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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

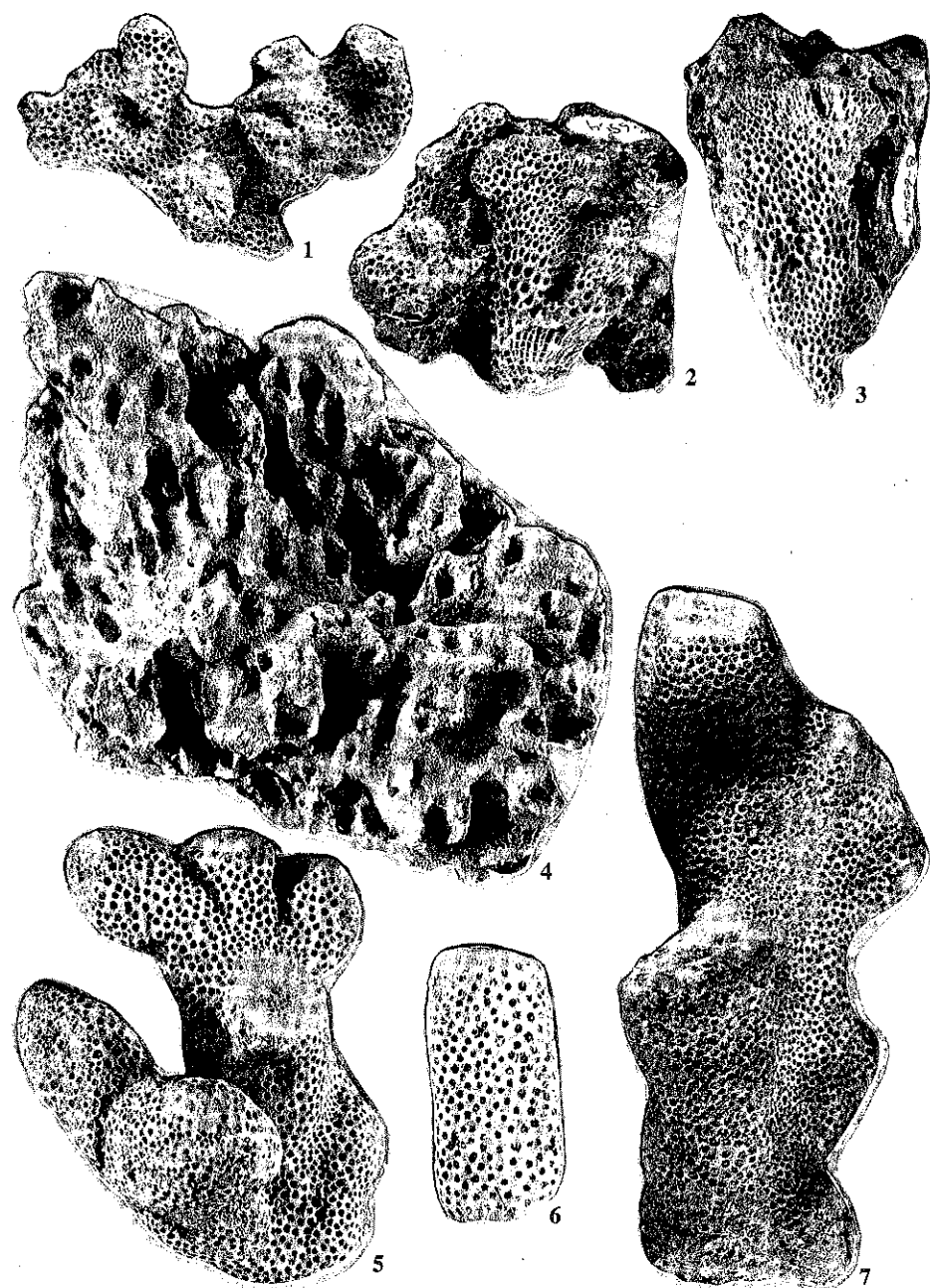
Genus *Pocillopora* Lamarck*Pocillopora guadalupensis* n. sp.

Plates 1, 2

*Pocillopora* [sp.] Squires, 1959, p. 399; 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.

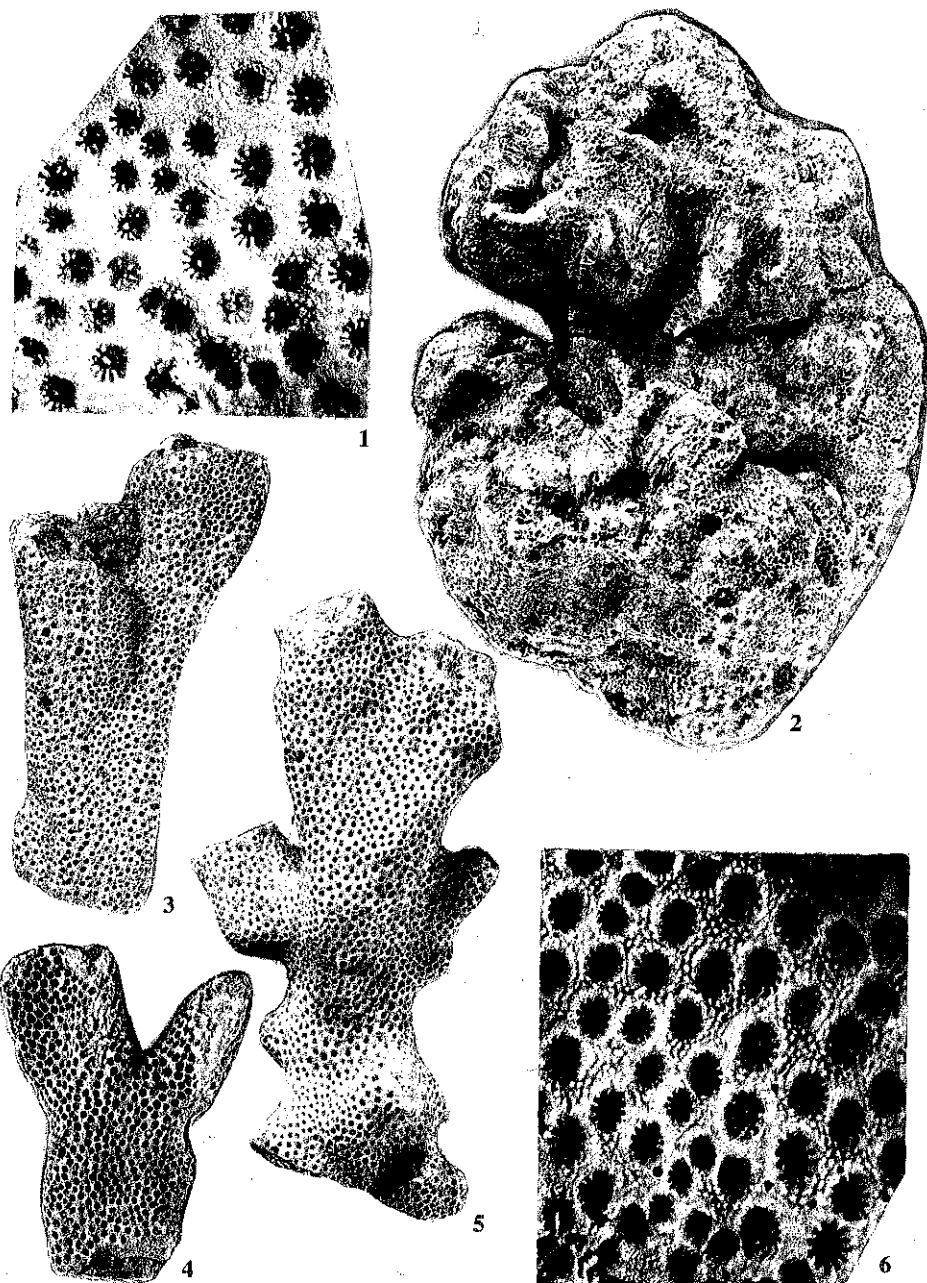
*Materials.*—Very numerous fragments and incomplete specimens (all representing the same species) in the collections of the Museum of Paleontology, University of California, Berkeley (UCMP localities B-6554, B-7336, D-1547, D-1548, D-1549, D-7297) and the Natural History Museum of San Diego Society of 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,  $\times 1.0$ ; Figure 4,  $\times 0.34$ . 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 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

**PLATE 2.** *Pocillopora guadalupensis* Durham, n. sp. Figures 1 and 6, approximately  $\times 10$ ; Figure 2, approximately  $\times 0.83$ ; Figures 3-5,  $\times 1.0$ . 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, "*Strylaphora* (?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 referable 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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