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Morphological variability of *Fomes fomentarius* basidiomata based on literature data

Introduction

The genus *Fomes* is a taxon accepted in the Polyporaceae family of Polyporales order in class Agaricomycetes, subphylum Agaricomycotina and phylum Basidiomycota. *Fomes fomentarius* is the type species of the genus (Donk, 1960). There are two morphological species in the genus *Fomes* recognized at present: *F. fomentarius* (L.) Fr. and *F. fasciatus* (Sw.) Cooke (Ryvarden, 1991). Although only mean basidiospore size is a helpful morphological characteristic in identification of the respective species, ITS and rpb2 sequence data and optimum temperature for hyphal growth *in vitro*, support separation of these two distinct species (McCormick et al., 2013a; Gáper et al., 2016).

F. fomentarius is an ecologically and economically important polypore wood decay macrofungus with major roles not only in nutrient cycling in forest ecosystems as decomposer of dead wood and plant litter, but also as a source of medicinal and nutraceutical products (Tello et al., 2005; Collado et al., 2007; Neifar et al., 2013; Dresch et al., 2015). There have also been reports that it can persist as an endophyte in healthy plants for many years (Baum et al., 2003; Parfitt et al., 2010). The species has been reported from Africa, Asia, Europe, South America (Chile) and North America (McCormick et al., 2013a, b; Gáper, Gáperová, 2014), but a revision of the *F. fomentarius* data from Chile is necessary (Gáper et al., 2016).

In recent years, the existence of three distinct ITS lineages/sublineages among *F. fomentarius* strains has been clearly established. The sublineage A1 consists of strains isolated from North America, whereas the sublineage A2 consists of strains recently

isolated only from Europe. The lineage B consists of strains isolated from Europe and Asia (Gáper et al., 2016). The presence of the two variable groups in Europe was further confirmed by molecular methods based on both *efa* region and LSU gene sequences comparison, so the *F. fomentarius* actually includes two sympatric cryptic species in Europe (Pristaš et al., 2013).

The present paper reviews the morphological variability of the *F. fomentarius* basidiomata with implications for reliable separation of *F. fomentarius* lineages/sublineages, basing on descriptions published in the literature. In contrast to the strain data (Dresch et al., 2015; Gáper et al., 2016), the morphological variability of *F. fomentarius* basidiomata is well documented.

Methods

All reliable information on *F. fomentarius* basidiomata was collected and corroborated through the evaluation of literature in libraries and searches in online databases using Google Scholar, SciFinder and Web of Knowledge. In this article, we present only a small fraction of the literature on the species within North America, namely McCormick et al. (2013a, b) because basidiomata morphology of *F. fomentarius* examined in their studies are consistent with formerly published descriptions (Overholts, 1953; Lowe, 1957; Gilbertson, Ryvarden, 1986). They examined macro- and micromorphological characters of basidiomata sampled from multiple woody plant hosts and geographic regions in the United States (McCormick et al., 2013a, b).

Results and discussion

General description of basidiomata

MACROCHARACTERS: basidiomata (Fig. 1) perennial, sessile, unguate (occasionally applanate or triquetrous), tough, woody with a blunt margin; upper surface of pileus crustose, glabrous, prominently zoned (occasionally slightly zonate or no zonation) and shallowly furrowed, marginal part finely tomentose or smooth; pore surface concave (occasionally flat to slightly concave or convex); pores round, small (2–5 per mm); context pale brown, soft-corky, tough and fibrous, azonate or concentrically zoned, up to 1–3 cm thick; granular core of varying size developing at upper part of the context close to the substratum consisting of very thick-walled and irregularly shaped hyphae (sclerids); tube layers not distinctly (exceptionally distinctly) stratified, brown and becoming filled with white mycelium.

MICROCHARACTERS: hyphal system trimitic; contextual generative hyphae thin-walled, hyaline with clamps, 2–5 μm in diam., inconspicuous; contextual skeletal hyphae thick-walled, aseptate, pale brown in KOH, 3–8 μm in diam.; contextual

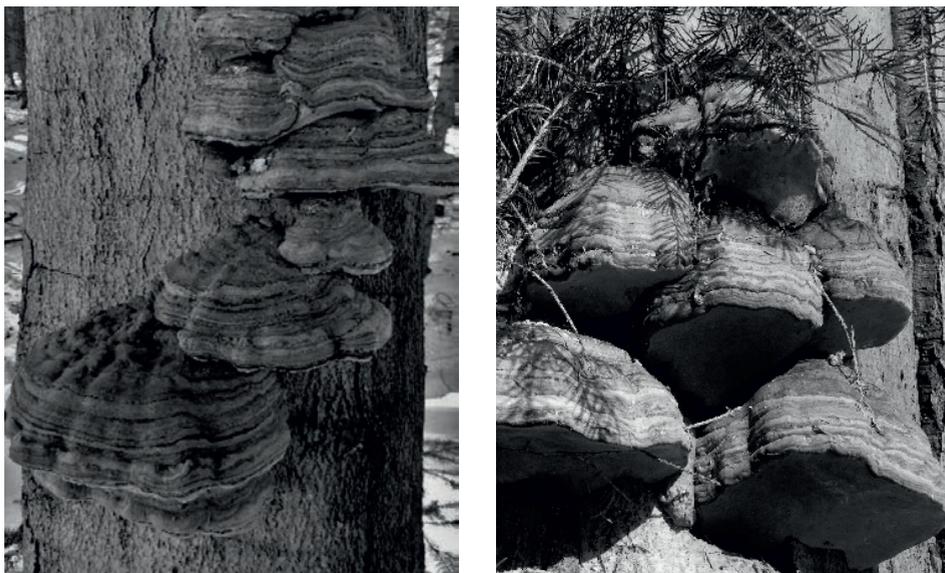


Fig. 1. *Fomes fomentarius* basidiomata typically unguulate in shape on beech (*Fagus sylvatica*) trunk. From M. Šebesta (unpub., 2015)

binding hyphae thick-walled, strongly branched, aseptate, pale brown, 1.5–4.5 μm in diam. Cystidia none, cystidioles often present in the hymenium, thin-walled, fusoid, 24–40 \times 3.5–7.5 μm , with a basal clamp. Basidia clavate, 4-sterigmate, usually with a basal clamp, developed only early in the spring. Basidiospores cylindric, hyaline, smooth, negative in Melzer's reagent.

Geographic variability of basidiomata

Above mentioned characters from basidioma macro- and micromorphology basically follow the description given by Ryvar den and Gilbertson (Gilbertson, Ryvar den, 1986; Ryvar den, Gilbertson, 1993). They generally correspond well with those reported in other comprehensive polyporological monographs and recent studies, but we detected some differences. On the other hand, some European and Asian data is identical (Ryvar den, Gilbertson, 1993; Nuñez, Ryvar den, 2001) (Tab. 1).

As described in Tab. 1, basidiomata pileus and pore surface colours, basidioma size, depth of tube layer and basidiospore size are the most variable characters within species. It seems that pileus surface colour in Europe is generally of lighter tones in comparison with basidiomata found in North America and Asia. The same pattern appears in pore surface colours, basidiomata from Europe are generally of lighter tones. The basidiomata width is 15 cm in North America and up to 40 cm in Asia, on the other hand, it may reach up to 50 cm in Europe. Maximum depth of tube layer is 8 mm in Europe and up to 10 mm in North America, in Asia it varies from 2 to 16 mm and in

Europe it varies from 2 to 10 mm (Jülich, 1984; Breitenbach, Kränzlin, 1986; Gilbertson, Ryvardeen, 1986; Zhao, Zhang, 1992; Ryvardeen, Gilbertson, 1993; Bondartseva, 1998; Nuñez, Ryvardeen, 2001; Bernicchia, 2005; McCormick, 2013a; Prasher, 2015).

Tab. 1. Geographic variation in macro- and micromorphological traits of the *Fomes fomentarius* basidioma

| Pileus surface colour |
|---|
| Europe: older party gray, marginal part light brown ^{1,2} ; older party gray, blackish, yellowish or yellowish brown; marginal part light reddish brown ³ , silvery white, grayish, gray-brown to nearly black ⁴ ; ocher to red brown when young, later light to dark gray ⁵ ; brown when young, later grayish brown and gray ⁶ |
| Asia: older party gray, marginal part light brown ⁷ ; older party gray, blackish, yellowish or yellowish brown; marginal part light reddish brown ³ , gray, gray-brown to black ⁸ ; gray, grayish brown, grayish black ⁹ |
| North America: brownish gray to nearly black ¹⁰ ; gray, brown, blackish gray, cinnamon, buff ¹¹ |
| Pore surface colour |
| Europe: pale brown ^{1,3} to pale gray ³ ; cream coloured when young, then light ocher to brownish ^{5,6} ; ochraceous to gray ² |
| Asia: pale brown ^{1,3} to pale gray ³ ; brownish to brown or black brown to black ⁸ ; light brown to grayish brown ⁹ |
| North America: brown to grayish brown ¹⁰ ; buff, brown, cinnamon ¹¹ |
| Basidioma size: width × height [cm] |
| Europe: up to 15 wide ¹ ; up to 20–40×5–15 (-20) ³ ; 10–25 (-30)×15–20 ⁵ ; up to 30–40 wide ² ; 5–50×3–25 ⁶ |
| Asia: up to 15 wide ⁷ ; up to 20–40×5–15 (-20) ³ ; 3–20 (-40)×2–15 (-27) ⁸ ; up to 12×18 ⁹ |
| North America: 2–15 wide ¹⁰ |
| Depth of tube layer [mm] |
| Europe: 2–6 ³ ; 2–5 (-8) ⁵ ; 5–7 ² ; ca. 10 ⁶ |
| Asia: 2–6 ^{3,8} up to 16 ⁸ , 7 ⁹ ; |
| North America: up to 10 ¹⁰ |
| Basidia size [µm] |
| Europe: 23–25×7–9 ¹ ; 25–30×8–11 ³ ; 21–25×7–9 ² ; 20–30×7–10 ⁵ ; 25–30×8–11 ⁶ |
| Asia: 23–25×7–9 ⁷ ; 25–30×8–11 ³ |
| Basidiospore size [µm] |
| Europe: 12–18 (-20)×4–7 ¹ ; 15–20×5–7 ³ ; 18.5–19×5.5–6 ⁵ ; 14–20×4.5–6.5 ² ; 6–24×5.5–6.5 ⁶ |
| Asia: 12–18 (-20)×4–7 ⁷ ; 15–20×5–7 ³ ; 12–19×5–6.5 (-8.5) ⁸ ; 15.6–18.6×5.1–6.1 ⁹ |
| North America: 12–18×4–7 ¹⁰ ; 10–21.25×2.5–7.5 ¹¹ |

¹ Ryvardeen, Gilbertson, 1993; ² Bernicchia, 2005; ³ Bondartseva, 1998; ⁴ Schwarze, 1992; ⁵ Breitenbach, Kränzlin, 1986; ⁶ Jülich, 1984; ⁷ Nuñez, Ryvardeen, 2001; ⁸ Zhao, Zhang, 1992; ⁹ Prasher, 2015; ¹⁰ Gilbertson, Ryvardeen, 1986; ¹¹ McCormick, 2013a

Concerning microscopic features, there are no significant differences in the size of basidia in Europe and Asia. Length of basidiospores from Asia is not less than 12 µm. Maximum width of basidiospores is up to 7 µm in Europe, whereas basidiospores found in North America and Asia may have up to 7.5 µm and 8.5 µm respectively (Jülich, 1984; Breitenbach, Kränzlin, 1986; Gilbertson, Ryvardeen, 1986; Zhao, Zhang, 1992; Ryvardeen, Gilbertson, 1993; Bondartseva, 1998; Nuñez, Ryvardeen, 2001; Bernicchia, 2005; McCormick, 2013a; Prasher, 2015).

According to Schwarze (1992) within the geographical area of distribution in Europe, the colouration, size and shape of the basidioma can vary based on where the specimen has grown. The colour of the pileus surface ranges from silvery white to nearly black although when it is wet it can appear to be black and when it is old and dry it can be bleached to an off-white colour. The colour is lighter at lower latitudes, at low elevations and on the south side of stems. Despite his studies covered basidiocarps collected in different places of origin in Great Britain and in mainland Europe, they revealed no discernible pattern (Schwarze, 1994). These differences have caused some fungal taxonomists to propose infraspecific divisions. Thus, the black basidiomata were previously classified as a *Fomes nigrescens*, *Ungulina fomentaria* subsp. *nigricans*, *F. fomentarius* subsp. *nigricans*, or *F. fomentarius* var. *nigrescens*. The lighter coloured basidiomata were classified as a *F. fomentarius* subsp. *fomentarius*. According to Zhao, Zhang's interpretation of the Chinese specimens examined, the basidiospores are also different; in *F. fomentarius* subsp. *nigricans* they are ovoid to subglobose (9–11×6.5–6.8 µm), while in *F. fomentarius* subsp. *fomentarius* they are cylindrical to oblong ellipsoid (12–19×5–6.5 µm) (Zhao, Zhang, 1992). Similarly, the small basidiomata with closely concentrically zoned pileus surfaces associated with birches were previously classified as a *Polyporus fomentarius* var. *lineatus* (Velenovský, 1922). In addition, there are a number of taxonomic synonyms, in the past described as separate taxa.

Basidiomata of *F. fomentarius* can range in size from ca. 5 to ca. 50 cm (Tab. 1). The species have been observed in northern Japan (Hokkaido Island) and northeastern China (Changbai Shan Nature Reserve; Xiao Xing'anling Mts.) to have two morphologically different types basing on basidioma size (Cheng, 2000). While the small-sized basidiomata (up to 20 cm wide) seem to be linked preferably with *Betula* spp., less frequently with *Populus* sp. and *Acer* sp., as the hosts, the large-sized basidiomata (over 20 cm wide) were found mostly on *Acer* sp., *Tilia amurensis*, *Quercus liaoi* and less frequently *Fraxinus mandshurica*, *Ulmus* sp. and *Betula platyphylla* (beeches are not distributed either in Hokkaido, or in the Changbai Shan Nature Reserve) (Cheng, 2000). Two types of *F. fomentarius* have also been reported from an old-growth beech (*Fagus japonica*, *F. crenata*) and oak (*Quercus serrata*, *Q. mongolica*) forest in a cool temperate area of Japan in the southern part of the Abukuma Mts. along the Pacific coast. Both types occurred frequently on beeches (Yamashita et al., 2010). The two types of *F. fomentarius* basidiomata were found growing together in the various localities (Cheng, 2000; Yamashita et al., 2010). These data correspond well with those reported in the Japanese polyporological monographs (Imazeki, Hongo, 1989; Igarashi, 1989, 1994; Takahashi, 2003). Apart from size, basidiomata may range also in shape. According to Gaudreau and co-authors it is either bracket- or boot-shaped (Gaudreau et al., 2005). The boot shaped form, however, is probably related to the following phenomenon. If a tree that *F. fomentarius* is growing on falls

down, the fungus will re-orient its direction of growth to account for its changed position, so specimens are sometimes seen with two different patterns of growth in the basidioma, at right angles to each other. This is to ensure that the fertile underside is always aligned with gravity so the basidiospores will fall into the air currents. According to Læssøe and Del Conte (1996) this species in Europe exists in two forms, the beech and the birch form, depending on the host. Beech form is semicircle-shaped and brown. Birch form is hoof-shaped, more slender and darker gray (Læssøe, Del Conte, 1996). The two forms have been already recognized by Lloyd in the early 20th century (Lloyd, 1915). According to this author, both forms are hoof-shaped. Beech form is larger with soft context and occurs in France. Birch form is smaller with harder context and occurs in the USA and Northern Europe (Lloyd, 1915). However, morphological analyses of 1 165 basidiomata samples within the Malenovický kotol nature reserve (Beskydy Mts., the Czech Republic) using the General Linear Model (GLM) confirmed a direct relationship between the shape of basidioma and its age rather than the host. The approximate age of transition of the basidiomata from the birch form to the beech form was around 5–6 years (Rybovičová, 2010). But some of the existing above mentioned phenotypic differences can be based on the interactions between the genotype and environment (Schwarze, 1999, 2004) and/or presence of different lineages/sublineages (Gáper et al., 2016). However, no clear differences between basidiomata, useful for reliable separation of the lineages/sublineages, have been observed so far. Nevertheless, a recent *F. fomentarius* basidiomata description in North American research articles (McCormick et al., 2013a, b) represents North American A1 sublineage (Gáper et al., 2016). Basidiomata of the *F. fomentarius* sublineage A1 are unguulate, applanate or triquetros; pileus surfaces gray, brown, blackish gray, cinnamon, buff; pore surfaces buff, brown, cinnamon, concave, flat to slightly concave or convex; pores 2–5 per mm; basidiospores $17.54(\pm 0.05) \times 5.27(\pm 0.03) \mu\text{m}$ (mean \pm SE) and ranged from $10.0\text{--}21.25 \times 2.5\text{--}7.5 \mu\text{m}$. Color of external portions of the basidiomata (pileus and pore surface colours) are more variable than internal portions (context and tube layers) (McCormick et al., 2013a). In both Asian and European literature such data is absent. As regards then, European literature alone, it is most possible that these descriptions are based on basidiomata of two other lineages/sublineages and thus we cannot discriminate between them.

Conclusions

The analysis of data present in literature shows that no clear differences can be observed between basidiomata of *Fomes fomentarius* which would be suitable for reliable separation of lineages/sublineages. Within geographical area of distribution in the world, these characteristics can vary considerably. The existing phenotypic differences

in *F. fomentarius* basidiomata morphology can be attributed either to different lineages/sublineages, or to interactions between the genotype and its environment.

The phenotypic basidioma traits of the North American A1 sublineage are known. However, it is most possible that the descriptions in European literature are based on basidiomata of both sublineage A2 and lineage B, and thus we cannot discriminate between them. Moreover, some European and Asian macro- and microcharacters are identical.

Therefore, the following recommendations which would be suitable for reliable separation of the lineages/sublineages can be made based on the review:

1. basidiomata differ macromorphologically mainly in pileus and pore surface colours, basidioma size and depth of tube layer,
2. basidiomata differ micromorphologically mainly in basidiospore size,
3. a detailed study of each of these three attributes, especially within Europe and Asia, would be suitable for separation of the above mentioned lineages/sublineages.

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Abstract

Currently two morphological species of the genus *Fomes* (Polyporaceae, Basidiomycota) are known: *F. fomentarius* (L.) Fr. and *F. fasciatus* (Sw.) Cooke. Both species are very important in the decomposition of wood and in the nutrient cycling in forest ecosystems. Moreover, *F. fomentarius* is also known as a source of medicinal and nutraceutical products. Recently the existence of three separate ITS lineages/sublineages among *F. fomentarius* strains has been clearly established – A1 (the strains isolated from North America), A2 (only from Europe) and B (from Europe and Asia). In this review the current knowledge of the morphological variability of *F. fomentarius* basidiomata has been summarized in respect of the reliable separation of its lineages/sublineages. Micro- and macrofeatures and geographic variability of the basidiomata have been described. Morphological traits of the *F. fomentarius* basidiomata can vary due to geographical distribution. These phenotypic differences can be based on the presence of several groups or interactions between the genotype and environment. However, no clear differences between basidiomata, useful for reliable separation of the lineages/sublineages, have been observed so far. A recent description in North American *Fomes* research articles is based on basidiomata of the A1 sublineage. It is most possible that the descriptions in European literature are based on basidiomata of two other lineages/sublineages and thus we cannot discriminate between them. In the future a detailed study of the macro- and microtraits – pileus and pore surface colors, basidioma size, depth of tube layer, and basidiospore size – is therefore proposed for reliable separation of the lineages/sublineages of *F. fomentarius*.

Key words: basidioma, cryptic species, morphological variability

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Zmienność morfologiczna owocników *Fomes fomentarius* na podstawie danych z literatury

Streszczenie

Obecnie znane są dwa morfologiczne gatunki z rodzaju hubiak *Fomes* (Fr.) Fr. (Polyporaceae, Basidiomycota): *F. fomentarius* (L.) Fr. i *F. fasciatus* (Sw.) Cooke. Obydwa są bardzo ważne w procesie rozkładu drewna oraz w obiegu składników pokarmowych w ekosystemach leśnych. Ponadto,

F. fomentarius jest również uznany jako źródło produktów leczniczych i nutraceutycznych. Ostatnio zostało wyraźnie określone istnienie trzech odrębnych linii rozwojowych ITS/sublinii pomiędzy szczepami *F. fomentarius* – A1 (szczone wyizolowane w Ameryce Północnej), A2 (tylko w Europie) i B (w Europie i Azji). W niniejszym przeglądzie aktualna wiedza o zmienności morfologicznej owocników *F. fomentarius* została zebrana w odniesieniu do rzetelnego wydzielenia linii rozwojowych/sublinii. Zostały tu opisane mikro- i makrocechy oraz zmienność geograficzna owocników. Cechy morfologiczne owocników *F. fomentarius* mogą się różnić ze względu na rozmieszczenie geograficzne. Różnice fenotypowe mogą bazować na obecności różnych grup lub interakcji pomiędzy genotypem a środowiskiem. Jednakże nie ma wyraźnych różnic między owocnikami, przydatnych do niezawodnego oddzielenia linii rozwojowych/sublinii, które do tej pory obserwowano. Nowsze opisy gatunków z rodzaju *Fomes* w Ameryce Północnej w artykułach naukowych opierają się na owocnikach z sublinii A1. Jest bardzo prawdopodobne, że opisy w literaturze europejskiej oparte są na owocnikach dwóch pozostałych linii rozwojowych/sublinii, a zatem nie możemy odróżnić ich między sobą. W przyszłości proponuje się do niezawodnego oddzielenia linii rozwojowych/sublinii *F. fomentarius* szczegółowe badania makro- i mikrocech: kolorów kapelusza i powierzchni porów, rozmiaru owocnika, głębokości warstwy rurek i rozmiaru bazydiospor.

Słowa kluczowe: różnicowanie morfologiczne, gatunki kryptyczne, owocnik

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