2 Revisiting the Cenozoic History and the Origin of the Eastern Pacific Coral Fauna

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Abstract

Distribution, composition and functioning of eastern Pacific (EP) coral communities and reefs have resulted from modern and ancient processes. While much has been learned from living systems, still many questions remain regarding how pre-Holocene events shaped modern EP coral communities and reefs. From the late Paleocene to late Miocene, fossil outcrops were spatially restricted to the Washington-Seattle and California regions, whereas from the late Miocene to late Pleistocene corals have been mainly recovered from the Gulf of California, but scarcely (just two outcrops) from western Mexico and Central America. From the Paleocene to Recent, 191 reef-building species, including living taxa without fossil representatives, have inhabited the eastern Pacific region. Of the 53 identified genera, 11 are living and 42 are regional (i.e., currently restricted to the Indo-Pacific or Caribbean and western Atlantic) or globally extinct; 49 species are living and 142 are extinct. Fourteen of the 48 living EP species have fossil records that extend back to the early (*Porites panamensis*) and middle (*Pocillopora capitata*) Pliocene, while the remainder appeared during the middle to late Pleistocene in the Gulf of California. Considering the age and number of taxa per assemblage, genera and species ranged from 1 to 21 (mean = 2.98 ± 3.75 SD), and 1–39 (mean = 3.87 ± 6.12 SD) respectively. The highest numbers of genera (>11) and species (>12) correspond with the middle Eocene to early Miocene of Central Chiapas, and the late Eocene of Panama. As such, EP coral communities and reefs probably never attained high species richness; in addition, depositional evidence and paleoenvironmental reconstructions of coral-bearing deposits from Washington-Seattle, Central California and the Gulf of California suggest that from late Paleocene to late Pleistocene, reefs were small and paucispecific as are today's formations. Based on coral occurrences, species richness increased during the Late Eocene/Early Oligocene (55 species), decreased during the early and middle Pleistocene (5 species), rose again during the late Pleistocene (13 species) and finally peaked again during Recent times (46 species). Bootstrap tests of the temporal changes in species richness indicate that except for the numbers recorded in Late Eocene-Early Oligocene, Late Pleistocene and Recent, changes elsewhere were non-significant. From the spatio-temporal distribution of the fossil outcrops, our knowledge regarding events directly related to the origin and evolution of the current coral fauna is biased since it represents the evolutionary history of subtropical coral communities and reefs from the Gulf of California. Quantitative analysis of presence/absence coral data suggests

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that during the last six million years, Gulf coral communities and reefs experienced dramatic turnover, in particular (a) the extinction of Caribbean-related regional endemics, and (b) since the middle Pleistocene, the steady arrival of Indo-Pacific taxa likely via the North Equatorial Counter Current. Lastly, morphologic, electrophoretic and molecular analyses clearly support a strong affinity of the eastern Pacific endemics, *Porites panamensis* and *Porites sverdrupi*, with the Caribbean and western Atlantic *Porites* clades, suggesting that the eastern Pacific poritid fauna resulted from local speciation of Caribbean/Atlantic populations and long-distance dispersal of Indo-Pacific taxa (e.g., *Porites australiensis*, *Porites lutea*). Hence, the vicariance and dispersal hypotheses regarding the origin of the eastern Pacific coral fauna, at least for some taxa, are complementary.

Keywords
Pacific American corals • Paleoecology • Faunal turnover • Dispersal and vicariance • Evolution

2.1 Introduction

Modern coral reefs in the eastern Pacific extend from the Gulf of California, Mexico to Ecuador, and the oceanic islands off western Mexico, Costa Rica, Colombia, Ecuador, and Chile (Cortés 2003). Yet, their distribution, composition and functioning have been intricately crafted by modern and ancient processes. Dana (1975) claimed that the modern eastern Pacific coral fauna may have resulted from the trans-Pacific dispersal of Indo-Pacific taxa. Today it is well known that ocean currents are associated with ongoing gene flow among populations of trans-Pacific species across a variety of taxonomic groups (e.g., echinoids, Lessios et al. 2003; fishes, Lessios and Robertson 2006; corals, Combosch et al. 2008; see Chap. 16, Lessios and Baums), but also with the potential of bringing new taxa into the eastern Pacific via the North Equatorial Counter Current during very strong ENSO events, as likely occurred during El Niño 1982–83 (molluscs, Emerson and Chaney 1995; echinoids, Lessios et al. 1996; fishes, Robertson and Allen 1996; and references therein). It is fair to say that the genetic similarity and introductions of many species are well in agreement with Dana's hypothesis.

By contrast, while much has been learned from living systems, many questions remain about how pre-Holocene events shaped modern coral communities and reefs in the eastern Pacific. Two facts are undeniable: (1) the pre-Pliocene reef coral faunistic similarity between the Pacific and Caribbean-Atlantic side of America (Vaughan 1917), and (2) the current faunistic similarity between the Indo-west and eastern Pacific regions (Squires 1959; Dana 1975; Glynn and Ault 2000; Glynn et al. 2007). However, when, where and how this change happened needs to be properly addressed in light of recent published data and current research. In order to reach this goal, this chapter will address several related issues: (1) an analysis of the large-scale evolutionary changes experienced by the coral fauna in the eastern Pacific over the last 60 million years up until the late Pleistocene, (2) a description and characterization of the composition and distribution of early (Late Miocene to Pleistocene) eastern Pacific reefs, and (3) a review of the role of dispersal and vicariance in shaping reef faunas following eastern Pacific isolation.

2.2 Large-Scale Temporal Patterns of the Eastern Pacific Coral Fauna

Seminal papers regarding large-scale spatio-temporal patterns of the eastern Pacific coral fossil fauna were published by Durham and Allison (1960), Durham (1966), Dana (1975), Heck and McCoy (1978), Colgan (1990), and Cortés (1997); few details apart, the studies addressed geographic affinities at a large spatial scale (i.e., eastern Pacific vs. Caribbean vs. Indo-Pacific), used epochs (i.e., Paleocene, Eocene) as the finest temporal resolution, and genera as the lowest taxonomic resolution. In an attempt to increase spatial, temporal and taxonomic resolution of the data, detailed databases from material collected at nearly 250 sites on the Pacific side of America (see López-Pérez 2005, 2008, 2012, for detailed information) were assembled (Tables 2.1 and 2.2) with the aid of recent published (López-Pérez 2005, 2008, 2012; Baron-Szabo 2006, 2008; Carreño and Smith 2007; López-Pérez and Budd 2009; Reyes-Bonilla et al. 2012; Paleobiology database http://paleodb.org/; and references therein) and unpublished information.

Table 2.1 summarizes the relative and/or absolute age of fossil assemblages, the geographic areas where corals have been recorded in the eastern Pacific during the Cenozoic, and major sources of information. It is apparent that from the late Paleocene to late Miocene fossil outcrops were spatially restricted to the

Table 2.1 Stratigraphic unit and relative/absolute ages of the 71 fossil assemblages of Tertiary and Quaternary eastern Pacific reef corals

Loc. ID	Stratigraphic unit	Formation	Geologic age	Age (Ma)	Source
1	Central California, CA	Martinez	L. Paleocene	58.7–55.8[o]	Gabb (1864, 1869), Dickerson (1914), Faustino (1931)
2	Mount Diablo, CA	Meganos	E. Eocene	55.8–48.6[m]	Dickerson (1914), Vaughan (1919)
3	Salem, Oregon	Capay	E. Eocene	55.8–48.6[m]	Baldwin (1964)
4	Kern County, CA	Domengine	E/M. Eocene	50–48[s]	Durham (1942b, 1943)
5	San Ignacio-San Juanico, BCS	Bateque	M. Eocene	48.6–40.4[n]	Squires and Demetrion (1992)
6	Central California, CA	Tejon	M. Eocene	48.6–40.4[p]	Nomland (1916)
7	Little Tar Spring, CA	Avenal	M. Eocene	48.6–40.4[q]	Wells (1940)
8	Western Washington	Crescent	M. Eocene	48.6–37.2[m]	Durham (1942a)
9	Northwest Peru	Chira	M. Eocene	46–43[r]	Vaughan (1922)
10	Central Chiapas	San Juan	M. Eocene	46–40[a]	Frost and Langenheim (1974)
11	Washington	Lincoln	L. Eocene/E. Oligocene	37.2–28.4[m]	Durham (1944)
12	Lake Alahuela, Panama	Gatuncillo	L. Eocene	37.2–33.9	Woodring (1957), Budd et al. (1992)
13	Brito, Nicaragua	Brito	L. Eocene	37.2–33.9	Vaughan (1919)
14	Central Chiapas	Ixtaclum	L. Eocene	36–33[a]	Frost and Langenheim (1974)
15	Contra Costa County, CA	–	E. Oligocene	33.9–28.4[m]	Nomland (1916)
16	Central Chiapas	Rancho Berlin	E. Oligocene	32–28[a]	Frost and Langenheim (1974)
17	Western Washington	Sooke	L. Oligocene	28.4–23[m]	Durham (1942a)
18	Seattle, Washington	Blakeley	L. Oligocene	28.4–23[m]	Durham (1942a, 1944)
19	Gatun Lake, Panama	Caimito	L. Oligocene	28.4–23	Woodring (1957)
20	Central Chiapas	La Quinta	L. Oligocene	28–24[a]	Frost and Langenheim (1974)
21	Canal Zone, Panama	La Boca	E. Miocene	23–16	Woodring (1957)
22	Central Chiapas	Santa Ana	E. Miocene	22–15[a]	Frost and Langenheim (1974)
23	Washington/Oregon	Temblor	E/M. Miocene	20.4–13.8[u]	Nomland (1917)
24	Nazca Ridge Guyot, Southern Pacific	–	M. Miocene	16–11.6	Allison et al. (1967), Durham (1980)
25	Valiente Peninsula, Panama	Valiente	M. Miocene	16–11	Coates et al. (2005)
26	Isla Montserrat, BCS	Carmen	L. Miocene/E. Pliocene	8–6[v]	López-Pérez (2008), López-Pérez and Budd (2009)
27	Imperial Valley, CA	Imperial	L. Miocene/E. Pliocene	6.5–6[b, l]	Vaughan (1917)
28	Los Algodones, BCS	El Refugio	E. Pliocene	5.3–3.6[v]	López-Pérez (2008), López-Pérez and Budd (2009)
29	Punta Chivato, BCS	San Marcos	L. Pliocene	3.6–2.6[v]	Simian and Johnson (1997), Johnson and Ledezma-Vazquez (2001)
30	Isla María Madre, Islas Marías, Nayarit	–	L. Pliocene	3.6–2.6[v]	Jordan and Hertlein (1926), Hertlein and Emerson (1959)
31	Central California	San Diego	L. Pliocene	3.6–2.6[m]	Hertlein and Grant (1960)
32	Isla San José, BCS	–	E-M Pliocene	>3[c]	López-Pérez (2008), López-Pérez and Budd (2009)
33	San Nicolas, BCS	San Nicolas	M-L Pliocene	<3.3–2[d, v]	López-Pérez (2008), López-Pérez and Budd (2009)
34	Las Barracas/B. Marquer, BCS	Marquer	L. Pliocene	3–2[e, v]	Durham (1950a), López-Pérez (2008), López-Pérez and Budd (2009)
35	Baltra Island, Galápagos Islands	–	L. Pliocene/Pleistocene	–	Hertlein (1972), Durham (1980)
36	Isla Coronados-1, BCS	–	Pleistocene	–	López-Pérez (2008), López-Pérez and Budd (2009)

(continued)

Table 2.1 (continued)

Loc. ID	Stratigraphic unit	Formation	Geologic age	Age (Ma)	Source
37	La Ventana-1, BCS	–	Pleistocene	–	López-Pérez (2008), López-Pérez and Budd (2009)
38	Isla Coronados-2, BCS	–	Pleistocene	–	López-Pérez (2008), López-Pérez and Budd (2009)
39	La Ventana-2, BCS	–	Pleistocene	–	López-Pérez (2008), López-Pérez and Budd (2009)
40	Isla Coronados-3, BCS	–	Pleistocene	–	López-Pérez (2008), López-Pérez and Budd (2009)
41	La Ventana-3, BCS	–	Pleistocene	–	López-Pérez (2008), López-Pérez and Budd (2009)
42	Isla Coronados-4, BCS	–	Pleistocene	–	López-Pérez (2008), López-Pérez and Budd (2009)
43	Isla Coronados-5, BCS	–	Pleistocene	–	López-Pérez (2008), López-Pérez and Budd (2009)
44	La Ventana-4, BCS	–	L. Pleistocene	>0.3[f]	López-Pérez (2008), López-Pérez and Budd (2009)
45	Isla Coronados-6, BCS	–	L. Pleistocene	–	López-Pérez (2008), López-Pérez and Budd (2009)
46	Arroyo Blanco, I. Carmen	–	L. Pleistocene	–	López-Pérez (2008), López-Pérez and Budd (2009)
47	Cabo Pulmo, BCS	–	L. Pleistocene	0.14–0.12[g]	Squires (1959), López-Pérez (2008), López-Pérez and Budd (2009)
48	Cañada Coronados, BCS	–	L. Pleistocene	0.127 ± .006[h]	Durham (1950b), López-Pérez (2008), López-Pérez and Budd (2009)
49	Puerto Balandra, I. Carmen	–	L. Pleistocene	0.117 ± .008[i]	Durham (1950b), López-Pérez (2008), López-Pérez and Budd (2009)
50	Timbabichi, BCS	–	L. Pleistocene	–	Squires (1959), López-Pérez (2008), López-Pérez and Budd (2009)
51	La Ventana-5, BCS	–	L. Pleistocene	–	López-Pérez and Budd (2009)
52	Punta Baja, I. Carmen	–	L. Pleistocene	0.117 ± .008[i]	Durham (1950b), López-Pérez (2008), López-Pérez and Budd (2009)
53	Bahía Oto, I. Carmen	–	L. Pleistocene	0.117 ± .008[i]	Durham (1950b), López-Pérez (2008), López-Pérez and Budd (2009)
54	Las Animas, BCS	–	L. Pleistocene	0.13–0.128[j]	De Diego-Forbis et al. 2003, López-Pérez (2008), López-Pérez and Budd (2009)
55	San Antonio, BCS	–	L. Pleistocene	0.13–0.12[k]	Johnson and Ledesma-Vázquez (1999)
56	South Punta Chivato, BCS	–	L. Pleistocene	0.117 ± .008[i]	Johnson and Ledesma-Vázquez (2001)
57	El Bajo, Loreto	–	L. Pleistocene	–	Johnson et al. (2007)
58	Isla San José, BCS	–	L. Pleistocene	–	Squires 1959
59	Isla San Diego, BCS	–	L. Pleistocene	–	Squires (1959)
60	Isla María Madre, Islas Marías, Nayarit	–	L. Pleistocene	–	Squires (1959)
61	Isla Cerralvo, BCS	–	L. Pleistocene	–	Squires (1959)
62	Puerto Escondido, Oaxaca	–	L. Pleistocene	–	Palmer (1928), Durham (1947)
63	Bahía Santa Inez, BCS	–	L. Pleistocene	0.117 ± .008[i]	Durham (1947), Hertlein (1957)
64	Isla María Cleofas, Islas Marías, Nayarit	–	L. Pleistocene	–	Hertlein and Emerson (1959), Squires (1959)
65	Isla Guadalupe, BC	–	L. Pleistocene	–	Durham (1980)
66	Isla Tiburón, Sonora	–	L. Pleistocene	–	Durham (1947, 1950b)
67	Isla San Marcos, BCS	–	L. Pleistocene	0.117 ± .008[i]	Durham (1947, 1950b)
68	Isla Monserrat, BCS	–	L. Pleistocene	–	Durham (1947, 1950b)
69	Bahía Magdalena, BCS	–	L. Pleistocene	–	Durham (1947)
70	Isla Coronados-8, BCS	–	L. Pleistocene	–	López-Pérez (2008), López-Pérez and Budd (2009)
71	Isla Coronados-9, BCS	–	L. Pleistocene	–	López-Pérez (2008), López-Pérez and Budd (2009)

Error terms are standard deviations
[a]Budd (2000), [b]Eberly et al. (1978), [c]Schwennicke (2005), [d]Ledesma-Vázquez (2002), [e]Dorsey et al. (2001), [f]Sirkin et al. (1990), [g]Muhs et al. (1994), [h]Johnson (2005), [i]Libbey et al. (1997), [j]DeDiego-Forbis et al. (2004), [k]Johnson et al. (1999), [l]McDougall et al. (1999), [m]Paleobiology database, [n]Schweitzer et al. (2006), [o]Brabb et al. (2008), [p]Lindberg and Squires (1990), [q]Dibblee (1973), [r]Kulm et al. (1990), [s]Squires (1997), [t]Prothero et al. (2009), [u]Bridges and Castle (2003), [v]Carreño and Smith (2007)

Washington-Seattle and California regions, whereas from the early Pliocene to late Pleistocene corals have been mainly recovered from the Gulf of California (see Fig. 1 in López-Pérez 2005). Nevertheless, aside from isolated late Pleistocene fossil coral occurrences at Guadalupe Island (Durham 1980), and Puerto Escondido (Palmer 1928) in western Mexico, and Baltra Island (Hertlein 1972; Durham 1980) in the Galápagos Islands, there is a lack of deposits in western Mexico and Central America. Also, another set of coral-bearing deposits has been recovered from central Chiapas (Eocene-Miocene: La Quinta Fm., Ixtaclum Shale Fm., San Juan Fm., Lecheria Fm., Rancho Berlin Fm., Río Lajas Fm., Santa Ana Fm., Balumtun Fm., Frost and Langenheim 1974), Nicaragua [Eocene: Brito Fm., Vaughan 1919), Costa Rica (Miocene: Limon Fm., Vaughan 1919), Panama (Eocene: Gatuncillo Fm. (Budd et al. 1992), Oligocene: Caimito Fm., Miocene: La Boca Fm., (Woodring 1957); Valiente Fm., (Coates et al. 2005)] and Colombia (Miocene: Usiacuri, Vaughan 1919). These units were deposited at the thermal equator during Eocene to Miocene times and, according to paleocoordinates (http://paleodb.org/), not in the eastern Pacific per se but rather midway between the Pacific and Caribbean Seas.

Whether these Central American assemblages formed part of the Cenozoic eastern Pacific fossil fauna deserves further scrutiny. For example, faunistic affinity between northwestern and Central America during Eocene to Miocene times can be considered relatively high at the genus level (32 %, n = 53) when compared with the low percentage of shared taxa (5.7 %, n = 11) at the species level. Regional species-level faunistic differences between northwestern and Central America are not unexpected; however, the extent to which this regional pattern is true or the result of poor taxonomy (Baron-Szabo 2006, 2008) needs to be carefully addressed, especially because Central American isthmus models suggest that, with an open passage, as much as 10^6 m^3 s^{-1} of surface water would pass from the Atlantic to the Pacific (Hay et al. 2002). This passage would connect Atlantic and Central American communities with northwestern (Seattle, Washington, California, and the Gulf of California, Mexico) communities and produce a continuous marine province and therefore a much more homogeneous coral fauna. Contrary to this view, recent geologic reconstructions (Kirby et al. 2008; Montes et al. 2012), based on new lithostratigraphic, biostratigraphic and strontium chemostratigraphic analyses, suggest that ocean circulation and the biogeographic connection between the Pacific and Caribbean was much more constricted in the early Neogene (Eocene to Miocene) than previously understood, and therefore relatively large faunistic differences between coral faunas may have occurred.

Table 2.2 Species list of Cenozoic hermatypic corals, eastern Pacific

Order Scleractinia
Family Acroporidae
Genus *Acropora*
†*Acropora panamensis* Vaughan 1919 (20)
†*Acropora saludensis* Vaughan 1919 (22)
Acropora valida (Dana 1846) (L)
Genus *Alveopora* (L)
†*Alveopora chiapanacae* Frost and Langenheim 1974 (20)
Genus *Astreopora* (L)
†*Astreopora antiguensis* Vaughan 1919 (19)
†*Astreopora duwamishensis* Durham 1942a (8)
†*Astreopora esperanzae* Frost and Langenheim 1974 (10)
†*Astreopora gatuncilloensis* Budd et al. 1992 (12)
†*Astreopora occidentalis* Nomland 1917 (23)
†*Astreopora sanjuanensis* Durham 1942b (4, 8)
†*Astreopora spinulosum* Frost and Langenheim 1974 (14)
Genus *Dendracis* (†)
†*Dendracis cantabrigiensis* Vaughan 1899 (12)
Genus *Montipora* (L)
†*Montipora schencki* Durham 1942a (8)
Family Actinacididae
Genus *Actinacis* (†)
†*Actinacis alabamensis* (Vaughan 1900) (12)
†*Actinacis barretti* Wells 1934 (10, 20)
Family Agariciidae
Genus *Cyathoseris* (†)
†*Cyathoseris allisoni* Frost and Langenheim 1974 (10)
†*Cyathoseris formosa* d'Achiardi 1875 (12)
Genus *Gardineroseris* (L)
Gardineroseris planulata (Dana 1846) (44, L)
Genus *Leptoseris* (L)
Leptoseris papyracea (Dana 1846) (L)
†*Leptoseris portoricensis* Vaughan 1919 (20)
Leptoseris scabra Vaughan 1907 (L)
†*Leptoseris sinuata* (Nomland 1916) (3)
Leptoseris solida (Quelch 1886) (L)
Genus *Pavona* (L)
Pavona chiriquiensis Glynn et al. 2001 (L)
Pavona clavus (Dana 1846) (37, 39, 41, 44, 48, 51, L)
Pavona duerdeni Vaughan 1907 (L)
Pavona frondifera (Lamarck 1816) (L)
Pavona gigantea Verrill 1869 (35, 42, 48, L)
Pavona maldivensis (Gardiner 1905) (L)
Pavona minuta Wells 1954 (L)
†*Pavona modeloensis* Frost and Langenheim 1974 (22)

(continued)

Table 2.2 depicts the systematic list of the 191 reef-building species, including living taxa without fossil representatives that inhabited the eastern Pacific (including

Table 2.2 (continued)

Order Scleractinia
†Pavona trinitatis Vaughan and Hoffmeister 1926 (22)
Pavona varians Verrill 1864 (L)
Pavona xarifae Scheer and Pillai 1974 (L)
Genus *Trochoseris* (*†*)
†Trochoseris aperta Duncan 1864 (14)
†Trochoseris gerthi Wells 1941 (9)
Family Agathiphylliidae
Genus *Agathiphyllia* (*†*)
†Agathiphyllia antiguensis (Duncan 1863) (12, 16)
†Agathiphyllia anguillensis (Vaughan 1919) (20)
†Agathiphyllia browni (Vaughan 1919) (12)
†Agathiphyllia hilli (Vaughan 1919) (16, 20)
†Agathiphyllia robusta Budd et al. 1992 (12)
†Agathiphyllia roxboroughi (Vaughan 1919) (20, 22)
†Agathiphyllia splendens (Vaughan 1919) (12)
Genus *Pattalophyllia* (*†*)
†Pattalophyllia grumi Catullo 1852 (10)
Family Astrocoeniidae
Genus *Astrocoenia* (*†*)
†Astrocoenia decaturensis Vaughan 1919 (12)
†Astrocoenia dilloni Durham 1942b (2)
†Astrocoenia guantanamensis Vaughan 1919 (10)
†Astrocoenia jukesbrownei Wells 1945 (12)
†Astrocoenia portoricensis Vaughan 1919 (16)
Genus *Madracis* (L)
†Madracis crescentensis Durham, 1942 (8)
†Madracis duncani Wells 1945 (12)
†Madracis stewarti Durham, 1942 (8)
†Madracis vaughani Wells, 1941 (9, 12)
†Madracis wellsi Bentson 1943 (4)
Genus Stephanocoenia (L)
†Stephanocoenia storrsi Wells 1941 (9)
Family Calamophylliidae
Genus *Antilloseris* (*†*)
†Antilloseris cantabrigiensis (Vaughan 1899) (10,14)
†Antilloseris vaughani Wells 1940 (7)
Family Columnastreidae
Genus *Haimesastrea* (*†*)
†Haimesastrea conferta Vaughan 1900 (9,10)
†Haimesastrea petrosa (Gabb 1864) (1)
Family Faviidae
Genus *Antiguastrea* (*†*)
†Antiguastrea cellulosa (Duncan 1863) (12, 16, 20)
†Antiguastrea prava Budd et al. 1992 (12)
Genus *Colpophyllia* (L)

(continued)

Table 2.2 (continued)

Order Scleractinia
†Colpophyllia duncani Wells 1935 (12)
†Colpophyllia elegans Budd et al. 1992 (12)
†Colpophyllia mexicanum Frost and Langenheim 1974 (20, 22)
†Colpophyllia nicholasi Squires and Demetrion 1992 (5)
†Colpophyllia reagani Durham 1942a (8)
†Colpophyllia willoughbiensis (Vaughan 1919) (12,16, 20)
Genus *Diploastrea* (L)
†Diploastrea aequalis Budd et al. 1992 (12)
†Diploastrea bacata Budd et al. 1992 (12)
†Diploastrea crassolamellata (Duncan 1863) (12,16, 20)
Genus *Diploria* (L)
†Diploria bowersi (Vaughan 1917) (27, 32)
†Diploria sarasotana Weisbord 1974 (29)
†Diploria wellsi (Durham 1942b) (4)
Genus *Favia* (L)
†Favia dominicensis Vaughan and Hoffmeister 1925 (22)
†Favia favioides (Wells 1945) (12)
†Favia hannai Durham 1942b (4)
†Favia maitreyiae López-Pérez 2012 (26)
†Favia tulsidasi López-Pérez 2012 (29)
†Favia weisbordi Wells 1934 (12)
Genus *Favites* (L)
†Favites crassiseptata Stemann 1992 (12)
†Favites magnificata Stemann 1992 (12)
†Favites polygonalis (Duncan 1863) (20)
Genus *Goniastrea* (L)
†Goniastrea canalis Vaughan 1919 (12, 20)
†Goniastrea longula Budd et al. 1992 (12)
†Goniastrea muralis Budd et al. 1992 (12)
Genus *Leptastrea* (L)
†Leptastrea hertleini Durham 1942b (4)
Leptastrea transversa Klunzinger, 1879 (L)
Leptastrea purpurea (Dana 1846) (L)
Genus *Leptoria* (L)
†Leptoria laxa Budd et al. 1992 (12)
†Leptoria pauca Budd et al. 1992 (12)
Genus *Montastraea* (L)
†Montastraea antilliana Wells 1945 (10)
†Montastraea bainbridgensis (Vaughan 1919) (16, 20)
†Montastraea canalis (Vaughan 1919) (25)
†Montastrea costata (Duncan 1863) (21)
†Montastrea eocenica Budd et al. 1992 (12)
†Montastraea gabbi (Vaughan 1919) (20)
†Montastrea imperatoris (Vaughan 1919) (25)
†Montastraea laurae Squires and Demetrion 1992 (5)

(continued)

Table 2.2 (continued)

Order Scleractinia
†Montastrea nodosa Budd et al. 1992 (12)
†Montastrea prima Budd et al. 1992 (12)
†Montastrea rotunda Budd et al. 1992 (12)
†Montastraea tampaensis (Vaughan 1919) (20,22)
Genus *Oulophyllia* (L)
†Oulophyllia californica Durham 1942b (4)
Genus *Plesiastrea* (L)
Plesiastrea versipora (Lamarck 1816) (24, L)
Genus *Solenastrea* (L)
†Solenastrea fairbanksi (Vaughan 1900) (27–30, 32)
Family Fungiidae
Genus *Cycloseris* (L)
Cycloseris curvata (Hoeksema 1989) (L)
Cycloseris distorta (Michelin 1842) (L)
Cycloseris vaughani (Boschma 1923) (L)
Family Meandrinidae
Genus *Dichocoenia* (L)
†Dichocoenia eminens Weisbord 1974 (27, 29)
†Dichocoenia merriami (Vaughan 1900) (27, 29, 32, 34)
Genus *Eusmilia* (L)
†Eusmilia bainbridgensis Durham 1942a (18)
†Eusmilia carrizensis Vaughan 1917 (27)
Genus *Meandrina* (L)
†Meandrina alahuelensis Budd et al. 1992 (12)
†Meandrina antiguensis (Vaughan 1919) (16)
Family Montlivaltiidae
Genus *Placosmilia* (*†*)
†Placosmilia copoyensis Frost and Langenheim 1974 (10)
†Placosmilia? aliciae López-Pérez 2012 (29, 33)
Family Mussidae
Genus *Cyclomussa* (*†*)
†Cyclomussa concinna Wells 1941 (9)
Genus *Leptomussa* (*†*)
†Leptomussa mexicanae Frost and Langenheim 1974 (14)
Genus *Mycetophyllia* (L)
†Mycetophyllia bullbrooki Vaughan and Hoffmeister 1926 (16)
Genus *Syzygophyllia* (*†*)
†Syzygophyllia hayesi Vaughan 1919
Genus *Trachyphyllia* (L)
†Trachyphyllia batequensis (Squires and Demetrion 1992) (5)
†Trachyphyllia bullbrooki (Hoffmeister 1926) (20, 22)
†Trachyphyllia clarki (Durham 1946) (14)
† Trachyphyllia hadleyi (Wells 1934) (12)
†Trachyphyllia heueri (Frost and Langenheim 1974) (20)
†Trachyphyllia sawkinsi (Vaughan 1926) (20, 22)
Family Pocilloporidae
Genus *Pocillopora* (L)
Pocillopora capitata Verrill 1864 (26, 40, 42–45, 47, 50–52, 54, 68, 71, L)
Pocillopora damicornis (Linnaeus 1758) (47, 50, 51, 54, L)
Pocillopora danae Verrill 1864 (L)
Pocillopora effusus Veron 2000 (L)
Pocillopora elegans Dana 1846 (42, 50, 61, L)
Pocillopora grandis Dana 1846 (L)
†Pocillopora guadalupensis Durham 1980 (65)
Pocillopora inflata Glynn 1999 (L)
Pocillopora ligulata Dana 1846 (L)
†Pocillopora maddenensis Budd et al. 1992 (12)
Pocillopora meandrina Dana 1846 (47, L)
Pocillopora verrucosa (Ellis and Solander 1786) (50, L)
Pocillopora woodjonesi Vaughan 1918 (L)
Genus *Stylophora* (L)
†Stylophora cambridgensis Wells 1934 (10)
†Stylophora chaneyi Durham 1942b (4, 5)
†Stylophora chiraensis Wells 1941 (9)
†Stylophora goethalsi Vaughan 1919 (19)
†Stylopora granulata Duncan 1864 (25)
†Stylopora imperatoris Vaughan 1919 (19)
†Stylophora lindavistae Frost and Langenheim 1974 (20)
Family Poritidae
Genus *Goniopora* (L)
†Goniopora cascadensis Vaughan 1919 (21)
†Goniopora elegans (Leymerie, 1846) (9)
†Goniopora hilli Vaughan 1919 (16, 20)
†Goniopora imperatoris Vaughan 1919 (5, 6, 20, 22)
†Goniopora reussiana (Duncan, 1865) (10, 12)
Genus *Porites* (L)
Porites arnaudi Reyes-Bonilla and Carricart-Ganivet 2000 (L)
Porites australiensis Vaughan 1918 (L)
†Porites baracoaensis Vaughan 1919 (20, 22)
Porites baueri Squires 1959 (L)
†Porites carrizensis Vaughan 1917 (26, 27, 29, 34)
†Porites douvillei Vaughan 1919 (16, 20)
Porites lichen Dana 1846 (L)
Porites lobata Dana 1846 (47, L)
Porites lutea Milne Edwards and Haime 1860 (L)
†Porites macdonaldi Vaughan 1919 (20)
Porites panamensis Verrill 1866 (26, 29, 34, 36–60, 62–64, 66, 67, 69–71, L)
†Porites portoricencis (Vaughan 1919) (20)
Porites rus (Forskal, 1775) (L)

(continued)

Table 2.2 (continued)

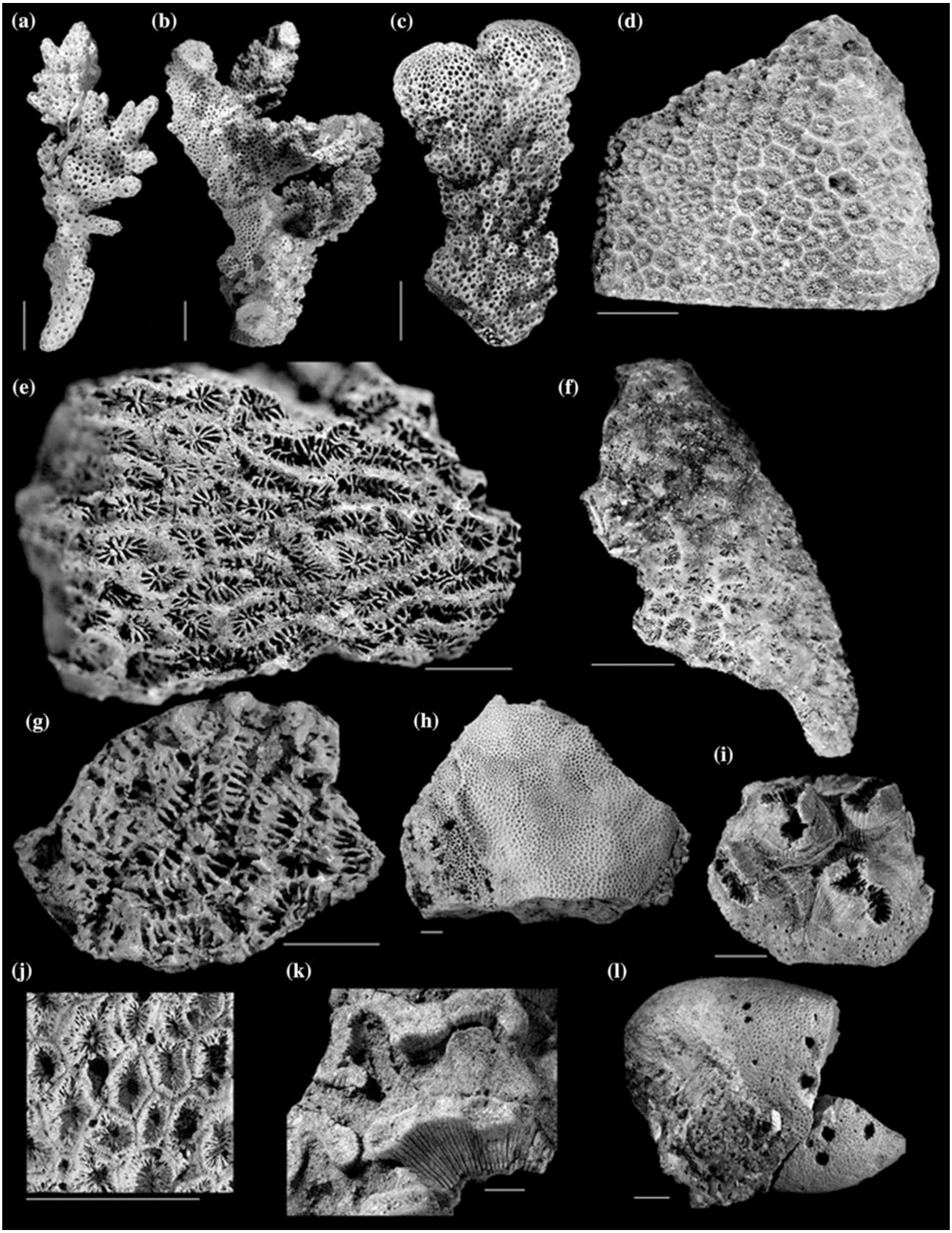
Order Scleractinia
Porites sverdrupi Durham 1947 (52, 53, 58, 60, 63, 64, 66, L)
†*Porites trinitatis* Vaughan and Hoffmeister 1926 (20, 22)
†*Porites waylandi* Foster 1986 (20, 25)
Family Rhipidogyridae
Genus Barysmilia (†)
†Barysmilia aenigma (Budd et al. 1992) (12)
Family Siderastreidae
Genus *Coscinaraea* (L)
†*Coscinaraea colei* Frost and Langenheim 1974 (22)
†*Coscinaraea panamensis* Stemann 1992 (12)
Genus *Pironastrea* (†)
†*Pironastrea antiguensis* Vaughan 1919 (20)
Genus *Psammocora* (L)
Psammocora brighami (Vaughan 1907) (L)
Psammocora contigua (Esper, 1797) (L)
Psammocora haimeana Milne Edwards and Haime 1851 (L)
Psammocora obtusangula Lamarck 1816 (L)
Psammocora profundacella Gardiner 1898 (L)
Psammocora stellata (Verrill 1866) (39, 47, 49, 65, L)
Psammocora superficialis Gardiner 1898 (L)
Genus *Siderastrea* (L)
†*Siderastrea annae* López-Pérez 2012 (29)
†*Siderastrea clarki* Nomland 1916 (15)
†*Siderastrea conferta* (Duncan, 1863) (16, 20, 21, 31)
Siderastrea glynni Budd and Guzmán 1994 (L)
†*Siderastrea mendenhalli* Vaughan 1917 (27)
†*Siderastrea radcliffi* Faustino 1931 (1)
†*Siderastrea scotia* Wells 1945 (10)
Siderastrea siderea (Ellis and Solander 1786) (20, 22, L)
†*Siderastrea vancouverensis* Vaughan 1923 (11, 17)
†*Siderastrea washingtonensis* Durham 1942a (18)
Genus *Sideroseris* (†)
†*Sideroseris durhami* Wells 1945 (10)
Family Synastreidae
Genus *Leptophyllastrea* (†)
†*Leptophyllastrea vaughani* Durham 1942a (8)
Family Thamnasteriidae
Genus *Thamnasteria* (†)
†*Thamnasteria sinuata* Nomland 1916 (6)

Valid names according to Foster (1986), Budd (1987, 1991), Budd and Johnson (1999), Reyes-Bonilla (2002), Baron-Szabo (2006, 2008), López-Pérez (2008, 2012), López-Pérez and Budd (2009). Numbers in parenthesis refer to stratigraphic unit/time where corals were recovered (see Table 2.1). † = Extinct, L = Living. Families, genera and species follow alphabetic order

Eocene to Miocene Central American communities) since the late Paleocene. Of the 53 identified genera, 11 are living and 42 are regionally extinct (currently restricted to Indo-Pacific or Caribbean and western Atlantic waters), or globally extinct. Among the living genera, except for the circumtropically distributed *Acropora*, *Porites*, *Siderastrea* and *Leptoseris*, the remaining taxa are currently restricted to the Pacific Ocean (Veron 2000). Among the regionally extinct genera, *Stephanocoenia*, *Dichocoenia*, *Meandrina*, *Eusmilia*, *Mycetophyllia*, *Colpophyllia*, *Solenastrea*, and *Diploria* are currently restricted to the Caribbean and western Atlantic (Budd 2000); whereas *Astreopora*, *Montipora*, *Diploastrea*, *Favites*, *Goniastrea*, *Leptastrea*, *Leptoria*, *Oulophyllia*, *Plesiastrea*, *Fungia*, *Trachyphyllia*, *Stylophora*, *Alveopora*, *Goniopora*, *Coscinaraea* and *Psammocora* are currently restricted to the Indo-Pacific (Veron and Kelley 1988). Finally, *Madracis* and *Siderastrea*, along with members of the paraphyletic Faviidae (*Favia* and *Montastraea*) (Fukami et al. 2004), are widely distributed across the Caribbean, western Atlantic, and Indo-Pacific. The remainder of the genera are globally extinct (Table 2.2).

Of the 191 species, 49 are living and 142 are extinct (Table 2.2). Of the living species, 48 are restricted to the Pacific whereas *Siderastrea siderea*, which was recorded in the late Oligocene La Quinta Formation and early Miocene Santa Ana Formation in Central Chiapas (Frost and Langenheim 1974), currently inhabits the Caribbean and western Atlantic area (Sekar et al. 2008). Fourteen of the 48 living eastern Pacific species (~30 %) have fossil records that extend back to the early (*Porites panamensis*) and middle (*Pocillopora capitata*) Pliocene, while the remainder appeared during the middle to late Pleistocene in the Gulf of California (López-Pérez 2008; López-Pérez and Budd 2009). Among the taxa with a fossil record, several of the major reef building species in the eastern Pacific are included, such as *Pocillopora damicornis* (Fig. 2.1a), *Pocillopora meandrina* (Fig. 2.1c), *Pocillopora elegans*, *Pocillopora verrucosa* (Fig. 2.1b), *Porites lobata* (Fig. 2.1l), *Pavona gigantea*, *Gardineroseris planulata* (Fig. 2.1j) (Glynn and Ault 2000; Reyes-Bonilla 2003), the more restricted but common *Psammocora stellata*, *Pavona clavus* (Fig. 2.1h), and the Gulf of California endemic *Porites sverdrupi* (López-Pérez et al. 2003).

Considering the age and number of genera and species per assemblage, the number of genera ranged from 1 to 21 (mean = 2.98 ± 3.75 SD), whereas the species ranged from 1 to 39 (mean = 3.87 ± 6.12 SD) (Fig. 2.2 a, b). The highest numbers of genera (>11) and species (>12) correspond with the middle Eocene to early Miocene of Central Chiapas (Frost and Langenheim 1974) and the late Eocene of Panama (Budd et al. 1992) whereas the remainder of the assemblages had less than seven genera (Kern County, California; Northwestern Peru; Punta Chivato, Baja California Sur, Mexico; Table 2.1) and up to nine species (Punta Chivato; Table 2.1).


(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
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◀ **Fig. 2.1** New records of fossil corals in the Gulf of California. **a** *Pocillopora damicornis* (Linnaeus 1758). SUI 100625. Late Pleistocene, locality BC 5, Timbabichi, Baja California Sur, Mexico. **b** *Pocillopora verrucosa* (Ellis and Solander 1786). SUI 100659. Late Pleistocene, locality BC 5, Timbabichi, Baja California Sur, Mexico. **c** *Pocillopora meandrina* Dana (1846). NHMLAC 11740. Late Pleistocene, locality BC 8, Cabo Pulmo, Baja California Sur, Mexico. **d** *Siderastrea annae* López-Pérez 2012. Holotype, SUI 100674. Early Pliocene San Marcos Formation, locality BC 15 Puerto de la Lancha, Isla Carmen, Gulf of California, Mexico. **e** *Favia maitreyiae* López-Pérez 2012. Holotype SUI 100686. Middle Pliocene Carmen Formation, locality BC 27, Isla Montserrat, Gulf of California, Mexico. **f** *Favia tulsidasi* López-Pérez 2012. Paratype SUI 100687. Early Pliocene San Marcos Formation, locality BC 15, Puerto de la Lancha, Isla Carmen, Gulf of California, Mexico. **g** *Diploria sarasotana* Weisbord, 1974. SUI 100690, Early Pliocene San Marcos Formation, locality BC 35, Ensenada El Muerto, Baja California Sur, Mexico. **h** *Pavona clavus* (Dana, 1846). SUI 100866. Late Pleistocene, locality BC 10, La Ventana, Baja California Sur, Mexico. **i** *Dichocoenia eminens* Weisbord, 1974. NHMLAC 38953. Late Miocene, northeastern Coyote Mountains, locality UCLA 631, Carrizo Creek, Imperial Formation, California. **j** *Gardineroseris planulata* (Dana 1846). SUI 100660, Middle Pleistocene, locality BC 11, La Ventana, Baja California Sur, Mexico. **k** *Placosmilia*? *aliciae* López-Pérez 2012. Holotype SUI 100680. Middle Pliocene, San Nicolas Formation, locality BC 4, San Nicolas, Baja California Sur, Mexico. **l** *Porites lobata* Dana, 1846. NHMLAC 11739. Late Pleistocene, locality BC 8, Cabo Pulmo, Baja California Sur, Mexico. Scale bars = 1 cm

This suggests that assemblages other than those that developed at the thermal equator during Eocene to Miocene times, were relatively less diverse through the entire Cenozoic. In light of recent Central America geologic reconstructions (Kirby et al. 2008; Montes et al. 2012) and the low Eocene to Miocene faunistic affinity observed between northwestern and Central American assemblages (see above), it can be argued that the eastern Pacific has never experienced extensive reef building or relatively high species diversity. Depositional accounts and paleoenvironmental reconstructions of coral-bearing deposits from Seattle (Washington), Central California (Durham 1942a, b, 1950a), and the Gulf of California support instead [except for relatively large Pleistocene reef patches at Carmen and Coronado islands (Fig. 2.3a) in the Gulf (Durham 1950b; Johnson et al. 2007; López-Pérez 2008)], small low-diversity (Fig. 2.3c, d) biostromal reefs

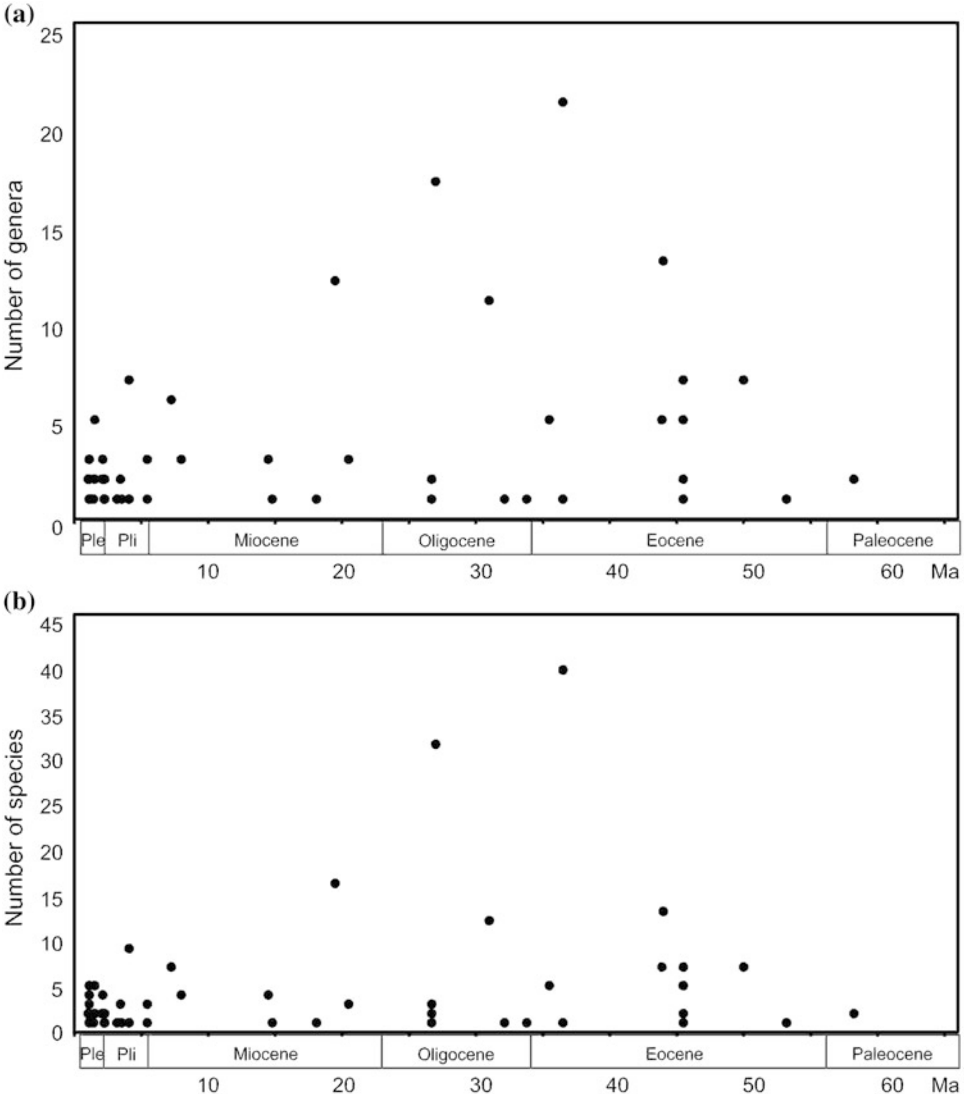

Fig. 2.2 Number of taxa recorded in 71 Cenozoic fossil assemblages, eastern Pacific region. Each point represents an assemblage and denotes locality richness. The geologic age plotted for each assemblage is the midpoint between oldest and youngest age estimates noted in Table 2.1. **a** Number of genera per assemblage, **b** number of species per assemblage

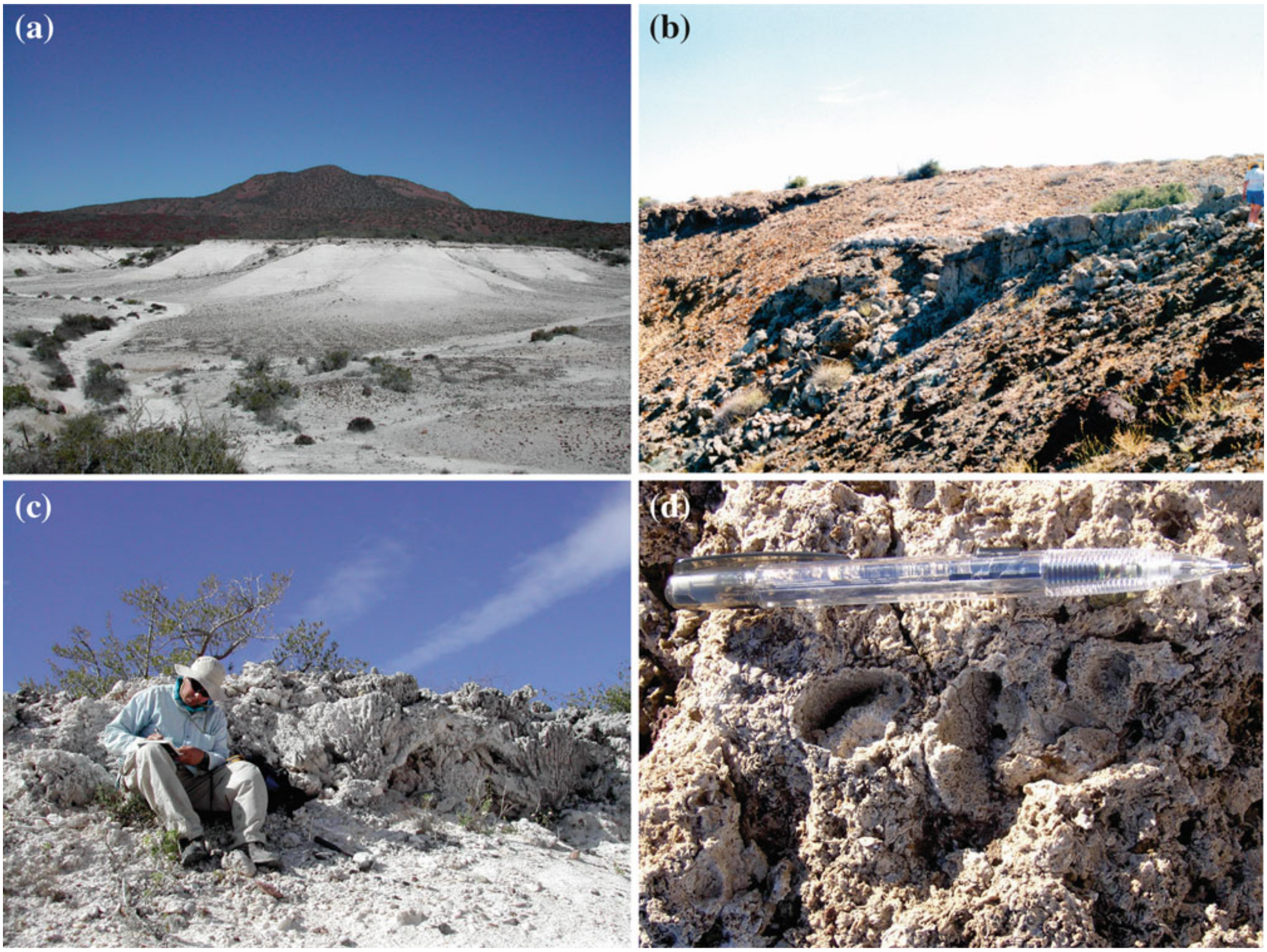

Fig. 2.3 Fossil outcrops and in situ corals in the Gulf of California, Mexico. **a** Cañada Coronados reef. Late Pleistocene *Porites panamensis* reef deposited in a large protected embayment at Isla Coronados (26°N, 111°W). **b** Punta Chivato fringing patch reef. Early Pliocene *Solenastrea fairbanksi* reef deposited in the open, exposed, high-energy environment on the north side of the Punta Chivato promontory (27°N, 111°W). **c** In situ Late Pleistocene *Porites panamensis* reef. West side of Cañada Coronados, Isla Coronados. Colonies may reach a maximum height of 1.1 m. **d** In situ Early Pliocene *Solenastrea fairbanksi* colonies. Early Pliocene reef, north side of Punta Chivato promontory (27°N, 111°W)

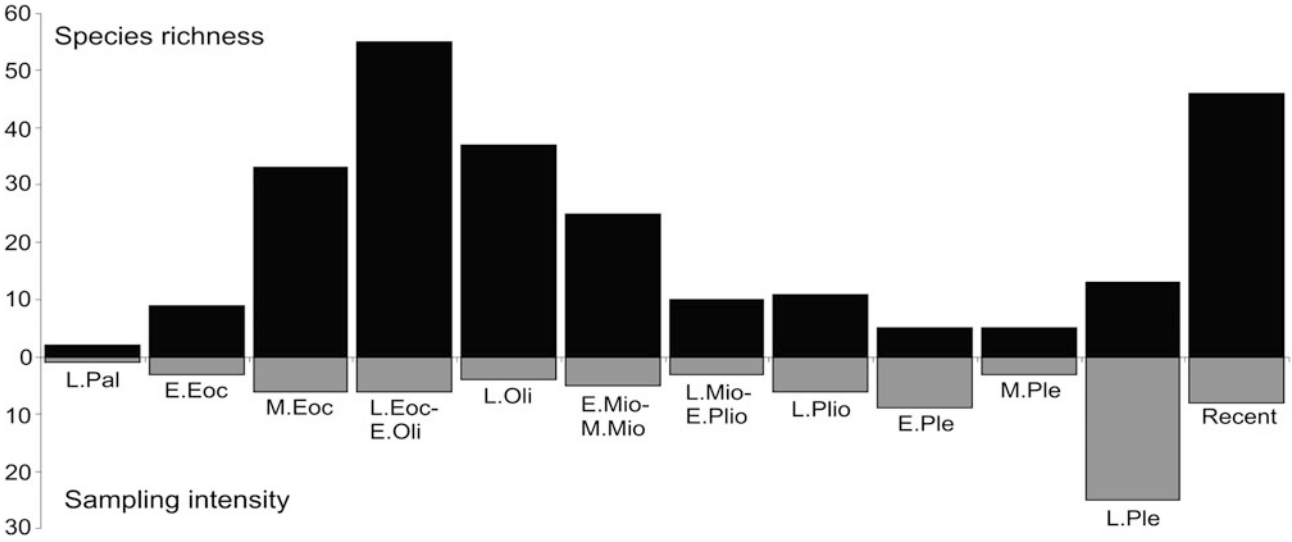

Fig. 2.4 Species richness and sampling intensity (i.e., number of sampled formations per time) of eastern Pacific coral reef species during the Cenozoic. *L.Pal* Late Paleocene, *E.Eoc* Early Eocene, *M.Eoc* Middle Eocene, *L.Eoc-E.Oli* Late Eocene-Early Oligocene, *L.Oli* Late Oligocene, *E.Mio-M.Mio* Early Miocene-Middle Miocene, *L.Mio-E. Plio* Late Miocene-Early Pliocene, *L.Plio* Late Pliocene, *E.Ple* Early Pleistocene, *M.Ple* Middle Pleistocene, *L.Ple* Late Pleistocene, *Recent* Recent time

formed on low-angle ramps or flat-lying terraces usually deposited in open, exposed, high-energy environments (Fig. 2.3b) or well preserved units deposited in small protected embayments. Although more data are needed, this information suggests that from the late Paleocene to the late Pleistocene, reefs were small and low in diversity as are today's coral communities and reefs in the eastern Pacific.

Large-scale temporal analysis suggests that, notwithstanding the well-known worldwide collapse in reef building at the end of the Cretaceous (Rosen 2000), numerous reef coral genera (73.3 %) and species (52 %) crossed the K/T boundary (Baron-Szabo 2006, 2008). Members of K/T surviving genera, *Haimesastrea petrosa* and *Siderastrea radclifi* were collected from Central California, and can be considered to be the oldest (late Paleocene) Cenozoic species known in the eastern Pacific (Table 2.2). Based on these coral occurrences, species richness increased during the Late Eocene/Early Oligocene (55 species), decreased during the early and middle Pleistocene (5 species), rose again during the late Pleistocene (13 species) and finally peaked during Recent times (46 species) (Fig. 2.4). Along with this trend, reef corals expanded and contracted their distributions poleward and vice versa, such that they were able to extend northward to Vancouver Island (~49.8°N) (http://paleodb.org/) during the late Oligocene (Durham 1942a, b, 1950a). Data suggest that these expansions and compressions of climatic belts, associated with global climate warming and cooling respectively (Hay et al. 2002; Thomas et al. 2006), were accompanied by increases-decreases in species richness in the eastern Pacific (Spearman $r = 0.739$, $n = 11$, $p < 0.05$), as has been reported for reef building corals elsewhere during the Cenozoic (Indo-Pacific, Veron 1995; Caribbean, Budd 2000).

Thus, temporal species richness trends in the eastern Pacific apparently responded to the climatic changes experienced during the Cenozoic. However, bootstrap tests (using 999 bootstrap samples) of species richness mean values for every sampled time interval (same as Fig. 2.4) indicated that the species richness observed in every time interval (except Late Eocene-Early Oligocene, Late Pleistocene and Recent) is not significantly different than the mean species richness expected by chance, therefore suggesting that the richness recorded in the eastern Pacific during Late Eocene-Early Oligocene, Late Pleistocene and Recent represents meaningful signals. This finding is relevant because it indicates that: (a) it is not unlikely that high species richness developed at the eastern Pacific thermal equator during the Late Eocene-Early Oligocene, which is in full agreement with the burst of coral taxa and the widespread distribution of reef biotas in the Caribbean and Indo-Pacific (Veron 1995; Budd 2000), (b) coral taxa were lost in the eastern Pacific and reached their lowest number during the Late Pleistocene (López-Pérez and Budd 2009), and (c) following the Late Pleistocene species richness rose toward the Recent with the arrival of Indo-Pacific taxa (Glynn and Ault 2000; Glynn et al. 2007). Nonetheless, aside from these three signals (Late Eocene-Early Oligocene, Late Pleistocene and Recent), clear evidence is lacking regarding true species richness in the eastern Pacific during most of the Cenozoic. Therefore, the large-scale historical trend suggested for most of the Cenozoic (Durham 1966; Frost 1977; Colgan 1990; Cortés 1997; Glynn and Ault 2000) is still debatable, and more data are needed.

2.3 Late Miocene to Modern Times: Shaping the Recent Eastern Pacific Coral Communities and Reefs

Large-scale spatio-temporal data have delineated major evolutionary trends in Cenozoic reef corals in the eastern Pacific (Durham 1966; Frost 1977; Colgan 1990; Cortés 1997; Glynn and Ault 2000, see Sect. 2.2). Nevertheless, new records of coral species (López-Pérez 2008, 2012; López-Pérez and Budd 2009); the lithology, age and paleoenvironment of buildups (Johnson and Ledesma-Vázquez 1999; Mayer and Vincent 1999; Halfar et al. 2001; DeDiego-Forbis et al. 2004; Johnson et al. 2007), and the relative absence of information from western Mexico and Central America (Palmer 1928; Hertlein 1972; Durham 1980), clearly imply that the only clues to the origin and evolution of the modern eastern Pacific coral fauna, come from the Late Miocene to Late Pleistocene buildups recovered from the Gulf of California. It is fair to say, however, that information from the gulf may be biased because it potentially represents the evolutionary history of subtropical coral communities and reefs, while information provided by eastern tropical Pacific (ETP) reefs (western Mexico and Central America) is lacking. Cortés (1993) observed that the

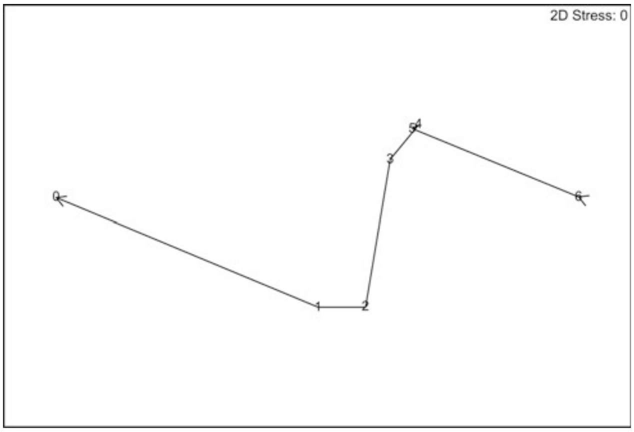

Fig. 2.5 Qualitative changes of coral reef communities and reefs in the Gulf of California, Mexico during the last six million years. Dissimilarities among time intervals (one million years duration; *6* oldest, *0* Recent) were generated with a Bray-Curtis index from an incidence matrix. Distance map produced by multidimensional scaling

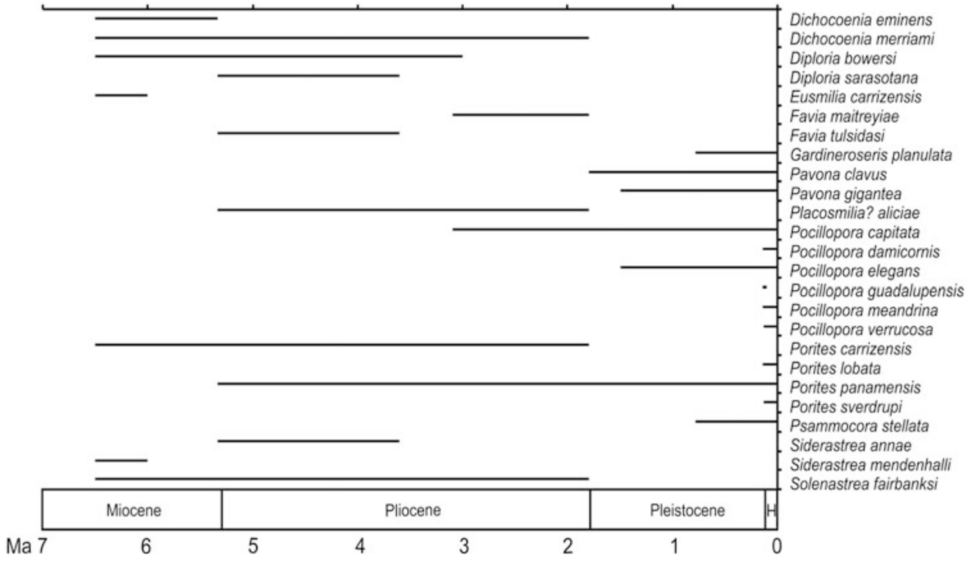

Fig. 2.6 Ranges of all known reef coral species (total = 25) in the Gulf of California during Late Miocene and recent times. Ranges are based on occurrences in 47 Gulf of California localities listed in López-Pérez (2008, Table 1). Ends of range lines are maximum age estimates for localities in which first and last occurrences take place. Only species with fossil occurrences are plotted. *H* Holocene

absence of ETP fossil reefs may be related to the poor structural integrity of reef frameworks and crustose coralline algal pavements, the relative absence of submarine cementation, and the high rates of bioerosion in this region. Along with the aforementioned negative effects, Greenstein and Pandolfi (2003) studied alteration in reef-coral death assemblages in the Florida Keys, and demonstrated that physico-chemical degradation (abrasion and dissolution) was greatest in reef-crest and patch-reef environments. It is possible that the relative absence of eastern Pacific fossil outcrops may be explained by the combined effect of high degradation of patch-reef environments coupled with one or several of the conditions advanced by Cortés (1993). Nevertheless, the data suggest that the apparent lack of fossil outcrops is deeply rooted in the relative absence of extensive and detailed studies in the eastern Pacific, as was recently demonstrated for the Gulf of California (Johnson and Ledesma-Vazquez 1999, 2001; DeDiego-Forbis et al. 2004; Johnson et al. 2007; López-Pérez 2008).

Quantitative analysis of published (López-Pérez 2008, 2012; López-Pérez and Budd 2009) and unpublished presence/absence coral data, collected during multidisciplinary and inter-institutional field expeditions to the Baja California Peninsula since 2002, suggest that during the last six million years, gulf coral communities and reefs experienced dramatic changes (Fig. 2.5). Several elements are particularly relevant. Six million years ago (late Miocene) the stony coral fauna was entirely distinct from the fauna currently inhabiting the Gulf of California and eastern Pacific (Glynn and Ault 2000; Glynn et al. 2007; see Chap. 5, Glynn et al.); indeed, the two temporally separated faunas are markedly different. During late Miocene time, the fauna was mainly composed of regional endemics (*Dichocoenia merriami*, *Diploria bowersi*, *Eusmilia carrizensis*, *Porites carrizensis*, *Siderastrea mendenhalli* and *Solenastrea fairbanksi*), and Caribbean species (*Dichocoenia eminens*) (Fig. 2.1i) (López-Pérez and Budd 2009) (Fig. 2.6). In spite of the large numbers of regional endemics, all of these species belonged to genera currently inhabiting the Caribbean. Figure 2.6 also shows the existence of three abrupt faunal shifts coupled with two periods of relative stasis in species composition. The shifts occurred at 6 to 5 Ma, 3 to 2 Ma, and 1 Ma to the Recent, with the last shift, by far, the most dramatic. While the first two shifts were related to the emergence of Caribbean-related endemic species in the gulf (*Siderastrea annae*, *Favia maitreyiae*, *Favia tulsidasi*, *Placosmilia*? *aliciae*, *Diploria sarasotana*; Fig. 2.1d–f, k, i), along with the appearance of *Porites panamensis* (Early Pliocene) and *Pocillopora capitata* (Middle Pliocene) (López-Pérez 2008) (Fig. 2.6), the last shift involved the extinction of regional endemics and the arrival of Indo-Pacific species currently inhabiting coral communities and reefs in the ETP region. Regarding faunal stasis, this occurred between 5 to 3 Ma and 2 to 1 Ma as a consequence of expansion and dominance of Caribbean-derived species in the Gulf of California (López-Pérez and Budd 2009). In summary, the change experienced in the Gulf during the last six million years is related to the extinction of Caribbean-related regional endemic species, and the steady arrival of Indo-Pacific taxa likely via the North Equatorial Counter Current (Fig. 2.6).

From the foregoing, two elements converged in the abrupt shift that shaped the current composition of coral communities and reefs in the Gulf and eastern Pacific: the extinction pulses that drove the local removal of Caribbean-related fauna between 3 and 1 Ma (López-Pérez and Budd 2009), and the immigration of species into the Gulf from the Indo-Pacific (Dana 1975; Glynn and Ault 2000; see also Chap. 5, Glynn et al.). As demonstrated by López-Pérez and Budd (2009), both pre-turnover (Caribbean-related) and post-turnover (Indo-Pacific) taxa do not coincide in space or time, thereby

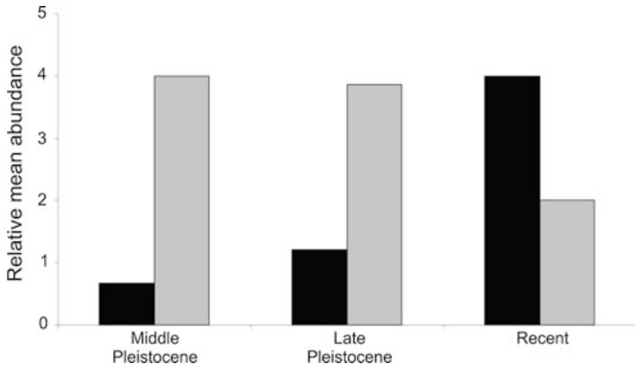

Fig. 2.7 Relative abundance variations of stony corals from middle Pleistocene to Recent times in coral communities and reefs, Gulf of California, Mexico. Gray = *Porites panamensis*, black = *Pocillopora capitata*. Relative values: *1* rare, *2* common, *3* abundant, *4* very abundant

ruling out the role of biological interactions or ecological replacement as playing the leading role in species extinctions. On the contrary, Indo-Pacific species probably invaded the Gulf at a steady but sporadic rate after the arrival of *Pavona clavus* during the lower to middle Pleistocene near the mouth of the Gulf (López-Pérez 2008). It is worth mentioning that, except for living *Porites panamensis* and *Pocillopora capitata* that spatio-temporally coexisted with pre-turnover taxa, no single regional endemic Caribbean-related coral species, or its descendant, has been recorded in the Gulf of California (Reyes-Bonilla and López-Pérez 2009) or elsewhere in the eastern Pacific (Glynn and Ault 2000). Nevertheless, related species of *Diploria, Dichocoenia, Solenastrea* and *Eusmilia* still persist on living Caribbean reefs (Budd et al. 1994), and *Favia* and *Siderastrea* also inhabit Indo-Pacific and Atlantic-Caribbean reefs. Recently, *Siderastrea glynni* was described from the Pacific side of Panama by Budd and Guzmán (1994), but later found to share identical sequence types with *Siderastrea siderea* currently living in the Atlantic. Therefore, it is unlikely that *S. glynni* represents the remnants of a population that was divided by the closure of the Central American Seaway (Forsman et al. 2005).

Relative abundance analysis of Gulf of California coral communities and reefs illustrates the emergence of modern reefs after the demise of Caribbean-related coral species (Fig. 2.7). The oldest record of *Porites panamensis* is in the Early Pliocene of Punta Chivato and in Puerto de La Lancha at Isla Carmen (López-Pérez 2008), where relatively small but abundant massive and branching colonies built small patch reefs along with Caribbean-related coral taxa. After the demise of the Caribbean-related coral fauna during the late Pliocene, *P. panamensis* flourished and constructed relatively large monospecific patch reefs from Punta Chivato to Isla Cerralvo during Pleistocene times (Johnson et al. 2007). In the Recent, this species became the most widespread taxon in the Gulf of California and eastern Pacific coral communities and reefs (Glynn and Ault 2000; Reyes-Bonilla and López-Pérez 2009). Figure 2.7 further illustrates the shift from *P. panamensis* to *Pocillopora* spp. in the Gulf. In particular, it is remarkable how *Pocillopora capitata*, first recorded during the middle Pliocene (López-Pérez 2008), has increased in abundance since the middle Pleistocene to Recent, while *P. panamensis* (thought still to be a common species) has become a relatively minor contributor to living Gulf of California south and central coral communities and reefs (Reyes-Bonilla and López-Pérez 2009). From this it can be hypothesized that the dominance of *Pocillopora* spp. in today's reefs may have a causal connection with the slightly historic decrement of *P. panamensis*, and also with the burst of speciation and ecological success of pocilloporid holobionts in the ETP. In other words, the relative high abundance of *Pocillopora* spp. over *Porites* in today's living coral communities and reefs in the gulf may be explained mainly by a dilution effect and not by the competitive displacement of *P. panamensis* by *Pocillopora* species.

2.4 The Modern Eastern Pacific Coral Fauna: A Tale of Dispersal and Vicariance

There are two hypotheses regarding the origin of the eastern Pacific coral fauna, commonly termed dispersal and vicariance. The dispersal hypothesis proposes that during the Plio-Pleistocene glaciations, and after the rise of the Isthmus of Panama, all of the eastern Pacific corals that were mainly Atlantic in origin became extinct and were replaced by an Indo-Pacific fauna (Dana 1975). In contradistinction, Heck and McCoy (1978) suggested that the modern eastern Pacific fauna was derived from previous Atlantic-Caribbean coral taxa through vicariance following the rise of the Isthmus of Panama. Evidence for the dispersal hypothesis was based on the relative absence of Plio-Pleistocene coral reef fossil outcrops on the Pacific side of America, the morphologic similarity between Indo-Pacific and eastern Pacific species, and the absence of transisthmian sibling taxa. Although Heck and McCoy (1978) criticized Dana's approach in favor of a more parsimonious explanation, they were unable to provide any alternative analysis, or unambiguously address the Atlantic-Caribbean origin of the eastern Pacific taxa.

Today it is widely accepted that the eastern Pacific coral reef fauna is almost entirely Indo-Pacific in origin (Glynn and Ault 2000; Glynn et al. 2007; Veron et al. 2015; see Chap. 5, Glynn et al.). In fact, based on the comparison of traditional morphologic characters (Squires 1959; Wells 1983; Ketchum-Mejía and Reyes-Bonilla 2001) as well as morphometric (Weil 1992; López-Pérez et al. 2003) and genetic (Weil 1992; López-Forment 2004; Forsman 2005, 2010; Combosch et al. 2008) analyses, it is estimated that approximately 66 % of the eastern Pacific coral fauna consists of Indo-Pacific immigrants. There are, however, studies suggesting that the ancestry of some eastern Pacific taxa may be closely related to Caribbean and western Atlantic species. For example, based on a morphometric comparison of selected taxa and a generic-level data analysis of Caribbean, eastern Pacific and Indo-Pacific coral species, Budd (1989) found a close relationship between the late Miocene Imperial Valley species and Plio-Pleistocene Caribbean faunas. In a similar analysis, based on the uninterrupted fossil record of *Porites* species in the Gulf of California during the Plio-Pleistocene, Reyes-Bonilla (1992) suggested that some Caribbean related species may have survived the Plio-Pleistocene extinctions that occurred in the eastern Pacific (López-Pérez and Budd 2009).

A few years ago, the genera *Siderastrea* and *Porites* were the best candidates for testing the hypothesis regarding the Caribbean origin for some eastern Pacific taxa because of their modern circumtropical distributions (Veron 2000), common occurrences in the fossil record (Veron and Kelley 1988; Budd 2000; López-Pérez 2008) and, at least for *Porites*, survival to the Plio-Pleistocene regional extinctions on both sides of the Central American Isthmus (Budd 2000; Lopez-Perez and Budd 2009). With a Central American Seaway connecting the Atlantic and Pacific, *Siderastrea mendenhalli* and *Siderastrea annae* were recorded in the Late Miocene/Pliocene of the Gulf of California, but they disappeared during the Pliocene/Pleistocene regional extinction (López-Pérez and Budd 2009). Recently, *Siderastrea glynni* appeared in the Pacific of Panama (Budd and Guzmán 1994), initiating a debate about the Atlantic origin of this species. Recent genetic analysis, however, demonstrated that this species shares identical sequence types with the Caribbean *S. siderea,* and therefore it is unlikely that *S. glynni* represents the remnants of a population that was divided by the closure of the Central American Seaway (~3.4 Ma; Coates and Obando 1996). Instead, *S. glynni* may have originated in response to a breach of the isthmus (~2 Ma), or a contemporary introduction by ship (Forsman 2005).

Contrary to *Siderastrea* species, several recent studies (Weil 1992; López-Forment 2004; Forsman 2005, 2010) clearly support the closest relation of *Porites panamensis* and *Porites sverdrupi* with the Caribbean and western Atlantic clades. For example, the electrophoretic analysis carried out by Weil (1992) suggests that *P. panamensis* is more closely related to *Porites colonensis* and *Porites astreoides* than to the Pacific species *Porites lobata*. In the same way, the maximum likelihood and parsimony analysis of the cytochrome oxidase 1 gene performed by López-Forment (2004) supported a close relationship between Gulf of California *P. sverdrupi* and Caribbean *Porites furcata*, *Porites porites* and *Porites divaricata*. Similarly, Forsman's (2006, 2010) analysis of the nuclear and ribosomal ITS region found that *P. panamensis* and *P. sverdrupi* are more closely related to the *P. furcata*-*P. divaricata* clade than to any Indo-Pacific poritid taxa. Finally, preliminary (although poorly supported; López-Pérez, unpublished data) phylogenetic analysis of morphometric data suggests the inclusion of *P. panamensis* and *P. sverdrupi* in Caribbean and western Atlantic clades, but unrelated to Indo-Pacific poritids. Therefore, the agreement among independent studies of genetic and morphologic data (Weil 1992; López-Forment 2004; Forsman's 2006, 2010), clearly supports the presence of a mix of Indo-Pacific (*P. lobata*, *P. lutea*, *P. lichen*, *P. australiensis*, *P. arnaudi*, *P. baueri*) and Caribbean/Atlantic derived *Porites* (*P. panamensis*, *P. sverdrupi*) in extant eastern Pacific coral communities and reefs. From the foregoing, the eastern Pacific poritid fauna resulted from long-distance dispersal of Indo-Pacific taxa, and from local speciation of Caribbean/Atlantic populations. Therefore, the hypotheses regarding the origin of the eastern Pacific coral fauna proposed by Dana (1975), and Heck and McCoy (1978), at least for some taxa, are complementary.

2.5 Summary and Future Research Agendas of Fossil Coral Fauna

Today both the pre-Pleistocene stony coral faunistic affinity between the Pacific and Caribbean-Atlantic side of America (Vaughan 1917) and the Pleistocene turnover with a bias towards an Indo-Pacific and eastern Pacific similarity (Dana 1975) is undeniable. New data, however, have helped to further disentangle the large-scale spatio-temporal patterns reported in a series of seminal papers published since 1960 (Durham and Allison 1960; Durham 1966; Dana 1975; Heck and McCoy 1978; Colgan 1990; Cortés 1997). So far, based on paleocoordinates of the coral deposits (http://paleodb.org/), and a much more restricted connection between the eastern Pacific and Atlantic/Caribbean during Eocene to Miocene times than previously envisaged (Kirby et al. 2008; Montes et al. 2012), the coral-bearing deposits recovered in Central America (Central Chiapas to Colombia) (Vaughan 1919; Woodring 1957; Frost and Langenheim 1974; Budd et al. 1992; Coates et al. 2005), once considered present at the thermal equator of the eastern Pacific region (Colgan 1990), should best be considered part of the Eocene-Miocene Caribbean Province. If future geologic studies support the hypothesis that Eocene to Miocene deposits from Central America are part of the Caribbean Province, then there is no reason to suggest that the eastern Pacific coral fauna was richer and supported more extensive reef building in pre-Holocene times (Durham 1966; Frost 1977; Colgan 1990; Cortés 1997; Glynn and Ault 2000) compared with eastern Pacific living coral communities and reefs. In support of this alternative view, data suggest that most of the eastern Pacific coral formations during the entire Cenozoic were small, low-diversity biostromal reefs deposited in low-angle ramps or flat-lying terraces in open, exposed, high-energy environments, or in small protected embayments (Durham 1942a, b, 1950b; Johnson et al. 2007; López-Pérez 2008). In summary, they are much like today's eastern Pacific coral communities and reefs.

Further bootstrap analysis of detailed spatio-temporal data demonstrated that the temporal trend of species richness in the eastern Pacific during the Cenozoic, currently suggested by large scale studies (Durham 1966; Frost 1977; Colgan 1990; Cortés 1997; Glynn and Ault 2000; López-Pérez 2005), may be spurious and, except for the richness recorded during the Late Eocene-Early Oligocene, Late Pleistocene and Recent times, they are not significantly different from a trend generated by chance. In other words, we lack clear evidence regarding the true species richness in the eastern Pacific (except for the above mentioned time slices), and therefore the large-scale trend through most of the Cenozoic era is still debatable.

Recently published information suggests that during the past six million years, Gulf of California coral communities and reefs experienced dramatic changes. The late Miocene coral fauna in the gulf was composed of regionally endemic species closely related to the Atlantic-Caribbean fauna (López-Pérez 2008; López-Pérez and Budd 2009) as a consequence of the existence of the Central American Seaway between the Atlantic and Pacific Oceans. During the late Miocene to Pliocene, an Atlantic/Caribbean-related fauna flourished throughout the gulf and constructed relatively large coral patches and reefs (López-Pérez 2008; López-Pérez and Budd 2009), until long after the connection between the Atlantic and Pacific was closed (~3.4 Ma; Coates and Obando 1996). Finally, the Atlantic/Caribbean-related coral fauna disappeared during the late Pliocene (~1.8 Ma) extinction pulses in the gulf and was replaced by the steady arrival of Indo-Pacific coral taxa (López-Pérez and Budd 2009) probably via the North Equatorial Counter Current.

Nevertheless, the late Pliocene extinction (López-Pérez and Budd 2009) pulses were apparently unable to eliminate some taxa (*Porites panamensis* and *Porites sverdrupi*), which strongly suggests that the hypotheses regarding the origin of the eastern Pacific coral fauna proposed by Dana (1975), and Heck and McCoy (1978) are to some extent complementary. There is a strong agreement between independent genetic (Weil 1992; López-Forment 2004; Forsman 2006, 2010) and morphologic analyses (López-Pérez, unpublished), which supports the phylogenetic relationship between the above species and Caribbean/Atlantic *Porites*. Thus, current information supports the presence of a mix of Indo-Pacific (*P. lobata*, *P. lutea*, *P. lichen*, *P. australiensis*, *P. arnaudi*, *P. baueri*) and Caribbean/Atlantic derived *Porites* (*P. panamensis*, *P. sverdrupi*) in modern eastern Pacific coral communities and reefs, indicating that contemporary eastern Pacific *Porites* resulted from long-distance dispersal of Indo-Pacific taxa and from local speciation of Caribbean/Atlantic ancestral populations of *Porites*.

Finally, the evolutionary history of the eastern Pacific coral fauna over the past 6 Ma (Late Miocene to Late Pleistocene) has been based on subtropical coral communities from the Gulf of California and, therefore, may, to some extent, be biased. It is therefore urgent to fully research coral-bearing fossil outcrops unambiguously deposited at the thermal equator (western Mexico and Central America) in the eastern Pacific during the geological past. In addition, several other research programs are required. For example, except for the taxonomic studies conducted by Baron-Szabo (2006, 2008) for the Paleogene, and by López-Pérez (2012) for the Late Miocene to Recent Gulf of California coral fauna, the taxonomy of a large number of eastern Pacific coral taxa needs to be carefully examined in order to unambiguously assess species richness and affinities among faunas (Budd et al. 1994). At the same time, a more intensive and widespread sampling design based on ecological quantitative techniques, similar to those used for sampling modern coral reef communities (i.e. transect and quadrat methods), must be implemented in new coral-bearing outcrops and previously studied exposures. This is especially important because recent published research conducted in the Gulf of California (López-Pérez 2008) has resulted in new localities and species records, even for previously studied exposures.

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