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A Review of Bambusicolous Ascomycetes

Dong-Qin Dai, Li-Zhou Tang and Hai-Bo Wang

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Abstract

Bamboo with more than 1500 species is a giant grass and was distributed worldwide. Their culms and leaves are inhabited by abundant microfungi. A documentary investigation points out that more than 1300 fungi including 150 basidiomycetes and 800 ascomycetous species with 240 hyphomycetous taxa and 110 coelomycetous taxa are associated with bamboo. Ascomycetes are the largest group with totally 1150 species. Families *Xylariaceae* and *Hypocreaceae*, which are most represented, have 74 species and 63 species in 18 and 14 genera, respectively, known from bamboo. The genus *Phyllachora* with a maximum number of species (22) occurs on bamboo, followed by *Nectria* (21) and *Hypoxylon* (20). The most represented host genera *Bambusa*, *Phyllostachys*, and *Sasa* are associated by 268, 186, and 105 fungal species, respectively. The brief review of major morphology and phylogeny of bambusicolous ascomycetes is provided, as well as research prospects.

Keywords: bamboo fungi, pathogens, morphology, phylogeny

1. Introduction

Bamboo, as the largest member of the grass family *Poaceae*, plays an important role in local economies throughout the world. They are used in furniture and construction, or as food for human and animals like panda. Bamboo is even used in Chinese traditional medicine for treating infections and healing of wounds [1]. Bamboo species is distributed in diverse climates, from cold mountain areas to hot tropical regions. They have very little natural toxicity and, therefore are easily prone to fungi and insect attacks [2]. It is reported that more than 1100 species of fungi have so far been described or recorded from bamboo host worldwide [3]. These include ca. 630 ascomycetes, 150 basidiomycetes, and 330 asexual morph taxa (100 coelomycetous and 230 hyphomycetous species) [3]. Bamboo fungi are important to agricultural and economic development, such as *Phallus indusiatus* Vent., which is the delicious edible

mushroom and usually called as “bamboo pith.” It has been cultivated worldwide and brings a high economic income. Some of bamboo fungi, however, are pathogens, most of which are ascomycetes. In this chapter, a review of bamboo ascomycetes is provided herein.

2. Importance of bamboo ascomycetes

Cultivation of economically important bamboos is often threatened by fungal infection and diseases which eventually result from serious damages on bamboo cultivation [4]. A number of foliage diseases (e.g., leaf spots and leaf blight) of bamboos have been recorded. However, fungi cause comparatively less damage to bamboo than culm diseases [5]. For example, during 1988–1990, 5300 hectares of bamboos were affected by *Balansia take* (Miyake) Hara which occurred on bamboo culms in Fujian, China. More than 200,000 bamboos were cut down and burned to prevent the pathogen from spreading. However, this caused serious economic losses. In 1960, Hino and Katumoto explained that the relative importance of different diseases affecting bamboos is difficult to assess because of the general lack of information accompanying the disease records [4]. Thus, pathologists have now started paying attention on the research of bamboo pathogens. A book entitled *Diseases of bamboos in Asia: an illustrated manual* listed 122 fungal diseases in Asia region, with 100 records in India and 15 in Thailand [5]. In China, 183 fungal pathogens associated with bamboo were recorded [6, 7]. Numbers of ascomycetous fungi recorded as bamboo pathogens were quite high. However, in the absence of molecular data, most of the fungal names recognized remained artificial. A sizable number of taxa were not even identified up to species level.

Shiraia bambusicola Henn. is one of the famous bamboo pathogens because of its medicinal value. The fungus produces large, pinkish ascostromata on living bamboo branches (**Figure 1**). Their fruiting bodies, as a traditional Chinese medicine, are used for curing rheumatoid arthritis [8], as well as extracting the metabolite, hypocrellin [9], which has promising applications



Figure 1. Ascstromata of *Shiraia bambusicola* collected from China.

in photodynamic therapy (PDT) [10] and in anticancer treatments [11]. Another well-known Chinese medicinal ascomycete is *Hypocrella bambusae* (Berk. & Broome) Sacc. This fungus produces similar ascostromata with *S. bambusicola* on branches of *Sinarundinaria* spp. Their ascostromata are also used to extract hypocrellin A and hypocrellin B. It is reported that hypocrellin B can be used to evaluate antiviral activity against the human immunodeficiency virus (HIV-1) [12]. In China, a costly medicinal unguent named Bamboo Parasitic Fungus Ointment is made of hypocrellin B. *H. bambusae* contains higher hypocrellin than that of *S. bambusicola*. Index Fungorum [13] recorded that the current name of this fungus is *Pseudonectria bambusae* (Berk. & Broome) Höhn. Without the full morphological study and molecular data in GenBank, its taxonomic placement still remains confused. Therefore, the study of taxonomy and phylogeny of bamboo fungi is urgently needed to be carried out to clarify these undetermined and confused taxa.

3. Bamboo ascomycetes: history

The term “fungorum bambusicolorum” (bambusicolous fungi), was first used by Iwao Hino [14], though the author did not give a definition. “Bambusicolous” means “living on bamboo” [3]. Kevin D. Hyde and colleagues in 2002 defined bambusicolous, which embodies fungi growing on any bamboo substrates, including leaves, culms, branches, sheathes, flowers, rhizomes, and roots [3]. Subsequently, the phrase “Bambusicolous fungi” has been widely used by mycologists worldwide [15, 16].

Lembosia Lévillé is the first mycologist, who mentioned the presence of a fungus on bamboo. In 1845, he described *Roumegueria goudotii* (Lév.) Sacc. ex Clem. & Shear (Basionym: *Dothidea goudotii* Lev.) occurring on leaves of *Chusquea* sp. and *Sphaeria bambusae* Lev. collected from the culms of *Bambusa bambos* (L.) Voss, in Tolima, Columbia [17]. Later, this author introduced two new species *Asterina microscopica* Lev. and *S. hypoxantha* Lev. from the leaves of *Chusquea* sp. and culms of *B. bambos*, respectively, in 1846 [18].

In 1854, Miles J. Berkeley recorded *Hypoxylon fuscopurpureum* (Schwein.) Berk. from *Phyllostachys* sp. and *Sasa* sp. [19]. The next year, Jean P.F.C. Montagne introduced a new species *S. fusariispora* Mont. on leaves of *Bambusa* sp. [20]. During 1871–1880, eight new ascomycetes were described from bamboo host, and between 1881 and 1920, the numbers got increased up to more than 100 species (Figure 2). However, the number of newly described species declined before and after the Second World War [3] (Figure 2). Nevertheless, during 1951–1990, publications of new species on bamboo got increased dramatically (Figure 2). Iwao Hino and Ken Katumoto made an earlier significant contribution on bambusicolous fungi during 1960–1970s, by recording 104 new species of ascomycetes [4, 21–29]. In 1961, Iwao Hino wrote *Icones fungorum bambusicolorum japonicorum*, and recorded 460 ascomycetous species worldwide, of which 175 species were from Japan [30]. In the following years, more records and checklists of fungi on bamboo were carried out by mycologists. Petrini Orlando and colleagues in 1989 mentioned 63 records from France [31]. Ove E. Eriksson and Yue Jinzhu published *Bambusicolous pyrenomyces, an annotated checklist* and listed 587 ascomycetous taxa in 1998 [32]. A checklist for 104 species from China is provided in 1999 by [33].

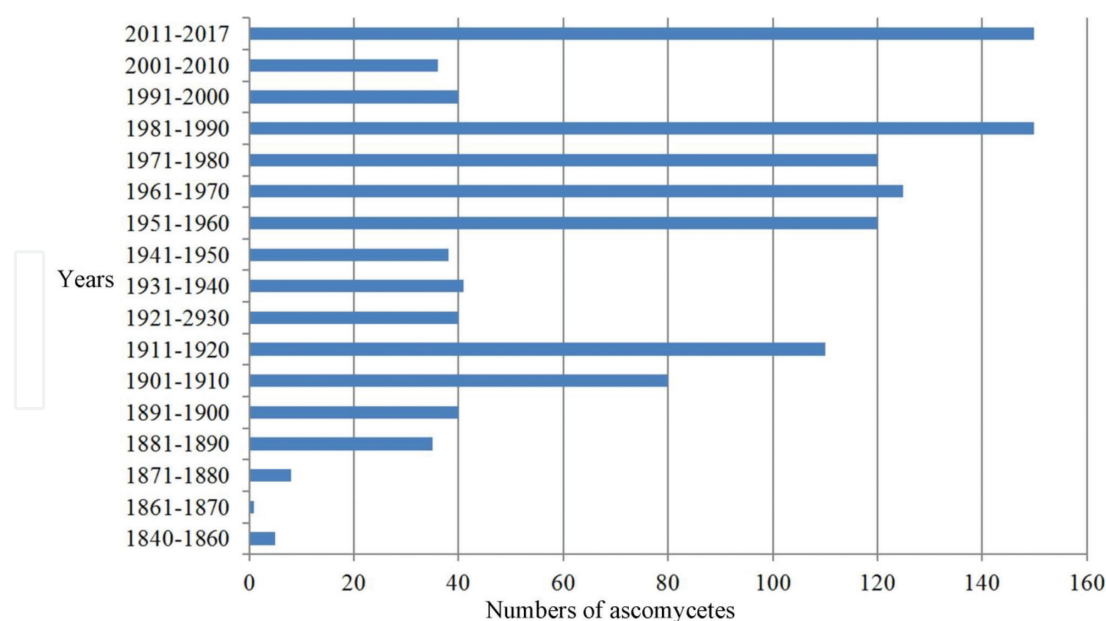


Figure 2. Number of fungi described from bamboo until 2017.

Recent contributions to the knowledge of bamboo-associated ascomycetes were the following. An article in 2000 reviewed 189 species of fungi, of which were 80 ascomycetes, 40 coelomycetous, and hyphomycetous fungi on bamboo substrates [34]. Kevin D. Hyde and colleagues reviewed bamboo fungi in detail in 2002 [3]. A total of 80 fungi were recorded on submerged bamboo in 2003, see [35].

During 2003–2008, the Japanese mycologists carried out a series of studies on bambusicolous fungi in Japan and introduced around 25 new taxa based on the morphological characters [15, 36–42]. In 2007, authors analyzed molecular diversity of bamboo-associated fungi from Japan, based on 257 endophytes strains, isolated from bamboo tissues; however, most isolates were not identified to species level [43]. Until 2009, the significant phylogenetic analysis was first used to classify the new taxa by [44].

Currently, during 2011–2017, approximate 145 new species and new records belonging to 65 genera, 37 families have so far been described or reported by mycologists [16, 45–52] based on taxonomic and phylogenetic analyses. In the short period of 6 years, six new families viz. *Anteagloniaceae* K.D. Hyde & Mapook [53], *Bambusicolaceae* D.Q. Dai & K.D. Hyde [54], *Occultabambusaceae* D.Q. Dai & K.D. Hyde [3], *Parabambusicolaceae* Kaz. Tanaka & K. Hiray [52], *Pseudoastrosphaeriellaceae* Phookamsak & K.D. Hyde [55], *Roussoellaceae* J.K. Liu et al. [56]. and 21 new genera viz. *Amphibambusa* D.Q. Dai & K.D. Hyde, *Bambusaria* Jaklitsch et al., *Bambusicola* D.Q. Dai & K.D. Hyde, *Bambusistroma* D.Q. Dai & K.D. Hyde, *Botryobambusa* Phook., J.K. Liu & K.D. Hyde, *Brunneoclavispora* Phook. & K.D. Hyde, *Embryonispora* G.Z. Zhao, *Flammeascoma* Phook. & K.D. Hyde, *Gregarithecium* Kaz. Tanaka & K. Hiray, *Kalmusibambusa* Phookamsak, Tennakoon, *Multilocularia* Phook., Ariyaw. & K.D. Hyde, *Neoanthostomella* D.Q. Dai & K.D. Hyde, *Neogaeumannomyces* D.Q. Dai & K.D. Hyde, *Neoramichloridium* Phookamsak et al., *Neophiosphaerella* Kaz. Tanaka & K. Hiray., *Neoroussoella* J.K. Liu, Phook.

& K.D. Hyde, *Occultabambusa* D.Q. Dai & K.D. Hyde, *Parabambusicola* Kaz. Tanaka & K. Hiray, *Pseudoastrophaeriella* Phookamsak et al., *Pustulomyces* D.Q. Dai & K.D. Hyde, *Seriascoma* Phook., D.Q. Dai & K.D. Hyde, associated with bamboo substrates were introduced by the natural classification [16, 45, 46, 52, 53, 55, 57–62].

4. Major morphological characters of bamboo ascomycetes

The morphological characters are important in fungal identifications. Most fungi produce their fruiting bodies on hyphae with two phases of reproductions (sexual and asexual reproduction). Thus, when an ascomycetous fungus bears its fruiting body by sexual reproduction, it usually produces an ascoma (**Figure 3**), and on the other hand, it produces either a conidioma or hyphomycetous fruiting structures. The major morphological characters of sexual morph are the type of ascomata, hamathecium, asci, and ascospores, and those of asexual morph are conidiomata, conidiophores, and conidiogenous cells [63, 64].

4.1. Morphological characters of sexual morph

4.1.1. Ascomata

The ascomata of bambusicolous fungi have various types, no matter what shapes or colors. They can form on bamboo leaves, culms, or even sheathes (**Figure 4**), with the positions being immersed, erumpent, or superficial (**Figure 5**). Some ascomata are stromatic, with unilocule to multilocules. Ascomata produce asci and ascospores within, when mature. An ostiole, where ascospores release, is commonly present at the top of an ascoma. Peridium is the wall of an ascoma and usually is composed of several layers of angular cells. The hamathecium is the sterile tissue, formed by hyaline filaments which are called paraphyses.

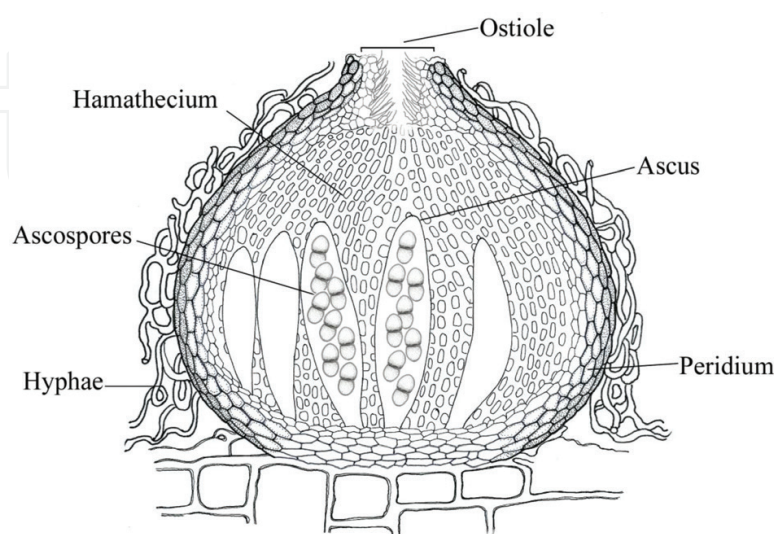


Figure 3. Line drawing of a fruiting body (ascoma) of sexual morph of ascomycete.



Figure 4. Ascomata on different bamboo substrates. (a), (b) on bamboo leaves. (c) on bamboo sheath. (d) on bamboo culm.

4.1.2. Asci

The morphology of asci is particularly of two major types, unitunicate and bitunicate (**Figure 6**). Asci are produced within the ascomata and act as platforms from which the spores are launched. However, some asci release the ascospores passively by dissolving the ascal wall at maturity, rather than active spore-shooting mechanism. Asci usually bear eight ascospores, though sometimes with four or six, and occasionally producing multiple numbers of ascospores.

4.1.3. Ascospores.

The ascospores of bambusicolous fungi exhibit a variety of shapes (**Figure 7**). The common shapes are ellipsoidal, fusiform, filiform, and so on. The color of ascospores can be hyaline, pale brown, brown to dark brown. The ascospores usually are single-celled or have one to two septa and sometimes multiseptate, like muriform spores. Their surfaces are smooth, striate to verrucose, or covered by a sheath.

4.2. Morphological characters of asexual morph.

The asexual morph of ascomycetous bambusicolous fungi is coelomycetous or hyphomyceteous [45–48], as in the asexual morph of *Bambusicola* and *Apiospora* Sacc. (\equiv *Arthrimum* Kunze)

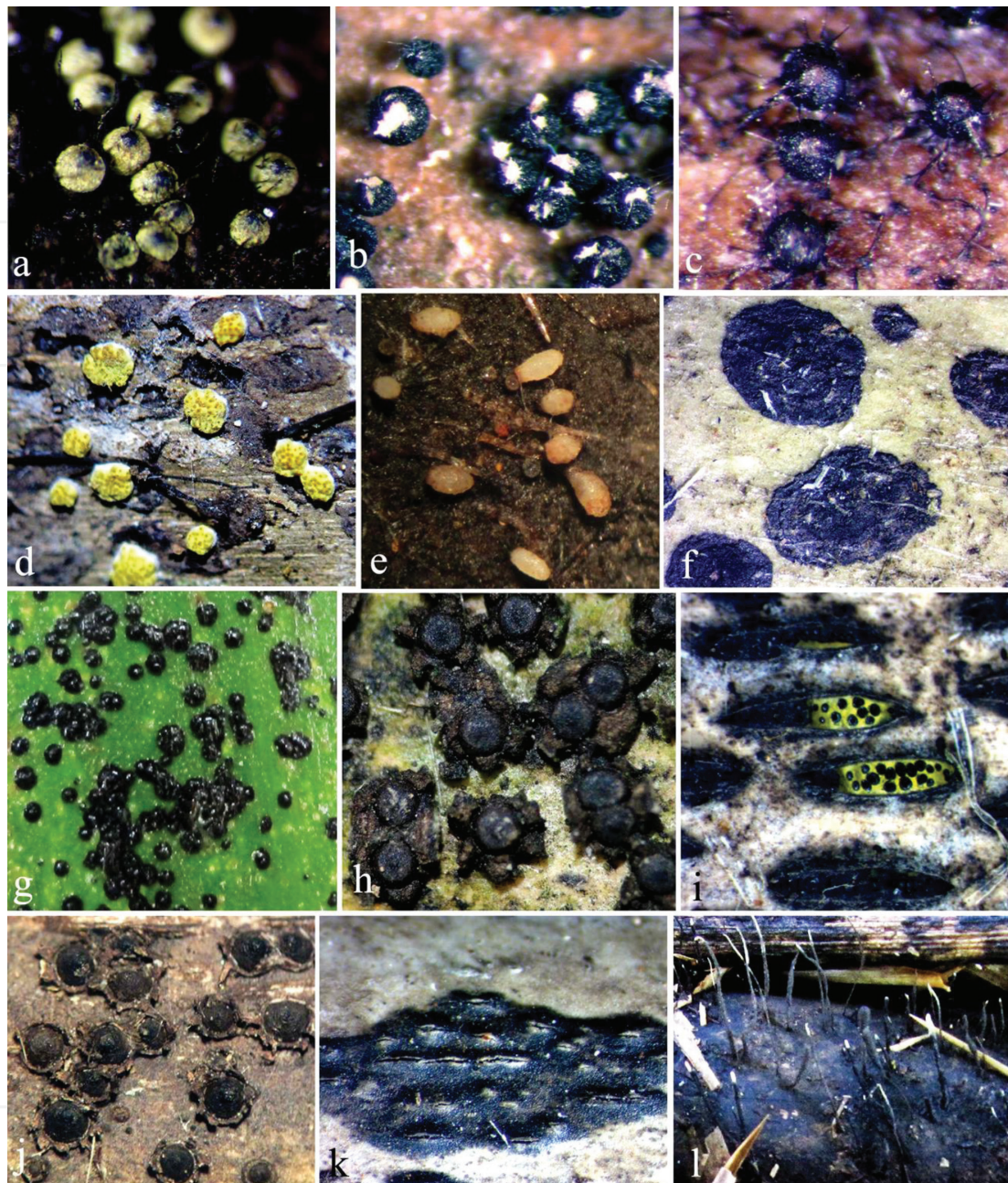


Figure 5. Various types of ascomata on bamboo. a–g, l: superficial ascomata; h–j: erupted ascomata; k: immersed ascomata; a–c, e, h: perithecia; d: stromata; f, g: flatten ascostromata; i: multiloculate stroma; j: conical stromatic ascomata; k: stromata; l: *xylarioid* stromata.

[16, 45]. The major morphologic characters are conidiomata, conidiophores, and conidiogenous cells. In the coelomycetous fungi, the conidia develop in a growing cavity, called conidiomata which can be acervuli, pycnidia, or sporodochium-like structures [64]. For hyphomycetous fungi, a conidium develops directly on the conidiophores which may be mononematous or synnematus and bear a single or more conidiogenous cells which usually are holoblastic, enteroblastic, phialidic, annelidic, or tretic. Conidium ontogeny has long been used as an

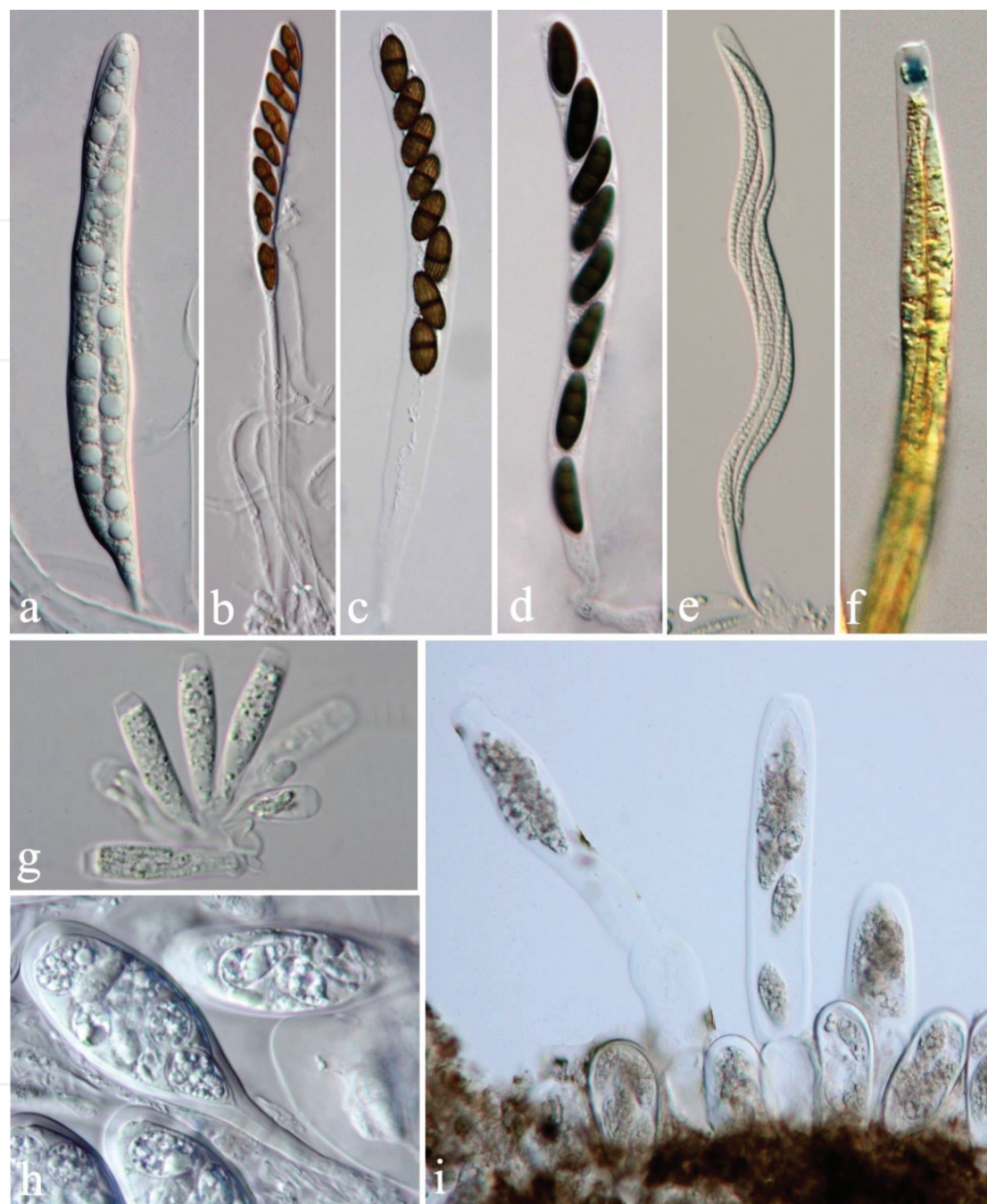


Figure 6. Asci types. a, b, c, h: bitunicate asci (note in b, jack-in-a-box spore release mechanism). d, e: unitunicate asci; f: unitunicate ascus with a special elastic ring at the tip; g: unitunicate asci with a flat apex; h: bitunicate ascus with a long narrow basal portion; i: fissitunicate asci.

important taxonomic feature in the diagnosis of conidial fungi [65]. Mostly, the conidiophores of coelomycetous fungi are reduced to conidiogenous cells, when they grow on the host substrate. However, some of them remain hyphomycetous (producing free conidiophores) on culture, as in *Arthrimum* [51].

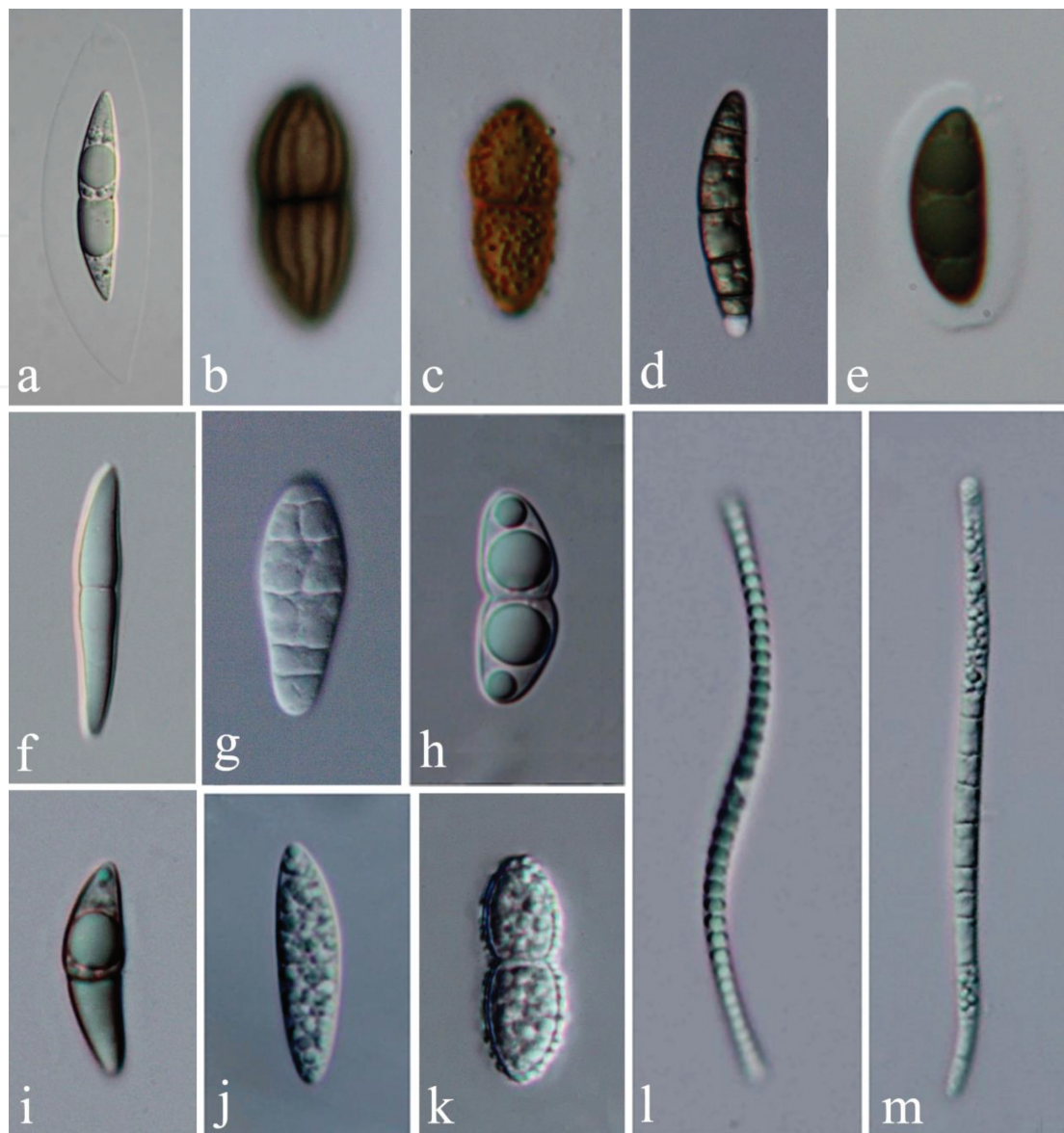


Figure 7. Ascospores types. a, e: ascospores surrounded by a sheath; b: striate ascospore; c, k: verrucose ascospores; d: dark brown, 6-septate ascospore; f, i, j: fusiform ascospores; g: muriform ascospore; h: smooth-walled ascospore; l, m: filiform ascospores.

5. Bamboo ascomycetes taxonomic distribution

The ascomycetes on bamboo are very diverse, together with their asexual morphs. In [30], the author recorded 460 species belonging to 218 genera in 43 families from all over the world. A reference [3] reported 630 species distributed in 121 families and 436 genera within ascomycota. According to our investigation on the basis of the current references, 800 ascomycetous species (**Figure 8**) belonging to 465 genera within 128 families were documented.

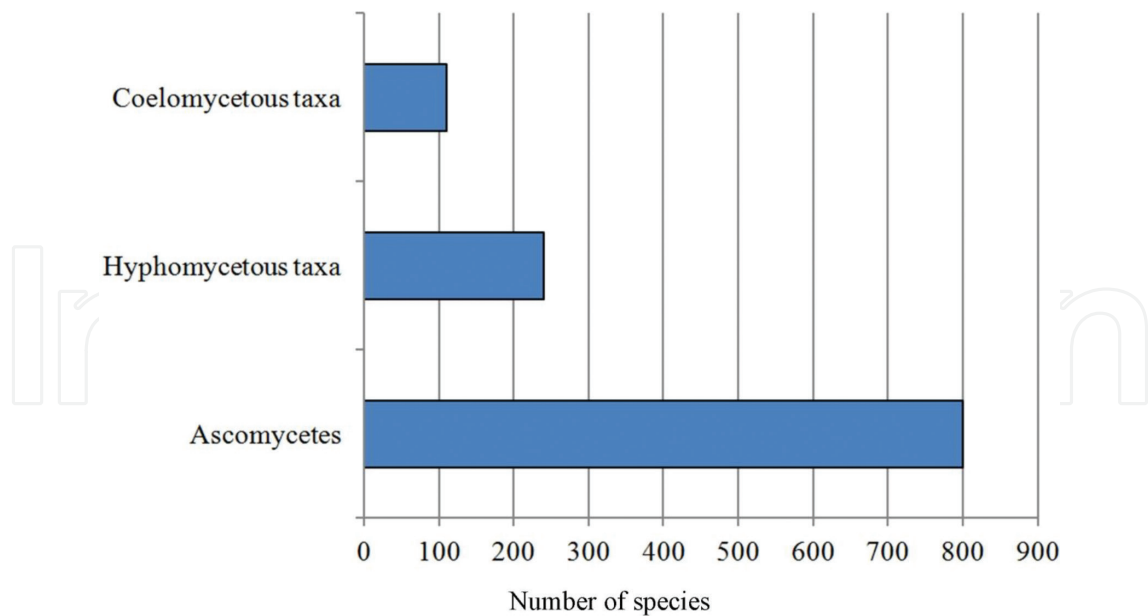


Figure 8. Numbers of ascomycetous, coelomycetous, and hyphomyceteous species on bamboo.

Families of *Xylariaceae* and *Hypocreaceae*, which are most represented, have 74 species and 63 species in 18 and 14 genera, respectively, known from bamboo (**Figures 9** and **10**). This was followed by the families, *Phyllachoraceae* and *Lasiosphaeraceae*, with 35 species in 9 genera and 33 species in 10 genera, respectively. *Roussoellaceae* with 32 species, *Clavicipitaceae* with 28

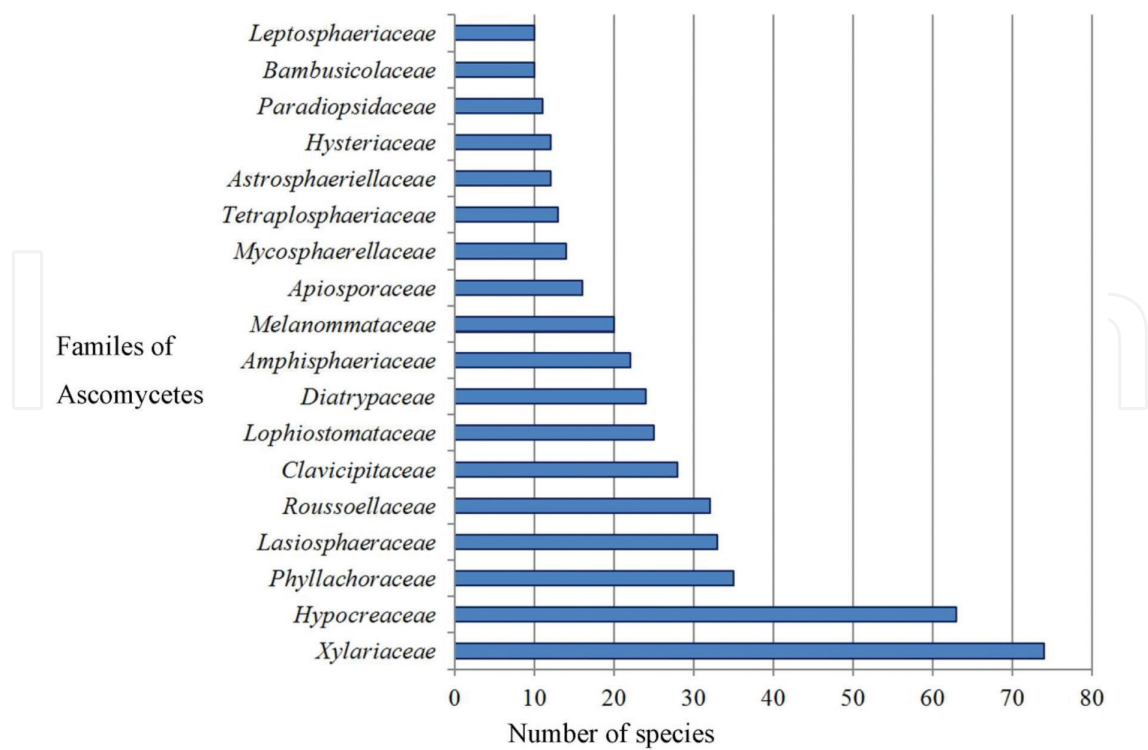


Figure 9. Ascomycete families with more than 10 recorded species on bamboo until 2017.

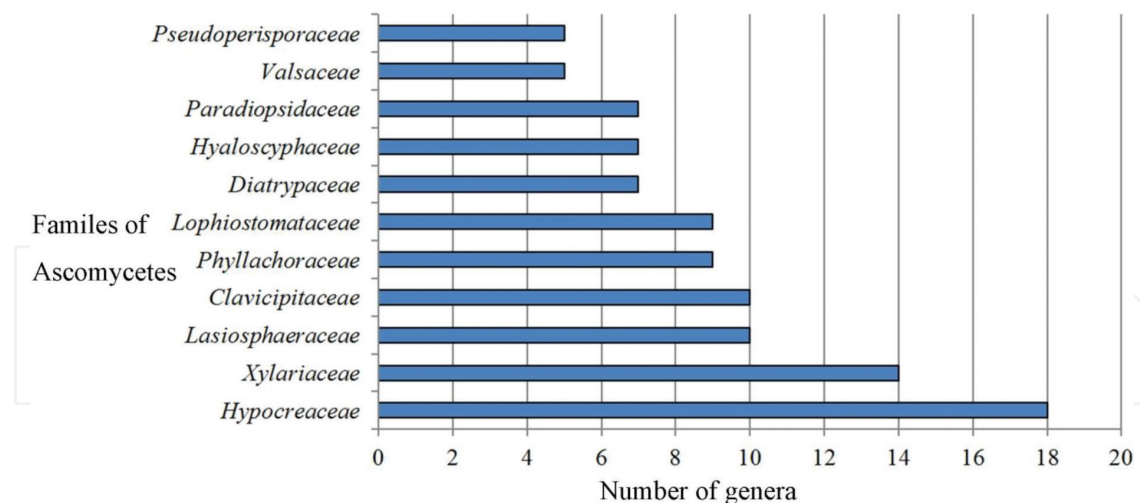


Figure 10. Ascomycete families with more than five genera recorded on bamboo until 2017.

species, *Lophiostomataceae* with 25 species, *Diatrypaceae* with 24 species, *Amphisphaeriaceae* with 22 species, and *Melanommataceae* with 20 species are the next common families on bamboo (Figure 9).

The genus *Phyllachora* with a maximum number of species (22) occurs on bamboo, followed by *Nectria* (21) and *Hypoxylon* (20) (Figure 11). *Phyllachora* species are the commonly known fungi on the grass families [3]. *Rosellinia* has hundreds of epithets listed, with 18 species occurring on bamboo. *Roussoella* is a well-known genus on bamboo and palm hosts, with 17 species known from the bamboo. Genera such as *Didymosphaeria* with 15 species, *Anthostomella* with 14, *Arthrinium* with 16, *Hypocrea* with 11, and *Astrosphaeriella* and *Chaetosphaeria* with 10 are also seen on bamboo. *Bambusicola* is a new genus introduced by [45] and contains 10 species as well found on bamboo culms during 2012–2017.

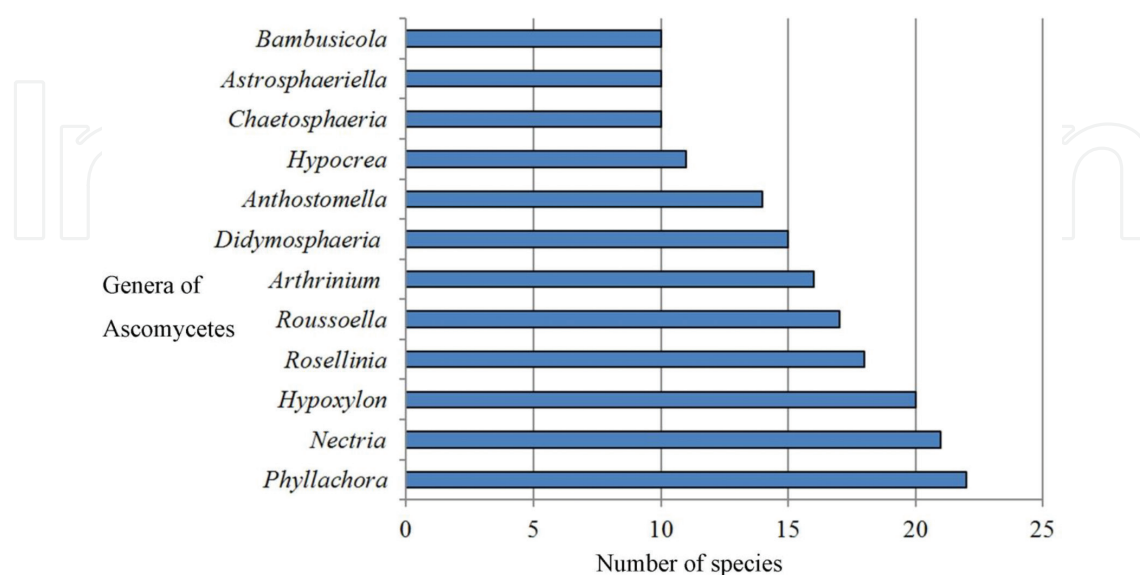


Figure 11. Ascomycetous genera with more than 10 recorded species on bamboo until 2017.

6. Bamboo ascomycetes: host distribution

Figure 12 showcases a picture of higher diversity of ascomycetes on the substrate genus *Bambusa*. More than 260 ascomycetous species are so far recorded from host *Bambusa*. This may be due to that the authors artificially treated mostly bamboo host names as *Bambusa* spp. The next bamboo genus with a higher fungal diversity is *Phyllostachys* with around 180 fungal species. *Phyllostachys* is one of the most common genera of bamboo. This may be the possible reason why it yielded a higher number of fungal taxa. There are 105 ascomycetous species occurring on *Sasa*, 73 on *Arundinaria*, 60 on *Chusquea*, and 56 on *Pleioblastus*. Such high species diversity at the subfamily level (*Bambusoideae*) undoubtedly has a significant impact on species numbers [3].

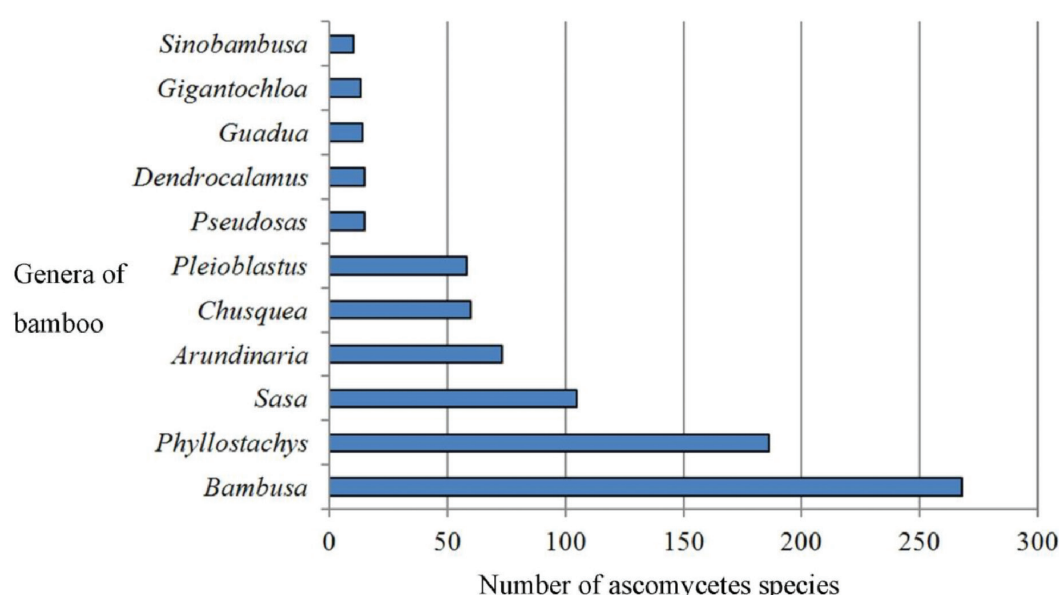


Figure 12. Bamboo genera with more than 10 recorded ascomycetous species until 2017.

7. Bamboo ascomycetes: tissue specificity

It is reported that most fungi grow on bamboo culms (514 fungal species) and leaves and only few recorded species from shoots, roots, or inflorescences [3]. An update of bamboo tissue types with their fungal species number is shown in **Figure 13** and according to which 665 fungal species have been collected from bamboo culms and 216 species were recorded from leaves, followed by sheaths (19 species) and branches (14 species). It is unknown whether fungi are tissue specific or are simply recurrent on certain bamboo tissues [3]. Most bamboo pathogens affect leaves, although a large number of ascomycetes (e.g., *Roussoella* spp. and *Astrosphaeriella* spp.) have been reported on decaying culms or branches.

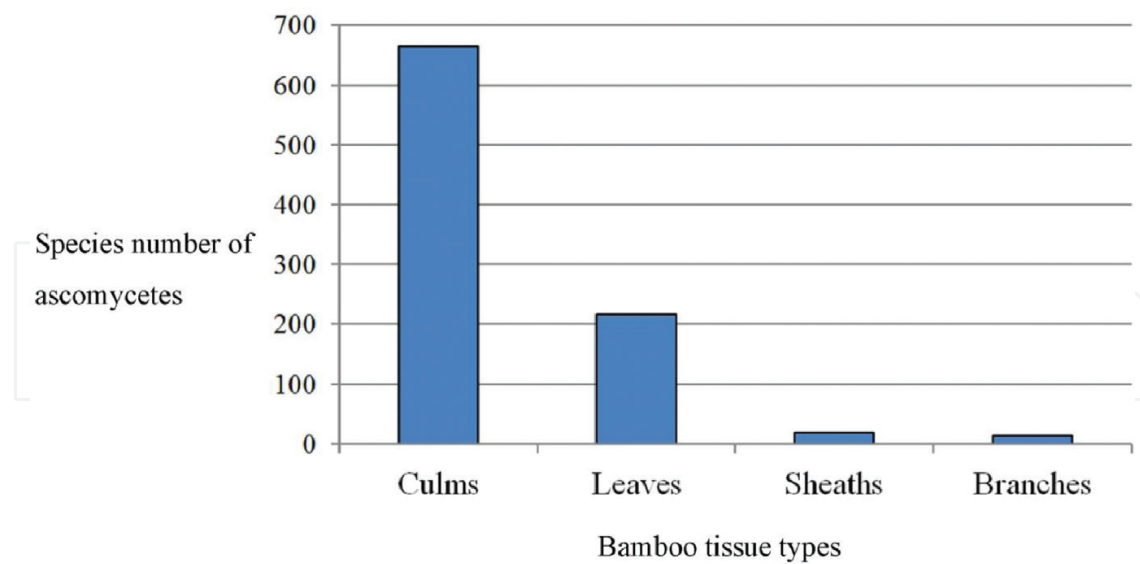


Figure 13. Bamboo ascomycetes: distribution by tissue types until 2017.

8. Phylogeny of bamboo ascomycetes

Phylogenetic analysis has been widely used to study the evolution and relationships among fungal individuals or groups. It is the modern method to clarify fungal species or fungal higher level placements (viz. genus, family, order, etc.). Initially, the studies of bamboo ascomycetes were carried out only based on the morphologic examinations. At the beginning of the twenty-first century, Japanese mycologists made the first contributed acknowledge on bamboo ascomycetes identifications and introduced a new fungal family to accommodate five new genera founded on bamboo [52]. To evaluate the validity of fungal taxa and clarify their phylogenetic relationships, the combined sequences of data with multi-genes (LSU (large subunit rDNA), SSU (small subunit rDNA), TEF (translation elongation factor 1- α gene region), and beta-tubulin) were firstly used to make the phylogenetic trees for bamboo-associated ascomycetes in [16]. Following, more new species, genera, and several new families were established by Thai and Chinese researchers based on morphology-phylogeny and the linking of sexual-asexual morphs [45, 55]. In their studies, ITS (internal transcribed spacers) and beta-tubulin genes were usually used to indentify fungal species like species in *Arthrinium* and *Myrothecium* [16, 51] and LSU, SSU, TEF, and RPB2 (RNA polymerase II second largest subunit) were used to clarify the relationships among genera, families, and orders [16, 52]. The evolution study of bamboo ascomycetes has not been carried out yet, probably due to most old species having no molecular data. More than 800 ascomycetous species with 240 hyphomycetous taxa and 110 coelomycetous taxa are so far recorded on bamboo; however, only less than 180 species have available sequences. Fresh specimens are required to recollect, and the existing species are waiting for reexamination or epitypification.

9. Research prospects of bamboo ascomycetes

Currently, 1300 fungi have been recorded on bamboo substrates. These are including 150 basidiomycetes [3], 800 ascomycetous species, 240 hyphomycetous taxa, and 110 coelomycetous taxa. It provides large opportunities on the utilization of fungi on bamboo. For example, species in *Hypoxylon* Bull., which form large stromata, can be easier to see on bamboo culms. In the recent years, a new secondary metabolite named lenormandins, which are further representatives of the well-known azaphilones [66], was found from *Hypoxylon* spp. More than 18 species in *Hypoxylon* have been occurred so far on bamboo (**Figure 11**). There may be some other interesting unknown azaphilones in *Hypoxylon* species, which may still wait for extraction. Numerous fungi from bamboo were documented, and some pathogens were isolated as well, such as *Arthrinium phaeospermum* (Corda), M.B. Ellis, and *Phyllachora graminis* (Pers.) Fuckel. Approximately 300 bamboo fungal diseases were so far reported [5–7, 67], which provides the essential step to understand ecosystem communication [3]. It is showed that some bamboo ascomycetes have a high value in medical treatment, such as *Engleromyces goetzi*, *H. bambusae*, and *S. bambusicola*. However, their effective compounds can be only obtained from stromata, which cannot be cultivated successfully at the moment [68]. The phylogenic relationship between *H. bambusae* and *S. bambusicola* needs to be carried out to understand the reason why *H. bambusae* produces more hypocrellin than the latter. Many interesting and subsequent studies on bamboo ascomycetes are still awaiting and needs to be conducted, and large numbers of new ascomycetous taxa on bamboo are also still waiting for collection and isolation.

10. Conclusions

Bamboo plays an important role in the forest ecosystem and is treated as an economic plant for human. Studying the bamboo fungi can provide the chances for controlling bamboo pathogens and promoting bamboo cultivation. Based on our study, more than 1300 bamboo ascomycetes have so far been described or recorded; however, most of them do not have detailed morphology or sequence data. Even some important ascomycetous species still need re-studying. The morphologic characters of bamboo ascomycetes are various in their ascomata, asci, and ascospores (**Figures 5–7**). They occur on different genera of bamboo host; however, most of the hosts have not been identified to species level. Bamboo ascomycetes are diverse in their taxonomic placements, with more than 120 families and 400 genera distributed according to the references. Phylogenic analyses of bamboo ascomycetes need more study and should focus on protein genes. It is recommended that more fresh specimens need to be collected in the future, and the existing species should be epitypified or designated as reference specimens. Efforts are required in naming the taxa to avoid confusion, such as *Hypocrella bambusae*. Host species names should be identified in the future for those willing to work on host specificity.

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