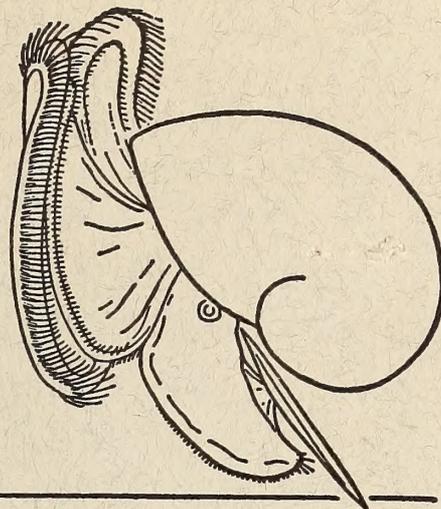


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THE VELIGER



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The Panamic-Galapagan Epitoniidae

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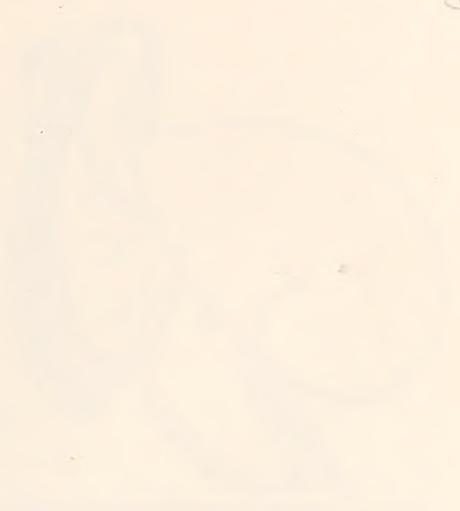
HELEN DUSHANE

Research Associate
Los Angeles County Museum of Natural History
Los Angeles, California 90007

(15 Plates; 5 Text figures; 1 Map)



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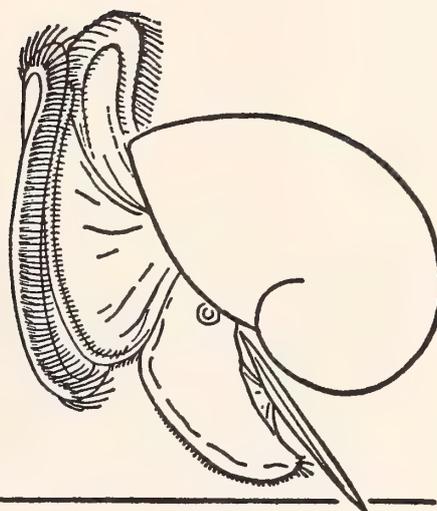
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The Panamic-Galapagan Epitoniidae

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(15 Plates; 5 Text figures; 1 Map)

INTRODUCTION

WITHIN THE CONTEXT OF TIME and space, the family Epitoniidae (Scalariidae), a group with seemingly fragile shells, is world-wide in distribution and has survived from the Jurassic age to the present time. Although the fossil record is meager and scattered, we have substantial proof that some of the species reported as fossil exist today (see Table 1). This paper will be concerned with the late Tertiary fossil and Recent species in the Panamic-Galapagan province. The Panamic-Galapagan province extends south from Isla Cedros on the Pacific side of Baja California (although some authors consider Bahía Magdalena as the northern limit [KEEN, 1971: 4]), including the Gulf of California, the west coast of Mexico and the offshore Mexican Islands, Central America, Colombia, Ecuador, the northern portion of Peru, and the offshore islands of the Galapagan archipelago (see Map).

Table 1

Comparison of Numbers of Recent and Fossil Species in Relation to Total Numbers of Species Within Genera

Genera and Subgenera	Recent &		Total
	Recent	Fossil	
<i>Epitonium</i>			
(<i>Asperiscala</i>)	21	2	23
(<i>Nitidiscala</i>)	17	1	18
(<i>Hirtoscala</i>)	3	0	3
(<i>Depressiscala</i>)	2	0	2
(<i>Sthenorytis</i>)	2	2	4
<i>Cirsotrema</i>	2	0	2
<i>Acirsa</i>	3	0	3
<i>Alora</i>	1	0	1
<i>Amaca</i> (s. l.)	1	0	1
(<i>Scalina</i>)	4	1	5
<i>Opalia</i>	1	0	1
(<i>Dentiscala</i>)	7	1	8
(<i>Nodiscala</i>)	5	1	6
Totals:	68	8	76

The extensive list of epitoniids from this province merits a complete revision. There are no comparable studies comprising the entire Panamic-Galapagan molluscan fauna, although BAKER, HANNA & STRONG (1930) reviewed the family in the Gulf of California. Since then, sporadic efforts have revealed new species within the Gulf of California region. STRONG & HERTLEIN (1939) reviewed the Allan Hancock Foundation collection from Panama and described 3 new species. Strong published keys to sub-

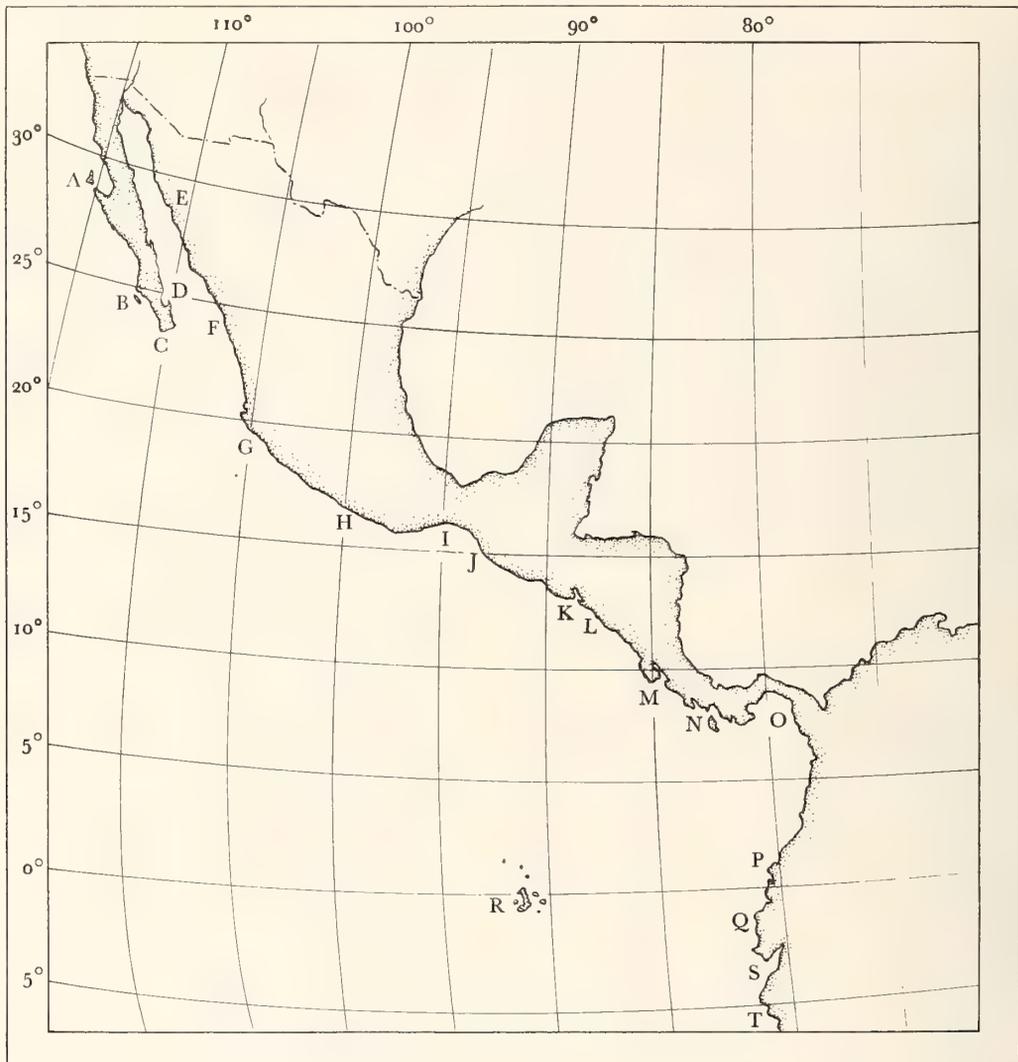
genera and species of Epitoniidae in the Minutes of the Conchological Club of Southern California (J. Q. BURCH, Ed., 1944 - 1945).

The nomenclatural work now possible in analyzing previously described species will probably prevent forgotten names from cropping up in the future. Comparison of photographs and descriptions of types in the British Museum (Natural History) with types from several museums in the United States has made it possible, with some degree of accuracy, to report geographical and bathymetric ranges, ecological habitats, and synonymies. A number of long lost species of Sowerby, Reeve, Hinds, and Carpenter have been located and a few hitherto overlooked species have come to light. A small percentage of the named species cannot be recognized positively on the basis of existing literature or photographs. Many errors on the part of early authors have been due, not to lack of astuteness on their part, but to the paucity of specimens to study. Even today, this sometimes presents a problem in the study of the Epitoniidae.

The epitoniid material in KEEN (1971) was based on my partially completed manuscript. At that time I had not yet had an opportunity to examine many of the types at the United States National Museum. Many changes of allocations and several altered synonymies became necessary in the interim between the time her book was published and the present review was submitted for publication.

Historical Aspects: The history of Panamic-Galapagan malacology is mainly one of naming new species brought back by various expeditions. Most of the early voyagers did not concern themselves with collecting small shells. DARWIN, on the *Beagle* (1832-1836), returned with a few mollusks which have been lost to science. Cuming, on the *Discoverer*, returned with the first epitoniids of which we have a record. The travels and voyages of Hugh Cuming to Central and South America (ca. 1822 - 1830) rank his amateur activities among those of professional scientists. Specimens from his collection were described and illustrated by Sowerby^{1st}, Sowerby^{2nd}, Broderip, Reeve, H. & A. Adams, Carpenter, and others from 1832 on and much of the material finally came to be deposited in the British Museum (Natural History). Hinds, on the voyage of the *Sulphur* (1836 - 1842) to the west coast of tropical America, returned with species described by Sowerby and Hinds in 1844; most of that type material, too, is at the British Museum (Natural History).

Because of the work of the Sowerbys, Broderip, Hinds, Reeve, and others, the descriptions of type specimens, though brief in many instances, are largely accurate, posing few problems for later workers.



Map of the Panamic-Galapagan Faunal Province

- | | |
|---|-----------------------------------|
| A. Isla Cedros, Baja California (Norte) | K. Golfo de Fonseca, San Salvador |
| B. Bahía Magdalena, Baja California (Sur) | L. Corinto, Nicaragua |
| C. Cabo San Lucas, Baja California (Sur) | M. Golfo de Nicoya, Costa Rica |
| D. La Paz, Baja California (Sur) | N. Isla Coiba, Panama |
| E. Guaymas, Sonora, Mexico | O. Golfo de Panama, Panama |
| F. Mazatlán, Sinaloa, Mexico | P. Punta Ancón, Ecuador |
| G. Manzanillo, Colima, Mexico | Q. Jipijapa (Xipixapa), Ecuador |
| H. Acapulco, Guerrero, Mexico | R. Islas Galápagos, Ecuador |
| I. Golfo de Tehuantepec, Chiapas, Mexico | S. Golfo de Guayaquil, Ecuador |
| J. Puerto Madero (Guacomayo), Chiapas, Mexico | T. Paíta, Perú |

There followed a period of monographs, reviews, and incidental papers. Chief among the contributors are C. B. ADAMS (1852), who produced the first major report on the molluscan fauna of Panama; CARPENTER (1856 to 1865), whose labors formed the basis for future systematic work in the United States; DEBOURY (1886 - 1919), whose many papers introduced several confusing genera among the epitoniids; DALL (1889 - 1928), a prolific writer, who did not designate type localities and sometimes, at a later date, exchanged the type for a better specimen. The cluttered nomenclature of these workers has made the task of systematists most difficult despite their works being the springboard for subsequent workers. Many synonymous names were proposed at this time; however, an attempt to clarify the confused nomenclatural problems surrounding the epitoniids is made here. Dr. Keen in 1964, 1965, and 1967 made 3 trips to the British Museum (Natural History), where, among others, she photographed most of the type specimens of *Epitonium*. Without these photographs the present work would have been immeasurably more difficult, if not impossible. Comparison of photographs of types in the British Museum with holotypes from several museums in the United States has made it possible, with some degree of accuracy, to work out synonymies. Modern collecting enables the reporting of geographical and bathymetric ranges, and ecological habitats to be made.

Specimens collected by C. B. Adams were acquired by the Museum of Comparative Zoology, Harvard University, in 1942. Carpenter's type specimens are housed in the British Museum (Natural History), the United States National Museum, Washington, D. C., the University of California, Berkeley, California, the Paleontological Research Institute, Ithaca, New York, and the Redpath Museum at McGill University, Montreal, Canada. Species named by deBoury are at the Muséum National d'Histoire Naturelle, Paris, France, and at the Zoologische Museum, Berlin, Germany. Dall's type specimens are at the United States National Museum.

Although Cuming was probably the first to use a dredge to obtain shells, Hinds also dredged extensively along the west American coast. The *Albatross*, a U. S. government sponsored expedition ship (1891, 1904-1905) dredged in deep water off the west coast of Central America to the Galápagos Islands. The material obtained was described by Dall over a period of many years.

The *St. George* was sent out (1924) with a group of scientists to the Pacific coast of South America. TOMLIN (1927) wrote a report on this, and although no new mollusks were obtained, he did record *Opalia diadema* (Sowerby) from the Galápagos Islands and *Epitonium replicatum* (Sowerby) from off the coast of Colombia.

The Allan Hancock Expeditions (1931 - 1941) to the west coasts of North and South America brought back a vast amount of marine material, parts of which, even today, have not yet been analyzed and studied. The Epitoniidae from this collection have been examined and 4 new species described by DUSHANE (1966, 1970a, 1970b). This material is now housed at the Los Angeles County Museum of Natural History, Los Angeles, California.

The Templeton Crocker Expedition (1936) and the Eastern Pacific *Zaca* expedition, sponsored by the New York Zoological Society, to the west coast of Mexico and Central America, were reported by HERTLEIN & STRONG (1951); 8 species of epitoniids new to science were described by them. The respective type specimens are at the California Academy of Sciences, Geology Type Collection, San Francisco, California.

The *Askoy* expedition of the American Museum of Natural History to Panama, Colombia, and Ecuador (1941) resulted in a range extension for one epitoniid (HERTLEIN & STRONG, 1955).

The *E. W. Scripps* cruise to the Gulf of California resulted in range extensions for 3 epitoniids (EMERSON & PUFFER, 1957). The *Puritan*-American Museum of Natural History Expedition to western Mexico, reported upon by EMERSON (1958) collected many species of epitoniids, some new to science, later described by DUSHANE (1970a).

Paleontologists who have added materially to our knowledge of the fossil record of the family Epitoniidae are: COOPER, 1888, 1894; ARNOLD, 1903, 1906; BÖSE, 1910; MOODY, 1916; PALMER, 1921; JORDAN & HERTLEIN, 1926; DALL & OCHSNER, 1928; GRANT & GALE, 1931; PALMER, 1937; DURHAM, 1937, 1942; OLSSON, 1942, 1961, 1964.

While the various expedition boats were busy dredging, amateurs were busy on foot. Certain of them took their avocation seriously enough to make worthwhile contributions to malacology. Their records of geographic distribution and habitat have added materially to the scope of this paper. There are too many to name all, but a few of the earlier amateurs who collected Epitoniidae are noteworthy because of the difficulties of travel at that time. Janos Xántus (1858 - 1861) collected at Cabo San Lucas, Baja California, Mexico. Both Dall and Carpenter worked with his material, which is at the United States National Museum. Charles Russell Orcutt (1882 - 1919) collected on the Mexican mainland and in Baja California. Part of his collection was acquired by the San Diego Natural History Museum, part by Pomona College, which, in turn, in 1958 was acquired by the University of California, Riverside (gastropods only), and part was sold. Representatives of some of the species obtained by Orcutt have not been collected subsequently. This has led to questions and misunderstandings on the

part of scientists. Orcutt did not collect in Bahía Magdalena proper, but on Isla Magdalena whose beaches front on an estuary (Laguna Magdalena), running roughly north and south. About 19 km north of the bay proper, the small harbor has been called variously Man-of-War Cove (Caleta del Navio), Bahía Magdalena, and Puerto Magdalena. This confusion of names has resulted in questions concerning Orcutt's reliability. Actually, he took passage on a boat out of San Diego, bound for Isla Margarita, to explore certain business possibilities there. The bark put in at Puerto Magdalena, situated on the eastern side of Isla Magdalena. Here, for about 10 days, Orcutt searched the beaches for shells. He probably covered an area roughly 8 km north and 8 km south of the tiny settlement. It is commendable that he collected as many species as he did (see DUSHANE, 1971: 64, 65).

Henry Hemphill (1830 - 1914) gathered land and littoral mollusks in Baja California, the bulk of which went to the California Academy of Sciences and some to both the San Diego Natural History Museum and to Stanford University. Herbert N. Lowe (1913 - 1934) made trips to Mexico and returned with material from which he described 4 new species of *Epitonium*; the types are in the Academy of Natural Sciences of Philadelphia.

Faunal and Malacozoological Research: Good faunal lists can be of great value to taxonomic research. In the past, inaccessibility of the region under consideration has prevented all but the most intrepid from collecting on shore or from accompanying expeditions. Lately, the improvement of roads has made travel a less hazardous undertaking. We have the results in a series of papers and checklists reporting on the molluscan fauna: MENKE (1847), who published the first catalogued report on the local fauna of the Gulf of California, unfortunately relied on information supplied him by Heinrich Melchers, who not only personally collected shells, but purchased them from ship's personnel in the port of Mazatlán; ZETEK (1918) published a list of 17 species of epitoniids from Panama; and STRONG & HANNA (1930) provided lists of mollusks from Isla Guadalupe, Islas Revillagigedo, Islas Tres Marias, Mexico. With the advent of "*Sea Shells of Tropical West America*" (KEEN, 1958), there followed a series of faunal lists of mollusks from the Gulf of California: McLEAN (1961), an appraisal of mollusks taken intertidally at Bahía de Los Angeles; DUSHANE (1962), a checklist of intertidal mollusks from Puertecitos; KEEN (1964), an analysis of mollusks from Isla Espiritu Santo; DUSHANE & POORMAN (1967), a checklist of intertidal and dredged mollusks from the Guaymas area; COAN (1968), an evaluation of benthic mollusks and conditions at Bahía de Los Angeles; DUSHANE & SPHON (1968), a checklist of intertidal and some dredged specimens from Bahía de

San Luis Gonzaga; DUSHANE & BRENNAN (1969), a preliminary survey of mollusks from dredging in the Con-sag Rock area.

In recent years the Mexican Government has established a series of marine stations dedicated to studying malacozoological problems in waters over which it has jurisdiction. In cooperation with the University of Arizona, a research laboratory is located near Punta Peñasco, Sonora. Considerable biological research is being conducted at the Vermilion Sea Field Station, Bahía de Los Angeles, Baja California, Mexico, established by the San Diego Natural History Society. At Ensenada, on the outer coast of Baja California, a small marine station is maintained by the Mexican Government. In Guaymas, Sonora, the Instituto Tecnológica y de Estudios Superiores de Monterrey maintains a department dedicated to marine ecology and other related sciences. At Mazatlán, Sinaloa, a small marine station is operated by the Mexican Government. On Isla Santa Cruz, Galápagos Islands, Ecuador, the Darwin Research Station, in operation for over 5 years, is involved in activities relating to all forms of marine research. It is hoped that the results of their combined research will culminate in greater knowledge regarding the fauna of the Panamic-Galapagan waters.

Population Systematics: To classify the epitoniids on the basis of shell characters alone is not enough (ROBERTSON, 1971: 62); this is a non-biological approach to systematics. An attempt has been made to derive non-morphological information from populations in order to comprehend more fully intra-population trends regarding ecology, biochemistry, and behavior. To this end we have made repeated trips to Baja California and the west coast of Mexico to study these trends. The populations seem to have definite shoreline boundaries and benthic limits beyond which they do not go. The epitoniids apparently occupy an area in the littoral and sub-littoral fauna from mean tide line to about 40 m, with a few exceptions which will be dealt with specifically later in the paper. The age of specialization has sometimes led workers to narrow the concept of genus and species to a bewildering point. They have exaggerated minor differences and have split categories beyond the bounds of sensibility. That there are degrees of intra-population variability is a fact well established by DALL (1917), STRONG (1930, 1945), McLEAN (1966), and others. The length and diameter of a shell for a given number of whorls and costae are probably the best characters for identifying species of *Epitonium*. The limits of specific variation in the number of costae are greater in those species having more costae. The presence or absence of coronation of the costae is sometimes predicated on the freshness of specimens. It is noteworthy that almost 50% of the epitoniids have color when freshly

taken, although most old descriptions claim that they are white. Many of those from early collections have suffered through having been described from beach-worn material, too abused to be of scientific value. I have attempted to rely on multiple defining characters (at least 3) in separating species. Specifically, these may be size of shell, color in live-taken specimens, length and diameter of shell, number of whorls, number of nuclear whorls in relation to the remainder, sculpture and shape of early whorls, number and placement of costae on the whorls, absence or presence of spiral sculpture, absence or presence of punctations, and absence or presence of a basal cord or disk, depth of suture, umbilicus, shape and placement of aperture, sculpture of operculum, geographical origin.

Physiological and Behavioral Aspects: Epitoniids are mesogastropods belonging to the ptenoglossan radula group (mollusks with needle-like recurved teeth, all of one sort). They are a fascinating family, partly because we know so little about them. The animal sometimes has an abnormally long acrembolic proboscis which has led FRETTER & GRAHAM (1962: 172) to theorize that perhaps the epitoniids have a method of feeding on either annelid worms or nemertean which would have to be anesthetized before being seized by the radula. The radula consists of a ribbon of cuticle with rows of teeth which lie flat within the buccal mass. As the radula slips forward, the teeth erect themselves almost vertically, ready to rasp. As the radula returns, a reverse action takes place. This action constitutes the food gathering habit of most prosobranch mollusks. A detailed account of this process is given in FRETTER & GRAHAM (1962: 186, 187). THORSON'S (1958) observation of *Opalia funiculata* [= *O. crenimarginata*] sucking on the juices of the sea anemone *Anthopleura xanthogrammica* does not tell which part of the host was being utilized. My own field observations have been that *O. funiculata* and the 2 California species *O. wroblewskyi chacei* and *Epitonium tinctum* attach themselves (for protection?) at the base of the anemone and not in the cup where the nematocysts are. Also, the anemone seems to be partially contracted while this is going on. All my observations were made in the intertidal zone and in daylight. However, HOCHBERG (1971: 22) adds to this observation with his own, "In Southern California, *Epitonium tinctum* lives in specific association with the small aggregate anemone, *Anthopleura elegantissima*, throughout its post-larval life. This, so-called, micropredator is active twice a day during periods of high water when the anemone beds are covered and the polyps expanded. In order to feed, the snail everts a long, acrembolic proboscis and slips it over the tip of a tentacle. The tentacle is held in place by the jaws and radula in combination with a muscular buccal bulb. Two stylets at the end of the proboscis inject a sali-

vary toxin or anesthetizing agent. The tip of the tentacle is cut or torn off and pulled into the digestive system upon retraction of the proboscis." Hochberg's excellent photographs corroborate his statements. ROBERTSON (1966: 7) has suggested that epitoniids have a cuticularized esophageal lining which may prevent injury from nematocysts.

The animals are consecutive hermaphrodites, laying their eggs in small clusters, each cluster affixed to the next by a mucous thread. Those species with a habitat in or near the sand substrate have sand-agglutinated egg capsules; the coral-associated species do not. As the eggs hatch, the veligers develop a smooth protoconch which is followed by whorls with costae or characteristic sculpture. ANKEL (1938b) has suggested that the costae are a defense against boring naticids, a suggestion which parallels our observations. Few epitoniid shells show damage from boring predators.

One other observation of interest is included here. The late Charles Turner (CARLISLE, TURNER & EBERT, 1964), senior marine biologist for the California Department of Fish and Game, in studying the environmental and behavioral habits of marine organisms in the artificial reef structures offshore from several Southern California beaches, recorded *Epitonium bellastratum* (Carpenter, 1864) from the stomachs of pile perch (*Rhacochilus vacca*) collected at 18m depth. All of the fish collected had absorbed the snail's brilliant purple dye into their flesh, effecting a violet-purple hue to the fish, readily observable under water. This is evidently the first recorded instance of the penetrating influence of the snail's dye into the flesh of fishes, with no resulting harmful effects on the fish.

METHODS AND FORMAT

Methods: The present review comprises those species of Epitoniidae inhabiting the littoral area from approximately Cedros Island, outer coast of Baja California to the northern portion of Peru, where waters of the Humboldt Current intermingle with the tropical offshore currents, from 28°12' N lat., 115°14' W long. to 4°27' S lat., 81°17' W long. This area encompasses an undulating coastline for the most part, known as the Panamic-Galapagan faunal province. Species occurring north of Cedros Island are omitted unless there is an overlap of populations, or unless there is a species distribution into the Southern Californian province.

Working methods were as follows: 1. A card file was started into which all references to type specimens were placed. References were carefully checked to reduce chance of error and to be certain of accurate dating.

2. To this file were added all references to Panamic-Galapagan epitoniids, whether lists or discussion. 3. At the same time, a notebook was used to record original descriptions, with as exact dating as could be ascertained, together with pertinent notes such as collecting data including bathymetric and geographical ranges, habitats and variation in shell size. At the end, 5 standard ring-binders were necessary to hold the material assembled. 4. Holotypic specimens were photographed and the photographs kept between plastic sheets with the written material. Of the type specimens discussed in this paper, very few proved to be unavailable, *i. e.*, those of deBoury and Böse. Some few holotypes have been lost to science and the facts are noted later in the paper.

At first it was thought necessary to examine all lots in the major museums, but this proved to be time consuming and unnecessary. On questionable items requests were made to study any available material. Astonishingly, amateur collectors have provided more and better specimens than the museums. Apparently, the work of KEEN (1958, 1971) has spurred collectors to become more discriminating in their selection of specimens and more discerning in their observations.

The following is a list of important institutions whose material has been of great value in this study; abbreviations are as used in the text:

Academy of Natural Sciences, Philadelphia, Pennsylvania	ANSP
Allan Hancock Foundation, University of Southern California, Los Angeles, California	AHF
American Museum of Natural History, New York City, New York	AMNH
British Museum [Natural History], London England	BM[NH]
California Academy of Sciences [Geology Type Collection], San Francisco, California	CAS[GTC]
Los Angeles County Museum of Natural History, Los Angeles, California	LACM
Museum of Comparative Zoology, Harvard Uni- versity, Cambridge, Massachusetts	MCZ
Paleontological Research Institute, Ithaca, New York	PRI
Redpath Museum, McGill University, Montreal, Canada	RM
Santa Barbara Museum of Natural History, Santa Barbara, California	SBM
San Diego Natural History Museum, San Diego, California	SDNHM
Southeastern Pacific Biological Oceanographic Program, United States National Museum, Washington, D. C.	SEPPOP

Stanford University [Paleontological Type
Collection], Stanford, California SU[PTC]
United States National Museum, Smithsonian
Institution, Washington, D. C. USNM

Through the efforts of Dr. Gerald Bakus of the Hancock Foundation, University of Southern California, the epitoniid material collected on the several trips of Captain Allan Hancock to the eastern Pacific (*Velero III*, 1931 to 1941) was made available to me several years ago. This collection, together with the many type specimens of Dall and Carpenter at the USNM formed the nucleus of material on which this paper is based.

Format: The synonymies of the genera and subgenera of the Epitoniidae presented by CLENCH & TURNER (1950, 1951, 1952) obviate the necessity of repeating it. Synonymy of species in the Panamic-Galapagan faunal area will be discussed here.

A conservative approach has been used, pending such time as a review of the family can be undertaken on a world wide basis. Much of the deBoury material waits for a student of French to translate and evaluate it. I am sincerely grateful to Jean Cate for having translated two of his more useful papers. Only the genera and subgenera *Epitonium*, *Asperiscala*, *Nitidiscala*, *Hirtoscala*, *Cirsotrema*, *Acirsa*, *Amaea*, *Scalina*, *Depressiscala*, *Sthenorytis*, *Alora*, *Opalia*, *Dentiscala*, and *Nodiscala* are used. Into the subgenus *Asperiscala* have been placed all those forms with a consistent pattern of cording or fine threads between the costae, including those where the spiral sculpture appears on only the early whorls. The forms with fine but uneven microscopic striae and a dark-colored body have been placed in the genus *Depressiscala*. The remaining genera and subgenera have characteristics that make them easy to identify. Brief summaries of each are given under the separate headings.

The following outline has been adopted for each species:

Synonymy: Original species name, author, date of publication, page number(s) and figure number(s), if any, followed by the same information for each author using the identical name. The first reference in the synonymy is to the original description unless otherwise stated.

Original description of type: Even if the description is in a foreign language, it is given verbatim. English translations are provided where found necessary for complete understanding.

Diagnosis: A complete diagnosis is given for those species of which live-taken specimens could be studied, or where the type specimen is in good condition. No

diagnosis is given in a few cases where the information is complete, or where only one beachworn specimen was obtained, with no further reports made on the species. Most descriptive terms are subjective; what is needed is a more objective method of defining species within a family group. Here, the size in length is defined as "small" = 0 to 5 mm; "medium" = 5 to 10 mm; and "large" = 10 mm and over. The range of variation in number of costae for each species is recorded in round numbers, as is the number of nuclear whorls and postnuclear whorls. In species where spiral sculpture is present, such as in the subgenus *Asperiscula*, the width of the spiral threads or cords is compared with the width of the interspaces. This is done, hopefully, for greater clarification of descriptive terms.

Discussion: Related information which does not fit into the "Diagnosis" is placed here. No attempt has been made to list all the locality data for each species, as some of the epitioids come from uncertain localities or with numerous records which would be cumbersome to report. In some cases where the species is a rarity, all locality data are used; otherwise only the north and south extremes of the known range, together with references to the specimens that form their bases, are given. Photographs of type specimens are included. If the type specimen is badly worn, an attempt has been made to include a photograph of a live-taken specimen.

Type Material: The repository of the holotype is listed with the accession (museum) number. The same information for synonymous taxa is also listed.

Type Locality: When reported by the original author, this is given, together with the collector's name, if known.

Geographical Distribution and Ecology: Extremes of the range, and the habitat are given.

Bathymetric Range: The depths from which the species has been obtained are recorded.

Geochronological Range: Because an effort has been made to report on the fossil material, the period or epoch, or both, is recorded.

A small section at the end of the paper is devoted to "Unresolved Species" followed by "Literature Cited," in which references are included for all genera, subgenera, species, and related papers mentioned. The "Index" includes all specific and generic names used.

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It takes many people to bring a project such as the present one to its proper conclusion. My gratitude is extended to

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My special appreciation goes to Mr. Gale Sphon of the Los Angeles County Museum of Natural History staff for numerous letters written in my behalf requesting the loan of type specimens.

For extraction of the radulae I am indebted to Dr. George Radwin and for the radular drawings to Mr. Anthony D'Attilio, both of the San Diego Museum of Natural History.

Personnel of the libraries at both the Los Angeles County Museum and the Hancock Library at the University of Southern California rendered help in finding difficult items. In addition, Mr. and Mrs. Crawford Cate permitted unlimited use of their personal library. Because of the generosity shown, it was possible to examine all the references cited. This helps to avoid errors which are often perpetuated through the years.

The following collectors have been generous with the loan of specimens and additional information on collecting data: Edith Abbott, San Dimas, Rose and John Q. Burch, Seal Beach, Jean and Crawford Cate, Florida, Elsie and Emery Chace, San Pedro; Anne Craig, Guaymas; Jacqueline and André DeRoy, Galápagos Islands, Faye Howard, Santa Barbara, Roy and Forrest Poorman, Pasadena, Dr. Donald Shasky, Redlands; and Laura Shy, Westminster.

Photographs, for which I am grateful, came from many sources. The definitive work of Dr. Myra Keen on her three trips to the British Museum (Natural History) resulted in my having photographs of otherwise inaccessible species which helped to clarify some rather puzzling nomenclatural problems. Credit is given here to individuals for their photographic work: Jean Cate, Figures 93, 148; Jacqueline DeRoy, Figure 115; Bertram Draper, Figures 35, 57, 100, 105, 113, 114, 116, 117, 119, 120,

122; Mead French, Figures 13, 15; Dr. Myra Keen, Figures 11, 28, 36, 39, 41, 43, 45, 59, 74, 77, 78, 81, 85, 94, 99, 111, 118, 125, 132; Dr. James McLean, Figures 6, 7, 17, 21, 22, 42, 47, 48, 49, 55, 63, 64, 65, 71, 82, 86, 87, 90, 91, 92, 95, 104, 107, 108, 109, 110, 121, 128, 130, 137, 140, 147, 149; Roy Poorman, Figures 10, 16, 18, 27, 37, 44, 53, 54, 58, 61, 76, 90, 112, 133, 134, 135, 141; Gale Sphon, Figures 9, 12, 20, 29, 30, 40, 46, 66, 70, 79, 84, 88, 106, 124, 126, 138, 139, 144, 145, 146; Armando Solis, Figures 5, 34, 60, 62, 67, 68, 69, 73, 75, 101, 102, 142; and Larry Reynolds, Figures 1, 2, 3, 4, 8, 19, 23, 24, 25, 26, 31, 32, 33, 38, 50, 51, 52, 72, 80, 83, 89, 98, 103, 123, 127, 129, 131, 136, 143 (the latter two of the Photographic Staff, Los Angeles County Museum); California Academy of Sciences, Figure 99; Perfecto Mary, Figures 14, 56.

To all of the persons mentioned above I am indebted for assistance, but any errors in determination or judgment are my own.

EPITONIAEAE

EPITONIIDAE

Epitonium Röding, 1798 [*Scala* of authors; *Scalaria* Lamarck, 1801]

Shells are usually colorless, somewhat turreted, sometimes umbilicate, with axial sculpture of heavy or slender costae, sometimes recurved; whorls are numerous, with varying degrees of convexity, coiled either loosely or tightly. Spiral sculpture may be present or absent. The aperture is round or oval, with an operculum that is thin and paucispiral.

(*Asperiscala*) deBoury, 1909

[Type species: (OD) *Scalaria bellastrata* Carpenter, 1864]

Shells are white or pink to dark gray or brown in color; costae usually recurved, sometimes with a spine on the shoulder of the whorl; with sculpture of heavy cords to fine striations, sometimes obsolete on the later whorls.

Epitonium (Asperiscala) acapulcanum Dall, 1917

(Figures 1, 2, 3, 4, 7)

Epitonium (Asperiscala) acapulcanum DALL, 1917: 475; BAKER, HANNA & STRONG, 1930: 50; pl. 2, fig. 8; M. SMITH, 1944: 7; KEEN, 1958: 271; fig. 90; KEEN, 1971: 424; fig. 611

Epitonium (Asperiscala) acapulcanum. - PILSBRY & LOWE, 1932: 120

Epitonium (Asperiscala) acapulcana. - STRONG, 1945: 22

Epitonium acapulcanum. - BURCH, 1945: 23; DUSHANE & SPHON, 1968: 240; BOSS *et al.*, 1968: 7

Epitonium (Asperiscala) xantusi DALL, 1917: 475; STRONG & HANNA, 1930: 19; BAKER, HANNA & STRONG, 1930: 50; pl. 3, figs. 1, 2; STRONG, 1945: 22; KEEN, 1958: 272; fig. 100

Epitonium (Asperiscala) xantusi. - PILSBRY & LOWE, 1932: 120; M. SMITH, 1944: 7

Epitonium xantusi. - BURCH, 1945: 23; DUSHANE & POORMAN, 1967: 424; BOSS *et al.*, 1968: 342

Epitonium (Asperiscala) keratium DALL, 1919: 340

Epitonium (Asperiscala) keratium. - STRONG, 1945: 22; BOSS *et al.*, 1968: 175

Epitonium keratium. - BURCH, 1945: 23; DUSHANE & BRENNAN, 1969: 358

Epitonium (Asperiscala) slevini STRONG & HERTLEIN, 1939: 193; pl. 18, fig. 9; STRONG, 1945: 22, 23

Epitonium slevini. - BURCH, 1945: 23

Epitonium (Asperiscala) slevini. - WILSON, 1967: 193 (paratypes 3686-3687, Taboga Island, Panama)

Explanation of Figures 1 to 10

Figure 1: *Epitonium (Asperiscala) acapulcanum* Dall, 1917. Holotype, USNM 59337; length 5 mm; width 2½ mm × 13

Figure 2: *Epitonium (Asperiscala) xantusi* Dall, 1917. Holotype, USNM 4107; length 5½ mm; width 3 mm × 11

Figure 3: *Epitonium (Asperiscala) keratium* Dall, 1919. Holotype, USNM 217878; length 10 mm; width 4½ mm × 6

Figure 4: *Epitonium (Asperiscala) slevini* Strong & Hertlein, 1939. Holotype, CAS[GTC] 724; length 4.3 mm; width 2 mm × 15

Figure 5: *Epitonium (Asperiscala) huffmani* DuShane & McLean, 1968. Holotype, LACM 1159; length 11 mm; width 7 mm × 4

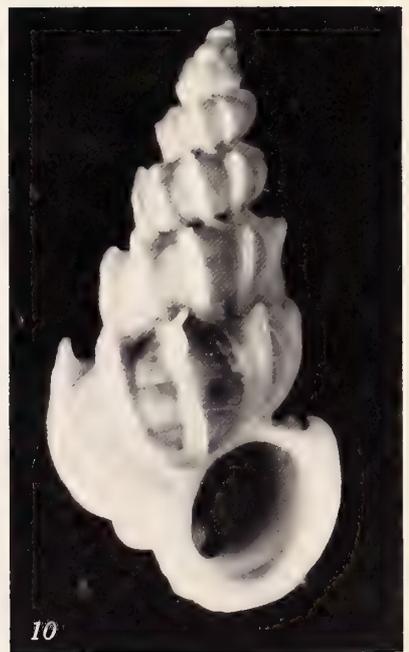
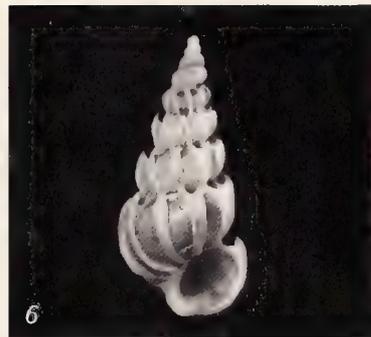
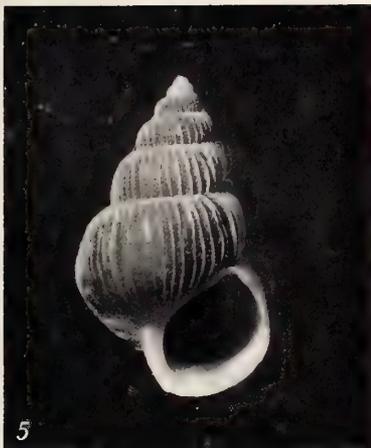
Figure 6: *Epitonium (Asperiscala) vivesi* Hertlein & Strong, 1951. Holotype, CAS[GTC] 9615; length 7 mm; width 3.2 mm × 3½

Figure 7: *Epitonium (Asperiscala) strongi* Bartsch, 1928. Holotype, USNM 367967; length 15.9 mm; width 8½ mm × 2.7

Figure 8: *Epitonium (Asperiscala) cookeanum* Dall, 1917. Holotype, USNM 211019; length 9½ mm; width 4 mm × 6

Figure 9: *Epitonium (Nitidoscala) eutaenium* Dall, 1917. Holotype, USNM 201201; length 11 mm; width 4 mm × 7.2

Figure 10: *Epitonium (Asperiscala) eutaenium* (Dall, 1917). Puertecitos, Baja California, Mexico, dredged in 11 m (DuShane Coll.); length 4 mm; width 2½ mm × 20.2



Epitonium strongi BARTSCH, 1928: 71; fig. 2

Epitonium (Nitidiscala) strongi. - STRONG, 1945: 26, 27

Original Description: "Shell small, white, acute, imperforate, with a slender three-whorled smooth nucleus and five subsequent whorls; varices 11, continuous over the suture up the spire which they nearly encircle; spiral sculpture of closely adjacent spiral threads covering the whorl; anterior faces of the varices smooth, without any spinosity at the shoulder. Length, 5; diameter, 2.5 mm." (DALL, 1917: 475)

Diagnosis: Shell small; nuclear whorls 3, smooth, glassy; subsequent whorls 5 to 6; costae 11 to 15, slightly reflected; riblets between costae evenly spaced and prominent, numbering about 20 on the last whorl, continuing in some cases on to the face of the costae; suture moderately deep; umbilicus lacking; parietal lip lying close to the costae; anterior end of lip with a strong wrinkled fasciole; aperture round; operculum thin and paucispiral. Length 5 to 10mm; width 2.5 to 4.5mm.

Discussion: Comparison of the holotype of *Epitonium (Asperiscala) acapulcanum* Dall, 1917, presumably from Acapulco, Mexico, with the types of *E. (A.) xantusi* Dall, 1917, *E. (A.) keratium* Dall, 1919, *E. strongi* Bartsch, 1928, and *E. (A.) slevini* Strong & Hertlein, 1939, shows them all to have the following characteristics in common: Ridges between the costae are evenly spaced and prominent, continuing in some cases on to the face of the slightly reflected costae. The anterior end of the lip has a strong, wrinkled fasciole behind the lip. The operculum is thin and paucispiral. The number of costae per whorl tends to be greater toward the southern end of the geographical range. This is a common intertidal species which may account for its synonymous names. C. R. Orcutt collected it intertidally on Isla Magdalena, off the outer coast of Baja California, Mexico, described as *E. (A.) keratium*. Xantus took *E. (A.) xantusi* intertidally at Cape San Lucas, Baja California, Mexico; *E. (A.) slevini* was dredged in from 3 to 16m off Taboga Island, Panama. *Epitonium strongi*, from Guayaquil, Ecuador, proves to belong to the subgenus *Asperiscala* with evenly spaced threads between the costae and a wrinkled fasciole behind the lip, specific characters of *E. (A.) acapulcanum*. Dr. Donald Shasky recently (March 1970) took 2 crab-inhabited shells at Punta Ancón, Ecuador. Live-taken specimens are rare, although there is a record from Consag Rock, in the upper reaches of the Gulf of California, Mexico, trawled in 30m, sand bottom, attached to shells of *Pteria sterna*, June 1968 (DuShane collection).

Type Material:

Epitonium (Asperiscala) acapulcanum: holotype USNM 59337

Epitonium (Asperiscala) xantusi: holotype, USNM 4107

Epitonium (Asperiscala) keratium: holotype, USNM 217878

Epitonium strongi: holotype, USNM 367967

Epitonium (Asperiscala) slevini: holotype, CAS[GTC] 724

Type Localities:

Epitonium acapulcanum: None given, but the name would suggest Acapulco, Mexico

Epitonium xantusi: Cabo San Lucas

Epitonium keratium: Isla Magdalena, outer coast of Baja California, Mexico

Epitonium slevini: Taboga Island, Panama

Epitonium strongi: Guayaquil, Ecuador

Geographical Distribution and Ecology: Magdalena Bay, Baja California throughout the Gulf of California, Mexico, south to Ecuador.

Bathymetric Range: Intertidal to depth of 30m.

Geochronological Range: Recent

Epitonium (Asperiscala) billeeanum (DuShane & Bratcher, 1965)

(Figures 13, 14, 15, and 155a, 155b)

Scalina billeeana DUSHANE & BRATCHER, 1965: 160; plt. 24, figs. 1-4; DUSHANE & POORMAN, 1967: 425

Epitonium (Asperiscala) billeeana. - DUSHANE, 1967: 87; DUSHANE & MCLEAN, 1968: 1, 2; fig. 1

Scalina (Ferminoscala) billeeana. - SPHON, 1971: 20

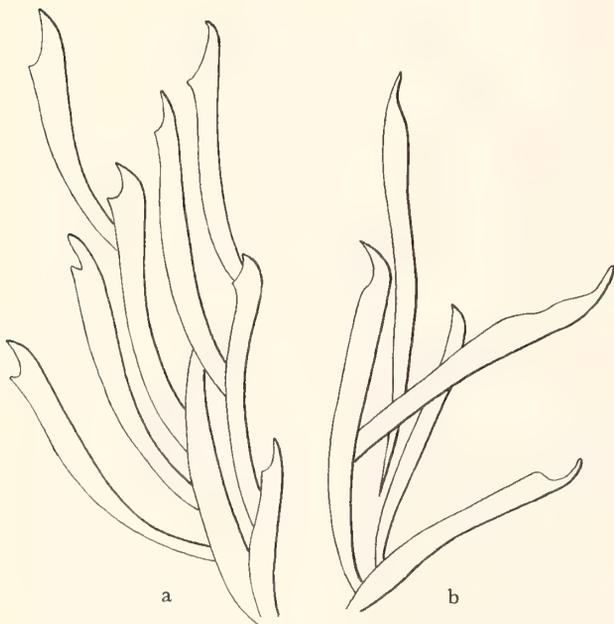
Epitonium (Asperiscala) billeeanum. - KEEN, 1971: 424; fig. 612

Original Description: "Shell small for genus, white under a thin, shining, yellowish buff periostracum; with three to four smooth, glassy nuclear whorls rapidly enlarging; postnuclear whorls six to seven, strongly convex; thin and fragile with strong cancellate sculpture of 16 to 18 raised spiral lines on the last whorl; outer lip thin, flaring on the inner margin; columella partially deflected over a narrow umbilicus. Height 7mm, maximum diameter 4mm. The operculum of this species is round, thin and horny with weak spiral incremental sculpture of variously spaced grooves." (DUSHANE & BRATCHER, 1965: 243)

Discussion: In general proportions *Epitonium (Asperiscala) billeeanum* resembles *E. (A.) frielei* (Dall, 1889) (CLENCH & TURNER, 1952: 301; plt. 139), which also

has an umbilicate shell with fine axial and spiral striae. However, *E. frielei* has fewer costae and its spiral ribs are weaker, in addition to having a habitat in depths of 113 to 243 m off the coasts of North Carolina and Florida; consequently, the relationship between the two species is probably superficial.

Thirty-one specimens, some with eggs, were taken at the type locality by Mrs. Billee Dilworth while diving in 2.4 to 3.0 m of water. Each yellow egg has 2 mucous threads which are joined to form a single thread, linking each egg to the main thread, in turn attached by threads to the coral host, *Tubastrea tenuilamellosa* (Milne-Edwards & Haime, 1848). The soft parts of the coral have orange zooids with yellow bases between them. The animals of *Epitonium (Asperiscala) billeeanum* seem to live on these bases. When alive, the animal is chrome-yellow and shows through the translucent shell making the latter appear to be a brilliant yellow. The radula is typical of *Ptenoglossa* (MOORE, 1960: 1-104) with an indefinite number of long hooked teeth, of which the outermost are the largest (Figures 1a, 1b).



Figures 155a and 155b

Epitonium (Asperiscala) billeeanum (DuShane & Bratcher, 1965)

Radular teeth of the holotype, $\times 550$

The radula is typical of *Ptenoglossa* with an indefinite number of long, hooked teeth, of which the outermost are the largest

Since the original description was published in 1965, much larger specimens are not uncommonly taken by divers in water from 2 to 14 m in depth at several localities throughout the Gulf of California, Mexico, southward to and including the Galápagos Islands, Ecuador. Some specimens taken attain the proportions of 25 mm in length and 15 mm in width.

Verona McKibbin, 1966, reported (*in litt.*) *Epitonium billeeanum* spawning on *Tubastrea tenuilamellosa* in a 1.5 m band, 2.4 m below the surface on San Pedro Nolasco Island, Gulf of California, Mexico. The water depth was 14 m, temperature 24.5°C. The 8 specimens are at Stanford University (PTC). Other localities from which *E. billeeanum* has been reported are: Cabo San Lucas, Gulf of California, Dr. James McLean diving at 6 m, 1966, specimens in the LACM; Manzanillo, Colima, Mexico, Laura and Carl Shy, several live specimens, diving at 2 to 4 m, 1970, specimens in Shy collection; Sombrero Chino Island, south of Santiago Island, Galápagos Islands, Ecuador, Jacqueline DeRoy, one dead specimen, 1964, in DuShane collection.

It is astonishing that the species could have been so long undetected. However, there is an underwater area from the low intertidal mark to 14 m in depth that had not been searched until the advent of SCUBA made it possible to explore this underwater belt.

This is a puzzling species since it does not seem to fit into any of the known genera or subgenera. Until such time as there is a complete study made of the genera on a world-wide basis with anatomical and ecological relations better known, it seems wise to leave it where it is. Dr. Robert Robertson (personal communication) indicates a similar coral-related species has been taken in the Indian Ocean (Maldive Islands).

Type Material:

Scalina billeeana: holotype, CAS[GTC] 12729

Type Locality:

Scalina billeeana: Southwest end of Cerralvo Island, Gulf of California, Mexico; lat. 24°09'N; long. 109°55'W

Geographical Distribution and Ecology: This species can be expected to occur from Cabo San Lucas, throughout the Gulf of California and south along the west Mexican coast to the Galápagos Islands. It lives in symbiotic association with the coral *Tubastrea tenuilamellosa*, from just below extreme low tide to approximately 14 m.

Bathymetric Range: From to 2 to 14 m in depth.

Geochronological Range: Recent

Epitonium (Asperiscala) canna Dall, 1919

(Figures 47, 48)

Epitonium (Asperiscala) canna DALL, 1919: 341; STRONG & HANNA, 1930: 19; LOWE, 1932: 113; pl. 9, figs. 7, 8; PILSBRY & LOWE, 1932: 120; LOWE, 1935: 31

Epitonium (Asperiscala) canna. - STRONG, 1945: 22; KEEN, 1958: 271; fig. 91; KEEN, 1964: 187; KEEN, 1971: 424; fig. 613

Epitonium cannum. - BURCH, 1945: 23

Epitonium canna. - DUSHANE & POORMAN, 1967: 424; BOSS *et al.*, 1968: 63

Epitonium reedi BARTSCH, 1928: 72; fig. 3

Epitonium (Nitidiscala) reedi. - STRONG, 1945: 27

Original Description: "Shell small, white, shading to yellowish on the spire, with six whorls excluding the (lost) nucleus, imperforate, with a deep suture and six strong varices, continuous up the spire which they about one-fourth encircle; the varices are concentrically striated on the anterior face, are very solid, and have no angulation at the shoulder; spiral sculpture of on the base of the last whorl numerous minute sharp threads with intercalary fine striae occupying the wider interspaces; this sculpture becomes obsolete at or behind the periphery; there is no basal disk or cord; height, 9; maximum diameter, 5 mm." (DALL, 1919: 341)

Diagnosis: Shell intermediate to large in size; nuclear whorls 2, solid, white, nearly always eroded; whorls 7 to 8, inflated, slightly reflected; suture deep; costae 6, rarely 7, strong and thick, with an angulation at the shoulder on live-taken specimens, fused at umbilicus; spiral threads between costae fine, no wider than interspaces; aperture oval; outer lip thickened, parietal lip less so with reinforcement of striated callus just outside inner lip. Operculum thin, dark, paucispiral. Length 5 to 22 mm; width 3 to 8 mm.

Discussion: This species is probably the most common of the *Asperiscala* in the Panamic province. Possibly because of its coarse sculpture and relatively large size it is more readily seen by collectors than some of the smaller, more fragile species.

DALL (1919: 341) described this species from a small beach specimen picked up by C. R. Orcutt on Isla Magdalena, Baja California, Mexico. BARTSCH (1928: 72) had a much superior specimen from which to draw his conclusions on *Epitonium reedi* from Ecuador. Comparison of the 2 holotypes indicates they are one species. Beach specimens are white and smooth, whereas fresh specimens show the brown flush between the costae that Bartsch noted in his description. It is unusual to find *E. canna* with more than 6 to 7 costae.

Type Material:

Epitonium (Asperiscala) canna: holotype, USNM 218099

Epitonium reedi: holotype, USNM 367968

Type Localities:

Epitonium canna: Isla Magdalena, Baja California, Mexico

Epitonium reedi: Ecuador

Geographical Distribution and Ecology: Throughout the Gulf of California, Mexico, Laguna Magdalena, Baja California (outer coast), Mexico south to Ecuador, exclusive of the Galápagos Islands. One specimen in the CAS[GTC], taken off Punta Abreojos, extends the known range northward on the outer coast of Baja California. This species is usually taken on rocky reef, covered with green algae and with sea anemones nearby.

Bathymetric Range: Intertidal and shallow water dredging.

Geochronological Range: Recent

Epitonium (Asperiscala) cookeanum Dall, 1917

(Figure 8)

Epitonium (Asperiscala) cookeanum DALL, 1917: 475; BAKER, HANNA & STRONG, 1930: 51; pl. 3, fig. 3; BURCH, 1945: 23; KEEN, 1958: 271; KEEN, 1971: 424; fig. 165

Asperiscala cookeana. - DALL, 1921: 114

Epitonium cookeanum. - OLDROYD, 1927: 56; KEEN, 1937: 35; BOSS *et al.*, 1968: 89

Epitonium (Asperiscala) cookeana. - STRONG, 1945: 22

Original Description: "Shell small, pink, solid, acute, imperforate, the nucleus lost, with eight well rounded subsequent whorls; with 10 rather solid, smooth continuous white varices making less than half a turn round the spire; spiral sculpture of extremely fine uniform threads covering the whorl between the varices; the terminal varix thicker than the others; all the varices broader at the intersection with the suture but not spinose. Length, 9.5; diameter, 4 mm." (DALL, 1917: 475)

Diagnosis: Shell small, white, sometimes with a pinkish cast between the costae; nuclear whorls 3, small, brown, glassy; later whorls 8, rounded; costae 10 to 12, solid, white, smooth, heavier at the suture, not reflected; threads between costae fine; suture deep; umbilicus lacking; aperture round; outer lip heavy, thinner parietally. Length, 7 to 10 mm; diameter, 3 to 5 mm.

Discussion: This is apparently a rare species, as few specimens have been reported. Eight specimens were collected by C. R. Orcutt, March 1917, reportedly from Magda-

lena Bay. At the time Orcutt made his collection, the small settlement on Isla Magdalena was called "Bahía Magdalena." Today it is referred to as "Puerto Magdalena."

DALL (1917: 475) named *Epitonium (Asperiscala) cookeanum* in honor of Miss J. M. Cooke of San Diego on the basis of one specimen obtained for her, presumably from La Paz, by Capt. Porter. The Fred Baker collection had one specimen from Ocean Beach, San Diego area, California. The CAS[GTC] has one beachworm specimen from Espíritu Santo Island, Gulf of California, Mexico; the LACM has one beach specimen collected intertidally by Dr. James McLean, 1966, at Cabo San Lucas, Baja California, Mexico.

Type Material:

Epitonium (Asperiscala) cookeanum; holotype, USNM 211019

Type Locality:

Epitonium (Asperiscala) cookeanum: None given

Geographical Distribution and Ecology: San Diego, California to La Paz and Espíritu Santo Island, Gulf of California, Mexico. Nothing is known of the habitat of the species.

Bathymetric Range: Unknown

Geochronological Range: Recent

Epitonium (Asperiscala) elenense (Sowerby, 1844)

(Figures 38, 39, 40, 41, and 156)

Scaloria elenensis SOWERBY, 1844a: 98; pl. 34, fig. 102; SOWERBY, 1844b: 29; REEVE, 1873: pl. 8, fig. 102; NYST, 1871: 107; TRYON, 1887: 70; pl. 14, fig. 44; DALL, 1917: 488

Scala elenensis. - ADAMS, 1853: 221

Epitonium elenense. - DALL, 1909: 190, 223

Epitonium (Nitidiscala) elenense. - KEEN, 1971: 432; fig. 648

Scaloria rariocostata CARPENTER, 1857b: 447 [not LAMARCK, 1822; not WOOD, 1828; not SOWERBY, 1844b]. Reprint, 1967: 447; CARPENTER, 1857a: 260, 270, 336; CARPENTER, 1860: 10; NYST, 1871: 131; DALL, 1917: 488; PALMER, 1951: 62; BRANN, 1966: 75; pl. 50, fig. 568; KEEN, 1968: 400, 401, 407; text fig. 38; pl. 57, fig. 49

Scaloria rariocostata. - CARPENTER, 1864c: 547

Scala rariocostata. - DEBOURY, 1919: 40

Epitonium (Punctiscala) carpenteri TAPPARONE-CANEFRI,

1876: 154 [nom. nov. pro *Scaloria rariocostata* Carpenter]

Scaloria rariocostata [sic]. - TAPPARONE-CANEFRI, 1876: 154

Scala carpenteri. - DEBOURY, 1919: 40

Epitonium (Punctiscala) carpenteri. - STRONG, 1945: 20; KEEN, 1958: 276

Epitonium carpenteri. - HERTLEIN & STRONG, 1951: 90; DUSHANE & POORMAN, 1967: 425

Epitonium thylax DALL, 1917: 487; ZETEK, 1918: 25; M.

SMITH, 1944: 7; BOSS *et al.*, 1968: 320

Epitonium (Nitidiscala) thylax. - STRONG, 1945: 7

Epitonium (s. l.) thylax. - KEEN, 1958: 276

Epitonium (Asperiscala) thylax. - KEEN, 1971: 428; fig. 628

Epitonium (Nitidiscala) phanium DALL, 1919: 342; PILSBRY & LOWE, 1932: 120; M. SMITH, 1944: 7; BOSS *et al.*, 1968: 253

Epitonium (Nitidiscala) phanium. - LOWE, 1932: 113; pl. 9, fig. 2; STRONG, 1945: 26, 27; KEEN, 1958: 274; fig. 126

Original Description: "*T. pyramidalis, laevi, imperforata; anfractibus contiguus; varicibus sex, ad suturam sub-plicatis, irregulariter continuis; apertura ovali; colore albo.*" (SOWERBY, 1844a: 29)

Diagnosis: Shell small to medium in size, conic, light brown shading into purple or pink with white costae in live-taken specimens; nucleus conic with 2 to 3 smooth, opaque whorls, nearly always eroded, remaining whorls 7 or 8, with about 30 to 35 spiral threads, half the width of the interspaces on the body whorl, seen only under magnification of 40×; suture distinct but not deep; costae 6 to 8, sharp edged, low, wider where they attach to the whorls and with a decided overlap at the intersection with the suture, some costae disjunct; aperture oval; lip narrow but entire, slightly patulous at the lower extremity; operculum thin, brown, paucispiral. Length, 3.2 to 10mm; width, 1.5 to 3mm.

Discussion: The description given by Sowerby is brief, but a photograph of the type is diagnostic and shows 3 subsequent species to be synonymous. Carpenter's *Scaloria rariocostata* was declared a homonym of *Scaloria rariocostata* Lamarck, 1822, which SOWERBY (1844: 93) changed to *Scaloria rariocostata*. CARPENTER (1864: 547), in at least one instance, misspelled the name, calling it *S. rariocosta*. He probably suspected synonymy with his species since he stated "*Scaloria rariocosta* [sic], (length 3.1mm), is perhaps the young of *Scaloria elenensis* Sowerby." The specimen described by Carpenter is a juvenile, found on a *Chama* from Mazatlán, Sinaloa, Mexico. TAPPARONE-CANEFRI (1876: 154) renamed Carpenter's species *Epitonium carpenteri*, but misspelled the original name as *rariocostat*. We are saved the necessity of clearing up the matter because WOOD, 1828 used the spelling *rariocostata* for another species in the same genus. Carpenter's name, in addition to being a primary homonym of Wood, 1828, is also a synonym of *S. elenensis* Sowerby.

DALL (1917: 488) placed *Scaloria rariocostata* Carpenter in the subgenus *Punctiscala*. The misallocation was perpetuated by STRONG (1945: 20) and by KEEN (1958: 276), but was rectified by KEEN (1968: 407) after examining the holotype which lacks spiral punctations and has a worn, chalky appearance.

DALL (1917: 487) described *Epitonium (Asperiscala) thylax*, from Panama, collected by Zetek, but failed to note that his *Epitonium (Nitidiscala) phanium* (1919: 341), collected by C. R. Orcutt at Isla Magdalena, is conspecific. In his description of the latter Dall notes the spiral sculpture but refers to it as "faint incremental lines." Since the US NM did not have specimens of Sowerby's species, Dall had nothing with which to compare his 2 species and did not realize their synonymy. Both Sowerby and Carpenter described their species from worn material in which the fine spiral sculpture is obliterated so that the whorls appear to be smooth.

Beach shells nearly always have the spiral striations so worn that strong magnification is needed to catch a hint of the sculpture. The striations are evident on live-taken specimens. Those from Oaxaca, Mexico, are more robust in appearance than ones from further north along the west Mexican coast. Two lots of live-taken *Epitonium elenense* were examined from the San Blas area, Nayarit, Mexico, collected by Gale Sphon who reported them living among small sea anemones, January, 1970; Anne Craig reported collecting specimens of this species in January 1970 on the face of shelly rock, feeding on sea anemones, and possibly spawning.

The radula of *Epitonium elenense* is in the form of 20 to 40 broad rows of hook-like uncini with some variability in length. The obtuse angles on the teeth are variable in their precise placement (Figure 156).

Type Material:

- Scalaria elenensis*: holotype, BM(NH)
Scalaria varicostata: holotype, BM(NH), Tablet 2040
Epitonium thylax: holotype, USNM 324465
Epitonium (Nitidiscala) phanium: holotype, USNM 218095

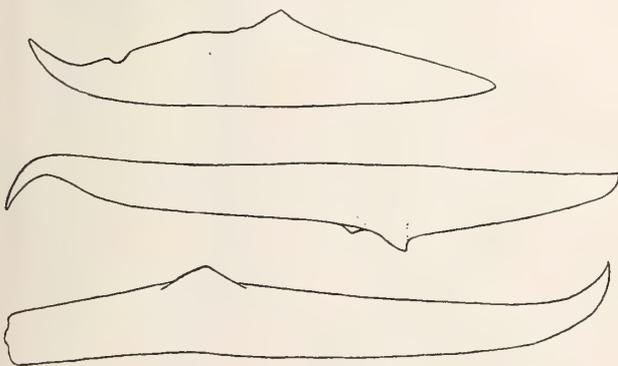


Figure 156

Epitonium (Asperiscala) elenense (Sowerby, 1844)

Uncini tend to be hook-like with some variability in length

Type Localities:

- Scalaria elenensis*: Panama
Scalaria varicostata: Mazatlán, Mexico
Epitonium thylax: Panama
Epitonium (Nitidiscala) phanium: Isla Magdalena, Baja California, Mexico

Geographical Distribution and Ecology: Bahía Concepción and Pulmo Reef, Gulf of California; Mazatlán, Sinaloa, Mexico, south to Panama. Symbiotic with sea anemones.

Bathymetric Range: Intertidal

Geochronological Range: Recent

Epitonium (Asperiscala) emydonesus Dall, 1917

(Figures 31, 32, 33)

- Epitonium (Asperiscala) emydonesus* DALL, 1917: 476; KEEN, 1971: 424; fig. 616
Epitonium (Asperiscala) cf. emydonesus [sic]. - HERTLEIN & STRONG, 1939: 370 [Pleistocene fossil]
Epitonium (Asperiscala) emydonesa [sic]. - STRONG, 1945: 22
Epitonium emydonedum [sic]. - BURCH, 1945: 23
Epitonium (Asperiscala) emydonesus [sic]. - HERTLEIN & STRONG, 1955: 116, 132
Epitonium emydonesus. - DUSHANE & POORMAN, 1967: 424; BOSS *et al.*, 1968: 117; KEEN, 1971: 424; fig. 616
Epitonium (Asperiscala) imperforatum DALL, 1917: 476
Epitonium (Asperiscala) imperforata. - STRONG, 1945: 22
Epitonium imperforatum. - BURCH, 1945: 23; BOSS *et al.*, 1968: 163
Epitonium (Asperiscala) manzanillense HERTLEIN & STRONG, 1951: 88; pl. 3, fig. 13; KEEN, 1958: 272; fig. 95

Original Description: "Shell minute, white, with two smooth, polished nuclear, and four and a half subsequent well-rounded whorls; varices 14, sharp, hardly reflected, not continuous over the suture, slightly crenulated by the spiral sculpture of distinct, close, rounded threads; base rounded, imperforate; aperture rounded. Length, 3.5 mm; diameter, 1.7 mm." (DALL, 1917: 476)

Diagnosis: Shell minute, white, fragile, broadly conic; nuclear whorls 3 to 4, horn color, smooth, glassy; post nuclear whorls 5, convex, rapidly increasing in size; suture deep; spiral threads rounded, strong, close, about 12 on the last whorl; space between threads same width; costae 14 to 21, thin, slightly reflected, sometimes with a slight angle at the shoulder, costae with a sharp angle at the bottom of the last whorl presenting a flat appearance; umbilicus small, hidden by parietal lip which is free from the costae; aperture slightly oval; lip reflected, broad,

lying against the costae on the parietal side, expanded anteriorly; operculum thin, dark, paucispiral. Length, 1 to 4.5 mm; width, 0.5 to 2.5 mm.

Discussion: This is a very small form requiring magnification of at least 20 \times to understand it well. The 3 nominal species, *Epitonium (Asperiscala) emydonesus* Dall, 1917 (p. 476), from the Galápagos Islands, in 72 m, *E. (A.) imperforatum* Dall, 1917 (p. 476), from off La Paz, Gulf of California, in 47 m, and *E. (A.) manzanillense* Hertlein & Strong, 1951 (p. 88; plt. 3, fig. 13), from Manzanillo, Colima, Mexico, in 54 m, have the same characteristic outline with strong spiral threads between the costae, a deep suture and flattened costae at the anterior end where they fuse into a very small umbilical chink, half hidden by the expanded lip. The 3 taxa are believed to be conspecific.

In shape this species somewhat resembles *Epitonium (Asperiscala) bellastratum* Carpenter, but is smaller and lacks the pointed costae of the Californian species. Nearly all collections have representatives of *E. emydonesus*, as it ranges over the entire Panamic-Galapagan province.

Hertlein (HERTLEIN & STRONG, 1939: 370) collected a late Pleistocene fossil specimen of what he tentatively identified as *Epitonium emydonesus*, from Isla San Salvador (James Island), Galápagos Islands, January 11, 1932, on a raised beach, 5 to 10 m above sea level. This appears to be the only fossil record.

Type Material:

Epitonium (Asperiscala) emydonesus: holotype, USNM 194995

Epitonium (Asperiscala) imperforatum: holotype, USNM 211391

Epitonium (Asperiscala) manzanillense: holotype, CAS[GTC] 9616

Type Localities:

Epitonium (Asperiscala) emydonesus: Galápagos Islands

Epitonium (Asperiscala) imperforatum: La Paz, Baja California, Mexico

Epitonium (Asperiscala) manzanillense: Manzanillo, Colima, Mexico

Geographical Distribution and Ecology: Throughout the Gulf of California, Mexico, south to the Galápagos Islands, Ecuador. Usually dredged from a sandy substrate.

Bathymetric Range: Dredged to depths of 72 m.

Geochronological Range: Pleistocene? to Recent

Epitonium (Asperiscala) eutaenium Dall, 1917

(Figures 6, 9, 10, 46)

Epitonium (Nitidoscala) eutaenium DALL, 1917: 479

Epitonium (Nitidoscala) eutaenium. - STRONG, 1945: 25; KEEN, 1958: 274

Epitonium eutaenium. - STRONG, 1945: 27; BOSS *et al.*, 1968: 123

Epitonium (Asperiscala) eutaenium. - KEEN, 1971: 424; fig. 617

Epitonium (Nitidoscala) centronium DALL, 1917: 480

Epitonium (Nitidoscala) centronium. - STRONG, 1945: 25, 27; KEEN, 1958: 273

Epitonium centronium BOSS *et al.*, 1968: 69

Epitonium (Asperiscala) centronium. - KEEN, 1971: 424; fig. 614

Epitonium (Asperiscala) vivesi HERTLEIN & STRONG, 1951: 88; plt. 3, fig. 11; KEEN, 1958: 272; fig. 98

Epitonium vivesi. - DUSHANE, 1962: 45; DUSHANE & POORMAN, 1967: 424; COAN, 1968: 121

Explanation of Figures 11 to 19

Figure 11: *Scalaria regulare* Carpenter, 1856. Syntypes (4), BM [NH] 1950.4.18.13-16; length 7 mm; width 3.3 mm $\times 5.2$

Figure 12: *Epitonium (Asperiscala) tinctorium* Dall, 1919. Lectotype (herein), USNM 218100; length 7 mm; width 3 mm $\times 7$

Figure 13: *Epitonium (Asperiscala) billeeanum* (DuShane & Bratcher, 1965). Holotype, CAS[GTC] 12729; length 7 mm; width, 4 mm; ventral view $\times 9$

Figure 14: *Tubastrea tenuilamellosa* (Milne-Edwards & Haime, 1848), host of *Epitonium billeeanum*. SU[PTC] 30667, collected at Bahía Santa Cruz, Oaxaca, Mexico $\times 1.2$

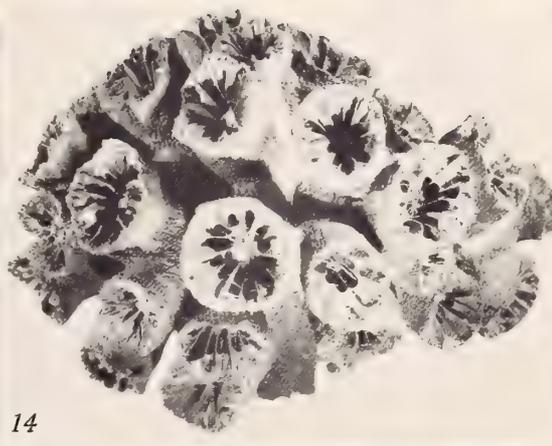
Figure 15: *Epitonium (Asperiscala) billeeanum* (DuShane & Bratcher, 1965). Same shell as in Figure 13, dorsal view $\times 9$

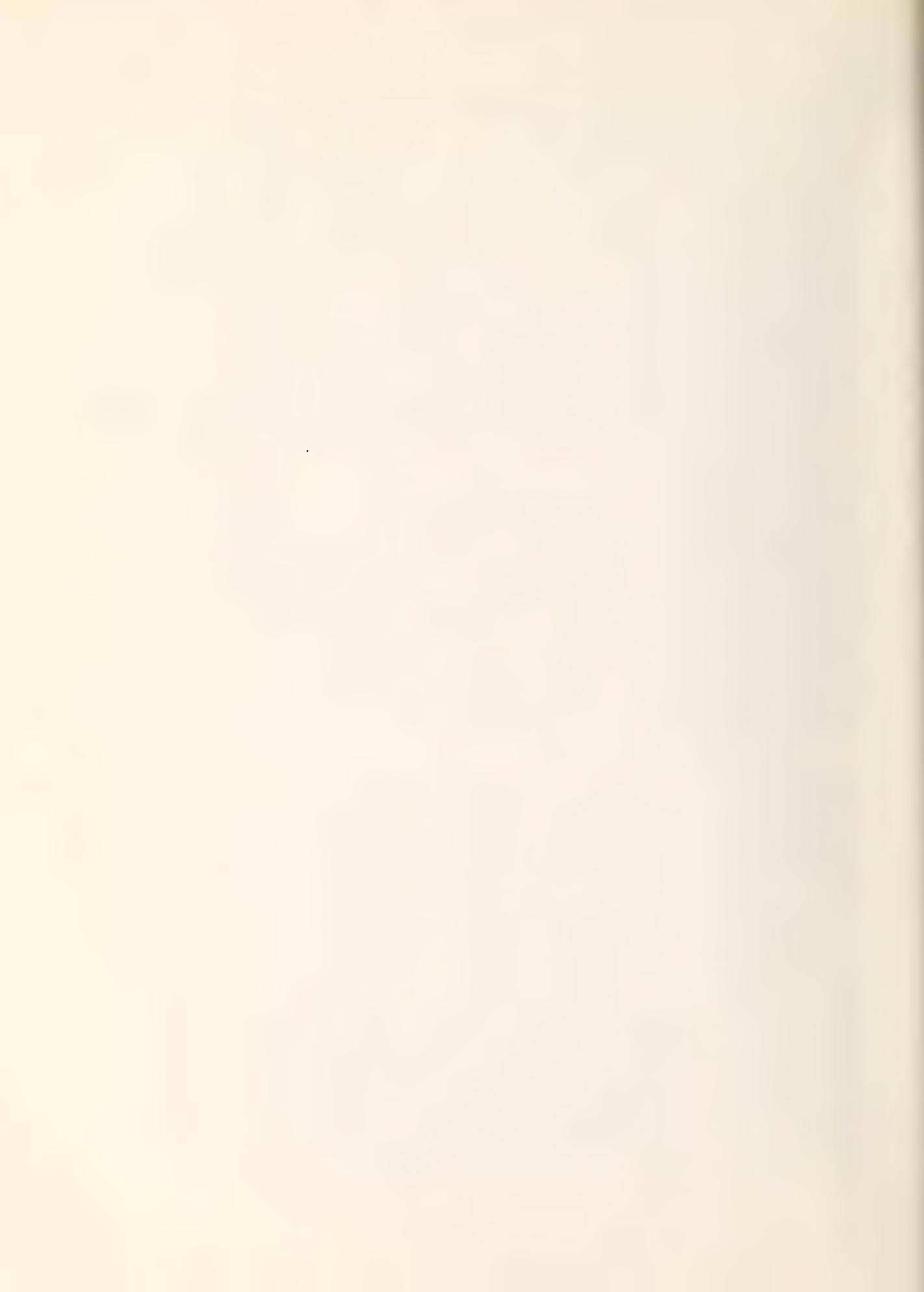
Figure 16: *Epitonium (Asperiscala) walkerianum* Hertlein & Strong, 1951. Puertecitos, Baja California, Mexico (DuShane Collection), length 8 mm; width 2 mm $\times 8.7$

Figure 17: *Epitonium (Asperiscala) walkerianum* Hertlein & Strong, 1951. Holotype, CAS[GTC] 9617; length 3.7 mm; width 1.2 mm $\times 6.7$

Figure 18: *Epitonium (Asperiscala) tinctorium* Dall, 1919. Bahía Concepción, Baja California, Mexico (DuShane Collection), length 6 mm; width 3 mm $\times 11\frac{1}{2}$

Figure 19: *Epitonium zeteki* Dall, 1917. Holotype, USNM 324463; length 6 mm; width 3 mm $\times 11$





Original Description: "Shell small, thin, slender, white, acute, with eight whorls, including the blunt smooth nucleus; varices eight, low, narrow, sharp, continuous over the deep suture into which they dip; a slight angle at the shoulder, the front faces of the varices smooth; aperture transversely oval, the lateral margins slightly produced. Length, 11; diameter, 4mm." (DALL, 1917:479)

Diagnosis: Shell small, slender, acute; nuclear whorls 3, white, opaque; whorls 7 to 8, well rounded, brown-purple on live-taken specimens; costae 7 to 8, white, narrow, extremely reflected with a strongly curved spine between the periphery and the suture, continuous, fusing anteriorly with the expanded lip; suture deep; spiral sculpture definite, dark brown, close on early whorls, further apart and fading on later whorls; aperture oval; lip expanded with a curved spine thickened by the last costa; operculum horn color, thin, paucispiral. Length, 4.2 to 11 mm; width, 2 to 4 mm.

Discussion: *Epitonium (Asperiscala) eutaenium*, *E. (A.) centronium*, both of Dall, and *E. (A.) vivesi* Hertlein & Strong show the same characteristic pattern of coronating costae, spiral sculpture definite and close on the early whorls, further apart and fading on the later whorls, with costae continuous over the base, fusing with the expanded inner lip, well rounded whorls, deep suture. Dall did not designate a type locality for his species, noting only the range as "Gulf of California." One wonders how he happened to overlook the spiral sculpture, erroneously placing his species in the subgenus *Nitidiscala*. Both of Dall's types were dead-taken specimens, therefore he described them as having white shells. Although HERTLEIN & STRONG (1951: 88; plt. 3, fig. 11) described *E. vivesi* from a live-taken specimen, as having a white shell, it is plain in the photograph of the holotype that the whorls are dark and the costae are white with sharply coronating points, easily broken.

This species varies in color from brown with white costae in live-taken specimens to white in dead ones. The few costae and slender outline make it distinct from any other Panamic-Galapagan species described in the subgenus *Asperiscala*. The synonymy of these 3 species has probably been overlooked because Dall's descriptions were based on specimens from which most of the costae and spines had been broken. The second costa from the left on the body whorl and the one directly behind the aperture on the type show the curved spine peculiar to all 3 species. The nuclear whorls of Dall's specimen are lacking although he described a blunt nucleus and mentioned 8 whorls which still remain.

The somewhat similar *Epitonium (Nitidiscala) hindsii* (Carpenter, 1856) usually has a larger shell with the same

number of whorls and costae, but it lacks the spiral sculpture and has more erect costae with less coronation to the spines.

Epitonium (Hirtoscala) reflexum (Carpenter, 1856) cannot be confused with *E. (Asperiscala) eutaenium* because it lacks spiral striations between the costae which, although reflected, are stronger and thicker, particularly near the suture. The Carpenter species consistently has 6 costae.

Type Material:

Epitonium (Nitidiscala) eutaenium: holotype, USNM 201201
Epitonium (Nitidiscala) centronium: holotype, USNM 211395
Epitonium (Asperiscala) vivesi: holotype, CAS[GTC] 9615

Type Localities:

Epitonium (Nitidiscala) eutaenium: Gulf of California, Mexico
Epitonium (Nitidiscala) centronium: Gulf of California, Mexico
Epitonium (Asperiscala) vivesi: San Domingo Point, Santa Inez Bay, Gulf of California, Mexico

Geographical Distribution and Ecology: Throughout the Gulf of California to the Galápagos Islands, Ecuador. Usually dredged on broken shell, weed, sand bottom. One specimen, collected by Dr. Donald Shasky, was crawling on wet sand at night.

Bathymetric Range: 7 to 42 m

Geochronological Range: Recent

Epitonium (Asperiscala) gradatum (Sowerby, 1844)

(Figures 36, 37)

- Scalaria gradata* SOWERBY, 1844a: 99; plt. 34, fig. 109
Scalaria gradata Hinds [sic]. - ADAMS, 1853: 221; NYST, 1871: 111 [from the Philippines]; REEVE, 1873: 19; plt. 1, fig. 2 [Amboyna]; TRYON, 1887: 62; plt. 13, fig. 88
Epitonium (Nitidiscala) gradatum. - KEEN, 1971: 432; fig. 649
Scalaria subnodosa CARPENTER, 1856b: 165; CARPENTER, 1857 a: 284, 336; CARPENTER, 1860: 10
Scalaria nodosa [sic]. - REEVE, 1874: plt. 1, fig. 2; TRYON, 1887: 62; plt. 13, fig. 88
Epitonium (s. l.) subnodosum. - KEEN, 1958: 276
Epitonium subnodosum. - PALMER, 1963: 333
Epitonium (Nitidiscala) subnodosum. - KEEN, 1971: 434
Epitonium (Nitidiscala) gaylordianum LOWE, 1932: 114; plt. 9, figs 3, 3a; STRONG, 1945: 26, 27; WILSON, 1967: 251 [paratypes 595, 3132 - 3136]
Epitonium (Nitidiscala) gaylordianum. - PILSBRY & LOWE, 1932: 120; M. SMITH, 1944: 7, fig. 62
Epitonium (Asperiscala) gaylordianum. - KEEN, 1958: 271; fig. 93
Epitonium (?Asperiscala) gaylordianum. - KEEN, 1971: 426; fig. 618

Original Description: "*T. pyramidalis, acuminata, laevi, imperforata; anfractibus numerosis, prope suturam elevatis; sutura profunda; varicibus rotundatis, sub-numerosis, distantibus, superne angulatis; apertura sub-ovali, postice angulata, labio interno tenui, colore albo.*"

"The whorls of this elegant species are elevated near the suture, and with the angles on the varices, have the appearance of steps. Brought by Mr. Hinds, from Amboyna." (SOWERBY, 1844: 99)

Diagnosis: Shell large for the subgenus, white; outline somewhat turreted; nuclear whorls nearly always broken; subsequent whorls 7 to 12, rounded; costae 12 to 16, slightly reflected; incised spiral lines indistinct between the costae, about 18 on the body whorl, tending to disappear near the suture and near the aperture, narrower than the raised cords; aperture oval, peritreme complete; outer lip reflected. Length, 23.4 to 35mm; width 7 to 12mm.

Discussion: The original assignment of *Scalaria gradata* Sowerby, 1844 to the Philippines (type locality) was an error perpetuated by Reeve, Tryon, and others. The allocation of the species to Ecuador by Sowerby (in the BMNH) would seem to be more nearly correct. Both REEVE (1873) and TRYON (1887: 62) noted that "*Scalaria nodosa* Carpenter," 1856b [*Epitonium subnodosum* (Carpenter, 1856), type locality, Panama] is probably a synonym of *S. gradata*. The dimensions are the same and the microscopic spiral sculpture could have been overlooked by early workers, particularly with beach worn shells. Carpenter had only one shell from which to draw his conclusions. This holotype seems to have been lost and there is no figure of it.

LOWE (1932: 114) described *Epitonium (Nitidiscala) gaylordianum*, a beach specimen from Montijo Bay, Panama, with a "trace of indistinct spiral incised lines." Apparently Lowe was not convinced of the validity of its assignment to the subgenus *Asperiscala*. Two specimens from Panama, in the author's collection, show very worn spiral cords, unevenly spaced, between which are very fine incised lines. This is probably an offshore species which accounts for the fact that specimens recovered have been dead and beachworn.

Type Material:

Scalaria gradata: syntype, BM(NH)

Scalaria subnodosa: holotype, lost

Epitonium (Nitidiscala) gaylordianum: holotype, ANSP
157987

Type Localities:

Scalaria gradata: Ecuador

Scalaria subnodosa: Panama

Epitonium (Nitidiscala) gaylordianum: Montijo Bay, Panama

Geographical Distribution and Ecology: Panama and Ecuador. The habitat is unknown; no live-taken specimens have been available.

Bathymetric Range: Unknown

Geochronological Range: Recent

Epitonium (Asperiscala) habeli Dall, 1917

(Figures 50, 51)

Epitonium habeli DALL, 1917: 483; STRONG, 1945: 27; BOSS *et al.*, 1968: 146

Epitonium (Nitidiscala) habeli. - STRONG, 1945: 26

Epitonium (Asperiscala) habeli. - KEEN, 1971: 426; fig. 619

Epitonium (Asperiscala) kelseyi BAKER, HANNA & STRONG, 1930: 48; pl. 2, fig. 7; STRONG, 1945: 22, 23; KEEN, 1958: 271; fig. 94; DUSHANE, 1970: 332

Original Description: "Shell small, acute, conical, white, with five rounded whorls exclusive of the (lost) nucleus; varices 16, low, rather thick, not reflected or angular, continuous over the suture and making about half the circuit of the spire; upper whorls delicately spirally striate, the sculpture becoming obsolete on the fourth and entirely absent from the last whorl; base rounded, with a small umbilical perforation; aperture rounded, the reflected margin produced near the axis in front. Length, 7.5; diameter, 4mm." (DALL, 1917: 483)

Diagnosis: Shell of medium size, thin, shiny, white, conic; nuclear whorls 3, white, opaque; post-nuclear whorls 5 to 8, rounded; costae 13 to 18, narrow over the whorls, expanded at the suture, with a small twisted tubercle at the shoulder; spiral threads between costae fine, irregular, more evident on the early whorls, less so on the 4th, 5th, 6th whorls, absent on the last 2 whorls; suture deep; aperture oval; lip expanded, thin, basal portion patulous; umbilicus partially hidden by expansion of parietal lip; operculum thin, horn colored, paucispiral. Length, 7.5 to 12.5 mm; width, 4 to 6 mm.

Discussion: The spaces between the threads are about 3 times greater than the width of the ridge. The threads become less noticeable on each succeeding whorl, until on the last whorl they usually disappear entirely. The deep suture and small, deep umbilicus, partially hidden, are characteristic of this species. The rounded tubercles on the costae mentioned by BAKER, HANNA & STRONG (1930:

48; type locality, San Francisco Island, Gulf of California, Mexico) are most peculiar, being twisted. Dall's worn specimen (type locality: Galápagos Islands) does not show this character, but in all other respects is identical. A relatively common species, *Epitonium (Asperiscala) habeli* Dall has gone undetected in many collections or has been erroneously assigned to the synonymous *E. (A.) kelseyi*.

Type Material:

Epitonium habeli: holotype, USNM 56055

Epitonium (Asperiscala) kelseyi: holotype, CAS[GTC] 4766

Type Localities:

Epitonium habeli: Galápagos Islands, Ecuador

Epitonium (Asperiscala) kelseyi: San Francisco Island, Gulf of California, Mexico

Geographical Distribution and Ecology: Gulf of California, Mexico to the Galápagos Islands, Ecuador.

Bathymetric Range: Intertidal to depths of 12 m

Geochronological Range: Recent

Epitonium (Asperiscala) huffmani

DuShane & McLean, 1968

(Figure 5)

Epitonium (Asperiscala) huffmani DUSHANE & McLEAN, 1968: 1, 2; fig. 1; DUSHANE, 1970: 3; SPHON, 1971: 11; KEEN, 1971: 426; fig. 620

Original Description: "Shell small, brown, periostracum lacking; nuclear whorls two, smooth, brown, glassy; third whorl white, axially ribbed; the following five whorls brown, strongly convex, rapidly enlarging, thin and fragile, with fine, white axial costae and white raised spiral threads between the costae, forming small, precise rectangles when intercepted by the costae; the final whorl lighter in color and the base of the shell fading to white adjacent to the columella; shell lacking a basal ridge; outer lip thin and white; umbilicus lacking; operculum missing in holotype. Dimensions (in mm): length 11, width 7 (holotype)." (DUSHANE & McLEAN, 1968: 1)

Diagnosis: An *Epitonium* distinguished from other west American species in having few, rapidly expanding, convex whorls, brown ground color, numerous low, white, axial ribs (about 50 on the last whorl), and fine white spiral ribs, the axial and spiral ribs forming small exact rectangles. Length, 4 to 11 mm; width, 2.5 to 7 mm.

Discussion: Since the original description was published, additional specimens of this species have been found:

At Guaymas, Sonora, Mexico, Anne Craig collected several specimens intertidally, freshly dead, with nuclear whorls intact, aperture stained with purple, which would suggest a possible symbiotic relationship with sea anemones; length, 11 mm; width, 7 mm.

At Puertecitos, Baja California, Joseph DuShane collected 2 dead specimens intertidally, October, 1970; length, 8 mm; width, 4.5 mm; and length, 6 mm; width, 4 mm.

On Venado Island, Panama, Dr. Donald Shasky collected 1 specimen intertidally, March, 1970; length, 4 mm; width, 2.5 mm.

At Salinas, Ecuador, Dr. Judith Terry Smith collected 1 specimen intertidally on the *Te Vega* Expedition, April 15, 1968; length, 5.5 mm; width, 3.5 mm.

On the north side of Santa Cruz Island, Galápagos Islands, Ecuador, Jacqueline DeRoy took 1 specimen intertidally, October, 1967; length, 11 mm; width, 7 mm.

No longer considered to be a rare species, further search may reveal live specimens from which we can determine the habitat of *Epitonium (Asperiscala) huffmani*.

Type Material:

Epitonium (Asperiscala) huffmani: holotype, LACM 1159

Type Locality:

Epitonium (Asperiscala) huffmani: Bahía Adair, Sonora, Mexico, lat. 31°21'N, long. 113°40'W

Geographical Distribution and Ecology: Throughout the Gulf of California, Mexico, south to the Galápagos Islands, Ecuador. No specific habitat is known.

Bathymetric Range: Intertidal

Geochronological Range: Recent

Epitonium (Asperiscala) indistinctum (Sowerby, 1844)

(Figures 27, 28, 29, 30)

Scalaria indistincta SOWERBY, 1844a: 95; pl. 35, fig. 141; SOWERBY, 1844b: 27; CARPENTER, 1857a: 285, 288, 336; CARPENTER, 1860: 10; NYST, 1871: 115; REEVE, 1873: pl. 14, fig. 109; TRYON, 1887: 61; pl. 12, fig. 76; DALL, 1917: 487

Scala indistincta. -H. & A. ADAMS, 1853: 221; DEBOURY, 1912: 183

Epitonium indistinctum. -STRONG, 1945: 23

Epitonium (s. l.) indistinctum. -KEEN, 1958: 276; fig. 147

Epitonium (Asperiscala) indistinctum. - KEEN, 1971: 426; fig. 621

Acirsa albemarlensis DALL & OCHSNER, 1928: 110; pl. 6, fig. 4 (Pleistocene fossil); BOSS *et al.*, 1968: 17

Epitonium chalceum OLSSON & SMITH, 1951: 44; pl. 3, fig. 3

Epitonium (s. l.) chalceum. - KEEN, 1958: 276; fig. 147

Original Description: "*T. elongata, imperforata, minute spiraliter striata; anfractibus numerosis, gradatim crescentibus, sutura distincta; varicibus numerosis, inaequalibus, rotundatis, decumbentibus, simplicibus; apertura parva, labio interno, antice sub-incrassato; colore albo.*" (SOWERBY, 1844a: 27)

Diagnosis: Shell white, elongate, acute, large; nuclear whorls 2½ to 4, horn color; following whorls convex, 7 to 10, thin, fragile, costae numerous, 23 to 32, thickened at the suture; a narrow brown line adjacent to and just below the suture occurring on all but the nuclear whorls; spiral sculpture of fine raised threads crenulating the costae slightly, evenly spaced; intersection of axial and spiral sculpture forming small rectangles within which are minute growth lines and spiral threads producing a textured appearance; aperture round; base imperforate; peritreme thin, incomplete, slightly patulous anteriorly; basal disk lacking, operculum dark brown, paucispiral.

Discussion: Comparison of a photograph of *Scaloria indistincta* (type locality San Blas, Nayarit, Mexico) with the types of *Acirsa albemarlensis* (Pleistocene fossil, type locality Galápagos Islands, Ecuador) and *Epitonium chalceum* (type locality Panama) indicates that these 3 taxa are conspecific. All show the same thickening of the costae at the sutures, with thread-like spiral sculpture, an imperforate base and approximately the same number of costae per whorl. The type of *S. indistincta* measures: length, 14 mm; width, 4½ mm; of *A. albemarlensis*, length, 10½ mm; width, 4.0 mm; while that of *E. chalceum* measures length, 23 mm; width, 7 mm.

This is apparently a rare species, probably not more than a dozen specimens having been reported since Sowerby described it in 1844. The narrow brown line, close to and just below the suture, was not mentioned by either DALL & OCHSNER (1928), or by OLSSON & SMITH (1951). Possibly the brown coloring had faded, as it does in *Epitonium (Asperiscala) tinctorium* Dall, by the time they had received the specimens for study. This species would seem to fit into the subgenus *Scalina* were it not for the fact that it has no basal disk.

Since so few specimens are known, it seems desirable to report here 4 that have been collected recently:

A small specimen (length, 4 mm; width, 1½ mm) was taken by Anne Craig, January 1970, at Matanchén Bay,

Nayarit, Mexico (3.2 km south of San Blas, the type locality). Attached by a thread, the *Epitonium* appeared to be feeding on the sea anemones living on the face of rocks and boulders. It has 2½ horn-colored, glassy, nuclear whorls and 6 postnuclear whorls. *E. (Asperiscala) elenense* (Sowerby) was found rather commonly under the same circumstances at the same locality.

A juvenile specimen of the same species was dredged off Acapulco, Mexico, in 81 m and has 4 white, opaque nuclear whorls, with 5 postnuclear whorls; length, 2½ mm; width, 0.75 mm (Anne Craig collection).

Dr. Donald Shasky took a crab-inhabited specimen at Venado Island, Panama in March, 1970 (length, 6 mm; width, 2½ mm). The 4 nuclear whorls are opaque white in color, enlarging rapidly, with distinct sutures between whorls. The 6 postnuclear whorls enlarge gradually. The shell is elongate with no umbilicus. The closely spaced costae merge into the perimeter of the slightly reflected, thin lip.

Laura and Carl Shy dredged a living specimen at 29 m off Manzanillo, Colima, Mexico in December, 1967 (length, 16 mm; width, 5½ mm).

Type Material:

Scaloria indistincta: holotype, BM(NH);

Acirsa albemarlensis: holotype, CAS[GTC] 2927

Epitonium chalceum: holotype, University of Alabama (Mus. Nat. Hist) 15597 (ex Maxwell Smith private collection)

Type Localities:

Scaloria indistincta: San Blas, Nayarit, Mexico

Acirsa albemarlensis: Galápagos Islands, Ecuador

Epitonium chalceum: Panama

Geographical Distribution and Ecology: From San Blas, Nayarit, Mexico south to Panama and the Galápagos Islands, Ecuador. Little is known about this species other than the material given above.

Bathymetric Range: Intertidal to 81 m.

Geochronological Range: Pleistocene to Recent.

Epitonium (Asperiscala) lowei (Dall, 1906)

(Figures 42 and 157)

Scala lowei DALL, 1906: 44; ORCUTT, 1915: 173; BOSS *et al.*, 1968: 191

Epitonium lowei. - DALL, 1917: 475; KEEN, 1937: 35; OLDROYD, 1927: 56; pl. 31, fig. 1

Asperoscala lowei. - DALL, 1921: 114; pl. 6, fig. 11

Epitonium (Asperiscala) lowei. - STRONG, 1922: 155; STRONG, 1945: 22, 23; BERRY, 1956: 153 (reprint) [as *cf. lowei*]; KEEN, 1971: 426; fig. 623

Original Description: "Shell small, conic, with five or more rapidly increasing whorls after the (lost) nucleus; color white, whorls very convex with deep sutures and a small, spiral umbilicus; there is no basal disk or cord; sculpture of about twenty-seven rather thick, strongly reflected, smooth, close-set varices, and very close, fine, spiral threads, covering the whole whorl between the varices, and separated by about equal sulci; aperture sub-circular, slightly higher than wide, the reflected margin wide at the outer lip, patulous at the inner base, narrow between the shoulder and the preceding whorl, and at the shoulder produced into a short, rather stout spine which, repeated on successive varices, coronates the whorls. Length (without nucleus), 7.0mm, diameter, 4.0mm." (DALL, 1906: 44)

Diagnosis: Shell medium in size, white, conic; nuclear whorls 4, white; in most cases the 4th nuclear whorl shows fine axial costae, with here and there a heavier one; teleoconch of 5 to 9 whorls, rapidly enlarging, convex; costae 25 to 32, strongly reflected with occasionally a heavier costa, with a spine at the whorl shoulder on all costae; raised spiral ridges between the costae, unevenly spaced, forming rectangles within which are 2 fine horizontal threads (magnification $\times 40$); sulci twice the width of the ridges; suture deep; umbilicus deep, spiral; aperture oval; lip thin, reflected, patulous at base, with a pointed spine at the shoulder; operculum dark brown, thin and paucispiral. Length, 3 to 17 mm; width, $1\frac{1}{2}$ to 9 mm. The radula of this species is rectangular, with compressed, conical, horn-like teeth, about 20 in one row (Figure 157).

Discussion: This species varies considerably in size. It resembles *Epitonium (Asperiscala) bellastriatum* (Carpenter [1864: 660] but has more numerous and more reflected costae, with much finer ridges between the costae, spaced farther apart. Both species belong to an offshore fauna. *Epitonium lowei* is usually associated with a marine fauna that extends from Anacapa Island, California to Punta Abreojos, Baja California, Mexico, and is rarely taken in the northern portion of the Gulf of California, Mexico. One live-taken specimen (length, 17 mm; width, 9 mm) was dredged at Bahía de Los Angeles, Gulf of California in 72m (DuShane Collection). One live-taken specimen (length, 5 mm; width, 2½ mm) (Shasky Collection) extends the range to Panama.

The original specimen of *Epitonium (Asperiscala) lowei* was returned to Lowe after a figure had been drawn of it. A second specimen was sent by Lowe (DALL, 1906: 44) from the same type locality (Avalon, Catalina Island, California), which became the "cotype." It has the same measurements as the original specimen. Apparently the

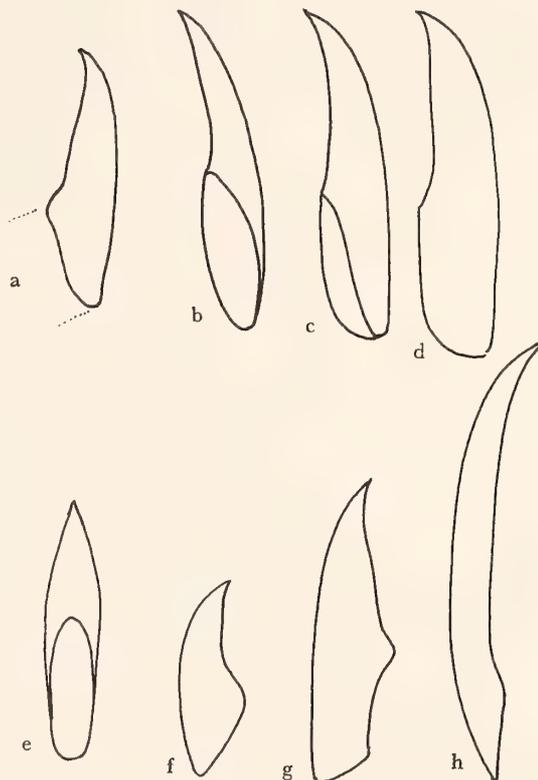


Figure 157

Epitonium (Asperiscala) lowei (Dall, 1906)

There are about 20 compressed, conical uncini in the row
a: area of attachment; b-c-d: tooth revolved from lateral to $\frac{3}{4}$ -view; e: tooth seen from attachment area; f: tooth from central area of ribbon; g: tooth from outer area of ribbon; h: orientation of tooth uncertain

holotype (Lowe Collection) is lost; the San Diego Museum of Natural History does not have it as might be supposed (*teste* Radwin).

Type Material:

Scala lowei: "cotype", USNM 191548

Type Locality:

Scala lowei: off Catalina Island, California

Geographical Distribution and Ecology: From Anacapa Island, California, to Punta Abreojos, Baja California,

Mexico; rarely in the Gulf of California and at Panama. Usually dredged from a sand bottom.

Bathymetric Range: 72 to 108m.

Geochronological Range: Recent

Epitonium (Asperiscala) macleani DuShane, 1970

(Figures 34, 35)

Epitonium (Asperiscala) macleani DUSHANE, 1970: 3; fig. 2;
SPHON, 1971: 11; KEEN, 1971: 426, fig. 624

Original Description: "Shell small, white, fragile, with approximately 32 fine costae of varying size, nuclear whorls two, smooth, rounded, light brown, first postnuclear whorl with axial striations; remaining whorls six; suture distinct, deeply impressed; umbilicus small and nearly covered by peritreme; surface between whorls with raised spiral threads, approximately 28 on the body whorl; whorls rapidly expanding, rounded, basal disk or cord lacking; aperture oval (lip broken in holotype); operculum unknown. Dimensions (in mm): length 7.0; width 3.5 (holotype)." (DUSHANE, 1970: 3)

Diagnosis: A species of small individuals, differing from all others in having rounded whorls, numerous low axial costae of differing strengths and numerous fine raised spiral threads, the same distance apart as the width of the sulci.

Discussion: This species seems to be restricted in range to the lower part of the western side of the Gulf of California, from Escondido Bay around the end of the peninsula of Baja California as far as Ventana Bay, but dredgings may well extend the range. The shells are extremely small and fragile, and previously may have been overlooked or broken by the contents of a dredge. An unidentified specimen of CARPENTER (1857b: 447) and figured in BRANN (1966: 74, fig. 566) could easily be *Epitonium (Asperiscala) macleani* although not reported to be from Mazatlán at this time.

Epitonium macleani is less globose than the brownish colored *E. (Asperiscala) huffmani* DUSHANE & McLEAN (1968: 1, 2; fig. 1); it has a white shell and somewhat similar sculpture. From *E. (A.) emydonesus* DALL (1917: 476) it differs in having more rounded whorls, a small but distinct umbilicus, and it lacks the flattened costae at the anterior end.

The 9 specimens collected by McLean, Oringer and Marincovich off Ventana Point, Baja California, Mexico, April, 1966, were all damaged in varying degrees. No

living specimens were taken. Thirteen dead specimens, dredged by DuShane in 18m on sand and broken shell bottom in February, 1971, off Escondido Bay, Baja California, Mexico, extended the range approximately 400 km north of the type locality. Five of these specimens are undamaged.

Type Material:

Epitonium (Asperiscala) macleani: holotype, LACM 1197

Type Locality:

Epitonium (Asperiscala) macleani: off Ventana Point, Baja California, Mexico (opposite Cerralvo Island), 24°04'N, 109°49'W

Geographical Distribution and Ecology: Southern end of the Gulf of California, to Ventana Bay, Baja California, Mexico. Dredged on sand and broken shell bottom.

Bathymetric Range: From 27 to 45 m in depth.

Geochronological Range: Recent

Epitonium (Asperiscala) minutica (deBoury, 1912)

(Figures 20 to 26)

Scala (Viciniscala?) minutica DEBOURY, 1912: 87; pl. 7, fig. 1

Scala minutica DEBOURY, 1919: 40

Epitonium (Asperiscala) minutica [sic]. - KEEN, 1971: 426; fig. 625

Epitonium pacis DALL, 1917: 476; BOSS *et al.*, 1968: 236; KEEN, 1971: fig. 625

Epitonium (Asperiscala) pacis. - STRONG, 1945: 22, 23; KEEN, 1958: 272; fig. 96

Epitonium onchodes DALL, 1917: 476; ZETEK, 1918: 25; BOSS *et al.*, 1968: 229

Epitonium (Asperiscala) onchodes. - STRONG, 1945: 23; HERTLEIN & STRONG, 1951: 88

Epitonium clarki T. S. OLDROYD, 1921: 115; pl. 5, fig. 13 [upper Pleistocene fossil] [not *Dentiscala clarki* Olsson & Smith, 1951]

Epitonium (Asperiscala) clarki. - GRANT & GALE, 1931: 857; DURHAM, 1937: 490

Epitonium cedrosensis JORDAN & HERTLEIN, 1926: 446; pl. 30, fig. 3 [Pliocene fossil]

Epitonium (Asperiscala) cedrosense. - GRANT & GALE, 1931: 857; DURHAM, 1937: 489

Epitonium dallasi JORDAN & HERTLEIN, 1926: 447; pl. 30, fig. 2 [Pliocene fossil]

Epitonium (Asperiscala) dallasi. - GRANT & GALE, 1931: 857; DURHAM, 1937: 489

Epitonium nesioticum DALL & OCHSNER, 1928: 111; pl. 6, figs. 5, 6 [Pleistocene fossil] [not *Dentiscala nesiotica* Dall, 1917]; BAKER, HANNA & STRONG, 1930: 48; BOSS *et al.*, 1968: 219

Original Description: "*S. testa alba, tenuis, paulum translucens, sat fragilis, elongata-conica, anguste sed profunde umbilicata, sutura sat obliqua, angusta et omnino disjuncta; anfract. summis costarum tantum commissi. Anfract. embryonales deficientes. Sequentes 6, valde convexi costis mediocriter obliquis, sat distantibus, tenuibus, acutis, vix prominuis ornat. Transversim nonnullae striae spirales, sat crebre dispositae adsunt. Ult. anfract costis 21 munitus. Basis convexa, funiculo circumbasati omnino destitutus. Columella funiculo nullo firmata. Apertura rotundata. Peristoma internum continuum et foliaceum. Peristoma externum tenue. Long. 35 mm, diam. maj. 17 mm. Habitat. - West Columbia."*

Diagnosis: Shell medium to large, horn color or white, with 3 brown, glassy, conic, nuclear whorls; 7 to 8 well-rounded body whorls; suture deep; costae 13 to 21, white, reflected, with wide interspaces, true varices at irregular intervals, short, sharp spine in front of suture; spiral sculpture of about 20 sharp threads on the last whorl, with wider interspaces in which there are about 8 axial striae crossing the threads between the costae and about 5 horizontal striulae within each rectangle; there is a smooth space in front which has no sculpture other than the costae and the axial striae, this is repeated around the narrow but deep umbilicus; aperture oval; reflected lip continuous, free from the costae, with a sharp spine; operculum dark brown, paucispiral. Length, 3 to 35 mm; width, 1½ to 17 mm.

Discussion: This is a commonly dredged species, with a wide range. It has been named and renamed, both as a fossil and as a Recent species, but deBoury appears to be the earliest author. DALL (1917: 476) named this species *Epitonium pacis*, from the vicinity of La Paz, Gulf of California, Mexico, dredged in from 18 to 81 m. His description agrees in every particular with that of deBoury. Dall also named a juvenile conspecific specimen from Panama Bay, *Epitonium onchodes*, the same year, probably without realizing the wide range of *E. (Asperiscala) minutica*. Dall's *E. onchodes* was dredged in 112 m on sand bottom; length, 3 mm; width, 1½ mm. T. S. OLDROYD (1921: 115) named and described a Pleistocene fossil from beds at Santa Monica, California, *E. clarki*; length, 19 mm; width, 8 mm. His description includes the characteristic fading of sculpture adjacent to the sutures, the short, sharp spines on the costae and the deep umbilicus. This species is also commonly reported from the Del Rey exposure, San Pedro, California, and from the General and Gaffey Avenues district, Los Angeles, California. JORDAN & HERTLEIN (1926: 446, 447) described 2 Pliocene fossils from Baja California (outer coast): *E. cedrosensis*, from Bernstein's Abalone Camp, Cedros Island

(length, 8½ mm; width, 3¼ mm); and *E. dallasi* (length, 7 mm; width, 4 mm) from 1.6 km southeast of Turtle Bay. Four whorls remain of each of the specimens. They show the rounded whorls, with definite spiral sculpture, reflected costae, although badly worn, and the pointed spine just short of the suture, the typical umbilicus, and the heavy outer lip with the spine at the top of the aperture. *Epitonium dallasi*, with 16 costae, is an extremely worn specimen showing much abrasion; *E. cedrosensis*, with 13 costae is well within the range of variability found in *E. minutica*. This species occurs in the Recent fauna off Cedros Island.

DALL & OCHSNER (1928: 11) described *Epitonium nesioticum* [not *Dentiscala nesiotica* Dall, 1917] from 4 specimens obtained by Ochsner from a Pleistocene deposit on Isla Isabela (Albemarle Island), the Galápagos group, Ecuador (length, 7½ mm; width, 3½ mm). To quote Ochsner in DALL & OCHSNER (1928: 11): "This species belongs to the Recent group of the genus which is typified on the California coast by *Epitonium bellastratum* (Carpenter)." DURHAM (1937: 490) suggests that *E. bellastratum*, *E. (Asperiscala) hemphilli* (Dall) and *E. (A.) clarki* T. S. Oldroyd are "all closely related, and it is possible that more material may show a gradation from one to another." It is interesting to note that the fossil forms of *E. (A.) minutica* occur north of Cedros Island; the Recent forms are not taken here, although they occur on the Galápagos Islands, Ecuador, both fossil and Recent. Neither *E. hemphilli* nor *E. bellastratum* occurs at the Galápagos Islands. There is no record of which I am aware of *E. minutica* being collected alive north of Cedros Island. One live specimen of this species was taken by the Allan Hancock Pacific Expeditions (*Velero III*), off Cedros Island at station 1705-49.

Type Material:

- Scala (Viciniscala?) minutica*: holotype, Zool. Mus. Berlin, Germany, no. 302 (fide deBoury)
Epitonium pacis: holotype, USNM 96821
Epitonium onchodes: holotype, USNM 211786a
Epitonium clarki: holotype, SU[PTC] 5948
Epitonium cedrosensis: holotype, CAS[GTC] 2116
Epitonium dallasi: holotype, CAS[GTC] 2122
Epitonium nesioticum: holotype, CAS[GTC] 2928

Type Localities:

- Scala (Viciniscala?) minutica*: west Colombia
Epitonium pacis: La Paz, Gulf of California, Mexico
Epitonium onchodes: Panama Bay
Epitonium clarki: Santa Monica, California
Epitonium cedrosensis: Bernstein's Abalone camp, Cedros Island, Mexico
Epitonium dallasi: Turtle Bay, Baja California, Mexico
Epitonium nesioticum: Isla Isabela (Albemarle Island), Galápagos Islands, Ecuador

Geographical Distribution and Ecology: Southern California (fossil), Cedros Island, Baja California, Mexico (fossil and Recent), south to Magdalena Bay (Recent), east side of Gulf of California (Recent), west coast of Mexico (Recent), Galápagos Islands (Recent and fossil). Dredged on sand and broken shell bottom.

Bathymetric Range: 18 to 137 m.

Geochronological Range: Pleistocene, Pliocene, Recent.

Epitonium (Asperiscala) obtusum (Sowerby, 1844)

(Figures 43, 44, 45, 49)

Scalaria obtusa SOWERBY, 1844a: 98; pl. 33, fig. 54; SOWERBY, 1844b: 29; C. B. ADAMS, 1852: 198 (reprint); CARPENTER, 1857a: 274, 336; CARPENTER, 1860: 10; NYST, 1871: 125; REEVE, 1873: pl. 7, figs. 48a, 48b; TRYON, 1887: 58; pl. 12, fig. 61

Scala obtusa. - H. & A. ADAMS, 1853: 221

Scalaria obtusa C. B. ADAMS [not Sowerby]. - CARPENTER, 1864a: 358 [reprint 1872: 173]

Epitonium obtusum. - DALL, 1909: 190, 223

Epitonium (Nitidiscala) obtusum. - STRONG, 1945: 25, 27; KEEN, 1971: 432; fig. 653

Epitonium (s. l.) obtusum. - KEEN, 1958: 276; fig. 149

Scalaria tiara CARPENTER, 1856b: 164; CARPENTER, 1857a: 284, 336; CARPENTER, 1860: 10; CARPENTER, 1864c: 624 [as *S? tiara*] [Reprint 1872: 110]

Epitonium (Nitidiscala) tiara. - DALL, 1917: 480 [not Panamic]; DALL 1921: 111 [as *E. (N)? tiara* (Carpenter)]; OLDROYD, 1927: 59 [not Panamic]; PALMER, 1958: 28, 188 [*E. (N.) ? tiara*]

Epitonium tiara. - ZETEK, 1918: 25; STRONG, 1922: 159; KEEN, 1937: 35 [not Panamic]; PALMER, 1963: 332; pl. 67, figs. 7, 8

Epitonium (Nitidiscala) tiara. - STRONG, 1930: 190; BURCH, 1945: 30 [not Panamic]; KEEN, 1958: 274

Epitonium (Nitidiscala) roberti DALL, 1917: 485; PILSBRY & LOWE, 1932: 120

Epitonium robertsi [sic]. - M. SMITH, 1944: 7

Epitonium (Nitidiscala) roberti. - STRONG, 1945: 25, 27; KEEN, 1958: 274; fig. 130; KEEN, 1971: 434; fig. 656

Epitonium roberti. - BOSS *et al.*, 1968: 485

Original Description: "*T. ventricosa, pyramidali, imperforata, laevi, anfractibus contiguis; varicibus numerosis, crassis, rotundatis, continuis, superne sub-angulatis; apertura rotundata, antice sub-marginata, labio interno spiraliter recurvo; colore albo.*"

"Rather short and thick, white, with numerous varices, which continue up the spire, from whorl to whorl, and are slightly angular above; the inner lip of the aperture is spirally twisted, and forms an undulated notch at its juncture with the outer lip." (SOWERBY, 1844: 29)

Diagnosis: Shell medium to large in size, pyramidal, heavy, solid, white; nuclear whorls $1\frac{1}{2}$ to $2\frac{1}{2}$; following 3 whorls showing spiral ribs on each whorl, often extending to the 4th whorl; remaining 4 to 5 whorls somewhat glassy, with no spiral sculpture between, rapidly expanding; costae usually 10 to 14, slightly reflected, heavy, continuous, angular at the shoulder on most specimens, live-taken specimens having a definite spine on all costae; base of last whorl marginated by an inconspicuous cord or incised line between the costae on some specimens, more obvious on small specimens; aperture oval; lip slightly reflected, almost obsolete where the costae join the inner lip, patulous, with a wrinkled fasciole at the anterior end, operculum thin, paucispiral. Length, 11 to 25 mm; width, $8\frac{1}{2}$ to 10 mm.

Explanation of Figures 20 to 30

Figure 20: *Scala (Viciniscala?) minutica* deBoury, 1912. Holotype, Berliner Zoologisches Museum, Germany, no. 302 (after DEBOURY, 1912, Journ. de Conchyl. 60 (2): pl. 7, fig. 1), length 35 mm; width 17 mm $\times 2.4$

Figure 21: *Epitonium pacis* Dall, 1917. Holotype, USNM 96821; length $12\frac{1}{2}$ mm; width 6 mm $\times 4\frac{1}{2}$

Figure 22: *Epitonium clarki* T. S. Oldroyd, 1921. Holotype, SU [PTC] 5948 (Pleistocene fossil); length 19 mm; width 8 mm $\times 2\frac{1}{2}$

Figure 23: *Epitonium onchodes* Dall, 1917. Holotype, USNM 211786a; length 3 mm; width $1\frac{1}{2}$ mm $\times 20$

Figure 24: *Epitonium dallasi* Jordan & Hertlein, 1926. Holotype, CAS[GTC] 2122; length 7 mm; width 4 mm $\times 9$

Figure 25: *Epitonium cedrosensis* Jordan & Hertlein, 1926. Holotype, CAS[GTC] 2116 (Pliocene fossil); length $8\frac{1}{2}$ mm; width $3\frac{3}{4}$ mm $\times 6\frac{1}{2}$

Figure 26: *Epitonium nesioticum* Dall & Ochsner, 1928. Holotype, CAS[GTC] 2928 (not *Dentiscala nesiotica* Dall, 1917); length 7 $\frac{1}{2}$ mm; width 3.3 mm $\times 9$

Figure 27: *Epitonium (Asperiscala) indistinctum* (Sowerby, 1844). Manzanillo, Colima, Mexico (Shy Collection); length 16 mm; width $5\frac{1}{2}$ mm $\times 5\frac{1}{2}$

Figure 28: *Scalaria indistincta* Sowerby, 1844. Holotype, BM[NH]; length 14 mm; width $4\frac{1}{2}$ mm $\times 4.1$

Figure 29: *Acirsa albemarlensis* Dall & Ochsner, 1928. Holotype, CAS[GTC] 2927; length $10\frac{1}{2}$ mm; width 4.0 mm $\times 6.2$

Figure 30: *Epitonium chalconeum* Olsson & Smith, 1951. Holotype, Univ. of Alabama (Mus. Nat. Hist.) 15597 (ex Maxwell Smith Collection); length 23.7 mm; width 7 mm $\times 3$



Discussion: Although KEEN (1971), at the author's suggestion, reported *Epitonium suprastriatum* and *E. tiara*, both of Carpenter, as synonyms of *E. obtusum* (Sowerby), further investigation proves that *E. suprastriatum* is a separate species. Charles Snell, while diving off La Paz, Gulf of California, took 12 specimens, which show clearly that *E. suprastriatum*, with no spiral sculpture, belongs in the subgenus *Nitidiscala*, whereas *E. obtusum* and *E. tiara* belong in the subgenus *Asperiscala*.

Unfortunately, earlier workers neglected to give complete diagnoses when they described new taxa. SOWERBY (1844: 29) described the spiral twisting of the inner lip of *Epitonium obtusum* but failed to give the number of costae and whorls and overlooked the indistinct spiral sculpture on the early whorls. On worn shells the spiral sculpture is lost and the twisting of the inner lip can appear as a single cord. Sowerby based his description on one specimen, brought by Cuming from Ecuador, taken at 11 m in sandy mud. C. B. ADAMS (1852: 179, reprint) listed *E. obtusum* as a dead shell found on the beach at Panama.

CARPENTER (1856b: 164) described one shell, collected intertidally by T. Bridges at Panama, as *Scalaria tiara* which has all the characteristics of *Epitonium obtusum*. PALMER (1958: 188) reported 3 specimens of *E. tiara* in the Cuming Collection (British Museum) with a locality label of "Matxlam." She questioned the placement of the species in the subgenus *Nitidiscala*. DALL (1917: 480) confused matters by declaring that the Carpenter species ranged from Catalina Island, California to Todos Santos Bay, Baja California, Mexico. This is certainly erroneous, but subsequent authors repeated the error (OLDROYD, 1927: 59; KEEN, 1937: 35; BURCH, 1945: 30).

DALL (1917: 485) described *Epitonium (Nitidiscala) roberti* from the Gulf of California, with no specific locality, overlooking the spiral sculpture on the early whorls, but with "base marginated by a slender, not prominent cord." On worn shells the spiral sculpture is lost.

With 238 specimens at hand (which I collected intertidally at Mazatlán, Sinaloa, Mexico) plus the many lots in several institutions, it is my opinion that the *obtusum-tiara-roberti* complex resolves itself into conspecificity with the necessity for a change of subgeneric placement from *Nitidiscala* to *Asperiscala*.

All specimens examined had faint spiral sculpture on the early whorls, unless very worn, some had a basal cord, others had an incised line instead of a cord, one had 2 basal cords. Extreme variants had 20 costae; sizes ranged from 5 to 20 mm in length, 3 to 7½ mm in width. At Banderas Bay, Nayarit, Mexico, the deme, numbering 36, displayed similar intergradation. It is strange that all 3 authors failed to note the spiral striations except for the

fact that none could possibly have had more than 3 of the 5 specimens. It is reasonable to suppose that all the mollusks were worn so that the characteristic sculpture and the basal line did not show except in the one specimen of Dall. The basal cord as a definitive characteristic is not consistent enough to warrant separation into a distinct species.

From *Epitonium (Asperiscala) habeli* Dall, 1917, its nearest congener, *E. obtusum* differs by having a heavier shell, less deep suture, costae that fuse with the lip, and no umbilicus.

Type Material:

Scalaria obtusa: (3) syntypes, BM(NH)

Scalaria tiara: (3) possible syntypes, BM(NH) 1963.20

Epitonium (Asperiscala) roberti: holotype, USNM 46251

Type Localities:

Scalaria obtusa: Punta Santa Elena, Ecuador

Scalaria tiara: Panama

Epitonium roberti: Gulf of California, Mexico

Geographical Distribution and Ecology: Gulf of California, west Mexican coast to Colombia. Under rocks at high mid-tide level; dredged in sandy mud.

Bathymetric Range: Intertidal to 11 m.

Geochronological Range: Recent

Epitonium (Asperiscala) regulare (Carpenter, 1856)

(Figure 11)

Scalaria regularis CARPENTER, 1856b: 164; CARPENTER, 1857a: 284, 336; CARPENTER, 1860: 10; CARPENTER, 1864c: 146 [reprint]; DALL, 1917: 488

Epitonium regulare. ZETEK, 1918: 25; PALMER, 1963: 332; pl. 67, figs. 10, 11

Epitonium (Nitidiscala) regulare. - PILSBRY & LOWE, 1932: 120

Epitonium regularis. STRONG, 1945: 27

Epitonium (Nitidiscala) regulare. - KEEN, 1958: 274

Epitonium (Asperiscala) regularis. - KEEN, 1971: 426; fig. 626

Original Description: "S. testa parva, turrata, alba; anfr. ix. parum attingentibus; costis x.-xii. validioribus, extantibus, lineis subspiralibus apicem versus continuis; striulis spiralibus subobsoletis; umbilico nullo." (CARPENTER, 1856b: 164)

Diagnosis: Shell medium in size, turreted, white; with 9 whorls and 10 - 12 costae; spiral striulae obsolete on the later whorls; not umbilicate. The height given by Carpenter is 7 mm, width 3.3 mm.

Discussion: With a description as brief as that given by Carpenter one remains uncertain as to just what he meant. In CARPENTER (1864c: 146, reprint) he compares *Epitonium regulare* with *E. tinctum* (Carpenter, 1864). The original description of *E. regulare* calls for 3 type specimens, yet in the BM(NH) there are 4 specimens filed under the one name. All 4 specimens have more costae than the Carpenter description states there are. The label for these 4 syntypic specimens (BM(NH) Reg. No. 1950.4.18.13/16) is not in Carpenter's handwriting (*teste Keen*). According to PALMER (1963: 332) the right hand specimen, Figure 11 of the present paper, is the holotype; this is an inaccurate statement that might be construed as fixation of the specimen as a lectotype. It is strange that NYST (1871) did not include this species in his list of the Panamic epitonids. This taxon must remain an enigma at present since it is impossible to know what Carpenter had in mind, particularly since the syntypes do not match the original description.

Type Material:

Scalaria regularis: (4) syntypes, BM(NH) 1950.4.18.13/16

Type Locality:

Scalaria regularis: Panama

Geographical Distribution and Ecology: Unknown.

Bathymetric Range: Unknown

Geochronological Range: Recent

Epitonium (Asperiscala) rhytidum Dall, 1917

(Figure 52)

Epitonium rhytidum DALL, 1917: 486; BOSS *et al.*, 1968: 273
Epitonium (Asperiscala) rhytidum. - KEEN, 1971: 428; fig. 627

Original Description: "Shell small, subcylindric, pinkish white, strongly sculptured, of about 10 whorls exclusive of the nucleus which is missing. The type specimen retains six whorls, rounded, and with a deep suture; varices 18 or 19, low, rounded, crenate; whorls spirally sculptured with (on the last whorl seven or eight) flattish cords; base flattish, nearly smooth, imperforate, margined by a strong cord; aperture rounded. Length of decollate type-specimen, 5.5; diameter, 2 mm." (DALL, 1917: 486)

Diagnosis: Shell small in size, white, strongly sculptured; whorls convex, 6 remaining in holotype; nuclear whorls missing; suture deep; costae 18, low, thick, continuing on the last whorl to the rather heavy basal ridge, with the portion of the whorl below the ridge flattened; costae

crenately sculptured by flat, spiral cords, 8 to 10 on the last whorl; imperforate; columella short and arched; lip reflected; aperture subcircular; operculum unknown. Length, 5.5 mm; width, 2 mm.

Discussion: This species does not fit well into the subgenus *Asperiscala*, but until deBoury's numerous sections have been carefully evaluated, it seems unwise to allocate Panamic-Galapagan species to doubtful subgeneric positions. With more specimens available a better diagnosis can be made.

Type Material:

Epitonium rhytidum: holotype, USNM 207604

Type Locality:

Epitonium rhytidum: Galápagos Islands, Ecuador

Geographical Distribution and Ecology: Known only by one specimen from off the Galápagos Islands.

Bathymetric Range: 72 to 1134 m

Geochronological Range: Recent

Epitonium (Asperiscala) tinctorium Dall, 1919

(Figures 12, 18)

Epitonium (Asperoscala) tinctorium DALL, 1919: 340; LOWE, 1932: 113; pl. 9, fig. 6; PILSBRY & LOWE, 1932: 120; M. SMITH, 1944: 7; BOSS *et al.*, 1968: 320

Epitonium (Asperiscala) tinctorium. - STRONG, 1945: 22, 23; KEEN, 1958: 272; fig. 97; KEEN, 1971: 428; fig. 629

Original Description: "Shell small, white, with a narrow purple-brown spiral line in front of the suture, of six or more whorls excluding the (lost) nucleus; the whorls adjacent, the axis imperforate, with 11 to 12 continuous varices which about half encircle the spire; the varices smooth, slightly reflected, wider where they cross the rather deep suture; there are no varical angles or spines; the whorls are uniformly finely spirally striated; aperture rounded; there is no basal cord or disk; no operculum was taken with the specimen; height of shell, 7; of last whorl, 3; diameter, 3 mm." (DALL, 1919: 340)

Diagnosis: Shell small, yellowish-brown with white costae; nuclear whorls 3, white, glassy; postnuclear whorls 8 or 9, rapidly enlarging; costae 8 to 12, slightly reflected, showing growth lines, thicker on the body whorl; spiral threads unevenly spaced between whorls; suture fairly deep; a purple-brown band on the whorls near the suture; aperture round; shell imperforate; lip slightly patulous

at bottom; operculum brown, thin. Length, 2 to $8\frac{1}{2}$ mm; width, 1 to $4\frac{1}{2}$ mm.

Discussion: Live-taken shells have white costae and yellow-brown whorls; beach specimens are white. The brown band between the costae is almost on the outer periphery of the whorl. In *Epitonium tinctorium* the costae show growth lines, the spiral striations are fine and irregularly spaced between the costae, but not on them, and the lip is heavier than in *E. zeteki*, its nearest congener. In *E. zeteki* the spiral striations are farther apart and sometimes cross the anterior faces of the costae. Fresh shells are easily identified but dead shells present a problem of identification unless these points are noted.

When Dall described *Epitonium (Asperiscala) tinctorium* he failed to choose a holotype from the 5 shells in the type lot. I have selected one as lectotype which most nearly parallels Dall's description and measurements. It is USNM 218100. Collected many years ago by C. R. Orcutt, it still retains the brown band between the costae, and the fine, spiral striations; the aperture is slightly damaged. The remaining 4 specimens are paralectotypes, USNM 698126.

This species belongs to an intertidal fauna down to depths of approximately 6m. It is most frequently taken from around rocks on rubble reefs and under rocks in tide pools, throughout the Gulf of California, on the outer coast of Baja California as far north as Magdalena Bay, and on the west coast of Mexico south possibly to Panama. I have not seen any specimens of *Epitonium tinctorium* from Panama, although it has been reported from there. The similarity to *E. zeteki* from Panama leads one to question if it has been confused with that species.

Type Material:

Epitonium (Asperiscala) tinctorium: lectotype herein, USNM 218100; 4 paralectotypes herein, USNM 698126

Type Locality:

Epitonium (Asperiscala) tinctorium: Magdalena Bay, Baja California, Mexico

Geographical Distribution and Ecology: Magdalena Bay, Baja California, throughout the Gulf of California, south on the west coast of Mexico, possibly to Panama. Usually found on rubble reefs.

Bathymetric Range: Intertidal zone down to approximately 6m.

Geochronological Range: Recent

Epitonium (Asperiscala) venado (Olsson & Smith, 1951)
(Figure 53)

Clathrus venado OLSSON & M. SMITH, 1951: 45; pl. 3, fig. 4

Epitonium (?Clathrus) venado. - KEEN, 1958: 272; fig. 104

Epitonium (Asperiscala) venado. - KEEN, 1971: 428; fig. 630

Original Description: "Shell of medium size, turbate, white, of about 9 whorls, the apical 2 being very small and smooth belong to the nucleus. Whorls convex, the coiling moderately close, the surface of the whorls not quite touching each other. No basal cord or disk. Varices 13, relatively thin, erect, of medium height, their edges entire when perfect, rounded or bearing an indistinct low spine at their shoulder point. Forward face of each varix is smooth or faintly roughened, the inner face concave, smooth. Intervarical surfaces with weak spirals which show as widely spaced raised threads, about 6 on the last whorl; these intervarical spirals being best developed in the middle zone, above the band bordering the suture to about the third and the base is smooth. Varices join together in the umbilical area to form a pillar cord. Aperture obliquely subovate, the peristome formed in part by the forward face of the last varix, flattened, flaring out slightly in front to form a shallow anterior canal. Length 9.9 mm, diameter 5 mm." (OLSSON & SMITH, 1951: 45)

Diagnosis: Shell medium in size, turbate; nuclear whorls 2, small, glassy; postnuclear whorls 7, rapidly expanding, convex; suture very deep; costae 13, thin, erect, slightly reflected, rounded, showing growth lines, with sometimes a small spine near the suture; spiral threads between costae fine, widely spaced, about 6 on the last whorl, upper one-third of each whorl lacking spirals; aperture oval; lip reflected, anteriorly with a strong, wrinkled fasciole behind the inner lip; operculum unknown.

Discussion: Although this species is quite similar to *Epitonium (Asperiscala) acapulcanum* Dall, there are some distinctive differences. The spiral threads are finer and much further apart; the interspaces are 5 to 6 times wider than the threads; the upper one-third of each whorl has no spiral sculpture. The spiral threads are unevenly spaced, about 6 on the last whorl. There is no umbilicus and the anterior end of the lip has a strong, wrinkled fasciole behind the lip. From *E. (A.) zeteki* Dall it differs by being larger, narrower, and having 13 instead of 11 costae, with spiral threads well spaced and lacking on the upper portion of each whorl. *Epitonium (A.) venado* is known only from Panama.

Type Material:

Clathrus venado: holotype, ANSP 187200

Type Locality:

Clathrus venado: Venado Beach, Panama

Geographical Distribution and Ecology: Known only from Panama; its habitat is unknown.

Bathymetric Range: Not known; holotype, the only specimen was picked up from the beach.

Geochronological Range: Recent

Epitonium (Asperiscala) walkerianum

Hertlein & Strong, 1951

(Figures 16, 17)

Epitonium (Asperiscala) walkerianum HERTLEIN & STRONG, 1951: 88; pl. 3, fig. 12; KEEN, 1958: 272; fig. 99; KEEN, 1971: 428; fig. 631

Epitonium walkerianum. - DUSHANE, 1962: 45; KEEN, 1964: 199; DUSHANE & BRENNAN, 1969: 358

Original Description: "Shell small, pure white, elongate-conic; nuclear whorls 4, smooth, white, forming an elevated spiral point to the shell without noticeable break in the outline; postnuclear whorls 5, rounded, separated by a distinct but rather shallow, rounded suture; axial sculpture of 20 low, rounded ribs, without spine or angulation, curving into the sutures where they meet and fuse, continuous over the spire which they nearly encircle, on the imperforate base continuing without change to the edge of the columellar lip; spiral sculpture of sharp, incised lines in the interspaces between the axial ribs, about 12 appearing on the last whorl; aperture nearly circular,

with the outer lip but little thickened and narrower than the columellar lip. The type measures: length, 3.7 mm; diameter, 1.2 mm." (HERTLEIN & STRONG, 1951: 88)

Diagnosis: The original description is so complete and accurate that a further diagnosis would only be repetitious.

Discussion: Although Hertlein & Strong thought their species to be similar to *Epitonium onchodes* Dall, the 2 species are distinct. *Epitonium onchodes* proves to be a synonym of *E. minutica* deBoury which has a shell very different from *E. (Asperiscala) walkerianum*. The former has a more obtuse shell, an umbilicus, spinose costae and strong spiral ridges. There is a difference in size between the two; *E. walkerianum* has a shell that measures 3 to 5 mm in length, whereas *E. minutica* has a shell from 13 to 35 mm in length. *Scala sericiflum* DALL (1889: 313), a Caribbean form from the coast of Honduras, appears to have a similar shell, but the likeness may be only superficial.

One specimen was dredged in 14 to 21 m off Punta Peñasco by the *Velero III*, AHF station 721-37, March 1937. The holotype was dredged in 22 m near Corinto, Nicaragua by the Templeton Crocker Expedition, station 200-D-19, 1936. Additional specimens were collected in beach drift at the same locality.

Type Material:

Epitonium (Asperiscala) walkerianum: holotype, CAS[GTC] 9617

Type Locality:

Epitonium (Asperiscala) walkerianum: Corinto, Nicaragua

Geographical Distribution and Ecology: From San Felipe, Gulf of California, along the west coast of Mexico, south to Nicaragua. In the northern portion of the Gulf of California this species is fairly common intertidally

Explanation of Figures 31 to 42

Figure 31: *Epitonium (Asperiscala) manzanillense* Hertlein & Strong, 1951. Holotype, CAS[GTC] 9616; length 3.7 mm; width 1.4 mm × 17½

Figure 32: *Epitonium (Asperiscala) imperforatum* Dall, 1917. Holotype, USNM 211391; length 4½ mm; width 2½ mm × 15

Figure 33: *Epitonium (Asperiscala) emydonesus* Dall, 1917. Holotype, USNM 194995; length 3½ mm; width 1.7 mm × 18

Figure 34: *Epitonium (Asperiscala) macleani* DuShane, 1970. Holotype, LACM 1197; length 7 mm; width 3½ mm × 8½

Figure 35: *Epitonium (Asperiscala) macleani* DuShane, 1970. Bahía Escondido, Baja California, Mexico (DuShane Collection); length 2½ mm; width 1 mm × 14½

Figure 36: *Scalaria gradata* Sowerby, 1844. Syntype, BM[NH] × 1.8

Figure 37: *Epitonium (Nitidiscala) gaylordianum* Lowe, 1932. Holotype, ANSP 157987; length 28½ mm; width 9½ mm × 2

Figure 38: *Epitonium thylax* Dall, 1917. Holotype, USNM 324465; length 6¼ mm; width 2.6 mm × 9.8

Figure 39: *Scalaria rivicostata* Carpenter, 1857. Holotype, BM [NH] Tablet 2040; length 4.4 mm × 10

Figure 40: *Epitonium (Nitidoscala) phanium* Dall, 1919. Holotype, USNM 218095; length 8 mm; width 4 mm × 7.2

Figure 41: *Scalaria elenense* Sowerby, 1844. Holotype BM[NH]; length 10 mm × 6

Figure 42: *Scala lowei* Dall, 1906. Cotype, USNM 191548; length 7 mm; width 4 mm × 5.1



at the edge of sand bars during low night tides. It is dredged from among mangrove leaves, sand and shell bottom.

Bathymetric Range: Intertidal to 23 m

Geochronological Range: Recent

Epitonium (Asperiscala) zeteki Dall, 1917

(Figure 19)

Epitonium zeteki DALL, 1917: 486; ZETEK, 1918: 25; BOSS *et al.*, 1968: 343

Epitonium (Asperiscala) zeteki. - M. SMITH, 1944: 8

Epitonium (Nitidiscala) zeteki. - STRONG, 1945: 22, 23, 27

Epitonium (Asperiscala) zeteki. - KEEN, 1958: 272; fig. 101; KEEN, 1971: 428; fig. 632

Original Description: "Shell small, white, thin, with about 8 whorls, the nucleus of about one and a half glassy rounded whorls (with a portion lost?); last whorl with obscure, close-set spiral striae, with no basal disk or cord; whorls rounded, suture deep; there are 11 sharp, erect, rather low varices, smooth on the front with no spines or angles, descending into the suture and regularly continuous over the spire, which they about half encircle; aperture nearly circular, axis imperforate. Height, 6.0; maximum diameter, 3.0 mm." (DALL, 1917: 486)

Diagnosis: Shell medium in size, thin; nuclear whorls 2, glassy, postnuclear whorls 8, rounded; costae 11, rounded, smooth, low, with no spines or angulations; spiral sculpture increasingly obsolete; suture deep; aperture round; peritreme complete; imperforate; operculum unknown.

Discussion: Although fairly close to *Epitonium (Asperiscala) acapulcanum* Dall, there are some characteristic differences. The 4th whorl below the nuclear whorl shows a separation of the spiral ridges; they become wider apart on succeeding whorls, until on the last whorl they are nearly obsolete. This species is more solid, has continuous costae, less emphatic spiral sculpture and increases more rapidly in diameter. It seems to be endemic to the fauna of Panama.

Type Material:

Epitonium zeteki: holotype, USNM 324463

Type Locality:

Epitonium zeteki: Panama

Geographical Distribution and Ecology: Panama; its habitat is unknown.

Bathymetric Range: Collected on the beach at Panama by James Zetek.

Geochronological Range: Recent

(*Nitidiscala*) deBoury, 1909

[Type species: (OD) *Scalaria unifasciata* Sowerby, 1844]
Spiral sculpture absent between whorls.

Epitonium (Nitidiscala) barbarinum Dall, 1919

(Figure 71 and Figure 158)

Epitonium (Nitidoscala) barbarinum DALL, 1919: 341; DALL, 1921: 117; BOSS *et al.*, 1968: 42

Epitonium barbarinum. - KEEN, 1937: 35; BURCH, 1945: 33; DUSHANE & POORMAN, 1967: 424

Epitonium (Nitidoscala) barbarina. - M. SMITH, 1944: 7

Epitonium (Nitidiscala) barbarina. - STRONG, 1945: 24; KEEN, 1958: 272; fig. 108

Epitonium (Nitidiscala) barbarinum. - KEEN, 1971: 430; fig. 640

Original Description: "Shell small, imperforate, white, with 11 varices continuous up the spire which they one-third encircle; anterior surface of the varices flattish, smooth; the shoulder is not angular or spinose; there are six whorls exclusive of the (lost) nucleus; suture deep; base rounded without a basal cord or disk; aperture sub-ovate, the inner lip thickened; height of shell, 19; of last whorl, 7.5; of aperture, 4; diameter, 6.5 mm." (DALL, 1919: 341)

Diagnosis: Shell white, medium in size, nuclear whorls 2 to 3, smooth, nearly always eroded, postnuclear whorls 7 to 8; costae 9 to 13, slightly reflected on fresh specimens, otherwise worn, ascending the spire continuously; suture moderately deep, umbilicus lacking; lip complete, aperture oval; operculum thin, light in color, paucispiral. Length, 7½ to 19 mm; width 4½ to 7½ mm.

Discussion: Dall gave the type locality as San Diego, California (Stearns Collection), but the latter's locality indications are sometimes open to question. This is a very common species on the west side of the upper Gulf of California. It has been thought by some that this is a spurious species in the Gulf of California, as most specimens seen in collections have been beach rolled. However, Dr. Donald Shasky and I have taken living specimens from Agua Chale (38½ km south of San Felipe) and

from Puertecitos (88km south of San Felipe), Gulf of California, Mexico, collected intertidally on algae-covered rocks, and dredged down to 18m on broken shell and sand substrate.

This species is very close to *Epitonium (Nitidiscala) tinctum* (Carpenter, 1864), a California species; it varies in some minor but essential ways; the costae on *E. tinctum* are sometimes spinose, thicker and reflected, coalescing into heavier costae near the lip; the aperture is slightly patulous, the inner lip thickened, and usually with a larger shell. Radular studies of these 2 species indicate no conspecificity. In *E. barbarinum* dentition is in the form of 20 - 40 broad rows of hook-like uncini with little variation along each row. The length of the teeth varies with the position of the teeth in the row, becoming progressively shorter with distance from the center. The obtuse angles on the teeth are variable as to their precise placement. In *E. tinctum* the tips of the teeth have a bifid structure with little variation in length (see Figures 158 and 159).



Figure 158

Epitonium (Nitidiscala) barbarinum Dall, 1919

The hook-like uncini vary with their position in the row

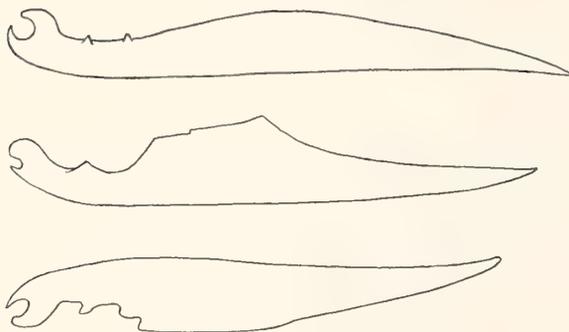


Figure 159

Epitonium (Nitidiscala) tinctum (Carpenter, 1864)

The bifid structure of the radular teeth is unlike any other thus far reported

Type Material:

Epitonium (Nitidiscala) barbarinum: holotype, USNM 46229

Type Locality:

Epitonium (Nitidiscala) barbarinum: San Diego, California (Stearns collection)

Geographical Distribution and Ecology: Upper Gulf of California, Mexico, on algae-covered rocks; dredged down to 18m on broken shell and sand substrate.

Bathymetric Range: Intertidal to 18m

Geochronological Range: Recent

Epitonium (Nitidiscala) basicum Dall, 1917

(Figure 86)

Epitonium basicum DALL, 1917: 485; ZETEK, 1918: 25; BURCH, 1945: 27; BOSS *et al.*, 1968: 42

Epitonium (Nitidiscala) basicum. - BURCH, 1945: 25; STRONG, 1945: 26; KEEN, 1958: 273; fig. 109

Original Description: "Shell white, with a brownish narrow band in front of the suture when fresh, with seven whorls exclusive of the (lost) nucleus; varices 11, low, rounded, cord-like, continuous over the suture into which they dip, and making nearly half a turn in ascending around the spire, one or two near the terminal are larger than the rest; interspaces smooth; base rounded, marginated by a strong cord, imperforate; aperture subovate, the margin narrow, somewhat patulous in front. Length, 15; diameter, 7mm." (DALL, 1917: 485)

Discussion: Other than the holotype of *Epitonium basicum* I have seen only a few specimens of Dall's taxon. There are 2 specimens of *E. basicum* in the USNM Collection, one from the Gulf of California (holotype); the other, in poor condition, came from the Stearns Collection, labeled "Panama," a not too reliable record. The SDMNH has one very worn and damaged specimen identified as *E. basicum* (No. 26483) from the Lowe Collection (collected by Capt. George Porter) with a notation questioning the locality (Baja California) and identification. No other specimens seem to be in museum or private collections. Worthy of comment is the fact that no major institution has collected this species on any of the various expeditions. Museums possessing specimens of *E. basicum* have apparently obtained them from private collectors long ago. It may well be that *E. basicum* does not really occur in the Panamic-Galapagan province.

There is an epitioid from the Hawaiian Islands, *Epitonium perplexum* (Pease, 1867) with 11 costae, a brown band in front of the suture and a strong cord between the costae on the basal whorl which seems to match the original description of Dall's taxon very well. It is possible

that Dall was mistaken in identification and geographical origin of his *Epitonium basicum*.

Type Material:

Epitonium basicum: holotype, USNM 56049

Type Locality:

Epitonium basicum: Gulf of California

Geographical Distribution and Ecology: Dead taken shells; no information on distribution available.

Bathymetric Range: Unknown

Geochronological Range: Recent

Epitonium (Nitidiscala) callipeplum Dall, 1919

(Figure 70)

Epitonium (Nitidoscala) callipeplum DALL, 1919: 341; BOSS *et al.*, 1968: 58

Epitonium (Nitidiscala) callipeplum [sic]. - STRONG, 1945: 26; [the name spelled correctly on p. 27]

Epitonium (Nitidiscala) callipeplum. - KEEN, 1971: 430; fig. 641

Original Description: "Shell small, lilac color on the spire, paling into white on the last whorl, with about eight whorls exclusive of the (lost) nucleus, imperforate; suture deep; axial sculpture of very faint incremental lines and 11 thin, low, narrow, continuous varices, dipping into the suture which encircles less than a quarter of the circumference of the spire; surface polished, aperture obliquely ovate; height of shell, 9; of last whorl, 5; diameter, 4mm." (DALL, 1919: 341)

Diagnosis: Shell medium in size, brown between white costae; nuclear whorls usually lost, but when intact number 2; postnuclear whorls 8, shining, rounded; costae 11, thin, narrow, low, some are disjunct; aperture obliquely oval, peritreme complete, anterior end of lip with slightly wrinkled fasciole; operculum unknown. Length, 9 to 11 mm; width, 4 to 5 mm.

Discussion: Few specimens of this species are known. It has been reported from Magdalena Bay, where Orcutt collected it (ANSP 151685); also from along the west coast of Mexico (DuShane Collection) to Panama (Shasky Collection), intertidally. This species is not easily confused with others from the Panamic fauna.

Type Material:

Epitonium (Nitidoscala) callipeplum: holotype, USNM 218096

Type Locality:

Epitonium (Nitidoscala) callipeplum: Beach at Magdalena Bay, Baja California, Mexico

Geographical Distribution and Ecology: Magdalena Bay, Baja California, west coast of Mexico south to Panama; under rocks on rubble reef

Bathymetric Range: Intertidal

Geochronological Range: Recent

Epitonium (Nitidiscala) columnella Dall, 1917

(Figure 107)

Epitonium columnella DALL, 1917: 483; ZETEK, 1918: 25; BOSS *et al.*, 1968: 85

Epitonium columella [sic]. - M. SMITH, 1944: 7

Epitonium (Nitidiscala) columnellum. - STRONG, 1945: 25, 27

Epitonium (s. l.) columnella. - KEEN, 1958: 276

Epitonium (Nitidiscala) columnella. - KEEN, 1971: 431; fig. 643

Original Description: "Shell small, white, with about five whorls exclusive of the (lost) nucleus; the whorls rather rapidly enlarging; varices 11, high, thin, angular and spinose at the shoulder, and distinctly angular at the margin of the base, on which the reflected portion is distinctly flattened, but with no basal disk or cord; base imperforate, aperture rounded, the reflected margin produced at the shoulder and in front. Length, 2.75; diameter, 1.75 mm." (DALL, 1917: 483)

Diagnosis: This is a small form, but the description does not match the holotype; therefore it is impossible to know what Dall intended. On the holotype 6 whorls remain; the aperture is shattered; costae are 11 with no indication of shoulder spines. There have been few reports of the species in the literature.

Discussion: Dall reported the species from Panama Bay in about 54m, but since then (1917) there seems to be no record of its having been collected.

Type Material:

Epitonium columnella: holotype, USNM 111220

Type Locality:

Epitonium columnella: Panama Bay

Geographical Distribution and Ecology: Panama Bay, otherwise unknown

Bathymetric Range: Dredged in about 54m

Geochronological Range: Recent

Epitonium (Nitidiscala) cumingii (Carpenter, 1856)

(Figures 109, 110, 111, 112)

- Scalaria cumingii* CARPENTER, 1856b: 165 [not *Eglisia cumingii* A. Adams, 1850]; CARPENTER, 1857a: 284, 336; CARPENTER, 1860: 10; COOPER, 1867: 34 [as "(Carpenter, 1865)"]; STRONG, 1930: 188
- Scalaria ? cumingii*. - CARPENTER, 1864c: 613, 660 [reprint 1872: 99, 146]
- Scala cumingi*. - ORCUTT, 1915: 78
- Epitonium cumingi*. - ZETEK, 1918: 25; M. SMITH, 1944: 7
- Epitonium (Nitidiscala) cumingi*. - STRONG, 1945: 26, 27
- Epitonium (s. l.) cumingii*. - KEEN, 1958: 276
- Epitonium cumingii*. - PALMER, 1958: 184; PALMER, 1963: 331; plt. 67, fig. 9
- Epitonium (Nitidiscala) cumingii*. - KEEN, 1971: 430; fig. 645
- Epitonium (Nitidoscala) colpoica* DALL, 1917: 478, 479; PILSBRY & LOWE, 1932: 120; M. SMITH, 1944: 7
- Epitonium (Nitidiscala) colpoicum*. - BAKER, HANNA & STRONG, 1930: 53; plt. 3, fig. 9; STRONG, 1945: 26; KEEN, 1958: 273; fig. 113; KEEN, 1971: 430, fig. 642
- Epitonium colpoicum*. - DUSHANE, 1962: 45; DUSHANE & POORMAN, 1967: 424; BOSS *et al.*, 1968: 84
- Epitonium (Nitidiscala) gissleri* STRONG & HERTLEIN, 1939: 124; plt. 18, fig. 8; STRONG, 1945: 26; KEEN, 1958: 274; fig. 120; WILSON, 1967: 252 (paratypes 3688-3689)

Original Description: "*S. testa 'S. mitraeformis' simili, sed paullum graciliore; anfr. x quarum iii. primi laeves; costis paucioribus, viii. - ix., minus coronatis, haud acutissimis, haud reflexis, striulis incrementi minutissime sculptis; anfr. valde separatis. Long. .35, long. spir. .25, lat. 14, div. 30°. Hab. Sinu Panamensi; legit. T. Bridges. Sp. un. in Mus. Cuming. The lines of growth on the varices show that the coronations were never so sharp and elevated as in S. mitraeformis.*" (CARPENTER, 1856b: 165)

Diagnosis: Shell small to medium in size, white, nuclear whorls 4, dark colored on live-taken specimens, glassy;

postnuclear whorls 7, rapidly expanding, rounded, disconnected, glassy; costae 8 to 10, rather wide, slightly reflected, easily fractured, continuous up the whorls; base rounded; lip wide, slightly patulous, supported by terminal ends of preceding costae; sutures very deep; aperture oval; operculum dark, paucispiral. Length, 4½ to 10mm; width, 2.3 to 6mm.

Discussion: The costae are very thin and easily fractured, with the result that few specimens are taken intact. In perfect specimens some of the costae have a wing, or extension preceding the dip into the suture. This species, with its disconnected whorls, would appear to be closely related to *Epitonium scalare* (Linnaeus, 1767).

CARPENTER (1864c: 613, 660) in reporting *Scalaria cumingii* from the southern California coast and from west Mexico and Panama (1860: 10; 1857a: 284, 336) confused later workers. What he had in mind is still a question. In the light of subsequent investigation it would appear that the Panama locality is more nearly correct, particularly since he described *Scalaria cumingii* (1856b: 165) in his paper on new species of shells from Panama, and stated that the type locality was Panama.

DALL's (1917: 478) type specimen of *Epitonium (Nitidiscala) colpoicum*, although slightly more squat, has the same number of costae and whorls, with only 1 mm difference in diameter. The type locality is the same. The recognition of 2 separate species in KEEN (1971: 430) now seems unjustified in the light of new material. Specimens from the northern Gulf of California tend to be slightly larger and higher; otherwise the two taxa are identical in all characters.

Epitonium (Nitidiscala) gissleri Strong & Hertlein, 1939 (p. 194; plt. 18, fig. 8), a synonymic taxon from Panama, shows the same thin, glassy whorls, deep suture, axial sculpture continuing to the junction with the columellar lip as *E. (N.) cumingii*.

Explanation of Figures 43 to 53

- Figure 43: *Scalaria tiara* Carpenter, 1856. Syntypes (3), BM[NH] 1963.20 × 4
- Figure 44: *Epitonium (Asperiscala) roberti* Dall, 1917. Bahía Concepción, Baja California, Mexico (DuShane Collection); length 6 mm; width 3 mm × 11
- Figure 45: *Scalaria obtusa* Sowerby, 1844. Syntypes (3), BM [NH] × 3
- Figure 46: *Epitonium (Asperiscala) centronium* Dall, 1917. Holotype, USNM 211395; length 4½ mm; width 2 mm × 7½
- Figure 47: *Epitonium reedi* Bartsch, 1928. Holotype, USNM 367968; length 12.7 mm; width 6.8 mm × 3

- Figure 48: *Epitonium (Asperoscala) canna* Dall, 1919. Holotype, USNM 218099; length 9 mm; width 5 mm × 3.2
- Figure 49: *Epitonium (Nitidiscala) roberti* Dall, 1917. Holotype, USNM 46251; length 12 mm; width 6½ mm × 4½
- Figure 50: *Epitonium (Asperiscala) kelseyi* Baker, Hanna & Strong, 1930. Holotype, CAS[GTC] 4766; length 11.9 mm; width 5½ mm × 5½
- Figure 51: *Epitonium habeli* Dall, 1917. Holotype, USNM 56055; length 7½ mm; width 4 mm × 9
- Figure 52: *Epitonium rhytidum* Dall, 1917. Holotype, USNM 207604; length 6½ mm; width 3½ mm × 9.8

- Figure 53: *Clathrus venado* Olsson & Smith, 1951. Holotype, AN SP 187200; length 9.9 mm; width 5 mm × 6



CLENCH & TURNER (1950: 136; 1951: 260) synonymize *Scalaria ligata* C. B. Adams, 1850 with *Epitonium albidum* d'Orbigny, 1842, but there are fundamental differences between the two species; the latter has more and lower costae (12 - 14), which are blade-like or narrow and a much larger shell (21½ mm). It has an extensive range in the Atlantic (see CLENCH & TURNER, 1951: 261). The shell of *S. ligata* from Panama (lectotype MCZ 186590) is figured well in TURNER (1956: 135; pl. 21, fig. 2) but has no accompanying description. MÖRCH (1875: 154) lists it as *sp. dub.*, but gives no supporting evidence. This species looks very much like *S. cumingii* Carpenter, but is so worn that it is difficult to arrive at a conclusion without more definitive material at hand. Until such time as a study of the epitonids can be made on a world-wide basis it seems preferable not to further synonymize these taxa.

Epitonium cumingii is a relatively common species both intertidally on rocky reefs and in dredgings to 18 m. Records indicate it may be taken from the northern end of the Gulf of California (Puertecitos, Baja California, DUSHANE, 1962; Guaymas, DUSHANE & POORMAN, 1967) south along the west Mexican coast to Panama (PILSBRY & LOWE, 1932; STRONG & HERTLEIN, 1939) and the Galápagos Islands (DeRoy Collection).

Type Material:

- Scalaria cumingii*: holotype, BM(NH) 1950.3.31.1
Epitonium (Nitidiscala) colpoica: holotype; USNM 46213
Epitonium (Nitidiscala) gissleri: holotype, CAS[GTC] 723

Type Localities:

- Scalaria cumingii*: Panama
Epitonium (Nitidiscala) colpoica: Panama
Epitonium (Nitidiscala) gissleri: Panama

Geographical Distribution and Ecology: Gulf of California to Panama and the Galápagos Islands, Ecuador; under rocks on reefs, dredged on sand bottom

Bathymetric Range: Intertidal to 18 m

Geochronological Range: Recent

Epitonium (Nitidiscala) curvilineatum (Sowerby, 1844)

(Figures 105, 106)

- Scalaria curvilineata* SOWERBY, 1844a: 94; pl. 33, fig. 59;
 SOWERBY, 1844b: 29; NVST, 1871: 103; REEVE, 1873-74:
 pl. 7, fig. 49; TRYON, 1887: 70; pl. 14, fig. 46
Scala curvilineata. - H. & A. ADAMS, 1853: 221
Epitonium (s. l.) curvilineatum. - KEEN, 1958: 276; fig. 144
Epitonium (Nitidiscala) curvilineatum. - KEEN, 1971: 432;
 fig. 646

- Epitonium imbrex* DALL, 1917: 486; ZETEK, 1918: 25;
 STRONG, 1945: 26, 27; BOSS *et al.*, 1968: 162

Original Description: "*T. ovali, laevi, tenui, imperforata; anfractibus paucis, rapide crescentibus; varicibus subnumerosis, curvilineatis, laevibus, simplicibus; apertura ovali, labio interno antice paululum expanso; colore pallide fulvo.* We have seen only one specimen, which is in Mr. Cuming's collection, from Sansonati, in Central America." (SOWERBY, 1844: 29)

Diagnosis: Shell white, large in size; nuclear whorls 2, postnuclear whorls 6, rounded, suture moderately deep; costae 15 to 22, arcuate, thin, low; aperture oval, operculum unknown. Length of type, 16 mm; width, 7½ mm.

Discussion: Little is known concerning this species. The holotype has not been found at the British Museum (Natural History) (*teste* Keen), thus we have only the illustration in Sowerby from which to draw our conclusions. DALL (1917: 486) described *Epitonium imbrex* from Panama as new; it matches the description of *Scalaria curvilineata*, but its small size (2.3 mm in length) makes recognition difficult. However, the curved costae are very similar to those in the Sowerby species. Comparison of the holotype of *E. imbrex* with the illustration in Sowerby of *S. curvilineata* makes synonymy seem inevitable. Unfortunately, there are no records available of Dall's form having been taken since the original description. The size ranges from 2.3 to 16 mm in length, from 1.0 to 7½ mm in width. The nearest congener appears to be *E. (Nitidiscala) durhamianum* Hertlein & Strong, 1951.

Type Material:

- Scalaria curvilineata*: holotype, not at BM(NH)
Epitonium imbrex: holotype, USNM 324464

Type Localities:

- Scalaria curvilineata*: Central America
Epitonium imbrex: Panama

Geographical Distribution and Ecology: Unknown

Bathymetric Range: Unknown

Geochronological Range: Recent

Epitonium (Nitidiscala) durhamianum Hertlein & Strong, 1951

(Figure 104)

- Epitonium (Nitidiscala) durhamianum* HERTLEIN & STRONG,
 1951: 89; pl. 3, fig. 9; KEEN, 1958: 274; fig. 118; KEEN,
 1971: 432; fig. 647

Epitonium durhamianum. - DUSHANE & POORMAN, 1967: 424; DUSHANE & BRENNAN, 1969: 358

Original Description: "Shell small, elongate-conic, white; nuclear whorls 4, pale horn color, smooth, forming an elevated spiral point to the spire without noticeable break to the outline; post nuclear whorls 7, the upper third of each whorl broadly, slopingly shouldered, the lower third well rounded, separated by a moderately deep suture; axial sculpture of 16 low, narrow, slightly reflected ribs, without spine or angulation, curving into the sutures where they meet and fuse, continuous over the spire which they nearly encircle, on the imperforate base continuing without change to the columellar lip; spiral sculpture absent; aperture oval, outer and columellar lips only moderately thickened. The type measures: length, 5.7 mm; diameter, 1.8 mm." (HERTLEIN & STRONG, 1951: 89; pl. 3, fig. 9)

Diagnosis: Shell rarely more than 8 mm in length, white, nuclear whorls 4, amber color on live-taken specimens, glassy, smooth; postnuclear whorls 6 to 8, with sloping shoulders; sutures moderately deep; costae 16, fusing at the sutures, low, very slightly reflected, rounded, continuous from whorl to whorl; base imperforate; lip slightly patulous; aperture oval; operculum thin, paucispiral. Length, $1\frac{1}{2}$ to 8 mm; width, $\frac{1}{2}$ to $2\frac{1}{2}$ mm.

Discussion: This species, with its narrow outline (long for its width) and its sloping shoulders is easily recognized. *Epitonium (Nitidiscala) politum* (Sowerby, 1844), a similar species, usually has a larger shell, the whorls are more rounded, less angular; costae are less numerous and are frequently disjunct; the peritreme is incomplete, although the thin lip is slightly patulous. Live-taken specimens of *E. (N.) durhamianum* are dredged in from 9 to 27 m. Records, although meager, indicate that *E. durhamianum* might have a discontinuous distribution. Present collections reveal occurrences in the northern portion of the Gulf of California (LACM-AHF station 721-37, Punta Peñasco) and in Nicaragua (HERTLEIN & STRONG, 1951), with no intermediate stations listed. Many more records are needed before a definite conclusion can be reached.

Type Material:

Epitonium (Nitidiscala) durhamianum: holotype, CAS[GTC] 9623

Type Locality:

Epitonium (Nitidiscala) durhamianum: Near Corinto, Nicaragua

Geographical Distribution and Ecology: Northern Gulf of California, Mexico, and Nicaragua; among mangrove leaves, sand and broken shell bottom.

Bathymetric Range: Dredged in from 9 to 27 m

Geochronological Range: Recent

Epitonium (Nitidiscala) hancocki DuShane, 1970

(Figure 73)

Epitonium (Nitidiscala) hancocki DUSHANE, 1970: 332; pl. 51, fig. 1; SPHON, 1971: 11; KEEN, 1971: 432; fig. 650

Original Description: "Shell white, glossy, axial costae 21, continuous from whorl to whorl, with a sharp spine at the shoulder of each whorl; nuclear whorls 3, smooth, convex, brown, glassy; post nuclear whorls 9; suture deeply impressed; umbilicus small, not hidden by parietal lip; surface area between costae lacking spiral threads, whorls rounded; basal cord lacking; aperture oval; outer lip reflected and formed by the last costae; operculum thin, paucispiral, yellowish brown in color. Dimensions: length 13.0 mm, width 5.2 mm (holotype)." (DUSHANE, 1972: 332; pl. 51, fig. 1)

Discussion: *Epitonium hancocki* differs from all other epitoniids known from the west coast of the Americas by having a tabulate outline, many costae and a glassy exterior. From *E. (Asperiscala) kelseyi* Baker, Hanna & Strong, 1930, which it most resembles, it differs by having no spiral sculpture and by having a thinner shell. From *E. implicatum* Dall & Ochsner, 1928 (fossil, probably Pliocene) it differs by having more costae, a sharp spine at the shoulder of each whorl and a small umbilicus. It differs from *E. sawinae* var. *catalinense* Dall, 1917 by having a sharp spine at the shoulder of each whorl, by having a more rounded base and a larger umbilicus hidden by the reflected costae. The type locality of *E. catalinense* is Catalina Island, California.

The range for *Epitonium hancocki* seems to be limited. One live-taken specimen was dredged in 90 m off the north end of Isla Santa Cruz (Indefatigable Island), Galápagos Islands, Ecuador, November, 1967, by Jacqueline and André DeRoy. Since then, they have dredged additional specimens at the same locality in from 90 to 200 m. The *Velero III*, Allan Hancock Foundation Expeditions, dredged one living specimen north of Isla Española (Hood Island), Galápagos Islands, station AHF 814-38, in 36 to 72 m, shell bottom, January, 1938 (holotype). One broken and doubtful specimen was reported from Hormigas de Afuera, Perú, in a mud sample at 80 m (LACM-AHF 569).

Type Material:

Epitonium (Nitidiscala) hancocki: holotype, LACM-AHF 1235

Type Locality:

Epitonium (Nitidiscala) hanoocki: off Isla Española (Hood Island), Galápagos Islands, Ecuador

Geographical Distribution and Ecology: Galápagos Islands and possibly Perú; sand and broken shell bottom

Bathymetric Range: Dredged in from 26 to 200 m

Geochronological Range: Recent

Epitonium (Nitidiscala) hexagonum (Sowerby, 1844)

(Figures 82, 85)

Scalaria hexagona SOWERBY, 1844a: 98; plt. 33, fig. 67; SOWERBY, 1844b: 29; C. B. ADAMS, 1852: 197 (reprint); CARPENTER, 1857a: 260, 274, 285, 336; CARPENTER, 1857b: 446 [reprint 1967: 466]; CARPENTER, 1860: 10; CARPENTER, 1864a: 358 [reprint 1872: 192]; NYST, 1871: 113; REEVE, 1873-74: plt. 4, fig. 27; TRYON, 1887: 70; plt. 14, fig. 45; PALMER, 1951: 62

Scala (Clathrus) hexagona H. & A. ADAMS, 1853: 222

Epitonium hexagonum. - ZETEK, 1918: 25

Epitonium (Nitidoscala) hexagonum. - DALL, 1917: 479; BAKER, HANNA & STRONG, 1930: 52; plt. 3, fig. 8; PILSBRY & LOWE, 1932: 120; M. SMITH, 1944: 7; figs. 65, 68

Epitonium (Nitidoscala) hexagona. - DALL, 1921: 115

Epitonium hexagona. - STRONG, 1922: 157

Epitonium hexagonum. - KEEN, 1937: 35; DUSHANE, 1962: 45; KEEN, 1964: 187

Epitonium (Nitidiscala) hexagonum. - STRONG, 1945: 25, 26; BURCH, 1945: 30; KEEN, 1958: 274; fig. 121; McLEAN, 1961: 464; KEEN, 1971: 432; fig. 651

Epitonium (Nitidoscala) propehexagonum DALL, 1917: 479; BAKER, HANNA & STRONG, 1930: 52; plt. 3, fig. 8; PILSBRY & LOWE, 1932: 120; STRONG, 1945: 25, 27 [as "*prehexagonum*"]

Epitonium propehexagonum. - BOSS *et al.*, 1968: 266

Original Description: "*T. brevis, laevi, imperforata; anfractibus contiguis; varicibus sex, crassis, prominentibus, ad spicem oblique continuis; apertura rotundata; colore albo.*"

"A short, imperforated, white species, with whorls closely united, and strong varices forming about six oblique, continuous lines along the spire." (SOWERBY, 1844a: 29)

Diagnosis: Shell medium to large in size, whorls sometimes pink in color, otherwise white; nuclear whorls 2 to 3, opaque, usually eroded; subsequent whorls 7 to 9; costae 6, rarely 7, thick, reflected, sometimes with a rounded angle at the shoulder, finely striated on the anterior

face, continuous over the suture, free of the wide, reflected outer lip, forming a continuous, oblique line from base to nuclear whorls; suture not deep; aperture oval, operculum unknown. Length, 5 to 29 mm; width, 2 to 11 mm.

Discussion: Since Sowerby did not cite dimensions with his description we have no way of knowing which of the 4 specimens in the BM(NH) is the holotype. The 4 syntypes presumably all came from Acapulco, Mexico.

DALL (1917: 479) procured a large specimen of the same species, but because of its size, deemed it to be new and described it as *Epitonium (Nitidiscala) propehexagonum*, recognizing its affinity to the Sowerby species. The characteristics of both species otherwise are identical. A few specimens in private collections exceed in size the holotype of Dall's species. *Epitonium (N.) hexagonum* seems not to range farther north than Los Angeles Bay on the west side of the Gulf of California (McLEAN, 1961), nor north of Magdalena Bay (collected by C. R. Orcutt, 1917 [SDMNH Collection]) on the Pacific side of Baja California. On the mainland of Mexico side of the Gulf it is strangely absent as far south as Acapulco (LACM-AHF 2596-54), whence its disjunct range seems to extend to Panama. This is probably an offshore species, as the specimens in collections are beach worn dead shells.

From *Epitonium (Hirtoscala) reflexum* (Carpenter, 1856), the nearest related species, *E. (Nitidiscala) hexagonum* differs by having a heavier shell, less deep sutures, thicker costae with rounded angles at the shoulder. From *E. (Asperiscala) canna* Dall it differs by having a more slender shell, with no spiral sculpture on the whorls.

Type Material:

Scalaria hexagona: (4) syntypes, BM(NH)

Epitonium (Nitidoscala) propehexagonum: holotype, USNM 153075

Type Localities:

Scalaria hexagona: Acapulco, Mexico

Epitonium (Nitidoscala) propehexagonum: Gulf of California and Mazatlán, Mexico

Geographical Distribution and Ecology: Magdalena Bay south and Los Angeles Bay, Gulf of California south; Acapulco, Mexico, to Panama; no live-taken specimens have been examined.

Bathymetric Range: intertidal to ? (no dredging records available)

Geochronological Range: Recent

Epitonium (Nitidiscala) hindsii (Carpenter, 1856)

(Figures 79, 80, 81, 83, 84, 87, 88)

Scaloria hindsii Carpenter, 1856b: 165; CARPENTER, 1857a: 284, 336; CARPENTER, 1860: 10; CARPENTER, 1864c: 538; TRYON, 1887: 84

Scala hindsii. - ORCUTT, 1915: 78; DEBOURY, 1919: 39; STRONG, 1930: 188-190

Epitonium hindsii. - ZETEK, 1918: 25

Epitonium (Nitidiscala) hindsii. - KEEN, 1958: 274; PALMER, 1963: 331; plt. 67, figs. 3-6; KEEN, 1971: 432; fig. 652

Epitonium apiculatum Dall, 1917: 480 [not DALL, 1889]; ZETEK, 1918: 25

Epitonium (Nitidoscala) ? apiculatum. STRONG & HERTLEIN, 1930: 19

Epitonium (Nitidoscala) apiculatum. - BAKER, HANNA & STRONG, 1930: 51, 52; plt. 3, figs. 4-6

Epitonium (Nitidiscala) apiculatum. - STRONG, 1945: 25, 27; HERTLEIN & STRONG, 1951: 88; KEEN, 1958: 272; fig. 106; McLEAN, 1961: 464; KEEN, 1962: 179

Epitonium (Asperiscala) apiculatum. - GLENCH & TURNER, 1952: 290; plt. 132, figs. 1, 2

Epitonium apiculatum. - BOSS *et al.*, 1968: 31

Epitonium (Nitidoscala) compradora Dall, 1917: 480

Epitonium cf. comprador [sic]. - JORDAN, 1936: 113

Epitonium (Nitidiscala) compradorum. - STRONG, 1945: 25, 27

Epitonium (Nitidiscala) compradora. - KEEN, 1958: 274; KEEN, 1971: 430; fig. 644

Epitonium compradora. - BOSS *et al.*, 1968: 86

Epitonium (Nitidoscala) cylindricum Dall, 1917: 480

Epitonium (Nitidiscala) cylindricum. - STRONG, 1945: 26, 27; KEEN, 1958: 274

Epitonium cylindricum. - BOSS *et al.*, 1968: 98

Epitonium (Nitidoscala) musidora Dall, 1917: 483

Epitonium musidora. - ZETEK, 1918: 25; KEEN, 1937: 35; BOSS *et al.*, 1968: 216

Epitonium (Nitidiscala) musidorum. - STRONG, 1945: 26

Epitonium (Nitidiscala) musidora. - BURCH, 1945: 33; KEEN, 1958: 274; fig. 123

Epitonium (Nitidoscala) pazianum Dall, 1917: 479; PILSBRY & LOWE, 1932: 120

Epitonium (Nitidiscala) pazianum. - STRONG, 1945: 25; KEEN, 1958: 274; KEEN, 1971: 432; fig. 654

Epitonium pazianum. - STRONG, 1945: 27 [as "pazinum"]; BOSS *et al.*, 1968: 243

Epitonium (Nitidiscala) bakhanstranum KEEN, 1962: 179; KEEN, 1971: 430; fig. 639

Epitonium bakhanstranum. - KEEN, 1964: 187; DUSHANE & BRENNAN, 1969: 358

Original Description: "S. testa 'S. Cumingii' simili, sed magis elongata, majore, anfr. x. haud profunde separatis; varicibus acutis viii., acutius coronatis, lineis regularibus, ad marginem alteram spirae parallelis, ascendentibus. Long. 1.04, long. spir. .79, lat. .4, div. 25°." (CARPENTER, 1856: 165)

Diagnosis: Shell medium to large in size, white, nuclear whorls 3, opaque; subsequent whorls 7 to 11; costae 8 to 14, sharp, high, thin, reflected, with an angle at the shoulder, free of the reflected outer lip; suture deep and at an angle giving the whorls a slanted appearance; aperture oval; operculum thin, paucispiral. Length, 3 to 26 mm; width, 1½ to 10 mm.

Discussion: CARPENTER (1856: 165) described a shell from Panama, naming it *Scaloria hindsii*. In 1865 he used the same name for a shell from the Californian fauna, later determined to be *Epitonium tinctum* (Carpenter, 1864) with 11 to 14 costae. STRONG (1930: 188-190) gave a clear interpretation of the puzzle. Although CARPENTER (1864: 538) listed *S. hindsii* collected by Col. Jewett at Santa Barbara, California, he acknowledged in a footnote (p. 539) that the species is of a southern type.

Because *Epitonium apiculatum* DALL (1917: 480) is a secondary homonym of *Scala apiculata* DALL (1889: 310) from the Atlantic fauna, KEEN (1962: 179) chose to rename a specimen from La Paz, Gulf of California, at the CAS, which Baker, Hanna & Strong identified as

Explanation of Figures 54 to 62

Figure 54: *Epitonium (Cirsotrema) togatum*, Hertlein & Strong, 1951. Live-taken specimen, Manzanilla, Colima, Mexico; length 16 mm; width 6 mm; Shy Collection × 5.6

Figure 55: *Epitonium (Cirsotrema) togatum*, Hertlein & Strong, 1951. Holotype, CAS[GTC] 9620; length 37½ mm; width 13.8 mm × 1.3

Figure 56: *Cirsotrema pentadesmium* Berry, 1963. Holotype, SU [PTC] 10058; length 8.2 mm; width 3.7 mm × 9.3

Figure 57: *Scaloria vulpina* Hinds, 1844. Holotype, BM[NH], lost; length 7½ mm [figure after Sowerby, 1844] × 7.6

Figure 58: *Trichotropis gouldii* A. Adams, 1857 [holotype, BM (NH) lost; specimen illustrated from Shy Collection]; length 14½ mm; width 9 mm × 6.2

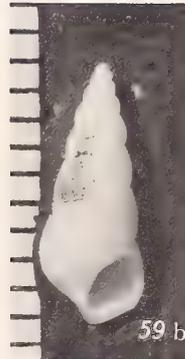
Figure 59a: *Acirsa menesthoides* Carpenter, 1864. Possible paratype BM[NH] 19621121; length 10.2 mm; width 4 mm × 3.2

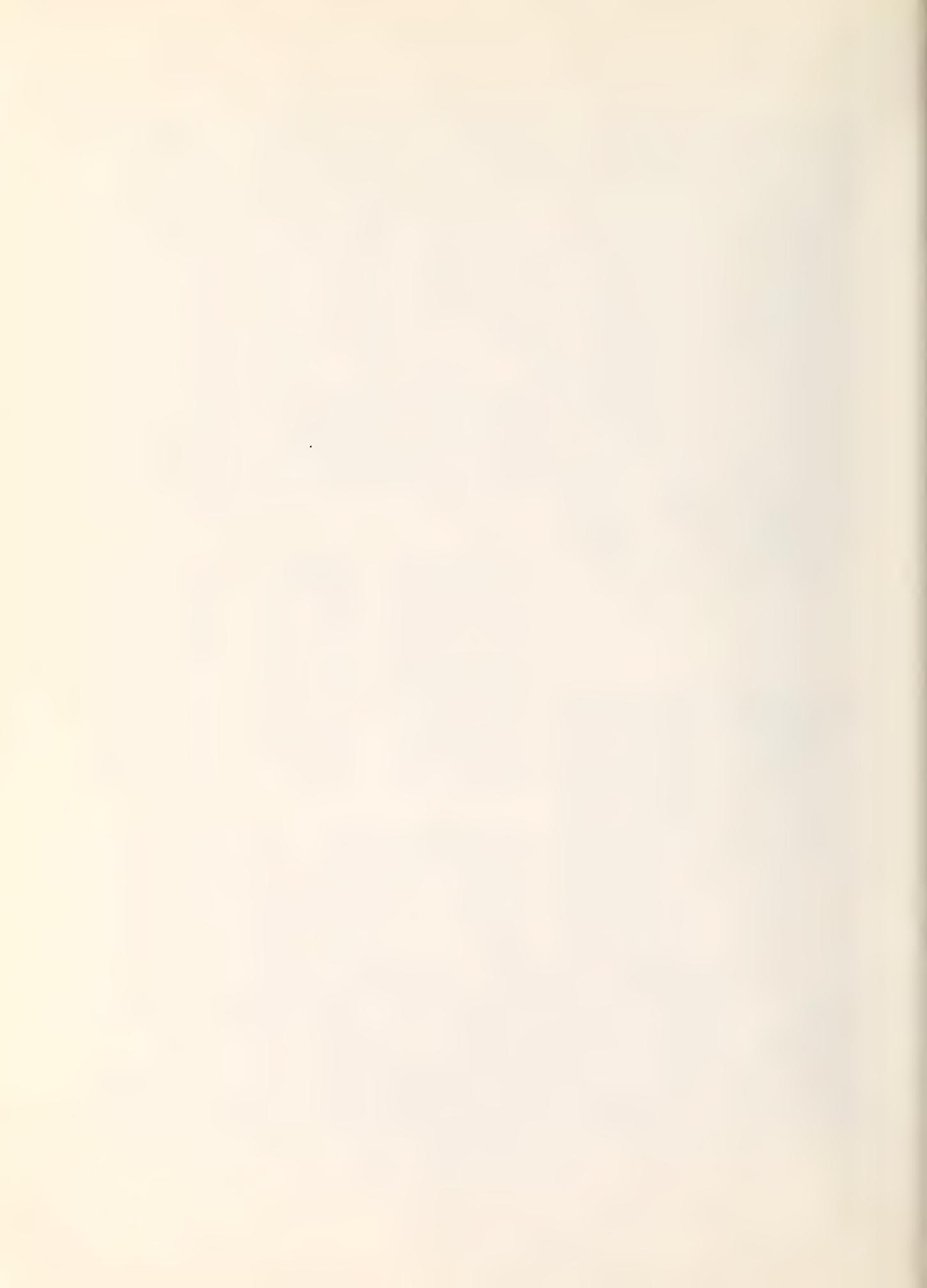
Figure 59b: *Rissoina berryi* Baker, Hanna & Strong, 1930. Holotype, CAS[GTC] 4608; length 9 mm; width 3¼ mm × 4

Figure 60: *Epitonium (Acirsa) cerralvoensis* DuShane, 1970. Holotype, LACM 1200; length 11.8 mm; width 3.7 mm × 3.6

Figure 61: *Recluzia insignis* Pilsbry & Lowe, 1932. Holotype, ANSP 155432; length 15 mm × 2.4

Figure 62: *Epitonium (Acirsa) murrha* DuShane, 1970. Holotype, LACM-AHF 1232; length 19.1 mm; width 6.9 mm × 3





E. apiculatum, without seeing the holotype, as *E. (N.) bakhanstranum*. The type of Dall's Panamic species is a chalky, immature specimen, lacking nuclear whorls. Comparison of photographs of the syntypes of *E. (N.) hindsii* (Carpenter) with the holotype of *E. (N.) bakhanstranum* Keen shows them to be conspecific. They each have the same number of thin, high costae (8), with an acute angle at the shoulder; convex whorls; an extremely deep suture; costae which are flatly reflected on the base, fusing into the reflected face of the aperture. Both taxa have a slant to the deep suture which gives the whorls a tipped appearance.

The following species, established by Dall based on beach-worm material, are placed in synonymy with *Epitonium hindsii* because they all have the same characteristics in common: *E. compradora* (1917: 480; no type locality given; range from Punta Abrejos, Baja California to the Gulf of California); *E. cylindricum* (1917: 480; type locality La Paz, Baja California); *E. musidora* (1917: 483; no type locality given); *E. pazianum* (1917: 479; type locality La Paz, California). The number of costae, which varies from 8 to 14, is within the range of variability of other epitoniid species.

Records indicate a northern range to Punta Abrejos, outer coast, Baja California (LACM-AHF 754-37) to Independencia Bay, Perú (LACM-AHF 380-35), with documentation of many stations throughout the Gulf of California southward.

Compared to *Scalaria cumingii* Carpenter, 1856 this species is more elongate, larger, and the costae have acute coronations. From *Epitonium hexagonum* (Sowerby, 1844) it differs by having a thinner, more delicate shell, with more costae and a deeper suture. Common as dead shells, only one live-taken specimen of *E. hindsii* has been seen, dredged off Puertecitos, Gulf of California, Mexico, in 11 to 15 m, December, 1964 (DuShane Collection).

Type Material:

- Scalaria hindsii*: 2 syntypes, BM[NH] 1963.21
Epitonium apiculatum: holotype, USNM 111219
Epitonium compradora: holotype, USNM 105527
Epitonium cylindricum: holotype, USNM 271037
Epitonium musidora: holotype, USNM 201203
Epitonium pazianum: holotype, USNM 111208
Epitonium bakhanstranum: holotype, CAS[GTC] 4763

Type Localities:

- Scalaria hindsii*: Panama
Epitonium apiculatum: none indicated
Epitonium compradora: none indicated
Epitonium cylindricum: La Paz, Gulf of California, Mexico
Epitonium musidora: none indicated
Epitonium pazianum: La Paz, Gulf of California, Mexico
Epitonium bakhanstranum: La Paz, Gulf of California, Mexico

Geographical Distribution and Ecology: Punta Abrejos, outer coast of Baja California, throughout the Gulf of California, Mexico, to Panama and Perú. Dredging records indicate this species is from a substrate comprised of mud or silty sand.

Bathymetric Range: Intertidal and dredged in from 11 to 198 m (all but one specimen dead)

Geochronological Range: Recent

Epitonium (Nitidiscala) politum (Sowerby, 1844)

(Figures 89, 90, 91, 92, 93, 96)

- Scalaria polita* Sowerby, 1844a: 30; SOWERBY, 1844b: 100; SOWERBY, 1847: plt. 34, fig. 99; NYST, 1871: 127; REEVE, 1873: plt. 10, fig. 77; TRYON, 1887: 69; plt. 14, fig. 43; DALL, 1917: 488
Scala polita. - H. & A. ADAMS, 1853: 222
Epitonium politum. - DALL, 1909: 223
Epitonium (Nitidiscala) politum. - KEEN, 1971: 432; fig. 655
Epitonium implicatum Dall & Ochsner, 1928: 111; plt. 6, fig. 1
Epitonium (Nitidiscala) appressicostatum Dall, 1917: 482
Epitonium (Nitidiscala) appressicostatum. - STRONG, 1945: 26, 27; KEEN, 1958: 272
Epitonium appressicostatum. - DURHAM, 1942: 121; EMERSON & PUFFER, 1957: 39 (as "cf."); DUSHANE & POORMAN, 1967: 424; BOSS *et al.*, 1968: 31; DUSHANE & BRENNAN, 1969: 358
Epitonium (Nitidiscala) pedroanum Willett, 1932: 88; plt. 5, fig. 3; STRONG, 1945: 27; BURCH, 1945: 30, 31
Epitonium pedroanum. - KEEN, 1937: 35; SPHON, 1971: 11

Original Description: "*T. tenui, elongata, laevi, imperforata; anfractibus numerosis, vix prominentibus; varicibus sub-numerosis, tenuis, in medis anfractu obsoletis; colore pallide griseo.* The whorls are numerous, and not very prominent. The varices appear as if worn away in the centre of the whorls. Taken by Mr. Cuming at Xipixappi, West Columbia, in sandy mud, ten fathoms deep." (SOWERBY, 1844a: 30)

Diagnosis: Shell medium in size, thin, polished, yellowish brown in color; nuclear whorls 3 to 5, smooth, glassy, amber colored; subsequent whorls 7 to 12, rounded; costae 9 to 15, white, nearly obsolete on the body whorls, slightly angulate at the shoulder, continuous over suture; suture moderately deep; base rounded; non-umbilicate; aperture oval, margin slightly angular in front. Length, 9 to 16 mm; width, 3½ to 5 mm.

Discussion: Fresh specimens are very glassy, sometimes brownish in color with the costae being mere threads.

Spiral striulae mark succeeding nuclear whorls after the first 2 on some specimens, but this characteristic is not constant in all specimens. Occasionally the costae are discontinuous in the suture.

Epitonium implicatum Dall & Ochsner, 1928, a Pleistocene mollusk from the Galápagos Islands, fits the description of *E. politum* very well, with whorls evenly rounded; surface smooth; costae 13, low, a little expanded at the suture; base rounded, imperforate.

Comparison of the types of *Epitonium appressicostatum* Dall, 1917, *E. implicatum* and *E. pedroanum* Willett, 1932, with the original figure of *E. politum* shows these 4 species to be conspecific. Records indicate a distribution of the species from San Pedro, California (LACM 1036, holotype, in 36m), into the northern end of the Gulf of California (AMNH, A-3634, west of Tiburon Island, in 393m) to James Bay, Santiago Island, Galápagos Islands, Ecuador (DeRoy Collection, in 22m).

Epitonium (Nitidiscala) politum differs from *E. (N.) aciculinum* by having glassy whorls, a slightly more bulbous shell, costae that are close and numerous on the nepionic whorls, discontinuous on later whorls, and a far greater geographical range. It also occupies a deeper subtidal level.

Type Material:

Scalaria polita: holotype, BM(NH)

Epitonium (Nitidiscala) appressicostatum: holotype, USNM 59334

Epitonium implicatum: holotype, CAS[GTC] 2932

Epitonium (Nitidiscala) pedroanum: holotype, LACM 1036

Type Localities:

Scalaria polita: West Colombia

Epitonium (Nitidiscala) implicatum: Galápagos Islands, Ecuador

Epitonium appressicostatum: Acapulco, Mexico

Epitonium (Nitidiscala) pedroanum: San Pedro, California

Geographical Distribution and Ecology: San Pedro, California to Panama and Ecuador. Records indicate a bottom of rocks, nullipores and broken shells, sandy mud.

Bathymetric Range: Dredged in from 11 to 393 m

Geochronological Range: Pleistocene and Recent

Epitonium (Nitidiscala) shyorum
DuShane & McLean, 1968

(Figure 75)

Epitonium (Epitonium) shyorum DuShane & McLean, 1968: 2; fig. 2; SPHON, 1971: 11

Epitonium (Nitidiscala) shyorum. - KEEN, 1971: 434; fig. 657

Original Description: "Shell small, white, tall, with 8 to 9 flaring costae, continuous from whorl to whorl, with an angular spine at the shoulder of each whorl; the ribs least pronounced on the lower portion of the body whorl; nuclear whorls 3, smooth, convex, brown, and glassy; postnuclear whorls 10; suture distinct but not deeply impressed; umbilicus lacking; surface area between costae lacking spiral sculpture; whorls flat sided, angulate at the shoulder and at the base; basal disk or cord lacking; aperture oval, but lip reflecting angulate outline of the costae, with a right angled spine on the shoulder; inner lip lacking; operculum missing in type. Dimensions (in mm): length 12; width 4 (holotype)." (DUSHANE & McLEAN, 1968: 2; fig. 2)

Discussion: This is a small, slender form, differing from others in having tabulate, spinose whorls, angulate base, incomplete peritreme and 9 costae per whorl. It does not suggest comparison with other Panamic species. The characteristic stepped outline of the shell and the absence of the inner lip readily distinguish it. Although originally placed in the subgenus *Epitonium* Röding, 1798, later consideration suggests assignment of the species to *Nitidiscala* deBoury, 1909.

Records for this species are scanty, but indicate its presence in the Gulf of California (LACM-AHF 682-37, Concepción Bay) and (AMNH 74767) Maria Magdalena Island, Tres Marias Islands, Mexico to Manzanillo, Colima, Mexico.

Type Material:

Epitonium (Epitonium) shyorum: holotype, LACM 1160

Type Locality:

Epitonium (Epitonium) shyorum: Manzanillo, Colima, Mexico

Geographical Distribution and Ecology: Concepción Bay, Gulf of California to Manzanillo, Colima, Mexico, from broken shell and sand bottom.

Bathymetric Range: Dredged in from 20 to 25 m

Geochronological Range: Recent

Epitonium (Nitidiscala) statuminatum (Sowerby, 1844)
(Figures 76, 77)

Scalaria statuminata Sowerby, 1844a: 102; pl. 35, fig. 127; SOWERBY, 1844b: 30; CARPENTER, 1857a: 230, 336; CARPENTER, 1860: 10; NYST, 1871: 135; REEVE, 1873: pl.

3, fig. 18; TRYON, 1887: 58; plt. 12, fig. 60; DALL, 1917: 488; ZETEK, 1918: 25

Scala (Opalia) statuminata. - H. & A. ADAMS, 1853-1858: 222
Epitonium statuminatum. - DALL, 1909: 223; M. SMITH, 1944: 7 [error in illustration, is fig. 60]; OLSSON, 1961: 38

Epitonium (Nitidiscala) statuminatum. - KEEN, 1958: 274; fig. 131; KEEN, 1971: 434; fig. 658

Epitonium (Nitidiscala) strongi LOWE, 1932: 115; plt. 9, fig. 5 [not *E. strongi* Bartsch, 1928]; WILSON, 1967: 252

Epitonium strongi Bartsch, 1928: 71, 72; figs. 2, 3

Epitonium (Nitidiscala) strongi Lowe. - M. SMITH, 1944: 7 [error in illustration, is fig. 64]

Epitonium (Nitidiscala) strongianum Lowe, 1932: 36 [new name for *E. strongi* Lowe, preoccupied]; STRONG, 1945: 26, 27

Original Description: "*T. parva, crasa, brevis, laevigata, imperforata; anfractibus contiguus, vix prominentibus, antice linea elevata cinctis; varicibus quinque, prominentibus, ad apicem continuis, antice crassis, postice in angulum elevatum expansis; apertura subrotunda, labio externo, antice tenui; colore, inter varices coeruleo.* A small, short, thick species, with very prominent ribs, which are elevated and expanded into a broad angle, at the upper part of the whorls, and very thick at the lower; they are united with each other so as to form five oblique prominent ridges along the spire. Brought by Mr. Cuming from Hayti in Peru." (SOWERBY, 1844a: 30)

Diagnosis: Shell white, shiny, thick, medium to large in size, with 10 contiguous whorls, rapidly expanding; costae start immediately on the nuclear whorl, continuing obliquely, expanding with each whorl into larger, angularly round, reflected costae; the costae on each whorl coalesce into the succeeding costae, with an overlap so that each costa merges into another at the suture, 5 in all; the last costa bounds the outer perimeter of the aperture on the right side; sutures deep; aperture round; basal disk present but not prominent; lip entire, heavy; operculum unknown.

Discussion: Sowerby failed to designate a holotype for *Scaloria statuminata*. Of the 3 syntypes in the BM(NH) the largest is in the best state of preservation and is here selected as the lectotype with the following dimensions: length, 20.37 mm; width, 8.51 mm.

LOWE (1932a: 115; plt. 9, fig. 5) named what he thought was a shell new to science from El Salvador and called it *Epitonium (Nitidiscala) strongi*. Because it is a primary homonym of *E. strongi* Bartsch, 1928 (p. 71, figs. 2, 3) LOWE (1932b: 36) changed the name of this taxon to *E. strongianum*. However, *E. strongianum* proves to be a synonym of *Scaloria statuminata*. Bartsch's species, *E. strongi*, belongs in the subgenus *Asperiscala* and is a synonym of *E. (A.) acapulcanum* Dall, 1917 (see under that title).

This is a rare species, not often found represented in collections. A specimen in the Shasky Collection from Panama (March 10, 1970) measures 22 mm in length, 10½ mm in width, and has 10 whorls, with the topmost nuclear whorl missing. Two specimens in the DuShane Collection were dredged off Mazatlán, Sinaloa, Mexico in 36 m (length, 15 mm; width, 7 mm; and length, 11 mm; width, 5½ mm) and seem to mark this point as the present northern limit of the range.

Type Material:

Scaloria statuminata: lectotype (1) (herein), BM(NH); paralectotypes (2) (herein), BM(NH)

Epitonium (Nitidiscala) strongi Lowe: holotype, ANSP 155535

Epitonium strongi Bartsch: holotype, USNM 367967

Type Localities:

Scaloria statuminata: Hayti (Paita), Perú

Epitonium strongi Lowe: El Salvador

Epitonium strongi Bartsch: Guayaquil, Ecuador

Geographical Distribution and Ecology: Mazatlán, Sinaloa, Mexico, to Perú.

Bathymetric Range: Intertidal to 36 m

Geochronological Range: Recent

Epitonium (Nitidiscala) suprastriatum (Carpenter, 1857)

(Figure 78)

Scaloria suprastrata Carpenter, 1857b: 446; CARPENTER, 1857a: 260, 336; CARPENTER, 1860: 10; NYST, 1871: 139; PALMER, 1951: 62; BRANN, 1966: 17

Epitonium (Nitidiscala) suprastriatum. - STRONG, 1945: 26; KEEN, 1958: 276; KEEN, 1968: 401, 408; plt. 59, fig. 101; text fig. 39

Original Description: "*S. t. turrita, gracilior, compacta; anfr. normalibus vii. attingentibus, rotundatis; costis xii. acutis, vix superne productis, lineis rectis, marginem alterum spirae parallelis, ascendentibus; anfr. primis spiraliter tenuissime striatis, adultis laevibus; umbilico nullo.* Differs from *S. mitraeformis* and its congeners in being broader, with the whorls not touching, and the shoulder-projections very slight. Only one nearly perfect and two young dead specimens, probably conspecific, were found. Long. '43, long. spir. '27, lat. '25, div. 40°." (CARPENTER, 1857: 446)

Diagnosis: Shell white, medium size; nuclear whorls 2½, opaque; subsequent whorls 7, inflated, coils not touching; suture very deep; costae 10 to 14 with a broad spine at the shoulder, somewhat reflected, dipping under the lip; aperture oval; lip reflected, entire, slightly patulous, broad spine posteriorly; operculum thin, paucispiral.

Discussion: This species can be easily confused with *Epitonium (Asperiscala) obtusum* (Sowerby, 1844) unless the following characters are noted. From Sowerby's species it differs by having no spiral sculpture on the early whorls and by having disjunct whorls with fewer costae, free of the lip, and an oval aperture.

KEEN (1968: plt. 59, fig. 101) photographed the syn-type of *Epitonium (Nitidiscala) suprastriatum* at the BM (NH) (1964), but the angle at which the photograph was taken fails to show the deep sutures and disconnected whorls described by Carpenter. Few collections include this species. Nine specimens, some collected alive by Charles Snell while he was diving off La Paz, Baja California, Mexico, extend the known range from Mazatlán westward across the Gulf of California.

Type Material:

Scalaria suprastrata: syntype, BM(NH) 2037

Type Locality:

Scalaria suprastrata: Mazatlán, Sinaloa, Mexico

Geographical Distribution and Ecology: La Paz, Baja California to Mazatlán, Sinaloa, Mexico. Habitat unknown

Bathymetric Range: Intertidal to 12 m

Geochronological Range: Recent

Epitonium (Nitidiscala) tabogense Dall, 1917

(Figure 108)

Epitonium (Nitidiscala) tabogense Dall, 1917:484; STRONG, 1945: 26; KEEN, 1958: 274; KEEN, 1971: 434; fig. 660

Epitonium tabogense. - ZETEK, 1918: 25; M. SMITH, 1944: 7; BOSS *et al.*, 1968: 313

Original Description: "Shell small, short, conic, white, with nearly three smooth nuclear whorls and four or five subsequent whorls; varices 11, sharp, erect, not continuous over the suture, not angulated or spinose at the shoulder, anteriorly smooth; base rounded, imperforate; aperture sub-circular, the thickened margin nearly interrupted over the body. Length, 3; diameter, 1.5 mm." (DALL, 1917: 484)

Discussion: The holotype is a juvenile specimen too young for comparison with adult topotype material.

Type Material:

Epitonium (Nitidiscala) tabogense: holotype, USNM 211786

Type Locality:

Epitonium (Nitidiscala) tabogense: Taboga Island, Panama

Geographical Distribution and Ecology: Off Taboga Island, Panama. Habitat unknown.

Bathymetric Range: From 112 m

Geochronological Range: Recent

Epitonium (Nitidiscala) willetti

Strong & Hertlein, 1937

(Figure 72)

Epitonium (Nitidiscala) willetti Strong & Hertlein, 1937: 171; plt. 35, fig. 5; STRONG, 1945: 27; KEEN, 1958: 274; fig. 134; KEEN, 1971: 434; fig. 661

Explanation of Figures 63 to 69

Figure 63: *Epitonium (Ferminoscala) brunneopicta* Dall, 1908. Holotype, USNM 97054; length 37 mm; width 10 mm × 1.3

Figure 64: ? *Eglisia nebulosa* Dall, 1919. Holotype, USNM 120702; length 19 mm; width 6 mm × 2.7

Figure 65: *Epitonium (Ferminoscala) ferminiana* Dall, 1908. Holotype, USNM 96818; length 38 mm; width 17 mm × 1.4

Figure 66: *Scala (Acrilla) pompholyx* Dall, 1890. Holotype, USNM 96474; length 14 mm; width 7.6 mm × 2.3

Figure 67: *Amaea (Scalina) deroyae* DuShane, 1970. Holotype, LA CM-AHF 1236; length 22.8 mm; width 7.3 mm × 3.7

Figure 68: from left to right:

Amaea (Scalina) ferminiana (Dall, 1908). Gulf of Tehuantepec, Mexico; length 40 mm; width 17 mm (DuShane Coll.) × 1½

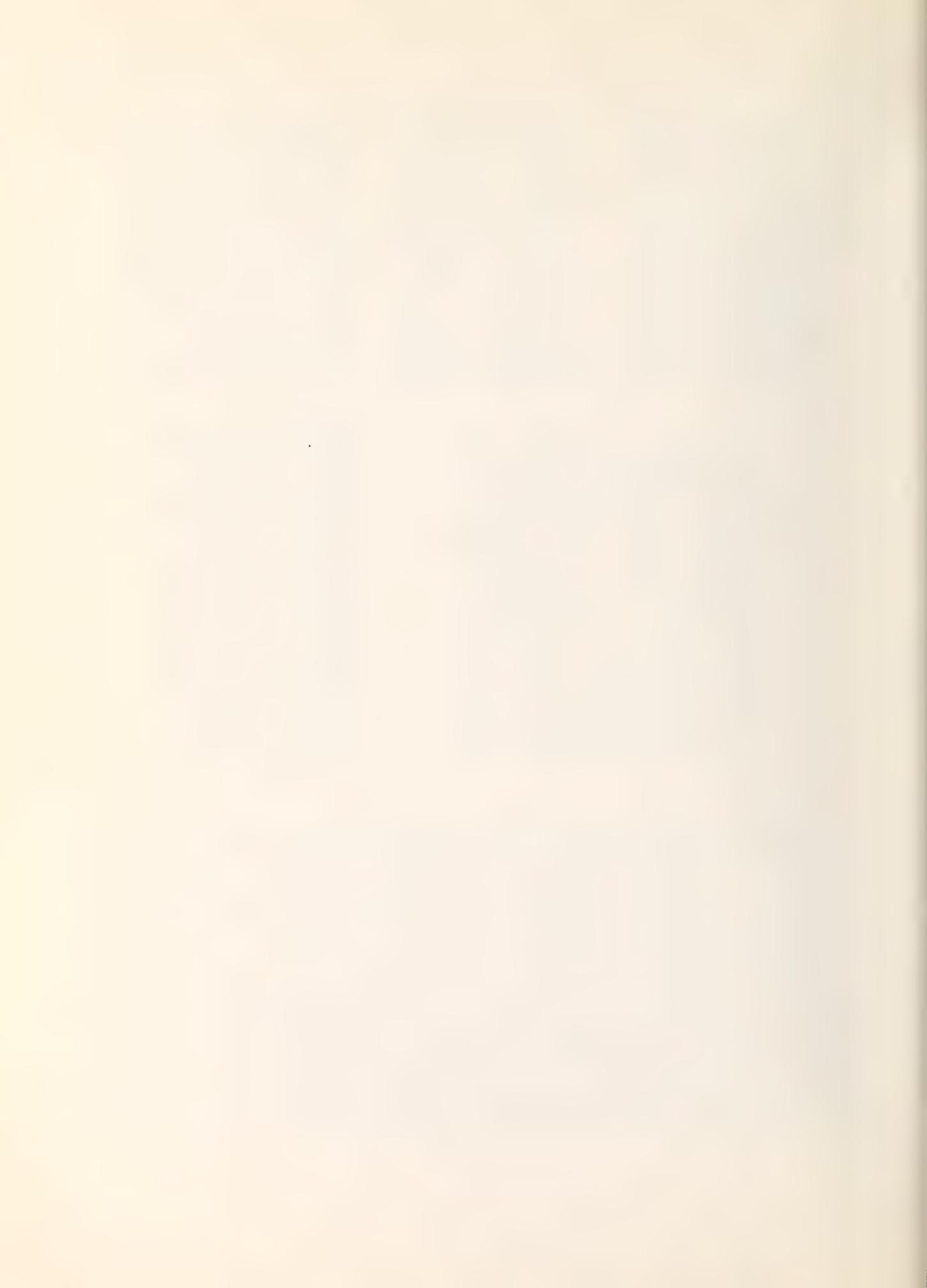
Amaea (Scalina) tehuandarum DuShane & McLean, 1968. Holotype, LACM 1161; length 39½ mm; width 15 mm × 1½

Amaea (Scalina) tehuandarum DuShane & McLean, 1968. Paratype (DuShane Coll.); length 34 mm; width 26 mm × 1.6

Amaea (Scalina) brunneopicta (Dall, 1908). Gulf of Tehuantepec, Mexico; length 35 mm, width 10 mm (DuShane Coll.) × 1.6

Figure 69: *Amaea (s. l.) contexta* DuShane, 1970. Holotype, LA CM 1199; length 15.4 mm; width 4½ mm × 4





Original Description: "Shell small, white, thin, turreted; nuclear whorls four, strongly rounded, elevated, smooth, changing abruptly to the sculpture of the succeeding whorls, of which there are five in the type; normal whorls well rounded, sutures deep; spiral sculpture absent; axial sculpture of eighteen, low sharp, erect, strongly retractive varices, continuous over the sutures where they make a marked curve to the left as they ascend the spire; at the shoulder of the whorls there is sometimes a slight expansion of the varices but no indication of a spine or coronation; on the base the varices become lower and decidedly curved; aperture nearly circular; lip thin, continuous; shell not umbilicated." (STRONG & HERTLEIN, 1937: 171; pl. 35, fig. 5)

Diagnosis: Shell small, fragile, white, turreted, nuclear whorls 2 to 4, rounded, opaque, smooth; postnuclear whorls 5 or 6, rounded; sutures deep; costae 18 to 22 or more, thin, erect, continuous over the sutures, definitely curved over the base so the costae are flatly reflected over it; umbilicus minute and hidden by the reflection of the continuous lip; aperture round; operculum unknown.

Discussion: Very few specimens of this species appear in collections. Two in the LACM-AHF, which possibly match this description, dredged during the Hancock-Pacific Expeditions, 1931-41 (*Velero III*) are from Salinas Bay, Costa Rica (Station 476-35) and from NW of Charles Island, Galápagos Islands, Ecuador (Station 802-38); one in the Poorman Collection dredged from 27 m, from the Guaymas, Mexico area and 3 specimens in the Shy Collection, from 31 m, off Manzanillo, Colima, Mexico comprise the total of known specimens, other than the 7 specimens taken by the Templeton Crocker Expeditions, 1932 (CAS) from off Mazatlán, Sinaloa, Mexico (type lot) in 22 m, all defective or juvenile. The type measures: length, 3.2 mm; width, 1.6 mm.

There seems to be an affinity among 4 species in the subgenus *Nitidiscala*, *Epitonium curvilineatum* (Sowerby, 1844) from Central America, *E. sawinae* (Dall, 1903) from off Catalina Island, California, *E. imbrex* Dall, 1917 from Panama, and *E. willetti* Hertlein & Strong, 1937 from off Mazatlán, Mexico. All have the same characteristics in general, but with great differences in size and type locality. Sizes vary from 2.3 to 16 mm in length; 1.0 to 7½ mm in width. Assuming identifications to be correct, DALL & BARTSCH (1910: 21) dredged *E. sawinae* from off Barkley Sound, British Columbia; the Hancock Expeditions (1931-41) dredged it commonly from off Anacapa Island, California south to the Coronados Islands and Cedros Island, outer Baja California, Mexico (additional records

are: off Punta Eugenia and Puerto Escondido, Gulf of California, Mexico). This Dall species with the type locality Catalina Island, California, is from a depth of 29 m and has a length of 10½ mm with a width of 4 mm. In a general statement DALL (1917: 481) suggested that *E. sawinae* ranged into the Gulf of California, but did not validate his suggestion with any specific data. STRONG & HERTLEIN (1937: 171) compared *E. willetti* from Mazatlán, Mexico, to *E. sawinae* stating, "The nearest species would seem to be *E. sawinae* Dall, 1903 which is more slender, with the varices almost always showing spines at the shoulder of at least some of the whorls."

Unfortunately, the type of *Epitonium curvilineatum* could not be located at the BM(NH) (*teste* Keen), so we have only the illustration in SOWERBY (1844: pl. 33, fig. 59; type locality, Central America) by which to make an evaluation.

Epitonium imbrex Dall (1917: 486) from Panama matches the description of all 3 species discussed, but is so small (length 2.3 mm; width 1.0 mm) that it is difficult to know what it is. There seem to be no records of either species having been taken since their original description, which in itself suggests synonymy. All 4 species have many costae, thin, erect; shell texture fragile; whorls swollen, basal whorl with flattened costae. Perhaps with continued research 3 of these species will be found to be synonymous with *E. curvilineatum*. At the present time the wide disparity of localities in which these similar species are found precludes conclusions being made. It is highly improbable that *E. sawinae* from the cold water fauna of British Columbia could be the same species as that found in Panama. If the identification of Dall & Bartsch could be found to be in error, then it would not be unreasonable to reconcile the several species as one, with a range from Anacapa Island, California to Ecuador. There seem to be no other epitioids from the Panamic-Galapagan province which have the same flatness of the costae on the basal whorl. For the present time, *E. willetti* will be treated as a separate species.

Type Material:

Epitonium (Nitidiscala) willetti: CAS[GTC] 6987

Type Locality:

Epitonium (Nitidiscala) willetti: Mazatlán, Sinaloa, Mexico

Geographical Distribution and Ecology: Gulf of California, Mexico to Costa Rica and Ecuador; dredged in mud, sand and broken shell substrate

Bathymetric Range: 14 to 36 m

Geochronological Range: Recent

(Depressiscula) deBoury, 1909

[Type species: (OD) *Scala aurita* Sowerby, 1844; synonym: *Pictoscala* Dall, 1917; type species (OD): *Scalardia lineata* Say, 1822 (not Röding, 1798; not Kiener, 1838)]

Shells purple-brown with white costae, oval aperture and fine spiral striae that do not form a pattern.

Epitonium (Depressiscula) aciculinum (Hinds, 1844)

(Figures 100, 101, 102)

Scalardia aciculina Hinds, 1844a: 125, figured; HINDS, 1844-45: 49, figured; SOWERBY, 1844: 100, pl. 34, fig. 100; CARPENTER, 1860: 10; NYST, 1871: 90; REEVE, 1873-1874: pl. 13, fig. 98; TRYON, 1887: 69; pl. 14, fig. 42; DALL, 1917: 487; KEEN, 1966: 268

Scala aciculina. - H. & A. ADAMS, 1853-1858: 221

Epitonium (Nitidiscala) aciculicum [sic]. - STRONG, 1945: 25

Epitonium (s. l.) aciculina. - KEEN, 1958: 276; fig. 221

Epitonium (Asperiscala) longinosanum DuShane, 1970: 1, 2-fig.1; SPHON, 1971: 11; KEEN, 1971: 426; fig. 622

Epitonium (Nitidiscala) aciculinum. - KEEN, 1971: 430; fig. 638

Original Description: "*Testa elongata, polita; anfractibus decenis subdisjunctis; costis rotundatis, superne angulatis; anfractu ultimo decemcostato; apertura ovali; umbilico parvo. Inhab.* West coast of intertropical America." (HINDS, 1844: 125)

Diagnosis: Shell medium to large in size, purple in live-taken specimens; nuclear whorls $2\frac{1}{2}$ to 4, glassy, rounded, smooth; postnuclear whorls 6 to 10, convex; costae 9 to 11, easily broken, white, continuous from whorl to whorl, with an occasional thicker one, reflected and with a sharp spine on the whorl shoulder; spiral striae uneven, visible only under $10\times$ magnification; columellar lip curved, peritreme continuous, reflected over the ends of the costae, outer lip thickened by the last costa; aperture oval, umbilicus lacking; operculum not seen.

Discussion SOWERBY's (1844: pl. 34, fig. 10) figure shows 13 whorls, 2 nuclear plus 11 postnuclear whorls. His figure shows that the shell is imperforate and needle-like in shape ("*aciculina*"). REEVE (1873-74: pl. 13, fig. 98) states that the shell is "small, elegantly acicular, purple-brown between the varices; whorls numerous, rather convex; varices white, rather distant, thin, rounded, nearly angular above, continuous." TRYON (1887: 69) says the shell is "narrow, chestnut brown; whorls 9, rather convex, crossed by somewhat distant, thin, white lamellae, sub-

angulated in the middle." DALL (1917: 487) describes the shell as a "purple brown species with about 12 arcuate varices and 10 whorls. It is imperforate and the varices are not spinose at the shoulder." Dall probably had not seen the shell but was reporting only what he saw from the figure. KEEN (1958: 276) cites the shell as 9 mm in length with 10 costae. KEEN (1966: 268), reporting on her trip to the British Museum (Natural History), stated that she did not find the type of *Scalardia aciculina*; however, she thought this was probably a valid species even though no recent specimens had been collected. Not until Margaret Cunningham returned from Mexico (February 1972) with 6 specimens (length 4 to 11 mm; width 1 to $2\frac{1}{2}$ mm) she had dredged in 9 m of water off a small cove approximately 48 km south of Las Varas, Nayarit, Mexico, did it become evident that *Epitonium (Asperiscala) longinosanum* DuShane, 1970 is a synonym of *S. aciculina*. The large size of the former (length, $16\frac{1}{2}$ mm; width, $5\frac{1}{2}$ mm), the type locality (outer coast of Baja California), and the good condition of the type that still retained sharp spines on the whorl shoulders, were misleading factors.

Epitonium (Depressiscula) aciculinum differs from *E. (Nitidiscala) politum*, a similar form, by having a more slender shell, costae that are continuous from whorl to whorl and are as far apart on the nepionic whorls as they are on the postnuclear whorls, and by occupying a shallower sub-tidal level.

Type Material:

Scalardia aciculina: holotype, probably lost, not in BM(NH)

Epitonium (Asperiscala) longinosanum: holotype, LACM 1196

Type Localities:

Scalardia aciculina: Central America

Epitonium (Asperiscala) longinosanum: Rancho Inocentes, Baja California (outer coast), Mexico

Geographical Distribution and Ecology: Outer coast of Baja California, Nayarit, Mexico and Central America. Dredged on sand and broken shell substrate.

Bathymetric Range: 9 to 54 m

Geochronological Range: Recent

Epitonium (Depressiscula) purpuratum (Dall, 1917)

(Figure 103)

Epitonium (Pictoscala) purpuratum Dall, 1917: 477; ZETEK, 1918: 25; M. SMITH, 1944: 7; STRONG, 1945: 20; KEEN, 1958: 275; BOSS *et. al.*, 1968: 270; KEEN, 1971: 434; fig. 663

Scala purpurata. - DEBOURY, 1919: 37

Original Description: "Shell small, dark purple, with seven well-rounded whorls, exclusive of the (lost) nucleus; minor varices linear, low, about 18 in number, major varices one or two, white and conspicuous; spiral sculpture [of] extremely fine striae visible under magnification; base rounded, imperforate, the disk feebly marked; aperture ovate; the thickened margin nearly or quite interrupted over the body. Length, 10; diameter, 4.5 mm." (DALL, 1917: 477)

Diagnosis: Shell dark purple-brown in color, medium in size; nuclear whorls 2, conic; postnuclear whorls 7 to 9, rounded; costae 13 to 19, white, low, with an occasional heavy costa; spiral sculpture of extremely fine, uneven striae between the costae; no basal disk or keel, although the color changes near the periphery of the basal whorl; interior of shell rust-brown; aperture oval; lip heavy, white, thin on the body whorl; operculum unknown. Length of shell 10 mm; width, 4½ mm.

Discussion: The holotype is very worn (2 specimens were obtained originally from the beach at Old Panama by Dr. MacDonald). The characteristics remain, although the nuclear whorls are missing. The specimens have faded to a dark brown with time as Dall distinctly mentioned the purple color in his description. For this species DALL (1917: 477) proposed a new subgenus, *Pictoscala*. His reason was the dark colored body with a feebly developed basal disk, but apparently he overlooked the subgenus *Depressiscula* deBoury (1909: 258) with the same description. Examination of the type of *Epitonium purpuratum* under magnification of 40 × reveals no basal keel, only a change of color at the periphery of the last whorl. Therefore, Dall's reasons for establishing a new subgenus do not seem valid since the subgenus *Depressiscula* is adequate to receive forms with dark colored whorls and white costae, with fine striae between the whorls and with an oval aperture.

One specimen in the Shasky Collection from El Rubio, Perú (length, 12 mm; width, 3 mm) matches well the photograph and description of the type. The color is a purple-brown and there are 17 costae, 2 nuclear whorls and 9 postnuclear whorls.

Type Material:

Epitonium (Pictoscala) purpuratum: holotype, USNM 252242

Type Locality:

Epitonium (Pictoscala) purpuratum: Beach at Old Panama

Geographical Distribution and Ecology: Panama to northern Perú; habitat unknown

Bathymetric Range: Unknown

Geochronological Range: Recent

(*Hirtoscala*) Monterosato, 1890

[Type species (SD, Cossmann, 1912): *Scalaria cantrainei* Weinkauff, 1866]

Costae with an exaggerated, sometimes tubular spine at the periphery of the whorl.

Epitonium (Hirtoscala) mitraeforme (Sowerby, 1844)

(Figure 74)

Scalaria mitraeformis Sowerby, 1844a: 12; SOWERBY, 1844b: 87; plt. 32, fig. 30; CARPENTER, 1856b: 165; CARPENTER, 1857a: 186, 336; CARPENTER, 1857b: 446; CARPENTER, 1860: 10; NYST, 1871: 121; REEVE, 1873: plt. 6, fig. 44; TRYON, 1887: 63; plt. 13, fig. 96; DALL, 1917: 487

Scala mitraeformis. - H. & A. ADAMS, 1853: 221

Epitonium (s. l.) mitraeforme. - KEEN, 1958: 276; fig. 148

Epitonium (Hirtoscala) mitraeforme. - KEEN, 1971: 428; fig. 635

Original Description: "*Sc. muricatae similima, sed magis tenui; varicibus augustioribus [sic], angulis magis elevatis; anfractibus magis distinctis; colore albo.*"

"The varices of this shell are less expanded, and the toothlike angles are more elevated than in *Sc. muricata*; the shell is also lighter and more elegantly formed. Length, 18 mm; width 8 mm." (SOWERBY, 1844: 12)

Diagnosis: Shell large in size, white, tabulated; whorls 10, rapidly enlarging; suture very deep; costae 12, somewhat narrow on the whorl, reflected, expanded on the periphery, becoming more reflected and elevated near the suture; aperture round; lip reflected, with a spine at the shoulder; operculum thin, horny, paucispiral.

Discussion: REEVE (1873-74) stated, "Shell pyramidal, spire acuminate, whorls contiguous, varices numerous, expanded into an aculeated small lobe near the suture; aperture ovate; outer lip marginated at the suture, then sharply lobed."

The original description leaves us wishing we might have a more explicit diagnosis. In defense of Sowerby, only 1 specimen from the Cuming Collection was available to him. Since then, only 1 other specimen (in the Shasky Collection, live-taken from the Gulf of Tehuantepec, Mexico, in 9 to 27 m; length, 20 mm; width, 7½ mm) compares favorably with a photograph of the type. Although somewhat similar to *Epitonium (Hirtoscala) reflexum* (Carpenter, 1856), *E. (H.) mitraeforme* is narrower, with less expanded and more numerous costae. Both species

apparently occur in the same bathymetric range, having been taken in moderately shallow water.

Type Material:

Scalaria mitraeformis: holotype, BM(NH)

Type Locality:

Scalaria mitraeformis: Guacomayo, Chiapas, Mexico

Geographical Distribution and Ecology: Southwest coast of Mexico (Gulf of Tehuantepec, Chiapas, Mexico)

Bathymetric Range: Dredged in 9 to 27 m

Geochronological Range: Recent

Epitonium (Hirtoscala) reflexum (Carpenter, 1856)

(Figure 94)

Scalaria reflexa Carpenter, 1856a: 235; CARPENTER, 1857a: 288, 336; CARPENTER, 1860: 10; NYST, 1871: 131; TRYON, 1887: 84; DALL, 1917: 488

Foveoscala reflexa. - DEBOURY, 1909: 257

Epitonium (Hirtoscala) reflexum. - KEEN, 1958: 272; KEEN, 1971: 430; fig. 636

Epitonium (Foveoscala) reflexum. - PALMER, 1963: 331; pl. 63, figs. 5, 6

Epitonium reflexum. - DUSHANE & BRENNAN, 1969: 358

Original Description: "*S. t. turrata, anfractibus x. valde disjunctis, laevibus; varicibus in anfractu utroque v. magnis, valde prominentibus, ad marginem reflexis, supra in spira brevi semitubulari productis; lineis varicum subspirilibus; vertice laevi; apertura circulari, ad basin haud umbilicata. Long. .6, lat. (spinas includens) .21, long. spir. .45 poll.; div. 40°.*"

"Most nearly allied to *S. mitraeformis* Sow. and remarkable for the large size of the varices, which are reflexed, and produced at the shoulder into a semi-tubular spout. The varical lines make about one revolution from the apex to the base. In the very young shell the varices are not shouldered, and are more numerous." (CARPENTER, 1856a: 235)

Diagnosis: Shell medium to large, white, conic; whorls 10, nearly disjunct; costae 5, expanded, rising to a tubular spout at the shoulder, strongly reflected below the periphery, sufficient to obscure the large, deep umbilicus, aperture round, lip reflected, broad, with a spine at the shoulder, patulous below; operculum dark, horny. Length 10 to 15 mm; width 4 to 5 mm.

Discussion: Since this is not generally an intertidal species, few collections include it, although it may commonly be obtained by shallow-water dredging. The photograph of the type in the BM(NH) shows clearly the characteristic tubular twisting of the costae as they rise from the periphery of the whorl. This is a species not easily confused with others in the Panamic-Galapagan province. Five living specimens were obtained from the east side of Santa Margarita Island, Baja California (outer coast) from the intertidal zone down to 1.8 m (LACM Collection); 12 living specimens were dredged from Tenacatita Bay, Jalisco, Mexico in 11 m from weed and sand substrate (DuShane Collection); one specimen was dredged off Corinto, Nicaragua (AMNH 90841).

Type Material:

Scalaria reflexa: holotype, BM(NH) 1962.1116

Type Locality:

Scalaria reflexa: San Blas, Nayarit, Mexico

Explanation of Figures 70 to 78

Figure 70: *Epitonium (Nitidoscala) callipeplum* Dall, 1919. Holotype, USNM 218096; length 9 mm; width 4 mm × 7

Figure 71: *Epitonium (Nitidoscala) barbarinum* Dall, 1917. Holotype, USNM 46229; length 19 mm; width 6½ mm × 3.2

Figure 72: *Epitonium (Nitidoscala) willetti* Strong & Hertlein, 1937. Holotype, CAS[GTC] 6987; length 3.2 mm; width 1.6 mm × 21

Figure 73: *Epitonium (Nitidoscala) hancocki* DuShane, 1970. Holotype, LACM-AHF 1235; length 13 mm; width 5.2 mm × 4

Figure 74: *Scalaria mitraeforme* Sowerby, 1844. Holotype, BM[NH]; length 18 mm; width 8 mm × 3.3

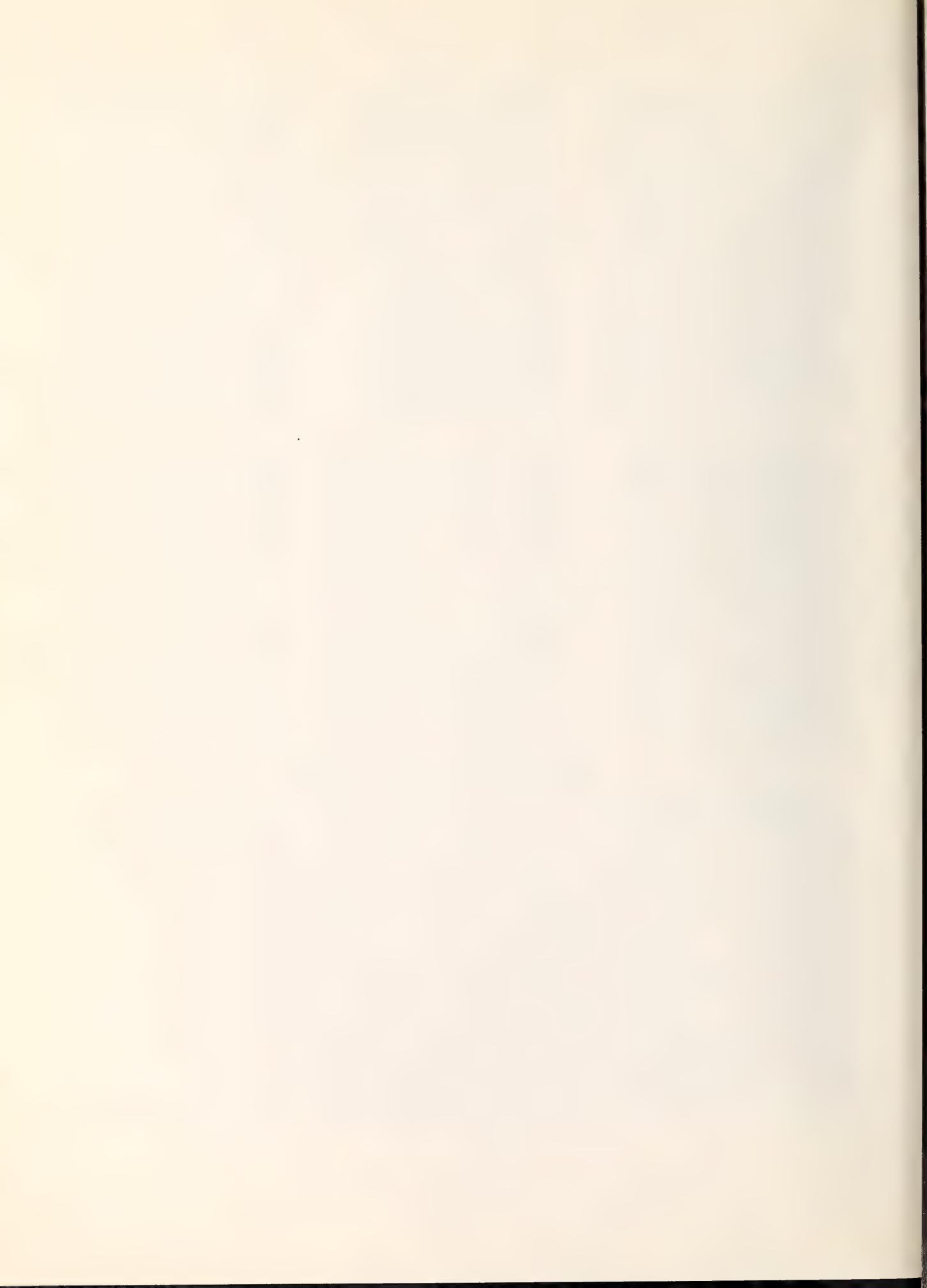
Figure 75: *Epitonium (Nitidoscala) shyorum* DuShane & McLean, 1968. Holotype, LACM 1160; length 12 mm; width 4 mm × 4.1

Figure 76: *Epitonium (Nitidoscala) strongi* Lowe, 1932. Holotype, ANSP 155535; length 19 mm; width 9.1 × 2½

Figure 77: *Scalaria statuminata* Sowerby, 1844. Lectotype (herein) (1), BM[NH] length 20.37 mm; width 8.51 mm; × 3.1 paralectotypes (herein) (2) BM[NH]

Figure 78: *Scalaria suprastrata* Carpenter, 1857. Syntype, BM[NH] Tablet 2037; length 11 mm × 5.4





Geographical Distribution and Ecology: Santa Margarita Island (entrance to Magdalena Bay), Baja California, Mexico, throughout the Gulf of California, and south to Nicaragua. Living specimens dredged from among weed on a sand substrate.

Bathymetric Range: Dredged in shallow water down to 9m, rarely taken intertidally.

Geochronological Range: Recent

Epitonium (Hirtoscala) replicatum (Sowerby, 1844)

(Figures 95, 97, 98, 99)

Scalaria replicata Sowerby, 1844a: 11; SOWERBY, 1844b: 84; plt. 32, figs. 23, 24; REEVE, 1873: plt. 6, fig. 39; NYST, 1871: 131; TRYON, 1887: 56, plt. 11, fig. 43; TOMLIN, 1927: 170

Scala replicata. - H. & A. ADAMS, 1853: 222

Epitonium replicatum. - TOMLIN, 1927: 120

Epitonium replicata. - DUSHANE & POORMAN, 1967: 424

Epitonium (Hirtoscala) replicatum. - KEEN, 1971: 430, 903; fig. 637

Epitonium bialatum Dall, 1917: 485; ZETEK, 1918: 25; LOWE, 1935: 31; STRONG, 1945: 25; HERTLEIN & STRONG, 1951: 89; BOSS *et al.*, 1968: 46

Scala (Stenorhytis) [sic] bialata. - DEBOURY, 1919: 39

Epitonium (Nitidoscala) bialatum. - STRONG, 1930: 39

Epitonium (Nitidiscala) bialatum. - KEEN, 1958: 273

Epitonium (Nitidiscala) wurtsbaughi Strong & Hertlein, 1939: 193; plt. 18, fig. 14; HERTLEIN & STRONG, 1955: 261; EMERSON & PUFFER, 1957: 39; KEEN, 1958: 274; fig. 135; KEEN, 1964: 199

Epitonium wurtsbaughi. - DUSHANE & POORMAN, 1967: 424

Epitonium (Nitidiscala) oerstedianum Hertlein & Strong, 1951: 89; plt. 3, fig. 10; KEEN, 1958: 274; fig. 124

Epitonium oerstedianum. - McLEAN, 1961: 464; DUSHANE, 1962: 45; DUSHANE & POORMAN, 1967: 424; DUSHANE & SPHON, 1968: 240; plt. 35, fig. 10

Original Description: "*T. sub ventricosa, brevis, laevi, anfractibus separatis; varicibus 8, distantibus, laminatis, valide replicatis, superne elevatim angulatis, ad suturam junctis, colore albo.*"

"This species and the three preceding, have an affinity [*Epitonium alata, E. fasciata, E. marmorata*] with each other; each has the whorls disunited, with broad, laminated, angulated, distant varices, which are united at the suture; those of *Sc. alata* are flat and broad, the angle of each varix is at some distance from the suture; those of *Sc. fasciata* have the angle much sharper, and higher in the whorl, and the shell is altogether more pyramidal; a similar form is observed in *Sc. marmorata*; but in this, the angle of the varices is very obtuse, and as low as that of

Sc. alata, the varices are also much narrower, and slightly reflected; the shell is beautifully marbled with brown between the varices. *Sc. replicata*, brought by Mr. Cuming from Lord Hood's Island, is a short, white shell, with a very acute angle on the upper part of each varix, near the suture. The varices are strongly folded back, so as to form a canal behind each." (SOWERBY, 1844a: 11)

Diagnosis: Shell medium to large in size, stout, conic, costae white, whorls dark gray on live-taken specimens; nuclear whorls 4, conical, glassy; postnuclear whorls 5 to 7, swollen, disunited, costae 7 to 8, white, thin, strongly reflected to form a canal behind each, spanning the suture, fusing with costae on upper whorls, narrow on whorls, greatly expanded at shoulder, anterior faces finely striated; suture very deep; aperture slightly oval; outer lip greatly expanded to form a broad, oval margin, free of the preceding whorl, resting against costae, produced at the shoulder and at the base; operculum dark, horny. Length, 6½ to 15mm; width, 4 to 10mm.

Discussion: Sowerby did not designate a holotype for *Scalaria replicata*. Of the 3 syntypes in the BM(NH) the largest is in the best state of preservation and is here selected as the lectotype. It was from Cuming's specimens that SOWERBY (1844a) described *S. replicata*. Because of duplication of names the type locality (Lord Hood's Island) for *S. replicata* has caused confusion. There are 2 Hood Islands. One, part of the Galapagan group, the other (Lat. 21°S, Long. 135°W) part of the Mendaña group of the Marquesas Islands. Cuming collected among the Galápagos Islands, but Darwin reported (DANCE, 1966: 151) Cuming was not at Hood Island; it is conceivable, however, that he dredged offshore.

CARPENTER (1857: 168) observed, "Another Hood's Island is in Lat. 21°S, long. 135°W. Which of these is the 'Lord Hood's Is.' often quoted in Mr. Cuming's Coll., is not known. It is possible that some species belonging to the Galapagan fauna have been passed over, from their being assigned to the Polynesian station."

TRYON (1887: 56) reported *Scalaria replicata* to be from both Lord Hood's Island and Kingsmill Island. The latter is part of the Mendaña group.

TOMLIN (1927: 170) stated that *Epitonium replicatum* was a Polynesian species collected on the "St. George" Expedition along the Pacific coast of America; one broken specimen was obtained at Gorgona Island, Colombia, South America.

On the basis of photographs of specimens of the syntypic lot in the BM(NH) the species is here interpreted as being from the Panamic fauna. If further study proves the species is to be rejected from the American fauna, the

synonym *Epitonium (Hirtoscala) bialatum* Dall, 1917 will be available.

Comparison of the types of *Epitonium bialatum* (type locality La Paz, Gulf of California, Mexico, in 18m), *E. wurtsbaughi* (type locality Panama in 5 to 16m) and *E. oerstedianum* (type locality Santa Inez Bay, Gulf of California, in 7 to 25m) with photographs of the syntypes of *E. replicatum* from the Galápagos Islands and descriptions of all 4 species shows them to be conspecific in their shell characters. It is hoped that future work on the radulae will confirm this opinion. It is common knowledge that throughout the Panamic-Galapagan area colonies of dwarf species of other molluscan families occur, so the fact that *E. oerstedianum* and *E. wurtsbaughi* were named from specimens smaller than those of *E. replicatum* and *E. bialatum* should alert us to the possibility of having the same phenomenon within the family Epitoniidae. Size alone cannot be used to differentiate species, for ecological and bathymetric conditions affect growth factors. All other characters, except size, are the same and a mixed lot of the 4 species is difficult, if not impossible, to separate.

Brown spots between the costae, observed on some specimens, could be the result of chemical disintegration of the animal showing through the thin walls of the whorls during decomposition. No brown spots have been observed on live-taken shells, although the area between the costae may vary in color from gray to pink or yellow. The narrow brown line in the sutures, between the nuclear whorls, mentioned in the description of *Epitonium oerstedianum*, is caused by the overlapping of the small nuclear whorls and is apparent in young specimens of all 4 species. Some specimens of *E. bialatum* appear to be stouter than specimens of the other 3 species, but the differences are not sufficient to separate it from them. In naming *E. oerstedianum* HERTLEIN & STRONG (1951: 89) agree that, "In many ways the unique type agrees with the description of the unfigured *E. bialatum* Dall but is half the length for the same number of whorls . . ."

Of 17 specimens collected in February, 1971 by DuShane outside Escondido Bay, Gulf of California, Mexico, 7 specimens dredged at 11m (sand substrate) were very small (length $3\frac{1}{2}$ to $8\frac{1}{2}$ mm; width $1\frac{1}{2}$ to 6 mm); 10 specimens collected intertidally were much larger (length 8 to 17 mm; width 5 to 9 mm), perhaps indicating that the individuals move into intertidal waters as they grow larger. These specimens fall within the accepted range of variation of the species.

This species has an extensive range, from the Gulf of California, Mexico (Guaymas, dredged in 31 m, Poorman Collection) to Santa Inez Bay, Gulf of California (CAS, station 145-D-1-3, type locality of *Epitonium oerstedianum*) to La Paz (type locality of *E. bialatum*, in 18m)

and the Tres Marias Islands (AMNH 54: 74637 [Puritan-American Expedition Acc. 7513]) to Bahía Honda, Veragua, Panama (CAS, station 27, 299, type locality of *E. wurtsbaughi*) and the Galápagos Islands, Ecuador (James Bay, Isla Santiago, dredged in 20m, DeRoy Collection).

Type Material:

Scalaria replicata: lectotype (herein), syntypes (2), BM(NH)
Epitonium bialatum: holotype, USNM 180798
Epitonium (Nitidiscala) wurtsbaughi: holotype, CAS[GTC] 725
Epitonium (Nitidiscala) oerstedianum: holotype, CAS[GTC] 9622

Type Localities:

Scalaria replicata: Lord Hood's Island, Galápagos Islands, Ecuador
Epitonium bialatum: La Paz, Gulf of California, Mexico
Epitonium (Nitidiscala) wurtsbaughi: Panama
Epitonium (Nitidiscala) oerstedianum: Santa Inez Bay, Gulf of California, Mexico

Geographical Distribution and Ecology: Gulf of California, Mexico, south to Panama and the Galápagos Islands.

Bathymetric Range: Rarely taken alive intertidally; usually dredged in from 5 to 25m.

Geochronological Range: Recent

(*Sthenorytis*) Conrad, 1862

[Type species (SD, deBoury, 1889): *Scalaria expansa* Conrad, 1862]

Whorls expanding rapidly, spire low; costae heavy; basal disk present.

Epitonium (Sthenorytis) diana (Hinds, 1844)

(Figures 118 to 121)

Scalaria diana Hinds, 1844a: 125; figured; HINDS, 1844-45: 48; figured; SOWERBY, 1844: 102; pl. 35, figs. 124, 125; CARPENTER, 1857a: 206, 336; CARPENTER, 1860: 10; NYST, 1871: 105 [as Hinds, 1843]; REEVE, 1873: pl. 12, figs. 89a, 89b; TRYON, 1887: 74; pl. 15, fig. 74; KEEN, 1966: 268; pl. 47, fig. 3

Scala (Opalia) diana [sic]. - H. & A. ADAMS, 1853: 222

Epitonium (s. l.) diana. - KEEN, 1958: 276; fig. 145

Sthenorytis diana. - OLSSON, 1964: 199

Epitonium (Sthenorytis) diana. - KEEN, 1971: 434, fig. 664

Epitonium (Sthenorytis) paradisi Hertlein & Strong, 1951: 90; pl. 3, fig. 7; KEEN, 1958: 276; fig. 139
Sthenorytis paradisi. - OLSSON, 1964: 199
Sthenorytis hertleini Olsson, 1964: 199; pl. 33, figs. 1, 1a, 1b

Original Description: "Testa ovata, acuminata, polita; anfractibus septenis connatis, costis valde alaeformibus ornatis; anfractu ultimo hexacostato, ad basin obtuse carinato; apertura rotundata, inferne subtruncata; peritremate extus alato; umbilico nullo." (HINDS, 1844: 125)

Diagnosis: Shell size normal for subgenus *Sthenorytis*, solid; nuclear whorls unknown; postnuclear whorls 6, well rounded, rapidly enlarging; sutures deep; costae 6 to 10, erect on early whorls, slightly reflected on later whorls, broadly expanded, forming coronating points, thick, heavy, with axial growth striations on the faces, confluent near the aperture; basal disk faintly developed; aperture round, not entire, produced at the shoulder into a large wing; operculum unknown.

Discussion: Although HINDS (1844: 125) in his original description gave the type locality as the Gulf of Nicoya, Costa Rica (65 m, in mud), later authors (SOWERBY, 1844: 102; REEVE, 1873: pl. 12, figs. 89a, 89b; TRYON, 1887: 74) erroneously reported the species to be from Amboyina in the Malayan Archipelago. Consequently the shell was for a long time omitted from American lists. However, CARPENTER (1857: 206, 336; 1860: 10) did recognize the species to be from Central America. A specimen in the LACM-AHF Collection (Hancock station 1030-40), length 19 mm (early whorls broken); width 22 mm; with 9 costae; from Outer Gorda Bank, Cabo San Lucas, Baja California compares favorably with the figured specimen in SOWERBY (1844: pl. 35, figs. 124, 125) and in KEEN (1958: fig. 145). Although the LACM-AHF specimen is much larger than the type of *Epitonium dianae* (length 8 mm), it is much smaller than the type of *E. paradisi* (length 35 mm; width 26½ mm) with 10 costae (type locality Gorda Bank, Cabo San Lucas, Baja California, from 128-146 m). *Epitonium paradisi* is here considered to be a synonym of *E. dianae*, having the same physical characteristics as Hind's species. *Epitonium (Sthenorytis) hertleini* OLSSON (1964: 199), a Neogene fossil from Ecuador in a good state of preservation, was recognized by Olsson as a closely related species, and is here considered to be a synonym of *E. dianae*. The apertural spine rounds the top of the aperture and terminates behind a costa on the body whorl. The other costae on each species ascend the whorl and curve to the left of the preceding costa, flattening out against the suture. In these respects these taxa differ from their nearest Panamic-Galapagan congener *E. (S.) turbinum* Dall, 1908,

which has the aperture entire, with heavier and thicker costae that flatten out as they approach the suture, but that are adherent to the costa immediately above, with a spur that extends to the costa immediately to the left, leaving a pit. At the suture a costa fills the entire space between the next 2 costae above. *Epitonium (S.) dianae* is closest to *E. (S.) pernobilis* Fischer & Bernardi, 1857 (p. 293; pl. 8, figs. 2, 3) from the Atlantic fauna, with fewer costae, but having the same pattern. This is a rare species, represented in few collections.

Type Material:

Scalaria dianae: holotype, BM(NH) 1950.4.18.3
Epitonium (Sthenorytis) paradisi: holotype, CAS[GTC] 9627
Sthenorytis hertleini: holotype, USNM 644060

Type Localities:

Scalaria dianae: Gulf of Nicoya, Costa Rica
Epitonium paradisi: Gorda Bank, Cabo San Lucas, Baja California, Mexico
Sthenorytis hertleini: Ecuador, (Neogene)

Geographical Distribution and Ecology: Cabo San Lucas, Baja California, Mexico, south to Costa Rica and Ecuador. Dredged in mud, sand, calcareous algae. The diversity of material from which the specimens were dredged may be accounted for by the fact that none of the specimens reported has been live-taken.

Bathymetric Range: 65 to 146 m

Geochronological Range: Recent and Neogene

Epitonium (Sthenorytis) turbinum Dall, 1908

(Figures 113 to 117 and Figure 160)

Epitonium (Sthenorhytis) [sic] *turbinum* Dall, 1908: 215, 317; pl. 9, figs. 5, 6, 8

Sthenorytis turbinum. - DALL, 1917: 477

Epitonium (Sthenorytis) turbinum. - HERTLEIN & STRONG, 1951: 90; DUSHANE, 1966: 311, 312; pl. 52, 5 figs.; BOSS *et al.*, 1968: 327; KEEN, 1971: 436; fig. 665 [not the holotype]

Epitonium (Ferminoscala) turbinum. - STRONG, 1945: 21

Sthenorytis turbina. - OLSSON, 1964: 199

Epitonium (Sthenorytis) toroense Dall, 1912: 6; DALL, 1925: 27; pl. 18, fig. 5; GRANT & GALE, 1931: 855; DURHAM, 1937: 482; BOSS *et al.*, 1968: 321

Sthenorytis toroense. - HANNA & HERTLEIN, 1927: 143

Original Description: "Specimen decollate, as figured, but showing the specific characteristics sufficiently well; form depressed-turbinate, aperture circular, very oblique; whorls coherent, rapidly enlarging, probably four or five originally; smooth, except for incremental lines; last whorl

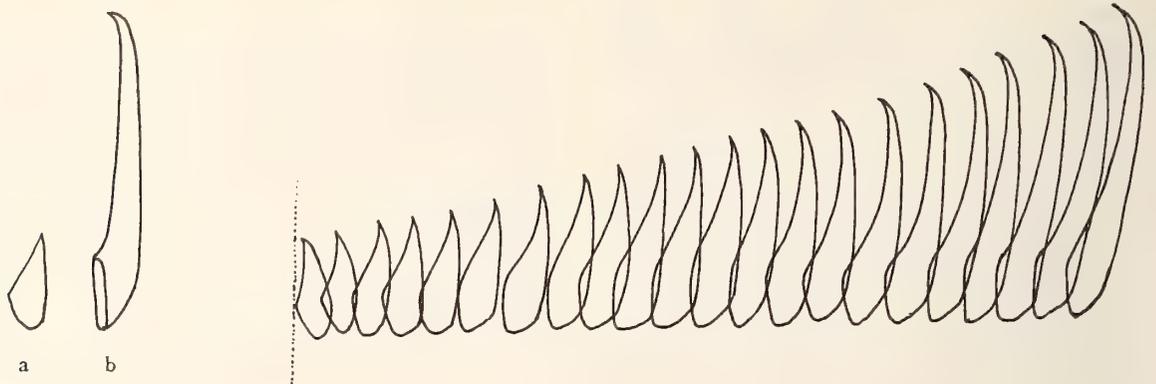


Figure 160

Epitonium (Sthenorytis) turbinum Dall, 1908

The symmetrical uncini are slender and pointed;
there are between 40 and 50 teeth in one row; a: at center of row;
b: at end of row

with ten strong, broad, sharp-edged varices of triangular section, the posterior portion pressed back upon and concealing the suture; basal disk faintly developed, the varices confluent on the base; umbilicus absent; peritreme circular. Height of last whorl, 22; diam. of last whorl, 28; of aperture exclusive of the varix, 11 mm.

"U. S. S. "Albatross," station 4642, four miles S. 41° E. from the east point of Hood Island, Galapagos Islands, in 300 fathoms, broken shell, bottom temperature 48.6° F, U. S. N. M. 110568.

"This is the most depressed species of this group (regarded by some authors as a genus) which has yet been described, as it is almost certain that the spire, when perfect, diminishes with proportionate rapidity to that of the portion figured. Its nearest relative, so far as known,

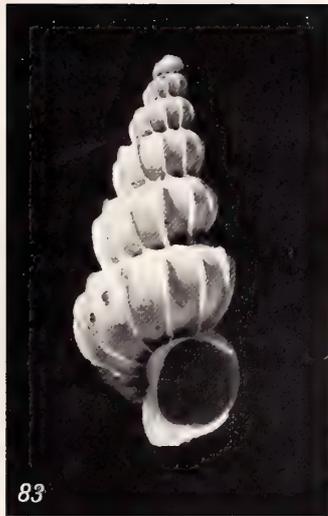
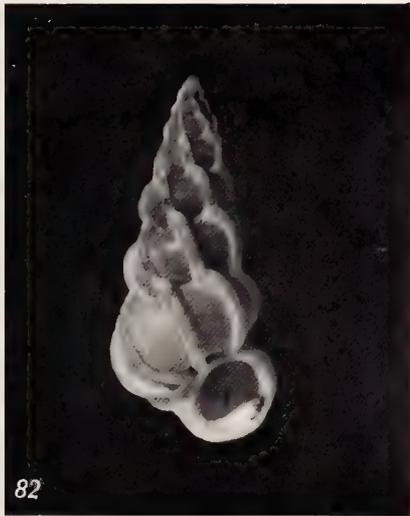
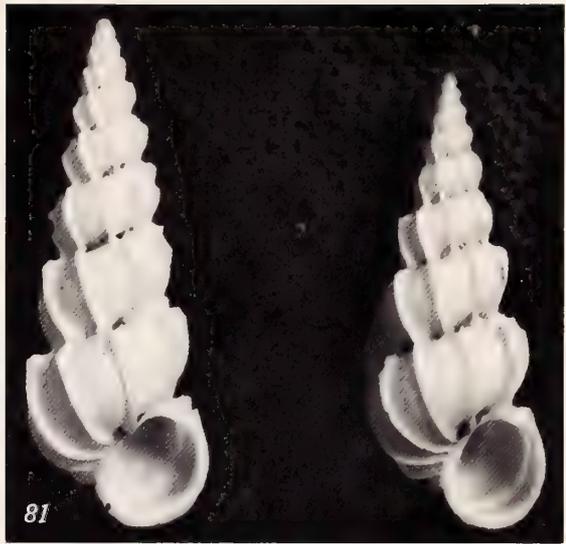
is the *S. stearnsii* Dall, of the Pliocene of San Diego, California, but this is considerably more elevated than the Galapagos species." (DALL, 1908: 317)

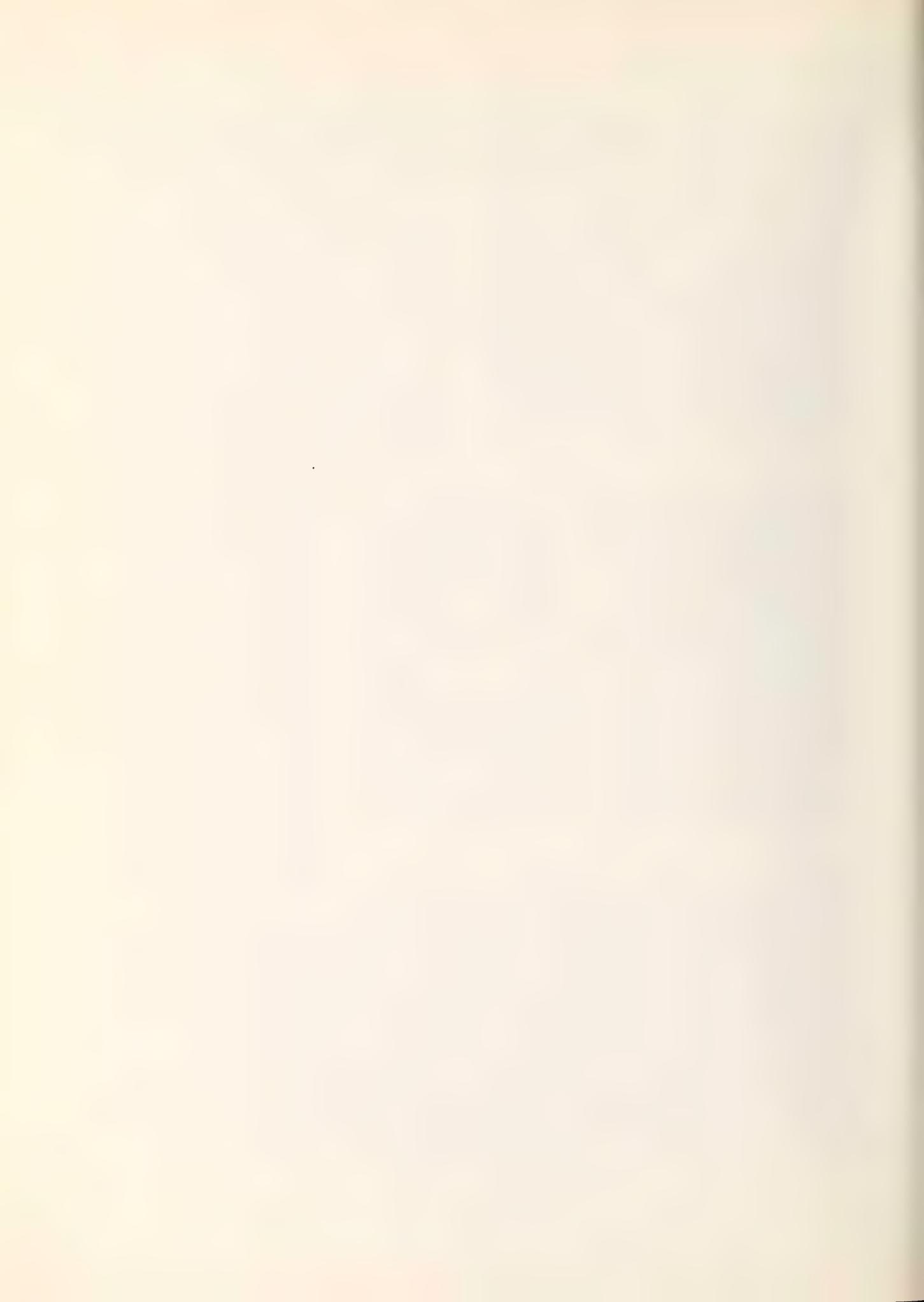
Diagnosis: Shell large, heavy, thick, turbinata, color off-white; nuclear whorls nearly always eroded; postnuclear whorls 9, continuous, rapidly enlarging, showing incremental growth lines and a faint basal disk; costae 9 to 12, sharp edged, wider where they attach to the whorl, with a spine at the tip, each costa flattening as it approaches the suture but adhering to the costa immediately above, with a spur that extends to the costa immediately to the left, leaving a pit at the suture, broadly reflected on the base, fusing with the lip; suture deep; aperture round, very oblique; lip heavy, reflected, continuous, with a

Explanation of Figures 79 to 88

Figure 79: *Epitonium apiculatum* Dall, 1917. Holotype, USNM 111219; length 4 mm; width 2 mm × 7
Figure 80: *Epitonium (Nitidiscala) bakhanstranum*. Keen, 1962. Holotype, CAS[GTC] 476; length 9.2 mm; width 3.3 mm × 5.7
Figure 81: *Scalaria hindsii* Carpenter, 1856. Syntypes (2) BM[NH] 1963.21; length (of larger specimen) 25 mm; width 10 mm × 2.6
Figure 82: *Epitonium (Nitidiscala) propehexagonum* Dall, 1917. Holotype, USNM 153075; length 21 mm; width 9 mm × 2.3
Figure 83: *Epitonium pazianum* Dall, 1917. Holotype, USNM 111208; length 20 mm; width 9 mm × 2.6

Figure 84: *Epitonium musidora* Dall, 1917. Holotype, USNM 201203; length 13 mm; width 5 mm × 6.5
Figure 85: *Scalaria hexagona* Sowerby, 1844. Syntypes (4) BM[NH]
Figure 86: *Epitonium basicum* Dall, 1917. Holotype, USNM 56049; length 15.7 mm × 2.6
Figure 87: *Epitonium compradora* Dall, 1917. Holotype, USNM 105527; length 4 mm; width 2½ mm × 2
Figure 88: *Epitonium cylindricum* Dall, 1917. Holotype, USNM 271037; length 4 mm; width 1½ mm × 5





spine on the shoulder; operculum black, thick, layered, circular, with a depressed center. Length, 25 to 40 mm; width, 22 to 30 mm.

Discussion: Few specimens, fossil or Recent, are known of this species. DALL (1912: 6) named a Pliocene fossil from Toro Point, Canal Zone, Panama, *Epitonium (Sthenorytis) toroense*, apparently having forgotten that he had previously described an identical species from off Hood Island in the Galapagan group, *E. (Sthenorhytis) [sic] turbinum* (1908: 317). Descriptions of these two species agree in every particular and comparison of the types confirms the fact that the Pliocene fossil is a synonym of *E. (S.) turbinum* HANNA & HERTLEIN (1927: 143) reported a specimen of *E. (S.) toroense*, with 12 costae, from the Pliocene (?) beds of Monserrate Island, Gulf of California, Mexico. DUSHANE (1966: 311; pl. 52, figs. 1-5) reported 3 dead specimens of *E. (S.) turbinum* from the Allan Hancock Foundation Collection (now at LACM-AHF); two of the specimens were dredged at 135 m, station 618-37, San Jaime Bank, Cape San Lucas, Baja California, Mexico; one specimen was dredged at station 572-36, north of San Pedro Nolasco Island, Gulf of California, Mexico, from 108 m. The only live-taken specimens (14 in number) have been from off the Galápagos Islands, dredged by Jacqueline and André DeRoy in from 170 to 200 m.

A congener, *Epitonium (Sthenorytis) stearnsii* (Dall, 1892) from California with very similar characteristics but with only 7 costae (length, 27 mm; width, 4 mm), although outside the scope of this paper is discussed here for comparison. The doubtful authenticity of Stearns' locality indications leads us to believe this is possibly a spurious specimen, and a form that should be treated as a *species inquirenda*. It is known from only one badly damaged specimen collected by Stearns, supposedly from the Middle Pliocene of Pacific Beach, California. In 80 years there have been no subsequent records of fossil or live-taken specimens from the California province.

The radula of *Epitonium (Sthenorytis) turbinum* consists of numerous (between 40 and 50 in one row) similar, symmetrical teeth (unci) which are slender and pointed at the end of each row.

The only other somewhat similar form from the Panamic-Galapagan fauna of the subgenus *Sthenorytis* is *Epitonium dianae* (Hinds, 1844) which has a less oblique aperture and a much different shape of the varicose axial ribbing. The produced structure of the costae of *E. dianae* gives a wing-like effect, not true of *E. (S.) turbinum*, which has reflected costae.

Type Material:

Epitonium (Sthenorhytis) turbinum: holotype, USNM 110568

Epitonium (Sthenorytis) toroense: holotype, USNM 214345 (previously reported as USNM 214340)

Type Localities:

Epitonium (Sthenorhytis) turbinum: Hood Island, Galápagos Islands, Ecuador

Epitonium (Sthenorytis) toroense: Toro Point, Canal Zone, Panama (Pliocene)

Geographical Distribution and Ecology: Cape San Lucas, Baja California (Recent), Gulf of California (Recent and fossil), Panama (fossil), Galápagos Islands, Ecuador (Recent). This species belongs to a deep water fauna; specimens have been dredged from very fine grayish green sand with numerous ophiuroids and some broken shells.

Bathymetric Range: 110 to 550 m

Geochronological Range: Pliocene, Recent

Cirsotrema Mörch, 1852

[Type species: (M) *Scalaria varicosa* Lamarck, 1822]

Shells with complicated sculpture of axial and spiral laminations, with a heavy basal ridge.

Cirsotrema togatum (Hertlein & Strong, 1951)

(Figures 54, 55)

Epitonium (Cirsotrema) togatum Hertlein & Strong, 1951: 89; pl. 3, figs. 1, 5; KEEN, 1958: 272; fig. 103; OLSSON, 1971: 89; fig. 77; KEEN, 1971, 428; fig. 633

Epitonium togatum. - DUSHANE & POORMAN, 1967: 424

Original Description: "Shell of medium size, with a slender, turritid spire, dingy white; nuclear and probably the first 1 or 2 postnuclear whorls lost; remaining whorls 10, narrowly tabulated, with deep sutures, regularly increasing in size, the upper whorls with the sculpture much worn; axial sculpture of (on the last whorl 20) retractive, strongly reflected ribs, continuous from suture to suture, of which every fourth, fifth or sixth is swollen to form a strong varix; spiral sculpture of 7 cords in the interspaces between the axial ribs and numerous fine striae; the reflected faces of the varices with close, wavy, axial striae, that of the intermediate axial ribs below the slightly coronated shoulder with 3 or more sharp, wavy, axial laminae, the points of which correspond to the spiral cords, and in some cases span the interspaces between the axial ribs; base with a strong spiral cord forming a narrow

spiral disk, the axial ribs expanded on the cord but become narrow where they fuse with the inner lip; aperture circular, the outer and basal lip thickened by the last varix. The type measures: length, 37.5 mm; maximum diameter, including the varices, 13.8 mm." (HERTLEIN & STRONG, 1951: 89)

Diagnosis: Shell large in size; nuclear whorls one and a half, showing early sculpture, somewhat glassy; third whorl down with strong axial ribs and evenly spaced spiral sculpture; fourth whorl shows sufficient expansion of the ribs to join the expansions of the neighboring ribs, leaving small openings through which the regular shell surface may be seen; lamination of the ribs extends above and below to give a third dimensional quality to the intricate sculpture; this pattern continues on all later whorls, increasing in strength with each whorl; whorls $9\frac{1}{2}$ to $10\frac{1}{2}$; suture very deep; umbilicus lacking; with a basal ridge, above and below which there are rather deep pits; aperture circular; lip slightly patulous, crenulated, thickened by the last rib; operculum dark and paucispiral. Size of shell varies from about 15 to $37\frac{1}{2}$ mm in length; 6 to 13.8 mm in width.

Discussion: I agree with CLENCH & TURNER (1950: 226) and with BERRY (1963: 143) in thinking that *Cirsotrema* are sufficiently different in characters to warrant generic status. For a detailed explanation and synonymy of the genus see CLENCH & TURNER (*op. cit.*). Beach rolled shells have lost much of the elaborate sculpture, but still retain enough of the fundamental characteristics to make identification possible. Records indicate a wide range for *C. togatum*. The *Velero III* (AHF station 1084-40) dredged one specimen off San Pedro Nolasco Island, Gulf of California, Mexico in 200 m on a rock substrate. The CAS Collection has 2 specimens from station 150-D-19 (Gorda Bank, Cabo San Lucas, Gulf of California, Mexico) dredged in 91 m from a sand substrate. An additional specimen was dredged south and east of Judas Point, Costa Rica (station 214-D-1-4) in $76\frac{1}{2}$ -112 m on a mud, shell and rock substrate. The DeRoys dredged specimens off Santa Fé Island (Barrington Island), Galápagos Islands, Ecuador, December, 1967 in 50 m. This is a rare species in the Panamic-Galapagan area, most specimens having been dredged, few having been taken alive. *Cirsotrema plexis* Dall, 1925 (p. 10) from Honshu Island, Japan appears to be closely related to *C. togatum*.

Type Material:

Epitonium (Cirsotrema) togatum: holotype, CAS[GTC] 9620

Type Locality:

Epitonium (Cirsotrema) togatum: Gorda Bank, Cabo San Lucas, Gulf of California, Mexico

Geographical Distribution and Ecology: From Guaymas, Sonora, Mexico south to the Gorda Bank, Gulf of California, to Manzanillo, Mexico, Costa Rica and to the Galápagos Islands. Dredged from mud, sand, shell, or gravel substrate.

Bathymetric Range: 32 to 113 m

Geochronological Range: Recent

Cirsotrema vulpinum (Hinds, 1844)

(Figures 56, 57)

Scaloria vulpina Hinds, 1844a: 126; figured; HINDS, 1844-45: 49; figured; SOWERBY, 1844: 106; pl. 35, figs. 117, 118; CARPENTER, 1857a: 206, 336; CARPENTER, 1860: 10; NYST, 1871: 145; REEVE, 1873: pl. 12, figs. 88a, 88b; pl. 15, figs. 113a, 113b; TRYON, 1887: 78; pl. 15, fig. 81; KEEN, 1966: 269

Scaloria vulpina. - DALL, 1917: 487 [as "Hinds, 1843"]

Scala (Opalia) vulpina. - H. & A. ADAMS, 1853: 222

Epitonium (s. l.) vulpina. - KEEN, 1958: 276; fig. 153

Epitonium (Cirsotrema) vulpinum. - KEEN, 1971: 428; fig. 634

Cirsotrema pentedesmium BETTY, 1963: 143

Epitonium pentedesmium. - DU SHANE & POORMAN, 1967: 424

Original Description: "*Testa elongata, fusca; anfractibus nonis rotundatis, connatis; costis obtusis, rotundatis, lineis elevatis decussatis; sutura profunda; anfractu ultimo novemcostato, ad basin obtuse carinato; apertura rotunda; umbilico nullo. 7.5 mm.*" (HINDS, 1844: 126)

Diagnosis: Shell small to medium, slender, acute; color reddish brown to pale orange to frost white; nuclear whorls 3, last nuclear whorl showing faint axial ribs; post-nuclear whorls 9, extremely convex, swollen about the periphery; axial ribs thick, sometimes forming a heavy varix; spiral sculpture of 5 dark brown cords over-riding the ribs; interspaces between the ribs and spiral cords pitted; suture deep; basal disk present, below are 2 to 3 dark brown spiral cords; aperture round; outer lip heavy, thick, over which the spiral cords ride; operculum light brown, horny, paucispiral. Size of shell varies from 3.2 to $13\frac{1}{2}$ mm in length; $1\frac{1}{2}$ to 4 mm in width.

Discussion: REEVE (1873-74) described the shell as "small, aciculated, reddish-brown; spire acuminate, whorls distinct, spirally striated; ribs few, irregular, thick, round; last whorl keeled below; aperture ovate, outer lip thick." TRYON (1887: 78) stated the shell is "orange brown, thick, spirally striated; whorls 10, well rounded, with strong, rib-like lamellae. Length, 6 mm."

It is strange that REEVE (1873-74), SOWERBY (1844: 106) and TRYON (1887: 78) all report that the species is from the Straits of Malacca, a channel between the South Malay Peninsula and Sumatra. CARPENTER (1857: 206) as well as KEEN (1958: 276; 1966: 269) agree with the original describer in stating Quibo, Veragua, Panama as the type locality. KEEN (*op. cit.*: 276) was unable to locate the type specimen in the BM(NH).

Cirsotrema vulpinum (Hinds) is so similar to *C. pentedesmium* Berry that the latter must be placed in synonymy. Although BERRY (1963: 143) uses different terminology to describe the shell, when the descriptions given by Hinds and Berry are compared, much the same result is obtained. Both agree that the shell is aciculated, spirally striated, deeply sutured, with a distinct basal disk, ribs heavy and rounded, with here and there a varix.

Because the type of *Cirsotrema vulpinum* is apparently lost, the only specimens extant are those taken in the Gulf of California, Mexico and south along the west Mexican coast. For this reason it is considered desirable to include those records here:

- 1937 Hancock Pacific Expeditions (station 682-37) off Concepción Bay, Gulf of California, Mexico; one specimen, length 13½ mm; width 4 mm; in 22 m (in LACM-AHF Collection)
- 1962 R. Poorman, off Guaymas, Sonora, Mexico; 7 specimens, length 6.3 to 10.3 mm; width 2.7 to 3.6 mm; in 18 m, on broken shell and rock bottom
- 1963 Margaret Cunningham, off San Carlos Bay, Guaymas area, Mexico; holotype of *Cirsotrema pentedesmium* (SU[PTC] 10058), length 8.2 mm; width 3.7 mm; in 27 to 54 m
- 1965 L. Shy, Guaymas, Sonora, Mexico; 2 specimens, length 9 mm; width 3 mm; in 18 m
- 1966 J. Bailey, Bahía de Los Angeles, Gulf of California, Mexico; 2 specimens (SBMNH one specimen, length 6 mm; width 2½ mm; one specimen Bailey Collection)
- 1967 Charles Snell, Banderas Bay, Nayarit, Mexico; 1 specimen, length 3.2 mm; width 1½ mm; diving at 9 to 18 m, under ledges, between boulders
- 1971 H. DuShane, Escondido Bay, Gulf of California, Mexico; 1 specimen, length 4½ mm; width 1½ mm; in 18 m, on sand and shell substrate

Type Material:

Scalaria vulpina: holotype, BM(NH) lost

Cirsotrema pentedesmium: holotype, SU[PTC] 10058

Type Localities:

Scalaria vulpina: Quibo (Isla Coiba), Veragua, Panama

Cirsotrema pentedesmium: Guaymas, Gulf of California, Mexico

Geographical Distribution and Ecology: Throughout the Gulf of California and south along the west Mexican coast to Panama; dredged on broken shell and rock bottom; diving at 9 to 18 m, under ledges

Bathymetric Range: Dredged in 18 to 54 m; obtained by diving at 9 to 18 m

Geochronological Range: Recent

Acirsa Mörch, 1857

[Type species: (M) *Scalaria borealis* Beck, 1839 (*nomen nudum*) = *Turritella costulata* Mighels & Adams, 1842]

Outer lip thin; axial and spiral sculpture of low ribs; with an indistinct basal keel.

Acirsa cerralvoensis (DuShane, 1970)

(Figure 60)

Epitonium (Acirsa) cerralvoensis DuShane, 1970: 3; fig. 3;
SPHON, 1970: 10

Acirsa cerralvoensis. - KEEN, 1971: 436; fig. 666

Original Description: "Shell of medium size, tall and slender, thin but strong, light brown in color, with 10-12 gradually enlarging, rounded whorls, two opaque nuclear whorls; suture moderately impressed; axial ridges pale brown, 16 on the fourth whorl, gradually becoming obsolete on succeeding whorls, spiral ridges wider than the interspaces, 19 on last whorl; peritreme incomplete, lip thin, columella arched; no basal ridge; operculum horn colored, paucispiral. Dimensions (in mm): length 11.8, width 3.7 (holotype)." (DUSHANE, 1970: 3)

Diagnosis: A species with a slender, pale brown shell, differing from other epitoniids from the Panamic-Galapagan molluscan province in having reduced axial costae and unevenly spaced spiral striae.

Discussion: No other epitoniid species from the west coast of the Americas has sculpture like this. Few specimens have been taken, thus it seems to be worthwhile to report them here:

All specimens are in the LACM Collection and all are from the Gulf of California, Mexico; 2 specimens off the west side of Cerralvo Island, in 13 m; 1 specimen off Cape San Lucas in 18-36 m; 1 specimen off Pulmo Reef in 7 m;

1 specimen off Puerto Refugio, Angel de la Guarda Island, in 38 m

Type Material:

Epitonium (Acirsa) cerralvoensis: holotype, LACM 1200

Type Locality:

Epitonium (Acirsa) cerralvoensis: West side of Cerralvo Island, Gulf of California

Geographical Distribution and Ecology: West side of the Gulf of California south and west to Cape San Lucas, Mexico; dredged on sand bottom

Bathymetric Range: From 7 to 38 m

Geochronological Range: Recent

Acirsa menesthoides Carpenter, 1864

(Figure 59)

Acirsa menesthoides Carpenter, 1864b: 478 [reprint 1872: 217]; CARPENTER, 1864c: 618 [reprint 1872: 104]; DALL, 1917: 474; PALMER, 1963: 334; plt. 63, figs. 7, 8; KEEN, 1971: 436; fig. 667

Scalaria (Acirsa) menesthoides. - TRYON, 1887: 84

? *Acirsa menesthoides*. - KEEN, 1958: 276

Rissoina berryi Baker, Hanna & Strong, 1930: 35; plt. 1, fig. 3; KEEN, 1971: 375

Original Description: "*A. testa nitida, turrata, majore, solidiore, pallide fusca; anfr. nucl. laevibus; norm. vi., subplanatis, suturis distinctis; lineis crebris spiralibus insculpta, quarum circ. viii. in spira monstrantur; testa adolescente lirulis radiantibus obsoletis decussata; apertura subovali; columella solida, imperforata. Long. 42, long. spir. .3, lat. .16 poll., div. 25°.*" (CARPENTER, 1864c: 478)

Diagnosis: Shell medium in size, white, solid; whorls 7; suture distinct; spiral sculpture of fine threads continuing on the base; peritreme incomplete; outer lip thin; aperture subovate; operculum unknown. Length, 10.2 mm; width, 4 mm.

Discussion: Very little is known of this species. One specimen was collected by J. Xantus from the area of Cape San Lucas, Baja California, Mexico. Placed in the USNM as the type, it was subsequently lost. A possible paratype, in the BM(NH), was photographed by KEEN (1964) and this figure is reproduced here.

It has recently come to my attention that BAKER, HANNA & STRONG (1930: 35) reported a new species, *Rissoina berryi*, from Cape San Lucas, Baja California, Mexico. Four beach specimens were collected by E. C. Johnson of the U. S. S. *Albatross* about 1914. The holotype is 9 mm in length and 3 $\frac{3}{4}$ mm in diameter. Upon examination, these specimens prove to be identical with *Acirsa menesthoides* Carpenter and thus *R. berryi* becomes a synonym. For comparison, both taxa are figured here.

Type Material:

Acirsa menesthoides: holotype, USNM lost; possible paratype, BM(NH) 1962.1121

Rissoina berryi: holotype, CAS[GTC] 4608

Type Locality:

Acirsa menesthoides: Cape San Lucas, Baja California, Mexico

Rissoina berryi: Cape San Lucas, Baja California, Mexico

Geographical Distribution and Ecology: Southern end of the Gulf of California, Mexico; habitat unknown

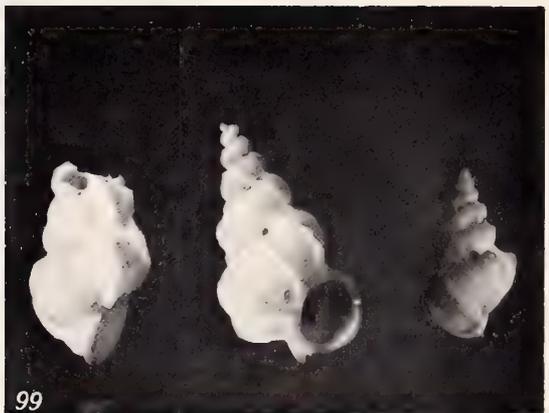
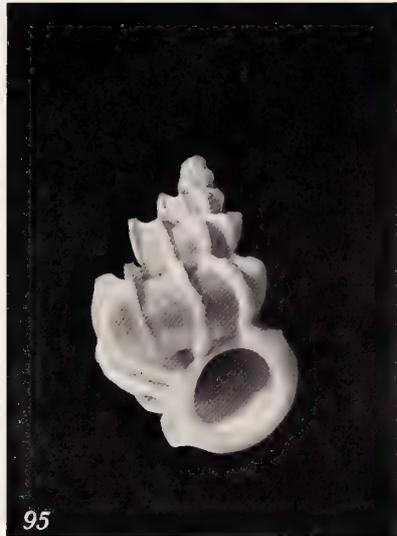
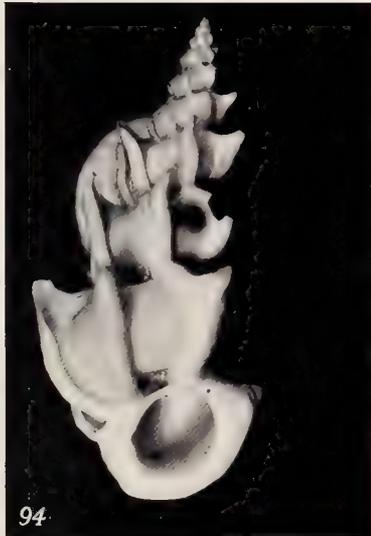
Bathymetric Range: Since J. Xantus collected it, we can assume this species may occur intertidally

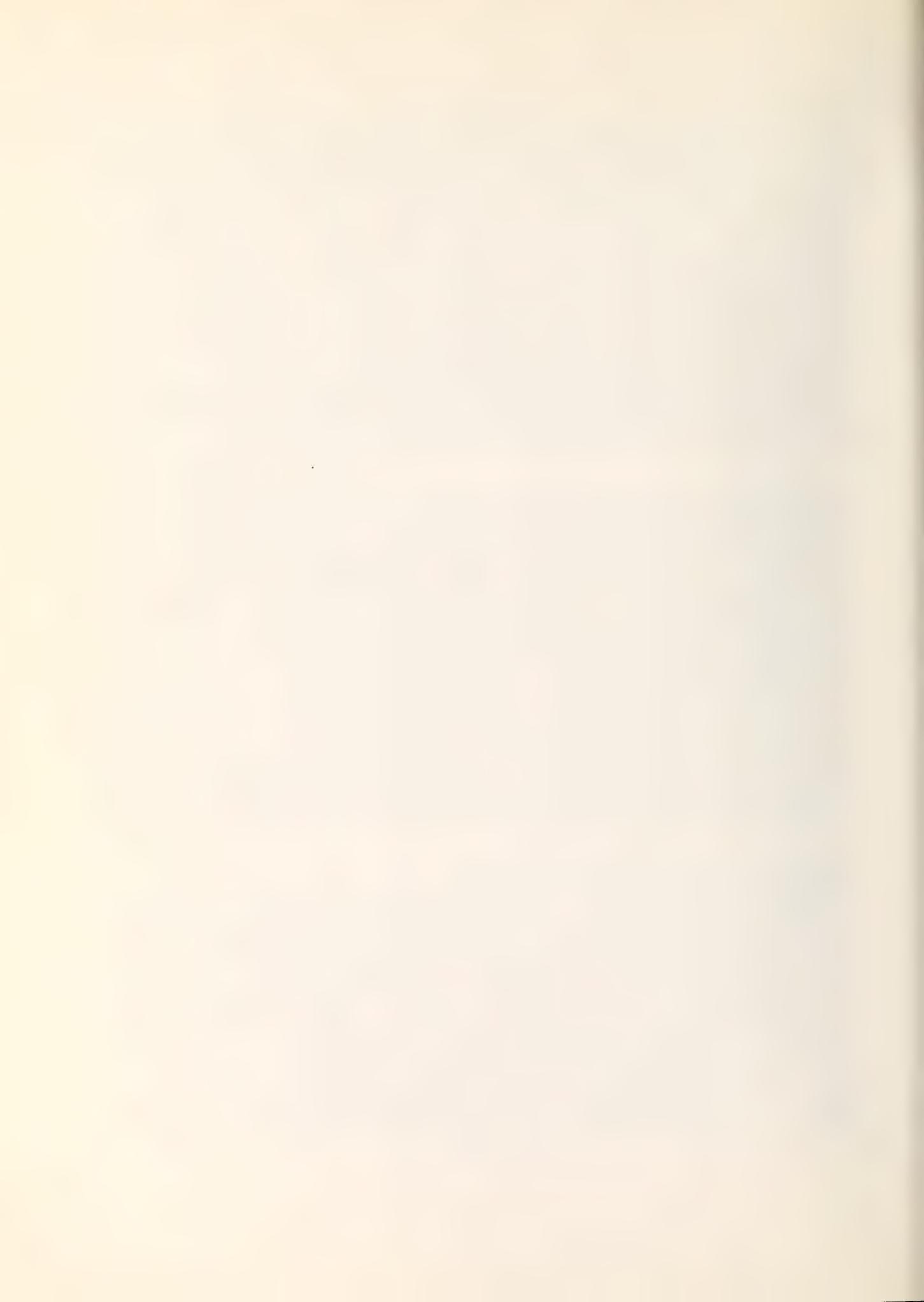
Geochronological Range: Recent

Explanation of Figures 89 to 99

Figure 89: *Epitonium implicatum* Dall & Ochsner, 1928. Holotype, CAS[GTC] 2932; length 18 mm; width 6 mm $\times 3\frac{1}{2}$
 Figure 90: *Epitonium appressicostatum* Dall, 1917. Syntype, USNM 59334; length 14 mm; width 4 $\frac{1}{2}$ mm $\times 4\frac{1}{2}$
 Figure 91: *Epitonium appressicostatum* Dall, 1917. Syntypes, USNM 59334 $\times 4\frac{1}{2}$
 Figure 92: *Epitonium (Nitidiscala) pedroanum* Willett, 1932. Holotype, LACM 1036; length 11.7 mm; width 3.7 mm $\times 4.7$
 Figure 93: *Scalaria polita* Sowerby, 1844 (after SOWERBY, 1844). Holotype, BM[NH] lost; no dimensions given $\times 2$
 Figure 94: *Scalaria reflexa* Carpenter, 1856. Holotype, BM[NH] 19621116; length 16 mm $\times 4$

Figure 95: *Epitonium bialatum* Dall, 1917. Holotype, USNM 180798; length 15 mm; width 10 mm $\times 2.6$
 Figure 96: *Epitonium (Nitidiscala) politum* (Sowerby, 1844). Live-taken specimen, dredged in 11 m, 1965, Puertecitos, Gulf of California, Mexico (DuShane Coll.); length 8 mm; width 2 $\frac{1}{2}$ mm $\times 9$
 Figure 97: *Epitonium (Nitidiscala) oerstedianum* Hertlein & Strong, 1951. Holotype, CAS[GTC] 9622; length 6 $\frac{1}{2}$ mm; width 4.2 mm $\times 8$
 Figure 98: *Epitonium (Nitidiscala) wurtsbaughi* Strong & Hertlein, 1939. Holotype, CAS[GTC] 725; length 7.2 mm; width 4.4 mm $\times 9$
 Figure 99: *Scalaria replicata* Sowerby, 1844. Lectotype (herein) (1); length 14 mm; paralectotypes (herein) (2) BM[NH] $\times 2.4$





Acirsa murrha (DuShane, 1970)

(Figure 62)

Epitonium (Acirsa) murrha DuShane, 1970: 4; fig. 4; SPHON, 1970: 11*Acirsa murrha*. - KEEN, 1971: 436; fig. 668

Original Description: "Shell of medium size, white, texture of opaque china; nuclear whorls two, opaque (first nuclear whorl missing in holotype); postnuclear whorl with faint indication of axial sculpture; second postnuclear whorl with incised spiral lines; remaining convex whorls 10, gradually enlarging; 19 retractive axial ridges on body whorl giving a sinuous appearance; penultimate whorl with 15 spiral cords, uneven in width, separated by narrow, incised lines riding over the axial ridges; suture moderately impressed basal ridge with 10-11 flat cords separated by incised lines; aperture oval, peritreme incomplete, umbilicus lacking, operculum unknown. Dimensions (in mm): length 19.1, width 6.9 (holotype)." (DUSHANE, 1970: 4)

Diagnosis: A large form with 19 low axial ribs over which the spiral sculpture crosses; differing from other *Acirsa* from the west coast of the Americas in having more pronounced axial sculpture on the body whorl.

Discussion: No other epitoniid from the west American coasts has the color or sculpture of this species. The north Atlantic species *Acirsa costulata* (Mighels & Adams, 1842) figured by CLENCH & TURNER (1950: 230) is similar in proportions but has weaker axial and spiral sculpture. Only one specimen was obtained by the *Velero III*, AHF station 944-39, March 1939, on gray sand, in 54m.

Type Material:*Epitonium (Acirsa) murrha*: holotype, LACM 1232**Type Locality:***Epitonium (Acirsa) murrha*: Secas Islands, Panama

Geographical Distribution and Ecology: Panama; dredged from gray sand bottom

Bathymetric Range: Dredged in 54m

Geochronological Range: Recent

Alora H. Adams, 1861[Type species: (M) *Trichotropis gouldii* A. Adams, 1857]

Shells globose, whorls rapidly expanding; both axial and spiral striations present; outer lip thin with an indistinct anterior notch.

Alora gouldii (A. Adams, 1857)

(Figures 58, 61)

Trichotropis gouldii A. Adams, 1857: 369*Alora gouldii*. - H. ADAMS, 1861: 272; KEEN, 1969: 439;

KEEN, 1971: 436; fig. 669

Recluzia insignis Pilsbry & Lowe, 1932: 80; plt. 9, fig. 3;

KEEN, 1958: 280; fig. 171

Original Description: "*T. testa ovato-fusiformi, vix rimata, alba, tenui; spira elata; anfractibus septem convexis, liris elevatis, spiralibus et lamellis tenuibus longitudinalibus concinne cancellatis, interstitiis transversim striatis; apertura ovali, antice producta, canali obsoleta; labio laevi, rotundato, antice subreflexo; labro margine simplici, acuto. Long. 1½ poll.*"

"... In a recent state the shell is probably covered with a thin light-brown epidermis. It differs from the typical genus in the canal of the aperture being almost obsolete." (A. ADAMS, 1857: 369)

Free Translation (by Dr. Myra Keen): Shell ovate, fusiform, very slightly umbilicate, white, thin; spire high; with seven convex whorls having raised lirae, the spire beautifully cancellate and the interspaces striate with thin longitudinal lamellae; aperture oval, produced anteriorly, canal obsolete; outer lip smooth, rounded, anteriorly slightly reflected, inner lip with simple sharp edge. Length 37mm.

Diagnosis: Shell white, thin, periostracum buff colored, small to medium in size, with 5 rapidly expanding, convex whorls, plus 3 nuclear whorls, the upper half of each nuclear whorl glassy, the lower half white; sutures deep; ribs 39, unevenly spaced; spiral sculpture of equally strong ribs, 18 on the body whorl, 7 on the penultimate whorl, intersection of axial and spiral ribs giving a beaded appearance to the surface of the whorl; the 2 spiral ribs next to the suture closer together than the others; fine threads on the interspaces formed by the axial and spiral ribs; aperture oval; outer lip thin, crenulated by the spiral ribs, produced anteriorly, inner lip incomplete; operculum unknown.

Discussion: The rather involved taxonomy of *Alora gouldii* (A. Adams, 1857) was succinctly outlined by KEEN (1969: 439). *Trichotropis gouldii* described by A. ADAMS (1857: 369) in a North Pacific genus, was moved to the genus *Alora* by HENRY ADAMS (1861: 272) with *Trichotropis gouldii* A. Adams, 1857 as type by monotypy. After 3 unsuccessful attempts to locate the type in the collections of the BM(NH) KEEN (1969: 439) concluded, "If the shell still remains in the Museum's collection, it has been mislabelled and the original notations obscured or lost."

Although much smaller in size (15 mm in length), *Recluzia insignis* Pilsbry & Lowe, 1932 from Panama meets all the requirements of Adams' original description. However, *Recluzia* belongs to a smooth, pelagic group, and so *R. insignis* should be removed from the family because of its sculpture and form. Laura and Carl Shy dredged 5 specimens (1965) in the Manzanillo, Mexico area from 30 m (15 to 37 mm in length). Study of these specimens and comparison with the holotype of *R. insignis* makes it possible to remove the species from the genus *Recluzia* to a genus and family more compatible; therefore, I propose that *Alora* be placed within the family Epitoniidae as a separate genus, with *Trichotropis gouldii* A. Adams as type species by monotypy, and with *R. insignis* as a synonym.

Type Material:

Trichotropis gouldii: holotype, BM(NH) type lost?
Recluzia insignis: holotype, ANSP 155432

Type Localities:

Trichotropis gouldii: West Panama
Recluzia insignis: Panama

Geographical Distribution and Ecology: Manzanillo, Mexico to Panama; habitat unknown

Bathymetric Range: Dredged from 30 m

Geochronological Range: Recent

Amaea H. & A. Adams, 1853

[Type species (SD, deBoury, 1909): *Scalaria magnifica* Sowerby, 1844]

Shells white, yellow-brown or dark brown; whorls joined; axial and spiral sculpture may be strong or weak, usually forming rectangles within which are extremely fine threads; with a basal ridge below which the sculpture is similar to that above.

Amaea (*s. l.*) *contexta* DuShane, 1970

(Figure 69)

Amaea (*s. l.*) *contexta* DuShane, 1970: 4; fig. 5; SPHON, 1970: 5

Amaea contexta. - KEEN, 1971: 438; fig. 675

Original Description: "Shell of medium size, slender, dark brown, with four smooth, white, glassy nuclear whorls

(missing in holotype), first postnuclear whorl axially ribbed; the following 10 whorls dark brown, convex; suture deeply impressed; axial sculpture of thin, strong ribs, about 24 on the body whorl, with occasionally a very heavy rib; these ribs continue to the columellar wall; spiral sculpture of about 18 ridges per whorl, beaded on the anterior face of the ribs; basal ridge present; outer lip formed by the extension of the last varix; aperture oval, umbilicus lacking; operculum lacking in holotype. Dimension (in mm): length 15.4, width 4.5 (holotype)." (DUSHANE, 1970: 4)

Diagnosis: An epitoniid differing markedly from other Panamic-Galapagan species; whorls 10, dark brown; sutures deeply impressed; axial ribs numerous on the body whorl with an occasional heavy rib; spiral sculpture weaker than the axial; intersections of axial and spiral sculpture beaded; basal ridge present; aperture oval; umbilicus lacking.

Discussion: The sculpture and color of this species are distinctive and unlike those in all other species of Epitoniidae from the west American coast. The generic allocation is uncertain, but since the general features suggest *Amaea* H. & A. Adams, 1853 it is placed here provisionally.

One specimen, the holotype, was dredged from Petatlan Bay, Guerrero, Mexico in 9 to 18 m, by the *Velero III*, station 265-34, February 3, 1934. Two smaller, damaged specimens with intact nuclear whorls were dredged by Laura and Carl Shy off Manzanillo, Colima, Mexico in 9 to 18 m, November 1967. These two specimens, while considerably smaller than the holotype, are uniformly dark brown, suggesting that the color of the holotype has faded.

Type Material:

Amaea (*s. l.*) *contexta*: holotype, LACM-AHF 1199

Type Locality:

Amaea (*s. l.*) *contexta*: Petatlan Bay, Guerrero, Mexico

Geographic Distribution and Ecology: Apparently restricted to a small area off the west Mexican coast from Manzanillo, Colima to Petatlan Bay, Guerrero, Mexico.

Bathymetric Range: Dredged in from 9 to 18 m

Geochronological Range: Recent

(*Scalina*) Conrad, 1865

[Type species (SD, Palmer, 1937): *Scalina staminea* Conrad, 1865]

Shells with basal ridge or keel below which sculpture is different from that above.

Amaea (Scalina) brunneopicta (Dall, 1908)

(Figures 63, 64)

Epitonium (Ferminoscala) brunneopictum Dall, 1908: 316; pl. 8, fig. 10; Boss *et al.*, 1968: 51

Epitonium brunneopictum. - DALL, 1917: 474; STRONG, 1945: 21

Epitonium (Scalina) brunneopictum. - GLENCH & TURNER, 1950: 287

Scalina ferminiana brunneopicta. - KEEN, 1958: 278; DUSHANE & POORMAN, 1967: 424

Amaea (Scalina) brunneopicta. - DUSHANE & MCLEAN, 1968: 5; fig. 6; KEEN, 1971: 436; fig. 670

? *Eglisia nebulosa* Dall, 1919: 348; Boss *et al.*, 1968: 218

Eglisia (?) *nebulosa*. - KEEN, 1958: 277; fig. 155

Original Description: "Shell slender, acute, pale brownish, with broad peripheral band and basal disk of darker brown, and about 11 whorls, exclusive of the (lost) nucleus; sculpture of the same type as in the preceding species [*Epitonium (Ferminoscala) ferminianum* Dall, 1908] with, between the sutures, 4 primary and about 6 secondary spirals beside the spiral striae; the axial lamellae are very small and sharp, regularly spaced, little raised and about 36 on the penultimate whorl, they appear as whitish lines on a brown background; basal disk sharply spirally threaded, little raised; aperture as figured, when fully grown probably with a thick varix. Length of shell, 37, of last whorl 14; of aperture, 8; diameter of basal disk, 9; max. diameter 10 mm." (DALL, 1908: 316)

Diagnosis: Shell slender, acute; size medium to large; color brown; whorls 13 to 14, convex, rounded in all stages; nuclear whorls lacking; first 2 whorls crenulated by the axial and spiral sculpture, 3rd whorl with 1 strong cord at the periphery, 4th and 5th whorls with 1 strong cord at the periphery with a weaker one on either side, 6th whorl with 3 strong cords at the periphery with 2 weaker cords on either side, from there on down the cords increase in number until, on the last whorl, there are 9 rounded, broader cords; sutures moderately deep; costae 25 to 40 on the last whorl, white, thin, sharp on early whorls, less sharply raised on later whorls; the cords intersected by the costae forming small, unevenly spaced rhomboids within which there are fine axial and spiral threads, with the axial threads crossing over the spiral cords forming the rhomboid; basal area brown, defined by a some-

what thickened cord, sculpture same as on the body whorl but fainter; lip white, thin, slightly crenulated by the spiral ribs crossing the last costa, patulous; peritreme incomplete, brownish color of the base can be seen as a brown spot anteriorly on the inside of the aperture; operculum dark brown, multispiral.

Discussion: The shells of this species vary in size from 11 to 44 mm in length and from 3 to 12 mm in width. Somewhat similar to *Amaea (Scalina) ferminiana* (Dall, 1908), the distinctions are great enough that one has no difficulty separating the two species. When the 2 occur together they are distinct species with no extremes of variation. From *A. ferminiana* the present species varies by having a more slender shell with all whorls rounded, by being smaller and appearing to be more fragile. It is probable that *Scala mitchelli* Dall, 1896 (p. 112), from off the Texas coast, forms another member of the subgenus *Scalina*. It resembles *A. (S.) brunneopicta*, but has a much stouter and larger shell.

At present, this seems to be the only species of *Scalina* taken as far north as Cedros Island on the outer coast of Baja California, *Albatross* station 2835, in 10 m. From there it ranges south and into the Gulf of California where several specimens were obtained by the *Ariel* off Cabo Haro, Guaymas, Mexico, by dredging in 36 to 72 m in August 1960; thence south along the west Mexican coast to Playa Blanca, Costa Rica by Hancock Expeditions, *Velero III* station 415-35, where it was dredged in 41 m in February 1935.

Dall erred when he surmised that *Amaea (Scalina) brunneopicta*, when fully adult, probably had a thick varix on the aperture. DALL's (1919: 348) *Eglisia nebulosa* from off Cabo San Lucas, Baja California proves, upon examination, to be a worn specimen of *A. brunneopicta*.

DALL (*loc. cit.*) reported that Carpenter had said that the shell was an *Eglisia*, but Dall thought it belonged with the epitoniids.

Type Material:

Epitonium (Ferminoscala) brunneopictum: holotype, USNM 97084

? *Eglisia nebulosa*: holotype, USNM 120702

Type Localities:

Epitonium (Ferminoscala) brunneopictum: Cedros Island, Baja California, Mexico

? *Eglisia nebulosa*: Cabo San Lucas, Baja California, Mexico

Geographical Distribution and Ecology: From Cedros Island, Mexico, throughout the Gulf of California, south on the west Mexican coast to Costa Rica; dredged from a mud bottom.

Bathymetric Range: 9 to 72 m

Geochronological Range: Recent

Amaea (Scalina) deroyae DuShane, 1970

(Figure 67)

Amaea (Scalina) deroyae, DuShane, 1970: 330; pl. 51, fig. 2;
SPHON, 1970: 5; KEEN, 1971: 436; fig. 671

Original Description: "Shell medium in size, thin, pale brown, nuclear whorls missing in holotype; remaining 13 whorls strongly convex, with a round shoulder; suture deeply impressed, aperture subcircular; axial sculpture foliaceous with about 31 costae on the body whorl; costae scalloped, with high areas at the intersections of the spiral sculpture; 6 to 8 spiral ridges on the body whorl; this reticulate pattern is found on all whorls; within the reticulations are minute axial and spiral threads; basal area set off by a strongly projecting ridge and characterized by low but well-defined reticulate sculpture; columella short, terminating in a shallow sinus; outer lip thin, with about 7 crenulations, umbilicus lacking; operculum missing in holotype. Dimensions: length, 22.8 mm, width, 7.3 mm (holotype)." (DUSHANE, 1970: 330)

Discussion: *Amaea (Scalina) deroyae* appears to be an analog of the Caribbean species *A. retifera* (Dall, 1889) (CLENCH & TURNER, 1950: 243; pls. 96, 106, figs. 1-4; DALL, 1902: pl. 30, fig. 9; and DALL, 1903: pl. 76, fig. 9 present good illustrations of the holotype of *A. retifera*). *Amaea deroyae* has the same sculptural characters, but has a shell apparently consistently smaller than that of

the Atlantic species. The Atlantic specimens attain a maximum height of about 30 mm, although the holotype is 13 mm, whereas the largest Pacific specimen measures 22 mm.

None of the Pacific specimens was taken alive. CLENCH & TURNER (1950: 245) describe the operculum of the Atlantic species; they give the range for *Amaea retifera* as North Carolina to Florida, the Gulf of Mexico and south to the Barbados, in from 23 to 216 m, with about 90 m being the median. It is a relatively abundant species as indicated by the records presented by CLENCH & TURNER (*op. cit.*). They compare *A. retifera* with *A. decussata* (Lamarck, 1801) from the East Indies, suggesting the relationship to be very close.

Amaea deroyae occurs in the Gulf of California: AMNH - Puritan - American Museum Expedition (76220), dredged off the southwest side of Isla San Diego, in 45 to 72 m, April 1957, one freshly dead specimen; SBMNH, trawled off Cabo Haro, Guaymas, in 80 to 162 m, September 1960, 5 specimens; south to the Tres Marias Islands, AMNH, Puritan - American Museum Expedition (67: 75204), dredged off Maria Magdalena Island, 2 specimens; and to the Galápagos Islands (type locality, Isla Isabela [Albemarle Island], AHF station 147-34, in 54 m, January 1934, 6 specimens).

Type Material:

Amaea (Scalina) deroyae: holotype, LACM 1236

Type Locality:

Amaea (Scalina) deroyae: Tagus Cove, Isla Isabela (Albemarle Island), Galápagos Islands, Ecuador

Geographical Distribution and Ecology: Throughout the Gulf of California to the Tres Marias Islands, Mexico,

Explanation of Figures 100 to 112

Figure 100: *Scalaria aciculina* Hinds, 1844 (after SOWERBY, 1844). Holotype, BM[NH] lost; length 9 mm × 7

Figure 101: *Epitonium (Depressiscula) aciculinum* (Hinds, 1844). Nayarit, Mexico (DuShane Coll.); length 10 mm; width 2½ mm × 3.8

Figure 102: *Epitonium (Asperiscula) longinosanum* DuShane, 1970. Holotype, LACM 1196; length 16½ mm; width 5½ mm × 3½

Figure 103: *Epitonium (Pictoscala) purpuratum* Dall, 1917. Holotype, USNM 252242; length 10 mm; width 5 mm × 5

Figure 104: *Epitonium (Nitidiscala) durhamianum* Hertlein & Strong, 1951. Holotype, CAS[GTC] 9623; length 5.7 mm; width 1.8 mm × 6.3

Figure 105: *Scalaria curvilineata* Sowerby, 1844 (figure after SOWERBY, 1844). Holotype BM[NH] apparently lost; length 16 mm; width 7½ mm × 3.1

Figure 106: *Epitonium imbrex* Dall, 1917. Holotype, USNM 324464; length 2.3 mm; width 1.0 mm × 5½

Figure 107: *Epitonium columnella* Dall, 1917. Holotype, USNM 111220; length 2¾ mm; width 1¾ mm × 1.9

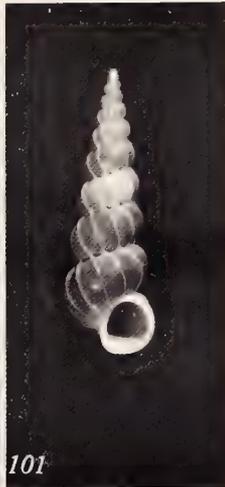
Figure 108: *Epitonium tabogense* Dall, 1917. Holotype, USNM 211786; length 3 mm; width 1½ mm × 9.6

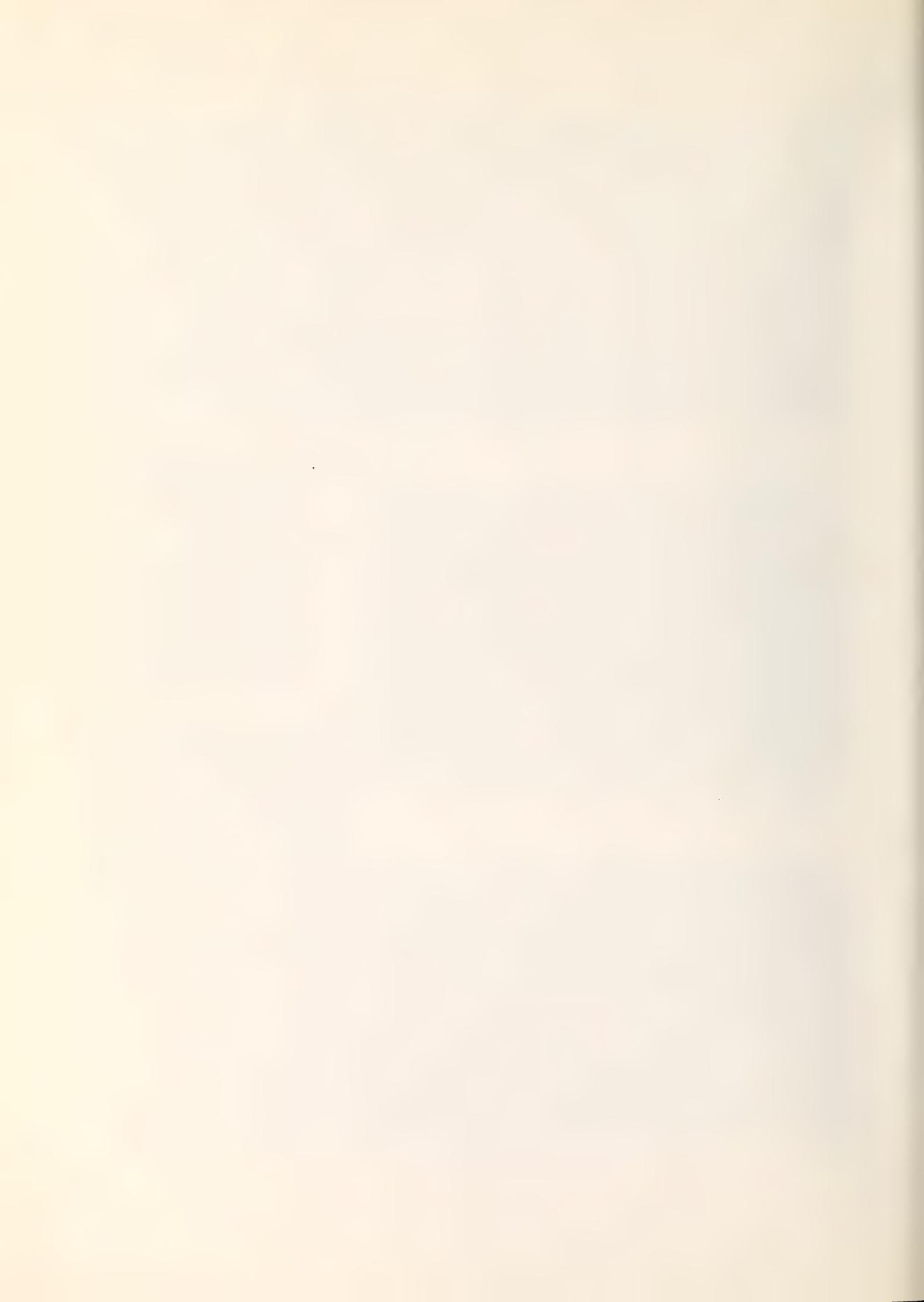
Figure 109: *Epitonium (Nitidoscala) colpoicum* Dall, 1917. Holotype, USNM 46213; length 9 mm; width 4½ mm × 2.6

Figure 110: *Epitonium (Nitidiscala) gissleri* Strong & Hertlein, 1939. Holotype, CAS[GTC] 723; length 4.8 mm; width 2.3 mm × 6

Figure 111: *Scalaria cumingii* Carpenter, 1856. Holotype, BM[NH] 1950.3.31.1 × 3.7

Figure 112: *Epitonium (Nitidiscala) cumingii* (Carpenter, 1856). Live-taken specimen, Guaymas, Sonora, Mexico (DuShane Coll.); length 11 mm; width 6 mm × 7.6





and the Galápagos Islands, Ecuador. Records are scanty, but the *Velero III* reported a rock and coral bottom.

Bathymetric Range: Dredged in 36 to 162 m

Geochronological Range: Recent

Amaea (Scalina) ferminiana (Dall, 1908)

(Figures 65 and 68)

Epitonium (Ferminoscala) ferminianum Dall, 1908: 316; plt. 8, fig. 8; DALL, 1917: 474; OLSSON, 1942: 228; plt. 9, fig. 6 (Pliocene fossil); CLENCH & TURNER, 1951: 287; BOSS *et al.*, 1968: 127

Epitonium ferminianum. - M. SMITH, 1944: 7; STRONG, 1945: 21

Epitonium (Ferminoscala) ferminoscala [*sic*]. - CLENCH & TURNER, 1950: 243

Scalina ferminiana. - KEEN, 1958: 278; fig. 167; KEEN, 1964: 199; OLSSON, 1964: 200; plt. 33, figs. 2, 2a

Amaea (Scalina) ferminiana. - DUSHANE & MCLEAN, 1968: 5; fig. 3; KEEN, 1971: 438; fig. 672

Scala (Acrilla) weigandi Böse, 1910: 228-230; plt. 12, fig. 8 (Tertiary fossil)

Original Description: "Shell large, solid, acute, with 11 or more closely adherent whorls, of a livid flesh color, fading to white, the terminal varix white; surface dull, not polished, axial sculpture of numerous low, small, sharp lamellae, slightly more prominent before the suture of the last two whorls; these are reticulated by half a dozen prominent, flattish spiral threads with wider interspaces in which run much finer threads; the basal disk is also covered with close-set, very fine spiral threads, and the suture is laid on its posterior margin; aperture rounded, slightly patulous in the prolongation of the axis, and in the fully adult shell with a thick, white varicose peritreme bevelled away from the actual aperture to the thicker portion of the varix behind. Length of shell, 38; of last whorl, 21; diameter of disk, 15.5, of last whorl, 17 mm." (DALL, 1908: 316)

Diagnosis: Shell large, acute, brown in color; whorls 11 to 15, convex, closely adherent; nuclear whorl perhaps disintegrated, apical whorl partially submerged, with decussate ornament; second whorl down with one strong cord at the periphery giving an angulate outline to the whorl, the remainder of the whorls with one strong cord at the periphery and 2 weaker ones on either side, these adjacent cords increase in strength resulting in a loss of angulation on the later whorls; sutures moderately deep; costae 45 to 50, white, low, of varying width, slightly more

prominent in front of the sutures; the spiral cords intersected by the costae forming small, very unevenly spaced rhomboids within which there are fine axial and spiral threads; basal area brown, defined by a small cord, sculpture the same as on the body whorl but fainter, with the costae more prominent than the spiral sculpture; lip white, thin, slightly crenulated by the spiral ribs crossing the last costae, patulous; peritreme incomplete; operculum dark brown, paucispiral.

Discussion: The shell size of this species varies from 23 to 76 mm in height and from 9 to 33 mm in width. Although somewhat similar to *Amaea (Scalina) brunneopicta* (Dall, 1908), this species has a much broader shell with the early whorls having an angulation caused by the peripheral cord. In addition, the basal area is usually the same shade of brown as the other portions of the shell, whereas *A. brunneopicta* is streaked with varying shades of brown. When BÖSE (1910: 228) described *Scala (Acrilla) weigandi* from the late Tertiary fauna of Tehuantepec, Mexico, he was probably unaware of Dall's description of *A. (S.) ferminiana*, although he compared his species to *A. retifera* (Dall, 1889), from the Atlantic. Böse obtained only 1 specimen, 23 mm in length, 9.3 mm in width, at Kilometer 70 on the Tehuantepec Road, Caribbean side of the peninsula. This specimen agrees in size and proportions with *A. ferminiana*. A specimen of Dall's species placed over the illustration given by BÖSE (1910: plt. 12, fig. 8) fits exactly. Further, the illustration shows the central cord on each whorl with 2 minor cords above and below it. There can be no doubt that *S. weigandi* is a synonym of *A. (S.) ferminiana*. OLSSON (1942: 228) reported *A. ferminiana* as a Pliocene fossil from the Burica Peninsula, Cosa Rica; again (1964: 199) as a Neogene fossil from northwestern Ecuador.

An uncommon species, Recent *Amaea (Scalina) ferminiana* range sparingly into the Gulf of California (type locality Point Fermin, U. S. S. *Albatross* station 3034, in 43 m). The southernmost record is that of the SEPBOB Program on the vessel *Anton Bruun*, station 625-A off the coast of Perú, in from 118 to 1333 m, June 1966 (3 specimens).

Type Material:

Epitonium (Ferminoscala) ferminianum: holotype, USNM 96818

Scala (Acrilla) weigandi: holotype, Berlin Museum, Germany

Type Localities:

Epitonium (Ferminoscala) ferminianum: Point Fermin, Gulf of California, Mexico

Scala (Acrilla) weigandi: Tehuantepec Road, Caribbean side of the peninsula

Geographical Distribution and Ecology: Gulf of California, west coast of Mexico south to Panama, Ecuador and Perú; usually taken from mud, bottom temperatures from 13.2 to 17½° C

Bathymetric Range: Dredged in 36 to 275 m

Geochronological Range: Recent and fossil (Neogene or late Tertiary), no specific epoch given by Böse; Pliocene

Amaea (Scalina) pompholyx (Dall, 1890)

(Figure 66)

Scala (Acrilla) pompholyx Dall, 1890: 332

Scala pompholyx. - STEARNS, 1893: 439; DEBOURY, 1919: 37 [as "Dall, 1889"]; BOSS *et al.*, 1968: 261

Scala (Ferminoscala) pompholyx. - DALL, 1917: 474 [as "Dall, 1889"]; STRONG, 1945: 21 [as "Dall, 1889"]

? *Amaea (Scalina) pompholyx*. - KEEN, 1971: 438; fig. 673

Original Description: "Shell thin, conical, inflated, white, with a pale yellow epidermis, smooth, polished, glassy nucleus, and nine or more whorls; spiral sculpture of fine numerous close-set rounded threads, with narrower interspaces, covering the whole surface, and a single stouter thread marginating the base, on which the suture runs; transverse sculpture of rather irregular rounded wrinkles following the incremental lines when present, but often absent, to some extent reticulating the stronger spirals; also of extremely thin, hardly raised, varical lamellae, about 32 on the last whorl; these are a little more elevated in the vicinity of the suture and a little fainter on the base; suture distinct, not deep; base imperforate; aperture subcircular, a little angulated below. Maximum longitude of shell, 14; of last whorl, 8; maximum diameter, 7.6." (DALL, 1890: 332)

Diagnosis: Shell thin, fragile; nuclear whorls lost; remaining whorls 7, inflated, rapidly enlarging; suture distinct; costae about 32, fine, more distinct near the sutures; spiral sculpture of fine threads, rounded, numerous, close-set; intersected by the axials to form small rectangles; base marginated by a single heavier cord, below which the sculpture changes; aperture oval, lip thin, slightly reflected; operculum unknown. Length, 14 mm; width, 7.6 mm (see below under Discussion).

Discussion: Other than the fact that DALL (1917: 474) mentions the range of this taxon to be from Cape San Lucas, Mexico to the Galápagos Islands, in deep water,

there seems to be no further mention in the literature regarding *Amaea (Scalina) pompholyx*. The type was taken by the *Albatross* (station 2807) near the Galápagos Islands in 1485 m (ooze, bottom temperature 38.4° F). DALL (1890: 332) mentioned in his description a pale yellow epidermis. When the type was examined no indication of it ever having had a periostracum was noted. At present the type (USNM 96474) differs from the original description somewhat since it has lost 2 nuclear whorls and a corresponding millimeter in height. Seven whorls remain; the dimensions are now 13 mm in height, 8 mm in width.

Although KEEN (1971: 438) questions the placement of this taxon in *Amaea*, it meets the requirements for the genus. The shell has a weak basal ridge with sculpture below different from that above. Between the worn costae are small spiral ribs which are cross-hatched with lesser axial threads, giving a beaded appearance to the interspaces between the costae. This taxon has a very fragile shell; the aperture is shattered on the type, although it was complete originally. DALL (1890: 332) placed his species in the subgenus *Acrilla*, but subsequently (1917: 474) changed it to the subgenus *Ferminoscala* (later changed to *Scalina*) with no explanation.

Type Material:

Scala (Acrilla) pompholyx: holotype, USNM 96474

Type Locality:

Scala (Acrilla) pompholyx: Off the Galápagos Islands, Ecuador

Geographical Distribution and Ecology: Cape San Lucas, Mexico to the Galápagos Islands, Ecuador (*vide* Dall). Dredged in ooze; bottom temperature, 38.4° F

Bathymetric Range: From 1485 m

Geochronological Range: Recent

Amaea (Scalina) tehuanaorum DuShane & McLean, 1968

(Figure 68)

Amaea (Scalina) tehuanaorum DuShane & McLean, 1968: 4; figs. 4, 5; SPHON, 1970: 5; KEEN, 1971: 438; fig. 674

Original Description: "Shell large, thin but strong, light brown, with 9 to 10 gradually enlarging postnuclear whorls (nuclear whorls missing); the first three or four whorls showing a decided angulation at the periphery, the fol-

lowing whorls markedly convex; sculpture strongly cancellate throughout, with 9 spiral ribs on the fourth whorl, increasing to 15 on the penultimate whorl; ribs more closely spaced and narrow below the deeply impressed suture, fine spiral striae between the spiral ribs; axial sculpture of 38-40 thin, white costae, raised into aculeated lamellae at the suture and reflected toward the direction of growth; fine axial striae between the axial costae; base of shell set off by a ridge consisting of a spiral cord of regular strength; base of shell with about 14 thin, closely spaced spiral cords, crossed by the much reduced axial ribs; umbilicus lacking; aperture simple, white; lip greatly thickened by one or more coalesced axial ribs; columella heavier and slightly deflected at its lower portion, with, on some specimens, a slight twisting behind the columellar lip; peritreme discontinuous and attached on the inner face of the last whorl, with cancellate sculpture of the base often seen showing through the glazed surface within the peritreme; operculum missing in type lot. Dimensions (in mm): length 39.5; width 15 (holotype)." (DUSHANE & McLEAN, 1968: 4)

Diagnosis: *Amaea (Scalina) tehuandarum* is distinguished from other Panamic-Galapagan species of *Amaea* in having intermediate proportions, a thickened mature lip, and a convex outline to the overall slope of the shell. It has a dark brown paucispiral operculum of 3 whorls.

Discussion: *Amaea (Scalina) tehuandarum* is closely related to *A. (S.) brunneopicta* (DALL, 1908: 316) and *A. (S.) ferminiana* (DALL, 1908: 318), but differs from both of these species in proportions. The shell is broader than that of *A. brunneopicta* and narrower than that of *A. ferminiana*. Both of the latter species have evenly tapering shells while that of *A. tehuandarum* is rapidly inflated, giving a convex outline to the overall slope of the shell. In addition, the thickened lip of *A. tehuandarum* is lacking in the two species of Dall, each of which has a thin, fragile lip. *Amaea ferminiana* attains twice the length of *A. tehuandarum*.

Although KEEN (1958: 278) treated the 2 species of Dall as differing only subspecifically, they do differ consistently in proportions and have generally been accepted as valid species. I have seen specimens from many localities at which both species occur. Both *A. ferminiana* and *A. brunneopicta* occur in the Gulf of Tehuantepec with *A. tehuandarum*. Specimens of *A. ferminiana* and *A. brunneopicta* (Figure 68) from this locality are illustrated here for comparison.

KEEN (1958: 278) considered *Scalina* as a full genus. CLENCH & TURNER (1950: 242) regard it as a subgenus

of *Amaea*. The genus *Amaea* H. & A. Adams, 1853 (type species *Scalaria magnifica* Sowerby [KIRA, 1962: 30; plt. 14, fig. 20]) shows on the type species a weak basal ridge without having the basal sculpture greatly different from that on the body whorl. In the subgenus *Scalina* Conrad, 1865 (type species *Scalina staminea* Conrad, 1865 [PALMER, 1937: 102; plt. 8, fig. 16]) a stronger basal ridge is apparent, the basal area is markedly concave and the basal sculpture is radically different from that on the body whorl. As shown by PALMER (1937) and CLENCH & TURNER (1951: 287), *Ferminoscala* Dall is a synonym of *Scalina* Conrad. CLENCH & TURNER (1950) placed the Caribbean species *Amaea retifera* Dall in the subgenus *Scalina* (inadvertently as *Ferminoscala*), since the basal ridge and concave base are quite apparent in that species. Possibly the Caribbean species *A. mitchelli* should also have been assigned by them to the subgenus *Scalina* rather than to *Amaea* (*s. s.*). It differs from *A. ferminiana* chiefly in having less pronounced axial and spiral sculpture.

Specimens of *Amaea (Scalina) tehuandarum* have been reported from a few localities other than the type locality (Gulf of Tehuantepec, collected by Dr. Donald Shasky, July 1963). One specimen in the LACM Collection was trawled in 54 m off Punta San Telmo in the southern part of the Gulf of California by Lloyd Findley in July 1965. The live-collected specimen has 10 postnuclear whorls and a paucispiral operculum of 3 whorls. It measures 44 mm in length and 17 mm in width. Another specimen in the LACM-AHF Collection was dredged by the *Velero III* (station 539-36) March 1936 off the spit at Bahía de Los Angeles, Gulf of California, Mexico, in 2 m on sand substrate. This specimen has 8 postnuclear whorls and measures 39 mm in length and 15½ mm in width. These 2 specimens are darker in color than those of the type series, none of which was live-collected, indicating that the color has probably faded in the type series. The southernmost record for this species is that of the SEPBOB Program, on the vessel *Anton Bruun* (station 625-A) off the coast of Perú, in from 118-133 m, June 1966 (1 specimen).

Type Material:

Amaea (Scalina) tehuandarum: holotype, LACM 1161

Type Locality:

Amaea (Scalina) tehuandarum: Gulf of Tehuantepec, Mexico

Geographical Distribution and Ecology: Gulf of California to Gulf of Tehuantepec, Mexico; dredged from sand or mud substrate

Bathymetric Range: 2 to 133 m

Geochronological Range: Recent

Opalia H. & A. Adams, 1853

[Type species (SD deBoury, 1886): *Scalaria australis* Lamarck, 1822]

Shells white or light gray to brown; solid, imperforate; axial sculpture of strong ribs that may sometimes be angulated; with or without basal ridge; with spiral sculpture of fine threads between each 2 of which is a row of small pits. A chalky outer layer over the entire shell is easily abraded. Aperture at an angle to the axis of the shell; lip thickened by last axial rib; operculum thin, paucispiral.

(Dentiscala) deBoury, 1886

[Type species (OD deBoury, 1886): *Turbo crenatus* Linnaeus, 1758]

Shells medium to large in size; white or off-white; ribs may become obscure on the whorls; suture usually deep; whorls convex, sometimes with sharply angulated shoulder and well-defined basal disk below which the ribs do not usually extend.

Opalia (Dentiscala) crenatoides (Carpenter, 1864)

(Figures 130, 131)

Opalia crenatoides Carpenter, 1864b: 47 (reprint 1872: 220); CARPENTER, 1864c: 619 (reprint 1872: 105); CARPENTER, 1864-1865: 31 (reprint 1872: 244); KEEP, 1893: 49; WHITE, 1896: 103; KELSEY, 1898: 89; M. SMITH, 1907: 58; LOWE, 1913: 27; ORCUTT, 1915: 20, 31; OLDRYD, 1918: 27; DUSHANE & POORMAN, 1967: 425

Opalia (? *crenatoides*, var.) *insculpta* Carpenter, 1866: 275-277 (reprint 1872: 324) [Pleistocene fossil]; STEARNS, 1894: 188; DALL, 1909: 189-191

Var. *crenatoides*. - TRYON, 1887: 77; pl. 16, fig. 1

Scala (Opalia) crenatoides. - BERRY, 1907: 42

Dentiscala crenatoides. - COSSMANN, 1912: 90

Opalia (Dentiscala) crenatoides. - DALL, 1917: 473

Scala crenatoides. - DEBOURY, 1919: 34, 36

Epitonium (Dentiscala) crenatoides. - BAKER, HANNA & STRONG, 1930: 47; pl. 2, figs. 1, 2; PILSBRY & LOWE, 1932: 120; STRONG, 1945: 18; KEEN, 1958: 278; fig. 156; PALMER, 1963: 333, 334; pl. 66, figs. 2, 3; KEEN, 1971: 440; fig. 678

Epitonium crenatoides. - KEEP (-BAILY), 1935: 180; LOWE, 1935: 20, 31; JORDAN, 1936: 113

Epitonium (Nodiscala) golischi Baker, Hanna & Strong, 1930: 44; pl. 2, figs. 1, 2

Opalia (Nodiscala) golischi. - STRONG, 1945: 19

Opalia (Dentiscala) golischi. - KEEN, 1958: 278; fig. 179

Opalia golischi. - DUSHANE & POORMAN, 1967: 425

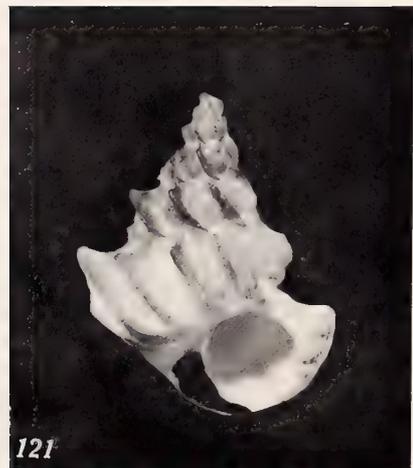
Original Description: "*D. testa turrata, alba, marginibus spirae rectis; anfr. nucl.? . . . ; norm. vi., compactis attingentibus; costis radiantibus circ. x., in spira plerumque obsoletis, ultimo anfractu validioribus, latis, haud exstantibus, attingentibus, spiram lineis fere rectis ascendentibus; suturis inter costas altissime indentatis; carina obtusa basali, suturae continua; inter costas radiantes undique, ut in suturis, indentata; costis interdum, propter lirulas spirales subobsoletes, subnodosis; columella haud umbilicata; base antice laevi. Long. .54, long. spir. .38, lat. .23 poll., div. 30°.*" (CARPENTER, 1864b: 47)

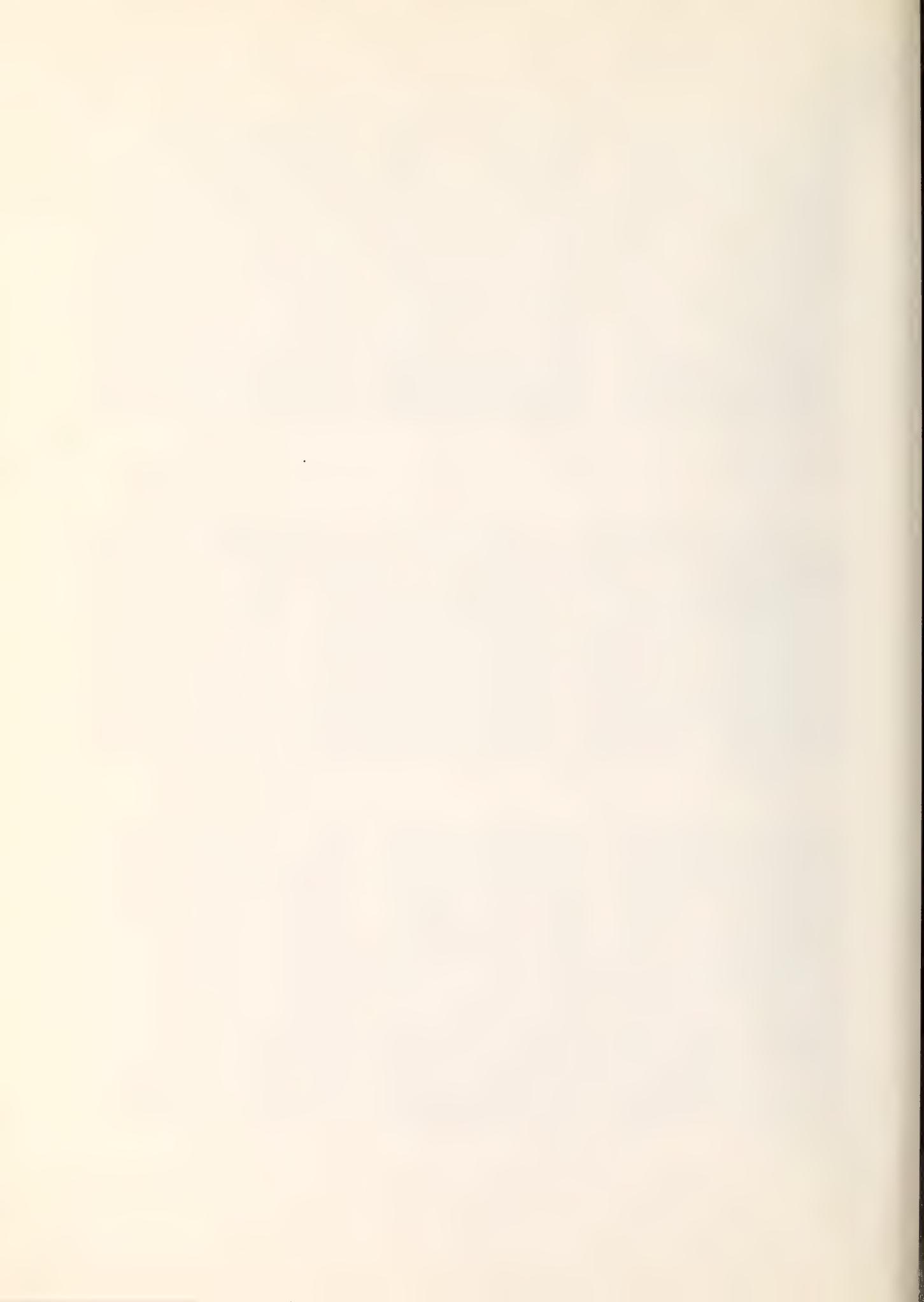
Diagnosis: Shell large for the subgenus, dull, off-white in color, calcareous outer coat; nuclear whorls 1½ to 2½, small, depressed helicoid; body whorls 8, rounded, each whorl crossed by about 10 unevenly spaced vertical ribs,

Explanation of Figures 113 to 121

Figure 113: *Epitonium (Sthenorytis) toroense* Dall, 1912, apical view. Holotype, USNM 214345 (Pliocene fossil) × 1.3
 Figure 114: *Epitonium (Sthenorytis) toroense* Dall, 1912, ventral view. Holotype, USNM 214345; length 18mm; width 18mm (Pliocene fossil) × 2.4
 Figure 115: *Epitonium (Sthenorytis) turbinum* Dall, 1908. Live-taken specimen, dredged in 170-200m south of Academy Bay, Isla Santa Cruz, Ecuador, July 1969 (coll. by DeRoy); length 39mm; width (without costae) 31mm (DuShane Coll.) × 1.3
 Figure 116: *Epitonium (Sthenorhytis)[sic] turbinum* Dall, 1908, apical view. Holotype, USNM 110568 × 2.4

Figure 117: *Epitonium (Sthenorhytis) [sic] turbinum* Dall, 1908, ventral view. Same shell as in Figure 116; length of last whorl 22mm; width 28mm × 1.3
 Figure 118: *Scalaria diana* Hinds, 1844. Holotype, BM[NH] 1950. 4.18.3; length 8mm; width 7.8mm × 5.6
 Figure 119: *Sthenorytis hertleini* Olsson, 1964, apical view. Holotype, USNM 644060 × 1.2
 Figure 120: *Sthenorytis hertleini* Olsson, 1964, ventral view. Same shell as in Figure 119; length 25mm; width 22mm × 1.2
 Figure 121: *Epitonium (Sthenorytis) paradisi* Hertlein & Strong, 1951. Holotype, CAS[GTC] 9627; length 35mm; width 26½mm × 1.2





low, rounded, overlapping the deep sutures to form pits; interspaces as broad as the ribs; sutures deep; the entire shell covered with spiral rows of very small, unequal punctations between minute spiral threads; basal disk joined by the extensions of the axial ribs to form deep pits above the disk; below the disk another series of pits extends to the anterior extremity of the shell; aperture subpyriform, anterior end with a wrinkled fasciole; lip heavy on mature specimens; operculum dark, paucispiral. Length, 13 to 19½ mm; width, 6 to 8 mm.

Discussion: No other *Opalia* thus far described has depressions above and below the basal disk, an important identifying characteristic.

This is a species apparently occupying the faunal area just below the low tide mark, as few live-taken specimens have been reported from above the 2 m level, and they have been taken alive off sea anemones by SCUBA divers. Beach specimens are common throughout the Gulf of California and as far south as the Galápagos Islands.

PALMER (1963: 333) gives an appraisal of the material on which Carpenter based his description of *Opalia crenatoides*, "The original material consists of the holotype which is badly worn with the apex eroded. The shell consists of 7 whorls with 9 longitudinal ribs on the body whorl. There is a strong basal cord and a thickened continuous lip. There are faint remnants of strong spiral ribs on the body whorl which are completely eroded on the whorls of the spire. The ribs are deep pitted into the suture."

CARPENTER (1866: 275 - 277) commented, "This and the Santa Barbara fossil, *O. var. insculpta*, are so close to the Portuguese *O. crenata*, that additional specimens may connect them." As I have seen no specimens of *Opalia crenata*, I cannot confirm this comparison. *Opalia (Dentiscala) insculpta* Carpenter proves to be a synonym of *O. (D.) funiculata* (Carpenter), *q. v.* DE BOURY (1913: 276) compared *Scalaria (D.) turrisformis* deBoury, 1913 from South Africa with *O. crenatoides*, feeling that they were very similar forms.

BAKER, HANNA & STRONG (1930: 44) had better, though limited, material from which to describe their synonymic species, *Opalia (Nodiscala) golischi*. Two immature specimens with juvenile lips were collected by Fred Baker in 1921 at San Francisco Island, Gulf of California, the type locality; length 13 mm, width 5.8 mm (holotype).

In the collection of Dr. Shasky are 2 specimens taken alive by him, one from a small cove south of Punta Colorado (Guaymas area), Mexico, 2 m below the surface, commensal on a sea anemone, in July 1962; its length is 12 mm, and its width is 5 mm; the second specimen was taken in sand under a rock at 7 m, at Cuastecoc-

mate, Jalisco, Mexico, in October 1968; its length is 13 mm and its width is 4½ mm.

Type Material:

Opalia crenatoides: holotype, USNM 15874

Epitonium (Nodiscala) golischi: holotype, CAS[GTC] 4770

Type Localities:

Opalia crenatoides: Cabo San Lucas, Baja California, Mexico

Epitonium (Nodiscala) golischi: San Francisco Island, Gulf of California, Mexico

Geographical Distribution and Ecology: Cape San Lucas, Mexico, throughout the Gulf of California, south along the west Mexican coast to the Galápagos Islands; commensal on sea anemones.

Bathymetric Range: 2 to 5 m

Geochronological Range: Recent

Opalia (Dentiscala) diadema (Sowerby, 1832)

(Figures 132, 133, and Figure 161)

Scalaria diadema Sowerby, 1832: 55; SOWERBY, 1844: 105; plt. 35, figs. 121, 122; CARPENTER, 1857b: 448 (reprint 1967: 448); CARPENTER, 1857a: 181; 336; NYST, 1871: 105; REEVE, 1873: plt. 11, figs. 84a, 84b [REEVE's figures appear to be *Scalaria funiculata* Carpenter, 1857]; TRYON, 1887: 78; plt. 16, figs. 99, 100; STEARNS, 1893: 439; DALL, 1917: 488

Scala (Cirsotrema) diadema. - H. & A. ADAMS, 1853: 223

Opalia diadema. - CARPENTER, 1864-1865: 31 (reprint 1872: 244); DUSHANE, 1962: 45; DUSHANE & POORMAN, 1967: 425; DUSHANE & SPHON, 1968: 240

Scala diadema. - DEBOURY, 1913: 277; DEBOURY, 1919: 36

Epitonium diadema. - TOMLIN, 1927: 170

Opalia (Dentiscala) diadema. - KEEN, 1958: 278; fig. 158 [actually a figure of *Opalia funiculata*]; MCLEAN, 1961: 464; KEEN, 1971: 440; fig. 679

Opalia diadema funiculata (Carpenter, 1857). - KEEN, 1968: 408; plt. 57, figs. 50a, 50b [fig. 50a: lectotype of *Opalia funiculata*]

Original Description: "*T. brevi, obtusa, imperforata, minutissime cancellata; anfractibus 7, prominentibus, ad suturam canaliferis, angulatim crenulatis; antice carina crassa cinctis; prope apicem rapide crescentibus; varicibus prope apicem crassis, prominentibus, penultimo anfractu subobsoletis; apertura ovali; margine crasso, antice posticeque angulato; colore albo.*"

"Much shorter and more obtuse than *Sc. crenatus*, with the whorls more prominent and excavated at the suture, at the fourth whorl the size increases suddenly, but afterwards more gradually." (SOWERBY, 1832: 55)

Diagnosis: Shell large, with calcareous outer coat; color off-white; nuclear whorls $1\frac{1}{2}$, nearly always eroded; body whorls 7, strongly convex, shouldered, with large, quite deep depressions at the juncture with the suture, axial ribs 10 to 13, rounded, ending in a small node at the shoulder to form a large, shallow depression from the shoulder to the suture, between each 2 ribs; interspaces wider than the ribs; basal disk heavy, joined by the extension of the axial ribs to form pits above the disk; a second basal disk extends from the lip at an angle downward and around the basal whorl to join the lip anteriorly; between the 2 disks is a deep circular depression with suggestions of unevenly spaced pits which do not conform to the pattern of ribs above; spiral threads cover the entire shell, unevenly spaced, wavy, with very small, deep punctations between; aperture oval; lip heavy, entire, patulous; operculum dark. Length $13\frac{1}{2}$ to 22 mm; width 6 to 7 mm.

Discussion: CARPENTER (1857: 360), in describing a new species, *Opalia funiculata*, declared in a footnote that "*Cirsotrema diadema* closely resembles *C. funiculata* from Mazatlan and Panama; at first thought identical by Mr. Cuming; differing simply in the size and obtuseness of the spiral portion." REEVE (1873, vol. 5 [no pagination]) noted that "the shell is keeled with a conspicuous rib below, sculpture with rounded, thick, longitudinal ribs nodose near the suture."

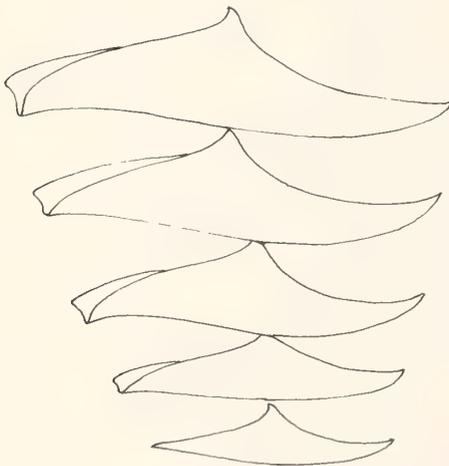


Figure 161

Opalia (Dentiscala) diadema (Sowerby, 1832)

The broad, short uncini have a hooked cusp about halfway down

No other *Opalia* thus far described has a second disk below the first and main one. The pupiform outline of the shell is characteristic.

The ANSP has 4 specimens taken by the Pinchot Expedition (H. A. Pilsbry, 1929), lot 143543, taken off Isla Pinzón [Duncan Island], Galápagos Islands, Ecuador. The Hancock Pacific Expeditions took 4 specimens, 1 off the reef north of Isla Isabela [Albemarle Island], 2 off the west coast of Isla San Salvador [James Island], both in the Galapagan group, and 1 at Independencia Bay, Peru, none live-taken. All 4 specimens are at the LACM. The deRoys have taken living specimens [6 or 7 in 10 years; 2 specimens were attached to sea anemones] under rocks at low tide, in Academy Bay, Santa Cruz Island [Indefatigable Island], Galápagos Islands.

Often confused with *Opalia funiculata* (Carpenter, 1857), a common species in the Panamic-Galapagan area, *O. diadema* (Sowerby, 1832) differs by having a ventricose shell with swollen whorls and 2 basal disks. The radula of *O. diadema* contains teeth that are broad, short and pointed, suggesting a carnivorous mode of feeding, with a hooked cusp about halfway down. The teeth are not associated on a well defined ribbon as they are in *Epitonium (Sthenorytis) turbinum* Dall, which has long, slender teeth with many more in a row. The radulae of the 2 species identify *O. diadema* as a distinct species, possibly endemic to the Galapagan littoral fauna and sympatric with *O. funiculata* at that locality. The hypothesis that *O. diadema* is endemic to the Galápagos Islands may, with further collecting elsewhere along the South American coast, prove to be erroneous.

Type Material:

Scalaria diadema: syntypes, BM(NH)

Type Locality:

Scalaria diadema: Isla San Salvador (James Island), Galápagos Islands, Ecuador

Geographical Distribution and Ecology: Galápagos Islands and Peru; symbiotic with sea anemones.

Bathymetric Range: Intertidal

Geochronological Range: Recent

Opalia (Dentiscala) exopleura (Dall, 1917)

(Figures 126, 127)

Acirsa exopleura Dall, 1917: 474; Boss *et al.*, 1968: 125

Scala exopleura. - DEBOURY, 1919: 37

Epitonium (Acirsa) exopleura. - STRONG, 1945: 20

Opalia (Opalia) exopleura. - KEEN, 1971: 438; fig. 676

Original Description: "Shell is littoriniform, acute, with seven whorls, including the somewhat styliform smooth nucleus; the sutures are appressed, the whorls only moderately convex, with very faint axial indications of ribbing, and sharp uniform spiral striation. A prominent thread upon which the suture is laid marks the periphery. The terminal varix is inconspicuous, the margin of the aperture being thickened inside with little outside expansion. Length, 3.6; diameter, 2 mm." (DALL, 1917: 474)

Diagnosis: Shell small, milk-white, solid, thick, subpyriform in shape; nuclear whorls $1\frac{1}{2}$, opaque, the first nuclear whorl deciduous; body whorls 5 to 8, rounded, enlarging rapidly; spiral sculpture of small threads, with microscopic pitting between, over entire shell; ribs 12, indistinct, not overlapping the sutures, but reaching to a very small subsutural collar; sutures not deep; indistinct basal ridge joined by the extensions of the axial ribs to form shallow depressions between; below the basal ridge the alternate rows of threads and pitting continue as wavy lines, slightly coarser than on the whorls; aperture oval, set at an oblique angle; lip heavy, patulous anteriorly; operculum unknown. Length $3\frac{1}{2}$ to 8 mm; width 2 to 4 mm.

Discussion: This species has been known only from the holotype taken at Cabo San Lucas, Baja California. Rarely do institutions seem to have it in their collections, although as dead shells it is quite commonly found on the west side of the Gulf of California as far north as Bahía Concepción (LACM Coll.) and from Mazatlán south to Manzanillo, Mexico. I have seen no livetaken specimens, which would imply that the species is an offshore form. I have collected enough specimens (96) to indicate that the fine spirals and punctations, plus the indistinct basal rib, with no pitting or crenulations at the sutures, place it in the subgenus *Dentiscala*. This form can be easily confused with worn specimens of *Opalia crenatoides* unless one remembers that the latter has pitting above and below the basal ridge.

Type Material:

Acirsa exopleura: holotype, USNM 74020

Type Locality:

Acirsa exopleura: Cabo San Lucas, Baja California, Mexico

Geographical Distribution and Ecology: From Cabo San Lucas north on the west side of the Gulf of California to Bahía Concepción; from Mazatlán south to Manzanillo, Mexico. Nothing is known of the habitat of this species.

Bathymetric Range: Unknown

Geochronological Range: Recent

Opalia (Dentiscala) funiculata (Carpenter, 1857)
[not Watson, 1883]

(Figures 122 to 125 and Figure 162)

- Scalaria (Cirsotrema) funiculata* Carpenter, 1857: 447 (reprint 1967: 447); CARPENTER, 1857a: 260, 284, 336; CARPENTER, 1860: 10; NYST, 1871: 109; HERTLEIN & STRONG, 1951: 89; PALMER, 1951: 62; BRANN, 1966: 17; KEEN, 1968: 408; plt. 57, figs. 50a, 50b; text fig. 40 (= *Opalia diadema funiculata*)
- Scalaria* sp. C. B. Adams, 1852. - CARPENTER, 1864a: 358 (reprint 1872: 192)
- Opalia funiculata*. - CARPENTER, 1864c: 547, 551 (as *Scalaria* sp.) (reprint 1872: 33, 37); CARPENTER, 1864-1865: 10 (reprint 1872: 244); McLEAN, 1969: 34; fig. 2; HOWARD, 1972: 21
- Not *Scalaria funiculata* Watson, 1883: 609; TRYON, 1887: 75; plt. 18, fig. 79 (this specimen is from Brazil and appears to be an *Opalia*; if so, *Scalaria funiculata* Watson, 1887 becomes a homonym of *Scalaria funiculata* Carpenter, 1857)
- Scala funiculata*. - DEBOURY, 1919: 34, 36
- Epitonium (Cirsotrema) funiculatum*. - KEEN, 1958: 272
- Opalia (Dentiscala) funiculata*. - KEEN, 1971: 440; fig. 680
- Opalia* (? *crenatoides*, var.) *insculpta* Carpenter, 1864c: 539, 619, 660 (reprint 1872: 25, 105, 146); CARPENTER, 1866: 275, 277 (reprint 1872: 322, 324; reprint in DALL, 1909: 189); COOPER, 1867: 34; COOPER, 1888: 255; STEARNS, 1894: 188; ARNOLD, 1903: 267; PALMER, 1958: 19, 20
- Opalia insculpta*. - CARPENTER, 1864-1865: 10 (reprint 1872: 244); VAN WINKLE, 1921: 4; plt. 1, figs. 10, 11; BURCH, 1947: 24
- Opalia crenatoides insculpta* Cooper [sic]. - ORCUTT, 1915: 31, 42
- Opalia (Dentiscala) insculpta*. - DALL, 1917: 473; STRONG, 1945: 18; ABBOTT, 1954: 162; PALMER, 1958: 28, 50, 191; plt. 22, figs. 4, 5
- Opalia insculpta* Arnold [sic]. - STRONG, 1922: 154
- Epitonium (Dentiscala) insculpta*. - BAKER, HANNA & STRONG, 1930: 48
- Epitonium (Dentiscala) insculptum*. - GRANT & GALE, 1931: 855
- Epitonium insculptum*. - WILLETT, 1938: 10
- Dentiscala crenimarginata* Dall, 1917: 473; PALMER, 1958: 191; KEEN, 1958: 272; McLEAN, 1961: 464; BOSS *et al.*, 1968: 94
- Scala crenimarginata*. - DEBOURY, 1919: 36
- Epitonium (Dentiscala) crenimarginata*. - DALL, 1921: 114; STRONG, 1922: 154
- Epitonium (Opalia) crenimarginata*. - STRONG, 1923: 42
- Epitonium (Dentiscala) crenimarginatum*. - OLDRYD, 1927: 53; BAKER, HANNA & STRONG, 1930: 47; plt. 2, fig. 6; PILSBRY & LOWE, 1932: 120; KEEP, 1935: 180; STRONG, 1937: 193; A. G. SMITH & GORDON, 1948: 190
- Epitonium crenimarginatum*. - KEEN, 1937: 35; WILLETT, 1938: 10; STRONG, 1945: 18
- Epitonium crenimarginata*. - LOWE, 1935: 31
- Opalia crenimarginatum*. - BURCH, 1947: 24
- Opalia crenimarginata*. - ABBOTT, 1954: 162; DuSHANE & POORMAN, 1967: 425

Dentiscala nesiotica Dall, 1917: 473 [not *Epitonium nesioticum* Dall & Ochsner, 1928]; STRONG, 1945: 18; BOSS *et al.*, 1968: 219

Scala nesiotica. - DEBOURY, 1919: 37

Epitonium (Dentiscala) nesiotica. - DALL, 1921: 114; STRONG, 1922: 154

Epitonium (Dentiscala) nesioticum. - OLDROYD, 1927: 53

Epitonium nesioticum. - KEEN, 1937: 35

Original Description: *C. t. subelongata, graciliore, alba; marginibus spirae rectis; anfr. ix. prope suturam valde impressum acute angulatis; costibus variantibus (xv.-xx.) haud acutis, angustioribus, ad angulam coronatis, supra basin vix continuis; anfr. ult. costis plerumque obsoletis, varicibus paucis validis; costa rotundata, suturam continuante, circa basin tumente, a costis radiantibus nodosa; costa spirali altera labio adjiciente; tota superficie minutissime decussata; labro a costis sinuato.*

"This shell agrees with *C. diadema* in almost every particular down to the minute decussation of the surface. The remarkable pupiform growth of the Peruvian shells however, contrasted with the very regular spire (with one more whirl in proportion) of the Panama and Mazatlan specimens, is thought by Mr. Cuming sufficient to separate the species. The Mazatlan shells are not so large as those in Mr. Cuming's collection, which measure *long.* '7, *long. spir.* '47, *lat.* '34, *div.* 37°." (CARPENTER, 1857b: 447)

Discussion: *Opalia funiculata* can be picked up on almost any rocky beach in California, throughout the Gulf of California, south to Ecuador and the Galápagos Islands. Several early workers failed to realize that one of the most common species of *Opalia* in the Panamic-Galapagan fauna has an extensive geographical distribution. Poor communication between these early scientists is perhaps

the reason each gave a different name to *O. funiculata*, simply because his specimen came from a different locality within the province. All have the characteristics described by Carpenter for his species.

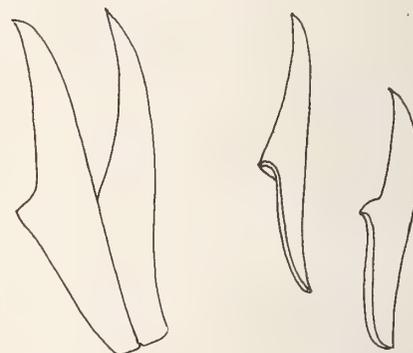


Figure 162

Opalia (Dentiscala) funiculata (Carpenter 1857)

The blunt, short uncini have a rounded cusp

After describing *Opalia insculpta*, a Pleistocene fossil from Santa Barbara, California, as a variety of *O. crenatoides* Carpenter (1864: 539), CARPENTER (1866) declares *O. insculpta* to be a southern form and contradicts himself (p. 660) when he states the species is found only as a fossil. Not until 1866 (p. 275) did he validate the species by describing it from the Pleistocene-Pliocene explaining that "*Opalia crenatoides* is a recent species with fewer varices than *insculptum* and appears to be quite distinct, though no doubt related."

Explanation of Figures 122 to 133

Figure 122: *Opalia insculpta* Carpenter, 1865. Holotype, Paleontol. Res. Inst. 7090 (formerly Cornell Univ. 4950); length 14 mm; width 7 mm × 4

Figure 123: *Opalia (Dentiscala) crenimarginata* Dall, 1917. Holotype, USNM 111207; length 17 mm; width 7 mm × 3.7

Figure 124: *Opalia (Dentiscala) nesiotica* Dall, 1917. Holotype, USNM 56900; length 10½ mm; width 5 mm × 6

Figure 125: *Scalaria (Cirsotrema) funiculata* Carpenter, 1857. Lectotype, KEEN, 1968, BM[NH]; length 21 mm × 2

Figure 126: *Opalia (Dentiscala) exopleura* (Dall, 1917). Tenacatita Bay, Jalisco, Mexico (DuShane Coll.); length 8 mm; width 4 mm × 8

Figure 127: *Acirsa exopleura* Dall, 1917. Holotype. USNM 74020; length 3.6 mm; width 2 mm × 13½

Figure 128: *Epitonium (Punctiscala ?) colimanum* Hertlein & Strong, 1951. Holotype, CAS[GTC] 9626; length 7.6 mm; width 2.8 mm × 6

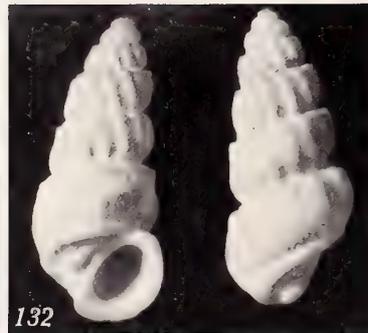
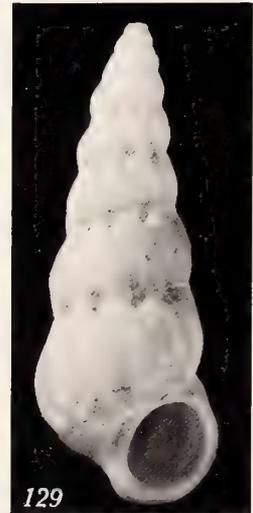
Figure 129: *Opalia (Dentiscala) mexicana* Dall, 1908. Holotype, USNM 59336; length 11½ mm; width 4 mm × 5½

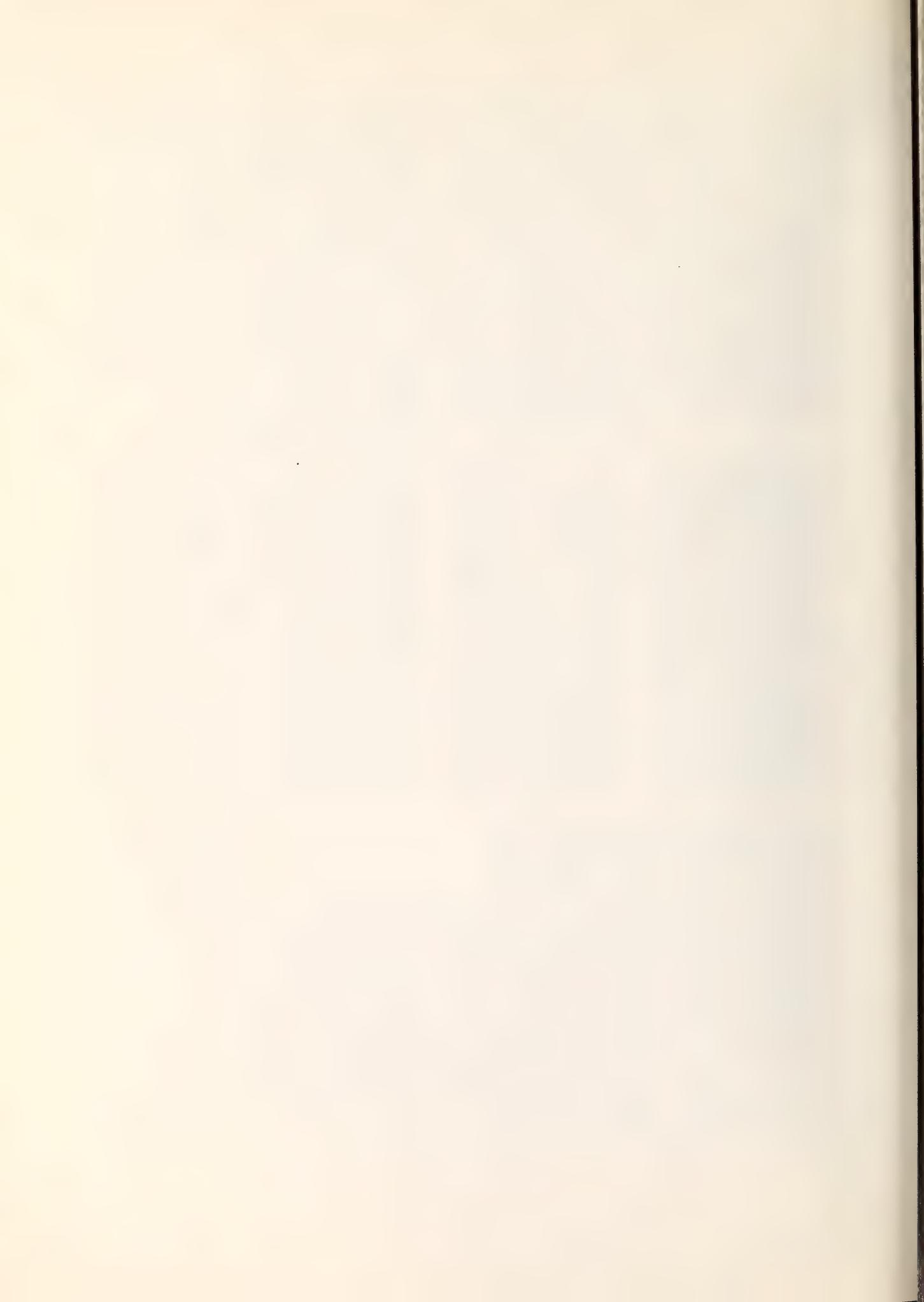
Figure 130: *Opalia golischi* Baker, Hanna & Strong, 1930. Holotype, CAS[GTC] 4770; length 13 mm; width 5.8 mm × 4

Figure 131: *Opalia crenatoides* Carpenter, 1864. Holotype, USNM 15874; length 13 mm; width 5½ mm × 5

Figure 132: *Scalaria diadema* Sowerby, 1832. Syntypes, BM[NH]; length 13½ mm × 2.9

Figure 133: *Opalia (Dentiscala) diadema* (Sowerby, 1832). Isla San Salvador, Galápagos Islands, Ecuador, December 1934, station 333-35, *Velero III* (LACM-AHF Collection); length 16 mm × 3.3





CARPENTER (1864: 547) states "*S. funiculata* and *S. diadema*, with their congeners, should be removed from *Cirsotrema* to *Opalia*," thus assigning the 2 species to a more compatible genus.

DALL (1917: 473) described *Opalia crenimarginata* from La Paz, Baja California with a length of 16mm, which in the opinion of later workers (Willett, Strong, Grant [WILLETT, 1938: 10]) "is identical with Carpenter's earlier *E. insculptum* and the latter name should be used for our Recent California species."

DALL (1917: 473) described as new a small specimen of *Opalia* which he had dredged in 29m off Catalina Island, California; he named it *O. nesiotica*; its length was 10½ mm. Dall based his opinion on the sharp spiral sculpture which covered the surface. This sharp sculpture lies in the chalky layer, easily abraded and worn off with wave action and rubbing against the substrate.

BAKER, HANNA & STRONG (1930: 47) and SMITH & GORDON (1948: 190) thought *Opalia insculpta* Carpenter was the fossil of *O. crenimarginata* Dall. The existence of *O. insculpta* at Monterey, California is doubted by SMITH & GORDON (*op. cit.*). PALMER (1958: 191) reports "The exterior of *O. insculpta* has been worn away except in the sutural region, [so] that the exact character of the longitudinal ribs cannot be described. However, prominent impressions of each reveal 14 ribs on the whorl." She further questions Carpenter's reasons for stating there was no spiral sculpture.

CARPENTER (1864: 551) states that the *Scalaria* sp. no. c. reported by C. B. ADAMS (1863) from Panama is *Opalia funiculata*.

WATSON (1883 in TRYON, 1887: 75; pl. 18, fig. 79) reported a new species, *Scalaria funiculata*, from Brazil. This species appears to be an *Opalia* and if so, it becomes a junior homonym of *O. funiculata* (Carpenter, 1857).

Some of the types of these 4 species are so badly worn that their true relationship to one another was not suspected in the past. Certain differences should always be expected due to differences in geographical backgrounds and the differences of these specimens are not sufficient to merit 4 different names. Comparison of the types shows them to be synonymous.

KEEN (1968: 408) thought that the two species *Opalia funiculata* and *O. diadema* were quite similar in appearance and chose the largest of the syntypic specimens of *O. funiculata*, from Panama, with a length of 21 mm, as lectotype. A specimen with immature lip, from Mazatlán, with a length of 16 mm, was selected as hypolectotype. KEEN (1971: 440; figs. 679, 680) listed the two species separately and subsequent radular studies prove them to be distinct, though probably related.

The radular teeth are blunt, short and have a somewhat rounded cusp at the center of each tooth in addition to the terminal ones (see Figure 162). The broad outline and blunt cusps suggest a carnivorous mode of feeding. *Opalia funiculata* is known to feed on sea anemones.

Type Material:

Scalaria (Cirsotrema) funiculata: lectotype [KEEN, 1968] BM (NH)

Opalia (? *crenatoides*, var.) *insculpta*: holotype, PRI 7090 [formerly Cornell University 4950] [Pleistocene fossil]

Dentiscala crenimarginata: holotype, USNM 111207

Dentiscala nesiotica: holotype, USNM 56900

Type Localities:

Scalaria (Cirsotrema) funiculata: Panama

Opalia (? *crenatoides*, var.) *insculpta*: Santa Barbara, California (Pleistocene fossil)

Dentiscala crenimarginata: La Paz, Baja California, Mexico

Dentiscala nesiotica: Catalina Island, California

Geographical Distribution and Ecology: California, Gulf of California, Mexico, south to Panama, Ecuador and the Galápagos Islands; symbiotic with sea anemones.

Bathymetric Range: Intertidal, with records of dead specimens down to 30m.

Geochronological Range: Pleistocene-Pliocene fossil, Recent

Opalia (Dentiscala) gereti (deBoury, 1913)

(Figure 146)

Scala Gereti deBoury, 1913: 274; pl. 10, fig. 3

Original Description: "*S. testa minuta, albo-sordida, valde crassa, solida, imperforata, compacta, conica, turriculata, in media parte inflata. Sutura parum obliqua, minime profunda, valde crenata, alveolata. Anfr. embryonales partim deficientes, notidi. Sequentes latiores, mediocriter convexi, costis axialibus obliquis, mediocriter prominulis, sed valde crassis, ad partem superiorem crenatis, instructi, in interstitiis liris tenuissimis atque punctatis ornati. Costae etiam punctatae sunt. Basis funiculo circumscripta, costis radiantibus obsoletissimis ornata. Columella funiculo crasso firmata. Apertura parva, valde ovalis, obliqua. Peristoma duplex; internum continuum valde conspicuum, nitidum; externum interruptum, punctatum. Labrum ad partem superiorem expansum. Long.: 4 mm.; diam. maj.: 2 mm.; alt. max. anfr.: 3 mm.*" (DEBOURY, 1913: 274)

Discussion: A translation (by Jean Cate) of the French description follows: "Shell of small size, of a dirty white color, thick, solid, imperforate, compact, conic, turriculate, reflected in the middle, ornamented with very thick and slightly projecting ribs. Suture slightly oblique, shallow, very strongly crenulated, with very evident pits. Protoconch partly broken, smooth, projecting much more straightly than the rest of the shell. The normal whorls, which from the beginning are larger than the protoconch, are not very convex, but enlarge rapidly in a manner to give the shell an inflated appearance. They are ornamented with slightly oblique ribs, not very projecting, but excessively thick, terminated at their upper part by a strong denticulation. Their lower part is also strongly projecting, which gives a bicrenulated appearance to the suture. The surface is further ornamented with fine cords, serrate and punctate. The ribs are equal. These are partly interrupted at their conjunction with the circumbasal cord, which is thick and very well developed. Inside this cord the ribs become partly obsolete and are almost submerged in the disk, which also is provided with punctations. The columellar funiculum is thick, but scarcely evident. Aperture small, very strongly ovate, very oblique on its long axis. Peristome double. The internal peristome is very visible, continuous and smooth. The external peristome is punctate like the rest of the shell. The lip is recurved and its upper part has a sort of expansion which is attached on one of the ribs of the preceding whorl. Anteriorly, the peristome slopes slightly and has hardly a trace of an auricle (?)."

The description matches well that of *Opalia funiculata* (Carpenter), but the photograph of the type does not. The photograph shows a small specimen with inflated whorls, lime encrusted between the ribs and in the suture. The dimensions are: length 4 mm, width 2 mm. deBoury stresses the point that only one basal disk is present, so this cannot possibly be *O. diadema* (Sowerby), besides being outside the known geographical range. Two specimens were obtained, but there seems to be no further mention of the species in the literature.

Type Material:

Scala Gereti: holotype, Muséum National d'Histoire Naturelle, Paris, 1115; paratype, Zoologisches Museum, Berlin, 512 (fide deBoury)

Type Locality:

Scala Gereti: Acapulco, Mexico

Geographical Distribution and Ecology: Not known

Bathymetric Range: Unknown

Geochronological Range: Recent

Opalia (Dentiscala) mexicana Dall, 1908

(Figure 129)

- Opalia (Dentiscala) mexicana* Dall, 1908: 251; ORCUTT, 1915: 102 [as *O. (D.) Mexicana*]; BOSS *et al.*, 1968: 204
Epitonium (Nodiscala) mexicanum - DALL, 1917: 474
Scala (Nodiscala) mexicana. - DEBOURY, 1919: 37
Epitonium (Nodiscala) mexicanum. - BAKER, HANNA & STRONG, 1930: 44
Opalia (Nodiscala) mexicana. - STRONG, 1945: 19, 20; KEEN, 1958: 278
Opalia (? Nodiscala) mexicana. - KEEN, 1971: 440; fig. 684

Original Description: "Shell small, slender, white, opaque, with two nuclear smooth whorls and seven subsequent whorls; nucleus small, blunt; subsequent whorls moderately rounded; suture distinct, with nine coronating points separated by deep and conspicuous pits; the ribs corresponding to the points are wide and thick but obsolete on the periphery, appearing again near the margin of the basal disk, where they are separated by shallow but distinct depressions; surface microscopically sculptured by sharp revolving lines reticulated by somewhat fainter incremental lines; basal disk slightly flattened, its periphery slightly angulating the whorl; aperture nearly circular, surrounded by a thick, slightly reflected peritreme. Height of shell, 11; of last whorl, 5; of peritreme, 2.7; maximum diameter, 4.0 mm." (DALL, 1908: 251)

Diagnosis: Shell medium in size, color dull white, calcareous outer coat present; nuclear whorls 2, blunt, small; body whorls 7, rounded, gradually enlarging; ribs 9, prominent, rounded, overlapping the sutures to form pits; interspaces as broad as the ribs; sutures deep; the entire shell covered with spiral rows of small threads between which are minute punctations; basal rib joined by the extensions of the axial ribs to form depressions between the ribs; below, the ribs gradually become obsolete with the punctate sculpture continuing to the anterior extremity of the shell; aperture subpyriform, anterior end with a wrinkled fasciole; lip heavy on mature specimens; operculum unknown. Length 7 to 20 mm; width 4 to 5 mm.

Discussion: DALL (1917: 474) changed the genus and subgenus of *Opalia (Dentiscala) mexicana* Dall, 1908 to *Epitonium (Nodiscala) mexicanum* arbitrarily and with no subsequent explanation. Since Dall's taxon meets the criteria for the subgenus *Dentiscala* deBoury, 1886, his original subgeneric allocation is used in this paper.

Opalia (Dentiscala) mexicana can be easily confused with *O. (D.) crenatoides* (Carpenter, 1864), particularly if the specimens are worn. From *O. crenatoides* it differs

by being smaller, by having a single row of depressions rather than pits above the basal ridge, with none below, and by a continuation of the punctate spiral sculpture below the basal ridge.

Two specimens in the DuShane collection from Santa Cruz, Nayarit, Mexico extend the known range north from Acapulco, Mexico.

Type Material:

Opalia (Dentiscala) mexicana: holotype, USNM 59336

Type Locality:

Opalia (Dentiscala) mexicana: Acapulco, Mexico

Geographical Distribution and Ecology: Coasts of Jalisco and Guerrero, Mexico. Since no live-taken specimens have been recorded the habitat of this species remains unknown.

Bathymetric Range: Unknown, but probably the species belongs to the littoral fauna.

Geochronological Range: Recent

(*Nodiscala*) deBoury, 1889

[Type species: (OD, deBoury, 1889) : *Scalaria bicarinata* Sowerby, 1884]

Shells small to medium in size; slender; usually brown; axial sculpture of closely set ribs that tend to become obsolete on the middle of the whorl but coalesce at the suture into crenulations, leaving pits between; basal ridge may be strong or weak; sometimes a thin inner lip protrudes from the surface of the thick outer lip.

Opalia (Nodiscala) colimana (Hertlein & Strong, 1951)

(Figure 128)

Epitonium (Punctiscala ?) colimanum Hertlein & Strong, 1951: 90; pl. 3, fig. 14

Epitonium (Punctiscala) colimanum. - KEEN, 1958: 276; fig. 138

Opalia (Dentiscala) colimana. - KEEN, 1971: 438; fig. 677

Original Description: "Shell small, elongate-conic, white; nuclear whorls with the tip broken, the two remaining whorls well rounded, rapidly enlarging, the first smooth, the second axially threaded; post nuclear whorls

6, well rounded, separated by a deep suture; axial sculpture of 10 strong, somewhat retractive, rounded ribs which hardly touch in the sutures where they alternate in most cases, interspaces rounded, wider than the ribs; base forming a distinct disk at the upper edge of which both ribs and interspaces terminate; entire surface with fine, wavy, spiral striations which continue over the tops of the ribs and show on the basal disk where they extend to the umbilical region; aperture round, outer lip thickened by the last rib, forming a flattened face with a slightly raised inner edge, columellar lip similarly raised but not as wide as the outer lip. The type measures: length, 7.6mm; diameter, 2.8mm." (HERTLEIN & STRONG, 1951: 90)

Diagnosis: Shell light brown in color, small, elongate-conic; nuclear whorls 2, glassy; one nepionic whorl showing faint axial growth lines, post nuclear whorls 6 to 8, well rounded; sutures deep; axial sculpture of 10 strong ribs, rounded, not overlapping the sutures, terminating at the basal disk; interspaces rounded, wider than the ribs; spiral striations cover all surfaces, including the heavy basal disk; spiral striations continue to umbilical area; aperture round; lip thickened by the last rib; an occasional heavy rib on the body whorl rides over the basal disk and terminates at the umbilical area; nucleus thin, dark brown, paucispiral in shape. Length, 7.6 to 12 mm; width, 2.8 to 3 mm.

Discussion: HERTLEIN & STRONG (1951: 90) questioned placing this species in the subgenus *Punctiscala* deBoury. CLENCH & TURNER (1951: 237) synonymized the subgenus *Punctiscala* deBoury with *Nodiscala* deBoury, placing both subgenera under *Opalia* H. & A. Adams. Specimens of the taxon of Hertlein & Strong have a very heavy basal disk, a distinguishing characteristic, with the ribs well rounded and definite, not crossing over the sutures.

The shells of this species vary from 7 to 12 mm in length. Laura and Carl Shy dredged 12 live specimens off Manzanillo, Colima, Mexico, in 22 m during December 1965.

Type Material:

Epitonium (Punctiscala ?) colimanum: holotype, CAS[GTC] 9626

Type Locality:

Epitonium (Punctiscala ?) colimanum: Manzanillo, Colima, Mexico

Geographical Distribution and Ecology: Known only from the type locality; dredged from gravelly sand.

Bathymetric Range: 22 to 55 m

Geochronological Range: Recent

Opalia (Nodiscala) crystallina (Carpenter, 1864)

(Figures 140, 141, 142)

Fenella crystallina Carpenter, 1864b: 478 (reprint 1872: 217);
CARPENTER, 1864c: 618 (reprint 1872: 104); PALMER,
1963: 295, 341; pl. 65, fig. 7

Alabina crystallina. - KEEN, 1971: 415

Epitonium (Nodiscala) espiritum Baker, Hanna & Strong, 1930:
46; pl. 2, fig. 6

Opalia (Nodiscala) espirita. - STRONG, 1945: 19, 21; KEEN,
1958: 278; fig. 161; KEEN, 1971: 440; fig. 682

Opalia espirita. - DUSHANE & POORMAN, 1967: 425

Original Description: "*F. testa alba, subdiaphana, turrita, rudiore; marginibus spirae rectis, parum divergentibus; anfr. nucl. ? . . . (decollatis); norm. v., valde rotundatis, suturis impressis; costis radiantibus circ. xvi., valde rotundatis, haud extantibus, interstitiis latis; striis spiralibus, regularibus, in anfr. penult. xvi.; apertura rotundata; basi rotundata; pertremate continuo; labro extus varicoso; labio calloso. Long. . 14, long. spir. . 11. lat. . 05 poll., div. 20°.*" (CARPENTER, 1864: 478)

Diagnosis: Shell small to medium in size, elongate-conic; color opaque white; nuclear whorls $2\frac{1}{2}$, smooth, opaque, rounded; immediately following whorl shows spiral sculpture; body whorls 7 to 8, all showing axial and spiral sculpture, upper half concave, the lower portion flattened; suture deep; ribs 10 to 15, rounded, with here and there a heavier one, following the contour of the whorls, terminating on the upper portion of each whorl in rounded, appressed tubercles at the suture; on the lower whorls each rib joins the rib above at the suture; on the upper

whorls the ribs are discrepant; below the shoulder each rib has a node, below which it resumes its rounded shape, ending in a barely perceptible rounded disk; the surface of the entire shell has small, wavy spiral threads, 30 to 35 on each whorl, with punctate interstices; the aperture is oval, set at an oblique angle; the lip heavy with the same sculpture as the rest of the shell; operculum dark. Length, 4 to 9mm; width, 2 to 4mm.

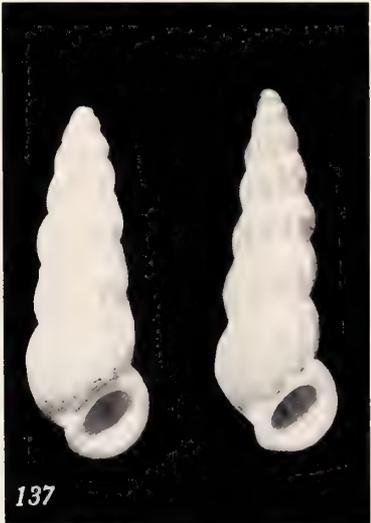
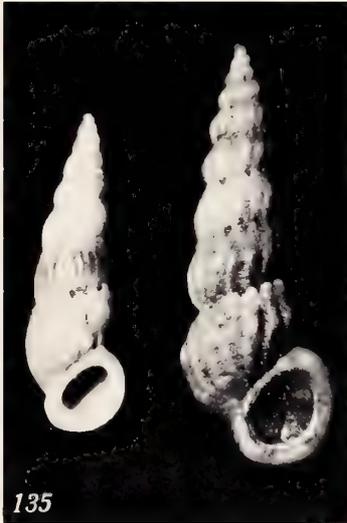
Discussion: This species differs radically from all other *Opalia* species in the Panamic-Galapagan fauna because of its slopingly concave shoulder and its noded ribs. CARPENTER (1864: 478) placed the one specimen he had in the genus *Fenella*, but examination of the holotype shows that it belongs in the Epitoniidae in the genus *Opalia* and the subgenus *Nodiscala*. The type of *Fenella crystallina* is a worn specimen, making it difficult to evaluate except for the general contour of the shell, the axial ribs faint over the shoulder, pointed in the sutures, with a small node at the shoulder of each rib and the spiral punctations. Comparison of this taxon with specimens of *Opalia (nodiscala) espirita* Baker, Hanna & Strong, 1930 shows that the two taxa are conspecific. The holotype and 2 immature specimens of *O. (N.) espirita* were collected by Fred Baker at Isthmus Bay, Espíritu Santo Island, Gulf of California, Mexico. One other paratype, labeled only "Gulf of California," was taken by Captain George Porter. Twelve specimens, some live-taken, were dredged by Laura and Carl Shy in December, 1965, off Manzanillo, Colima, Mexico, in 22m. One specimen from Bahía Bacochibampo, Guaymas, Mexico, in 36m, and another specimen obtained from shrimp trawlers, from

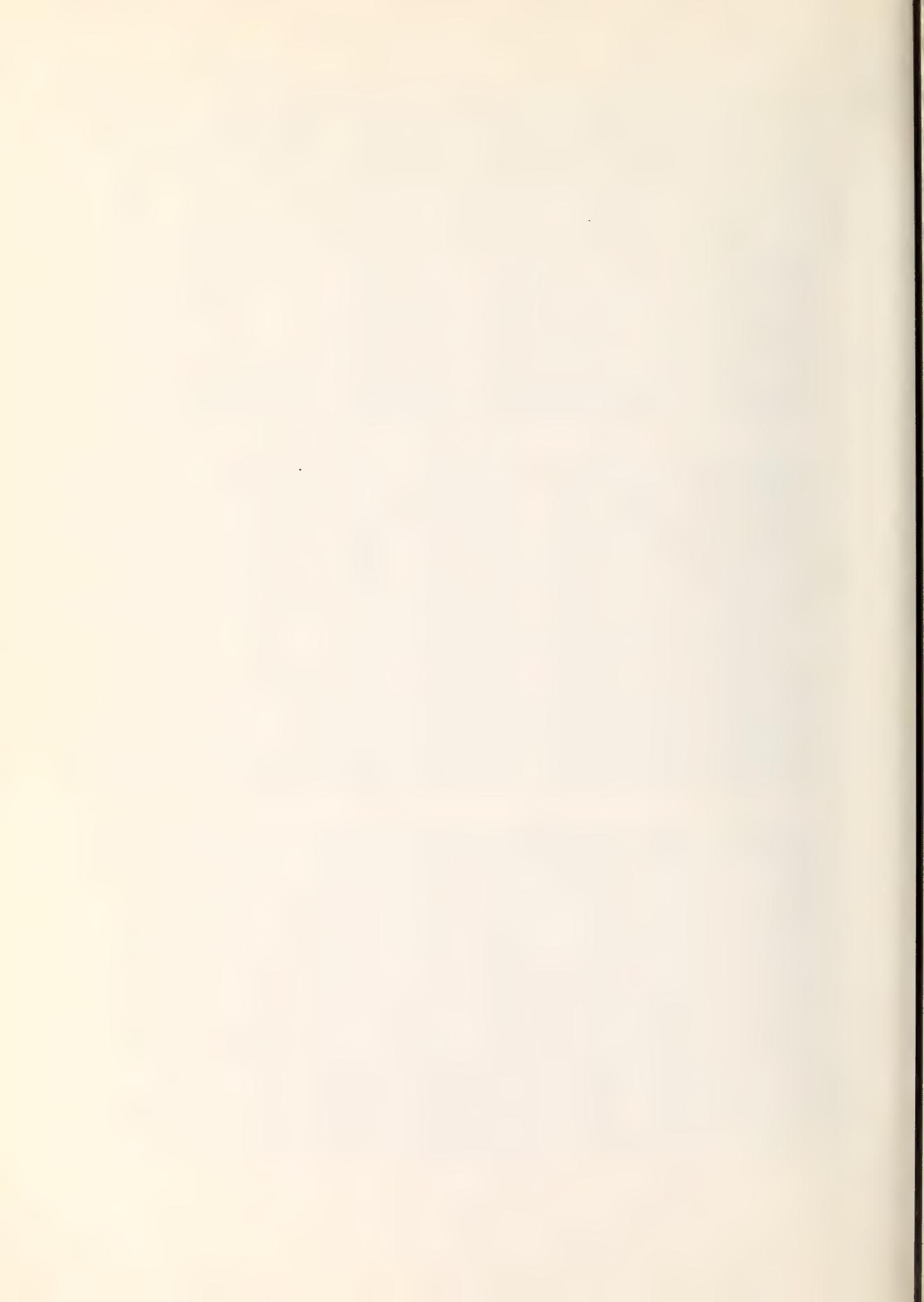
Explanation of Figures 134 to 146

Figure 134: *Epitonium (Nodiscala) ordenanum* Lowe, 1932. Holotype, ANSP 157988; length 7mm; width 2mm × 7
Figure 135: *Epitonium (Nodiscala) ordenanum* Lowe, 1932. Holotype on left. *Opalia (Nodiscala) spongiosa* Carpenter, 1866, on right; Manzanillo, Colima, Mexico (DuShane Coll.); length 9mm; width 5mm × 15
Figure 136: *Epitonium (Nodiscala) sanjuanense* Lowe, 1932. Holotype, ANSP 157989; length $10\frac{1}{2}$ mm; width 3mm × 7
Figure 137: *Opalia (Dentiscala) clarki* Olsson & Smith, 1951. Holotype, ANSP 187201 (figure to right); length 12.2mm; width 3.9mm × 3.9
Figure 138: *Opalia retiporosa* Carpenter, 1866. Holotype, USNM 11843; length 7mm; width 2.3mm × 7
Figure 139: *Opalia spongiosa* Carpenter, 1866. Holotype, USNM 14830; length $8\frac{1}{2}$ mm; width 3mm × 8

Figure 140: *Epitonium (Nodiscala) espiritum* Baker, Hanna & Strong, 1930. Holotype, CAS[GTC] 4778; length 6mm; width $2\frac{1}{2}$ mm × 6
Figure 141: *Opalia (Nodiscala) crystallina* (Carpenter, 1864). Puertecitos, Gulf of California, Mexico (DuShane Coll.); length 5mm; width $1\frac{3}{4}$ mm × 15
Figure 142: *Fenella crystallina* Carpenter, 1864. Holotype, USNM 15888; length 4mm; width 2mm × 9½
Figure 143: *Opalia (Dentiscala) mazatlanica* Dall, 1908. Holotype, USNM 168669; length $12\frac{1}{2}$ mm; width $4\frac{1}{2}$ mm × 5
Figure 144: *Opalia tremperi* Bartsch, 1927. Holotype, USNM 362454; length 7.8mm; width $2\frac{1}{2}$ mm × 7
Figure 145: *Opalia bullata* Carpenter, 1865. Holotype, Redpath Museum, Montreal, Canada, no. 76; length 8mm; width $2\frac{1}{2}$ mm × 7

Figure 146: *Scala Gereti* deBoury, 1913. Holotype, Mus. Nation. d'Hist. Natur. Paris, no. 1115; length 4mm; width 2mm (after DEBOURY, 1913) × 10.7





off the coast of Chiapas, Mexico, are both in the Shasky collection. One specimen, collected by Edith Abbott at Puertecitos, Baja California on a sand flat at low tide, places the species in the northern reaches of the Gulf of California. Specimens from the upper portion of the Gulf of California tend to be smaller than those from the Manzanillo area. Few institutions have this species; most of the known specimens are held by private collectors.

From *Opalia (Nodiscala) spongiosa* Carpenter, a more common species, *O. (N.) crystallina* differs by having a less elongate shell, with a more subdued basal disk and with the first post-nuclear whorl showing spiral rather than axial sculpture.

Type Material:

Fenella crystallina: holotype, USNM 15888

Epitonium (Nodiscala) espiritum: holotype, CAS[GTC] 4778

Type Localities:

Fenella crystallina: Cabo San Lucas, Baja California, Mexico

Epitonium (Nodiscala) espiritum: Espiritu Santo Island, Gulf of California, Mexico

Geographical Range and Ecology: Gulf of California south to Chiapas, Mexico

Bathymetric Range: Intertidal to 36m

Geochronological Range: Recent

Opalia (Nodiscala) infrequens (C. B. Adams, 1852)

(Figures 134, 135, 143, 144, 145, 147)

Rissoa infrequens C. B. Adams, 1852: 403 (reprint: 179); TURNER, 1956: 57; plt. 12, fig. 2

Epitonium (Pliciscala) infrequens. - BARTSCH, 1915: 34

Rissoina infrequens. - KEEN, 1971: 375, 903

Opalia bullata Carpenter 1864c [not *Scala bullata* Sowerby, 1844]; CARPENTER, 1864c: 537, 660 (reprint 1872: 23, 146); CARPENTER, 1865: 397 (reprint 1872: 287); COOPER, 1867: 35; ORCUTT, 1915: 38; PALMER, 1944: 100; HOWARD, 1972: 21

Scala (Psychrosoma) crosseana Tapparone-Canefri, 1876: 154 (replacement name for *Opalia bullata* Carpenter, 1865); TRYON, 1887: 84 (synonym of *Opalia bullata* Carpenter, 1865, not *Scala bullata* Sowerby, 1844)

Opalia (Nodiscala) bullata. - PALMER, 1958: 20, 23, 50, 192; plt. 22, fig. 6 [under *Opalia spongiosa*], [as *Epitonium retiporosum* and *E. spongiosum*, p. 28]; KEEN, 1971: 440; fig. 681

Opalia (Dentiscala) mazatlanica Dall, 1908: 250; ORCUTT, 1915: 102; DALL, 1917: 474; BOSS *et al.*, 1968: 201

Epitonium (Nodiscala) mazatlanicum. - DALL, 1917: 474; BAKER, HANNA & STRONG, 1930: 44

Scala (Nodiscala) mazatlanica [sic]. - DEBOURV, 1919: 37

Opalia (Nodiscala) mazatlanica. - STRONG, 1945: 19, 21; KEEN, 1958: 278

Opalia tremperi Bartsch, 1927: 3; plt. 1, fig. 8; OLDROYD, 1927: 279; STRONG, 1930: 42; STRONG, 1937: 7; KEEN, 1946: 8

Epitonium (Opalia) tremperi. - GRANT & GALE, 1931: 854

Epitonium tremperi. - KEEN, 1937: 36

Epitonium (Nodiscala) tremperi. - STRONG, 1945: 19; BURCH, 1945: 19

Epitonium (Nodiscala) ordenanum Lowe, 1932: 114; plt. 9, figs. 3, 3a; PILSBRY & LOWE, 1932: 120

Opalia (Nodiscala) ordenanum [sic]. - M. SMITH, 1944: 7; fig. 63

Opalia (Nodiscala) ordenana. - STRONG, 1945: 21; KEEN, 1958: 278; fig. 164

Original Description: "Shell very long, ovate conic: white: with, on each whorl, sixteen very obtuse slightly elevated indistinct ribs, which are separated only by striae, and a few microscopic revolving striae: apex subacute: spire with the outlines nearly rectilinear: whorls seven, contracted above, otherwise convex or subangular with a moderately impressed suture: last whorl long, subangular: aperture oblique, subovate, scarcely effuse: labrum much excurved, well thickened: umbilicus wanting. Length .24 inch; breadth .075 inch." (C. B. ADAMS, 1852: 403)

Diagnosis: Shell small, slim, conic, brown, varying in shading, dead shells white, soft calcareous outer coat; nuclear whorls 2, glassy, brown; body whorls 8, evenly punctate between the spiral sculpture of small raised threads; well defined suture; ribs 15 to 20, rounded, coalescing at the suture, overlapping the edge of the preceding whorls to form cusps, with an occasional heavier rib; aperture oval, large; lip strongly expanded and thickened, complete, with the same sculpture as on the whorls; outer lip rounded, inner lip set at an angle against the body whorl; operculum dark, oval, paucispiral, with the nucleus uppermost. Length, 7 to 12mm; width, 2 to 4mm.

Discussion: Although C. B. Adams placed his species (with Panama as the type locality) in the Rissoidae, which later authors copied, BARTSCH (1915: 34) recognized that it belonged in the Epitoniidae and placed it in the subgenus *Pliciscala* with no comment regarding his decision. However, the type species of *Pliciscala* deBoury 1887 (a European Eocene form) has a basal disk and strong axial sculpture that bears no resemblance to the species named by C. B. Adams.

One Pleistocene fossil specimen collected at Santa Barbara by Col. Jewett was first referred to *Opalia bullata* by CARPENTER (1864: 537, 660); he did not describe it

until 1865 (p. 397). PALMER (1958: 192) synonymized *O. bullata* with *O. spongiosa* and *O. retiporosa*, all of Carpenter, which now seems unjustified. CARPENTER (1864-1866: 222), in describing *O. retiporosa* compared the shell with that of *O. bullata*, stating that it was similar, but different in sculpture. *Opalia spongiosa* and *O. retiporosa* differ from *O. bullata* by having much more shouldered whorls, ribs that coalesce near the aperture into the basal disk, and a less oval aperture. *Opalia spongiosa* and *O. retiporosa* are here considered to be synonymous. TAPPARONE-CANEVRI (1876: 154), believing incorrectly that *O. bullata* was a homonym of *Scala bullata* Sowerby, 1844, renamed Carpenter's species *Scalaria (Psychrosoma) crosseana*. TRYON (1887: 84) correctly reinstated *O. bullata*. The type specimen of *O. mazatlanica* Dall, 1908 (p. 250; type locality Mazatlán, Mexico) is a beach-rolled shell that has lost much of its calcareous outer surface and sculpture, but shows the minute pitting and ribs overlapping the suture, typical of *O. infrequens*. It is the largest of the synonymous types: length, 12 mm; width, 4 mm. DALL (1917: 474) changed the generic and subgeneric assignments and called the species *Epitonium (Nodiscala) mazatlanicum*, giving no reason for doing so. *Opalia tremperi* Bartsch, 1927 (p. 3; type locality San Clemente Island, California) described from a single specimen, has also been reported by KEEN (1946: 8) to have been dredged in shallow water off Santa Cruz Island, California. *Opalia tremperi* agrees in every detail with *O. infrequens* and is herein considered to be synonymous. The type is 7.8 mm long and 2.5 mm wide. A. M. STRONG (1937: 4-8) commented: "*Opalia tremperi* Bartsch is described as having faint axial ribs forming cusps in the sutures. The figure shows the characteristic punctate surface . . . There is no indication of a basal disk or peripheral cord . . . It is not typical of *Opalia* nor does it agree in all ways with the species which have been placed in the subgenus *Nodiscala*." LOWE (1932: 114) described *Epitonium (Nodiscala) ordenanum*, dredged from 36 m off San Juan del Sur, Nicaragua. The type is complete with nuclear whorls and shows the characteristics described by other authors in naming their species. It has a brown shell with 15 slender ribs; length, 7 mm; width, 2 mm.

Type Material:

- Rissoa infrequens*: holotype, MCZ Harvard 186418
Opalia bullata: holotype, Redpath Museum, Montreal, Canada, no. 76
Opalia (Dentiscala) mazatlanica: holotype, USNM 168669
Opalia tremperi: holotype, USNM 362454
Epitonium (Nodiscala) ordenanum: holotype, ANSP 157988

Type Localities:

- Rissoa infrequens*: Panama

- Opalia bullata*: Santa Barbara, California (Pleistocene)
Opalia (Dentiscala) mazatlanica: Mazatlán, Mexico
Opalia tremperi: San Clemente Island, California
Epitonium (Nodiscala) ordenanum: San Juan del Sur, Nicaragua

Geographical Distribution and Ecology: From Santa Cruz Island, California, along the Southern California coast to Mazatlán, Mexico, and Panama. There are no records of habitat.

Bathymetric Range: Intertidal to 36

Geochronological Range: Pleistocene and Recent

Opalia (Nodiscala) sanjuanensis (Lowe, 1932)

(Figures 136, 137)

- Epitonium (Nodiscala) sanjuanense* Lowe, 1932: 115; pl. 9, fig. 4; PILSBRY & LOWE, 1932: 120; M. SMITH, 1944 :7 [as *Nodoscala*]
Opalia (Nodiscala) sanjuanense. - STRONG, 1945: 19, 21
Opalia (Nodiscala) sanjuanensis. - KEEN, 1958: 278; fig. 166; KEEN, 1971: 440; fig. 685
Opalia sanjuanensis. - DUSHANE & POORMAN, 1967: 425
Opalia (Dentiscala) clarki Olsson & Smith, 1951: 44-46; pl. 3, fig. 5 [not *Epitonium clarki* Oldroyd, 1921]
Opalia (Nodiscala) clarki. - KEEN, 1958: 278; fig. 160

Original Description: "Shell small, milk white, elongate conic, of nine well rounded whorls, evenly covered over entire surface with faint spiral, punctate incised lines. Suture well defined. There are twelve prominent rounded ribs. Aperture oval with strong, much thickened varix. On each of the two preceding whorls is an equally strong varix. Alt. 10.5 mm., diam. 3.5 mm.

Operculum dark brown, paucispiral with nearly basal nucleus, lightly marked with growth wrinkles." (OLSSON & SMITH, 1951: 44)

Diagnosis: Shell medium in size, milk-white, slender-conic; nuclear whorls 2, opaque, blunt; subsequent whorls 6 to 7, well rounded, gradually enlarging; spiral sculpture of alternate rows of fine threads and punctate pitting over entire shell; ribs 10 to 13, somewhat sinuous, extending from the base to the suture, overlapping the sutures to leave pits between; interspaces as wide as the ribs; sutures moderately deep; aperture oval, oblique; lip heavy, reflected, pitted; operculum dark brown, thin, paucispiral. Length, 10 to 12 mm; width, 3½ to 4½ mm

Discussion: Comparison of the types of *Opalia (Nodiscala) sanjuanensis* with *O. (N.) clarki* shows that these

two species have the same characteristics and are therefore conspecific.

The intervarical surface reported by Olsson & Smith to be smooth except for minute spiral lines visible only under a microscope contains sculpture of fine threads on which there are punctations visible under magnification of 40 \times . The operculum is dark, thin and corneous. The outer lip is much thickened.

According to CLENCH & TURNER (1950: 233), members of the subgenus *Dentiscala* deBoury may or may not have a basal ridge, but deep pits at the termination of the ribs are characteristic of this subgenus. It is true that *Opalia crenata* (Linnaeus, 1758) and *O. (Dentiscala) hotesseriana* (d'Orbigny, 1842), the two species to which they make comparison, have pits, and thus *O. clarki* Olsson & Smith was placed by them in this subgenus; the type was worn and did not show the punctate surface layer. It belongs in the subgenus *Nodiscala* as correctly interpreted by KEEN (1958: 278). The punctate layer, one of the important systematic characters, is very thin and suffers from abrasion when beach rolled. One specimen of *O. sanjuanensis*, taken alive intertidally from under a rock at Agua Chale, Gulf of California, Mexico, by the author has a dark brown paucispiral operculum. The outer lip is very thick, the whorls are rounded and more inflated than the one in the Shy collection, which was dredged in 36m off Manzanillo, Mexico. Another specimen taken by the author at Puertecitos in the northern end of the Gulf of California shows the same bulbous characteristics as the Agua Chale specimen. One dead-collected specimen in the ANSP collection (lot 81479), was taken by J. G. Malone off Santa Rosalia, Gulf of California, Mexico, in 1901. This is a rare species, not represented in most collections.

Type Material:

Epitonium (Nodiscala) sanjuanense: holotype, ANSP 157989
Opalia (Dentiscala) clarki: holotype, ANSP 187201

Type Localities:

Epitonium (Nodiscala) sanjuanense: San Juan del Sur, Nicaragua
Opalia (Dentiscala) clarki: Panama

Geographical Distribution and Ecology: West side of the upper Gulf of California to Manzanillo, Colima, Mexico and Venado Beach, Panama. Taken under rocks intertidally; dredging records unknown

Bathymetric Range: Intertidal to 36m

Geochronological Range: Recent

Opalia (Nodiscala) spongiosa Carpenter, 1866

(Figures 138, 139)

- Opalia spongiosa* Carpenter, 1864c: 613, 660 (reprint 1872: 99, 146); CARPENTER, 1864-1865: 31 (reprint 1872: 244); CARPENTER, 1864-1866: 222; COOPER, 1867: 34; COOPER, 1870: 67; ORCUTT, 1915: 70
- S[calaria] (Opalia) spongiosa*. - NYST, 1871: 135
- Scalaria spongiosa*. - TRYON, 1887: 84
- Epitonium (Nodiscala) spongiosum*. - DALL, 1917: 474
- Nodiscala spongiosa*. - DALL, 1921: 114
- Epitonium spongiosum*. - BAKER, HANNA & STRONG, 1930: 44; KEEN, 1937: 35; WILLETT, 1943: 13
- Opalia (Nodiscala) spongiosa*. - STRONG, 1945: 19, 21; PALMER, 1958: 20, 23, 28, 40, 50, 192, 193; KEEN, 1971: 442; fig. 686
- Opalia retiporosa* Carpenter, 1864c: 613, 660 (reprint 1872: 99, 146); CARPENTER, 1864-1865: 31 (reprint 1872: 244); CARPENTER, 1864-1866: 222; COOPER, 1867: 35; LOWE, 1904: 20; ORCUTT, 1915: 70; PALMER, 1958: 23, 28, 50, 192, 193; DUSHANE & POORMAN, 1967: 424
- Scalaria (Opalia) retiporosa*. - TRYON, 1887: 84
- Scala retiporosa*. - ORCUTT, 1915: 78; DEBOURY, 1919: 34
- Epitonium (Opalia) retiporosa*. - MOODY, 1916: 43
- Epitonium (Nodiscala) retiporosum*. - DALL, 1917: 474; STRONG & HANNA, 1930: 19
- Nodiscala retiporosa*. - DALL, 1921: 114
- Epitonium (Nodiscala) retiporosa*. - STRONG, 1922: 155; OLDROYD, 1927: 53; STRONG, 1945: 19, 21; A. G. SMITH & GORDON, 1948: 190; KEEN, 1958: 278; fig. 165
- Epitonium (Nodiscala) retiporosum*. - BAKER, HANNA & STRONG, 1930: 45; pl. 2, fig. 3; GRANT & GALE, 1931: 855
- Opalia (Nodiscala) retiporosa*. - DURHAM, 1937: 505; pl. 57, fig. 19
- Epitonium retiporosum*. - KEEN, 1937: 35
- Opalia (Nodiscala) retiporosa*. - KEEN, 1958: 278; fig. 165
- Opalia retiporosa*. - DUSHANE, 1962: 45

Original Description: "*O. t. turrata, parva, albida, marginibus spirae rectis; anfr. ix. subplanatis suturis impressis; costis undulantibus circ. xiii., plerumque (nisi ad suturas crenulatus) obsolete; tota superficie lineis punctorum creberrimis spiralibus, punctis creberrimis, minutis, altissimis; circa basim imperforatum costa antica latissima, spirali; apertura ovata, valde callosa; operculo auratiaco, paucispirali. Long., 0.36; long. spir., 0.26; lat. 0.12; div. 20°.*" (CARPENTER, 1866: 222)

Diagnosis: Shell brown when live-taken, slender-conic, medium in size; nuclear whorls 2½, glassy, brown; post-nuclear whorls 8 to 9 (Southern California specimens tend to have 7 postnuclear whorls), whorls somewhat

rounded, axial and spiral sculpture present over entire shell; ribs 10 to 15, sinuous, prominent, rounded, overlapping the sutures to leave deep pits between, with tubercles at the periphery, more prominent on the last whorl; interspaces as wide as the ribs; sutures deep; spiral rows of punctations over entire shell, about 28 rows on the last whorl, alternate rows smaller in size; basal disk joined by the extensions of the axial ribs to form depressions between; punctate sculpture continues to the anterior extremity of the shell; aperture subpyriform, set at an oblique angle; lip heavy and reflected on mature specimens, punctate; operculum brown, paucispiral. Length 7 to 13½ mm; width 2½ to 5½ mm.

Discussion: Although CARPENTER (1864c: 613) by implication suggests the synonymy of *Opalia spongiosa* and *O. retiporosa*, 80 years passed before workers accepted the similarities between the two taxa. STRONG & WILLETT (1945: 19) agree that the two are conspecific. PALMER (1958: 192), having examined the types, synonymizes the two. Palmer also felt that *O. bullata* Carpenter was a synonym, but *O. bullata* is very different. CARPENTER (1864c: 660) compared *O. retiporosa* to *O. bullata*, stating that the shells were similar, but different in sculpture. Unfortunately, Carpenter had very poor specimens from which to make his diagnoses. CARPENTER (1864-1866: 222) states of *O. retiporosa*: "The texture has a rotten appearance; yet one of the specimens was stained with purple, and contained the dried remains of the animal, with its operculum. In the endeavor to extract this, the shell gave way." Carpenter referred to the two species as new several times in his earlier publications before he finally described them in 1866.

Live-taken *Opalia (Nodiscala) spongiosa* must be dredged, but occasionally beach worn material may be found. The species is both fossil and Recent, having been

live-taken by the *Velero III*, Hancock Pacific Expeditions off Santa Cruz Island, California; by John Q. Burch in 45 m off Redondo Beach, California; by Baker, Hanna & Strong off Cape San Lucas, Mexico (CAS [GTC]); by various collectors in from 18 to 72 m in the Gulf of California south to Manzanillo, Colima, Mexico. The American Museum of Natural History took it in 30 m off Maria Madre Island, Tres Marias Islands, Mexico, and the DeRoys in Academy Bay, Santa Cruz Island, Galápagos Islands, Ecuador. As fossil it has been collected by George Kanakoff at Playa del Rey, California, Upper Pleistocene formation; from shell washings at Monterey Bay, California (Cooper); between Hill and Broadway Streets at Fourth Street, Los Angeles, California, Pliocene formation (Moody).

Comparison of the types of all 3 of the Carpenter species of *Opalia* with various lots from several institutions makes it apparent that *O. spongiosa* and *O. retiporosa* are synonymous; since Carpenter listed *O. spongiosa* first, that name has priority. *Opalia bullata*, with more ribs (15 to 20), no basal disk and no tubercles at the shoulder, is considered a distinct species in this paper. PALMER (1958: 192) questions the importance of dividing *Opalia* into subgenera. *Opalia spongiosa* has a poorly developed basal disk with both axial and spiral sculpture continued below it. Previous workers have allocated it to the subgenus *Nodiscala*. There is a question as to the advisability of any subgeneric placement among the *Opalia*.

Type Material:

Opalia spongiosa: holotype, USNM 14830

Opalia retiporosa: holotype, USNM 11843

Type Localities:

Opalia spongiosa: Monterey, California

Opalia retiporosa: Santa Barbara Island, California

Explanation of Figures 147 to 154

Figure 147: *Rissoa infrequens* C. B. Adams, 1852 [*Opalia (Nodiscala) infrequens* (C. B. Adams, 1852)]. Holotype, MCZ Harvard 186418; length 6½ mm; width 2 mm × 7.6

Figure 148: *Scalaria principalis* Sowerby, 1844. Syntype, BM[NH] [after SOWERBY, 1844: plt. 34, fig. 75]; Length 20 mm; width 9 mm × 2.4

Figure 149: *Scalaria ducalis* Mörch, 1875. 1 of 3 syntypes, BM[NH] Length 20 mm; width 9 mm × 2

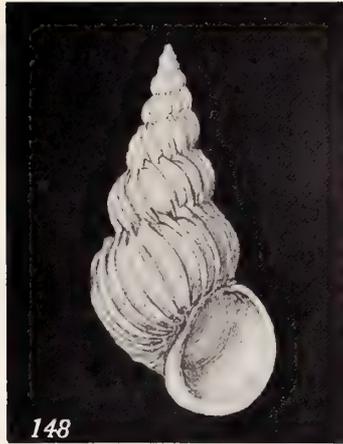
Figure 150: *Epitonium (Nitidiscala) skoglundae* DuShane, spec. nov. Holotype, LACM 1612; length 5 mm; width 3 mm × 12.8 dorsal view

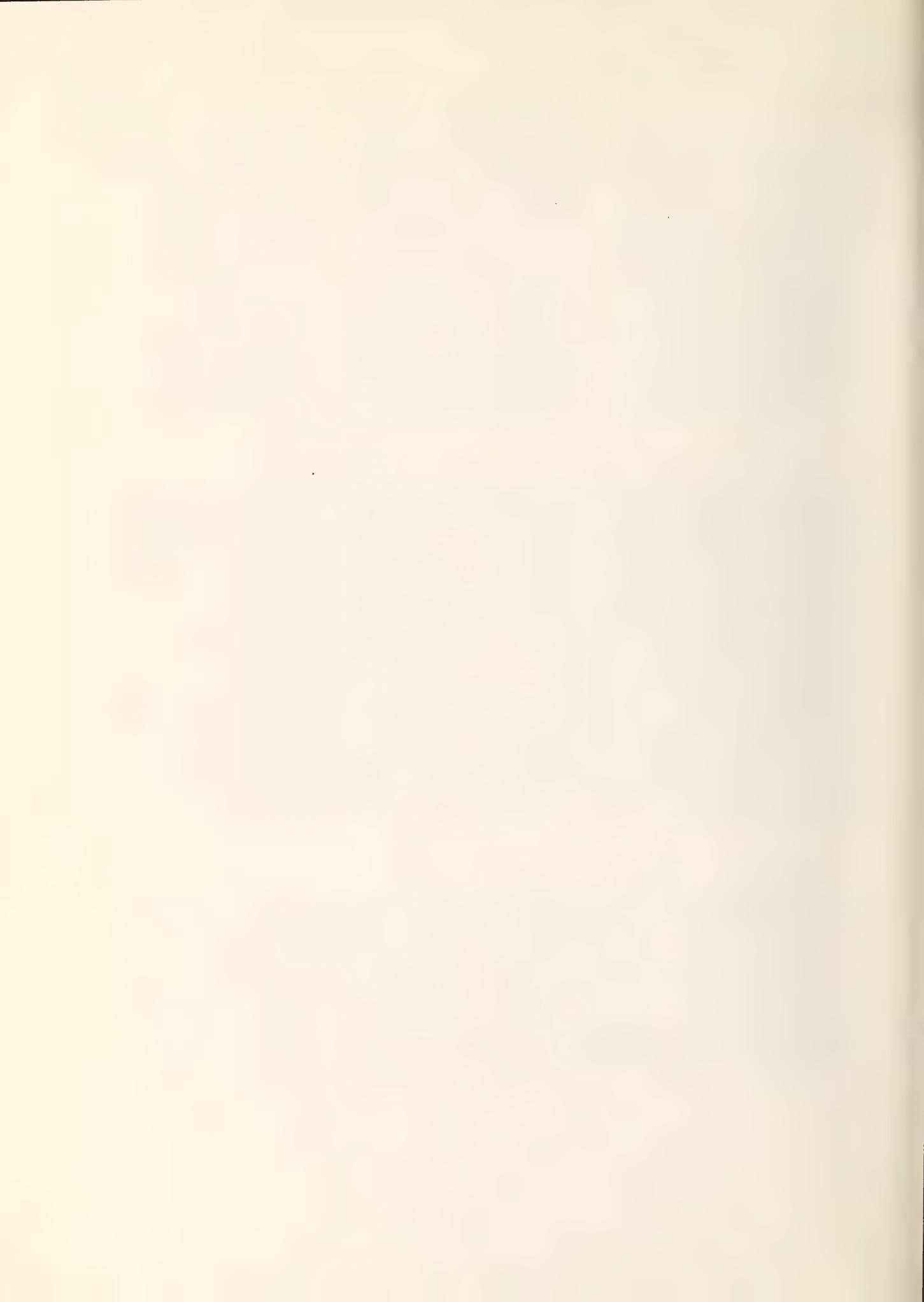
Figure 151: *Epitonium (Nitidiscala) skoglundae* DuShane, spec. nov. Holotype, LACM 1612; length 5 mm; width 3 mm × 12.8 ventral view

Figure 152: *Opalia (Dentiscala) paulula* DuShane, spec. nov. Holotype, LACM 1611; length 3½ mm; width 1.3 mm × 18.3

Figure 153: *Epitonium (Nitidiscala) skoglundae* DuShane, spec. nov. Holotype, LACM 1612; length 5 mm; width 3 mm × 12.8 apical view

Figure 154: *Opalia (Dentiscala) paulula* DuShane, spec. nov. Paratype (DuShane Coll.); length 2 mm; width 1 mm × 11½





Geographical Distribution and Ecology: California south, into the Gulf of California, and south along the west Mexican coast to the Galápagos Islands, Ecuador. Usually dredged on a sand bottom.

Bathymetric Range: 18 to 72 m

Geochronological Range: Pleistocene, Pliocene, and Recent

UNRESOLVED SPECIES

Scalaria crassilabrum Sowerby, 1844

Scalaria crassilabrum Sowerby, 1844: 103; SOWERBY, 1847: plt. 35, figs. 115, 116; REEVE, 1873-1874: plt. 16, figs. 120a, 120b

Scalaria crassilabris [sic]. - MENKE, 1850: 177; CARPENTER, 1857a: 238; CARPENTER, 1857b: 542; NYST, 1871: 102; DALL, 1917: 487

Original Description: "*Sca. testa albida, imperforata, elongata, spiraliter minutissime striata; anfractibus septem, biangulatus, subobsolete costellatis; varicibus nullis; apertura subrotunda, margine crasso, expanso, minute striato.*" (SOWERBY, 1844: 103)

Discussion: REEVE (1873-1874) stated: "Shell nearly white, imperforate, elongated, spirally very minutely striated; whorls seven, biangular, rather obsoletely ribbed; varices none; aperture rather rounded; with thick, expanded, minutely striated margin." In his original description of *Scalaria crassilabrum*, SOWERBY (1844) cited Ticao, Philippine Islands as the type locality. MENKE (1850) reported it came from Mazatlán, Mexico and Sansonati, Central America. NYST (1871) questioned the localities given by Menke. CARPENTER (1857a) prefaced Menke's faunal list of Mazatlán shells with the statement that although ostensibly all the species listed came from Mazatlán and were collected by M. Melchers personally, Menke admitted he received a box at the same time from a ship at Mazatlán. This admission casts doubt on *S. crassilabrum* as a species from Mazatlán. The Reeve figure of *S. crassilabrum* looks like an *Opalia* which could be easily compared with *O. spongiosa* (Carpenter, 1866), a species Carpenter had not yet described when MENKE's (1850) list was published. The problem can only be resolved by comparison with the type in the BM[NH]. If

the two species prove to be synonymous, the Sowerby name is available.

Epitonium ducale (Mörch, 1875)

(Figures 148, 149)

Scalaria ducalis Mörch, 1875: 143 (no description) [*Scalaria principalis* (Pallas) of Sowerby, 1844, not of Pallas, 1774]; DALL, 1917: 488

Epitonium ducale. - DALL, 1909: 223

Scala ducalis. - DEBOURY, 1912: 89, 91 (type of *Delicatiscala* deBoury, 1912)

Scalaria simillima Tapparone-Canefri, 1876: 154 (objective synonym)

Original Description: "*T. pyramidalis, sub-ventricosa, tenui, laevi; anfractibus vix contiguus; varicibus numerosis, laminatis, ad suturam dilatatis, irregulariter junctis; apertura magna; labio interno spiraliter incrassato, colore albo.*"

"The ribs are much more numerous, the shell more ventricose, and the whorls more rapidly increasing in size than in *Sc. communiformis*, Xipixappi, West Columbia, Mr. Cuming. This shell agrees with Mr. Pallas's figure which is copied by Martini, in every respect but size." (SOWERBY, 1844:88)

Discussion: Apparently SOWERBY (1844: 88; plt. 34, fig. 75) figured a specimen from Colombia which he thought matched the figure of *Turbo principalis* Pallas, 1774. Actually, this species is generally conceded to be from the West Indies. MÖRCH (1875: 143) recognized Sowerby's misidentification and named the Colombian form *Scalaria ducalis*. TAPPARONE-CANEFRI (1876: 154) did likewise, so his name, *S. simillima*, falls as a synonym. Because Sowerby did not describe this as a new species, KEEN (1964, 1965, 1967) was not alerted to look for it during her trips to the British Museum. Thus, the specimen named *Epitonium ducale* (Mörch, 1875) is the unrecognized holotype of the Sowerby figure. However, the type lot consisting of the 3 specimens in the BM(NH) has since been made available for study. These shells do not compare closely to any species from the Panamic-Galapagan fauna. Rather, they are similar to the figures of *Epitonium* (*Epitonium*) *albidum* (d'Orbigny, 1842) given by CLENCH & TURNER (1951: 261), a variable form from the Atlantic. *Epitonium ducale* is light in structure; the surface is shiny and there are 8 to 9 convex whorls, rapidly expanding; the 15 to 16 costae are low and slightly reflected; the suture is deep; the shell is nearly imper-

forate, with a thin, slightly reflected outer lip, narrow in the parietal area and attached to the costae; the aperture is oval; operculum unknown. Of the 3 specimens in this lot, the largest is the holotype which measures, length 20 mm; width, 9 mm, with 9 whorls and 15 costae. The other 2 specimens are somewhat damaged. One measures, length 19 mm; width 9 mm with 8 whorls and 16 costae, the outer lip fractured. The last specimen measures, length 18 mm; width 6 mm, with 9 whorls and 15 costae, the aperture and last whorl badly damaged. The 3 shells are mounted on the original tablet which reads, on the back, "Sc. *Principalis* Pallas, Xipixappi West Colombia, 10 fms., from muck. H. C." In pencil has been added: "Sow. *non* Pallas = *ducalis* Mörch, 79/5."

One cannot help but conjecture that the shell has been misallocated and that it really belongs to the Atlantic fauna.

Type Material:

Scalaria ducalis: 3 syntypes, BM(NH)

NEW SPECIES

Species of the subgenus *Nitidiscala* are common in the eastern Pacific, 16 species being recognized. During the past months specimens of a species new to science have been given to me for identification. This taxon is here described:

Epitonium (Nitidiscala) skoglundae DuShane, spec. nov.

(Figures 150, 151, 153)

Description: Shell small in size, china white, sturdy; nuclear whorls $1\frac{1}{2}$, opaque, showing scarcely discernible axial riblets under $40\times$ magnification; subsequent whorls 5, rounded; sutures distinct; axial costae 25 to 32, continuous from whorl to whorl, very slightly reflected; spiral threads lacking on surface between costae which are sharp, thin edged, but heavier where they join the whorl, curved to follow the contour of the whorl, with a small pit at the suture before joining the next costa above; lip heavy, with a strong wrinkled fasciole anteriorly; aperture round, partially shattered on type; operculum unknown. Length 5 mm; width 3 mm.

Type Material:

Epitonium (Nitidiscala) skoglundae: holotype, LACM, Invertebrate Zoology Type Collection, no. 1612

paratypes (5): LACM, Invertebrate Zoology Type Collection, no. 1613

paratypes (2): Carol Skoglund Collection

paratypes (2) DuShane Collection

Type Locality:

Epitonium (Nitidiscala) skoglundae: Fort Amador, Panama Canal Zone, Lat. $8^{\circ}56'N$; Long. $79^{\circ}33'W$, 10 specimens, none alive, taken at mid-tide level among gravel, March, 1972

Discussion: *Epitonium skoglundae* differs from all other epitoniids known from the west coast of the Americas by having a rounded contour, with many costae not standing away from the whorls as in many species of epitoniids, and with a china-like texture.

A pigmy in size (length 4 to 5 mm; width 1.85 to 3 mm) and with more costae, this Panamic species has the same characteristic arrangement of the costae as *Epitonium turbinum* Dall, 1908 from the Galápagos Islands, but in no other way is similar. The costae curve, following the contour of the whorl; at the suture each costa twists to the left as it dips into the suture, and joins the next costa above.

The name honors Carol Skoglund of Phoenix, Arizona, an avid collector, who brought this epitoniid back from a collecting trip to Panama.

The other taxon is a remarkable new species referable to the genus *Opalia*, subgenus *Dentiscala*.

Opalia (Dentiscala) paulula DuShane, spec. nov.

(Figures 152, 154)

Description: Shell white, small, solid, tabulate in outline; nuclear whorls $3\frac{1}{2}$, opaque, rounded; subsequent whorls 5, suture deep; ribs 12, with here and there a heavier one, slightly projecting to form crenulations around the top of each whorl before dipping onto the tabulate area leading to the crenulated and pitted suture; ribs become obsolete on the last third of the body whorl; spiral cording riding over the fine, regular ribs, twice the width of the spirally punctate interspaces; base sculptured with about 11 fine threads and minute pitting; aperture oval, expanded into a heavy, continuous peri-

stome, the internal one visible, continuous and smooth, the external one finely corded and punctate; anterior lip patulous; operculum unknown. Length $3\frac{1}{2}$ mm; width 1.3 mm.

Type Material:

Opalia (Dentiscala) paulula: holotype, LACM, Invertebrate Zoology Type Collection, no. 1611
paratype (1): DuShane Collection

Type Locality:

Opalia (Dentiscala) paulula: Cuastecomate Bay, Jalisco, Mexico, Lat. $19^{\circ}13'N$; Long. $104^{\circ}44'W$; 2 specimens dredged at 11 m, sand and shell substrate, 5 February 1969, leg. DuShane

Discussion: No other *Opalia* in the eastern Pacific has the sculpture of this species. The pitting at the suture is reminiscent of *Opalia (Dentiscala) crenatoides* (Carpenter, 1864), but the present taxon lacks the basal ridge of

most species in the subgenus *Dentiscala*. It has a more tabulate outline than either *O. (D.) funiculata* Carpenter, 1857 or *O. (D.) diadema* (Sowerby, 1832), and is very much smaller (length 2 to $3\frac{1}{2}$ mm; width 1 to 1.3 mm).

The name *paulula* is a Latin adjective meaning "very little."

Table 2

Depth Provenance of Species

	Intertidal	Low Intertidal to 40m	40m and Deeper	Unknown	Total
	14	28	16	11	69

Table 3

Zoogeographical Distribution

Species	Southern California	Isla Cedros	Bahia Magdalena	West coast Baja Calif.	Cabo San Lucas	Gulf of California	West coast of Mexico	Nicaragua	Panama	Ecuador	Galapagos Islands	Peru
<i>Epitonium</i>												
<i>(Asperiscala)</i>												
<i>acapulcanum</i>		×	×	×	×	×	×		×	×		
<i>billeeanum</i>					×	×	×				×	
<i>canna</i>			×	×	×	×	×			×		×
<i>cookeanum</i>	×		×		×	×						
<i>elenense</i>						×	×		×	×		×
<i>emydonesus</i>						×	×		×		×	
<i>eutaenium</i>						×	×				×	
<i>gradatum</i>									×	×	×	
<i>habeli</i>						×	×				×	
<i>huffmani</i>						×	×		×	×	×	
<i>indistinctum</i>							×		×		×	
<i>lowei</i>				×					×	×		
<i>macleani</i>						×						
<i>minuticosta</i>	×	×	×	×		×	×				×	
<i>obtusum</i>						×	×		×			×
<i>regulare</i>									×			
<i>rhytidum</i>									×			
<i>tinctorium</i>			×			×	×		×		×	
<i>venado</i>									×			×
<i>walkerianum</i>						×	×	×				×
<i>zeteki</i>									×	×		×
<i>(Depressiscala)</i>												
<i>aciculinum</i>				×			×	×				×
<i>purpuratum</i>									×			×
<i>(Nitidiscala)</i>												
<i>barbarinum</i>	×					×						
<i>callipeplum</i>			×				×					
<i>columnellum</i>									×			
<i>cumingii</i>						×	×		×		×	×

Table 3 [continued]

Species	Southern California	Isla Cedros	Bahía Magdalena	West coast Baja Calif.	Cabo San Lucas	Gulf of California	West coast of Mexico	Nicaragua	Panama	Ecuador	Galápagos Islands	Peru
<i>curvilineatum</i>								×	×			
<i>durhamianum</i>						×		×				
<i>hancocki</i>											×	
<i>hexagonum</i>			×			×	×		×			
<i>hindsii</i>				×		×	×		×			×
<i>politum</i>	×	×		×		×	×	×	×	×	×	
<i>shyorum</i>						×	×					
<i>skoglundae</i>									×			
<i>statuminatum</i>							×		×			×
<i>suprastriatum</i>						×	×					
<i>tabogense</i>									×			
<i>willetti</i>						×	×	×	×	×	×	
(<i>Sthenorytis</i>)												
<i>dianae</i>					×			×		×		
<i>turbinum</i>					×	×			×		×	
(<i>Hirtoscala</i>)												
<i>mitraeforme</i>							×					
<i>reflexum</i>			×			×	×	×				
<i>replicatum</i>						×	×		×		×	
(<i>Cirsotrema</i>)												
<i>togatum</i>					×	×	×		×		×	
<i>vulpinum</i>						×	×		×			
<i>Amaca</i>												
(<i>s. l.</i>)												
<i>contexta</i>							×					
(<i>Scalina</i>)												
<i>brunneopicta</i>		×		×	×	×	×				×	
<i>deroyae</i>						×	×				×	
<i>ferminiana</i>						×	×		×			×
<i>pompholyx</i>					×						×	
<i>tehuanarum</i>						×	×					×
<i>Acirsa</i>												
<i>cerralvoensis</i>					×	×						
<i>menesthoides</i>					×							
<i>murrha</i>									×			
<i>Alora</i>												
<i>gouldii</i>							×		×			
<i>Opalia</i>												
(<i>Dentiscala</i>)												
<i>crenatoides</i>					×	×	×				×	
<i>diadema</i>											×	×
<i>exopleura</i>					×	×	×				×	×
<i>funiculata</i>	×	×	×	×	×	×	×		×	×	×	×
<i>gereti</i>							×					
<i>mexicana</i>							×		×		×	×
<i>paulula</i>							×					
(<i>Nodiscala</i>)												
<i>colimana</i>							×					
<i>crystallina</i>					×	×	×					
<i>infrequens</i>	×			×			×	×				
<i>sanjuanense</i>							×	×	×			
<i>spongiosa</i>	×				×	×	×				×	

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¹ *Italic numbers (123)* refer to plate figures; Roman numbers refer to the pages; **bold face figures (123)** refer to text figures; new species, described herein, are indicated by **bold face Italics**; non-molluscan taxa are printed in Roman type and are not cross-indexed under the species name.

² Genus names following a dash (-) indicate that the same species was also assigned to the genera listed and that the name may be found in the synonymy of the valid assignment.

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ERRATA

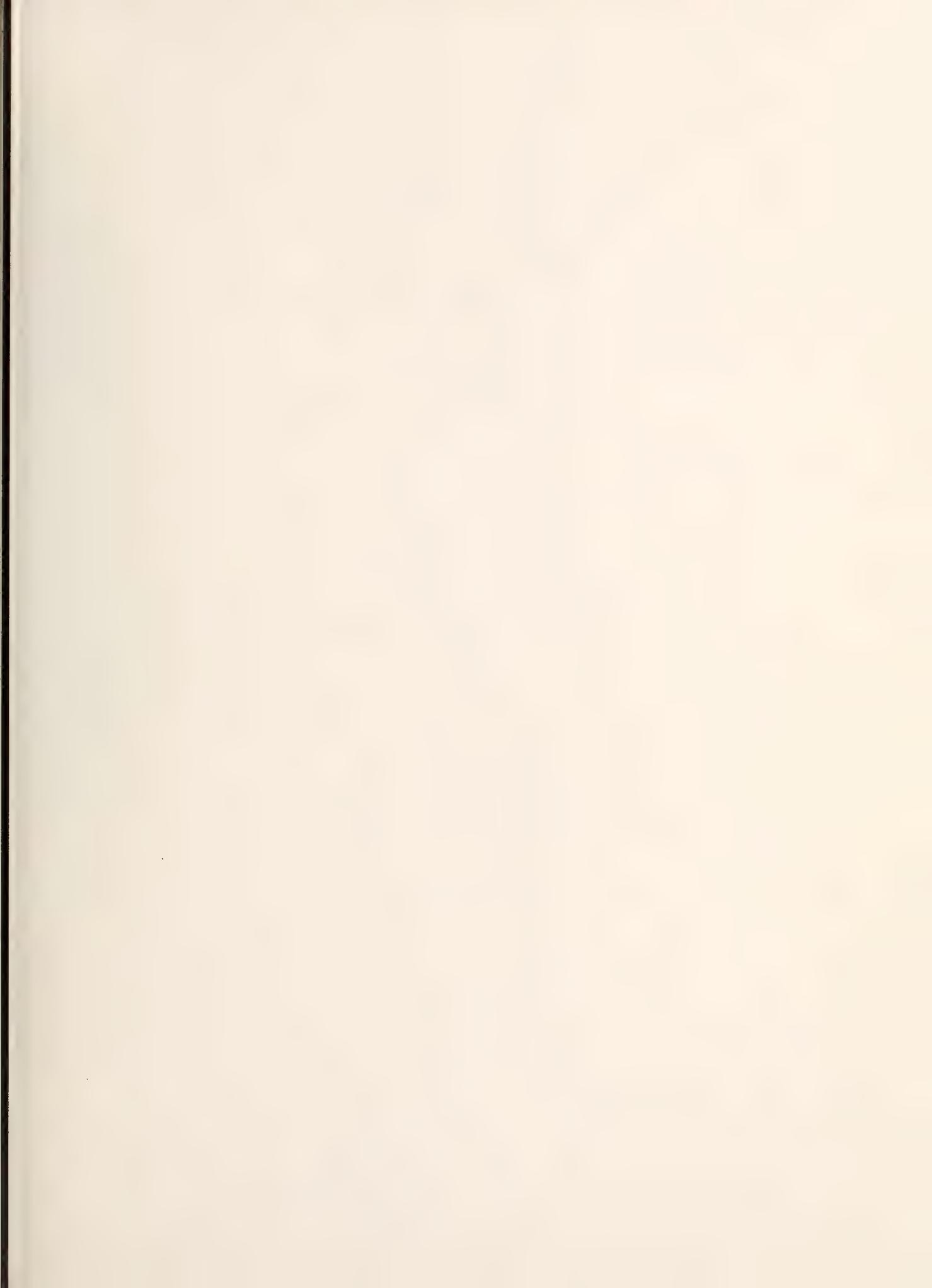
In the following list the numbers refer to page, column, and line from the top; the term after the colon is the error, and following the dash is the correction.

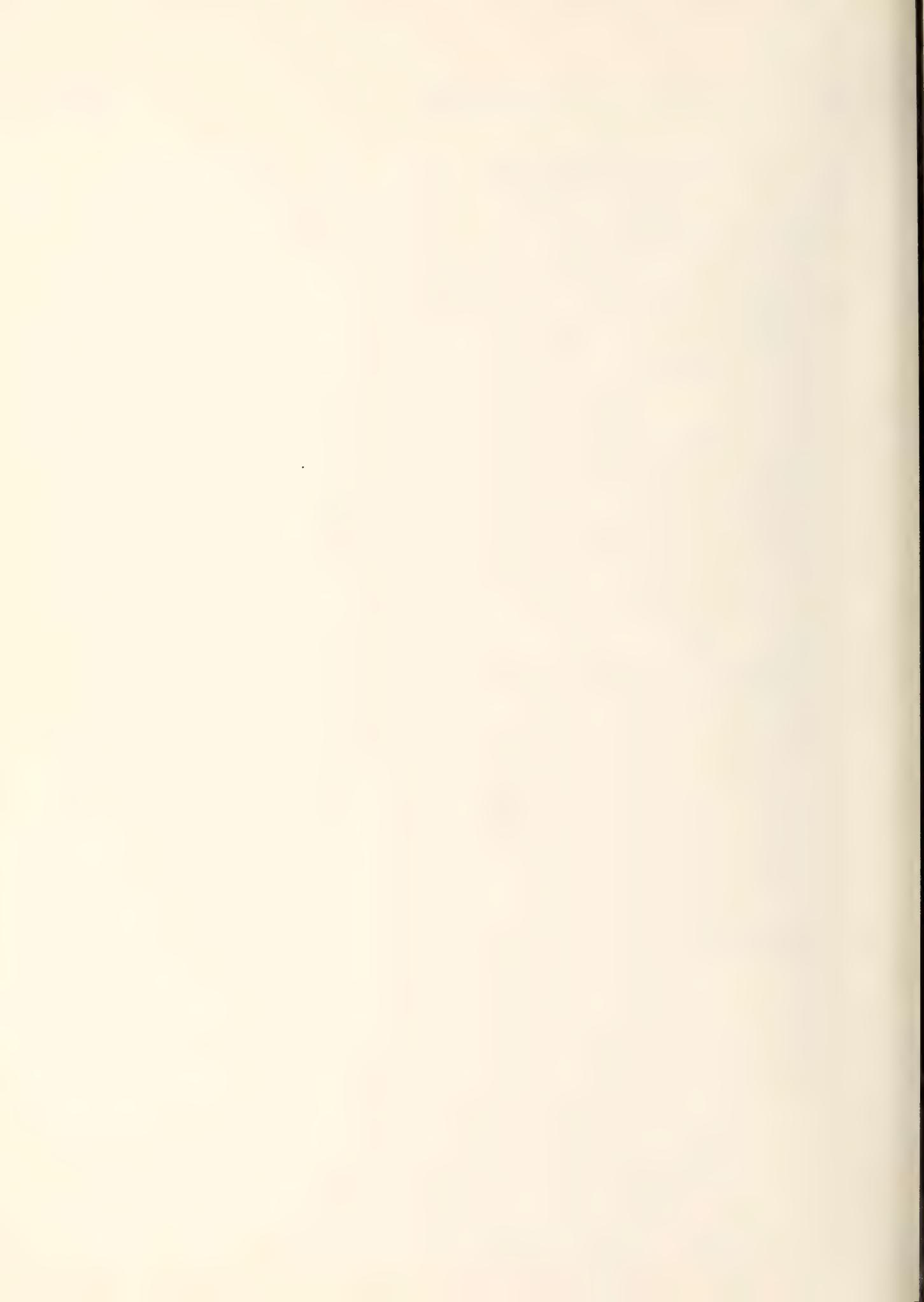
- 10/1/21: (Figures 1a, 1b) — (Figures 155a, 155b)
 26/2/45: *elenense* — *elenensis*
 31/1/28: *colpoica* — *colpoicum*
 31/1/32: *colpoica* — *colpoicum*
 36/1/19: (N.) — (D.)
 38/2/30: *brunneopicta* — *brunneopictum*
 38/2/34: *ferminiana* — *ferminianum*
 42/1/34: (*Nitiscala*) — (*Nitidiscala*)
 42/2/34: *mitraeforme* — *mitraeformis*
 53/1/ 4: (Figures 63, 64) — (Figures 63, 64, 68)

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Epitonium (Nitidoscala) colpoicum DALL, 1917: 478, 479

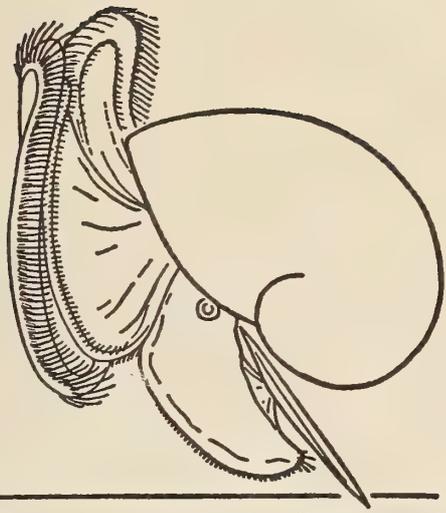
and in the present line 16 delete: DALL, 1917: 478, 479; and insert a dash (-) before PILSBRY . . .





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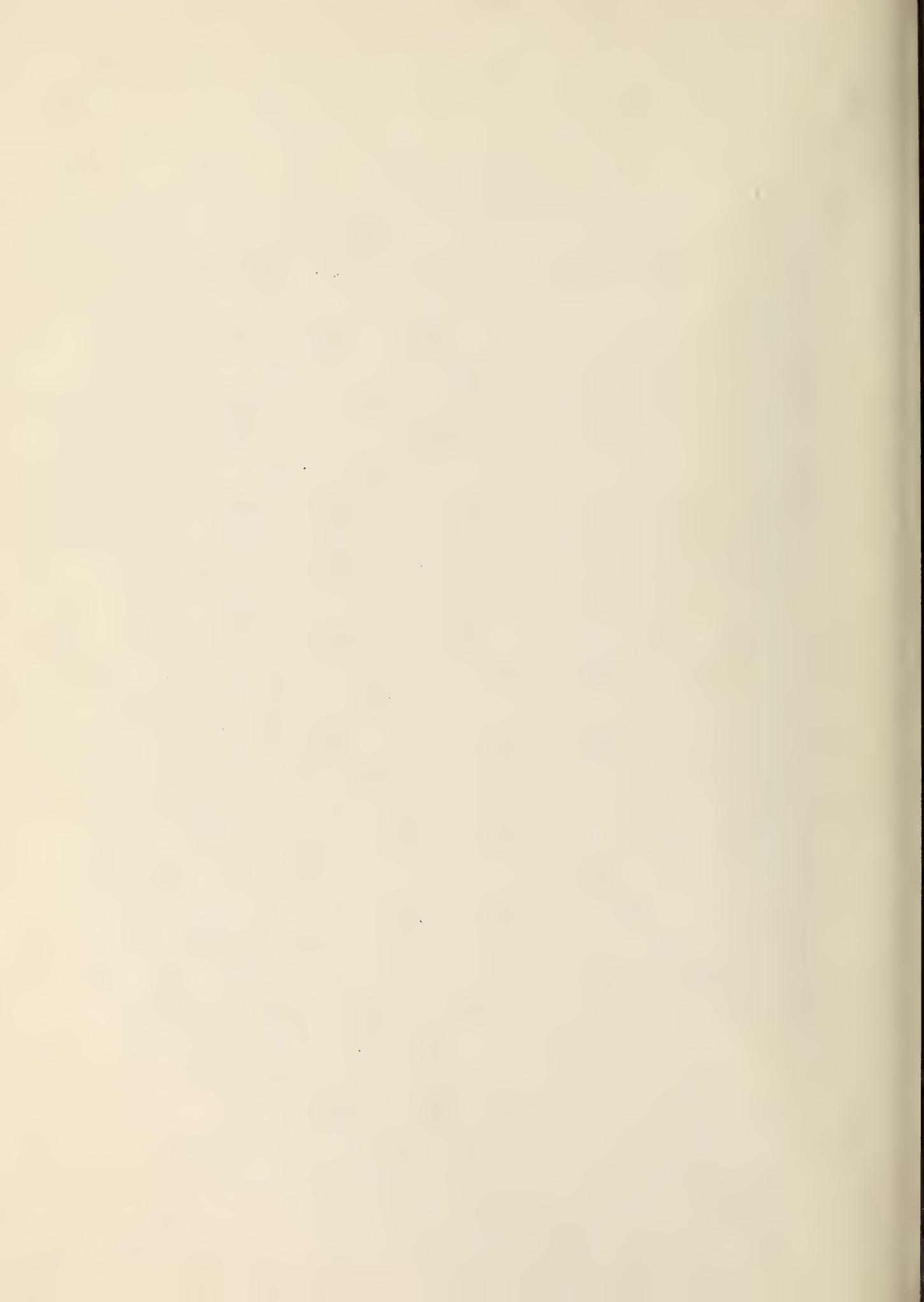
Growth Rates, Depth Preference and Ecological Succession of Some Sessile Marine Invertebrates in Monterey Harbor

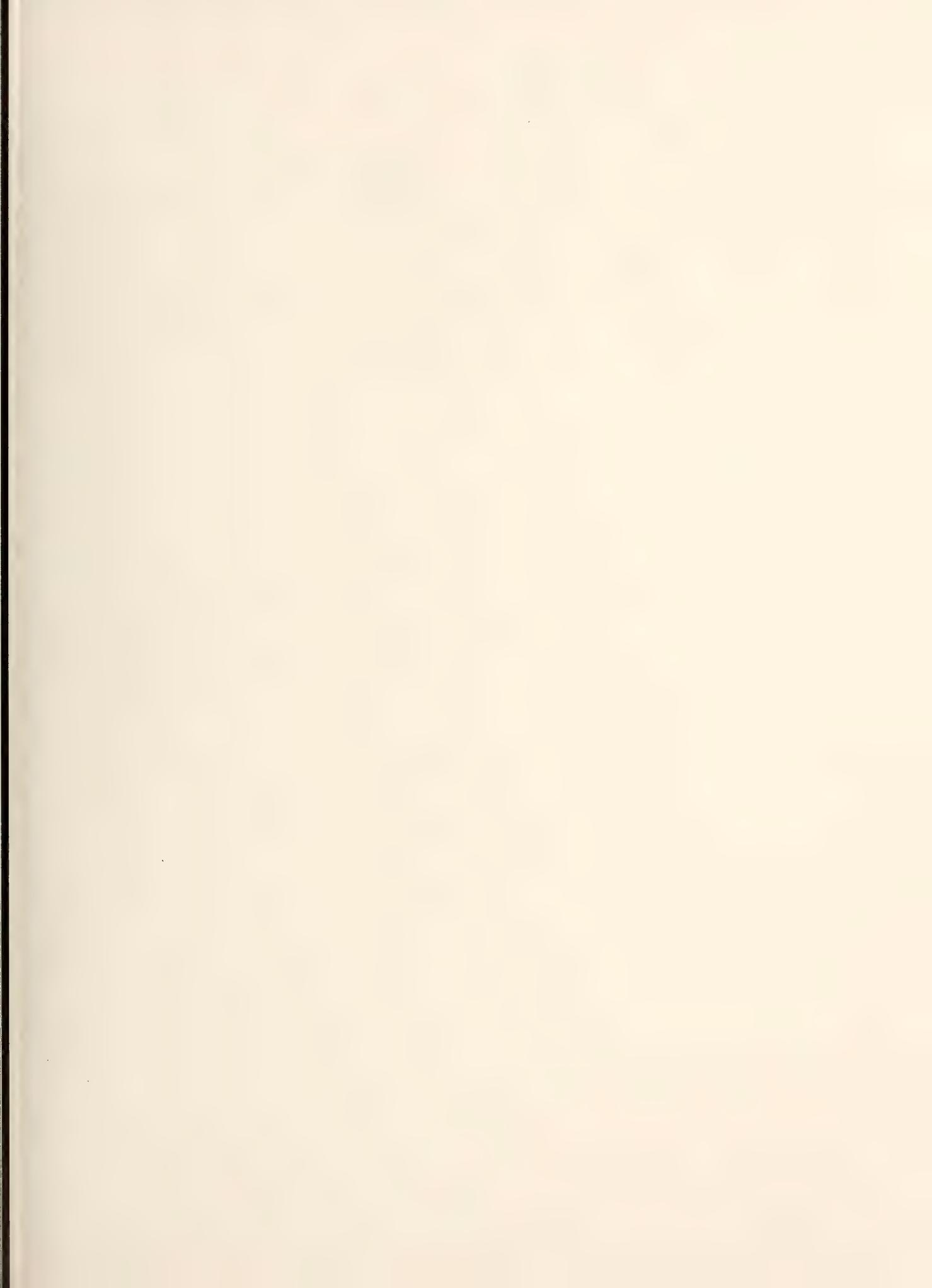
BY

E. C. HADERLIE

Department of Oceanography, Naval Postgraduate School,
Monterey, California 93940

(44 Text figures)

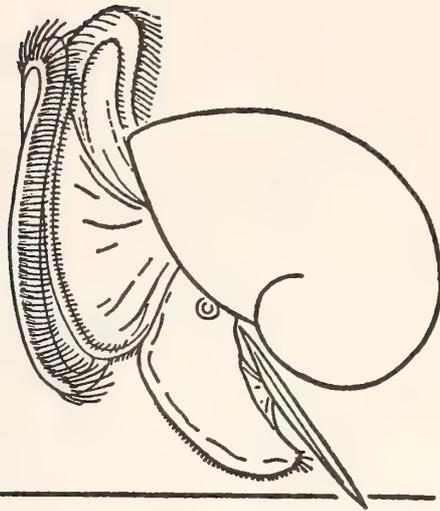






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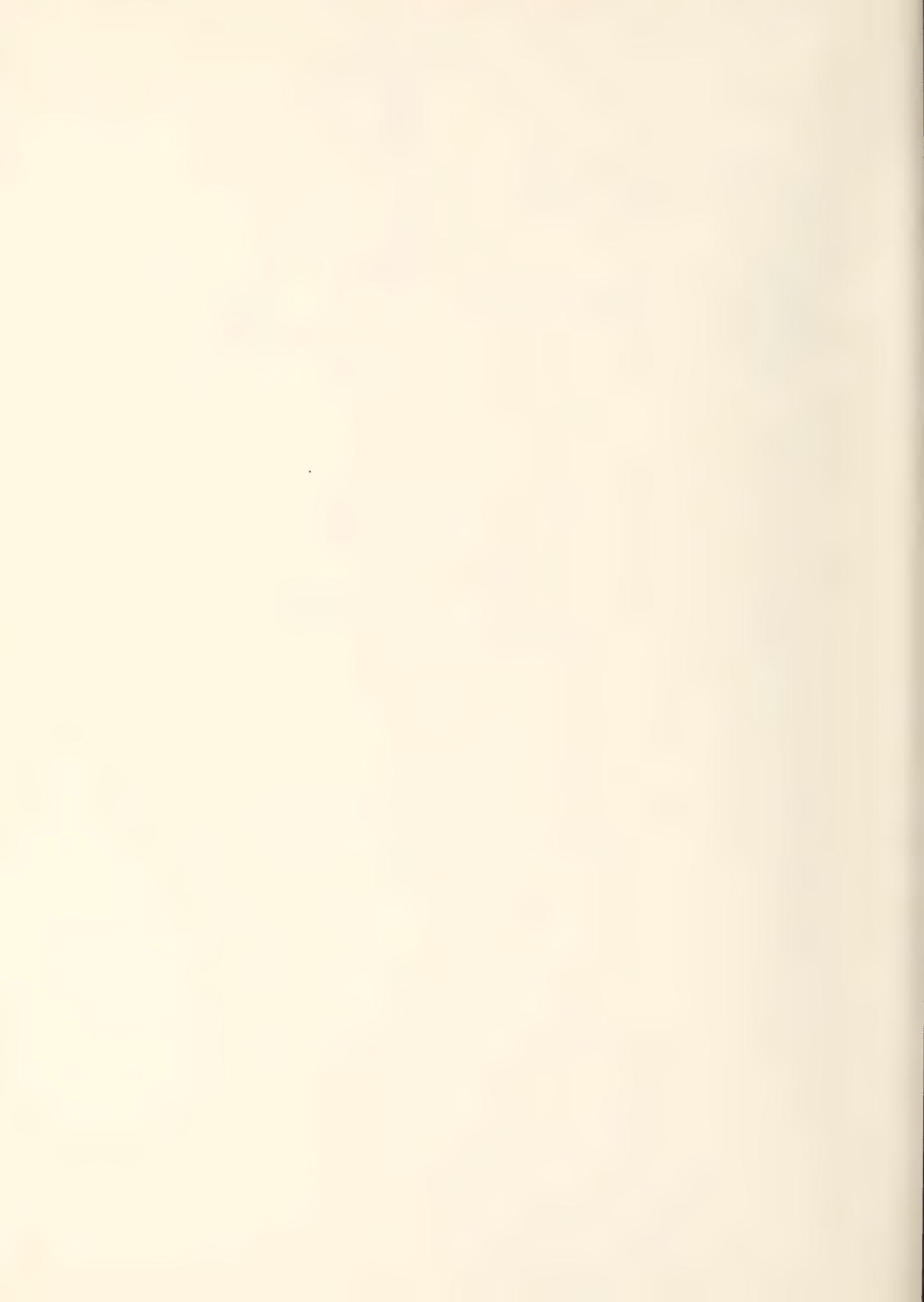
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INTRODUCTION

EXCEPT FOR CERTAIN SPECIES of mollusks such as mussels that have been extensively investigated, few specific studies on the growth rates of sessile marine invertebrates have been made on the California coast. COE (1932) and COE & ALLEN (1937) carried out classic long-term studies on the season of attachment and made some measurements on growth rates of sedentary marine organisms at La Jolla, and over a period of many years G. E. MacGinitie made observations on the growth rates of invertebrates in the laboratory and under natural conditions in Newport Bay (MACGINITIE & MACGINITIE, 1949). In the San Francisco Bay region GRAHAM & GAY (1945) studied growth rates of foulers in the estuary at Oakland. Since 1966 extensive studies on fouling organisms in Monterey Harbor have been in progress and data on seasons of settlement, growth rates, depth preference and the ecological succession of communities have been collected (DELGADO, 1971; HADERLIE, 1968, 1969, 1970; HADERLIE & MELLOR, 1973; MOMMSEN, 1966; MILLER, 1966). Growth rates and longevity of some of the calcareous foulers from Monterey Bay have been roughly calculated from data collected by periodically inspecting fouling panels (SMITH & HADERLIE, 1969).

The investigation reported on here was an attempt to gain more precise data on a few of the most common sessile marine invertebrates found in Monterey Harbor. During a period of 18 months from 1 October 1970 to 1 April 1972 a series of collecting surfaces were exposed at various depths where animals soon settled, attached, and began to grow and develop. Many of these newly settled animals were carefully marked and then individually followed for many months. In this way fairly precise information was gained on rates of growth at different depths, at different seasons, under conditions of little or intense crowding, etc. In addition to this primary objective of the study, data on specific depth preference for several species were obtained and general observations on longevity and ecological succession were made.

The author wishes to acknowledge the help of Mr. J. C. Mellor for considerable assistance in the fieldwork and my wife, Mrs. A. E. Haderlie, for assistance in the laboratory. The Naval Facilities Engineering Command provided financial support.

AREA OF STUDY

This study was restricted to a site under Monterey Municipal Wharf No. 2 at a point approximately 1000 m from the shore (Figure 1). This commercial wharf was constructed in 1926 and is supported by concrete piles spaced

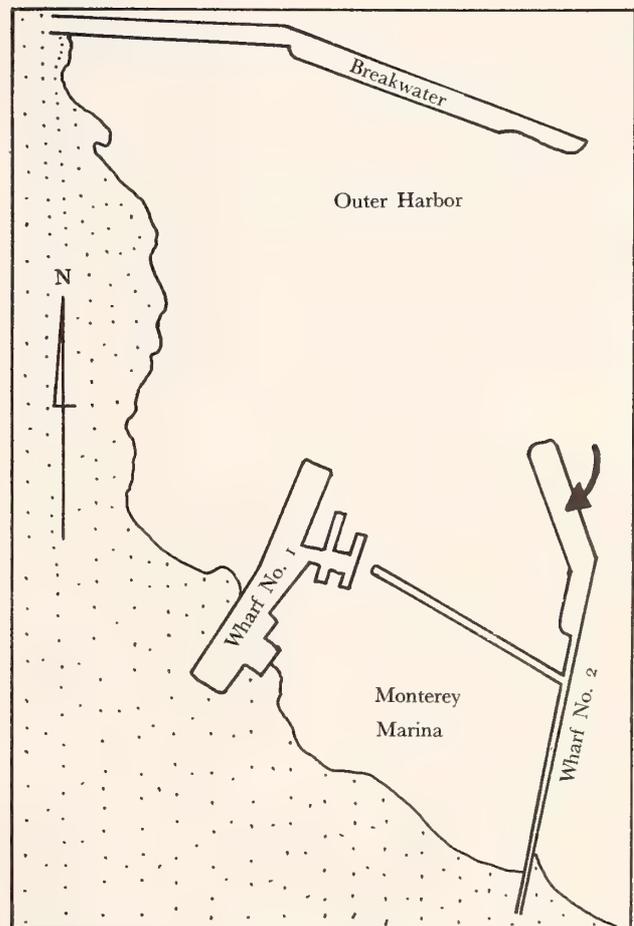


Figure 1

Map of Monterey Harbor showing test site under Municipal Wharf No. 2 (test site indicated by arrow)

about 3 m apart. A series of wooden fender piles are located along each edge of the wharf. All of these piles are covered with a luxurious growth of fouling organisms and it appears to take several years before a stable climax com-

munity becomes established. This community is dominated by acorn barnacles, *Balanus nubilis* Darwin, 1854; *Balanus glandula* Darwin, 1854; *Balanus crenatus* Bruguière, 1789; *Balanus tintinnabulum* (Linnaeus, 1758); anemones, *Metridium senile* (Linnaeus, 1767); *Anthopleura xanthogrammica* (Brandt, 1835); *Anthopleura elegantissima* (Brandt, 1835); *Corynactis californica* Carlgren, 1936; bay mussels, *Mytilus edulis* Linnaeus, 1758; hydroids; polychaetes; ascidians, and many encrusting and arborescent bryozoans. Not all of these appeared on the experimental collecting surfaces but most did. The study site was under the middle of the wharf so that light was subdued and no direct sunlight reached the area except in the early morning. As a result practically no macroscopic plants settled on the collecting surfaces. The water depth at the study site is about 6.9 m at median lower low water (MLLW); the maximum spring tidal fluctuation is approximately 2.7 m. The water freely circulates under the wharf and is not excessively polluted although occasional oil and gasoline spills occur in the vicinity.

Throughout the period of study reported on here daily temperature of the surface water was recorded and is summarized in Figure 2.

MATERIALS AND METHODS

Some sessile benthic marine invertebrates have definite natural surfaces on which they prefer to settle and develop; others seem to show no preference. In the artificial environment of a harbor, substrate preferences can sometimes be noted. In the climax communities found on the piles under Monterey Municipal Wharf No. 2 the dominant anemones show a particularly clear distribution: the large white plumose anemone *Metridium senile* is primarily found on the wooden piles whereas the small, brightly colored *Corynactis californica* is to be found mainly on the concrete piles. Other anemones, such as the green *Anthopleura xanthogrammica*, are found in equal

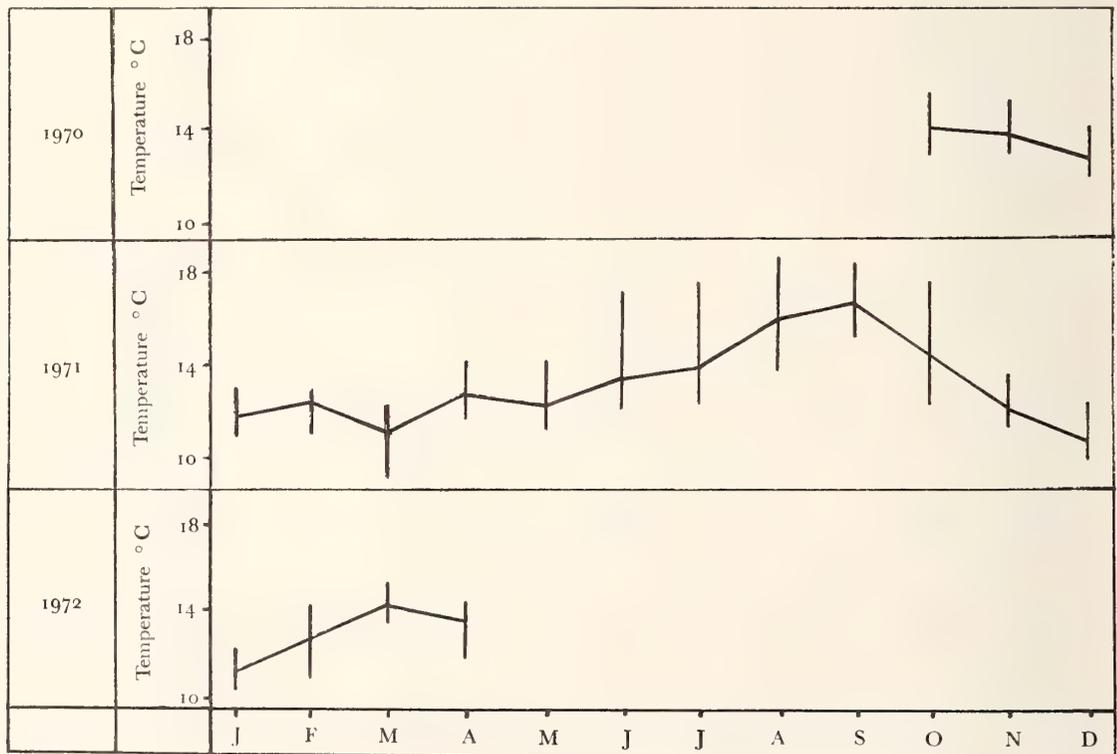


Figure 2

Summary of surface water temperature in Monterey Harbor during this study. Vertical bars indicate monthly range of temperature; connecting lines indicate monthly average temperature

numbers on both kinds of piles and this seems to be true of most of the other pile dwellers.

In studies on fouling organisms in the harbor, several kinds of experimental surfaces such as glass, plywood, concrete, masonite, fiberglass and stainless steel have been used in the past. Douglas fir boards, timbers, or plywood seemed to provide the best all-round collecting surfaces and this material is cheap and easy to obtain and therefore was employed exclusively in the present study. It must be admitted, however, that for most sessile invertebrates stone or concrete would be a more natural substrate for settlement and growth. Furthermore, all of the boards, panels and timbers used in this study were exposed in the water in a vertical orientation, and some sedentary forms prefer to settle on horizontal surfaces. MACGINITIE & MACGINITIE (1949) have pointed out that some species of benthic organisms grow at quite different rates when on horizontal or vertical surfaces. It must be recognized then that rates of growth reported here are not necessarily the rates that would be measured under absolutely "natural" conditions.

Three different arrangements of substrate were used during the course of this study:

1. Experimental Piles: In a long-term investigation of shipworm settlement and growth in Monterey Harbor a series of 10×10 cm clear douglas fir timbers were used as substrate (HADERLIE & MELLOR, 1973). In addition to collecting borers these timbers attracted many of the common sessile invertebrates of the harbor. As the study on borers overlapped the period of study reported on here, these timbers were used to determine depth preference in the water column for many of the surface dwellers.

Two 10×10 cm timbers approximately 5.4 m long were secured together with a 90 cm overlap to form one long "experimental pile" over 9 m in length. This pile was sharpened and weighted on one end and placed vertically in the water with the lower end driven into the bottom and the upper end extending some distance above the highest tide. The pile was secured by stainless steel bands to cross pieces placed between the concrete piles of the wharf. A continuous substrate was therefore available to settling larvae that extended from the bottom up through the water column to above high tide level.

These piles were left in place for 6-month periods, then removed and the surfaces carefully analyzed for attached organisms. During periods of submergence the piles were examined periodically by divers and notations of larval settlement were made but no other data were collected until the piles were removed and taken to the laboratory for analysis. A series of four of these piles were exposed

for consecutive 6-month periods from 1 January 1970 to 1 January 1972.

2. Intertidal Staff: The experimental piles described above provided data on the kinds, numbers, sizes and depth distribution of sessile animals that were present on a vertical surface after 6 months exposure to the marine environment. They did not, however, make it possible to follow the rates of growth of various species from month to month. To make such measurements possible it was decided to use a continuous vertical substrate that could be removed monthly for analysis and measurement and then returned to the water. Such an arrangement extending through the entire water column seemed impractical, so it was limited to the intertidal area. The plan at first was to use a 15 cm wide douglas fir board 3 m long but it was obvious this would be difficult to handle for periodic laboratory analysis so, instead of a board, a piece of ca. 6 mm thickness marine grade douglas fir plywood was used. The plywood was 2.5 m long and 15 cm wide and for ease of handling and examination in the laboratory was cut into 25 cm sections. Each section carried a distinctive label as to its position. A rigid stainless steel rack consisting of side channels was used to hold these sections in place in a vertical series. When in place the top section of this plywood staff was just awash at the highest spring tide of +2.1 m. The staff extended as a continuous surface down to near the lowest tide level.

On the first of each month for the entire 18-month period of this study the sections of the staff were slid out of the rack, placed in tubs of sea water and taken to the laboratory where they were held in aquaria of running sea water until examined. Analysis consisted of placing each 15×25 cm plywood section or panel in a pan of cold sea water and scanning the entire surface with a binocular stereoscopic microscope ($7\times$ to $30\times$ magnification). A grid consisting of stainless steel wires positioned 1 inch apart was placed over the panel during microscopic examination and the position, size and identity of selected animals that had settled and attached to the panel were recorded on graph paper. On each succeeding month these same selected individuals were re-located on the grid and remeasured. Only firmly attached forms were followed so there was no chance of not following the same individual from month to month. In addition to measuring the size of individual organisms each month, changes in populations, new settlements and ecological succession were noted. Following examination, the plywood staff sections were replaced in their rack to allow another month of growth and development. The plywood sections were never out of the harbor water for more than 4 hours while being analyzed

and during these periods they were immersed continually in sea water except when being handled.

Some observers have noted that there is sometimes a slightly different population of pile-dwelling animals on the surfaces of piles facing different directions, e.g., certain forms grow more readily on the north side of a pile than on the south. In the conditions of dim light and reduced current and wave action at the study site under Wharf No. 2 in Monterey such differences have not been detected. It should be pointed out, none-the-less, that the surface of the intertidal staff that was examined monthly was the surface that continually faced south during periods of exposure to harbor water.

3. Sub-tidal Collecting Panels: To supplement observations made on the intertidal staff, and to partially compensate for not having staff sections extend down through the entire water column to the bottom, a series of plywood panels was exposed in stainless steel racks suspended at three different levels below low tide level. The racks used were the same as those employed in previous fouling studies (Haderlie, 1968) where each rack held six $20 \times 25 \times 0.6$ cm douglas fir panels. Each panel was held vertically in the rack and separated from its neighbor by a 7.2 mm space.

The three racks were designated and positioned as follows: the shallow rack was suspended at 90 cm below MLLW (= approximately 30 cm below lowest tide), the midwater rack at 3.6 m below MLLW and the deep rack at 6.9 m below MLLW or just above the bottom.

Previous studies in the harbor have shown that the larvae of many of the attached invertebrate species settle at various times throughout the year, some settling continuously. To make it possible to study the growth of different individuals that have settled at different seasons without the complicating factors of competition with older organisms already settled and growing, new panels were added to these racks monthly. In other words, when the three racks were initially placed in the water on 1 October 1970 each contained but one panel. Each month after that a new panel was added until at the end of 6 months the racks were full. It became obvious at the end of 6 months that the midwater panels were collecting the greatest diversity of species. A second midwater rack was therefore placed beside the original one and this allowed for additional panels to be exposed monthly for another 6 months. A total of 6 panels was therefore employed in the shallow and deep positions, and twelve panels in the mid-water position. All of these panels, once immersed, remained in the racks until the project was terminated on 1 April 1972. Some panels had been exposed for the full 18 months, others for progressively shorter periods to a minimum of 6 months. Each month they were removed and taken to

the laboratory for analysis. They were handled exactly as the staff sections described above.

DEPTH PREFERENCE AND VERTICAL ZONATION

The vertical zonation of animals on the rocky shores of the California coast is obvious and often the delineation between zones is sharp. This zonation is not so clear on pilings in harbors, yet at Monterey such vertical stratification of some organisms can be clearly seen.

LANG (1968) made an investigation of the pile-dwelling animals under Monterey Municipal Wharf No. 2. Using Scuba diving gear he carefully mapped the distribution of the most common pile-dwellers on a series of concrete piles at different places under the wharf. He identified a total of 98 species of invertebrates living on these pilings. Most of these were free-moving, non-attached forms such as worms, crustaceans, mollusks and echinoderms. Lang's observations have been continued and extended and we now have identified over 150 invertebrate species from the piles.

The concrete piles on which these studies were made have been in place since 1926, so the climax community of pile-dwellers is presumably old and relatively stable. No substantial change in the populations has been detected in the past 6 years of observations except for the gradual disappearance of mussels due to predation by sea otters. No new concrete piles have been added in recent years, but wooden piles in the vicinity are replaced periodically and this has given opportunity to study the initial colonization of a newly placed pile and the establishment of piling communities. The process is slow and all indications are that creosoted wooden piles require 5 to 10 years to become covered with a luxurious fouling growth which then appears to become stable. None-the-less, many newly placed creosoted piles will be colonized as soon as placed in the water. One new fender pile was found to carry a very heavy settlement of young *Balanus crenatus* two weeks after it was put in place. It is not known if the concrete piles require a shorter or longer period to achieve a climax community.

Figure 3 illustrates the vertical distribution of a few of the more obvious attached invertebrates found in the climax community of concrete pile-dwellers in Monterey Harbor. The data for Figure 3 were taken from piles in the immediate vicinity of the site of the experimental studies to be described below. To the casual observer looking at the piles from above water during a very low tide the



Crisulipora occidentalis Robertson, 1910
Bugula neritina (Linnaeus, 1758)
Bugula californica Robertson, 1905
Chitinozoma groenlandica (Mörch, 1853)
Spirorbis sp.
Bowerbankia gracilis O'Donoghue, 1926
Balanus tintinnabulum (Linnaeus, 1758)
Balanus aquila Pilsbry, 1916
Chthamalus dalli Pilsbry, 1916
Balanus glandula Darwin, 1854

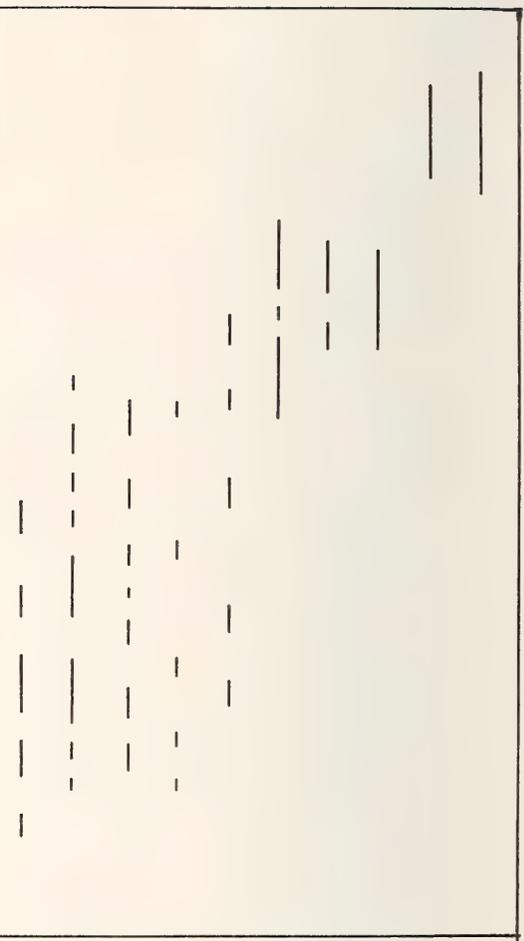


Figure 4
 Marine invertebrates on Experimental Pile No. 1
 July 1970 (6 months exposure)

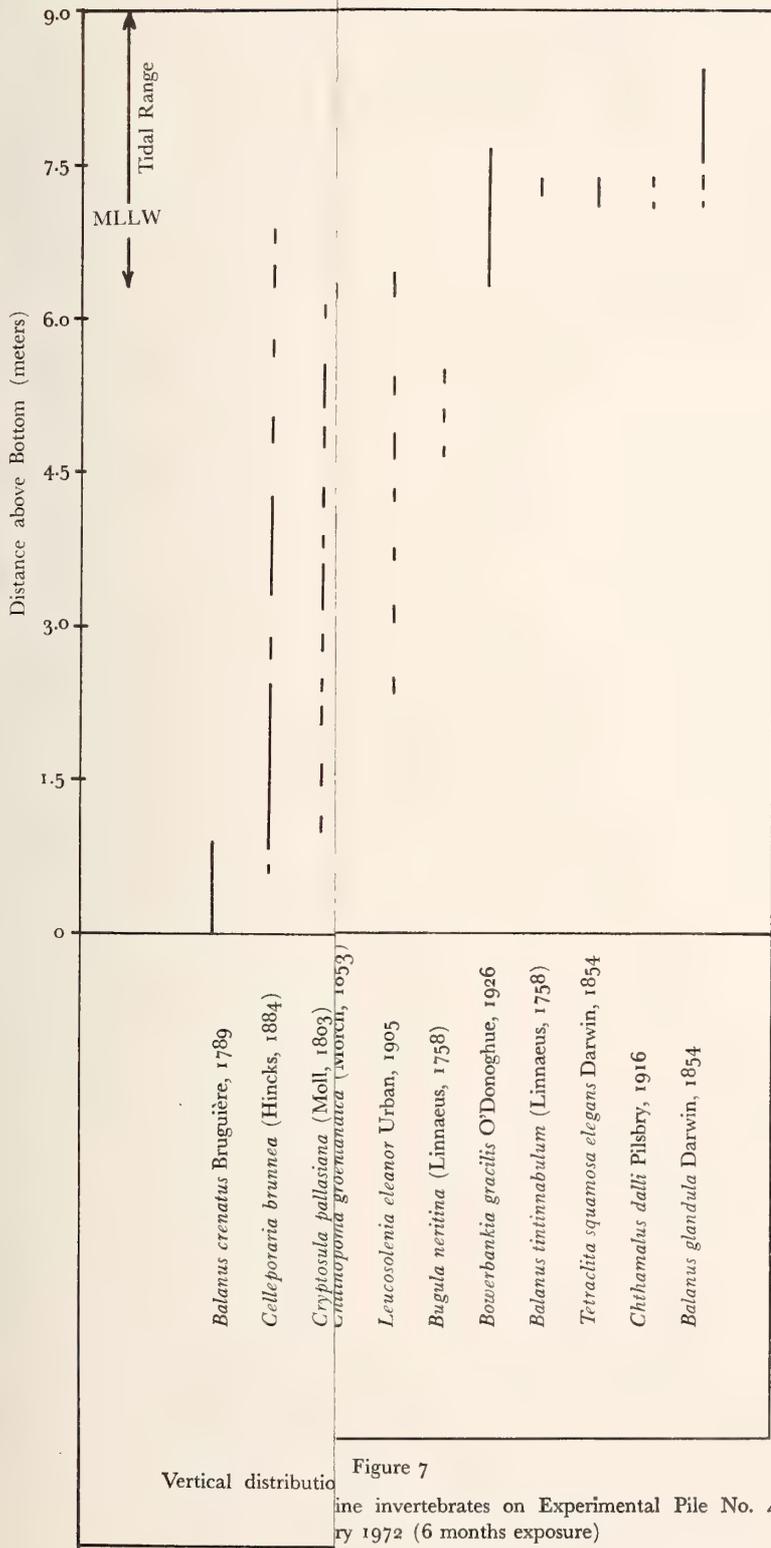
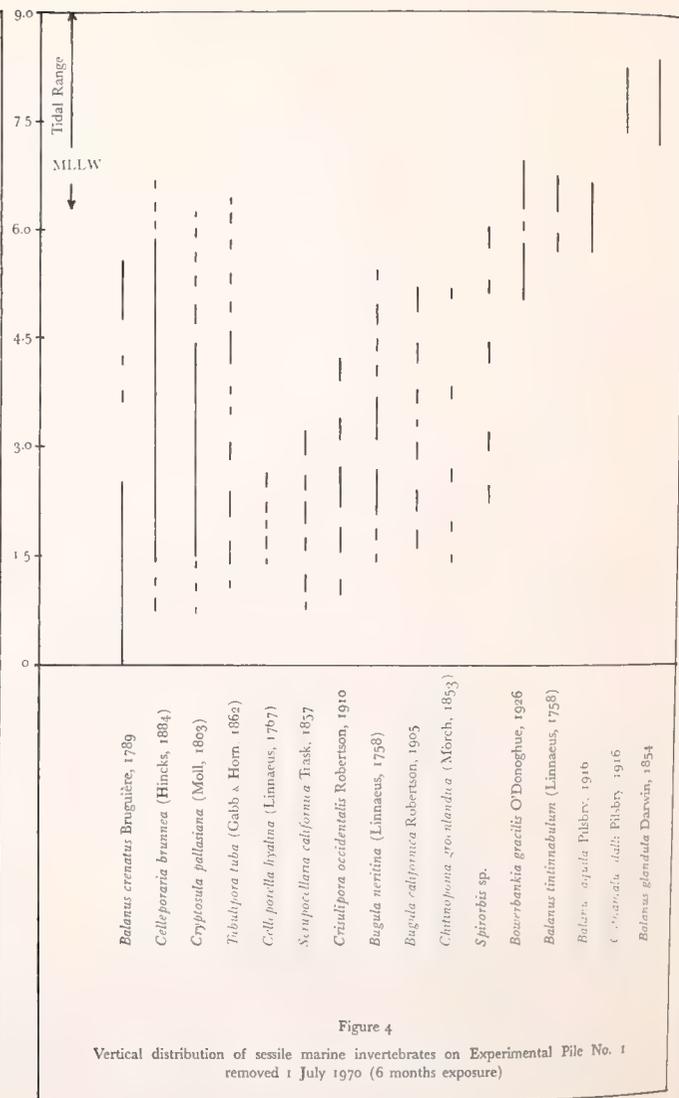
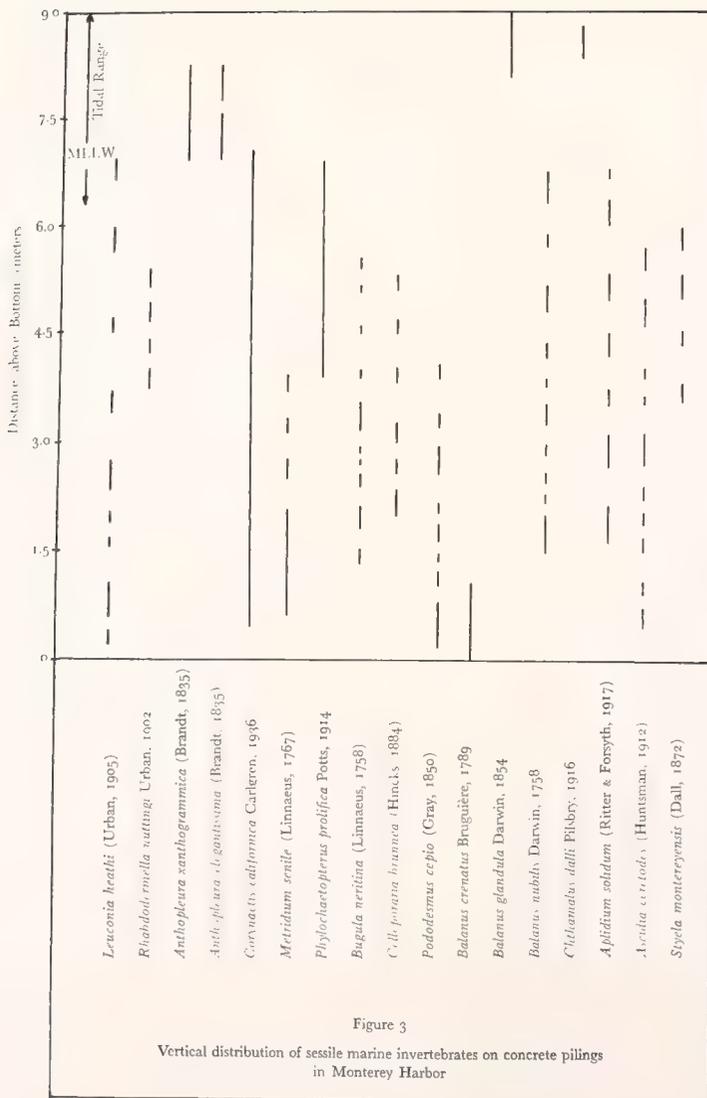


Figure 7
 Vertical distribution of marine invertebrates on Experimental Pile No. 4 in January 1972 (6 months exposure)



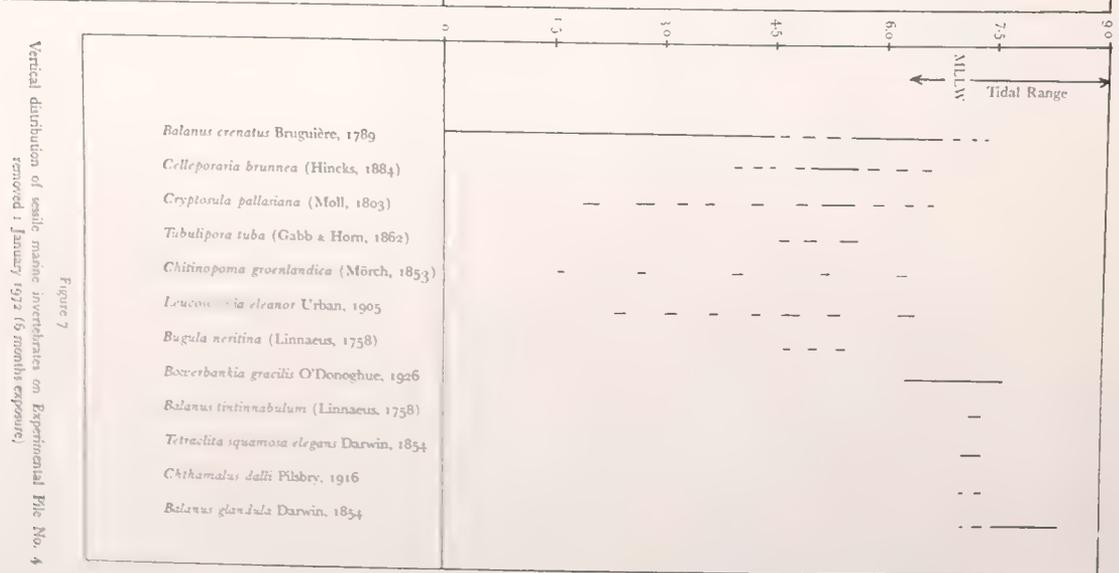
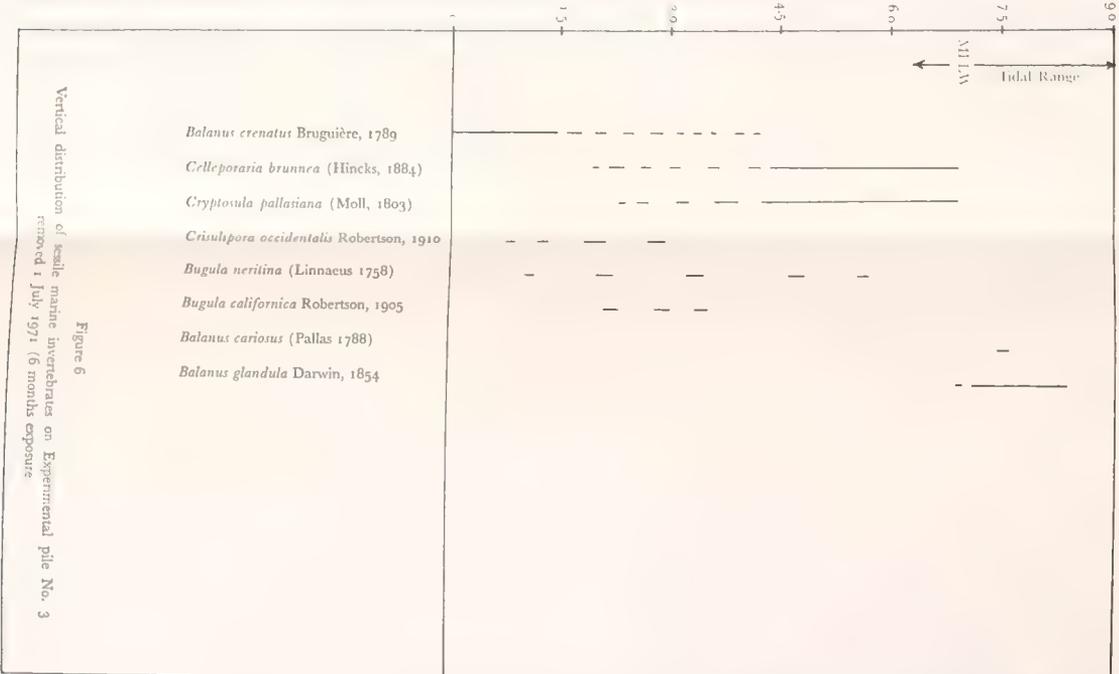
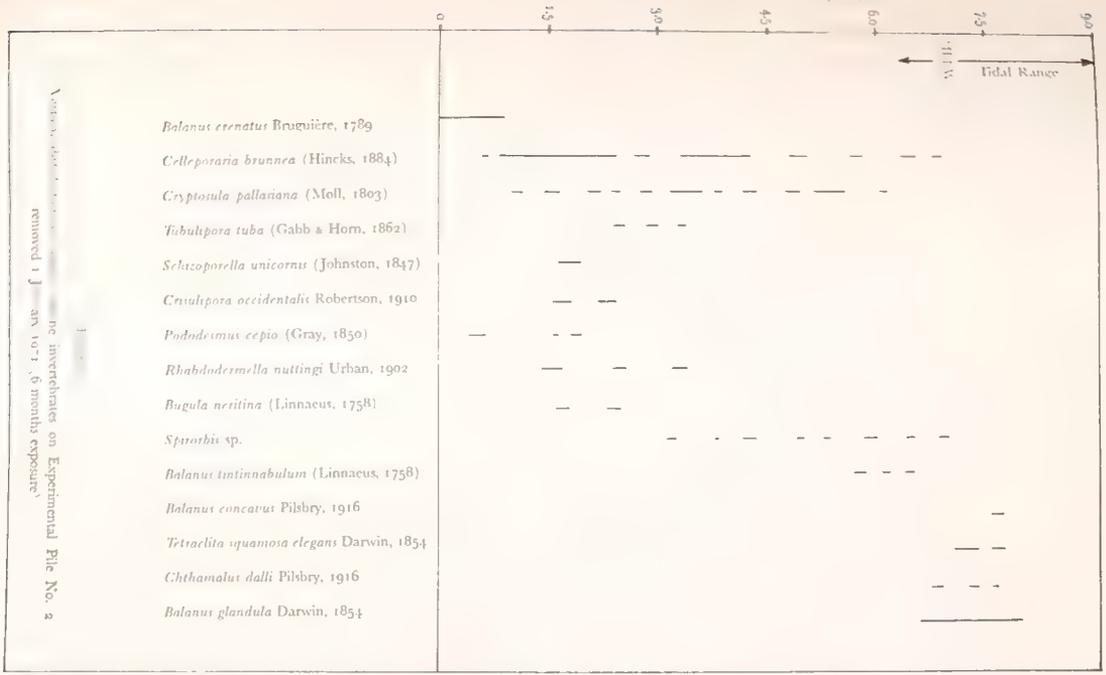
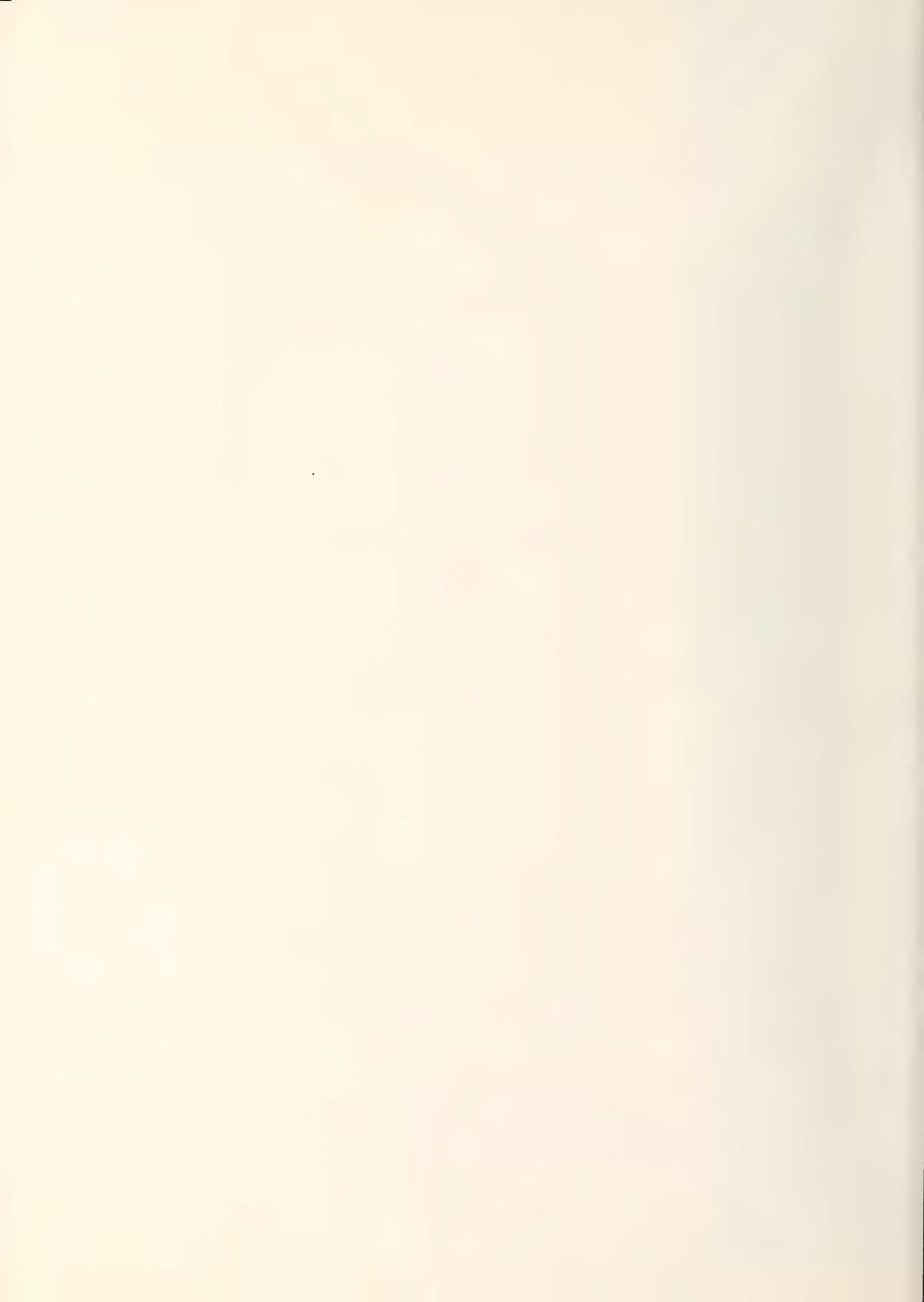


Figure 5

Figure 6

Figure 7



most obvious zonation is the distribution of anemones. The large green solitary anemone *Anthopleura xanthogrammica* with a few individuals of the aggregate forms, *A. elegantissima*, are common from about 1.2 m down to 30 cm above MLLW where they are abruptly replaced by the small anemone *Corynactis californica*. These bright red and orange anemones form dense colorful bands around the piles at the very lowest tidal level and below and then continue in smaller numbers down the pile to near the bottom. The large white plumose anemone *Metridium senile* is found on the concrete piles in numbers only in the bottom half of the water column, but on wooden piles, especially where there is adequate light, *Metridium* is much more abundant and occurs up into the intertidal zone in great numbers. The acorn barnacles also show distinct zonation on these old concrete piles. *Balanus glandula* and *Chthamalus dalli* form dense masses in the upper intertidal zone. Lower down the giant barnacle *Balanis nobilis*, often achieving 10 cm or more in basal diameter on these old piles, is distributed from the lowest tide level down the pile for about 6 m. Many of these barnacles are covered with colonies of *Corynactis* and other animals such as the encrusting bryozoans *Celleporaria brunnea* and *Cryptosula pallasiana*. Near the bottom of the concrete piles the giant barnacles are replaced by often dense populations of *Balanus crenatus*. Between MLLW and about 3 m below many piles carry enormous colonies of the polychaete tube-dweller *Phylochaetopterus prolifica*. The intertwining tubes of these worms create a swollen collar around the piles and a habitat for dozens of other small mobile pile-dwellers.

In order to make more precise observations on initial colonization of wharf piles, a series of experimental piles were employed in this investigation. As described above, the piles consisted of 10 × 10 cm douglas fir timbers that were placed vertically in the water alongside the regular piles with the lower ends driven into the bottom and the upper ends extending above the high tide line. Each pile remained in the water for 6 months before removal for analysis. Four piles were exposed for 6-month periods in the same location extending from 1 January 1970 to 1 January 1972. Figures 4–7 illustrate the vertical distribution of the major sessile invertebrates found on each of the experimental piles after 6 months exposure to the water in Monterey Harbor.

Some differences are apparent in numbers of different species settling and vertical distribution of settlers during the four different periods. This was expected, for all previous studies in the harbor have shown considerable variation from year to year in the pattern of settlement of fouling organisms. Yet many consistencies were found and

piles exposed in January or in July carried approximately the same species and in the same spacial distribution. This again illustrates that for the major fouling organisms in Monterey Harbor there is no single season of settlement and growth.

On all of the experimental piles the most obvious consistent pattern of vertical distribution was observed in the case of acorn barnacles and the encrusting bryozoans. Near the bottom of all the piles *Balanus crenatus* was present in great numbers and in most cases, especially near the bottom, covered 100% of the pile surface. After six months these barnacles ranged in size from 4 to 10 mm basal diameter. The barnacles extended up from the bottom of the pile as pure stands for distances varying from about 1 to 5 m when they began to thin out and were replaced by the encrusting bryozoans *Celleporaria brunnea* and *Cryptosula pallasiana*. After taking the place of the barnacles, these bryozoans often covered the piles completely with circular, overlapping colonies up to 40 mm across. These dominant bryozoans extended up the piles in decreasing numbers to near the low tide line. The intertidal part of the piles was dominated by other acorn barnacles, especially *Balanus glandula*. Other species of foulers were usually distributed in rather discontinuous fashion in and among the dominant forms mentioned above. In Figures 4–7, the solid continuous lines indicate essentially continuous distribution along the designated part of the pile but not necessarily 100% coverage. The broken lines indicate discontinuous distribution through the range given.

In the intertidal zone the acorn barnacles exhibited an interesting distribution. *Balanus glandula* was the dominant species and in the mid- and upper-tidal zones often covered the pile completely with individuals up to 12 mm diameter (after 6 months or less of growth). The upper limit of these barnacles was 1.5 m above MLLW. The small barnacle *Chthamalus dalli* (up to 5 mm basal diameter) was found interspersed with *Balanus glandula*. *Balanus tintinnabulum* occurred on three of the four piles in the low intertidal and subtidal zone. It was never abundant but occasionally was very large. The pile removed 1 July 1970 after 6 months exposure carried one *B. tintinnabulum* 30 mm in basal diameter and several others of slightly smaller size.

Tetraclita squamosa elegans had not been encountered in previous fouling studies in Monterey Harbor but was found on two of the four experimental piles in this investigation. This barnacle had a very limited range, being found only in the lower intertidal zone between 15 and 75 cm above MLLW. The barnacles ended abruptly at each end of their range. On the pile removed 1 January 1972 the band of *Tetraclita* covered practically 100% of all four

surfaces in the 15 to 45 cm range. Most of these averaged 8 mm in diameter but a few were 10 mm. *Tetraclita* must settle during July through December in Monterey Harbor, for they were found only on the two piles in the water during this period on alternate years.

Balanus aquila appeared on only one pile and was distributed from the lowest intertidal zone down to 1.2 m below lowest tide. These barnacles were most heavily concentrated at the -90 cm level where dozens of them were found. Some of these were very large, up to 35 mm in basal diameter (after six months or less growth).

As explained earlier under "Materials and Methods," a staff of plywood panels or segments was exposed in the intertidal area for 18 months and examined monthly. Curiously, fewer species of animals settled on these than on the experimental piles, but where settlement occurred in both places the animals settled in similar numbers and at the same level. The results of analysis of these intertidal staff panels will be considered below.

ECOLOGICAL SUCCESSION

SCHEER (1945) found a definite ecological succession of animal communities on submerged panels in Newport Harbor, California. On most surfaces there was a bacteria-diatom-bryozoan-mussel sequence. HADERLIE (1969) reported a similar succession in Monterey Harbor except that ascidians in general followed the bryozoans in the sequence, and the ascidians appeared only on panels that had been submerged nine to twelve months. No matter which month of the year a panel was initially submerged the fouling communities went through basically the same sequence. Differences at various depths were noted, however, and panels in shallow water carried somewhat different populations than those near the bottom. During the present investigation these observations have been extended, for many of the panels used here were in the water for up to 18 months before terminal removal whereas earlier studies had lasted only a year.

As before, it was found that regardless of month of initial exposure to the marine environment the panels at any one depth accumulated a fouling growth in definite sequence, except on midwater panels that were subject to occasional massive barnacle settlement. After about twelve months exposure most of the panels at any one depth came to have a similar fouling community that simply enlarged but did not change appreciably for the next six months. Therefore, to simplify the discussion below only an analysis of panels that were initially submerged on 1 October

1970 at the start of the investigation will be given. A similar analysis involving essentially the same sequences could be made for panels initially submerged on any other month.

Intertidal Staff Panels

The panels or segments making up the staff that covered the intertidal zone collected different organisms at various depths. In general, soon after exposure the lower panels became covered with a slime film of bacteria and benthic diatoms. By the end of the second month of exposure the lower panels carried heavy growths of the hydroid *Obelia* sp. and associated animals such as *Hermisenda crassicornis* (Eschscholtz, 1831) and *Caprella californica* Stimpson, 1857. Encrusting bryozoans then made their appearance and the soft fuzzy growth of *Bowerbankia gracilis* O'Donoghue, 1926, often covered the lower panels and this growth persisted on many panels for several months. After four months of exposure the barnacle *Balanus glandula* settled on many of the high and mid-intertidal panels. During the latter period of the study bryozoans that dominated the lower panels were gradually replaced by massive growths of ascidians such as *Ascidia ceretodes*. Toward the end of the investigation many panels began to crumble and disintegrate due to the activities of the boring gribble *Limnoria quadripunctata* Holthuis, 1949.

Shallow Panels (90 cm below MLLW):

During the first two months of exposure the shallow panels accumulated a slime film of bacteria and ultimately a growth of benthic diatoms (*Melosira* sp., *Isthmia* sp., *Navicula* sp., plus others unidentified.) Colonies of the hydroid *Obelia* sp. often followed the diatoms. During the third month macroscopic colonies of the encrusting bryozoan *Celleporaria brunnea* were found all over the panels; these colonies grew rapidly so that by the sixth month the colonies were practically all in contact and the panel nearly 100% covered with *Celleporaria* with a few colonies of *Cryptosula pallasiana* and a few bushy tufts of *Bugula neritina*. Relatively small settlements of the barnacle *Balanus crenatus* occurred during the third month and again periodically during the next month but few settled or survived after a few months apparently due to competition with encrusting bryozoans. During the tenth to the twelfth month the ascidian *Ascidia ceretodes* appeared as scattered individuals attached to or between the bryozoans. The ascidians grew rapidly and after two to four months practically covered the panel as globular forms up to 50 mm in diameter. All of the underlying bryozoans and barnacles were smothered and from month 14 to 18 only *Ascidia* and large bushes of *Bugula neritina* covered

the panel. The wet weight of the fouling growth on some of these panels after 18 months submergence was often as much as 2 kg and most of this was due to the ascidians on the panel. Of course, many small mobile animals lived among the sedentary forms but these are not considered here.

Midwater Panels (3.6 m below MLLW):

The ecological sequence on the midwater panels was somewhat obscured by the periodic massive settlement of *Balanus crenatus* larvae. During the period of study being considered here *B. crenatus* larvae settled during nearly every month of the year, but in various numbers (see Figure 9). Thus, whenever a release of larvae occurred the young barnacles would settle on the other animals such as the ascidian *Ascidia ceretodes* already on the panel.

The midwater panels went through the same basic early ecological sequence as the shallow panels. After 2 months exposure *Celleporaria* appeared and grew rapidly followed by *Cryptosula*. When barnacles settled on the panels between the bryozoan colonies, the bryozoans often grew up over the barnacles and smothered them. In other cases, however, a massive settlement of *Balanus* could swamp the panel and before long only barnacles side by side covered the panel to the total exclusion of the earlier bryozoans. When this occurred the barnacles could no longer grow in diameter, but became very tall, thin and tubular. *Ascidia ceretodes* appeared on the panels after ten months exposure followed by a few specimens of *Styela montereyensis*, *Ciona intestinalis* and *Aplidium solidum*. By the end of 18 months the ascidians came to dominate the midwater panels and most of the barnacles were dead.

Deep Panels (6.9 m below MLLW):

Data from the deep panels submerged during this study were incomplete for most of the living organisms on the panels died or were killed half way through the period and the panels never recovered their fouling growth. These panels were suspended near the bottom and may have been subject to predation by seastars and gastropods.

In November 1970 during the second month of initial exposure the deep panels received a heavy settlement of *Balanus crenatus* (yet curiously none settled on the midwater panels just a few feet above). At the same time a few encrusting bryozoans settled. By late January 1971 (after four months of exposure) the barnacles were large, crowded and were lifting up and destroying the *Celleporaria* colonies. The tall tubular barnacles began to break off in February and were replaced by the March settlement. During April a few of the original barnacles released nauplii and the new crop from the March settle-

ment grew rapidly. Then suddenly on 1 May 1971 all the barnacles on all the deep panels were found to be dead. The shells were still attached but no living barnacles were left. Moving slowly over the dead barnacles were dozens of individuals of the nudibranch *Acanthodoris pilosa*. Earlier studies (HADERLIE, 1971) indicated, as does the present one, that *Acanthodoris* is a predator on *Balanus crenatus*. The panels remained fairly sterile until October 1971 when a few *Ascidia ceretodes* settled on the remains of the encrusting bryozoans and began to grow.

GROWTH RATES

Growth rates and longevity studies on only a relatively few sessile marine invertebrates have been made. For commercially important shellfish such as oysters and mussels considerable data have been collected and published, but for most other attached forms little or nothing is known. This lack of information is surprising, for it is a relatively easy matter to mark or relocate these non-mobile animals in their natural environment for observations and measurement. Such measurements that have been made indicate that as in all growth studies many variables enter into the picture and it becomes very difficult to know if the individuals or populations one is studying represent average growth rates or something above or below average. The temperature of the water, its turbidity and turbulence, salinity, oxygen content, the amount of food in the water, the depth at which settlement occurs, and even the orientation of the substrate on which sessile animals settle can influence their rate of growth. Once settled, a dense aggregation of individuals can stunt or alter growth rates due to competition for space and for available food. Only by studying many individuals and populations over a long period of time can really accurate data on average growth rates be accumulated.

The present study is a start in this direction but the data collected can be criticized on at least two grounds: first, a period of 18 months is not long enough to detect yearly differences in growth rates, and second, the animals observed in this investigation settled and grew on vertically placed wooden panels and timbers which represent an unnatural substrate in nature. A much more satisfactory method of study would be to observe and measure the animals in place on truly natural stone substrates and to do this for many years. In the intertidal zone this would be no great problem, but to do this for subtidal species would be difficult.

This investigation is therefore admittedly short-term and the choice of experimental substrate for ease of study

has introduced unknown variables in the growth studies. Yet the information gained may give some indications of general growth rate patterns in some of the common sessile invertebrate animals found in Monterey Harbor.

Hundreds of individual animals or colonies were identified, marked and followed during the course of this investigation. Many of these individuals that were being measured monthly survived for many months and reached maturity, some released larvae or sex products. Others, after being followed for some weeks or months, met with one disaster or another and either died or disappeared. Individuals separated by some distance may have grown fairly normally for several months, but ultimately they became crowded and then growth became abnormal or impossible. In the growth curves shown in Figures 8–44, each curve represents one individual animal or colony studied, but often many individuals were followed that had similar growth and would show the same or a very similar curve. The size given is basal or maximum diameter of an individual or colony except for elongated forms such as the sponge *Rhabdodermella* or the ascidian *Styela* where the size given is maximum length or height of the animal. The initial point on each growth curve is the size of the animal or colony when first detected on the panel and generally indicates that the animal or colony settled during the preceding month. When the growth curve extends to the far right of the graph (1 April 1972) it indicates the animal or colony was still alive when the panels were removed and the project terminated. When the curve stops before 1 April 1972 it indicates the animal or colony had died, was lost, or was smothered by other species on the panel. As explained above, a new fresh panel was placed in the rack on the first of every month for the first 6 months of study in the case of the shallow and deep racks and one each month for 12 months in the case of the mid-water rack. For barnacles, serpulids and encrusting bryozoans only those animals settling on newly placed panels were selected for study and subsequent periodic measurement. Therefore, each consecutive growth curve or set of curves for these animals represents individuals growing on different panels. Ascidians, sponges, some arborescent bryozoans and a few other forms settled only on older panels with already established fouling communities. In choosing specific animals for study and measurement an attempt was made to select those that were separated far enough from similar forms so that there was no excess crowding or stunting of growth, but this was not always possible.

In the discussion below the major groups and individual species studied will be considered. Much more information was collected on certain species than on others and this will be noted in each case.

Barnacles

Balanus crenatus

The acorn barnacle *Balanus crenatus* is one of the most common of the sub-tidal fouling organisms in Monterey Harbor and settles sporadically throughout the year at all sub-tidal depths but most commonly in deeper water. In this investigation it was therefore possible to study growth rates in individuals that settled at different depths and at different months during the year. Figures 8–10 give some typical growth curves for *B. crenatus* when growing on panels in the shallow, midwater and deep positions. On the shallow panels settlement occurred during the second, third and fourth month of the study. Most of the barnacles grew rapidly for about 6 months and achieved a basal diameter of from 10 to 20 mm, then most individuals died. A few continued to live but did not grow after 6 months. A few individuals, such as the one represented in the top curve of Figure 8, were still alive after 16 months of observations but had remained the same size for six months.

Settlement extended over a longer period of time on the midwater panels as indicated by Figure 9, but the curves are roughly of the same shape as those from individuals on the shallow panels. The most spectacular growth rate of any *Balanus crenatus* individual followed in this study was one that grew to 10 mm in basal diameter during the single month of June 1971.

Settlement was most intense on the panels in the deep position and *Balanus crenatus* individuals were generally so crowded as to make growth measurements meaningless. On these panels it was not unusual to have such a massive settlement that when the barnacles had grown to a basal diameter of from 2 to 5 mm they would all be in contact and the panel 100% covered. These animals then grew only in height and often became tall and tubular in shape. Early in March 1971 the most massive settlement of all took place and all panels exposed in the deep position were covered with young barnacles. By 1 April 1971 these panels were very heavy with an incredible growth of practically pure stands of *B. crenatus* covering every part of each panel. Some of the panels previously carried fairly extensive growths of encrusting bryozoans but the barnacle settlement was so massive as to smother and cover everything. After only one month many of these barnacles were only 2 mm in basal diameter but they extended up for 10 to 15 mm and expanded into a swollen upper end that averaged 5 mm in diameter. After two months some of these tall barnacles were up to 35 mm high and the upper end swollen to 10 mm diameter, but still with a 2 mm basal diameter. These animals were thus cone-shaped and were

totally different in form from the usual pyramidal acorn barnacle.

The numbers of settling barnacles on these deep panels made it impossible to determine "normal" growth rates. The few curves shown in Figure 10 are from individuals that were at first somewhat separated but became crowded later. Some of the barnacles that settled during November 1970 were sexually mature, despite their crowding, by 1 April 1972 and released nauplii.

Balanus tintinnabulum

Balanus tintinnabulum is a large, colorful barnacle that in Monterey Harbor grows in the low intertidal and shallow subtidal areas. It is commonly a solitary form, but occasionally several individuals will grow close together even on one another's shell. The species does not form extensive beds such as is found in *B. crenatus* and *B. glandula*.

In this investigation several *Balanus tintinnabulum* settled on panels in the shallow position during December 1970 and January 1971. Growth curves for typical individuals are shown in Figure 11. These barnacles grew rapidly and after 8 to 9 months had achieved a basal diameter of 25–35 mm. Many of the individuals followed were still alive on 1 April 1972 when the study was terminated so their longevity was not determined.

Balanus aquila

This is another large barnacle found in the lower intertidal zone down to midwater depths in Monterey Harbor. Only a few individuals of this species settled on panels during this study and their growth curves are shown in Figure 12. Settlement occurred from January through March 1971 and these barnacles grew rapidly at about the same rate as *Balanus tintinnabulum*.

Balanus flos

Balanus flos is not a common barnacle in Monterey Harbor but over the years it has been recorded periodically from fouling panels. In this study one individual settled on a panel in the intertidal staff series at the very lowest tide level. The barnacle settled in November 1970 and achieved a basal diameter of 13 mm by April 1971 but then failed to grow any more and was found to be dead on 1 July 1971 (Figure 13).

Balanus glandula

Balanus glandula is the commonest local barnacle in the high intertidal zone and occurs as dense populations on all the pilings in the harbor. This species settled on many of the panels in the intertidal staff series from 1.8 m above

MLLW (Panel #2) to 30 cm above MLLW (Panel #7). Figure 14 gives a number of growth curves for individuals that settled at various times throughout the study and at different levels. From these curves it would appear that *B. glandula* grows somewhat more slowly high up in the intertidal than it does in midregions. Several of the individuals followed were still alive after one year of observation.

Chthamalus dalli

This small brownish barnacle is commonly found interspersed with *Balanus glandula* on the piles. Individuals rarely exceed 5 mm in basal diameter. Only relatively few *Chthamalus* settled on experimental panels during this study and all of these were on the intertidal staff panel located 1.2 m above MLLW. Settlement occurred during December 1971 so these were observed for only a few months. Growth curves for two individuals of this group are shown in Figure 15.

Encrusting Ectoprocts (Bryozoa)

Encrusting bryozoans are among the most common sessile animals in Monterey Harbor and on experimental panels exposed during the past six years have often covered the panels at times to the exclusion of nearly everything else. Settlement of certain species occurred throughout the year and at nearly all depths of the harbor and often these settlements were so intense that in one or two months the young colonies were all in contact with one another. Other species settled only seasonally or sporadically and in lesser numbers.

Determining long-term growth rates and longevity for these organisms proved difficult for two reasons: first, in species that had heavy settlement the colonies soon came in contact and additional growth then became difficult or impossible, and second, in all cases the bryozoan colonies were ultimately completely overgrown and replaced by other organisms such as barnacles or ascidians.

Celleporaria brunnea

Celleporaria brunnea was the commonest encrusting bryozoan that settled on the experimental surfaces in this study. Colonies of this animal are orange in color and under magnification even tiny colonies consisting of only a few individual zooids could be recognized. Settlement was often intense and many wooden panels in the shallow and deep positions were nearly 100% covered with colonies of this species after three months exposure.

Figures 16–18 show representative growth curves for several colonies at the shallow, midwater and deep positions. In all cases an attempt was made to select colonies for observation that were somewhat separated from others, but practically invariably the colonies would ultimately come in contact with each other and growth would cease. In a few cases colonies that normally grow symmetrically at the periphery of the colony would extend up the side walls of barnacles that were already in place. The maximum size any one colony achieved during this study was 60 mm colony diameter after seven months of growth (Figure 16). Most colonies grew to 20–40 mm before coming in contact with each other. The curves indicate that growth rates are much the same throughout the year, but seem to be slower in the deeper water. Ultimately on all panels *Celleporaria* was smothered by later settling forms such as the barnacle *Balanus crenatus* or the ascidian *Ascidia ceretodes*. The flatworm *Hoploplana californica* Hyman, 1953, was commonly seen associated with *Celleporaria* and actively fed on the living zooids, yet these predators did not seem to reduce growth rates significantly for they tended to feed on the older, non-dividing individuals near the center of the colony.

On the pilings in Monterey Harbor colonies of *Celleporaria* obviously live longer and take on a different ultimate morphology than was found to be the case on the experimental panels. In places large, heavy, globular clusters of *Celleporaria* up to 60 mm in diameter can be found. These clusters are hard and come to resemble a hermatypic coral growth.

Celleporella hyalina

Celleporella hyalina was found to settle throughout much of the year on the shallow and midwater panels but in far fewer numbers than in the case of *Celleporaria brunnea*. Colonies grew rapidly to 20–30 mm diameter and growth rates were much the same at both depths and during all months (Figures 19 & 20). Colonies of *Celleporella* rarely came in contact with one another and each colony seemed to be relatively short-lived, for after 3 to 4 months of growth the colony would begin to die and would soon be covered with some other organism (particularly *Celleporaria brunnea*).

Cryptosula pallasiana

Like *Celleporaria brunnea*, the encrusting *Cryptosula pallasiana* was found to have a rapid and aggressive colony growth. *Cryptosula* settled only on shallow and midwater panels and in modest numbers. Never was one individual panel ever covered exclusively with colonies of this species but occasionally very large single colonies were observed

that were over 70 mm in maximum diameter. When *Cryptosula* colonies came in contact with each other while growing on a flat surface they tended to curl up away from the substrate and grow outward for some distance with the bases of the two colonies in contact. *Cryptosula* was often observed to grow up over large barnacles and seemed to have a more aggressive growth than any other encrusting bryozoan, for it occasionally even smothered *Celleporaria brunnea*. Figures 21 and 22 show typical growth curves for *Cryptosula*. Growth rates appear to be about the same at both depths and for most months.

Tubulipora tuba

The only encrusting cyclostomate bryozoan followed in this study was *Tubulipora tuba*. The colony of this species consists of a zoarium composed of suberect or erect white calcareous tubules. The colony is fan-shaped when young but as more tubules are added it becomes more or less circular in outline. In this investigation *T. tuba* settled on panels at all depths and often in great numbers. A week after a heavy settlement a panel often appeared to have white salt grains scattered all over and these proved to be young colonies of *T. tuba*. Individual colonies rarely achieved a maximum diameter of more than 10 mm and growth rates were much the same at all depths and at different times during the year (Figures 23–25). *Tubulipora* was not found to be aggressive in its growth habits and commonly became completely smothered by *Celleporaria* or *Cryptosula*.

Arborescent Ectoprocts (Bryozoa)

In addition to the ubiquitous encrusting forms, many species of erect, arborescent or bushy bryozoans occur in Monterey Harbor. Four of these species settled on experimental panels during this study and their growth stages were monitored. The colonies of these forms stand up from the substrate like small bushes. Some assume a relatively squat form, others are quite tall. In the measurements given in the growth charts for these animals the maximum height of the colony was used for one tall species; the maximum diameter of the bushy colonies for the squat species.

Bugula neritina

The most common of the arborescent forms settling on panels was *Bugula neritina*. The colonies were invariably brownish purple in color, even when very young, so were easy to recognize. Settlement occurred only on the shallow and midwater panels and only after the panels had been

exposed for several months. Figures 26 and 27 show typical growth curves for colonies of this species. Growth rates were approximately the same at each depth and different times during the year. Colonies on the midwater panels, however, did not grow as large or survive as long as on the shallow panels. Several colonies on the shallow panels were followed for 14 months after settlement and they were still alive and over 120 mm high when the project was terminated. Indeed, on many of the shallow panels removed on 1 April 1972 colonies of *Bugula neritina* contributed a biomass second only to ascidians.

Bugula californica

Bugula californica settled in far smaller numbers and the colonies were never as large as were those of *B. neritina*. The colonies of *B. californica* could be easily identified by the tan color, the presence of numerous golden avicularia, and the generally squat shape of the bushy colony. The species settled only on shallow and midwater panels and grew at about the same rates at both positions. More settled at the midwater depth and grew to larger size than in shallower water (Figures 28 & 29).

Crisulipora occidentalis

In earlier fouling studies in Monterey Harbor colonies of the erect bryozoan *Crisulipora occidentalis* were often the dominant organisms, particularly on the panels in the deep position, where they often made up over $\frac{3}{4}$ of the fouling biomass (HADERLIE, 1968). During this investigation far fewer larvae of this species settled on the experimental panels, yet individual colonies ultimately attained a size comparable to those seen previously. As explained above, the deep panels used in this study completely lost their accumulated fouling growth half way through the study for unknown reasons. As a result no colonies of *Crisulipora* were recorded from these panels where from previous experience one would have expected maximum settlement. Figures 30 and 31 give growth curves for the individual colonies monitored on the shallow and midwater panels.

Scrupocellaria californica

This erect species is easily distinguished from other local forms by the presence of long, whip-like and extremely mobile vibracula. The species settled in modest numbers on panels at all depths during the early spring and summer months. Growth rates were found to be very high (in one case the colony diameter increased from 10 to 30 mm in one month) and were much the same at all

depths. Figures 32 and 33 give growth curves for typical colonies.

Serpulid Worms

On the rocks and the concrete wharf pilings in Monterey Harbor, numerous species of serpulid worms are found. In fouling studies so far conducted in the harbor only a few of these have settled on wooden panels and during this investigation only two species were recorded and monitored.

Spirorbis sp.

As noted in a previous paper (HADERLIE, 1969) the calcareous tubes of the serpulid *Spirorbis* occur in at least four morphological forms in Monterey Harbor. Each tube has different sculpturing or direction of coiling; in some cases tubes are distinct mineralogically. Yet when extracted from the tubes the worms themselves appear to be identical. In previous fouling studies the *Spirorbis* with a sculptured, counter-clockwise coiled tube was most commonly encountered, but during this investigation the form most abundant on the experimental panels and the one monitored for growth had a smooth tube coiled clockwise. This form also seems to be the dominant one on the rocks in the intertidal zone of the Monterey area. Until the systematics of this genus is worked out it seems wise to merely refer to the animal as *Spirorbis* sp.

These sessile worms settled in great numbers on several of the panels in the shallow and midwater positions, especially the latter, and throughout most months of the year. They did not succeed in settling on panels that already carried an extensive fouling growth of other organisms, but were found only on newly exposed panels. Their ultimate growth potential seemed to be rarely attained, for they were practically invariably smothered by growths of bryozoans or barnacles after a few months. Figures 34 and 35 illustrate the rate of growth of typical individuals up to the time they became covered by other fouling growth.

Chitinopoma groenlandica

The only other serpulid followed during this study was *Chitinopoma groenlandica*. In deeper waters of Monterey Bay this is a very commonly encountered fouling animal, but in the harbor water it settled only in modest numbers on shallow and midwater panels during the course of this study. As in the case of *Spirorbis* sp. these organisms were often completely smothered by encrusting bryozoans after a few months, so the full growth potential was not realized (Figure 36).

Ascidians

Previous fouling studies in Monterey Harbor have shown that ascidians settle on wooden fouling panels only after several months of exposure and after a community of encrusting bryozoans has been established. This normally occurred from about the ninth to the twelfth month after initial exposure of the panel. The same observation was made during this study and by the end of 18 months the ascidians, particularly *Ascidia ceretodes*, had grown to such an extent as to dominate the fouling growth on panels at all depths.

Ascidia ceretodes

At the end of the 18 months of this investigation panels exposed at all depths were dominated by large numbers of the solitary ascidian *Ascidia ceretodes*. This was particularly true of the shallow and midwater panels, but was also true on the deep panels that had lost most of the other fouling growth. The individual animals achieved a maximum length of 50 mm, but there were often dozens of these on a single panel and the ascidians covered practically everything. *Balanus crenatus* sometimes settled in numbers on the tunics of older ascidians but the barnacles never grew to large size. Rates of growth of *Ascidia ceretodes* and the maximum size achieved was much the same at all depths (Figures 37-39).

Aplidium solidum

This ascidian has been found to occur commonly on wharf pilings and on intertidal and shallow subtidal experimental panels in Monterey Harbor. In some cases, at the end of one year, large slabs of this compound ascidian dominated intertidal panels (HADERLIE, 1968). During the course of the present study this species did not settle on the intertidal panels but did settle in small numbers on shallow and midwater panels after one year of exposure. As can be seen from Figure 40, growth rates were comparable at both depths and were often spectacular, giving rise to very large colonies in a period of a few months.

Ciona intestinalis

On the styrofoam floats in the Monterey Marina the large solitary ascidian *Ciona intestinalis* is a very common animal, yet during the past six years of study of foulers settling on panels in the harbor this species was not encountered until the present investigation. On a few of the shallow and midwater panels that had been exposed for

about eleven months several individuals of *Ciona* settled and rapidly grew to a maximum size of 112 mm in length. The rate of growth was similar at each depth (Figure 41).

Styela montereyensis

This large stalked ascidian is a common member of the wharf piling fauna and often grows to a length of 25 cm or more. During the course of this study *Styela* settled on both shallow and midwater panels, usually only one or two individuals per panel. Some of these settled during the 8th month of exposure of the panels. None of the panels remained in the water long enough for the animals to achieve full growth, but several were over 120 mm long when the panels were removed. The rate of growth was similar at both depths (Figure 42).

Sponges

Two species of sponges settled on the experimental panels during this study. These were often observed for several months before they were either overgrown or broke off and were lost.

Rhabdodermella nuttingi

Figure 43 illustrates the growth rates of several individuals of the slender, vase-like *Rhabdodermella nuttingi*. On the deep panels these sponges appeared to have a more rapid rate of growth than on the shallow panels. Curiously none of this species appeared on the midwater surfaces.

Leuconia heathi

This sponge has a globose or pear shape and settled in modest numbers on a few of the shallow and midwater panels. It had a growth rate similar to that of *Rhabdodermella* on the deep panels (Figure 44).

SUMMARY

1 During the 18-month period from 1 October 1970 to 1 April 1972 a series of collecting surfaces were exposed to the marine environment in Monterey Harbor with the objective of collecting sessile or sedentary marine invertebrates that attached to the surfaces.

2 Experimental surfaces consisted of douglas fir timbers and panels. The timbers were arranged into experimental piles and extended from the bottom up through the water column to above high tide level. Panels were exposed in

racks continuously through the intertidal zone and at three selected subtidal depths.

3 Individual invertebrates of many species that settled on the experimental surfaces were marked and measured monthly to determine growth rates and longevity. Growth curves for individuals or colonies of various species that settled at different depths and at different times throughout the year were prepared from data collected.

4 Depth preference for different species and ecological succession of communities were noted and studied.

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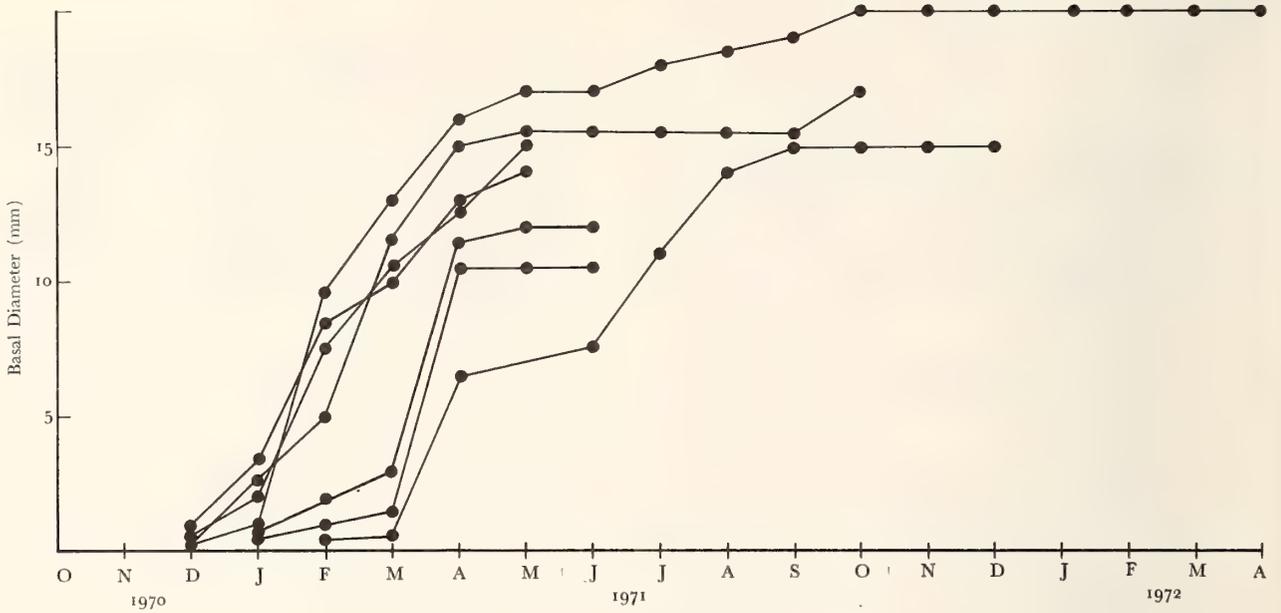


Figure 8
Balanus crenatus
growth curves (shallow water panels)

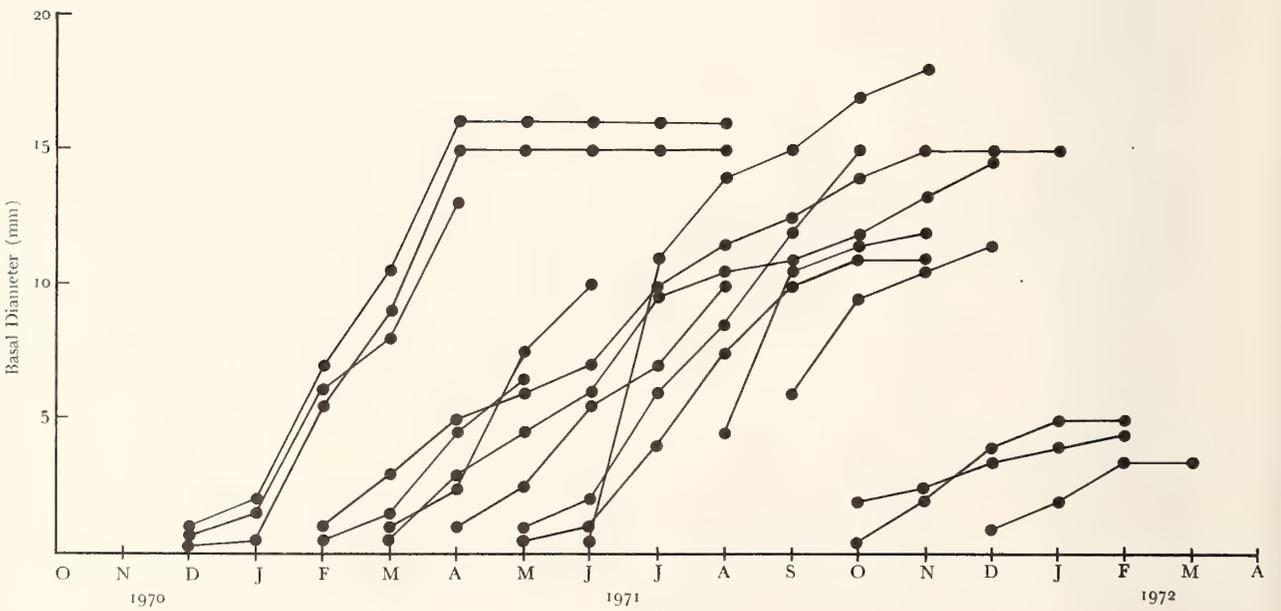
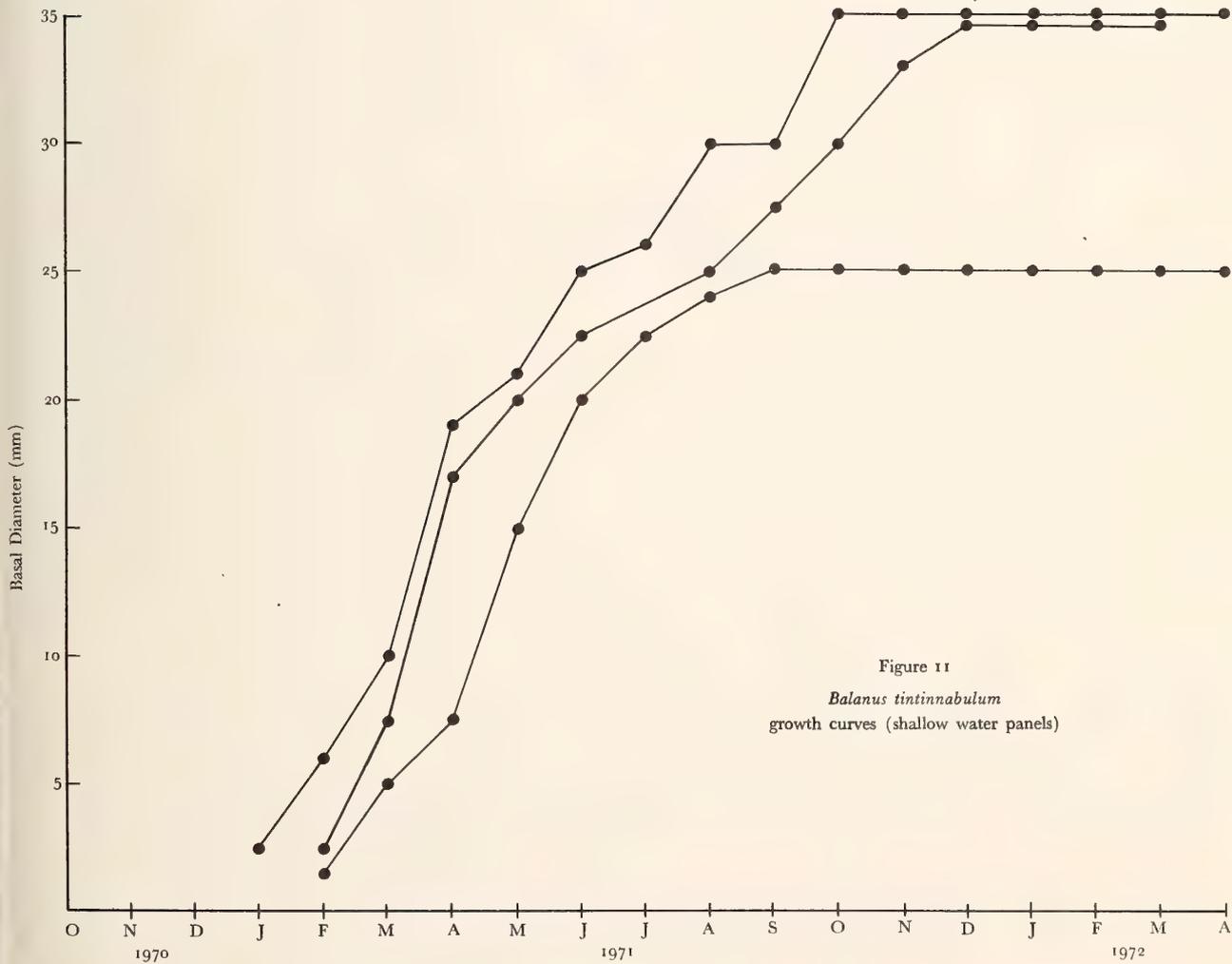
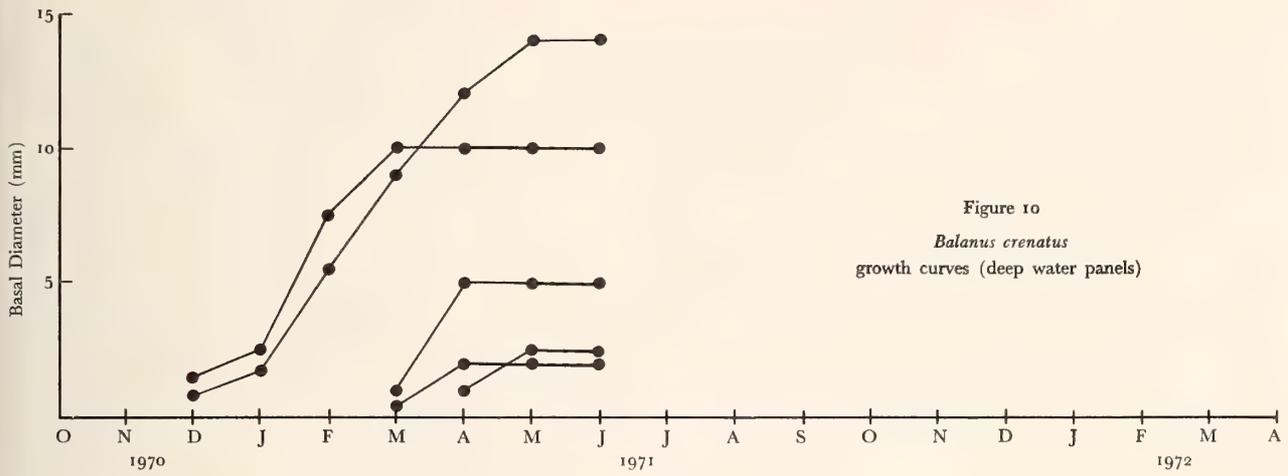
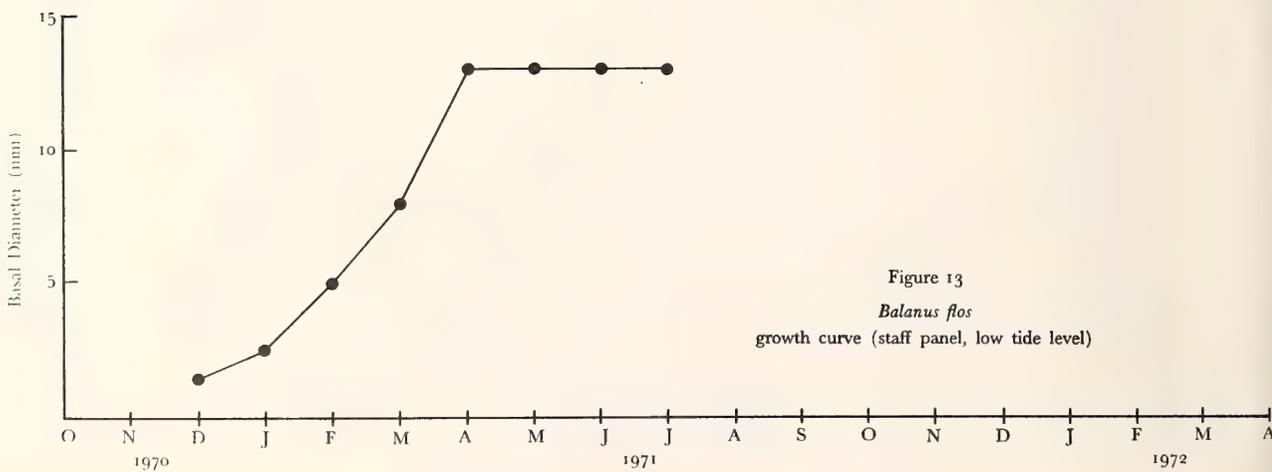
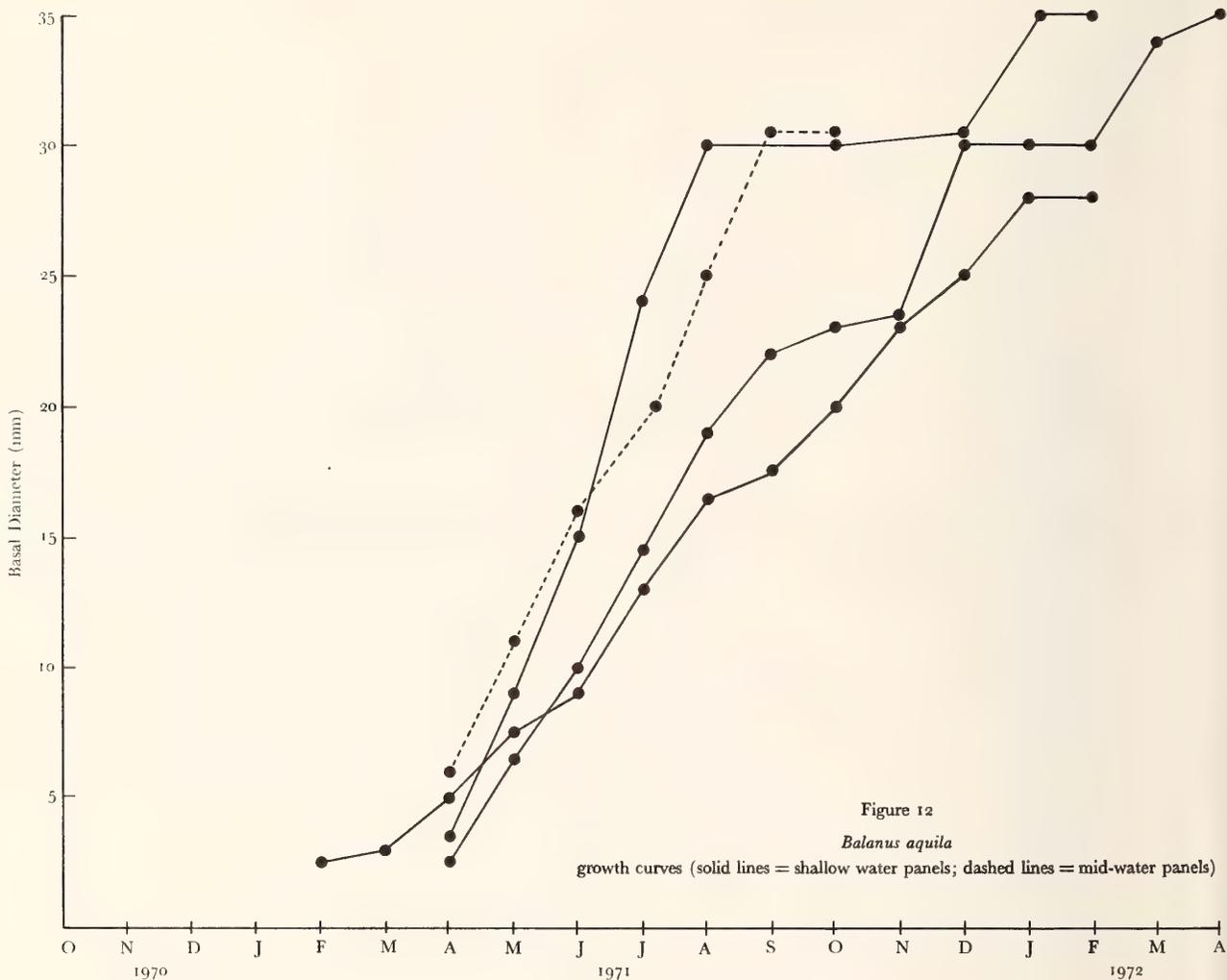


Figure 9
Balanus crenatus
growth curves (mid-water panels)





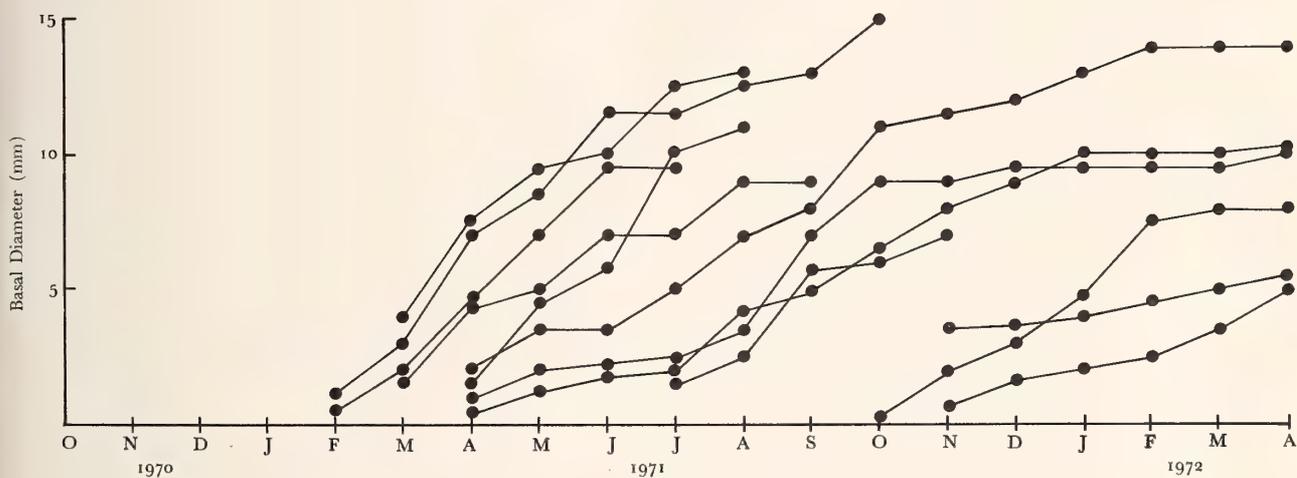


Figure 14

Balanus glandula

growth curves (intertidal staff panels; numbers refer to height of panel:
 2: 1.57m above MLLW; 3: 1.5m above MLLW; 4: 1.2m above MLLW;
 5: 0.9m above MLLW; 6: 0.67m above MLLW; 7: 0.3m above MLLW)

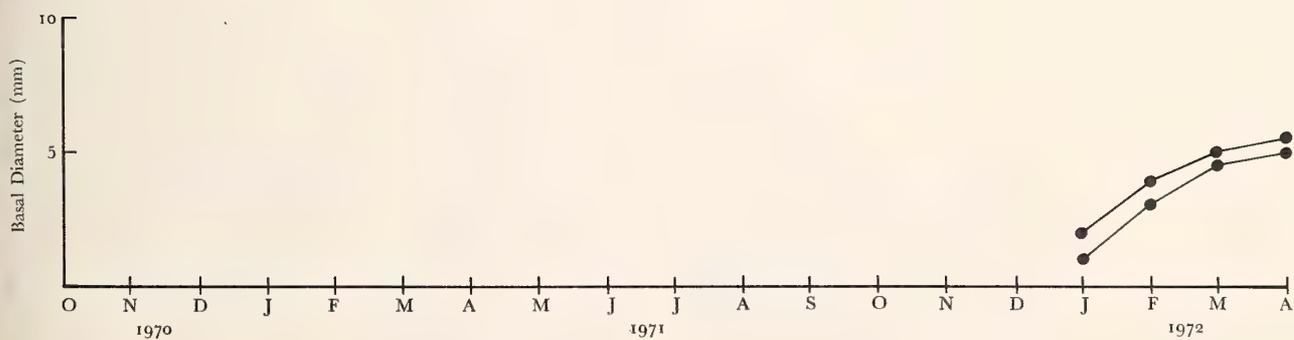


Figure 15

Chthamalus dalli

growth curves (staff panel; 1.2m above MLLW)

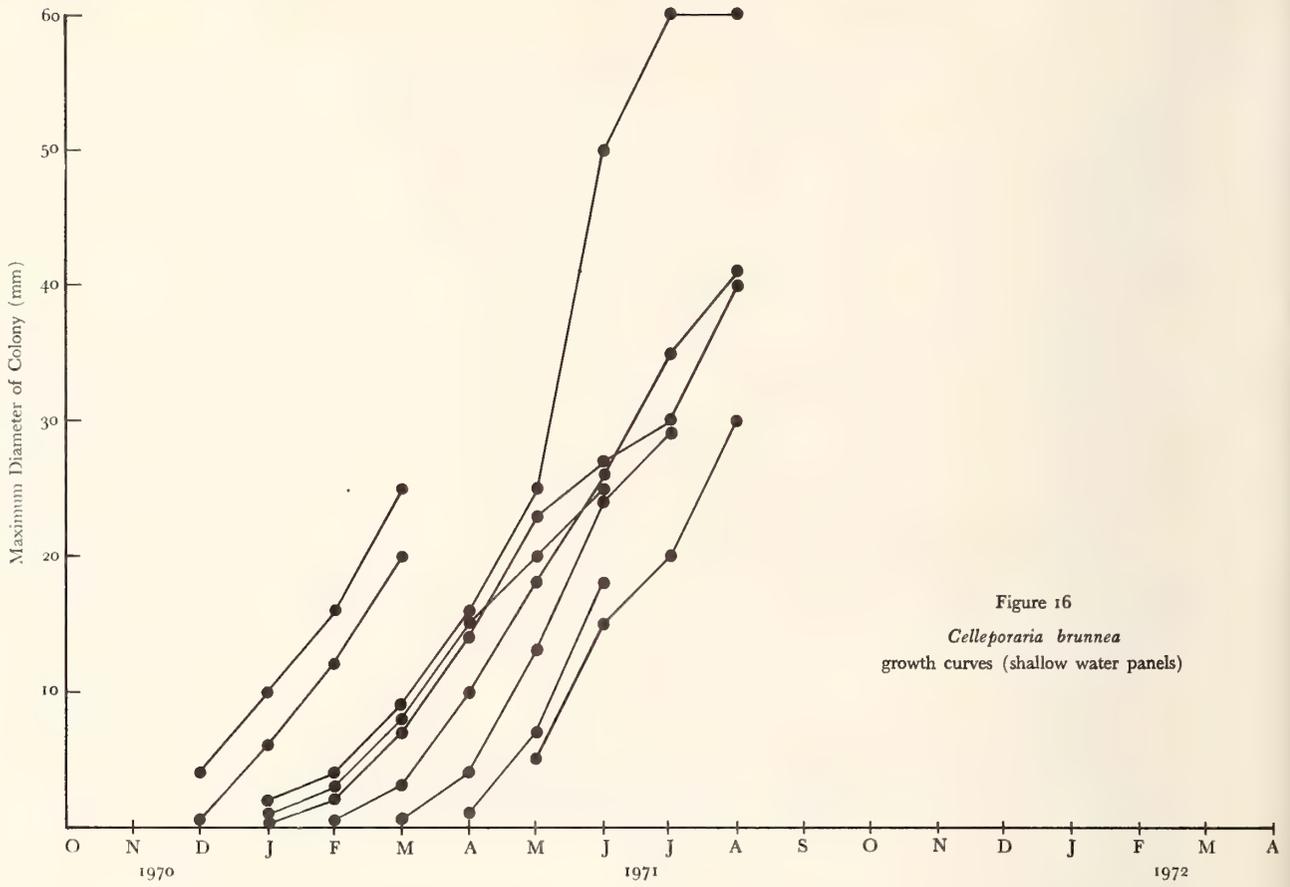


Figure 16
Celleporaria brunnea
growth curves (shallow water panels)

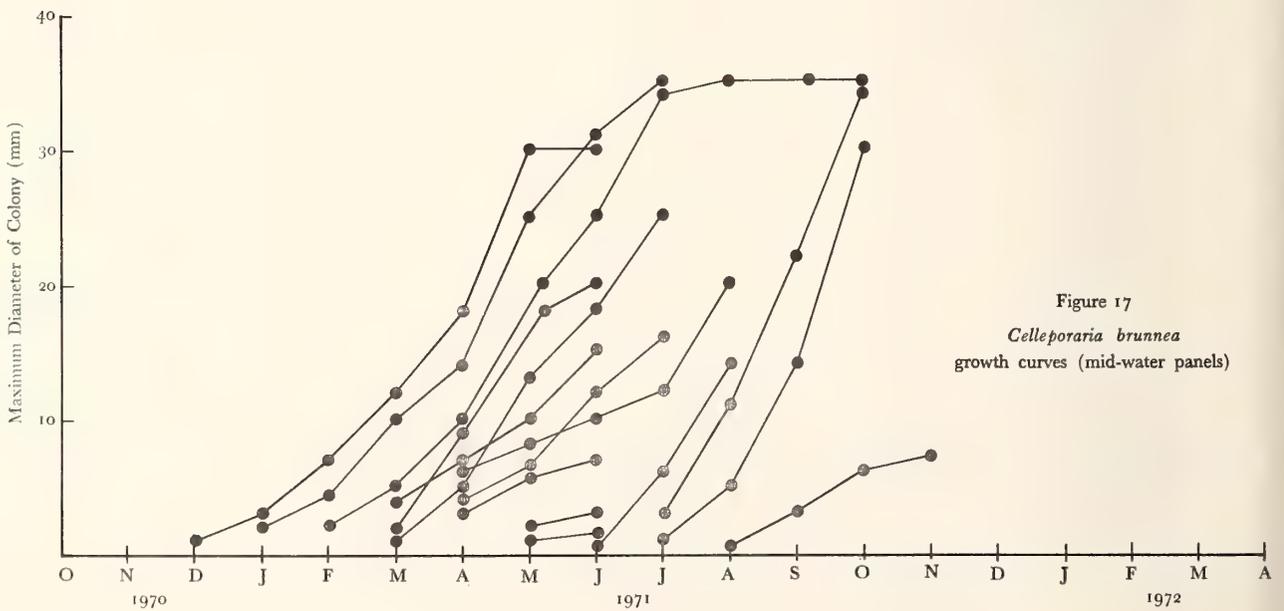


Figure 17
Celleporaria brunnea
growth curves (mid-water panels)

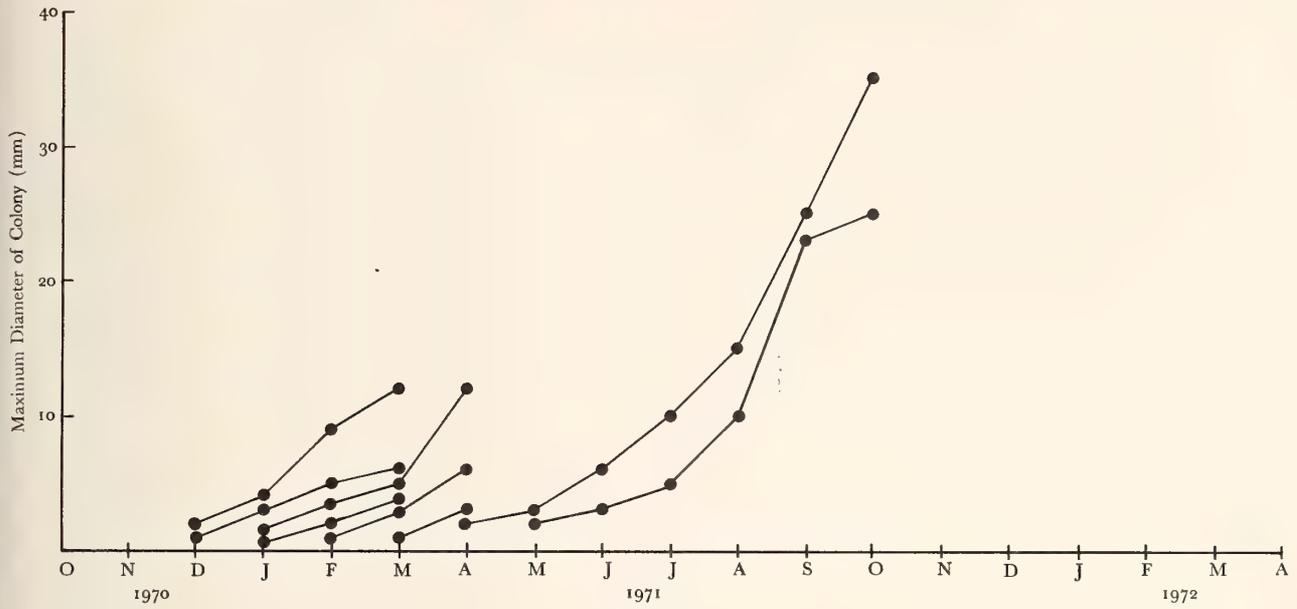


Figure 18
Celleporaria brunnea
growth curves (deep water panels)

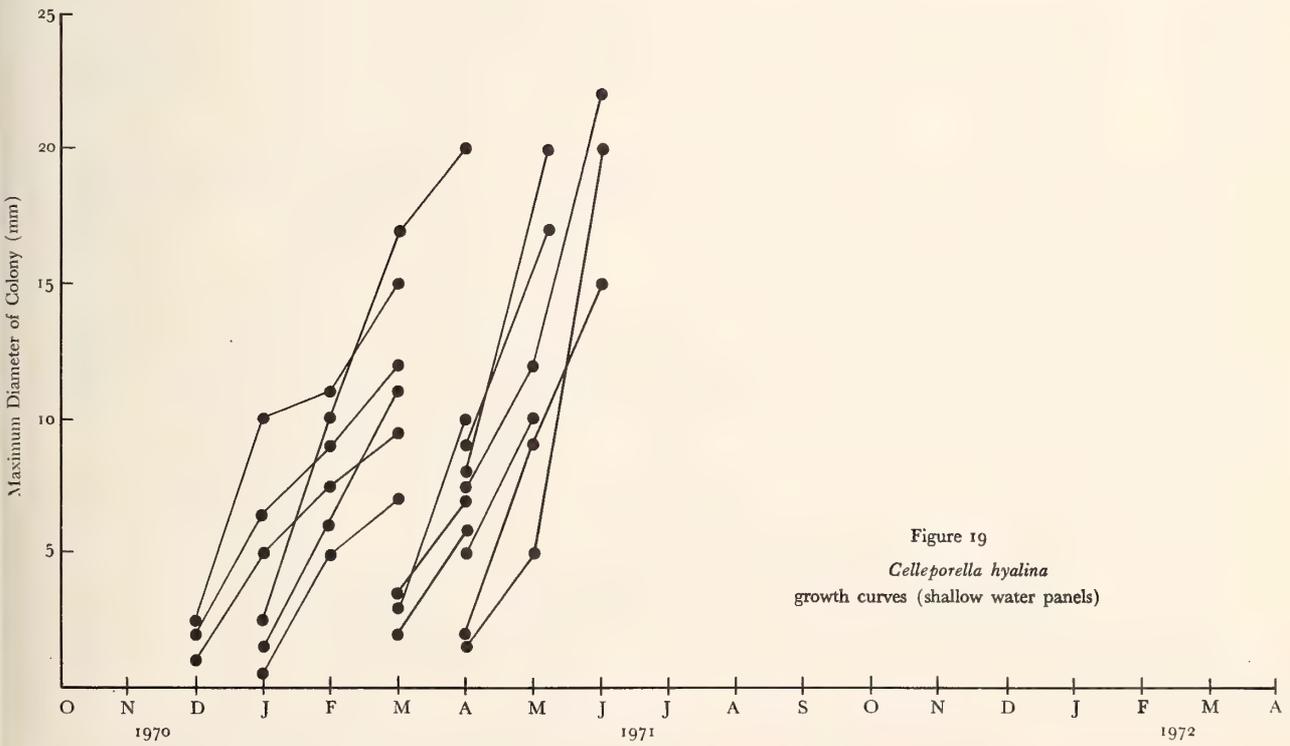


Figure 19
Celleporella hyalina
growth curves (shallow water panels)

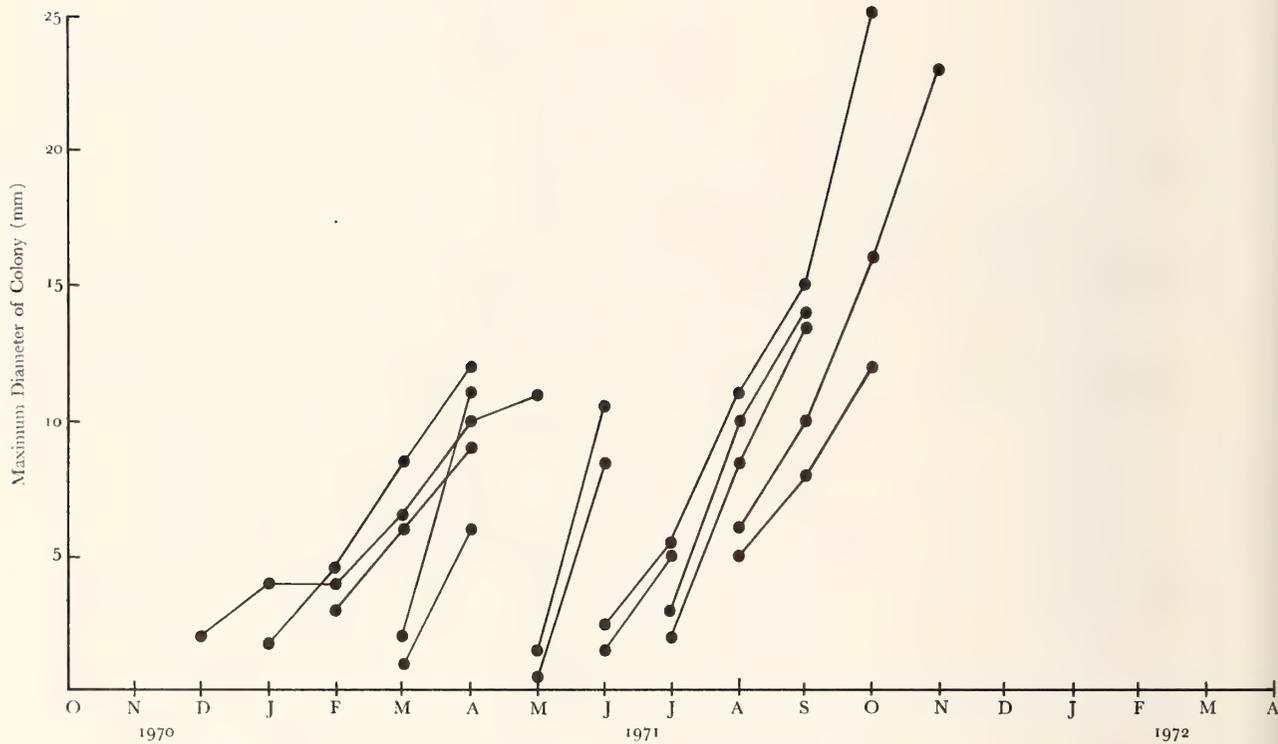


Figure 20
Celleporella hyalina
 growth curves (mid-water panels)

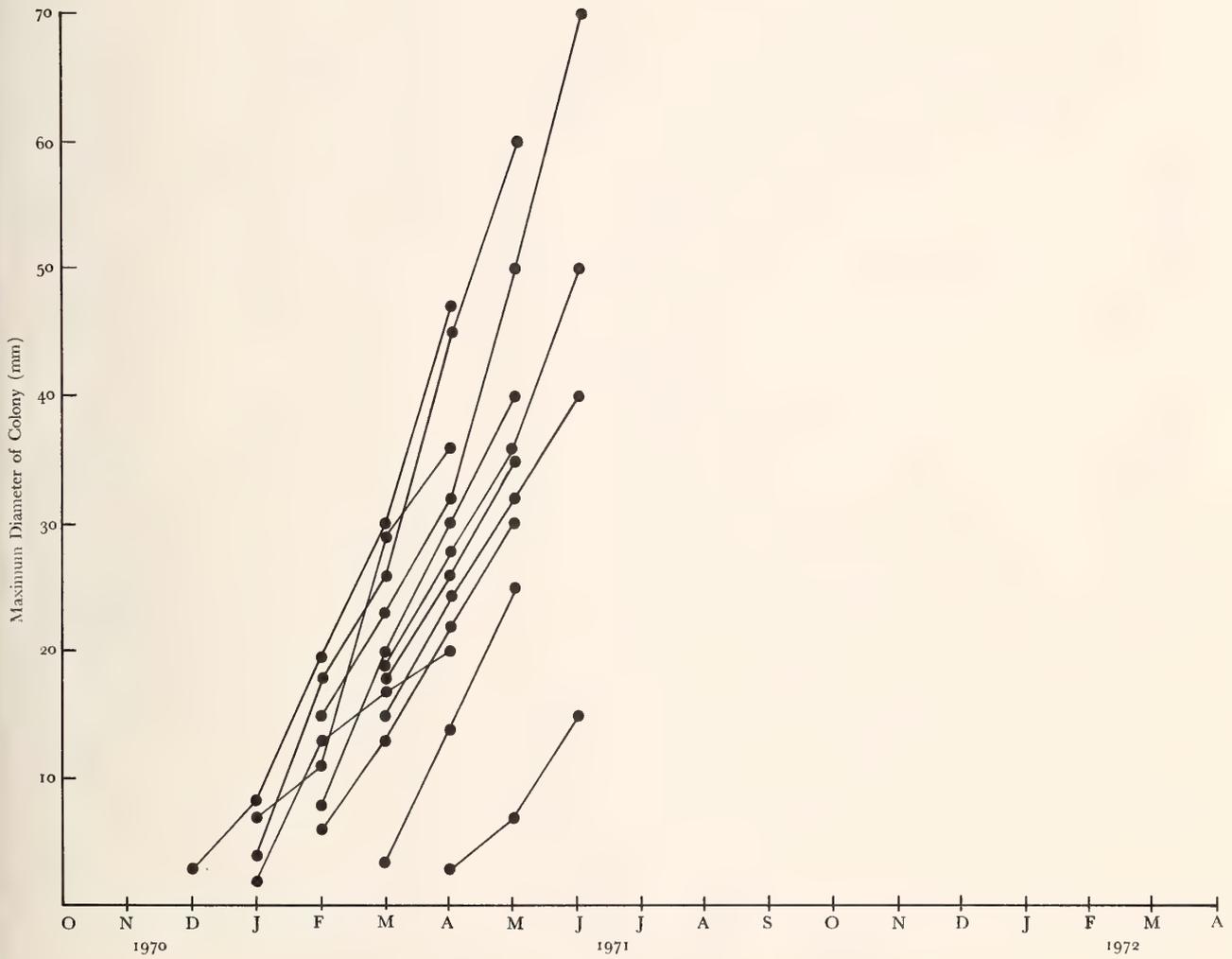


Figure 21
Cryptosula pallasiana
growth curves (shallow water panels)

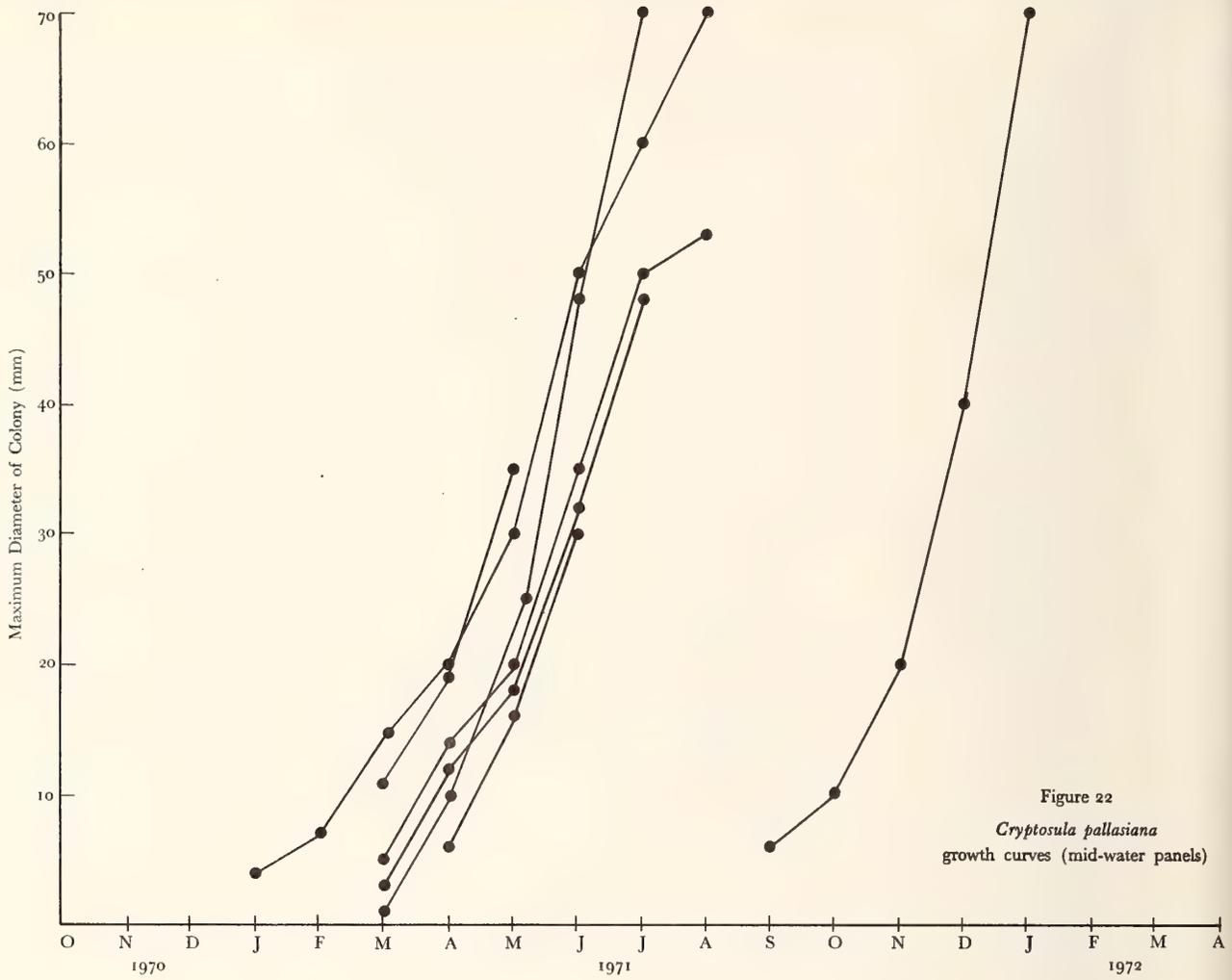


Figure 22
Cryptosula pallasiana
growth curves (mid-water panels)

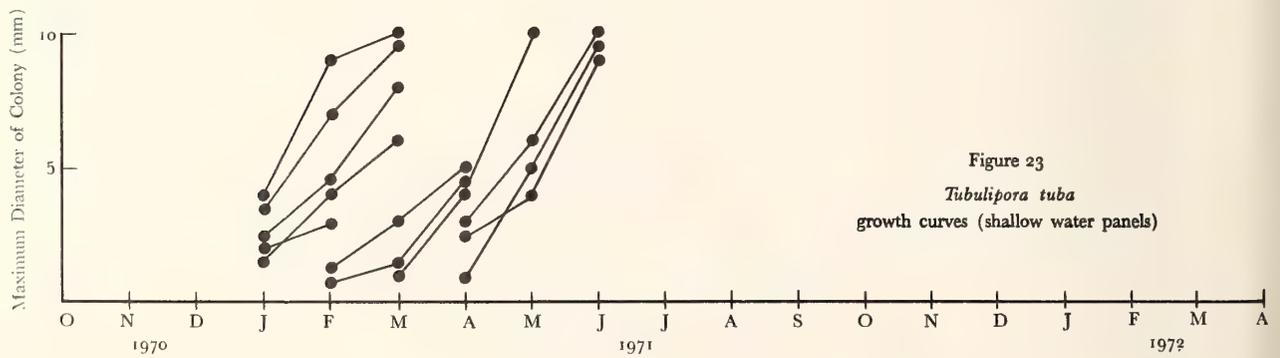


Figure 23
Tubulipora tuba
growth curves (shallow water panels)

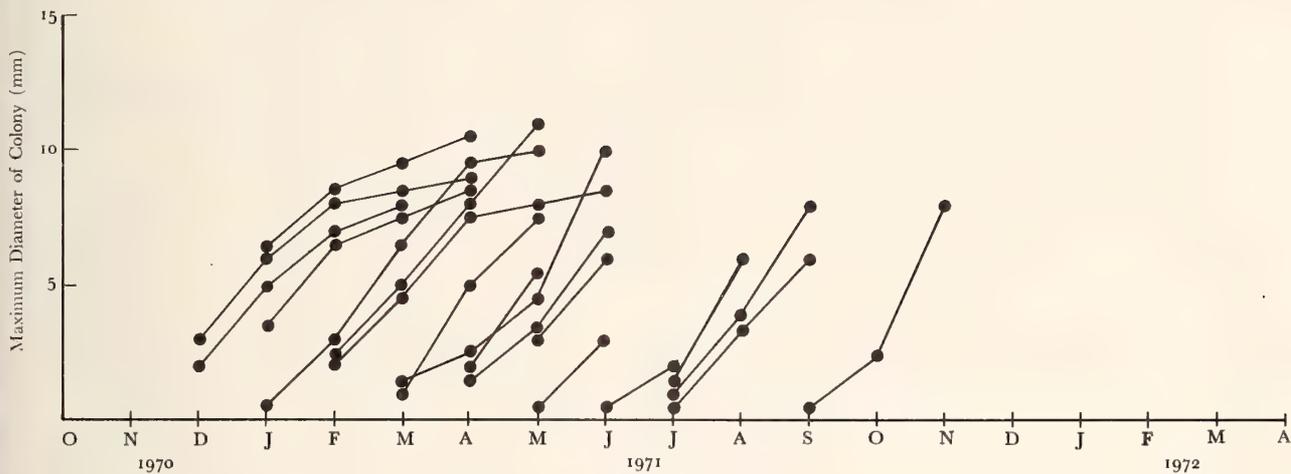


Figure 24
Tubulipora tuba
growth curves (mid-water panels)

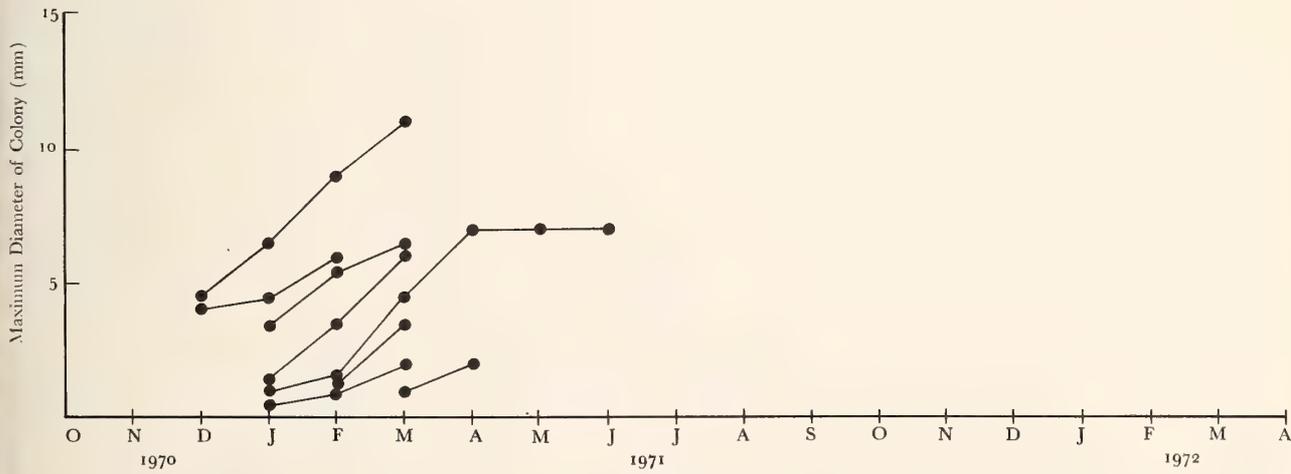


Figure 25
Tubulipora tuba
growth curves (deep water panels)

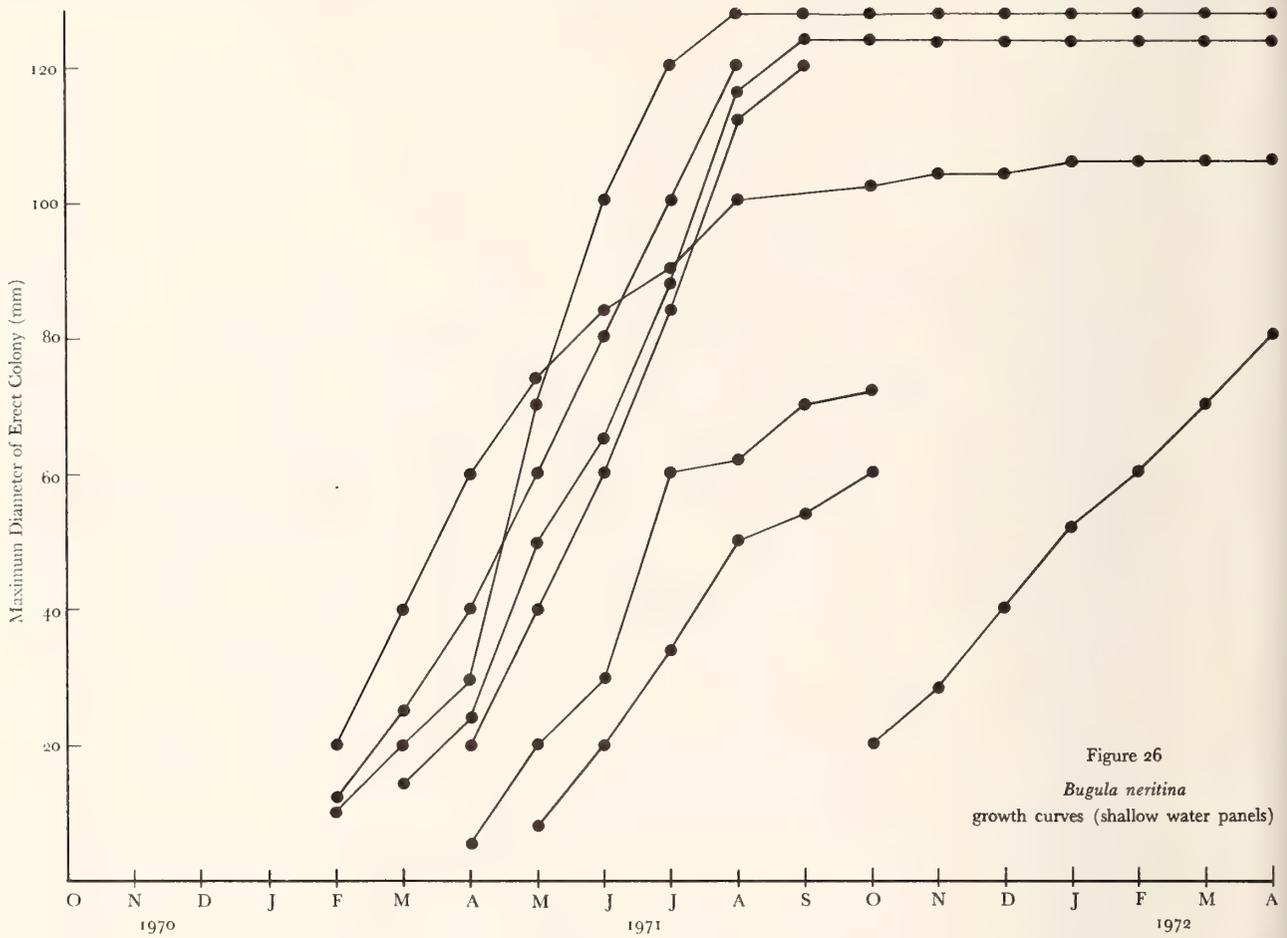


Figure 26
Bugula neritina
growth curves (shallow water panels)

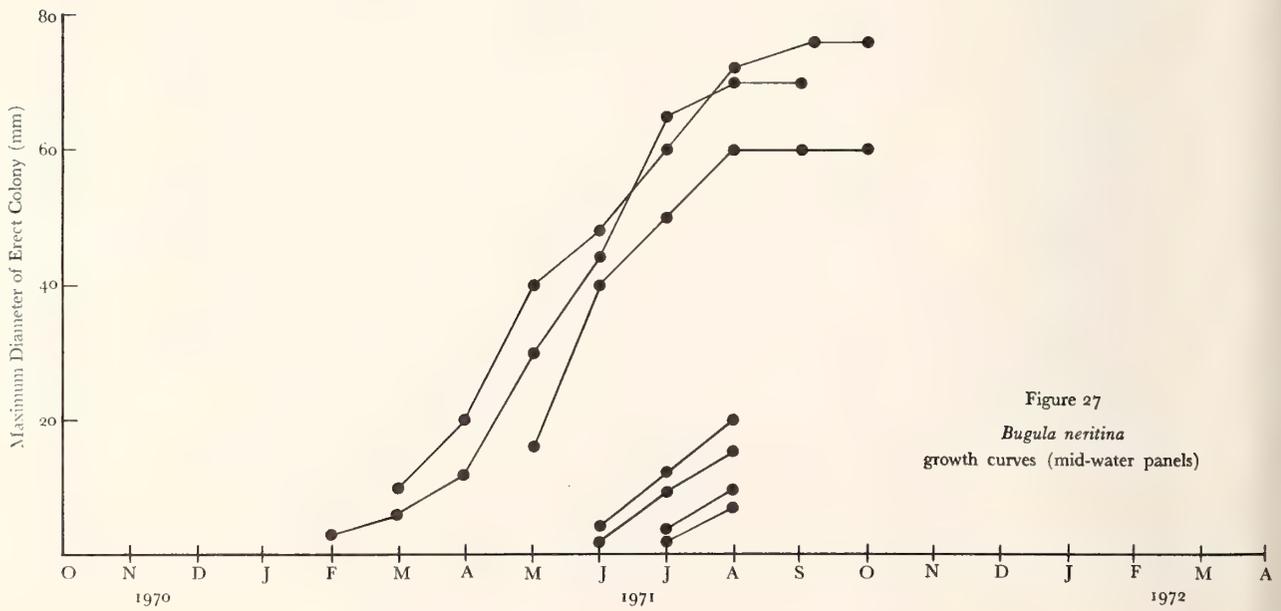


Figure 27
Bugula neritina
growth curves (mid-water panels)

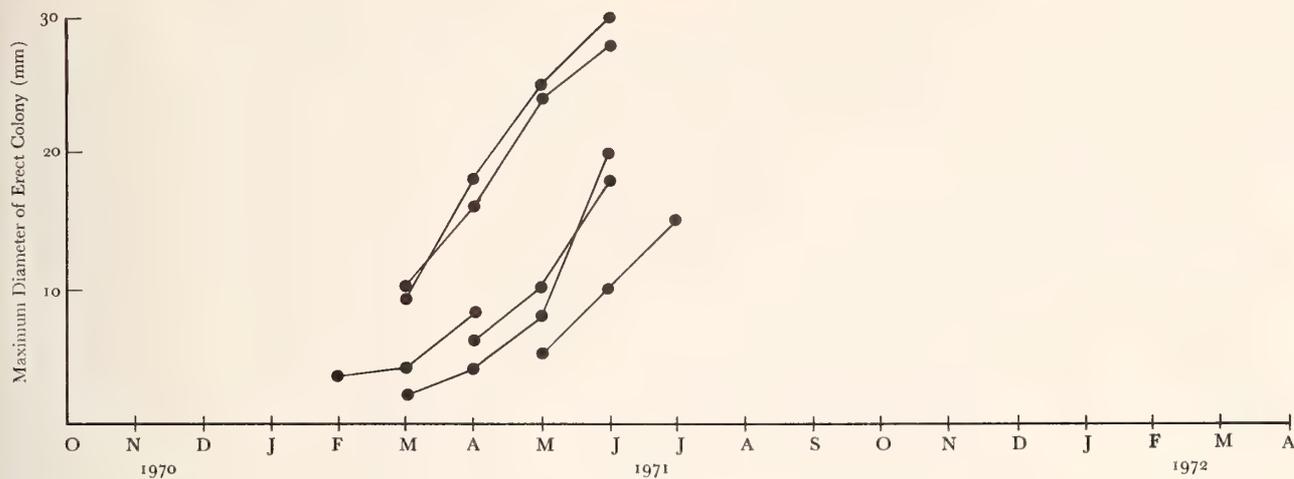


Figure 28

Bugula californica
growth curves (shallow water panels)

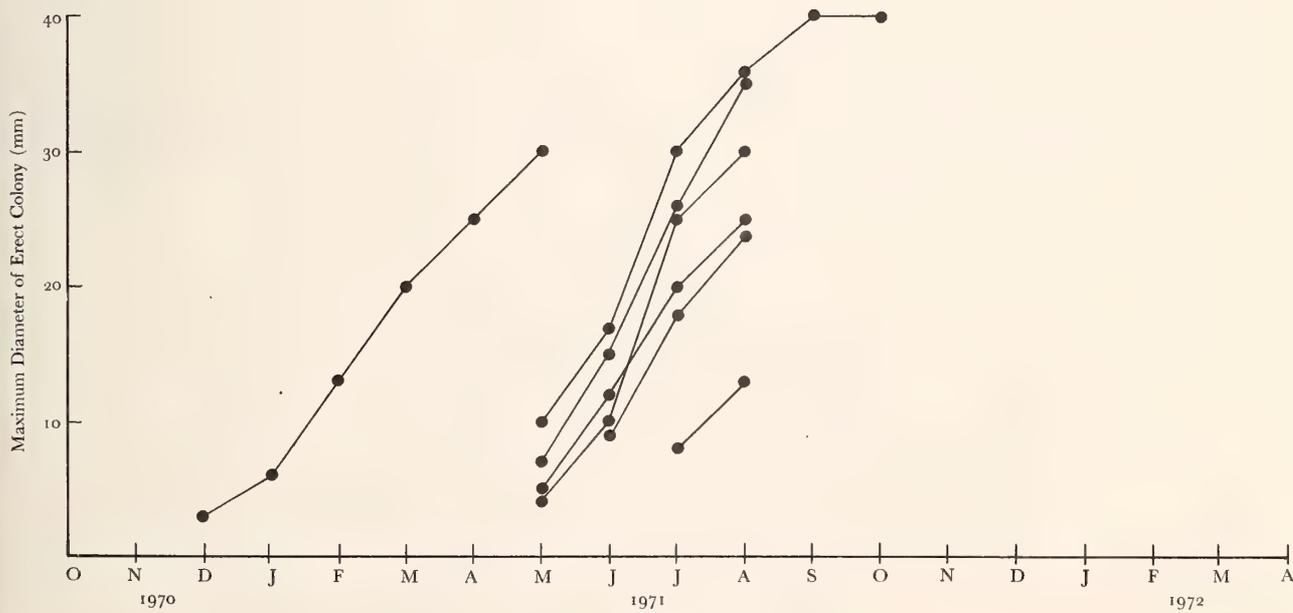


Figure 29

Bugula californica
growth curves (mid-water panels)

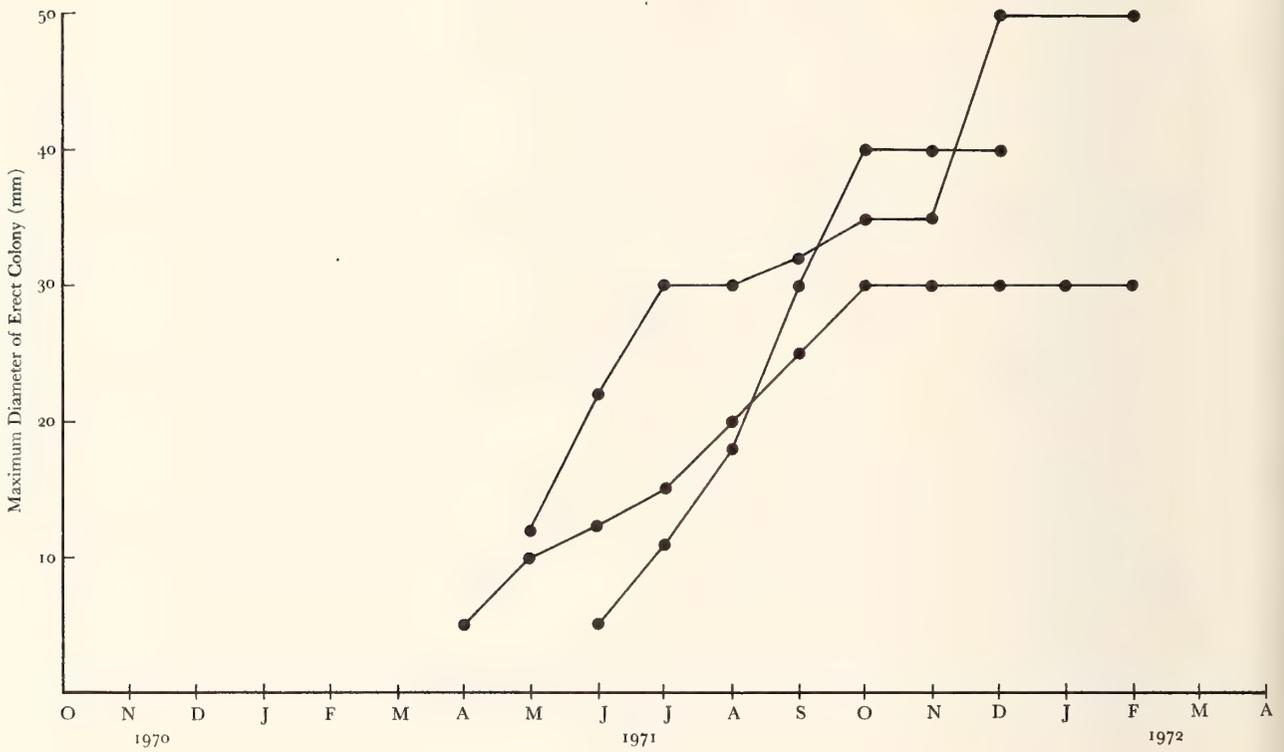


Figure 30
Crisulipora occidentalis
growth curves (shallow water panels)

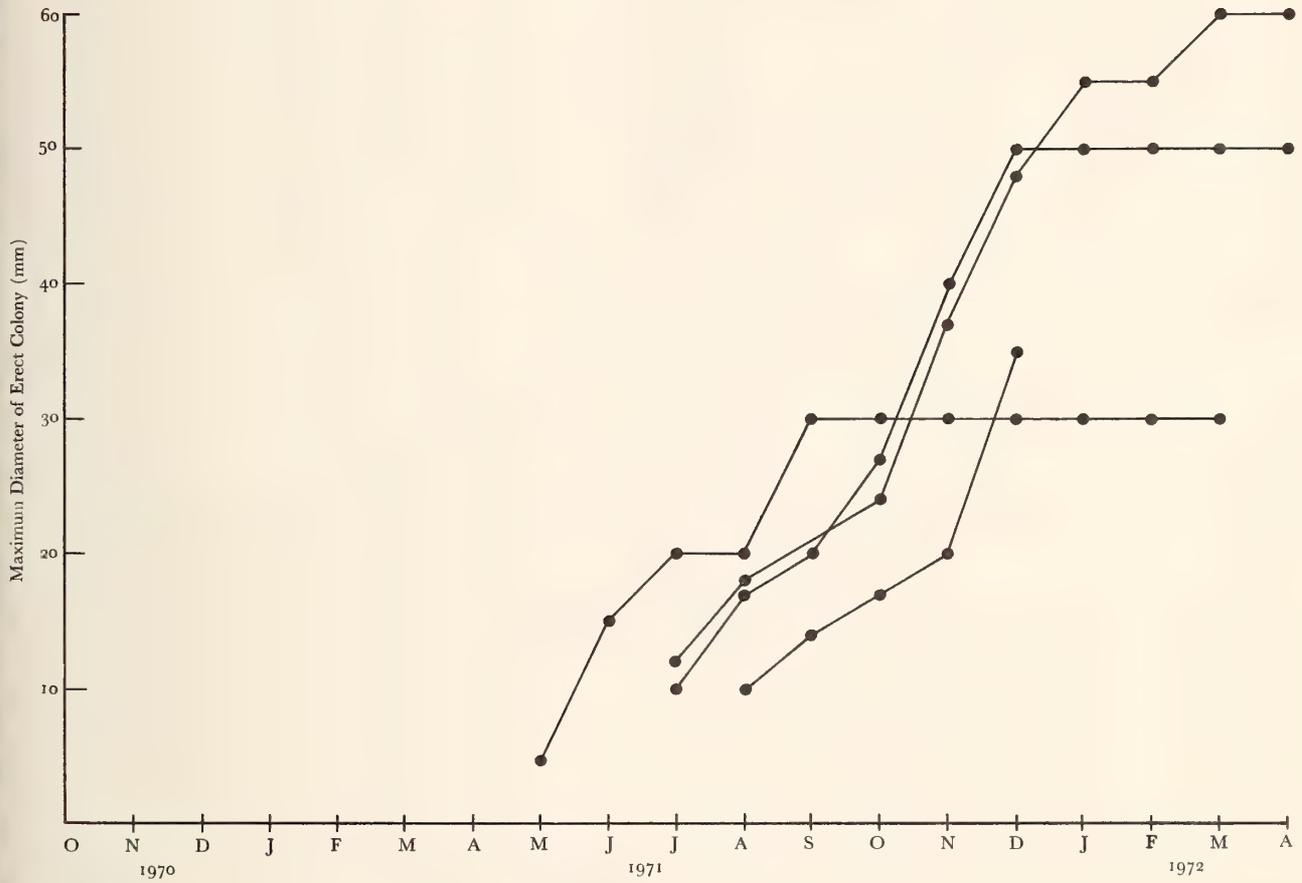


Figure 31
Crisulipora occidentalis
 growth curves (mid-water panels)

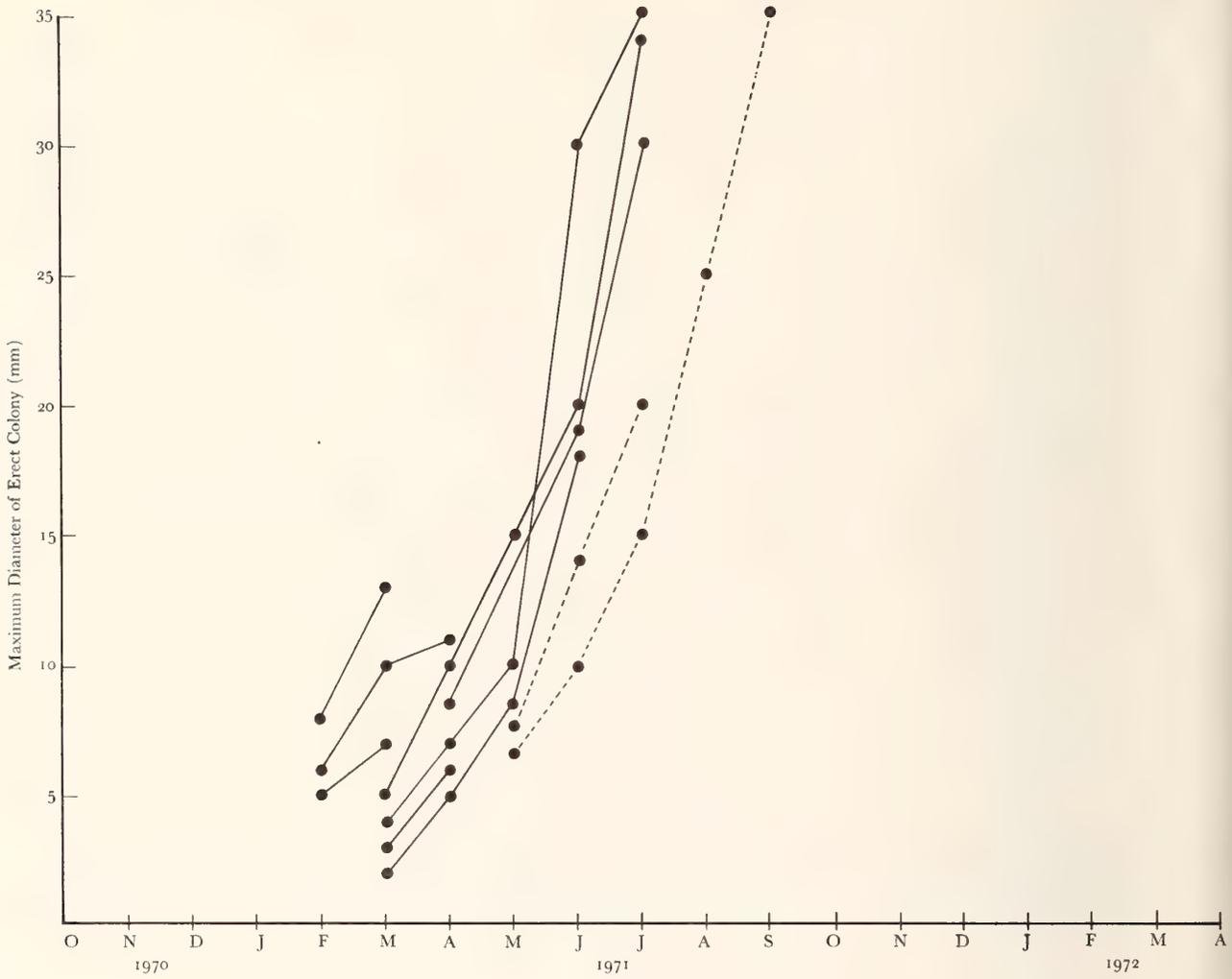


Figure 32
Scrupocellaria californica
growth curves (solid lines = shallow water panels; dashed lines = deep water panels)

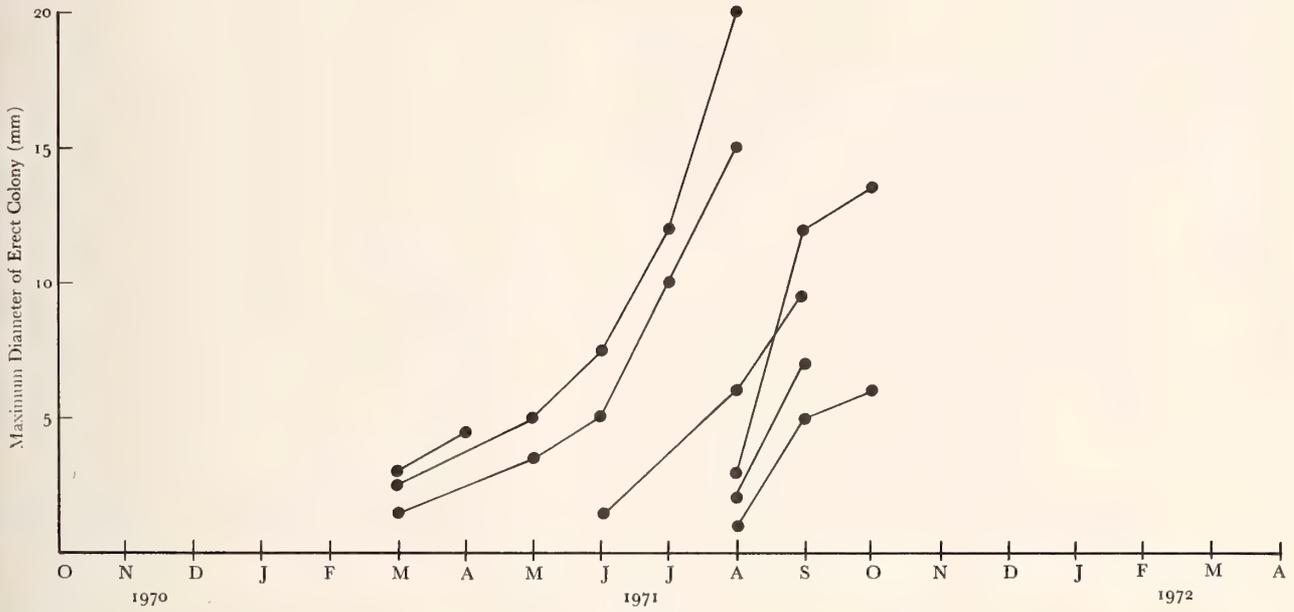


Figure 33

Scrupocellaria californica
growth curves (mid-water panels)

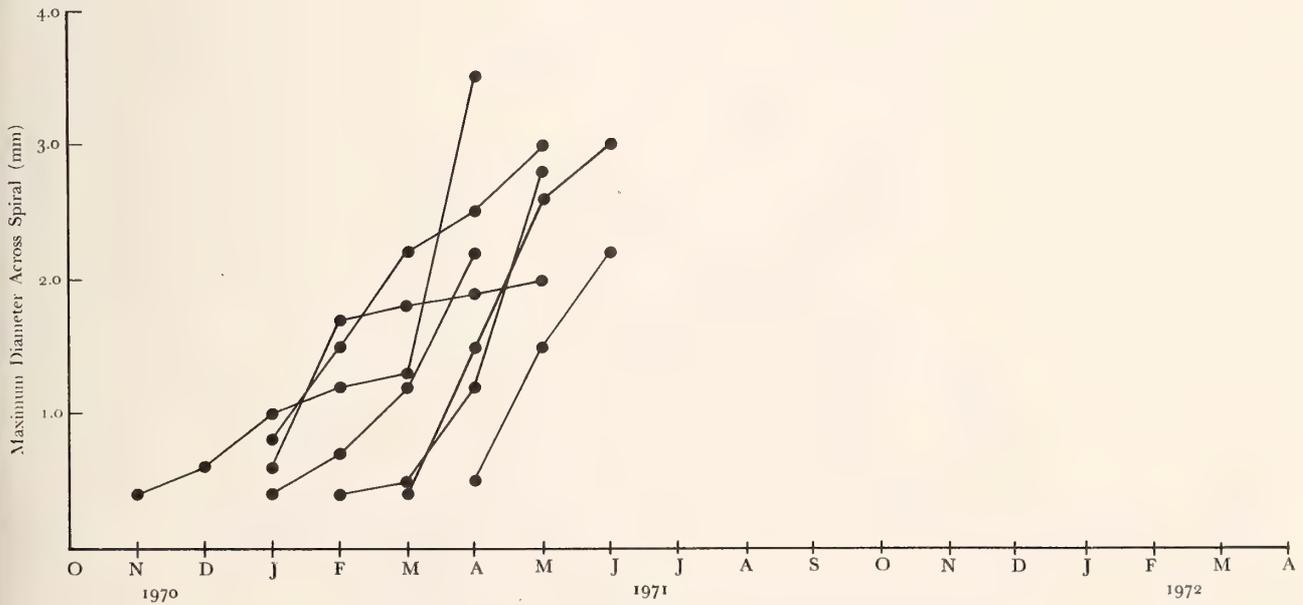


Figure 34

Spirorbis sp.
growth curves (shallow water panels)

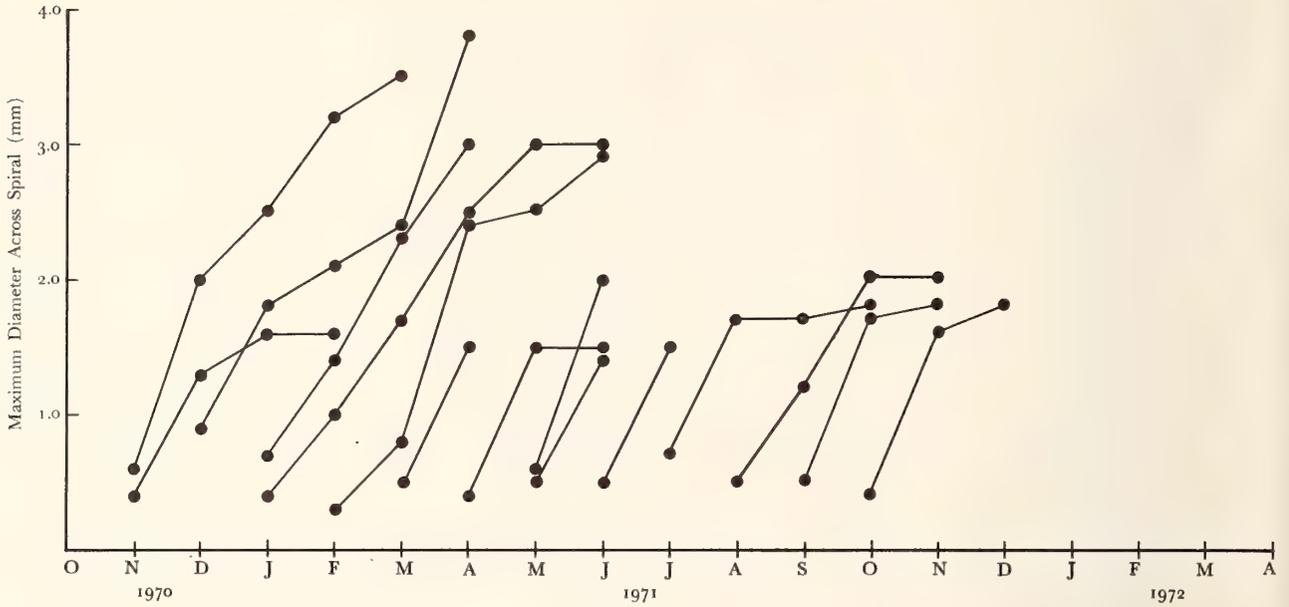


Figure 35
Spirorbis sp.
growth curves (mid-water panels)

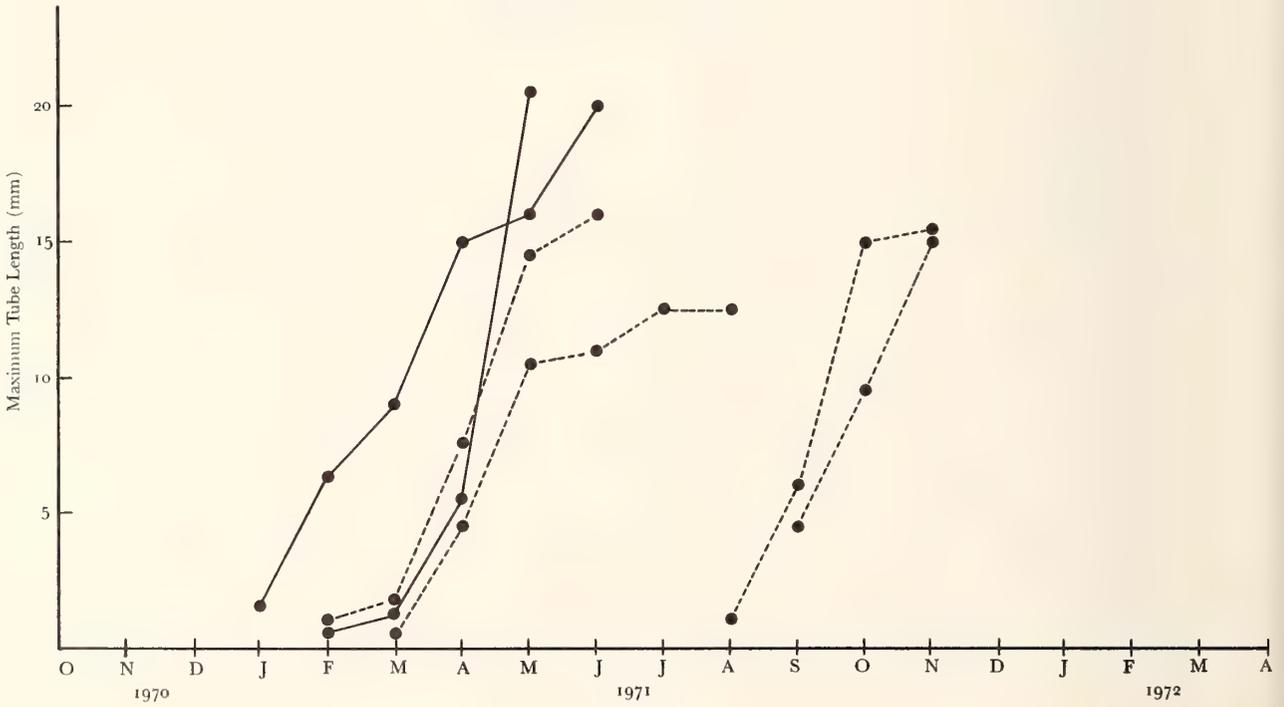


Figure 36
Chitinopoma groenlandica
growth curves (solid lines = shallow water panels; dashed lines = mid-water panels)

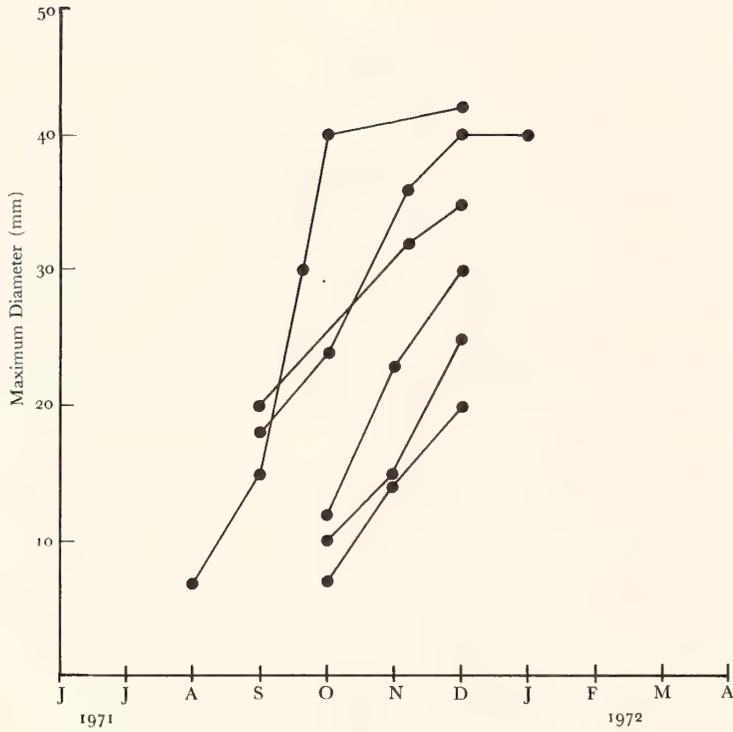


Figure 39
Ascidia ceretodes
growth curves (deep water panels)

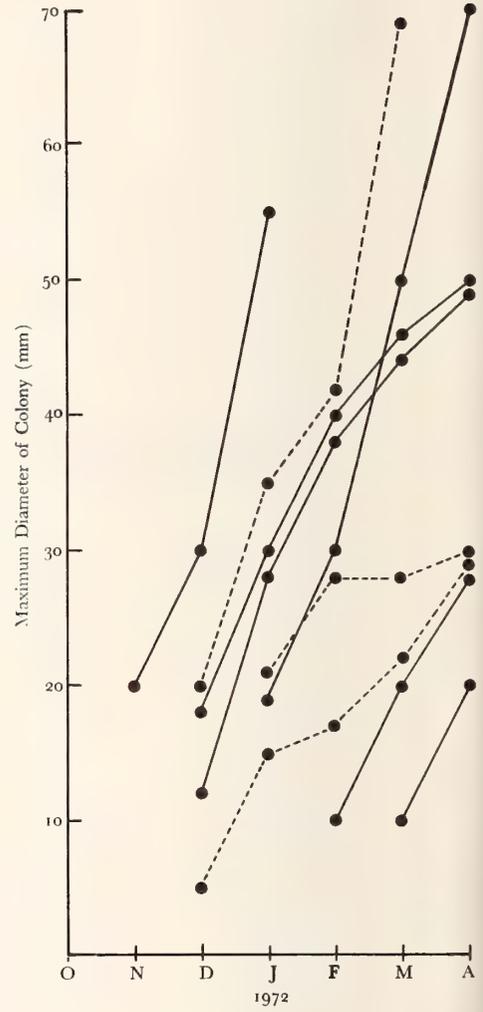


Figure 40
Aplidium solidum
growth curves (solid lines = shallow water panels; dashed lines = mid-water panels)

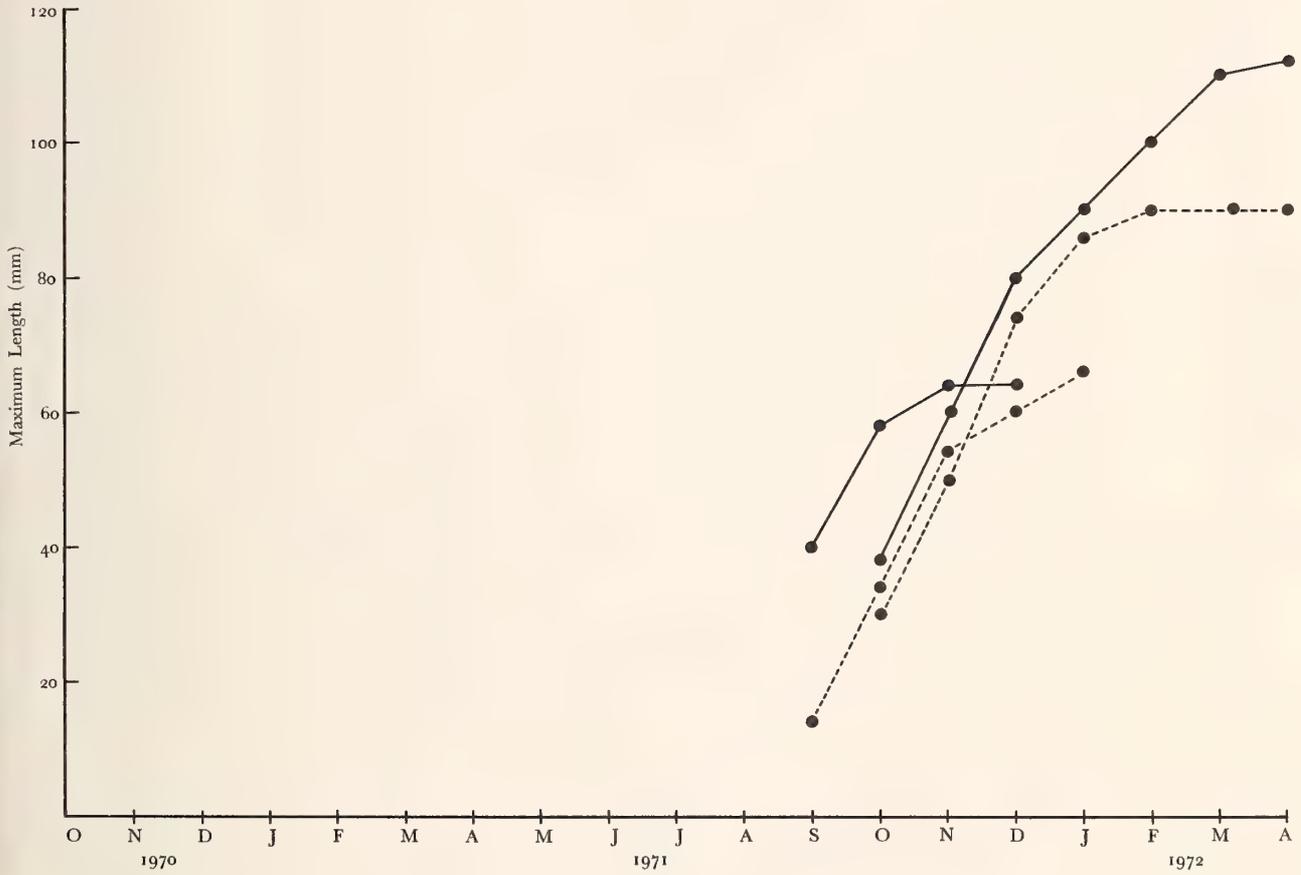


Figure 41
Ciona intestinalis
growth curves (solid lines = shallow water panels; dashed lines = mid-water panels)

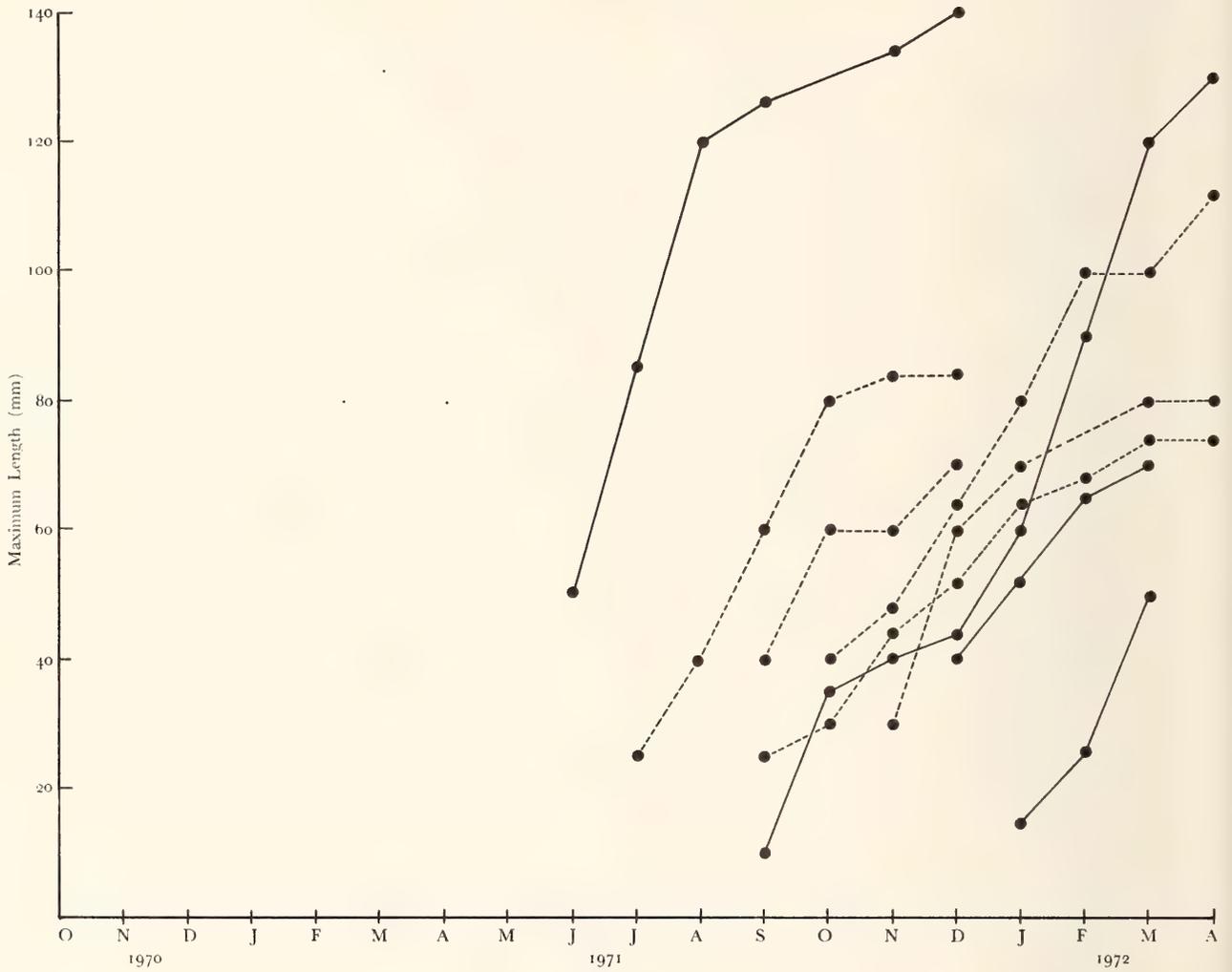


Figure 42
Styela montereyensis
growth curves (solid lines = shallow water panels; dashed lines = mid-water panels)

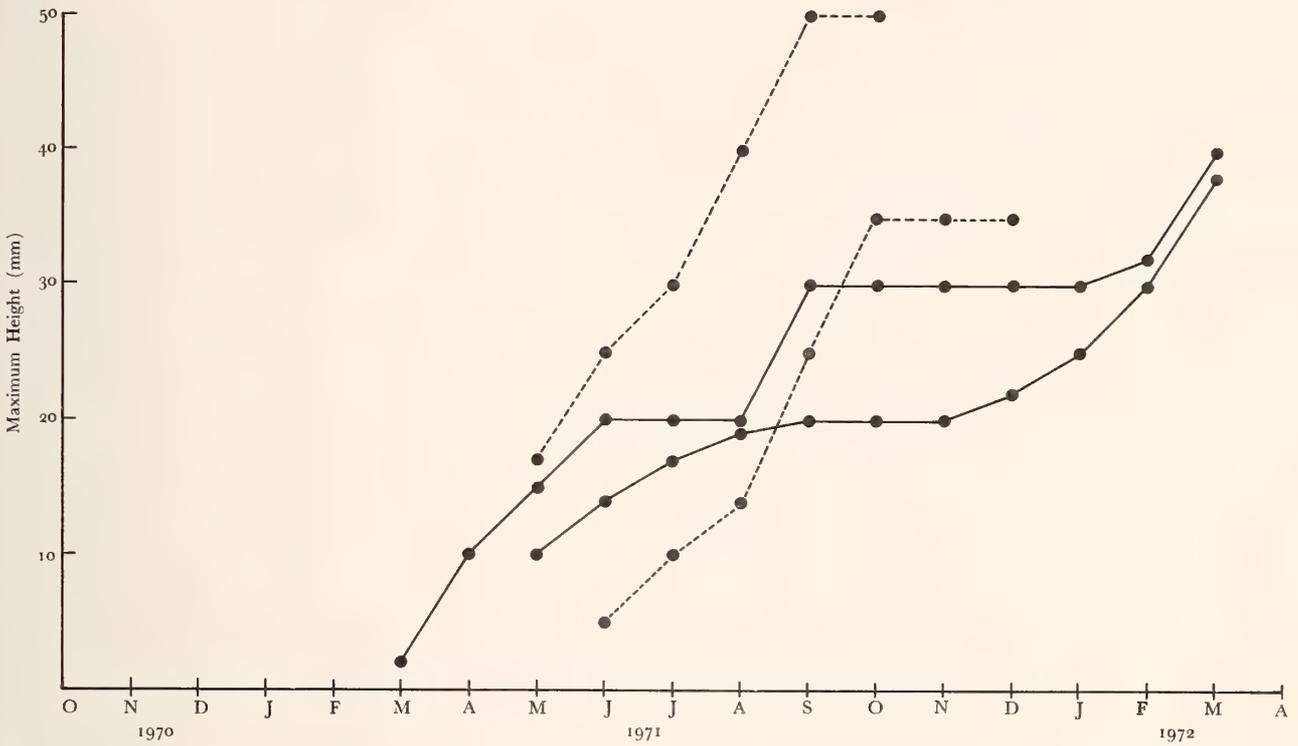


Figure 43

Rhabdodermella nuttingi

growth curves (solid lines = shallow water panels; dashed lines = deep water panels)

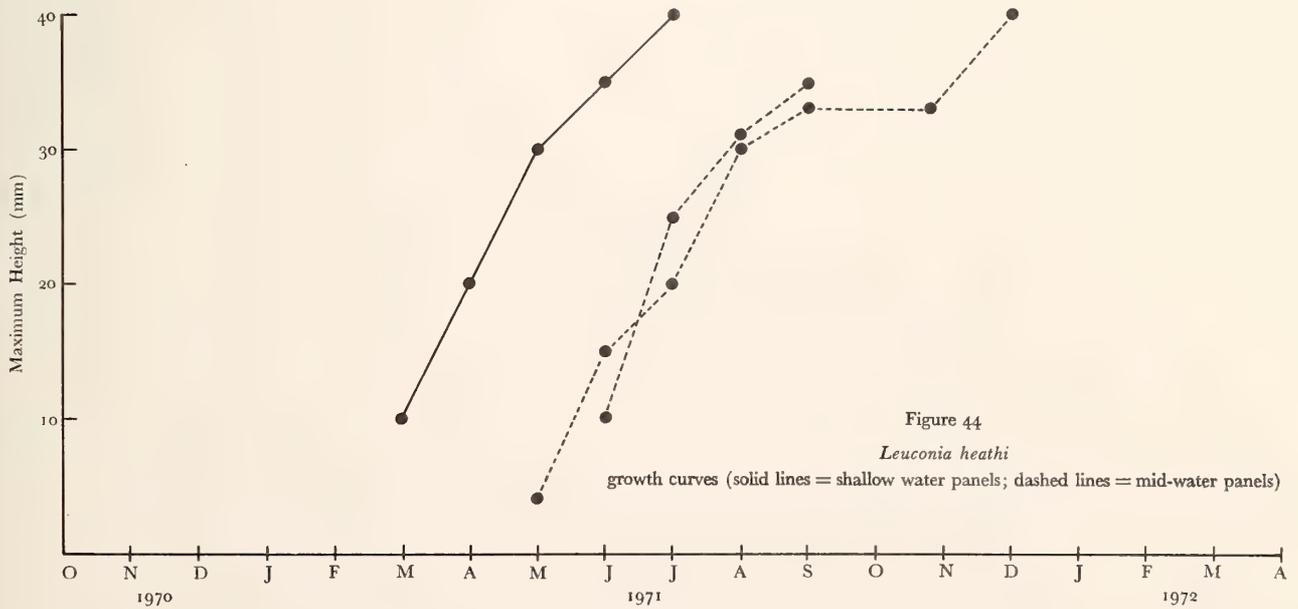
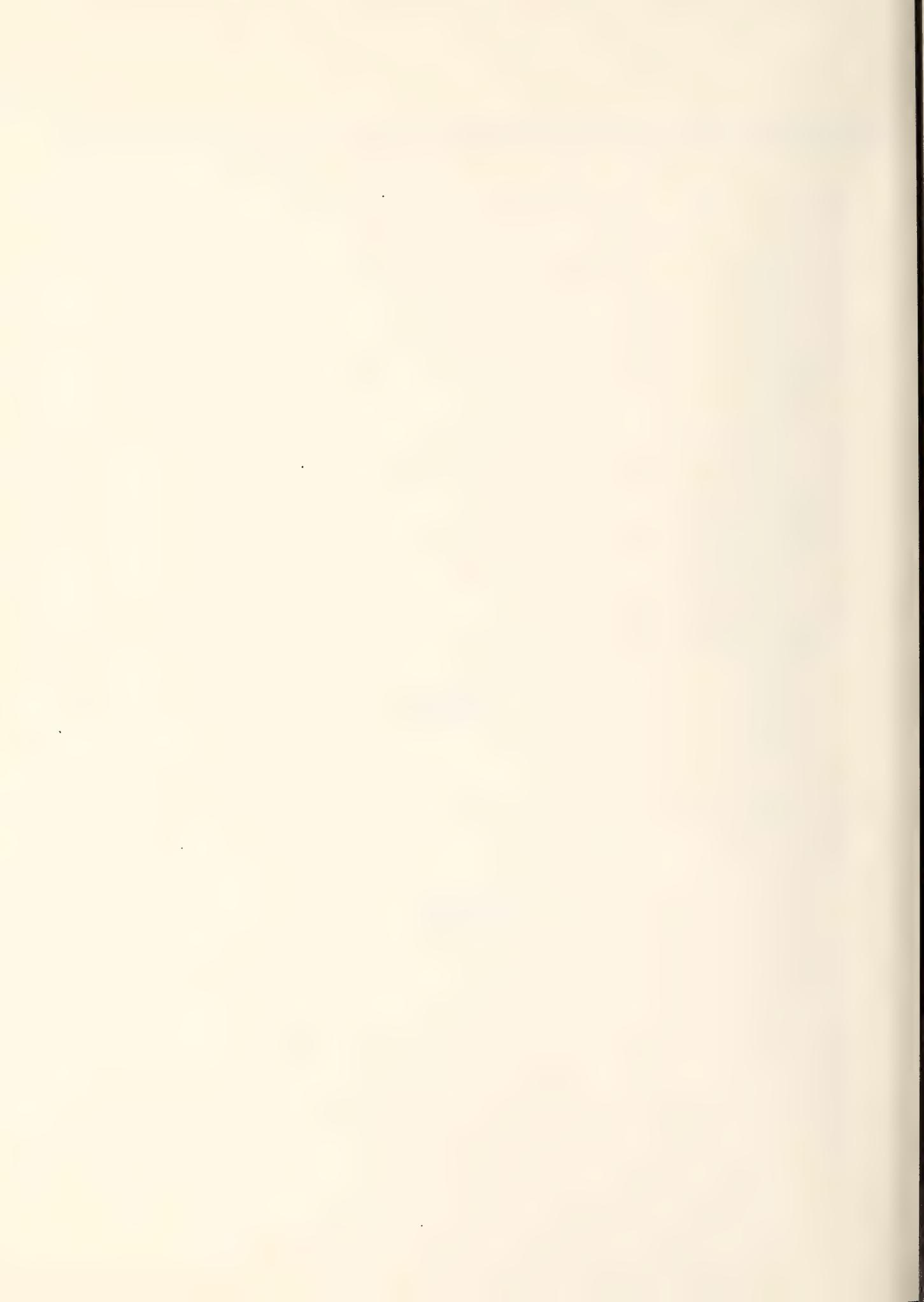
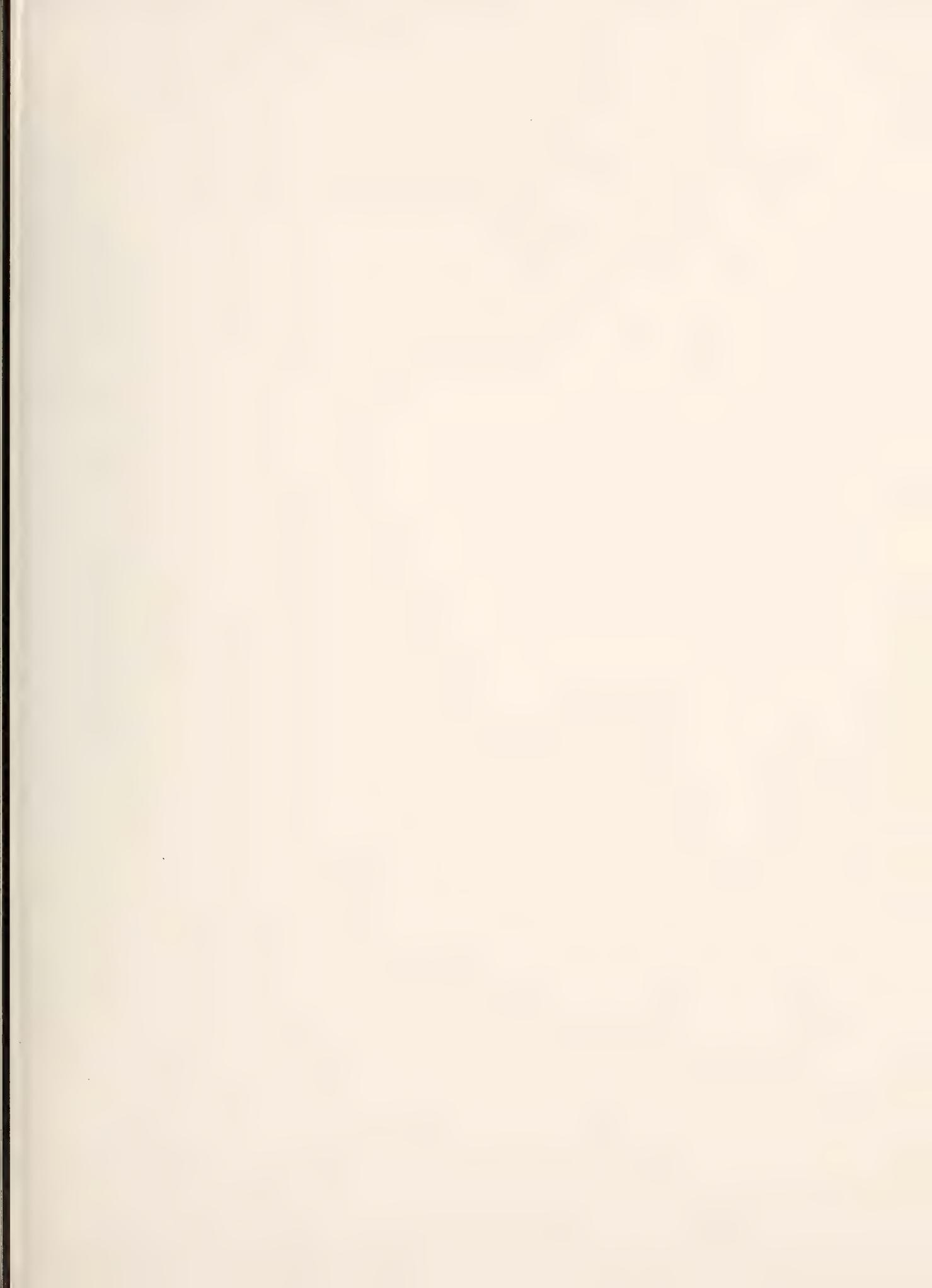


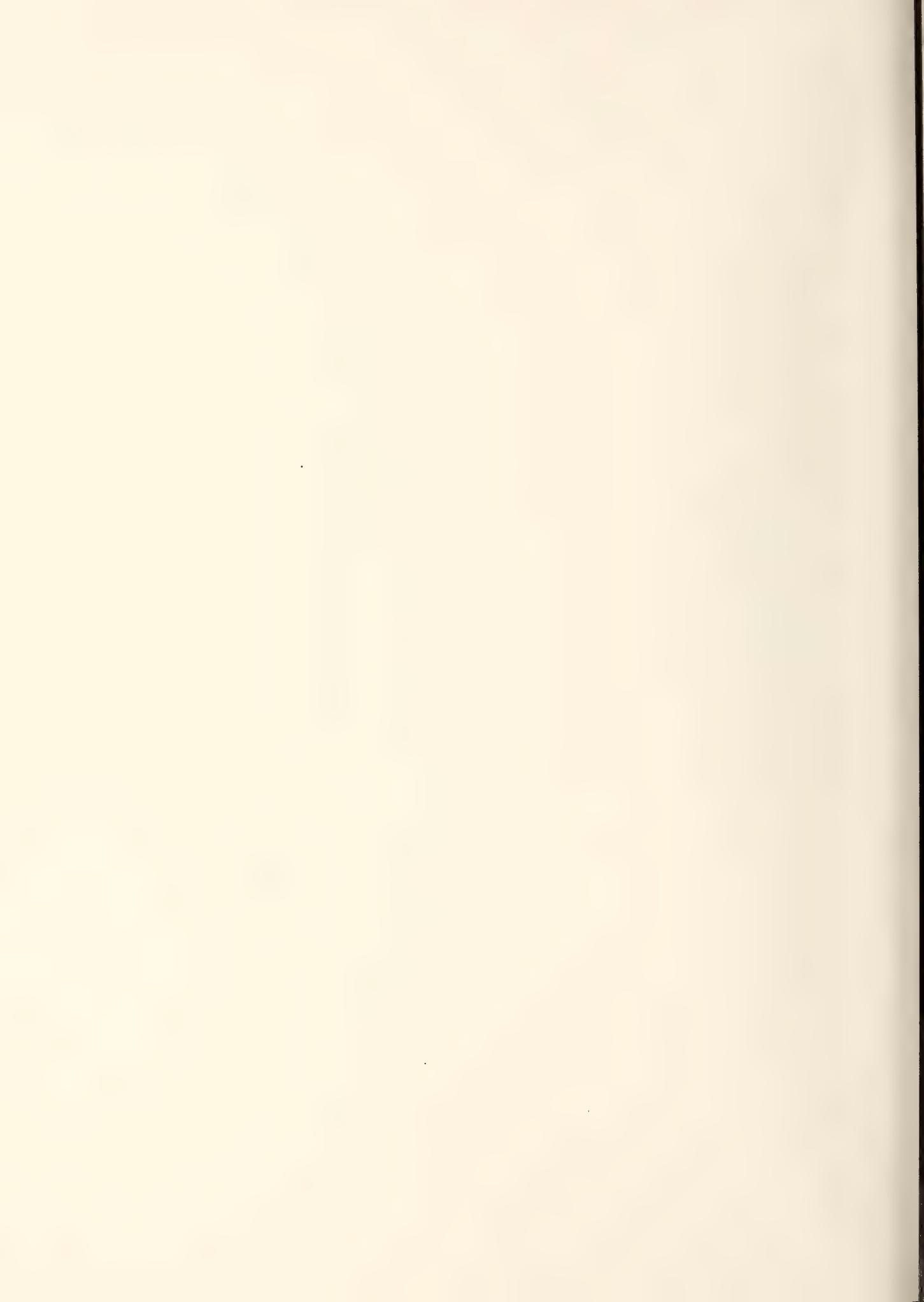
Figure 44

Leuconia heathi

growth curves (solid lines = shallow water panels; dashed lines = mid-water panels)

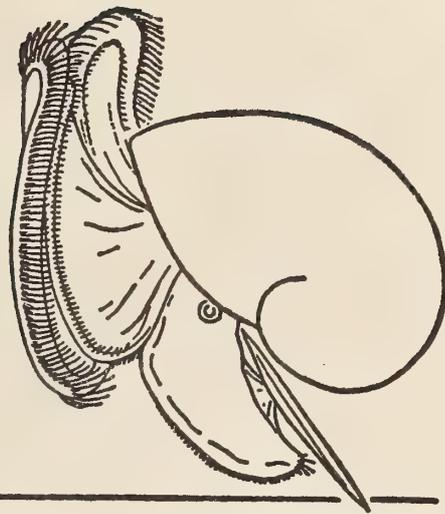






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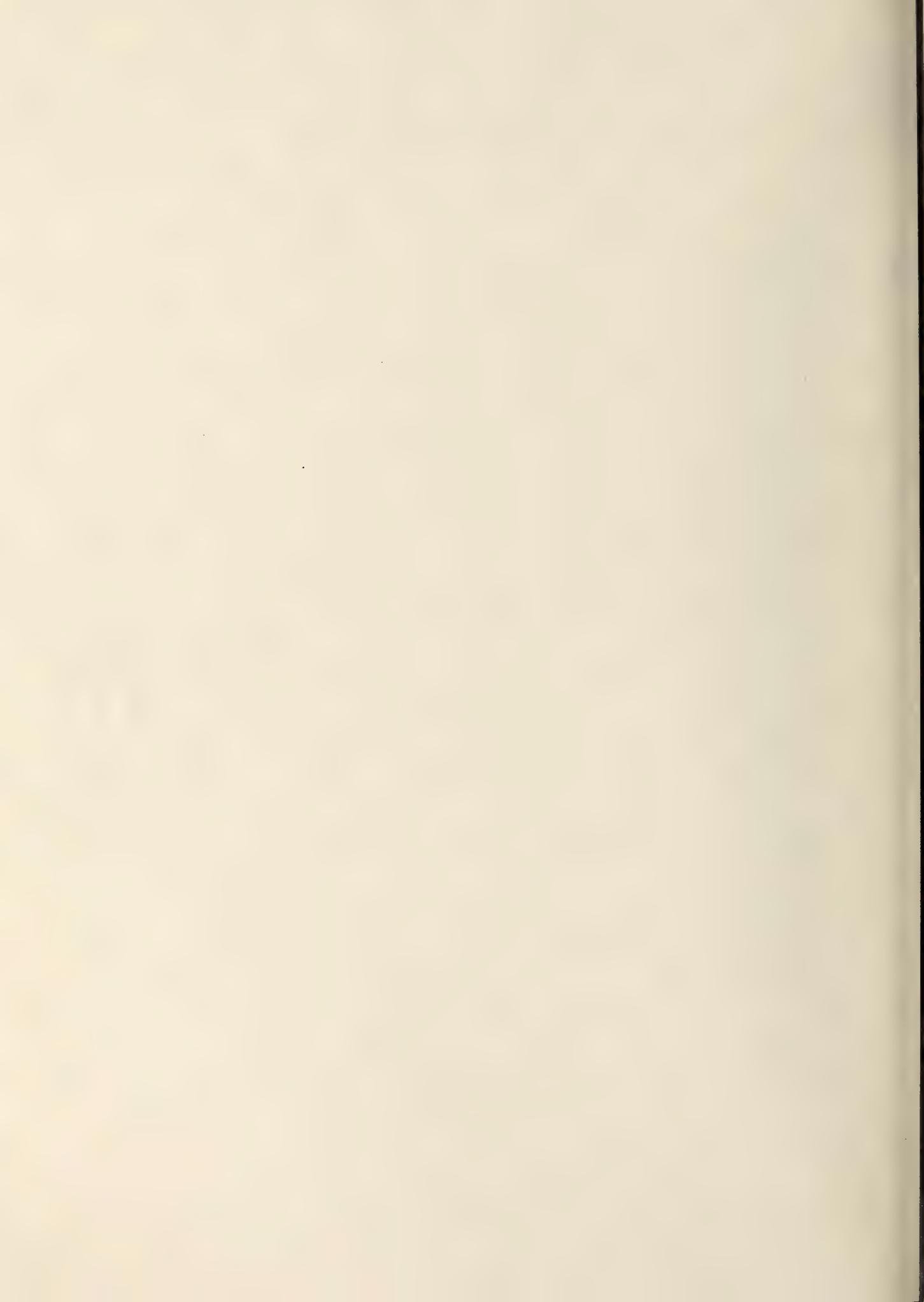
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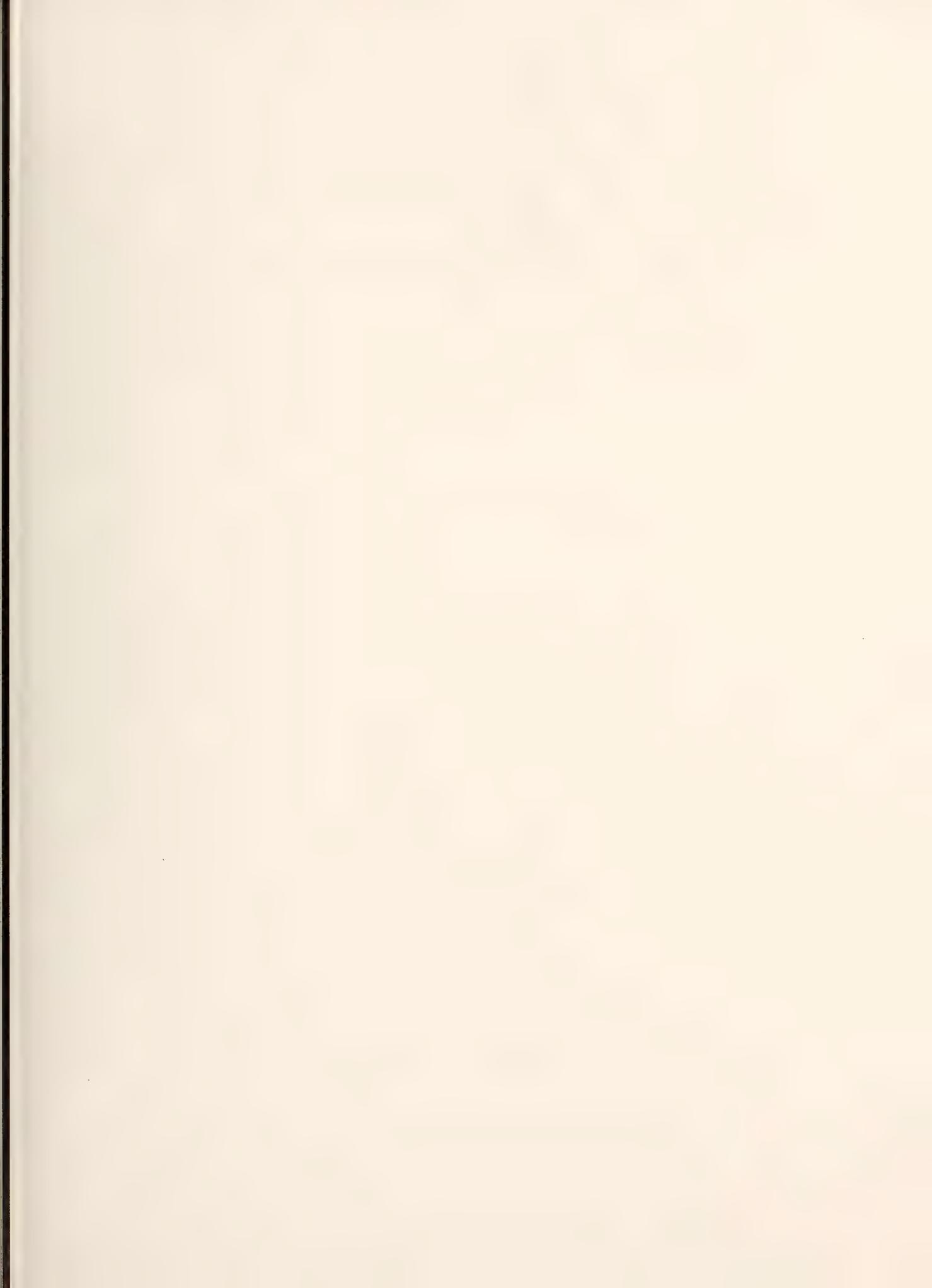
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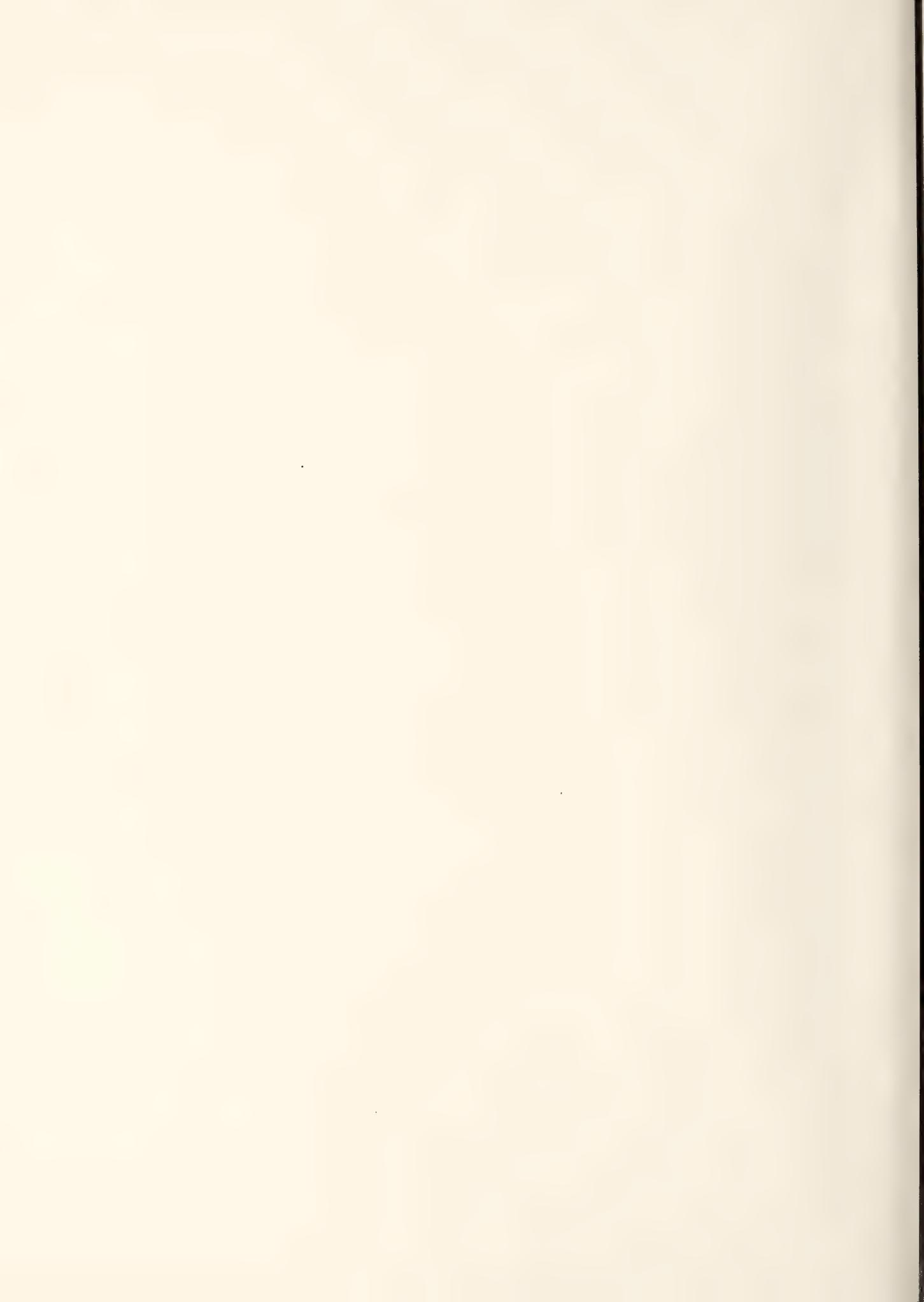
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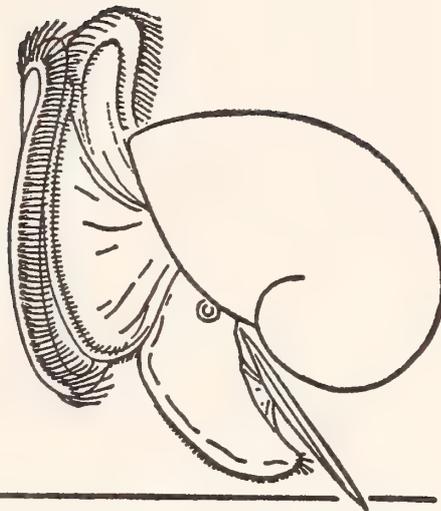






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SUPPLEMENT

The Biology of Chitons

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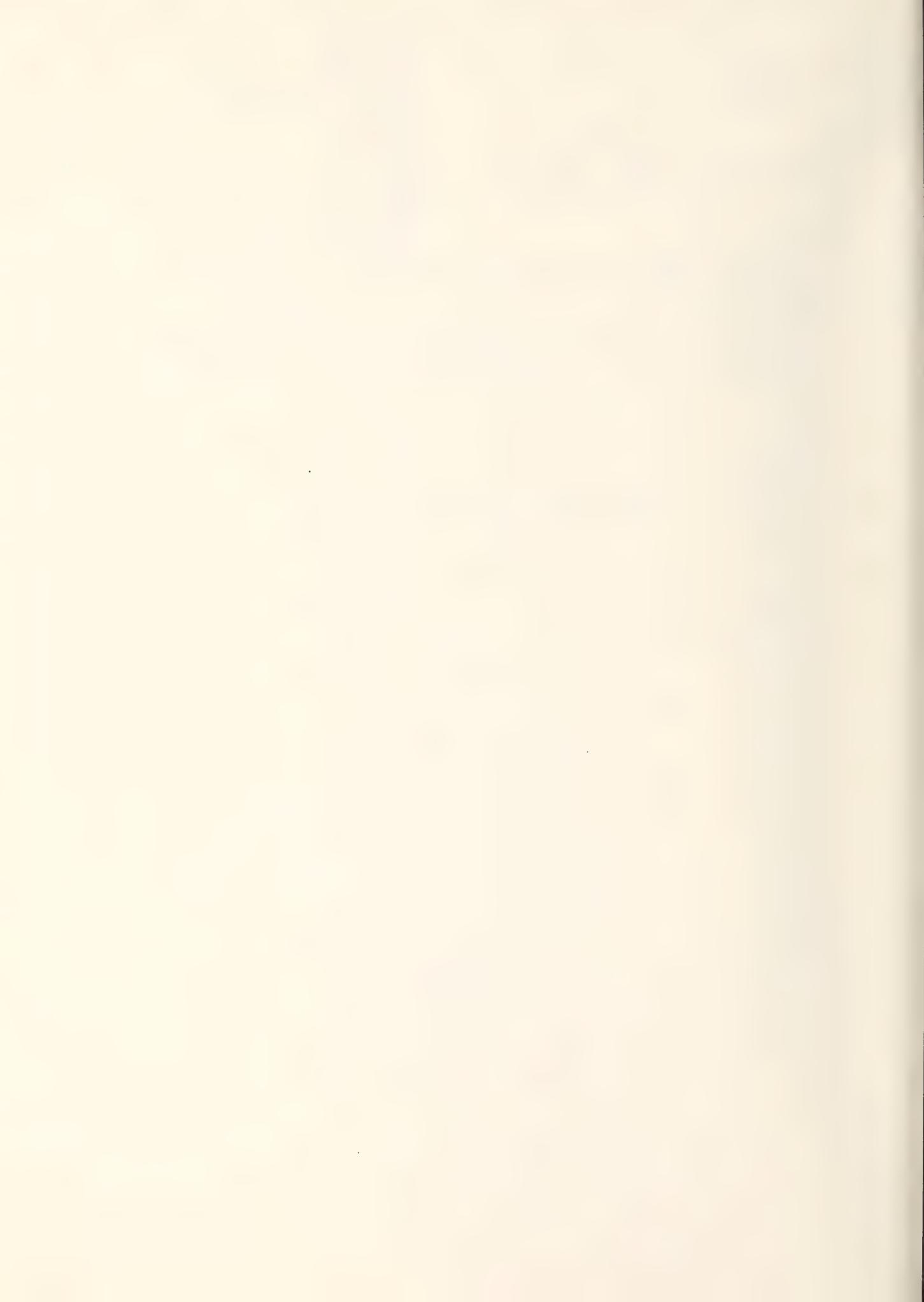


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Introduction

EACH SPRING APPROXIMATELY 30 undergraduates majoring in biology come to Hopkins Marine Station for ten weeks in order to dedicate most of their waking hours to the task of learning, from the animals they study, information neither known by the faculty of Hopkins nor stored in any library. The resultant accumulation of new knowledge either appears piecemeal as papers by individual authors in a spectrum of publications or, now for the third time, as an aggregate of papers in a special supplement to the *Veliger*. We let the following papers be testimony to the surprising yield of worthwhile information that can come from undergraduates given the freedom and equipment to do their own work.

Not as obvious as the published results, except to those of us fortunate enough to be involved in the course, is the fun, the challenge, the excitement, the frustration, the exhaustion, the maturation and finally the pride that the students show as they proceed through what is known as Spring Course. Perhaps the biggest gain for the students is a first hand appreciation of what being investigatory biologists is like; they find it quite different from being students of extant knowledge.

Credit for personal gains that the students obtained through this experience goes in large part to the three persons who developed the concept and the format of the course: Dr. Donald Abbott, Dr. John Phillips, and Dr. Lawrence Blinks. The interested reader should consult the introductions to the Supplements to Volumes 6 and 11 of the *Veliger* for their detailed description of the workings of the Spring Course. Dr. Donald Abbott and Dr. John Phillips have brought continuity to the course by being totally involved in it again this spring. They were joined by Dr. Isabella Abbott, Mr. Charles Baxter, Dr. Robin Burnett, Dr. Frederick Fuhrman, Dr. Malvern Gilmartin, Mr. Chris Harrold, and Dr. George Mpitsos. In addition the staff at Hopkins Marine Station all helped make the course workable.

For this Spring Course, that of 1974, we decided to work on chitons for they fit well the criteria we deemed important: they were common enough that thirty researchers working simultaneously wouldn't destroy the local population; there was clear continuity in the group of organisms called chitons so that results of one worker

could reasonably be compared to those of another; most species could be studied in the field under adverse weather conditions; their taxonomy was fairly well established; and most importantly, they comprised a group about which there were numerous unanswered questions. The bibliography on chitons, compiled by Allyn G. Smith at the California Academy of Sciences, while large (almost 200 entries), was small enough that a student could read all that was known about the aspect of chiton biology he or she had chosen, without using an excessive amount of limited research time. And indeed chitons turned out to be quite interesting; they proved once again that the more an organism is examined, the more interest and the more questions it provides to the examiner. By way of adding a bit to the knowledge of chitons, we have all realized better how much awaits future work. Therefore, while we present these papers in hopes the reader will learn through them more about the chiton, we mostly hope that they will stimulate more work on this animal.

LIST OF EDITORS

Robin Burnett, Donald P. Abbott, Isabella Abbott, Charles Baxter, Frederick A. Fuhrman, Malvern Gilmartin, Christopher Harrold, George Mpitsos, John Phillips, Betsy Lyman, and Rudolf Stohler.

We dedicate this collection of papers to the late Dr. L. D. Howard who, upon retirement from his medical practice, spent several years doing research here at Hopkins Marine Station. He was a generous friend to us all. He valued inquiry and valued the Marine Station as a site particularly conducive to the discovery of new knowledge. We therefore feel the following contributions coming from Hopkins are an appropriate tribute to Dr. Howard.

ACKNOWLEDGMENTS

We thank the following people for the generous contributions they gave to help defray the costs of publication dedicated to Dr. L. D. Howard. Without their help, printing of this supplement would have been greatly delayed.

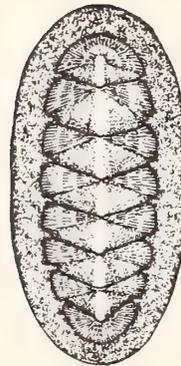
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ROBIN BURNETT

Hopkins Marine Station of Stanford University
Pacific Grove, California 93950



Description of the Habitats of Several Intertidal Chitons

(Mollusca : Polyplacophora)

Found along the Monterey Peninsula of Central California

BY

JON KIM ANDRUS¹ AND W. BILL LEGARD²

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

(1 Text figure)

INTRODUCTION

CHITONS MAKE UP a conspicuous portion of the intertidal fauna of the California coastline. Various species are known to be characteristic of particular intertidal zones (RICKETTS & CALVIN, etc.), yet little is known about their specific habitats. Only two researchers have given this topic more than cursory treatment in print; BARNAWELL, (1954) for *Mopalia* spp. and BARNES (1972) for *Tonicella lineata* (Wood, 1815).

We selected six areas of the Monterey Peninsula shoreline, differing in exposure and substrate, and examined the specific habitats of the following chiton species: *Cryptochiton stelleri* (Middendorff, 1846); *Cyanoplax hartwegii* (Carpenter, 1855); *Ischnochiton regularis* (Carpenter, 1855); *Katharina tunicata* (Wood, 1815); *Mopalia ciliata* (Sowerby, 1840); *Mopalia hindsii* (Reeve, 1847); *Mopalia lignosa* (Gould, 1846); *Mopalia muscosa* (Gould, 1846); *Nuttallina californica* (Reeve, 1847); *Placiphorella velata* Carpenter in Dall, 1878; *Stenoplax heathiana* Berry, 1946; and *Tonicella lineata*. These habitats are herein described. Also included is a description of the habitat where juvenile chitons were most commonly found.

MATERIALS AND METHODS

From April 22 to May 9, 1974, each study site was surveyed during the lower low tides. Descriptions of plant and ani-

mal associates of each species of chiton were recorded, along with detailed chiton density maps (maps on file at Hopkins Marine Station, Pacific Grove, California). Species were collected and identified using BURGHARDT & BURGHARDT, 1969, the key to chitons in LIGHT, *et. al.*, (1964); and a preliminary copy of the chiton key appearing in SMITH & CARLTON (1975). From May 10 to May 28, all 6 study sites were examined for habitat parameters characteristic of the most abundant chiton species. Relative surf and sun exposure, substrate conditions and vertical distribution (as determined by algae distribution—DOTY, 1946) were noted. Sites were examined at high tide as well as low water, to determine the surf strength.

STUDY SITES

Figure 1 shows the locations of the sites on the Monterey Peninsula.

Yankee Point consists of large granite platforms split by many deep channels. Isolated shallow tidepools and deep pools, with sparse flora and abundant fauna, are exposed to strong surf action.

Carmel Point consists of a broad belt of large granite boulders bordered by a sandy beach; it experiences moderate surf action. The boulders provide for few tidepools, and only a few small, protected channels are present.

Stillwater Cove is protected by a natural off-shore breakwater of rocks. The study site substratum consists mainly of horizontal tables of shale exposed at low tide, at the north edge of a sandy beach.

The Cypress Point site resembles the site at Yankee Point, but the slope of the terrain is steeper and large algae are more abundant.

¹ Permanent address:

P. O. Box 2509, El Macero, CA 95618

² Permanent address:

2745 South Ingalls Way, Denver, CO 80227

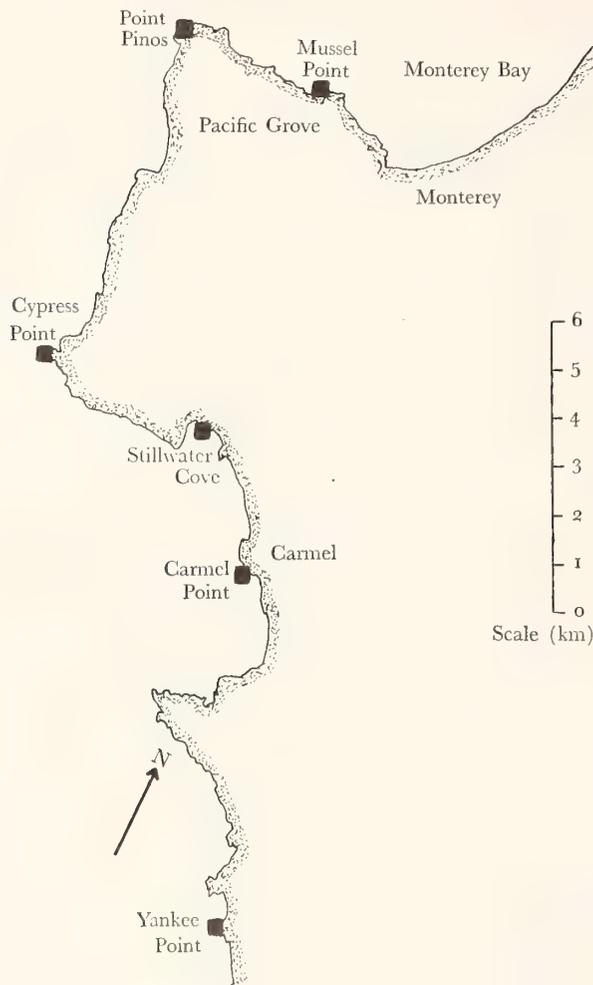


Figure 1

Map of Monterey Peninsula, California, showing the locations of the six study areas

Point Pinos marks the south entrance to the Monterey Bay. Granite promontories and large, isolated rocks are exposed to strong surf. These formations partially protect the study area which was an area along the shoreline and was composed of boulders separated by channels and pools.

Mussel Point is exposed at the south side of Monterey Bay. The granite substrate often forms vertical surfaces with distinct algal zonation.

The data collected during our study are presented in table and figure form. Table 1 lists algal and animal associates, surf strength, vertical range, and additional comments useful in finding each species.

Description of Habitats Characteristic of Species Studied

Cryptochiton stelleri

Cryptochiton stelleri was found next to and in very deep tidepools and channels. They were not predominantly on huge rocks on sandy beaches, contrary to the findings of MACGINITIE & MACGINITIE (1968). We encountered individuals at the + 0.3 m tidal level, totally exposed to full sunlight. This conflicts with reports that individuals are sensitive to light and only remain out of water when it is foggy (RICKETTS & CALVIN, 1968).

Cyanoplax hartwegii

Cyanoplax hartwegii was found in two distinct habitats: 1) under *Pelvetia fastigiata* (J. G. Agardh) DeToni; and 2) in small, wet crevices or depressions. Occasionally individuals were found under *Fucus distichus* Linnaeus. Apparently, constant moisture and protection from direct surf are major characteristics of the *C. hartwegii* habitats. Less than 2% of those studied were exposed to direct surf, perhaps because they cannot maintain attachment when exposed to wave shock. Macroalga cover was not always present, though crustose coralline algae or *Hildenbrandia occidentalis* Setchell were consistent companions at all locations except the wet shale at Stillwater Cove. *Cyanoplax hartwegii*'s common occurrence under fronds of *Pelvetia* is described by RICKETTS & CALVIN (1968), and we confirm this association. We found no avoidance of direct sunlight, as long as sufficient moisture was present (e.g., wet shale at Stillwater Cove), an observation in conflict with one recorded by RICKETTS & CALVIN (*op. cit.*).

Ischnochiton regularis

Ischnochiton regularis was found only on the bottom of smooth rocks, 15 cm to 30 cm in diameter, resting on a rocky bottom. The only other organisms found on these rocks were unidentified microscopic green and blue-green algae. Individuals were usually found in groups of two or three per rock. All seemed to avoid direct sunlight. No mention of *I. regularis* habitat was found in the literature.

Table 1

List of Chiton Species with Corresponding Algal and Animal Associates, Vertical Range, Average Spring Surf Strength, and Additional Comments

Associated algae	Associated animals	Surf strength	Vertical range	Comments
<i>Cryptochiton stelleri</i>				
<i>Calliarthron tuberculosum</i> (Postels & Ruprecht)	<i>Anthropleura elegantissima</i> (Brandt, 1835)	Weak	Below	<i>C. stelleri</i> occurs in or next to deep pools and channels, but is more abundant subtidally
<i>Corallina vancouveriensis</i> (Yendo)	<i>Strongylocentrotus purpuratus</i>			
<i>Cystoseira osmundacea</i> (Menzies) C. A. Agardh	<i>Tonicella lineata</i>		+0.3 m	
<i>Egregia menziesii</i> (Turner) Areschoug				
<i>Iridaea flaccida</i>				
<i>Cyanoplax hartwegii</i>				
Crustose coralline algae	<i>Collisella limatula</i> (Carpenter, 1864)	Moderate	+1.05 m to +0.45 m	<i>C. hartwegii</i> occurs under <i>P. fastigiata</i> or in small wet crevices where crustose coralline algae are abundant
<i>Corallina vancouveriensis</i>	<i>Collisella pelta</i> (Rathke, 1833)		Up to +1.5 m in shallow pools	
<i>Endocladia muricata</i>	<i>Collisella scabra</i> (Gould, 1846)			
<i>Fucus distichus</i>	<i>Mopalia muscosa</i>			
<i>Gigartina papillata</i> (C. A. Agardh) J. G. Agardh	<i>Nuttallina californica</i>			
<i>Hildenbrandia occidentalis</i>	<i>Tetraclita squamosa rubescens</i>			
<i>Pelvetia fastigiata</i>				
<i>Peyssonnelia meridionalis</i>				
<i>Ischnochiton regularis</i>				
Unidentified green and blue-green microscopic algae	None	Moderate to weak	+0.15 m to -0.3 m	<i>I. regularis</i> occurs on bottom of smooth rocks, often in clusters
<i>Katharina tunicata</i>				
<i>Corallina vancouveriensis</i>	<i>Anthropleura xanthogrammica</i>	Very strong	+0.8 m to 0.0 m	<i>K. tunicata</i> is usually found on crustose coralline algae, often on sides of channels, and often exposed to direct sun. <i>I. flaccida</i> also usually present
Crustose coralline algae	<i>Notoacmea scutum</i> (Rathke, 1833)			
<i>Egregia menziesii</i>	<i>Strongylocentrotus purpuratus</i>			
<i>Fucus distichus</i>	<i>Tonicella lineata</i>			
<i>Hildenbrandia occidentalis</i>				
<i>Iridaea flaccida</i>				
<i>Mopalia ciliata</i>				
Crustose coralline algae	<i>Mytilus californianus</i>	Weak	+0.75 m to below 0.0 m	<i>M. ciliata</i> is commonest in well-protected crevices
<i>Endocladia muricata</i>	<i>Tetraclita squamosa rubescens</i>			
<i>Pelvetia fastigiata</i>				
<i>Mopalia hindsii</i>				
Crustose coralline algae	<i>Pagurus samuelis</i>	Moderately	+0.9 m to +0.3 m	Most exposed of <i>Mopalia</i> spp. Much algal growth on back. In crevices
<i>Egregia menziesii</i>				
<i>Hildenbrandia occidentalis</i>				
<i>Iridaea flaccida</i>				
<i>Petrocelis franciscana</i> (Setchell & Gardner)				
<i>Mopalia lignosa</i>				
Crustose coralline algae	<i>Stenoplax heathiana</i>	Weak to very weak	+0.45 m to below -0.6 m	Under rocks in protected coves and channels. Least exposed of <i>Mopalia</i> spp.
<i>Cladophora trichotoma</i> (C. A. Agardh) Kutzing	<i>Tegula funebris</i> (Adams, 1854)			
<i>Cystoseira osmundacea</i>				
<i>Gigartina papillata</i>				
<i>Hildenbrandia occidentalis</i>				
<i>Iridaea flaccida</i>				
<i>Peyssonnelia meridionalis</i>				
<i>Ulva</i> spp.				

Table 1 (continued)

Associated algae	Associated animals	Surf strength	Vertical range	Comments
<i>Mopalia muscosa</i>				
Crustose coralline algae	<i>Anthopleura elegantissima</i>	Moderate to weak	+0.9 m to +0.45 m. Up to +1.5 m in tidepools	In tight depressions, wedged between barnacles and mussels, and in shallow tidepools
<i>Fucus distichus</i>	<i>Anthopleura xanthogrammica</i>			
<i>Gigartina papillata</i>	<i>Collisella pelta</i>			
<i>Hildenbrandia occidentalis</i>	<i>Nuttallina californica</i>			
<i>Iridaea flaccida</i>	<i>Tegula funebris</i>			
<i>Pelvetia fastigiata</i>				
<i>Peyssonnelia meriodalis</i>				
<i>Nuttallina californica</i>				
<i>Cladophora trichotoma</i>	<i>Cyanoplax hartwegii</i>	Very strong to moderately weak	+1.35 m to 0.0 m. Usually +1.05 m to +0.6 m	In tight depressions, wedged between barnacles and mussels, and in shallow tidepools
<i>Corallina vancouveriensis</i>	<i>Dodecaceria fistulicola</i> (Ehlers, 1901)			
Crustose coralline algae	<i>Mopalia muscosa</i>			
<i>Endocladia muricata</i>	<i>Mytilus californianus</i>			
<i>Gigartina papillata</i>	<i>Pollicipes polymerus</i>			
<i>Hildenbrandia occidentalis</i>	<i>Tetraclita squamosa rubescens</i>			
<i>Pelvetia fastigiata</i>				
<i>Peyssonnelia meridionalis</i>				
<i>Postelsia palmaeformis</i>				
<i>Placiphorella velata</i>				
<i>Agardhiella tenera</i> (J. G. Agardh) Schmitz	None	Weak	Below -0.3 m	On sides of rocks and channel walls; in constant shade
<i>Corallina vancouveriensis</i>				
<i>Cystoseira osmundacea</i>				
<i>Gigartina corymbifera</i> (Kutzing) J. G. Agardh				
Red crustose				
<i>Ulva</i> spp.				
<i>Stenoplax heathiana</i>				
<i>Pelvetia fastigiata</i>	<i>Mopalia lignosa</i>	Very weak	Below +0.15 m	Under rocks resting on sandy bottom
Red crustose algae				
<i>Tonicella lineata</i>				
<i>Calliarthron tuberculosum</i>	<i>Anthopleura xanthogrammica</i>	Moderately strong to weak	Below 0.0 m. Up to +1.2 m in tidepools	In pools and depressions. High density subtidally. Crustose coralline algae always present
<i>Cladophora trichotoma</i>	<i>Cryptochiton stelleri</i>			
Crustose coralline algae	<i>Katharina tunicata</i>			
<i>Hildenbrandia occidentalis</i>	<i>Pagurus samuelis</i> (Stimpson, 1857)			
<i>Peyssonnelia meridionalis</i>	<i>Strongylocentrotus purpuratus</i>			

Katharina tunicata

Katharina tunicata was abundant in two distinct habitats: 1) in low numbers at the *Iridaea flaccida* (Setchell and Gardner) Hollenberg and Abbott level of almost vertical granite surfaces, a habitat found at almost all the study sites; and 2) in higher numbers in shallow, exposed tidepools with crustose coralline algae covering the bottom; this habitat occurred only at Yankee and Cypress Points. In addition, small individuals (less than 6 cm long) were found in depressions inhabited by *Strongylocentrotus purpuratus* (Stimpson, 1857) and *Anthopleura xanthogrammica* (Brandt, 1835). At Yankee Point we observed a

size gradient with larger animals further from the surf. The largest were found in the protected channels on the leeward walls. Our results agree with previous work (MACGINITIE & MACGINITIE, 1968) in that individuals were found along open, rocky coasts, not necessarily in direct surf, but not in a habitat as well protected as Stillwater Cove.

Mopalia ciliata

Mopalia ciliata was the chiton least encountered, perhaps because it was inconspicuous. Tucked in crevices among *Mytilus californianus* Conrad, 1837, *Tetraclita*

squamosa rubescens Darwin, 1854, crustose coralline algae, *Pelvetia fastigiata* and *Endocladia muricata* (Postels and Ruprecht) J. G. Agardh, members of this species often had their girdle buried in sand. Found mainly below the $+0.75$ m tidal level and noted subtidally at Mussel Point, this animal was exposed to little or no surf.

Mopalia hindsii

We found *Mopalia hindsii* to be more exposed to air during low tides than the other *Mopalia* species. Individuals were usually in crevices nestled among associated algae, and often covered with a thick algal growth on the valves.

Mopalia lignosa

Mopalia lignosa has the most specific habitat of the chitons in this study. Individuals inhabited the undersides of movable rocks resting on rocky bottom. Some animals were found on the sides of rocks or in deep, smooth crevices and occasionally at the bottom of high tidepools.

Mopalia muscosa

Mopalia muscosa was found predominantly in two habitats: 1) in wet, protected, large crevices from the $+0.45$ m to $+0.9$ m tidal levels; and 2) in high, protected tidepools up to $+1.5$ m tidal level. In addition, individuals were found under algae (*Fucus distichus* and *Pelvetia fastigiata*), and under rocks. At Stillwater Cove, a high density also was found on slight irregularities along flat, horizontal, very wet shale. None were exposed to direct surf. More than 97% of the individuals examined were in direct contact with moisture; either touching a pool of water (in tidepools or crevices), lying partially buried in moist sand, or sitting under wet macroalgae. More than 90% of the individuals examined had their anterior ends lower than their posterior ends and in contact with moisture. Almost all individuals (with the exception of those at Stillwater Cove) were found near either *Peyssonnelia meridionalis* Hollenberg and Abbott or crustose coralline algae.

Nuttallina californica

Nuttallina californica was found in three distinct situations. Listed in order of highest to lowest density, these were: 1) the bottom of bare rock depressions the size of their bodies; 2) squeezed between the bases of *Tetraclita squamosa rubescens*, *Pollicipes polymerus* (Sowerby, 1833),

and *Mytilus californianus*; and 3) wedged in small crevices in high, shallow tidepools. Rare individuals were found in large, shallow depressions at the base of *Pelvetia fastigiata* and *Postelsia palmaeformis* Ruprecht. Surf strength at depression localities varied widely from very strong at Yankee Point to moderately weak at Stillwater Cove. *Nuttallina californica* was found in areas both with and without macroalgae, though highest densities were in the macroalgae-free depressions. Apparently, a major habitat factor is the need for protection from the direct shearing force of the surf. Only about 5% were not firmly entrenched in a crevice, depression, or space where the surf's force was depleted. MACGINITIE & MACGINITIE (1968) say *N. californica* inherit and live in deep depressions in rocks exposed at low tide, and feed on debris which collects in these depressions. We found individuals on rocks exposed to a wide range of surf strengths, but few such rocks were in areas of weak surf. More than 98% of the animals were in the presence of erect or crustose coralline algae. None were found on flat areas, unless sessile animals or high-profile algae were present. The largest individuals were found in the high, shallow tidepools, but here the density was very low.

Placiphorella velata

Placiphorella velata were found on the flat sides of movable rocks and on the walls of deep tidepools, always below the -0.3 m tidal level. The individuals were always found in shade and always with red crustose coralline algae. Their avoidance of sunlight has been previously noted (RICKETTS & CALVIN, 1968). This species was rare intertidally, being more common subtidally.

Stenoplax heathiana

Stenoplax heathiana generally was found on the sides of large, rather bare rocks resting on a sandy bottom; this is in accord with observations by JOHNSON & SNOOK (1935) and RICKETTS & CALVIN (1968). There seemed to be no size-habitat relationship. One reason these animals can occur on a barren substrate is they eat large bits of drift algae that lodge at the base of the rocks (MACGINITIE & MACGINITIE, 1968).

Tonicella lineata

BARNES (1972) notes that the presence of encrusting coralline algae is critical to the habitat of *Tonicella lineata* in the area he studied. Our observations support this. *Tonicella lineata* was rarely found without coralline algae

and was most abundant in coralline-dominated tidepools or subtidally with corallines, both erect forms and crustose about 2 mm thick. It additionally was found next to *Strongylocentrotus purpuratus* and among *Anthopleura xanthogrammica*. *Tonicella lineata* was rarely exposed to direct surf, occurring primarily below the 0.0 m tide level, though sometimes found at higher levels in tidepools. Point Pinos was the only site where *T. lineata* was found in crevices, in the open. Only one animal was found at Stillwater Cove.

Juvenile Chitons

The habitat of the majority of juvenile chitons was: a) low in the intertidal ranging between the 0 and +0.9 m tidal levels; b) damp; c) shady or dark; d) protected from wave shock by surrounding boulders, overhanging ledges, or by being within crevices. This zone corresponded to that of tunicates and sponges. Yet a young chiton was never found on either, but rather on bare rock or rock encrusted with such algae as *Corallina gracilis* forma *densa* Collins, and members of the genera *Lithothamnion*, *Lithophyllum*, and *Hildenbrandia*.

SUMMARY

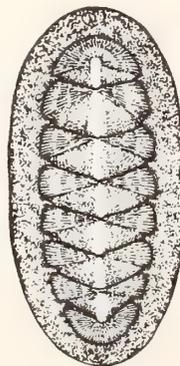
1. The habitats of 12 intertidal chitons from six sites on the Monterey Peninsula in central California picked for variability in surf exposure and substrate type, were described in terms of physical factors and biological associates. The chitons were *Cryptochiton stelleri*, *Cyanoplax hartwegii*, *Ischnochiton regularis*, *Katharina tunicata*, *Mopalia ciliata*, *M. hindsii*, *M. lignosa*, *M. muscosa*, *Nuttallina californica*, *Placiphorella velata*, *Stenoplax heathiana*, and *Tonicella lineata*.
2. The most important environmental parameters in determining chiton habitats proved to be surf strength, light exposure, substrate composition, moisture and biological associates.

ACKNOWLEDGMENTS

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Niche Apportionment among the Chitons
Cyanoplax hartwegii and *Mopalia muscosa*
and the Limpets *Collisella limatula* and *Collisella pelta*
under the Brown Alga *Pelvetia fastigiata*

BY

MICHAEL STEWART CONNOR¹

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

(8 Text figures)

INTRODUCTION

Chitons and limpets represent two different classes of the phylum Mollusca; yet they seem to perform very similar functions in the intertidal community. They are slow-moving, grazing herbivores occurring together throughout the intertidal zone. The similarity of their food and habitat provoked a closer investigation of their apportionment of resources within the sympatric areas.

In the portion of the intertidal zone of the central California coast marked by the brown alga *Pelvetia fastigiata* (J. G. Agardh) DeToni, two common species each of chitons and limpets can be found: *Cyanoplax hartwegii* (Carpenter, 1855) and *Mopalia muscosa* (Gould, 1846), and *Collisella pelta* (Rathke, 1833) and *Collisella limatula* (Carpenter, 1846). While *Cyanoplax* can be found in its greatest abundance in this area (RICKETTS & CALVIN, 1968), *Collisella pelta*, *Collisella limatula* and *Mopalia* can be found throughout the intertidal area (TEST, 1945; ANDRUS & LEGARD, 1975). EATON (1968) and CRAIG (1968) distinguished the different food preferences of *Collisella limatula* and *C. pelta*.

To identify habitat differences among these intertidal herbivores, I conducted a general survey of their spatial distribution and of the behavioral aspects of resource apportionment. The study was conducted from April to June, 1974 in the high intertidal portion of three areas of Monterey County, California: Mussel Point, Point Pinos

and Carmel Point. All three intertidal areas consist of granite rock outcroppings surrounded by sand.

DIFFERENCES BETWEEN *Cyanoplax*
AND *Mopalia* HABITATS

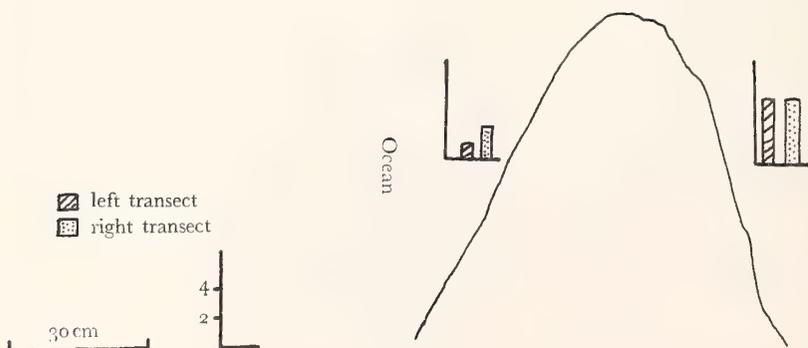
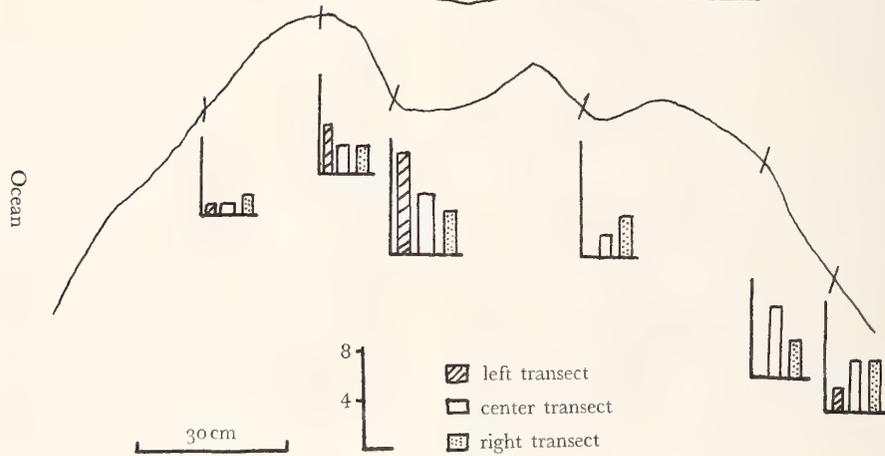
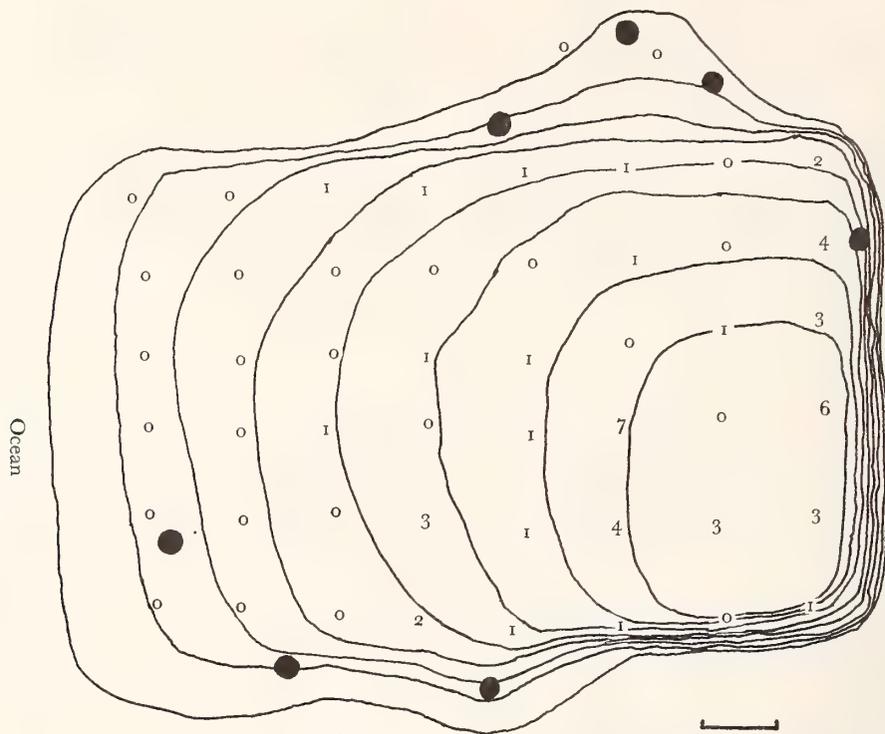
Transects were run at Mussel Point and Point Pinos through the *Pelvetia* zone. Quadrats 30 cm x 30 cm were placed along the transect with additional quadrats extending laterally to the entire width of any rock touched by the transect. The number of chitons and limpets inside each quadrat was recorded.

These transects (Figure 1) indicate that *Cyanoplax* is more abundant in the areas more protected from wave shock: higher rocks, crevices and the shoreward side of rocks. *Mopalia* occurs at the lower boundary of the *Pelvetia* zone in regions less protected from wave action and at a lower tidal level. The limpets are found throughout the transects.

At Carmel Point a survey was made at the same vertical height on the protected and open sides of the point. On the protected side of the point, *Cyanoplax* can be found at densities of 5-6/m²; while on the open-coast side of the point, only *Mopalia* at a density of 1-2/m² can be found at a similar tidal height. The sand grain size on the open side of the point ($md\phi = -0.991$) is much larger than on the protected side ($md\phi = 0.453$) where *Cyanoplax* is found (Figure 2). While relative wave motion or wave shock cannot be precisely determined from differences in grain size (SHEPARD, 1963), differences as large as those observed

¹ Permanent address:

108 Stimson Place, Wilmington, DE 19810



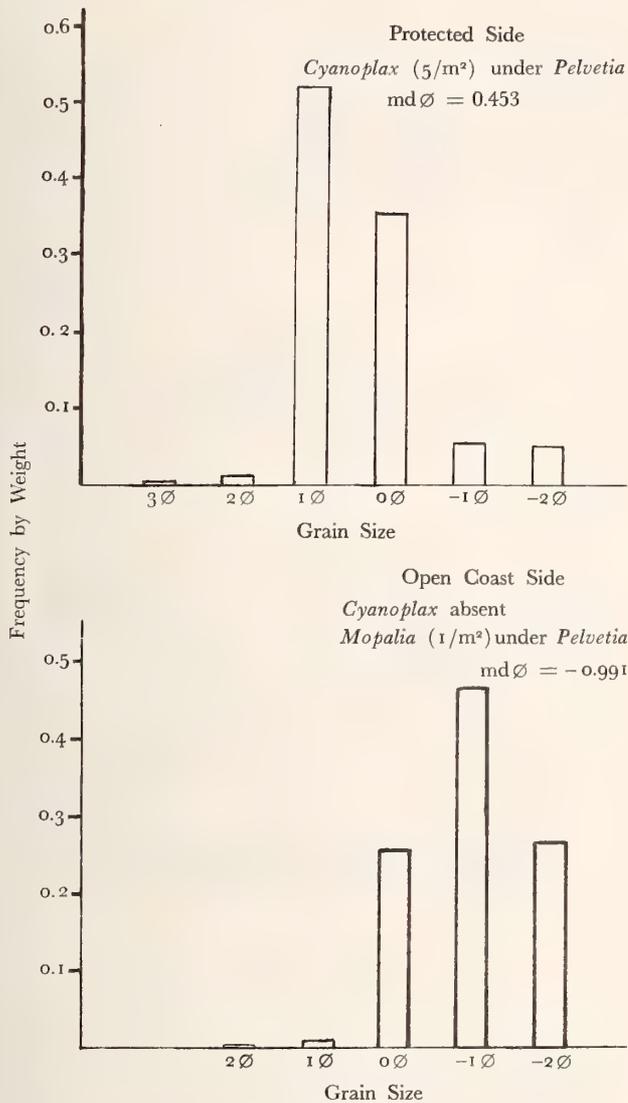


Figure 2

Particle size of sand grains on two sides of Carmel Point. The *Pelvetia* zone is at the same vertical height on both sides of the point.

(← on facing page)

Figure 1

Distribution of *Cyanoplax* and *Mopalia* along transects run through the *Pelvetia* zone. Numerals and bar graphs show number of *Cyanoplax* per 30 cm × 30 cm quadrat. Darkened circles represent single *Mopalia* individuals.

- a. Topographical map of rock at Point Pinos. Contour lines represent 10 cm of vertical displacement.
- b. & c. Cross-sectional representation of transects at Mussel Point viewed perpendicular to the surf line. The bars of the graphs represent the number of *Cyanoplax* in laterally adjacent quadrats at the same vertical height.

between the two sides of the point indicate that large differences in wave energy must be present in these two habitats (KRUMBEIN, 1944-1947).

FOOD COMPETITION BETWEEN

Cyanoplax AND *Collisella limatula*

Chitons in the *Pelvetia* zone at Mussel Point and Point Pinos were randomly chosen; their position and the positions of the neighboring chitons and limpets were noted, and the body length of each animal was recorded. Mapping of chiton neighbors (Figure 3) indicated *Collisella limatula* to occur significantly further away (\bar{x} = 12.19 cm; Student's t-test: $P < 0.05$) from *Cyanoplax* than *Cyanoplax* was from itself (\bar{x} = 10.74 cm). *Collisella pelta* showed no such effect (\bar{x} = 11.49 cm; $0.2 < P < 0.4$).

Size studies (Figure 4) demonstrated that *Collisella limatula* within 20 cm of *Cyanoplax* were significantly smaller (\bar{x} = 1.50 cm; $P < 0.01$) than *C. limatula* at least 50 cm away from the nearest *Cyanoplax* (\bar{x} = 1.80 cm).

Work by ROBB (1975) has indicated that *Cyanoplax hartwegii* found under *Pelvetia* has a diet consisting mostly of *Pelvetia* and secondly *Hildenbrandia occidentalis* Setchell. *Collisella limatula* depends mostly on *Hildenbrandia* and other crustose algae for its food (EATON, 1968) while *Collisella pelta* under *Pelvetia* eats mostly *Pelvetia* and other frondose algae (CRAIG, 1968). Given the common occurrence of large stands of *Pelvetia* in the intertidal zone, this alga is probably not a limiting food, but *Hildenbrandia* is less abundant by several orders of magnitude. Food competition, then, may account for the tendency of *Collisella limatula* to be further away from *Cyanoplax* and to be larger when *Cyanoplax* is not in its immediate vicinity.

HOMESITE COMPETITION BETWEEN

Cyanoplax AND *Collisella pelta*

Data shown in Figure 3 were subjected to statistical analysis to determine the degree of specific and interspecific aggregation. Clumping around individuals of *Cyanoplax* is evident; *Cyanoplax* apparently occurs mostly in the vicinity of other *Cyanoplax* (G -test = 58.3), but *Collisella pelta* (G = 29.1) and *C. limatula* (G = 14.9) also show a significant tendency to aggregate near *Cyanoplax* ($P < 0.001$). The difference between *Cyanoplax*'s and *Collisella pelta*'s clumping cannot be distinguished (Arcsin transformation of percentages of the total number of animals within 10 cm of the chiton [Box 16.10, SOKAL & ROHLF, 1969]: $0.1 < P < 0.2$); while *Cyanoplax* shows significantly more clumping with other *Cyanoplax* than with *Collisella limatula* ($0.1 < P < 0.05$).

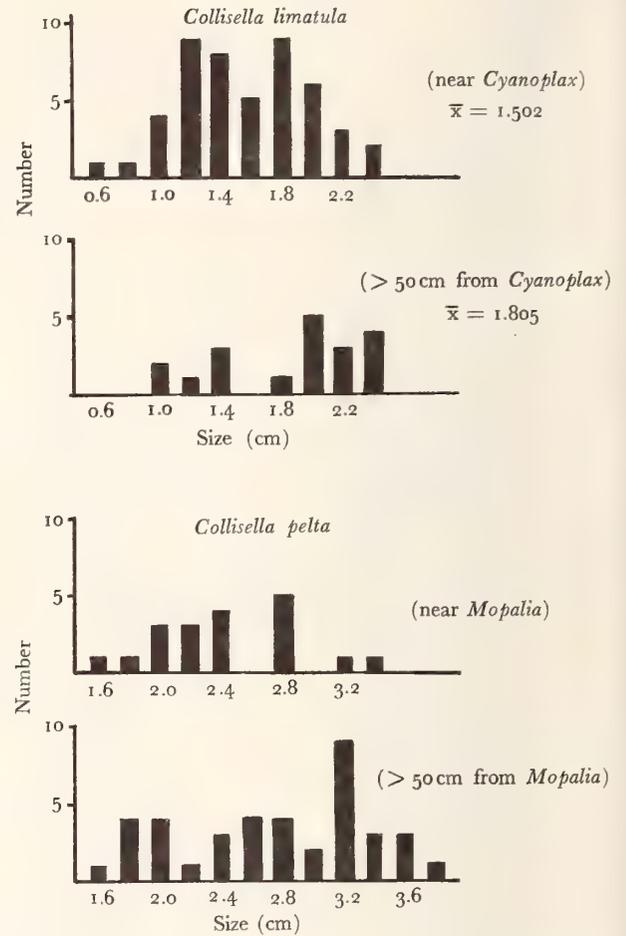
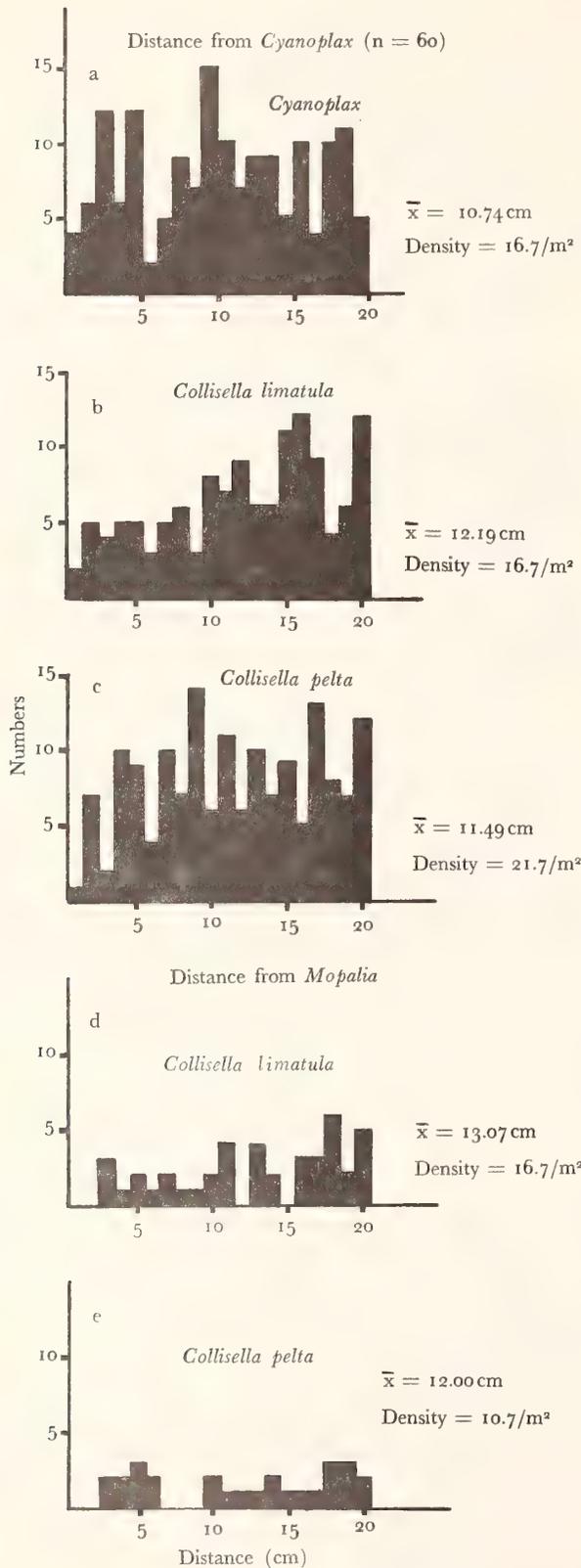


Figure 4

Size frequency of limpets within 20 cm versus those more than 50 cm from the nearest *Cyanoplax* or *Mopalia*.

(← adjacent column)

Figure 3

Distance from chitons to all neighbors within 20 cm. Density is the interpolated density of animals around each chiton (animal number / m^2). a., b. & c. represent distance from each *Cyanoplax* to other *Cyanoplax* (a.), *Collisella limatula* (b.) and *Collisella pelta* (c.). d. & e. represent distance from each *Mopalia* to *Collisella limatula* (d.) and *Collisella pelta* (e.).

Evidently there are certain locations on the rocks which are favorite resting areas for the organisms, but within these favored areas comparative exclusions can occur. Ly-

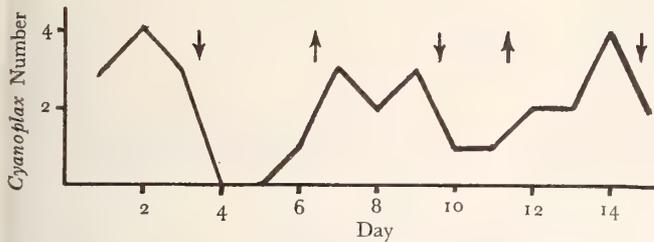


Figure 5

Effects of changing *Collisella pelta* density on the number of *Cyanoplax* in a commonly used home area. Normal *Collisella pelta* density was doubled (\downarrow), or all *Collisella pelta* were removed (\uparrow).

MAN (1975) has shown different *Cyanoplax* individuals to repeatedly use the same set of home areas and these results suggest that *Cyanoplax* and *Collisella pelta* might compete for these specific home areas. When the number of *Collisella pelta* on a rock face also containing *Cyanoplax* and *Collisella limatula* was experimentally doubled (from 6/0.1 m² to 12/0.1 m²) in an area commonly used for homes by *Cyanoplax*, *Cyanoplax* density decreased (Figure 5). *Collisella limatula* was not affected. When the *Collisella pelta* were removed, the *Cyanoplax* returned. Observations suggested that appropriate sites were occupied on a "first come, first served" basis.

EXCLUSION BEHAVIOR

OF *Mopalia muscosa* TOWARDS *Collisella pelta*

While the density of *Collisella limatula* within 20 cm of *Cyanoplax* was the same as its density near *Mopalia* (16.7/m²; see Figure 3), *Collisella pelta* was much less dense in the vicinity of *Mopalia* (10.7/m²) than around *Cyanoplax* (21.7/m²; G-test of independence: 0.01 < P < 0.025). *Collisella pelta* within 30 cm of *Mopalia* were significantly smaller (Figure 4; \bar{x} = 2.39 cm; P < 0.05) than those at least 50 cm away from *Mopalia* (\bar{x} = 2.75 cm).

In order to test whether *Mopalia* selectively excludes *Collisella pelta* from its immediate area, *C. pelta* from a similar habitat were placed 1 cm from the girdle of a submerged *Mopalia*. A control *C. pelta* was placed on a matched substrate about 20 cm from the *Mopalia*. After one hour the distance of the *C. pelta* from its starting position was measured. In the ten trials run (Figure 6), the *C. pelta* near the *Mopalia* always moved further (Mann-Whitney U-test: \bar{x} = 9.8 cm; P < 0.001) than the controls

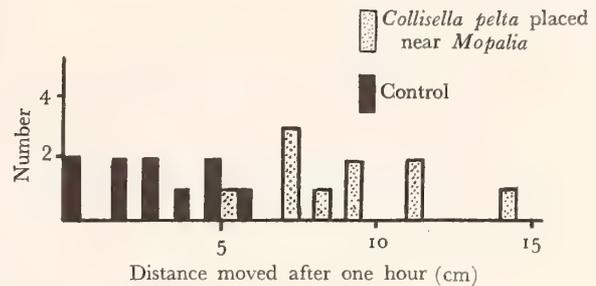


Figure 6

Exclusion of *Collisella pelta* by *Mopalia*.

Abscissa is distance moved after one hour by *Collisella pelta* placed 1 cm from *Mopalia*'s girdle. Controls were placed on a matched substrate about 30 cm away.

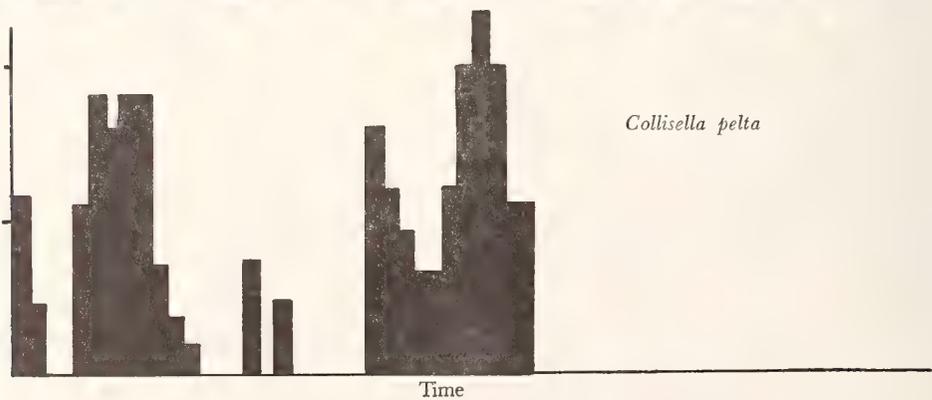
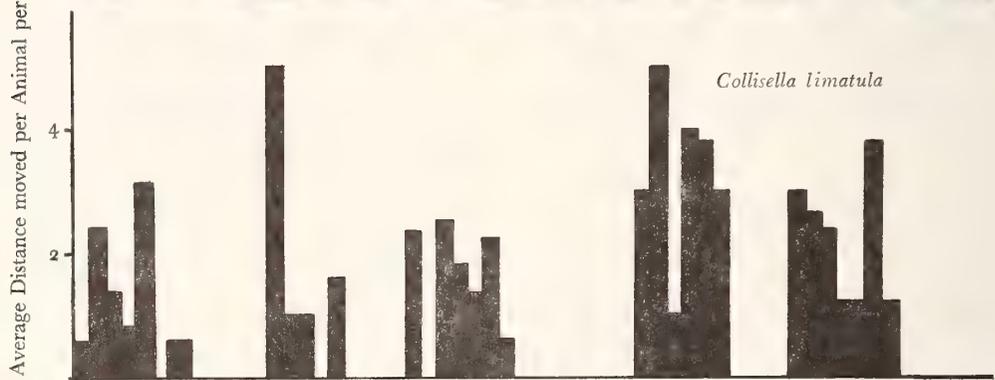
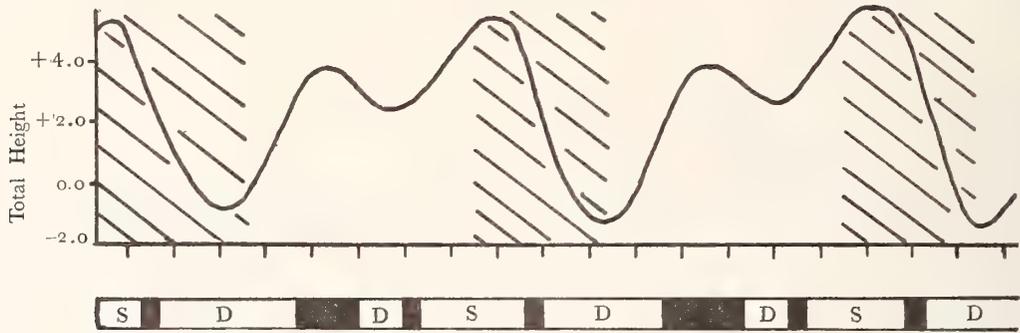
(\bar{x} = 3.0 cm). Contact did not seem to be a prerequisite for moving, but in half the cases the chiton was seen to actively push the limpet away with its girdle. This behavior was also twice observed naturally in the field. *Collisella pelta* was the only animal observed to be actively excluded by *Mopalia*. When *Cyanoplax* and *Collisella limatula* were placed next to *Mopalia*, no reaction occurred.

Feeding studies of *Mopalia muscosa* (BARNAWELL, 1954; BOOLOOTIAN, 1964; SMITH, 1975) show that *Pelvetia* is not a source of food for *M. muscosa*. *Mopalia* must rely on less abundant stands of *Gigartina papillata* (C. A. Agardh) J. G. Agardh or *Endocladia muricata* (Postels and Ruprecht) J. G. Agardh in the *Pelvetia* zone. As mentioned earlier, *Collisella pelta* in this intertidal zone has been reported to eat primarily *Pelvetia*; however, *C. pelta* in other zones eats both *Gigartina* and *Endocladia*. The incursion of *C. pelta*, then, could represent a threat to *Mopalia*'s relatively limited food supply.

MOVEMENT DIFFERENCES

AMONG THE LIMPETS AND CHITONS

In the Mussel Point area, I selected a rocky outcropping covered with *Pelvetia*, under which *Cyanoplax hartwegii*, *Mopalia muscosa*, *Collisella pelta* and *Collisella limatula* were found. Movement of these animals was observed for two 24-hour periods, one 48-hour period and one 60-hour period. The movement of thirteen *Cyanoplax* was plotted every hour during the 48-hour and the 60-hour watches. The movement of eleven *C. pelta* was plotted over a 36-hour period, and the movement of five *C. limatula* was plotted over a 60-hour period. Positions of all animals were checked every hour (Figure 7).



Time

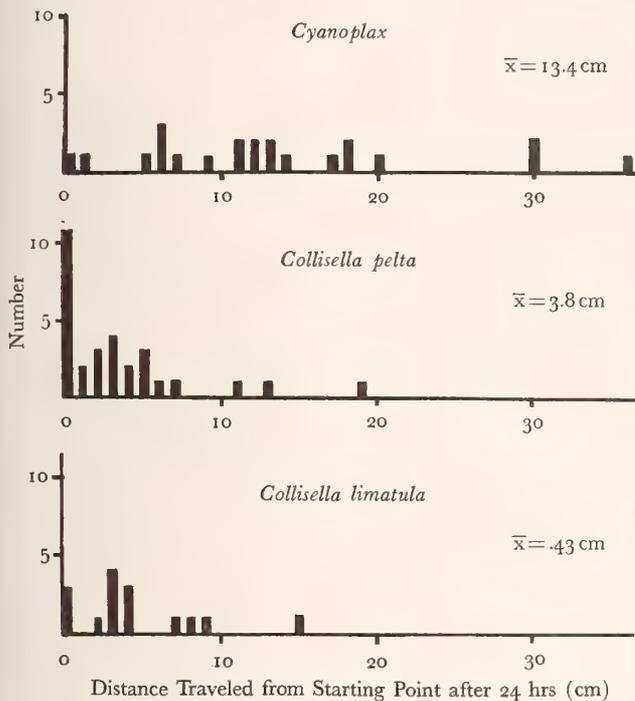


Figure 8

Distance travelled from starting point after one day for limpets and *Cyanoplax*.

Field observations of *Cyanoplax* movement (LYMAN, 1975) and *Collisella pelta* (using scoring method of LYMAN, op. cit.) movement showed the two species to be quite similar. Both moved more at night, and more when either awash or exposed than when submerged (*C. pelta* average movement—night, 1.2 cm/hr; day, 0.3 cm/hr; $P < 0.001$; exposed, 1.1 cm/hr; submerged, 0.5 cm/hr; $P < 0.01$). *Collisella limatula*, on the other hand, moved more when submerged or awash ($\bar{x} = 1.8$ cm/hr) than when dry ($\bar{x} = 0.3$

(← on facing page)

Figure 7

Movement of *Cyanoplax hartwegii*, *Collisella limatula* and *Collisella pelta* in relation to tidal cycle and day-night cycle. Observations were conducted in the field every hour for 60 hours for *Cyanoplax* and *Collisella limatula*, and 36 hours for *Collisella pelta*. Cross-hatched area represents night. S = submerged; D = dry; and shaded area = awash. *Cyanoplax* data collected in conjunction with LYMAN, 1975.

cm/hr; $P < 0.001$), but moved equally during the night and day ($0.5 < P < 0.75$). EATON (1968) has also observed greater submerged movement in *C. limatula*, and SMITH (1975) observed *Mopalia muscosa* to move mostly at night when submerged.

While *Cyanoplax*, *Collisella limatula* and *Collisella pelta* all show some degree of specific homing (LYMAN, 1975; EATON, 1968; and CRAIG, 1968), *Cyanoplax* is the most nomadic of the three species. To quantify this movement, plots were made of the distance of each animal from its starting point after 24 hours (Figure 8). The traveling distance of *Cyanoplax* ($\bar{x} = 13.4$ cm) was much greater than that of either *Collisella pelta* ($\bar{x} = 3.8$ cm; Mann-Whitney U-test: $P < 0.001$) or *C. limatula* ($\bar{x} = 4.3$ cm; $P < 0.001$). No difference could be distinguished between *C. pelta* and *C. limatula* ($0.4 < P < 0.5$), which move more erratically within the same general area. Average movement of the animals during the entire study was *Cyanoplax*: 1.3 cm/hr; *Collisella limatula*: 1.1 cm/hr; *Collisella pelta*: 0.8 cm/hr; a difference insufficient to totally cause the above results.

DISCUSSION

HUTCHINSON (1957) has proposed that two sympatric species will coexist only if each exploits some aspect of the common environment in a different way. If limiting, the environment must be partitioned in terms of food preference, food procurement and the requisite microhabitats necessary to tolerate physical and biological stresses.

The evidence presented here combined with other findings can be used to demonstrate that these four intertidal herbivores partition their environment by food preference, spatial restriction and temporal restriction. This evidence is summarized in Table 1. In instances of potential resource competition, mitigating factors separate the niches. For example, *Mopalia* and *Collisella pelta* may be potential food competitors; but their activity varies with submergence, and *Mopalia*'s aggressive behavior forces *C. pelta* to occupy different areas. *Cyanoplax*'s nomadic behavior, as opposed to the home area behavior of the limpets, spatially limits its disturbance of the food niche of *Collisella limatula*, and distinguishes it from *C. pelta* which retains individual home areas for longer periods of time than *Cyanoplax*.

The results of this survey therefore seem to support the generally accepted ecological principle that congeneric species (PAINE, 1962; KOHN, 1959; BOWERS, 1964; JEFFRIES, 1966; HAVEN, 1971) and confamilial species (MAGNUM, 1964; CROKER, 1967) will show definite niche separation despite apparent similarities in habitat and behavior.

Table 1

Ecological and Behavioral Differences in Four *Pelvetia*-Zone Herbivorous Mollusks

Species	Principal food	Day/night activity	Submerged/dry movement	Habitat: wave exposure	Comments
<i>Mopalia muscosa</i>	<i>Endocladia</i> ^{5 6} <i>Gigartina</i> ^{5 6}	Night ⁵	Submerged-awash ⁵	Unprotected ⁷	Territorial; actively excludes <i>C. pelta</i>
<i>Cyanoplax hartwegii</i>	<i>Pelvetia</i> , mostly; some <i>Hildenbrandia</i> ⁴	Night ¹	Dry-awash ¹	Protected ⁷	Highly nomadic
<i>Collisella limatula</i>	<i>Hildenbrandia</i> ³	No difference ^{3 7}	Submerged-awash ^{3 7}	—	Smaller size near <i>Cyanoplax</i>
<i>Collisella pelta</i>	<i>Pelvetia</i> , mostly Fronlose algae ²	Night ^{2 7}	Dry-awash ⁷	—	Smaller size near <i>Mopalia</i> Prevents <i>Cyanoplax</i> from returning to home areas

¹according to LYMAN (1974)²according to CRAIG (1968)³according to EATON (1968)⁴according to ROBB (1975)⁵according to SMITH (1975)⁶according to BARNAWELL (1954) and BOOLOOTIAN (1964)⁷according to this study

SUMMARY

Niche partitioning by the chitons *Cyanoplax hartwegii* and *Mopalia muscosa*, and the limpets *Collisella limatula* and *Collisella pelta*, two classes of mollusks with similar functions in the intertidal community, under the brown alga *Pelvetia fastigiata* was studied. *Cyanoplax* and *Mopalia* were found to partition a common habitat by different microhabitat preferences and behavioral patterns. Food niche overlap with *Collisella pelta* was lessened by *Mopalia*'s aggressive behavior. Food niche overlap with *Collisella limatula* and resting area overlap with *Collisella pelta* were lessened by *Cyanoplax*'s nomadic behavior.

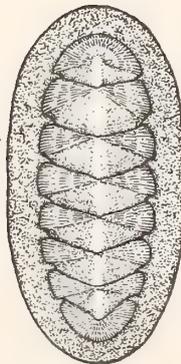
ACKNOWLEDGMENTS

This project would never have been completed were it not for Mr. Charles Baxter, whose widespread knowledge of biology and unfailing interest and support for the project sustained me through the doldrums that are a part of any hard work. I would also like to thank the rest of the HMS staff, particularly Dr. Robin Burnett who worked on this paper as if it were his own.

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Spawning Behavior and Larval Development
in *Mopalia lignosa* and *Mopalia muscosa*
(Mollusca : Polyplacophora)
in Central California

BY

JAMES M. WATANABE¹ AND LARRY R. COX²

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

(3 Text figures)

INTRODUCTION

THE GENUS *Mopalia* (Mollusca, Polyplacophora) is represented by 14 species along the California coast (BURGHARDT & BURGHARDT, 1969). Among the common forms in central California are *Mopalia muscosa* (Gould, 1846), *Mopalia lignosa* (Gould, 1846), *Mopalia ciliata* (Sowerby, 1840), and *Mopalia hindsii* (Reeve, 1847). Though relatively well known taxonomically, little is known of the spawning behavior and larval development of this genus. HEATH (1905) made brief mention of spawning in *M. lignosa* and *M. muscosa* in the field. THORPE (1962) studied spawning in *M. lignosa*, *M. muscosa*, *M. ciliata*, *M. hindsii*, *M. importata* (Carpenter in Pilsbry, 1892), and *M. porifera* (Pilsbry, 1892). He also made some general observations on the larval development of *M. ciliata*. Comparable information on larval development in other species of this genus is not available. We chose to study development in *M. muscosa* and *M. lignosa* in part to fill this gap and because these species are common and known to spawn in the spring (HEATH, 1899; BOOLOOTIAN, 1964). Our aim was to determine the main sequence of events in larval development and its time schedule. The development of *M. muscosa* was followed by Cox, while that of *M. lignosa* was followed by Watanabe. A strong effort was made to standardize experimental procedures and presentation of results so that comparisons between the two would be valid and clear. The work was carried out at Hopkins Marine Station of

Stanford University during the months of April-June, 1974.

METHODS AND MATERIALS

Specimens of *Mopalia lignosa* were collected under low rocks at Mission Point, Carmel Bay, California. *Mopalia muscosa* were collected at the same location and from rocks in the mid-tide zone of Point Pinos, Pacific Grove, California. HEATH (1905: 392) maintains that *Katharina tunicata* (Wood, 1815) attains sexual maturity at 2 years, reaches a length of 25 mm the first year and add 8-11 mm the second year. He states that this is also characteristic of both *M. lignosa* and *M. muscosa*, therefore only larger animals (50-60 mm long) were taken, to insure sexual maturity. Once in the laboratory, the chitons were maintained in circulating seawater aquaria.

Embryos were reared in 5-inch finger bowls cleaned with concentrated nitric acid followed by detergent and thorough rinsing. Fertilized eggs were pipetted from the aquaria (see Spawning), rinsed in fresh sea water several times and placed in thin layers in bowls with one-half-inch of sea water. Both natural sea water filtered through coarse filter paper and artificial sea water (Instant Ocean Synthetic Sea Salts) were used. Little difference was found between the two and only filtered natural sea water was used for embryos from the late free-swimming stage on. From 0.1 to 0.3 ml of a mixture of 0.5 g streptomycin and 300 000 units of penicillin in one liter of distilled water was added to the bowls to control bacterial growth. Water in the bowls was changed by decanting off about one-half the volume of water and pouring the remainder of the cul-

¹ Permanent address:

748 East Glendora Avenue, Orange, CA 92665

² Permanent address:

P. O. Box 341, Big Pine, CA 93513

ture, containing nearly all the larvae, into a clean finger bowl. This was done every 4 hours for the first 12 hours of development and twice daily for the later stages. The finger bowls were covered with glass plates and maintained partially immersed in running sea water at 13.5°-15.8°C. Around the time of settling, eroded fragments of *Mytilus* shell covered with a green algal film were added to most of the bowls as a settling surface.

Observations of the structure and behavior of living larvae were made in finger bowls under a dissecting microscope and in wet whole mounts under a compound microscope. For permanent whole mounts, larvae were fixed in Bouin's fluid and stained in dilute acidulated Grenacher's borax carmine (GALIGHER & KOZLOFF, 1964). Due to the large amount of yolk in the larvae, little internal differentiation could be discerned.

SPAWNING

To obtain gametes, attempts were made to induce spawning in the laboratory using methods which have produced positive results in gastropods and other invertebrates. The methods tried were the following (*M.l.* = *Mopalia lignosa*, *M.m.* = *Mopalia muscosa*. Numerals preceding these indicate numbers tested):

1. Dilation of gonopores by insertion of glass probe, followed by placement of animals in standing seawater; 2 *M.l.*, 1 *M.m.* No spawning in 1 hour. Ref. GOULD (1967) for *Urechis*.
2. Electrical stimulation of gonopores (15v @ 50 cycles AC for 5 sec.) followed by placement in standing seawater; 3 *M.l.*, 2 *M.m.* No spawning in 1.5 hours. Ref. IWATA (1950) for *Mytilus edulis* Linnaeus, 1758.
3. Electrical stimulation of exposed lateral nerve cord (15v @ 50 cycles AC for 5 sec.) followed by placement in standing seawater; 1 *M.l.*, 1 *M.m.* No spawning in 1 hour. Ref. HARVEY (1956) for echinoids.
4. Injection of 0.2 ml 0.5 M KCl into perivisceral hemocoel or through pallial groove followed by placement in standing seawater; 3 *M.l.*, 3 *M.m.* Caused strong body contraction in 3 minutes but no spawning in 4 hours. Ref. HARVEY (1939) for echinoids.
5. Injection of nerve tissue homogenate into perivisceral hemocoel, followed by placement in standing seawater; 1 *M.m.* No spawning in 1 hour. Ref. DAVIS, MPITSO, & PINNEO (1973) for *Pleurobranchaea*.
6. Eggs dissected from ovaries and treated for one hour with 3 ml 0.1N NaOH in 100 ml seawater, inseminated

with sperm obtained by dissection; 1 *M.l.*, 1 *M.m.* Eggs not fertilizable with active sperm.

Ref. WOLFSOHN (1907) for *Acmaea*.

7. Several ml sperm solution obtained from dissected male gonad added to aquaria containing chitons; 7 *M.l.*, 5 *M.m.* No spawning in 5 hours. Ref. HEATH (1905) that sperm released by males may cause female spawning.

8. Water in tank containing chitons allowed to stand and become stale. Temperature slightly elevated (15°C); 7 *M.l.*, 7 *M.m.* Spawning occurred though not consistently. Ref. GRAVE (1932) for *Chaetopleura apiculata* (Say).

Still water at temperatures slightly above ambient ocean temperature seem to be common conditions for natural spawning. *Ischnochiton magdalenensis* (= *Stenoplax heathiana* Berry, 1946) was observed spawning in tide pools during early morning low tides (HEATH, 1899: 5). GRAVE (1932) and CHRISTIANSEN (1954) obtained spawning in *Chaetopleura apiculata* and *Lepidopleurus asellus* (Spengler), respectively, by allowing them to sit in non-circulating sea water at slightly elevated temperatures for several hours. While similar conditions were present when *Mopalia lignosa* spawned in the laboratory, these conditions were not sufficient for consistent release of gametes. Male and female *Mopalia muscosa* spawned together on one occasion in a tank with circulating seawater at a temperature of approximately 13°C. Isolated females spawned in finger bowls in which the water had been allowed to stand for a day. Thus, no coherent pattern of spawning conditions could be established.

THORPE (1962) reports that *Mopalia muscosa* and *M. lignosa* may spawn in the laboratory at times corresponding to certain phases of the local tidal cycle. We could not resolve any such correlation.

Detailed observations of spawning behavior were made only for *Mopalia lignosa*. In two instances, once in the late afternoon and once at night, 7 to 10 chitons placed in a large plastic dish pan partially filled with non-circulating seawater spawned after several hours. The pan was tilted so that the water reached only part way up the inclined bottom. During spawning, the girdle was elevated anteriorly and postero-laterally. In both sexes the posterior tip of the girdle margin was raised to form a spout through which a single stream of gametes was released. The four males observed spawning were more active than females during the process. They released intermittent spurts of sperm in long, thin streams which pooled in masses at the bottom of the tank and diffused into the water only slowly. The duration of each continuous sperm release was 3-5 minutes, separated by intervals of 5-15 minutes. Two of the three females observed spawning were partially out of

water, with only their posterior ends submerged; all remained stationary. Eggs flowed slowly out in single file, loosely held together by a thin mucus sheath, and piled up behind the animal.

Small disturbances, including a brief removal from water, interrupted but did not permanently stop spawning. THORPE (1962) reported that in his experience only the close proximity of a strong, hot light would halt spawning: agitation and inversion of the animals would not.

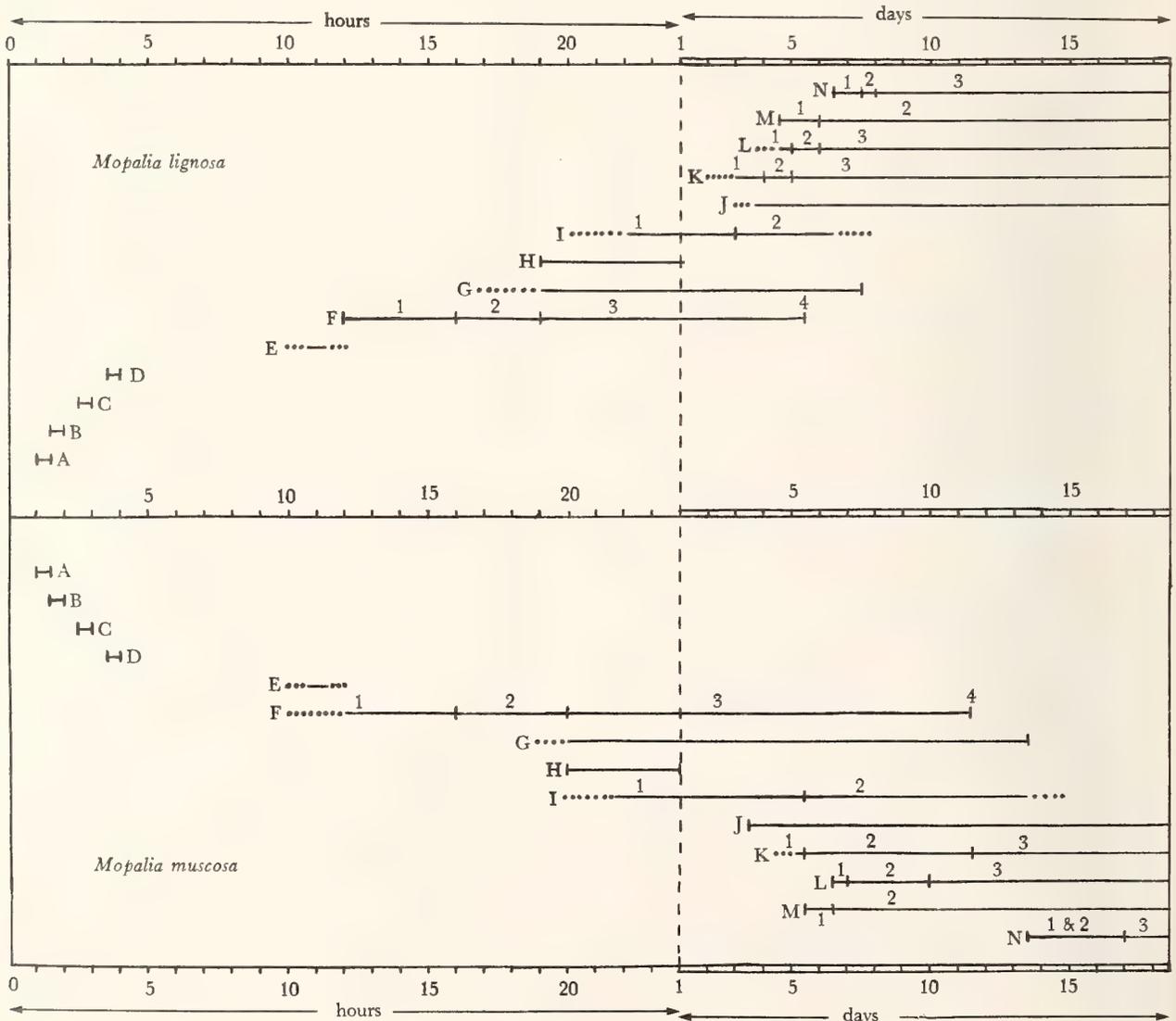
DEVELOPMENT OF *Mopalia lignosa*

A time schedule of development for *Mopalia lignosa* is given in Figure 1. The various stages of development are shown in Figure 2.

Early Development

The eggs were light green and about 0.2 mm in diameter. They were very yolky and were surrounded by a transparent, frilly chorion (Figure 2 A). Once fertilization occurred, a small space appeared between the egg and the chorion (Figure 2 B). Cleavage was typically spiral (Figure 2 C-F).

Gastrulation begins with an invagination of the macromeres (HEATH, 1899: 50). A slight invagination was observed in several embryos 10-12 hours after fertilization but was never positively identified as the blastopore. Beating of the prototrochal cilia began about 12 hours after fertilization. Just before hatching (19 hours), the strongly beating cilia stopped for several minutes. When beating resumed, small portions of the chorion broke away and



the trochophore struggled out anterior end first using both muscular contractions of the body and ciliary beat (Figure 2 H). The hatching process occupied approximately 5 minutes.

Free Swimming Trochophore

The newly hatched trochophores were broadly egg-shaped with the prototrochal band encircling the body at its greatest girth. Several long cilia at the anterior end of the body, which make up the apical tuft, were present at or before hatching (Figure 2 I). The apical tuft was surrounded by a field of much shorter cilia. A similar teleotrochal field of short cilia occurred around the posterior end of the body (Figure 2 I). By the third day after fertilization these fields had expanded to cover the body of the trochophore. About this same time the larval eyes appeared as simple pigment spots on the lateral margins of the body just posterior to the prototroch. They persisted until well after metamorphosis.

The prototrochal cilia beat such that the body was continually rotating around its axis in a clockwise direction when viewed from the anterior end. Sometimes the larvae

halted their rapid swimming and hovered in a head-up position, maintaining their places in the water column with the slow beat of the prototrochal cilia. The apical tuft appeared in part to serve a sensory function, for when a swimming larva contacted an obstacle with it, it backed away and swam in another direction.

Mantle and Shell Development

Large epidermal cells, noted by HEATH (1899) in *Stenoplax heathiana* and OKUDA (1947) in *Cryptochiton stelleri* (Middendorff, 1846), appeared scattered over the dorsal body surface 2 to 3 days after fertilization (Figure 2 K-L). Shortly after this, a series of alternating ridges and grooves, transversely oriented, began forming on the dorsal surface. Five days after fertilization, 8 ridges and 7 grooves were present. The large cells became aligned along the tops of the ridges (Figure 2 M-N). This system of ridges and grooves marked the site of the developing mantle. By 4.5 days, the mantle field had become well-delineated by the mantle fold (Figure 2 M). Short spicules appeared first at the anterior margin of the mantle and by six days after fertilization they completely encircled it (Figure 2 Q-R).

Herein, the term "settled" refers to larvae which have lost the prototrochal cilia and become permanent crawlers. "Metamorphosed" refers to larvae which have lost the apical tuft and have shell plates forming.

As the larvae began to settle (5.5 days), the head became partially covered by the mantle field. The shell plates first appeared after about 6.5 days. Plates 2-7 (counting the cephalic or head plate as number one), the first to form, appeared as thin, opaque slivers in the grooves between successive dorsal ridges (Figure 2 Q). The cephalic plate formed a day later, by which time the apical tuft had disappeared. The 7 plates enlarged anteriorly and posteriorly until they overlapped one another (Figures 2 S-U), and expanded laterally to completely obscure the body (Figures 2 V-W). A small pallial groove was formed (Figure 2 W), but no ctenidia were present. These began appearing approximately 8 weeks after fertilization, the posterior-most ones being formed first. By this time the larval eyes had disappeared. The 8th (caudal) plate formed approximately 6 weeks after fertilization.

Foot Development

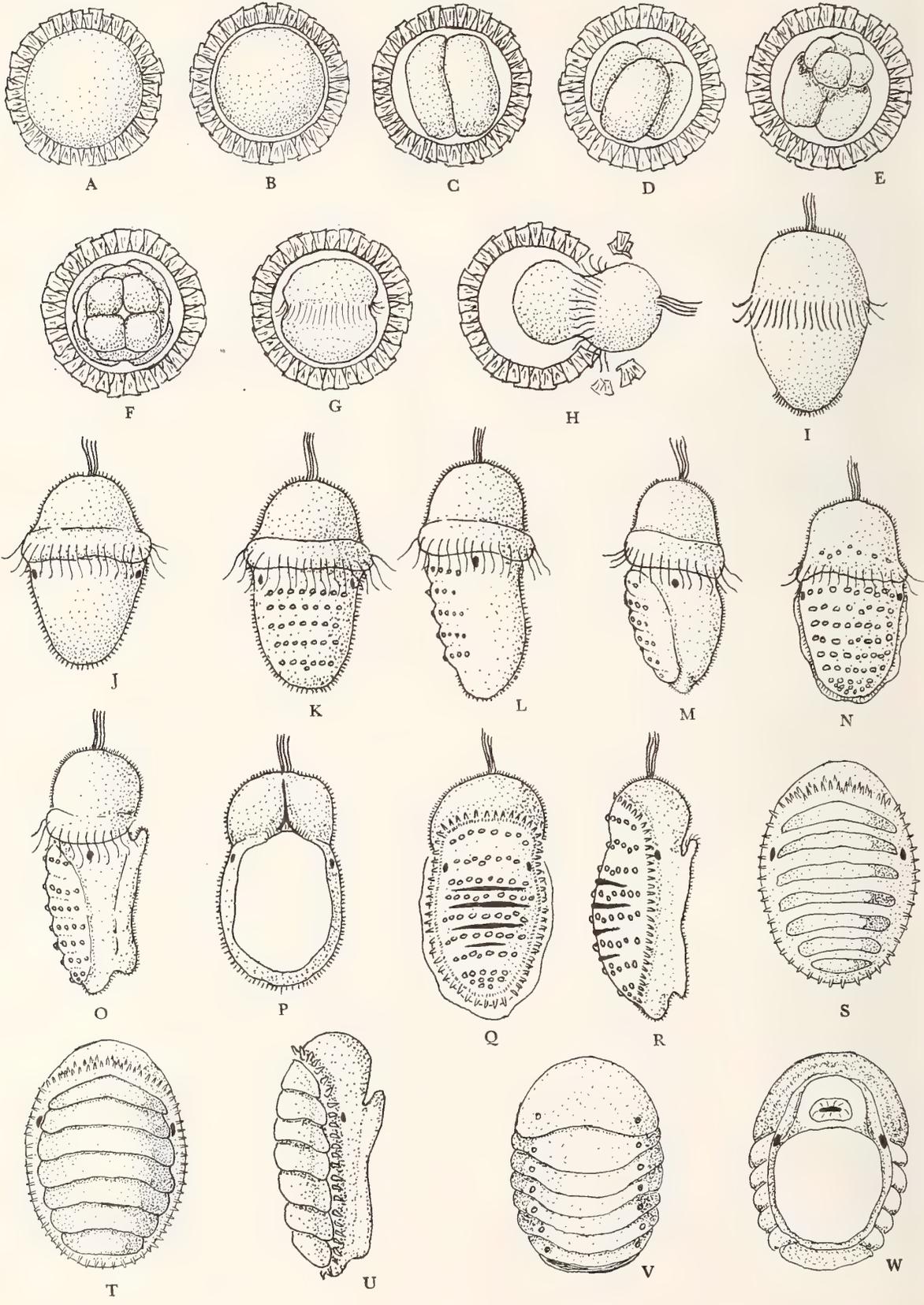
The foot began to form on the ventral surface of the body, just posterior to the prototroch and the mouth (Figure 2 M), about 4-5 days after fertilization. Within a day it was well-differentiated, and a heavily ciliated flap appeared at

(← on facing page)

Figure 1

Time schedule of development for *Mopalia lignosa* and *Mopalia muscosa* in hours and days after fertilization. A vertical bar indicates the exact beginning and end of an event as observed. A dotted line indicates that the exact times were not determined. These times are representative and do not indicate the limits of individual variation.

- | | |
|---|---|
| A. First cleavage | K. Mantle field |
| B. Second cleavage | 1. Large cells appear on the dorsal surface |
| C. Third cleavage | 2. Mantle fold develops |
| D. Fourth cleavage | 3. Mantle field extends onto head |
| E. Gastrulation | L. Foot |
| F. Prototroch | 1. initial bulge |
| 1. faint ciliary action within the chorion | 2. ciliated flaps develop anteriorly |
| 2. strong ciliary action within the chorion | 3. well-developed foot |
| 3. Swimming activity | M. Spicules |
| 4. disappearance of cilia | 1. across dorsal surface of head only |
| G. Apical tuft | 2. all around mantle field |
| H. Hatching | N. Shell plates |
| I. Somatic cilia | 1. CaCO ₃ deposits first seen |
| 1. only at anterior and posterior ends | 2. seventh plate forms |
| 2. distributed over body | 3. plates expand and overlap one another |
| J. Larval eyes | |



its anterior margin (Figures 2 o-p). Whether or not this structure aided in early feeding was not determined.

Approximately 5 days after fertilization, the larvae began to spend increasing amounts of time crawling on the bottom rather than swimming with their still-present prototrochs. This was accompanied by a dorso-ventral flattening of the body. The crawling larvae often attached with the posterior end of the foot and waved their free anterior end from side to side. They used the anterior portion of the foot to gain firmer attachment when needed. Once the prototroch cilia disappeared, the larvae became permanent crawlers and apparently began feeding, crawling slowly forward while moving their heads from side to side. Dark material became visible in the central region of the body.

Head Development

At hatching, the head region was clearly marked off by the prototroch. In the free-swimming trochophore, it was relatively undifferentiated, its most prominent feature being the apical tuft (Figure 2 i). As the foot and mantle formed, it became more flattened (Figure 2 r). Our studies did not determine whether the mantle grew forward over the head, or if the head itself formed new mantle tissue. At about 6.5 days, a groove appeared along the mid-ventral line of the head, being wider at the prototroch and tapering anteriorly (Figure 2 p). Its function was not determined. By 18 days after fertilization, the head had attained essentially its

(← on facing page)

Figure 2

Development of *Mopalia lignosa*

A. Unfertilized egg within chorion. B. Fertilized egg showing the perivitelline space. C. First cleavage (1 hr). D. Second cleavage (1.5 hrs). E. Third cleavage (2.5 hrs). F. Fourth cleavage (3.5 hrs). G. Prototrochal cilia begin beating within chorion (12 hrs). H. Hatching (19 hrs). I. Newly hatched trochophore (about 1 day). J. Free-swimming trochophore. Eye spots appear (3 to 3.5 days). K, L. Dorsal ridges and foot forming (dorsal and lateral views, respectively; about 4 days). M. Mantle fold evident (lateral view; 4.5 days). N - P. Settling stage (dorsal, lateral, ventral views, respectively): 8 dorsal ridges and ciliated flap of foot present (about 5 days). Q, R. Settled larva (dorsal and lateral views, respectively); shell plates 2 to 7 begin forming (6.5 days). S - U. Shell plates expand and apical tuft lost (dorsal, dorsal, lateral views, respectively; 7 - 8 days). V, W. Juvenile chiton (dorsal and ventral views, respectively; 24 days).

adult form (Figure 2 w). Feeding motions of the radula were observed under a compound microscope at this time.

By 8 weeks after fertilization, the juvenile chitons had all the features of an adult: eight shell plates were present, the girdle margin had grown out from under the plates and was covered with spicules, ctenidia had begun to form, and the larval eyes had disappeared.

DEVELOPMENT OF *Mopalia muscosa*

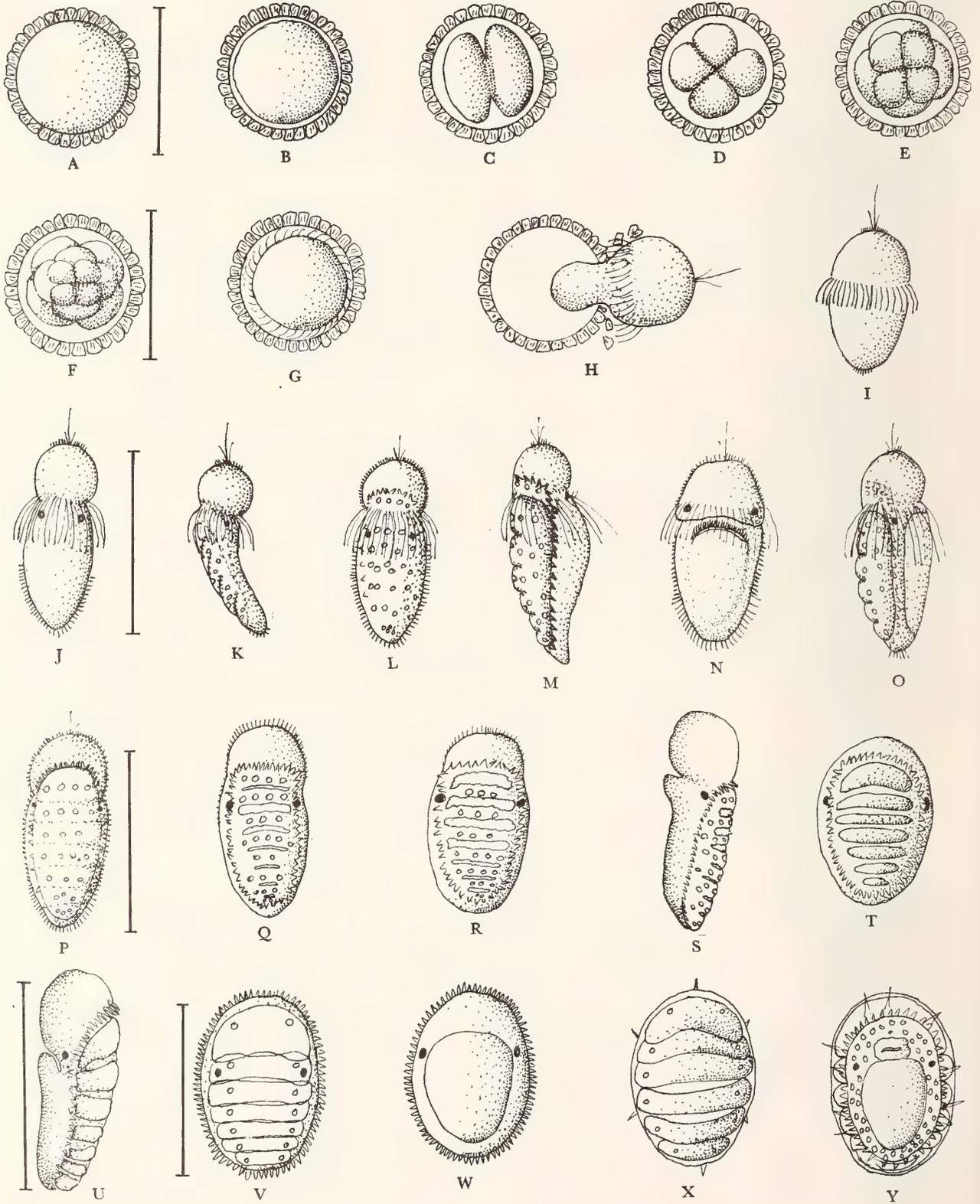
A schedule of development and illustrations of the various stages appear in Figure 1 and Figure 3. Further details on the ontogeny of form and behavior are given below.

Early Development

The eggs of *Mopalia muscosa* are either green or golden brown, 0.29 mm in diameter, and are encased in a bristly chorion. The vitelline membrane of an unfertilized egg lies in close proximity to the chorion (Figure 3 A). A few minutes after fertilization, a gap was visible between the egg and chorion (Figure 3 B). Cleavage followed the typical spiral pattern (Figures 3 C-F). Division after the fourth cleavage and gastrulation were not followed in detail. The first prototroch cilia were seen at 10 hours and the ciliated ring appeared complete 12 hours after fertilization (Figure 3 G). The cilia beat slowly and feebly at first, but their movements increased in frequency and amplitude until hatching at 20 hours (Figure 3 H), when their action was sufficiently powerful to break away pieces of the chorion as the trochophore emerged. The trochophore larvae usually hatched with the apical tuft foremost, but some emerged with part of the prototroch first.

Free Swimming Trochophore

The trochophores were roughly egg-shaped with the prototroch a little above the equator (Figure 3 I). The apical tuft, developed prior to hatching, was surrounded by a field of smaller somatic cilia. A similar field of telotrochal somatic cilia occupied the posterior end (Figure 3 J). These 2 patches of somatic cilia expanded anteriorly and posteriorly until they surrounded the body at 5.5 days. The larval eyes, 2 red pigmented spots embedded in the epithelium covering the body, appeared laterally just posterior to the prototroch at 3.5 days, and were still visible at 32 days (Figures 3 J-Y). In swimming, the larvae rotated continuously in a clockwise direction (as viewed anteriorly): their



bodies oriented vertically with the apical tuft up when hovering. Swimming of a larva was interrupted only when it ran into another larva or the side of the bowl, which caused an asynchronous beat. Ciliary action then stopped for less than a second and resumed slowly. Larvae usually swam along the bottom with the apical tuft in front, randomly moving both horizontally and vertically, but only occasionally swimming to the surface.

Mantle and Shell Development

The post-trochal region appeared elongated at 3.5 days (Figure 3 J). About 5 days after fertilization, it began to flatten dorso-ventrally, and large cells appeared, forming irregular rows on the dorsal surface (Figure 3 K). This was also reported by HEATH (1899) in *Stenoplax heathiana* and by OKUDA (1947) in *Cryptochiton stelleri*. A row of short, pointed spicules then formed anterior to the prototroch, and extended almost entirely across the dorsal surface of the head. A sparse scattering of spicules later appeared laterally on the periphery of the mantle field, and by 6.5 days, spicules formed a complete ring around the circumference of the mantle field. At 5.5 days, transverse grooves began to form dorsally, aligned between the bands of large cells (Figure 3 M), and the latter formed more regular rows, except in the posterior region. The mantle field continued

to expand, and by 11.5 days had extended over the postero-dorsal head region. Mantle growth on the head was accompanied by the loss of the prototroch (Figure 3 P).

Shell plate formation began around 13.5 days with the deposition of seven thin lines of opaque material along the transverse grooves of the mantle field (Figure 3 Q). During their early development, the order of size from the largest to the smallest (counting the cephalic plate as number one) was 2, 3, (4, 1), 5, 6, 7 (Figure 3 Q). This order suggests the sequence of development. Enlargement of the plates continued until they came into mutual contact and extended laterally to the ring of spicules around the mantle field (Figures 3 R-Y). The mantle field itself extended until the rest of the larva was completely hidden. The eighth (caudal) plate did not form until approximately 6 weeks after fertilization. Ctenidia began to form in the pallial groove about two weeks after this, the posterior-most ones being the first to develop.

Foot Development

The foot began to form during the free-swimming stage (6.5 days). It gradually extended as a ventral bulge, and a conspicuous ciliated flap formed on the anterior edge of the foot on the 7th day (Figure 3 N). By the 10th day, the foot was well formed.

Development of the foot was accompanied by a gradual change in locomotion. The 3-day larvae swam rapidly, predominantly near the surface. However, at 6 days, they began to spend more time on the bottom, occasionally adhering to it with their posterior ends. Here they swung freely from the point of attachment or rotated due to proto-trochal action for 1 to 2 seconds; then either they were knocked loose by movement of water in the bowl or freed themselves by swimming action of the prototroch. Once freed, they resumed swimming. As the foot developed further, the trochophores spent increasing periods of time on the bottom. At 9 or 10 days, they attached to the bottom by both the anterior and posterior ends of the foot and rocked from side to side from these two points. Their prototrochs were noticeably smaller and had disappeared by 12.5 days. The larvae were then considered "settled," crawling being their only means of locomotion.

Head Development

External differentiation of the head was minimal until the disappearance of the apical tuft at 11.5 days, which was about the same time as first deposition of the shell plates. As the mantle field extended, the head became flattened

(← on facing page)

Figure 3

Development of *Mopalia muscosa*

A. Unfertilized egg within chorion. B. Fertilized egg, showing perivitelline space. C. First cleavage (1 hr). D. Second cleavage (1.5 hrs). E. Third cleavage (2.5 hrs). F. Fourth cleavage (3.5 hrs). G. Prototroch complete (12 hrs). H. Hatching (20 hrs). I. Early trochophore showing anterior and posterior fields of somatic cilia (1 day). J. Post-trochal region elongated; eye spots (3.5 days). K. Post-trochal region flattened dorsoventrally (5.5 days). L. Spicules on head and beginning of cell alignment on dorsal surface of mantle field (5.5 days). M. Grooves on dorsal surface of mantle field, foot beginning to bulge (6 days). N. Ciliated flap on anterior foot (7 days). O. Foot more differentiated (7 days). P. Settled larva, loss of prototroch (11.5 days). Q. Shell plate deposition, loss of apical tuft (13.5 days). R, S. Mantle field begins to extend onto head (14 days). T, U. Shell plates enlarging (15 days). V. Shell plates in mutual contact (17 days). W. Foot well developed (17 days). X. Juvenile chiton in curled position, 7th plate hidden from view (21 days). Y. Ventral view, head and mouth well formed, but neither 8th plate nor first pair of ctenidia have appeared.

and was soon covered by the mantle dorsally (Figure 3 v). Radular movements were observed in the mouth at 21 days.

SETTLING STIMULI

Metamorphosis in both *Mopalia lignosa* and *M. muscosa* was delayed or prevented by the lack of an appropriate settling substratum. Only two larvae out of several hundred observed underwent complete metamorphosis on glass.

In *Mopalia lignosa*, fully metamorphosed juveniles (shell plates present, no apical tuft, no prototroch cilia) appeared by 7 days after fertilization when water-worn *Mytilus* shells with a film of microscopic algae were added 4.5 days after fertilization. In a bowl left without shells for 14 days, the apical tuft was still present and no shell plates had appeared, though most of the larvae had lost their prototroch cilia and had been crawling 6 days after fertilization. When *Mytilus* shells were added on day 14, fully metamorphosed juveniles were noted within a day.

Similarly, no substratum was added to three bowls containing seawater and *Mopalia muscosa* larvae, while pieces of *Mytilus* shell with an algal film were added to another three such bowls at 5 days after fertilization. In the bowls without the shells, only two larvae ever formed dorsal plates. The rest apparently stopped development, retained the prototroch cilia and never metamorphosed; all subsequently died 14 to 17 days after fertilization. Development in the bowls with *Mytilus* shell progressed normally.

The advantage of a substrate-sensitive settling response is clear. The ability to delay metamorphosis until a suitable substratum is present increases the chances that larvae will settle under conditions favorable for post-larval development. Such a settling response has been shown to exist in *Tonicella lineata* (Wood, 1815) by BARNES (1972) and was briefly mentioned by HEATH (1899: 62-63) for *Stenoplax heathiana*. It has also been found in other mollusks (BAYNE, 1964; THOMPSON, 1964; SWENNEN, 1961; and SCHELTEMA, 1961), as well as in other invertebrate groups.

DISCUSSION

Mopalia muscosa and *M. lignosa*, while similar in many aspects of development, show some differences, particularly in the timing of events. They are compared below to each other, to *Mopalia ciliata* for which some details are available (THORPE, 1962), and to a few more distantly related species.

Development from cleavage through hatching takes place at similar rates in *Mopalia lignosa* and *M. muscosa*, and at 13°C, the larvae hatch roughly 20 hours after fertilization. Development of *M. ciliata* at "normal ocean temperature" is a little slower, and the larvae hatch 36-42 hours after fertilization (THORPE, 1962). Structures arising during the free-swimming stage appear within 2 days of each other in *M. lignosa* and *M. muscosa*; details are not available for *M. ciliata*. Settling can be contrasted in all 3 species: *M. lignosa* loses its prototroch cilia at about 5.5 days, while *M. ciliata* and *M. muscosa* lose theirs on the 8th and 11th days, respectively. For the remainder of development, *M. lignosa* adheres to a schedule 4 days ahead of that for *M. muscosa*.

A major difference in the development of these three species of *Mopalia* is in the ontogeny of the plates. THORPE (1962) states that "the anterior valves are the first to be apparent" in *M. ciliata*. In both *M. lignosa* and *M. muscosa*, the cephalic plate did not form until after the appearance of the plates posterior to it. The caudal plate in *M. ciliata* develops on the 8th day (THORPE, *op. cit.*). In contrast, in both *M. lignosa* and *M. muscosa* the caudal plate doesn't appear until the 6th week.

Mopalia lignosa and *M. muscosa* show sequences of developmental events similar to those of the few other chitons studied. The major differences appear in the timing rather than the nature or order of events. *Tonicella lineata*, according to BARNES (1972), hatches at 2 days and the larvae settle at 3 days. CHRISTIANSEN (1954) reported that *Lepidopleurus asellus* hatched at 20 to 21 hours and settled at about 10 days. HEATH (1899) reported a period of 7 days between fertilization and hatching in *Ischnochiton magdalenensis* (= *Stenoplax heathiana*). OKUDA (1947) noted that *Cryptochiton stelleri* did not hatch until 70 hours or more after fertilization. The larvae emerged with external features which did not develop in *M. lignosa* and *M. muscosa* until the later free-swimming stages. Settling in *Cryptochiton* began 12 to 20 hours after hatching and liberation from the jelly mass.

A curious feature is the placement of the larval eye. In spiralian development, larval eyes usually occur anterior to the prototroch. The larval eyes of chitons are located more posteriorly, behind the head region proper. They apparently still serve a sensory function, since they are innervated by the pallial nerve cord (HEATH, 1904). HEATH (*op. cit.*) puts forth the following interesting hypothesis:

"Now it is obvious that if the chiton eye were situated in front of the velum, as in the annelids, it would be most unfavorably placed after metamorphosis. Under the circumstances the most available situation would be the furrow about the proboscis, where it would be continually obscured and would be practically useless even if provided with tentacles. It seems most reasonable to suppose that as the structures character-

istic of the chitons appeared in the phylogenetic development, the eye-spots gradually shifted their position into the present more favorable location."

SUMMARY

1. Spawning behavior and external features of the larval development were studied in the chitons *Mopalia muscosa* and *M. lignosa* during the months of April-June, 1974, at Pacific Grove, California.
2. Specimens of *M. lignosa* spawned in the laboratory after several hours in containers of standing seawater. Males moved around during spawning while females remained stationary.
3. Electrical stimulation, injection of 0.5 M KCl or homogenate of nervous tissue failed to induce spawning. Eggs obtained through dissection were unfertilizable, even after treatment with 3 ml of 0.1 N NaOH in 100 ml seawater.
4. The sequence of events in the development of the two species is the same, though some differences in timing exist. First cleavage, second cleavage, third cleavage, and hatching occurred about 1 hr., 1.5 hrs., 2.5 hrs., and 20 hrs., respectively, in both species.
5. After hatching, the larvae of both species swam freely for a period. *Mopalia lignosa* settled about 5.5 days after fertilization and *M. muscosa* about 11.5 days after fertilization. During the free-swimming period, the larval eyes, mantle and foot developed.
6. Larvae were considered settled when the prototroch cilia were no longer present, and metamorphosed when the shell plates appeared and the apical tuft was lost. This happened at 6.5 days for *Mopalia lignosa* and 13.5 days for *M. muscosa*. The shell plates of *M. muscosa* appeared to develop in the following order: 2, 3, 1 & 4, 5, 6, 7, 8. No such sequence was noted for *M. lignosa*. The caudal plate in both species did not form until about 6 weeks after fertilization.
7. Both species seemed to exhibit a substrate-sensitive settling response, though further work is needed to verify this.

ACKNOWLEDGMENTS

We would like to express our thanks to Dr. Donald P. Abbott for his guidance and willingness to assist us in this project. We would also like to thank the rest of the faculty and staff of Hopkins Marine Station for their assistance,

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An Association Between
Nuttallina californica and *Cyanoplax hartwegii*,
Two West Coast Polyplacophorans (Chitons)

BY

RICHARD LOUIS GÓMEZ¹

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

(1 Text figure)

INTRODUCTION

THE HABITATS AND HABITS of *Cyanoplax dentiens* (Gould, 1846) have received little attention. Those papers that have investigated *C. dentiens* (HEATH, 1905; BERRY, 1917; 1948) indicate a far ranging intertidal habitat for it but make no mention of interactions between it and other organisms. Presented is a report on a finding that this small (≤ 1 cm.) chiton *Cyanoplax dentiens* (LIGHT, 1964; SMITH, 1975) is often found under the moderately large (≈ 40 mm) chiton *Nuttallina californica* (REEVE, 1847). Field and laboratory studies show that: a) this association is not random; b) *C. dentiens* is negatively phototactic; c) *C. dentiens* can actively crawl under *Nuttallina*; and d) *C. dentiens* can detect and seek out *Nuttallina*.

FIELD STUDIES

A total of over 100 *Nuttallina* from Carmel Beach, Carmel, California; Point Pinos, Pacific Grove, California; and Mussel Point, Pacific Grove, California, were removed; only under those *Nuttallina* from Point Pinos were many *Cyanoplax dentiens* found. The association between *Nuttallina* and *C. dentiens* was restricted to vertical and angled rock faces with moderate to little light exposure in the mid-zone of the *Nuttallina* range (90 to 120 cm tidal height).

Over 100 *Cyanoplax dentiens* were collected from Point Pinos. Individual intertidal rocks were exhaustively examined and all *C. dentiens* encountered were removed. Only 10% of these were not found under *Nuttallina*, a frequency well below that expected for a chance association. Approximately 25 *Acmaea* and 10 chitons of species other than *Nuttallina* were investigated, but no *C. dentiens* were found under any of these animals.

A 12-hour night watch was conducted of 5 *Nuttallina*, 3 with *Cyanoplax dentiens* naturally occurring and 2 with *C. dentiens* introduced under them. The positions of all chitons had been previously mapped out and marked two days prior to the watch. A red light was used at regular one-hour intervals to observe the chitons and the distance they had travelled. To be able to make regular readings even at high tide, the investigator wore a wet suit and face-mask. During the watch 3 *Nuttallina* left their locations; 2 returned to take up their original position. No *C. dentiens* moved during the watch despite the fact that those exposed by the moving *Nuttallina* encountered heavy wave shock. Desiccation may play a larger role in the association than wave shock since *Nuttallina* move primarily at night (MOORE, 1975), a time when desiccation rates are low.

LABORATORY STUDIES

It seemed likely that *Cyanoplax dentiens* could detect the presence and direction of a nearby "host" *Nuttallina* since the low field density of the latter would make chance encounter an unlikely event. In order to test for the ability

¹ Permanent address:
3798 Highland Drive, Carlsbad, CA 92008

to detect chemical cues carried down a flow of water from a *Nuttallina* a simple Y-maze experiment was conducted. Three 12-hour trials were run using ten fresh *Cyanoplax* starting at the base of the Y for each trial. At the top of one arm of the Y was placed a *Nuttallina* and a glass vial was placed at the top of the other arm in order to approximately match any possible turbulence in the fresh sea water which was allowed to flow equally down each arm towards the base (Figure 1). Pooled results indicated non-random movement (chi-square test; $p < 0.01$), with 18 *C. dentiens* moving over 1 cm toward the *Nuttallina* and 3 over 1 cm away. A control without a *Nuttallina* showed random movement.

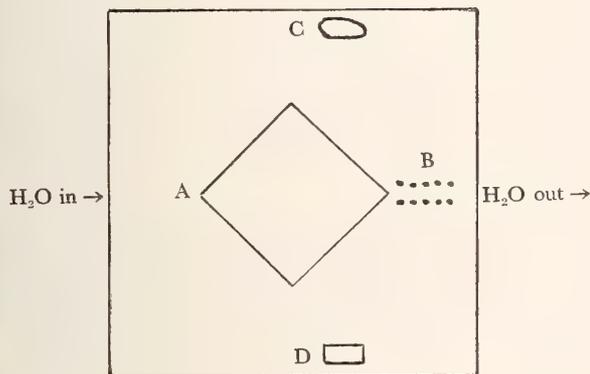


Figure 1

Y-maze test. Flowing current in a tray was equally divided by Y-structure (A) and carried past the 10 *Cyanoplax dentiens* (B). Twelve hours were allowed for movement of the *Cyanoplax dentiens* toward either the *Nuttallina californica* (C) or the glass vial (D).

A phototactic test of *Cyanoplax dentiens* was run in a wooden tray with a 200-watt light bulb at one end, and a gentle flow of water perpendicular to the light-dark axis. Fifteen *C. dentiens* were placed along the mid-line of the tray and tested for 12 hours. Fourteen went 2 cm or more away from the light, indicating negative phototaxis.

On three occasions *Cyanoplax dentiens* kept in finger bowls with *Nuttallina* were observed to move under their "host." The *Nuttallina* neither conspicuously lifted its girdle to accommodate the *Cyanoplax* nor did it make an obvious attempt to avoid the smaller chiton. Once under the *Nuttallina*, the *Cyanoplax* oriented lengthwise along the pallial groove, but showed no preference to facing anteriorly or posteriorly relative to the "host."

DISCUSSION

Cyanoplax dentiens, in using *Nuttallina californica* as a microhabitat, is benefited in several ways: protection against desiccation, sunlight, predators and against other physical parameters. *Cyanoplax dentiens* further restricts its habitat by not locating itself under either those *Nuttallina* outside of the mid-zone of the *Nuttallina* range or those exposed to stronger light; the latter restriction perhaps is a result of its apparent negative phototaxis.

Cyanoplax dentiens can seek out and detect *Nuttallina*, as the Y-maze test indicated, presumably using a chemical cue. This ability implies coevolution has occurred.

SUMMARY

- 1) *Cyanoplax dentiens* was found underneath *Nuttallina californica*, along its pallial groove.
- 2) The association was restricted primarily to those *Nuttallina* on a shady vertical or angled rock face in the mid-zone of the *Nuttallina* range.
- 3) *Cyanoplax dentiens* appeared to be negatively phototactic.
- 4) *Cyanoplax dentiens* possibly uses *Nuttallina* as its micro-habitat for purposes of protection against desiccation, harsh sunlight, predators, etc.
- 5) *Cyanoplax dentiens* was found capable of detecting and seeking out *Nuttallina californica*.

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The Diet and Feeding Habits
of *Nuttallina californica* (Reeve, 1847)
from Two Contrasting Habitats in Central California

BY

RAE NISHI¹

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

(2 Text figures)

INTRODUCTION

INDIVIDUALS OF *Nuttallina californica* (Reeve, 1847) are widely distributed along the western coast of the United States (the Strait of Juan de Fuca, Washington to San Diego, California [BURGHARDT & BURGHARDT, 1969]), yet information on their diet and feeding habits is largely speculative. According to MACGINITIE & MACGINITIE (1968: 386) *Nuttallina* are largely sedentary animals, found in deep, form-fitting depressions in the hard substratum, and seldom or never venture out to feed. MacGinitie and MacGinitie suggest that such animals have forsaken the grazing habit and subsist on algal debris which settles in the depressions. The absence of detailed studies supporting or contradicting this view motivated the present study.

Mussel Point, Pacific Grove, California provides several kinds of habitats, of which two were selected for study. One consists of crevices in vertical rocky surfaces at the +0.9 m to +1.2 m tidal level, exposed to heavy surf action, and on the western portion of the Point. Here animals commonly found with *Nuttallina* are the barnacles *Tetraclita squamosa* Darwin, 1854 and *Chthamalus* spp., and the mussel *Mytilus californianus* Conrad, 1837. The second habitat consists of beds of calcareous tubes formed by the colonial cirratulid worm *Dodecaceria fistulicola* Ehlers, 1901. Here *Nuttallina* are found in depressions 1 to 2 cm deep on the mostly horizontal surface of the beds at about the +0.3 m tidal level and exposed to moderate surf. The *Dodecaceria* beds were located on the eastern portion of the Point. Few other animals are found upon the *Dodecaceria* bed itself

but neighboring it (on the exposed rocky substratum) are *Tegula funebris* (Adams, 1855), *Phragmatopoma californica* Fewkes, 1889 and *Anthopleura xanthogrammica* Brandt, 1835.

The objective of this study was to compare the diet and feeding habits of *Nuttallina californica* in these two habitats. Specifically, to define their diet, determine the sources of the food eaten, and compare the foods eaten with those apparently available in the microhabitat.

METHODS

A specific site at each of the two study areas as well as one site at Carmel Beach were chosen. At each site food resources in the vicinity of *Nuttallina californica* were determined by randomly placing a 25 x 25 cm grid over the site and measuring the area covered by each macroscopic alga. This was done 4 times at each location. The relative abundance or availability of each alga was taken as the area covered by that alga divided by the total area covered by all of the algae present. At each location all of the *N. californica* found within the areas surveyed for algal cover were collected. This included a total of 25 animals from rocky crevices at Mussel Point and Carmel Beach and 26 animals from a *Dodecaceria* bed at Mussel Point. The specimens were immediately preserved in a 10% formaldehyde solution to stop further digestion. Gut contents were analyzed by removing the digestive tract from the stomach to the small intestine and squeezing out its contents on to a microscope slide. This was examined under a dissecting microscope and the macroscopic pieces of algae identified, counted, and removed. A compound microscope was used

¹ Permanent address:
1816 Las Lanas Lane, Fullerton, CA 92633

to identify the smaller pieces of algae on the basis of color, cell structure and size. Relative abundance of each type of alga within the guts was estimated by counting the number of pieces of each alga found (with rough attempts to correct for gross differences in size), and dividing by the total number of pieces of algae found.

RESULTS AND DISCUSSION

From preliminary gut content analyses it was immediately apparent that instead of merely scraping at algae with its radula, *Nuttallina* was taking in large pieces. Length of the largest piece in the gut of each of 34 animals was measured and the number standardized to the size of the chiton by expressing it as the percent of body length. These figures show *N. californica* is capable of consuming pieces of algae

up to 20% of its body length, although the average size was 12% of the body length. No appreciable difference in algal fragment size between *Nuttallina* of the different habitats could be seen. Microscopic algae such as diatoms and blue-green algae were also found in all of the animals, yet the abundance of large algal pieces comes from macroscopic algae. The frequency of occurrence of various macro-algae in the guts of different individuals is shown in Figure 1. The most frequently occurring algae in the animals from rocky crevice communities are *Corallina* spp. (80% of the individuals examined), *Endocladia muricata* (Postels & Ruprecht) J. G. Agardh (60%), and *Cladophora trichotoma* (C. A. Agardh) Kützing (48%); the most frequently consumed algae by *Dodecaceria* bed animals were *Gelidium* spp. (53%) and *Cladophora trichotoma* (76%). These figures correspond roughly to the relative frequency with which these algae are found in the habitats from which these animals came.

The relation of the algal distribution in the habitat vs. average diet at the 3 field sites is shown in Figure 2. *Corallina* spp. make up a much higher percentage of the gut contents of *Nuttallina* collected at all 3 locations than would be expected by the composition of the flora in these habitats. In addition crustose corallines are found in considerably smaller amounts in the guts than expected by their presence in the habitat. This suggests that *Nuttallina* may preferentially seek out erect corallines over crustose forms. This may be due to limitations imposed upon their feeding habits by the manner in which their radulas work. The radula in these chitons appears to be best adapted for use in consuming large bushy algae by tearing them into pieces or swallowing them whole if they are small enough. The radula does not appear to function as a scraping organ, which would be best suited in consuming crusts.

According to Dr. I. A. Abbott (personal communication), the plants most commonly found in the study areas in terms of biomass and therefore to be expected in drift feeders are: the flowering plant *Phyllospadix* sp., the brown alga *Macrocystis pyrifera* (Linnaeus) C. A. Agardh, and red algae *Rhodomenia* spp.; *Botryoglossum farlowianum* (J. G. Agardh) DeToni, *Botryocladia pseudodichotoma* (Farlow) Kylin, and *Gigartina corymbifera* (Kützing) J. G. Agardh. None of these was found within the guts of the *Nuttallina californica* examined. Thus it is highly unlikely that the *Nuttallina* studied were feeding upon drift plants.

Since the diet of *Nuttallina californica* indicates feeding by grazing on larger algae, and these are not available within deep depressions in the *Dodecaceria* bed, feeding activity must occur when animals emerge from their shelters at high tide. Preliminary studies support this hypothesis. Numerous *Nuttallina* were observed crawling out of their depressions when the bed was awash on an incoming tide;

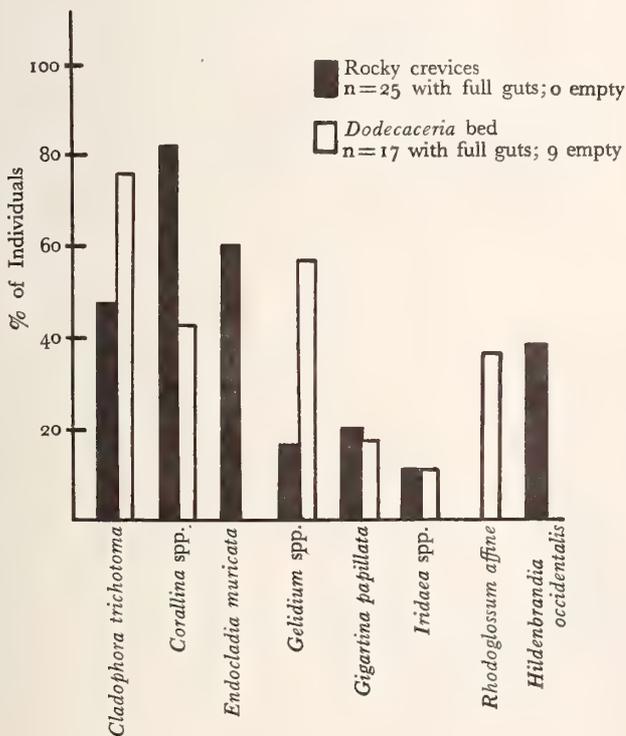


Figure 1

Comparison of the frequency of occurrence of macroscopic algae in the guts of *Nuttallina californica* from rocky crevices (n = 25, with full guts) with those from *Dodecaceria* beds (n = 26, of which 9 contained no food). Percentages were calculated on the basis of the 17 animals with full guts)

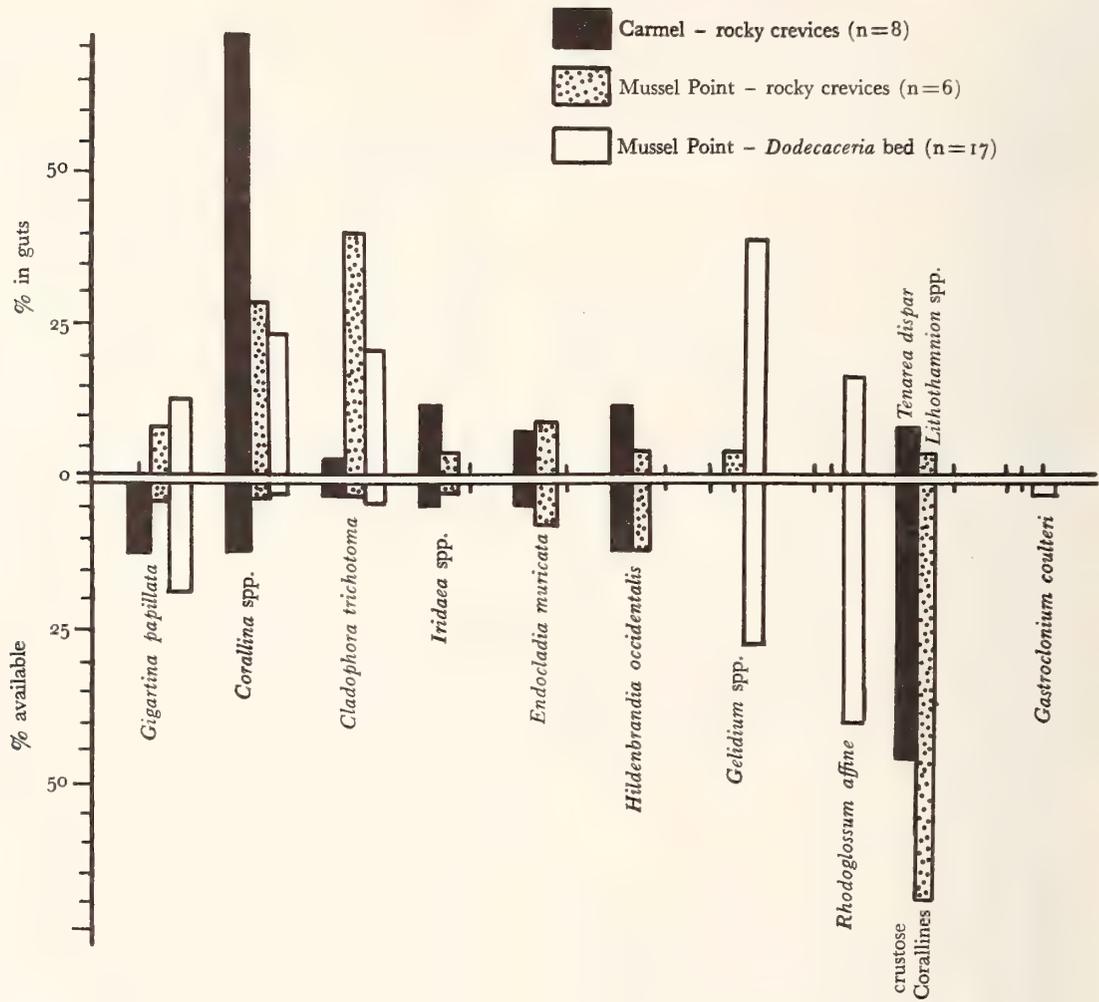


Figure 2

Comparison of algal composition in terms of percent of total algal cover at study sites with corresponding relative abundance of the algae in the gut contents of *Nuttallina californica* collected from each area at the time of the survey. From Carmel rocky crevices n = 8; from Mussel Point rocky crevices n = 6; and from Mussel Point *Dodecaceria* beds n = 17

however, further studies need to be done in order to determine whether this movement is correlated with feeding activity.

**NATURAL HISTORY NOTES
ON THE TWO POPULATIONS OF
*Nuttallina californica***

The populations of *Nuttallina californica* studied in the two contrasting habitats differed markedly in their external appearances. *Nuttallina californica* from the *Dodecaceria* bed possessed valves so worn that species-characteristic markings were erased. The shells of these chitons were beige in color and pitted by a blue-green alga, *Entophysalis deusta* (Meneghini) Drouet & Daily. This coloration exactly matched that of the *Dodecaceria* bed. In addition, the girdle bristles were predominantly white with scattered reddish brown ones. In contrast the rocky crevice *Nuttallina* possessed black valves with occasional white stripes down either side of a shiny dorsal ridge. The girdle bristles were primarily reddish-brown with more white ones towards the outer edge of the girdle. These *Nuttallina* were often found with a profuse growth of algae on both valves and girdle. These included *Endocladia muricata* (Postels & Ruprecht) J. G. Agardh, *Corallina* spp., *Polysiphonia hendryi* Gardner, *Cladophora trichotoma* (C. A. Agardh)

Kützing, *Rhodoglossum affine* (Harvey) Kylin, *Peyssonnelia* sp., and *Microcladia* sp.

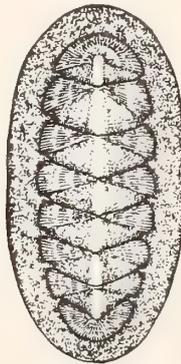
Representative specimens collected from the *Dodecaceria* bed were positively identified as *Nuttallina californica* by Mr. Allyn G. Smith of the California Academy of Sciences.

ACKNOWLEDGMENTS

I would like to thank Dr. Donald P. Abbott and Dr. Robin Burnett for their helpful comments in aiding me to write this paper, James Watanabe, Stuart Seiff, and Betsy Lyman in assisting me in collecting animals, and Allyn G. Smith for identification of the *Nuttallina*. My deepest and most profound thanks go to Dr. Isabella A. Abbott for her patient aid in identifying gut contents, her constant encouragement throughout this study, and her advice in writing this paper.

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The Diet of the Chiton *Cyanoplax hartwegii* in Three Intertidal Habitats

BY

MARK F. ROBB¹

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

(3 Text figures)

INTRODUCTION

ALTHOUGH CHITONS are abundant along California shores, studies of their food and feeding have been limited largely to species of *Mopalia* (e.g. BARNAWELL, 1960; BOOLOOTIAN, 1964), *Placiphorella* (see MCLEAN, 1962), and *Cryptochiton* (MACGINITIE & MACGINITIE, 1968). The purpose of this study was to examine the diet of the chiton *Cyanoplax hartwegii* (Carpenter, 1855) in different habitats. I also include a few notes on the slit formula of the plates of *C. hartwegii*.

INTERTIDAL HABITATS

OF *Cyanoplax hartwegii*

Cyanoplax hartwegii on the Monterey Peninsula, California, is found in the mid and upper intertidal zones. Three general habitats where large numbers of *C. hartwegii* were present were studied.

First, at approximately the +60 cm tide level, *Cyanoplax hartwegii* was most common underneath the brown alga *Pelvetia fastigiata* (J. G. Agardh) DeToni on otherwise nearly bare rock in an area of low wave action. Here *Pelvetia* covered approximately 70% of the rock area, providing a shady and moist environment even during daylight hours and at low tide. Because of shading by algae and by other rocks, only about 5% of the rock was exposed to sunlight at low tide. *Pelvetia* was by far the dominant alga; small amounts of *Hildenbrandia occidentalis* Setch-

ell, *Petrocelis franciscana* Setchell and Gardner, *Gigartina papillata* (C. A. Agardh) J. G. Agardh, *Fucus distichus* Linnaeus, and crustose corallines were also present. *Cyanoplax hartwegii* occurred in numbers up to 25 per m² in the *Pelvetia* habitat.

At a higher tide level, +60 cm to +1.2 m, *Cyanoplax hartwegii* was found in crevices which provided a moist, shady, and wave-sheltered environment. *Endocladia muricata* (Postels and Ruprecht) J. G. Agardh, *Hildenbrandia occidentalis*, *Gigartina papillata*, *Cladophora* spp., and crustose corallines were the most common algae present. *Cyanoplax hartwegii* occurred in much smaller numbers, about 5 per m² of total rocky surface, in the crevice habitat.

Finally, some tidepools at the +60 cm to +1.2 m tide level contained crevices which maintained a shady, protected habitat with minimal exposure to surf. *Cyanoplax hartwegii* occurred in such pools at densities of up to 15 per m². *Gigartina leptorhynchos* J. G. Agardh, *Petrocelis*

		No. slits in head valve				
		8	9	10	11	12
No. slits in tail valve	8	0	1	3	0	2
	9	0	2	5	2	0
	10	0	1	5	7	1
	11	0	0	2	0	0
	12	0	0	0	0	0

n=31

Figure 1

Number of *Cyanoplax hartwegii* with a specific slit formula¹ Permanent address:

846 Forest Avenue, River Forest, IL 60305

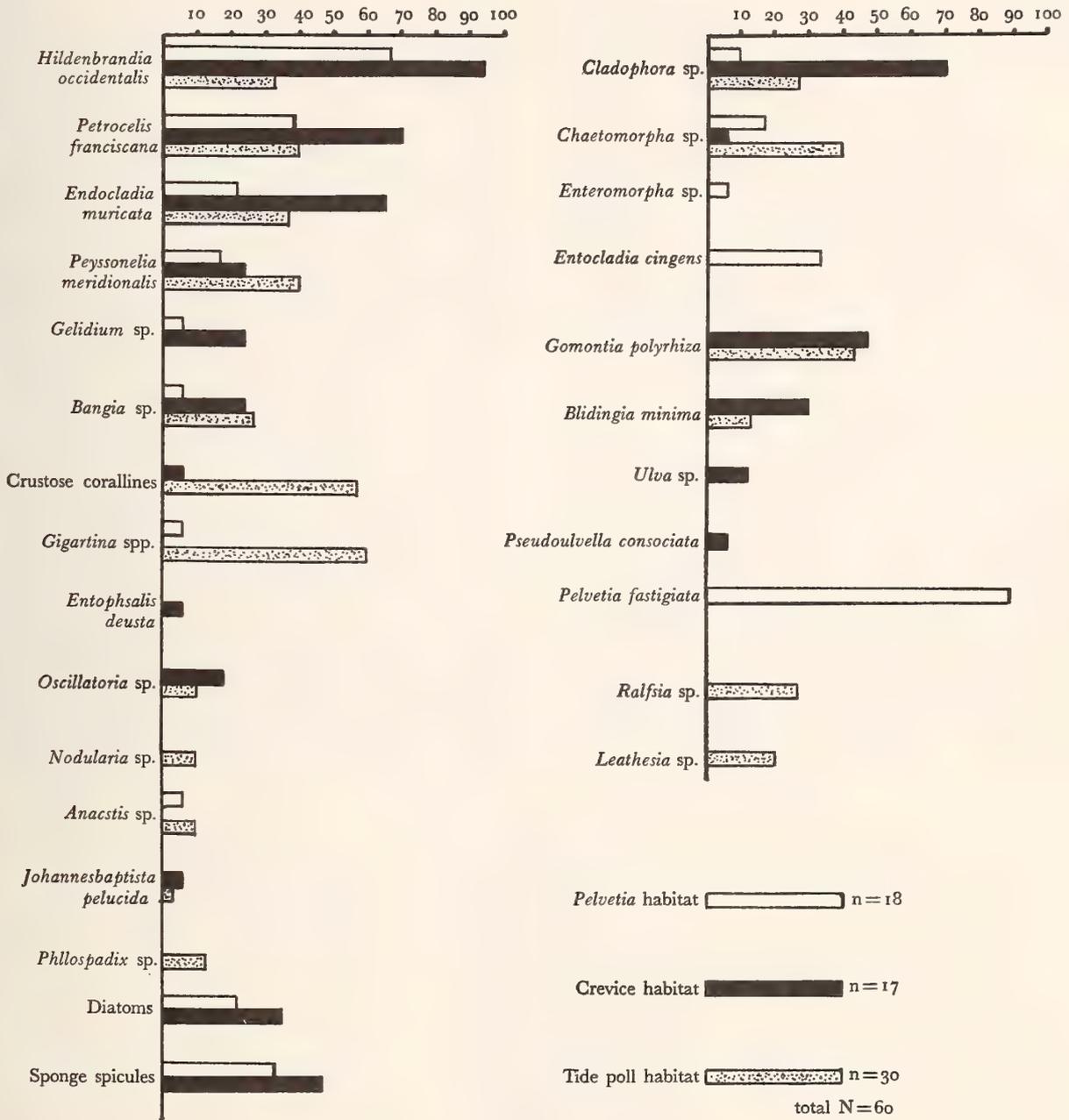


Figure 2

The percentage of the total number of guts where a specific alga was found in chitons from three habitats

franciscana, *Prionitis lanceolata* (Harvey) Harvey, crustose corallines, and microscopic green algae were the most common algae present.

MATERIALS AND METHODS

I collected *Cyanoplax hartwegii* from the above habitats and immediately placed them in a buffered 10% formaldehyde solution to stop further digestion and preserve the algae in the gut. The stomach and intestine were slit open and the content distributed to one or more slides, spread and teased out, and mounted in 50% glucose syrup for examination under a compound microscope. Identifications of the algae were made using SMITH (1969) and were verified by Dr. I. A. Abbott. The digestive diverticulum was not extensively examined since several dissections yielded only blue green algae and yeast cells.

Specimens of *Cyanoplax hartwegii* were identified as such on the basis of size, color, shape, insertion plate slit formula, and comparison with museum specimens of *C. hartwegii* and *Cyanoplax dentiensi* (Gould, 1846) identified by Allyn G. Smith and kindly provided by the California Academy of Sciences. Average insertion plate slit formulas (11-1-11 for *C. hartwegii*, 11-1-10 for *C. dentiensi*) proved unreliable for identification. In specimens conforming to *C. hartwegii* in all other respects, numbers of slits ranged 9-12 in the head valve and 8-11 in the tail valve

(Figure 1). The formula 11-1-10 occurred most often, which is the slit formula given for *C. dentiensi*.

RESULTS

The results of the gut content analyses of 65 *Cyanoplax hartwegii* from the various habitats are shown in Figures 2 and 3.

Since *Pelvetia* made up 70% of the plant cover of the *Pelvetia* habitat, it is not surprising that the 18 *Cyanoplax hartwegii* taken here ate large amounts of this alga. *Pelvetia* occurred in 89% of the digestive tracts and comprised the bulk of the material in each individual. *Hildenbrandia occidentalis*, and *Petrocelis franciscana* were found in much smaller quantities in many individuals.

In the crevice habitat where *Pelvetia* was absent, *Cyanoplax hartwegii* ate moderate amounts of *Hildenbrandia*, *Petrocelis*, *Endocladia*, and *Cladophora* spp. The relative quantities of these algae in the digestive system varied in the 17 individuals examined, but for the population as a whole they occurred in roughly equal amounts in the total gut content.

In the tidepool habitat the 30 *Cyanoplax hartwegii* examined displayed a more varied diet. *Gigartina leptorhynchos* appeared in many *Cyanoplax* here, but many other algae were present in small quantities, including crustose corallines. Even when *Gigartina* and crustose cor-

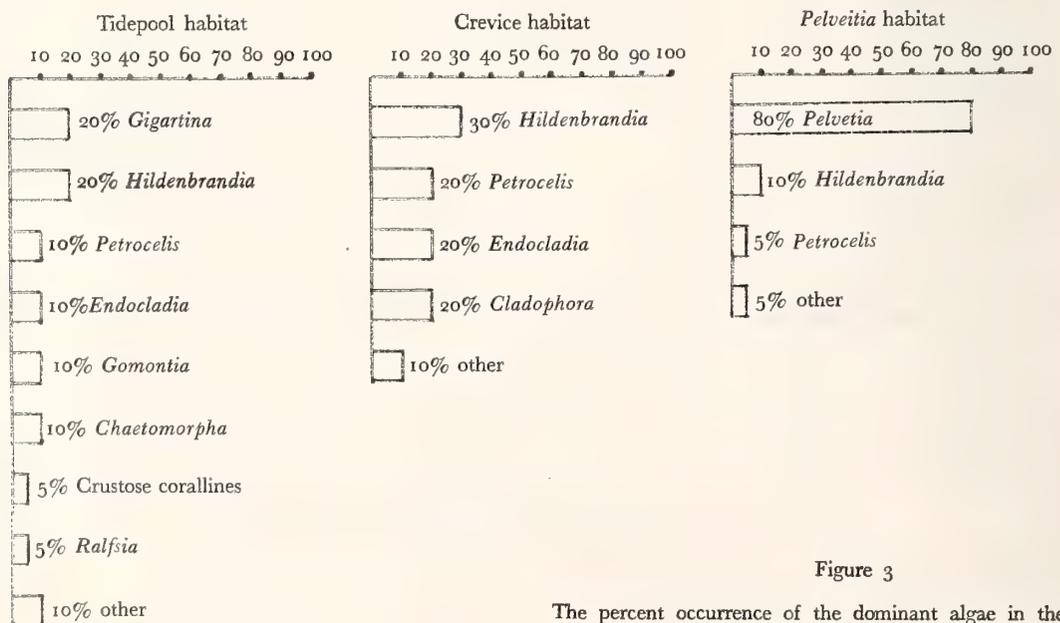


Figure 3

The percent occurrence of the dominant algae in the total gut content of chitons from three habitats

allines were present in the *Pelvetia* habitat and crevice habitat, they were not eaten. Thus, it would appear that there is a preference for *Pelvetia*, *Hildenbrandia*, *Petrocelis*, *Endocladia*, and *Cladophora* spp. when these are present.

In the gut of *Cyanoplax hartwegii*, larger algal species (e.g. *Pelvetia*) and encrusting algae (e.g. *Hildenbrandia*) appear in very small pieces indicating feeding by rasping. However, algae with slender branches or highly dissected blades (e.g. *Endocladia muricata*, *Gigartina leptorhynchus*) appear in the gut in much larger pieces, reminiscent of algal fragments found in the guts of *Nuttallina californica* (Reeve, 1847) by NISHI (1975), and suggestive of feeding by biting or tearing algal branches.

SUMMARY

1. Stomach contents were examined in 65 specimens of *Cyanoplax hartwegii* taken from three different intertidal microhabitats near Monterey, California.
2. In the *Pelvetia* bed habitat, *Pelvetia* made up 80% of the total diet, while in the higher crevice habitat, the algae *Hildenbrandia*, *Endocladia*, *Petrocelis*, and *Cladophora* spp. comprised 90% of the diet and were eaten in relatively equal amounts.
3. In the high tidepool habitat, *Cyanoplax hartwegii* ate a much wider variety of algae. *Gigartina* and *Hildenbrandia* together made up 40% of the diet. Crustose corallines and *Gigartina* occurred in all habitats exam-

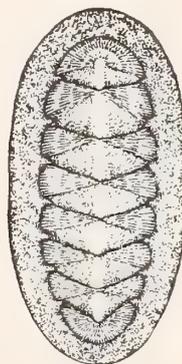
ined, but were eaten by *Cyanoplax* only in the tidepools.

ACKNOWLEDGMENTS

I would like to express my thanks to Dr. Isabella A. Abbott for technical help in all aspects of the gut content analysis and identification of algae. My appreciation cannot be measured. Her guidance in all areas of the study, and her insight and beauty as a sincere, warm human being made my time at Hopkins Marine Station an experience I will never forget.

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The Diet of the Chiton *Mopalia lignosa* (Gould, 1846)

(Mollusca : Polyplacophora)

BY

FRANCES T. FULTON¹

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

INTRODUCTION

Mopalia lignosa (Gould, 1846), a common chiton of the rocky intertidal zone around the Monterey Peninsula, California, is found most often under rocks between about +0.45 m to -0.45 m tidal levels, where even during lowest tides the environment stays moist. Its food habits have never been reported, though the diets of some related species are known. *Mopalia hindsii* (Reeve, 1847) is omnivorous; those collected in San Francisco Bay had ingested about 59% animal matter (BARNAWELL, 1960). The gut of

M. muscosa (GOULD, 1846) from Santa Monica, California, was found to contain largely red and green algae (BOOLOOTIAN, 1964); in San Francisco Bay the same species ingested diatoms, other algae, and a smaller amount (15%) of animal food (BARNAWELL, *op. cit.*). The present study was carried out to determine the diet of *M. lignosa*, in relation to the foods available in the habitat.

MATERIALS AND METHODS

Animals were collected throughout a 5-week period from April 23 through May 30, 1974, from three central California sites: Point Pinos, Pacific Grove, Carmel Point,

¹ Permanent address:

26745 Paseo Robles, Carmel, CA 93921

Table 1

Description of Collecting Areas

Tidal heights are given for location of *Mopalia lignosa*; algae listed were typically 20 - 30cm above this height. Complete species names of algae are given in Table 4

	Habitat Description		
	Point Pinos	Stillwater Cove	Carmel Point
Substratum	Granite	Sandstone	Granite
Tidal level	-0.45 to -0.6 m.	-0.3 to -0.45 m.	-0.3 to -0.45 m.
Size of Study Area	3 by 6 meters, low tidepool	6 by 12 meters, flat	30 mm by 6 meters, crevice
Wave Action	Heavy	Calm	Heavy
Dominant Algae	<i>Ulva</i> spp., <i>Gigartina papillata</i> , erect and crustose Corallines, <i>Petrocelis franciscana</i> , <i>Hildenbrandia occidentalis</i> , <i>Cladophora</i> spp., diatom mats.	<i>Ulva</i> spp., <i>Phyllospadix</i> sp., <i>Smithora</i> sp., <i>Enteromorpha</i> spp., <i>Cladophora</i> spp., <i>Gigartina papillata</i> , erect and crustose Coralline spp., <i>Porphyra perforata</i> , <i>Gigartina leptorhynchos</i> , <i>Petrocelis franciscana</i> , <i>Hildenbrandia occidentalis</i> , <i>Peyssonelia meridionalis</i> .	<i>Egregia menziesii</i> , <i>Gigartina papillata</i> , <i>Ulva</i> spp., crustose Coralline spp.
Other Chitons	<i>Mopalia muscosa</i>	<i>Stenoplax fallax</i> (Carpenter in Pilsbry, 1892)	<i>Tonicella lineata</i> (Wood, 1815) <i>Mopalia hindsii</i>

Carmel; and Stillwater Cove, Pebble Beach. These habitats are characterized in Table 1. The microhabitat inhabited by *Mopalia lignosa* is restricted to the undersides of rocks 30 cm. or more in diameter, usually where irregularities raised the bottom surface slightly above a coarse sand and small rock bottom. This habitat was also inhabited by worms, sponges, and tunicates; drift algae tended to collect at the base of such rocks. The most conspicuous algae found growing in the surrounding lighted areas were recorded to help characterize the general habitat area. Animals were collected during morning low tides, and 23 of the 42 animals taken were dissected the same morning. The remainder were kept in plastic tanks with circulating seawater and with no food for 2 to 6 days prior to dissection to determine the time required for the gut to empty. Gut contents of each animal were observed *in situ*, then removed and examined under a compound microscope. Four slides from each animal, representing the contents of the stomach, digestive diverticula, small intestine and the large intestine, were examined. Plant material was identified with the assistance of Dr. Isabella Abbott. Most algal fragments were clearly identifiable to genus and sometimes species. Fecal pellets were examined when present.

Six chitons on one rock at Stillwater Cove were marked in the field and checked for evidence of movement over a 7 day period. Marking was made by gluing numbered circles of waterproof paper to the dorsal plates of the chitons with "Zip-Grip" (Devcon Co., Danvers, Mass.). Movement was determined by measuring distances between animals and established reference points on the rocks.

In addition, 8 animals were placed in aquaria containing running seawater, starved for 5 weeks and then fed *Ulva* spp. Four of these starved animals were dissected. Fecal pellets from all 8 animals were examined.

RESULTS

The degree of fullness of the sections of the digestive system is tabulated in Table 2 for freshly collected and starved chitons. Only freshly collected animals had full stomachs. The guts of starved animals were distended with mucus, probably from the animal itself, and contained only trace amounts of food.

The stomachs contained pieces of brightly colored algae, from a few mm up to 3 cm long. The digestive diverticulum never showed recognizable algal material. Enigmatic granular spheres, 8-16 μ m in diameter, often in membrane-

Table 2

Location of Algae in Guts of Animals
Large and small intestines were analysed separately, but yielded the same data

Days after collection	Number examined	Number with algae in stomach	Number with algae in small/large intestine
0	23	20 a	21 a
1	4	3 b	3 b
2	4	2 c	4 b
3	4	0 d	2 b
4	3	0 d	2 c
5	2	0 d	1 c
35-42	2	0 d	1 c

Legend: a: considered full
b: partially full
c: only a trace
d: totally empty

bounded clusters, were observed in almost every animal, most frequently in diverticulum preparations, but also in other sections of the gut.

Mopalia lignosa feeds largely on plant material (Table 3). The plants found in the gut contents included 13 taxa of red algae, 7 taxa of green algae, 3 taxa brown algae, several kinds of diatoms, and 1 flowering plant. Frondose algae such as *Ulva* spp. were found more frequently than crustose algae such as *Peyssonelia*. It was impossible to identify more specifically the coralline algae since the pieces ingested were small. Not all species of algae present in the habitat were found in the gut contents (Table 4).

On the other hand 65% of the total number of algae species (exclusive of diatoms) found in the gut were not observed in the immediate habitat. Six species, or 40% of this total not observed in the habitat were microscopic algae, unlikely to have been observed macroscopically. None of these minute species, however, constituted more than an average of 1 or 2% of the food eaten. Diatoms occurring as small films on sand, small rocks and other algae were very common, and constituted the largest amount of plant material (Table 3). Several definite, mostly naviculoid species were observed in the contents, but these were not further identified.

The bulk of the plant material ingested by the Point Pinos animals was diatoms and *Ulva* spp.; these were also

Table 3

Plants and other Materials Found in the Gut Contents of 38 *Mopalia muscosa* from three localities on the Monterey Peninsula. Values given are the average percentage of total gut content occupied by each material.
N = the number of individuals examined

	Point Pinos (N=13)	Carmel Point (N=13)	Stillwater Cove (n=12)
Diatoms	24.5	11.5	12.9
<i>Ulva</i> spp.	20.5	11.0	17.5
Laminariales	0.0	12.0	4.5
<i>Gelidium</i> spp.	4.5	8.2	0.0
<i>Gigartina</i> spp.	5.0	8.5	0.0
<i>Enteromorpha</i> sp.	6.0	4.5	2.5
<i>Endocladia muricata</i>	2.5	6.0	1.3
Delesseriaceae	0.0	0.0	4.0
Corallines	1.0	1.0	6.0
<i>Peyssonelia meridionalis</i>	2.5	1.5	0.0
<i>Iridaea</i> sp.	0.0	2.0	0.0
<i>Hildenbrandia occidentalis</i>	2.0	1.0	0.05
<i>Petrocelis franciscana</i>	0.0	1.5	0.0
<i>Erythrotrichia carnea</i>	0.05	0.05	1.5
<i>Erythrocladia irregularis</i>	0.0	0.0	1.2
<i>Cladophora</i> spp.	2.5	0.0	1.5
<i>Percursaria dawsonii</i>	0.05	0.05	1.5
<i>Endocladia cingens</i>	0.05	0.05	3.0
<i>Centroceras clavulatum</i>	0.0	0.0	1.4
<i>Ectocarpus</i> spp.	0.0	1.0	0.05
<i>Phyllospadix</i> sp.	0.0	0.0	1.5
<i>Chaetomorpha</i> sp.	1.5	0.0	0.0
<i>Polysiphonia</i> sp.	0.0	0.0	1.0
<i>Endophyton</i> sp.	0.0	0.0	0.0
<i>Pelvetia fastigiata</i>	0.0	0.0	0.05
Animal material	2.3	2.5	3.3
Rocks and sand	25.05	27.6	35.2

the dominant algae in the environment. *Enteromorpha* spp. appeared in three-fourths of the animals but in small amounts. *Peyssonelia meridionalis* appeared in over half the animals and *Hildenbrandia occidentalis* in a third of them, also in small amounts.

Ulva spp. and diatoms were likewise the two most important and widely eaten foods at Carmel Point. Brown algae (order Laminariales) completely filled the guts of 2

(adjacent column →)

Table lists both the Algal Types found within approximately a meter of animal examined and the algal types actually found in the guts of the animals

Table 4

Algae Found in Habitat	Algae Found in the Gut
Green	
<i>Cladophora</i> spp.	<i>Cladophora</i> spp.
<i>Enteromorpha</i> sp.	<i>Enteromorpha</i> sp.
<i>Ulva</i> spp.	<i>Ulva</i> spp.
	<i>Chaetomorpha</i> spp.
	<i>Percursaria dawsonii</i>
	Hollenberg & Abbott, 1968
	<i>Endocladia cingens</i>
	Setchell & Gardner, 1920
	<i>Endophyton</i> sp.
(Brown)	
<i>Egrecia menziesii</i>	
(Turner) Areschough, 1876	
	Laminariales
	<i>Ectocarpus</i> spp.
	<i>Pelvetia fastigiata</i>
	(J. Ag.) DeToni, 1895
(Red)	
Crustose corallines	
Erect corallines	"Corallines"
<i>Hildenbrandia occidentalis</i>	<i>Hildenbrandia occidentalis</i>
Setchell & Gardner, 1917	
<i>Gigartina leptorhynchos</i>	<i>Gigartina</i> spp.
J. Agardh, 1885	
<i>Gigartina papillata</i>	
(C. Agardh) J. Agardh, 1826	
<i>Petrocelis franciscana</i>	<i>Petrocelis franciscana</i>
Setchell & Gardner, 1917	
<i>Peyssonelia meridionalis</i>	<i>Peyssonelia meridionalis</i>
Hollenberg & Abbott, 1968	
<i>Porphyra perforata</i>	
J. Agardh, 1883	
<i>Smithora naiadum</i>	
(Anderson) Hollenberg, 1959	
	<i>Endocladia muricata</i>
	(Postels & Ruprecht) J. Ag., 1847
	<i>Gelidium</i> spp.
	Delesseriaceae
	<i>Iridaea</i> sp.
	<i>Centroceras clavulatum</i>
	(C. A. Agardh) Montagne
	<i>Polysiphonia</i> sp.
	<i>Erythrotrichia carnea</i>
	(Dillwyn) J. Agardh, 1883
	<i>Erythrocladia irregularis</i>
	Rosenvinge, 1909
Diatoms	Diatoms
<i>Phyllospadix</i> sp.	<i>Phyllospadix</i> sp.

animals from Carmel Point but they averaged only 12% of the algae present in the 12 guts analyzed. Red algae were also important, forming close to 30% of the diet of *Mopalia lignosa* here. This represents 10 species; 3 of them, *Endocladia muricata*, *Gelidium* spp., and *Gigartina* spp. made up the bulk.

As in the other two locations, the major foods of *Mopalia lignosa* at Stillwater Cove were *Ulva* spp. and diatoms, together comprising about 30% of the gut contents. Two animals had 55% of their guts full of *Ulva* spp. A crustose coralline appeared in 58% of Stillwater Cove animals and made up 6% of the bulk. A variety of brown and red algae, not seen from other sites, was found in trace amounts. Approximately 1% of the flowering plant *Phyllospadix* was also observed in 2 of these animals.

The animal material identified was composed of: foraminifera bryozoans, small crustacea or pieces thereof, sponge spicules, and bristles (probably from chitons). Animal matter comprised less than 3% of the total contents; 5% being the greatest bulk found in any one animal. This result is compared with results for *Mopalia hindsii* and *M. muscosa* in Table 5.

Table 5

Table compares Percentages of Animal, Vegetable and other material found in the guts of three species of *Mopalia*. "Other" refers largely to inorganic debris. The number of animals examined by each worker follows "n = "

Species	% Vegetable	% Animal	% "Other"
<i>Mopalia lignosa</i> n = 38	68	2.7	29.3
<i>Mopalia hindsii</i> n = 242 BARNAWELL, 1960	31	59.0	10.0
<i>Mopalia muscosa</i> n = 110 BARNAWELL, 1960	78	15.0	7.0

Nearly all animal guts contained sponge spicules. Chiton bristles appeared infrequently, but when observed, were covered with algae and detritus. *Entocladia cingens*, *Erythrotrichia carnea* and *Endophyton* sp. were three such epiphytes.

Forty-eight hours after starved laboratory animals were fed *Ulva* spp., they produced fecal pellets containing *Ulva* fragments.

Six animals on one rock were closely observed. Each of these animals moved during the week-period of observations. Two of the 6 disappeared off the rock; of the remaining, the furthest moved 8 cm during the 7 days. Trails of fecal pellets were found near approximately 1/4 of the animals collected in the morning; no fecal pellets were found at other times of the day. This implies they had fed at night.

DISCUSSION AND SUMMARY

Mopalia lignosa on the Monterey Peninsula appear to be herbivores; an average of 68% of the gut contents is of plant origin, consisting principally (11-20%) of green algae (*Ulva* spp.) and several species of diatoms, with a variety of other algal species in smaller amounts. Small plant particles in the small and large intestine were without pigment or protoplasm, only the cell walls remaining. On the other hand, if pieces were large, they were often passed through the gut unchanged in color or cell shape. Animal material found in the gut consisted of small crustacea, or fragments of them, foraminifera and bryozoans of sizes and shapes suggestive of inadvertent feeding. These never averaged more than 3.3% of the bulk of the total contents.

Only freshly dissected animals had full stomachs. The amount of mucus present in the gut increased as the gut emptied of food when animals were deprived of food 6 days.

Full stomachs in freshly dissected chitons and trails of fecal pellets upon collection of these animals suggest early morning or nocturnal feeding.

ACKNOWLEDGMENTS

I wish to express my thanks and gratitude to Dr. Isabella Abbott for her help in identifying algae in the guts of *Mopalia lignosa*, and for her help in compiling this paper. With her constant aid this research was made possible.

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Diet, Activity and Feeding in *Tonicella lineata* (Wood, 1815)

BY

PETER ANDREW DEMOPULOS¹

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

(6 Text figures)

INTRODUCTION

Tonicella lineata (Wood, 1815) is a common and distinctive chiton of the Pacific coast. In western North America it extends from the Aleutian Islands to San Diego, California and is also relatively abundant in northern Japan (BURGHARDT & BURGHARDT, 1969). In the area of Monterey Bay, California, it ranges from intertidal pools to 65 m depth (SMITH & GORDON, 1948: p. 205). Such a wide distribution in latitude and depth implies exposure to a varied spectrum of physical and biological factors. However, the microhabitat in which *Tonicella lineata* and other species of *Tonicella* are found is surprisingly narrow, for this genus appears to require the presence of coralline algae, either crustose or erect, as a substratum (BARNES, 1972, and YAKOVLEVA, 1952).

The larvae of *Tonicella lineata* settle only if presented with a coralline algal substratum (BARNES, 1972). Also, this species displays a disruptive dorsal coloration which blends well with the surface of coralline algae, offering an excellent defense against visual predation.

In view of this seeming dependence on coralline algae, it has been proposed (BARNES, 1972), but not supported with quantitative data, that corallines are used by *Tonicella* as food. The present report concerns the diet of *T. lineata* and the possible existence of activity and feeding patterns. A distinction between intertidal and subtidal populations is also discussed.

DIET INVESTIGATION MATERIALS AND METHODS

Specimens were collected at Mussel Point, Pacific Grove, California, from three relatively distinct habitats: a high intertidal tidepool (at approximately the +4 ft tidal level);

a low intertidal region characterized by an abundance of *Phyllospadix scouleri* Hooker; and subtidal rocks at depths of 6 to 10 m within the canopy of *Macrocystis pyrifera* (Linnaeus) C. A. Agardh. Coralline algae predominate in each region. A list of coralline and other algae found in each habitat is provided in Table 1. Identifications were verified by Dr. Isabella Abbott of Stanford University.

A total of 25 *Tonicella lineata* (6 tidepool, 11 intertidal and 8 subtidal) were collected at varying times throughout the day-night and tidal cycles. Specimens were preserved immediately in a solution of 10% buffered formaldehyde in sea water.

The content of the entire digestive tract, from stomach to anus, of each animal was subjected to microscopic examination, and a visual estimate was made of the various constituents of biologic and inanimate origin. Along with gut content determinations, the relative fullness of the anterior digestive tract was recorded for all specimens. Three categories were employed. These are: "full" (greater than 70% of the digestive tract filled with ingested material), "moderate fullness" (30-70% filled), and "empty" (less than 30% of the digestive tract containing ingested matter).

RESULTS

The percentages of the identifiable gut content constituents in animals from each habitat are presented in Figures 1-3. Coralline algae always represented the major food ingested. It was not possible to distinguish between species of coralline algae on the basis of fragments in the gut for the rasping of the radula removes cell layers and not whole regions of the algal thallus, hindering identification.

The category, "Detritus and Substrate," was predominantly mineral material, some almost certainly CaCO₃ from corallines (chalky white grains, dissolving with production of gas on treatment with 1% HCl). Other material in this category appeared to be decomposed plant or animal tissue, but no clear cell structure was observed. In any

¹ Permanent address:

6530 83rd Place SE, Mercer Island, WA 98040

Table 1

Predominant Algae and their Percentage of Total Algal Cover in the Three Habitats Studied

Tidepool Habitat	%	Low-Intertidal Habitat	%	Subtidal Habitat	%
¹ <i>Corallina officinalis</i> var. <i>chilensis</i> (Decaisne) Kützing	55	¹ <i>Hydrolithon decipiens</i> (Foslie) Adey	50	¹ <i>Calliarthron tuberculosum</i> (Postels and Ruprecht) Dawson	30
¹ <i>Calliarthron tuberculosum</i> (Postels and Ruprecht) Dawson	15	<i>Peyssonnelia meridionalis</i> Hollenberg and Abbott	15	¹ <i>Hydrolithon decipiens</i> (Foslie) Adey	30
¹ <i>Lithophyllum grumosum</i> Foslie	7	¹ <i>Calliarthron tuberculosum</i> (Postels and Ruprecht) Dawson	10	¹ <i>Lithophyllum proboscideum</i> Foslie	30
<i>Peyssonnelia meridionalis</i> Hollenberg and Abbott	7	<i>Iridaea</i> spp.	6	<i>Rhodymenia pacifica</i> Kylin	10
<i>Cladophora graminea</i> Collins	3	<i>Ulva</i> sp.	6		
¹ <i>Hydrolithon decipiens</i> (Foslie) Adey	3	¹ <i>Lithothamnium phymatodeum</i> Foslie	5		
<i>Prionitis lanceolata</i> Harvey	3	<i>Cladophora graminea</i> Collins	4		
<i>Endocladia muricata</i> (Postels and Ruprecht) J. G. Agardh	3	<i>Callophyllis</i> spp.	4		
¹ <i>Melobesia mediocris</i> (Foslie) Setchell and Mason (on <i>Phyllospadix</i>)	2				
<i>Hildenbrandia occidentalis</i> Setchell	1				
<i>Gastroclonium coulteri</i> (Harvey) Kylin	0.3				
<i>Iridaea</i> spp.	0.3				
<i>Laurencia crispa</i> Hollenberg	0.4				

¹ = Coralline alga

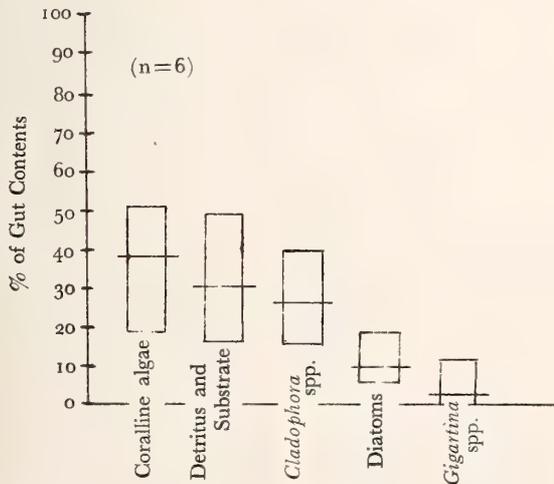


Figure 1

Gut contents of six *Tonicella lineata* from tidepool habitat. Bars indicate range. Horizontal line within bar indicates mean.

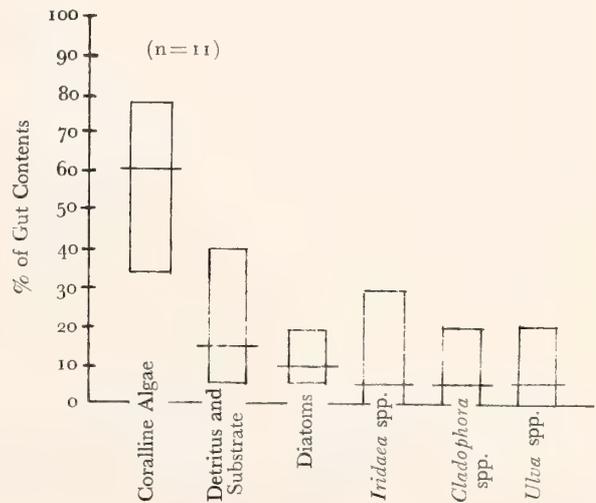


Figure 2

Gut contents of 11 *Tonicella lineata* from low intertidal habitat. Bars indicate range. Horizontal line within bar indicates mean.

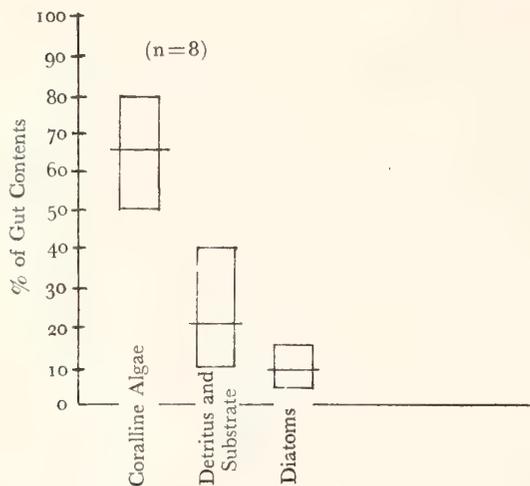


Figure 3

Gut contents of 8 *Tonicella lineata* in subtidal habitat. Bars indicate range. Horizontal line within bar indicates mean.

event, the percentage of coralline algae ingested is probably even higher than indicated graphically, for a substantial part of the "Detritus and Substrate" category very likely represents coralline algal structural material.

Figure 6 illustrates the relations between "fullness" of the anterior digestive tract and time of day. Subtidal speci-

mens were fuller at night. No consistent variation in the "fullness" of intertidal animals with time of day was observed.

ACTIVITY MATERIALS AND METHODS

Activity patterns were investigated in the field on subtidal and intertidal populations over a 24-hour period. In the subtidal survey, two separate rock faces with algal distributions conforming to that listed in Table 1 and bearing a combined total of 11 *Tonicella lineata*, were chosen. Positions of all animals were recorded at 4-hour intervals, using a 50 cm x 50 cm quadrat frame. Intertidally, the tide-pool habitat described previously was chosen for study. Specimens were marked with numbered squares of waterproof paper attached to the valves with an acrylic glue (Tm "Zip-Grip 10," Devcon Corp., Danvers, Mass.). Fifteen specimens were observed hourly, tide permitting, throughout a 24-hour period. Ten of these were marked and placed in the tidepool site one week before study; 5 were returned to this site one day before study.

RESULTS

Movements of the subtidal and intertidal populations are given in Figures 4 and 5 respectively. All estimates are minimal for only net displacement in a straight line was

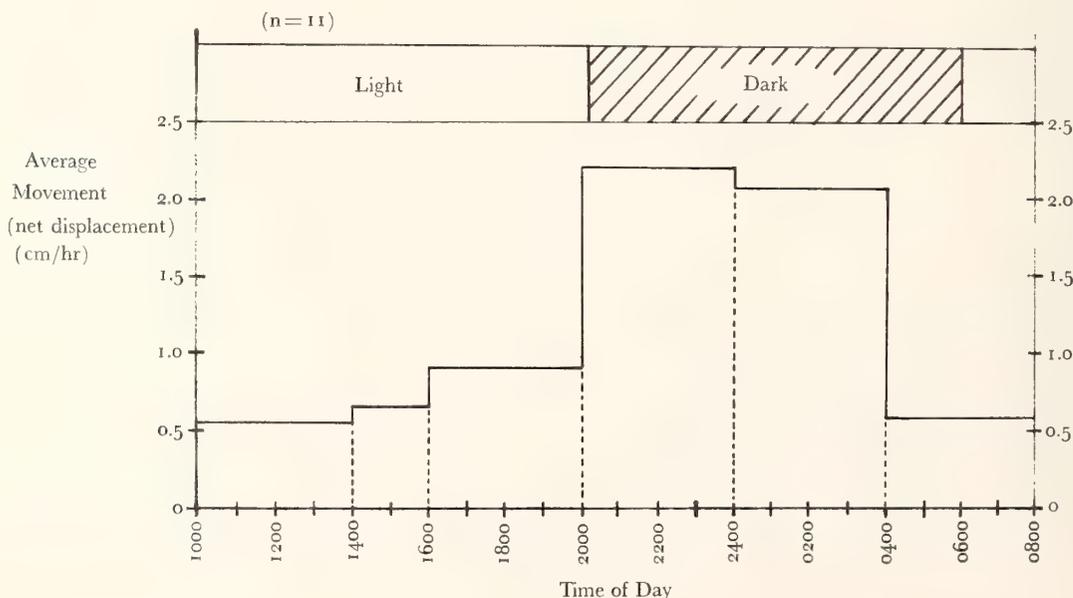


Figure 4

Activity of 11 *Tonicella lineata* in subtidal habitat over one 24-hour period.

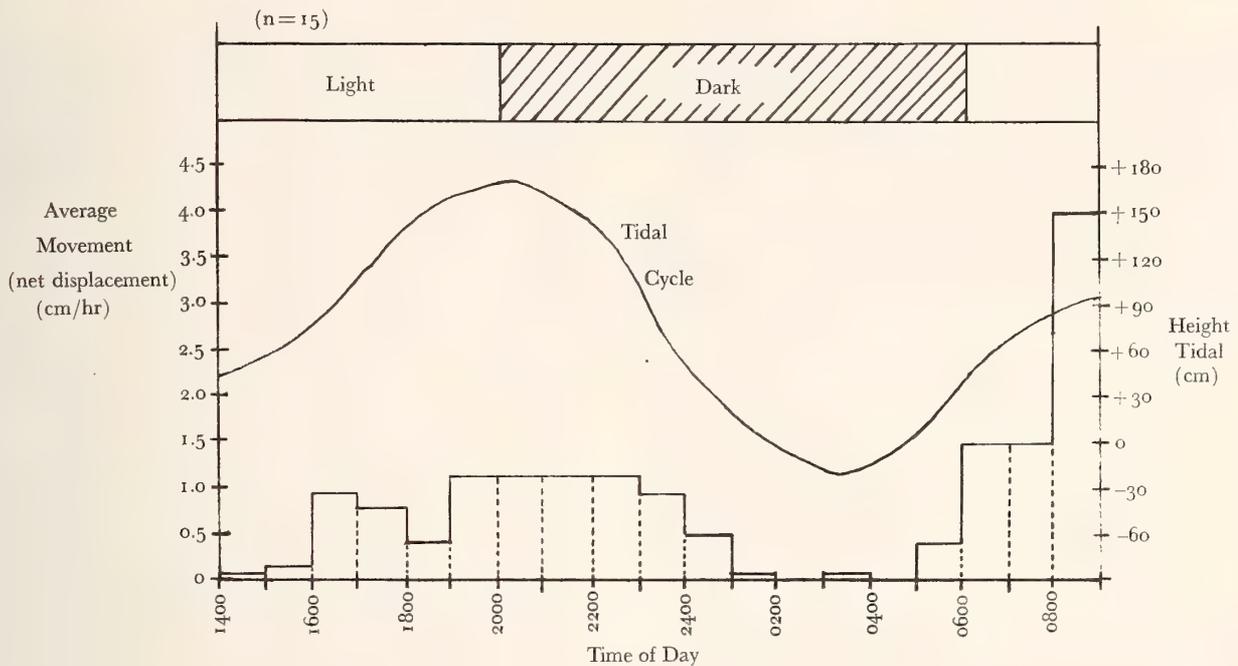


Figure 5

Activity of 15 *Tonicella lineata* in intertidal habitat over one 24-hour period.

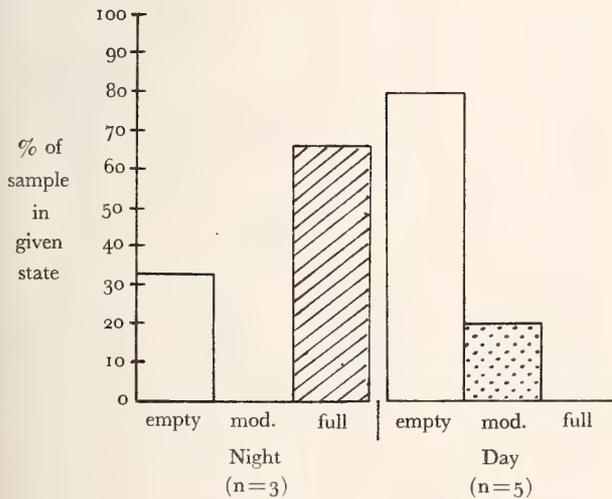


Figure 6

Relative "fullness" of the anterior digestive tract of subtidal specimens versus time of day. Diagonal lines indicate "full" digestive tracts, stippling "moderate fullness", and unmarked bars represent "empty" specimens (explanation of categories on page 42).

measured. For the intertidal animals, movement from 1900-2300 hrs was determined by dividing the total movement during the four-hour period by 4 and plotting it in 4 hourly increments. Further observations were not possible because of rough surge.

During the 24-hour surveys of activity, 3 of the 11 subtidal individuals exhibited homing, returning before sunrise to the positions and orientations noted at the initiation of the watch. Intertidally, 3 of the 15 marked chitons homed with the approach of low tide at the end of the complete 25-hour tidal cycle.

TAXONOMY

Consistent differences in size and coloration are found between intertidal and subtidal populations of *Tonicella lineata*. BARNES (1972) voiced the suspicion that a taxonomic differentiation between subtidal and intertidal communities exists in Oregon and Washington, and indicated that further work was in progress relating to this question.

Sex, length and width measurements, valve and girdle coloration, and numbers of anterior and posterior valve

notches were recorded for 36 specimens (6 subtidal and 30 intertidal, including tidepool). A difference ($p < 0.2$) (Student's t-test) in the total number of valve notches was found. Intertidal animals consistently exhibited a greater sum of anterior and posterior notches.

Subtidal specimens are typically smaller (1 to 2 cm in length) with purple lines on the girdle, and lavender and pink hues closely matching the coralline substrate. Intertidal individuals, ranging 2 to 4 cm in length, have darker valve and mantle coloration with yellow lines on the girdle.

DISCUSSION

Coralline algae clearly comprise the majority of material ingested by *Tonicella lineata*; the narrowness of microhabitat exhibited in the field is reflected in the limited number of algal genera and species ingested (see Figures 1 to 3 and Table 1). It is nonetheless surprising that no red algae other than coralline algae were ingested by subtidal specimens, for reds such as *Rhodomenia* spp. were available. The absence of green algae in the guts of subtidal animals and brown algae in digestive tracts of intertidal animals corresponds to the scarcity of greens subtidally and browns intertidally in the sites studied. Brown algae were also scarce subtidally, and absent from the gut contents of subtidal animals.

Diatoms averaged about 10% of the gut contents in all habitats studied. Microscopic observation reveals fewer intact, more "digested" diatoms in the posterior portions of the gut. As diatoms are common epiphytes on coralline algae, they may be passively ingested with the corallines and subsequently utilized as a food source.

Coralline algae, due to the considerable calcium carbonate content, would appear to provide a poor source of nutrition per bulk weight. However, they are abundant and grazing competition is probably low.

The findings that activity in *Tonicella lineata* conforms to a diel cycle subtidally and a tidal cycle intertidally are noteworthy. Nocturnal activity subtidally would be advantageous in avoiding predators with vision. Although such predators have not been demonstrated for this chiton, the close visual conformity that *T. lineata* displays with its coralline substrate strongly suggests such a possibility. Likewise, decreased activity with low tide may be advantageous in the intertidal zone, for heightened activity in an aerial environment would result in respiratory inefficiency (B. ROBBINS, 1975) and increased exposure to desiccation.

The correspondence of relative "fullness" of the anterior digestive tract in subtidal specimens with the observed

cyclic activity patterns suggests that increased activity is associated with increased feeding. Intertidally, the gut "fullness" data do not support a similar conclusion.

Subtidal individuals of *Tonicella lineata* were generally smaller and differently colored than those from the intertidal area; they had fewer valve notches, and a somewhat different activity pattern. Whether these represent taxonomic, ecological, or age differences in the two populations is unclear. Experiments in which members of the two populations are transplanted and juxtaposed might be helpful in clarifying this question.

SUMMARY

1. *Tonicella lineata* characteristically occurs on a coralline algal substratum.
2. Coralline algae comprise an average of more than 50% of its diet.
3. Subtidally, *Tonicella lineata* exhibits increased activity nocturnally. Intertidally, heightened activity coincides with periods of high water.
4. Indications of homing behavior were observed in some intertidal and subtidal individuals.
5. Intertidal and subtidal populations of *Tonicella lineata* differ in body size, color, activity pattern, and number of valve notches.

ACKNOWLEDGMENTS

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Predation on the Chiton *Cyanoplax hartwegii*

(Mollusca : Polyplacophora)

BY

ANNE E. DEBEVOISE¹

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

INTRODUCTION

On California rocky shores *Cyanoplax hartwegii* (Carpenter, 1855) occurs in higher tidepools, damp crevices, and under dense stands of algae at intertidal heights of +45 cm to +1.2 m above mean lower low water (ANDRUS & LEGARD, 1975). In the Monterey Bay region the densest populations (up to 30/m²) are found on rocks covered by heavy beds of the brown alga, *Pelvetia fastigiata* (J. G. Agardh) DeToni, at a tidal height of about +0.9 m to +1.05 m, in areas protected from strong wave action. Few erect plants grow under the *Pelvetia* cover, but a film of encrusting red algae and microscopic species are generally present.

According to ROBB (1975), in this habitat *Pelvetia* is a major food of *Cyanoplax hartwegii*. In addition, *Pelvetia* might be expected to offer protection to the chitons against wave surge and desiccation, and to provide an excellent screen against predators. Preliminary field observations carried out at low and intermediate tides both day and night revealed no instances of predation on *C. hartwegii* but disclosed a number of species deemed potential predators including the carnivorous snails *Thais emarginata* (Deshayes, 1839) and *Acanthina spirata* (Blainville, 1832), the hermit crabs *Pagurus samuelis* (Stimpson, 1857) and *Pagurus granosimanus* (Stimpson, 1859), the crabs *Pachygrapsus crassipes* (Randall, 1839) and *Hemigrapsus nudus* (Dana, 1851), the sea stars *Pisaster ochraceus* (Brandt, 1835), *Patiria miniata* (Brandt, 1835) and *Leptasterias pusilla* (Fisher, 1911), and the western gull *Larus occidentalis* (Audubon, 1839). The present investigation posed the questions: 1) do some or all of these organisms prey on *C. hartwegii*, and 2) does the *Pelvetia* bed habitat provide significant protection for the chitons against some or all of these predators? To answer these questions, predation on naturally occurring populations and on populations situated where extant *Pelvetia* was removed, was studied in the field. Concurrent with these field observations, artificial test situations were set up in laboratory aquaria to induce interaction between potential predators

and *Cyanoplax*. I herein report on these studies, conducted in the spring of 1974.

FIELD STUDIES

Methods and Results:

A *Pelvetia fastigiata* covered granite rock with a surface area of about 1.5 m² was chosen as a site to study the role of *Pelvetia* as a deterrent to predation on *Cyanoplax*. The rock was surrounded by sand at a tidal height of about +90 cm and was located off of a protected point of the Hopkins Marine Station property in Pacific Grove, California. To the natural population of 25 *Cyanoplax* were added 30 additional *Cyanoplax*. After the population stabilized for 5 days to 45 chitons, all the *Pelvetia* from one side of the rock was removed, exposing half of the *Cyanoplax* population. A common predator of intertidal molluscs, *Pisaster ochraceus*, was used as the test predator. Four *Pisaster* were added to each side of the test rock 30 minutes before the oncoming tide washed over the rock. During the next tidal cycle, any *Pisaster* that left the rock was replaced; this happened on eight occasions on the side where *Pelvetia* remained and only twice on the bare side. During the tidal cycle, 10 chitons from the bare side and only 2 from the *Pelvetia* side were eaten (a significant difference; $p < 0.05$, Chi-squared test). This finding supports the concept that *Pelvetia* offers *Cyanoplax* protection.

Although numerous *Tegula* sp. and various *Acmaea* spp. were present, none were eaten, even though it has been demonstrated by LANDENBERGER (1968), MAUSEY (1966), and PAINE (1969) that both species are eaten by *Pisaster* at a higher rate than chitons.

To determine the effect of *Larus occidentalis*, the western gull, on the *Cyanoplax* population, a survey of Granite Point within Pt. Lobos State Reserve, Monterey County, California was made in conjunction with MOORE's (1975) study. The study site and the procedures are described by MOORE (1975).

Cyanoplax was conspicuous only within an area approximately 20 m x 3 m which had scattered dense layers of *Pelvetia*; its density there was estimated to be 4 *Cyano-*

¹ Permanent address:

5072 San Joaquin Drive, San Diego, CA 92109

plax/m². No *Cyanoplax* shell plates were found in over 100 regurgitation pellets of the gulls, while Moore found plates of 62 individuals of the more exposed and abundant chiton, *Nuttallina californica* (Reeve, 1847). Thus there is no indication that this common foraging bird feeds on the locally available *Cyanoplax*.

LABORATORY STUDIES

Methods and Results:

In order to test for predation under controllable conditions, *Cyanoplax* and potential predators were kept in aquaria both in the presence and in the absence of algal covering. One set of experiments was conducted in indoor aquaria measuring 60 x 30 x 30 cm, and provided with a constant flow of unfiltered seawater at 14°C. The natural day-night cycle was maintained, occasionally being interrupted at night with artificial lights. Two rocks, one bare, one covered with *Pelvetia fastigiata*, each with a surface area of about 300 cm², were placed at opposite ends of each aquarium, on a 2 cm layer of coarse sand and shell fragments. On each rock three *Cyanoplax* were placed: 1 small

(1-2 cm), 1 medium (2-3 cm), and 1 large (3-4 cm). Potential predators, in various densities, were added to the middle of the aquaria. Observations were made at 12 hour intervals, and dead or missing chitons were replaced immediately. Chitons found on the bottom of the rock, or on the side of the tank were placed back on top of their assigned rock.

Further tests were made in two 1.5 m² screened-off sections of outdoor cement tanks containing running seawater at a depth of 0.5 m, and at 15 ± 1°C. In each section a *Pelvetia* covered rock and a bare rock, each about 30 cm in diameter, were suspended about 2 cm from the bottom but totally submerged. This was done to insure that chitons placed on the rocks would remain there; starfish then placed in the tank could reach and climb up on the rocks without apparent difficulty. Six chitons (2 large, 2 medium, and 2 small) were placed on each rock. Eight *Pisaster ochraceus* were then added to each section and the number of *Cyanoplax* consumed was monitored daily for one week. *Patiria miniata* was also studied with identical conditions and methods.

A list of species tested and a quantitative summary of the results can be found on Table 1.

Table 1

Table Summarizes the Different Predation Rates on *Cyanoplax* by the Various Potential Predators, tested in indoor and outdoor aquaria, plus field observations. Also listed is any preferred chiton size or preference for chitons on bare rock, demonstrated by each predator

Predators:	Test location ¹	Test period (days)	No. predators/ experiment ²	No. of <i>Cyanoplax</i> / experiment ³	Predation rate: No. chitons/ predator/day	Preferred chiton size (cm)	Preference for exposed chitons
<i>Pisaster ochraceus</i>	A	28	1	3-3	0.75	2	yes
	O	7	8	6-6	0.25	2	yes
	F	1	8	45/m ²	1.2	2	yes
<i>Hemigrapsus nudus</i>	A	12	1	3-3	0.25	—	no
<i>Pachygrapsus crassipes</i>	A	28	3	3-3	0.055	—	no
<i>Leptasterias pusilla</i>	A	23	5→1	3-3	0.04	1	no
<i>Patiria miniata</i>	A	26	3→1	3-3	0.095	—	yes
	O	7	8	6-6	0	—	no
<i>Larus occidentalis</i>	F	14	18	4/m ²	0	—	no
<i>Thais emarginata</i>	A	28	3	3-3	0	—	no
<i>Acanthina spirata</i>	A	28	3	3-3	0	—	no
<i>Pagurus</i> spp.	A	28	30	3-3	0	—	no

¹A represents aquaria, O, the outdoor tanks, and F, the field investigations.

²A fixed number of predators were used for each testing period except for *L. pusilla* and *P. miniata* where densities from 5 to 1 and 3 to 1 respectively, were tested.

³For aquaria and outdoor tanks: number of chitons on bare rock listed prior to dash-number on *Pelvetia* covered rock is listed after dash. For field observations, number indicates chitons/m².

Of all animals tested, *Pisaster ochraceus* was the most voracious in the small aquaria; they ate an average of 0.75 chiton per day. There was a preference for chitons over 2 cm, and for those on bare rocks (both results significant at $p < 0.05$ chi square test). No chitons were taken from a rock covered by *Pelvetia*. In the large tanks, within one week 12 (7 large, 5 medium and 0 small) from the bare rock and one medium chiton from the rock covered by *Pelvetia fastigiata*, were taken.

Over a 12 day period using one large *Hemigrapsus nudus*, three chitons were eaten.

During a two week test, three *Pachygrapsus crassipes* ate three chitons. Both *Hemigrapsus* and *Pachygrapsus* may have eaten chitons which had moved from their rock to the side of the tank.

Leptasterias pusilla were observed to eat three *Cyanoplax* 1 cm in length over a four week period.

Within the small aquaria *Patiria miniata* were observed to partially eat three *Cyanoplax*, but in the larger outdoor tanks no predation occurred, which suggests that *Patiria* is not a significant predator under natural conditions.

The 2 carnivorous snails *Thais emarginata* and *Acanthina spirata*, and the hermit crabs *Pagurus* spp. were all tested as potential predators for 4 weeks and no predation was observed.

DISCUSSION

This study indicates that *Pisaster ochraceus* is an important predator on *Cyanoplax hartwegii* under artificial conditions. Yet, in the intertidal zone densities of 30 *Cyanoplax*/m² can be observed. These high densities are found at a tidal height of +0.9 m to +1.2 m, thus they are typically covered by water for only 7 hours a day, and consequently are potential prey for *Pisaster* only a fraction of the day, since this predator feeds mostly underwater. However the present investigation indicates that the presence of *Pelvetia* may be a more important deterrent to predation than the short exposure period. Perhaps *Pisaster* avoids *Pelvetia* because the algal mass blocks firm attachment or perhaps the movement of the fronds with the waves is itself a deterrent.

Despite the predation found in the laboratory by *Pachygrapsus crassipes* and *Hemigrapsus nudus*, they are probably not major predators on *Cyanoplax hartwegii*. This is supported by HIATT (1948) who ranked the feeding preferences of *Pachygrapsus* in order of decreasing importances

as: 1) live algae, 2) detritus, and 3) littoral animals, on which it is chiefly a scavenger and less often a predator. HIATT also reports that *Hemigrapsus* subsists primarily on detritus and infrequently on algal fronds.

Predation by *Leptasterias pusilla*, *Pachygrapsus crassipes* and *Hemigrapsus nudus* was low in the indoor aquaria. However, if this rate is characteristic of natural predation, the effect on the population of the slow growing chitons may be important.

Cyanoplax hartwegii is well adapted to the *Pelvetia fastigiata* community. *Pelvetia* offers an abundant food source, protection from wave surge and desiccation and from *Pisaster ochraceus*.

SUMMARY

According to both the experiments and field observations, potential predators of *Cyanoplax hartwegii* are ranked as follows:

	<i>Leptasterias pusilla</i> (on chitons = 1 cm)
<i>Pisaster ochraceus</i> > > >	<i>Pachygrapsus crassipes</i> (occasional)
	<i>Hemigrapsus nudus</i> (occasional)

The algal covering of *Pelvetia fastigiata* is a protective barrier against predation by *Pisaster ochraceus*, and possibly from birds; all the other potential predators tested showed no preference for chitons on bare rocks as opposed to those covered by *Pelvetia*.

ACKNOWLEDGMENTS

I wish to extend my thanks to my advisors: Malvern Gilmartin, Robin Burnett, Donald Abbott, Charles Baxter, Joe Balesteri, and to my fellow researcher, Michael Moore.

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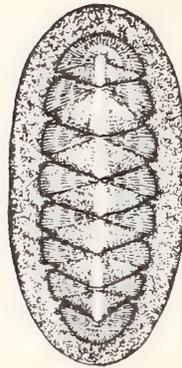
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Foraging of the Western Gull *Larus occidentalis* and its Impact on the Chiton *Nuttallina californica*

BY

MICHAEL MATTHEW MOORE Jr.¹

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

INTRODUCTION

Nuttallina californica (Reeve, 1847) is an intertidal chiton often found in association with the mussel *Mytilus californianus* (Conrad, 1837), and the barnacle *Pollicipes polymerus* (Sowerby, 1833), on Californian rocky shores (RICKETTS & CALVIN, 1952).

This report is about predation on *Nuttallina californica* by the western gull, *Larus occidentalis* (Audubon, 1839). The gulls are voracious and opportunistic feeders (HUBBS *et al.*, 1970). After feeding, the birds regurgitate undigested material, particularly the bones, shells and exoskeletons of their prey; consequently examination of regurgitation pellets (hereafter "pellets") yields information on the gulls' food choice.

MATERIALS AND METHODS

The study was conducted from May 10 to June 1, 1974 at Granite Point, a precipitous rocky peninsula located in the Point Lobos State Park Reserve, Monterey County.

The 18 western gulls observed during the study appeared to have already established breeding territories. They were studied during the beginning of their breeding season (HARPER, 1971; TINBERGEN, 1953), and each gull was seen daily near a specific nesting site. Breeding animals restricted much of their foraging to the nearby rocky intertidal zone and offshore waters. Alien gulls were rarely seen in the study area.

Granite Point proved excellent for my study. The gulls were rarely disturbed and the brooding sites on bare rock were far enough from tourist trails that the pellets were not disturbed.

After the gulls were counted, accessible brooding sites were marked and old pellets were collected and characterized. Each of the sites was then visited daily and fresh pellets were collected.

Many of the old pellets had fallen apart and their contents scattered, thus quantification was difficult. Fresh pellet size was used to estimate the number of old pellets at a site. This was done by spreading the contents of fresh pellets to the same density as that of the remains of old pellets and comparing the areas covered.

The population of *Nuttallina californica* around Granite Point was estimated by counting the number of *N. californica* per square meter in quadrates every 10 m along the shore. Areas of markedly differing densities were thus defined and the numbers of *N. californica* were found by multiplying the average density of *N. californica* by the area size. The totals for each area were added, which gave an estimate of the total number of *N. californica* in the study area.

Finally, early morning activities of foraging gulls were observed on three separate days.

RESULTS AND DISCUSSION

A total of 37 fresh pellets and an estimated total of 65 old pellets were collected and analyzed. The results are shown in Table 1.

While plates of the barnacle *Pollicipes polymerus* were the most common material found in the pellets, an observation in accord with MARTINI (1966), over a quarter of the pellets examined contained the plates of at least one *Nuttallina*.

Of 24 old pellets containing *Nuttallina*, only two had plates of 3 animals and none had more than that. The 4 fresh pellets containing *Nuttallina* had plates from 3, 8, 9, and 11 animals. A likely explanation seems that one or

¹ Permanent address:

2615 Graceland Avenue, San Carlos, CA 94070

Table 1
Data on the Number of Regurgitation Pellets
in which individual animals were found

Animal	Number of Pellets in which animal is found
<i>Pollicipes polymerus</i>	65
Fish	43
<i>Nuttallina californica</i>	28
Limpets	16
<i>Katharina tunicata</i>	8
Crab	6
Isopod	5
<i>Mytilus californianus</i>	5
<i>Mopalia muscosa</i>	1
Sea Urchin	1
Total Pellets = 102	

several gulls changed their feeding habits during the course of the study, either by feeding in an area containing a higher density of *Nuttallina* or by deliberately seeking out *Nuttallina* in greater numbers.

$$\frac{18 \text{ gulls}}{\text{Area}} \times \frac{1 \text{ pellet/day}}{\text{gull}} \times \frac{0.6 \text{ chitons}}{\text{pellet}} \times \frac{90 \text{ days}}{\text{breeding season}} = \frac{972 \text{ Nuttallina}}{\text{area—breeding season}}$$

The data indicate that gulls feeding in the *Pollicipes polymerus* area concentrate most heavily on *P. polymerus* (Table 1). This might be explained by the easy accessibility of *P. polymerus* to the gull or by the gull actively seeking out the *P. polymerus*, due to its taste or some other factor. In 22 of the 28 pellets containing *Nuttallina californica*, *P. polymerus* was also present. The gulls were likely eating the *N. californica* and *P. polymerus* in proportion to the numbers they were encountered. The 43 pellets containing *P. polymerus* but no *N. californica* may represent foraging in a zone with a high *P. polymerus* to *N. californica* ratio.

The low number of *Mytilus californianus* shells in the pellets is probably due to the gulls' habit of breaking open the mussels and eating the flesh, instead of ingesting the whole shell. The high densities of *M. californianus* and

Pollicipes polymerus probably act as "predation-buffer" for the *Nuttallina californica* as has been found for predation on these organisms by starfish (LANDENBERGER, 1968).

Isopods were found only in fresh pellets; if left over night these lightweight pellets would be swept away by wind. Thus, the isopods probably made up more of the gulls diet than Table 1 indicates. Barnacle shells, chiton plates, mussel shells, and limpet shells appeared to be quantitatively recoverable from month-old pellets.

The contents of the pellets indicate opportunistic feeding of the gulls and indicate the gulls often feed as a group, concentrating a day's effort on a habitat. On the morning of May 24 all the gulls were observed to be feeding on schooling fish, and all but one of the pellets that day and the next contained only fish bones.

The effect of predation by the western gulls on *Nuttallina californica* can be estimated by assuming three things. First, the foraging of the gulls is limited to the general area around Granite Point, due to the gulls' breeding behavior and to the abundant food sources around the point. The second assumption is that each gull regurgitates one pellet per day. The final assumption is that there is an average of 0.6 *N. californica* per pellet. This is based on the overall ratio of 62 *Nuttallina* in the 102 pellets found. The breeding season of the western gull is roughly 90 days (SCHREIBER, 1970; TINBERGEN, 1953), so the best estimate to be made is as follows:

The number of *Nuttallina* in the area was estimated at 6 500, the average density being approximately 3 *Nuttallina*/m² around the point; consequently the gulls preyed on approximately 15% of the *Nuttallina* around the point during the breeding season. This estimate could clearly be improved with the attainment of more precise data; yet it serves to indicate the possibility that the western gull consumes a significant proportion of *Nuttallina* in some localities.

SUMMARY

In a study of the contents of western gulls' regurgitation pellets, *Pollicipes polymerus*, the gooseneck barnacle, was shown to be the most abundant material. The chiton

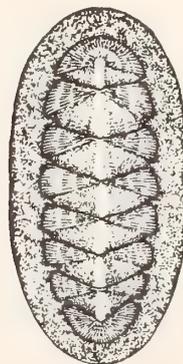
Nuttallina californica was also found to occur in the pellets in relatively high frequency, indicating that the western gull is a major predator on *Nuttallina*, perhaps taking 15% of the population around the study site per breeding season.

ACKNOWLEDGMENTS

I wish to thank Alan Baldrige, Judson Vandevere, Anne DeBevoise, Bob Tenold, Chris Harrold, James Beck, and Robin Burnett. In addition I am indebted to Point Lobos State Park Reserve for allowing this study to be carried out.

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Predation Upon Subtidal *Tonicella lineata* of Mussel Point, California

(Mollusca : Polyplacophora)

BY

STUART R. SEIFF¹

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

INTRODUCTION

IN THE KELP BEDS off Mussel Point, Pacific Grove, California, the chiton *Tonicella lineata* (Wood, 1815) is abundant on subtidal *Lithophyllum* encrusted rocks. While colors and patterns make them inconspicuous on a background of coralline algae, they appear vulnerable to predation by nonvisual predators such as starfish.

MAUZEY *et al.* (1968) state that, on occasion, the sea stars *Dermasterias imbricata* (Grube, 1857), *Evasterias troschellii* (Stimpson, 1862), and *Orthasterias koehleri* (deLoriol, 1897) eat subtidal individuals of *Tonicella* in the Pacific Northwest. No published information is available on predation of subtidal *Tonicella* in Californian waters. I herein report on laboratory experiments and subtidal observations pertaining to the discrimination of nonvisual predators against *Tonicella* and the possible reasons for the lack of predation.

METHODS AND RESULTS

Tonicella seem quite vulnerable to predation by nonvisual predators while situated on the *Lithophyllum* covered rocks in the Mussel Point kelp bed. However, their abundance implies that they are not heavily preyed upon.

A 24 hour subtidal observation period was undertaken to observe, in a natural setting, the activities of subtidal *Tonicella* and associated fauna. The area selected was a coralline encrusted rock in the Mussel Point kelp bed measuring 1.2 x 0.6 x 0.25 m. There were 16 *Tonicella* present at the site, along with 2 *Pisaster brevispinus* (Stimpson,

1857), 1 *P. giganteus* (Stimpson, 1857), 5 *Patiria miniata* (Brandt, 1835), and 1 *Mitra idae* (Melvill, 1893). Observations were made every four hours. During this time no *Tonicella* were consumed, though starfish were observed on top of the chitons at various times. There is, thus, no apparent predation on *Tonicella* by the species just mentioned.

In order to further investigate the lack of predation, several laboratory experiments were performed. During the course of study, a total of 92 *Tonicella* were exposed to 48 starfish in test aquaria. This resulted in 4 300 starfish hours of exposure during which time only 3 apparently healthy *Tonicella* were eaten. These were all consumed by *Pisaster brevispinus*.

Strongylocentrotus purpuratus (Stimpson, 1857) ate a *Tonicella* when the tank temperature rose above 14°C as a result of a running seawater system malfunction. The phenomenon of temperature affecting predation on *Tonicella* is discussed by BARNES (1972: 17-18).

However, none of the following potential predators consumed *Tonicella* in aquaria during at least 48 hours exposure: the seastars *Pisaster giganteus*, *Orthasterias koehleri*, and *Leptasterias* spp., and the carnivorous gastropods *Mitra idae* and *Conus californicus* (Hinds, 1844). During the various tests, starfish were often observed with *Tonicella* beneath them. Thus, lack of contact between the starfish and chitons was not a factor in the low predation levels.

In more specific studies, 15 subtidal *Tonicella*, 15 *Nuttallina californica* (Reeve, 1847), and 15 *Cyanoplax* spp., all between 1.9 and 3.0 cm in length, were allowed to attach to the bottom of a 43 x 27 x 25 cm aquarium. The potential nonvisual predators *Pisaster ochraceus* (Brandt, 1835), *P. giganteus*, *P. brevispinus*, *Patiria miniata*, and *Orthasterias koehleri* were introduced. The seawater temperature was

¹ Permanent address:

337 South Camden Drive, Beverly Hills, CA 90212

14 ± 1°C. The results (Table 1), after 3 days exposure, show that no *Tonicella* were eaten while the other chitons were. This differential predation was significant using the chi square test ($p < 0.01$).

Table 1

Species Present during Preference Feeding Test

The remains of 2 additional *Nuttallina* were found on the bottom of the aquarium; the identity of the predator was unknown

Species	No.	Species (No.) preyed on
<i>Pisaster ochraceus</i>	1	<i>Nuttallina</i> (3), <i>Cyanoplax</i> (6)
<i>Pisaster giganteus</i>	1	
<i>Pisaster brevispinus</i>	1	<i>Cyanoplax</i> (1)
<i>Patiria miniata</i>	1	
<i>Orthasterias koehleri</i>	1	<i>Nuttallina</i> (1), <i>Cyanoplax</i> (1)
Unobserved		<i>Nuttallina</i> (2)

In order to be certain that the *Tonicella* in the previous experiment were of the proper size for consumption by the starfish, 15 *Tonicella*, ranging in size from 3.1 to 1.2 cm, were placed in another aquarium with the same individual predators for 3 days. None were eaten. These results indicate that starfish preferentially consumed other chitons, and did not eat *Tonicella* even when they were the only available food source and a wide size range existed.

A series of laboratory experiments was conducted to examine several possible reasons for the lack of predation. All of the experiments were conducted either in 43 x 27 x 25 cm aquaria or 33 x 28 x 13 cm plastic trays filled with running seawater at 14 ± 1°C. The number and size of *Tonicella* varied with the individual experiment, as did the species, size and number of the predators.

1. To determine whether contact between a starfish and a *Tonicella* would produce a repellent in the form of a pH change, the valves and feet of 5 *Tonicella*, not exposed to starfish, were tested with pH paper. The paper was placed on the wet back and foot of each chiton and readings of 7.5 ± 0.1 were obtained. After contact with the starfish, *Orthasterias koehleri*, the pH readings of both the valves and feet remained 7.5 ± 0.1. Thus, no indication was found

that an altered pH was the means by which *Tonicella* avoid predation.

2. The presence of a chemical repellent within *Tonicella* was tested for by use of a suspension of whole *Tonicella*. Every hour 2 live *Tonicella* (approximately 1.25-2 cm) were ground up using a mortar and pestle. The tissue and fluid were added to a tray containing 5 *Cyanoplax* spp. and the predators *Pisaster brevispinus*, *P. giganteus*, *P. ochraceus*, and *Orthasterias koehleri*. A control tray containing the same numbers of animals was also set up, but no suspension of *Tonicella* was added. In this experiment the running seawater was turned off so as not to dilute the suspension. Fresh seawater was added every hour with the new suspension. After 3 hours, a *Cyanoplax* spp. was eaten by the *Orthasterias koehleri* in the tray containing the *Tonicella* suspension. There is thus no evidence for an active chemical repellent.

3. Cellulose sponge impregnated with suspension of *Cyanoplax* spp. was attached to the backs of 5 *Tonicella* in an attempt to determine if *Cyanoplax* possess a chemical, attractive to starfish, which *Tonicella* might lack. The sponge was affixed using Devcon "Zip-Grip 10". The *Tonicella* were placed in a tray with 1 *Pisaster brevispinus*, 1 *P. ochraceus*, and 1 *Orthasterias koehleri*. After 96 hours of exposure, none of the *Tonicella* with the sponge were eaten. It would thus seem that *Cyanoplax* does not have a chemical attractant.

4. As chemical properties alone do not appear to account for the low rate of predation on *Tonicella*, the function of the valves was more closely investigated. Four *Tonicella* were inverted and affixed to glass slides using Devcon "Zip-Grip 10" (Devcon Corp., Danvers, Mass.). They were placed in a tray with 1 *Orthasterias koehleri*, 1 *Pisaster brevispinus*, and 1 *P. ochraceus*. Within 3 days, 2 *Tonicella* were consumed, 1 by *P. brevispinus* and 1 by *P. ochraceus*. It thus appears that inverted *Tonicella* are very susceptible to predation by sea stars.

5. When *Tonicella* are not inverted, the valves are the first part of the chiton that a predator comes in contact with. Microscopically, the valves of *Tonicella* appear smooth and shiny, unlike most other chitons. To test whether or not a starfish's tube feet could hold onto the smooth valves of a *Tonicella*, one was placed under a starfish. When removal of the chiton was attempted, the tube feet held on. Therefore, the protection seems due to a nonmechanical property of the valves.

6. In determining whether the texture of *Tonicella* valves alone is sufficient to repel starfish and other predators, the

valves of 5 *Tonicella* were epoxyed to the backs of 5 *Cyanoplax*. These were placed in a tank with 5 normal *Cyanoplax*, 1 *Pisaster brevispinus*, 1 *P. giganteus*, 1 *P. ochraceus*, 1 *Orthasterias koehleri*, and 1 *Patiria miniata*. Within 2 days, *P. brevispinus* had eaten 2 *Cyanoplax* with *Tonicella* valves, and *Orthasterias koehleri* had eaten 2 with and 2 without. Thus, 4 of the 5 *Cyanoplax* with *Tonicella* valves were consumed. It appears that for the *Tonicella* valves to be effective against predation, the *Tonicella* must be alive.

DISCUSSION

Pisaster brevispinus appears to be the dominant nonvisual, subtidal predator of *Tonicella*, and its rate of predation is low. According to NAKASHIMA (1974), only 0.25% of the diet of *P. brevispinus* in the Mussel Point kelp bed is composed of *Tonicella*.

In the Pacific Northwest, *Dermasterias*, *Evasterias*, and *Orthasterias* consume small amounts of *Tonicella* (MAUZEY *et al.*, 1968). Additionally, *Pisaster ochraceus* primarily eats chitons, including *Tonicella*, during the winter when the starfish mass together in groups and become rather sessile. The grazing movements of the chitons bring them into contact with the starfish (MAUZEY, 1966). The diet of *Leptasterias hexactis* (Stimpson, 1862) has been reported to be composed of 45% *Tonicella* in intertidal areas where there is little else to eat (MAUZEY *et al.*, *op. cit.*). In contrast, local *Tonicella* were not consumed by these starfish when in aquaria, yet these starfish did consume other chitons.

The concept of 2 species of *Tonicella*, one intertidal and one subtidal, has been advanced by BARNES (1972). Perhaps a taxonomic distinction between the *Tonicella* collected from Mussel Point and those studied by Mauzey in the Pacific Northwest could account for the difference in the predation.

Explanations for the low predation on the Mussel Point *Tonicella*, which appear to be easy prey, may include difficulties encountered by starfish when removing *Tonicella* from various substrates, lack of a chemical attractant, possession of a chemical repellent, or some form of a tactile inhibitor of predation. Cryptic coloration, however, is not a possibility here as starfish are not visual predators.

That both inverted *Tonicella* and *Cyanoplax* with *Tonicella* plates attached to their backs were eaten sug-

gests that *Tonicella*'s protection is dependent on its being alive and upright. Thus, a living dorsal surface may be the site of protection. Whatever the protection, it is not 100% effective as indicated by the 4 apparently healthy *Tonicella* that were eaten.

SUMMARY

Starfish predation on *Tonicella lineata* in the Pacific Northwest has been reported as common. However, subtidal *Tonicella* from Mussel Point, Pacific Grove, California, are rarely consumed in aquaria by starfish which will consume other species of chiton. A chemical repellent, or some kind of tactile inhibitor of predation are deemed possible explanations. The mechanism of the protection of the local population from predation is not known but appears to be associated with the dorsal surface of living animals.

ACKNOWLEDGMENTS

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Temporal and Spatial Activity Patterns of the Intertidal Chiton

Mopalia muscosa

BY

SUANNE YVONNE SMITH¹

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

(2 Text figures)

INTRODUCTION

THE STUDY OF ANIMALS in the field often reveals aspects of behavior not discoverable from observations on captive animals. Behavioral studies on intertidal organisms in the field are usually carried out during periods of low tide. Observations at high tide are more difficult to make, particularly at night, and animal behavior under these conditions remains largely unexplored. A search of the literature revealed no such work done on chitons.

This study, carried out on *Mopalia muscosa* (Gould, 1846), was directed toward revealing its temporal and spatial patterns of activity. Attention was also focused on partitioning, and on the possible occurrence of individual homesites and territories or home ranges. Homing ability in some Polyplacophora has been noted previously (CROZIER, 1921; THORNE, 1967, 1968).

FIELD STUDY SITE AND METHODS

The present study was carried out during the Spring of 1974 on the rocky shores of Mussel Point, Pacific Grove, California. *Mopalia muscosa* is common here, particularly in the mid tide zone. The site selected was a surface 1.2 x 1.3 m on a sculptured granitic outcropping, occurring between the + 0.54 m and + 1.26 m tide level on the eastern edge of the point. Surf conditions at the site during high tide varied from a gentle surge to breaking waves.

The macroalgae occurring in the study site were *Gigartina papillata* (C. A. Agardh) J. G. Agardh, *Petrocelis franciscana* Setchell and Gardner, *Endocladia muricata* (Postels and Ruprecht) J. G. Agardh, *Iridaea flaccida* (Set-

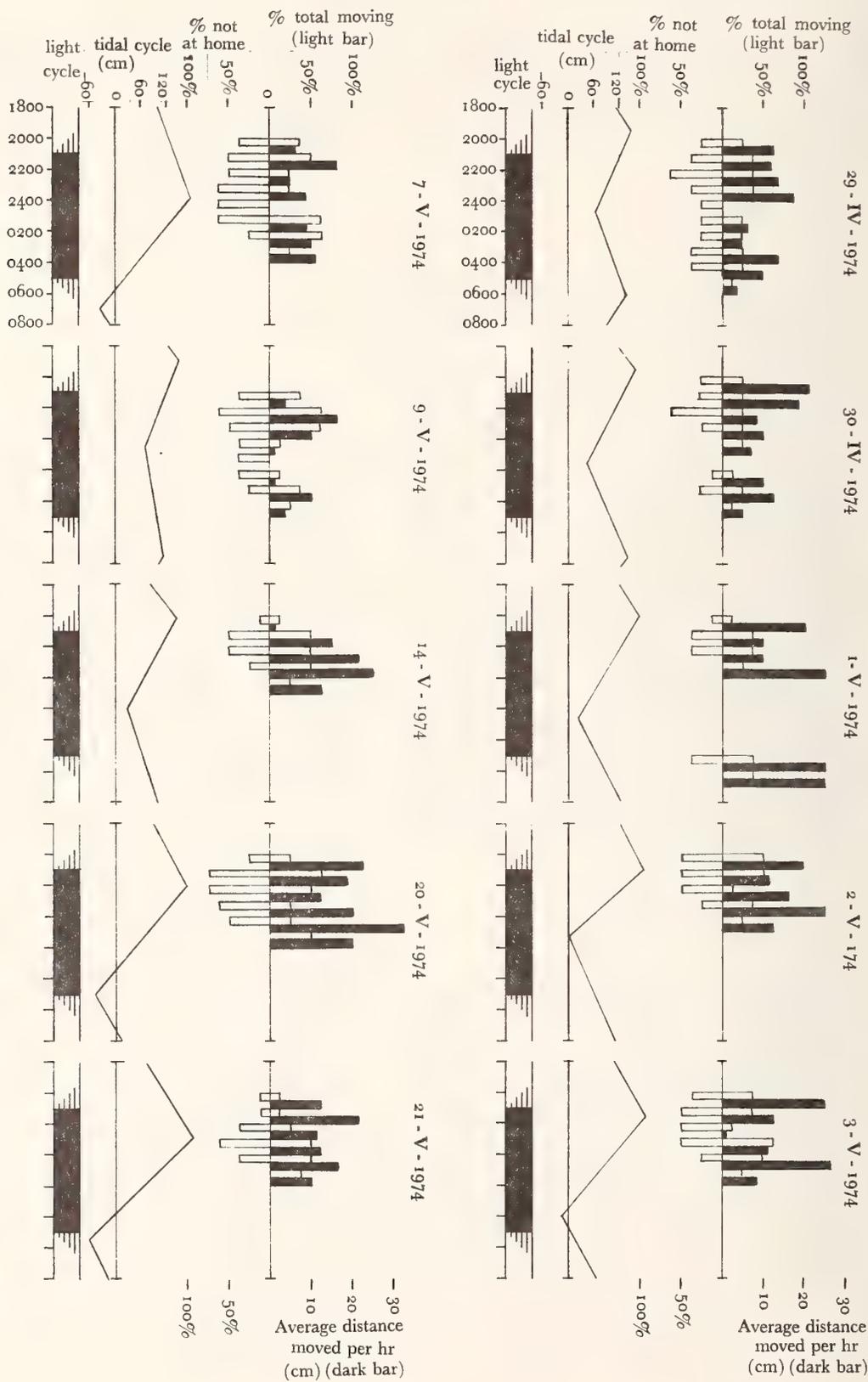
chell and Gardner) Hollenberg and Abbott, *Pelvetia fastigiata* (J. G. Agardh) DeToni, *Gigartina leptorhynchos* J. G. Agardh, and *Gigartina corymbifera* (Kützing) J. G. Agardh in order of decreasing percent cover. Immediately adjacent to this area, the rocks were covered with *Pelvetia* and here the relative abundance of *Mopalia muscosa* dropped. The resident animals in the study area, in order of decreasing numbers of individuals, included the annelid *Phragmatopoma californica* (Fewkes, 1889), the anemone, *Anthopleura elegantissima* (Brandt, 1835), the snail *Tegula funebris* (Adams, 1854), hermit crabs (*Pagurus* spp.), the young limpets, *Collisella digitalis* (Rathke, 1833) and *Collisella scabra* (Gould, 1846), the chitons *Mopalia muscosa* and *Cyanoplax hartwegii* (Carpenter, 1855), the anemone *Anthopleura xanthogrammica* (Brandt, 1835), the chiton *Nuttallina californica* (Reeve, 1847), and the crab *Pachygrapsus crassipes* Randall, 1839. Herbivores occurring on the adjacent rocks consisted primarily of *Cyanoplax* and the limpets *Collisella pelta* (Rathke, 1833), *C. limatula* (Carpenter, 1864), and *Notoacmea scutum* (Rathke, 1833). None of these latter limpet species occurred in the area where *M. muscosa* was studied. *Tegula* were found in approximately equal densities in and adjacent to the study site, whereas the numbers of *C. digitalis* and *C. scabra* declined in the neighboring areas.

The activity of eight individuals of *Mopalia muscosa* in the study site was monitored over a five-week period from April 28 to May 30, 1974. Marking the chitons was unnecessary due to distinctive individual differences in algal growth on their plates. The substrate was also unmarked, and natural landmarks were used as reference points to note the positions of animals. The chitons could, in this way, be observed with minimal disturbance.

An initial 48-hour watch indicated that the *Mopalia* moved only at night, therefore an intensive surveillance of the chitons was conducted from just before dusk to shortly

¹ Permanent address:

2777 Sarah Lane, Eugene, OR 97401



after dawn, with intermittent daytime observations. The night time observations were made at intervals of 15 minutes to one hour. For each observation the chitons' new positions and the distances traveled from their previously noted positions were recorded. These night observations were made with a flashlight, using a red filter to reduce disturbance during their dark cycle. Observations on submerged animals were made with the use of a wet suit, face plate, and snorkel.

DIURNAL AND TIDAL ACTIVITY PATTERNS

The data on movements are summarized in Figure 1; original data are on file in the library at Hopkins Marine Station.

During daylight hours and when exposed by the tide, *Mopalia muscosa* were not active, and were in fairly protected locations. Six of the 8 sites were adjacent to a sandy bottom and in a depression, crevice, or at the base of a rock. Individuals were often partially or completely buried by the sand. Another daytime site was under or next to *Anthopleura elegantissima* and *A. xanthogrammica*. After foraging, the 8 individuals in the rocky area homed for 69 out of the 71 excursions monitored. Homing is defined here as the return to exactly the same site the individual left earlier that night. In one instance, a rock washed into the home of a foraging chiton and blocked it. This individual settled about 7 cm away, and then consistently

(← on facing page)

Figure 1

Date, time, light, tidal height, and movements of 8 *Mopalia muscosa* during ten 14-hr periods of observation. Positions of animals were recorded at intervals of 15 min to 1 hr throughout the 14 hours for these ten dates. Four additional nights these chitons were observed, only the observations were sporadic. These additional data are included in an Appendix on file at Hopkins Marine Station. Each vertical white bar above the axis indicates the percentage of the total number of animals moving sometime within that hour; the dark vertical bar shows the average distance these animals moved during that hour. Below the line the vertical white bar indicates the percentage of the total number of animals away from their homes, which does not always equal the percentage moving. Absence of bars means all animals were examined and found to be immobile at their home sites.

homed to this new site for 5 observed journeys over the following 15 days. The only other occasion a chiton failed to home occurred when one individual traveled 20 cm beyond its customary range of 40 cm from home. Instead of returning, it stayed at a site similar to its old home, about 35 cm away, and subsequently was lost from the study area.

Foraging occurred only at night, when the chitons were submerged or awash. Not all of the animals monitored moved every night: during the 14 nights of observation the total number of times a particular individual left home varied from 4 to 14, with a mean of 9.

If the rock was submerged or awash by an incoming tide at the onset of dusk, the animals moved away from their homes. If the study site was dry, activity was delayed until the chitons were wetted by the incoming tide. The chitons began the return journey to their homesites at such a time that they were back at their homesites before sunrise or before a receding tide uncovered them, whichever came first. Thus no animal in the study site was left either conspicuously exposed to avian predators or stranded in a position where desiccation rates were high.

Similar activity patterns were found for *Chiton tuberculatus* Linnaeus by CROZIER (1921) and for *Acanthozostera gemmata* (Blainville) by THORNE (1967, 1968).

Figure 1 illustrates other intriguing variations in activity. More individuals were active at spring tides (May 7, May 20 and 21, 1974) than at neap tides (April 29 and May 9, 1974). There was a period of inactivity during high tide at night when the individuals were away from home (May 3, May 7 and May 20, 1974). In addition, some individuals remained out, but inactive, during the high low tides that occurred in the middle of the night (April 29 and May 9, 1974); these individuals were located at the lowest vertical positions in the study area and during these low tides were never entirely uncovered. On one occasion an individual was found away from its home during a low tide that left it totally uncovered. That particular animal halted movement until the next incoming tide, which occurred while it was still dark.

These observations suggest that the chitons predict the time and perhaps the height of low tides. Westersund (1975) found evidence of endogenous tidal rhythms in his work with *Mopalia muscosa*, which could explain the animals' activity to anticipate coming events. He also found the extent of their activity reflected the magnitude of the tides. This is corroborated by my field observations.

Additional observation 3 months after the initial study found 5 of the original 8 chitons in the same homesites previously occupied. Six months later, 3 of these chitons were still at the same sites.

HOME RANGES, DIET AND INTERACTION WITH NEIGHBOURS

Fifty-three chiton journeys were continually monitored while an additional 18 journeys were monitored only sporadically (due to adverse weather conditions). Figures

2a and 2b show the various pathways the individuals followed. The distances traveled from the homesites ranged from 5 to 50 cm, most being between 25 and 40 cm. Only on one occasion, already described, did an individual move farther than 50 cm from his home.

Each *Mopalia muscosa* appeared to have a series of established pathways within a radius of 50 cm from their home-

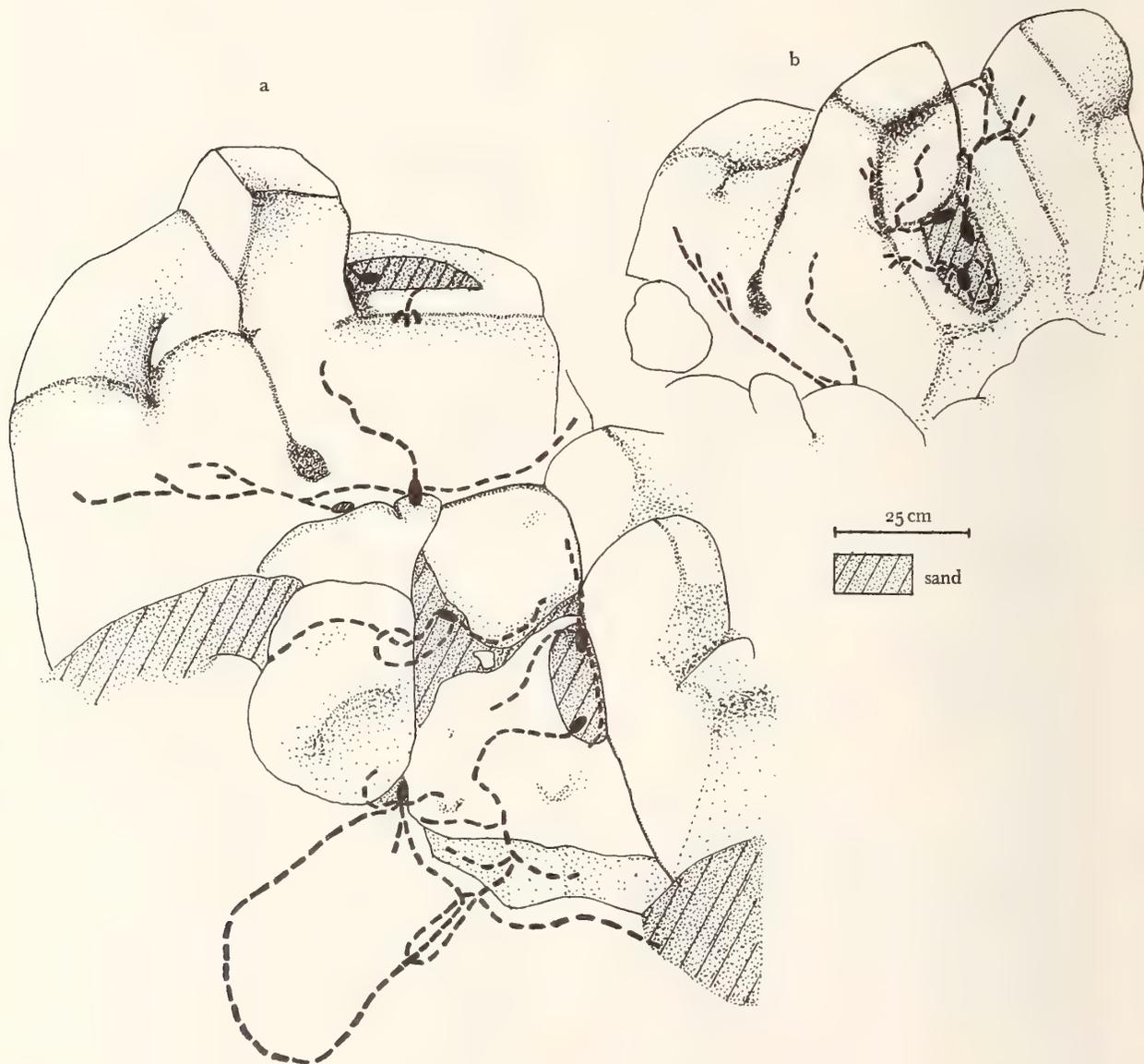


Figure 2

Rocky intertidal study area:

(a) shows the position of home sites (oval areas) and respective home ranges with regularly followed pathways, indicated by broken lines, in the study area. Note most of the home sites are in the

sandy regions (heavily stippled areas bearing diagonal lines).

(b) is another view of section A, both views are at approximately a 45° angle looking into the study area.

sites. These pathways were followed fairly closely and consistently, though they did not always appear to coincide with any obvious contours of the substrate. The same path, was normally used on both the outgoing journey and the return home, though this was not always the case. In general, a chiton left home, traveled to a certain location within its home range, and remained there "until it was time" to return home. The locations to which foraging chitons traveled usually had much macroalgae present; yet some locations were void of any macroalgae. On several occasions, feeding on *Gigartina papillata* was observed.

Quantitative studies of the diet of *Mopalia muscosa* were not undertaken, but the gut contents of 5 chitons from very similar habitats in areas adjacent to the study site were analyzed qualitatively. The guts contained a wide variety of algal material along with small amounts of animal matter and a lot of sand. Those algae that appeared most often were identified (with the assistance of Dr. Isabella A. Abbott) as *Gigartina* spp., *Cladophora* sp., *Endocladia muricata* (Postels and Ruprecht) J. G. Agardh, and *Hildenbrandia occidentalis* Setchell. Also included were *Petrolcelis franciscana* Setchell & Gardner, *Chaetomorpha* sp. and a variety of blue-green and coralline algae. BOOLOOTIAN (1964) also found *M. muscosa* to be a nonspecific herbivore, feeding on what was available, along with small amounts of animal matter he believed was accidentally ingested.

The home ranges of individual chitons, as determined by the paths they followed, did not appear to overlap. Only on 2 out of the 63 chiton journeys monitored did a chiton enter into another's home range. On one of these occasions the resident individual left its home, approached the intruder's girdle and remained there for about half an hour. The resident chiton then left the intruder and traveled a wide semicircle of about a 50 cm radius in its home range before returning home again. The intruder remained for a little over an hour before moving off to a new site.

Collisella pelta were absent from the study area but were abundant on rocks in adjacent areas, indicating possible competitive exclusion. CONNOR (1975) demonstrated that *C. pelta* exhibits an avoidance reaction to *M. muscosa* pushing *C. pelta* when it encountered the limpet in its territory.

BEHAVIOR IN OTHER HABITATS

Limited observations were made on 6 *Mopalia muscosa* located in a tide pool adjacent to the main study site, and on 2 individuals located on a cement substrate immediately above this pool. The 6 individuals in the tide pool did not home or follow regular pathways, but rather wandered

throughout the pool. At dawn, they settled in sites out of direct sunlight and there spent the day. Activity at low tide during the night decreased in the pool but did not halt altogether as in the chitons of the rocky habitat which were exposed to air during low tide. The 2 chitons located on the cement substrate above the tide pool, like the rocky habitat individuals, returned to specific homes after foraging at night during the high tides. They, too, generally followed specific pathways within limited home ranges. None of the 8 chitons was active during the day and all showed a tidal rhythm in some degree.

SUMMARY

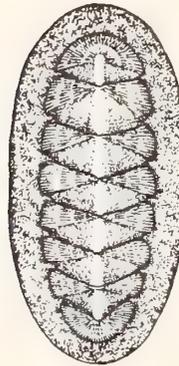
1. The movements of 8 *Mopalia muscosa* inhabiting the rocky intertidal area were followed during 14 days over a one month period (April 28-May 30). All were regularly covered and uncovered by the tides.
2. The animals moved about only at night when submerged or awash. They were inactive during the day and when exposed by low tides at night.
3. Each animal occupied a specific home site when inactive; home sites on rocks near or in sand, or adjacent to sea anemones (*Anthropleura* spp.).
4. In foraging, individuals normally followed specific pathways leading no more than 50 cm from the home site, and returned along the same path.
5. Diet consisted mainly of red algae; the animals appear to be relatively unselective herbivores.
6. A competitive herbivore, *Collisella pelta*, appeared to be excluded from the home range of *M. muscosa*.
7. Animals observed in a tidepool showed similar basic activity patterns but failed to home or completely halt movement during low tides at night, as seen in those directly exposed to the tidal cycle.

ACKNOWLEDGMENTS

My thanks go to Christopher Harrold and Dr. Robin Burnett for their assistance and advice, and Dr. Isabella A. Abbott and Bob Sellers for help in algae identifications. Most of all I would like to extend my sincere appreciation to Charles Baxter for his undying enthusiasm and unlimited advice.

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Activity Patterns of the Chiton *Cyanoplax hartwegii*

(Mollusca : Polyplacophora)

BY

BETSY WENTWORTH LYMAN¹

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

(4 Text figures)

INTRODUCTION

THE CHITON *Cyanoplax hartwegii* (Carpenter, 1855) has been studied taxonomically (e.g., TRYON & PILSBRY, 1892; BERRY, 1922), and RICKETTS & CALVIN (1952) note that the chiton is found under clumps of *Pelvetia* during the day and prefers relatively quiet waters. There appears to be little known about the animal beyond this. To gather more information on its biology I observed the daily and nightly activities of a population of *C. hartwegii* on Mussel Point in Pacific Grove, California, during the spring of 1974. My findings on when and where the animals move, their homing behavior and phototactic behavior are herein reported along with a discussion on possible selective advantages of this behavior.

HABITAT OF *Cyanoplax*

The Mussel Point *Cyanoplax hartwegii* were commonly found under the brown alga *Pelvetia fastigiata* (J. G. Agardh) DeToni in areas of moderate or weak surf action. The animals were generally on bare granite or on the encrusting red algae *Hildenbrandia occidentalis* Setchell, *Petrocelis franciscana* Setchell and Gardner, or crustose corallines. Numerous tufts of the red algae *Gigartina papillata* (C. A. Agardh) J. G. Agardh, *Endocladia muricata* (Postels and Ruprecht) J. G. Agardh and some *Coralina officinalis* Linnaeus were found in these areas. Such mobile fauna as the snail *Tegula funebris* (Adams, 1854); the limpets *Collisella pelta* (Rathke, 1833), *C. digitalis* (Rathke, 1833), *C. limatula* (Carpenter, 1864), and *C. scabra* (Gould, 1846), the crab *Pachygrapsus crassipes* (Randall, 1839), the hermit crabs, *Pagurus* spp. and a variety of gammarid amphipods were frequently found

in all my study areas. Of the sessile animals present, the anemone *Anthopleura elegantissima* (Brandt, 1835), the small barnacle *Chthamalus* sp. and annelid worm *Phragmatopoma californica* (Fewkes, 1889) were the most common.

ACTIVITY PATTERNS

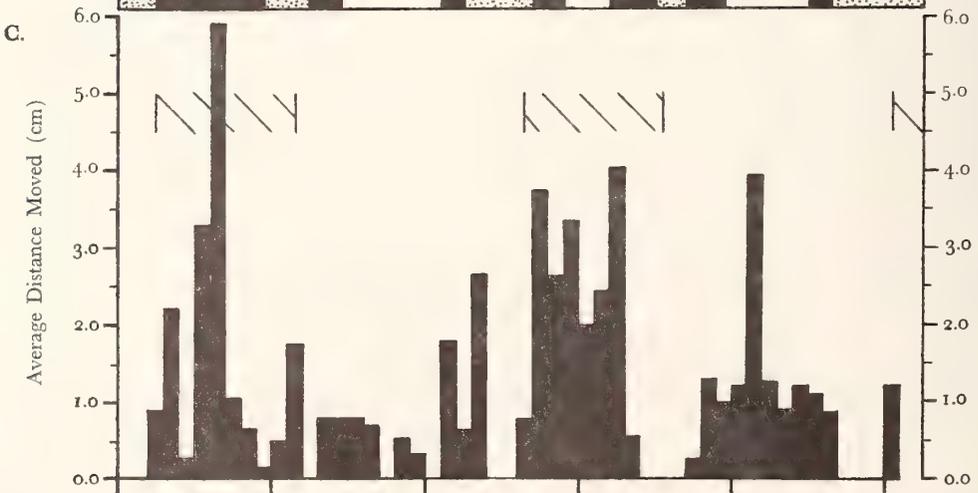
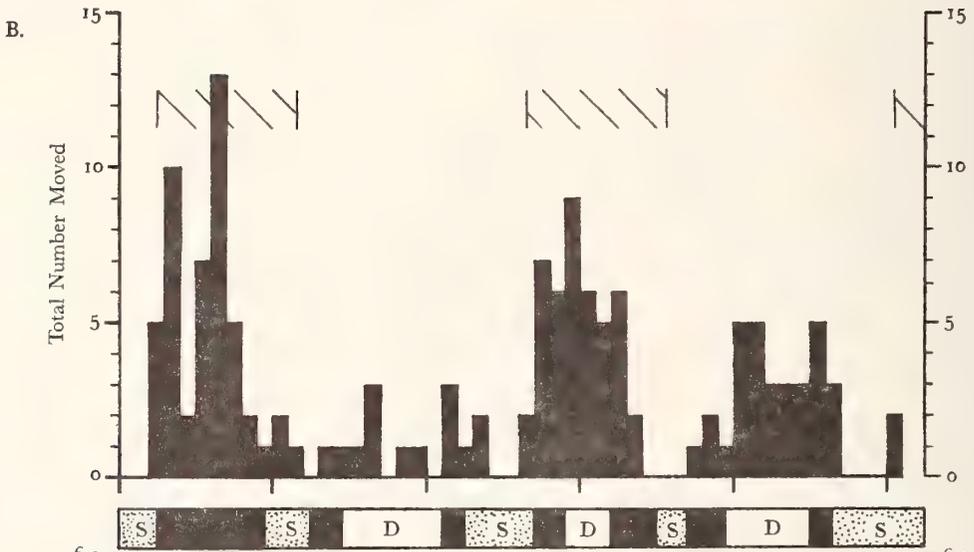
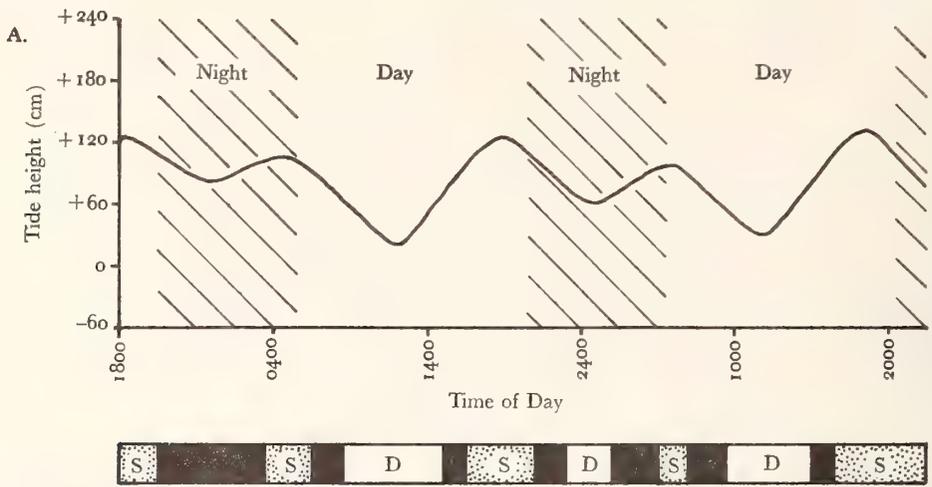
To mark individual chitons whose movements were to be followed, small numbered labels of waterproof paper were attached to the shell plates utilizing a reportedly non-toxic, quick-drying contact glue ("ZIP-GRIP" 10; Devcon Corporation, Danvers, Mass.). To monitor the positions of the chitons, I used a 50 cm x 50 cm grid marked off in 10 cm intervals which was aligned to marked reference points on the transect during times of data collection.

To investigate the chitons' diurnal activity patterns, I labelled *in situ* 13 *Cyanoplax hartwegii* from Mussel Point found living within an area approximately 3 m x 1 m between the + 0.75 m and + 1.2 m tidal levels. Starting approximately 6 hours after the labelling, the animals were observed at one hour intervals beginning at 1800 on May 13th and ending at 2000 on May 15th, and their positions were recorded for each observation. Night-time observations were made using a dim red flashlight. A second set of hourly observations was made on the same population from 2000 on May 19th to 0800 on May 22nd, a time when the tidal cycle was 6 to 7 hours out of phase with the previous cycle. The number of animals located each hour varied from 10 to all 13.

The results of the two watches are shown in Figures 1 and 2. These indicate that the animals moved much more at night than in the day, a pattern observed in other species of polyplacophorans (HEATH, 1899; GLYNN, 1970; SMITH, 1975). There is also an indication that the animals moved more when they were dry (completely exposed to air) or awash (covered less than half the time by lapping

¹ Present address:

P. O. Box 3692, Stanford, CA 94305



waves) than when they were submerged (covered more than half the time). Assignments of the categories "awash," "submerged" and "dry" were subjective and conditions could vary at one particular tidal height, depending upon the surge. The relation of activity to tidal height and conditions of exposure to sea and air is illustrated in Figure 4. In Figure 3, the data are organized to show the relationship of activity to conditions of tidal exposure and the light cycle.

During the day, fewer animals moved when submerged than when dry (Mann-Whitney U-Test; $P < 0.001$) or awash ($P < 0.01$), and a slightly larger number moved when dry than when awash ($0.1 < P < 0.2$). For the average distance moved, there is a similar relationship: lesser movement while submerged than awash ($0.05 < P < 0.1$) or dry ($P < 0.05$) and slightly greater movement when dry than when awash ($0.2 < P < 0.4$). At night, activity patterns were similar — i.e., the animals moved more when awash ($P < 0.002$) or dry ($P < 0.002$) than when submerged. Their activity was approximately equal during both their dry and awash periods. Contrasting diurnal with nocturnal patterns, more animals were moving nightly while submerged ($0.05 < P < 0.1$), awash ($P < 0.001$), and dry ($P < 0.001$) than during the day. They also moved greater distances at night while awash ($0.02 < P < 0.04$) and dry ($P < 0.002$) than during the day. There was very little difference between day and night movement when they were submerged ($P < 0.1$).

PHOTOTACTIC BEHAVIOR

Negative phototaxis has been observed in some chiton species (CROZIER, 1920; HEATH, 1899; WESTERSUND, 1975) and is possibly related to their nocturnal behavior; consequently I tested *Cyanoplax hartwegii* for a light response. Sixteen animals, laboratory and dark adapted for 12 days,

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Figure 1

Activity patterns of 13 *Cyanoplax hartwegii* observed hourly from May 13th to May 15th, 1974

- A. Conditions of tide and light. The horizontal bars indicate tidal exposure of *Cyanoplax*: S = submerged; D = dry; and blacked out areas = awash. Light cycle is indicated on each graph
- B. Total number of animals that moved each hour
- C. Average distance moved by the animals each hour

were placed in the middle of a shallow tray, with eight facing toward a light source and eight away. The light source was a 500-watt incandescent bulb placed about six inches above one end of the tray and about 11 inches away from the chitons. After the chitons had settled (usually 2 to 3 minutes), the light was turned on for 20 minutes. I ran 4 trials with the same 16 chitons, rinsing and turning the tray 180° and allowing the animals to dark adapt for 30 minutes between trials. The first 3 trials were run with the animals on a thin film of seawater. Hoping to diminish any response to heat from the bulb, I ran the fourth test with the animals totally submerged in fresh seawater. The results were similar for all the tests: out of 64 choice situations, 52 responses were away from the light, two were toward the light, and ten showed no response.

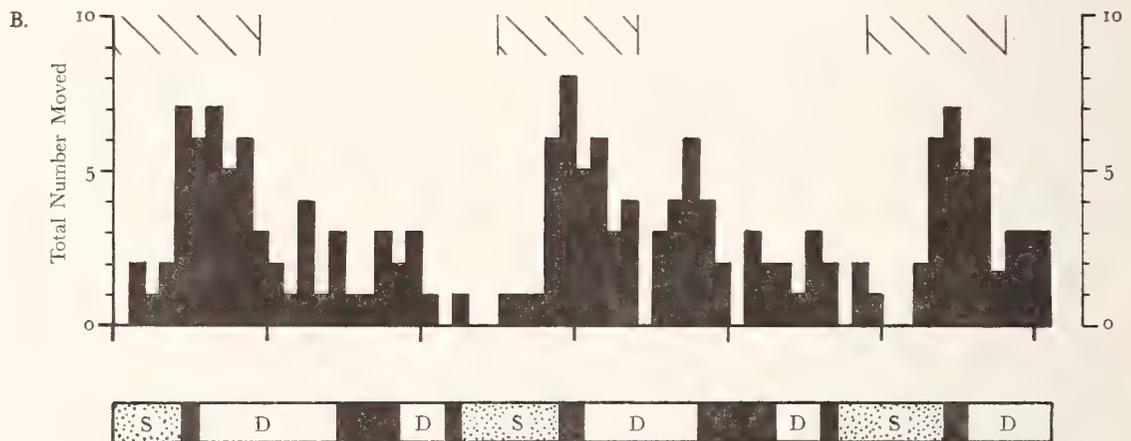
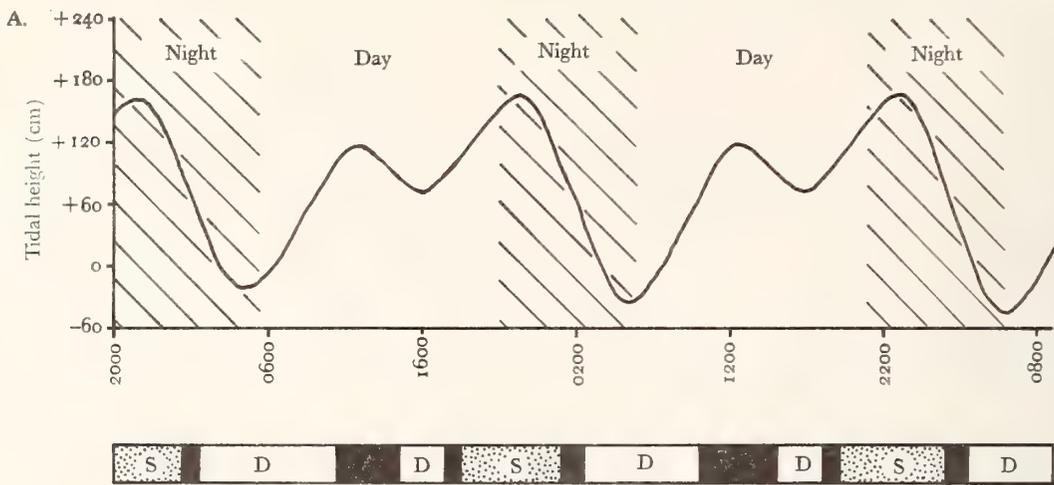
HOMING BEHAVIOR

My activity studies showed that the chitons' overall activity is greater during periods when they are not submerged. In those studies, some animals returned to their starting points after periods of movement while others did not.

To examine further the incidence of homing behavior, I marked 84 chitons with numbered labels and recorded their positions once daily during low tide for 14 days, starting April 27th, 1974. Homing was considered to exist when animals were repeatedly found in a precise location or homesite. Only 10 of these animals displayed homing over the entire period, while another 22 homed for periods varying from 3 to 13 days. I displaced the 11 most consistent homers not more than 10 cm from their respective homes. Only two returned home within 24 hours; three weeks later, only one was found in its original home.

I returned on June 1st to the same area at low tide and attempted to locate the 84 marked chitons. One-third (28) were found, of which 17, though for the most part not in their original homesites, were still in their original areas (either under the same *Pelvetia* clump or not more than 20 cm from it). Of the remaining 11 animals, 9 had moved to different *Pelvetia* clumps ranging from 30 to 104 cm away. Only 2 left the *Pelvetia* community altogether and both were found on exposed granite among clusters of *Anthopleura elegantissima*. One had traveled 65 cm, and the other had gone an impressive 186 cm, made notable by the fact that, in order to reach this new area, the animal either had to cross a stretch of sand, or follow a rather lengthy, circuitous route over a rock bridge.

The above results clearly show that individual chitons may reside at, or consistently return to, a homesite for a period of at least two weeks, and they indicate that homing



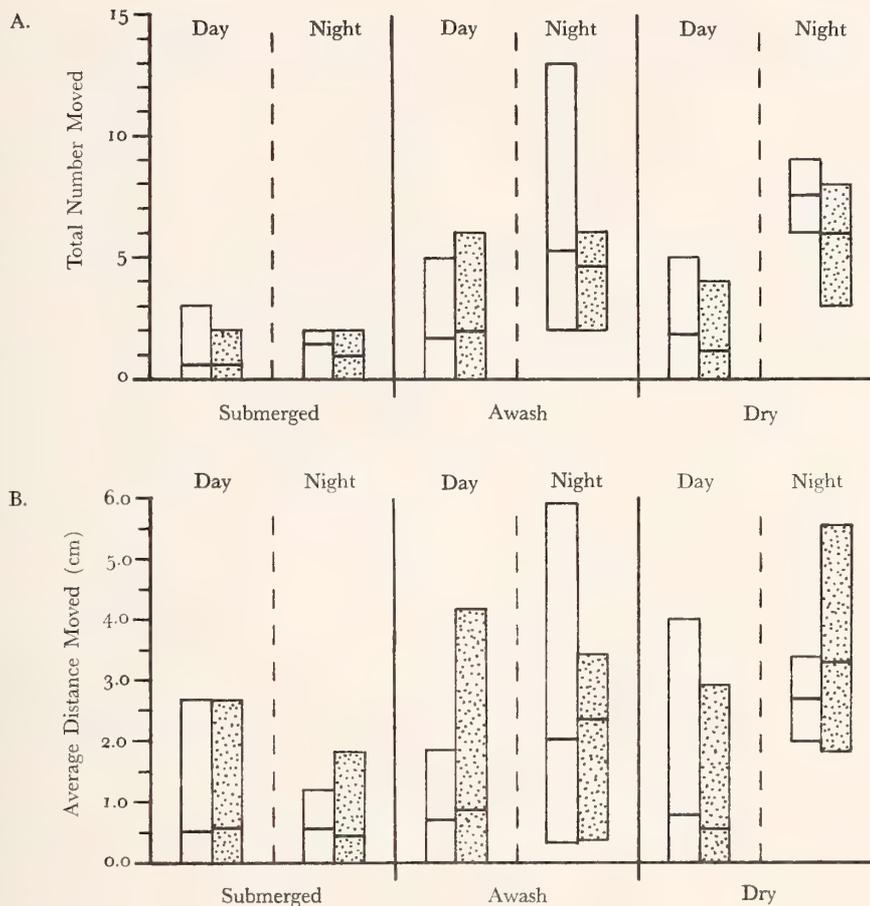


Figure 3

Activity shown in relation to conditions of tidal exposure and the light cycle. The bottom of the vertical bars indicates the minimum levels of activity recorded for a given condition. The top indicates the maximum and the line within the bar indicates the mean of

recorded values. Clear bars represent data from May 13th to May 15th; stippled bars represent data from May 19th to May 22nd.
 A. Total number of animals that moved
 B. Average distance moved by the animals

is a rather transient phenomenon. However, the results of the activity studies show that at low tide, when observa-

tions for homing were made, more of the chitons are moving and, therefore, they are less likely to be in their homesites. Thus, the chitons may be more consistent in their homing behavior than my studies suggest.

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Figure 2

Activity patterns of 13 *Cyanoplax hartwegii* observed hourly from May 19th to May 22nd, 1974. Key and explanations are the same as in Figure 1

DISCUSSION

In populations of *Cyanoplax hartwegii* living under *Pelvetia*, movement was mainly nocturnal. Some animals were active during the day, which behavior may in part be

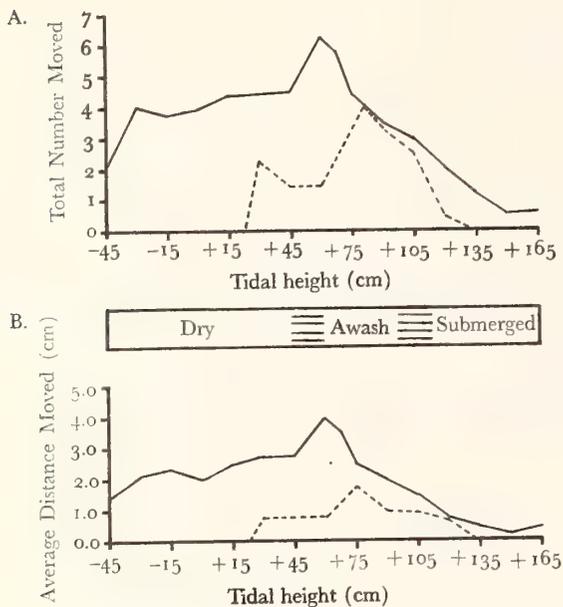


Figure 4

Activity versus the tidal height. Approximate conditions of tidal exposure are indicated on the horizontal bar. Dotted line represents activity from May 13th to May 15th; solid line represents activity from May 19th to May 22nd

- A. The sum of the total number of animals that moved during a particular tidal height for the entire watch divided by the number of times that tidal height occurred during the watch
- B. The sum of the average distance moved by the animals during a particular tidal height for the entire watch divided by the number of times that tidal height occurred during the watch

related to the fact that the *Pelvetia* affords some protection from heat, desiccation, and predation. The chitons moved more during periods when they were dry or awash than while submerged. This is not the case for the chiton *Mopalia muscosa* (Gould, 1846) whose activity is far greater when submerged (Smith, 1975). Possible advantages of this behavior to *Cyanoplax* are discussed below.

Many *Cyanoplax hartwegii* are located on smooth rock, and they cling less firmly and are thus more readily dislodged from the rock substratum than *Mopalia muscosa* or *Nuttallina californica* (Reeve, 1847), which are found in the same area. It is possible that the strength of the surge is strong enough to detach moving *Cyanoplax*, but not ones which are inactive on the rock.

Another possible advantage of decreased activity during submerged periods is suggested by CONNOR (1975) and

concerns the animal's diet. *Cyanoplax hartwegii* were frequently observed feeding on *Pelvetia* and this alga makes up the great bulk of their gut contents (Robb, 1975). While the *Cyanoplax* are submerged, the *Pelvetia* clumps, attached by one relatively small holdfast to the rock, are afloat and considerably agitated by the surge. This would make feeding on the thallus difficult. This is not the case when the chitons are merely awash or dry, and it is during these periods, in the day or night when *Pelvetia* lies prostrate on the rocks, that I have observed the animals feeding on branches of the alga.

Although I did not find consistent homing behavior in *Cyanoplax hartwegii*, they did appear to prefer certain areas on the substrate to others. These "campsites" were frequently occupied by a chiton during the animal's less active periods. Sometimes the same chiton would home to one location consistently for days, but eventually it would leave and another *Cyanoplax* would take its place. There were over a dozen such locations on the transect used for the two lengthy watches and I could see this phenomenon occurring in other transects where I had marked *C. hartwegii*. The high frequency of habitation of these particular sites versus other possible sites suggests strongly that these sites are "recognizable" by the animals, possibly by recognition of chemical cues. THORNE (1967) suggests that such an accumulation of chemicals on the substratum at the homesite is the cue for homing in the chiton *Acanthozostera gemmata* (Blainville). Most of the sites appeared to offer the *Cyanoplax* some protection, being located in a crevice, depression, tidepool, or among *Phragmatopoma* or *Anthopleura elegantissima*. It seems likely, whatever the mechanism involved, that this behavior has some survival value for the animal, such as consistent protection from desiccation.

SUMMARY

1. The chiton *Cyanoplax hartwegii* found on Mussel Point in Pacific Grove, California under the brown alga *Pelvetia fastigiata*, is more active at night and is negatively phototactic in the laboratory. Protection afforded by the *Pelvetia* habitat might explain the considerable daytime activity that does occur.
2. The tidal cycle affects the animals' activity, greatest activity occurring at dry and awash periods. Lesser activity during the high tides may be due to the strength of the surge or to the difficulty in feeding on *Pelvetia* during these times.
3. Although strict homing is not exhibited by *Cyanoplax hartwegii*, certain "campsites" on the substratum are

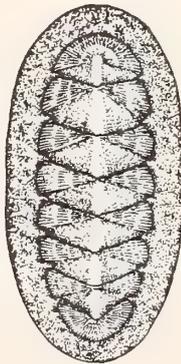
occupied successively by different individuals. This behavior may have survival value as these sites may be consistently well-protected spots.

ACKNOWLEDGMENTS

I am grateful to the faculty and staff of Hopkins Marine Station and my Biology 175H classmates for being an integral part of an unforgettable learning experience. Particular thanks go to the Drs. Isabella A. and Donald P. Abbott for their enthusiasm, sincerity, and hospitality. Even more particular thanks are given to Dr. Robin Burnett, whose patience, willing help, copious advice and equally abundant criticism have been greatly appreciated. Also, I thank Mr. Allyn G. Smith of the California Academy of Sciences for confirming several identifications of chitons.

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Exogenous and Endogenous Control of Movement in the Chiton *Mopalia muscosa*

(Mollusca : Polyplacophora)

BY

KRISTEN R. WESTERSUND¹

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

(2 Text figures)

INTRODUCTION

THE CHITON *Mopalia muscosa* (Gould, 1846) is flexible in habit and habitat. In the present study on the Monterey Peninsula, California, *M. muscosa* was found at low tide 1. in permanent tide pools; 2. attached to the undersides of large rocks in sand with *Mopalia lignosa* (Gould, 1846); 3. in the midst of tight clusters of sea anemone, *Anthropleura elegantissima* (Brandt, 1835); 4. in the shade of various macroscopic algae; 5. in bare rock crevices with only microscopic and crustose algae; and 6. on exposed surfaces where their shells are often bleached white by the sun. BARNAWELL (1954) notes that *M. muscosa* is one of the few species of *Mopalia* that can do well in the estuarine conditions of San Francisco Bay. This variety of habitats implies behavioral flexibility as well as wide physiological tolerances.

Field observations by SMITH (1975), myself, and others indicate that *Mopalia muscosa* moves mostly at high tide and at night. In an observation which led to the present research, chitons in a high tide pool began to move at sunset. At the same time, a rising tide splashed the tide pool with waves, and the water temperature dropped rapidly from 24°C to 15°C. The chitons may have begun to move in response to the onset of darkness, the disturbance of the pool by wave splash, the lowered temperature, or an endogenous cycle. A series of experiments was planned to determine the effect of each stimulus isolated from the rest. All work was carried out at the Hopkins Marine Station of Stanford University during the period April-June, 1974.

EFFECTS OF LIGHT, TURBULENCE, TEMPERATURE AND WATER LEVEL ON MOVEMENT

Methods: Five aquaria, each containing 5 *Mopalia muscosa*, were placed in darkrooms equipped with running sea water. In each tank, 3 of the chitons were freshly collected, and the other 2 had been in the laboratory 1 to 2 weeks. Individual animals were not marked, but were recognized by size and adhering algal cover. Each aquarium was held under a different set of test conditions for a period of 12 hours, as shown in Figure 1, and explained below. Tanks A, B, and D were held in the same darkroom, while Tanks C and E were isolated in separate darkrooms.

At the start of the experiment and every 30 minutes thereafter, the position of the center or midpoint of the animal was established to the nearest centimeter. The straight-line distance between consecutive midpoint positions was calculated and recorded as the distance moved (net displacement) per hour. Observations under dark conditions were made with a flashlight covered with a red filter, to which the chitons appeared to give no response.

Results and Discussion: The control animals in Tank A (Figure 1-A) held at constant darkness, temperature, and turbulence, showed little movement. Small peaks of activity were noted which (unfortunately) occurred when conditions were changed in other tanks. Since the control was held in the same room with Tanks B and D, the manipulations carried out on these other tanks may have altered the noise level or some other factor in the room to cause these small activity peaks. It is also possible that these were random fluctuations.

¹ Permanent address:
Star Route, Pendleton, OR 97801

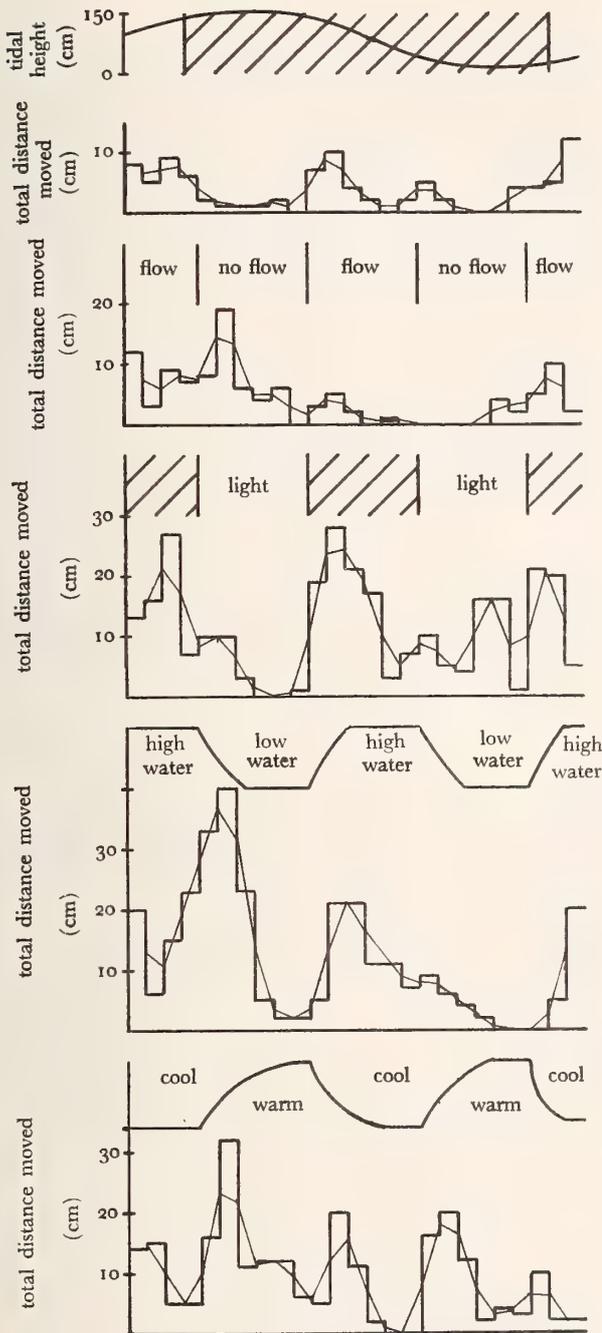


Figure 1

Total distance moved versus time (25 hrs) for 5 chitons in each of 5 aquaria held under conditions explained below. At the top of the figure is a curve representing the height of the tide and shading representing night. In the activity curves, each vertical bar represents total distance animals moved in a one-hour interval. The finer lines

The animals in Tank B, subjected to varying turbulence (Figure 1-B) showed no obvious response to this gentle stimulus.

In Tank C, exposed to alternate periods of light and darkness (Figure 1-C), there was less movement during light than during dark periods; and the first onset of a dark period was accompanied by a sharp increase in activity.

In Tank D (Figure 1-D), the animals responded to a falling water level by moving down the sides of the tank, keeping half submerged until they reached the bottom. Although the aquarium bottom remained wet during the artificial low tides, the chitons moved very little until the "tide" rose again.

Animals kept in Tank E with a temperature cycle (Figure 1-E) showed increased activity at the onset of each change.

The results indicate that movement may be stimulated by decreases in incident light, or by a change in water temperature or water level.

ENDOGENOUS RHYTHMS

The results obtained above indicate that movement may be stimulated by some exogenous factors; the following experiment was performed in order to resolve a possible endogenous rhythm.

Methods: Eight chitons from low tide pools and 8 from other habitats were collected and placed in aquaria equipped with running sea water at 14°C in constant darkness. Animals ranged in length from 5 to 9 cm. Observations were made with the aid of a dim red light. The position of the midpoint of each chiton was checked every 45 minutes over 25 hour periods, starting after the chitons had been in the aquaria .5, 3, 13 and 19 days. Movement (net

show general trends by connecting averages of adjacent data points.

A. In this control, nothing was varied. Sea water circulated at 14°C, the tank was kept full, and the room was kept dark. These were also the conditions in the other tanks, except for those that were varied, as explained below and shown above each of the other activity graphs. B. The gently turbulent flow of sea water was stopped or restarted every 3 hours. Temperature change was minimal. C. Cool bright overhead fluorescent lights were turned on or off every 3 hours. D. The tank was alternately drained or refilled every 3 hours. The tank took about 1 hour to refill and 1.5 hours to drain. During the 3 hour filling period, the water was kept flowing, but during the draining period, the water was shut off. Therefore a small temperature cycle probably accompanied the "tidal" cycle. 3. The incoming stream of water was changed from a source at 14°C to a source at 25°C or back again every 3 hours. After 1.5 hours, the temperature of the tank was within 1°C of the incoming water temperature.

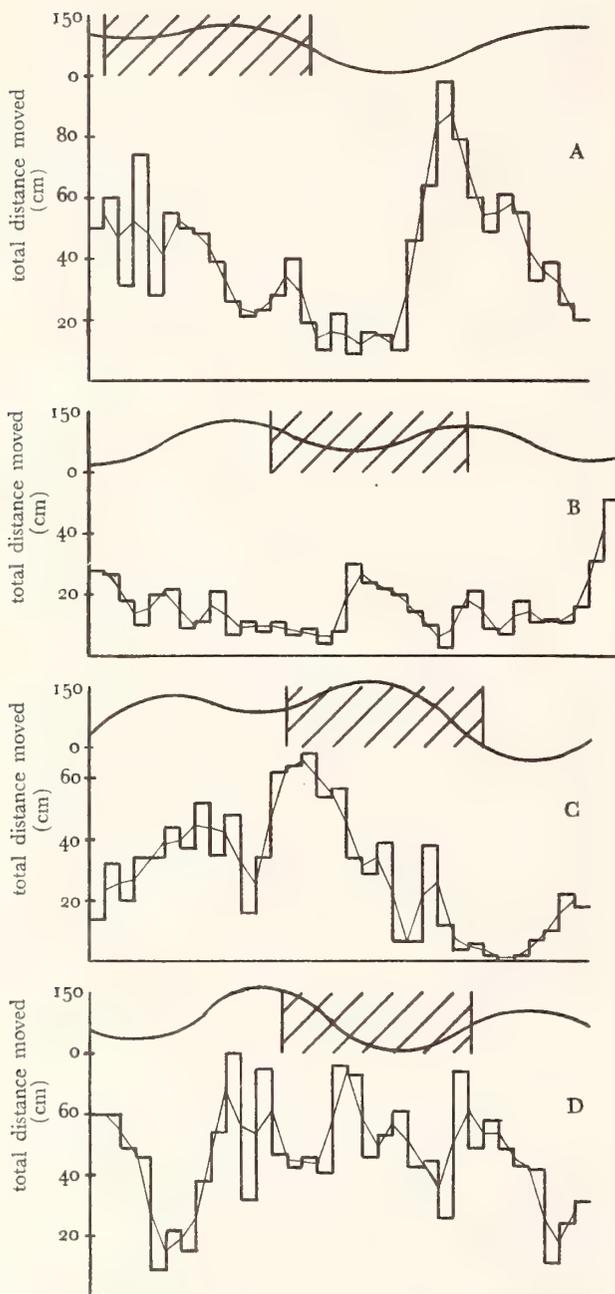


Figure 2

Total distance moved versus time (25 hrs) for 16 chitons maintained in constant dark and observed after 0.5 (A), 3 (B), 13 (C), and 19 (D) days in aquaria. External conditions of light and tide are shown for each observation period. Chitons were observed every 45 minutes; consequently, vertical bars represent total dis-

placement) was recorded as in the previous experiment. **Results and Discussion:** Figure 2-A shows the total activity of all 16 animals for a 25 hour period starting 12 hours after they were placed in aquaria. Minimum activity, corresponding to actual lower low tide, is followed immediately by an increase in activity. After 3 days in the tank (Figure 2-B), a sharp increase in activity of the animals still corresponds to the rising tide following the lower low tide, but there is less overall activity. After 13 days (Figure 2-C) activity is again low during the lower low tide and the overall activity is again high. No tidal cycle is clearly resolvable after 19 days in the tanks (Figure 2-D). The results obtained are very suggestive of a tidal rhythm of movement. The lull in activity at low tide periods coincide with the field observations of SMITH (1975) who found that *Mopalia muscosa* that were uncovered by the tide had already "homed," while other animals slightly lower in the intertidal that were not going to be exposed did not home, but did reduce their movement. Activity was greatest during spring tides, days #1 and #13. These results suggest the animals may predict monthly fluctuations of tidal height. Further studies are needed to confirm and expand on these preliminary conclusions.

SUMMARY

1. *Mopalia muscosa* appears to be exogenously stimulated to move by decreases in incident light, or by a change in water temperature or water level.
2. *Mopalia muscosa* responds to an artificially lowered water level by moving down, staying half submerged. The chitons move very little in an empty tank until it is refilled.
3. *Mopalia muscosa* show evidence of an endogenous tidal rhythm in their movement. Under constant aquarium conditions, they move less at times corresponding to low tide, especially the lower low tide, and they move much more soon after.
4. *Mopalia muscosa* under constant aquarium conditions show more overall movement and clearer tidal cycles during spring tides. The same monthly cycle may enable them to predict the heights of low tides.
5. No endogenous diurnal activity pattern was detected.

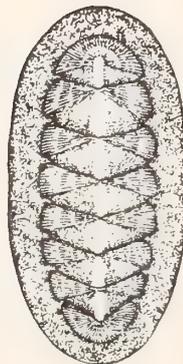
tances moved in a 45 minute period. As in Figure 1, finer lines show general trends. Note the recurring pattern of reduced activity at low tides followed by sharply increasing activity soon afterward.

ACKNOWLEDGMENTS

I would like to thank and acknowledge the help of: Dr. Robin Burnett, who advised me during this study and the writing of this paper; David W. Phillips, who gave advice and loaned equipment; Dr. W. G. Evans, who advised and encouraged me to study tidal rhythms; and Margaret Westersund, my wife, who worked with me observing chitons at all hours.

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(15 July 1975)



A Behavioral Light Response in the Chiton *Stenoplax heathiana*

BY

KEITH BAUER¹

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

(5 Text figures)

INTRODUCTION

MANY SPECIES OF CHITONS have aesthetes, unique photoreceptors whose structure has been examined (e.g. OME-LICH, 1967), but whose role in behavior has received little attention. The most common light-mediated behaviors noted among chitons are: 1) phototaxis (usually found to be negative); 2) diurnal activity patterns; and 3) shadow responses (HEATH, 1899; and BOYLE, 1972). The first two behaviors require only photoreceptors that are able to detect the presence of light and of light intensity gradients. The shadow response, on the other hand, requires the ability to detect sudden decrements in light intensity. Since the approach of possible predators could very well be signalled by a shadow, the ability to detect a sudden drop in light intensity may be of selective value. Obviously, a shadow response can only occur when animals are illuminated; on the other hand, since the sensitivity of most photoreceptors is attenuated by long exposures to light, due to bleaching of the visual pigment, it might be expected, that the shadow response of chitons would weaken during the day. However, in another mollusk, *Lima scabra* (Born), the strength of the sensory response to shadowing increases during light adaptation, and a photoreceptor mechanism for this phenomenon has been proposed (MITSOS, 1973). The present investigation, on the chiton *Stenoplax heathiana* Berry, 1946, obtained the first measurements of an increase in a **behavioral** response to shadowing during light adaptation.

MATERIALS AND GENERAL METHODS

Specimens of *Stenoplax heathiana* were collected intertidally off Mussel Point, Pacific Grove, California, in May, 1974, and were used in experiments not more than 3 weeks after collection. The animals were maintained unfed in tanks of running seawater at a temperature of about 14°C.

The response to shadowing in this animal consists primarily of a movement of the dorsal surface towards the substrate, hereafter termed a "clamp-down". In order to measure this clamp-down response, the dorsal surfaces of the animals were first carefully dried, and a pin, fashioned into a hook, was glued to their plates at about the middle of the body. After allowing the animals to adjust to this condition for at least 24 hours, a specimen was selected and placed in a wax-bottomed pan filled with sea-water kept at about 14°C by a Peltier cell. A string from a force transducer was hooked around the pin on the specimen's dorsal surface and pulled taut. The output of the transducer was then coupled to a polygraph, giving a permanent record of relative changes in string tension. In order to eliminate all lateral movement, a tight enclosure was built around the animals using pins inserted in the wax. With this enclosure in place, string tensions could be changed only by vertical movement of the chiton's plates.

Two light sources were used during the course of the experiment. Monochromatic test flashes were supplied by a high intensity diffraction grating using a 100-watt tungsten-halide lamp; the intensity of this source was controlled by a linear neutral density wedge; a camera shutter was used to control the duration of the test flashes. Background adaptation lights were provided by a heat-filtered 18-watt

¹ Permanent address:

430 San Domingo Way, Los Altos, CA 94022

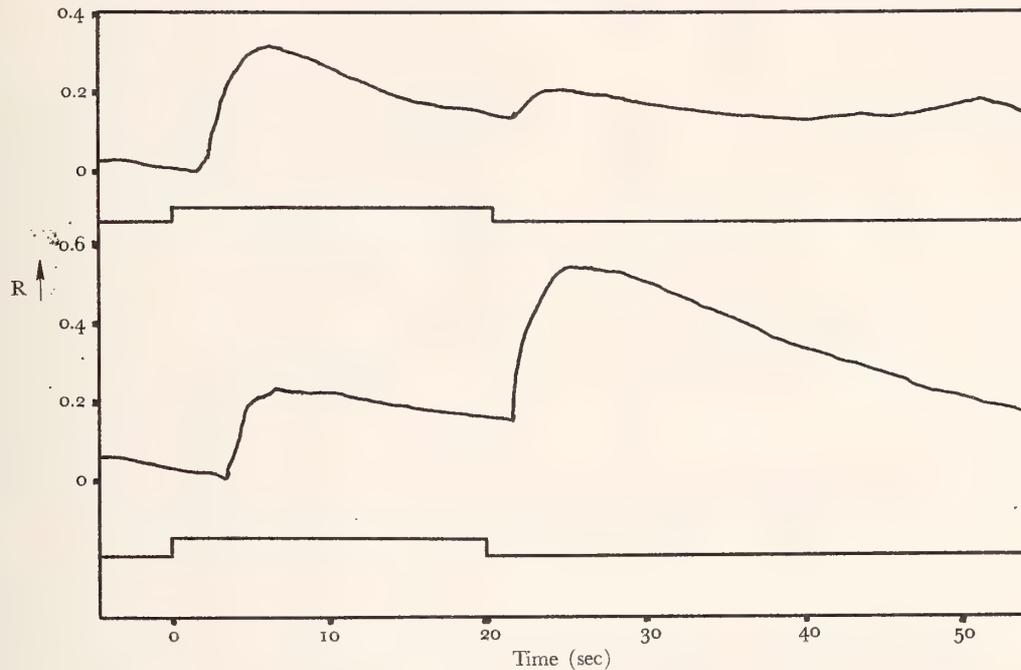


Figure 1

A. Response of *Stenoplax* to test flashes of light during dark (λ of the test flash = 500 nm). B. Response to the same test flash just subsequent to approximately 30 minutes of light adaptation. (Vertical axis indicates response magnitude in upper traces.

The lower traces indicate the duration of test flashes: upward deflection indicates the onset of the stimulus and downward deflection indicates the cessation of the stimulus. Stimulus duration about 20 seconds.)

tungsten lamp equipped with a Corning 5-58 filter, with a transmission maximum at about 450 nm, and a Wratten 22 filter which cut off wavelengths of light below 560 nm.

EXPERIMENTS AND RESULTS

When presented with a 20 second test stimulus from the monochromatic source ($\lambda = 500$ nm), *Stenoplax* displayed a behavioral clamping down to both the presentation of the flash ("on-response") and to its removal ("off-response"). The behavior as measured was the same for each stimulus; a rapid lowering of the dorsal surface began 1 to 3 seconds after the onset of the stimulus, and continued for about five seconds. The chiton then returned to its

original position, a process which was highly variable in duration and lasted up to several minutes (see Figure 1). The actual displacement of the animal's plates during this process was only about 1 mm; the tension of the string from the strain gauge may have decreased the normal displacement slightly.

The clamp-down response could be evoked by other stimuli as well. Stroking the dorsal surface of the animals with a pin, disturbing the water in the tray, or any sharp movement which might affect the tray, such as a tap on the table-top close to the animal, resulted in a clamp-down. Some animals clamped down in the absence of stimuli perceivable by the investigator. The clamp-down responses elicited by all types of stimuli were indistinguishable from one another. Only clamp-downs that occur-

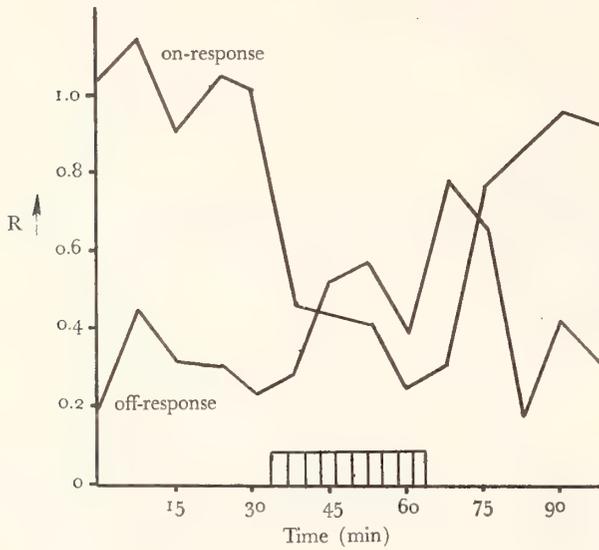


Figure 2

Average of five runs showing magnitudes of on-response and off-response during light and dark adaptation. Animals were dark adapted for one hour prior to the start of the experiment. The striped bar shows the period of light adaptation (about 30 minutes). Response magnitude, in this and in all figures, is in arbitrary units which are in proportion to uncalibrated values recorded by the polygraph.

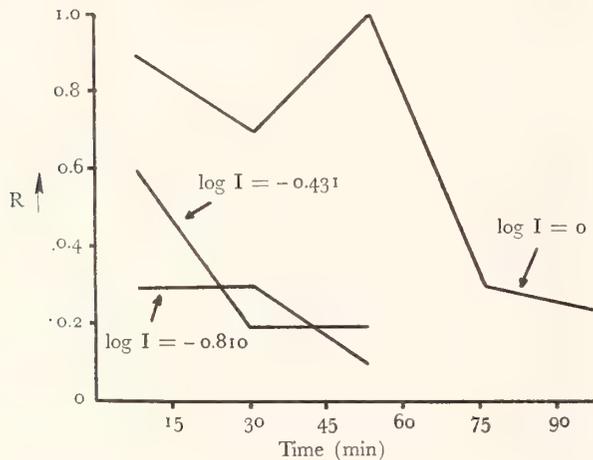


Figure 3

Magnitude of the off-response after 30 minutes light adaptation under different intensity conditioning lights. Different intensities were achieved using neutral density filters. The adaptation light was removed at time = 0.

red from 1 to 3 seconds after the presentation of a light stimulus were counted as responses to light.

In order to determine the relative effects of light and dark adaptation on the on- and off-responses, specimens were first allowed to dark adapt for at least one hour. Then test flashes, each 20 seconds in duration and given at least 6 minutes apart, were presented from the monochromator. The test flashes used within any one sequence were identical in intensity, and had a wavelength of 500 nm. After dark adaptation, the on-response was of much greater magnitude than the off-response (Figure 2). The animals were then light-adapted for about 30 minutes. The monochromatic test flashes were again used to test the magnitude of the responses. During and immediately after the light adaptation, the on-response was considerably weakened, while the off-response usually increased during presentation of the adaptation light, and was always stronger just subsequent to its removal (Figure 2).

The magnitude of the effect of light adaptation was found to be dependent upon the intensity of the adaptation light: the stronger the light used to adapt the animal prior to testing, the more the off-response was increased (Figure 3). It does not appear to matter whether the on-stimulus is given before the off-stimulus or vice-versa, and furthermore, the rates of change of the two responses are not necessarily correlated (Figure 4). In *Lima scabra*, the same effect has been noted and shown to be highly dependent on the wavelength of the adaptation light (Mpirsos, 1973). The effect of using 3 different ranges of wavelengths of the adaptation light on the magnitude of the off-response was examined in *Stenoplax* as well; however, no significant wavelength dependence could be discerned (Figure 5).

DISCUSSION

While *Stenoplax* is predominantly a nocturnal animal which seeks the undersides of rocks during the day, it can be found exposed early in the morning (HEATH, 1899). In addition, presumably the moon can sometimes provide sufficient light for some predators to see *Stenoplax* when it is out grazing. Consequently *Stenoplax's* ability to detect and to react to a sudden change in light intensity may reflect its ability to detect and react to changes in lighting produced by an approaching predator. Since chitons are unable to outrun many potential predators, a clamp-down to impede removal from the substrate is probably their best defense.

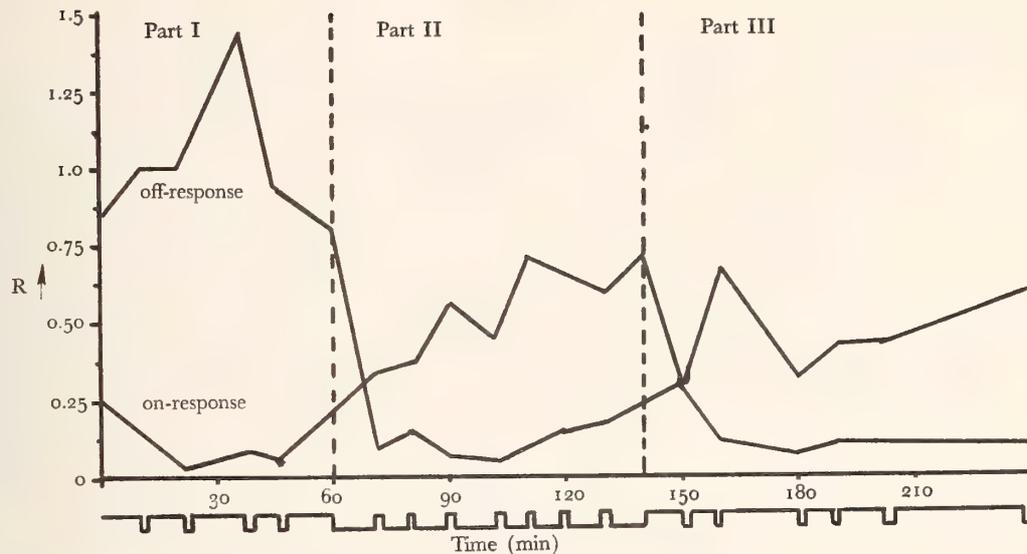


Figure 4

Magnitude of the on- and off-responses during various stimulus regimes. Animals were light adapted for 20 minutes prior to the start of the experiment using the monochromator, which was used throughout to give test flashes. During Part I, the light was interrupted intermittently for about 20 seconds to give "off-on" stimuli. For Part II, the light was turned off and the responses of the animal were followed during dark adaptation using short flashes of "on-off" stimuli. In Part III, a return to the first stimulus regime was used to follow the responses during light adaptation. Note that the rate of change of the off-response is greater than that of the on-response during dark adaptation, while during light adaptation the reverse is true. Lower trace same as in Figure 1.

From a behavioral viewpoint, at least, *Stenoplax* seems to rely on its "on-receptors" during periods of low illumination and on its "off-receptors" during periods of high illumination for its primary source of information about sudden changes in intensity levels. This may give the animal a wider range of ambient illumination in which a potential predator can be detected. Physiologically, the weakening of the clamp-down in response to the on-stimulus during light adaptation can be accounted for by bleaching of the visual pigment. The increase in the off-behavior during light adaptation is much harder to explain. The only animal in which the sensory off-response has been

shown to increase during light adaptation is the file clam *Lima scabra*. A wavelength dependence of this effect led to a proposed mechanism involving two visual pigments. The present study has turned up no such wavelength dependence in *Stenoplax*, suggesting that this mechanism is probably not functioning here. However, it can not be conclusively ruled out, solely on the basis of this study. In order to more fully investigate this problem, a neurophysiological approach would be ideal; unfortunately preliminary attempts to record from the lateral nerve cord, which is known to innervate the aesthetes, were unsuccessful.

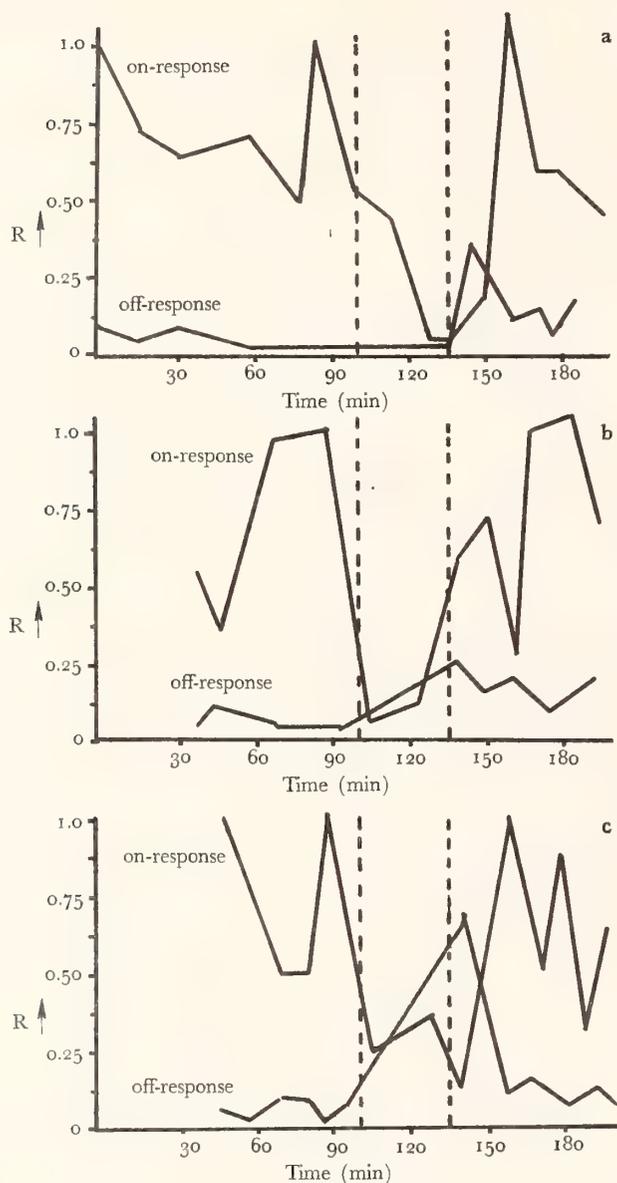


Figure 5

Magnitude of the on- and off-responses under three different colored conditioning lights: A. White light; B. Blue light (Corning 5-58 filter); C. Red light (Wratten 22 filter). Dashed lines indicate onset and removal of the adaptation light.

SUMMARY

The chiton *Stenoplax heathiana* was shown to respond to both the onset (on-response) and the removal (off-response) of a light stimulus. In both cases the response consisted of a slight clamp-down to the substrate, presumably to help maintain the animal's grip on the substrate. If the animal is light adapted, the magnitude of the off-response increases while that of the on-response decreases. These responses were shown to be independent of the wavelength of the light used to light-adapt the animal, which indicates that the differences did not result from stimulating two separate visual pigments. Thus, while this effect has clear adaptive significance, its physiological mechanism has not been determined.

ACKNOWLEDGMENTS

I would like to thank Dr. George J. Mpitsos for his advice and encouragement throughout this project, and especially for his critical reading of this paper. I would also like to thank the staff of Hopkins Marine Station for their kind assistance.

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Isometric Responses of the Somatic Musculature of *Cryptochiton stelleri*

(Mollusca : Polyplacophora)

BY

JOHN T. HARRISON¹

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

(1 Text figure)

INTRODUCTION

THE MUSCULATURE OF MOLLUSKS has attracted the attention of physiologists for many years largely because molluscan smooth muscle exhibits two unusual properties. One is the unusually great capacity for development of tension by smooth muscles of bivalves. The other is the occurrence of "catch," a change in physical state, first described in the clam *Pecten maximus* by VON UEXKÜLL (1912), and since extensively investigated in *Mytilus edulis* (e. g., TWAROG, 1967). Molluscan muscles exhibit a wide variety of ultrastructural organization varying from classic smooth muscles to highly complex striated fibers and including smooth muscles containing paramyosin that possess catch properties. Thus the phylum cannot be characterized by any one type of physiological response of somatic muscles.

Even though a comprehensive anatomical characterization of the musculature of *Tonicella* is available (HENRICI, 1912), there appear to have been no attempts to isolate preparations of somatic muscles of polyplacophorans for study of their physiological properties. The procedures described here were designed to investigate the contractive properties of one group of somatic muscles of one species of Polyplacophora, *Cryptochiton stelleri* (Middendorff, 1846). These preliminary results of isometric responses of the dorsal oblique muscle show that the responses resemble those found not only in other mollusks, but in Crustacea as well.

MATERIALS AND METHODS

Adult specimens of *Cryptochiton stelleri* were collected subtidally at Mussel Point, California, and maintained in a large seawater system tank prior to use. From each animal, an anterior dorsal oblique muscle was isolated and tied off with silk thread at the dorsal insertion. A 10 to 15 mm segment was then excised and the untied end secured in a plexiglass muscle clamp having imbedded Ag/AgCl-electrodes, and the entire system was maintained at about 15°C for the duration of the experiment. The muscle was secured at its working length as measured in the intact animal and allowed to equilibrate for about 20 minutes.

Isometric responses were coupled by a Grass FT.03 Force Transducer to a Grass Model 5 Polygraph through a Model 5PIC Low Level D.C. Preamplifier.

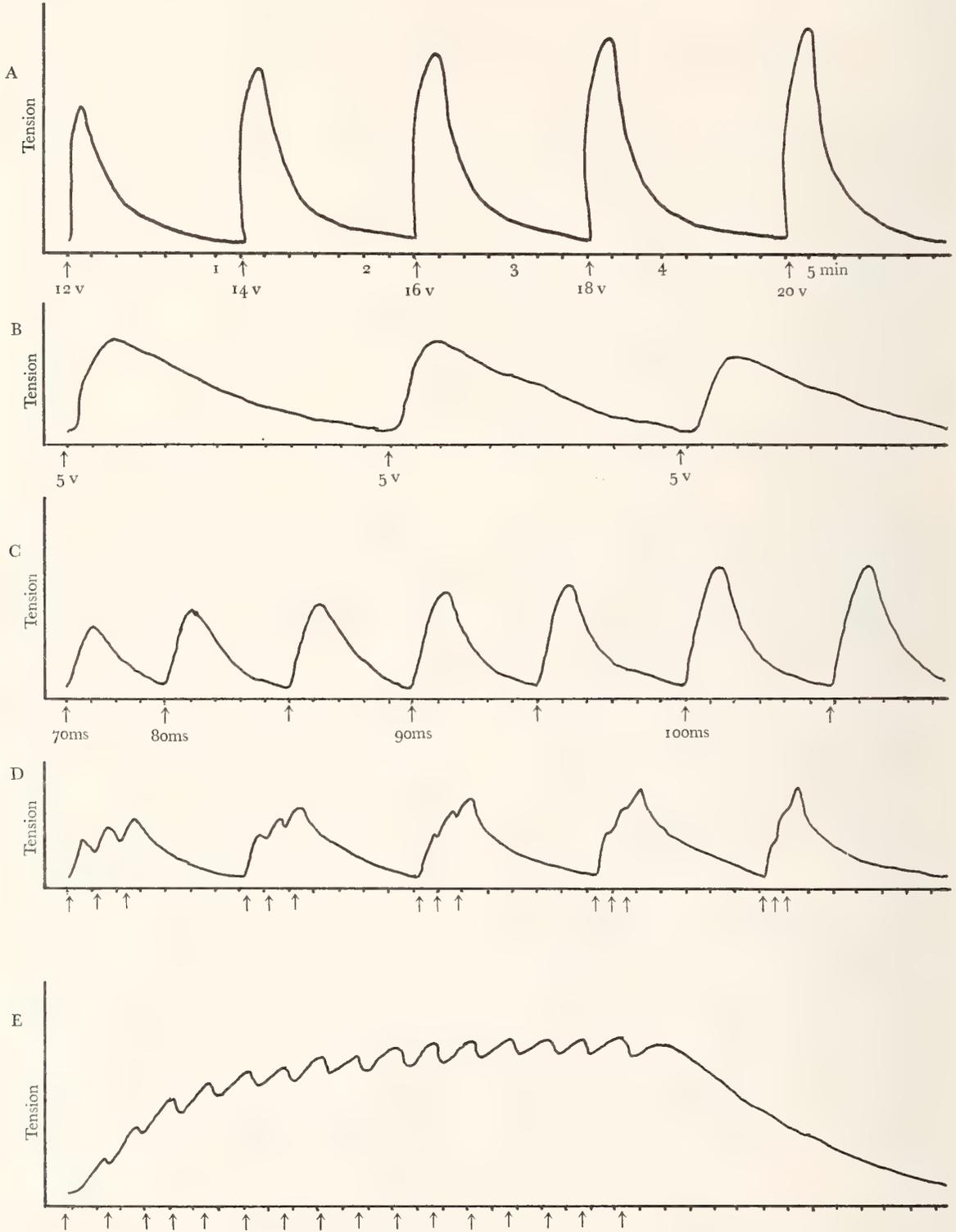
RESULTS

A representative sample of isometric responses from anterior oblique muscle preparations of *Cryptochiton stelleri* to various regimes of electrical stimulation is illustrated in Figure 1. The contractions may be generalized into two basic types of waveform: a rapidly ascending and decaying "phasic" form, and a slower "tonic" response that is characterized by a period of latency preceding the development of tension and by a more linear and elongate curve of relaxation.

The waveforms shown in Figure 1A are typical of the response to D.C. stimulation with a duration of a few sec-

¹ Permanent address:

353 Tennessee Lane, Palo Alto, CA 94306



onds. Peak contraction is attained in from 3 to 6.5 seconds, depending upon the strength of stimulus, while the decay from peak to half-peak ranges from 4.5 to 11 seconds in different individual preparations. The latter variation is not dependent upon stimulus intensity. By contrast, tonic contractions such as those in Figure 1B average 27 seconds to peak and 44 seconds to half-decay, neither value showing any dependence upon stimulus strength. The stimulus mode which elicits the tonic response is also moderate duration D.C., the only difference being the reversal of polarity at the stimulator. In addition, both responses may be evoked by various regimes of pulsed stimulation, as long as the appropriate polarity is employed for the phasic or tonic waveform. Figure 1C illustrates a phasic waveform elicited by a train of pulses of varying duration.

Both the phasic and the tonic responses are iterative in that they cannot be induced by single brief stimuli but require repetitive or continuous activation. It is also evident that for the phasic waveform both the rate of development of tension and the degree of tension achieved are dependent upon the amount of charge passed across the membrane. Thus, the increasing phasic summation (Figure 1D) reflects the decrease in interval between pulses and can be extrapolated to approximate the type of waveform in Figure 1C. By contrast, summation in the tonic mode is accompanied by the latency of response and retains a characteristic sawtooth appearance (Figure 1E). In the phasic mode, a tetanic contraction can be achieved which, for a muscle of working length 9 mm under a rest tension of 17.5 g, peaks at a maximum tension of 24.6 g.

As in other smooth muscles, a constant tension produces a gradual elongation which, in the isometric preparation,

is recorded as a steady decrease in resting tension. Furthermore, a protracted regime of occasional low level phasic stimulation will cause the rest tension to stabilize.

In preliminary experiments on the dorsal oblique muscle of *Cryptochiton stelleri*, reproducible responses could not be elicited with acetylcholine ($10^{-6}M$), 5-hydroxytryptamine (10^{-5} to $10^{-7}M$), or norepinephrine.

Teased muscle fibers examined by phase contrast microscopy exhibit a diameter of 3.5 to 5 μm and appear several millimeters long. Under high magnification, contractile fibrils are visible and of uniform diameter, with no indication of striation. Thus light microscopy revealed only one type of fiber. Other details of fine structure are not readily apparent although the presence of occasional membrane processes is indicated. The entire muscle is encased in a sheet of connective tissue.

DISCUSSION

Although the characteristics of the phasic waveform from a dorsal oblique muscle of *Cryptochiton stelleri* are generally comparable with those of other molluscan non-striated muscles such as the opaque adductor of *Pecten* (PROSSER, 1973: 747), both the character and the means of elicitation of the tonic response are anomalous. Significantly, there is no evidence of differentiation between fibers or contractile fibrils that would indicate fast and slow response capabilities. Consequently, the source of the variation in response must be sought elsewhere.

Preliminary reports on the development of tension in crayfish motor fibers as a consequence of membrane hyperpolarization (REUBEN *et al.*, 1967: 634) have recently been confirmed in other crustaceans (UCHITEL & GARCIA, 1974: 111). The characteristics of the evoked waveform include a period of latency and a time to peak and time to half decay considerably longer than those of normally elicited responses. Furthermore, the contraction following hyperpolarization has been proven independent of normal intracellular mechanisms for release and sequestration of Ca^{++} and is a function of inward diffusion of Ca^{++} from the bathing medium in response to the imposed electrochemical gradient.

On the basis of the waveform similarities, the tonic response of the chiton smooth muscle is tentatively suggested to be attributable to a similar hyperpolarization mechanism. The individual muscle fibers are known to be several millimeters in length, and in the process of isolation many fibers have been cut, leaving a channel for the establishment of intracellular variation in potential. The reversal of polarity is suggested to set up an electrochemical

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Figure 1

A composite of isometric responses of somatic muscle preparations from *Cryptochiton stelleri*, horizontal axis in 10 second intervals.

- A - phasic responses to 2 second D. C. stimuli (voltages indicated)
- B - tonic waveforms elicited by 5 second stimuli of 5 volts, polarity reversed from A
- C - phasic response to normal polarity D. C. pulses, 10 pulses per second, duration as indicated
- D - phasic summation: D. C. (4 volts, 2 seconds) separated by intervals of 10, 8, 6, 4, and 2 seconds
- E - tonic summation: reverse polarity D. C. (20 volts, 3 seconds) at points indicated

gradient which promotes the diffusion of Ca^{++} inward across the membranes of intact cells as a result of hyperpolarization. The discrepancies in time course from those reported by Uchitel and Garcia are to be expected because of significant ultrastructural differences between the two muscles, and are equally reflected in the respective phasic responses.

The similarity of the phasic and tonic waveforms to those obtained on a faster time scale for crustacean striated muscle points out the phylogenetic transcendence of the basic functional principles of muscular response. Further characterization, both electrophysiological and pharmacological, of this preparation will enhance our appreciation of its adaptive structural properties.

SUMMARY

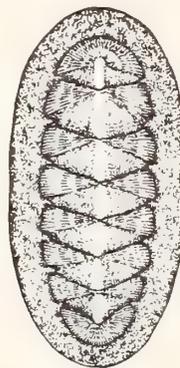
Electrophysiological data were gathered on an isolated segment of the somatic musculature of *Cryptochiton stelleri*, a subtidal Polyplacophoran.

1. The muscles were found to be iterative, single short stimuli evoking no response.
2. Both steady D.C. (2 sec.) and trains of short duration pulses evoke a short term phasic response, although the time relations differ slightly.

3. Steady D.C. of polarity opposite to the above yields a longer tonic contraction.
4. Both the tonic and the phasic responses will summate, but only in the phasic mode will the muscle sustain a state of tetanus.
5. The tonic response is hypothetically attributed to membrane hyperpolarization and subsequent Ca^{++} influx, and as such probably does not occur *in vivo*.

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The Resistance of Five Species of Polyplacophorans to Removal from Natural and Artificial Surfaces

BY

TODD A. LINSENMEYER¹

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

(5 Text figures)

INTRODUCTION

ACCORDING TO AREY & CROZIER (1919), the mechanism by which Polyplacophora attach themselves to surfaces is suction, primarily from the mantle. HOFFMANN (1931) comments that the role of the ventral muscle and the foot are of equal importance in fastening to surfaces. Detailed research on this subject, however, is lacking.

This investigation was designed to determine the forces required to remove several species of Polyplacophora from various surfaces, and to elucidate the mechanism by which they resist removal.

MATERIALS AND METHODS

Mopalia lignosa (Gould, 1846), *Mopalia muscosa* (Gould, 1846), *Nuttalina californica* (Reeve, 1847), *Katharina tunicata* (Wood, 1815), and *Stenoplax heathiana* Berry, 1946 were collected intertidally off the Monterey Peninsula in California in April and May, 1974. After collection, undamaged chitons were held in running sea water aquaria until tested. Chitons were used within 4 days of collection and each animal was used in only one trial.

Prior to testing, chitons were allowed to attach to the test surface for a period of two hours. The device sketched in Figure 1 was used to determine the resistance to removal by a force parallel to the surface. Approximately three grams were added to the container every two seconds until the animal broke free of the surface. The device had a mechanical advantage of two so that the force required to remove the chiton was taken as twice the weight of the container.

To determine resistance to removal by a force perpendicular to the surface, a cloth-backed picture hanger was glued to the dried plates of an animal (using the contact glue "ZIP GRIP" 10, Devcon Co., Danvers, Mass.), and connected by a string to the device illustrated in Figure 2. Weights were added at the rate of three grams every two seconds.

Following each test, the area of the foot and the total area of the ventral surface were determined by placing the chiton on a transparent grid. Resistance to removal is expressed as grams per square centimeter of foot area, since the foot proved to be the primary site of attachment.

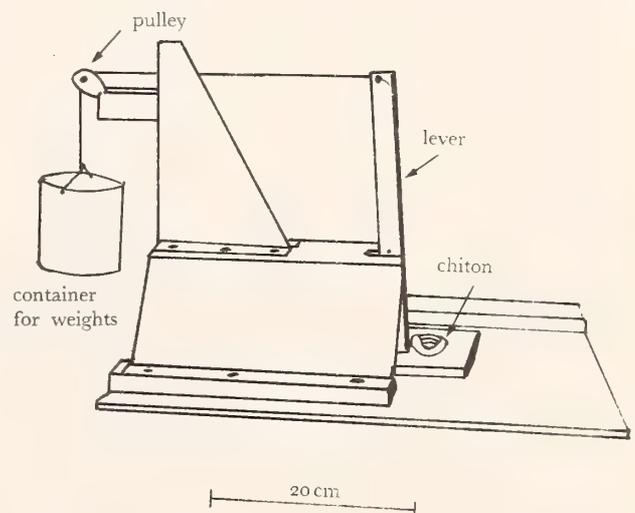


Figure 1

Device used to determine resistance to removal by a force parallel to the attachment surface

¹ Permanent address:
776 Pahumele Place, Kailua, HI 96734

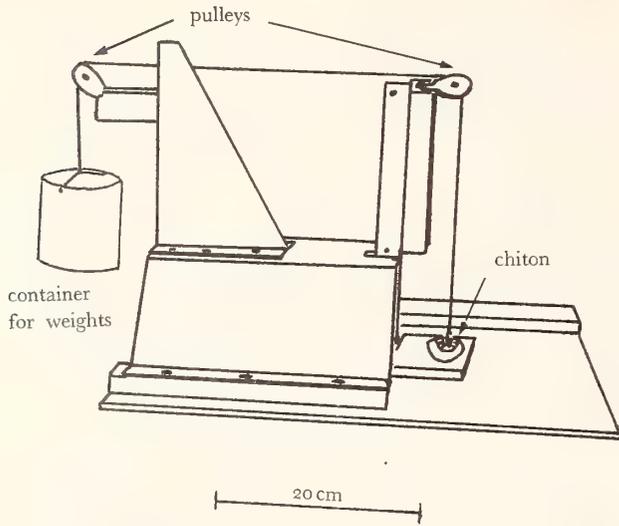


Figure 2

Device used to determine resistance to removal by a force perpendicular to the attachment surface

The relation between roughness of the surface to which the chiton was attached and resistance to removal was also determined. Tests were conducted using chitons attached to smooth glass or Plexiglas, #120 waterproof emery cloth having an average grit size of 120 μ m and flat natural granite.

In order to evaluate the role of reduced atmospheric pressure (suction) under the foot as a method of attachment, individual *Mopalia muscosa*, attached to Plexiglas plates, were placed in a vacuum desiccating jar. Piano wire, attached to the glued hook on the animal, exited the jar through a small hole and was connected to the device illustrated in Figure 2. Tests were run at atmospheric pressure and under vacuums of 127 and 380 mm of mercury below atmospheric pressure.

Additionally, chitons were allowed to settle on substrates with varying pore size: fritted glass with a pore diameter of less than 15 μ m, a 1 mm² mesh wire screen, and Plexiglas containing numerous 3 mm diameter holes. Their ability to cling, after two hours, was tested.

RESULTS AND DISCUSSION

Figure 3 shows the resistance of chitons to removal by forces parallel to a Plexiglas surface, in g/cm² of foot surface, for each species. *Nuttallina*, which inhabits rocks sub-

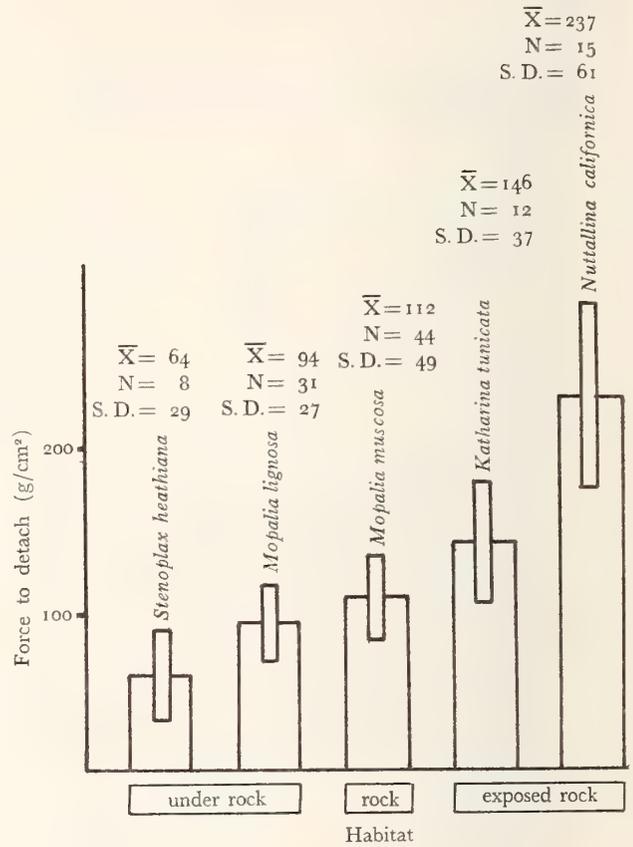


Figure 3

A comparison of the lateral force required to detach the five species of Polyplacophora in relation to the degree of wave action to which they are normally exposed. Bar graphs show mean and standard deviation

ject to heavy surf, exhibited a mean resistance to removal of 237 g/cm². This was more than double the resisting force of the three species occupying the most protected habitats: the two under-rock species, *Stenoplax heathiana* and *Mopalia lignosa*, had mean values of 64 and 94 g/cm² respectively, and *Mopalia muscosa*, found on the top surface of protected rocks, had a mean value of 112 g/cm². *Katharina tunicata*, which, like *Nuttallina*, occupies a surf-exposed habitat, had a comparatively high mean resistance to removal of 146 g/cm². Thus, the resisting force had a direct adaptive relationship to the habitat occupied by each of the species.

It was observed in all species that the plates and mantle were forcefully displaced as the loading increased, while

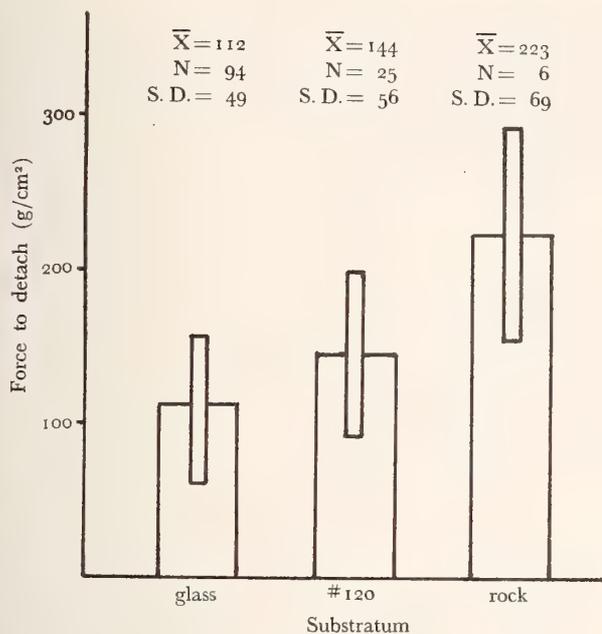


Figure 4

The lateral force required to detach *Mopalia muscosa* from various substrata. Bar graphs show mean and standard deviation

the foot remained fixed. This strongly implies that the foot plays the major role in attachment.

The lateral forces required to remove *Mopalia muscosa* from the three types of surfaces are shown in Figure 4. *Mopalia muscosa* had a mean resistance of 112 g/cm² when settled on Plexiglas, 144 g/cm² when on #120 emery cloth and 233 g/cm² when on granite. The animals had a mean resistance to a vertical (lifting) force of 82 g/cm² on natural rock. Thus substrate roughness had a significant effect on the resistance to detachment by forces both lateral to and normal to the attachment surface. During the tests using forces normal to the surface, the plates and mantle lifted off the surface by as much as 5 mm without detachment of the foot, again implicating the foot as the organ of attachment.

No significant differences were detected in the resistance of *Mopalia muscosa* to lifting forces applied at atmospheric pressure and under vacuums of 127 and 380 mm of mercury below atmospheric pressure (Figure 5).

Chitons could clearly attach to porous glass, wire screen, and Plexiglas with 3 mm holes. This result also argues against suction as a major factor involved in the resistance of chitons to removal. A chiton on the 3 mm thick Plexiglas with 3 mm holes passed part of its foot through a hole

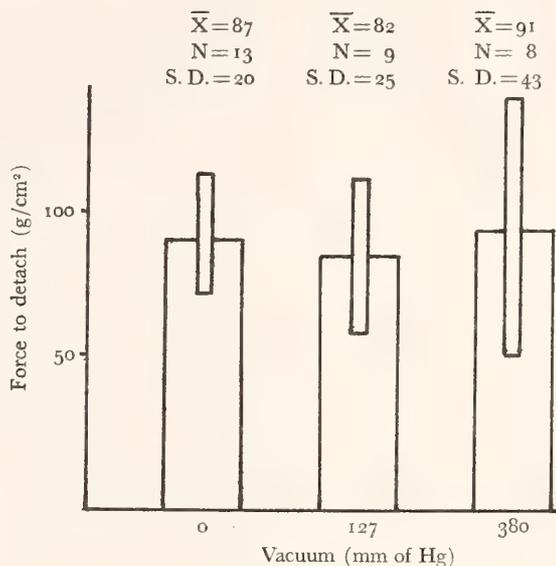


Figure 5

The vertical lifting force required to detach *Mopalia muscosa* from a Plexiglas plate at atmospheric pressure and at vacuums of 127 and 380 mm of mercury below atmospheric pressure. Bar graphs show mean and standard deviation

and expanded it on the opposite side, providing a mechanical wedging which held the chiton to the surface. Similarly, portions of the chiton's foot penetrated the wire screen and expanded on the opposite side.

When chitons were detached from smooth surfaces, a relatively insoluble mucus-like residue (hereafter "mucus") the shape of the chiton's foot remained on the surface. The chiton's resistance to removal from such smooth surfaces may be largely due to the adhesive effect of the mucus they secrete.

It appears that on rough surfaces, the bonding of chitons to the surface is partially adhesive, due to mucus, and partially mechanical as the foot conforms well to surface irregularities. Furthermore, the foot appears to be the sole organ of attachment.

SUMMARY

1. The lateral force required to dislodge the chitons *Mopalia lignosa*, *Mopalia muscosa*, *Nuttallina californica*, *Katharina tunicata*, and *Stenoplax heathiana* was directly related to the degree of exposure to wave action in the habitat of each species.

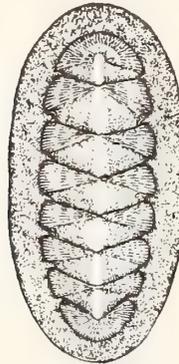
2. The rougher the surface to which a chiton was attached, the greater the force required to remove the specimens from the surface.
3. The foot plays the major role in attachment by secreting an adhesive mucus material and by mechanically conforming to surface irregularities with its tissue.
4. Suction does not appear to play a major role in the attachment of species tested.

ACKNOWLEDGMENTS

I wish to express my appreciation for the help and encouragement received from the faculty and staff of Hopkins Marine Station. Special thanks to Dr. Gilmartin, my advisor, for his time and many helpful suggestions throughout this study.

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The Relations Between Body Weight and Habitat Temperature and the Respiratory Rate of *Tonicella lineata* (Wood, 1815)

(Mollusca : Polyplacophora)

BY

ELIZABETH ANNE KINCANNON¹

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

(6 Text figures)

INTRODUCTION

INTERTIDAL MOLLUSKS are known to show compensatory changes in metabolic rate in response to different temperature regimes. For example, some species from high latitudes have the same rates of oxygen consumption as do related tropical species at warmer temperatures (see reviews by BULLOCK, 1955; and SEGAL, 1961). Furthermore, this compensation, or acclimation, has been shown between two spatially separated populations of the same species. Low level populations of the limpet *Collisella limatula* (Carpenter, 1864) show cold acclimation of heart rate while high intertidal *C. limatula* from a few meters away show warm acclimation (SEGAL, 1956). KENNY (1958) suggests that this should apply to the Polyplacophora as well; the chiton *Clavaronia hirtosa* (Blainville) from low intertidal zones shows a lower upper lethal temperature than those from comparatively higher, warmer zones. However, no definitive work on acclimation as a function of microgeographic separation has been done on the Polyplacophora.

This study was designed to answer the following questions:

1. Can chitons acclimate to altered temperatures within a few weeks?
2. If so, are subtidal animals acclimated to a lower temperature than intertidal ones of the same species?
3. Are intertidal animals, which are exposed to wide fluctuations in habitat temperature, better able to acclimate to experimental temperatures than subtidal animals, which experience a more limited temperature range?

The species *Tonicella lineata* (Wood, 1815) was selected for study because of its wide vertical distribution. In addition to being abundant subtidally (BARNES, 1972: 67), the species has been found by the author to occupy sites in the intertidal zone up to 0.9 m above mean lower low water. Exchange of individuals between deepwater and shallow populations is probably small or nonexistent (DEMOPULOS, 1975).

Acute respiratory rates (oxygen consumption rates of animals collected and held at constant temperature for one day before measurement) were compared with rates of acclimated animals (held 3 weeks at constant temperature prior to measurement), at a series of 5 temperatures. Rate of oxygen consumption was used as an indicator of metabolic rate. Since many factors other than temperature affect respiratory rate, notably body weight and activity level, an attempt was made to study and correct for these variables. There is evidence (BULLOCK & RAO, 1954) that temperature affects the relationship between body weight and respiratory rate. Consequently, weight-rate regressions were done at each temperature for each population, using the formula $M = k \cdot W^b$, where M = metabolic rate, k = a constant, W = weight of the organism, and b = the regression coefficient.

MATERIALS AND METHODS

All intertidal *Tonicella* were collected from Carmel Point, Carmel, California, between 0 and 0.6 m above mean lower low water. Subtidal *Tonicella* were collected at a depth of 6 m to 7.8 m off Mussel Point, Pacific Grove, California. In the laboratory, all were held under constant light in aquaria equipped with air stones. Constant temperature was maintained by means of running sea water and immer-

¹ Permanent address:

164348 Prudencia Drive, Whittier, CA 90603

sion heaters. Three holding tanks were maintained in this manner at 8°C, 13°C, and 18°C; temperature was checked daily and fluctuated $\pm 2^\circ\text{C}$ in the two warmer tanks, less in the 8°C tank. Large glass jars covered with plastic screens served both to keep the chitons submerged and to keep the populations separate.

Rates of oxygen consumption were expressed on the basis of wet weight which was measured by blotting the *Tonicella* with paper towels before weighing. Fourteen chitons were weighed after 29 hours in an 80°C oven. They were then combusted at 600°C for 48 hours. Those initially weighing over 2 g were combusted 6 days and reweighed. Percentages of dry to wet weight, and ash-free to dry weight, were subsequently calculated and plotted as a function of wet weight.

Rates of oxygen consumption were measured at experimental temperatures of 3°C, 8°C, 13°C, 18°C and 23°C using the direct Warburg method of constant volume manometry as described by UMBREIT *et al.* (1972). After collection, *Tonicella* were kept in the holding tank closest in temperature to that at which they would be tested. Before the experiment they were weighed, placed in the Warburg reaction vessel, and covered with a measured volume of sea water filtered through a 0.22 μm Millipore filter. Oxygen consumption by particles less than 0.22 μm was assumed to be negligible. Two-tenths of a ml of 10% KOH was added to a filter paper wick located in the side-arm. After one hour of equilibration in the water bath, manometer readings were taken at one-hour intervals for 6 to 12 hours, depending upon the time required for respiratory rates to stabilize. Hourly rates of oxygen uptake were calculated and averaged over the time interval showing the most consistent rates.

Notes on the animals' activity and degree of submersion were kept throughout each experiment. Only the rates of those chitons which appeared unhurt, remained submerged, and did not move more than a few cm were used in further calculations. Each chiton was used in only one experiment, after which it was liberated.

Acute respiratory rates were measured 22 to 26 hours after collection for 6 *Tonicella* at each temperature. Rates of acclimated animals were measured after 3 weeks using 2 specimens for each combination of acclimated and experimental temperatures. A regression analysis was performed on each set of acute rates measured, using a double logarithmic transformation (SOKAL & ROHLF, 1969). The method of least squares (*Ibid.*, Box 14.1) determined the regression coefficients, and Fisher's F-test (*Ibid.*, Box 8.1) tested the significance of the lines. In the comparison of regression lines with each other, the F-test was used to compare slopes (*Ibid.*, Box 14.8), while Student's t-test

(*Ibid.*, Box 9.6) compared the means after a determination that the variances were similar (Fisher's F-test as above).

The mean weight of all chitons collected was 0.70 g. Rates of oxygen consumption for this weight were obtained from the regression line at each temperature and plotted on a rate vs. temperature graph. Assuming that *b*, the slope of the regression line, remains constant with acclimation, rates of acclimated animals were standardized to this same weight and plotted with the same procedure as the acute rates. Since all rate-temperature curves were plotted semi-logarithmically, their slopes are directly proportional to Q_{10} as calculated by the formula:

$$Q_{10} = \left(\frac{R_1}{R_2} \right)^{10/t_1-t_2}$$

(PROSSER, 1973, p. 363).

RESULTS AND DISCUSSION

Wet Weight as a Measure of Metabolizing Tissue:

Figure 1 shows dry weight as a percentage of wet weight and ash-free dry weight as a percentage of dry weight for a nearly fifty-fold range of weights of *Tonicella*. Appar-

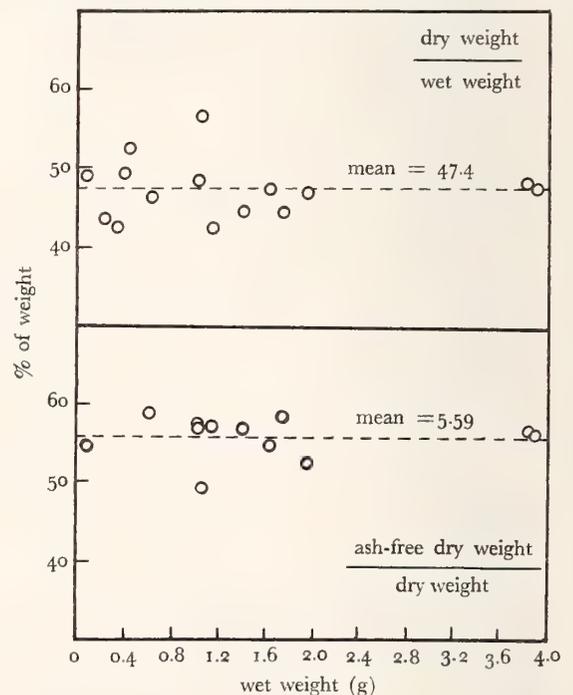


Figure 1

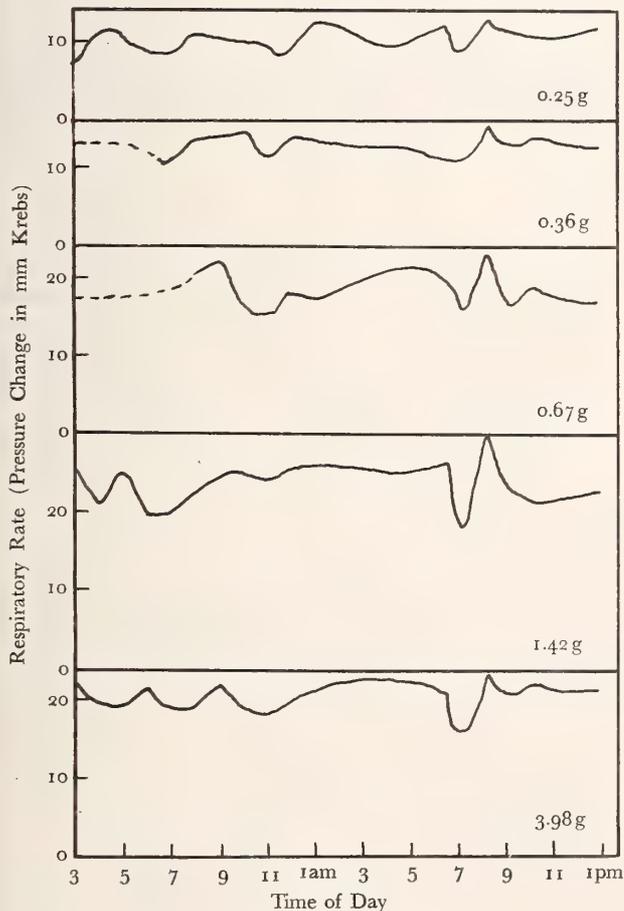
Relationship between wet, dry, and ash-free dry weights in selected *Tonicella lineata* of various sizes. Upper plot is dry weight as percentage of wet weight; lower plot is ash-free dry weight as percentage of dry weight

ently the proportion of water (upper graph) and ash-weight (lower graph) in *Tonicella* does not depend upon total wet weight.

Ash-free dry weight excludes the bulk of a chiton's non-metabolizing tissue—the shell plates. However, other non-metabolizing elements such as fats and connective tissue will combust and thus form part of the ash-free dry weight. These could conceivably be present in larger amounts in larger animals, leaving less metabolizing tissue in proportion, and thus contribute to an overall decrease in weight-specific metabolism in larger creatures. However, ash-free dry weight has commonly been used as a measure of the amount of metabolizing tissue in an organism. Since ash-free dry weight represents a fairly constant proportion of wet weight, I chose to compute weight-specific respiration in terms of wet weight.

Stability of Respiratory Rates:

To determine whether respiratory rates measured over a 6 to 12-hour period are representative of an entire 24-



hour period, 5 chitons were tested for 24 hours. Change in manometric pressure is plotted against time in Figure 2. Although many species show a diurnal or tidal respiratory rhythm, this is clearly not the case for *Tonicella*. (The irregularity near 0800 hours was reflected by the thermo-barometer and is not due to changes in respiration.)

Effect of Body Weight upon Respiratory Rate:

Rates of oxygen consumption as a function of body weight at 5 different temperatures in subtidal and intertidal populations are plotted in Figures 3 and 4 respectively. Slopes and 95% confidence limits for each regression line appear in Table 1. Correction for weight by means of

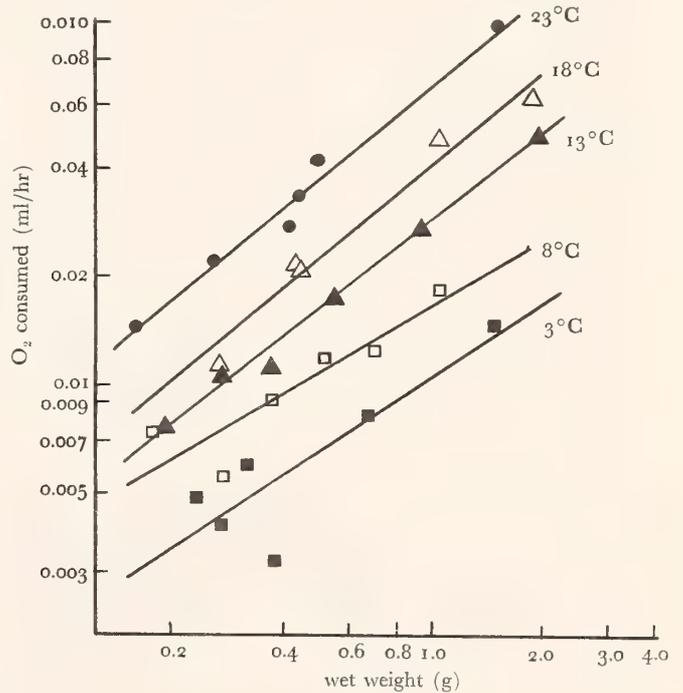


Figure 3

Oxygen consumption as a function of body weight for subtidal *Tonicella lineata*. Rates were measured at 5 temperatures 24 hours after collection. Each point represents one animal

(← adjacent column)

Figure 2

Respiratory rates of *Tonicella lineata* measured over a 24-hour period. Change in manometer reading as plotted is proportional to oxygen consumption. Weights are those of the chitons tested

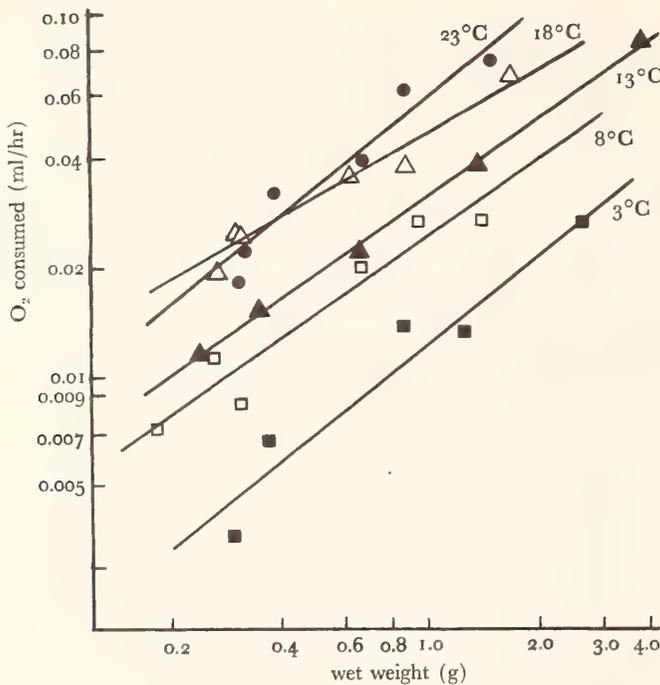


Figure 4

Oxygen consumption as a function of body weight for intertidal *Tonicella lineata*. Rates were measured at 5 temperatures 24 hours after collection. Each point represents one animal

regression analysis greatly reduced the variance in even these small samples of rates; this suggests that at any given temperature, weight is a more important determinant of respiratory rates in *Tonicella* than are other factors such as sexual and nutritional states.

Statistical comparison of the regression lines revealed no consistent pattern of change in the slopes (b-values) as a function of temperature. The slopes of subtidal animals (Table 1) suggest a pattern of decreasing b-values with decreasing temperature, but this is not a statistically significant trend and does not appear in the intertidal population. It may be concluded from this that b for this species does not change with temperature, large and small *Tonicella* are equally affected by temperature, and Q_{10} does not vary with size. These conclusions represent an exception to the general rule. For example, in intertidal invertebrates studied by EDWARDS & IRVING (1943), BULLOCK & RAO (1954) and NEWELL (1970), b decreased with temperature and Q_{10} decreased with body weight. The results presented here for *Tonicella* are therefore quite significant, and need to be confirmed with more data and clearer statistical conclusions.

These data also suggest that vertical location does not affect the relationship between body weight and respiratory rate; there are no consistent differences in b between subtidal and intertidal *Tonicella* tested at the same temperature. An average of all 10 slopes obtained yields a b-value of 0.73 for this species. This is similar to those of other mollusks as reported by PROSSER (1973: 193) and close to ZEUTHEN's (1970) generalized metazoan value of 0.74.

Effect of Temperature upon Acute Respiratory Rate:

Figure 5 shows acute rates of oxygen consumption for a hypothetical 0.70 g chiton plotted against temperature. These points are derived from the regression lines in Figures 3 and 4, and their significance is determined by the confidence limits of those lines. It is apparent that the curve for intertidal *Tonicella* does not lie below that for

Table 1

Statistics for the Weight Regression Lines Shown in Figures 3 and 4

Values are based on a double logarithmic transformation. Ninety-five per cent confidence limits for the y values (rates) are obtained by constructing parallel lines at a vertical distance of $2 \cdot s_{y \cdot x}$ above and below the regression line on log scale

Population	Intertidal					Subtidal				
	23°C	18°C	13°C	8°C	3°C	23°C	18°C	13°C	8°C	3°C
b	0.80	0.57	0.70	0.69	0.81	0.84	0.86	0.80	0.59	0.68
95% confidence limits ($2 \cdot s_{y \cdot x}$)	.151	.085	.032	.166	.188	.089	.124	.060	.180	.254

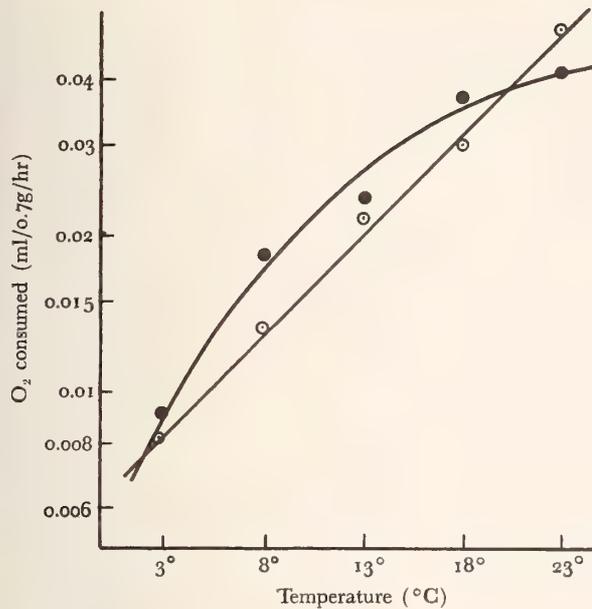


Figure 5

Rate versus temperature curves for intertidal (●) and subtidal (○) *Tonicella lineata*, measured acutely. Points represent the intersection of a perpendicular, erected at 0.70 g, with weight regression lines at each temperature

subtidal *Tonicella*. Subtidal chitons therefore do not appear to be cold-acclimated; these results suggest that they may even be warm-acclimated since their rates are generally lower than those of the intertidal population. Although this seems unlikely, the question cannot be resolved until it is known to what aspect of the thermal regime these animals are responding. According to temperature data from nearby Moss Landing, California (Harold, Christopher, personal communication, 1974), intertidal animals are frequently exposed at low tide to air temperatures both higher and lower than those of the ocean. If they are acclimating to the lowest temperature in their environment, they could indeed appear cold-acclimated in comparison with subtidal chitons.

VERNBURG & VERNBURG (1970: 132) have suggested that the temperate-zone crabs *Uca pugnax* (Rathbun, 1901) are better able to adapt to temperature extremes than are their tropical relatives *Uca rapax* (Rathbun, 1918) because they are exposed to more temperature fluctuations. This argument may apply to *Tonicella* in that subtidal chitons are exposed to a more narrow temperature range and would be expected to be less flexible in respiratory response than

intertidal ones. From Figure 5, subtidal *Tonicella* show a constant Q_{10} near 2.5, while intertidal ones appear to decrease their Q_{10} s in higher temperatures. SEGAL (1956) has found similar patterns in his work with heart rate in *Acmaea*, although BULLOCK & RAO (1954) stated that Q_{10} generally increases with temperature in mollusks such as *Mytilus californianus* (Conrad, 1837). Since a lower Q_{10} would be advantageous for an intertidal animal exposed at midday low tide to the sun, this preliminary result should be further tested by repetition of these experiments, including temperatures higher than 23°C.

Relation of Acclimatation to Temperature:

Rates for each population of acclimated *Tonicella* corrected to a standard body weight using acutely measured b-values are plotted in Figure 6. Very little can be said about the subtidal population (Figure 6-B) because of the intertwining curves. However, it appears that acclimation has occurred to some extent in the intertidal population (Figure 6-A). The rate-temperature curve for 13°C acclimated animals falls below that for 8°C acclimated animals at all points, although the distinction between 13°C and 18°C curves is less clear. This is probably due to greater temperature fluctuations in the two warmer tanks than in the 8°C holding tank. These results come after a relatively short period of acclimation, and experiments conducted for a longer time are necessary to determine whether or not subtidal *Tonicella* in fact can acclimate. Nonetheless, they support the argument of the preceding section that intertidal *Tonicella* are capable of compensating for changes in their environmental temperature and possibly can do so better than the subtidal *Tonicella*.

The curves in Figure 6-A do not show the same pattern of decreasing Q_{10} with increasing temperature as do the acutely measured rate-temperature curves. However, the absolute shape of these curves is not as accurate, since only one or two experimental animals determined each point and b-values were not measured for acclimated animals. The curves in Figure 6 are useful only in comparison with each other.

There remains the possibility that acclimation observed in the laboratory is due to factors other than temperature. Starvation is an obvious possibility; NEWELL (1970: 391) reports that this is common and results in a decrease in respiratory rate. However, at least one group of intertidal *Tonicella* (8°C acclimated, tested at 23°C) had higher rates than did the corresponding acutely measured group, and the *Tonicella* were observed to defecate fecal pellets throughout their 3 weeks in the holding tanks. Possibly more variation would have been introduced by trying to feed the *Tonicella* than by starving them.

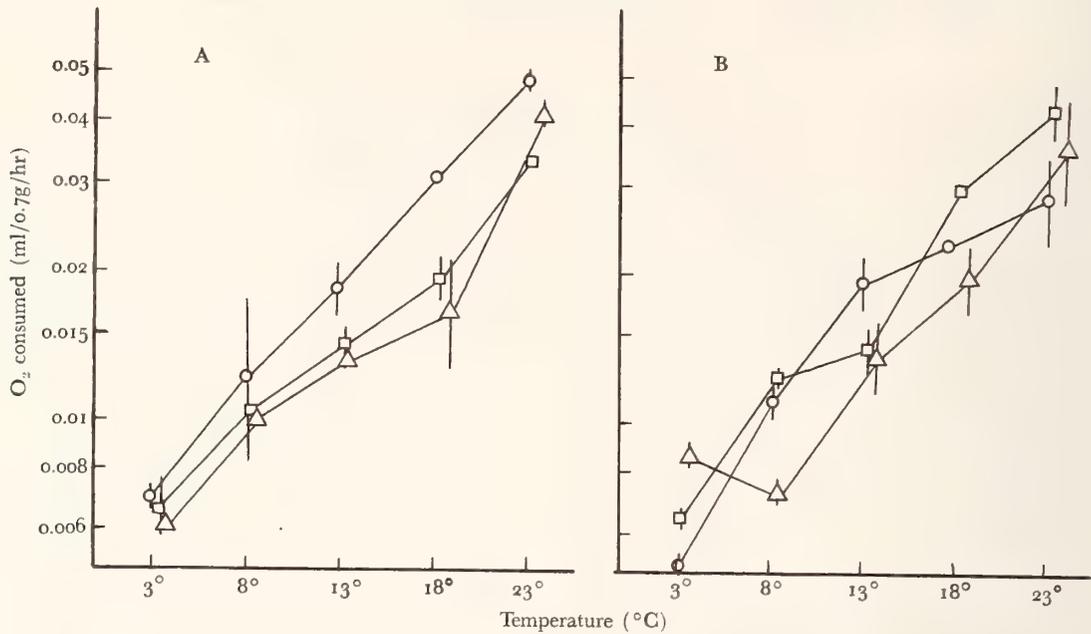


Figure 6

Rate versus temperature curves for intertidal (A) and subtidal (B) *Tonicella lineata* acclimated to various temperatures in the laboratory for 3 weeks (8°C - ○; 13°C - □; 18°C - △). Each point is the mean of two animals, corrected to a standard weight of 0.70 g as in Figure 5; vertical lines represent the range

Future Studies:

An interesting question remaining is whether or not Q_{10} changes with laboratory acclimation. For the purposes of this project no change was assumed, but this needs verification. Another topic is that of standard vs. active metabolism and its effect on Q_{10} ; the Q_{10} s found in this project are higher than those given by NEWELL (1970) for standard metabolism. Finally, once it has been determined that a population of *Tonicella* can acclimate, transplantation experiments would be helpful to test whether animals from one habitat can acquire the ability to acclimate over a short period of time.

SUMMARY

1. Two vertically separated populations of *Tonicella lineata* (Wood, 1815) were tested for acute and acclimated respiratory rates at a series of five temperatures.
2. *Tonicella* show no diurnal or tidal rhythm in respiratory rate.
3. Q_{10} seems unaffected by body weight in both populations.

4. Subtidal *Tonicella* are not acclimated in the field to a colder temperature than are intertidal *Tonicella*, but may be less able to compensate for temperature change.
5. Intertidal *Tonicella* show a pattern of acclimation after three weeks in the laboratory; results from subtidal animals are ambiguous.

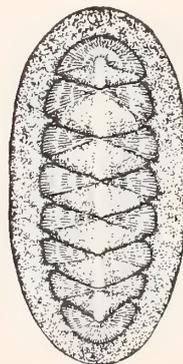
ACKNOWLEDGMENTS

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Effect of Temperature and Salinity on the Oxygen Consumption of the Chiton, *Mopalia lignosa*

BY

CYNTHIA SUE LEBSACK¹

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

(2 Text figures)

INTRODUCTION

THE CHITON *Mopalia lignosa* (Gould, 1848) is a common inhabitant of the intertidal zone on Californian shores. Although it usually retreats to sheltered regions during the day and at low tide, it must be able to cope with relatively wide variations in temperature and salinity, both on a seasonal basis and during a single tidal cycle. Temperature and salinity in the environment do not necessarily fluctuate together. In winters, for example, animals may experience relatively high salinities and low temperatures when submerged, and low salinities and low temperatures during rains at low tide.

Studies of the combined effects of temperature and salinity on metabolic rates have been carried out on such marine organisms as the crabs *Hemigrapsus oregonensis* (Dana, 1851) and *H. nudus* (Dana, 1851) by DEHNEL (1960), and the gill tissues of oysters and mussels by VAN WINKLE (1968). However, no studies of this sort have been made on chitons.

I here report the effects of simultaneously imposed temperature and salinity variations on the respiratory rate of *Mopalia lignosa*. All studies were carried out at the Hopkins Marine Station of Stanford University, Pacific Grove, California, during the period April-June, 1974. The chitons used in the experiments were collected at various points on the rocky shores of the Monterey Peninsula.

MATERIALS AND METHODS

Respiration rates were measured using Warburg-Barcroft manometers kept in a water bath held at a constant temperature. A wick of filter paper wetted with 0.2 ml of 10% KOH was placed in the side arm of the respiration chamber in order to absorb CO₂, and the vessels were agitated. The vessel constants were measured using a Gilmont-Warburg calibrator.

Salinities were obtained by dissolving "Instant Ocean Synthetic Sea Salt" (Aquarium Systems, Inc.), in appropriate amounts of distilled water and were checked with a salinometer. Normal sea water from the environment (100%) was determined to be 33.94%.

Animals taken from the field were held in running sea water at $13.5 \pm 0.5^\circ\text{C}$ for at least three days before use. I assumed the relation between respiratory rate (V_{O_2}) and body weight (W) followed the equation: $V_{O_2} = KW^{0.74}$ where K is a constant. The value of 0.74 is the generalized value for animals given by PROSSER (1973) and is close to the average value (0.73) found by KINCANNON (1975) for the chiton *Tonicella lineata* (Wood, 1815). Using the above equation, the measured respiratory rates were corrected to that of a hypothetical 10 gram chiton. The weight of the animals varied from 5.5-18.5 grams. Sample size varied from 3 to 6 animals at each temperature salinity combination.

Individual chitons were placed in separate Warburg vessels and covered with 70 ml of synthetic sea water at the salinity to be tested. They equilibrated for one hour

¹ Permanent address:

910 Nob Hill Road, Redwood City, CA 94061

at a given temperature. Readings were then taken hourly for six hours. The average number of μl of O_2 consumed/gram/hour was taken as the respiratory rate. Each of the three temperatures within the environmental range encountered by *Mopalia lignosa* (8°C , 13.5°C , and 19°C) was combined with four different salinities (90%, 100%, 110%, and 120% of normal sea water) to yield separate experimental conditions.

KINCANNON (1975) has shown that there is no conspicuous diurnal rhythm which affects chiton respiration, thus experimental runs were made at various times during a day.

RESULTS

Respiration rates vs. temperature for the 4 salinities are shown in Figure 1. Their Q_{10} values are listed in Table 1. Like most poikilotherms, chitons respire at an increased rate at higher temperatures: $36.2 \mu\text{l}/\text{gram}/\text{hour}$ at 100% sea water and 19°C versus $14.27 \mu\text{l}/\text{gram}/\text{hour}$ at 100% sea water and 8°C . The Q_{10} value calculated using the 13.5°C and 19°C values for animals in 100% sea water is 2.0. However, using the 8°C and 13.5°C values, a much higher Q_{10} of 2.7 is obtained for the same animals.

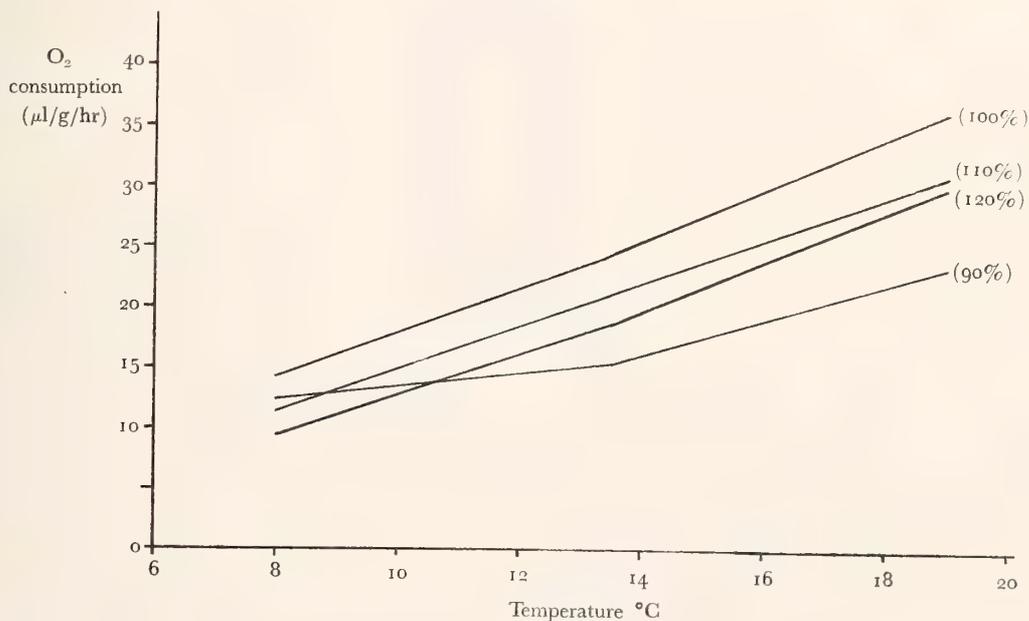


Figure 1

Mean oxygen consumption versus temperature at salinities of 90%, 100%, 110%, and 120% sea water

Table 1

Q_{10} Values for the Intervals $8^\circ - 13.5^\circ\text{C}$ and for $13.5^\circ - 19^\circ\text{C}$ for the four test salinities

% Seawater	Temperature Interval	
	$8^\circ\text{C}-13.5^\circ\text{C}$	$13.5^\circ\text{C}-19^\circ\text{C}$
90	1.5	2.1
100	2.7	2.0
110	3.0	2.0
120	3.4	2.3

Respiration as a function of salinity for each experimental temperature is plotted in Figure 2. For each temperature, animals in 100% sea water respired at a significantly higher rate than at any other salinity.

DISCUSSION

Most marine mollusks are osmoconformers with varying degrees of stenohalinity (PROSSER, 1973). KINNE (1971),

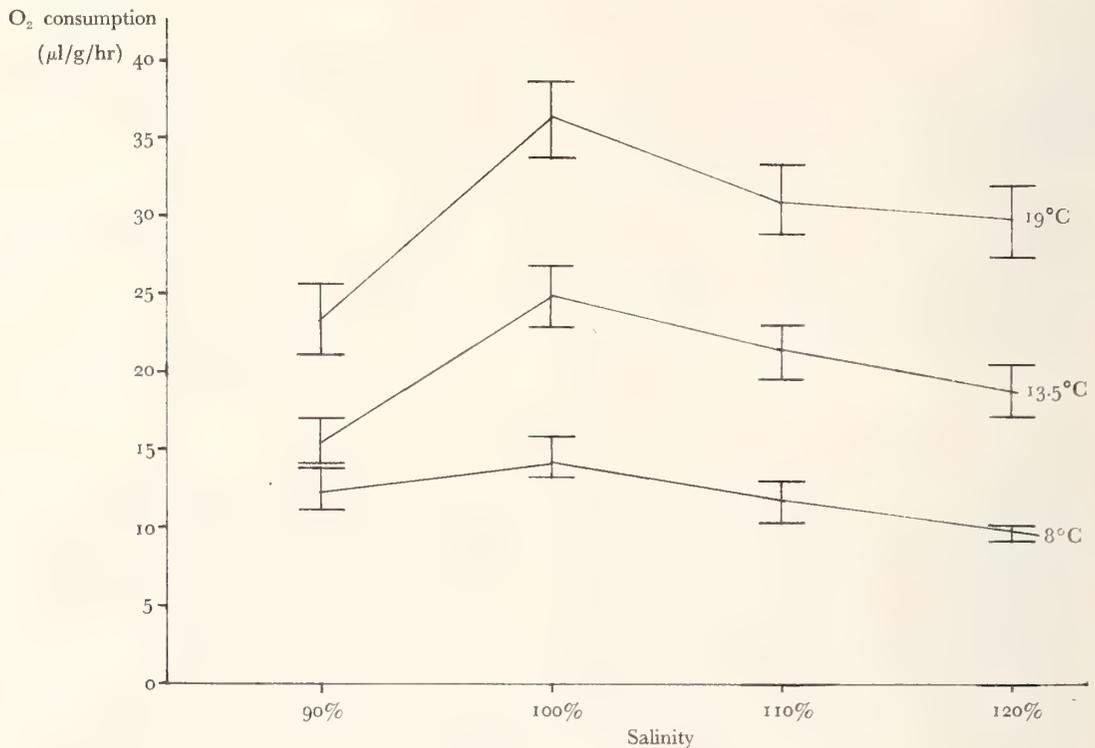


Figure 2

Mean oxygen consumption and standard errors versus salinity at 8°C, 13.5°C, and 19°C. Letters next to individual data points indicate significant differences, using Student's t-test, from 100% S. W. values obtained at the same temperature.

A = $p < 0.005$; B = $p < 0.025$; C = $p < 0.05$

states that although not much is known on how salinity affects invertebrate metabolism, there are some general trends in the responses of species. One of these trends is that animals which are stenohaline decrease respiration at both the higher and lower salinities. This reduction in respiratory rate may be mediated through any of the following routes: (1) increasing or decreasing the body water or salt content; (2) changing of internal ion rates; (3) hormonal, neuromuscular, and enzymatic interference (4) behavioral changes (KINNE, *op. cit.*). In addition there is probably a reduction in the concentration of cellular metabolites in animals placed in hypotonic solutions, and a reduction of oxygen tension in those exposed to hypertonic media, both of which could lower respiratory rate. The least change in respiration due to osmotic stress was found, in both hyper- and hypoosmotic solutions, at 8°C. Perhaps at this temperature the metabolism is nearly minimal for maintenance, and the chiton actively controls against further lowering.

In 100% sea water the Q_{10} between 8°C and 13.5°C is higher than that between 13.5°C and 19°C; this agrees with many observations on other animals that Q_{10} decreases with increasing temperature (PROSSER, 1973). The Q_{10} 's increase from the lowest salinity to the highest for the colder temperature interval but remain quite constant at the higher temperature interval (Table 1). Work should now be done to elucidate the physiological processes responsible for this low temperature change of Q_{10} with salinity.

SUMMARY

1. *Mopalia lignosa* respire at a higher rate as the temperature increases.
2. Deviation in salinity from normal sea water causes a decrease in respiration rate.

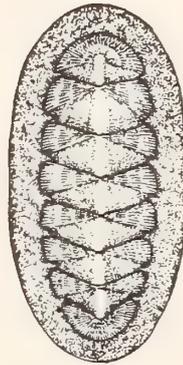
3. At low, but not higher, temperatures, the Q_{10} increases with salinity.

ACKNOWLEDGMENTS

I would like to extend a sincere thanks to Christopher Harrold for his instruction on use of the Warburg, to Dr. Robin Burnett for his patience and help with statistics, and to Charles Baxter for his advice, aid, and encouragement on this project. To the staff and students of Hopkins Marine Station, thank you for making this academic pursuit such an enjoyable one.

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Aerial and Aquatic Respiration in the Chitons

Nuttallina californica and *Tonicella lineata*

BY

BRUCE A. ROBBINS¹

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

(5 Text figures)

INTRODUCTION

MARINE MOLLUSKS which occupy middle and upper intertidal regions must be adapted to periodic exposure to air. While adaptations toward avoiding desiccation are usually apparent, the means by which these animals cope with respiratory problems during periods of emersion is not so immediately evident. Studies of intertidal mollusks have demonstrated an ability to breathe air in several species, and some investigations (SANDISON, 1966; MICALLEF & BANNISTER, 1967) have revealed capacities for aerial respiration even greater than those possible in the submerged state. Adaptations to air breathing typically involve 1) increased rigidity of the ctenidial lamellae (STEEN, 1971) and 2) increased vascularization of the mantle skirt (NEWELL, 1970).

Several species of Polyplacophora occur in the upper intertidal region and face the problems of exposure. However, the only study known to me on aerial respiration in chitons concerned the low intertidal species *Cryptochiton stelleri* (Middendorff, 1846) (PETERSEN & JOHANSEN, 1973).

The work described here involved *Nuttallina californica* (Reeve, 1847), which is found at +0.9 to 1.5 m tidal levels and is frequently exposed to air, and *Tonicella lineata* (Wood, 1815), which occupies subtidal to low intertidal zones and is very rarely uncovered. These species were compared with respect to respiratory anatomy, efficiency of aerial respiration, and recovery from exposure upon resubmersion, in an attempt to reveal possible adaptive advantages of *Nuttallina* over *Tonicella* under humid exposed conditions.

ANATOMICAL OBSERVATIONS

The general anatomy and function of the chiton respiratory system has been described in detail by YONGE (1939).

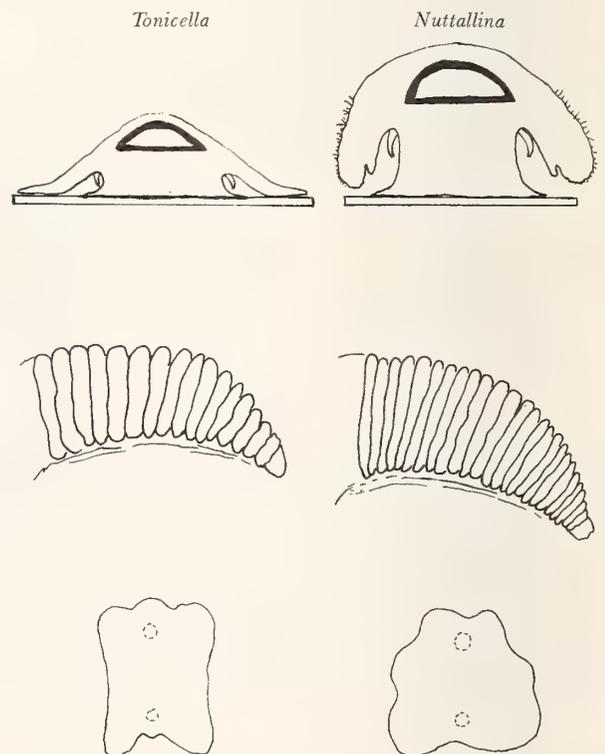


Figure 1

Top: Schematic cross-sections of *Tonicella* and *Nuttallina* showing ctenidia in the pallial groove. Center: Ctenidia lateral views.

Bottom: Typical cross-sections of the ctenidia

¹ Permanent address:

1123 Donaire Way, Pacific Palisades, CA 90272

Nuttallina and *Tonicella* were examined for variations of this basic pattern in terms of structure, number, and orientation of the ctenidia, as well as shape and variability of the pallial groove. Representative cross-sections of the two species are shown in Figure 1, along with the typical ctenidial structure of each.

The number of ctenidia per animal is known to be variable, but preliminary counts gave *Tonicella* 22-29 and *Nuttallina* 30-48 ctenidia along each side of the foot. The greater number of gills in *Nuttallina*, which reaches a larger adult size, agrees with the observations of JOHNSON (1969). The general morphology of the ctenidia appears very similar in the two species, although closer examination reveals that *Nuttallina* ctenidia are somewhat stouter and contain $\approx 50\%$ more lamellae. These filaments do not appear to possess greater self-support than do those of *Tonicella*.

Major differences between the two respiratory systems include the shape of the pallial cavity and the involvement of the girdle in its regulation. As seen in Figure 1, *Nuttallina* has a relatively deep pallial groove bounded by a highly thickened and bristly girdle. The orientation of the girdle is variable and under voluntary control; it may be partially or totally raised, promoting exposure of the gills (Figure 2a), or clamped against the foot, shielding the gills and undoubtedly decreasing their efficiency (Figure 2b).

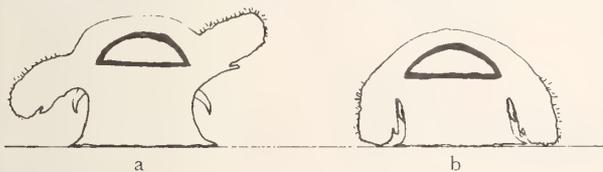


Figure 2

- a. Schematic cross-section of *Nuttallina* with girdle partially raised on the left side and totally raised on the right.
 b. Schematic cross-section of *Nuttallina* with girdle in the clamped-down position. Note ctenidia pressed against the foot

The latter behavior is generally avoided, except in response to a local disturbance or to critical levels of desiccation. Normally, as observed in the laboratory, the girdle is partially raised along one side of the foot. In contrast, *Tonicella* maintains a shallower pallial groove of constant shape, with the smooth thin girdle pressed flat against the substrate and lifted only locally as entrance and exit ports for water circulation. There is no active response to shield gills from desiccation.

Responses to exposure were studied as chitons clinging to horizontal glass plates were taken out of water. It was

found that *Nuttallina* could hold water in the pallial groove for several hours with its girdle down, but in its normally raised position the gills were freely exposed to air. *Tonicella* usually developed air pockets in its pallial groove, though it too could hold water beneath the gills under moist conditions. In both animals, when the gills were exposed to air they collapsed against the foot or the back of the pallial groove. In this state they were kept moist with a mucus-like secretion.

RESPIRATION STUDIES

Materials and Methods:

Chitons were collected weekly from the Mussel Point area surrounding Hopkins Marine Station, Pacific Grove, Calif. *Nuttallina* were obtained intertidally at the +0.9 m to +1.5 m tidal level on exposed rock faces, while *Tonicella* were found subtidally in rocky areas at -4.5 m to -7.5 m. Animals were scrubbed to remove any commensal algae, and a standard "wet weight" determined after blotting for 30 seconds on a paper towel. Chitons were then placed in "restraining chambers" (Figure 3) designed to minimize

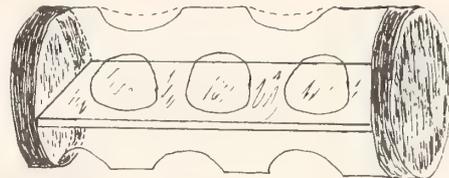


Figure 3

The "restraining chamber" in which animals were maintained during experimentation. Actual size: 1.5 cm diameter; 3 cm length

activity and facilitate future manipulation. Restraining chambers were constructed of 1.5 x 3 cm glass plates enclosed in perforated plastic tubing capped at both ends. *Nuttallina* and *Tonicella* weighing between 0.5 and 1.0 gram fit easily into these chambers, where they remained throughout the experiment. Chambers were placed in an aquarium supplied with circulating, well-aerated sea water at 13.5°C where the chitons were allowed to equilibrate in a horizontal position under constant light for 3-5 days.

Oxygen consumption was measured on individual animals under successive conditions of submersion, exposure

to humid air, and secondary submersion. Respiration rates were determined by the direct method of Warburg using standard manometric technique as described by UMBREIT *et al.* (1972). Restraining chambers were adapted to fit available Warburg vessels so as to maintain animals in the submerged condition and horizontal position. All phases of the experiment were conducted at 13.5°C with vessels agitated to maximize diffusion of oxygen.

Submerged rates of oxygen consumption were first determined with chambers immersed in glass fiber-filtered sea water, and readings taken half-hourly for a period of 4-6 hours. Chambers were then removed, drained for 1 minute on paper towels, and returned to vessels containing 0.3 ml sea water to maintain humidity. Aerial respiration rates were then recorded under these conditions for the next 12 hours. Finally, filtered sea water was replaced to its original level in the vessels and post-exposure respiration followed for 4-9 hours.

Each run consisted of a maximum of 3 *Nuttallina* and 3 *Tonicella*. Final data were compiled from 10 of each species, 7 of which were followed through resubmersion. Additionally, several of each species were run as controls which were handled exactly as were the experimental animals, but were maintained submerged throughout the experimental period. Data were expressed as oxygen consumption in $\mu\text{l O}_2/\text{g wet weight}/\text{hr}$ for each of the three experimental phases, and as ratios of aerial rate/ submerged rate and resubmerged rate/ submerged rate for each individual.

Results:

Both *Nuttallina* and *Tonicella* displayed remarkably constant oxygen consumption rates during the primary

submerged and aerial phases of the experiment, possibly reflecting the standardization of activity imposed by the restraining chambers. A greater variation of rate with time was observed during the resubmersion period.

Table 1 summarizes the average primary submerged rate, aerial/submerged rate ratios, and resubmerged/submerged rate ratios for experimental and control animals of each species. Results for experimental animals are depicted in Figure 4. Individuals of both species exhibited aerial respiration at a level significantly ($p < 0.001$; paired points t-test) below that of the initial submerged rate,

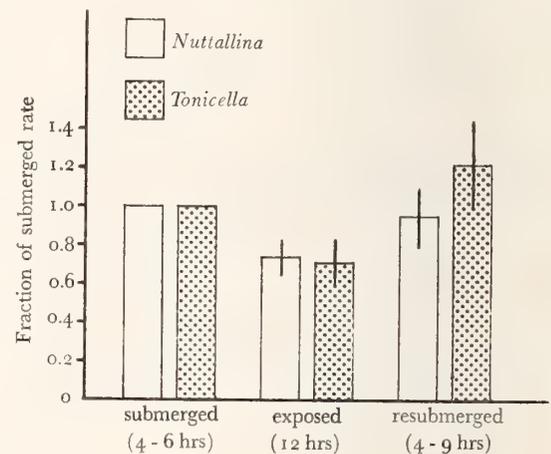


Figure 4

Mean relative respiratory rates of 10 *Nuttallina* and 10 *Tonicella* during successive periods of submersion, and 7 animals of each species after resubmersion. Lines through bars indicate standard deviation

Table 1

Weight-Specific Oxygen Consumption of *Nuttallina californica* and *Tonicella lineata*

under submerged conditions; average fractional changes in respiratory rate during 12 hours of aerial exposure, followed by resubmersion. Controls were maintained submerged during all phases of the experiment. Number in parentheses is the number of individual animals studied. Variation shown is ± 1 Standard Deviation

	<i>Nuttallina</i>		<i>Tonicella</i>	
	Experimental	Control	Experimental	Control
Wet weight (grams)	0.912 \pm 0.198 (10)	0.908 \pm 0.186 (4)	0.733 \pm 0.141 (10)	0.833 \pm 0.182 (3)
Submerged rate ($\mu\text{l/g wet wt}/\text{hr}$)	60.0 \pm 9.8 (10)	59.6 \pm 11.3 (4)	50.8 \pm 8.6 (10)	51.2 \pm 7.1 (3)
Aerial rate/ submerged rate	0.738 \pm 0.088 (10)	1.09 \pm 0.10 (4)	0.717 \pm 0.118 (10)	1.02 \pm 0.03 (3)
Resubmerged rate/ submerged rate	0.945 \pm 0.159 (7)	1.11 \pm 0.06 (4)	1.22 \pm 0.237 (7)	0.980 \pm 0.218 (3)

while controls showed a slight elevation of rate during this period. Furthermore, the average fractional decrease in rate upon exposure was very similar (≈ 0.73) for both *Nuttallina* and *Tonicella*. The pattern of post-exposure respiration, however, differed significantly ($p < 0.025$; Student's t-test) between the two. While *Nuttallina*'s resubmerged rate returned to 94.5% of its initial submerged rate and was depressed below the associated control, that of *Tonicella* rose 22% above its original wet rate and was elevated above its control.

DISCUSSION

Anatomical studies present little evidence for any adaptation to aerial respiration in *Nuttallina*. Excepting the observed differences in numbers of ctenidia and filaments, the basic orientation and structure of the gills in *Nuttallina* and *Tonicella* appear very similar. The expected adaptation towards increased rigidity is apparently absent in the ctenidia of *Nuttallina*; the gills collapse upon exposure as do those of *Tonicella*.

Manometric studies confirm that *Nuttallina* has no significant advantage in aerial respiration over *Tonicella*. Respiration rates were equally depressed in both species, reflecting the lessened efficiency of the gills in minimal retained water reservoirs and in the collapsed state. Studies of *Cryptochiton stelleri* showed a greater decline in rate upon exposure, with aerial rates averaging 3 to 5 times less than the submerged value (PETERSEN & JOHANSEN, 1973).

Preliminary experiments (unpublished) show that *Nuttallina* survives longer than *Tonicella* under humid exposed conditions. The nature of *Nuttallina*'s advantage is suggested by the observed post-exposure respiratory behavior. The elevated oxygen consumption of *Tonicella* upon resubmersion probably indicates that an oxygen debt was accrued during the period of decreased oxygen uptake accompanying exposure. *Nuttallina* has no such increase in respiratory rate and evidently avoids anaerobiosis during emersion periods. In this manner it is not forced to cope with the problems of acid-product accumulation and eventual re-oxidation of those products. Intertidal *Cryptochiton stelleri* show a pattern of post-exposure respiration similar to that of *Nuttallina*; more significantly, no accumulation of lactate in the body fluid has been observed during exposed conditions (PETERSEN & JOHANSEN, 1973). Similar chemical analysis for lactate or succinate in body fluid of exposed *Nuttallina* and *Tonicella* would help confirm the presence or absence of oxygen debt.

This evidence suggests an internal regulatory control rather than a structural alteration through which *Nuttal-*

lina has adapted to exposure. NEWELL (1970) has reviewed in detail the recognized physiological responses of intertidal animals to a decreased availability of oxygen. Possible mechanisms of avoiding oxygen debt include: 1) excretion of anaerobic products; 2) maintenance of stores of oxygen within respiratory pigments in the body; 3) reduction of activity and general body metabolism during restrictive periods. The latter possibility is supported by observations that *Nuttallina* becomes extremely sluggish and remains sessile when emersed. Similar behavior was noted in *Cryptochiton stelleri* (PETERSEN & JOHANSEN, 1973).

Finally, the possibility must be considered that measurements in the laboratory may not accurately reflect behavior during exposure in the field. Animals were always maintained on flat glass surfaces during manometric and observational studies of responses to emersion. However, field studies show *Nuttallina* to be found wedged in cracks or depressions in the substratum, with the girdle molded to the contour of the local environment. A similar preference was noted in the laboratory, where *Nuttallina* grouped into corners of aquaria rather than remaining on flat surfaces. This preferential "wedging" is possibly an adaptive response which allows for a raised girdle and maximum gill exposure while simultaneously protecting the gills and maintaining a large water reservoir in the pallial groove during aerial exposure (Figure 5). In this manner, the collapse of the ctenidia would be avoided and efficiency of respiration maximized in the emersed state.

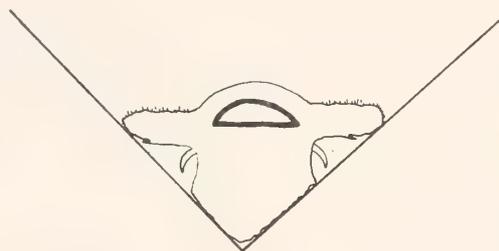


Figure 5

Schematic cross-section of *Nuttallina* "wedged" in the corner of an aquarium. Note the raised girdle, the exposed gills, and the large water-holding capacity of the pallial groove

SUMMARY

The respiratory anatomy and function of intertidal *Nuttallina californica* and subtidal *Tonicella lineata* were compared in an attempt to elucidate adaptations of the

former to frequent aerial exposure. Ctenidial structure was found to be very similar, without additional self-support in *Nuttallina*. Most significant is the thicker more actively flexible girdle in *Nuttallina* which permits control of gill exposure and possibly maintains a reservoir of water beneath the gills in the naturally exposed state. Manometric studies have shown aerial respiration rates to be equally depressed to 73% of the submerged rate in both species. Though *Nuttallina* has not apparently adapted for increased efficiency of air breathing, studies of recovery from extended periods of exposure have indicated a probable oxygen debt present in *Tonicella* and absent in *Nut-*

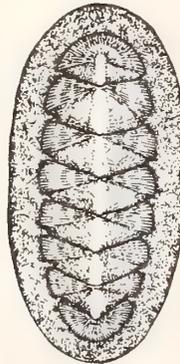
tallina. Field and laboratory observations suggest that *Nuttallina* decreases its metabolic activity when uncovered. However, further work is necessary to confirm these conclusions and to elucidate the physiological basis of *Nuttallina*'s resistance to oxygen debt during periods of exposure.

ACKNOWLEDGMENTS

I would like to thank Dr. Fred Fuhrman for his helpful assistance and advice, and Dr. Donald P. Abbott for making this whole venture possible.

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The Effects of Air Exposure and External Salinity Change on the Blood Ionic Composition of *Nuttallina californica*

BY

STEPHEN C. PIPER¹

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

(1 Text figure)

INTRODUCTION

THE BLOOD OF MARINE MOLLUSKS, with the exception of the cephalopods, is similar to but not identical with sea water in inorganic composition. The analyses of various workers are well summarized by ROBERTSON (1964). In general, the concentrations of sodium and magnesium are the same in the blood and in sea water while potassium and calcium are more concentrated in the blood. Except for blood ion values for *Katharina tunicata* (Wood, 1815) in conditions of fluctuating salinity (STICKLE & AHOKAS, 1975), data are nonexistent for blood ionic composition for the whole classes Amphineura and Scaphopoda.

Polyplacophoran mollusks are common members of the intertidal fauna of the Pacific Coast of North America. *Nuttallina californica* (Reeve, 1847) is a small chiton, seldom more than 5 cm long, that is fairly restricted to the middle intertidal zone of exposed shores from Puget Sound to the Coronado Islands. *Nuttallina californica* is usually found in moderately exposed rocky crevice habitats. It is subject to large fluctuations of sea water salinity caused by such factors as rain run-off, evaporation, and summer fog, and is exposed to air about 10 to 20 hours a day (RICKETTS & CALVIN, 1968). This study is an examination of the concentrations of 4 inorganic cations in the hemolymph of *Nuttallina californica* over a range of experimental salinities and in conditions of exposure to air.

MATERIALS AND METHODS

Specimens of *Nuttallina californica* were collected from the eastern end of the Great Tidepool at Point Pinos, Monterey County, California during the month of May, 1974.

To minimize possible intraspecific adaptive differences, the animals were collected from a small area, all at approximately the same vertical level, +1.05 m to +1.5 m above mean low-low tide. The animals varied from 2.5 to 8 grams in weight. After being brought into the laboratory, they were placed in plastic tubs in sea water of similar salinity, 33.97‰, to that sampled at the collection area and designated 100% sea water. Each tub contained 4 liters of sea water and not more than 17 animals; 2 tubs of the 8 were used for each experimental condition. The animals were kept in the 100% sea water without food for at least 44 hours but not more than 68 hours prior to the experiment. The experiments were carried out in plastic tanks containing 4 liters of experimental solution and continuously aerated with porous stone diffusers. The animals were kept submerged throughout the experiments with a rigid wire screen. The tanks were covered with aluminum foil lids to reduce evaporation and consequent salinity change and were set in a water bath maintained at 13° to 14.5°C; air temperature varied from 14.5° to 15.5°C inside the covered tubs during the experiment.

Salinities used in this study were 50%, 100% and 150% of sea water. To prepare 150% sea water, Instant Ocean, supplied by Aquarium Systems, Inc., Eastlake, Ohio, was added in sufficient quantity to bring 100% sea water to 150%. At time 0, the 100% sea water was poured from each tub, leaving the chitons attached, and 4 liters of either 50%, 100%, or 150% sea water were added. In addition, other tubs were drained leaving the chitons exposed to air throughout the experiment.

Measurements of ion levels were made on samples of blood withdrawn from the area of the heart and pericardial cavity. The heart, contained within the pericardium, lies directly beneath shell valves 7 and 8, and the fluid was withdrawn directly by puncturing the dorsal body wall between these two valves and inserting a piece of capillary tubing. No significant difference was found between sam-

¹ Permanent address:
205 Calle Higuera, Camarillo, CA 93010

ples taken as indicated and from positions more anterior. Usually three and occasionally two animals were used at a sample time. At the same times, samples of the sea water solutions were taken. Sampling was for intervals up to 55 hours.

All samples were analyzed shortly after collection using a Perkin-Elmer 303 Atomic Absorption Spectrophotometer. The analytic procedure was based on suggestions given in the Perkin-Elmer 303 Analytic Methods Manual. For K^+ analysis, aliquots of 50 or 100 μ l of untreated blood were diluted to 5.05 or 10.10 ml respectively with a solution of 1000 ppm Na^+ to reduce effects of ionization. For Ca^{2+} , Mg^{2+} , and Na^+ analysis, aliquots of 100 μ l were diluted to a volume of 50.10 ml with a solution of 1000 ppm K^+ to reduce ionization effects. The potassium standards were prepared by adding Na^+ solution, HNO_3 and distilled water to 1000 ppm stock solution supplied by Harleco, Philadelphia, Pa., resulting in standards with 1000 ppm Na^+ , 1% HNO_3 ; Ca^{2+} , Mg^{2+} , and sodium standards were made by adding K^+ solution, HNO_3 and distilled water to 1000 ppm standard stock solution, resulting in standards with 1000 ppm K^+ and 1% HNO_3 .

After 24 hours, the 50% and 150% solutions of one set of animals were replaced with 100% sea water. At the same time, 100% sea water was added to one set of animals that had been exposed to air.

Although animals were weighed at the time blood was taken, no significant correlation between animal size and ionic composition was observed. A total of 91 *Nuttallina californica* were examined during the experiment. Blood was taken from each animal at only one time.

RESULTS

For chitons maintained in 100% sea water, the blood concentrations of Na^+ and Mg^{2+} were not significantly different from the concentrations of these ions in sea water. Much of the variability in the data is thought to have been contributed by "machine drift," during spectrophotometer operation, which was not completely corrected for by adjusting all the experimental blood ion values to values which correspond to sea water ion values corrected to their mean. The high blood Na^+ and Mg^{2+} values for 100% sea water at hour 27.5 probably result from uncorrected drift. Blood K^+ and Ca^{2+} concentrations were significantly higher than the concentrations of these ions in sea water (see Table 1). The results of tests for significant differences between blood and 100% sea water ion levels, based upon the "Student's t-test," are presented in Table 1; changes in ionic composition of the blood of experimental animals

(on facing page →)

Figure 1

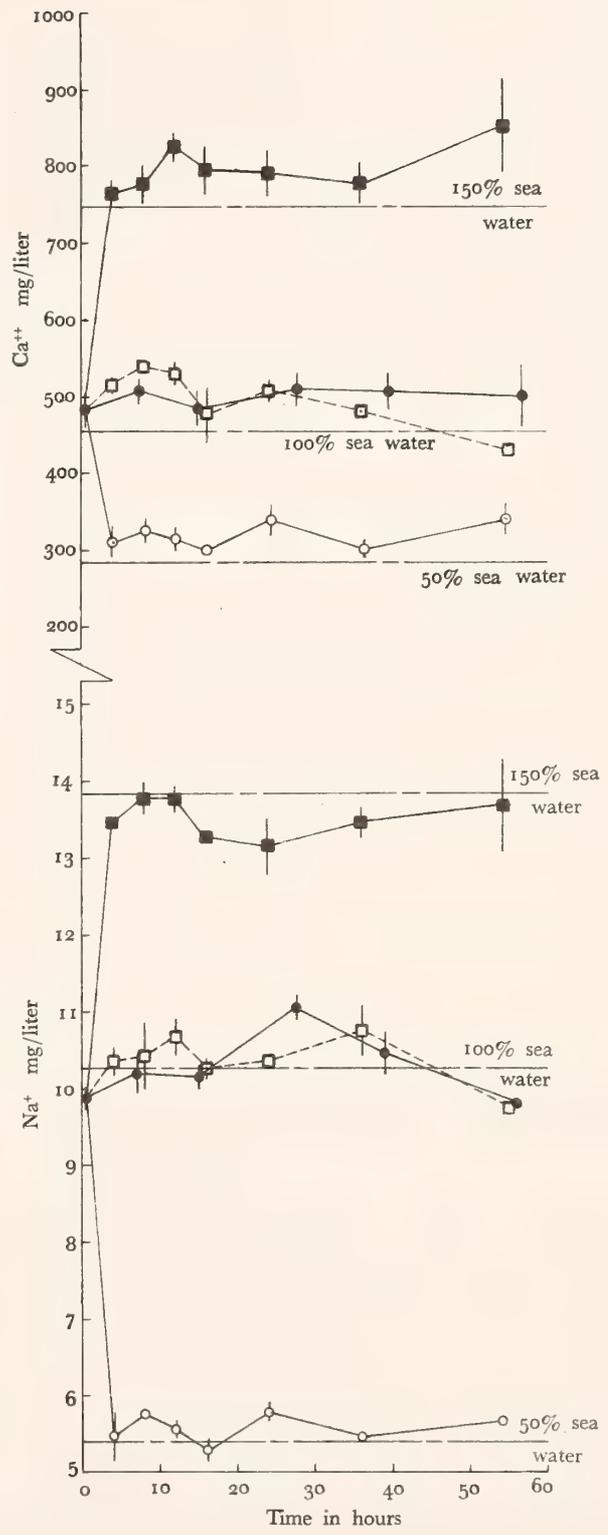
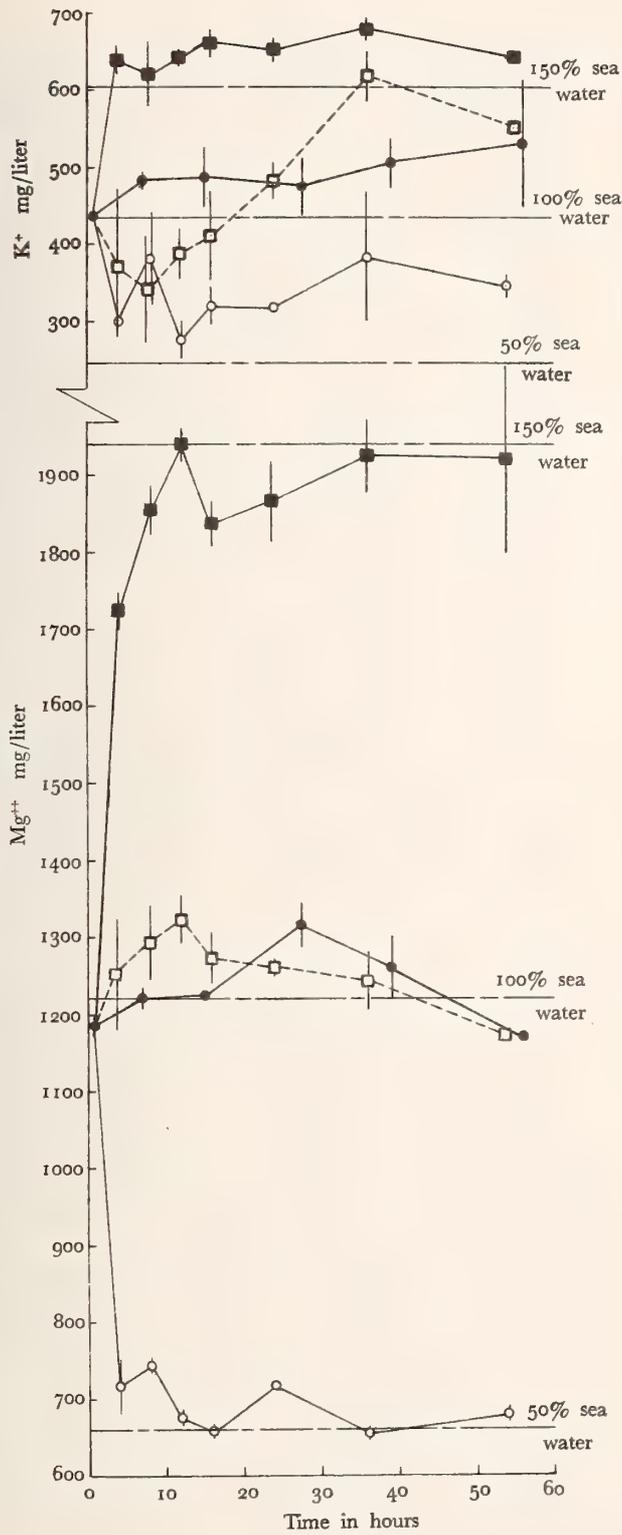
Changes in ionic composition of the blood of experimental animals during observation

- — Blood ionic levels in animals in 100% sea water
 - — Blood ionic levels in animals in 50% sea water
 - — Blood ionic levels in animals in 150% sea water
 - - - - Blood ionic levels in animals in exposed conditions
- Vertical lines represent standard deviations

Table 1

Concentration of Ions in Blood of *Nuttallina californica* Compared to Ion Concentrations in 100% Sea Water in which the animals were maintained. The "Student's t-test" was used to determine significance levels. All ion values are given as mg/liter

	Na^+	Mg^{2+}	K^+	Ca^{2+}
Blood concentration	10243.8	1225.4	482.0	499.6
Sea water concentration	10234.4	1220.6	434.4	456.4
Number of blood samples	16	16	13	16
Number of water samples	6	6	6	6
Blood sample standard deviation	±6438.0	±45.7	±31.9	±46.4
Water sample standard deviation	±754.8	±62.0	±41.4	±40.9
Significance level	N.S.	N.S.	99.9%	90.0%



during the period of observation are shown in Figure 1.

When the chitons were placed in 50% and 150% sea water, the concentrations of blood Na^+ and Mg^{2+} after a period of time were not different from the concentrations of these ions in the experimental solutions. K^+ and Ca^{2+} were higher in the blood than in sea water at all salinities to at least the 95% level of "t-test" significance, except the blood Ca^{2+} of animals in 100% sea water which was higher with only 90% significance.

The blood and sea water ion levels in 50% and 150% sea water were measured outside the range of ion standards and are not accurate absolute values (e.g., note in Figure 1 that the measured Ca^{2+} mean for 100% sea water is not twice the measured Ca^{2+} mean for 50% sea water). Valid comparisons of relative ion concentrations can be made only at one salinity for a single ion; however, comparisons of the time required for new equilibrium values to be reached are possible, among salinities and among ions. Due to the variability in the data, highly accurate equilibration periods or even half-equilibration periods can not be determined. Rough estimates of the equilibration periods were made by graphically determining the time required for the blood ions to attain their estimated new equilibrium levels. These estimates are presented in Table 2. The equilibration periods for all the cations measured were slightly longer in the 150% sea water than in 50% sea water. In both 50% and 150% sea water, Mg^{2+} had the longest equilibration period; K^+ had the shortest while Ca^{2+} and Na^+ had equilibration periods of intermediate length.

Table 2

Estimated Equilibration Periods of Ions in 50% and 150% sea water. Equilibration periods were estimated by determining the time required for the blood ions to attain their estimated new equilibration levels

	Equilibration Time in hours			
	K^+	Na^+	Ca^{2+}	Mg^{2+}
50% sea water	3-5	3-5	3-7	8-12
150% sea water	4-8	6-10	6-10	10-14

The chitons exposed to air showed no significant differences from the animals in 100% sea water with respect to their Na^+ and Ca^{2+} levels. Blood Mg^{2+} , however, was

higher in exposed animals than in animals immersed for the first 16 hours (Student's t-test; $p < 0.05$). Blood K^+ , on the other hand, was lower in exposed animals than in those in 100% sea water to hour 16 ($p < 0.05$) and then gradually became significantly higher.

The animals immersed in 100% sea water remained in good condition until hour 39. After this time they were only slightly attached to the bottom of the tubs, although they still responded when their feet were touched. Animals exposed to air remained in good condition during exposure and upon return to 100% sea water. Some of the animals in 150% sea water showed no adverse effects from immersion in water of this salinity. Others showed poor attachment, but upon return to 100% sea water, these animals all responded when their feet were touched. The animals maintained in 50% sea water were in good condition until the thirty-sixth hour and did not revive upon return to 100% sea water; however, they showed a foot response throughout the experiment.

DISCUSSION

In this study mean values of ion concentrations in *Nuttallina californica* in 100% sea water exhibited the typical molluscan pattern in that sodium and magnesium concentrations were almost the same in the blood and sea water, while calcium and potassium were maintained at higher levels in the blood than in the ambient sea water.

In addition, in 50% and 150% sea water, the blood ions eventually assumed the same relationship with the sea water ions as was observed in 100% sea water; K^+ and Ca^{2+} were maintained higher than ambient sea water ion levels at all salinities, while Na^+ and Mg^{2+} eventually conformed at all salinities. A Donnan equilibrium situation can not be invoked in explanation of these results since all the diffusible blood cations would be expected to show raised levels. Selective protein binding of K^+ and Ca^{2+} could explain their elevated levels at all salinities but PROSSER (1973) has concluded that "in all marine animals the differences remaining after dialyses are so small compared with the ionic differences between normal blood and sea water that protein binding must be considered insignificant as a regulating mechanism." Therefore it appears that *Nuttallina californica* actively maintains its blood K^+ and Ca^{2+} levels above environmental concentrations at all experimental salinities.

As indicated by the estimated equilibration periods, the relative rates of change of all blood ion levels were slightly smaller in animals in 150% sea water than in 50% sea water. It is possible that this difference is due to cell damage in the dilute salinity; WINTERSTEIN (1916) has shown

that cell injury leads to increased cell permeability to salts and water. It is also possible that the difference between the ion changes in 50% and 150% sea water is related to the difference in calcium concentration in these two experimental solutions. ALEXANDER *et al.* (1939) suggested that calcium binding to cephalin molecules makes a tight molecular structure and thus reduces tissue permeability, and MARTIN (1953) pointed out that calcium binding regulates the degree of coiling of chondroitin-sulfuric acid, thus altering the pore size of a structure. Therefore, the greater concentration of calcium in 150% sea water may have reduced tissue permeability to both water and ions. Another possible explanation for the apparent faster rates of ion level change in 50% sea water may be differences in the ability of *Nuttallina californica* to clamp down in the two salinities; STICKLE & AHOKAS (1975) have found faster hemolymph osmolality fluctuations in unattached than attached specimens of *Katharina tunicata*. *Nuttallina californica* was observed to swell considerably in 50% sea water, which may have decreased its ability to tightly clamp its girdle to the substrate and decrease its exposure to water of low salinity.

The estimated equilibration periods suggest that the relative rates of change of the blood ions under consideration are: $K^+ > Ca^{2+} \approx Na^+ > Mg^{2+}$. In contrast, STICKLE & AHOKAS (1975) found the rate series $Mg^{2+} > K^+ > Na^+ > Ca^{2+}$ for *Katharina tunicata* and $Na^+ > Mg^{2+} > K^+ > Ca^{2+}$ for *Thais lamellosa* (Gmelin, 1791), while TUCKER (1970) found $Ca^{2+} > K^+ > Na^+ > Mg^{2+}$ for *Scutus breviculus* (Blainville, 1817). The ion flux rate series expected if the concentration changes were due to integument permeability alone is: $K^+ > Na^+ > Ca^{2+} > Mg^{2+}$ due to the increasing diameter of the hydrated ions. The similarity of this latter series with that observed for *Nuttallina californica* suggests that integument permeability may be the major factor determining relative rates of change, although the rate series is based on only 3 points in twelve hours.

The animals maintained in humid drained tubs for 55 hours probably did not lose significant amounts of body water during this interval. The concentrations of Na^+ and Ca^{2+} ions were never significantly different from the levels of those in control animals in 100% sea water. The changes in blood K^+ and Mg^{2+} levels of animals in exposed conditions are interesting. K^+ initially became lower than the same ion of control animals in 100% sea water, returned to the control level by the 24th hour, and continued to rise until it became significantly higher than the K^+ level of immersed animals. Mg^{2+} , on the other hand, initially became significantly more concentrated in the blood of exposed animals, returned to the control level by the 20th hour, and then dropped slightly below the Mg^{2+} level of

the control animals. Later it returned to the level in immersed animals. It has been demonstrated that moderate increases in potassium ions (50% to 100% and more) have a stimulatory action on the neuromuscular system (e.g., WELLS, 1928; ROSS & PANTIN, 1940). BETHE (1927) found that an increase in potassium in the external medium augmented rhythmical movements in medusae, phoronid worms and various crustaceans. ROBERTSON (1953) suggests that the higher muscular activity of members of the Cephalopoda compared with the Lamellibranchia or Gastropoda may be related to the high K^+ concentrations maintained in the blood by members of this class.

In addition, ROBERTSON (1953) points out that solutions of magnesium chloride can be used to narcotize marine animals and has shown that activity and blood magnesium level are inversely related in a series of crustaceans; he suggests that an increase in blood magnesium and decreased activity are causally related. A study of the isolated walking legs of *Carcinus* indicates that perfusion with a fluid containing 1.5 to 2 times the blood concentration of magnesium depresses neuromuscular transmission (KATZ, 1936) and perfusing with a fluid containing only 5% to 20% of the blood Mg^{2+} concentration enhances the submaximal muscular response (BOARDMAN & COLLIER, 1946). Findings that the mechanical response to nerve stimulation varies inversely with the magnesium concentration in the perfusing fluid have also been reported in three other decapods, *Maia*, *Panulirus*, and *Cambarus* (WATERMAN, 1941).

The foregoing findings suggest the possibility that the initial rise in blood magnesium levels and decrease in blood potassium levels observed when specimens of *Nuttallina californica* were subjected to exposed conditions may have particular significance to the biology of these animals. NISHI (1975) has observed low activity in *N. californica* to be correlated with low tides, or times of exposure, and high activity to be correlated with high tides and immersion. The decrease in blood K^+ and increase in Mg^{2+} levels observed when animals were exposed may act to depress neuromuscular activity and reduce muscle tone in *N. californica* during low tides, its periods of relative inactivity. B. ROBBINS (1975) has found the metabolic rate of *N. californica* in exposed conditions, as measured by oxygen consumption, to be approximately 70% of the rate observed when animals were submerged in sea water. Upon return to water, the exposed animals did not show the temporary increase in rate that would suggest the repayment of an oxygen debt. Therefore, his results suggest that glycolysis is depressed during periods of exposure. The changes in K^+ and Mg^{2+} levels may be correlated with these suggested modifications in metabolism. The rise in

blood K^+ level and decrease in blood Mg^{2+} level at about the 20th hour (maximum length of exposure per day) may indicate a physiological anticipation of a high tide and a period of high activity by the animals.

Ion changes in *Nuttallina californica* when exposed to the air, a condition with which it is regularly confronted, is a topic which merits further study.

SUMMARY

1. The concentrations of sodium, potassium, calcium and magnesium in the blood of *Nuttallina californica* have been measured and they show the typical molluscan trend.
2. Over a range of experimental salinities from 50% to 150% sea water, blood values of Na^+ and Mg^{2+} were the same as the respective sea water ion values, while blood potassium and calcium levels were higher than the levels of the same ions in the experimental solutions. Potassium and calcium may be actively regulated whereas Na^+ and Mg^{2+} are in passive equilibrium.
3. The rate of flux was apparently greater in 50% than in 150% sea water for all ions; the rate series appears to be: $K^+ > Na^+ \approx Ca^{2+} > Mg^{2+}$.
4. In animals in exposed conditions, sodium and calcium levels were held fairly constant. Potassium was initially lowered, magnesium raised; these changes may be correlated with an observed lowering of metabolism on exposure to air.

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Responses to Osmotic Stress in the Chiton *Cyanoplax hartwegii*

(Mollusca : Polyplacophora)

BY

VIRGINIA L. MCGILL¹

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

(1 Text figure)

INTRODUCTION

INHABITANTS OF THE middle and high intertidal zones frequently face extreme fluctuations in the salinity of their environmental water due to factors such as evaporation, rain and fresh-water run-off. Salinities have been measured to range, for short periods of time, from 14‰ to 45‰ in pools and crevices (BOYLE, 1969). Preliminary experiments indicated the small intertidal chiton *Cyanoplax hartwegii* (Carpenter, 1855) is quite capable of surviving such changes; the possibilities of osmoregulation and volume regulation in *Cyanoplax* were therefore investigated.

METHODS

Cyanoplax hartwegii were collected at Point Pinos, Monterey County, California in April and May, 1974. Specimens were taken at the +1.2 m tidal level from granite rock underneath the brown macroalga *Pelvetia fastigiata* (J. G. Agardh) DeToni. Animals at this tidal height are at times uncovered by the tide for 18 hours or longer (DOTY, 1946).

Animals were allowed to equilibrate in aquaria with running sea water for 7 to 10 days before being used. The different concentrations, equal to 75%, 90%, 95%, 105%, 110% and 125% of normal sea water (SW) were made by dilution of sea water with distilled water for hypotonic media and by addition to sea water of synthetic sea salts (trade name: Instant Ocean, Aquarium Systems, Inc.) for hypertonic media. The salinity of ambient sea water was determined to be 33.9‰ using a Hytech Portable Laboratory Salinometer (Bissett-Berman Corp.).

To keep chitons immersed and to facilitate weighing, animals were placed in individual "cages" made of plastic petri dishes with holes for circulation of water. The petri dishes were then placed in finger bowls containing approximately 200 ml of the experimental salinities. Glass covers were used to minimize evaporation. The finger bowls were maintained at $13.5^{\circ}\text{C} \pm 1.0^{\circ}\text{C}$ for 24 hours.

At set times the pre-weighed petri dishes and the attached chitons' dorsal surfaces were blotted dry; each chiton and its dish were then weighed on a Mettler H15 analytical balance. In 16 replicate weighings of two animals, the largest deviation was 0.6% of initial body weight; thus the weighing procedure was deemed reliable. Animals were left attached to avoid introducing additional stresses due to forced removal.

After 24 hours of exposure to the experimental salinity, samples of body fluid for freezing point depression determinations were obtained by syringe, inserting the needle between shell valves VII and VIII into the body cavity (BOYLE, 1969). Microscopic examination revealed blood cells and verified that the solution obtained was hemolymph without gut or gonad contamination. Fluid samples of 1 μl to 10 μl were drawn into capillary tubes which were then plugged with paraffin. Similar samples were taken from the finger bowl baths. Differences in concentration between body fluid and the corresponding baths were determined by WELSH, SMITH & KAMMER's (1968) modification of Gross's comparative melting point method.

RESULTS

The mean percent difference between concentrations of body fluid and the respective baths was calculated for the 75%, 90%, 110% and 125% SW. The mean of these four sample means was 0.1% with a Standard Error (S.E.) of

¹ Permanent address:

27342 Via Burgos, Mission Viejo, CA 92675

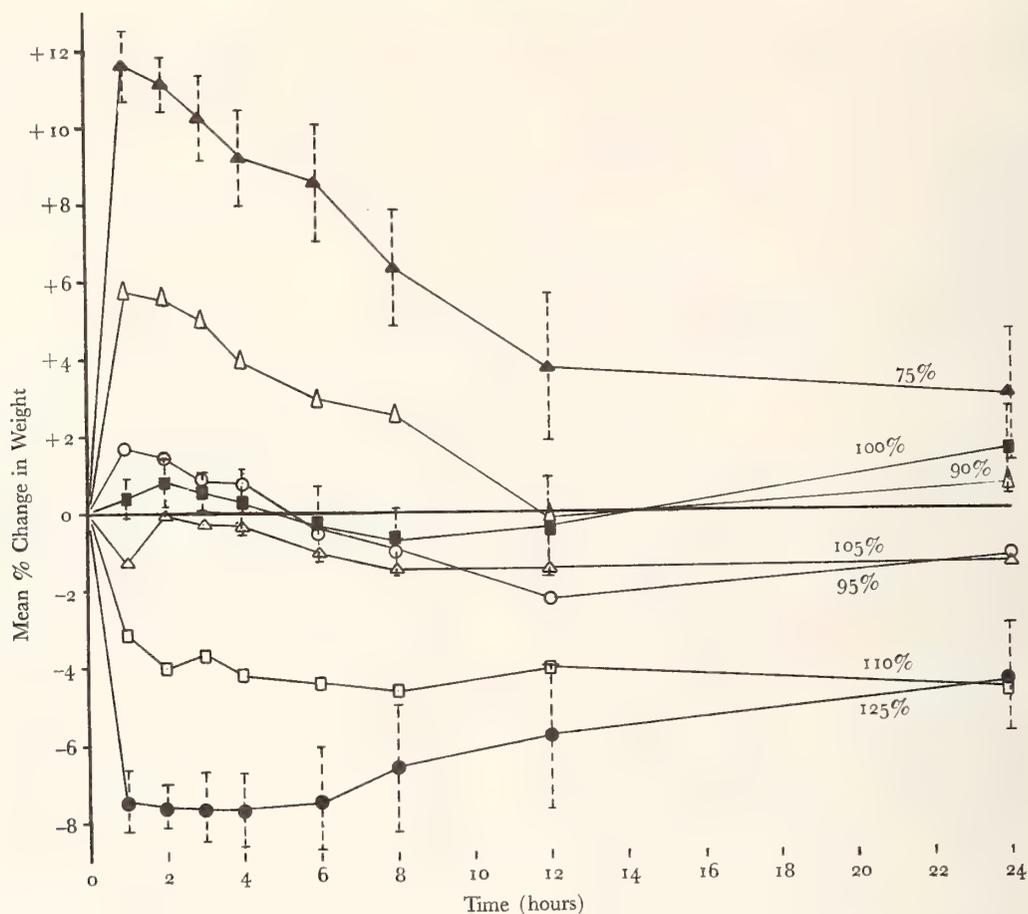


Figure 1

Mean weight change (as % change from initial weight) in *Cyanoplax hartwegii* exposed to seven salinities (as % of normal sea water). Vertical dashed lines represent \pm standard error (S. E.) $N = 7$ (90% S. W., 105% S. W.); $N = 8$ (95% S. W., 100% S. W.); $N = 11$ (110% S. W., 125% S. W.); $N = 12$ (75% S. W.)

1.2%. *Cyanoplax hartwegii* was therefore in osmotic equilibrium with its environment since its internal concentration was within 1 to 2% of the external concentration for each salinity tested (ROBERTSON, 1964).

The mean weight changes during 24 hours of exposure to different salinities, expressed as percent change from initial weight, are summarized in Figure 1. Standard errors of the means are shown for 75%, 100% and 125% sea water. Those for the other salinities are similar and are omitted for figure clarity. Sample sizes are given in the figure legend. *Cyanoplax hartwegii* responded to salinity changes by rapid changes in weight, reaching its maximum measured change within one hour in hypotonic sea water and a few

hours in hypertonic sea water. The maximum weight change was +11.6%, after one hour exposure to 75% SW. Hypotonic solutions resulted in larger and more rapid weight changes in the first hours and also resulted in faster returns from the maximum towards the original weight than did hypertonic solutions. After 1 and 2 hours, the absolute value of the mean percent change was significantly greater in 75% SW than in 125% SW (Student's t -test; $p < 0.02$ for one hour and $p < 0.001$ for two hours). The data clearly show that *Cyanoplax hartwegii* volume regulates when placed under osmotic stress.

Desiccation at $66^{\circ}\text{C} \pm 1^{\circ}\text{C}$ to constant weight showed water to constitute 51.6% ($N = 9$; S.E. = 1.5%) of the total

wet weight of *Cyanoplax*. Similar values have been reported for another chiton (BOYLE, 1970). This figure was used to calculate the maximum percent change in weight that would occur if *Cyanoplax* behaved as a simple osmometer. Table 1 shows that *Cyanoplax* approaches, but does not equal, a perfect osmometer, the deviation from the expected change increasing with increasing osmotic stress.

Table 1

Comparison of Expected versus Actual Maximum Percent change in body weight during 24 hours in six experimental salinities

% of Normal Sea Water	Expected Max. % Change	Actual Max. % Change	± S.E.
75	+17.2	+11.60	0.86
90	+ 5.7	+ 5.72	1.02
95	+ 2.7	+ 1.70	0.40
105	- 2.5	- 1.52	0.99
110	- 4.7	- 4.67	0.81
125	-10.3	- 7.65	0.96

Throughout the experiment, all chitons remained attached to their petri dishes. None swelled enough to prevent contact of the girdle with the dish. *Cyanoplax hartwegii* does not appear to attempt exclusion of the environment during osmotic stress; all animals moved at some time and there was no evidence of a prolonged tight attachment to the dish. None of the chitons died during the experiment; they were sacrificed at the end of the experiment.

DISCUSSION

Cyanoplax hartwegii is an osmoconformer over the range 75% sea water to 125% sea water. This is equal to a salinity range of 25.5‰ to 42.4‰. Osmotic conformance has been shown for other species of Polyplacophora (BOYLE, 1969; HYMAN, 1967; SIMONSEN, 1975) and also for other marine mollusks (PROSSER, 1973; ROBERTSON, 1964).

When exposed to osmotic stress, *Cyanoplax* quickly undergoes volume changes due to influx or efflux of water down the osmotic gradient. Volume regulation by the chiton decreases the original change in body weight and

volume, returning them to near normal. This ability varies among mollusks: some such as *Acmaea* spp. show no volume regulation (PROSSER, 1973), while others, like the opisthobranch *Aplysia fasciata* (Poiret, 1789), may regulate their weight past its original value (ROBERTSON, 1964).

The actual weight change of *Cyanoplax* in some salinities is less than expected for simple osmometers; a similar result is seen in many gastropods and bivalves (ROBERTSON, 1964). The amount of bound (osmotically inactive) water is generally insufficient to explain entirely this deviation (PROSSER, 1973). Thus it seems likely that volume regulation in *Cyanoplax* is effective even during the first hour of exposure to osmotic stress.

Volume regulation limits swelling of the chiton's foot, allowing maintenance of attachment. *Cyanoplax hartwegii* appears to adhere weakly to its substrate compared to *Nuttalina californica* (Reeve, 1847), another high intertidal chiton subject to similar osmotic stresses. Yet *Nuttalina*'s volume regulatory ability is considerably poorer than that of *Cyanoplax* (Simonsen, 1975). It may be that the weak grip of *Cyanoplax* provided strong selective pressure for development of its ability to volume regulate. Rapid regulation back to normal size is necessary for the chiton to remain attached to the rock. Thus, failure to tightly grip the substrate during osmotic stress may be an adaptive behavioral response in *Cyanoplax* since maximizing exposure to the environment hastens the ultimate achievement of normal size. Long periods of exposure at low tide may make this rapid fluctuation in weight a better survival strategy than an attempt to slow osmoconformance by adhering tightly to the substrate. The absence of mortality during the 24-hour experiment demonstrates survival of osmotic stress by *Cyanoplax* for a period of time longer than that normally encountered intertidally. This ability to tolerate salinity changes and to rapidly volume-regulate seems to be an important adaptation of *Cyanoplax hartwegii* to its habitat.

SUMMARY

1. The intertidal chiton *Cyanoplax hartwegii* was found to be an osmoconformer over the range 75% to 125% of normal sea water concentration (25.5‰ to 42.4‰ salinity).
2. The initial rapid weight change was subsequently reduced by volume regulation. After 24 hours, *Cyanoplax hartwegii* had returned to within a few percent of initial weight.

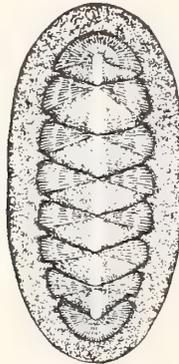
3. Survival was 100% after 24 hours of exposure at 13.5°C to above salinity range.
4. No behavioral modifications were noted in response to changes in salinity. Animals remained attached, but moved about and did not grip the substrate tightly.
5. The ability to withstand fluctuations in the salinity of its environmental water and its rapid regulation of volume are considered to be important factors in the adaptation of *Cyanoplax hartwegii* to conditions in the upper mid-tide zone.

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I would like to express my thanks to Charles H. Baxter, my advisor, and to Dr. Robin D. Burnett. Their advice and encouragement made this project feasible and very rewarding. I am also very grateful to Carol Stratford for her frequent assistance in collecting chitons.

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Response to Osmotic Stress in Vertically Separated Populations of an Intertidal Chiton, *Nuttallina californica*

(Mollusca : Polyplacophora)

BY

MARILOU SIMONSEN¹

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

(1 Text figure)

INTRODUCTION

Nuttallina californica (Reeve, 1847), a common intertidal chiton, has a large vertical range and is found in a variety of habitats. Though the species is eurytopic, individuals appear to maintain their particular position in the intertidal area for extended periods (MACGINITIE & MACGINITIE, 1968). Salinity variations from 14% to 45% have been measured in pools and crevices in the intertidal area (BOYLE, 1969); the range and duration of osmotic stress would be a function of position in the intertidal area. Chitons are typically isosmotic with seawater, as are most marine mollusks, but intertidal species subjected to salinity fluctuations may have developed adaptive responses to osmotic change (PROSSER, 1973). Previous osmotic studies on the chiton, *Sypharochiton pelliserpentis* (Quoy and Gaimard, 1835), in New Zealand (BOYLE, 1969 and 1970) showed this species to be an osmoconformer.

The topic explored in this paper is the response to osmotic stress in individuals of *Nuttallina californica* selected from 2 micro-habitats differing in vertical height and wave exposure in a way which has resulted in difference in osmotic stress histories.

MATERIALS

The study was carried out on individuals taken from Mussel Point at Hopkins Marine Station, Pacific Grove, California. One group of animals, taken from the lower intertidal zone, was from a vertical face of granite normal to the incoming surf. These organisms thus were not ex-

posed to sitting water or extensive evaporation. They were found along with the coralline algae *Corallina vancouveriensis* (Yendo), *Lithophyllum proboscideum* (Foslie) and the barnacle, *Balanus glandula* (Darwin, 1854). The other set of animals, taken from the high intertidal zone, was from an area protected from direct surf action by offshore rocks. The chitons were collected on horizontal ledges, making them exposed to salinity fluctuations from evaporation or precipitation. In the lower part of this range were *Endocladia muricata* (Postels & Ruprecht) J. G. Agardh, *Gigartina papillata* (C. A. Agardh) J. G. Agardh, *Tetraclita squamosa* (Darwin, 1854) and *Pollicipes polymerus* (Sowerby, 1833).

The chitons in the low intertidal zone were collected at a tidal range of 0.63 m to 1.11 m which is almost completely below the plus 1.05 m critical level (DORY, 1957) where they are subjected to air exposure less than 10.25 hours a day. Directly above this level there is an almost twofold increase in exposure time and then it gradually increases until at 1.5 m the maximum exposure is twenty-three hours. The high intertidal *Nuttallina* were collected between 1.2 m and 1.56 m and lie in the latter range.

Middle sized chitons were chosen, the mean size of the experimental animals from the low intertidal population was 1.86 g and 2.10 g for the high intertidal population.

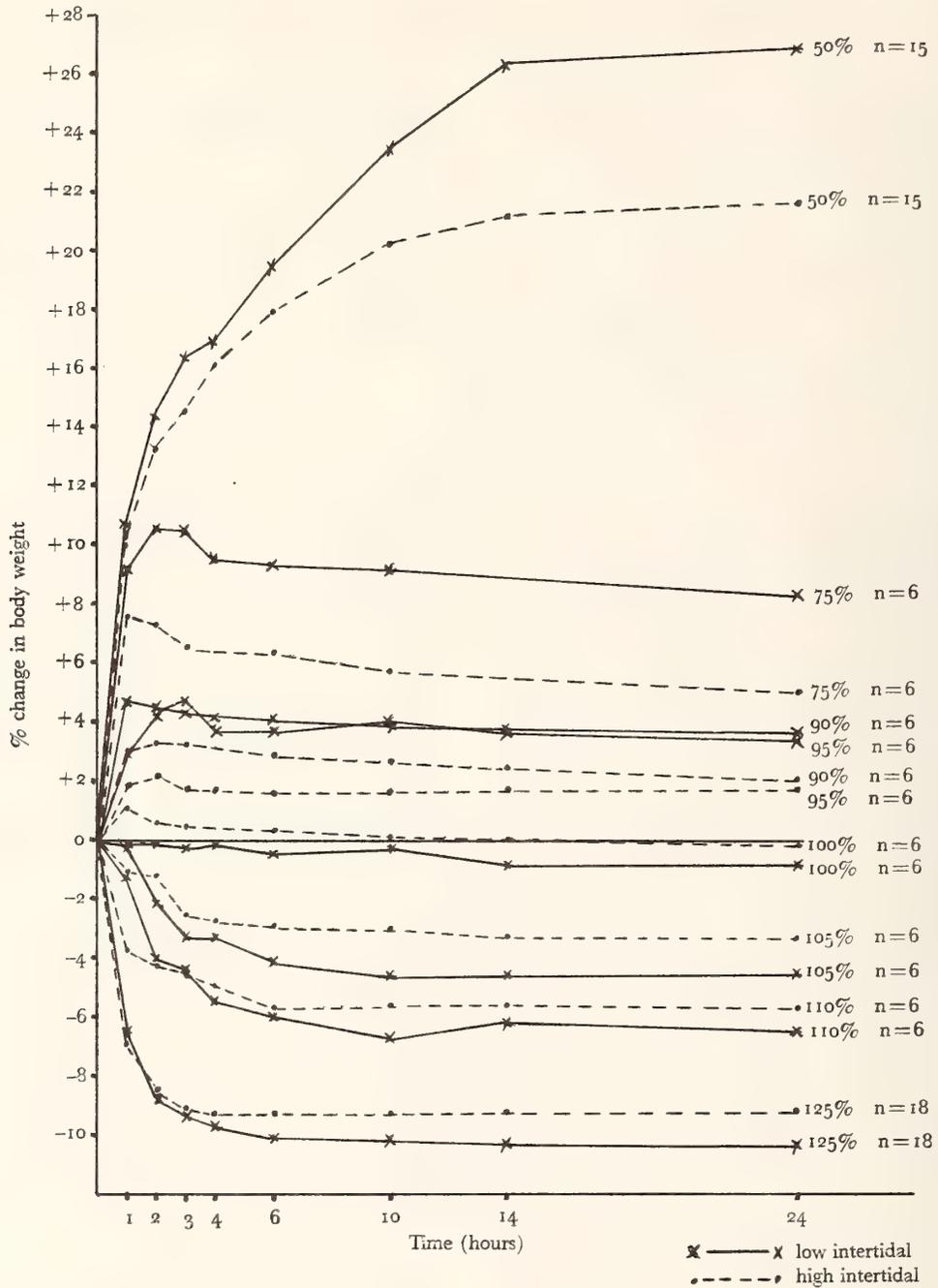
METHODS AND RESULTS

A. Change in Weight Following Osmotic Stress

In order to test for possible differential response to osmotic stress in the 2 populations, a series of laboratory experiments involving measuring weight changes of stressed animals was conducted. A method of weighing the chiton with

¹ Permanent address:

105 Edgewater Drive, Rio Vista, CA 94571



its substrate was devised to avoid the stress of constantly detaching the chiton. Plastic petri dishes with holes drilled in the top to allow free exchange of water were used as containers and were blotted dry and weighed with the chitons. Experimental animals were collected and placed in the dishes, kept in running sea water, for 48 hours to allow them to acclimate and partially empty their guts.

The salinity of the ambient and circulating seawater was determined by a salinometer to be 33.9%. Using this information the experimental salinities of 50%, 75%, 90%, 95%, 100%, 105%, 110%, 120%, and 125% of the concentration of local seawater were mixed from "Instant Ocean Synthetic Sea Salts" (Aquarium Systems, Inc.).

For each solution 6 or more chitons from each site were blotted and weighed with their containers before being placed in 250 ml finger bowls of test solution. The bowls, covered to reduce evaporation, remained in the sea table at a constant temperature of $14^{\circ} \pm 1^{\circ}\text{C}$. At intervals of 1, 2, 3, 4, 6, 10, 14, and 24 hours the chitons were removed, blotted dry and weighed.

In order to distinguish between a behavioral and a physiological difference in the two groups' response to osmotic stress, 8 chitons from each site were put in small mesh bags and placed on their backs in finger bowls to prohibit their excluding the external medium. Salinities of water in the bowls, exposure and weighing was as before.

Results: Low intertidal chitons gained more weight due to osmotic uptake of water, and at a slightly faster rate than the high intertidal chitons in dilutions of sea water (Figure 1). Weight changes are presented as percent change of original body weight.

In the 95%, 90% and 75% seawater a small decrease toward the original weight occurred with time in both groups. No decrease was seen in the 50% medium where the high intertidal *Nuttallina* gained an average of 19.4% of their body weight, significantly less than the mean gain of 28.4% for the low intertidal chitons ($P < 0.001$, $n = 30$, Student's t-test).

(← on facing page)

Figure 1

Mean weight changes (as % of original body weight) of *Nuttallina californica* in experimental solutions of various salinities. Test salinities in percent of ambient seawater and number of animals tested are indicated. The standard errors of the means were all less than 3% of the percent change indicated and thus too small to be indicated graphically.

Low intertidal chitons initially lost weight at a slower rate than the high intertidal ones in hypertonic seawater, but this was reversed after 1 to 2 hours so that they ultimately evidenced a greater percentage change in weight. For the 120% medium, after 24 hours, the low intertidal animals lost an average of 8.9% and the high intertidal chitons lost 6.6% ($P < 0.001$, $n = 36$).

The high intertidal *Nuttallina* that were placed in the mesh bags in 50% seawater gained 19.3% while the low intertidal chitons gained 26.4%. No significant difference between weight gain in attached versus unattached animals was found (Student's t-test).

B. Freezing Point Depression

The internal body fluid and the external medium of the chitons were examined for differences in osmotic concentration using a modification of the method by Gross (WELSH, SMITH, & KAMMER, 1968). *Nuttallina* from both the high and the low intertidal groups were placed in various salinities as previously described. At 12 and 24 hours one animal was removed from each salinity, weighed and bled by inserting a hypodermic needle between the seventh and eighth plates and extracting with a syringe a small sample of pericardial fluid (BOYLE, 1969). These samples were placed in capillary tubes, sealed and frozen along with samples of the solutions.

Results: The results of the freezing point depression experiments show *Nuttallina* to be an osmoconformer. The mean of the osmotic pressures of the internal fluid was within 1.8% of that of the external fluid, which is within the limits of the definition by WILBUR & YONGE (1964) of osmotic equilibrium (± 1 to 2%). Equilibrium had been reached before the 12th hour as there was no appreciable difference between the 12 and the 24 hour samples.

C. Theoretical Osmometer

To discover how closely *Nuttallina* follows the predictions for a gravimetric osmometer, 8 chitons, 4 from each group, were weighed and dried to constant weight in a 75°C drying oven. The percent body water was calculated as was the theoretical weight change that would be predicted to occur in each salinity if the chiton was a perfect osmometer with no bound water.

Results: Water constitutes 61% (Range = 58%-66%) of the body weight of the low intertidal *Nuttallina* and 56% (Range = 53-60%) of the high intertidal animals. The predicted weight gain in 50% seawater is 61% for the low intertidal chitons, yet they gained an average of only 28.4%, significantly less than predicted (chi-squared =

17.35, $P < 0.01$). The predicted change for the high intertidal chiton is 56%, yet the actual average weight gain was 19.4%, again significantly less ($\chi^2 = 23.83$, $P < 0.005$).

DISCUSSION

High intertidal *Nuttallina californica*, although osmoconformers, have developed means to cope with the higher osmotic stresses associated with their environment. Behavioral changes, such as partial exclusion of water in osmotic imbalance by clamping down, do not completely account for their osmotic response; their equilibrium point for hypotonic solutions remains the same whether or not they are attached. It may, however, affect the rate at which equilibrium is reached, a quantity not measured for unattached animals.

In hypotonic solutions the chitons from the high intertidal area gained less than the low intertidal chitons. Both groups, however, showed a decrease in body weight after reaching an extreme, except in 50% seawater; thus volume regulation does occur. The difference between the 2 groups must be due either to the efficiency of volume regulation or to differences in the threshold of stress required to initiate regulation. By having a lower threshold volume regulation of the high intertidal chitons would start sooner, thereby reducing the weight gained. Since the chiton is not an osmoregulator it never returns to its original weight while still in the hypotonic solution.

The theoretical weight changes deviate from the observed changes for the 50% and 75% solutions. This can partly be explained by assuming that 10-15% of the body water is bound by protein and osmotically inactive (PROSSER, 1973), but some type of mechanism working on a switch basis, such as ionic excretion or the making of monosaccharides from stored polysaccharides, must also be present to account for the difference between the two populations.

Since in hypertonic solutions there is no appreciable return of body weight toward the original weight it is unclear if any volume regulation occurs especially since the actual weight changes come close to the theoretical weight changes.

The greater ability for high intertidal *Nuttallina californica* to withstand osmotic stress could have a genetic basis as in selective larval settling or differential survival.

This ability seems more likely, though, to be ontogenetic by development of differences in tissues or metabolism as a result of exposure to the stress. Further work needs to be done before this can be answered.

SUMMARY

1. High intertidal *Nuttallina californica* can cope with osmotic stress better than the low intertidal chitons as shown by their smaller weight change.
2. The low intertidal chitons have a slower initial rate of weight loss in hypertonic seawater.
3. Attached and unattached animals reach the same equilibrium point, so behavior alone can't explain the differences in osmotic response.
4. There is a large deviation from predicted weight changes in 50% and 75% seawater which shows that both populations do exhibit some regulation, but with a difference in effectiveness.

ACKNOWLEDGMENTS

I am indebted to the faculty and staff of Hopkins Marine Station, especially to Mr. Chuck Baxter and Dr. Robin Burnett for their advice and encouragement during the course of this experiment.

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Blood Glucose Concentration and Regulation in *Cryptochiton stelleri*

(Mollusca : Polyplacophora)

BY

PHILIP F. MICHAEL¹

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

(3 Text figures)

INTRODUCTION

SEVERAL INVESTIGATORS have found indications of regulation of the blood glucose levels of mollusks (MARTIN, 1966; GODDARD, 1969). Although the concentration of glucose in the blood of *Cryptochiton stelleri* (Middendorff, 1846) has been measured (MYERS, 1920; TUCKER & GIESE, 1962), the ability of this species to regulate has not been examined. Its large size permits serial sampling of blood, and in view of this, studies were undertaken on *Cryptochiton stelleri* in the Spring of 1974 at Hopkins Marine Station, first to determine the normal glucose concentration in the blood, and then to seek evidence for any regulatory mechanism. The results clearly indicate a regulating response opposing changes in the blood glucose concentration.

METHODS AND MATERIALS

Cryptochiton stelleri, ranging in size from 700 to 1500 g, were collected subtidally from the kelp beds just off Mussel Point in Monterey Bay, California and kept in a large sea water tank at 13.5°C for one to two weeks before use.

A single polyethylene catheter (PE 60) was placed in each animal 12 to 24 hours before initiation of the experiment and subsequent samples and injections were made through the catheter. The catheter was inserted according to the method of MARTIN *et al.* (1958), either dorsally between the seventh and eighth valves into the pericardial cavity, or just ventral to and between the fourth and fifth valves into the haemocoel or lateral sinus. Some difficulty

was encountered in locating the catheter accurately in the desired position. Danger of puncturing the heart or missing the lateral sinus, for example, could not be avoided and could only be accounted for after each experiment when the animals were dissected to determine sex and catheter position.

Blood samples were analyzed for glucose concentrations by the Glucostat method (Worthington Biochemicals Corp.), an enzyme system specific for D-glucose. Analysis was performed on 0.3 ml samples diluted with 0.7 ml of H₂O and with 0.5 ml each of 1.8% Ba(OH)₂ · 8H₂O and 2% Zn(SO₄) · 7H₂O. Total reducing power was determined on the deproteinized blood by the method of Nelson and Somogyi (Hawk *et al.*, 1954).

RESULTS

a. Normal Blood Sugar Level

D-glucose concentrations in the blood of 25 *Cryptochitons*—13 males, 9 females, and 5 of unknown sex—were determined during the month of May. Although the chitons were grouped by sex, no significant difference was found between the glucose concentrations of males and females ($P < 0.1$ Student's *t*-test).

The results are summarized in Figure 1. One male (glucose concentration of 35.6 mg%) differed so widely from the mean that it was not included in calculating the mean.

Twelve of the chitons were sampled 2 or 3 times at intervals from 1 to 24 hours and were found to maintain reasonably constant blood glucose concentrations. The average of the standard deviations for all these animals was 0.6 mg%, and the largest standard deviation was 1.4 mg%.

¹ Permanent address:

502 Siskiyou Boulevard, Ashland, OR 97520

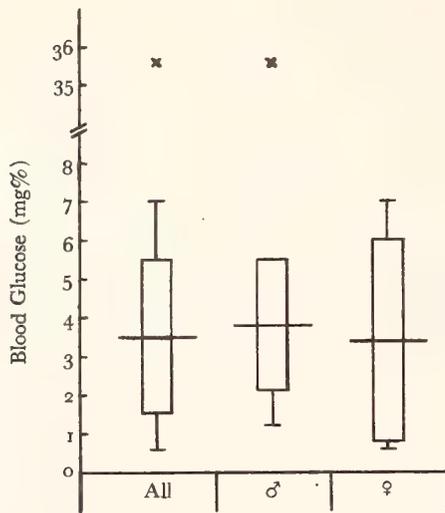


Figure 1

Blood glucose concentrations found in male and female *Cryptochiton stelleri*. Means and ranges are indicated by horizontal lines, standard deviations by boxes. x is value from one chiton which was not included in calculating the mean

Blood samples for 3 of the *Cryptochitons* were also assayed for total reducing power, yielding values from 0.1 mg% above to 2.0 mg% below those for D-glucose, essentially equal within experimental error. Therefore, glucose is the major reducing component in the blood.

b. Glucose Injection

Glucose solution (400 mg/ml) was injected directly into the blood of 6 *Cryptochitons* in a dose of 311 mg/kg. This quantity is sufficient to raise the blood glucose level by 75 mg% on the basis of the blood volume reported by MARTIN *et al.* (1958).

Blood sugar concentrations, before and after injection, were measured in serial samples taken from each chiton. The results are summarized in Figure 2. The high initial glucose values and the wide variation in the rate of the response of the chitons was probably due to a lack of good mixing since it was not always possible to place the collecting catheter in a position of good circulation. However, despite the variation, in each case the blood glucose level clearly returned to a point well below that expected from mere establishment of a passive equilibrium. The blood of chitons 1, 2, and 3 returned to virtually normal glucose concentrations, and it is expected that chitons 4, 5, and 6 would have also, had the experiment been prolonged. No

evident difference appeared between the chitons with the catheter in the haemocoel and those with it in the pericardial cavity.

The water surrounding chitons 1, 2, 3, and 4 which were kept in closed containers, was also tested for glucose and, in all cases, less than 10% of the original glucose injection was found in the water. Thus, decrease in blood glucose could not have been due to excretion of glucose.

c. Insulin Injection

Four *Cryptochitons* were injected with large doses of insulin 6 hours after injection with glucose as described in the previous section. Two animals received a 20 units/kg dose of insulin solution (13 units/ml) and 2 received a 200 units/kg dose of a more concentrated insulin solution (130 units/ml). The insulin used was Calbiochem bovine pancreas insulin, recrystallized and assayed at 25.9 units/mg. Figure 3 summarizes the results and indicates that the insulin had no noticeable effect on the blood glucose level. It did not increase the rate of fall of the blood glucose concentration.

The lower glucose values for the two chitons sampled in the lateral sinus probably result from good circulation there which insures rapid mixing. In light of this result, it might be advantageous in all similar future experiments with *Cryptochitons* to use the lateral sinus for injection and sampling.

d. Norepinephrine and Serotonin Injection

Norepinephrine and serotonin, each injected into 4 *Cryptochitons* in doses of 1 mg/kg (1 mg/ml solution), were found to cause no significant changes in blood glucose concentrations during 4 to 5 hours after injection.

DISCUSSION

Blood sugar concentrations in *Cryptochiton stelleri* have been observed by MYERS (1920) who reported a value of 41 mg%, and by TUCKER & GIESE (1962) who found concentrations from 3.7 to 11.7 mg%, with the lowest values recorded in the Spring. The present study confirms Tucker's very low spring glucose concentrations and, in addition, indicates that the blood sugar level is quite constant, both among members of the population and within each individual. MARTIN (1966) notes a general constancy in the blood sugar levels of other mollusks also.

A low blood glucose level probably is of adaptive advantage to the chiton, since, as MARTIN (1966) notes, most

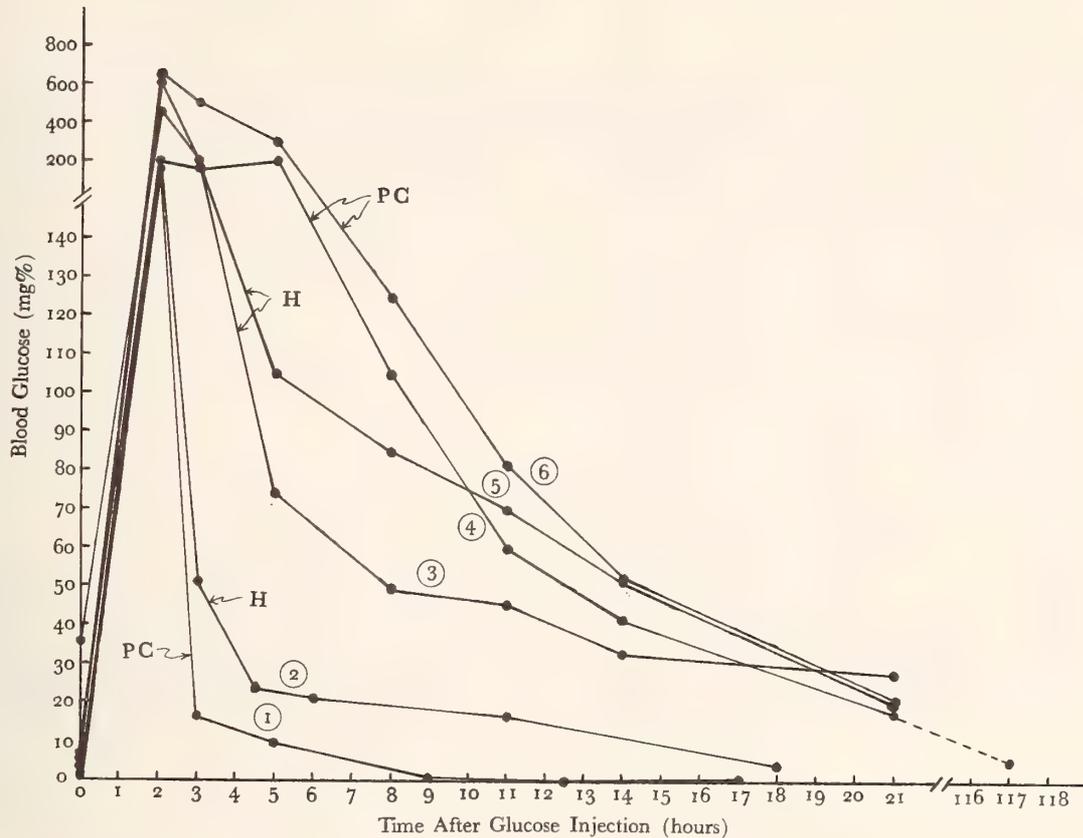


Figure 2

Blood glucose response of six *Cryptochiton* after injection of 311 mg glucose/kg. H: sampling catheter in haemocoel; PC: catheter in pericardial cavity

mollusks filter their blood for urine production and must then actively reabsorb any sugar present. However, the very low supply of blood sugar also presents *Cryptochiton* with the problem of adequately meeting its energy requirements, since it does not appear to have a significant concentration of any other reducing compound in its blood. The chiton is often observed to exist long periods without eating, so it must be able to mobilize energy stores, such as glycogen, to maintain an adequate blood sugar concentration. It seems likely, especially considering the great stability found in the sugar levels, that *Cryptochiton* possesses some mechanism of active regulation to accomplish that purpose.

To indicate further the existence of any regulating mechanism, the response of the chiton to artificially in-

creased blood glucose levels was measured. It was observed, as expected if *Cryptochiton* does indeed regulate, that the sugar concentration rapidly returned toward a level near the original value without significant loss of glucose to the surroundings. The glucose might well have been deposited as glycogen for storage since TUCKER & GIESE (1962) have found significant amounts of glycogen present in the chiton. BARRY & MUNDAY (1959) have noted a similar phenomenon of apparent regulation in *Patella vulgata* (Linnaeus, 1758).

Although regulation of blood glucose in *Cryptochiton* has not been studied previously, evidence for a possible mechanism of sugar regulation has been sought actively in other mollusks. GODDARD (1969) has obtained the most interesting results, having induced both hyperglycaemia and

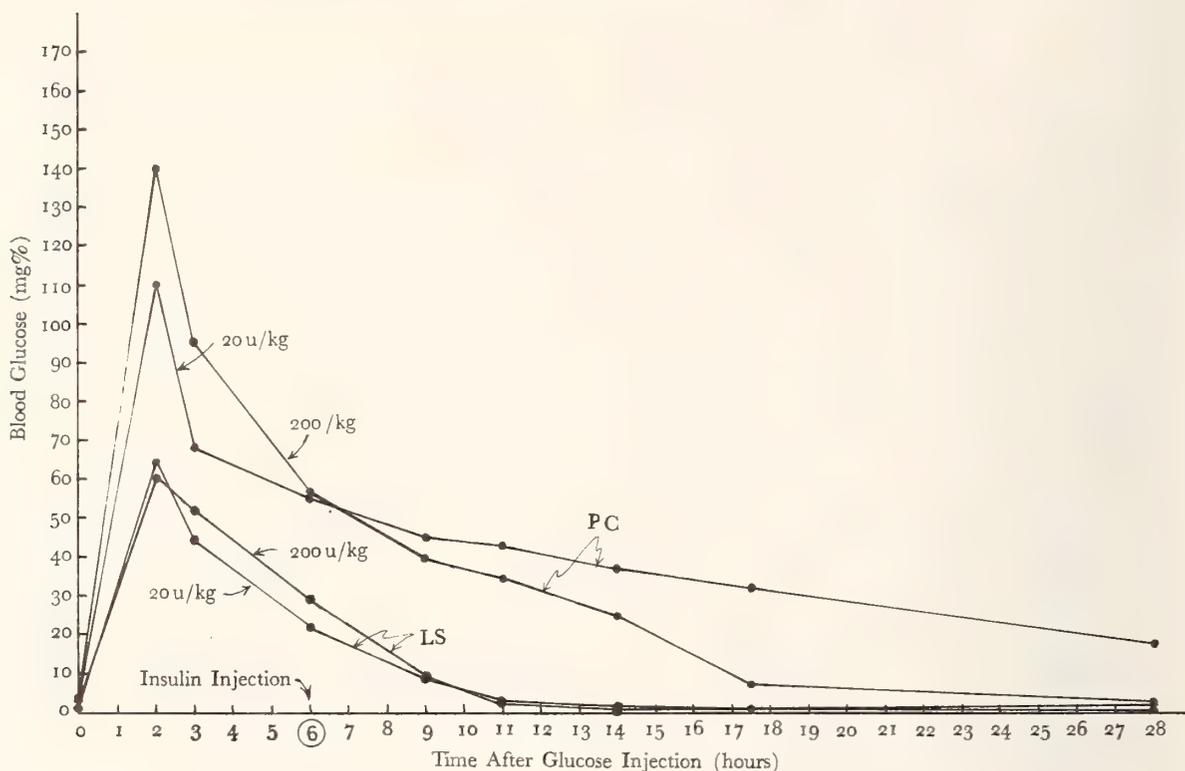


Figure 3

Blood glucose response to insulin injected in doses of 20 and 200 units/kg 6 hours after glucose injection of 311 mg glucose/kg. PC: Sampling catheter in pericardial cavity; LS: catheter in lateral sinus

hypoglycaemia in *Octopus dofleini* (Wülker, 1910) with tissue extracts. Although the precise interpretation of his results is somewhat unclear, they provide a definite indication that some functional hormonal control system for glucose regulation may be active within the mollusk. In addition, most of the vertebrate sugar-regulating amines have been found in the mollusks. Many investigators have tried, with mixed success, to record an effect of those hormones, as well as insulin and glucagon, on the sugar levels of mollusk blood.

GODDARD (1968) and KASINOTHAN (1963) reported a questionable hypoglycaemic effect of mammalian insulin on *Octopus dofleini* and *Meretrix casta* (Chemnitz), respectively. However, such large dosages were required that insulin probably plays a small role in any actual regulating mechanism they might possess. The present study indicates

that even large doses of insulin have no observable effect on the blood sugar concentration of *Cryptochiton*.

GODDARD (1968) found no effect from norepinephrine or serotonin on blood glucose of *Octopus dofleini*. However, TIFFON (1967) has elicited a rise in glucose concentration upon injection of serotonin into the haemocoel of *Achatina fulica* (Bowdich, 1822). The present study indicates that neither norepinephrine nor serotonin has any effect on *Cryptochiton* blood sugar levels, at least within 5 hours after injection.

The research reported here provides strong evidence that a form of carbohydrate regulation exists in *Cryptochiton stelleri*. However, much more work is needed to strengthen these results and provide insight into the actual mechanism of such regulation. Studies might include monitoring the glycogen content after glucose injection as well as the effects of molluscan tissue extracts.

SUMMARY

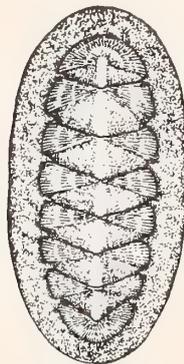
1. Blood glucose levels were determined for *Cryptochiton stelleri*. The mean was 3.5 mg% \pm 2.0 mg% and no significant difference was found between the sexes.
2. After injection of large dosages of glucose, the chitons were found to regulate their blood sugar levels back to or near normal in 9 to 24 hours.
3. Crystalline bovine insulin, in doses of 20 units/kg and 200 units/kg was found to have no effect on the blood sugar concentration.
4. Norepinephrine and serotonin, in doses of 1 mg/kg, were found to have no effect on the blood sugar concentration.

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I would like to acknowledge and thank my advisor, Dr. Frederick Fuhrman, for his ready advice and practical cooperation. More importantly, his encouragement and quiet enthusiasm was a real source of inspiration throughout the project. In addition, I would like to thank Chris Harrold for collecting the subtidal *Cryptochiton*s.

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Active Absorption of D-Glucose and D-Galactose by Intestinal Tissue of the Chiton, *Cryptochiton stelleri* (Middendorff, 1846)

BY

KENNETH B. ROBBINS¹

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

(4 Text figures)

INTRODUCTION

THE ABSORPTION OF NUTRIENTS is one important physiological function of animal intestine. Absorption of nutrients has been well-studied in vertebrates (for reviews, see WILSON, 1962; CRANE, 1968; CURRAN, 1973), revealing accumulation against an apparent concentration gradient by means of the carrier-mediated process termed active transport (for a review of membrane carrier transport, see NEAME & RICHARDS, 1972). Little work has been done with invertebrates, however.

The study of monosaccharide active transport in invertebrate intestine has encompassed only two classes of Echinodermata (see LAWRENCE & MAILMAN, 1967; FERGUSON, 1964), one class of Arthropoda (RANDAL & DERR, 1965), and two classes of Mollusks (LAWRENCE & LAWRENCE, 1967; WRIGHT, 1968). Very little is known about the exact site of monosaccharide absorption in invertebrates, or the nature of the mechanism by which that absorption occurs.

The first investigation demonstrating active transport of monosaccharides by a molluscan intestine was done by LAWRENCE & LAWRENCE (1967) using the amphineuran *Cryptochiton stelleri* (Middendorff, 1846). D-glucose and 3-0-methylglucose were found to be accumulated from the incubation medium into everted sacs of proximal anterior intestine, while D-galactose was accumulated by everted sacs of posterior intestine. Further studies have revealed a sodium coupled galactose transport system in the posterior intestine of this organism (LAWRENCE & MAILMAN, 1967; PUDDY, 1970; LAWRENCE *et al.*, 1972).

Little or no work has been done on the kinetics or specificity of the monosaccharide transport systems in the intestinal tissue of *Cryptochiton stelleri* due to the experimental limitations of the everted sac technique. I decided to approach the problem of sugar uptake and related enzyme kinetics of this organism by measuring the accumulation of sugar in intestinal tissue itself, as CRANE & MANDELSTAM (1960) did with hamster intestine. There are two basic reasons for preferring this technique. First, it is difficult to elucidate the actual transport mechanism using everted sacs, as at least two separate processes are occurring to yield net transport across the intestinal wall: initial transport into the epithelial cells, followed apparently by diffusion through the many underlying cell layers to the serosal fluid. The connective tissue itself, which is 200 μm thick in the anterior intestine (FRETTER, 1937), may act as a significant barrier to free diffusion. With the use of tissue slices, however, sugar need only enter the epithelial cells to be measured, and underlying tissue serves as a repository similar to the serosal fluid of the everted sac. A second advantage of the tissue accumulation technique is that slices from different locations on the intestine and from different animals can be pooled and distributed among flasks so that the sugar absorbing potential of the tissues in each flask is uniform. This is not possible using everted sacs, as the transport rate of each sac varies. The use of tissue samples with equivalent absorbing potential is essential in the study of saturation kinetics, which is an important means of characterizing any transport mechanism.

The properties of D-glucose, D-galactose, and, in certain circumstances, 3-0-methylglucose transport were thus studied using a tissue accumulation technique. The two regions of intestine studied showed specific accumulation of one or more of these sugars. Transport was notably slow com-

¹ Permanent address:

1123 Donaire Way, Pacific Palisades, CA 90272

pared to sugar absorption by hamster intestinal tissue. The D-galactose transport system of the proximal posterior intestine of *Cryptochiton stelleri*, however, was found to be more sensitive to low sugar concentrations than the mammalian equivalent.

MATERIALS AND METHODS

Chitons (*Cryptochiton stelleri*) of both sexes weighing between 600 and 1200 g were obtained subtidally near Mussel Point, Pacific Grove, California. They were kept in aerated seawater at 13°C at least 3 weeks before use.

The procedure for determining monosaccharide accumulation in intestinal tissue was a modification of that of CRANE & MANDELSTAM (1960). The intestine and associated digestive gland was removed from an experimental animal and placed in chiton Ringer solution (LAWRENCE & LAWRENCE, 1967). The digestive gland was carefully teased away from the intestine and the intestine was elongated. The proximal half of the anterior intestine and the proximal 30 cm of the posterior intestine were the only portions studied in these experiments.

Fifteen centimeter portions of the experimental tissues were everted over a glass rod, rinsed in chiton Ringer solution, and cut with scissors to yield a number of 2-4 mm wide tissue rings. These were distributed evenly among incubation flasks containing 50 ml of chiton Ringer solution, thus assuring a uniform sample in each flask.

Incubation flasks were given a 15-minute preincubation period followed by the addition of specific unlabeled and ^{14}C -labeled monosaccharides to the medium. Both preincubation and incubation were carried out at 18°-20°C on a rotary shaker (60 rpm) under 100% oxygen. Concentrations of sugar in the incubation medium ranged from 0.2-10 mM. Incubation periods ranged from 0-8 hours.

Following incubation, two tissue samples containing 6-8 intestinal tissue slices were removed from an incubation flask, blotted lightly, weighed, homogenized in 2.0 ml 2.0% $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$ followed by 2.0 ml 1.8% $\text{Ba}(\text{OH})_2$ for the purpose of deproteinization, and centrifuged at low speed. The filtrate was analyzed for the appropriate monosaccharides. Original intestinal tissue, tissue dipped in the experimental medium, original medium samples and final medium samples were also analyzed for sugar content.

Determinations of D-glucose and D-galactose were made by both the chemical and radioactive techniques. Analysis of 3-O-methylglucose was done only by the radioactive method. Chemical determinations were done colorimetrically using the Glucostat and Galactostat reagents (Worthington Biochemical Corporation). D-glucose- $U\text{-}^{14}\text{C}$, D-galactose- $1\text{-}^{14}\text{C}$, and 3-O-methyl ^{14}C -D-glucose were obtained

from New England Nuclear Corporation. Tracer concentrations in the incubation media were $0.040 \mu\text{C}/\text{ml}$ ($3 \times 10^{-6}\text{M}$), added to the non-radioactive analogues which were present at final concentration. Radioactivity was determined by liquid scintillation counting in a solution of Omnifluor in Dioxane (8 g/l) using proportional counting by a Nuclear Chicago Unilux II Scaler. Quenching was consistent for known standards and all experimental samples.

Data are presented as millimolar concentrations of sugar in the tissue water. Tissue water was determined to be approximately 80% of tissue wet weight for both anterior and posterior intestinal samples, by comparing the wet weights and dry weights (after 24 hours at 100°C) of pooled samples.

RESULTS

D-galactose at an original concentration of 4.5 mM in the medium was found to be concentrated to 7.0 mM within posterior intestinal tissue after a 3 hour incubation. Results of the accumulation of 3.0 mM D-galactose over an 8-hour period by posterior intestinal tissue are presented in Figure 1. D-galactose at a medium concentration of 4.5 mM gave an anterior intestinal tissue concentration of 4.4 mM after 8 hours, apparently indicating the lack of a D-galactose transport system in this region of the intestine.

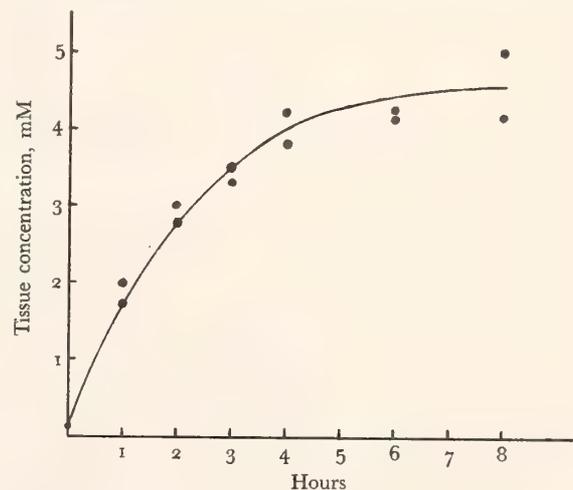


Figure 1

Uptake of D-galactose by posterior intestinal tissue over an 8-hr incubation period. Initial medium concentration was 3.0 mM. Samples were taken in duplicate at 0, 1, 2, 3, 4, 6, and 8 hours and analyzed chemically and radioactively for D-galactose. Both methods yielded similar results; radioactive analysis is presented here

Original tissue D-galactose concentrations were less than 0.4 mM, and thus were not a problem in analysis.

The results of an experiment demonstrating saturation kinetics over a three-hour incubation period by the D-galactose transport system of the posterior intestine are presented in Figure 2. D-galactose accumulation has been divided into a hypothetical diffusion component and saturable, carrier-mediated component, the latter being the difference between total transfer and the diffusion component. On this basis the maximum velocity of the transport system (V_{max}) is 0.8 millimoles D-galactose/1 tissue fluid/hr, and K_m , the concentration of substrate necessary to give half the maximum velocity, is less than 0.1 mM.

D-glucose at an original medium concentration of 5.5 mM was found to be concentrated to approximately 8.0 mM in both anterior and posterior intestinal tissue over a three-hour period (Figure 3). Three-O-methylglucose, a non-metabolizable glucose analogue in other transport systems (CURRAN, 1973: 188) was not concentrated by posterior intestinal tissue. The accumulation of D-glucose, but not of 3-O-methylglucose, was substantiated by an ex-

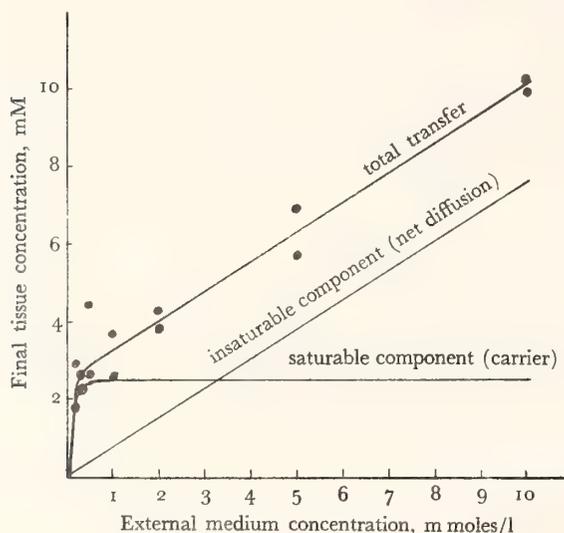


Figure 2

Relationship of the rate of D-galactose uptake to the concentration of D-galactose in the incubation medium. Rate of uptake is plotted as the concentration of D-galactose in posterior intestinal tissue after a 3-hr incubation period. Radioactive and chemical analysis gave equivalent results; radioactively-determined data are presented here. Total transport is divided into a hypothetical insaturable component and a saturable component, attributed to net diffusion and carrier transport, respectively. On this basis, V_{max} equals 0.81 mM per hour, and K_m 0.1 mM. V_{max} may actually be somewhat higher, due to the possible effects of outward transport which were not considered in analysis

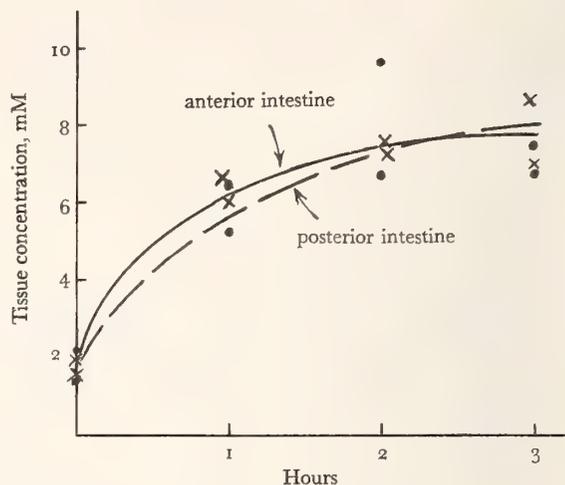


Figure 3

The uptake of D-glucose by intestinal tissue. Proximal anterior and proximal posterior intestinal tissue were incubated for 3 hrs in a 5.5 mM D-glucose medium. Hourly samples were recovered in duplicate and analyzed by radioactive and chemical techniques. Chemical analysis gave slightly higher values for the first 2 hours, due to the presence of 1.8 mM D-glucose and 3.1 mM D-glucose in original anterior and posterior tissue samples. Complete exchange diffusion seemed to occur by the third hour, however, as radioactive and chemical analysis gave equivalent results. Radioactively-determined data are presented here, as these data definitely indicate accumulation of D-glucose from the medium and are less biased to high tissue/medium D-glucose ratios

periment in which 3-O-methylglucose tracer exhibited only passive diffusion in both a D-glucose and 3-O-methylglucose medium (Figure 4). This demonstrates that the difference in transport of the two sugars is due to carrier specificity rather than the need for a metabolic substrate in the medium.

The analysis of D-glucose transport was complicated by the presence of an average of 3 mM D-glucose in the original intestinal tissue of chitons starved for 3 weeks. Chemical analysis thus gave higher D-glucose concentrations than tracer analysis for the first few hours of tissue incubation in a D-glucose medium. By the fourth hour, however, radioactive and chemical analysis gave approximately the same results. This was assumed to indicate the replacement of original cellular D-glucose with D-glucose from the medium by the process of exchange diffusion.

D-galactose transport in the posterior intestine was not greatly inhibited by the presence of a relatively high concentration of D-glucose, thus ruling out competition of

these two sugars for the same carrier. A concentration of 0.2 mM D-galactose in the presence of 3.0 mM D-glucose gave a tissue/medium D-galactose concentration ratio

(T/M) averaging 14.5, while a 0.2 mM control gave a T/M of 17.0 over a three-hour period.

DISCUSSION

A number of assumptions was made in the calculation and interpretation of data. Tissue water was approximated at 80% of tissue wet weight, and sugar was assumed to be spread uniformly throughout that fluid. Tissue water, however, is actually a composite of adherent medium, extracellular fluid and intracellular fluid. There are furthermore a variety of cell types composing the tissue, not all of which may be participating in absorption. The sugar concentrations presented are thus averages of all the uncontrollable factors related to tissue structure and do not represent true intracellular concentrations.

It is assumed that transport is a one-way process over the time interval studied, and the possible effects of diffusion and outward transport were not dealt with quantitatively in simple uptake experiments. These effects over a three-hour period may be considerable, however, since an everted sac is presumably filled with sugar by the action of diffusion over that interval.

Other assumptions made were that all transported sugars were free in solution in the cells, that tissue slicing damage was minimal, and that the contents of all cells and organelles were released upon homogenization. The effects of metabolism were ignored, since chemical and radioactive tracer analysis gave approximately the same results in all experiments when original tissue concentrations were accounted for.

In consideration of all these factors, the concentrations of sugar determined in these experiments are biased, if at all, towards a lower tissue/medium concentration ratio. Thus, an accumulation of sugar above medium concentration by a tissue definitely indicates active transport, while no accumulation ($T/M \leq 1$) does not necessarily negate that possibility.

It is also important to realize that the rate of sugar absorption by intestinal tissue varies from one animal source to another, thus making the comparison of rates in separate uptake experiments impossible.

Experimental results thus indicate active transport of D-galactose by the proximal posterior intestine and of D-glucose by both the anterior and posterior intestine. D-glucose transport by the proximal anterior intestine, and D-galactose transport by the posterior intestine were both observed in the everted sac studies of LAWRENCE & LAWRENCE (1967). The fact that D-galactose was not accumulated by anterior intestinal tissue which accumulated D-glucose, and the fact that D-galactose transport by pos-

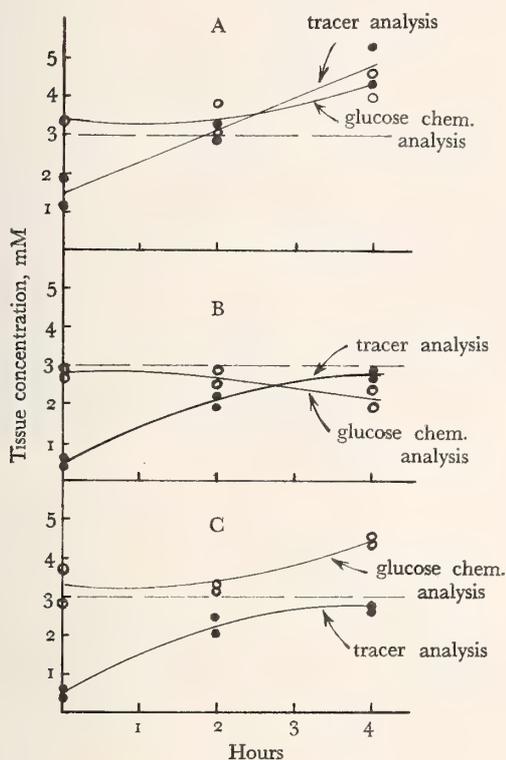


Figure 4

Specificity of the posterior intestinal D-glucose transport system. Incubations of posterior intestinal tissue were carried out in the monosaccharide media described below. Samples were taken in duplicate at 0, 2, and 4 hrs, analyzed chemically for D-glucose and radioactively to determine the behavior of tracers in each environment. The contribution of added tracers to the total sugar concentration was negligible (3×10^{-6} M)

A. D-glucose at 3.0 mM plus 0.04 μ C/ml D-glucose-U- 14 C. Both D-glucose and labeled D-glucose were accumulated by the tissue. The initial difference between chemical and radioactive analysis was due to the presence of 3.0 mM glucose in the tissue before addition of sugar to the medium. This was apparently completely exchanged for D-glucose from the medium by the fourth hour of incubation.

B. Three-o-methylglucose at 3.0 mM plus 0.04 μ C/ml 3-o-methyl- 14 C-D-glucose. Labeled 3-o-methylglucose was not apparently concentrated by the tissue. Presumably, original tissue glucose dropped due to passive diffusion.

C. D-glucose at 3.0 mM plus 0.04 μ C/ml 3-o-methyl- 14 C-D-glucose. D-glucose concentration, determined chemically, rose within the tissue as in A. Labeled 3-o-methylglucose, however, behaved similarly to the labeled 3-o-methylglucose in B, and apparently was not concentrated.

terior intestinal tissue was not substantially inhibited by high concentrations of D-glucose support the belief of LAWRENCE & LAWRENCE (*op. cit.*) that at least two monosaccharide transport systems are operating in the intestine of this organism.

The velocity of D-galactose accumulation in the experiment demonstrating saturation of galactose transport (Figure 2) is represented by the final tissue concentration after a three-hour incubation period. The experimental values thus do not directly represent initial rates, as is desired. However, transport is slow enough that it is assumed the final concentrations are proportional to initial rates. Transport analyzed in this way yields a curve which can be divided hypothetically into a saturable and unsaturable component, the linear unsaturable component being attributed to net diffusion. The value for V_{max} determined for the saturated D-galactose system, 0.8 mM/hr, may actually be somewhat lower than the true value due to the effects of outward transport which were not considered in this experiment. Nevertheless, even with a two-fold increase in rate, transport remains extremely slow when compared to a corresponding mammalian system. The D-galactose transport system of hamster intestine, for example, has a V_{max} of 120 mM/hr (CRANE, 1960). The difference in rates is not unexpected, however, as there are great differences in the metabolic rates and energy requirements of these two organisms. The low temperature environment (11°-14°C) of *Cryptochiton stelleri* may, in particular, depress the rate of any carrier-mediated transport process (LAWRENCE & LAWRENCE, 1967a).

Another unique feature of D-galactose transport in *Cryptochiton stelleri* is the extremely low K_m of the system. The value cannot be accurately determined from the graph of carrier transport in Figure 2, but it is definitely in the range of 0.1 mM or less. The corresponding K_m for hamster intestinal D-galactose transport is 2.2 mM (CRANE, 1960). The D-galactose transport system of *Cryptochiton stelleri* thus responds most efficiently at low concentrations, perhaps compensating somewhat for the low transport rate.

The D-glucose transport system in the proximal posterior intestine seems to be extremely specific, as 3-0-methylglucose is not apparently concentrated. LAWRENCE & LAWRENCE (1967) did not detect an accumulation of D-glucose in everted sacs of posterior intestine. Nevertheless, a decrease in D-glucose concentration and no decrease in 3-0-methylglucose concentration was noted in the serosal compartment. The decrease in D-glucose was attributed to metabolism. My results suggest, however, that D-glucose was not metabolized, but merely accumulated in the tissue, while 3-0-methylglucose was not accumulated. The absorption of D-glucose within the posterior intestinal tissue without unidirectional transport across the intestinal wall

seems reasonable, as GABE & PRENANT (1949) have reported significant glycogen stores in that tissue for three species of chitons. Presumably, D-glucose was actively transported into epithelial cells, but was not converted to glycogen during the course of the experiments.

Although this study demonstrates the accumulation of sugar by intestinal tissue, a process which most certainly is important in the trans-intestinal transport process, no investigation of *Cryptochiton stelleri* has yet determined the entire mechanism by which sugars and other nutrients are transported across the intestinal wall and into the body fluids. Histological studies of chiton intestine have been done (FRETTER, 1937; GABE & PRENANT, 1949), but no cells show the characteristic microvilli of mammalian epithelia. In mammals, transport is localized in the microvilli region of the epithelial cells (WILSON, 1962), thus explaining the unidirectional flux of nutrients across the gut wall. Exactly how unidirectional flux is achieved by the intestinal epithelia of *Cryptochiton stelleri* remains the greatest enigma of this invertebrate transport system.

SUMMARY

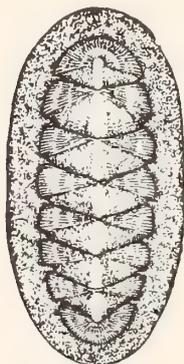
1. The uptake of D-glucose and D-galactose by the intestine of *Cryptochiton stelleri* (Middendorff, 1846) was studied in vitro by the accumulation of sugar within intestinal tissue.
2. Proximal anterior intestinal tissue actively absorbs D-glucose.
3. Proximal posterior intestinal tissue actively absorbs D-glucose and D-galactose, via separate transport systems.
4. The posterior intestinal D-glucose transport system is apparently incapable of transporting 3-0-methylglucose, a non-metabolizable glucose analogue in other transport systems.
5. D-galactose uptake by the posterior intestine is very slow in mammalian terms ($V_{max}=0.81$ mM/hr), although the D-galactose transport system of *Cryptochiton stelleri* shows a greater sensitivity ($K_m=0.1$ mM) to D-galactose than does the equivalent system in hamster intestine. This indicates a slow but efficient accumulation of D-galactose at low concentrations by this invertebrate.

ACKNOWLEDGMENTS

The author wishes to thank Dr. Frederick A. Fuhrman and the rest of the faculty and staff of Hopkins Marine Station for encouragement in this endeavor.

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Lipid and Glycogen Levels in the Tissues
of Two West Coast Chitons,
Mopalia muscosa and *Nuttallina californica*

BY

ROBERT TENOLD¹

ABSTRACT

ANALYSIS WAS DONE ON the foot, gut, digestive gland, and gonad using the methanol-ethyl ether method for lipids and the phenol-sulfuric acid method for glycogen. Species differences were found only in the foot tissues. Female

Mopalia muscosa (Gould, 1846) had a lower percentage of lipid in the foot tissue than did female *Nuttallina californica* (Reeve, 1847). Comparing both sexes, *M. muscosa* was found to have a higher level of glycogen in the foot tissue than *N. californica*. In the tissues of both species studied lipids are quantitatively the more important storage materials. Original paper containing full findings is in library of Hopkins Marine Station.

¹ Permanent address:

Route 3, Box 102, The Dalles, OR 97058

Nitrogenous Materials Released
from *Mopalia muscosa* (Gould, 1846),
an Intertidal Chiton

BY

RICH WILLIAMS

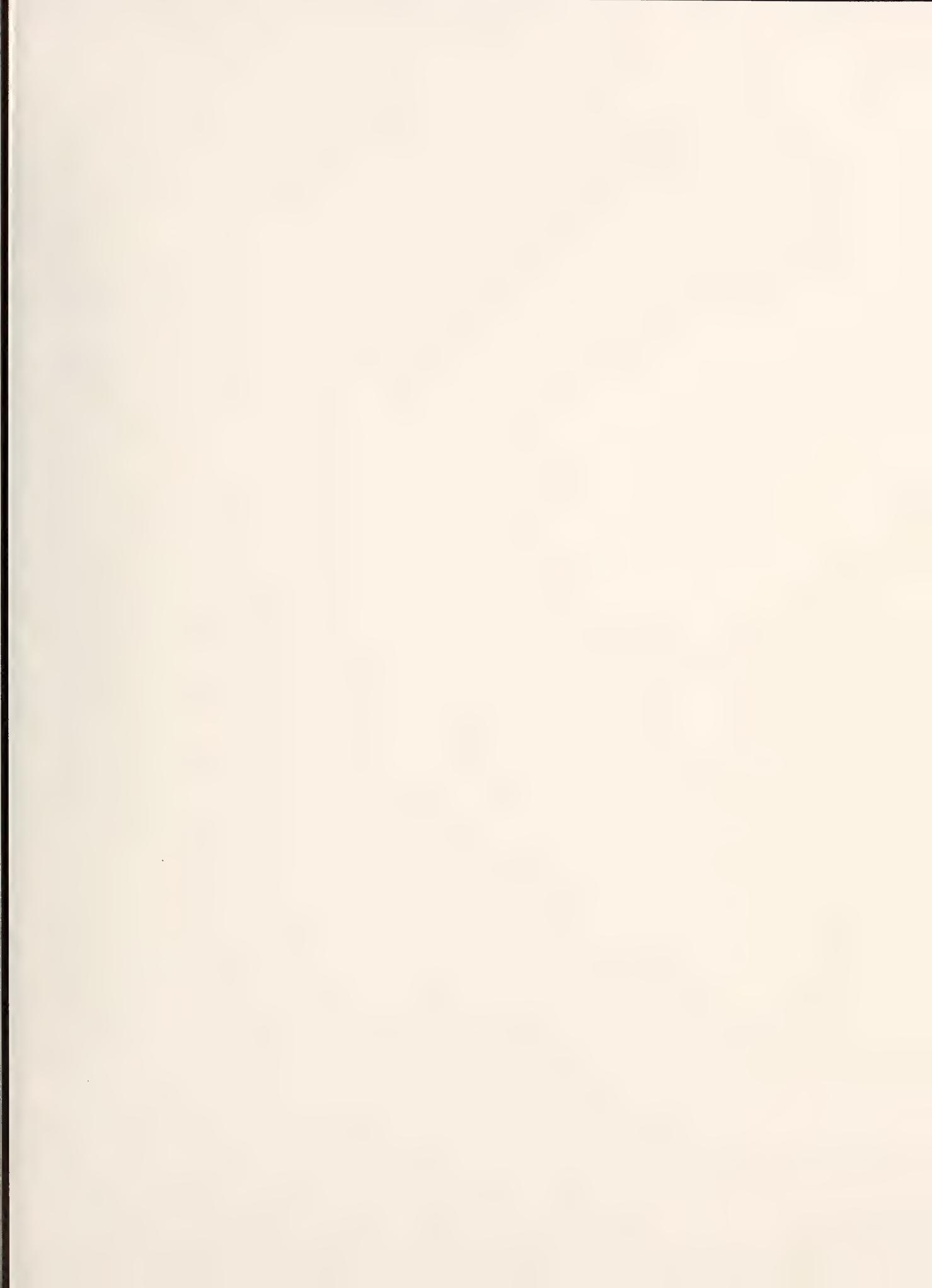
ABSTRACT

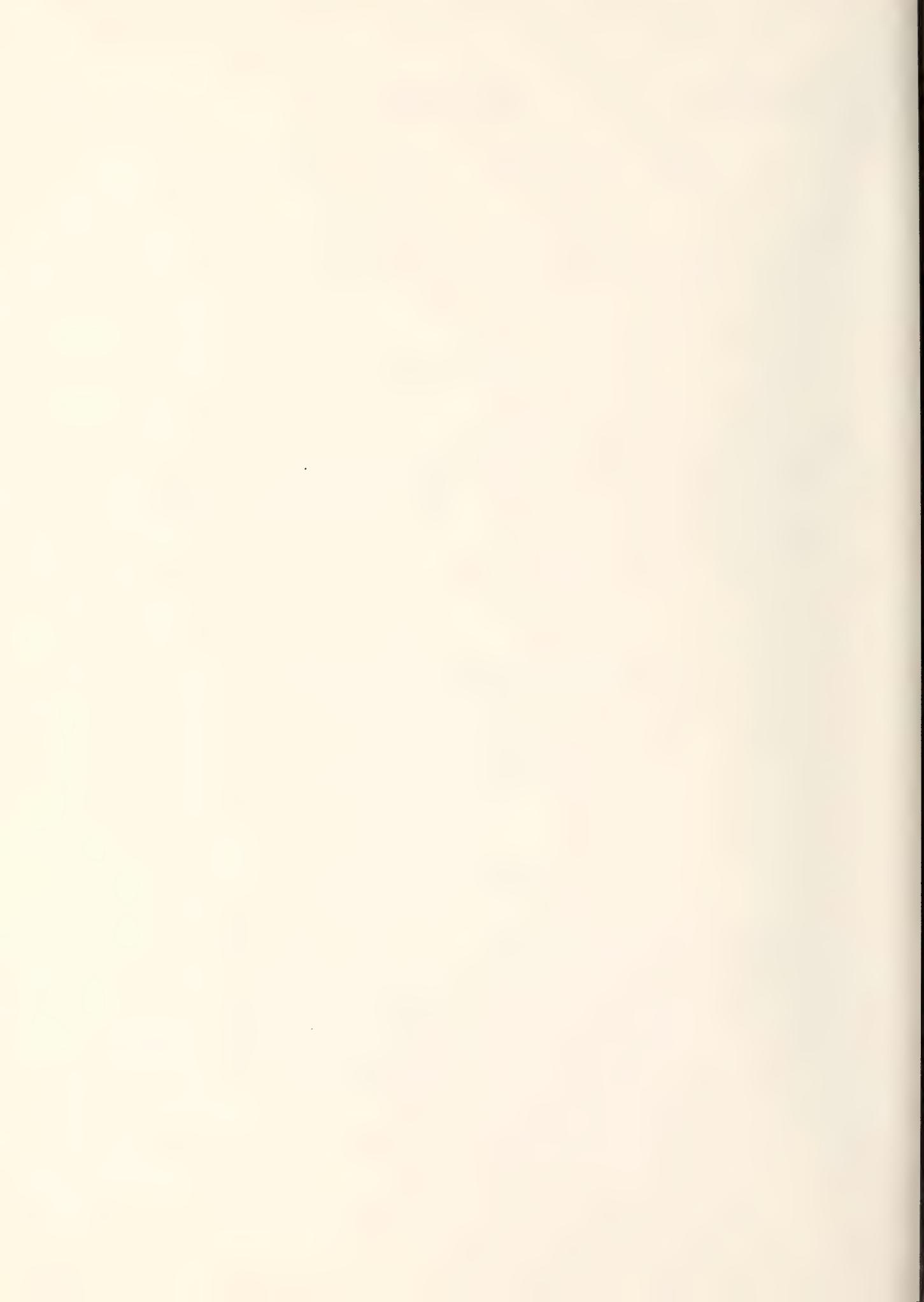
A STUDY WAS UNDERTAKEN to identify the nitrogenous waste products released from the intertidal chiton *Mopalia muscosa* (Gould, 1846). The Solorzano method was used to test for the presence of ammonia or urea, or both, while ninhydrin positive nitrogenous compounds were identified by the Spies method. Large variability within each sample

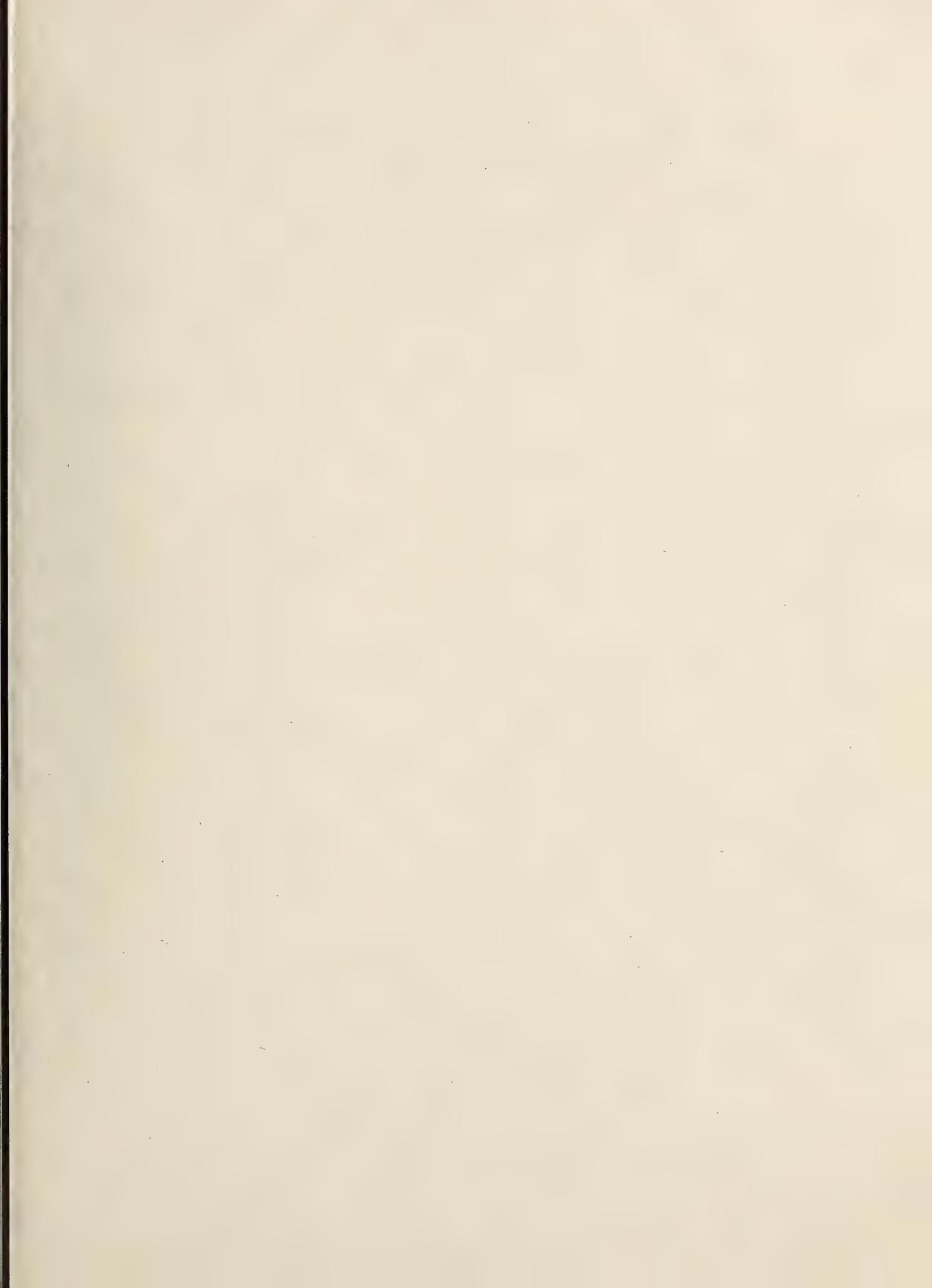
collected from each of five chitons did not allow a significant comparison between levels of ammonia and urea, although both nitrogenous compounds were present. However, in three of the *M. muscosa* high levels of ninhydrin positive material were found in comparison to the ammonia and urea levels. For one chiton these levels were $220.4 \pm 27.2 \mu\text{g}$ of ninhydrin positive nitrogen, $42.4 \pm 4.7 \mu\text{g}$ of urea nitrogen, and $51.4 \pm 12.0 \mu\text{g}$ of ammonia nitrogen. The ninhydrin positive nitrogen was released from this *M. muscosa* at a rate of 0.48 mg/100 g/day. The original paper is on file at the library, Hopkins Marine Station, Pacific Grove, California 93950.

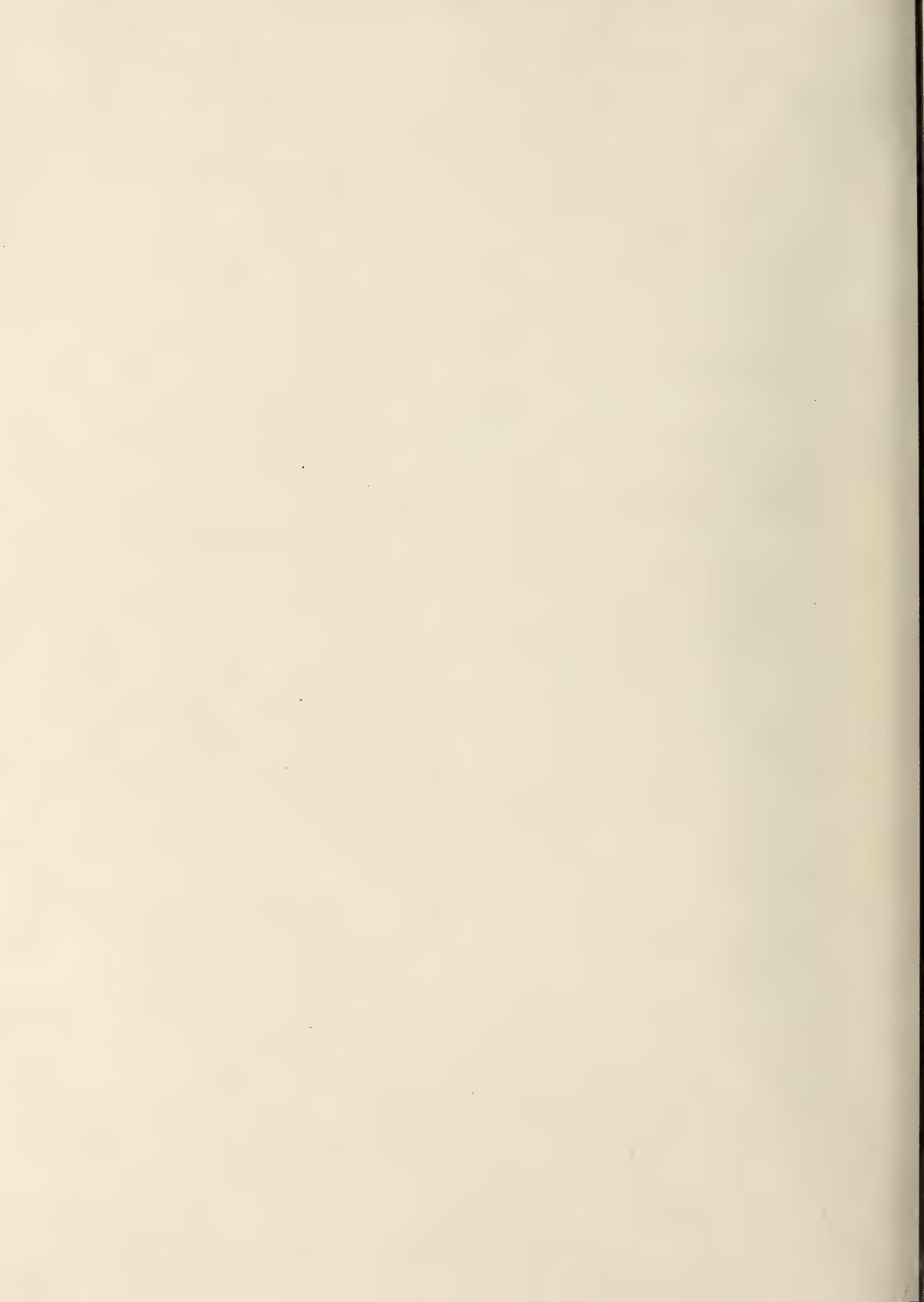
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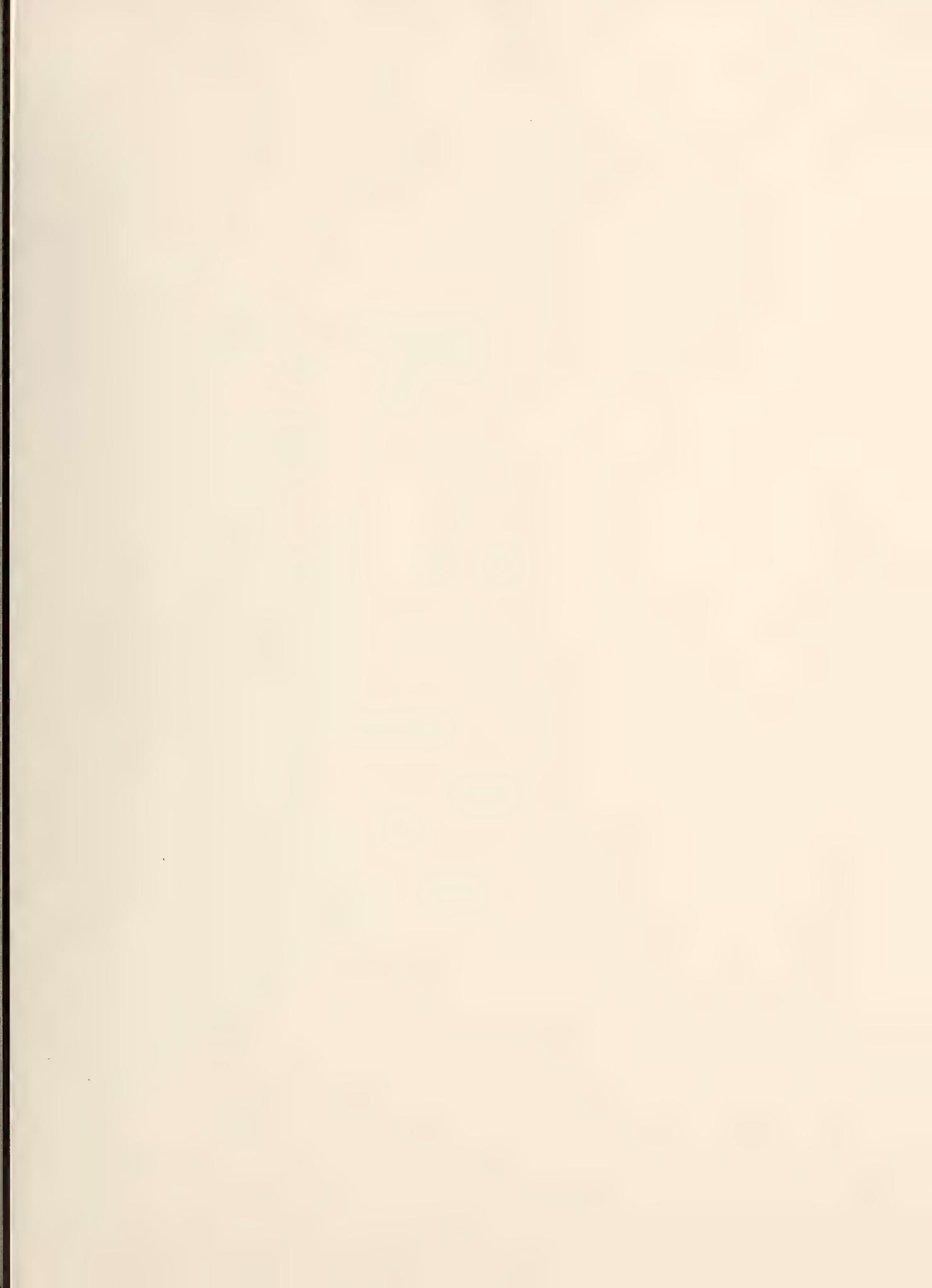
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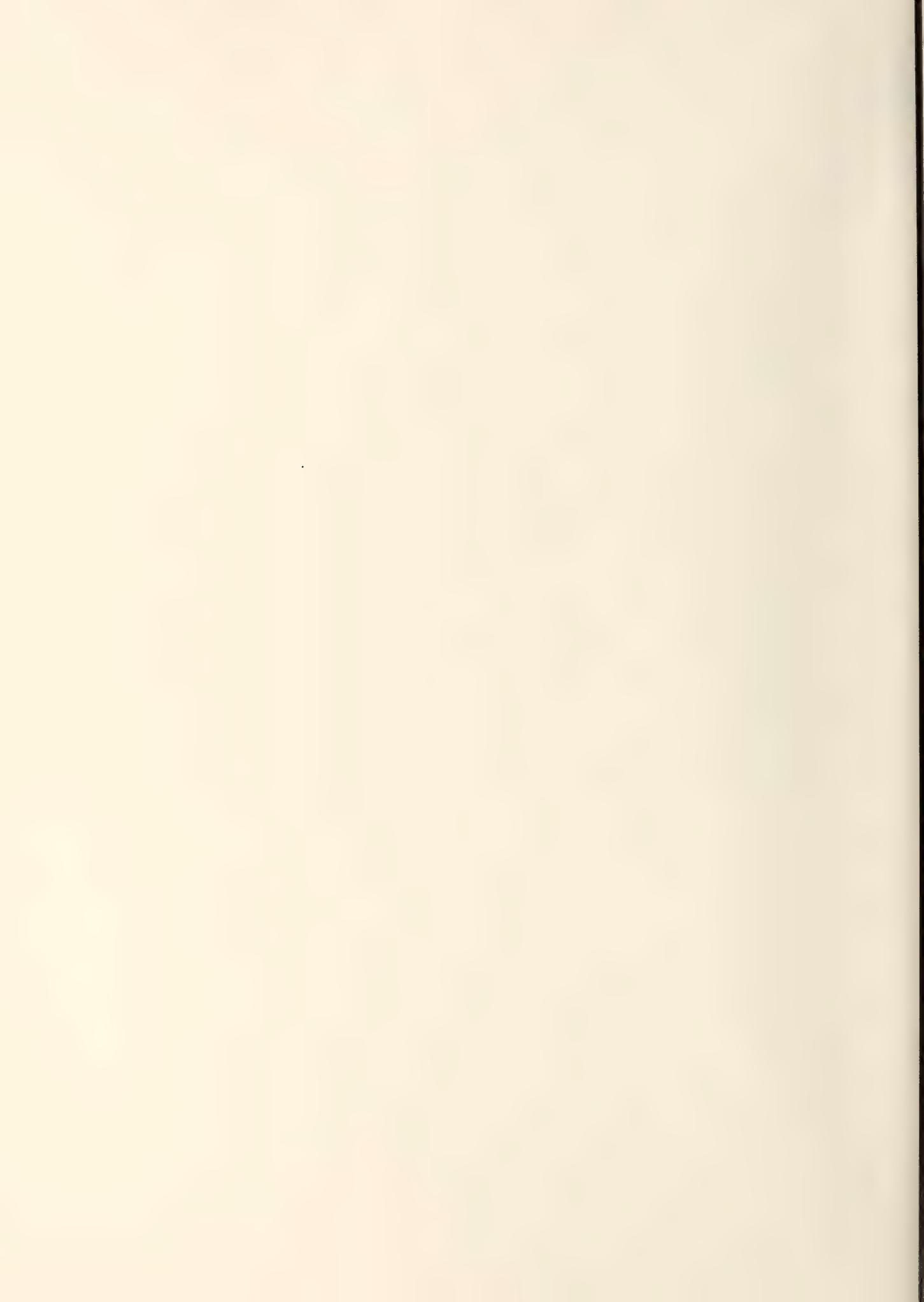


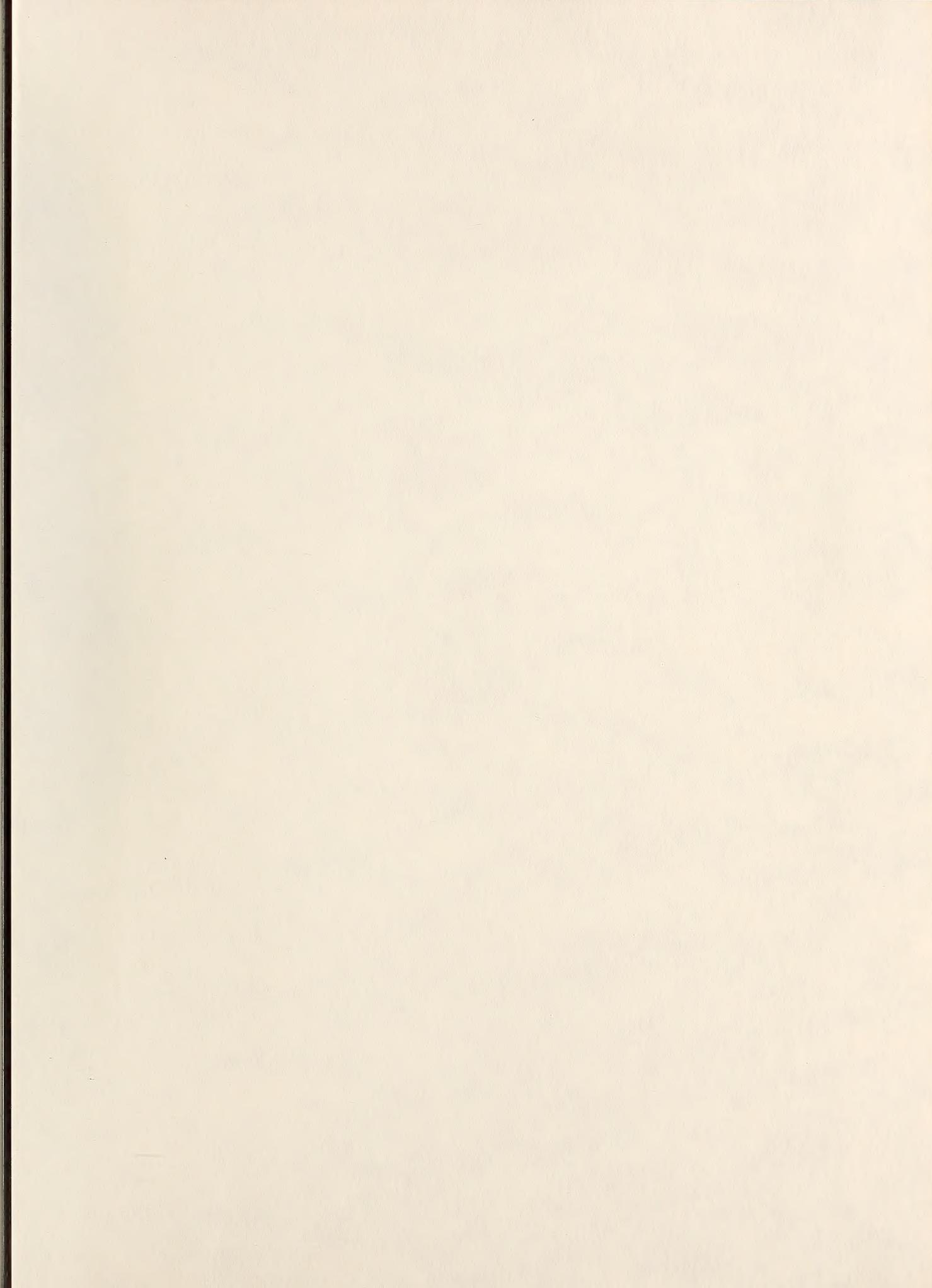




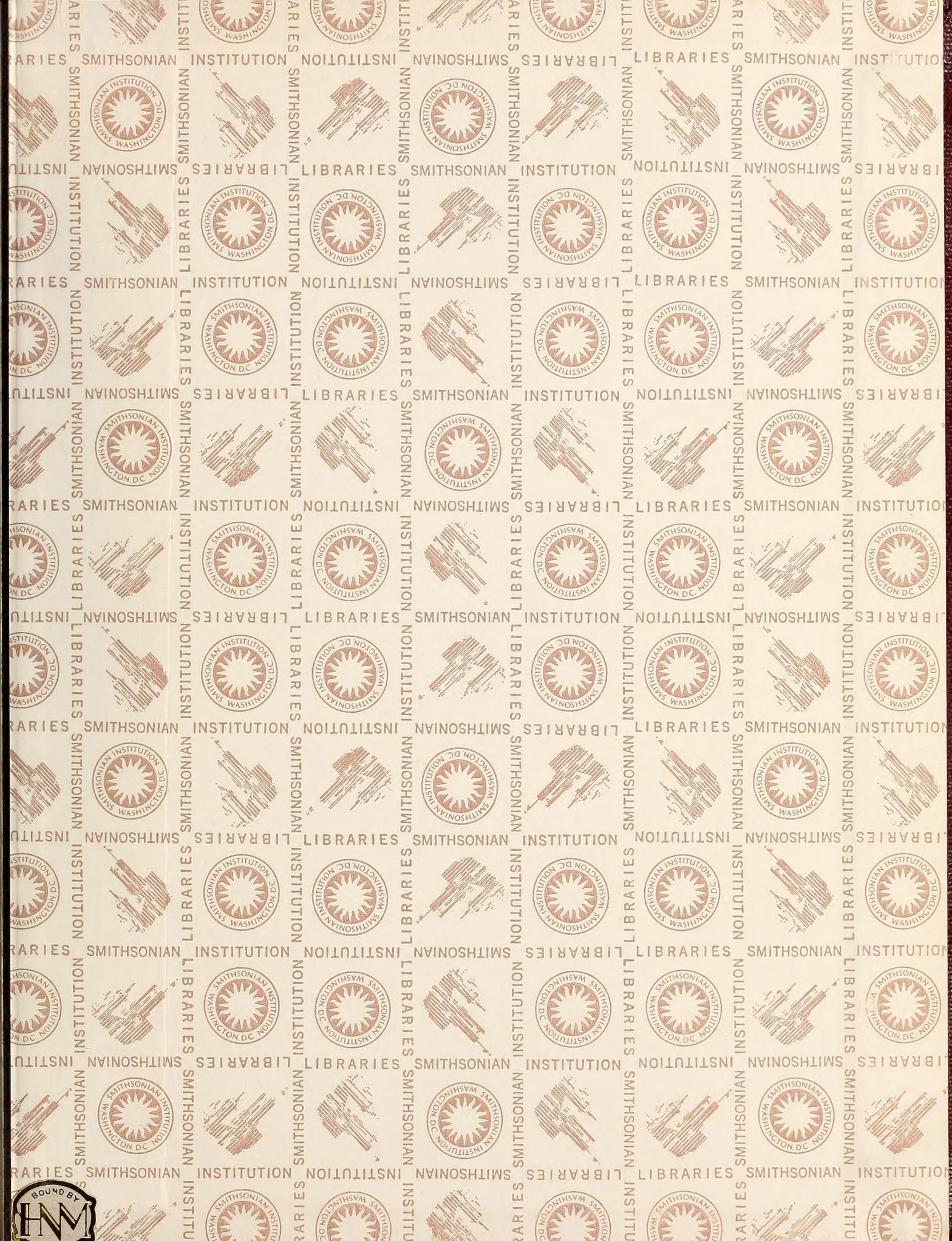












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