A buried mystery

Like a buried treasure, truffles are hidden underground. Broadly speaking, certain fungi which reach fruition underground are known as truffles (also called hypogeous fungi). This is an evolutionary step that has emerged in different groups of fungi, converging into the same type of fruiting bodies. There are both hypogeous Ascomycetes and Basidiomycetes. Among the Basidiomycetes, we can find agaricales related with truffles (Hydnangium), boletales (Rhizopogon), and falales (Hysterangium and Phallogaster), etc. The intermediate link is known as the semihypogeous fungi, which form a transition between the two states. Examples include the genus Macowanites (rusulales) or the agarical Endoptychum agaricoides.



Truffles grow under the soil (Terfezia claveryi)

This process is believed to arise as an adaptation to arid and extreme climates, where the soil attenuates the contrasts that occur above ground. One factor that supports this theory is the lack of truffles in tropical forests. They are especially abundant in midlatitude forests, such as Mediterranean ecosystems or Australian eucalypt forests. Oregon forests are also well known for their truffles. With some exceptions (e.g. various *Sclerogaster* and hypogeous Zygomycetes), truffles are mycorrhizal fungi, associated in symbiosis with the roots of higher plants. Over 40 different species of truffles only associated with oaks are found in Spain. Some alien species are related to eucalyptus plantations or other trees (see table on ecology of Iberian truffles) (see table 3).

Based on genetic studies, it is known that the refuge for the black truffle (and possibly other species of truffles) during the last glaciation was the Iberian Peninsula. After the retreat of the ice, the fungus spread from here to colonize France and Italy.

How do truffles disperse their spores?

Since they develop underground, many hypogeous fungi must be eaten by an animal in order to disperse their spores along with their feces, after passing through the digestive system. Animals like wild boars, rabbits, squirrels, badgers, dormice, voles or mice avidly seek and eat many hypogeous fungi. These animals play a key role in the spread of truffles and the complex relationships that exist between the trees, their mycorrhizal fungi and fauna. And not only large animals eat truffles, there are specialized insects such as flies and beetles which feed on them also. Truffles are often eaten only occasionally, although some animals rely on them for their basic food supply, such as some Australian truffle-eating marsupials or the California redbacked vole (Maser et al, 2008).

Many animals detect truffles by their aromas (although not all are fragrant to humans). These aromas do not appear until the spores are mature, and scientists think that they are not activated until they have passed through the digestive system of an animal.



How to pick truffles

Not all species of truffles have commercial value, while those that do are divided into several categories. The places where some species of truffles grow can be found because they produce a clearing at the base of host trees called a burn or truffière.



After the dog marks the truffle's position, the gatherer digs it up with a special knife (picture: www.trufamania.com)

Thanks to their sense of smell, some animals, such as pigs, locate truffles without training. In Spain, the use of pigs is forbidden because they damage mycorrhizal roots which truffles depend on, so specially trained dogs are therefore used. The training is based on relating the smell of a truffle with a treat. The dog marks the place where the truffle is located with his paws so that the gatherer can then dig it up with his special truffle knife.

Dogs can be taught to only locate truffles with commercial or scientific value.

Since truffle flies (Helomyza tuberivora) lays their eggs on truffles, we can find the precious truffle by looking for these insects on the surface of the truffière, preferably on a sunny day. Many species of truffles (genus *Picoa, Terfezia*, etc.), can be detected by a crack which opens on the surface of the ground. In this case, the help of a trained dog is unnecessary, since lots of practice and detailed observation of the terrain will enable us to find the truffles hidden beneath the cracks. The period for harvesting truffles depends on each species, although spring is the most normal time of year.



Desert truffle crack (picture: J. Fajardo)

Black gold in the kitchen

Some species of truffles are greatly valued as a gourmet delicacy, reaching very high prices in the markets. These are used as seasonings. Fresh truffle flavor lasts for only a few days, but they can also be sold canned or frozen. In some cases lower quality Asian truffles are marketed at a lower price than their Mediterranean counterparts.

Ethnomycology of Truffles

On the Iberian Peninsula there are several species of hypogeous fungi which are traditionally collected. Often the relationship between truffles and host plants, such as rockroses, is popularly known. These fungi are collected to eat at home or in the case of truffles, for sale to wholesalers.



Species	Common name in Spanish	Where it is collected
Choiromyces gangliformis	Criadilla jarera	Extremadura
Melanogaster variegatus	Naranjones	Murcia
Picoa spp.	Bolnegros, monegrillos, negrillos, ta- cones de perro	Southeastern Spain
Rhizopogon spp.	Patatas de monte, turmas	Eastern Spain
Sarcosphaera crassa	Orejones	Eastern Spain
Terfezia spp.	Criadillas, patatas de tierra, turmas	Southern and Central Spain
Tuber aestivum	Trufa blanca, trufa de verano	Eastern Spain
Tuber mesentericum	Trufa de pino	Eastern Spain
Tuber nigrum	Trufa negra	Eastern Spain

Table 1. Truffles traditionally gathered in Spain

Chocolate truffles

Chocolate truffles sold in pastry shops have nothing to do with real truffles; they are simply a confectionery imitation with completely different aromas and taste.

Truffle cultivation

In the field of controlled mycorrhization, the most important sector is the production of trees inoculated with truffles that have a high market value, especially black truffle. Nurseries which specialize in these plants supply truffle growers. The best results are obtained on agricultural land, always in limestone soils.

A new line is desert truffle cultivation, based on producing rock roses (Helianthemum spp.) mycorrhizated with Terfezia spp.



Rhizopogon sp.



Tuber melanosporum



From left to right: Picoa lefebvrei and Terfezia claveryi



Genera and species of Iberian truffles

Genus	Species
Balsamia	B. vulgaris
Choiromyces	Ch. gangliformis
Chondrogaster	Ch. pachysporus
Delastria	D. rosea
Descomyces	D. albus
Elaphomyces	E. anthracinus, E. citrinus, E. granulatus, E. mutabilis, E. trappei
Endogone	E. lactiflua
Endoptychum	E. agaricoides
Fischerula	F. macrospora
Gastrosporium	G. simplex
Gautieria	G. graveolens, G. morchellaeformis, G. otthii, G. trabutii
Genabea	G. cerebriformis, G. sphaerospora
Genea	G. compacta, G. fragrans, G. hispidula, G. lespiaultii, G. sphaerica, G. subbaetica, G. thaxterii, G. verrucosa
Geopora	G. cooperi. Otras especies del género son semihipogeas
Glomus	G. flavisporum, G. macrocarpum, G. microcarpum
Gymnomyces	G. dominguezii, G. meridionalis, G. sublevisporus
Hydnangium	H. aurantiacum, H. carneum
Hydnocystis	H. clausa
Hydnotrya	H. tulasnei
Hymenogaster	H. arenarius, H. bulliardii, H. citrinus, H. griseus, H. hessei, H. knappii, H. luteus, H. lycoperdineus, H. muticus, H. niveus, H. olivaceus, H. populetorum, H. tener, H. thwaitesii, H. vulgaris

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Genus	Species
Hysterangium	H. clathroides, H. crassum, H. inflatum, H. rickenii, H. stoloniferum
Macowanites	M. ammophilus, M. vinaceodorus (semihipogeos)
Mattirolomyces	M. terfezioides
Melanogaster	M. ambiguus, M. broomeianus, M. macrosporus, M. tuberiformis, M. variegatus
Octavianina	0. asterosperma
Pachyphloeus	P. prieguensis
Phallogaster	P. saccatus (semihipogeo)
Picoa	P. juniperi, P. lefebvrei, P. melospora
Protoglossum	P. aromaticum
Pyrenogaster	P. pityophilus
Reddellomyces	R. donkii
Rhizopogon	R. corsicus, R. luteolus, R. marchii, R. occidentalis, R. pannosus, R. roseolus, R. rocabrunae
Ruhlandiella	R. reticulata, R. truncata
Sarcosphaera	S. crassa (semihipogeo)
Sclerogaster	S. compactus
Terfezia	T. albida, T. alsheikii, T. arenaria, T. claveryi, T. eliocrocae, T. extremadurensis, T. fanfani, T. leptoderma, T. olbiensis, T. pini, T. pseudoleptoderma
Tuber	T. aestivum, T. asa, T. borchii, T. brumale, T. excavatum, T. malençonii, T. melanosporum, T. mesentericum, T. nitidum, T. oligospermum, T. panniferum, T. puberulum, T. rapaedorum, T. rufum, T. uncinatum
Wakefieldia	W. macrospora
Zelleromyces	Z. giennensis

Table 2. Data: Calonge et al. (1999), García (2011), Moreno et al. (2005), Bordallo et al (2013), own data.



Ecology of Iberian truffles

In certain cases, hypogeous fungi can be associated with various plants. The table below shows the cases of more specific symbiosis on the Iberian Peninsula (in other countries truffles are often cited as being associated with plant species that do not always correspond with Iberian symbiosis): With over 100 species of truffles, the high diversity of hypogeous fungi is outstanding within the rich Iberian mycota. These fungi are located especially in southern and eastern Spain, where the greatest variety can be found in shrublands and Mediterranean forests.

Ecology	Species
Eucalyptus plantations (<i>Eucalyptus spp</i> .)	<i>Chondrogaster pachysporus, Descomyces albus, Hydnangium carneum, Hysterangium inflatum, Labyrinthomyces donkii,</i>
Grasslands	Gastrosporium simplex
Holm oak (<i>Quercus ilex</i> subsp. <i>ballota</i>)	Balsamia vulgaris, Elaphomyces anthracinus, Gautieria morchellaeformis, Genea compacta, Genea lespiaultii, Genea sphaerica, Genea subbaetica, Genea verrucosa, Gymnomyces dominguezii, Gymnomyces meridionalis, Hymenogaster bulliardi, Hymenogaster citrinus, Melanogaster ambiguus, Tuber aestivum, Tuber excavatum, Tuber malençonii, Tuber nigrum, Tuber panniferum, Tuber puberulum, Tuber rapaedorum, Tuber rufum, Wakefieldia macrospora
Pastures with <i>Helianthemum spp</i> .	Picoa juniperi, Picoa lefebvrei, Terfezia albida, Terfezia claveryi, Terfezia eliocrocae
Pastures with <i>Xolantha</i> guttata	Terfezia arenaria, Terfezia extremadurensis, Terfezia fanfani, Terfezia leptoderma
Pine forests (<i>Pinus spp</i> .)	Geopora cooperi, Hymenogaster luteus, Protoglossum aromaticum, Pyrenogaster pityophilus, Rhizopogon spp., Sclerogaster compactus, Tuber oligospermum, Zelleromyces giennensis
Poplar forests (<i>Populus spp</i> .)	Hymenogaster citrinus, Tuber rufum
Shrublands of <i>Cistus spp.</i>	Balsamia vulgaris, Choiromyces gangliformis, Delastria rosea, Elaphomyces trappei, Genabea cerebriformis, Hysterangium clathroides var. cistophilum, Tuber asa, Tuber oligospermum

Table 3. Data: Moreno et al. (2005), Bordallo et al (2013), own data.





Different Iberian species of the genus Tuber: 1.- T. aestivum. 2.- T. excavatum. 3.- T. melanosporum. 4.- T. mesentericum. 5.- T. panniferum. 6.- T. rufum. Pictures: www.trufamania.com

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