830 basidiomycote, zygomycote and glomeromycote truffles

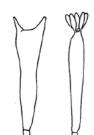
Truffles constitute a form group where the tuber-like fruitbodies are formed ± underground (hypogaeus) and spore dispersal is passive via digging animals. This strategy has arisen multiple times during the evolution of the fungal kingdom, both amongst the Ascomycota, Basidiomycota and Zygomycota and within the Glomales (A-mycorrhizaforming fungi), where truffle-like asexual structures can be found. The fungal wheels shown here have the basidiomycote and other non-ascomycote truffles on the first page spread and the ascomycotes (the "true truffles") on the second.

Truffles

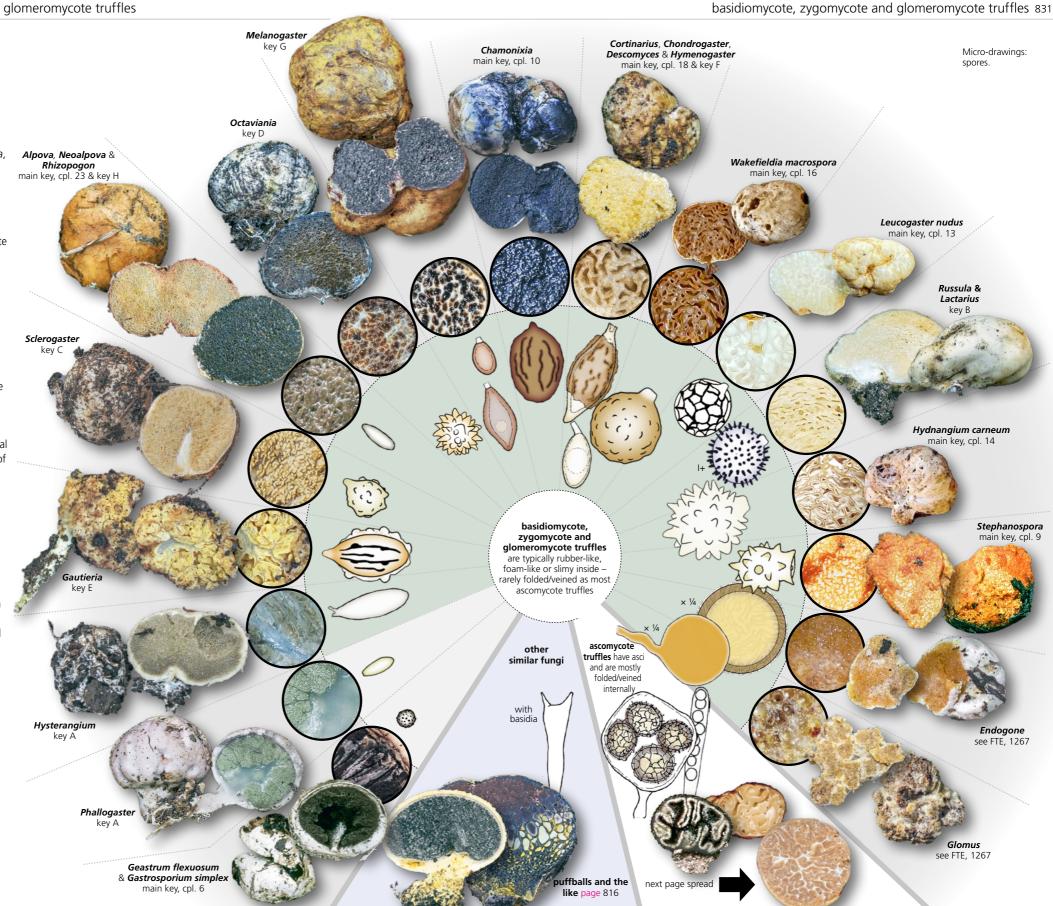
Almost all truffles are ectomycorrhizal. They are dispersed by animals, and various mammals are attracted by their often pungent odours. Boar, deer, mice, and other mammals dig up the fruitbodies to feed on them. Some rodents hoard truffles. Spores from some of the species tolerate passage through the gut.

The odours vary from species to species, and some may resemble mammal pheromones. It is probably compounds of the latter nature that make true truffles an exclusive ingredient in fine cuisine.

The spores are formed internally and the mechanism for active release has been lost. Within the basidiomycote truffles this means that the sterigmata on the basidia and the apiculus on the spores are absent or have changed, and that the spores are typically more symmetrical than in basidiomycotes with active dispersal. Within the ascomycotes the cylindrical ascus has typically evolved into a \pm balloon-like shape, but in some species the cylindrical shape has been maintained. The ascospores tend to be extremely large (20–50 μ m long).



False truffle basidia: left, a 2-spored basidium from *Hymenogaster*; right, a 6-spored basidium without sterigmata from *Hysterangium*.



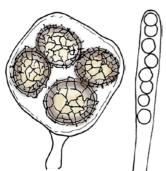
Successful truffling requires a certain "feel" for the ecology of the species. One simple prerequisite is the presence of suitable ectomycorrhizal partners, mainly trees and shrubs, e.g. Corylus, Tilia, Fagus, Quercus or ectomycorrhizal conifers. Relatively light mull soils can often be rewarding to rake through, mainly in

A shortcut can be taken by looking out for animal scrapes, e.g. from deer or squirrels – or, even better, train a dog!

veined or spongy you are in luck.

OTHER SIMILAR FUNGI:

- witch's eggs may look similar but mature above ground (page 814).
- puffballs and the like typically become dusty at maturity and normally mature above ground (page 816).
- cleistothecial fungi produce tiny fruitbodies with tiny asci (see FTE 2 page 1500).



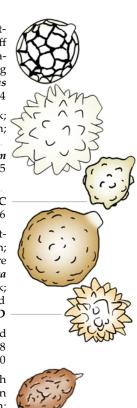
Types of truffle asci: left, a balloon-shaped type from *Tuber aestivum*; right, a cylindrical ascus from *Hydnocystis*.



834 basidiomycote truffles basidiomycote truffles

_		ore measurements are without ornament.
	1.	Spores globose and more than 42 µm wide (sometimes with stringlike appendages)
	2.	Spores formed in asci; fruitbody typically strongly internally folded
		Spores formed on basidia or spore formation unknown; fruitbody interior usually more uniform, e.g. foam-rubber-like 3
	3.	Spore mass (gleba) powdery at maturity 4 Spore mass not powdery at maturity 7
	4.	Spores globose and more than 15 μm wide, with a dark ornament Elaphomyces – see FTE 2 p. 1276 Spores different 5
	5.	Spores more than 9 μ m wide, with a spiny or netlike ornament see <i>Scleroderma</i> , p. 819 Spores smaller, warty 6
	6.	In warm, calcareous scrub and forests; fruitbodies with a thick peridium; with many thin, white hyphal cords. Spores globose, dark greyish brown, 4–6 µm, densely warty; rare (Sweden) <i>Geastrum flexuosum</i> In dry, steppe-like vegetation; fruitbodies with a pale outer peridium and a greyish inner; with a thick, white hyphal cord. Spores subglobose to drop-shaped, pinkish buff, finely warty (3.5–) 4–5 µm; rare (S, reaching S Sweden)
	7.	Cut fruitbodies resemble a cut witch's egg in colour and texture; base with hyphal cords; spores smooth and hyaline under the microscope
	8.	Fruitbodies orange or bluish (), sometimes only when bruised
	9.	Both surface and spore mass orange; spores with triangular spines and a truncate end. Fruitbody 10–40 mm wide; spore mass \pm chambered; spores 10–16 × 7.5–12 µm; in warm calcareous forests; rare (S, including UK). Stephanospora caroticolor Surface blueing or reddening; spores different 10
	10.	Surface deep blue when bruised and at maturity; spores brown, longitudinally wrinkled. Fruitbody 10–30 mm wide; spore mass labyrinthine-chambered, greyish brown with a short, white columella; spores $18-20\times12-15~\mu m$; in \pm calcareous conifer forests, usually in rotten stumps; rare (N–NW)
	11.	Spores with an amyloid, spiny ornament
		Spore ornament not amyloid
	12.	Spores globose to subglobose











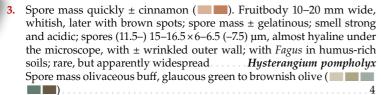


836 key A – Hysterangium and Phallogaster key B – Lactarius and Russula 837

Key A – Hysterangium and Phallogaster

1.	Spores ± globose and wartysee Sclerogaster, key C
	Spores ellipsoid to spindle-shaped, smooth, but sometimes with a loos-
	ening outer wall 2

Spores 4–5.5×1.5–2.5 µm; fruitbody very witch's-egg-like. Fruitbody up to 15 mm wide, pale; stem 10-20 mm high; spore mass gelatinous, greenish; on debris with much dead wood; rare (S) ... Phallogaster saccatus



Spores 9–12 µm long Spores longer than (11–) 12 µm 6

5. With Eucalyptus; spores with an outer wall that loosens crest-like; the outer layer of the fruitbody (peridium) exclusively of narrow hyphae. Fruitbody 10-25 mm wide, whitish, immediately clay-pink when touched, later brownish; spore mass \pm gelatinous, glaucous green; smell radish- to melon-like; spores 9–12×3–4 μm; rare (S) Hysterangium inflatum With deciduous and coniferous trees; spores with a wrinkled outer layer; the outer layer of the fruitbody with a layer of globose cells. Fruitbody 20-25 mm wide, initially whitish, but soon orange-brown; spore mass \pm gelatinous, \pm olivaceous buff; spores 9–12 × 4–6 µm; rare, but widespread Hysterangium coriaceum

Outer layer of the fruitbody (peridium) exclusively of narrow hyphae. 7 Outer layer with a layer of globose cells 8

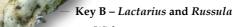
Fruitbody wrapped in a thick layer of thin, white hyphal cords; spores on average 12-15 µm long. Fruitbody 10-30 mm wide, whitish, later with brown spots; spore mass ± gelatinous, glaucous green; spores spindle-shaped and with a slightly wrinkled outer wall, 12–15×5–7 µm; in calcareous soil with deciduous trees; rare, but widespread ... Hysterangium calcareum Fruitbody with a thick basal hyphal cord and with rather few surface cords; spores on average 16-20 µm long. Fruitbody 5-15 mm wide, whitish, later with brown spots; spore mass ± gelatinous, dark olivaceous buff; spores spindle-shaped with a uneven outer wall, 15–22×5–7 µm; in mixed forest; rare, but widespread. Hysterangium clathroides ss. auct.

Spores up to 16 µm long. Fruitbody 20–25 mm wide, initially whitish, but soon orange-brown; with a thick hyphal cord; spore mass \pm gelatinous, glaucous green; smell fruity; spores ± spindle-shaped with distinctly longitudinally wrinkled outer wall, 11–16 × 3–5.5 (–7) µm; in Spores longer than 16 µm 9

Spores 17–26 × 5–7 μm. Fruitbody 10–30 mm wide, initially whitish, later ± orange-brown, with numerous white hyphal cords, including a thicker basal; spore mass ± gelatinous, olivaceous buff to brownish olive; spores spindle-shaped; with deciduous trees; rare, but widespread.

..... Hysterangium stoloniferum

Spores $16-17 \times 4.5-6.5 \, \mu m$. Fruitbody $10-20 \, mm$ wide, whitish; spore mass ± gelatinous, glaucous green; spores spindle-shaped, outer wall wrinkled; in deciduous forests, rare, but widespread ... Hysterangium nephriticum¹

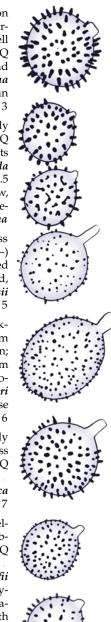


1.	With a stem or a remnant of one (a columella) internal in the f	ruit-
	body	
	Without any traces of a stem	4

- 2. With a well-developed stem and curled remnants of gills; spores on average wider than 11 µm. Fruitbody 12-38 mm wide, brownish orange with browner spots; spore mass labyrinthine, buff-yellow; smell absent; taste mild; spores (9–) 10.5-15.5 (-18) × (8–) 10-15 (-17) μ m, Q 1–1.15, with up to 2.5 (–3) µm long, isolated spines; with Abies and Picea; rare (S) Russula mattiroloana Only with inner traces of a stem; spores on average narrower than
- 3. Spores with entirely isolated spines, $8-11(-12.5)\times7-9(-11)$ µm. Fruitbody 5–35 mm wide, cream; spore mass buff-yellow, foam-rubber-like; spore Q 1.1–1.3, with up to 1.5 µm high spines; in nutrient-rich deciduous forests and parks; rare, but widespread Russula candida Spores with somewhat connected spines, $9.5-12.5 (-15) \times (8-) 8.5-10.5$ (-13) µm. Fruitbody 14-28 mm wide, cream; spore mass buff-yellow, foam-rubber-like; spore Q 1.1–1.3, with up to 2 µm high spines; with de-
- 4. With white milk. Fruitbody 10–30 mm wide, reddish; spore mass foam-rubber-like, whitish, later cinnamon; milk hot; spores (11.5–) $12-14.5 (-15) \times (10-) 11-13 \mu m$, Q 1.1–1.2, with up to 2 μ m long, isolated spines; basidia 1-spored; with deciduous trees; rare, but widespread, reaching S Scandinavia Lactarius stephensii Without white milk, but sometimes with water-clear milk
- 5. With sparse, water-clear milk; flesh with lactiferous hyphae (milkhyphae); spores broadly ellipsoid, Q 1.2-1.3. Fruitbody 10-20 mm wide, ± reddish brown; spore mass foam-rubber-like, reddish brown; taste mild; smell fruity; spores $14-18.5 \times 12-15 \mu m$, with up to 2 μm long, isolated or slightly connected spines; with deciduous and coniferous trees; rare (S) Lactarius soehneri Without milk; flesh without lactiferous hyphae; spores usually globose to subglobose (Q 1–1.2).
- Basidia 1-spored; spores 13–15 (–15.5) × 12.5–14.5 (–15) µm. Fruitbody 10–20 mm wide, whitish to yellowish brown, later brownish; spore mass foam-rubber-like ± yellowish brown; smell and taste unknown; spore Q 1.0–1.1, with up to 3 μm long, isolated spines; rare (Germany)

Spores with 0.5–1 μ m long spines. Fruitbody 10–30 mm wide, \pm yellowish brown, later with darker brown spots; spore mass foam-rubber-like, \pm yellowish brown; taste mild; spores 9.5–12.5 \times 8.5–11 µm, Q 1.0–1.1; with deciduous trees; rare (Czech Republic, Germany)

Spores with 1–3 µm long spines. Fruitbody 10–30 mm wide, ± claybuff, later with brown spots; spore mass foam-rubber-like, ± cinnamon; smell fruity; taste mild; spores (8–) 9.5–12.5 (–14) µm, Q 1; with deciduous and coniferous trees; scattered (S–SE, reaching S Germany) Russula cerea







^{1.} Hysterangium thwaitesii should have a hyphal, hyaline lower layer in the peridium and a rather smooth outer wall on the spores, while *Hysterangium nephriticum* should have a lower layer of more globose, brown cells and a more wrinkled outer spore wall

838 key C – *Sclerogaster*, key D – *Octaviania* key E – *Gautieria* 839



Key C – Sclerogaster





Sclerogaster gastrosporoides





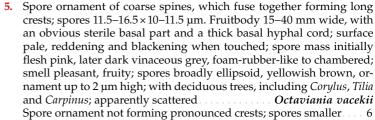
Key D – Octaviania





- **3.** The spore ornament forms a ± regular pattern of conical spines . . . 4 The spore ornament forms a more striped, irregular pattern 5





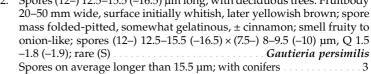


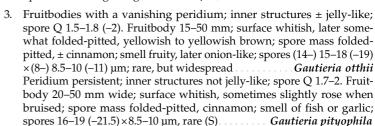


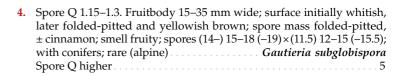


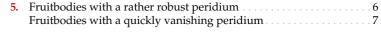
Key E – Gautieria

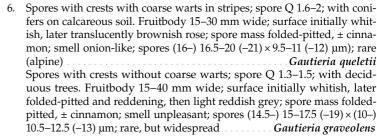
1.	Spores wider 2 Spores wider 4	
2.	Spores (12–) 12.5–15.5 (–16.5) µm long; with deciduous trees. Fruitbody	





















- 7. Spores (13–) 14–17 (–18) μm wide. Fruitbody 20–65 mm wide; surface initially whitish, later folded-pitted and yellowish brown, reddening when touched; spore mass folded-pitted, ± cinnamon; smell strongly pear- or peach-like; spores 19–24 (–26) × (13–) 14–17 (–18) μm, Q 1.3–1.6; with deciduous trees on calcareous soils; rare (S)
 - Gautieria macrocoilia
 Spores 10–14.5 µm wide 8



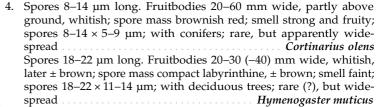








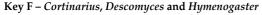




- 6. Spores 13–20 μm long; with Eucalyptus. Fruitbody up to 60 mm wide, whitish, when bruised yellowish to brownish; spore mass ± clay-buff; spores spindle-shaped to lemon-shaped, 13–20×7–11 μm, with a warty to netlike, loosening outer wall; rare, mainly SW Descomyces albus Spores on average longer than 20 μm; with other hosts
- 7. Spores on average longer than 25 μmSpores on average shorter than 25 μm9
- Spores $23-35 \times 10-15$ µm; fruitbody surface initially yellowish, when bruised reddish brown to almost blackish. Fruitbodies 10-30 (-60) mm wide; spore mass compact labyrinthine, soon dark greyish brown; smell fruity to more acidic; with deciduous trees; scattered.

Spores 35–50 (–90) × 12–15 µm; fruitbody surface initially whitish, when touched pale buff, browning to blackish. Fruitbody 10–30 mm wide; spore mass compact labyrinthine, ± clay-buff; smell unknown; with deciduous and coniferous trees; rare (?), apparently widespread *Hymenogaster calosporus* ss. auct.





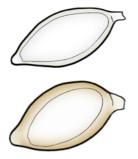
Sequence studies on European material have shown that *Hymenogaster* is far more species rich than normally assumed, and the key is a simplification.

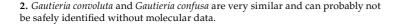
- 1. Spores smooth or almost so 2
 Spores with a wrinkled-warty, ± loosening outer wall 3
- 2. Spore mass buff-yellow (). Fruitbodies 5–20 mm wide, whitish, pale buff to clay-pink; spore mass compact labyrinthine, buff-yellow to cinnamon-buff; smell aromatic, pleasant; spores 18–22 × 7–11 µm, mostly narrowly lemon-shaped, many deformed, pale greyish yellow; with deciduous trees; rare, but widespread



Spore mass \pm cinnamon (). Fruitbodies 20–40 mm wide, whitish, later \pm brown; spore mass very compact labyrinthine with branched veins, cinnamon to dark brownish rose; smell unpleasantly pungent; spores $20-22 \times 12.5-15$ µm, lemon- to pear-shaped; smooth to almost so, brownish yellow; with deciduous trees; rare (S)

Hymenogaster bulliardii





^{3.} Including Hymenogaster thwaitesii.

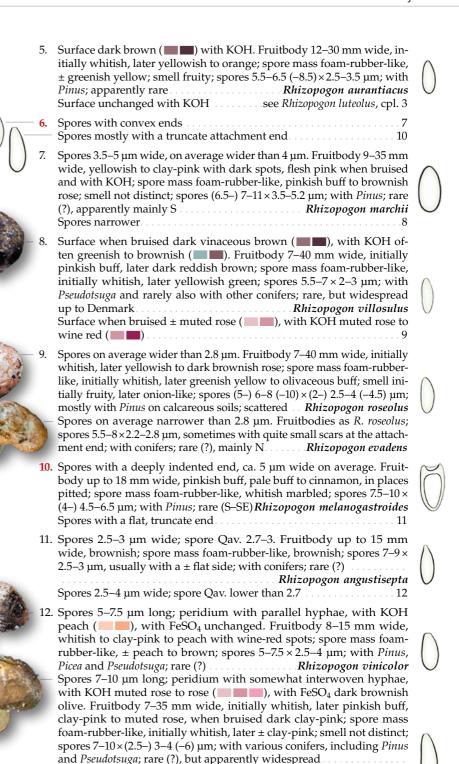
^{4.} Including *Hymenogaster olivaceus*. Gross 1969 (Über Hymenogasterfunde mit Sporen von 25–35 μ mittlerer Länge. *Zeitschrift für Pilzkunde* 35(3–4): 157–178) describes a number of species with spores up to 35 μ m in length.

^{5.} *Hymenogaster hessei, Hymenogaster decorus* and *Hymenogaster rehsteineri* are included here.

842 key G – Melanogaster, key H – Rhizopogon

	Ke	y G – Melanogaster	
	1.	Spores on average shorter than 10 μm $$2$ Spores on average longer than 11 μm $$4$	
	2.	Spores on average shorter than $6\mu m$. Fruitbody $10-15m m$ wide, \pm curry yellow; spore mass chambered, black; spores $5.5-6.5\times2.8-3.3\mu m$; with deciduous and coniferous trees; rare, but widespread	0
		Spores on average longer than 7 µm	
	3.	Spores almost cylindrical; spore Qav. 1.8–2.0. Fruitbody 20–60 mm wide, \pm yellowish brown; spores 6.5–11 × 3.5–5 μ m; in mull soil with Fagus, Tilia or other deciduous trees, both in parks and forests; scattered	
	4.	Spores almost lemon-shaped with an obvious papilla, $14-18 (-20) \times 7-9 (-12) \mu m$. Fruitbody $20-50\times 10-30 \ mm$, greyish brown; with Fagus, Corylus or other deciduous trees; scattered Melanogaster ambiguus Spores without an obvious papilla	
	5.	Spores egg-shaped to ellipsoid, broadly rounded at one end, Q 1.4–1.6. Fruitbody 20–60 mm wide, \pm reddish brown; spores 9–15 × 6–8.5 μ m; mostly with <i>Fagus</i> ; rare, but apparently widespread. <i>Melanogaster tuberiformis</i> ⁶ Spores \pm spindle-shaped, Q 1.9–2.2. Fruitbody 20–60 mm wide, \pm reddish brown; spores 12–16 × 6–7 μ m; with <i>Fagus</i> or other deciduous trees; rare (?), mainly S <i>Melanogaster macrosporus</i>	
	Ke	y H – Rhizopogon	
	1.	Fruitbody covered by adpressed hyphal cords 2 Fruitbody at most with scattered adpressed hyphal cords 6	
0	2.	Spores mostly with a truncate attachment end 3 Spores with convex ends 4	
	3.	Surface with reddening hyphal cords, turning muted rose () with KOH. Fruitbody 18–27 mm wide, curry yellow to pinkish buff with dark spots; spore mass foam-rubber-like, ± pinkish buff to reddish brown; spores 5–8 × 2–3.8 µm; with <i>Pinus</i> ; rare (?), but widespread <i>Rhizopogon verii</i> ? Surface ± curry yellow, turning glaucous green or clay-buff () with KOH. Fruitbody 10–50 mm wide, pale buff, curry yellow to cinnamon-	
		buff; spore mass foam-rubber-like, \pm clay-buff to brownish olive; smell slightly fruity; spores 5–8.5 (–11)×2–4 μ m; with $Pinus$; common	
	4.	Surface reddening (), especially after addition of KOH. Fruitbody 20–40 mm wide; initially whitish, later curry yellow, when bruised muted rose; spore mass foam-rubber-like, glaucous green to olivaceous buff; smell fruity; spores $5-8\times2-3.5$ µm; with <i>Pinus</i> ; rare (?), but widespread	
	<u></u>	Melanogaster intermedius is sometimes regarded as a distinct species with slight-	

^{6.} *Melanogaster intermedius* is sometimes regarded as a distinct species with slightly larger spores.



..... Rhizopogon pseudoroseolus⁹

^{7.} Rhizopogon subolivascens is very similar or identical, and if so, it is the correct name.

^{8.} *Rhizopogon subalpinus* can possibly be separated by a peridium of narrow hyphae mixed with wider cells. *Rhizopogon ochraceorubens* is very similar, but should have more slender, $30-40 \times 4-4.5 \, \mu m$ sized basidia.

^{9.} *Rhizopogon abietis* is probably a synonym.