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'What are fungi?' A Revisit

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ABSTRACT

The concept of fungi based on an absorptive mode of nutrition that prevailed till the 1970s changed with discoveries brought about subsequently by molecular phylogeny studies. The term 'fungi' was thenceforth confined to the opisthokontan lineage, termed popularly as the Kingdom Fungi, while the *Oomycetes*, *Hyphochytriomycetes* and *Labyrinthulomycetes* that belonged to the Kingdom *Straminipila* were relegated to 'pseudofungi' or 'fungi-like organisms'. We argue here that the term 'fungi' should be used in a broad sense based on a nutritional mode and ecological function. We support our arguments based on those of a number of other eminent mycologists. We further suggest that to avoid ambiguity, the opisthokontan lineage of fungi should be termed as belonging to the Kingdom *Mycetae*. The term 'fungi' then would constitute a polyphyletic group of 'mycetaen fungi' and 'straminipilan fungi' that are found in the Kingdom *Straminipila*.

Keywords: Opisthokont, Fungi, Kingdom, *Mycetae*, Straminipila, mycetaen, straminipilan.

Seventeen years after a similar question was discussed by Cavalier-Smith (2001) and at a time when systematists are gradually succeeding in establishing an accurate, evolutionary and phylogenetic classification of organisms, a revisit to the topic on what fungi are, is still relevant.

Fungi as understood till 1980

There have been various definitions and taxonomic organizations of fungi by earlier mycologists, such as Saccardo in his Sylloge Fungorum of 1884 and in the books of Gwynne-Vaughan and Barnes in 1926 and Gaumann and Dodge in 1928. Many of these, based on the two Kingdom classification of organisms, classified fungi under plants and included bacteria under fungi as 'Schizomycetes'. For the sake of brevity, we will not consider these and confine to definitions after an arbitrary time period after 1950, subsequent to the exclusion of bacteria, the prokaryotes, from others that are eukaryotes.

Thus, Bessey, E.A. (1950) defined fungi as 'chlorophyll-less nonvascular plants whose reproductive or vegetative structures do not permit them to be assigned to positions among recognized groups of algae or higher plants, and as excluding the Bacteria (which are typically one-celled and lack a typical nucleus) and the *Mycetozoa* (which have an animal type of structure and reproduction)'. Ainsworth (1973) considered the following features to be important for an organism to be considered a fungus: "(1) Free-living, parasitic or mutualistic symbionts, devoid of chlorophyll. (2) Cell wall composition is very variable, majority contain chitin and glucan. (3) Reserve food materials are oil, mannitol and glycogen. (4) Except some unicellular members, majority are filamentous."Alexopoulos and Mims (1979) defined fungi as achlorophyllous, saprobic or parasitic organisms with unicellular or more typically, filamentous soma (thallus), usually surrounded by cell walls that characteristically consist of chitin and other complex carbohydrates, nutrition absorptive, except in the slime molds (Division *Gymnomycota*) where it is phagotrophic, propagation typically by means of spores produced by various types of sporophores; asexual and sexual reproduction usually present. This definition is very similar to that of Alexopoulos in his earlier book published in 1962.

The concept of fungi during the period of 1950 to 1980 was as follows.

1. Eukaryotic, devoid of chlorophyll.
2. Unicellular or filamentous.
3. Heterotrophic and osmotrophic in nutrition, except for the slime molds.
4. Cell wall made of chitin or glucans.

Fungi, as defined by various authors till this period included posteriorly uniflagellate, anteriorly uniflagellate and biflagellate zoosporic fungi (chytrids, *Hyphochytriomycetes* and *Oomycetes*, respectively), the *Zygomycetes*, *Ascomycetes*, *Basidiomycetes* and the asexual fungi (**Table 1**).

Concepts OF fungi that emerged since the 1970s

Our understanding of fungi underwent a major change with the publication of Whittaker (1969) who concluded that the conventional two Kingdom classification of eukaryotes was inadequate and proposed a five kingdom classification, which elevated Fungi to the level of a Kingdom. He also created the Kingdom *Protista* that included a heterogenous assemblage of unicellular organisms. The idea was further supported by Whittaker and Lynn Margulis (1978). Whittaker's circumscription of the Kingdom Fungi included all

Table 1: Classification of fungi over time by various mycologists

Ainsworth (1973)	Alexopoulos and Mims (1979)	McLaughlin et al. (2001)	Cavalier-Smith (2001)	Alexopoulos, Mims and Blackwell, 2002	Hibbett et al. (2007)	Webster and Weber (2007)	Adl et al. (2012)
Kingdom *Mycota* -	Kingdom *Myceteae* -	*Mycota* -	Kingdom *Fungi* -	Kingdom *Fungi* -	Kingdom *Fungi*	Kingdom *Fungi* Kingdom *Straminipila* And Kingdom *Protozoa*	*Fungi*
					Phylum *Microsporidia*	-	*Microsporidia*
Division *Eumycota*			Subkingdom 1. *Eumycota*			Kingdom *Fungi*	
Subdivision *Mastigomycotina* Class *Chytridiomycetes* Class *Hyphochytrio-mycetes* Class *Plasmodiophoro-mycetes*	Division *Mastigomycota* Subdivision *Haplomastigo-mycotina* Class *Chytridiomycetes* Class *Hyphochytridio-mycetes* Class *Plasmodiophoro-mycetes*	*Eumycota*, *Chytridiomycota*	Phylum *Archemycota* Subphylum *Dictyomycotina* Class *Chytridiomycetes* Class *Enteromycetes* Subphylum *Melanomycotina* Infraphylum *Allomycotina* Class *Allomycetes*	Phylum *Chytridiomycota*	Phylum *Chytridiomycota* Phylum *Neocallimastigo-mycota* Phylum *Blastocladio-mycota*	*Chytridio Mycota*	*Neocalli-mastigaceae* *Chytridiomycota* *Blastocladiales*
			-	Kingdom *Straminipila*	-	Kingdom *Straminipila*	-
Class *Oomycetes* Class *Hypho-chytriomycetes*	Subidivision *Diplomastigomyco-tina* Class *Oomycetes* Class *Hypho-chytriomycetes*	*Pseudomycota* *Oomycota* *Hyphochytrio-mycota*	-	Phylum *Oomycota* Phylum *Hupho-chytridiomycota* Phylum *Laburin-thulomycota*	-	*Hyphochytrio-mycota* *Labyrinthulom ycota* *Oomycota*	-
-	Division *Amastigomycota*	*Eumycota*	-	Kingdom *Fungi*	-	Kingdom *Fungi*	-
Subdivision *Zygomycotina*	Subdivision *Zygomycotina*	*Zygomycota*	Infraphylum *Zygomycotina*	Phylum *Zygomycota*	Phylum *Glomeromycota* *Phylum Incertaesedis*	*Zygomycota*	*Mucoromycotina* *Mortierellaceae* *Entomophthorales* *Zoopagales* *Kickxellomyco-tina*
-	-	-	Subkingdom *Neomycota*	-	Śubkingdom *Dikarya*	-	*Dikarya*
Subdivision *Ascomycotina* Subdivision *Basidiomycotina*	Subdivision *Ascomycotina* Subdivision *Basidiomycotina*	*Dikaryomycota*	Phylum *Ascomycota* Phylum *Basidiomycota*	Phylum *Ascomycota* Phylum *Basidiomycota*	Phylum *Ascomycota* Phylum *Basidiomycota*	*Ascomycota* *Basidiomycota*	*Ascomycota* *Basidiomycota*
Classes *Acrasiomycetes* *Labyrinthula*les *Myxomycetes* *Plasmodiophoro-mycetes* [?]	Subdivision *Acrasiogymnomyc otina* Class *Acrasiomycetes* Class *Myxomycetes* Subdivision *Plasmodiogymno mycotina* Class *Protosteliomycetes*	- -	- -	Protists Phyla *Plasmodio-phoromycota* *Dictyostelio-mycota* *Acrasiomycota* *Myxomycetes*	- -	- -	- -

groups considered traditionally as fungi by mycologists, as given above and as circumscribed by Ainsworth (1973) (**Table 1**).

Advances in cell wall chemistry, biochemical pathways and electron microscopy in the 1970s had begun to show differences within fungi, as they were understood up to that time. Moore (1980) was probably the first to limit the use of 'fungi' to eukaryotes that were 'heterotrophic, not phagotrophic; often with walls and multinucleate hyphae; walls, when present, with β-glucan and usually chitin, at least in spore walls; lysine biosynthesis by aminoadipic acid (AAA) pathway; mitochondria and peroxisomes present, or secondarily lost as in Microsporidia; flattened mitochondrial cristae; plastids and tubular mastigonemes absent." This effectively excluded *Myxomycetes*, *Oomycetes* and *Hyphochytriomycetes*.

By the 1980s, it was clearly established that *Chytridiomycetes*, *Zygomycetes*, *Trichomycetes*, *Ascomycetes* and *Basidiomycetes* formed a monophyletic group related most closely to Kingdom *Animalia* (Cavalier-Smith, 1987). This lineage was called 'fungi' by the author, a terminological practice that has become the norm today. *Oomycetes*, which had hitherto been considered fungi, but which were shown to belong to the Kingdom '*Chromista*', also called the Kingdom *Straminipila*, were marginalized as 'pseudofungi'. These phylogenetic relationships, based firmly on molecular sequences are now well established and beyond dispute (Cavalier-Smith, 2001; Steencamp, *et al*., 2006; Adl *et al*., 2012; Baldauf *et al*. 2013).

Thus, organisms that were considered fungi till the period even up to 1980 are now known to belong to two distinct lineages. One of these forms a monophyletic group of the Superkingdom *Opisthokonta* that includes the Kingdom *Animalia*, and the others, namely the *Oomycetes*, *Hyphochytriomycetes* and *Labyrinthulomyctes* belong to the Kingdom *Straminipila* or Kingdom *Chromista*. We will henceforth in this articlce call these the opisthokontan lineage of fungi and the straminipilan lineage of fungi, respectively, in line with our arguments that follow.

Terms used for 'Fungi'

Fungi, together as a polyphyletic assemblage, or as a monophyletic, opisthokontan lineage have been named variously in nomenclature (Table 1).

- Whittaker (1969) called them 'Kingdom *Fungi'*.
- Ainsworth (1973) used the term '*Mycota'*.
- Alexopoulos and Mims (1979) used the term 'Kingdom *Myceteae'*.

Terminologies of these authors referred to a polyphyletic assemblage, which included 'fungi' belonging to both the opisthokontan lineage and the straminipilan lineages.

The opisthokontan lineage of fungi have been termed variously as 'Kingdom *Fungi'*, 'Fungi' and '*Eumycota'* by various authors.

- 'Kingdom *Fungi'*, a term originally used by Whittaker was also the one adopted by Moore (1980), Cavalier-Smith (1987, 2001) and Hibbett *et al*. (2007) . These authors have used this term exclusively for the monophyletic, opisthokontan lineage of fungi. The formal nomenclatural term recommended by Hibbett *et al*. (2007) is 'Kingdom: *Fungi* R. T. Moore, *Bot. Mar*. 23: 371 (1980)'.
- The term 'Fungi', but not Kingdom *Fungi*, has been used by Kirk *et al*. (2008), Adl *et al*. (2012) and Baldauf *et al*. (2013) to refer to the opisthokontan lineage of fungi. Adl *et al*. (2012), in their classification, did not recognize a Kingdom level, or even any other suprageneric hierarchy. According to Baldauf *et al*. (2013), 'Fungi' belong to a larger, monophyletic clade, the *Holomycota* that comprises not only fungi with their absorptive mode of nutrition, but also many related phagotrophic, unicellular forms. These include the *Rozellida*, which are mostly known from environmental sequences, the *Nucleariida*, which are strictly amoeboid and *Fonticula alba*, which is also an amoeba that was previously classi? ed as a slime mold. The unicellular and strictly parasitic *Microsporidia* are also part of the *Holomycota*. Holomyciota share a common ancestor with *Holozoa*, the latter comprising Kingdom *Animalia* or *Metazoa*, as well choanozoans (**Fig. 1**).
- Silar *et al*. (2016), who also recognize *Holomycota*, have used the term '*Eumycota'* for the opisthokontan fungi. The term has also been used by Ainsworth (1973) and McLaughlin and McLaughlin (2001) for these fungi.. These latter two authors recognized the distinct evolutionary lineages of opisthokontan and straminipilan fungi, but brought them together under the umbrella of '*Mycota'*. According to them, the *Mycota* encompassed the '*Eumycota'* comprising the opisthokontan and the 'Pseudomycota' that comprised the straminipilan fungi.

'Kingdom *Fungi'* has been the most popular term for the opisthokontanlineage of fungi. This has led to the usage of the term 'fungi' exclusively to members of this group

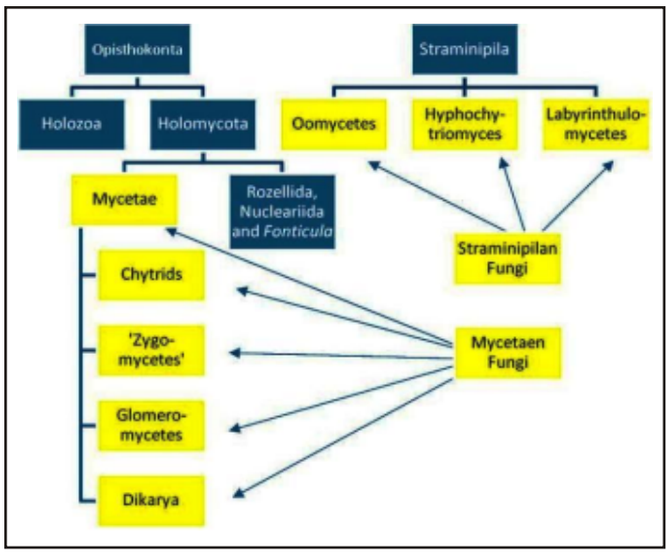

Fig. 1. Representation of Mycetaen fungi and Straminipilan Fungi.

(Cavalier-Smith, 1987, 2001; Hibbett *et al*. 2007; Kirk *et al*., 2008; Adl *et al*., 2012), or to members of one of the lineages of the larger group, the *Holomycota* (Baldauf *et al*., 2013). *Oomycetes*, *Hyphochytriomycetes* and *Labyrinthulomycetes* have now been relegated to "fungal-analogues", "untrue fungi", 'pseudofungi' or 'fungal-like organisms", implying that these are not 'fungi'.

Thus, 'fungi' is mostly used at present in an evolutionary sense, as a monophyletic group.

Arguments for defining fungi as a polyphyletic group

Many mycologists have strongly recommended that the term 'fungi' should be used in a broad ecological and functional sense, instead of strictly on the basis of evolution. Several arguments have been forwarded to support this view.

- Nearly seventy years ago, Bessey (1950) wondered whether the fungi were monophyletic or arose from different ancestors, making way to a consideration of the term fungi being used in a polyphyletic sense.
- Barr (1992)expressed the view that a definitionof fungi based solely on phylogeny was inconsistent with pragmatic needs of mycologists for whom a consideration of ecological or nutritional groupings would be more suitable. He further argued that considering the role that plant pathology has played in mycology and the enormous role of oomycetes in causing plant diseases, a non-inclusion of these organisms, as well as the *Hyphochytriomycetes* and slime molds in a study of mycology could lead to a neglect in their teaching. The solution lies in recognizing a polyphyletic assemblage. According to him, the name "fungi" should be retained in the popular or colloquial, polyphyletic sense to include kingdoms, or parts of kingdoms, that make up logical groups for the benefit of the applied biologist, mycologist or phytopathologist. He suggested the term 'Union of Fungi' to include opisthokontan fungi, as well as the straminipilan ones.
- McLaughlin and McLaughlin (2001) also observed that 'the term fungi has assumed an ecological meaning for all organisms with a similar nutritional mode'. Based on this interpretation, they addressed the monophyletic opisthokontan lineage, as well as 'pseudofungi' *sensu* Cavalier-Smith, which comprised the *Oomycetes*, *Hyphochytriomycetes* and *Labyrinthulomycetes* together as '*Mycota'* (**Table 1**).
- Dick (2001), in his monumental monograph of the *Oomycetes*, *Hyphochytriomycetes* and *Labyrinthulomycetes* addressed these organisms as 'straminipilous fungi', thus emphasizing the need to understand fungi in a broad ecological and functional role, rather than on a strictly evolutionary relationship.
- Alexopoulos *et al*. (2002) recognized the term 'fungi' to represent a polyphyletic assemblage. They considered three groups of fungi. Fungi of the Kingdom Fungi comprised the *Chytridiomycota*, *Zygomycota*, *Ascomycota* and *Basidiomycota*. Those belonging to the Kingdom *Stramenopila* consisted of the *Oomycetes*, *Hyphochytriomycetes* and the *Labyrinthulomycetes*. The protozoans, *Plasmodiophoromycetes*, dictyostelids, *Acrasiomycetes* and myxomyceteal were also treated by them as part of mycology.
- Webster and Weber (2007) also agreed with Barr and others 'who take a biological approach to the subject and regard fungi as organisms sharing all or many key ecological or physiological characteristics'. They circumscribed 'fungi' based on their lifestyle and in a manner that included both fungi belonging to the opisthokontan lineage, as well as those that had been classified under the Kingdom *Straminipila*, the latter too being considered fungal phyla.
- Kirk et al. (2008) have also followed a broad,

polyphyletic interpretation of fungi, which included all of Kingdom *Fungi* and certain members of the Kingdom *Chromista* and Kingdodm *Protozoa*.

- Beakes *et al*. (2014) also recommended that "fungi" should be considered a biological lifestyle. They further advised that it was important that the straminipilan fungi "continue to be considered an integral part of mycology and not be excluded or marginalized because of their different evolutionary origins".

There are many compelling reasons for considering fungi in a broad, polyphyletic sense. Exclusion of the *Oomycetes*, *Hypochytriomycetes* and *Labyrinthulomycetes* from 'fungi' would be a great loss to the science of mycology.

From a practical point of view, especially plant pathology and industrial mycotechnology, the straminipilan fungi deserve as much attention from mycologists, plant pathologists and biotechnologists. Downy mildew diseases caused by *Sclerospora* and *Plasmopara*, as well as *Phytophthora* that also causes soft rot diseases on diverse economic crop plants require to be studied as intensively as the rust and smut diseases caused by the "true" basidiomycetous fungi.

By ignoring straminipilan fungi, one would be excluding the study of a large part of ecosystem functioning and dynamics from mycology. In some ecosystems, these groups actually play a larger part than the opisthokontan fungi. For example, members of *Labyrinthulomycetes* appear to contribute much more in terms of biomass and energy transfer mechanisms in the marine ecosystem than the opisthokontan fungi (Raghukumar, 2017). The *Oomycetes*, which like the *Labyrinthulomycetes* appear to be of marine origin (Beakes et al., 2014) play a significant role as parasites of marine organisms. Indeed, the inclusion of these organisms under 'fungi' will make mycology much more interesting to marine microbiologists and marine biologists alike, since opisthokontan fungi, as far as the evidence points out today, seem only to be secondary invaders of the sea.

Estimation of fungal diversity based on DNA sequencing has presently skyrocketed as compared to the conservative estimate of 1.5 million proposed by Hawksworth (1991). Even in the absence of a live specimen and based exclusively on environmental nucleic acid sequence analysis, new taxa such as *Hawksworthiomyces* have been described (de Beer *et al*., 2016). In such a scenario, it is unfortunate that the unfolding rich diversity of *Oomycetes*, *Hyphochytriomycetes* and *Labyrinthulomycetes*, conventionally considered and studied as Fungi for a long time is not considered. We believe that there is an urgent need for a consensus among biologists to appreciate the extent and biodiversity dimensions in fungi that includes both the opisthokontan and straminipilanlineages of fungi.

It appears that segregation of the straminipilian fungi as "pseudofungi" is unwarranted as this will lead to mycologists neglecting such a large group of important genera and species in future. Since none other than mycologists and plant pathologists have any knowledge or expertise to make meaningful scientific contributions to this group of fungi, progress of research on these fungi will be severely hampered.

In view of the above, Raghukumar (2017) subscribed to the views of those who advocated that fungi should be considered in a broad ecological sense to include straminipilan, as well as opisthokontan lineages that fulfilled the criteria of being eukaryotic organisms with an osmotrophic or absorptive mode of nutrition.

If fungi are considered polyphyletic, those who study straminipilan fungi are mycologists, as much as those who study opisthokontan fungi. As a corollary, one could say that fungi are biological entities studied by mycologists. We stresss that mycologists should continue to spare their best efforts in studying and understanding fungi in the broadest sense.The knowledge that we have acquired through advances in biochemistry and molecular biology of these groups should be meaningfully used for a better understanding of the biodiversity in the mycological realm in its broadest sense.The loss of opportunities and scientific knowledge would indeed be serious if mycologists in future years do not wish to study all these groups together.

Choices for defining Fungi

We are confronted with two logical choices to address the two groups of fungi, depending on whether we view them as from an evolutionary point of view or that of nutritional mode and ecological function.

(1) If fungi are defined strictly based on their evolutionary lineage, they would be restricted only to members of the '*Holomycota'* (Baldauf *et al.,* 2013). *Holomycota*, which term implies 'total fungi' is a mixed bag, consisting of 'fungi' with an absorptive mode of nutrition, as well as organisms with a phagotrophic mode. In such a case, the definition of fungi needs to be modified to include organisms with two different modes of nutrition. Fungi, then will not strictly comprise organisms understood as those with an absorptive

nutrition, but as an assemblage that also includes phagotrophic organisms. This will go against the common understanding of mycologists of fungi being organisms with absorptive nutrition.

(2) Alternatively, if we adopt the term fungi only for organisms with an absorptive mode of nutrition, our concept of fungi should be expanded to make the term polyphyletic.

We reiterate what we have stated before that the second of the two choices given above, that 'fungi' should be defined in a broad sense based on lifestyle and ecological function in a manner very similar to that of 'algae'. The term 'algae' is used in a polyphyletic sense, and are understood as 'eukaryotic, nonvascular, photosynthetic organisms' and encompass straminipilan (diatoms, brown algae), viridiplantae (green algae) and the red algae. Barr (1992) indeed cited the use of the term 'algae' to support his argument.

The term 'fungi' then would embrace the opisthokontan lineage generally called as Kingdom *Fungi*, as well as *Oomycetes*, *Hyphochytriomycetes* and *Labyrinthulomycetes* that belong to the Kingdom *Straminipila*.

Terminologies for the polyphyletic assemblage of fungi

A definition of fungi that includes the opisthokontan, as well as the straminipilan lineages of organisms with the same ecological functioning, will make the exclusive use of the terms Fungi or the Kingdom *Fungi* only for the opisthokontan lineage illogical and would obviously lead to confusion. This point has also been raised by Barr (1992) and Webster and Weber (2007). It would then be reasonable to apply an alternative term for the opisthokontan fungi. There appear to be two choices if a polyphyletic interpretation of fungi is accepted.

1. Eumycotan fungi and Straminipilan fungi: Barr (1992), as well as McLaughlin and McLaughlin (2001) recommended that the opisthokontan lineage of fungi be called the Kingdom *Eumycota*. Silar (2016) employed the same term. However, in our opinion this term too is ambiguous, since it also implies that only fungi belonging to *Eumycota* are 'true fungi'. In like terms, it is misleading to call the straminipilan group of fungi as 'pseudo-fungi' or 'fungal-like organisms', because it implies that these are not fungi. However, these indeed are fungi in the ecological sense that we have defined them. We suggest that these should be named 'Straminipilan fungi' in the manner discussed by Dick (2001).

2. Holomycotan and straminipilan fungi: *Holomycota* (Baldauf *et al*., 2013) is a clearly defined group. Fungi belonging to Holomycota could then be considered holomycotan fungi and the other group would be straminipilan fungi. However, the term '*Holomycota'* signifies the totality of fungi, thus automatically excluding the use of 'straminipilan fungi'. Therefore, this combination of terms is not be acceptable.

3. Mycetaen fungi and Straminipilan fungi: The opisthokonttan group of fungi have been referred to as the Kingdom *Myceteae* by Alexopoulos and Mims (1979) to include both the opisthokontan and straminipilan fungi. A simpler version, Kingdom *Mycetae* has been popular among a large number of mycologists and teachers (eg., Launchbaugh and Urness, 1992; Manoharachary *et al*., 2016). We suggest that this term is appropriate in place of Kingdom *Fungi* for the opisthokontan lineage. A similar proposal to use the term Kingdom *Mycetae* for the opisthokontan lineage and calling these mycetaen fungi, while the *Oomycetes*, *Hyphochytriomycetes* and *Labyrinthulomycetes* corresponded to the straminipilan fungi has also been made by Raghukumar (2017) (**Fig. 1**).

CONCLUSION

We recommend that mycologists should consider the usage of the term 'fungi' in a polyphyletic sense to include the opisthokontan, as well as straminipilan organisms with an absorptive mode of nutrition. We further suggest that the term Kingdom *Fungi* should be replaced by Kingdom *Mycetae*.

In conclusion, fungi belong to two distinct evolutionary groups. One group belongs to the Kingdom *Mycetae*, or just *Mycetae* of *Holomycota*, which are a group of opisthokontan organisms, related to Kingdom *Animalia* or *Holozoa*. The second group comprises the groups *Oomycetes*, *Hyphochytriomycetes* and *Labyrinthulomycetes* that belong to the Kingdom *Straminipila*. The two groups are respectively called the mycetaen fungi and the straminipilan fungi (Fig. 1). This approach will lead to a positive outlook on what fungi are and facilitate a deeper and broader appreciation in understanding of fungal biodiversity in its total perspective.

Fungi would then be defined as 'Unicellular, or filamentous eukaryotic organisms that possess an osmotrophic mode of nutrition'.

The broad characteristics of fungi, based on those of Webster and Weber (2007) are as follows.

1. Nutrition: Heterotrophic (lacking photosynthesis), osmotrophic, feeding by absorption rather than ingestion.
2. Vegetative state: Non-motile, single-celled or in

the form of mycelium of hyphae showing internal protoplasmic streaming.

3. Cell wall: Typically present, usually based on chitin, cellulose or other polysaccharides.

4. Nuclear status: Eukaryotic, uni- or multinucleate, the thallus being homo- or heterokaryotic, haploid, dikaryotic or diploid.

5. Life cycle: Simple or complex.

6. Reproduction: Asexual, sexual or parasexual (i.e. involving nuclear fusion followed by gradual de-diploidization) and/or asexual (i.e. purely mitotic nuclear division).

7. Propagules: By means of non-motile or motile spores. Motile spores may be posteriorly uniflagellate, anteriorly uniflagellate or biflagellate.

8. Sporocarps: May be present in mycelial forms. Microscopic or macroscopic and showing characteristic shape.

9. Habitat: Ubiquitous in terrestrial, freshwater and marine habitats.

10. Ecology: Important ecological roles as saprotrophs, mutualistic symbionts, parasites, or hyperparasites.

11. Distribution: Cosmopolitan.

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