Invertebrate Megafossils of Pleistocene (Sangamon Interglacial) Age From Isla de Guadalupe, Baja California, Mexico

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INTRODUCTION

The presence of marine invertebrate fossils on the dominantly volcanic Isla de Guadalupe, Mexico (29° N, 118° 20′ W), approximately 275 km off the west central coast of Baja California, has been mentioned periodically in the literature (Johnson 1953, Chace 1958, Squires 1959, Hubbs 1960, 1967, Goldberg 1965, Hubbs and Jehl 1976). Johnson (1953: 235) reported an Isla de Guadalupe "upper Tertiary or Quaternary" marine faunule "from the Melpomene Cove seacliff, about 75 feet above sea level and interbedded within the pyroclastic series" (Fig. 1). Johnson considered the stratification and cross-bedding of the sequence to be suggestive of water deposition. Fossils reported from this deposit were an unidentified gastropod, echinoid spines, fish scales, and foraminifera, the latter apparently serving as the basis for the general age assignment. We have not reinvestigated this locality, but if the description is accurate, especially regarding elevation and interbedding, we suspect it to be of a different age and depositional history than the unit described herein.

In 1957 Carl L. Hubbs and Emery P. Chace discovered a fossiliferous sedimentary deposit near the island's present sea level. Collections were made then and on subsequent trips in 1960, 1963, 1965, 1966, and 1969. On the basis of part of these collections, Chace (1958) first reported the presence of a warm-water Pleistocene faunule on Isla de Guadalupe. A hermatypic coral and echinoid spines from this faunule were sent to J. W. Durham at Berkeley in 1958 and several times subsequently. A sample of the coral was sent by Chace to D. F. Squires, who noted (Squires 1959:339) that it was "a remarkable occurrence of *Pocillopora* . . . apparently closely related to *P. palmata* Palmer, and specimens of *P. robusta* Verrill," indicating "a northern shift of approximately 8 degrees of latitude from the most northerly occurrence of *Pocillopora* outside the Gulf of California at the present time." Goldberg (1965:R126) dated a sample of the Guadalupe *Pocillopora* obtained from Hubbs as "130,000 years [before present] by the uranium 234:thorium-230 technique and 110,000 years by the uranium-234:uranium-238 technique." Edward C. Wilson and Hubbs conducted further, unpublished, studies on fossils obtained from the deposit. In June of 1975, David R. Lindberg visited Isla de Guadalupe and collected invertebrate fossils from a previously unstudied locality belonging to the same unit. Specimens studied are deposited in the Department of Paleontology, San Diego Museum of Natural History (SDMNH), San Diego, California; Department of Geology, California Academy of Sciences (CASG), San Francisco, California; and the University of California Museum of Paleontology (UCMP), Berkeley, California. In the appendix to this paper, the *Pocillopora* species is described as new (Durham 1980).

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[3] Deceased, 30 June 1979.

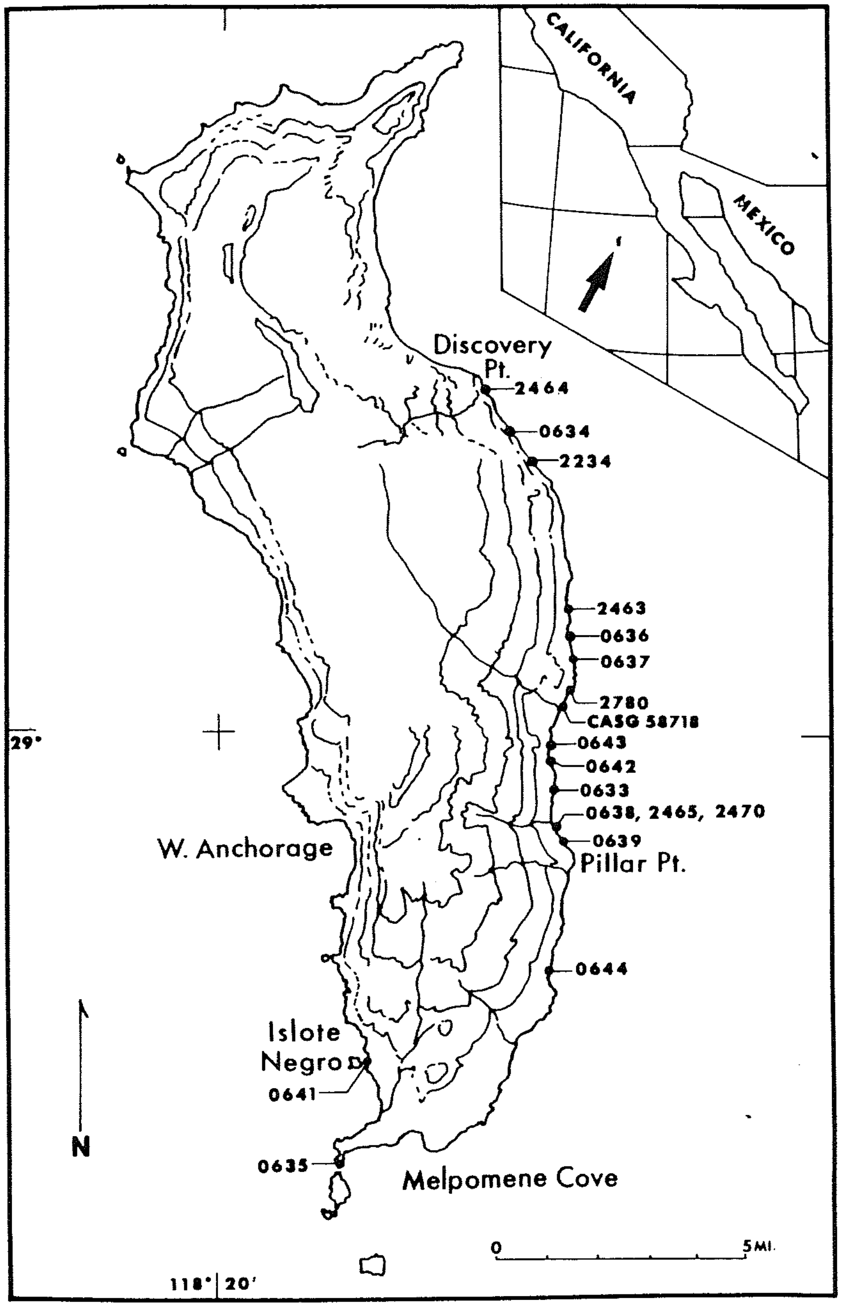

FIGURE 1. *Map of Isla de Guadalupe, Baja California, Mexico, showing features referred to in text and Pleistocene fossil localities.*

THE DISCOVERY POINT FORMATION

Isla de Guadalupe rises steeply over 4,500 m from the ocean bottom with its highest point approximately 1,524 m above sea level. It is one of few emergent volcanoes of the Baja California Seamount province (Menard 1955) and rests upon a basement of oceanic crust supposed, on paleomagnetic evidence, to be 12 million years of age or older (Doyle and Gorsline 1977). Batiza (1977) cites unpublished work by H. W. Menard indicating that Isla de Guadalupe is flanked symmetrically by magnetic anomaly 5B, 15.5 million years old, and is built on the axis of an extinct spreading center. Approximately 80 km of deep ocean separate Isla de Guadalupe from the continental crust of the margin of the Baja California borderland (Doyle and Gorsline 1977: fig. 1). The island consists of two partly overlapping shield volcanoes that are overlain by a thick series of flank and fissure eruptions. The northern shield volcano is the younger of the two (Batiza 1977); its oldest exposed rocks are subaerial flows of alkali olivine basalt that have been radiometrically dated at 7 ±2 million years before present (Engel and Engel 1971). This places the island in existence since at least the latest Miocene epoch (Berggren and Van Couvering 1974: fig. 1).

The fossiliferous rocks at low elevation consist of coarsely clastic sediments that grade laterally from conglomerate, locally with pebbles of volcanic origin, to a biostrome formed chiefly of hermatypic coral fragments and mollusk shells. It is partly concealed by younger shoreline talus deposits which occur at the base of the steep cliffs surrounding much of the island. At most localities there seems to be no Pleistocene wave-cut bench, terrace, or platform. Exposed subaerial lava flows are erosionally truncated at and near present sea level. The sediments are moderately to well indurated, usually with calcitic cement. There is no basal conglomerate like those which characterize many deposits of similar age on the mainland. In places one can see the irregular contact between the sediments and eroded surfaces of the lava. Interbedding as described by Johnson (1953) at the Melpomene Cove locality was nowhere observed.

The name "Discovery Point Formation" was proposed and the deposit described by Wilson and Hubbs, in manuscript, as follows:

> The type section of the formation is at Discovery Point [Fig. 1] on the east shore of the island. A description of this locality and the nature of the formation there is given in the locality register (SDMNH Locality 0634) [included below]. The Discovery Point Formation extends discontinuously along much of the eastern side of Isla Guadalupe, around the southern end, and up the western side at least as far as Islote Negro. The west side of the island was investigated only for about 1 km north of the south end at Islote Negro, at West Anchorage, and briefly at a few other spots. At some localities where [the deposit] lies between large blocks of talus close to sea level, it is thick enough for sea caves to have been formed in it. These caves may be highly fossiliferous, with fossils on the ceilings, walls, and floors. At other localities, the formation is only a few inches in thickness, coating the talus or ledges along the seashore. Some former exposures seem to have been covered by recent talus slides and many exposures must have been destroyed by wave action. The existing exposures extend from the present sea level to about 1 to 8 meters above the present high tide line. The uniform distribution of the formation suggests that the island has been tectonically stable since at least Pleistocene times. It has not been determined whether or not the formation extends into the submarine area or if there are submerged terraces. Divers operating around the island have not reported fossils.

Although the deposit is at and near present sea level, the fossils and lithology indicate that it was laid down subtidally, and this is consistent with higher former sea levels inferred for the Sangamon interglacial stage.

LITHOLOGY

The fossiliferous matrix from Locality CASG 58718 consists of a poorly indurated, tan, arenaceous, pebble conglomerate consisting predominantly of angular grains of volcanic rock, comminuted shell debris, and quartz and lava sand. A smaller number of rounded to subrounded grains are present. The rock is highly porous and the sand grains and pebbles are coated with clay. A hand specimen from Locality SDMNH 0634 is well indurated and contains a higher proportion of shell debris and a few pumiceous clasts in addition to angular to subangular volcanic pebbles. The pebbles are mostly scoriaceous. Angular quartz grains, some showing striations on unworn crystal faces, are present. The rock is cemented by tan to pinkish gray calcite, presumably redeposited from the detrital invertebrate remains.

In composition and fabric, both these rock samples suggest deposition in shallow subtidal depths, following minor mechanical sorting, with source rocks no great distance from the deposit. The angular lithic fragments and quartz grains appear to have undergone little transport or mechanical abrasion. A component interpreted as beach rubble is present. Rounded clasts in the sample from CASG 58718 are almost certainly wave-worn. They and some of the marine invertebrate remains may have been transported onshore initially by waves, as occurs at present. Lindberg, for example, at Isla de Guadalupe in June 1975, observed storm-generated waves tossing onshore living *Tegula regina* (Stearns 1892), a gastropod which lives at depths of 9 m and more (McLean 1969). Material deposited in the intertidal zone would have been removed by subsequent wave scouring before induration could occur. The clay component coating the pebbles and sand grains was probably distributed interstitially at a later time.

The topographic setting was similar to the island's present periphery, where steep cliffs shed landslide debris into the intertidal and supratidal zones. Additional terrestrial debris is introduced into these zones as sediments carried down the arroyos which transect the island. Some reworking of the sediments by wave action has been suggested (Hubbs and Jehl 1976), but the dominance of angular grains in the sample from CASG 58718 indicates that, for this site at least, reworking was minimal. Shells of minute, delicate gastropods and bivalves, which are present intact in several samples, and unworn foraminiferan tests, give no evidence of reworking.

REGISTER OF LOCALITIES

All localities refer to Isla de Guadalupe, Baja California, Mexico. (Abbreviations: SDMNH—San Diego Museum of Natural History, Department of Paleontology; CASG—California Academy of Sciences, Department of Geology; UCMP—University of California, Berkeley, Museum of Paleontology.)

SDMNH 0633. East side of island; north edge of large sea cave, approximately ½ inch south of 29° latitude line on U. S. Hydrographic Office map 1688 (1962). Coll. E. C. Wilson, 2 March 1965.

SDMNH 0634. East side of island; conglomerate from ceiling of Discovery Cave, approximately 2¼ inches north of 29° latitude line and opposite "50" fathom sign on U. S. Hydrographic Office map 1688 (1962). Coll. E. C. Wilson, 1 March 1965.

SDMNH 0635. East side of island; intertidal conglomerate at center of northernmost of two small islands due south of the weather station. At low tide the islands form a peninsula as shown on U. S. Hydrographic Office map 1688 (1962), north to Isla de Adentro and west of the "G" in "Good landing." Coll. E. C. Wilson, 3 March 1965.

SDMNH 0636. East side of island; estimate 6.4 km south of SDMNH 0634. Coll. E. C. Wilson, 1 March 1965.

SDMNH 0637. East side of island; approximately 0.16 km north of large sea cave and 0.8 km south of the Nursery, 4 to 6 m above sea level. Coll. C. L. Hubbs *et al.*, 1 March 1965.

SDMNH 0638. East side of island; coquina between two caves approximately halfway between Pillar Point and the point midway between Pillar and Red Cinder Cone Points, just south of a canyon. Coll. C. L. Hubbs *et al.*, 25 April 1963.

SDMNH 0639. East side of island; coquina, approximately 0.5 km north of Pillar Point. Coll. C. L. Hubbs *et al.*, 25 April 1963.

SDMNH 0640. Exact locality unknown. Coll. E. P. Chace and C. L. Hubbs, 17 December 1957.

SDMNH 0641. West side of the island; coquina, southern end, east side of Islote Negro, 3 to 6 m above sea level, formed in two rock slides. Coll. C. L. Hubbs, 19 April 1957.

SDMNH 0642. East side of island; 28° 59.6′ N, 118° 13.6′ W (Hydrographic Office map 1688 [1956]), cliff talus, 1 to 5 m above sea level. Coll. C. L. Hubbs *et al.*, 27 January 1957.

SDMNH 0643. East side of island; 28° 59′ 25″ N. Coll. C. L. Hubbs and E. P. Chace, 17 December 1957.

SDMNH 0644. East side of island; 28° 56′ 18″ N. Coll. C. L. Hubbs and E. P. Chace, 17 December 1957.

SDMNH 0645. East side of island; about midway on the island. In cliff, 1 to 5 m above high tide line. Coll. C. L. Hubbs, January 1960.

SDMNH 2233. East side of island; within 0.8 km of 29° 4.7′ N (Hydrographic Office map 1688 [1956]), between Discovery and Dyke Points, southerly of two exposures. Coll. C. L. Hubbs, 2 April 1966.

SDMNH 2234. As SDMNH 2233, but northerly of two exposures. Coll. C. L. Hubbs, 2 April 1966.

SDMNH 2463. East side of island; the Nursery, cave shelf approximately 3 to 4 m above sea level. Coll. C. Nelson and Lo-Chai Chen, 2 May 1967.

SDMNH 2464. East side of island; 29° 6′ N (Hydrographic Office map 1688 [1957]), Discovery Point, in small sea caves. Coll. C. Nelson, 2 May 1967.

SDMNH 2465. East side of island; approximately 28° 58.4′ N (Hydrographic Office map 1688 [1957]). Coll. C. Nelson and C. L. Hubbs, 3 May 1967.

SDMNH 2470. East side of island; approximately 28° 58.4′ N (Hydrographic Office map 1688 [1957]). Coll. C. L. Hubbs, 3 May 1967.

SDMNH 2780. East side of island; 29° 0.6′ N, 118° 13.3′ W (Hydrographic Office map 1688 [1956]), approximately 0.5 km southwest of Red Cinder Cone Point. Coll. C. L. Hubbs, 18 February 1969.

CASG 35020. Same as SDMNH 0643.

CASG 58718. East side of island; approximately 750 m north of Lobster Camp located at 29° 0′ 10″ N, 118° 13′ 40″ W (Defense Mapping Agency Hydrographic Center chart 21661 [1976]), approximately 3 m above sea level. Coll. D. R. Lindberg and J. E. Sutton, 5, 7, and 8 July 1975.

UCMP B-6554. Same as SDMNH 0643.

UCMP B-7336. Same as SDMNH 0642.

UCMP D-1547. Same as SDMNH 0633.

UCMP D-1548. Same as SDMNH 0634.

UCMP D-1549. Same as SDMNH 0637.

UCMP D-7297. Same as CASG 58718.

AGE AND CORRELATION

The radiometric age determinations obtained from the coral by Goldberg (1965), 110,000 and 130,000 years B.P. (before present), fall within the range of the Sangamon interglacial stage

TABLE 1. Invertebrate megafossils from Isla de Guadalupe, Mexico.

Localities Taxa	CASG 58718	SDMNH 0633	SDMNH 0634	SDMNH 0635	SDMNH 0636	SDMNH 0637	SDMNH 0638	SDMNH 0639	SDMNH 0640	SDMNH 0641	SDMNH 0642	SDMNH 0643	SDMNH 0644	SDMNH 0645	SDMNH 2233	SDMNH 2234	SDMNH 2462	SDMNH 2463	SDMNH 2464	SDMNH 2465	SDMNH 2470	SDMNH 2780	Province	Tide level	Recent
CNIDARIA																									
Anthozoa																									
Pocillopora guadalupensis Durham, n. sp.	x	x	x	x		x	x	x			x	x	x		x	x			x	x	x		(I)		
ANNELIDA																									
Polychaeta																									
Dexiospira sp.												x													
Serpulidae	x		x													x			x						
Sabellidae			x																x						
ARTHROPODA																									
Crustacea																									
Tetraclita squamosa (Bruguière)	x	x	x							x						x			x	x	x		B	L	x
Paguridae																					x				
Eriphia (?) sp.										x															
Hapalogaster sp.										x															
Majidae										x															
Cycloxanthops cf. *C. novemdentatus* (Lockington)	x		x																				C	S	x
Xanthidae		x	cf								x	x									x				
Pinnixa sp.																					x				
Pachygrapsus sp.			x																						
Petrolisthes edwardsii (Saussure)			x																		x		P	L	
MOLLUSCA																									
Polyplacophora																									
Callistochiton palmulatus Pilsbry										x													C	S	x
Nuttallina californica (Reeve)										x													C	L	x
Lepidozona, n. sp.										x													C	L	E
Gastropoda																									
Haliotis fulgens guadalupensis Talmadge	cf	cf	cf				cf	cf		cf	cf	cf							x			x	C	S	E
Sinezona rimuloides (Carpenter)																						x	B	S	x
Fissurella volcano Reeve	x	x	x	x	x	x	x			x	x	x		x		x			x	x		x	C	L	x
Collisella digitalis (Rathke)			x							x		x											C	L	x
Collisella limatula (Carpenter)	x	x	x			x	x	x		x	x	x		x					x	x		x	B	L	x
Collisella scabra (Gould)	x	x	x				x			x									x			x	C	L	x
Lottia gigantea Sowerby	x						x			x													C	L	x
Norrisia norrisi (Sowerby)	cf	cf	x			x	x			x	x	x		cf								x	C	SL	x
Tegula eiseni Jordan	x	x	x	x	x	x	x	x		x	x	x		x	x					x	x	x	C	L	
Tegula gallina (Forbes)		x	x			x	x	x		x	x					x				x			C	L	x
Homalopoma luridum (Dall)	x																						C	L	x
Astraea undosa (Wood)	cf	x					x							x								x	C	S	x
Tricolia sp.																						x			
Littorina keenae Rosewater	x	x	x		x		x			x	x	x		x						x			C	L	x
Barleeia haliotiphila Carpenter																						x	C	L	
Barleeia subtenuis Carpenter																						x	C	L	
Alvinia purpurea (Dall)																						x	C	S	x
Alvinia oldroydae (Bartsch)																						x	B	S	x
Amphithalamus inclusus Carpenter																						x	C	S	x
Rissoella excolpa Bartsch																						x	P	?	
Rissoella tumens (Carpenter)																						x	P	?	

Symbols:cf=tentative identification. Province column—B, biprovincial; C, Californian; I, Indo-Pacific; P, Panamic. Tide level column—L, littoral; S, sublittoral; SL, littoral and sublittoral. Recent column—x, present in Recent fauna of Isla de Guadalupe; E, endemic to Isla de Guadalupe.

TABLE 1. (Cont.)

Taxa \ Localities	CASG 58718	SDMNH 0633	SDMNH 0634	SDMNH 0635	SDMNH 0636	SDMNH 0637	SDMNH 0638	SDMNH 0639	SDMNH 0640	SDMNH 0641	SDMNH 0642	SDMNH 0643	SDMNH 0644	SDMNH 0645	SDMNH 2233	SDMNH 2234	SDMNH 2462	SDMNH 2463	SDMNH 2464	SDMNH 2465	SDMNH 2470	SDMNH 2780	Province	Tide level	Recent
Truncatella guadalupensis Pilsbry																x					x	x	C	L	E
Heliacus sp.																			x						
Petaloconchus cf. *P. montereyensis* Dall										x															
Petaloconchus sp.			x																	x					
Vermetus (Thylaeodus) cf. *V. compactus* (Carpenter)			x																	x					
Dendropoma lituella (Moerch)																						x	C	L	x
Bittium sp.																						x			
Hipponix cranioides Carpenter	x	x	x				x	x		x	x			x				x		x		x	B	L	x
Cypraea cernica Sowerby	cf	x	x								x	cf		cf									I	S	
Sinum sp.	x																							S	
Erato columbella Menke		x																					B	S	x
Trivia solandri (Sowerby)			x																				B	S	x
Bursa californica (Hinds)			x									x											B	S	x
Murexiella cf. *M. lappa* (Broderip)																				x			P	S	
Purpura pansa Gould		x	x																				P	L	
Thais biserialis (Blainville)								x												x			P	L	
Thais planospira (Lamarck)		x	x				x			x	x			x						x		x	P	L	
Morula lugubris (C. B. Adams)		x	x				x					x											B	S	x
Columbella aureomexicana (Howard)			x											x									P	L	
Columbella sp.																						x			
Mitrella guttata (Sowerby)	x		x				x							x									P	L	
Latirus sp.								x																	
Mitra rupicola Reeve							x																P	S	
Volvarina taeniolata Moerch	x																						B	SL	x
Conus californicus Hinds			x									x		x									C	SL	x
Conus purpurascens Sowerby	x											x											P	L	
Conus princeps Linnaeus											x												P	L	
Conus fergusoni Sowerby												x											P	SL	
Odostomia navisa Dall & Bartsch																						x	B	?	x
Odostomia aepynota Dall & Bartsch																						x	B	?	x
Odotomia terebellum (C. B. Adams)																						x	B	?	x
Odostomia sp.																						x			
Turbonilla (Chemnitzia) sp.								x											x						
Pedipes liratus Binney																					x		B	L	
Bivalvia																									
Barbatia reeveana (Orbigny)		x								x				x									B	S	
Brachidontes adamsianus (Dunker)	x																						B	L	x
Ostrea sp.	x																								
Lasaea sp.	x																								
Codakia distinguenda (Tryon)		x																		x			P	S	
Ctena mexicana (Dall)		x										x											P	S	
Chama squamuligera Pilsbry & Lowe		x						x		x		x								x			P	SL	x
Chione squamosa (Carpenter)																						x	P	S	
ECHINODERMATA																									
Echinoidea																									
Eucidaris thouarsii Valenciennes	x	x	x			x			x								x			x	x		P	S	x
non-cidaroid																						x			

Symbols:cf=tentative identification. Province column—B, biprovincial; C, Californian; I, Indo-Pacific; P, Panamic. Tide level column—L, littoral; S, sublittoral; SL, littoral and sublittoral. Recent column—x, present in Recent fauna of Isla de Guadalupe; E, endemic to Isla de Guadalupe.

(Berggren and Van Couvering 1974). In harmony with this late Pleistocene age assignment, the fossil faunule, as far as determinable, except for the coral, consists entirely of extant species.

Coral and mollusk specimens from several late Pleistocene formations in southern California have also yielded radiometric age determinations within the range ascribed to the Sangamon interglacial. These deposits include: Palos Verdes sand, 115,000 ±20,000 years B.P. (Fanale and Schaeffer 1965; based on He/U ratios in bivalve and gastropod shells) and 130,000 to 140,000 years B.P. (Kaufman and Broecker *in* Fanale and Schaeffer 1965; based on Th^{230}/U^{238}); Cayucos terrace, 130,000 ±30,000 and 140,000 ±30,000 years B.P. (Veeh and J. W. Valentine 1967; based on Th^{230}/U^{238}); and San Nicolas Island lower terrace, 120,000 ±20,000 and ≥120,000 years B.P. (J. W. Valentine and Veeh 1969; by Th^{230}/Th^{232}). Amino acid age estimates agree with the radiometric determinations on the Cayucos and San Nicolas Island terraces (LaJoie *et al.* 1975).

Inferred paleotemperatures, discussed below, do not allow correlation at an equal level of precision, but are consistent with a late Pleistocene climatic model based on the Palos Verdes sand and other correlative deposits in southern California and northern Baja California (J. W. Valentine 1961, J. W. Valentine and Meade 1961, P. C. Valentine 1976).

Hopkins (1967), from little-deformed late Cenozoic marine sequences in Alaska, estimated a Sangamon interglacial sea level of +10 m. Lipps *et al.* (1968), working on Santa Barbara Island off southern California, identified a strandline at +9 m as possibly Sangamon. Land *et al.* (1967) in Bermuda, Oaks (1965) in Virginia, Butzer and Cuerda (1962) in southern Mallorca, and Lipps *et al.* (1968) in southern California recognized sea stands at between 30 and 40 m above present sea level which correlate with pre-Illinoian interglacials, either Yarmouth or Aftonian. Goldberg (1965) noted that radiometric determinations in the 130,000-year range seemed to define an interval just preceding the last major pre-Recent regression when sea level stood about 10 m higher than today. Flint (1971) summarized late Quaternary eustatic sea level fluctuations as follows: the maximum height of sea level during the Sangamon interglacial stage as questionably +20 m; the lowest position of sea level during the Wisconsin glacial maximum as questionably −100 m; and little or no fluctuation since the end of the Wisconsin stage. Milliman and Emery (1968) indicated a maximum lowering to about −130 m between 14,000 and 16,000 years B.P.; and Heusser (1960) suggested a post-Wisconsin rise of 1 to 2 m above present sea level.

Based on this historical model and assuming tectonic stability for Isla de Guadalupe during the late Quaternary, we interpret the fossil locality of Johnson (1953) at Melpomene Cove as pre-Sangamon and possibly associated with the +30 to +40 m pre-Illinoian transgression. The Discovery Point Formation, with upper limit 1 to 8 m above present sea level, was deposited in shallow subtidal water prior to the marine regression of the Wisconsin glacial stage. It stood higher (possibly considerably higher) above the lowered sea level of Wisconsin time than it does now. Post-Wisconsin transgressions, if any, may have removed lower portions of the formation by direct wave action and undercutting—a process continuing today.

Hubbs and Jehl (1976) by implication suggested that reworking had caused a temporal mixture of tropical and warm-temperate faunal elements in the formation, and at least superficial reworking may have accompanied recession of the post-Sangamon sea level to its Wisconsin low. Both tropical and warm-temperate elements occur, however, throughout the thickness of the formation. Neither group is noticeably more abraded than the other. The main effect of changing sea level was probably removal, not redeposition, of Discovery Point sediments.

PALEONTOLOGY

The megafauna obtained from the Discovery Point Formation (Table 1) consists of eighty-six species of marine invertebrates: one scleractinian coral, three polychaete worms, ten crustaceans, fifty-nine gastropods, eight bivalves, three chitons, and two echinoids. The faunule contains species whose modern occurrence is principally in subtropical and tropical regions (Panamic) and others which characteristically inhabit warm-temperate waters (Californian). Most of the species (>80 per cent), whether mainly of Californian or Panamic distribution, occur at present along the western coast of Baja California between Isla Cedros (approximately 28° N) and Cabo San Lucas (approximately 23° N). Also noteworthy is the presence of a small element (one gastropod and the coral) with Indo-Pacific affinities.

TABLE 2. Taxa extraneous to the Surian province.

(1) Species not now ranging south of Isla Cedros
Callistochiton palmulatus (P)
Lepidozona n. sp. (P, E)
Haliotis fulgens guadalupensis (P, E)
Alvinia purpurea (P)
Truncatella guadalupensis (P, E)
Dendropoma lituella (at Cedros) (P)

(2) Species not now ranging north of Cabo San Lucas on the outer coast of Baja California.
Rissoella tumens (at Cabo San Lucas)
Rissoella excolpa (at Cabo San Lucas)
Thais planospira (at Cabo San Lucas)
Mitra rupicola
Conus princeps
Ctena mexicana
Chione squamosa

P = present in Recent fauna of Isla de Guadalupe. E = endemic to Isla de Guadalupe.

The Panamic marine molluscan province coincides approximately with that portion of the west coasts of North and South America with marine hydroclimates dominated by the Pacific Equatorial Water Mass. The Californian province is influenced by the North Pacific Subarctic Water Mass (Sverdrup *et al.* 1942), the southward-flowing California Current and, characteristically, the presence of cold-water upwelling near shore during at least a part of the year. For exposed-coast faunal communities, the boundary between the Californian and Panamic provinces lies at approximately 23° N, near Cabo San Lucas; for embayment and protected-shore communities, it lies at about 28° N, near Isla Cedros and Bahía Sebastián Vizcaíno (J. W. Valentine 1961). The portion of the outer coast of Baja California between Isla Cedros and Cabo San Lucas is characterized by Californian molluscan species in exposed-coast biotopes and Panamic species in protected and embayed situations and has been named the Surian province (J. W. Valentine 1966). A similar set of provinces, based on the distribution of Holocene Ostracoda, has recently been recognized (P. C. Valentine 1976). The Surian province has a very small number of endemic, "index," mollusk species, of which none occur in the Discovery Point faunule. Moreover, Isla de Guadalupe lacks large embayments which, on the Baja California mainland, are reservoirs of typically Panamic species. Therefore, for the following analysis we recognize two zoogeographic groupings, designating as "Californian" those species which at present range north of Isla Cedros, and as "Panamic" those which range south of Cabo San Lucas (Table 1). Species whose modern ranges are entirely north of Isla Cedros or entirely south of Cabo San Lucas are listed in Table 2. Species which range both north and south of the Surian province are termed "biprovincial." The northern boundary of the Californian province lies near Point Conception, California, approximately 35° N. The southern boundary

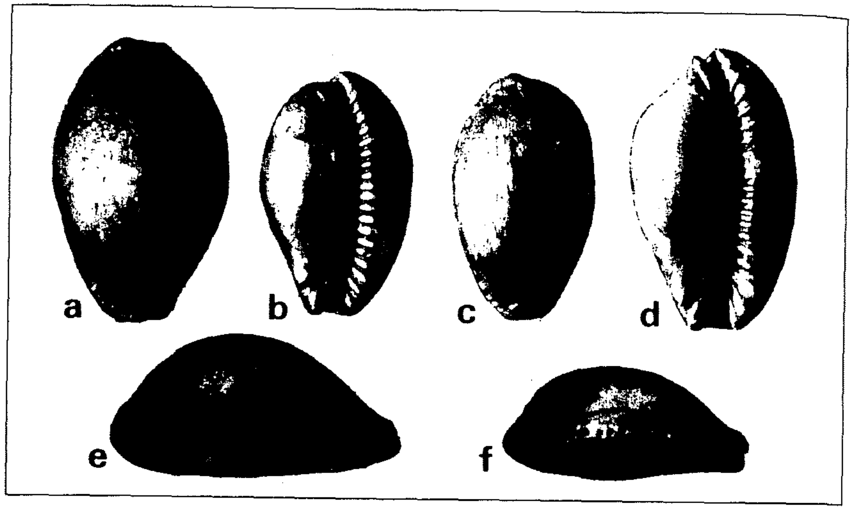

FIGURE 2. Cypraea cernica *Sowerby from Discovery Point Formation.*

of the Panamic province is stated by Keen (1971) to occur at Punta Aguja, Peru. In general, Panamic species are thermophilic, with their northward distribution limited by minimum temperatures. The southern distribution of Californian species is, conversely, presumed to be limited by maximum temperatures.

Several gastropod fragments and two entire specimens from six localities represent the only cowry known from the Discovery Point Formation and are referable to the Indo-Pacific *Cypraea (Erosaria) cernica* Sowerby 1870 (Fig. 2). The existence of *C. cernica* at Isla de Guadalupe during the Pleistocene represents an extension of over 3,200 km from its presently known distribution. The Recent range of *C. cernica* encompasses the entire Indo-Pacific region including Mauritius, Australia, New Caledonia, Okinawa, Japan, Hawaii, and the Tuamotu Archipelago (Burgess 1970). Despite the great distance involved this extension of range is not surprising considering the power of dispersal exhibited by *C. cernica* in attaining its present distribution. The Cypraeidae have a long pelagic larval stage and eleven Recent Indo-Pacific cypraeids (including two *Erosaria*) occur in the tropical eastern Pacific (Keen 1971). The currents available for transport of Recent Indo-Pacific species to the eastern Pacific have been discussed by Abbott (1966).

Indo-Pacific molluscan species (exclusive of opisthobranchs) known to occur in the Recent fauna of the tropical eastern Pacific have been summarized by Emerson (1978). Robertson (1976: 17) cautioned that "apparent novelties among eastern Pacific marine mollusks may be outliers from the Indo-West-Pacific that are already known." Conversely, it may be expected that some species described from the tropical eastern Pacific (especially the oceanic islands) will eventually be found in the Indo-Pacific region. The occurrence of *C. cernica* in the Pleistocene of Isla de Guadalupe emphasizes the necessity of considering the Indo-Pacific fauna when identifying fossil or Recent specimens from the eastern Pacific. (Kellogg [1976] reported *C. cernica* as the first Indo-Pacific mollusk recognized in the fossil record of the eastern Pacific. However, Bratcher and Burch [1971] synonymized *Hastula gnomon* Keen 1943, described from the Miocene of California, with *H. albula* [Menke 1843], an Indo-Pacific species also found in the Recent faunas of Isla Clarión and Isla Socorro, Mexico.)

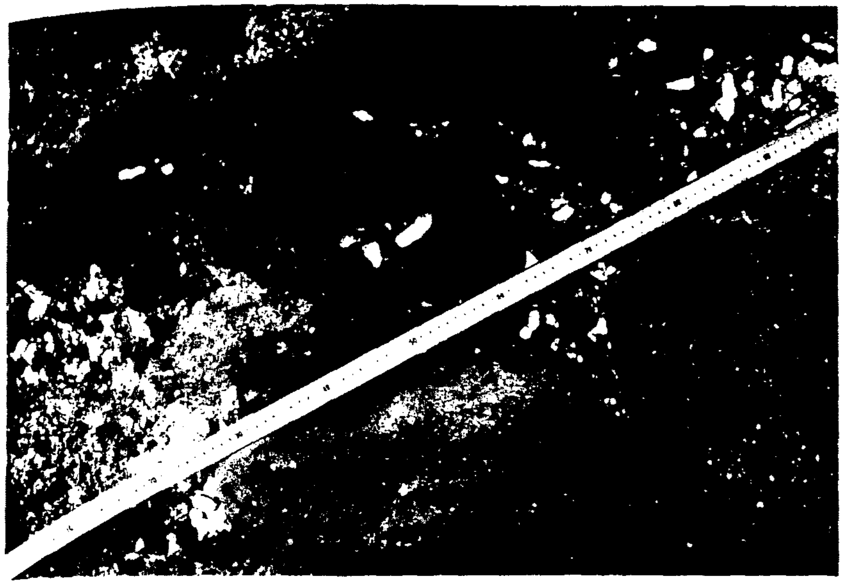

FIGURE 3. *Exposure of Discovery Point Formation at Locality CASG 58718 containing large lava cobbles and detrital invertebrate remains.*

The Discovery Point megafauna represents a mixture of intertidal and shallow subtidal, rocky shore communities. A rock substratum is indicated by the presence of species of *Haliotis, Collisella, Lottia, Chama,* and *Tetraclita*. An abundance of the hermatypic coral *Pocillopora guadalupensis* Durham, n. sp., indicates the proximity of substantial coral growth but not necessarily structural reef development. The genera *Codakia, Barbatia,* and *Ctena* were probably nestlers in pockets of sand. In aggregate, this faunal composition suggests a complex, outer coast environment with microhabitats ranging from protected to exposed. Comparable environments, with sand, coral, and rock substrata closely associated, are moderately widespread in the Recent Panamic province. Fossils from the Discovery Point Formation show no evidence of massive transport. The coral fragments are mostly abraded but in indentations on some specimens the calices are intact. Such wear and breakage as is apparent most likely resulted from local surf action rather than from transport over long distances. Faunal evidence indicates relatively little bathymetric displacement as well, since all taxa now live intertidally or at shallow subtidal depths. *Cypraea cernica* lives at depths of 12 to 183 m, but beach shells in excellent condition may be locally common (Cate 1960, 1962, Burgess 1970).

Part of the sample consists of beach rubble, perhaps displaced downslope through the effect of storm waves. Several unidentified polychaete tube casts, two specimens of the sessile gastropod *Hipponix cranioides,* and one *Chama squamuligera* are attached to a cobble which was probably dislodged from the intertidal zone. Specimens at Locality CASG 58718 were found embedded among lava cobbles (Fig. 3) such as compose many Recent beaches on Isla de Guadalupe.

In addition to the detrital megainvertebrate remains, a small microfauna occurs in the

Discovery Point Formation. Robert W. Crouch, who examined a sample from Locality SDMNH 2780, submits the following identifications:

- Foraminiferida
  - *Cibicides fletcheri* Galloway and Wissler
  - *Diocibicides biserialis* Cushman and Valentine
  - *Gavelinopsis turbinata* (Cushman and Valentine)
  - *Neoconorbina* sp., cf. *N. terquemi* (Rzebak)
- Coral fragments (much abraded)
- Echinoid spines.

Concerning the foraminifera in the sample, Crouch comments (pers. comm. October, November 1977), "all have been recorded from this latitude (Recent) in water depths of 5 to 30 meters. The abraded corals are a different matter; they were no doubt buffeted by wave action and torn loose from the substrate and deposited in slightly deeper water below the wave influence. The forams, however, were preserved with no sign of abrasion." Absence of the foraminiferan genera *Bolivina* and *Uvigerina* indicates a maximum depth of deposition of less than 40 m. Deposition as shallow as 5 to 15 m is compatible with inferred Sangamon interglacial sea levels. The megafaunal evidence does not require deposition any deeper than this.

PALEOTEMPERATURES

An estimate of paleotemperatures during the depositional period of the Discovery Point Formation has been made from three lines of biological evidence: (1) the temperature range indicated by the extreme thermophilic and cryophilic mollusk species present in the faunule, (2) the thermophilic and cryophilic mollusk species taken in aggregate, and (3) the presence of the hermatypic coral, *Pocillopora guadalupensis* Durham, n. sp. (see Appendix). All proceed on the assumption that the thermal-tolerances of these invertebrates were the same in the past as they are at present. The first method has been used for southern Californian Pleistocene faunas by J. W. Valentine and Meade (1961), who stated, "in a thermally mixed fossil assemblage the thermophilic species establish a lower limit to the maximum (effective) temperature. . . . That is, water temperatures must have been *at least* high enough during appropriate seasons to support the most warmth-loving species—the species least tolerant of low temperatures. Similarly, frigophilic [=cryophilic] species place an upper limit on the minimum temperature. Together the warm- and cool-water elements define the minimum temperature *range* represented by a fossil fauna."

In this case the method yields untenable results. *Mitra rupicola* appears to be the most critically thermophilic element in the Discovery Point faunule. Its Recent range extends from Panama to Ecuador (Keen 1971) and the lowest average annual minimum sea-surface temperature within this range is 20° C (Sverdrup *et al.* 1942). Cerohorsky (1976) synonymized *M. rupicola* with *Mitra muricata* (Broderip 1836). This extends the northern range of the *Mitra* from Panama (*M. rupicola*) to Cabo San Lucas (*M. muricata*) but does not affect our use of it as the most critically thermophilic element because the minimum sea-surface temperature experienced by the species occurs in the southern portion of its range. We interpret five species as the most critically cryophilic elements in the faunule: *Callistochiton palmulatus* and *Alvinia purpurea*, both with Recent ranges extending from Monterey, California, to Isla de Guadalupe (Smith 1963, as *C. palmulatus mirabilis*, a synonym of *C. palmulatus;* and Lindberg unpubl.), and three other species which are strictly Guadalupe endemics. The maximum sea-surface temperature within this range, to the nearest 1° C, is 20° C (Robinson 1973). Thus the minimum temperature suggested by the extreme thermophilic element is equal to the maximum temperature suggested by the extreme cryophilic elements. While this implies a single temperature at which the extreme elements could, hypothetically, coexist, we consider it unlikely that a thermal regime with no variation could have existed in the nearshore environment at Isla de Guadalupe.

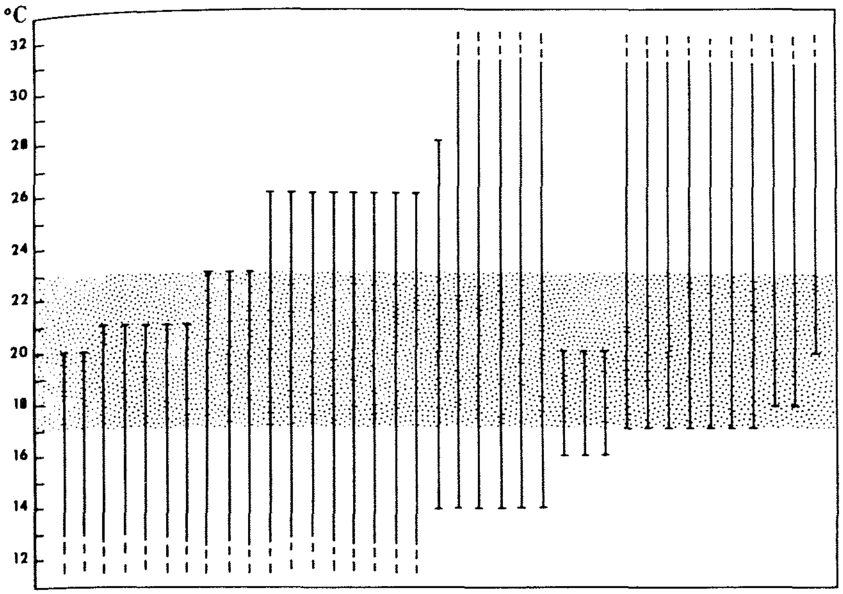

FIGURE 4. *Recent thermal ranges of 37 mollusk species in Discovery Point Formation and inferred annual paleotemperature range, to nearest 1° C (pattern). Temperature data from Robinson (1973) and Sverdrup* et al. *(1942); molluscan range data from various sources.*

If the extreme thermophilic and cryophilic elements are not separately considered, the thermophilic (Panamic) and cryophilic (Californian) mollusks taken in aggregate suggest a sea-surface temperature range of 17° to 23° C (Fig. 4). Only taxa identified to species are included in this analysis. Biprovincial species are excluded; their range end-points are not critical here. Ninety-two per cent of taxa considered have Recent ranges which include sea-surface temperatures of 17° to 20° C. Sixty-five per cent (81 per cent of thermophiles, 52 per cent of cryophiles) have Recent ranges spanning sea-surface temperatures of 17° to 23° C. Outside the latter limits, the number decreases sharply. Above 23° C only 38 per cent of the cryophilic species remain present; below 17° C only 44 per cent of the thermophilic species remain.

An important constraint on inferences drawn from this method is the observation (Hutchins 1947, P. C. Valentine 1976) that organisms are limited in distribution not only by survival temperatures but by a narrower temperature range within which repopulation (including reproduction and larval development) can occur. If the southward distribution of any of our cryophilic species is limited not by survival temperature but by winter repopulation temperature, it is possible that they could have existed on Isla de Guadalupe as nonreproducing waifs in a warmer environment than here inferred. Conversely, a cooler marine environment might support thermophilic waifs.

The proportion of Panamic and Californian species offers little help in choosing between the alternatives: Panamic and Californian forms are present in approximately equal numbers. Three of the Californian taxa are Guadalupe endemics, otherwise known only from the Recent fauna of the island. Unless they had a broader Pleistocene distribution which left no mainland fossil record, these could not be waifs from more northern regions. Yet, clearly, their limiting temperatures must be outside the range now reached at the island.

Squires (1959) states that, in tropical waters, active reef growth is largely confined to areas with a mean annual thermal range of 25° to 29° C (although component corals of the reefs may exist well outside these limits), and that 18° C is the minimum temperature at which a few hardy hermatypic corals may be present. Wells (1956) noted that a few hermatypic corals can live at temperatures as low as 15° C, but that most are found in waters above 18° C. Although the *Pocillopora* is abundant in the Discovery Point Formation samples, no reef structures were found, and there is no secondary evidence of true structural reef development (*e.g.*, more than one species of coral, or obligate reef-associated invertebrates). The coral growth may have been similar to, although less taxonomically diverse than, that currently present near El Pulmo, Baja California Sur, in the southern Gulf of California, where, according to Squires (1959), the coral community is locally concentrated on rock ledges and is dominant only in certain areas. Squires (*op. cit.*) cited an annual temperature range of 17° through 26° C for Bahía El Pulmo and suggested that for part of the year the water there is too cold for active reef growth.

In summary, the maximum sea-surface temperature suggested by 52 per cent of the cryophile Mollusca (23° C), the minimum temperature suggested by 81 per cent of the thermophile Mollusca (17° C) and the range of temperature suggested by the coral (≥18° C, <25° C) lead us to infer an annual temperature range of 17° to 18° through 23° C for the nearshore waters of Isla de Guadalupe during the deposition of the Discovery Point Formation.

DISCUSSION

Comparison can be made with Recent thermal conditions, based on data from Robinson (1973). At Isla de Guadalupe, the late Sangamon annual minimum temperature was 1° to 2° C higher than the Recent annual minimum; the late Sangamon annual maximum temperature was 3° C higher than the Recent annual maximum. The late Sangamon annual temperature range was 5° to 6° C, slightly greater than the Recent annual range of 4° C. The Recent monthly temperature at Isla de Guadalupe averages 1.95° C higher than that along the Baja California mainland at the same latitude, and the annual range (4° C) is less than the mainland annual range (5° C). Similarly, the late Sangamon annual range (5° to 6° C) was the same or less than that inferred (J. W. Valentine 1961) for a comparable stretch of mainland coast in the late Pleistocene (6° C). The late Sangamon annual maximum temperature for Isla de Guadalupe was the same (23° C) indicated by J. W. Valentine (1961: fig. 13; "August" temperature) for this portion of the mainland coast in the late Pleistocene, and the late Sangamon annual minimum (17° to 18° C) was the same or one degree higher (J. W. Valentine *op. cit.*: fig. 11; "February" temperatures).

These comparisons suggest that the same general relationship between the marine thermal regime at Isla de Guadalupe and the mainland regime existed during Sangamon time as exists between the island and the peninsula today, except that temperatures averaged 2° to 3° C warmer. The insular regime during the late Sangamon was more equable than that along the mainland, as it is at present. Also as at present, this equability was expressed as a higher minimum annual temperature, such as occurs in the Recent during the spring months. The presence of seasonal upwelling near the mainland and its absence around Isla de Guadalupe (Dawson 1951, Emerson 1956) was probably the cause, then as now.

The discrepancy between insular and mainland temperatures today is most marked in May, when insular temperatures are 2.7° C higher, and is minimal in November, when temperatures are equal (data from Robinson 1973). The warmer Recent sea-surface temperatures in the vicinity of the island result from an offshore northward displacement of isotherms which begins in June and continues through October. The 18° C isotherm, which we theorize may not have moved south of Isla de Guadalupe (latitude 29° N) during the depositional period of the Discovery Point Formation, today stands north of the island from June through November. The most southerly Recent position of this isotherm is 25° N between the months of February and April. Thus a minimum northward shift of 4 degrees of latitude is necessary to accommodate Isla de Guadalupe south of the range of this isotherm throughout the year.

The partly Californian, partly Panamic, and dominantly Surian molluscan fauna of the Discovery Point Formation is unlike the faunas of other eastern Pacific islands or the mainland. Emerson (1967) summarized the provincial relationships of the Recent molluscan faunas of the tropical eastern Pacific oceanic islands. Cocos and the Galapagos Islands have molluscan faunas which belong to the Panamic molluscan province, as well as some endemic species and a few Indo-Pacific taxa. Clipperton Island mollusks are about half Panamic and half Indo-Pacific. The known fauna of the Islas Revillagigedos is largely Panamic with about 25 per cent Californian species.

The Recent marine molluscan fauna of Isla de Guadalupe belongs largely to the Californian province. According to the definitions employed above in the section on paleontology, 74.7 per cent of the Recent Mollusca are Californian, 19 per cent are biprovincial, and 6.3 per cent are Panamic (faunal list modified after Chace 1958; range data from several sources). Nine species, 5.6 per cent, are strictly endemic to the island and two others occur otherwise only in the Surian region of Baja California. One Indo-Pacific species, *Morula uva* (Röding 1798), is reported (Keen 1971). If present mainland distributions are considered indicative of source-areas for the Isla de Guadalupe marine fauna, approximately 80 per cent of the mollusk species could have colonized the island from southern California waters. Approximately 59 per cent could have had a Surian source.

Chace (1958: 322) considered 34 of 193 Recent mollusk species at Isla de Guadalupe to "belong to the Panamic Fauna, occurring on the mainland between San Diego and Panama." As noted earlier, for outer-coast mollusks the northern boundary of the Panamic province falls near Cabo San Lucas. By this criterion, only 17 of the Mollusca listed by Chace are exclusively Panamic. In addition, we question Chace's identification of "*Bursa calcipicta* Dall"; all specimens of *Bursa* which we have seen from Isla de Guadalupe are *Bursa californica* (Hinds 1843), which ranges from Monterey Bay, California, to the Gulf of California (McLean 1969). *Crenella megas* Dall, listed by Chace, is probably a synonym of *Megacrenella columbiana* (Dall 1897), which ranges north to the Aleutian Islands (Keen 1971) and was also included in Chace's faunal list. *Liotia heimi* Strong and Hertlein, said by Chace to be known only from Isla de Guadalupe and Panama, is a synonym of *Parviturbo stearnsii* (Dall 1918) (McLean *in* Keen 1971), which ranges north on the outer coast of Baja California to Isla Asunción. The occurrence of "*Cystiscus*" *minor* (Adams) at Isla de Guadalupe was not substantiated during later studies of Panamic Marginellidae (Coan and Roth 1966, Coan and Roth *in* Keen 1971). Some other identifications are questionable in light of later work (Keen 1971, Lindberg in prep.). This leaves only 10 species which do not otherwise range north of the Panamic province in the strict sense. None are reported to be common at Isla de Guadalupe. They do nevertheless establish the possibility of colonization of the island from Panamic sources. The rest of the taxa which have partly Panamic ranges also occur in the Surian region on the outer coast of Baja California. None of the extra-Surian Panamic species in the Recent fauna are present in the Discovery Point faunule.

Evolution of the molluscan fauna of Isla de Guadalupe from late Sangamon time to Recent has consisted of: (1) the local extinction of a number of major Panamic elements (species with part or all of their modern distribution south of the Surian region), and their replacement by

Californian elements; (2) the apparent extinction of at least one of the Californian species; and (3) the apparent introduction of many new Californian and a few Panamic province species. In addition, an unknown number of unrecorded introductions and extinctions must have occurred. At the same time the hermatypic coral biotope has disappeared. It is difficult to assess the effect of the coral's disappearance on the molluscan fauna because none of the mollusks in the Discovery Point faunule is known to be an obligate associate of coral. Thirty-two of the mollusk species known from the Recent fauna of the island have been recovered from the Discovery Point Formation (Table 1). All are either Californian or biprovincial. One conspicuous Californian province fossil mollusk, *Tegula eiseni* Jordan, is unknown in the Recent fauna of Isla de Guadalupe. Two others, *Barleeia haliotiphila* and *Barleeia subtenuis*, are unknown in the Recent fauna but may have been overlooked by collectors. None of the strictly Panamic species of the Discovery Point Formation occur in the island's Recent fauna. *Acanthina lugubris* (Sowerby) and *Haliotis cracherodii* Leach, two of the most conspicuous species in the Recent intertidal zone, are not known from the Discovery Point Formation. One Indo-Pacific species, *Cypraea cernica*, has become locally extinct; another, *Morula uva*, may have established itself.

Of particular interest among the mollusks which are present in both the Recent and fossil faunas are three taxa which are known only from Isla de Guadalupe: *Haliotis fulgens guadalupensis*, *Truncatella guadalupensis*, and *Lepidozona* n. sp. Because the chances are remote that these strictly insular endemics evolved, became locally extinct, and then were reintroduced to the island without leaving either surviving mainland populations or any trace in the rich mainland Pleistocene fossil record, they provide evidence for a core group of mollusks which were present on the island in Sangamon time and lasted through the Wisconsin glacial stage into the Holocene. The *Lepidozona* is morphologically most similar to the warm-temperate to boreal *Lepidozona mertensii* (Middendorff 1846) (A. J. Ferreira pers. comm.); and the *Haliotis* is a subspecies of the Californian *H. fulgens* Philippi 1845. *Truncatella guadalupensis* differs from *T. californica* Pfeiffer 1857, which ranges from southern California to the northern Gulf of California, in having a strong vertical rib or varix behind the outer lip and in details of suture and whorl proportion. It bears a striking resemblance to *T. succinea* C. B. Adams 1845 of the Caribbean area and *T. guerinii* Villa and Villa 1841, which is widespread in the Indo-Pacific region.

The Discovery Point faunule, therefore, may be thought of as having a "persistent" component—those taxa which survived on the island into Recent times—and a "transient" component—taxa now locally extinct. The "persistent" component, as already stated, consists entirely of Californian and biprovincial elements. These presumably were constitutionally better equipped to withstand the cooler marine conditions accompanying the Wisconsin glaciation, while the Panamic species and the coral, *Pocillopora*, were eliminated. During the Wisconsin glacial stage, temperatures probably dropped too low for survival of many thermophilic taxa. Also, with depression of the isotherms during this stage the mainland ranges of many thermophiles must have retreated southward; any taxa which had existed on Isla de Guadalupe only as nonreproducing waifs might no longer have received recruitment from their original sources.

The "transient" component consists mainly of thermophiles, but also includes *Tegula eiseni* and possibly *Barleeia haliotiphila* and *B. subtenuis*. Why these Californian species should have become locally extinct is not clear. Ten of the fourteen neogastropods in the Discovery Point faunule are "transient"; so are six of the eight bivalves. Any hypothesis which seeks to explain the extinction in ecological/trophic terms has to account for a similar response in these two ecologically and trophically dissimilar groups. By contrast only one of twelve archaeogastropod taxa became locally extinct. Some species may have been very short-term transients, like the southern spiny lobster *Panulirus gracilis* Streets 1871 observed by Hubbs (1967), and introduced during periodic local and temporary current changes. Zinsmeister (1974) gave criteria for recognizing such species in fossil assemblages. His criteria 2 and 3 are not met by any species in the Discovery Point faunule; his criterion 1 requires a larger sample than is now available.

Isla de Guadalupe has been capable of supporting a shallow-water marine fauna since at least the late Miocene. At that time the deterioration of widespread tropical thermal regimes which characterized the later Tertiary and Quaternary periods (Durham 1950, Addicott 1969) was not as far advanced as at present. Since its beginning as an island, Isla de Guadalupe has come under the influence of alternating tropical, temperate, and subarctic water masses (Ingle 1973: fig. 4). The southward flow of the California Current was the dominant oceanographic factor throughout this interval, as it has been since at least the Cretaceous period (Sliter 1972). Superimposed thereon are climatic oscillations with isotherms shifting north and south along the coast, their migrations detectable by the composition of the megafossil and microfossil records. For most of its history, Isla de Guadalupe has been within the zone of tropical-subtropical planktonic foraminiferal biofacies (Ingle *loc. cit.*), corresponding to waters 20° C and warmer. Under these conditions the shallow-water invertebrate fauna would have been predominantly "Panamic" (remembering that at these times the northern boundaries of the proto-Panamic province were well north of their present positions).

Subsequent cooling, the incursion of first temperate and finally subarctic waters, caused the local extinction of many Panamic forms and their replacement by cryophiles. This may have occurred gradually but more likely in a series of pulses, of which the transition from Sangamon to Recent faunas is only the latest and possibly the most dramatic. Each extinction altered the community composition of the fauna and hence the possibilities of establishment of new taxa. In between cold pulses, local warming may have allowed re-establishment of certain Panamic taxa (such as the 10 tropical species on the island today), their success or failure at colonization depending at least partly on the existing community makeup of the insular fauna.

SUMMARY

Marine invertebrate fossils, mainly mollusks, occur in a superficial deposit, the Discovery Point Formation, around the periphery of Isla de Guadalupe. The fossiliferous sediments grade laterally from conglomerate containing volcanic pebbles to a biostrome formed chiefly of hermatypic coral fragments and mollusk shells. Radiometric dating indicates a Sangamon interglacial age. The deposit apparently was laid down at shallow subtidal depths on irregular volcanic basement; a component interpreted as beach rubble is present.

More than 80 per cent of the taxa occur today on the Baja California mainland between Isla Cedros (28° N) and Cabo San Lucas (23° N); others are extralimital, either north or south. One gastropod species and a hermatypic coral, both now extinct on Isla de Guadalupe, have Indo-Pacific affinities. The faunule suggests a complex, outer-coast environment. Modern thermal tolerances of the invertebrates suggest late Sangamon marine temperatures 1° to 3° C higher than Recent, with an annual range of 5° to 6° C (compared to 4° C Recent range): more equable than the climate inferred for the adjacent mainland, probably because of the absence of upwelling.

The Recent marine molluscan fauna of Isla de Guadalupe is largely Californian. Evolution of the island's molluscan fauna from late Sangamon to Recent time has consisted of the local extinction of major tropical elements and their replacement by Californian forms, the apparent extinction of at least one conspicuous Californian species, and the apparent introduction of many new Californian and a few Panamic province species.

ACKNOWLEDGMENTS

We are grateful to Arnold Ross (formerly of San Diego Museum of Natural History) who made available the SDMNH fossil material and supplied valued procedural advice; E. C. Wilson (Los Angeles County Museum of Natural History) who worked on an earlier version of the manuscript and offered many helpful suggestions; W. K. Emerson (American Museum of Natural History) for encouragement and constructive criticism; J. W. Durham (University of California Museum of Paleontology) for consultation and critique of the text; and R. W. Crouch (Los Osos, Calif.) who kindly contributed identifications and interpretation of microfossils. We gratefully acknowledge the aid of the following individuals who loaned material, identified specimens, or otherwise advised us concerning their various specialties: R. Batiza, C. N. Cate, E. P. Chace, D. D. Chivers, A. J. Ferreira, A. M. Keen, P. I. LaFollette, J. H. McLean, P. U. Rodda, the late G. E. Radwin, G. G. Sphon, R. R. Talmadge, and D. W. Taylor.

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APPENDIX

A New Fossil *Pocillopora* (Coral) from Guadalupe Island, Mexico

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In late 1957, Carl L. Hubbs of the Scripps Institution of Oceanography, in company with Emery P. Chace, discovered a fossiliferous deposit on Guadalupe Island and collected numerous fossils. Among the fossils was a hermatypic coral which was forwarded to me by Hubbs. The coral was identified as belonging to the genus *Pocillopora* at that time and later mentioned as "reef coral" by Hubbs (1967). Other small collections subsequently made by Hubbs and various associates as well as by David R. Lindberg have also been deposited in the collections of the Museum of Paleontology at the University of California, Berkeley (UCMP). Coral material was also deposited at various times in the Natural History Museum of the San Diego Society of Natural History. Chace independently forwarded a specimen of the coral to Donald F. Squires who subsequently (Squires 1959) also identified it as a *Pocillopora*. About a decade ago the coral was identified as a new species by E. C. Wilson, now at the Los Angeles County Museum of Natural History. He has generously made all his data available to me in preparing the present description. The coral is particularly important because it represents the northernmost extent of the range of hermatypic corals known for the outer coast of North America during the Pleistocene and because it is more closely related to central and western Pacific species of *Pocillopora* than to the more southeastern Pacific species of the genus.

SYSTEMATIC DESCRIPTION

Order SCLERACTINIA Bourne
Family POCILLOPORIDAE Gray
Genus *Pocillopora* Lamarck

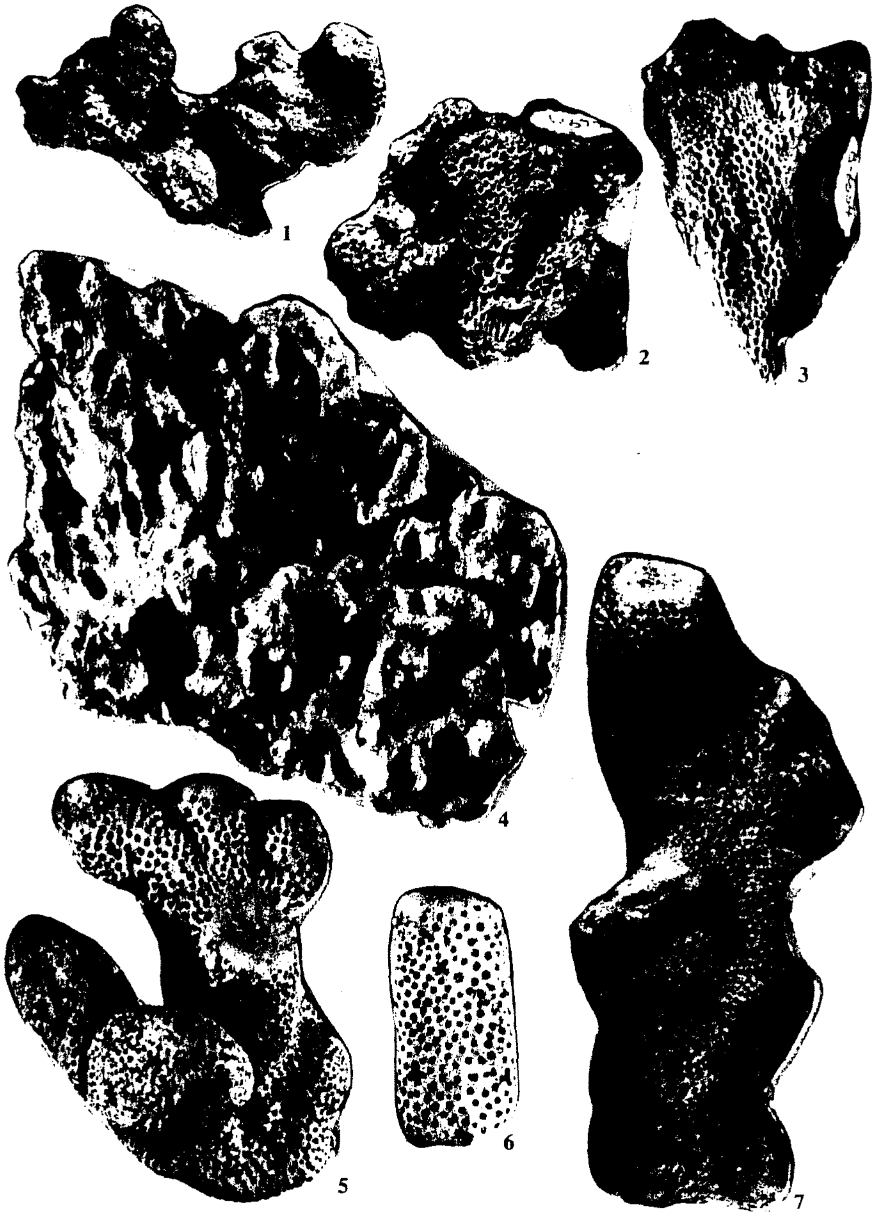
Pocillopora guadalupensis n. sp.

Plates 1, 2

Pocillopora [sp.] Squires, 1959, p. 309; Hubbs and Jehl, 1976, p. 421; "reef coral," Hubbs, 1967, p. 340.

Corallum usually ramose, rarely massive; in ramose forms branches usually heavy, varying from flattened to terete, terminations irregular; verrucae usually absent but a few broken branches have scattered heavy verrucae near the ends; calices deep, varying from about 0.5 mm to 1 mm in diameter; spacing of calices variable, in flattened areas usually distant about one-fourth to one-half a diameter but sometimes on ends of branches with only a common wall between them; on massive branches occasional calices distant more than a diameter from one another; 12 prominent septa present, usually extending nearly halfway to columella; very rarely a calice with 24 septa; columella prominent, usually styliform but sometimes slightly flattened, situated on well-developed directive septum, extending nearly halfway to surface; intercalicular surface with numerous prominent, usually pointed but sometimes flattened spinules; adcalicular spinules usually forming a slightly raised rim around calice.

Dimensions.—Holotype (UCMP-14544, pl. 1, fig. 7) a broken branch with terete branchlets (most typical morphology), height 98 mm, basal diameter about 26 mm; paratype (UCMP-14545, pl. 1, fig. 5), end of branch with flattened, heavy branchlets, height about 69 mm, diameter of basal broken surface, about 21 mm; paratype (UCMP-14551, pl. 1, fig. 1), a fragmentary branch with nodose verrucae (not typical of most specimens), height 54 mm, basal diameter 14 by 17 mm; paratype (UCMP-14553, pl. 2, fig. 2) a massive corallum, somewhat meandroid on top, height about 88 mm, about 80 by 87 mm at base; paratype (UCMP-14549,



pl. 1, fig. 6), a fragment of an elongate terete branch, height 37.5 mm, maximum diameter 12.7 mm; paratype (UCMP-14558, pl. 2, fig. 5), a fragmentary atypical specimen with numerous small broken branchlets, calices and surface detail very well preserved, height 82.5 mm; paratype (UCMP-14554) with abraded flattened base, worn, massive, maximum diameter about 295 mm, height about 210 mm (second largest available specimen); paratype (San Diego Society of Natural History no. 19042, pl. 1, fig. 4), a worn, massive corallum, originally with tall meandroid branches, height about 335 mm, maximum diameter about 315 mm.

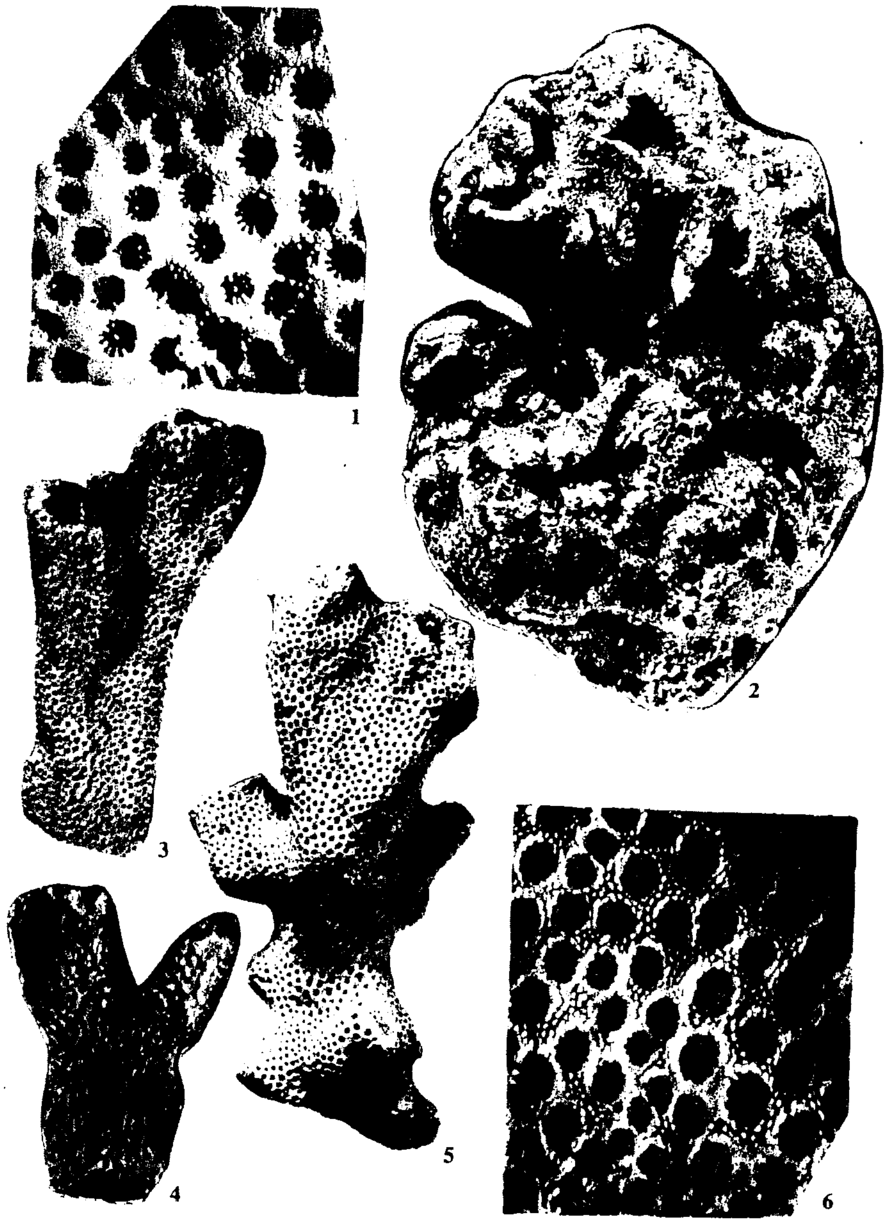
Materials.—Very numerous fragments and incomplete specimens (all representing the same species) in the collections of the Museum of Paleontology, University of California, Berkeley (UCMP localities B-6554, B-7336, D-1547, D-1548, D-1549, D-7297) and the Natural History Museum of San Diego Society of Natural History (locs. 0633 to 0635, 0637 to 0639, 0642 to 0644, 2233, 2234, 2464, 2465, 2470).

Types.—All designated types, except one paratype, are in the University of California Museum of Paleontology (UCMP) invertebrate collections: Holotype UCMP-14544, loc. B-6554; paratypes UCMP-14545, 14547, 14550, 14551, and 14554, all from loc. B-6554; paratype UCMP-14548, loc. B-7336; paratype UCMP-14646, 14549, 14552, 14553, all from loc. D-7297; paratype in San Diego Soc. Nat. Hist. Mus. no. 19042, their loc. 0633.

Comparisons.—The calicular characters of this species are very suggestive of *Pocillopora ligulata* Dana and its allies (*P. eydouxi* Milne-Edwards and Haime, *P. modumanensis* Vaughan, and *P. woodjonesi* Vaughan) but it is distinguished from them by the abundant verrucae of those species and their common absence on the Guadalupe Island specimens. On the available specimens of *P. ligulata* from the Hawaiian Islands the septa are usually slightly shorter than on the new species.

Taxonomy and nomenclature of the species of *Pocillopora* known from the eastern Pacific have varied considerably in the last three decades (see: Durham 1947, 1966; Durham and Barnard 1952; Glynn 1974; Glynn and Stewart 1973; Glynn, Stewart, and McCosker 1972; Porter 1972) and are still in a state of flux. In my earlier papers (Durham 1947; Durham and Barnard 1952) I employed a regional nomenclature largely based on the work of Verrill. Subsequently Squires (1959), using a more conservative taxonomy, considered the eastern Pacific taxa to be conspecific with central and western Pacific species and used their names (which had priority) for the species described by Verrill. For a few years (see Durham 1966) I used the nomenclature adopted by Squires but further studies caused me to largely revert to the earlier nomenclature (see identifications in Glynn, Stewart, and McCosker 1972 and Porter 1972). As a consequence the following names (some of which may be synonyms) have been employed for species and subspecies of *Pocillopora* from the eastern Pacific: *bulbosa* Ehrenberg 1834; *capitata* Verrill 1864; *cespitosa* Dana 1846; *damicornis* (Linnaeus) 1758; *elegans*

PLATE 1. Pocillopora guadalupensis *Durham, n. sp. Figures 1-3, 5-7, x1.0; Figure 4, x0.34.* FIGURE 1, *paratype UCMP 14551, loc. B-6554, atypical branch with nodose verrucae (tips broken).* FIGURE 2, *paratype UCMP 14547, loc. B-6554, three near-terminal fragments in matrix, central one flattened, with complete apex.* FIGURE 3, *paratype UCMP 14550, loc. B-6554, flattened termination of branch in matrix.* FIGURE 4, *paratype San Diego Soc. Nat. Hist. no. 19042, loc. 0633, a large, massive, eroded corallum, tops of branches removed.* FIGURE 5, *paratype UCMP 14545, loc. B-6554, branch with heavy, somewhat flattened branchlets–detail of Plate 2, Figure 1 from near center of basal frontal area.* FIGURE 6, *paratype UCMP 14549, loc. D-7297, fragment of terete branch.* FIGURE 7, *holotype UCMP 14544, loc. B-6554, part of a typical heavy branch, many* Dexiospira *tubes in calices (only a few calices well preserved).*



Dana 1846; *lacera* Verrill 1869; *meandrina* Dana 1846; *nobilis* Verrill 1864; *palmata* Palmer 1928; *porosa* Verrill 1869; *pumila* Verrill 1870; *robusta* Verrill 1870; *verrucosa* (Ellis and Solander) 1786.

The Museum of Paleontology coral collections contain representatives of nearly all the nominal taxa listed above and include material (in part fossil) from Nasca Ridge, Galapagos Islands, Panama, Cocos Island, western Mexico, Gulf of California, Clipperton Atoll, and Guadalupe Island. The Guadalupe Island *Pocillopora* has been compared with specimens from all these areas and is clearly distinct from all of them, being characterized by the usual absence of verrucae and the consistent presence of 12 well-developed septa and a prominent columella. The nominal species listed above consistently have well-developed verrucae and most specimens have the septa and columella poorly developed and sometimes absent. The Guadalupe Island species is more closely related to *P. ligulata* and its allies from the central and western Pacific than to the eastern Pacific species. This relationship seems strange, but is perhaps to be explained by the isolated geographic position of Guadalupe Island. The island is of volcanic origin, about 275 km offshore from Baja California and 1,100 km northwest of the nearest known eastern Pacific outer coast (exclusive of Gulf of California) occurrence of *Pocillopora* (both Pleistocene and Recent). Hubbs (1967) reports a radiometric date of about 7 million years from the volcanic rocks of which the island is formed, indicating that it has been in existence since the late Miocene, thus affording ample time for chance colonization from a central or western Pacific source and subsequent local evolution.

Glynn and Stewart (1973) in a study (largely based on *Pocillopora damicornis*) on the distribution of coral reefs in the Pearl Islands (Gulf of Panama) concluded that minimum temperatures of 20° to 21° C had a debilitating effect on the growth of coral. Inasmuch as coral reefs have not been recognized in the Guadalupe Island deposits, it seems probable that the mean surface water temperatures at the time the *Pocillopora* existed were slightly above 20° to 21° C. Glynn, Stewart, and McCosker (1972: fig. 8) observed that the various species of *Pocillopora* in the Panama area occurred to a depth of about 33 m, but were most abundant in "shallow depths." This suggests that the Guadalupe Island species probably lived at quite shallow depths inasmuch as the locality was apparently at the extreme northern margin of the habitable area for the genus *Pocillopora*.

Glynn (1974), working in the Gulf of Panama, described unattached mobile colonies of the hermatypic coral genera *Pavona*, *Porites*, and *Agariciella*, characterized by a high sphericity and proposed the term "corallith" for them. He presented evidence suggesting that most of the movement of the colonies was caused by browsing fish. He observed that colonies with this characteristic morphology are found in various other scleractinian genera as well as the Paleozoic tabulate coral *Favosites*. He also noted (p. 196) that "unattached colonies of

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PLATE 2. Pocillopora guadalupensis *Durham, n. sp. Figures 1 and 6, approximately x10; Figure 2, approximately x0.83; Figures 3-5, x1.0.* FIGURE 1, *paratype UCMP 14545, loc. B-6554, enlargement of slightly eroded area, displaying septal pattern, near base of same specimen as Plate 1, Figure 5–contrast with uneroded surface detail in Figure 6.* FIGURE 2, *paratype UCMP 14553, loc. D-7297, a corallith* sensu *Glynn (1974).* FIGURE 3, *paratype UCMP 14546, loc. D-7297, fragment of branch, dividing at top.* FIGURE 4, *paratype UCMP 14548, loc. B-7336, part of branch with flattened cross-section.* FIGURE 5, *paratype UCMP 14558, loc. D-1549, branch with many more branchlets than usual, only rare suggestions of verrucae, surface detail mostly very well preserved.* FIGURE 6, *paratype UCMP 14552, loc. D-7297, uneroded surface showing spinules–compare with slightly eroded surface in Figure 1 where septal pattern is well displayed.*

Pocillopora move in a tumbling fashion with relative ease." One of the larger paratypes (UCMP-14553, pl. 2, fig. 2) of the Guadalupe Island species appears to fall within the corallith concept. No attachment area can be recognized and calices are present on all surfaces except where post-mortem abrasion has occurred, indicating that the colony had rotated considerably during life so that polyps had been able to maintain themselves. The gross shape is a somewhat elongated hemisphere, with the apparent lower surface much less convex than the upper. Incipient stubby meandrine branches are present on the "upper" surface, indicating that it was uppermost for longer intervals than the "lower" surface. In the Gulf of Panama the coralliths usually occur in depths of 5 to 9 m, below mean lower low water, just below the zone of coral reefs. Thus there is a suggestion that the Guadalupe Island specimen lived in a similar shallow depth.

The genus *Pocillopora* is now living only in the Pacific and Indian Oceans although during the mid-Cenozoic it had a pantropical distribution. Recently Geister (1977) has shown that a species of *Pocillopora* was widely distributed in late Pleistocene deposits of the Caribbean and that the genus was seemingly absent during the earlier Pleistocene and much of the Pliocene. A significant number of radiometric dates is available from the deposits in which the genus occurs and show that no occurrences are older than about 120,000 years B.P. Ages as young as 26,020 ±675 and 39,550 to 31,500 years B.P. have been reported for two low terrace occurrences, but other data suggest that these may be minimum ages only. At least some of these Caribbean occurrences are thus synchronous with the occurrence of *Pocillopora* on Guadalupe Island. Geister previously (1975) had designated the Pleistocene *Pocillopora* from San Andrés Island (Caribbean) as *P.* cf. *palmata* Palmer but in his 1977 discussion he avoids using a specific name and merely notes that the Caribbean form "closely resembles" *P. palmata*. Squires (1959) concluded that the Guadalupe Island species was closely related to *P. palmata* Palmer which he felt should not be included within the concept of *P. robusta* Verrill (a synonym of *P. elegans* Dana according to Squires) as I (Durham 1947) had done. Geister (1977) likewise concluded that *P. palmata* Palmer was a part of the *P. robusta-P. elegans* complex but left the specific nomenclature of the Caribbean Pleistocene species open until a better understanding of the taxonomy of the genus is available. One "cotype" of *P. palmata* Palmer (original of his pl. 11, fig. 2) is in the Museum of Paleontology collections (UCMP no. 30326). Although Palmer (1928) described his species as having six septa, the calices, where not weathered, on this "syntype" consistently show a prominent columella and 12 septa, substantiating Squires' suggestion that *P. palmata* should be compared with *P. eydouxi* and *P. woodjonesi*. To avoid future confusion, the specimen in the Museum of Paleontology (no. 30326) is here designated the lectotype of *P. palmata* Palmer (1928). At this time the relationship to the Caribbean species is uncertain but in contrast to Geister's description (1977) of his species as having one to two calices per verruca, the lectotype of *P. palmata* has from three to six calices per verruca.

Geister (1977) notes that I had informed him that *Pocillopora* was a member of the eastern Pacific fauna during the Pliocene. This conclusion is based on the occurrence of *Pocillopora* in late Pliocene-early Pleistocene terrace deposits in the Galapagos Islands, and on its occurrence as fossil on an unnamed guyot on Nasca Ridge about 1,540 km west of the coast of Chile. The Nasca Ridge occurrence (long. 85° 25′ W, lat. 25° 44′ S) is from a dredge haul from depths between 210 and 227 m (over twice the depth at which hermatypic corals can live). It was reported by Allison, Durham, and Mintz (1967) where the occurrence was given a probable Miocene age on the basis of a shipboard coral identification (*Plesiastrea*) from a nearby locality by J. W. Wells. Unfortunately the specimen on which Wells' determination was made was subsequently lost in the mail. The fossil material reported in Allison, Durham, and Mintz is now given UCMP loc. D-7298 rather than B-6555 (now reserved for Recent organisms only) as cited in that publication. The fossil corals include

Pocillopora sp., UCMP hypotype no. 14555
Porites sp., UCMP hypotype no. 14560-a, b, c
Leptoseris (?) sp., UCMP hypotype no. 14577, frondose, unifacial.

A fourth coral, "*Stylophora* (?fossil)," was included in the 1967 list. Numerous incipient colonies of this coral are growing on the *Porites* but are of obviously younger age (Recent?). J. W. Wells (pers. comm., 12-3-74) informs me that this coral is referrable to *Madracis* [*Madracis* sp. cf. *M. pharensis* (Heller)] (UCMP hypotype no. 14559). Plate tectonics suggest that the age of the fossils could equally well be either Pliocene or Miocene.

The fossil *Pocillopora* from the Galapagos Islands is from locality UCMP B-3595 on Baltra Island. It (hypotype UCMP no. 14556) is an external mold, clearly assignable to *Pocillopora*, collected from a bed unconformably beneath a lava flow which Cox and Dalrymple (1966: table 2, sample G 30) assigned to the Matuyama reversed magnetic polarity epoch. The Matuyama epoch had a duration of about 700,000 to nearly 2,500,000 years, so it is obvious that this *Pocillopora* occurrence is either of early Pleistocene or Pliocene age. Although the evidence is scanty, it demonstrates the existence of *Pocillopora* in the eastern Pacific prior to the late Pleistocene (Sangamon) occurrence on Guadalupe Island and together with the Nasca Ridge occurrence indicates that the genus has been a continuous member of the eastern Pacific biota since at least the middle Cenozoic.

Notwithstanding this history, the characteristics of the Guadalupe Island *Pocillopora* suggest that it represents an invasion of the eastern Pacific by a different stock of the genus than that present in the more southern parts of the eastern Pacific. The lectotype of *P. palmata* Palmer designated above is described as coming from Pleistocene terrace deposits (Palmer 1928: 22 and legend to pl. 2, fig. 2) along the Mexican coast near Escondido Bay, Oaxaca. Although *P. palmata* is a distinct species, its septal characteristics show that it is also related to the *P. ligulata* group of species and it is suggested that it might represent a local colonization at the same time as the Guadalupe Island invasion. Thus it is tempting to suggest that the Puerto Escondido terrace is of the same age (Pleistocene: Sangamon) as the 2,500 km-distant Guadalupe Island deposits.

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PREHISPANIC MAN