Late Miocene to Pleistocene Reef Corals in the Gulf of California

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ABSTRACT
A new collection of fossil reef corals from the late Miocene Imperial Formation, the early Pliocene San Marcos Formation, the middle to late Pliocene Carmen Formation, and the Pleistocene, Gulf of California, Mexico, has yielded four new species Siderastrea annae n. sp., Placosmilia? aliciae n. sp., Favia maitreyiae n. sp., and Favia tulsidasi n. sp. Additionally, new occurrences of the previously described Pocillopora damicornis (Linnaeus, 1758), Pocillopora verrucosa (Ellis & Solander, 1786), Pocillopora meandrina Dana, 1846, Gardineroseris planulata (Dana, 1846), Pavona clavus (Dana, 1846), Porites lobata Dana, 1846, Diploria sarasotana Weisbord, 1974, as well as Dichocoenia eminens Weisbord, 1974, are reported. Morphometric analysis failed to distinguish between S. californica Vaughan, 1917, and S. mendenhalli Vaughan, 1917, therefore the former is synonymized with the latter. The fauna occurred either in low-angle ramps or flat-lying terraces of variable extension. Most outcrops were small, and reminiscent of more extensive deposits usually formed in open, exposed, high-energy environments. However, well preserved units deposited in protected embayments are also present. Except at Isla Coronados and La Ventana where multiple coral terraces occur, coral bearing units represent single spatiotemporal growth episodes. The present analysis shows that the reef coral fauna between late Miocene to late Pleistocene in the Gulf of California can be considered depauperate when compared to the Caribbean fauna; nonetheless, it bears many more species than previously thought.

RESUMEN
Una colección reciente de corales fósiles del Mioceno tardío de la Formación Imperial, del Plioceno temprano de la Formación San Marcos, del Plioceno medio-tardío de la Formación Carmen y del Pleistoceno del Golfo de California, México ha contribuido con cuatro especies nuevas: Siderastrea annae, Placosmilia? aliciae, Favia maitreyiae y Favia tulsidasi. Adicionalmente, se reportan nuevos ámbitos geográficos para Pocillopora damicornis (Linnaeus, 1758), Pocillopora verrucosa (Ellis & Solander, 1786), Pocillopora meandrina Dana, 1846, Gardineroseris planulata (Dana, 1846), Pavona clavus (Dana, 1846), Porites lobata Dana, 1846, Diploria sarasotana Weisbord, 1974, y Dichocoenia eminens Weisbord, 1974, previamente registrados para el Indo-Pacífico y Caribe. Análisis morfométricos fueron incapaces de distinguir entre S. californica Vaughan, 1917, y S. mendenhalli Vaughan, 1917, por lo tanto S. californica se sinonimizó con S. mendenhalli. La fauna fósil se desarrolló en rampas con pendientes moderadas o terrazas de dimensión variable. Los afloramientos coralinos son pequeños y reminiscientes de depósitos más extensos que usualmente se desarrollaron en ambientes con alta energía del oleaje. Sin embargo, también existen depósitos que se desarrollaron en pequeñas bahías protegidas. Excepto en Isla Coronados y La Ventana donde se desarrollaron múltiples terrazas, los corales representan episodios de crecimiento únicos en tiempo y espacio. El análisis demuestra que la fauna coralina entre el Mioceno tardío y el Pleistoceno tardío en el Golfo de California puede ser considerada pobre si se compara con la fauna del Caribe, sin embargo posee muchas más especies de lo que previamente se pensó.

INTRODUCTION
Fossil reef corals have previously been reported from the Cenozoic of the eastern Pacific, where up to 151 coral species including synonyms have been recorded (López-Pérez, 2005). Between the late Miocene and Recent time, fossil-bearing units are spatially restricted to the Gulf of California, and there is a lack of outcrops in western México and Central America (Palmer, 1928; Hertlein, 1972). Since Fairbanks (1893) first recorded the existence of an unusually interesting coral fauna from Imperial Valley, California, 13 species included in nine genera have been reported in the Gulf of California area. Coral taxa were treated in a handful of papers published by Vaughan (1917), Durham (1947, 1950), and Squires (1959). The rest of the Gulf of California literature has added fossiliferous localities to the record (Jordan & Hertlein, 1926; Hertlein, 1957, 1966; Hertlein & Emerson, 1959; Emerson, 1960; Emerson & Hertlein, 1964; Simian & Johnson, 1997; Johnson & Ledesma-Vázquez, 1999; Gastil et al., 1999; DeDiego-Forbis et al., 2004). Rather than being caused by the impoverished and to some extent homogenous fauna of the Gulf of California, this mainly resulted from the focus of the studies. With the exception of the works of Vaughan (1917), Durham (1947, 1950), and Squires (1959), whose main concerns were hermatypic corals, most reports were incidental in nature and studies focused on aspects other than corals.
An inter-institutional and multidisciplinary research team targeted Pliocene to Pleistocene coral communities in the Gulf of California to assemble a detailed geologic and taxonomic framework for already known and new coral-bearing units. The focus of the present study is solely on the systematic of the reef corals and its purpose is to describe several new taxa, as well as provide expanded descriptions of some previously described taxa retrieved from the late Miocene to late Pleistocene of the Gulf of California. Further implications in paleoecology, paleogeography, and evolution of the group in the Gulf of California were discussed by López-Pérez (2008) and López-Pérez & Budd (2009).

**STRATIGRAPHY AND GEOLOGIC SETTING**

The fauna described below was collected from fossil coral outcrops showing coral development in the Gulf of California area (Text-fig. 1). The ages of the outcrops range between late Miocene to late Pleistocene. A general account of the nature and depositional setting of the coral-bearing units is followed by a brief synopsis of the lithology, age, and paleoenvironment of each unit.

**Coral-bearing Units**

Coral-bearing units form low-angle ramps (Punta Chivato area, San Nicolas, Isla Montserrat; Text-fig. 1; Appendix 1), or flat-lying terraces (Isla Coronados, Las Animas, Cabo Pulmo; Text-fig. 1; Appendix 1) of variable extension. They usually rest with an angular unconformity on the tilted volcanics of the Miocene Comondú Group in the Bahía Conception area (Ledesma-Vázquez & Johnson, 2001), Miocene El Cien Formation at Las Animas (DeDiego-Forbis et al., 2004), and early Pliocene Trinidad Formation at Rancho Algodones (Martínez-Gutiérrez & Sethi, 1997). Most outcrops are small, reminiscent of more extensive deposits that are interpreted to have been formed in open, exposed, high-energy environments. However, well-preserved units deposited in protected embayments are also present (South Punta Chivato, Cañada Coronados, Puerto Balandra, Las Animas; Text-fig. 1; Appendix 1). Marine deposits are common and widespread from Santa Rosalía to Cabo Pulmo (Ortlieb, 1991), although those recording reef development are scarce. Except at Isla Coronados and La Ventana, where multiple coral terraces occur, they represent single spatiotemporal growth episodes. Finally, in contrast with the Indo-Pacific and Caribbean where coral reefs have a wide bathymetric range (ca. 0-50 m) and therefore most reef-building episodes preserve several reef environments (Pandolfi, 1996), Gulf of California coral communities developed in shallow waters (< 15 m) as suggested by actual coral development at the Baja California Peninsula (Reyes-Bonilla & López-Pérez, 2009), and therefore coral-bearing units generally represent single reef environments.

**Imperial Formation**

The Imperial Formation is a lithologic unit described from the Coyote Mountains in southern California (Hanna, 1926; Text-fig. 2). In general, the Imperial Formation overlies the Mesozoic and older metamorphic basement, and contacts represent rocky shorelines containing marine borings and filled predominantly with Quaternary age sediments (Watkins, 1990). The Imperial Formation unconformably overlies the Alverson Formation and local nonmarine units, and represents marine conditions with the occurrence of green micaeous shale, calcareous sandstone, and yellow biotstratal claystone (Kidwell, 1988). Corals were collected by Ann F. Budd (Department of Geoscience, University of Iowa) from the calcareous sandstone of the Latrania Member at Barrett Canyon, northeast of Coyote Mountains, and Alverson Canyon (Text-fig. 2; Appendix 1), deposited under shallow marine conditions (Foster, 1979, 1980a). A more detailed analysis regarding the stratigraphic setting of the collecting localities was provided by Foster (1979, 1980a).

Studies indicate that the boundary between members of the formation is time-transgressive and that the unit includes multiple biofacies that are difficult to correlate. However, radiometric ages from rocks overlying and underlying fossiliferous facies constrain the age of the Imperial Formation between 6 and 6.5 Ma (Eberly & Stanley, 1978, for rocks underlying the Imperial Formation in the Coyote Mountains; McDougall et al., 1999, for rocks overlying the Imperial Formation in Whitewater Canyon).

**San Marcos Formation**

The San Marcos Formation is the lower member of a much larger lithologic unit referred to as the Salada Formation by the Maryland Oil Company (Anonymous, 1924) that used it to describe all of the marine Pliocene of Baja California. As designated by Anderson (1950), the San Marcos Formation overlies unconformably tilted Oligocene to Miocene andesites, basalts, tuffs, and volcanic breccias of the Comondú group (McFall, 1968). The San Marcos Formation is a sequence of clastic sediments, gypsum, and pebbly limestone at San Marcos Island, but consists of ca. 61 m of volcanic gravels, sandstones, and siltstones at Isla Carmen (Anderson, 1950).

Corals were collected from a pebbly limestone facies to the north of Punta Chivato and Ensenada El Muerto in the Punta Chivato area, and calcareous sandstone at Puerto de la Lancha in Isla Carmen (Text-figs 3-4; Appendix 1). The coral-bearing unit is relatively small at Puerto de la Lancha and north of Punta Chivato (Puerto de la Lancha, ca. 70 m in length with a maximum width of 15 m and a maximum thickness of 5 m; Punta Chivato, 107 m in length with a maximum width of 20 m and a maximum thickness of 1-4 m), but is large at
Text-fig. 1. Study area in the Gulf of California, northwestern México. Detailed information about each locality is listed in Appendix 1.
Ensenada El Muerto (> 500 m in length with a maximum width of 50-60 m and a maximum thickness of 5 m). At the localities, corals do not form a rigid reef structure; instead they make up scattered colonies that are poorly preserved and are mixed with andesite black pebbles in the Punta Chivato area. Based on the presence of index fossils (Durham, 1950; Simian & Johnson, 1997) and comparison with the Miocene Comondu Group, the coral facies were deposited under vigorous wave activity immediately after the Pliocene-Miocene unconformity during the early Pliocene.

### Carmen and Marquer Formations

The Carmen Formation crops out around the eastern shore of Bahía Salinas and along the shore of Bahía Oto at Isla Carmen. Anderson (1950) defined the unit as a succession of ca. 460 m thick volcanic pebble and cobble conglomerate, which is poorly bedded, and contains scattered interbeds of volcanic sandstone usually 0.3-0.7 m thick with fragmentary marine fossils. Dorsey et al. (2001) carried out a more detailed study of the sequence in the northeastern side of Isla Carmen and found ca. 1,200 m of thick bedded conglomerate, bedded conglomerate sandstone, bathyal marine marlstone and mudstone, dacite breccia, and conglomerate and bioclastic limestone. At Bahía Oto (Text-fig. 4), the Carmen Formation is a flat-lying sequence formed by calcareous beds and volcanic conglomerate capped by light-gray limestone, where scattered intermediate-sized heads of massive *Porites panamensis* Verrill, 1866, were collected (Appendix 1). This section contains the upper conglomerate and youngest bioclastic unit identified at Punta Perico (Dorsey et al., 2001: 100) and deposited in a high-energy marine-shelf setting. At Isla Montserrat (Text-fig. 4), the Carmen Formation is a unit ca. 12-34 m thick of basal conglomerate capped with light-gray fossiliferous limestone. *Pocillopora capitata* Verrill, 1864, *P. panamensis*, and *Favia maitreyiae* n. sp. collected at 200-220 m (Appendix 1) are abundant and loose, not bound together, and not attached to a firm substratum, but rather they are surrounded by Quaternary siliciclastics and Pliocene bioclastic sandstone.

The Marquer Formation consists of siliciclastic and bioclastic sediments, including calcareous conglomerates containing pebbles, calcareous sandstones, marls, coquina, algal limestone, and coral reef material (Anderson, 1950). Most of the sediments, however, represent carbonate bioclastic accumulations in shallow marine environments (Durham, 1950). Intermediate size heads (ca. 7-10 cm in height) of *Porites panamensis* were recovered from Bahía Marquer (Text-fig. 4; Appendix 1), formally designated as the type locality of the formation; here extensive reef (ca. 140 m in length with a maximum width of ca. 92 m and a maximum thickness of ca. 3 m) composed of the above species forms the upper part of the sequence. At Las Barracas (Text-fig. 3; Appendix 1), *Porites carrizensis* Vaughan, 1917, was collected from the limestone (1-2 m) that caps the northeastern corner of Mesa Las Barracas, whereas *Dichocoenia merriami* (Vaughan, 1900) was collected from the thick (ca. 36 m) unit of soft lime-rich siltstone underlying the limestone. Occurrence of the sand dollar *Encope shepherdi* Durham, 1950, at Bahía Marquer and Las Barracas suggests a late Pliocene age for the outcrops.

The age, lithology, and faunal relationships between the Carmen and Marquer formations are still not clear. The Carmen and Marquer formations were proposed by Anderson (1950) to represent middle and late Pliocene sequences, as suggested by the large-scale correlation of Durham (1950) based on mollusks; however, the beds show strong eithological similarities (Anderson, 1950: 19). Natland (1950) suggested a late Pliocene age for foraminiferal assemblages at Punta Perico, which is considered the type locality for the Carmen Formation. This interpretation was further supported by Dorsey et al. (2001) who suggested middle to late Pliocene ages (ca. 3.1-1.8 Ma) for the Carmen Formation based on planktonic foraminiferal biostratigraphy. In addition, molluscan paleogeographic studies conducted by Smith (1991a, b) indicate that mollusks do not differentiate among formations. Further data are needed to determine the relative or absolute age of the outcrops.
Text-fig. 3. Collecting localities at Punta Chivato (above) and Bahía San Nicolas area (below) in the Gulf of California, northwestern México. Detailed information about each locality is listed in Appendix 1. Adopted from Simian & Johnson (1997), and Ledesma-Vázquez (2002).
Text-fig. 4. Collecting localities at Coronados (above), Montserrat (below left), and Carmen (below right) islands in the Gulf of California, northwestern México. Detailed information about each locality is listed in Appendix 1.
Text-fig. 5. Collecting localities at Timbabichi (above), Las Animas (below left), and Isla San José (below right) in the Gulf of California, northwestern México. Detailed information about each locality is listed in Appendix 1. Adopted from DeDiego-Forbis et al. (2004).
**San Nicolas Formation**

San Nicolas Formation is a lithologic unit described from the Bahía Concepción area in Baja California Sur (Ledesma-Vázquez, 2002). It was deposited during the crustal extension of the Proto-Gulf in the basin of San Nicolas. The San Nicolas Formation overlies the tilted Oligocene-Miocene Comondú Group, and represents marine conditions represented by the lowermost Toba San Antonio Member, the Los Volcanes alluvial fan, the transitional Lodolita Arroyo Amarillo Member, and the marine La Ballena Member (Johnson & Ledesma-Vázquez, 2001; Ledesma-Vázquez, 2002). A relatively large number of overturned specimens of the coral *Placosmilia? alliciae* n. sp. were collected from a fine sediment (mudstone) matrix not far above the Miocene-Pliocene unconformity (Text-fig. 3; Appendix 1). The matrix is associated with abundant internal molds of a wide range of molluscan fossils belonging to the Arroyo Amarillo Member. According to Ledesma-Vázquez (2002), the age assigned to the lowermost Toba San Antonio unit is a maximum of 3.3 ± 0.5 Ma. The type of sediment, the fauna, and the completeness of the fossils suggest that the strata were deposited in a sandy tidal flat with important wave activity (Johnson & Ledesma-Vázquez, 2001).

**El Refugio Formation**

The El Refugio Formation represents the youngest marine unit in the San José del Cabo Basin (Fletcher et al., 2003). The El Refugio Formation conformably overlies the Trinidad Formation; it is composed of a ca. 380-m thickness of light-gray, medium to coarse arkosic sandstones as well as some fine-grained sandstone, shale, and limestone (Martínez-Gutiérrez & Sethi, 1997). The unit is considered to represent a regressive sequence based on its coarse grain size, ripple marks and fine cross laminations, abundant bioturbation, and coarse shell deposits. A large number of specimens of *Solenastrea fairbanksi* Vaughan, 1917, were collected from yellow medium-grained sandstone at Arroyo El Peyote near to Rancho Algodones (Text-fig. 6; Appendix 1) that is mixed with coquina along with complete and fragmented marine mollusks. The age of the formation is not well constrained (Fletcher et al., 2003). Based on molluscan affinities (Smith, 1991b) and its conformable contact with the Trinidad Formation (Martínez-Gutiérrez & Sethi, 1997; Pérez-López, 2002), the unit is considered as early Pliocene. A more detailed analysis regarding the stratigraphic setting of the collecting localities was provided by Martínez-Gutiérrez & Sethi (1997) and Pérez-López (2002).

Text-fig. 6 (*at right*). Collecting localities at La Ventana (*above*) and the San José del Cabo area (*below*) in the Gulf of California, northwestern México. Detailed information about each locality is listed in Appendix 1. Adopted from Martínez-Gutiérrez & Sethi (1997).
A large number of Pleistocene reefs and flat-lying marine terraces of variable extension from which coral taxa were collected are distributed from Punta Chivato to Cabo Pulmo (Text-figs. 1-6; Appendix 1). Most of the Pleistocene reefs and marine terraces have been, to some extent, carefully described in the literature (Durham, 1950; Squires, 1959; Ashby et al., 1987; Sirkin et al., 1990; Ortlieb, 1991; Muhs et al., 1994, 2002; Libbey & Johnson, 1997; Johnson & Ledesma-Vázquez, 1999, 2001; Ransom, 2000; Ledesma-Vázquez & Johnson, 2001; Mayer et al., 2002; DeDiego-Forbis et al., 2004) and no further detail in stratigraphy or age is added here, except the identity of some coral taxa (see Systematic Paleontology, below).

**TEXT-FIg. 7.** Two-dimensional Cartesian coordinates collected for 36 landmarks on transverse thin-sections of corallites of *Pavona*. Extremal landmarks; SUI 100860, *P. clavus*, Pleistocene, Punta Arenas, Baja California, México. Point numbers 1 and 18 were used to define the baseline; these landmarks were selected to characterize the development and structure of the corallite wall and septa.

**TEXT-FIg. 8.** Two-dimensional Cartesian coordinates collected for 27 landmarks on transverse thin-sections of corallites of *Solenastrea*. Extremal landmarks; SUI 45606c, *S. fairbanksi*, late Miocene, Imperial Valley, California. Point numbers 1 and 14 were used to define the baseline; these landmarks were selected to characterize the development and structure of the septa.

**Pleistocene units**

A large number of Pleistocene reefs and flat-lying marine terraces of variable extension from which coral taxa were collected are distributed from Punta Chivato to Cabo Pulmo (Text-figs. 1-6; Appendix 1). Most of the Pleistocene reefs and marine terraces have been, to some extent, carefully described in the literature (Durham, 1950; Squires, 1959; Ashby et al., 1987; Sirkin et al., 1990; Ortlieb, 1991; Muhs et al., 1994, 2002; Libbey & Johnson, 1997; Johnson & Ledesma-Vázquez, 1999, 2001; Ransom, 2000; Ledesma-Vázquez & Johnson, 2001; Mayer et al., 2002; DeDiego-Forbis et al., 2004) and

**TAXONOMIC METHODS**

Taxa were identified using a combination of qualitative and quantitative identification protocols. Gulf of California specimens were sorted into qualitative groups using a suite of morphologic criteria derived from Wells (1956), Budd (1991), Budd et al. (1992, 1994a), Budd & Johnson (1999), and a conventional set of diagnostic characters and illustra-
tions (Frost & Langenheim, 1974; Veron & Kelley, 1988; Veron, 2000; NMITA: http://nmita.iowa.uiowa.edu). To facilitate species recognition within each qualitative group, a suite of morphologic characters was selected that facilitated subdivision of the group into finer morphologic subgroups. Regarding landmark techniques (see Landmark Techniques, below), "characters" are considered as independent and discrete morphologic structures that can be identified using topographic criteria (after Budd & Klaus, 2001), whereas in traditional morphometrics (see Traditional Morphometrics, below), "characters" consist of linear distance measures of corallite architecture and counts.

Characters in each case were put into an agglomerative unweighted pair-group average cluster analysis (UPGMA). As suggested by Budd et al. (1994a) and Budd & Johnson (1996), Mahalanobis distances (instead of squared Euclidean distances) were used to maximize between-group variation relative to within-group variation. Differences among the clusters were examined by performing iterative canonical discriminant analysis until the highest percentages of the colonies were correctly classified. Differences among subgroups were analyzed using one-way analysis of variance and Duncan’s multiple comparison tests. The statistical methods were performed using SPSS (ver. 10.0.5).

Species names were assigned to morphologic subgroups by quantitative comparison with holotypes of all formally described species from the late Miocene to Recent Gulf of California and Caribbean region (Appendix 1). However, in cases where qualitative groups consist of fewer than 10 specimens, or when there is a lack of reliable calical structures and/or because structures were not available in large enough quantity to distinguish species using a statistical population approach, the subgroups were identified by qualitative comparison with previously described fossil and Recent species. Specifically, species identification in *Pocillopora* and *Psammocora* was attained following the latter approach.

**Landmark techniques**

When working with Recent material, species recognition is based on skeletal characters that are related to both skeletal growth and skeletal density structures (Budd & Klaus, 2001) (i.e., species can be distinguished using three-dimensional data on corallite structures). However, in fossil material, calical surfaces are absent, worn, or recrystallized (Budd & Klaus, 2001; Pandolfi et al., 2002) and, as a consequence, a two-dimensional morphometric approach is needed. Two-dimensional morphometric analysis is based on the analysis of landmark data identified on transverse thin-sections (Budd et al., 1994a). Cartesian coordinates (x-y) for landmarks of skeletal structures observed in transverse thin-sections of *Pavona* (Text-fig. 7) and *Solenastrea* (Text-fig. 8) groups were digitized using the Image Processing and Analysis in Java (ImageJ; written by Wayne Rasband, available at http://rsb.info.nih.gov/ij/download.html). Data were collected on six mature calices

Text-fig. 9. Scanning electron micrographs showing some of the characters measured in the morphologic groups. SUI 100844, *Pavona gigantea*, Recent, Panamá (above); USNM M547362, *Porites sverdrupi*, Recent, Isla Carmen, Gulf of California, México (below). CRL, greatest calical diameter; CDL, calical spacing; CR, distance across columellar ring; CW, columellar width; FSL, length of the first septum clockwise from the largest; LDS, length of dorsal septum; LLS, length of lateral septum; LSL, length of the largest septum; LVS, length of ventral septum; NB, bifurcate septum; SSL, length of the second septum clockwise from the largest; WT, wall thickness.
from each of the 47 colonies of *Pavona* and 50 colonies of *Solenastrea*. The landmarks consist of spatially homologous points designed to reflect skeletal structures, maxima of curvature, and extremal points (Bookstein, 1991), which mainly reflect the shape of the septal margin and corallite wall. Size and shape coordinates in the form of thin-plate spline coefficients, commonly known as partial warps, were determined using the Integrated Morphometrics Programs (IMP; written by Dennis E. Slice, available at http://www.canisius.edu/~sheets/morphosoft.html). Centroid size is the one measure of size that is mathematically independent of shape, and it represents the sum of the distances between the location of the centroid of the landmark configuration and each individual landmark. Partial warps are used for visualizing shape change as a deformation (Zelditch *et al*., 2004). Whereas centroid size has been widely used in coral taxonomy, partial warps have been preferred over commonly used Bookstein coordinates (Budd & Coates, 1992; Potts *et al*., 1993; Budd & Johnson, 1996; Budd & Klaus, 2001), because they provide a visually interpretable description of shape change as a deformation, they involve the same number of variables as there are statistical degrees of freedom, and they employ the Procrustes distance as a metric (Zeldich *et al*., 2004).

**Traditional morphometrics**

Two-dimensional landmark techniques are preferred over traditional morphometrics because they are based on biologically meaningful components of shape rather than size (Bookstein, 1991). However, when preservation or qualitative characteristics (*i.e.*, lack of reliability to identify landmarks) precluded the use of geometric morphometrics as subgroup recognition criteria, recognition was based on traditional morphometrics.
Although traditional morphometrics is influenced by components of size (Zelditch et al., 2004), it has been successful and widely used to recognize species in various fossil and living scleractinian groups in the Caribbean (Brakel, 1977; Foster, 1986, 1987; Budd, 1991; Budd & Johnson, 1999) and eastern Pacific (Budd, 1990; Weil, 1992; López-Pérez et al., 2003).

Although subgroup recognition protocols varied among qualitative groups, it is based on counts and linear measurements of characters made on calical surfaces or corallites cross sections. Counts and linear measures were determined such that they retrieve information regarding corallite characters, which are diagnostic in recognizing fossil and Recent species from the Indo-Pacific (Veron & Pichon, 1976, 1982; Veron & Kelley, 1988), eastern Pacific (Wells, 1983; Ketchum & Reyes-Bonilla, 2001; López-Pérez et al., 2003), and Caribbean (Foster, 1986; 1987; Budd, 1991; Budd & Johnson, 1999). Characters related to septum development, corallite diameter, wall thickness, number of pali, and degree of development of the columella for each qualitative group (Text-fig. 9; Tables 1-3) were collected on six mature calices from various places of each of the colonies.

**RESULTS**

*Pavona* group

Discriminant analysis of partial warp scores revealed three clusters identified as *Pavona clavus* (Dana, 1846), *P. duerdeni* Vaughan, 1907, and *P. gigantea* Verrill, 1869, the former and the latter occurring in Pleistocene strata of the Gulf of California. The results show that: (a) two canonical variables have significant values for Wilk’s Lambda, suggesting three significantly distinct groups, (b) 100% of the specimens are correctly classified, and (c) clusters do not overlap on plots of the first two canonical variables (Text-fig. 10A). As suggested by shape differentiation associated with CV1 depicted by the thin-plate spline, the most useful traits to discriminate among groups are related to: (a) localized differences in the orientation of tertiary septa (*i.e.*, tertiary septa bending towards secondary septa), (b) closeness between the bases of tertiary and secondary septa, and (c) the apparent contraction of the grid between the center of the corallite (landmark 1) and landmarks 15 and 29. Shape differentiation associated with CV2 is mainly related to the bending of the tertiary septa toward the secondary septa.

Similar to landmark techniques, discriminant analysis of traditional characters supports the presence of *Pavona clavus* and *P. gigantea* in Pleistocene sediments of the Gulf of California, and *P. duerdeni* as distinct from the rest of the species. The results show that: (a) only one canonical variable has significant values for Wilk’s Lambda, suggesting three significantly distinct groups, (b) 100% of the specimens are

**Table 2. Landmarks on transverse thin sections of corallites of Solenastrea.**

<table>
<thead>
<tr>
<th>Number</th>
<th>Type*</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>3</td>
<td>Center of corallite</td>
</tr>
<tr>
<td>2</td>
<td>3</td>
<td>Base of tertiary septum</td>
</tr>
<tr>
<td>3</td>
<td>3</td>
<td>Innermost point on tertiary septum</td>
</tr>
<tr>
<td>4</td>
<td>2</td>
<td>Point of maximum curvature at theca margin between tertiary and secondary septum</td>
</tr>
<tr>
<td>5</td>
<td>3</td>
<td>Base of secondary septum</td>
</tr>
<tr>
<td>6</td>
<td>3</td>
<td>Innermost point on secondary septum</td>
</tr>
<tr>
<td>7</td>
<td>2</td>
<td>Point of maximum curvature at theca margin between secondary and tertiary septum</td>
</tr>
<tr>
<td>8</td>
<td>3</td>
<td>Base of tertiary septum</td>
</tr>
<tr>
<td>9</td>
<td>3</td>
<td>Innermost point on tertiary septum</td>
</tr>
<tr>
<td>10</td>
<td>2</td>
<td>Point of maximum curvature at theca margin between tertiary and primary septum</td>
</tr>
<tr>
<td>11</td>
<td>3</td>
<td>Base of primary septum</td>
</tr>
<tr>
<td>12</td>
<td>3</td>
<td>Innermost point on primary septum</td>
</tr>
<tr>
<td>13</td>
<td>2</td>
<td>Point of maximum curvature at theca margin between primary and tertiary septum</td>
</tr>
<tr>
<td>14</td>
<td>3</td>
<td>Base of tertiary septum</td>
</tr>
<tr>
<td>15</td>
<td>3</td>
<td>Innermost point on tertiary septum</td>
</tr>
<tr>
<td>16</td>
<td>2</td>
<td>Point of maximum curvature at theca margin between secondary and tertiary septum</td>
</tr>
<tr>
<td>17</td>
<td>3</td>
<td>Base of secondary septum</td>
</tr>
<tr>
<td>18</td>
<td>3</td>
<td>Innermost point on secondary septum</td>
</tr>
<tr>
<td>19</td>
<td>2</td>
<td>Point of maximum curvature at theca margin between secondary and tertiary septum</td>
</tr>
<tr>
<td>20</td>
<td>3</td>
<td>Base of tertiary septum</td>
</tr>
<tr>
<td>21</td>
<td>3</td>
<td>Innermost point on tertiary septum</td>
</tr>
<tr>
<td>22</td>
<td>2</td>
<td>Point of maximum curvature at theca margin between tertiary and primary septum</td>
</tr>
<tr>
<td>23</td>
<td>3</td>
<td>Base of primary septum</td>
</tr>
<tr>
<td>24</td>
<td>3</td>
<td>Innermost point on primary septum</td>
</tr>
<tr>
<td>25</td>
<td>2</td>
<td>Point of maximum curvature at theca margin between primary and tertiary septum</td>
</tr>
<tr>
<td>26</td>
<td>3</td>
<td>Base of tertiary septum</td>
</tr>
<tr>
<td>27</td>
<td>3</td>
<td>Innermost point on tertiary septum</td>
</tr>
</tbody>
</table>

*Types: 1, juxtaposition of structures; 2, maxima of curvature; 3, extreme points.
Table 3. List and description of all morphologic characters measured on the surfaces of fossils and modern morphologic groups.

<table>
<thead>
<tr>
<th>Character</th>
<th>Code</th>
<th>Description</th>
<th>Applicable morphologic group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calical diameter</td>
<td>CRL &amp; CRS</td>
<td>Linear measure of the greatest and shortest calical diameter</td>
<td>Gardineroseris, Pavona, Siderastrea, Porites, *Favia, Solenastrea, Dichocoenia, Placosmilia, Diploria</td>
</tr>
<tr>
<td>Calical spacing</td>
<td>CDL &amp; CDS</td>
<td>Longest and shortest distance between centers of neighboring corallites</td>
<td>Gardineroseris, Pavona, Siderastrea, Porites, *Favia, Solenastrea, Dichocoenia</td>
</tr>
<tr>
<td>Number of septa</td>
<td>NS</td>
<td>Count of the number of septa projecting into the calyx</td>
<td>Gardineroseris, Pavona, Siderastrea, Porites, Favia, Solenastrea, Dichocoenia, Placosmilia, Diploria</td>
</tr>
<tr>
<td>Number of major septa</td>
<td>NMS</td>
<td>Count of the number of septa that reach the columella</td>
<td>Gardineroseris</td>
</tr>
<tr>
<td>Length and width of largest septum</td>
<td>LSL &amp; LW</td>
<td>Linear measure of the distance from the calical wall to the end of largest septum; width measured at midpoint</td>
<td>Gardineroseris, Pavona, Siderastrea, Favia, Solenastrea, Dichocoenia, Placosmilia, Diploria</td>
</tr>
<tr>
<td>Length and width of first septum to the right of largest</td>
<td>FSL &amp; FW</td>
<td>Length and width measured as noted above on first septum in the clockwise direction from largest</td>
<td>Gardineroseris, Pavona, Favia, Solenastrea, Dichocoenia, Placosmilia, Diploria</td>
</tr>
<tr>
<td>Length and width of second septum to the right of largest</td>
<td>SSL &amp; SW</td>
<td>Length and width measured as noted above</td>
<td>Gardineroseris, Pavona, Placosmilia, Diploria</td>
</tr>
<tr>
<td>Columella length and width</td>
<td>CL &amp; CW</td>
<td>Linear measure of the greatest diameter of the columella and the diameter normal to this axis at the midpoint</td>
<td>Gardineroseris, Pavona, Siderastrea, Porites, Favia, Solenastrea, Dichocoenia, Placosmilia, Diploria</td>
</tr>
<tr>
<td>Number of neighboring corallites</td>
<td>NC</td>
<td>Count of the number of adjacent corallites</td>
<td>Gardineroseris, Pavona, Porites, Favia, Solenastrea</td>
</tr>
<tr>
<td>Wall thickness</td>
<td>WT</td>
<td>Linear measure between thecal margins of nearest neighboring corallites</td>
<td>Gardineroseris, Pavona, Siderastrea, Porites, Favia, Solenastrea, Dichocoenia, Placosmilia, Diploria</td>
</tr>
<tr>
<td>Length and width of dorsal septum</td>
<td>LDS &amp; WDS</td>
<td>Linear measure of the distance from the calical wall to the end of dorsal septum; width measured at midpoint</td>
<td>Porites</td>
</tr>
<tr>
<td>Length and width of ventral septum</td>
<td>LVS &amp; WVS</td>
<td>Length and width measured as noted above on ventral septum</td>
<td>Porites</td>
</tr>
<tr>
<td>Length and width of lateral septum</td>
<td>LLS &amp; WLS</td>
<td>Length and width measured as noted above on lateral septum</td>
<td>Porites</td>
</tr>
<tr>
<td>Number of bifurcate septa</td>
<td>NB</td>
<td>Count</td>
<td>Porites</td>
</tr>
<tr>
<td>Number of pali</td>
<td>PL</td>
<td>Count</td>
<td>Porites</td>
</tr>
<tr>
<td>Distance across columnellar synap- ticular ring</td>
<td>CR1 &amp; CR2</td>
<td>Linear measure of longest and shortest distance across ring</td>
<td>Porites*, Solenastrea</td>
</tr>
<tr>
<td>Number of centers</td>
<td>C</td>
<td>Number of centers per corallite</td>
<td>Dichocoenia</td>
</tr>
<tr>
<td>Corallite elevation</td>
<td>CE</td>
<td>Linear measure from the surface of the calice to the base of the corallite</td>
<td>Dichocoenia</td>
</tr>
</tbody>
</table>

*Average of longest and shortest distance: a, CRL/C; b, number of septa per 5 mm.
correctly classified, and (c) the clusters do not overlap on plots of the first two canonical variables (Text-fig. 10B). A combination of variables related to the inverse of calical diameter (-CRS, -CRL), the width of largest septum (-LW), and calical spacing (-CDL, -CDS) is most strongly correlated with first canonical variable that distinguished between the clusters for *P. clavus*, *P. duerdeni*, and *P. gigantea* (Table 4).

Univariate comparisons among the three species (Text-fig. 11) show that there is a clear size trend in calical characters. *Pavona gigantea* is distinguished by large corallite diameter, calical spacing, and septal development, followed by *P. clavus* and *P. duerdeni*, whereas *P. clavus* is distinguished by a relatively large number of septa.

**Siderastrea group**

Preliminary average linkage cluster analysis revealed four clusters identified as *Siderastrea mendenhalli* Vaughan, 1917, *S. californica* Vaughan, 1917, *S. siderea* (Ellis & Solander, 1786), and *S. annae* n. sp. An initial discriminant analysis revealed that the morphologic distance between the clusters identified as *S. mendenhalli* and *S. californica* is not meaningful (F = 1.68; p = 0.15). Therefore, they are not sufficiently distinct to be considered as two species, so these specimens were reassigned and the analysis rerun. The results showed that: (a) two canonical variables have significant values for Wilk’s Lambda, suggesting three significantly distinct groups, (b) 93.9% of the specimens are correctly classified, and (c) clusters overlap on plots of the first two canonical variables (Text-fig. 12). A combination of variables related to columella development (CL) and the inverse of the number of synapticular rings (-NSY) was most strongly correlated with the first canonical variable, which distinguished between the clusters for *S. siderea*, and the *S. mendenhalli* and *S. annae* group; a combination of variables related to calical diameter (CRL) and the number of septa (NS) was most strongly correlated with the second canonical variable, which distinguished between the clusters for *S. mendenhalli* and *S. annae* (Table 5).

Univariate comparison among the three species (Text-fig. 13) showed that *Siderastrea siderea* is distinguished by its small columella and large number of synapticular rings. *Siderastrea*

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Table 4. Pearson’s correlations among the original variables and the canonical variables (CV) in the final canonical discriminant analysis distinguishing species of *Pavona*.

<table>
<thead>
<tr>
<th>Original variable</th>
<th>CV1</th>
<th>CV2</th>
</tr>
</thead>
<tbody>
<tr>
<td>CRS</td>
<td>-0.217*</td>
<td>0.119</td>
</tr>
<tr>
<td>CRL</td>
<td>-0.184*</td>
<td>0.099</td>
</tr>
<tr>
<td>LW</td>
<td>-0.177*</td>
<td>0.008</td>
</tr>
<tr>
<td>CDL</td>
<td>-0.163*</td>
<td>0.070</td>
</tr>
<tr>
<td>CDS</td>
<td>-0.153*</td>
<td>0.062</td>
</tr>
<tr>
<td>SW</td>
<td>-0.141*</td>
<td>-0.063</td>
</tr>
<tr>
<td>LSL</td>
<td>-0.133*</td>
<td>0.115</td>
</tr>
<tr>
<td>SSL</td>
<td>-0.107</td>
<td>0.083</td>
</tr>
<tr>
<td>WT</td>
<td>-0.047</td>
<td>0.010</td>
</tr>
<tr>
<td>NS</td>
<td>0.118</td>
<td>-0.279*</td>
</tr>
<tr>
<td>FSL</td>
<td>-0.041</td>
<td>0.234*</td>
</tr>
<tr>
<td>CW</td>
<td>-0.035</td>
<td>-0.134*</td>
</tr>
<tr>
<td>FW</td>
<td>0.056</td>
<td>0.103</td>
</tr>
<tr>
<td>NC</td>
<td>-0.005</td>
<td>0.087</td>
</tr>
<tr>
<td>CL</td>
<td>0.020</td>
<td>-0.056</td>
</tr>
<tr>
<td>% variance explained</td>
<td>92.8</td>
<td>7.2</td>
</tr>
</tbody>
</table>

*Heavily weighted characters.

Text-fig. 10. Plots of scores on the first two canonical variables in the final canonical discriminant analysis distinguishing species of *Pavona*. (A) Partial warp scores. Thin-plate spline representing shape differentiation associated with CV1 and CV2. (B) Traditional morphometrics. Each point represents one colony. The polygons enclose clusters of colonies belonging to the following species: cross, *P. clavus*; circle, *P. duerdeni*; square, *P. gigantea*.
Text-fig. 11. Plots showing means and 1 standard error intervals for measurements of species of *Pavona*. Characters with meaningful differences are plotted. Character descriptions and codes are indicated in Table 3. 1, *P. clavus*, n = 19; 2, *P. duerdeni*, n = 3; 3, *P. gigantea*, n = 5.
mendenhalli is distinguished by its large columella thickness, whereas S. annae is distinguished by its small corallite and fewer septa.

**Porites group**

Discriminant analysis of the measured characters revealed four clusters identified as *Porites panamensis*, *P. lobata* Dana, 1848, *P. carrizensis*, and *P. sverdrupi* Durham, 1947. The results showed that: (a) three canonical variables have significant values for Wilk's Lambda, suggesting four significantly distinct groups, (b) 91.9% of the specimens are correctly classified, and (c) the clusters slightly overlap on plots of the first two canonical variables (Text-fig. 14). A combination of variables related to the number of pali (PL) and columella length (CL) is most strongly correlated with the first canonical variable, which distinguished between the clusters for *P. lobata*, and the *P. sverdrupi*, *P. panamensis* and *P. carrizensis* groups; a combination of variables related to calical spacing (CS) and the length of lateral septa (LLS) is most strongly correlated with the second canonical variable which distinguished between the clusters for *P. sverdrupi*, *P. panamensis*, and *P. carrizensis* (Table 6).

Univariate comparisons among the three species (Text-fig. 15) show that *Porites carrizensis* is distinguished by a large calical diameter and spacing, and better developed septa. *Porites lobata* is distinguished by the presence of the columella and a high number of pali. *Porites panamensis* is morphologically similar to *P. sverdrupi* at the corallite level; however, the former is distinguished by its small calical diameter, its relatively better developed columella, and its shorter ventral septa.

**Favia group**

Discriminant analysis of measured characters revealed three clusters identified as *Favia fragum* (Esper, 1795), *F. maitreyiae* n. sp., and *F. tulsidasi* n. sp. The results showed that: (a) two canonical variables have significant values for Wilk's Lambda, suggesting three significantly distinct groups, (b) 100% of the specimens are correctly classified, and (c) the clusters do not overlap on plots of the first two canonical variables (Text-fig. 16). A combination of variables related to the columella length (CL) and the number of septa (NS) is most strongly correlated with the first canonical variable, which distinguished between the clusters for *F. fragum*, *F. maitreyiae*, and *F. tulsidasi* (Table 7).

Univariate comparisons among the three groups (Text-fig. 17) show that *Favia fragum* is distinguished by its large caliella and more numerous shorter septa. *Favia maitreyiae* n. sp. is distinguished by its large widely spaced corallites and its larger septa, whereas *F. tulsidasi* n. sp. is distinguished by its small, shortly spaced corallites and its less numerous short septa.

**Solenastrea group**

Discriminant analysis of partial warp scores revealed three clusters identified as *Solenastrea bournoni* Milne Edwards & Haime, 1849, *S. hyades* (Dana, 1846), and *S. fairbanksi*; the former two are restricted to the Caribbean, and the latter occurs in late Miocene to Pliocene strata of the Gulf of California. The results showed that: (a) two canonical variables have significant values for Wilk’s Lambda, suggesting three significantly distinct groups, (b) 100% of the specimens are correctly classified, and (c) the clusters slightly overlap on plots of the first two canonical variables (Text-fig. 18). A combination of variables related to the calical diameter (CD) and the length of lateral septa (LLS) is most strongly correlated with the first canonical variable, which distinguished between the clusters for *S. bournoni*, *S. hyades*, and *S. fairbanksi* (Table 8).

Univariate comparisons among the three species (Text-fig. 19) show that *Solenastrea bournoni* is distinguished by its small calical diameter, its relatively better developed caliella, and its shorter ventral septa.

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**Table 5. Pearson’s correlations among the original variables and the canonical variables (CV) in the final canonical discriminant analysis distinguishing species of *Siderastrea*.**

<table>
<thead>
<tr>
<th>Original variable</th>
<th>CV1</th>
<th>CV2</th>
</tr>
</thead>
<tbody>
<tr>
<td>CL</td>
<td>0.820*</td>
<td>0.259</td>
</tr>
<tr>
<td>NSY</td>
<td>-0.297*</td>
<td>-0.020</td>
</tr>
<tr>
<td>CRL</td>
<td>-0.266</td>
<td>0.731*</td>
</tr>
<tr>
<td>NS</td>
<td>-0.273</td>
<td>0.615*</td>
</tr>
<tr>
<td>WT</td>
<td>0.117</td>
<td>0.562*</td>
</tr>
<tr>
<td>CRS</td>
<td>-0.299</td>
<td>0.518*</td>
</tr>
<tr>
<td>LW</td>
<td>-0.070</td>
<td>0.095</td>
</tr>
<tr>
<td>% variance explained</td>
<td>90.5</td>
<td>9.5</td>
</tr>
</tbody>
</table>

*Heavily weighted characters.
Text-fig. 13. Plots showing means and 1 standard error intervals for measurements made of species of *Siderastrea*. Characters with meaningful differences are plotted. Character descriptions and codes are indicated in Table 3. 1, *S. mendenhalli*, n = 7; 2, *S. siderea*, n = 5; 3, *S. annae*, n = 6.
are correctly classified, and (c) the clusters do not overlap on plots of the first two canonical variables (Text-fig. 18A). As suggested by shape differentiation associated with CV1 depicted by the thin-plate spline, the most useful traits to discriminate among groups are related to the strong bending of the tertiary septa toward the secondary septa.

Discriminant analysis of measured characters supports the presence of *Solenastrea fairbanksi* in late Miocene to Pliocene sediments of the Gulf of California, and *S. bournoni* and *S. hyades* as distinct from the former. The results show that: (a) two canonical variables have significant values for Wilk’s Lambda, suggesting three significantly distinct groups, (b) 97.6% of the specimens are correctly classified, and (c) the clusters do not overlap on plots of the first two canonical variables, although they are morphologically closer than expected from partial warp scores analysis (Text-fig. 18B). A combination of variables related to the wall thickness (WT), the inverse of the shortest distance across the columellar synapticular ring (-CR2), and the inverse of the width of the first septum to the right of the largest (-FW) is most strongly correlated with the first canonical variable, which distinguished between the clusters for *S. fairbanksi*, *S. bournoni*, and *S. hyades* (Table 8).

Univariate comparisons among the three species (Text-fig. 19) show that *Solenastrea hyades* is distinguished by a large calical spacing and wall thickness, whereas *S. bournoni* is distinguished by its small calical diameter. *Solenastrea fairbanksi* has better developed septa, a large columellar synapticular ring, and a small corallite wall.

### Dichocoenia group

Discriminant analysis of the measured characters revealed four clusters identified as *Dichocoenia eminens* Weisbord, 1974, *D. merriami*, *D. caloosahatcheensis* Weisbord, 1974, and *D. stokesi* Milne Edwards & Haime, 1848; the latter two are restricted to the Caribbean. The results show that: (a) only one canonical variable has significant values for Wilk’s Lambda, suggesting four significantly distinct groups, (b) 96.9% of the specimens are correctly classified, and (c) except for the *D. caloosahatcheensis* and *D. merriami* clusters, the groups do not overlap on plots of the first two canonical variables (Text-fig. 20). Although pairwise comparisons between morphologic groups show that the distances between *D. merriami*, *D. caloosahatcheensis*, and *D. stokesi* are statistically meaningful, they are smaller than those obtained for among “morphs” of *Porites panamensis*. However, these results, along with colony shape and morphologic attributes other than corallite characters, support the validity of the species (see Discussion sections under *Dichocoenia* in Systematic Paleontology, below).

A combination of variables related to the corallite elevation (CE), wall thickness (WT), and the development of the first septum right of the largest (FSL, FW) is most strongly cor-

### Table 6. Pearson’s correlations among the original variables and the canonical variables (CV) in the final canonical discriminant analysis distinguishing species of *Porites*

<table>
<thead>
<tr>
<th>Original variable</th>
<th>CV1</th>
<th>CV2</th>
<th>CV3</th>
</tr>
</thead>
<tbody>
<tr>
<td>PL</td>
<td>0.643*</td>
<td>-0.055</td>
<td>0.085</td>
</tr>
<tr>
<td>CL</td>
<td>0.336*</td>
<td>0.008</td>
<td>0.160</td>
</tr>
<tr>
<td>CS</td>
<td>0.015</td>
<td>0.459*</td>
<td>-0.392</td>
</tr>
<tr>
<td>LLS</td>
<td>0.101</td>
<td>0.430*</td>
<td>-0.318</td>
</tr>
<tr>
<td>LVS</td>
<td>0.062</td>
<td>0.398*</td>
<td>-0.352</td>
</tr>
<tr>
<td>WVS</td>
<td>-0.142</td>
<td>0.380*</td>
<td>-0.353</td>
</tr>
<tr>
<td>CD</td>
<td>0.042</td>
<td>0.378*</td>
<td>-0.331</td>
</tr>
<tr>
<td>WT</td>
<td>-0.107</td>
<td>0.350*</td>
<td>0.194</td>
</tr>
<tr>
<td>NC</td>
<td>-0.016</td>
<td>-0.178*</td>
<td>0.122</td>
</tr>
<tr>
<td>NB</td>
<td>0.083</td>
<td>-0.360</td>
<td>-0.441*</td>
</tr>
<tr>
<td>WDS</td>
<td>-0.169</td>
<td>0.413</td>
<td>-0.415*</td>
</tr>
<tr>
<td>WLS</td>
<td>-0.136</td>
<td>0.330</td>
<td>-0.388*</td>
</tr>
<tr>
<td>CW</td>
<td>0.239</td>
<td>0.002</td>
<td>0.281*</td>
</tr>
<tr>
<td>LDS</td>
<td>0.183</td>
<td>0.104</td>
<td>-0.259*</td>
</tr>
<tr>
<td>CR</td>
<td>0.101</td>
<td>0.126</td>
<td>-0.236*</td>
</tr>
<tr>
<td>NS</td>
<td>0.006</td>
<td>-0.025</td>
<td>0.046</td>
</tr>
<tr>
<td>% variance explained</td>
<td>90.3</td>
<td>7.7</td>
<td>2</td>
</tr>
</tbody>
</table>

*Heavily weighted characters.
Text-fig. 15. Plots showing means and 1 standard error intervals for measurements of species of *Porites*. Characters with meaningful differences are plotted. Character descriptions and codes are indicated in Table 3. 1, *P. panamensis*, n = 73; 2, *P. lobata*, n = 22; 3, *P. carrizensis*, n = 10; 4, *P. sverdruyi*, n = 19.
related with the first canonical variable, which distinguished between *D. merriami*, *D. caloosahatcheensis* and *D. stokesi*, and *D. eminens*; a combination of variables related to columella thickness (CW) and shortest calical diameter (CRS) is most strongly correlated with the second canonical variable, which distinguished between the clusters for *D. caloosahatcheensis* and *D. stokesi* (Table 9).

Univariate comparisons among the four species (Text-fig. 21) show that *Dichocoenia eminens* is distinguished by a large calical diameter, wide spacing, and corallite elevation. *Dichocoenia caloosahatcheensis* has a small number of septa, whereas *D. merriami* is distinguished by low corallite elevation and large wall thickness. *Dichocoenia stokesi* is distinguished by having a small columella, and a proportionally large corallite length relative to corallite width.

**SYSTEMATIC PALEONTOLOGY**

Comments upon previously described taxa are kept to a minimum, and no attempt is made to revise generic concepts.

**Repositories**

Specimens studied are deposited in the Santa Barbara Museum of Natural History, Santa Barbara, California (AHF), the Museo de Historia Natural de la Universidad Autónoma de Baja California Sur, La Paz, Baja California Sur, México (MHNUABCS), the Natural History Museum of Los Angeles County, Los Angeles, California (NHMLAC), the Smithsonian Tropical Research Institute, Panama (STRI), the Paleontology Repository, Department of Geoscience, University of Iowa, Iowa City (SUI), the University of California Museum of Paleontology, University of California, Berkeley (UCMP), the United States Geological Survey (USGS), the National Museum of Natural History, Washington, DC (USNM), and the Yale Peabody Museum, New Haven, Connecticut (YPM).

Order **SCLERACTINIA** Bourne, 1900

Family **POCILLOPORIDAE** Gray, 1842

Genus **POCILLOPORA** Lamarck, 1816

Type Species.—*Pocillopora acuta* Lamarck, 1816, by subsequent designation (Wells, 1956).

Diagnosis.—Colonies submassive to branching, rarely encrusting, plocoid, usually covered with verrucae. Septa and columella often poorly developed. Coenosteum covered by granules.

Discussion.—The genus is represented by 17 common, widely distributed species in the Indo-Pacific, yet also has what appears to be many regional endemics in the central and eastern Pacific (Veron, 2000).

The first record of *Pocillopora* was in the Eocene of the Caribbean (Vaughan & Wells, 1943). During the Oligocene,
Text-fig. 17. Plots showing means and 1 standard error intervals for measurements of species of *Favia*. Characters with meaningful differences are plotted. Character descriptions and codes are indicated in Table 3. 1, *F. maitreyiae* n. sp., n = 10; 2, *F. tulidasi* n. sp., n = 5; 3, *F. fragum*, n = 3.
it ranged from the Mediterranean to the Caribbean, but the genus disappeared from the Caribbean by the end of the Pleistocene (Geister, 1977). Indo-Pacific and eastern Pacific species, in which septa and columella are inconspicuous and highly variable, are greatly in need of revision. All of the species forming the continuum \([\textit{Pocillopora damicornis} \text{ (Linnaeus, 1758)}, \textit{P. danae} \text{ Verrill, 1864}, \textit{P. verrucosa} \text{ (Ellis & Solander, 1786)}, \textit{P. meandrina} \text{ Dana, 1846}, \textit{P. elegans} \text{ Dana, 1846}, \text{and} \textit{P. capitata}; \text{Vaughan, 1907; Squires, 1959}]\) occur in the Recent of the eastern Pacific and have been synonymized either in the Indo- or eastern Pacific by one author or another (Squires, 1959; Veron & Pichon, 1976; Glynn & Leyte-Morales, 1997; Reyes-Bonilla & López-Pérez, 1998; Reyes-Bonilla, 2002). More detailed molecular and morphometric studies are needed to determine whether these represent distinct valid species.

The first record of \textit{Pocillopora} in the eastern Pacific corresponds to an unidentified specimen found at the Astoria group in the Oligocene of Washington (Nomland, 1917). Up to seven records have been mentioned for eastern Pacific representatives between the Pliocene and Pleistocene (López-Pérez, 2005), however, based in the analysis of a large collection of specimens, \textit{P. damicornis}, \textit{P. verrucosa}, and \textit{P. meandrina} are added to the Gulf of California fossil record.

<table>
<thead>
<tr>
<th>Original variable</th>
<th>CV1</th>
<th>CV2</th>
</tr>
</thead>
<tbody>
<tr>
<td>WT</td>
<td>0.773*</td>
<td>0.082</td>
</tr>
<tr>
<td>CR2</td>
<td>-0.508*</td>
<td>0.504</td>
</tr>
<tr>
<td>FW</td>
<td>-0.413*</td>
<td>0.280</td>
</tr>
<tr>
<td>LW</td>
<td>-0.268*</td>
<td>0.209</td>
</tr>
<tr>
<td>NS</td>
<td>0.128</td>
<td>-0.074</td>
</tr>
<tr>
<td>NC</td>
<td>0.051</td>
<td>0.008</td>
</tr>
<tr>
<td>CDS</td>
<td>0.257</td>
<td>0.635*</td>
</tr>
<tr>
<td>CRS</td>
<td>-0.238</td>
<td>0.605*</td>
</tr>
<tr>
<td>CRL</td>
<td>-0.288</td>
<td>0.559*</td>
</tr>
<tr>
<td>FSL</td>
<td>0.010</td>
<td>0.535*</td>
</tr>
<tr>
<td>CDL</td>
<td>0.370</td>
<td>0.534*</td>
</tr>
<tr>
<td>LSL</td>
<td>-0.303</td>
<td>0.530*</td>
</tr>
<tr>
<td>CR1</td>
<td>-0.441</td>
<td>0.523*</td>
</tr>
<tr>
<td>% variance explained</td>
<td>72.5</td>
<td>27.5</td>
</tr>
</tbody>
</table>

*Heavily weighted characters.

Text-fig. 18. Plots of scores on the first two canonical variables in the final canonical discriminant analysis distinguishing species of \textit{Solenastrea}. (A) Partial warp scores. Thin-plate spline representing shape differentiation associated with CV1 and CV2. (B) Traditional morphometrics. Each point represents one colony. The polygons enclose clusters of colonies belonging to the following species: cross, \textit{S. fairbanksi}; circle, \textit{S. bournoni}; square, \textit{S. hyades}.

\textit{Pocillopora capitata} Verrill, 1864

Pl. 1, Fig. 3

\textit{Pocillopora capitata} Verrill, 1864: 60.
\textit{Pocillopora capitata} var. \textit{porosa} Verrill, 1869: 99.
\textit{Pocillopora porosa} Verrill, Durham, 1947: 16-17, pl. 8, fig. 5.
\textit{Pocillopora robusta} Verrill. Durham, 1947: 17-18, pl. 7, figs 1-2, pl. 8, fig. 6.
Text-fig. 19. Plots showing means and 1 standard error intervals for measurements made on species of *Solenastrea*. Characters with meaningful differences are plotted. Character descriptions and codes are indicated in Table 3. 1, *S. fairbanksi*, n = 28; 2, *S. hyades*, n = 6; 3, *S. bournoni*, n = 7.
Description.—Colonies ramose, branching. Corallum openly branched or forming variably sized rounded mounds. Branches large, usually cylindrical to elliptical (0.63-3.8 cm in diameter), occasionally slightly subflabellate, rounded or flattened on top. Verrucae subacute, rarely rounded, generally elongate but variable in size, irregularly distributed, wanted or obsolete on top.

Calices circular to elliptical; those on end of branches or verrucae generally polygonal. Calices small (0.5-1.1 mm), of moderate depth. Distance between neighboring corallites moderate (0.6-1 mm), highly variable at colony level. Coenosteum solid and minutely granulated. Septa 12, in two cycles; presence and degree of development highly variable at intra- and intercolony levels; in some cases opposite septa well developed and connecting at bottom with columella. Columella small, styliform, often wanting.


Material Examined.—115 SUI specimens (100627, 100693, 100695, 100838-100840, 100890, 100920, 100935-100958, 100962-100966, 100974, 100986-100990, 100992, 100994, 100996, 102051, 102063-102065, 102073-102123, 102328-102336, 102352-102377, 102384-102387, 102390-102391); 4 YPM specimens (4033, 3872, 3889, 3898); 1 UCMP specimen (15491).

Occurrence.—Isla Coronados (locs. BC 36, 39-42), Isla Carmen (locs. BC 12, A 3508), Isla Montserrat (locs. BC 25, 27; A 3567, 3569), Timbabichi (locs. BC 20; A 3596), Las Animas (BC 6, 7), La Ventana (Locs. BC 10-11), Cabo Pulmo (loc. BC 8).

*Pocillopora capitata* ranges in age from middle Pliocene to Recent. Outside of the Gulf of California, it occurs in the Mexican Pacific (Reyes-Bonilla & López-Pérez, 1998), and in Costa Rica, Panamá, Colombia, and Ecuador (Reyes-Bonilla, 2002). Outside of the eastern Pacific, its presence is still unclear (Veron, 2000).

Discussion.—Durham (1947) synonymized *Pocillopora pumila* and *P. palmata* Palmer, 1928, with *P. robusta*, and retained *P. capitata*, *P. porosa*, and *P. robusta* as valid species. In contrast, Squires (1959) considered *P. capitata*, *P. capitata var. robusta*, *P. robusta*, and *P. capitata var. pumila* as synonyms of *P. elegans*. Due to their flabellate branch shape and well-developed septa and columella, this species clearly belongs to *Pocillopora eydouxi* Milne Edwards & Haime, 1860 (Reyes-Bonilla, 2002), whereas branches of *P. elegans* are flabellate to subflabellate with less developed, more numerous verrucae.

Colony shape and septal and columellar development of *Pocillopora capitata* from the Gulf of California are highly plastic. Septal and columellar development, along with the presence of verrucae and shape of the branch tips, were highly important in establishing species, varieties, and synonyms.

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Table 9. Pearson’s correlations among the original variables and the canonical variables (CV) in the final canonical discriminant analysis distinguishing species of *Dichocoenia*.

<table>
<thead>
<tr>
<th>Original variable</th>
<th>CV1</th>
<th>CV2</th>
<th>CV3</th>
</tr>
</thead>
<tbody>
<tr>
<td>CE</td>
<td>0.881*</td>
<td>0.197</td>
<td>0.224</td>
</tr>
<tr>
<td>WT</td>
<td>0.474*</td>
<td>0.326</td>
<td>0.327</td>
</tr>
<tr>
<td>FSL</td>
<td>0.307*</td>
<td>0.189</td>
<td>0.220</td>
</tr>
<tr>
<td>FW</td>
<td>0.202*</td>
<td>-0.155</td>
<td>-0.100</td>
</tr>
<tr>
<td>CW</td>
<td>0.207</td>
<td>0.810*</td>
<td>0.250</td>
</tr>
<tr>
<td>CRS</td>
<td>0.326</td>
<td>0.432*</td>
<td>0.185</td>
</tr>
<tr>
<td>LSL</td>
<td>0.270</td>
<td>0.313*</td>
<td>0.031</td>
</tr>
<tr>
<td>NS</td>
<td>0.129</td>
<td>-0.173</td>
<td>0.731*</td>
</tr>
<tr>
<td>CRL/C</td>
<td>0.283</td>
<td>0.050</td>
<td>0.318*</td>
</tr>
<tr>
<td>LW</td>
<td>0.132</td>
<td>0.209</td>
<td>0.264*</td>
</tr>
<tr>
<td>% variance explained</td>
<td>84.7</td>
<td>10.1</td>
<td>5.2</td>
</tr>
</tbody>
</table>

*Heavily weighted characters.

Text-fig. 20. Plots of scores on the first two canonical variables in the final canonical discriminant analysis distinguishing species of *Dichocoenia*. Each point represents one colony. The polygons enclose clusters of colonies belonging to the following species: cross, *D. merriami*; circle, *D. stokesi*; square, *D. calosabatchensis*; triangle, *D. eminens*.
in the species (Verrill, 1868-1870, 1869; Durham, 1947; Squires, 1959; Wells, 1983). The first characters are highly variable, either combining strong septal development with a weak columella or vice-versa without any consistent pattern. Similarly, branch morphology apparently represents a continuum from lacerate to flattened ends, largely influenced by environmental conditions or attacks by corallivores (Wells, 1983). Because of this, no successful separation based on corallite morphology or colony shape is consistent with the species proposed by Verrill (1868-1870, 1869) and retained by Durham (1947).

*Pocillopora capitata* is morphologically similar to *P. ligulata* Dana, 1846, and *P. elegans*. Unlike *P. capitata*, however, *P. ligulata* has widely spaced and irregularly distributed verrucae, whereas *P. elegans* has flabellate to subflabellate branches with smaller, rounded, numerous verrucae (Table 10).

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**Pocillopora damicornis** (Linnaeus, 1758)

*Pl. 1, Figs 1-2*


*Pocillopora lacera* Verrill, 1869: 100.

*Pocillopora caespitosa* Dana. Vaughan, 1907: 86-87, pl. 10, figs 1-2, pl. 11, figs 1-2.

*Pocillopora porosa* Verrill. Durham, 1947: 16-17, pl. 8, fig. 5, pl. 10, fig. 8.

*Pocillopora damicornis* var. caespitosa Dana. Durham & Barnard, 1952: 20, pl. 1, figs 3a-c.

**Description.**—Colonies ramose, branching. Corallum strongly lacerate or forming variably sized, more or less irregular colonies or rounded mounds. Branch size and shape variable. Branches covered with irregularly distributed subdeveloped...
branches that resemble verrucae. Verrucae and branches intergrading into each other. True verrucae lacking.

Calices circular to elliptical but those on ends of branches generally polygonal. Calices small to intermediate in size (0.4-1.5 mm) and of moderate depth. Distance between neighboring corallites moderate (0.5-1.5 mm), highly variable at colony level. Coenosteum solid and minutely granulated. Septa in two cycles, 12 in number; presence and development highly variable at intra- and intercolony levels; in some cases opposite septa developed and connected at bottom with columella. Columella small, styliform, often wanting.

Type.—Syntype, USNM 681, *Pocillopora cespitosa*.

Material Examined.—6 SUI specimens (100625-100626, 100925, 100927, 102389); 1 USNM specimen (681).

Occurrence.—Isla Montserrat (loc. A 3596), Timbabichi (loc. BC 20), Las Animas (loc. BC 6), La Ventana (loc. BC 10), Cabo Pulmo (loc. BC 8).

*Pocillopora damicornis* ranges in age from Miocene to Recent. It occurs in the Miocene of Butung Island, in the Pliocene of Java and New Guinea, in the Plio-Pleistocene of Ceram and Christmas Island, and in the Pleistocene of Japan (Veron & Kelley, 1988). It also occurs in the Recent of the Mexican Pacific (Reyes-Bonilla & López-Pérez, 1998), and in Costa Rica, Panamá, Colombia, Ecuador, and Chile (Reyes-Bonilla, 2002). Outside of the eastern Pacific, it ranges from the western Indian Ocean and Red Sea to the central Pacific (Veron, 2000).

Discussion.—A specimen from Las Animas (Pl. 1, Fig. 1) strongly resembles lacerate forms from semiprotected environments, whereas Timbabichi, Las Animas, La Ventana and Cabo Pulmo specimens (*e.g.*, Pl. 1, Fig. 2) have branches a few millimeters high like those found in areas of moderate to extreme wave action (Pl. 1, Fig. 2).

Unlike species in which the septa and columella are inconspicuous (see *Pocillopora* Discussion, above), *P. damicornis* is distinguished by having branches that are devoid of true verrucae or have intergrading branches and verrucae (Table 10).

**Table 10. Morphologic characters distinguishing species of *Pocillopora.***

<table>
<thead>
<tr>
<th>Species</th>
<th>Distribution</th>
<th>Colony shape</th>
<th>Branches</th>
<th>Verrucae</th>
<th>Additional references*</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. capitata</em> Verrill, 1864</td>
<td>middle Pliocene to Recent; eastern Pacific</td>
<td>openly branched to rounded mounds, variable size</td>
<td>large, cylindrical to elliptical, round or flattened on top</td>
<td>subacute, elongated, irregularly distributed, rare on top</td>
<td>2, 4, 5, 6, 8, 9</td>
</tr>
<tr>
<td><em>P. damicornis</em> (Linnaeus, 1758)</td>
<td>Miocene to Recent; Indo-Pacific, eastern Pacific</td>
<td>strongly lacerate or irregular rounded mounds</td>
<td>size and shape variable</td>
<td>true verrucae lacking</td>
<td>1, 3, 4, 5, 6, 7, 8, 9, 10</td>
</tr>
<tr>
<td><em>P. elegans</em> Dana, 1846</td>
<td>late Pleistocene to Recent; Indian Ocean, Indo-Pacific, eastern Pacific</td>
<td>slightly openly branched to rounded mounds</td>
<td>upright, cylindrical to elliptical at base, subflabellate to flabellate on top, flattened ends</td>
<td>round, small, numerous, regularly distributed</td>
<td>1, 6, 7, 8, 9, 10</td>
</tr>
<tr>
<td><em>P. verrucosa</em> (Ellis &amp; Solander, 1786)</td>
<td>late Pleistocene to Recent; Red Sea, Indo-Pacific, eastern Pacific</td>
<td>slightly openly branched to rounded mounds</td>
<td>upright, cylindrical to elliptical at base, rarely subflabellate to flabellate on top</td>
<td>irregular in size, short, numerous</td>
<td>1, 3, 6, 7, 9, 10</td>
</tr>
<tr>
<td><em>P. meandrina</em> Dana, 1846</td>
<td>late Pleistocene to Recent; Indian Ocean, Indo-Pacific, eastern Pacific</td>
<td>irregular to rounded mounds, variable size</td>
<td>upright, thick, ends strongly flabellate</td>
<td>round, small, numerous, regularly distributed</td>
<td>1, 2, 3, 6, 7, 9, 10</td>
</tr>
</tbody>
</table>

Description.—Colonies ramose, branching. Corallum moderately openly branching to rounded mounds. Branches upright, variable in size, cylindrical to elliptical at base, usually subflabellate to flabellate on top, with flattened ends; thickness variable. Verrucae usually rounded, numerous, generally small, regularly distributed.

Calices circular to elliptical; those on ends of branches and verrucae polygonal. Calices small to intermediate in size (0.5-1.4 mm); depth variable. Distance between neighboring corallites moderate (0.4-1.5 mm), highly variable at colony level. Coenosteum solid and minutely granulated. Septa in two cycles, 12 in number, equal to subequal; presence and development highly variable at intra- and intercolony levels. Columella absent or inconspicuous, small and styliform when present.

Holotype.—Syntype, USNM 720, Pocillopora elegans.

Material Examined.—6 SUI specimens (100629, 100632, 100658, 102311-102313); 1 USNM specimen (720).

Occurrence.—Isla Coronados (loc. BC 41), Timbabichi (loc. BC 20).

Pocillopora elegans ranges in age from late Pleistocene to Recent. Outside of the Gulf of California, it occurs from Nayarit to Oaxaca (Reyes-Bonilla & López-Pérez, 1998) and Islas Revillagigedo (Ketchum & Reyes-Bonilla, 2001), México. It also occurs in Costa Rica, Panamá, Colombia, Ecuador, and Clipperton Atoll (Reyes-Bonilla, 2002). Outside of the eastern Pacific, it ranges from the eastern Indian Ocean to the central Pacific (Veron, 2000).

Discussion.—The taxonomic status of Pocillopora elegans was discussed in some detail by Reyes-Bonilla (2002). In general, there is disagreement about whether P. elegans is a valid species (Veron & Pichon, 1976; Veron, 2000), and whether it is present in the eastern Pacific. Squires (1959) considered P. capitata, P. capitata var. robusta, P. robusta, and P. capitata var. pumila to be synonyms of P. elegans on the basis of their poorly developed septa, but because the septa and columella are highly variable at inter- and intracolonial levels (see Pocillopora Discussion, above), their taxonomic value is ambiguous. I reviewed the specimens upon which Squires (1959: 410) established the presence of the species in the Pleistocene of Cabo Pulmo, southern Cerralvo, Isla Carmen, and Isla Montserrat, and the material resembles the morph currently identified as P. capitata in the Gulf of California, therefore their presence in those places is doubtful.

Pocillopora elegans is morphologically similar to P. verrucosa and P. capitata. Unlike P. verrucosa, P. elegans has rather uniform, rounded, numerous verrucae; it is distinguished from P. capitata by its subflabellate to flabellate branches and its less acute, more numerous verrucae (Table 10).

Pocillopora verrucosa (Ellis & Solander, 1786)
Pl. 1, Fig. 9

Madrepora verrucosa Ellis & Solander, 1786: 172; Vaughan 1918: 77-78, pl. 23, fig 1 [n. comb.].
Pocillopora ligulata Dana, 1846 in 1846-1849: 531-532, pl. 50, figs 2, 2a.

Description.—Colonies ramose, branching. Corallum openly branching to rounded mounds. Branches generally upright, cylindrical to elliptical at base, occasionally subflabellate to flabellate on top, with flattened ends; thickness variable. Verrucae irregular in size, generally small, numerous, regularly distributed.

Calices circular to elliptical; those on ends of branches and verrucae polygonal. Calices small to intermediate in size (0.5-1.4 mm); depth variable. Distance between neighboring corallites moderate (0.4-1.5 mm), highly variable at colony level. Coenosteum solid and minutely granulated. Septa in two cycles, 12 in number, equal to subequal; presence and development highly variable at intra- and intercolony levels. Columella absent or inconspicuous, small and styliform when present.

Type.—Type (status not researched), YPM IZ 3881, Pocillopora verrucosa.

Material Examined.—1 SUI specimen (100659); 1 YPM specimen (3881); 10 MHNUABCs specimens (613-616, 676-677, 737-740).

Occurrence.—Timbabichi (loc. BC 20).

Pocillopora verrucosa ranges in age from Pliocene to Recent. Outside of the Gulf of California, it occurs in the Pliocene of New Guinea (Veron & Kelley, 1988). In the Recent, it occurs from Baja California Sur to Oaxaca (Reyes-Bonilla & López-Pérez, 1998), México. It also occurs in Costa Rica, Panamá, Colombia, Ecuador, and Clipperton Atoll (Reyes-Bonilla, 2002). Outside of the eastern Pacific, it ranges from the Red Sea to the central Pacific (Veron, 2000).

Discussion.—See Pocillopora elegans Discussion (above). Pocillopora verrucosa is morphologically similar to P. elegans and P. capitata. Unlike P. elegans, however, P. verrucosa has thinner branches; it is distinguished from P. capitata by its less acute, more numerous verrucae (Table 10).
**Pocillopora meandrina** Dana, 1846

Pl. 1, Fig. 8

*Pocillopora meandrina* Dana, 1846 in 1846-1849: 533, pl. 50, figs 6, 6a-b.

*Pocillopora nobilis* Verrill, 1864: 59.

*Pocillopora meandrina* var. *nobilis* Verrill. Vaughan, 1907: 98-99, pl. 14, figs 3-4, pl. 22, figs 1, 1a, 2, 2a, pl. 23.

*Pocillopora meandrina* Dana, 1846 in 1846-1849: 533, pl. 50, figs 6, 6a-b.

*Pocillopora nobilis* Verrill, 1864: 59.

*Pocillopora meandrina* var. *nobilis* Verrill. Vaughan, 1907: 98-99, pl. 14, figs 3-4, pl. 22, figs 1, 1a, 2, 2a, pl. 23.

**Diagnosis.**—Colonies ramose. Corallum slightly irregular to rounded mounds of variable size. Branches upright, thick; ends expanded in one plane and of greater diameter than their bases. Branches covered with numerous, regularly distributed verrucae. Verrucae usually round, small.

Calices circular to elliptical, intermediate in size (0.7-1.5 mm), slightly shallow. Distance between neighboring corallites moderate (0.5-1.5 mm), highly variable at colony level. Coenosteum solid, minutely granulated. Septa in two cycles, 12 in number, equal to subequal; presence and development highly variable at intra- and intercolony level; in some cases opposite septa are developed and connected at bottom with columella. Columella small, styliform, often wanting; highly variable.

**Type.**—Type (status not researched), YPM IZ 1970, *Pocillopora meandrina*.

**Material Examined.**—1 SUI specimen (102388); 1 NHMLAC specimen (11740); 1 YPM specimen (1970).

**Occurrence.**—Cabo Pulmo (loc. BC 8).

*Pocillopora meandrina* ranges in age from late Pleistocene to Recent. Outside of the Gulf of California, it occurs from Nayarit to Oaxaca (Reyes-Bonilla & López-Pérez, 1998) and Islas Revillagigedo (Ketchum & Reyes-Bonilla, 2001), México, and in Costa Rica, Panamá, and Clipperton Atoll (Reyes-Bonilla, 2002). Outside of the eastern Pacific, it ranges from Oaxaca, México (Leyte-Morales, 1995a, b) to Colombia (Reyes-Bonilla, 2002). Based on the analysis of a large collection of specimens, *G. planulata* is added to the Gulf of California fossil record.

**Gardineroseris planulata** (Dana, 1846)

Pl. 2, Figs 1-9

*Agaricia planulata* Dana, 1846 in 1846-1849: 338.

*Asteroseris planulata* Verrill, 1901: 155, pl. 27, figs 8, 8a.

*Agaricia ponderosa* Gardiner, 1905: 927, pl. 89, figs 5-6.

*Gardineroseris planulata* Wells, 1983: 228-229, pl. 9, figs 1-6.

**Description.**—Colony form cerioid. Corallum highly variable in shape, encrusting or massive with laminar margins, slightly columnar, with moderately undulating upper surface. Budding generally circumoral, di- and tristomodeal also present. Valleys of variable size regularly enclose variable number of calices. Valleys separated by intermediate to high collines. Calices moderate in depth, polygonal, variable in size (3.5-8 mm in length; 2.5-5 mm in width). Septa numerous (41-96), arranged in 3 or 4 cycles, with 9-14 major septa reaching columella; secondary septa < ½ length of primaries; quaternary septa rarely beyond corallite wall. Septa thickness slightly heterogeneous. Septa covered with randomly distributed granules. Columella discontinuous between centers, trabecular, small.

**Types.**—Holotype, YPM IZ 4309, *Gardineroseris planulata*; hypotype, USNM 46946, *G. planulata*; hypotype, USNM 46945, *G. planulata*.
**Measurements (in mm) of the Holotype.**—CL, 4.18; CS, 3.26; CDL, 3.63; CDS, 3.01; NS, 57; NMS, 10; LSL, 1.5; LW, 0.05; FSL, 0.62; FW, 0.04; SSL, 1.06; SW, 0.05; CL, 0.51; CW, 0.18; NC, 5; WT, 0.13.

**Material Examined.**—25 SUI specimens (63665, 63819, 63830-63834, 100610-100611, 100613, 100615-100616, 100618-100622, 100624, 100660, 100706-100707, 100830, 100928, 100932, 102503); 4 USNM specimens (46945-46946, 78849, 100524); 1 NMB specimen (40425); 1 UCMP specimen (160253); 1 YPM specimen (4309).

**Occurrence.**—La Ventana (loc. BC 28).

*Gardineroseris planulata* ranges in age from late Miocene to Recent. Outside of the Gulf of California, it occurs in the late Miocene and Pliocene of the Dominican Republic, the Pinecrest Sandstone of the Tamiami Formation of Florida, and the Bowden Formation of Jamaica (Stemann, 1991). It occurs in the Pliocene of Java and Papua New Guinea, and in the Pleistocene of Timor and Ryukyu Islands (Veron & Kelley, 1988). It also occurs in the Recent of Oaxaca (Leyte-Morales, 1995a, b), México, and in Costa Rica, Panamá, Colombia, and Ecuador (Reyes-Bonilla, 2002). Outside of the eastern Pacific, it ranges from the western Indian Ocean and Red Sea to the central Pacific (Veron, 2000).

**Discussion.**—The Gulf of California record is composed mainly of typical "planulata"-like specimens with low collines (Pl. 2, Figs 7-8), whereas Caribbean representatives are typical "ponderosa"-like with high collines (Pl. 2, Figs 4-5), although surface preservation of the Gulf of California specimens precluded an unambiguous differentiation among morphs. More importantly, however, are the striking quantitative differences between Gulf of California, Recent eastern Pacific, and Caribbean representatives of the species. As suggested by discriminant analysis (not presented), morphologic differences are greater than those found in similar analyses among populations on other Gulf of California taxa; nonetheless, aside from size differences, Neogene Caribbean and Gulf of California material are indistinguishable from modern eastern Pacific colonies (Pl. 2, Figs 6, 9).

*Gardineroseris planulata* is morphologically similar to *Pavona venosa* (Ehrenberg, 1834) and *P. varians* Verrill, 1864. Unlike *P. venosa*, *G. planulata* has more closely spaced septa and a better-developed columella; it is distinguished from *P. varians* by its septal number and the presence of acute collines.

Genus **PAVONA** Lamarck, 1801

**Type Species.**—*Madrepora cristata* Ellis & Solander, 1786.

**Diagnosis.**—Colonies massive, columnar, with frond-like bifacial laminas. Corallite wall poorly defined, sometimes separated by ridges. Costosepta exerted.

**Discussion.**—The first record of *Pavona* was in the late Cretaceous and early Eocene of the Caribbean and Europe (Vaughan & Wells, 1943). During the Oligocene to Miocene, the genus was cosmopolitan, but disappeared in the Mediterranean and Caribbean by the end of the Miocene (Vaughan & Wells, 1943). In the Indo-Pacific, the genus consisted of eight species ranging in age between Oligocene to Recent (Veron & Kelley, 1988). In the eastern Pacific, previous records suggest the presence of *P. gigantea* in late Pleistocene sediments of Isla Carmen (Duran, 1950), but based on recently collected material described herein, *P. clavus* is added to the Gulf of California fossil record.

**Pavona clavus** (Dana, 1846)

Pl. 2, Figs 10-12, Pl. 3, Figs 1-3

*Pavona clavus* Dana, 1846 in 1846-1849: 332-333, pl. 24, figs 4a, b.

*Pavonia clivosa* Verrill, 1869: 395-396; 1870: 544-545, pl. 9, fig. 8.

*Pavona galapagensis* Durham & Barnard, 1952: 44-45, pl. 5, figs 16a, b.

*Solenastrea ecuadoriana* Durham & Barnard, 1952: 59, pl. 5, fig. 23.

**Description.**—Colonies cerioid to subcerioid. Corallum massive, encrusting to columnar, occasionally with laminar margins. Colony surface usually smooth, well rounded. Budding mainly circumoral.

Calices circular to slightly elliptical, of intermediate size (1.8-2.0 mm in length; 1.57-1.7 mm in width), moderately spaced (1.7-2.6 mm). Corallite size and theca thickness highly variable at colony level and among colonies from same locality. Costosepta generally 14-18, as many as 28, of two alternating orders: larger and smaller; larger generally reaching columella, slightly thicker; smaller ¾-⅔ length of larger. Costosepta covered with abundant, minute, randomly distributed granules. Columella solid, small, either slightly styliform or dorsally compressed.


**Measurements (in mm) of the Syntype USNM 62699.**—CRL, 2.88; CRS, 2.31; CDL, 3.93; CDS, 2.64; NS, 20.83; LSL, 1.20; IW, 0.09; FSL, 0.75; FW, 0.08; SSL, 1.05; SW, 0.08; CL, 0.39; CW, 0.20; NC, 4.83; WT, 0.47.
Material Examined.—73 SUI specimens (100694, 100696-100699, 100701-100703, 100814, 100817, 100819-100820, 100822, 100824-100828, 100845-100890, 100892-100893, 100898, 100929-100931, 100979, 102308-102309); 6 UCMP specimens (160152, 160221, 160252, 161609); 2 USNM specimens (221, 62699); 2 AHF specimens (2, 3).

Occurrence.—La Ventana (locs. BC 10, 11, 28-32), Isla Coronados (loc. BC 38).

*Pavona clavus* ranges in age from Miocene to Recent. Outside of the Gulf of California, it occurs in the Miocene of Nias, Plio-Pleistocene of Ceram, and in the Pleistocene of Java, Sumatra, Nias, and New Caledonia in Southeast Asia (Veron & Kelley, 1988). In México, it occurs in the Recent of Jalisco, Colima, Oaxaca (Reyes-Bonilla & López-Pérez, 1998), and Islas Revillagigedo (Ketchum & Reyes-Bonilla, 2001). It also occurs in Costa Rica, Panamá, Colombia, Ecuador, and Clipperton Atoll (Reyes-Bonilla, 2002). Outside of the eastern Pacific, it ranges from the Red Sea to the central Pacific (Veron, 2000).

Discussion.—*Pavona clavus* is morphologically similar to *P. duerdeni* (Pl. 3, Figs 9-12) and *P. minuta* Wells, 1954. Unlike *P. duerdeni*, however, colonies of *P. clavus* lack paralleled ridges or hillocks (Pl. 3, Figs 9-10). At the corallite level, *P. clavus* has larger corallites and more exserted primary costosepta than *P. duerdeni* or *P. minuta*.

*Pavona gigantea* Verrill, 1869

Pl. 3, Figs 4-8

**Pavonia gigantea** Verrill, 1869: 394-395; Durham, 1947: 20, pl. 3, figs 1-2, 7.

**Description.**—Colonies cerioid to subcerioid. Corallum massive, encrusting to slightly columnar; large colonies invariably with laminar margins. Colony surface usually smooth, undulated. Budding mainly circumoral.

Calices circular to slightly elliptical, of large size (2.3-2.6 mm) and widely spaced (2.0-3.3 mm). Corallite size and theca thickness highly variable at colony level and among colonies from same locality. Costosepta generally 12-14, as many as 18, of two alternating orders: larger and smaller; larger generally reaching columella, thicker; smaller ¾-⅔ length of larger. Costosepta covered with minute, randomly distributed granules. Columella solid, variable in size, eventually absent.


Measurements (in mm) of the Hypotype.—CRL, 2.37; CRS, 2.07; CDL, 2.13; CDS, 2.87; NS, 13.16; LSL, 0.85; LW, 0.18; FSL, 0.40; FW, 0.05; SSL, 0.72; SW, 0.15; CL, 0.17; CW, 0.07; NC, 7; WT, 0.26.

Material Examined.—8 SUI specimens (100661, 100672, 100843-100844, 102303, 102305-102307); 2 UCMP specimens (14865, 160137); 1 USNM specimen (62702); 1 YPM specimen (1679A).

Occurrence.—Isla Coronados (locs. BC 38, 41).

*Pavona gigantea* ranges in age from middle Pleistocene to Recent. It occurs in Pleistocene salt flats of Isla Carmen (Durham, 1947). Outside of the Gulf of California, it occurs from Nayarit to Oaxaca including the Islas Revillagigedo (Reyes-Bonilla & López-Pérez, 1998), México. It also occurs in Costa Rica, Panamá, Colombia, Ecuador, and Clipperton Atoll (Reyes-Bonilla, 2002).

Discussion.—*Pavona gigantea* is easily differentiated from *P. clavus* by its much larger corallites and less numerous septa.

Family SIDERASTREIDAE Vaughan & Wells, 1943

Genus SIDERASTREA de Blainville, 1830

**Type Species.**—Madrepora radians Pallas, 1766; holotype currently lost (Budd & Guzmán, 1994).

**Diagnosis.**—Colonies massive, branching or encrusting. Corallites cerioid, rounded, or polygonal, formed by extratenuicular budding. Wall structure synapticulothecal. Septa straight, fine. Columella formed by few pinnules.

**Siderastrea mendenhalli** Vaughan, 1917

Pl. 4, Figs 1-4

Siderastrea mendenhalli var. minor Vaughan, 1917: 375, pl. 102, fig. 1.

*Siderastrea californica* Vaughan, 1917: 375, pl. 102, figs 2, 2a, 3-4.

**Description.**—Colonies cerioid. Corallum massive, small, attached, with smooth, slightly undulated surface. Calices polygonal, generally hexagonal or pentagonal, intermediate in diameter (4.3-5.8 mm). Corallite wall solid, continuous, generally straight, relatively thick (ca. 0.24 mm). Synapticulae arranged in 3 or 4 rings, intermediate in thickness (ca. 0.12 mm). Septa relatively thin, equal in thickness, usually continuous between adjacent corallites. Septal margins finely dentate, with 13-15 dentations per primary septum. Four septal cycles, sometimes with fourth incomplete or members of fifth present; generally 40-48 septa per corallite. First, second, and fourth cycles free; third cycle fused with secondary near columella. Columella solid, thick (ca. 1.1 mm). Calicular fossa relatively shallow.


**Measurements (in mm) of the Holotype USNM 68290.**—CRL, 5.28; CRS, 4.6; NS, 46.5; IW, 0.18; CL, 1.17; WT, 0.18; NSY, 3.66.

**Material Examined.**—1 SUI specimen (102275); 5 USNM specimens (63032, 65300, 68290-68292).

**Occurrence.**—Barrett Canyon (loc. USGS 7616), Coyote Mountains (loc. UCLA 631), Alverson Canyon (loc. USGS 3923).

*Siderastrea mendenhalli* is known from the late Miocene to early Pliocene of the Gulf of California, and the Pliocene in the Dominican Republic (Budd et al., 1994b).

**Discussion.**—*Siderastrea mendenhalli* and *S. californica* were erected as distinct species on the basis of corallite size, and septal number and development (Vaughan, 1917). Morphometric analysis of corallite characters on which species distinction was based failed to distinguish between the two species; instead, the types of *S. californica* totally overlapped with specimens and types of *S. mendenhalli*, and pairwise comparison among groups rendered Mahalanobis’s distances equal or minor to those found among populations of other coral species (among *S. californica* and *S. mendenhalli*, Mahalanobis = 16.85; among north and south *P. panamensis* populations, Mahalanobis = 57.27). Similarly, in a morphometric analysis of *Siderastrea*, Foster (1980b) found considerable overlap between *S. mendenhalli* and *S. californica* and suggested that the species are not sufficiently distinct to warrant separation into two species. Based on these results, *S. californica* is here synonymized with *S. mendenhalli*.

*Siderastrea mendenhalli* is morphologically similar to *S. siderea*. Unlike *S. siderea*, however, *S. mendenhalli* has a thick columella, a shallower fossa, and fewer synapticular rings (Table 11).

**Siderastrea annae n. sp.**

Pl. 4, Figs 5-6, Pl. 5, Figs 1-4

**Diagnosis.**—Colonies small, encrusting. Corallites of intermediate size. Corallite wall zig-zagging, moderately thick. Septa dentate, relatively few, equally thin, in three cycles. Columella thick, solid, with fossa of moderate depth.

**Description.**—Colonies cerioid. Corallum small (3-6 cm in diameter), attached, encrusting to massive with a smooth outer surface. Calices polygonal, generally hexagonal, or pentagonal, intermediate in diameter (3.5-4.6 mm). Corallite wall solid, continuous, generally in zig-zag pattern, relatively thin (ca. 0.18 mm). Synapticulae arranged in 3 (rarely 4) rings, intermediate in thickness (ca. 0.1 mm). Septa relatively thin, slightly unequal in thickness, usually discontinuous between adjacent corallites that give corallite wall characteristic zig-zag pattern. Septal margins dentate, with up to 7 dentations per primary septum. Three septal cycles, rarely with members of fourth cycle; generally 35-40 septa per corallite. First and second cycles free; third cycle fused with secondary near columella. Columella solid, relatively thick (ca. 1.15 mm). Calicular fossa of moderate depth.

**Etymology.**—Named in honor of Ann F. Budd for her important and large contribution to coral taxonomy.

**Types.**—Holotype, SUI 100674; paratypes, SUI 100673, 100675.

**Type Locality.**—Loc. BC 15, Puerto de la Lancha, Isla Carmen, San Marcos Formation, Baja California Sur, México. Early Pliocene.

**Measurements (in mm) of the Holotype.**—CRL, 4.18; CRS, 3.41; NS, 34.83; IW, 0.16; CL, 1.31; WT, 0.20; NSY, 3.16.

**Material Examined.**—6 SUI specimens (100673-100675, 102140-102141, 102148).

**Occurrence.**—Puerto de la Lancha (loc. BC 15).

*Siderastrea annae* is known only from the early Pliocene of
Puerto de La Lancha at Isla Carmen.

Discussion.— *Siderastrea annae* n. sp. is morphologically most similar to *S. mendenhalli*, which also forms small, attached colonies, with similar columella development and numbers of synapticular rings. Unlike *S. mendenhalli*, however, *S. annae* n. sp. has much smaller corallites, less numerous septa in three cycles, and a deeper fossa. It is also morphologically similar to *S. radians* (Pallas, 1766), which also has corallites with a deep fossa and similar number of septa; unlike *S. radians*, the new species has larger corallites and a larger number of synapticular rings (Table 11).

Table 11. Morphologic characters distinguishing species of *Siderastrea*.

<table>
<thead>
<tr>
<th>Species</th>
<th>Distribution</th>
<th>Septa per corallite</th>
<th>Corallite diameter (mm)</th>
<th>Columella</th>
<th>Corallite wall</th>
<th>Additional references*</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. annae</em> n. sp.</td>
<td>Early Pliocene; Gulf of California</td>
<td>35-40</td>
<td>3.5-4.6</td>
<td>thick, solid; intermediate fossa depth</td>
<td>relatively thin, 3-4 synapticular rings; septa usually alternate between calices</td>
<td>none</td>
</tr>
<tr>
<td><em>S. glynni</em> Budd &amp; Guzman, 1994</td>
<td>Recent; eastern Pacific</td>
<td>40-48</td>
<td>2.5-3.5</td>
<td>intermediate thickness, papillose; shallow fossa</td>
<td>intermediate thickness, 3-4 synapticular rings; septa usually continuous between calices</td>
<td>10</td>
</tr>
<tr>
<td><em>S. mendenhalli</em> Vaughan, 1917</td>
<td>late Miocene to early Pliocene; Dominican Republic, California</td>
<td>48-54</td>
<td>3-5</td>
<td>thick; shallow fossa</td>
<td>thick, 3-4 synapticular rings; septa usually continuous between calices</td>
<td>1, 5, 10, 11</td>
</tr>
<tr>
<td><em>S. radians</em> (Pallas, 1766)</td>
<td>middle Pliocene to Recent; Caribbean, Bermuda, Brazil, w. Africa</td>
<td>30-40</td>
<td>2.5-3.5</td>
<td>thick, solid; intermediate fossa depth</td>
<td>thick, 2-3 synapticular rings; septa usually continuous between calices</td>
<td>2, 4, 6, 10, 11</td>
</tr>
<tr>
<td><em>S. savignyana</em> Milne Edwards &amp; Haime, 1850</td>
<td>Recent; Red Sea, Indian Ocean</td>
<td>28-35</td>
<td>2.5-4</td>
<td>thick, solid; intermediate fossa depth</td>
<td>very thick, 2-3 synapticular rings; septa usually continuous between calices</td>
<td>7, 9, 10</td>
</tr>
<tr>
<td><em>S. siderea</em> (Ellis &amp; Solander, 1786)</td>
<td>Early Miocene to Recent; Caribbean, ?W Africa</td>
<td>44-50</td>
<td>3-5</td>
<td>thin, papillose; deep fossa</td>
<td>thin, 3-5 synapticular rings; septa alternate between calices</td>
<td>2, 4, 6, 10, 11</td>
</tr>
<tr>
<td><em>S. silicensis</em> Vaughan, 1919</td>
<td>Early Miocene to early Pleistocene; Florida, Dominican Republic</td>
<td>48 - &gt; 60</td>
<td>&gt;&gt; 4.5</td>
<td>intermediate thickness; deep fossa</td>
<td>thin, 3-5 synapticular rings; septa continuous between calices</td>
<td>8, 10, 11</td>
</tr>
<tr>
<td><em>S. stellata</em> Verrill, 1868</td>
<td>Recent; Brazil</td>
<td>ca. 48</td>
<td>ca. 3 (in series)</td>
<td>thin, papillose; very deep fossa</td>
<td>thin, 3-4 synapticular rings; septa usually continuous between calices</td>
<td>3, 4, 10</td>
</tr>
<tr>
<td><em>S. pliocenica</em> Vaughan, 1919</td>
<td>middle Pliocene to early Pleistocene; Florida</td>
<td>40-48</td>
<td>4.5-5</td>
<td>thick, solid; shallow fossa</td>
<td>thick, 4-5 synapticular rings; septa usually continuous between calices</td>
<td>5, 10, 11</td>
</tr>
</tbody>
</table>

*References: 1, Vaughan, 1917; 2, Yonge, 1935; 3, Laborel, 1969; 4, Laborel, 1974; 5, Foster, 1980a; 6, Foster, 1980b; 7, Scheer & Pillai, 1983; 8, Budd, 1989; 9, Veron, 1993; 10, Budd & Guzman, 1994; 11, Budd et al., 1994b.*
Genus **PSAMMOCORA** Dana, 1846

**Type Species.**—*Pavona obtusangula* Lamarck, 1816, by subsequent designation (Wells, 1956).

**Diagnosis.**—Colonies massive, columnar, laminar, or encrusting. Corallites small, shallow, separated by ramifying costosepta. Costosepta with granulate margins. Corallite walls indistinct. Collines enclosing one to a group of calices. Columella formed by pinnules.

**Discussion.**—The first record of *Psammocora* was in the Miocene of the Caribbean (Vaughan & Wells, 1943). It has been recorded in the Pleistocene of Japan and New Guinea (Veron & Kelley, 1988). In the eastern Pacific, the genus is represented by four species distributed between the Gulf of California and Isla de Pascua, Chile (Reyes-Bonilla, 2002). It was recorded in the late Pliocene-early Pleistocene of Seymour Island, Galapagos (Hertlein, 1972), and the late Pleistocene of Isla Coronados (Durham, 1947, 1950).

**Psammocora stellata** (Verrill, 1866)

*Pl. 5, figures 5, 6*

*Stephanocora stellata* Verrill, 1866: 330.
*Stephanaria stellata.* Verrill, 1868-1870: 545-546, pl. 9, figs 4, 4a.

**Diagnosis.**—Colonies cerioid. Corallum small, with submassive to irregular relatively short contorting branches with distinctive encrusting bases. Colony surface usually irregular, covered with relatively small collines enclosing valleys of rather variable number of calices. Development of collines highly variable. Budding circumoral.

Calices circular to polygonal at edges, relatively small (1.5-2.5 mm in diameter) although highly variable at intracolonial level; fossa relatively shallow. Corallite wall synaptilothecal, poorly defined or absent. Costosepta generally 12-21, highly variable at colony level, covered with sharp, moderately large, randomly distributed granulations on sides and edges. Columella development variable, usually poorly developed, often absent.

**Types.**—Syntype, USNM 20849, *Stephanocora stellata*; hypotype, UCMP 15494, *Psammocora stellata*.

**Material Examined.**—13 SUI Specimens (100676, 100704-100705, 101006-101007, 102304, 102314-102320); 1 USNM specimen (20849); 1 UCMP specimen (15494).

**Occurrence.**—Isla Coronados (locs. BC 37, A 3547), Punta Baja (loc. BC 12), Las Animas (locs. BC 6, 7), La Ventana (loc. BC 11).

*Psammocora stellata* ranges in age from late Pleistocene to Recent. Outside of the Gulf of California, it occurs in Islas Revillagigedo (Reyes-Bonilla & López-Pérez, 1998) and Oaxaca (Glynn & Leyte-Morales, 1997), México. It also occurs in Costa Rica, Panama, Colombia, Ecuador, and Cliperton Atoll (Reyes-Bonilla, 2002). Outside of the eastern Pacific, it occurs in Hawaii and Southeast Asia (Veron, 2000).

**Discussion.**—Aside from two well-preserved colonies recovered from loc. BC 37, material is rather worn, therefore precluding specimen measurement. Corallum morphology allowed the unambiguous assignment of the specimens to *Psammocora stellata*.

Family **PORITIDAE** Gray, 1842

Genus **PORITES** Link, 1807

**Type Species.**—*Porites polymorphus* Link, 1807.

**Diagnosis.**—Colonies massive, branching, columnar, laminar or encrusting. Corallites small (< 2 mm). Septa 12 in number, arranged in two cycles following a bilateral-symmetric pattern (after Bernard, 1905). Septa formed by 1-4 trabeculae; innermost can form pali. With little or no coenosteum.

**Discussion.**—The first record of *Porites* was in the Eocene of the Caribbean and Tethys (Vaughan & Wells, 1943), but since the early Miocene, it has been one of the most important reef-building corals. Today, a total of 14 nominal species of *Porites* are recognized in the eastern Pacific, but only 9 species are considered valid: *P. arnau di* Reyes-Bonilla & Carricart-Ganivet, 2000; *P. australiensis* Vaughan, 1918; *P. baueri* Squires, 1959; *P. lichen* Dana, 1846; *P. lobata*; *P. lutea* Milne Edwards & Haime, 1860; *P. panamensis*; *P. rus* Forskaal, 1775; and *P. sverdrupi* (Reyes-Bonilla, 2002; López-Pérez et al., 2003). All except *P. rus* occur in the Mexican Pacific area (Reyes-Bonilla & López-Pérez, 1998). Five names have been proposed for eastern Pacific representatives between the Pliocene and Pleistocene (López-Pérez, 2005). Based on the analysis of a large collection of specimens, *P. lobata* is added to the Gulf of California fossil record.

**Porites carrizensis** Vaughan, 1917

*Pl. 6, Figs 1, 4*

*Porites carrizensis* Vaughan, 1917: 375-376, pl. 102, figs 5, 5a-b, 6, 6a.

**Description.**—Corallum small, massive, encrusting, nodular or subhemispherical with smooth, undulated surface. Calices
circular to polygonal, intermediate in size (1.4-1.8 mm in diameter), shallow in depth (0.3-0.5 mm), with narrow (<1 mm), regular spacing. Theca elevation variable, composed of one (rarely two) trabeculae, straight. Septa in two cycles, 12 in number, composed of one trabecula forming irregular surface denticle, thick. Dorsal septum often relatively reduced in length (<¾ lateral septa), with four lateral pairs; ventral triplet either fused or free. Pali five in number, moderate in size, equally developed; none before dorsal directive septa. Columella usually absent; poorly developed when present. Outer synapticular ring incomplete; palar synapticular ring usually complete.

**Types.**—Holotype, USNM 68293, *Porites carrizensis*; paratype, USNM 86840, *P. carrizensis*.

**Measurements (in mm) of the Holotype.**—CD, 1.73; CS, 1.87; LDS, 0.42; WDS, 0.15; LVS, 0.68; WVS, 0.15; LLS, 0.69; WLS, 0.14; NC, 6; NS, 12; NB, 0.16; PL, 5; CL, 0; CW, 0; CR, 0.46; WT, 0.27.

**Material Examined.**—25 SUI specimens (SUI 45710-45711, 45714-45715, 45717, 45724, 45730-45731, 100911, 102152-102158, 102168-102172, 102261-102262, 102272, 102480); 2 USNM specimens (68293, 68840).

**Occurrence.**—Barrett Canyon (loc. USGS 07616), Coyote Mountains (loc. UCLA 631), Alverson Canyon (loc. USGS 3923), Punta Chivato (loc. BC 3), Ensenada El Muerto (loc. BC 35), Puerto de la Lancha (loc. BC 15), Isla Montserrat (loc. BC 25-27), Las Barracas (loc. BC 2).

*Porites carrizensis* ranges in age from late Miocene to Pliocene. It occurs in the late Miocene-early Pliocene Imperial Formation of south-central California, the San Marcos Formation of Puerto de la Lancha, Punta Chivato, and Ensenada El Muerto, the middle Pliocene Carmen Formation of Isla Montserrat, and the late Pliocene Carmen Formation of Las Barracas.

**Discussion.**—*Porites carrizensis* is morphologically similar to *P. astreoides* Lamarck, 1816, and the massive morph of *P. panamensis*. Unlike *P. astreoides*, *P. carrizensis* has shallower calices and a better developed palus; it is distinguished from *P. panamensis* by its larger calices (Table 12).

**Porites lobata** Dana, 1846

*Pl. 6, Figs 2-3*

*Porites lobata* Dana, 1846: 562, pl. 55, fig. 1.

*Porites excavata* Verrill, 1868-1870: 504-505.

*Porites paschalensis* Vaughan in Arnold, 1906: 50, pl. 50, figs 9-10.

**Description.**—Corallum large, massive. Colony shape highly variable, ranging from hemispherical and helmet-shaped to colonies with columnar expansions; large colonies with thick ledges around base; surface smooth, undulate. Calices circular but generally polygonal, intermediate in size (1-2 mm in diameter), variable in depth (0.3-0.8 mm), with wide (<1 mm), regular spacing. Theca elevation variable, composed of 2-3 trabeculae, straight. Septa in two cycles, 12 in number, composed of two trabeculae that form small irregular surface denticles; lateral pairs and dorsal directive septum better developed; ventral triplet free. Pali generally six, rarely eight, in number, weakly to moderately well developed; pali in front of lateral pairs better developed, similar in size or smaller than septal denticles. Columella tubercle present, either as vertical rod or laterally compressed. Palar synapticular ring irregularly completed.


**Measurements (in mm) of the Syntype USNM 652.**—CD 1.28, CS 1.42, LDS, 0.32; WDS, 0.07; LVS, 0.33; WVS, 0.06; LLS, 0.46; WLS, 0.08; NC, 6; NS, 12; NB, 2; PL, 6; CL, 0.25; CW, 0.07; CR, 0.59; WT, 0.09.

**Material Examined.**—14 MHNUABCs specimens (1028-1029, 1032, 1049, 1054, 1056, 1058-1059, 1062, 1079, 1083, 1105, 1425); 1 NHMLAC specimen (11739); 2 USNM specimens (652, 68279); 1 YPM specimen (1677A).

**Occurrence.**—Cabo Pulmo (loc. BC 8).

*Porites lobata* ranges in age from late Pliocene to Recent. It occurs in the late Pliocene-early Pleistocene Era Beds of New Guinea and doubtfully in the Pleistocene of New Caledonia (Veron & Kelley, 1988). It also occurs in the Recent of Nayarit, Jalisco, Colima, and the Islas Revillagigedos (Reyes-Bonilla & López-Pérez, 1998), and recently was recovered from Guerrero (Reyes-Bonilla et al., 2005) in the Mexican Pacific. It also has been reported in Costa Rica, Panamá, Colombia, Ecuador, and Chile (Reyes-Bonilla, 2002). Outside of the eastern Pacific, it ranges from the western Indian Ocean and Red Sea to the central Pacific (Veron, 2000).

**Discussion.**—*Porites lobata* is easily distinguished from other fossil Gulf of California poritid species by the number of pali and the presence of a columella (Table 12).

**Porites panamensis** Verrill, 1866

*Pl. 6, Figs 5-11*

*Porites panamensis* Verrill, 1866: 329-330; non *P. panamensis*
Porites californica Verrill, 1868-1870: 504.
Description.—Colonies intermediate in size (13-30 cm in diameter), massive. Corallum highly variable in shape, ranging from encrusting to nodular and ramose (branch thickness = 12.7-38.1 mm). Colony smooth with slightly undulated surface or bumps developing into lobes as columnar expansions generally short and rounded at top.
Calices circular to irregularly polygonal, small to intermediate in size (0.9-1.6 mm in diameter), shallow in depth (0.3-0.5 mm), with narrow, regular spacing. Theca elevation variable, composed of one (rarely two) trabeculae, straight. Septa in two cycles, 12 in number, composed of one (rarely two) trabeculae that form small, irregular surface denticles. Dorsal septum often relatively reduced in length (< ¾ lateral septa), with four lateral pairs; ventral triplet either fused or free. Pali five in number, moderate in size, equally developed; none before dorsal directive septa. Columella tubercle usually absent, weakly developed when present. Palar synapticular ring irregularly complete.

Types.—Syntype, YPM 585A, Porites panamensis; holotype, YPM 1599A, B, P. californica; holotype, YPM 6845, P. porosa; holotype, YPM 6844A, B, P. nodulosa.

Measurements (in mm) of the Syntype.—CD, 1.25; CS, 1.16; LDS, 0.35; WDS, 0.09; LVS, 0.48; WVS, 0.09; LLS, 0.47; WLS, 0.1; NC, 6.66; NS, 12; NB, 1.33; PL, 5; CL, 0; CW, 0; CR, 0.34; WT, 0.10.

Porites panamensis Verrill, 1866
described as P. californica.

Porites porosa Verrill, 1868-1870: 504.

Porites nodulosa Verrill, 1868-1870: 505-506.

Porites panamensis Verrill, 1866
described as P. californica.

Porites porosa Verrill, 1868-1870: 504.

Porites panamensis Verrill, 1866
described as P. californica.

Porites porosa Verrill, 1868-1870: 504.

Porites panamensis Verrill, 1866
described as P. californica.

Porites porosa Verrill, 1868-1870: 504.

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described as P. californica.

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described as P. californica.

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described as P. californica.

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described as P. californica.

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described as P. californica.

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described as P. californica.

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described as P. californica.

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described as P. californica.

Porites porosa Verrill, 1868-1870: 504.

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described as P. californica.

Porites porosa Verrill, 1868-1870: 504.

Porites panamensis Verrill, 1866
described as P. californica.

Porites porosa Verrill, 1868-1870: 504.
Puerto Balandra at Isla Carmen, and the late Pleistocene of Punta Chivato, Punta San Antonio, Las Animas, Cabo Pulmo, Timabichichi, El Bajo, and El Sombrerito. It occurs in the Pleistocene of Isla Tiburón, San Marcos, Bahía Magdalena, Islas Marías, and Oaxaca (Palmer, 1928; Hertlein & Emerson, 1959; Squires, 1959). It also occurs in the Recent of the Gulf of California and Mexican Pacific, from San Felipe (30°N) to Oaxaca (15°N), and at Bahía Magdalena, on the western coast of the Baja California Peninsula (24°N) (López-Pérez et al., 2003). It has been reported in Costa Rica, Panamá, Colombia, and Ecuador (Reyes-Bonilla, 2002). Outside of the eastern Pacific, it was doubtfully reported for the late Pliocene-early Pleistocene Era Beds of New Guinea (Veron & Kelley, 1988).

**Discussion.**—Colony shape, and the measures related to corallite diameter, the number of pali, and the number of septa (CD 0.8-2.2; PL 2-7; NS 10-22) were found to be highly plastic in this species. Similarly, the examination of more than 300 specimens of *Porites* suggested that characters related to the development of the corallite wall and septa are highly variable. On this basis, no successful separation based on corallite morphology is consistent with the species proposed by Verrill (1866, 1868-1870); instead species types appear scattered throughout the plot (results not shown).

From the early Pliocene to Recent, colony morphology varies from encrusting to ramose; the massive (Pl. 6, Fig. 5) and ramose (Pl. 6, Figs 6-9) morphologies are the end members of a continuum. *Porites panamensis*, *P. californica*, and *P. porosa* represent the massive morph commonly retrieved from Pliocene to Recent localities in the Gulf of California, whereas in late Pleistocene records of *P. panamensis* north of La Paz (from Las Animas to Punta Chivato, except for Punta San Antonio), it is dominated by the ramose "nudolosa" form (Pl. 6, Fig. 7). Discriminant analysis using colony shape as the criterion for distinguishing a priori groups (i.e., ramose, massive) was unsuccessful at recovering any consistent pattern of corallite morphology either during the Pleistocene or the Recent; instead, colonies with different shapes appeared scattered throughout the plot (results not shown). These results were supported by electrophoretic analysis performed on Gulf of California material, in which enzyme differences were larger among geographic areas than among morphs (Paz-Garcia, 2005).

The massive morph of *Porites panamensis* is morphologically similar to *P. carrizensis* (see Discussion for *P. carrizensis*, above), whereas fragments or small colonies of the ramose morph are easily confused with *P. sverdrupi* (Table 12). Squires (1959) considered *P. sverdrupi* to be morphologically similar to *P. nudolosa*, therefore increasing the stratigraphic range of the former species to the Pliocene (Squires, 1959: 422). I have been able to carefully analyze the material upon which Squires (1959) based his conclusions, and have found that all of his specimens belong to the ramose morph of *P. panamensis*.

*Porites sverdrupi* Durham, 1947
Pl. 7, Figs 1-4

*Porites sverdrupi* Durham, 1947: 23, pl. 12, fig. 4, pl. 13, fig. 2; López-Pérez et al., 2003: 685-687, figs 3, 6.

**Description.**—Corallum relatively small (<15 cm in diameter), branching (branch thickness = 5-7 mm). Calices circular to irregularly polygonal, small to intermediate in size (0.9-1.6 mm in diameter), shallow in depth (0.3-0.5 mm), with narrow, regular spacing. Theca elevation variable, composed of two trabeculae, straight. Septa in two cycles, 12 in number. Dorsal septum often relatively reduced in length (<¾ lateral septa), with four lateral pairs; ventral triplet either fused or free. Pali five in number, moderate in size, equally developed; none before dorsal directive septa. Columella tubercle usually absent, weakly developed when present. Pala synapticular ring irregularly complete.

**Type.**—Holotype, USNM M547362, *Porites sverdrupi*.

**Measurements (in mm) of the Holotype.**—CD, 1.30; CS, 1.30; LDS, 0.42; WDS, 0.15; IVS, 0.49; WVS, 0.12; WLS, 0.12; NC, 6.62; NS, 12; NB, 1.25; PL, 5.12; CL, 0; CW, 0; CR, 0.57; WT, 0.12.

**Material Examined.**—2 SUI specimens (100679, 100926); 19 MNHUABCS specimens (751-756, 775, 988-994, 1773-1776, 1780); 1 USNM specimen (M547362).

**Occurrence.**—Bahía Oto (loc. BC 16), Punta Baja (loc. BC 12).

*Porites sverdrupi* ranges in age from the late Pleistocene to Recent. It occurs in the late Pleistocene of Bahía Oto and Punta Baja at Isla Carmen. It was erroneously identified by Squires (1959: 422) in the Pliocene and Pleistocene of the Gulf of California. It also occurs in the Recent of the Gulf of California from Isla Angel de la Guarda, México (29°N) to Isla San José (25°N) (López-Pérez et al., 2003).

**Discussion.**—*Porites sverdrupi* is morphologically similar to the ramose morph of *P. panamensis* (see Discussion of *P. panamensis*, above, and López-Pérez et al., 2003). Unlike *P. panamensis*, *P. sverdrupi* has more slender (<7 mm diameter) and less straight branches. At the corallite level, the development of the columella (*P. panamensis > P. sverdrupi*), and the corallite size and septal development (*P. sverdrupi > P. panamensis*) are
also important in species identification (Table 12).

Family MONTLIVALTIIDAE Dietrich, 1926
Genus PLACOSMILIA Milne Edwards & Haime, 1848

Type Species.—Turbinolia cymbula Michelin, 1846, by subsequent designation (Wells, 1956).


Discussion.—The first record of Placosmilia was in the Upper Cretaceous of Europe (Vaughan & Wells, 1943; Wells, 1956), but by the Middle Eocene, it extended to Central Chiapas, which is typically considered to be Caribbean (Frost & Langenheim, 1974).

The species described here is distinct from any flabellloid species fossil or living, currently assigned to the families Faviidae, Meandrinidae, Mussidae, or Trachyphylliidae. Morphologically, it is similar to Placosmilia copoyensis Frost & Langenheim, 1974, from the Middle Eocene of Central Chiapas, México. However, the striking convergence in colony form among families (Budd & Johnson, 1999), along with the lack of a suite of well-preserved specimens, precludes an unambiguous determination.

Placosmilia? aliciae n. sp.
Pl. 7, Figs 5-9, Pl. 8, Figs 1-9


Description.—Flabellloid, free-living colonies formed by intramural, polystomodeal budding. Single, highly contorted corallith with several generally indistinct centers per series. Valley width generally 4-8 mm wide, but to 12 mm in clearly distinct centers. Clearly distinct centers generally located at end of, and in bifurcations of, series. Centers rather indistinct at center of series. Epitheca poorly developed or absent.

Costae well-developed, corresponding to septa, unequal, with thinner costae extending from quaternary septa. Septa generally in four cycles, with total number per 5 mm ranging from 10-12. Septa unequal in thickness at mid-length with primary thicker than secondary; secondary thicker than tertiary; tertiary slightly thicker than quaternary. Primary septa extending to columella (3.2-3.6 mm); secondary septa ca. ¾ of primary (1.8-2.5 mm); tertiary septa ca. ⅕ of primary (0.8-1 mm); quaternary septa extending < ⅕ of distance to columella. Septal margins with minute, acute teeth, 0.9-1.8 mm in diameter, spaced 0.4-0.7 mm apart. Septal faces covered with conical spines 0.1-0.2 mm in diameter, arranged in rows. Columella trabecular, seeming laminar at surface, continuous, ca. ⅔ (0.9-1.1 mm) of valley width. Paliform lobes well-developed in front of primary septa. Septal lobes absent. Endothecal and exothecal dissepiments absent.

Etymology.—I take pleasure in naming this species after the late Mrs. Alicia Pérez, in recognition of her loving presence.

Types.—Holotype, SUI 100680; paratypes, SUI 100681-100683.

Type Locality.—Loc. BC 4, San Nicolas, San Nicolas Formation, Baja California Sur, México. Middle Pliocene.

Measurements (in mm) of the Holotype.—CRS, 4-8; LSL, 3.2-3.6; FSL, 0.8-1; SSL, 1.8-2.5; CW, 0.9-1.1; NS/5 mm, 10-12.

Material Examined.—21 SUI specimens (100680-100684, 102216-102220, 102266, 102411-102420).

Occurrence.—Punta Chivato (loc. BC 3), Ensenada El Muerto (BC 35), San Marcos Formation. San Nicolas (loc. BC 4), San Nicolas Formation.

Placosmilia? aliciae is only known from the early to middle Pliocene of the Gulf of California.

Discussion.—Frost & Langenheim (1974) described Placosmilia copoyensis from the San Juan Formation, middle Eocene of Central Chiapas. Like the new species described here, it has thin valleys and contorted coralliths with similar septal arrangement and ornamentation. However, the number of septa per 5 mm is reduced, and there is a lack of endothecal and exothecal dissepiments. Trachyphyllia geoffroyi (Audouin, 1826) and T. bilobata (Duncan, 1863) are morphologically similar to P?. aliciae n. sp., however, the last lacks the second trabecular fan system that forms the inner prominent lobes characteristic of the Trachyphylliidae.

The main morphological differences among specimens of Placosmilia? aliciae n. sp. are related to the growth stages of the species. The first represents a small circular solitary corallite with the same septal arrangement and ornamentation (i.e., teeth and granulation; Pl. 8, Figs 5, 7-9), whereas the
second represents an elongated, highly sinuous form of larger coralliths.

Family **FAVIIDAE** Gregory, 1900
Genus **FAVIA** Oken, 1815

**Type Species.**—*Madrepora fragum* Esper, 1795, by subsequent designation (Wells, 1956). Holotype is currently lost (Scheer, 1990).


**Discussion.**—As shown by Budd & Johnson (1999) and Fukami et al. (2004), the genus *Favia* is paraphyletic and in need of revision. As currently defined, it is represented by ca. 20 species, widely distributed in the Indo-Pacific, Atlantic, and Caribbean (Veron, 2000).

The first record of *Favia* is in the Cretaceous of the Tethys (Vaughan & Wells, 1943). The genus has been reported in the Tertiary of the Mediterranean and Indo-Pacific (Chevalier, 1962; Pfister, 1980; Veron & Kelley, 1988). In the eastern Pacific, the genus appears in the middle Eocene of California (Durham, 1942) and in the early Miocene of Chiapas (Frost & Langenheim, 1974). Based on the analysis of a large collection of specimens, *F. maitreyiae* n. sp. and *F. tulsidasi* n. sp. are added to the Gulf of California fossil record.

**Favia maitreyiae** n. sp.
Pl. 9, Figs 1-5

**Diagnosis.**—Colony massive, plocoid, with predominantly intramural budding. Calices with 1-2 centers, elliptical to polygonal in shape.

**Description.**—Colonies massive, plocoid, with predominantly intramural budding; new buds forming by equal to subequal bifurcation. Calices with single and double (rarely 3) centers, elliptical to polygonal in shape, with minimum diameter of 6-8 mm.

Costae moderately developed, subequal, continuous. Septa in three cycles, with ca. 30 total septa per corallite. Septa unequal in thickness with primary slightly thicker than secondary; both thicker than tertiary. Primary and secondary septa extending to columella; tertiary septa free, extending 1/3-1/2 of distance to columella. Septal faces covered with rare, randomly distributed spines. Columella spongy, discontinuous, ca. 1/3 of corallite width. Paliform lobes absent. Wall septothecal, thinner than primary septa. Endothecal and exothecal dissepiments rare, thick. Coenosteum porous. Distance between corallite walls 1.6 mm.

**Etymology.**—Named in honor of the author’s daughter, Maitreyi López Alarcon.

**Types.**—Holotype, SUI 100686; paratype, SUI 100685.

**Type Locality.**—Loc. BC 26, Isla Montserrat, Carmen Formation, Baja California Sur, México. Middle Pliocene.

**Measurements (in mm) of the Holotype.**—CL, 9.96; CS, 6.56; CDL, 9.23; CDS, 3.44; NS, 34.33; LSL, 3.68; LW, 0.36; FSL, 0.78; FW, 0.25; SSL, 2.95; SW, 0.41; CL, 1.39; CW, 0.74; NC, 6.16; WT, 1.84.

**Material Examined.**—31 SUI specimens (100685-100686, 101010-101011, 101013-101014, 101018, 102032-102049, 102055-6, 102059, 102066, 102071).

**Occurrence.**—Isla Montserrat (locs. BC 25-27), Carmen Formation.

**Favia maitreyiae** n. sp. is known only from the middle Pliocene of the Isla Montserrat.

**Discussion.**—*Favia maitreyiae* n. sp. is morphologically similar to *Favia* n. sp. aff. dominicensis Budd & Johnson (1999), a Miocene species from the Dominican Republic. It differs primarily from the latter in its septothecal wall, its relatively large corallites, and its higher budding frequency (Table 13).

**Favia tulsidasi** n. sp.
Pl. 10, Figs 1-5

**Diagnosis.**—Colonies predominantly encrusted, plocoid, with extramural budding. Calices with one center, circular to elliptical in shape.

**Description.**—Colonies small, predominantly encrusting, plocoid, with predominantly extramural (rarely intramural) budding. Calices with single center, circular to elliptical in shape, with minimum diameter of 3-4 mm.

Costae moderately developed, equal, continuous. Septa in three cycles, with ca. 24 total septa per corallite. Septa unequal in thickness, with primary and secondary slightly thicker than tertiary. Primary and secondary septa extending to columnella; tertiary free or fused, extending 1/3-3/4 of distance to columnella. Septal faces covered with abundant, cone-shaped, randomly distributed spines. Columella spongy, discontinuous, ca. 1/3 of corallite width. Paliform lobes absent. Wall septothecal, thinner than primary septa. Endothecal and exothecal dissepiments rare, thick. Coenosteum porous. Distance between corallite walls 1.6 mm.

**Etymology.**—Named in honor of the author's daughter, Maitreyi López Alarcon.

**Types.**—Holotype, SUI 100686; paratype, SUI 100685.

**Type Locality.**—Loc. BC 26, Isla Montserrat, Carmen Formation, Baja California Sur, México. Middle Pliocene.

**Measurements (in mm) of the Holotype.**—CL, 9.96; CS, 6.56; CDL, 9.23; CDS, 3.44; NS, 34.33; LSL, 3.68; LW, 0.36; FSL, 0.78; FW, 0.25; SSL, 2.95; SW, 0.41; CL, 1.39; CW, 0.74; NC, 6.16; WT, 1.84.

**Material Examined.**—31 SUI specimens (100685-100686, 101010-101011, 101013-101014, 101018, 102032-102049, 102055-6, 102059, 102066, 102071).

**Occurrence.**—Isla Montserrat (locs. BC 25-27), Carmen Formation.

**Favia maitreyiae** n. sp. is known only from the middle Pliocene of the Isla Montserrat.

**Discussion.**—*Favia maitreyiae* n. sp. is morphologically similar to *Favia* n. sp. aff. dominicensis Budd & Johnson (1999), a Miocene species from the Dominican Republic. It differs primarily from the latter in its septothecal wall, its relatively large corallites, and its higher budding frequency (Table 13).
distributed spines. Columella spongy, \(< ca. \frac{1}{3}\) of corallite width. Paliform lobes absent. Wall septothecal, thinner than primary septa. Endothecal and exothecal dissepiments absent. Distance between corallite walls 0.81 mm.

**Etymology.**—Named in honor of the author’s son, Tulsidas Balam López Alarcon.

**Types.**—Holotype, SUI 100688; paratypes, SUI 100687, 100689.

**Type Locality.**—Loc. BC 15, Puerto de la Lancha, Isla Carmen, San Marcos Formation, Baja California Sur, México. Early Pliocene.

**Measurements (in mm) of the Holotype.**—CL, 7.18; CS, 5.78; CDL, 8.33; CDS, 7.35; NS, 22.83; LSL, 2.55; LW, 0.33; FSL, 1.46; FW, 0.25; SSL, 1.96; SW, 0.28; CL, 1.11; CW, 0.48; NC, 6.16; WT, 1.8.

**Material Examined.**—16 SUI specimens (100687-100689, 102132, 102142-102147, 102149-102151, 102163-102164, 102167).

**Occurrence.**—Puerto de la Lancha (loc. BC 15), San Marcos Formation.

*Favia tulsidasi* n. sp. is known only from the early Pliocene of Puerto de la Lancha at Isla Carmen.

**Discussion.**—*Favia tulsidasi* n. sp. is morphologically similar to *Favia vokesae* Budd & Johnson, 1999, a Miocene to Pliocene species from the Dominican Republic and Costa Rica, and to *F. fragum*, a Late Miocene to Recent Caribbean species. *Favia tulsidasi* n. sp. is distinguished by its septothecal wall, smaller single center corallites, and fewer septa (Table 13).

**Genus DIPLORIA** Milne Edwards & Haime, 1848

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**Table 13. Morphologic characters distinguishing species of Favia.**

<table>
<thead>
<tr>
<th>Species</th>
<th>Distribution</th>
<th>Colony form</th>
<th>Corallite diameter (mm)</th>
<th>Corallite shape</th>
<th>Centers per corallite</th>
<th>Additional references*</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>F. maitreyiae</em> n. sp.</td>
<td>middle Pliocene; Isla Montserrat, Gulf of California</td>
<td>plocoid</td>
<td>6-8</td>
<td>angular to rounded</td>
<td>1-3</td>
<td>--</td>
</tr>
<tr>
<td><em>F. tulsidasi</em> n. sp.</td>
<td>early Pliocene, Isla Carmen, Gulf of California</td>
<td>plocoid</td>
<td>3-4</td>
<td>rounded</td>
<td>1</td>
<td>--</td>
</tr>
<tr>
<td><em>F. dominicensis</em> Vaughan, 1925</td>
<td>early Miocene to middle Miocene; Dominican Republic</td>
<td>plocoid</td>
<td>5-8</td>
<td>angular</td>
<td>1-2</td>
<td>2, 3, 4, 6</td>
</tr>
<tr>
<td><em>F. fragum</em> (Esper, 1795)</td>
<td>late Pliocene to Recent; Caribbean</td>
<td>plocoid</td>
<td>2.5-3.5</td>
<td>rounded</td>
<td>1-2</td>
<td>4, 5, 6</td>
</tr>
<tr>
<td><em>F. gravida</em> Verrill, 1868</td>
<td>Recent; Brazil</td>
<td>plocoid</td>
<td>2.5-4</td>
<td>rounded</td>
<td>4-6</td>
<td>1, 4, 6</td>
</tr>
<tr>
<td><em>F. leptophylla</em> Verrill, 1868</td>
<td>Recent; Brazil</td>
<td>plocoid</td>
<td>5-7</td>
<td>rounded</td>
<td>1-3</td>
<td>1, 4, 6</td>
</tr>
<tr>
<td><em>F. aff. dominicensis</em> Budd &amp; Johnson, 1999</td>
<td>lower to middle Miocene; Dominican Republic</td>
<td>plocoid</td>
<td>5-7</td>
<td>angular</td>
<td>1-2</td>
<td>4</td>
</tr>
<tr>
<td><em>F. vokesae</em> Budd &amp; Johnson, 1999</td>
<td>late Miocene to late Pliocene; Dominican Republic, Costa Rica, Bahamas</td>
<td>plocoid</td>
<td>3.5-5</td>
<td>rounded</td>
<td>1-2</td>
<td>4</td>
</tr>
<tr>
<td><em>F. maoadentrensis</em> Budd &amp; Johnson, 1999</td>
<td>late Miocene to early Pliocene; Puerto Rico</td>
<td>meandroid</td>
<td>1.5-5</td>
<td>rounded</td>
<td>1-6</td>
<td>4</td>
</tr>
</tbody>
</table>

*References: 1, Verrill, 1868-1870; 2, Vaughan & Hoffmeister, 1925; 3, Frost & Langenheim, 1974; 4, Budd & Johnson, 1999; 5, Veron, 2000; 6, Budd et al., 1994b.*
**Type Species.**—*Meandrina cerebriformis* Lamarck, 1816.

**Diagnosis.**—Colonies massive, meandroid, formed by intra- and extramural budding. Series long, sinuous, with indistinct centers. Costae well developed. Columella trabecular, continuous. Endothecal dissepiments well developed. Wall structure septothecal. Paliform lobes weakly developed or absent.

**Discussion.**—As shown by Budd & Johnson (1999: 36), the genus is paraphyletic and in need of revision. As known, the genus is represented by three species occurring in the Gulf of Mexico, Caribbean, Bermuda, and western Atlantic, from south Florida to Venezuela.

The first record of *Diploria* was in the late Miocene of the Caribbean (Budd et al., 1994b). According to Budd & Johnson (1999: 42), the upper Cretaceous to Miocene records from Europe (Vaughan & Wells, 1943) are meaningless because the European forms are distinctively different from those in the Caribbean. In the eastern Pacific, the genus consists of *D. bowersi* (Vaughan, 1917) (see below) from the late Miocene of the Gulf of California. Based on the analysis of a large collection of specimens, *D. sarasotana* Weisbord, 1974, is added to the Gulf of California fossil record.

*Diploria bowersi* (Vaughan, 1917)

Pl. 11, Figs 1-2

*Diploria bowersi* Vaughan in Arnold, 1906: 22 (*nomen nudum*).  
*Maeandra bowersi* Vaughan, 1917: 374, pl. 101, figs 1, 1a.

**Description.**—Colonies massive, subhemispherical, permanently attached, intermediate in size (10-30 cm). Colony form meandroid, with variable, long, gently sinuous series formed by multidirectional intra- and extramural budding. Valleys separated by wide (> valley width) porous coenosteum. Valley width small (3-5.5 mm). Calicular platform U-shaped, with medium (2-4 mm) relief.

Costae well developed, equal, continuous, corresponding to all septa. Septa in three cycles, with total number of septa per 5 mm ranging 4-6, equal in thickness. Primary septa extending to columella; secondary and tertiary septa free, variable in development. Columella trabecular, continuous, approximately ⅓ of valley width. Paliform lobes present. Wall septothecal. Endothecal dissepiments rare, vesicular, thin; exothecal dissepiments common, vesicular, thick.

**Type.**—Holotype, USNM 68289, *Diploria bowersi*.

**Material Examined.**—4 SUI specimens (100692, 102295, 102298, 102221); 1 USNM specimen (68289).

**Occurrence.**—Carrizo Creek (loc. USGS 07616), Ensenada El Muerto (loc. BC 35), Isla San José (loc. BC 23).

*Diploria bowersi* occurs in the late Miocene Imperial Formation of south-central California, the early Pliocene San Marcos Formation of Ensenada El Muerto, and Pliocene sediments of Isla San José at the Gulf of California.

**Discussion.**—*Diploria bowersi* resembles *D. labyrinthiformis* (Linnaeus, 1758) from the late Pliocene to Recent in the Caribbean. *Diploria bowersi* is distinguished from *D. labyrinthiformis* by its reduced valley and coenosteum width, its reduced number of septal cycles, and its reduced number of septa per 5 mm.

**Diploria sarasotana** Weisbord, 1974

Pl. 10, Fig. 6

*Diploria sarasotana* Weisbord, 1974: 351-353, pl. 35, figs 1-2, pl. 36, fig 1.

**Description.**—Colonies massive, subhemispherical, permanently attached. Colony form meandroid, with variable, moderately long, sinuous series formed by multidirectional intra- and extramural budding. Valleys contiguous. Valley width medium (5-10 mm). Calicular platform V-shaped, with high (4-10 mm) relief.

Costae well developed, equal, continuous, corresponding to all septa. Septa in three cycles, with total number of septa per 5 mm ranging 6-12, equal in thickness. Primary septa extending to columella; secondary and tertiary septa free, variable in development. Columella trabecular, continuous, approximately ⅓ of valley width. Paliform lobes present. Wall septothecal. Endothecal dissepiments rare, vesicular, thin; exothecal dissepiments common, vesicular, thick.

**Type.**—Holotype, USNM 99999, *Diploria sarasotana*.

**Material Examined.**—2 SUI specimens (100690, 102215); 1 USNM specimen (99999).

**Occurrence.**—Ensenada El Muerto (loc. BC 35).

*Diploria sarasotana* ranges in age from early to Late Pliocene. Outside of the Gulf of California, it occurs in the early to late Pliocene Tamiami Formation, Sarasota, Florida.

**Discussion.**—*Diploria sarasotana* resembles *D. strigosa* (Dana, 1846) from the Pliocene to Recent in the Caribbean. *Diploria sarasotana* is distinguished from *D. strigosa* by its fewer septa.
and wider valley.

Genus **Solenastrea** Milne Edwards & Haime, 1848

**Type Species.**—*Astrea turonensis* Michelin, 1847, by subsequent designation (Wells, 1956).

**Diagnosis.**—Colonies massive, hemispherical or encrusting with irregular upgrowths, plocoid. Costae poorly developed. Coenosteum trabecular. Columella trabecular. Paliform lobes present.

**Discussion.**—The genus is represented by two uncommon but widely distributed species occurring in the Caribbean and western Atlantic, from North Carolina to Venezuela. The eastern Pacific, Durham & Barnard (1952) described *Solenastrea ecuardoriana* on the basis of a single beachworn specimen thought to have been collected on the shore at Isla La Plata, Ecuador, although detailed analysis (Wells, 1983) suggested that it is only a beachworn fragment of *Pavona clavus*.

The first record of *Solenastrea* was in the Oligocene of Europe (Vaughan & Wells, 1943). During the early Miocene, it ranged from the Mediterranean to the Caribbean, but the genus disappeared in the Mediterranean by the end of the Miocene (Budd, 1991). According to Budd (1991), the genus consisted of three species in the Caribbean and western Atlantic: *S. hyades*, *S. bournoni*, and *S. fairbanksi*. The former two species extended from Miocene to Recent time, whereas *S. fairbanksi* apparently was restricted to the late Miocene to Pliocene of the Gulf of California (Vaughan, 1917; Jordan & Hertlein, 1926; Hertlein & Emerson, 1959). *Solenastrea fairbanksi* was questionably synonymized with *S. bournoni* on the basis of corallite similarity, however, based on both character measurement and thin-section analysis of a larger sample size, the two species were considered as different (see Results). Therefore, in the eastern Pacific, the genus consists solely of *S. fairbanksi*, which arose in the middle Miocene of Isla Tiburón (Gastil et al., 1999). During the late Miocene-early Pliocene to middle Pliocene, its distribution ranged from south-central California to Isla María Madre (Vaughan, 1917; Jordan & Hertlein, 1926; Hertlein & Emerson, 1959) and questionably to Cartagena, Colombia (Vaughan, 1919).

*Solenastrea fairbanksi* (Vaughan, 1900)

Pl. 11, Figs 3-7

*Stephanocoenia* fairbanksi Vaughan, 1900: 151, pl. 17, figs 11, 11a.
*Stephanocoenia* fairbanksi var. **columnaris** Vaughan, 1900: 151, pl. 17, figs 10, 10a.
*Solenastrea* fairbanksi var. **normalis** Vaughan, 1917: 373, pl. 96, figs 2, 2a-c, pl. 97, figs 1, 1a.
*Solenastrea* fairbanksi var. **minor** Vaughan, 1917: 373, pl. 97, figs 2, 2a-c.

**Description.**—Colonies massive, hemispherical or encrusting with occasional irregular upgrowths, or columnar. Colony surface usually smooth, well rounded. Epitheca absent to weak. Costae elongate, extending to colony edge. Calices generally circular, but corallites at level of coenosteum often polygonal. Calices of intermediate size (2.5-2.8 mm), moderate in depth, moderately spaced (2.6-3.4 mm). Size, theca thickness, and distance between neighboring corallites highly variable at colony level and among colonies from same locality. Corallite wall slightly elevated.

Costae short, subequal, alternating, minutely granulose on surface, extending or not to those of adjacent calices. Septa in 3 cycles, 24 in number, with first and second usually extending to colulmella. First and second cycles equal to subequal in thickness, thicker at wall, each thicker than third cycle. Third cycle ¼-¾ length of second cycle, fused or not to second; when free, larger tertiary septa tending to curve toward second cycle. Spines small, evenly distributed in septal sides. Columella trabecular, usually formed by inner ends of those septa that reach columella. Paliform lobes well developed before both first and second cycles; when tertiary septa fuse with secondary septa, pali are better developed before second cycle.


**Measurements (in mm)** of Syntype USNM 68283A.—CRL 2.85, CRS 2.61, CDL 3.77, CDS 2.73, NS 23, LSL 0.95, LW 0.11, FSL 0.57, FW 0.075, CL 0.25, CW 0.22, SD1 0.57, SD2 0.51, NC 6.33, WT 0.44.


**Occurrence.**—Barrett Canyon (loc. USGS 7616), Coyote Mountains (loc. UCLA 631), Alverson Canyon (loc. USGS
Table 14. Morphologic characters distinguishing species of Solenastrea.

<table>
<thead>
<tr>
<th>Species</th>
<th>Distribution</th>
<th>Corallite diameter (mm)</th>
<th>Third cycle</th>
<th>Wall thickness (mm)</th>
<th>Additional references*</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. fairbanksi</em> (Vaughan, 1900)</td>
<td>?middle Miocene to middle Pliocene; Gulf of California, ?Colombia</td>
<td>2.7-2.9</td>
<td>fused or free</td>
<td>thin (0.3-0.038)</td>
<td>1, 4</td>
</tr>
<tr>
<td><em>S. hyades</em> (Dana, 1846)</td>
<td>early Miocene to Recent; Caribbean, North Carolina, Venezuela</td>
<td>2.3-2.8</td>
<td>fused</td>
<td>thick (0.8-1)</td>
<td>2, 3, 4</td>
</tr>
<tr>
<td><em>S. bournoni</em> Milne Edwards &amp; Haime, 1849</td>
<td>late Oligocene to Recent; Caribbean, Florida, Venezuela</td>
<td>2.1-2.3</td>
<td>free</td>
<td>intermediate (0.57-0.63)</td>
<td>2, 3, 4</td>
</tr>
</tbody>
</table>


Distribution.—*Solenastrea fairbanksi* ranges in age from middle Miocene to middle Pliocene. It occurs in the middle Miocene of Isla Tiburón (Gastil et al., 1999), the late Miocene-early Pliocene Imperial Formation of south-central California, the San Marcos Formation of Puerto de la Lancha at Isla Carmen, Punta Chivato, and Ensenada El Muerto, the early to middle Pliocene El Refugio Formation of Rancho Los Algodones, the middle Pliocene sediments of Isla María Madre (Jordan & Hertlein, 1926; Hertlein & Emerson, 1959), and in Pliocene sediments of Isla San José. It was doubtfully recorded at Isla Cerralvo, México (Emerson & Hertlein, 1964), and Cartagena, Colombia (Vaughan, 1919).

Discussion.—Calice size and the measures related to the distance between corallites (WT, CDL, CDS) are highly plastic in this species. In this regard, Vaughan (1917) recognized the closeness of this species with *Solenastrea hyades* and *S. bournoni* from the Caribbean and western Atlantic. Later, Budd (1991) questionably synonymized *S. fairbanksi* with *S. bournoni* based on the occurrence of corallites resembling those of *S. bournoni* in the upper surface and center of larger colonies of *S. fairbanksi*. The analysis of a larger suite of colonies reveals that such similarity mainly resulted from the top to bottom colony variability already recognized by Budd (1991). Small corallites resembling those of *S. bournoni* are likely to occur in the upper surface and crowded sites of larger colonies of *S. fairbanksi*. The corallites of the former species have a complete septal cycle. In smaller corallites of *S. fairbanksi*, the third cycle is often incomplete, presenting 20-22 septa.

There are no clear trends across varieties as recognized by Vaughan (1900, 1917) because colonies appear scattered throughout the plot. However, there are clear differences among localities. In general, Punta Chivato specimens have polygonal calices, larger corallites, and a small distance between calices; in contrast, colonies recovered from Rancho Algodones have circular corallites and larger distance between calices. As noticed by Budd (1991), corallites increase in size from colony top to bottom, but there is no clear trend in spacing or costae.

*Solenastrea fairbanksi* is distinguished from *S. hyades* (Pl. 12, Figs 1-3) by its larger, more regular, and well rounded colonies, its smaller calices, and the fused third septal cycle of the latter species. Its colony form resembles that of *S. bournoni* (Pl. 11, Figs 8-9), but is distinguished from the latter species on the basis of its larger calices, its better developed third septal cycle, its smaller corallite spacing, and the free third septal cycle (Table 14).

Family MEANDRINIDAE Gray, 1847
Genus *DICHOCOENIA* Milne Edwards & Haime, 1848

Type Species.—*Dichocoenia stokesi* Milne Edwards & Haime, 1848

Diagnosis.—Colonies massive, hemispherical or platy, plocoid or plocomeandroid. Budding intramural, mono- to tristomeodal. Costae poorly developed. Coenosteum granulose. Columella trabecular.

Discussion.—The genus is represented by two widely distributed species occurring in the Caribbean, Gulf of Mexico, and western Atlantic, from southern Florida to Venezuela.

The first record of *Dichocoenia* was in the upper Cretaceous of the Caribbean, but in the Miocene, it ranged from the Mediterranean to the Caribbean (Vaughan & Wells, 1943). In the Caribbean and western Atlantic, the genus consisted of
six species: *D. caloosahatcheensis*, *D. stokesi*, *D. eminens*, *D. tuberosa* Duncan, 1863, and *Dichocoenia stellaris* Milne Edwards & Haime, 1849, the former two extending from the Pliocene to the Recent. In the eastern Pacific, the genus consisted of *D. merriami* from the late Miocene to early Pliocene of southern California Imperial Formation; however, based on the analysis of a large collection of specimens, *D. eminens* is added to the Gulf of California fossil record.

**Dichocoenia merriami** (Vaughan, 1900)  
Pl. 12, Figs 4-6, Pl. 13, Figs 7-8

*Favia merriami* Vaughan, 1900: 142, pl. 15, figs 5, 5a-c.  
*Dichocoenia merriami* var. *crassisepta* Vaughan, 1917: 371, pl. 94, figs 3, 3a.

**Description.**—Colonies plocoid, rarely meandroid, subspherical, massive, or platy, with undulated surface. Budding intratentacular, with 1-2 (rarely 3) centers. Calices circular to elliptical with compressed sides, rarely trilobate, small to intermediate in size (1.5-12.1 mm in length), with small (0.5-4.5 mm) interthecal distance, high intracolonial variation; theca elevation small (1-3.9 mm in exertness). Septal number: one center, 20-38; two centers, 39-58; three centers, 57-117. Faces smooth, granulated, with 3 (rarely 4) complete cycles; first and second cycles reaching columella, equal to subequal in thickness; third cycle ⅔-⅚ of length of first cycle; when present, fourth cycle < ⅓ of first cycle. Paliform lobes usually in front of first and second cycles, weakly developed. Costae alternate, corresponding to septa, weakly developed. Wall septothecal. Columella tubercle present, trabecular, continuous, between centers in form of axial lamella.

**Types.**—Hypotype, USNM M325289, *Dichocoenia merriami*; holotype, M325291, *D. merriami* var. *crassisepta*.

**Measurements (in mm) of the hypotype.**—CL 7.90, CS 4.55, NS 35.75, LL 2.01, LW 0.51, ML 1.3, MW 0.23, CT 1.26, WT 2.66, CE 1.79.

**Material examined.**—44 SUI specimens (15625, 15628, 100614, 100623, 100628, 100633, 100832, 100841, 100842, 100891, 102159-102161, 102225-102233, 102267-102271, 102278-102280, 102282-102289, 102291, 102294, 102298, 102404, 102505-102506); 8 NHMLAC specimens (002-1-009-1); 2 USNM specimens (M325289, M325291).

**Occurrence.**—Barrett Canyon (loc. USGS 7616), Coyote Mountains (loc. UCLA 631), Alverson Canyon (loc. USGS 3923), Ensenada El Muerto (loc. BC 35), Las Barracas (loc. BC2), Isla San José (loc. BC 22).

**Discussion.**—In describing *Dichocoenia merriami* affinities, Vaughan (1917) mentioned the morphologic closeness with *D. stokesi* (Pl. 13, Figs 1-3), and with a species later described as *D. caloosahatcheensis* (Pl. 12, Figs 7-9). Morphometric analysis of calices with one, two, and three centers showed a high similarity among the three species, nonetheless when standardized by largest calical diameter/number of centers per corallite (CRL/C), species formed distinct meaningful groups. In general, morphologic differences among species are so slight and morphologic variability so large, that in the opinions of Vaughan (1917) and Weisbord (1974), they might be considered the same or variants; however, the attachment of *D. caloosahatcheensis* is peduncular (Pl. 12, Fig. 8) and it has fewer septa than *D. stokesi* and *D. merriami*; *D. stokesi* has long, relatively thin calices and a thinner columella than *D. merriami* (Table 15).

**Dichocoenia eminens** Weisbord, 1974  
Pl. 12, Figs 10-12, Pl. 13, Figs 4-6

*Favia eminens* Weisbord, 1974: 426-433, pl. 53, figs 1-3, pl. 54, figs 1-2, pl. 55, figs 1-3.

**Description.**—Colonies plocoid to meandroid, subspherical, massive. Budding intratentacular; one to three centers. Attachment peduncular. Calices circular to elliptical, intermediate in size (6.5-32.6 mm in length), with large (2.5-11.3 mm) interthecal distance; thecal elevation large (2.5-7.5 mm in exertness). Septal number: one center, 36-44; two centers, 46-103; three centers, 62-120; smooth, granulated faces; three (rarely four) complete cycles; first and second reaching columella, with first thickest; third cycle ⅔ length of first; fourth cycle when present < ¼ of first. Paliform lobes usually in front of first and second cycles, weakly developed. Costae alternate, corresponding to septa, weakly developed. Wall septothecal. Columella tubercle present, trabecular, continuous, between centers in form of axial lamella.

**Types.**—Paratype, USNM M325293, *Dichocoenia eminens*; paratype, USNM M325305, *D. eminens*.

**Measurements (in mm) of Paratype USNM M325293.**—CL 9.21, CS 4.64, NS 44.66, LL 1.9, LW 0.33, ML 1.05, MW 0.13, CT 1.33, WT 11.63, CE 8.99.

**Material Examined.**—31 SUI specimens (100612, 100617, 100630-100631, 100815-100816, 100818, 100828, 102222,
Dichocoenia eminens ranges in age from late Miocene-early Pliocene to early Pleistocene. Outside of the Gulf of California, it occurs in the early to late Pliocene Quebrada Chocolate Formation and Quebrada Chocolate of Costa Rica, early to late Pliocene Tamiami Formation of Sarasota, Florida, late Pliocene Shark’s Hole Formation of Isla Barrientos, Panama, and in the early Pleistocene Caloosahatchee Formation of Shell Creek, Florida.

Discussion.—Dichocoenia eminens is easily distinguished from D. merriami by its long protuberant corallites and prominent costae. Nonetheless, in the Caribbean, it is morphologically similar to Barysmilia intermedia Duncan, 1863, and D. tuberosa was further synonymized with D. stokesi by Gregory (1895). As demonstrated by the morphometric analysis (Text-fig. 21), however, corallites of D. stokesi are smaller and less protuberant than in D. eminens, whereas D. tuberosa has a smaller corallite diameter (Table 15).

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Table 15. Morphologic characters distinguishing species of Dichocoenia.

<table>
<thead>
<tr>
<th>Species</th>
<th>Distribution</th>
<th>Attachment</th>
<th>Size/# centers per corallite (mm)</th>
<th>Theca elevation (mm)</th>
<th>Wall thickness (mm)</th>
<th>Additional references*</th>
</tr>
</thead>
<tbody>
<tr>
<td>D. merriami</td>
<td>Late Miocene to late Pliocene; Gulf of California</td>
<td>flat</td>
<td>6.7-7.5</td>
<td>1.5-2.1</td>
<td>3.2-3.8</td>
<td>2, 4, 5</td>
</tr>
<tr>
<td>(Vaughan, 1900)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>D. stokesi</td>
<td>early Pliocene to Recent; Caribbean, Florida, Venezuela</td>
<td>flat</td>
<td>6.3-9.3</td>
<td>2.7-2.8</td>
<td>2.7-3.3</td>
<td>4, 5</td>
</tr>
<tr>
<td>Milne Edwards &amp; Haime, 1848</td>
<td></td>
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<tr>
<td>D. caloosahatcheensis</td>
<td>early Pliocene to early Pleistocene; Dominican Republic, Curacao, Florida, Costa Rica</td>
<td>pedunculate</td>
<td>5.8-6.4</td>
<td>2.5-2.7</td>
<td>1.8-3.8</td>
<td>2, 4, 5</td>
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<td>Weisbord, 1974</td>
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<tr>
<td>D. eminens</td>
<td>early Pliocene to early Pleistocene; Caribbean, Costa Rica, Florida, Panama</td>
<td>pedunculate</td>
<td>9.5-10.5</td>
<td>6.5-7.5</td>
<td>7.2-8.7</td>
<td>3, 4, 5</td>
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<td>Weisbord, 1974</td>
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<tr>
<td>D. tuberosa</td>
<td>Late Miocene; Dominican Republic, Costa Rica</td>
<td>pedunculate</td>
<td>2.5-3</td>
<td>5-6.8</td>
<td>6.5-8</td>
<td>1, 2, 3, 4, 5</td>
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<tr>
<td>Duncan, 1863</td>
<td></td>
<td></td>
<td></td>
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</table>

*References: 1 = Duncan, 1863; 2 = Vaughan, 1917; 3 = Vaughan, 1919; 4 = Weisbord, 1974; 5 = Budd et al. (1994b).
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**APPENDIX 1**

Locality register, with global positioning satellite coordinates taken between June 2002 and January 2005 for each locality.

BC 1, South Punta Chivato; elevation 6 m; N27°04.382',
BC 12, Punta Baja, Isla Carmen; elevation 10 m; N25°49.139', W111°12.870'. Geologic age: late Pleistocene. Faunal list: *Porites panamensis*.


BC 15, Puerto de la Lancha, Isla Carmen; elevation 30 m; N26°03.284', W111°06.372'. Formation: San Marcos. Geologic age: early Pliocene. Faunal list: *Porites panamensis*, *Por. carrizensis*, *Solenastrea fairbanksi*, *Siderastrea annae* n. sp., *Favia tuloidasi* n. sp.

BC 16, Bahía Oto, Isla Carmen; elevation 7 m; N26°02.550', W111°09.730'. Formation: Carmen. Geologic age: middle to late? Pliocene, 3.1-1.8 Ma. Faunal list: *Porites panamensis*.

BC 17, Puerto Balandra 1, Isla Carmen; elevation 2 m; N26°01.395', W111°09.960'. Geologic age: late Pleistocene. Faunal list: *Porites panamensis*.

BC 18, Puerto Balandra 2, Isla Carmen; elevation 1 m; N26°00.949', W111°09.843'. Geologic age, late Pleistocene. Faunal list: *Porites panamensis*.


BC 20, Timbabichi; elevation 5 m; N25°16.756', W110°56.004'. Geologic age: late Pleistocene. Faunal list: *Porites panamensis*, *Pocillopora capitata*, *Por. damicornis*, *Ps. elegans*, *Por. verrucosa*.


BC 22, Isla San José 1; elevation 56 m; N25°01.168', W111°35.172'. Geologic age: middle Pliocene. Faunal list: *Dichocoenia merriami*.

BC 23, Isla San José 2; elevation 105 m; N25°00.737', W110°34.856'. Geologic age: middle Pliocene. Faunal list: *Solenastrea fairbanksi*, *Diploria boursi*.


BC 26, Isla Montserrat 3; elevation 213 m; N25°40.470', W111°01.837'. Formation: Carmen. Geologic age: middle to late? Pliocene. Faunal list: *Porites panamensis*, *Pocillopora capitata*, *Favia maitreyiae* n. sp.

BC 27, Isla Montserrat 4; elevation 202 m; N25°40.520', W111°01.784'. Formation: Carmen. Geologic age: middle to late? Pliocene. Faunal list: *Porites panamensis*, *Pocillopora capitata*, *Favia maitreyiae* n. sp.

BC 28, La Ventana 3; elevation 15 m; N24°02.474', W109°49.577'. Geologic age: middle? Pleistocene. Faunal list: *Porites panamensis*.

BC 29, La Ventana 4; elevation 21 m; N24°02.200', W109°49.332'. Geologic age: middle? Pleistocene. Faunal list: *Porites panamensis*.

BC 30, La Ventana 5; elevation 19 m; N24°02.033', W109°49.175'. Geologic age: middle? Pleistocene. Faunal list: *Porites panamensis*, *Ps. clavus*.


BC 32, La Ventana 7; elevation 54 m; N24°01.834', W109°49.130'. Geologic age: early Pleistocene. Faunal list: *Porites panamensis*.
Pavona clavus.

BC 33, Las Animas 3; elevation 17 m; N24°32.672', W110°44.358'.
Geologic age: late Pleistocene. Faunal list: Porites panamensis, Pocillopora capitata, Poc. damicornis, Psammocora stellata.

BC 34, El Bajo; elevation 10 m; N26°06.085', W111°19.626'.
Geologic age: late Pleistocene. Faunal list: Porites panamensis.


BC 36, Isla Coronados 1; elevation 9.8 m; N26°06.718', W111°16.670'. Geologic age: late Pleistocene. Faunal list: Porites panamensis, Pocillopora capitata.

BC 37, Isla Coronados 2; elevation 11.95 m; N26°06.719', W111°16.665'. Geologic age: late Pleistocene. Faunal list: Porites panamensis, Psammocora stellata.

BC 38, Cañada Coronados, Isla Coronados; elevation 12-14 m; N26°06.563', W111°16.376'. Geologic age: late Pleistocene. Faunal list: Porites panamensis, Pavona clavus, Pav. gigantea.


BC 40, Isla Coronados 5; elevation 17.5 m; N26°06.502', W111°16.198'. Geologic age: middle Pleistocene. Faunal list: Porites panamensis, Pocillopora capitata.

BC 41, Isla Coronados 6; elevation 19.5 m; N26°06.499', W111°16.165'. Geologic age: middle Pleistocene. Faunal list: Porites panamensis, Pocillopora capitata, Poc. elegans, Pavona gigantea.

BC 42, Isla Coronados 7; elevation 22.5 m; N26°06.708', W111°16.158'. Geologic age: middle Pleistocene. Faunal list: Porites panamensis, Pocillopora capitata.

BC 43, Isla Coronados 8; elevation 23.95 m; N26°06.713', W111°16.164'. Geologic age: middle Pleistocene. Faunal list: Porites panamensis.


PLATES
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<td>Pocillopora damicornis (Linnaeus, 1758), figured specimens, Late Pleistocene, Baja California Sur, México. Scale bars = 1 cm.</td>
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</tr>
<tr>
<td>3. SUI 100625. Locality BC 5, Timbabichi.</td>
<td>25</td>
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<td>4. SUI 100626. Locality BC 8, Cabo Pulmo.</td>
<td>25</td>
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<tr>
<td>3. Pocillopora capitata Verrill, 1864, figured specimen, SUI 100627, Late Pleistocene, locality BC 10, La Ventana, Baja California Sur, México. Scale bar = 1 cm.</td>
<td>22</td>
</tr>
<tr>
<td>4. Pocillopora elegans Dana, 1846, figured specimens, Baja California Sur, México. Scale bars = 1 cm.</td>
<td>26</td>
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<td>4-5. SUI 100629. Late Pleistocene, locality BC 41, Isla Coronados.</td>
<td>26</td>
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<td>6. SUI 100632. Recent, El Bajo, Loreto.</td>
<td>26</td>
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<td>7. SUI 100658. Late Pleistocene, locality BC 5, Timbabichi.</td>
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