

Dictyosphaera macroreticulata and *Valeria lophostriata* from the late Mesoproterozoic Chaporadih Formation, Chhattisgarh Supergroup and their significance

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The present study enriches the records of the Proterozoic eukaryotic fossils with well-preserved specimens of the genus *Dictyosphaera macroreticulata* and *Valeria lophostriata* reported from the late Mesoproterozoic Chaporadih Formation of the Chandarpur Group, Chhattisgarh Supergroup. Results of integrated studies, involving Confocal Laser Scanning Microscopy (CLSM) over the Transmitted Light Microscopy (TLM), are presented to understand the submicron level morphology of Organic Walled Microfossils (OWM). In the global context, *Tappania*, *Dictyosphaera*, and *Valeria* constitute a biozone of which the latter two are important constituents. These elements are part of the widely distributed and long-ranging forms that are found in the latest Palaeoproterozoic to early Neoproterozoic (Tonian) organic-walled microfossils assemblages. Collectively, their occurrence in the Chhattisgarh Supergroup demonstrates a new record of eukaryotic fossils from the Proterozoic succession of India.

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INTRODUCTION

The modern world, full of multicellular plants, animals, and fungi, is a result of the advent of nucleated cells known as eukaryotes. In the Precambrian, evidence of eukaryotic organisms in the fossil records is rare. Their occurrence contributes uniquely to our understanding of the pattern and diversification of micro and macro-evolutionary processes through deep times. The general belief is that the eukaryotes evolved around 2000 Ma (Berney and Pawlowski, 2006). Based on biomarker studies (steranes) Brocks *et al.* (1999) suggested their origin in 2500-2800 Ma old shales of Australia. Later, this discovery was contested and found to be a contaminant (Brocks *et al.*, 2003; Kirschvink and Kopp, 2008). As of now the oldest indigenous steranes which could be convincingly associated with eukaryotes come from the c. 750 Ma Chuar Group (Summons *et al.*, 1988; Pawlowska *et al.*, 2013). Over the last fifty years, many fossils have been described as eukaryotic fossils from the Proterozoic rocks, both at the level of conventional palaeontology and molecular studies (Chernikova *et al.*, 2011; Knoll, 2014; Bonneville *et al.*, 2020; Carlisle *et al.*, 2021). These fossils, distinctly documented worldwide in marine sedimentary successions, play a significant role in understanding the patterns of the earth's atmospheric and biological evolution in deep time (Loron *et al.*, 2021; Miao *et al.*, 2021).

Besides various other Proterozoic fossils, the acritarchs – a group of decay resistance organic-walled microfossils - are taxonomically considered as eukaryotic microorganisms (Huntley *et al.*, 2006; Knoll *et al.*, 2006; Singh and Sharma, 2014; Butterfield, 2015). They are conventionally interpreted as unicelled photosynthetic protists, though some may represent multicellular algae (Butterfield, 2000). Whereas, a few have been tentatively interpreted as fungi (Butterfield, 2005; Loron *et al.*, 2019b) and thick-walled resting stage or cyst in the life cycle of marine phytoplankton (Strother, 1996). Some Proterozoic acritarchs have been interpreted as dinoflagellates after bio-molecular studies (Moldowan and Talyzina, 1998; Meng *et al.*, 2005). In particular, a few acritarchs show close similarity to the non-motile stage (phycoma) in the life cycle of modern prasinophytes, a group of well-known primitive green algae. The evolutionary pattern and abundance fluctuation of acritarchs in the fossil records have been put concerning changes in ocean chemistry, global glaciation, the diversification of metazoans, and variations in atmospheric CO₂ conditions. However, uncertainties over the biological affinities and phylogenetic relationship of acritarchs records in the Proterozoic biosphere are extensively debated (Huntley *et al.*, 2006). The current understanding of acritarchs palaeobiology is mainly based on morphological criteria, including ultrastructural studies of cell walls and analyses of distributional patterns in the sedimentary record. Similarly, the lack of detailed knowledge about the chemical structure of modern algae, fungi, and other microorganisms

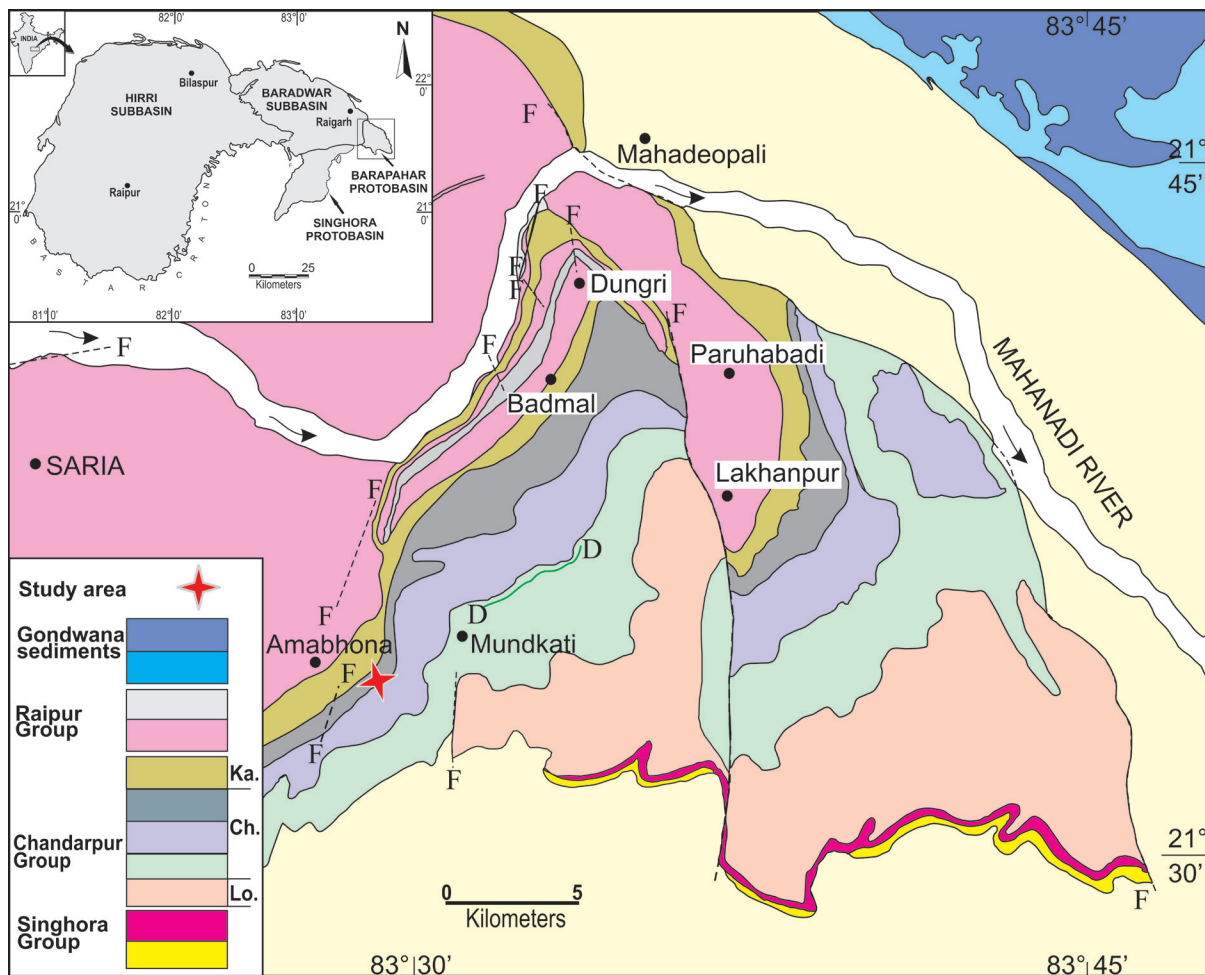


Figure 1. Generalized geological map of the Barapahar Protobasin – a part of Baradwar subbasin (redrawn after GSI, 1979) showing the location of the study area. Abbreviation: Lo. – Lohardh Formation; Ch. - Chaporadih Formation; Ka.- Kansapathar Formation)

is a major barrier in understanding the affinities of organic-walled microfossils (Schopf *et al.*, 2006). After the Great Oxidation Event (GOE, 2.4 Ga), about a billion-year (1.8 – 0.8 Ga) period of earth history underwrite noteworthy mile spot in the Proterozoic ocean, especially the origin and evolution of eukaryotes despite atmospheric and climatic stability (Holland, 2006; Hamilton *et al.*, 2016; Olson *et al.*, 2016; Large *et al.*, 2018; Mukherjee *et al.*, 2018).

Not all, but only morphologically complex acritarchs, having distinct vesicle ornamentations and sculpture, are generally assigned as eukaryotic fossils and also provide important information about taxonomic diversity and morphological disparity (Huntley *et al.*, 2006). Distinct sphaeromorph acritarchs *viz.*, *Dictyosphaera macroreticulata* and *Valeria lophostriata* are among the oldest known morphologically and taxonomically recognized eukaryotic fossils which are widely distributed in the latest Palaeoproterozoic to early Neoproterozoic (Tonian) organic-walled microfossils assemblages of Australia, Africa, Canada, China, and Siberia (Knoll *et al.*, 2006; Nagovitsin, 2009; Javaux, 2011; Singh and Sharma, 2014; Agić *et al.*, 2015; Cohen and Macdonald, 2015; Vorob'eva *et al.*, 2015; Sergeev *et al.*, 2016; Adam *et al.*, 2017; Agić *et al.*, 2017; Miao *et al.*, 2019; Singh *et al.*, 2019b; Loran *et al.*, 2021). In the past few years, continuous attempts have been made to

understand the life cycle and affinity of these acritarchs based on morphology and vesicle (Moczydlowska and Willman, 2009; Moczydlowska *et al.*, 2010; Agić *et al.*, 2015; Pang *et al.*, 2015).

During the last decade, studies on the late Palaeoproterozoic to early Neoproterozoic Chhattisgarh Supergroup provided evidence for our understanding of the lithostratigraphy, chronostratigraphy, evolution, and age of this prominent Proterozoic sedimentary basin of India (Patranabis-Deb *et al.*, 2007; Patranabis-Deb and Chaudhuri, 2008; Chakraborty *et al.*, 2010; Bickford *et al.*, 2011a; Dhang and Patranabis-Deb, 2012; Chakraborty *et al.*, 2015; Chakraborty and Barkat, 2020; Chakraborty *et al.*, 2020; George and Ray, 2020). Except for a few reports of stromatolites from this supergroup (Schnitzer, 1969; Moitra, 2003; Gupta, 2004) fossil contents were poorly documented from the Chhattisgarh Supergroup. In recent years different litho-units of the Chhattisgarh Supergroup were analyzed for documenting the palaeobiological remains of the basin to assess the biostratigraphic potential of recorded remains (Babu and Singh, 2013; Singh and Babu, 2013; Singh and Sharma, 2016; Singh *et al.*, 2019a, b). In our continuing effort to understand the evolutionary history of the Chhattisgarh Supergroup, we discovered an association of *Dictyosphaera* and *Valeria* bearing morphologically complex acritarchs

Table 1. Generalized lithostratigraphic succession of the Chhattisgarh Supergroup (Das *et al.*, 1992; Patranabis-Deb and Chaudhuri, 2008; Mukherjee and Ray, 2010) Age data source: 1. Bickford *et al.* (2011), 2. Pandey *et al.* (2012), 3. Das *et al.* (2009). * Fossiliferous unit.

GROUP	FORMATION	LITHOLOGY	AGE	
CHHATTISGARH SUPERGROUP	Kharsia	Nandeli Shale	Gypsiferous purple shale and dolomite Sandstone and conglomerate	
		Sarnadih Sandstone		
	Unconformity			
	Raipur	Churtela Shale	Purple shale and Tuff	1000 Ma (Tuff) ¹
		Saradih Limestone	Dolomite/Stromatolitic Limestone	
		Gunderdehi Shale	Calcareous shale with stromatolitic limestone	
		Sarangarh Limestone	Flaggy limestone and shale	
	Chandarpur	Kansapathar Formation	Quartz arenite	1641 ±120 Ma (Dolerite Intrusive) ²
		Chaporadih Formation*	Glauconitic sandstone/siltstone, black shale	
		Lohardi Formation	Subarkose with basal conglomerate	
Unconformity				
Singhora	Chhuipali Formation	Stromatolitic limestone and Variegated shale	c.1500 Ma (Tuff) ³	
	Bhalukona Formation	Quartz arenite and minor shale		
	Saraipali Formation	Variegated shale/siltstone, tuff/porcellanite		
	Rehatikhoh Formation	Sandstone with conglomerate at the base		
Archean Basement (Sonakhan & Sambalpur Granites)				

from the Chandarpur Group of rocks, exposed in the Baradwar sub-basin, Bastar Craton in Central India. In the present study, we discuss the results of sub-micron level morphology, using Confocal Laser Scanning Microscopy (CLSM) over the Transmitted Light Microscopy. The CLSM is a laser-induced non-destructive, non-intrusive analytical technique preferred to understand the cellular anatomy and ultrastructure study of the Precambrian microfossils (Schopf and Kudryavtsev, 2009; Schopf *et al.*, 2015; Schopf *et al.*, 2016). CLSM provides 2-D and 3-D high-resolution images, as well as 3-D reconstructions of autofluorescent objects excited with the aid of laser-induced light operating at the variable wavelength (Schopf *et al.*, 2006).

GENERAL GEOLOGY AND AGE

~2300 meters thick Proterozoic Chhattisgarh Supergroup is an unmetamorphosed, less deformed sedimentary succession lying over the Bastar Craton (Mukherjee *et al.*, 2014). The rocks of this succession exposed over ~33000 km² area in parts of Chhattisgarh and Odisha states of Peninsular India (Fig. 1). Lithostratigraphically, it is divided into four groups *viz.*, the Singhora, the Chandarpur, the Raipur, and the Kharsia in ascending order (Das *et al.*, 1992; Mukherjee *et al.*, 2014; Chakraborty *et al.*, 2015) (Fig. 2) (Table-1). The Chhattisgarh Supergroup in the western part is comprised of only the Chandarpur and Raipur Groups, whereas in the eastern part all the four groups are exposed.

In the easternmost part, ~1000 m thick succession of mixed siliciclastic-carbonate rocks association unconformably overlies the basement constituted by the Sambalpur granite (Pascoe, 1973). The Chandarpur Group, middle part of the Chhattisgarh Supergroup, is well exposed in and around Amabhona area, which is about 32 km NNW of Bargarh city in the Odisha State. It is sub-divided into

three distinct formations *i.e.*, Lohardi, Chaporadih, and Kansapathar in stratigraphic order (Table-1). The Lohardi Formation unconformably overlies on the erosional surface of the Singhora Group of rocks (Das *et al.*, 2001) which is represented by matrix-supported polymictic conglomerate, thinly bedded arkose, sub-arkose, and wack arenite showing fining upward sedimentation pattern. The overlying Chaporadih Formation is characterized by lithologic heterogeneity and constituted of three major lithological components namely the green mudstone, green and black shale, sandstone – mudstone, and sub-arkosic sandstone. The sandstone – mudstone are the dominant constituents of this formation and occupy almost 65% of its thickness. The green mudstone and shale with small isolated lenses of sandstone are well developed in the basal part over the Lohardi Sandstone that shows a cyclic representation of sand-mud heterolithic. The sequence is overlain by black shale (> 20-meter-thick) in the upper part with a thick sheet of arkosic sandstone. The Kansapathar Formation overlies the mud-dominated Chaporadih Formation, consisting mainly of well-sorted scarp forming sandstone. The sediments of the Chandarpur Group are intensely folded, faulted, and show rapid facies changes (Patranabis-Deb, 2004).

The available geochronological data on the Chhattisgarh basin are inconsistent. EPMA dating of monazite and SHRIMP dating of zircon of the Khariar and Shingora tuffs show a concentration of ages around ~1500 Ma (Das *et al.*, 2009; Bickford *et al.*, 2011b). On the contrary, SHRIMP II and LA-ICP-MS dating of zircon from the different stratigraphic units of the Singhora Group yielded the youngest age population between c. 1619 Ma and c. 2543 Ma, implying the initiation of sedimentation >1600 Ma (Das *et al.*, 2017). A basic dyke intruding the overlying Chandarpur sediments at Damdama area, Raigarh district has yielded 1641 ± 120 Ma Rb – Sr isochron date (Pandey *et al.*, 2012). The SHRIMP, U–Pb analysis of zircon from Rhyolitic tuffs (Sukhda and Dhamda tuffs) found at the top of the Raipur Group yielded an age of ca. 975–1000 Ma (Patranabis-Deb *et al.*, 2007; Bickford *et al.*, 2011a). These rhyolitic tuffs are considered as representing

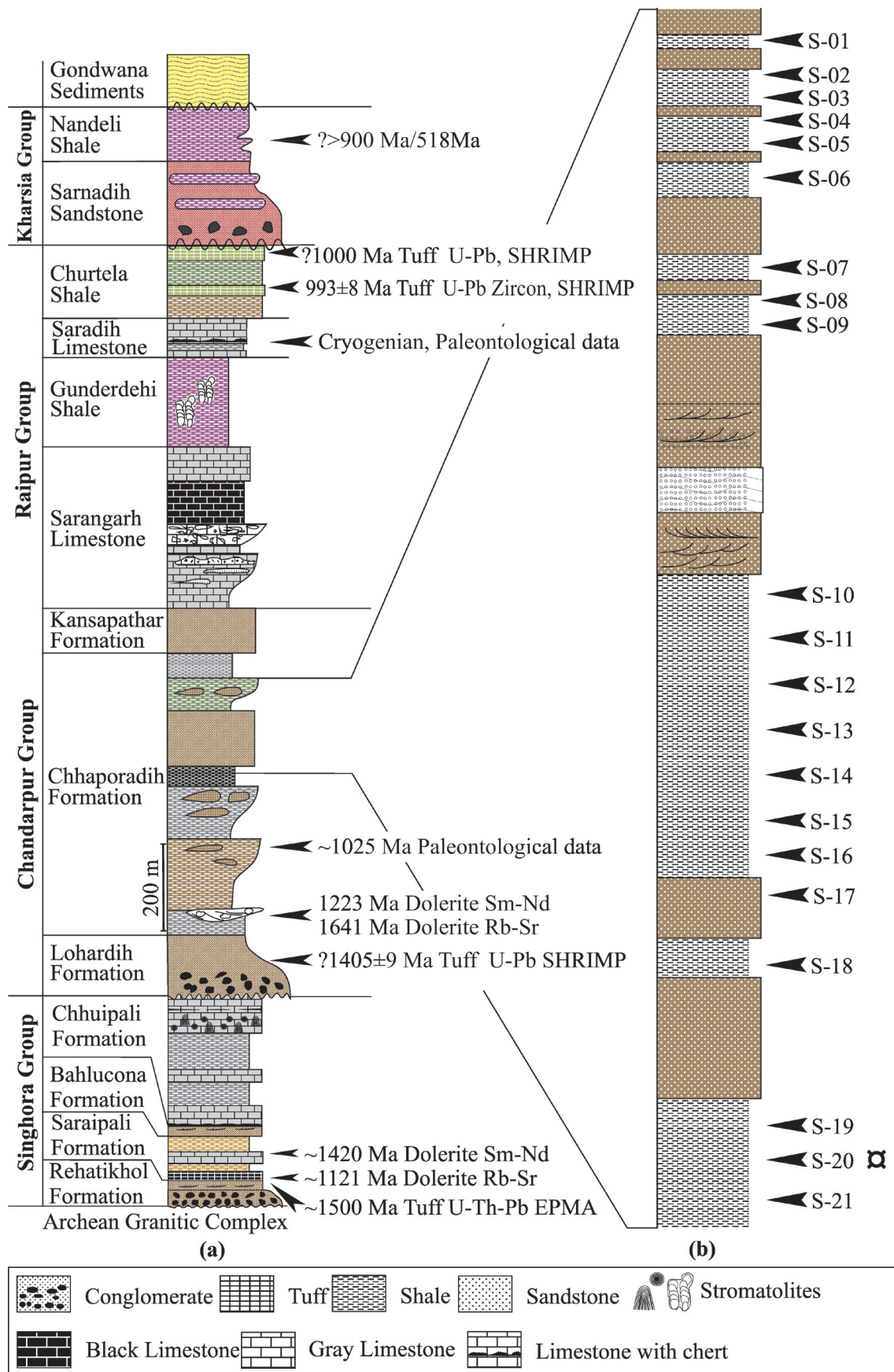


Figure 2. Generalized lithostratigraphic column: a. Chhattisgarh Supergroup (after Patranibs-Deb and Chaudhuri, 2008) and b. Amabhona Ghat Section showing the sample locations.

a major thermal event denoting the closer of sedimentation in the Chhattisgarh basin (Patranabis-Deb and Chaudhuri, 2008) similar to the Vindhyan basin (Malone *et al.*, 2008). Later, tuffs have been recorded at various other levels in the underlying formations making the stratigraphic positions of dated tuffs questionable (Mukherjee and Ray, 2010). Thus, the geochronological data suggest that the Chhattisgarh Supergroup is Palaeoproterozoic-Mesoproterozoic in age. These dates are not well-matched with the recently recorded palaeontological data (Singh *et al.*, 2019b).

Previously recorded palaeobiological evidence from the entire Chhattisgarh succession is meager and restricted to the reporting of stromatolites (Schnitzer, 1969; Moitra, 2003; Gupta, 2004). The occurrence of vauchericean algae *Jacutianema solubila* and other associated age diagnostic organic-walled microfossils from the rocks of the Chandarpur Group indicate the latest Mesoproterozoic age equivalent to ~1025 Ma Lakhanda microbiota of Russia (Singh and Sharma, 2016). Additionally, microfossils recovered from the chert found in the Saradih Dolomite (the unit below the Sukhda tuff) indicate Tonian to Cryogenian age (Singh and Babu, 2013) whereas, the occurrence of helically coiled cyanobacterial microfossil *Obruchevella* from the same horizon suggest that the age extended up to the early Ediacaran (Singh *et al.*, 2019b). These studies suggested Mesoproterozoic-Neoproterozoic age for the entire succession contrary to the recent geochronological data that support the late Palaeoproterozoic to Mesoproterozoic age for the Chhattisgarh Basin. Acritarchs and other organic-walled microfossils from the Precambrian successions are becoming increasingly important proxies in establishing the biostratigraphy and determining the age and depositional environment of sedimentary succession (Huntley *et al.*, 2006; Singh and Sharma, 2014, 2016; Singh *et al.*, 2019a, b).

MATERIALS AND METHODS

For palaeobiological studies, samples were collected from the lower heterolithic unit of the Chaporadih Formation, exposed in Pahari *nala* flowing down at Amabhona Ghat section (2.64 Km ESE of Amabhona Village) (Long.: 21°33'59.33"N; Lat.: 83°29'47.62"E) in the Barapahar region of the Bargarh district, Odisha, India. The dominant lithology at this section is mud-sand heterolithic with gentle dipping strata. Organic-walled microfossils are recovered from this section as marked in Fig.-2.

The low- manipulation acid digestion technique (Butterfield *et al.*, 1994) was applied for the recovery of microfossils and organic residue, using 40% hydrofluoric acid. This technique avoids the fragmentation and destruction of microfossils and morphological characters *viz.*, long tubular processes, long filaments, and large size vesicles. Specimens were further individually picked from macerated residue and were individually mounted on the glass slides with the help of Canada Balsam (R.I. = 1.5).

Transmitted Light Microscopy (TLM) - Transmitted Light Microscopic (TLM) studies were conducted on the

fossils recovered from the carbonaceous shale. About 120 palynological slides were examined under Olympus BX51 transmitted light microscope at 40X and 100X (under oil immersion lens) magnifications for documenting the finer morphological details of microorganisms. Further specimens are photographed on Olympus DP 26 digital camera and size measurements were taken on CellCense Standard software. England Finder coordinates are given for each specimen with the arrow on the oriented slide.

Confocal Laser Scanning Microscopy (CLSM) - To understand the sub-micron scale morphology of organic-walled microfossils *Dictyosphaera macroreticulata* and *Valeria lophostriata* the Confocal Laser Scanning Microscopy (CLSM) were performed by using standard protocols (Schopf *et al.*, 2006; Singh *et al.*, 2019a). Three-dimensional confocal fluorescence imaging was obtained on Leica TCS SP8 Confocal Laser Scanning biological microscope system equipped with two Melles Griot lasers, a 488 nm 20 mW-output argon-ion laser, and a 633 nm 10mW-output helium-neon laser (Melles Griot, Carlsbad CA). The images were acquired using a 100× oil-immersion objective (numerical aperture = 1.4). The observations were made with fluorescence-free microscopy immersion oil. Filters were used in the light-path of the system to remove wavelength 660 nm (for 633 nm laser excitation) from the kerogen-derived fluorescence emitted by the specimens. Sets of the acquired image were subsequently processed and examined on LAS-X imaging software.

Sample Repository - All illustrated specimens in the palynological slides, photomicrographs, and associated samples are deposited in the Birbal Sahni Institute of Palaeosciences, Lucknow. These can be retrieved vide statement no. BSIP-1571.

SYSTEMATICS

The carbonaceous shales from the Chaporadih Formation have yielded the majority of well-preserved as well as, geographically long-ranging Organic Walled Microfossils (OWMs). These are constituted of subsphaeroidal – spheroidal vesicles of the acritarch forms belonging to Sphaeromorphida subgroup (Fensome *et al.*, 1990) followed by mono-specific botuliform microfossils representing Gongrosia phases of a vauchericean xanthophyte alga *Jacutianema solubila* (Butterfield, 2004; Singh and Sharma, 2016). The taxonomic richness of smooth-walled spheromorphic acritarch genus *Leiosphaeridia* is present in almost all samples. In taxonomic composition, the organic-walled microfossils are excellent/good, three-dimensionally preserved, slightly compressed due to mutual compressions, and display bark brown coloration of organic matter. The most significant microfossils in the Chaporadih assemblage are morphologically assigned complex acritarch *Dictyosphaera macroreticulata* and *Valeria lophostriata* (Plates I-III). On the size parameters, vesicles vary in size (40-250 µm), are ornamented/unornamented, thick to thin-walled, and single-

layered. Compression and compaction folds, dense concentric striations, and polygonal plates on the vesicle wall as well as deformation in specimens are common characteristics in microfossils. Such complex morphologies are diagnostically recognized as extant grade eukaryotes (Knoll *et al.*, 2006; Nagovitsin, 2009; Javaux, 2011; Singh and Sharma, 2014; Agić *et al.*, 2015; Cohen and Macdonald, 2015; Vorob'eva *et al.*, 2015; Sergeev *et al.*, 2016; Adam *et al.*, 2017; Agić *et al.*, 2017; Miao *et al.*, 2019; Singh *et al.*, 2019b; Loron *et al.*, 2021). Systematics and geographical distributions of the identified OWMs are provided below.

Group **Acritarcha** Evitt 1963

Subgroup **Sphaeromorphitae** Downie, Evitt and Sarjeant, 1963

Genus **Valeria** Jankauskas, 1982, emended Nagovitsin, 2009

Type species **Valeria lophostriata** (Jankauskas, 1979) Jankauskas, 1982.

Valeria lophostriata (Jankauskas, 1979) Jankauskas, 1982 (Pl. I, Figs. 1–3; 1.1–3.2; Pl. II, Figs. 1–5; Pl. III, Figs. 1–3; 1.1–1.3)

Occurrence: Lower heterolithic shale of the Chaporadih Formation, Chandarpur Group.

Description: Originally spheroidal organic-walled vesicle, oval to sub-angular outline, consists of equidistantly and closely spaced striations on the inner/outer surface of vesicle wall (Pl. I, Figs. 1.1, 2.1; Pl. II, Fig. 1). Appear dark brown in color. Vesicle wall moderately thin, translucent, fold thick. Vesicle diameter ranges between 56–200 µm. Striations about 0.3–0.5 µm in width and 0.2–0.3 µm in spacing. More than 30 well-preserved and complete specimens are measured.

Remarks: In the present assemblage, striations visible on the edge of some of the specimens exhibit a cross-hatch pattern (Pl. I, Figs. 1.1, 2.1, 3.1, 3.2), reflecting back-facing sides of the vesicle surface (Pl. II, Figs. 2, 4.1). CLSM analysis of the examined specimens in the present work demonstrates the densely organized cross hatched striations pattern on vesicle surface in light microscopy (Pl. III, Fig. 1), however, CLSM imaging display the presence of short hairy processes (up to 2–4 µm long) on the entire vesicle (Pl. III, Fig. 1.3) as well as few specimens characterizes fine concentric striations (Pl. III, Fig. 2.2) with cristate surface patterns on the vesicle (Pl. III, Fig. 2.1).

Age and distribution: *Valeria lophostriata* is a geographically widespread taxon invariably known from more than 30 localities of the latest Palaeoproterozoic to Tonian successions (Hofmann, 1999). Palaeoproterozoic: the Changzhougou Formation and Chuanlinggou Formation of the Changcheng Group, North China (Yan, 1995; Miao *et al.*, 2019). Mesoproterozoic: the Ruyang Group, North China (Agić *et al.*, 2015; Pang *et al.*, 2015; Agić *et al.*, 2017); the Mallapunyah Formation, Roper Group and ~811–716 Ma Alinya Formation, Australia (Javaux, 2007a, b; Riedman and Porter, 2016; Javaux and Knoll, 2017); the Bylot Supergroup, Canada (Hofmann and Jackson, 1994); the Qaanaaq Formation, Thule Supergroup, Northwest Greenland (Samuelsson *et al.*, 1999); the Sarda Formation, Bahraich Group, Ganga Basin, India (Prasad and Asher, 2001); the Zigazino-Komarovo

Formation, Kamo Group; Russia (Nagovitsin, 2009); the Greyson Formation, Belt Supergroup, Montana (Adam *et al.*, 2016; Adam *et al.*, 2017); the Mbuji-Mayi Supergroup, Democratic Republic of Congo (Baludikay *et al.*, 2016); the lower Shaler Supergroup, Arctic, Canada (Loron *et al.*, 2019a); the Xiamling Formation, North China (Miao *et al.*, 2021). Neoproterozoic: the Dashkinsky Formation, Tonian Ust'-Kirbin, Chapoma and Karuyarvinskaya Formations, Russia (Jankauskas *et al.*, 1989; Samuelsson, 1997; Pavlov *et al.*, 2002); the Båtsfjord Formation, Norway (Vidal and Siedlecka, 1983); the Chuar Group, Arizona, USA (Vidal and Ford, 1985; Nagy *et al.*, 2009; Porter and Riedman, 2016).

Genus **Dictyosphaera** Xing and Liu, 1973

Type species **Dictyosphaera macroreticulata** Xing and Liu, 1973

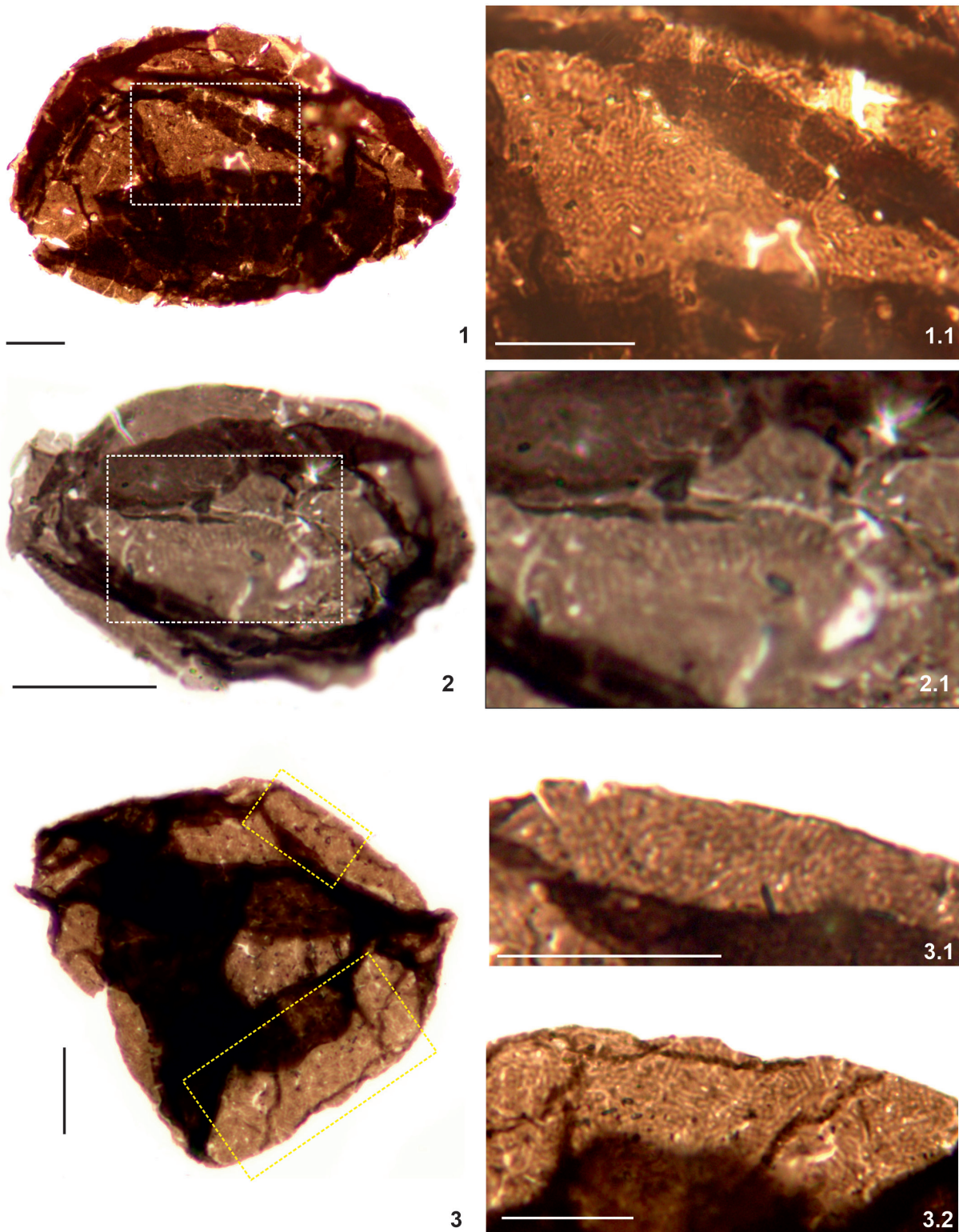
Dictyosphaera macroreticulata Xing and Liu, 1973 (Pl. III, Figs. 3, 3.1; 3.2)

Occurrence: Lower heterolithic shales of the Mesoproterozoic Chaporadih Formation, Chandarpur Group, Odisha, India.

Description: Uni-layered spheroidal organic-walled vesicle, moderately thick-walled, comprising sub-rounded-to-sub-angular reticulate surface pattern with positive relief defining concave pits on entire vesicle surface. The vesicle diameter ranges from 40–80 µm, reticulates broadly 1.5–02 from µm in diameter. A total of 05 complete specimens were measured.

Remarks: Specimens of *D. macroreticulata* observed in the present material have a maximum vesicle diameter of 80 µm with 1.5–02 µm wide tessellated polygons on the vesicle (Pl. III, Fig. 3.1) which shows close resemblance with the specimens of the Ruyang Formation (Agić *et al.*, 2017). Present specimens also differ from *D. smaugi* by its small hexagonal/polygonal tessellated surface ornamentations covering the whole vesicle (Pl. III, Fig. 3.1). Confocal Laser Scanning studies of the examined specimen of *Dictyosphaera macroreticulata* (Pl. III, Fig. 3) having a reticulate surface sculpture formed by polygonal or hexagonal low ridges with positive relief delimiting concave pits (mesh) are prominently visible in the confocal image (Pl. III, Fig. 3.2) parallel to the previous explanation given after SEM studies for eukaryotic interpretation (Javaux *et al.*, 2004b).

Age and distribution: The stratigraphic range of this genus is Palaeoproterozoic to early Neoproterozoic (Tonian). Palaeoproterozoic: the Gaoshanhe Group, China (Hu and Fu, 1982; Xiao *et al.*, 1997). Mesoproterozoic: the Baicaoping and Beidajian Formation, Ruyang Group, China (Xing and Liu, 1973; Yan and Zhu, 1992; Yin and Yuan, 2003; Yin *et al.*, 2005; Li *et al.*, 2012; Agić *et al.*, 2015; Agić *et al.*, 2017); the Velkerri Formation, Roper Group, Australia (Javaux *et al.*, 2001; Javaux *et al.*, 2004a; Javaux and Knoll, 2017), the Greyson Formation, Belt Supergroup, Canada (Adam *et al.*, 2016; Adam *et al.*, 2017); the Escape Rapids and Grassy Bay Formations, Shaler Supergroup, Canada (Loron *et al.*, 2019a); the Fort Confidence Formation, Dismal Lakes Group, Canada (Loron *et al.*, 2021); the Xiamling Formation, North China (Miao *et al.*, 2021). Neoproterozoic: the Gouhou Formation, Huaibei region, North China (Tang *et al.*, 2015).



EXPLANATION OF PLATE I

Organic Walled Microfossil *Valeria lophostriata* from the Chaporadih Formation, Chandarpur Group. Scale bar for each specimen = 25 μm. 1. Slide no. BSIP 16993, England Finder No. H34/3; 2. Slide no. BSIP 8429/14B, England Finder No. E57/4; 3. Slide no. BSIP 16994, England Finder No. F32/3; 1.1, 2.1, 3.1, 3.2. show the enlargement of the regions in box and show view of cross hatched vesicle striation.

DISCUSSION

Records of early eukaryotes

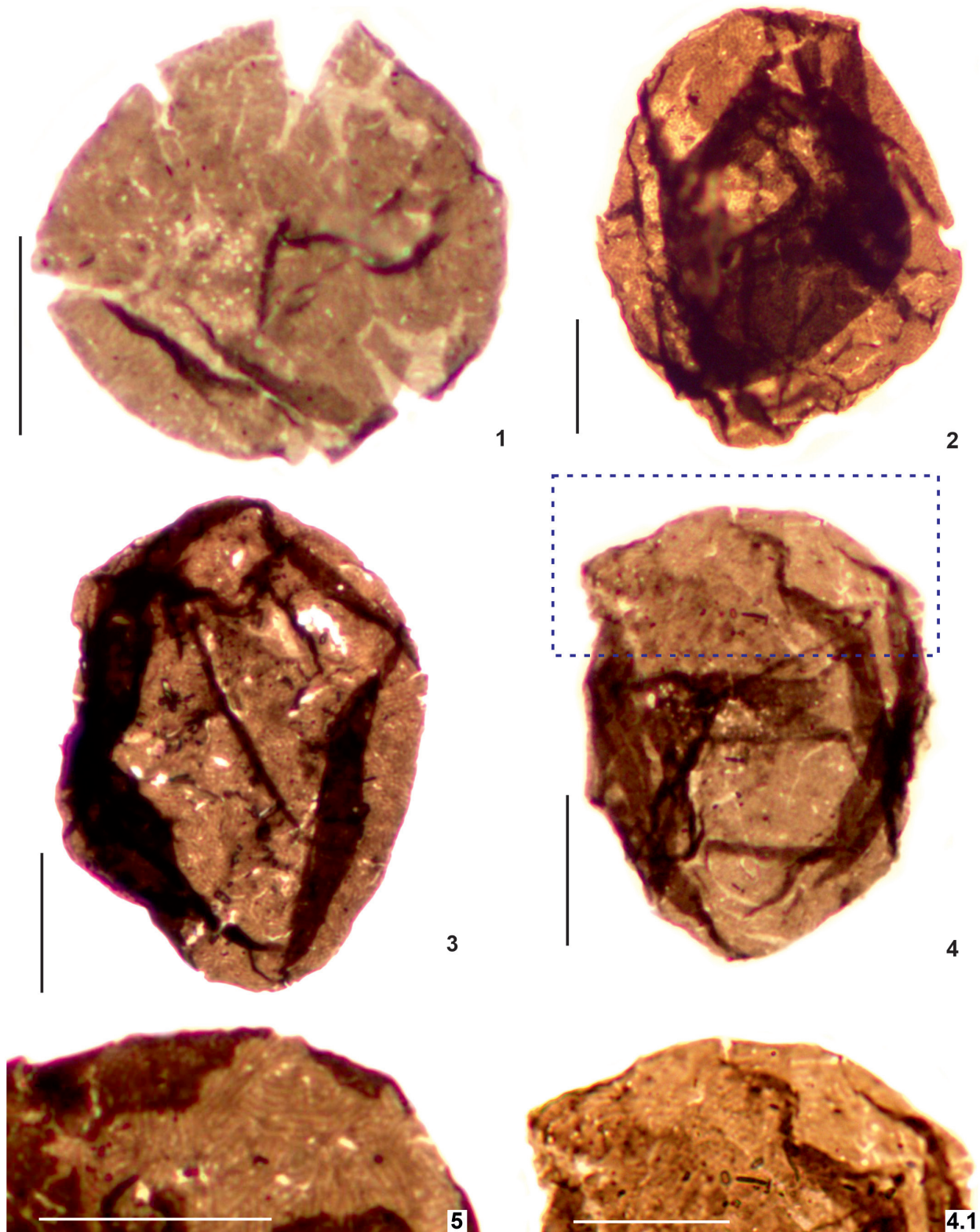
In the earth's history, the mid-Proterozoic time (ca. 1850–850 Ma) is not only known as 'Boring Billions' but also considered as a slingshot for the evolution and diversification of complex life as inferred from the existing palaeontological and molecular clock studies (Javaux *et al.*, 2013; Knoll, 2014; Sharpe *et al.*, 2015; Mukherjee *et al.*, 2018; Wang and Luo, 2021). However, some researches support the hypothesis of little happened on earth in terms of biological evolution due to the low level of oxygen in the atmosphere and ocean (Poulton *et al.*, 2004; Zhang *et al.*, 2021a; Zhang *et al.*, 2021b). Sedimentary successions are true archives to explore what happened during this period. Acid resistance organic-walled microfossils (acritarchs) are considered as earth's earliest non-marine eukaryotes during the Precambrian Eon and an essential tool for biostratigraphic correlation of sedimentary sequences; especially those successions which are geo-chronologically poorly established. Series of biological innovations *viz.*, such as fusion of multiple unicellular prokaryotic cells, endosymbiosis, the transition from proto-eukaryotic last common ancestor, the origin of multicellularity, sexual reproduction as well as cyst formation, etc., are considered as the steps towards the evolution of eukaryotes and higher forms during the Precambrian and their evidence are recorded throughout the fossil records (Javaux, 2011; Xiao, 2013; Butterfield, 2015; Cohen and Macdonald, 2015; Agić and Cohen, 2021).

Fossil eukaryotes are recognized based on size, distinct processes, median split and preservable walls (Knoll *et al.*, 2006; Agić *et al.*, 2015). In general, the cells of eukaryotic organisms are large (>60 µm) (Butterfield, 2015). For a considerable time, characteristic intracellular inclusions in microfossils were believed to represent nucleus and their large sizes were considered as representative eukaryotes (Schopf, 1968; Schopf and Blacic, 1971; Schopf, 1999). Later in most of the cases, these claims were contested (Xiao, 2005; Berney and Pawlowski, 2006; Pang *et al.*, 2013). Molecular clock estimates suggest the radiation of eukaryotes around Mesoproterozoic-Neoproterozoic Boundary ~ 1100 Ma (Berney and Pawlowski, 2006).

Our understanding of the advent, evolution, and diversification of eukaryote during the Proterozoic time has continuously improved dramatically since the purported report of eukaryotic body fossil *Grypania spiralis*- a coiled carbonaceous fossils-documented from the 1980-1800 Ma Negaunee Iron Formation of Michigan (Han and Runnegar, 1992), however, it is widely debated for its eukaryotic affinity (Sharma and Shukla, 2009). The common eukaryotic fossils in the early records are spinose and otherwise ornamented carbonaceous 'acanthomorphic acritarchs' (Cavalier-Smith, 2002). Studies revealed that eukaryotic fossils with complex morphology initially appeared in the stratigraphic units of late Palaeoproterozoic ca. 1.65 -1.6 Ga Changcheng Group (Lamb *et al.*, 2009; Miao *et al.*, 2019; Miao *et al.*, 2021), the Ruyang Group (Yin *et al.*, 2005; Agić *et al.*, 2015; Agić *et al.*, 2017) of China; ca. 1650 Ma old Mallapunyah Formation, Roper Group of Australia (Javaux *et al.*, 2004b; Javaux and

Knoll, 2017; Javaux and Lepot, 2018) and the ca. 1700 – 1600 Ma old Semri Group, Vindhyan Supergroup of India (Prasad *et al.*, 2005; Singh and Sharma, 2014; Bengtson *et al.*, 2017). Although, exceptionally preserved fossils of red alga *Bangiomorpha* favor the emergence of Crown Group eukaryote ~1047 million years ago (Gibson *et al.*, 2018), yet the Stem Group of eukaryotes record represent emergence during ~1800 - ~1600 million years ago (Knoll, 2014). The exact timing of such innovations is still debatable for example, the first appearance of Stem Group Eukaryotes or Last Eukaryotic Common Ancestors (LECA) (Carlisle *et al.*, 2021). Available diversification models, palaeodiversity data revealed that the eukaryotic domain developed various biological innovations during the late Palaeoproterozoic-early Mesoproterozoic. Additionally, studies revealed that during the Mesoproterozoic time eukaryotes were taxonomically, metabolically, and ecologically diversified with the initiation of photosynthesis, osmotrophy, and predation (Javaux and Knoll, 2017; Loron *et al.*, 2021). Series of investigations are continuously made to understand these aforesaid global patterns played a significant role to understand the evolutionary development of early eukaryotes in Precambrian Eon. Several distinct types of micro and macrofossils are recorded after the Great Oxidation Event (GOE) from the Proterozoic sedimentary successions and claimed as eukaryotes with the oldest antiquity (Lamb *et al.*, 2009; Javaux *et al.*, 2010; Retallack *et al.*, 2013a; Retallack *et al.*, 2013b; Singh and Sharma, 2014; Tang *et al.*, 2020). Despite these biological innovations the signatures of eukaryotic fossils in the Archaean sedimentary successions are less and non-convincing due to doubtful interpretations. Javaux *et al.* (2010) have claimed large spheroidal vesicle (diameter up to 300 µm) as potential Stem Group eukaryotes, documented from the Mesoarchaeon (~3200 Ma) shales and siltstones of Moodies Group, South Africa. Eukaryotic fossils recorded from different formations of the world claimed their antiquity from 2.2 Ga to 1.8 Ga. Such fossils are *Grypania spiralis* (Han and Runnegar, 1992; Sharma and Shukla, 2009); *Diskagama buttonii* (Retallack *et al.*, 2013b); carbonaceous ribbons and blades (Yan and Liu, 1997; Sharma, 2006; Babu and Singh, 2011; Zhu *et al.*, 2016); large sphaeromorphic acritarchs (Lamb *et al.*, 2009).

Comprehensive reviews revealed that distinct types of OWMs assemblages are recorded from the latest Palaeoproterozoic-Neoproterozoic sedimentary successions globally and some are claimed to represent eukaryotes on the basis of complex vesicle and its wall structure, median split, large spines (Lamb *et al.*, 2009; Javaux, 2011; Singh and Sharma, 2014; Agić *et al.*, 2015; Cohen and Macdonald, 2015; Adam *et al.*, 2017; Singh *et al.*, 2019b). These OWMs are morphologically differentiated and characterized by *Dictyospehara*, *Gigantosphaeridium*, *Shuiyousphaeridium*, *Tappania*, and *Valeria* type organic-walled microfossils association. *Tappania-Dictyosphaera-Valeria* is a widely distributed principal constituent of late Palaeoproterozoic to early Mesoproterozoic successions and is considered as a biozone (Adam *et al.*, 2017). Besides, Singh and Sharma (2014) documented distinct morphologically complex acritarch species *Shuiyousphaeridium echinatum* from the > 1650 Ma old rocks of the Chitrakut Formation of the Semri Group and claimed the oldest occurrence of eukaryotic fossils from India after China (1600 Ma) and Australia (1450 Ma).



EXPLANATION OF PLATE II

Organic Walled Microfossil *Valeria lophostriata* from the Chaporadih Formation, Chandarpur Group. Scale bar for each specimen = 25 μ m. 1. Slide no. BSIP 16992, England Finder No. O40/2; 2. Slide no. BSIP 16641, England Finder No. O40; 3. Slide no. BSIP 16991, England Finder No. J53/3; 4. Slide no. BSIP 16994, England Finder No. O40/4; 5. Slide no. BSIP 16641, England Finder No. S42/4; 4.1, 5. Magnified view of vesicle striations.

Chaporadih eukaryotes and their implications

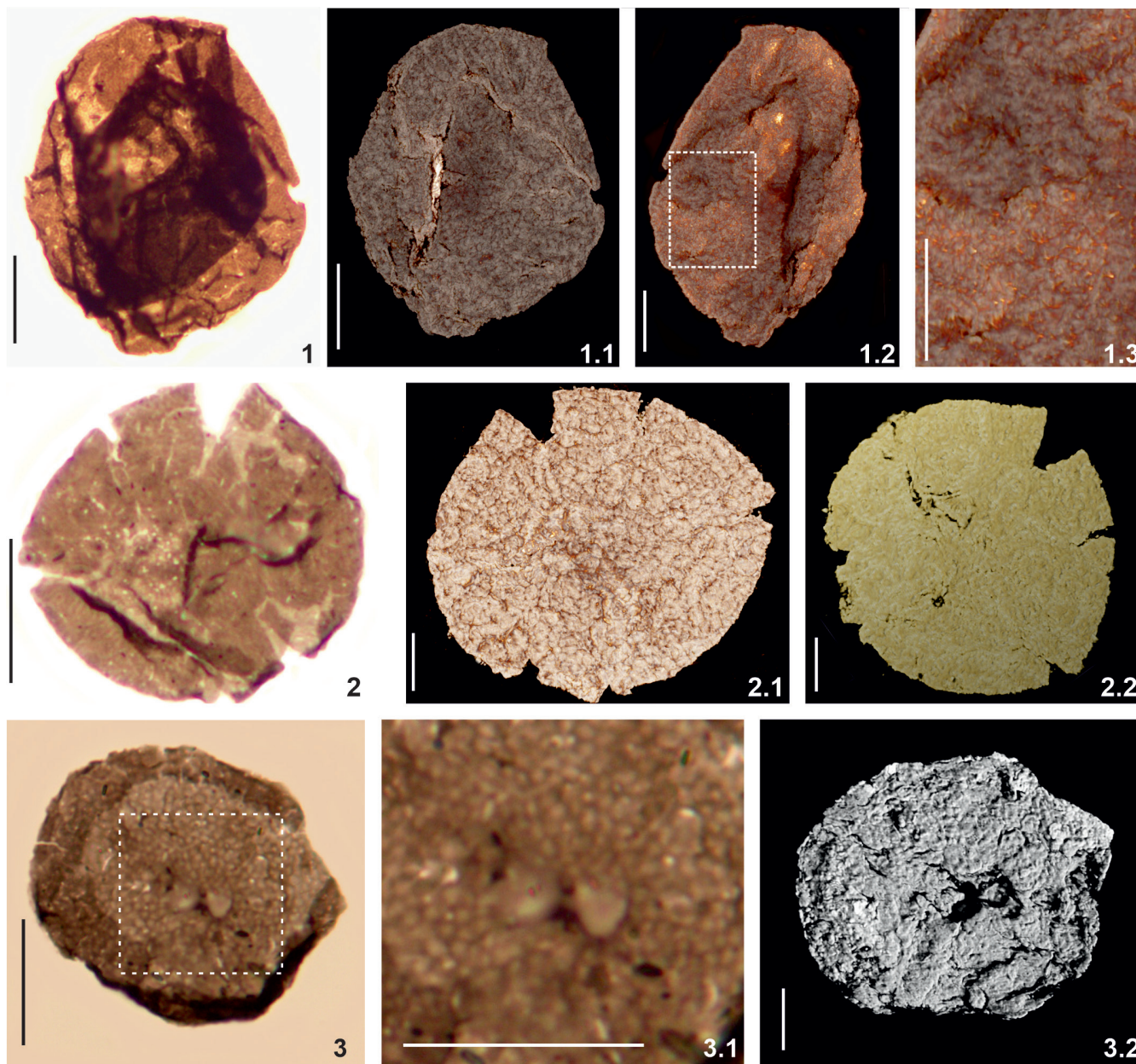
The late Mesoproterozoic Chaporadih Formation of the Chandarpur Group contains well preserved ornamented OWMs assemblage including diagnostically recognized eukaryotic taxa *Dictyosphaera macroreticulata* and *Valeria lophostriata* (Plate I-III) along with co-occurrence of botuliform microfossil *Jacutianema solubila*, smooth-walled sphaeromorphic acritarchs *Leiosphaeridia* spp. and *Trachysphaeridium levis* (Singh and Sharma, 2016).

Based on the complex morphological characteristics such as tessellated hexagonal platelets on thick-walled vesicles as observed after CLSM investigation in the present study (Plate-III, Figs. 3, 3.1; 3.2) as well as on the light microscopy and scanning electron microscopy, *Dictyosphaera* has been assigned as a eukaryotic fossil (Xiao, 2013; Agić *et al.*, 2015; Agić *et al.*, 2017) with possibly algal affinity previously observed by Yin *et al.* (2005) and Moczydlowska *et al.* (2010). Usually, the *Dictyosphaera macroreticulata* is considered as an index taxon of early Mesoproterozoic successions, due to its restricted occurrence in the early Mesoproterozoic Ruyang Group, China (Yin *et al.*, 2005; Agić *et al.*, 2015; Agić *et al.*, 2017); the Roper Group, Australia (Javaux and Knoll, 2017) and the Belt Supergroup of Montana (Adam *et al.*, 2017) and found co-occurring with *Valeria* and *Tappania* (Adam *et al.*, 2017; Javaux and Knoll, 2017; Loron *et al.*, 2021). Recently, this species has been documented from the <1013-892±13Ma Grassy Bay Formation, Canada (Loron *et al.*, 2019a). Similarly, the age of the Chaporadih Formation has been considered as late Mesoproterozoic (~1025 Ma) based on the occurrence of xanthophyte algal fossil *Jacutianema solubila*. Additionally, Detrital zircon SIMS U-Pb ages from the Porcellanite samples of the Lohardih Formation (stratigraphic unit just below the Chaporadih Formation) yield a maximum depositional age of <1263 ± 17Ma (Singh *et al.*, 2021). Thus, the record of *Dictyosphaera macroreticulata* from the latest Mesoproterozoic Chaporadih Formation constitutes only the first occurrence from India (another species *D. tactica* from China, Laurentia, and Arctic Canada) extends the biostratigraphic range of *Dictyosphaera* into the entire Mesoproterozoic and up to early Neoproterozoic.

Xing and Liu (1973) initially established the genus *Dictyosphaera* with type species *Dictyosphaera macroreticulata* from the ~1800-1600 Ma Chuanlinggou Formation, Yenliao region of northern China. With minimum morphological characteristics, the additional species of *Dictyosphaera* are *D. gyrorugosa*, *D. incrassate*, *D. sinica*, and *D. delicata*. Later, Tang *et al.* (2015) have described a new species *Dictyosphaera tacita* from the Tonian Gouhou Formation, Anhui Province of China on the basis of the smooth external surface and the presence of hexagonal platelets only on the interior vesicle. The specimens of *Dictyosphaera tacita* have smaller hexagons (0.5–0.9 µm) and the vesicle diameter larger (100–120 µm) than those of *D. macroreticulata* (2–6 µm platelets, 10–20 µm vesicle diameter), *D. sinica* (0.5–1.5 µm platelets, 15–45 µm vesicle diameter), and *D. delicata* (1–3 µm platelets, 50–300 µm vesicle diameter). Recently, a new species *Dictyosphaera smaugi* Loron *et al.*- spheroidal vesicle having irregular size hexagonal surface ornamentations covering less than one-third of the vesicle, have been described from

the Fort Confidence Formation, Dismal Lakes Group, Canada (Loron *et al.*, 2021, p. 7, Fig. 5.1). However, in a new taxonomic assessment of the *Dictyosphaera*, Agić *et al.* (2015) synonymized the above-mentioned species in a single biological species *D. macroreticulata*, described as 10 to 300 µm vesicles ornamented by a reticulate polygonal pattern consisting of interlocking 1–6 µm polygonal plates. Additionally, they also suggested that *Dictyosphaera-Shuiyousphaeridium* plexus both are the developmental stages of a single species. However, worldwide other occurrences of the *Dictyosphaera* have been documented without co-occurrence of *Shuiyousphaeridium* (Adam *et al.*, 2017; Javaux and Knoll, 2017; Loron *et al.*, 2019a) except for Ruyang assemblage. Even in the present study, no co-occurrence of *Shuiyousphaeridium* and *Dictyosphaera* have been documented, so in our opinion, *Dictyosphaera-Shuiyousphaeridium* both are two distinct morphologies and have no connection in the biological life cycle as proposed by Agić *et al.* (2015).

Another peculiar organic-walled microfossil in the Chaporadih Formation is *Valeria lophostriata*. It is characterized by distinctive vesicle wall ornamentation—uniformly and closely spaced parallel concentric striations (Hofmann, 1999; Pang *et al.*, 2015). *Valeria lophostriata* is one of the oldest known morphologically complex sphaeromorphic acritarch that has been widely accepted as a Precambrian eukaryotic fossil. The specimens of this distinctive complex morphology globally known from the nearly three dozen localities extending from the late Palaeoproterozoic to the Neoproterozoic age (Tonian) (Hofmann and Jackson, 1994; Hofmann, 1999; Javaux, 2007b; Nagovitsin, 2009; Javaux, 2011; Pang *et al.*, 2015; Porter and Riedman, 2016; Javaux and Knoll, 2017; Loron *et al.*, 2021; Miao *et al.*, 2021). It was originally described as *Kildinella lophostriata* from the Riphean Zigalga Formation in the southern Urals (Jankauskas, 1979), later reassigned to the genus *Valeria* by Jankauskas (1982). Subsequently, Yan and Liu (1993) established the species *Valeria lophostriata* reported from the late Palaeoproterozoic (~1670 Ma – 1625 Ma) Chuanlinggou Formation in North China. This species has been reported from the ~1650 Ma Mallapunyah Formation of Roper Group in Australia (Javaux *et al.*, 2004b). Another species *Valeria elongata* (50 µm X 200 µm) was described by Nagovitsin (2009) from the Mesoproterozoic (~1526 Ma-1105 Ma) Dzhelindukon Formation, Kamo Group of the Central Angara Basin in southern Siberia on the basis of spindle-shaped vesicles with meridional rather than concentric striations. These striations were probably formed through the Belousov Zhabotinsky (B-Z) oscillatory reaction (Hofmann, 1999). The B-Z reaction model is an oscillating reaction-diffusion (R-D) system that has been used in various nonlinear biological systems and processes, and also played a key role in the pattern development and intracellular transport of *Valeria* striations (Tabony, 1994). Additionally, the biomechanical analysis of the *Valeria lophostriata* using the thin-walled spherical pressure vessel model (Sharma *et al.*, 2009; Pang *et al.*, 2015) suggests that the concentric striations may have functioned as a mechanism to guide biologically programmed to execute excystment mechanism (Pang *et al.*, 2015). Moreover, the CLSM image of the *Valeria lophostriata* in the present study provides better observable details such as the existence of numerous micron size hairy



EXPLANATION OF PLATE III

Optical photomicrographs (1 - 3) and confocal laser scanning micrographs (1.1 – 3.2) of the Chhattisgarh organic-walled microfossils. Scale bar is 25 µm for each specimen. 1 - 1.3, 2 – 2.2. *Valeria lophostriata* 1.1. Front appearance, 1.2. back appearance, 1.3 showing short hairy processes on vesicle surface under CLSM; 2.1. crinate surface pattern on the vesicle, 2.2. Concentric striations on the vesicle; 3 – 3.1. *Dictyosphaera macroreticulata* 3.1. reticulate surface pattern on the vesicle; 1. Slide no. BSIP 16641, England Finder No. O40; 2. Slide no. BSIP 16992, England Finder No. O40/2; 3. Slide no. BSIP 16992, England Finder No. G29/2.

processes projecting over the vesicle (Plate III, Figs. 1.2, 1.3). An alternative explanation for these hairy processes could be that these were possibly used for locomotion against the wave direction.

Besides the present study, the Chaporadih Formation of the Chhattisgarh Supergroup was previously investigated for palaeontology records (Singh and Sharma, 2016). Studies revealed an important diversity of organic-walled microfossils, including unambiguous eukaryotes *Dictyosphaera*

macroreticulata, *Valeria lophostriata* and *Jacutianema solubila*. The other interesting and stratigraphically important associated age diagnostic OWMs in the Chaporadih Formation include *Pterospermopsisimorpha*, *Germinosphaera*, *Ourasphaera*, *Octoedryxium*, *Trachyhystrichosphaera*, *Pololeptus*, *Cheilophilum*, *Navifusa*, and *Simia* (Singh *et al.*, 2021) are widely documented from the late Mesoproterozoic and early Neoproterozoic assemblages of Arctic Canada, Australia, China, India, Siberia, Russia, and USA.

CONCLUSIONS

In the present documentation lower heterolithic sediments of the latest Mesoproterozoic – early Neoproterozoic Chaporadih Formation comprises an assemblage of Organic-Walled Microfossils dominated by ornamented and unornamented acritarch taxa followed by a few acanthomorphic acritarchs and cyanoprokaryotes. The present paper adds a new occurrence of *Dictyosphaera* and *Valeria* bearing OWMs association in the late Mesoproterozoic succession of the world. It documents a well-preserved population of two distinct unambiguous organic-walled microfossil *Dictyosphaera macroreticulata* and *Valeria lophostriata* for the first time from the ~ 1025 Ma carbonaceous shale of the Chaporadih Formation of the Chandarpur Group of the Chhattisgarh Supergroup. These two elements are part of global biozone comprising *Tappania-Dictyosphaera-Valeria*. Complex morphology viz., large vesicle; wall structures and diverse striation and tessellated hexagonal platelet patterns in the specimens demonstrate a eukaryotic affinity for the Chaporadih microfossils. In addition, a new biostratigraphic range (up

to late Mesoproterozoic) is proposed for *Dictyosphaera macroreticulata* along with other co-occurrences and can be considered as Mesoproterozoic age diagnostic taxa. Available palaeontological records, such as the occurrence of acanthomorphic acritarch *Tappania* Yin, from the Singhora Group – the lower stratigraphic unit of the Chhattisgarh Supergroup (Singh *et al.*, 2019b) and present reports of eukaryotic fossils from the Chaporadih Formation of the Chandarpur Group makes the Chhattisgarh basin unique in case, which holds all the globally accepted eukaryotic fossils in a single Proterozoic sedimentary succession and is part of *Tappania, Dictyosphaera* and *Valeria* biozone.

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