

PALEONTOLOGY

Differences in extinction rates drove modern biogeographic patterns of tropical marine biodiversity

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Marine biodiversity in the Coral Triangle is several times higher than anywhere else, but why this is true is unknown because of poor historical data. To address this, we compared the first available record of fossil cheilostome bryozoans from Indonesia with the previously sampled excellent record from the Caribbean. These two regions differ several-fold in species richness today, but cheilostome diversity was strikingly similar until the end of the Miocene 5.3 million years ago so that the modern disparity must have developed more recently. However, the Miocene faunas were ecologically very different, with a greater proportion of erect and free-living species in the Caribbean compared to the less well-known Coral Triangle. Our results support the hypothesis that modern differences in diversity arose primarily from differential extinction of Caribbean erect and free-living species concomitant with oceanographic changes due to the uplift of the Isthmus of Panama, rather than exceptional rates of diversification in the Indo-Pacific.

INTRODUCTION

Marine species richness in the Coral Triangle region of Southeast Asia, commonly referred to as the Coral Triangle, is two to several times greater than in the tropical western Atlantic (1). Most well-studied marine groups exhibit the same pattern. The greatest reported differences are for reef fishes (3689 versus 891 species) (2); reef corals (627 versus 73 species) (3); and coral reef-associated crustaceans, which are about 10 times more diverse in the Indo-West Pacific than in the Caribbean (4). The same pattern applies to bivalves and gastropods (5), and larger benthic foraminifera (6). A similar diversity contrast has been suggested for less well-studied cheilostome bryozoans. More than 500 species have been reported from Indonesia (7), and more than 300 from the Philippines (8), whereas only 221 and 232 species are estimated to be present in the Recent cheilostome fauna of the Caribbean (9) and the Gulf of Mexico (10), respectively. The data are based on extensive regional surveys in both regions but almost certainly underestimate total regional diversity because they are based on old taxonomy. More critical recent morphometric and genetic analyses of a limited number of Caribbean genera have revealed numerous complexes of cryptic species (11), and the same is likely for the Indo-West Pacific (12).

When and why these striking differences arose and how they have been maintained are controversial questions. Biologists have long invoked five conflicting theoretical mechanisms as explanatory models of high Coral Triangle diversity, variously viewing the region as a (i) center of origin, (ii) center of overlap, (iii) center of accumulation, (iv) center of survival, or (v) center of mid-domain overlap (13). Depending on the target group investigated and whether or not both fossil and present-day data are analyzed, results are more consistent with different mechanisms, suggesting that a single theory alone is inadequate to explain the high diversity in the region (13, 14).

Time-calibrated molecular phylogenies for reef-associated tetraodontiform fishes (15) and gastropods (16) suggest that their main species diversification in the Coral Triangle region occurred around 20 to 25 million years (Ma) ago. However, the paleontological record has been too little studied, and there are no comparative data for fossil species to

provide a definitive quantitative test (17). In contrast, the Caribbean is also a major center of Cenozoic tropical marine biodiversity with extensive paleontological data on species richness of corals, mollusks, bryozoans, and foraminifera from the Oligocene to today (18). Diversity in most groups has generally increased over the past 25 Ma until a regional mass extinction about 2 Ma ago (19, 20).

Although still limited, we now have some comparative paleontological data from Indonesia to compare with the excellent Caribbean record. A detailed study of Miocene corals from Indonesia demonstrated species richness of about 100 species for each stage of the Miocene, which is only about 25% greater than contemporaneous faunas from the Caribbean (19). In addition, preliminary analyses of ostracods from the tropical western Pacific showed that species richness has increased over the past 25 Ma, with a big jump to approximately modern values beginning about 5 Ma ago (21). However, comparable data for Caribbean ostracods are sparse.

We used extensive paleontological collections of Caribbean and Indonesian cheilostome bryozoans (22) to address the timing of the divergence in species richness between the two regions and to evaluate the relative contributions of differential rates of origination and extinction to the patterns we observe today. Cheilostome bryozoans offer a model system because they are abundant, small, and well-preserved components of Cenozoic tropical shelf sediments (23). Moreover, their skeletal complexity provides a wealth of morphological characters enabling a precise species-level taxonomy (24), whereas variations in their life history and ecology are readily apparent from differences in colony form. Caribbean faunas are well documented from the early Miocene (approximately 18 Ma ago) to the Recent in Florida, the Dominican Republic (DR), and Panama (25, 26). Indonesian collections are from East Kalimantan and extend from 17.5 to 5.3 Ma ago (22). The fossil samples analyzed are provisionally assumed to be representative of the two regions as a whole. We reanalyzed all available fossil collections to develop a new, taxonomically standardized Caribbean database to compare with the Indonesian material (data sets S1 to S11).

RESULTS

Cheilostome origination and extinction in the Caribbean

Caribbean cheilostome species richness increased nearly threefold from the early to the middle-late Miocene (18.3 to 5.3 Ma ago) and changed

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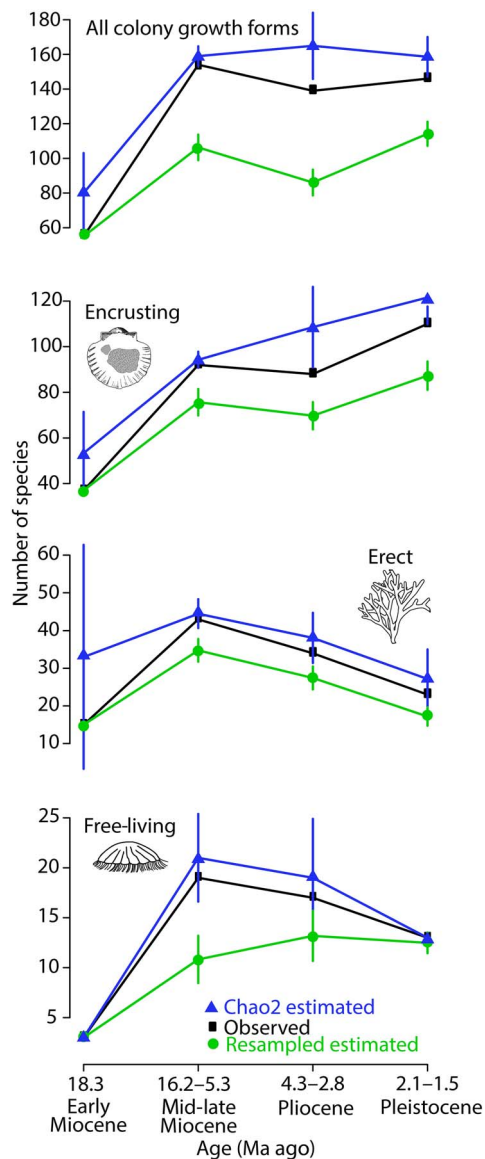


Fig. 1. Changes in Caribbean cheilostome species richness over the past 18 Ma. Observed counts (black squares), Chao2 estimates (blue triangles), and resampled estimates (green dots) of cheilostome species diversity over geological time for all colony growth forms combined and for encrusting, erect, and free-living only.

little afterward (Fig. 1 and fig. S1). The generally strong agreement between the observed and estimated patterns of diversity suggests that these patterns are highly robust. However, trends in diversity for three major categories of colony form—encrusting, erect, and free-living—are strikingly different. Encrusting species diversity increases throughout the time series. In contrast, erect and free-living species diversity increased from the early to middle-late Miocene (18.3 to 5.3 Ma ago) but subsequently declined steadily. These patterns become even more striking when categories of colony form are expressed as percentages of the entire fauna within each time interval (Fig. 2). The proportions remained stable until 5.3 Ma ago when erect species precipitously declined, whereas free-living species peaked before declining over the past 2 Ma in favor of encrusting species.

Encrusting colony forms make up the largest proportion (80%) of the 124 extant species in our fossil data set that are still extant. Only 20% of the 42 erect and 15 free-living species in the data set are still living today, confirming earlier results based on less complete data (27–29). High rates of extinction of erect species are epitomized by the genus *Metrarabdotos*, with only 2 of 14 species recorded in our data set extant (30), and for free-living species by the genus *Discoporella*, with 3 of 11 species still extant (29).

Patterns of diversity change were examined by counting the numbers of species within each 1-Ma time interval. The results indicate significant species origination at 18.3 Ma ago (Fig. 3). The Chipola Formation contains the oldest occurrences for all the cheilostome bryozoan species recorded in its fauna with the sole exception of *Nellia tenella*, which first appeared 70 to 65 Ma ago and has been considered a “living fossil.” Thirty of the 54 first occurrences were restricted to the Chipola Formation, and their subsequent demise produced the first peak of extinction at 18 Ma ago. The remaining 24 species were also found in younger units, with the majority extant (fig. S2). Diversification peaked around 7 Ma ago and subsequently around 4 Ma ago.

Patterns of extinction show two clear peaks at 5 Ma ago (Miocene-Pliocene boundary) and 2 to 1 Ma ago, driven mainly by erect and free-living taxa. The bulk of species responsible for the extinction peak at 5 Ma ranges back to 18 to 15 Ma ago, whereas the 2-Ma extinction peak is caused by the disappearance of species that range back to 10 to 8 Ma ago.

Comparison of Caribbean and Indonesian diversity

Cheilostome species richness, which is dominated by encrusting species, is similar in the two regions over the range represented by the Indonesian collections, which cover the middle-late Miocene (16 to 5 Ma ago) (Fig. 4). Although there are fewer species in the Indonesian collections than in the Caribbean (107 and 151 species, respectively) due to less intensive sampling (65 collections versus 111 collections), estimates of diversity based on Chao2 and resampling are not significantly different. This result is further supported by the similar shapes of the individual-based cumulative collecting curves for the two regions being compared, which suggest that the differences in total numbers of cheilostome species reflect real differences in true diversity (Fig. 5).

In addition to estimate of regional diversities determined by pooling samples together and assuming them to be representative of the two regions as a whole, we also calculated species richness for each site. In Indonesia, local species richness ranges from 1 to 32 (median, 7.5; mean, 9); no pattern of distribution can be recognized according to facies type, environment, or age of the sample (22). In the Caribbean, local species richness ranges from 1 to 44 (median, 18; mean, 18.6), with the variability in apparent diversity partly a function of preservation (25). These differences are statistically significant (t test, $P = 6.213 \times 10^{-14}$).

The two faunas are ecologically very different because of the greater proportion of erect (28% versus 24%) and free-living (12% versus 5%) species in the Caribbean compared to Indonesia. As it is apparent from the shapes of the cumulative collecting curves (Fig. 5), not all the growth forms are sampled with the same completeness. All the collecting curves for the Caribbean level out, suggesting that the sampling is saturated, whereas collecting curves for Indonesia differ greatly depending on the colony form. The collecting curve for erect species rises steeply before leveling out, the collecting curve for encrusting species shows a slight tendency toward flattening, but the collecting curve for free-living species suggests that the sampling was not saturated.

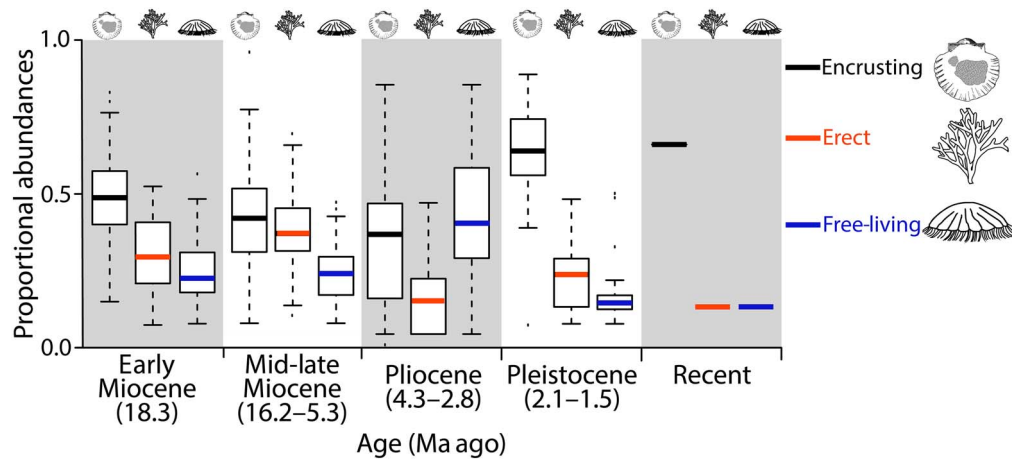


Fig. 2. Neogene-Recent histories of Caribbean cheilostome bryozoan colony growth forms. Results are shown as proportional abundances. “Recent” refers to the proportions of species present in our fossil data sets that are still living today.

DISCUSSION

The similarity in Indonesian and Caribbean Miocene cheilostome diversity is statistically robust despite differences in the mode and density of sampling, the latter being far more limited in Indonesia. Thus, the modern differences in cheilostome diversity must have arisen within just the last 5 Ma. New collections from the Coral Triangle are needed to determine when the regional differences arose. Nevertheless, our results clearly negate the hypothesis that high cheilostome diversity in the Coral Triangle today is the result of exceptionally high diversification over tens of millions of years (31).

The newly integrated Caribbean record also demonstrates that Caribbean cheilostome diversity increased throughout the Miocene until stalling in the Pliocene due to mass extinction of erect and free-living species associated with the collapse in Caribbean planktonic productivity following the final closure of the Central American Seaway (32). Total cheilostome diversity did not decline, however, because of the continued diversification of encrusting species that make up most of the faunas in both regions. Caribbean extinction exhibited two peaks at the beginning of the Pliocene and Pleistocene epochs roughly 5 and 2 Ma ago. The Pliocene extinction is confounded with a shift in the primary sampling locations from the DR in the Miocene to Panama in the Pliocene, but the records of exceptionally well-studied genera with collections from throughout the Caribbean suggest that the pattern is robust (27, 30).

The Caribbean extinction of erect and free-living cheilostomes coincided with the closure of the Isthmus of Panama. Morphological evidence for clonal propagation strongly supports the hypothesis of a causal mechanism between the extinction of free-living species and the collapse in primary productivity due to oceanographic changes (29, 33). The exceptionally low abundance and diversity of Indonesian erect and free-living species is a mystery, especially because these colony forms are generally more robust, better preserved, more conspicuous, and therefore more likely to attract attention than fragile, generally smaller, and easily overlooked encrusting species (34). However, in terms of the proportions of species classified according to major colony forms, the Indonesian diversity in the middle-late Miocene reflects modern tropical bryozoan faunas, which, on average, contain 78% of encrusting species, 19% of erect species, and 3% of free-living species (34). Cryptic encrusters are the most common bryozoans in modern tropical reefs pantropically.

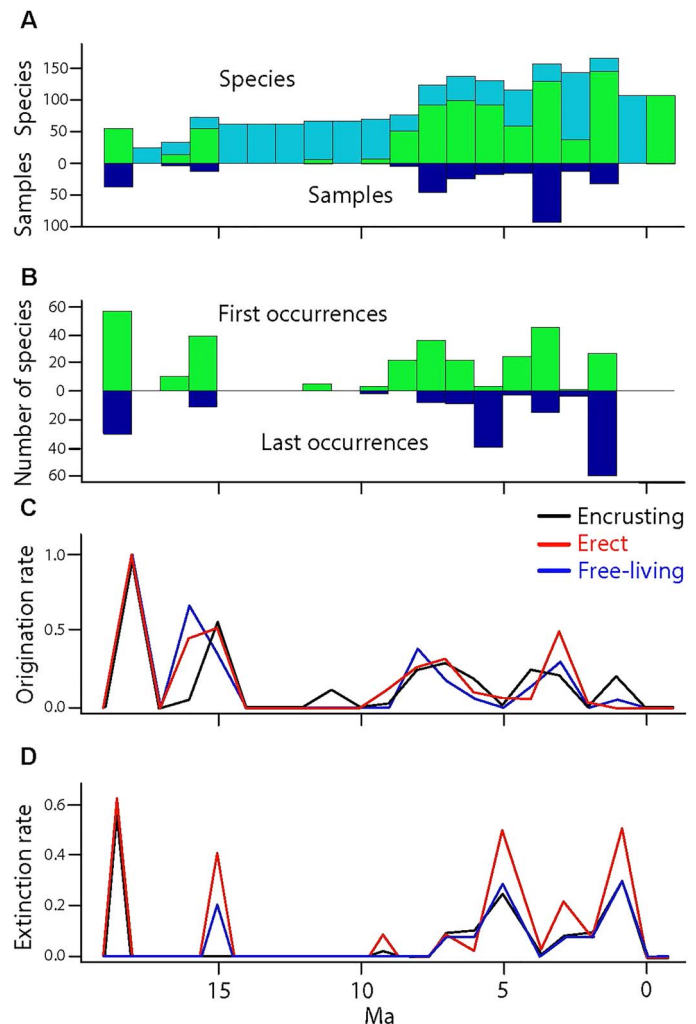


Fig. 3. Measures of cheilostome taxonomic turnover and sampling intensity in the Caribbean for 1-Ma time intervals for the past 18 Ma. (A) Range-through species richness (in green, the number of species effectively found in each 1-Ma time interval) and numbers of samples, (B) numbers of first and last occurrences in each sampled million year interval, (C) origination, and (D) extinction rates per colony growth form (black, encrusting; red, erect; blue, free-living) per million year subinterval.

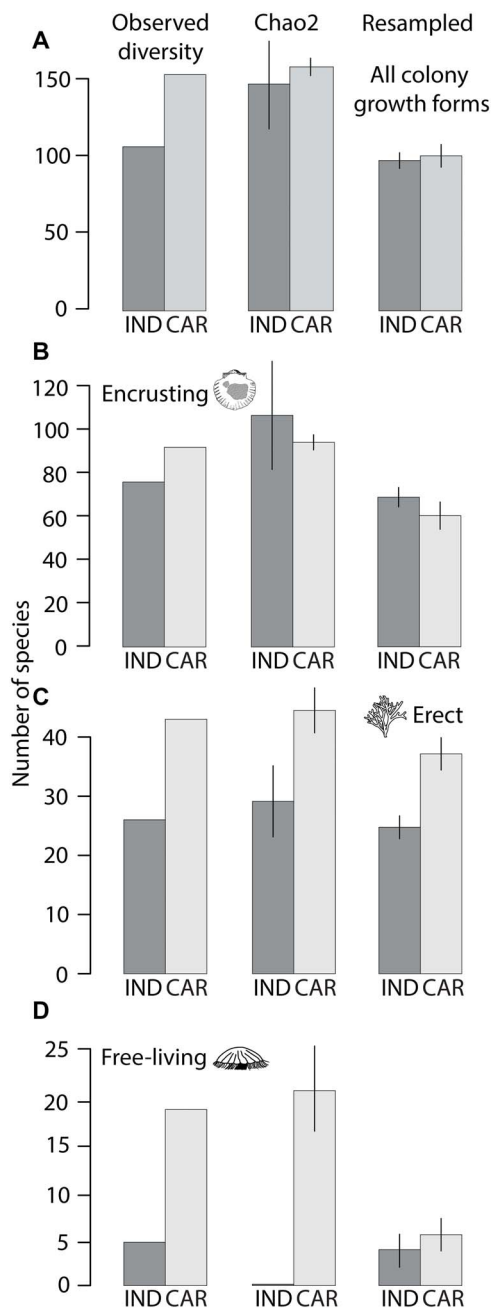


Fig. 4. Observed, Chao2, and resampled estimated measures of cheilostome species diversity in the middle-late Miocene (16 to 5 Ma ago) in Indonesia (IND) and the Caribbean (CAR). Results are presented for all colony growth forms combined and for encrusting, erect, and free-living only.

The history of cheilostome diversity in the Caribbean is very similar to that of reef corals, mollusks, and fishes in that progressively higher diversity was halted, and in the case of corals reversed, from about 5 to 2 Ma ago (35). Similar mass extinction of highly diverse coral and cheilostome faunas occurred approximately 6 Ma ago when the Mediterranean was isolated from the Atlantic during the Messinian salinity crisis from which diversity never fully recovered. We conclude that the exceptional diversity of the Coral Triangle today reflects the absence of

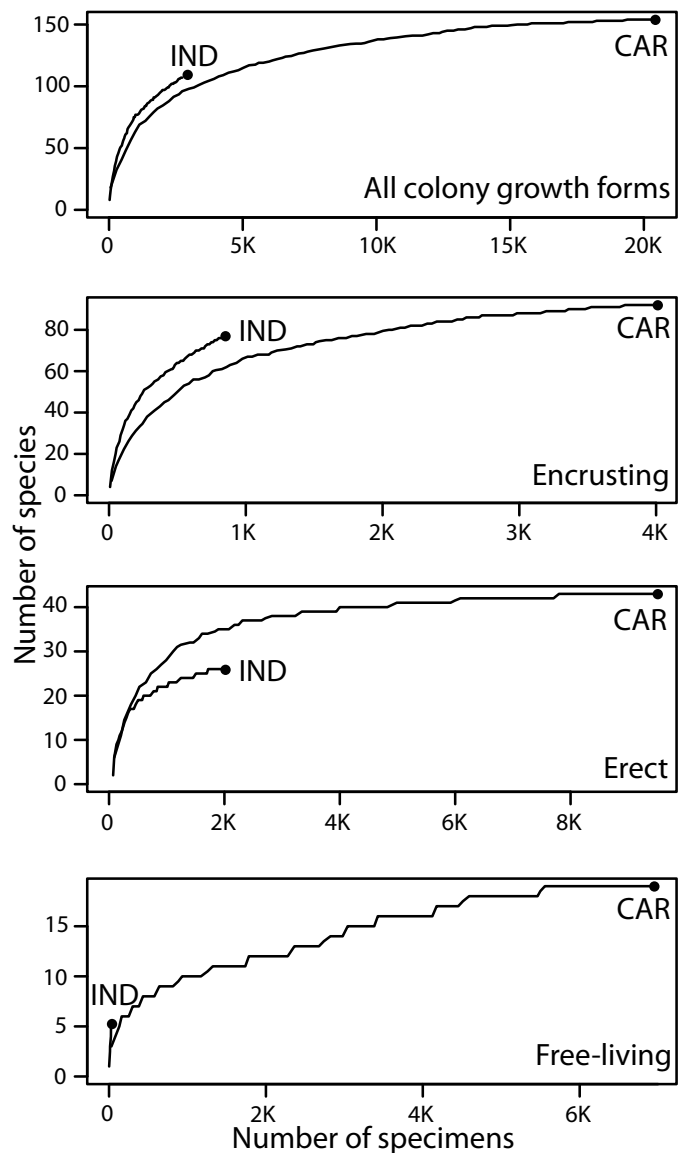


Fig. 5. Diversity of cheilostome bryozoan species for the middle-late Miocene for Indonesia and the Caribbean. Cumulative collection curves are for the middle-late Miocene for all colony growth forms combined and for encrusting, erect, and free-living only.

mass extinction as much as any exceptional rates of diversification compared to more peripheral regions.

MATERIALS AND METHODS

Cheilostome bryozoans from standardized bulk sediment samples in existing museum collections were used to determine species diversity from Indonesia and the Caribbean. Collections from Indonesia are from East Kalimantan and are housed at the Natural History Museum, London (NHMUK). Collections from the Caribbean include (i) early Miocene samples from the Chipola Formation in Florida, deposited at the Florida Museum of Natural History (FLMNH) in Gainesville; (ii) middle-late Miocene samples from the Baitoa, Gurabo, and Cercado

formations in the DR and the Gatun Formation in Panama; and (iii) Pliocene and Pleistocene samples from several formations in the Bocas del Toro and Limon basins in Panama. All the DR and Panama specimens are housed at the National Museum of Natural History (NMNH), Smithsonian Institution, Washington, DC.

To understand the effects of sampling on diversity estimates, we compared observed richness with Chao2 diversity and resampled richness (Figs. 1 and 4). Chao2 is a nonparametric estimator of the number of undetected species calculated by adding a correction factor to the observed species richness that corresponds to the square of the number of uniques (species occurring in one sample) divided by two times the number of duplicates (species occurring in two samples), with 95% confidence interval (36, 37). This estimator is based on incidence data and provides a nonparametric lower bound of true species richness under the assumption of homogeneity among samples. Resampled-based species richness was estimated by individual-based collecting curves as the median of 100 random draws of taxon occurrences without replacement (Fig. 5 and fig. S1). This approach attempts to normalize variation in sampling completeness between the two sets of collections by drawing random subsamples to reduce the number of samples considered in each set of collections. A randomization distribution of species richness for each set of collections is obtained by repeated resampling followed by counting the number of species in each selection of samples (19). Confidence intervals are provided by the 5th and 95th percentiles of permutation distributions.

To compare regional diversity of the Caribbean during the Neogene, we divided the data set into four intervals with a similar sample size: early Miocene, middle-late Miocene, Pliocene, and Pleistocene. The Indonesian data set is limited to a single interval, the middle-late Miocene, so it is for the comparison with the Caribbean. Ages of localities were taken from several sources (22, 25, 26).

Collections used for the comparison of the two regions are from a similar range of habitats including shallow nearshore environments with seagrass meadows and patch reefs (inferred paleodepth of <5 m) to deeper shelf edge reefs (inferred paleodepth of 60 to 100 m) (38, 39). In both regions, samples are from a single sedimentary basin. DR collections are from sites little more than 100 km across in the Cibao region of the northern DR (25). Indonesian collections are from sites extending about 200 km across in the Kutai Basin (22).

Stratigraphic ranges of each taxon were estimated as extending from the lower boundary of the age of the sample in which the taxon first occurred to the upper boundary of the age assigned to the sample in which the taxon last occurred (fig. S2). Taxonomic turnover was estimated within a set of stratigraphic intervals that were 1 Ma in duration (Fig. 3). Per-interval richness was estimated both by the number of species that occurred in each bin and by counting range-through taxa that were not recovered from the bin but occurred in both earlier and later bins. Numbers of species that first or last occurred in each bin were counted and divided by total within-bin richness to produce rates of origination and extinction.

Diversity and taxonomic turnover were estimated for the full fauna and also after dividing the assemblages into three major colony growth forms following the study of Cheetham *et al.* (25): encrusting, erect, and free-living. Abundance of individuals was measured as minimum numbers on an approximate scale that codes the number of specimens in each species in a collection as 1 for 1 to 9 specimens, 10 for 10 to 99 specimens, and 100 for 100 or more specimens. All analyses were conducted in R Statistical Environment (40). All faunal data sets necessary for reproducing figures are available in the Supplementary Materials.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/4/4/eaag1508/DC1>

fig. S1. Diversity of Caribbean cheilostome bryozoan species for four time intervals from the early Miocene to the Pleistocene.

fig. S2. Stratigraphic ranges of the 285 Neogene Caribbean cheilostome bryozoan species included in our data sets.

data set S1. Diversity and abundance of cheilostome bryozoans in the Miocene Chipola Formation and the DR.

data set S2. TU and DR Miocene samples.

data set S3. Diversity and abundance of cheilostome bryozoans in the Miocene of Panama.

data set S4. PPP Miocene samples.

data set S5. Diversity and abundance of cheilostome bryozoans in the Pliocene of Panama.

data set S6. PPP Pliocene samples.

data set S7. Diversity and abundance of cheilostome bryozoans in the Pleistocene of Panama.

data set S8. PPP Pleistocene samples.

data set S9. Diversity and abundance of cheilostome bryozoans in the Miocene of East Kalimantan, Indonesia.

data set S10. Miocene samples from East Kalimantan.

data set S11. Extant species.

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