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Review

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

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ABSTRACT

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.

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. carcinomale* 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

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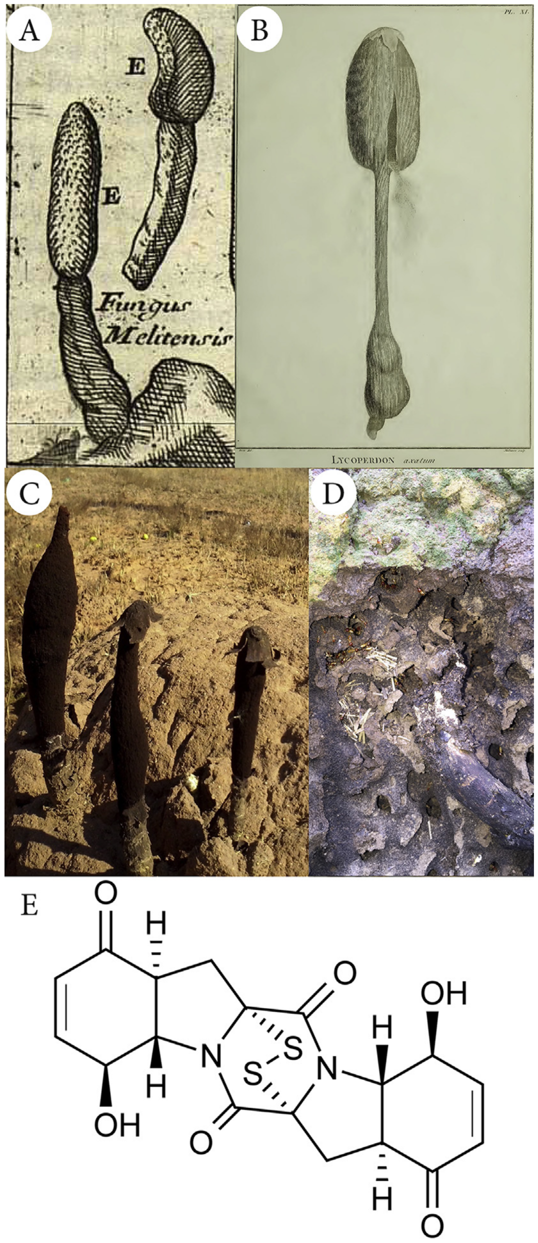

Fig. 1. (A) The first apparent depiction of *Podaxis* (as *Fungus melitensis*) by Boccone (1697). (B) Depiction of *Podaxis senegalensis*/*Podaxis axatus*/*Podaxis calyptratus* (as *Lycoperdon axatum*) by Bosc (1792). (C) *Podaxis* sp. Fruiting bodies emerging from a termite mound in South Africa (© Z. Wilhelm de Beer). (D) *Podaxis* sp. fruiting body originating in the grass storage chamber of a *Trinervitermes* mound in South Africa (From Conlon et al., 2016). (E) An antimicrobial Epicorazine reportedly produced by *Podaxis* sp. (Drawn from: Al Fatimi et al., 2006).

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. *Scleroderma pistillare*, *C. pistillare* and *M. indica*) and *L. carcinomale* (a.k.a. *Scleroderma 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 aegyptiacus* 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 arabicus*), *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. aegyptiacus*), *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, 1899). 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: *P. 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

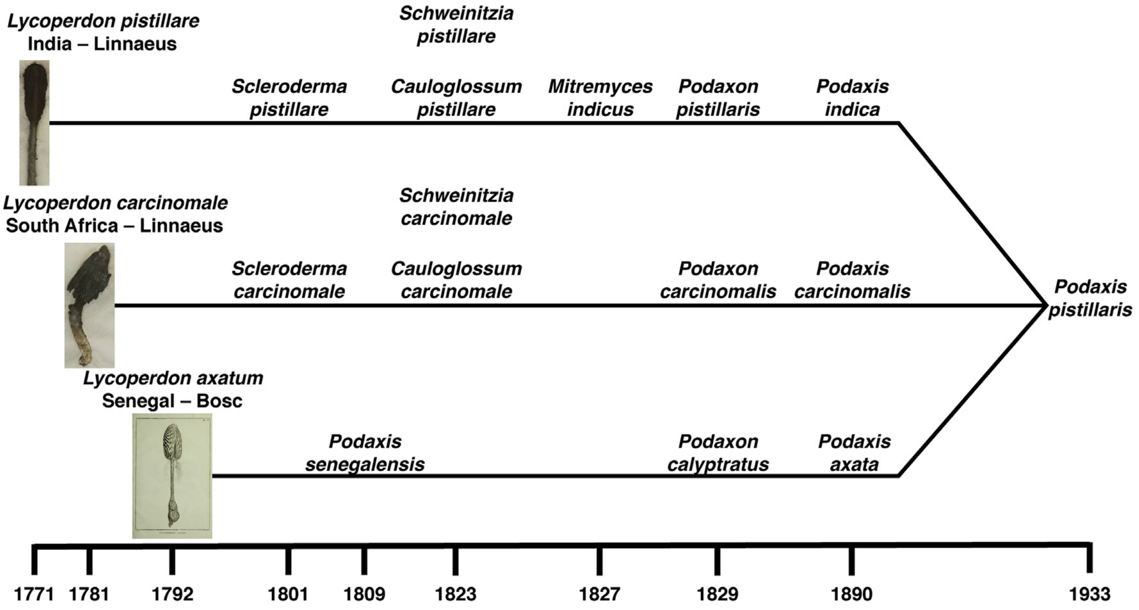

Fig. 2. The name changes of the first three described specimens of *Podaxis* until their reduction to a single species as *Podaxis pistillaris* in 1933 (Morse). Images of fruiting bodies are provided for the two type specimens (*L. pistillare* and *L. carcinomale*) described by Linnaeus (1771, 1781) for which the location is known (© Permission of The Linnaean 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).

historic species names for *Podaxis*, the vast majority of fungarium specimens are labelled as a single, global, polymorphic species surviving in extremely different environments (Morse, 1933; Conlon et al., 2016). Although some recent work has sought to use genetic barcoding to disentangle the confusing taxonomy of *Podaxis* (Conlon et al., 2016; Medina-Ortiz et al., 2017), the lack of genetic data for type specimens makes it difficult to identify whether a phylogenetic clade represents a new species or if it corresponds to one or more previously-described species. The naming of almost every specimen of *Podaxis* as a single species also hinders efforts to understand other aspects of the biology of the genus as it is almost impossible to tell which species is being discussed in the literature. This consideration could be especially important when considering that traditional uses for *Podaxis* fruiting bodies can vary between medicines, poisons and hair dyes (Boccone, 1697; Linnaeus, 1781; Muhsin et al., 2012).

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, 1965; 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 (Šobotník 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

(Johnson et al., 2017), have larger spores with thicker walls than their termite-associated cousins (Conlon et al., 2016). This could help the spores resist desiccation and is likely only one of many adaptations *Podaxis* has to its desert lifestyle. It has also been reported that *Podaxis* cultures grow optimally at 40 °C, a much higher temperature than many non-extremophilic basidiomycetes (Khan et al., 1979), suggesting that this represents another adaptation to life in desert environments. With phylogenetic analyses showing that desert-living *Podaxis* cluster into Old World and New World clades (Conlon et al., 2016), it is possible that each clade experienced a separate evolutionary trajectory and thus exhibits different adaptations for desert life. There is also the possibility that a third, independently evolved, desert clade exists; containing *Podaxis* from desert areas of Australia (Hennings, 1904).

3. Future perspectives

To have several closely-related species exhibiting such extremely different and unusual lifestyles makes *Podaxis* a potentially promising model organism for the study of fungal adaptations to varying and even extreme biotic and abiotic environments. Not only does it provide the possibility to compare between different lifestyles but the existence of multiple separate lineages for each lifestyle, separated by oceans, means that it may also be possible to compare different evolutionary trajectories within lifestyles to test patterns of convergent evolution. Studies of *Podaxis*, and mycology in general, 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 fungal 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 germination of spores from type specimens can be a hugely useful resource for disentangling the taxonomic uncertainty surrounding *Podaxis*. It is, however, less useful when the location of the type specimen is unknown or lost. In this case, it may be possible to identify potential neotypes: new type specimens to replace lost or destroyed pre-existing types. The generation of neotypes would also provide the opportunity to provide much more metadata than is available with many of the older type specimens. Linnaeus' description of the type specimen of *P. pistillaris* is a particularly good example of where environmental metadata is lacking from an original type description as the only location information provided is: “India” (1771). Considering that Linnaeus was writing at a time when “India” included modern-day India, Pakistan and Bangladesh, this narrows the collection location of the *P. pistillaris* type specimen down to just over 4,300,000 Km^2 including vastly different environmental conditions. However, even when the fungarium record may be lacking, it is not always impossible to identify where an original specimen may have been collected. Through a combination of detective work and citizen science, we have already had some success in collecting *Podaxis* specimens from the location of the 19th century explorer William Burchell's camp site in South Africa (Buys et al., 2018), where he painted a *Podaxis* fruiting body. While, to our knowledge, the fruiting body in the painting did not become a type specimen, this highlights the potential of using citizen science to both aid in the discovery of fruiting bodies and for collecting potential neotypes from the same location of the original type when the type specimen has been lost. Through the analysis of spore morphology, which can differ significantly between phylogenetic clades (Conlon et al., 2016), it should then be possible to determine how similar a new specimen is to descriptions of the original type. With the description of the type specimen of *P. pistillaris* including a note that it was collected in India by König (Linnaeus, 1771), it may be possible to use similar methods to narrow down the collection location of this specimen. Based on descriptions of König's travels (Rottbøll, 1783), it seems likely that the collection location of the type specimen of *P. pistillaris* was in Southern, modern-day, India.

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 arid 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 (Muhsin 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.

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