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Indian Myxomycetes: A Comprehensive Review and Future Prospects

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Abstract

Myxomycetes, commonly called slime molds or plasmodial slime molds, are a unique group of protists combining features of both protozoans and fungi. Nearly 535 species have been recorded from India, reflecting its remarkable diversity for this group of organisms. Although earlier reviews have largely emphasized taxonomy, comparatively little focus has been placed on ecological, cultural, and applied aspects of myxomycetes. The purpose of this review is to provide a comprehensive synthesis of Indian contributions, integrating taxonomic, ecological, experimental, and applied perspectives, and highlights emerging research directions and future prospects in the field.

Keywords – biochemical – cultivation – ecology – India – physiology – slime molds – taxonomy

Introduction

There are approximately 1,100 species of myxomycetes, commonly known as slime molds, worldwide, which makes them a diverse group of eukaryotic microorganisms (Lado 2005–2025). The most commonly observed stages of the myxomycetes life cycle are fruiting bodies and plasmodia, which can be found in decaying wood and leaf litter. In 1858, de Bary coined the term 'Mycetozoa' for this category of organisms. He described the relationship between these organisms and protozoans (animals). However, in 1960 and 1961, Martin chose to use the term Myxomycetes instead of Mycetozoa to emphasize the association of these organisms with fungi rather than protozoans (Martin 1960). Olive (1975) supported the idea of a connection to animals and preferred to label them as Mycetozoans.

Myxomycetes display a relatively intricate life cycle (Clark & Haskin 2010). They produce spores within their fruiting structures, which represent the reproductive stage of these organisms. When conditions are favorable, the spores germinate, producing one to four haploid protoplasts (or cells) without walls. Some of these protoplasts develop flagella shortly after being released, while others retain an amoeboid shape. The cells with flagella are called swarm cells, while the non-flagellated cells are referred to as myxamoebae (Clark & Haskin 2016). Two compatible swarm cells or myxamoebae fuse to form a diploid zygote. This diploid zygote begins to absorb nutrients and evolves into a free-living multinucleate mass of protoplasm known as a plasmodium, which is the most distinctive feature of the myxomycete life cycle, hence the term plasmodial slime molds.

Due to their spore-producing structure, myxomycetes were historically grouped with fungi; however, recent genetic studies have placed them more closely with amoebozoans (Shadwick et al 2009, Tice et al. 2016) In the traditional classification framework, myxomycetes are placed into five

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orders—Echinosteliales, Liceales, Trichiales, Stemonitales, and Physarales. This classification is based on various morphological traits, including the presence of capillitium or the calcification of their fruiting bodies (Massee 1892, Macbride 1922, Jahn 1928, Martin 1960). Currently, myxomycetes are classified under the superclass Eumycetozoa within the kingdom Amoebozoa (Adl et al. 2005). This current system of classification adheres to the International Code of Zoological Nomenclature as well as the classification system for protists recommended by the International Society of Protistologists (Adl et al. 2007).

India, characterized by its varied climatic conditions and abundant ecological diversity, offers an ideal environment for numerous species of myxomycetes. The primary environmental elements that affect the distribution of these organisms include temperature, moisture, and rainfall (Stephenson 1989, Ndiritu et al. 2009). The Indian subcontinent presents an optimal climate for myxomycetes to thrive, allowing them to be gathered as fruiting bodies or plasmodia from decaying wood or leaf litter.

Over time, numerous regional investigations have documented the occurrence of myxomycetes across India. However, most of these studies have emphasized species identification and checklists (Ranade et al. 2012), with limited attention to ecological roles, environmental responses, or molecular mechanisms. Earlier reviews have largely summarized biodiversity surveys from different regions (Ranade et al. 2012, Lakhanpal et al. 2021). The present review provides a comprehensive account of myxomycete research in India, encompassing not only biodiversity assessments but also biochemical, physiological, and molecular investigations. In doing so, it aims to advance the understanding of Indian myxomycetes and outline future directions for interdisciplinary research.

Historical perspective on the study of myxomycetes in India

Initial Documentation and Botanical Surveys of myxomycetes

In India, most of the information related to myxomycetes has come from biodiversity surveys conducted by various researchers across different areas of the country. The earliest known record of myxomycetes from the Indian subcontinent goes back to approximately 1830 when Dr. Wright discovered *Physarum cinereum* (Batsch) Pers. in Madras (Lakhanpal & Mukerji 1981a). This groundbreaking collection represents the beginning of myxomycete research in India. Following this, in 1862, J. C. Habson noted the presence of *Hemitrichia serpula* (Scop.) Rost. in Bombay (Lakhanpal & Mukerji 1981a). Between 1854 and 1882, E. S. Berkeley identified 11 additional species from southern India, such as *Physarum pusillum*, *Didymium difforme*, *Diderma hemisphericum*, *Didymium squamulosum*, *D. melanospermum*, *Diachea leucopodia*, *Comatricha typhoides*, *Lycogala epidendrum*, and *Tubifera ferruginosa* from the Nilgiris, along with *Fuligo septica* from Cannanore and *Stemonitis herbatica* from Pondicherry (Lakhanpal & Mukerji 1981a). These specimens were subsequently validated by A. Lister and stored in the herbaria of the British Museum (Natural History) in London and the Royal Botanic Gardens in Kew (Thind 1977). By the end of the 19th century, only 15 species of myxomycetes had been documented in India (Kharat 1999).

Further advancements occurred in the early 20th century through the groundbreaking collections made by Drake (1911–1927), who obtained 124 specimens representing 74 species from locations such as Shimla, Dalhousie, Nainital, Mussoorie, Serampore, and Darjeeling (Kharat 1999). A significant number of these specimens were identified by G. Lister (Kharat 1999). However, until this time, there were no published accounts available. The first organized research emerged in 1924 when G. Lister released "Mycetozoa from North India," which was based on 36 collections made by Mrs. Drake (1912–1919), thus establishing the groundwork for the scientific examination of Indian myxomycetes (Lister 1924).

After Lister's seminal contribution, Bruhl & Gupta (1927) became the second group to publish findings on Indian myxomycetes with their work "Indian Slime-Fungi (Myxomycetes or Mycetozoa)" from West Bengal, in which they documented 16 species. The next significant milestone occurred in 1934, when Lodhi published "Indian Slime Moulds," the first comprehensive monograph addressing Indian myxomycetes, providing descriptions and illustrations of 43 species, primarily based on Mrs. Drake's collections. During the same timeframe, between 1932 and 1934, G. Fareau obtained specimens of 12 species of myxomycete from the Paini Hills in South India; these were identified by E.M. Wakefield and later archived at the Kew Herbarium (Thind 1977).

Myxomycetes were briefly referenced by Uppal and collegues in 1935; however, Lakhanpal (1983) identified the years between 1935 and 1952 as a gap when no studies on Indian slime molds were carried out. During this time, Mundkur (1938) compiled a list of myxomycetes in his supplement to Indian Fungi, originally published by Butler & Bisby (1960), which was later enhanced by Vasudeva in 1962 to include 27 genera, 79 species, and eight varieties, laying an essential groundwork for future taxonomic research in India.

Research interest was rekindled around 1952 when Erandy reported a new species from Southern Travencore (Erandy 1953). From 1954 to 1965, Agnihothrudu conducted thorough surveys throughout South India, documenting 30 species and describing numerous new taxa through a series of notes (Agnihothrudu 1954b, 1955, 1956a, b, c, 1958, 1959, 1961, 1963, 1965). He also noted 56 species, including two new ones, from Assam. Simultaneously, further regional research contributions were made by Ghosh & Datta (1962a, b, c, 1963) from Orissa, Kar (1964a) from Calcutta, Singh & Pushpavathy (1965, 1966) from Delhi, and Agnihothrudu & Chinappa (1966, 1969) from Karnataka. Additional progress was made by Indira during the period 1966–1971, who described and illustrated species from Tamil Nadu (Indira 1966, 1968a, b, c, 1969a, b, c, 1971).

A significant body of research was conducted in the northwestern Himalayas by Thind and co-workers between 1955 and 1971 (Thind & Sohi 1955, 1956a, b, c, Thind & Rehill 1957, 1958, 1959, Thind & Manocha 1957, 1958, 1963, 1964, Thind & Sehgal, 1960, 1963, 1964, Thind & Dhillon 1967, Thind & Lakhanpal 1968a, b, Thind & Khara 1969, Thind et al. 1957, 1971), during which they documented 165 species, comprising 17 new species, two new varieties, and four new forms. Thind subsequently compiled these findings along with earlier reports in his 1977 monograph "The Myxomycetes of India," in which he described a total of 186 species, three varieties, and six forms (Thind 1977). The pioneering Indian myxomycologists who laid the foundation for taxonomic and floristic studies of myxomycetes in the country are illustrated in Fig. 1. In 1966, Dr. P. U. Indira made history as the first Indian to earn a Ph.D. in myxomycetes (Indira 1966, Lakhanpal 1983). In early 1970s, comprehensive studies on Indian myxomycetes were initiated across various regions, leading to significant enhancements in the country's taxonomic and ecological databases. Lakhanpal (1971, 1972, 1973, 1974, 1975, 1978) and the collaboration of Lakhanpal & Mukerji (1976a, b, c, d, e, f, g, h, 1977a, b, c, d, 1978a, b, c) carried out detailed surveys in Delhi and Himachal Pradesh, while Dhillon (1976, 1977a, b) and Dhillon & Nannenga-Bremekamp (1977, 1978) concentrated on the western Himalayas. Further contributions came from Kowalski & Lakhanpal (1973) in Himachal Pradesh and Sekhon (1976, 1978, 1979a, b, 1980) in Chandigarh. Chopra (1984), in his doctoral thesis, contributed substantially to the knowledge of Indian myxomycetes by adding 48 species and three varieties as new records for the country. Shortly thereafter, Sharma (1986) carried out extensive surveys in the Eastern Himalayas and documented 139 taxa in total, of which 14 species and three varieties represented new additions to the Indian myxomycete flora.

Parallel efforts were undertaken in western and central India. Uppal et al. (1935) were among the pioneers to make initial references to myxomycetes, followed by observations from Chavan & Kulkarni (1974), Thite (1975), and Patwardhan & Joshi (1975). A notable advancement took place with Ranade (1978), who collected and recorded 81 species across 23 genera from 18 sites in western Maharashtra. During the late 1970s, further records were added by Ranade & Mishra (1977), Patil & Mishra (1977), and Mishra & Ranade (1979), who recognized seven species, including *Physarum pusillum* (Berk. & Curt.) G. Lister, *Diderma circumscissilis* Patil, Mishra & Ranade, and *D. mariei* Patil, Mishra & Ranade. Additional floristic research was subsequently carried out by Nanir, which significantly enriched knowledge of the myxomycete flora of western Maharashtra and the Marathwada region. Nanir described new species and published a sustained series of contributions on Indian myxomycetes and the myxomycetes of Marathwada, including taxonomic treatments and regional accounts (Nanir 1979, 1981, 1983, 1984, 1985, 1992, Nanir & Rokade 1985, 1991a, b, 1992, 1993a, b, Nanir et al. 1991, 1993a, b, 1998).

Over the subsequent decades, floristic surveys conducted in different areas of Maharashtra and surrounding regions further expanded the catalog of known species. Rokade (1989) documented a total of 106 species from the Khandesh region, while Chimankar (1993) recorded 109 species across five districts in East Vidarbha. In the Western Ghats, Salunkhe (1995) identified 105 species and one variety from the Dang Forest, including 16 species that were newly described. Kharat (1999) reported findings from the Pachmarhi Hills in Madhya Pradesh, noting 126 species and one variety. Tembhurne (2011) conducted a survey in southeastern Maharashtra and found 107 species belonging to 23 genera. Subsequently, Mishra and co-workers described additional new myxomycete taxa from western Maharashtra, including new species and new taxa of *Diderma* (Mishra et al. 2013, Mishra & Phate 2013a, b).

Ranade et al. (2012) published the first comprehensive checklist of Indian myxomycetes, cataloguing 373 species and highlighting their absence from several northeastern states (Arunachal Pradesh, Meghalaya, Nagaland, Manipur, Tripura, and Mizoram) as well as from Telangana and Andhra Pradesh. Subsequent surveys expanded this baseline, with Manoharachary et al. (2012) and Manoharachary & Rajithasri (2015) documenting 35 species from Andhra Pradesh and Telangana. This knowledge was further extended by Manoharachary & Nagaraju (2017), who reported approximately 30 additional taxa as new records for Telangana, thereby considerably broadening the distributional range of the group in southern India.

Regional explorations continued to enrich the database of Indian myxomycetes. Moreno et al. (2018) reported four nivicolous taxa—*Didymium dubium*, *Lamproderma ovoideum*, *L. ovoideum var. cucumer*, and *Trichia alpina*—from the northwestern Himalayas (Himachal Pradesh), representing the first records of nivicolous myxomycetes from alpine habitats in India. Similarly, Hashmi et al. (2020) recorded four species from Jammu and Kashmir, including *Arcyria major*, *Trichia decipiens*, and *Stemonitis fusca* as new state records, underscoring the underexplored diversity of this region.

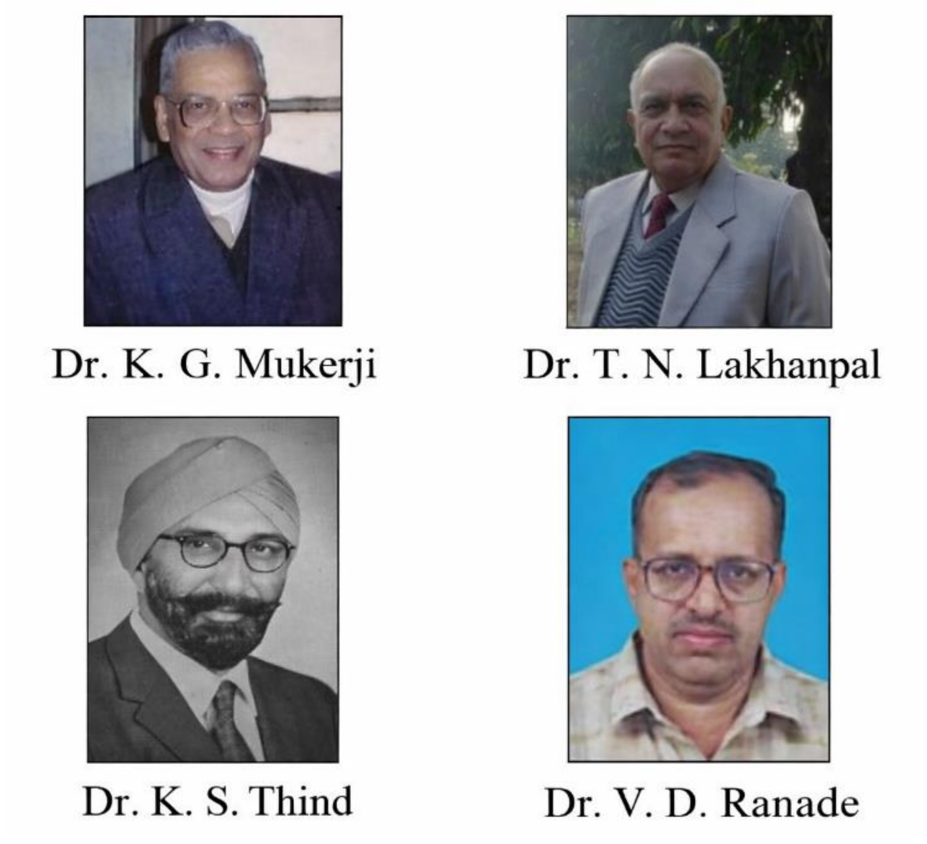

Fig. 1 – Pioneering Indian myxomycologists who made foundational contributions to the documentation, taxonomy, and floristic exploration of myxomycetes in India: a Dr. K. G. Mukerji. b Dr. T. N. Lakhanpal. c Dr. K. S. Thind. d Dr. V. D. Ranade.

From coastal ecosystems, Phate (2023c) reported 26 species from the Alibag area of Raigad district, Maharashtra, providing new insights into the distribution of myxomycetes in littoral habitats. In southern India, Kumar et al. (2023) surveyed tropical dry evergreen forests along the southeastern coastal belt and documented 11 taxa across Ceratiomyxales, Trichiales, Stemonitidales, and Physarales, including several first records for Tamil Nadu such as *Ceratiomyxa fruticulosa var. arbuscula*, *Arcyria insignis*, *Hemitrichia serpula*, and *Stemonitis flavogenita*. Most recently, a preliminary survey from Kerala recorded 42 species of myxomycetes, of which 20 represented new additions to the state's flora (Arunkumar et al. 2025).

Based on these cumulative contributions, the total number of myxomycete species recorded from India now approaches 535. These findings underscore the extraordinary diversity of Indian myxomycetes and reflect the cumulative work of numerous researchers over time. Although significant advancements have been made, many ecological niches—such as deserts, alpine snow areas, and various extreme habitats—remain inadequately explored, presenting considerable opportunities for future discoveries and ecological research.

Ecology and Habitat Studies

The early Indian studies on myxomycetes predominantly focused on taxonomy and systematics, with minimal emphasis on ecological dimensions. Gray & Alexopoulos (1968) pointed out the lack of ecological understanding regarding these intriguing organisms, stressing the lack of data necessary to determine the factors that affect their fruiting behavior and geographical spread. The initial ecological findings were made by Thind & Sohi (1955, 1956a, b, c), Thind & Rehill (1957, 1958, 1959), Thind et al (1957), Thind & Manocha (1963, 1957, 1958, 1964), Thind & Sehgal (1960, 1964, 1963), Thind & Dhillon (1967) Thind & Lakhanpal (1968a, b), Thind & Khara (1969) as well as Singh & Pushpavathy (1965, 1966), who intermittently noted variables such as elevation, season, and weather conditions during their collections. Following this, Indira (1968a) undertook groundbreaking ecological studies in the Coorg district of Mysore, detailing the habitat preferences and distribution of 22 species. She identified species such as *Perichaena chrysosperma*, *Stemonitis nigrescens*, *Badhamia macrocarpa*, *Physarum crateriforme*, *P. compressum*, and *P. rigidum* from the bark of living trees in both Coorg and Madras. However, it remained unclear whether these samples were isolated in moist chambers or gathered directly from nature. In another study, Indira (1968b) reported that calcareous myxomycetes (Physarales) favored substrates such as decayed leaves, twigs, and debris, while non-calcareous types (Stemonitales and Trichiales) were found more frequently on dead wood and bark.

In 1970, Rama Rao described a species found in the alkaline soils of Andhra Pradesh, while Lakhanpal (1971, 1972, 1973, 1974, 1975) continued to include ecological observations such as altitude and seasonal patterns in his collections. Around the same period, Lakhanpal & Mukerji (1975) investigated substrate specificity and identified four *Licea* species from bark and dung. Later, Lakhanpal (1975) & Thind (1973) recorded corticolous species, noting that only about 21 species had been identified from living bark in India, many of which were rare or newly described. Sood & Lakhanpal (1980) and Lakhanpal & Chopra (1982) further expanded these records. The latter work reported species such as *Licea parasitica*, *Echinostelium colliculosum*, and *E. minutum* from the bark of *Pinus wallichiana* (Lakhanpal & Chopra 1982). More recently, Phate & Chavan (2015) documented a rare microhabitat for *Stemonitis inconspicua* from Maharashtra, highlighting the continued discovery of specialized ecological niches for Indian myxomycetes.

A broader ecological and physiological perspective was later provided by Mubarak Ali (1993) in his doctoral dissertation, which examined various aspects of the ecology and nutrition of Indian myxomycetes, thereby strengthening the foundation for experimental ecological studies in the country. In the late 1970s, Venkataramani (1978) proposed that substrate specificity was influenced by calcium content and pH. Later, Lakhanpal & Chopra (1980) tested this hypothesis by studying the effects of substrate pH and height on myxomycete growth.

In the early 1980's, notable advancements were achieved. In his doctoral research, Chopra (1984) conducted one of the most thorough ecological studies titled "Biology of Corticolous

Myxomycetes” at Himachal Pradesh University in Shimla. He analyzed the bark of *Pinus wallichiana*, *Cedrus deodara*, and *Quercus incana*, identifying 82 species distributed across 22 genera and 10 families. His research indicated that the bark of *Cedrus deodara* provided the optimal environment for myxomycete fructification. Around the same time, Lakhanpal & Mukerji (1981b) examined the seasonal distribution in both the northwestern Himalayas and Delhi. Concurrent studies further enriched ecological knowledge. Venkataramani & Kalyansundaram (1986) linked distribution patterns to environmental variables, determining that calcareous species exhibited greater tolerance to tropical climates, flat terrains, and elevated temperatures, whereas non-calcareous species preferred temperate environments, hilly areas, cooler seasons, and moderate rainfall. Furthermore, Rahman (1987) explored the relationships between myxomycetes and associated bacteria, while Chopra (1984) looked into ecological factors including tree species preferences, bark specificity, incubation time, pH, substrate height, and monthly trends in fructification for corticolous forms in Shimla. A new phase of ecological research emerged much later. Ragu (2000) investigated the role of myxomycetes in the decomposition of wood and litter in pine plantations and shola forests within the Nilgiri Hills of Tamil Nadu. He noted that myxomycetes colonized logs that were moderately decayed in plantations and logs that were either moderately or significantly decayed in forests, usually after being colonized by Basidiomycetes. It was found that nitrogen activity was higher in logs with plasmodia, indicating their significant role in the decomposition processes within forests.

These groundbreaking studies signified a shift from taxonomy to ecology, emphasizing how altitude, pH, calcium levels, host species, and substrate decomposition affect the distribution of myxomycetes. While often secondary, they established a foundation for contemporary ecological research in India.

Application of Moist-Chamber Culture Technique in India

In India, the moist-chamber culture method has been effectively employed to investigate the occurrence of corticolous myxomycetes. This technique was first introduced by Thind et al. (1971) and since that time, a number of researchers have successfully utilized it to isolate various species from the bark of different tree varieties and other substrates, significantly improving our knowledge of their diversity and ecological roles.

The majority of corticolous myxomycetes reported from India have been gathered using this technique, which was originally developed by Gilbert & Martin (1933). This approach continues to be one of the most reliable methods for collecting species that inhabit bark. A consolidated summary of corticolous myxomycete species isolated in India using the moist-chamber culture technique, along with their substrates and host trees, is presented in Table 1.

Table 1 Summary of myxomycete species isolated in India using the moist-chamber technique.

No.	Reference	Species Isolated	Substrate/Host
1	Thind (1971)	*Licea biforis, L. pedicellata, L. tenera*	Bark of living trees
2	Lakhanpal & Mukerji (1975)	*Licea perexigua, L. scyphoides L. tenera, L. varibilis*	Bark of living trees Bark of *Cedrus deodara* Horse dung
3	Lakhanpal (1975)	*Calomyxa metallica, Perichaena depressa, Machrideola robusta, Machrideola cornea, Stemonitis herbatica*	Bark of *Cedrus deodara* Living tree bark *Rhododendron* sp. *Pinus excelsa* Maize leaves
4	Dhillon (1976)	*Licea belmontiana, L. castanea, L. testudinacea, Cribraria minutissima, Physarum* sp.	Bark of *Abies* sp. and *Aesculus* sp.

Table 1 Continued.

No.	Reference	Species Isolated	Substrate/Host
5	Sood & Lakhanpal (1980)	*Licea operculata,* *Cribraria pachydictyon* *Echinostelium cribrarioides* *Arcyria nigella* *Hemitrichia leonticha* *Comatricha nodulifera*	Bark of *Pinus excelsa*, *Cedrus deodara*, *Rhododendron* sp.
6	Lakhanpal & Chopra (1982)	*Licea parasitica, Echinostelium colliculosum, E. minutum*	Bark of *Pinus wallichiana*
7	Chopra (1984)	*Licea floriformis, L.hydrogyrangium, L. lilacina, L. morchelloides, L. nigrodenticulata, L. chelonoides, L. denudescens, L. kleistobolus, L. parasitica, L. pseudoconica, L. pusilla, L. pvamaca, L. scyphoides* var. *reticulata, Paradiacheopsis acanthodes, P. bremekampii Comatricha ellae, C. rigidirete*	Bark of *Pinus wallichiana, Cedrus deodara, Quercus incana*

Studies on Agar Cultures

The use of agar-based media to cultivate myxomycetes was first introduced by Klebs in 1900. Initial cultural investigations concerning Indian myxomycetes began in the early 1960's when Kar (1962, 1964b) successfully grew *Physarella oblonga* and *Physarum wingatense*. These foundational efforts were later expanded by Indira (1964, 1965, 1969a, b, c, 1971), Indira & colleagues (1963, 1971, 1974), and Lakhanpal & Mukerji (1976a, b, c, d, e, f, g, h), followed by Lakhanpal (1981), which signified a crucial period for experimental myxomycete research in India.

In addition to systematic and taxonomic studies (Indira 1968a, b, Kalyanasundaram 1975), substantial advancements in *in vitro* cultivation were achieved. For the first time, several species were successfully cultured from spore to spore in controlled laboratory conditions, such as *Arcyria cinerea*, *Diachea splendens*, *Stemonitis herbatica*, *Lamproderma scintillans*, *Comatricha suksdorfii*, *Physarum compressum*, *P. cinereum*, *P. gyrosum*, *P. serpula*, *P. vernum* and *Fuligo septica* (Indira & Kalyanasundaram 1963, Indira 1965, 1969a, b, 1971, Kalyanasundaram & Venkataramani 1974, Kalyanasundaram 1974, Venkataramani et al. 1977).

A comprehensive investigation by Indira & Kalyanasundaram (1971) explored how various agar media like soil extract, wood decoction, leaf decoction, Bengal gram, carrot, and oat agar affected *Stemonitis herbatica*, demonstrating that robust plasmodial growth occurred on soil extract, Bengal gram, carrot, and oat-based mediums. They also found that germination could take place from a single spore, although the germination potential decreased with spore age, and while light was not required for the initiation of fruiting, completing the process necessitated a phase of light followed by darkness. Germination rates were somewhat higher in the absence of light, with the ideal temperature for development ranging from 22 °C to 30 °C. Later, Indira & Venkataramani (1974) proposed that directly placing spores on agar was more effective for culturing plasmodia than transferring pre-germinated spores from liquid media.

Nanir (1978) introduced a new method known as the substrate decoction technique for the isolation of myxomycetes. That same year, Venkataramani (1978), in his doctoral research titled "Studies on Myxomycetes: Distribution in India and Some In Vitro Studies" (University of Madras), developed a coconut milk agar medium and performed in vitro studies on nine different species, including *Comatricha suksdorfii*, *Physarum gilkeyanum*, *P. nicaraguense*, *Didymium flexuosum*, *D. melanospermum*, *Craterium leucocephalum*, *Fuligo septica*, and *P. bogoriense*. Sporulation was successfully achieved in five of these species, while a novel “paper cone technique” was created for those that stayed vegetative, which triggered sporulation in four additional species.

Following this, Lakhanpal & Sood (1981a) explored spore germination, swarm cell fusion, plasmodium formation, and sporophore development in five species, thus enhancing the understanding of life-cycle management under controlled laboratory conditions. After a considerable gap, Singh (2005) conducted thorough physiological studies for his doctoral project titled “Physiology of Growth and Reproduction of Light-Sensitive Myxomycete Species”. From 26 species gathered in Varanasi and Chandauli (Uttar Pradesh), he succeeded in cultivating five species. These were *Fuligo septica*, *F. cinerea*, *Diderma effusum*, *Didymium squamulosum*, and *D. iridis*. His findings revealed that spores of *D. iridis* exhibited optimal germination at pH 5 and 25 °C, with weak bark decoctions promoting germination. He also showed that swarm cells and myxamoebae proliferated quickly in organic media, minerals played a crucial role in plasmodial growth, and carbohydrate- and protein-rich media with an osmotic concentration of 0.2 M, pH 5, and temperatures ranging from 20°C to 25°C provided the best conditions for plasmodial development.

Together, these investigations established agar culture as an effective method for researching Indian myxomycetes, facilitating systematic studies on spore germination, plasmodial development, and sporulation. By enhancing the types of media and culture methods, they offered crucial experimental frameworks that still guide physiological and developmental research on these organisms.

Physiological and Biochemical Investigations

Initial physiological studies in India concentrated on how light and pigments affect the growth of myxomycetes. Ganju & Mukherjee (1969) found that sporangial development in *Didymium iridis* was preferentially triggered by short wavelengths of light, a phenomenon linked to the existence of two flavonoid pigments. Notably, this response was confined to illuminated areas, indicating that light signals do not transfer throughout the plasmodium.

Research later turned to exploring the biochemical characteristics of spore wall pigments. Loganathan et al. (1989) studied twelve species from the orders Physarales, Stemonitales, and Liceales, identifying melanin as the main pigment in spore walls through physicochemical analyses, UV, and IR spectroscopy. Subsequently, Kalyanasundaram et al. (1994) found that melanin is present not only in dark-spored taxa but also in light-spored varieties, often accompanied by solvent-extractable pigments. Building on this, Loganathan (1995), in his doctoral research, examined spore wall pigments in *Stemonitis herbatica*, *Lycogala epidendrum*, *Trichia decipens*, and *T. favoginea*, asserting that the melanins in myxomycetes have complex structures, containing aliphatic and aromatic components along with protein and polysaccharide connections.

The effect of light on growth and reproduction was further explored by Paramasivan (1990) in *Stemonitis herbatica*. Although sporulation was not entirely dependent on light, exposure to light fostered the development of larger sporangia, bigger spores, and enhanced germination rates. Biochemical analysis indicated elevated levels of amino sugars, proteins, and melanin in light-exposed cultures, while cultures grown in the dark accumulated greater amounts of galactosamine, lipids, and nitrogen in their skeletal frameworks. Complementary research by Singh (2005) on *Didymium iridis* indicated that its light-sensitive brown plasmodium contained flavonoid pigments that influenced morphogenesis. Blue light hindered plasmodial growth but stimulated sporulation, whereas red light had the opposite impact. Together, these findings underscore the dual function of pigments—as both photoreceptors and as structural components of the spore wall.

Numerous studies have also investigated plasmodial metabolism and the secretion of enzymes. Mubarak Ali & Kalyanasundaram (1991) identified the production of extracellular amylase by *Physarum flavicomum* and *S. herbatica* that was not reliant on their associated bacteria. Later, Mubarak Ali et al. (1992) discovered that amylase secretion occurs solely during the vegetative phase and is inhibited during sporulation, only to resume upon spore release, thus connecting enzyme secretion to metabolic changes during reproduction. Likewise, Ragu (2000) showcased the ability of *Physarum gyrosum* to degrade wood and litter in the Nilgiri forests, isolating carboxymethyl cellulase and xylanase from plasmodia. These enzymes showed peak activity under acidic conditions (pH 5.0 to 5.5) and moderate temperatures (40 °C to 55 °C), contributing directly to the breakdown of cellulose and hemicellulose.

The microbial relationships of myxomycetes have also been studied. Balaji (2000) established diazotrophy in monoxenic cultures, demonstrating that *Physarella oblonga* associated with *Enterobacter cloacae* displayed significant nitrogenase activity in aerobic conditions. Sujatha (2000) went further to illustrate the bioremediation potential of plasmodial-bacterial consortia, which tolerated and decomposed heavy metals, hydrocarbons, azo dyes, and fungicides more efficiently than each partner could alone. In-depth studies of the *P. oblonga–E. cloacae* pairs revealed effective diesel degradation over a wide pH spectrum, with plasmid-encoded resistance traits in the bacteria being activated in conjunction with plasmodia (Sujatha 2000) . Protein expression studies have offered additional insights. Venkataramani et al. (1981) reviewed protein patterns during sporulation in *Physarum nicaraguense*, uncovering stage-specific expression associated with differentiation.

Such biochemical insights enhance our understanding gained from studies on pigments and enzymes, highlighting that research on Indian myxomycetes has significantly improved our knowledge of plasmodial physiology, metabolism, and ecological functions.

Molecular studies

Sujatha (2000) offered significant insights into the genetic foundations of metabolic versatility within myxomycete–bacterial associations at the molecular level. Her doctoral research revealed that the capabilities for degradation and resistance observed in the *Physarella oblonga–Enterobacter cloacae* consortia were primarily due to traits encoded by plasmids in the bacterial partner. A large megaplasmid extracted from *E. cloacae* contained genes that provided resistance to hydrocarbons, heavy metals, and fungicides, as demonstrated by the complete absence of these traits in plasmid-cured strains. Notably, standard cultures of *E. cloacae*, while morphologically and biochemically similar, did not possess these resistance factors, indicating that a prolonged interaction with the plasmodium may have encouraged plasmid acquisition and/or modified gene expression patterns.

These discoveries highlight the significance of horizontal gene transfer and symbiotic associations in influencing the metabolic and ecological capabilities of myxomycete–bacterial consortia, emphasizing their importance as model systems for examining co-evolutionary processes and practical bioremediation applications.

Cytological investigations

Thorough cytological studies carried out by Indira (1969c) investigated protoplasmic streaming and structural features in three varieties of plasmodia—phaneroplasmodium (*Physarum compressum*), aphanoplasmodium (*Stemonitis herbatica*), and an intermediate variant (*Arcyria cinerea*).

The initial cytological studies enhanced the comprehension of the variety in plasmodial organization and emphasized the functional variations in protoplasmic streaming behaviors among different groups of myxomycetes. Despite being somewhat narrow in focus, this research highlighted the capacity of cytology to connect structural and physiological viewpoints in the biology of myxomycetes.

The Author's Contribution to Myxomycete Research

The foundational agar culture studies started by Kar (1962, 1964b) and further developed through the significant contributions of Indira (1964, 1965, 1969a, b, c, 1971, 1974), Lakhanpal & Mukerji (1976a, b, h), Venkataramani (1978), and Singh (2005) have led to new systematic advancements in this area of research. Previous investigations successfully showcased cultivation methods for specific species, including *Physarella oblonga*, *Physarum compressum*, *Arcyria cinerea*, and *Fuligo septica*. Nonetheless, these studies were often constrained by the limited number of species analyzed, the narrow scope of taxonomic coverage, and the lack of comparative physiological insights.

With this groundwork already laid, my research has meaningfully progressed the cultural and physiological knowledge of Indian myxomycetes by presenting the first comprehensive study to culture a wide taxonomic range on agar media, including representatives from the orders Physarales, Trichiales, and Stemonitales (Phate 2015). Eleven species—*Physarum melleum*, *Diachea subsessilis*, *Fuligo septica* (Phate 2023b), *Diderma hemisphericum*, *Hemitrichia serpula* (Phate & Mishra 2014a), *Arcyria denudata* (Phate 2023a), *A. incarnata*, *Stemonitis flavogenita*, *S. fusca*, *S. smithii*, and *S. axifera* (Phate & Mishra 2014b) — were successfully cultured on various media. Several of these represent the first cultural records from India, including spore-to-spore cultures of *Arcyria denudata* (Phate 2023a), *Diachea subsessilis* (Phate 2019), and *Stemonitis axifera* (Phate & Mishra 2014). Others were sustained up to the plasmodial stage, thereby considerably broadening the range of cultivable species documented in the country. Comparative assessments highlighted species-specific and regional variations in germination rates, plasmodial behavior, and media efficacy, illustrating the ecological diversity present within Indian myxomycetes.

A significant methodological innovation of my research was the creation of Indigenous Corn Flour Agar (CFA), a new medium that has proven to be highly efficient for both germination and plasmodial development, now complementing standard media such as oat agar, carrot agar, and water agar. Moreover, optimal cultural conditions were determined. For examples, members of the Physarales were able to endure a wider temperature (22–25 °C) and humidity (80–95%) range, while members of the Trichiales and Stemonitales demonstrated narrower preferences (25 °C, 95% RH). Water availability was identified as a crucial factor for germination and plasmodial development in the Trichiales and Stemonitales, yet it was relatively less important for the Physarales (Phate 2015).

Past research in India indicated that only a limited number of myxomycete species could be cultivated on agar. Therefore, the current study adds further species to the collection of myxomycetes that have been successfully cultured from India, thus broadening the scope of cultural research pertaining to this group. A comprehensive list of myxomycete species that have been successfully cultivated in vitro (spore-to-spore) in India, based on earlier studies and the present investigation, is summarized in Table 2.

Table 2 Summary of myxomycete species cultivated in vitro (spore-to-spore) in India.

No.	Reference	Name of the species
1	Kar (1963a, b, 1964a,b)	*Licea* sp. *Physarella oblonga* (Berk. and Curt.) Morgan *Physarum wingatense* Macbr.
2	Indira (1964, 1965, 1966, 1969a, b, c, 1971, 1974), Indira & Kalyanasundaram (1963, 1971) Indira & Venkataramani (1974)	*Arcyria cinerea* (Bull.) Pers. *Stemonitis herbatica* Peck *Physarum compressum* Alb. and Schw. *P. cinereum* (Batsch) Pers. *P. gyrosum* Rost. *P. serpula* Morgan *P. vernum* Somm. Ex Fries
3	Lakhanpal & Mukerji (1976h)	*Didymium muscorum* Lakhanpal and Mukerji
4	Lakhanpal (1983)	*D. karstenil* Nann.- Brem. *D. intermedium* Schroct. *D. squamulosum* (Alb. and Schw.) Fries *Physarum nicaraguense* Macbr.
5	Phate (2023)	*Arcyria denudata* (L.) Wettst.
6	Phate (2019)	*Diachea subsessilis* Peck
7	Phate & Mishra (2014b)	*Stemonitis axifera* (Bull.) T. Macbr.

Discussion

Indian myxomycete research has evolved considerably over the past century, progressing from scattered taxonomic records to more integrative approaches that include ecology, physiology, cytology, and preliminary molecular studies. Taxonomic surveys remain the foundation, with nearly 535 species documented across diverse regions (Lakhanpal 1981, Ranade et al. 2012, Manoharachary & Nagaraju 2017, Phate 2023, Kumar et al. 2023). These efforts have firmly established India as a centre of significant myxomycete diversity. However, ecological research remains uneven, with intensive studies largely confined to the Himalayas and central India, while coastal, desert, alpine, and mangrove ecosystems are underrepresented (Lakhanpal 1981, Chopra 1984, Phate 2023c, Kumar et al. 2023).

A major strength of Indian research lies in the development of agar culture and *in vitro* studies, which have enabled controlled investigations into spore germination, plasmodial growth, and sporulation. Innovations such as Corn Flour Agar, substrate decoction, and the paper cone method have expanded the scope of experimental myxomycetology, leading to several species being cultured spore-to-spore for the first time (Kar 1962, 1964b, Indira 1964, 1968a, b, 1969a, b, c, 1971, Lakhanpal & Mukerji 1976a, b, c, d, e, f, g, h, Singh 2005, Phate 2015). Physiological and biochemical investigations on pigments, enzyme secretion, and light responses have provided additional insights into metabolic versatility and ecological roles (Ganju & Mukherjee 1969, Loganathan et al. 1989, Kalyanasundaram et al. 1994, Paramasivan 1990, Singh 2005, Mubarak Ali & Kalyanasundaram 1991, Mubarak Ali et al. 1992, Ragu 2000). Nevertheless, these studies have largely been restricted to a few model taxa, limiting broader generalizations.

Knowledge Gaps

Despite more than a century of research, several critical areas of Indian myxomycete biology remain insufficiently explored. Large ecological niches such as deserts, alpine snow banks, mangroves, and urban environments are poorly documented, with only sporadic ecosystem-based reports available from India (Lakhanpal & Mukerji 1981a, Phate 2023c, Kumar et al. 2023). Most culture-based investigations have focused on a limited number of taxa, resulting in a strong bias in available physiological and developmental datasets (Kar 1962, 1964b, Indira 1964, 1968a, b, 1969a, b, c, 1971, Lakhanpal & Mukerji 1976a, b, c, d, e, f, g, h, Singh 2005, Phate 2015).

Cytological studies on Indian myxomycetes are remarkably scarce (Indira 1969c), and modern molecular investigations addressing genetics, genomics, phylogeny, and evolutionary relationships are almost entirely absent from Indian research programs, with most national syntheses remaining morphology-based (Lakhanpal & Mukerji 1981a, Ranade et al. 2012). Furthermore, the functional roles of myxomycetes in ecosystem processes—particularly in decomposition dynamics, nutrient cycling, and interactions with microbial communities—remain poorly resolved, being addressed only in a few isolated studies (Balaji 2000, Sujatha 2000).

Future Perspectives

Looking forward, research on Indian myxomycetes has significant potential for advancement through interdisciplinary approaches. Detailed biodiversity assessments in lesser-studied ecosystems such as deserts, alpine areas, mangroves, and coastal forests are crucial for enhancing the existing distribution database. A stronger focus on ecological studies that correlate species presence with microclimatic, edaphic, and seasonal factors will facilitate predictions regarding how these organisms may react to climate change. At the experimental level, culture studies need to be extended across a broader taxonomic spectrum, incorporating innovative media formulations and refined laboratory protocols. The integration of molecular and genomic tools offers exciting opportunities to resolve phylogenetic relationships, unravel the genetic regulation of life-cycle stages, and shed light on evolutionary adaptations. Functional investigations that examine myxomycete-microbe interactions are also vital, especially in exploring their roles in decomposition, nutrient cycling, and ecosystem functioning. Lastly, practical research avenues like bioremediation, enzyme and pigment investigation, and the development of microbial consortia-based biotechnology offer promising opportunities, with the potential to convert fundamental research findings into tangible environmental solutions.

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Conflict of Interest

None

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