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A key to the species of *Hyphodontia* sensu lato

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Abstract

A dichotomous key to all currently accepted species of *Hyphodontia* in the broad sense is presented. It consists of a key to genera (*Alutaceodontia*, *Botryodontia*, *Chaetoporellus*, *Deviodontia*, *Hastodontia*, *Hyphodontia* s. str., *Kneiffiella*, *Lagarobasidium*, *Lyomyces*, *Palifer*, *Rogersella*, *Schizopora*, *Xylodon*) and detailed keys to species level within genera. The key also includes taxa which were published under preliminary names (such as '*Hyphodontia* species A') and some taxa which require taxonomic clarification (like *Hyphodontia macrescens*). Some recently describes *Hyphodontia* species are placed in the keys to *Palifer* and *Xylodon* due to their morphology.

Key words

Basidiomycota, cystidia, global species diversity, Hymenochaetales, taxonomy

Introduction

Hyphodontia J. Erikss. (Hymenochaetales) in its broad sense is a genus of resupinate non-poroid Basidiomycota. Its species commonly occur on dead wood worldwide from Arctic tundra (Mukhin 2006) to evergreen equatorial forests (Hjortstam et al. 1998). In the latter case they belong in the strict sense mainly to *Botryodontia* and *Schizopora*. The latest global monograph of the genus (Langer 1994) included descriptions of 53 *Hyphodontia* species and 4 *Schizopora* species.

The aim of our work was to construct a key, which can serve as a tool for further studies of *Hyphodontia* s. l., especially when describing new species. The key includes 126 validly published species, four unnamed taxa (e.g. *Hyphodontia* sp. 1), and three

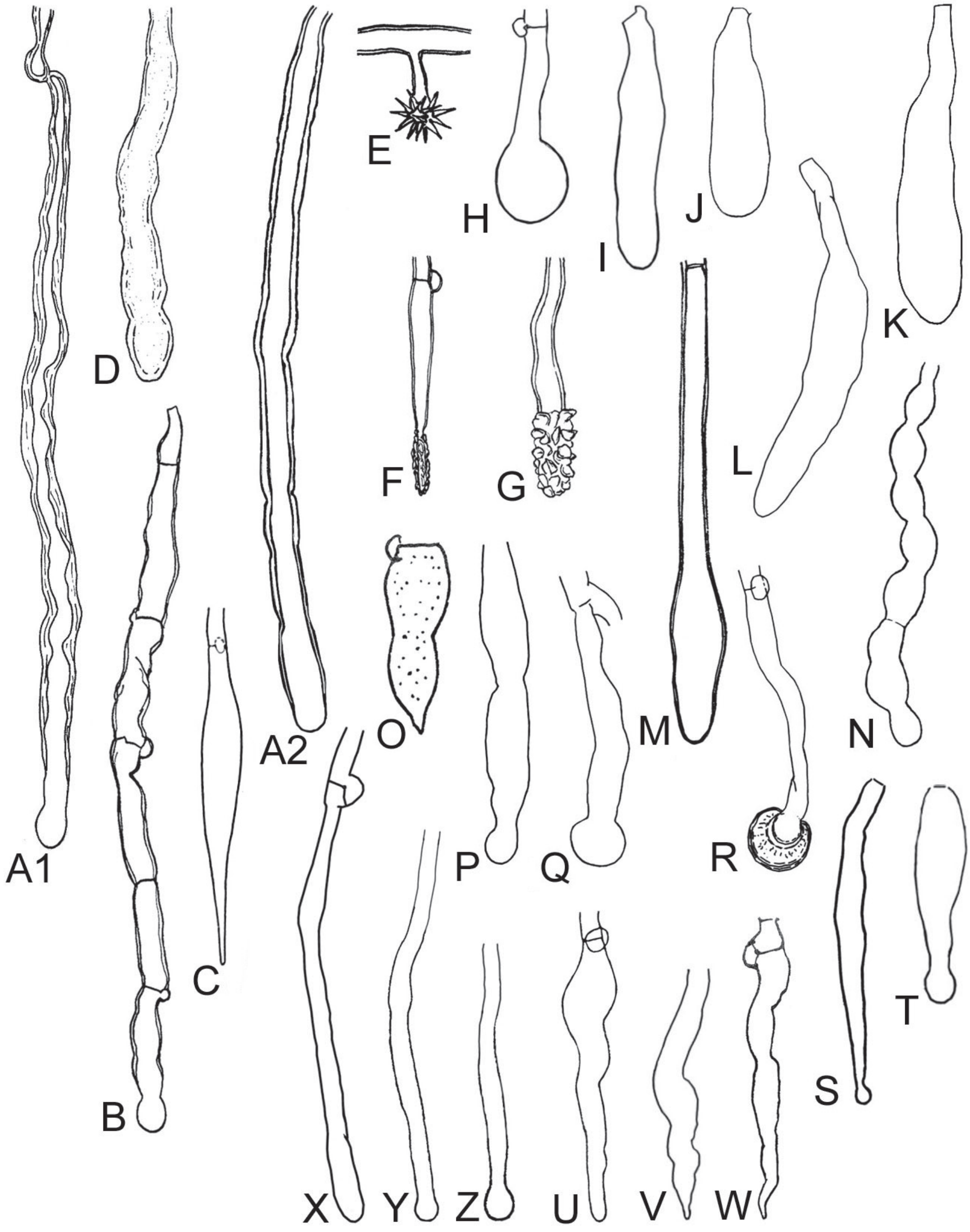

Figure 1. Types and shapes of cystidial elements in *Hyphodontia* s.l.: **A1** skeletocystidium **A2** tubular **B** septocystidium **C** hastocystidium **D** gloeocystidium **E** astrocystidium **F** lagenocystidium **G** cylindrical apically encrusted (lamprocystidium-like) **H** vesicular or bladder-like (embedded) **I** cylindrical **J** subclavate **K** clavate **L** fusoid **M** spatuliform **N** moniliform (torulose) **O** ventricose submucronate **P** subcapitate **Q** capitate **R** capitate with resinous cap **S** capitulate **T** lecythiform **U** tapering (subulate with blunt apex) **V** acute **W** acuminate (subulate with pointed apex) **X** hyphoid cylindrical **Y** hyphoid subcapitate; Z, hyphoid capitate. See also Appendix.

taxa with affinity formulation (e.g. *Kneiffiella* cf. *abieticola*), for which brief or detailed descriptions have been published. The taxa requiring taxonomic clarification, e.g. species with poor types (*Kneiffiella byssoidea*, *Xylodon nudisetus*, *X. rimosissimus*; Parmasto et al. 2004), are included in the key equally with 'good' taxa.

For identification convenience, the species are assigned to 13 derivative genera, adopted by Hjortstam and Ryvarden (2009). However, among these genera the independence of *Hastodontia*, *Hyphodontia* s. str., *Kneiffiella*, and *Lagarobasidium* only is confirmed by molecular phylogenies (Larsson et al. 2006; Yurchenko and Wu 2014). Species of *Fibrodontia* were excluded because they belong to trechisporoid lineage (Larsson 2007). *Palifer seychellensis* Dämmrich & Rödel was excluded from consideration because of unusual cystidia with double umbrella-like incrustations and probable belonging to the genus *Sceptrulum* K.H. Larss. (Karasiński 2014). In addition to the concept of *Hyphodontia* s. l., the genus *Botryodontia* in the key as several species in this genus have been earlier combined in *Hyphodontia* s. l. as well. *Botryodontia* is related to *Oxyporus* (Sell et al. 2014), and is a presumed member of the hymenochaetoid clade.

Because of the diffuse generic borders within *Hyphodontia* s. l., the species are listed in the key with their main synonyms when combined in different genera. Recently described *Hyphodontia* species, that have never been combined in other genera, are included in the appropriate subordinate keys according to their morphology. For example, *H. septocystidiata* is keyed within *Palifer* and *H. heterocystidiata* within *Xylodon*. Morphological types of cystidia, important for the identification of genera and species, are illustrated on Fig. 1. Spore quotient (length/width ratio) is denoted in the key as Q. Distribution of each species in parts of the world is given after "distr."

Keys

Key to the segregated genera and some species within *Hyphodontia* s. l.

1 Spores warted or minutely echinulate, globose, slightly thick-walled................................ ....***Rogersella*** [*R. griseliniae* (G. Cunn.) Stalpers (*Hyphodontia griseliniae* (G. Cunn.) E. Langer 'griselinae', *R. asperula* Liberta & A.J. Navas)]; distr.: Macaronesia, Africa, southwest Indian Ocean islands, South America, New Zealand, Oceania The other known species in the genus, *R. eburnea* Hjortstam & Högholen, should according to its morphology (subceraceous basidioma, smooth hymenophore, gelatinized subhymenial hyphae, subclavate basidia, suballantoid spores) be classified as *Phlebia* s. l.

– Spores smooth, globose to cylindrical or allantoid, thin- to thick-walled..... **2**

2 Clamps lacking at all septa.. **3**

– Clamps present at some, at many, or at all primary septa **6**

3 Basidia obovate to clavate **4**

– Basidia cylindrical-utriform **5**

4 Hymenophore granulose to irpicoid-labyrinthoid; capitate cystidia absent.... .... ***Botryodontia***...**(Key A)**

– Hymenophore poroid; small capitates cystidia numerous............................ .... ***Xylodon poroideoefibulatus***

5 Basidia with 4 sterigmata ....***Botryodontia tetraspora***

– Basidia with 2 sterigmata ....***Kneiffiella efibulata***

6 Lagenocystidia or lagenocystidia-like elements (like small lamprocystidia) present in hymenium...**7**

– Lageno- and similar encrusted cystidia lacking..**8**

7 With rare to numerous lagenocystidia, or with apically richly encrusted, short cylindrical cystidia ....***Hyphodontia* s. str**...**(Key D)**

– With lamprocystidia-like elements.................................. ***Palifer***...**(Key H)**

8 Hymenophore distinctly irpicoid or poroid **9**

– Hymenophore smooth to odontioid and hydnoid, seldom slightly irpicoid or with spathulate aculei **12**

9 Hyphal system monomitic..**10**

– Hyphal system dimitic, trimitic or pseudodimitic (subdimitic) with skeletal-like hyphae in subiculum 11

10 Spores allantoid, about 0.8 μm broad .... ***Chaetoporellus*** (***Ch. latitans***)...**(Key B)**

– Spores subglobose to cylindrical or suballantoid, at least 2 μm broad........... ....***Xylodon***...**(Key J)**

11 In hymenium moniliform cystidia .... ***Xylodon bresinskyi***

– Constricted cystidia absent .... ***Schizopora***...**(Key I)**

12 Spores allantoid, 0.5–1.5(–2) μm broad...**13**

– Spores subglobose to cylindrical or suballantoid, broader, than 2 μm **16**

13 Tubular thick-walled cystidia present..........................***Kneiffiella***...**(Key E)**

– Tubular thick-walled cystidia absent, but cylindrical thin-walled cystidia sometimes present...**14**

14 Hymenophore with aculei reaching 1–2 mm long; spores significantly curved, 4–5 μm long........................... ***Chaetoporellus*** (***Ch. curvisporus***)...**(Key B)**

– Hymenophore with aculei less than 1 mm long; spores slightly or moderately curved, 5–8 μm long...**15**

15 Spores 6–8 × 1.5(–2) μm; cystidia cylindrical to torulose, mostly 50–75 × 4–7 μm; some samples with conidia 8–10 × 3–4 μm in hymenium... ....***Alutaceodontia*** (Parmasto) Hjortstam & Ryvarden [*A. alutacea* (Fr. : Fr.) Hjortstam & Ryvarden (*Hyphodontia alutacea* (Fr. : Fr.) J. Erikss.]; distr.: Eurasia, North and South America

– Spores 5–6 × 1–1.5 μm; only with subclavate cystidioles or basidioles, 8–10 × 3–3.5 μm, and projecting cylindrical and subcapitate hyphal ends; conidia unknown ....***Xylodon scopinellus***

16 Hyphal system dimitic with skeletal hyphae, or subdimitic because of the presence of thick-walled hypha-like bases of tubular cystidia, or pseudodimitic due to skeletoid (skeletal-like) hyphae in aculeal trama or dissepiment **17**

– Hyphal system monomitic, but subicular hyphae and hyphae in aculeal trama can be thick-walled **19**

17 With tubular cystidia .... ***Kneiffiella*...(Key E)**

– Typical tubular cystidia lacking, but elements of intermediate morphology between hyphae and tubular cystidia present in aculeal trama **18**

18 Aculeal trama with skeletocystidia: long, narrow, thick-walled, often yellow-pigmented in mass, naked of covered with tablet-shaped crystals; capitate or subcapitate hyphal ends or cystidia absent in aculei; basidia when mature suburniform.. ***Fibrodontia***

– Aculeal trama with skeletal-like hyphae or with thick-walled hyphoid cystidia, often encrusted (crystals not flattened); capitate or subcapitate cystidial elements present in aculei; basidia more or less utriform ...***Xylodon*...(Key J)**

19 Spores cyanophilous with distinctly thickened or thick wall...................... **20**

– Spores acyanophilous (rarely somewhat cyanophilous) thin- or slightly thick-walled **21**

20 Capitate cystidia often with a resinous cap; cylindrical cystidia embedded .... ***Xylodon crassisporus***

– Capitate cystidia if present, lack the resinous cap; cylindrical cystidia if present, distinctly projecting .... ***Lagarobasidium*...(Key F)**

21 Hymenophore coarsely odontioid, raduloid or semiporoid, with aculei 1–5(–7) mm long; cystidia clearly capitate, with broadened base, projecting clearly over the basidia, 50–85 × 7–10 µm; basidia nearly subcylindrical .... ***Deviodontia*** (Parmasto) Hjortstam & Ryvarden [*D. pilicystidiata* (S. Lundell) Hjortstam & Ryvarden (*Hyphodontia pilicystidiata* (S. Lundell) J. Erikss. '*pilaecystidiata*')]; distr.: Europe Langer (1994) proposed to treat this taxon in *Hyphoderma* because of large capitate cystidia and spores with granular contents.

– Hymenophore smooth to hydnoid, raduloid or poroid; aculei rarely up to 3 mm long; projecting capitate cystidia, if present, often smaller, and frequently classified as capitate hyphal ends or cystidioles; basidia usually utriform 22

22 Septocystidia present, distinct .... ***Hyphodontia* s. str...(Key D)**

– Septocystidia absent or little differentiated **23**

23 Hymenophore smooth to slightly tuberculate; generally two types of cystidia: (1) moniliform, embedded or slightly projecting, (2) projecting, capitate cystidia or hastocystidia, apically often with resinous excretion; spores subcylindrical .... ***Hastodontia*...(Key C)**

– If with moniliform cystidia, then hymenophore odontioid or hydnoid, or spores ellipsoid; projecting capitate cystidia naked or with resinous cap; hastocystidia if present, lacking apical excretion; spores globose to suballantoid.................... **24**

24 Hymenophore usually odontioid, sometimes almost smooth to hydnoid or poroid; usually with tufts of projecting hyphal ends or cystidia in hymenophoral aculei; hymenial surface usually cream-colored; spores thin-walled, rarely somewhat thick-walled, subglobose to suballantoid, acyanophilous,

rarely somewhat cyanophilous; cystidia subulate to cylindrical, capitate or moniliform; subicular hyphae naked to richly encrusted ...***Xylodon***...**(Key J)**

– Hymenophore smooth to tuberculate; typically no tufts of projecting hyphal ends or cystidia; hymenial surface white or with age pale cream, in herbarium material white, cream or yellowish; spores thin- to somewhat thick-walled, globose to oblong, slightly or distinctly cyanophilous; cystidia capitate or fusoid, or of both types; subicular hyphae usually encrusted ....***Lyomyces***...**(Key G)**

Key A. *Botryodontia*

1 Cystidia long (40–180 µm), cylindrical, tubular, more or less thick-walled ... **2**

– Cystidia never tubular, thin-walled, sometimes indistinct, 15–40 µm long.... **4**

2 Spores 3–5 × 2–2.5 µm; hymenophore minutely warted............................. ***B. tetraspora*** (S.S. Rattan) Hjortstam & Ryvarden [*Hyphodontia efibulata* f. *tetraspora* S.S. Rattan; *H. tetraspora* (S.S. Rattan) Hjortstam; *Kneiffiella tetraspora* (S.S. Rattan) Hjortstam & Ryvarden]; distr.: South Asia

– Spores 4–6.5 × 3–4 µm; basidioma farinaceous-granulose or hymenophore odontioid to irpicoid.. 3

3 Basidioma farinaceous-granulose; spores with thin or thickened walls, 5–6(–6.5) × 3–4 µm ....***B. crassispora*** P. Roberts [*Kneiffiella crassispora* (P. Roberts) Hjortstam & Ryvarden]; distr.: Africa

– Basidioma odontioid or raduloid-irpicoid; spores thin-walled, 4–5 × 3–3.7 µm..............***B. subglobosa*** (Sheng H. Wu) Hjortstam [*Hyphodontia subglobosa* Sheng H. Wu; *Kneiffiella subglobosa* (Sheng H. Wu) Hjortstam]; distr.: East Asia

4 Hymenophore irpicoid-labyrinthoid; gloeocystidia present in hymenium, clavate or irregular-shaped (sinuous); spores broadly ellipsoid to subglobose, 4–7 × 3.3–5.5 µm....... ***B. millavensis*** (Bourdot & Galzin) Duhem & H. Michel; distr.: Europe

– Hymenophore semi-odontioid to odontioid; gloeocystidia absent; spores ellipsoid, 5–6.5 × 3.5–4.5 µm **5**

5 Hymenophoral aculei 0.1–0.3 mm long; spores (5–)5.5–6(–6.5) × 4–5 µm.......................................***B. cirrata*** (Hjortstam & Ryvarden) Hjortstam [*B. denticulata* Hjortstam; *B. formosana* (Sheng H. Wu & Burds.) Hjortstam; *Hyphodontia formosana* Sheng H. Wu & Burds.]; distr.: pantropical

– Hymenophoral aculei 0.4–0.5(–0.75) mm long; spores 5–5.5(–6) × (3.5–)3.8–4(–4.3) µm... ....***B. semispathulata*** Hjortstam & Ryvarden; distr.: South America

Key B. *Chaetoporellus* Bondartsev & Singer

1 Hymenophore odontioid or sometimes almost smooth; cystidia 35–70 × 4–7 µm; spores 4–5 × 1–1.5(–2) µm ....

.... ***Ch. curvisporus*** (J. Erikss. & Hjortstam) J. Erikss. & Hjortstam (*Hyphodontia curvispora* J. Erikss. & Hjortstam); distr.: Europe, Central America
– Hymenophore poroid with rounded, lacerate or labyrinthiform pores; cystidia 30–35 × 4–5 µm; spores 3–4 × 0.5–1 µm .... ***Ch. latitans*** (Bourdot & Galzin) Bondartsev & Singer [*Hyphodontia latitans* (Bourdot & Galzin) Ginns & Lefebvre]; distr.: Europe, North America, Oceania

Key C. *Hastodontia* (Parmasto) Hjortstam & Ryvarden

1 With capitate projecting cystidia, 30–60 × 4–5 µm, capped by resinous matter (the matter usually disappearing in microscopic slides); acute cystidia absent; spores 4.5–5.5 × 2–2.5 µm........ ***H. halonata*** (J. Erikss. & Hjortstam) Hjortstam & Ryvarden (*Hyphodontia halonata* J. Erikss. & Hjortstam); distr.: Europe
– No capitate cystidia; with projecting hastocystidia, about 50 µm long, 5–7 µm wide, some of them apically with a globe of resinous matter (the matter easily dissolving in slides); spores 5–7 × 2–3 µm........ ***H. hastata*** (Litsch.) Hjortstam & Ryvarden [*Hyphodontia hastata* (Litsch.) J. Erikss.]; distr.: temperate north hemisphere

Key D. *Hyphodontia* J. Erikss. s. str.

1 Hymenophore poroid .... ***H. borbonica*** Riebesehl, E. Langer & Barniske; distr.: southwest Indian Ocean islands
– Hymenophore smooth to hydnoid.. **2**
2 Capitate or subcapitate cystidial elements lacking .... ***H. wrightii*** Hjortstam & Ryvarden [*Palifer wrightii* (Hjortstam & Ryvarden) Hjortstam & Ryvarden]; distr.: South America
The species was included in *Hyphodontia* s. str. by Gorjon (2012).
– Capitate or subcapitate cystidial elements present **3**
3 With capitate or subcapitate septocystidia (usually with 2–3 septa), distinctly protruding above the hymenium; hymenophore smooth to grandinioid **4**
– Capitate or subcapitate cystidia usually with a basal septum only, little protruding above the hymenium, or hypha-like and arranged in tufts at aculeal apices; hymenophore smooth to hydnoid.. **8**
4 Lagenocystidia more or less numerous **5**
– Lagenocystidia absent or occasional **6**
5 Spores 4.5–5 × 3–3.5 µm; septocystidia up to 80 µm long........................... .... ***H. alutaria*** (Burt) J. Erikss.; distr.: cosmopolitan
– Spores 6–7.5 × 4–4.5 µm; septocystidia up to 110 µm long.............................. .... ***H. subdetritica*** S.S. Rattan (*H. propinqua* Hjortstam); distr.: Asia, Africa
6 Spores 3.5–5 × 2–3 µm; septocystidia 80–120 µm long, slightly thick-walled **7**

– Spores 5–8 × 4–5.5 µm; septocystidia 60–73 × 6–7 µm, thin-walled ....***H. subpallidula*** H.X. Xiong, Y.C. Dai & Sheng H. Wu; distr.: East Asia

7. Hymenophore smooth or finely tuberculate; subicular hyphae thin-walled, 2−3 µm wide, moderately densely packaged; septocystidia 4–6 µm wide; spores 3.5–5.5 × 2–3 µm ......***H. pallidula*** (Bres.) J. Erikss.; distr.: Eurasia, North America

– Hymenophore odontioid; subicular hyphae with thickened walls, 4−5 µm wide, loosely arranged; septocystidia 7−8 µm wide; spores 4.5−5 × 3 µm...... .... ***H. alba*** Sheng H. Wu; distr.: East Asia
According to Hjortstam and Ryvarden (2009), this species has features of *Hyphoderma* and *Lyomyce*s.

8 Hymenial surface smooth; no capitate cystidia; lagenocystidia few, sometimes absent .... ***H. subdetritica*** (see step 5)

– Hymenial surface odontioid to hydnoid; capitate cystidia present; lagenocystidia scattered to numerous **9**

9 Spores up to 4.5 µm long, globose to broadly ellipsoid, slightly thick-walled .... ***H. sphaerospora*** (N. Maek.) Hjortstam [*H. arguta* var. *sphaerospora* (N. Maek.) N. Maek.]; distr.: East and Southeast Asia, South America

– Spores up to 5–6 µm long, ellipsoid to cylindrical, occasionally subglobose, thin- to slightly thick-walled **10**

10 Spores ellipsoid, occasionally subglobose, (4–)4.5–6 × (3–)3.5–3.7(–4) µm ... .***H. arguta*** (Fr. : Fr.) J. Erikss. [*H. lageniformis* Sang H. Lin & Z.C. Chen, *H. stipata* (Fr. : Fr.) Gilb.]; distr.: cosmopolitan
H. lageniformis is synonymized with *H. arguta* (Langer 1994), and evidently is a variety of the latter, with smaller spores (4.5 × 3–4 µm) and shorter basidia (10–11 µm, according to the original description).

– Spores narrowly ellipsoid to cylindrical, 4.3–5.3 × 2–3 µm...................... **11**

11 Hymenophoral aculei up to 3 mm long; spores 4.5–5 × 2–2.5(–3) µm; mucronate (apically papillate) cystidia present; lagenocystidia scattered; capitate cystidia in aculeal apices; basidia 10–15 µm long ....***H. ochroflava*** (Pat.) Nakasone; distr.: Southeast Asia

– Hymenophoral aculei up to 6 mm long; spores 4.3−5.3 × 2.5−3 µm; no mucronate cystidia; capitate cystidia also on lateral surfaces of aculei; lagenocystidia numerous; basidia 22−28 µm long ....***H. dhingrae*** Samita & Sanyal; distr.: South Asia

Key E. *Kneiffiella* P. Karst.

1 Clamps absent at all septa **2**

– Clamps present at all or most primary septa... **3**

2 Spores subglobose to ellipsoid, 4−4.5(−5) × (2.5–)3(−3.5) µm..................... .... ***K. byssoidea*** (H. Furuk.) Hjortstam & Ryvarden '*byssoideus*' [*Hyphodontia byssoidea* (H. Furuk.) N. Maek. '*byssoideum*']; distr.: East Asia

– Spores oblong to cylindrical, adaxially flat or concave, 5–5.5 × 2–2.5 µm..... ....***K. efibulata*** (J. Erikss. & Hjortstam) Jülich & Stalpers (*Hyphodontia efibulata* J. Erikss. & Hjortstam); distr.: Europe

3 Spores broadly ellipsoid to short cylindrical, Q = 1.4–2.2 ....**4**

– Spores cylindrical to allantoid, Q = (1.9–)2.3–4 ....**11**

4 Spores broadly ellipsoid to ellipsoid, Q = 1.4–1.7; hymenophore odontioid to hydnoid..**5**

– Spores narrowly ellipsoid to short cylindrical, Q = (1.6–)1.8–2.2; hymenophore smooth to odontioid **7**

5 Subicular hyphae with clamps at all primary septa; spores 4.5–6 × 3–4.5 µm ... **6**

– Subicular hyphae partly simple septate; sometimes clamps only scattered on sibicular hyphae and on projecting hyphae in the aculei; spores 3.5–5 × 2.5–3.5 µm.............***Hyphodontia orasinusensis*** Gilb. & M. Blackw. [*Kneiffiella crassa* (Rick) Hjortstam & Ryvarden, non *Hyphodontia crassa* Z.C. Chen & Sang H. Lin; *K. stereicola* (Bres.) Nakasone]; distr.: North America

6 Hymenophore hydnoid with aculei 1–3 mm long; tubular cystidia 6–8 µm broad; spores often broadly ellipsoid, 4.5–5.5(–6) × 3.5–4.5 µm....***K. barba-jovis*** (Bull. : Fr.) P. Karst. [*Hyphodontia barba-jovis* (Bull. : Fr.) J. Erikss., *H. irpicoides* (P. Karst.) Burds. & M.J. Larsen]; distr.: Eurasia, North America

– Hymenophore odontioid or minutely hydnoid, with aculei less 1 mm long; tubular cystidia 4–6 µm broad; spores ellipsoid, 5–6 × 3–3.5 µm ....***K.* cf. *abieticola*** (Hjortstam and Ryvarden 2007b); distr.: South America

7 Some tubular cystidia with excreted resinous matter near or on apex; excretion stable or slowly disappearing in 5% KOH solution **8**

– Tubular cystidia without resinous excretion in apical part...........................**9**

8 Hymenial surface smooth to odontioid, cream to beige; spores 2.5–4.5 × 1.5–2.5 µm, ellipsoid to cylindrical; tubular cystidia reaching about 100 × 8 µm in size, with the wall up to 2 µm thick; cystidial apical or subapical excretion crust-like, preserving in KOH; subicular hyphae 2–3 µm broad, with wall up to 1 µm thick .... ***K. microspora*** (J. Erikss. & Hjortstam) Jülich & Stalpers (*Hyphodontia microspora* J. Erikss. & Hjortstam); distr.: cosmopolitan

– Hymenial surface odontioid, ochraceous; spores 4–5.5 × 2.5–3 µm, cylindrical to somewhat depressed adaxially; tubular cystidia reaching about 1000 × 14 µm in size, with wall up to 1.5 µm thick; cystidial apical or subapical excretion granular, dissolving in KOH; subicular hyphae 3–4 µm diam, with wall up to 0.5 µm thick ....***K. palmae*** (Rick) Hjortstam & Ryvarden [*Hyphodontia palmae* (Rick) E. Langer]; distr.: South America, East Asia This taxon is conspecific with *K. microspora* according to Hjortstam and Larsson (1995).

9 Hymenial surface smooth; tubular cystidia usually 80–100 µm long, normally encrusted in the middle part by coarse crystals ....***K. alienata*** (S. Lundell) Jülich & Stalpers [*Hyphodontia alienata* (S. Lundell) J. Erikss.]; distr.: Europe, Africa, North and South America

– Hymenial surface warted to odontioid; tubular cystidia mostly 100–150 µm long, naked, sometimes scarcely encrusted **10**

10 Tubular cystidia cylindrical, with walls up to 2.5 µm thick.......................... ....***K. abieticola*** (Bourdot & Galzin) Jülich & Stalpers [*Hyphodontia abieticola* (Bourdot & Galzin) J. Erikss.]; distr.: Eurasia, North America

– Tubular cystidia thin-walled and tapering in upper half, in lower half with walls up to 1.5 µm thick ***Hyphodontia* sp. A** (Eriksson and Ryvarden 1976; Ginns and Lefebvre 1993); distr.: North America

11 Hymenophore smooth (under the lens often porose-reticulate or finely furfuraceous) **12**

– Hymenophore warted, odontioid or distinctly floccose **15**

12 Spores 1.5–2 µm broad.. **13**

– Spores 2–3 µm broad... **14**

13 Spores 4.5–6 µm long; tubular cystidia up to 10 µm broad, reaching about 300 µm in length... ***K. altaica*** (Parmasto) Hjortstam & Ryvarden (*Hyphodontia altaica* Parmasto); distr.: Asia

– Spores 6–8 µm long; tubular cystidia up to 7(–8) µm broad, reaching about 150(–200) µm in length ....***K. subalutacea*** (P. Karst.) Jülich & Stalpers [*Hyphodontia subalutacea* (P. Karst.) J. Erikss.]; distr.: cosmopolitan

14 Tubular cystidia very long (up to 250–280 µm) and very thick-walled (up to 6 µm); spores 7–10 µm long... .... ***K. decorticans*** (Gresl. & Rajchenb.) Hjortstam & Ryvarden (*Hyphodontia decorticans* Gresl. & Rajchenb.); distr.: South America

– Tubular cystidia usually not exceeding 120 µm in length, moderately thick-walled; spores 5.5–7 µm long...***K. cineracea*** (Bourdot & Galzin) Jülich & Stalpers [*Hyphodontia cineracea* (Bourdot & Galzin) J. Erikss. & Ryvarden]; distr.: Europe, West Asia, South America

15 Tubular cystidia very thick-walled (up to 6 µm); spores 2.5–3 µm broad...... ....***K. decorticans*** (see step 14)

– Tubular cystidia moderately thick-walled (0.5–2.5 µm); spores 1.5–2.2 µm broad **16**

16 Spores cylindrical, slightly concave adaxially, 4.7–5.5 µm long; basidia 7–13 µm long; walls in subicular hyphae thickened to thick (up to 1.2 µm).......... ....***K. tubuliformis*** Sheng H. Wu [*Hyphodontia tubuliformis* (Sheng H. Wu) Hjortstam & Ryvarden]; distr.: East Asia

– Spores allantoid, 5.5–8 µm long; basidia 12–20 µm long; walls in subicular hyphae usually thin or somewhat thickened (less 1 µm)........................... **17**

17 Hymenophore distinctly floccose to odontioid; tubular cystidia often in clusters at apices of the aculei.. ....***K. floccosa*** (Bourdot & Galzin) Jülich & Stalpers [*Hyphodontia floccosa* (Bourdot & Galzin) J. Erikss.]; distr.: Eurasia, North America *Hyphodontia intermedia* (Bourdot & Galzin) Parmasto is considered as a synonym of *K. floccosa* (Hjortstam and Ryvarden 1988). According to the

descriptions in Bourdot and Galzin (1928), there are some differences in spore morphology between the two taxa: spores in *Odontia alutacea* subsp. *intermedia* Bourdot & Galzin are 6–7.5(–9) × 1.5–2 µm, and in *O. alutacea* subsp. *floccosa* Bourdot & Galzin – 4.5–7.5 × 1.5–2.5 µm.

– Hymenophore minutely furfuraceous to slightly warted; tubular cystidia not aggregated..***K. subalutacea*** (see step 13)

Key F. *Lagarobasidium* Jülich

1 Cylindrical, thick- or very thick-walled cystidia present, 140–360 µm long... **2**

– Cylindrical cystidia, if present, then thin-walled and 70–110 µm long **3**

2 Basidioma odontioid, with large, 140–360 × 10–12 µm, usually aseptate tubular cystidia in aculeal trama; projecting capitate cystidia apically 12–19 µm broad; spores 5–6 × 4–5 µm, with thickened wall.. .... ***L. magnificum*** (Gresl. & Rajchenb.) Hjortstam & Ryvarden (*Hyphodontia magnifica* Gresl. & Rajchenb.); distr.: South America

– Basidioma smooth to grandinioid, with skeletocystidia 140–160 × 5–9 µm, often with adventitiuos septa; projecting capitate (spatuliform) cystidia apically 6–7 µm broad; spores 7–8 × 5–6 µm, thick-walled.. ... ***L. calongei*** M. Dueñas, Tellería, Melo & M.P. Martín; distr.: Macaronesia

3 Cystidia of one type: projecting, clavate to spathuliform in outline; hymenophore first smooth, then papillose to odontioid; hyphae with numerous crystals; spores ellipsoid, 4–5.5(–6) × 4–4.5(–5) µm......***L. detriticum*** (Bourdot) Jülich [*Hyphodontia detritica* (Bourdot) J. Erikss., *Hyphodontia magnacystidiata* Lindsey & Gilb., *H. nikolajevae* Parmasto, *Hypochnicium detriticum* (Bourdot) J. Erikss. & Ryvarden, *Lagarobasidium nikolajevae* (Parmasto) Jülich, *L. pruinosum* (Bres.) Jülich]; distr.: Eurasia, South America, southwest Indian Ocean islands *L. pruinosum* is evidently a form of *L. detriticum* with narrowly clavate cystidia that are not spathuliform in outline.

– Cystidia of two types: (1) projecting, capitate with small capitulum, (2) immersed, cylindrical or somewhat moniliform; hymenophore smooth; hyphae naked; spores subglobose to broadly ellipsoid and broadly ovoid, (4–)5–6(–6.5) × 4–5(–5.5) µm..........***L. pumilium*** (Gresl. & Rajchenb.) Hjortstam & Ryvarden (*Hyphodontia pumilia* Gresl. & Rajchenb.); distr.: South America

Key G. *Lyomyces* P. Karst.

1 Spores globose to broadly ellipsoid, (5.5–)6–7 × 5–6.3 µm; cystidia, basidia, and especially basidioles moderately to richly encrusted by fine crystals; cylindrical or subcylindrical cystidia present, up to 53 × 7 µm; basidioma often very thin, hypochnoid; subicular hyphae naked ....

.... ***L. incrustatus*** (Kotir. & Saaren.) Hjortstam & Ryvarden (*Hyphodontia incrustata* Kotir. & Saaren.); distr.: Europe

– Spores broadly ellipsoid to oblong, 2.5–4.5 µm broad; cystidia and basidioles smooth to moderately encrusted, basidia usually smooth; cylindrical cystidia absent or intermediate in shape to subulate and fusiform; basidioma usually moderately thick; subicular hyphae naked to moderately encrusted **2**

2 Capitate cystidia/cystidioles present, usually numerous................................ **3**

– Capitate cystidia/cystidioles absent **4**

3 Spores narrowly ellipsoid to subcylindrical, (4.5–)5–5.7 × (2.5–)3–3.5 µm, thin-walled; subicular hyphae thin-walled; subhymenial hyphae usually non-encrusted .... ***L. erastii*** (Saaren. & Kotir.) Hjortstam & Ryvarden (*Hyphodontia erastii* Saaren. & Kotir.); distr.: temperate Eurasia

– Spores broadly ellipsoid to ellipsoid, sometimes narrowly ellipsoid, 4.5–6(–7) × (3–)3.5–4(–4.5) µm, when mature somewhat thick-walled; subicular hyphae thick-walled; subhymenium rich of crystalline material ....***L. sambuci*** (Pers.: Fr.) P. Karst. [*Hyphodontia sambuci* (Pers. : Fr.) J. Erikss., *H. hariotii* (Bres.) Parmasto, *Hyphoderma sambuci* (Pers.: Fr.) Jülich, *Rogersella sambuci* (Pers.: Fr.) Liberta & A.J. Navas]; distr.: cosmopolitan

4 Basidia with 2(3) sterigmata; spores broadly ellipsoid, 5–6 × 3.5–4.5 µm; no typical cystidia, only fusiform cystidioles 18–24 × 4(–6) µm; hyphae often encrusted, up to 3 µm wide ....***L. bisterigmatus*** (Boidin & Gilles) Hjortstam & Ryvarden (*Hyphodontia bisterigmata* Boidin & Gilles); distr.: southwest Indian Ocean islands

– Basidia with 4 sterigmata; spores oblong, 4.5–7.5 × 3–4.5 µm; with fusiform cystidia 25–35 × 5–7 µm; hyphae naked, up to 4 µm wide.......................... .... ***L. boninensis*** (S. Ito & S. Imai) Hjortstam & Ryvarden [*Hyphodontia boninensis* (S. Ito & S. Imai) N. Maek. '*boninense*']; distr.: East Asia, Oceania

Key H. *Palifer* Stalpers & P.K. Buchanan

1 Spores thick-walled... **2**

– Spores thin-walled **3**

2 Projecting, naked, thin-walled septocystidia present in aculei and hymenium between them, 40–80 × 4–5 µm; spores 3.2–4.3 µm broad ....***Hyphodontia septocystidiata*** H.X. Xiong, Y.C. Dai & Sheng H. Wu; distr.: East and Southeast Asia, Central America
This species is considered to be in the genus *Palifer* due to the presence of numerous short, thick-walled, apically encrusted cystidia.

– True septocystidia absent, but some encrusted cystidia with adventitious septa; spores 3–3.5 µm broad ... ***Hyphodontia rickii*** (Hjortstam & Ryvarden) Gresl. & Rajchenb. [*Lagarobasidium rickii* (Hjortstam & Ryvarden) Hjortstam & Ryvarden, *Hypochnicium rickii* Hjortstam & Ryvarden]; distr.: South America

According to Gorjón (2012), this species should be excluded from *Lagarobasidium* because of encrusted cystidia, similar to those in *P. gamundiae* and *H. erikssonii*.

3 Hymenophore smooth or slightly grandinioid; cylindrical cystidia naked, apically obtuse or capitulate, 40–150 × 4.5–7 µm ..***P. verecundus*** (G. Cunn.) Stalpers & P.K. Buchanan [*Hyphodontia verecunda* (G. Cunn.) Hjortstam & Ryvarden]; distr.: South America, New Zealand According to Gorjón (2012), *H. verecunda* possesses true lagenocystidia, but in other features fits *Xylodon*.

– Hymenophore grandinioid to odontioid; large cylindrical cystidia absent... 4

4 Spores oblong to cylindrical, (5–)6–6.5 µm long ....***P. gamundiae*** (Gresl. & Rajchenb.) Hjortstam & Ryvarden (*Hyphodontia gamundiae* Gresl. & Rajchenb.); distr.: South America

– Spores broadly ellipsoid to ellipsoid, 4–6 µm long **5**

5 Spores 4–5 × 3–3.5 µm; capitate cystidia apically 8–12 µm broad, usually naked ....***Hyphodontia erikssonii*** (R. Galan & J.E. Wright) Hjortstam & Ryvarden; distr.: South America This taxon was included in *Hyphodontia* s. str. by Hjortstam et al. (2005) and Hjortstam and Ryvarden (2009). However, instead of true lagenocystidia, it possesses cylindrical, naked or apically encrusted elements, called in the protologue as "hyphis paraphysoideis".

– Spores 5–6 × 4–4.5 µm; capitate cystidia apically 7–10 µm broad, usually with resinous cap ......***P. hjortstamii*** (Gresl. & Rajchenb.) Hjortstam & Ryvarden (*Hyphodontia hjortstamii* Gresl. & Rajchenb.); distr.: South America According to Gorjón (2012), this species has encrusted cystidia and spores almost identical to *H. erikssonii*, and can be treated as a probable synonym of the latter.

Key I. *Schizopora* Velen.

1 Basidioma pileate, broadly dimidiate or with tapering base, sometimes with effused part; hyphal system trimitic with skeletal and binding hyphae; binding hyphae almost lacking a lumen, tortuous, up to 3.5 µm in diam, both in subiculum and trama ....***Sch. trametoides*** Núñez; distr.: Southeast Asia

– Basidioma effused or effused-reflexed; hyphal system dimitic or seemingly dimitic, with skeletals or skeletal-like hyphae **2**

2 In hymenium numerous bottle-shaped cystidia, apically with stellate group of big, rhomboid crystals...***Sch. cystidiata*** David & Rajchenb. [*Hyphodontia cystidiata* (David & Rajchenb.) Hjortstam & K.H. Larss.]; distr.: Africa, southwest Indian Ocean islands According to Hjortstam and Ryvarden (2009), this species does not belong to *Schizopora*, but is possibly related to *Poriodontia*.

– Cystidia apically without stellate incrustations **3**
3 Spores 2.8–4(–4.3) µm long **4**
– Spores 4–6.5 µm long **5**
4 Hyphal system dimitic, skeletals abundant in subiculum, 3.5–6 µm diam.; capitate cystidial elements present in hymenium and dissepiment edges, lacking a cap of resinous matter; fusoid cystidia present, about 20 × 4 µm; basidia 2-sterigmate; spores 3–4 × 2.3–3 µm, many spores with a conspicuous papilla at one or both ends, reminiscent of conidia formation .... ***Sch. crassihypha*** Douanla-Meli; distr.: Africa
– Hyphal system seemingly dimitic, skeletal-like hyphae 2.5–5 µm diam, abundant in central trama; capitate cystidial elements present in subiculum, trama and hymenium, often provided with a cap of resinous matter; fusoid cystidia absent; basidia 4-sterigmate; spores 3.7–4.3 × 2.8–3.3 µm, without papillae..... ***Sch. ovispora*** (Corner) Hjortstam & Ryvarden [*Hyphodontia ovispora* (Corner) T. Hatt., *H. tropica* Sheng H. Wu nom. inval.]; distr.: East Asia
5 Hyphal system dimitic with skeletals **6**
– Hyphal system subdimitic: some hyphae in trama very thick-walled **8**
6 Pores 1–2(–4)/mm; spores (5–)5.5–6(–6.5) × (3.3–)3.5–4(–4.5) µm; hymenophore irpicoid, denticulate, labyrinthiform, rarely poroid or irregularly-hydnoid; capitate cystidia usually few.. ....***Sch. paradoxa*** (Schrad. : Fr.) Donk [*Hyphodontia paradoxa* (Schrad. : Fr.) E. Langer & Vesterh., *Sch. versipora* (Pers.) Teixeira]; distr.: cosmopolitan
– Pores (3)4–6(−8)/mm; spores (3−)4−5 × 3−3.5(−4) µm; hymenophore poroid; capitate cystidia common, especially as 'tramal vesicles' 7
7 Subulate or fusoid cystidia in hymenium common, apically with crystalline incrustation; capitate cystidia in hymenium inabundant; spores 4–5 × 3–3.5 µm .... ***Sch. flavipora*** (Berk. & M.A. Curtis) Ryvarden [*Hyphodontia flavipora* (Berk. & M.A. Curtis) Sheng H. Wu, *H. nongravis* (Lloyd) Sheng H. Wu, *H. subiculoides* (Lloyd) Sheng H. Wu, *Sch. hypolateritia* (Berk. ex Cooke) Parmasto, *Sch. phellinoides* (Pilát) Domański, *Sch. subiculoides* (Lloyd) Ryvarden, *Sch. trichiliae* (Van der Byl) Ryvarden]; distr.: cosmopolitan
– Subulate or fusoid cystidia in hymenium scattered, mostly naked; capitate cystidia in hymenium abundant; spores (3−)3.5−4.8(−5) × (2.8−)3−3.5(−4) µm .... ***Sch. carneolutea*** (Rodway & Cleland) Kotl. & Pouzar; distr.: Australia This name is synonymized with *Sch. flavipora* by Hjortstam and Ryvarden (2007a).
8 Hymenophore poroid with angular or elongate pores, sometimes irpicoid; capitate cystidia usually numerous; spores (4–)4.5–5(–5.5) × (2.8–)3–3.5 (–3.8) µm .... ***Sch. radula*** (Pers.: Fr.) Hallenb. [*Hyphodontia radula* (Pers.: Fr.) E. Langer & Vesterh.]; distr.: cosmopolitan
– Pores soon torn into narrow teeth, in old specimens teeth aggregated into groups; cystidia absent or not pronounced; spores 5−6 × 2.5−3 µm ....***Sch. archeri*** (Berk.) Nakasone [*Xylodon archeri* (Berk.) Kuntze]; distr.: Australia, New Zealand

Key J. *Xylodon* (Pers.) Gray

1 Hymenophore poroid, predominantly poroid or irpicoid/raduloid **2**
– Hymenophore smooth to odontioid or hydnoid **12**
2 All hyphae simple-septate ***X. poroideoefibulatus*** (Sheng H. Wu) Hjortstam & Ryvarden (*Hyphodontia poroideoefibulata* Sheng H. Wu); distr.: East Asia
– Hyphae clamped at all primary septa **3**
3 Tapering or acuminate cystidia present in hymenium **4**
– Hymenial cystidia apically rounded to capitate; tapering cystidial elements absent **8**
4 Spores cylindrical to suballantoid .... ***X. nothofagi*** (G. Cunn.) Hjortstam & Ryvarden [*Hyphodontia nothofagi* (G. Cunn.) E. Langer, *Schizopora nothofagi* (G. Cunn.) P.K. Buchanan & Ryvarden]; distr.: New Zealand
– Spores broadly ellipsoid to ellipsoid **5**
5 Hyphal system pseudodimitic due to thick-walled (up to 1.5 µm) hyphae in subiculum and dissepiment; cystidia moniliform, often with a small acuminate apical segment .... ***X. bresinskyi*** (E. Langer) Hjortstam & Ryvarden (*Schizopora bresinskyi* E. Langer); distr.: Europe
– Hyphal system monomitic, hyphal walls up to 0.5 µm thick; cystidia not moniliform or only faintly constricted **6**
6 Spores 4–5.5 µm broad; pores up to 2 mm deep; subiculum up to 0.5 mm thick; capitate hyphal ends usually absent in subiculum, but present in dissepiment; tapering hymenial cystidia reaching 50 × 8 µm in size; basidia 5–7 µm broad, usually not repetitive; .... ***X. apacheriensis*** (Gilb. & Canf.) Hjortstam & Ryvarden [*Hyphodontia apacheriensis* (Gilb. & Canf.) Hjortstam & Ryvarden]; distr.: North America
– Spores up to 4(–4.5) µm broad; pores to 0.3 mm deep; subiculum to 0.15 mm thick; capitate hyphal ends in subiculum numerous; tapering hymenial cystidia reaching about 30 × 6 µm in size; basidia 4.5–5 µm broad, often repetitive... 7
7 Pores rounded; spores (3–)3.3–4 µm broad .... ***X. niemelaei*** (Sheng H. Wu) Hjortstam & Ryvarden (*Hyphodontia niemelaei* Sheng H. Wu subsp. *niemelaei* Sheng H. Wu); distr.: East Asia, Africa, South America
– Pores somewhat elongated; spores 3.7–4(–4.5) µm broad .... ***X. gracilis*** (Hjortstam & Ryvarden) Hjortstam & Ryvarden (*Hyphodontia niemelaei* subsp. *gracilis* Hjortstam & Ryvarden); distr.: South America
8 Spores suballantoid .... ***X. syringae*** (E. Langer) Hjortstam & Ryvarden (*Hyphodontia syringae* E. Langer); distr.: East Asia
– Spores subglobose to oblong **9**
9 Pores 1−3/mm; spores subglobose to broadly ellipsoid **10**
– Pores 4−7/mm; spores narrowly ellipsoid to oblong, 4−5.5 × 2.5−3.2 µm ... **11**
10 Pores about 3/mm; margin filamentous-arachnoid, without rhizomorphs; spores subglobose, 4.2−5 × 4−4.3 µm; capitate cystidia 15−23 ×

4.5–3 µm .... ***X. hallenbergii*** (Sheng H. Wu) Hjortstam & Ryvarden (*Hyphodontia hallenbergii* Sheng H. Wu); distr.: East Asia

– Pores 1–2/mm; margin with white rhizomorphs; spores broadly ellipsoid/ellipsoid, (4–)4.3–5.5(–6) × 3.5–4(–4.3) µm; capitate cystidia 20–27 × 6–7 µm .... ***Hyphodontia rhizomorpha*** C.L. Zhao, B.K. Cui & Y.C. Dai; distr.: East Asia

11 Pores 4–6/mm, up to 0.35 mm deep; capitate cystidia 10–45 × 3.5–5 µm, apically capped with resinous matter; basidia 14–20 µm long; spores 4.5–5.5 µm long .... ***X. taiwanianus*** (Sheng H. Wu) Hjortstam & Ryvarden (*Hyphodontia taiwaniana* Sheng H. Wu); distr.: East Asia

– Pores 6–7/mm, to about 1 mm deep; capitate cystidia 11–13.5 × 4–6 µm, without resinous cap; basidia 9–12.5 µm long; spores (4–)4.3–5 µm long .... ***Hyphodontia pseudotropica*** C.L. Zhao, B.K. Cui & Y.C. Dai; distr.: East Asia

12 Spores allantoid, 1–1.5 µm broad .... ***X. scopinellus*** (Berk.) Hjortstam & Ryvarden [*Odontia scopinella* (Berk.) Berk.]; distr.: Australia, New Zealand

– Spores subglobose to cylindrical or suballantoid, at least 2 µm broad **13**

13 Apically acute cystidia or acuminate hyphal ends regularly present in hymenium and/or at sterile apices of aculei **14**

– All cystidia apically blunt (but can be tapering), or acuminate elements rare and only at aculeal apices or occasionally in hymenium **35**

14 Acuminate hyphal ends or acuminate cystidia confined to sterile aculeal apices **15**

– Acuminate cystidia or cystidioles also in hymenium **20**

15 With hypha-like, thick-walled tramal cystidia, somewhat constricted and flexuous, often richly encrusted and with adventitious septa, apically blunt, subcapitate or acute .... ***X. lanatus*** (Burds. & Nakasone) Hjortstam & Ryvarden (*Hyphodontia lanata* Burds. & Nakasone); distr.: North and South America, East Asia

– Thick-walled tramal cystidia absent **16**

16 With hastocystidia, 40–60 × 6–8 µm, at aculeal apices .... ***X. hastifer*** (Hjortstam & Ryvarden) Hjortstam & Ryvarden (*Hyphodontia hastifera* Hjortstam & Ryvarden); distr.: South America

– No hastocystidia; acuminate hyphal ends in aculei 2–4 µm broad **17**

17 With enclosed, more or less constricted (torulose) cystidia; capitate and subcapitate cystidia often provided with resinous cap **18**

– Torulose cystidia absent; capitate and subcapitate cystidia naked, seldom with resinous cap **19**

18 Cylindrical sterile elements in hymenium (if present) up to 4 µm broad; torulose cystidia with oily contents (like gloeocystidia), sometimes very rare; spores ellipsoid, 4–5 × 3–3.5 µm...... ***X. brevisetus*** (P. Karst.) Hjortstam & Ryvarden [*Hyphodontia breviseta* (P. Karst.) J. Erikss.]; distr.: temperate north hemisphere

– Subclavate/short cylindrical cystidia common or scattered in hymenium, 4.5–8.5 µm broad; torulose cystidia with non-oily contents; most basidiospores broadly ellipsoid, some subglobose, 4–5.5(–6) × (3–)3.5–4(–4.5) µm..***Hyphodontia subclavata*** Yurchenko, H.X. Xiong & Sheng H. Wu; distr.: East Asia

19 Spores ellipsoid to oblong, convex or flat adaxially, 5.5–6.5(–7) × 3.5–4.5 µm; capitate cystidia present in hymenium...***X. pruni*** (Lasch) Hjortstam & Ryvarden [*Hyphodontia pruni* (Lasch) Svrček]; distr.: Eurasia, North Africa, North America

– Spores ellipsoid, flat or depressed adaxially, (5–)6–7 × 2.5–3.5 µm; capitate cystidia absent, subcapitate elements very few ....***Hyphodontia novozelandica*** Gorjón & Gresl.; distr.: New Zealand

20 All hyphae covered with dark yellow or brown granular material, dissolving and turning violet in KOH....... ***X. australis*** (Berk.) Hjortstam & Ryvarden [*Hyphodontia australis* (Berk.) Hjortstam]; distr.: Australia, South America

– The hyphal incrustations colorless or pale colored, not turning violet in KOH..**21**

21 Hymenophore smooth to minutely odontioid, with the longest aculei reaching 0.05–0.3 mm in length..**22**

– Hymenophore odontioid to hydnoid and almost irpicoid, with aculei reaching 0.5–3 mm long... **31**

22 Spores cylindrical to suballantoid, (2–)2.5–3(–3.5) µm broad **23**

– Spores subglobose to oblong, 3–4 µm broad..**25**

23 Basidioma very thin (mostly about 25 µm thick); hymenial surface smooth ... . ***Hyphodontia tenuissima*** Yurchenko & Sheng H. Wu; distr.: East Asia

– Basidioma usually 50 µm or more thick; hymenial surface scarcely aculeate (in younger parts smooth) to densely odontioid.......................................**24**

24 Hymenial surface whitish or greyish, with sterile peg-like projections (11–15 projections/mm).. ***Hyphodontia vietnamensis*** Yurchenko & Sheng H. Wu; distr.: Southeast Asia

– Hymenial surface yellowish or cream-colored, with at least partly fertile aculei (about 5 aculei/mm) ....***X. crustosus*** (Pers.: Fr.) Chevall [*Hyphodontia crustosa* (Pers.: Fr.) J. Erikss., *H. burtii* (Peck) Gilb.]; distr.: cosmopolitan
The species is very variable, especially in macromorphology and spore morphology. Hjortstam and Ryvarden (1997) noted a specimen from Colombia under the name *Hyphodontia* cf. *crustosa*, with ellipsoid spores. A morphological variant called *Hyphodontia crustosa* "*jacutica*" (Eriksson et al. 1981), or *H. jacutica* (Eriksson and Ryvarden 1976), differs from *H. crustosa* by narrowly ellipsoid spores, and this may represent a taxon of its own.

25 Spores subglobose; hymenophore smooth or scanty odontioid.................**26**

– Spores broadly ellipsoid to oblong; hymenophore smooth to densely odontioid..**27**

26 Basidia bisterigmate; spores 5.5–7 × 4.5–6 µm, thin-walled; subulate cystidia 18–25 × 4.5–6 µm; hymenophore smooth......***X. bisporus*** (Boidin & Gilles) Hjortstam & Ryvarden (*Hyphodontia bispora* Boidin & Gilles); distr.: Europe

– Basidia with (2)4 sterigmata; spores about 5 × 3.8–4 µm, slightly thick-walled; subulate cystidia 30–40 × 3.5–5 µm; hymenophore at first smooth, later with minute, separated aculei ....***X. crustosoglobosus*** (Hallenb. & Hjortstam) Hjortstam & Ryvarden (*Hyphodontia crustosoglobosa* Hallenb. & Hjortstam); distr.: South America

27 Capitate (including lecythiform) elements present in hymenium **28**

– Capitate cystidial elements absent, or present only in aculei or in subhymenium...**29**

28 Hymenial surface salmon-colored when dry; hymenial cystidia of three types: tapering, 2–3.5 µm wide, capitate, and lecythiform; spores ellipsoid ....***Hyphodontia macrescens*** (Banker) Ginns & Lefebvre; distr.: North America According to Hjortstam and Ryvarden (2009), this is a name of unknown application.

– Hymenial surface ochraceous- or cinnamon-yellow; cystidia of two types: tapering, 3–5 µm wide, and lecythiform; spores ellipsoid to narrowly ellipsoid..................***X. rimosissimus*** (Peck) Hjortstam & Ryvarden [*Hyphodontia rimosissima* (Peck) Gilb. sensu Gilbertson (1962)]; distr.: North America

29 Hymenophoral aculei consisting of strongly flexuous hyphae with blunt, subcapitate or capitulate apices..***X. candidissimus*** (Berk. & M.A. Curtis) Hjortstam & Ryvarden [*Hyphodontia candidissima* (Berk. & M.A. Curtis) E. Langer]; distr.: North and South America

– Hymenophoral aculei, if present, consisting apically of acute cystidial elements..**30**

30 Hymenophore smooth to minutely tuberculate, white to yellowish; basidioma not stratified, except at the differentiation zone of subhymenium and subiculum; hymenial surface more or less matt ***X. juniperi*** (Bourdot & Galzin) Hjortstam & Ryvarden [*Hyphodontia juniperi* (Bourdot & Galzin) J. Erikss. & Hjortstam]; distr.: Eurasia, Macaronesia, North and South America

– Hymenophore distinctly warted to odontioid (basidioma can be partly smooth), yellowish to ochraceous; basidioma when well developed, somewhat stratified; hymenial surface more or less glossy.................................... ....***X. stratosus*** (Hjortstam & Ryvarden) Hjortstam & Ryvarden (*Hyphodontia stratosa* Hjortstam & Ryvarden); distr.: Africa, South America

31 Spores cylindrical to suballantoid, 2.5–3.5 µm broad ....***X. quercinus*** (Pers.: Fr.) Gray [*Hyphodontia quercina* (Pers.: Fr.) J. Erikss.]; distr.: temperate north hemisphere

– Spores subglobose to narrowly ellipsoid, (3.2–)3.5−4.5 µm broad **32**

32 Basidioma up to 0.8 mm thick between aculei; torulose, apically rounded cystidia with 2−9 constrictions present...................................***Hyphodontia anmashanensis*** Yurchenko, H.X. Xiong & Sheng H. Wu; distr.: East Asia

– Basidioma about 0.05 mm thick between aculei; constricted cystidia if present, with 1−5 constrictions and apically acute...**33**

33 Spores narrowly ellipsoid or oblong, 5–6.3 × 3–4 μm; capitate hyphal ends, if present, without resinous cap; cystidia ventricose-submucronate, thin- or slightly thick-walled towards the base... ....***X. submucronatus*** (Hjortstam & Renvall) Hjortstam & Ryvarden (*Hyphodontia submucronata* Hjortstam & Renvall); distr.: Africa

– Spores subglobose to ellipsoid, 4.5–5(–5.5) × (3.5–)4–4.5 μm; capitate hyphal ends in hymenium often with resinous caps; cystidia fusoid with 1–5 constrictions, acuminate, thin-walled...**34**

34 Hymenophoral aculei flattened, incised, rarely conical or subcylindrical....... ....***X. spathulatus*** (Schrad. : Fr.) Kuntze [*Hyphodontia spathulata* (Schrad. : Fr.) Parmasto]; distr.: cosmopolitan

– Hymenophoral aculei triangular at base, subulate above, arranged in more or less parallel rows.................................... ***Hyphodontia fimbriiformis*** (Berk. & M.A. Curtis) Ginns & Lefebvre '*fimbriaeformis*'; distr.: North America Hjortstam and Ryvarden (2009) synonymized this name with *X. spathulatus*.

35 Astrocystidia present on subicular hyphae ....***Hyphodontia astrocystidiata*** Yurchenko & Sheng H. Wu; distr.: East Asia

– Astrocystidia lacking in subiculum..**36**

36 Thick-walled, hypha-like, more or less encrusted, constricted and septate cystidia present, projecting in bundles at aculeal apices.................................**37**

– All cystidia thin-walled or slightly thick-walled in lower part, aseptate......**40**

37 Spores cylindrical 2–2.5(–3) μm wide; hymenial cystidia subcapitate.....***X. nespori*** (Bres.) Hjortstam & Ryvarden [*Hyphodontia nespori* (Bres.) J. Erikss. & Hjortstam, *Odontia papillosa* (Fr.) Bres. sensu Nikolajeva, 1961]; distr.: cosmopolitan Spores in *O. papillosa*, according to Nikolajeva (1961), are larger than *X. nespori* measuring 5–8 × 2–3.5 μm.

– Spores broadly ellipsoid to oblong 3–4(−5) μm wide **38**

38 Capitate hyphal ends (vesicles) present in subiculum***X. lanatus*** (see step 15)

– No capitate hyphal ends in subiculum **39**

39 Cystidia at aculeal apices flexuous and subcapitate; aculei fertile at base; basidia 15−17 μm long...........***X. serpentiformis*** (E. Langer) Hjortstam & Ryvarden (*Hyphodontia serpentiformis* E. Langer); distr.: East Asia, Macaronesia *Hyphodontia crassa* Sang H. Lin & Z.C. Chen was considered as synonym of *H. serpentiformis* by Dai et al. (2004).

– Cystidia straight or slightly wavy, apically hypha-like, forming sterile peg-like fascicles; basidia 15−35 μm long ....***Hyphodontia echinata*** Yurchenko & Sheng H. Wu; distr.: East Asia

40 Lepto- or gloeocystidia present, of tramal or subhymenial origin, longer, than 30 μm, or if shorter, then reaching 8–15 μm in width.............................**41**

– Lepto- or gloeocystidia absent, or if hymenial leptocystidia present, then up to 30 × 8 μm, or somewhat thick-walled in lower 1/2–2/3 ....**48**

41 Hymenophore smooth to tuberculate **42**

– Hymenophore odontioid to hydnoid...**43**

42 Cystidia of three types: enclosed cylindrical gloeocystidia, capitate and hyphoid cystidia; cylindrical hyphoid cystidia 40−70(−80) × (3−)4−5(−5.5) µm..***X. tuberculatus*** (Kotir. & Saaren.) Hjortstam & Ryvarden (*Hyphodontia tuberculata* Kotir. & Saaren.); distr.: Europe

– Cystidia of one type, cylindrical or subcylindrical, 90−100 × 4−6 µm; gloeocystidia absent ....***X. tenuicystidius*** (Hjortstam & Ryvarden) Hjortstam & Ryvarden (*Hyphodontia tenuicystidia* Hjortstam & Ryvarden nom. inval.); distr.: South America

43 Capitate cystidial elements present in hymenium or subiculum, sometimes projecting from aculeal apices **44**

– Capitate cystidial elements lacking..**47**

44 Hyphae in aculeal trama thin- to slightly thick-walled; spores thin-walled, the biggest ones 5–5.5 × 3.5 µm **45**

– Aculeal trama with thick-walled or pseudoskeletal hyphae; spores often slightly thick-walled or distinctly thick-walled, the biggest ones 6–7 × 4–4.5 µm...**46**

45 Lepto- or gloeocystidia mostly of tramal origin, submoniliform, sometimes cylindrical, 40–60(–125) × 4–5(–7) µm, enclosed, sometimes difficult to find; capitate cystidia in hymenium and in aculeal apices, sometimes in subiculum, naked and apically 3.5–5.5 µm broad, or provided with a cap of resinous matter; spores ellipsoid..........................***X. brevisetus*** (see step 18)
Hyphodontia* cf. *breviseta, briefly described and illustrated in Kotiranta and Saarenoksa (2000) also keys here. It has long (about 100 µm and more), acute sterile aculeal apices, consisting of strictly parallel, tightly agglutinated, amyloid hyphae; gloeocystidia more 90 µm long; spores (4.5–)5–5.5 × 3–3.5(–4) µm. In *H. breviseta*, following to the same authors, sterile aculeal apices are shorter (near 70 µm), and consisting of subparallel, loosely arranged, inamyloid hyphae; gloeocystidia usually (45–)50–70 µm long; spores 4–4.5(–6) × (2.7–)3–3.5(–5) µm. Distr.: Europe

– Leptocystidia of subhymenial origin, cylindrical, fusoid or clavate, often apically projecting, 35–50 × (5.5–)6–8(–9) µm; capitate cystidia only embedded in subiculum and aculeal trama, naked, apically 5–8 µm broad; spores narrowly ellipsoid to oblong ....***Hyphodontia heterocystidiata*** H.X. Xiong, Y.C. Dai & Sheng H. Wu; distr.: East Asia
The species is referred by Gorjón (2012) to the *H. breviseta* complex.

46 Capitate cystidia enclosed or projecting, mostly capped with resinous matter; leptocystidia enclosed; spores thick-walled, (5–)5.5–6(–7) × 4–4.5 µm ....***X. crassisporus*** (Gresl. & Rajchenb.) Hjortstam & Ryvarden (*Hyphodontia crassispora* Gresl. & Rajchenb.); distr.: South America

– Capitate cystidia in subiculum only, without resinous cap; leptocystidia enclosed or projecting up to 30 µm; spores thin- to slightly thick-walled, 4–6 × 3–4 µm.. ***Hyphodontia sinensis*** H.X. Xiong, Y.C. Dai & Sheng H. Wu; distr.: East Asia

47 Hymenophore odontioid-hydnoid, with aculei 0.2–0.8 mm long; leptocystidia of tramal and subhymenial origin, cylindrical to torulose, 15–70 × 5–8 µm; spores 4–5 × 3–3.5 µm... ***X. lenis*** Hjortstam & Ryvarden (*Hyphodontia mollis* Sheng H. Wu); distr.: East Asia

– Hymenophore odontioid, with aculei up to 0.4 mm long; leptocystidia only hymenial, subcylindrical, clavate, almost pyriform, 20–35 × 4.5–15 µm; spores 5–6 × 3.5–4.5 µm ....***Hyphodontia pelliculae*** (H. Furuk.) N. Maek.; distr.: East Asia

48 Capitate, subcapitate or capitulate cystidial elements abundant to scattered, but regularly present in hymenium or at aculeal apices **49**

– Capitate and similar cystidial elements absent or occasional......................**68**

49 Resinous caps present on some or many capitate cystidia.........................**50**

– Capitate cystidia lacking resinous cap **53**

50 Hymenial surface with fairly sparse aculei (1–3/mm), separated or connected by crests...**51**

– Hymenial surface densely tuberculate to densely odontioid (6–10 aculei/mm), without crests..**52**

51 Aculei separated; capitate cystidia 4.5–5.5(–6) µm broad, often lacking resinous cap; spores subglobose to broadly ellipsoid, 3.5–4.5(–5) µm broad ... .***X. asperus*** (Fr.) Hjortstam & Ryvarden [*Hyphodontia aspera* (Fr.) J. Erikss., *H. granulosa* (Pers.: Fr.) Ginns & Lefebvre nom. superfl.]; distr.: temperate Eurasia

– Aculei often connected by crests; capitate cystidia 3–4.5 µm broad, usually with a cap of resinous matter; spores ellipsoid, 3.5–4 µm broad................... ....***Hyphodontia subspathulata*** (H. Furuk.) N. Maek.; distr.: East Asia
Hjortstam and Ryvarden (2009) consider this name as a synonym of *X. spathulatus*. However, in Maekawa's description (1993) no acuminate, constricted gloeocystidia were mentioned.

52 Basidioma white or cream-colored, with age pale ochraceous; aculei narrowly conical or subcylindrical; hyphal texture in subiculum and trama loose; spores (5–)5.5–6.5(–7) × 3.5–4.5(–5) µm..................***X. pruni*** (see step 19)

– Basidioma creamish or often pale ochraceous and reddish ochraceous; aculei conical to almost semiglobose; hyphal texture in subiculum and trama fairly dense; spores 5–6 × 3.5–4 µm..***X. verruculosus*** (J. Erikss. & Hjortstam) Hjortstam & Ryvarden [*Hyphodontia verruculosa* J. Erikss. & Hjortstam; *H. papillosa* (Fr.) J. Erikss. p.p., sensu Eriksson and Ryvarden (1976); *Lyomyces papillosus* (Fr.) P. Karst.]; distr.: Europe
In many taxonomical works *Hyphodontia verrucolosa* is considered to be a synonym of *H. rimosissima*. However, Hjortstam and Ryvarden (2009) treated *X. verruculosus* separately from *X. rimosissimus* (see step 28).

53 Spores 7.5–10 µm long, ovoid to suballantoid; aculeal apices with subulate or hypha-like, apically capitulate cystidia ....***X. adhaerisporus*** (E. Langer) Hjortstam & Ryvarden (*Hyphodontia adhaerispora* E. Langer); distr.: southwest Indian Ocean islands

– Spores up to 7 µm long, subglobose to oblong, never concave adaxially; aculeal apices with hypha-like, tapering, capitate or capitulate cystidia...........**54**

54 Capitate cystidia apically 8–12 µm broad, projecting about 20 µm.. ***X. capitatus*** (G. Cunn.) Hjortstam & Ryvarden [*Hyphodontia cunninghamii* Gresl. & Rajchenb., non *Hyphodontia capitata* (Boidin & Gilles) Hjortstam]; distr.: Australia, New Zealand

– Capitate or subcapitate cystidia apically up to 6(–7) µm broad, projecting or enclosed..**55**

55 Capitate cystidia predominating at aculeal apices, naked or slightly encrusted ....***Hyphodontia capitatocystidiata*** H.X. Xiong, Y.C. Dai & Sheng H. Wu; distr.: East Asia

– Aculeal apices consisting predominantly of tapering or cylindrical cystidia or hyphal ends, otherwise capitate cystidia richly encrusted (incrustation dissolving in KOH)...**56**

56 With fairly straight, hyphoid, projecting cystidia, somewhat broadened apically and thick-walled there, and somewhat broadened basally..................... ....***X. borealis*** (Kotir. & Saaren.) Hjortstam & Ryvarden (*Hyphodontia borealis* Kotir. & Saaren.); distr.: temperate Eurasia This taxon was depicted under the name *Hyphodontia* aff. *nudiseta* in Langer (1994).

– Hyphoid cystidia if present, then not broadened and thick-walled apically.....**57**

57 Spores (5–)5.5–6.5(–7) µm long...**58**

– Spores 3.8–5(–6) µm long **61**

58 Hymenophoral aculei 10–15/mm; capitate, subcapitate and capitulate cystidia 20–60 × 4–6 µm, typically present in aculei....................................... ....***X. fimbriatus*** (Sheng H. Wu) Hjortstam & Ryvarden (*Hyphodontia fimbriata* Sheng H. Wu); distr.: East Asia, South America

– Hymenophoral aculei 6–12/mm; capitate and similar cystidia 15–40 × 3–5 µm, often absent in aculei...**59**

59 Spores thin-walled, 3.5–4.5(–5) µm broad; projecting hyphal ends in aculei subulate, obtuse, capitulate ....***X. pruni*** (see step 19)

– Spores slightly thick-walled when mature, 3.5−4 µm broad; projecting hyphal ends in aculei nearly cylindrical or tapering.......................................**60**

60 Hymenial cystidia tibiiform to lecythiform.. ...***X. bugellensis*** (Ces.) Hjortstam & Ryvarden sensu Hjortstam and Ryvarden (2007a) [*Hyphodontia bugellensis* (Ces.) J. Erikss.]; distr.: Macaronesia, Africa In earlier works (Eriksson and Ryvarden 1976; Langer 1994) this name was synonymized with *Hyphodontia pruni*.

– Hymenial cystidia cylindrical or subcapitate ....***X. subscopinellus*** (G. Cunn.) Hjortstam & Ryvarden [*Hyphodontia subscopinella* (G. Cunn.) Greslebin & Rajchenb.]; distr.: Australia, New Zealand

61 Subulate cystidial elements regularly present at aculeal tips and/or in hymenium...**62**

– Subulate cystidia absent, rare, or little distinguishing from cylindrical hyphal ends **64**

62 Many capitate cystidia with olive brownish contents; all hyphae thin-walled; spores narrowly ellipsoid, 3–3.5(–4) µm broad .... ***Hyphodontia* sp. 2** (Kotiranta and Saarenoksa 2000); distr.: Europe

– Capitate cystidia colorless; subicular hyphae with thickened to moderately thick walls; spores broadly ellipsoid to ellipsoid, 3.5–4 µm broad **63**

63 Cystidia subulate, rarely capitate; tramal hyphae with thickened walls; spores thin- or slightly thick-walled.. ....***Hyphodontia* sp. 1** (Kotiranta and Saarenoksa 2000); distr.: Europe. European samples, treated under the name *X. nudisetus*, and having, besides subulate cystidia, also slightly capitate ones (Langer 1994), possibly belong here (Kotiranta and Saarenoksa 2000).

– Cystidia subcapitate and almost subulate; tramal hyphae thin-walled; spores thin-walled ....***X. pruniaceus*** (Hjortstam & Ryvarden) Hjortstam & Ryvarden (*Hyphodontia pruniacea* Hjortstam & Ryvarden); distr.: Africa

64 With skeletal-like, strongly light-refractive hyphae in aculeal trama and partly in subiculum......................***X. rudis*** (Hjortstam & Ryvarden) Hjortstam & Ryvarden (*Hyphodontia rudis* Hjortstam & Ryvarden); distr.: South America

– Skeletal-like hyphae absent, hyphae in aculeal trama thin- to slightly thick-walled **65**

65 Hyphae in aculeal apices richly encrusted; spores 4−5 µm long.................**66**

– Hyphae in aculeal apices scarcely to moderately encrusted; spores up to 5.5−6 µm long...**67**

66 Capitate cystidia in hymenium between aculei, 15−18 µm long; hyphae in aculei (peg-like fascicles) flexuous, 2.5−3.5 µm wide; spores 4–5 × 3–3.5 µm................. .... ***Hyphodontia microfasciculata*** Yurchenko & Sheng H. Wu; distr.: East Asia

– Capitate cystidia mainly in aculei, 30–60 µm long; hyphae in aculeal apices straight, 3−4 µm wide; spores 4.3–4.5 × 4–4.3 µm ....***X. tenellus*** Hjortstam & Ryvarden; distr.: South Americ

67 Hymenophoral aculei more or less scattered, usually 1–3/mm; spores subglobose to broadly ellipsoid, 5–6 × (3.5–)4–5(–5.8) µm ....***X. asperus*** (see step 51)

– Hymenophoral aculei more crowded; spores broadly ellipsoid, (4.2–)4.5–5(–5.5) × 3.5–4 µm .... ***Hyphodontia* sp. 3** (Kotiranta and Saarenoksa 2000); distr.: Europe

68 Spores 2.2–3 µm broad...**69**

– Spores ≥ 3 µm broad..**70**

69 Spores (6–)6.5–7 × 2.2–2.5 µm; cystidia or hyphal ends in aculei tapering, thin- to moderately thick-walled; hymenophore densely odontioid; subicular hyphae (2.5–)3–4 µm diam; basidia 25–30 × 4.5–5 µm .... **X. nesporina** (Hallenb. & Hjortstam) Hjortstam & Ryvarden (*Hyphodontia nesporina* Hallenb. & Hjortstam); distr.: South America

– Spores 4.5–6 × 2.5–3 µm; cystidia or hyphal ends in aculei cylindrical, thin-walled; hymenophore smooth to grandinioid; subicular hyphae 2–3 µm in diam; basidia about 15 × 3.5–4 µm .... ***Hyphodontia papillosa*** (Fr. : Fr.) J. Erikss. sensu Gilbertson (1974); distr.: North America The concept of this species in Gilbertson differs from the concept of *H. verruculosa* (Ginns and Lefebvre 1993; see step 52), and resembles *X. nespori* with naked cystidia (see step 37).

70 Cystidia or hyphal ends in aculei with crystalline incrustations **71**

– Cystidia or hyphal ends in aculei naked or almost naked **72**

71 Cystidia torulose; spores thick-walled when mature .... **X. bugellensis** sensu Bernicchia and Gorjón (2010) [*Hyphodontia bugellensis* sensu Melo and Tellería (1997); see also step 60]; distr.: Europe, Southwest Asia

– Cystidia subulate, often with somewhat broadened base; spores thin-walled .... **X. knysnanus** (Van der Byl) Hjortstam & Ryvarden [*Hyphodontia knysnana* (Van der Byl) D.A. Reid]; distr.: Africa, South America

72 Hymenophoral aculei 2–4/mm; cystidia 3–4 µm broad, usually flexuous; spores ellipsoid, (6–)6.5–7(–7.5) × (3–)3.5–4 µm.. .... **X. lutescens** (Hjortstam & Ryvarden) Hjortstam & Ryvarden (*Hyphodontia lutescens* Hjortstam & Ryvarden); distr.: South America Langer (1994) noted that this taxon should be treated in the genus *Hyphoderma* because of *Hyphodontia*-like hyphae are absent and spores are with granular contents. However, Hjortstam and Ryvarden (2009) referred *X. lutescens* to the same morphological group as *X. asperus* and *X. brevisetus*.

– Hymenophoral aculei crowded, more than 4/mm; cystidia basally up to 7 µm broad, straight or weakly flexuous; spores subglobose to ellipsoid, 4.5–6 × 3–4.5 µm... **X. nudisetus** (Warcup & P.H.B. Talbot) Hjortstam & Ryvarden (*Hyphodontia nudiseta* Warcup & P.H.B. Talbot; see also step 63); distr.: East Asia, Australia

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Appendix

Species and specimens from which various cystidial elements were depicted (Fig. 1; collection acronyms follow *Index Herbariorum* – http://sweetgum.nybg.org/science/ih): A1, *Lagarobasidium calongei* (MA-Fungi 73256, from Dueñas et al. 2009); A2, *Kneiffiella floccosa* (MSK-F 4755); B, *Hyphodontia pallidula* (MSK-F 6937); C, *Hastodontia hastata* (GB 94809, from Eriksson and Ryvarden 1976); D, *X. brevisetus* (MSK-F 5105); E, *Hyphodontia astrocystidiata* (TNM F24764); F, *H. arguta* (TNM F24822); G, *H. rickii* (CIEFAP Rick 208 47, from Gorjón 2012); H, *Xylodon lanatus*, (TNM F1225); I, *X. lenis* (TNM F21833); J, *Hyphodontia subclavata* (TNM F24744); K, *H. heterocystidiata* (TNM F, Wu 9209-33); L, *H. heterocystidiata* (TNM F, Wu 911107-38); M, *Lagarobasidium detriticum* (MSK-F 4146); N, *Hyphodontia anmashanensis* (TNM F15201); O, *Xylodon spathulatus* (MSK-F 5663); P, *X. fimbriatus* (TNM F111); Q, *X. asperus* (TNM F17159); R, *Hyphodontia subclavata* (TNM F24742); S, *Lyomyces sambuci* (MSK-F 4155); T, *Xylodon fimbriatus* (TNM F7890); U, *Hyphodontia anmashanensis* (TNM F15201); V, *Xylodon candidissimus* (TNM F9278); W, *X. juniper* (TNM F15343); X, *X. tuberculatus* (MSK-F 7352); Y, Z, *X. brevisetus* (MSK-F 5105).

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Top 50 most wanted fungi

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Abstract

Environmental sequencing regularly recovers fungi that cannot be classified to any meaningful taxonomic level beyond "Fungi". There are several examples where evidence of such lineages has been sitting in public sequence databases for up to ten years before receiving scientific attention and formal recognition. In order to highlight these unidentified lineages for taxonomic scrutiny, a search function is presented that produces updated lists of approximately genus-level clusters of fungal ITS sequences that remain unidentified at the phylum, class, and order levels, respectively. The search function (https://unite.ut.ee/top50.php) is implemented in the UNITE database for molecular identification of fungi, such that the underlying sequences and fungal lineages are open to third-party annotation. We invite researchers to examine these enigmatic fungal lineages in the hope that their taxonomic resolution will not have to wait another ten years or more.

Key words

Fungi, environmental sequencing, taxonomic orphans, metabarcoding, taxonomy feedback loop

Introduction

Fungi form a large and diverse kingdom of heterotrophic eukaryotes. Recent studies suggest that there may be more than 6 million extant species of fungi (Taylor et al. 2014), a number that contrasts sharply with the ca. 100,000 formally described species (Hibbett et al. 2011). Several factors contribute to the discrepancy between the estimated and the known number of fungal species. In particular, the subterranean or otherwise difficult-to-observe nature of much of fungal life sets mycology apart from the study of many other groups of multicellular eukaryotes (Blackwell 2011). Molecular (DNA sequence) data have revolutionized the scientific study of fungi, and DNA sequence data are now a routine source of information in fungal systematics, taxonomy, and ecology across the fungal tree of life (Stajich et al. 2009). Fungal environmental sequencing (molecular ecology) studies, where some particular environmental habitat or substrate is examined for fungal diversity, span these disciplines in seeking to detail what fungi are present and what their ecological and functional roles are in the system studied.

Molecular ecology studies regularly struggle to identify the recovered fungi to meaningful taxonomic levels. Lack of reference sequences, mis-annotated reference sequences, and reference sequences annotated only to, e.g., kingdom or phylum level combine to make taxonomic identification of newly recovered sequence data challenging (Nilsson et al. 2012). These issues are to some extent mitigated by initiatives such as the UNITE database for molecular identification of fungi (Kõljalg et al. 2013), but they remain significant challenges to any molecular ecology effort. In particular, environmental sequencing studies regularly recover fungal sequences that are difficult to assign to any fungal lineage at all, even at the phylum level. The discovery and subsequent description of the class *Archaeorhizomycetes* (Schadt et al. 2003; Rosling et al. 2011) and the phylum *Cryptomycota* (Lara et al. 2010; Jones et al. 2011) both involve environmental samples that initially could not be assigned to any resolved taxonomic level. Similarly, the global soil sequencing study of Tedersoo et al. (2014) recovered 16 large groups of fungal sequences that could not be classified to any meaningful taxonomic level beyond Fungi. Indeed, more or less all environmental sequencing studies feature a non-trivial proportion of sequences simply classified as “Unidentified fungi” (cf. Hardoim et al. 2015) due to the lack of more explicit taxonomic information. There is no taxonomic feedback loop in place to highlight the presence of these enigmatic lineages to the mycological community, and they often end up in sequence databases for years without attracting significant research interest.

In our work with environmental sequencing of fungi, we regularly run across these unidentified lineages. We typically encounter them through sequences of the internal transcribed spacer (ITS), the formal fungal barcode (Schoch et al. 2012) and the marker of choice in fungal molecular ecology studies (Lindahl et al. 2013; Tedersoo et al. 2015). A quick BLAST search in the International Nucleotide Sequence Database Collaboration (INSDC: GenBank, ENA, and DDBJ; Nakamura et al. 2013) or UNITE typically hints at the impossibility of coming up with any resolved taxonomic affiliation, and the matter is left at that. This situation is untenable in the long run. These lineages will give rise to identification problems for other research groups too, such that a limited number of taxonomic orphans will affect the scientific results of a large number of research efforts negatively. This is not in the best interest of mycology. In the present study we seek to bridge the gap between fungal taxonomy and molecular ecology by putting the spotlight on the 50 largest of these unidentified lineages at the phylum, class, and order levels. Our effort takes the form of an automatically updated search function targeting the largest taxonomic orphans in the UNITE database. The lists of the largest orphans and the constituent sequences are subject to third-party sequence annotation, such that anyone who has information on these species is invited to share it with the scientific community. The lists are updated monthly, and by highlighting these fungal lineages we hope to speed up their characterization and formal description.

Materials and methods

UNITE clusters all public fungal ITS sequences (~500,000 at the time of this writing) to approximately the genus/subgenus level (called a "compound cluster") using a clustering threshold of 80% sequence similarity. A second round of clustering inside each such compound cluster seeks to produce molecular operational taxonomic units (OTUs) at approximately the species level; these OTUs are called *species hypotheses* (SHs; Kõljalg et al. 2013). The species hypotheses are open for viewing and querying (http://unite.ut.ee/search.php) through uniform resource identifiers (URIs) such as https://plutof.ut.ee/#/datacite/10.15156/BIO/SH154595.07FU. Each SH has a unique digital object identifier (DOI, 10.15156/BIO/SH154595.07FU for the example above) to enable precise species-level taxonomic communication across publications and studies also in the absence of precise Latin names.

Although UNITE offers various search functions targeting the compound clusters and species hypotheses, none of the search functions were designed to find truly poorly known lineages. To remedy this, we devised a search function to retrieve fungal lineages for which little to no taxonomic information is available. The user is presented with two main choices: 1) the taxonomic level to be considered (phylum, class, or order), and 2) whether the list of compound clusters should be ordered by the number of constituent sequences or by the number of studies in which the sequences were found. In addition, the user can exercise control over how the output is shown through several other options.

Taxonomic scope (phylum, class, or order)

To enable exploration of different hierarchical levels in the classification system, the search function supports three different levels: phylum, class, and order. Thus, the search function will retrieve clusters of sequences where none of the sequences are identified at the phylum, class, or order level depending on the choice of the user.

Sorting of the list of taxa (sequence or study count)

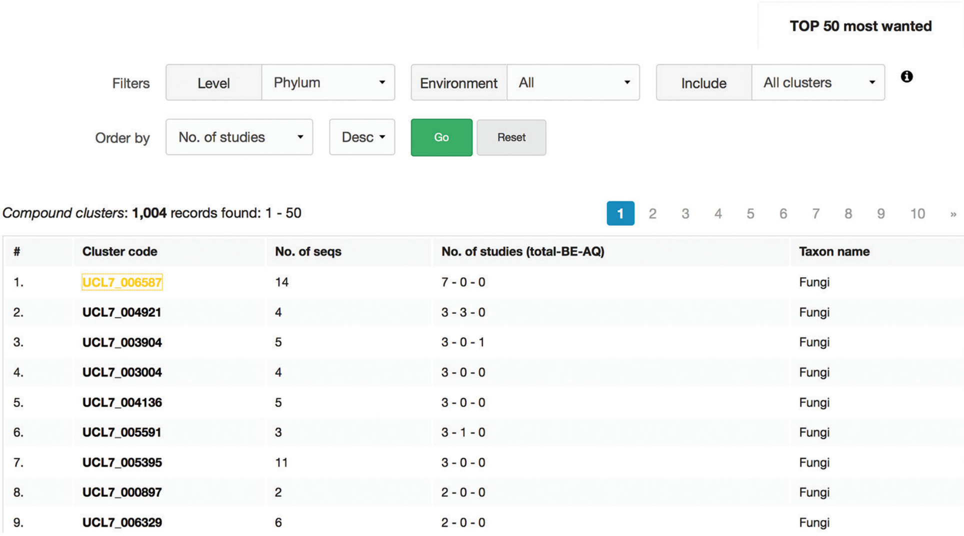
Multiple independent recoveries of some particular fungal sequence type would strengthen one's belief that the lineage indeed corresponds to a biological reality. In analogy, for sequence types found only in a single study, some sound skepticism is perhaps in place given the sequence quality-related issues involved in studies based on cloning as well as next-generation sequencing (Hyde et al. 2013; Lindahl et al. 2013; Hughes et al. 2015). However, there are examples to the contrary for both of these situations: sequence types found only in one particular study have proved to be authentic, and "species" found in several different studies have proved to be chimeras (Brown et al. 2015; Nilsson et al. 2015). This search parameter offers some degree of flexibility by allowing the user to specify whether the number of sequences or the number of studies should be used to order the list of compound clusters.

Each search will retrieve all clusters of sequences fulfilling the criteria. Thus, there are 3 (phylum, class, and order) * 2 (order by sequences or by studies) = 6 lists of "poorly known" fungal lineages. Some degree of overlap among these lists is likely; a compound cluster where all sequences are unidentified at the order level may also qualify as a cluster where all of the sequences are unidentified at the phylum level. No attempt was made to account for such redundancy.

A concern was that these sequences could be subject to quality issues. Alternatively they could be false positives in that they lacked explicit taxonomic annotation but nevertheless were easy to assign to a known taxonomic lineage. To minimize these concerns, we examined the 50 largest lineages at the phylum, class, and order levels (as ordered by the number of constituent studies) through BLAST searches in UNITE and the INSDC following Kang et al. (2010) and Nilsson et al. (2012). The full length of the sequences as they were deposited in INSDC/UNITE, as well as the ITS2 and 5.8S separately, were used for these searches. Many of the sequences were annotated to the barest minimum and lacked, for example, metadata on country and substrate of collection. In an attempt at restoring as much of these data as possible, we examined the underlying papers when specified in the corresponding INSDC entries.

Results

The phylum-level search returned 1,004 compound clusters, of which 830 (83%) were singletons. Out of the 1,364 class-level clusters, 1,056 (77%) were singletons; and out of the 1,738 order-level clusters, 1,290 (74%) were singletons. The results presented here focus on the 50 topmost entries in each of these lists. The largest of the phylum-level clusters comprised 30 sequences, and the average number of sequences in the 50 topmost clusters was 7.4 (standard deviation: 4.9). At the class level, the largest cluster comprised 60 sequences (average cluster size 8.5 sequences, standard deviation 9.7). At the order level, the largest cluster comprised 60 sequences (average cluster size 9.5 sequences, standard deviation 9.5). The cluster with the highest



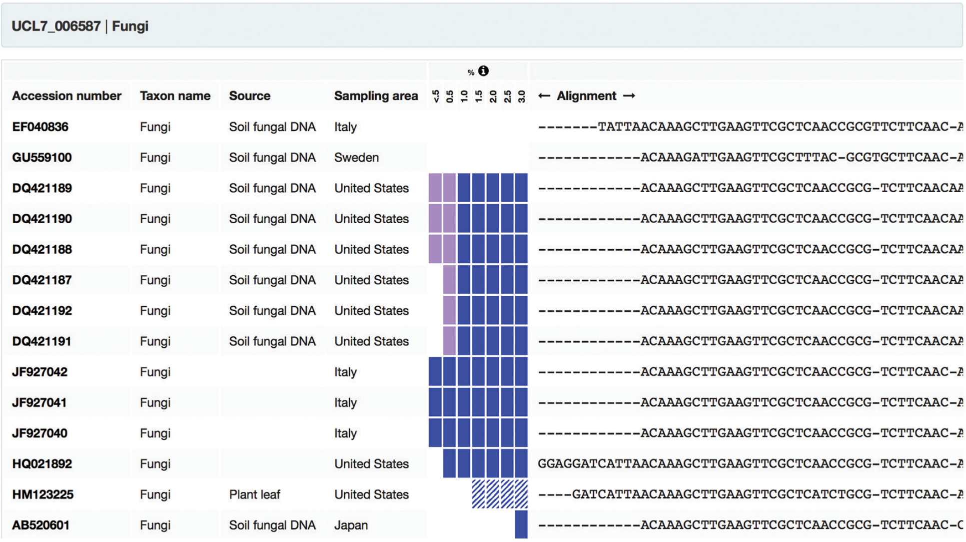
#	Cluster code	No. of seqs	No. of studies (total-BE-AQ)	Taxon name
1.	UCL7_006587	14	7 - 0 - 0	Fungi
2.	UCL7_004921	4	3 - 3 - 0	Fungi
3.	UCL7_003904	5	3 - 0 - 1	Fungi
4.	UCL7_003004	4	3 - 0 - 0	Fungi
5.	UCL7_004136	5	3 - 0 - 0	Fungi
6.	UCL7_005591	3	3 - 1 - 0	Fungi
7.	UCL7_005395	11	3 - 0 - 0	Fungi
8.	UCL7_000897	2	2 - 0 - 0	Fungi
9.	UCL7_006329	6	2 - 0 - 0	Fungi

Figure 1. A web-based screenshot of the upper part of the top 50 list of compound clusters where all sequences are unidentified at the phylum level. The clusters are ordered by the number of contributing studies in this screenshot.

number of independent recoveries had been found in 23 different studies and was unidentified at the order level.

The lists, with accompanying multiple sequence alignments and geo/ecological metadata, are available for viewing and third-party annotation at https://unite.ut.ee/top50.php (Figs 1–3 from September 2015). Our taxonomic examination of the lineages at the compound cluster level was unsuccessful – we could not assign any of the lineages to any known fungal lineage with confidence. For some lineages, there were hints or clues pointing to a tentative assignment of the sequences to phylum or class level, but the disparate or heterogeneous nature of the available reference sequences did not lend confidence to any robust assignment. In line with the UNITE policy, no speculative (non-robust) assignments were made in these lineages. In other cases, the publicly available reference sequences offered absolutely no guidance as to the taxonomic affiliation of the query sequences (e.g., "Uncultured eukaryote"). In 39 cases, we found the sequences to be associated with quality-related problems, mainly a chimeric nature (cf. Nilsson et al. 2012). We marked those sequences as substandard/chimeric and re-ran the search function to make sure that none of the top 50 clusters in the compound cluster list would be obvious cases of compromised sequence data as of the date of the preparation of this paper.

Our data assembly effort to restore data on the country and host of collection resulted in 60 sequences being tagged with a country of collection and 261 with a substrate of collection. Data on country and substrate of collection for the 50 largest compound clusters that were not identified at the phylum, class, and order level, respectively, are shown in Figs 4–5 (September 2015). Soil, living plants, and mycor-



UCL7_006587 | Fungi

Accession number	Taxon name	Source	Sampling area	%	← Alignment →
EF040836	Fungi	Soil fungal DNA	Italy		-------TATTAACAAAGCTTGAAGTTCGCTCAACCGCGTTCTTCAAC-A
GU559100	Fungi	Soil fungal DNA	Sweden		------------ACAAAGATTGAAGTTCGCTTTAC-GCGTGCTTCAAC-A
DQ421189	Fungi	Soil fungal DNA	United States		------------ACAAAGCTTGAAGTTCGCTCAACCGCG-TCTTCAACAA
DQ421190	Fungi	Soil fungal DNA	United States		------------ACAAAGCTTGAAGTTCGCTCAACCGCG-TCTTCAACAA
DQ421188	Fungi	Soil fungal DNA	United States		------------ACAAAGCTTGAAGTTCGCTCAACCGCG-TCTTCAACAA
DQ421187	Fungi	Soil fungal DNA	United States		------------ACAAAGCTTGAAGTTCGCTCAACCGCG-TCTTCAACAA
DQ421192	Fungi	Soil fungal DNA	United States		------------ACAAAGCTTGAAGTTCGCTCAACCGCG-TCTTCAACAA
DQ421191	Fungi	Soil fungal DNA	United States		------------ACAAAGCTTGAAGTTCGCTCAACCGCG-TCTTCAACAA
JF927042	Fungi		Italy		------------ACAAAGCTTGAAGTTCGCTCAACCGCG-TCTTCAAC-A
JF927041	Fungi		Italy		------------ACAAAGCTTGAAGTTCGCTCAACCGCG-TCTTCAAC-A
JF927040	Fungi		Italy		------------ACAAAGCTTGAAGTTCGCTCAACCGCG-TCTTCAAC-A
HQ021892	Fungi		United States		GGAGGATCATTAACAAAGCTTGAAGTTCGCTCAACCGCG-TCTTCAAC-A
HM123225	Fungi	Plant leaf	United States		----GATCATTAACAAAGCTTGAAGTTCGCTCATCTGCG-TCTTCAAC-A
AB520601	Fungi	Soil fungal DNA	Japan		------------ACAAAGCTTGAAGTTCGCTCAACCGCG-TCTTCAAC-C

Figure 2. A compound cluster displayed in the web browser of the user. The INSDC accession numbers and their taxonomic annotation are shown in columns 1 and 2. The DNA source and the country of collection are shown in columns 3 and 4. Column 5 shows the inclusiveness of the species hypotheses at the 97% similarity level (rightmost filled column), the 97.5% similarity level (second-to-rightmost filled column), and so on up to 100% similarity. The aligned sequence data are shown in column 6.

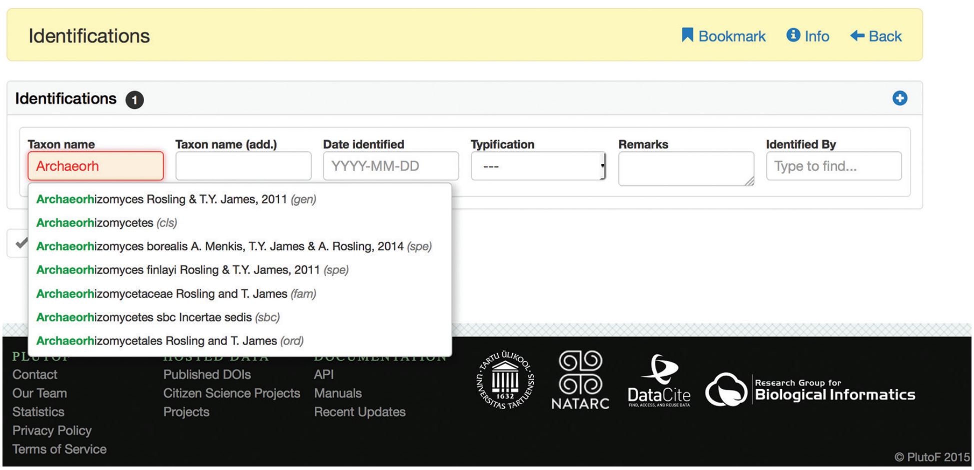


Figure 3. Web-based third-party taxonomic annotation of the sequences in a species hypothesis is demonstrated. Third-party annotation requires non-anonymous registration, and such annotations are subject to peer review. Annotations are tagged with the name of the annotator as well as the date. Multiple annotations for individual entries are supported.

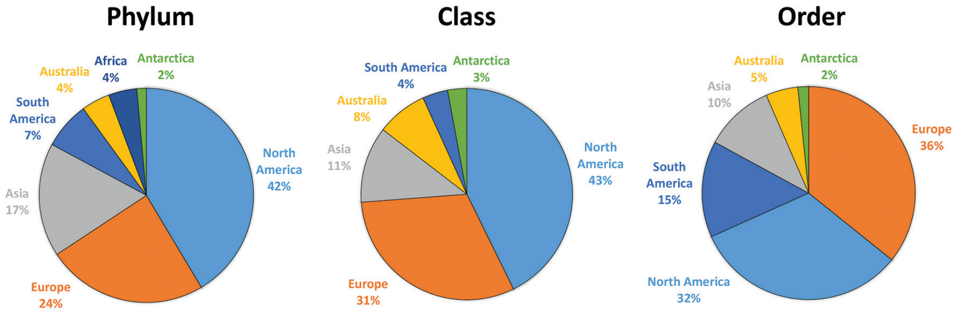


Figure 4. Geographical distribution of the top 50 most wanted fungi at the phylum, class, and order level. Each fungal sequence was assigned to country of origin according to its INSDC entry (or underlying publication as applicable) and then summarized based on the continents: Africa (dark blue), Antarctica (green), Asia (grey), Australia (yellow), Europe (orange), North America (light blue), and South America (blue).

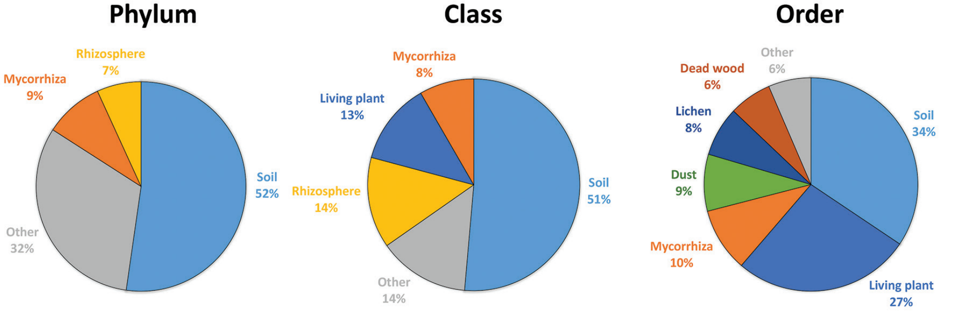


Figure 5. The most common substrates associated with the top 50 most wanted fungi at the phylum, class, and order level. Each fungal sequence was assigned to substrate according to its GenBank entry (or underlying publication as applicable). The major substrates included soil (light blue), living plants (blue), mycorrhiza (orange), dust (green), lichen (dark blue), dead wood (red), and other (grey). To improve readability, rare substrates (<3 occurrences) were merged into the 'other' category.

rhiza stand out as frequently sampled substrates. Europe and North America stand out as frequent targets for environmental sequencing studies. These are well-known biases towards the most commonly targeted molecular ecology substrates and the Western world, respectively (Ryberg et al. 2009; Tedersoo et al. 2011; Lindahl et al. 2013), and should not necessarily be taken to mean that fungal diversity is the highest in these substrates and geographical locations. Along the same line, it is pleasing to note that all seven continents are represented in Figure 4, hinting perhaps at the increasingly ambitious sampling efforts undertaken by the mycological and molecular ecology communities. Somewhat unexpectedly, perhaps, dust and lichens seem to be relatively rich sources of sequences and species hypotheses that cannot be identified at the order level.

Discussion

This paper presents a set of lists of fungi for which taxonomic assignment is very troublesome at present. These lists matter, because the underlying fungi are regularly recovered in environmental sequencing efforts, where they contribute to the proportion of unidentified sequences. Mycology is a comparatively small discipline that struggles for funding (cf. Pautasso 2013), and it would be beneficial for mycology to show that when researchers sequence fungi as a part of their scientific pursuits, they get clean, unequivocal results. That is not the case at present. Worse, the taxonomic discovery potential of environmental sequencing is not made full use of by the mycological community. History shows that evidence of unknown lineages of fungi may sit in sequence databases for upwards of 10 years before receiving scientific attention and formal recognition. Indeed, several of the present lineages feature sequence data that are at least that old. We hope that these lists – largely consisting of sequences from environmental sequencing efforts – will establish a feedback loop back to taxonomy. We furthermore hope that anyone who has information that sheds light on the taxonomic affiliation of these lineages would be willing to share this information with the research community through the third-party sequence annotation tools of UNITE (or otherwise). Even phylum-level annotations, as applicable, would help. UNITE serves as data provider for a range of sequence identification pipelines and databases (Bates et al. 2013; https://unite.ut.ee/repository.php), and any such contributed taxonomic information would be shared with all downstream resources.

We examined all sequence types from the 50 largest compound clusters for telltale signs of a technically compromised nature, such as chimeric insertions or low read quality (cf. Nilsson et al. 2012, 2015). In this process we found and excluded 39 substandard sequences, after which the search was re-run. We could not assert with confidence that any of the remaining lineages were technically compromised. However, such examinations should ideally be carried out in light of other sequences from closely related lineages, of which none or very few are available for these lineages. Our sequence quality control was, therefore, not carried out under optimal conditions. Even so, all sequences passed the quality measures we exercised. Importantly, none of the lineages examined were singletons – on the contrary, the largest one comprised 60 sequences, and most were recovered in two or more different studies (with 23 being the largest number of studies). Although independent recovery of some particular sequence type does not rule out, e.g., a chimeric nature, it does increase the likelihood that the sequence is genuine.

It is not immediately clear that all of these lineages indeed are fungi, although at least one fungus-specific primer seems to have been involved in the generation of many of them. Many studies have reported the occasional (even frequent) co-amplification of, e.g., plants and metazoans with fungus-specific primers (cf. Tedersoo et al. 2011; 2014). We are certainly open to the possibility that one or more of the present lineages will prove to be non-fungal organisms in the end. Since they evidently are prone to co-amplification with fungus-specific primers or otherwise are retrieved in research efforts targeting fungi, it would seem important to be able to tell them from fungi in the sequence identification step. Getting the naming of these sequences right, even if they are not fungal, would thus still appear to be of relevance to mycology.

Precise and robust taxonomic assignment of these ITS sequences is not possible at present due to the lack of similar reference sequences in the public sequence databases. Sequence data from the much more conserved, neighboring small and large subunit genes (18S/SSU and 28S/LSU, respectively) would presumably have alleviated this problem by allowing phylogenetic placement in the context of known SSU and LSU sequences. However, ITS sequences are typically sequenced and deposited without significant parts of the SSU and LSU, particularly in environmental sequencing efforts, rendering this approach difficult. Deeply sequenced metagenomes – as well as emerging sequencing technologies producing very long reads – offer a route by which to retrieve parts of the ITS region attached to either the SSU or LSU, or indeed span them both. Thus, the increasing popularity of metagenomics and genomics may solve many of these cases over time. However, also someone doing traditional systematics and taxonomy can contribute. Supplying, as a minimum, an ITS sequence with each new species description would offer structure to available sequence data and would significantly reduce interpretation difficulties of species names (Hyde et al. 2008). Similarly, GenBank is known to contain thousands of sequences from type material – sequences that are not annotated as stemming from type material at present. GenBank has recently implemented standards for marking and querying sequences from type material (Schoch et al. 2014), and we hope that the mycological community will be quick to embrace these standards for newly generated as well as already deposited sequences. Another helpful move would be to provide an ITS sequence with each new fungal genome. For technical reasons, ITS and other ribosomal sequences tend to be hard to assemble and are therefore left out from many genome sequencing efforts (Schoch et al. 2014).

We are working to add additional flexibility in the generation of these lists. Some researchers may, for example, be interested only in unknown fungi found in the built environment, or in a medical context, or from aquatic environments. We will seek to address these needs by compiling a set of keywords for each such research field. For the built environment, these keywords would include, e.g., "house", "dust", "building", and "gypsum". For the search function, we will then require that a compound cluster contains at least one sequence where at least one of these keywords occurs either in the title of the underlying scientific study or in the FEATURES field of the corresponding INSDC/UNITE entry. The search function would then retrieve compound clusters with at least one fungal sequence that has a relation to the built environment. We will similarly endeavor to add support for the genus and species levels in the search function.

We refer to this list as the "most wanted" fungi. That is not meant to suggest that these fungi are the ecologically or economically most important extant fungi. Indeed, we make no claim as to the importance of these fungi from whatever point of view. We do make a claim to their uniqueness though, because it is frustrating, in the year 2016, not to be able to assign a name to a fungal sequence even at the phylum level.

When it comes to taxonomic discovery potential, we argue that these lineages definitely should be counted among the most interesting candidates. Even if we assume that some proportion of the present lineages in fact are technical artifacts or represent non-fungal organisms, it is reasonable to assume that some proportion of them indeed represent new or previously unsequenced lineages of fungi. None of them are at least 80% similar to sequences with richer taxonomic annotations; many are much more distant from known reference sequences than that. Common rules of thumb for ITS sequence similarity thresholds (Schoch et al. 2012, 2014; Irinyi et al. 2014) suggest that these lineages each represent at least a new (or previously unsequenced) genus, and in some cases an order or potentially even higher. We hope that the present publication will serve to put the spotlight on these uncharted parts of the fungal tree of life, and we invite the reader to examine them through our online tools or otherwise. These lists of the most wanted fungi are recomputed automatically on a monthly basis. We hope that they will speed up the formal recognition of the underlying species, and we challenge users to try to identify these species – because we failed ourselves. Until formal scientific names are available for these species, UNITE provides DOIs to promote unambiguous communication, and data harvesting, across datasets and studies.

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The date of collection and name of collector for *Cortinarius kioloensis* was incorrect. The herbarium accession number for *Cortinarius atrotomentosus* was incorrect. The authors apologize for these errors. The correct type specimen data are provided below.

Page 5:
Cortinarius kioloensis **Wood**
Type. AUSTRALIA. New South Wales: Batemans Bay, Kioloa State Forest, Eucalypt woodland, 19 May 1983, A.E. Wood & J.J. Bruhl (holotype: UNSW 83/781).

Page 17:
Cortinarius atrotomentosus **Harrower, sp. nov.**
Type. USA, Florida: Wakulla Co., Crawfordville, Apalachicola National Forest (30°12'06"N; 84°26'33"W), on soil under *Quercus virginiana*, 4 Dec. 2010, TFB 13848, (holotype: TENN 065535).