

Thermally anomalous assemblages revisited: Patterns in the extraprovincial latitudinal range shifts of Pleistocene marine mollusks

Kaustuv Roy Department of Biology, University of California, San Diego, La Jolla, California 92093

David Jablonski Department of Geophysical Sciences, University of Chicago, 5734 South Ellis Avenue, Chicago, Illinois 60637

James W. Valentine Museum of Paleontology and Department of Integrative Biology, University of California, Berkeley, California 94720

ABSTRACT

Pleistocene faunas of the eastern Pacific shelf are characterized by thermally anomalous species assemblages—i.e., coexisting species that inhabit different climatic regimes today. We used data on the latitudinal ranges of 2887 extant molluscan species to determine the biological basis of the Pleistocene faunal migrations. Overall, the species exhibiting the most extensive range shifts (termed extraprovincial species) were not drawn randomly from the available species pool, and the pattern is climatically asymmetrical. The latitudinal ranges of southern extraprovincial species are significantly wider on average than those of the species pool from which they were drawn, but the ranges of northern extraprovincials resemble those of their parent pool. This contrast is primarily a consequence of the biogeographic structure of the eastern Pacific fauna; water-mass boundaries are more effective barriers for southern species migrating north in response to changing climatic conditions than for northern species moving south. Our analysis of Pleistocene marine mollusks provides a biological and environmental context for species response to environmental change and permits predictions about the movement of eastern Pacific species relative to major environmental barriers in the face of future global change.

INTRODUCTION

Pleistocene marine assemblages have long been known to contain thermally anomalous associations—i.e., co-occurring species that today inhabit distinct climatic regimes. This pattern has been particularly marked for the eastern Pacific mollusks (early references include Carpenter, 1866; Arnold, 1903; Smith, 1919). Increasing knowledge of Pleistocene biogeography has shown that these anomalies are part of a more general pattern of community breakup and species reassembly in response to climatic changes. Individualistic species response to climate change was evidently the rule during the Pleistocene, as documented for terrestrial floras (e.g., Davis, 1986; Webb, 1992; Prentice et al., 1991; Servant et al., 1993), insects (reviewed by Elias, 1994), mammals and herpetofaunas (Graham and Grimm, 1990; Holman, 1993), as well as benthic marine organisms (e.g., Valentine and Jablonski [1993] for mollusks and Cronin and Ikeya [1987] for ostracods). While such geographic shifts bear significantly on many evolutionary and ecological questions (including the design of biological reserves, see Graham and Grimm, 1990; Jablonski, 1991), few studies have addressed the biological basis for the differential extent of migration, particularly in marine organisms. In this paper, we show that the species that exhibit the most significant range shifts, having crossed provincial boundaries relative to their present-day distributions, are not a random sample of the eastern Pacific fauna. This pattern has implications for the origin of thermally anomalous assemblages and for their biological consequences.

CALIFORNIAN PLEISTOCENE FAUNA

The Pleistocene molluscan record of the extratropical eastern Pacific shelf is well documented by large collections from nearly 400 localities (Valentine, 1989). Over 75% of the living molluscan species of the Californian province (extending from Cedros Island [28°N], Baja California, to Point Conception [34.5°N], California; see Valentine, 1966) are also present as Pleistocene fossils; no common or ecologically important species are missing (Valentine, 1989; Valentine and Jablonski, 1993). However, of the 750 species in our Californian Pleistocene database, 90 live only to the north or south of the Californian province today (Fig. 1). These extraprovincial

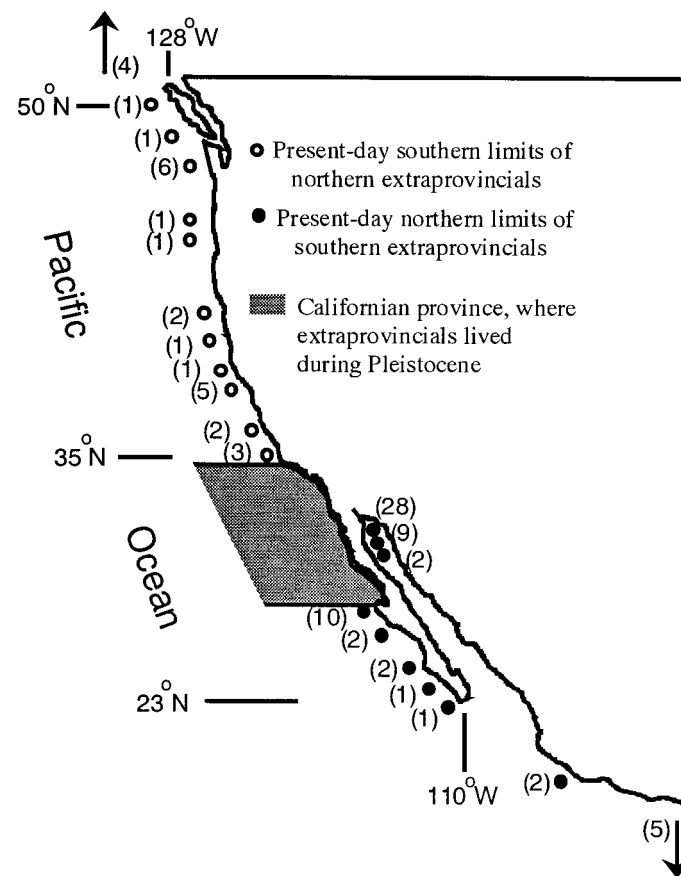


Figure 1. Present-day distribution of Pleistocene extraprovincial molluscan species along eastern Pacific shelf. Numbers in parentheses are number of extraprovincial species whose ranges end at that latitude. Arrows indicate that southern limits of four northern extraprovincial species and northern limits of five southern extraprovincial species fall outside area shown.

TABLE 1. COMPARISON OF LATITUDINAL RANGES

Fauna	No. of Species	Median latitudinal range (°)	Probability (<i>p</i>)	
			Mann-Whitney U test	Kolmogorov-Smirnov test
Holocene	2797	18		
Extraprovincial (all) Panamic	90 1804	25 21	<0.0001	0.0009
S. extraprovincial Oregonian and Arctic	62 812	33 17.5	<0.0001	<0.0001
N. extraprovincial	28	19	0.58	0.22

species are the focus of this study. The vast majority of Pleistocene mollusks of the Californian province show evidence of migration (i.e., their latitudinal range endpoints do not coincide with their present range limits; Valentine and Jablonski, 1993) and can be termed “extralimital” at some localities. However, the distinction between species that crossed provincial boundaries (i.e., extraprovincial species) and those that only migrated within the province is important, not only because of the scales of migration involved, but also because of the nature of the physical barriers crossed. Eastern Pacific provincial boundaries coincide with contacts between contrasting water masses or water types with distinctive temperature regimes and hence represent important physical barriers to species migration (see Valentine, 1966; Roy et al., 1994); extraprovincial species thus crossed much more formidable physical barriers than did those that shifted intraprovincially. The Pleistocene pattern described here is robust to sampling bias because it depends not on negative evidence but on the Pleistocene co-occurrence of species that today are disjunct.

METHODS

The Pleistocene faunal distributions were compared to the latitudinal ranges of 2887 species of bivalves and gastropods living today in waters shallower than 200 m from Peru to the Arctic Ocean. The Holocene latitudinal ranges of these species were compiled from museum collections and the primary molluscan literature (see Jablonski and Valentine, 1990; Roy et al., 1994). The Pleistocene data set comprises about 750 molluscan species that are known to have been present in the Californian region during the past ~1 m.y. Of these, 62 species are represented today by populations living only in provinces to the south of the Californian province, whereas 28 live only to the north. We compared the present latitudinal ranges of (1) all extraprovincial Pleistocene species to those of the rest of the Holocene fauna, (2) the southern extraprovincial Pleistocene species to the rest of the Panamic species—i.e., the species pool from which they were drawn, and (3) the ranges of the northern extraprovincial species to those of the rest of the species living to the north of the Californian province. Because the frequency distributions of ranges are not normal, nonparametric statistics were used throughout.

RESULTS AND DISCUSSION

The present-day latitudinal ranges of the extraprovincial Pleistocene species tend to be significantly wider than those of the rest of the eastern Pacific fauna (Table 1; Fig. 2A). However, an interesting asymmetry emerges when the southern extraprovincials are

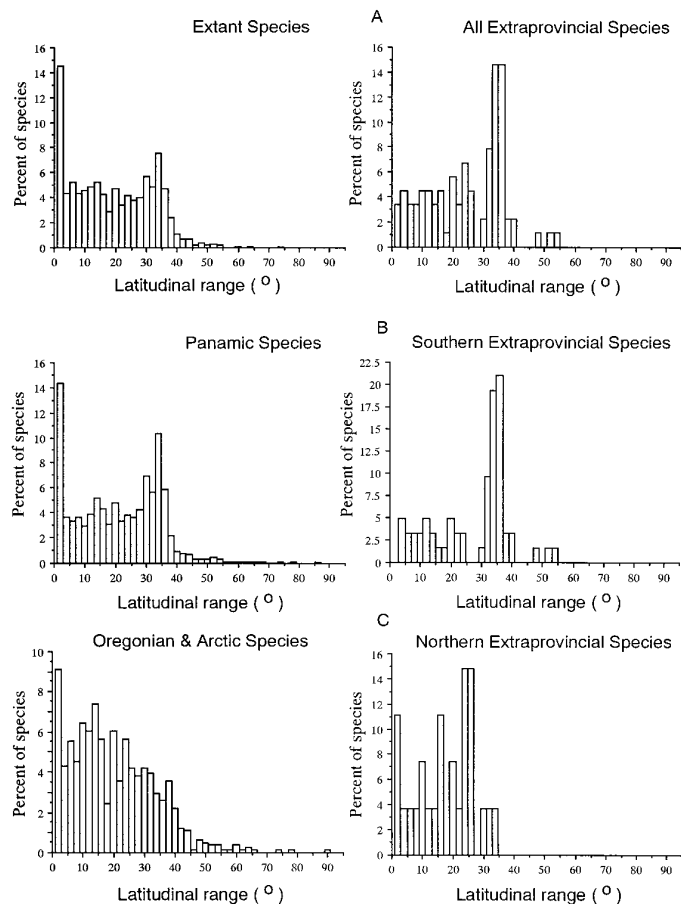


Figure 2. Comparisons of frequency distributions of latitudinal ranges of eastern Pacific molluscan species. Each bar represents 2° of latitude. See Table 1 for statistical treatments.

treated separately from the northern ones. The southern extraprovincial species are drawn from the widespread end of the frequency distribution of geographic ranges of their source biota in the Panamic province, and the frequency distributions of these extraprovincials are significantly different from those of their source biota (Table 1 and Fig. 2B). In contrast, the latitudinal range frequency distribution of the northern extraprovincials is statistically indistinguishable from that for the Oregonian and Arctic province species—i.e., the pool from which the northern extraprovincials were drawn (Table 1 and Fig. 2C).

The difference between the northern and southern extraprovincial species can be understood in terms of eastern Pacific biogeography. For southern forms that expanded their ranges during warming trends, the warmer waters found to the north tend to be at shallow depths. Furthermore, species that range into very shallow waters (intertidal to 1 m) tend to have extensive geographic ranges and physiological tolerances (see Jackson, 1974; Jablonski and Valentine, 1981; Jablonski et al., 1985), and so these are the species preadapted for extensive migrations. In contrast, for northern forms migrating southward during cooling trends, cooler waters can be found in both shallow and deep environments, and cool upwelling patches provide opportunities for latitudinal range extensions beyond water-type boundaries (Valentine, 1955; Emerson, 1956). Therefore, in this case, migrators can be drawn from any depth on the shelf, and the water-mass barriers are “leaky” filters that are less demanding of thermal or other tolerances for the northern forms

TABLE 2. COMPARISON OF MINIMUM BATHYMETRIC RANGES

Fauna	No. of Species	Species. in 0-1 m (%) [*]	Average minimum depth (m) [†]	Mann-Whitney U test §
Panamic	1565	61±2	9±0.6	$p = 0.003$
S. extraprovincial Oregonian and Arctic	53 667	77±12 55±4	2±1 14±1	
N. extraprovincial	22	50±21	12±5	$p = 0.76$

^{*} Error estimates represent 95% confidence interval.
[†] Error estimates represent 1 standard error of the mean.
[§] Based on the entire range of data; they include species with minimum bathymetric ranges deeper than 1 m.

than for the southern ones. A given provincial barrier is thus perceived differently by northern and southern species.

Two lines of evidence support this interpretation of barrier effectiveness. First, a significantly greater percentage of the northern latitudinal range endpoints of extant eastern Pacific mollusks cluster at the major provincial boundaries, compared to the southern range endpoints. The five provincial boundaries between the equator and 71°N account for 31% ± 2% of all the northern range endpoints, but only 17% ± 2% of the southern range endpoints (error bars represent 95% confidence limits calculated following Raup, 1991); the distributions of northern and southern latitudinal range endpoints are also significantly different on the basis of both Kolmogorov-Smirnov and Mann-Whitney U tests ($p < 0.0001$). This result indicates that the contacts between different water masses serve as effective barriers to the migration of southern species but are less effective when approached from the north. Second, a comparison of the present-day bathymetry of the Pleistocene southern extraprovincials to that of the rest of the Panamic species shows that the former not only have a significantly higher percentage of species in the shallowest waters, but overall have significantly shallower depth distributions than the species pool from which they were drawn (Table 2). The same, however, is not true for the northern extraprovincial species, where the percentage of shallowest water forms is indistinguishable from that of the Oregonian and Alaskan species pool (Table 2). Further, this contrast demonstrates that the patterns observed here are not simply due to a sampling bias toward shallow-water species in the fossil record, as might be suspected if both sets of Pleistocene extralimitals were composed of shallow-water forms.

Thermally anomalous molluscan assemblages might be generated by factors other than climatic change (see DeVries and Wells, 1990, for a Holocene example). Of the hypotheses formulated for the Pleistocene mollusks of the eastern Pacific, reworking of deep-water species into shallow assemblages (Woodring et al., 1946) appears unlikely, given the postmortem behavior of shells (see Zinsmeister [1974] and Kidwell and Bosence [1991] on hydrodynamic transport). At any rate, most of the extraprovincial species are known to range into fairly shallow waters. Our results also argue against the hypothesis that the thermally anomalous eastern Pacific molluscan assemblages resulted from temporary changes in current patterns that transported tropical larvae into cooler waters, giving rise to isolated, ephemeral populations (Zinsmeister, 1974). Not only are the extraprovincial species locally abundant in Pleistocene

assemblages, but some of these species lack a planktotrophic larval stage (e.g., the northern *Searlesia dira* and *Nucella lima*) and thus are unlikely to take advantage of short-term fluctuations in current patterns (Valentine, 1980). Some extraprovincial species do have pelagic larval stages, but that may simply reflect the correlation of dispersal ability and geographic range (Scheltema, 1971, 1988; Jablonski, 1986).

A general correlation between faunal histories for the eastern Pacific and thermal histories derived from stable isotopes lends support to a climatic explanation for the extraprovincial migrations. Improved dating of Pleistocene terraces has shown that molluscan assemblages rich in northern extralimital species generally correspond to cooler-than-present intervals, whereas assemblages with many extralimital southern species correspond to intervals characterized by climates warmer than the present (see Valentine, 1980; Kennedy et al., 1988, 1992; Muhs et al., 1994). This is also consistent with recent findings that significant changes in the composition of marine species assemblages can occur over ecological time scales in response to warming trends (see Barry et al., 1995). Our results suggest that environmental tolerances of individual species (and associated latitudinal ranges) played a fundamental role in determining the responses of marine species to such changes and that the biogeographic situation mediated these responses.

The model of faunal response presented here depends on the relative differences in water temperature and other physical factors across provincial boundaries rather than on absolute magnitudes of such differences. Although each of the eastern Pacific provinces recognized today can be traced back through the Pleistocene (see Valentine, 1961; Kennedy, 1978; Valentine and Jablonski, 1991), it is clear that oceanic paleotemperatures off California have fluctuated in a complex manner during that time. For example, Muhs and Kyser (1987), using stable isotopic compositions of fossil mollusks, have inferred cooler-than-present water temperatures off the California coast during oxygen-isotope substages 5a, 5c, and 5e. This inference is consistent with faunal data (e.g., Kennedy, 1978), but the reasons for such among-interglacial variations are poorly understood. However, the model presented here should be robust to such second-order fluctuations so long as the relative differences between the water masses across provincial boundaries are maintained, as seems to be indicated by the maintenance of strong provinciality throughout Pleistocene time.

Our results also have implications for the design of biological reserves and for modeling the biotic consequences of future global change. Previous studies have used Pleistocene examples to argue for incorporating into such models the individualistic response of species to climate change (see Graham and Grimm, 1990; Jablonski, 1991). However, although the Pleistocene is replete with empirical observations about community breakup and reassembly, in most cases the controls of environmental parameters and physiological tolerances on species distributions are poorly understood (see Davis, 1990; Cronin and Schneider, 1990). Our analysis of Pleistocene marine mollusks puts the individualistic species responses into a biological and environmental context that permits predictions about the movement of eastern Pacific species relative to major environmental barriers in the face of future global change. Furthermore, given the nature of the changes described here, the insights gained from this study are probably also applicable to the nonmolluscan species in benthic marine communities, including commercially important demersal fishes and crustaceans.

ACKNOWLEDGMENTS

Supported by National Science Foundation grants EAR90-05744, EAR91-96068, and EAR93-17114. We thank E. V. Coan and P. H. Scott for updated information on the distributions of extratropical bivalves; J. H.

McLean, G. L. Kennedy, and L. T. Groves (Natural History Museum of Los Angeles County) for advice and access to Holocene and Pleistocene molluscan collections; and J. Barry, T. M. Cronin, S. M. Kidwell, and two anonymous reviewers for valuable comments.

REFERENCES CITED

- Arnold, R., 1903, The paleontology and stratigraphy of the marine Pliocene and Pleistocene of San Pedro, California: California Academy of Sciences Memoir 3, 420 p.
- Barry, J. P., Baxter, C. H., Sagarin, R. D., and Gilman, S. E., 1995, Climate-related, long-term faunal changes in a California rocky intertidal community: *Science*, v. 267, p. 672–675.
- Carpenter, P. P., 1866, On the Pleistocene fossils collected by Col. E. Jewett at Santa Barbara, California, with description of new species: *Annals and Magazine of Natural History*, ser. 3, v. 17, p. 274–278.
- Cronin, T. M., and Ikeya, N., 1987, The Omma-Manganji ostracod fauna (Plio-Pleistocene) of Japan and the zoogeography of circumpolar species: *Journal of Micropalaeontology*, v. 6, p. 65–88.
- Cronin, T. M., and Schneider, C. E., 1990, Climatic influences on species: Evidence from the fossil record: *Trends in Ecology and Evolution*, v. 5, p. 275–279.
- Davis, M. B., 1986, Climatic instability, time lags, and community disequilibrium, in Diamond, J., and Case, T. J., eds., *Community ecology*: New York, Harper & Row, p. 269–284.
- Davis, M. B., 1990, Biology and paleobiology of global climate change: Introduction: *Trends in Ecology and Evolution*, v. 5, p. 269–270.
- DeVries, T. J., and Wells, L. E., 1990, Thermally-anomalous Holocene molluscan assemblages from coastal Peru: Evidence for paleogeographic, not climatic change: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 81, p. 11–32.
- Elias, S. A., 1994, Quaternary insects and their environments: Washington and London, Smithsonian Institution Press, 284 p.
- Emerson, W. K., 1956, Pleistocene invertebrates from Punta China, Baja California, Mexico: *American Museum of Natural History Bulletin* v. 111, p. 317–342.
- Graham, R. W., and Grimm, E. C., 1990, Effects of global change on the patterns of terrestrial biological communities: *Trends in Ecology and Evolution*, v. 5, p. 289–292.
- Holman, J. A., 1993, British Quaternary herpetofaunas: A history of adaptations to Pleistocene disruptions: *Herpetological Journal*, v. 3, p. 1–7.
- Jablonski, D., 1986, Larval ecology and macroevolution in marine invertebrates: *Bulletin of Marine Science*, v. 39, p. 565–587.
- Jablonski, D., 1991, Extinctions: A paleontological perspective: *Science*, v. 253, p. 754–757.
- Jablonski, D., and Valentine, J. W., 1981, Onshore-offshore gradients in Recent eastern Pacific shelf faunas and their paleobiogeographic significance, in Scudder, G. G. E., and Reveal, J. L., eds., *Evolution today*: Pittsburgh, Carnegie-Mellon University, p. 441–453.
- Jablonski, D., and Valentine, J. W., 1990, From regional to total geographic ranges: Testing the relationship in Recent bivalves: *Paleobiology*, v. 16, p. 126–142.
- Jablonski, D., Flessa, K. W., and Valentine, J. W., 1985, Biogeography and paleobiology: *Paleobiology*, v. 11, p. 75–90.
- Jackson, J. B. C., 1974, Biogeographic consequences of eurytopy and stenotopy among marine bivalves and their evolutionary significance: *American Naturalist*, v. 108, p. 541–560.
- Kennedy, G. L., 1978, Pleistocene paleoecology, zoogeography and geochronology of marine invertebrate faunas of the Pacific Northwest coast (San Francisco Bay to Puget Sound) [Ph.D. thesis]: Davis, University of California, 824 p.
- Kennedy, G. L., Wehmiller, J. F., and Muhs, D. R., 1988, Late Pleistocene climatic change: Evidence from coastal San Luis Obispo County, central California: *American Quaternary Association biennial meeting*, 10th, Program and Abstracts, p. 126.
- Kennedy, G. L., Wehmiller, J. F., and Rockwell, T. K., 1992, Paleoecology and paleozoogeography of Late Pleistocene marine-terrace faunas of southwestern Santa Barbara County, California, in *Quaternary coasts of the United States: Marine and lacustrine systems*: SEPM Special Publication 48, p. 343–361.
- Kidwell, S. M., and Bosence, D. W. J., 1991, Taphonomy and time-averaging of marine shelly faunas, in Allison, P. A., and Briggs, D. E. G., eds., *Taphonomy: Releasing the data locked in the fossil record*: Topics in Geobiology, v. 9, p. 115–209.
- Muhs, D. R., and Kyser, T. K., 1987, Stable isotope compositions of fossil mollusks from southern California: Evidence for a cool last interglacial ocean: *Geology*, v. 15, p. 119–122.
- Muhs, D. R., Kennedy, G. L., and Rockwell, T. K., 1994, Uranium-series ages of marine terrace corals from the Pacific coast of North America and implications for last-interglacial sea level history: *Quaternary Research*, v. 42, p. 72–87.
- Prentice, I. C., Bartlein, P. J., and Webb, T., III, 1991, Vegetation and climate change in eastern North America since the last glacial maximum: *Ecology*, v. 72, p. 2038–2056.
- Raup, D. M., 1991, The future of analytical paleobiology, in Gilinsky, N. L., and Signor, P. W., eds., *Analytical paleobiology. Short courses in paleontology*, 4: Knoxville, Tennessee, Paleontological Society, p. 207–216.
- Roy, K., Jablonski, D., and Valentine, J. W., 1994, Eastern Pacific molluscan provinces and latitudinal diversity gradient: No evidence for “Rapport’s Rule”: *Proceedings, National Academy of Sciences*, v. 91, p. 8871–8874.
- Scheltema, R. S., 1971, Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods: *Biological Bulletin*, v. 140, p. 284–322.
- Scheltema, R. S., 1988, Planktonic and non-planktonic development among prosobranch gastropods and its relationship to the geographic range of species, in Ryland, J. S., and Tyler, P. A., eds., *Reproduction, genetics and distributions of marine organisms*: Fredensborg, Denmark, Olsen and Olsen, p. 183–188.
- Servant, M., Maley, B., Turcq, B., Absy, M.-L., Brenac, P., Fournier, M., and Ledru, M.-P., 1993, Tropical forest changes during the Late Quaternary in African and South American lowlands: *Global and Planetary Change*, v. 7, p. 25–40.
- Smith, J. P., 1919, Climatic relations of the Tertiary and Quaternary faunas of the California region: *California Academy of Sciences Proceedings*, 4th ser., v. 9, p. 123–173.
- Valentine, J. W., 1955, Upwelling and thermally anomalous Pacific coast Pleistocene molluscan faunas: *American Journal of Science*, v. 253, p. 462–474.
- Valentine, J. W., 1961, Paleoeologic molluscan geography of the Californian Pleistocene: University of California Publications in Geological Sciences, v. 34, p. 309–442.
- Valentine, J. W., 1966, Numerical analysis of marine molluscan ranges on the extra-tropical northeastern Pacific shelf: *Limnology and Oceanography*, v. 11, p. 198–211.
- Valentine, J. W., 1980, Camalu: A Pleistocene terrace fauna from Baja California: *Journal of Paleontology*, v. 54, p. 1310–1318.
- Valentine, J. W., 1989, How good was the fossil record? Clues from the Californian Pleistocene: *Paleobiology*, v. 15, p. 83–94.
- Valentine, J. W., and Jablonski, D., 1991, Biotic effects of sea level change: The Pleistocene test: *Journal of Geophysical Research*, v. 96, p. 6873–6878.
- Valentine, J. W., and Jablonski, D., 1993, Fossil communities: Compositional variation at many time scales, in Ricklefs, R. E., and Schluter, D., eds., *Species diversity in ecological communities: Historical and geographical perspectives*: Chicago, University of Chicago Press, p. 341–348.
- Webb, T., III, 1992, Past changes in vegetation and climate: Lessons for the future, in Peters, R. L., and Lovejoy, T. E., eds., *Global warming and biological diversity*: New Haven, Connecticut, Yale University Press, p. 59–75.
- Woodring, W. P., Bramlette, M. N., and Kew, W. S. W., 1946, *Geology and paleontology of Palos Verdes Hills, California*: U.S. Geological Survey Professional Paper 207, 145 p.
- Zinsmeister, W. J., 1974, A new interpretation of thermally anomalous molluscan assemblages of the California Pleistocene: *Journal of Paleontology*, v. 48, p. 84–94.

Manuscript received June 13, 1995

Revised manuscript received August 28, 1995

Manuscript accepted September 7, 1995