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CORALLINE ALGAE FROM THE MIOCENE MAHAKAM DELTA (EAST KALIMANTAN, SOUTHEAST ASIA)

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ABSTRACT: **Miocene crustose coralline algae (CCA) from Southeast Asia are poorly known, although the Miocene is the epoch of the onset of the biodiversity hotspot in the region and CCA are crucial to understanding the evolutionary history of reef building. To fill this knowledge gap, CCA from early and middle Miocene reefs and related carbonates in the Kutai Basin in East Kalimantan (Borneo, Indonesia) have been studied. The Kutai Basin was dominated by siliciclastic sediments of the proto-Mahakam Delta. Locally, carbonate buildups occur lateral to, or within, the deltaic succession. CCA in the Kutai Basin occur in carbonate beds that were deposited in a low-energy shallow-water platform setting and in association with coral reefs, encrusting the corals or bioclasts. Two main CCA assemblages are recognized herein: (1) a shallow-water assemblage (S-assemblage), dominated by *Neogoniolithon* spp., thick crusts of *Spongites* spp., and *Hydrolithon* spp.; and (2) the D-assemblage, which consists mainly of thin crusts of *Lithothamnion* spp., *Mesophyllum* spp., and *Sporolithon* spp., and is interpreted to have developed in darker waters. Light reduction in reefs in the proto-Mahakam Delta is interpreted to reflect either increased water depth or higher turbidity resulting from higher siliciclastic input. Assemblages with intermediate composition (I-assemblages) also occur. Common CCA with large cell fusions and groups of heterocysts, typical features of modern reef CCA, in the S-assemblages in the middle Miocene of East Kalimantan reflect the initiation of the reef-building CCA flora in the Indo-Pacific region. The occurrence of this kind of CCA confirms the biogeographic differentiation of a tropical reef flora.**

INTRODUCTION

Crustose coralline algae (CCA) play important roles in coral reefs as they function as constructional agents and are a stabilizing grout for the coral-sustained buildup (Bak 1976; Tierney and Johnson 2012). They also enhance invertebrate recruitment by chemically inducing larval settlement and subsequent metamorphosis (Heyward and Negri 1999; Steller and Cáceres-Martínez 2009). Sea urchins, abalones, scleractinian corals, and octocorals have similar chemosensory recognition of coralline algae surface or their bacterial biofilms for induction of larval settlement and later development (Morse et al. 1988, 1996; Huggett et al. 2006). Recruitment and development of scleractinian-coral larvae are crucial to maintaining reef building (Ritson-Williams et al. 2009).

This paper deals with CCA associated with Miocene reefs in East Kalimantan (Borneo, Indonesia). The purposes of this study are (1) to identify CCA taxa and analyze their distribution within the studied reefs and reef-related deposits; (2) to define CCA assemblages on the basis of their taxonomic composition and explore their application as paleoenvironmental indicators; (3) to confirm the paleobiogeographical separation of tropical CCA assemblages from those of the better-known Mediterranean/intermediate latitudes; and (4) to track the oldest records of CCA taxa crucial in building modern reefs in the Indo-Pacific region.

Published reports on Cenozoic CCA from Borneo are scarce and relatively old (Lignac-Grutterink 1943; Johnson and Ferris 1949; Keij 1963, 1964; Johnson 1966). Ishijima (1978) described a presumably Cretaceous coralline species from West Kalimantan, the type of which has been recently reassessed by Iryu et al. (2012). A number of other papers have described coralline algae from Paleogene and Neogene deposits of localities in Southeast Asia and the western Pacific area (Ishijima 1943, 1944, 1954, 1965; Johnson and Ferris 1949; Johnson 1954, 1957, 1961, 1964a). These publications comprise accounts of fossil coralline algae including many newly established species, and their stratigraphic distribution. The descriptions and original diagnoses of most reported species, however, have little or no significance according to the modern criteria used for delimiting taxa (Braga et al. 2010), and the illustrations usually show only limited aspects of the anatomical features needed to identify CCA species. As a result, despite the numerous species names introduced for Paleogene and Neogene algae from the western Pacific, only a few of the separate species recognized in the Miocene of East Kalimantan can be assigned to previously established species.

There are also very few studies on extant coralline algae from Indonesia, and only the accounts of CCA from the Spermonde Archipelago in Sulawesi (Verheij and Prud'Homme van Reine 1993; Verheij 1994) and short monographs dealing with particular taxa (Verheij 1992, 1993a, 1993b, 1993c) have been carried out with a modern taxonomic perspective. Verheij and Woelkerling (1992) lectotypified the newly described species in the reports on CCA from the Siboga Expedition by Foslie (1901a, 1901b, 1904) and Weber-van Bosse (1926), but these species require critical reassessment with an updated taxonomic approach. In the last two decades several accounts and monographs (e.g., Keats et al. 1996; Baba 2000; Ringeltaube and Harvey 2000) have increased the generally poor knowledge of tropical Pacific CCA.

Fossil CCA can be used as paleoenvironmental indicators (Adey and McIntyre 1973; Adey 1979, 1986; Bosence 1991) as they give information about turbulence, turbidity, and especially water depth of the settings in which they grew. As photoautotrophic red algae, they are light dependent and the different taxa show a bathymetric distribution (Adey 1979, 1986;

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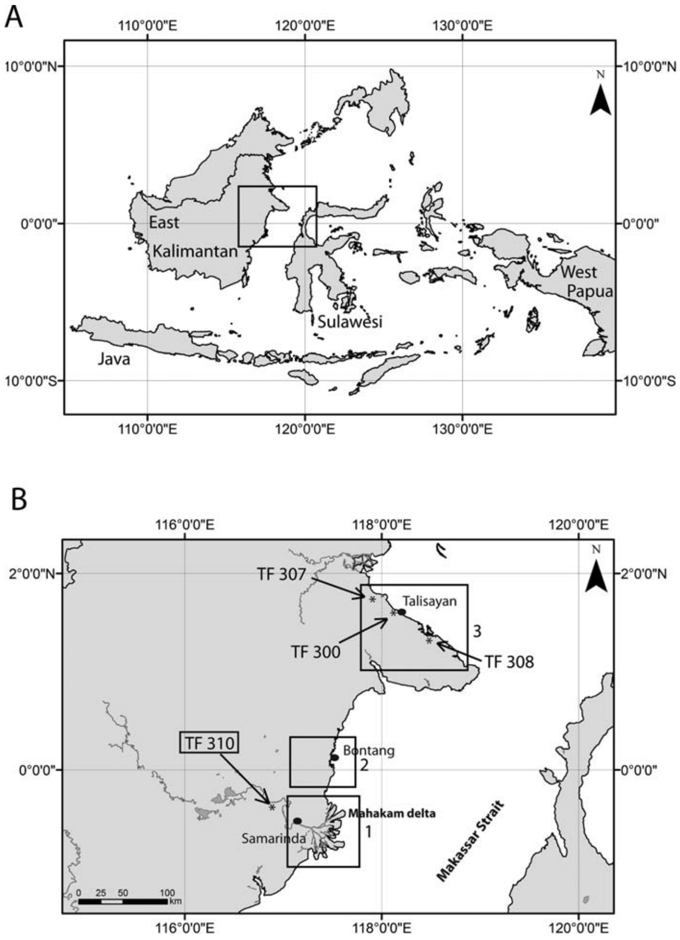

FIG. 1.—Map of study area. **A**) Southeast Asia. **B**) Detail of inset in A, East Kalimantan with the four study areas: TF310 = Senoni, 1 = Samarinda area, 2 = Bontang area, 3 = Mangkalihat peninsula with three sample sites, see also Table 1.

Bosence 1991; Webster et al. 2009; Braga 2011). CCA have a high preservation potential due to their calcitic cell walls and, consequently, they are a group with an excellent fossil record (Bosence 1991). This is an exceptional source of temporal information that allows combining paleontological and molecular data to test phylogenetic models and to calibrate the molecular clocks with a precision difficult to achieve in other groups of organisms (Aguirre et al. 2010). The Miocene was the epoch of the onset of reef growth in the coral triangle (Wilson and Rosen 1998) and peaking biodiversity in the area (Renema et al. 2008). As Aguirre et al. (2010) suggest, a cladogenesis within the mastophoroids and lithophylloids, the main shallow reef CCA, should be expected during the Oligocene and Miocene, the age of the outcrops sampled for this study.

MATERIALS AND METHODS

Five hundred nineteen samples of fossil coralline algae (crusts on corals, rhodoliths, and thallus fragments) were selectively collected at 17 stations (14 logged sections, Figs. 2–3; and three sampling sites, Fig. 1) in the Miocene limestone outcrops of East Kalimantan. In each section, samples were positioned in sedimentary units defined by lithofacies and fossil components. One to three ultrathin sections (48 × 28 mm; 10–15 µm thick) were cut from each rock sample (a total of 680 thin sections), and studied using optical microscopy to identify specimens to the most precise taxonomic level possible. We do not discuss the so-called thin laminar thalli, unistratose CCA with very small cells and conceptacles, as they are usually either micritized or impossible to identify, even at the subfamily level, due to lack of preserved diagnostic features. Members of the genus *Phymatolithon* were not recognized in the samples, although some plants assigned to *Lithothamnion* actually might belong to *Phymatolithon*. *Phymatolithon* and *Lithothamnion* are distinguished by the shape of the epithallial cells, which are usually not fossilized because they are not fully calcified, and by the relative size of the subepithallial cells, which cannot be identified in the absence of the epithallial cells. Cell and conceptacle dimensions were measured on microscope photographs with the tools of AxioVision (version 4.6; Carl Zeiss 2002) software. Cell length is the distance between primary pit connections, and cell width perpendicular to it (Chamberlain 1993). Conceptacles were measured following methods outlined in Adey and Adey (1973).

Following Schindel and Miller (2010), we use taxon labels to name specimens that cannot be assigned to any of the already-described species. A taxon label consists of information about geographical location plus voucher specimen number and collector of the selected type. Labeling of our samples includes TF (for Throughflow, the title of the research project), station number (see Table 1 for geographic information), AR (initials of the collector, Anja Rösler), and sample number.

Facies description in the lithological logs follows the nomenclature of Dunham (1962) for carbonate lithofacies and Insalaco (1998) for growth

TABLE 1.—*Location and age of sampling stations.*

TF n°	Latitude	Longitude	Sector	Locality	Age
TF51/57	−0.5857	117.1190	Samarinda, Stadion/Palaran	Stadion reef	Serravallian
TF78	−0.5185	117.1027	Samarinda, SungaiKunjang	Crab locality	Serravallian
TF130	−0.4812	117.1141	Samarinda, Batu Putih	The rooster's crest	Langhian
TF77	−0.4766	117.1166	Samarinda, Batu Putih	Station 77	Langhian
TF52	−0.4689	117.1213	Samarinda, Batu Putih	Batu Putih 2	Langhian
TF76	−0.4663	117.1218	Samarinda, Batu Putih	Batu Putih 1	Langhian
TF79	−0.4323	117.1378	Samarinda, Batu Putih	Batu Cermin	Langhian
TF311	−0.4313	117.1346	Samarinda, Batu Putih	Roosters Crest	Langhian
TF59	−0.0182	117.3535	Bontang, Southern Hemisphere	South. Hem.	late Burdigalian
TF153	0.0964	117.3804	Bontang, Mine	Rainy Section	late Burdigalian
TF126	0.1513	117.3044	Bontang, Mine	3D-Reef	late Burdigalian
TF128	0.2075	117.2867	Bontang, Mine	Monkey Section	late Burdigalian
TF310	−0.3311	116.8473	Senoni	Senoni	early Burdigalian
TF300	1.6228	118.1297	Mankalihat, Talisayan	Palm Oil Plantation	Serravallian
TF307	1.7621	117.8686	Mankalihat, Talisayan	Taballar Bridge	Aquitanian
TF308	1.3425	118.4819	Mankalihat, Talisayan	BP Village	Burdigalian

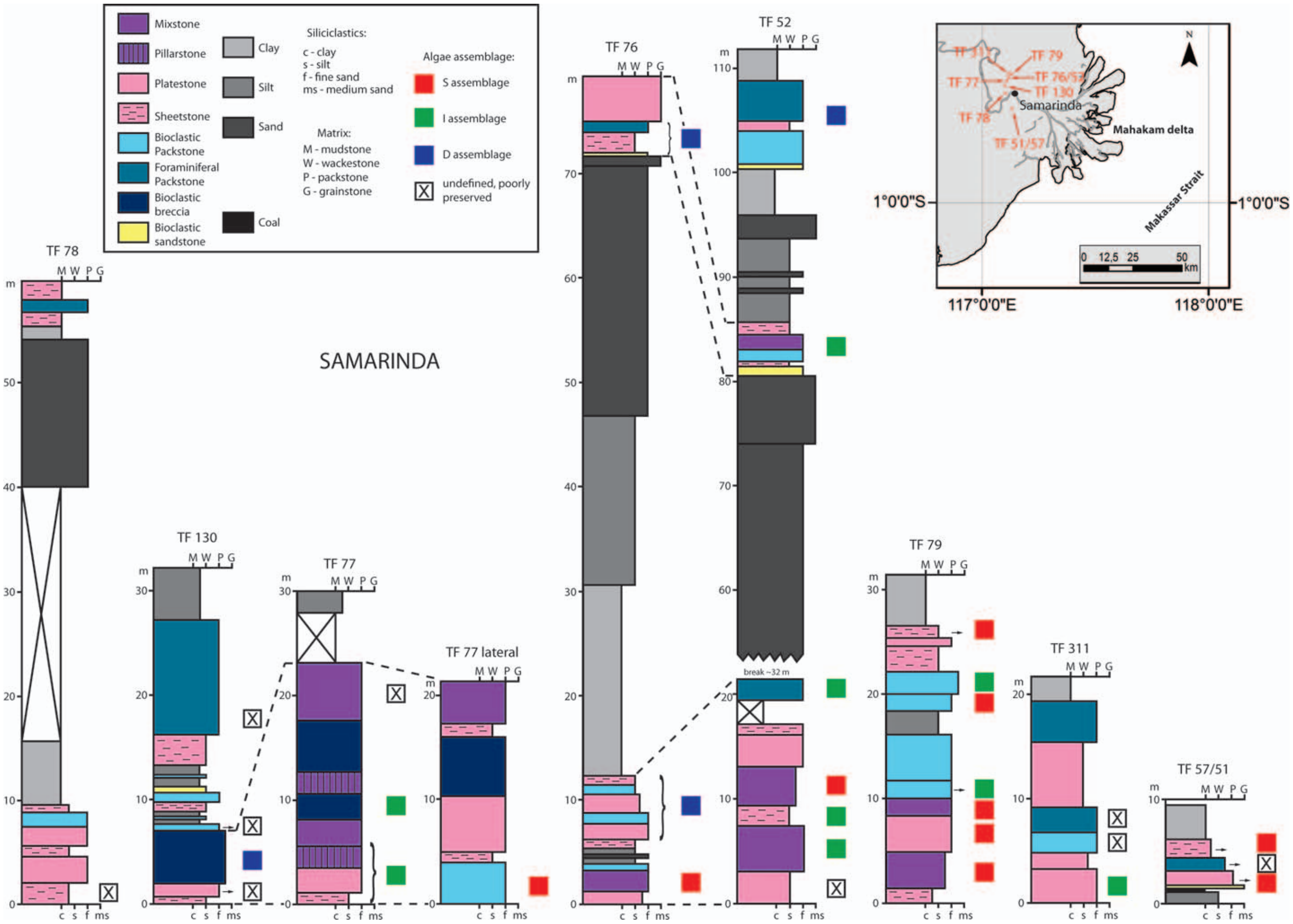

FIG. 2.—Logs of lithofacies and coral growth fabrics of studied outcrops in Samarinda area, with records of CCA assemblages; dashed lines indicate correlation of units.

fabrics in coral reefs. All studied samples are deposited at the Departamento de Estratigrafía y Paleontología of the University of Granada.

GEOLOGICAL SETTING

Miocene CCA occur associated with reef limestone units in the Kutai Basin in East Kalimantan (Indonesia), in Borneo. Miocene carbonates in the Kutai Basin are shallow-water marine deposits related to siliciclastic sediments of the proto-Mahakam Delta (Wilson et al. 1999; Wilson 2005). High rates of Neogene erosion of the Borneo landmass resulted in active eastward progradation of the Mahakam Delta, which infilled the Kutai basin with sediments 9 to 14 km thick (Chambers and Daley 1995; Hall and Nichols 2002). Only a small proportion of the sediment volume corresponds to carbonates (2%–3%, Marshall et al. 2015).

CCA have been sampled in carbonates formed in two distinct paleoenvironmental settings: low-energy shallow-water platform of the Taballar Limestone (Wilson and Evans 2002) in the Mangkalihat Peninsula, and patch reefs within delta deposits of the Kutai Basin (Figs. 1–3).

CCA are generally scarce in mudstone, wackestone/floatstone, and packstone units that are characteristic of the Taballar Limestone outcrops (Wilson and Evans 2002). CCA samples have been collected there at isolated sites (Fig. 1), in which limited exposures prevent measuring stratigraphic sections. The age of the CCA samples has been inferred from the larger benthic foraminifers (LBF) recorded at the same site. Samples from the oldest locality (TF 307, Fig. 1) are Te5 Letter Stage in age (corresponding to Aquitanian, early Miocene, of the standard chronostratigraphic scale; Renema 2007) based on occurrence of *Borelis*, and absence of *Flosculinella* and *Pseudotaberina*. Samples from site TF 308 (Fig. 1) can be assigned to Tf1 Letter Stage zone (Burdigalian, early Miocene; Renema 2007) as suggested by the occurrence of *Flosculinella* and *Pseudotaberina* (most likely *P. malabarica*). The youngest samples (TF 300, Fig. 1) belong to Tf2 Letter Stage zone (middle Miocene as indicated by the appearance of *Cycloclypeus annulatus*; Renema 2007).

The majority of CCA samples were collected in patch reefs in the proto-Mahakam Delta, in which reef carbonates occur within and interfinger with fine-grained deltaic siliciclastic sediments (Wilson 2005). Individual carbonate bodies are up to 2–4 km across with thicknesses of up to 40 m (Wilson 2005), which can vary several tens of meters along strike within a single patch reef. According to their stratigraphic position, four groups of patch reefs were identified:

1. Early Burdigalian reef (TF 310, Fig. 3). CCA of this age were collected in one of the two patch reefs cropping out in Senoni (Wilson 2005; Renema et al. 2015). CCA are scarce and occur as crusts on corals

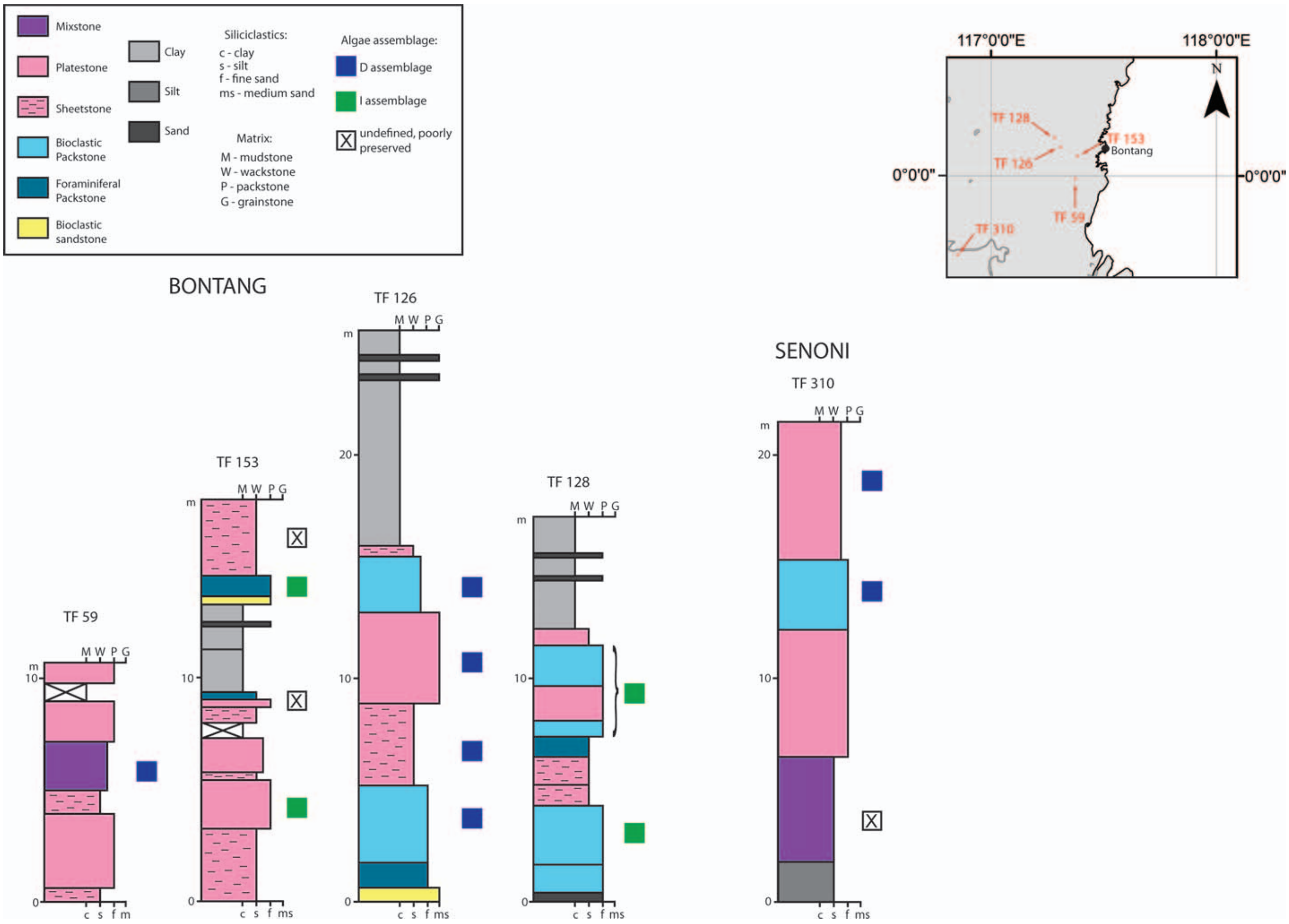

FIG. 3.—Logs of lithofacies and coral growth fabrics of studied outcrops in Senoni and Bontang area, with records of CCA assemblages.

in platestone to mixstone growth fabrics and as crusts on coral fragments in bioclastic deposits (Fig. 3). The LBF assemblage is indicative of the early Burdigalian due to the abundance of *Miogypsinoides* (most likely *M. dehaarti*), combined with rare occurrences of *Nephrolepidina ferreroi* and *Miogypsina* (probably *M. tani*), suggesting deposition between 17 and 20 Ma (Lunt and Allan 2004; Renema 2007). The absence of *Eulepidina* and *Lepidosemicyclina polymorphalbifida*, which are usually quite abundant in Indo-Pacific early Miocene reef deposits (Raju 1974; Lunt and Allan 2004), suggests an age younger than Aquitanian and older than mid-Burdigalian, thus supporting an early Burdigalian age.

2. Late Burdigalian reefs. CCA were sampled in four patch reefs (TFs 59, 153, 126, 128) in the Bontang area (Figs. 1 and 3) associated with platestone and mixstone fabrics and bioclastic packstone. According to Novak et al. (2013), the age of the patch reefs in the Bontang area is late Burdigalian due to the occurrence of the LBF *Nephrolepidina*, *Miogypsina* cf. *globulina*, *Lepidosemicyclina polymorpha*, *Flosculinella bontangensis*, and the coccolith *Sphenolithus heteromorphus*.

3. Langhian reefs (TFs 78, 130, 77, 76, 52, 79, 311, from south to north). Several patch reefs were sampled in the Samarinda area. A Langhian age has been assigned to these localities, based on an integrated magnetostratigraphic and biostratigraphic study (Marshall et al. 2015). CCA occur as crusts on corals in platestone and mixstone fabrics and as rhodoliths in bioclastic sandstone at the base of one of the reefs (TF76, Fig. 2).

4. Late Serravallian reef (TF 51/57). CCA occur encrusting corals in coral sheetstone and platestone in the Stadion patch reef south of Samarinda (Fig. 2). The age of this reef is late Serravallian, according to LBF and magnetostratigraphy (Marshall et al. 2015; Santodomingo et al. 2015).

RESULTS

All recorded CCA in East Kalimantan are associated with coral reefs or coral-rich shallow-water limestones. They mainly occur encrusting coral skeletons or coral fragments and only locally appear forming nodules together with foraminifera and highly recrystallized peyssonneliacean red algae. No CCA occur on thin to very thin corals that are dominant in beds with very high siliciclastic content.

Thirty-one species have been distinguished, belonging to the order Corallinales (families Hapalidiaceae, 10 species; and Corallinaceae, 16 species) and the order Sporolithales (five species) (Figs. 4–5, S1–S2). Dichotomous keys with the diagnostic characters of the recognized taxa can be found in Tables S1 and S2 of the Supplementary Data. The identified species, the station where they have been recorded and their stratigraphic distribution is shown in Table 2.

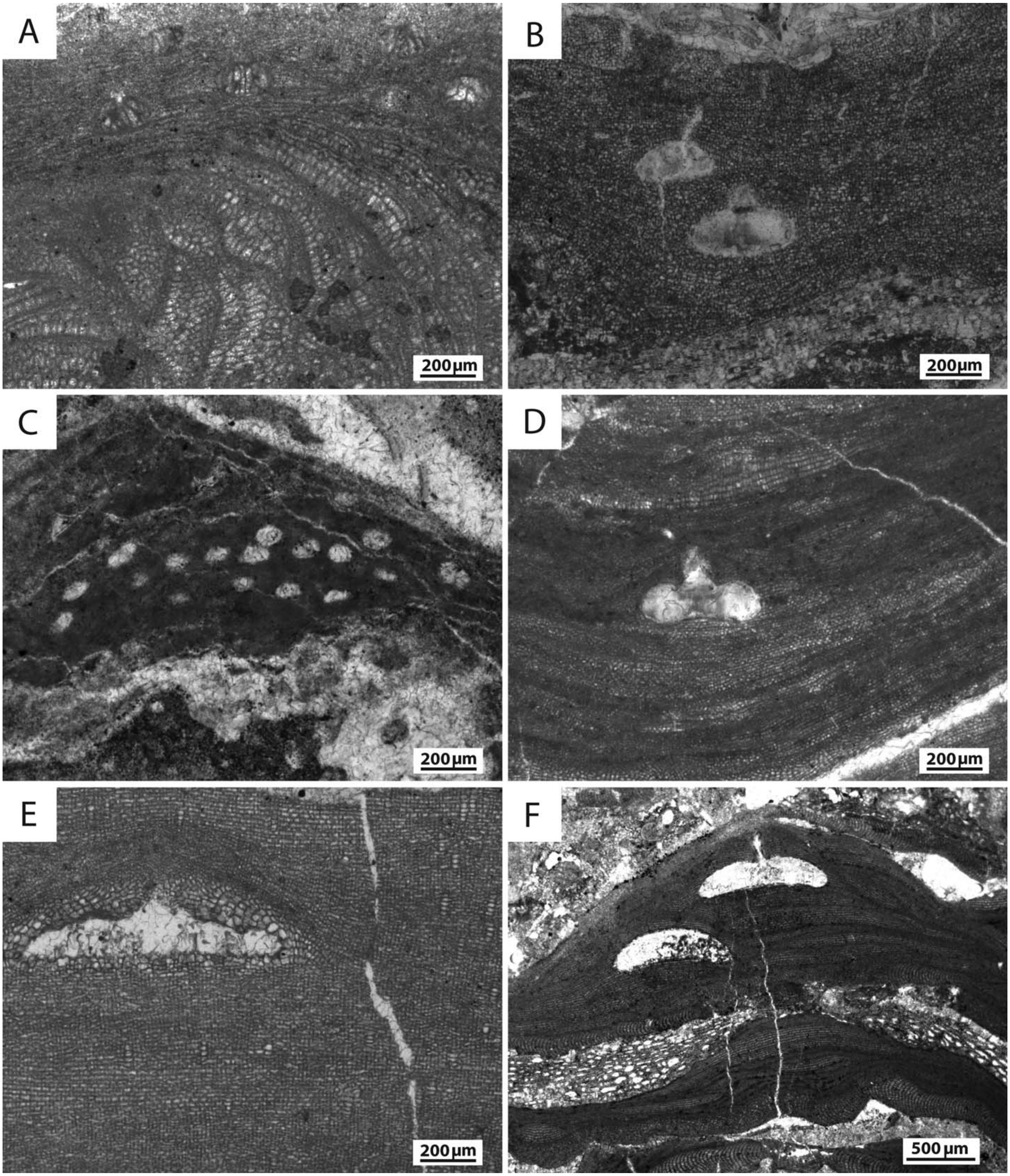

FIG. 4.—Representative CCA of the S-assemblage. **A**) *Aethesolithon problematicum* Johnson 1964. **B**) *Hydrolithon reinboldii* (Weber-van Bosse and Foslie) Foslie. **C**) *Hydrolithon rupestre* (Foslie) Penrose. **D**) *Spongites fruticulosus* Kützing. **E**) *Neogoniolithon fosliei* Setchel and Mason. **F**) *Neogoniolithon* TF78_AR307.

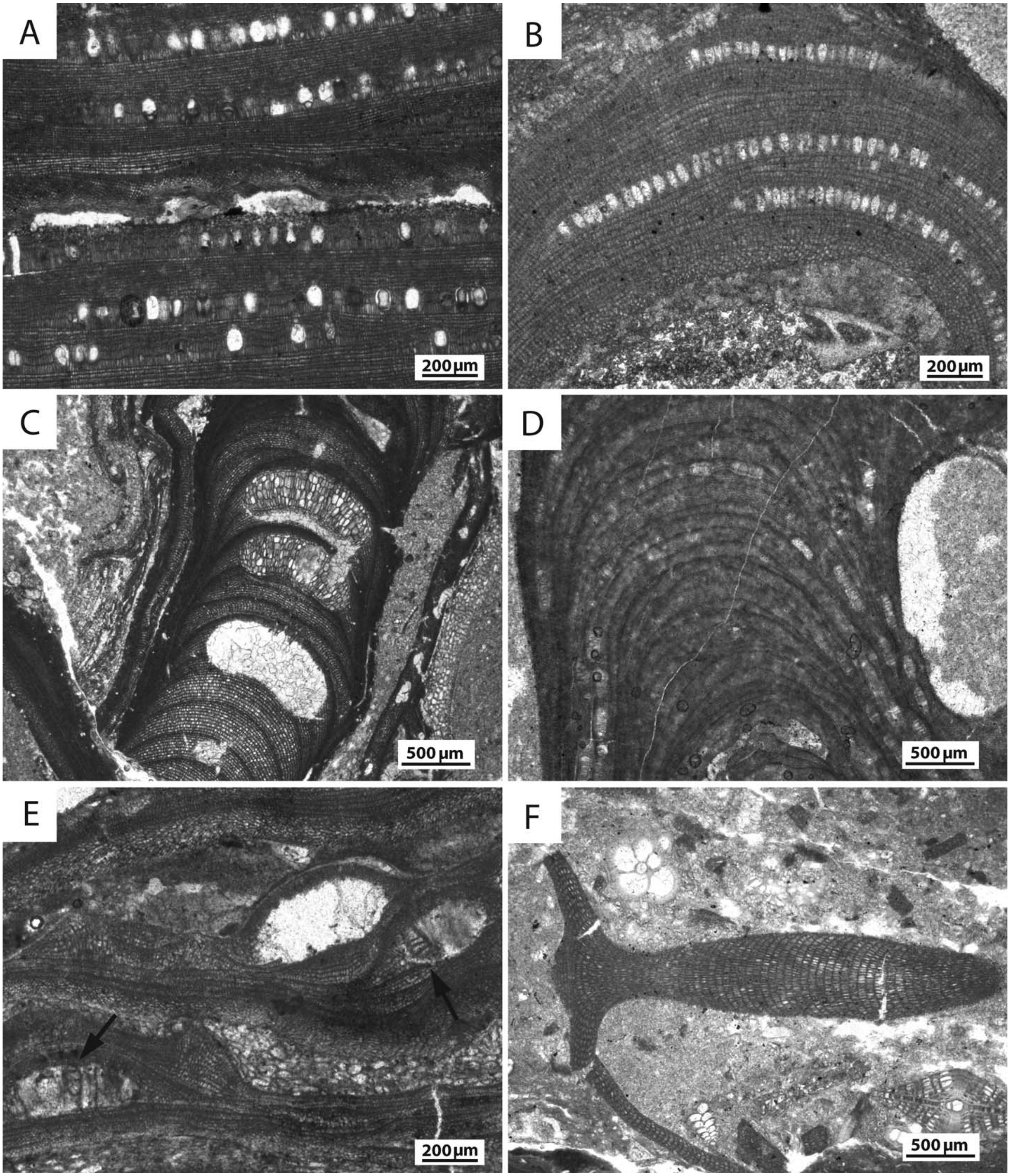

FIG. 5.—A–E) Representative CCA of the D-assemblage. **A**) *Sporolithon ptychoides* Heydrich. **B**) *Sporolithon molle* (Heydrich) Heydrich. **C**) *Mesophyllum guamense* Johnson. **D**) *Lithothamnion ramosissimum* (Reuss) Piller. **E**) *Lithothamnion huseinii* with preserved tetraspores (arrows). **F**) "*Lithophyllum pseudoamphiroa*" Johnson, not diagnostic for any assemblage.

TABLE 2.—*Recorded species in sampled stations and their stratigraphic distribution.*

Species	TF- Stations	Aquitanian	early Burdigalian	late Burdigalian	Langhian	Serravallian	Recent
“Lithophyllum pseudoamphiroa”	52, 57, 76, 77, 79, 126, 153, 307, 308, 310,311	X	X	X	X	X	
Sporolithon TF128_AR237A	128, 130, 310		X	X	X		
Sporolithon TF307_AR564	307	X					
Sporolithon molle	76, 77, 126, 307, 310, 311	X	X	X	X		X
Sporolithon TF76_AR49	57, 76, 79				X	X	
Sporolithon ptychoides	76, 77, 79, 126, 128, 153, 310		X	X	X		X
Mesophyllum indicum	77				X		
Mesophyllum TF59_AR216	59, 153			X			
Mesophyllum guamense	79, 126,130,310		X	X	X		
Lithothamnion TF79_AR353	79, 310		X		X		
Lithothamnion TF79_AR348	79,126			X	X		
Lithothamnion TF76_AR50	76				X		
Lithothamnion ramosissimum	310		X				
Lithothamnion TF126_AR121	126			X			
Lithothamnion TF126_AR149	126, 307	X		X			
Lithothamnion huseinii	52, 76, 79, 130, 153, 307, 310	X	X	X	X	X	
Lithophyllum pustulatum	307	X					X
Mastophora TF76_AR09	52, 57, 76, 7, 126, 310, 308		X	X	X	X	
Lithoporella minus	52, 311, 310, 308	X	X	X		X	X
Lithoporella melobesioides	310, 307, 126, 128, 76, 57	X	X	X	X	X	
Neogoniolithon fosliei	52, 57, 311				X	X	X
Neogoniolithon TF126_AR135	51, 57, 76, 77, 79, 101, 126, 128, 307, 310	X	X	X	X	X	
Neogoniolithon TF78_AR307	153, 52, 57, 78, 79			X	X	X	
Spongites fruticulosus	57, 76, 77, 78, 79, 310		X		X	X	X
Spongites TF77_AR582A	77, 300				X	X	
Aethesolithon problematicum	77, 79				X		
Hydrolithon rupestre	77, 79				X		X
Hydrolithon TF76_AR46	76, 79, 128			X	X		
Hydrolithon TF77_AR581	77				X		
Hydrolithon TF79_AR316	79				X		
Hydrolithon reinboldii	126, 128			X			X
Hydrolithon cf. *munitum*	77, 126, 311			X	X		X

Three CCA assemblages can be distinguished in the studied reefs according to the main components (Table 2). The S-assemblage is commonly dominated by thick crusts of one, or combinations of the taxa *Neogoniolithon* spp., *Spongites* spp., *Hydrolithon* spp. and *Aethesolithon problematicum* Johnson 1964a. These taxa are included within the subfamily Mastophoroideae according to its traditional taxonomy (Harvey et al. 2003; see also Figs. 4 and S1).

The D-assemblage is dominated by *Lithothamnion* spp., *Mesophyllum* spp., and *Sporolithon* spp., and consists mainly of thinner crusts on corals and coral fragments and locally comprises rhodoliths. *Lithothamnion* and *Mesophyllum* belong to the subfamily Melobesioideae while *Sporolithon* is one of the few genera of the order Sporolithales (Figs. 5 and S2).

In the I-assemblage none of the groups of taxa characterizing the other two assemblages significantly dominates, or the dominating taxa are of nondiagnostic character (for example “*Lithophyllum pseudoamphiroa*” Johnson 1964a). There are also units in which poor preservation or scarce records of CCA prevent the assignment of samples to any of the distinguished assemblages (see Figs. 2 and 3 for occurrences of these assemblages in the logged sections).

DISCUSSION

CCA assemblages show bathymetric ranges in modern coral reefs in the Caribbean and Pacific Ocean, presumably based on light requirements of different taxa (Adey et al. 1982; Adey 1986; Bosence 1991; Cabioch et al. 1999; Braga 2011). In present-day reef-related settings, species and genera belonging to the subfamily Mastophoroideae in its traditional concept (Harvey et al. 2003) dominate shallow-water assemblages, while melobesioids and *Sporolithon* are more common in deeper assemblages (Adey et al. 1982; Adey 1986; Bosence 1991; Braga 2011). A similar paleobathymetric distribution of CCA genera and subfamilies has been recognized in Miocene reefs and shelf deposits in which paleodepth can be independently constrained, such as the Mediterranean Tortonian and Messinian (upper Miocene) platform carbonates in southeastern Spain (Braga and Martín 1988; Braga and Aguirre 2001), the Llucmajor reef in Mallorca in the Balearic Islands (Perrin et al. 1995), Messinian reefs in the Salento Peninsula (southern Italy), and Cariatiz in southeastern Spain (Braga et al. 2009). These depth-related CCA patterns have been applied to interpret paleobathymetry in Cenozoic fossil reefs and associated deposits (Webster and Davies 2003; Braga and Aguirre 2004; Webster et al. 2004, 2009; Brachert et al. 2006; Braga et al. 2010). The S-assemblage recognized in Miocene CCA of East Kalimantan is mainly composed of thick crusts of members of the subfamily Mastophoroideae in the sense of Harvey et al. (2003), such as *Hydrolithon*, *Neogoniolithon*, *Spongites*, and *Aethesolithon*, and therefore, can be interpreted as characteristic of shallow-water environments (they dominate in clear tropical waters typically until 30–40 meters; Adey et al. 1982; Iryu et al. 1995). The relatively high proportions of fine-grained siliciclastic sediment in the reef facies suggest that CCA grew in turbid waters and, consequently, the high illuminance required by the S-assemblage could only be attained in very shallow water. Consequently the S-assemblage, which occurs in most cases in mixstone and platestone facies (Figs. 2–3), is indicative of very shallow environments. CCA crusts in S-assemblages are locally thick and comprise a relatively high proportion of the reef deposit. As water turbidity causes a decrease in CCA abundance and crust thickness (Fabricius and De'ath 2001; Perry and Smithers 2006), well-developed CCA growths suggest intervals of arrested siliciclastic influx and limited resuspension of sediment in the reef setting.

D-assemblages include taxa, such as the genera *Lithothamnion*, *Mesophyllum*, and *Sporolithon* (Figs. 5 and S2), most abundant in darker settings, which in clean waters correspond to deep (from 35–50 meters on, Adey et al. 1982; Lund et al. 2000; Abbey et al. 2011) or cryptic environments, such as caves or crevices. In the Miocene Mahakam reefs, however, low illumination may have prevailed in relatively shallow settings due to high turbidity. The D-assemblage is the only one found in some Miocene reefs in East Kalimantan (TF 59, 126, 310). The absence of shallower CCA, in combination with the paleoenvironmental requirements of associated larger benthic foraminifers, corals, and bryozoans, suggests that these reefs grew in mesophotic conditions (Novak et al. 2013). CCA in rhodoliths belong to the D-assemblage in accordance with the muddy bioclastic deposits in which they are locally recorded at the initiation of reef development (TF 76, meter ~ 75; Fig. 2) or as small nodules encrusted with foraminifera in bioclastic packstone (TF 126, Fig. 3). In the case of TF 76 this rhodolith layer could be interpreted as a transgressive marker bed *sensu* Nalin et al. (2007), at the delta front.

Lithophyllum pustulatum (Lamouroux) Foslie 1904 species group, commonly consisting of thin plants, is the only lithophylloid recorded in the studied Miocene reefs in East Kalimantan. This species is also the type of *Titanoderma* Nägeli (Nägeli and Cramer 1858) which has been accepted by many authors as an independent genus (Irvine and Chamberlain 1994; Bailey 1999). Species of *Lithophyllum* Philippi (Philippi 1837), with diverse, sometimes complex growth forms, are typical components of the CCA assemblages in present-day coral reefs in the Indo-Pacific, locally accounting for up to 25%–30% of CCA diversity (Adey et al. 1982; Verheij 1994; Baba 2000; Ringeltaube and Harvey 2000). The absence of thick *Lithophyllum* species cannot be attributed to a sampling artifact as the number of sampling sites and studied samples can be considered representative of the Miocene reefs and CCA in east Borneo. As they share similar ecologic needs in modern reefs with the recorded taxa, the absence of multistratose *Lithophyllum* plants should be attributable to evolutionary (or historical) biogeography. Fossil lithophylloids in the Mediterranean are known from the Late Cretaceous (Maslov 1956; Braga et al. 2005). Thin fossil thalli of *Lithophyllum* gr. *pustulatum* (Lamouroux) Foslie 1904 are known in the late Oligocene in the Pacific (Bassi et al. 2009; Clague et al. 2010) and thin "bistratose" CCA (such as *Distichoplax* Pia) have been reported from the Paleogene in Borneo (Keij 1963, 1964). Reliable records of thick, multistratose *Lithophyllum* species in the Indo-Pacific are mainly known from Pleistocene and younger rocks (Johnson 1961, 1957). Johnson (1964), however, described *Lithophyllum alternicellum* Johnson 1964a, a new species of thick-branching CCA from the Bonya Limestone in Guam, which is middle Miocene in age according to the larger benthic foraminifera reported by Cole (1963). Similar thick-branching CCA were also described by Johnson (1964a) as *Lithophyllum alternatum* from the Alifan Limestone, a formation overlying the Bonya Limestone. Both species are close to *L. kotschyanum* species group and, therefore, *Lithophyllum alternicellum* Johnson 1964a is the oldest known Pacific thick lithophylloid, similar to the representatives of the genus in modern coral reefs. In contrast, thick multistratose litophylloids are common in the Caribbean Sea and in the Mediterranean (such as *Lithophyllum racemus* (Lamarck) Foslie 1901c) since the early Miocene (Lemoine 1917; Basso et al. 1996). Thick multistratose members of *Lithophyllum* presumably arrived in the Indo-Pacific sometime during the middle Miocene and probably diversified during the Pleistocene.

Neogoniolithon fosliei (Heydrich) Setchell and Mason 1943 and *Hydrolithon reinboldii* (Weber-van Bosse and Foslie) Foslie 1909, extant species which were only known from Pleistocene deposits (Webster et al. 2004; Abbey et al. 2011; Faichney et al. 2011) are reported here in older reefs of East Kalimantan. *H. reinboldii* occurs in late Burdigalian successions (TF 128, Fig. 3) and *N. fosliei* occurs in Langhian and Serravallian successions (TF 57, Fig. 2). This is the earliest occurrence of these species, which are common components of the CCA assemblages of present-day Indo-Pacific reefs.

Other CCA found in the Miocene Mahakam Delta resemble modern Indo-Pacific reef taxa, but lack heterocysts, which are cells with larger dimensions than the surrounding cells in the thallus, and correspond to trichocytes in the living plant. This is the case of *Hydrolithon* TF79_AR316 (Fig. S1), similar in vegetative anatomy and conceptacle shape and size to *H. gardineri* (Foslie) Verheij and Prud'homme van Reine 1993, and *Hydrolithon* TF76_AR46 (Fig. S1), which shows features characteristic of *Hydrolithon breviclavium* (Foslie) Foslie 1909.

Groups of heterocysts buried in the thallus in horizontal rows or vertical columns are a very common morphological trait of modern reef CCA. They are used to distinguish species such as *Hydrolithon onkodes* (Heydrich) Penrose and Woelkerling 1992, one of the most common reef CCA, from the similar species *H. munitum* Penrose 1996 that lacks buried trichocytes (Penrose 1996). Although their physiologic function, and even their validity as taxonomic characters, is discussed (Walker 1984; Chamberlain 1985), these features can be considered as typical for reef-related CCA. Thick thalli with pervasive large cell fusions, such as the ones characteristic of *Hydrolithon reinboldii* (Weber-van Bosse and Foslie) Foslie 1909, are also distinctive of tropical CCA. Bittner et al. (2011) and Kato et al. (2011) suggested using trichocytes in large horizontal fields to distinguish and resurrect *Porolithon* as a distinct genus from *Hydrolithon*, but these taxonomic implications remain a topic of discussion (Woelkerling et al. 2012). The first well-documented occurrence of groups of heterocysts in fossil CCA was reported associated with coral reefs from the Oligocene of the Mediterranean Basin (*Neogoniolithon raripunctatum* Mastrorilli 1968; Vannucci et al. 2010; Braga and Bassi 2001). The common occurrence of algae with large cell fusions (*H. reinboldii*, *Aethesolithon problematicum* Johnson 1964a) and those possessing groups of heterocysts (*N. fosliei* and *Hydrolithon* TF77_AR581, Fig. S1) in the S-assemblages in the middle Miocene of East Kalimantan can be interpreted as the inception of the CCA flora, which will play a significant role in reef building in the Indo-Pacific region. Specimens of *Hydrolithon* similar to *H. reinboldii* have been recorded in the middle Miocene of Queensland Plateau in northeastern Australia (Martín and Braga 1993) together with *Aethesolithon*. The latter genus was described in the Miocene of Guam (Johnson 19964) and has also been found in Miocene rocks from Guatemala (Johnson and Kaska 1965). No CCA plants with groups of heterocysts or pervasive large cell fusions occur in the coeval Miocene reefs in the Mediterranean Basin or in carbonate deposits in higher latitudes, marking a biogeographic differentiation of CCA species which cannot be recognized in pre-Miocene times (Braga et al. 2010). Potential paleobiogeographic patterns at the species level for other CCA taxa, such as *Sporolithon* and members of the subfamily Melobesioideae, is hindered by the lack of a consistent and reliable taxonomy, which prevents the use of species names for biogeographic analyses.

Species richness of CCA in the Miocene of East Kalimantan is comparable to species richness in present-day CCA accounts in West Sulawesi in Indonesia on the eastern side of the Mahakam Strait (Verheij and Prud'homme van Reine 1993). These authors reported 21 CCA species in the Spermonde archipelago. A total of 32 CCA species have been identified in the Miocene deposits of the Kutai Basin, in a time span of about 10 myr, but the species richness is different in each stratigraphic interval recognized. Only nine species have been recorded in the poorly represented Aquitanian platform limestones. The number of species is limited to 13 in the early Burdigalian reef of Senoni in which only D-assemblages occur. A higher CCA diversity, similar to the modern one, is encountered in early Burdigalian and Langhian reefs (18 and 24 species respectively), in which S-, D-, and I-assemblages are represented in diverse paleoenvironments. The species richness decreases in the Serravallian as only S-assemblages appear in the Stadion reef (TF51/57).

CONCLUSIONS

Crustose coralline algae (CCA) are common in early and middle Miocene patch reefs within dominantly siliciclastic successions of the proto-Mahakam Delta in East Kalimantan (Borneo, Indonesia). They can also be found in laterally equivalent Miocene shallow-water carbonates in the Mangkalihat peninsula.

CCA occur as crusts on corals and coral fragments and only locally as rhodoliths in bioclastic sandstone beds. According to their components, three types of CCA assemblages have been distinguished: (1) S-assemblages dominated by *Neogoniolithon* spp., thick crusts of *Spongites* spp., and *Hydrolithon* spp.; (2) D-assemblages which consist mainly of thin crusts of *Lithothamnion* spp., *Mesophyllum* spp., and *Sporolithon* spp., and (3) I-assemblages with intermediate composition. The S-assemblages occur mainly in platestone and mixstone fabrics and their components are characteristic of well-illuminated shallow waters. D-assemblages grew in dimly lit waters in deeper settings or under higher turbidity.

Components of S-assemblages from middle Miocene reefs show features, such as pervasive large cell fusions and groups of heterocysts, typical of CCA in modern reefs, and probably represent the earliest members of the extant reef CCA flora in the Indo-Pacific region.

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SUPPLEMENTAL MATERIAL

Data is available from the PALAIOS Data Archive: http://www.sepm.org/pages.aspx?pageid=332.

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