COASTAL EVOLUTION OF SOUTHERN CALIFORNIA AS INTERPRETED FROM BENTHIC FORAMINIFERA, OSTRACODES, AND POLLEN

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ABSTRACT

Three paleoecological studies were conducted on five lagoons and marshes in San Diego County in 1973–1975 and initial results were published in 1976. This paper integrates the earlier results with new palynological evidence, microfossil, and sedimentological data to provide a regional perspective of lagoon, salt-marsh, and climate changes in southern California over the past 8000 years. Foraminiferal species are illustrated and a revised taxonomy is presented. Ostracodes in the surface samples and boreholes of this region are illustrated for the first time.

Surface sample data show the relation between microfossil faunal assemblages, modern salinity, tidal exchange, water depth, and salt-marsh elevation in open lagoons at Tijuana estuary, San Diego and Mission bays, and Agua Hedionda, and for hypersaline-to-brackish marshes in the Los Peñasquitos wetlands. Drillhole lithofacies in Los Peñasquitos, Tijuana, and Mission Bay marshes were dated with seven radiocarbon ages in addition to those published in 1976. The microfossil surface sample data were used to interpret the drillhole records showing the paleoecological evolution of the wetlands and the variation within and between lagoons located less than 40 km apart. Abundances of planktonic and other nearshore foraminifera show that Los Peñasquitos lagoon was much more open in the mid-Holocene compared to today. Palynological data provide the first documentation of mangrove migration as far north as San Diego in the mid-Holocene, which implies warmer winters and wetter summers at that time. Palynostratigraphic data also permit refined timing of recent changes (past 300 years) in lagoonal environments based on use of historical dates for introduced plant species.

INTRODUCTION

Population census data for foraminiferal, ostracode, and palynomorph occurrences in surface samples from five southern Californian lagoon marsh areas (Fig. 1) were obtained during ecological surveys in 1973–75 as baseline material for a study of of coastal lagoon geomorphological evolution (Scott, 1976a, b; Scott and others, 1976). These data are updated, extended, and re-evaluated in this paper. Four lagoons are continuously open to tidal exchange: San Diego Bay, Mission Bay marsh, Agua Hedionda lagoon, and Tijuana slough/estuary. In contrast, Los Peñasquitos lagoon has usually been closed in historical time by a beach barrier.

Fossil associations were also studied in drillholes to document environmental changes over the past several thousand years, particularly since European settlement in Missionary time, ca. 1769-1830. The studies of the 1970s aimed to provide reference points for the 1972 California Coastal Zone Act that sought to restrict development within 400 m of the shoreline that existed when California obtained statehood in 1859. In the early 1970s, however, there was no reliable method to accurately determine the 1859 coastline of California. Subsequent studies have shown how marsh foraminifera can be used to identify past sea level with an accuracy of ± 10 cm (see Scott and others. 2001), and how the pollen of introduced plants can date the past 300 years of salt-marsh sediments in San Diego County (Mudie and Byrne, 1980; Cole and Wahl, 2000). The current revision of the 1976 data enhances our understanding of the evolution of salt marshes in southern California and shows how microfossil and pollen data can be used in coastal-zone research worldwide.

An updated foraminiferal and ostracodal taxonomy is presented here, with illustrations of their major taxa, graphs of the foraminiferal distributions for both the modern (1976) and borehole data, and additional radiocarbon dates. New mid-late Holocene pollen data for Los Peñasquitos lagoon also show how palynology can enhance microfossil-based interpretations of the evolution of coastal wetlands. For Tijuana lagoon, we calculate sedimentation rates based on exotic pollen markers and compare them with the geochronological data of Weis and others (2001), and we relate them to new reports on historical changes in sedimentation in the Tijuana (Callaway and Zedler, 2004) and Los Peñasquitos watersheds (City of San Diego, 1973; Cole and Wahl, 2000). This approach helps refine the chronology of lagoon sedimentation rates for the last 200 years, which is not readily provided by ¹⁴C ages because they have been affected by uncertain marine reservoir effects and radioactive atoms from human nuclear activities since 1950.

PREVIOUS WORK

Prior to the mid-1970s, several studies on the region's coastal environments had been documented: Purer (1942) described the general plant ecology of San Diego coastal salt marshes, Phleger and Bradshaw (1966) studied the physical variability of the Mission Bay marsh environments, Gorsline (1967) documented the sedimentology of southern Californian coastal bays, and Carpelan (1969) investigated the regional lagoon hydrodynamics, Bradshaw (1968) detailed the biology and ecology of Los Peñasquitos lagoon, Mudie (1970) surveyed the coastal wetland vegetation of northern San Diego County marshes, and Macdonald and Barbour (1974) reviewed the characteristics of Pacific Coast salt marshes. These pioneer studies led to intensive salt marsh studies on Tijuana Estuary (e.g., Zedler,

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FIGURE 1. Aerial view of the five lagoon and coastal wetlands (marked as white areas) that are discussed in this paper.

1977, 2001), and Mission Bay (Mudie and Byrne, 1980) and Los Peñasquitos lagoon (Mudie and Byrne, 1980; Hubbs and others, 2008). The early studies on foraminifera and ecological variability in Mission Bay included the important study of Phleger and Bradshaw (1966) that reported rapid changes in salinity, water temperature, oxygen content, and sunlight that occur in a salt marsh over one tidal cycle, and in which they attempted to explain why intertidal environments had lower species diversity than subtidal environments. Later, Zedler (2001) reported on the short- and longterm changes in plant species dominance and distribution in the open estuary at Tijuana and in other southern Californian marshes. Nichols (1956) and Phleger (1967) broadly examined marsh foraminifera in Mission Bay and Tijuana slough and later, Scott, Medioli, and others showed that benthic foraminifera allow detection of ancient sea levels to an accuracy of ± 10 cm (Scott, 1976a, b; Scott and others 1976; Scott and Medioli, 1978, 1980).

Foraminiferal studies farther south in Baja California also helped our early 1970s analyses because most of the nearshore benthic (and tranported planktics) foraminifera were similar to those in the southern Californian coastal lagoons. Those Baja California studies included Todos Santos lagoon south of the Viscaino Peninsula (Walton, 1955), San Miguel estuary (Stewart, 1958), Ojo de Liebre (Scammons lagoon), two other Viscaino Bay lagoon/marsh systems north of the Viscaino peninsula (Phleger and Ewing, 1962) and marine ostracoda from the Pacific Coasts of North and Central America (Swain and Gilby, 1974-this reference was used to identify the ostracodes in this study). Lankford and Phleger (1973) documented the foraminifera in the nearshore turbulent zone of from Baja California to British Columbia. In contrast to the similarity of San Diego and Baja California benthic foraminiferal faunas, the intertidal salt-marsh vegetation on the southern Viscaino peninsula changes radically where subtropical-tropical mangroves (Rhizophora mangle [red mangrove], Avicennia [black mangrove], and Laguncularia racemosa [white mangrove]), and Conocarpus (buttonwood) become part of the lagoonal flora (Whitmore and others, 2005).

Bradshaw and Mudie (1972) determined the tidal prisms, lagoon volumes, salinity ranges, and areal coverage of marsh in the lagoons of the present study (Table 1). Other early ecological studies include reports on Los Peñasquitos lagoon (Mudie and others, 1974), Agua Hedionda lagoon (Bradshaw and others, 1976), San Diego Bay (Browning and others, 1973), and San Dieguito and Batiquitos lagoons (Mudie and others, 1976). The only published studies of Holocene pollen in southern California are for Los Peñasquitos lagoon (Cole and Wahl, 2000), Santa Barbara Basin (Heusser, 1978; Mensing and others, 1999), upper Newport Bay (Davis, 1992), Santa Rosa Island (Cole and Liu, 1994), Los Flores Creek (Anderson and Byrd, 1998), and Alamitos Bay (Boxt and others, 1999).

In 1980, a concerted effort began that aimed to restore the San Dieguito watershed and lagoon to their original state by means of a community-based watershed management plan. The effort focused on remediating (a) the reduced water supply from the upper watersheds and (b) the obstruction of tidal exchange by partial barriers (road/rail embankments) across the entrance channels that close-off in summer as the result of low lagoon volumes and channel constriction. Without full runoff and tidal flow, the wetland

 TABLE 1. Physical and chemical parameters for each area discussed here. Not all parameters were available for Tijuana, Mission Bay, San Dieguito, San Mateo, and Santa Margarita.

Study site	Drainage area (mi ²)	Tidal volume (ft3 mhhw)	Tidal prism (ft3)	Annual salinity	Tidal marsh (% area)
Tiajuana Slough	1750	ND	10.89×10^{6}	36-56 (marsh)	>90
San Diego Bay	119	15000×10^{6}	3000×10^{6}	31–35	<10
Mission Bay	440	ND	250×10^{6}	36-56 (marsh)	1
Los Penasquitos	178	28×10^{6}	$0-7 \times 10^{6}$	15-68	90
Agua Hedionda	28	$81 imes 10^6$	30×10^{6}	32–34	negligible

Drill-hole Material Dated Age (BP) Marsh Location Depth (cm) Lab. No. Los Peñasquitos LJ-2992 1930 ± 40 LP-1 190 Macoma nasuta Los Peñasquitos LP-1 460 Ostrea lurida I I_2003 5170 ± 60 Los Peñasquitos LP-1 860 Ostrea lurida LJ-2998 6210 ± 50 Los Peñasquitos LP-3 190 Ostrea lurida LJ-2996 3310±60 Los Peñasquitos LP-3 530 Ostrea lurida LJ-2997 5480 ± 70 Mission Bay MB-1 312 Chione undulata LJ-3351 2360 ± 60 Tijuana slough red-brown peaty clay LJ-3103 1210 ± 50 TJ-4 110 *Los Peñasquitos LJ-2994 4730 ± 140 LP-2 665 Cerithidea californica 985 LJ-2995 *Los Peñasquitos LP-2 6210 ± 70 Chione fructiflaga

TABLE 2. Radiocarbon dates from the La Jolla Radiocarbon Laboratory at Scripps Institution of Oceanography, San Diego, California (Linick et al., 1977).

areas become hypersaline in summer, and stagnant channel waters become anoxic and malodorous. In San Dieguito Valley, landfill from construction of a large racetrack in the 1960's further obstructs tidal flow and creates extremely stagnant conditions.

METHODS

COLLECTION OF SAMPLES

Samples were collected in the early to late 1970s using various sampling methods, depending on the environment. In intertidal areas, a 10-cm-diameter plastic tube was used to obtain a 1-cm-thick 10-cm³ surface sample. In subtidal areas, a small boat with an "orange peel" grab sampler was used to collect 10-cm³ surface samples. Samples were preserved in the field in formaldehyde, which was mixed with rose Bengal stain to detect live specimens. For shallow cores (<1 m deep) in marshes with clayey sediment, a posthole auger was used (Medioli and Scott, 1976). For deeper sampling, especially where there was sand (e.g., Los Peñasquitos), it was necessary to adopt a wash-boring drillhole technique in which samples were taken with a bailer-corer as the casing was advanced (Scott and others, 1976).

PROCESSING

Processing methods for foraminiferal retrieval involved washing sediment through a pair of stainless-steel screens consisting of a coarse sieve (500-µm mesh) that retained large particles and a fine sieve (63-µm mesh) through which silt and clay passed. Once dry, the foraminifera were separated from the sand by flotation on carbon tetrachloride. Marsh samples were examined in liquid (combination of alcohol and water) because the process of drying and removing plant material would have also eliminated the microfossils. Wet samples were first decanted to remove most of the organics and obtain a foraminiferal concentrate, then whole sample totals were counted in Petri dishes as they could not be split (the wet splitter was introduced in 1993), and representative specimens were placed on micropaleontological slides for further study. For the dry, floated foraminiferal samples, an Otto dry sediment splitter was used to obtain samples of 300-400 specimens (Scott and others, 2001). The residues were examined to make sure we did not lose the agglutinated foraminifera from floating process.

Radiocarbon dates for the cores were obtained from the Mt. Soledad Radiocarbon Laboratory of the University of

California San Diego (Table 2, from Linick, 1977). The analyses were done primarily on mollusc shell material from the Los Peñasquitos and Mission Bay cores and on peat recovered from drilling Tijuana slough. Results are reported in conventional ¹⁴C years without correction for a marine reservoir effect.

Processing for palynologic studies involved wet-sieving 5to 10-cm³ samples through a 125-µm screen to remove coarse sediment, followed by chemical processing to remove the carbonates with 10% hydrochloric acid, then addition of cold 42% hydrofluoric acid to dissolve silica, and, finally, treatment in acetolysis mixture to remove organic debris (see Mudie and Byrne, 1980). Processed residues were stained with Safranin and mounted in glycerin gel. Charcoal counts included only microcharcoal <125 µm.

Local and exotic pollen taxa were identified using the reference collections of P. Mudie (housed at Geological Survey Canada Atlantic) and R. Byrne (University of California. Berkeley), and publications on Chenopodiaceae pollen (Mudie and others, 2005). In salt-marsh environments, pollen assemblages are dominated by herbaceous salt-marsh plants, particularly the halophytes Salicornia virginica (now Sarcocornia pacifica), Arthrocnemon subterminale (formerly Salicornia subterminalis), and Batis maritima (Mudie and others, in press). The "ferns" category also includes Lycopodiaceae (clubmosses and spikemosses). For the present study in using pollen primarily as chronostratigraphic and climatological markers, it is important to note that the salt-marsh taxa were removed from the pollen sum in determining relative abundances of non-arboreal pollen (NAP) taxa in LP-1. A similar procedure was also used by Cole and Wahl (2000), who excluded Chenopod-Amaranth pollen. However, our specialized reference collection of salt-marsh plant pollen (see also Mudie and others, 2005) allowed distinction of the native salt-marsh species from the non-obligate halophytic taxa Atriplex, Chenopodium, and Salsola, many of which have been recently introduced, Cole and Wahl (2000) also did not distinguish Spartina pollen from other salt-marsh and upland grasses and cereals.

RESULTS

FORAMINIFERAL DISTRIBUTIONS IN LAGOONS AND MARSHES

San Diego Bay

San Diego Bay, the largest inlet on the southern California coast (Figs. 1, 2), is the port for most of the

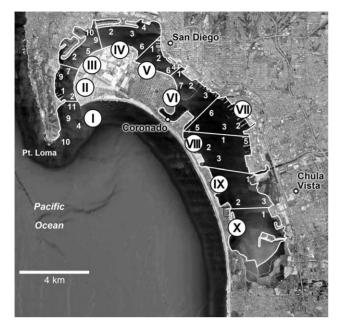
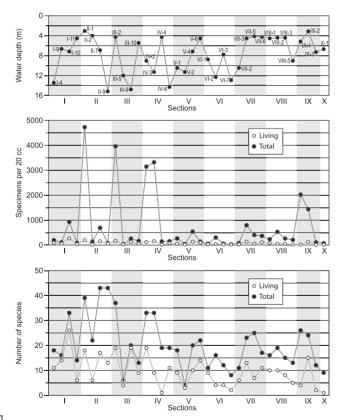


FIGURE 2. Aerial view of San Diego Bay showing locations of the surface sample stations. Data from Appendix 1.

US Navy's west-coast fleet and has many potential sources of environmental disturbance. The drainage basin area that was 803 mi² in 1850 was reduced to 119 mi.² by1900 and is probably even smaller today. Water depths (Fig. 3) of 2–14 m are considerably altered because of dredging.



1 FIGURE 3. Graphs of water depth, number of specimens, ansd number of species at each station in San Diego Bay. Data from Appendix 1.

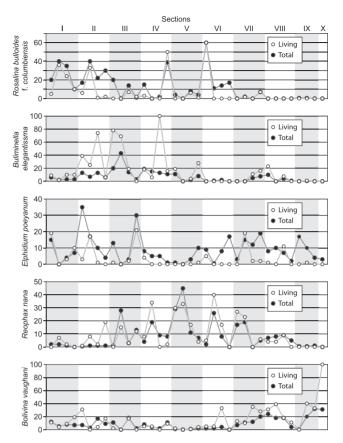


FIGURE 4. Percentage distribution for selected species from San Diego Bay stations. Living = % live specimens in each population; Total = % in assemblage. Data from Appendix 1.

This lagoon yielded 45 foraminiferal taxa; species diversity and total abundance peak in sector II (Figs. 3, 4) and decrease markedly in sectors III–XI. The most common taxa in sectors I–IV assemblages tend to be calcareous and include *Rosalina bulloides* (d'Orbigny) f. *columbiensis* (Cushman), *Buliminella elegantissima* (d'Orbigny), and *Elphidium* spp. *Rosalina bulloides* f. *columbiensis* detached from seaweed may float farther into the bay. It is not in contact with the polluted bottom waters of the inner bay, and is rarely found living in the bay sediments. *Bolivina vaughani* Natland and *Elphidium* spp. appear more tolerant of organic-rich sediments because they reoccur in the inner bay (Fig. 4). *Reophax nana* Rhumbler and other agglutinated species dominate sections III–VII (Fig. 4, Appendix 1).

Agua Hedionda Lagoon

This lagoon was altered significantly in the early 1970s by housing development on the adjacent farmland. The lagoon entrance also was considerably changed by construction of a road with two bridges across the inlet, resulting in restricted tidal flow (Fig. 5). The lagoon has less organic pollution than San Diego Bay but the foraminiferal faunas are very similar (Appendix 2), although more abundant calcareous species and lower agglutinated foraminiferal numbers (Fig. 6) were found in Aqua Hedionda. Species such as *Ammonia beccarii* (Linné) dominate the shallower

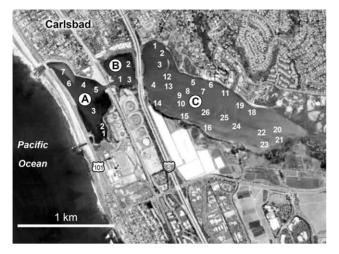


FIGURE 5. Aerial view of Agua Hedionda lagoon, showing locations of sample stations. A, outer basin; B, middle basin; C inner basin. Data from Appendix 2.

depths (2–4 m, Fig. 5), especially in the inner part of the lagoon, where *Rosalina*, *Elphidium* spp., and *Buliminella elegantissma* are common (Fig. 7, Appendix 2).

Los Peñasquitos Lagoon

Los Peñasquitos lagoon (Fig. 8) is largely isolated from the ocean except during and shortly after major flood events. When flooding occurs, the freshwater head washes out the sand barrier across the entrance channel, and opens the lagoon to the ocean. Within a few weeks, the entrance usually closes off again because the tidal prism there is insufficient to counter the strong offshore tidal currents that move sand back into the channel mouth.

This is the only inlet we sampled systematically for foraminifera, five times from August 1973 to August 1974

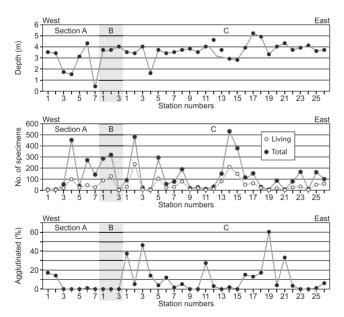


FIGURE 6. Graphs of water depths, number of specimens, and percentage of agglutinated species at each station in Agua Hedionda lagoon. Data from Appendix 2.

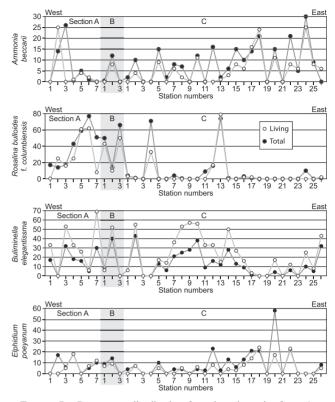


FIGURE 7. Percentage distribution for selected species from Agua Hedionda lagoon stations Living = % live specimens in each population; Total = % in assemblage. Data from Appendix 2.

(Figs. 9, 10). Total species numbers were highest during the winter/spring when the inlet was open, but the water became anoxic in the summer when the entrance closed (Fig. 9). Species numbers were highest at station 2 (Fig. 9) at 2 m water depth. The deepest site (station 4) had the lowest diversity because the bottom water never flushed

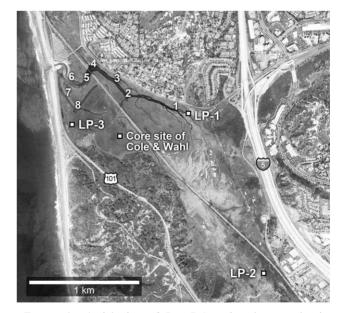


FIGURE 8. Aerial view of Los Peñasquitos lagoon, showing locations of surface sample stations 1–8 and drillhole locations. Data from Appendix 3.

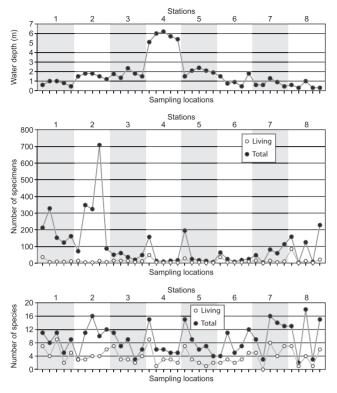


FIGURE 9. Graphs of water depths, number of specimens by season, and number of species at each station in Los Peñasquitos lagoon. Living = % live specimens in each population; Total = % in assemblage. Data from Appendix 3.

sufficiently to become normally oxygenated. Living numbers were low throughout the year at all stations, but the total numbers of 8–16 species for each station were high (Fig. 10). Unlike San Diego Bay and Agua Hedionda, calcareous species were the dominant forms and there were few agglutinants. The most abundant species were *Ammonia beccarii, Elphidium* spp., and *Quinqueloculina seminulum* (Linné) (Appendix 3).

MICROFOSSILS IN CORES FROM LOS PEÑASQUITOS

Sediment samples were obtained from three holes (Figs. 8, 11–16) drilled in the Los Peñasquitos wetland area along the axis of the valley, where sediment accumulation was expected to be greatest and therefore provide the most comprehensive paleo-records. The lithologies varied, with mostly nearshore sediments (shells, coarse sand, minor silt) closest to the ocean in drillhole LP-3.

Drillhole LP-1) contained a mixture of fluvially dominated sediment in the upper section, with open-marine nearshore sediments in the middle, and enclosed bay sediments at the base. The upper 0–4.6 m (Fig. 12) yielded very low numbers of foraminifera that included *Trochammina inflata* (Montagu) from 2.5–2.9 m and from 4.6–7.8 m, and an increase in *Elphidium* spp. downhole (48–180/10 cc). Below 7.8m, total numbers increased to >1000/10 cc but diversity only increased slightly. Planktic foraminifera occurred from 6.25–12.8 m, and the foraminiferal sequence terminated in nonfossiliferous hard clay at 13.2 m (Appendix 4).

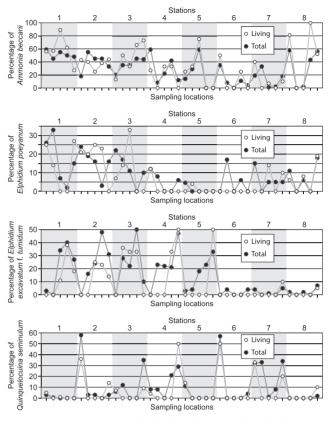


FIGURE 10. Percentage distribution for selected species from Los Peñasquitos lagoon stations (L and T), showing the changes by season. Living = % live specimens in each population; Total = % in assemblage. Data from Appendix 3.

Drillhole 2 (Fig. 13) was located farthest inland and largely contained fluvial sediment with sparse marsh elements in the upper few meters. Nearshore sediments were present below 4.5 m. Recovered sediments included the oldest of any drilled in this project, with a ¹⁴C age of 6200 ± 50 BP obtained from shell 2 m above the bottom. This hole contained few foraminifera (*Trochammina inflata*) in the upper section: 0–5.5 m (Fig. 13). A ¹⁴C age of $5,480\pm70$ was obtained from *Ostrea* shell at 5.3 m (Scott and others, 1976). From ~6 m to the base of the core, *Elphidium* spp. and *Ammonia beccarii* are abundant (Appendix 5), indicating that this site probably was an open-ocean mudflat prior to ~5000 BP.

Drillhole 3 was positioned just behind the beach barrier and therefore most influenced by oceanic conditions (Fig. 14). The upper 1 m was mostly lagoonal with *Ammonia beccarii* and *Elphidium excavatum* (Terquem) f. *clavatum* (Cushman) dominant. From 1.2–1.5 m, low numbers of *Trochammina inflata* suggested a marsh interval, followed by 4.5 m of nearshore/estuarine conditions with calcareous species in abundances of 200–300 specimens/10cc (Appendix 6).

LOS PEÑASQUITOS LAGOON PALYNOLOGY

Sampled transects across Los Peñasquitos marsh indicate that low, middle, and high marshes, and inland delta floodplains are characterized by different pollen assemblag-

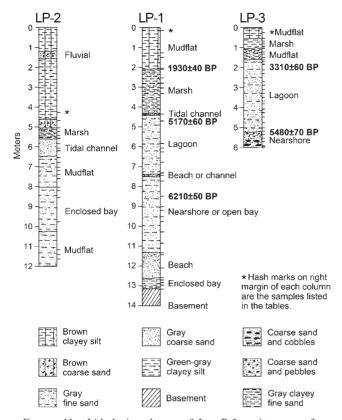


FIGURE 11. Lithologic columns of Los Peñasquitos cores from drillholes LP-1 to LP-3 indicating lithology, depths of samples, C-14 ages, and lithofacies interpretations. Data from Appendices 4–6.

es. Salt-marsh areas are all dominated by *Sarcocornia* pollen but the low-tide zone is marked by the presence of *Spartina alterniflora* (cord grass) pollen that is distinguished from *Distichlis* (salt grass) and other Poaceae by its large size (>45 μ m). The middle marsh has more *Batis* (saltwort) and *Frankenia* pollen, while the high marsh has more annual *Salicornia* species and high abundances of Asteraceae pollen of *Lasthenia* (goldfields) and *Jaumea* (saltmarsh daisy). The freshwater marsh contains almost no Chenopodiaceae pollen but has common *Typha* (cattail), Cyperaceae, and *Urtica* (stinging nettle) pollen.

Pollen of exotic plants provides one of the most accurate ways to chronologically age-date sediments deposited since the European occupation of southern California in 1769 (Mudie and Byrne, 1980). Older palynostratigraphic data also are important for validating ¹⁴C ages obtained from mollusc shells in marginal marine environments where the amount of correction for an old-carbon or marine-reservoir effect is very uncertain (e.g., Ingram, 1998). However, this potential error can be evaluated by cross-correlating stratigraphic data of lagoonal and freshwater lake pollen

The southern Californian record of arboreal (tree and shrub) pollen (Fig. 15) includes several historical datums, such as those of the exotic tree *Eucalyptus*, which was introduced to California in 1859 and extensively planted in San Diego County after 1902–1910 (Mudie and Byrne, 1980). Other exotic trees or shrubs subsequently introduced to the San Diego area include *Phoenix canariensis* (Canary Island date palm) between 1888 and 1904, *Acacia* spp. between 1910–1933, and *Pinus thunbergi* (Japanese

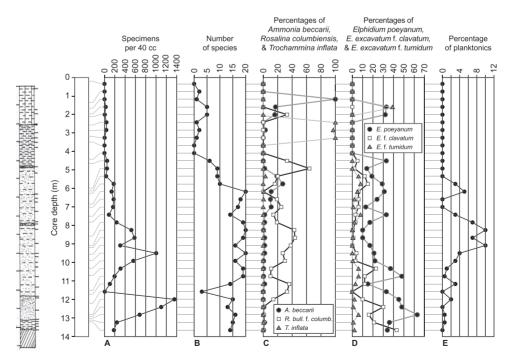


FIGURE 12. Downcore distributions of selected foraminiferal species in Los Peñasquitos drillhole LP-1. Data from Appendix 4.

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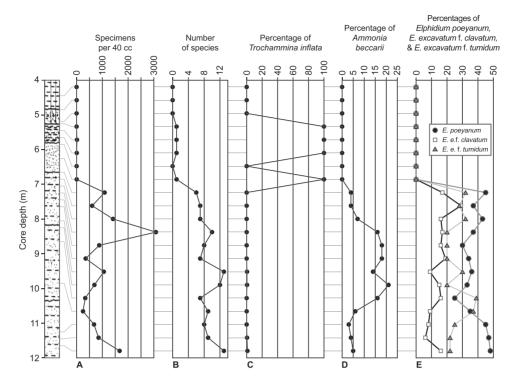


FIGURE 13. Downcore distributions of selected foraminiferal species from Los Peñasquitos drillhole LP-2. Data from Appendix 5.

dwarf pine), between 1945 and 1950. In LP-1, the first occurrences of these taxa mark the youngest pollen subzone (referred to here informally as subzone 3b, which also includes common pollen of *Juniperus* (probably an exotic horticultural species) and *Nicotiana glauca* (tree tobacco), a South American shrub that became wide-spread in southern California by 1920–1930. The base of

this subzone is characterized by herb-pollen assemblages (Fig. 16) correlative with those from Boulton Creek, Long Beach that were dated as 1770–1830 BP (Boxt and others, 1999).

Downhole changes in the arboreal pollen (AP) assemblages from LP-1 (Fig. 15) provide information on terrestrial climates and ecological conditions in prehistoric time.

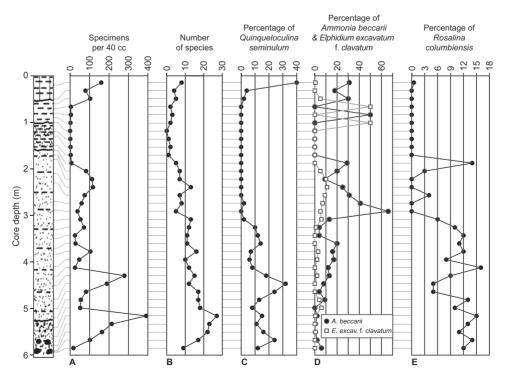


FIGURE 14. Downcore distributions of selected foraminiferal species from Los Peñasquitos drillhole LP-3. Data from Appendix 6.

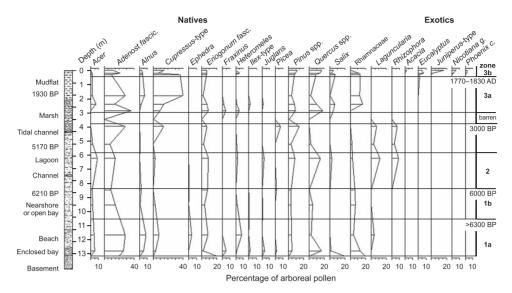


FIGURE 15. Pollen diagram of relative abundances and zonation of arboreal (tree and shrub) pollen from Los Peñasquitos drillhole LP-1. Shown are lithology and radiocarbon dates (left), approximate dates (top right) for first occurrences of exotic taxa such as *Eucalyptus*, ornamental *Juniperus*, tree tobacco (*Nicotiana glauca*), and date palm (*Phoenix canariensis*), and ages of palynozone boundaries (right). Abbreviations: *Adenost fascic* = *Adenostoma fasciculata; Eriogonum fasc.* = *Eriogonum fasculatum*.

Several taxa that first occur in subzone 3a at 3000 BP decline at the base of zone 3b when European colonization began. The increase in Alnus (alder), Salix (willow), and Cupressus (Cypress) in subzone 3a, above the barren interval at 280-400 cm, may signal the start of a morehumid period in the last 3000 yrs and corresponds to subzone 1b of Heusser (1978), which has a basal date of 2263±60 BP. The older assemblages in LP-1 all contain more hardwood tree pollen, including Acer (maple), Juglans (walnut), and Picea (spruce), and persistently present chaparral shrub Heteromeles arbutifolia (toyon). Zone 2 from 400-850 cm in LP-1 is clearly marked by pollen of the Rhizophora mangle (red mangrove) and Laguncularia (white mangrove). Zone 2 is also characterized by increases in Quercus (oak), Rosaceae (Adenostoma, Heteromeles), and Rhamnaceae pollen, and broadly corresponds to Heusser's hypsithermal zone 1c in the Santa Barbara Basin. Heusser's pollen zone 1c/2 boundary has an estimated basal age of 7745 BP in that basin, but is ~ 6000 BP in LP-1.

In LP-1, the oldest zone 1 (850–1320 cm) is marked by increases in the chaparral shrubs *Adenostoma* (chamise) and Rhamnaceae (probably mostly *Ceanothus*) and the presence of *Ephedra* (Mormon tea) mark the oldest zone 1 (850– 1320 cm). Subzones 1b and 3b similarly have increases in *Alnus* (alder) and *Salix* (willow) indicating a more humid climate. However subzone 1b lacks the major increase in *Pinus* or *Filicales* (ferns) that characterizes Heusser's (1978) oldest zone 2, dated 7,745–12,135 BP. In subzone 3a, nonsalt-marsh, non-arboreal pollen (NAP-ex), and fern spore assemblages above 280 cm (Fig. 16) show a similar zonation to the tree pollen assemblages, with a rise in Asteraceae (compositae), Poaceae (grasses), "ferns" (mostly

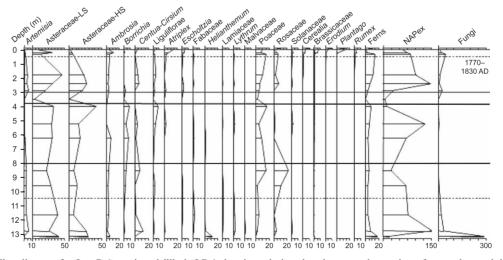


FIGURE 16. Pollen diagram for Los Peñasquitos drillhole LP-1 showing relative abundances and zonation of non-salt marsh herb pollen (NAP), total herb pollen abundances excluding salt-marsh taxa (NAP-ex), and numbers of fungal spores per gram dry weight of sediment. The NAP taxa here include the sub-shrub *Borrichia* and some shrubby Lamiaceae, Malvaceae, and Rosaceae taxa.



FIGURE 17. Aerial view of Tijuana (TJ) slough, showing drillhole locations.

the spikemoss *Selaginella*), and total NAP.A rapid rise in NAP-ex between 180–240 cm is accompanied by the replacement of *Glomus*-type fungal spores commonly associated with soil erosion, and a rise in ascospores associated with grassland and cereal crops. Subzone 3b is marked by a decline in all ferns, and the appearance of field weeds, including the Brassicaceae (mustards and canola) and the exotics *Erodium cicutarium, Rumex acetosella*, and *Plantago lanceolata* that first appeared in California either just before the Mission Era began in 1769, or after 1820 when there was widespread land clearance (Mudie and Byrne, 1980), while increases in *Ambrosia* and *Atriplex* signal the clearing of land for agriculture and grazing.

A maximum in total Asteraceae pollen (including *Artemisia, Borrichia, Centaurea, Cirsium,* Liguliflorae, and undifferentiated low- and high-spine Asteraceae) marks the top 400–630 cm of the NAP zone 2. This event correlates in part with zone II at Los Flores Creek, Camp Pendleton (Anderson and Byrd, 1998) and zone 2 on Santa Rosa Island (Cole and Liu, 1994), which have basal ages of <4,230 and 4,665 BP, respectively. In LP-1, the extrapo-



FIGURE 18. Aerial view of Mission Bay (MB) salt marsh, showing drillhole locations.

lated age of the base of zone 2 is 5,600 BP. *Polypodium verrucosum*, a tropical species, is the dominant fern spore in this mid-Holocene zone. Zone 1 (630–1320 cm) has the greatest diversity of native herb species, and its lower subzone 1a has a downward increase in fungal spores, which could be expected for a terrigenous deposit above the basal clay paleosol.

TIJUANA SLOUGH AND MISSION BAY MARSH

Physical Characteristics

In the mid-1970s, the Tijuana and Mission Bay areas were among the most floristically diverse marsh systems in California (Zedler, 2006). Average salinity in both marshlands is similar, ranging from 56 in the high marsh to 36 in the low marsh (Scott, 1976a). However, the Tijuana wetland area (20.2 \times 10⁵ m² in 1976) experiences large short-term changes in vegetation; for example, after a storm in 1984, the ocean entrance was closed for eight months, resulting in a temporarily depauperate marsh. Tijuana slough (Fig. 17) is presently the only southern California salt marsh not completely altered by man-made road or rail construction and it was designated as a wildlife area in 1980. In contrast, the original extensive marshland area $(111.85 \times 10^5 \text{ m}^2)$ of Mission Bay was greatly enlarged into a marina by dredging in the 1950s and only a small, pristine wetland area of 1.4×10^5 m² remained in 1976 that remains protected and used as a field station by the University of California, San Diego (Fig. 18).

Drillhole Lithology and Foraminiferal Faunas

The lithologies of these two marsh areas are quite different (Fig. 19). The \sim 2-m-long cores from drillholes TJ-4 and TJ-5 in the Tijuana beach barrier have marsh sediments, and the one from TJ-4 has with a peat layer in the middle that yielded a ¹⁴C age of 1210±50 BP. In the two Mission Bay cores, the high-marsh lithofacies is only 50-cm thick, below which varying sandy/silty low-marsh-mudflat

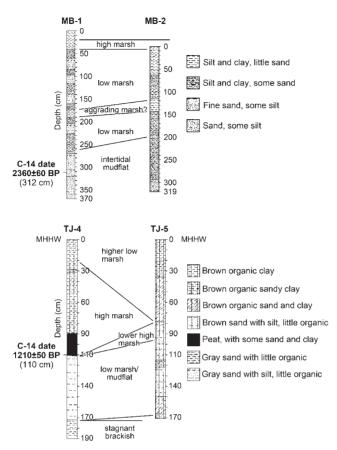


FIGURE 19. Lithologic columns of Mission Bay drillholes MB-1 and MB-2, and Tijuana slough drillholes TJ-4, and TJ-5, indicating lithology, sample intervals downcore, radiocarbon dates, and environmental interpretations.

sequences occur (down to the base at 370 cm in MB-1). A radiocarbon date for shell from 312 cm in MB-1 indicates a basal age of $>2360\pm60$ BP.

Tijuana contained a unique foraminiferal assemblage on the surface and in holes TJ-4 (Fig. 20) and TJ-5 (Fig. 21). Both foraminiferal records show high variability and completely different faunas in the upper 100 cm, below which abundances drop to <100/sample. The TJ-5 core had large populations of Polysaccammina hyperhalina Scott in Petrucci and others (1983) above 100 cm, but the species is not present in the TJ-4 core taken from ~ 200 m away. In the TJ-5 drillhole, there are more changes between high and low marsh, with abundant foraminifera down to 100 cm whereas the TJ-4 section has high abundances only down to 50 cm. The lithologies and lithofacies of the drillholes are also quite different. From 0-20 cm, TJ-4 has a low-marsh assemblage with a high percentage of Miliammina fusca (Fig. 20, Appendix 7), followed by a high-marsh assemblage (30-110 cm) dominated by Trochammina inflata and T. macrescens Brady f. polystoma (Bartenstein and Brand), and with total numbers decreasing markedly below 90 cm. From 170-184 cm, the ostracode Limnocythere cf. L. sanctipatricii (Brady and Robertson) is the only abundant microfossil. The genotype was originally called Cythere inopinata Baird (1843) but the genus was changed to Limnocythere by Brady (1868) (= Limnicythere Brady, 1868). It was very abundant in the low-salinity San Mateo brackish marsh (Scott, 1976a). The sandy peat from 90-110 cm did not yield any microfossils and probably indicates a freshwater environment, although a high percentage of chenopod pollen indicates close proximity to dense salt-marsh vegetation.

Drillhole TJ-5 (Fig. 21), located closer to the beach, yielded samples that were markedly different and contained

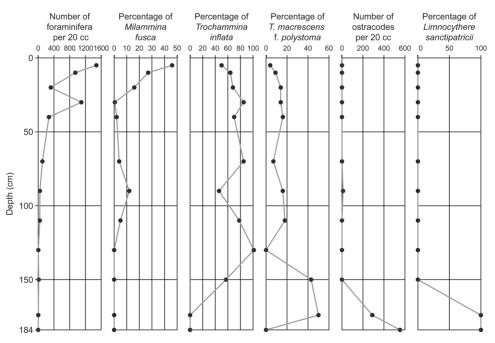


FIGURE 20. Downcore distributions of selected foraminiferal species in drillhole TJ-4. Data from Appendix 7.

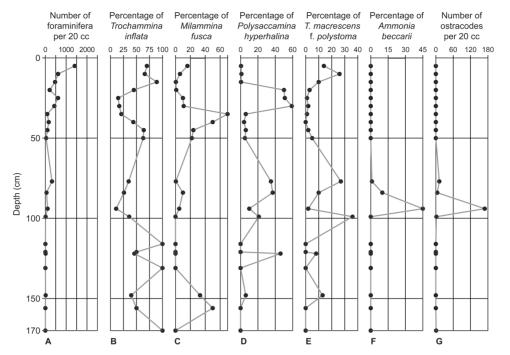


FIGURE 21. Downcore distributions of selected foraminiferal species in drillhole TJ-5. Data from Appendix 8.

high-marsh assemblages throughout most of the sequence. However, a low-middle marsh section occurred from 25– 100 cm, which was characterized by *Polysaccammina hyperhalina* and *Miliammina fusca* (Brady) above 77 cm, followed by high ostracode numbers and high percentages of *Ammonia beccarii* suggesting a low-middle marsh with relatively high salinities. The base of this core was predominantly high marsh with *Trochammina* spp. dominant in low total numbers (Appendix 8).

The modern populations of Mission Bay (Scott 1976a) contained more calcareous species in the low marsh than in Tijuana (Appendices 9, 10). Foraminiferal results (Figs. 22, 23) for the two MB drillholes were quite similar with the exception of an almost barren interval in MB-2 from 10–

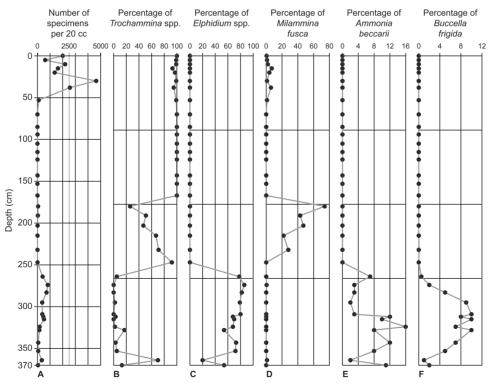


FIGURE 22. Downcore distributions of selected foraminiferal species in drillhole MB-1. Data from Appendix 9.

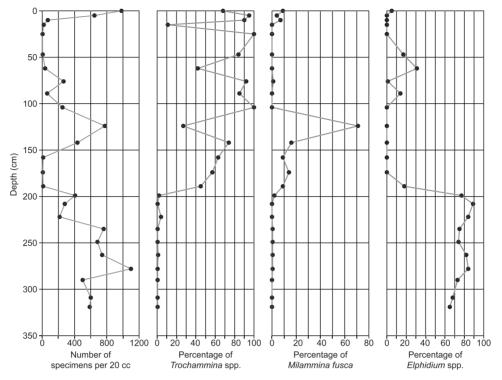


FIGURE 23. Downcore distributions of selected foraminiferal species in drillhole MB-2. Data from Appendix 10.

60 cm. Drill-hole MB-1 (Fig. 22, Appendix 9) contained an abundant high-marsh fauna from 0–53 cm that declined to <10 specimens/20 cc from 53–247 cm. At 167–232 cm *Miliammina fusca* dominated at low numbers (3–54/20 cc). Specimen numbers increased below 264 cm, with *Elphidium excavatum* (three formae: *gunteri* [Cole], *clavatum* [Cushman], and *tumidum* [Natland]) and high percentages of *Trochammina* spp. reappearing at the base (360–370 cm). The low-marsh Mission Bay DH MB-2 sequence (Fig. 23) exhibits the same trend as MB-1 except for a virtually barren zone from 10–70 cm (Fig. 19). In both drillholes, the more open-marine species *Buccella frigida* (Anderson) appeared in the lower sections, suggesting greater marine influence before 2000 BP (Appendix 10).

Comparison of the lithologies from the lagoon and baymarsh areas reveals very different prehistoric records. Tijuana records a diversity of environments, including freshwater peat and occurrences of *Linnocythere* cf. *L. sanctipatricii* and other ostracodes at the base with abundant *Polysaccammina hyperhalina*. There is much more silt and clay in the TJ-5 samples than in the Mission Bay drillholes where *P. hyperhalina* is not common. In Mission Bay, clearly defined low-marsh/mudflat assemblages of calcareous foraminifera (*Buccella* and *Elphidium* spp.) suggest the presence of an open mudflat earlier than 2000 BP, implying that the modern Mission Bay salt marsh expanded greatly during the past two millennia.

Drillhole Palynology

The palynology of introduced species recovered from Mission Bay drillhole MB-1 was described by Mudie and Byrne (1980). The base of the high marsh was reached at

50 cm in this drillhole and dated as earliest Mission time (1769-ca. 1834), and four pollen markers indicated a higher sedimentation rate after 1950. Pollen studies for TJ-4 and TJ-5 are still in progress. However, initial results indicate that palynological assemblages in both drillholes are dominated by pollen of Sarcocornia and other salt-marsh chenopods, with Spartina becoming co-subdominant above 40 cm. This is coincident with the first occurrence of the exotic Pinus thunbergi introduced ca. 1950. Pollen of Triglochin (a genus that includes both brackish and salt marsh species) increases downhole. Both TJ coreholes contained common dinoflagellate cysts (dinocysts), mainly Lingulodinium polyedrum, a species that frequently causes red tides off San Diego in summer. In contrast, dinocysts were only found in one Los Peñasquitos sample, at 180-cm depth.

DISCUSSION

Earlier papers focused mainly on modern foraminiferal distributions in San Diego County without presenting a coherent picture of system dynamics (Scott, 1976a, b; Scott and others, 1976). There was little discussion of the significance of the data in regard to either regional trends or landscape changes, and palynological data were not included. We present below a more detailed discussion and interpretation of the now expanded data set.

PALYNOLOGY

Mudie (1975) summarized unpublished studies of pollen in surface samples from an east-west transect from the Cuyamaca Mountains to San Diego Bay in San Diego County and a south-north transect along the California coast. In essence, an altitudinal transect of surface assemblages established that the pollen input from local salt-marsh vegetation can be distinguished from regional vegetation signals by the predominance of Chenopodiaceae pollen and presence of local markers such as *Batis maritima, Frankenia palmeri*, and *Triglochin maritima*. These results were supported by detailed transect data of Wahl (2003) and local observations of Cole and Wahl (2000). More recent electron microscope studies (Mudie and others, 2005) allow further discrimination of obligate halophyte species (e.g., perennial *Sarcocornia*, annual *Salicornia* species, *Suaeda*) from other facultative halophytes (e.g., *Atriplex, Chenopodium*) that may indicate indicate land clearance as opposed to permanently saline soils.

The palynological data for Los Peñasquitos lagoon is the longest chronological record for any coastal or island site in southern California, which has no large deep lakes. Previous long records (up to 30,000 BP) were only available in the offshore region, such as Santa Barbara Basin (Heusser, 1978; Mensing and others, 1999) where the ages of pollen zones were based on the varve chronology developed by A. Soutar for CLIMAP in 1976 (Heusser, 1978). These offshore palynological data are biased by pollen sorting that increases with distance from the onshore vegetation source, but the dominant tree pollen and fluctuations in herb pollen can be compared to the data from Los Peñasquitos lagoon. The age of the base of the deepest drillhole (LP-1) that records enclosed bay and beach environments is younger than 9000 BP and probably younger than the 7745-BP age of Heusser's zone 1c/2 boundary. Los Peñasquitos pollen zone 2 spans the interval from about 6000-3000 BP and, by analogy with the modern floral distribution; it was characterized by a warmer climate with wetter summers. The benthic foraminifera are species adapted to the fluctuating tidal environment, and they apparently survived this climatic interval. The youngest pollen zone 3 corresponds to the start of the Neoglacial cooler, wetter interval that began 2500-3000 BP and roughly correlates with the beginning of the salt marsh in this estuary. Coeval with this event is the establishment of the modern chaparral scrubland dissected by river valleys with riparian woodlands dominated by Alnus and Salix.

A large peak in micro-charcoal was found at 180 cm, with a C¹⁴ age of $1,930\pm40$ BP, slightly older than the rise in charcoal influx after 1500 BP recorded in San Joaquin marsh (Davis, 1992). In the short core from Los Peñasquitos studied by Cole and Wahl (2000), the microcharcoal peak was dated as ~2600 BP. These microcharcoal peaks occur long after the rise on Santa Rosa Island dated at ca. 3940 BP, which places it during the 5200–3250-BP interval of maximum aridity (Cole and Liu, 1994). These early indications of prehistorical vegetation destroyed by fire were not accompanied by increases in marsh sedimentation rates like those of the past 300 years.

The discovery of the *Rhizophora* and *Laguncularia* mangrove pollen between 3–6 kBP in LP-1 is significant because in Baja California today these mangrove trees/ shrubs occur in the frost-free, summer monsoonal region that extends from the tropics to $\sim 25.5^{\circ}$ N on the west coast and to 28° N on the east coast. A detailed survey of

mangrove occurrences in Baja California in the 1970s (Mudie, 1975 unpublished report to Foundation for Ocean Research, Scripps Institution of Oceanography) showed that presently no mangrove tree species grow north of 26°N. In the eastern Sea of Cortez, there are red mangroves at 25°N in Topolobampo lagoon (Phleger and Ayala-Castañares, 1969) and three mangrove tree species in the southwestern Sinoloan desert at Kino Bay and Guyamas, but only the black mangrove (Avicennia) extends as far north as 28.86°N (Aburto-Oropeza and others, 2008). Los Peñasquitos is located at 32.5°N, and the occurrence of Laguncularia and Rhizopora pollen demonstrates that red and white mangroves grew much farther north between 3000-6000 BP. The present-day northernmost co-occurrence of these two species is in the climate transition between Mediterranean and subtropical climate regions of western Baja California and in the summer-wet coastal area of the northeastern Sea of Cortez.

The Los Peñasquitos pollen record thus suggests that winter conditions were warmer during the mid-Holocene hypsithermal, coinciding with higher sea levels reported in other parts of the world. A foraminiferal response to the warmer conditions seems to be evident in the increase of more-marine nearshore conditions evident in LP-1 and particularly in LP-2 from 3310–5480 BP, where there is an increase from <10 to 15–20 species including *Rosalina bulloides* f. *columbiensis* and other calcareous species (Figs. 14, 24, 25). The combined data indicate higher sea level during this period.

It is worth noting here the fate of *Avicennia* and *Laguncularia* shrubs experimentally planted in the Mission Bay marsh in the 1960s. The seeds were first germinated in a greenhouse and the plants had to be protected from winter frost, suggesting they could not have naturally survived in this location during the last 3000 years. While *Avicennia* grew vigorously, the less cold-tolerant *Laguncularia* and one trial *Rhizophora* transplant did not survive, indicating that the mid-Holocene climate of Los Peñasquitos lagoon was substantially different than now.

FORAMINIFERA

The interpretation of the foraminiferal data for the lagoons of San Diego Bay, Los Peñasquitos, and Agua Hedionda is essentially the same as previously reported (Scott, 1976a, b; Scott and others, 1976), although some taxonomy is modified here to enhance the application of these data to other coastal areas (e.g. Mexico, Texas, Louisiana). The *Elphidium excavatum* "group" was poorly understood and divided among several genera and species. When examined critically using the intergradational series technique (Miller and others 1982) and the illustrations in this paper (Fig. 26), it became apparent that several of the named taxa that are ecophenotypes of Elphidium excavatum that correspond to different water temperatures: These had been distinguished as E. excavatum f. clavatum (colder water), E. selseyensis (more-temperate water), and E. lidoensis (warmer water). Additionally, re-examination of the material has shown that the warm-water E. gunteri Cole, mostly observed in the Gulf of Mexico, is also another morphotype of E. excavatum. The dominant

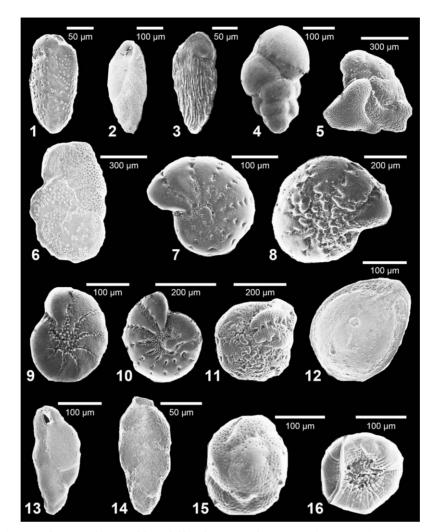


FIGURE 24. Scanning electron microscope images of foraminifera from San Diego County lagoons and marshes. 1 Bolivina vaughani Natland. 2 Buliminella elegantissima (d'Orbigny), apertural view. 3 Bolivina aculuta Bandy. 4 Bulimina marginata d'Orbigny. 5, 6 Dyocibicides biserialis Cushman and Valentine: 5, dorsal view; 6, ventral view. 7 Elphidium excavatum (Terquem) f. clavatum (Cushman). 8 E. excavatum f. tumidum Natland. 9 E. excavatum f. excavatum (Terquem). 10 E. discoidale (d'Orbigny). 11 E. excavatum f. gunteri Cole. 12 Fissurina lucida (Williamson). 13 Fursenkoina pontoni (Cushman). 14 F. sandiegoensis (Uchio). 15, 16 Glabratella ornatissima (Cushman): 15, dorsal view; 16, ventral view.

Elphidium species in southern California was previously identified by Scott and others (1976) as *E. translucens* (Natland). However, re-examination of specimens from the original samples housed at Dalhousie University has concluded that these are *E. poeyanum* (d'Orbigny, here Figs. 25.13, 25.14).

The ambient environments represented by individual species or assemblages are important as paleoecological parameters. For example, a percentage increase of offshore calcareous or planktic forms represents a greater flux of open-ocean water into a coastal area (Lankford and Phleger, 1973). Calcareous benthic and planktic foraminifera were most common in surface samples near the entrances of San Diego Bay (sections I–IV), Agua Hedionda (sections A, B), and Los Peñasquitos (stations 4–8), and occurred in the nearshore and open-lagoon facies of LP-1 and LP-3 before ~ 2000 BP.

In Los Peñasquitos lagoon, only LP-3, the drillhole closest to the ocean, contained notable occurrences in the last 300 yrs of calcareous offshore species within assem-

blages dominated by saline lagoonal species. The absence of offshore species in upper parts of other Los Peñasquitos drillhole sections suggests that this lagoon started to fill in and become semi-isolated from tidal inflow before the landuse changes of the Missionary Era. The lagoon was more severely impacted in the 1800s, by railroad and highway construction across the main channel that restricted the natural migration of the entrance channel during storms.

In contrast to the relatively common occurrence of planktic foraminifera in the youngest sediments at Los Peñasquitos, dinocysts were absent from all but one mid-Holocene sample in the >6500 year record. In the unobstructed Tijuana estuary, however, the tidal channel facies in samples from drillholes TJ4 and TJ5 (<2500 BP) contained *Lingulodinium polyedrum* (= *Gonyaulax polyedra*). This taxon is responsible for the present-day southern California red tides (Mudie and others, 2001).

The two southernmost marsh areas present contrasting foraminiferal distributions in both the surface and subsurface environments (Scott, 1976a, Scott and others, 1976). In SCOTT AND OTHERS

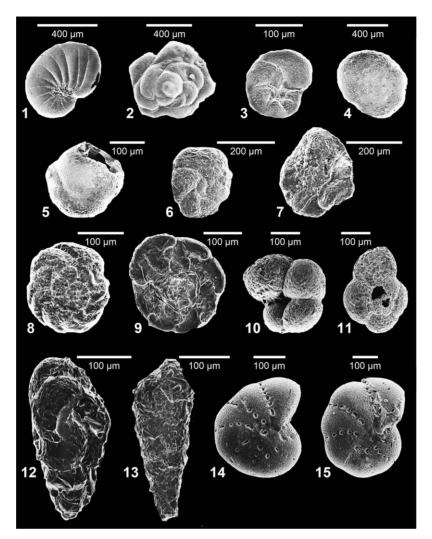


FIGURE 25. Scanning electron microscope images of foraminifera from San Diego County lagoons and marshes. 1 *Florilus basispinatus* (Cushman and Moyer). 2–5 *Rosalina bulloides* (d'Orbigny) f. *columbiensis* (Cushman): 2, dorsal view of specimens deformed to fit on substrate; 3, normal specimen, ventral view; 4, solightly infilled specimen, ventral view. 5 *R. bulloides* f. *bulloides* side view of broken-open float chamber. 6, 7 *Trochammina ochracea* (Williamson): 6, dorsal view; 7, ventral view. 8, 9 *T. kellettae* Thalmann: 8, dorsal view; 9, ventral view. 10, 11 *T. pacifica* (Cushman): 10, ventral view; 11, dorsal view. 12 *Eggerella advena* (Cushman). 13 *Textularia earlandi* Parker. 14, 15 *Elphidium poeyanum* (d'Orbigny).

Mission Bay, the dominant low-marsh species in the surface transect were *Elphidium* spp. (= *Cribroelphidium* in Scott, 1976a) with some *Quinqueloculina* spp. and few *Polysaccammina hyperhalina* (= *Protoschista findens* in Scott, 1976a). In contrast, at Tijuana Slough 40 km south of Mission Bay, the low marsh was dominated by *Polysaccammina hyperhalina*. High-marsh surface samples from both areas had significant populations of *Discorinopsis aguayoi* and *Trochammina* spp.

The samples from Mission Bay drillhole MB-1 (Fig. 22) had a very large number of specimens with almost 100% *Trochammina inflata* Montagu and *T. macrescens* Brady f. *polystoma* (Bartenstein and Brand) in the upper 50 cm, a barren zone from 50–150 cm, and a weak but diverse fauna with *Miliammina fusca* (Brady) from 150–250 cm that was replaced by calcareous species of *Ammonia* and *Buccella* from 250–300 cm to the base at 370 cm. This predominantly calcareous assemblage indicates the presence of a low-marsh mudflat or shallow intertidal environment in Mission Bay, dated as 2380 BP at 312 cm. This observation is

thought provoking because prior to the dredging in the 1950s, the inner bay area should have contained more extensive marshland, not more-open bay conditions. The barren zone and M. *fusca* fauna that overlie the mudflat deposits are also interesting because they resemble present-day disturbed faunas.

Both of the Tijuana Slough drillholes are located behind the beach ridge, less than 200 m apart. In barrier lagoons, commonly a channel breaks through the beach ridge but leaves adjacent ridge areas intact. This feature could account for the variability between in the Tijuana drillholes, and the absence of a peat layer in the more-seaward TJ-5 supports this suggestion (Appendices 7, 8). However, the dominance of *P. hyperhalina* in upper TJ-5 and absence in TJ4 suggests that the two stratigraphic sequences are not coeval. It is also unusual that this species was not be found in the present-day marsh faunas at San Mateo, Santa Margarita and San Dieguito that were sampled at about the same time as Tijuana marsh (Scott, 1976b). These data indicate the presence of large inter-site variations over short

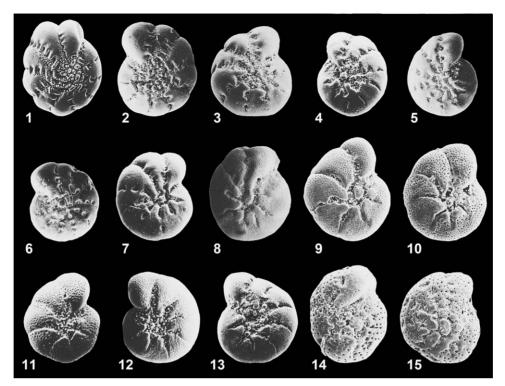


FIGURE 26. Scanning electron microscope images of *Elphidium excavatum* formae in this study (all $\sim 70 \times$). **1–4** *Elphidium excavatum* (Terquem) f. *tumidum* Natland. **5** *E. excavatum* f. *selseyensis* Heron-Allen and Earland. **6–8** *E. excavatum* f. *clavatum* Cushman. **9–14** *E. excavatum* f. *lidoensis* Cushman. **15**, **16** *E. excavatum* f. *gunteri* Cole.

distances in dynamic beach-barrier environments, and the need for age-dating cored lagoonal lithofacies showing large differences between microfossil assemblages.

OSTRACODES

Previously, ostracodes from the sampled areas (Fig. 27) were only cursorily discussed (Scott and others, 1976). Now it is evident that some hypersaline or hyposaline ostracode species and associated layers of the gastropod Cerithidea cf. \hat{C} . californica (Haldeman) occur in the lagoons that are isolated from the ocean. Because Cerithidea cannot survive more than two weeks of freshwater conditions (Scott and Cass, 1977), and layers of this shell suggest hypersaline environments followed by freshwater flooding. Layers with few foraminifera but abundant Cyprideis beaconensis LeRoy), a ubiquitous lagoonal ostracode also suggest hypersalinity. These beds probably represent summer closure of the lagoon entrance, which would have resulted in excessive evaporation, hypersalinity, anoxia, fish kills, and a decline in typical lagoonal foraminifera. This ostracode species appears to develop external spines in such high-salinity conditions. Limnocythere cf. L. sanctipatricii appears when hyposaline conditions prevail, which is usually in the winter rainy season. This ostracode was most common in the San Mateo and Santa Margarita marshes (Scott, 1976b) where there was continuous flow of freshwater from rivers, but it was also dominant near the base in drillhole TJ-4 (Fig. 20), suggesting a fresh-tobrackish interval in pre-European times. Also present were species of Cypridopsis, Candona, and Xestoleberis; these ostracode genera typically inhabit brackish-water environments from the Pacific coasts of North and Central America (e.g., Swain, 1974; Swain and Gilby, 1974). The ostracodes in the open-marine nearshore environments tend to occur in relatively low abundance but with higher species diversity.

PALEOENVIRONMENTAL HISTORY

The Los Peñasquitos drillholes provide the most comprehensive record of the long-term paleoenvironmental history because they span the longest time interval and the palynological records provide a background of climate and vegetation change. The introduction of exotic weeds beginning in the mid-18th Century marks the start of changes in native vegetation that accompanied European development such as deforestation, ranching, road and dike construction, agriculture, and the introduction of fastgrowing trees such as exotic Eucalyptus. Mudie and Byrne (1980) showed that the average sedimentation rates over the 2,500 BP prior to the mid-18th Century were 9.0-12.8 cm/ century for Los Peñasquitos, Tijuana, and Mission Bay marshes and 4 cm/century for San Dieguito marsh. In contrast, the sedimentation rates that followed in Mission Bay and Los Peñasquitos marshes average 46-53 cm/ century, peaking at 10 cm/decade in the 1950-1975 interval concomitant with large-scale urban development. Cole and Wahl (2000) reported a similar rate of 43 cm/century in the 20th Century. Our 10 cm/decade values are also comparable to vertical accretion rates of 0.7-1.2 cm/yr between 1963-1998 determined by 137Cs dating of low- and middle-marsh sediments in cores from Tijuana estuary (Weis and others, 2001). Other Tijuana Estuary sedimentation rates measured

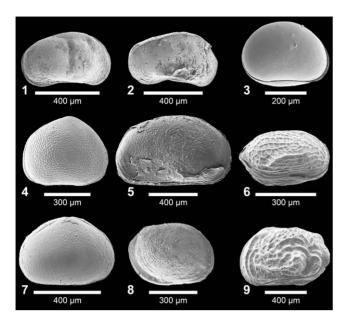


FIGURE 27. Scanning electron microscope images of ostracodes from San Diego coastal lagoons. 1, 2 Limnocythere sanctipatricii (Brady and Robertson): 1, external side view; 2, internal view. 3 Candona sp. 4, 7 Cypridopsis vidua (Müller). 5 Cyprideis beaconensis (LeRoy). 6 Cytheruridae. 7 Megacythere cf. M. johnsonoides Swain. 8 Loxoconcha tamarindoidea Swain. 9 Perissocytheridea cf. P. meyerabichi (Hartmann).

using feldspar marker layers (Wallace and others, 2005) yielded results of 2–8 cm/yr during 1993 winter flooding of *Spartina* low marsh, and 1.3 cm/yr (9.5 cm per storm season from 2000–2004) in the north channel of this estuary.

Comparison of the paleoecological data from the southern California lagoons also indicates how much change has occurred since European colonization. Tijuana Slough straddles the US/Mexico border but does not have a road or railway embankment across its inlet. This channel entrance can migrate and breach the lowest points of the beach barrier, possibly explaining why this marshland remains in a more natural state even though its watershed has been highly modified. The small remnant marsh of Mission Bay has been protected in its "natural" state and its foraminifera do not indicate much anthropogenic impact other than the effects of adjacent dredging, despite the exotic pollen record indication of a large increase in sedimentation rate since 1950.

In contrast, Los Peñasquitos, Agua Hedionda, and San Diego Bay have undergone considerable modifications as result of road construction, and agriculture, as well as dredging. San Diego Bay and Agua Hedionda lagoon were extensively dredged, and most of their wetlands were eliminated, making it difficult to compare them with the other tidal-lagoon areas still containing extensive wetlands. However, the San Diego Bay and Agua Hedionda microfaunas indicate continuously open oceanic connections similar to those in lower parts of the Los Peñasquitos drillhole sections. The prehistoric microfaunas from Los Peñasquitos match fairly closely with those presently found in inner San Diego Bay (sections VII–X) but contain many more specimens of nearshore turbulent zone genera such as *Cibicides* and *Rosalina*. Agua Hedionda has a less-diverse

fauna than either San Diego Bay or the lower part of Los Peñasquitos LP-3, suggesting that inlet dredging impacted the subtidal environments in addition to removing saltmarsh.

As a final note, Google[®] maps and local reports show that the oceanic entrances to Los Peñasquitos and San Dieguito lagoons are now open most of the year as a result of channel dredging in response to community demands for maintainance of the lagoons in as natural a state as possible. In July 2010, the senior author (DBS) observed that the ocean inlets to Los Peñasquitos and San Dieguito lagoons were open during summer. The dredging now allows these inlets to be open almost all year and they are almost back to their natural state. Drs. Bradshaw and Mudie, together with many community groups, played a key role in promoting the value of these areas over the past 40 years: their persistence has finally come to fruition.

CONCLUSIONS

Foraminiferal distributions in surface samples from open lagoons at Tijuana Estuary, San Diego and Mission bays, and Agua Hedionda, and from periodically closed hypersaline-to-brackish marshes in the Los Peñasquitos wetlands show the relation between microfossil faunal assemblages and modern environmental conditions. Taxonomic revision and illustration of foraminifera and ostracodes from a diversity of southern Californian lagoon and marsh environments refines earlier interpretations of the paleoenvironmental evolution of southern Californian lagoons, and permits comparison with similar environments worldwide. Foraminifera and ostracodes in the coastal wetlands of San Diego County are sensitive indices of shoreline migration, tidal exchange, and salinity that can be used to determine Holocene sea-level.

Pollen records from Los Peñasquitos lagoon are particularly valuable in determining changes in sedimentation rates associated with anthropogenic activities such as local agricultural and urban development. Exotic-pollen datums enable precision dating of sediments deposited after the first European settlement in 1769. There have been major geomorphological as well as biotic changes in most of the lagoons and wetlands investigated. Some changes reflect natural long-term fluctuations in climate and vegetation during the past 8000 BP, but in post-Missionary time (after the 1769-1830 interval), major changes in the southern Californian coastal ecosystems include increased salinity, destruction of marshland by dredging or siltation, restriction of tidal flow by road and railroad embankments and reduction of freshwater inflow by inland reservoirs. Foraminifera show that Los Peñasquitos lagoon was much more open in the mid-Holocene than today, as evidenced by abundant planktic taxa, which prefer the open ocean, and by occurrences of nearshore benthic species. Sustained dredging of tidal channels may restore this wetland pre-Missionary Era conditions. In Tijuana lagoon, where there is little obstruction of the tidal exchange by urban construction, variable microfossil faunas in sections <200 m apart suggest that the beach barrier shifted dynamically over the past 2000 years.

The presence of red (*Rhizophora mangle*) and white (*Laguncularia racemosa*) mangrove tree pollen in the 3000–6000-BP interval at Los Peñasquitos drillhole 1 indicates that in the mid-Holocene this subtropical lagoon vegetation migrated at least as far north as 32.5°N from its present nearest locations of 25.5–28.8°N in Baja California. This is the first time that this mangrove shift has been documented for California in the literature for the Holocene.

The Los Peñasquitos mangrove pollen record implies that the climate was warmer in winter and wetter in summer during the mid-Holocene hypsithermal, while the foraminifera indicate that the subtropical open-lagoon conditions coincided with higher sea levels recorded in many other parts of the world.

TAXONOMIC LIST

- Ammobaculites dilatatus Cushman and Brönnimann, 1948a, p. 39, pl. 7, figs. 10, 11.
- Ammobaculites exiguus Cushman and Brönnimann, 1948a, pl. 7, figs. 7, 8.
 Ammobaculites salsus Cushman and Brönniman, 1948b, p. 16, pl. 3, figs. 7–9.
 Ammotium salsum (Cushman and Brönniman) in Parker and Athearn, 1959, p. 340. pl. 50, figs. 6, 13.
- Ammonia beccarii (Linné) = Nautilus beccarii Linné, 1758, p. 710.
- Astrononion incilis Lankford in Lankford and Phleger, 1973, p. 115, pl. 3, fig. 11.
- Bolivina advena Cushman var. acutula Bandy, 1953, p. 180, pl. 24, fig. 7. Bolivina aculuta Bandy = Bolivina advena Cushman var. acutula
- Bandy, 1953, p. 180, pl. 24, fig. 7. *Brizalina acutula* (Bandy) *in* Lankford and Phleger, 1973, p. 115, pl. 4; Scott and others, 1976, p. 74. (Fig. 24.3)
- Bolivina minuta Natland, 1938, p. 146, pl. 5, fig. 10.

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- *Bolivina pseudoplicata* Heron-Allen and Earland, 1930a, p. 81, pl. 3, figs. 36–40. *In* Lankford and Phleger, 1973, p. 115, pl. 4, fig. 6. (Fig. 24.1)
- Bolivina vaughani Natland, 1938, p. 146, pl. 5, fig. 11. Brizalina vaughani (Natland) in Lankford and Phleger, 1973, p. 115, pl. 4, fig. 9; Scott and others, 1976, p. 74.
- Buccella frigida (Cushman) = Pulvinulina frigida Cushman, 1921 (1922), p. 144. Eponides frigidus (Cushman) in Cushman, 1941, p. 37, pl. 9, fig. 17. Buccella frigida (Cushman) in Andersen, 1952, p. 144.
- Buccella parkerae Anderson. Lankford and Phleger, 1973, p. 116, pl. 4 fig. 20.
- *Buccella tenerrima* (Bandy) = *Rotalia tenerrima* Bandy, 1950, p. 278, pl. 42, fig. 3. *In* Lankford and Phleger, 1973, p. 116, fig. 19.
- *Bulimina marginata* d'Orbigny, 1826, p. 269, pl. 12, figs. 10–12. *In* Lankford and Phleger, 1973, p. 116, pl. 4, fig. 11. (Fig. 24.4)
- Buliminella elegantissma (d'Orbigny) = Bulimina elegantissima d'Orbigny, 1839, p. 51, pl. 7, figs. 13, 14. In Cushman, 1919, p. 606; Scott and others, 1976, p. 74; Lankford and Phleger, 1973, p. 116, pl. 4, fig. 12. (Fig. 24.2)
- Buliminella subfusiformis var. tenuata Cushman, 1927, p. 149, pl. 2, fig. 9. Buliminella tenuata Cushman in Scott and others, 1976, table 2.
- Cancris auriculus (Fichtel and Moll) = ?Nautilus auriculus Fichtel and Moll, 1798, p. 108, pl. 20, figs. d–f. In Lankford and Phleger, 1973, p. 116, pl. 4, fig. 21.
- *Cassidulina subglobosa* Brady, 1881, p. 60; type-fig. in Brady, 1884, pl. 54, figs. 17a–c. *In* Barker, 1960, p. 112, pl. 54, fig. 17.
- *Cyclogyra planorbis* (Schultze) = *Cornuspira planorbis* Schultze, 1854, p. 40.
- *Dyocibicides biserialis* Cushman and Valentine, 1930, p. 31, pl. 10, figs. 1, 2; *In* Lankford and Phleger, 1973, p. 119, pl. 6, figs. 16, 17. (Figs. 24.5, 24.6)
- Eggerella advena (Cushman) = Verneuilina advena Cushman, 1921, p. 9 (141). Eggerella advena (Cushman) in Loeblich and Tappan, 1953, p. 36; Lankford and Phleger, 1973, p. 119, pl. 1, fig. 18. (Fig. 25.12)
- *Elphidium crispum* (Linné) = *Nautilus crispus* Linné, 1758, Systema Naturae: G. Engelmann (Lipsiae), 10, v. 1, p. 709.
- *Elphidium discoidale* (d'Orbigny) = *Polystomella discoidalis* d'Orbigny, 1839, p. 56, pl. 6, figs. 23, 24. *Cellanthus cf. discoidale* (d'Orbigny) *in* Lankford and Phleger, 1973, p. 117, pl. 3, fig. 16. (Fig. 24.10)

- *Elphidium excavatum* f. *clavatum* (Cushman) *In* Loeblich and Tappan, 1953, p. 98, pl. 19, figs. 8–10. *Cribroelphidium* cf. *clavatum* (Cushman) *in* Lankford and Phleger, 1973, p. 117, pl. 3, fig. 24. (Figs. 24.7, 26.6–26.8).
- *Elphidium excavatum* f. *excavatum* (Terquem) = *Polystomella excavatum*, Terquem, p. 429, pl. 2, figs. a–d. (Figs. 26.9).
- *Elphidium excavatum* f. *gunteri* Cole = *Elphidium gunteri* Cole, 1931, p. 34, pl. 4, figs. 9, 10. *Cellanthus gunteri* (Cole) *in* Lankford and Phleger, 1973, p. 116, pl. 3, fig. 17. (Figs. 26.15, 26.16)
- Elpidium excavatum f. lidoensis Cushman = Elpidium lidoensis Cushman, 1936, p. 86, pl. 15, no. 6. (Fig. 26.9–26.14).
- *Elphidium excavatum* f. *selseyensis* (Heron-Allen and Earland) = *Polystomella striatopunctata* (Fichtel and Moll) v. *selseyensis* Heron-Allen and Earland, 1930a, p. 448. (Fig. 26.5)
- Elphidium excavatum f. tumidum Natland = Elphidium tumidum Natland, 1938, p. 144, pl. 5, figs. 5, 6. (Figs. 24.8, 26.1–26.4)
- *Elphidium incertum* (Williamson) var. *clavatum* Cushman, 1930b, p. 20, pl. 7, figs. 10a, 10b.
- Elphidium poeyanum (d'Orbigny) = Polystomella poeyana d'Orbigny, 1839, p. 55, pl. 6, figs. 5, 6. (Figs. 25.14, 25.15)
- Elphidium poeyanum (d'Orbigny) f. spinatum (Cushman and Valentine)
 Elphidium spinatum Cushman and Valentine, 1930, p. 21, pl. 6, figs. 1, 2. Cribroelphidium spinatum (Cushman and Valentine) in Lankford and Phleger, 1973, p. 118, pl. 3, fig. 23.
- Lankford and Phleger, 1973, p. 118, pl. 3, fig. 23. Elphidium translucens Natland, 1938, p. 144, pl. 5, figs. 3, 4. Elphidium spinatum var. translucens Natland in Uchio, 1960, p. 62, pl. 4, figs. 23, 24. Cribroelphidium spinatum var. translucens (Natland) in Lankford and Phleger, 1973, p. 118, pl. 3, fig. 22.
- Fissurina lucida (Williamson) = Entosolenia marginata var. lucida Williamson, 1848, p. 17, pl. 2, fig. 17. Entosolenia lucida (Williamson) in Cushman and Gray, 1946, p. 30, pl. 5, figs. 16–18. Fissurina lucida (Williamson) in Lankford and Phleger, 1973, p. 119, pl. 3, fig. 7. (Fig. 24.12)
- Florilus basispinatus (Cushman and Moyer) = Nonion pizarrense Berry var. basispinata Cushman and Moyer, 1930, p. 54, pl. 7, figs. 18a, b. Nonionella basispinata (Cushman and Moyer) in Walton, 1955, p. 1010, pl. 101, figs. 16, 17. Florilus basispinatus (Cushman and Moyer) in Lankford and Phleger, 1973, p. 119, pl. 4, fig. 17. (Fig. 25.1)
- Fursenkoina pontoni (Cushman) = Virgulina pontoni Cushman, 1932, p. 17, pl. 3, fig. 7. Fursenkoina pontoni (Cushman) in Lankford and Phleger, 1973, 119, pl. 4, fig. 17.
- Fursenkoina sandiegoensis (Uchio) = Virgulina sandiegoensis Uchio, 1960, p. 63, pl. 6, figs. 17, 18. Fursenkoina cf. sandiegoensis (Uchio) in Scott and others, 1976, p. 75. (Figs. 24.13, 24.14)
- Gavelinopsis campanulata (Galloway and Wissler) = Globorotalia campanulata Galloway and Wissler, 1927, p. 58, pl. 9, fig. 14. Gavelinopsis campanulata (Galloway and Wissler) in Lankford and Phleger, 1973, p. 120, pl. 5, fig. 13.
- Glabratella ornatissma (Cushman) = Discorbis ornatissma Cushman, 1925, p. 42, pl. 6, figs. 11, 12. Trichohyalus ornatissima (Cushman) in Lankford and Phleger, 1973, p. 128, 129, pl. 5, figs. 3–6. Glabratella ornatissma (Cushman) in Scott and others, 1976, p. 75. (Figs. 24.15, 24.26)
- Hanzawaia mexicana Lankford in Lankford and Phleger, 1973, p. 122, pl. 6, fig. 20.
- Haplophragmoides advenum Cushman, 1925, p. 38, pl. 6, fig. 1. Alveophragmium advenum (Cushman) in Lankford and Phleger, 1973, p. 114, pl. 1, fig. 7.
- Haplophramoides columbiensis Cushman, 1925, p. 39, pl. 6, fig. 2. Alveolophragmium columbiensis (Cushman) in Lankford and Phleger, 1973, p. 114, pl. 1, fig. 8; Scott and others, 1976, p. 74.
- *Miliammina fusca* (Brady) = *Quinqueloculina fusca* Brady, 1870, p. 286, pl. 11, figs. 2, 3; *Miliammina fusca* (Brady) *in* Phleger and Walton, 1950, p. 280, pl. 1, figs. 19a, b.
- *Oolina melo* (d'Orbigny) = *Entoselina melo* d'Orbigny, 1839, p. 20, pl. 5, fig. 9. *Oolina melo* (d'Orbigny) *in* Lankford and Phleger, 1973, p. 123, pl. 3, figs. 8, 9.
- Patellina corrugata Williamson, 1858, p. 46, pl. 3, figs. 86–89. In Lankford and Phleger, 1973, p. 124, pl. 5, fig. 7.
- Pateoris hauerinoides (Rhumbler) = Quinqueloculina subrotunda (Montagu) forma hauerinoides Rhumbler, 1936, p. 206, 217, 226, figs. 167, 208–212. Pateoris hauerinoides (Rhumbler) in Lankford and Phleger, 1973, p. 124, pl. 2, fig. 14.

- Polysaccammina hyperhalina Medioli, Scott, and Petrucci, 1983 in Petrucci and others, 1983, p, 72–75, pl. 2, figs. 1–8. Protoschista findens (Parker) in Scott, 1976a, p. 170.
- Polysaccammina ipohalina Scott, 1976b, p. 318, pl. 2, figs. 1–4, text figs. 4a–c.
- Quinqueloculina compta Cushman, 1947, p. 87, pl. 19, fig. 2. In Lankford and Phleger, 1973, p. 126, pl. 1, fig. 24.
- Quinqueloculina costata d'Orbigny, 1826, p. 301, pl. 4, fig. 8.
- *Quinqueloculina elongata* Natland, 1938, p. 141, pl. 4, fig. 5. *In* Lankford and Phleger, 1973, p. 126, pl. 1, fig. 19.
- Quinqueloculina laevigata d'Orbigny, 1826, p. 301, no. 6. In Lankford and Phleger. 1973, p. 126, pl. 2, figs. 5,6.
- *Quinqueloculina lamarckiana* d'Orbigny, 1839, p. 189. pl. 11, figs. 14, 15. *In* Lankford and Phleger, 1973, p. 126, pl. 1, fig. 23.
- Quinqueloculina seminulum (Linné) = Serpula seminulum Linné, 1758, p. 786. Quinqueloculina seminulum (Linné) in d'Orbigny, 1826, p. 301.
- Reophax nana Rhumbler, 1911, p. 182, pl. 8, figs. 6–12. In Lankford and Phleger, 1973, p. 127, pl. 1, fig. 4.
- *Rosalina bulloides* d'Orbigny, 1839, p. 98; type-fig. published separately in v. 8, pl. 3, figs. 2–5.
- Rosalina bulloides f. columbiensis (Cushman) = Discorbis columbiensis Cushman, 1925, p. 43, pl. 6, fig. 13. Rosalina columbiensis (Cushman) emend. Lankford and Phleger, 1973, p. 127–128, pl. 5, figs. 10–12. (Fig. 25.5)

Remarks: This species was cultured by Myers (1943), as illustrated in Loeblich and Tappan. (1964) and in San Diego by Scott in 1973. It produced an inflated *bulloides*-form float chamber when the salinity of the culture rose to 60, suggesting that the chamber is an escape mechanism from intertidal areas in regions like southern California with high summer temperatures. *Planorbulina mediterranensis* d'Orbigny has also been observed with a similar float chamber from Greek marshes (Scott et al., 1979).

Originally placed in the genus *Discorbis* by Cushman, this species was later emended by Lankford (in Lankford and Phleger, 1973) as *Rosalina columbiensis*, We consider *R. bulloides* (d'Orbigny) to be a senior synonym with two formae: *bulloides* and *columbiensis*. Loeblich and Tappan (1964) reproduced the life cycle postulated by Myers (1943), which showed the transformation from the attached form (*Rosalina bulloides*) to the planktic form ("*Tretomphalus*" *bulloides*). However, the connection between these morphotypes was not established until the salinity experiment by Scott in 1974 (unpublished). Thus, the planktic form now is referred to as *R. bulloides* f. *bulloides* and the benthic form as *R. bulloides* f. *columbiensis*.

- Saccammina difflugiformis (Brady) = Reophax difflugiformis Brady, 1879, p. 51, pl. 4, figs. 3a, b. Saccammina difflugiformis (Brady) in Thomas and others, 1990, p. 234, pl. 2, figs. 10–12.
- *Spirillina vivipara* Ehrenberg, 1843, p. 223, 442, pl. 3, VII, fig. 41. *In* Lankford and Phleger, 1973, p. 128, pl. 6, fig. 2.
- Textularia earlandi Parker, 1952, p. 458 (footnote). (Fig. 25.13)
- Textularia schencki Cushman and Valentine, 1930, p. 8, pl. 1, fig. 3. In Lankford and Phleger, 1973, p. 128, pl. 1, figs. 13, 14.
- Trifarina fluens (Todd) = Angulogerina fluens Todd in Cushman and Todd, 1947, p. 67, pl. 16, figs. 6, 7. Trifarina angulosa (Williamson) in Lankford and Phleger, 1973, p. 129, pl. 3, figs. 29, 30. Trifarina fluens (Todd) in Feyling-Hanssen and others, 1971, p. 242, pl. 2, figs. 12–15, pl. 18, fig. 10.
- Trochammina inflata (Montagu) = Nautilus inflata Montagu, 1808, p. 81, fig. 3. Trochammina inflata (Montagu) in Parker and Jones, 1859, p. 347.
- *Trochammina kellettae* Thalmann, 1932, p. 313, fig. 28, nos. 8, 9. (Figs. 25.8, 25.9)
- Trochammina macrescens Montagu f. polystoma (Bartenstein and Brand) = Jadammina polystoma Bartenstein and Brand, 1938, p. 381, figs. 1, 2. Trochammina macrescens f. polystoma Montagu in Scott and others, 2001, p. 143, pl 3, figs. 19a–c.

- *Trochammina ochracea* (Williamson) figs. 25, nos. 6, 7 = *Rotalia ochracea* Williamson, 1858, p. 55, pl. 4, fig. 112, pl. 5, fig. 113; *Trochammina squamata* Parker and Jones, 1865, p. 407, pl. 15, figs. 30, 31; Parker, 1952, p. 460, pl. 3, fig. 5.0, p. 45, pl. 4, figs. 4, 5. *Trochammina kellattae* Thalmann, 1932, p. 313 *in* Lankford and Phleger, 1973, p. 130, pl. 3, fig. 5. (Figs. 25.6, 25.7)
- *Trochammina pacifica* Cushman, 1925, p. 39, pl. 6, figs. 3a-c. *In* Lankford and Phleger, 1973, p. 130, pl. 3, fig. 2. (Figs. 25.10, 25.11) *Trochammina vesicularis* Goës, 1894, p. 31, pl. 1, figs. 235–237.

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APPENDICES 1-10

Microfaunal checklists.

- Appendix 1. San Diego Bay
- Appendix 2. Agua Hedionda.
- Appendix 3. Los Peñasquitos.
- Appendix 4. Los Peñasquitos drillhole LP-1.
- Appendix 5. Los Peñasquitos drillhole LP-2.
- Appendix 6. Los Peñasquitos drillhole LP-3.
- Appendix 7. Tijuana drillhole TJ-4.
- Appendix 8. Tijuana drillhole TJ-5.
- Appendix 9. Mission Bay drillhole MB-1.
- Appendix 10. Mission Bay drillhole MB-.

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SCOTT AND OTHERS

Authors Queries

Journal: Journal of Foraminiferal Research Paper: fora-41-03-05 Title: COASTAL EVOLUTION OF SOUTHERN CALIFORNIA AS INTERPRETED FROM BENTHIC FORAMINIFERA, OSTRACODES, AND POLLEN

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