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A DIVERSE PATCH REEF FROM TURBID HABITATS IN THE MIDDLE MIOCENE (EAST KALIMANTAN, INDONESIA)

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ABSTRACT: The Kutai Basin (East Kalimantan, Indonesia) contains a rich and well-preserved Miocene fossil record of small patch reefs that developed under the influence of high siliciclastic input associated with the progradation of the Mahakam Delta. In this study, we reconstruct the biodiversity and paleoenvironments on one of these delta-front, mixed carbonate-siliciclastic systems that developed at the Serravallian–Tortonian boundary near the city of Samarinda. In two newly exposed sections, we analyzed the sedimentology and distribution of the main fossil biota including corals, foraminifers, coralline algae, and bryozoans. Seven facies are herein defined, including two dominated by platy corals and two by larger benthic foraminifera. Facies distributions were driven by changes in depth and variations in terrigenous input within a range of delta-front habitats. Despite the turbid conditions, fossil assemblages are highly diverse, including 69 coral species and 28 bryozoan species that occur in coral-dominated facies. Crustose coralline algae were mainly associated with the coral-dominated facies. Larger benthic foraminifera showed broader ecological tolerance within the range represented in the studied sections and thus are common in most facies. These diverse patch reef ecosystems were able to cope with high siliciclastic input during the early development of the Miocene coral reef biota.

INTRODUCTION

Coral reefs are declining worldwide as a result of human activities (Hughes et al. 2003; Hoegh-Guldberg 2011). Anthropogenic stressors include local activities such as overfishing and water pollution from urban areas, and at broader scale, global warming and declining pH (Bellwood et al. 2004; Hughes et al. 2007). Global warming has changed rainfall patterns (Xie et al. 2010) that, in combination with coastal expansion and deforestation around river basins, have led to increased discharges of sediments into the oceans. As a consequence, many coral reefs have undergone phase shifts into systems tolerant of sediment input (Hughes et al. 2007; Hoegh-Guldberg et al. 2007).

Understanding the dynamics of coral reefs living under terrigenous input contributes to a better understanding of the ecological processes that support reef resilience. Terrigenous influx is a key control on the development of coral reefs, because (1) it leads to increased water turbidity, reducing light available for light-dependent organisms; and (2) smothering of biota due to high sedimentation regimes (Rogers 1990; Nugues and Roberts 2003; Fabricius 2005). Numerous studies have shown that prolonged exposure to sediment discharge from rivers has a negative impact on corals and other reef biota leading to decreased coral reef health (Rogers 1990; Katwijk et al. 1993; Stafford-Smith 1993; Fabricius and De'ath 2001; Fabricius 2005). There is also a generally accepted view that coral diversity tends to be low in reefs that are substantially influenced by siliciclastic input (Van Woesik et al. 1999; DeVantier et al. 2006; De'ath and Fabricius 2010). In contrast, other

studies challenge the idea of a negative effect of high rates of sedimentation on reef development (Kleypas et al. 1999; Larcombe et al. 2001; Perry et al. 2012; Browne et al. 2012). Indeed, Perry et al. (2012) found that periods of most rapid accretion over the past ~ 700 years coincide with phases of reef development dominated by fine-grained terrigenous sediment accumulation.

Paleoecological studies are key to understanding the dynamics of the environmental parameters that drive coral reef development and diversity at broader temporal and spatial scales (Perry et al. 2009; Roff et al. 2013). In the geological record there are numerous examples of coral assemblages developing in turbid-water environments since at least the Late Triassic (Rosen et al. 2002) in the Mediterranean (Hayward 1982; Braga et al. 1990; Morsilli et al. 2011; Pomar et al. 2012) and the Caribbean (McNeill et al. 2000; Klaus et al. 2008). In fact, the fossil record of Southeast Asia, the region that hosts today the most diverse marine ecosystems on Earth (commonly referred to as the Coral Triangle; Bellwood et al. 2005; Hoeksema 2007), is rich in well-preserved coral assemblages that mainly developed under high sediment influx (Gerth 1923; Umbgrove 1929; Wilson 2005; Novak et al. 2013).

Sedimentology and carbonate dynamics of Miocene reefs in the Coral Triangle have been studied in a regional context (Wilson and Lokier 2002; Wilson 2005), revealing the potential high diversity of patch reefs that formed in mixed carbonate-siliciclastic deposits (Wilson 2005). Still, little is known about the species composition, development, and detailed paleoecology of those Miocene turbid environments. Due to urban

development in the area, numerous new outcrops are exposed regularly, increasing the number of sections through patch reefs beyond those available for study by Wilson (2005).

In the current study, we characterize a new example of coral-rich facies that occur within mixed carbonate-siliciclastic systems in the region referred to as the Stadion coral carbonates (Stadion CC) as they are exposed on the highway leading to *Stadion Utama Kaltim*, which opened in 2008. The main goals of this study are: (1) to describe the assemblages of corals, benthic foraminifera, coralline algae, bryozoans, and mollusks occurring in the Stadion CC sections; (2) to perform a paleoenvironmental reconstruction based on the analyses of the sedimentology and biota; (3) to describe the developmental stages of the Stadion CC sections; and (4) to discuss the importance of terrigenous input as a controlling factor for modern coral reefs.

GEOLOGICAL SETTING

The study area is located within the Kutai Basin in East Kalimantan (Fig. 1), a depositional basin that originated during the middle Eocene when the Makassar Straits and Philippine Sea opened (Cloke et al. 1999; Wilson and Moss 1999). Throughout the Miocene, large amounts of clastic sediments formed rapidly prograding deltas (Hall and Nichols 2002). In particular, during the middle Miocene more than 4 km of shelf to fluvial sediments were deposited as the Mahakam Delta system prograded to its current position (Wilson and Moss 1999; Hall and Nichols 2002; Marshall et al. 2015). The modern Mahakam Delta is located on a low wave-energy coast. Its dynamics are tide dominated so that the deltaic sediments are characterized by high silt and clay contents as little sand is sorted by longshore currents (Allen and Chambers 1998; Storms et al. 2005).

The Miocene Mahakam Delta succession (Fig. 2A) begins with shale-dominated shelf deposits and includes several carbonate intervals that are exposed as prominent ridges such as the Batu Putih patch reefs (Moss and Chambers 1999; Wilson 2005; Lokier et al. 2009; Marshall et al. 2015). Stratigraphically above the Batu Putih patch reefs, deltaic sedimentation takes place and sandstone progressively becomes the dominant lithology, often directly above coal beds. Based on magnetostratigraphic analyses that correlate the Samarinda polarity pattern and the geomagnetic polarity timescale, an average sedimentation rate of ~ 75 cm/kyr has been estimated throughout the Samarinda sequence (Marshall et al. 2015). The Stadion CC is a second set of fossiliferous carbonates (Fig. 2). Within 20 m above the Stadion CC, fluvial sedimentation resumes as thick sandstone and nonfossiliferous shale (Marshall et al. 2015).

The age of the Stadion locality has been placed close to the Serravallian–Tortonian boundary (11.6 Ma) using integrated magnetostratigraphy and biostratigraphy (Marshall et al. 2015). Thus, the Stadion CC is younger than other Samarinda carbonate sections previously studied by Wilson (2005).

Terminology

Facies descriptions in this work follow the nomenclature and characterizations developed by Insalaco (1998). These terms are an extension of the boundstone category applied by Dunham (1962) to facies that are dominated by *in situ* bioconstructors (corals, sponges, bryozoans, etc.) in growth position that may or may not form a true framework. From this approach, the term growth fabric is used to describe the structure of coral facies. The term framework, *sensu stricto*, is applied when a degree of rigidity, wave resistance, and intergrowth can be inferred for the growth fabric (Insalaco 1998). The Insalaco nomenclature is based on the growth form of scleractinian corals as the primary descriptor. Thus, a facies dominated ($> 60\%$) by branching corals is named a pillarstone, by platy to tabular corals (width to height ratio ≤ 3)

to $\sim 3:1$) is a platestone, by thin-plate to sheet-like corals (width to height ratio $> 30:1$) is a sheetstone, by domal massive corals is a domestone, and finally, by a variety of coral growth morphologies is a mixstone. Regarding the geometry of the bioconstructions, the term biostrome is applied to bioclastic accumulations that are distinctly bedded and do not thicken into lenses so that their upper and lower surfaces are flat and parallel. In contrast, bioherm is used to define rigid structures that caused modification of seabed topography and therefore are likely to have distinct ecological zonation (Cummings 1932).

Although extensively used in paleoenvironmental interpretations, the terms reef and patch reef have countless contradictory and ambiguous definitions (see review in Fagerstrom 1987; Rosen 1990). Therefore, we constrain our direct comparisons to previous studies in Kalimantan region (Moss and Chambers 1999; Wilson and Lokier 2002; Wilson 2005, 2008; Lokier et al. 2009; Novak et al. 2013). In East Kalimantan, the term patch reef has been applied to modern coral communities characterized as small isolated assemblages, which develop in shallow waters on the delta front, eight kilometers from the mouth of the Berau River (Tomascik et al. 1997). A similar approach was used for the interpretation of Miocene fossil coral assemblages located in the delta front of the Mahakam delta, in which the term patch reef has been applied to carbonate structures that “developed in shallow waters, form low-relief coral buildups, lack rigid frameworks, and had gently sloping margins of a few degrees” (Wilson 2005). It is important to note that Wilson’s definition implies the use of the term reef in a broad sense due to the “lack of rigid framework” of the carbonate structures. Likewise, in the present study, the term patch reef is used in concordance with Wilson (2005), to describe coral carbonates regardless of the lack or presence of rigid frameworks (Moss and Chambers 1999; Wilson and Lokier 2002; Wilson 2008; Lokier et al. 2009; Novak et al. 2013).

From our descriptive approach, we use the word biostrome independently from the term coral carpets as proposed by Riegl and Piller (2000a, 2002), because the use of coral carpets implies an environmental interpretation by analogy with modern coral settings. While coral carpets can be preserved as biostromes, not all biostromes have been interpreted as coral carpet successions (e.g., algal biostromes, Bosence 1983; Benisek et al. 2009; bryozoan biostromes, Taylor and Zaborski 2002). These concepts provide the background for further interpretations of the different facies within the Stadion CC.

METHODS

The Stadion CC are exposed in two outcrops: Stadion CC-1 located at 0.585° S, 117.120° E (Fig. 1C); and Stadion CC-2 at 0.586° S, 117.120° E (Fig. 1D). These outcrops are 150 m apart, at the crossroad of the stadium highway and a local coal mine road. The two studied sections are 8–10 m thick (Figs. 1C–D), with an eastward dip of 55° . Both consist of lateral exposure of a few tens of meters but are partially covered by vegetation (Figs. 1C–D). Both sections were logged and sampled to identify lithological units, sedimentary structures, relative abundance of carbonaceous content, sediments, and fossil components, and main taphonomic features. Photographs were taken to describe morphology and lateral variation and the units were correlated and summarized in two logs (Fig. 2B). Annotated photographs with shaded facies overlays are provided in Figure 3. Lithological samples were collected from each unit for further microfacies analysis utilizing 21 standard thin sections (28×48 mm). Lithology and facies descriptions follow Folk (1980) for siliciclastics, and Dunham (1962) and Insalaco (1998) for carbonates.

The carbonate content of the sediment matrix was determined using Total Inorganic Carbon (TIC) analysis. Fifty mg of each sample was ground and then analyzed with the front-end acid digestion instrument CM 5240, which converts inorganic carbonate into CO_2 . The CO_2 was transported into a UIC Inc. CM 5014 Coulometer that measures the TIC

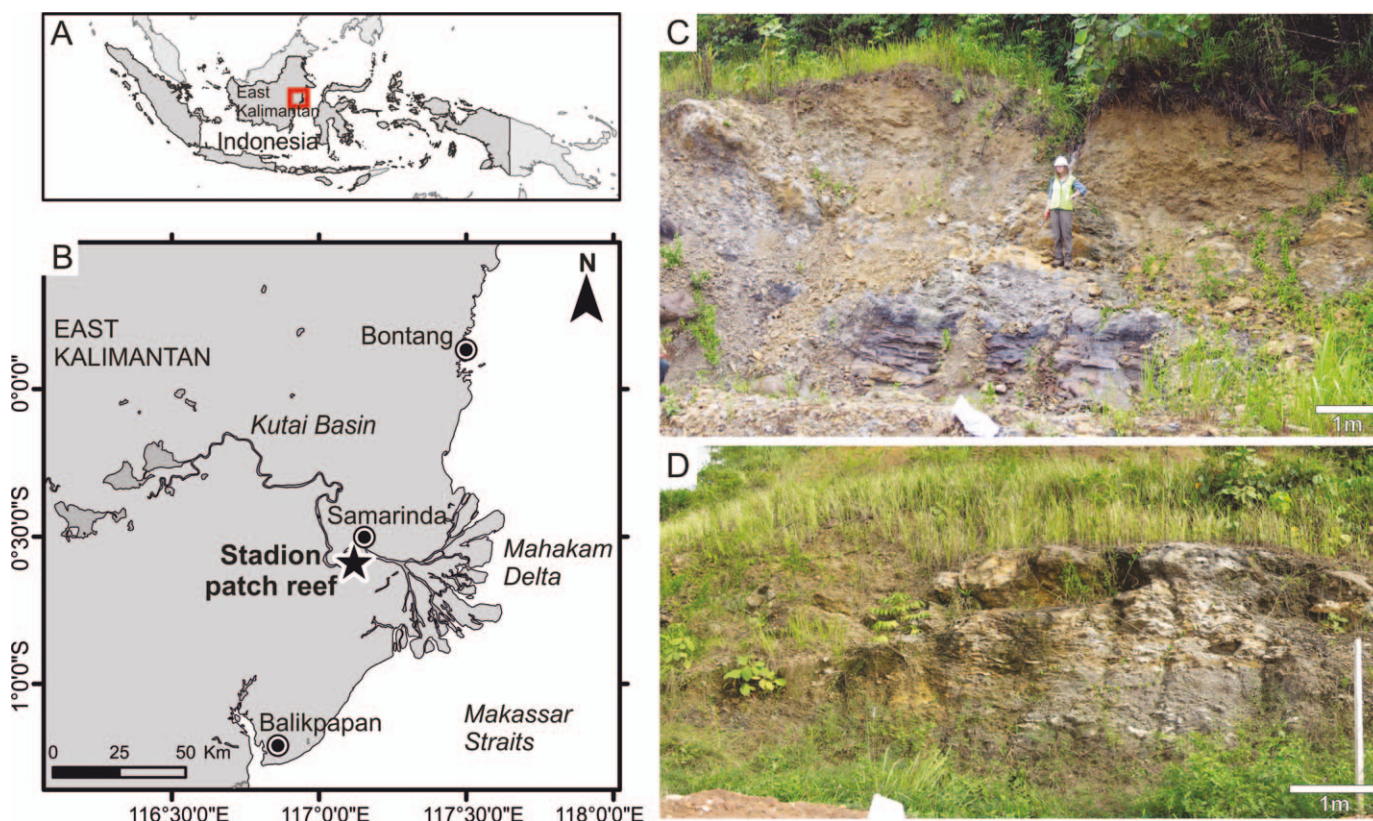


FIG. 1.—Location of the Stadion patch reef. A) Location of East Kalimantan in Indonesia. B) Location of Samarinda city and the Stadion patch reef, east of the present-day Mahakam Delta. C) Outcrop photograph of locality Stadion CC-1. D) Outcrop photograph of locality Stadion CC-2.

percentage from which the CaCO_3 percentage was calculated. A 12% carbon standard was used for the instrument calibration.

Fossil Content

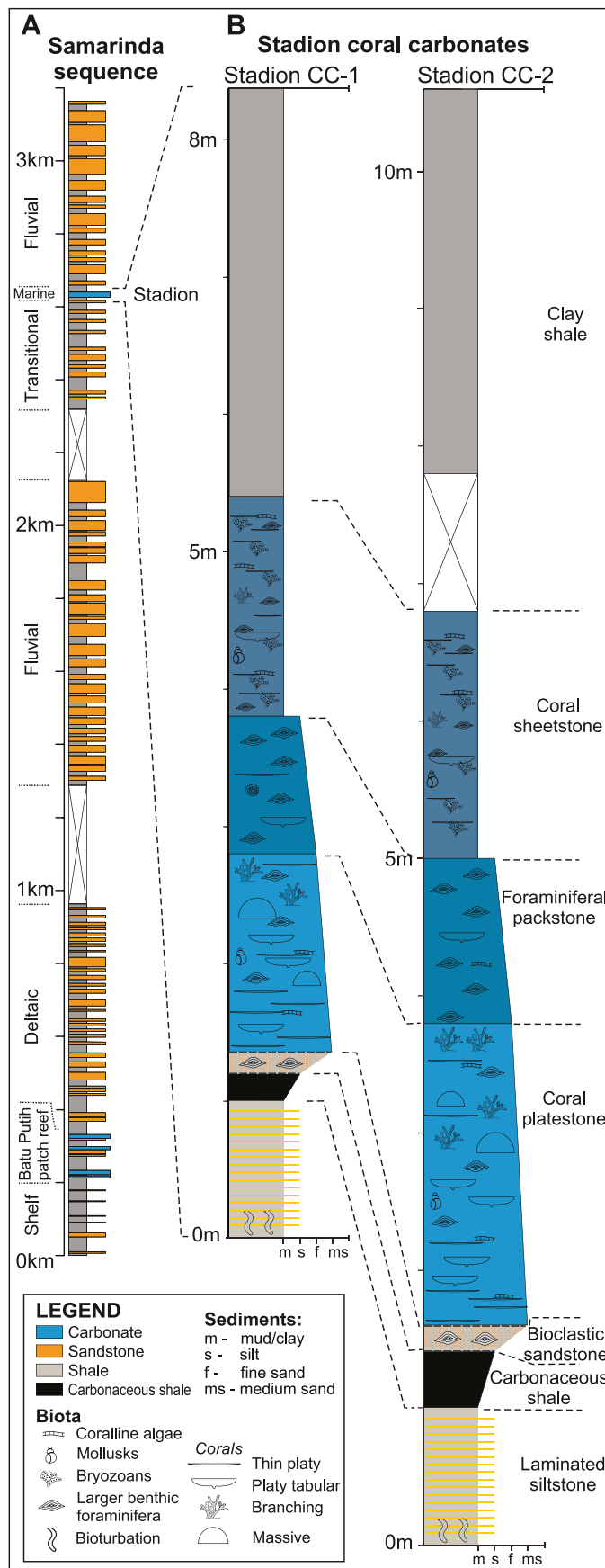
The Stadion CC sections preserve a diverse assemblage that includes corals, foraminifers, coralline algae, bryozoans, and mollusks. In addition, some echinoid spines, serpulid tubes, small brachiopods, and crustacean chelae were found within the sediments or cemented to coral surfaces. In this study, only the former five main groups are discussed based primarily on the relative abundance of these taxa. The primary datasets used to describe the distributions of these five main taxa within the study interval include field observations, hand specimens and bulk samples collected from the fossiliferous units, and thin sections. Bulk samples were collected randomly within each unit and also along 4–5-m-long line transects. Transects were placed at each observed change of composition within each unit, thus nine transects were measured at Stadion CC-1 and seven equivalent transects at Stadion CC-2 (Fig. 3).

Bulk samples consisted of approximately 5 to 7 kg mix of sediment and fossil material obtained from each outcrop unit. The bulk samples were soaked in water, washed, and sieved through 5 mm, 2 mm, 500 μm , and 125 μm sieves in the laboratory.

Fossil specimens were identified to the lowest taxonomic grade possible, according to their preservation and the taxonomic framework available for each group. Some taxa were left in open nomenclature pending detailed taxonomic description that is beyond the scope of this study. Representative specimens of corals, bryozoans, and mollusks are deposited at the Natural History Museum (London), larger benthic foraminifera at the Naturalis Biodiversity Center (Leiden), and coralline algae at the Departamento de Estratigrafía y Paleontología at the University of Granada.

Corals were studied from 53 bulk samples as well as specimens individually collected from the outcrop surface. High taxonomic richness and the lack of a rigorous regional taxonomic framework for Miocene reef corals restricted our ability to identify taxa in the field, so transects were used to estimate percentages of the different types of coral growth forms, including massive, branching (ramose and phaceloid), solitary, and platy, the latter subclassified as thin platy and platy tabular (Insalaco 1998; Rosen et al. 2002). The relative abundance of sediment and corals in each unit was estimated along each transect. Specimens recovered from bulk samples were counted and weighed, and relative abundances were estimated as a percentage of each taxon per unit (see Supplementary Data, Appendix A). External morphological characters of corals, such as colony forms and calice features, were used for taxonomic identifications in the laboratory and taxa names were assigned following the recent revision on Indo-Pacific fossil corals by Johnson et al. (2015). *Acropora* specimens were placed within “species groups” (Wallace 1999). Well-preserved corals, which had weathered out of the outcrop, were also collected to enhance taxonomic lists and identifications.

Larger benthic foraminifera were examined in 11 thin sections (28×48 mm) and as specimens picked from 14 bulk samples (500 μm to 2 mm fractions; ~ 300 foraminifera per sample). Taxon abundances were estimated relative to the total number of foraminifera identified in each sample or thin section (see Supplementary Data, Appendix B). A semiquantitative approach was applied to evaluate benthic foraminiferal assemblages within the 125–500 μm fraction from each sample. In each sample, ~ 100 specimens were sorted, identified, and scored as abundant if they represented more than 40%, common between 15% and 40%, frequent from 5% to 15%, and rare if less than 5%. The percentage of planktonic/benthic foraminifera was also calculated (see Supplementary Data, Appendix C).



Coralline algae were selectively collected in the field and subsequently studied in a total of 32 ultra-thin sections (10–15 μm thick). Relative abundances of taxa of coralline algae were estimated by measuring the proportional cross-sectional area occupied by each taxon in relation to the total coverage of coralline algae (Perrin et al. 1995). Structures built by coralline algae such as crusts, rhodoliths, and foralgaliths, which are compact nodules with foraminifers (Prager and Ginsburg 1989), were recognized in hand specimens and in thin sections. Growth forms were described using the terms of Woelkerling et al. (1993).

Bryozoans were found encrusting the bases of platy corals and coral branches, and as colony fragments picked from sediment fractions larger than 500 μm from ten bulk samples. Bryozoan specimens were identified to the genus or family level. Relative abundances of taxa were estimated by counting the number of encrusting colonies on the corals and fragments of erect species scattered in the sediments. The proportion of corals encrusted by bryozoans was also estimated by comparing the number of coral specimens and/or fragments encrusted by bryozoans and the total number of coral specimens and/or fragments contained in the bulk samples. Colony growth forms of bryozoans included two main categories, encrusting and erect, and their respective proportions were calculated in terms of both species richness and specimen abundance.

Statistical Analysis

To assess changes in the community composition among facies and between the two sections, nonmetric multidimensional scaling (NMDS) ordinations were produced for corals and larger benthic foraminifera. Coral abundances were estimated as weight percentages standardized using the “Wisconsin double standardization” where species are first standardized by maxima, and then site by site totals (Oksanen et al. 2013). NMDS plots based on transformed data from percentages of the number of fragments and/or colonies showed a similar pattern of clustering to that obtained from their respective weight percentages; hence the former plots are not included here. Analyses of similarity (ANOSIM) were used to test for intergroup differences, and similarity of percentages analysis (SIMPER) was used to identify species that were most responsible for the discrimination between facies and outcrops. Statistical analyses were performed using the vegan package (Oksanen et al. 2013) within the R statistical software environment (R-Core Team 2013).

RESULTS

Seven main lithological units were recognized and correlated across both sections (Fig. 2B). Each of the lithofacies extended laterally at least 150 m, as along-strike exposures were identified no farther than 50 m north from Stadion CC-1 and 300 m south from Stadion CC-2. Thus the horizontal size of the structure is interpreted to be larger than 150 m and less than 300 m.

Facies Types

A combined analysis of the sedimentary composition and main fossil contents of the seven lithological units showed that each unit corresponds to a distinctive facies type (Figs. 2B, 3–4). Table 1 provides a summary of the most relevant characteristics of the facies and their respective fossil contents.

FIG. 2.—Measured sections. A) Composite section through the Samarinda sequence which preserves the Miocene progradation of the Mahakam Delta System. B) Detailed sections through the Stadion patch reef showing correlations between units. Details of lithology indicated alongside. For paleoenvironmental interpretations see Figure 11.

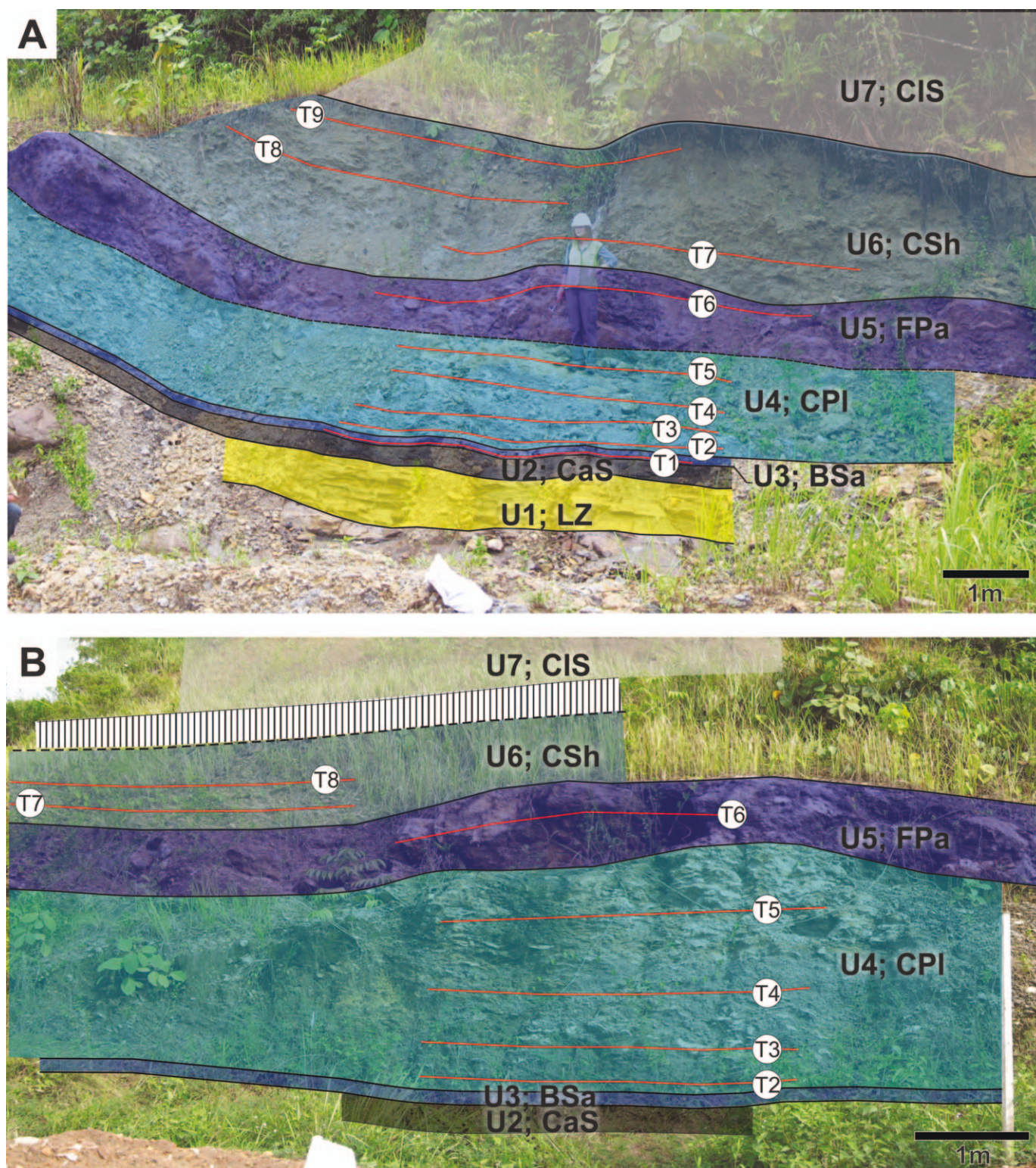


FIG. 3.—Outcrops of the Stadion coral carbonate sections showing lithological units (U1 to U7) and facies. **A)** Locality Stadion CC-1. **B)** Locality Stadion CC-2. Laminated siltstone = LZ; carbonaceous shale = CaS; bioclastic sandstone = BSa; coral platestone = CPI; foraminiferal packstone = FPa; coral sheetstone = CSh; clay shale = CIS. Red contours indicate line transects (T1 to T9).

Laminated Siltstone Facies.—This facies is characterized by a laminated siltstone with thin mudstone layers (3–10 mm) and occasional ripple marks (Fig. 4A). The laminated siltstone facies can be recognized in lithological Unit 1. The lower part of the unit is intensely bioturbated.

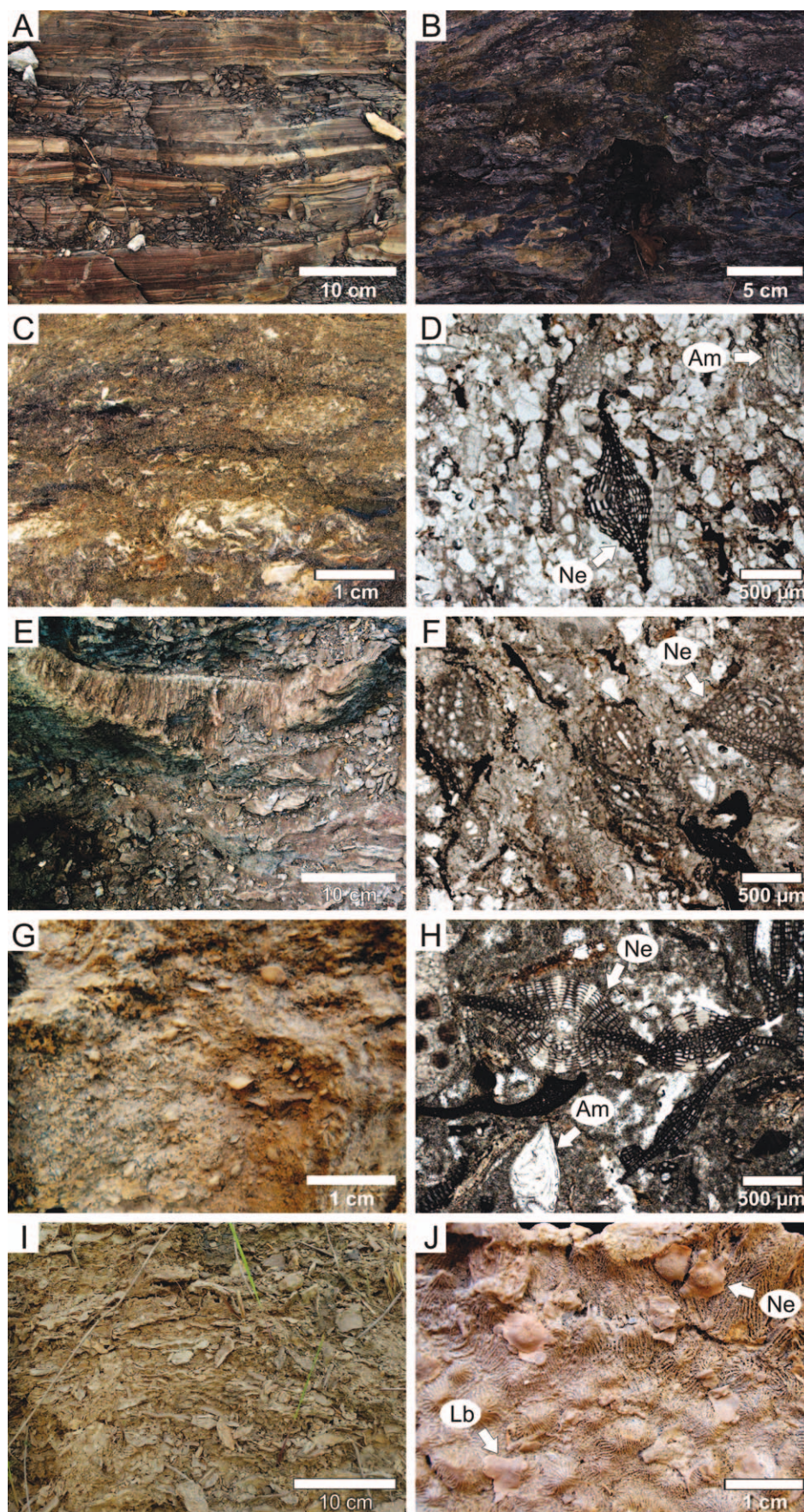
Toward the top, the siltstone alternates with fine-grained sandstone beds and thin carbonaceous shale layers (< 1 cm). Invertebrate fossils are absent. The exposed facies is about 1 m thick in both sections, with its base covered.

TABLE 1.—Principal characteristics of the Stadion coral carbonates, including facies types, lithologies, and main fossil groups.

Unit	Facies type	Lithology	Foraminifers	Corals	Coralline algae	Bryozoans	Mollusks
7	CIS	Fossil barren clay-shale	Absent	Absent	Absent	Absent	Absent
6	CSH	Coral sheetstone within a clay-rich matrix	Dominance of elongated forms of <i>Lepidosemicyclina bifida</i> (37%), followed by <i>Amphistegina</i> (30%) and <i>Nephrolepidina</i> (29%). <i>Operculina</i> , <i>Cibicoides</i> , and <i>Elphidium</i> common in finer fraction; Planktonic foraminifera increase from base to top (<1 to 11%)	Main carbonate-forming group. Highly diverse, 56 species, and well-preserved specimens. Mainly thin-plate corals of <i>Porites</i> sp. 1 (41%), and the agariciids <i>Leptoseris</i> spp. (17%). Most colonies are 1 to 5 mm thick; n=3042	Very abundant crusts, mainly <i>Neogoniolithon</i> spp. (80%) and other mastophoroids, encrusting corals, some protuberant, and some forming foragaliths; n=25	Twenty-eight species. Mostly encrusting (78%) the under surfaces of platy corals as large colonies, up to 10 cm width; <i>Steginoporella</i> sp. (27%) is the most common species. Among the erect forms (22%), with <i>Vincularia</i> spp. (11%) as the most common species; n=695	Two fragments of oysters and one gastropod <i>Angaria</i> sp. Poorly preserved specimens; n=3
5	FPA	Foraminifera packstone	Main carbonate-forming group. <i>Nephrolepidina</i> (63%) dominate. Subordinate <i>Amphistegina</i> (19%) and <i>Lepidosemicyclina</i> (12%). <i>Cycloclypeus</i> present, but in low abundances (3.5%); Planktonic foraminifera absent	Low abundance, very recrystallized, and low species richness, mainly represented by the genus <i>Porites</i> in massive (44%), ramose (30.5%) and platy (10%) forms; n=16	Low abundance, very recrystallized, hard to identify, some <i>Lithophyllum pseudoamphiroa</i> ; n=4	Absent	Absent
4	CPI	Coral platestone	High diversity. Dominance of <i>Nephrolepidina</i> (45%) and <i>Amphistegina</i> (39%). Some <i>Lepidosemicyclina</i> (13%); No planktonic foraminifera	Main carbonate-forming group. Forty-eight species in 43 genera. Thin-plate forms decreased from the base (82%) to the top (27%); in the middle part, platy-tabular <i>Porites</i> sp.1 (24%) and <i>Progyrosmilia</i> sp. 2 (23%), and small massive <i>Porites</i> sp. 3 (33%) dominate. At the top, phaceloid <i>Galaxea</i> spp. (15%) and ramose <i>Porites</i> sp. 2 (10%) become more abundant; n= 1471	<i>Neogoniolithon</i> sp., <i>Hydrolithon</i> sp. and thick crusts of <i>Spongites</i> encrusting corals, partly with forams; n=6	Absent	Eighteen taxa, including 14 genera. Mostly herbivore gastropods (52%), followed by suspension feeders (28%). Poorly preserved specimens, yet identifiable; n=79
3	BSa	Bioclastic packstone	Low diversity. Smaller and robust forms of <i>Amphistegina</i> (47%) and <i>Nephrolepidina</i> (39%) dominate. A few <i>Lepidosemicyclina</i> (12%); Planktonic foraminifera present (2%)	Absent	Absent	Absent	Gastropods, including <i>?Calliostoma</i> sp. Poorly preserved; n=4
2	CaS	Carbonaceous shale	Absent	Absent	Absent	Absent	Absent
1	LZ	Laminated siltstone interbedded with mudstone	Absent	Absent	Absent	Absent	Absent

Carbonaceous Shale Facies.—This facies is characterized by dominance of carbonaceous shale with occasional thin clay and silt layers (Fig. 4B). The carbonaceous shale of Unit 2 is 20 cm thick in Stadion CC-1 and 40 cm thick in Stadion CC-2. This unit has a sharp contact with the

laminated siltstone facies at the base and a gradual change into the mixed siliciclastic-carbonate facies toward the top. The carbonaceous content decreases upward as clay and silt content increases. Small pieces of amber were observed in the lower part of this unit.



Bioclastic Sandstone Facies.—This facies is characterized by larger benthic foraminifera and mollusk bioclasts in a predominantly moderate to well-sorted fine sand matrix, composed of a mix of subangular to subrounded fine-grained quartz. This facies occurs in Unit 3, which is a 20-cm-thick transitional bed of mixed siliciclastic and bioclastic carbonate components (Fig. 4C). Contacts at the base and the top are gradual. Compared to the underlying facies, the carbonaceous content is lower (<10%) while the average carbonate content is higher (36%). Larger benthic foraminifera comprise about 15% of the sediment (Fig. 4D). A few planktonic foraminifera were observed in the finer fractions (2%).

Coral Platestone Facies.—This mixed carbonate and siliciclastic facies is characterized by a coral framework with thick-platy corals that develop a platestone growth fabric (*sensu* Insalaco 1998). This facies can be recognized in Unit 4, where corals and other bioclasts occur in a gray matrix with an average of 45% CaCO₃ (Figs. 4E–F). The thickness of this unit is 1.1 m at the Stadion CC-1 and 3 m at the Stadion CC-2. The transition from the underlying bioclastic sandstone facies is gradual from sand to a silt-rich sediment matrix with abundant fossils. Corals constitute the main carbonate-forming component of this unit (60%–70%, Fig. 5). Most corals are densely packed in growth position, with their calicular surfaces facing upward and bioclastic sediment in the interstices (Fig. 4E). Relative abundances of the different coral growth forms change from the base to the top of the unit (Fig. 5). Corals first appear in transect 2 (Fig. 5), mainly as thin-platy forms (1 to 7 mm thick) and delicate ramose corals (1 to 6 mm in diameter). More robust forms are abundant in the middle of this unit, including ramose corals (up to 16 mm in diameter), platy-tabular (4 to 7 cm thick), and small massive forms (10 to 15 cm high). At the upper part of the unit, the growth fabric consists of relatively similar proportions of small massive (21.2%), phaceloid (17%), and platy-tabular corals (16.4%) (Fig. 5). Larger benthic foraminifera appear as a subordinate component (10%) within the siliciclastic matrix. Coralline algae occur in low abundances (5%), mainly as encrusting plants. The majority of mollusks recovered from the Stadion CC belong to this unit. Some echinoid spines were also observed within the sediments.

Foraminiferal Packstone Facies.—This facies is characterized by packstone dominated by larger benthic foraminifera (Figs. 4G–H). It occurs in Unit 5 with relatively uniform thickness of 1 m at Stadion CC-1 and 1.2 m at Stadion CC-2. It has the highest carbonate content (72%). The contacts with the units below and above are sharp. Corals were observed as a subordinate component (15%), preserved in growth position, and evenly distributed among thin-platy, massive, tabular, and ramose forms. From the base to the top, no changes in the fossil assemblages were observed. Coralline algae, *Halimeda* fragments, echinoid spines, and entirely recrystallized gastropods occur as minor components.

Coral Sheetstone Facies.—This facies is characterized by dominant thin-platy corals forming a sheetstone fabric (*sensu* Insalaco 1998). It occurs in Unit 6 where corals are the main component (40%–60%) of this mixed carbonate-siliciclastic bed (Fig. 4I). The thickness is 1.6 m at Stadion CC-1 and 1.8 m at Stadion CC-2. Carbonate content within the sediment matrix averages 30%, decreasing from 40% to 11% upsection. The upper part of the unit is characterized by a decline in coral

abundance. Among the corals, thin-platy forms dominate (65%–95%). These thin-platy corals are mostly 1–5 mm thick, and densely packed in growth position. Platy-tabular corals (30%) up to 3 cm thick were also observed, mainly toward the top of the bed, and some clusters of branching corals were sparsely distributed along the transects. The siliciclastic sediment matrix is yellow and clay-rich with abundant larger benthic foraminifera (20%–30%). Crustose coralline algae occur in low proportions (5%), mainly encrusting corals together with foraminifera (Fig. 4J). Bryozoans are commonly found encrusting the under surfaces of thin-platy corals, colonizing 27% of the corals. Sparse cidaroid echinoid spines, gastropods, and fragments of bivalves also occur.

Clay-Shale Facies.—This facies is dominated by clay and devoid of fossils. It occurs in the uppermost exposure of Unit 7 at the Stadion CC sections. Although the top of the outcrop is covered by vegetation with no other deposits exposed, several hundred meters of thick deltaic sandstones are visible further up the section (Cibaj 2009).

Fossil Assemblages

Rich fossiliferous biofacies are characteristic in the four middle facies of the Stadion sections, including the coral-dominated facies (coral platestone and sheetstone) and foraminifer-dominated facies (bioclastic sandstone and foraminiferal packstone). The other facies are barren in fossils. Percentages of abundance for the five main fossil groups studied in the Stadion sections are illustrated in Figure 5 and principal taxa are summarized in Table 1. Most fossil taxa recovered from the Stadion CC sections have complete or partial calcitic skeletons with higher potential of preservation, such as coralline algae (Bosence 1991), foraminifera (Lowenstam and Weiner 1983), octocoral sclerites (Bayer and Macintyre 2001), echinoderm spines (Su et al. 2000), and polychaete tubes (Vinn et al. 2009), among others. Even though scleractinian corals deposit aragonitic skeletons, those were recrystallized and transformed from original aragonite into secondary calcite as it is commonly found in corals older than Pleistocene age (Constantz 1986; McGregor and Gagan 2003; Reuter et al. 2005).

Corals.—A high richness of coral species was recorded from the studied sections (Table 1; Fig. 6). A total of 69 species belonging to 41 genera were identified from the 4686 studied specimens. They include 66 species from 38 genera of scleractinians. Other taxa were the hydrozoan *Millepora* sp., and the octocorals *Heliopora* sp. (Fig. 6G) and *Isis* sp. (see Supplementary Data, Appendix A). A few octocoral sclerites (3–5 mm long) were also recovered. A small percentage of the specimens (<1%) could not be identified. The 157 specimens collected from the outcrop surface only yielded two additional taxa, *Leptoseris* aff. *mycetoseroides* and *Lobophyllia* sp. The latter two taxa could not be assigned to any specific facies so were left out of the statistical analyses.

Statistical ordinations showed that the coral assemblages were significantly different between the coral sheetstone and coral platestone facies (Fig. 7; ANOSIM $R = 0.278$, $p\text{-value} = 0.022$) but not between the Stadion CC-1 and Stadion CC-2 sections ($R = 0.078$, $p\text{-value} = 0.206$). External morphological features of corals were well preserved in the coral platestone facies allowing taxonomic identifications. Internal microstructures of coral skeletons were highly recrystallized and some specimens have a friable consistency. The reconstruction of the coral succession

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FIG. 4.—Lithofacies characteristic of the Stadion patch reef. **A**) Laminated siltstone. **B**) Carbonaceous shale. **C**) Bioclastic sandstone. **D**) Micrograph of bioclastic sandstone thin section showing well sorted fine-sand and larger benthic foraminifera. **E**, **F**) Coral platestone. **E**) Large tabular colony of *Progyrosmilina* sp. **F**) micrograph of thin section showing *Nephrolepidina ferreroti*. **G**, **H**) Foraminiferal packstone. **H**) Micrograph of thin section showing *Nephrolepidina* and *Amphistegina*. **I**, **J**) Coral sheetstone showing multiple stacks of thin platy coral colonies. **J**) Detail of larger benthic foraminifera encrusting on coral surface of a *Pavona* sp. Common larger benthic foraminifera include *Nephrolepidina* = Ne, *Amphistegina* = Am, and *Lepidosemicyclina bifida* = Lb.

species from the underlying foraminiferal packstone facies were present in the coral sheetstone facies.

Foraminifera.—In the coarser fractions (0.5–2 mm and >2 mm), assemblages of larger benthic foraminifera varied among the lithofacies (Table 1, Fig. 5; Supplementary Data, Appendix B). Ordination analyses showed two distinctive groups (Fig. 7B), a first one preserved in the bioclastic sandstone, coral platestone, and foraminiferal packstone facies and a second group found in the coral sheetstone facies (ANOSIM $R = 0.706$, p -value = 0.001). No significant differences were found between the two Stadion CC sections (ANOSIM $R = 0.461$, p -value < 0.001). Small and robust forms of *Amphistegina* and *Nephrolepidina* (Fig. 8A) dominated in the bioclastic sandstone facies, with rare occurrences of thin and flatter *Lepidosemicyclina*. In the coral platestone facies richness increased slightly, with *Amphistegina* and *Nephrolepidina* still dominant, albeit with increased abundance of *Lepidosemicyclina*, and subordinate *Operculina*. Although very abundant, they were less rich in the foraminiferal packstone facies than in the coral platestone facies, and again contained abundant *Amphistegina*, with subordinate *Nephrolepidina* and *Lepidosemicyclina*. In the uppermost fossiliferous unit, the coral sheetstone facies, there was an abrupt change in larger benthic foraminifera composition as *Lepidosemicyclina bifida* (Fig. 8C) became the most abundant taxon with subordinate *Nephrolepidina* (e.g., Fig. 8A), *Amphistegina* and *Operculina*, and rare occurrences of flat discoidal *Cycloclypeus annulatus* (Fig. 8B).

Among the 125 μ m fractions recovered from the bulk samples, benthic foraminifera were present in the bioclastic sandstone, coral platestone, and coral sheetstone facies, but absent from the clay-shale facies (see Supplementary Data, Appendix C). In general, foraminiferal tests were poorly preserved and taxonomic identifications were only possible at the genus level. Six taxa were identified, from which *Amphistegina* spp. (Fig. 8D) were the most abundant, followed by *Operculina* spp. (Fig. 8E), *Elphidium* spp. (Fig. 8G), and *Cibicidoides* spp. (Fig. 8H). Small differences could be noticed among the facies types: abundances of *Cibicidoides* and *Elphidium* increased from frequent at bioclastic sandstone and coral platestone facies, to common in coral sheetstone facies. Similarly, miliolids (Fig. 8F) were rare in the bioclastic sandstone and coral platestone facies but common in coral sheetstone facies. Samples from the coral sheetstone facies were moderately well preserved and contained the highest benthic foraminiferal richness.

Coralline Algae.—Abundances, growth forms, and groups commonly associated with coralline algal assemblages in the successive carbonate units are shown in Table 1 and detailed data per taxon in the Supplementary Data, Appendix D. Coralline algae were present as a subordinate component in the coral platestone, foraminiferal packstone, and coral sheetstone facies. Abundances were higher in coral platestone and coral sheetstone facies, mainly encrusting corals, forming foralgaliths, and also as fragments within the matrix (Fig. 5). Assemblages and growth forms of coralline algae did not vary significantly between the coral-dominated facies, but both were characterized by abundant mastophoroids (Fig. 9), mainly *Neogoniolithon* spp. (Figs. 9A–B). In the foraminiferal packstone facies, coralline algae were less abundant and very recrystallized, limiting taxonomic identification.

Bryozoans.—Although bryozoans were restricted to the coral sheetstone facies (Table 1, Fig. 5), they included 28 species, with 3 cyclostomes, 25 cheilostomes (9 anascan-grade and 16 ascophoran-grade species), and rare ctenostome borings visible on the undersurfaces of corals (see Supplementary Data, Appendix E). Species richness and specimen abundance was very similar in the two sections: 25 species (302 specimens) at the Stadion CC-1 and 24 species (393 specimens) at the Stadion CC-2. Twenty-one of the species that occur in both sections were the most abundant taxa. In contrast, the four species found exclusively in Stadion CC-1 and the three species unique to Stadion CC-2 were represented by a

few or even a single colony. The dominant taxa among erect colonies were the articulated anascan *Vincularia berningi* (11%) and the fenestrate ascophoran *Triphyllozoon* sp. (7%), both found as scattered fragments and as specimens cemented to coral surfaces and a few colony bases. Among encrusters the anascans *Steginoporella* sp. (27%; Fig. 10B), *?Crassimarginatella* sp. (3%), *Cranosina rubeni* (Fig. 10A), *Antropora* cf. *subvespertilio* (Fig. 10D), the cribrimorph *Puellina* spp., and the ascophorans *Reptadeonella* sp. A (Fig. 10C) and *Hippopodina* cf. *feegeensis* (5%) usually developed large colonies on coral undersides; only a few specimens were observed encrusting the surfaces of ramose corals. Unidentifiable cheilostome species accounted for 33% at Stadion CC-1 and 17% at Stadion CC-2, mainly represented by fenestrate phidolopodid fragments.

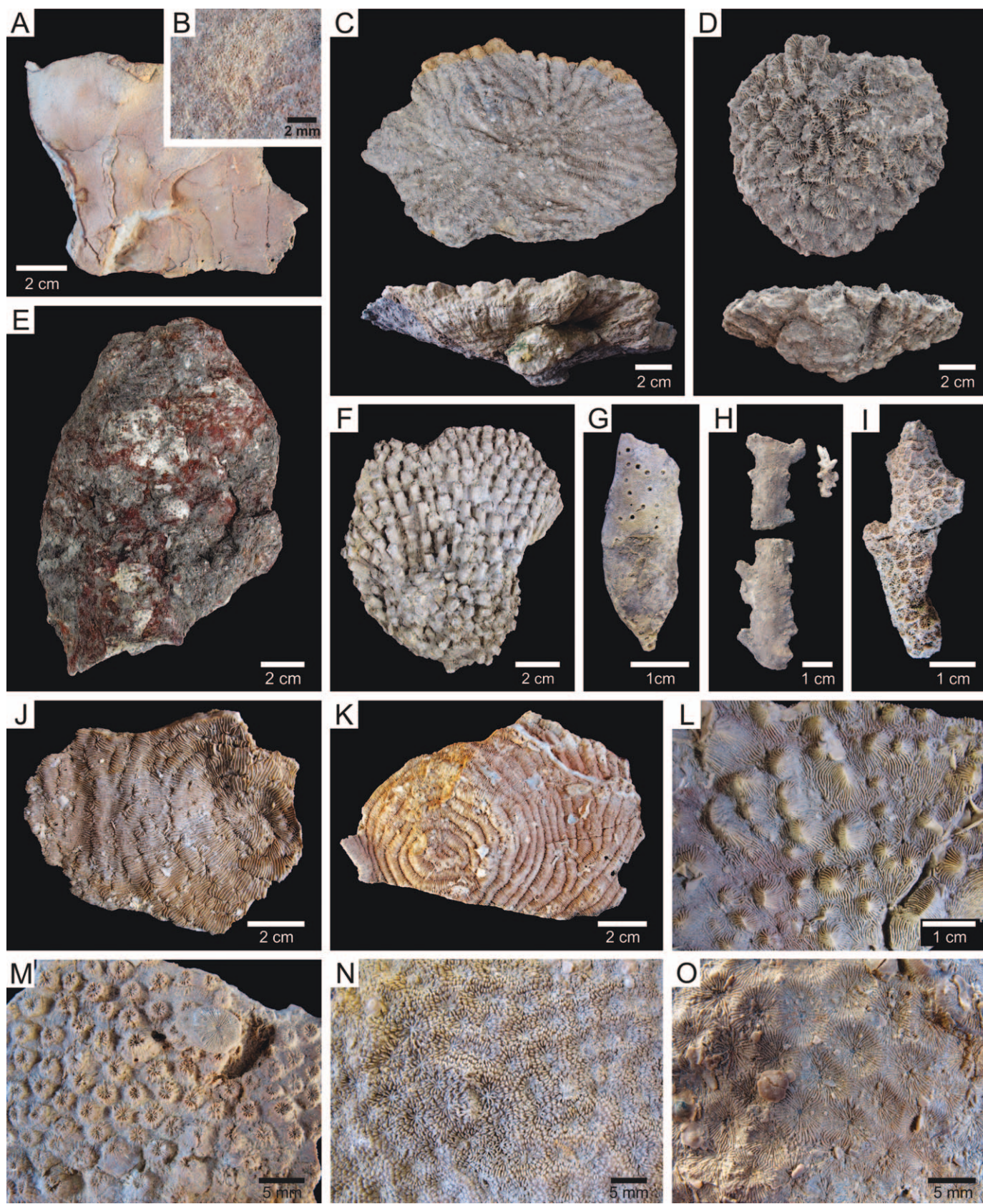
Most taxa were encrusters (78%), typically two-dimensional colonies of low relief. The remaining 22% of the species were erect, mostly flexible because of jointing and anchored to a substrate by rootlets, or rigid fenestrate with a cemented base. A single ctenostome species occurs as borings in the corals. Almost the same proportions of growth forms occur in terms of specimen abundance: 81.6% of specimens were encrusters, 18.3% were fragments of erect species, and only one specimen (0.1%) was boring a coral substrate (Fig. 5).

Mollusks.—Eighty-six poorly preserved specimens were recovered, including representatives of three bivalve families and at least eleven gastropod families (see Supplementary Data, Appendix F). Aragonitic mollusks are rare and mainly represented by very small, incomplete, and highly recrystallized shells. Gastropods with an outer calcitic shell layer and/or relatively thick shells (e.g., Trochidae and Turbinidae; Gainey and Wise 1980; Beesley et al. 1998) are comparatively common in the Stadion CC sections. The majority of bivalves present at the studied sections are epifaunal taxa that aggregate calcitic foliated, and therefore relatively hard and chemically resistant shells (Kennedy et al. 1969; Taylor and Layman 1972).

Most mollusks were recovered from coral platestone facies, in which 92% of the total number of specimens were collected. Bivalves are predominately preserved as fragments and include oysters (e.g., *Lopha, sensu lato*), pectinids, and one specimen of the Lucinidae *?Anodontia (Pegophysema)*. The most common gastropod families are Turritellidae ($n = 13$), Trochidae (*?Euchelus* sp., $n = 12$), and Turbinidae (*Astraea* sp., $n = 6$; opercula of two species). Other identifiable families include Cerithiidae, Scaliolidae, Rissoidae, Iravadiidae, Triphoridae, and Pyramidellidae, each with very low abundances ($n < 4$). Gastropods are represented by herbivores, suspension feeders, and parasites (Fig. 5). Predatory taxa are entirely lacking, although they are dominant in modern reef-associated gastropod faunas (Taylor 1977) due to the preservation constraint.

DISCUSSION

Most of the fossils found in the Stadion sections are light-dependent benthic taxa, including zooxanthellate corals, larger benthic foraminifera, and coralline algae, that lived as distinct communities during deposition of bioclastic sandstone, coral platestone, foraminiferal packstone, and coral sheetstone facies (units 3 to 6), indicating that in those settings light reached the benthic environment. The varying composition of the communities in these facies may suggest a variation in light levels, most likely related to changes in depth and/or alterations in terrestrial input (Perrin et al. 1995; Wilson 2005, 2012; Bassi and Nebelsick 2010; Novak et al. 2013). Terrigenous input can drive the response of light-dependent biota through: (1) the amount of siliciclastic input; (2) the frequency of input (i.e., constant or episodic); (3) grain size; and (4) associated nutrient input (Sanders and Baron-Szabo 2005; Wilson 2005; Lokier et al. 2009). Disentangling the role of each factor involved with terrigenous input is difficult, as each interacts with other factors, such as depth and hydrodynamic regimes, to produce similar effects on the amount of light



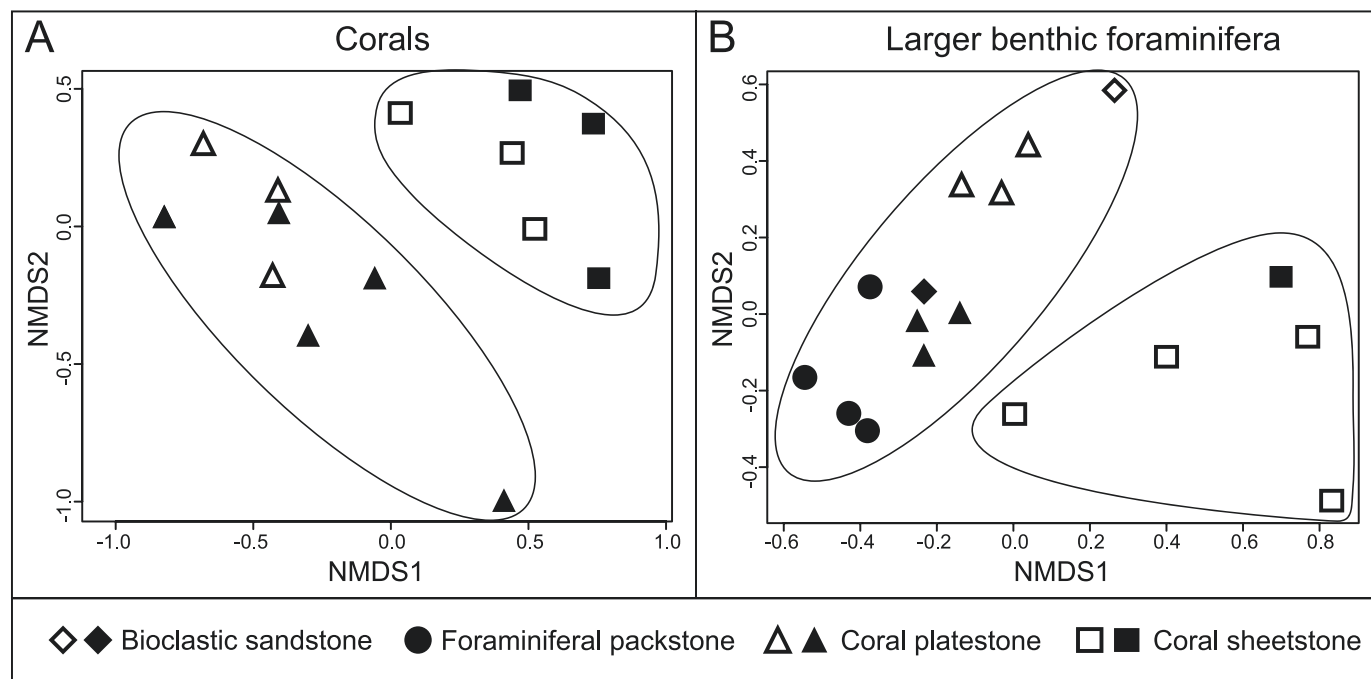


FIG. 7.—Nonmetric multidimensional scaling analysis of fossils from the study interval. A) Coral assemblages. B) Larger benthic foraminiferal assemblages. Open symbols correspond to Stadion CC-1 and filled symbols to Stadion CC-2.

available to the benthic community. Thus, paleoenvironmental interpretations based on the light-dependent components of Stadion communities are relative and require independent evidence to verify. In this study, the growth forms and taxonomic composition of fossil assemblages were analyzed because these two aspects are key to interpret paleoenvironments, as has been shown in previous studies for scleractinian corals (Perrin et al. 1995; Pandolfi 1996; Perrin 2000; Klaus et al. 2008; Johnson et al. 2009), larger benthic foraminifera (Hallock and Glenn 1986; Hottinger 1997; Hohenegger et al. 1999; Renema and Troelstra 2001), and coralline algae (Bosence 1983; Perrin et al. 1995; Braga et al. 2009).

Facies Interpretation and Paleoenvironmental Evolution

The Stadion CC were deposited during a transgressive interval within a 3-km-thick section of alternating shallow marine, deltaic, and fluvial deposits that accumulated between 16 and 11 Ma (Marshall et al. 2015). The observed geometry and lateral continuity of the deposits that extend at least 150 m between the two studied sections suggests that the Stadion CC could have developed as a low-relief patch reef (Moss and Chambers 1999; Wilson 2005). The main factors controlling this patch reef were most likely depth and episodic variation in the nature and rate of terrigenous sedimentation (Fig. 11).

At the base of the Stadion CC sections, the lack of marine fossils in the laminated and occasionally rippled siltstone and fine-grained sandstone facies suggests a low-energy depositional environment within a delta-plain setting (Allen and Chambers 1998). Increase in marine influence

leading to the development of coastal swamps or estuarine mangrove environments can be inferred from the appearance of thin carbonaceous layers, first occasionally at the top of the laminated siltstone facies and becoming more abundant until they form the distinctive carbonaceous shale facies (Figs. 11A–B). The first occurrence of larger benthic foraminifera marks the transition into a fully marine environment, characterized by deposition of bioclastic sandstone (Fig. 11C). The foraminiferal assemblage in the bioclastic sandstone facies, dominated by smaller and robust specimens of *Amphistegina* and *Nephrolepidina* with subordinate miogypsinids and *Operculina*, supports the interpretation of shallow-water conditions and an increase of energy levels in the environment (Hallock and Glenn 1986). Similar communities of foraminifera occur in the subsequent coral platestone facies, although smaller and more robust forms decrease, and slightly thinner and elongated forms increase, upsection.

Corals are preserved in growth position in the coral platestone facies indicating autochthonous deposition and fully marine conditions. The platy morphology of corals has been recognized as an adaptation to low-light environments (Rosen et al. 2002; Sanders and Baron-Szabo 2005) that could have resulted as a response to terrigenous input, consistent with the silty siliciclastic matrix of the facies. Although significant, the overall siliciclastic input was low as indicated by the robustness of platy-tabular and small massive colonies (Figs. 6C–E, 11D); in addition, relatively constant sedimentation rates are likely as the corals present no signs of partial mortality during development. The subsequent appearance of phaceloid and ramose morphologies toward the top of the coral

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FIG. 6.—Representative corals from the Stadion patch reef. A, B) *Porites* sp.1, NHMUK AZ6718, from the coral sheetstone facies. A) Fragment of a platy colony of *Porites* sp. 1 and B) detail of corallites. C–H) Some corals from the coral platestone facies. C) *Progyrosmilia* sp., NHMUK AZ6575. D) *Symphylia recta*, NHMUK AZ7214. E) *Porites* sp. 3, NHMUK AZ7238. F) *Galaxea* sp., NHMUK AZ6477. G) *Heliopora* sp., NHMUK AZ7230. H) *Acropora* sp. *elegans* group, NHMUK AZ7302. I–O) Some corals from the coral sheetstone facies. I) *Goniopora planulata*, NHMUK AZ6606. J) *Leptoseris* sp., NHMUK AZ7329. K) *Pachyseris* sp. 4, NHMUK AZ6722. L) *Pavona* cf. *varians*, NHMUK AZ7351. M) *Cyphastrea* sp., NHMUK AZ6979. N) *Psammocora* sp., NHMUK AZ7159. O) *Coscinaraea* sp., NHMUK AZ6833.



FIG. 8.—Representative foraminifera from the Stadion patch reef. Common foraminifers from the coarse fraction (> 0.5 mm) include **A**) *Nephrolepidina martini*, **B**) *Cycloclypeus annulatus*, and **C**) *Lepidosemicyclina bifida*. Foraminifers from the fine fraction (> 125 µm to 0.5 mm) include **D**) *Amphistegina* sp., **E**) *Operculina* sp., **F**) miliolid, **G**) *Elphidium* sp., and **H**) *Cibicidoides* sp.

platestone facies can be indicative of an environment with relatively higher sedimentation rates of silt-size siliciclastics (Perrin et al. 1995; Sanders and Baron-Szabo 2005). The initial stage of the coral platestone facies was characterized by low coral abundances (< 10%) and dominance of thin-platy forms (Fig. 5), suggesting plausible constratal

framework (Insalaco 1998) with corals barely exceeding the rates of siliciclastic deposition. Once this pioneer coral community was established, the framework may have become partially suprastratal as suggested by higher abundances of corals arranged with more colony intergrowth and the appearance of small massive and branching growth

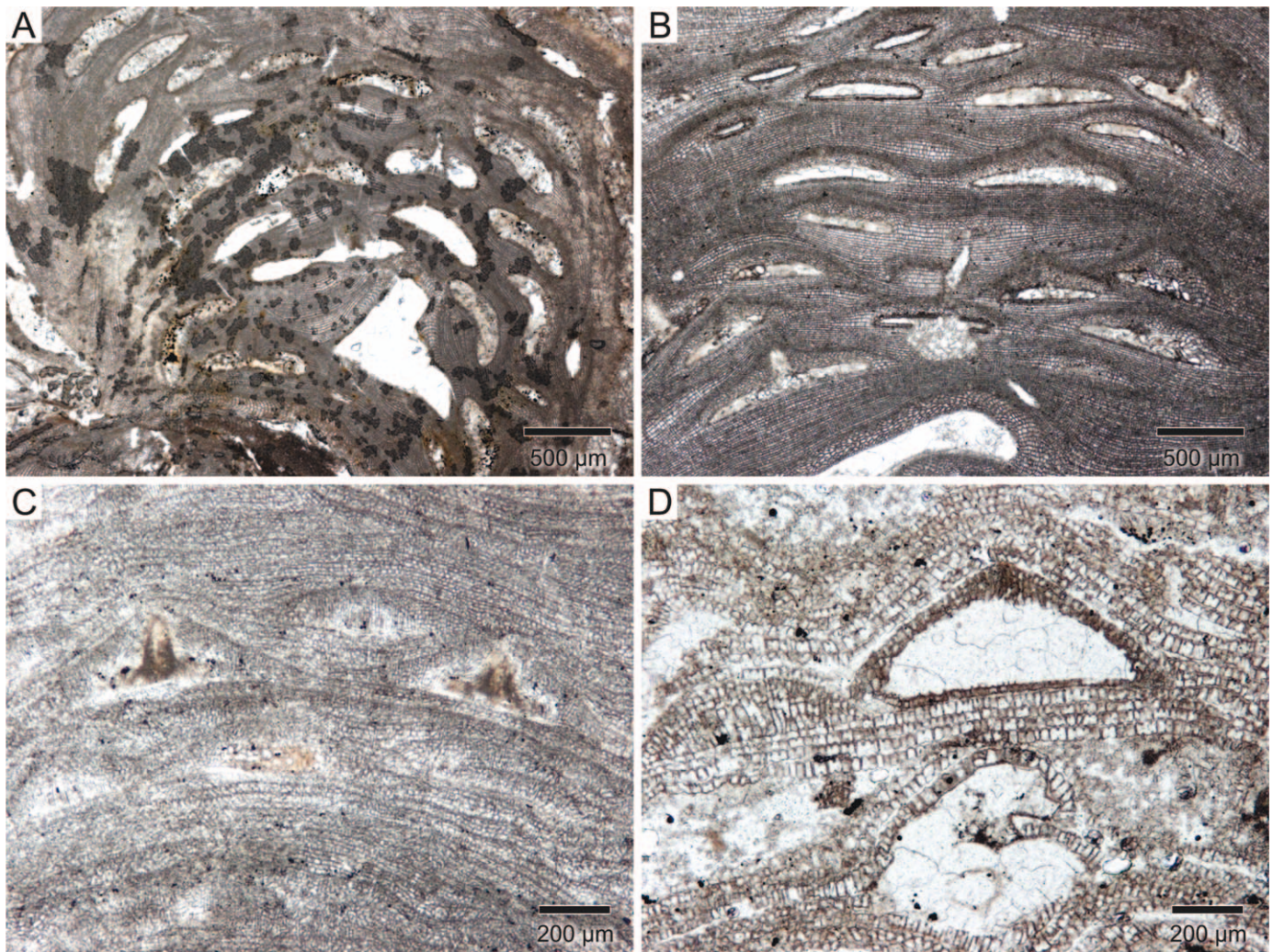


FIG. 9.—Representative crustose coralline algae of the Stadion patch reef. A) *Neogoniolithon* sp., AR274-3. B) *Neogoniolithon fosliei*, AR262-1. C) *Spongites* sp., AR267-1. D) *Lithoporella* sp., AR263D-1.

forms (Insalaco 1998). However, any growth above seafloor was limited to a few decimeters, resulting in the relatively flat parallel geometry of the bed after compaction. Gastropods from the coral platestone facies such as Turbinidae, Trochidae, Cerithiidae, and Turritellidae are typical inhabitants of reefs and other shallow marine habitats (Taylor 1968; Héros et al. 2007). The absence of encrusting bryozoans in the coral platestone facies, despite the abundant offer of coral substrates for their colonization, can be explained as a preservation issue due to the cementation of sediments on coral surfaces, as it has been suggested by Taylor and Di Martino (2014).

Coralline algal assemblages provide the most reliable signal for an interpretation of paleodepth for the coral platestone facies. Mastophoroids are well-known components of the algae communities that live on shallow parts of modern coral reefs, mainly in the first 30 m depth (Adey 1986; Minnery 1990; Verheij and Erftemeijer 1993; Iryu et al. 1995). Relatively high abundance of thick crusts of members of the subfamily Mastophoroideae (such as *Neogoniolithon* and *Spongites*) has also been well constrained to shallow-water environments in tropical Miocene reefs (Perrin et al. 1995; Braga et al. 2009, 2010). While the paleodepth interpretation of coralline algae with affinity for low light is ambiguous, the photophilic (high-light affinity) property of thick mastophoroid

species constitutes an unequivocal indication of a shallow paleodepth for the coral platestone facies. High sediment input rates have characterized the Kutai Basin since its early formation (van de Weerd and Armin 1992; Allen and Chambers 1998). In the modern Mahakam delta-front system water transparency is very low, with Secchi disc estimation at maximum of 13 m depth (Budhiman et al. 2012), due to high quantities of suspended sediments (Storms et al. 2005). Therefore, by analogy to modern conditions around the Mahakam delta, the co-occurrence of mastophoroids and platy coral communities within a terrigenous-rich matrix suggests that coral development took place at a few meters depth, likely less than 10 m depth. The abrupt transition from the coral platestone facies to the foraminiferal packstone facies may indicate an increase in clastic sedimentation past the tolerance level of coral species (Fig. 11E).

In the foraminiferal packstone facies, the dominance of flatter forms of *Nephrolepidina* combined with the presence of *Cycloclypeus* suggests a decrease of light levels, most likely due to a depth increase (Hallock 1981; Hallock et al. 1986; Renema 2006). This increase in turbidity was not likely to have been caused by increased nutrient input, as elevated CaCO_3 content of the foraminiferal packstone facies suggests continued low terrigenous input. Corals are the secondary component within this facies, providing additional evidence for a reduction in light levels. The presence

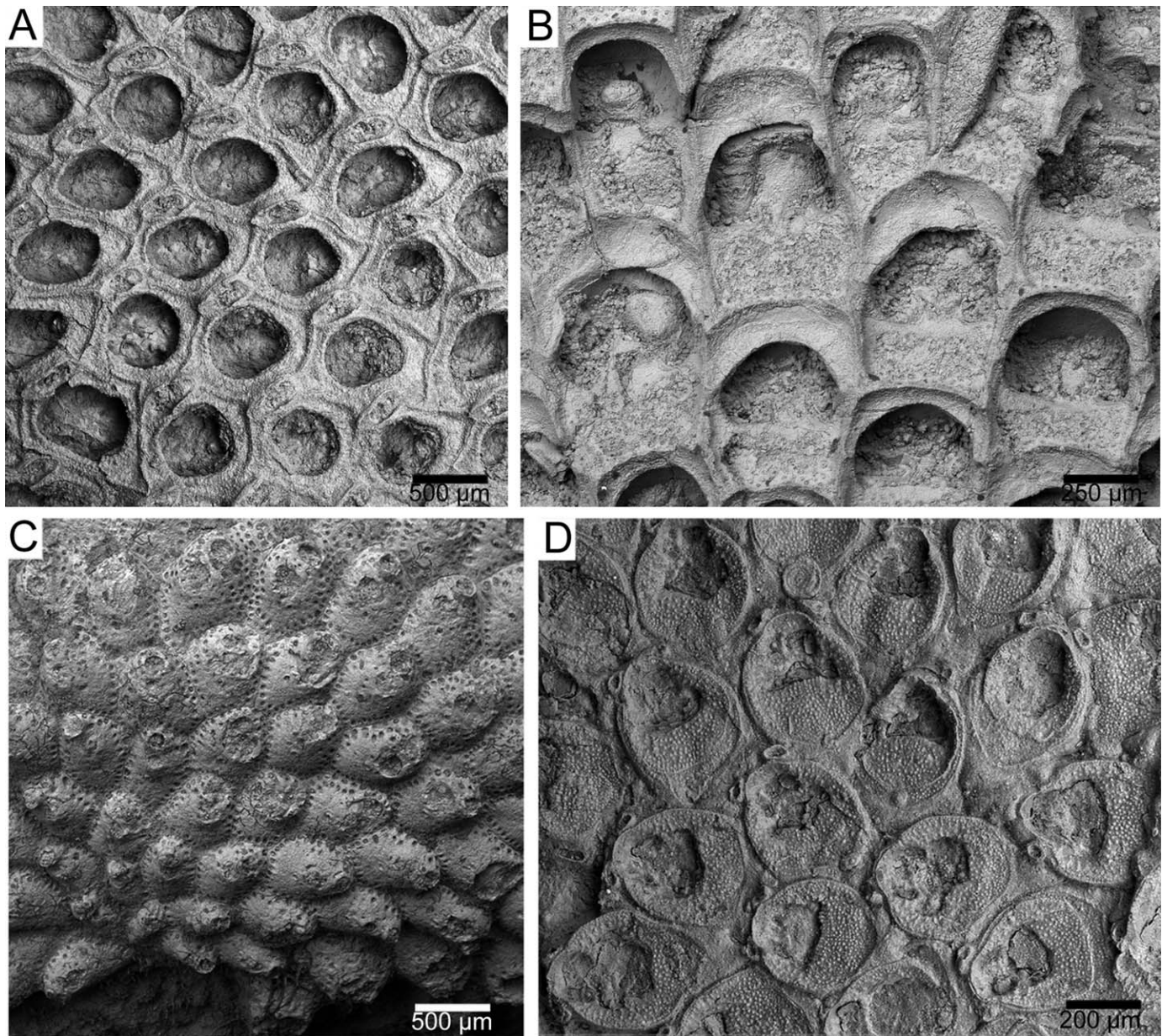


FIG. 10.—Representative bryozoans from the Stadion patch reef. A) *Cranosina rubeni*. B) *Steginoporella* sp. C) *Reptadeonella* sp. A. D) *Antropora* cf. *subvespertilio*.

of unidentifiable crustose corallines and fragments of geniculate corallines merely confirm that the foraminiferal packstone facies was deposited in the photic zone but cannot provide a more refined interpretation.

Subsequently, the recolonization of thin-plate corals in the coral sheetstone facies could be a response to a stabilized environment by larger benthic foraminifers and a change of the grain-size composition from silt to clay (Fig. 11F). Previous studies have shown that thin-plate corals are successful in turbid environments if the input contains finer fractions of sediments (Lokier et al. 2009). Flat forms are more common in the foraminiferal assemblage that is dominated by *Lepidosemicyclina bifida* and includes abundant *Amphistegina* and *Nephrolepidina*. It has been proposed that increased surface area to volume ratios provide a morphological response of foraminifera to facilitate the capture of light in low-light environments by symbionts (Hallock et al. 1986). On the other hand, corals in the coral sheetstone facies are typically thinner than

5 mm, suggesting that lower light availability occurred under conditions of clay input in comparison to the silt input that characterized the coral platestone facies. Corals growing at their tolerance limits can develop helical spiraling colony forms to maximize both light capture and ability to shed sediment (Rosen et al. 2002; Sanders and Baron-Szabo 2005). Ragged margins were observed in some thin-plate colonies (Figs. 6A, K), suggesting that episodic higher discharges of clay produced partial mortality, followed by regrowth during intervals of lower sediment stress (Sanders and Baron-Szabo 2005). Agariciids are among the most common corals of the coral sheetstone facies and provide more evidence for a turbid habitat. Agariciid corals are the principal inhabitants of many modern mesophotic reefs (Kahng et al. 2010), mainly associated with deep and clear waters in the Indo-Pacific (Maragos and Jokiel 1986), Red Sea (Fricke et al. 1987), and Caribbean (Reed 1985). In fact, *Leptoseris* species are the deepest-known zooxanthellate corals that live

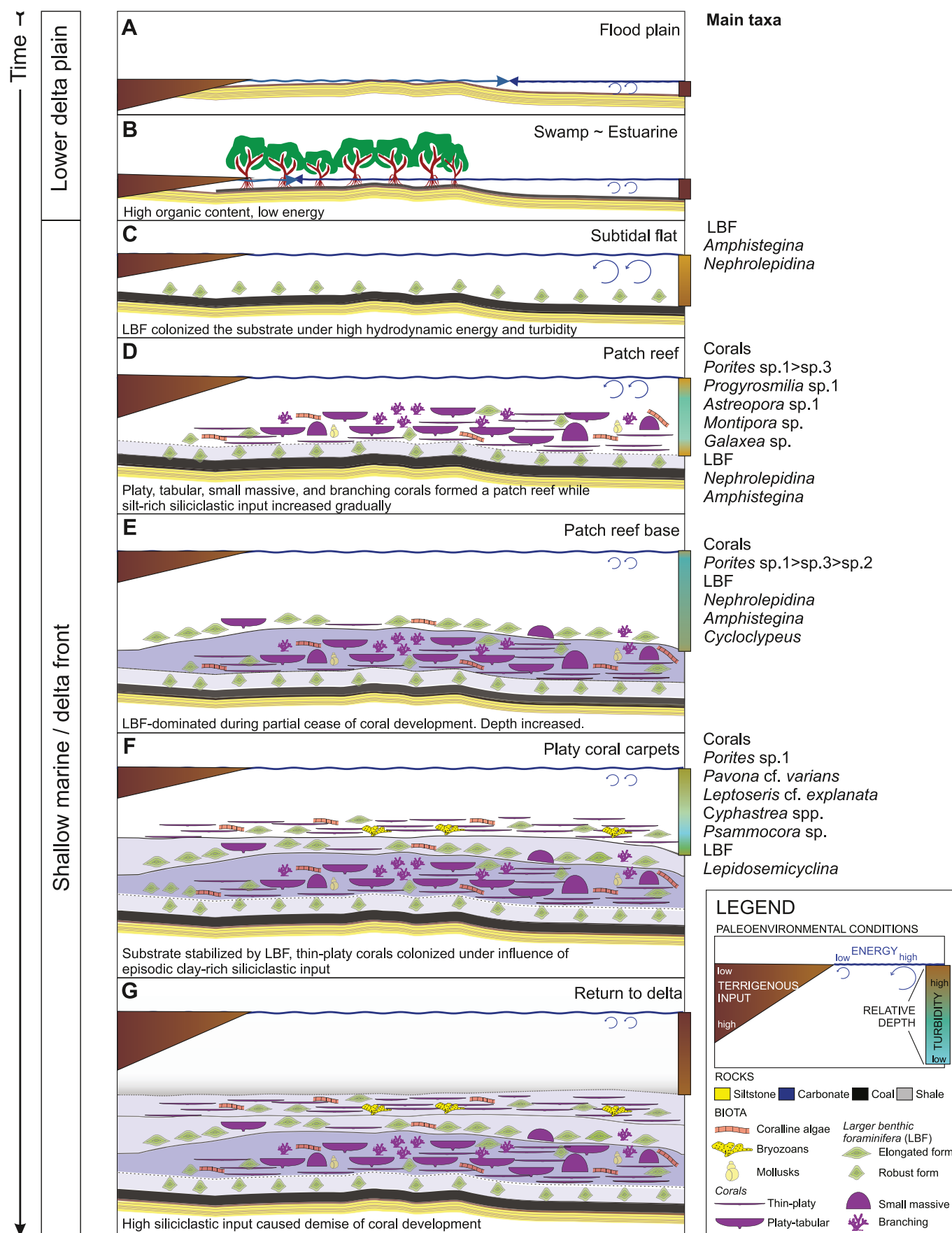


FIG. 11.—Interpretation of depositional environments of the Stadion patch reef.

today at depths of ~ 150 m (Kahng and Maragos 2006), suggesting that not only growth forms but also the taxonomic composition of coral communities in low-light environments could be analogous between turbid shallow waters, such as the Stadion CC habitats, and clear deep waters as in the modern examples. The coral community did not acquire ecological differentiation at this stage, but remained as thin veneers following the seafloor morphology, similar to coral carpets described elsewhere (Riegl and Piller 2000a, 2000b). The rich community of bryozoan epibionts preserved on the underside of agariciids and other taxa, indicates that corals may have grown suprastratally, even though the sheetstone facies was built almost entirely of thin-plate corals. Abundant larger benthic foraminifera and crustose coralline algae were observed partially overgrowing the calicular surfaces of thin-plate corals, suggesting significant partial mortality of the corals before burial. For some taxa, coral growth can be enhanced in turbid habitats (Edinger et al. 2000), and rapid growth allows colonies to survive high levels of partial mortality, promoting rapid accretion of coral carbonates in turbid environments (Perry et al. 2012). Higher nutrient input associated with episodic terrigenous influx can also be inferred at this stage, based on the proliferation of large encrusting colonies of filter-feeding organisms such as bryozoans (Moissette et al. 2007).

The abundance of mastophoroid corallines indicates relatively high light levels in this shallow habitat influenced by siliciclastics. Thus, thin-plate agariciid corals, elongated foraminifera, the occurrence of mastophoroid coralline algae, and a clay-rich matrix all suggest a habitat characterized by episodic high terrigenous input in calm waters at a paleodepth of approximately 10 m. The absence of fossils and any carbonate contents in the overlying clay-shale facies suggests an environmental shift that was intolerable for coral communities (Fig. 11G).

The laminated siltstone and carbonaceous shale were likely deposited within peat swamp or mangrove estuarine environments in a deltaic flood plain setting. In contrast, the bioclastic sandstone, coral platestone, foraminiferal packstone, and coral sheetstone developed on the delta front, probably at depths <10 m, and fully marine environmental conditions. The capping clay shale records the termination of marine-dominated habitats suitable for reef biota.

Diversity of Fossil Assemblages

Species richness varied among the studied fossil assemblages. Corals were the main carbonate-forming group as well as the most diverse group. The substrate provided by corals is likely to have enhanced overall diversity in the Stadion settings by hosting bryozoans, mollusks, and coralline algae. The bryozoan community had a medium diversity in comparison to other studied localities of Miocene age in East Kalimantan (Di Martino et al. 2015), yet did not contribute significantly to carbonate accretion. The record of mollusks in the Stadion section is biased due to a lack of aragonite preservation. Mollusks are typical of other Miocene reef successions in East Kalimantan. They also occur in other modern habitats and several fossil localities (Wright et al. 2003, and references therein). Larger benthic foraminifera were present in the greater number of fossil facies due to their higher ability to tolerate terrigenous input with respect to corals (Lokier et al. 2009) and because they are efficient colonizers of soft substrates (Hohenegger et al. 1999; Renema 2008). The taxonomic richness of larger benthic foraminifera of the Stadion CC is lower than clear-water faunas but is comparable to modern low-light marine environments of Indonesia (Renema and Troelstra 2001; Renema 2008). Higher richness in clear waters is probably due to increased habitat partitioning along an extended photic gradient (Hallock 1987; Renema and Troelstra 2001; Novak and Renema 2015). In this study, analysis of larger benthic foraminifera was used mainly as a paleoenvironmental proxy rather than as a diversity indicator. Even though coralline algae are important paleodepth indicators, in the Stadion patch

reef their abundance and diversity was relatively low and restricted to a few mastophoroids species and *Sporolithon* (Rösler et al. 2015). Therefore, discussion about diversity in the Stadion CC sections is focused on the richest taxa found represented by corals and bryozoans.

Corals.—The 69 coral taxa identified from these sections indicate that high coral richness could develop under turbid conditions in the Stadion CC. Of course, corals are smothered and die at high levels of terrigenous input (Van Woesik et al. 1999; Fabricius 2005), but these findings clearly show that below this lethal threshold, turbid environments can support rich coral communities over ecologically significant time scales. Likewise, the Stadion coral assemblages were not building large-scale high-relief reef structures, supporting the idea that high coral species diversity can be independent of reef development (Johnson et al. 2008). Thus, high siliciclastic input is a major control on the functioning of reef-coral communities even though a high diversity of coral species would be able to thrive under turbid conditions (Klaus et al. 2011).

The Stadion coral assemblages are the richest known for a Miocene setting in the Indo-Pacific. Previous records in the area (Wilson 2005; Lokier et al. 2009) include at least ten coral genera, one quarter the richness discovered in this study. In terms of species richness, the maximum number of species per locality recorded so far is 34 species in a middle Miocene site in Fiji (Bromfield and Pandolfi 2012), and 36 species for a Burdigalian patch reef located about 80 km to the north of the Stadion CC (Novak et al. 2013). Coral assemblages of late Oligocene age in similar mixed carbonate-siliciclastic settings in Sabah, Malaysian Borneo are also less rich, with a maximum of 37 genera per site (McMonagle et al. 2011; McMonagle 2012).

Comparisons of the Stadion patch reef assemblages with modern assemblages are complicated by the possibility of time-averaging processes inherent in any fossil assemblage (Pandolfi and Greenstein 1997; Pandolfi 2002). Although the richness of the Stadion assemblages could reflect a time-averaged effect, it is notable that the Stadion patch reef contains a similar number of species as communities living today in clear waters on the nearshore Great Barrier Reef, estimated to be around 60 species per site (Van Woesik et al. 1999), although a larger study of 135 reefs in the Great Barrier Reef system identified an average coral richness of 39.5 taxa per site (DeVantier et al. 2006). The Stadion patch reef is almost three times as diverse as coral assemblages currently growing under high river and tidal influence, in which observed average coral richness per site varied from 20 to 24 species per site (Van Woesik et al. 1999).

There are significant differences in the abundances of the dominant *Porites* species between the coral platestone and coral sheetstone facies (Fig. 7A). Studies on *Porites* species at the Great Barrier Reef have shown that colonies of this genus are able to tolerate long-term sediment input and low-light levels, in relatively calm waters for long periods of time (Stafford-Smith and Ormond 1992; Stafford-Smith 1993; Anthony 1999; Perry et al. 2009).

Acroporids are characteristic of the platestone facies, while agariciids are more common and diverse in the sheetstone facies (Table 2). Although acroporids are mainly known to prefer clear- and shallow-water habitats on modern reefs, some *Astreopora* and the *A. elegans*-group (Fig. 6H) species that are typical of the coral platestone facies are also known from low-light environments such as shallow turbid reefs and reef slopes (Wallace 1999; Veron 2000). A higher abundance and diversity of agariciids in the coral sheetstone facies, including *Pachyseris*, *Leptoseris*, and *Pavona* species, could be explained by their ability to grow and colonize disturbed habitats as observed in modern Indo-Pacific (Tomascik et al. 1997) and Caribbean reefs (Jackson and Hughes 1985). In the Leitha Limestone (Austria), middle Miocene coral assemblages dominated by a platy *Leptoseris* species developed as coral carpets with a rich associated bryozoan community that is comparable to the Stadion CC (Reuter et al. 2012). Even though both coral carpet communities have been interpreted to

TABLE 2.—Percentage contribution by the top 24 coral species to the Bray-Curtis similarity (SIMPER analysis) in species biomass (weight in grams) at the coral platestone (= CPL) and coral sheetstone (= CSh) facies in the Stadion patch reef.

	Coral species	Contrib	SD	Ratio	av. F4, CPL	av. F6, CSh	Cumulative
1	<i>Porites</i> sp.1	0.183	0.132	1.390	728.9	2679.9	0.214
2	<i>Progyrosmilia</i> sp.2	0.066	0.103	0.639	448.9	247.8	0.291
3	<i>Leptoseris</i> cf. <i>explanata</i>	0.063	0.101	0.621	6.6	649.7	0.364
4	<i>Porites</i> sp.3	0.056	0.099	0.569	545.5	—	0.431
5	<i>Cyphastrea</i> cf. <i>divaricata</i>	0.046	0.057	0.805	—	442.6	0.485
6	<i>Pavona</i> cf. <i>varians</i>	0.042	0.053	0.797	—	743.9	0.534
7	<i>Leptoseris</i> sp.7	0.035	0.049	0.710	328.3	—	0.575
8	<i>Psammocora</i> sp.1	0.033	0.046	0.714	—	366.4	0.614
9	<i>Pachyseris</i> sp.4	0.030	0.031	0.973	33.3	429.1	0.649
10	<i>Astreopora</i> sp.1	0.021	0.060	0.355	340.3	—	0.674
11	<i>Astreopora</i> sp.2	0.021	0.021	0.994	245.2	155.9	0.698
12	<i>Goniopora planulata</i>	0.021	0.035	0.596	1.1	288.2	0.723
13	<i>Montipora</i> cf. <i>venosa</i>	0.021	0.032	0.655	252.1	12.4	0.748
14	<i>Galaxea</i> sp.1	0.020	0.035	0.555	215.2	3.9	0.770
15	<i>Merulina</i> sp.1	0.018	0.042	0.437	—	304.8	0.792
16	<i>Progyrosmilia vacua</i>	0.017	0.030	0.547	—	303.3	0.811
17	<i>Fungophyllia</i> sp.1	0.013	0.021	0.629	37.1	88.4	0.827
18	<i>Cyphastrea</i> cf. <i>imbricata</i>	0.013	0.031	0.430	—	143.7	0.843
19	<i>Symphyllia</i> sp.1	0.010	0.014	0.717	103.2	33.7	0.855
20	<i>Porites</i> sp.2	0.010	0.012	0.825	61.6	111.6	0.866
21	<i>Coscinaraea</i> sp.1	0.009	0.020	0.473	4.4	185.6	0.877
22	<i>Alveopora</i> sp.1	0.009	0.013	0.694	100.2	1.1	0.887
23	<i>Stylophora</i> sp.1	0.009	0.017	0.502	59.6	53.7	0.897
24	<i>Goniopora</i> sp.2	0.008	0.019	0.402	64.2	26.2	0.906

occur under similar high siliciclastic environments, species richness of the Stadion in the Indo-Pacific is much higher than the one of the impoverished carpets of the Leitha Limestone in the Paratethys.

Bryozoans.—Twenty-eight bryozoan species occurred within the Stadion coral environments and these new records increase our knowledge of this poorly studied group in fossil communities of the Indo-Pacific (Di Martino and Taylor 2012, 2014). The undersides of platy corals supported a relatively rich encrusting bryozoan community. These surfaces may have formed long-lived, cryptic habitats for the settlement of bryozoan larvae, offering a large surface area for the growth of encrusting bryozoans and adequate vertical space for erect colony growth. Despite high richness, the abundance of bryozoans is due primarily to a few common encrusting species, particularly *Steginoporella* sp. and *Reptadeonella* sp. In the studied units, these two cheilostomes covered more substrate space than any other species. Furthermore, *Steginoporella* sp. often overgrows older colonies of the same species by frontal budding. Congeneric species encrusting the undersurfaces of foliaceous reef corals in Jamaica at the present day show a similar tendency to monopolize the substrate (Jackson and Winston 1982; Jackson 1984). In Jamaican successions *Steginoporella* is an extremely fast growing taxon (Jackson and Hughes 1985), whereas *Reptadeonella* grow much more slowly. *Steginoporella* colonies are much more common than *Reptadeonella* in disturbed microhabitats such as the edges of coral colonies (Jackson and Hughes 1985). Although colony fragmentation renders, it is impossible to distinguish with certainty between coral edges and inner zones. The distribution of *Steginoporella* sp. and *Reptadeonella* sp. may reflect the same pattern showed by congeneric Jamaican species.

Comparison with Coeval Regional Patch Reefs

Wilson (2005) described seven other Miocene delta-front patch reefs located in the Kutai Basin that likely developed in turbid shallow waters (≤ 10 m) with low-light penetration during lowstand to transgressive intervals. The Stadion reefs described herein developed under similar

conditions but also add new elements that aid in understanding the dynamics of Miocene turbid-water coral communities. Here we compare the Stadion patch reef with the Bontang patch reef (Novak et al. 2013) and two of the seven reefs described by Wilson (2005). The Batu Putih carbonates occur about 2.3 km below the Stadion CC in the Samarinda sequence, and the Dibelakan Parliament has been considered as a lateral extension of the youngest carbonates of the Batu Putih patch reef (Wilson 2005). The Bontang patch reef (Novak et al. 2013) is about 83 km to the north and late Burdigalian in age. As with most Miocene patch reefs in the region, initial coral development in the Stadion patch reef occurred during a transgressive interval. Although disseminated leaves and carbon detritus were observed at the base of the succession in Batu Putih and Dibelakan Parliament patch reefs (Wilson 2005), the development of the patch reef on top of a carbonaceous shale makes the Stadion coral assemblages different from all previously described patch reefs of the region. Coral assemblages occurring immediately after carbonaceous deposition shows that a relatively minor change in depth could trigger coral development in the ancient Kutai Basin.

In terms of biotic composition, mastophoroid coralline algae are dominant in the Stadion CC in contrast to the dim-light Melobesioidea assemblage observed in the Batu Putih, Dibelakan Parliament, and Bontang patch reefs (Wilson 2005; Novak et al. 2013). Coral assemblages follow a relatively similar succession, which in the case of the Batu Putih patch reef has been described as ideal because it shows a change from sheet-platestone to mixstone and pillarstone (Wilson 2005; Lokier et al. 2009). In the Bontang patch reef, which exhibits a change of facies from sheetstone into platestone, this idealized succession is only partially developed (Novak et al. 2013). In the coral platestone facies of the Stadion patch reef this succession of thin-platy to tabular, small massive and branching coral growth forms occurs as a thin, “condensed succession” without sharp differentiation into distinct facies.

Common coral genera mentioned by Wilson (2005) are also present in the Bontang patch reef (Novak et al. 2013) and the Stadion patch reef, yet direct taxonomic comparisons can only be performed between the latter two. Although poritids (*Porites* and *Goniopora*) are abundant in the four settings, the Bontang patch reef hosts more common merulinid taxa

(former Faviidae), while in the Stadion CC, acroporids (*Astreopora* spp.) and agariciids are more abundant.

Thus, a spectrum of three different types of biotic assemblages within these turbid environments can be recognized: (1) the Stadion patch reef with characteristic photophilic coralline algae and “condensed succession” of coral development; (2) Batu Putih and Dibelakan Parliament patch reefs with coralline algae tolerant of a broader range of turbid low-light habitats and an “ideal” succession of reef development (Wilson 2005); and (3) the Bontang patch reef (Novak et al. 2013), also with coralline algae that can thrive in turbid low light but an incomplete succession of corals restricted to sheet and platestones. Such differences in the composition of coralline algae and corals could be interpreted as a response of the biota to slightly different levels of light within the low-light levels characteristic of these shallow turbid habitats. In particular, the Stadion patch reef developed in the upper limits of low-light regime, but the Bontang patch reef (Novak et al. 2013) developed at the lower boundaries of low-light levels. The Batu Putih and Dibelakan Parliament patch reefs (Wilson 2005) developed within the whole range of low-light levels resulting in more habitat partitioning among biota. According to Wilson (2005), turbid conditions on the delta-front limited coral development on the the Batu Putih and Dibelakan Parliament patch reefs to habitats less than 10 m deep. The lithology and fossil assemblages found in the Stadion patch reef suggest that the Stadion patch reef occupied a similar habitat. In the case of the Bontang reef, mesophotic conditions resulted from both high terrigenous input and deposition below fairweather wave base (Novak et al. 2013).

Another possible explanation for the differences found among the three fossil assemblages in question is the relative position of the patch reefs within the delta system. In deltaic environments, turbidity and light penetration are controlled primarily by position within the deltaic complex. In the modern Mahakam delta system, the maximum concentration of suspended particles is found in the mouth of the main delta lobes, while the minimum concentration is observed in the offshore region (Budhiman et al. 2012). Similarly, sand decreases in grain size in an offshore direction (Storms et al. 2005). Superimposed on these onshore-offshore trends is a north-south variation caused by the southward flow of the Indonesian Throughflow current that generally persists throughout the year (Murray and Arief 1988) and favors a higher concentration of carbonates on the northern part of the shelf (Roberts and Sydow 2003). Thus, the Stadion patch reef may have developed north of an active delta lobe, while the Bontang (Novak et al. 2013), Batu Putih, and Dibelakan Parliament patch reefs (Wilson 2005), may have been located closer to different active delta lobes. However, additional data, not available in the present study, are needed to test this hypothesis.

Shallow Turbid Reefs and Coral Diversity

The reef-coral fauna recovered from the Stadion patch reef is one of the richest Miocene assemblages yet discovered and provides a record of the transition from foraminifera- to coral-dominated carbonates (Wilson and Rosen 1998). This faunal transition is likely related to the initiation of the modern-day Indo-West Pacific biodiversity hotspot as recorded by diverse coral assemblages from the late Oligocene in Malaysian Borneo (McMonagle et al. 2011). These Oligocene faunas, and the various patch reefs that have been described from the Kutai basin, all developed in turbid habitats, yet contain significant diversity. This suggests that such habitats may well have played a stronger role in coral diversification during the Miocene than has previously been attributed to them.

CONCLUSIONS

Carbonate bodies of the Stadion CC sections in East Kalimantan, Indonesia can be interpreted as a shallow-water patch reef, in which the

main controls for coral development were depth and varying levels of water turbidity related to the amount, frequency, and grain size of siliciclastic input. Evidence gathered in this study supports a paleodepth interpretation for the Stadion patch reef within turbid waters at a maximum of 10 m depth. Different facies were most likely deposited following a proposed deepening sequence comprising: (1) laminated siltstone; (2) carbonaceous shale; (3) bioclastic packstone; (4) coral platestone; (5) foraminiferal packstone; (6) coral sheetstone; and (7) clay shale.

Larger benthic foraminifera were present in all fossiliferous facies, supporting their role as the most siliciclastic-tolerant group. Although the environmental conditions for coral development within the Samarinda sequence were ephemeral, the Stadion patch reef had a rich coral assemblage that could cope with changing terrigenous input. Yet their demise was due to increased siliciclastic input exceeding the tolerance of any coral species. Corals enhanced the overall diversity in these turbid settings by hosting bryozoans, coralline algae, mollusks, and echinoderms.

Comparisons to coeval patch reefs in East Kalimantan show that platy corals are dominant in these environments, with some taxa found in most sites but other taxa more unevenly distributed among habitats. Communities of larger benthic foraminifera tend to be similar among all patch reefs, but calcareous coralline algal assemblages vary significantly according to light availability, with characteristic assemblages in lower and higher light habitats within the Samarinda turbid settings during the Miocene. Bryozoans are diverse and their presence in the studied fossil record is usually associated with thin platy coral assemblages. Mollusks are poorly preserved in platy-coral dominated settings. Large, ecologically sampled collections and multitaxa analysis of fossil assemblages are important to the better understanding of paleoenvironmental conditions. The high diversity of coral species in the Stadion patch reef highlights the importance of marginal turbid habitats as a reservoir of diversity during the origins of the Coral Triangle hotspot.

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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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