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REVIEW

Evolution in taxonomic studies in Polypores

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Definite report of polypores have been found from Tertiary to Quaternary i.e., during the period of 25 my to 15 my which is evident by the occurrence of poroid fossil basidiocarps of some species such as *Ganodermites libycus*, *Lithopolyporales zeerabadensis* and *Fomes idahoensis*. According to International Rules of Botanical Nomenclature *Systema Mycologicum* Vol.1 published in 1821 by E. M. Fries is regarded as the starting point for taxonomic studies of polypores. The earliest taxonomic studies of polypores were exclusively based on gross morphological characters of the basidiocarps. However, initially Fries recognized only 3 genera of polypores namely, *Daedalea, Merulius and Polyporus* based on exomorphological features but finally he recognized 8 genera : *Merulius, Daedalea, Hexagonia, Favolus, Lenzites, Cyclomyces, Trametes* and *Polyporus* . Following Fries several mycologists erected several genera of polypores such as *Fomitopsis, Ganoderma, Tyromyces* etc. But when more and more workers began to study polypores from taxonomic point of view they found that exomorphology is unreliable character. Taxonomists, therefore, searched for more reliable features which are constant. The concept of Fries of taxonomic studies of polypores then found a change in the hands of subsequent workers. The main credit to point out the taxonomic importance of micromorphological characters of hyphae goes to Corner who introduced the concept of "hyphal system" and opened a new era in the field of taxonomy. Corner described that the polypores may consist of morphologically distinct hyphae which he classified into 3 basic groups namely, generative, skeletal and binding hyphae .When only generative hyphae are present in a basidiocarp Corner called it as monomitic, when two types of hyphae are involved (generative and either skeletal or binding hyphae) he called it dimitic, and he called the basidiocarp with all the three types of hyphae as trimitic. Hymenial structures also have taxonomical importance. Characteristics of basidia and basidiospores are very important at species and in some cases at generic level. Different kinds of sterile hymenial structures are found in polypores along with basidia. These have been regarded as characters of generic importance. These include cystidia, acanthophyses, gloeocystidia, dichophytic elements and hyphal pegs. Type of rots (white rot and brown rot) caused by the polypores have been incorporated as an important character in their taxonomic studies. Later workers introduced some biochemical tests including xanthochroic test, gum guaic test, amyloidy, dextrinoidy etc. Cytological aspects such as stichobasidial and chiastibasidial characters have been found to be important characters in segregation of genera. A great change occurred in the concept of taxonomic studies of polypores when cultural studies were introduced. Through several papers Nobles showed that cultural characters and certain biological characters have great taxonomic value in studying polypores. From these studies she formulated a hypothesis that white rotter polypores possess tetrapolar sexuality and positive result in oxidase tests while brown rotter ones possess bipolar sexuality and negative result in oxidase tests. Interfertility test is another important aspect which was introduced in taxonomic studies of polypores. Solution of confused situation in the systematics of some species of polypores particularly of the closely related species requires consideration of additional criteria from interfertility study.

* Ninth Professor S. R. Bose Memorial Lacture

Interfertility study is, therefore, used for confirmation of conspecificity and synonymy of morphologically similar and dissimilar species. The electrophoretic analysis of total protein of polypores have been found to be important aspect in their taxonomic studies. It is considered that for the morphological revision of taxa protein analysis offers an additional taxonomic criterion. Modern mycologists think that overlapping and variable morphological characteristics have made the classification of polypores unreliable and unstable. In solving taxonomic problems and phylogeny of polypores they have introduced Internal Transcribed Spacer (ITS) rDNA sequence. Among various molecular methods introduced including DNA-DNA hybridization, RFLP, and sequence analyses, phylogenetic analyses of amino acid or DNA sequences are known to have the highest resolving power . DNA sequence data of 18S, 26S, ITS, and mitochondrial rDNAs are most frequently used in recent phylogenetic studies of polypores.

Key words: Taxonomy, polypore, exomorphology, anatomy, hyphal system, hymenial structures, cultural study, oxidase test, interfertility test, sexuality, electrophoretic analysis, ITSrDNA.

INTRODUCTION

Polypores are fungi having basidiocarp with basidia on tubes forming pores of various types. Polypores are mostly wood rotting fungi. In some areas of the wood of *Callixylon*, one of the oldest known trees, the tracheid walls are characterized by erosion troughs, which represent areas of delignification by the enzymatic activities of the fungus. The patterns produced on the tracheid walls in *Callixylon*, a fossil plant, are similar to those formed by living basidiomycetous fungi responsible for white rot (Otjen and Blanchette, 1986) . It can not be stated that this fungus was a polypore but it provides evidence that association between fungi and vascular plants begins around the same time when wood development begun.

In the tracheids of the fern *Zygopteris,* hyphae of the bsidiomycete *Palaeoancistrus martinii* (300 my old) possessing clamp connecitions has been found (Dennis 1970). *Palaeofibulus* is another fossil fungus with clamp connections known from Middle Triassic permineralised peat of Antarctica (Osborn *et al.,* 1989). These definitely belong to Basidiomycetes but basidiocarps of none of these above mentioned fossil fungi have been reported. So, whether they were polypores is not known. Definite report of polypores have been found from Tertiary to Quaternary i.e., during the period of 25 my to 15 my which is evidenced by the occurrence of poroid fossil basidiocarps of some species. They are *Ganoderma libycus* (Fleischmann *et al.,* 2007), *Lithopolyporales zeerabadensis* (Kar *et al.,* 2003) and *Fomes idahoensis* (Andrews and Lenz, 1947).

Taxonomic studies of polypores—Friesian System

Taxonomic studies of polypores started in 1821. According to International Rules of Botanical Nomenclature *Systema Mycologicum* Vol.1 published in 1821 by E. M. Fries is regarded as the starting point for nomenclature of polypores. This earliest taxonomic studies of polypores were exclusively based on gross morphological characters of the basidiocarps. The exomorphological features included colour, surface, texture and hymenial configuration which are readily seen. Colour of basidiocarp of polypores varies greatly such as white, red, black, brown etc.; surface of basidiocarp may be smooth and shiny, hairy, crustose, zonate etc.; texture may be thin to thick, soft, hard, fleshy, cartilaginous, woody etc.; hymenial configuration shows great variations such as lamellate, daedaloid, hexagonal, poroid, dentoid etc. Shape of basidiocarp also varies considerably such as resupinate i.e., appressed to substrate with exposed hymenium; effuso-reflexed i.e., appressed to surface and also bracket shaped with hymenium on lower surface or pileate i.e., bracket shaped with upper portion sterile and exposed hymenium on lower surface. Pileate basidiocarps may be sessile or stipitate, when stipitate the stipe of basidiocarp may be centric, eccentric or lateral.

However, initially Fries recognized only 3 genera of polypores namely, *Daedalea, Merulius* and *Polyporus* based on exomorphological features. But gradually he added more and more genera, always giving emphasis on the characters of hymenial configuration, although other macromorphological characters of basidiocarps were also taken into consideration. Fries (1874) ultimately recognized 8 genera as follows : *Merulius*—Hymenium with folds that are joined into shallow pits or pores; *Daedalea* — Hymenium with daedaloid pores; *Hexagonia*— Basidiocarp sessile, hymenium with hexagonal pores; *Favolus*— Basidiocarp stipitate or substipitate, hymenium with hexagonal pores arranged in radiating rows, *Lenzites*— Hymenium with radiating lamellae; *Cyclomyces*— Hymenium with concentric lamellae; *Trametes*—Hymenium with circular to angular pores, pore tubes sunk to unequal depths; and *Polyporus* — Hymenium with circular to angular pores, pore tubes sunk into an even depth forming a distinct stratum.

Following Fries several mycologists such as Gillet (1878), Karsten (1881). Quelet (1886), Lloyd (1898-1925),Patouillard (1900), Murrill(1907, 1908) studied more and more polypores and erected several genera of polypores. All these studies were mainly based on external characters of basidiocarps including hymenial configuration, surface of basidiocarp, consistency and colour of basidiocarps. Karsten erected the genera such as *Fomitopsis, Ganoderma* and *Tyromyces* in 1881.

Growth form i.e., whether the basidiocarp is annual, biennial or perennial, is also considered as an important character in taxonomic studies of polypores.

Introduction of anatomical features in taxonomy

When more and more workers began to study polypores from taxonomic point of view they found that exomorphology is an unreliable character. They found that there are combination of different types of hymenial features in a single basidiocarp of some specimens of a species. They also found that different basidiocarps of the same species show various types of hymenial configurations. Mention may be made of the type specimens of *Gloeophyllum imponens* which show different types of hymenial configurations from lamellate, daedaloid to poroid in different basidiocarps.

Taxonomists, therefore, searched for more reliable features which are constant. The concept of Fries of taxonomic studies of polypores then found a change in the hands of subsequent workers. They realized that micromorphological characters should be considered along with macromorphology. Patouillard (1900) is the pioneer worker to introduce anatomical characters in taxonomic study of polypores. Patouillard (1900) in his *Essai Taxonomique* introduced hyphal characters, characters of basidia, basidiospores and cystidia. Later this concept i.e., delimiting genera on the basis of micromorphological characters, was applied by other workers namely Rea (1922), Bourdot and Galzin (1928), Donk (1933), Pilat (1936-1942), Bondertzev and Singer (1941), Imazeki (1943), Imazeki and Toki (1954) and others. In all these studies micromorphological characters got much emphasis. But the credit to point out greatly the taxonomic importance of micromorphological characters of hyphae goes to Corner (1932) who introduced the concept of "hyphal system" and opened a new era in the field of taxonomy. Corner (1932) studied the sporophore of *Polystictus xanthopus* Fr. and demonstrated the presence of different types of hyphae inside the basidiocarp. He (1932) boldly stated, "the hyphal system of the fruitbody must be considered foremost in the morphology of polypores as it will provide the key to a natural classification". Later, through more papers (1950, 1953) he drew further attention of mycologists all over the world. His works now became fundamental to all modern generic concepts in fungi and a new field of study was thus initiated. Corner (1953) described that the polypore may consist of morphologically distinct hyphae which he classified into 3 basic groups namely, generative, skeletal and binding hyphae and defined them as follows: generative hyphae are thin-walled and septate hyphae which takes the longitudinal course in growimg region; skeletal hyphae~are unbranched, thick-walled, commonly aseptate and constructional hyphae of the first order in the growing region; and binding hyphae are much branched, thick-walled, aseptate hyphae of very intricate and limited growth, developing behind the growing point.

When only generative hyphae are present in a basidiocarp Corner called it as monomitic; when two types of hyphae are involved (generative and either skeletal or binding hyphae) it is called dimitic; with all the three types of hyphae, the basidiocarp is called trimitic (Corner 1953).

Corner's concept of hyphal system has been broadly accepted by modern mycologists, though some more terms have been added to accommodate certain modified forms of these hyphae.

Generative hyphae are septate, septa simple or with clamp connections, thin-walled or thick-walled to solid. Thick-walled generative hyphae are referred to as sklerified generative hyphae by Donk (1964). Sometimes thick-walled generative hyphae possess irregular thickening of their walls. This character is considered as one of the important characters of the genus *Daedalea*. The genus *Amylosporus* is characterized by presence of whorled clamp connections and simple septa on the same hypha. Sometimes special forms of generative hyphae called gloeopleurous hyphae occur in basidiocarps of some polypores such as *Daedalea ostreiformis, Fomitopsis officinalis, Rigidoporus vinctus* etc. Gloeopleurous hyphae are thin-walled generative hyphae, rather wide, rarely showing septa, usually hyaline and with deeply stained contents.

Skeletal hyphae are thick-walled to solid, usually aseptate and unbranched but sometimes they show branches towards the distal ends as in *Datronia mollis, Trametes versicolor* etc. These skeletal hyphae are described as arboriform type of skeletal hyphae by Teixeira (1962).

Binding hyphae may develop branch of varying length. Binding hyphae are called long type when the branches are long and tapering; they are called "coralloid type" when they bear many short branches and become coral-like in appearance, eg. the species of *Hexagonia*; they are called "bovista type" when binding hyphae possess much narrower branches arising from wider stems as found in the species of *Polyporus*.

Hymenial structures also have taxonomical importance. Characteristics of basidiospores are very important at species and in some cases at generic level. They may be globose, subglobose, ellipsoid, cylindrical, allantoids, navicular, warty and smooth. In *Amylosporus, Heterobasidion* and *Diacanthodes* the basidiospores are finely warted.

Different kinds of sterile hymenial structures are found in polypores along with basidia. These have been regarded as characters of generic importance. These include cystidia, acanthophyses, gloeocystidia, dichophytic elements and hyphal pegs.

Cystidia may be more or less of the same size as basidia, thin-walled or thick-walled, smooth or encrusted at the apex and of variable shape from clavate to ventricose. Occasionally thick-walled pointed apical ends of skeletal hyphae and also of the branches of binding hyphae may penetrate into the pores through the hymenium behaving as cystidia. But these are not true cystidia and found particularly in the species of *Lenzites* and *Hexagonia*.

Sterile hyphal ends having a number of short pin-like projections on their surface towards their distal ends called acanthophyses are encountered in some polypores such as *Flavodon flavus* and *Rigidoporus zonalis*.

Hyaline, smooth, tubular or sinuous structures with refractive contents occur in the hymenial layer of some polypores called gloeocystidia. They are important identifying characters at species level. Mention may be made of a fungus like *Heteroporus biennis* which is characterized by presence of gloeocystidia in their basidiocarp.

Dichophytic elements i.e., hyaline strongly coralloid structures formed by repeated emergence of fine processes at the terminal ends of some hyaline thick-walled hyphae occur in some species of *Microporus*.

Introduction of type of rots caused by polypores and some biochemical tests in taxonomy

Type of rot caused by the polypores has been incorporated as an important character in their taxonomic studies. Mainly two types of rots are caused by polypores- white rot and brown rot. In case of white rot both cellulose and lignin are utilized at approximately equal rates by polypores. As a result the wood becomes whitish. On the other hand brown rotters utilize cellulose and hemicelluloses, lignin remains unaffected. As a result the wood becomes dark brown. So, polypores can be clearly separated into two groups- white rotters and brown rotters. A white rotter polypore can not be grouped with a brown rotter.

Later workers studied polypores based on macromorphology, anatomical features, habit, type of rot produced and also introduced some biochemical tests including xanthochroic tests, gum guaic test, amyloidy, dextrinoidy etc. If hyphae and basidiospores are stained with Melzer's reagent and they become yellow, they are called inamyloid, if they turn grey to blue they are called amyloid and dextrinoid if become reddish brown. An amyloid species can not be grouped with a dextrinoid or an inamyloid one.

Introduction of some cytological aspects in taxonomy

Cytological aspects have also been included in taxonomic studies of polypores. Stichobasidial and chiastibasidial characters have been found to be important characters in segregation of genera.

Introduction of cultural studies in taxonomy

A great change occurred in the concept of taxonomic studies of polypores when cultural studies were introduced. Cultural characters of higher fungi were studied as early as 1889 by Brefeld (Brefeld 1889). Long and Harsch (1918) made cultural studies of a large number of wood rotting fungi. Fritz (1923) was the first to indicate the importance of microscopic characters in culture and described 18 species of wood rotting fungi. Bavendamm (1928) observed that brown diffusion zones were formed when cultures of certain species known to cause white rots were grown on agar media containing gallic acid or tannic acid, but zones were not produced by the species which cause brown rots. He designated these reactions as "positive" and "negative" respectively. This observation of Bavendamm was confirmed by Davidson *et al.* (1942), Nobles (1943) and many others. Although cultural characters of higher fungi were studied as early as 1889 by Brefeld (Brefeld 1889), Nobles (1958) was the first to incorporate cultural characters to solve the taxonomic problems of polypores. Through several papers she (1958, 1964, 1971) showed that cultural characters and certain biological characters have great taxonomic value in studying polypores. The macroscopical features of cultures vary greatly among the species of polypores. Besides, all the corresponding anatomical features of a species occurring in its basidiocarps are also produced in culture. Sometimes fertile basidiocarps are also developed in culture bearing basidia and basidiospores similar to those developed in basidiocarps produced in nature. Nobles emphasized on correlative studies on the morphological, cultural and certain biological characters such as the type of rot and type of sexuality of a species in taxonomic study. Several workers have followed this concept of Nobles (1948,1958) such as Van der Westhuizen (1963, 1971), Roy and De (1980), De and Roy (1981) and many others. Bondartzeva (1961) in her critical review on the classifications of the family of Polyporaceae referred about the works of Nobles as "a very promising beginning". She studied macromorphological and micromorphological features of cultures of a large number of polypores along with oxidase test, sexuality and interfertility tests. From these studies she formulated a hypothesis that white rotter polypores possess tetrapolar sexuality and positive result in oxidase tests while brown rotter ones possess bipolar sexuality and negative result in oxidase tests. In modern taxonomic studies type of sexuality is regarded as an important character in segregation of genera. A species of polypore possessing bipolar sexuality can not be placed in the same group with another species having tetrapolar sexuality. Similarly white rotter polypore can not be grouped with a brown rotter one and a species giving positive result in oxidase test can not belong to the same taxonomic group with a species giving negative result in oxidase test.

Interfertility test is another important aspect which was introduced in taxonomic studies of polypores. Solution of confused situation in the systematics of some species of polypores particularly of the closely related species requires consideration of additional criteria from interfertility study. Interfertility studty is, therefore, used for confirmation of conspecificity and synonymy of morphologically similar and dissimilar species. Interfertility tests are carried out placing inocula from two single spore cultures obtained from two different basidiocarps at a distance from each other in a culture plate. After a few days hyphae from their line of contact are observed under microscope. If clamps are observed in the hyphae, these two basidiocarps are regarded as conspecific, if clamps are not observed they are regarded to be of different species. Several mycologists (Bose 1952, Nobles, *et al.,* 1957, Roy and Pal 1994) have followed this aspect and showed that interfertility test can prove the conspecificity of a species and this can be used in the solution of taxonomic problems.

Introduction of electrophoretic analysis of total soluble protein in taxonomy 0f polypores

The electrophoretic analysis of total protein of polypores have been found to be important aspect in their taxonomic studies. Electrophoresis affords opportunities for studying intraspecific variabilities in fungi. Specific electrophoretic profiles of proteins of higher basidiomycetes have been obtained using mono- and two-dimensional electrophoresis. Proteins and enzymes in representatives of higher Basidiomycetes have shown specific electrophoretic mobility and the number of protein bands common for certain species are considerably greater at the generic rank than at the subgeneric rank. Studies on the gel electrophoretic analysis of total soluble proteins showed that the banding patterns of the three species namely *Daedaleopsis flavida, Lenzites adusta* and *Lenzites japonica* are different among themselves. This indicates that these three polypores are individual species each one being different from the other taxonomically and thus not synonymous as has been opined by some mycologists. On the other hand *Daedalea quercina* and *Trametes dickinsii* which are considered to be different species by many mycologists have been found to be synonymous as banding patterns of these two species are similar. Thus electrophoretic analysis of total soluble protein of polypores have been found to be important aspect in their taxonomic studies.

There is, however, a difference of opinion regarding the utility of protein pattern as a taxonomic tool for classification of fungi. The protein patterns are markedly influenced by age and experimental conditions (Sadhukhan and Sen, 1979). However the application of such methods leads to a number of problems which failing to resolve makes the application of electrophoretic data for taxonomy and phylogeny of fungi void. These problems are: age, seasonal, ecological, geographical, morphogenetical variabilities of proteins, peculiarities of electrophoretic spectra of proteins from different parts of the basidiocarp and the influence of freezing or drying of the material on the fractionational composition of proteins (Wasser and Brun, 1991).

In spite of distinctions in the estimation of the results of the electrophoretic analysis of fungal proteins which are available in literature most of the authors (Gams and Julich, 1984; Kammerer *et al.*, 1985; Papa and Polini, 1987; Bielenin *et al.*,1988) consider this method to be rather promising for comprehensive systematic investigation. It is considered that for the morphological revision of taxa protein analysis offers an additional taxonomic criterion.

Introduction of molecular aspects in taxonomy of polypores

The taxonomy of polypores is primarily based on morphological characteristics, such as the shapes of basidiocarps and hymenophores, hyphal systems, and forms and sizes of basidiospores, and secondarily on mycological features like host relationships and rot types (brown versus white) (Donk, 1964). However, overlapping and variable morphological characteristics have made the classification of polypores unreliable and unstable. In solving taxonomic problems and phylogeny of polypores Internal Transcribed Spacer (ITS) rDNA sequence data have been introduced. A close relationship of *Polyporus squamosus* and *Datronia mollis* has been inferred from rDNA studies (Binder and Hibbert, 2002). Through DNA fingerprinting it has been ascertained that North Eastern China and South Western China isolates of *Heterobasidion annosum* are actually *Heterobasidion parviporum* and *Heterobasidion annosum* s.str. is so far identified only from Altai region outside Europe (Dai *et al.*, 2003). Molecular systematics has been shown to be a valuable tool in modern fungal taxonomy. Among various molecular methods including DNA-DNA hybridization, RFLP, and sequence analyses, phylogenetic analyses of amino acid or DNA sequences are known to have the highest resolving power. DNA sequence data of 18S, 26S, ITS, and mitochondrial rDNAs are most frequently used in recent phylogenetic studies of polypores. Sequences of 18S rDNAs are conserved and have been used in phylogenetic analyses of fungi of higher taxonomic ranks such as classes or orders. On the other hand, ITS rDNAs are so variable that they often cannot be aligned accurately between genera and are now commonly used in the systematics of species within a genus. However, mitochondrial (mt)SSU rDNAs are reported to evolve 16 times faster than 18S rDNAs, but are less variable than ITS rDNAs. Thus they are believed to have a potential to fill phylogenetic gaps at a family level between those available from 18S and ITS rDNAs.

Nearly full-length sequences of 18S and ITS rDNAs for polypores can be amplified by PCR, but only partial sequences of mt SSU rDNAs have been amplified so far. For this reason, mt SSU rDNA sequences have not been popular among molecular systematists, and phylogenetic investigation of polypore fungi based on partial sequences of mt

SSU rDNA has been found unsatisfactory. The mitochondrial small subunit ribosomal DNA (mt SSU rDNA) is generally considered to be one of the molecules that are appropriate for phylogenetic analyses at a family level. In order to obtain universal primers for polypores of Hymenomycetes, mt SSU rRNA genes were cloned from *Bjerkandera adusta, Ganoderma lucidum, Phlebiopsis gigantea,* and *Phellinus laevigatus* and their sequences were determined. Phylogenetic relationships were resolved quite efficiently by mt SSU rDNA sequences, and they were proved to be more useful in phylogenetic reconstruction of *Ganoderma*. From phylogenetic analyses of several genera of Hymenomycetes and strains of the genus Ganoderma, it is clear that mt SSU rDNA sequences can be used as molecular markers to resolve phylogenetic relationships of both higher and lower rank of taxa, because the region is composed of conserved and variable domains. In addition, insertion and deletion events as well as the primary sequence can be used as important molecular markers to resolve phylogenetic relationships.

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