Late Pleistocene Marine Paleoecology and Zoogeography in Central California

GEOLOGICAL SURVEY PROFESSIONAL PAPER 523-C
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By W. O. ADDICOTT

CONTRIBUTIONS TO PALEONTOLOGY

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Invertebrate assemblages analogous to the Aleutian molluscan province indicate a former cool-temperate marine climate

UNITED STATES GOVERNMENT PRINTING OFFICE, WASHINGTON : 1966
CONTENTS

Abstract .................................................................................................................. C1
Introduction ............................................................................................................. 2
Acknowledgments ................................................................................................... 2
Earlier studies ......................................................................................................... 2
Geologic setting...................................................................................................... 3
Point Año Nuevo localities .................................................................................... 3
Santa Cruz localities ............................................................................................. 3
Faunal composition ............................................................................................... 4
Paleoecology ........................................................................................................... 6
Mode of formation ................................................................................................ 6
Probable size of late Pleistocene fauna ................................................................. 8
Bathymetry ............................................................................................................ 8
Paleoecology—Continued
Substratum ............................................................................................................ C9
Marine hydroclimate ............................................................................................ 9
Regional marine paleoclimate ............................................................................. 11
Outer-coast biotope ............................................................................................ 11
Protected-coast biotope ...................................................................................... 13
Zoogeography ....................................................................................................... 15
Modern molluscan provinces ............................................................................. 16
Late Pleistocene molluscan provinces ................................................................. 16
Discussion ............................................................................................................ 17
References ............................................................................................................ 19

ILLUSTRATIONS

[Plates follow index]

PLATE 1. Mollusks and coral.
   2. Mollusks.
   3. Mollusks and echinoid.
   4. Mollusks and barnacle.

FIGURE 1. Index map of Half Moon Bay-Monterey area, central California .................. C3
   2. Index map of the Pacific coast showing places referred to in text ................................ 7
   3. Average annual temperature at surface and at 100 feet in northeastern Pacific Ocean ... 10
   4. Modern shallow-water molluscan provinces of the northeastern Pacific Ocean ........ 12
   5. Modern and inferred late Pleistocene shallow-water marine climate ...................... 14
   6. Late Pleistocene shallow-water molluscan provinces ............................................ 15

TABLES

TABLE 1. Late Pleistocene larger invertebrates ................................................................ C4
   2. Pleistocene mollusks from Point Año Nuevo and Santa Cruz, California, listed by Arnold 4
   3. Late Pleistocene Foraminiferida from Point Año Nuevo and Santa Cruz, California ... 5
   4. Late Pleistocene Ostracoda from Point Año Nuevo, Calif ....................................... 5
   5. Mollusks not previously reported as fossil ................................................................ 6
   6. Modern bathymetric ranges of selected sublittoral mollusks ..................................... 8
   7. Mollusks from the southwestern Santa Cruz Mountains that are extralimital ............ 9
   8. Southern mollusks in the upper Pleistocene Millerton Formation ............................ 14
   9. Late Pleistocene invertebrates from three-quarters mile southwest of Bandon, Oreg. 17
  10. Mollusks from central California to Oregon open-coast assemblages that are now restricted to the Aleutian molluscan province ......................................................... 18
  11. Pleistocene invertebrates from Willapa Bay, southwestern Washington .................. 19
CONTRIBUTIONS TO PALEONTOLOGY

LATE PLEISTOCENE MARINE PALEOECOLOGY AND ZOOGEOGRAPHY
IN CENTRAL CALIFORNIA

By W. O. Addicott

ABSTRACT

Open-coast molluscan assemblages of late Pleistocene age from
northwestern Baja California to Oregon can be grouped to
represent three faunal provinces. The composition of these
units differs significantly from that of modern shallow-water
zoogeographic provinces of the near-shore northeastern Pacific
Ocean area. Late Pleistocene invertebrates of the outer-coast
briotope from central California to Oregon have modern ranges
that overlap in the vicinity of southern British Columbia (lat
48° N.). These assemblages represent the newly recognized
Nuevian molluscan province named for the relatively large open­
coast assemblages from Point Año Nuevo, Calif. (lat 37.1° N.).
To the south, molluscan assemblages broadly comparable to those
of the modern Oregonian province (lat 34.5°–48° N.) occur from
Estero Bay (lat 35.5° N.) south to the Channel Islands (lat 34°
N.). This faunal unit is referred to as the Cayucan province
(restricted). South of the Channel Islands mixed assemblages
with both extralimital northern and southern mollusks character­
ize the open-coast biotopes of southern California and north­
western Baja California. This faunal unit has been named the
Verdean molluscan province (Valentine, 1961).

In the Santa Cruz–Point Año Nuevo area of central California,
the open-coast late Pleistocene biotopes are represented by 101
larger invertebrate taxa, principally mollusks. Also represented
are 27 taxa of Foraminiferida, the largest late Pleistocene
assemblage known from the Pacific coast, and 18 species of
ostreids. The megafossil assemblages represent a fossil assemblage con­
sisting of three principal elements: a rock-boring pelecypod ele­
ment, an epifaunal gastropod element, and a sandy infaunal
pelecypod element. The mollusks inhabited a level-bottom inner
sublittoral biotope consisting of a fine sand substratum with
local rock protuberances. The fossil assemblages are compara­
ble to Sheldrick's (1953) Macoma-Paphia and Strongylocentrotus-
Argobaculum communities of the near-shore northeastern
Pacific Ocean. Bathymetric data on living mollusks suggest
maximum water depths of 15–20 fathoms; physical data suggest
shallower depths, about 10–14 fathoms. Locally the fossil as­
semblages are preserved undisturbed. Usually they are re­
worked or transported, but evidence of significant mixing with
representatives of other communities is lacking. Zoogeographic
criteria suggest relatively cooler surface-water temperatures
during the late Pleistocene interval represented by these de­
posits. There is a moderately large element of extralimital
species that today range no farther south than the latitude of
Puget Sound (48° N.). The foraminifers, with one exception,
have comparable zoogeographic affinities. Former average
surface-water temperatures of about 7.5°C are suggested for the
winter–early-spring period. This is about 4° lower than present­
day temperatures. Yearly high temperatures during the
late-summer–early-fall period may have averaged about 13°C,
about 2° lower than present-day temperatures. The late
Pleistocene marine climate was cool temperate, whereas the
modern climate is temperate.

The relatively cooler late Pleistocene hydroclimate indicated
by fossil assemblages from the lowest emergent terrace in the
coastal area of central California to Oregon differs markedly
from that in the southern California area, where contemporane­
ous fossil assemblages commonly contain both southward- and
northward-ranging extralimital species. Greater climatic ex­
tremes are required by the faunal distributions in southern
California. They have been interpreted as occurring within the
framework of a generally warmer marine climate because of
the sizeable subtropical to tropical molluscan element. The
outer-coast assemblages in the northern part of the late Pleisto­
cene Verdean province are bracketed, however, by assemblages
of predominantly northern aspect in central California and in
northern Baja California, suggesting that the near-shore marine
climate of this part of the northeastern Pacific Ocean may have
been somewhat cooler than at present. The more southern po­
sition of isotherms during the late Pleistocene in central Cali­
fornia and Oregon reflects an overall cooling and relatively
narrow range of temperature, perhaps due to proximity to gla­
cial melt water. The cool-water aspect of the northwestern Baja
California assemblages may be related to heightened seasonal
upwelling as the presence of a few warm-water specimens seems
to indicate a relatively broader range of temperatures than
now prevails in that area. The cool-water aspect of some of
the faunal units conflicts with relatively warm interglacial
paleotemperature estimates from zoogeographic and oxygen
isotope studies of foraminifers from deep-water oceanic cores,
although these are generally from more equatorial areas of
other oceans.

The only significant protected-coast assemblages from the
central California–Oregon area occur in the upper Pleistocene
Millerton Formation of Tomales Bay (lat 38.2° N.). These
assemblages contain extralimital southern species that sug­
gest a warm-temperate hydroclimate. The deposits are diffi­
cult to relate to the open coastal area and may not be con­
temporaneous. Population of this protected biotope by
warm-limited southern mollusks with long larval stages might
have occurred during winter months of northward-flowing
near-shore currents provided water was sufficiently warm.
INTRODUCTION

Segments of the lowest emergent coastal terrace in central California, northern California, and southern Oregon contain scattered assemblages of shallow-water mollusks of late Pleistocene age. The faunal assemblages represent open-coast communities that differ significantly in composition and zoogeographic aspect from the modern invertebrate fauna of this part of the Pacific coast. The largest and perhaps most significant faunal assemblages are from the Point Año Nuevo–Santa Cruz area of central California. The faunal assemblages mark the southern outport of a heretofore unrecognized late Pleistocene molluscan province characterized by northern mollusks and foraminifers that are no longer living off the central California coast. Although the late Pleistocene fauna of the Point Año Nuevo–Santa Cruz area was originally noted by Arnold (1908), its occurrence has been generally overlooked in subsequent studies of Pleistocene mollusks of California, and the original faunal list recorded less than one-third the number of invertebrate taxa herein identified.

The Pleistocene invertebrates from the central California–Oregon area differ compositionally from the well-known late Pleistocene assemblages that occur farther south along the coast—from Estero Bay, Calif. (lat 35.4° N.) to northwestern Baja California. In the northern part, from Estero Bay to the Santa Monica Mountains, molluscan assemblages are broadly comparable to the modern fauna but differ by having a few northern and southern species whose modern ranges do not quite include the fossil localities. Late Pleistocene assemblages south of the Santa Monica Mountains, however, are characterized by an element of warm-water mollusks displaced far to the north of their modern distributional limits and at some localities by extralimital northern species.

The purpose of this report is to enumerate the cool-water late Pleistocene assemblages of the central California–Oregon area, in particular the largely undescribed fauna of the Point Año Nuevo–Santa Cruz area. These new faunal data are used in discussion of paleoecologic interpretations and zoogeographic reconstruction of the shallow water, near-shore shelf invertebrate communities. Finally, a more refined definition of the late Pleistocene molluscan provinces of the southern California–Oregon area is outlined and contrasted with the distribution of similar modern molluscan provinces and marine climatic zones of the near-shore eastern Pacific Ocean.

Collections from the Point Año Nuevo and Santa Cruz localities were made during the period 1962-64. Specimens were collected individually as well as by both dry and wet screening at the outcrop. Bulk and screened samples were returned to the laboratory, where they were examined for microscopic mollusks, Foraminifera, and other minute organisms.

ACKNOWLEDGMENTS

I am indebted to Patsy B. Smith and J. E. Hazel of the U.S. Geological Survey for identification of the Foraminiferida and Ostracoda, respectively, and for data on their modern distribution. E. C. Allison, T. G. Gibson, J. G. Vedder, and J. W. Valentine read the manuscript and offered helpful suggestions and criticism. A. G. Smith, California Academy of Sciences, examined the chitons, and James McLean of the Los Angeles County Museum identified some of the trochids. Thanks are due A. Myra Keen for permission to study Pleistocene and Recent material at Stanford University and for examination of vermitid mollusks. L. G. Hertlein granted access to the collections at the California Academy of Sciences that were used for comparative purposes. Jack Miller assisted in securing collections from Point Año Nuevo and prepared much of the material from these areas. W. C. Bradley and Robert Curry helped collect material from the Santa Cruz and Point Año Nuevo localities. The specimens illustrated herein were photographed by Kenji Sakamoto of the U.S. Geological Survey.

EARLIER STUDIES

Mollusks regarded as Pleistocene by Ashley (1895, p. 349) were reported from the Santa Cruz area with the observation that "at places Haliotis and some other shells are quite plentiful." Inasmuch as Haliotis is not present in Pleistocene collections from this area, it seems possible that Ashley's reference was to aboriginal kitchen midden accumulations, which usually contain abundant Haliotis and some of which appear to be stratified.

Arnold's (1908, p. 355-356) list of 32 gastropods and pelecypods from Santa Cruz and Point Año Nuevo is the first definite record of Pleistocene marine invertebrates from this area. In a subsequent list (Arnold in Branner and others, 1909, p. 7) three taxa identified only to genus were omitted. Several studies of the physical aspects of marine terraces of the southern Santa Cruz Mountains were summarized or referenced in Bradley's (1957) investigation of the 100-foot terrace near Santa Cruz. Brief mention of some of the burrowing pelecypods that occur in the terrace platform near Santa Cruz was made by Bradley (1956) and Addicott (1963a). Assemblages from three localities in the Santa Cruz area were listed by Hoskins (1957).
GEOLOGIC SETTING

POINT AÑO NUEVO LOCALITIES

Pleistocene fossils occur at two localities near Point Año Nuevo (fig. 1). The principal locality, M1690, is on the south side of the point, about 1 mile east-northeast of Año Nuevo Island. A second locality, M2147, is on the north side of the point, about 2 miles north of Año Nuevo Island. Both localities are about 1 mile offshore from the associated late Pleistocene shoreline.

Many exposures of the terrace deposits consist of unfossiliferous fine sand. Fossiliferous deposits presumed to have initially blanketed the terrace platform apparently have been redistributed or removed from these areas by wave or current action.

On the south side of Point Año Nuevo the wave-cut platform is directly overlain by a stratum of fossiliferous sand and sandy gravel that reaches a maximum thickness of 2–3 feet. In the vicinity of the fossil locality the terrace platform is cut into a massive siltstone unit characterized by blocky fracture and iron-stained surfaces. These exposures were mapped as the Miocene Monterey Formation by Hall and others (1959). The bedrock surface is broken by numerous steeply inclined burrows containing large specimens of Penitella penita. Other pelecypods inhabiting pockets or burrows in the terrace platform are Zirfaea pilsbryi, Saxidomus giganteus, and Protothaca staminea ruderalata. The fossiliferous stratum is overlain, locally, by light-gray to tan fine sand.

Much of the fossiliferous stratum at this locality is reworked. Evidence of reworking is furnished by abundant nonarticulated pelecypod valves, a large percentage of broken or abraded shell material, and crude sorting. Reworked parts usually consist of rounded to subangular rock fragments and sand. Areas of undisturbed marine deposits are identified by abundant articulated valves of Macoma inquinata and Saxidomus nuttalli oriented in their normal living positions. There are also many specimens of the near-surface or nestling pelecypod Protothaca staminea with articulated valves. The undisturbed areas consist of gray fine micaceous sand.

The fossiliferous stratum gains altitude eastward from locality M1690 to a point about three-quarters of a mile east of this locality, beyond which the terrace is truncated by a gravel-filled stream channel graded to a lowered sea level. Large articulated valves of Saxidomus or Tresus are visible from the beach near the eastern limit of the fossiliferous stratum, but the fossiliferous bed is inaccessible owing to near-vertical sea cliffs.

North of Point Año Nuevo, the terrace platform dips under the beach but reappears nearly 2 miles to the north near Green Oaks Creek where it is about 10–15 feet above sea level. It is carved out of sandstone of the Pliocene Purisima Formation. Large areas of the platform have been swept clean of sediment, and its surface is extensively pitted with holes of boring pelecypods, many of which still contain valves of large Penitella penita. Collections from this area are principally from burrows, but a few additional specimens were obtained from local exposures of reworked fine fossiliferous sand (loc. M2147).

SANTA CRUZ LOCALITIES

Pleistocene mollusks occur in sea cliffs along a half-mile segment of shoreline just west of Point Santa Cruz (fig. 1). Many of the mollusks in this area are boring or nestling species that occur in the terrace platform or in water-worn boulders lying directly above the platform. The principal locality in this area, M1691, is near the top of a sea cliff at the outer edge of an incipient sea stack. Access is hazardous. The terrace surface here is about 15 feet above sea level. It is cut into fossiliferous sandstone of the Pliocene Purisima Formation. The rock-boring faunal element is dominated by Platycop succulentus. A radiocarbon date on pelecypod shells from this area reported by Bradley (1956) was older than 39,000 years.

Original sand deposits are preserved at locality M1691 as pockets underneath and between large, rather...
The late Pleistocene fauna of the southwestern Santa Cruz Mountains area includes at least 101 larger invertebrate taxa (table 1). Mollusks are the dominant vertebrate taxa (table 1). Mollusks are the dominant

Plese I. cf. Pedina marmorea

Barleeia marmorea

Calliostoma ligatum
cf. (Carpenter) (pl. 2, figs. 4, 5)

Protothaca staminea

San Miguel, Calif.

Mollusks are nearly three times as numerous as pelecypods. Most of the mollusks identified here are figured on plates 1-4.
Astrononion gallowayi
L'Juccella
Rosalina columbiensis
Robertinoides charlottensis
Buliminella elegantissima
Buliminella
Buccella inusitata
Bolivina vaughani
Nonionella basispinata

1964). See figure 4 for limits of molluscan provinces.

(Identified by Elphidium
Spirilina
Cassidulina
Trichohyalus pustulatus

Identifications from Recent
Uvigerina
Pachyderma
Costata

Carter, 1964),

Hazel (written commun.,

lamellosa.

Univ., recovered

Pregon,

zone. Bandy's faunule consisted of 11 species and sub­

identified with

Samidomus giganteus,

Arctic to Aleutian?

M. niocenica

(1960),

Lankford (1962), Loeblich and Tappan (1953) and

Cushman

(Ehrenberg)

Arctic to Panamic.

Arctic to Oregonian.

Arctic to Panamic.

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ima Formation, as its modern bathymetric range is generally much deeper than the associated foraminifers and mollusks would suggest.

| Table 5.—Mollusks not previously reported as fossil |
| Gastropoda: |
| Lirularia funiculata (Carpenter) |
| Lirularia lirulata conica (Carpenter) |
| Lacuna porrecta caequata Carpenter |
| Cerithiopsis cf. C. columna Bartsch |
| Cerithiopsis paramoae Bartsch |
| Cerithiopsis rosei Bartsch |
| Cerithiopsis cf. C. steinbergeri Bartsch |
| Diaphana brunnea Dall |
| Odostomia cf. O. heringi Dall |
| Odostomia stephenseae Dall and Bartsch |
| Odostomia lacomaensis Dall and Bartsch |

Pelecypods:
Adula cf. A. diegensis (Dall)
Adula californiensis (Gould)

PALEOECOLOGY

Speculations on former environmental parameters such as bathymetry and temperature, deduced from biologic and physical evidence, are founded on the uniformitarianism principle of analogy with modern examples. Upper Pleistocene deposits clearly offer a favorable arena in which to interpret the fossil record in terms of modern distribution of marine life and physical properties of their environment. Some factors that permit a much greater degree of refinement in paleoecologic analysis of upper Pleistocene deposits than in older units are: (1) the brief time interval between genesis of the marine upper Pleistocene deposits and the present, possibly on the order of 100,000 years; (2) the presumed contemporaneity or near-contemporaneity of marine deposits of the lowest emergent terrace that can be identified for hundreds of miles along the Pacific coast (Cooper, 1958; Valentine and Liff, 1964; Hoskins, 1957), (3) readily determinable depths of maximum inundation within the upper part of the inner sublittoral zone of Hedgepeth (1957), (4) the slight tectonic disturbance of deposits, (5) the presence of a closely analogous modern depositional environment in the near-shore segment of the submerged post-Wisconsin terrace along the Pacific coast, and (6) the excellent preservation and relatively large size of the marine invertebrate fauna compared with pre-Pleistocene faunas at any given latitude.

Of principal concern in paleoecologic study of the Santa Cruz assemblages is the shallow-water marine climate during deposition. Also of interest are the nature of the substrata of the late Pleistocene sea in this area and the bathymetry at specific localities. Whereas physical characteristics are useful in this respect, the fossil assemblage furnishes evidence upon which temperature speculations can be made. Although zoogeographic implications of the fauna are discussed in a subsequent section, some of the conclusions from the comparison of fossil and modern occurrences are important in the interpretation of marine paleotemperatures and are included here. Place names referred to hereafter are shown on an index map of the Pacific coast (fig. 2).

MODE OF FORMATION

An important step in paleoecological analysis is appraisal of the mode of formation (Johnson, 1960, 1962) of individual fossil assemblages. Both biologic and physical criteria are pertinent to the determination of whether or not a given assemblage represents a transported accumulation (thanatocoenosis or death assemblage) and if so to what extent inhabitants of different biotopes have been brought together. Both the Point Año Nuevo and Santa Cruz assemblages show evidence of reworking of shell material such as abraded shells and abundant shell debris in the crudely sorted deposits. Yet some parts of these deposits have not been reworked. The undisturbed deposits are dominantly fine grained and micaceous and contain abundant articulated valves of several species of pelecypods. One species, Protolithaca staminea, is very abundant at Santa Cruz. Its valves have remained so tightly closed that the interior is devoid of sediment. Most of the articulated pelecypods have ligaments preserved. Some still have patches of periostracum adhering to the shell. Further, some of the abundant infauna—such as the Tresus, Oerithiopsis—may be oriented in their normal living position with the siphonal end of the articulated tests directed upwards and the long axis of the shell normal to the bedding. These taxa are conspecific with some of the dominant mollusks in Sheldorf's Macoma-Paphia community (1935, p. 274), a shallow inner sublittoral level-bottom community of the Puget Sound area, Washington. The less abundant associated gastropod-barnacle-echinoid element seems closely comparable to his Strongylocentrotus-Argo-
buccinum community (p. 280), a hard-bottom sublittoral to upper bathyal community. Some of the Puget Sound species listed as dominants by Sheldorf (1935) that are represented in the outer-coast late Pleistocene assemblages of central California are Macoma inquinata, Protolithaca staminea, Tresus giganteus, Tresus
nuttalli, Strongylocentrotus, Fusitriton oregonensis, Trichotropis cancellata, and Chlamys hercia.

Successive communities of somewhat differing aspect inhabited the terrace platform and overlying sediments. Initial population of the fossiliferous localities occurred after the breaker zone of the rising sea passed inshore. An association of rock-boring pelecypods such as Platydodon and Penitella, nesting mollusks, and epifaunal elements probably dominated the biotope until the rocky surfaces became inundated by sand. In the succeeding life association, species boring and nesting in the platform surface were replaced by sand dwellers such as Saxidomus, Tresus, and Macoma. From all indications, the large invertebrate assemblages represent conditions that obtained during the stillstand of the sea during Pleistocene time. When the overlying water column was approximately 80 feet at the Año Nuevo localities on the basis of the occurrence of the shoreline angle at a present-day altitude of about 100 feet (Bradley, 1965).

During withdrawal of the sea from its maximum shoreline, these localities must have been subjected to the retreating zone of vigorous marine abrasion, a high-energy environment that extends down to about 30 feet below sea level (Dietz and Menard, 1951; Bradley, 1958). Most exposures of terrace cover in the Santa Cruz area seem to have undergone extensive reworking. The occurrence of relatively undisturbed beds of marine fossils at some localities suggests that the late Pleistocene sea must have retreated rapidly from its highest reach. Under conditions of gradual retreat, the high-energy breaker zone probably would have destroyed all traces of the original inner sublittoral fossiliferous deposits. Some admixture of littoral invertebrates might also be expected under these circumstances. Clearly this is not the case. The undisturbed fossiliferous deposits at Santa Cruz underlie a protective ocean-bottom boulder field composed of concretions weathered out of the underlying Purisima Formation. At Point Año Nuevo the reasons for their preservation are uncertain. Possibly the undisturbed sediments occupied slight depressions or pockets in the depositional surface or were overlain by moderate thicknesses of marine sediments, which acted as an effective buffer from the erosive action of the retreating surf zone.

There is no suggestion of faunal mixing in the molluscan assemblages from the central California localities. Evidently the fine-sand-scattered rocky bottom substrata were sufficiently widespread on the surf-cut platform to preclude mixing with specimens from a different biotope. For example, none of the dominant species of Shelford's Pandora-Yoldia community (1935), an inner sublittoral muddy-bottom community.
associated with modern analogs of the late Pleistocene assemblages in the Puget Sound area, occur in the fossil collections.

PROBABLE SIZE OF LATE PLEISTOCENE FAUNA

Sampling of the late Pleistocene fauna at three localities near Santa Cruz has yielded 96 molluscan taxa. In a comprehensive study of the Recent mollusks of the Monterey Bay area, Smith and Gordon (1948, p. 154–155) recorded some 220 mollusks, “many of them gastropods” from “the shallow part of the neritic zone” (5–40 fathoms). These were dredged from a substratum of fine dark sand containing scattered fragments of shale, presumably analogous to the late Pleistocene biotopes represented by the Santa Cruz and Point Año Nuevo assemblages. The authors described a smaller group of mollusks (95) from a Miocene shale reef biotope that occurs at depths of 8–40 fathoms in Monterey Bay. Allowing for some duplication of species in these two biotopes, a total assemblage of nearly 300 species of mollusks is indicated for the middle and upper parts of the inner sublittoral zone of Monterey Bay and the surrounding area. The late Pleistocene collections may represent, therefore, about one-third of the molluscan fauna that might have been present during the late Pleistocene. Comparison with the modern inner sublittoral fauna of Puget Sound would be more meaningful, but comparable quantitative data are not available for that area. If such comparative data were available, a somewhat smaller late Pleistocene assemblage might be expected inasmuch as the invertebrate fauna of the Puget Sound–Queen Charlotte Islands area (Oldroyd, 1924) contains fewer shell-bearing molluscan taxa than that of the Monterey Bay area.

The combined fossil assemblages from the Santa Cruz area are somewhat smaller than the largest recorded late Pleistocene assemblages referable to the exposed coast biofacies, a fauna of 153 mollusks from Point Loma near San Diego, southern California (Valentine and Meade, 1961, p. 10–12), and a faunal assemblage of more than 150 taxa from San Nicolas Island (Vedder and Norris, 1963, p. 50).3

BATHYMETRY

The composition of the larger invertebrate assemblages is indicative of the shallow part of the inner sublittoral zone (0–50 fathoms) of Hedgpeth (1957). Most of the species range from the intertidal zone down to 20–25 fathoms. Some range even deeper. Yet there are several inner sublittoral species whose ranges seem to restrict the bathymetric interval (table 6). These data indicate an overlap in the range of about 15–20 fathoms. It is interesting to note that some of the northward-ranging species such as Fusitriton orogonensis and Calyptraea fastigiata are taken inshore or intertidally in the northern part of their range but submerge toward the south and are obtained only by dredging at middle sublittoral depths. The mollusks recorded from 10 fathoms and deeper off Monterey Bay, Calif., such as Cyclina atonna, may also occur in shallower depths farther north.

Foraminifera from localities M1690 and M1691 suggest an inner-continental-shelf environment with water depths probably less than 100 meters (Patsy B. Smith, written commun., November 1964).

Ostracodes from locality M1691 at Santa Cruz indicate rather shallow inner sublittoral water depths according to J. E. Hazel (written commun., June 1965). The assemblage from Point Año Nuevo, however, suggests somewhat deeper inner sublittoral or possibly outer sublittoral depths.

Physical data tend to corroborate the depths suggested by faunal evidence. The difference in altitude of the wave-cut platform between the Santa Cruz and Año Nuevo localities (15–20 ft) and the shoreline angle

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3 There is a larger unrecorded open-coast assemblage consisting of about 240 species from Emerald Bay near Laguna Beach, Calif. (J. O. Vedder, oral commun., July 1965).

---

| Table 6.—Modern bathymetric ranges of selected sublittoral mollusks in the Point Año Nuevo and Santa Cruz assemblages |
|-----------------|-----------------|
| Species         | Bathymetric data and source |
| Gastropods      | Trichotropis insignis Midden-dorf. |
| Puncturella galeata (Gould) | 10–50 fathoms (Burch, 1946, no. 90, p. 28); 10–75 fathoms (Abbott, 1954, p. 90). |
| Puncturella multistriata | 20–30 fathoms off San Juan Islands, Washington (Oldroyd, 1924, p. 183). |
| Bacia micans (Carpenter) | 5–25 fathoms, Monterey Bay area (Smith and Gordon, 1948). |
| Trichotropis cancellata (Duelos) | 15–25 fathoms, San Juan Islands (Oldroyd, 1924, p. 146); “Commonly dredged in cold, shallow water” (Abbott, 1954, p. 168). |
| Trichotropis insignis (Meden-dorf) | 10–50 fathoms, Monterey Bay (Smith and Gordon, 1948, p. 195), deeper than 75 fathoms off southern California, inshore in Puget Sound area (Valentine and Emerson, 1961, p. 617). |
| Fusitriton orogonensis (Red-field) | 10–60 fathoms, Monterey Bay (Smith and Gordon, 1948, p. 195), deeper than 75 fathoms off southern California, inshore in Puget Sound area (Valentine and Emerson, 1961, p. 617). |
| Cyclina atonna | 10–40 fathoms, Monterey Bay Columbia (Quayle, 1960, p. 70). |
| Pelecypod | Mysella tumida (Carpenter) |
| Mysella tumida (Carpenter) | 15–50 fathoms off California (Burch, 1945, no. 40, p. 15, 24); intertidal to 48 fathoms in British Columbia (Quayle, 1960, p. 76). |
The fossiliferous deposits are about 1–3 feet thick. This is less than the relief on the lowest emergent late Pleistocene terrace platform at Santa Cruz, about 5 feet (Bradley, 1957, p. 430). Relief on the analogous submerged terrace offshore from Santa Cruz may be as much as 10 feet (Bradley, 1957, p. 426). These differences suggest that rock protuberances may have extended above the thin cover of sand, providing refuge for rock-boring pelecypods, a substratum for the gastropod and barnacle epifauna, and attachment for marine algae.

**MARINE HYDROCLIMATE**

A significant feature of the central California fauna is the large representation of extralimital northern species of mollusks and foraminifers in the Point Año Nuevo assemblage and, to a lesser extent, in the Santa Cruz assemblage. About 20 percent of the larger invertebrates has modern distributional patterns that are entirely north of the fossil locality. These species and their known ranges are listed in table 7. Three additional forms—*Cerithiopsis* cf. *C. columna*, *Thais lamellosa*, and *Macoma inquinata*—are now living at or near their southern limit in the latitude of Santa Cruz. Of the more than 80 species of larger invertebrates for which distributional data are available, only 3 do not include the latitude of Puget Sound (48° N.) within their range. These species occur only north of the Puget Sound area (table 7).

### Table 7.—Mollusks from the southwestern Santa Cruz Mountains that are extralimital with respect to their known modern distribution

<table>
<thead>
<tr>
<th>Species</th>
<th>Modern latitudinal range</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Gastropods:</strong></td>
<td></td>
</tr>
<tr>
<td><em>Lepeta concentrica</em> (Middendorff)</td>
<td></td>
</tr>
<tr>
<td><em>Lirularia funiculata</em> (Carpenter)</td>
<td></td>
</tr>
<tr>
<td>cf. <em>L. lirulata conica</em> (Carpenter)</td>
<td></td>
</tr>
<tr>
<td><em>Lacuna porrecta exaequata</em> Carpenter</td>
<td></td>
</tr>
<tr>
<td><em>Brittium eschrichti</em> (Middendorff)</td>
<td></td>
</tr>
<tr>
<td><em>Cerithiopsis paramoea</em> Bartsch</td>
<td></td>
</tr>
<tr>
<td>cf. <em>C. stejnegeri</em> Bartsch</td>
<td></td>
</tr>
<tr>
<td><em>Trichotropis cancellata</em> (Duclos)</td>
<td></td>
</tr>
<tr>
<td>cf. <em>T. insignis</em> Middendorff</td>
<td></td>
</tr>
<tr>
<td><em>Oenopota ? fidicula</em> (Gould)</td>
<td></td>
</tr>
<tr>
<td><em>tabulata</em> (Carpenter)²</td>
<td></td>
</tr>
<tr>
<td><em>Diaphana brunnea</em> Dall</td>
<td></td>
</tr>
<tr>
<td><em>Odostomia</em> cf. <em>O. beringi</em> Dall</td>
<td></td>
</tr>
<tr>
<td>cf. <em>O. columbiana</em> Dall and Bartsch</td>
<td></td>
</tr>
<tr>
<td><em>stephensae</em> Dall and Bartsch</td>
<td></td>
</tr>
<tr>
<td><em>tacomaensis</em> Dall and Bartsch</td>
<td></td>
</tr>
<tr>
<td><strong>Pelecypods:</strong></td>
<td></td>
</tr>
<tr>
<td><em>Saxidomus giganteus</em> (Deshayes)</td>
<td></td>
</tr>
<tr>
<td><em>Tresus capaz</em> (Gould)</td>
<td></td>
</tr>
<tr>
<td><em>Macoma expansa</em> Carpenter</td>
<td></td>
</tr>
<tr>
<td><em>Mya truncata</em> Linne</td>
<td></td>
</tr>
</tbody>
</table>
The Recent distribution of mollusks from the central California localities then strongly suggests comparison with the modern fauna at the approximate latitude of Puget Sound, northwestern Washington. A minimum latitudinal shift of 11° in the range of certain mollusks since the late Pleistocene is thereby implied (table 7). As previously indicated, many of the dominant taxa from modern shallow-water inner sublittoral communities of the Puget Sound area (Shelford, 1935) are abundant in the central California assemblages.

The modern distribution of the Foraminiferida from the marine terrace deposits tends to confirm the evidence for large postdepositional displacement of ranges to the north, and thereby suggests a former cooler marine hydroclimate. Four of the six foraminifers that are abundant or common in the Point Año Nuevo sample (loc. M1690) are now restricted to either the “Arctic” or “Arctic-Aleutian” provinces according to data assembled by Patsy B. Smith (table 3). The two other commonly occurring species include these provinces within their range but also occur farther south. All the other species excepting Bolivina vaughani include at least part of the Aleutian subprovince (southern boundary 48° N.) within their range. Bolivina vaughani has been found living as far north as Bodega Bay, Calif., about 100 miles north of the Santa Cruz area (Lankford, 1962); recently specimens tentatively identified as B. vaughani have been dredged off the Oregon coast (Gerald Fowler, oral commun., April 1965).

Ostracodes from the Point Año Nuevo locality are also of northern aspect in terms of their present-day latitudinal distribution along the coast. Eight taxa for which distributional data are available have modern ranges that overlap in the vicinity of Puget Sound (lat 48° N.) according to J. E. Hazel (written commun., June 1965). Two of the species have modern ranges that include the latitude of the fossil locality (37.1° N.), whereas the remainder are northern forms with southern endpoints between 43° and 48° N., several hundreds of miles to the north (table 4). Hazel emphasizes, however, that because the literature and available samples on Pacific coast ostracodes are relatively meager, zoogeographic inferences drawn from Recent distributions must be considered tentative.

Surface and near-surface water temperatures in the vicinity of northern Washington and southern British Columbia are generally lower than those off central California in the vicinity of the fossil localities (U.S. Hydrog. Office, 1947; Robinson, 1957, fig. 38). Robinson’s surface-water temperature charts of the northeastern Pacific Ocean for the period 1941–52 indicate an average annual inshore temperature differential of about 3°C between Santa Cruz, Calif., and the Straits of Juan de Fuca, Wash., in the low tide to 100-foot-depth range (fig. 3). If these data are representative of longer term temperature conditions, inshore surface-water temperatures near the southern boundary of the Aleutian molluscan province (lat 48° N.) average about 13°C in the warmest months (July–September) and about 7°C in the coolest months (January–March). Comparable maximums and minimums for central Cali-
California in the vicinity of Santa Cruz (lat 37° N.) are 15°C (August–October), and 11½°C (December–April). In this context, the data on modern distribution of shallow-water mollusks in the central California Pleistocene assemblages suggest average winter to early spring temperatures of about 74°C, about 4° lower than present-day temperatures. The suggested average late summer to early fall temperature of about 13°C is about 2° lower than present-day temperatures.

The effect of depth on temperatures in the low-tide-to-100-foot range in middle latitudes appears to be nil during the winter to early spring period (Bolin and Abbott, 1963; Robinson, 1957, fig. 50). In the warmest part of the year, however, a thermocline occurs at depths of 50–100 feet in the northeastern Pacific Ocean (Robinson, 1957, p. 68). Data on vertical temperature distribution in Monterey Bay (Bolin and Abbott, 1963, fig. 2e) indicate that a difference of as much as 2°C may occur between the surface and a depth of about 15 fathoms during the summer months. In all probability, then, average maximum summer surface temperatures in the Pleistocene were somewhat higher than those at depths comparable to the fossil localities, 10–15 fathoms.

**REGIONAL MARINE PALEOClimATE**

It is necessary to utilize average values from the modern thermal regime in zoogeographic paleotemperature inferences. However, seasonal as well as long-term cyclic temperature changes are often masked in charts of average maximum or minimum surface-water temperatures. Monthly sea-surface temperature charts for the northeastern Pacific Ocean (Robinson, 1957), for example, show a complex pattern of near-shore temperature distribution, yet the annual averages show a fairly simple pattern. Furthermore, the near-shore complexities are not at all predictable from the pattern of oceanic isotherms, which is generally aligned in an east-west direction. Rarely do the oceanic isotherms intersect the shoreline of the northeastern Pacific Ocean perpendicularly. Assignment of discrete temperature values to fossil assemblages is particularly subjective; great care should be exercised in quantifying these phenomena. Large displacements of faunal units do seem meaningful, however, if they can be satisfactorily compared with modern faunal provinces. Such distributional shifts are characteristic of late Pleistocene molluscan assemblages from Oregon to Baja California.

**Outer-COast Biotope**

The evidence from other occurrences of late Pleistocene invertebrates of the inner sublittoral exposed-coast biotope from northern California and southern Oregon suggests that cool water was not a local phenomenon. Molluscan assemblages from Crescent City (Addicott, 1963b), Cape Blanco (Bandy, 1950; Addicott, 1964), and Bandon (table 8) all contain extralimital northern species including significant representations of species now restricted to the Aleutian molluscan province of British Columbia and southern Alaska.

The inferred late Pleistocene occurrence of cool water far south of its modern southern limits along the margin of the northeastern Pacific Ocean could be the manifestation of a uniformly cooler marine climate in this area or intensified upwelling in near-shore areas. The coastal segment from Point Conception to Washington is a present-day area of seasonal upwelling of cool water during the late winter, spring, and summer (Bolin and Abbott, 1963, p. 28). It is a well-known fact that local intensification of the upwelling process takes place on the south sides of some of the major points along the Pacific coast. Prevailing north winds move surface water offshore, allowing cool water from below to rise to the surface. The result is a strong temperature contrast between the north and south sides of principal points or capes during periods of strong northerly winds. Although many of the cool-water Pleistocene assemblages occur on or near modern points—Point Año Nuevo, Crescent City, and Cape Blanco—these features were not present as such during deposition of the fossiliferous deposits. In the vicinity of these points, the late Pleistocene shorelines were relatively straight and were well inshore from the fossil localities. Notwithstanding the apparent geographic relationship to potential modern sites of intensified upwelling, it seems that the anomalous southern occurrences of these cool-water assemblages are not the manifestation of local pockets of cool water, because the requisite coastal configuration was not developed near the late Pleistocene localities.

Regional intensification of seasonal upwelling characteristic of the central and northern parts of the Oregonian molluscan province might produce a thermal regime in which a much broader range of temperatures than now exists would occur, provided that temperatures returned to normal levels during intervening periods. Under a broader spectrum of temperatures it would not be unreasonable to expect an invertebrate fauna that would include some southward- and northward-ranging species that do not now occur within the area. Clearly this is not the case with the faunal data from the area considered herein. The zoogeographic unity of the central California–southern Oregon outer-coast late Pleistocene assemblages suggests, rather, a lowering of both seasonal maximum and minimum temperatures to values comparable to those of the southern part of British Columbia.
Although the interpretation of a cool near-shore water mass neatly fits the known data from central California and more northern open-coast assemblages, it is not compatible with the zoogeographic evidence from the outer-coast molluscan assemblages of southern California. The zoogeographic aspect of faunal data from south of the Channel Islands (lat 34° N.) is principally warm temperate to subtropical; however, there are extralimital northern species in some of these assemblages. The thermal regime of the southern California area was doubtlessly more complex than at present. Many workers have interpreted it as being generally warmer, but with local areas of more intense seasonal upwelling to account for the anomalous northern forms. A review of the southern California–northern Mexico late Pleistocene molluscan fauna and in particular some of the zoogeographic evidence suggestive of cool water in these areas seems appropriate.

The occurrence of cool-water outer-coast molluscan assemblages in the San Diego and northwestern Baja California area is noteworthy. Open-coast localities from Point Loma, Calif. (Webb, 1937), to Punta Baja, northwestern Baja California (Emerson and Addicott, 1958; Valentine and Meade, 1961), contain several extralimital northern species. Molluscan assemblages from Punta Cabras (Addicott and Emerson, 1959) and Punta Baja contain a significant element of locally extinct northern species, about 20 percent. Warm-water species are poorly represented in the collections or absent. Modern distributional limits of the northern forms are within the modern Californian province (fig. 4). The number of significantly displaced species in these assemblages, northern mollusks now living in the Oregonian province (fig. 4), is very small. Although the faunal data do not indicate distributional shifts after late Pleistocene time as great as those in central California–Oregon assemblages, they do indicate relatively cooler marine climate than now exists in these areas. Valentine (1954) and Emerson (1956a) postulated that their occurrence in an otherwise warmer climatic framework was due to intensified seasonal upwelling in local near-shore areas. Present-day upwelling in these areas seems to account for similar, but less numerous, records of cool-water northern marine invertebrates and algae (Emerson, 1956a).

Valentine and Meade's (1961, p. 41) paleotemperature determinations from oxygen isotope studies indicate that some of the southern species from exposed coast biotopes of southern California have isotopic temperatures far lower than would be predicted from their modern distribution. Instead, the temperatures are similar to values inferred from zoogeographic distribution of associated northern species. Some of the iso-
topic temperatures from southern forms in protected biotopes are also much lower than temperatures inferred from their modern distribution.

A small Californian element reportedly occurs in late Pleistocene assemblages of the Gulf of California and the west coast of Mexico as far south as Oaxaca (Valentine, 1961, p. 398). These assemblages and the details of their occurrence are too poorly known, however, to determine whether they are contemporaneous with the late Pleistocene fauna of Baja California and farther north or to speculate on their climatic significance.

The evidence of coiling-direction preference in the foraminifer *Globigerina pachyderma* in cores from the outlying basins in the southern California borderland may also be pertinent. Bandy (1960) presents evidence for a Pleistocene sinistral coiling population of this planktonic foraminifer succeeded about 11,000 years ago, by a right-hand coiling population. Modern sinistral coiling in this species is limited to the cool waters of high latitudes (above 60° N.). The cool neritic hydroclimate suggested by the sinistral coiling *Globigerina* existed offshore from a near-shore area which was abundant faunal evidence of a late Pleistocene episode of marine climate that was at times warmer than at present.4

To summarize, this area of warm inshore marine climate seems anomalous in the context of the unusually cool aspect of the central California–Oregon area to the north and the scattered suggestions of cooler climate in parts of northwestern Baja California.5 In a larger sense, however, cool marine climate associated with interglacial high stands of the sea is unexpected and contrary to the zoogeographic and oxygen isotope studies of planktonic foraminifers from the Pleistocene sequence in oceanic cores (Emiliani, 1955, 1961; Ericson and Wollin, 1956). Possibly the relative southerly shift of surface isotherms in the central California–Oregon area was a local cooling brought about by proximity to glacial melt water. The cool aspect of the northern Baja California assemblages more likely is related to intensified upwelling as the occasionally occurring extralimital southern mollusks in these assemblages would seem to be indicative of a relatively broader range of marine temperature.

4The projection of a uniformly cool oceanic climate much beyond the reach of radiocarbon dating is highly speculative. The basin cores may not have reached levels contemporaneous with the in situ and inshore deposits of the lowest emergent marine terrace.

5Average high and low surface temperatures inferred from data on fauna in central California, 12° and 7.5°C, are considerably cooler than comparable figures on open-coast assemblages from southern California, about 20° and 11°C (Valentine and Meade, 1961, p. 25, 32). Comparable temperatures of 14° and 11°C were inferred for two open-coast assemblages in northwestern Baja California by Valentine and Meade (1961, p. 29).

### PROTECTED-COAST BIOTPE

In the central California–Oregon area, the protected bay or estuarine facies of late Pleistocene age are represented only in the Tomales Bay and San Pablo Bay areas. The modern distribution of faunal elements in the Tomales Bay area suggests warm-temperature conditions. About 25 percent of the fossil mollusks of the Tomales Bay area (Dickerson, 1922; Weaver, 1949; Valentine, 1961; Johnson, 1962) occurs north of their modern ranges. These species and their modern northern end-points of range are listed in table 8. Their former occurrence at this latitude requires water temperatures above those which now exist in this area. These assemblages seem to represent the modern Californian province (northern limit 34.5° N.), whereas open-coast assemblages near Santa Cruz several miles to the southeast are compositionally analogous to the fauna of the southern part of the Aleutian province (southern boundary 48° N. lat.). The Californian and Aleutian provinces (fig. 5) may be characterized by warm-temperate and cool-temperate climates respectively (Hall, 1964, p. 231). If the Millerton fauna is contemporaneous with the outer-coast terrace assemblages, the apparent telescoping of the late Pleistocene analogs of the modern Californian and Aleutian provinces, with the resultant absence of assemblages comparable to the intervening modern Oregonian province, suggests a much different thermal regime than now exists in this area. The known late Pleistocene distributions would thereby indicate lower near-surface temperatures in offshore, exposed coastal areas and a somewhat warmer marine climate in protected bay environments. This is not unlike conditions observed in southern California. There is an important difference, however; the outer-coast assemblages, from Santa Cruz northward, do not contain extralimital southern forms.
Figure 5.—Diagrammatic representation of modern and inferred late Pleistocene shallow-water marine climate of the near-shore northeastern Pacific Ocean. Late Pleistocene climatic boundaries after Valentine (1961), in part.

### Table 8.—Southern mollusks in the upper Pleistocene Millerton Formation

<table>
<thead>
<tr>
<th>Species</th>
<th>Modern northern limit of range (California)</th>
<th>Distance from northern endpoint (miles)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apodina sea squirt</td>
<td>Point Conception (Fitch, 1953)</td>
<td>232</td>
</tr>
<tr>
<td>Chione californiensis</td>
<td>Carpentaria (Fitch, 1953)</td>
<td>380</td>
</tr>
<tr>
<td>Chione cf. C. undata (Sowerby)</td>
<td>Goleta (Fitch, 1953)</td>
<td>360</td>
</tr>
<tr>
<td>Chione undata similina</td>
<td>Santa Rosa Island (Dall, 1921)</td>
<td>356</td>
</tr>
<tr>
<td>Corbula porcella (Dall)</td>
<td>Redondo Beach (Burch, 1944)</td>
<td>460</td>
</tr>
<tr>
<td>Laevicardium substratum (Conrad)</td>
<td>Mugu, Ventura County (Burch, 1944)</td>
<td>410</td>
</tr>
<tr>
<td>Leptopetra latiora (Conrad)</td>
<td>Point Reyes (Fitch, 1953)</td>
<td>20</td>
</tr>
<tr>
<td>Littorina unutata (Conrad)</td>
<td>Monterey (Burch, 1944)</td>
<td>130</td>
</tr>
<tr>
<td>Profitectes lucicutis (Carpenter)</td>
<td>Elkhorn Slough (Fitch, 1953)</td>
<td>130</td>
</tr>
<tr>
<td>Senela decisa Conrad</td>
<td>San Pedro (Burch, 1944)</td>
<td>400</td>
</tr>
<tr>
<td>Trachycardium quadragenarium</td>
<td>Monterey Bay (Fitch, 1953)</td>
<td>130</td>
</tr>
<tr>
<td>Crepidula onyx Sowerby</td>
<td>Monterey (Burch, 1946)</td>
<td>130</td>
</tr>
<tr>
<td>Epitonium kindae (Carpenter)</td>
<td>Monterey (Palmer, 1938)</td>
<td>110</td>
</tr>
<tr>
<td>Nassarius delos (Woodring)</td>
<td>Balboa (Chase, 1962)</td>
<td>400</td>
</tr>
<tr>
<td>Shastus littoralis (Hinds)</td>
<td>Morro Bay (Burch, 1945)</td>
<td>203</td>
</tr>
<tr>
<td>Turcica caffea (Gabb)</td>
<td>Monterey (Burch, 1946)</td>
<td>130</td>
</tr>
</tbody>
</table>

1 Occurrence in upper Pleistocene sedimentary deposits of San Pablo Bay area (Weaver, 1949, p. 105).

### Notes

- The modern oceanic cycle includes a period of strong northward-flowing currents near shore which are usually active from October to March along the central and northern California coast (Schwartzlose, 1963, p. 21).
- These currents have minimal speeds of 0.5–0.9 knots as measured by time elapsed between drift bottle.
releases and recoveries. If one assumes this speed and Thorson's 3-week average pelagic larval stage for marine mollusks (1957, p. 480), it is conceivable that mollusk larvae could be transported about 500-900 miles. Reference to the relative displacement from modern end-points of range (table 8) shows that the maximum distance is about 560 miles, well within the theoretical boundaries suggested above.

As indicated earlier, the population of Tomales Bay by southern forms may not have been contemporaneous with the open-coast biocenoses. The fauna of the Millerton Formation may have lived during a relatively warmer interglacial period temporally unrelated to the outer-coast marine terrace faunas—a possibility supported by the absence of warm-water forms from the relatively large open-coast faunas of central California and the overlap of modern ranges of their faunal constituents near the Straits of Juan de Fuca (lat 48° N.). Moreover, the characteristic northern species that are abundant in outer-coast late Pleistocene assemblages of the central California—Oregon area—such as *Macoma inquinata*, *Tresus capax*, *Saxidomus giganteus*, and *Mya truncata*—are not recorded from Johnson's Millerton localities (1962, locs. 1-4), which contain some open-coast species.

**ZOOGEOGRAPHY**

Studies of late Pleistocene molluscan faunas of northwestern Mexico and southern California were initiated by Arnold's (1903) early study of the San Pedro Pleistocene. During the following 50 years or so, assemblages from many local areas in southern California were put on record. During the last decade increasing attention has been focused on interpreting late Pleistocene marine environments represented by the fossil assemblages and on the recognition of Pleistocene molluscan provinces. The abundant and well-preserved late Pleistocene mollusks of northwestern Baja California area and southern California have intrigued many workers. Notable among recent studies is the synthesis of the enormous amount of data from this area by Valentine (1961). Included in his geographic analysis was the recognition of three late Pleistocene molluscan provinces similar in some respects to the modern provinces that occur between Canada and northern Mexico (Valentine, 1961). These provinces (and the comparable modern molluscan provinces) are, from north to south: Cayucan (Oregonian), Verdean (California), and Magdalenan (Panamic and northern overlap with the Californian province). (See figs. 4 and 6.)

**Figure 6.**—Late Pleistocene shallow-water molluscan provinces of the lowest exposed marine terrace of Baja California to Oregon. After Valentine (1961, fig. 9), in part.
MODERN MOLLUSCAN PROVINCES

Molluscan provinces of the near-shore northeastern Pacific Ocean (fig. 4) are defined as areas containing a characteristic assemblage of species. Whereas faunal integrity characterizes the province, a rapid rate of change of fauna defines the boundaries (Newell, 1948, p. 159). Differences in marine climate are believed to be the basis of geographic differentiation of animal distributions. The boundary between the Californian and Oregonian provinces at Point Conception (lat 34.5° N.), for example, marks a significant change in inshore, near-surface marine temperatures. Superimposed upon the normal latitudinal temperature gradient are factors of current anomalies and upwelling in near-shore areas which greatly intensify the gradient in this area. The annual climatic cycle of the California coast north of Point Conception consists of three recognizable seasons: a late winter to late summer period of northerly winds and southward-flowing currents, a period of relative calm during the fall, and a brief winter period of southerly winds and northward-flowing currents (Bolin and Abbott, 1963, p. 28). South of Point Conception, however, ocean currents of the continental borderland are in an almost continual counterclockwise eddy, which seems to break down the normal southward-flowing current operative off the central California coast throughout about two-thirds of the year. Studies of near-shore currents in this area by means of drift bottles (Schwartzlose, 1963, p. 21) suggest that very little surface water passes from the near-shore southern California area into the region north of Point Conception. The period of northerly winds off central California coincides with the onset of upwelling of cool water which tends to suppress near-shore surface temperatures during the first half of the year and thereby creates a strong gradient at either end of the upwelling belt, an area that extends from Point Conception northward as far as Oregon and Washington (Bolin and Abbott, 1963, p. 43). For the Channel Islands area south of Point Conception, for example, Hubbs (1960, p. 110) reports a 10°C temperature gradient in summer seawater temperatures from the west end of San Miguel Island to the south side of Santa Cruz Island.

A fairly strong gradient of decreasing annual surfacewater temperature occurs along the northwestern coast of Washington (Robinson, 1957, fig. 38), and is most pronounced during the last half of the year (Robinson, 1957, figs. 8-30). This period coincides with the normal spawning season of many mollusks in that area (Quayle, 1960). The gradient may therefore act as a barrier to the southern dispersal of cold-limited species characteristic of the Aleutian province.

Short-term changes in the climatic regime of the area north of Point Conception that seem to be of a cyclic nature have been observed during a decade of careful monitoring of oceanographic conditions off central California (Bolin and Abbott, 1963). During these periods some unusual distributions of warm-water plankton have been observed in which species have been collected far north of their normal limits of distribution (Balech, 1960; Bernier, 1960). Similar unusually warm cycles could explain the presence of southern species in the late Pleistocene fauna of Tomales Bay. They might permit some southern warm-limited forms with relatively long larval stages to travel far north of their normal range, possibly during a period of relatively warm climate. Given access to a protected, shallow-water bay free from the influence of seasonal upwelling which acts to depress yearly maximum temperatures, these southern species might be able to establish a reproducing population isolated by considerable distance from its distribution in the outer-coast biotope to the south.

LATE PLEISTOCENE MOLLUSCAN PROVINCES

Whereas the boundaries of Valentine’s (1961) late Pleistocene molluscan provinces compare rather closely with those of modern provinces (figs. 4, 6), the composition of assemblages from comparable biotopes in each province differs significantly from that of their modern counterparts. Two seemingly distinct facies of shallow-water biota are involved. One represents a protected bay or estuarine biotope which, in California at least, includes many southern species with modern ranges that are displaced to the south of the fossil occurrences. The other is from an open- or exposed-coast environment which, in southern California, commonly contains a perplexing mixture of extralimital northern and southern species.

The abundance of faunal data is such that the late Pleistocene analog of the Californian province (Ver- dean province of Valentine, 1961) is satisfactorily defined. It is doubtful that new data can significantly modify its presently known boundaries or composition. Yet the southern and northern provinces are poorly

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1 Woodward (1856), Schenck and Keen (1936), Hall (1961), and others consider this a separate and distinct province; Dall and Bartee (1907) and Newell (1948) consider it part of the Oregonian province. Aleutian is used herein to characterize the faunal unit of the Puget Sound—Queen Charlotte Island area as a matter of convenience in discussing conditions at its southern boundary (lat 48° N.). Full provincial rank is not necessarily implied as it is perhaps doubtful considering Newell’s (1948) analysis of range data. His name for this faunal unit (Columbian) seems, however, to be a synonym of Woodward's (1856) earlier-named Aleutian province.
defined, by comparison, because of the paucity of faunal data. Valentine's definition (1958, 1961) of the northern province, the Cayucan, was admittedly based on very few and incomplete data. The Santa Cruz–Point Año Nuevo fauna, not considered in his definition of the Cayucan province, together with recently described open-coast assemblages of northern California and southern Oregon (Addicott, 1963, 1964), provide a better definition of the late Pleistocene molluscan distribution in this area. These newly considered faunal data modify, as will be subsequently shown, the original concept of that province.

DISCUSSION

The known late Pleistocene faunal data of central and northern California are from the Santa Maria basin, Santa Cruz, Point Año Nuevo, San Francisco Bay, Tomales Bay, and Crescent City. Additional occurrences are known from Cape Blanco and Bandon, Oreg., and Bay Center, Wash.

Open-coast assemblages from Santa Cruz, Point Año Nuevo, Cape Blanco and Bandon (table 9)* are characterized by a persistent element of cool-water forms that now live far to the north. This element amounting to as much as 30 percent of one assemblage, is now almost entirely restricted to the Aleutian province of British Columbia and southern Alaska (southern boundary lat 48° N.).

TABLE 9.—Late Pleistocene invertebrates from three-quarters of a mile southwest of Bandon, Oreg. (CAS loc. 23)

Gastropods:
- Lepeta concentrica (Middendorff)
- ?Pupillaria sp.
- Crepidula cf. C. grandis Middendorff
- Trichiropis cf. T. insignis Middendorff
- Fusinus sp.
- Thais lanellosa (Gmelin) (possibly Recent beach drift)

Pelecypods:
- Mytilus cf. M. edulis forma gianematus Gould
- Pododesmus macrochiasms (Deshayes)
- Transscenia tantilla (Gould)
- Macoma cf. M. incongrua (von Martens)
- Macoma inquinata (Deshayes)
- Mya truncata Linné
- Hiatella sp.

Brachiopods:
- Hemythiris sp.
- Terebratulina unguicula (Carpenter)

Barnacle: Balanus sp.

A review of some of the factors involved in synthesizing widely scattered occurrences of late Pleistocene invertebrates into faunal provinces seems appropriate.

*In addition to the collection at the California Academy of Sciences (table 9), there is a larger unrecorded collection at the University of California, Berkeley, that is being studied by V. A. Zullo.

First, it is assumed that virtually contemporaneous assemblages are being lumped. The extensive coastal terrace that occurs along the California coast at an altitude of less than 100 feet, as a rule, is believed to be synchronous and to represent a relatively higher stand of an eustatic sea level. There is ample evidence of local and broad-scale warping of this marine surface, which locally causes the shoreline angle to depart from horizontal. New techniques of radiometric dating utilizing minute quantities of uranium and thorium in marine fossils hold considerable promise in making refined correlation of upper Pleistocene terrace deposits in tectonically active areas such as the Pacific coast.

Second, the assemblages are closely comparable bathymetrically. Moreover, modern depth ranges of these taxa do not indicate a pronounced distributional break within this bathymetric interval. Third, the fossil deposits represent comparable substrata. At most places, they directly overlie the bedrock surface and are composed of a thin skin of sand or sandy gravel. Both infauna and epifauna are usually represented, and thereby provide a broad base for recognizing fossil molluscan communities. Finally, classification of an assemblage as protected or open coast, if not clearly determinable from faunal composition, can usually be checked by analogy with modern shorelines, which usually mirror closely the late Pleistocene shorelines.

The southern faunas of the Santa Maria basin at Cayucos (Valentine, 1958) and near Point Sal (Woodring and Bramlette, 1950) do not contain representatives of the Aleutian province. They contain only a very few species that are not represented in the modern fauna of the southernmost part of the modern Oregonian province (Valentine, 1958). Most of the extralimital forms are southern species now restricted to the California molluscan province. Although there are two northern forms with present-day southern end points in the vicinity of Monterey Bay in these assemblages, there is no evidence of the great latitudinal shifts of ranges such as occur in the more northern late Pleistocene assemblages.

If the Cayucos fauna is comparable bathymetrically and ecologically to the Santa Cruz and more northern exposed-coast faunas of northern California and southern Oregon, it surely does not represent the same province. It has none of the greatly displaced species of the Aleutian province which characterize the northern assemblages. Yet it seems to be distinct from the exposed-coast assemblages of the Los Angeles basin in that it lacks their characteristic element of warm water, Panamic mollusks.

These open-coast assemblages represent a province of rather limited latitudinal extent, from the Santa Monica
Mountains (lat 34° N.) to a point between Cayucos (lat 35.5° N.) and Santa Cruz (lat 37° N.). The modern analog of this faunal unit is the Oregonian province (lat 34°-48° N.); Valentine (1958) characterizes these assemblages as being almost purely Oregonian in aspect. As an alternative to treatment as a unique province, these assemblages could be regarded as a transitional faunal unit comparable to some of the known overlaps between modern molluscan provinces.

The problematic warm-temperate fauna of the Millerton Formation was originally included in the Cayucan province as the only significant representative of the protected coast biofacies (Valentine, 1958). If this fauna is contemporaneous with the outer-coast terrace assemblages of the Santa Cruz area, an unusual juxtaposition of faunal elements from noncontiguous modern faunal provinces, the Aleutian (southern boundary lat 48° N.) and the Californian (northern boundary lat 34.5° N.) provinces, is indicated. Neither biofacies is mixed as in some late Pleistocene assemblages from southern California where both Panamic and Oregonian forms frequently occur together (Woodring and others, 1946; Valentine, 1955; Emerson, 1956b; Kanakoff and Emerson, 1959).

New faunal data from the Santa Cruz area and other recently described assemblages from northern California and southern Oregon make it advisable to redefine the late Pleistocene molluscan province represented by open-coast assemblages from the Santa Cruz area northward to southern Oregon. At the time that the Cayucos assemblages were designated as being typical of this area (Valentine, 1958, 1961), the more northern assemblages were very poorly known. Subsequent investigations indicate that the Cayucos assemblages are not typical of the more northern area. It is therefore proposed that their use in characterizing the late Pleistocene molluscan assemblages to the north be discontinued and that the Santa Cruz and Point Año Nuevo assemblages, the largest and best known from the area, be adopted as the standard of reference for the late Pleistocene molluscan province lying north of the outer-coast assemblages of the Santa Maria and Santa Barbara-Ventura basins here included in the Cayucan province (restricted). That province can take the substitute name Nuevan for the Point Año Nuevo assemblage. Mollusks characteristic of this faunal province are: Lepeta concentrica, Trichotropis, Sazidomus giganteus, Tresus capax, Macoma inquinata, and Mya truncata. The exclusively Aleutian species from the known open-coast assemblages of central California to southwestern Oregon are listed in Table 10. They range from 8 percent of the molluscan assemblage at Crescent City to 31 percent at Bandon.

<table>
<thead>
<tr>
<th>Province</th>
<th>Santa Cruz (lat 36.9°)</th>
<th>Point Año Nuevo (lat 37.1°)</th>
<th>Crescent City (lat 41.8°)</th>
<th>Cape Blanco (lat 42.8°)</th>
<th>Bandon (lat 43.1°)</th>
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<tbody>
<tr>
<td>Gastropods</td>
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<td>Lepeta concentrica (Middendorff)</td>
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<td>Lepeta fusiformis (Carpenter)</td>
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<td>Lepeta punctata (Carpenter)</td>
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<td>Lepeta truncata (Carpenter)</td>
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<td>Trichotropis f. jenkinsi (Middendorff)</td>
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<td>Odostomia murchisoni (Middendorff)</td>
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<td>Odostomia serrata (Carpenter)</td>
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<td>Odostomia rugosa (Carpenter)</td>
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So few protected-coast assemblages are known from north of southern California that it is extremely difficult to characterize this biofacies. The Tomales Bay assemblages include some species now restricted to south of Point Conception (Table 8). As mentioned earlier, it is convenient to think of these assemblages as more representative of the late Pleistocene Verdean province because of these California faunal elements. They may or may not be contemporaneous with the outer-coast assemblages. If contemporaneous, a condition of overlap not unlike that at the modern Panamic-Californian province boundary (Emerson, 1956a, p. 329) is indicated. The only other known occurrence of this biofacies is a small faunule, presumably of comparable age, from Willapa Bay, southwestern Washington (Kincard, 1957). The assemblage consists of 12 species (Table 11), all of which have modern geographic ranges that include the fossil locality. These species are common to both the modern Oregonian and Aleutian provinces.

Many late Pleistocene fossil assemblages from the Puget Sound area, Washington, and from southwestern British Columbia have been successfully dated by the radiocarbon technique. The marine part of the lowest emergent terrace in California, however, has proven to be too old to be dated by this technique (Kulp and others, 1952; Bradley, 1956; Orr, 1960). Some upper
Pleistocene deposits in the Pacific Northwest, however, are older than the range of radiocarbon resolution, about 30,000–40,000 years, and could possibly be contemporaneous with the California and Oregon terrace deposits. They are the Nickomel Formation (Wagner, 1959) of the Fraser River area, British Columbia, and the Cherry Point Silt (Easterbrook, 1963, p. 1470) of northwestern Washington. Marine mollusks and barnacles occur in both units, but only the fauna of the Nickomel Formation is recorded. Assemblages from the Nickomel Formation suggest water depths of 5–15 fathoms (Wagner, 1959, p. 50). The largest assemblages (loc. 7) contain 40 mollusks, all but one of which occur within their known modern range. The extralimital species, *Odostomia siliqua*, is known only from the type locality in the Aleutian Islands. Wagner determined from the median of midpoints analysis (Schenck and Keen, 1937) that the latitude of the collection was 51° N. (the actual latitude of loc. 7 is 49.1° N.). This calculation was corrected, however, to a “corresponding present-day latitude” (Wagner, 1959, p. 44, 47) of 60.9° N. from a chart prepared by Schenck (1945). The reason for the correction was that the median of midpoints calculated for modern assemblages from British Columbia and Washington fail to agree with the actual midpoint by 2°–12° of latitude, the midpoints regularly plotting 2° or more farther south than the collection.9

Clearly, the Nickomel fauna is closely comparable with that of the Aleutian province (lat 48°–56° N.) and is only slightly displaced, if displaced at all. It is a much cooler water assemblage than those from the Santa Cruz to Cape Blanco area of California and Oregon to the south.

9 Although the Nickomel fauna may have lived in cooler water than currently exists at this latitude, the suggestion of conditions comparable with those about 10° farther to the north are at odds with the basic data. Of the ranges of 40 species known from loc. 7 (Wagner, 1959, p. 8–9), 19, or nearly 50 percent, do not occur north of 60° N. in the modern fauna, and 40 percent of the species occurs no farther north than 58°, about 200 miles south of the assumed modern equivalent.


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PLATES 1–4
PLATE 1

FIGURES 1, 2, 4. *Thais lamellosa* (Gmelin).

1. Height 64 mm, width 38 mm. USNM 649222. Loc. M1690.
2. Height 55 mm, width 33 mm. USNM 649223. Loc. M1690.
3. Height 26.5 mm, width 15.9 mm. USNM 649224. Loc. M1691.


3. Length 41.5 mm, width 31.5 mm. USNM 649225. Loc. M1691.
10. Length 27.5 mm, width 23.5 mm, thickness 5.3 mm. USNM 649226. Loc. M1691.

5. *Amphissa columbiana* Dall. Height 19.7 mm, width 9.6 mm. USNM 649227. Loc. M1691.

6. *Serpulorbis* sp. Length (incomplete) 16.5 mm, width 5.7 mm. USNM 649228. Loc. M1690.


11, 30, 32. *Fusitriton oregonensis* (Redfield).

11. Length (incomplete) 21 mm, width 18.5 mm. USNM 649232. Loc. M1690.


14. *Polinices* sp. Height 13.3 mm, width (incomplete) 11.5 mm. USNM 649237. Loc. M1690.

15. *Acanthina spirata* (Blainville). Height 23.6 mm, width 13 mm. USNM 649238. Loc. M1691.

16. *Nassarius mendicus* forma indisputabilis Oldroyd. Height 17.6 mm, width 8.6 mm. USNM 649239. Loc. M1690.

17, 18. *Ocenebra lurida munda* Dall in Williamson. Height 13.2 mm, width 6.9 mm. USNM 649240. Loc. M1690.

19. *Cylichna attonsa* Carpenter. Height 10.5 mm, width 3.8 mm. USNM 649241. Loc. M1690.


22, 23. *Trophonopsis multicostatus* (Eschscholtz). Height 27.5 mm, width 8.7 mm. USNM 649244. Loc. M1690.


24, 28. Height 15.8 mm, width 32.5 mm. USNM 649245. Loc. M1690.
29. Height 12.1 mm, width 27 mm. USNM 649246. Loc. M1690.


27. *Paritulum occidentale* Bartes. Greatest length 2.5 mm, diameter of aperture 0.6 mm. USNM 649248. Loc. M1691.

31. *Nassarius fassatus* forma coioterus (Woodring). Height 57 mm, width 27 mm. USNM 649249. Loc. M1691.
PLEISTOCENE MOLLUSKS AND CORAL FROM CENTRAL CALIFORNIA
PLATE 2

FIGURE

1. Polinices sp. Height 15.5 mm, width 18.3 mm. USNM 649350. Loc. M1691.
2, 3. Puncturella galeata (Gould). Height 10.1 mm, length 15.5 mm, width 12 mm. USNM 649251. Loc. M1690.
4, 5. Diodora aspera (Echscholtz in Rathke). Height 4.2 mm, length 12.6 mm, width 8 mm. USNM 649292. Loc. M1691.
6. Megatechna bimaculata (Dall). Height 2.9 mm, length 19.7 mm, width 12.3 mm. USNM 649253. Loc. M1691.
7, 8. Puncturella multisirrata Dall. Height 8.6 mm, length 18.9 mm, width 14.4 mm. USNM 649254. Loc. M1690.
9. Mitrella tuberosa (Carpenter). Height 7.3 mm, width 3.3 mm. USNM 649256. Loc. M1690.
10. Mitrella carinata (Hinds). Height 6.2 mm, width 3.3 mm. USNM 649257. Loc. M1691.
11. Mitrella carinata forma gausapata (Gould). Height 6.8 mm, 3.4 mm. USNM 649258. Loc. M1691.
12, 28. Bittium echrichti (Middendorf).
12. Immature specimen. Height 3.1 mm, width 1.7 mm. USNM 649259. Loc. M1691.
28. Height 11.3 mm, width 4.4 mm. USNM 649260. Loc. M1690.
13. Cerithiopsis cf. C. stejnegeri Barstch. Height 3.6 mm, width 1.6 mm. USNM 649261. Loc. M1691.
15, 16. Transenella tallula (Gould). Length 8.2 mm, height 7.3 mm. USNM 649263. Loc. M1690.
18. Cerithiopsis rowelli Barstch. Height 2.8 mm, width 1.2 mm. USNM 649265. Loc. M1690.
19. Cerithiopsis n. sp.? aff. C. kalia Barstch. Height (incomplete) 3.6 mm, width 2 mm USNM 649266. Loc. M1690.
20, 31. Lirularia lirulata conica (Carpenter).
20. Height 4.9 mm, width 4.7 mm. USNM 649267. Loc. M1691.
31. Height 3.8 mm, width 3.4 mm. USNM 649268. Loc. M1691.
22. Balcis cf. B. micans (Carpenter). Height 5.4 mm, width 2.2 mm. USNM 649270. Loc. M1691.
23. Amphissa columbiana Dall. Immature specimen. Height 8.1 mm, width 3.1 mm. USNM 649271. Loc. M1690.
25, 34. Barlesia marrorea (Carpenter).
25. Height 2.9 mm, width 1.5 mm. USNM 649274. Loc. M1691.
34. Height 2.5 mm, width 1.4 mm. USNM 649275. Loc. M1691.
26. Odostomia tacomensis Dall and Barstch. Height 3.7 mm, width 2.2 mm. USM 649276. Loc. M1690.
27, 50. Ocnebra interfossa Carpenter.
27. Height 14 mm, width 6.6 mm. USNM 649277. Loc. M1691.
50. Height 19.1 mm, width 9.3 mm. USNM 649278. Loc. M1690.
29. Epitonium indiannorum (Carpenter). Height 7.4 mm, width 3.3 mm. USNM 649279. Loc. M1690.
30, 48. Nassarius fossatus (Gould).
30. Height 30 mm, width (incomplete) 15.2 mm. USNM 649280. Loc. M1691.
48. Immature specimen. Height 11.5 mm, width 13.5 mm. USNM 649281. Loc. M1690.
32, 37, 38. Lacuna solidula compacta (Carpenter).
32. Height 2.5 mm, width 2.2 mm. USNM 649282. Loc. M1691.
37. Height 2.8 mm, width 2.2 mm. USNM 649283. Loc. M1691.
38. Height 2.7 mm, width (incomplete) 2 mm. USNM 649284. Loc. M1691.
33. Diaphana brunnea Dall. Height 1.6 mm, width 1.1 mm. USNM 649285. Loc. M1691.
35. Height 1.5 mm, width 1 mm. USNM 649286. Loc. M1691.
36. Height 1.5 mm, width 1 mm. USNM 649287. Loc. M1691.
39. Odostomia cf. O. beringi Dall. Height 5.3 mm, width 2.6 mm. USNM 649288. Loc. M1690.
40. Odostomia cf. O. columbiana Dall and Barstch. Height 4.8 mm, width 2.2 mm. USNM 649289. Loc. M1690.
41. Odostomia aelli ana Carpenter. Height 6.2 mm, width 3.4 mm. USNM 649273. Loc. M1691.
42. Odostomia cf. O. steptensae Dall and Barstch. Height 6.7 mm, width 2.5 mm. USNM 649290. Loc. M1690.
43. Cerithiopsis paramoea Barstch. Height 6.9 mm, width 2.3 mm. USNM 649291. Loc. M1691.
44. Onoprotas tabulata (Carpenter). Height 8.9 mm, width 4 mm. USNM 649292. Loc. M1690.
45, 47. Lacuna porrecta ezaequata Carpenter.
45. Height 5.3 mm, width 4.1 mm. USNM 649293. Loc. M1691.
47. Height 4.1 mm, width 3.4 mm. USNM 649295. Loc. M1691.
46. Lacuna carinata Gould. Height 5.7 mm, width 4 mm. USNM 649294. Loc. M1691.
49. Odostomia teneiisculpta (Carpenter). Height 11.9 mm, width (incomplete) 4.9 mm. USNM 649296. Loc. M1690.
51. Searlesia dira (Reeve). Height 39.5 mm, width 19.7 mm. USNM 649297. Loc. M1691.
PLEISTOCENE MOLLUSKS FROM CENTRAL CALIFORNIA
PLATE 3

2. Platyodon cancellatus Conrad. Length (incomplete) 51 mm, height (incomplete) 31.5 mm. USNM 649299. Loc. M1691.
5. 12. Crepidula adunca Sowerby. Length 6.1 mm, width 3.9 mm, height 3.7 mm. USNM 649302. Loc. M1691.
6. Mya truncata Linné. Length (nearly complete) 34 mm, height 24 mm. USNM 649303. Loc. M1690.
7, 9. Lepeta concentrica (Middendorff).
7. Length 12.7 mm, width 10.5 mm, height 4.7 mm. USNM 649304. Loc. M1690.
9. Length (nearly complete) 13.4 mm, width 4.5 mm, height 5.7 mm. USNM 649305. Loc. M1690.
8, 20. Olivella cf. O. pedroana (Conrad).
8. Height 12.7 mm, width 6 mm. USNM 649306. Loc. M1690.
20. Height 11.0 mm, width 5.5 mm. USNM 649307. Loc. M1690.
10, 11. Velutina laevigata (Linné). Height 3.9 mm, width 4.4 mm. USNM 649308. Loc. M1691.
15. Tresus nuttalli (Conrad). Length 56 mm, height 59 mm. USNM 649311. Loc. M1691.
17. Olivella biplicata (Sowerby). Height 20.5 mm, width 11.4 mm. USNM 649313. Loc. M1691.
18. Strongylocentrotus sp. Length 7.2 mm, width 1.4 mm. USNM 649314. Loc. M1691.
PLEISTOCENE MOLLUSKS AND ECHINOID FROM CENTRAL CALIFORNIA
PLATE 4

**Figure**


6, 8. *Balanus crenatus* Bruguière.

6. Tergum. Length 3.4 mm, width 2.1 mm. USNM 649320. Loc. M1690.

8. Scutum. Length 3.7 mm, width 4.4 mm. USNM 649321. Loc. M1690.


10, 11. *Cryptomya californica* Conrad.

10. Length 18.7 mm, height 11 mm. USNM 649324. Loc. M1691.

11. Length 18.9 mm, height 13 mm. USNM 649325. Loc. M1691.


17. *Ostrea* sp. Internal view of an immature specimen. Length 2.9 mm, height 3.1 mm. USNM 649330. Loc. M1691.


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