= Phellodon =

Phellodon is a genus of tooth fungi in the family Bankeraceae . Species have small- to medium @-@ sized fruitbodies with white spines on the underside from which spores are released . All Phellodon have a short stalk or stipe , and so the genus falls into the group known as " stipitate hydnoid fungi " . The tough and leathery flesh usually has a pleasant , fragrant odor , and develops a cork @-@ like texture when dry . Neighboring fruitbodies can fuse together , sometimes producing large mats of joined caps . Phellodon species produce a white spore print , while the individual spores are roughly spherical to ellipsoid in shape , with spiny surfaces .

The genus , with about 20 described species , has a distribution that includes to Asia , Europe , North America , South America , Australia , and New Zealand . About half of the species are found in the southeastern United States , including three species added to the genus in 2013 ? 14 . Several Phellodon species were placed on a preliminary Red List of threatened British fungi because of a general decline of the genus in Europe . Species grow in a symbiotic mycorrhizal association with trees from the families Fagaceae (beeches and oaks) and Pinaceae (pines) . Accurate DNA @-@ based methods have been developed to determine the presence of Phellodon species in the soil , even in the extended absence of visible fruitbodies . Although Phellodon fruitbodies are considered inedible due to their fibrous flesh , the type species , P. niger , is used in mushroom dyeing .

= = Taxonomy = =

Phellodon was circumscribed in 1881 by Finnish mycologist Petter Karsten to contain white @-@ toothed fungi . Karsten included three species : P. cyathiformis , P. melaleucus , and the type , P. niger (originally published with the epithet nigrum) . P. nigrum was originally described by Elias Fries in 1815 as a species of Hydnum . Some early authors did not consider Phellodon distinct enough to be a separate genus , and folded species assigned to this genus into Hydnellum .

Hydnellum is classified in the family Bankeraceae , which was circumscribed by Marinus Anton Donk in 1961 . Donk 's original family concept included the genera Bankera and Phellodon , whose species produce hyaline (translucent) and echinulate spores (covered with small spines) . Donk also noted that Bankeraceae species lacked clamp connections . When clamp connections were discovered in Phellodon fibulatus and tuberculate spore ornamentation (the presence of small nodules on the spores) was found in P. niger , Kenneth Harrison thought the family Bankeraceae was superfluous , and placed Phellodon and Bankera in the family Hydnaceae . This taxonomic rearrangement was rejected by Rudolph Arnold Maas Geesteranus in 1974 , who showed that the tuberculate spores of P. niger were the result of an immature specimen . Richard Baird and Saeed Khan investigated spore ornamentation in North American Phellodon species using scanning electron microscopy , and rejected the placement of Phellodon in the Bankeraceae , preferring to leave it and Bankera in the Hydnaceae . Modern molecular phylogenetic analysis places Phellodon in the thelephoroid clade (roughly equivalent to the order Thelephorales) along with the related genera Bankera , Hydnellum , and Sarcodon . Although the status of the Bankeraceae has not been fully clarified with molecular genetic techniques , Phellodon is classified in this family by authorities on fungal taxonomy .

The generic name is derived from phell- , meaning " cork " , and -don , meaning " tooth " . In North America , Phellodon species are commonly known as " cork hydnums " . The British Mycological Society , in their recommended list of common names for fungi in the United Kingdom , name Phellodon species in the form " descriptor word " plus " tooth " : fused tooth (P. confluens) , grey tooth (P. melaleucus) , black tooth (P. niger) , and woolly tooth (P. tomentosus) .

= = Description = =

The fruit bodies of Phellodon species have caps and stipe , and thus fall into the general category " stipitate hydnoid fungi " . The cap surfaces are initially velvety to tomentose , eventually becoming

matted . The surface is rough , with pits and ridges , and sometimes with concentrical zones of color or texture . The color can vary considerably , from cream to yellowish , brownish , greenish , greyish or black . Neighboring fruitbodies can fuse together , forming intertwined caps and partially fused stipes . Alexander H. Smith wrote of P. tomentosus , " It often occurs in large mats of fused caps almost producing a ceiling over large areas of the moss under conifers . " Phellodon fruitbodies can envelop nearby grass or twigs . The stipe is thickly tomentose or smooth , typically the same color as the cap or darker . In P. niger , the outer covering of the stipe is a thick felty layer of mycelium that absorbs water like a sponge . The hymenophore (the fertile , spore @-@ bearing surface) is on the underside of the cap . The spines become grey at maturity . In conditions of high humidity , P. niger can form striking drops of black liquid on the actively growing caps .

The fibrous flesh is single to double @-@ layered ; duplex layering results from differences in compactness or in the alignment of the constituent hyphae . Tough and leathery when fresh , the flesh develops a corklike texture when dry . In the dried state it often has an odor of fenugreek or curry powder . Phellodon species are often free of insect damage , suggesting that they may have defensive chemicals that deter predation . Fruitbodies are not considered edible due to their fibrous flesh .

The hyphal system is monomitic , containing only generative hyphae . These hyphae are not less than 6 ?m in diameter . All European species lack clamp connections , but they are present in the North American species P. fibulatus and P. mississippiensis . The basidia (spore @-@ bearing cells) are four @-@ spored . Cystidia are either absent , or present infrequently as incompletely differentiated cystidioles (sterile cells about the size of an immature basidium) . In mass , the spores are white . Spores are broadly ellipsoid to roughly spherical , and echinulose (covered with small spines) . They are also hyaline and inamyloid .

= = Habitat and distribution = =

Fruit bodies grow on the ground . Phellodon species , like all members of the order Thelephorales , are thought to be mycorrhizal , forming symbiotic relationships with trees . Usual hosts include species from the families Fagaceae (beeches and oaks) and Pinaceae . The ectomycorrhizae that P. niger forms with Norway spruce (Picea abies) has been comprehensively described . It is distinguished from the ectomycorrhizae of other Thelephorales species by the unique shape of its chlamydospores . Stable isotope ratio analysis of the abundance of the stable isotope carbon @-@ 13 shows that P. niger has a metabolic signature close to that of saprotrophic fungi , indicating that it may be able to obtain carbon from sources other than a tree host .

Many Phellodon species are known from the southeastern United States , where they have been extensively researched . According to Baird and colleagues , there are nine distinct Phellodon species from Great Smoky Mountains and the surrounding southern Appalachian Mountains . Three additional species from this area , P. mississippiensis , P. brunneo @-@ olivaceus , and P. fuligineoalbus were added to the genus in 2013 ? 14 .

= = Conservation = =

Phellodon species , like other members of the family Bankeraceae , are sensitive to air pollution and soil pollution , and are in general decline in western Europe . In a preliminary assessment for a red list of threatened British Fungi , P. confluens , P. tomentosus , and P. melaleucus are considered vulnerable , and P. niger is rare .

Conservation efforts for stipitate hydnoid fungi are hampered by a dearth of information about their basic ecology , and so molecular genetic techniques are increasingly employed in attempts to better understand these fungi . In the case of Phellodon tomentosus , for example , there is little correlation between fruitbody appearance and below @-@ ground mycelium , making it hard to determine the distribution and rarity of the fungus with standard surveying techniques . Phellodon melaleucus and P. niger were included in a Scottish study to develop species @-@ specific PCR primers that can be used to detect the mycelia of stipitate hydnoids in soil . DNA testing of collections labelled as P.

melaleucus and P. niger from the United Kingdom revealed additional cryptic species . PCR analysis can be used to determine the presence of a Phellodon species up to four years after the appearance of fruitbodies , allowing a more accurate determination of their possible decline and threat of extinction .

= = Chemistry = =

Phellodon species contain thelephoric acid , a metabolite of the shikimic acid pathway . Thelephoric acid is a terphenyl quinone ? a 1 @,@ 4 @-@ benzoquinone wherein positions carbon @-@ 2 and carbon @-@ 5 are substituted with phenyl groups . The hirsutane derivative phellodonic acid is found in P. melaleucus . Phellodonic acid , which exhibits antibiotic activity towards bacteria and other fungi , was the first bioactive compound reported from any member of the order Thelephorales . A total synthesis was described for phellodonic acid in 2008 using cis @-@ 1 @,@ 2 @-@ dihydrocatechol as the starting material . The compound atromentin was reported to occur in fruitbodies of P. melaleucus , but this was not confirmed in a later analysis . P. niger has been a source for several bioactive compounds : the cyathane @-@ type diterpenoids , nigernin A and B ; a nitrogenous terphenyl derivative , phellodonin ; 2 ' , 3 ' -diacetoxy @-@ 3 @,@ 4 @,@ 5 ' , 6 ' , 4 ' '-pentahydroxy @-@ p @-@ terphenyl ; grifolin ; and 4 @-@ O @-@ methylgrifolic acid . P. niger has also been used for mushroom dyeing , in which it produces gray @-@ blue and green colors .

= = Species = =

Phellodon was originally circumscribed with three species . Joost Stalpers included 13 Phellodon species in his 1993 monograph on the Thelephorales . The tenth edition of the Dictionary of the Fungi (2008) indicated 16 species in the genus . As of September 2015 , Index Fungorum lists 18 species of Phellodon , not including the three eastern United States species added in 2013 ? 14 .

Phellodon atratus K.A.Harrison (1964) ? California , United States
Phellodon brunneo @-@ olivaceus R.E.Baird (2013) ? United States
Phellodon confluens (Pers .) Pouzar (1956) ? China , eastern United States , Europe
Phellodon excentrimexicanus R.E.Baird (1985) ? Mexico
Phellodon fibulatus K.A.Harrison (1972) ? North Carolina , United States
Phellodon fuligineoalbus (J.C.Schmidt) Baird (2013) ? United States
Phellodon implicatus R.E.Baird & S.R.Khan (1986) ? Florida , United States
Phellodon indicus Khara (1978) ? Himachal Pradesh , India
Phellodon maliensis (Lloyd) Maas Geest . (1966) ? Australia , New Zealand
Phellodon melaleucus (Sw. ex Fr .) P.Karst. (1881) ? Europe , North America
Phellodon mississippiensis R.Baird (2014) ? Mississippi , United States
Phellodon niger (Fr .) P.Karst. (1881) ? Europe , North America
Phellodon nothofagi McNabb (1971) ? New Zealand
Phellodon plicatus (Lloyd) Maas Geest . (1966) ? Australia
Phellodon putidus (G.F.Atk.) Banker (1906) ? North America
Phellodon radicatus R.E.Baird (1985) ? North America
Phellodon rufipes Maas Geest . (1971) ? Japan
Phellodon secretus Niemelä & Kinnunen (2003) ? Finland
Phellodon sinclairii (Berk .) G.Cunn. (1958) ? New Zealand
Phellodon tenuis R.E.Baird (1988) ? Brazil
Phellodon tomentosus (L.) Banker (1906) ? Europe , North America