

**Rethinking the genus *Hyphodontia* s.l.
(Hymenochaetales, Basidiomycota) – investigations
on a worldwide scope including new taxonomy,
phylogeny, and identification keys**

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1. Introduction

1.1 The genus *Hyphodontia* sensu lato

Hyphodontia J. Erikss. is a basidiomycetous genus in the family Schizoporaceae (www.indexfungorum.org, November 2017), belonging to the order Hymenochaetales (Larsson et al. 2006). Eriksson described the genus in 1958, based on the generic type *Hyphodontia pallidula* (Bres.) J. Erikss. Since then, the genus has grown through the addition of new species descriptions and new combinations. The first discovered species were *Corticium sambuci* Pers., *Hydnum paradoxum* Schrad. and *Hydnum spathulatum* Schrad., whose descriptions were published in 1794 and are known today as *Lyomyces sambuci* (Pers.) P. Karst., *Xylodon paradoxus* (Schrad.) Chevall. and *Xylodon spathulatus* (Schrad.) Kuntze. In 1994, Langer's monograph was published. This is still the only work with species descriptions for all *Hyphodontia* species worldwide. Langer demonstrated 60 species, of which 52 are still counted today to *Hyphodontia* s. l. An important milestone in the history of the taxonomy of *Hyphodontia* s.l. is marked by the first molecular phylogeny of the Hymenochaetales with 29 ribosomal DNA sequences of different *Hyphodontia* s.l. species (Larsson et al. 2006). It shows that *Hyphodontia* s.l. is not monophyletic, but instead polyphyletic. Since this publication, it is still common to use *Hyphodontia* s.l. for all species which morphologically fit to species of these clades. In 2002 and 2009, Hjortstam and Ryvarden divided *Hyphodontia* s.l. into several genera based on morphological features, because a high number of taxa did not fit the original concept. The elaborated checklist of Hjortstam and Ryvarden (2009) contains 98 species in *Hyphodontia* s.l., which are split into 14 genera: *Alutaceodontia* (Parmasto) Hjortstam & Ryvarden, *Botryodontia* (Hjortstam & Ryvarden) Hjortstam, *Chaetoporellus* Bondartsev & Singer, *Deviodontia* (Parmasto) Hjortstam & Ryvarden, *Fibrodontia* Parmasto, *Hastodontia* (Parmasto) Hjortstam & Ryvarden, *Hyphodontia* J. Erikss., *Kneiffiella* P. Karst., *Lagarobasidium* Jülich, *Lyomyces* P. Karst., *Palifer* Stalpers & P.K. Buchanan, *Rogersella* Liberta & A.J. Navas, *Schizopora* Velen. and *Xylodon* (Pers.) Gray. Today, 85 of these species are still counted to *Hyphodontia* s.l. The genus *Fibrodontia* was removed from Hymenochaetales after DNA sequences of *Fibrodontia gossypina* Parmasto revealed a relationship with Trechisporales (Binder et al. 2005). The third work which includes all *Hyphodontia* s.l. species worldwide was the key of Yurchenko and Wu (2016). They keyed out 126 species, four published but unnamed taxa (e.g. *Hyphodontia* sp. 1) and three taxa with an affinity formulation. The concept followed

Hjortstam and Ryvarde (2009) by classifying recently described species into the existing genera, without formulating new combinations. In 2017, Riebesehl and Langer presented the latest checklist, with new combinations and new keys to all *Hyphodontia* s.l. species. This work was also based on Hjortstam and Ryvarde (2009), but took account of recent findings from molecular phylogenies too (e.g. Yurchenko and Wu 2014). They accepted 120 species, classified into seven genera: *Hastodontia*, *Hyphodontia*, *Kneiffiella*, *Lagarobasidium*, *Lyomyces*, *Palifer* and *Xylodon*. Following this study, eleven more species have been described: *Hyphodontia bubalina* Min Wang, Yuan Y. Chen & B.K. Cui, *H. chinensis* C.C. Chen & Sheng H. Wu, *H. mollissima* L.W. Zhou, *H. mongolica* Min Wang, Yuan Y. Chen & B.K. Cui, *H. reticulata* C.C. Chen & Sheng H. Wu, *H. subtropica* C.C. Chen & Sheng H. Wu, *H. zhixiangii* L.W. Zhou & Yu.Sh. Gafforov, *Lyomyces allantosporus* Riebesehl, Yurchenko & E. Langer, *L. mascarensis* Riebesehl, Yurchenko & E. Langer, *L. organensis* Yurchenko & Riebesehl and *L. orientalis* Riebesehl, Yurchenko & E. Langer. Furthermore, Chen et al. (2017) clarified that *Hyphodontia nongravis* (Lloyd) Sheng H. Wu is an independent species, and not a synonym for *Xylodon flaviporus* (Berk. & M.A. Curtis ex Cooke) Riebesehl & E. Langer. This gives the current number of 132 species in *Hyphodontia* s.l. (December 2017). After the addition of the newly described species to the genera concepts by Riebesehl and Langer (2017), *Hyphodontia* consists of 11, *Hastodontia* of 2, *Kneiffiella* of 24, *Lagarobasidium* of 4, *Lyomyces* of 21, *Palifer* of 6 and *Xylodon* of 64 species.

The morphology of *Hyphodontia* s.l. comprises different features which could be used to separate the seven genera. The basidiomata are generally resupinate, with a smooth, grandinioid, odontoid or poroid hymenophore. Intermediate forms are also possible. They are mostly whitish or yellowish in colour. The hyphal system is monomitic, dimitic, trimitic or pseudodimitic. Most species have clamp connections, but not necessarily on every septum. Cystidia of different types are possible. Suburniform holobasidia are common, but e.g. clavate or cylindrical forms could also occur. The basidia usually have four sterigmata, two sterigmata are rare. The basidiospores are mainly allantoid, ellipsoid, globose, ovoid or cylindrical in shape. Hyalin, inamyloid and thin-walled spores are common, thick-walled spores occur less often (Riebesehl & Langer 2017).

Generally, the genera can be differentiated by some criteria, but exceptions are present, so that an identification key is important for a determination. *Hyphodontia* is clearly characterized by the presence of capitate septo- and/or lagenocystidia. Lamprocystidia with a strongly encrusted apex, are present in *Palifer*. *Hastodontia* shows moniliform cystidia and thin-walled

spores, paired with a smooth or slightly grandinioid hymenophore. Tubular tramacystidia are present in *Kneiffiella* and *Lagarobasidium*. *Kneiffiella* mainly have thin-walled, and *Lagarobasidium* thick-walled, spores. *Xylodon* and *Lyomyces* overlap on several points. Tuberculate, coralloid, irpicoid or poroid hymenophores and thick-walled spores are only present in *Xylodon*, but smooth, grandinioid or odontoid hymenophores and thin-walled spores, are present in both genera (Riebesehl & Langer 2017). Ultimately, a key is important for the identification of species in these two genera, even with a lot of experience in *Hyphodontia* s.l.

Additional morphological features, drepanocysts and malocysts, could be observed in cultures of *Hyphodontia* s.l. Drepanocysts are ending hyphae, which bend and clasp around other hyphae. Malocysts are formed on the sides of hyphae, and are roundish in shape, with a tip. The function of these cell types is unknown (Langer 1994).

The distribution of *Hyphodontia* s.l. species is in principle worldwide, with different inhabited areas depending on single species. It can vary between small habitats for some species, and a cosmopolitan distribution for others, e.g. *Lyomyces bisterigmatus* (Boidin & Gilles) Hjortstam & Ryvarden is only known from the southwest Indian Ocean islands, while *Hyphodontia arguta* (Fr.) J. Erikss. has a cosmopolitan distribution (Yurchenko and Wu 2016). *Hyphodontia*, *Kneiffiella*, *Lyomyces* and *Xylodon* species have been found all over the world. *Hastodontia* is only known from the northern hemisphere, *Lagarobasidium* is not known from Australia and Africa, but is present in the southwest Indian Ocean islands and Macaronesia, and *Palifer* is distributed in South America, Central America, Asia and New Zealand. In principle, distribution data for *Hyphodontia* s.l. species should be considered incomplete, because this group has not been sufficiently explored (Riebesehl and Langer 2017).

Usually *Hyphodontia* s.l. species belong to the wood decomposers, causing a white-rot in angiosperms, as well as in gymnosperms (Eriksson and Ryvarden 1976, Yurchenko and Wu 2014). Nevertheless, other observations have also been reported. Nordén et al. (1999) detected *Hastodontia hastata* (Litsch.) Hjortstam & Ryvarden, *Hyphodontia pallidula*, *Kneiffiella abieticola* (Bourdot & Galzin) Jülich & Stalpers, *Xylodon asperus* (Fr.) Hjortstam & Ryvarden and *X. brevisetus* (P. Karst.) Hjortstam & Ryvarden on brown-rotted spruce stumps. These species are similarly known from white-rotting wood (Langer 1994). *Kneiffiella lanata* (Burds. & Nakasone) Riebesehl & E. Langer is reported living inter alia on palm tree

inflorescences of the genus *Sabal* Adans. (Burdson and Nakasone 1981). *K. palmae* Rick ex Hjortstam & Ryvarden, *Xylodon candidissimus* (Berk. & M.A. Curtis) Hjortstam & Ryvarden and *X. gracilis* (Hjortstam & Ryvarden) Hjortstam & Ryvarden are known for living on palms (Hjortstam et al. 2005, Langer 1994). *Lagarobasidium detriticum* (Bourdot & Galzin) Jülich, *Lyomyces griseliniae* (G. Cunn.) Riebesehl & E. Langer, *Xylodon borealis* (Kotir. & Saaren.) Hjortstam & Ryvarden and *X. gracilis* could also be found on pteridophytes (Kotiranta and Saarenoksa 2000, Langer 1994). Bamboo has been documented as a possible substrate for *Lyomyces bisterigmatus* and *Palifer septocystidiatus* (H.X. Xiong, Y.C. Dai & Sheng H. Wu) Riebesehl, Yurchenko & E. Langer, and halms of Poaceae for *L. capitato-cystidiatus* (H.X. Xiong, Y.C. Dai & Sheng H. Wu) Riebesehl & E. Langer (Boidin and Gilles 2003, Xiong et al. 2009, 2010). Furthermore, *Xylodon adhaerisporus* (Langer) Hjortstam & Ryvarden grows on *Clematis* L. and *X. bisporus* (Boidin & Gilles) Hjortstam & Ryvarden on *Staehelina dubia* L. (Boidin and Gilles 2003, Langer 1994).

Other fungi could also serve as a possible substrate: *Phellinus* Quél. is confirmed for *Hyphodontia pallidula*, and *Xylobolus frustulatus* (Pers.) P. Karst. for *Lyomyces macrescens* (Banker) Riebesehl & E. Langer (Ginns and Lefebvre 1993, Langer 1994).

Hyphodontia sp. (s.l.), *Xylodon flaviporus* and *X. raduloides* (Pers.) Riebesehl & E. Langer have been observed in the human respiratory system (Cui et al. 2013, James et al. 2016, Pounder et al. 2007), as well as *Hyphodontia* sp. (s.l.), which has been linked to a fungal keratitis of the human eye (Tananuvat et al. 2012).

An endophytic lifestyle is also possible (Dodd et al. 2010, Ragazzi et al. 2003). However, Ragazzi et al. only found *Hyphodontia* s.l. in declining *Quercus* species, and not in healthy trees.

Ponge (1990) detected a mycorrhizal form for *Hyphodontia* s.s. and the decomposition of animal remains.

Lichenized lifestyles were proven for *Hyphodontia pallidula*, *Lyomyces crustosus* (Pers.) P. Karst. and *Xylodon brevisetus*, with algal species related to *Coccomyxa* Schmidle and *Elliptochloris* Tschermak-Woess as photobiotic partners (Voytsekhovich et al. 2015).

Until now, the following enzymes have been found in *Hyphodontia* sp. (s.l.): laccase, as well as lignin, manganese, and manganese dependent versatile peroxidases (Kinnunen et al. 2017). Erkel et al. (1994) discovered Hyphodontal, an antifungal inhibitor of reverse transcriptases.

The production of crystals in *Hyphodontia* s.l. is common. They can occur as a layer over and in the whole basidiocarp, connected with hyphae or typically organized on cystidia. Keller (1985) investigated the crystals of cystidia in four *Hyphodontia* s.l. species: *Hyphodontia alutaria* (Burt) J. Erikss., *H. arguta*, *Xylodon brevisetus* and *X. paradoxus*. It was found to be calcium oxalate, which arises during cell wall decomposition of wood, and is a widespread phenomenon in white-rot fungi (Anagnostakis 1983, Guggiari et al. 2011).

1.2 Goals of the thesis

Fungi play a dominant role in terrestrial ecosystems, and represent one of the three large eukaryotic lineages (Nagy et al. 2017). Accumulation curves of newly described species over time, showed that higher taxa were more or less completely described whereas the accumulation curve for fungi is still increasing. The recent study by Hawksworth and Lücking (2017), extrapolated a total of 2.2 to 3.8 million species of fungi. Currently, around 120.000 species are accepted. This leads to the conclusion that only 3 to 8 % of the fungal species have been described. Since 2010, around 1.600 species have been described each year; in the previous 40 years it was around 1.300 per year (Hawksworth and Lücking 2017).

The aim of this study is to make a contribution to the unknown fungal diversity. *Hyphodontia* s.l. is an understudied group, especially in the tropics. The fungarium collection at the Department of Ecology in the University of Kassel, contains a high number of unstudied *Hyphodontia* s.l. specimens, collected from different continents. Essentially, this study was inspired by a big collection from La Réunion Island, because biodiversity hotspots are recognized as regions where unknown species could occur (Myers et al. 2000, Scheffers et al. 2012).

Initially, an attempt was made to identify the specimens from La Réunion Island. This work was very time-consuming, because there was no current worldwide identification key, and it led to the decision that a new key was essential for good identification. Nevertheless, one specimen could be identified very quickly as a new species: *Hyphodontia borbonica* Riebesehl, E. Langer & Barniske. It has lagenocystidia combined with a poroid hymenophore (Riebesehl et al. 2015). At the time, this combination was not present in *Hyphodontia* s.l. While working on the new key, another new key to all *Hyphodontia* s.l. species worldwide, was published by Yurchenko and Wu (2016). It follows the concept of Hjortstam and

Ryvarden (2009) with 13 genera, into which recently described species were organised, but without formulating new combinations. Riebesehl and Langer (2017) combined the morphological classification after Hjortstam and Ryvarden (2002, 2009) with the relationships obtained from DNA analyses (e.g. Larsson et al. 2006). This led to six genera and a seventh genus, which was not sufficiently supported via DNA sequences. Six genera after Hjortstam and Ryvarden (2009) could no longer be supported. Furthermore, Riebesehl and Langer (2017) added 35 new combinations in *Hyphodontia* s.l. to the classification system with seven genera, and provided eight ITS sequences of holotype material and further three ITS sequences of previously unsequenced species. On the basis of the new identification keys from Riebesehl and Langer (2017) and Yurchenko and Wu (2016), it was also possible to identify four other new species from Brazil, La Réunion and Taiwan: *Lyomyces allantosporus*, *L. mascarensis*, *L. organensis* and *L. orientalis* (Yurchenko et al. 2017). A contribution to the distribution of *Hyphodontia* s.l. species could be made by collaborating on collections from Central Asia. Six species could be reported for the first time in this region: *Hyphodontia alutaria*, *H. pallidula*, *Kneiffiella alutacea* (Fr.) Jülich & Stalpers, *Lyomyces crustosus*, *L. erastii* (Saaren. & Kotir.) Hjortstam & Ryvarden and *L. sambuci* (Gafforov et al. 2017).

2. Publications

2.1 *Hyphodontia borbonica*, a new species from La Réunion

2.2 *Hyphodontia* s.l. (Hymenochaetales, Basidiomycota): 35 new combinations and new keys to all 120 current species

2.3 Clarification of *Lyomyces sambuci* complex with the descriptions of four new species

2.4 *Hyphodontia* (Hymenochaetales, Basidiomycota) and similar taxa from Central Asia

3. Summary and perspectives

This thesis dealt with the fungal genus *Hyphodontia* s.l. Changing the classification system to treat the species from the broad *Hyphodontia* s.l. concept by a division into other genera was continued. Hjortstam and Ryvarde (2002, 2009) began the concept, but only took morphological features into account. This thesis revised the system and considered findings from molecular systematics. 35 new combinations were formulated. New identification keys were prepared, according to the new genera classifications. Overall, 37 DNA sequences were obtained and made publicly available on NCBI GenBank. The first generated sequences were successful for 13 species, and sequences of holotype material for 12 species, with regard to the fungal barcode ITS. It was possible to describe five new species out of collections from Brazil, La Réunion and Taiwan. Furthermore, the distribution of *Hyphodontia* s.l. species in Central Asia was investigated.

Hawksworth and Lücking (2017) showed that the accumulation curve for describing new fungal species is not yet saturated. Around 1.600 new species of fungi were described every year (Hawksworth and Lücking 2017). With regard to *Hyphodontia* s.l., 24 new species were described in the last five years (Tab. 1). Most of the new species were found in Southeast Asia. This is due to active mycologists working with this group in these parts of the world. Nevertheless, more new *Hyphodontia* s.l. species could also be expected from other regions. Further new species might be suspected while studying difficult species, or species complexes. The species complex of *Lyomyces sambuci* was one topic of this thesis (Yurchenko et al. 2017), as well as the question whether *Lyomyces palmae* and *Hyphodontia microspora* are one or two species (Riebesehl and Langer 2017). But there are still more difficult species, for which a deeper investigation could reveal new species, e.g. *Lyomyces pruni* and *Xylodon bugellensis* (Ces.) Hjortstam & Ryvarde. This is also a case where it is unclear whether they are two or only one species. In Riebesehl and Langer (2017), the concepts of Eriksson and Ryvarde (1976) and Langer (1994) are followed, with a synonymization of the species. But other scientists treat them as two species (e.g. Hjortstam 1991). A molecular analysis with new sequences, could be helpful here. Another example is *Hyphodontia alutaria* and *Hyphodontia pallidula*. These taxa were generally counted as being different species, but phylograms show a high similarity in their ITS sequences (e.g. Riebesehl et al. 2015), which would normally point to them being one species. In addition, the morphological differences are not very large. Riebesehl and Langer (2017) still used the

genus *Palifer*, because currently, it is impossible to base a decision on DNA sequences. Only one ITS sequence is available so far. An additional study is important to resolve the status of *Palifer*: Is it an independent genus, or should it be integrated into *Xylodon*? Several more instances in *Hyphodontia* s.l. are known to be unsolved.

Table 1: Newly described species in *Hyphodontia* s.l. from the last five years (2013-2017)

Year	Species	Country
2013	<i>Lyomyces tenuissimus</i>	Taiwan
	<i>Xylodon anmashanensis</i>	Taiwan
	<i>Xylodon echinatus</i>	Taiwan
	<i>Xylodon subclavatus</i>	Taiwan
2014	<i>Hyphodontia dhingrae</i>	India
	<i>Lyomyces microfasciculatus</i>	China, Taiwan, Vietnam
	<i>Lyomyces vietnamensis</i>	Vietnam
	<i>Xylodon astrocystidiatus</i>	Taiwan
	<i>Xylodon pseudotropicus</i>	China
	<i>Xylodon rhizomorphus</i>	China
2015	<i>Hyphodontia borbonica</i>	La Réunion
2016	<i>Kneiffiella subefibulata</i>	China
	<i>Xylodon dimiticus</i>	China
2017	<i>Hyphodontia bubalina</i>	China
	<i>Hyphodontia chinensis</i>	China
	<i>Hyphodontia mollissima</i>	China
	<i>Hyphodontia mongolica</i>	China
	<i>Hyphodontia reticulata</i>	Japan, Taiwan
	<i>Hyphodontia subtropica</i>	China, Vietnam
	<i>Hyphodontia zhixiangii</i>	Uzbekistan
	<i>Lyomyces allantosporus</i>	La Réunion
	<i>Lyomyces mascarensis</i>	La Réunion
	<i>Lyomyces organensis</i>	Brazil
<i>Lyomyces orientalis</i>	Taiwan	

In conclusion, it can be said that much more research can be imagined, simply to solve the problematic cases already identified, and that it is also conceivable that more new species could be found, especially in biodiversity hotspots or understudied regions.

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List of abbreviations

aff.	affinity to (from latin: affinis)
alt.	altitude
asl.	above sea level
BLAST	Basic Local Alignment Search Tool
BS	bootstrap support
DNA	deoxyribonucleic acid
dupl.	duplicate
e.g.	for example (from latin: exempli gratia)
emend.	revised by (from latin: emendatus)
Fig.	figure
GIS	Geographic Information System
GPS	Global Positioning System
ibid.	in the same place (from latin: ibidem)
ITS	internal transcribed spacer
KOH	potassium hydroxide
LCB	lactophenol cotton-blue solution
leg.	collected by (from latin: legit)
ME	Minimum Evolution
NCBI	National Centre for Biotechnology Information
PCR	polymerase chain reaction
PP	posterior probability
rDNA	ribosomal desoxyribonucleic acid
rLSU	ribosomal large subunit
rRNA	ribosomal ribonucleic acid
s.l.	in the broad sense (from latin: sensu lato)
s.s.	in the narrow sense (from latin: sensu stricto)
s.str.	in the narrow sense (from latin: sensu stricto)
sp.	species (singular)
sp. nov.	new species (from latin: species nova)
spp.	species (plural)
Tab.	table
var.	variety (from latin: varietas)

Contributions from the authors to the publications

This dissertation includes four publications.

2.1 Riebesehl J, Langer EJ, Ordynets A, Striegel MM, Witzany C (2015)

***Hyphodontia borbonica*, a new species from La Réunion. Mycol Prog 14:104. doi: 10.1007/s11557-015-1126-z**

The study was designed by Riebesehl. The collecting of the samples was done by Langer and Barniske, and the description of the new species was elaborated by Riebesehl under assistance of Ordynets and Striegel. The line drawings were made by Riebesehl and Langer, and the photographs by Witzany and Riebesehl. Riebesehl did the laboratory work, followed by the phylogeny. The emendation of the genus was done by Riebesehl and Langer, and the identification key by Riebesehl. The corresponding author Riebesehl wrote the manuscript under assistance of Langer, Ordynets and Witzany.

2.2 Riebesehl J, Langer E (2017) *Hyphodontia* s.l. (Hymenochaetales, Basidiomycota): 35 new combinations and new keys to all 120 current species. Mycol Prog 16(6):637–666. doi: 10.1007/s11557-017-1299-8

This study was designed by Riebesehl. Riebesehl did the laboratory work, followed by the phylogeny. The list of species was done by Riebesehl and the new combinations by Riebesehl, Langer and Yurchenko. The identification keys were constructed by Riebesehl and the emendations of the genera by Riebesehl and Langer. The corresponding author Riebesehl wrote the manuscript under assistance of Langer.

2.3 Yurchenko E, Riebesehl J, Langer E (2017) Clarification of *Lyomyces sambuci* complex with the descriptions of four new species. Mycol Prog 16(9):865–876. doi: 10.1007/s11557-017-1321-1

This study was designed by Yurchenko and Riebesehl. The collecting of the samples was done by Yurchenko, Riebesehl, Bauer, Chen, Hennen, Schröder, Striegel, E. and G. Langer. The description of the new species was elaborated by Yurchenko under assistance of Riebesehl. The line drawings and the photographs were taken by Yurchenko. Riebesehl did the laboratory work, followed by the phylogeny. The corresponding author Yurchenko wrote the manuscript together with Riebesehl and under assistance of Langer.

2.4 Gafforov Y, Riebesehl J, Ordynets A, Langer E, Yarasheva M, Ghobad-Nejhad M, Zhou LW, Wang XW, Gugliotta AM (2017) *Hyphodontia* (Hymenochaetales, Basidiomycota) and similar taxa from Central Asia. *Botany* 95(11):1041–1056. doi: 10.1139/cjb-2017-0115

The design of the study and the collecting of the samples were done by Gafforov with support from Yarasheva. Gafforov and Ordynets made the morphological examinations and the re-identifications. The photograph was taken by Gafforov and the map by Gafforov and Yarasheva. The laboratory work was processed by Gafforov and the phylogeny by Riebesehl. The identification key was prepared by Riebesehl and Langer. The first author as well as all coauthors contributed to the writing of the manuscript.

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