multilocus phylogeny, where incongruity between each individual phylogeny switches to concordance (as depicted by the dotted arrow in Fig. 2B, this node being the one where this transition occurs with the least polymorphic marker). Applying the GCPSR method in such cases results in following the most conservative individual phylogeny at each node and identifying species limits at the most inclusive clade of each possible option. Thus, it can be argued that GCPSR is a conservative inference method, which *subtracts* phylogenetic information from the most variable markers rather than *adding* information from each locus. An alternative approach would be to acknowledge that the chosen loci display different resolution power and opt to combine their phylogenetic information, as depicted in Fig. 2B (plain arrows). In this case, relevant nodes can be inferred following the most polymorphic marker, and species limits would contrastingly be defined by the least inclusive clade of each phylogeny. This approach, though, abandons the bases of GCPSR and should probably be referred to as

Fig. 2 GCPSR vs multilocus phylogenies: the GCPSR method with three equally polymorphic loci (A, reproduced from Taylor et al. 2000) or with three asymmetrically resolving loci (B). The GCPSR-based delineation of species limits identifies the node in the multilocus phylogeny where individual phylogenies switch from incongruity to concordance. Note that this approach does not consider some of the phylogenetic signal from individual, more polymorphic loci, and delineates species by the most inclusive clade among the three phylogenies. In contrast, a merging-based (multilocus) approach combines the phylogenetic signal conveyed by the three loci and delineates species by the least inclusive clades among the three phylogenies



“additive-” or “combined multilocus analysis,” rather than GCPSR. Given the above shortcomings, it is perhaps not surprising that some of the authors of the original Taylor et al. (2000) paper appear to have subsequently revised their views and abandoned the requirement for polygenic differentiation (see Dettman et al. 2003).

The phylogenetic methodology introduced a decade ago by Kerry O’Donnell and collaborators (Taşkın et al. 2010; O’Donnell et al. 2011) to unravel the extent of *Morchella* diversity, and widely applied in the genus since (Taşkın et al. 2012; Du et al. 2012a, b, 2019b; Pildain et al. 2014; Richard et al. 2015; Loizides et al. 2016; Baroni et al. 2018), is based on such a combination of asymmetric phylogenetic markers (Fig. 2B). Indeed, it had become apparent from the first extensive analyses that the ITS rDNA locus has much more resolution than the LSU rDNA, *RPB1*, *RPB2*, and *REF1* loci (Du et al. 2012b), although in the *Mel-17* to *Mel-38* subclades (often called the *Elata* subclade) this asymmetry is much less obvious, therefore, applying GCPSR might still be possible with the five selected loci. This, however, has never been the case in *Morchella* and a clear “merging” strategy has been applied to infer clades and species, rather than a search for the deepest node where concordance to incongruity of individual phylogenies occurs. As an example, *Morchella norvegiensis* Jacquet. ex R. Kristiansen (*Mel-19*) and *M. purpurascens* (Krombh. ex Boud.) Jacquet. (*Mel-20*) should not be recognized as distinct species following a strict GCPSR approach, because they are not resolved by the ITS phylogeny and the node where concordance to incongruity is taking place between the different phylogenies is the inclusive clade encompassing the two phylopecies. Likewise, *M. brunnea* M. Kuo (*Mel-22*) and *M. fekeensis* H.H. Doğan, Taşkın & Büyükalaca (*Mel-28*) should not be distinguished at species level by GCPSR, since they are not resolved by *RPB1* and *RPB2*, neither should be *Mel-23* from *M. conifericola* Taşkın, Büyükalaca & H.H. Doğan (*Mel-32*) which are not distinguished by *RPB2*. Semantics aside, it becomes obvious from the above examples that the multilocus phylogenetic method introduced to unravel more diversity a decade ago is not founded on the exact same evolutionary grounds as classic GCPSR (as originally outlined in Taylor et al. 2000 and advocated by Petrželová and Sochor 2019), but rather adds or combines the information derived from the different loci analyzed.

It must be stressed that the above examples are not intended to dismiss or belittle the usage of the current multilocus method widely applied in *Morchella*, or even the classic GCPSR method, but simply to temper overconfidence in the *Mel/Mes* clades delineated and call for caution when phylogenies need to translate into a meaningful taxonomy. It is precisely because of such intrinsic limitations that a broader spectrum of analyses

is necessary in the delimitation of species, expressed in multidisciplinary approaches broadly termed as “integrative,” “multisource,” or “polyphasic” taxonomy (Dayrat 2005; Will et al. 2005; Stadler et al. 2014). Rather than relying on a single tool or a single source of information, integrative taxonomical approaches utilize multi-source data to reach taxonomic conclusions, complementing multilocus analyses with population genetics, morphological, developmental, and behavioral analyses, chemotaxonomy, cytology, and ultrastructural and reproductive studies, as well as analysis of distributional patterns, ecological niches, and host associations (Will et al. 2005; Padiál et al. 2010; Schlick-Steiner et al. 2010; Barrett and Freudenstein 2011; Stech et al. 2013; Carstens et al. 2013; Zervakis et al. 2014; Zamora et al. 2015; Wei et al. 2016; Kuhnert et al. 2017; Haelewaters et al. 2018; Sochorová et al. 2019; Liu et al. 2020; Samarakoon et al. 2020; Wittstein et al. 2020; Zamora and Ekman 2020; Maharachchikumbura et al. 2021). It is only by the use of such integrative approaches and carefully evaluating all lines of evidence that a number of closely related and insufficiently clarified lineages in *Morchella*, such as the *M. angusticeps/M. eximoides* pair, the *M. norvegiensis/M. purpurascens/M. laurentiana/Mel-38* complex, or the *M. pulchella/M. septentrionalis/M. conifericola/Mel-23* cluster, can be satisfactorily resolved (see Table 1).

Cryptic, semicryptic, or pseudocryptic?

Empirical data provide the foundations on which species hypotheses are formed (Sites and Marshall 2004). Yet, despite the wealth of information that can be obtained from long-term observations and multisource analyses, integrative assessments of *Morchella* are few. This has all too often resulted in superficially circumscribed and poorly described taxa, and has been the root of much confusion and instability within the genus. Because many species are nowadays randomly detected through DNA sampling rather than long-term observations and hypothesis-driven approaches, important morpho-ecological information is lost in the process (Koukol and Delgado 2021). This lack of information in turn results in a poor or incomplete understanding of the morphological, behavioral, and ecological traits of the described taxa which, following unsuccessful attempts to reconstruct their profiles and identify diagnostic traits *in vitro*, are dismissed as “cryptic.” Truly cryptic (or “sibling species” as once termed by Mayr 1942), however, are probably less common in nature than assumed, and many taxa often labeled “cryptic” are in fact *pseudocryptic*, or in other words species whose diagnostic traits have been overlooked (Knowlton 1993; Sáez et al. 2003; Will et al. 2005; Sáez and

Lozano 2005; Lajus et al. 2015; Karanovic et al. 2016; Westrop et al. 2018).

Crypticism has been overestimated in *Morchella*, where the majority of species are perhaps best defined as *semicryptic* (having subtle or unstable morpho-ecological traits and considerable phenotypic overlap with other taxa), or *pseudocryptic* (having reasonably reliable diagnostic traits that have been largely overlooked), rather than genuinely cryptic. A number of species, such as *Morchella anatolica* Işiloğlu, Spooner, Allı & Solak, *M. rufobrunnea* Guzmán & F. Tapia, *M. tridentina* Bres., *M. disparilis* Loizides & P.-A. Moreau, *M. steppicola* Zerova, or *M. exuberans* Clowez, Hugh Sm. & S. Sm. are in fact very well-delimited and so morphologically distinct they can be instantly recognized in the field or even directly from photographs (Zerova 1941; Kuo 2008; Loizides et al. 2015). Other species such as *M. arbutiphila* Loizides, Bellanger & P.-A. Moreau, so far exclusively associated with *Arbutus*, or the autumnal *M. galilaea* Masaphy & Clowez are ecologically or phenologically distinct and can also be reliably identified by non-molecular methods (Taşkın et al. 2015; Loizides et al. 2016). The situation becomes more complicated when it comes to semicryptic taxa, due to high inter-individual plasticity of their sporocarps and absence of clear-cut (dichotomous) diagnostic traits. Because many characters in semicryptic species are unstable and largely overlap with those of other taxa, their morphological identification based on a single dichotomous character (monothetic model) is not really feasible. To overcome this problem, a polythetic system of identification was introduced in recent years (Loizides et al. 2015, 2016, 2021), in which a larger set of traits are taken into consideration, none in themselves a strict prerequisite, but rather complementing each other in the identification process. Thus, by increasing the number of potentially informative traits, identification is often possible on a “best match” basis rather than consistently occurring dichotomous characters, which may or may not be present. Several macromorphological and developmental features have been shown to be of taxonomic value in morels, such as the process of maturation of ascocarps from pale to dark or vice versa (see Table 2). The orientation and darkening (or non-darkening) process of the sterile ridges, together with the shape and alignment of the pits, are important, as is any rufescence and the stipe color, surface, and its length proportionately to the pileus. The attachment of the pileus to the stipe (*sinus*) is also a taxonomically useful character and occasionally diagnostic (e.g., *M. disparilis*). Microscopically, a number of often neglected features can provide valuable taxonomic information, such as the acroparaphyses, the ectal excipulum and hyphoid hairs of the stipe, the apices, number and orientation of the septa of the paraphyses, or the ornamentation, shape, and average size of the ascospores (see Kuo et al. 2012; Loizides et al.

2015, 2016, 2021; Baroni et al. 2018; Clowez and Moreau 2018a, 2018b; Table 2).

Still, in the absence of adequate field data and comprehensive morphoanatomical analyses, many of these taxonomically important characters are frequently ignored. For instance, a new species recently published in the FUSE series of *Sydowia* (Hernández-Restrepo et al. 2016), *Morchella pakistanica* S. Jabeen & A. N. Khalid, has been described from a single collection of what looks like a deformed ascocarp (fig. 14A of Hernández-Restrepo et al. 2016). Not only taxonomically important features (including the process of maturation, stipe, spore ornamentation, acroparaphyses, stipe hairs, and ectal excipulum) are all absent from the original description, but ascospores appear to be grossly immature, as the dimensions of $7.5\text{--}10 \times 4.5\text{--}6.5 \mu\text{m}$ given are unrealistically small for a morel. Moreover, even though this species nests in the *ISemilibera* clade accommodating species with a pileus that is only partially attached to the stipe (“half-free morels”), no information on the *sinus* of the new species is provided. Other critical features like the acroparaphyses and the hyphoid hairs of the stipe are repeatedly ignored in contemporary descriptions or emendations of taxa (e.g., Yatsiuk et al. 2016; Baran and Boroń 2017; Pinzón-Osorio and Pinzón-Osorio 2017; Badshah et al. 2018; Du et al. 2020), despite being arguably the most informative microanatomical characters in morels (Kuo et al. 2012; Loizides et al. 2015, 2016, 2021; Clowez and Moreau 2018a; Baroni et al. 2018). The same is true for the macromorphological profile of many taxa and the process of maturation of their ascocarps, which are rarely reported due to lack of sufficient in situ observations. Imagery and photographs, when provided, are often of poor quality or depict a single ascocarp, sometimes dried ascocarps, or even the wrong species. All these lead to a proliferation of poorly circumscribed and dubiously described taxa, which in turn results in their dismissal as “cryptic,” followed by an overreliance on molecular tools and eventually in an uninformative and chronically unstable taxonomy.

How can phylogenies translate into a meaningful taxonomy?

The phylopecies concept pioneered and propelled in *Morchella* by O’Donnell et al. (2011) and widely endorsed in subsequent studies (Taşkın et al. 2012; Du et al. 2012a, 2012b, 2019b; Pildain et al. 2014; Richard et al. 2015; Loizides et al. 2015, 2016, 2021; Baroni et al. 2018) continues to provide a sound basis for species delimitation at the molecular level. Phylogenetic data, however, should be carefully compared to and complemented with morpho-ecological, chorological, and

other data that can be critical in inferring recent speciation events and building robust species concepts.

- We agree with the “criterion of minimal sampling” proposed by Petrželová and Sochor (2019) and urge prospective authors to refrain from proposing new taxa based on single finds, insufficiently represented collections, or in the absence of a robust morpho-ecological understanding of the described taxa, especially if the differences with other species are below the average in that group. While it is technically possible to quickly put a name on a putatively undescribed lineage randomly detected by DNA sampling, poorly circumscribed and superficially described taxa do not provide taxonomy a good service, but lead to a proliferation of “ghost taxa” and synonyms. In order to correct such mistakes and restabilize taxonomy, considerable time, effort, and resources are then diverted from other original research (Koukol and Delgado 2021). To discourage the opportunistic introduction of poorly circumscribed taxa, we recommend that several (3+) collections from two or more different localities should be rigorously analyzed using a multisource approach before proposing a new taxon. Including three or more collections in the analysis allows for a better assessment of infraspecific (both genetic and phenotypic) variability and consequently reduces the margin of error in inferring interspecific limits.
- Phylogenetic criteria requiring all species to differ equally in all loci, such as the criterion of “polygenic differentiation” proposed by Petrželová and Sochor (2019), are considered unreasonably conservative and rejected, because they can lead to artificial taxonomic arrangements not accurately reflecting evolutionary history.
- We also call for caution in the introduction of any absolute quantitative threshold in gene divergence, as barcoding thresholds may fluctuate depending on a given dataset. Such automated application of an artificial cutoff point could on one hand deny the status of species to recently isolated lineages, while on the other hand may lead to allelic heterogeneity being misinterpreted as speciation (Stadler et al. 2020).
- The informal *MellMes* designators have served well as a temporary coding system for phylopecies detected by molecular tools; therefore, their usage for lineages lacking sufficient data to be formally described or linked to an existing binomial is appropriate. However, for phylospecies whose taxonomic identity has been conclusively resolved (either through the proposal of a new name or typification of an old one), we strongly urge for the pertinent use of Linnaean binomials, in order to normalize and stabilize taxonomy and nomenclature in the genus (Table 1).
- Equally importantly, deciphering the phylogenetic identity of a number of classical, yet to be clarified binomials such as *M. crassipes* (Vent.) Pers., *M. elata* Fr., *M. hortensis* Boud., *M. intermedia* Boud., *M. ovalis* (Wallr.) Boud., *M. rielana* Boud., *M. rigida* (Krombh.) Boud., *M. rotunda* (Pers.) Boud., and *M. umbrina* Boud., should constitute a high priority, as epitypification of early-described taxa will significantly reduce the risk of further synonymies in the future.
- For species descriptions and taxonomically informative morphoanatomical analyses, we recommend following the polythetic model and methodology outlined in Loizides et al. (2016) and further expanded in Clowez and Moreau (2018a, b), Baroni et al. (2018), and Loizides et al. (2021).
- Ascospores are very late (and unevenly) maturing in morels and measurements from dried specimens are often unreliable (see also Baral 1992); therefore, spores should be measured from naturally ejected prints obtained on a glass slide. To work out meaningful averages (Me, Q, Qm), ascospores from at least three or four different ascocarps should be measured in water, with a minimum of 30 spores measured from each ascocarp. Spore ornamentation must be carefully evaluated through scanning electron microscopy, when possible, or at least in the appropriate staining medium in light microscopy (see Chen and Liu 2005; Loizides et al. 2016; and Clowez and Moreau 2018b for suitable stains).
- Additional taxonomically informative characters, such as the paraphyses and acroparaphyses (including their apices and the number and orientation of their septa), as well as the ectal excipulum and hyphoid hairs (terminal elements) of the stipe, should all be included in the description and adequately depicted.
- The process of maturation and developmental stages of ascocarps, the alignment and discolouration of their ridges, the shape and arrangement of primary and secondary pits, and the *sinus*, as well as the color and surface of the stipe and its average length proportionate to the pileus, are all important features that must also be thoroughly documented from fresh ascocarps at various stages of maturity.
- Accurate information of ecological and distributional patterns, substrate preferences, and putative plant associations/specificities is critical and can often clinch the diagnosis among semicryptic taxa.

For the purpose of adopting a uniform and intelligible descriptive terminology, a glossary of morphoanatomical characters and their taxonomic usage is provided in Table 2.

Table 2 Glossary of descriptive terminology of morphoanatomical characters in *Morchella*

<p>Acroparaphyses: A term introduced by Loizides et al. (2016) for the paraphysoid elements of the sterile ridges. These are morphologically and topologically distinct from the paraphyses, the latter found intermingled with the asci in the fertile pits. Acroparaphyses are typically fasciculate, shorter than the paraphyses, and sometimes of critical taxonomic importance: some morels have shorter and more thick-walled acroparaphyses than others, while a number of species have capitate elements and others not. The sterile ridges often become eroded in overmature specimens and acroparaphyses collapse or become obscured by extraparietal pigment, therefore are best observed in younger specimens where the ridges are intact</p> <p>Alveoli: The fertile pit-like cavities, effectively the hymenium of the fungus, formed by the network of interconnecting ridges on the pileus. The depth and especially the shape and alignment of the alveoli are usually important taxonomic features. Some morel species have \pm regularly arranged ridges forming rectangular, oblong, angular, or rounded alveoli, while others have highly irregular or labyrinthoid alveoli. In many species, smaller secondary alveoli can form inside the primary alveoli</p> <p>Asci: The spore-bearing sac-like cells in the fertile pits. In morels, they often appear flexuous or somewhat contorted, can be monoseriate or irregularly biseriata, are inamyloid, and typically simple septate at the base. Depending on whether they are located at the base or the sides of the pits, they can be centrally or laterally attached at the base. Of limited or no taxonomic value; previous reports of croziers in some morel species (Clowez et al. 2014) are spurious</p> <p>Ascogonia: The “female” gametangia before fertilization by “male” gametangia (sometimes also called antheridia). After fertilization, the ascogonium becomes the first dikaryotic cell of the ascome, from which arise dikaryotic ascogenous hyphae. Although Kirschner (2019, fig. 9) cited <i>Morchella</i> “conica” (with a picture likely illustrating <i>M. importuna</i>) as an example of loss of ascogonia and antheridia, Clowez and Moreau (2018a, 2020) observed and illustrated frequent, broad, and thick-walled cells in the subhymenium of all studied species of <i>Morchella</i>, emitting ascogenous hyphae interpreted as ascogonia</p> <p>Apothecium: Another term for <i>mitra</i> or <i>pileus</i></p> <p>Ascospores: See <i>spores</i></p> <p>Cap: See <i>mitra</i></p> <p>Chambers: Refers to the channels, cavities, and chambers formed internally in ascocarps of some morel species. Although the vast majority of morel ascocarps are hollow, at least two species, <i>M. exuberans</i> and <i>M. steppicola</i>, have internal chambers visible when the ascocarp is sectioned longitudinally</p> <p>Crests: Another term for <i>ridges</i></p> <p>Developmental process: An important behavioral feature in morels referring to the process of maturation of ascocarps, i.e., from pale to dark or vice versa. Some species of the /Elata clade can be confused with species of the /Esculenta clade when immature because their ascocarps have initially pale colors but then gradually darken. Conversely, <i>M. tridentina</i>, both species of the /Rufobrunnea clade and several species of the /Esculenta clade produce ascocarps that are initially darker and gradually become paler at maturity. Similarly, the stipe can in some species be short proportionately to the pileus when young, but as the ascocarp matures, it becomes elongated and often longer than the pileus, contrary to other taxa where the stipe remains relatively short</p> <p>Ectal excipulum: A term used for the outer layer of the sterile surface of ascocarps. In morels, the <i>ectal excipulum</i> refers to the hyphal system of the outer layer of the stipe that typically gives rise to variously shaped terminal elements (<i>hyphoid hairs</i>), often an important taxonomic trait (see, e.g., Loizides et al. 2015, 2016, 2021)</p>	<p>Lacunose: From <i>lacuna</i>, referring to a gap, cavity, or depression in tissue (Stearn 1985). In stipitate ascomycetes, it is usually used to describe the external surface of the stipe when it is covered with ribs, ridges, and depressions (e.g., Kuo et al. 2012; Nguyen et al. 2013; Loizides et al. 2016)</p> <p>Lipids or lipid bodies: See <i>extrapolar lipid bodies</i></p> <p>Maturation process: See <i>developmental process</i></p> <p>Mitra: The part of the ascocarp that incorporates the hymenium. Also referred to as <i>pileus</i>, <i>cap</i>, or <i>apothecium</i></p> <p>Ophiomorphous: A characteristic “snakehead” shape seen in the apices of paraphyses and acroparaphyses of many morel species (see, e.g., Loizides et al. 2016, 2021)</p> <p>Paraphyses: The sterile hyphal elements of the hymenium, usually bifurcate or less often trifurcate and typically intermingled with the asci or occurring in small fasciculate groups. Some species have multiseptated (3–4) paraphyses that sometimes become inflated and constricted at the septa (moniliform), while others have paraphyses with fewer septa (1–2) on average that are usually confined to the lower third or at the base. Although variable in shape and size, the paraphyses apices and their septation can sometimes provide useful taxonomic clues</p> <p>Pileus: See <i>mitra</i></p> <p>Pits: See <i>alveoli</i></p> <p>Ridges: The sterile rib-like interconnecting structures on the pileus that give morels their honeycomb appearance. Ridges are a key diagnostic feature and are further distinguished in <i>primary</i> (longitudinal) and <i>secondary</i> (transversal or interconnecting). Species of the /Esculenta clade (sect. <i>Morchella</i>) typically have \pm irregular ridges, while species of the /Elata (sect. <i>Distantes</i>) and /Rufobrunnea (sect. <i>Rufobrunnea</i>) clades have regularly arranged or sinuous ridges and usually interconnecting secondary ridges. The color and process of maturation of the ridges are important: a number of <i>Distantes</i> species have ridges that are initially pale but gradually darken at maturity, sometimes acquiring pinkish or purplish tinges in the process</p> <p>Rufescence: The tendency of the ascocarps of a species to stain reddish or orange. Both species of the /Rufobrunnea clade, several species of the /Esculenta clade, and a couple of species of the /Elata clade produce ascocarps that are often rufescent</p> <p>Sinus: Also referred to as <i>sulcus</i> or <i>vallécule</i>, the sinus is the cavity formed by the inward bent of the pileus at its point of attachment to the stipe, somewhat equivalent to the way lamellae are attached to the stipe in basidiomycetes. An important taxonomic trait, the sinus can be deep, shallow, abrupt, rounded, wide, or altogether absent. It is best observed in younger ascocarps, as in overripe specimens, it may sometimes shrink or disappear as the stipe becomes inflated. In “half-free” morels of the /Semilibera clade, the sinus is exceptionally deep and the stipe is attached to the pileus approximately halfway up, leaving the pileal margin completely detached from the stipe</p> <p>Spores: The microscopic units by which fungi reproduce either sexually or asexually. In morels, spores are typically ellipsoid to broadly ellipsoid and appear smooth under a light microscope, but in reality are ornamented when viewed under SEM or in the appropriate staining medium. Six basic types of ornamentation were identified by Clowez and Moreau (2018b), though the spore measurements given by them were taken mostly from exsiccata and might not always be representative of the true range for each species. Because morel spores are very variable and late maturing, measurements from exsiccata can often produce grossly misleading readings; therefore, morel spores should always be measured from a print</p> <p>Lanceolate: A “sword-like” shape of paraphyses and acroparaphyses of several morel species</p> <p>Stem: See <i>stipe</i></p>
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Table 2 (continued)

Extrapolar lipid bodies: The *guttules* often externally attached to the poles of naturally ejected *Morchella* spores. These are hardly ever observable in exsiccata material or in KOH preparations and are of no diagnostic value as far as the identity of the species is concerned

Guttules: See *extrapolar lipid bodies* above

Hairs: See *hyphoid hairs*

Heteroparaphyses: A term introduced by Jacquetant (1984) for some highly irregular structures sometimes seen in the hymenium and sterile ridges that appear to be contorted or deformed paraphyses and acroparaphyses. Such malformations are more often observed in the transitional zone between the hymenium and the ridges and are nowadays considered to be of no taxonomic value

Hyphoid hairs: The terminal hyphal elements of the *ectal excipulum* of the stipe, also referred to as *hairs* or *terminal elements*. These are taxonomically important microscopic structures that can range from long and slender, to clavate, fusiform, catenulate, capitate, or are sometimes irregular and poorly differentiated. They are typically hyaline, although intraparietal pigment and incrustations can sometimes be present in different stages of growth

Stipe: The sterile stalk-like part of the ascocarp supporting the spore-bearing portion (pileus). In morels, the average length of the stipe proportionately to the pileus varies from species to species and can give valuable clues as to the species' identity. The stipe in species of the /Rufobrunnea clade is initially covered in a distinct gray pruinescence, a key diagnostic feature for this clade. At least two species, *M. steppicola* and *M. exuberans*, produce ascocarps with a stipe that is extensively chambered internally

Sulcus: Another term for *sinus* or *vallécule*

Terminal elements: See *hyphoid hairs*

Vallécule: A term introduced by Boudier (1897) for what is now referred to as a *sinus* or a *sulcus*

Final thoughts and recommendations

According to Wheeler (2004), the “causes for the decimation of morphology and taxonomy include misunderstandings that stem from the non-experimental nature of taxonomy, preferential support for new technologies and a cynical equation of success with money.” Up to now, methodologically flawed, scientifically unsound, and taxonomically compromised papers often referred to as “taxonomic vandalism” (Jäch (2007a, 2007b; Kaiser et al. 2013; Páll-Gergely et al. 2020) had been confined to predatory or non-peer-reviewed journals and self-published outlets. The paper by Phanpadith et al. (2019) is the first, to the best of our knowledge, gross taxonomic malpractice of such extraordinary magnitude to be published in such a “high-profile” and highly impacted Q1 journal. Certainly, an exhaustive discussion on the crisis in taxonomy and exploitative publishing lies beyond the scope of this review and the paper by Phanpadith et al. (2019) may or may not constitute a paradigm shift in scholarly publishing. But in an ever-increasing demand for citations, publications in highly impacted journals and fast, hassle-free publishing, the proliferation of generalist pay-to-publish journals, disassociated from academic societies and operating on corporate profit-driven models, is alarming (Beall 2013, 2021; Cobey et al. 2018; Teixeira da Silva et al. 2019). Indeed, in a recent analysis of the impact pay-to-publish has on research quality, van Vlokhoven (2019) concluded that “moving to APC [article processing charge]-based open access makes journals, including the top journals, more lenient” and lower-quality articles could thus be “an unintended consequence of open-access publishing.” In theory, these negative effects could be compensated by

the publishing market itself if lower-quality articles were scarcely cited, as this would eventually lower the impact factor and demand for publishing services in a given journal, therefore prompting an incentive for the journal to offer high-quality papers. In reality, this is seldom the case, as low-quality publications can also be heavily cited if they are accepted without critics, or even negatively cited by critics themselves, still contributing to a high impact factor. An alternative system to criticize and eventually retract works without rewarding the criticized paper and journal with citations could mitigate some of these problems in the post-publication stage.

In this newly emerging landscape, the overwhelming burden for prepublication quality control falls on editors' and reviewers' shoulders, as there seems to be no easy way to ensure pay-to-publish journals will retain the high-quality standards most of their readership would expect and require (Brembs 2018). Careful selection of the appropriate specialist reviewers in each field is crucial but not always easy, as specialists are few and have little time to spare. Fair rewards for their services, either in the form of financial compensation and/or direct academic acknowledgement in an open review process, along with editors' and reviewers' names and comments to be published together with the published article, could provide both an incentive and share some accountability on the validity of the published works. A modified system of academic evaluation, taking into account the reviews undertaken by each researcher other than just published papers and citations, could be a step in the right direction reinforcing the crucial role of the peer-review process (<https://plos.org/resource/open-peer-review/>). Additional quality controls on taxonomic novelties could be provided by external

academic institutions, which have no conflict of interest between the social purpose of science and the commercial purpose of publishing. The International Association for Plant Taxonomy, which publishes the International Code of Nomenclature for algae, fungi, and plants, already operates through committees voting on nomenclatural issues, a system which could be modified to also oversee the quality of works when taxonomic novelties are published, while further supervision could be provided by the International Commission on the Taxonomy of Fungi (<https://www.fungaltaxonomy.org>).

Considering the critical role DNA phylogenies play in fungal taxonomy, making sequence alignments available on Treebase (<https://treebase.org/treebase-web/home.html;jsessionid=D7417F487C513B1B2991D0B42BCC9EF4>) and/or directly to reviewers upon submission, as some journals have already introduced (e.g., *Mycologia*, *Mycological Progress*), must become a prerequisite for the admission of new papers. These could then become part of supplemental information upon acceptance of the paper, so they are openly accessible to ensure reproducibility of the published works. Precisely because DNA sequencing is such a powerful tool, it has all too often been used to mask methodological deficiencies and substandard taxonomy, creating a false sense of security for authors, editors, and reviewers alike. We cannot emphasize enough the need for patient and careful field work, sound sampling methodologies, and multisource approaches in the circumscription of taxa. As is becoming increasingly evident, the integrative model is not only more robust than any single-method approach in delimiting species, but can ultimately lead to a deeper understanding of biodiversity (Pante et al. 2015; Sheth and Thaker 2017; Haelewaters et al. 2018; Sochorová et al. 2019; Lücking et al. 2020; Stadler et al. 2020; Vinarski 2020; Wibberg et al. 2020; Maharachchikumbura et al. 2021). DNA-based phylogenies and morphology are inherently intertwined and can both fail if used single-handedly, uncritically, or out of context to delimit species. Much like morphological and morphometric approaches have in the past failed to recognize species or have misinterpreted intraspecific polymorphism as speciation, DNA-based phylogenies can equally over- or under-split lineages, especially if employed without minimal technical training, overall experience in the studied group, and external controls in the pre- and post-publication stages. Overconfidence in new technologies and dismissal of other valuable sources of information can lead to simplistic approaches that deviate both from the critical thinking and methodology that characterize rigorous scientific thought.

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Author contribution ML conceptualized and initiated this review with the help of MS and BA. ML wrote the first draft of the manuscript together with JMB who wrote the first draft of the phylogenetic part. JMB also designed Figs. 1 and 2. PA contributed significant edits and additions to the entire manuscript, especially the phylogenetic part and recommendations. ML, JMB, BA, VH, PA, GM, and GZ contributed to the point-by-point critique of Phanpadith et al. (2019). ML, JMB, and PAM compiled and edited the taxonomic, nomenclatural, phylogenetic, and phylogeographic information provided in Table 1. ML drafted Table 2 with significant help from PAM and GZ on key terminology. All other authors provided useful edits, suggestions, and support the recommendations proposed in this review. All authors are unanimous in their demand for more stringent quality controls in academic publishing.

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Declarations

Competing interests The authors declare no competing interests.

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