Reviewing the taxonomy of Podaxis
Conlon, Benjamin H.; Aanen, Duur K.; Beemelmanns, Christine; de Beer, Z Wilhelm; De Fine Licht, Henrik H.; Gunde-Cimerman, Nina; Schiøtt, Morten; Poulsen, Michael

Published in:
Fungal Biology

DOI:
10.1016/j.funbio.2019.01.001

Publication date:
2019

Document version
Publisher's PDF, also known as Version of record

Document license:
CC BY

Citation for published version (APA):
Review

Reviewing the taxonomy of Podaxis: Opportunities for understanding extreme fungal lifestyles

Benjamin H. Conlon a,*, Duur K. Aanen b, Christine Beemelmanns c, Z. Wilhelm de Beer d, Henrik H. De Fine Licht e, Nina Gunde-Cimerman f, Morten Schiøtt g, Michael Poulsen a

a Section for Ecology and Evolution, Department of Biology, University of Copenhagen, Copenhagen, Denmark
b Laboratory of Genetics, Plant Sciences Group, Wageningen University, Netherlands
c Leibniz Institute for Natural Product Research and Infection Biology, Hans-Knoll-Institute, Chemical Biology, Jena, Germany
d Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria, South Africa
e Department of Plant and Environmental Sciences, University of Copenhagen, Denmark
f Laboratory of Genetics, Plant Sciences Group, Wageningen University, Netherlands
g Department of Biology, Biotechnical Faculty, University of Ljubljana, Ljubljana, Slovenia

A R T I C L E   I N F O

Article history:
Received 27 August 2018
Received in revised form 13 December 2018
Accepted 8 January 2019
Available online 11 January 2019

Keywords:
Basidiomycota
Drought
Extremophile
Low water activity
Termitae

A B S T R A C T

There are few environments more hostile and species-poor than deserts and the mounds of Nasutitermitinae termites. However, despite the very different adaptations required to survive in such extreme and different environments, the fungal genus Podaxis is capable of surviving in both: where few other fungi are reported to grow. Despite their prominence in the landscape and their frequent documentation by early explorers, there has been relatively little research into the genus. Originally described by Linnaeus in 1771, in the early 20th Century, the then ~25 species of Podaxis were almost entirely reduced into one species: Podaxis pistillaris. Since this reduction, several new species of Podaxis have been described but without consideration of older descriptions. This has resulted in 44 recognised species names in Index Fungorum but the vast majority of studies and fungarium specimens still refer to P. pistillaris. Studies of Podaxis' extremely different lifestyles is hampered by its effective reduction to a single-species genus. Here we examine the history of the taxonomy of Podaxis before focusing on its extreme lifestyles. From this, we consider how the muddled taxonomy of Podaxis may be resolved; opening up further avenues for future research into this enigmatic fungal genus.

© 2019 The Authors. Published by Elsevier Ltd on behalf of British Mycological Society. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

The fungal genus Podaxis has fascinated scientists and explorers for centuries. Its first apparent depiction (As Fungus melitensis; Fig. 1A) (Boccone, 1697) was accompanied by a description of its collection from Malta, Sicily and Tunisia as well as a recommendation that it is “well suited to the treatment of dysentery” (Boccone, 1697). Linnaeus later described the first species from a specimen collected in India as Lycoperdon pistillare (Fig. 2) (Linnaeus, 1771); before describing a second species, Lycoperdon carcinomale (Fig. 2), from termite mounds on the Cape of Good Hope, South Africa (Linnaeus, 1781). The description of L. carci- nomale included a recommendation that the spores are an effective treatment for “cancerous ulcers” (Linnaeus, 1781; Thunberg, 1785). The third “beautiful species” was described from “a small sandy isle on the Senegal River” by Bosc as Lycoperdon axatum (Fig. 1B; Fig. 2) (Bosc, 1792). It is from here that the taxonomy of Podaxis becomes complicated; challenging any attempt to study the species in detail.

1. Taxonomy

In 1800, there were three described species of the genus we now call Podaxis: L. pistillare, L. carcinomale and L. axatum (Linnaeus, 1771, 1781; Bosc, 1792). However, they were mis-classified as part of the genus Lycoperdon. The two species described by Linnaeus (Linnaeus, 1771, 1781) were sanctioned by Persoon but moved to the genus Scleroderma (Fig. 2) (Persoon, 1801). Subsequently, using the L. axatum specimen described by Bosc (1792), Desvaux described a new genus: Podaxis (Desvaux, 1809). He renamed L. axatum as the generic type species Podaxis senegalensis (Fig. 2) (Desvaux, 1809). Although he made no mention of Linnaeus’ two species (Linnaeus, 1771, 1781), it is possible that any attempt by Desvaux to study these specimens was hampered by ongoing
hostilities between Sweden and France during the Napoleonic Wars; meaning the only specimen available was the one described by the French mycologist Bosc (1792).

Apparently without considering Desvaux’s work, L. pistillare and L. carcinomale were later placed in a new genus: Schweinitzia (Fig. 2) (Greville, 1823a). However, shortly after, it became apparent that the generic name Schweinitzia was already taken and the genus was renamed Cauloglossum (Fig. 2) (Greville, 1823b). Five years later, L. pistillare (now Cauloglossum pistillare) was moved to the genus Mitremyces and named Mitremyces indicus (Fig. 2) (Sprengel, 1827). The three species originally described by Linnaeus (1771; 1781) and Bosc (1792) were now in three different genera: Podaxis, Cauloglossum and Mitremyces (Fig. 2) (Desvaux, 1809; Greville, 1823b; Sprengel, 1827). This was somewhat resolved by Fries who, in 1829, described the family Podaxidei and recognised Podaxis (Desvaux, 1809) as a valid generic name. However, Fries argued that Podaxis was incorrectly derived from the original Greek and that Podaxon would be more grammatically correct (Fries, 1829). He then renamed L. pistillare (a.k.a. Cauloderma pistillare, C. pistillare and M. indica) and L. carcinomale (a.k.a. Cauloderma carcinomale and Cauloglossum carcinomale) as Podaxon pistillaris and Podaxon carcinomalis respectively (Fig. 2). However, without explanation, he renamed L. axatum (Desvaux’s P. senegalensis) as Podaxon calyptratus (Fig. 2) (Fries, 1829); the third new specific name for a single specimen!

After a wild start to the 19th Century, in which three species in the genus we now call Podaxis received seven different generic names in just under thirty years, the renaming calms down following Fries (1829); the only major change being the renaming of the family to Podaxideae (later changed to Podaxaceae) (Corda, 1842). However, several new species were described in the following century. Three new species were described based on specimens collected in Angola from: sand dunes near the ocean (Podaxon loandensis), sand dunes on the banks of a river near Moçâmedes (Podaxon mossamedensis) and sand dunes and forests (Podaxon elatus) (Welwitsch and Currey, 1870). Podaxon arabicus was described from the vicinity of Aden, Yemen (Patouillard, 1897) and Podaxon aegypticus was described from the Sinai Peninsula (Fischer, 1889).

In 1890, the generic name returned to Podaxis when the first monograph of the genus was published (Massee, 1890). In this, Massee identified those species for which multiple names existed whilst also reducing several recently-described species to synonyms and adding two new species to the genus (Massee, 1890). In doing this, Massee identified seven species: Podaxis indica (Fig. 2) (Following Sprengel’s specific name and including Podaxis pistillaris and Podaxis arabisicus), Podaxis carcinomalis (Fig. 2) (including Podaxis elatus), Podaxis axata (Fig. 2) (the fourth specific name for the specimen described by Bosc and including P. senegalensis, Podaxis calyptratus and Podaxis loandensis), Podaxis mossamedensis, Podaxis aegyptica (renaming P. aegypticus), Podaxis farlowii (the first North American Podaxis specimen, collected from New Mexico) and Podaxis emerici (Massee, 1890).

Numerous new species were described in the next 43 years, including Podaxis muelleri from near the dry Gascoyne River in Western Australia (Hennings, 1904), Podaxis termitophilus from termite mounds in Madagascar (Jumelle and Perrier de la Bathie, 1907) and Podaxis argentinius from Argentina (Spegazzini, 1889). By 1933, there appear to have been 25 recognised species of Podaxis, although there were 52 different genus and species names (Morse, 1933), from every continent aside from Europe; even though the first apparent record of the fungus describes it as living in Malta and Sicily (Boccone, 1697). It was at this point that the second monograph of the genus was produced (Morse, 1933). Based on the examination of predominantly North American specimens, only one type specimen and ignoring that the type species was P. senegalensis, almost the entire genus was reduced to a single species: Podaxis pistillaris (Fig. 2). Only P. argentinius, Podaxis patagonicus, Podaxis paolii and Podaxis ferrandii were not reduced to P. pistillaris and, even then, with a note that they were likely to be reduced in the future (Morse, 1933). Although some authors rejected this reduction (Heim, 1939, 1977; Ingold, 1965), the classification was widely adopted (Bottomley, 1948; Doidge, 1950).

Since this reduction, several new species of Podaxis have been described. However, descriptions were often made relative to P. pistillaris without the authors necessarily taking the pre-Morse (1933) species names for Podaxis into account (Ahmad, 1941; Batista, 1950; McKnight, 1985; De Villiers et al., 1989; Moreno and Mornand, 1997; Priest and Lenz, 1999). In 2018, despite over 40
Fig. 2. The name changes of the first three described specimens of Podaxis until their reduction to a single species as Podaxis pistillaris in 1933 (Morse). Images of fruiting bodies are provided for the two type specimens (L. pistillare and L. carcinomale) described by Linnaeus (1771, 1781) for which the location is known (© Permission of The Linnean Society of London). As the location of the type specimen of L. axatum is unknown, we provide the image which accompanied its original description (Bosc, 1792).

2. Ecology

Despite appearing to contain numerous species with a global distribution, most of the descriptions of Podaxis come from dry, sandy, habitats near ephemeral water sources (Hennings, 1904; Morse, 1933), or from the mounds of grass-harvesting termites in the sub-family Nasutitermitinae (Linnaeus, 1781; Zoberi, 1972; McKnight, 1985; De Villiers et al., 1989). Although this suggests that, regardless of habitat, the production of fruiting bodies requires a high availability of moisture, there are very few environmental similarities between the Namib Desert (Johnson et al., 2017) and the interior of a termite mound (Brossard et al., 2007; Field and Duncan, 2013); this further supports the notion that Podaxis is a poly-specific genus (Ingold, 1969; Heim, 1977; Conlon et al., 2016; Medina-Ortiz et al., 2017) and raises the possibility that Podaxis is an ideal model genus for the study of basidiomycete adaptations to extreme biotic and abiotic environments.

2.1. Interactions with termites - an extreme biotic environment

Despite common reports of Podaxis growing on the mounds of Nasutitermitinae (Linnaeus, 1781; Jumelle and Perrier de la Bathie, 1907; Priest and Lenz, 1999; Conlon et al., 2016), the exact nature of the relationship between termites and Podaxis is unknown. Aside from Podaxis and the termites, no large fungi or plants are seen to grow on the mounds of Nasutitermitinae while prokaryotic life is also reported to be scarce (Fig. 1C) (Lee and Wood, 1971). Podaxis fruiting bodies appear to originate from the faeces-lined grass-storage chambers of living termite mounds (Fig. 1D) (Conlon et al., 2016). However, with Podaxis only being reported when its fruiting bodies appear, it is unclear if it has a permanent or transient presence in termite mounds.

If Podaxis is parasitic on termite mounds, it may possess adaptations to overcome the wide range of chemical defences produced by the Nasutitermitinae (Sobotník et al., 2010). These defences include a variety of antimicrobial and cytotoxic compounds (Rosengaus et al., 2000), which impregnate the walls of the mound (Lee and Wood, 1971). However, the production of numerous antimicrobial compounds by Podaxis, such as epicorazine (Fig. 1E) (Al-Fatimi et al., 2006; Feleke and Doshi, 2018), also raises the possibility that the fungus prevents colonisation by other microorganisms and therefore is tolerated by the termites.

2.2. Survival in deserts - an extreme abiotic environment

The interior of a Nasutitermitinae mound contains optimal growth conditions, with high nutrient availability and relatively constant conditions, for any fungus which can overcome termite chemical defences (Brossard et al., 2007; Field and Duncan, 2013). A desert, by contrast, would be expected to contain low nutrient availability with large temperature fluctuations outside of the optimal growing conditions for many fungi (Johnson et al., 2017). Although moisture can be hard to come by in the desert, Podaxis fruiting bodies are often reported shortly after rainfall in gullies where the rainwater can collect (Morse, 1933), near the coast (Welwitsch and Currey, 1870) or in periodically dry river systems; which are supported by a network of aquifers just below the surface (Hennings, 1904; Leonhard et al., 2013). This suggests that desert-living Podaxis can make use of numerous and varied water sources.

To aid its survival in inter-rain periods, Podaxis collected from the Namib Desert, where average annual rainfall is below 60 mm.
and even extreme biotic and abiotic environments. Not only does it provide the possibility to compare between different lifestyles but it can be greatly enhanced by the ability to germinate spores from fungarium specimens into culture (Conlon et al., 2016). In the case of Podaxis, the unusually high optimal-growth temperature of 40 °C (Khan et al., 1979) can help improve germination success by reducing temperature-sensitive contaminants. When permitted by the fungarium, this would allow for a wealth of biodiversity, collected over centuries, to be incorporated into modern-day experiments.

Unfortunately, research into Podaxis is hindered by a lack of information on the species being studied. While genetic evidence can show that there are at least six clades of Podaxis (Conlon et al., 2016; Medina-Ortiz et al., 2017), there is only one type specimen of Podaxis (Podaxis rugospora) (De Villiers et al., 1989) with nucleotide data in the NCBI databases (Conlon et al., 2016). One of the most promising avenues to resolve this is the sequencing of genes or even whole genomes from more type specimens for inclusion in phylogenetic analyses. The resulting tree could then be useful to identify distinct clades with low genetic variability and link these to any type specimens within the clades.

While the inclusion of type specimens in phylogenetic analyses may sound promising, fungaria can understandably be reluctant to allow destructive sampling of valuable type specimens. It is here that the ability to sequence from minute amounts of spores, and particularly the ability to germinate spores into cultures can be crucial. Podaxis spores will readily fall from fruiting bodies in fungarium collections with almost no harm to the specimen itself. DNA for sequencing can be extracted directly from spores or the spores can be germinated making it possible to grow ample amounts of fungal biomass without damaging the fungarium specimen (Conlon et al., 2016). The generation of cultures from fungarium specimens could help establish collaborations between the dried specimens of traditional fungarium collections and fungaria with culture collections such as the DSMZ (Deutsche Sammlung von Mikroorganismen und Zellkulturen), the ATCC (American Type Culture Collection) and the CBS (Centraalbureau voor Schimmelcultures). However, it would be important, where possible, to include the maximum amount of metadata possible to aid any future studies using these strains.

The resolution of the taxonomic confusion in Podaxis could open up a diverse array of new avenues for research. While it is currently not possible to determine the species of Podaxis used in experimental studies, knowledge of the species and lifestyle of a specimen could allow for a much broader understanding of how fungi can adapt to different abiotic and biotic extreme environments. This would be enhanced by the ability to germinate fungarium spores into cultures. With some of the highest concentrations of fungal species diversity on earth found in fungarium collections, it would not only be relatively quick and simple to collect a diverse array of species and specimens but it would also enable the incorporation of a wealth of historical biological information into contemporary experiments and culture collections. Of particular interest could be the secondary chemical compounds which Podaxis appears to produce in abundance (Al-Fatimi et al., 2006; Feleke and Doshi, 2018). Analysis of these compounds could help to illuminate the exact nature of Podaxis’ relationship with termites, how it can survive in a chemically-defended biotic environment and how it survives amid abiotic environments, such as the desert, which experiences extreme fluctuations in temperature and UV radiation. With some of the earliest descriptions of Podaxis recommending its use as a medicine (Boccone, 1697; Linnaeus, 1781), as well as its continued use as a traditional medicine (Muhisin et al., 2012), it is possible that Podaxis produces numerous medically-useful compounds. With Podaxis being so poorly studied it is likely that many of these compounds would be new to science.
Acknowledgements

We are grateful for financial support from the German Research Foundation (DFG, CRC1127 ChemBioSys, and BE 4799/3-1) and the Daimler and Benz Foundation to CB, the Villum Foundation to HHDFL (Grant No. 10122), and the Independent Research Fund Denmark (DFF - 7014-00178) to MP.

References

Fries, E., 1829. Systema Mycologicum. Sumtibus Ernesti Mauritii, Greifswald, Germany.
Hennings, P., 1904. Fungi australiensis II. Hedwigia 43, 187–188.
Linnanen, C., 1771. Manitia plantarum altera generum editionis VI et specierum editionis II. Laurenti Salvi.
Linnanen, C., 1781. Supplementum plantarum* Systematis vegetabilium* editionis decimae tertiae,‘ Generum plantarum* editionis sextae et‘ Specierum plantarum* editionis secundae (quod opus partim C. a LINNE, partim F. EHRHART curaverunt), editum a Carolo a LINNE [fil.]. Impensis Orphanotrophi.
Rottelli, F., 1783. Beschrieven over nogle Planter fra de malabarske Kyst. Copenhagen, Denmark.