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Biogeography of Reef-Building Corals in the Mariana and Palau Islands in Relation to Back-Arc Rifting and the Formation of the Eastern Philippine Sea

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Abstract An interesting aspect of the scleractinian reef-building fauna of the Mariana Arc Islands is their relatively low diversity (ca. 254 species) when compared to other Northwest Pacific regions, such as the Phillippine Islands (ca. 411 spp.), Ryukyu and Japan Islands (ca. 381 spp.), Caroline Islands (ca. 395 spp.), and Marshall Islands (ca. 300 sp.). Out of these relatively high coral diversity island groups the Palau Archipelago in the Western Caroline Islands has a reef-building coral fauna of about 385 species, and is especially interesting for comparison with the Mariana Arc coral fauna because of the islands similar size and age, but different geologic histories.

According to current plate tectonic hypotheses the Mariana Forearc was once part of the Palau -Kyushu Ridge, from where it has been displaced to its present position at the eastern margin of the Philippine Sea by two episodes of back-arc rifting and basin development followed by active arc volcanism. A model is developed which suggests that during part of the back-arc basin formation phase of the first episode the migrating forearc may have been drowned to a depth that precluded the presence of hermatypic reef-building corals. Subsequently, during the active volcanic arc phase of the first episode, hermatypic reef-building corals could then be recolonized on shoaling West Mariana Ridge highs. The absence of marginal sea formation along the southern part of the Palau-Kyushu Ridge also suggests that shoal-water conditions and the presence of reef-building hermatypic corals along the Palau Archipelago was not interrupted during the formation of the Eastern Philippine Sea. If the Mariana Forearc was emergent during its migration from the Palau-Kyushu Ridge it is hypothesized that the coral fauna would be more similar to that of the Palau Archipelago. Evidence is given for the above model based upon the timing and stratigraphic sequence of carbonate and volcanic units on the Palau-Kyushu Ridge and Mariana Forearc and Western Mariana remnant arc ridges, Deep Sea Drilling Program data, and characteristics of the present hermatypic reef-building coral faunas of the Palau Archipelago and Mariana Forearc.

Keywords: hermatypic corals, biogeography, Eastern Philippine Sea, Mariana Islands, Palau Islands.

One of the most interesting aspects of natu-ral history is the distribution of plants and animals, both in a local context at community and ecosystem levels, and more broadly at geographic levels. Biogeography is particularly interesting at geographic scales because it invokes pathways and mechanisms by which organisms become distributed within their ranges. In this paper a brief review of reef-building coral diversity within the Northwest Pacific Ocean is given, followed by a focus on the biogeography of such corals in the Mariana and Palau Islands in relation to back-arc rifting and the formation of the Eastern Philippine Sea (Figs. 1 and 2).

Approach to the Concept of Coral Diversity

Since diversity can be measured in a number of ways, the concept of the term as used here is simply the number of taxa within a defined geographic region. Reef-building coral diversity of a geographic region is generally related to the amount of collecting effort and the degree to which all the coral habitats have been sampled. As an example, there may have been a great amount of collecting effort from shallow-water habitats within a certain geographic region, but until the deeper-water habitats are also sampled the diversity estimates will generally be underestimated. Before scuba was used as an aid to sampling, estimates of reef-

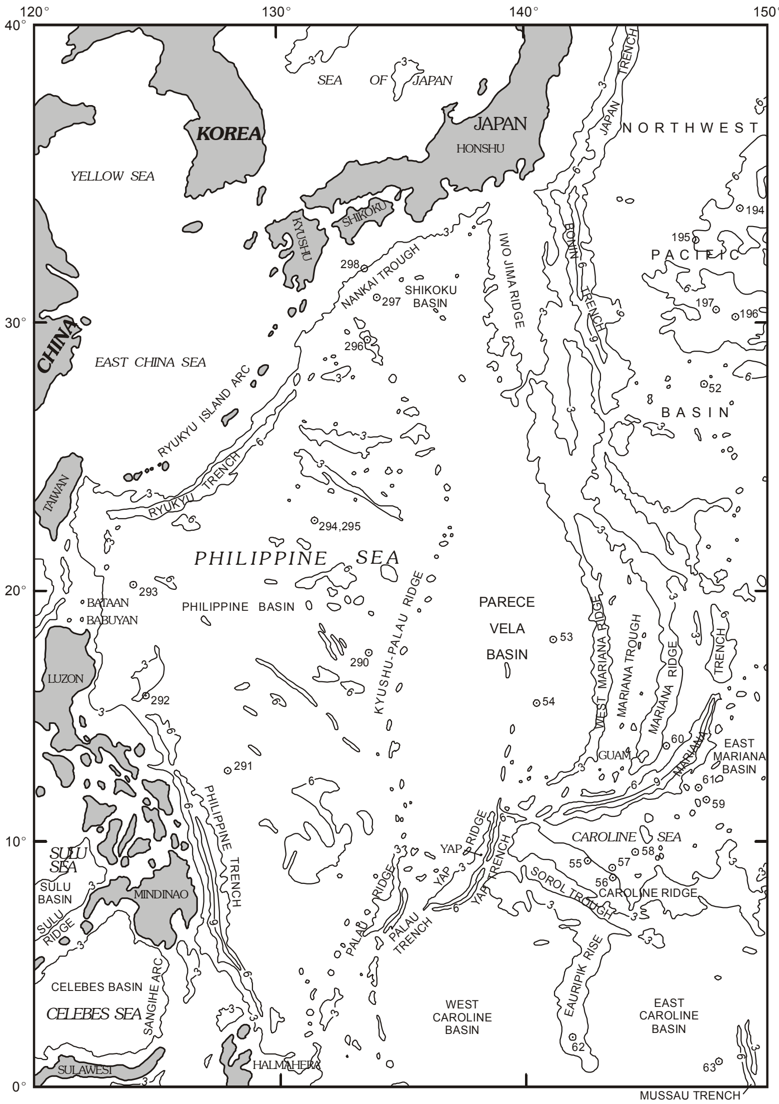

Fig. 1. Bathymetric map of the Philippine Sea and surrounding areas. Numbers refer to Deep-Sea Drilling coring sites. Contour interval=3000 meters. After Chase *et al.* (1971).

building coral diversity were generally based upon shallow-water collections, occasionally augmented with limited ship-board dredged specimens, that generally resulted in an underestimate of overall actual diversity. In the last decade or so, earlier coral diversity estimates for an increasing number of geographic locations have been greatly revised from an overall increased sampling effort as well as from scuba sampling from deeper water habitats.

Reef-building coral diversity estimates used in this paper are based upon the authors collec-

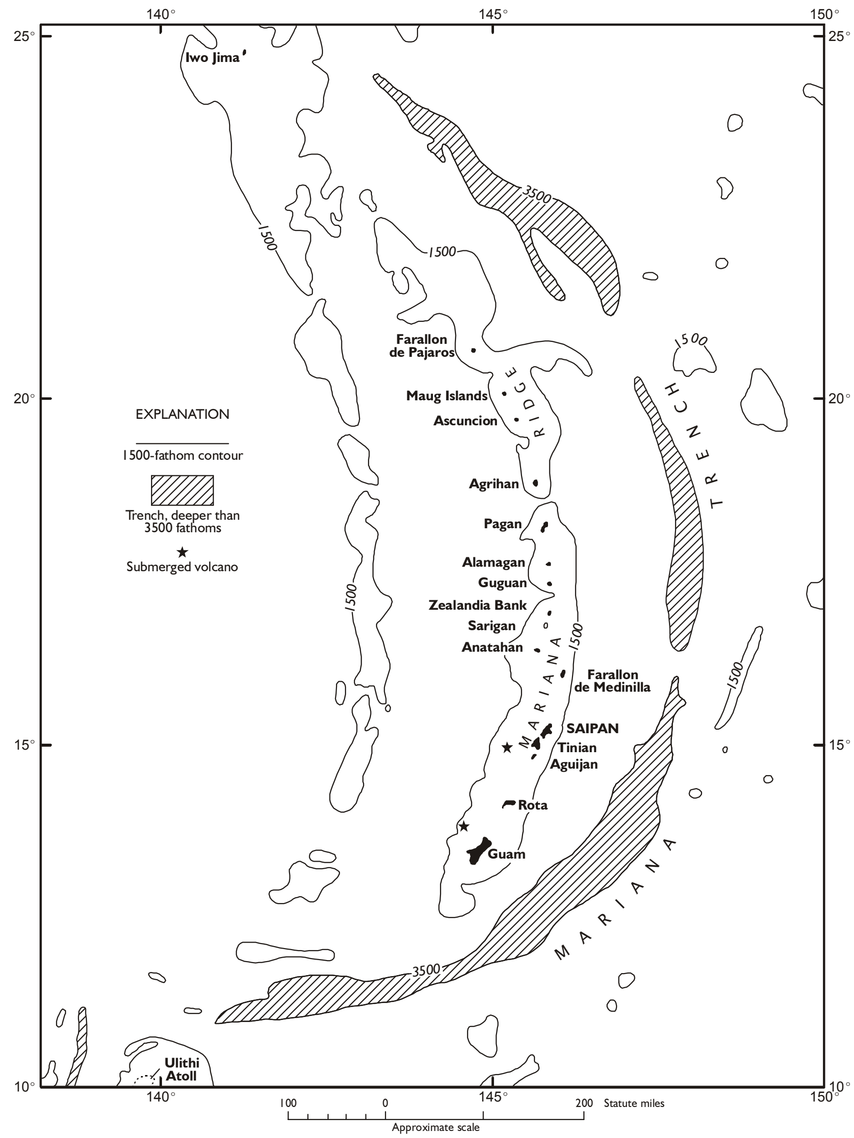

Fig. 2. Bathymetric map of the Mariana arc. After Hess (1948).

tions for the Mariana and Caroline Islands, partly upon the authors collections and literature reviews for the Marshall Islands, and for the most part upon relatively recent comprehensive reviews of the literature and some collections by the author for Japan and Ryukyu Islands and Philippine Islands.

Table 1 gives an estimate of both the collecting effort and the degree to which the reef-building coral habitats have been sampled within the Mariana, Caroline, and Marshall Island groups. A collecting station, as defined here, indicates a distinct uniform habitat and geographic location from which one or more

Table 1. Number of collecting stations, number of specimens collected at the collecting stations, percent of coral habitats sampled, and percent of collecting station effort for various islands within the Southern Marianas, Northern Marianas, Eastern Caroline, Western Caroline, and Marshall Island groups.

Geographic Location	A Collecting Stations for each Island	B Number of Specimens Collected	C Percent of Coral Habitats Sampled	D Percent of Collecting Station Effort
Southern Mariana Islands				
1. Guam	1724	9771	95	74.2
2. Rota	116	253	10	5.0
3. Aguijan	16	79	5	0.7
4. Tinian	121	594	20	5.2
5. Saipan	333	1421	50	14.3
6. Farallon de Medinella	6	94	2	0.3
7. Galvez Bank	7	164	3	0.3
8. Santa Rosa Reef	2	12	<1	0.1
Totals	2325	12388		
Northern Mariana Islands				
1. Esmerelda Bank	1	1	<1	0.5
2. Anatahan	29	364	10	13.9
3. Sarigan	6	33	5	2.9
4. Zealandia Bank	2	16	10	1.0
5. Guguan	20	115	7	9.6
6. Alamagan	2	9	<1	1.0
7. Pagan	78	428	20	37.3
8. Agrihan	17	146	7	8.1
9. Asuncion	8	58	3	3.8
10. Maug Islands	46	280	15	22.0
11. Farallon de Pajaros	6	35	<2	2.9
Totals	209	1485		
Totals for all the Mariana Islands	2534	13873		
Eastern Caroline Islands				
1. Ulithi Atoll	25	116	3	4.6
2. West Fayu Atoll	24	86	2	4.4
3. Woleai Atoll	8	33	1	1.2
4. Truk Islands	261	1545	10	48.2
5. Ponape	196	1054	7	36.2
6. Kosrae	28	324	4	5.2
Totals	542	3158		
Western Caroline Islands				
1. Palau Islands	264	1541	7	77.2
2. Yap Islands	78	402	5	22.8
Totals	342	1943		
Totals for all of Caroline Islands	884	5101		
Marshall Islands				
1. Kwajalein Atoll	31	234	5	30.7
2. Eniwetok Atoll	10	528	7	69.3
Totals	101	762		

corals have been collected, but does not include stations from which quantitative data or species lists only have been compiled. Each species listed from a geographic area in Table 2 is represented by one or more voucher specimens deposited in the University of Guam Marine Laboratory Museum collections. The amount of time spent at each collecting station ranged from 10 to 60 minutes, with an average of about 20 minutes. The number of coral specimens collected is the total tabulated from all the collecting stations for an island. The amount of collecting station effort for each island (Table 1, Column D) is given as a relative percent of all the stations of an island group, and the amount of coral habitat sampled (Table 1, Column C) is given as an estimate of the percent of an islands total area occupied by reef-building corals from which specimens have been collected. Table 1 shows considerable variation in the relative percentage of collecting station effort and percentage of coral habitat sampled between island groups as well as between islands within an island group. In general, islands that are more easily accessed by commercial transportation or have marine research institutions located on them have higher numbers of collecting stations and collected specimens, especially from Guam where the author has resided and been collecting corals since 1965. With greater collection effort it is expected that more new species records would be found in large island groups that have had a low percentage of their potential coral habitats collected from, such as Palau, and the least number of new species records from islands where a significant percentage of the coral habitats have been sampled, such as Guam and Saipan.

Distribution of Reef-Building Corals within the Northwest Pacific Ocean and Philippine Sea

Recent comprehensive reviews of reef-building coral diversity within the major island groups of the Northwest Pacific Ocean and Philippine Sea list 381 species and 76 genera from Japan and Ryukyu Islands (Veron, 1992; Nishihira, 1988), 411 species and 77 genera from the Philippine Islands (Veron and Hodgson, 1989), 395 species and 69 genera from the Eastern and Western Caroline Islands (collections made by Randall and others from 1966–1994), ca. 300 species and 62 genera from the Marshall Islands (Wells, 1954; and collections made by Randall and others from 1970–1976), and 253 species and 56 genera from the Mariana Islands (Randall and Myers, 1983; and collections made by Randall and others from 1965–1994). An interesting aspect of the reef-building coral fauna of the Mariana Islands is their significantly lower diversity when compared to other Northwest Pacific Ocean and Philippine Sea island groups. The Mariana Islands appears as a lower coral diversity anomaly surrounded by other higher coral diversi-ty island groups. A comparison of coral species from the Northwest Pacific Ocean and Philip-pine Sea island groups also reveal that the Mariana fauna, as well as that of the Caroline and Marshall Islands, are for the most part an attenuation of the high-diversity Western Pacific region. There are very few endemic reef-building coral species found east of the Philippine Islands in the North Pacific.

Biogeography of the Reef-Building Corals of the Mariana and Palau Islands in Relation to the Formation of the Eastern Philippine Sea

Out of the relatively high coral diversity island groups within the Northwest Pacific Ocean and Philippine Sea, the Palau Islands in the Western Caroline Islands has a reef-building coral fauna of about 385 species and 66 genera. The Palau fauna is especially interesting for comparison with the less diverse Mariana coral fauna of about 254 species and 56 genera, because of the two island groups somewhat similar size, origin, age, and related but different geologic histories.

Table 2 shows that 244 reef-building coral species are common to both the Palau and Mariana Islands, and that all 56 genera collected from the Mariana Islands are found in the Palau Islands. There are 141 coral species collected from Palau that have not been collected in the Marianas, and ten species collected from the Marianas that have not been collected in Palau. In regard to the ten Mariana coral species that have not been collected from Palau: two are pocilloporid species that probably occur in Palau if the proper high-energy seaward reef slopes were better investigated; two are *Madracis* species, one of which is rare and has only been collected from a single station from Guam; one is an undescribed but common ramose *Coscinaraea* species dredged from the lower (ca. 100 m) seaward reef slopes from a number of Mariana Islands stations, and probably occurs in Palau if similar habitats were dredged; four are widespread cycloserid and

Table 2. List of coral species collected from the Palau Islands, Southern Mariana Forearc Islands, and Northern Marianna Volcanic Arc Ridge Islands.

Coral Order, Family and Species	Palau Islands	Southern Mariana Islands	Northern Mariana Islands
Order SCLERACTINIA			
Family ASTROCOENIIDAE			
Stylocoeniella armata (Ehrenberg, 1834)	x	x	x
Stylocoeniella guentheri (Bassett-Smith, 1890)	x	x	x
Family THAMNASTERIIDAE			
Psammocora contigua (Esper, 1797)	x	x	
Psammocora digitata Edwards & Haime, 1851	x	x	x
Psammocora explanulata van der Horst, 1922	x	x	
Psammocora haimeana Edwards & Haime, 1851	x	x	x
Psammocora nierstraszi van der Horst, 1921	x	x	x
Psammocora obtusangula (Lamarck, 1816)	x	x	
Psammocora profundacella Gardiner, 1898	x	x	x
Psammocora stellata (Verrill, 1866)	x	x	
Psammocora superficiales Gardiner, 1898	x	x	
Psammocora sp. 1 (collines)	x	x	x
Psammocora sp. 2 (columnar, pink)	x	x	
Psammocora sp. 3 (columnar, brown)	x		
Family POCILLOPORIDAE			
Seriatopora aculeata Quelch, 1886	x	x	
Seriatopora caliendrum Ehrenberg, 1834	x	x	
Seriatopora hystrix Dana, 1846	x	x	x
Seriatopora sp. 1 (thick blunt tips)	x	x	
Stylophora mordax (Dana, 1846)	x	x	x
Stylophora pistillata Esper, 1797	x		
Palauastrea ramosa Yabe & Sugiyama, 1941	x		
Pocillopora ankeli Sheer & Pillai, 1974	x	x	x
Pocillopora damicornis (Linnaeus, 1758)	x	x	x
Pocillopora dame Verrill, 1864	x	x	x
Pocillopora elegans Dana, 1846	x	x	x
Pocillopora eydouxi Edwards & Haime, 1860	x	x	x
Pocillopora ligulata Dana, 1846	x	x	x
Pocillopora setchelli Hoff meister, 1929	x	x	x
Pocillopora meandrina Dann, 1846	x	x	x
Pocillopora verrucosa Edwards & Haime, 1860	x	x	x
Pocillopora woodjonesi Vaughan, 1918	x	x	x
Pocillopora sp. 1 (nodular branching)		x	
Pocillopora sp. 2 (compact branching)		x	
Madracis asanoi Yabe & Sugiyama, 1941	x		
Madracis kirbyi Veron & Pichon, 1976		x	
Madracis palaoensis Yabe & Sugiyama, 1936	x	x	
Madracis sp. 1 (small button)		x	
Family ACROPORIDAE			
Acropora (A.) abrotanoides (Lamarck, 1816)	x	x	
Acropora (A.) aculeus (Dana, 1846)	x	x	
Acropora (A.) acuminata (Verrill, 1864)	x	x	
Acropora (A.) aspera (Dana, 1846)	x	x	
Acropora (A.) austera (Dana, 1846)	x		
Acropora (A.) azurea Veron & Wallace, 1984	x	x	x
Acropora (A.) bushyensis Veron & Wallace, 1984	x		
Acropora (A.) carduus (Dana, 1846)	x		
Acropora (A.) cerealis (Dana, 1846)	x	x	x
Acropora (A.) clathrata (Brook, 1891)	x		
Acropora (A.) cytherea (Dana, 1846)	x		

Table 2. (continued)

Coral Order, Family and Species	Palau Islands	Southern Mariana Islands	Northern Mariana Islands
Acropora (A.) dendrum (Bassett-Smith, 1890)	x		
Acropora (A.) digitifera (Dana, 1846)	x	x	x
Acropora (A.) dispar Nemenzo, 1967	x		
Acropora (A.) divaricata (Dana, 1846)	x		
Acropora (A.) echinata (Dana, 1846)	x		
Acropora (A.) elseyi (Brook, 1892)	x		
Acropora (A.) florida (Dana, 1846)	x	x	
Acropora (A.) formosa (Dana, 1846)	x	x	
Acropora (A.) gemmifera (Brook, 1892)	x	x	x
Acropora (A.) granulosa (Edwards & Haime, 1860)	x	x	
Acropora (A.) grandis (Brook, 1892)	x		
Acropora (A.) hebes (Dana, 1846)	x	x	
Acropora (A.) horrida (Dana, 1846)	x		
Acropora (A.) humilis (Dana, 1846)	x	x	x
Acropora (A.) hyacinthus (Dana, 1846)	x		
Acropora (A.) irregularis (Brook, 1892)	x	x	x
Acropora (A.) kyirstyae Veron & Wallace, 1984	x		
Acropora (A.) longacyathus (Edwards & Haime, 1860)	x	x	
Acropora (A.) loripes (Brook, 1892)	x	x	x
Acropora (A.) lovelli Veron & Wallace, 1984	x	x	
Acropora (A.) lutkeni Crossland, 1952	x	x	
Acropora (A.) microphthalma (Verrill, 1869)	x		
Acropora (A.) millepora (Ehrenberg, 1834)	x		
Acropora (A.) monticulosa (Bruggemanni, 1879)	x	x	x
Acropora (A.) multiacuta Nemenzo, 1967	x	x	
Acropora (A.) nana (Studer, 1878)	x		
Acropora (A.) nasuta (Dana, 1846)	x	x	x
Acropora (A.) nobilis (Dana, 1846)	x		
Acropora (A.) ocellata (Klunzinger, 1897)	x	x	x
Acropora (A.) palmerae Wells, 1954	x	x	x
Acropora (A.) pulchra (Brook, 1891)	x		
Acropora (A.) quelchi (Brook, 1893)	x	x	x
Acropora (A.) rambleri (Bassett-Smith, 1890)	x	x	x
Acropora (A.) robusta (Dana, 1846)	x		
Acropora (A.) samoensis (Brook, 1891)	x		
Acropora (A.) secale (Studer, 1878)	x	x	
Acropora (A.) selago (Studer, 1878)	x	x	x
Acropora (A.) smithi (Brook, 1893)	x	x	x
Acropora (A.) spicifera (Dana, 1846)	x		
Acropora (A.) striata Verrill, 1866	x	x	
Acropora (A.) studeri (Brook, 1893)	x	x	
Acropora (A.) subglabra (Brook, 1891)	x		
Acropora (A.) surculosa (Dana, 1846)	x	x	x
Acropora (A.) tenella (Brook, 1892)	x		
Acropora (A.) tenuis (Dana, 1846)	x	x	x
Acropora (A.) teres (Verrill, 1866)	x	x	
Acropora (A.) valenciennesi (Edwards & Haime, 1860)	x		
Acropora (A.) valida (Dana, 1846)	x	x	x
Acropora (A.) vaughani Wells, 1954	x	x	
Acropora (A.) verweyi Veron & Wallace, 1984	x	x	
Acropora (A.) virgata (Dana, 1846)	x	x	
Acropora (A.) yongei Veron & Wallace, 1984	x		
Acropora (A.) sp. 1	x		
Acropora (A.) sp. 2	x		

Table 2. (continued)

Coral Order, Family and Species	Palau Islands	Southern Mariana Islands	Northern Mariana Islands
Acropora (A.) sp. 3	x		
Acropora (A.) sp. 4	x		
Acropora (A.) sp. 5	x		
Acropora (A.) sp. 6	x	x	
Acropora (A.) sp. 7 (thick branch)	x	x	
Acropora (I.) brueggemanni (Brook, 1893)	x		
Acropora (I.) cuneata (Dana, 1846)	x		
Acropora (I.) palifera (Lamarck, 1816)	x	x	x
Anacropora forbesi Ridley, 1884	x		
Anacropora matthaii Pillai, 1973	x		
Anacropora puertogalerae Nemenzo, 1964	x		
Anacropora spinosa Rehberg, 1892	x		
Anacropora sp. 1	x		
Astreopora eliptica Yabi & Sugiyama, 1941	x	x	x
Astreopora gracilis Bernard, 1896	x	x	x
Astreopora listeri Bernard, 1896	x	x	
Astreopora moretonensis Veron & Wallace, 1984	x		
Astreopora myriophthalma (Lamarck, 1816)	x	x	x
Astreopora ocellata Bernard, 1896	x	x	x
Astreopora randalli Lamberts, 1890	x	x	x
Montipora acanthella Bernard, 1897	x	x	
Montipora angulata (Lamarck, 1816)	x		
Montipora berryi Hoffmeister, 1925	x	x	x
Montipora caliculata (Dana, 1846)	x	x	x
Montipora colei Wells, 1954	x	x	x
Montipora danae Edwards & Haime, 1851	x	x	
Montipora digitata (Dana, 1846)	x		
Montipora edwardsi Bernard, 1897	x		
Montipora efflorescens Bernard, 1897	x		
Montipora ehrenbergii Verrill, 1875	x	x	x
Montipora elschneri Vaughan, 1918	x	x	x
Montipora cf. *equituberculata* Bernard, 1897	x	x	
Montipora floweri Wells, 1954	x	x	x
Montipora foliosa (Pallas, 1766)	x	x	
Montipora foveolata (Dana, 1846)	x	x	x
Montipora fragilis Quelch, 1886	x		
Montipora gaimardi Bernard, 1897	x		
Montipora granulosa Bernard, 1897	x	x	
Montipora grisea Bernard, 1897	x	x	x
Montipora hirsuta Nemenzo, 1967 (non Bernard)	x		
Montipora hispida (Dana, 1846)	x		
Montipora hoffmeisteri Wells, 1954	x	x	x
Montipora incrassata (Dana, 1846)	x		
Montipora informis Bernard, 1897	x		
Montipora lobulata Bernard, 1897	x	x	x
Montipora monasteriata (Forskål, 1775)	x	x	x
Montipora cf. *planiuscula* (Dana, 1846)	x	x	x
Montipora pulcherrima Bernard, 1897	x	x	
Montipora socialis Bernard, 1897	x	x	x
Montipora stellata Bernard, 1897	x		
Montipora tuberculosa (Lamarck, 1816)	x	x	x
Montipora turgescens Bernard, 1897	x		
Montipora undata Bernard, 1897	x		
Montipora venosa (Ehrenberg, 1834)	x	x	x

Table 2. (continued)

Coral Order, Family and Species	Palau Islands	Southern Mariana Islands	Northern Mariana Islands
Montipora verrilli Vaughan, 1907	x	x	x
Montipora verrucosa (Lamarck, 1816)	x	x	x
Montipora sp. 1 (green spine)	x	x	x
Montipora sp. 2 (ramose tuber.)	x		
Montipora sp. 3 (Pago)	x	x	x
Montipora sp. 4 (Ramose pap.)	x		
Montipora sp. 5 (thick branch)	x	x	x
Montipora sp. 6 (spiny grey)	x		
Family AGARICIIDAE			
Pavona cactus (Forskål, 1775)	x	x	
Pavona clavus (Dana, 1846)	x	x	x
Pavona decussata (Dana, 1846)	x	x	
Pavona difflens (Lamarck, 1816)	x	x	x
Pavona divaricata (Lamarck, 1816)	x	x	
Pavona duerdeni Vaughanm, 1907	x	x	x
Pavona explanulata (Lamarck, 1816)	x	x	
Pavona frondifera (Lamarck, 1816)	x		
Pavona minuta Wells, 1954	x	x	x
Pavona maldivensis (Gardiner, 1905)	x	x	x
Pavona varians Verrill, 1864	x	x	x
Pavona venosa (Ehrenberg, 1834)	x	x	x
Pavona sp. 1 (collines)	x	x	x
Pavona sp. 2 (white dot)	x	x	x
Pavona sp. 3 (monticules)	x	x	x
Gardineroseris planulata (Dana, 1846)	x	x	x
Coeloseris mayeri Vaughan, 1918	x		
Leptoseris explanata Yabe & Sugiyama, 1941	x	x	x
Leptoseris foliosa Dineson, 1980	x	x	
Leptoseris gardineri van der Horst, 1921	x	x	
Leptoseris hawaiiensis Vaughan, 1907	x	x	x
Leptoseris incrustans (Quelch, 1886)	x	x	x
Leptoseris mycetoseroides Wells, 1954	x	x	x
Leptoseris scabra Vaughan, 1907	x	x	x
Leptoseris solida (Quelch, 1886)	x	x	x
Leptoseris papyracea (Dana, 1846)	x	x	
Leptoseris yabei (Pillai & Scheer, 1976)	x		
Leptoseris sp. 1 (pink)	x	x	
Leptoseris sp. 2 (cones)	x		
Pachyseris rugosa (Lamarck, 1816)	x		
Pachyseris speciosa (Dana, 1846)	x	x	x
Family SIDERASTREIDAE			
Coscinaraea columna (Dana, 1846)	x	x	x
Coscinaraea exesa (Dana, 1846)	x		
Coscinaraea sp. 1 (ramose)		x	x
Family FUNGIIDAE			
Cycloseris costulata Ortmann, 1889	x	x	x
Cycloseris cyclolites Lamarck, 1816	x	x	
Cycloseris hexagonalis Edwards & Haime, 1848	x	x	
Cycloseris sinensis Edwards & Haime, 1851		x	
Cycloseris tenuis Dana, 1846		x	
Cycloseris vaughani (Boschma, 1923)		x	
Diaseris fragilis Alcock, 1893	x	x	
Diaseris distorta Michelin, 1842		x	
Fungia (F.) fungites (Linnaeus, 1758)	x	x	x

Table 2. (continued)

Coral Order, Family and Species	Palau Islands	Southern Mariana Islands	Northern Mariana Islands
Fungia (V.) concinna Verrill, 1864	x	x	x
Fungia (V.) granulosa Klunzinger, 1879	x	x	
Fungia (V.) repanda Dana, 1846	x	x	
Fungia (V.) spinifera Claereboudt & Hoeksema, 1987	x	x	
Fungia (D.) danai Edwards & Haime, 1851	x	x	
Fungia (D.) horrida Dana, 1846	x	x	
Fungia (D.) scabra Doderlein, 1901	x		
Fungia (D.) scruposa Klunzinger, 1879	x		
Fungia (P.) paumotensis Stutchbury, 1833	x	x	
Fungia (L.) scutaria Lamarck, 1801	x	x	x
Helipfungia actinijormis (Quoy & Gaimard, 1833)	x		
Ctenactis albateutaculata Hoeksema, 1989	x	x	
Ctenactis echinata (Pallas, 1766)	x	x	
Ctenactis crassa (Dana, 1846)	x		
Herpolitha limax (Esper, 1797)	x	x	x
Herpolitha weberi (van der Horst, 1921)	x	x	
Polyphyllia talpina (Lamarck, 1801)	x	x	
Sandalolitha dentata Quelch, 1884	x	x	
Sandalolitha robusta (Quelch, 1886)	x	x	x
Lithophyllon undulatum Rehberg, 1892	x		
Lithophyllon mokai Hoeksema, 1989	x		
Podabacia crustacea (Pallas, 1766)	x	x	
Podabacia sp. 1	x		
Family PORITIDAE			
Porites (P.) annae Crossland, 1952	x	x	
Porites (P.) australiensis Vaughan, 1918	x	x	x
Porites (P.) cylindrica Dana, 1846	x	x	
Porites (P.) densa Vaughan, 1918	x		
Porites (P.) eridani Umbgrove, 1940	x	x	x
Porites (P.) cf. *evermanni* Vaughan, 1907	x		
Porites (P.)lichen Dana, 1846	x	x	x
Porites (P.) lobata Dana, 1846	x	x	x
Porites (P.)lutes Edwards & Haime, 1860	x	x	x
Porites (P.) murrayensis Vaughan, 1918	x	x	x
Porites (P.) cf. *myrmidonensis* Veron, 1985	x		
Porites (P.) nigrescens Dana, 1846	x		
Porites (P.) solida (Forskål, 1775)	x	x	
Porites (P) stephensoni Crossland, 1952	x	x	x
Porites (P.) superfusa Gardiner, 1898	x	x	x
Porites (P.) sp. 1 (nodular)	x	x	x
Porites (P.) sp. 2 (spiny coen.)	x		
Porites (P.) sp. 3 (lumpy yell.)	x	x	x
Porites (S.) convexa Verrill, 1864	x	x	x
Porites (S.) horizontalata Hoff meister, 1925	x	x	x
Porites (S.) rus (Forskål, 1775)	x	x	x
Porites (S.) sp. 1 (encrusting)	x	x	
Porites (N.) sillimaniana Nemenzo, 1976	x		
Porites (N.) vaughani Crossland, 1952	x	x	
Porites (N.) sp. 1 (ramose)	x		
Stylaraea punctata Klunzinger, 1879	x	x	
Goniopora columna Dana, 1846	x	x	x
Goniopora djiboutiensis Vaughan, 1907	x	x	
Goniopora eclipsensis Veron & Pichon, 1982	x	x	x
Goniopora fruiticosa Saville-Kent, 1893	x	x	x

Table 2. (continued)

Coral Order, Family and Species	Palau Islands	Southern Mariana Islands	Northern Mariana Islands
Goniopora lobata Edwards & Haime, 1860	x	x	x
Goniopora minor Crossland, 1955	x	x	x
Goniopora pandoraensis Veron & Pichon, 1982	x	x	
Goniopora somaliensis Vaughan, 1907	x	x	x
Goniopora stokesi Edwards & Haime, 1851	x		
Goniopora tenuidens Quelch, 1886	x	x	x
Goniopora cf. *traceyi* Wells, 1954	x		
Alveopora allingi Hoffmeister, 1925	x	x	x
Alveopora fenestrata (Lamarck, 1816)	x	x	
Alveopora spongiosa Dana, 1846	x		
Alveopora superficiales Sheer & Pillai, 1976	x	x	x
Alveopora verrilliana Dana, 1872	x	x	
Alveopora virdis Quoy & Gaimard, 1833	x	x	x
Alveopora sp. 1 (small calices)	x		
Family FAVIIDAE			
Caulastrea echinulata (Edwards & Haime, 1849)	x		
Caulastrea furcata Dana, 1846	x		
Caulastrea tumida Matthai, 1928	x		
Caulastrea sp. 1 (fused calices)	x		
Barabattoia amicorum (Edwards & Haime, 1850)	x		
Favia danae Verrill, 1872	x	x	
Favia favus (Forskål, 1775)	x	x	x
Favia helianthoides Wells, 1954	x	x	x
Favia laxa (Klunzinger, 1879)	x		
Favia lizardensis Veron, Pichon & Wijsman-Best, 1977	x		
Favia maritima Nemenzo, 1971	x	x	
Favia matthaii Vaughan, 1918	x	x	x
Favia pallida (Dana, 1846)	x	x	x
Favia rotumana (Gardiner, 1899)	x	x	x
Favia rotundata Veron, Pichon & Wijsman-Best, 1977	x		
Favia stelligera (Dana, 1846)	x	x	x
Favia sp. 1 (small calice)	x		
Favites abdita (Elks & Solander, 1786)	x	x	x
Favites chinensis (Verrill, 1866)	x		
Favites complanata (Ehrenberg, 1834)	x		
Favites flexuosa (Dana, 1846)	x	x	x
Favites halicora (Ehrenberg, 1834)	x		
Favites pentagons (Esper, 1794)	x		
Favites russelli (Wells, 1954)	x	x	x
Goniastrea aspera Verrill, 1865	x		
Goniastrea australensis (Edwards & Haime, 1857)	x		
Goniastrea edwardsi Chevalier, 1971	x	x	x
Goniastrea favulus (Dana, 1846)	x		
Goniastrea palauensis (Yabe, Sugiyama & Eguchi, 1936)	x		
Goniastrea pectinata (Ehrenberg, 1834)	x	x	x
Goniastrea retiformis (Lamarck, 1816)	x	x	x
Goniastrea sp. 1	x		
Leptoria phrygia (Elks & Solander, 1786)	x	x	x
Platygyra daedalea (Ellis & Solander, 1786)	x	x	x
Platygyra lamellina (Ehrenberg, 1834)	x		
Platygyra pini Chevalier, 1975	x	x	x
Platygyra sinensis (Edwards & Haime, 1849)	x		
Platygyra cf. *verweyi* Wijsman-Best, 1976	x		
Oulophyllia crisps (Lamarck, 1816)	x	x	x

Table 2. (continued)

Coral Order, Family and Species	Palau Islands	Southern Mariana Islands	Northern Mariana Islands
Oulophyllia sp. 1	x		
Montastrea annuligera (Edwards & Haime, 1849)	x		
Montastrea curta (Dana, 1846)	x	x	x
Montastrea magnistellata Chevalier, 1971	x	x	x
Plesiastrea versipora (Lamarck, 1816)	x	x	x
Diploastrea heliopora (Lamarck, 1816)	x	x	
Leptastrea bottae (Edwards & Haime, 1849)	x	x	x
Leptastrea cf. *immersa* Klunzinger, 1879	x	x	x
Leptastrea pruinosa Crossland, 1952	x		
Leptastrea purpurea (Dana, 1846)	x	x	x
Leptastrea transversa Klunzinger, 1979	x	x	x
Cyphastrea chalcidicum (Forskål, 1775)	x	x	x
Cyphastrea microphthalma (Lamarck, 1816)	x	x	x
Cyphastrea serailia (Forskål, 1775)	x	x	x
Cyphastrea cf. *ocellina* (Dana, 1864)	x	x	x
Cyphastrea sp. 1	x	x	
Echinopora gemmacea (Lamarck, 1816)	x		
Echinopora hirsutissima Edwards & Haime, 1849	x		
Echinopora horrida Dana, 1846	x		
Echinopora lamellosa (Esper, 1795)	x	x	x
Echinopora mammiformis (Nemenzo, 1959)	x		
Family OCULINIDAE			
Galaxea astreata (Lamarck, 1816)	x		
Galaxea fascicularis (Linnaeus, 1767)	x	x	x
Acrhelia horrescens (Dana, 1846)	x	x	
Family MERULINIDAE			
Hydnophora grandis Gardiner, 1904	x		
Hydnophora microconos (Lamarck, 1816)	x	x	x
Hydnophora pilosa Veron, 1985		x	
Hydnophora rigida (Dana, 1846)	x		
Hydnophora exesa (Papas, 1766)	x	x	
Merulina ampliata (Ellis & Solander, 1786)	x	x	
Merulina scabricula Dana, 1846	x		
Scapophyllia cylindrica (Edwards & Haime, 1848)	x	x	x
Paraclavarina triangularis (Veron & Pichon, 1980)	x		
Family MUSSIDAE			
Scolymia vitiensis Bruggemann, 1877	x		
Scolymia australis (Edwards & Haime, 1849)	x	x	x
Acanthastrea sp. *amakusensis* Veron, 1990	x	x	x
Acanthastrea echinata (Dana, 1846)	x	x	x
Acanthastrea hillae Wells, 1955	x	x	
Lobophyllia corymbosa (Forskål, 1775)	x	x	x
Lobophyllia costata (Dana, 1846)	x	x	x
Lobophyllia hataii Yabi, Sugiyama & Eguchi, 1936	x	x	
Lobophyllia hemprichii (Ehrenberg, 1834)	x	x	x
Lobophyllia pachysepta Chevalier, 1975	x		
Symphyllia agaricia Edwards & Haime, 1849	x		
Symphyllia radians Edwards & Haime, 1849	x		
Symphyllia recta (Dana, 1846)	x		
Symphyllia valeniennesii Edwards & Haime	x	x	
Family PECTINIIDAE			
Echinophyllia aspera (Ellis & Solander, 1786)	x	x	x
Echinophyllia echinata (Saville-Kent, 1971)	x	x	
Echinophyllia sp. 1	x		

Table 2. (continued)

Coral Order, Family and Species	Palau Islands	Southern Mariana Islands	Northern Mariana Islands
Mycedium elephantotos (Pallas, 1766)	x	x	
Pectinia alicicornis (Saville-Kent)	x		
Pectinia elongata Rehberg, 1892	x		
Pectinia lactuca (Pallas, 1766)	x		
Pectinia paeonia (Dana, 1846)	x	x	
Oxypora lacera (Verrill, 1864)	x		
Oxypora glabra Nemenzo, 1959	x		
Family CARYOPHYLLIIDAE			
Euphyllia (E.) glabrescens (Chamisso & Eysenhardt, 1821)	x	x	x
Euphyllia cristata Chevalier, 1971	x		
Euphyllia anacora Veron & Pichon, 1980	x		
Euphyllia divisa V eron & Pichon, 1980	x		
Plerogyra simplex Rehberg, 1892	x	x	x
Plerogyra sinuosa (Dana, 1846)	x		
Physogyra lichtensteini Edwards & Haime, 1851	x		
Family DENDROPHYLLIIDAE			
Turbinaria frondens (Dana, 1846)	x		
Turbinaria mesenterina (Lamarck, 1816)	x		
Turbinaria peltata (Esper, 1794)	x		
Turbinaria reniformis Bernard, 1896	x	x	x
Turbinaria stellulata (Lamarck, 1816)	x	x	x
Turbinaria sp. 1	x		
Order COENOTHECALIA			
Family HELIOPORIDAE			
Heliopora coerulea (Papas, 1766)	x	x	x
Order STOLONIFERA			
Family TUBIPORIDAE			
Tubipora musica Linnaeus, 1758	x	x	
Order MILLEPORINA			
Family MILLEPORIDAE			
Millepora dichotoma Forskål, 1775	x	x	x
Millepora exaesa Forskål, 1775	x		
Millepora foveolata Crossland, 1952	x		x
Millepora intricata Edwards & Haime, 1857	x		
Millepora latifolia Boschma, 1966	x	x	
Millepora murrayi Quelch, 1884	x		
Millepora platyphylla Hemprich & Ehrenberg, 1834	x	x	x
Millepora tenera Boschma, 1949	x		
Millepora tuberosa Boschma, 1966	x	x	x
Millepora sp. 1	x		
Total species	385	253	159
Total genera	66	56	43

diaserid species dredged from the lower reef slopes (ca. 100 m), and probably occur in Palau if similar habitats were dredged; and one is a hydnophorid species collected from two stations on Guam.

1. General geologic history of the Eastern Philippine Sea

According to current plate tectonic hypotheses the Mariana Fore-arc Ridge was once a part of the Palau-Kyushu Ridge, from where it has been displaced to its present position at the eastern margin of the Philippine Sea by several episodes of arc ridge rifting, basin development, and active arc volcanism. A brief geologic history that led to the formation of the Eastern Philippine Sea Basin and the migration of t he Mariana Fore-arc Ridge to its present location is given in the following series of events that have been summarized from Karig, 1975; Hilde *et al.*, 1977; Mrozowski and Hayes, 1980; Scott *et al.*, 1980; Meijer *et al.*, 1983; Reagan and Meijer, 1984: 1) Prior to about 45 million years (my) ago the Pacific Plate was subducting beneath the Asian Continent and a transform fault boundary most likely occupied what is now the Palau-Kyushu Ridge, 2) A change in the direction of motion of the Pacific Plate about 43 my ago to a more westerly direction initiated subduction along the trend of the trans form fault boundary, 3) The Palau-Kyushu Ridge was then formed by arc volcanism along the trend of the subduction zone between 43 and 32 my ago, 4) The Palau-Kyushu Ridge rifted apart about 32 my ago, beginning formation of the Parece-Vela Basin by backarc spreading, and eastward displacement of the fore-arc region of the Palau-Kyushu Ridge north of the Palau Islands, 5) About 20 my ago arc volcanism commenced immediately west of the old eastward rifted Palau-Kyushu fore-arc, forming the West Mariana island arc ridge, 6) Arc volcanism on the West Mariana island arc ridge continued until about 9 to 5 my ago, 7) About 5 my ago the West Mariana arc ridge rifted beginning the formation of the Mariana Trough by back-arc spreading and diplacement of the West Mariana fore-arc region eastward to eventually become the present fore-arc region of the Mariana island arc ridge, and 8) Sometime prior to 1.3 my ago, arc volcanism formed the presently active Mariana volcanic island arc ridge immediately west of the old eastward rifted west Mariana fore-arc.

In searching for explanations for the lower reef-building coral diversity in the Mariana Islands it will be argued here that the geologic history of the two island groups in relation to the formation of the Eastern Philippine Sea can most satisfactorily provide some answers.

2. Time-distance emplacement of the fore-arc stratigraphic units during the formation of the Eastern Philippine Sea

Uplifted sections of Mariana fore-arc islands of Tinian, Saipan, and particularly on Guam (Cloud *et al.*, 1956; Doan *et al.*, 1960; Tracey *et al.*, 1964) have preserved the most complete accessible stratigraphic record of deposits that span the historical development of the Eastern Philippine Sea (Karig, 1975; Scott *et al.*, 1980; Meijer *et al.*, 1983; Reagan and Meijer, 1984).

On the southernmost Mariana island of Guam, volcanic deposits of the Facpi (late middle Eocene) and Alutom (late Eocene to early Oligocene) Formations (as revised by Reagan and Meijer, 1984) were laid down prior to rifting when the fore-arc was part of the Palau-Kyushu Ridge system. Intraformational reefal and nonreefal limestones also occur within the Alutom volcanic deposits (Schlanger, 1964; Reagan and Meijer, 1984; Siegrist and Randall, 1992). Presence of reefal limestones indicate near sea level conditions for at least part of the eruptive Alutom deposits.

According to Scott *et al.* (1980) there is no evidence of arc volcanism preserved in either the island fore-arc or back-arc system during the early period of Parece-Vela Basin formation. There is also apparently a hiatus of shallow water calcareous deposition in the Mariana fore-arc during a significant period of time during the formation of the Parece-Vela Basin as well. The Miocene eruptive sequence exposed on Guam (Umatac Formation) was deposited after arc volcanism was initiated along the West Mariana Ridge. The Maemong Limestone deposits that crop out along the southwest mountain slopes and in the Talofofo River Basin of southern Guam were previously included as a member of the Umatac Formation by Tracey *et al.* (1964). According to Tracey (pers. comm. in Siegrist and Randall, 1992) Maemong Limestone beds along the southwest mountain slopes that crop out on Facpi volcanic flows should now be considered youngest Oligocene on the basis of recent correlations between Deep Sea Drilling Project results and Paris Basin Tertiary sections, and the Maemong Limestone deposits which unconformably overlies Umatac volcanics in the Talofofo Basin is to be considered lower Miocene. Apparently these Maemong Limestone deposits reflect temporal and spacial north-to-south shallowing of waters around emerging volcanic highs (Schlanger, 1964; Siegrist and Randall, 1992).

Further shoaling along the fore-arc brought more waters into the photic zone, which on Guam produced a number of middle and upper Miocene carbonate units that include the Bonya, Alifan, Janum, and Barrigada Limestones. Although Tracey *et al.* (1964) mapped these limestones as separate time-stratigraphic units, they may represent, in part, facies modifications of each other (Siegrist and Randall, 1992). The Mariana Limestone of Pliocene-Pleistocene age is the most extensive carbonate unit on Guam, Rota, Aguijan, and Tinian, but at many sites fossil control evidence of the age has not been uncovered (Siegrist and Randall, 1992). The time-distance implacement of carbonate units since the opening up of the Mariana Trough is somewhat tenuous because of uncertainties of the exact timing of the Mariana fore-arc rifting and age of the late Miocene-Pliocene-Pleistocene limestones. If the time of rifting is placed at about 5 my ago, the Mariana Limestone, as well as part of the Barrigada Limestone have been implaced during the opening of the Mariana Trough and the earlier carbonate units during the shoaling of the West Mariana Ridge. In summary, regardless of the timing of rifting of the Mariana fore-arc, stratigraphy as represented in the present Mariana fore-arc deposits, supports the hypothesis of rather continuous shallow-water carbonate deposition throughout the Neogene and continuing to the present time.

3. Effect of the formation of the Eastern Philippine Sea on the biogeography of corals of the Mariana Islands

It appears that the development of the Eastern Philippine Sea has had an important effect on the biogeography of reef-building corals in the Mariana Islands principally because of two historical events.

The first of these historical events was the probable drowning of the Mariana fore-arc below the depth for hermatypic corals to live during the Oligocene opening of the Parece-Vela Basin. Supporting this view is the absence of Oligocene reefal carbonates in the present Mariana fore-arc islands. With emergence or shoaling of the fore-arc to depths favorable for reef corals during the development of the West Mariana Ridge the hermatypic coral fauna would have to be reintroduced. Had the fore-arc remained emergent during the formation of the Parece-Vella Basin, it would have most likely carried with it the early Oligocene reef coral fauna that was extant on the Palau-Kyushu Ridge at the time of rifting. The timing of the fore-arc submergence may have been crucial, because the appearance of genera in the Eocene that are now the most diverse and important reef builders, such as *Acropora*, *Montipora*, and *Porites*, were undergoing significant speciation at that time. Out of the 141 corals from Palau that have not been found in the present Mariana Islands, about 40 percent of them are *Acropora*, *Montipora*, and *Porites* species.

The second of the historical events that has had an important effect on the reef-building coral biogeography of the Mariana Islands was that during the development of the Eastern Philippine Sea the present day Mariana fore-arc has been displaced hundreds of kilometers northward and eastward away from the high coral diversity Western Pacific biogeographic region into the mainstream of the westward-flowing North Equatorial Current. Evidence for such a displacement comes from paleomagnetic latitude analysis on rocks from DSDP Holes 447A, 448, and 448A sampled at present day 18°N Lat. on the Palau-Kyushu Ridge that indicate implacement at 5° to 10° north or south of the equator (Scott *et al.*, 1980).

Displacement of the Mariana fore-arc into the mainstream of the North Equatorial Current is significant because corals are dispersed almost exclusively by ocean currents which have carried planulae and gametes from their place of origin to other geographic regions of their range. Jokiel (1990) shows that rafting of settled coral planulae on floating objects may also be an important dispersal agent as well. Examination of reef-building coral isopangeneric lines on a map of the Pacific Ocean show a general attenuation in an eastward direction from the high diversity Western Pacific region Veron (1986). Currents in the Mariana Islands are flowing toward the high diversity Western Pacific rather than from it. The eastward-flowing Equatorial Counter Current has most likely been an important conduit during the Tertiary for dispersal to the Eastern and Western Caroline and Marshall Islands. Furthermore, the Marshall Islands higher coral diversity in comparison that of the Mariana Islands may be a result of the Marshall Islands relatively geologically recent movement through the Equatorial Counter Current region as a result of the Pacific Plates northwestern movement. The Marshall Islands, particularly the southern Marshalls, are still being affected by dispersal from the west via the Equatorial Counter Current. Although the Equatorial Counter Current is a rather narrow conduit for dispersal, satellite imagery shows that its effective latitudinal range for dispersal is greatly enhanced by seasonal displacement, El Niño phenomenon, and eddies and gyres generated by climatic events.

Since shoaling and emergence of the Mariana fore-arc during the development of the West Mariana Ridge to the present time, the most important agent for dispersal of reef-building corals to the Mariana Ridge appears to have been the westward-flowing North Equatorial Current which transports coral gametes, planulae, and rafted propagules from the Marshall Islands. The Mariana Islands reef-building coral fauna appears to be an attenuation of the Marshall Islands fauna, as the two island groups have a greater percentage of species in common than do the Mariana and Palau Islands. The present coral fauna of the Mariana Islands is for the most part composed of those species which are good dispersers, those with the most widespread ranges, which is what would be expected with the above proposed pathway of coral dispersal. As an example, Richmond (1987) has shown that *Pocillopora* species are very good dispersers, and it is interesting that there are nearly as many species of this genus in the Mariana Islands as are in the Palau and Marshall Islands.

Distribution of Reef-Building Corals in the Mariana Islands

1. General geographic and geologic setting

The Mariana Islands consists of 15 principal emergent islands scattered along a mostly submergent ridge axis that lies west of the Mariana Trench subduction zone (Figs. 1 and 2). A number of shallow banks with reef-building corals and deeper submarine prominences lacking them also occur along the ridge axis. The islands can be divided into two distinct geologic groups consisting of the six southern islands of Guam, Rota, Aguijan, Tinian, Saipan, and Farallon de Medinella that lie on the old Mariana fore-arc ridge axis; and the nine northern islands of Anatahan, Sarigan, Guguan, Alamagan, Pagan, Agrihan, Asuncion, Maug, and Farallon de Pajaros that are offset 25 to 35 km west of the southern group along the young Mariana active volcanic arc ridge axis. Zealandia Bank, which has two small islets that are generally awash is located between Sarigan and Guguan, and a number of other small emergent islets are also associated with some of the other principal islands. As a group the six southern islands can be characterized as relatively old inactive volcanic islands overlain on much, or all, of their emergent surfaces by limestone deposits. In contrast all the nine northern islands are geologically young active volcanic islands and lack significant emergent limestone deposits. Pagan has a few narrow emergent bands of Holocene limestone, generally less than two meters in elevation, at several locations along the eastern, northern, and western shorelines (Siegrist and Randall, 1989).

2. Distribution of corals

The most conspicuous aspects of reef-building coral distribution within the Mariana Islands is the lower diversity in the northern island group and the variation in the number of species collected within and between islands of both the northern and southern island groups (Tables 1–3). All but one of the 159 reef-building coral species, *Millepora foveolata*, and all 43 genera collected from the Northern Mariana Islands were also collected from the Southern Mariana Islands. There are 94 species and 14 genera collected from the Southern Mariana Islands that were not found in the Northern Mariana Islands.

The significant difference in reef-building coral diversity between the Northern and Southern Mariana Islands is in part due to the reduced effort (number of collecting stations and number of specimens collected) and the

Table 3. The distribution of the number of reef-building coral genera and species collected from the various island in the Mariana Islands.

	Genera	Species
SOUTHERN MARIANA ISLANDS		
Guam	56	253
Rota	38	167
Aguijan	34	132
Tinian	40	141
Saipan	52	206
Farallon de Medinella	7	22
Total Southern Islands	57	255
NORTHERN MARIANA ISLANDS		
Anatahan	36	99
Sarigan	15	20
Guguan	18	43
Alamagan	6	6
Pagan	38	131
Agrihan	32	67
Asuncion	12	12
Maug	33	66
Farallon de Pajaros	5	5
Total Northern Islands	43	159
Total of all the Mariana Islands	56	254

smaller percentage of potential coral habitats sampled from in the northern islands (Table 1). At most islands there is a direct correlation between the number of collecting stations and species diversity (Tables 1 and 3). Regardless of the reduced collecting and habitat sampling effort in the northern islands, a number of other factors could also be important constraints on diversity there.

Lower species diversity is partly a result of reduced habitat diversity in the northern islands. Arborescent species of *Acropora* are absent on islands in both the northern and southern island groups where barrier reef lagoons or well-protected leeward coasts or embayments are lacking. Even in the well-defined deepwater crater lagoon at Maug Island, no arborescent *Acropora* species were found.

Lower coral diversity may be related to the younger geologic age of the northern islands, but apparently it does not require long periods of time for newly emergent islands to acquire a fairly diverse coral fauna. The northern islands developed by arc volcanism sometime after the fore-arc rifted away from the West Mariana Ridge and thus have had a significantly shorter period of time to aquire their present coral fauna than the southern fore-arc islands. The oldest dated rocks from the volcanically active northern islands are 1.3 my (Meijer *et al.*, 1983), and thus the present coral fauna of 159 species has presumably been acquired since that time.

Frequent disturbance from volcanic eruptions and typhoons may keep coral diversity low by keeping the communities in an early stage of successional development in the northern islands. There is no disturbance from volcanic eruptions in the southern islands, and typhoon effects are more severe on the predominantly smaller northern islands where there is no significant protected habitats to act as refugia. Less frequent disturbance in the southern islands may even tend to enhance coral diversity according the model of successional regulation by intensity and frequency of disturbance proposed by Connell (1978).

Higher latitudes of the North Equatorial Current that sweeps by the northern islands may be less effective as a dispersal agent because of fewer islands to the east as a source of planulae.

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マリアナ諸島およびパラオ諸島の造礁性サンゴの生物地理：特に背弧拡大と，東フィリピン海の成立との関連において

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伊豆マリアナ島弧の造礁性サンゴ相の一つの大きな特徴は，その低い種多様性にある．そこでは，約 250 種類が産するが，それを他の北西太平洋の地域と比較してみると，フィリッピン諸島で 400 種類，琉球諸島と日本周辺域で 400 種類，カロリン諸島で 370 種，マーシャル諸島で 300 種類などである．これら，サンゴの種多様性の高い地域のうち，西カロリン諸島にあるパラオ諸島では，350 種類の造礁性サンゴを産し，マリアナとの比較において，興味深い地域である．なぜならマリアナとパラオは，同じくらいのサイズで，同じくらいの地質年代を持ち，しかし地史が異なるからである．

近年のプレートテクトニクス理論によれば，マリアナ前弧はかつて九州-パラオ海嶺の一部であったが，活発な島弧火山活動による背弧拡大と海盆形成によって，フィリッピン海の東端の現在の位置に移動してきた．この背弧海盆形成の時代において，移動しつつある前弧は，造礁性サンゴが生息できない深さまで沈降したと考えられる．その後，活発な活動的火山性島弧の時代に，造礁性サンゴは浅海化した西マリアナ海嶺の高まりに再びサンゴ礁を形成することができた．九州-パラオ海嶺の南部に沿って縁海の形成が無かったという事は，東フィリッピン海が形成する間，パラオ諸島に沿っては浅海の環境と造礁性サンゴの生育がとぎれることなく継続した，ということを示すものである．もしマリアナ前弧が九州-パラオ海嶺から移動してくる間，浅海化していたなら，サンゴ相はパラオ諸島と，より似たものとなっていたはずである．これらの考え方の証拠となるものは，九州-パラオ海嶺，マリアナ前弧，西マリアナ海嶺における炭酸塩岩と火山性堆積物の年代と層序，DSDP（深海底掘削計画）によるデータ，そして現在の造礁性サンゴ相の特徴である．