Tropical Natural History 23 (2023): 82-96

Fungal Spores from Neogene Sediments of the Hongsa Basin, Lao PDR

THUNYAPAT SATTRABURUT[1*], BENJAVUN RATANASTHIEN[2] and YUPA THASOD[2]

[1]*Faculty of Environment and Resource Studies, Mahidol University, Nakhon Pathom 73170, THAILAND*
[2]*Department of Geological Sciences, Faculty of Science, Chiang Mai University, Chiang Mai 50200, THAILAND*
[*]Corresponding author. Thunyapat Sattraburut (thunyapat.sat@mahidol.ac.th)
Received: 16 November 2022; Accepted: 1 May 2023

ABSTRACT. – Fungal spores in Neogene organic-rich sediments from the Hongsa coalfield in northwestern Lao PDR were studied in detail. Fungal spores and the significance of palynological associations are employed for interpreting depositional environment and paleoclimate. The palynological assemblages, recovered from 34 samples, were rich and diversified, consisting mainly of pollen grains of vascular plants, spores of pteridophytes, and fungal spores. Of all 67 fungal taxa from 22 genera identified in this study, 21 are Amerosporae, 20 Phragmosporae, 18 Didymosporae, and 8 Dictyosporae. Although diversified, they yielded low to very low frequencies compared to total palynomorphs. Most palynological and fungal spores in this investigation indicate a Miocene age of the deposits. The presence of *Dyadosporites*, *Brachysporisporites*, *Diporicellaesporites*, *Pluricellaesporites*, and *Dictyosporites* of sub-tropical to warm temperate forests associated with a large number of pteridophytes and evergreen to deciduous vegetation can reinforce the hypothesis of terrestrial origin in a humid and warm climate. Variations in relative abundance and diversity of fungal spores in this study indicate paleoenvironmental fluctuations during deposition, which also conform to the climate interpreted from each palynological zone.

KEYWORDS: fossil fungal spores, depositional environment, paleoenvironment, paleoclimate, Hongsa coalfield

INTRODUCTION

Fungal remain is one of the non-pollen palynomorphs (NPPs) which is generally found in preparations of palynology (Kalgutkar and Jansoniun, 2000; Shumilovskikh et al., 2021). However, they have received far less attention than palynomorphs of vascular plants (Taylor et al., 2015) and are perhaps being ignored in the reports. Although their remains have been reported since the Paleozoic, they became more widespread in terms of abundance and diversity during the Paleocene to Pliocene (Elsik, 1976; Elsik, 1996; Premaor et al., 2018). Various distinctive fungal spores have been compared to their extant affinities to modern genera (Kalgutkar and Sigler, 1995; Premaor et al., 2018) and can be used to interpret paleoecological conditions and climatic oscillations during the time the fungi were fossilized. The descriptive morphology of NPPs combined with their possible assignment to extant taxa and discussions on their stratigraphic position can be used as paleoecological indicators (Shumilovskikh and van Geel, 2020).

Recently, the study of fungal remains of different ages and areas all around the world as a proxy has become an area of growing interest (e.g., Ediger and Alişan, 1989; Kumar, 1990; Singh and Chauhan, 2008; Geel et al., 2011; Tripathi, 2011; Musotto et al., 2012; Atfy et al., 2013; Guimarães et al., 2013; Martínez et al., 2016; O'Keefe, 2017; Calhim et al., 2018; Kumar, 2018; Premaor et al., 2018; Nuñez Otaño et al., 2021; Romero et al., 2021). Moreover, the study of fossil fungi is important for understanding biodiversity changes, especially during the middle Miocene Climate Optimum (MMCO) which was the warmest interval of the last 23 million years (Romero et al., 2021). According to Sattraburut et al. (2021a), the Hongsa sediments were assigned to be of middle to late Miocene. Nevertheless, no detailed palynological studies on fossil fungi have been carried out from the Hongsa sediments nor from other Lao PDR areas. Thus, this paper aims to present the first detailed report of fossil fungi in the Hongsa Basin and its relevance to the paleoenvironment and paleoclimatic studies.

Geological Setting and Stratigraphy

The Hongsa Basin lies in Xayabouly Province in northwest Lao PDR. It is located at latitudes 19°39´N and 19°43´N and longitudes 101°14´E and 101°24´E. It lies about 40 km northeast of the Huai Kon-Muang Nguen border checkpoint (Figs. 1a and 1b). The basin is roughly triangular and covers approximately 60 km^2 between northern Thailand and southern China. The tectono-stratigraphic evolution of the Hongsa Basin is related to the Indian and Eurasian collision in the Middle Eocene (around 45 Ma), and subsequent events during the early Cenozoic Era in Southeast Asia. Numerous half-graben basins were formed as a result of extensional stress due to strike-slip movements dominating during the Eocene to Oligocene (Burri, 1989; Hall and Morley, 2003; Friederich et al., 2016). The uncertain time frame of sedimentation of the Hongsa Basin may have begun between the Oligocene to Pliocene (Morley and Racey, 2011) because of the failure to find any mammalian fossils to define the age of deposition.

The northern flank of the Hongsa Basin is bound by the ENE-WSW trend of the fault set, while the western flank is bound by the NW-SE trend of a normal fault. The basement rocks of the basin are predominantly red Mesozoic clastic terrigenous sedimentary rocks, mainly

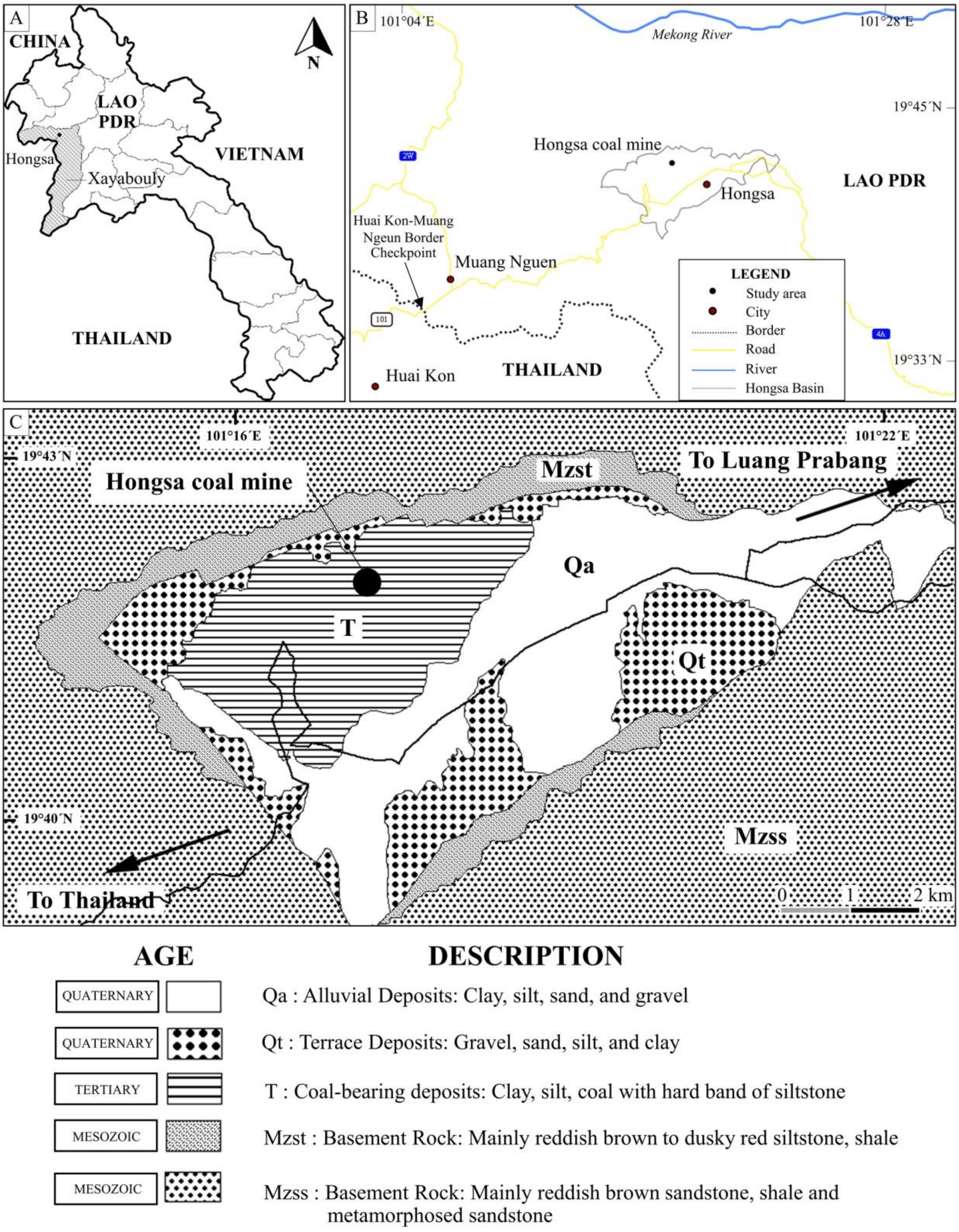

FIGURE 1. Study site. (a) Political map of Lao PDR. The study area is in Xayabouly Province. (b) Location map of the Hongsa Basin with the position of the Hongsa coal mine indicated. (c) Detailed geologic map of the Hongsa area (modified from Hofmann et al., 2008).

sandstone and siltstone (Fig. 1c). Neogene and Quaternary sediments unconformably overlie the Mesozoic basement rocks. The coal-bearing Neogene sediments comprise light grey silt and clays with some siltstone hard bands, reaching over 100 m in the cumulative thickness of coal. Quaternary sediments are alluvial and terrace deposits from the Mekong River, consisting mainly of clays, silt, sand, and gravel.

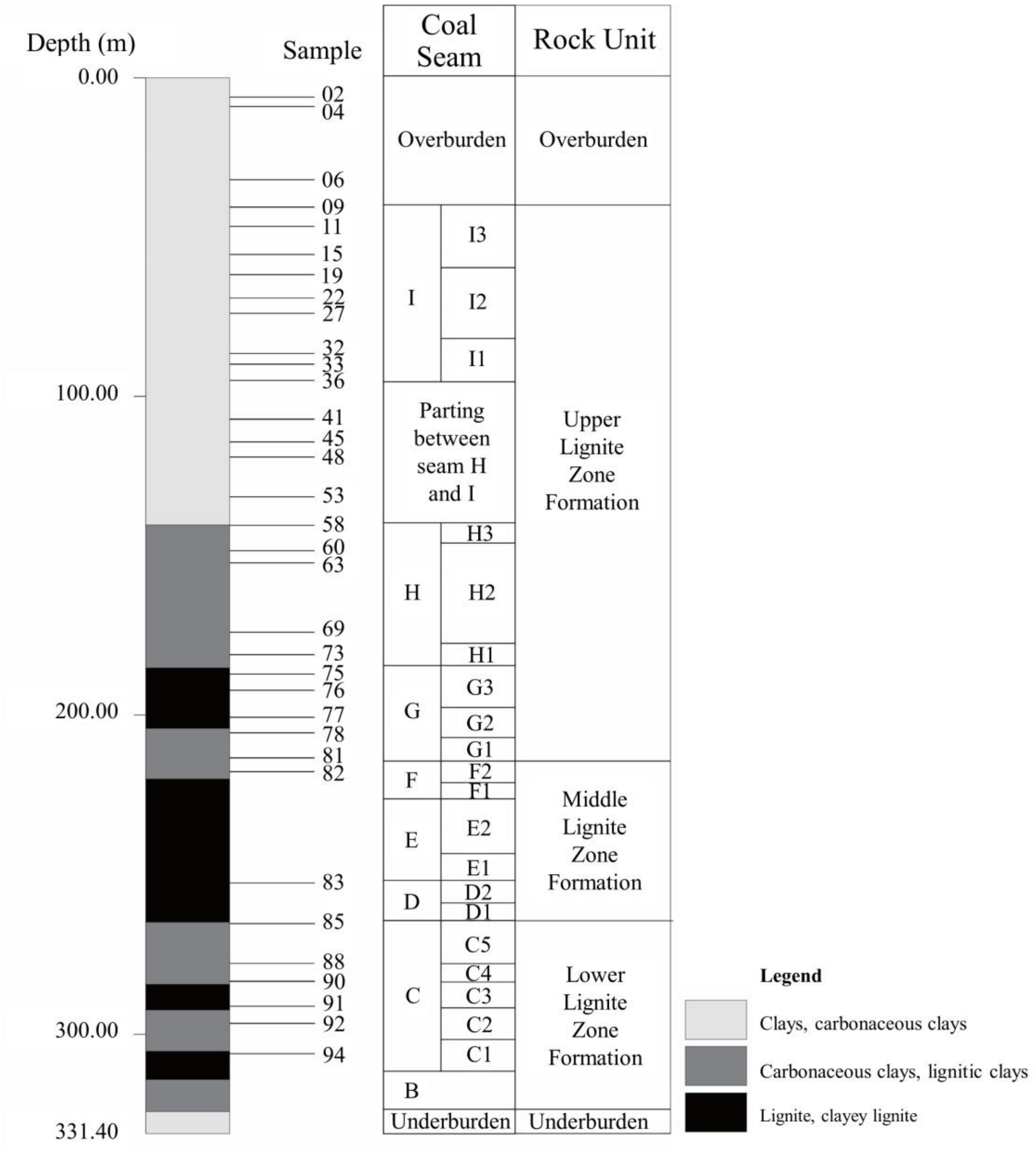

FIGURE 2. Simplified lithological profile showing the stratigraphic position of selected samples in a drill core.

The Hongsa coal deposit is regarded as an important energy resource of Laos. The coal mine has been operated by Hongsa Power Co. Ltd. since 2015. Coals of lignite B to lignite A in rank have been excavated and supplied to three mine-mouth thermal power plants. The Hongsa coal deposit consists of Neogene fine-grained terrigenous sediments and coal seams that had been brought up to the surface by tectonism, partially eroded, and partially covered by recent fluvial sediments. The main stratigraphic work in this deposit was developed by Hofmann et al. (2008), involving the rock unit and coal seam subdivisions. The sedimentary rock units are divided from the lowermost to uppermost units as the Underburden, Lower Lignite Zone Formation, Middle Lignite Zone Formation, Upper Lignite Zone Formation, and Overburden, respectively (Fig. 2). Nine coal seams were named A to I units from bottom to top. Each unit was split into numerous sub-seams. Geological structures in the Hongsa coal deposit are quite complex, with folds, normal and reverse faults, and inversion faults typically recognized.

Organic-rich sediments were deposited in an anoxic freshwater mire or forest swamp in the seasonal tropical forest, with a moderate amount of sediment supplied by low-energy water flow (Sattraburut et al., 2021b). Palynological investigation suggests that the Hongsa coal deposit witnessed a climatic change from a warmer subtropical to a cooler warm temperate condition during the middle to late Miocene. During deposition, the forest was dominated by broad-leaved trees, along with a variety of ferns on the forest floor, indicating the high humidity of shaded growth (Sattraburut et al., 2021a).

MATERIALS AND METHODS

Thirty-four samples of a drill core collected from the central part of the Hongsa coal mine were chosen for the study. The core was provided by Hongsa Power Co. Ltd. The samples consisted mainly of dark grey carbonaceous clays, with some minor carbonaceous silty clays They were collected at varying intervals from a total core length of 331.40 m in every sub-coal seam, spaced approximately 10 m apart (Fig. 2). Before collecting the samples, the exposed surface of the cores was scraped to remove the oxidized and weathered material.

The physical and chemical extraction of non-pollen palynomorphs was carried out using standard palynological techniques modified from Traverse (1988), Faegri and Iversen (1989), Moore et al. (1991), and Wood et al. (1996). Palynological treatments were conducted at the Northeastern Research Institute of Petrified Wood and Mineral Resources (In Honour of His Majesty the King), Nakhon Ratchasima Rajabhat University, Thailand. The methodology involved grinding and removing inorganic fractions by treating samples with hydrochloric acid and hydrofluoric acid, without using oxidation methods. Residues from each sample were then sieved using 150 µm nylon filters. Fungal spores and palynomorphs retained on each sieve were separately mounted in colorless glycerine jelly for microscopic studies.

The taxonomic study was carried out using a transmitted-light microscope at the Department of Geological Sciences, Faculty of Science, Chiang Mai University, Thailand, under a magnification of 400x. Fungi were described, compared, and classified according to relevant literature (mainly Ediger and Alişan, 1989; Kumar, 1990; Kalgutkar and Jansonius, 2000; Martínez et al., 2016; Premaor et al., 2018). The artificial morphological system (Saccardo System) was adopted for classification, based on the number of cells, disposal of septa, and the presence of apertures (Pirozynski and Weresub, 1979). This study adopted classifications at the genus and species level from Kalgutkar and Jansonius (2000). Biostratigraphic ranges were applied according to Kalgutkar and Jansonius (2000), Saxena and Tripathi (2011), and Saxena et al. (2021).

RESULTS

Palynofloral investigation of the Hongsa sediments was reported by Sattraburut et al. (2021a). The assemblages of palynomorphs and NPPs are diversified through the stratigraphic analysis intervals, composed predominantly of pollen grains of angiosperms and gymnosperms, spores of pteridophytes, and fungal spores. The percentage of palynomorphs and fungal spores recorded along the interval of 331.40 m is presented in Fig. 3. The taxonomic list of fungal species identified in this study is presented in Table 1. The stratigraphic distribution of the taxa in each level is shown in Fig. 4, and photomicrographs of the recorded taxa which are presented in Plates 1 to 3 (Appendix).

The studied samples yielded well-preserved fungal spores in low to deficient numbers (0.25-13.86%, mean 2.02%) compared to other palynomorphs such as pollen grains and spores. Generally, all levels of the selected intervals are characterized by a few occurrences of fossil fungi. The only exception is sample 04 at 10.25 m from the Overburden, where fungal spores exist in significantly higher amounts than in the other samples, comprising 13. 86% of total palynomorphs.

Abundant fungal spores of various forms, ranging from unicellular to multicellular structures of different sizes and shapes with variable frequencies, were found throughout the sediment intervals. The fungal assemblages recovered from the Hongsa Basin consisted of 67 species placed into 22 genera, divided into four spore groups. The Phragmosporae group, characterized by three or more cells with two or more transverse septa, had the highest number of genera, including 20 species from 9 genera. The Amerosporae group, which is unicellular with or without aperture, included 21 species from 7 genera. The Didymosporae group, consisting of two-celled forms, comprised 18 species from 4 genera, while this study identified 8 species belonging to 2 genera of the Dictyosporae group.

The Phragmosporae group possesses the highest number of fungal taxa, including *Diporicellaesporites*, *Multicellaesporites,* and *Pluricellaesporites. Diporicellaesporites* are elongate, diporate, and multicellate fungal spores. *Multicellaesporites* are inaperturate and usually consist of 3 to 5 cells with a longitudinal slit or furrow. *Pluricellaesporites* are monoporate and have 3 or more cells that are symmetrical or nearly symmetrical around the long axis. *Dicellaesporites* are prominent among Didymospores. They are inaperturate, isopolar, and two-celled. Dictyospores or muriform spores are inaperturate and variable in shape. Most Dictyospores in this study belong to the genus *Dictyosporites*. They are multicellular, inaperturate, and all have a brownish coloration.

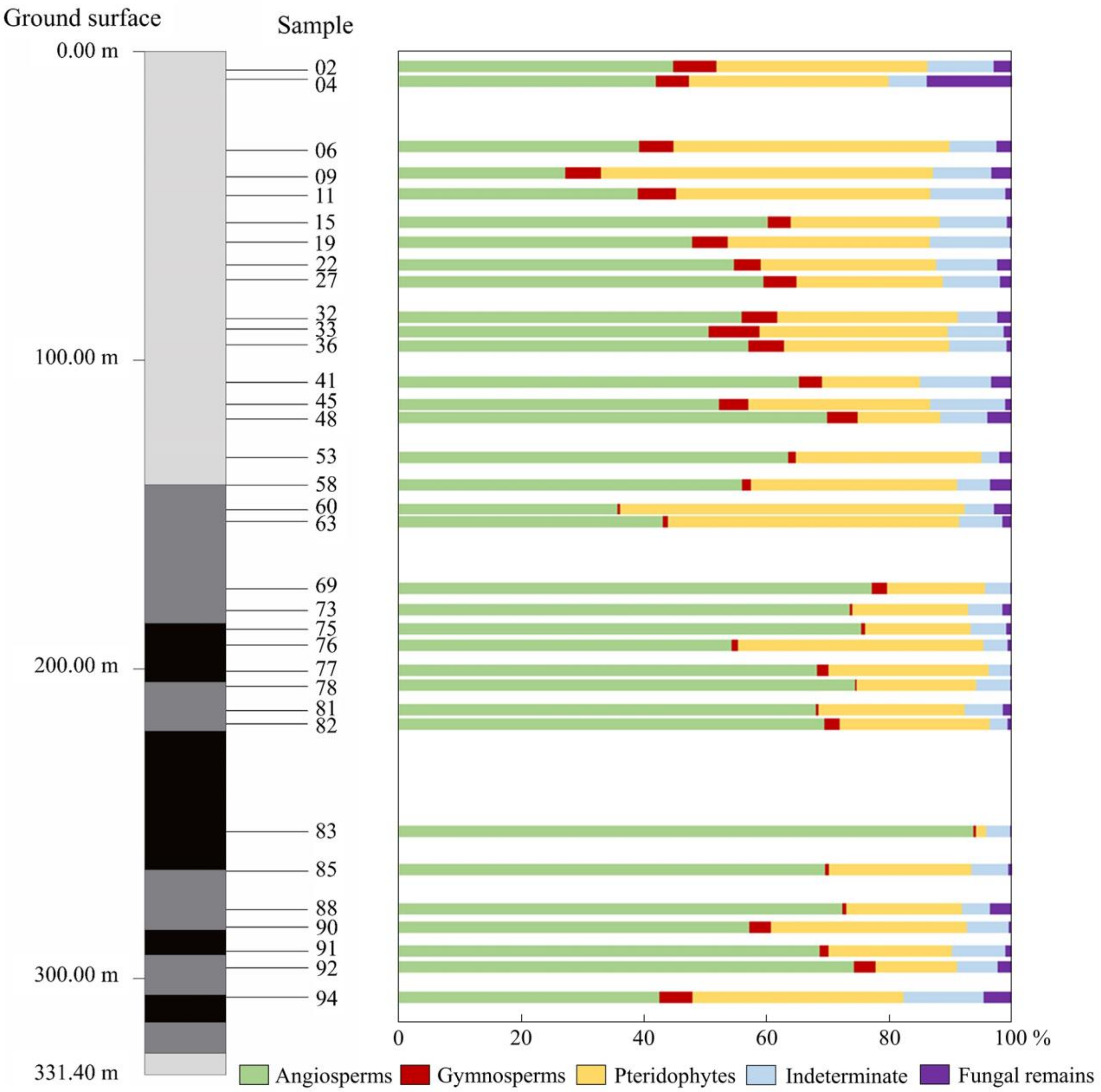

FIGURE 3. Percentage diagram of angiosperms, gymnosperms, indeterminate, and fungal spores in the Hongsa Basin.

DISCUSSION

Age

A large number of fossil fungi are not specific to any age, such as *Fusiformisporites* (Martínez-Hernández and Tomasini-Ortiz, 1989), *Diporicellaesporites* (Zhang, 1980; Kalgutkar and Braman, 2008; Saxena and Tripathi, 2011), and *Hypoxylonites* (Elsik, 1990). The presence of most fungal spores in this study suggests that the deposits are of Miocene age, which is consistent with the age assigned by previous palynological investigations (Sattraburut et al., 2021a). This indicates that the Hongsa sediments were deposited during the middle to late Miocene. This result corresponds to the time-stratigraphic correlation of sedimentary basins in northern Thailand and southern China, which are nearby the Hongsa Basin. According to various palynological studies, the ages of the northern Thailand basins range from the late Oligocene to middle Miocene, while the southern China basins are middle Miocene to Pliocene in age (Wang, 1996; Songtham, 2000; Songtham et al., 2003, 2005; Wang, 2006; Xu et al., 2008; Sepulche et al., 2009; Yao et al., 2011; Grote, 2015).

However, our study found inconsistencies in the ages of a few fungal taxa. For instance, *Fractisporonites canalis*, which consists of chains of fungal spores and hyphal fragments consisting of 8 or more cells, had been found during the late Cretaceous but was absent in the Paleogene.

TABLE 1. Fossil fungal taxa identified and illustrated in this study.

Group and species	Plates and figs.
Amerosporae	
Diporisporites ellipsoides Kalgutkar and Jansonius (2000)	Plate 1, fig. (a)
Diporisporites elongatus van der Hammen (1954)	Plate 1, fig. (b)
Exesisporites neogenicus Elsik (1969)	Plate 1, figs. (c), (d)
Exesisporites sp. cf. *E. annulatus* Kalgutkar (1993)	Plate 1, fig. (e)
Hypoxylonites africanus Kalgutkar and Jansonius (2000)	Plate 1, figs. (j), (k)
Hypoxylonites ellipsoideus Kalgutkar and Jansonius (2000)	Plate 1, figs. (m), (n), (o)
Hypoxylonites fusiformis Elsik (1990)	Plate 1, fig. (r), (s)
Hypoxylonites gulfensis Elsik (1990)	Plate 1, fig. (l)
Hypoxylonites ovalis Elsik (1990)	Plate 1, fig. (q)
Hypoxylonites sp. Elsik (1990)	Plate 1, fig. (p)
Hypoxylonites sp. cf. *H. curvatus* Elsik (1990)	Plate 1, fig. (t)
Inapertisporites circularis Kalgutkar and Jansonius (2000)	Plate 1, figs. (f), (g)
Inapertisporites elongatus Kalgutkar and Jansonius (2000)	Plate 1, fig. (h)
Inapertisporites ovalis Kalgutkar and Jansonius (2000)	Plate 1, fig. (i)
Monoporisporites neoglobosus Kalgutkar and Jansonius (2000)	Plate 1, figs. (u), (v)
Monoporisporites oviformis Kalgutkar and Jansonius (2000)	Plate 1, fig. (w)
Monoporisporites sp. van der Hammen (1954)	Plate 1, figs. (x), (y)
Monoporisporites sp. cf. *M. abruptus* Sheffy and Dilcher (1971)	Plate 1, fig. (z)
Spirotremesporites sp. cf. *S. disciformis* Elsik (1990)	Plate 1, figs. (aa), (ab), (ac)
Striadiporites bistriatus Ke and Shi (1978)	Plate 1, figs. (ad), (ae)
Striadiporites reticulatus Varma and Rawat (1963)	Plate 1, figs. (af), (ag)
Didymosporae	
Dicellaesporites aculeolatus Sheffy and Dilcher (1971)	Plate 1, fig. (ah)
Dicellaesporites elongatus Ramanujam and Rao (1978)	Plate 1, fig. (ai)
Dicellaesporites littoralis Salard-Cheboldaeff and Locquin (1980)	Plate 1, fig. (am)
Dicellaesporites perelongatus Kalgutkar and Jansonius (2000)	Plate 1, fig. (aj)
Dicellaesporites sp. Elsik (1968)	Plate 1, fig. (ak)
Dicellaesporites sp. cf. *D. africanus* Salard-Cheboldaeff and Locquin (1980)	Plate 1, fig. (al)
Didymoporisporonites discitypicus Kalgutkar and Jansonius (2000)	Plate 1, fig. (an)
Didymoporisporonites panshanensis Ke and Shi (1978)	Plate 1, fig. (ao)
Dyadosporites hilatus Kalgutkar and Jansonius (2000)	Plate 1, fig. (ap)
Dyadosporites inaequalis Kalgutkar (1993)	Plate 1, fig. (aq)
Dyadosporites okayi Kalgutkar and Jansonius (2000)	Plate 1, figs. (ar), (as)
Dyadosporites reticulatus Kalgutkar and Jansonius (2000)	Plate 1, fig. (au)
Dyadosporites subovalis Kalgutkar and Jansonius (2000)	Plate 1, fig. (at)
Fusiformisporites elongatus Ramanujam and Rao (1978)	Plate 1, fig. (av)
Fusiformisporites lineolatus Sheffy and Dilcher (1971)	Plate 1, fig. (az)
Fusiformisporites mackenziei Parsons and Norris (1999)	Plate 1, fig. (ba)
Fusiformisporites rugosus Sheffy and Dilcher (1971)	Plate 1, fig. (ax)
Fusiformisporites sp. Rouse (1962)	Plate 1, figs. (aw), (ay)
Phragmosporae	
Anatolinites sp. Elsik et al. (1990)	Plate 2, fig. (a)
Brachysporisporites sp. Lange and Smith (1971)	Plate 2, fig. (b)
Diporicellaesporites acuminatus Sheffy and Dilcher (1971)	Plate 2, fig. (c)
Diporicellaesporites ellipticus Zhang (1980)	Plate 2, fig. (h)
Diporicellaesporites sp. Elsik (1968)	Plate 2, figs. (d), (e), (f), (g)
Fractisporonites canalis Clarke (1965)	Plate 2, fig. (i)
Fractisporonites sp. Clarke (1965)	Plate 2, fig. (j)
Multicellites fusus Kalgutkar and Jansonius (2000)	Plate 2, fig. (k)
Multicellites grandiusculus Kalgutkar and Jansonius (2000)	Plate 2, figs. (l), (m)
Multicellites sp. Kalgutkar and Jansonius (2000)	Plate 2, figs. (n), (o)
Multicellaesporites sp. Elsik (1968)	Plate 2, fig. (p)
Pluricellaesporites patagonicus Martínez et al. (2016)	Plate 2, fig. (q)
Pluricellaesporites sp. Elsik and Jansonius (1974)	Plate 2, fig. (u)
Pluricellaesporites sp. cf. *P. delicatus* Ke and Shi (1978)	Plate 2, fig. (r)
Pluricellaesporites sp. cf. *P. psilatus* (Clarke 1965)	Plate 2, fig. (t)
Pluricellaesporites sp. cf. *P. serratus* Sheffy and Dilcher (1971)	Plate 2, fig. (s)
Quilonia multicellata Kalgutkar and Jansonius (2000)	Plate 2, fig. (v)
Quilonia sp. Jain and Gupta (1970)	Plate 2, fig. (w)
Quilonia sp. cf. *Q. attenuata* Kalgutkar and Jansonius (2000)	Plate 2, fig. (x)
Scolecosporites sp. Lange and Smith (1971)	Plate 2, figs. (y), (z), (aa), (ab), (ac), (ad)
Dictyosporae	
Dictyosporites moruloides Kalgutkar and Jansonius (2000)	Plate 3, fig. (a)
Dictyosporites ovalis Kalgutkar and Jansonius (2000)	Plate 3, figs. (b), (c)
Dictyosporites sp. Felix (1894)	Plate 3, figs. (d), (e)
Dictyosporites sp. cf. *D. dictyosus* Kalgutkar and Jansonius (2000)	Plate 3, fig. (g)
Dictyosporites sp. cf. *D. ovoideus* Salard-Cheboldaeff and Locquin (1980)	Plate 3, fig. (h)
Dictyosporites sp. cf. *D. symmetricus* Kalgutkar and Jansonius (2000)	Plate 3, fig. (i)
Dictyosporites tirumalacharii Kalgutkar and Jansonius (2000)	Plate 3, fig. (f)
Staphlosporonites irregularis Kalgutkar and Jansonius (2000)	Plate 3, fig. (j)

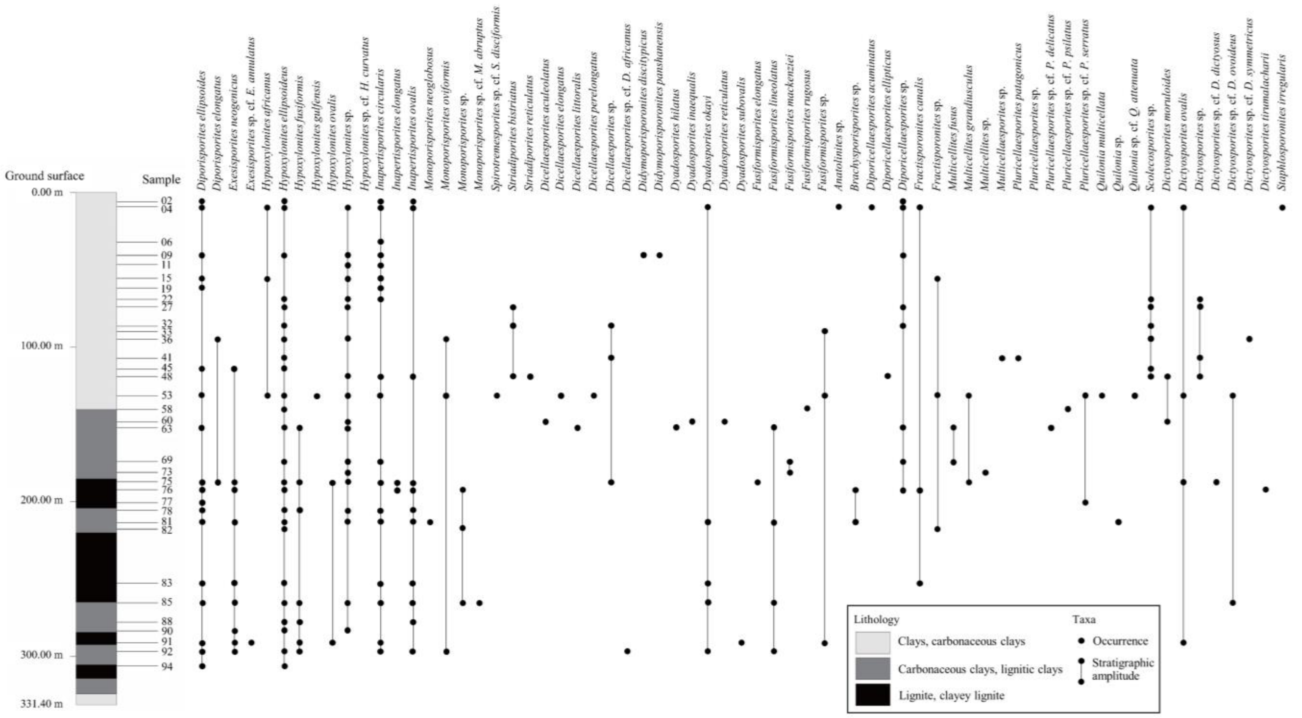

FIGURE 4. Stratigraphic distribution of fungal taxa in the Hongsa basin.

The tabular structure of *Fractisporonites canalis* possibly indicates the presence of a parasitic fungus (Kalgutkar and Jansonius, 2000) or closely resembles the external spore formation known as actinomycetes (Hermann and Podkovyrov, 2008). They can survive under extreme conditions (Trenozhnikova and Azizan, 2018) and are prominently found in soil, water bodies, and plant remains (Bhatti et al., 2017). Furthermore, some fungal taxa (e.g., *Diporisporites ellipsoides*, *Dictyosporites ovalis*, *Inapertisporites circularis*, *Inapertisporites elongatus*, *Monoporisporites abruptus*) have only been recorded in sediments from the middle to late Eocene. Based on the ages assigned to these fossil fungal spores, it can be presumed that some of the fungal taxa were reworked or transported from other areas of deposition, possibly the Paleogene bedrock boundary of the Hongsa Basin. This is also consistent with the various colors of sporomorphs of ferns reported in the basin (Sattraburut, 2020), which were interpreted as in situ and reworked, indicating that some of the sediment influx was derived from other areas of deposition and probably different ages. The presence of recycled sporomorphs and fungal spores in the Hongsa sediments suggests that the material making up the Miocene sediments in this area was partly derived from the Paleogene rocks. The petrography of immature sandstone and siltstone from Miocene strata also shows poorly sorted and subangular grains, suggesting that the source area was not far from the basin (Sattraburut, 2020).

Depositional environment and paleoclimate

Fossil fungi are suitable as reliable proxies to understand the depositional environment and paleoclimate. Although fungi commonly suggest diverse ecological trends, certain fossil fungal spores in sediments can be useful in determining the depositional environment and paleoclimate based on the ecological implications compared to their extant taxa with known environmental conditions (Atfy et al., 2013). Fossil fungi occur in both terrestrial and aquatic environments, but the terrestrial group prevails due to their greater distribution, diversity, and frequency. Most fungal taxa are dependent on vascular plants for their existence, and although they are reported to be associated with soil, air, and water, fungi actually derive their nutrition from plant material (Cannon and Hawksworth, 1995). The assemblages in this study suggest terrestrial taxa, such as *Dicellaesporites*, *Diporicellaesporites*, *Multicellaesporites*, and *Pluricellaesporites*. They generally occur as saprophytes, living on dead or decaying organic matter.

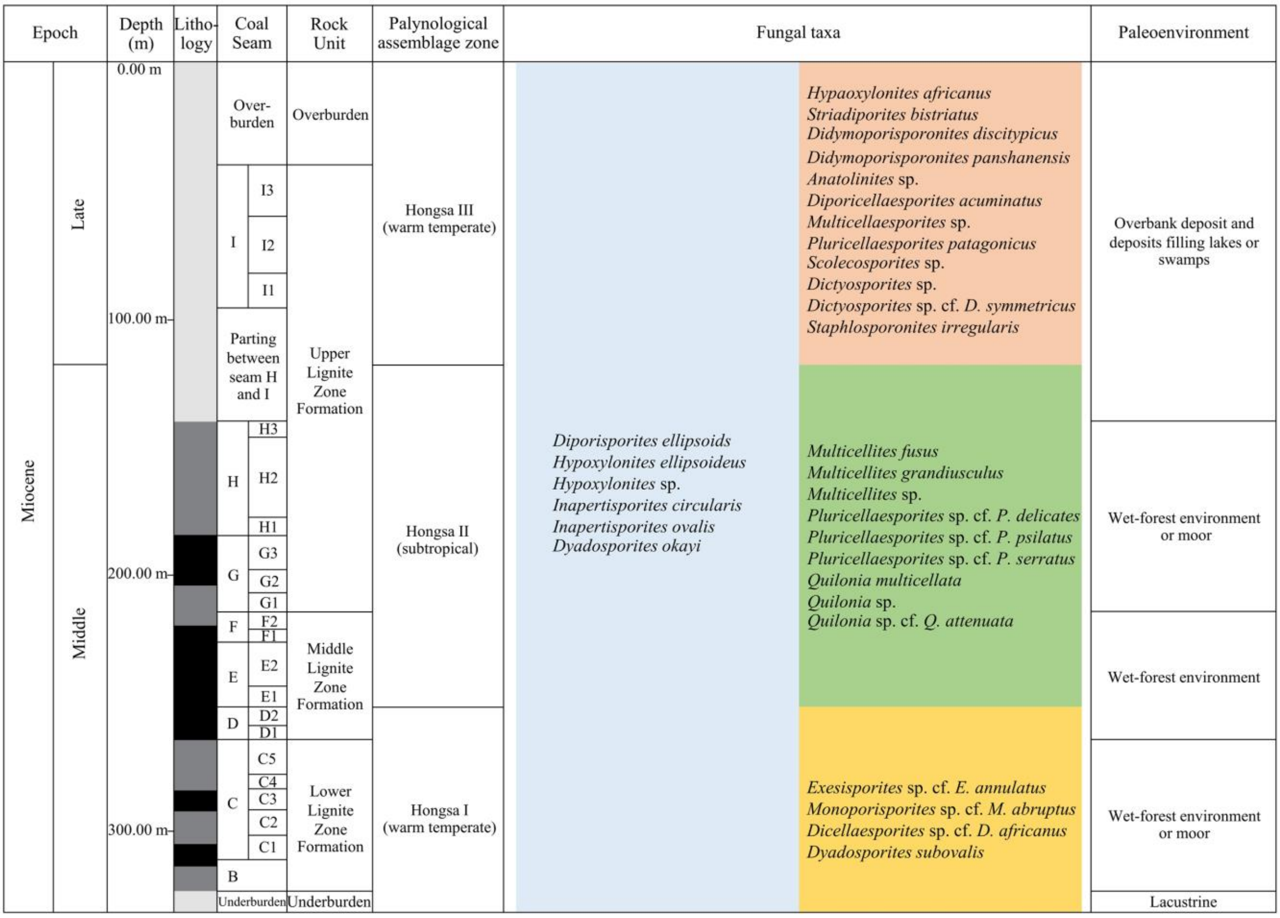

FIGURE 5. The paleoenvironmental interpretation and stratigraphic distribution of selected fungal species compared with palynological zones in the Hongsa Basin (modified after Sattraburut et al., 2021a; Sattraburut, 2020). The interpretation of paleoenvironment is based on the integration of lithological, coal petrological, and palynological data.

Some fossil fungi, such as *Dyadosporites*, *Brachysporisporites*, *Diporicellaesporites*, *Pluricellaesporites*, and *Dictyosporites*, can be compared with modern hyphomycetes. Most of the spores in this study are similar to the conidia of extant hyphomycetes. These hyphomycetes grow as dematiaceous saprotrophs in decaying and dead woods, plant debris, litter, or other organic remains on the ground floor beneath the forest canopy under suitable humidity and temperature (Kalgutkar and Braman, 2008).

The existence of *Exesisporites* indicates a warm climate during the deposition (Elsik, 1969). In this study, a high number of *Hypoxylonites* are reported. *Hypoxylonites* are commonly found in deposits around the world (Elsik, 1981). They are usually known from rocks or sediments that reflect cooling environments (Elsik, 1990) or a warm-humid to temperate forest (Martínez et al., 2016). *Inapertisporites circularis*, which is found through the selected intervals, may have been associated with woods of *Fagus* (Soomro et al., 2010) or parasitized vascular plants of humid grassland such as freshwater swamp (Kirk et al., 2008). *Inapertisporites* also are a good indicator of high precipitation (Dilcher, 1965). *Monoporisporites*, *Quilonia*, and *Striadiporites* are usually found in shallow pond-like habitats (Santos, 2008; Atfy et al., 2013).

Fossil spores of *Brachysporisporites* are commonly compared with the extant genus *Brachysporium* (Réblová and Seifert, 2004), which is a saprotrophic, dematiaceous hyphomycete. Some anamorphic relationships between *Brachysporisporites* and *Monotosporella* have also been considered (Ellis, 1959; Sadowski et al., 2012). *Monotosporella* is frequently found growing on decaying wood submerged in freshwater (Tsui et al., 2001). However, it can also be found in woody plants outside of aquatic habitats (Raja et al., 2007). Spores of *Multicellites* are broadly found in the Eocene aquatic angiosperm rhizome *Eorhiza arnoldii* (Robinson and Person, 1973).

Overall, the rich diversity of fungal spores in the Hongsa sediments suggests that the climate was warm and humid during the time of sediment deposition, which is in consistent with the palynomorphs previously recorded in this area (Sattraburut et al., 2021a). The fungal spores were associated with pteridophyte spores, and there was a very high relative abundance of angiosperm palynomorphs in the Hongsa sediments. These finding support the hypothesis that the sediments were deposited in a sub-tropical to warm temperate evergreen and deciduous forest where saprotroph fungi were predominant. The deposits were likely from freshwater lakes or swamps where both lowland and highland vegetation thrived, possibly in the vicinity of the basin.

Changes in the relative abundance and diversity of fungal remains can also indicate paleoenvironmental fluctuations (Kloosterboer-van Hoeve et al., 2006). Sattraburut et al. (2021a) reported that three palynological zones in the Hongsa Basin, divided from bottom to top as Hongsa I, II, and III (Fig. 5). The vegetation of the Hongsa Basin during the Hongsa II consisted of more tropical to subtropical floras than the Hongsa I and III zones, which were assigned to warm temperate vegetation. While some fungal taxa were presented throughout the selected sediment intervals, some taxa only existed within specific palynological zones (Fig. 5).

In addition, it is noteworthy that fossil fungal spores in the Hongsa I and III zones are less diverse and have lower relative abundance than those in the Hongsa II zone. Both temperature and moisture are important factors in explaining fungal abundance and richness (Talley et al., 2002). Fungi are usually more abundant in tropical forests than in other ecosystems (Tedersoo et al., 2014). Consistent with our study, the Hongsa II zone, which is characterized by a subtropical climate, exhibits greater diversity and abundance than the Hongsa I and III zones. This supports the presence of specific fungal taxa and their richness being associated with the climate inferred from the palynological zones within the Hongsa Basin.

Paleoenvironment interpretation

The deposition in the Hongsa Basin began with the Underburden, which is composed of inorganic clay-sized sediments in the deeper part of the basin. This layer is interpreted as a deposit from stagnant water conditions or lacustrine sediment. The significant amount of clay-sized particles in this rock unit suggests that they were suspended for a prolonged period before aggregating and depositing. Based on the mineral compositions, mainly quartz and kaolinite, it indicates a warm and humid climatic condition during the deposition (Sattraburut, 2020).

Sedimentation continued with the formation of the Lower Lignite Zone Formation, which is the deepest part of the basin where organic-rich sediments were deposited. The sequence is completed with fine-grained lacustrine sediments and lignite, which were formed in a wet-forest swamp and moor. According to the palynological assemblage, the Lower Lignite Zone corresponds to the Hongsa I zone and is dominated by broad-leaved trees in warm temperate climatic conditions. This is consistent with the presence of certain fungal taxa, such as *Exesisporites*.

The Middle Lignite Zone Formation comprises thick and high-quality coal seams. According to Sattraburut (2017), the lignite in this zone is mainly composed of humic coals, indicating relatively wet conditions during peat formation. Some fungal taxa, such as *Inapertisporites circularis*, can be associated with vascular plants in humid conditions. Based on the palynological zone, the lowest part of the Hongsa II zone is assigned to the Middle Lignite Zone Formation, which indicates subtropical climatic conditions in a forest swamp.

The Upper Lignite Zone Formation consists mainly of fine-grained organic-rich sediments and lignite. According to the palynological assemblage, this rock unit is assigned to the Hongsa II to the middle of the Hongsa III zones. From the bottom, it comprises a high amount of tropical to subtropical vegetation compared to the top, which is mostly composed of warm temperate trees, including conifers (Sattraburut, 2020). These data reinforce the hypothesis that the Hongsa area underwent a climatic change from tropical to warm temperate conditions, confirmed by some taxa that are only found within this rock unit. Most taxa of *Multicellites*, *Pluricellaesporites*, and *Quilonia* are commonly found within the Hongsa II zone. These taxa are relevant to shallow aquatic habitats and humid climates in the deposition area, indicating a subtropical environment.

The Overburden, which is the uppermost part of the succession, consists of both inorganic and some organic-rich sediments. Palynological studies reveal a significant quantity of conifers and temperate-like plants, reflecting the warm temperate climate assigned to the Hongsa III zone. Fungal spores found in this unit also reflect a warm and humid climate.

Overall, the depositional scenario of the Hongsa Basin can be envisaged as follows. The basin was formed due to extensional stress resulting from tectonic activity in Southeast Asia during the Tertiary. The basin displays a succession of sedimentary facies ranging from lacustrine deposits to forest swamps with occasional flooding and overbank deposits under subtropical to warm and humid conditions. The prevalence of fine-grained sediment points to the low-energy transportation of current flow. Sediment sources in the Hongsa Basin were derived from both within and outside the basin as a result of the uplifting of basement rocks. The Neogene succession was overlain by Quaternary fluvial and alluvial coarse clastic sediments.

CONCLUSIONS

The study of Neogene successions from the Hongsa Basin in the Lao PDR reveals the first detailed record of well-preserved fungal spores. The assemblages suggest a warm and humid climate of forest swamps or shallow pond-like habitats colonized by sub-tropical to warm temperate evergreen and deciduous vegetation. Changes in relative abundance and diversity of fungal spores indicate that the Hongsa area underwent paleoenvironmental fluctuations during the deposition period. These fungal assemblages also serve as a stratigraphic indicator for the deposit age of the Miocene, in accordance with palynomorphs of vascular plants.

ACKNOWLEDGMENTS

The authors express their gratitude to Hongsa Power Co. Ltd. for granting permission and providing access to the information and data on the Hongsa coal mine, as well as the core samples used in this study. Authors also thank the Northeastern Research Institute of Petrified Wood and Mineral Resources (In Honour of His Majesty the King), Nakhon Ratchasima Rajabhat University, Thailand, and the Department of Geological Sciences, Faculty of Science, Chiang Mai University, Thailand, for their technical support in the laboratories. The first author would like to thank Dr. Wipanu Rukmai for teaching the palynomorph preparation procedures. Finally, the authors would like to express their appreciation to the anonymous reviewers for their careful reading of the manuscript and their insightful comments and suggestions.

LITERATURE CITED

Afty, H., Brocke, R. and Uhl, D. 2013. A fungal proliferation near the probable Oligocene/Miocene boundary, Nukhul Formation, Gulf of Suez, Egypt. Journal of Micropalaeontology, 32: 183-195.

Bhatti, A.A., Haq, S. and Bhat, R.A. 2017. Actinomycetes benefaction role in soil and plant health. Microbial Pathogenesis; 111: 458-467.

Burri, P. 1989. Hydrocarbon potential of Tertiary intermontane basins in Thailand. In: Thanasuthipitak, T., and Ounchanum, P. (Eds.). Proceeding of the International Symposium on Intermontane Basins: Geology & Resources, Chiang Mai University, Chiang Mai, 3-12.

Calhim, S., Halme, P., Petersen, J.H., Læssøe, T., Bässler, C. and Heilmann-Clausen, J. 2018. Fungal spore diversity reflects substrate-specific deposition challenges. Scientific Reports, 8: 5356.

Cannon, P.F. and Hawksworth, D.L. 1995. The diversity of fungi associated with vascular plants: the known, the unknown and the need to bridge the knowledge gap. Academic Press, London.

Clarke, R.T. 1965. Fungal spores from Vermejo Formation coal beds (Upper Cretaceous) of central Colorado. Mountain Geologist, 2: 85-93.

Dilcher, D.L. 1965. Epiphyllous fungi from Eocene deposits in western Tennessee, USA. Paleontographica, 116B: 1-54.

Ediger, V.Ş. and Alişan, C. 1989. Tertiary fungal and algal palynomorph biostratigraphy of the Northern Thrace Basin, Turkey. Review of Palaeobotany and Palynology,58: 139-161.

Ellis, M.B. 1959. Clasterosporium and some Allied Dematiaceae-Phragmosporae II. Mycological Papers (C.M.I.),72: 1-75.

Elsik, W.C. 1968. Palynology of a Paleocene Rockdale lignite, Milam County, Texas. I. Morphology and taxonomy. Pollen et Spores, 10: 263-314.

Elsik, W.C. 1969. Late Neogene palynomorph diagrams, northern Gulf of Mexico. Transactions of the Gulf Coast Association of Geological Societies, 19: 509-528.

Elsik, W.C. 1976. Microscopic fungal remains and Cenozoic palynostratigraphy. Geoscience and Man, 15(1): 115-120.

Elsik, W.C. 1981. Fungal palynomorphs: notes for a palynology short course. Louisiana State University, Louisiana.

Elsik, W.C. 1990. Hypoxylonites and Spirotremesporites, form genera for Eocene to Pleistocene fungal spores bearing a single furrow. Palaeontographica,216: 137-169.

Elsik, W.C. 1996. Fungi. In: Jansonius, J., and McGregor, D.C. (Eds.). Palynology: principles and applications. American Association of Stratigraphic Palynologists Foundation, Dallas: 293-206.

Elsik, W.C. and Jansonius, J. 1974. New genera of Paleogene fungal spores. Canadian Journal of Botany, 52: 953-958.

Elsik, W.C., Ediger, V.S. and Bati, Z. 1990. Fossil fungal spores: Anatolinites nov. gen. Palynology, 14: 91-103.

Faegri. K. and Iversen, J. 1989. Textbook of pollen analysis (4th ed). Publisher John Wiley and Sons, Chichester.

Felix, J. 1894. Studien über fossile Pilze. Zeitschrift der Deutschen Geologischen Gesellschaft, 46: 269-280.

Friederich, M.C., Moore, T.A. and Flores, R.M. 2016. A regional review and new insights into SE Asia Cenozoic coal-bearing sediments: Why does Indochina have such extensive coal deposit? International Journal of Coal Geology, 166: 2-35.

Geel, B., Gelorini, V., Lyaruu, A., Aptroot, A., Rucina, S., Marchant, R., Damsté, J.S.S. and Verschuren, D. 2011. Diversity and ecology of tropical African fungal spores from a 25,000-year palaeoenvironment record in southeastern Kenya. Review of Palaeobotany and Palynology, 164: 174-190.

Grote, P.J. 2015. Paleobiogeographic and paleoenvironmental changes in Thailand since the Miocene: Evidence from plant fossils. School of Biology, Institute of Science Suranaree University of Technology, Nakhon Ratchasima.

Guimarães, J.T.F., Nogueira, A.C.R., Silva, J.B.C., Soares, J.L. and Silveira, R. 2013. Fossil fungi from Miocene sedimentary rocks of the central and coastal Amazon Region, North Brazil. Journal of Paleontology, 87(3) :484-492.

Hall, R. and Morley, C.K. 2003. Sundaland basins. Washington, DC: American Geophysical Union. In: Clift P, Kuhnt W, Hayes DE, editors. Continent-ocean Interactions Within the East Asian Marginal Seas. Eos, Transaction American Geophysical Union, 106(1): 153-184.

Hermann, T.N. and Podkovyrov, V.N. 2008. On the Nature of the Precambrian Microfossils Arctacellularia and Glomovertella. Paleontological Journal, 42(6): 655-664.

Hofmann, L., Blunck, S., Dittrich, W., Kraemer, T., von Schwarzenberg, T. and Wall G. 2008. Mine Master Plan for the Hongsa Mine Mouth Power Project, Lao P.D.R.: Final Report. RWE Power International, Koeln.

Jain, K.P. and Gupta, R.C. 1970. Some fungal remains from the Tertiaries of Kerala Coast. The Palaeobotanist, 18: 177-182.

Kalgutkar, R.K. and Jansoniun, J. 2000. Synopsis of fossil fungal spores, mycelia and fructifications. American Association of

Stratigraphic Palynologists Foundation, Contributions Series, 39: 1-429.

Kalgutkar, R.M. 1993. Paleogene fungal palynomorphs from Bonnet Plume Formation, Yukon Territory. Contributions to Canadian Paleontology, Geological Survey of Canada, Bulletin, 444: 51-105.

Kalgutkar, R.M. and Braman, D.R. 2008. Santonian to ?earliest Campanian (Late Cretaceous) fungi from the Milk River Formation, southern Alberta, Canada. Palynology, 32: 39-61.

Kalgutkar, R.M. and Sigler, L. 1995. Some fossil fungal form-taxa from the Maastrichtian and Palaeogene ages. Mycological Research, 99(5): 513-522.

Ke, P. and Shi, Z.Y. 1978. Early Tertiary spores and pollen grains from the coastal region of the Bohai (in Chinese). Academy of Petroleum Exploration, Development and Planning Research of the Ministry of Petroleum and Chemical Industries and the Nanjing Institute of Geology, and Paleontology, Chinese Academy of Sciences, Peking.

Kirk, P.M., Cannon, P.F., Minter, D.W. and Stalpers, J.A. 2008. Dictionary of the Fungi (10th ed). CABI, Wallingford.

Kloosterboer-Van Hoeve, M.L., Steenbrink, J., Visscher, H. and Brinkhuis, H. 2006. Millennial-scale climatic cycles in the Early Pliocene pollen record of Ptolemais, northern Greece. Palaeogeography, Palaeoclimatology, Palaeoecology, 229: 321-334.

Kumar, A. 2018. First record of palynomorph assemblages from the Arshad Sandstone (Late Cretaceous), Sirte Basin, north-central Libya. Arabian Journal of Geosciences, 11: 740.

Kumar, P. 1990. Fungal Remains from the Miocene Quilon Beds of Kerala State, South India. Review of Palaeobotany and Palynology, 62: 13-28.

Lange, R.T. and Smith, P.H. 1971. The Maslin Bay flora, South Australia. 3. Dispersed fungal spores. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, 11: 663-681.

Martínez, M.A., Bianchinotti, V., Saxena, R.K., Cornou, M.E. and Quattrocchio, M.E. 2016. Fungal spores from the Palaeogene El Foyel Group of Ñirihuau Basin, Argentina. Papers in Palaeontology, :1-20.

Martínez-Hernández, E. and Tomasini-Ortiz, A.C. 1989. Esporas, hifas y otros restos de hongos fósiles de la cuenca Carbonifera de Fuentes-Río Escondido (Campaniano-Maastrichtiano), Estado de Coahuila. Universidad Nacional Autónoma de México, Instituto de Geología, Revista, 8: 235-242.

Moore, P.D., Webb, J.A. and Collinson, M.E. 1991. Pollen Analysis (2nd ed). Blackwell Scientific Publications, Oxford.

Morley, C.K. and Racey, A. 2011. Tertiary Stratigraphy. In: Ridd, M.F., Barber, A.J. and Crow, M.J. (Eds.). The Geology of Thailand. The Geological Society of London, London: 223-271.

Musotto, L.L., Bianchinotti, M.V. and Borromei, A.M. 2012. Pollen and fungal remains as environmental indicators in surface sediments of Isla Grande de Tierra del Fuego, southernmost Patagonia. Palynology, 36(2): 162-179.

Nuñez Otaño, N.B., Bianchinotti, M.V. and Saparrat, M.C.N. 2021. Palaeomycology: a modern mycological view of fungal palynomorphs. In: Marret, F., O'Keefe, J.M.K., Osterloff, P., Pound, M. and Shumilovskikh, L. (Eds.). Applications of Non-Pollen Palynomorphs: from Palaeoenvironmental Reconstructions to Biostratigraphy. Geological Society, London.

O'Keefe, J.K.M. 2017. Fungal palynomorphs from the Miocene Health Formation, Tumbes Province, Peru. Palynology, 41: 309-326.

Parsons, M.G. and Norris, G. 1999. Paleogene fungi from the Caribou Hills, Mackenzie Delta, northern Canada. Palaeontographica, 250: 77-167.

Pirozynski, K.A. and Weresub, L.K. 1979. The classification and nomenclature of fossil fungi. In: Kendrick, B. (Ed.). The whole fungus, the Sexual-Asexual Synthesis. University of Calgary, Alberta: 653-688.

Premaor, E., Saxena, R.K., Souza, P.A. and Kalkreuth, W. 2018. Fungal spores and fruiting bodies from Miocene deposits of the Pelotas Basin, Brazil. Revue de Micropaléontologie, 61: 255-270.

Raja, H.A., Stchigel, A.M., Miller, A.N., Crane, J.L. and Shearer, C.A. 2007. Hyphomycetes from the Great Smoky Mountains National Park, including three new species. Fungal Diversity, 26: 271-286.

Ramanujam, C.G.K. and Rao, K.P. 1978. Fungal spores from the Neogene strata of Kerala in South India. Proceedings of the IV International Palynological Conference, Lucknow.

Réblová, M. and Seifert, K.A. 2004. Cryptadelphia (Trichosphaeriales), a new genus for holomorphs with Brachysporium anamorphs and clarification of the taxonomic status of Wallrothiella. Mycologia, 96: 343-367.

Robinson, J.M. and Person, C.P. 1973. A silicified semiaquatic dicotyledon from the Eocene Allenby Formation of British Columbia. Canadian Journal of Botany, 51: 1373-1377.

Romero, I.C., Nuñez Otaño, N.B., Gibson, M.E., Spears, T.M., Fairchild, J., Tarlton, L., Jones, S., Belkin, H.E., Warny, S., Pound, M.J. and O'Keefe, J.M.K. 2021. First Record of Fungal Diversity in the Tropical and Warm-Temperate Middle Miocene Climate Optimum Forests of Eurasia. Frontiers in Forests and Global Change, 4: 768405.

Rouse, G.E. 1962. Plant microfossils from the Burrard Formation of western British Columbia. Micropaleontology, 8 :187-218.

Sadowski, E.M., Beimforde, C., Gube, M., Rikkinen, J., Singh, H., Seyfullah, L.J., Heinrichs, J., Nascimbene, P.C., Reitner, J. and Schmidt, A.R. 2012. The anamorphic genus Monotosporella (Ascomycota) from Eocene amber and from modern Agathis resin. Fungal Biology, 116: 1099-1110.

Salard-Cheboldaeff, M. and Locquin, M.V. 1980. Champignons présents au Tertiaire le long du littoral de l' Afrique équatoriale: 105e Congrès National des Sociétée savantes, Caen. Sciences, fascicule, 1: 183-195.

Santos, D.B. 2008. A Paleopalinologia na reconstituição da paisagem Paleógena na Formação Itaquaquecetuba (Mineradora Itaquareia 1). Universidade de Guarulhos, São Paulo.

Sattraburut T. 2017. Depositional Environments of Hongsa Coal Deposits, Xayabouly Province, Lao PDR. Chiang Mai University, Chiang Mai.

Sattraburut, T. 2020. Characteristics of Sediments and Plant Fossils Deposited in Hongsa Coalfield, Xayabouly Province, Lao PDR. Chiang Mai University, Chiang Mai.

Sattraburut, T., Ratanasthien, B. and Thasod, Y. 2021a. Palaeovegetation and palaeoclimate of Tertiary sediments from Hongsa Coalfield, Xayabouly Province, Lao PDR – Implication from palynofloras. Songklanakarin Journal of Science and Technology, 43(3): 648-659.

Sattraburut, T., Thasod, Y., Ratanasthien, B. and Kandharosa, W. 2021b. Petrographic and chemical characterization of coals from Hongsa coal mine, Xayabouly Province, Lao PDR. Suranaree Journal of Science and Technology, 28(1): 030037(1-11).

Saxena, R.K. and Tripathi, S.K.M. 2011. Indian fossil fungi. The Palaeobotanist, 60: 1-208.

Saxena, R.K., Wijayawardene, N.N., Dai, D.Q., Hyde, K.D. and Kirk, P.M. 2021. Diversity in fossil fungal spores. Mycosphere, 12(1): 670-874.

Sepulchre, P., Jolly, D., Ducrocq, S., Chaimanee, Y. and Jaeger, J.J. 2009. Mid-Tertiary palaeoenvironments in Thailand: Pollen evidences. Climate of the Past Discussions, 5: 709-734.

Sheffy, M.V. and Dilcher, D.L. 1971. Morphology and taxonomy of fungal spores. Palaeontographica, 133: 34-51.

Shumilovskikh, L. and van Geel, B. 2020. Non-Pollen Palynomorph. In: Henry, A.G. (Ed.). Handbook for the Analysis of Micro-Particles in Archaeological Samples. Springer Nature Switzerland AG, Cham.

Shumilovskikh, L., O'Keefe, J.M.K. and Marret, F. 2021. An overview of the taxonomic groups of non-pollen palynomorphs. In: Marret, F., O'Keefe, J.M.K., Osterloff, P., Pound, M. and Shumilovskikh, L. (Eds.). Applications of Non-Pollen Palynomorphs: from Palaeoenvironmental Reconstructions to Biostratigraphy. Geological Society, London.

Singh, S.K. and Chauhan, M.S. 2008. Fungal remains from the Neogene sediments of Mahuadanr Valley, Latehar District, Jharkhand, India and their palaeoclimatic significance. Journal of the Palaeontological Society of India, 53(1): 73-81.

Songtham, W. 2000. Palynological investigation of Na Hong Basin, Mae Chaem district, Chiang Mai province. Geological Survey Division, Department of Mineral Resources, Bangkok.

Songtham, W., Ratanasthien, B., Midenhall, D.C., Singharajwarapan, S. and Kandharosa, W. 2003. Oligocene-Miocene climate changes in Northern resulting from extrusion tectonics of Southeast Asian landmass. Science Asia, 29: 221-233.

Songtham, W., Ratanasthien, B., Watanasak, M., Midenhall, D.C., Singharajwarapan, S. and Kandharosa, W. 2005. Tertiary basin evolution in Northern Thailand: A Palynological point of view. Natural History Bulletin of the Siam Society, 53(1) :17–32.

Soomro, S., Leghari, S.M., Lashari, R., Rajar, A.W. and Abbasi, Q.D. 2010. Fossil fungal spores from Brown Coal of Sonda, District Thatta, Sindh, Pakistan. Sindh University Research Journal, Science Series, 42: 73-84.

Talley, S.M., Coley, P.D. and Kursar, T.A. 2002. The effects of weather on fungal abundance and richness among 25 communities in the Intermountain West. BMC Ecology, 2: 7.

Taylor, T.N., Krings, M. and Taylor, E.L. 2015. Fungal Spores. In: Taylor, T.N., Krings, M. and Taylor, E.L. (Eds.). Fossil Fungi. Academic Press, London.

Tedersoo, L., Bahram, M., Põlme, S., Kõljalg, U., Yorou, N.S., Wijesundera, R., Ruiz, L.V., Vasco-Palacios, A.M., Thu, P.Q., Suija, A., et al. 2014. Global diversity and geography of soil fungi. Science, 346(6213): 1256688.

Traverse, F. 1988. Palaeopalynology. Springer Netherlands, Heidelberg.

Trenozhnikova, L. and Azizan, A. 2018. Discovery of Actinomycetes from Extreme Environments with Potential to Produce Novel Antibiotics. Central Asian Journal of Global Health, 7(1): 337.

Tripathi, A. 2011. Fungal remains from Early Cretaceous Intertrappean Beds of Rajmahal Formation in Rajmahal Basin, India. Cretaceous Research, 22: 565-574.

Tsui, C.K.M., Goh, T.K., Hyde, K.D. and Hodgkiss, I.J. 2001. New species or records of Cacumisporium, Helicosporium, Monotosporella and Bahusutrabeeja on submerged wood in Hong Kong streams. Mycologia, 93: 389-397.

Van der Hammen, T. 1954. El desarrollo de la flora Colombiana en los periodos geológicos. I. Maestrichtiano hasta Terciario más inferior. Boletín Geológico, 2: 49-106.

Varma, C.P. and Rawat, M.S. 1963. A note on some diporate grains recovered from Tertiary horizons of India and their potential marker value. Grana Palynologica, 4: 130-139.

Wang, W.M. 1996. A palynological survey of Neogene strata in Xiaolongtan Basin, Yunnan province of South China. Acta Botanica Sinica, 38(9): 743-748.

Wang, W.M. 2006. Correlation of pollen sequence in the Neogene palynofloristic regions of China. Palaeoworld, 15: 77-99.

Wood, G.D., Gabriel, A.M. and Lawson, J.C. 1996. Chapter 3 Palynological techniques - processing and microscopy. In: Jansonius, J. and McGregor, D.C. (Eds.). Palynology: principles and applications. American Association of Stratigraphic Palynologists Foundation, College Station, Texas.

Xu, J.X., Ferguson, D.K., Li, C.S. and Wang, Y.F. 2008. Late Miocene vegetation and climate of the Lühe region in Yunnan, southwestern China. Review of Palaeobotany and Palynology, 148: 36-59.

Yao, Y.F., Bruch, A.A., Mosbrugger, V. and Li, C.S. 2011. Quantitative reconstruction of Miocene climate patterns and evolution in Southern China based on plant fossils. Palaeogeography, Palaeoclimatology, Palaeoecology, 304: 291-307.

Zhang, Z. 1980. Lower Tertiary fungal spores from Lunpole Basin of Xizang, China. Acta Palaeontologica Sinica, 19: 296-301.

Appendix

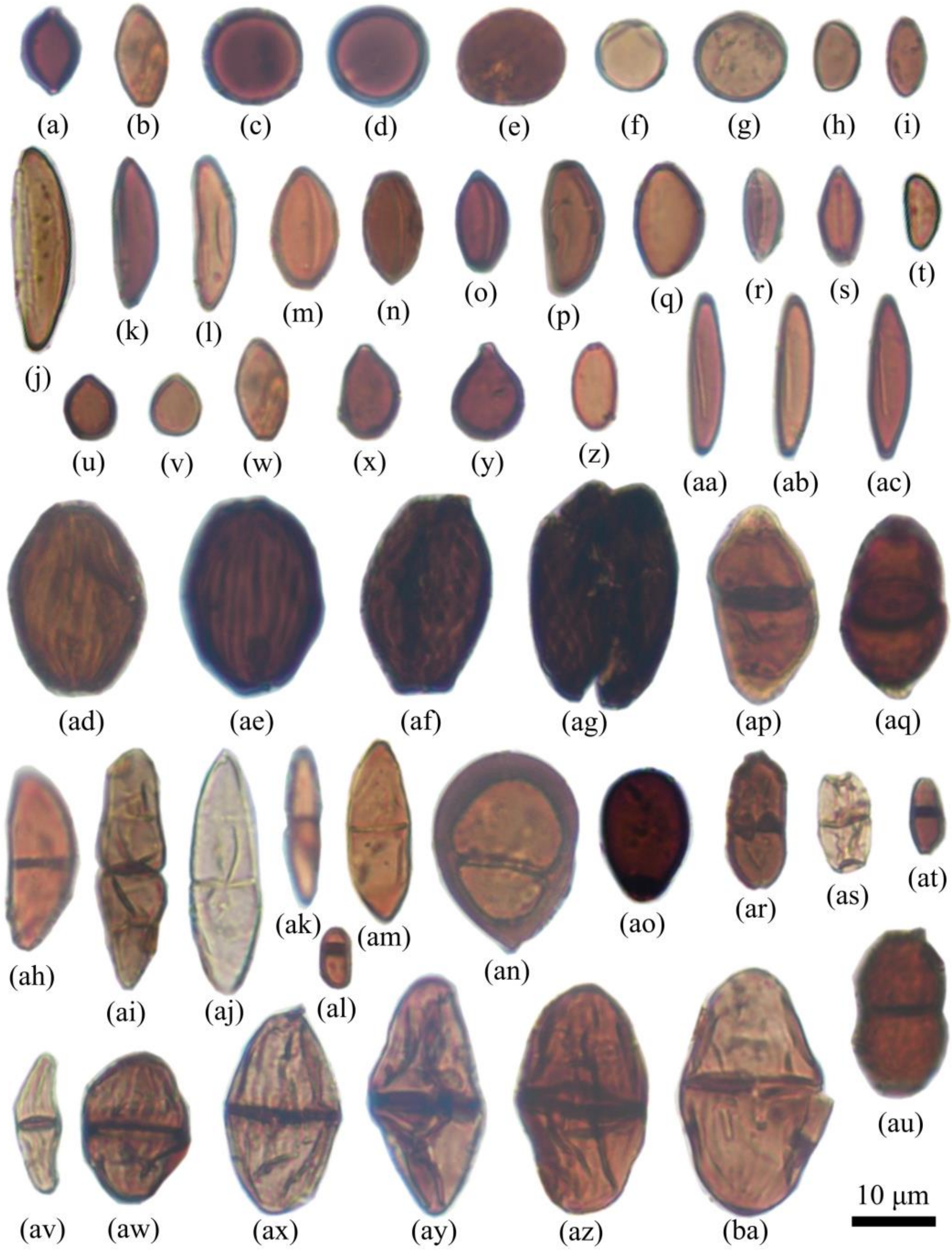

PLATE 1. Photomicrographs of selected Amerosporae and Didymosporae spores (graphic scale equivalents to 10 μm). Depth (m), coal seams, and sample numbers are provided (details are separated by '/'). (a) *Diporisporites ellipsoides* (187.00/G3/75); (b) *Diporisporites elongatus* (94.80/I1/36); (c-d) *Exesisporites neogenicus* (c: 187.00/G3/75, d: 187.00/G3/75); (e) *Exesisporites* sp. cf. *E. annulatus* (290.85/C3/91); (f-g) *Inapertisporites circularis* (f: 187.00/G3/75, g: 187.00/G3/75); (h) *Inapertisporites elongatus* (192.00/G3/76); (i) *Inapertisporites ovalis* (205.20/G2/78); (j-k) *Hypoxylonites africanus* (j: 10.25/OB/04, k: 131.25/HI/53); (l) *Hypoxylonites gulfensis* (131.25/HI/53); (m-o) *Hypoxylonites ellipsoideus* (m: 151.90/H2/63, n: 264.75/D1/85, o: 187.00/G3/75); (p) *Hypoxylonites* sp. (212.75/G1/81); (q) *Hypoxylonites ovalis* (187.00/G3/75); (r-s) *Hypoxylonites fusiformis* (r: 290.85/C3/91, s: 151.90/H2/63); (t) *Hypoxylonites* sp. cf. *H. curvatus* (10.25/OB/04); (u-v) *Monoporisporites neoglobosus* (u: 212.75/G1/81, v: 212.75/G1/81); (w) *Monoporisporites oviformis* (94.80m/I1/36); (x-y) *Monoporisporites* sp. (x: 217.20/F2/82, y: 192.00/G3/76); (z) *Monoporisporites* sp. cf. *M. abruptus* (264.75/D1/85); (aa-ac) *Spirotremesporites* sp. cf. *S. disciformis* (aa: 131.25/HI/53, ab: 131.25/HI/53, ac: 131.25/HI/53); (ad-ae) *Striadiporites bistriatus* (ad: 73.75I2/27, ae: 118.90/HI/48); (af-ag) *Striadiporites reticulatus* (af: 118.90/HI/48, ag: 118.90/HI/48); (ah) *Dicellaesporites aculeolatus* (148.30/H2/60); (ai) *Dicellaesporites elongatus* (131.25/HI/53); (aj) *Dicellaesporites perelongatus* (131.25/HI/53); (ak) *Dicellaesporites* sp. (187.00/G3/75); (al) *Dicellaesporites* sp. cf. *D. africanus* (296.35/C2/92); (am) *Dicellaesporites littoralis* (151.90/H2/63); (an) *Didymoporisporonites discitypicus* (40.60/I3/09); (ao) *Didymoporisporonites panshanensis* (40.60/I3/09); (ap) *Dyadosporites hilatus* (151.90/H2/63); (aq) *Dyadosporites inaequalis* (148.30/H2/60); (ar-as) *Dyadosporites okayi* (ar: 252.20/E1/83, as: 212.75/G1/81); (at) *Dyadosporites subovalis* (290.85/C3/91); (au) *Dyadosporites reticulatus* (148.30/H2/60); (av) *Fusiformisporites elongatus* (187.00/G3/75); (aw, ay) *Fusiformisporites* sp. (aw: 131.25/HI/53, ay: 89.90/I1/33); (ax) *Fusiformisporites rugosus* (140.20/H3/58); (az) *Fusiformisporites lineolatus* (296.35/C2/92); (ba) *Fusiformisporites mackenziei* (173.75/H2/69). OB = Overburden, HI = soil parting between seams H and I.

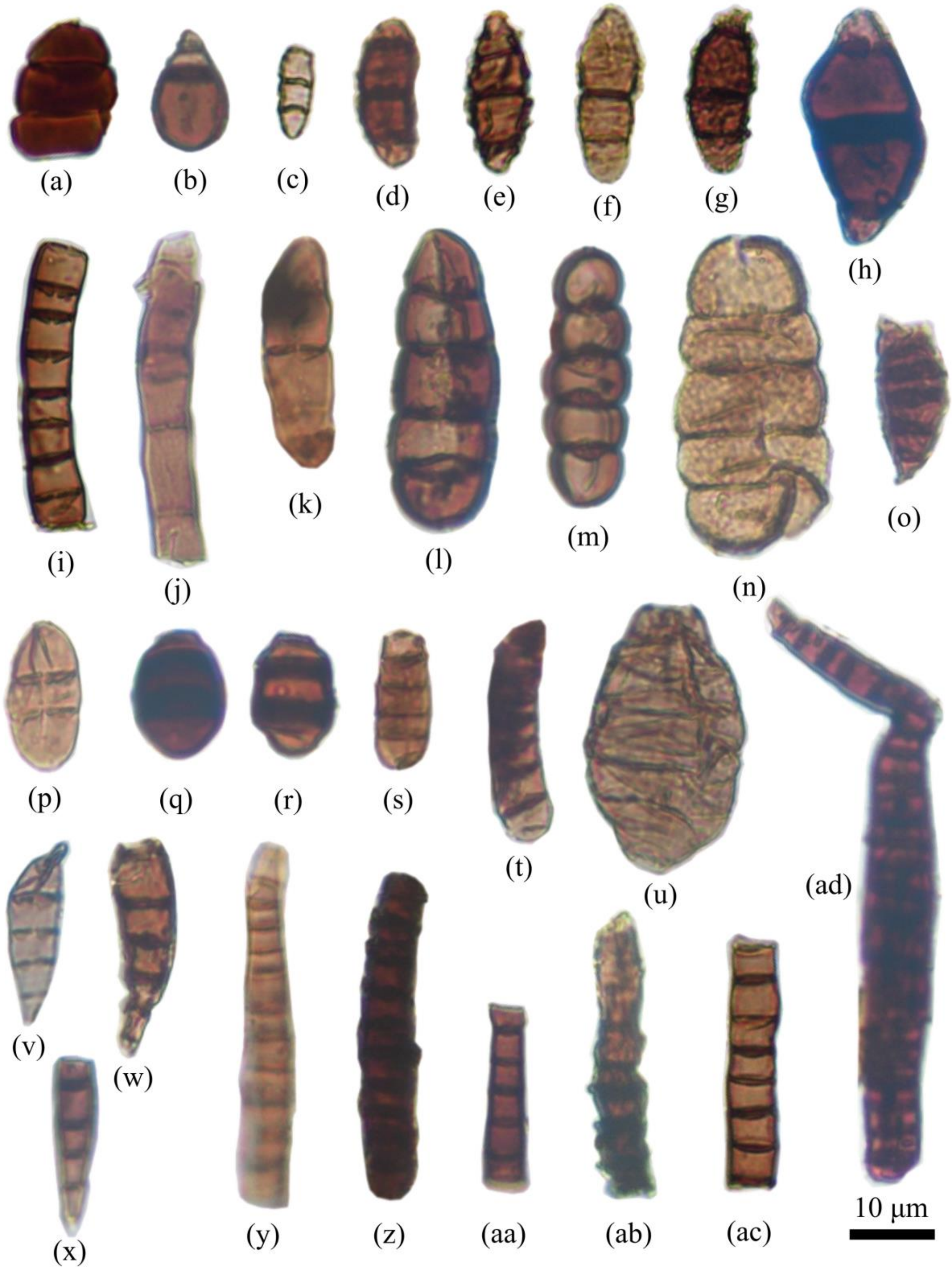

PLATE 2. Photomicrographs of selected Phragmosporae spores (graphic scale equivalents to 10 µm). Depth (m), coal seams, and sample numbers are provided (details are separated by '/'). (a) *Anatolinites* sp. (210.50/G1/80); (b) *Brachysporisporites* sp. (192.00/G3/76); (c) *Diporicellaesporites acuminatus* (10.25/OB/04); (d-g) *Diporicellaesporites* sp. (d: 151.90/H2/63, e: 6.55/OB/02, f: 6.55/OB/02, g: 40.60/I3/09); (h) *Diporicellaesporites ellipticus* (118.90/HI/48); (i) *Fractisporonites canalis* (10.25/OB/04); (j) *Fractisporonites* sp. (131.25/HI/53); (k) *Multicellites fusus* (151.90/H2/63); (l-m) *Multicellites grandiusculus* (l: 131.25/HI/53, m: 131.25/HI/53); (n-o) *Multicellites* sp. (n: 187.00/G3/75, o: 180.75/H1/73); (p) *Multicellaesporites* sp. (107.25/HI/41); (q) *Pluricellaesporites patagonicus* (107.25/HI/41); (r) *Pluricellaesporites* sp. cf. *P. delicatus* (151.90/H2/63); (s) *Pluricellaesporites* sp. cf. *P. serratus* (200.20/G2/77); (t) *Pluricellaesporites* sp. cf. *P. psilatus* (131.25/HI/53); (u) *Pluricellaesporites* sp. (131.25/HI/53); (v) *Quilonia multicellata* (131.25/HI/53); (w) *Quilonia* sp. (212.75/G1/81); (x) *Quilonia* sp. cf. *Q. attenuata* (131.25/HI/53); (y-ad) *Scolecosporites* sp. (y: 94.80/I1/36, z: 73.75/I2/27, aa: 86.35/I1/32, ab: 114.15/HI/45, ac: 10.25/OB/04; ad: 140.20/H3/58). OB = Overburden, HI = soil parting between seams H and I.

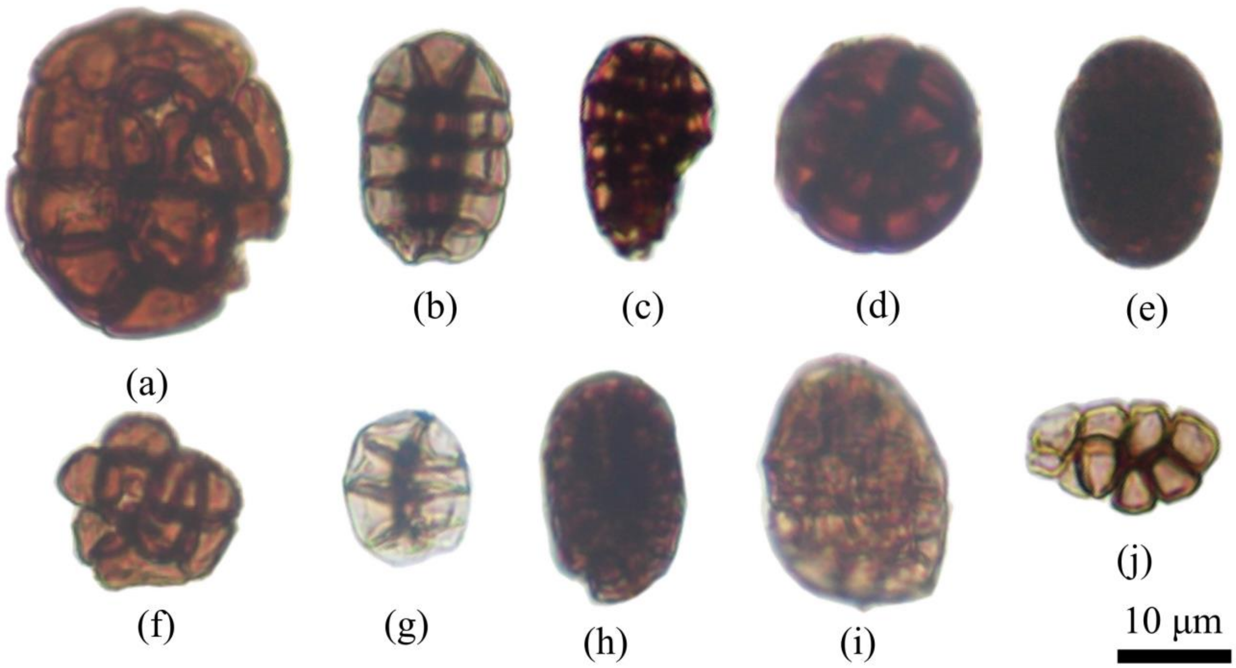

PLATE 3. Photomicrographs of selected Dictyosporae spores (graphic scale equivalents to 10 µm). Depth (m), coal seams, and sample numbers are provided (details are separated by '/'). (a) *Dictyosporites moruloides* (148.30/H2/60); (b-c) *Dictyosporites ovalis* (b: 131.25/HI/53, c: 10.25/OB/04); (d-e) *Dictyosporites* sp. (d: 107.25/HI/41, e: 68.95/I2/22); (f) *Dictyosporites tirumalacharii* (192.00/G3/76); (g) *Dictyosporites* sp. cf. *D. dictyosus* (187.00/G3/75); (h) *Dictyosporites* sp. cf. *D. ovoideus* (131.25/HI/53); (i) *Dictyosporites* sp. cf. *D. symmetricus* (94.80/I1/36); (j) *Staphlosporonites irregularis* (10.25/OB/04). OB = Overburden, HI = soil parting between seams H and I.