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# THE WESTERN SOCIETY OF MALACOLOGISTS

## ANNUAL REPORT FOR 1999

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## VOLUME 32

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# THE WESTERN SOCIETY OF MALACOLOGISTS

ANNUAL REPORT FOR 1999

VOLUME 32

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- No. 3** Hans Bertsch. 1993. Twenty-five year index to publications of the Western Society of Malacologists: Author, taxonomic, geographic and subject indices. 68 pp. \$15.00
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# WESTERN SOCIETY OF MALACOLOGISTS ANNUAL REPORT FOR 1999, VOLUME 32

Abstracts and Papers from the 32<sup>nd</sup> Annual Meeting of the Western Society of Malacologists  
held at California State University, Fullerton, 13-17 June 1999

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# ABSTRACTS AND PAPERS

## **Mollusks, multiple molecules and model-based methods: recent developments in metazoan phylogenetic analysis**

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The interrelationships of the higher molluscan taxa and the phylogenetic position of Mollusca within Metazoa have been persistent problems for molluscan systematists. Molecular sequence data, primarily from the nuclear small-subunit (18S) ribosomal RNA gene, have been very useful for studying relationships among the animal phyla in general. However, 18S data have not provided much insight into the position of Mollusca relative to other eutrochozoans, and have failed to support molluscan monophyly. A suite of nuclear protein-coding genes -- including elongation factor 1-alpha, RNA polymerase II, and the alpha subunit of sodium-potassium ATPase, among others -- are being used to investigate relationships among the eutrochozoan phyla and to estimate divergence times among the major animal lineages. These data, in conjunction with analyses of existing COI, 18S and EF1-alpha data sets, will allow investigation of the strength of support for molluscan paraphyly and should provide more insight regarding the position of Mollusca among the metazoans. Results from preliminary analyses of these data will be presented.

## **An episodic rafting model: an explanation for dispersal of direct developing genera**

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During studies of several cowrie genera that exhibit direct development, the question of how direct developing genera disperse over distances of several thousand kilometers in geologically short periods of time is noteworthy. A review of the literature revealed that genera with planktonic larval stages are easily dispersed by oceanic currents. The question for direct developers has not been studied in any depth.

The specific distribution pattern that raised the question is that of members of the genus *Muracypraea* Woodring, 1957. The genus apparently originated in Venezuela in the early Miocene. By the middle Miocene species in this genus had dispersed to the present day Dominican Republic and southern Baja California. The dispersal from Venezuela to the Dominican Republic can be explained by island hopping following currents as the present day Greater and Lesser Antilles were located closer to Venezuela in the early Miocene. Tectonic plate movement has displaced these islands to their more easterly position over time. This explanation does not work as well in the dispersal from Venezuela to Baja California as

present coastal surface currents are predominantly southward along the entire Central American coast and these patterns may have been similar prior to the closing of the Panamanian Strait.

The episodic rafting model is based on the concept that the west coast of Central America is subject to intense cyclonic tropical storms on a regular basis. These tropical storms often cause local disruptions of current patterns that can last from a few days to a few weeks depending on storm severity. These disrupted current patterns could result in shallow water detritus, carrying eggs and animals, being moved against the prevailing current for distances of 50 to 100 km per storm episode. The probability of such a rafting event landing in a suitable habitat and resulting in a viable population is small, but given enough replications over time a significant number of successful rafting events could occur.

### **Opisthobranch biodiversity of the Punta Eugenia region, Baja California Sur: a CONABIO-sponsored investigation**

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Six research expeditions to one of the most isolated yet biogeographically important areas of the Baja California peninsula resulted in major new information regarding the seasonality, reproductive behavior, and density of intertidal and subtidal opisthobranch mollusc populations. Almost 25% of the observed fauna represent new species or new distributional records for the entire Pacific coast of the Baja California peninsula.

### ***XENOPHORA* AS BIOINDICATORS IN THE HAWAIIAN ARCHIPELAGO, A PRELIMINARY STUDY**

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#### **Abstract**

During the growth of the Hawaiian *Xenophora peroniana kondoi* Ponder, 1983, the gastropod adheres increasingly larger objects from both benthic flora and fauna. It also serves as a hard substrate needed by seven phyla of larval settlers otherwise unable to survive at depths of 200 to 800 meters on soft fine sand substrate. Benthic objects are selected and positioned by the proboscis and foot to the peripheral shell margins. This preliminary paper presents a study of three different populations of this species of *Xenophora* taken using various gear and methods and to report on the possible effects of severe storms at these sites and four sites seen documented by video camera.

## Introduction

*Xenophora peroniana kondoi* Ponder, 1983, the carrier shelled gastropod in Hawaii, was first taken by the United States Fish Commission Steamer ALBATROSS in 1902 as part of the exploration for commercial fisheries specimens off Oahu and at the other main Hawaiian Islands. The holotype came from station 3810 on the south side of Oahu as were 12 paratypes (Ponder, 1983). This report adds further information obtained from bicatch in 1967-1968 by the National Marine Fisheries Services Research Vessel TOWNSEND CROMWELL at several sites where the ALBATROSS had explored earlier for fin-fish and shrimp. The first site chosen in this study was the Pailolo Channel in 1968 winter cruise, TC40 Stations 91-92. The second choice of stations was from the 1968 Spring cruise TC35, station 32 from the less protected area south of Oahu on Molokai's Penguin Bank. The third site was off Honolulu, Oahu in the south-facing Mamala Bay. Although aware of storm effects on populations nearer shore by and on the reefs (Burch, Burch and Thorsson, 1985), it also was interesting to find that the deeper water populations of sea urchins and forams were also affected by the storms (Burch & Burch, 1998). Thus, this study was initiated on populations of *Xenophora* occurring at the depths of the sea urchins and forams.

## Materials and Methods

Material from the National Marine Fisheries Services was sorted by University of Hawaii Marine Options students on a National Science Foundation grant to Dr. Dennis Devaney at the Bishop Museum in 1981-1983 under the senior author's direction. The samples were taken by shrimp trawls of varying sizes, mesh, and length of time towed. Specimens of *Xenophora* were obtained as part of the bicatch.

The Burch 10 m steel salmon troller used a hardware cloth-covered rectangular dredge (with a 76 by 20 cm opening and 76 cm depth) and a half-size Clarke dredge (Clarke, 1972) to obtain fauna, flora, and sediments. Trawls were of 10 to 15 min duration, and were taken from beyond the reefs to depths of 600 meters.

The locations of all sites are shown in Figure 1. The Burch collecting stations in Mamala Bay, Oahu are identified in Figure 2. In addition, video camera records of *Xenophora* were taken by both the University of Hawaii HURL project and the National Marine Fisheries Service from manned University of Hawaii research submersibles at depths of 200 to 400 meters at various sites.

## Results and Discussion

Stations 91-92 of the TOWNSEND CROMWELL Cruise 40 were sampled during the winter of 1968, repeating earlier explorations for fin-fish and shrimp in areas trawled in 1902 by the U. S. Fish Commission Steamer ALBATROSS. The TOWNSEND CROMWELL stations used benthic shrimp trawls at an average depth of 440 meters for two hours each. The specimens of *Xenophora* from these stations were utilized by growing and enlarging larval settlers, which were overlaid by organic debris selected by the enlarging *Xenophora*. These opportunistic settlers consisted of at least twenty-three species from seven phyla (Table 1). The most common of these were *Bentharca asperula* (Bivalvia) which were attached by their byssus, and the brachiopods *Basiola beecheri* (Dall, 1895) and *Laqueus hawaiiensis* (Dall, 1895), which were attached by their fragile pedicles to the dorsal surface of the *Xenophora*. Lacking a pedicle, the minute *Disciniscus* sp. only settled on the uppermost whorls of adult *Xenophora*. The polychaete *Spirobranchus laticapulus* Marenzeller, 1878, first reported in Hawaii by Bailey-Brock (1972), were abundant on adult *Xenophora*, with the tube growing from near the margin towards the apex, or tending to grow laterally around the shell's whorl if the initial attachment was higher on the shell.

Various benthic fauna was picked up from the sediments and attached to the shells of *Xenophora* (Table 2). Live or dead *Bentharca asperula* encountered in the sediment were attached to the fourth or later whorls of the shell of *Xenophora*. These bivalves were positioned usually by the small sharper angle of either valve and occasionally so close that they formed almost an entire cover. *Glycymeris molokaia* were also commonly picked up, positioned as were the *Bentharca* so that the convex surface lay pointed towards the substrate to raise the *Xenophora* free from the substrate (St. Jean, 1977). Smaller bivalves were not utilized, perhaps because they were uncommon near the substrate surface. Gastropods from the collecting area must be comparatively few, although opercula of the larger *Natica hilaris* Sowerby, 1914, were occasionally positioned at the margin of adult *Xenophora*. Short fragments of *Fissidentalium complexum* (Dall, 1895) and heavy spines of sea urchins from those depths were attached lengthwise. Other echinoids found were small *Echinocyamus* sp., which were positioned with the dorsal side facing the sediment as were those of the larger *Lagena* sp. Both were attached only to the penultimate and final whorls of the *Xenophora*. Most were only fragmentary with just the inner layer of remains visible, indicating that they were freshly dead.

The second site of the study was from TOWNSEND CROMWELL station TC35-32 to the southeast of Oahu and on the somewhat protected northwest part of Penguin Bank off Molokai. Compared to the more protected Pailolo Channel fauna described previously, among all of the phyla represented the fauna was diminished (Tables 3 and 4). There was an increase in *Xenophora* with only biogenic particles of increasing size alone. Here too, *Xenophora* were of smaller diameter and height but with a greater size range.

During the 1970s and 1980s, the Burch JANTHINA VII took several hundred dredge hauls beyond the reefs off Honolulu to 600 meters. *Xenophora* were taken together with other benthic organisms. Similar to the *Xenophora* from Penguin Bank (TC35-32) these had increasingly large unidentifiable organic debris and were barren of any fauna derived from larval settlement.

Samples were taken before, during, and after the storm season and Hurricane Ewa of November 1982. Only 21 specimens of *Xenophora*, including both juveniles and adults, were dredged, but only one was taken alive (Burch & Burch, 1987). They occurred in only 10 of the 107 stations examined at 200 to 600 meters (Fig. 2). The south side of Oahu has seven terraces of coral reefs extending far below to far above the present reef reflecting various exposed or submerged reefs in the past (Stearns, 1969). The terraces are close to shore permitting reef debris to fall down and accumulate at greater depths but preventing such material from being transported to shallower water. From late 1970 through March 1980 prolonged and severe southern storms occurred, which the local weather people called "100 year storms" (Haraguchi, 1974, 1980). In the calmer weather after these storm seasons Burch station sediments to beyond 400 meters were heavy with segments of intertidal and near-shore coralline algae species of *Halimeda*.

None of the *Xenophora* from Mamala Bay had attached *Bentharca asperula*, even though at one station we dredged both a dead *Xenophora* and a live *Bentharca*, which demonstrated that the two species did occur in the same area. In sediments at stations where *Xenophora* were taken from equal depths, thin-shelled uncommon specimens of bivalves and small heavy-shelled *Verticordia* were also collected (Burch & Burch, 1995). There were also enormous numbers of *Glycymeris* from minute to those of far greater size than adult *Xenophora* could utilize. They were all from a shallow water species, as were the many minute to large Arcidae that were also available. *Fissidentalium complexum* (Dall, 1895) was rarely taken in Mamala Bay. With the heavy sediment layer of *Halimeda* not present from stations before the storm, it is not surprising that subtidal and shallow water fauna and flora were present at 200 meters after the storm. It also was interesting to see that the juvenile *Xenophora* stages were only found after the 1980 storm and after the hurricane of 1982. As with the populations of *Chaetodiadema pallidum* Agassiz & Clark, 1907, the temporary populations of *Xenophora* were destroyed leaving only a few live ones at Oahu (Burch & Burch, 1998).

Based on video tape records at submarine stations (Fig. 1), we were able to show the following: 1) the apparent beginnings of new populations of *Xenophora* near Oahu, 2) population densities of *Xenophora* and adjacent colonies of *Chaetodiadema pallidum*, 3) the stance of the *Xenophora* that resulted from debris they had attached to their peripheries, 4) locomotion of *Xenophora*, which appeared to be by usage of the foot to thrust the shell up and forward, and 5) collection of specimens by the mechanical arms of the submersible.

### Acknowledgements

We thank the National Science Foundation for the three-year contract to the late Dr. Dennis M. Devaney of the Bishop Museum, Honolulu, which enabled the senior author to hire University of Hawaii students to sort, identify, and catalog the invertebrate material collected by the National Marine Fisheries, Honolulu Laboratory. We are grateful for the support of University of Hawaii scientists Dr. Edith Chave, Brian Midson, Jane Culp, the submersible managers of the University, Dr. Alexander Malahoff, Director of the School of Earth Science and Technology, Dr. Sherwood Maynard of the University of Hawaii Marine Options Program, the scientists and computer personnel from the National Marine Fisheries Service, Honolulu Laboratory, especially biologist Robert B. Moffitt, Bishop Museum librarians and Dr. Robert H. Cowie and Regina Kawamoto of the Department of Natural Sciences of the Bishop Museum. Our special thanks to Wesley M. Thorsson, retired US Coast Guard Captain for help aboard the Burch JANTHINA VII. Paul Haraguchi furnished much appreciated weather information.

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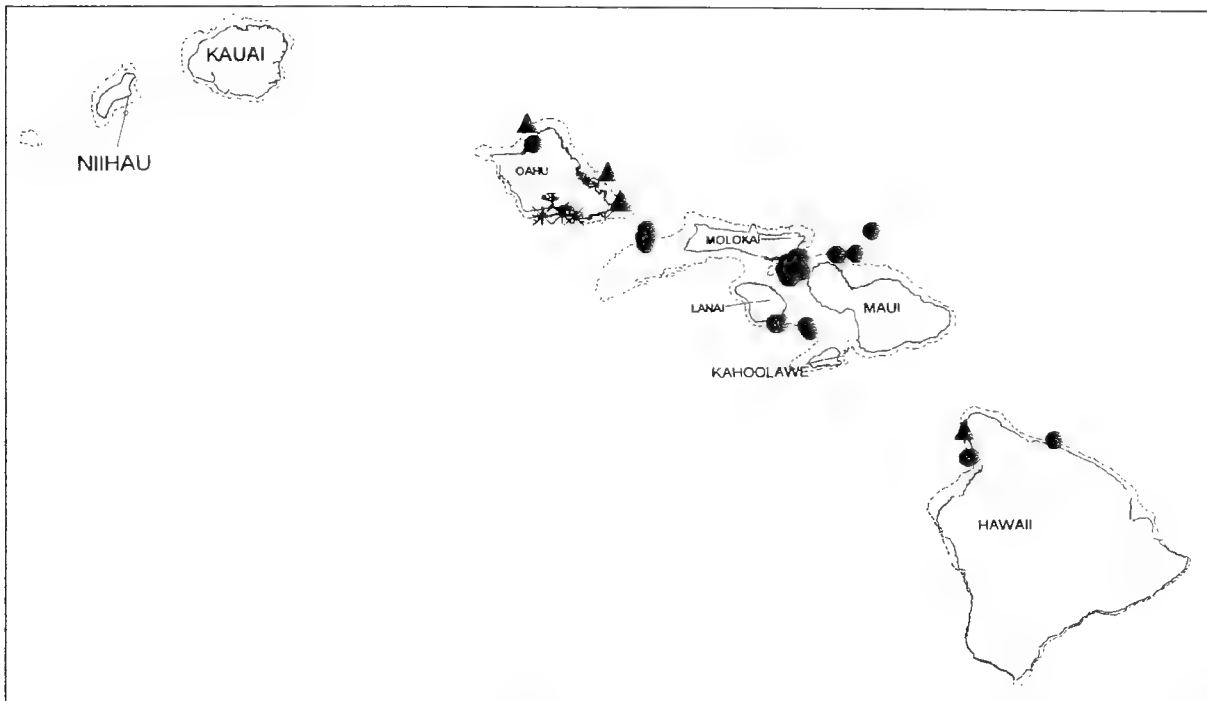


Figure 1. Locations of sampling stations in the Hawaiian Islands (Latitude  $18^{\circ}55'N$  to  $22^{\circ}30'N$ , Longitude  $154^{\circ}40'W$  to  $160^{\circ}21'W$ ). Symbols: NMFS trawl stations = circles, HURL and NMFS submarine stations = triangles, and Burch dredge stations = stars.

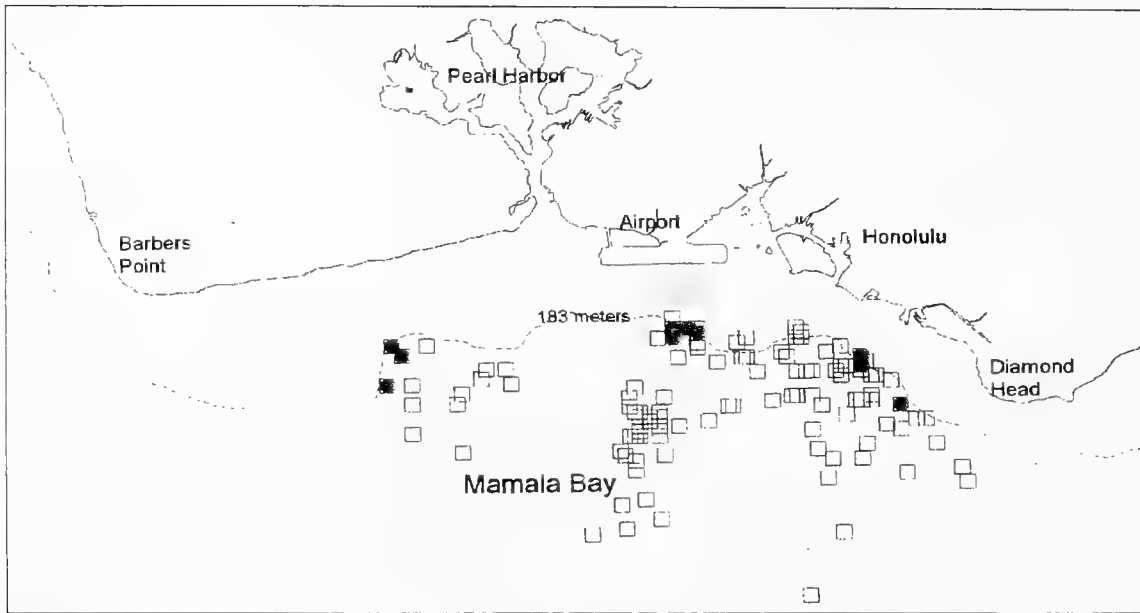


Figure 2. Locations of Burch dredge stations off the south shore of Oahu (Latitude 21°13'N to 21°25'N, Longitude 157°40'W to 160°21'W). Symbols: Dredge station locations = open boxes; stations from which *Xenophora* was collected = solid circles.

Table 1. Opportunistic settler fauna on *Xenophora* from Station TC40:91-92.

Phylum, Class	Attached Fauna	Abundance
Protozoa, Foraminifera	<i>Biarrizina proteiformis</i> (Goes, 1882)	rare
	<i>Carpenteria monticularis</i> Carter, 1877	common
	<i>Miniacina miniacea</i> (Pallas, 1766)	rare
	<i>Sagenina divaricans</i> Cushman, 1910	rare
	<i>Sagenina frondescens</i> (Brady, 1879)	rare
Cnidaria, Scleractinia	<i>Anthemiphyllia pacifica</i> Vaughan, 1907	rare
	<i>Endopachys grayi</i> Milne-Edwards & Haime, 1848	rare
	<i>Premocyathus</i> sp.	rare
Cnidaria, Scyphozoa	<i>Stephanoscyphus simplex</i> Kirkpatrick, 1890	common
Ectoprocta	3 species	abundant
Annelida, Polychaeta	<i>Spirobranchus laticapax</i> Marenzeller, 1878	abundant
	Arenaceous sp. (ventrally)	rare
Brachiopoda	<i>Basiola beecheri</i> (Dall, 1920)	abundant
	<i>Disciniscus</i> sp. Dall, 1920	rare
	<i>Laqueus hawaiiensis</i> (Dall, 1920)	abundant
Arthropoda, Balanoidea	Alive & dead, several ages, dorsally	common
Arthropoda, Lepadomorpha	Alive, several ages, ventrally	common
Mollusca, Bivalvia	<i>Bentharca asperula</i> (Dall, 1881)	abundant
	<i>Isognomon</i> sp. (juvenile)	rare
	<i>Neopycnodonta cochlear</i> (Poli, 1795) (juvenile)	rare
Mollusca, Gastropoda	<i>Emarginula hawaiiensis</i> Dall, 1895	rare



Table 2. Benthic fauna attached by *Xenophora* from Station TC40-91-92.

Phylum, Class	Attached Fauna	Abundance
Cnidaria, Scleractinia	<i>Anthemiphyllia</i> sp. * <i>Cyphastrea ocellina</i> Dana, 1846 <i>Endopachys grayi</i> Milne-Edwards & Haime, 1848	rare rare rare
Brachiopoda	<i>Basiola beecheri</i> (Dall, 1920) * <i>Laqueus mauiensis</i> (Dall, 1920) *	abundant abundant
Mollusca, Bivalvia	<i>Bentharca asperula</i> (Dall, 1881) *	abundant
Mollusca, Gastropoda	<i>Glycymeris molokaia</i> Dall, Bartsch, & Rehder, 1938 <i>Conus acutangulus</i> Lamarck, 1810 costellarid ** <i>Emarginula hawaiiensis</i> Dall, 1895 <i>Gaza</i> sp. mitrid ** <i>Natica hilaris</i> Sowerby, 1914 <i>Pupa pudica</i> (A. Adams, 1854) turrid sp. 1 ** turrid sp. 2 **	abundant rare rare rare rare rare uncommon uncommon rare rare
Mollusca, Scaphopoda	<i>Fissidentalium complexum</i> (Dall, 1895)	common
Echinodermata, Echinoidea	<i>Echinocyamus</i> sp. Echinoid, heavy spines <i>Lagena</i> sp.	rare common common

\* filter feeder, fallen into sediment

\*\* washed down from shallower depth

Table 3. Opportunistic settler fauna on *Xenophora* at Station TC35-32.

Phylum, Class	Attached Fauna	Abundance
Protista, Foraminiferida	<i>Biarrizina proteiformis</i> Goes, 1882 <i>Carpenteria monticularis</i> Carter, 1877	rare rare
Cnidaria, Scleractinia	<i>Anthemiphyllia</i> sp.	rare
Cnidaria, Scyphozoa	<i>Stephanocyphus simplex</i> Kirkpatrick, 1890	rare
Ectoprocta	one colony	rare
Annelida, Polychaeta	arenaceous tubular (ventral surface) <i>Spirobranchus laticapus</i> Marenzeller, 1885	rare common
Arthropoda, Balanoidea	both live and dead on dorsal surface	common
Mollusca, Bivalvia	<i>Bentharca asperula</i> (Dall, 1881) (all dead) <i>Isgnomon</i> sp. (juvenile)	uncommon rare

Table 4. Benthic fauna attached by *Xenophora* at Station TC35-32.

Phylum, Class	Attached Fauna	Abundance
Cnidaria, Scleractina	reef coral fragments	rare
Brachiopoda	fragments only	rare
Mollusca, Bivalvia	<i>Bentharca asperula</i> (Dall, 1881) (dead) <i>Glycymeris molokaia</i> Dall, Bartsch, & Rehder, 1938 Pectenidae fragment <i>Spondylus</i> sp. unidentified bivalve fragment <i>Verticordia deshayesiana</i> (Fisher, 1862)	uncommon common rare rare rare rare
Mollusca, Gastropoda	<i>Architectonica</i> sp. <i>Cypraea</i> fragment Gastropod, eroded fragment <i>Natica hilaris</i> Sowerby, 1914 (operculum) <i>Solariella</i> sp.	rare rare rare rare rare
Mollusca, Scaphopoda	<i>Fissidentalium complexum</i> (Dall, 1895) fragments	rare

### The role of parasites and bacteria in the displacement of a native mudsnail by an exotic competitor

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Many studies of species invasion demonstrate the instrumental role that freedom from natural predators plays in enabling proliferation of exotic species. The influence of microscopic natural enemies, i.e. parasites and bacteria, on invasion success however is almost always overlooked despite these organisms' ubiquity and often extreme influence on life history and population dynamics. Given typically high parasitism rate in molluscs, it is imperative to incorporate evaluation of these "unseen" players into analyses of invasion success. The exotic mudsnail, *Batillaria attramentaria*, was introduced to the West Coast of North America in the late 1920's with aquaculture imports of *Crassostrea gigas*, and has been displacing the native mudsnail, *Cerithidea californica*.

Here I report results of experiments designed to determine the role of parasites and bacteria in aiding the proliferation of *Batillaria* and displacement of *Cerithidea* in marshes of northern California. Overall prevalence in both species was not significantly different (14% in *Batillaria*; 15% in *Cerithidea*), however the exotic snail was only infected by one trematode species (potentially a non-native species itself) while the native snail was parasitized by 11 species. Susceptibility experiments with one particular species of native parasite indicated complete immunity by the exotic snail even under intensified exposure conditions. In a second set of experiments, bacteria were found to create anoxic conditions that killed native *Cerithidea* at a rate 7 times higher than *Batillaria*. Increased resistance to both parasitic infection and bacterial effects confer a marked advantage to *Batillaria* and contribute to a growing mechanistic understanding of its successful invasion.

**Repatriacion de los datos, Bajo el patrocinio de CONABIO  
(Comision Nacional para el Conocimiento y Uso de la Biodiversidad):  
Pacific coast of Mexico specimens of opisthobranchs  
in California (U.S.) museums**

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In 1998 we were able to study the Pacific Coast and Gulf of California opisthobranchs that are deposited in California museums. This study was supported by the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO) in order to establish a data base of opisthobranch molluscs collected from Mexican waters, and to obtain a better idea of opisthobranch biodiversity in northwest Mexican marine waters.

The collections of opisthobranchs that we reviewed are housed in the Los Angeles County Museum of Natural History (LACMNH), Santa Barbara Museum of Natural History (SBMNH), and California Academy of Sciences (CAS). The lots of identified species are as follows.

SBMNH: These collections yielded a total of 25 lots of opisthobranchs, the majority of which came from the northern part of the Baja California peninsula and the Gulf of California.

LACMNH: Approximately 600 identified lots of opisthobranchs were contained in the collections. We searched the entire collection, recording those species lots from Mexican Pacific waters. The entire region was represented, but the greatest number of lots were from Bahía San Carlos, Puerto Peñasco, and Guaymas. Most records were intertidal, but some were subtidal.

CAS: These collections contained the largest number (more than 1,500 lots) of identified western Mexican opisthobranchs from sites along the coasts of Baja California, Baja California Sur, Sonora, and other Mexican states. CAS also has significant holdings from western Central America and the Islas Galápagos, but these were not reported for the Mexican CONABIO data base. The CAS collections extend throughout nearly the entire twentieth century and contain a large number of type specimens, including holotypes and paratypes. The majority of types are validly named (i.e., currently accepted) species, although some are synonyms of previously named species (e.g., *Aclesia rickettsi*, named by MacFarland in 1966, has since been recognized as a synonym of *Stylocheilus longicauda* Quoy & Gaimard, 1824). Holotype specimens of some of the more recently named species include *Chromodoris baumanni* Bertsch, 1970, *Phyllaplysia padinae* Williams & Gosliner, 1973, *Eubranchus cucullus* Behrens, 1985, *Bajaeolis bertschi* Gosliner & Behrens, 1986, and *Tritonia myrakeenae* Bertsch & Mozqueira, 1986.

The information obtained from the specimens deposited in these California museum collections is now in the data base of CONABIO. In addition to the living intertidal and subtidal opisthobranchs that we encountered in the Punta Eugenia Zona Prioritaria (see Bertsch, Angulo, Arreola y Sanchez herein, and Bertsch, Angulo y Arreola, in press, *The Festivus*), we have examined a total of 1,937 specimens and lots in our studies supported by the CONABIO grant. During the middle of 2001, these data will be completely accessible to all researchers throughout the world on the Internet page of CONABIO ([www.conabio.gob.mx](http://www.conabio.gob.mx)).

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## **A second look at Eastern Pacific recent species of the bivalve genus *Gari***

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A study has been conducted of the type and other material of the Recent eastern Pacific species of the genus *Gari*. There are seven species of *Gari* (*Gobraeus*). (1) *Gari* (*G.*) *californica* (Conrad, 1849) (synonyms: *Psammobia rubroradiata* Carpenter, 1864; *P. lilacina* Wilkins, in Palmer, 1958 [in synonymy]) occurs from Kachemak Bay, Alaska, to Bahia Magdalena, Baja California Sur, Mexico, but with a gap between Puget Sound and Mendocino County, California. Based on the material currently available in the United States, it cannot be distinguished from the northwestern Pacific *G. katusensis* (Yokoyama, 1922), which is also regarded as a synonym, along with *G. k. atsumiensis* Hayasaka, 1961. (2) *Gari* (*G.*) *fucata* (hinds, 1845) (synonym: *Siliquaria edentula* Gabb, 1869), occurs from Ventura County, California, to Punta Eugenia, Baja California Sur, Mexico, and perhaps as far south as Bahia Magdalena. (3) *Gari* (*G.*) *lata* (Deshayes, 1855) (synonym: *Psammobia regularis* Carpenter, 1864), occurs from Bahia Magdalena, Baja California Sur, Mexico, throughout the Gulf of California, south to Santa Elena, Ecuador. Records of *Gari regularis* from northern Baja California are based on misidentified small, elongate, inflated specimens of *G. californica*. (4) *Gari* (*G.*) *maxima* (Deshayes, 1855) occurs from Mazatlán, Mexico, to Panama. (5) *Gari* (*G.*) *panamensis* Olsson, 1961, occurs from the central Gulf of California to Playas, Ecuador. (6) *Gari* (*G.*) *solida* (Gray, 1838) (synonyms: *Psammobia solida* Philippi, 1844; *P. crassa* Hupé 1854), occurs from Arica to Rio Inio, Chile. (7) A probable new species of *Gari* (*G.*) occurs in the Galapagos Islands, thus far represented by only a single, small, broken specimen. An eighth species, *Gari* (*Dysemea*) *helenae* Olsson, 1961, occurs from Laguna Ojo de Liebre, Baja California Sur, Mexico, throughout the Gulf of California, south to Isla Salango, and the Galapagos Islands, Ecuador. Its relationship to the western Atlantic *Gari circe* (Mörch, 1876) and *G. linhares* Simone, 1998, remain to be resolved. Several lectotype designations will be made, and a list will be provided of New World Recent and fossil taxa that have been placed in *Gari*.

## **Alien snails in the Pacific: homogenization of the Pacific island non-marine snail fauna**

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There are probably about 5000 native Pacific island land snail species, many of them endemic to single islands or archipelagos. The freshwater snail fauna is smaller and less narrowly endemic. These faunas are being replaced by 100-200 synanthropic species introduced both deliberately and accidentally. Much

publicity has centered on the introduction of the giant African snail, *Achatina fulica*, and subsequently of predatory snails, notably *Euglandina rosea*, in ill-conceived attempts at biological control. *Euglandina rosea* is probably the major cause of the extinction of endemic tree snails (Partulidae) in French Polynesia and is heavily implicated in the drastic decline of partulids in Samoa, Guam and elsewhere, and of achatinellid tree snails in Hawaii. Other non-predatory species are becoming widespread throughout the Pacific (e.g., various species of Subulinidae). In Hawaii, these species have occupied previously degraded habitat from which native species had probably already disappeared. Elsewhere (e.g., Samoa), some of these species, especially subulinids, occur in vast numbers in native forests. Their impacts on the native faunas are unknown: they may compete with native species, and almost certainly provide a food resource sustaining populations of predatory snails. Other species are still not established widely in the Pacific but seem to be spreading rapidly (e.g., *Parmarion martensi*), often associated with horticultural commerce, or are potential serious threats should they be more widely introduced (e.g., *Pomacea canaliculata*). The rate of introduction of new species is not slowing. Once established, these introduced species are probably impossible to eradicate. Conservation efforts must therefore focus on prevention of their introduction and spread, by strict implementation of quarantine measures combined with public education.

### **The effects of the exotic mussel, *Musculista senhousia*, on macrofaunal assemblages in an urbanized Southern California lagoon**

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*Musculista senhousia* Benson in Cantor is an Asian mussel that is capable of having a range of effects within invaded ecosystems. This small mytilid typically lives on soft sediments, where it creates a byssal cocoon. When the mussel occurs in high densities (5,000 – 10,000 m<sup>2</sup>), the dense mats that form can fundamentally alter the nature of the benthic habitat. Studies on inter-relationships between *M. senhousia* and resident biota in Mission Bay, San Diego, California, have revealed that the effects of the mussel appear scale-dependent. The mats created by *M. senhousia* increase the structural complexity of the benthos, and many small macrofauna able to live within this biogenic habitat are facilitated. Most macrofaunal organisms found in higher abundances within mussel beds respond to the physical structure of the mat, although the biological activities of the mussel do affect some taxa. At larger scales, however, organisms not able to live within the mussel mats can be outcompeted. For example, large clams are often reported to be in lower abundances in the presence of *M. senhousia*, and experimental work in Mission Bay has demonstrated that two species of cockles (*Chione* spp.) can be severely inhibited by the presence of the mussel and its mats. These competitive interactions may be partially responsible for a long-term decline in surface-dwelling cockles in Mission Bay tidal creek habitats.

**Genetic evidence supporting the existence of *Lottia austrodigitalis*  
as a sibling species to *Lottia digitalis*, and an examination  
of differential habitat utilization in the zone of sympatry**

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In 1978, Philip Murphy proposed that the common California limpet, *Lottia digitalis* has a southern sibling species *Lottia austrodigitalis*. Both species show two distinct morphotypes that correspond to a rock and gooseneck barnacle microhabitat. In the zone of sympatry, Murphy proposed that *L. digitalis* occurs in higher frequency in the barnacle habitat while *L. austrodigitalis* occurs in higher frequency in the rock habitat. We hypothesize that the proposed sibling species pair actually exists. To test this hypothesis, limpets will be taken from allopatric populations and genetically sampled for allele frequency differences at multiple enzyme loci. If the first hypothesis is supported, we will determine if the sibling species show differential habitat utilization in the zone of sympatry by electrophoretic comparison of rock and barnacle populations. Finally, we plan to test the hypothesis that interspecific competition plays a key role in the observed differential habitat utilization by comparing species frequency and shell growth between species within treatment plots that differ in population density. Based on preliminary electrophoretic research, we suspect that a sibling species pair does exist and that further analysis will support this. Recognizing sibling species in biological studies is imperative. In addition, sibling species are ideal for studying how speciation occurs and how it is maintained. Lastly, if competition is influencing ecological separation in the zone of sympatry, then it is possible that a seldom recognized evolutionary process, "character displacement", may be at work here.

**Paleoenvironments, paleoecology, and molluscan paleontology  
of a late Pleistocene bay, Oceanside, San Diego County, California**

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A thick upper Pleistocene stratigraphic section exposed near Oceanside represents a transgressive sequence of fluvial and alluvial sandstones and paleosols, littoral sandstones and siltstones, and sublittoral crossbedded sandstones. Fossils collected from this sequence include sparse remains of terrestrial mammals (fluvial/alluvial facies), low diversity assemblages of infaunal and epifaunal molluscs (sandflat/mudflat facies), and high diversity assemblages of infaunal and epifaunal molluscs, crustaceans, fishes, and mammals (nearshore marine facies).

The molluscan assemblage recovered from the sandflat/mudflat facies includes *Nassarius tegula*, *Pinna* sp., *Anomia peruviana*, *Ostrea lurida*, *Argopecten aequisulcatus*, *Laevicardium elatum*, *Lucinisca nuttalli*, *Parvilucina approximata*, *Tellina meropsis*, *Chione californiensis*, and *Megapitaria squalida*.

The molluscan assemblage recovered from the nearshore marine facies is more diverse and contains species that lived in a wider range of habitats that include back-bay mud flats (*Cerithidea californica* and

*Melampus olivaceus*), rocky substrates (*Astraea undosa*, *Tegula aureotincta*, and *Crepidula onyx*), kelp (*Norrisia norrisi*), eel grass (*Acmaea depicta*), sand flats (*Conus californicus*, *Anadara perlabiata*, *Donax californicus*, *Chione* sp., *Dosinia ponderosa*, *Megapitaria squalida*, and *Protothaca lacinata*), and mud flats (*Nassarius tegula*, *Laevicardium elatum*, *Trachycardium panamense*, and *Macoma nasuta*). A few shells of the bean clam, *Donax gouldii*, reflect an open coast, surf-pounded sandy beach habitat. This diverse mixture of habitats indicates that deposition of this facies occurred in a centrally located region that was receiving sediment and dead shells from many areas of this ancient estuary/bay.

## **Challenges for molluscan research in the next millennium**

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This symposium provides ample evidence that we are about to start the next millennium of molluscan research with fresh approaches that range from paleontological to molecular methodologies, and these are especially effective when they are combined with centuries-old emphases on systematics, biogeography, and natural history of molluscs. This presentation will feature current (and by no means comprehensive) examples of how molluscs are likely to remain important to humans in the next century and beyond. Third millennium malacologists are likely to become increasingly involved in: 1) assessing biodiversity; 2) controlling invaders; 3) thwarting parasite vectors; 4) comparing genomes; 5) aligning gene sequences; 6) boosting aquaculture productivity; and 7) applying biomineralization processes. Such diverse goals serve to emphasize the vibrant importance of promoting further molluscan research.

## **Strategies for coding questionably aligned DNA sequences**

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Currently, many new phylogenetic hypotheses for mollusks are constructed using molecular data, particularly DNA sequences. Often the various methods lead to different hypotheses, and the question of selection of the "correct" tree is at issue. Instead of choosing a tree on the basis of personal preference, I try here to work out arguments in a bottom-up approach. I will deal with one particular problem, namely of how to represent similarity statements in questionably aligned sequences. I will not discuss how to recognize questionable alignment, but presume it. Some sequences are easily aligned, others offer various options depending on the parameters (e.g., gap-weight, ti/tv-ratio) used, as well as the methodology (e.g., computer facilitated, manual). The question arises of how to represent questionably aligned sequence data. A number of methods (elision, missing data, polymorphic, case sensitive, gaps as presence-absence matrix, data contraction, data exclusion) are evaluated based on consequences for the explanatory concept of homology, and effects during character state optimization in terms of test of conjunction and contradictions with original data. For small numbers of highly dissimilar taxa two new coding strategies are presented: block coding and stretch coding. A strict comparison to practices in morphology is carried out. Once appropriate representation of DNA data as perceptual entities is achieved, then interesting questions relating to character evolution of DNA sequences are possible. In a second inferential step of abductive hypothesis generation at the composite hypothesis level, relationships

of organisms as evidenced by the distribution of their properties emerge. The consideration of these problems is needed to provide the foundation in foundherentist justification of parts of a cladogram, the latter being derived beliefs.

**The pea crab *Orthotheses haliotidis* new species (Decapoda: Brachyura: Pinnotheridae) in the Australian abalone *Haliotis asinina* Linnaeus, 1758 and *H. squamata* Reeve, 1846 (Gastropoda: Vetigastropoda: Haliotidae)**

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A new species of pinnotherid crab, *Orthotheses haliotidis* Geiger & Martin, 1999, is described from two species of Australian abalone, *Haliotis asinina* Linnaeus, 1758, and *H. squamata* Reeve, 1846. Its morphology is recorded using light and scanning electron microscopy. The report is the second record of the predominantly American genus *Orthotheses* in the western Pacific, the first confirmed record of a pinnotherid crab from any species of abalone, and the first record of a pinnotherid associated with *H. squamata*.

**Genetic studies of *Mytilus* invasions on the west coast of North America**

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Bay mussels in the *Mytilus edulis* species complex have had a tortuous taxonomic history which has obscured patterns of invasion worldwide. Genetic data suggest that there are three species present in the northern hemisphere: *Mytilus trossulus*, *M. edulis*, and *M. galloprovincialis*. *Mytilus trossulus* is native to the west coast of North America (WNA). *Mytilus galloprovincialis* has invaded this coast, apparently in the 1930's, but this invasion was unnoticed because of morphological similarity until genetic studies in 1988 revealed the presence of two distinct species. Since then, several genetic studies using a variety of methods and loci have described the distribution of the native and introduced mussel in WNA. Combined, these studies indicate that *M. galloprovincialis* is essentially the sole bay mussel in populations south of San Francisco Bay, that the two species overlap and hybridize in central California, and that *M. trossulus* dominates north of San Francisco Bay. *M. galloprovincialis* appears to have now spread north as far as Cape Mendocino. There also appears to be a separate introduction in the Puget Sound region associated with mussel farms. Genetic analysis of museum material from the mid 1800's reveals the presence of *M. trossulus* in southern and central California, indicating an unnoticed replacement of native mussels by introduced mussels. The native and introduced mussels are not ecologically equivalent and the consequences of this replacement in southern California are unknown.



## Geology and paleontology of the basal Upper Cretaceous in San Diego County, Southern California

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Upper Cretaceous (upper Campanian/lower Maastrichtian) marine sedimentary rocks in San Diego County, southern California, are represented by the Rosario Group, comprising the Cabrillo Formation and underlying Point Loma Formation. Upper Cretaceous rocks are unconformably overlain by Eocene and Pleistocene units, and unconformably overlie the Cretaceous Lusardi Formation, Jurassic metavolcanics, and granitic basement rocks. The contact between the Point Loma Formation and the Lusardi Formation was previously undescribed and their stratigraphic relationships were unclear.

New building cuts and utility trenches on Palmer Way in Carlsbad, northern San Diego County, briefly revealed an unconformable contact between the basal Point Loma and uppermost Lusardi formations, and exposed at least two meters of indurated conglomerate that make up the basal part of the Point Loma Formation. The conglomerate is sparsely fossiliferous, but has yielded an interesting assemblage of species, several of which are new, indicative of an intertidal(?) to very shallow, nearshore marine, rocky bottom habitat. The most abundant species are the rudistid bivalve *Coralliochama orcutti* White, and a new species of neritid gastropod, *Otostoma* n.sp. Saul and Squires [in preparation]. Other new or probable new species, most of which are not well enough preserved for immediate description, include a *Xenophora*, a melanopsid(?), perhaps two trochaceans(?), and a patellacean limpet (all gastropods), bivalves in the genera *Crassatella* and *Limopsis*, a bryozoan, and a colonial coral. The fauna differs from that of the conglomerate in the Cabrillo Formation on Point Loma. Sandstones above the basal conglomerate on Palmer Way are also sparsely fossiliferous, but have yielded specimens of a locally unusual exogyrine oyster that compare well with *Amphidonte parasitica* (Gabb).

### Feeding preferences of invasive and native turban snail predators

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Novel ecological function may contribute to the successful establishment of invasive species. The recent expansion of Kellet's whelk (*Kelletia kelletii*) from south of Point Conception into central California added a novel functional feeding mode to the guild of invertebrate predators that consume subtidal turban snails. Whelks feed with a proboscis while sea stars, common predators of turban snails, feed with an eversible stomach. In laboratory experiments, I compared consumption rates and feeding preferences of *Kelletia* and three sea stars (*Pisaster giganteus*, *Astrometis sertulifera* and *Orthasterias koehleri*) for five *Tegula* species from either southern or central California (two and three, respectively). If the novel

feeding mode of the whelk is advantageous when handling naïve prey, relative feeding rates should be higher. For central California *Tegula*, *Kelletia* consumed higher proportions of poorly defended species, suggesting some degree of optimal behavior relative to sea stars. To explore the potentially confounding effects of local adaptation, I compared *Kelletia* and *Pisaster* collected from southern and central California. If predators are well adapted to local prey, consumption rates should be high for sympatric prey and lower for allopatric prey. There was no evidence of local adaptation by *Pisaster* and only slight support of local adaptation by *Kelletia*. Establishment of an invasive species is a function of many factors, and for *Kelletia*, its novel feeding mode appears to contribute weakly to its success.

### **Comparing size-frequency distributions of a subtidal whelk in native and invaded habitats**

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Invasive species often experience an ecological release in non-native habitats due to the absence of coevolved natural enemies. This release can lead to invader population explosions and significant changes in life history characteristics. The recent expansion of Kelle's whelk (*Kelletia kelletii*) into central California is an opportunity to study differences in population structure in native and invaded habitats. I compared size-frequency distributions for whelks in southern and central California over a 5 yr period. In the native habitats, whelk size ranges were greatest, densities were highest, and distribution was nearly continuous. In central California, whelks were primarily small adults, densities were low, and populations were patchy. Whelks in Monterey Bay potentially consist of several closely overlapping cohorts with some evidence of weak, episodic recruitment. This recruitment pattern may be the result of planktonic larvae carried northward during ENSO events, making central California populations larval sinks of southern California source populations. In addition, whelk populations in central California are severely impacted by local predators that are either absent or uncommon in southern California.

### **Progress on the taxonomic manual: *Shell-bearing Gastropoda of the Northeastern Pacific***

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Work is in progress on a taxonomic reference manual treating approximately 1360 species ranging from Alaska to the outer coast of Baja California. Although this fauna had been considered well known, alpha taxonomy for marine gastropod families remains unfinished. Approximately 25 new genera and 265 new species will be described separately in advance of the book or described within the book. Taxa are diagnosed and discussed at all levels of classification. Generic treatments include references to type species and citation of recent authors using a similar generic concept. Species treatments include single-line synonymies for all taxa and synonyms, consisting of original combination, pagination and figures, and, in brackets, references to subsequent type figures, catalog numbers of primary types and abbreviated type localities. The general bibliography includes references to all generic and species-level taxa,

including synonyms. Each family has a separate bibliography of recent work on systematics and phylogeny. Illustrations are black and white photographs of shells with composite plates prepared in PhotoShop. Half of the text is now in draft and the remaining part is in detailed outline form, including revisions of the turrids and pyramidellids, the two most ignored families for the Northeastern Pacific. Taxonomic problems most in need of further investigation are noted. The format provides the essentials of a formal monograph and also serves as an identification manual for the long neglected eastern Pacific marine gastropod fauna. Timely completion of the project is contingent upon receiving grant support for a skilled collaborator.

**Results from a 10-year study of a *Cypraea mauritiana* Linnaeus  
(Gastropoda: Cypraeidae) population on Oahu, Hawaii**

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The large, heavy-shelled cowrie, *Cypraea mauritiana*, lives in intertidal and shallow subtidal reef structures exposed to wave action. Although some gastropod species have projected age spans of 3-4 decades based on growth rates and shell annulations, longevity estimates for gastropods with determinate growth, like cowries, are difficult to make without following individual survival over time. Individuals in the population of *C. mauritiana* on the eastern-facing, wave-exposed breakwall of the Hawaii Institute of Marine Biology at Moku O Loe, Kaneohe Bay, Oahu, Hawaii, have been marked and censused every two years since 1988. Two individuals marked in 1988 were present in 1998 and several others were at least 4-6 years old at that time. Additional observations on activity patterns and movements will be presented.

**Using parallel cladogenesis and molecular specificity to define  
species boundaries in squid - luminous bacterium symbiosis**

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Mutualistic associations between bacteria and their eukaryotic hosts have a variety of mechanisms that provide the specificity for symbiont recognition and colonization. Although most symbiotic bacteria are capable of infecting their particular host partner, very few are able to switch partners. The sepiolid squid-bioluminescent bacteria symbiosis is one such system where closely related bacterial strains are capable of infecting similar host species.

In the coastal areas of Southern France, eight sympatric species of squids exist, harboring two symbiont species, *Vibrio fischeri* and *Vibrio logei*. Whether the presence of two different species of luminous bacteria is dependent upon the squid species and their populations, or the ecological dynamics of the surrounding environment, has been explored. This can be demonstrated by a variety of colonization experiments, where aposymbiotic juveniles are first inoculated with one or both species of *Vibrio*, and tested for specificity to their particular host squid under changing environmental conditions.

Along with these competition experiments, immunocytochemistry using genetic markers in the symbionts have provided evidence for spatial differentiation between the different species. Both techniques have allowed the measurement of both temporal and spatial differentiation between competing symbiont species, and provides additional clues to the evolution of specificity in these symbioses.

## **Plio-Pleistocene offshore molluscan communities and their spatial distribution in shelf-to-slope transects in the Kuroshio Current, Northwestern Pacific Rim**

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Major recurring molluscan assemblages are recognized in the Plio-Pleistocene offshore muddy facies on the Pacific side of SW Japan. The spatial distribution of the molluscan assemblages in shelf-to-slope transects is regular and common among the sedimentary basins from central Honshu to the Ryukyu Islands. The following assemblages appear toward the deeper facies along any key horizons: (1) *Glycymeris rotunda* assemblage, composed of suspension-feeding bivalves (outer shelf); (2) *Hindsia* assemblage, dominated by carnivorous and saprophagous gastropods (shelf edge); (3) *Limopsis tajimae* assemblage, dominated by a large, suspension-feeding limopsisid bivalve (upper slope); and (4) nuculoids assemblage, dominated by minute deposit-feeding bivalves (slope to basin plain).

This regular horizontal change of the benthic biofacies is characterized by replacement of feeding habits. It is noteworthy that the *Hindsia* assemblage is most often associated with abundant shells of pteropods, planktonic foraminifers, and otoliths. This fact indicates that the gastropod dominant assemblage may be formed under the influence of flux from intensified biological production near the shelf-break front. Therefore the regularity of the horizontal change may be related to surface-water conditions as well as bottom conditions. This regularity appeared since the Pliocene on the Pacific side of Japan. Deep-water molluscan biofacies in SW Japan was reformed in its trophic structures during the late Miocene to early Pliocene. It remains an open question whether the Pliocene reformation of an offshore fauna is unique to the NW Pacific or is common to the Pacific Rim.

## **Predicting the long-term impacts and spread of the zebra mussel, *Dreissena polymorpha***

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The zebra mussel (*Dreissena polymorpha*) is one of the most important recent invaders to North American freshwater, both environmentally and economically. Much of the success of the zebra mussel as an invader has been attributed to its lifestyle and life history which are similar to marine benthic invertebrates, but unique in freshwater. The long history of research on the physiology and ecology of zebra mussels in eastern and western Europe greatly influenced facilitated our study of zebra mussels in North America and can help us make predictions about the long-term impacts of this novel ecological

type in freshwater ecosystems. The use of simulation modeling and spatially explicit models will also help us predict the likely long-term impacts and spread of these invaders across wide geographic areas and in areas where they have not yet invaded.

## **AGE AND PALEOENVIRONMENT SUGGESTED BY MOLLUSKS FROM THE PURISIMA FORMATION AND RELATED ROCKS (LATE MIOCENE – PLIOCENE), SAN FRANCISCO BAY AREA, CENTRAL CALIFORNIA**

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### **Introduction**

A mega-invertebrate fauna of 168 taxa, [2 brachiopods, 147 mollusks (1 polyplacophora, 85 bivalves, 60 gastropods, and 1 scaphopod), 8 echinoids, and 11 arthropods] has been reported from the “Purisima” Formation in northern California (Powell, 1998), although a few of the taxa need verification. These taxa can be divided into three molluscan assemblages which, with one exception (Pillar Point; see below), suggests normal marine conditions at water depths less than 50 m and water temperatures the same as, or possibly slightly cooler (coastal San Mateo County) or slightly warmer (Santa Cruz Mountains), than exist along the adjacent coast today. Coupled with age determinations from many sources (see Powell, 1998), these taxa suggest an age range of late Miocene through Pliocene.

Outcrops of the “Purisima” Formation occur from Point Reyes National Seashore in the north to Santa Cruz and the Sargent Oil Field area in the south and are found in four major structural blocks: Ben Lomond, La Honda, Pigeon Point, and San Francisco blocks (Fig. 1). Sedimentary rocks attributed to the Purisima Formation are lumped under the name “Purisima” Formation because they represent relatively shallow marine conditions and are late Miocene through Pliocene in age. Lithologic members of the type Purisima Formation are not, or only poorly, recognized outside of the type area and so the name Purisima is used here in quotes. Also, the stratigraphic histories of each of the fault-bounded blocks is different, suggesting that the “Purisima” Formation may represent more than one formation in the sense of sediments deposited in a continuous depositional basin. However, the occurrence of age diagnostic molluscan taxa allows correlation to the standard California molluscan stages, and a stratigraphic succession of molluscan fauna in the “Purisima” Formation can be developed.

### **Biostratigraphy**

Three molluscan faunas are recognized in the “Purisima” Formation in the greater San Francisco Bay area. From lowest to highest they are the La Honda, the Pillar Point, and the Santa Cruz. These molluscan assemblages allow correlation across the structural block boundaries and suggest ages for individual outcrops.

The La Honda fauna is best expressed in the La Honda structural block and is named for occurrences in the type area of the Purisima Formation, near the town of La Honda. Other “Purisima” Formation outcrops containing a similar fauna occur at Lobitos Creek, Pomponio State Beach, Purisima Creek, and the Sargent Oil Field area, and questionably at Point Reyes, Redondo Beach, San Gregorio, Cascade Creek, Gazos Creek, Año Nuevo west of Año Nuevo Creek, Mountain Charlie Road in the Santa Cruz Mountains, and Scotts Valley. This fauna indicates shallow water depths (< 50 m) and normal marine

conditions with water temperatures similar to off the adjacent coast today. It contains the extinct mollusks *Chione* cf. *C. securis* Shumard, *Dendostrea? vespertina* (Conrad), *Mytilus coalingensis* Arnold, and *Swiftopecten parmeleei* (Dall), which suggest correlation with the "Jacalitos-Etchegoin" provincial molluscan stage, indicating a late Miocene to early Pliocene age.

The Pillar Point fauna is recognized only at Pillar Point, west of the Seal Cove fault and differs from other faunas in representing deeper water (> 100 m). It contains *Lituyapecten purisimaensis* (Arnold), which occurs only in the "Purisima" Formation and can not be used to determine age because of its restricted geographic distribution. The Pillar Point fauna contains *Conchocele disjuncta* Gabb, *Lituyapecten purisimaensis* (Arnold), *Lucinisca annulata* (Reeve) and *Panope? sp.*, along with unidentified vertebrate remains. Together, *Conchocele disjuncta* Gabb and *Lucinisca annulatum* (Reeve) suggest water depths between 100 m and 750 m (depth data from Bernard, 1983) which is in agreement with foraminiferal data from the same section which suggests upper to middle bathyal depths (150 to 1,500 m) (R. S. Boettcher, written comm., 1996).

The Santa Cruz fauna suggests shallow water depths [usually < 10 m, but perhaps as deep as 50 m (Norris, 1986)] and normal marine conditions. It is probably best exposed in the sea cliffs at Capitola city beach and New Brighton/Sea Cliff State Beaches in the Santa Cruz area, but also crops out at Año Nuevo State Park east of Año Nuevo Creek, in the San Gregorio and Lobitos members of the Purisima Formation (Cummings et al., 1962) in the La Honda structural block, and at Moss Beach northeast of the Seal Cove Fault. Extinct taxa from this fauna include *Macoma addicotti* Nikas, *Nanochlamys nutteri* (Arnold), *Searlesia portolaensis* (Arnold), *Nassarius grammatus* (Dall), and *Psephaea oregonensis* (Arnold), indicating correlation with the early to late Pliocene "San Joaquin" provincial molluscan stage.

Other exposures of "Purisima" Formation have few taxa, which are not age diagnostic, and can not be assigned to a molluscan fauna described above. A few localities have significant faunas (especially in the Sargent Oil Field area) and they are of the same age as the Purisima Formation, but they should not be assigned to that formation as they differ lithologically from the type Purisima Formation and likely represent a different depositional basin.

## Conclusions

Fossils from "Purisima" Formation outcrops are divided into three faunas (La Honda, Pillar Point, and Santa Cruz) which differ in taxa present, depositional environments they represent, and probably age. These faunas are not well dated and it is possible that they are ecologically based, but in the case of the La Honda and Santa Cruz fauna they form a stratigraphic succession from older to younger based on correlations with provincial California molluscan stages and in outcrop at Año Nuevo (Powell, 1998). The stratigraphic succession of molluscan faunas in the "Purisima" Formation allows some correlation of widely scattered outcrops across structural block boundaries suggesting that older and younger portions of the Formation and may aid in development of models of paleogeography and fault movement and hazards.

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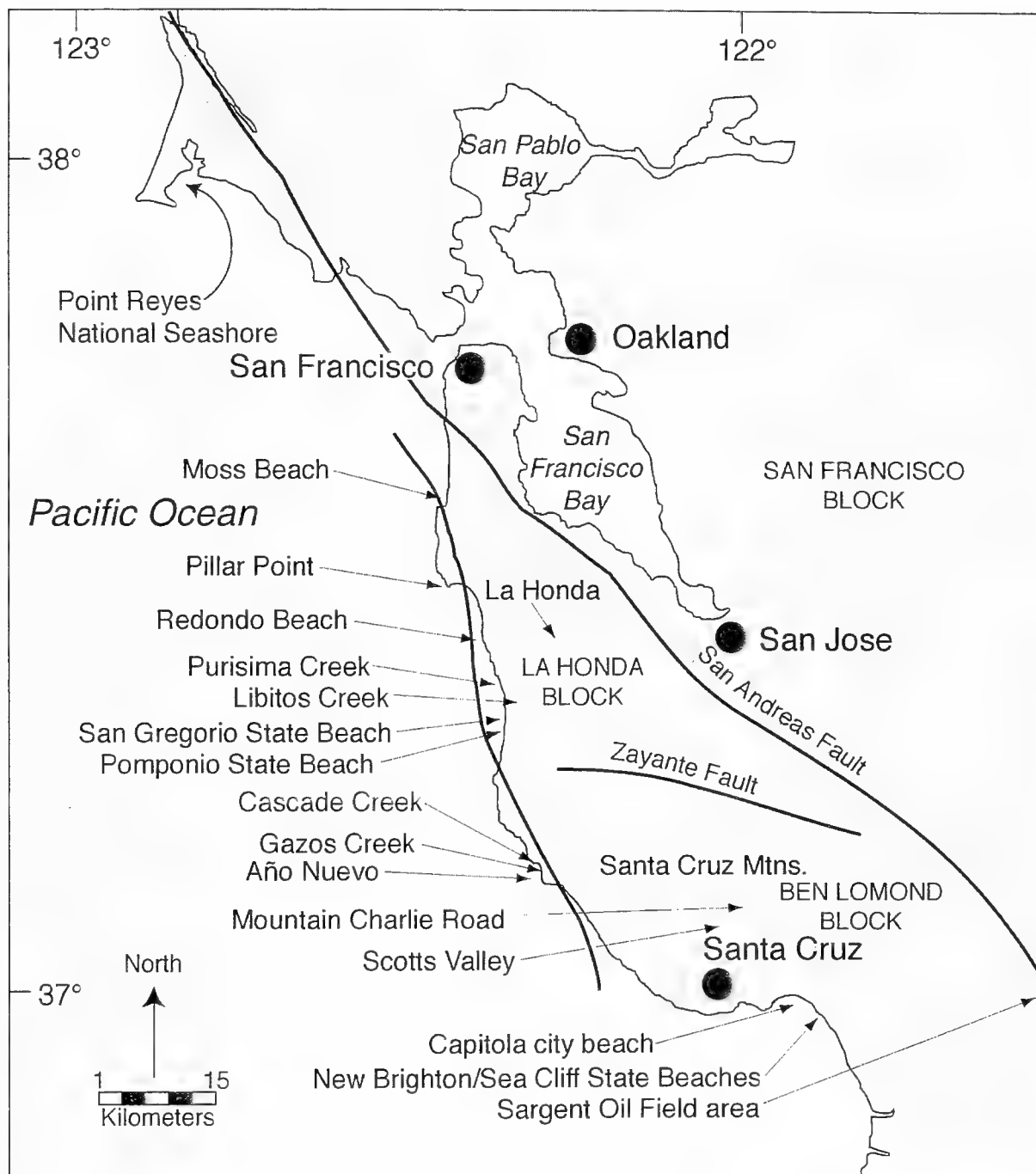


Figure 1. Index map of "Purisima" Formation outcrop areas in central California.

# A preliminary chronostratigraphy based on molluscan biogeography for the late Quaternary of southern California

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## Introduction

Five late Quaternary chronostratigraphic zones have been tentatively identified in southern California using marine molluscan faunas (Fig. 1; Table 1). From youngest to oldest they occur at (1) < 12,000, (2) 105,000(?) -  $\approx$  40,000, (3)  $\approx$  125,000, (4)  $\approx$  350,000 - 150,000, and (5)  $\approx$  600,000 - 300,000, years B.P. The fossil faunas studied show three biogeographic character states: (1) cooler than present water temperatures, (2) water temperatures similar to today, and (3) warmer than present water temperatures. Within the cooler and warmer water character states there is variation allowing for further subdivision. These zones are not based on individual taxa or assemblages but on the biogeographic affinities of faunas with more than 25 molluscan taxa.

The chronozones are informally numbered from youngest to oldest. The fauna from chronozone 1 is essentially modern with no or very rare extra-limital taxa. Faunas from chronozone 2 contain a significant percentage of north-ranging taxa and a few northern extra-limital taxa. Faunas from chronozone 3 contain a significant percentage of south-ranging taxa and a few southern extra-limital taxa, as well as occasional northern extra-limital taxa that may be reworked. Chronozone 4 faunas show a higher percentage of south-ranging taxa and southern extra-limital taxa are moderately common. Chronozones 3 and 4 are similar faunally but can be differentiated by the percentage of south-ranging and southern extra-limital taxa. These chronozones are also easily identified using amino-acid racemization studies. Finally, faunas of chronozone 5 show both cool and warm water faunas and commonly contain a small percentage of extinct taxa. This chronozone may be further subdivided in the future.

The molluscan faunas used here are coupled with geomorphic, amino acid, and stratigraphic position to develop a stratigraphic sequence. This sequence is integrated with the stratigraphic ranges of extinct taxa and radiometrically dated faunas from both within and outside of southern California to date the chronozones. Dates of the older chronozones are imprecise and preliminary.

Quaternary deposits in California generally reflect sea level fluctuations superimposed on a rising coastline. With a known sea level curve (Shackleton and Opdyke, 1973) and uplift rates (Lajoie et al., 1991) we can deduce, generally, where Quaternary deposits of known ages are likely to be found (Fig. 1). For example sea level was about -100 m (below present sea level) in California during the last glacial maxima (20,000 to 15,000 years ago; Powell, 1994). Pleistocene standlines along the California coast typically indicate uplift rates in the range of 0.1 to 0.4 m/ka (Lajoie et al., 1991). These data give a range of uplift of only about 1.5 m to 8.0 m above the -100 m former sea level elevation for the probable highest occurrence of marine deposits from the last glacial maxima. Fossil mollusks generally occur below sea level so the above depth would be the highest occurrence of this age material, assuming the given uplift rate. Applying this method to the chronozones here suggests deposits from chronozone 1 which are entirely below sea level, deposits from chronozone 2 may be partly below present sea level and/or partially above. The deposits from all chronozones should be above present sea level, assuming uplift rates above. When marine deposits are old enough they may not be represented only as emergent marine terraces but also as basinal deposits. These basinal deposits reflect sedimentation below the



fluctuating sea level and so include both highstand and lowstand deposits. In addition, older deposits are likely to be found at even higher elevations as strandline deposits, but deeper in basinal deposits.

## Zonation

### Chronozone 1: 12,000 year B.P. – present

Mollusks from this chronozone suggest water temperatures essentially similar to those along the adjacent coast today but also suggest possibly slightly warmer or slightly cooler water temperatures depending on the relative age of the deposits. The slightly cooler water temperatures are older and the warmer water temperatures are younger as would be expected with a rising sea level since the last glacial event 20,000 - 15,000 years ago.

The slightly warmer water temperatures are based on the occurrence of the bivalve *Laevicardium elatum* (Sowerby) at the Terminal Island coal hopper, San Pedro (Fig. 4), a site correlated with this chronozone by amino acids (D. Ponti, pers. comm., 1999). *Laevicardium elatum* (Sowerby) has been reported in southern California during historic times (Dall, 1921) but has not been reported in recent decades in the Los Angeles area so its occurrence in this fauna may suggest slightly warmer conditions than present. The Terminal Island coal hopper site represented a protected bay environment that might account for slightly higher temperatures than normal at that latitude.

The slightly cooler water temperatures are based on the presence of *Mya truncata* (Linnaeus) from samples dredged from Cordell Bank off central California (Fig. 3) which were dated by c-14 at about 10,800 years B.P. (Powell et al., 1992). This is an extra-limital northern taxon that does not occur today south of Puget Sound, Washington. The remaining fauna indicates deposition at about the latitude of the fossil locality (37°N-38°N) in water depths between the intertidal zone and 50 m. No other faunas are referred to this chronozone.

A cold water chronozone between chronozone 1 and chronozone 2 in southern California has been recognized from faunas off southern Oregon (USGS collections), in central California (Powell and McGann, 1991; Powell, 1994), and off San Benedicto Island, Revillagigedo Islands, Mexico (USGS collections) in the eastern Pacific, but has not been recognized to date off southern California. This chronozone has been dated between 20,000 –15,000 years B.P. (Powell and Chin, 1984; Powell and McGann, 1991).

### Chronozone 2: 105,000 (?) - ≈ 40,000 years B.P.

Chronozone 2 contains mollusks that represent temperatures similar to today off southern California, to slightly cool water temperatures. No southern extra-limital taxa, and none to few, northern extra-limital taxa are present. This chronozone correlates with the Mesa and upper part of the Pacific amino acid assemblage zone of Ponti (1989) and is characterized in Los Angeles County by a fauna similar to that along the adjacent coast today. Notable by their absence are the bivalves *Amiantis*, *Argopecten* and *Chione*. Also in the San Pedro area the “southerly” taxon *Donax* is rare, and, at least at 3<sup>rd</sup> Street and Mesa Avenue in San Pedro, appear to be totally reworked (Ponti, 1989). In coastal Orange and San Diego Counties *Chione* and *Donax* are present in faunas attributed to this chronozone and do not appear to be reworked (USGS collections).

Other localities containing suggested cool water faunas that are correlative with chronozone 2 occur at the Crawfish George’s locality in San Pedro and in the Ventura Basin. Crawfish George’s contains both southern and northern extra-limital molluscan taxa, but it is assumed that the southern extra-limital taxa are reworked. This assumption is based on most of the fauna, including the commonly collected species,

representing the same to slightly cooler water temperatures than exists along the adjacent coast today, as well as amino acid racemization studies (Ponti, 1989). The occurrence of reworked specimens in the Pleistocene of San Pedro is common, also based on amino-acid studies (D. Ponti, unpublished data). The emergent Punta Gorda marine terrace in the Ventura Basin has been dated at 60,000 - 40,000 years B.P. (Lajoie et al., 1982), but no fauna has been reported from these deposits. It should be noted that the Ventura Anticline where these deposits occur has experienced much higher uplift rates (maximum of 6.7 - 7.6 m/ka, Lajoie et al., 1982) than determined elsewhere in California (0.3 - 0.5 m/ka, Lajoie et al., 1982; 0.1 - 0.4 m/ka, Lajoie et al., 1991).

Also included in this chronozone is the Bird Rock terrace deposits, Point Loma, San Diego County (Kern, 1977; Kennedy et al., 1982; 87,000 - 83,000 years B.P., Muhs et al., 1994) (Fig. 3). Deposits from the first terrace in the northern San Joaquin Hills, Orange County (106,000 years B.P.; Grant et al., in press) (Fig. 3) are questionably referred to this chronozone but a fauna from this site has not been recorded or examined so deposits of this age ( $\approx$  105,000 years B.P.; oxygen-isotope stage 5c) may be better placed in chronozone 3. But the relative size of the sea level rise compared with that  $\approx$  125,000 years ago suggest cooler water conditions and inclusion here.

Outside of southern California deposits attributed to chronozone 2 have been reported and/or numerically dated from Whisky Run terrace at Coquille Point, Oregon (72 ka, Kennedy et al., 1982; 82 ka, Muhs et al., 1990); the lowest terrace at Point Arena, Mendocino County (76 ka, Muhs et al., 1990; 88 ka, Muhs et al., 1994) (Fig. 3); Año Nuevo Point (Addicott, 1966) (Fig. 3); the Q1 terrace (of Hanson et al., 1992) in the San Luis Obispo area, San Luis Obispo County (Muhs et al., 1994) (Fig. 3); the first terrace on San Nicolas Island in Santa Barbara County (Vedder and Norris, 1963; Muhs et al., 1994) (Fig. 3); the Lighthouse terrace at Punta Banda, Baja California Norte, Mexico (Rockwell and other, 1989; Muhs et al., 1994) (Fig. 3); the lower terrace at Turtle Bay, Baja California Sur, Mexico (Emerson et al., 1981) (Fig. 3); and possibly the fauna reported by Valentine (1980) from Camalú, Baja California Norte, Mexico (Fig. 3). Although Valentine attributed his fauna to deposits from chronozone 3, the occurrence of several extra-limital northern taxa and only a single worn specimens of a southern extra-limital taxon argues for inclusion here of the deposit and reworking of the warm water taxon.

### Chronozone 3: $\approx$ 125,000 years B.P.

This chronozone contains a fauna similar to off the adjacent coast today along with common south ranging taxa and rare to common southern extra-limital taxa. Northern extra-limital taxa are rare and, when present, are commonly represented by *Patinopecten caurinus* (Gould) which appear to be reworked from older deposits.

In the Los Angeles Basin the common south ranging and southern extra-limital taxa in this chronozone include the bivalves *Anadara perlabiata* (Grant & Gale), *Argopecten ventricosus* (Sowerby), *Chione gnidia* (Broderip & Sowerby), *Chione picta* Willett, *Crassinella* spp., *Felaniella parilis* (Conrad), *Nucula exigua* Sowerby, *Petricolaria cognata* (Adams), *Trachycardium panamense* (Sowerby), and the gastropods *Diodora arnoldi* McLean, *Eupleura muriciformis* (Broderip), and *Tegula eiseni* Jordan. Southern ranging bivalves are, for unknown reasons, much more common than southern ranging gastropods in this chronozone. The extinct gastropod *Cancellaria tritonidae* (Gabb) makes its youngest occurrence in this chronozone, while the extinct, endemic bivalve *Cyclocardia hilli* Willett appears to be restricted to this chronozone, but is only known from the Newport Bay area, Orange County (Figs. 3 and 4).

This chronozone includes the lower part of the Pacific amino acid assemblage zone of Ponti (1989) in the Los Angeles Basin. In southern California faunas attributed to this chronozone have been recorded from

the second terrace on San Nicolas Island, Santa Barbara County (Vedder and Norris, 1963; Muhs et al., 1994) (Fig. 3); Point Dume in Ventura County (Addicott, 1964) (Fig. 4); 2<sup>nd</sup> Street and Gaffe Street in San Pedro (USGS collections), 15<sup>th</sup> Street and Leland Ave., San Pedro (Chace, 1966), the lower stratum at Knoll Drive, San Pedro (Valentine, 1961), and possibly Signal Hill (DeLong, 1941) (although Signal Hill may represent chronozone 4) (Fig. 4), all in Los Angeles County; most localities in the Newport Bay, Orange County area (Bruff, 1946; Kanakoff and Emerson, 1959) (Fig. 4); Torrey Pines State Park, San Diego County (Valentine, 1960) (Fig. 3); and the Nestor terrace on the Point Loma Peninsula, San Diego County (Kern, 1977; Muhs et al., 1994) (Fig. 3). These sites are included here because of amino-acid correlations and all contain a percentage of southern extra-limital taxa.

Terrace faunas outside of southern California which are attributed to this chronozone are based on the presence of a warm water fauna, amino acid correlations, numerical dating, include the following: Q2 terrace (of Hanson et al., 1992) in the San Luis Obispo area, San Luis Obispo County (Muhs et al., 1994) (Fig. 3); Sea Cave terrace at Punta Banda, Baja California Norte, Mexico (Rockwell et al., 1989; Muhs et al., 1994) (Fig. 3); fossiliferous marine deposits at low altitude on Isla Guadalupe, Baja California Norte, Mexico (Lindberg et al., 1980; Muhs et al., 1994) (Fig. 3); the upper terrace at Turtle Bay, Baja California Sur, Mexico (Emerson et al., 1981) (Fig. 3); the Magdalena Terrace at Magdalena Bay, Baja California Sur, Mexico (Omura et al., 1979) (Fig. 3); and tentatively the terraces at Cabo Pulmo at the southern tip of Baja California Sur, Mexico (Squires, 1959; Muhs et al., 1994) (Fig. 3).

This chronozone is correlated with oxygen isotope stage 5e based on numerical age determinations from California and because the molluscan faunas contain southern extra-limital taxa. Dated occurrences include the Tripod terrace at Cayucos, San Luis Obispo County (130 ka, Veeh and Valentine, 1967;  $\approx$  101 ka to  $\approx$  125 ka, Stein et al., 1991; 117-121 ka, Muhs et al., 1994) (Fig. 3); the Q2 terrace at San Luis Obispo, San Luis Obispo County (99-117 ka, Muhs et al., 1994) (Fig. 3); the 2<sup>nd</sup> terrace on San Nicolas Island, Santa Barbara County (120-111 ka, Muhs et al., 1994) (Fig. 3); the 2<sup>nd</sup> terrace on San Clemente Island, Los Angeles County (127 ka, Muhs and Szabo, 1982; 114-108 ka, Muhs et al., 1994) (Fig. 3); the Nestor terrace on the Point Loma Peninsula, San Diego County (131-109 ka, Ku and Kern, 1974; 143-133 ka, Stein et al., 1991; 126 ka, Muhs et al., 1994) (Fig. 3); the Sea Cave terrace at Punta Banda, Baja California Norte, Mexico (128 ka-117 ka, Muhs et al., 1994) (Fig. 3); marine deposits on Isla Guadalupe, Mexico (131-114 ka, Muhs et al., 1994) (Fig. 3); and at Cabo Pulmo near the southern tip of Baja California Norte, Mexico (144-117 ka, Muhs et al., 1994) (Fig. 3).

#### Chronozone 4: $\approx$ 350,000 - 150,000 B.P.

Chronozone 4 generally contains a warm water fauna with common south ranging taxa, rare to common southern extra-limital taxa, and no northern extra-limital taxa. In southern California this chronozone is easily confused with chronozone 3 but can be most confidently distinguished using amino acid racemization studies or stratigraphic position. Faunally this chronozone can be distinguished by its higher percentage of southern extra-limital taxa than chronozone 3 ( $\approx$  125,000 years B.P.) and other extinct taxa. Mollusks characteristic of this chronozone, but not restricted to it, include those of the previous chronozone, and commonly the bivalve *Dosinia ponderosa* (Schumacher) and the gastropod *Macron aethiops* (Reeve). The extinct bivalve *Cyclocardia* sp., aff. *C. occidentalis* (Conrad) of Woodring et al. (1946) makes its youngest occurrence in this zone. Preliminary data suggests that this species of *Cyclocardia* became extinct during the Upper Bent Springs/Bixby amino acid zones (oxygen isotope stage 9). Other extinct taxa, which may have their youngest occurrence in this chronozone (or the next older chronozone), include the bivalve *Flabellipecten stearnsii* Dall, and the gastropods *Calicantharus fortis* (Carpenter) and *Crepidula princeps* Conrad. Younger occurrence of *Crepidula princeps* Conrad (i.e., Kanakoff and Emerson, 1959 in Newport Bay, Orange County) probably represent reworked specimens.

Ponti (1989) includes the lower part of this chronozone in his Harbor amino acid assemblage zone and his upper Bent Springs/Bixby amino acid assemblage zone. Deposits referred to this chronozone occur at Bixby Slough (USGS collections) (Fig. 4); the Defense Fuel Reserve quarries in Torrance (USGS collections) (Fig. 4); and possibly some sites at Signal Hill (DeLong, 1941) (Fig. 4). Also showing the characteristic warm water fauna and correlated with amino acid studies are the upper part of the Palos Verdes Sands, the lower part of the San Pedro Sands in the Palos Verdes/San Pedro area, and the Bay Point Formation at Mission Bay, San Diego County. Outside of southern California deposits of this age have not been recognized with certainty.

The age of this chronozone zone is uncertain. Amino-acid data correlate with oxygen isotope stage 7 and possibly 9, suggesting an age of between 350 - 150 ka (Ponti, 1989).

#### Chronozone 5: $\approx$ 600,000 - 300,000 B.P.

Deposits attributed to chronozone 5 generally contains a mix of warm water faunas and cool water faunas with a small percentage of both southern and northern extra-limital taxa. Usually the percentage of southern extra-limital taxa is smaller than for northern extra-limital taxa. Our opinion is that a detailed stratigraphy study of deposits of this age would show no mixing of southern and northern extra-limital taxa, but that they are restricted to individual zones representing highstands and lowstands of sea level within the broad time period attributed to this chronozone. In southern California, especially in the Los Angeles Basin, this chronozone generally contains deeper water deposits (as demonstrated by the entrained fossils) than previous chronozones, usually > 50 m. Mollusks characteristic of this chronozone in the Los Angeles Basin, but not restricted to it, include the bivalves *Chlamys jordani* Arnold, *Clinocardium nuttallii* (Conrad), *Mya truncata* Linnaeus, *Patinopecten caurinus* (Gould) and the gastropods *Antiplanes* spp., *Boreotrophon pedroana* (Arnold), *Boreotrophon* spp., and *Punctulla* spp. The extinct bivalves *Cyclocardia* sp., aff. *C. occidentalis* (Conrad) of Woodring et al. (1946) and *Flabellipecten stearnsii* Dall, and the gastropods *Bittium giganteum* Bartsch, *Calicantharus fortis* (Carpenter), and *Crepidula princeps* Conrad occur in this zone.

Ponti (1989) includes this chronozone in the lower part of his upper Bent Springs/Bixby and possibly all of his lower Bent Springs amino acid assemblage zones. Deposits referred to this chronozone include the type sections of the Timms Point Silt and Lomita Marl in San Pedro. Also included here and correlated by amino acid studies are the Chandler Gravel Pit South in Torrance, Los Angeles County (USGS collections) (Fig. 4). Based on published literature, the Broadway fauna, mostly exposed in downtown San Diego, San Diego County (Deméré, 1981), is probably referable to this chronozone. Outside of southern California deposits of this age have not been recognized with certainty.

No radiometric dates of deposits from this chronozone zone are available so its age range is uncertain. Amino-acid data suggest correlation with oxygen isotope stage 11 to possibly 15, suggesting an age of between about 600 and 350 ka (Ponti, 1989).

### **Conclusions**

A preliminary chronostratigraphy for southern California based on the ecologic character, extinct taxa, and numerical age techniques has been presented. Five chronozones are recognized over the past 600,000 years. Chronozone 1 (<12,000 years B.P.) contains faunas similar, or possibly slightly cooler or warmer, than off the adjacent coast today. Younger faunas suggest warmer conditions than older faunas within this zone. Fossils from chronozone 2 (between about 105,000 (?) - 40,000 years B.P.) suggest slightly cooler water conditions than exist along the adjacent coast today with occasional north ranging extra-limital taxa. Chronozone 3 ( $\approx$  125,000 years B.P.) faunas contain southern extra-limital taxa and

occasionally northern extra-limital taxa (possibly from reworking) and suggest slightly warmer water conditions than exist along the adjacent coast today as the cool water taxa generally appear to be reworked. Faunas from chronozone 4 (350,000 - 150,000 years B.P.) are similar to those from chronozone 3, but no extra-limital northern taxa have been reported and several extinct taxa are commonly found in faunas attributed to this age. Chronozone 5 (600,000 - 300,000 years B.P.) generally contains faunas suggesting deeper water than the previous chronozones. These faunas include several extinct taxa and deposits of this age commonly contain both southern and northern extra-limital taxa, although northern extra-limital seem to be more extensive. Dating of these zones is tentative and new data will refine these age calls.

The data presented here are preliminary and are likely to be further refined in the future. Also in addition to the chronozones described are a few outside of southern California that will have to be integrated with the southern California to develop a complete chronostratigraphy of the northeastern Pacific. It is hoped that this study will lead to develop "index" fossils to aid paleontologists and geologists in the field to make an educated guess at the age of marine Pleistocene sediments.

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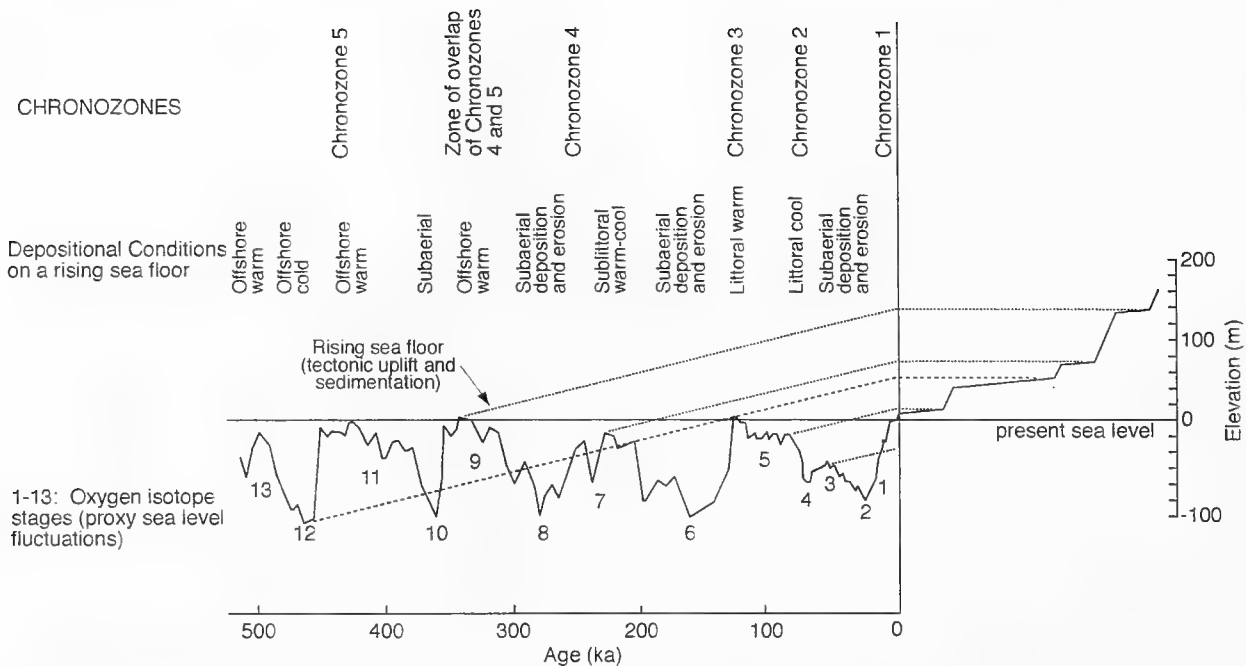


Figure 1. Diagram showing sea level curve, depositional conditions on a rising sea floor, and the late Quaternary chronozones for southern California. This diagram is based on paleontologic and amino acid data from fossil marine molluscan assemblages. The heavy dashed line represents a hypothetical sea floor that rises by tectonic uplift and sedimentation. In most slowly uplifting areas older littoral sediments are found at progressively higher elevations. Deposition during the minor sea level highstands of isotope stage 3 and younger deposits are still submerged below present sea level. In areas of subsidence (i.e., western Los Angeles basin) successively older stratigraphic units are buried progressively deeper below the surface. The proxy sea level curve is based on oxygen-isotope data from foraminifers in deep sea cores (Shackelton and Updyke, 1973). The sea level curve includes oxygen-isotope stages that correlate with sea level highstands (odd numbers) and lowstands (even numbers).



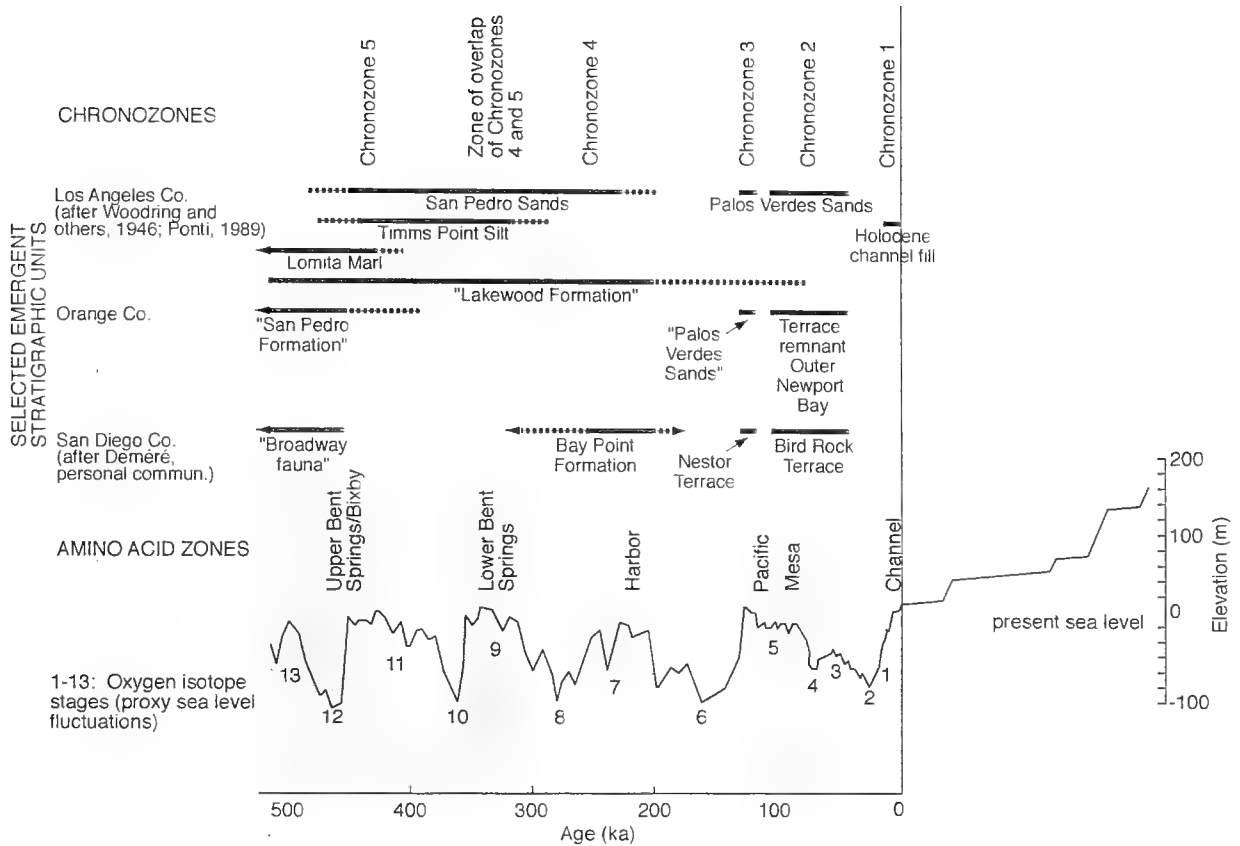


Figure 2. Sea level curve, amino acid zones of Ponti (1989), late Quaternary chronozones for southern California, and age ranges of selected emergent stratigraphic units in the Los Angeles Basin, coastal southern Orange County, and the San Diego Basin. The Lomita Marl, Timms Point Silt, San Pedro Sand, and Palos Verdes Sand reflect various depositional environments related to sea level fluctuations and gradual basin shallowing. The Lomita, Timms Point, and San Pedro are offshore and sublittoral correlatives of the littoral deposits on the third, fourth, and higher marine terraces cut into the Palos Verdes Hills. The Palos Verdes Sand is the littoral sediment on the two lowest terraces, which truncate the uplifted and tilted older stratigraphic units. The sublittoral and offshore correlatives of the Palos Verdes are submerged below present sea level. The proxy sea level curve is based on oxygen-isotope data from foraminifers in deep sea cores (Shackelton and Updyke, 1973). The sea-level curve includes oxygen-isotope stages that correlate with sea level highstands (odd numbers) and lowstands (even numbers).

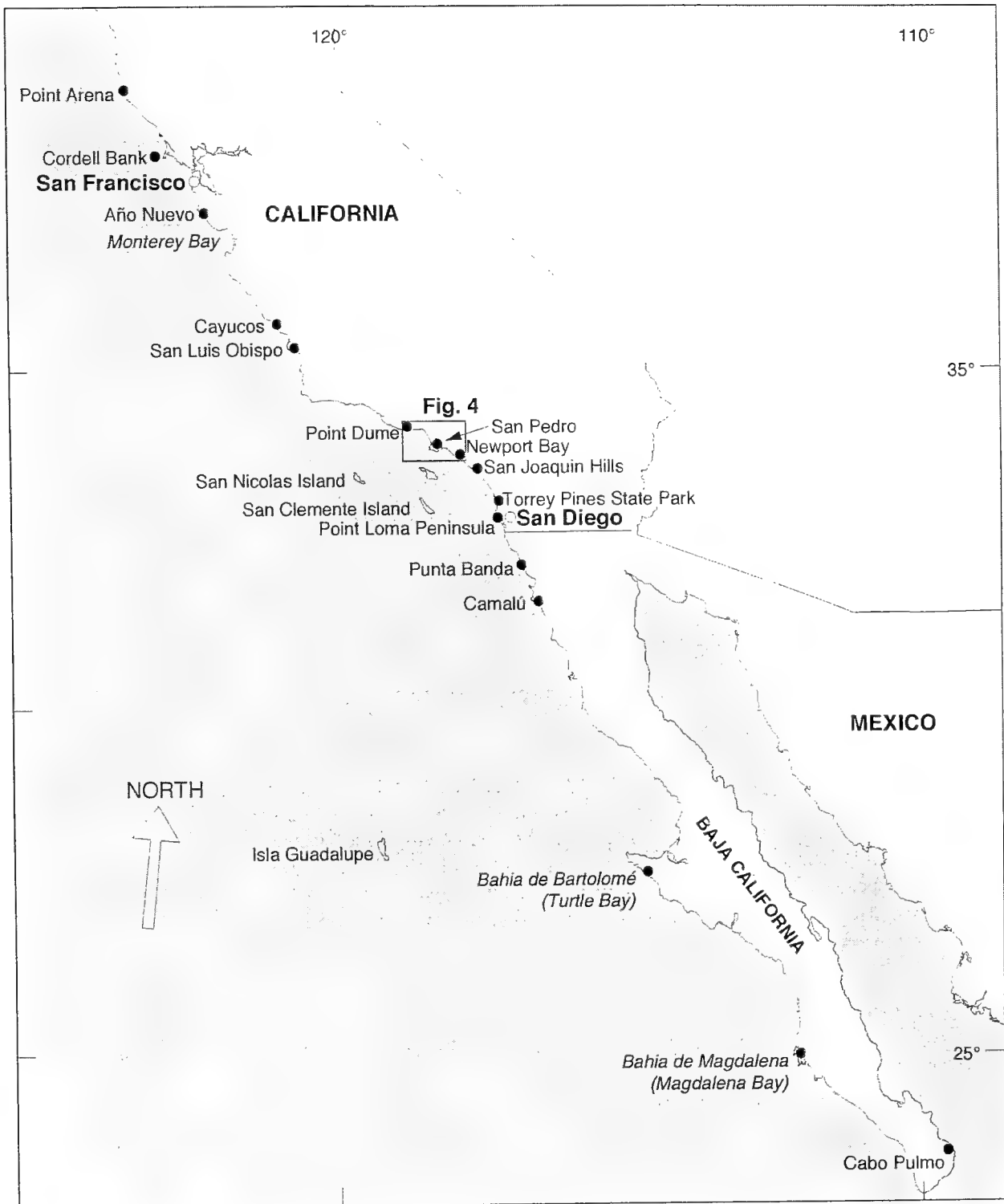


Figure 3. Index map of fossil localities in California and Mexico.

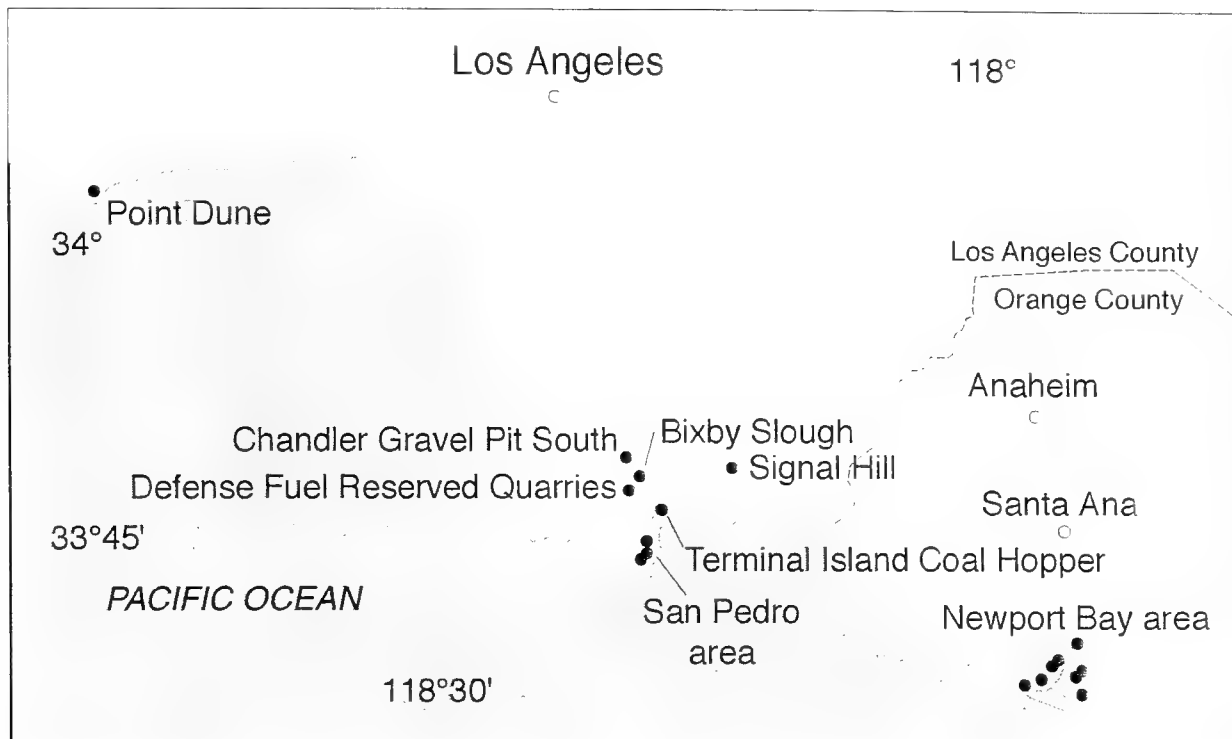


Figure 4. Index map of fossil localities in the greater Los Angeles Basin, including the San Pedro and Newport Bay areas.

Table 1. Preliminary data for late Quaternary chronozones in southern California.

Chronozone	Tentative age range (years B.P.)	Biogeographic character of the fauna	Suggested amino acid zone correlation	Suggested oxygen-isotope stage(s) correlation
1	<12,000	Slightly cooler to slightly warmer? than present.	Channel AAZ of Lajoie (ms).	1
2	105,000(?) to circa 40,000	Slightly cooler than present. Few extra-limital northern taxa.	Mesa and upper part of Pacific AAZ of Ponti (1989).	5c-3
3	Circa. 125,000	Slightly warmer than modern fauna. Few extra-limital southern taxa. Few extra-limital northern taxa (probably reworked)	Lower part of Pacific AAZ of Ponti (1989).	5e
4	350,000 to 150,000	Warmer water fauna with common southern extra-limital taxa	Harbor and upper Bent Springs/Bixby AAZ of Ponti (1989)	9-7
5	600,000 to 300,000	Mixture of warm water and cool water faunas	Lower part of upper Bent Springs/Bixby and possibly all of lower Bent Springs AAZ's of Ponti (1989)	15-11

Chronozone	Correlated deposits in southern California	Correlated deposits outside southern California
1	Terminal Island Coal Hopper, San Pedro (herein)	West of Cordell Bank (Powell et al., 1992)
2	Crawfish George's, Bird Rock Terrace deposits, first terrace, San Joaquin Hills (?).	Whisky Run terrace, OR; lowest terrace, Point Arena, CA; Año Nuevo, CA; Q1 terrace, San Luis Obispo, CA, 1 <sup>st</sup> terrace, San Nicolas Island, CA; Lighthouse terrace, Punta Banda, MX, lowest terrace, Turtle Bay, MX; (?) Camalú, MX.
3	2 <sup>nd</sup> terrace, San Nicolas Island; Point Dume; 2 <sup>nd</sup> terrace, San Clemente Island; 2 <sup>nd</sup> & Gaffey, San Pedro; 15 <sup>th</sup> & Leland, San Pedro; lower stratum, Knoll Drive, San Pedro; (?) Signal Hill; some outcrops at Newport; Torey Pines State Park; Nestor terrace.	Tripod terrace, CA; Q2 terrace, San Luis Obispo, CA; Sea Cave terrace, MX; Isla Guadalupe, MX, upper terrace, Turtle Bay, MX; Magdalena Terrace, MX, (?) Cabo Pulmo, MX.
4	Bixby Slough; DFR quarries; Signal Hill (?); Bay Point Formation.	None with certainty.
5	Type Timms Point Silt; type Loma Marl; Chandler Gravel Pit.	Broadway fauna, San Diego, CA.

Five late Quaternary chronostratigraphic zones can be recognized using mollusk faunas from southern California. From youngest to oldest they occur at (1) < 10 ka, (2) between 105 and 85 ka, (3) about 125 ka, (4) between about 350 and 150 ka, and (5) between about 500 and 300 ka. The molluscan faunas studied show three biogeographic character states: (1) cooler than present water temperatures, (2) water temperatures similar to today, and (3) warmer water temperatures. Within the cooler and warmer water biogeographic character states there is variation allowing for further subdivision. These zones are not based on individual taxa or assemblages but on the biogeographic affinities of faunas of more than 25 taxa.

The < 10 ka fauna is essentially modern with no extra-limital taxa. Faunas dated between 105 and 85 ka contain a significant percentage of north ranging taxa and a few northern extra-limital taxa. Faunas dated at about 125 ka contain a significant percentage of south ranging taxa and a few southern extra-limital taxa, as well as occasional northern extra-limital taxa. Faunas dated between 350 ka and 150 ka show a higher percentage of south ranging taxa and southern extra-limital taxa can only be distinguished from the previous chronozone by degree. Faunas of the 500 to 300 ka chronozone also show both cool and warm water faunas and may be further subdivided in the future.

The molluscan faunas used here are coupled with geomorphic and amino acid data to develop a stratigraphic sequence. Integrated with this sequence are extinct taxa and radiometrically dated faunas from other regions which allows dating of these chronozones.

## **Significance of macrofossils from the "San Pedro" Formation, Coyote Hills, Orange County, southern California**

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### **Introduction**

The "San Pedro" Formation in the Coyote Hills, Orange County, southern California, contains a molluscan assemblage of 156 taxa (78 bivalves, 75 gastropods, and 3 scaphopods; table 1) collected from 156 localities. In addition foraminifers, annelid worms, bryozoans, echinoids, arthropods, and vertebrates are known from these collections. These fossils are divided into two assemblages: an upper, temperate to warm-water assemblage and a lower, cool-water assemblage. Likewise the Formation is divided into two informal members, but these members are not coincident with the two assemblages. Exposures of the "San Pedro" Formation occur fairly extensively in the West Coyote Hills (including Ralph Clark Regional Park) (maximum thickness near 100 m) but are much thinner and poorly exposed in the East Coyote Hills (maximum thickness about 20 m).

### **Geology**

According to Yerkes (1972) the "San Pedro" Formation in the Coyote Hills is exposed locally south of the Whittier fault zone in a thin bank just north of La Habra and in the central parts of the East and West Coyote Hills oil fields. It is composed of interbedded silts, silty sands, sands, and pebbly sands, and is informally divided into two members. Based on well data, Yerkes (1972) cited a maximum thickness of 520 m (1750 ft) for the formation, although he recognized a maximum thickness of only 99 m (325 ft) in outcrop. We recognized a maximum thickness of only about 84 m (275 ft) in the West Coyote Hills. The upper member is composed mostly of sand and pebbly sand with local conglomerate beds and contains scattered beds of shallower water fossils. The lower member is mostly composed of silts and silty sands with scattered deeper water mollusks. Both the top and base of the formation are expressed as unconformities or not exposed.

The "San Pedro" Formation in the Coyote Hills is not equivalent to the San Pedro Formation as redefined by Woodring et al. (1946) in the type area, but is significantly older.

## Biostratigraphy

The upper fauna is represented at only a few sites in the West Coyote Hills and Ralph Clark regional Park. Mollusks from these sites generally indicate normal marine conditions on a protected to open coastline in shallow water (< 25 m). Two southern extra-limital taxa are present: *Argopecten ventricosus* (Sowerby) and *Trachycardium panamense* (Sowerby), which do not occur north of Baja California today. Other warmer water taxa include the bivalves *Chione* spp. and *Donax californicus* Conrad, and the gastropods *Bursa californica* (Hinds), *Crucibulum spinosum* (Sowerby), *Nassarius* cf. *N. cerritensis* (Arnold), and *Terebra pedroana* Dall. These taxa indicate water temperatures similar to, or warmer than, off the adjacent coast today. The fauna is not well dated, but based on the presence of southern extra-limital taxa and no extinct taxa the fauna may date between  $\approx$  350,000 and 125,000 years BP. However, Welton et al. (MS) cite *Pecten bellus* (Conrad) 4 or 5 meters stratigraphically below another collection containing the warmer water taxa *Crucibulum?* sp., *Donax californicus* (Conrad), *Leporimetis obesa* (Deshayes), and *Gari fucata* (Hinds), suggesting either a major unrecognized unconformity between the two fossil localities or that the age of the warmer water fauna is significantly older than that stated above and is late Pliocene to earliest Pleistocene in age.

The lower fauna occurs fairly extensive in both the West and East Coyote Hills. Mollusks from exposures referred to this member suggests normal marine conditions, but offshore in water depths around 50 m. Two northern extra-limital bivalves are present: *Patinopecten caurinus* (Gould) and *Pandora wardiana* Adams, which do not occur south of central California today, indicating cooler water than present along the adjacent coast during deposition of these rocks. This fauna is characterized by the bivalves *Cyclocardia* aff. *C. occidentalis* (Conrad), *Panope abrupta* (Conrad), *Patinopecten caurinus* (Gould), and *Pecten bellus* (Conrad) and the gastropods *Crassispira zizyphus* Berry and *Crepidula princeps* (Conrad). Together these taxa and other extinct taxa indicate an early Pleistocene or possibly late Pliocene age for the informal lower member of the "San Pedro" Formation in the Coyote Hills (Table 2).

## Conclusions

Pleistocene marine rocks crop out in the Coyote Hills in Fullerton, La Habra, and Buena Park, Orange County, southern California. These rocks have been referred to the "San Pedro" Formation but differ in age significantly from the type San Pedro and so are referred to in quotes for outcrops in the Coyote Hills. They have been divided into two lithologic units: a mostly silt and silty sand underlying mostly sand, pebbly sand, and conglomerate unit. They are also divided into two biostratigraphic units that do not correlate with the stratigraphic units. The lower biostratigraphic unit consists mostly of mollusks, which represent moderately deep water (circa. 50 m), and cooler water than exist along the adjacent coastline today. The upper biostratigraphic unit also consists mostly of mollusks, but they represent shallow water depths (probably circa. 10 m or less) and a marine environment similar to off the adjacent coast today to slightly warmer. Based on extinct taxa, the lower biostratigraphic unit is late Pliocene to early Pleistocene in age. The age of the upper biostratigraphic unit is uncertain but could be anywhere between late Pliocene and late Pleistocene, but a late Pleistocene age is suggested.

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Table 1. Faunal list of megainvertebrate fossils from the “San Pedro” Formation in the Coyote Hills, Orange County, California. Taxa in bold are extinct. Taxa double underlined have modern ranges no further south than the latitude of the fossil locality (34°N). Taxa underlined have modern ranges no further north than the latitude of the fossil locality (34°N)

Taxa	Ralph C. Clark Regional Park	West Coyote Hills (includes Yerkes, 1972 collections)	East Coyote Hills
ANNELIDA			
POLYCHAETA			
Serpulidae, indet.	-	x	x
MOLLUSCA			
BIVALVIA			
<i>Amiantis callosa</i> (Conrad, 1837)	x	-	-
<u><i>Argopecten ventricosus</i> (Sowerby, 1842)</u>	x	? sp.	-
Cardiidae, indet.	x	x	-
<u><i>Chione californiensis</i> (Broderip in Broderip &amp; Sowerby, 1835)</u>	-	x	-
<u><i>Chione undatella</i> (Sowerby, 1835)</u>	x	-	-
<i>Chlamys behringiana</i> (Middendorff, 1849)	-	x	-
<i>Chlamys hastata</i> (Sowerby, 1843)	x	x	-
<b><i>Chlamys opuntia</i> (Dall, 1898)</b>	-	<b>x</b>	-
<i>Chlamys rubida</i> (Hinds, 1845)	-	x	-
<i>Chlamys</i> sp.	x	x	-
<i>Clinocardium</i> sp.	-	x	-
<i>Compsomyax subdiaphana</i> (Carpenter, 1864)	-	x	-
<i>Crassadoma giganteus</i> (Gray, 1825)	x	-	-
<i>Crassinella?</i> sp.	-	x	-
<i>Cryptomya californica</i> (Conrad, 1837)	x	x	-
<i>Cyathodonta pedroana</i> Dall, 1915	x	x	-
<b><i>Cyclocardia</i> sp., cf. <i>C. occidentalis</i> (Conrad, 1855)</b>	-	<b>x</b>	-
<b><i>Dendostrea?</i> <i>vespertina</i> (Conrad, 1854)</b>	-	<b>x</b>	<b>x</b>
<i>Diplodonta orbella</i> (Gould, 1851)	x	-	-
<u><i>Donax californicus</i> Conrad, 1837</u>	x	-	-
<i>Donax gouldii</i> Dall, 1921	-	x	-
<i>Epilucina californica</i> (Conrad, 1837)	-	x	-
<u><i>Gari fucata</i> (Hinds, 1845)</u>	x	x	-
<i>Glycymeris septentrionalis</i> (Middendorff, 1849)	-	x	-
<i>Humilaria kennerleyi</i> (Reeve, 1863)	-	x	-
<i>Leporimetis obesa</i> (Deshayes, 1855)	x	x	-
<i>Leptopecten latiauratus</i> (Conrad, 1837)	-	x	-
Lithophaginae, indet.	x	x	-
<i>Lucinisca nuttalli</i> (Conrad, 1837)	x	x	-
<i>Lucinoma annulata</i> (Reeve, 1850)	x	x	-
Lucinidae, indet.	x	x	-
<b><i>Lyropecten cerrosensis</i> (Gabb, 1866)</b>	-	<b>x</b>	-
<i>Macoma indentata</i> Carpenter, 1864	-	x	-
<i>Macoma nasuta</i> (Conrad, 1837)	-	x	-
<i>Macoma secta</i> (Conrad, 1837)	-	x	-
<i>Macoma</i> sp.	-	x	-
<i>Mactromeris hemphilli</i> (Dall, 1894)	-	x	-
<i>Mactrotoma californica</i> (Conrad, 1837)	x	x	-
<i>Miodontiscus prolongatus</i> (Carpenter, 1864)	-	x	-
<i>Modiolus rectus</i> (Conrad, 1837)	x	x	-

<i>Mytilus californianus</i> Conrad, 1837	-	cf.	-
<i>Mytilus trossulus</i> Gould, 1850	-	X	-
<i>Nuculana taphria</i> (Dall, 1896)	X	X	-
<i>Nuculana</i> sp.	-	X	-
<i>Nutricola tantilla</i> (Gould, 1853)	-	X	-
<i>Ostrea conchapila</i> Carpenter, 1857	X	X	-
<u><i>Pandora wardiana</i> Adams, 1860</u>	-	X	-
<i>Pandora</i> sp. (small)	-	X	-
<i>Panopea abrupta</i> (Conrad, 1849)	X	X	-
<i>Parvilucina tenuisculpta</i> (Carpenter, 1864)	-	X	-
<u><i>Patinopecten caruinus</i> (Gould, 1850)</u>	X	X	-
<b><i>Pecten bellus</i> (Conrad, 1857)</b>	<b>X</b>	<b>X</b>	<b>X</b>
Pectinidae, indet.	-	X	-
<i>Periploma planiusculum</i> Sowerby, 1834	-	X	-
<i>Pododesmus macrochisma</i> (Deshayes, 1839)	X	X	-
<i>Protothaca tenerrima</i> (Carpenter in Gould & Carpenter, 1857)	-	X	-
<i>Protothaca</i> sp.	-	?	-
<i>Saxidomus nuttalli</i> Conrad, 1837	X	X	-
<i>Semele venusta</i> (Reeve, 1853)	-	X	-
<i>Semele?</i> sp.	-	X	-
<i>Siliqua</i> sp.	-	X	-
<i>Solamen</i> sp., cf. <i>S. columbiana</i> Dall, 1897	-	X	-
<i>Solen</i> sp.	-	X	X
<i>Spisula</i> sp.	-	X	-
<i>Tagelus</i> sp., cf. <i>T. californianus</i> (Conrad, 1837)	-	X	-
<i>Tagelus</i> sp., cf. <i>T. subteres</i> (Conrad, 1837)	-	X	-
<i>Tellina bodegensis</i> Hinds, 1845	-	X	-
<i>Tellina</i> sp., cf. <i>T. modesta</i> (Carpenter, 1864)	-	X	-
Tellinidae, indet.	X	X	-
Teredinidae, indet.	-	X	-
<i>Thracia trapezoides</i> Conrad, 1849	-	X	-
<i>Tivela stultorum</i> (Mawe, 1823)	X	X	-
<u><i>Trachycardium panamense</i> (Sowerby, 1833)</u>	X	-	-
<i>Trachycardium quadragenarium</i> (Conrad, 1837)	X	X	-
<i>Tresus nuttalli</i> (Conrad, 1837)	X	X	-
Veneridae, indet.	-	X	-
GASTROPODA			
<i>Acanthina spirata</i> (Blainville, 1832)	-	X	-
<i>Acteocina culcitella</i> (Gould, 1853)	-	X	-
<i>Acteocina harpa</i> (Dall, 1871)	-	X	-
<i>Acteocina inculta</i> (Gould, 1855)	-	cf.	-
<i>Amphissa reticulata</i> Dall, 1916	-	X	-
<i>Astraea gibberosa</i> (Dillwyn, 1817)	X	X	-
<i>Astraea undosa</i> (Wood, 1828)	X	-	-
<i>Astyris gausapata</i> (Gould, 1850)	-	X	X
<u><i>Boreotrophon</i> sp., cf. <i>B. multicostatus</i> (Eschscholtz, 1829)</u>	-	X	-
<i>Boreotrophon pedroana</i> (Arnold, 1903)	-	X	-
<i>Bursa californica</i> (Hinds, 1843)	X	X	-
<b><i>Calicantharus fortis</i> (Carpenter, 1866)</b>	<b>X</b>	<b>cf.</b>	<b>-</b>
<i>Calliostoma annulatum</i> (Lightfoot, 1786)	X	-	-
<i>Calliostoma canaliculatum</i> (Lightfoot, 1786)	cf.	X	-
<i>Calliostoma gemmulatum</i> Carpenter, 1864	-	X	-
<i>Calliostoma variegatum</i> Carpenter, 1864	-	X	-
<i>Calliostoma</i> sp.	X	X	-
<i>Calyptraea</i> sp.	-	X	-
<b><i>Cancellaria arnoldi</i> Dall, 1909</b>	-	<b>X</b>	<b>-</b>



<b><i>Cancellaria tritonidea</i> Gabb, 1866</b>	-	X	-
<i>Clathurella</i> sp.	-	?	-
<i>Conus californicus</i> Reeve, 1844	X	X	-
" <i>Crassispira montereyensis</i> " (Stearns, 1871)	-	X	-
<b><i>Crassispira zizyphus</i> (Berry, 1940)</b>	X	X	-
<i>Crepidula adunca</i> Sowerby, 1825	X	X	-
<i>Crepidula onyx</i> Sowerby, 1824	-	X	-
<b><i>Crepidula princeps</i> Conrad, 1856</b>	-	X	-
<i>Crockerella</i> sp., cf. <i>C. conradiana</i> (Gabb, 1866)	-	X	-
<i>Crucibulum spinosum</i> (Sowerby, 1824)	X	X	-
<i>Cryptonatica affinis</i> (Gmelin, 1791)	-	X	-
<i>Cylichna attonsa</i> Carpenter, 1864	-	X	-
<i>Cymatosyrinx hemphilli</i> (Stearns, 1871)	-	X	-
<i>Epitonium bellastrata</i> (Carpenter, 1864)	X	-	-
<i>Epitonium indianorum</i> (Carpenter, 1864)	-	X	-
<i>Epitonium sawinae</i> (Dall, 1903)	X	X	-
<i>Erato vitellina</i> Hinds, 1844	-	X	-
<i>Fusinus</i> sp., cf. <i>F. barbarena</i> (Trask, 1855)	sp.	X	-
<i>Haliotis cracherodii</i> Leach, 1814	-	X	-
<i>Halistylus pupoideus</i> (Carpenter, 1864)	-	X	-
<i>Haminoea vesicula</i> (Gould, 1855)	X	-	-
<i>Homalopoma paucicostatum</i> (Dall, 1871)	-	X	-
<i>Kelletia</i> sp.	-	X	-
<i>Kutziella variegata</i> (Carpenter, 1864)	-	X	-
<i>Lacuna unifasciata</i> Carpenter, 1857	-	X	-
<i>Lirobittium lomaensis</i> (Bartsch, 1911)	sp.	cf.	-
<i>Lirobittium rugatum</i> (Carpenter, 1864)	-	X	-
<i>Littorina scutulata</i> Gould, 1849	-	X	-
<i>Megasurcula carpenteriana</i> (Gabb, 1865)	X	X	-
<i>Mitra idea</i> Melville, 1893	X	-	-
<u><i>Nassarius</i> sp., cf. <i>N. cerritensis</i> (Arnold, 1903)</u>	-	X	-
<i>Nassarius fossatus</i> (Gould, 1849)	X	X	-
<i>Nassarius mendicus</i> (Gould, 1849)	X	X	-
<i>Nassarius perpinguis</i> (Hinds, 1844)	X	X	-
<i>Nassarius tegula</i> (Reeve, 1853)	-	X	-
Naticidae, indet.	X	X	-
<i>Neptunea tabulata</i> (Baird, 1863)	-	X	-
<i>Neverita reclusiana</i> (Deshayes, 1839)	X	X	-
<i>Ocenebra foveolata</i> (Hinds, 1844)	X	X	-
<i>Olivella baetica</i> Carpenter, 1864	X	X	cf.
<i>Olivella biplicata</i> (Sowerby, 1825)	X	X	-
<i>Olivella</i> sp.	-	X	-
<i>Opalia borealis</i> Keep, 1881	-	X	-
<i>Ophiidermella inermis</i> (Reeve, 1843)	sp.	X	-
<i>Polinices draconis</i> (Dall, 1903)	sp.	X	-
<i>Polinices lewisii</i> (Gould, 1847)	-	X	-
<i>Polygireulima rutila</i> (Carpenter, 1864)	-	X	-
<i>Pseudomelatoma</i> sp., cf. <i>P. pencillata</i> (Carpenter, 1864)	-	X	-
<i>Scabrotrophon</i> sp., cf. <i>S. lasius</i> (Dall, 1919)	-	X	-
<i>Sinum scopulosum</i> (Conrad, 1849)	-	X	-
<i>Tegula pulligo</i> (Gmelin, 1791)	-	X	-
<u><i>Terebra pedroana</i> Dall, 1908</u>	sp.	X	-
<i>Turbonilla</i> sp.	-	X	-
Turridae, indet.	-	X	-
<i>Turritella cooperi</i> Carpenter, 1864	-	X	-
<i>Volvulella cylindrica</i> (Carpenter, 1864)	-	X	-

SCAPHOPODA			
<i>Dentalium neohexamun</i> Sharp & Pilsbry, 1897	x	x	-
<i>Dentalium pretiosum</i> Sowerby, 1860	-	x	-
<i>Dentalium</i> sp.	x	x	-
ARTHROPODA			
CRUSTACEA			
<i>Balanus?</i> sp. (Barnacle)	x	x	x
<i>Cancer</i> sp. (Crab)	-	x	-
<i>Coronula?</i> sp. (Whale Barnacle)	-	x	-
<i>Randallia ornata</i> (Randell, 1839)	x	-	-
indet. crab fragments	x	x	-
ECHINODERMATA			
ECHINOIDEA			
Clypeasteriod, indet.	-	x	-
<i>Dendraster venturaensis</i> Kew, 1920	sp.	x	-
indet. echinoid spines	-	x	-

Table 2. Age range of extinct molluscan taxa from the "San Pedro" Formation, Coyote Hills, Orange County, California..

Taxa	Late Miocene	Early Pliocene	Late Pliocene	Early Pleistocene	Middle Pleistocene	Late Pleistocene
MOLLUSCA						
BIVALVIA						
<i>Chlamys opuntia</i> (Dall)	-	X	X	X		
<i>Cyclocardia</i> sp., aff. <i>C. occidentalis</i> (Conrad)		-	?	-	X	X
<i>Dendostrea?</i> <i>vespertina</i> (Conrad)	X	X	X	?	-	-
<i>Flabellipecten stearnsii</i> (Dall)	-	X	X	X	X	?
<i>Lyropecten cerrosensis</i> (Gabb)	X	X	X	-	-	-
<i>Pecten bellus</i> Conrad	-	X	X	X	-	-
GASTROPODA						
<i>Cancellaria arnoldi</i> (Dall)	-	-	X	?	-	-
<i>Cancellaria tritonidae</i> (Gabb)	-	X	X	X	X	X
<i>Caliantharus fortis</i> (Carpenter)	X	X	X	X	X	X
<i>Crepidula princeps</i> (Conrad)	X	X	X	X	X	X
ECHINODERMATA						
ECHINOIDEA						
<i>Dendraster venturaensis</i> Kew	-	-	?	X	-	-

## Understanding latitudinal diversity patterns in the sea: a molluscan perspective

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Latitudinal diversity gradients characterize many marine and terrestrial organisms, and are commonly considered to be one of the most fundamental global biodiversity patterns. However, despite a long debate, the processes that underlie such gradients remain enigmatic. In addition, there is considerable debate about how pervasive this pattern is among marine organisms. Analyses of distributional patterns of shallow marine mollusks living on the eastern Pacific and western Atlantic shelves contradict some current hypotheses about the controls on such gradients, and reveal the important role played by biogeographic barriers and evolutionary history.

Integration of modern day coastal biogeography with paleobiological data reveals a dynamic picture of molluscan biodiversity. Evolutionary rate differences underlie the primary diversity gradient but the shape of this gradient is controlled by spatial distribution of biogeographic boundaries that are determined by prevailing physical conditions.

### Exposed sandy shore molluscan assemblages from the Pliocene of Chula Vista, San Diego County, California

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Excavation for the new Veteran's Home of California, Chula Vista, exposed approximately 75 ft of the Pliocene-age San Diego Formation with deposits rich in fossils of marine mammals and marine invertebrates. The upper 50 ft of section consisted of friable sandstones containing exposed sandy shore fossil invertebrates. The lower 25 ft of section consisted of compact massive and locally concretionary sandstone beds containing remains of marine mammals (including articulated skeletons) associated with shells of inner sublittoral (0-175 ft) to outer sublittoral (175 to 700 ft) marine mollusks (see Fig. 1). A broad shoaling pattern (from down-section to up-section) in a slowly subsiding sedimentary basin is reflected in the exposed section. Sublittoral deposits at the bottom grade upwards into littoral deposits at the top. This pattern is supported by both sedimentologic and paleontologic evidence.

Previous paleontological studies of the San Diego Formation have focused almost solely on taxonomy and have failed to document the biostratigraphic and paleoenvironmental aspects of the molluscan species. At the Veteran's Home site the upper beds contain fossils indicative of exposed sandy shore paleoenvironments. Molluscan taxa strictly characteristic of the sandy shore include *Tivela stultorum*, *Tellina bodegensis*, *Siliqua lucida*, *Amiantis* sp., *Periploma planiuscula*, *Yoldia cooperi*, *Pandora punctata* and *Spisula catilliformis*. Associated species in this assemblage that may also occur in protected bays include *Macoma nasuta*, *Macoma secta*, *Tresus nuttallii*, *Cryptomya californica*, and *Polinices* sp. Their occurrence of these latter species on exposed sandy beaches is generally limited to subtidal areas where wave action is minimal.

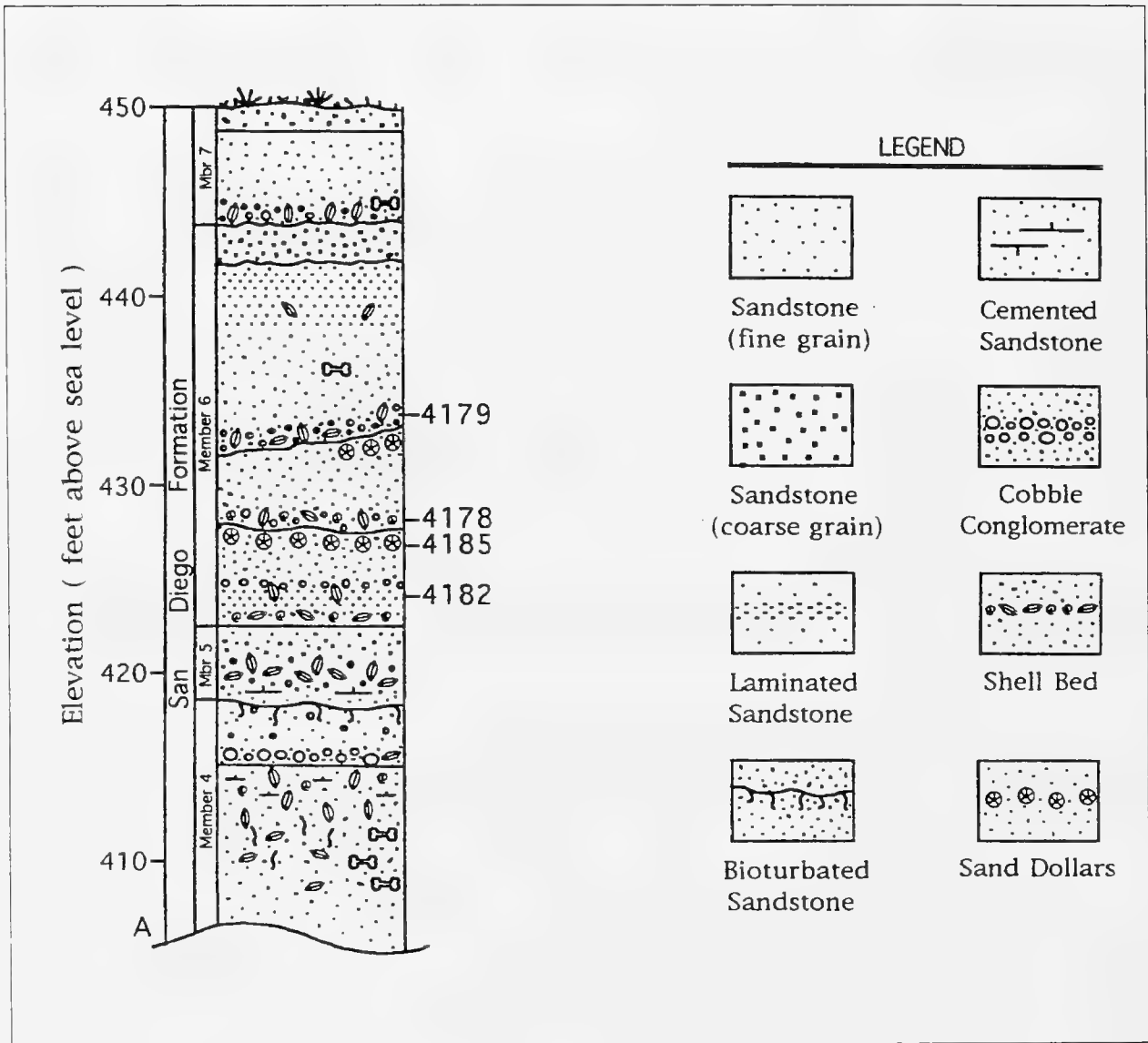


Figure 1. Measured stratigraphic section for the Veterans Home project site showing the San Diego Formation members 4 through 7. Locality numbers are shown for only the friable sandstones containing exposed sandy shore fauna

### Patterns of species transfer and invasion associated with ships

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The human-mediated transfer and introduction of nonindigenous species into North American waters has been occurring for approximately 4 centuries. Although a variety of transfer mechanisms or vectors are responsible for resulting invasions, the transfer of species in and on ships continues to contribute strongly to the pattern of invasions. Historically, many species were transferred on the bottoms or associated with

dry ballast (i.e., sand and rocks) of ships. In this century, dry ballast has been replaced by the use of ballast water for stability. Today, the transfer of species with ballast water of ships is considered a primary mechanism of invasion, although its relative importance may vary spatially and among taxonomic groups. The on-going process of invasion clearly exerts a significant influence on the structure and function of aquatic (i.e., marine and freshwater) communities throughout the world, but the actual patterns and effects of invasion remain poorly resolved due to limited data in many regions. As a result, our understanding of invasion processes, and especially the relationship between supply and invasion, remains in its infancy. Importantly, the ability of management efforts to reduce the rate of invasions requires a much higher resolution analysis than presently exists for patterns of invasion. Standardized and quantitative measures of invasion patterns, both in space and time, are fundamental building-blocks of invasion biology and should be a priority for current research and management efforts.

## BIVALVES OF THE OPINAE FROM THE NORTH AMERICAN PACIFIC SLOPE

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Opinae is a subfamily of Astartidae having distinctively carinated shells with a defined posterior area, high beaks, and high cardinal hinge teeth. The genus *Opis* ranges from Early Jurassic through Late Cretaceous and comprises subtrigonal, obliquely elongated shells with only cardinal hinge teeth, 3b in the right valve and 2 and 4b in the left valve. In typical *Opis* from Europe 4b is stronger than 2. The ligament is narrow (Chavan, 1969). *Opis* spp. from the Pacific Slope differ in three characteristics from typical *Opis*: 1) in the left valve, cardinal tooth 2 is stronger than 4b; 2) in the right valve, the presence of a lamellar, second cardinal, 5b appressed to the posterior valve margin is suggested by a vertically grooved area facing tooth 4b; 3) the ligament area is external near the beaks but deeply submerged posteriorly. This type of ligament attachment was described by Whiteaves (1879) in the first recognized Pacific slope species *Opis vancouverensis* from British Columbia. These differences suggest that the Pacific slope species constitute a new subgenus.

The geologically oldest Pacific Slope Cretaceous species is *Opis californica* Stanton, 1895 of Valanginian? age from the Knoxville beds, Tehama Co., California. Another Early Cretaceous species, *Opis shastalis* Anderson, 1938 does not appear to be an *Opis* or in the Opinae. Six Late Cretaceous species can be recognized:

- 1). A new species, *Opis* n. sp. A, of Turonian age from the upper Baker Canyon Member and the lower Holz Shale Member of the Ladd Formation in the Santa Ana Mountains, Orange Co., California, has a rough surface and a well marked radial sulcus along the posterior area.
- 2). *Opis rosarioensis* Anderson & Hanna, 1935 based on one specimen from "Punta Abajo" has been considered to be from the Rosario Formation and of late Campanian-early Maastrichtian age, but matrix within the shell strongly suggests the Punta Baja Formation at Punta Baja, Baja California, Mexico. The specimen is most similar to *Opis* n. sp. B of early Campanian age from the middle to upper (but not uppermost) Holz Shale Member of the Ladd Formation in the Santa Ana Mountains, Orange Co., California. If the holotype of *O. rosarioensis* was from the Punta Baja Formation and is the same species as specimens from the middle Holz Shale, its age is early Campanian. It would then suggest that possibly the age of the Punta Baja Formation ranges from early Campanian (based on the *Opis*) to late middle Campanian (based on *Metaplacenticeras*). *Opis* n. sp. B has a smooth surfaced shell with deeply sunken lunule.

- 3). *Opis* n. sp. C. Above the occurrences of *Opis* n. sp. B in the uppermost Holz Shale Member of the Ladd Formation, Santa Ana Mountains, Orange Co., California, are specimens with a higher shell, narrower beaks, and higher cardinal teeth. They are of early middle Campanian age.
- 4). *Opis vancouverensis* Whiteaves, 1879 has a yet higher shell with more elongate cardinal teeth and rougher sculpture. Whiteaves' specimen was from outcrops of the Cedar District Formation on the SW side of Denman Island, British Columbia. *Metaplacenticerias* provides a late middle Campanian age for these strata and for the Pleasants Member of the Williams Formation in the Santa Ana Mountains, Orange Co., California which also yields *O. vancouverensis*.
- 5). *Corbula triangulata* Cooper, 1894 was based on specimens from Point Loma, San Diego Co., California. Stanton (1895) recognized Cooper's species as an *Opis* and indicated that the small specimen is the lectotype (Fig. 1a). Cooper's larger specimen seems to have been lost and recognition of the species *O. triangulata* based on the small lectotype has been difficult. *Opis* n. sp. A, B, C, and *O. vancouverensis* from the Santa Ana Mountains have previously all been referred - as cf. or AFF. - to *O. triangulata*. Recent salvage collecting at building sites, especially near Carlsbad, San Diego Co., has provided good specimens of adults from the Point Loma Formation (Fig. 1b). *Opis triangulata* is a large *Opis* with well marked concentric ribbing in the beak area. The beaks are higher than those of *O. vancouverensis* and the ventral margin relatively shorter. Ammonites from the Point Loma Formation provide a late Campanian-early Maastrichtian age.
- 6). *Opisoma pacifica* Anderson, 1958 is from the Garzas beds of the Moreno Formation, Merced Co., California, associated with *Baculites columna* Morton (Matsumoto, 1960), and of about middle Maastrichtian age. Anderson (1958) placed this species in *Opisoma* Stoliczka, 1871 because he considered *O. pacifica* to resemble *Opisoma geinitziana* Stoliczka, 1871 from India. Stoliczka, however, designated *Opisoma paradoxum* (Buvignier, 1843) as type species of *Opisoma*, and *O. geinitziana* lacks important characteristics of *Opisoma*, -- e.g., opisthogyrous beaks, ligament attachment upon a nymph, medioanterior carination -- and is not an *Opisoma*. Stoliczka's specimen (pl. 10, fig. 11b) is probably an *Opis* with a transposed hinge, i.e., a right valve with left valve cardinals. The peculiar shape of these species suggests that they were recliners on the substrate rather than burrowers.

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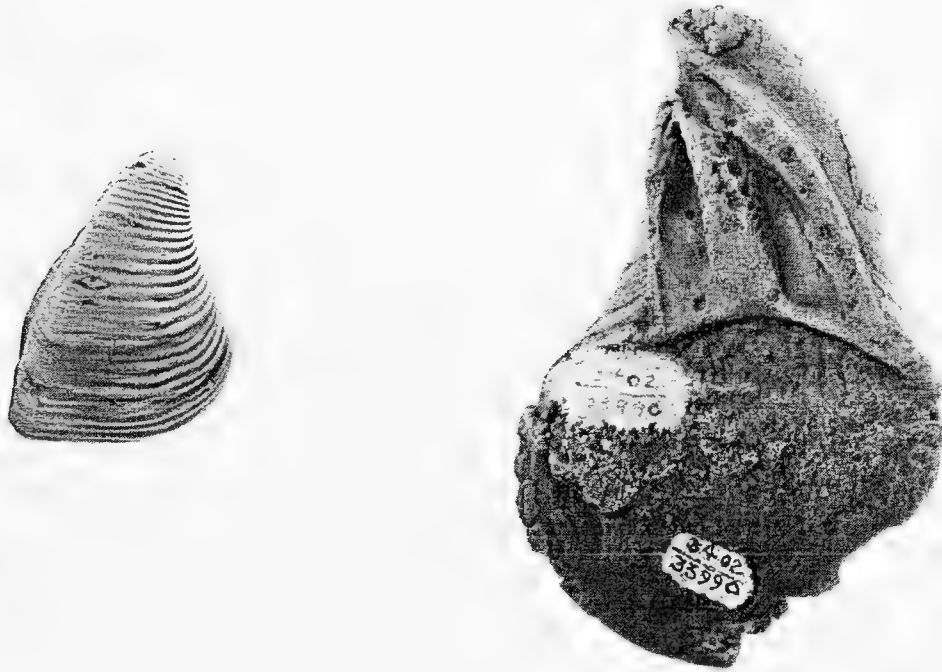


Figure 1. *Opis triangulata* (Cooper, 1894). A (left): Lectotype CAS 624 from Point Loma Formation, Point Loma, San Diego Co., California, right valve, X2. B (right): Hypotype SDNHM 33990 from Point Loma Formation, SDNHM loc. 3402, near Carlsbad Airport, San Diego Co., California, right valve hinge, X1.

### **Sampling bias in the Neogene of California: diversity and extinction in the Pectinidae**

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The fossil record is widely recognized as a powerful tool in the study of temporal trends in diversity. However, to utilize the fossil record to its fullest potential requires quantitative assessment of the effect of sampling bias on the diversity patterns in question. The Neogene fossil record of California is relatively well sampled and provides a good system for studying the effects of sampling on diversity patterns.

A compiled database for the family Pectinidae that includes over 2500 species occurrences at 3000 Neogene localities in California is used to analyze the effects of sampling on both species diversity and extinction rates using the Lazarus metric. Two major peaks in extinction rates prior to the late Pliocene are followed by peaks in the Lazarus metric. This implies that, excluding the late Pliocene, the extinction rate of pectinid species remained relatively constant throughout the Miocene and early Pliocene. The

peak in first occurrences, and concurrent increases in species diversity during the late Miocene is also preceded by a period of high Lazarus metric and the abrupt increase in diversity in the late Miocene may be an artifact of sampling. Sampling standardization of the pattern indicates that pectinid diversity actually increased gradually through the Miocene and early Pliocene before suffering high extinction rates during the Plio/Pleistocene. This analysis shows that the Plio/Pleistocene peak in extinction is not an artifact of sampling and it is this event which has had the most influence in shaping the present diversity of Pectinidae.

### **Rise and fall of Early Tertiary (Paleogene) shallow marine gastropod faunas of the west coast of North America**

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This is the first inventory of all reported genera/subgenera of shallow-marine gastropods found in Paleogene rocks between Seattle, Washington and southern Baja California, Mexico. From Paleocene through middle Eocene ("Tejon Stage"), these gastropods were tropical-water taxa that emigrated from the Old World Tethyan Sea region. Their arrival onto the west coast of North America reached its peak number (132) during the middle early Eocene (about 52 Ma = "Capay Stage"), which coincided with a major, global-warming trend. Representative taxa include *Ectinochilus (Macilentos)*, *Eocernina*, *Galeodea (Mambrina)*, *Pachycrommim*, *Pseudoperissolax*, and *Xenophora*. During the late Eocene to earliest Oligocene Galvinian Stage (about 35 Ma), the tropical taxa began to disappear and were replaced by cooler-water taxa. This trend continued during the Oligocene, when global cooling was even more pronounced. Representative cool-water genera include *Liracassis*, *Bruclarkia*, and *Priscofusius*.

Throughout the Paleogene on the west coast there were eurythermal taxa (e.g., *Calyptraea*, *Crepidula*, *Euspira*, *Neverita*, *Sinum*, *Turritella*). They were tropical in the early Paleogene to late Eocene, but later became tropical to temperate or tropical to boreal. Most of them were present as single species whose geologic ranges extend from the early Paleogene into the Oligocene.

### **Argonauts of the late Miocene, Los Angeles Basin, Southern California**

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Enigmatic fossils of late Miocene age resembling nautiloids, but having thin shells without septa, are here recognized as egg cases ("paper nautili") from epipelagic octopods of the family Argonautidae. Available specimens are from three Los Angeles Basin areas, namely the Santa Monica Mountains, the Puente-Chino Hills, and the Palos Verdes Peninsula (Figure 1). All occurrences are in laminated, fine-grained, biogenic sediments, primarily siltstone. Calcareous nannoplankton and foraminifers from the Los



Angeles Basin samples provide an age of 7 ma and indicate temperate waters with depositional depths of 500 meters in anoxic conditions. The Puente Formation in the Chino Hills has yielded mass mortality clusters of egg cases with the remains of algae, bathypelagic fish, and delectopectens. Delectopectens also occur with Miocene argonauts in Japan (Noda et al., 1986).

This is the first formal notice of fossil argonauts from the eastern Pacific. The largest southern California assemblage of these fossils found thus far is from the Puente Formation of late Miocene age in the Puente/Chino Hills of the eastern Los Angeles Basin. Neogene argonauts have been reported from Japan, Sumatra, Australia, New Zealand, Austria, and Italy, the geologically earliest record of argonauts being from the Oligocene of Japan (Kobayashi, 1954).

Modern argonauts live and reproduce primarily in tropical to subtropical seas at epipelagic depths, but they drift under favorable wind and current conditions with some frequency into neighboring temperate seas (e.g., Dall, 1871; Kobayashi, 1954; Noda et al., 1986). As the egg cases are fragile and without chambers, this drift does not correspond to that of empty *Nautilus* shells, but is of the living *Argonauta* animals (Noda et al., 1986). These pelagic animals feed subsurface during the day and rise to the surface by night where they attach to any available item – jellyfish, stomatopod larvae, pteropod shells, pumice, etc., and each other, forming floating chains of 20–30 argonauts – to increase their buoyancy during spawning (Nesis, 1977). The male has no shell or egg case and, at less than 7 mm, is ten times smaller than the female. The male argonaut attaches to the female by suckers and its hectocotylus (sex organ), sheathed in the left third arm, is freed to attach to the female's egg case and crawl within. All males die after their first and only mating, but females may mate nightly. Eggs are laid nightly inside the case wall near the front of the case. The case contains three “batches” of eggs, the most immature near the aperture, the most mature farthest from the aperture. Eggs apparently hatch on the third night. Although neither length of spawning periods or maximum age of females is known, females are become mature at mantle lengths of about 11–13 mm, and may grow to over 30 mm (Nesis, 1977).

Argonauts are planktivores feeding largely on pelagic gastropods, predominantly heteropods of the families Atlantidae and Carinariidae and pteropods of the family Cavoliniidae (Nesis, 1977). Not only are they able to propel themselves in pursuit of food, but they are also sufficiently motile to swim against slow water flow, to rotate their shell, and to swim ventral side down or on a side (Nesis, 1977). Argonauts and their larva have been collected between depths of 500 m and the surface, but are predominantly found within 100 m of the surface. Their remains have been recovered from the stomachs of tuna and other large game fish, some of which feed mainly at depths between 100–300 m (Nesis, 1977).

All modern argonauts have keels and belong to the genus *Argonauta*. At least 25 specific names are available (Kobayashi, 1954), several of which are synonyms, RESULTING IN SEVEN OR FEWER ACTUAL SPECIES: *A. ARGO* Linnaeus, 1758, *A. pacificus* Dall, 1871, *A. boettgeri* Maltzan, 1881, *A. nodosus* Lightfoot, 1786, *A. hians* Lightfoot, 1786, *A. cornutus* Conrad, 1854, and *A. nouryi* Lorois, 1852. Keen (1971, p. 894) gives the range of *A. cornutus*, *A. nouryi*, and *A. pacificus* as the tropical eastern Pacific. Two species, *A. nouryi* and *A. pacificus* periodically range into warm temperate southern California seas. *Argonauta hians* is cosmopolitan and occurs in the southern Gulf of California in the spring. In contrast to these keeled species, the Japanese Oligocene and Miocene and the Los Angeles Basin Miocene argonauts lack strong ribs and keels. The Los Angeles Basin argonauts exhibit characteristics of the genus *Mizuhobaria* Noda, Ogasawara, and Nomura, 1986. which, in addition to being smooth and keelless, has rounded rather than angulate shoulders to the whorl.

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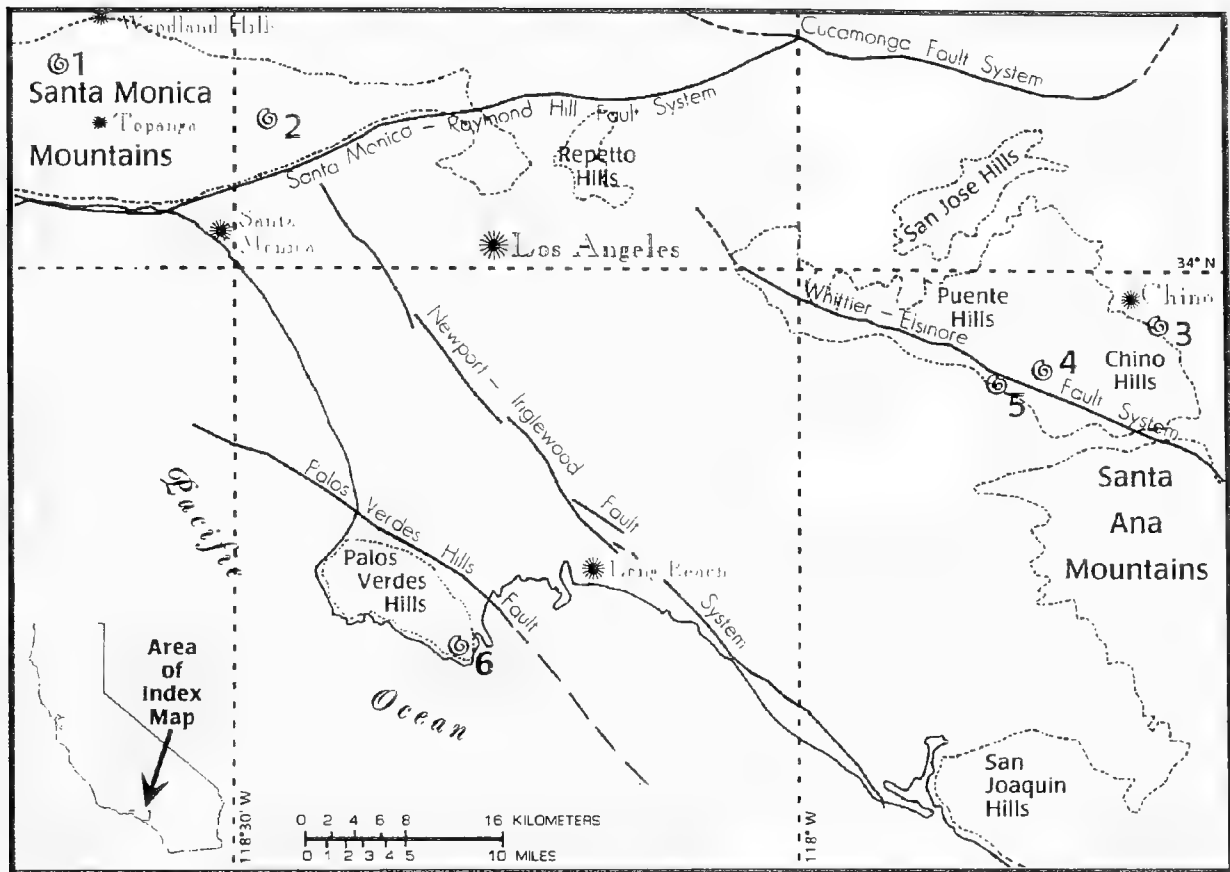


Figure 1. Fossil argonaut localities in the Los Angeles Basin. 1 = Topanga Canyon, lower part of upper Modelo Formation, 7 specimens; 2 = Stone Canyon Reservoir, Modelo Formation, 1 specimen; 3 = Chino Hills, Puente Formation, Yorba Member, many specimens; 4 = Carbon Canyon, Puente Formation, Yorba Member, 1 specimen; 5 = Olinda Landfill, Puente Formation, Yorba Member, many specimens; 6 = "San Pedro Golf Club", upper Altamira Shale, 1 specimen.

## Latitudinal patterns of allozyme heterozygosity in bivalves

Scott Storms

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Genetic diversity is now well recognized as important in conservation biology, both in ensuring long term species viability and in defining the units of conservation. Traditional species based approaches to conservation have been aided by well-studied patterns of species diversity, such as the latitudinal diversity gradient. However, latitudinal patterns of genetic diversity are less well understood, and could be important in setting conservation priorities. In this study I examined previously published allozyme data for forty species of bivalve mollusks and found a significant positive correlation between allozyme heterozygosity and latitude. Further tests of taxonomic affinity, substrate type, and depth range showed

no significant relation with allozyme heterozygosity. Several models have been proposed to explain allozyme polymorphism as a function of environmental heterogeneity. To test if the correlation between latitude and enzyme polymorphism could be explained by such a mechanism, I separated allozyme systems into environmentally and non-environmentally coupled groups, and repeated the analysis. The results of this analysis do not support environmental heterogeneity as a mechanism to explain the observed pattern. This suggests that other factors, such as effective population size, may be more important in determining the latitudinal patterns in allozyme heterozygosity seen in these bivalves.

## **The earliest recorded polyplacophorans from the Late Cambrian of Utah**

**Michael Vendrasco and Bruce Runnegar**

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Silicified assemblages of Late Cambrian polyplacophorans from the Notch Peak Formation of western Utah are dominated numerically by a new species of *Matthevia*. Over 1,500 isolated head, intermediate, and tail valves were recovered from this formation. Valves of two additional new species belonging to the paleoloricate polyplacophoran families *Mattheviidae* and *Septemchitonidae* have also been discovered. The presence of members of both families in these beds indicates there was a diversity of polyplacophorans by the Late Cambrian.

Biometric data reveal the distinctiveness of the valve types of each species in the Notch Peak Formation assemblages and show the differences between *mattheviid* species. Furthermore, the data indicate a gradation in the length to width ratio and apical area length between the *mattheviid* valves and those of modern polyplacophorans.

The *mattheviid* head and, in some cases, intermediate valves exhibited holoperipheral growth, a style characteristic of modern polyplacophoran tail valves. The *mattheviid* tail valves exhibited mixoperipheral growth, which occurs in the intermediate valves and in some tail valves of modern polyplacophorans. *Mattheviid* valves are also unique in possessing one or two tunnels. These tunnels, which presumably had a sensory function, became reduced and subsequently lost in the *mattheviid* lineage. The early polyplacophoran valves also seem to have consisted purely of tegmentum, which makes up the outer layer of modern polyplacophoran valves. The *mattheviid* and other early chiton valves appear also to have contained canals homologous to the esthete channels in modern polyplacophorans.

In spite of the differences in valve shape from modern polyplacophorans, *mattheviids* share a number of synapomorphies. The size, shape, and spacing of the granules in *mattheviid* valves fall within the range of variation of modern polyplacophoran valves. The apical shelf, beak, bilateral symmetry, and overlapping nature of the *mattheviid* valves all suggest a polyplacophoran affinity as well.

## 1999 EXECUTIVE BOARD MEETING

Meeting called to order (Seapy) at 4:10 PM, 13 June 1999

Attending: Terry Arnold, Hans Bertsch, Jules Hertz, Kim Hutsell, George Kennedy, George Metz,  
Roger Seapy

- Motion to approve minutes (M: Bertsch; S: Metz): accepted unanimously.
- Treasurer report (Metz): George recommended to transfer interest from the \$10,000 CD to the general fund when it rolls over in July. Accepted as corrected (M: Kennedy, S: Hertz)
- Nominating Committee report (Seapy):

President	Ronald Shimek
First VP	Hans Bertsch
Second VP	open
Treasurer	Steve Long
Secretary	Terry Arnold
Members at Large	Cynthia Trowbridge, Roland Anderson

Motion (M: Kennedy) to accept the nominations: passed unanimously. Regarding the open Second VP job, Seapy anticipates that Chris Kitting will accept nomination to the position.

- Student Grant Awards (Seapy, for Henry Chaney, Chair, Student Grant Committee): award decisions not made as of this date; to be announced in July.

Motion (M: Kennedy, S: Metz): "The Student Grant committee shall complete their selection by the Annual Meeting to be confirmed by the Executive Board." Passed unanimously.

- 2000 Meeting (Seapy): scheduled as a joint meeting with AMS to be held in late June at San Francisco State University.
- 2001 Meeting (Bertsch): to be held in San Diego in the last half of June. Possible venue is the Handelry in Mission Valley.
- Annual Report (Kennedy): working deadline for revised abstracts & papers will be 15 July.
- Other business (Seapy): proposal to expend \$1500 as the WSM contribution to the student grant fund will be presented at the general meeting. Passed unanimously.

Adjourned at 5:27 PM.

Respectfully submitted,

Terry S. Arnold  
Secretary

## 1999 ANNUAL BUSINESS MEETING

Called to order (Seapy) at 3:35 PM, 15 June 1999.

- Minutes of Executive Board of Directors were read and approved.
- Treasurer's Report (Metz): 159 individual members, 68 institutional members.
- Nominating Committee Report (Seapy):

President	Ronald Shimek
First VP	Hans Bertsch
Second VP	Open (Christopher Kitting, tentative)
Treasurer	Steve Long
Secretary	Terry Arnold
Members at Large	Cynthia Trowbridge, Roland Anderson

Additional nominations: none. Nominations approved and accepted unanimously.

- Student Grant Fund: \$1340 from donations. Motion (M: Metz) to allocate \$1500 for the Student Grant Fund in 2000. Passed unanimously.
- 2000 Meeting (Seapy): WSM will meet jointly with AMS in late June to early July at San Francisco State University.
- 2001 Meeting (Bertsch): to be held in San Diego in last half of June.
- Annual Report (Kennedy): extended abstracts to full papers will be published if submitted by late July.
- Other Business: none

Adjourned at 4:10 PM.

Respectfully submitted,

Terry S. Arnold  
Secretary

**TREASURER'S REPORT**  
**(1 October 1998 - 30 September 1999)**

**INCOME**

Membership dues	1866.00	
Student Grant donations, members	200.00	
Student Grant donations,		
Santa Barbara Malacological Society	500.00	
San Diego Shell Club	500.00	
Southwestern Malacological Society	500.00	
California Malacozoological Society	150.00	
Total Grants	1850.00	
Symposium fund donations	70.00	
Royalties	119.06	
Meeting Income 1999	2645.00	
Auction Income 1999	1654.05	
Interest Income 1999	1088.14	
<b>TOTAL INCOME</b>		<b>9292.25</b>

**EXPENSES**

Administrative (Fees, Dues, Officer Expense, Office Expense)	173.16	
1999 Student Grant	3225.00	
Annual Report 1997 & 1998 (Combined Issue)	2358.10	
Meeting expenses 1999	2441.57	
<b>TOTAL EXPENSES</b>		<b>8197.82</b>

<b>Net Gain</b>		<b>1094.43</b>
<b>Balance brought forward (10/1/98)</b>		<b>2725.16</b>
<b>Current Balance</b>		<b>3819.59</b>

<b>Savings (Does not include all of current interest)</b>		
CD 188-004405-0	4139.72	
CD 008-037930-8	10136.22	
CD 188-001886-4	2565.08	
<b>Total</b>		<b>16841.02</b>

<b>Total Assets</b>		<b>20660.61</b>
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## STUDENT GRANT AWARDS

Recipients of the 1999 WSM Student Grant Awards are:

SHIREEN J. FAHEY, San Francisco State University

Proposal: "The hypothesis of nudibranch mollusc phylogenies using morphological, molecular and biochemical character sets"

Funding: \$975

SARAH GILMAN, University of California, Davis

Proposal: "Limpet limits: An examination of the factors influencing the northern range limit of *Collisella scabra*"

Funding: \$1,000

MATHEW C. KAY, University of Oregon

Proposal: "Reproduction and early life history of the flat abalone *Haliotis wallalensis*, and implications for the role of boulder fields in the early life history of abalone"

Funding: \$500

JOHN C. MALONE III, University of California, Los Angeles

Proposal: "Effects of resource heterogeneity on growth and survival of marine gastropod grazers"

Funding: \$750

The 1999 WSM Student Grant Awards were made possible by gifts from:

Individual donations by the members of the WSM  
California Malacozoological Society  
San Diego Shell Club  
Santa Barbara Malacological Society  
Southwestern Malacological Society  
Western Society of Malacologists

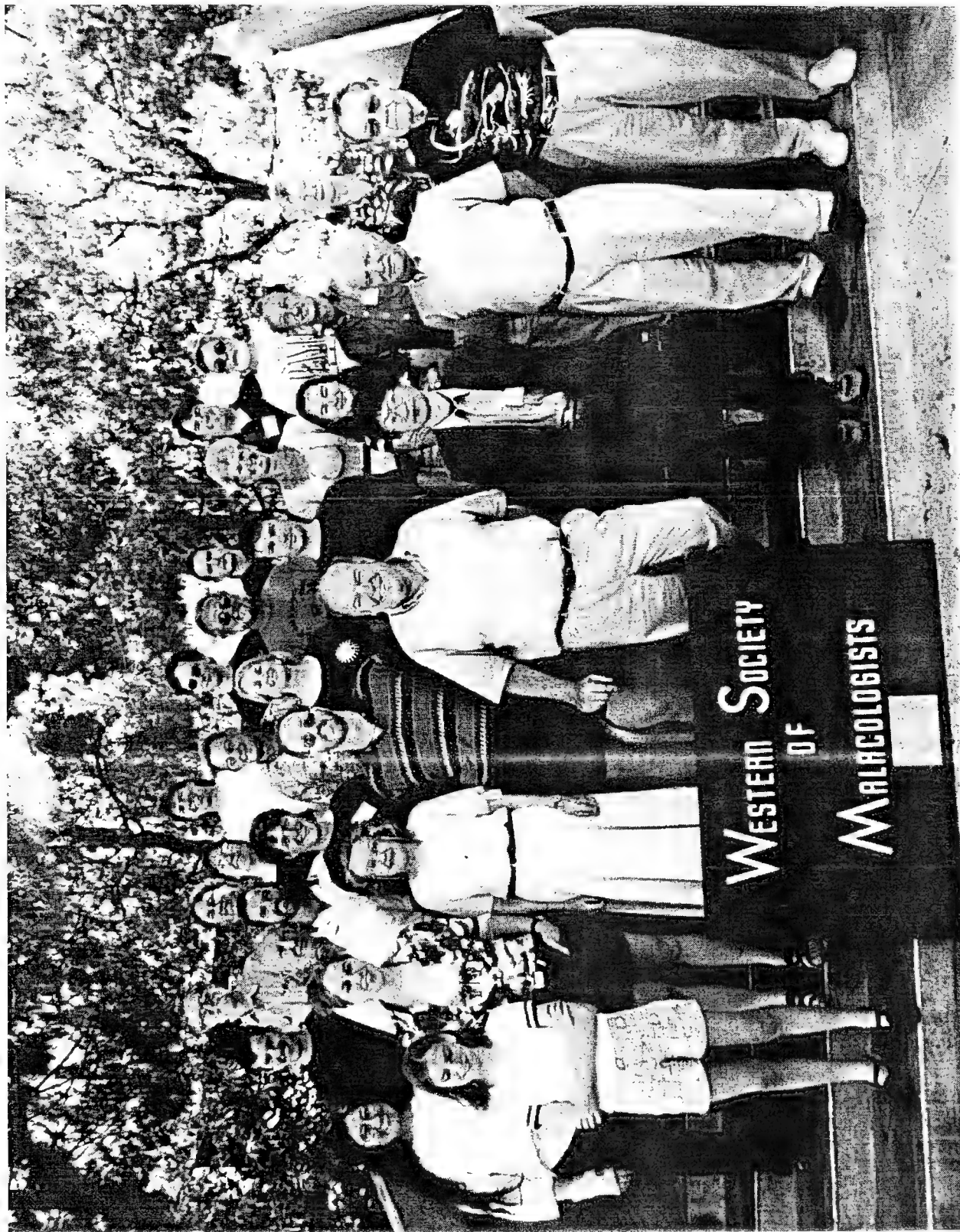
## BEST STUDENT PAPER AWARD

Recipient of the Best Student Paper Award at the 1999 Annual Meeting of WSM:

MICHAEL VENDRASCO, University of California, Los Angeles

"The earliest recorded polyplacophorans from the Late Cambrian of Utah"





Annual Meeting Group Photograph, California State University, Fullerton, 15 June 1999

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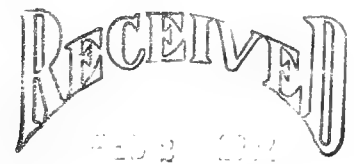
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# ABSTRACTS AND PAPERS

## The burying behavior of the sepiolid squid *Euprymna scolopes* Berry, 1913 (Cephalopoda: Sepiolidae)

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### Abstract

Sepiolid squids are known for burying in the sand during daylight hours. The burying activity of the sepiolid squid *Euprymna scolopes* was examined to determine how it managed to respire, how it behaved when threatened while buried, and how it avoided burying in intertidal sand. It was allowed to bury in four different substrates. Inking behavior, time to settle, latency to bury, time to bury, method of burial, breathing while buried, and response to a threat were noted. There were significant differences in burying times and activities related to substrate type. The squids used a fixed routine in burying themselves. They formed two small breathing holes in the substrate and may have formed a mucus-lined breathing chamber. When facing a continuing threat, the squid first blew water out of a breathing hole, then water and sand, then diffuse ink, and finally a concentrated ink blob. Thus, these squids showed both a stereotyped modal action pattern in responses and a variable reaction to environmental differences.

### Introduction

Boletzky and Boletzky (1970) and Boletzky (1987) reported the process some sepiolids use to bury themselves. The species investigated settle onto the bottom and create a depression in the sand with jets of water blown out of their funnel. They then blow water jets forward and backward and are covered by the resultant sand cloud. The burying process is finished with the second pair of arms (the “dorso-lateral pair”), which extend outward together along the surface of the sand. Then they sweep a “handful” of sand over the head and body with the arm tips pointed medially until the squid is completely covered with sand. While these authors considered their findings as preliminary, they concluded that the process was basically the same in the six Mediterranean species of sepiolids studied. Mather (1986) also investigated the burying process in the cuttlefish *Sepia officinalis*. While she did not report arms sweeping sand over the dorsal surface, as in the sepiolids, she did observe the same forward and backward blowing of sand and a dorsal mantle wiggle, and considered these to be stereotyped behaviors indicative of a “modal action pattern” (*sensu* Barlow, 1977).

Boletzky and Boletzky (1970) noted two peculiarities during their study on sepiolids burying in the sand: the position of the eyes while buried and the mechanism of breathing while buried. The eyeballs are rotated vertically so that the pupils face upwards. Respiration while buried is accomplished not by mantle expansion and contraction, as is normal in cephalopods (Morton, 1967), but by the use of a “skirt”



attached at the base of the funnel. This skirt is pulled back allowing the funnel to exhale and then the funnel is extended forward creating a suction, bringing water through it into the mantle. Thus, the skirt of the funnel acts as a diaphragm. Respiration is accomplished by the action of alternate water currents between the funnel and the mantle cavity, where the gills are situated.

Sepioids are good models for laboratory studies on cephalopods (Hanlon et al., 1997). Representative species from the subfamilies Rossiinae and Sepiolinae can easily be cultured because of their small size (Arnold et al., 1972; Summers and Colvin, 1989). Sepioids have also been cultured extensively to study commensal light-emitting bacteria, which live in their light-emitting organs (e.g. Montgomery and McFall-Ngai, 1993).

*Euprymna scolopes* Berry, 1913, a small (up to 35 mm ML) member of the subfamily Sepiolinae, is endemic to the Hawaiian Islands (Berry, 1913; 1914). While nocturnal, like other sepioids, *E. scolopes* is unusual in that it ranges into very shallow water, just 2-4 cm deep (Anderson and Mather, 1997). During the day it buries itself in the sand (Shears, 1986; 1988). When it emerges from the sand it keeps a "sand coat" on its dorsal surface, which is presumed to give it camouflage (Singley, 1983; Shears, 1986, 1988). Moynihan (1983) described the behavior of *E. scolopes* and made preliminary observations on capture sites, methods of capture, and aquarium husbandry, with brief comments on its burying behavior, feeding, escape behaviors, and body patterns and colors.

Despite this background, there are few studies on the behavior of *Euprymna scolopes* in the wild, probably because of its nocturnal activity pattern. Anderson (1997) investigated how the squids avoid getting stranded in intertidal sand when the tide fell while they were buried. Anderson and Mather (1996) focused on its escape behaviors and documented their interesting variety and lack of predictability, from which they concluded that individuals of *E. scolopes* must have a high level of neural complexity. This potential flexibility and remaining uncertainties suggested it was an appropriate subject for further behavioral studies. Thus, we decided to study the relationship between burial behavior and grain size in *Euprymna scolopes*. We also investigated how it respired while buried and the sequence of burying actions.

## Methods

Studies of the behavior of *Euprymna scolopes* were performed at the Hawaiian Institute of Marine Biology (HIMB) on Coconut Island, the marine biological laboratory of the University of Hawaii, located in Kaneohe Bay on the island of Oahu. Sediment samples of intertidal and subtidal sand were taken at several sites at the north end of Coconut Island, where *E. scolopes* have previously been reported (Anderson, 1997; Anderson and Mather, 1996; Anderson and Mather, 1997). Samples were taken subtidally directly offshore at low tide through 1 m of water, only from the top 2 cm of substrate because *E. scolopes* are small and only bury deep enough to cover themselves (Anderson, 1997). The sediment samples were sent to the Seawater Chemistry Laboratory of the School of Oceanography, University of Washington, for analysis of grain size and organic content.

*Euprymna scolopes* were collected between 30 March and 7 April 1999 by snorkeling at night near the University of Hawaii's Lilipuna Pier across from Coconut Island in Kaneohe Bay. Adult *E. scolopes* at least 1 cm length were captured. They were sitting on top of the sand at night and could easily be netted and then put in a plastic holding container (see Anderson, 1997). Animals were then placed inside a lidded bucket hanging on the pier and transported to the holding facilities on Coconut Island until the next morning, when laboratory work was performed in an indoor sea water lab. Lighting duration was approximately 8 h a day, achieved by switched fluorescent light fixtures in an otherwise dark room.

Five *Euprymna scolopes* were individually allowed to bury during the day in different grain sizes of substrate. Like the cuttlefish studied by Mather (1986), sepiolids bury under the stimulus of light and daytime hours (Singley, 1983; Shears, 1986, 1988). Each squid was allowed to bury 10 times in each substrate over five days. No squid was allowed to bury in the same substrate twice. For each substrate, we determined whether they inked or not as they were placed in the water, the time to settle, the latency to bury from time of settlement, refusals to bury, and the duration of digging. Based on preliminary testing, the squids' "refusal to bury" was arbitrarily determined to be 2 min after tank entry (see Mather, 1986).

Several substrates with different grain sizes were used. "Black" sand" (a brown magmatic sand; mean grain size = 0.85 mm, SD = 0.67) was purchased from a nursery. Aquarium gravel (mean grain size = 4.9 mm, SD = 1.7), intertidal sand (mean grain size = 0.48 mm, SD = 0.24), and subtidal sand (mean grain size = 0.47 mm, SD = 0.41) were also used. All substrates were rinsed with seawater prior to testing.

All testing took place in a 40 l clear glass aquarium tank. Substrates were 5 cm thick to allow the animals sufficient depth for burying themselves. Burying behaviors were filmed in ambient light using a Sony Hi8 video camera and a Minolta still camera model 430a (ISO 400 film with a 55-mm macro lens) for later in-depth analysis.

## Results

The organic carbon content of the intertidal and subtidal substrate samples taken at HIMB on Coconut Island was significantly different ( $t_7 = -3.07$ ;  $p < 0.02$ ), as was the organic nitrogen ( $t_7 = -1.99$ ;  $p < 0.04$ ). The intertidal substrate samples were composed of 4% silt and 96% sand with mean grain size 0.48 mm, while the subtidal samples were 6% silt and 94% sand, mean grain size 0.47 mm, according to the Wentworth scale (Stokes and Judson, 1968). Although the mean grain sizes were similar, the silt/sand proportions were significantly different ( $t_4 = -5.73$ ,  $p < 0.01$ ).

We characterized the first phase of burying as "pre-settling." When placed in a tank with one of the substrates, the squid would swim above the substrate a mean time of 13 sec ( $n = 200$ ,  $SD = 9.9$ ) before settling to the bottom. In 22.5% of the trials the squid inked at least once before settling to the bottom. The squid all turned a dark, red-brown color upon settling, regardless of the substrate type.

There was a significant difference in the latency of *E. scolopes* to bury between the four substrates tested ( $F_{3,196} = 154.77$ ,  $p < 0.001$ ). The squids had a mean latency of 13 sec ( $n = 50$ ,  $SD = 9.8$ ) to bury in subtidal sand, 31 sec ( $n = 49$ ,  $SD = 10.4$ ) in intertidal sand, 99 sec ( $n = 19$ ,  $SD = 33.3$ ) in black sand, and 105 sec ( $n = 5$ ,  $SD = 8.8$ ) in gravel. There were no refusals to bury in subtidal sand, one (2%) in intertidal sand, 31 (62%) in black sand and 43 (86%) in gravel. These were significantly different ( $\chi^2_4 = 74.91$ ;  $p < 0.001$ ). The mean burial time was 48 sec ( $n = 50$ ,  $SD = 20.5$ ) in subtidal sand and 80 sec ( $n = 49$ ,  $SD = 41.0$ ) in intertidal sand. These differences were also significant ( $F_{48,49} = 3.912$ ,  $p < 0.001$ ).

The burying behavior can be described as follows. After the pre-settling stage, the squids would settle onto the substrate, where they would pause before burying. On most substrates, the squids would first give one forceful ventral water jet directed posteriorly and then pause. On subtidal sand, the squids would sometimes not pause but began burying quickly (mean latency 13 sec,  $n = 50$ ,  $SD = 9.8$ ), with repeated posterior water jets creating a depression in the substrate, and then would stir up the soft substrate until it settled down and covered them. After settling onto the larger-grained substrates and pausing, a squid would create a depression in the sand or gravel by blowing water jets with the funnel, always first posteriorly and then anteriorly and continuing to alternate directions for 1-3 jets in each direction. The arms were braced against the sand to keep the squid from moving forward during the posteriorly-directed

jets, and the ventral posterior tip of the mantle resting on the substrate kept the squid from moving backward during anteriorly-facing blows.

Secondary burial actions (the “second phase” of Boletzky and Boletzky, 1970) were accomplished in four stages by “sweeping” sand over the body with the second pair of arms. Typically, a squid would extend the second pair of arms up through the substrate just forward of the eyes. The two arms would then extend forward synchronously, approximately twice the mantle length in parallel, scoop up a small amount of sand or mud by placing the arm tips down on the substrate and rotating the suckered surface medially while digging into the substrate. The substrate was collected by the distal 15% of the ends of the arms. The arms were then retracted to deposit the substrate back over the top of the body. If the substrate was soft, this action appeared to be a sweeping action. If the substrate was instead large-grained gravel, the squid would actually lift the grains and throw them on top of its head and mantle, while both curling the middle portion of its arms upward and retracting them. In the second step, both arms went out forward anterolaterally at approximately 45° to the longitudinal axis of the body, collected a sample of the substrate and deposited it over the body as before. This action was then repeated with arms extending posterolaterally at a 45° angle to the body midline, and then once again directly posteriorly. While collecting substrate posteriorly, the armtips did not come together. It was at this last position that the stretched arms could be most accurately measured, as they scooped substrate a mantle’s length behind the posterior tip of the mantle. These four actions were repeated in sequence as often as necessary to complete the burying of the squid’s body.

We also observed behaviors while buried. Once *Euprymna scolopes* was completely buried, there was a slight pause in its actions, then it blew a jet of water straight upward out of the top of each mantle margin slit. Each burst of water appeared as a sandy “geyser” erupting from the surface of the substrate. A small round hole in the sand, approximately 2 mm in diameter, remained over the top of each slit. The squid presumably generated a respiratory current through these very small holes.

The eyes of *E. scolopes* were totally covered by the sediments, but the squid could apparently see through this layer. This was confirmed by moving a hand suddenly towards the glass tank but without touching it. In response, the squid would first blow a water jet out of one of the holes, again seen as a distortion of the water accompanied by the movement of a few sand grains. Following a second hand movement, another, presumably stronger, jet of water was accompanied by enough movement of sand and mud that it resembled a “sand geyser.” If we repeated our hand threat a third time, the squid would blow a diffuse jet of ink up through one of the holes. This was not an ink blob but instead an ink “plume.” This plume held its shape in the water column longer than the sand geyser, eventually dissipating after about 30 sec. In response to continued “threats” while buried, the provoked squid would blow out a cohesive blob of ink that would maintain its shape for several minutes. The squid never emerged from the sand in response to these disturbances.

## Discussion

We have demonstrated that *Euprymna scolopes* can differentiate between several types of substrate. Latencies to bury, the duration of burying, and the refusals to bury differed significantly in the different substrates tested. Squids were probably differentiating between the substrates after their physical contact with the substrate and were possibly sensing chemical components in addition to touch. Anderson (1997) proposed that *E. scolopes* was able to avoid burying in intertidal sand on the basis of its texture, but our results suggest that grain size of subtidal and intertidal sand is most likely not a factor because the mean size was nearly identical in both habitats. However, we found the proportion of silt in the subtidal sand was significantly greater, and we therefore suspect that organic content could be the factor that was

discriminated by the squids. While this seems likely, it still is possible that these squids use other factors not assessed or a combination of cues to determine substrate suitability for burial.

Species-specific differences were observed in the second phase of the burial process. *Euprymna scolopes* gathered substrate from four different directions to throw on itself. It would repeat this four-step process using the same pattern. Boletzky and Boletzky (1970) and Boletzky (1983) stated that in phase two of the burial process of other sepiolids, a squid would gather sand using this technique from all around its head. Instead, *E. scolopes* use this process of sand gathering in a strictly ordered and set fashion, unless interrupted, with some squids attempting to pick up gravel grains unsuccessfully, and then attempt to deposit these "imaginary" gravel grains onto themselves. This is strongly reminiscent of the classic "fixed action pattern" described by Lorenz and Tinbergen (1938) in egg retrieval of greylag geese.

As in other cephalopod species *Euprymna scolopes* can vary the thickness of its ink into at least two consistencies. Hanlon and Messenger (1996) state that cephalopod species can create ink in either of two forms: a pseudomorph that resembles the body of the animal emitting it, or a diffuse cloud that acts as a "smoke screen" to block the taste or smell of predators. Schafer (1956) suggested that those cephalopods that produce ink could be divided taxonomically into two groups, based on whether they produce pseudomorphs or diffuse clouds of ink. Further research is needed to establish squid control of ink types.

All squid observed in this study turned dark, and thus visible, immediately upon settling to the substrate. There may be a possible ecological advantage for this color, as a prelude to a potential escape response. A potential predator might be attracted momentarily, but be deceived into following a similar appearing dark blob of ink, while the squid that released it turns pale and jets away undetected. Alternatively, the dark color might conceal of the sepiolid's shadow by matching the shadow's intensity against the substrate (Hanlon and Messenger, 1996).

The division of burying behaviors into fixed sequences and "choice" decision points reinforces the flexibility of behavior found to be characteristic of other cephalopods (Hanlon and Messenger, 1996), and is likewise the case for the evasive actions of *Euprymna scolopes* (Anderson and Mather, 1996). *Euprymna scolopes* and cuttlefish (Mather, 1986) show this flexibility in similar responses to gravel substrates. Each refused digging many times in this medium, or refused and simply remained on the gravel surface. When given a chance, cuttlefish lifted off gravel, settled again and buried in sand (Mather, 1986). In contrast to their flexibility, both the arm actions reported here and the funnel jets in Mather (1986) followed a fairly fixed sequence. Such mixtures of fixed and flexible behaviors offer an excellent opportunity to study assessment and choices governing behavior.

There is also an opportunity to extend the study of behavioral control in another dimension, to evaluate the similarities and differences in a relatively fixed behavior across related species. Behavioral similarities such as head movements in ducks, nest building similarities in birds, and the nuptial gifts of flies, are presumed homologous, *i.e.*, due to common ancestry (Drickamer, Vessey and Meikle, 1996). The relatively stereotyped digging sequence reported here is similar in related sepiolid squids studied by Boletzky and Boletzky (1970), although the burying action by the arms has not been observed in cuttlefish. *Euprymna scolopes* has an extended spatial scope of substrate retrieval compared to the cuttlefish. The study of the many deep-water sepiolids' burying behaviors would broaden our understanding of this comparative pattern. Such comparisons will be extended in the future by evaluating the burying behavior of the sepiolid *Rossia pacifica* Berry, 1911.

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**The Natural History of *Doriopsilla gemela* Gosliner, Schaefer and Millen, 1999 (Opisthobranchia: Nudibranchia), at Bahía de los Angeles, Baja California, México**

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During the past several decades, I have conducted a long-term taxonomic and ecologic study of opisthobranch molluscs at Bahía de los Angeles, Baja California, México (approximately 29° 03' N; 113° 32.3" W). Publications from this research include Bertsch, 1991, 1993, 1995a, 1995b, and 1997; Bertsch, Miller & Grant, 1998; and Millen & Bertsch, 2000. *Doriopsilla gemela* is one of the most common subtidal nudibranchs at two of the study sites, Cuevitas and Punta la Gringa (both northeast of town). At these Bahía de los Angeles locations, this species has a distinct annual cycle, reaching maximum sizes in June, with the small adults of the next generation taking over in September (Fig. 1).

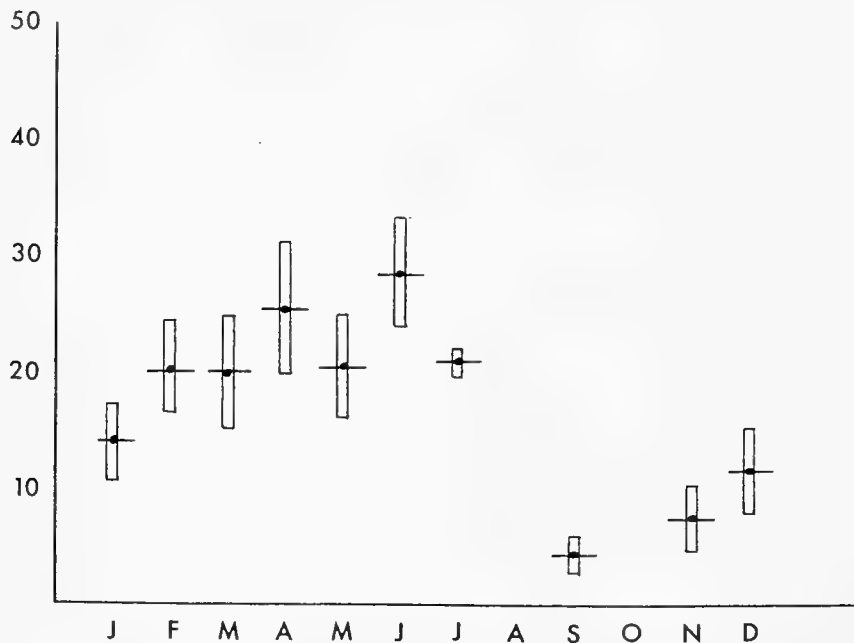


Figure 1. Monthly average sizes of *Doriopsilla gemela* (January 1992-January 1995) in mm; bar height represents mean  $\pm$  one standard deviation.

*Doriopsilla gemela* is quite host specific. It occurs on its prey item, pink masses of the sponge, *Pseudosuberites pseudos*, or highly camouflaged on a yellow sponge (that may be a different color form or species of sponge). Most specimens are found on these sponges, except during the late spring reproductive period.

Eggs are laid on the super-abundant algal covering, that is, inside *Colpomenia* "bubbles" or on *Padina* sheets. I have observed rolling, pelagic *Colpomenia* (broken off from their growth sites) being carried by the tidal or water currents, with "hitchhiking" or "taxi-ing" eggs or specimens of the "yellow-gilled porostome" (the common name for this species of nudibranch). As reported by Gosliner, Schaefer and Millen (1999), *Doriopsilla gemela* has lecithotrophic development (not feeding in the larval stage). I suggest it may use algal transport to augment its dispersion capabilities to other sponge prey throughout its wide geographic range.

This species has been reported from central and southern California; Bahía Tortugas, Pacific coast of Baja California Sur, México, and Bahía de los Angeles, Gulf coast of Baja California.

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## Eastern Pacific species of the venerid genus *Cyclinella* (Bivalvia)

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In spite of the number of available names, there are only three eastern Pacific species of *Cyclinella*. (1) *Cyclinella jadisi* Olsson, 1961, occurs from the head of the Gulf of California to Guayas Province, Ecuador, from the intertidal zone to 31 m. (2) *Cyclinella producta* (Carpenter, 1856) occurs from Laguna Ojo de Liebre, Pacific coast of Baja California Sur, throughout the Gulf of California, to Tumbes Province, Peru, on intertidal mudflats; *C. singleyi* Dall, 1902, is a synonym. (3) *Cyclinella subquadrata* (Hanley, 1844) occurs from Isla Cedros, Pacific coast of Baja California, throughout the Gulf of California, to Lima Province, Peru, from the intertidal zone to 75 m. *Venus kroeyeri* Philippi, 1847; *Artemis macilenta* Reeve, 1850; *Arthemis saccata* Gould, 1851; *Cyclinella galera* Pilsbry & Olsson, 1941; and *C. kroeyeri ulloana* Hertlein and Strong, 1948, are regarded as synonyms of *C. subquadrata*. Other Recent taxa that have been referred to *Cyclinella* are discussed.

## What sort of bilaterian ancestor gave rise to Mollusca (and ourselves)?

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Recent phylogenetic analyses of morphological and 18S rDNA data sets have revealed overall congruence in recognizing three main groups of bilaterian animals. These new groupings are very different from conventional views. Mollusca is presently viewed as a member of the clade, Lophotrochozoa (or Eutrochozoa), along with annelids and other protostome animals with spiralian development, and also lophophorates (e.g., brachiopods and phoronids). This grouping does not include arthropods, which are no longer considered sister taxon of annelids but instead are members of Ecdysozoa, along with nematodes and other protostome animals that molt their exoskeleton. A third major clade of bilaterian animals, Deuterostomia, is now restricted to chordates (ourselves), echinoderms, and hemichordates. This presentation will focus on the rooting of Bilateria, which is a problem because only relatively distant outgroups such as cnidarians and ctenophores are available, but remains an extremely important obstacle to accurate reconstruction of bilaterian ancestry. For example, recent analyses have favored a basal position for acoel flatworms within Bilateria, and this would have critical implications for understanding the polarity of embryonic and larval evolution within Bilateria. Evidence will be presented that leads to a different interpretation for these results, suggesting that the rooting at acoel flatworms is an artifact of spurious attraction to distant outgroups. When acoels are removed from the data set, 18S rDNA estimates agree largely with morphological estimates, with a more conventional split between deuterostome and protostome bilaterians. Moreover, it appears increasingly likely that spiralian development is derived from a deuterostome-like ancestor.



**Deep-sea species of *Halgerda* (Nudibranchia, Doridina)  
with a revised phylogeny of the genus**

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Four new species of *Halgerda* from the deep western Pacific Ocean were dredged near New Caledonia and the Philippines. The depth of these new species ranges from 90 m to 420 m. They differ from other *Halgerda* species in several aspects of reproductive morphology. Phylogenetic analysis places these four new species in a highly derived clade, closely associated with *H. punctata* Farran, 1905. The ranges and depths of four additional, previously described *Halgerda* species (*H. brunneomaculata* Carlson and Hoff, 1993, *H. malessio* Carlson and Hoff, 1993, *H. carlsoni* Rudman, 1978 and *H. dalanghita* Fahey and Gosliner, 1999) are also extended. A refined hypothesis of evolution is proposed for the genus. Numerous specimens from 28 species were examined anatomically. Literature from four additional species was reviewed. Fifty-three characters were considered from these examinations. The outgroup, *Asteronotus* Ehrenberg, 1831, was used to polarize the characters. The phylogeny obtained from the analysis of the characters supports the hypothesis that *Halgerda* is a monophyletic group. A species previously placed with the genus *Sclerodoris* Eliot, 1904 is examined and determined to be a member of the genus *Halgerda*. Phylogenetic analysis places this species, *H. paliensis* comb. nov., as a basal member of the genus. A new species, *H. sp. 1* is presented as the sister taxon to a basal member of the genus.

**Fact, theory and tradition in the study of molluscan origins**

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Discussions of phylogenetic relationships and origins often use figures called “archetypes,” or “reconstructed common ancestors.” Here we discuss one such creature, the hypothetical ancestral mollusk or HAM. HAM first appeared in 1853 as T. A. Huxley’s archetypal mollusc and has speciated often since then. Radiations have occurred within both paleo and Recent taxa (from the paleontological and neontological literature, respectively). Eight species have appeared in the last 25 years alone and six species remain extant today. We performed both phenetic and cladistic analyses of the character states present in these figures. Our best approximation of the phylogeny of HAM (based on known ancestor - descendant relationships and stratigraphy) requires 28 more steps than the most parsimonious tree found by cladistic analysis. Phenetic trees based on neighbor joining and UPGMA analyses require one and ten more steps, respectively. The evolution of HAM exhibits all the typical processes and developmental heterochronies thought to encompass organic morphological evolution and both phenetic analysis and cladistic analyses have problems relating pedomorphic taxa. HAM has not aided evolutionary biologists or paleontologists in solving problems, but has had the opposite effect, by requiring that theories be

treated within its framework. Often real data end up being “tested ”against a hypothetical anatomy to determine whether a hypothesis shall be accepted or rejected. It has been argued that HAM serves a valuable role as a pedagogical teaching aid. Unfortunately, these imaginary animals do not come clearly labeled with warnings about the harm that they might do if mistaken for real organisms.

## **The Intermediate Disturbance Hypothesis and River Continuum Concept do not work for western stream mollusks**

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### **Abstract**

The Intermediate Disturbance Hypothesis (IDH) proposes that species diversity (usually gamma diversity) in a non-equilibrium system is greatest in an intermediate disturbance régime. As applied to streams, it is often coupled with river classification schemes. For freshwater streams, benthic invertebrate gamma diversity will be greatest in the midportion (rithron) and will decline both toward the headwaters (crenon) and lowest segment (potamon). Plots of any such system will thus be unimodal curves. Another stream disturbance/diversity hypothesis in broad usage, the River Continuum Concept (RCC), assumes relative equilibrium and rapid response to disturbance in streams but makes very similar predictions as regards stream benthic invertebrate gamma diversity. The models differ in that the IDH assumes physical diversity controls paramount while the RCC assigns precedence to biotic interactions. Survey of the Sacramento River (California) system freshwater mollusk fauna indicates that both the IDH and RCC are inadequate to explain observed mollusk diversity patterns and their system location. Alpha and gamma diversity peak in the crenon (large limnocrenes; springs generally), in habitats with relatively little disturbance. Further, greatest sympatric diversity and endemism occur in the same habitats. Hydrobiid dominance may be a partial explanation. Eastern U. S. unionid faunas may not fit the IDH-RCC models either. Relative scarcity of crenon taxa, due to virtual exclusion of glochidial hosts from the crenon, perhaps renders comparison moot. Unionid diversity may peak in the potamon. The importance of spring habitats to mollusks and other freshwater invertebrates is often neglected. More thorough survey of crenon habitats may yield similar results for other invertebrate groups. Alternatively, literature/model overemphasis of temperate U. S. streams, and insects as representative of all invertebrates, may mask multiple diversity and distribution patterns worldwide. For streams, one size likely does not fit all.

### **Introduction**

The Intermediate Disturbance Hypothesis (Connell, 1975, 1978; Petraitis *et al.*, 1989) has become a truism of modern ecology, so much so as to be termed “one of the success stories of ecological science” (Rosenzweig, 1995). The IDH maintains that diversity, in a system that is not in equilibrium, is greatest in an intermediate disturbance regime. For most applications, diversity is taken to mean number of species (species richness), not necessarily but sometimes paralleled or replaced by abundance or biomass measures. Various diversity definitions have been assumed to be relevant to the hypothesis; but the most frequently cited is gamma ( $\gamma$ ) diversity, that is, species richness across a range of related microhabitats, as compared between similar areas (Rosenzweig, 1995). Often, however, usage has been extended to include

alpha ( $\alpha$ ) diversity as well (Petraitis *et al.*, 1989). Disturbance could include many causative factors; but specifically is almost always assessed indirectly, generally in terms of standard habitat parameters, *e.g.*, temperature, conductivity, pH, insolation, dissolved oxygen, humidity. Such disturbance measures may show either a parallel relationship to disturbance (examples would include productivity, salinity, dissolved oxygen, and temperature in most habitats) or an inverse relationship (depth, atmospheric oxygen pressure). The IDH applies only to those situations, assumed to be the majority, in which standard habitat parameters vary considerably, either irregularly or regularly. The hypothesis was originally intended by neontologists to apply to short- to medium-term disturbances, *i.e.*, those occurring on a scale of frequency stretching perhaps to centuries or even millenia, but not catastrophes on a geologic scale. Graphically, the relationship between diversity and disturbance is best expressed as a unimodal but not symmetric curve, most frequently portrayed as in Figure 1.

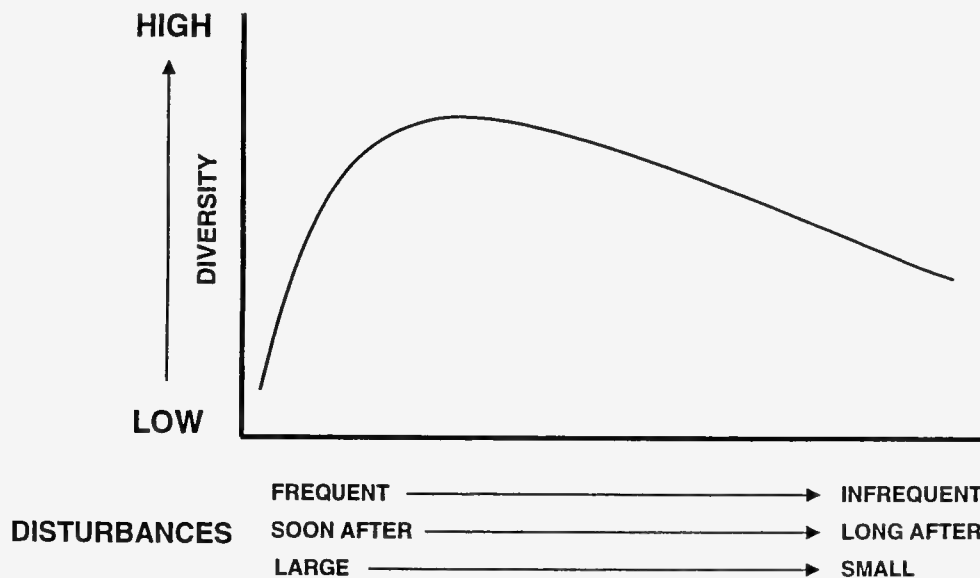


Figure 1. Relationship between diversity and disturbance in the IDH (modified slightly from Connell, 1978): a unimodal curve with the peak at intermediate disturbance levels as determined by three different measures.

The IDH has been applied to a variety of situations since its first formulations. These include forests, Gobi Desert rodents, African herbivorous mammals weighing more than 10 kg; coral reefs, marine epifaunal invertebrates generally; continental shelf bivalves, North Atlantic benthic macrofauna, freshwater stream insects, and freshwater macrophytes (Eggeling, 1947, Osman, 1977; Connell, 1978; Sousa, 1979; Haedrich *et al.*, 1980; Jablonski, 1984; Petraitis *et al.*, 1989; Anderson, 1992; Rosenzweig, 1995). More recently, it has been proposed by paleobiologists to apply to certain large-scale phenomena in the geologic record (diversity of lower Paleozoic shelly shelf benthos, response (speciation) to extinction events: Rosenzweig & Abramsky, 1993, Allmon, 1994, Rosenzweig, 1995, and Allmon *et al.*, 1998). Reviews of neontological applications (Petraitis *et al.*, 1989; Rosenzweig, 1995) have generally concluded the IDH to be most successful in marine applications (less so in terrestrial) and with animals (less successful with plants). One general explanation of the difference in applicability has been suggested by Connell (1978; see also Rosenzweig, 1995). In marine systems, there may be a direct correlation between disturbance and productivity, while terrestrial systems may often show an inverse correlation. As

most standard habitat parameters are effectively indirect measures of productivity, they might show opposite skew in terrestrial vs. marine habitats; but still should peak at intermediate levels.

As applied to streams, the IDH is often coupled with river classification schemes like that of Illies and Botosaneanu (1963). For freshwater streams, benthic invertebrate gamma diversity will be greatest in the midportion (rithron) and will decline both toward the headwaters (crenon) and lowest segment (potamon). Plots of any such system will thus be unimodal curves. Another stream disturbance-diversity hypothesis in broad usage, the River Continuum Concept (RCC: Vannote *et al.*, 1980; Minshall *et al.*, 1985), is predicated in very different terms. It assumes relative equilibrium and rapid response to disturbance in streams but makes very similar predictions with regard to stream benthic invertebrate gamma diversity, seen here also as directly related to disturbance régime and plotted similarly.

## Stream Classification

As applied to surface water streams, the IDH is often coupled with river classification schemes of various sorts. The two most commonly used currently (*e.g.* Allan, 1995, Hauer & Lamberti, 1996) are geomorphic or physiographical classifications, which often treat such streams as branching systems of various orders, and more biotically oriented systems like that of Illies and Botosaneanu (1963). Examples of terminology for each of these are given in Figure 2. We will emphasize the biotic classification here; but use both systems as appropriate. According to Illies & Botosaneanu (1963), the surface water part of a river system is most usefully conceived as comprised of three successive components (Figure 2, right side). The crenon includes such headwater features as intermittent or seasonally active streams; the smallest permanent streams; and permanent seeps, springs and spring runs. Headwaters in mountainous areas with considerable height, may have permanent glaciers and associated run-off streams. These constitute a special case (for the general case, we will largely ignore these latter). Groundwater-influenced features lower in the system may also be considered part of the crenon. In the headwaters *s.s.*, ground water influence will be paramount. Waters will be very cold, clear, and oligotrophic, with minor concentrations of dissolved nutrients typically. Shortly after reaching the surface, relatively oxygen-deficient ground water may quickly acquire and sustain relatively high levels of dissolved oxygen (more soluble in cold water at normal atmospheric pressures). Macrophytes are often low in quantity and diversity; substrates are often coarse and relatively stable; gradients are often relatively low to moderate. The crenon is low in productivity by most measures but relatively stable as regards most habitat parameters.

Not all stream headwaters fit into a single category. Glacial streams carry a high and variable sediment load and are often very turbid. Streams originating from glaciers frequently have a high gradient, very unstable substrate, and braided and otherwise shifting channels. Other features are much like those of the crenon segments of the system: high dissolved oxygen, few macrophytes (low in diversity also), very cold waters. Glacial meltwater streams vary considerably in volume and permanence seasonally, as well as in long-term persistence [the other three river system components are geologically long-term phenomena]. This mix of features is sufficiently distinct from that of the groundwater-based crenon as to require a special term, the oreon, for them. This second headwater stream type on a world-wide basis may be subordinate in frequency and volume to groundwater streams; but nonetheless may be dominant locally or regionally. Another special case may be hyporheic rheocrene springs and more diffuse groundwater influx into rithron and potamon stream segments. These have received increasing attention recently as diversity hot spots and refuges for stream faunas in low water situations. In our view, these should be classed as a part of the crenon. Unfortunately, many stream studies have overlooked these microhabitats or lumped them with more typical rithron and potamon habitats. Field detection of such sites is relatively straightforward, as habitat parameters differ from those surrounding (water temperature and turbidity, *e.g.*, are lower).

The rhithron (middle stream reaches, including creeks and upper parts of the mainstem river) may be characterized generally as rather cool; may range from clear to turbid and oligotrophic to mesotrophic; may have high to moderate dissolved oxygen concentrations, often variable at least seasonally; have common to abundant macrophytes; and have semistable, often rather variable substrates. Productivity is higher than that of the crenon and most habitat measures show some, but not extreme, variation. The lowermost reaches of the river system, including much of the mainstem stream and mouth, constitute the potamon. This section has relatively warm and turbid water; can be best characterized as mesotrophic to eutrophic in terms of dissolved nutrients; and often has rather low to moderate dissolved oxygen concentrations. Potamon substrates are most frequently rather soft (fine: muds to silts) and semistable to unstable. In this part of the system, macrophytes typically are common to abundant and diverse. Locally, productivity is relatively high; but disturbance frequency and variability of many habitat parameters peaks also.

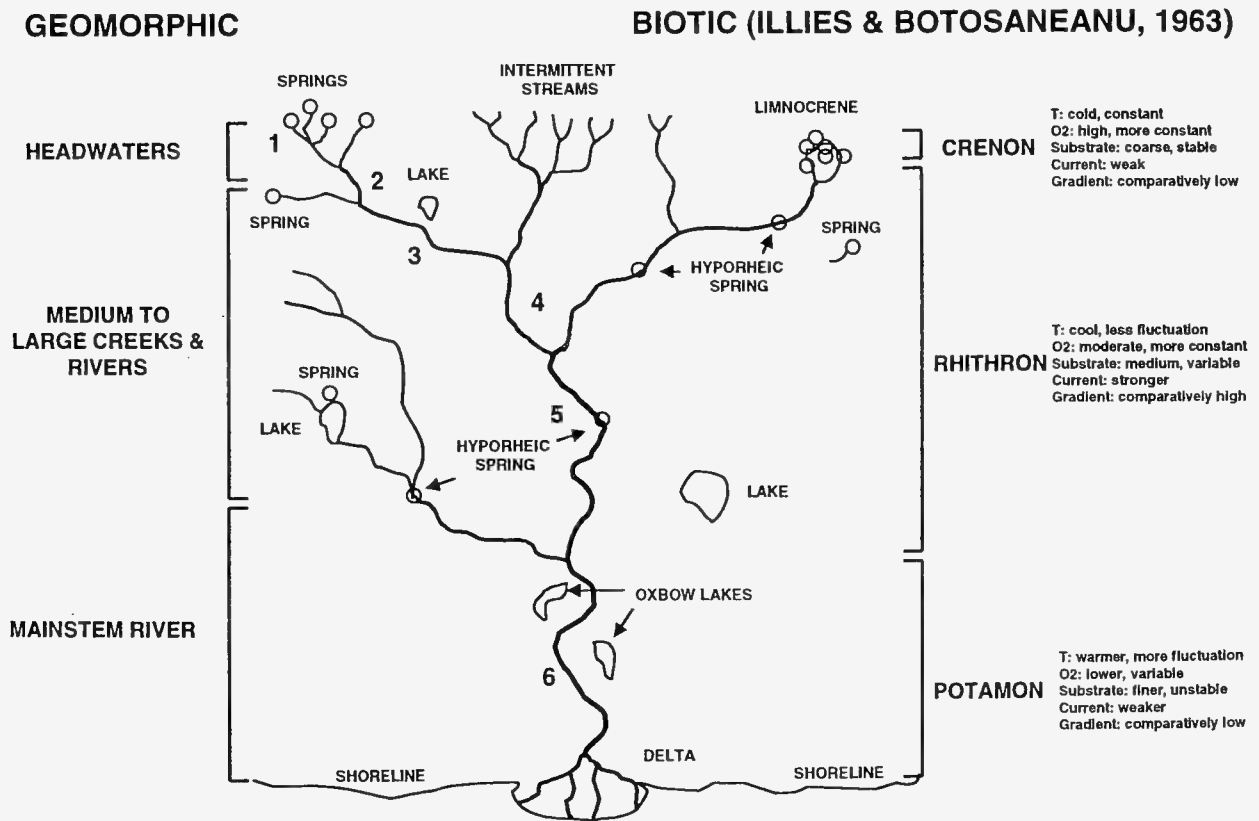


Figure 2. Examples of two commonly used stream classification schemes: geomorphic (stream order classification on left), and biotic (originally based upon fish distribution; modified from Illies and Botosaneanu, 1963 on right).

### Stream Disturbance and Diversity

The IDH proposes that diversity (again, usually defined as  $\gamma$  diversity) in a non-equilibrium system is greatest in an intermediate disturbance régime. As noted above, this generally implies that  $\gamma$  diversity for streams will be greatest in the midportion (rhithron) and will decline both toward the headwaters (crenon) and lowest segment (potamon). Plots of any such system will thus be unimodal curves as in Figure 1. Note that the surface stream (river) system in this view is regarded as more analogous to marine habitats than to terrestrial and hence should exhibit a direct correlation between disturbance and productivity.

Energy flow patterns are more similar to those of habitats in marine settings; marine and freshwater habitats are more closely comparable than freshwater and terrestrial. They are assessed with similar habitat parameters; and the freshwater benthic biota, including both faunal and floral components, is very different from the terrestrial and more closely related to the marine, ecologically and sometimes historically. This is not to underrate the complex relations between the terrestrial and freshwater ecosystems; nor the similarly involved relations of their biota, a substantial part of which may be shared, at least for certain life stages. For a comprehensive review of these interrelations, see Gray (1988).

The IDH is not the only hypothesis relating disturbance and diversity in freshwater surface streams. Especially notably, the River Continuum Concept of Vannote *et al.*, 1980 (see also Minshall *et al.*, 1985; Cushing *et al.*, 1996) was formulated specifically to apply to such habitats and their biota. It has been widely used since its original formulation (Benke *et al.*, 1988; Cushing *et al.*, 1996; Grubaugh *et al.*, 1996; Naiman & Bilby, 1998). Interestingly, the RCC deduces a similar relationship despite somewhat differing assumptions. Succinctly, the RCC proposes that diversity, in a river in dynamic equilibrium, is greatest in an intermediate disturbance regime. Diversity here is defined exactly as in the IDH. Disturbance is also similarly defined and measured. The RCC, however, presumes that river systems typically (again excepting geologic-scale catastrophes, either in size or timing or both) maintain themselves in an effective equilibrium. The perspective here is that a river is better viewed as a continuum from origin to mouth, rather than as distinct segments. Vannote *et al.* (1980) contends that rivers generally recover quickly from standard disturbances. Two features of river systems are thought to bring this about. Rivers in this view are argued to contain many habitat patches scattered through the system, allowing quick recolonization after, or adjustment to, the typical range of physical disturbances. RCC supporters also contend that biotic interactions are at least as important as physical factors in determining river biota diversity and distribution; the IDH holds that physical factors are paramount as compared to relatively weak biotic interactions. In either case, combined effects of many ecosystem properties affecting diversity positively are thought to peak at intermediate levels typically. The RCC sees maximum benthic macroinvertebrate species richness (sometimes also biomass and/or abundance) as most likely to occur *ca.* stream order 3-5 (Vannote *et al.*, 1980; Minshall *et al.*, 1985; Cushing *et al.*, 1995). As with the IDH, the result is a unimodal asymmetric curve (Fig. 3).

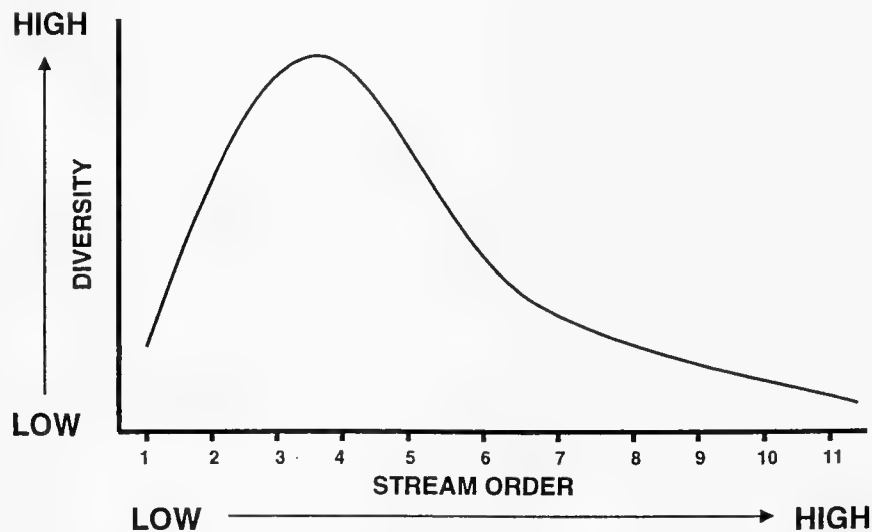


Figure 3. Relationship between benthic invertebrate diversity and stream order in the RCC (redrawn from Vannote *et al.*, 1980; Minshall *et al.*, 1985). Diversity here also peaks at intermediate disturbance levels as typically measured.

For the RCC, this result stems from interaction between local extinction from disturbance and local extinction from competition. At low disturbance levels, biotic interactions are strong. Most extinction (local extirpation, not absolute species extinction) is caused by competition and competitive exclusion is very important. Lower order (high in the system: Figure 2 left) sites are thought to have low per-site ( $\alpha$ ) diversity and also low diversity ( $\gamma$ ) overall. At intermediate disturbance levels, biotic interactions are moderately important, extirpation or local extinction is influenced equally by disturbance and competition; and competitive exclusion remains of some, though diminished, importance. Particular sites here would have high per site ( $\alpha$ ) diversity, and overall diversity ( $\gamma$ ) of this part of the continuum is high. Areas with high disturbance levels are likely to be areas in which biotic interactions are not very important, and local extinction is more likely to be caused by physical disturbance. Competitive exclusion is similarly of less significance as a factor influencing diversity, and both  $\alpha$  and  $\gamma$  diversity in such areas are expected to be low.

## Methods

We recently attempted to apply the IDH to western U. S. freshwater stream mollusks. As a part of a larger project assessing herbicide spill damage we surveyed the Sacramento River system, California, the second largest freshwater drainage in the western U. S., above Shasta Lake, for mollusks. The survey was mostly limited to the Upper Sacramento River, the McCloud River, the Pit River, and their tributaries, from their origins to the river confluence forming the Sacramento River proper in what is now Shasta Lake. Between 1992 and 1995 some 228 sites were surveyed, plus three additional ones below Shasta Lake (Frest & Johannes, 1995). These sites are reported on here. Later, 100 additional sites were added to the study (Frest & Johannes, 1997). For locations, descriptions, and faunal lists of these, see Frest & Johannes (1997). The 1997 sites increased system diversity somewhat but strengthen conclusions based on the 1995 data. Detailed descriptions of sampling strategy, taxonomy, and treatment are given in Frest and Johannes (1995).

## Results

Our survey of the Upper Sacramento River, California, system freshwater mollusk fauna indicates that both the IDH and RCC are inadequate to explain observed mollusk diversity. Our original 228 Upper Sacramento system sites plus three lower sites on the Sacramento proper had a total of 57 mollusk species, three non-native and 54 native, divided between 16 bivalves and 51 gastropods. Some 19 were undescribed taxa, predominantly hydrobiids; these will be formally named elsewhere. Almost all of these are believed to be strictly endemic to the Sacramento system. Plots of species occurrence show a pattern typical of diverse river systems (Figure 4). However, most strict endemics occur only in the crenon, with a few extending into the rithron or even lower in the system. There are no strict rithron endemics and at most one strict potamon endemic, the extinct Delta hydrobe *Savaginius yatesianus* (Cooper, 1894) (Taylor, 1981). A sizable number of taxa occur in all three river areas indiscriminately; but this segment of the fauna is smaller than that strictly endemic to the crenon (see also Fig. 7 below).

Species diversity in the 228 Upper Sacramento sites ranges to 16 taxa, with a substantial number of sites lacking mollusks altogether (Fig. 5). Sites without mollusks may be so for several reasons. Portions of the system were affected historically by hydraulic gold mining, a practice that still continues today, though at only a tiny fraction of the intensity more than a century ago. The 1991 Cantara spill of the pesticide metam sodium into the Upper Sacramento proper particularly affected rithron and potamon sites in that stream (Frest & Johannes, 1995). Hydroelectric dams impact portions of the Pit, mostly resulting in decreased diversity in some impounded rithron and crenon sites. Still, sites without mollusks occur in all habitats in the system. The lowest reaches of the River proper, especially those areas below

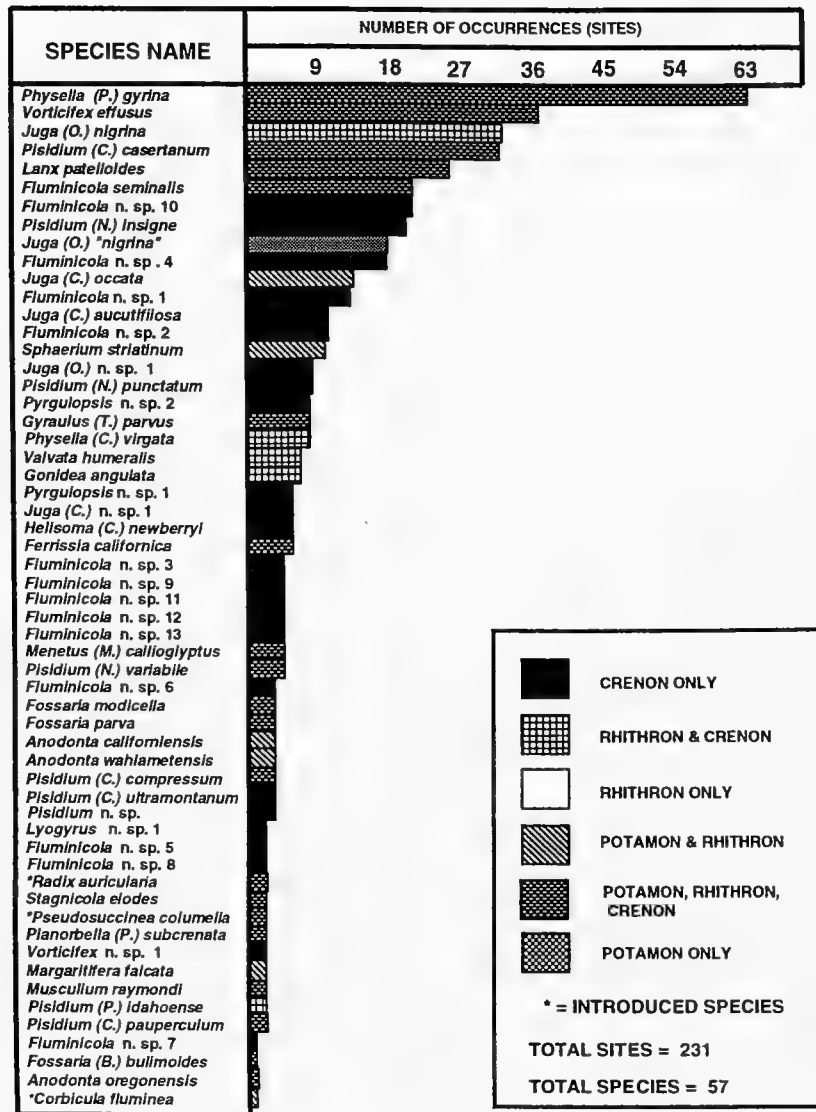


Figure 4. Species rankings (number of sites with each) for Upper Sacramento system freshwater mollusks. A rather typical species diversity curve in the sense of Rosenzweig (1995) overall: but note crenon occurrence of most strict endemics and most species.

Shasta Dam, are incorporated into the Central Valley Project and are generally heavily modified. Moreover, much of the historic mollusk fauna is extirpated from the lowermost half of the system and must be reconstructed from the literature and museum records. Hence, we concentrated on sites above Shasta Dam and its impoundment, Shasta Lake. Excluding sites lacking mollusks, median mollusk site ( $\alpha$ ) diversity is about 3 taxa and mean diversity approximately 3.7. Including sites with no mollusks appreciably changes median diversity to less than 2 and lowers mean diversity to about 1.7. Ranges for crenon and rhithron sites largely overlap if all sites are considered together, as done in Figure 5, although the highest diversity sites belong exclusively to the crenon. This becomes clearer if the two major Sacramento tributaries, the Upper Sacramento River and the Pit River (including the McCloud) are



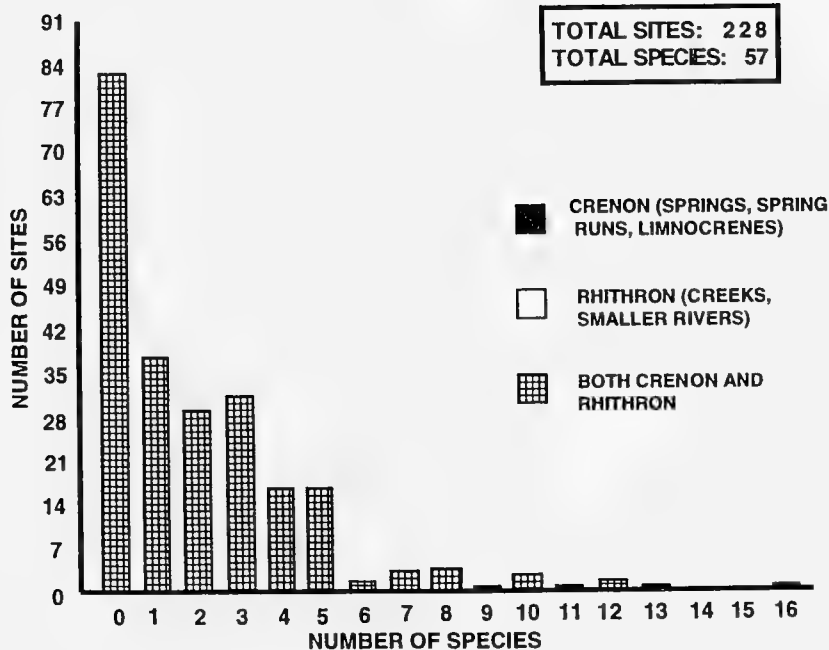


Figure 5. Taxon diversity of Upper Sacramento system freshwater mollusk sites (cumulative results: for breakdown, see next two figures). Most sites have low  $\alpha$  diversity but high  $\alpha$  diversity sites occur almost exclusively in the crenon.

considered separately, as done in Figure 6. Mollusk diversity in the Upper Sacramento itself may reach 7 species, although the high diversity sites here all appear to be spring-influenced and perhaps could best be classed as hyporheic or rheocrene, hence part of the crenon. In any case, again ignoring sites lacking mollusks, median  $\alpha$  diversity is higher in Upper Sacramento tributaries and particularly in crenon sites (1-8 taxa: median 4, mean 5: note also that in smaller tributaries, all sites with diversity greater than 3 are crenon sites). Upper Sacramento sites proper had a median  $\alpha$  diversity of just over 3 species and a mean  $\alpha$  diversity of 2.3 taxa. Pit River mainstem (rhithron) sites are more diverse (to 12 taxa), with median  $\alpha$  diversity about 6 and mean  $\alpha$  diversity approximately 6.2. Here again, high diversity sites are associated with hyporheic springs. The Pit tributaries are still more diverse, ranging to a maximum of 16 taxa. Note again that only crenon sites occupy the upper half of this range. However, most crenon sites in the smaller tributaries have a low  $\alpha$  diversity. Overall, the Pit River tributary sites had a mean  $\alpha$  diversity of approximately 4.25 and a median of about 3. Purely rhithron sites in both the Upper Sacramento and Pit drainages also had comparatively low  $\gamma$  diversity collectively (10 and 19 vs. 16 and 41 respectively for smaller tributaries). Gamma diversity is perhaps more clearly examined in Figure 7. Here, the native species were assigned first to one of two groups: those occurring exclusively in particular river segment habitat types or those found in some combination of them. None were exclusive to the potamon or rhithron; but 25 were found solely in the crenon and the next largest category (19) could occur in all three river segment habitat types. Total ( $\gamma$ ) diversity, including the nonnative forms showed striking differences for each stream segment. Some 48 taxa were found in the crenon, 30 in the rhithron, and 28 in the potamon. Thus, in this system,  $\gamma$  diversity declines substantially from headwaters to the mainstem.

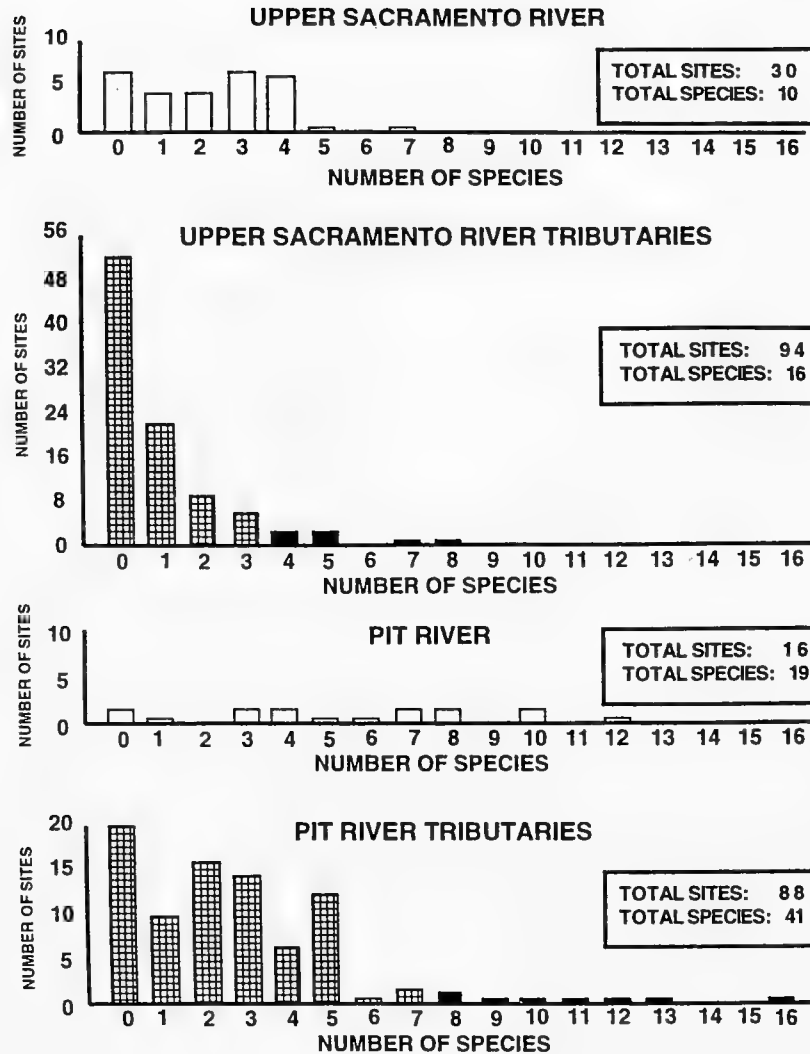
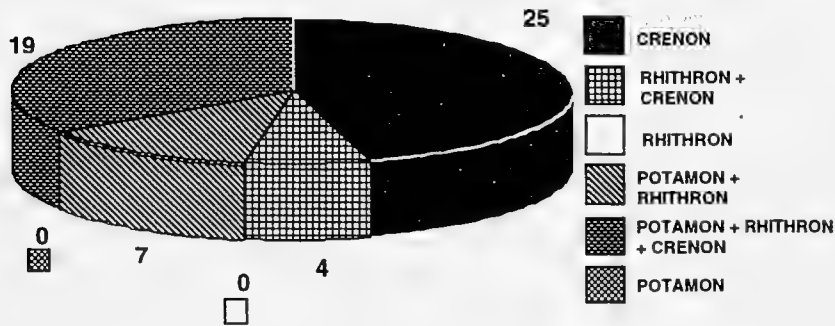


Figure 6. Alpha ( $\alpha$ ) species diversity of Upper Sacramento system freshwater mollusk sites, with separate tabulations for the Upper Sacramento and Pit rivers and their tributaries. Alpha ( $\alpha$ ) diversity is higher in the Pit system: but highest  $\alpha$  diversity sites are in Pit and Upper Sacramento tributaries.

### Discussion

In the Upper Sacramento system, both  $\alpha$  and  $\gamma$  diversity peak in the crenon. Most diverse were large limnocrenes, found only in the headwater areas. Strict endemism (taxa found nowhere else) and system endemism are strongly linked to headwaters location. Site ( $\alpha$ ) diversity is more complex, with low diversity sites found in each stream segment or region. However,  $\alpha$  diversity is still clearly highest in the crenon (large limnocrenes). Gamma diversity, even when large limnocrenes are discounted, remains much higher in the crenon. This is because of the occurrence there of substantial numbers of endemic taxa, many restricted to one or a few spring sites. These are as often small as large. Other western US streams which we have surveyed in detail follow the same pattern (Rogue and Umpqua drainages,

## ENDEMIC OCCURRENCES



## OCCURRENCES BY STREAM SEGMENT

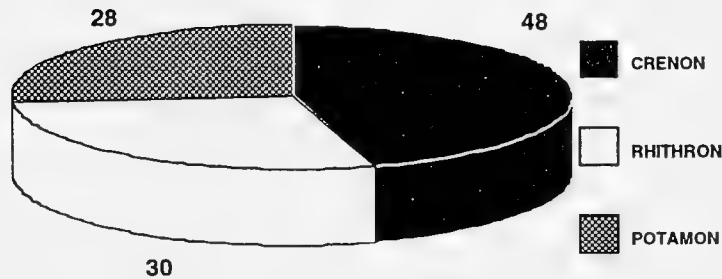


Figure 7. Gamma ( $\gamma$ ) species diversity of Upper Sacramento system freshwater mollusk sites. Native taxa assigned to river segment or segment combination above; overall species diversity in each segment below. Note high degree of endemism in the crenon and high  $\gamma$  diversity here as well.

Oregon: Frest & Johannes, 1999, 2000a; Klamath drainage, Oregon and California: Frest & Johannes, 1998, 2000b; middle and upper Snake River drainage, Idaho: Frest & Johannes, unpub.). It thus appears that, for western US stream mollusks, diversity peaks in crenon habitats with relatively little small-scale disturbance. Productivity is low, but stability in most factors is high and most are dependable (permanent and varying little). Further, greatest sympatric diversity and endemism appear to peak in the same habitats (crenon). For example, one large Upper Sacramento tributary appears to have up to 4 sympatric hydrobiids in the springsnail genus *Fluminicola s.l.* at the same limnocrone site (Frest & Johannes, 1995). One Klamath drainage small tributary has several limnocrone sites with up to 6 sympatric *Fluminicola* (Frest & Johannes, 1999). Rhithron and potamon sites in the same drainages do not exceed two sympatric *Fluminicola*. This sort of diversity situation may perhaps better fit other diversity models; for example the Sanders (1968) diversity-stability hypothesis.

Are western US freshwater stream mollusk faunas merely a rare exception to the IDH and RCC? One persistent criticism of both the IDH and RCC is that they were based mostly upon data collected from temperate-zone (eastern U. S.) or western European streams (Giller & Malmqvist, 1998). Western U. S. river systems do differ somewhat, but would still seem to fit well enough into the general framework. In this region crenon habitat water conditions typically are: very cold, very clear, strongly oligotrophic, very high dissolved oxygen, few to no macrophytes, and stable coarse substrates. Rhithron equivalents would

be: cold, clear, oligotrophic, moderate dissolved oxygen, some macrophytes, semistable and rather variable substrates; in the potamon: cool, somewhat turbid, mesotrophic, moderate dissolved oxygen that is somewhat variable in concentration, some to common macrophytes, and unstable to very unstable substrates. This would seem close enough to the situations described by Illies & Botosaneanu (1963) as to make application of the IDH appropriate. Similarly, the RCC has been expanded to worldwide coverage (Cushing *et al.*, 1996) and western U. S. stream applications are quite common in the literature (for examples, see Naiman & Bilby, 1998 and references therein). Hydrobiid dominance of the malacofauna is typical of many western streams, including the Sacramento system (Fig. 2) but it is hard to see why hydrobiids should constitute an exception. Moreover, given their very strong world-wide deployment in fresh waters, including those of the eastern U. S. and Europe (Hershler & Ponder, 1998) this would not be a minor exception. Certainly Dillon (2000) sees no reason to treat hydrobiid ecologic features differently from those of other freshwater mollusk groups.

It is a truism of stream ecology, as in limnology, that insects are the primary focus of benthic invertebrate research, often to the near exclusion of other groups. This shows up quite strongly in textbooks (for recent examples, see: Hauer & Lamberti, 1996; Giller & Malmqvist, 1998; Naiman & Bilby, 1998). The RCC's emphasis on biotic interactions would remain generally valid if it could be convincingly argued that biotic interactions of mollusks differ substantially from those of other freshwater benthic groups, such as insects. However, a recent summary and critical analysis of the freshwater mollusk ecologic literature (Dillon, 2000) would not seem to support such a supposition. Another possibility is that existing studies of the relationship between stream size and diversity are methodologically deficient. We favor this notion in some ways. In reviewing stream surveys for this study, we found very few in which much attention was paid to the crenon. In most cases, only a few spring or headwater sites were inventoried. In fact, we found none in which the crenon biota of a typical stream system was comprehensively evaluated. It should be obvious that most drainages show a dendritic pattern. While it is clear that in the final sense each river system has only one potamon, it is not obvious to us that survey of small numbers of crenon sites would give a fair representation. The concept of a stream system as a stick or snake, rather than a tree, is simplistic and likely most inappropriate for the crenon areas. Note that, even in our crenon sites, the range of diversity, especially  $\alpha$ , includes a large number of low-diversity sites (Figs. 5, 6). But realistic representation of either  $\alpha$  or  $\gamma$  diversity in the crenon of most freshwater streams cannot be achieved unless most crenon sites are inventoried. Were this done more often for benthic freshwater insects, perhaps benthic mollusks would prove not to differ after all! Finally, some consideration must be given to the possibility that both models are substantially defective. Both universal applicability to the world's streams and applicability to freshwater groups other than insects have been challenged previously (Giller & Malmqvist, 1998).

Finally, we would suggest another avenue for mollusk tests of the RCC and IDH on their home grounds. Eastern U. S. unionid faunas are sufficiently well known that the relationship of diversity to river segment habitat should be easy to establish. In terms of biomass, if not diversity as well, this group clearly dominates the benthic invertebrate fauna in much of the eastern U. S. We doubt that such studies will fit the traditional picture better, although the relative scarcity of crenon taxa, here due to virtual exclusion of fish larval hosts from the crenon of many streams, perhaps renders comparison moot. Minimally, we would argue that no single model of the relationship between diversity and disturbance in freshwater streams is likely to prove appropriate to all benthic groups and all streams. One size seldom fits all.

## Acknowledgements

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# Systematic review and phylogenetic analysis of the nudibranch genus *Melibe* (Opisthobranchia: Dendronotacea) with descriptions of three new species

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Three new species of the genus *Melibe* are described from the Philippines and Okinawa. Specimens of *Melibe engeli* Risbec, 1937 are recorded and described from the Hawaiian Islands and the Philippines and an additional photo is noted from southern Japan. These represent the first published records of this species since its original description. The anatomy of an additional nine species of *Melibe* is re-examined. These include: *M. australis* (Angas, 1864), *M. bucephala* Bergh, 1902, *M. leonina* (Gould, 1852), *M. liltvedi* Gosliner, 1987, *M. megaceras* Gosliner, 1987, *M. papillosa* (de Filippi, 1867), *M. pilosa* Pease, 1860, *M. rosea* Rang, 1829 and *M. viridis* (Kelaart, 1858). Consistent anatomical differences suggest that *M. pilosa* and *M. papillosa* represent distinct species. This review of the morphological variability within the genus provides the basis for a phylogenetic analysis of the group. *Melibe* is shown to represent a monophyletic clade. Members of the genus *Tethys* represent the sister group of *Melibe*.

## Phylogeny, biogeography and evolution of color in the genera *Hypselodoris* and *Thorunna* (Nudibranchia: Chromodorididae)

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Phylogenetic reconstruction is the only testable means by which evolutionary relationships between taxa can be examined. The resulting hypothesis of relationship is used to answer questions broader than who is related to whom. Phylogenies have been used to trace the evolution of different traits, to test the appropriateness of group names and to understand biogeographic events. Here questions regarding the evolution of color pattern in similarly colored sympatric nudibranchs and the geographic distribution of different species are addressed in light of phylogenetic hypotheses. Three phylogenies are presented: A preliminary phylogeny of the family Chromodorididae and complete phylogenies of the genera *Hypselodoris* and *Thorunna*. It is immediately apparent from the phylogeny of the Chromodorididae that similar color patterns have evolved multiple times in distantly related, sympatric taxa. In examining the other more detailed species level phylogenies we find there is no one pattern to explain the evolution of color in these nudibranchs. Biogeographical patterns found in the Indo-Pacific and Eastern Pacific species of *Hypselodoris* are also discussed.

## **Pulmonate Mollusca persisting in California delta marshes with high tidal and physical/chemical extremes**

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Several marshes along the outer San Joaquin/Sacramento River Delta have been monitored for years as some have been restored to higher tidal action, after levees largely isolated these sites from San Francisco Bay tides and from the outer River Delta. As a result, salinities and other environmental parameters have often changed with tidal action. Among restored and reference sites, winter salinities ranged 0.5–10 ppt (2–30% seawater) and summer salinities ranged 1–20 ppt (3–60% seawater). Temperatures in these shallows ranged 10–25 °C near the Bay and 5–30 °C further (20Km) from the Bay. Water clarity was only 5–15 cm in each marsh.

Marsh benthos yielded live Mollusca that represent bivalves and pulmonate gastropods, with almost no other Mollusca. A freshwater pulmonate snail, *Physella integra*, was the most abundant mollusk (year-round) at both restored sites fed by a reclaimed water marsh. Other invertebrates and fishes also were most abundant there, where salinities were lowest, ranging 0.9–2.2 ppt (brackish), water clarity was down to 5 cm, and temperatures were extreme. The other low-salinity site had more variable salinity, low pulmonate population densities, but high abundances of *Macoma balthica* bivalves. Pulmonate slugs were detected at even saltier marshes (~5 ppt), with higher temperature extremes. Based on nearby sediments, bivalves including Asian clams, *Potamocorbula amurensis*, once were common near most sites.

Thus, these several Mollusca persist among extreme conditions in brackish marshes, while prosobranch gastropods and other Mollusca are virtually absent, despite abundant, other Mollusca only seaward or only up river.

## **Native predators limit the abundance of a subtidal whelk in a recently invaded habitat**

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Species that invade new regions and habitats often experience ecological release due to the absence of coevolved natural enemies. This release can lead to invader population explosions and result in significant direct and indirect impacts on invaded communities. The recent expansion of Kelle's whelk (*Kelletia kelletii*) into central California added a novel species to kelp forest communities. These whelks act both as important predators of native prey species and as a novel prey resource for native predators (primarily sea otters, but also crabs and drilling gastropods). Field experiments in Monterey Bay identified potential predators of the whelk and determined types and frequencies of shell damage. Results indicate that invasive whelk populations in central California are severely impacted by native predators that are either absent or uncommon in southern California. In Monterey Bay, high levels of predation on the whelk by native predators and an apparent failure of local reproductive effort suggest that this is a whelk population "sink" which may become locally extinct. Such an extinction would represent a rare marine example of native predators controlling an invader.



## **Land snails and slugs in Delaware, USA: Systematic survey reveals new distribution records**

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Knowledge of species distributions is necessary for making informed decisions about the world. Current understanding of Delaware's terrestrial mollusk distributions is inadequate. The most comprehensive existing land snail and slug distribution maps for eastern North America report distributions to the level of county only. With only three counties in the state of Delaware, distribution resolution is very poor. Many areas of Delaware have been poorly surveyed. In this study, we have sampled land snails and slugs from each of the 238 5x5-km squares in Delaware, giving resolution about 80 times greater than existing distribution maps. Because most species are minute, we have collected leaf litter samples to sieve later in the lab to recover small species. We have also searched visually in the field for slugs and larger snails. We report dozens of new species records at the county and state level. We show that protected natural areas tend to have greater mollusk diversity. Species occurring in few squares include taxa on the edges of their ranges, species restricted to uncommon habitats, introduced species that have not yet spread, or species that are actually rare. As part of a larger study on land gastropods of the Delmarva Peninsula, this work will result in an atlas showing gastropod distributions in the area. The atlas will aid amateur and professional naturalists as well as workers in the fields of conservation, agriculture and ecology.

## **Hawaiian endemic succineid land snails: Preliminary study of phylogeny and biogeography**

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The Hawaiian land snail fauna is extraordinarily diverse and unique, and an ideal model for evolutionary study. Hawaii is home to at least 750 mostly endemic non-marine snail species; unfortunately 70% to 90% of these are now extinct. Succineidae are among the few Hawaiian land snails that have remained relatively abundant. Succineids occur in many parts of the world but only in Hawaii have they adopted such a broad range of habitats, from xeric duneland to montane rainforest. Despite the evolutionary and ecological significance of the endemic Hawaiian succineids, almost no research on this group has been undertaken since the early 1900s. The process of evolutionary radiation in this group can be investigated by constructing a phylogenetic tree of the Hawaiian Succineidae using molecular techniques and then, using museum specimens, evaluating range sizes of the succineid species. Hypothetically, these range sizes relate to island age, where older islands have more species with smaller ranges (in the context of the "taxon cycle" hypothesis of adaptive radiation). In this study, I examine a subset of the Hawaiian Succineidae, testing the utility of 16S rRNA and COI genes for phylogenetic reconstruction in the group. Preliminary results suggest that species on older islands do indeed have smaller ranges, but additional data are needed to confirm or reject this.

# **The history of malacology at the Carnegie Museum of Natural History and opportunities for collection based research**

**Charles F. Sturm, Jr and John Rawlins**

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The Carnegie Museum of Natural History was founded in 1895. Malacology has been an integral part of the Museum of Natural History since its establishment in 1895. Included in this paper is a section with biographical material on the major individuals associated with the malacology collection. This biographical material includes the areas of malacology in which these individuals were active. Following the biographical vignettes, is a detailed breakdown of the collection. This analysis was completed in June 2000. By knowing the interests of previous scientists at the Museum and the current holdings of the collection, one will see that the Museum's collection is particularly strong in the freshwater and terrestrial mollusks.

## The Carnegie Museum of Natural History:

The Carnegie Museum of Natural History was one of the original components of what is now The Carnegie. The Museum of Natural History moved to its present site in 1907 having outgrown its prior quarters. The Museum is composed of three scientific divisions: Earth Sciences, Life Sciences and Anthropology. The Division of Life Sciences is in turn made up of the Sections of Botany, Invertebrate Zoology, Mammals, Reptiles and Amphibians, and Birds.

The holdings in the Museum's scientific collections number well over 17 million specimens. Worldwide in scope, these collections were assembled by the Museum's curators and scientific staff. In addition, the collections have been augmented by exchanges with other institutions and donations from other scientists and amateur natural history enthusiasts.

The other major divisions of the Museum are the Division of Education and Division of Exhibits. The former conducts some 500 classes a year as part of its outreach program to the southwestern Pennsylvania region. It also provides programs to local organizations and loans specimens to teachers for use in school programs. The Division of Exhibits has recently opened the Hall of American Indians, the Hall of African Mammals, and the Hall of Arctic Life. A small portion of the scientific collections is used in the exhibits to augment their educational mission.

## Malacologists at the Carnegie:

H. H. Smith served as the first "curator" of invertebrate zoology at the Carnegie Museum of Natural History. He was employed in what we would now consider a consultant basis and was instrumental in acquiring the beginnings of the malacological collection. Smith was born in Manlius, NY in 1851. He graduated from Cornell University. He became curator in 1895 and retired from that position, due to ill health, in 1903. He moved south to Alabama where he became Curator of the Alabama State Museum. He passed away in 1919.

The Carnegie Museum's molluscan collection had its beginning with the 3,000 species collected by Smith, in addition to other specimens purchased from FR Holland and donated by George Clapp. Despite being at the Carnegie for only eight years, Smith set the stage for others who were to follow.

From 1870 to 1886, Smith made several trips to Brazil and collected mollusks among other natural history specimens. Smith also took trips to the West Indies, Mexico and Columbia, further pursuing his interests in Natural History. When Smith retired to Alabama, he undertook extensive field trips throughout the State collecting freshwater and terrestrial mollusks. Despite collecting all manners of specimens, Smith's particular interests were the Unionids and Pleuroceridae of the southeastern United States. Arnold Ortmann succeeded Smith as curator.

Ortmann was born in 1863 in Magdeberg, Prussia. He studied at the Universities of Kiel, Strassburg and Jena. He received his Ph.D. from the latter institution in 1885. Ortmann came to the United States in 1894 and was Curator of Invertebrate Paleontology at Princeton University. He left Princeton in 1903 to come to the Carnegie Museum of Natural History. While still at Princeton, he worked on the Report upon the Tertiary Invertebrates of the Princeton Expedition to Patagonia.

Upon coming to the Carnegie, Ortmann undertook extensive studies of decapod crustaceans. Following these studies, he began an intensive study of unionids found in the drainage patterns on either side of the Appalachian Mountain Range. His work on unionids resulted in several major monographs and numerous shorter papers. As early as 1909, Ortmann had commented on the effects of pollution in our waterways and its effect on the Unionid populations. Ortmann also published on the Naiads of South American based primarily on the Haseman Collection. Haseman made this collection during an expedition to South America. At the time, it represented material from regions of the Amazon basin not yet collected by other scientists.

In addition to his duties at the Museum, Ortmann was on the faculty of the University of Pittsburgh. He rose to the level of Professor and the University conferred the degree of Sc.D. upon him in 1911. Ortmann died suddenly in 1927 at the age of 64. Upon his death, Stanley Truman Brooks was appointed to care for the collection.

Brooks was born in Mound City, Kansas in 1902. He studied at the University of Kansas and undertook his graduate studies at the University of Pittsburgh where he received his Ph.D. in 1929. He had worked under Ortmann. Upon Ortmann's death, Brooks was appointed custodian of the mollusks at the Museum. Upon earning his Ph.D., he was elevated to a curatorial position. Brooks wrote his thesis on the land snails of Pennsylvania. Brooks also studies the molluscan fauna of Kansas. In addition, he spent several summers studying the fauna of Newfoundland, Canada.

Brooks was the first person to publish a catalog of the type holdings of the collection. In 1931, he published a catalog of the Pelecypoda followed by one on the Amphineura and Gastropoda. Brooks left the Museum in 1945. Upon leaving, he worked as a scientific specialist for the U.S. Military. He left this position in 1947. Subsequent positions that he held were with the U.S. Public Health Service, the American Tobacco Company and the National Research Council. Brooks passed away in 1958 at the age of 56.

Gordon Kutchka was born in Muehleim, Germany in 1906. He earned his M.S. from the University of Pittsburgh in 1937. Kutchka started as an assistant in the Section of Invertebrates in 1929, and was appointed to the permanent staff in 1939. He became a curator in 1946 and held the position of Assistant Curator until 1951 when he left the Museum. In 1938, due to anti-German sentiments, Kutchka changed his last name to MacMillan. From 1944 to 1945, he served with the Armed Forces. After leaving the

Museum, he worked for the Allegheny County Sanitary Authority (Pennsylvania) until 1971, where he held the position of Chemist.

While at the Carnegie, MacMillan worked primarily on terrestrial gastropods. He published one paper on the land snails of West Virginia with Brooks and later published a comprehensive monograph on the terrestrial gastropods of West Virginia. He also studied the terrestrial gastropods of Utah, Wyoming, Montana, Kansas and Nebraska. In all, MacMillan published over 50 papers. He died in 1981 at the age of 75.

After MacMillan left the Carnegie, Juan Jose Parodiz was appointed to replace him as Curator. Parodiz was born in Buenos Aires, Argentina and attended the Instituto Nacional Ciencias Naturales, where he received his degree. Parodiz studied paleontology and malacology while in Argentina. While later serving in the Argentinian Navy, he participated in several oceanographic expeditions to the south Atlantic and sub Antarctic region. Parodiz worked at the Museo Argentino de Ciencias Naturales for almost 20 years before moving to the United States.

In 1951 Parodiz accepted a position at the Carnegie Museum and shortly thereafter was appointed Curator of Invertebrate Biology, a position he held for some 30 years. For roughly the last 20 years he has been Curator Emeritus and has continued to work on the South American naiads and Neogene fossils of the southeastern United States. Parodiz published over 100 papers. He collected throughout South America in addition to the eastern United States. Parodiz's activities have greatly enlarged the Museum's collections in the naiads and terrestrial and freshwater gastropods of North and South America, both fossil and recent. He has been a member of the American Malacological Society since 1949 and served as president in 1965.

Two other men, Victor Sterki and George Clapp, played a significant role in the development of the malacology collection at the Carnegie Museum. Victor Sterki was born in Solothurn, Switzerland in 1846. He studied at the University of Bern and Munich University and earned his M.D. in 1878. Sterki practiced medicine for several years in Europe before emigrating to the U.S. in 1883. Sterki settled in Ohio where he set up his medical practice. He eventually retired in 1900 and pursued the study of natural history full-time. Sterki was an assistant in the Section of Invertebrates from 1909 to 1933.

Sterki's main malacological interests included the gastropod family Pupillidae and the bivalve family Sphaeriidae. The Carnegie acquired his Pupillidae collection of almost 4,000 lots. Later the Museum acquired his Sphaeriidae collection, which numbered over 12,000 lots at the time of Sterki's death. In addition, the malacological library benefited by the addition of Sterki's library, which contained 275 bound and unbound monographs as well as 1,500 reprints. He passed away in 1933 at the age of 87. At the time of his death, Sterki was working on a monograph of the Sphaeriidae of the World, a work that was never finished. The journal *Sterkiana* was named in his honor.

George Clapp was born in 1859. He was actively involved in the educational institutions that were located in Pittsburgh. He became a trustee of the Carnegie Institute in 1896 and continued to serve in this capacity for 53 years. This service ended only with his death. He also served as a trustee for the University of Pittsburgh and the Carnegie Institute of Technology (Carnegie-Mellon University). The University of Pittsburgh honored him with a Sc.D. in 1915 and named their biology department building, Clapp Hall, in his honor.

Clapp's first contribution to the Section of Invertebrates was a collection of 546 specimens representing 60 species of shells from Allegheny County, Pennsylvania. This was one of some 190 donations made by Clapp to the Museum. He was appointed Honorary Curator of Malacology in 1900. Overall, he donated more than 15,000 lots to the Section. Though his collection contained marine, freshwater and terrestrial

mollusks from around the world, most of the material he donated represented terrestrial shells of North America north of Mexico. Clapp's service to the people of Pittsburgh continued until his death in 1949 at the age of 90.

### The Malacology Collection:

The bulk of the collection is housed in sixty cases, each with triple columns of glass-topped drawers. The Sphaeriidae collection is housed in four cases, each with two columns of drawers. The total collection consists of over 115,000 lots containing an estimated 3.5 million individual specimens. Approximately 40 percent of the collection is formally catalogued. The uncatalogued portion contains older material as well as specimens collected or acquired since 1979, including Cenozoic fossil material and terrestrial taxa collected worldwide by Carnegie entomologists, stored in the entomological sample residue collection. The following components are discussed in order of importance in the Carnegie Museum collection.

**Type Collection:** There are 1335 lots of "type" specimens. Primary and secondary types account for 1202 lots. The rest are topotypes that represent either uncommon taxa or taxa that are from localities that no longer exist. Most of the types are freshwater or terrestrial taxa from North and South America, or terrestrial gastropods from Japan.

**Freshwater Bivalves:** There are 11,467 lots of Unionacea, 9,827 from North America, 439 from South America, 316 from other parts of the world and 885 unsorted lots. The largest portion of the North American material was collected by A.E. Ortmann in the early 1900's from Pennsylvania and the Appalachian region. From many of the localities that Ortmann collected, the Unionids are either threatened or extinct. Haseman collected a major portion of the South American Unionacea from 1909-1911. This collection was further augmented by collections made by Parodiz. There are 439 lots, exclusive of type material, in the South American collection. The Corbiculidae number 102 lots and are particularly strong in their South American material. Parodiz collected most of these. Because of visits by South American malacologists to the collection, Parodiz believes this South American collection is among the best curated collections in North America. The Sphaeriidae number 16,119 lots, of which approximately 12,000 lots are from the Sterki collection.

**Terrestrial Gastropods:** There are 28,427 lots of North American land snails. There are also 15,750 lots from other localities around the world. The unsorted material includes 6,483 lots, much of which is from North America.

**Freshwater Gastropods:** There are 11,685 lots of freshwater gastropods. The majority of these are from North and South America.

**Marine Mollusca:** There are 15,951 lots of marine gastropods, 4,258 lots of marine bivalves and 388 lots of other classes. This material is worldwide in scope.

**Cenozoic Fossils:** The collection has 2,966 lots, mostly from the Pliocene – Pleistocene of Florida. This collection is augmented by the holdings in the Section of Invertebrate Paleontology.

**Alcohol Collection:** There are estimated 6,000 lots, primarily unionids, in the alcohol collection.

**Library Holdings:** The Section's library contains more than 100 boxes of reprints. Among the books are many classics in complete sets, including *Conchologia Iconica* (20 volumes) and *Conchylien Cabinet*, First Edition. There are also complete sets of many of the worldwide malacological journals. The library of the Section is augmented by the libraries of the Museum and the Carnegie Library of Pittsburgh, both of which are on the same campus.

Since 1985, the malacology collection has been under the oversight of Dr. John Rawlins, an entomologist. Currently, there is a search underway for a curator of a combined Section of Invertebrate Paleontology and Invertebrate Zoology [subsequently filled by Timothy A. Pearce].

Additional information about the malacology collection at the Carnegie Museum of Natural History can be obtained by e-mail (csturmjr@pitt.edu) from C. F. Sturm, Jr., Research Associate.

**Changes in host-plant use of sacoglossan (=ascoglossan)  
sea slugs on introduced macroalgae**

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On European, American, and Australasian shores, oligophagous marine herbivores associate with the introduced green macroalga *Codium fragile* ssp. *tomentosoides*. On Scottish shores, the ascoglossan sea slug *Elysia viridis* preferred to associate with and consume the introduced *C. fragile* to the native *C. tomentosum*. Growth rates and maximum body sizes of *E. viridis* on introduced hosts were greater than on natives. Although the native host *Cladophora rupestris* induced a high rate of slug metamorphosis, recently metamorphosed juvenile *E. viridis* (from *Codium fragile*-feeding parents) were generally not able to feed or grow on the native alga; in contrast, juveniles from *Cladophora*-feeding parents could eat *Cladophora*, although their performance was highly variable. Small, post-larval slugs could not effectively puncture cell walls and extract algal food from *Cladophora*; slugs fed far more readily on the thin-walled *C. fragile*. The new association on Scottish shores appears to be a host-switch such that *Codium*-feeders and their offspring had limited capacity to complete their life cycle on the native host *Cladophora*. Larval metamorphosis in *E. viridis* was greatest on potential host species, but larvae also responded to non-host macrophytes and adult conspecifics. Generality of larval settlement and metamorphosis enables oligophagous adult consumers to exploit spatially unpredictable novel hosts, to capitalize on newly available host plants, and to exhibit spatial and temporal variation in host-plant associations. [Full paper was recently published: Trowbridge, C. D. & C. D. Todd. 2001. Host-plant change in marine specialist herbivores: Ascoglossan sea slugs on introduced macroalgae. *Ecol. Monogr.* 71: 219–243.]

**NE Pacific sacoglossan (=ascoglossan) opisthobranchs:  
Review and prospectus**

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The species richness and geographic ranges of the sacoglossan (=ascoglossan) opisthobranch fauna have been well characterized for northeastern Pacific shores, particularly in the Californian province, but the natural history and ecology of these gastropods have been comparatively less well studied. Over half of the described sacoglossan genera and approximately two-thirds of the families are represented on northeastern Pacific region. At least 24 species of sacoglossans occur: 16 species are known stenophagous herbivores and one feeds on opisthobranch eggs. Eight species occur on cold-temperate northeastern Pacific shores (Alaska to northern California), 18 species inhabit the Gulf of California and warm-temperate to tropical Pacific shores, and four species occur in the Aleutian, Oregonian, Californian, and Panamic provinces. Five of the species have been studied appreciably more than the others: *Elysia hedgpethi* (Marcus, 1961), *Alderia modesta* (Lovén, 1844), *Placida dendritica* (Alder & Hancock, 1843), *Aplysiopsis enteromorphae* (Cockerell & Eliot, 1905), and *Stiliger fuscovittatus* Lance, 1962. The paucity of study on other species is not necessarily due to low abundance. This natural history review of the regional sacoglossan fauna synthesizes the scattered literature about the stenophagous gastropods and highlights the major gaps that malacologists should seek to fill in the study of this highly specialized order. [Full paper was recently published: Trowbridge, C. D. 2002. Northeastern Pacific sacoglossan opisthobranchs: Natural history review, bibliography, and prospectus. *Veliger* 45: 1-24.]

**A new book on the marine bivalve mollusks of Western North America**

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A book has just been published on the marine bivalve mollusks of western North America. Eleven years in the making, the manuscript documents and describes all bivalves from northern Baja California, Mexico, to the Alaskan Arctic, encompassing habitats from the intertidal zone down to abyssal depths of more than 4,500 meters. The new monograph details 472 species and includes photographs and/or line drawings of each, along with a description of its shell, habitat, and ecology, and references to relevant literature. A particular effort has been made to ensure the book's utility to those outside this geographic area. In this regard, the monograph contains copiously illustrated keys and character tables; over 4,700 full bibliographic references for important literature on each family, genus, and species, and anatomical figures of most genera treated in the text. Three new bivalve species are formally described in the book, belonging to the Thyasiridae, Tellinidae and Mactridae. Several additional new species are figured but not officially named.

## 2000 EXECUTIVE BOARD MEETING

Meeting called to order (Seapy) at approximately 5:00 PM, 12 July 2000

Attending: Hans Bertsch, Cynthia Trowbridge, Chris Kitting, Jules Hertz, George Metz, Roger Seapy, Doug Eernisse, Terry Arnold

- Motion to approve minutes (M: Metz; S: Eernisse): accepted unanimously.
- Treasurer report (Metz): Details of financial report reviewed (included this volume).
- History of 1999-2000 Offices (Seapy): Steve Long resigned as Treasurer in Nov. 1999, and all materials were returned to Metz, who agreed to resume as Treasurer for the remainder of the year. Ron Shimek resigned as President in March 2000. Roger Seapy agreed to resume as President.
- Nominations (Seapy):

President	Hans Bertsch
First VP	Chris Kitting
Second VP	open
Secretary	Terry Arnold
Treasurer	Cynthia Trowbridge
Members-at-Large	George L. Kennedy, Edna Narenjo-Garcia
- Motion (M: Bertsch; S: Metz) to accept the nominations passed unanimously. Seapy agreed to continue to seek an appropriate person for the open Second VP position. [Ángel Valdés has subsequently agreed to the position.]
- Student Grant Awards (Seapy, for Henry Chaney, Chair, Student Grant Committee): Total of \$2,178 in hand and an additional \$500 expected from Santa Barbara Club. Three awards were recommended (Melissa Frey, \$1,000; Kristina Louie, \$1,000; and J. Travis Smith, \$675). Motion (M: Metz; S: Bertsch) to approve the awards as recommended was unanimously passed.
- Motion (M: Kennedy, S: Metz): "The Student Grant committee shall complete their selection by the Annual Meeting to be confirmed by the Executive Board." Passed unanimously.
- 2001 Meeting (Bertsch): scheduled to be held in late June [20-23] in San Diego.
- 2002 Meeting (Kitting): to be held tentatively at Asilomar Conference Grounds on Monterey Peninsula, tentatively 12-15 July.
- Annual Report (Seapy & Kim Hutsell): currently working to complete the 1999 report. Doug Eernisse volunteered to be Editor as of Vol. 33 (2000), with Kim Hutsell resuming as Production Editor.
- Other business (Metz): proposal to expend \$1000 as the WSM contribution to the student grant fund will be presented at the general meeting. Passed unanimously.

Adjourned at 6:25 PM.

Respectfully submitted,  
Terry Arnold, Secretary)



## 2000 ANNUAL BUSINESS MEETING

At 16:02 Roger Seapy, President (continuing) called the meeting to order.

The President read the Secretary's Report provided by T. Arnold for 1999, and the minutes of the executive meeting of July 7, 2000. The secretary's report was discussed. It was moved, seconded and voted that the report be approved as read.

The Treasurer's report for 1999 was provided by George Metz, copies were provided all members. The report was discussed and all questions answered. It was moved, seconded and voted that the report be approved as read.

The President (continuing) reported that in November 1999 the Treasurer elect, Steve Long had resigned and that he had appointed George Metz to continue in that office. Seapy also reported that President-elect Ronald Shimek resigned in April 2000, and Seapy agreed to serve a second term as President.

The Student Grant Committee submitted the following Student Grants for approval:

1. Melissa A. Frey. Doctoral program. University of California, Davis. Competitive interactions of closely related rocky intertidal snails: insights into species divergence? Award: \$1,000.
2. Kristina D. Louie. Doctoral candidate. University of California, Los Angeles.  
The effect of reproductive strategy and dispersal capability on genetic isolation in two eelgrass dependent mollusks, Taylor's seahare (*Phyllaplysia taylori*) and the Pacific eelgrass limpet (*Tectura depicta*). Award: \$1,000.
3. J. Travis Smith. Doctoral program. University of California, San Diego (Scripps). Species level pattern of tropical American Pectinidae. Award: \$675.

Approval of the above recommendations was moved, seconded and voted to accept.

President Seapy reported the recommendations of the Nominating Committee as follows:

President (2001)	Hans Bertsch
First Vice President (2002 President)	Christopher L. Kitting
Second Vice-President (2003 President)	Open
Secretary	Terry Arnold
Treasurer	Cynthia D. Trowbridge
Members-at-large	George L. Kennedy Edna Naranjo Garcia

There being no nominations from the floor, approval of the proposed officers for the coming year was moved, seconded and unanimously approved.

Hans Bertsch reported on the 2001 meeting, which was announced for June 27-July 1 [later modified to June 20-24], 2001 at the Ramada Inn, San Diego California. Bertsch provided information about the accommodations, symposia, meeting facilities and general thoughts about the meeting.

Chris Kitting reported on the preliminary plans for the 2002 meeting, which will if possible be held July 12-15, 2002, at the Asilomar Conference Center, Monterey California. Discussions of possible joint meetings and general plans were provided.

Roger Seapy then reported that the Annual Report for 1999, as yet had not been published, but should be completed by the end of the year. Discussions of the reasons for the delay followed. President Seapy announced the appointment of Doug Eernisse as the Editor and Kim Hutsell as the Production Editor of the Annual Report.

Under new business, it was reported that the AMS had agreed to share the proceeds of the joint auctions with the WSM.

The Treasurer moved that the WSM donate \$1500 to the Student Grant Fund for the 2001 fiscal year. The motion was seconded, voted and approved.

Roger Seapy presented the WSM gavel to incoming president Hans Bertsch.

President Bertsch recommended that the group give a vote of thanks to Roger Seapy and George Metz for their continued services.

Hans reported on the disposition of the WSM's display cabinets, which had been donated to the Biology Department of a university in Baja California.

Steve Lonhart requested that consideration be given to providing applicants a critique on grant proposals submitted to the Student Grant committee. This would provide valuable feedback to the students both in terms of their proposals and applications. Several members spoke in favor of the suggestion. Hans agreed to discuss the proposal with the grant committee.

There being no further business, the meeting was adjourned.

Respectfully submitted,

George Metz, Treasurer (for Terry Arnold, Secretary)

**WESTERN SOCIETY OF MALACOLOGISTS  
TREASURER'S REPORT**

1 October 1999 - 30 September 2000

**INCOME**

Membership dues		\$1,787.00
Student Grant donations, members	263.00	
Student Grant donations,		
Santa Barbara Malacological Society	500.00	
San Diego Shell Club	300.00	
N.C.M.C.	150.00	
Total Student Grant donations		1,213.00
Symposium Fund donations		152.00
Royalties		51.09
Interest income		343.42
<b>TOTAL INCOME</b>		<b>3,546.51</b>

**EXPENSES**

Administrative (Fees, Dues, Office Expense)		156.99
2000 Student Grant		2,675.00
Publication of 1999 Annual Report (deferred to FY 2001)		
2000 Joint AMU/WSM Meeting		1,200.00
2001 WSM Meeting		600.00
<b>TOTAL EXPENSES</b>		<b>4,631.99</b>
<b>Net (Loss)</b>		<b>(1,085.48)</b>
<b>Balance brought forward 10/1/99</b>		<b>3,819.59</b>
<b>Current Balance</b>		<b>2,734.11</b>
<b>Savings (Does not include all of current interest)</b>		
CD 188-004405-0		4,322.76
CD 008-037930-8		10,694.89
CD 188-001886-4		2,683.77
<b>Total</b>		<b>17,701.42</b>
<b>Total Assets</b>		<b>20,435.53</b>

**WSM**  
**STUDENT GRANT ACTIVITIES**  
**2000**

Recipients of the 2000 WSM Student Grant Awards are:

Melissa A. Frey, University of California, Davis.

Proposal: "Competitive interactions of closely related rocky intertidal snails: insights into species divergence? "

Funding: \$1,000

Kristina D. Louie, University of California, Los Angeles.

Proposal: "The effect of reproductive strategy and dispersal capability on genetic isolation in two eelgrass dependent mollusks, Taylor's Seahare (*Phyllaplysia taylori*) and the Pacific eelgrass limpet (*Tectura depicta*)."

Funding: \$1,000

J. Travis Smith, University of California, San Diego (Scripps Institution of Oceanography)

Proposal: "Species level pattern of tropical American Pectinidae."

Funding: \$675.

The Student Grants were made possible, by gifts from the following contributors;

Individual donations by the members of the WSM  
Northern California Malacozoological Club  
San Diego Shell Club  
Santa Barbara Malacological Society  
The Western Society of Malacologists

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