The evolutionary status of fungi

†B. S. Mehrotra

Mehrotra BS 1992. The evolutionary status of fungi. *Palaeobotanist* **41** : 23-28.

This review reflects on the uncertainties revolving round the origin of fungi and the paucity of the fossil record of these organisms. The main cause for the lack of fossil data is perhaps the insufficient attention these organisms have received and not that they have evaded the attempts to bring them to light. A brief review of the criteria generally used in propounding the hypotheses for the evolution of the modern fungi has also been made.

Key-words—Evolution, Status, Fungi.

†*B. S. Mehrotra, 23 C. Y. Chintamani Road, Allahabad.*

सारॉंश

कवकों की विकासीय स्थिति

बी० एस० मेहरोत्रा

प्रस्तुत समीक्षा में कवकों की उत्पत्ति तथा इनके अल्प अश्मित अभिलेखों को ध्यान में रखते हुए विवेचना की गई है। कवकों के कम अश्मित अभिलेखों का कारण सम्भवतः इनकी ओर कम ध्यान देना है न कि इनके कम अभिलेखों का होना। कवकों के विकास हेतु इस शोध-पत्र में एक परिकल्पना भी प्रस्तुत की गई है।

TYPICAL of botanists of his time Professor Sahni had a much broader based knowledge of botany and whatever he did it was characterised by depth and precision. Besides his outstanding contribution to palaeobotany, what he did in palaeomycology still holds true. For example, two species of fossil fungi discovered by him and Rao in 1943, viz., *Perisporiacites varians*, with dark spherical closed bodies, and *Palaeosordaria lagena*, with flask-shaped perithecia, resembling the modern genus *Sordaria*, still figure in the latest edition of Dictionary of Fungi prepared by Ainsworth and Bisby.

Biological evolution has been defined as a change in the diversity and adaptation of populations of organisms (Mayr, 1974, 1978). In fact, it is the diversity of the organic world which is one of the main factors for the never ending interest of a biologist in the group of organisms of his choice. The great diversity of fungi, characterised by wide range of body types, reproductive mechanisms and associations and their complex eucaryotic internal organisation, which enables them to adapt to all possible environmental extremes and to accomplish biosynthetic processes being utilised by man for his gains since posterity, are two of the many reasons which have kept a mycologist ever busy in a never ending quest for more and more bizarre forms of fungi. Perhaps no other single major group in the Plant Kingdom has such a great degree of diversification than the Fungi (Delevoryas, 1966).

ORIGIN AND EVOLUTION OF FUNGI

We cannot say for sure whether the fungi originated during the Precambrian or the Phanerozoic Era, and also how they have subsequently evolved during geologic time. A perusal of the fossil records of the two eras convinces us on the truth of this statement.

Precambrian

The history of Precambrian life is still mysterious inspite of the use of modern biochemical, geological and mineralogical methods. It is generally believed that conditions of life at that remote epoch when life originated on the earth were

Essays in Evolutionary Plant Biology
Editors : B. S. Venkatachala, David L. Dilcher & Hari K. Maheshwari
Publisher : Birbal Sahni Institute of Palaeobotany, Lucknow

anoxic. During this period anaerobic procaryotic organisms came into being. Gradually with the evolutionary changes in the environment, first the partially aerobic procaryotes and later the chiefly aerobic ones had evolved. Perhaps this latter phase of evolution was a polyphyletic one and took place in a shorter time than the anaerobic evolution of the procaryotes (Knoll, 1990). The oxygen was added to the atmosphere later when certain photosynthetic procaryotes, chiefly cyanobacteria (blue-green algae) came into existence.

The presence of bacteria and blue-green algae during the Precambrian seems to be well documented. Since 1950's, numerous ancient sedimentary deposits, the stromatolites, have been found in the form of mounds or pillars made up of many thin layers piled one on top of another. They were first discovered in the Precambrian strata from Western North America by Walcott and later in Gunflint Iron Formation (age about 2 Ga years old) near Lake Superior in Ontario by Tyler and Barghoorn (1954). Stromatolitic cherts near the base of the formation were found to contain abundant microfossils preserved as organic, haematitic, or pyritic structures. With the discovery of living stromatolites in several coastal habitats notably in a lagoon at Shark Bay on the western coast of Australia, the biological origin of fossil stromatolites, chiefly by activities of blue-green algae and bacteria, seems to have been confirmed. The age of the sedimentary deposits has, however, been doubted as it can be determined on the basis of the nearest underlying and overlying datable rock units and the radioactive isotope method has an accuracy of plus or minus 5 per cent (Schopf, 1978).

It is generally believed that procaryotic micro-organisms preceded the eucaryotic. The endosymbiotic hypothesis proposes that the eucaryotes arose polyphyletically from the primitive photosynthetic procaryotes (Edwards, 1976). But how and when this change over from procaryotic to eucaryotic life occurred is a mystery. The distinction between Precambrian procaryotes and eucaryotes is commonly based on a statistical study of the sizes of known Precambrian microfossils and comparison with modern examples. The evolution of eucaryotes brought not only a change in average size but also significant alterations in the internal organisation of the cells, including the change from membraneless nuclei and organelles in procaryotes to membrane bounded nuclei and organelles in eucaryotes. The two groups also differ in physiology. While procaryotes are chiefly responsible for fermentation and produce unsaturated fatty acids, the eucaryotes respire and form saturated and/or polyunsaturated fatty acids (Schopf, 1978). The earliest eucaryote-like fossils probably were less than 1.5 Ga yrs old. Two types of such fossils are: (i) branched filaments made up of cells with distinct cross walls that resemble hyphae of fungi or green algae from the Olkhim Formation of Siberia, about 725 million years old and, (ii) complex flask-shaped microfossils of fungi or algae from the Kwagunt Formation, about 300 million years old.

At present we do not have sufficient evidence either to substantiate or reject the concluding remark of the eminent mycologist G.W. Martin (1968) that 'fungi (may) have been present for over two billion years, from Precambrian time, in aquatic habitats', especially when we know that the Precambrian Era has not received the attention of palaeomycologists as it deserved.

Phanerozoic

Reports of fungi from the Phanerozoic Era are generally of those which were fossilised with vascular plants. Most of these records are from the Carboniferous to Tertiary, with a considerable increase during the latter period as angiosperms, serving as hosts of the parasitic fungi, were abundant then. One such example is that of a number of ascomycetous leaf ectoparasites from the Middle Eocene (45 Ma) of Tennessee (Dilcher, 1963, 1965).

Approximately 500 species of fossil fungi belonging to a broad range of taxonomic categories have been reported, many of them prior to 1900. Most are a result of chance discoveries and no systematic treatment of the data has been assembled (Tiffney & Barghoorn, 1974). The known record of fossil fungi is of little value for tracing the evolutionary history of fungi through the geologic time or during the modern period. Some of the reasons for this are:

1. Reports of fossil fungi are influenced by the preference of individual investigators and their interest in a particular geological stratum or the type of fossils (micro- or macro-scopic). Just as in the case of reports of modern fungi (Mehrotra, 1977) such reports fail to reflect upon the geographical distribution of fossil fungi. For example, "Sclerotinites" reported from Palaeozoic and Tertiary, employing thin and polished sectioning techniques, are a result of the special interest of petrologists in coal deposits.
2. Identification of fossil fungi is commonly based on a vague resemblance (Tiffney & Barghoorn, 1974), such as of external appearance of minute fruiting bodies or hyphal strands.

A few errors have been subsequently rectified. For example, the reports of fossil algae by Duncan (1876) are now classified as Phycomycetes, and some specimens identified as Hemisphaeriales (Ascomycetes) are now placed in the Chytridiales (Phycomycetes) by Bradley (1967).

3. Records depend on the material of which the fungus is constituted (size and composition of the organism; Tiffney & Barghoorn, 1974); and the availability of the stratum in which it could be preserved. For example, the parasitic fungi, obligate ones in particular, can be related to the presence of particular group of host plants. Savile (1976), therefore, had pertinently pointed out that in the case of obligate parasites both hosts and parasites reflect each other's age.

EVOLUTIONARY STATUS OF MODERN FUNGI

The concept of evolution has ever been of great help in not only bringing order to the study of any biological group but also in providing a broader perspective necessary for an overall understanding of a group and to provide an ultimate basis for a satisfactory taxonomy, so essential for a correct approach to any phase of mycology. With over 65,000 species of living fungi presently known and an ever-increasing number of new species, mycologists have been busy determining the evolutionary patterns within the fungi in general and within the taxonomic groups of fungi of their choice in particular. In the absence of fossil record of value, phylogeneticists have based their phylogenetic hypotheses on imagination (Bessey, 1950), speculation, inference, and intuition (Muller, 1978).

Two views have prevailed regarding the phylogeny of fungi. In one, the emphasis has been on the algal ancestry (either polyphyletic or monophyletic) and in the other on the protozoan ancestry, with the latter finding favour of majority of the workers. It is also likely that some groups of fungi may have evolved from the algae and others from Protozoa. An alternative view which did not attract many followers suggested that fungi may not have evolved from either the algae or the Protozoa. This theory of the independent origin of fungi was suggested by Wolf (1960) in view of the wonderful chemosynthetic potentialities possessed by many fungi and that are unknown in algae or Protozoa. Martin (1968) has discussed at length current hypotheses regarding the phylogeny of fungi.

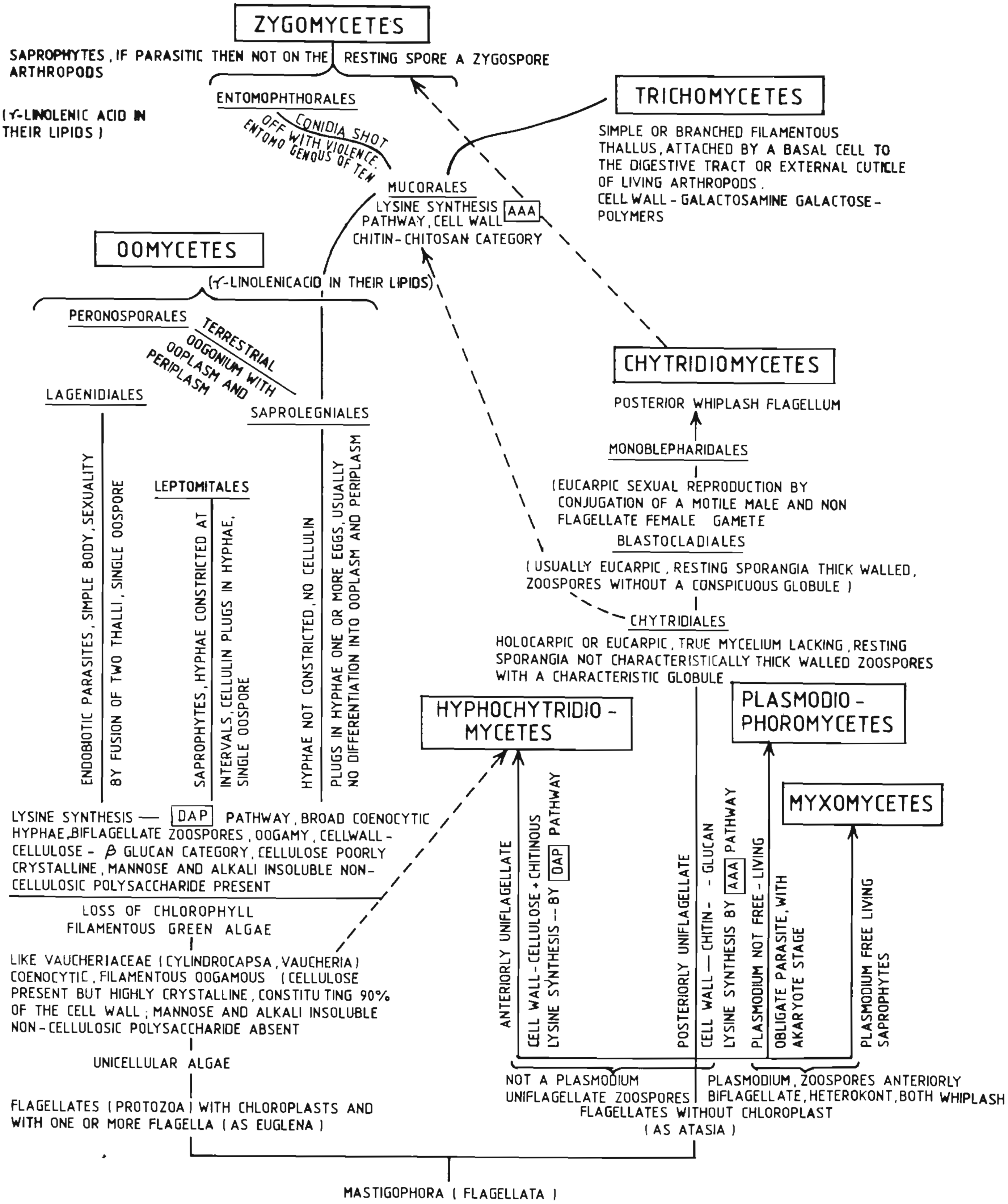
In the absence of a fossil record which might indicate the evolutionary trends of the fungi, different phylogeneticists have laid partly or completely differing criteria for their evolutionary hypotheses. General principles of evolution and their application to phylogenetic theories of fungi have been discussed in detail by Savile (1968). Raper (1968) commented on the role of genetics in the evolutionary history of fungi. Some of the more significant criteria which have influenced students of phylogeny are briefly discussed here with the hope that this discussion will be of help to those interested in evaluating existing phylogenetic theories.

1. *Morphology*—The foremost criterion supporting any hypothesis of fungal evolution is morphology. But too much emphasis on form has resulted in relating fundamentally unrelated groups or species of fungi in which similarity in structure is largely due to similar habitat and parallel evolution. Simple morphology and life cycles are generally considered more primitive than complex ones but they can be regressive forms of the convergent or more highly evolved groups. Attempts, therefore, have been made to de-emphasize morphology and to stress other criteria.

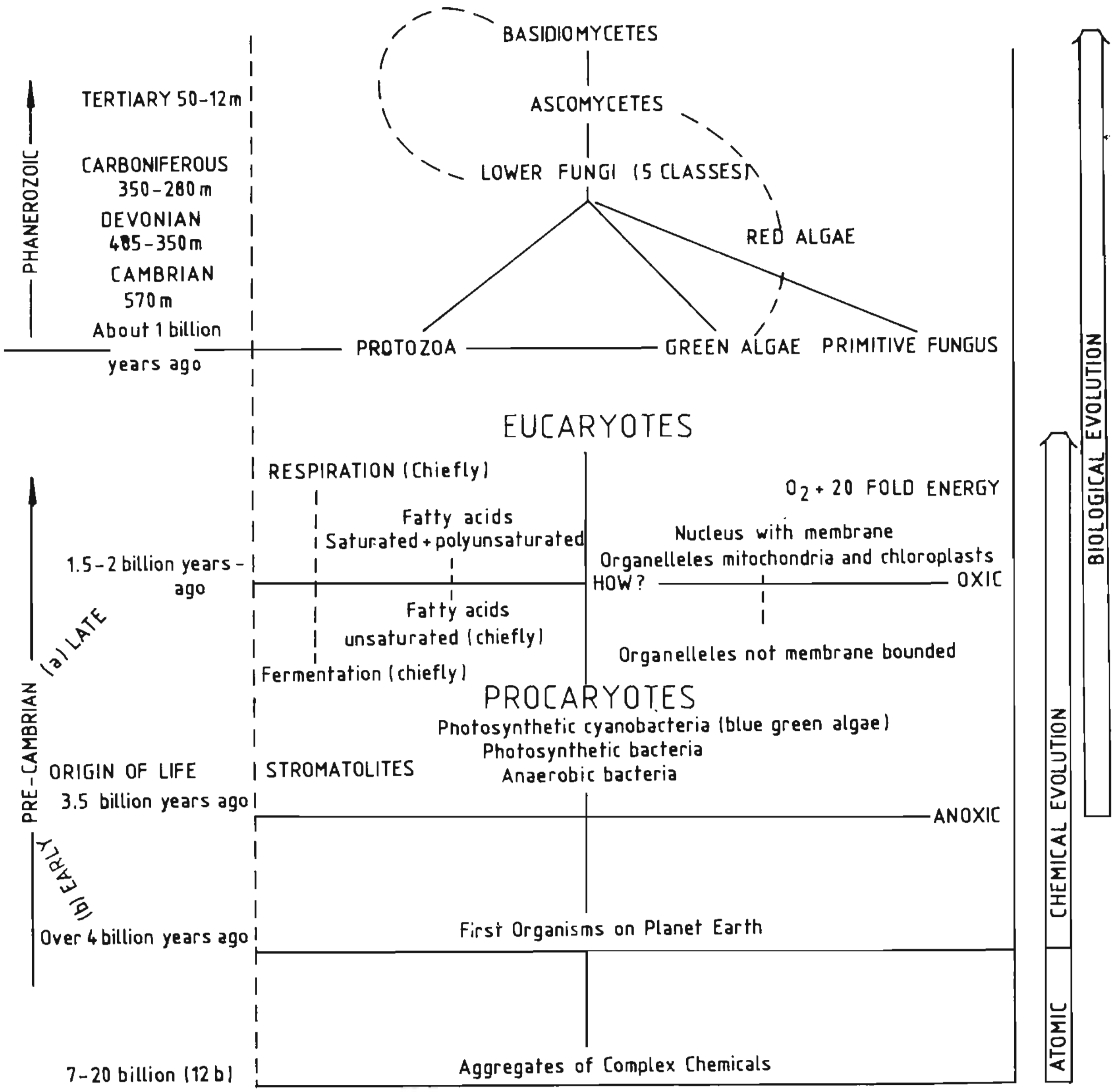
2. *Function of structures*—Burnett (1968) suggested that the function of a structure is a significant criterion as it can provide for a rationalisation of structure and can indicate the kinds of selective agencies which are likely to have been operative in the development of a particular feature. Since, it is not possible to ascribe a definite functional significance to all structures, this feature can be of limited value in specific areas.

3. *Nutrition and synthetic capacity*—Saprophytic fungi are believed to have evolved from parasitic ones. During this process they have developed the competence to synthesize each specific nutrilite formerly obtained from the host (Raper, 1968). Cantino (1955) considered the loss of synthetic competence as of prime importance in the evolution of water moulds from ancestral forms having high synthetic capacity. However, application of this criterion to all groups of fungi is not possible because the synthetic capacity of most fungi is not known in such detail as that worked out for water moulds.

4. *Biochemical characters*—In simple organisms biochemistry often proves more reliable than gross morphology in indicating genetic relationship (Savile, 1960). Certain biochemical characters such as cell wall composition (Bartnicki-Garcia, 1968), metabolic pathways adopted for the production of metabolites such as lysine (Vogel, 1963), and the sedimentation behaviour of the



Text-figure 1—Probable course of evolution of lower fungal groups.



Text-figure 2—Probable course of evolution of Fungi.

enzymes involved in tryptophan biosynthesis (Bartnicki-Garcia, 1970) have been emphasized. Based on these and other important criteria evolutionary trends within the Lower Fungi are illustrated in Text-figure 1.

5. *Co-evolution of fungal parasites and their hosts*—The earliest evolved parasitic organisms have to co-exist with their hosts and both may directly or indirectly interact with each other. However, in no case has it been demonstrated that either of the partners was exerting reciprocal selective pressure over a period of geological time, and therefore examples of strict co-evolution have yet to be demonstrated (Morris, 1990).

Leppik (1967) proposed a theory of the coevolution of the rust order Uredinales and their hosts through geologic time. Species on a more primitive host are considered primitive to those on an advanced host. For example, one on a fern is primitive to one on a gymnosperm, and one on the latter host is more primitive to that on an angiosperm.

Text-figure 2 summarises our knowledge of the evolutionary status of fungi.

CONCLUSION

From this brief and frank appraisal of the evolutionary status of fungi it is amply clear that among all micro-organisms fungi have been the most neglected group although they offer great promise for unravelling the mystery of the first appearance of heterotrophic eucaryotic life. Perhaps the early attempts of palaeobotanists lacked the desire to unearth the early fossil history of fungi because they were too busy with problems of the evolution of higher plants. Concerted effort of palaeomycologists is very much needed and will be rewarding.

ACKNOWLEDGEMENTS

I am grateful to Dr B. S. Venkatachala, Director, Birbal Sahni Institute of Palaeobotany, for his kind invitation to present a paper on this topic at the Symposium, and to Professor David Dilcher for going through the manuscript at its initial stage and making some useful suggestions during his sojourn to Allahabad University.

REFERENCES

Bartnicki-Garcia S 1970. Cell wall composition and other biochemical markers in fungal phylogeny. *In* Harborne JB (Editor)—*Phytochemical phylogeny* : 81-103. Academic Press, London.

Bessey EA 1950. *Morphology and taxonomy of fungi.* Blakiston, Philadelphia.

Bradley WH 1967 Two aquatic fungi (Chytridiales) of Eocene age from the Green River Formation of Wyoming. *Am. J. Bot.* **54** : 577-582.

Burnett JH 1968. *Fundamentals of mycology.* Edward Arnold, London.

Cantino EC 1955. Physiology and phylogeny in the water moulds. *Q. Rev. Biol.* **30** : 138-149.

Delevoryas T 1966. *Plant diversification.* Holt, Rinehart, and Winston, Inc.

Dilcher DL 1963. Eocene epiphyllous fungi. *Science* **142** : 667-669.

Dilcher DL 1965. Epiphyllous fungi from Eocene deposits in western Tennessee, U.S.A. *Palaeontographica* **B116** : 1-54.

Duncan PM 1876. On some unicellular algae parasitic within Silurian and Tertiary corals with a notice of their presence in *Calcaola sandalina* and other fossils. *Q. J. geol. Soc. Lond.* **32** : 205-211.

Edwards P 1976. A classification of plants into higher taxa based on cytological and biochemical criteria. *Taxon* **25** : 529-542.

Knoll AH 1990. Precambrian evolution of prokaryotes and protists. *In* Briggs DEG & Crowther PR (editors)—*Palaeobiology, a synthesis* : 9-16. Blackwell Scientific Publications, Oxford.

Leppik EE 1967. Some viewpoints on the phylogeny of rust fungi. VI. Biogenic radiation. *Mycologia* **59** : 568-579.

Martin GW 1968. The origin and status of fungi (with a note on the fossil record). *In* Ainsworth GS & Sussman AS (editors)—*The fungi.* **3** : 635-648. Academic Press, New York.

Mayr E 1974. The challenge of diversity. *Taxon* **23** : 3-9.

Mayr E 1978. Evolution. *The fossil record and evolution* : 7-15. W. H. Freeman & Co., San Francisco.

Mehrotra BS 1977. The current status of studies on the fungal flora of India : an overview. *Bull. bot. Surv. India* **19** : 293-300.

Morris SC 1990. Coevolution. *In* Briggs DEG & Crowther PR (editors)—*Palaeobiology, a synthesis.* Blackwell Scientific Publications, London.

Muller E 1978. Taxonomy and phylogeny of fungi. *In—Progress in Botany* (40) : 339-357. Springer Verlag, Berlin.

Raper JR 1968. On the evolution of fungi. *In* Ainsworth GS & Sussman AS (editors)—*The fungi* **3** : 677-693. Academic Press, New York.

Sahni B & Rao HS 1943. A silicified flora from the Intertrappean cherts around Sausar in the Deccan. *Proc. natn. Acad. Sci. India* **13** : 36-75.

Savile DBO 1968. Possible interrelationships between fungal groups. *In* Ainsworth GS & Sussman AS (editors)—*The fungi.* **3** : 649-675. Academic Press, New York.

Savile DBO 1976. Evolution of the rust fungi (Uredinales) as reflected by their ecological problems. *Evol. Biol.* **9** : 137-207.

Schopf JW 1978. The evolution of the earliest cells. *In—Readings from scientific American* : 47-62. W. H. Freeman & Co., San Francisco.

Tiffney BH & Barghoorn ES 1974. The fossil record of the fungi. *Occasional papers, Farlow Herbarium of Cryptogamic Botany* (7) : 1-42.

Vogel HJ 1963. *In* Bryson V & Vogel HJ (editors)—*Evolving genes and proteins* : 25-40. Academic Press, New York & London.

Wolf FA 1960. Concepts regarding fungi—then and now. *A,S.B. Bull.* **7** (4) : 59-61.