

Calcified rivulariaceans from the Ordovician of the Tarim Basin, Northwest China, Phanerozoic lagoonal examples, and possible controlling factors



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ABSTRACT

A distinctive association of rivulariacean-like calcified microfossils is recognized in back-reef lagoon facies on the Bachu-Tazhong Platform in the Lianglitag Formation (Katian Stage, Upper Ordovician) of the Tarim Basin, based on investigation of 4500 thin sections from 35 well drill cores. The genera include *Hedstroemia*, *Ortonella*, *Zonotrichites*, *Cayeuxia*, and *Garwoodia*, most of which have features comparable with present-day calcified cyanobacteria such as *Rivularia*, *Calothrix* and *Dichothrix* (Rivulariaceae, Nostocales). A similar association is present in lagoonal and other restricted nearshore shallow-marine carbonate environments during much of the Paleozoic and Mesozoic. This suggests the sustained presence of a rivulariacean-dominated cyanobacterial association characteristic of back-reef/lagoonal environments. At the present-day, uncalcified *Rivularia*, *Calothrix* and *Dichothrix* remain common in back-reef, lagoon, mangrove-swamp, rocky shore, salt-marsh, and saline lake environments. The ability of these cyanobacteria to grow in environments low in inorganic nitrate and phosphate could help to explain this distribution. Cenozoic decline in marine calcified rivulariaceans is attributed to global reduction of seawater carbonate saturation state. The Phanerozoic record of calcified rivulariacean cyanobacteria appears to sensitively reflect long-term variations in the carbonate and nutrient chemistry of marine environments.

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1. Introduction

Cyanobacteria have a soft body-fossil record of at least ~1900 Ma (Hofmann, 1976) and possibly much earlier (Schopf, 2006), and are widely assumed to have been extant when signs of oxygenation appeared ~3000 Ma ago (Buick, 2008). Some cyanobacteria can stimulate CaCO₃ precipitation within or upon their sheath by photosynthetic uptake of inorganic carbon (Pentecost and Riding, 1986; Merz, 1992), and this calcification can produce filamentous microfossils (Riding, 2012) that date back at least ~1200 Ma (Kah and Riding, 2007) and probably ~2500 Ma (Klein et al., 1987). Marine calcified cyanobacteria are locally common during the Paleozoic and Mesozoic (Konhauser and Riding, 2012) and played important sedimentological roles in building reefs, stromatolite and thrombolites, as well as in producing finer-grained and fragmentary material (Riding, 1991a; Flügel, 2004).

Examination of well-preserved ~450 Ma calcified cyanobacteria from the Katian (Late Ordovician) of the Tarim Basin revealed an association of the genera *Hedstroemia*, *Ortonella*, *Cayeuxia*, *Zonotrichites* and *Garwoodia* in back-reef lagoon facies of the Bachu-Tazhong Platform. *Cayeuxia* and *Zonotrichites* are common in similar environments in the Jurassic and Cretaceous (Riding, 1991a). Similarly, *Hedstroemia*, *Ortonella* and *Garwoodia* occur in restricted and semi-restricted environments in the Paleozoic (Mamet, 1991). These genera, particularly *Hedstroemia*, *Cayeuxia*, *Ortonella* and *Zonotrichites*, resemble extant cyanobacteria such as the rivulariaceans *Rivularia*, *Calothrix* and *Dichothrix*. Here we suggest that this persistent association of genera in Paleozoic-Mesozoic marine carbonate back-reef/lagoonal environments in part reflects the ability of rivulariaceans to cope with nitrogen and phosphate limitation. The decline in calcification of these organisms in marine environments during the Cenozoic could reflect progressive long-term reduction in seawater carbonate saturation state. We support our data from Ordovician *Rivularia*-like calcified fossils in China with a global review of their occurrence during the remainder of the Phanerozoic. This suggests that calcified rivulariaceans and accompanying taxa constitute a long-lived Phanerozoic association typical of protected

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shallow-marine environments that can be linked to seawater, including nutrient, composition. This new insight into the paleoecology of these organisms could assist the environmental interpretation of ancient platform interiors.

2. Geological setting

The Tarim Basin in Xinjiang Province is bordered by the Kunlun, Altun, Tianshan and Kuluketake mountains (Fig. 1). Precambrian, Paleozoic and Mesozoic rocks occur around the margins of this extensive desert basin, which is up to 500 km wide and over 1000 km in length. The underlying Tarim Block consists of pre-Neoproterozoic basement, a late Neoproterozoic to Early Permian marine succession, and Late Permian-Quaternary continental facies (Jia, 1997). It experienced several stages of tectonic development that show both similarities and differences from those of North and South China (Zhang et al., 2012), and can be divided into a number of subunits (Fig. 1; Jia et al., 1995).

Current reconstructions locate the Tarim Block at low latitudes throughout the Ordovician (Cocks and Torsvik, 2002; Webby, 2002) when extensive carbonate platforms developed on the Tazhong and Bachu uplifts, as revealed by outcrop, well and seismic data (Fig. 1C, Feng et al., 2007; Zhao et al., 2009). These 2 to 6 km thick carbonate platforms been penetrated by 35 drilling wells that provide the samples for our research (Fig. 1). They include the lower part of the Lower Ordovician, and middle and upper parts of the Upper Ordovician. Most of the Middle Ordovician and the lower Upper Ordovician have been removed by erosion. The Upper Ordovician in the Bachu-Tazhong Platform is largely represented by two formations: the Lianglitag and Sangtamu. The Sangtamu Formation is mainly a mixed terrigenous clastic and carbonate deposit of greenish sandy argillaceous mudstone interbedded

with argillaceous limestone (Feng et al., 2007; Zhang et al., 2007; Cai and Li, 2008; Yang et al., 2011).

The Lianglitag Formation contains the conodonts *Yaoxianognathus yaoxianensis*, *Belodina confluens*, and *Baltoniodus alobatus*, and is attributed to the Katian Stage (Li et al., 2009). Based on lithological and paleobiological data, the Lianglitag Formation can be divided into three members from bottom to top: (1) argillaceous limestone (50–550 m), consisting of dark micrite and grainstone, interbedded with irregular siliceous mudstone; (2) grainstone (50–150 m), dominated by grainstone and reef limestone; and (3) argillaceous-stripped limestone (20–100 m), composed of micrite interbedded with striped mudstone, and some grainstone and reef limestone (Yang et al., 2000; Yang et al., 2010). This succession has been divided into three depositional sequences (Gao et al., 2014). During the SQ1 and SQ2 stages (Early to Middle Katian), the Bachu-Tazhong platform was a rimmed carbonate platform. Reef limestones, built by corals, stromatoporoids, and calcareous algae, characterized the southern and northern margins of the Bachu-Tazhong Platform (Gu et al., 2005; Cai et al., 2008; Li et al., 2009; Wang et al., 2009; Yang et al., 2010; Wang et al., 2013; Gao et al., 2014; Zhang et al., 2014, 2015). Mainly wackestone and lime mudstone occur in the interior, indicating a restricted platform, including tidal flat and lagoon facies (Fig. 2A, B; Yang et al., 2010; Gao et al., 2014). During the SQ3 Stage (Late Katian), the Bachu-Tazhong Platform became more open and appeared to have lost its reef-margins (Fig. 2C; Gao et al., 2014).

Previous research revealed numerous calcimicrobes preserved in the Lianglitag Formation. Of these, *Girvanella*, *Subtifloria*, *Razumovskia*, *Acuasiphonoria*, *Hedstroemia*, *Cayeuxia*, *Bija*, *Apophoretella*, *Ortonella*, *Zonotrichites* and *Bevocastria* are regarded as cyanobacteria, *Proaulopora*, *Phacelophyton* and *Gomphosiphon* as probable cyanobacteria, and *Renalcis*,

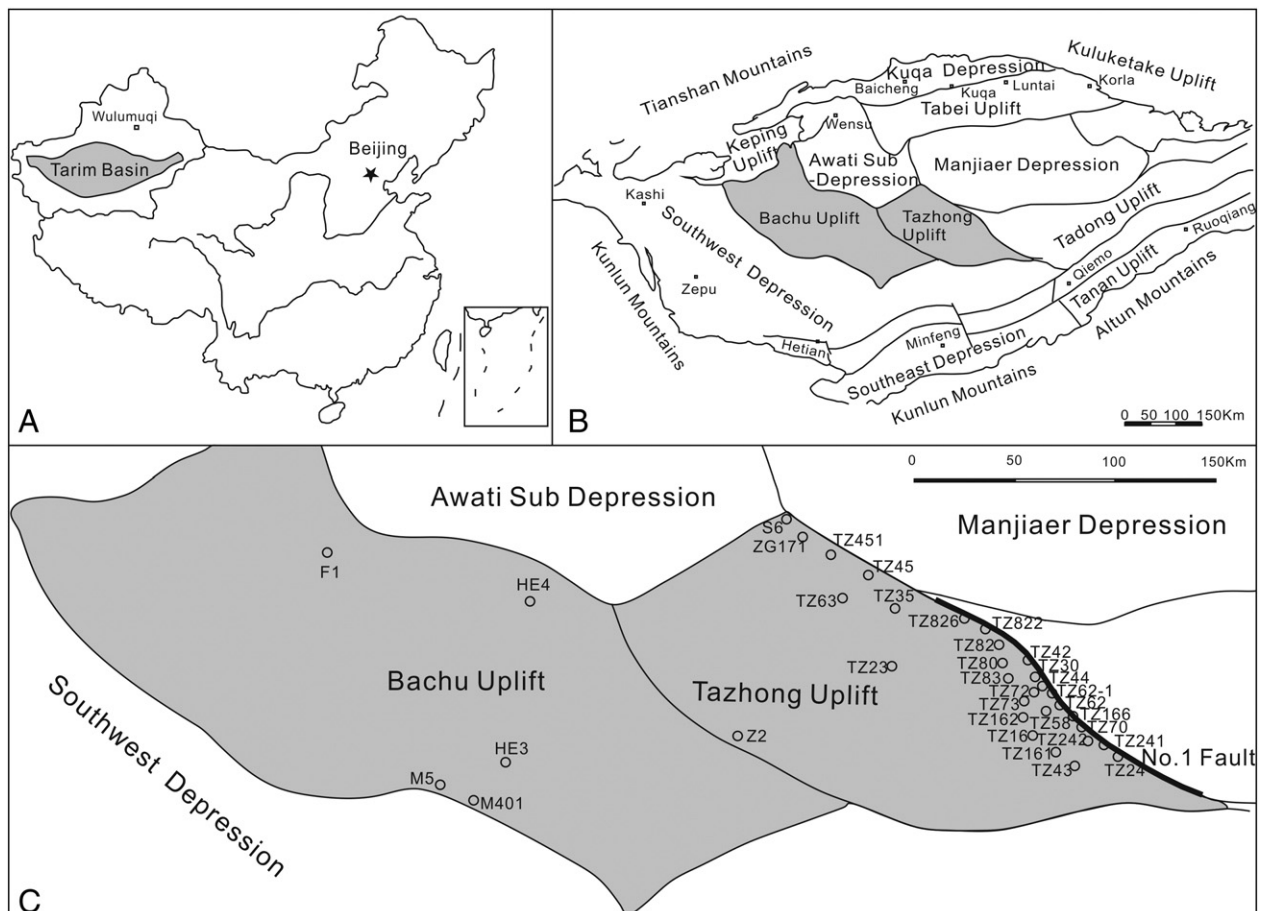


Fig. 1. A. Location of the Tarim Basin. B. Tectonic/depositional divisions. C. Locations of wells in this study.

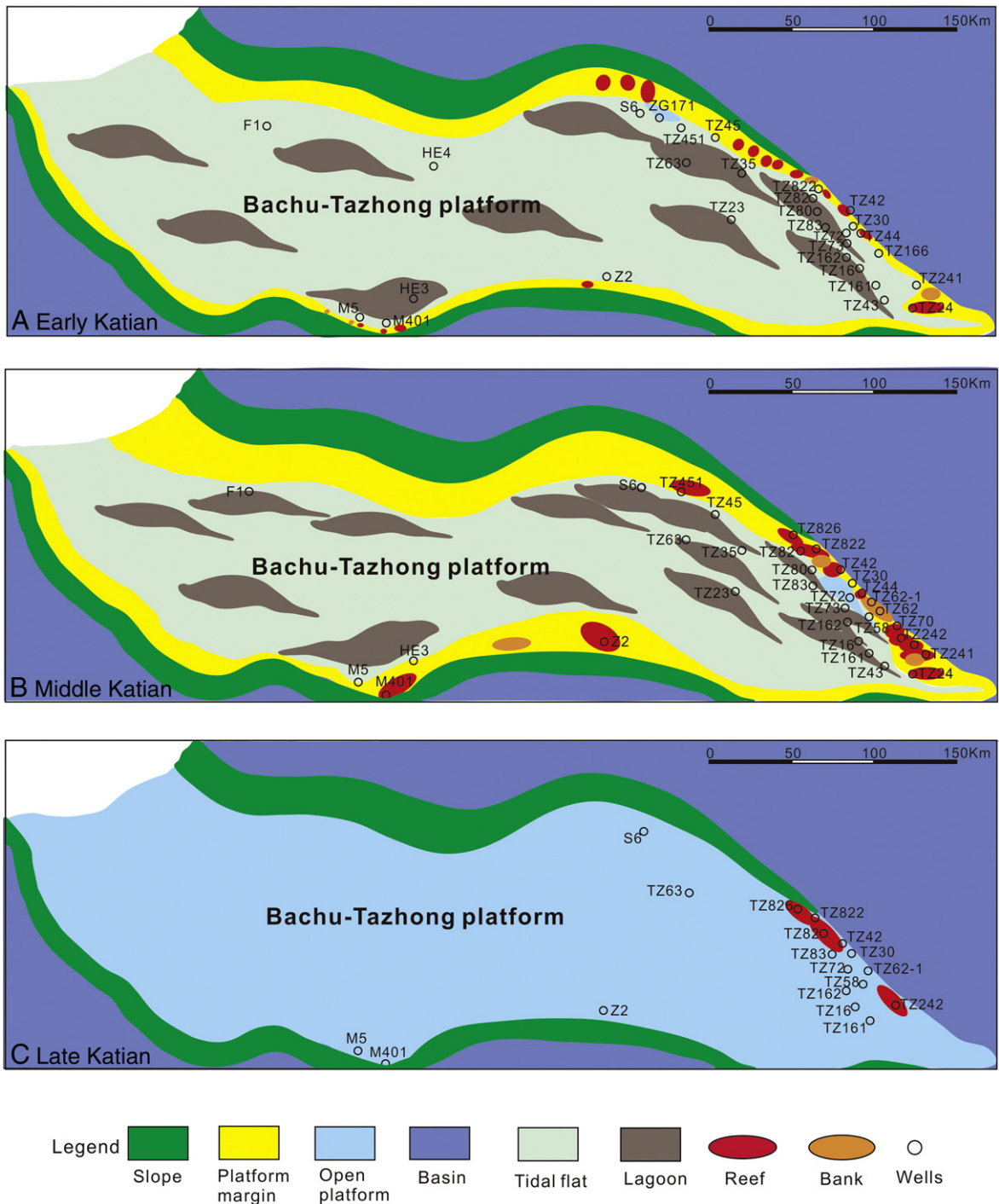


Fig. 2. Lithofacies paleogeography of the Bachu-Tazhong platform during Katian Stage (Late Ordovician) Lianglitag Formation deposition (modified from Zhang et al., 2007; Feng et al., 2007; He et al., 2007; Zhao et al., 2009; Lin et al., 2011; Gao et al., 2014).

Izhella, *Wetheredella*, *Rothpletzella* and *Garwoodia* are classed as Microproblematica (Riding and Fan, 2001; Liu et al., 2011, 2015). Paleocological distributions of these calcimicrobes in the Lianglitag Formation deserve further study.

3. Materials and methods

Drill cores of the Lianglitag Formation from 35 wells in the Bachu and Tazhong uplifts (Fig. 1) were systematically examined and sampled, and more than 4500 large (5 × 7 cm) thin sections were prepared. These samples cover the full succession of the Lianglitag

Formation in these areas. The thin sections were investigated using transmitted light microscopy and microphotography (see Liu et al., 2015 for details).

4. Results

4.1. Recognition of lagoonal facies

Marginal reef (Fig. 3A, B), bank (Fig. 3C, D), open platform (Fig. 3E, F), and tidal flat (Fig. 3K, L) facies in the Lianglitag Formation are fairly

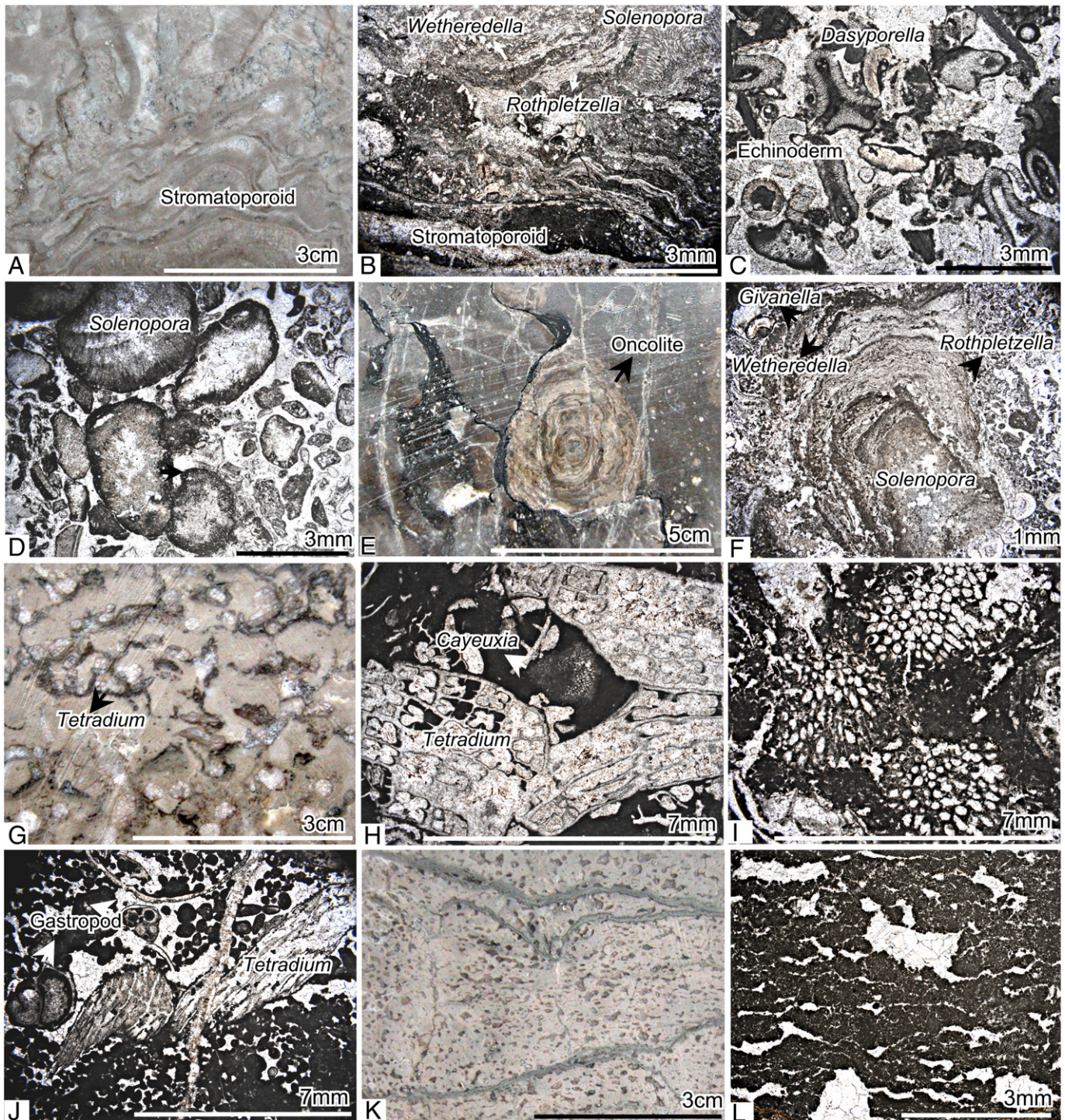


Fig. 3. Macrophotographs of drill cores and microphotographs of thin sections of lagoonal and related facies of the Lianglitag Formation (Katian, Late Ordovician). A, Marginal reef, formed by stromatoporoids and red algae, O₃l, TZ822-8-108-85; B, Similar, O₃l, M401-24-70-25; C, Marginal bioclastic grainstone with echinoderms and dasycladaleans, O₃l, TZ822-1-43-4; D, Similar, with 'solenoporaceans', O₃l, TZ822-4-73-27; E, Open platform, oncolite packstone, O₃l, TZ30-1-15-12; F, Open platform, oncolite formed by *Girvanella*, *Wetheredella* and *Rothpletzella*, O₃l, TZ72-10-104-15; G, Lagoonal wackestone, with *Tetradium*, O₃l, TZ16-17-58-40; H, Similar, with *Tetradium* and calcimicrobes (such as *Cayeuxia* (Fig. 3H), *Hedstroemia*, *Ortonella*, *Zonotrichites*, *Garwoodia*), ostracodes, O₃l, TZ161-30-50-39; J, Similar, with *Tetradium* and gastropods, O₃l, TZ73-12-54-32; K, Tidal flat micrite with birds-eye structure, O₃l, TZ16-17-58-47; L, Similar, O₃l, TZ82-14-54-4.

readily recognized, based on distinctive lithological characters, sedimentary structures, and fossil communities.

Lagoons are typically isolated by distance and/or by physical barriers, such as sand shoals or reefs, from the open sea (Harris et al., 1985; Read, 1985). The back-reef lagoonal environment differs substantially from the open sea in hydrodynamics, salinity and nutrients (Schäfer, 1972; Han et al., 1989). Lagoon facies are typically fine-

grained, with distinctive communities that can show low diversity and high individual abundance (Hallam, 1965; Feng, 2001). We used these characteristics to identify lagoonal facies in the Lianglitag Formation.

The lithology of the lagoon facies is mainly micritic and peloidal limestone, with a community of abundant *Tetradium* (Fig. 3G, H, J), an unidentified organism (Fig. 3I), numerous calcimicrobes (such as *Cayeuxia* (Fig. 3H), *Hedstroemia*, *Ortonella*, *Zonotrichites*, *Garwoodia*), ostracodes,

gastropods (Fig. 3J), and occasional green algae (*Dimorphosiphonoides*, Liu et al., 2011). The main community difference between lagoonal and marginal and open platform facies is its relatively low-diversity, and scarcity of echinoderms (Fig. 3C), bryozoans, brachiopods, dasycladaleans (Fig. 3C), red algae (Fig. 3D), stromatoporoids (Fig. 3A, B), oncolites, and reef encrusters formed by calcimicrobes, such as *Girvanella*, *Wetheredella* and *Rothpletzella* (Fig. 3B, E, F). The lagoonal deposits are often interdigitated with tidal flat facies (Fig. 3K, L), characterized by fossil-poor micrite with birds-eye fenestrae. The abundance of carbonate mud suggests a restricted, relatively low energy environment, and close association with tidal flat facies indicates very shallow-water. These features are consistent with the low diversity and scarcity of stenohaline marine organisms. We infer an inner platform location protected by – and often distant from – a higher energy, locally reefal, margin (Fig. 2A, B).

Lagoonal facies has been recognized in the lower part of the Lianglitag Formation in 22 wells, including S6, TZ43, TZ166, TZ162, TZ161, TZ80, TZ83, TZ16, TZ23, TZ35, TZ82, TZ451, TZ30, TZ241, TZ72, TZ73, TZ822, TZ63, as well as TZ45 in the Tazhong platform and HE3, M401, and M5 in the Bachu platform, all of Early Katian age (Fig. 2A). The marginal reef facies in wells of TZ451, TZ82, TZ241, and M401 developed when the northern and southern margin reef zones expanded towards the inner platform during the Middle Katian (Fig. 2B).

4.2. Calcified cyanobacteria in lagoonal facies

Calcimicrobes were identified in thin sections of the lagoon facies from the 22 wells studied. Their occurrence and distribution in wells TZ82, TZ241, TZ822, TZ822, M401, TZ161, TZ23, M5, TZ63, and TZ43 are shown in Fig. 4. In the lagoon facies, *Hedstroemia*, *Ortonella*, *Zonotrichites*, *Cayeuxia*, and *Garwoodia* are abundant (Fig. 5), whereas some other calcimicrobes are only very occasionally present; these include e.g., *Proaulopora* (TZ241, TZ822, Fig. 4), *Bevocastria* (TZ161, Fig. 4), *Girvanella* (TZ161, TZ23, Fig. 4), and *Rothpletzella* (TZ161, TZ23, Fig. 4). *Hedstroemia*, *Ortonella*, *Zonotrichites*, *Cayeuxia*, and *Garwoodia* therefore constitute a commonly recurring association in the lagoonal environment in many of the wells examined.

Hedstroemia, *Ortonella*, *Zonotrichites*, and *Cayeuxia* are similar in overall organization, but are distinguished by differences in branching patterns and filament morphology and size. In our samples they occur as a total of 8 species: *H. halimedoidea*, *H. biofilosa*, *O. furcata*, *O. kershopenensis*, *O. tenuissima*, *Z. lissaviensis*, *C. moldavica*, *C. piae* (Liu et al., 2015). Some of these genera were previously compared with green algae (e.g., Pia, 1927; Johnson, 1961; Roux, 1985), but this overlooks substantial differences in their size and detailed organization (Riding, 1977). Monty (1967) compared *Ortonella* with the extant cyanobacterium *Scytonema*, and the affinity of *Garwoodia* remains uncertain (Feng et al., 2010; Liu et al., 2015). We regard *Zonotrichites*, *Hedstroemia*, *Ortonella*, and *Cayeuxia* as calcified cyanobacteria comparable with extant rivulariaceans (see Liu et al., 2015), such as *Rivularia* (Fig. 5Q, R), *Calothrix* and *Dichothrix* (Rivulariaceae, Nostocales).

We also investigated the occurrence of these and other calcimicrobes in other facies, in all 35 wells, such as marginal reefs, marginal banks, and open platform, exemplified here by wells TZ82, TZ241, TZ822, TZ822, M401, TZ161, TZ23, M5, and TZ63 (Fig. 4). Marginal reefs commonly contain a wide variety of calcimicrobes, including *Girvanella*, *Rothpletzella*, *Wetheredella*, *Apophoretella*, *Renalcis*, *Izhella*, *Phacelophyton*, *Proaulopora*, *Gomphosiphon*, *Bija*, and *Acuasiphonoria* (TZ82, TZ241, TZ822, M401, and Fig. 4), whereas occurrences of *Hedstroemia*, *Ortonella*, *Zonotrichites*, *Cayeuxia*, and *Garwoodia* are very scarce in these reefs (e.g., TZ241, TZ822, M401; Fig. 4). Similarly, marginal banks and open platform facies often contain abundant *Girvanella*, *Rothpletzella*, and *Wetheredella* (TZ82, TZ241, TZ822, M401, TZ61, M5, TZ63, Fig. 4), but few or no occurrences of *Ortonella* and *Garwoodia* (TZ82, TZ241, TZ822, M401, TZ161, Fig. 4). These distributions underscore the close association of *Hedstroemia*, *Ortonella*, *Zonotrichites*, *Cayeuxia*, and *Garwoodia*, and their abundant recurrence, in lagoonal environments in our Ordovician

Tarim samples. This suggests a close ecological relationship between these specific calcimicrobes and the lagoonal environments they inhabited.

5. Phanerozoic lagoonal calcified cyanobacteria

The documented Proterozoic record of calcified cyanobacteria is currently quite uneven. *Renalcis*-like calcimicrobes occur in the ~1900 Ma Rocknest Formation (Grotzinger and Hoffman, 1983), in the ~1080–780 Ma Little Dal Group (Turner et al., 1993), and possibly in the ~635 Ma Noonday Formation (Corsetti and Grotzinger, 2005). *Girvanella*-like filaments resembling calcified sheaths have been reported from ~2500 Ma (Klein et al., 1987), ~1200 Ma (Kah and Riding, 2007), from the Little Dal (Turner et al., 1993), and from the ~750–700 Ma Draken Formation (Knoll et al., 1993). However, so far as we are aware, there have been no reports of fossils resembling *Hedstroemia* or allied forms from the Precambrian.

5.1. Early Paleozoic

Calcimicrobes are widespread and locally abundant in the Cambrian, for example, *Girvanella*, *Renalcis*, *Gemma*, *Tarthinia*, *Korilophyton*, *Kordephtyon*, *Epiphyton*, *Tubomorphophyton*, *Obruchevella*, *Subtifloria*, *Razumovskia*, *Proaulopora*, *Botomaella*, *Bija*, and *Wetheredella* (Korde, 1973; Riding, 1991b, 2001). Adachi et al. (2014a) reported a probable *Hedstroemia* from the Qingxudong Formation (Upper Toyonian-lower Amgan) of Hunan Province. ‘Epiphyton’ reported by Zhang et al. (2014) from the Maozhuang Formation, Cambrian Series2-Series3, Wuhai area, North China, may be compared with *Hedstroemia*, and appears to occur in an open shallow-marine setting. *Kordephtyon*, *Botomaella* and *Bija* often occur in reefs (Adachi et al., 2014b). However, convincing reports of *Hedstroemia*, *Ortonella*, and similar fossils in lagoonal environments during the Cambrian are scarce.

Walker (1972) reported some low-diversity communities from the Lowville and Chaumont Formations of the Middle-Late Ordovician Black River group, New York State, with abundant *Hedstroemia*, *Tetradium*, and a few bryozoans, which broadly resembles the Tarim lagoonal community and is also interdigitated with tidal flat facies. A low-diversity community from the Upper Ordovician of the Williston Basin, Canada, includes abundant *Ortonella* and *Hedstroemia* in a stressed restricted environment (Pratt and Haidl, 2008). Kwon et al. (2012) reported *Ortonella* associated with *Dimorphosiphonoides* (misidentified as *Ortonella*) and *Rhabdotetradium* (similar to *Tetradium*) from a lagoonal environment in the Late Katian of Jiangxi and Zhejiang, South China. Bian and Zhou (1990) reported *Ortonella*, *Garwoodia*, and *Zonotrichites* (misidentified as *Ortonellina*) from the Late Ordovician of South China, which was also regarded as a restricted environment.

Watkins (1992) reported a low diversity Wenlockian community of Middle Silurian, with abundant *Hedstroemia*, from Gotland, Sweden, whose simple trophic structure and stratigraphic setting suggests deposition in a restricted lagoon or back-barrier setting, associated with tidal flat facies. However, *Hedstroemia* is also common in reefs the same succession (Riding and Watts, 1981). Soja and Riding (1993) reported possible *Hedstroemia* from oncoidal wackestones in the Early to Mid-Silurian of the Alexander terrane, Alaska that suggest quiet-water, back-reef environments in protected areas of the shelf.

5.2. Late Paleozoic

Laporte (1963) noted abundant fragments of *Garwoodia* in the Manlius Limestone of Early Devonian, New York State, which has been interpreted as a shallow water, lagoonal deposit. *Ortonella* and *Garwoodia* are common in lagoonal environments, and were both first described from the Early Carboniferous (Garwood, 1931; Mamet, 1991). Shen et al. (2012) reported both genera as prominent

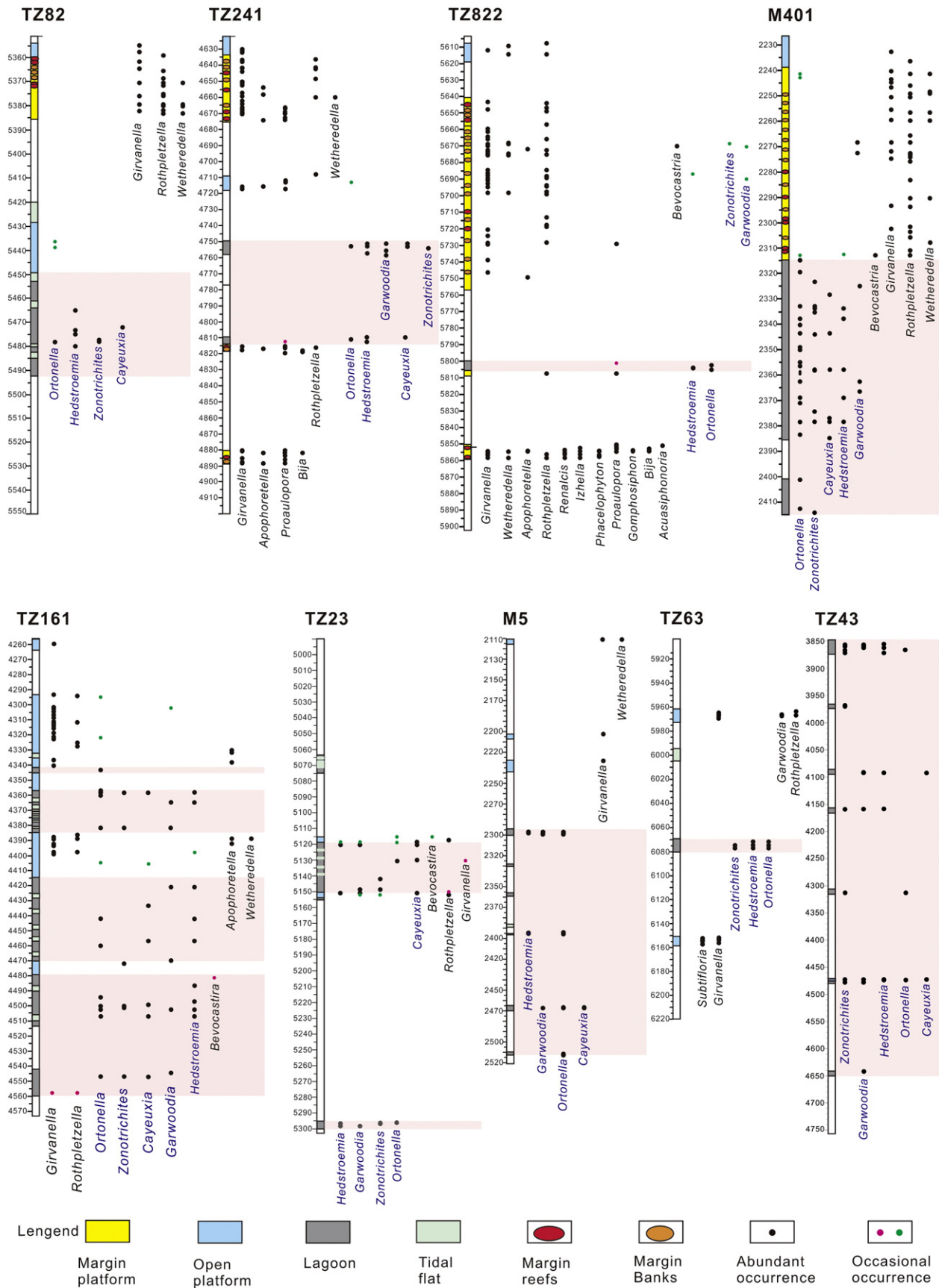


Fig. 4. Stratigraphic and sedimentary distribution of cyanobacteria and other calcimicrobes in TZ82, TZ241, TZ822, M401, TZ161, TZ23, M5, TZ63, TZ43. Those occurring in lagoonal environments are highlighted in pink, with the most common forms highlighted in purple.

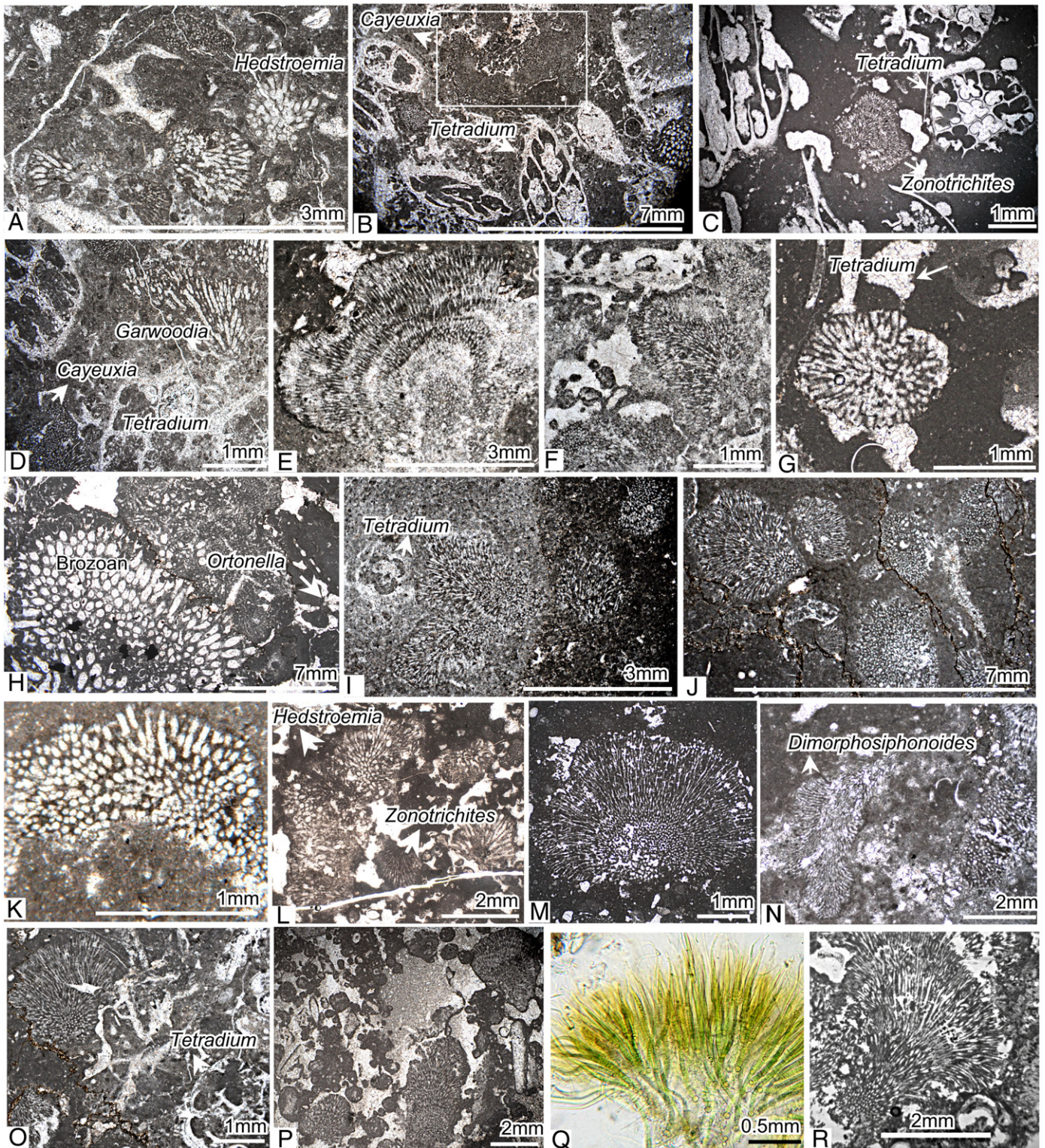


Fig. 5. Calcified cyanobacterial and calcimicrobial associations from Late Ordovician lagoonal facies of the Bachu-Tazhong platform and present-day analogs. A, B, D, O_{3l}, No. TZ23-9-47-36, *Hedstroemia*, *Garwoodia* and *Cayeuxia* associated with *Tetradium*; C, *Zonotrichites* associated with *Tetradium*, O_{3l}, from 4696.56 m of well TZ73; E, *Ortonella*, O_{3l}, No. HE3-12-48-47; F, *Cayeuxia*, O_{3l}, from 5050.50 m of well TZ30; G, *Hedstroemia* associated with *Tetradium*, O_{3l}, from 4812.96 m of well TZ73; H, *Ortonella* associated with unidentified organism, O_{3l}, TZ16-15-13-12; I, *Cayeuxia*, O_{3l}, M5-19-40-31; J, *Zonotrichites*, O_{3l}, M5-19-40-30; K, *Garwoodia*, O_{3l}, from 4091.75 m of TZ43; L, *Hedstroemia*, O_{3l}, from 5465.73 m of TZ82; M, *Ortonella*, O_{3l}, from 5136.04 m of TZ80; N, *Zonotrichites* associated with *Dimorphosiphonoides*, O_{3l}, from 5137.83 m of TZ80; O, *Zonotrichites*, associated with *Tetradium*, O_{3l}, TZ166-3-52-33; P, *Cayeuxia*, O_{3l}, from 4813.53 m of TZ73; Q, Present-day *Rivularia bullata* (credit Malcolm Storey); R, Calcified freshwater *Rivularia*, Late Pleistocene (Portman et al., 2005).

components in the Mississippian of the Williston Basin, Canada, in a succession of upward-shoaling lagoonal sediments. *Ortonella* occurs in Artinskian shelf-lagoon facies of Permian, Carnic Alps, Austria

(Flügel, 1981) and *Hedstroemia* is reported to be abundant in the upper Capitan massive (Babcock, 1977), although whether this includes lagoonal facies is not clear.

5.3. Mesozoic

Flügel (1979) reported abundant associated of *Cayeuxia*, *Zonotrichites* and *Ortonella* from the restricted reef-back environment of the Upper Triassic (Norian and Rhaetian) in the Northern Calcareous Alps. Henrich (1984) reported a flora dominated by *Cayeuxia*, *Zonotrichites*, and *Ortonella* in lagoonal carbonates of the Wetterstein limestone (Upper Triassic, Northern Calcareous Alps). *Cayeuxia* is common in Pliensbachien platform interior facies in Morocco (Della Porta et al., 2012). Flügel (1979) reported abundant *Cayeuxia* and *Garwoodia* from restricted lagoon environments of the Upper Jurassic of the Northern Alps. Additional examples of lagoonal or back-reef rivulariacean-like genera include *Cayeuxia* in the Middle Jurassic of Scotland (Hudson, 1970), Middle Oxfordian of the eastern edge of the Paris Basin (Vincent et al., 2006), Late Jurassic–Early Cretaceous of Germany, Romania and Greece (Dragastan, 1985; Dragastan et al., 1998; Dragastan and Richter, 2011), Jurassic and Lower Cretaceous of Italy (Mancinelli and Ferrandes, 2001), and Kimmeridgian–Berriasian of the Northern Calcareous Alps (Schlagintweit and Dragastan, 2004).

This brief overview suggests that one or more of these genera (*Hedstroemia*, *Ortonella*, *Zonotrichites*, *Cayeuxia*, *Garwoodia*) formed a common association in lagoonal/back-reef and platform interior environments at many times during the Paleozoic and Mesozoic. This recurring long-term pattern suggests a persistent ecologic link between these particular taxa and lagoonal environments.

6. Discussion

6.1. Uncalcified rivulariaceans in modern lagoons

Hedstroemia, *Botomaella*, *Cayeuxia* and similar fossils broadly resemble calcified rivulariaceans (Nostocales) (Riding, 1991a). These distinctive cyanobacteria, such as *Rivularia*, *Calothrix*, and *Dichothrix*, are morphologically similar, being characterized by having tapered trichomes with a basal heterocyst, even though they are genetically heterogeneous (Berrendero et al., 2008; Whitton and Mateo, 2012). Heterocystous cyanobacteria, including rivulariaceans, are less conspicuous in the present-day oligotrophic ocean (Zehr, 2011) than in littoral marine environments, and also occur in lakes, ponds and fast-flowing streams (Khoja et al., 1984). A brief literature survey indicates that coastal rivulariaceans at the present-day are commonly observed in

back-reef, salt-marsh, lagoon, saline lake and mangrove-swamp, as well as rocky shore habitats (Table 1).

6.2. Environmental factors

Extant rivulariaceans form a diverse group (Sihvonon et al., 2007; Whitton and Mateo, 2012) that is widely distributed in marine and non-marine environments. Rivulariaceans occur in symbiotic associations with a range of algae, including as epiphytes on *Sargassum* (Carpenter, 1972) that gives them a pelagic distribution (Goetze et al., 2010), and are also epiphytic in this role on coastal mangroves (Hicks and Silvester, 1985). *Calothrix* is abundant in fore-reef environments at St Croix (Adey and Steneck, 1985), occurs on the reef crest at One Tree Reef (Hatcher and Larkum, 1983), and is a major nitrogen fixer on windward reefs at Eniwetok Atoll (Gerber and Marshall, 1974). *Calothrix* is common in seagrass beds at Mauritius (Jagtap, 1993). Rivulariaceans contribute to the biofilm community in the splash zone of rocky shores (Whitton, 1987; Gerard et al., 1999; McGlathery et al., 2013). *Calothrix* forms pustular mats in the arid supratidal zone at Baja California (Javor and Castenholz, 1981; Johnson et al., 2011), and subaqueous mats in hypersaline Gavish Sabkha (Gerdes et al., 1985). In hot springs at temperatures <48 °C, *Calothrix* occurs in grazer-resistant mats (Ward et al., 2012). Consequently, rivulariaceans are well-suited to tolerate the large fluctuations in temperature, salinity, pH that can characterize lagoons, as well as to periodic emergence and desiccation. Rivulariaceans are also unusually well-adapted to limitations in major nutrients such as N and P that can also affect marine, including lagoonal (Dufour and Berland, 1999; Torrétion et al., 2000), and mangrove-swamp environments (Alvarenga et al., 2015).

Khoja et al. (1984) noted that localization of *Rivularia* in a protected marine embayment in Scotland, where it is subjected to temperature, salinity and pH fluctuations, rather than in less restricted offshore environments, might reflect its ability utilize dissolved organic phosphate from seaweed decay. Rivulariaceans are able to hydrolyze organic phosphate which can be an important component of dissolved P in aquatic environments (Whitton et al., 1991; Yelloly and Whitton, 1996) and can be associated with at least moderate phosphorus deficiency (Sinclair and Whitton, 1977). They often occur in environments with highly variable P concentrations (Livingstone and Whitton, 1984) where organic P typically exceeds inorganic P (Whitton and Mateo, 2012; Mateo et al., 2015). Rivulariaceans are also important as heterocystous N₂-fixing cyanobacteria (Herrero et al., 2001; Mateo et al., 2015), able to convert nitrogen into bioavailable forms such as nitrate

Table 1
Common occurrences of uncalcified *Rivularia*, *Calothrix* and *Dichothrix* in lagoonal and similar present-day restricted environments.

Environment	<i>Rivularia</i>	<i>Calothrix</i>	<i>Dichothrix</i>	Location	References
Sheltered bay	Abundant		Abundant	S-E. Scotland	Khoja et al. (1984), Yelloly and Whitton (1996)
Sheltered bay		Abundant	Abundant	South Florida	Capone and Taylor (1977)
Lagoon	Common			North coast of Bali	Seregeg (1989)
Back-reef lagoon	Abundant	Abundant		Aldabra Atoll, Indian Ocean	Potts and Whitton (1977)
Mangrove	Abundant			Zanzibar Island	Lugomela and Bergman (2002), Kyaruzi et al. (2003)
Mangrove	Abundant	Rare	Abundant	Saudi Arabia, Red sea	Hussain and Khoja (1993)
Mangrove	Abundant	Abundant		Sinai Peninsula	Potts (1979)
Mangrove		Abundant		Parangipettai, India	Ramachandran and Venugopalan (1987), Santra et al. (1988)
Mangrove		Abundant	Abundant	East coast, India	Sakthivel and Kathiresan (2013), Silambarasan et al. (2012)
Mangrove	Abundant			Southern Africa	Lambert et al. (1989)
Mangrove	Abundant	Abundant		Gulf of Elat	Potts (1980)
Rock shore		Abundant		Heron Island, Great Barrier Reef	Diez et al. (2007)
Rock shore			Abundant	Hong Kong	Nagarkar (2002)
Rock shore	Abundant	Abundant		Gulf of Eilat	Potts (1980)
Salt-marsh	Rare			Scotland	Polderman and Polderman-Hall (1980)
Salt-marsh	Common	Common		NW Iberian Peninsula	Calvo et al. (1999)
Salt-marsh	Common	Common		Southern England	Polderman (1978)
Salt-marsh	Rare	Rare		N-W. Scotland	Wilkinson (1979)
Salt-marsh	Rare	Rare		S.Wales	Wilkinson (1982)
Salt-marsh	Abundant	Frequent		Laguna Guerrero Negro, Mexico	Javor and Castenholz (1981)
Saline lake	Common			Australia	Taylor (1975)

and ammonia. This role has also been widely confirmed in lagoonal and related environments, e.g., in a sheltered bay in Scotland (Khoja et al., 1984), Aldabra Atoll lagoon (Potts and Whitton, 1977), intertidal Gulf of Eilat (Potts, 1980), beach rock at Heron island (Díez et al., 2007), and a mangrove belt at Zanzibar Island (Lugomela and Bergman, 2002). Thus, Whitton and Mateo (2012) argued that since present-day rivulariaceans are mostly associated with environments where long periods of phosphate limitation are interrupted by episodes of high phosphate flux in which the available P is mostly organic, they benefit from their ability to efficiently utilize organic phosphate, and nitrogen fixation becomes especially important during the period when the cyanobacterial filaments have elevated phosphate.

In lagoonal carbonate environments isolated from terrestrial input, the nutritional abilities of cyanobacteria, including rivulariaceans, can be significant. For example, the water entering the interior lagoon at Tikehau Atoll (French Polynesia), with an area of 400 km², water depth 25 m, and normal salinity (Abed et al., 2003), undergoes changes in nutrients (Charpy-Roubaud et al., 1990), including increase in nitrogen content of the waters crossing the reef. Charpy-Roubaud et al. (1990) attributed this to cyanobacterial nitrogen fixation. They found that nitrogen production makes the atoll a net exporter of nitrogen, and that phosphate input from the ocean is largely balanced by organic phosphorus output from the mineralization of organic compounds in the lagoon. Thus, the occurrence of rivulariaceans in back-reef and lagoonal habitats likely not only reflects their tolerance of fluctuating physical and chemical conditions, but also their abilities for N₂-fixation and organic phosphate utilization in conditions that could otherwise be limiting for these key elements. Thus, *Rivularia*, *Calothrix*, and *Dichothrix* can indicate waters with low levels of inorganic P and N, and their abilities for N₂-fixation and organic phosphate utilization constitute ecophysiological strategies (Mateo et al., 2015).

6.3. Cenozoic decline in marine calcified rivulariaceans

Marked reduction in the abundance of marine heavily calcified cyanobacteria during the mid-Cretaceous (Riding, 1982; Arp et al., 2001) has been attributed to decline in carbonate saturation state, possibly linked to increase in biocontrolled planktic calcifiers (Riding, 1993). Sheath-calcified cyanobacteria are locally conspicuous in present-day calcareous creeks and lakes (Golubic, 1973; Pentecost, 1987), but are rarely reported from Cenozoic marine environments. One of the few well-documented Cenozoic examples is the presence of relatively large (30–40 micron diameter) tubes attributed to *Girvanella* from early Messinian (~7 Ma) marine deposits in Sardinia, whose occurrence coincides with localized resurgence of microbialites during the Mediterranean Messinian Crisis (Saint-Martin, 2010). Present-day reports of marine cyanobacteria that appear to be sheath calcified are similarly very scarce (e.g., Winland and Matthews, 1974), but include rivulariaceans (Golubic and Campbell, 1981; Planavsky et al., 2009). The scarcity of well-calcified marine cyanobacteria during the past ~100 Ma contrasts with their relatively common occurrence in reefal environments from Cambrian to Early Cretaceous, underscoring the bioinduced nature of cyanobacterial calcification (Pentecost and Riding, 1986; Kempe and Kazmierczak, 1994; Konhauser and Riding, 2012).

7. Conclusions

Hedstroemia, *Ortonella*, *Zonotrachites*, *Cayeuxia*, and *Garwoodia*, most of which resemble extant rivulariaceans, were widespread in restricted lagoonal and associated environments from at least the Ordovician to Cretaceous. The common occurrences of uncalcified *Rivularia*, *Calothrix* and *Dichothrix* in modern similar restricted environments (e.g., back-reef, lagoons, rocky shores, mangrove-swamps, salt-marshes, and saline lake) likely not only reflects their tolerance of fluctuating physical and chemical conditions, but also their abilities for N₂-fixation and organic

phosphate utilization. Phanerozoic calcified rivulariaceans are not restricted to lagoons, and can also be common in reefs. Nonetheless, the recurring association of morphologically similar genera, particularly *Hedstroemia*, *Ortonella*, *Zonotrachites*, and *Cayeuxia*, suggests a distinctive and extraordinarily long-lived community, well-adapted to restricted nearshore conditions. Decline in marine calcified rivulariaceans, and cyanobacteria in general, since the mid-Cretaceous could reflect global reduction of seawater carbonate saturation state. Calcified rivulariacean cyanobacteria may therefore be subtle indicators of changes in aquatic carbonate and nutrient chemistry over extended geologic time-scales.

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