British Naturalists' Association
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A Question of Morels

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True morels (genus *Morchella* Dill. ex Pers.: Fr.) was typified by Christian Hendrik Persoon in 1794 with *Morchella esculenta* designated as the type species. They are fungi that are classified as Ascomycota, Pezizomycetes, Morchellaceae and genus Morchella. They Produce the largest fruit bodies within the ascomycota and can reach a height of 20cm. The hymenium has a typical highly folded and exposed honeycomb appearance producing a very large surface area for spore dissemination. They are highly prized for their gastronomic qualities and are highly sort after especially in temperate areas of the world, mainly fruiting in early spring but there are a couple of autumnal species. Morels are some of the most valuable special forest products in Western North America, and the annual commerce related to morels is thought to be between $5 million to $10 million per year in this region. In China, the annual export of dried morels increased five-fold from 181,000 kg to 900,000 kg during the past 5 years, averaging $160 US dollars per kg. Morel festivals are held in several countries but perhaps the most noted occurs in Michigan in Northern America each year and the most famous is in Boyne City. In 1984 it celebrated its 25th anniversary when the champion on that day found over 500 morels in 90 minutes. Apparently, the all-time record was over 900 morels collected by one person in 1970.

Morchella esculenta by TOMMES-WIKI - Own work, CC BY-SA 3.0, https://commons.wikimedia.org/w/index.php?curid=27753655

The genus is distributed worldwide but recent molecular phylogenetic studies suggest that individual species exhibit high continental endemism in the Northern Hemisphere, and approximately 20 species have been recorded on more than one continent The highest species diversity of true morels is concentrated in Europe and West Asia, East Asia (mainly China), and North America but currently two of the worldwide diversity hotspots are found in the Mediterranean and adjacent regions. More than 20 species have been found in turkey and Cyprus has 11 species. The genus has been the source of considerable taxonomical classification especially with regard to the number of species and traditional classification relies on morphological features and also environmental and ecological associations. These results lead to the classical binominal Latin name as devised by Linnaeus and even using this method it indicated that morels have an intricate genus. Due to insufficient microscopic detail and high levels of variability in form and colour of ascocarps during different developmental stages affected by ecological and climate factors, the species number in Morchella by traditional identification varies from 3 to 50 or more, which has also caused confusing use of homonyms and synonyms.

With the advent of molecular biological techniques, the latest study suggests 79 species and this includes several new species that have been described from Australia, Canada, Cyprus, Israel, Spain, and Turkey. This is likely to change over time given the current interest in Morel investigation and classification. However nucleic acid sequencing (which has become substantially quicker and cheaper) reveals in-depth changes that have revolutionized traditional classification.

Molecular classification has revealed three easily distinguishable evolutionary lineages (clades) and these are currently recognized as:
(i) the basal Rufobrunnea Clade (sect. *Rufobrunnea*, or "white morels")
(ii) the Elata Clade (sect. *Distantes*, or "black morels")
(iii) the Esculenta Clade (sect. *Morchella*, or "yellow morels").

These have been classified 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-1a (TEF1), the nuc rDNA region encompassing the internal transcribed spacers 1 and 2, along with the 5.8S rDNA (ITS), and partial nuc 28S rDNA D1-D2 domains (28S). This data has also been used with the application and principles of the genealogical concordance phylogenetic species recognition (GCPSR).

Using these techniques, it has distinguished (as of 2021) 79 phylogenetic species (phylospecies) in three major clades across the globe: 45 in the Elata Clade, 32 in the Esculenta Clade and 2 species in the Rufobrunnea Clade. The big problem is using binominal names and these can be unambiguously assigned to only a part of the phylospecies, and therefore species are usually denoted by a clade abbreviation followed by an Arabic number (Mel-1 to Mel-45 for the Elata Clade and Mes-1 to Mes-32 for the Esculenta Clade. An example of some of these codes with and without traditional names is given in the figure. You can see sometimes multiple names have been used for the same morel. Considering that phenotypic traits are often highly changed by plasticity eg environmental conditions) and/or intraspecific variability the identification of discriminating macro-and microscopic characters that correspond to the phylogenetic species present the most current challenging problem. Currently most of the unassigned codes are found within the morels recently classified from China.

Of the three clades the basal lineage is assumed to be the more primitive (section Rufobrunnea) and is estimated to have evolved and diverged in the late Jurassic. This clade is represented by two extant species, *M. rufobrunnea*, which has been grown commercially in America and *M. anatolica*. The origin of the later-diverging sister clades, Elata (black morels, section Distantes and Esculenta (yellow morels, section Morchella) was dated to the early Cretaceous, approximately 125 Mya. Early ancestral area reconstruction (AAR) tests postulated a western North American origin of morels but had not included in the analyses *M. anatolica*, whose phylogenetic identity remained at the time unresolved. This cast doubts over the accuracy of the original reconstructions, since both species of the ancestral Rufobrunnea clade are present in the Mediterranean, while *M. anatolica* is altogether absent from North America. Following new collections of *M. anatolica* and *M. rufobrunnea* from the Mediterranean islands of Cyprus, Kefalonia, Lesvos, Malta, and Zakynthos, revised AAR tests were performed to update the historical biogeography of the genus. The results, inferred from multilocus analysis, challenge previous reconstructions and now suggest the Mediterranean basin as the most likely place of origin for morels. The question then is, how did *M.rufobrunnea* arrive in the Mediterranean basin and three possible mechanisms have been suggested; 1. The result of recent anthropogenic introductions from North America; which has now been discarded. 2. It may be the result of refugia from the Pleistocene glaciations or 3. Long distance spore dispersal (LDD) has been suggested as the most likely expansion mechanism. Whether the transcontinental tree-associated species are the result of LDD or refugia, however, remains an unanswered question, and it seems more studies are therefore needed to decipher the complex evolutionary history of these widespread lineages.

The exact ecology of morels is still uncertain but it is clear that not all species have the same requirements. Morels were always thought to be saprotrophic, however there is now a strong link between morels and trees. The formation of mycorrhizae-like structures has been seen in certain species. The Yellow morel clade generally appear to be more abundant in temperate northern and continental regions, where they are usually associated with broadleaved trees, while the black morels clade is more widespread in southern and Mediterranean regions, where they are mostly associated with conifers. Arbruscular associations which are more primitive have been associated with trees such as *Fraxinus excelsior* or *Olea europaea.* Endophytic associations are another type of fungal plant relationship and even this has been found in cheatgrass (*Bromus tectorum*), which confirmed the presence of at least two *Morchella* species (*M. sextellata*, *M. snyderi*) colonising the stems of this grass. Ecological associations can be highly specialized e.g., recently described *Morchella arbutiphila*, appears to be confined to the Mediterranean basin where it is exclusively associated with *Arbutus*, or extremely cosmopolitan with *M. tridentin* being found on least four continents and linked to no less than 15 tree-hosts. What has become apparent recently is a small number of late-diverging lineages within the Distantes clade (*Morchella eximia*, *M. exuberans*, *M. importuna*, *M. sextelata* and *M. tomentosa*) that are facultative or obligate pyrophiles and can fruit in vast numbers in the first and second springs following a forest fire. The exact mechanism is not known but foragers and growers are taking advantage of this phenomenon and are deliberately burning ground in known morel regions.

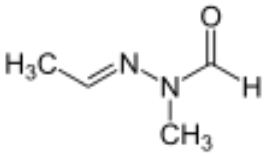
Morchella elata By Holger Krisp - Own work, CC BY 3.0 https://commons.wikimedia.org/w/index.php?curid=19083626

As regards identification of morels the amateur naturalist can now generally speaking only classify them as belonging to a clade complex, e.g., white, yellow or black. Technically *M. esculenta* has been given its own separate position on the clade tree but *M. elata* has not and its place and name still remain hotly contested. With very detailed morphological

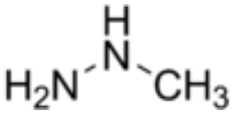
component identification and a definitive guide then sub identification is possible to a certain level but to truly identify the specimen then nucleic acid sequencing is necessary. Does this matter? If you are just trying to identify the morels at a basal level and /or to eat them, then the answer is no. A simple guide to distinguishing the 2 main morels in the UK follows with a typical representative picture. Esculenta clade (Sect. *Morchella*) There are ridges that are buff or ochraceous, never dark at maturity, usually irregularly arranged, sinus absent or present, ascocarps usually ovoid, sometimes rufescent. Elata clade (Sect. *Distantes*) Ridges at least at maturity dark brown or black, partially longitudinally arranged or ± parallel, sinus always present, ascocarps almost never rufescent, usually conical or cylindrical. The only other distinctive species is *m. vulgaris*. The biggest problem for foragers is the mistaken identity of the false morel as a true morel. There is only one false morel really to consider. Unfortunately, the false morel *Gyromitra esculenta* carries the epithet esculenta which means tasteful or good to eat. However, *G. esculenta* is potentially deadly. Although it appears at roughly the same time and in similar geographical locations it can be differentiated from true morels because in the Gyromitra species, its cap is folded in a brain shape and carries more internal divisions and tend to have a furrowed rather than hollow stem. There used to Be a second larger false morel in the UK named *G. gigas* as it was considerably bigger than the usual False Morel but in some author's opinions it is now extinct in UK. Worldwide the true number of false morel species has not been ascertained but ranges between 12 and 18. The false morel however carries with it cultural and gastronomic significance and in most cases unfortunately results in illness and certain death. Although potentially fatal if eaten raw, *G. esculenta* is a popular delicacy in Scandinavia, Eastern Europe, and North America. It used to be popular in some districts of the eastern Pyrenees however it is now prohibited from sale. There is some evidence that populations of *G esculenta* appear to vary geographically in their toxicity which could explain why people from certain areas and certain countries are more likely to get ill. A study from France has shown that mushrooms collected at higher altitudes have lower concentrations of toxin than those from lower elevations, and there is some evidence that fungi found in west North America contain fewer toxins than those to the east. However, poisonings in the west have been reported but overall frequency tends to remain high in Europe. Finland seems to still hold a fascination with false morels and they can still be sold fresh, but it must now be accompanied by warnings and instructions on correct preparation. This involves parboiling before preparation but evidence suggests that even this procedure may not make *G. esculenta* entirely safe for consumption. The main active constituent is gyromitrin and is also known as acetaldehyde *N*-methyl-*N*-formyl hydrazone.

False Morel; *Gyromitra esculenta*
Photo: Roy Stewart

The structure is shown here:



Gyromitrin is rapidly broken down upon heating or in acid media such as stomach acid to N, N methyl formyl hydrazine (MFH) with release of acetaldehyde. A slower hydroxylation results in the formation of monomethyl hydrazine (MMH). The structure of MMH is shown here:



The principle toxic agent (MMH) was also used as a rocket propellant. The toxin affects the liver, central nervous system, and sometimes the kidneys. Severe cases may lead to delirium, coma and death after five to seven days. The lethal dose of gyromitrin has been estimated to be 10–50 mg kg1

So, has the question of morels been answered? Not exactly, but hopefully it has shown how the natural world is still fascinating and wonderful and how recent technological advances and molecular biology is not only enlightening the subject but also making it even more curious.

Roy Stewart is Chairman of South Yorkshire branch and a BNA Trustee. This article has been adapted as a web article, from the original article published in Country-*Side* Winter 2021 issue.

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