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EOCENE–MIOCENE SHALLOW-WATER CARBONATE PLATFORMS AND INCREASED HABITAT DIVERSITY IN SARAWAK, MALAYSIA

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ABSTRACT: **The Indo-Pacific marine biodiversity hotspot originated between the late Eocene and the early Miocene. Its origin coincides with an increase in availability of shallow-marine habitats driven by the opening of the South China Sea and the collision of Australia with the Pacific arcs and the southeast Asian margin. However, little is known about the distribution and diversity of past Indo-Pacific marine habitats. Understanding habitat diversity is key for understanding the significance of biodiversity origins and a necessary prerequisite for interpreting biodiversity patterns through time. Here we describe and interpret past carbonate platform environments in Sarawak, Malaysia during a time of active tectonism. We examine upper Eocene to lower Miocene marine shallow-water carbonate deposits from six localities in two limestone formations: the large ramplike Melinau carbonate platform (middle Eocene to early Miocene) and the unattached Subis carbonate platform (early Miocene). Deposits examined in this study represent paleoenvironments. Our analysis reveals an increase in habitat diversity from the Eocene to the Miocene. Mesophotic to oligophotic low-energy environments are typical for the Eocene sites. The corals first appear in the Oligocene deposits, but genuine reef depositional settings are not observed until the Miocene. This study provides both insight into the evolution of the carbonate platform environments along the Sarawak margin, and context for the origin of the Indo-Pacific marine biodiversity hotspot.**

INTRODUCTION

Biodiversity hotspots are geographical regions characterized by exceptionally high species diversity (Reid 1998). The diversity is facilitated through the availability of ecologically diverse habitats (MacArthur and MacArthur 1961). Habitat heterogeneity allows coexistence of both generalist and specialist taxa resulting in an increase in origination rates and a decrease in extinction rates (Connell 1978). Availability of marine habitats is controlled by tectonic (at both a local and global scale), eustatic, climatic, and oceanographic processes (Rosen 1984). In shallow-marine (shoals, inner-ramp, and platform margin) environments, habitat heterogeneity is typically facilitated through a range of tidal regimes and wave energy, but structural complexity of habitats can be increased by the taxa themselves (e.g., reefs) (Roberts and Ormond 1987). Here we examine the role of environmental change on habitat distribution and diversity that formed the foundation for the Indo-Pacific biodiversity hotspot.

Since the early Miocene, the Indo-Pacific region (30°S–30°N, 90°–160°E) features as a hotspot of global marine diversity (Wilson and Rosen 1998; Renema et al. 2008; Lohman et al. 2011). This coincides with a significant increase in carbonate area in the region and is characterized by a shift in the main carbonate producers from larger benthic foraminifera to corals (Wilson 2008). An abrupt increase in coral abundance (measured as area of coral-dominated carbonate platforms) is reported from the early Miocene (Wilson 2008). The apparent paucity of coral records from the Oligocene of the Indo-Pacific, known as the Paleogene gap (Wilson and Rosen 1998), is not a consequence of the paucity of Oligocene carbonates in the region (Wilson 2002). So far, Oligocene fossil corals (mostly fragmented) have been found in massive carbonate bioclastic packstone facies that are abundant in the Oligocene in the Indo-Pacific, but coral framestone is rare (Saller and Vijaya 2002). It is assumed, therefore, that scleractinian corals are not preserved in this setting. However, abundant occurrence of corals has been reported from environments otherwise dominated by large benthic foraminifera (McMonagle et al. 2011).

The occurrence of large benthic foraminifera and scleractinian corals is determined by a set of often-interrelated environmental parameters such as temperature, turbidity, depth, substrate, hydrodynamic energy, and pH (Hottinger 1983; Connell 1997; Renema and Troelstra 2001). Over long timescales these are influenced by variations in regional tectonics, global sea level, climate, and oceanographic parameters (Rosen 1984; Flügel 2010). High marine diversity in the early Miocene of the Indo-Pacific coincides with an expansion in the frequency of occurrence of shallow-marine habitats suitable for coral-reef development (Renema et al. 2008), which was mediated by the opening of the South China Sea (~ 45–17 Ma) and the collision of Australia with the Pacific arcs and the Southeast Asian margin (starting ~ 20–25 ma) (Hall 1996, 2002, 2009; Hutchison 2004; Hall et al. 2011). To investigate the paleoenvironmental conditions during this critical period for the early development of the South China Sea and the Indo-Pacific marine biodiversity hotspot (i.e., the late Eocene to early Miocene), we examine past shallow-marine carbonate environments and the composition of their main carbonate producers from Sarawak, Malaysia.

GEOLOGICAL SETTING

Regional Geology

The southern margin of the South China Sea lies in the convergence zone between Eurasia, Australia, and the Pacific/Philippine Sea plates,

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where a complex mosaic of oceanic plates, arcs, and microcontinental fragments occurs (Hall 1996, 2002, 2009; Hutchison 2004; Hall et al. 2011). During the Eocene and the Oligocene much of northern Borneo was an active margin locally, with large-scale carbonate platforms developing offshore (Liechti 1960; Adams 1970; Hutchison 2005; Wannier 2009). The active margin was characterized by a large subduction zone (Lohman et al. 2011) that, up to the middle Eocene, formed an accretionary wedge where Sarawak is today. The subduction ceased through the docking of the Luconia Continental Block onto the northwest Borneo margin. This resulted in a large shelf area that subsequently was uplifted and provided suitable environments for the development of large carbonate platforms. The collision of Australia with the Pacific arcs and the Southeast Asian margin started ~ 20–25 million years ago and resulted in a change in the tectonic regime, such as the counterclockwise rotation of Borneo and the early Miocene onset of a compressional tectonic regime in the South China Sea (Hinz and Schlüter 1985; Hall 2002). At this time, carbonates began developing on smaller scale local tectonic highs (Liechti 1960; Noad 2001). Observed variations in formation thicknesses, constituent biota, and lithologies indicate that the carbonate sedimentation along the southern margin of the South China Sea is strongly influenced by differential subsidence (controlled by tectonics) and local changes in depositional environment, such as siliciclastic input (Wilson 2002).

Geology of Sarawak

Sarawak is situated in the northwest of Borneo and is divided into three zones based on surface geological mapping (Haile 1974): (1) the Kuching Zone, (2) the Sibu Zone, and (3) the Miri Zone. These are dominated by siliciclastic sediments derived from the uplift and weathering of the Rajang and Crocker Accretionary Complex under humid tropical conditions (Hutchinson 2005). Deposits of the Kuching Zone in the south are oldest, and young toward the Miri Zone in the northwest. Although limestone deposits are not widespread in Sarawak, they occur almost continuously from the late middle Eocene (late Lutetian) to the earliest early Miocene (Aquitanian) in the Miri Zone. All of the study sites addressed in this paper occur in the Miri Zone. The Melinau and Subis (Tangap) Limestone formations include the most extensive carbonate platforms in Sarawak (Hutchison 2005). Prior to the late Eocene, northern Sarawak was a deep marine foreland basin that shallowed toward the south (Hutchison 2005). The deep marine deposits are characterized by interbedded sandstone and shale lithologies found in the Mulu and the Kelalan Formation. The late Eocene collision of the Luconia Continental Block triggered regional uplift and the shallowing of the Sarawak basin (Hutchinson 1996). On the resulting broad shallow shelf the platform carbonates of both the Melinau and Subis Limestones were deposited along with nonmarine to inner neritic marine deposits of the Nyalau and Setap Shale formations (Hutchison 2005). In the Oligocene, carbonate deposition also expanded to offshore Sarawak in the Central Luconia Province, culminating in the upper Miocene extensive buildups formed as a response to sea-level changes (Epting 1980).

METHODS

Study Sites

Samples for this study were collected from the Melinau and the Subis (Tangap) Limestone formations (Fig. 1) (Hutchison 2005). The Melinau Limestone is a large carbonate platform that was deposited over a 30 Ma interval from the middle Eocene to the early Miocene (based on foraminiferal biostratigraphy) (Adams 1965; Cotton et al. 2014) and has been interpreted as forming in a wedge-top basin (Adams 1965; Wannier 2009). The Melinau Limestone extends northeast–southwest for over 100 km but the limestone deposits are not continuous and consist of individual, geographically distinct, carbonate units. The thickest (around 2200 m) deposits are found in the Gunung Mulu National Park but both the vertical and horizontal extent and depositional environments of the deposits vary along the length of the platform (Liechti 1960; Adams 1965;

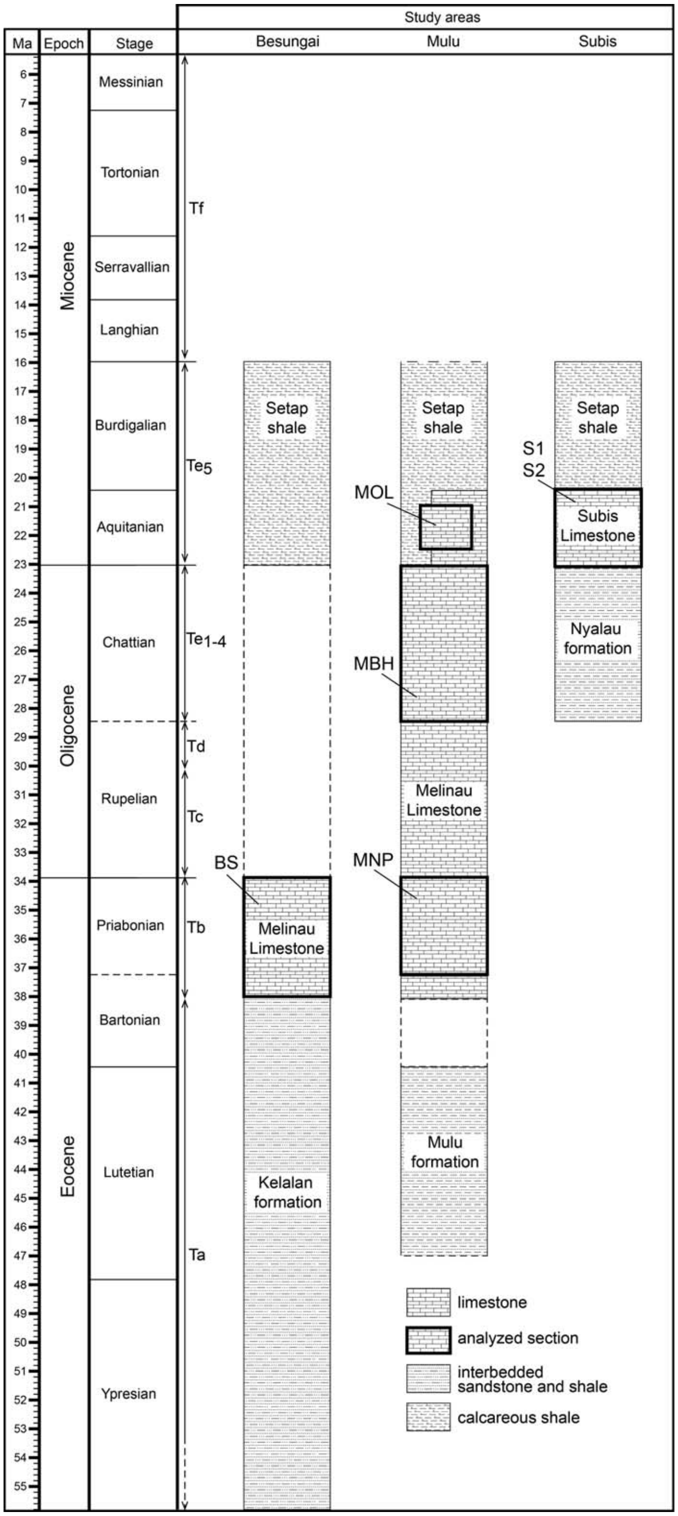

FIG. 1.—Chronostratigraphic context of our study areas based on Hutchison (2005). BS = Besungai, MBH = Mulu Broken Hill, MNP = Mulu National Park, MOL = Mulu Olistolith, S1 = Subis 1, S2 = Subis 2.

Hutchison 2005). Additionally, a high-angled reverse fault (in north-south direction) extends along the whole of the Gunung Mulu outcrop. Lithologies from the Gunung Mulu National Park are mostly foraminifera- and algae-rich bioclastic packstones that were deposited in shallow-marine environments (Adams 1965). Coral-rich carbonate blocks (olistoliths) of late Chattian to early Aquitanian age are scattered in the overlying Setap Shale Formation (located just outside of the Gunung Mulu National Park) and most likely originated from a reef at the edge of the platform (Fig. 1) (Wannier 2009). Displaced carbonate blocks of Oligocene age, with internal stratigraphic position preserved, are also found in the black shale deposits of the Setap Shale Formation (middle Oligocene–early Miocene) (Wannier 2009). Additional localities of the Melinau Formation are found 50 km southeast from the Gunung Mulu National Park: Batu Gading, Batu Besungai, and Batu Bukit. The Melinau Formation dips toward the northeast from Batu Besungai, across Batu Bukit toward Batu Gading. An angular contact of *Nummulites javanus*-rich sandy limestone with the underlying Kelalan Formation can be observed at Batu Besungai (Adams and Haak 1962). The sandy limestone wedges out toward the northeast and is therefore absent at Batu Gading. The upper Eocene massive Melinau limestone is foraminifera- and algae-rich, lies on top of the sandy limestone, and is present at all three Batu sites. The Melinau limestone is overlain by the lower Miocene calcareous shales of the Setap Shale Formation at Batu Besungai. However, in the Batu Gading section, the Setap Shale Formation overlies a late Oligocene–early Miocene coral-rich breccia that is completely absent in the Batu Besungai section (Fig. 1) (Adams and Haak 1962; Hutchison 2005; Wannier 2009).

The Subis Limestone (Tangap) Formation stretches over 25 km^2. It lies between the underlying sandy Nyalau Formation (predominantly littoral shallow neritic deposition) and the overlying fossil-rich Sibuti Member Formation (part of the Setup Formation, deeper neritic) (Fig. 1). The limestone deposits (lower Miocene) at Batu Niah are almost 400 m thick and were deposited as an unattached carbonate platform on a bathymetric paleohigh (Liechti 1960; Adams 1965; Hutchison 2005). Lower parts of the limestone are characterized by a foraminiferal/algal packstone that contains siliciclastics. That lithology changes gradually into a coral/algal rich grainstone and boundstone toward the top of the platform (Liechti 1960; Adams 1965; Roohi 1994; Hutchison 2005).

Study sites were selected based on previous descriptions (Adams and Haak 1962; Adams 1965; Wannier 2009), accessibility, preservation quality, reported age (middle Eocene to early Miocene), and fossil content (Hutchison 2005). The Melinau Formation is found at the Besungai (N 3.77160° E 114.43886°), Mulu Broken Hill (N 4.033036° E 114.795019°), Mulu National Park (N 4.023056° E 114.812806°) and Mulu Olistolith (N 4.03275° E 114.788611°) localities, whereas the Subis Limestone (Tangap) Formation outcrops at localities Subis 1 (N 3.77935° E 113.78082°) and Subis 2 (N 3.77856° E 113.78769°) (Fig. 2). The thickness of the units at the study sites varied considerably from a single isolated limestone block (Mulu Olistolith) to an over 100-m-thick bedded limestone section (Subis 1).

Sampling Design

Lithological samples were taken from logged sections through the carbonate platforms at Besungai, Mulu Broken Hill, and the two Subis localities (Fig. 1). In localities with well-preserved bedding one sample was collected from each bed. In localities with massive limestone, beds were evenly divided into intervals within sections (1–10-m-thick intervals, depending on the thickness of the section) and initial samples were collected from each interval of the subdivided sections. When a change in sediment composition was observed between initial samples, further representative samples were collected. Where bedding was not obvious (in the isolated blocks at the Mulu National Park locality and the Mulu Olistolith locality) systematic collection was undertaken to ensure adequate representation of the lithofacies.

From around 200 lithological samples, 55 were selected to represent significant changes in lithology/facies thereby capturing all major habitats. Thin sections (76 × 51 mm) were prepared from those samples for constituent grain type analysis (Ginsburg 1956). The number of thin sections varied per locality depending on differences in extent of the localities and sediment composition of adjacent lithological samples: Besungai (60 m thick) = 16 samples; Mulu National Park (isolated limestone blocks) = 5 samples; Mulu Broken Hill (30 m thick) = 4 samples; Mulu Olistolith (isolated limestone block) = 4 samples; Subis 1 (over 100 m thick) = 20 samples; Subis 2 (10 m thick) = 6 samples.

Stratigraphy

Collected samples were put in a temporal context based on foraminiferal occurrences. In shallow-marine tropical rocks/deposits, larger benthic foraminifera (LBF) are an excellent tool for biostratigraphical analysis, due to their frequent occurrence, high abundance, and restricted stratigraphic ranges. Hence, foraminiferal assemblages can be assigned to a LBF zone with an accuracy of up to 3 million years (Lunt and Allan 2004; Renema, 2007). Moreover, foraminiferal deposits in Sarawak are common, diverse, and well studied (Adams and Haak 1962; Adams 1965; Wannier 2009). Here the biozonation scheme of Renema (2007) is used. Our samples are categorized into three age groups: late middle to late Eocene, late Oligocene, and early Miocene.

Constituent Grain Type Analysis

The spatial patterns of skeletal constituent types, the distribution of sediment producing organisms, and physical characteristics of marine environments are correlated (Illing 1954; Ginsburg 1956) and can be used to describe and differentiate between both modern (Boss and Liddell 1987) and past marine environments (Pandolfi et al. 1999). The paleoenvironments and community composition from the two geological formations were described by calculating relative abundances of grain type constituents in each of the 55 lithological samples. Additionally, carbonate lithology was classified using the modified Dunham classification scheme (Dunham 1962).

The constituent grain composition was measured from thin sections using the point-counting method (Chayes 1956; Ginsburg 1956) and a petrographic microscope with a motorized stage. The constituent type (both skeletal and nonskeletal) of at least 300 equally spaced points was recorded. Skeletal constituents were divided into 11, and nonskeletal constituents into three categories (see Supplementary Data). The skeletal categories used in this study are corals, eight foraminiferal categories (*Nephrolepidina*, *Eulepidina*, *Cycloclypeus*, *Miogypsina*, *Nummulites*, *Amphistegina*, milioline forms, and undifferentiated foraminifera), green algae, and red coralline algae. *Nephrolepidina*, *Eulepidina*, *Cycloclypeus*, *Miogypsina*, *Nummulites*, and *Amphistegina* are large benthic foraminifera. The category, undifferentiated foraminifera, contains foraminifera that due to the poor preservation or fragmentation could not be identified and assigned to the other foraminiferal categories. That means that this category could contain individuals belonging to the other foraminiferal categories; and therefore, this category was excluded from all statistical analyses. However, the category was included when discussing total number of foraminifera (total foraminifera). The recorded nonskeletal categories were micrite, terrigenous material, and diagenetic features (cements and stylolites). The category, diagenetic features, was subtracted from the total number of constituent types and was not used for any analysis, since they do not contribute information about the environments at the time of deposition.

A sampling curve was generated to ensure that the sample size (300 counted points) was adequate for statistical analysis (Raup 1975). Relative abundances of the most abundant groups of skeletal elements were depicted in a ternary plot. Relative abundance of foraminifera in the

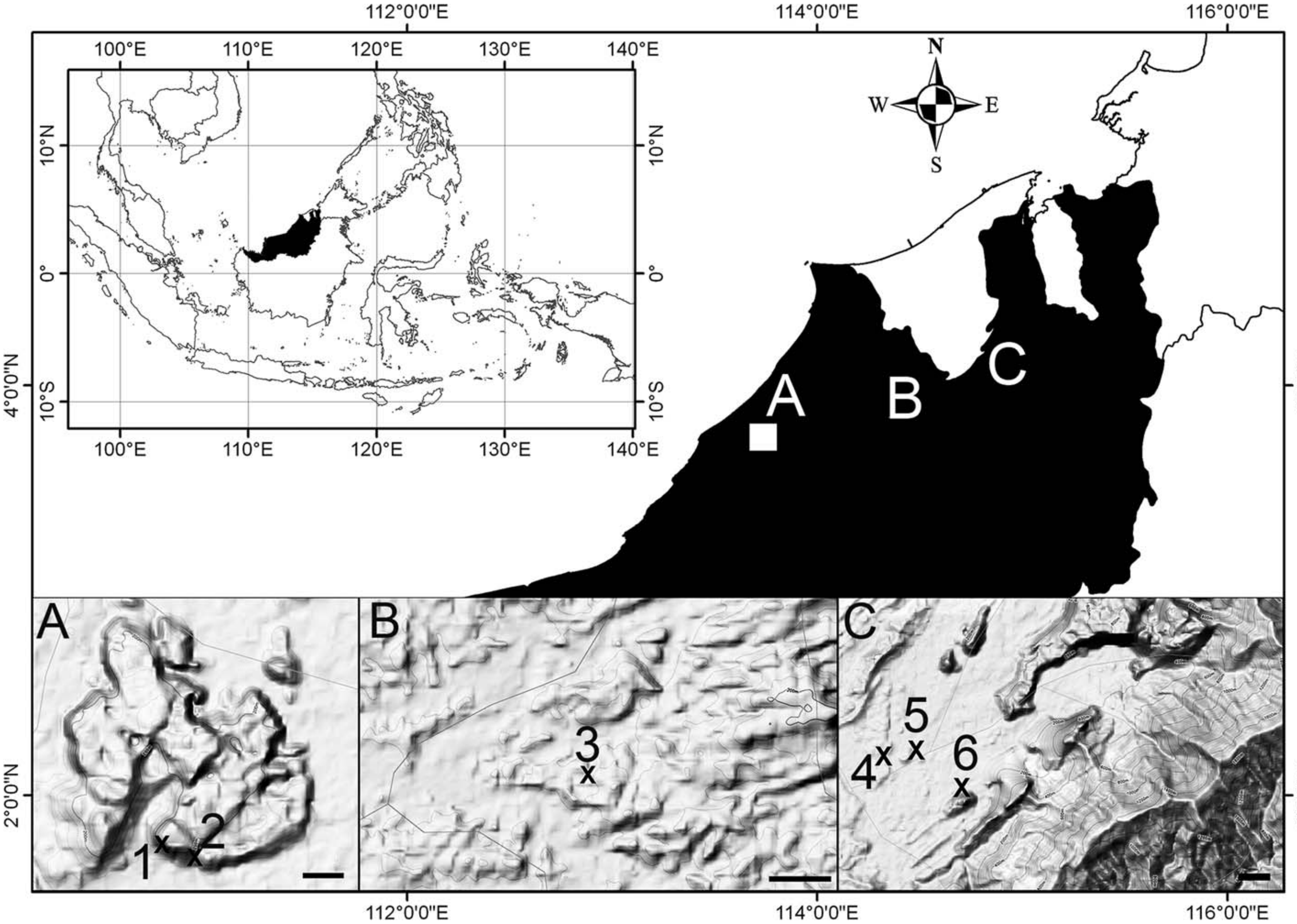

FIG. 2.—Map of Sarawak showing sites (A, B, C) and six localities within sites. **A**) Topographic map of the Subis site with localities Subis 1 (1) and Subis 2 (2). **B**) Topographic map of the Besungai site and locality (3). **C**) Topographic map of the Mulu site with localities Mulu Olistolith (4), Mulu Broken Hill (5), and Mulu National Park (6). Scale bar = 1 km.

plot was shown as the sum of the relative abundances of all foraminiferal categories present in the respective sample. Relative abundance of algae for each sample comprised green and red coralline algae. The coefficient of variation was calculated for each of the three most abundant groups of skeletal constituents to quantify their variation in our three age categories. Overall differences in the relative abundance of constituent types was calculated using a Bray-Curtis dissimilarity index (Bray and Curtis 1957), one of the most robust and effective dissimilarity measures for ecological data (Faith et al. 1987). To assure that the dissimilarity index is not influenced by high abundances of some constituent types, we first square-root transformed all constituent type abundances (Field et al. 1982). To test if the dissimilarities between all pairs of paleoenvironments (compared both spatially and temporally) were statistically significant, we used the nonparametric test ANOSIM (analysis of similarities) (Clarke 1993; Pandolfi and Minchin 1996). ANOSIM compares distances within samples and across samples, such that if two samples are different in their constituent composition, within-sample distances would be smaller than across-sample distances. Significance levels were generated using a randomization approach. We visualized the relative distances among samples using nonmetric multidimensional scaling (nMDS) ordination of the Bray-Curtis dissimilarity matrix (Anderson 1971; Giraudel and Lek 2001). Rotational vector fitting was used to relate the constituent types to the ordination allowing us to quantify the strength of this relationship through a correlation coefficient (r2) (Faith and Norris 1989; King and Richardson 2008). The vector points in the direction of the gradient. The length of the vector indicates the strength of the gradient, i.e., correlation between the ordination and the constituent type. Significance of vectors was estimated by using 999 random permutations (Oksanen et al. 2012). All statistical analyses were carried out using R 2.15.2 software (R Development Core Team 2012).

RESULTS AND INTERPRETATION

Stratigraphy

Based on the co-occurrence of *Nummulites javanus*, *Discocyclina*, *Nummulites pengaronensis*, and *Pellatispira*, the Besungai locality is inferred to be the Tb zone, i.e,, to range from the late middle Eocene to the late Eocene (Fig. 1) (Lunt and Allan 2004; Renema 2007). We assigned the Mulu National Park locality to the Tb zone as well but have limited it to only the late Eocene (Fig. 1) due to the presence of *Discocyclina*. The Mulu Broken Hill locality is deposited during the Te_{1-4} zone, i.e., late Oligocene in age (Fig. 1), since *Nephrolepidina* and *Eulepidina* co-occur in absence of *Miogypsina*. Both Subis localities and the Mulu Olistolith are dated to the Te_5 zone (the early Miocene) (Fig. 1) based on the presence of *Nephrolepidina* (Subis 1 and Subis 2), *Eulepidina* (Subis 1, Subis 2 and Mulu Olistolith), *Miogypsina* (Subis 1 and Subis 2), and *Miogypsinoides* (Mulu Olistolith) (Lunt and Allan 2004; Renema 2007).

Sampling Adequacy

The sampling curve leveled off for new constituent types after 100 points (Fig. 3). This indicates that sampling of 300 points per thin section is more than adequate for statistical analyses (Fig. 4) (see Supplementary Data).

Late Middle to Late Eocene Paleoenvironments

The Besungai Locality.—The Besungai locality of the Melinau Limestone shows obvious bedding which dips 19° to the north (190°) (Fig. 2B). Active quarrying at this location has cut obliquely across the strike providing excellent exposure. A 60-m-thick section of the Besungai locality was logged and characterized by two distinct parts: a lower-bedded deposit of alternating shale–fossiliferous quartz wacke beds followed by sandy limestone and massive limestone deposits toward the top (Fig. 5). The lower part of the section is unconformably underlain by flysch of the Kelalan Formation (Cretaceous). The distinction between the two formations (the Kelalan and Melinau) is conspicuous due to this angular contact. Up section four distinct facies were observed: (1) shale: this facies consists of fine-grained unfossiliferous dark gray clay and silts. (2) sandstone: high siliciclastic content, poorly sorted with coarse quartz sand in a clay-rich matrix and small vertical burrows, possibly *Skolithos,* characterize this facies. Mollusk fragments and lenses of fine sediment containing foraminifera and indistinct cross-bedding are also present. (3) *Nummulites javanus* packstone: high abundance (up to 54%) of *Nummulites javanus* surrounded by sandy limestone matrix is characteristic for this facies. No nummulithoclasts are seen in this facies. The input of terrigenous material (largely quartz silts and sands) varies significantly (from 1% to 49%). No obvious sedimentary structures are observed and beds appear to be laterally continuous sheets rather than channelized or forming high-relief structures. (4) Foraminiferal–algal wackestone to packstone: this facies is characterized by large benthic foraminifera (*Opercuilina*, *Discocyclina*) and coralline algal fragments with abundant micrite, and composes the top 40 m of the logged section. Lower Miocene shale deposits of the Setap Shale Formation unconformably overlie these upper Eocene deposits.

The Mulu National Park Locality.—The limestone outcrop of the Mulu National Park locality is located in the southern part of the Gunung Mulu National Park near the old entrance to the Royal Mulu Resort (Fig. 2C). The studied outcrop, which measures horizontally over 60 m and is around 30 m high, is representative for the late Eocene blocks, which show severe surface weathering and no obvious bedding. Additionally, shearing faults are observed in the limestone. Large benthic foraminifera together with coralline algae constitute approximately half of all constituent types. The whole locality represents the same facies type: foraminiferal–algal packstone. The facies is characterized by high abundance (up to 26%) of large benthic foraminifera (*Discocyclina, Nummulites*) and coralline algal debris (up to 27%) embedded in a matrix of gray homogenous micrite.

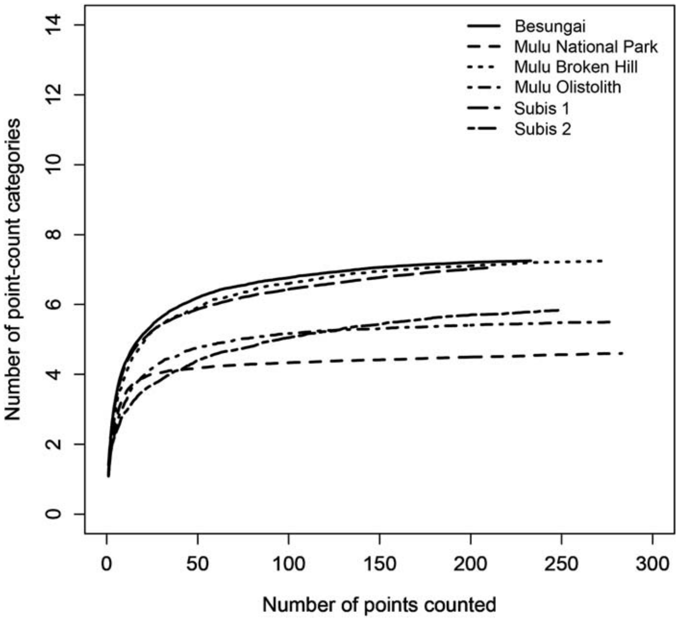

FIG. 3.—Mean sampling curves derived from point counts from each locality. New constituents encountered quickly level out after 50–100 points counted, implying adequate sampling for statistical analysis. The y-axis includes both skeletal and nonskeletal constituent types.

Paleoenvironmental Interpretation.—High relative abundances of large benthic foraminifera, coralline algae, and fine micrite matrix suggest mesophotic to oligophotic (Pomar 2001; Brandano and Corda 2002; Ćosović et al. 2004; Novak et al. 2013) low-energy environments (Folk 1965; Kroeger et al. 2006; Gramigna et al. 2011) in both the upper part of the Besungai and the Mulu National Park localities of the Melinau Limestone (Table 1). This could be interpreted as shallow-shelf or turbid lagoonal setting (Ahr 1973, 1998; Burchette and Wright 1992; Loucks et al. 1998; Geel 2000). However, a greater range of environments are determined to have been preserved at Besungai. Accumulations of robust *Nummulites javanus* in low-relief structures suggest a relatively high hydrodynamic energy, and thus a shallow- to mid-ramp (at least above storm-wave base) depositional environment and possible reworking to form banks (Aigner 1983, 1985; Aly et al. 2001; Nebelsick et al. 2005; Jorry et al. 2006). This is supported by the relatively small amounts of micrite and little sign of nummulithoclasts (Loucks et al. 1998). The transition from fine-grained, clay-rich through poorly sorted wackes to the *Nummulites* banks is suggestive of a shallowing-upward sequence. Greater amount of terrigenous material in the Besungai locality than the Mulu National Park locality may suggest a nearer-shore paleoenvironment. All described environments are typical for the oligotrophic depositional environments and are consistent with an inner-ramp setting (Brasier 1995a, 1995b; Racey 2001). The disconformity observed at the Besungai locality indicated the absence of Oligocene deposits, and may be a result of a rapid, eustatic sea-level fall that occurred at the Eocene/Oligocene boundary due to the rapid expansion of the Antarctic ice sheets (Zachos et al. 2001, 2008) or possibly a continuation of late Eocene uplift (Hutchinson 1996). Arguably, the nearer-shore environments interpreted at Besungai would be more susceptible to these processes.

Oligocene Paleoenvironments

Mulu Broken Hill Locality.—The Mulu Broken Hill locality is situated outside of the Gunung Mulu National Park, southwest of the Mulu Airport (Fig. 2C). The hill was quarried in the recent past and its top has been flattened during airport building works, leaving most of the limestone blocks dislodged from their original stratigraphic context. However, the late Oligocene locality situated on the southern side of the hill appears undisturbed. The locality extends horizontally approximately 30 m with bedding planes dipping almost vertically (Fig. 5). Foraminifera and coralline algae dominate the deposits. Two alternating facies are recognizable in this locality: (1) foraminiferal–algal packstone: this facies contains large benthic foraminifera and coralline algal fragments

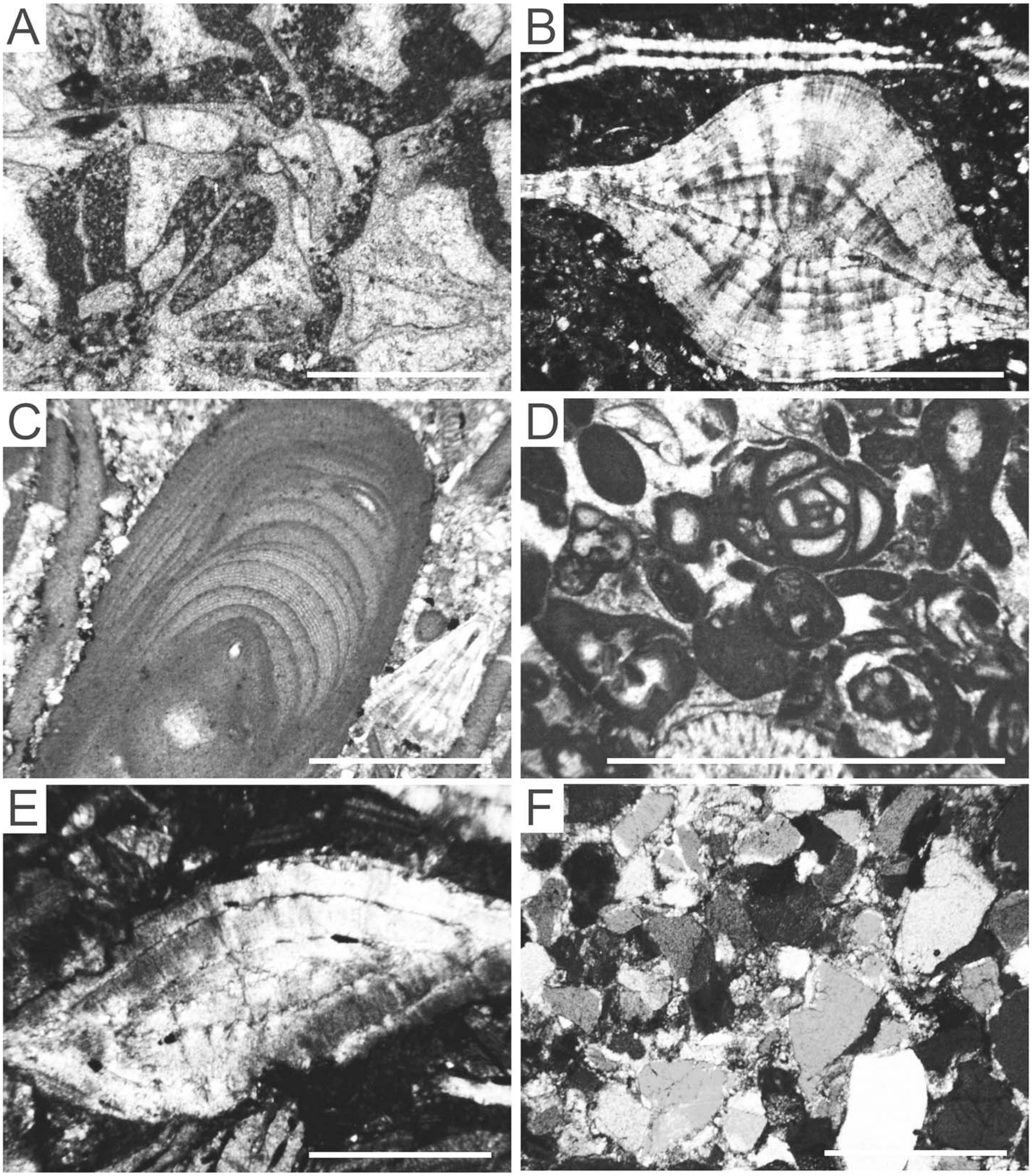

FIG. 4.—Examples of some common constituent types (photographs of thin sections) from the latest middle Eocene to the early Miocene of Sarawak, Malaysia. **A**) Coral from sample 11MOL200/001. **B**) Foraminifera (*Cycloclypeus* and *Nephrolepidina*) from sample 11Subis133. **C**) A fragment of coralline red algae from sample 11Subis133. **D**) Miliolid foraminifera from sample 11Subis23. **E**) Foraminifera (*Nummulites javanus*) from sample 11Besungai083. **F**) Terrigenous material from sample 11Besungai088. See Supplementary Data for additional information on the samples. Scale bar = 1 mm.

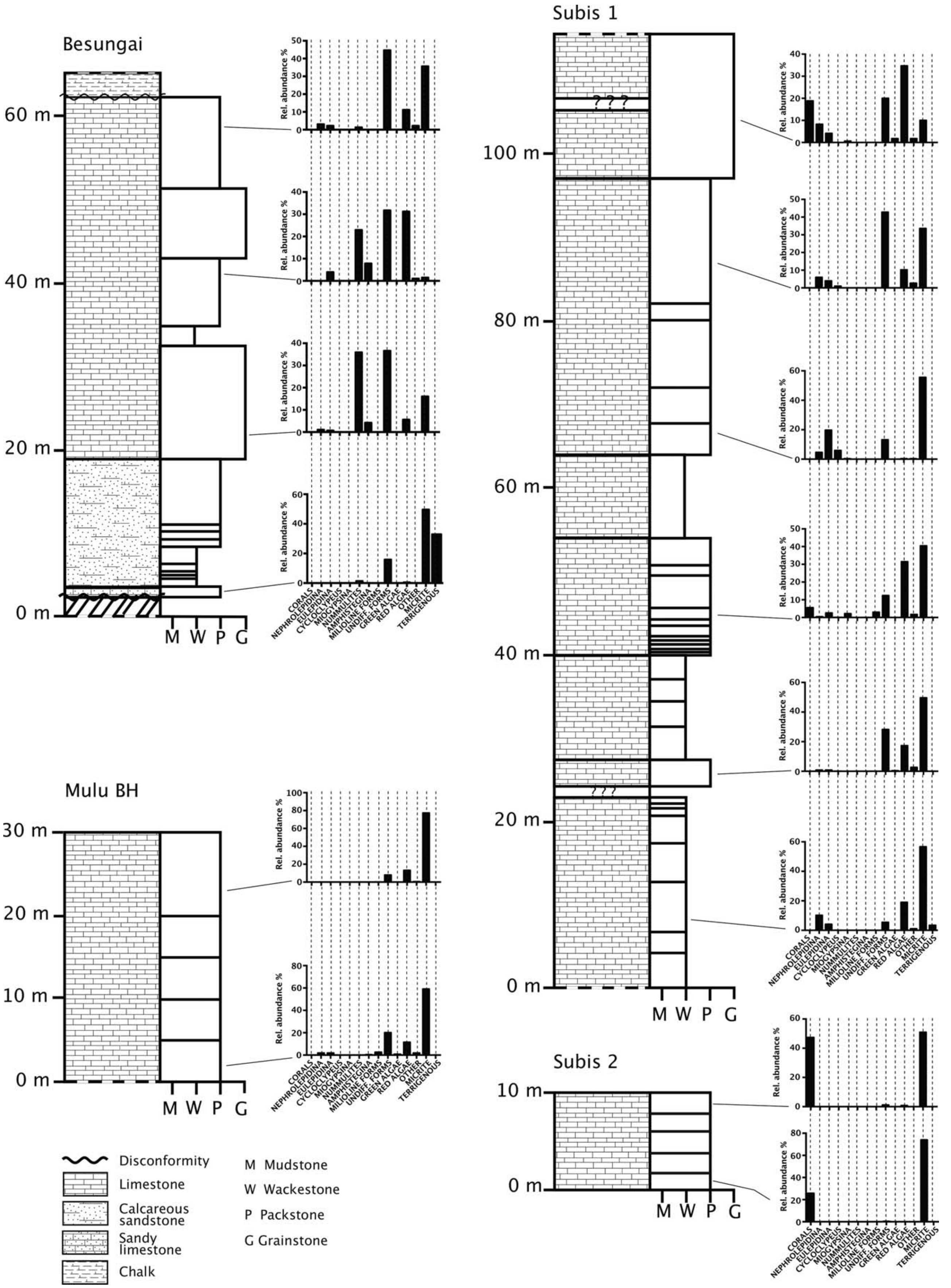
Besungai
60 m
40 m
20 m
0 m
M W P G
Mulu BH
30 m
20 m
10 m
0 m
M W P G
Subis 1
100 m
80 m
60 m
40 m
20 m
0 m
M W P G
???
Subis 2
10 m
0 m
M W P G
Rel. abundance %
CORALS
NEPHROLEPIDINA
EULEPIDINA
CYCLOCLYPEUS
MIOGYPSINA
NUMMULITES
AMPHISTEGINA
MILIOLINE FORMS
UNDIFF. FORMS
GREEN ALGAE
RED ALGAE
OTHER
MICRITE
TERRIGENOUS
Disconformity
Limestone
Calcareous sandstone
Sandy limestone
Chalk
M Mudstone
W Wackestone
P Packstone
G Grainstone

TABLE 1.—*Summary of study localities with regard to facies types and paleonvironmental conditions.*

Site	Age	Facies present	Light	Nutrients	Hydrodynamic energy	Position on the ramp/platform
Besungai	late middle Eocene to late Eocene (Tb)	(4) Foraminiferal—algal wackestone to packstone (3) Nummulites javanus packstone (2) Sandstone (1) Shale	mesophotic to oligophotic	oligotrophic	high to low-energy	from mid-ramp to inner-ramp
Mulu National Park	late Eocene (Tb)	(1) Foraminiferal—algal packstone	mesophotic to oligophotic	oligotrophic	low-energy	inner-ramp
Mulu Broken Hill	late Oligocene (Te1-4)	(2) Coral—skeletal fragment packstone (1) Foraminiferal—algal packstone	euphotic to mesophotic	oligotrophic	low-energy	fore-reef, inner-ramp
Mulu Olistolith	early Miocene (Te5)	(1) Coral framestone facies	euphotic to mesophotic	oligotrophic	higher energy	unknown
Subis 1	early Miocene (Te5)	(5) Coral framestone facies (4) Grainstone (3) Coral floatstone (2) Foraminiferal—algal wackestone to packstone (1) Sandy silt	euphotic to mesophotic	oligotrophic	low to higher energy	fore-reef, isolated platfrom
Subis 2	early Miocene (Te5)	(1) Coral—foraminiferal packstone	euphotic to mesophotic	oligotrophic	low-energy	fore-reef, isolated platfrom

embedded in a gray micritic matrix. (2) Coral–skeletal-fragment packstone: fragmented corals, green algae, and other unidentifiable skeletal elements embedded in gray micrite are typical for this facies.

Paleoenvironmental Interpretation.—Specific to this locality, in comparison with the two older (Eocene) localities, is the first evidence for the presence of corals. Coral (with their symbiotic algae) and green algae are typical for oligotropic and euphotic to mesophotic environments (Table 1). However, all skeletal elements are fragmented and not preserved *in situ* which would indicate transport and redeposition (Nebelsick and Kiene 1997; Pandolfi et al. 1999; Nebelsick et al. 2000). The high abundance of micrite excludes possibility of high-energy environments (Folk 1965). These conditions are consistent with a fore-reef paleoenvironment (James and Bourque 1992).

Miocene Paleoenvironments

Mulu Olistolith Locality.—The Mulu Olistolith is a 13 m^3 isolated block surrounded by shale deposits of the Setap Shale Formation. It is located around 700 m westward from the Mulu Broken Hill locality (Fig. 2C). This lower Miocene locality not only yielded the highest coral abundance recorded in our study but also *in situ* preservation of corals. The other two most abundant constituent grain types found in this locality are large foraminifera and coralline algae (Fig. 5). The whole locality is a coral framestone facies, characterized by high abundance of *in situ* mostly massive corals (up to 81%) and other skeletal fragments such as large benthic foraminifera (*Eulepidina*, *Nephrolepidina*, and *Miogypsinoides*) and coralline algae that are embedded in a fine micrite matrix.

Subis Localities.—The lower Miocene Subis localities are located in the south of the Gunung Subis area, on the edge of what has previously been identified as an unattached platform (Fig. 2A) (Liechti 1960; Adams 1965; Haile and Ho 1991; Hutchison 2005). The area is actively quarried and the bedded deposits of the Subis 1 locality are well exposed in the SY Quarry. The Subis 2 locality is situated 700 m to the east of the quarry and access to it was limited due to vegetation (Fig. 2A). Thickness of the beds at the Subis 1 locality varies from 20 cm to 8 m up the logged section whereas the thickness of the Subis 2 beds is relatively constant at approximately 2 m (Fig. 5). The Subis 1 deposits are relatively horizontal (21°, 160°S) but the Subis 2 section dips at a steep angle (47°, 170°S) away from the center of the platform. Large benthic foraminifera, coralline algae, and corals are the dominant constituent grain types in these localities. Although abundance of corals varies throughout the whole Subis 2 section, corals are present in all beds, making up from 1%–47% of the fossil content. In contrast, at the Subis 1 locality corals are present in only a few beds in the lower part of the section but are more common toward the top. Four different facies were observed in the Subis 1 section: (1) sandy silt: this facies is characteristic of the lowest part of the section. It contains large benthic foraminifera (*Eulepidina*) in a fine-grained matrix and in some beds contains terrigenous material (approximately 3%). (2) Foraminiferal–algal wackestone to packstone: skeletal elements (large benthic foraminifera and coralline algae) are enclosed in a light-gray micrite matrix. (3) Coral floatstone: facies characteristic of the top of the section contains mostly coral fragments embedded in a fine beige micrite. (4) Grainstone: this facies contains coral fragments, large benthic foraminifera (*Nephrolepidina*, *Eulepidina*), and coralline algae. The skeletal fragments are reworked and rounded. In contrast, only one

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FIG. 5.—Stratigraphic sections of four localities (Besungai, Mulu Broken Hill, Subis 1 and Subis 2) indicating lithologies, bedding, and faunal constitutents. Dunham (1962) carbonate classification categories are indicated adjacent to the stratigraphic sections: M = mudstone, W = wackestone, P = packstone, and G = grainstone. Bar diagrams show changes in relative abundance of constituent types along the section. Each bar diagram represents a single sample. The samples shown here are a subset (15 samples) of all analyzed samples (55 samples). Samples were chosen from the bottom and top of each section and evenly spaced every 20 m in two longer sections (Besungai and Subis 1).

distinct facies is observed in the Subis 2 locality: coral–foraminiferal packstone. This facies contains mainly corals and large benthic foraminifera associated with subordinate coralline algae and mollusk fragments embedded in a fine white matrix. (5) Coral framestone facies were also observed in cliffed sections above Subis 2 and in one adjacent quarry; however, the sites were not suitable for sample collection because of the danger of falling rocks. Recrystallized branching corals were observed.

Paleoenvironmental Interpretation.—The Mulu Olistolith and Subis localities show different depositional environments. Absence of bedding in the Mulu Olistolith locality and the coral framestone facies (as described above) suggest the nearby presence of a reef (Table 1) (James and Bourque 1992; Flügel 2010). However, it is difficult to determine the extent of the reef. Although corals were found *in situ* in framestone it is not possible to place the olistolith in the context of a ramp/platform. It was most likely patchy or a fringing reef rather than a substantial barrier reef because there is no *in situ* evidence of reef framestone in the rest of the Melinau Limestone. Prior to the late Oligocene hemipelagic sediments were typical of the Melinau basin (Wannier 2009). Wannier (2009) suggested that the Mulu Olistolith represents the remains of a narrow reefal area preserved only in the rafted blocks scattered within the younger Setap Shale Formation, indicating rapid subsidence. The facies observed in the Subis 1 section suggest a changing depositional environment during growth of the Subis platform with decreasing terrigenous sediment input through time. Higher abundance of corals toward the top of the section might indicate an increasingly stable environment allowing the proliferation of corals or the progradation of the reef framework over previous shallow-shelf or turbid lagoonal sediments (Table 1) (Ahr 1973, 1998; Burchette and Wright 1992; James and Bourque 1992; Geel 2000; Flügel 2010). The shallow-shelf or turbid lagoonal sediments contain some corals, but these are reworked and transported, and in combination with foraminifera and coralline algae embedded in micrite matrix are typical for mesophotic to oligophoic low-energy environments (Folk 1965; Pomar 2001; Zamagni et al. 2007; Novak et al. 2013). The grainstone facies observed toward the top of the section suggests a higher-energy/shallower-water environment (Folk 1965). This pattern might correspond with changes from a predominantly reef shoal environment (in the lower parts of the logged section) to a reef framework at the top of the Subis Limestone Formation. Coral–foraminiferal packstone facies observed in the Subis 2 locality situated on the flanks of Subis 1 locality suggests a fore-reef slope environment (James and Bourque 1992; Flügel 2010).

Changes in Biotic Composition

The relative abundance of foraminifera continuously decreases through time. Corals first appear in samples from the late Oligocene and rapidly increase in abundance thereafter (Fig. 6). The ANOSIM test showed a significant dissimilarity in constituent composition among both sites ($R = 0.3889$, $p = 0.001$) and age groups ($R = 0.3007$, $p = 0.001$). This could indicate the presence of different environments in different ages. The coefficients of variation of the three most abundant groups of skeletal constituents (corals, total foraminifera, total algae) show no obvious pattern within age categories or localities (Table 2).

The nonmetric multidimensional scaling (NMDS) ordination of lithological samples shows a gradual change from Eocene foraminifera-dominated environments to Miocene coral-dominated ones (NMDS axis 1). NMDS axis 2 shows a gradient from deep to shallow (from oligophotic to euphotic) based on the environmental preferences of the observed foraminifera (Hallock 1986; Novak et al. 2013). Most constituent type categories have a significant influence on the ordination (Table 3).

The ternary plot of abundances of the three most abundant skeletal constituent types (corals, total foraminifera, and total algae) reveals an increase in their variation from the Eocene to Miocene (Fig. 7). The Eocene samples occupy only a limited area on the plot. This area increases in the Oligocene samples. In contrast, the early Miocene samples spread across most of the plot surface enclosing both the Eocene and Oligocene samples (Fig. 7). This can be due to an increase in the rock volume, preserved lithologies, or habitat diversity. Increase in rock volume can be excluded since the volume of limestone deposits in the Melinau Limestone Formation is more extensive than the younger Subis Limestone (Tangap) Formation (Fig. 2). The preservation of different lithofacies types is an ever-present issue in paleontology (Smith and Benson 2013) in addition to taphonomic considerations (such as fragmentation, encrustation, and bioerosion) (Behrensmeyer et al. 2000; Nebelsick et al. 2010), and could also bias the results. However, both our quantitative and qualitative data agree with previously described carbonate platform environments from Sarawak (Liechti 1960; Adams and Haak 1962; Adams 1965, 1970; Haile 1974; Hutchison 2005; Wannier 2009). Therefore we interpret the increase of polygon area on the ternary plot from the Eocene to the Miocene as an increase in habitat diversity.

DISCUSSION

Interpretation of past shallow-marine carbonate environments and their community composition in Sarawak reveals an increase in habitat diversity from the Eocene to Miocene. Mesophotic/oligophotic foraminifera/algae-associated slope environments are typical for the Eocene study areas. Coral-reef–associated environments (reef shoals and patchy reefs) emerge sometime from the Oligocene into the early Miocene when coral-reef framestoneis found. However, foraminifera/algae-associated environments do not disappear in the Miocene (Fig. 7). The Eocene environments have low biotic structural complexity whereas increasing reef association enhances the rugosity (measurement of substrate topographic complexity) of the Miocene environments. Increased structural complexity is positively correlated with increases in habitat diversity (Simpson 1949; MacArthur and MacArthur 1961; MacArthur 1967; Lack 1969; Roberts and Ormond 1987; Dustan et al. 2013). We raise the hypothesis that the increase in the variability of habitats initiated the increase in marine diversity (Roberts and Ormond 1987; Tews et al. 2004; Tokeshi and Arakaki 2011) contributing to the origin of the Indo-Pacific marine biodiversity hotspot sometime between the Eocene and the early Miocene (Renema et al. 2008). This pattern of habitat diversity increase is not unique for Sarawak but has also been reported from the Tonasa Limestone in South Sulawesi (Wilson and Bosence 1996), the offshore Malampaya buildup from the island of Palawan (the Philippines) (Fournier et al. 2005), and the Kerendan platform in Central Kalimantan (Indonesia) (Saller and Vijaya 2002) during the same time interval.

Results from point-counting analysis of thin sections and the analysis of the skeletal constituent types provide both quantitative data on the most important carbonate producers and statistically robust measurements to evaluate past marine environments in Sarawak. The point-counting data combined with the field study of rock fabrics, depositional geometries, and stratigraphic sequences allowed the evaluation of spatial and temporal patterns in Sarawak carbonate platform development. Due to the fragmentary distribution of the localities only a fraction of each carbonate platform could be sampled. This could have resulted in an underrepresentation of the variation in constituent types in some of the time intervals. This is particularly true of the Oligocene where only a few sections could be measured, potentially resulting in an underrepresentation of the available habitats in this interval.

The apparent increase in habitat diversity was accompanied by a gradual change in the dominant carbonate constituent. Foraminifera-

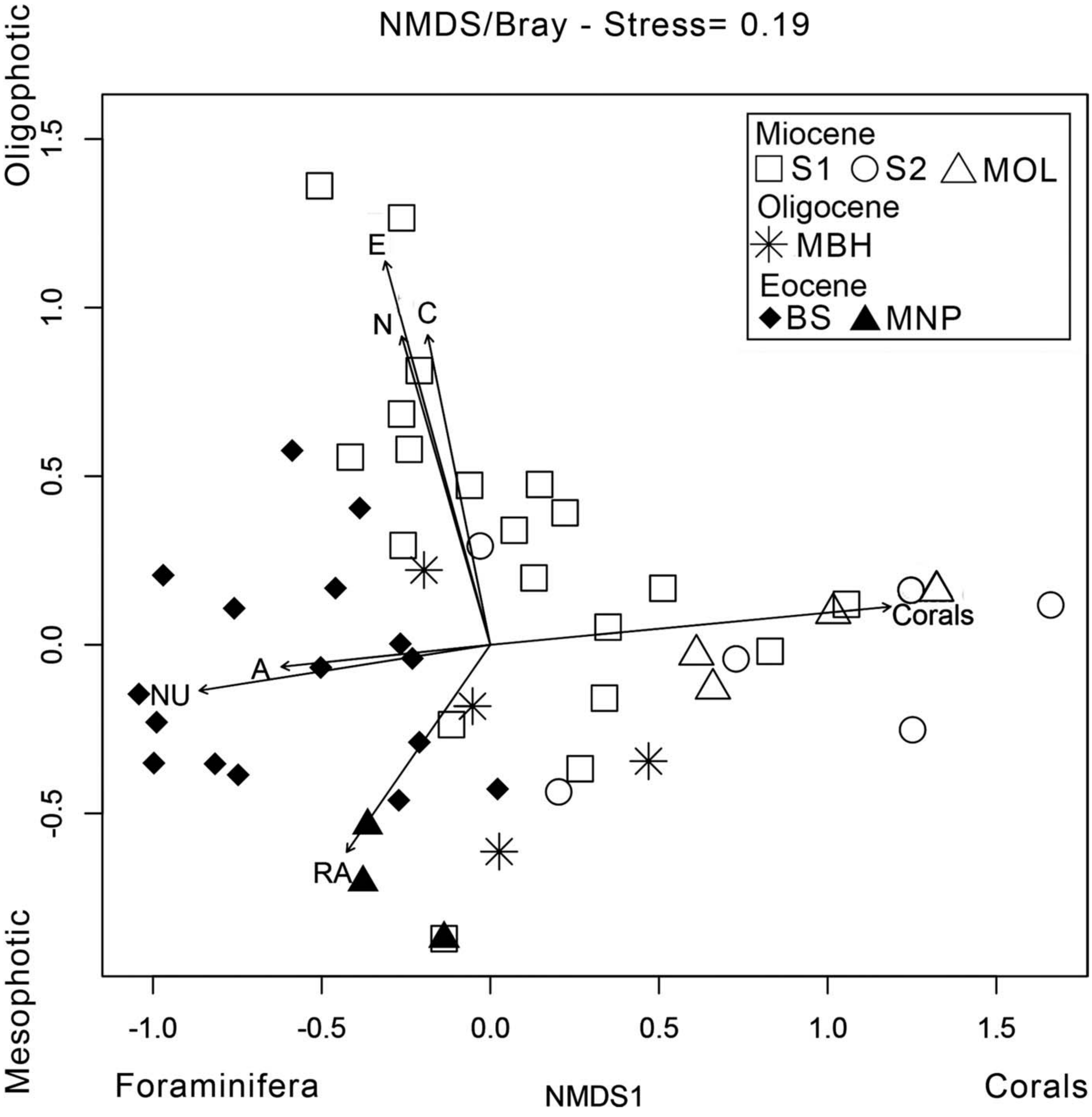

FIG. 6.—Nonmetric multidimensional scaling (NMDS) ordination of lithological samples from six localities from Sarawak based on skeletal constituent types. Arrows are vectors that show which constituent type drives the similarity among samples. The length of the arrow indicates the strength of the constituent type prediction, i.e., weak predictors have shorter arrows than strong predictors. The NMDS1 axis shows a gradient from the foraminifera-dominated environments in the Eocene samples to coral-dominated environments in the Miocene samples. Shallow (mesophotic)/deep (oligophotic) gradient indicated on the NMDS2 axes. A = *Amphistegina*, BS = Besungai, C = *Cycloclypeus*, E = *Eulepidina*, MBH = Mulu Broken Hill, MI = milioline foraminifera, MNP = Mulu National Park, MOL = Mulu Olistolith, N = *Nephrolepidina,* NU = *Nummulites*, RA = red coralline algae, S1 = Subis 1, S2 = Subis 2.

dominated carbonates were characteristic of the late middle and late Eocene whereas from the late Oligocene into the early Miocene corals became the main carbonate producers. Overall patterns of the foraminifera-dominated versus the coral-dominated carbonates in the Indo-Pacific show an abrupt change to coral dominance at the Oligocene-Miocene boundary (Wilson 2008). However, our results support studies from Sabah (Malaysia) (McMonagle et al. 2011), Central Kalimantan (Indonesia) (Saller and Vijaya 2002), and Palawan Island (the Philippines) (Fournier et al. 2005) that show an earlier start to coral dominance in the Oligocene. The generality of this is currently unknown because to date it has only been recorded at three localities in Borneo and one from the Philippines and therefore, might be specific only to large carbonate platforms of the southern margin of the South China Sea. Regardless, capturing the diversity and spatial distribution of late Eocene–early

TABLE 2.—*Coefficients of variation of the three most abundant groups of skeletal constituents (corals, total foraminifera, total algae) in our three age categories and six localities.*

	Coefficient of variation		
	Corals	Foraminifera	Algae
Age			
late Middle–late Eocene	0	0.24	0.69
late Oligocene	2	0.35	0.27
early Miocene	1.11	0.77	0.83
Site:			
Besungai	0	0.2	0.78
Mulu National Park	0	0.21	0.28
Mulu Broken Hill	2	0.35	0.27
Mulu Olistolith	0.19	0.75	0.92
Subis 1	1.57	0.56	0.62
Subis 2	0.73	0.87	1.38

TABLE 3.—*The goodness of fit statistic of the constituent types on the ordination is shown here as a squared correlation coefficient (r^2). The significance of fitted vectors of the constituent types is assessed using 999 random permutations (p).*

Constituent type vector	r2	p
corals	0.8048	0.001
Nephrolepidina	0.5135	0.001
Eulepidina	0.7877	0.001
Cycloclypeus	0.4975	0.001
Miogypsina	0.0229	0.538
Nummulites	0.4319	0.001
Amphistegina	0.2197	0.002
milioline foraminifera	0.0446	0.317
green algae	0.0141	0.711
coralline red algae	0.3166	0.001

Miocene marine habitats provides important clues to interpret temporal patterns in the origination of biodiversity.

Carbonate deposits in the Eocene formed a large-scale carbonate platform, whereas in the Miocene carbonates developed on smaller scale local tectonic highs (Liechti 1960; Adams and Haak 1962; Adams 1965, 1970; Hutchison 2005; Wilson et al. 2013). The shape of the platform is determined by the underlying topographical relief and is driven by tectonic events. During the Eocene the Melinau limestone was deposited on the Rajang accretionary prism, which has undergone uplift due to the docking of the Luconia block in the middle Eocene. The upper Eocene tectonic environment has been interpreted as a subsiding shelf (Liechti 1960; Adams 1965) or possibly a wedge-top basin (Wannier 2009) distant from land. No reef buildups have been observed (Wilson 2002) and therefore an unrimmed or ramp platform is most likely in this setting (Bosence 2005). The Miocene onset of compressional tectonics in the South China Sea mediated the development of the unattached Subis platform (Hinz and Schlüter 1985; Hall 2002). Interplay of the tectonic regime and more variable eustatic sea level from the Eocene to the early Miocene (Zachos et al. 2001, 2008) might have controlled the increase in diversity of habitats we observed. Local tectonism has been identified as a main driver of the increase in the habitat diversity in the region (Wilson and Bosence 1996; Saller and Vijaya 2002; Fournier et al. 2005).

We found substantial evidence for changes in abundance of the dominant community constituent (foraminifera or corals) from the late middle Eocene to the early Miocene, but so far we have no data on their diversity. A complex relationship exists between foraminiferal abundance and their diversity in the Indo-Pacific: during the Eocene foraminiferal abundance is high but diversity is low; in the Oligocene abundance is still relatively high but diversity begins to increase; diversity continues to increase during the early Miocene (reaching a maximum in the middle Miocene) but with a concomitant decrease in abundance (Renema 2007). Coral abundance and diversity are also not necessarily related (Johnson et al. 2008)—coral dominated carbonates (high abundance) can be the result of the proliferation of just a few coral species (low diversity). In the Indo-Pacific, Eocene coral diversity is low (Wilson and Rosen 1998) and the post-early Miocene diversity is high (Bromfield and Pandolfi 2011), but our understanding of the exact timing and rate of the increase is limited, and spans the Oligocene to early Miocene interval. Our future taxonomic analysis will reveal if increases in coral abundance are accompanied by increases in their diversity.

Modern coral reefs and the biodiversity they support are under threat due to rapidly changing environments (Roberts et al. 2002) and anthropogenic stressors (Pandolfi et al. 2003, 2011). Environmental change is not unique to the present day and is always accompanied by taxonomic and distributional changes in marine ecosystems (Eiserhardt et al. 2013). The change from foraminifera-dominated to coral-dominated environments we observed during the Oligocene to Miocene illustrates this point. The main drivers of this change appear to be local tectonics and an increase in habitat diversity. Historical processes (i.e., tectonics) and habitat heterogeneity have been argued to be factors driving the biogeography of modern corals in the region (Keith et al. 2013). Therefore, our discovery of stepwise origin of coral-dominated carbonate environments provides insight into the development of the Indo-Pacific marine biodiversity hotspot.

CONCLUSIONS

Investigation of the paleoenvironmental conditions on shallow-water carbonate platforms during the time of active tectonism (opening of the South China Sea) provided an opportunity to assess the Eocene–Miocene habitat diversity in Sarawak, Malaysia and its implication for the origin of the Indo-Pacific marine biodiversity hotspot.

1. The Eocene study sites are characterized by foraminiferal–algal associations characteristic of mesophotic–oligophotic environments.
2. The first coral fragments were recorded at an Oligocene site deposited in a fore-reef environment.
3. Miocene deposits (in some parts of the section) show a high abundance of corals associated with fossil reefs.
4. The middle Eocene to the lower Miocene limestone deposits from Sarawak show an increase in habitat diversity accompanied by a decrease in foraminiferal abundance and an increase in coral abundance through time.
5. The observed pattern of faunal turnover shows that corals were already increasing in abundance during the Oligocene. However, this increase preceded reef expansion in the Indo-Pacific region previously reported to have occurred from the early Miocene (Wilson 2008).

SUPPLEMENTAL MATERIAL

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

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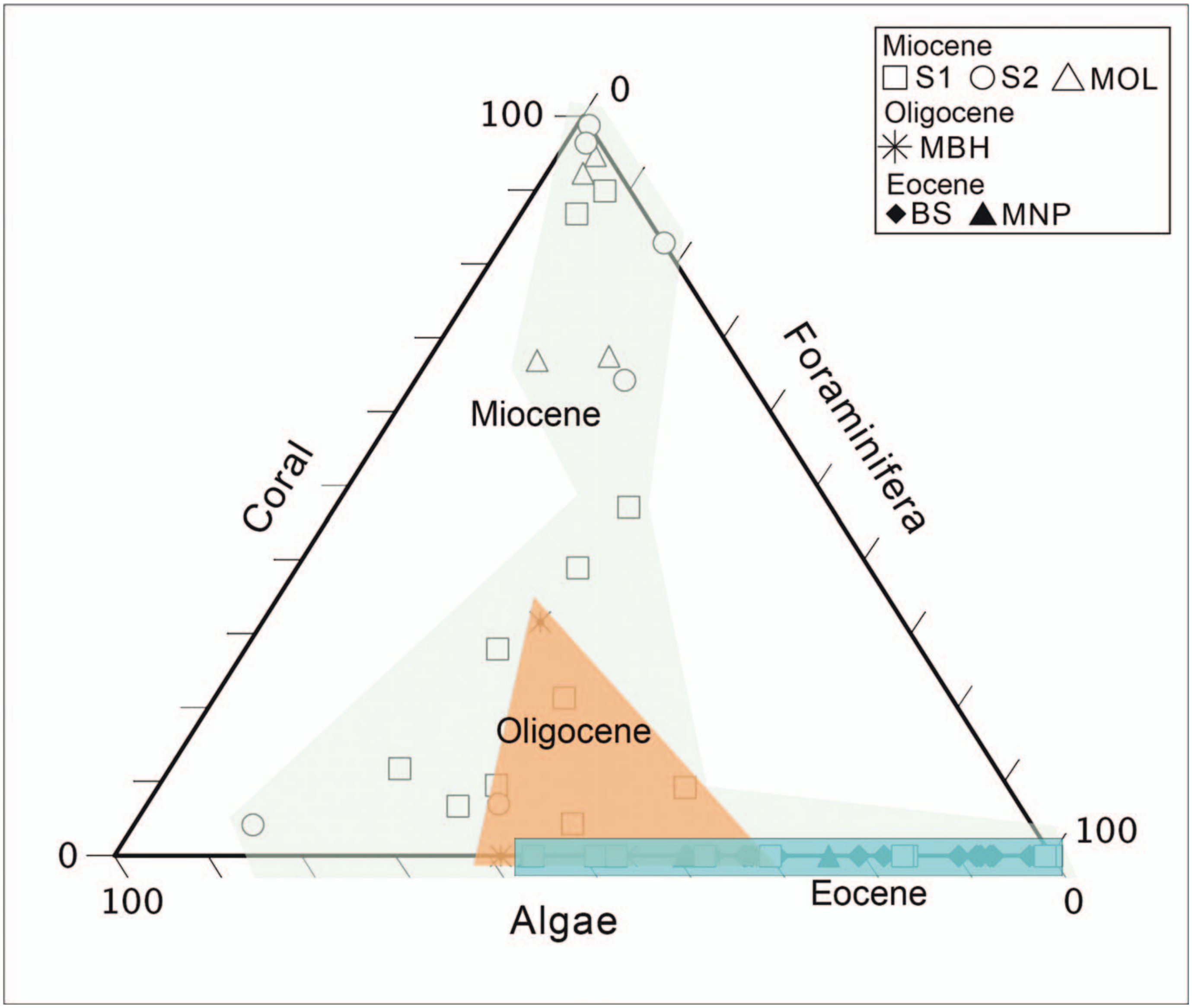

FIG. 7.—Ternary plot showing relative abundances of the three most dominant constituent types—corals, total foraminifera and total algae—from each of 55 samples collected from six study localities (BS = Besungai, MNP = Mulu National Park, MBH = Mulu Broken Hill, S1 = Subis 1, S2 = Subis 2, and MOL = Mulu Olistolith) in Sarawak, Malaysia. The polygons enclose samples of the same age (blue = Eocene, orange = Oligocene, gray = Miocene). The variation in constituent composition increases from the Eocene to the Miocene.

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