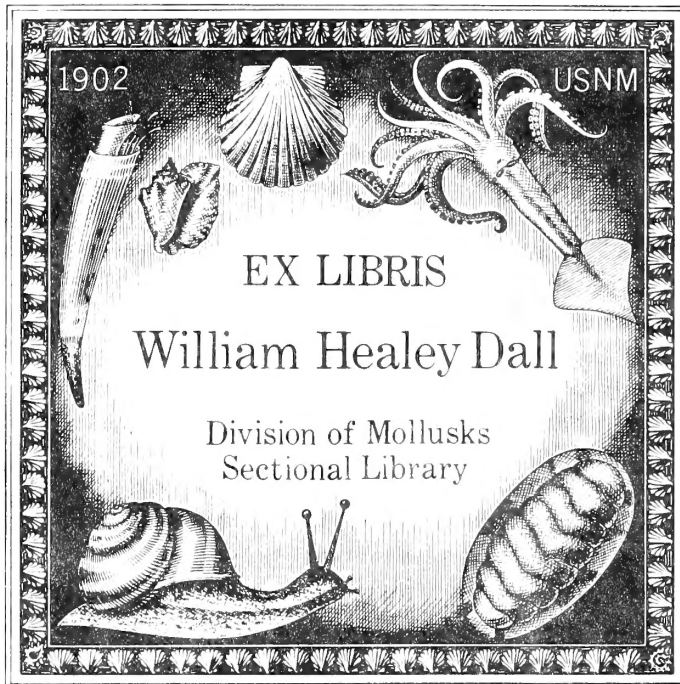
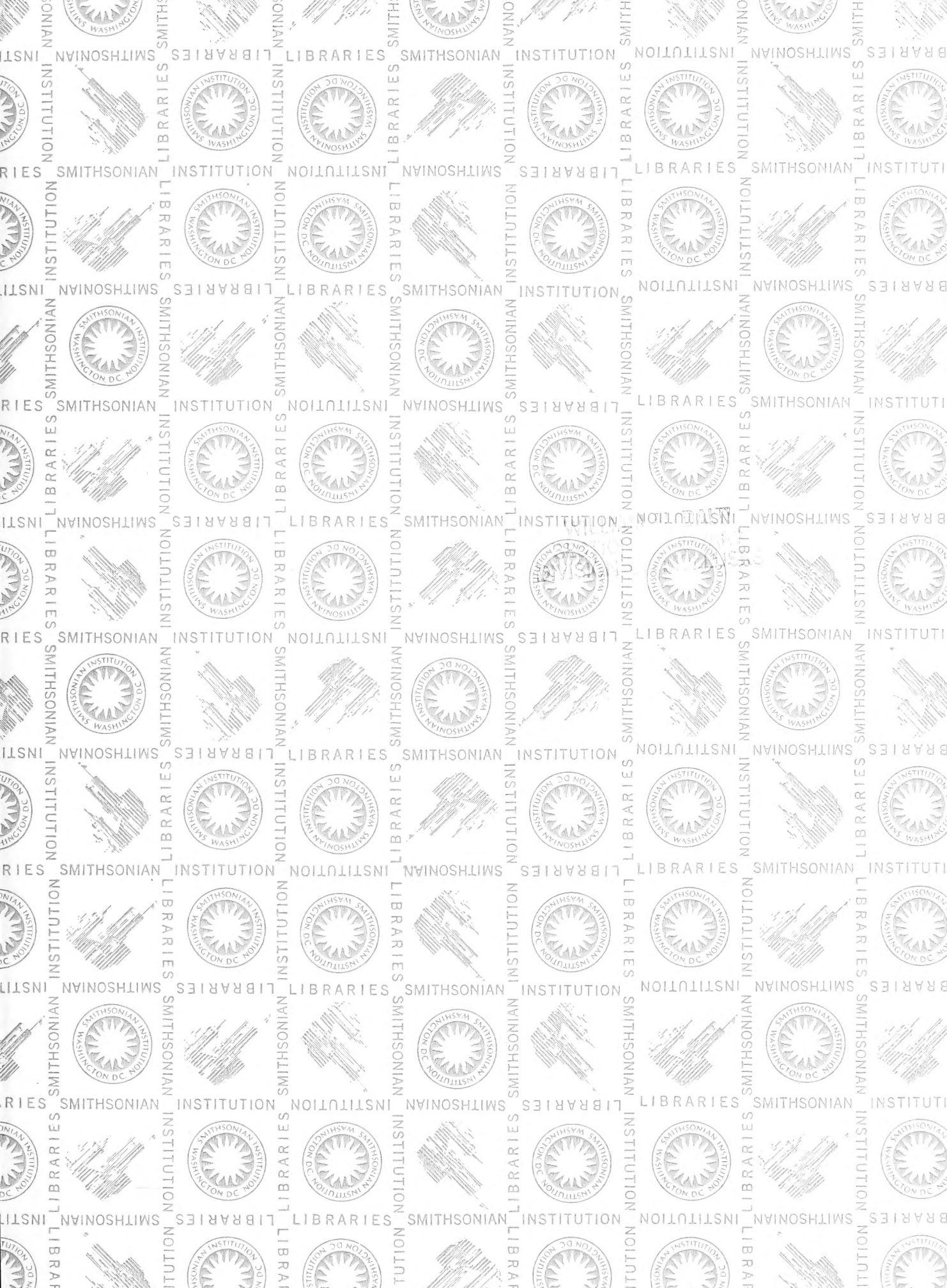


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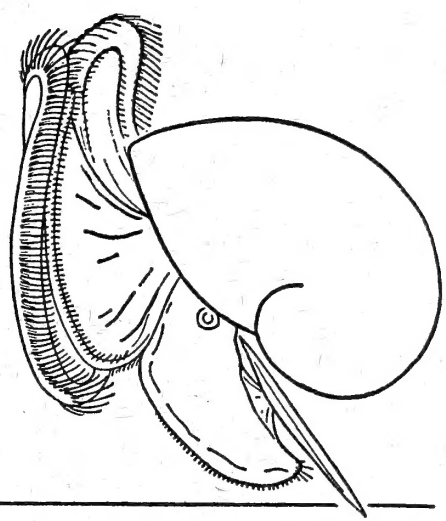
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# THE VELIGER



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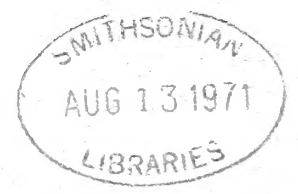
SUPPLEMENT

## The Northwest American Tellinidae

BY

EUGENE V. COAN

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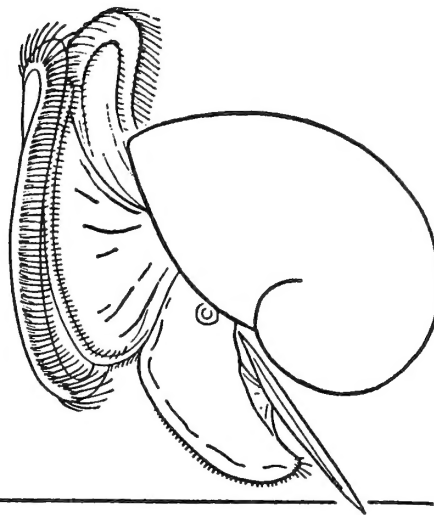






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**Note:** The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

**ORDER**, Suborder, **DIVISION**, Subdivision, **SECTION**,  
SUPERFAMILY, FAMILY, Subfamily, *Genus*, (*Subgenus*)

*New Taxa*

# The Northwest American Tellinidae

BY

EUGENE V. COAN

Research Associate

California Academy of Sciences, Golden Gate Park, San Francisco, California 94118

(12 Plates; 30 Text figures)

## INTRODUCTION

A MUCH NEEDED TAXONOMIC REVIEW of the Tellinacea occurring from the Arctic coast of Alaska to the central portion of the outer coast of Baja California has been conducted. Preliminary nomenclatural conclusions with regard to the entire Tellinacea were presented to the June 1967 meeting of the American Malacological Union, Pacific division (COAN, 1968a). Only the data on the Tellinidae are published here.

The Tellinidae, one of the largest families of Bivalvia, and of considerable ecologic and potential economic importance, have not been critically revised on the northwest Pacific coast in recent years. A review can bring the nomenclature and certain aspects of the taxonomy of organisms to such a level as to be of immediate benefit to workers in a variety of disciplines (such as ecology, physiology, and paleontology), provide a firm basis for further and more advanced kinds of taxonomic research, and lead to the discovery and initial outlining of problems of current interest in biogeography, paleontology, and comparative morphology.

The historical perspectives of this project within the context of West American marine malacology will first be discussed, especially emphasizing progress toward nomenclatural stability; then some of the basic issues of systematic and population biology that are taken into consideration will be outlined.

**Historical Considerations.** – The history of malacology on this coast can be divided into a series of overlapping periods. Aside from those species named in the North Atlantic that also occur in the North Pacific, West American nomenclature is relatively free from problems posed by the pre-Linnean entanglements of 1758 - 1830 – the “Linnean Era,” as we may term it. The few species-level names applicable to our fauna from this period have been

investigated in the present study as carefully as was practical. The definitive search for type specimens and the selection of lectotypes for these species is more properly the task of European workers with access to European collections; it is unfortunate that this has generally not yet been properly done (for instance, see *Macoma balthica*).

The early history of malacology on the West American coast is mainly one of sporadic naming of new taxa collected by expeditions between 1830 and about 1845. One might call this the “Era of Exploration.” As far as the Tellinacea are concerned, the most important of these expeditions were (1) the voyage of the *Blossom* to the Bering Sea and the Arctic Ocean, with species described by Broderip, Sowerby, and Gray in 1829 and 1839, (2) the travels of Thomas Nuttall in California and Oregon, with material described by Conrad in 1837, (3) the voyage of the *Sulphur* to Mexico and California, with mollusks described by Hinds from 1842 to 1845, and (4) the travels of Hugh Cuming in Central and South America in the 1820's and 1830's, his collected material described by Broderip, Sowerby, Carpenter, and many others from 1832 on.

The type specimens from the *Blossom*, originally in the Zoological Society of London, are mostly lost to science. A careful search was made in an attempt to locate the tellinaceans from this expedition in the British Museum (Natural History) (see *Macoma brota*), but none could be found (KEEN, verbal communication).

The types of species described by Conrad are mainly in the British Museum (Natural History) and have been discussed by KEEN (1966a). She did not select lectotypes, however, properly leaving this task to specialists in various groups.

Many of the specimens collected and described by Hinds are housed in the British Museum (Natural History) (KEEN, 1966b). Finally, the Cuming collection also

went to the British Museum, and Cuming's travels and the history of his material have been discussed by DANCE (1966). Dr. Keen was able to locate many of these type specimens and photograph them.

The species collected on these early expeditions were, in general, well described and illustrated, and few problems have been encountered in allocating the species-level names, although many of the original specimens have been lost. The losses occurred because there were no large national collections at the time nor was the importance of the preservation of original materials recognized.

The period from about 1845 to 1880 may, in part, be considered the "Era of Monographs." Works from this period dealt with species of large taxonomic units from the entire world. Chief among these of importance in the study of the Tellinidae are KÜSTER & RÖMER (1841-1873), HANLEY (1844-1845, 1846), DESHAYES (1855), SOWERBY (1866b-1869), TRYON (1869), and BERTIN (1878). One might think that these workers, aided by the large collections at their disposal and a world-wide point of view, would have been able to make significant contributions. This was generally not the case, and many difficult problems arise as a result of their publications. Several were shell dealers and were possibly interested in proliferating the number of named species in order to increase the value of their merchandise. They often described new taxa with incorrect or unknown localities, without comparisons, with brief, cryptic, virtually useless Latin descriptions, and without illustrations. Sometimes type material was sold and never ended up in present-day collections, at least in recognizable form. Dr. Keen's extensive studies at the British Museum (Natural History) bettered West American malacology in that she located the type specimens of many Deshayes and Sowerby species.

In two cases (*Tellina nuculoides* and *Leporimetes obesa*), older names were encountered for relatively well known species. These names were both from monographs, one described from an incorrect locality, the other originally allocated to an incorrect genus and subsequently ignored. It seems to be the consensus of West Coast malacologists that such names, even if they are technically *nomina oblita*, should be recognized and used. The ecological and physiological literature on West American species is not now large, and the nomenclatural work possible at present will probably prevent forgotten names from cropping up frequently in the future.

The period from about 1850 to 1921 in the eastern Pacific might be termed the "Era of Faunal Accounts." Such accounts were books and papers on the mollusks, treating either the entire fauna or that of one limited area. This category includes the account of C. B. ADAMS

(1852a, 1852b) on Panama, the books and papers by CARPENTER, especially his catalogue of Mazatlán shells (1857c) and his more general books on West America (1857b, 1864a, 1872), and the many important works of DALL (especially 1891, 1900a, 1909, 1916a, 1921a). The quality of work done by these authors was superior to that of the monographers or, for that matter, to contemporary work in most areas of the world.

Although Adams, Carpenter, and Dall were not West Coast residents, they did much to summarize previous literature and describe new species in a useful and careful manner. The type specimens of nearly all of these species are extant and well labeled. Those of Adams are mainly in the Museum of Comparative Zoology at Harvard University and have been reviewed by TURNER (1956). Those of Carpenter are partly in the British Museum (Natural History) and partly in museums in North America, mainly in the United States National Museum and the Redpath Museum (PALMER, 1945, 1951, 1958, 1963; BRANN, 1966; KEEN, 1968; COAN, 1969c).

One might term the period from 1900 to 1965 the "Era of the Paleontologist and the Amateur." The thorough and comprehensive work of Carpenter and Dall in reviewing previous literature and describing new species, aided by large collections, placed West American molluscan systematics farther ahead and on firmer nomenclatural ground than that of most other areas of the world. The kind of systematic work needed, studies of geographic distribution, correlated with paleontology, had to wait until principles of biology and geology caught up with molluscan systematics. The chief professional contributions to malacology were those made by paleontologists working on Recent and fossil material, such as ARNOLD (1903), GRANT & GALE (1931), KEEN (1937, 1958b), WEAVER (1943), KEEN & BENTSON (1944), HERTLEIN & STRONG (1949-1950, 1955), and OLSSON (1961).

In this period, among the most active workers on Recent molluscan systematics was a group of amateurs in southern California, whose contributions were rather good in terms of their concepts of what constituted a species and of population and geographic variation (BURCH & BURCH, 1943; BURCH, 1945a-1945c).

Some features of the development of marine molluscan systematics are illustrated by means of the following Table of the dates of proposal of new names definitely applicable to the entire northwest American Tellinacea (new names and Pleistocene synonyms are included but not misspellings, *nomina nuda*, species described "in synonymy," nor synonyms possibly or definitely from other areas of the world, or from the Pliocene or earlier:

Dates (in 25-year periods)	Valid Taxa	Invalid Taxa
1758 - 1782	1	-
1783 - 1807	1	-
1808 - 1832	3	2
1833 - 1857	18	13
1858 - 1882	8	6
1883 - 1907	7	10
1908 - 1932	6	6
1933 - 1957	-	1
1958 - 1969 (12 years)	1	-
Totals:	45	38

It can be seen that the number of synonyms is nearly equal to the number of valid taxa (is equal to it, if one counts probable synonyms from the Pliocene or earlier). A new tellinacean species has not been discovered since 1921, the species recently described (DUNNILL & COAN, 1968) being a reinterpretation of previously known material.

Thus, what is required of West American marine molluscan systematics now is chiefly the task of analyzing previously described species and arranging them in a meaningful classification. In doing this, nomenclature must be stabilized by a thorough search for applicable names and for the type specimens upon which they were based. Taxonomists now attempt to ground their analysis of species as well as they can on a biological species concept and on a study of many specimens from a wide array of places and times. This task is best accomplished by a review of entire genera, families, or superfamilies at one time in order to understand better their members' distributions and the relationships of one species to others in the same area and in other areas and ages.

The need for a more stable nomenclature and classification of the Tellinidae is now great. For example, one researcher in southern California is working on the phylogeny of the superfamily; a worker in central California has recently completed a project on substrate relationships and feeding in *Tellina nukuloides* and *T. modesta*; another in central California has completed work on the ecology of *Macoma balthica*; someone in northern California is working on reproductive cycles of *Macoma nasuta* and *M. secta*; and a student in British Columbia has completed a project on the benthic ecology of eight species of *Macoma*. In the present study, the need for changing the names of several species on which these workers have already published is pointed out.

**Principles and Assumptions.** - I have attempted to rely on a biological species concept, one with multiple defining factors, as best outlined by MAYR (1963, 1969). This concept uses as its chief basis the cohesion of co-adapted gene complexes, established by continuous interbreeding within the area occupied by populations of animal species. This,

together with the disruptive effect of selection, enhancing differences between closely related species in their areas of overlap, results in a degree of continuity within species and a degree of discontinuity between them that would not be present were there not such forces.

From the morphological standpoint, the problem of recognizing such biological species in the coastal marine environment seems to be a simpler one than on land. This may be true because one is dealing with distribution along a line, however convoluted, rather than within a complex area, and because there may be a relatively higher degree of panmixis, randomness of interbreeding over a large area, than is generally present on land (MAYR, 1963: 316). Such panmixis may be especially characteristic of a majority of clams, most of which have pelagic larvae (THORSON, 1950, 1961). The importance of pelagic gametes in this regard is unknown.

With these concepts in mind, I looked for continuously occurring, morphologically similar populations throughout the range of presumed species but also expected some degree of variation in morphology along the range and some degree of variation among members of populations of one area. I also expected morphologically similar species inhabiting the same range but differing ecologically.

Because of the presumed degree of panmixis present in the coastal environment, I anticipated making little use of the concept of subspecies (MAYR, 1963: 348), which has been misused in marine mollusks for the expression of intra-population variation, as explained by McLEAN (1966). I find myself somewhat in disagreement with MAYR (1963) on the matter of fossil subspecies and believe one should go to some lengths to avoid using them. The problem does not often arise, however, because of the gaps in our knowledge of the fossil record.

The nature of the process of analysis and classification of relatively large taxonomic groups requires a review of many specimens in widespread collections. As a result, such a study cannot be a detailed one in comparative morphology. Decisions had to be made quickly on the identity of museum specimens, although some review and reexamination were utilized where difficulty was encountered. In attempting to achieve systematic order in this manner, I tried to be careful not to "force" order where there was unsatisfyingly little. I have outlined cases in which, with methods appropriate to analysis and classification, I cannot be certain where to draw the lines between species. Such problems require the still more careful studies of comparative morphology and ecology, dealing with small species-groups only.

It is not always possible to do a thorough job of systematic revision of supra-specific taxa in connection with a review of the present sort, because one is dealing with the

limited number of species of a single area. For example, the arrangement used here above the species-level within the Tellinidae is provisional only. The magnitude of review required for a more complete generic revision of this family would be a large task in itself.

What one can and should do, on the other hand, is to arrange species within the fauna studied into species-groups and attempt to relate these groups to Cenozoic forms of the area covered and to the Recent and Quaternary faunas of adjacent areas. One cannot expect to be able to carry this out in the same detail that is appropriate to the analysis of species of the Recent fauna.

However, one can make a number of comparative statements and from these form hypotheses about the biogeography and evolution of the species. For instance, it has been possible in the Tellinidae to suggest which species-groups have had a long history on our coast and which have arrived from elsewhere. It has often been possible to suggest areas of the world from which such species have come, or, in some cases, areas that have been recipients of West American species. Sometimes these geographic statements bring insights into isolating factors that may have resulted in speciation.

#### ACKNOWLEDGMENTS

It would be impossible to conduct a project of the present sort, one which synthesizes a great deal of information from many sources and bridges biology and geology, without the help of many persons, such as the curators of museums throughout the world, amateurs who have provided data from their collections, and colleagues who have given me advice on difficult questions.

Many of these almost two hundred individuals and institutions that have been of assistance in this research will be apparent from the taxonomic portion of the text. Several persons, however, deserve special recognition. Dr. Myra Keen of Stanford University photographed many type specimens for me on her visits to the British Museum (Natural History) and provided guidance and encouragement. Mr. Barry Roth of the California Academy of Sciences made the line drawings. Thanks are also extended to Drs. Donald P. Abbott and George S. Myers of Stanford University, Dr. Warren O. Addicott of the United States Geological Survey, Dr. Kenneth J. Boss of Harvard University, Mr. Robert M. Dunnill, formerly of the University of Victoria, Drs. Leo G. Hertlein and Victor A. Zullo of the California Academy of Sciences, Dr. Joseph Rosewater of the United States National Museum, Dr. Norman Tebble of Oxford University, and

Mr. D. L. F. Sealy of the British Museum (Natural History). This research was supported by U. S. National Institutes of Health Predoctoral Fellowship 4-F-1-GM-22925 from the National Institute of General Medical Sciences, and publication costs were partially financed by a grant from the Theodore Roosevelt Memorial Fund of the American Museum of Natural History.

#### METHODS AND FORMAT

**Methods.** – The present review covers those species of the Tellinidae inhabiting the northwest coast of America, from the Arctic coast of Alaska to the middle of the outer coast of Baja California – the beginning of the Panamic province – at about the latitude of the border between Baja California Norte and Baja California Sur, Isla Cedros, and Punta Eugenia. Species occurring in this area and in the Panamic province but not further northward were omitted, as these have been discussed by KEEN (1958b) and OLSSON (1961).

The first step in this project was a search for potentially applicable species-level names and their synonyms by canvassing literature on the Recent fauna and the Tertiary as far back as the Pliocene.

The original description of each taxon was located and the exact date of publication established as carefully as possible. A relatively thorough but non-critical list of references was accumulated, which included all of the significant accounts. Xerox copies or photocopies of the most important of these accounts were interleaved or pasted into notebooks.

An attempt was then made to locate the type specimens which formed the basis for each name. In this endeavor, I was greatly aided by visits made by Dr. Myra Keen to the British Museum (Natural History) and by the cooperation of many curators and museums. During my two visits to the Museum of Comparative Zoology at Harvard University and the United States National Museum, I spent a large portion of my time locating, verifying, and photographing type material. The same was true of some other museums I visited. When necessary, I selected one specimen from among the type material to serve as lectotype. Of the many type specimens searched for, I was able to study photographs of all except those of Middendorff and Schrenck in Leningrad, U. S. S. R.

Photographs of type or otherwise interesting material made possible continuing reexamination and reconsideration. In my own photographic work I used an Asahi Pentax "Spotmatic" single lens reflex camera, extension tubes, Kodak "Panatomic-X" film, and whatever combina-

tion of sunlight, roomlight, spotlights, and desk lamps was available in each institution. Most of the film was commercially developed and printed. Prints were filed in the notebooks in plastic folders. Both internal and external views of valves were photographed when possible.

At the same time I was gathering information about type specimens, I began to go through the tellinaceans in each of the major collections, maintaining complete records of every lot studied as to tentative identification, catalogue number, approximate number of specimens, locality, and whatever data were available on habitat. Notes were also made about unusual specimens, maximum sizes, and variation among the specimens. In the Tellinidae about 3500 lots were examined. A special effort was made to locate the sources of published records of rare species, isolated occurrences, and range limits.

The decision-making process with regard to species and synonyms involved examination of photographs of and notes about type specimens, review of lists of specimens studied, and consideration of conclusions reached by previous workers, in light of the principles and limitations discussed above.

As time went on, my ideas about synonymies and distribution inevitably changed. With complete records of all material seen, it was possible to borrow specimens about which doubt had arisen. My second visits to the United States National Museum and the Museum of Comparative Zoology were necessitated chiefly by the large number of specimens that I needed to reexamine.

Most important of the collections studied was that of the United States National Museum. The West American tellinacean material in this institution was arranged in drawers as Dall had left it in about 1916.

The following is a list of important institutions in the present study, nearly all of which I visited myself. Abbreviations are as used in the text:

Academy of Natural Sciences, Philadelphia, Pennsylvania – ANSP  
 American Museum of Natural History, New York, New York  
 British Museum (Natural History), London, England – BM(NH)  
 California Academy of Sciences, San Francisco, California – CAS  
 [GTC – Geology Type Collection]  
 Hopkins Marine Station (Stanford University), Pacific Grove, California  
 Los Angeles County Museum of Natural History, Los Angeles, California – LACM  
 Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts – MCZ  
 National Museum of Canada, Ottawa, Ontario, Canada – NMC  
 Pacific Marine Station (University of the Pacific), Dillon Beach, California  
 San Diego Natural History Museum, San Diego, California – SDNHM

Santa Barbara Museum of Natural History, Santa Barbara, California – SBMNH

Stanford University, Stanford, California – SU [PTC – Paleontology Type Collection]

United States Geological Survey, Menlo Park, California – USGS

United States National Museum, Smithsonian Institution, Washington, District of Columbia – USNM

University of California at Berkeley, California – UCB

University of California at Davis, California (the author's collection, recently acquired by UC at Davis)

University of California at Los Angeles, California – UCLA

It is unfortunate that material in the Hancock Foundation, University of Southern California, was not yet in sufficient order to be useful in this study, for specimens in it will change distributional records somewhat. After a discussion with Dr. Garth of that institution, I decided that it would be best not to attempt to include even the obvious records from that collection, for to do so would be to “skim the cream” off the collection, which should be studied as a whole. It will be possible to do this in a year or two.

Material from the major private collections of the following persons was also studied: Dr. S. Stillman Berry, Redlands, California; Dr. I. McT. Cowan, Vancouver, British Columbia, Canada; Mrs. Faye B. Howard, Santa Barbara, California; Mr. Barry Roth, San Francisco, California; and Mr. Robert R. Talmadge, Eureka, California.

When decisions about species and synonyms had been made, brief diagnoses were written. These followed a descriptive formula emphasizing diagnostic characters. In the case of the genus *Macoma*, a key was written to aid in identification.

Internal details of shells have not been emphasized, but, as a first step in this regard, sketches of inside views were made of each of the species from typical, but not necessarily type, material, showing hinge structures and the positions of adductor, retractor, pallial, and cruciform muscle scars. They were not camera lucida-controlled. Representative drawings for each species are reproduced in the present report.

Most descriptive terms used are relative and require further clarification. In the future, these should be more precisely defined mathematically. Size terms used herein (large, medium, and small) are additionally defined in millimeters. Most shape terms (overall lateral shape, relative length of ends, degree of roundness and truncation) are clarified by the drawings and photographs of each species. As an example of the meaning of “flattened” or “compressed,” one may take *Tellina idae*, which measures 5.2 times as long as its diameter and 3.2 times as wide as its diameter. *Macoma obliqua*, described as “inflated,”

measures 2.6 times as long as its diameter and 1.9 times as wide as its diameter. "Thin" may be defined as "easily broken by careless handling." A thick shell is one broken only with considerable effort.

Localities were plotted on outline maps so that isolated occurrences and range records could be double-checked. West American Coast Pilots of Arctic Alaska through Panama (Hydrographic Office publications 10, 11, and 26; United States Coast Pilots 7, 8, and 9), United States Geological Survey state maps of Alaska, Washington, Oregon, and California, Canadian Geological Survey map MCR 3 of British Columbia, and the American Automobile Association map of Baja California, proved especially useful in plotting localities. It was necessary to obtain the original data lists from the *Albatross* collections (especially TOWNSEND, 1901), because sometimes localities listed on USNM labels for particular stations proved to be in error. For range data, I relied almost entirely on material I examined myself, although I have included a few recently published distributional data on specimens I have not seen when I felt there was little question about their accuracy and when they significantly supplemented other records.

When northwest American species have been reported from other coasts, I have not given distributional data in detail, and have relied chiefly on recently published accounts and figures, such as those of KIRA (1962) and HABA (1964) on Japan, GOLIKOV & SCARLATO (1967) on Siberia, HABA & ITO (1965) on northern Japan, Siberia, and the Bering Sea, SOOT-RYEN (1958) and OCKELMANN (1959) on Greenland and the North Atlantic. For north-west American species that have been reported from the Panamic province, I have taken distributional information mainly from KEEN (1958b) and OLSSON (1961).

Ecological data on the Tellinidae have been gleaned from the labels of specimens studied, from the as yet only partially published thesis of DUNNILL (Master of Science, Department of Biology, University of Victoria, 1968) (DUNNILL & ELLIS, 1969), and from the published accounts of BURCH (1945a-1945c), SOOT-RYEN (1958) and OCKELMANN (1959). There are a few other published data in the form of benthic studies and the like, but it is time-consuming to search for these and determine the authenticity of the identifications. This is more properly the task of a benthic ecologist working on a few selected species. Depths are reported in meters, and a conversion table from fathoms to meters was constructed with the use of a computer.

The problem of citing the paleontologic range of species covered in this report proved to be a greater one than anticipated. The literature on the Cenozoic formations of West America is very large, and there remain many un-

solved stratigraphic problems. Little would be accomplished by merely listing records from earlier than the early Pleistocene. Many of these records may be in error, and as many taxonomic problems must be solved for fossil species as for Recent ones. It became apparent from the volume of literature and from the number of described species that a major review of fossil Tellinacea is now needed and, indeed, that a review would probably yield much useful information on stratigraphy and the evolution of this superfamily. Such a review must start from a study of type specimens and a review of material from which published records were made. Material must be interpreted in light of the latest insights into stratigraphy and systematics, and workers will have to take into account the paleontology of the entire northern Pacific basin and migratory routes into it and out of it during the Cenozoic.

In many cases, I have suggested species from the Pliocene or earlier that may either be regarded as synonymous with or ancestral to Recent species, and for some I have hypothesized evolutionary pathways. The outline is not thorough but goes beyond anything yet in print. The evaluation of these earlier species-level names was aided considerably by the major reviews of WEAVER (1943) and KEEN & BENTSON (1944).

The literature on the late Pleistocene has been thoroughly and critically reviewed in light of the synonymies proposed for Recent species. In some cases I have re-examined specimens, although most records were taken at face value. More re-examination should be made. I also covered papers on formations considered to be early Pleistocene, especially those of the San Pedro area, California. I have discussed the literature on the Saugus part of the "Fernando group" and the Santa Barbara formation but have omitted specific mention of other formations thought to border on the Plio-Pleistocene boundary, such as the Pico portion of the "Fernando group," the San Diego formation, and the Merced formation. Major recent accounts on the Pleistocene are WAGNER (1960) on southwestern British Columbia, ADDICOTT (1966) on central California, VALENTINE (1961) and VALENTINE & MEADE (1961) on southern California and northern Baja California.

**Format.** — The present format departs somewhat from that used by other recent workers. The innovations employed may be especially well suited to the presentation of a study of this sort.

(1) The applicable synonymous species-level names are listed in chronological order, with the name in use listed first and "first revisions" indicated. Under each name are listed accounts published under those names and also accounts of type material pertinent to each (even if the



latter were published under other synonymous names). These accounts are listed in chronological order with major changes in generic or subgeneric allocation indicated in brackets following the account in which they were first employed. It is to be assumed that nearly all following accounts used the same name combinations. Other pertinent comments are also included in brackets.

The works listed do not represent a complete catalogue of literature, but are the major ones concerning living and fossil northwest American material, especially those containing previously unpublished information and taxonomic innovations. Some recent foreign papers are cited. Not included are books written largely for amateurs nor general works on marine biology.

Aside from the standard taxonomic conventions and abbreviations (the latter are listed at the end of this section), a few special conventions are used in the synonymies. For instance, "not of's" are listed first in cases of misidentification, but last in cases of homonymy. Numbers following dates (as 1851: 27) are page numbers.

(2) The type material pertinent to the valid name and its northeastern Pacific synonyms is discussed; type material of other nominal species is mentioned when it is important to the present study.

Measurements given are of the greatest lengths of type specimens. When type material is no longer extant the dimensions from original accounts or of original illustrations are given. (In most early accounts the figures were printed at natural size without special indication.) Photographs of type specimens or original illustrations are included.

(3) Type localities of the various nominal species are given. There seems little reason to restrict previously broad type localities (such as "California") or to designate type localities for species originally described without them (such as *Leporimetis obesa*) unless it is necessary to do so for nomenclatural reasons. This is usually done in connection with the definition of subspecies (MAYR, 1969). The designation of lectotypes for Carpenter's species restricts the type locality to one of his several original localities. The original collector is also cited and sometimes major collections are mentioned when this clarifies the history of the specimens.

(4) A nomenclatural commentary may be given to explain nomenclatural complications not made clear in the synonymy or in the discussion of type material.

(5) Description. A short diagnosis of each species is given, which emphasizes distinguishing characters. Internal details are not discussed in detail but are illustrated with drawings. Photographs of specimens other than type material may be included.

(6) Geographic Distribution and Ecology. The major end-points of the range are given, together with references to the specimens that form their bases. The intermediate range data are summarized.

The sources of ecologic information on each species other than from museum labels or personal experience are indicated. I mention also the approximate number of lots examined.

(7) Geologic Distribution and Biogeography. The final section is a summary of paleontologic records from the published accounts. I have not listed all Pleistocene records, but generally have given only the end-points and indicated the published accounts that form their bases. This is followed by an account of the seemingly related fossil species from earlier than the Pleistocene and related living species in other provinces.

References are included under "Literature Cited" for all genera, species, and papers mentioned.

Conventions, symbols, and abbreviations used, other than those for museums listed above, are as follows:

<i>cf. (conferre)</i>	- to be compared to, "probably identical to"
<i>ex (Gray) MS</i>	- from the manuscript name of (Gray)
ICZN	- International Commission on Zoological Nomenclature, or International Code of Zoological Nomenclature (STOLL, <i>et al.</i> , 1964)
"in synonymy"	- a name proposed in the synonymy of another and therefore not available
m	- meter(s)
mm	- millimeter(s)
<i>nomen dubium</i>	- a name representing an unidentifiable taxon
<i>nomen nudum</i>	- an unavailable name lacking any description, definition, or other indication
not, not of	- as in the case of homonyms or misidentifications
pair	- the two valves of one specimen
USFC	- United States Fish Commission ( <i>Albatross</i> ) station number

## SYSTEMATIC ACCOUNT

### Family TELLINIDAE Blainville, 1814

Within the Tellinacea this family is that most highly evolved for feeding on bottom deposits, although not all species rely solely on this food source; some also filter feed. YONGE (1949) reviewed the functional morphology of the Tellinidae, considering also the evolutionary relationships of the superfamily. BOSS (1966) in a recent, significant account on the Tellinidae reviews much of the previous anatomical and functional literature.

The Tellinidae may be defined as those Tellinacea that are relatively elongate, inequivalve, with a posterior flex-

ure, especially in the right valve, but no conspicuous gape. The ligament is external, but not seated on a conspicuous nymph. There are two cardinal teeth in each valve, and lateral teeth may or may not be evident. The separate siphons are relatively elongate and motile compared to those in other families and can be contracted into a sheath. They contain an extra middle layer of circular muscles but do not have the rows of sensory cells characteristic of the Psammobiidae.

The outer demibranch does not overhang the inner, and there are either one or two food tracts, as contrasted to as many as three in the other families. The ctenidia are mostly flat and homorhabdic, and the ventral tips of the inner (anterior) demibranch are not inserted into a distal oral groove. The ventral mantle edge just dorso-anterior to the cruciform muscles has special folds for the collection of pseudofeces. The stomach is of "type 5" (PURCHON, 1960), in that the typhlosole enters the right caecum as well as the left. The rectum does not have the circular muscles of some other families. The heart is elongate, with an aortic bulb.

The posterior cruciform muscle is often divided, with a smaller anterior element. The sense organ associated with the cruciform muscle communicates to the outside directly, not by means of a duct.

The entire family is much in need of a thorough, world-wide revision. Until this is carried out, division of the family into subfamilies and genera should be conservative. I use only the genera *Tellina*, *Leporimetis*, and *Macoma*, with subgenera tentatively suggested for the species-groups recognized. The following quotation from KEEN (1969) with regard to the genus *Tellina* is as applicable to the entire family.

"Most modern attempts to divide *Tellina*, *s. l.*, into a number of genera, each with several subgenera, abound in inconsistencies. Evolutionary history of the family in different ocean basins seems to have resulted in many parallel forms or homeomorphs, so that subdivision on one set of characters (*e. g.*, shell outline) runs counter to that on another (*e. g.*, hinge details or musculature). A proper review being beyond the scope of the present summary, the expedient of a conservative classification is adopted herein, treating most generic taxa as subgenera of *Tellina*."

Even division of the family into two subfamilies seems premature, being based largely on the presence or absence of lateral hinge teeth. I suspect that the loss of these is polyphyletic, although most Macominae probably will be found to have bases other than the lack of lateral teeth and sculpture. They seem to be especially well adapted to and characteristic of quiet areas with fine substrates.

*Tellina* Linnaeus, 1758

[Type species: *Tellina radiata* Linnaeus, 1758, by subsequent designation of CHILDREN, 1823]

Into the genus *Tellina* are placed, pending a revision of the family, those forms with lateral hinge teeth in one or both valves, especially the right (missing in adult specimens of a few species although present in juveniles). A majority of the species are elongate, relatively compressed, conspicuously sculptured, brightly colored, and are tropical to subtropical.

(*Peronidia*) Dall, 1900a

[Type species: *Tellina albicans*, Gmelin, 1791, by original designation]

Medium to large in size (30 to 110 mm); heavy; compressed; equivalve or with left valve larger; elongate; equilateral or longer anteriorly; rounded anteriorly; pointed, truncate, twisted to right posteriorly; shell surface smooth, with fine concentric grooves or ridges, often stronger at ends of shell and in right valve; no escutcheon or lunule present; lateral teeth approximately equidistant from cardinals, weak, even absent in adults of some species, strongest in left valve and anteriorly, pallial sinuses approximately equal or slightly longer in right valve, only slightly detached from pallial line.

*Tellina* (*Peronidia*) *lutea alternidentata*  
Broderip & Sowerby, 1829

(Plate 1, Figures 1 to 3; Text figure 1)

*Tellina alternidentata* Broderip & Sowerby

BRODERIP & SOWERBY, 1829: 363

SOWERBY, in GRAY, 1839: 153; plate 44, figure 5

*Tellinea lutea* Wood, of authors, not of Wood

[not WOOD, 1828: 3; plate 1 (*Tellina* 3)]

MIDDENDORFF, 1849: 578

GREWINGK, 1850: 286 [see also DALL, 1904]

MIDDENDORFF, 1851: 258-259; plate 21, figures 2, 3

CARPENTER, 1857b: 219, 221, 223, 301

CARPENTER, 1864a: 523 [1872: 9]

SCHRENCK, 1867: 563-564

SOWERBY, 1867: plate 19, figures 97a, 97b

DALL, 1900a: 304, 322, 326; plate 4, figures 15, 16

[*Tellina* (*Peronidia*)

DALL, 1904: 116

I. OLDROYD, 1925: 169; plate 1, figure 9

GRANT & GALE, 1931: 363

BURCH & BURCH, 1943: 14

BURCH, 1945a: 9; 1945b: 16; 1945c: 30

MACGINITIE, 1959: 180

*Tellina lutea venulosa* Schrenck, of authors, not *Tellina venulosa* Schrenck

[not SCHRENCK, 1861: column 412]

[not SCHRENCK, 1867: 556-559, 972; plate 22, figures 2-5]

DALL, 1916a: 36

DALL, 1921a: 46

I. OLDROYD, 1925: 169; plate 1, figure 11

GRANT & GALE, 1931: 363

BURCH, 1945a: 9; 1945b: 16

#### Type Material:

*Tellina alternidentata* – Lost (KEEN, verbal communication).

The description and 60 mm-long figure (SOWERBY, in GRAY, 1839) are sufficient to identify the species. Plate 1, Figure 1.

*Tellina lutea* Wood (not a synonym) – Lost (KEEN, verbal communication). The original specimen was about 76 mm long. See Nomenclatural Commentary. Plate 1, Figure 2.

*Tellina venulosa* Schrenck (not a synonym) – Presumably in the Zoologische Institut, Leningrad. I have not been able to obtain information about the type material.

#### Type Localities:

*Tellina alternidentata* – Icy Cape, Arctic Alaska; voyage of the *Blossom*.

*Tellina lutea* – None given in original account, but probably from Japan.

*Tellina venulosa* – Sakhalin Island, between "Wjachtu and Choji."

#### Nomenclatural Commentary:

Considering the name "*lutea*" [Latin: yellow] and the early date of WOOD (1828), I feel confident that the original material of *Tellina lutea* came from Japan. *Tellina guildfordiae* Griffith & Pidgeon, 1833, ex Gray MS, seems to be the same thing. I have seen only a few Japanese specimens that fit this concept (USNM 343959, 228959, "C1588"; SU 13821), none from north of southern Hokkaido. Specimens from north and east of this point are pink or purple within. Japanese authors consider the yellow and pink morphological forms as distinct species (OMORI, 1966). I am here provisionally recognizing the pink, North Pacific specimens as a subspecies, *T. lutea alternidentata*. The Japanese species-name used for such northern specimens, *T. zyonoensis* Hatai & Nishiyama, 1938, is regarded as a synonym. It is possible that the present status may be retained if further study of material from northern Japan proves that populations are continuous, south to north, yellow to pink. If the two species are, indeed, separable, then West American workers can simply drop the "*lutea*" from the name.

There is a distinct species in the western Pacific, *Tellina venulosa* Schrenck, 1861. It is more curved ventrally, more produced posteriorly, and has a higher pallial sinus. It

overlaps the distribution of the above complex from Sakhalin Island south. SCHRENCK (1867) described three varieties, "*forma semisulcata*," "*var. (ubique) sulcata*," and "*var. laevigata*," which are presumably synonyms. Since none of Schrenck's type specimens have recently been illustrated, one cannot be certain that the species is on firm nomenclatural ground. Use of the name *T. venulosa* for smooth eastern Pacific specimens of *T. lutea alternidentata* is in error.

#### Description:

Large (to 110 mm); elongate; moderately inflated; heavy; left valve more convex; equilateral to slightly longer posteriorly; rounded anteriorly; pointed and truncate posteriorly; smooth or with fine concentric ridges; often worn, leaving a few concentric rings of outer shell material; periostracum heavy, greenish; pink within, sometimes with an orange hue (Plate 1, Figure 3). Other internal details as in Text figure 1.

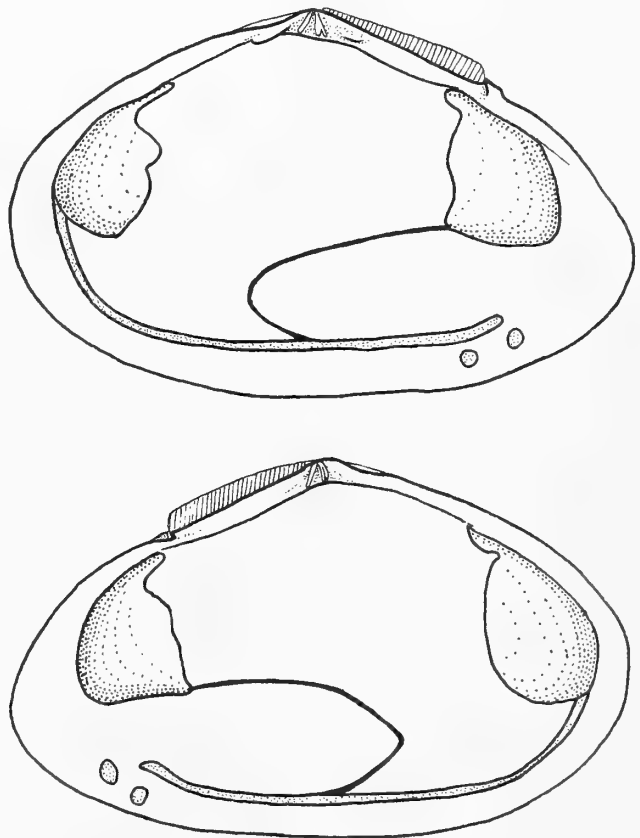


Figure 1

*Tellina lutea alternidentata*, internal view of valves  
MCZ 78910, Swikshak, Alaska; 102 mm

**Geographic Distribution and Ecology:**

Cape Krusenstern, Arctic coast of Mackenzie, Canada (BM[NH] 1860.1.23.5), Arctic coast of Alaska, along the coasts of the Bering Sea, through the Aleutian Islands as far east as Kanatak, Cook Inlet, Alaska (CAS 28932, 28933), and as far south as Hokkaido (USNM 344700). (*Tellina lutea lutea* is probably restricted to Japan, from southern Hokkaido south.) It has been taken from the intertidal area to 84 m, probably on exposed coasts, in sand.

**Material seen:** 193 West American lots.

**Geologic Distribution and Biogeography:**

This species is known in the Pleistocene of Kodiak Island (MADDREN, 1919; TWENHOFEL, 1952) and the Pliocene of Nome, Alaska (MACNEIL, MERTIE & PILSBRY, 1943). There are also records in the Miocene of Alaska. WOODRING, STEWART & RICHARDS (1941) suggest that *Tellina oldroydi* Wiedey, 1928, described from the Miocene of southern California, may be related.

*Tellina (Peronidia) bodegensis* Hinds, 1845

(Plate 1, Figures 4, 5; Text figure 2)

*Tellina bodegensis* Hinds

- HINDS, 1845: 67; plate 21, figure 2  
 MIDDENDORFF, 1849: 578-579  
 CARPENTER, 1857b: 207, 211, 219, 224, 234, 302, 349  
 CARPENTER, 1864a: 583, 600, 639, 683 [1872: 69, 86, 125, 169]  
 DALL, 1900a: 304-305 [*Tellina (Peronidia)*]  
 ARNOLD, 1903: 158, 392; plate 15, figure 7  
 PACKARD, 1918: 275, 382; plate 25, figure 5  
 OLDROYD, 1924: 52, 214; plate 41, figure 5  
 I. OLDROYD, 1925: 168; plate 44, figure 5  
 GRANT & GALE, 1931: 362, 922; plate 20, figure 13  
 BURCH & BURCH, 1943: 14, 15, 24 (text figure)  
 BURCH, 1945a: 4 (text figure), 8; 1945b: 16; 1945c: 30  
 KEEN, 1966b: 267

*Tellina (Peronidia) santarosae* Dall

- DALL, 1900a: 305, 321, 325; plate 3, figure 6; plate 4, figures 1, 2  
 I. OLDROYD, 1925: 168  
 BURCH & BURCH, 1943: 15  
 BURCH, 1945a: 8, 9; 1945b: 16; 1945c: 30

**Type Material:**

- Tellina bodegensis* – BM(NH) 1874.12.11.372, holotype, pair, about 33.5 mm. Plate 1, Figure 4  
*Tellina santarosae* – USNM 60212, lectotype herein, left valve, figured by Dall, 51.8 mm; USNM 663881, paratotypes, one pair and one valve. Plate 1, Figure 5.

**Type Localities:**

- Tellina bodegensis* – “Russian Bodegas” [area north of Bodega Bay], California; R. B. Hinds, 13 m, in sand.  
*Tellina santarosae* – Santa Rosa Island, California; S. Bowers.

**Nomenclatural Commentary:**

Southern specimens of this species differ, on an average, from northern material, but I do not think the generally flatter shape, thinner shell, and minor sculptural differences warrant the subspecific recognition suggested by BURCH (1945a).

**Description:**

Medium-sized (to 60 mm); elongate; flattened; adults thick; longer, rounded anteriorly; pointed, slightly trun-

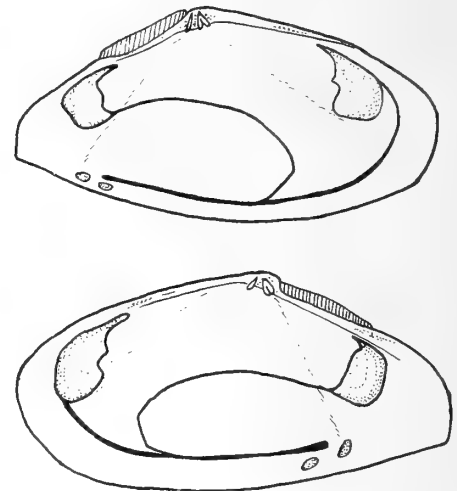


Figure 2

*Tellina bodegensis*, internal view of valves  
 Roth collection 1286, Monterey, California; 53.8 mm

**Explanation of Plate 1**

Figure 1: *Tellina lutea alternidentata*. Original illustration of *Tellina alternidentata*; 60 mm

Figure 2: *Tellina lutea lutea*. Original illustration of *Tellina lutea*; specimen was 76 mm

Figure 3: *Tellina lutea alternidentata*. Specimen illustrated by SOWERBY (1867: pl. 19, fig. 97a), BM(NH) 1874.12.11.364; 76 mm

Figure 4: *Tellina bodegensis*, holotype, BM(NH) 1874.12.11.372; 33.5 mm

Figure 5: *Tellina bodegensis*. Lectotype (herein) of *Tellina santarosae*, USNM 60212; 51.8 mm



Figure 1



Figure 2

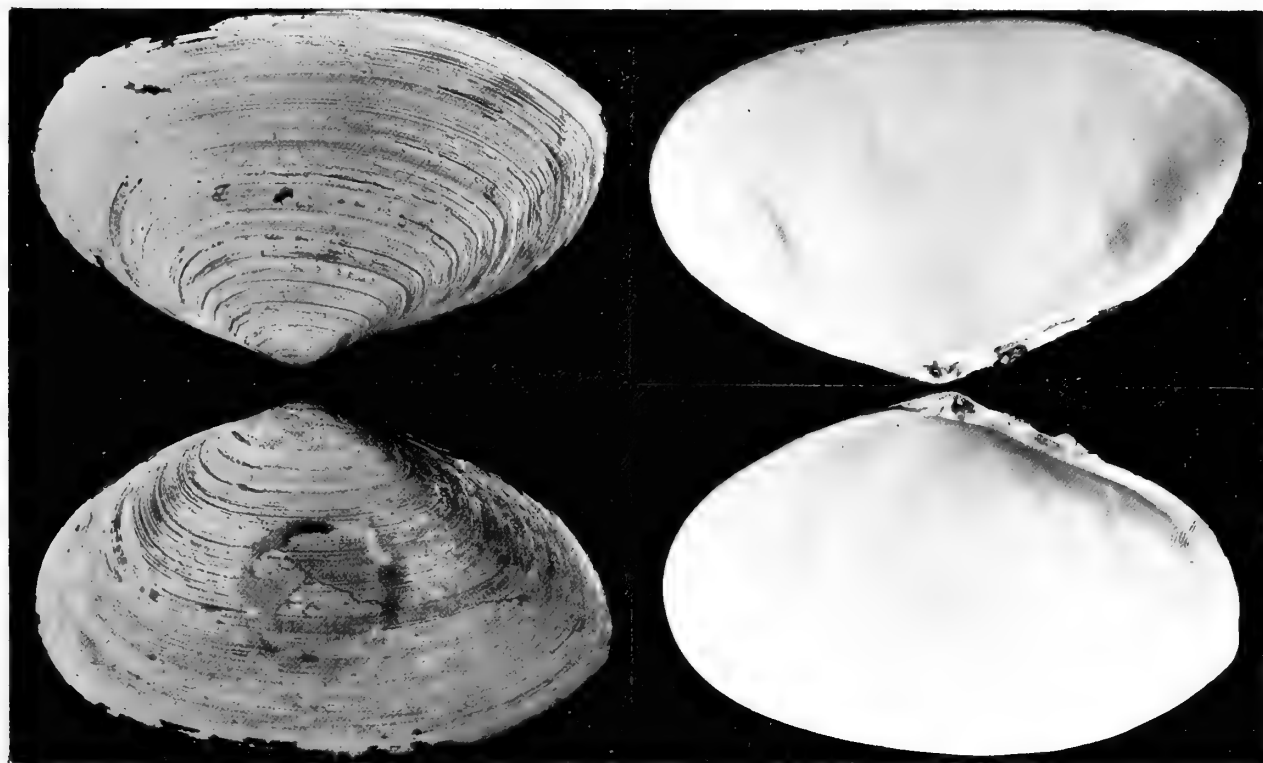


Figure 3

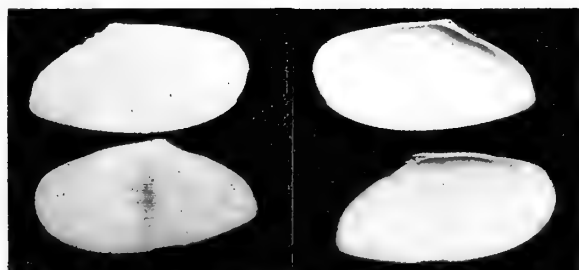


Figure 4



Figure 5



cate posteriorly; sculpture of heavy, closely spaced concentric ribs; white, sometimes with a slight yellow or pink hue internally. Other internal details as in Text figure 2.

#### Geographic Distribution and Ecology:

La Paz Bay, Graham Island, Queen Charlotte Islands, British Columbia (COWAN, 1964), to Rosario, Baja California Norte (Berry Collection 13491), with numerous intermediate records; possibly as far south as Bahía Magdalena, Baja California Sur (SU 284/8). Specimens at Stanford (SU 284/7) from La Paz, Baja California Sur, probably represent a labeling error. It is found in the intertidal area to 96 m, mainly on open coast, but occasionally in bays, in sand (BURCH, 1945a; SMITH & GORDON, 1948). MACGINITIE (1935) reports that this species comes to the surface if exposed by the tide for too long a time. Its abundance on exposed beaches indicates that it may be a dominant in a *Tellina* community, similar to the *Tellina* communities described by THORSON (1957).

**Material seen:** 164 lots.

#### Geologic Distribution and Biogeography:

This is one of the several species of tellinaceans that has a long and well documented geologic history. It is known in the late Pleistocene from Cayucos, California (VALENTINE, 1958), to Bahía Magdalena, Baja California Sur (JORDAN, 1924, 1936), with many intermediate records. There are records in the early Pleistocene of the San Pedro area, California (ARNOLD, 1903; T. OLDROYD, 1925; BURCH, 1947; VALENTINE & MEADE, 1961), in Californian formations transitional between the Pliocene and the Pleistocene, in the Pliocene of California, the Miocene of Oregon and California, and the Oligocene of Washington. *Tellina oregonensis* Conrad, 1848, described from the Miocene of Oregon, may be ancestral and seems closely related to the following: *T. emacerata* Conrad, 1849, from the Miocene of Oregon; *T. aragonia* Dall, 1909, from the Miocene of Oregon; *T. clallamensis* Reagan, 1908, from the Miocene of Washington; and *T. eugenia* Dall, 1909, from the Oligocene of Washington.

I know of no Asian or Caribbean homologue.

(*Tellinella*) MÖRCH, 1853,  
ex Gray MS

[Type species: *Tellina virgata* Linnaeus, 1758, by subsequent designation of STOLICZKA, 1870]

Medium to large in size (30 to 80 mm); medium in thickness and degree of inflation; equivalve or with left valve slightly larger; elongate; approximately equilateral; rounded anteriorly; pointed, truncate, and twisted to right posteriorly; shell surface with medium to fine concentric ribs or lamellae; oblique lamellae present on ante-

rior end in some species; sculpture strongest in right valve; posterior end with one or two strong radial ribs; escutcheon and lunule present in some species; some ligamental material present anterior to beaks; lateral teeth strong, strongest in right valve; anterior lateral closest to cardinal complex; pallial sinuses long, reaching almost to anterior adductor muscle scar, approximately equal in size, slightly to moderately detached from pallial line.

*Tellina (Tellinella) idae* Dall, 1891

(Plate 2, Figure 6; Text figure 3)

*Tellina idae* Dall

DALL, 1891: 183-185, 191; plate 6, figure 3, plate 7, figures 1, 4

DALL, 1900a: 301, 326; plate 4, figures 10, 11

ARNOLD, 1903: 158-159, 392; plate 15, figure 6 [*Tellina (Angulus)*]

I. OLDROYD, 1925: 164-165; plate 14, figure 4

GRANT & GALE, 1931: 358, 922; plate 20, figures 12, 14a, 14b

BURCH & BURCH, 1943: 10-11

BURCH, 1945a: 5-6; 1945b: 16 [*Tellina (Tellinella)*]

#### Type Material:

USNM 120098, holotype, pair, 46.9 mm; Plate 2, Figure 6

#### Type Locality:

Long Beach-San Pedro area, California; Mrs. G. L. Trobridge; I. S. Oldroyd Collection

#### Nomenclatural Commentary:

None necessary.

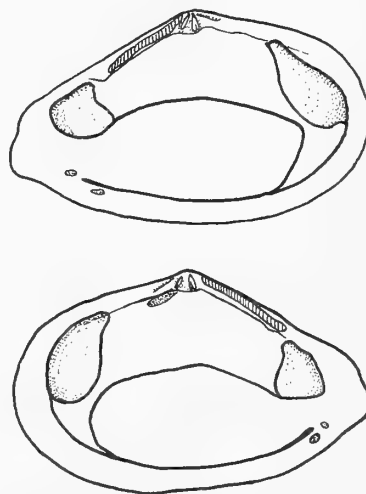


Figure 3

*Tellina idae*, internal view of valves  
SU 274, San Pedro, California; 59 mm

**Description:**

Medium-sized (to 60 mm); elongate; flattened; thin; approximately equilateral; rounded anteriorly; pointed posteriorly, with a strong fold and escutcheon; sculpture of well-spaced concentric lamellae; white inside and outside. Other internal details as in Text figure 3.

**Geographic Distribution and Ecology:**

Santa Barbara, California (UCB 2390), to San Diego, California (SDNHM 13052; SU 274/1) with several intermediate records. It is found from the intertidal area in bays (only before pollution?) to 91 m offshore, in sand.

**Material seen:** 100 lots.

**Geologic Distribution and Biogeography:**

*Tellina idae* is more common as a fossil than it is in the living fauna. In the late Pleistocene it has been recorded from Santa Monica, California (HOOTS, 1931; GRANT & GALE, 1931; VALENTINE, 1956), to Bahía San Quintín, Baja California Norte (ORCUTT, 1921a; JORDAN, 1926; MANGER, 1934) with several intermediate records. In the early Pleistocene, there is a record in the northwestern portion of the Los Angeles basin, California (RODDA, 1957, as "cf."), and one in the San Pedro area, California (GRANT & GALE, 1931). In southern California it has frequently been reported from formations transitional between the Pliocene and Pleistocene and from the Pliocene.

There are several records of the species in the Miocene, and it may be related to, if not identical to, *Tellina insurana* Hanna, 1924 (new name for *T. tenuistriata* Davis, 1913, a homonym, also unnecessarily renamed *T. davisii* Salisbury, 1934), from the Miocene of central California, and *T. tenuilineata* Clark, 1918, from the Oligocene of central California. *Tellina englishi* Clark, 1915, from the Miocene of central California is also related but more elongate.

I know of no similar Asian or Caribbean species.

(*Cadella*) Dall, Bartsch & Rehder, 1938

[Type species: *Tellina lechriogramma*, Melvill, 1893, by original designation]

Small in size (under 20 mm); thick; rather inflated; approximately equivalve; ovate to ovate-elongate; longer, narrowly rounded anteriorly; rounded, only slightly truncate, not conspicuously twisted posteriorly; shell surface smooth or with conspicuous concentric sculpture; no lunule or escutcheon present; right valve with two cardinals; left valve with posterior cardinal lamellar or obscure; right valve with two conspicuous laterals, approximately equidistant from cardinals; left valve without laterals; pallial sinuses deep, approximately equal in size, only partially confluent with pallial line; usually tinted pink.

This subgenus is close to *Acorylus* Olsson & Harbison, 1953 (type species: *Tellina suberis* Dall, 1900b). Boss (1966) places the Caribbean species *T. gouldii* Hanley, 1846, in *Acorylus*.

*Tellina (Cadella) nuculoides* (Reeve, 1854)

(Plate 2, Figures 7, 8; Text figure 4)

*Donax nuculoides* Reeve

REEVE, 1854: plate 8, figure 59

SOWERBY, 1866a: 312; plate 4, figure 105

TRYON, 1869: 114

BERTIN, 1881: 117 [as "nuchloides"]

*Maera salmonea* Carpenter

CARPENTER, 1864a: 627, 639 [1872: 113, 125]

CARPENTER, 1864b: 423 [1872: 235]

SOWERBY, 1867: plate 29, figure 155 [*Tellina*]

DALL, 1900a: 302-303 [*Tellina (Moerella)*]

ARNOLD, 1903: 157, 388; plate 13, figure 7

PACKARD, 1918: 276; plate 25, figures 3a, 3b, plate 46

OLDROYD, 1924: 51; plate 41, figures 3a, 3b

I. OLDROYD, 1925: 165-166; plate 44, figures 3a, 3b

GRANT & GALE, 1931: 359

BURCH & BURCH, 1943: 11

BURCH, 1945a: 5-6; 1945b: 16, 21; 1945c: 30

PALMER, 1958: 15, 22, 26, 32, 34, 38, 48, 105-106, 338; plate 13, figures 17-19

**Explanation of Plate 2**

Figure 6: *Tellina idae*, holotype, USNM 120098; 46.9 mm

Figure 7: *Tellina nuculoides*. Original illustration of *Donax nuculoides*; 17 mm

Figure 8: *Tellina nuculoides*. Lectotype (herein) of *Maera salmonea*, USNM 73449; 13.1 mm

Figure 9: *Tellina meropsis*, lectotype (herein), USNM 123410; 14.6 mm

Figure 10: *Tellina meropsis*. Lectotype (herein) of *Angulus gouldii*, USNM 13652; 13 mm

Figure 11: *Tellina meropsis*. Lectotype (herein) of *Tellina paziana*, USNM 108580; 9 mm

Figure 12: *Tellina carpenteri*. Lectotype (herein) of *Angulus variegatus*, USNM 15467b; 12.7 mm

Figure 13: *Tellina carpenteri*. Holotype of *Tellina arenica*, CAS GTC 9233; 24.6 mm



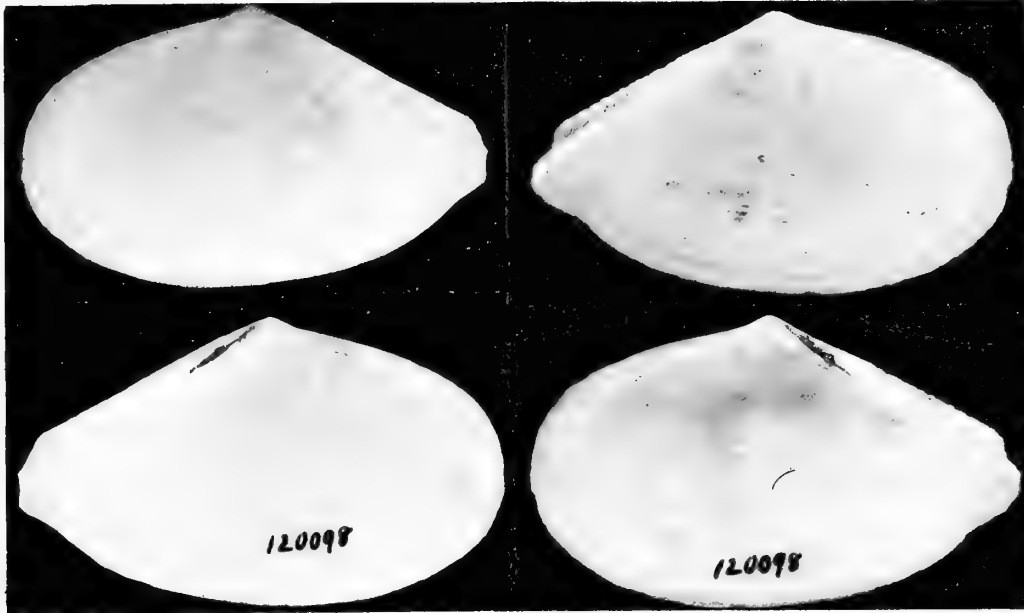


Figure 6

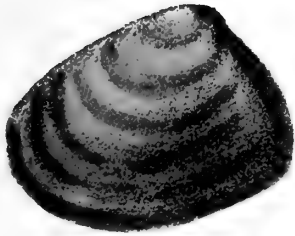


Figure 7

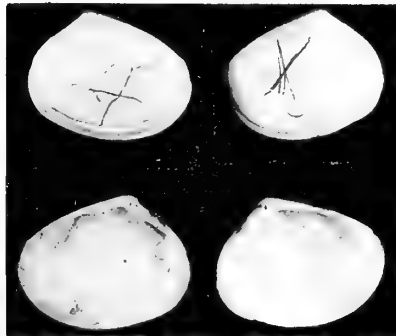


Figure 8

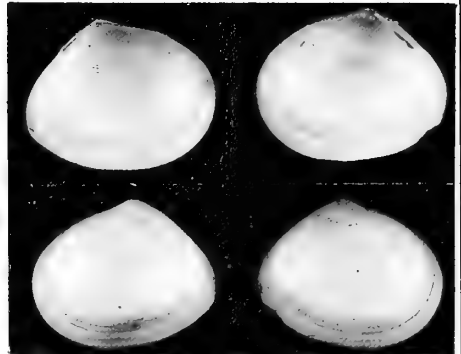


Figure 9

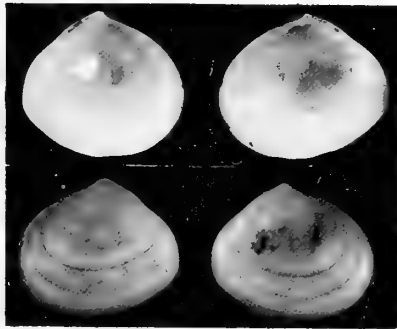


Figure 10

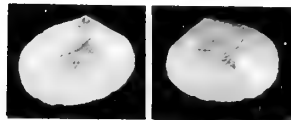


Figure 11



Figure 12

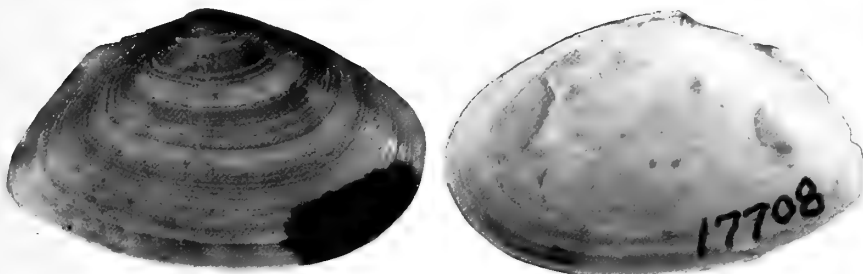


Figure 13



**Type Material:**

*Donax nuculoides* – Lost. Reeve's description and 17 mm-long figure are sufficient to identify the species. Plate 2, Figure 7.

*Maera salmonea* – USNM 73449, lectotype herein, pair, 13.1 mm; USNM 663882, paralectotypes, 4 valves.

PALMER (1958) suggested that the specimen should be regarded as a neotype. However, it is certainly original material and bears Carpenter's initials. The fact that the word "type" was not written on the label does not mean that it was not from among the originally examined specimens. Plate 2, Figure 8.

**Type Localities:**

*Donax nuculoides* – "Russian Bodegas" [area north of Bodega Bay], California; R. B. Hinds.

*Maera salmonea* – Either Vancouver Island, British Columbia, or Neah Bay, Washington. The specimen is probably from the latter locality and would have been collected by J. G. Swan.

**Nomenclatural Commentary:**

It is unfortunate that workers have missed Reeve's name for so long, but in spite of the fact that the type specimen is lost, there is little doubt as to its identity.

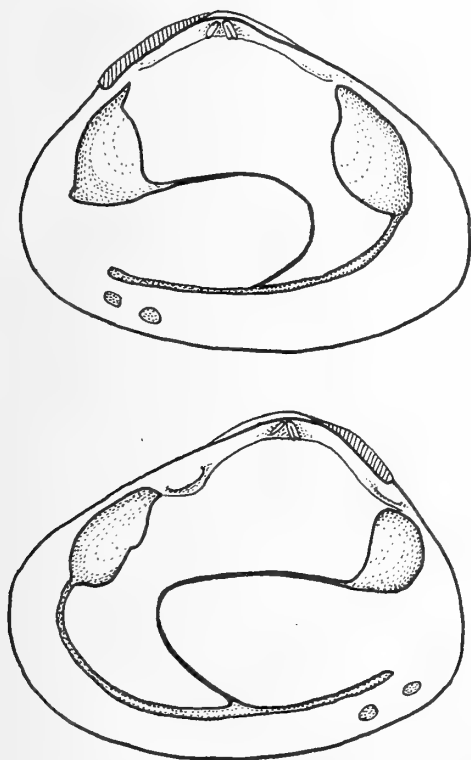


Figure 4

*Tellina nuculoides*, internal view of valves  
MCZ 88265, Vancouver Island, British Columbia; 12.6 mm

**Description:**

Small (to 19 mm); ovate; moderately inflated; thick for size; longer, rounded anteriorly; rounded, slightly truncate posteriorly; posterior dorsal margin rather straight; smooth; often covered with a shiny greenish periostracum; externally reddish, with reddish concentric lines; internally reddish. Other internal details as in Text figure 4.

**Geographic Distribution and Ecology:**

Attu Island, Aleutian Islands (USNM 108633), and Saint George Island, Pribiloff Islands (USNM 217129), through the Aleutian Islands, southern Alaska, British Columbia, Washington, Oregon, California, and south to Islas Los Coronados, Baja California Norte (UCLA 20458), with many intermediate records. It occurs from the intertidal area to 73 m, in protected areas, in a variety of bottom types (rock, gravel, sand, and mud), but is most common on coarse sand. It is a suspension feeder (MAURER, 1967a-1967c, 1969). Talmadge (in correspondence) observed it crawling in tight curves in sand at low tide.

**Material seen:** 118 lots.

**Geologic Distribution and Biogeography:**

*Tellina nuculoides* is known in the late Pleistocene from Cayucos, California (VALENTINE, 1958), to Huntington Beach, California (VALENTINE, 1959), with three intermediate records. In the early Pleistocene, there are records from the San Pedro area, California (ARNOLD, 1903; T. OLDRYD, 1925; BURCH, 1947). I would question the Californian Miocene records.

There is a closely related species in Japan, *Tellina lubrica* Gould, 1861, which differs in being longer anteriorly and attaining a larger size. The type of the latter was re-discovered in the course of the present study (USNM 1688).

(*Angulus*) Megerle von Mühlfeld,  
1811

[Type species: *Tellina lanceolata* Gmelin, 1791,  
by subsequent designation of GRAY, 1847]

Small to medium in size (under 40 mm); thin; inflated to compressed; equivalve or with left valve more convex; oval to elongate; almost equilateral to longer anteriorly; broadly to sharply rounded anteriorly; pointed to rounded and broadly truncate posteriorly; moderately twisted to right posteriorly; shell surface smooth or with fine concentric sculpture, strongest in right valve; no escutcheon or lunule present; lateral teeth conspicuous in right valve only, anterior one close to cardinals, posterior weaker and

more distant; often with internal anterior radial strengthening ribs, strongest in left valve; pallial sinuses long, slightly longer in right valve, confluent with pallial line along most of their length.

Workers have placed West American species in the subgenus *Moerella* Fischer, 1887. For the same reasons outlined by Boss (1968) with regard to Atlantic species, I use the subgenus *Angulus* for similar West American species. *Tellina (Angulus) meropsis* fits least well into this subgenus.

*Tellina (Angulus) meropsis* Dall, 1900  
(Plate 2, Figures 9 - 11; Text figure 5)

- Tellina (Moerella) meropsis* Dall  
DALL, 1900a: 303, 317, 325; plate 3, figure 1  
I. OLDROYD, 1925: 166  
GRANT & GALE, 1931: 359, 908, 922; plate 14, figures 9a, 9b, plate 20, figures 9a, 9b  
BURCH & BURCH, 1943: 11-12  
BURCH, 1945a: 6; 1945b: 16; 1945c: 30  
KEEN, 1958b: 170; figure 389  
OLSSON, 1961: 401-402, 542; plate 69, figures 9, 9a  
*Angulus gouldii* Carpenter, ex Hanley MS, not *Tellina gouldii* Hanley  
CARPENTER, 1864a: 639, 665 [1872: 125, 151]  
CARPENTER, 1865b: 132-133 [1872: 300-301]  
PALMER, 1958: 105 [under *Tellina (Moerella) meropsis*] [not HANLEY, 1846: 272; plate 56, figure 26]  
*Tellina (Moerella) paziana* Dall [First reviser: OLSSON, 1961]  
DALL, 1900a: 303, 318, 325; plate 3, figure 8  
KEEN, 1958b: 172-173; figure 401

#### Type Material:

- Tellina meropsis* - USNM 123410, lectotype herein, pair, 14.6 mm; USNM 663883, paralectotypes, 3 pairs. The specimen figured by DALL (1900a) was from another lot. Plate 2, Figure 9.  
*Angulus gouldii* - USNM 13652, lectotype herein, pair, 13 mm. The lots from San Diego are not in the USNM collection. PALMER (1958) did not look for the type of this species on the grounds that this was merely a misuse of Hanley's name. However, Carpenter was unaware of Hanley's description and fully described the species as a new one, so it must be regarded as being of Carpenter (with

a type specimen) and as a homonym. Plate 2, Figure 10.  
*Tellina paziana* - USNM 108580, lectotype herein, figured right valve, 9 mm; USNM 663877, paralectotype, left valve. Plate 2, Figure 11.

#### Type Localities:

- Tellina meropsis* - San Diego, California; I. S. Oldroyd.  
*Angulus gouldii* - Isla Cedros, Baja California Norte; W. O. Ayres  
*Tellina paziana* - Southwest of Punta San Lorenzo, north of La Paz, Baja California Sur; USFC 2823, in 48 m, among broken shells.

#### Nomenclatural Commentary:

*Tellina paziana* was based on juvenile specimens of *T. meropsis*, as concluded by OLSSON (1961). Misidentified specimens of *T. meropsis* with slight concentric ribbing account for Californian records of the Panamic *Tellina (Merisca) reclusa* Dall, 1900a.

#### Description:

Small (to 20 mm); ovate; inflated; longer, rounded anteriorly; truncate posteriorly, with a low fold; smooth or with traces of fine concentric lamellae; white inside and outside. Other internal details as in Text figure 5.

#### Geographic Distribution and Ecology:

Pacific Grove, California (Berry Collection 3305), probably as a result of larval settlement in an especially warm year, as the species has not been taken in the Monterey area since Carpinteria, California (SU 43378), throughout southern California, the outer coast of Baja California, the Gulf of California, and south to Santa Elena, Ecuador (OLSSON, 1961). It is found from the intertidal area in bays to 48 m offshore on protected outer coast, in sand.

**Material seen:** 82 northwest American lots.

#### Geologic Distribution and Biogeography:

*Tellina meropsis* is known in the late Pleistocene from the northwestern portion of the Los Angeles basin, California (HOOTS, 1931; RODDA, 1957), to Laguna San Ignacio, Baja California Sur (HERTLEIN, 1934), with several intermediate records. It has also been reported from the

### Explanation of Plate 3

- Figure 14: *Tellina modesta*. Lectotype (herein) of *Angulus modestus*, USNM 4245; about 8 mm  
Figure 15: *Tellina modesta*. Lectotype (herein) of *Angulus modestus obtusus*, USNM 19429; 17 mm  
Figure 16: *Tellina modesta*, CASGTC 13619, southwest shore of Monterey Harbor, California; 16 mm  
Figure 17: *Leporimetis obesa*. Lectotype (herein) of *Tellina obesa*,

- BM(NH) without registry number; 83 mm  
Figure 18: *Leporimetis obesa*. Holotype of *Tellina turgida*, BM (NH) 1967577; about 75 mm  
Figure 19: *Leporimetis obesa*. Holotype of *Tellina alta* and *Scrobicularia biangulata*, BM(NH) 1861.5.20.117; 45 mm  
Figure 20: *Macoma calcarea*. Original illustration of *Tellina calcarea*; 28.3 mm

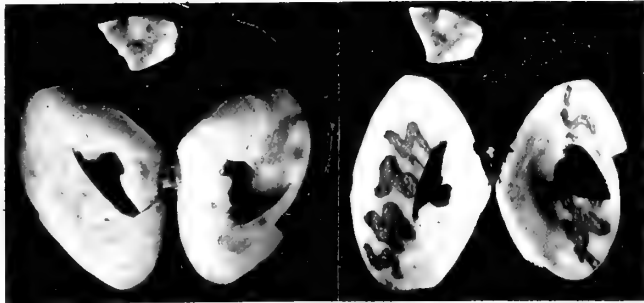


Figure 14

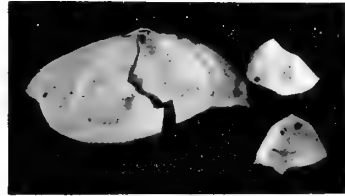


Figure 15

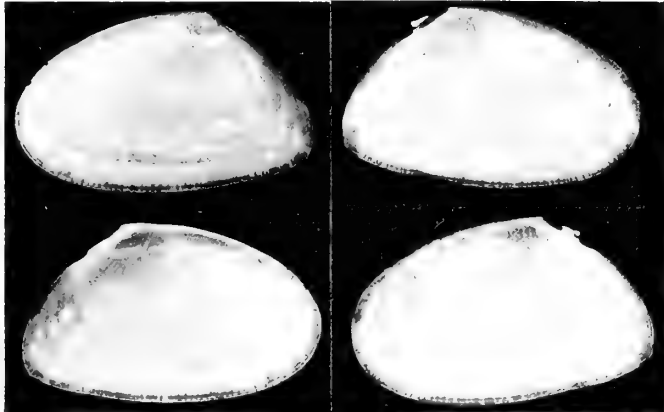


Figure 16

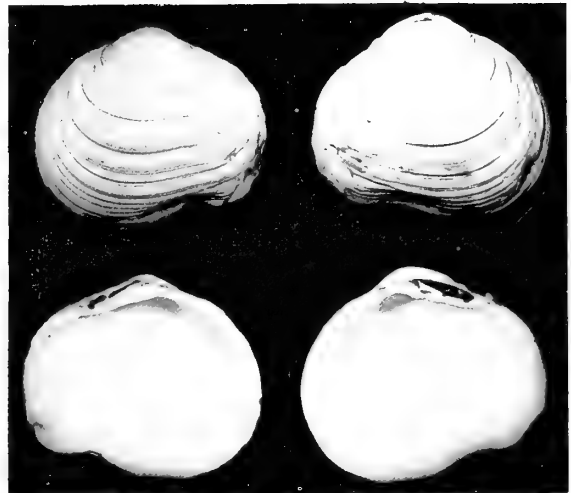


Figure 17

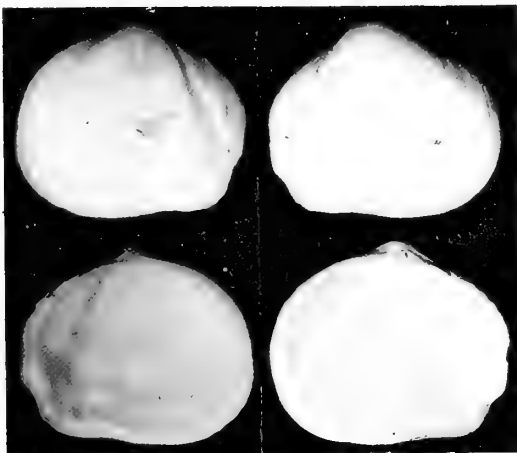


Figure 18

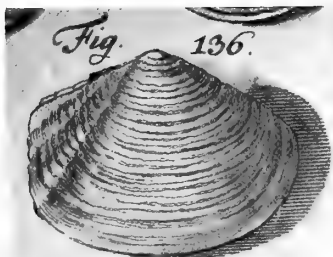


Figure 20

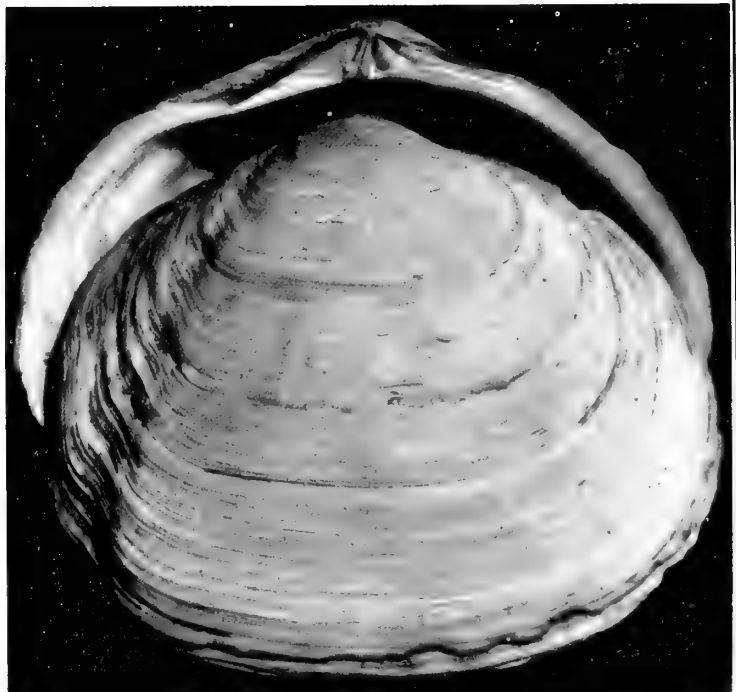


Figure 19



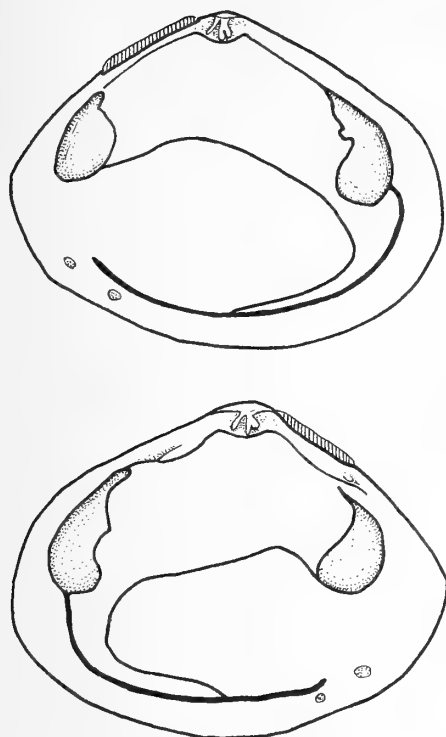


Figure 5

*Tellina meropsis*, internal view of valves  
MCZ 70108, San Diego, California; 16.5 mm

Pleistocene (or Pliocene?) of Isla Carmen, Baja California Sur (HERTLEIN, 1957; EMERSON & HERTLEIN, 1964), and of Santa Elena, Ecuador (HOFFSTETTER, 1952). There is one record in a southern Californian formation transitional between Pliocene and Pleistocene.

It is most similar to *Tellina mera* Say, 1834, from the Caribbean; *T. meropsis* differs from this species in being more rounded, shorter posteriorly, and usually heavier.

*Tellina (Angulus) carpenteri* Dall, 1900  
(Plate 2, Figures 12, 13; Text figure 6)

*Tellina (Angulus) carpenteri* Dall, new name for *T. variegata* (Carpenter), not of Gmelin  
DALL, 1900a: 303, 320  
PACKARD, 1918: 276; plate 15, figure 10  
OLDROYD, 1924: 51, 209, 214; plate 10, figure 4, plate 41, figures 10a, 10b  
I. OLDROYD, 1925: 166; plate 29, figure 2, plate 44, figures 10a, 10b  
GRANT & GALE, 1931: 361

BURCH & BURCH, 1943: 12, 25 (text figure)  
BURCH, 1945a: 3 (text figure), 7; 1945b: 16; 1945c: 30  
*Angulus variegatus* Carpenter, not *Tellina variegata* Gmelin  
CARPENTER, 1864a: 611, 627, 639 [1872: 97, 113, 125]  
CARPENTER, 1864b: 423-424 [1872: 235-236]  
PALMER, 1958: 15, 22, 26, 38, 48, 104-105, 388; plate 13, figures 12-16  
[not *Tellina variegata* Gmelin, 1791: 3237]  
*Tellina (Moerella) arenica* Hertlein & Strong  
HERTLEIN & STRONG, 1949: 68-69, 97; plate 1, figures 5, 11  
KEEN, 1958b: 170-171; figure 393

#### Type Material:

*Angulus variegatus* - USNM 15467b, lectotype herein, left valve, 12.7 mm; USNM 663890, paralectotype, small pair. Plate 2, Figure 12.

*Tellina arenica* - CASGTC 9233, holotype, right valve, 24.6 mm; CAS, one paratype. Plate 2, Figure 13.

#### Type Localities:

*Angulus variegatus* - Either Catalina Island, California, or Neah Bay, Washington. The former would have been collected by J. G. Cooper, the latter by J. G. Swan. The lectotype is more likely from Neah Bay, because large, heavy valves are more common in shallow water there than in southern California.

*Tellina arenica* - CAS Loc. 17708, Arena Bank, southern end of Gulf of California, in 79 m.

#### Nomenclatural Commentary:

This species may have two forms in southern California, a large, flat, light-colored, offshore one and a smaller, more inflated, more brightly colored one in bays. The

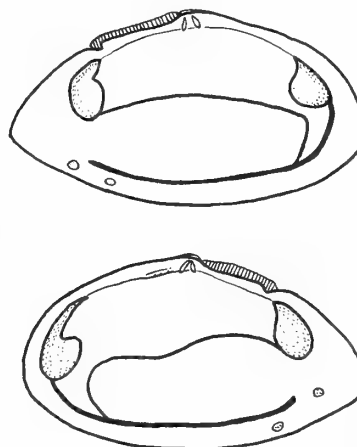


Figure 6

*Tellina carpenteri*, internal view of valves  
MCZ 139930, west coast of Vancouver Island, British Columbia  
15 mm

relationship between these two is uncertain. The fact of importance here, however, is that the type specimens of the two nominal species are morphologically of the former category, so I regard the two as synonyms.

#### Description:

Small (to 20 mm); elongate, more so than in *Tellina modesta*; moderately inflated, somewhat more so than in *T. modesta*; almost equilateral to longer anteriorly; rounded anteriorly; more pointed posteriorly than in *T. modesta*, but broadly truncate; smooth or with low concentric undulations; without a conspicuous internal radial strengthening rib; pink to rosy; color sometimes throughout, sometimes in patches. Other internal details as in Text figure 6.

#### Geographic Distribution and Ecology:

Ketchikan, Alaska (UCLA 20466), through British Columbia, Washington, Oregon, California, Baja California and the Gulf of California, to Panama (KEEN, 1958b). It has been taken in the intertidal area in bays and offshore to 441 m, in a variety of bottom types (BURCH, 1945a). On exposed coasts, it seems to average somewhat farther offshore and in finer substrates than the next species, and BANDY (1958) reports that it constitutes 20 - 22% of the molluscan fauna between about 300 and 500 m in southern California. Specimens (reported as *Tellina arenica*) were as abundant as 95.5 per m<sup>2</sup> between 2 and 30 m in sandy-silt to sand in Bahía de los Angeles, Gulf of California (COAN, 1968b). BURCH (1945a) records the species as spawning in summer in Anaheim Bay, California.

**Material seen:** 143 northern West American lots.

#### Geologic Distribution and Biogeography:

In the late Pleistocene *Tellina carpenteri* has been recorded from Goleta, California (OLDROYD & GRANT, 1931), from Bahía San Quintín, Baja California Norte (ORCUTT, 1921b; JORDAN, 1926), and from Bahía Magdalena, Baja California Sur (JORDAN, 1924, 1936). There are a few records in the early Pleistocene of the San Pedro area, California (T. OLDROYD, 1925; SCHENCK, 1945; BURCH, 1947).

I know of no related fossil or Asian species. It may be similar to *Tellina probrina* Boss, 1964, from the western Atlantic.

*Tellina (Angulus) modesta* Carpenter, 1864  
(Plate 3, Figures 14 - 16; Text figure 7)

*Angulus modestus* Carpenter  
CARPENTER, 1864a: 602, 639, 681 [1872: 88, 125, 167]  
CARPENTER, 1865c: 56

DALL, 1900a: 304 [*Tellina (Angulus)*]

OLDROYD, 1924: 51

I. OLDROYD, 1925: 167

GRANT & GALE, 1931: 361

BURCH & BURCH, 1943: 12-13 [*Tellina (Oudardia)*]

BURCH, 1945a: 7-8; 1945b: 16

PALMER, 1958: 17, 22, 26, 38, 103, 338; plate 13, figures 4-9

*Angulus modestus obtusus* Carpenter, not *Tellina obtusa* Sowerby

CARPENTER, 1864a: 639 [1872: 125]

CARPENTER, 1865c: 56

PALMER, 1958: 22, 26, 34, 38, 48, 103-104, 338; plate 13, figures 10, 11 [under *Tellina buttoni*]

[not *Tellina obtusa* SOWERBY, 1817: 175; plate 179]

*Tellina (Oudardia) buttoni* Dall, new name for *Tellina modesta obtusa* (Carpenter), not *T. obtusa* Sowerby

DALL, 1900a: 304, 320-321, 326; plate 4, figures 12, 13

DALL, 1900b: 1036, 1203; plate 47, figure 18

ARNOLD, 1903: 157-158, 394; plate 15, figures 2, 9

PACKARD, 1918: 275-276; plate 25, figures 7a, 7b

OLDROYD, 1924: 51-52, 214; plate 41, figures 7a, 7b

I. OLDROYD, 1925: 167-168; plate 44, figures 7a, 7b

GRANT & GALE, 1931: 361-362

BURCH & BURCH, 1943: 13, 25 (text figure)

BURCH, 1945a: 3 (text figure), 8; 1945b: 16; 1945c: 30

#### Type Material:

*Angulus modestus* - USNM 4245, lectotype herein, badly broken pair, about 8 mm. Carpenter's second specimen is lost. Plate 3, Figure 14.

*Angulus modestus obtusus* - USNM 19429, lectotype herein, badly broken pair (left valve missing), originally stated to be about 17 mm; USNM 663876, paralectotype, smaller pair. There are also USNM specimens labeled as having been collected at Neah Bay, Washington, by J. G. Swan, but there is uncertainty about their origin; the catalogue numbers with the specimens do not agree with the record books. Plate 3, Figure 15.

#### Type Localities:

*Angulus modestus* - Puget Sound, Washington; C. B. R. Kennerly.

*Angulus modestus obtusus* - San Pedro, California; J. G. Cooper.

#### Nomenclatural Commentary:

As first surmised by BURCH & BURCH (1943), there seems no good basis for separating Carpenter's two subspecies, and I regard them as synonyms. The type specimens of both have a distinct internal radial strengthening rib.

Misidentified specimens of this species account for records of *Tellina hiberna* Hanley, 1844c, from California (reported as *T. panamensis* Dall, 1900a). The latter is Panamic (KEEN, 1958b; OLSSON, 1961), and differs in being smaller, longer posteriorly, iridescent externally, more inflated, and lacking an internal radial rib.



**Description:**

Small (to 20 mm); elongate, but generally higher than the preceding species; moderately inflated; longer, rounded anteriorly; pointed, fairly truncate posteriorly, but more smoothly rounded than in the last species; unworn shells smooth, shiny; with an internal radial strengthening rib; white externally and internally (Plate 3, Figure 16). Other internal details as in Text figure 7.

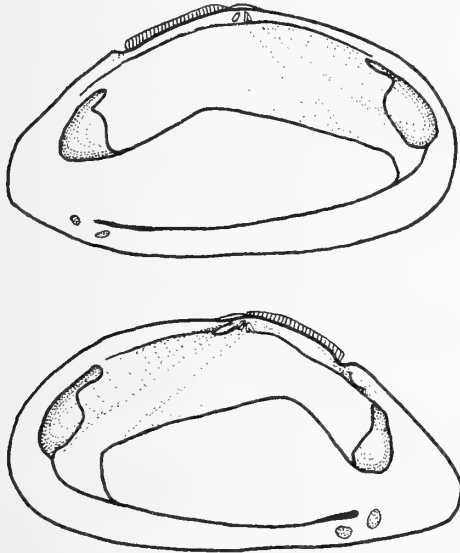


Figure 7

*Tellina modesta*, internal view of valves  
MCZ 48170, Olga, Orcas Island, Washington; 21 mm

**Geographic Distribution and Ecology:**

Montagu Island, Alaska (LACM unnumbered) and Hinchinbrook Island, Alaska (MCZ 101898; ANSP 177931), to Bahía San Bartolomé, Baja California Sur (USNM 554319 and several other lots). It occurs in the intertidal area to 10 m in bays and on more exposed coasts below wave level to 91 m, in silty-sand to fine sand (MAURER, 1969). Offshore this species occurs in shallower water and in coarser sediments than the preceding one. BANDY (1958) found that it constituted 28% of the mollusks in depths of about 12 m in southern California, and BARNARD (1963) named a *Tellina* - *Nothria* community from a 10 - 30 m zone in southern California based on it. JONES (1964) found it most common between 0 and 46 m, and MAURER (1967a-1967c, 1969) reports that it is mainly a deposit feeder.

**Material seen:** 151 lots.

**Geologic Distribution and Biogeography:**

*Tellina modesta* has a rather well documented history. It is known in the late Pleistocene from Point Año Nuevo, California (ADDICOTT, 1966) to Laguna San Ignacio, Baja California Sur (JORDAN, 1924; HERTLEIN, 1934). There are records in the early Pleistocene from the northwestern portion of the Los Angeles basin (RODDA, 1957) and the San Pedro area, California (ARNOLD, 1903; T. OLDROYD, 1925; CLARK, 1931; BURCH, 1947; VALENTINE, 1961), and in southern Californian formations transitional between the Pliocene and Pleistocene. There seem to be similarities between this species and *T. hannibali* Clark, 1915, from the Miocene of central California, and *T. wilsoni* Anderson & Martin, 1914, from the Miocene of southern California.

I know of no related Asian or Atlantic species.

*Leporimetis* Iredale, 1930

[Type species: *Tellina spectabilis* Hanley, 1844b, by original designation]

Medium to large in size (50 to 100 mm); medium in thickness to thick; inflated, often most so anteriorly; equi-valve; rounded to rounded-quadrate; slightly longer posteriorly, equilateral, or longer anteriorly; rounded anteriorly; rounded to broadly truncate posteriorly, with a radial sulcus and ridge setting off postero-dorsal slope; very slightly twisted to right posteriorly; shell surface with concentric ribs and often radial striae; escutcheon and lunule present in some species; two cardinal teeth present in each valve; lateral teeth absent in both valves; ligament sunken below dorsal margin; pallial sinuses moderate in length, approximately equal in the two valves to longer in left valve, slightly to moderately detached from pallial line.

This generic name seems to be a senior synonym of *Florimetis* Olsson & Harbison, 1953, although the latter may be used as a subgenus. A world-wide review of this complex of species would be useful.

*Leporimetis obesa* (Deshayes, 1855)

(Plate 3, Figures 17 - 19; Text figure 8)

*Tellina obesa* Deshayes

DESHAYES, 1855: 354

KEEN, 1966a: 170-171 (text figure 1)

*Tellina turgida* Deshayes ["First Revision" herein]

DESHAYES, 1855: 354

KEEN, 1966a: 170

*Tellina alta* Conrad, 1837, not of Conrad, 1833 [*alba*, of authors, a misspelling]

- CONRAD, 1837: 258  
 HANLEY, 1846: 332; plate 62, figure 200  
 CARPENTER, 1857a: 213  
 CARPENTER, 1857b: 195, 302, 349  
 CARPENTER, 1864a: 526, 536, 540, 639-640 [*Lutricola*]  
 [1872: 12, 22, 26, 125]  
 DALL, 1900a: 306 [*Metis*]  
 DALL, 1900b: 1044  
 ARNOLD, 1903: 160  
 I. OLDROYD, 1925: 169; plate 57, figure 3  
 KEEN, 1966a: 170-171  
 [not of CONRAD, 1833: 41]  
*Scrobicularia biangulata* Carpenter [*biangularis*, misspelling,  
 of authors ]  
 CARPENTER, 1856: 230 [1872: 12]  
 CARPENTER, 1857a: 213  
 CARPENTER, 1857b: 195, 303  
 GRANT & GALE, 1931: 363-364, 922; plate 20, figure 16  
 [*Apolymetis*]  
 BURCH & BURCH, 1943: 16, 24 (text figure)  
 BURCH, 1945a: 4 (text figure), 9-10, 24 (text figure);  
 1945b: 16; 1945c: 30  
 DURHAM, 1950: 89-90, 169, 170; plate 24, figure 1, plate  
 25, figure 12  
 KEEN, 1958b: 178  
 PALMER, 1958: 26, 45, 48, 107, 399; plate 14, figure 5

#### Type Material:

- Tellina obesa* - BM(NH) without registry number, lectotype herein, the pair with more flexuous posterior-ventral margin (as seen from inside), 83 mm; paralectotype, slightly smaller pair. Plate 3, Figure 17.  
*Tellina turgida* - BM(NH) 1967577, holotype, pair, about 75 mm. Plate 3, Figure 18.  
*Tellina alta* and *Scrobicularia biangulata* - BM(NH) 1861. 5.20.117, holotype of both species, pair, 45 mm. Carpenter was not aware that this specimen was Conrad's type. Plate 3, Figure 19.

#### Type Localities:

- Tellina obesa* - "China Seas," presumably in error; Cuming Collection. Probably from southern California.  
*Tellina turgida* - "Catbalonga; Philippines," presumably in error; Cuming Collection. Probably from southern California.  
*Tellina alta* and *Scrobicularia biangulata* - Santa Barbara, California; T. Nuttall.

#### Nomenclatural Commentary:

KEEN (1966a) discussed the history of the two Deshayes species. As in other such cases in the present study,

workers on this coast would prefer to adopt so-called *nomina oblita*, rather than petition for the conservation of more widely used names. The second-occurring Deshayes name has been chosen because of the uses (evidently in error) of *Tellina turgida* in the Philippines and in the Indian Ocean. There seem to be species that resemble *Leporimetis obesa*, one in the Indo-Pacific and one in South Africa, both rare and poorly understood.

#### Description:

Large (to 100 mm); ovate; inflated; heavy; somewhat longer posteriorly; beaks prominent; rounded anteriorly; rounded, slightly truncate, folded posteriorly; sculpture of low ribs and undulations; traces of dark periostracum present; mostly yellow within, rarely white. Internal details as in Text figure 8.

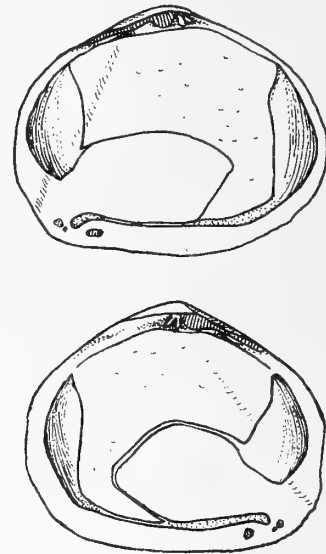


Figure 8

*Leporimetis obesa*, internal view of valves  
 MCZ 199410, Newport Bay, California; 51 mm

#### Geographic Distribution and Ecology:

Point Conception, California (SU 4500), to Bahía Magdalena, Baja California Sur (Berry Collection 24737; SDNHM 22626), with several intermediate records. Spe-

#### Explanation of Plate 4

- Figure 21: *Macoma calcarea*. Original illustration of *Tellina lata*; 47 mm  
 Figure 22: *Macoma calcarea*. Original illustration of *Tellina proxima*; 24 mm

- Figure 23: *Macoma calcarea*. Holotype of *Macoma sitkana*, US NM 108656; 41.6 mm  
 Figure 24: *Macoma calcarea*. Holotype of *Macoma calcarea obliqua*, Zoologisk Museum, University of Oslo; 46.5 mm



Figure 21

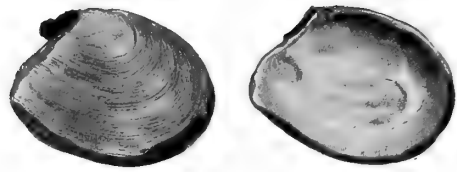


Figure 22

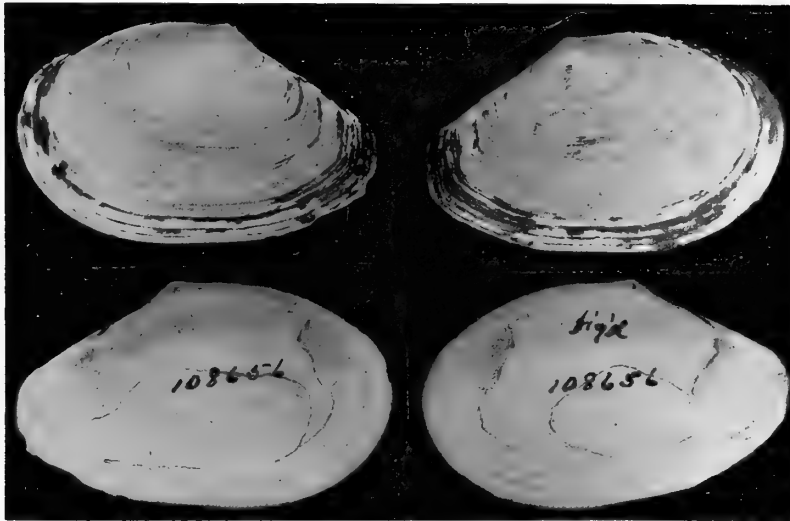


Figure 23



Figure 24



cimens in collections from San Francisco (MCZ 257633), Pacific Grove (SBMNH K9), and Guaymas (UCLA 24185) probably represent labeling errors. This species is found in bays, or below wave line on open, protected coast, in the intertidal area to 46 m, in sand (BURCH, 1945a).

**Material seen:** 92 lots.

#### Geologic Distribution and Biogeography:

This species has a long and well documented history in the eastern Pacific. It is known in the late Pleistocene from Tomales Bay, California (DICKERSON, 1922; ADDICOTT, 1966), to Bahía Magdalena, Baja California Sur (DALL, 1918; SMITH, 1919; JORDAN, 1924, 1936). There is a record in the Pleistocene (undifferentiated) of Las Islas Tres Marias, Nayarit (HERTLEIN, 1934).

There are records from the early Pleistocene of the San Pedro area, California (ARNOLD, 1903; T. OLDROYD, 1925; BURCH, 1947; CLARK, in NATLAND, 1957), and many records in southern Californian formations transitional between the Pleistocene and the Pliocene, as well as several Pliocene records. It is also known from the Miocene and seems to be the same as *Arcopagia medialis* Conrad, 1857a, from the Miocene of Monterey County, California, and *A. unda* Conrad, 1857d, from the Miocene of Santa Barbara County, California. Other species described in the genus from the Tertiary of the eastern Pacific may not be related.

I know of no similar Asian forms. The affinities of this species seem closest to two currently living in the Panamic province and to the one in the Caribbean. It is closest to *Leporimetis cognata* (Pilsbry & Vanatta, 1902), which occurs from Bahía Magdalena, throughout the Gulf of California, to northern Peru (OLSSON, 1961). *Leporimetis obesa* differs from *L. cognata* in being larger, heavier, yellow within, having a heavier hinge, and in lacking radial threads.

#### *Macoma* Leach, 1819

[Type species: *Macoma tenera* Leach, 1819, by monotypy; = *Tellina calcarea* Gmelin, 1791]

Into the genus *Macoma* are placed, pending a revision of the family, those forms lacking lateral hinge teeth. A majority of the species are relatively more rounded than *Tellina*, more inflated, smooth, white, often chalky, and are chiefly arctic and sub-arctic.

It is difficult to pick key characters for species of *Macoma*, as nearly every feature chosen is gradational, and exceptions can be found. In the following key, qualitative and sometimes relative rather than quantitative

choices are emphasized, and interpretations of terms may create some difficulty. Certain figures are cited for the preliminary choices to aid in decision making. In this dichotomous key, which works best with live-collected, adult specimens, a balance of several characters is used to distinguish, for the most part, between what I believe to be natural groups. Of necessity, some species are keyed out twice. *Macoma frigida* is not included because of its uncertain West American occurrence.

- 1a. Anterior ventral edge of pallial sinus detached and more or less paralleling pallial line for at least  $\frac{1}{4}$  of way to posterior adductor muscle scar (true of both valves) (Figure 9) ..... 2
- 1b. Anterior ventral end of pallial sinus not detached from pallial line for a substantial distance, although it may overlap slightly near point of juncture (usually in one valve only) (Figure 28) ..... 18
- 2a. Very thin, fragile and inflated; periostracum thin, never thick; rounded to ovate (Plate 9, Figure 50) ..... 3
- 2b. Thick to thin, but not markedly thin; may be somewhat inflated; periostracum thick to thin (Plate 5, Figure 26) ..... 4
- 3a. Produced to quadrate posteriorly; left valve flexed; conspicuously more inflated anteriorly ..... *Macoma carlottensis*
- 3b. Rounded to only slightly quadrate posteriorly; left valve not flexed; anterior end only slightly more inflated ..... *Macoma leptonoidea*
- 4a. Pallial sinuses approximately equal in size and short, reaching about  $\frac{3}{4}$  of way to anterior adductor muscle scar and periostracum shiny, thin (Figure 25) ..... 5
- 4b. Pallial sinuses unequal in size, that in left valve longer, often reaching almost to anterior adductor muscle scar; periostracum dark, silky or shiny (if sinuses subequal, periostracum not shiny) (Figure 9) ..... 8
- 5a. Large (over 30 mm); tendency to form a posterior dorsal flange ..... 6
- 5b. Small (under 30 mm); not flexed posteriorly; no such flange present ..... 7
- 6a. With a conspicuous posterior flexure; often produced posteriorly; elongate ..... *Macoma indentata* (place 1)
- 6b. Quadrate posteriorly, not strongly flexed or produced; ovate ..... *Macoma secta* (place 1)
- 7a. Rostrate posteriorly; longer anteriorly ..... *Macoma yoldiformis*
- 7b. Produced posteriorly, not rostrate; longer anteriorly to equilateral ..... *Macoma acolasta*
- 8a. Small (usually under 30 mm); thin; periostracum dark or shiny; elongate to rounded (shell, if thick, decidedly small or periostracum decidedly shiny) (Plate 7, Figure 36) ..... 9
- 8b. Medium-sized to large (over 30 mm); thick; periostracum dark to silky, never shiny (shell, if thin, decidedly elongate, not rounded) (Plate 4, Figure 23) ..... 13
- 9a. Rather inflated; rounded to oval; periostracum dull ..... 10
- 9b. Not inflated; oval to elongate; periostracum shiny ..... 11
- 10a. Oval, not quadrate posteriorly; more inflated ..... *Macoma loveni*
- 10b. Quadrate posteriorly; less inflated ..... *Macoma crassula*
- 11a. Heavier; larger (mostly over 25 mm); pointed posteriorly ..... *Macoma lama* (place 1)
- 11b. Thinner; smaller (under 25 mm); posterior end more rounded ..... 12

- 12a. Flattened; rounded postero-dorsally; Arctic to Shelikof Strait ..... *Macoma moesta moesta*  
 12b. More inflated, especially anteriorly; no postero-dorsal rounding; Shelikof Strait to Puget Sound ..... *Macoma moesta alaskana*  
 13a. Rotund to triangular; pallial line often striose (Figure 14)  
 13b. Oval to elongate; pallial line only slightly striose, if at all (Figure 10) ..... 15  
 14a. Rotund; moderately inflated; almost equilateral, with posterior end slightly shorter ..... *Macoma obliqua*  
 14b. Triangular; flattened; posterior end conspicuously shorter ..... *Macoma middendorffi*  
 15a. With a conspicuously beveled escutcheon ..... *Macoma elimata*  
 15b. Without an escutcheon ..... 16  
 16a. Produced posteriorly and slightly pointed, with ventral posterior margin upturned; relatively thinner and smaller (mostly less than 50 mm) than next two species ..... *Macoma calcarea*  
 16b. Posterior end quadrate to rounded, not produced; ventral posterior margin not upturned; relatively heavier and larger (over 50 mm) than the above ..... 17  
 17a. Posterior end rounded; thick ..... *Macoma lipara*  
 17b. Posterior end quadrate; thinner ..... *Macoma brota*  
 18a. Pallial sinuses reaching to or almost to anterior adductor muscle scars (Figure 28) ..... 19  
 18b. Pallial sinuses terminate only  $\frac{1}{2}$  to  $\frac{3}{4}$  of way to anterior adductor muscle scars (Figure 27) ..... 20  
 19a. Pallial sinus in left valve nearly always reaching center of anterior adductor muscle scar and fusing with it; twisted to right posteriorly ..... *Macoma nasuta*  
 19b. Pallial sinuses do not reach or reach only to bases of anterior adductor muscle scars; equivalve, not twisted posteriorly ..... *Macoma inquinata*  
 20a. Pallial sinuses unequal; thick, shiny periostracum present; posterior end usually shorter, its dorsal and ventral slopes even; thick ..... *Macoma lama* (place 2)  
 20b. Pallial sinuses about equal; periostracum thin, less shiny; equilateral or posterior end longer (rarely shorter), its dorsal slope often broken by a flange or its ventral one by an indentation; thick to thin ..... 21  
 21a. Small (usually under 30 mm); with no tendency to form postero-dorsal flange; often thick and rounded; often reddish ..... *Macoma balthica*  
 21b. Large (over 30 mm); with tendency to form postero-dorsal flange ..... 22  
 22a. Very thin, inflated; rounded posteriorly; flange only slightly developed ..... *Macoma expansa*  
 22b. Heavy; produced or quadrate posteriorly; flange conspicuous ..... 23  
 23a. With a conspicuous posterior flexure; often produced posteriorly; elongate ..... *Macoma indentata* (place 2)  
 23b. Quadrate posteriorly, not strongly flexed or produced; ovate ..... *Macoma secta* (place 2)

(*Macoma*) Leach, 1819

Small to large in size (20 to 100 mm); medium in thickness to heavy; moderately inflated; equivalve or with left valve somewhat larger; rounded to elongate; equilateral to longer anteriorly; rounded anteriorly; rounded to broadly truncate, twisted to right posteriorly; periostracum dark, silky, or shiny; beveled escutcheon present in some species; pallial sinuses long, longer in left valve, detached from pallial line along much of their length.

Species group of *Macoma* (*Macoma*) *calcarea* (Gmelin)

Medium-sized to large in size (30 to 60 mm); chalky to smooth; periostracum dark to silky, rarely shiny.

*Macoma* (*Macoma*) *calcarea* (Gmelin, 1791)

(Plate 3, Figure 20; Plate 4, Figures 21 - 24; Plate 5, Figure 25; Text figure 9)

*Tellina calcarea* Gmelin

[CHEMNITZ, 1782: 140; plate 13, figure 136 - non-binomial]

GMELIN, 1791: 3236

CARPENTER, 1857b: 221, 232

CARPENTER, 1864a: 584, 639 [*Macoma*, synonym of *M. lata*] [1872: 70, 125]

DALL, 1900a: 299, 307

DALL, 1900b: 1046

OLDROYD, 1924: 53, 209; plate 10, figure 2 [figure is of *M. brota*]

I. OLDROYD, 1925: 173-174; plate 42, figure 5 [figure is of *M. brota*]

GRANT & GALE, 1931: 369-370 [in part only]

BURCH & BURCH, 1943: 19-20

BURCH, 1945a: 11; 1945b: 17

SOOT-RYEN, 1958: 24

MACGINITIE, 1959: 181-182; plate 24, figures 5-7, plate 26, figures 6-9

OCKELMANN, 1959: 125-128; plate 2, figure 10

DUNNILL & COAN, 1968: 8-17; figures 5-10

DUNNILL & ELLIS, 1969: 10-13, 33; figures 4(1), 9(e)

*Tellina lata* Gmelin [First Reviser: probably DALL, 1900a] [LISTER, 1687: plate 407, figure 253 - pre-Linnaean]

GMELIN, 1791: 3237

MIDDENDORFF, 1849: 578, 601; plate 8, figures 8-10

MIDDENDORFF, 1851: 257-258; plate 23, figures 1-5

CARPENTER, 1857b: 219, 221, 223, 301

### Explanation of Plate 5

Figure 25: *Macoma calcarea*. Holotype of *Macoma calcarea longisinuata*, Zoologisk Museum, University of Oslo; 33.4 mm

Figure 26: *Macoma elimata*, holotype, NMC 46070; 27.2 mm

Figure 27: *Macoma brota*. Original illustration (lectotype herein) of *Tellina edentula*; 53.2 mm

Figure 28: *Macoma brota*, CASGTC 13620; CAS locality 20463. Unalaska Island, Aleutian Islands, Alaska; 75 mm

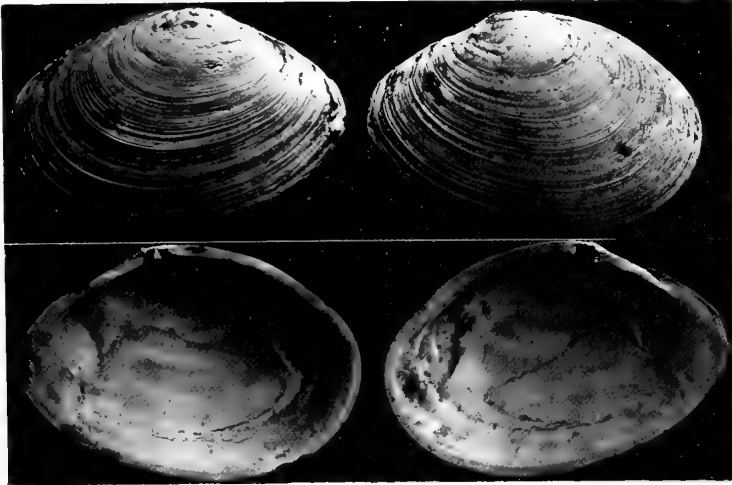


Figure 25

Figure 26

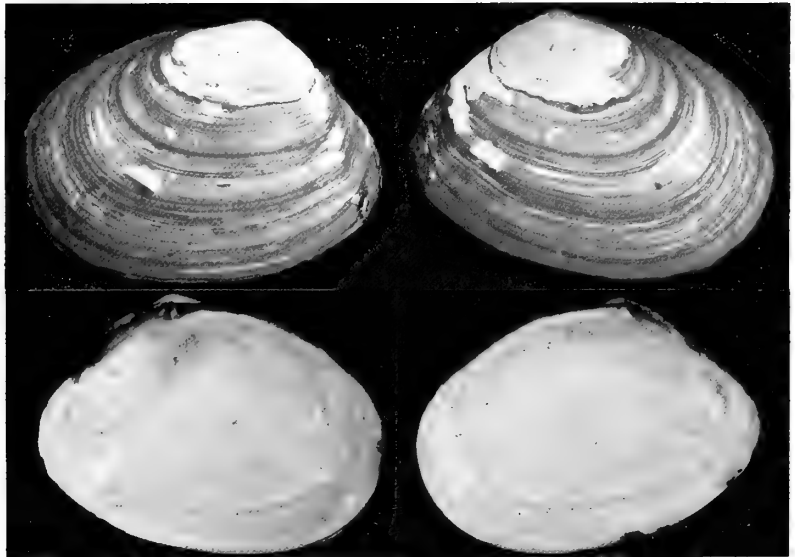


Figure 27

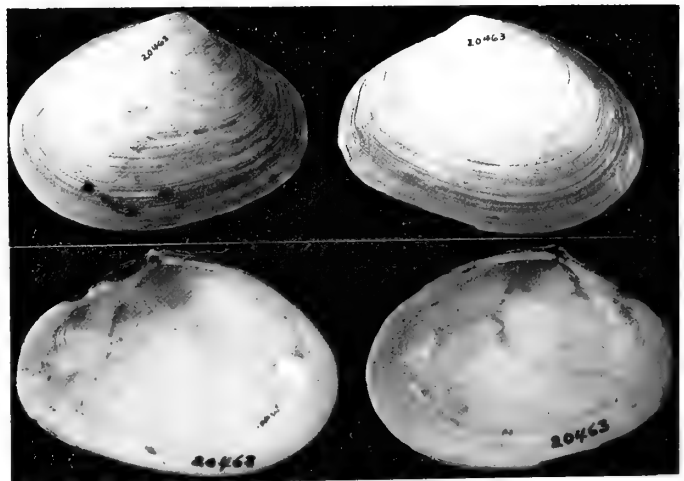


Figure 28





CARPENTER, 1864a: 584, 602, 639 [*Macoma*] [1872: 70, 88, 125]

KRAUSE, 1885: 37-38

DALL, 1900a: 299

*Tellina proxima* Sowerby, in Gray, *ex* Brown MS

SOWERBY, in GRAY, 1839: 154; plate 44, figure 4

CARPENTER, 1857b: 178, 221

CARPENTER, 1864a: 584, 602 [*Macoma*] [1872: 70, 88]

*Tellina lata nasuta* Middendorff, 1849, not *Tellina nasuta* Conrad

MIDDENDORFF, 1849: 578

[not CONRAD, 1837: 258-259]

*Macoma sitkana* Dall

DALL, 1900a: 307, 323, 326; plate 4, figures 6, 7

I. OLDROYD, 1925: 171

BURCH, 1945a: 11; 1945b: 17

*Macoma calcarea obliqua* Soot-Ryen, not *M. obliqua* (Sowerby)

SOOT-RYEN, 1932: 15-17, 36; plate 2, figures 4-6

[not SOWERBY, 1817: 137-138; plate 161, figure 1]

*Macoma calcarea sootryeni* Petrov, *ex* Scarlato, 1953 MS

(unpublished thesis), new name for *M. calcarea obliqua* Soot-Ryen, not of (Sowerby)

PETROV, 1966: 230

*Macoma calcarea longisinuata* Soot-Ryen

SOOT-RYEN, 1932: 17, 36; plate 2, figures 1-3

### Type Material:

*Tellina calcarea* – Based on Chemnitz' figures, but the type specimen cannot be found in the Zoologiske Museum, University of Copenhagen (Knudsen, in correspondence). The figure measures 28.3 mm long and unfortunately is not a good representation of the species. Plate 3, Figure 20.

*Tellina lata* – The figure in LISTER (1687) is 47 mm long and of sufficient quality to identify the taxon. This specimen seems not to be extant in the Zoological Collections, University Museum, Oxford University (Hull, in correspondence). Plate 4, Figure 21.

*Tellina proxima* – Lost (Keen, verbal communication). The figure is 24 mm long and is adequate to allocate the name. Plate 4, Figure 22.

*Tellina lata nasuta* – Probably in Zoological Institute, Leningrad; inquiries there remain unanswered.

*Macoma sitkana* – USNM 108656, holotype, pair, 41.6 mm. Plate 4, Figure 23.

*Macoma calcarea obliqua* – Zoologisk Museum, University of Oslo, holotype, pair, 46.5 mm. Plate 4, Figure 24.

*Macoma calcarea longisinuata* – Zoologisk Museum, University of Oslo, holotype, pair, 33.4 mm. Plate 5, Figure 25.

### Type Localities:

*Tellina calcarea* – Iceland and Faeroe Islands.

*Tellina lata* – "Norwegian Sea."

*Tellina proxima* – "Arctic Ocean," presumably the Alaskan coast; voyage of the *Blossom*.

*Tellina lata nasuta* – Several localities given by Middendorff; one from northwestern Russia is listed first.

*Macoma sitkana* – Sitka Harbor, Alaska; W. H. Dall, 27 m.

*Macoma calcarea obliqua* – Station 9, northwest of Ostrov Vrangelya, East Siberian Sea (73°15' N, 175°30' E), 44 m.

*Macoma calcarea longisinuata* – Station 30, north of Ostrov Kotel'nyy, Novosibirskiye Ostrova (76°34' N, 139°00' E), 20 m.

### Nomenclatural Commentary:

For an author to have been considered the "first reviser" of the two Gmelin species, he would have had to cite both as being of Gmelin, or mentioned both of Gmelin's usages in his synonymics, considered them to represent the same species, selected one of the names to stand as the name of the species, and relegated the other to synonymy. Since it was not until comparatively recent times that Chemnitz' species were considered to have been validated only by later authors, the first publication meeting all of these requirements seems to be DALL (1900a).

The species exhibits considerable variation, and it is possible that the situation is more complex than that represented by one circum-arctic name. For instance, there are some very large specimens in collections from the Bering Sea (CAS 20455, 60 mm), much larger than any Atlantic material I have seen. These may represent something else, or perhaps even hybrids with *Macoma brota* Dall. As is the case with many arctic species, this problem ought to be approached statistically from a world-wide viewpoint. Until this is done, I have chosen to be nomenclaturally conservative. There is little question that *M. sitkana* should be regarded as a synonym, more question about *M. calcarea sootryeni* and *M. calcarea longisinuata*.

This species has occasionally been cited as *Macoma sabulosa* (Spengler, 1798), a European synonym.

### Description:

Medium-sized (to 55 mm, rarely to 60 mm); ovate-elongate; moderately inflated; fairly thin; rounded anteriorly; pointed, slightly truncate posteriorly; ventro-posterior margin upturned; chalky-white externally, with remnants of thin, dark periostracum ventrally in adult;

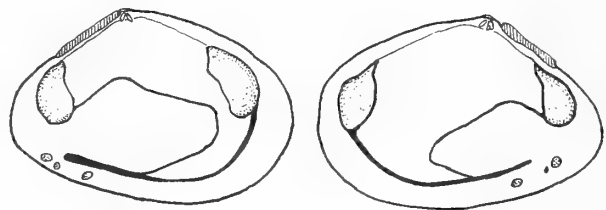


Figure 9

*Macoma calcarea*, internal view of valves  
USNM 223783, north of Unimak Island, Alaska; 47 mm

periostracum shiny in juvenile; pallial sinuses detached from pallial line, that in left valve larger. Other internal details as in Text figure 9.

#### Geographic Distribution and Ecology:

Circum-arctic; throughout the Bering Sea, the Aleutian Islands, southern Alaska, British Columbia, and south to Victoria (ANSP 65841) and Sooke, Vancouver Island, British Columbia (SU 52025). I have seen no specimens from Washington. *Macoma calcarea* occurs in numbers of up to 226 per m<sup>2</sup> from 2 to 320 m, most common over 50 m, in silty-sand to sand (SOOT-RYEN, 1958; OCKELMANN, 1959; MACGINITIE, 1959; DUNNILL, 1968; DUNNILL & ELLIS, 1969).

**Material seen:** 169 West American lots.

#### Geologic Distribution and Biogeography:

In the Pleistocene, this species is known from the Arctic coast of the Northwest Territories (DALL, 1919, 1924), Arctic Alaska (MEEK, 1923), Saint Paul Island (DALL, 1899), the Kenai Peninsula (TWEHOFEL, 1952, as "cf."), Middleton Island (MILLER, 1953, as "cf."), southeastern Alaska (DALL, 1904; KNOPF, 1912; CHAPIN, 1918; SMITH, 1919; TWEHOFEL, 1952); British Columbia (NEWCOMBE, 1914; SMITH, 1919; CRICKMAY, 1925, 1929b; DRAYCOT, 1951; ARMSTRONG & BROWN, 1954; WAGNER, 1960), and the Puget Sound area, Washington (ARNOLD & HANNIBAL, 1913; HERTLEIN & CRICKMAY, 1925; HENDERSON, 1927), although the last records should be reëxamined and some may prove to be of the next species.

There are records from the Pliocene of Alaska and California, the Miocene of Alaska and Oregon, and the Oligocene of Washington. An ancestral form may be *Macoma arctata* (Conrad, 1849), from the Miocene of Astoria, Oregon, which is very similar to *Tellina arctata juana* Reagan, 1908, from the Miocene of Washington; *M. arctata wynoocheensis* Weaver, 1912, from the Miocene of Oregon; and *M. twinensis* Clark, 1925, from the Oligocene of Washington.

This species evidently had its origin in the northern Pacific basin and reached the northern Atlantic only during the last period of submergence of the Bering Strait area, as it is unknown earlier than Pleistocene in the northern Atlantic (RICHARDS, 1962; British Museum [Natural History], 1963).

*Macoma orientalis* Scarlato, in Golikov & Scarlato, 1967, from Siberia to northern Japan, is a western Pacific relative of this species. It differs in being thinner, more inflated, more expanded antero-dorsally, more rounded posteriorly, and in having a more shiny, adherent periostracum. The pallial sinus is directed more dorsally.

*Macoma (Macoma) elimata* Dunnill & Coan, 1968  
(Plate 5, Figure 26; Text figure 10)

*Macoma elimata* Dunnill & Coan

DUNNILL & COAN, 1968: 1-11; figures 2-6

DUNNILL & ELLIS, 1969: 11, 15-16, 33; figures 4 (2), 9 (f)

*Macoma calcarea* (Gmelin), of authors, not of Gmelin  
[not GMEIN, 1791: 3236]

ARNOLD, 1903: 161, 394; plate 16, figure 2 [but not the figure?]

WOODRING, BRAMLETTE & KEW, 1946: 84, plate 33, figure 6

#### Type Material:

NMC 46070, holotype, pair, 27.2 mm; paratypes widely distributed. Plate 5, Figure 26.

#### Type Locality:

North end of Moresby Island, Satellite Channel, Vancouver Island, British Columbia; R. M. Dunnill, 54 m, silty-sand.

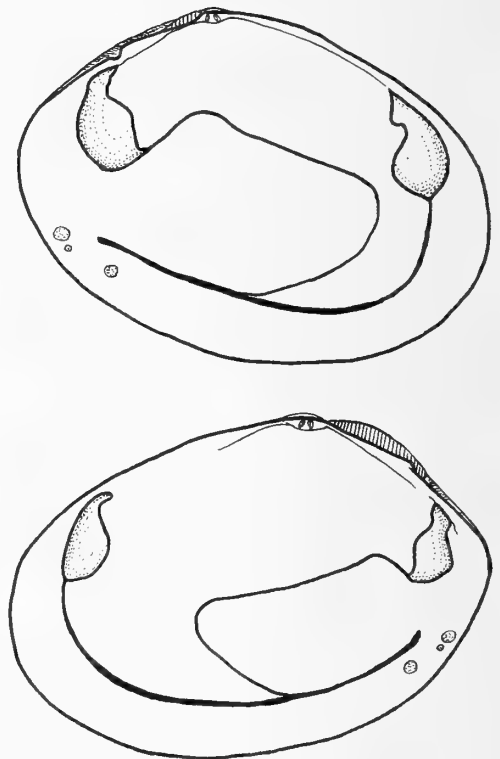


Figure 10

*Macoma elimata*, internal view of valves  
USNM 108672, north end of Vancouver Island, British Columbia  
35.3 mm

**Nomenclatural Commentary:**

This species has been reported from the Pleistocene of southern California in error, as *Macoma planiuscula* GRANT & GALE, 1931.

**Description:**

Medium-sized (to 33 mm); elongate; moderately inflated; thin; longer, rounded anteriorly; truncate posteriorly; postero-dorsal margin straight, with a conspicuously beveled escutcheon; periostracum thin, greenish-gray, little eroded; pallial sinuses detached from pallial line, that in left valve larger. Other internal details as in Text figure 10.

**Geographic Distribution and Ecology:**

Craig (UCLA 20512) and Ketchikan (UCLA 20514), Alaska, to Redondo Beach, California (LACM A4052; SU unnumbered). It has been found in numbers up to 217 per m<sup>2</sup> in 9 to 435 m, most common over 50 m; in silty-sand to sand (DUNNILL, 1968; DUNNILL & COAN, 1968; DUNNILL & ELLIS, 1969).

**Material seen:** 65 lots.

**Geologic Distribution and Biogeography:**

There are no certain records in the late Pleistocene. Those of CRICKMAY (1929a) at Deadman Island, San Pedro, California, were derived from reworked early Pleistocene material. There are many records in the early Pleistocene, from Santa Barbara, California (KEEN & BENTSON, 1944), to the San Pedro area, California (WILLETT, 1937; T. BURCH, 1947), in which it has been reported as *Macoma calcarea*, *M. planiuscula*, or *M. nasuta*. There is also material in those southern Californian formations transitional between Pliocene and Pleistocene. I have studied material from each of these areas.

The species may be related to *Macoma albaria* (Conrad, 1849), from the Miocene of Oregon. *Tellina obruta* Conrad, 1848, from the same formation, may be an earlier synonym. If I am correct about these relationships, specimens of this species-complex do not have a beveled escutcheon before the early Pliocene.

*Macoma (Macoma) brota* Dall, 1916  
(Plate 5, Figures 27, 28; Text figure 11)

*Macoma brota* Dall, new name for *Tellina edentula* Broderip & Sowerby, not of Spengler  
DALL, 1916a: 36 [*nomen nudum*]  
DALL, 1916b: 413  
OLDROYD, 1924: 52-53  
I. OLDROYD, 1925: 170-171; plate 9, figure 2

GRANT & GALE, 1931: 368

BURCH & BURCH, 1943: 19

BURCH, 1945a: 10-11; 1945b: 17; 1945c: 30

DUNNILL & ELLIS, 1969: 8-10, 33; figures 3 (2), 9 (a)

*Tellina edentula* Broderip & Sowerby, not of Spengler

BRODERIP & SOWERBY, 1829: 363

SOWERBY, in GRAY, 1839: 154; plate 41, figure 5, plate 44, figure 7

CARPENTER, 1857b: 175, 195, 219, 223, 301

CARPENTER, 1864a: 526, 584, 600, 627, 639 [*Macoma*]  
[1872: 12, 70, 86, 113, 125]

KRAUSE, 1885: 37

DALL, 1900a: 307

[not SPENGLER, 1798: 96-97]

**Type Material:**

*Tellina edentula* - Lost, according to Dr. Keen. Since the two figures given by SOWERBY, in GRAY (1839) are somewhat different from each other, I select plate 44, figure 7 as lectotype. This figure measures 53.2 mm in length, and it is the closer of the two to the "type" of Dall's *Macoma brota*, USNM 108668. Plate 5, Figure 27.

**Type Locality:**

Bering Strait, Alaska; voyage of the *Blossom*.

**Nomenclatural Commentary:**

See next species.

**Description:**

Large (to 65 mm); ovate to ovate-elongate; moderately inflated; rather heavy; longer, rounded anteriorly; broadly truncate posteriorly; periostracum thin, dark to silky, present only as ventral fragments in adult; pallial sinuses detached from pallial line, that in left valve somewhat larger (Plate 5, Figure 28). Other internal details as in Text figure 11.

**Geographic Distribution and Ecology:**

Bathurst Inlet, Mackenzie, Arctic Canada (MCZ 192915), along the entire eastern shore of Bering Sea, through the Aleutian Islands, as far east as Adak Island (USNM 108612), south coast of Alaska, British Columbia, to Puget Sound, Washington (USNM 184278 and several other lots). It is found in numbers of up to 75 per m<sup>2</sup> from 14 to 260 m, most common over 35 m in silt to sand (DUNNILL, 1968; DUNNILL & ELLIS 1969).

**Material seen:** 102 lots.

**Geologic Distribution and Biogeography:**

*Macoma brota* has been reported in the Pleistocene of the Canadian Arctic (DALL, 1919, 1924) and southwestern British Columbia (CRICKMAY, 1925, 1929b). It seems

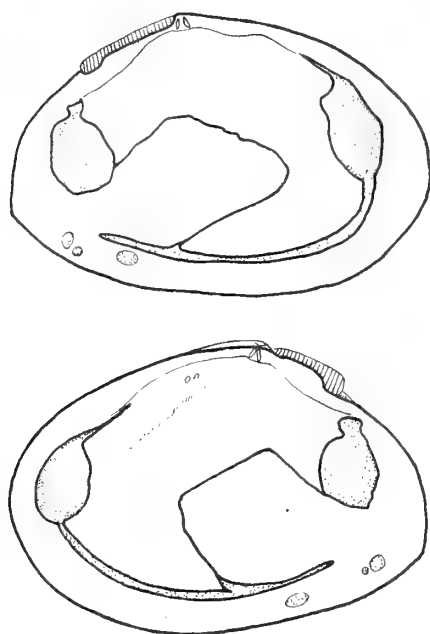


Figure 11

*Macoma brota*, internal view of valves  
USNM 108664, southeast of Alaska Peninsula, Alaska; 69 mm

to be closely related to *M. astori* Dall, 1909, from the Pliocene of Coos Bay, Oregon. The latter has also been reported from the Miocene. This Miocene material ought to be compared with *M. grewingkii* Dall, 1904, from southern Alaska. Grewingk's figure (plate 7, figure 1) seems to be drawn backwards with regard to the position of the pallial sinus.

An Oligocene ancestor of this Miocene species may be *Macoma lorenzoensis* (Arnold, 1908) from central California, which may be synonymous with *M. lorenzoensis arnoldi* Tegland, 1933, from the Oligocene of Washington. There may be some relation of these last to *Tellina benedenii* Nyst & Westendorp, 1839, from the Pliocene and Pleistocene of Europe, even though the latter has lateral teeth.

It is possible that *Macoma brota* represents populations that were "trapped" north of Bering Strait when it closed in the early Pliocene. If this species is related to *Tellina benedenii*, then the loss of lateral teeth took place later in eastern Atlantic-Arctic populations than it did in populations remaining in the Pacific.

*Macoma (Macoma) lipara* Dall, 1916  
(Plate 6, Figure 29; Text figure 12)

*Macoma brota lipara* Dall

DALL, 1916a: 36 [nomen nudum]

DALL, 1916b: 414

OLDROYD, 1924: 53, 209; plate 10, figure 1

I. OLDROYD, 1925: 171; plate 42, figure 6

GRANT & GALE, 1931: 368-369

BURCH & BURCH, 1943: 19

BURCH, 1945a: 11; 1945b: 17

DUNNILL & ELLIS, 1969: 9, 24, 26-27, 33; figures 3 (1), 9 (b)

#### Type Material:

USNM 223032, holotype, pair, 72.7 mm. Plate 6, Figure 29.

#### Type Locality:

Off Fort Rupert, Queen Charlotte Strait, Vancouver Island, British Columbia; USFC 4201, about 259 m, in mud.

#### Nomenclatural Commentary:

GRANT & GALE (1931) suggested that *Macoma astori* Dall, 1909, from the Pliocene of Coos Bay, Oregon, might be an older name for this species. I do not concur.

#### Description:

Large (to 75 mm); ovate; moderately inflated; heavy for size; somewhat longer, rounded anteriorly; rounded posteriorly, with only a slight degree of truncation; periostracum very thin, silky to shiny; pallial sinuses detached from pallial line, that in left valve larger. Other internal details as in Text figure 12.

#### Geographic Distribution and Ecology:

There seems to be an isolated population in the southeastern corner of the Bering Sea (USNM 210287, 212948).

#### Explanation of Plate 6

Figure 29: *Macoma lipara*, holotype, USNM 223032; 72.2 mm

Figure 30: *Macoma middendorffi*, lectotype (herein), USNM alcoholic type collection 40945; 58.9 mm

Figure 31: *Macoma obliqua*. Lectotype (herein) of *Tellina obliqua*, BM(NH) Fossil Mollusca Section 43058; 45.6 mm

Figure 32: *Macoma incongrua*. Lectotype (herein) of *Tellina incongrua*, Zoologisches Museum, Humboldt-Universität 7624; 24.4 mm

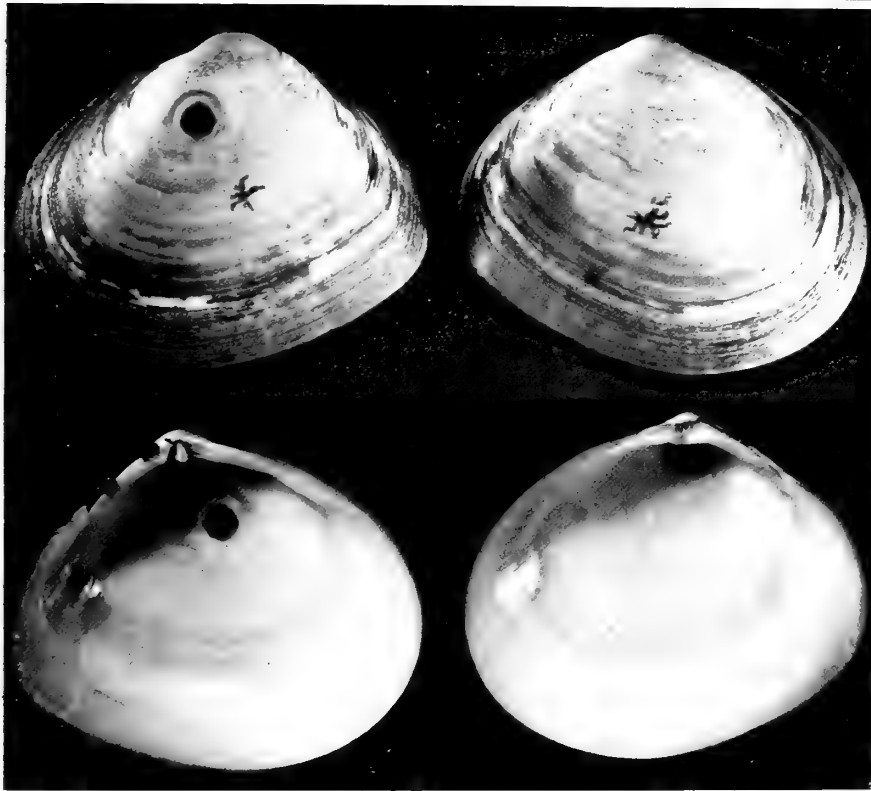


Figure 32

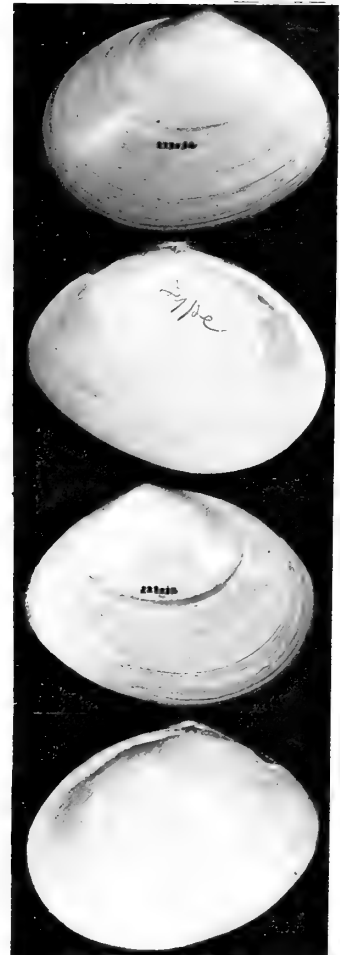


Figure 29



Figure 31

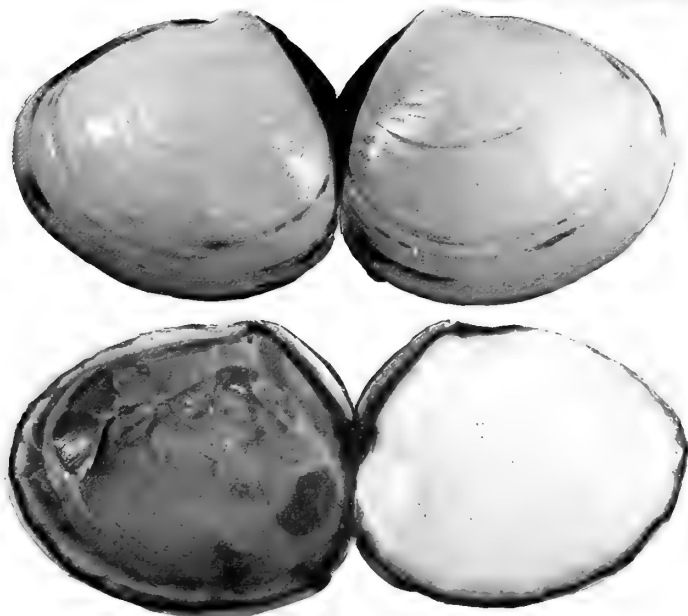


Figure 30



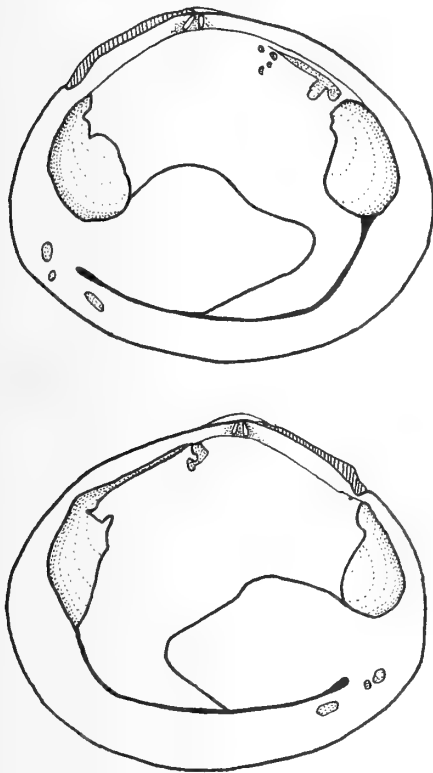


Figure 12

*Macoma lipara*, internal view of valves  
MCZ 223485, Malcolm Island, British Columbia; 70 mm

The latter of these two lots seems to be intermediate between this species and *Macoma brota*. This situation requires additional investigation. The main distribution is from Port Etches (USNM 108697) and Galena Bay (LACM 5498), Alaska, to Eureka, California (Talmadge Collection). There is one lot from Cordell Bank, near San Francisco, California (CAS 33047), but this may be fossil. It has been found in numbers of up to 23 per m<sup>2</sup> from 26 to 259 m, especially over 40 m, in silt to fine sand (DUNNILL, 1968; DUNNILL & ELLIS, 1969).

**Material seen:** 32 lots.

#### Geologic Distribution and Biogeography:

There are no records of this species in the Pleistocene, except that of ADDICOTT (1966) in central California, the specimen having been derived from the Pliocene Purisima formation by reworking. Like the preceding species, this seems allied to, but not identical with *Macoma astori* Dall, 1909, from the Pliocene of Oregon.

#### *Macoma (Macoma) middendorffi* Dall, 1884

(Plate 6, Figure 30; Text figure 13)

*Macoma* "(edentula?)" *middendorffi* Dall [*middendorffii* of authors, a misspelling]

DALL, 1884: 347, 348

DALL, 1886: 308-309; plate 4, figure 11

DALL, 1900a: 306

I. OLDROYD, 1925: 170; plate 53, figure 1

GRANT & GALE, 1931: 372-373

BURCH, 1945a: 10; 1945b: 17

*Tellina edentula* Broderip & Sowerby, of authors, not of Broderip & Sowerby

[not *Tellina edentula* BRODERIP & SOWERBY, 1829: 363]

MIDDENDORFF, 1849: 578

MIDDENDORFF, 1851: 259-260; plate 21, figure 1

#### Type Material:

*Macoma middendorffi* - USNM alcoholic type collection  
40945, lectotype herein, pair, 58.9 mm. Plate 6, Figure 30.

#### Type Locality:

Ostrov Beringa, Komandorskiye Ostrova, Union of Soviet Socialist Republics; L. Stejneger.

#### Nomenclatural Commentary:

None necessary.

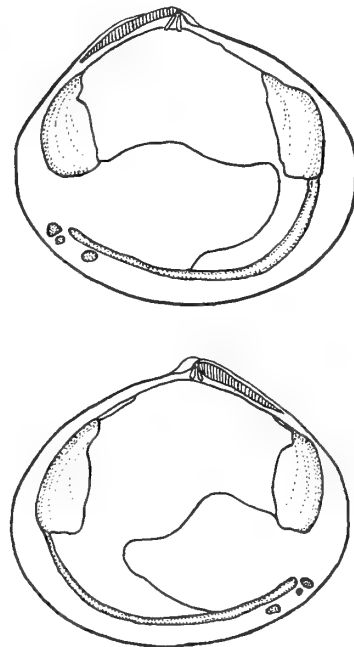


Figure 13

*Macoma middendorffi*, internal view of valves  
USNM 108595, Ostrov Beringa, Komandorskiye Ostrova, U. S. S. R.  
56 mm

**Description:**

Large (to 60 mm); trigonal; flattened; very heavy; somewhat longer, rounded anteriorly; rounded, somewhat truncate posteriorly; sculpture of rounded growth lines; periostracum inconspicuous; pallial sinuses partially detached from pallial line, that in left valve larger; pallial line striose. Other internal details as in Text figure 13.

**Geographic Distribution and Ecology:**

Point Barrow, Alaska (USNM 207073), the Bering Sea, along the west coast of Alaska, the Aleutian Islands, and in Siberia. Dall's record from Chirikoff Island, Alaska, is based on what appears to be a worn, broken specimen of *Macoma obliqua*. Depth records are from 27 to 32 m, in sand (DALL, 1886).

**Material seen:** 28 lots.

**Geologic Distribution and Biogeography:**

This species is known from the Pleistocene of Nome (MOFFIT, 1913; SMITH, 1919; MACNEIL, MERTIE & PILSBRY, 1943) and Kodiak Island (MADDREN, 1919; TWENHOFEL, 1952), Alaska. Records from Oregon (SMITH, 1919; HERTLEIN & CRICKMAY, 1925) probably represent misidentifications. It is also known in the Pliocene and Miocene of Alaska.

It seems closest to *Macoma obliqua* and perhaps represents populations of this species-group that remained in the Bering Sea, when, in the early Pliocene, *M. obliqua* became isolated in the Atlantic-Arctic.

*Macoma (Macoma) obliqua* (Sowerby, 1817)

(Plate 6, Figure 31; Plate 7, Figure 33; Text figure 14)

*Tellina obliqua* J. SOWERBY, 1817, not of WOOD, 1815 [conserved name, ICZN pending, COAN & SEALY, 1969]  
SOWERBY, 1817: 137-138; plate 161, figure 1  
WOOD, 1848: 228; plate 21, figures 7a-7d  
WOOD, 1874: 152, 216  
British Museum (Natural History), 1963: 106; plate 38, figures 7-9  
COAN, 1969a: 277-279  
[non WOOD, 1815: 152; plate 41, figures 4, 5]

*Tellina incongrua* von Martens, of authors, not of von Martens  
[NOT VON MARTENS, 1865: 430-431]

DALL, 1900a: 306 [*Macoma*]

OLDROYD, 1924: 52, 209; plate 10, figure 5

I. OLDROYD, 1925: 170; plate 42, figure 10

GRANT & GALE, 1931: 373

BURCH & BURCH, 1943: 18-19, 25 (text figure)

BURCH, 1945a: 3 (text figure), 10; 1945b: 17; 1945c: 30

MACGINITIE, 1959: 180

DUNNILL & ELLIS, 1969: 18-21, 33; figures 6 (2), 9 (m)

**Type Material:**

*Tellina obliqua* - BM(NH) Fossil Mollusca Section 43058, lectotype herein, larger left valve, 45.6 mm; paralectotype, smaller right valve. Plate 6, Figure 31.

*Tellina incongrua* (not a synonym) - Zoologisches Museum, Humboldt Universität, Berlin, 7624, lectotype herein, pair, figured by RÖMER, in KÜSTER & RÖMER (1871), 24.4 mm (von Martens' measurement of 33 mm is probably in error); paralectotypes, other specimens in same lot. Plate 6, Figure 32.

**Type Localities:**

*Tellina obliqua* - Red Crag, Suffolk, England; Pleistocene; G. R. Leathes.

*Tellina incongrua* - Yokohama, Japan.

**Nomenclatural Commentary:**

Specimens from the eastern Pacific are so very different from specimens from Japan that I initially considered naming the West American form a new species or subspecies. However, in investigating the relationships between the Pacific boreal fauna and that of the Miocene, Pliocene, and Pleistocene of the Atlantic Ocean, I discovered that the eastern Pacific species is identical with *Macoma obliqua* (Sowerby), described from the Red Crag (Pleistocene) of England (COAN, 1969a).

DALL (1900a) suggested that *Tellina rotundata* Sowerby, 1867, might be a synonym of *Macoma incongrua*, but an examination of the holotype showed that it is *M. balthica* (Linnaeus, 1758). Dall also suggested that *M. californiensis* Bertin, 1878, was a synonym. Photographs of the two syntypes of the latter, kindly provided by l'École des Mines, Paris, prove these to be specimens of

**Explanation of Plate 7**

Figure 33: *Macoma obliqua*, USNM 223682, Sitka Harbor, Alaska; 40.7 mm

Figure 34: *Macoma frigida*, lectotype (herein), BM(NH) 1907. 10.28.37-38; about 24 mm

Figure 35: *Macoma moesta moesta*. Holotype of *Tellina moesta*, BM(NH) without registry number; about 26 mm

Figure 36: *Macoma moesta moesta*. Lectotype (herein) of *Macoma krausei*, USNM 108606; 22.7 mm

Figure 37: *Macoma moesta moesta*. Lectotype (herein) of *Macoma oneilli*, NMC 4240; 21.4 mm

Figure 38: *Macoma moesta alaskana*. Lectotype (herein) of *Macoma alaskana*, USNM 108652; 14.4 mm

Figure 39: *Macoma crassula*. Holotype of *Tellina crassula*, BM(NH) without registry number; 16 mm

Figure 40: *Macoma crassula*. Lectotype (herein) of *Macoma inflata*, Redpath Museum 6151; about 13 mm





Figure 33

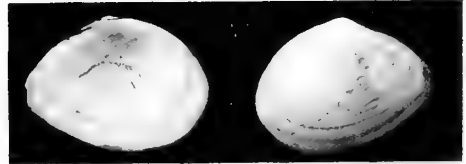


Figure 34



Figure 35

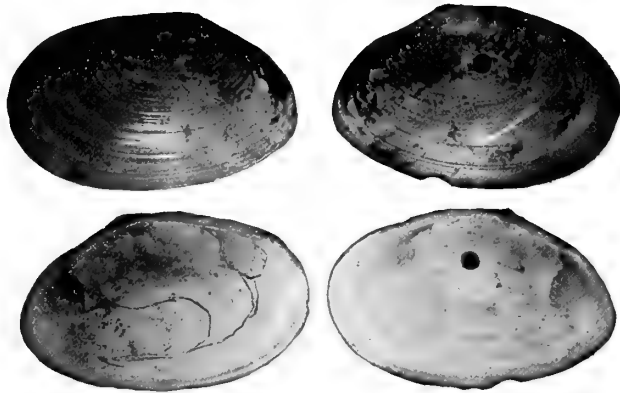


Figure 36

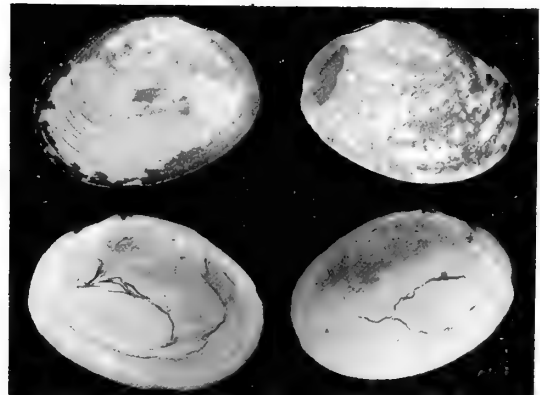


Figure 37

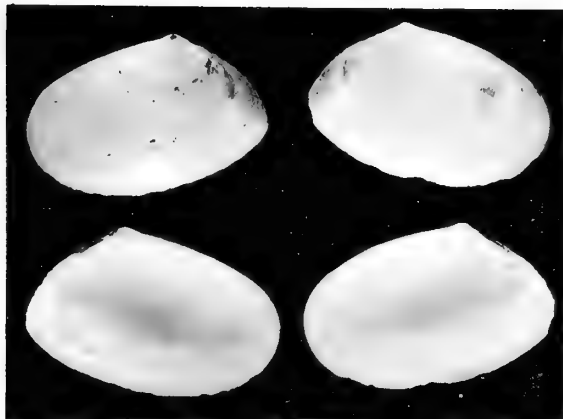


Figure 38



Figure 39

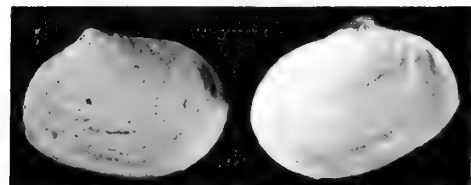


Figure 40



*Macalia bruguieri* (Hanley, 1844b), mislabeled as to locality, for this species is Asian.

#### Description:

Medium-sized (to 50 mm); ovate; inflated; heavy; almost equilateral to longer anteriorly; rounded anteriorly; slightly truncate posteriorly; sculpture of rounded growth lines; traces of dark periostracum present throughout;

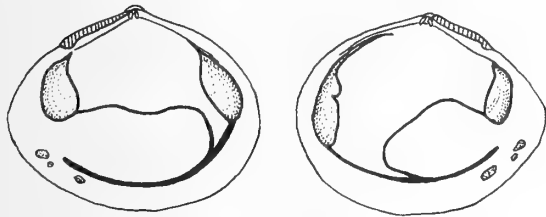


Figure 14

*Macoma obliqua*, internal view of valves  
USNM 223682, Sitka, Alaska; 40.7 mm

pallial sinuses partially detached from pallial line, that in left valve larger; pallial line vertically striated (Plate 7, Figure 33). Other internal details as in Text figure 14.

#### Geographic Distribution and Ecology:

Point Barrow, Alaska (USNM 207073), along the western coast of Alaska, throughout the Aleutian Islands as far east as Ostrov Beringa (USNM 108594), along the southern coast of Alaska, British Columbia, and as far south as off the northern portion of the outer coast of Washington (USNM 210313, 207220, 409608). Published records from near San Pedro, California (MATTOX, 1955; BANDY, 1958), probably represent identification errors (Jones, in correspondence), possibly of *Macoma carlotensis*. There is, however, one specimen (USNM 209537), a single, worn valve, from off Point La Jolla, California, in about 282 m. Without additional evidence, I would consider this to be either a fossil or a mislabeled lot. It has been taken in numbers of up to 151 per m<sup>2</sup> from the intertidal area to 183 m, especially over 50 m, in gravel to sand (DUNNILL, 1968; DUNNILL & ELLIS, 1969).

**Material seen:** 203 lots.

#### Geologic Distribution and Biogeography:

*Macoma obliqua* is known in the Pleistocene of Nome, Alaska (MOFFIT, 1913; MACNEIL, MERTIE & PILSBRY, 1943), southwestern British Columbia, Puget Sound, Oregon (ADDICOTT, 1966), and southern California (OLD-

ROYD & GRANT, 1931; RODDA, 1951), with a number of intermediate records.

Members of this species-complex were apparently among the first group of boreal *Macoma* to reach the Atlantic as a result of the late Miocene submergence of Bering Strait. Representatives are apparently *M. lyelli* Dall, 1894, from the late Miocene of Martha's Vineyard, Massachusetts, and *M. cookei* Gardner, 1943, from the late Miocene of Virginia. *Macoma obliqua* is present in the late Pliocene of England and Europe and the Pleistocene of England, Belgium, and Iceland; it has apparently become extinct in the Atlantic since the Pleistocene.

In the Recent fauna it is closest to *Macoma incongrua*, which occurs from the Kurile Strait, Kamchatka, south through Japan to Korea. I believe that the two should be regarded as distinct species in spite of the proximity of their ranges.

*Macoma obliqua* differs from *M. incongrua* in being more rounded posteriorly, heavier, and less twisted to the right posteriorly. The pallial sinuses do not extend as far dorsally; that in the left valve does not reach as far toward the anterior adductor muscle scar nor merge with it as it does in *M. incongrua*. The pallial sinuses parallel the ventral pallial line for a greater distance.

*Macoma incongrua* may be closely related to the next species, *M. frigida*.

#### *Macoma (Macoma) frigida* (Hanley, 1844)

(Plate 7, Figure 34; Text figure 15)

#### *Tellina frigida* Hanley

HANLEY, 1844b: 143-144

HANLEY, 1846: 327; plate 19, figure 119

KRAUSE, 1885: 36

#### Type Material:

BM(NH) 1907.10.28.37-38, lectotype herein, separated pair, about 24 mm, marked "T" and "X"; paralectotype, un-separated pair. Plate 7, Figure 34.

#### Type Locality:

Kamchatka; Petit collection to Hanley collection.

#### Nomenclatural Commentary:

I am not certain that this is a distinct species. The type specimens may even be unusual specimens of *Macoma calcarea*.

#### Description:

Small (to 30 mm); elongate; inflated; heavy; longer, rounded anteriorly; pointed posteriorly; periostracum dark, present as ventral fragments; shiny internally; pal-

lial sinuses detached from pallial line, that in left valve larger. Other internal details as in Text figure 15.

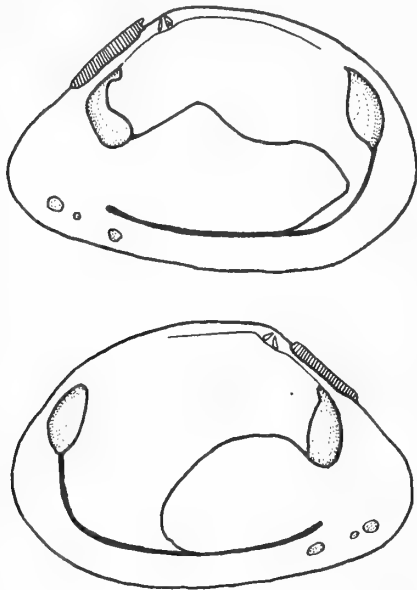


Figure 15

*Macoma frigida*, internal view of valves  
USNM 34034, "north of Bering Strait";  
left valve, 27 mm; right valve, 20 mm

#### Geographic Distribution and Ecology:

"North of the Bering Strait" (USNM 34034) and Kamchatka (type lot). The occurrence in Alaska is uncertain, and no ecologic data are available.

#### Geologic Distribution and Biogeography:

No fossil record. See previous species.

Species-group of *Macoma (Macoma) moesta* (Deshayes)

Small to medium in size (under 40 mm); chalky to smooth; periostracum dark to shiny.

*Macoma (Macoma) moesta moesta* (Deshayes, 1855)

(Plate 7, Figures 35-37; Text figure 16)

*Tellina moesta* Deshayes

DESHAYES, 1855: 361

SOWERBY, 1868: plate 52, figure 307

DALL, 1916a: 36 [*Macoma*]

I. OLDROYD, 1925: 173

GRANT & GALE, 1931: 370, 922; plate 20, figure 3

BURCH, 1945a: 11; 1945b: 17

SOOT-RYEN, 1958: 23

MACGINITIE, 1959: 182-184; plate 21, figure 3, plate 23, figure 10, plate 24, figures 1-3

OCKELMANN, 1959: 129-131; plate 2, figure 13

*Macoma krausei* Dall

DALL, 1900a: 307, 322, 326; plate 4, figure 8

DALL, 1916a: 36 [as a synonym of *Macoma moesta*]

*Macoma oneilli* Dall

DALL, 1919: 20; plate 2, figure 1

I. OLDROYD, 1925: 173; plate 40, figure 7

BURCH, 1945a: 14

#### Type Material:

*Tellina moesta* - BM(NH), without registry number, holotype, pair, about 26 mm. Plate 7, Figure 35.

*Macoma krausei* - USNM 108606, lectotype herein, pair, figured by DALL (1900a), 22.7 mm; USNM 663880, paralectotypes, 4 pairs and 1 valve. Plate 7, Figure 36.

*Macoma oneilli* - NMC 4240, lectotype herein, about 21.4 mm; NMC 40576, paralectotype, right valve; USNM 216896, "virtual paralectotype," pair. Plate 7, Figure 37.

#### Type Localities:

*Tellina moesta* - "Northern Ocean"; Cuming collection.

*Macoma krausei* - Off Icy Cape, Arctic Alaska; Captain E. E. Smith, 13 to 27 m, in sand.

*Macoma oneilli* - Dolphin and Union Strait, Mackenzie, Arctic Canada; Canadian Arctic Expedition station 43a, F. Johansen, 91 m, in mud.

#### Nomenclatural Commentary:

A defense of this synonymy is given by MACGINITIE (1959). There are additional synonyms in the Atlantic-Arctic. See also the next subspecies.

#### Description:

Small (to 30 mm); oval to oval-elongate; flattened; thin; longer, rounded anteriorly; broadly truncate to somewhat pointed posteriorly; periostracum thin, adherent, shiny; pallial sinuses partially detached from pallial line, that in left valve larger. Other internal details as in Text figure 16.

#### Geographic Distribution and Ecology:

Circum-arctic; Point Barrow (USNM 606408 and other lots), along the Arctic and west coasts of Alaska, throughout the Aleutian Islands, as far west as Kamchatka, and as far east as Chignik Bay on the Alaska Peninsula (USNM 663900). Low tide level to 260 m, in a variety of bottom types, mostly silt (SOOT-RYEN, 1958; OCKELMANN, 1959). Southern records of this species are in error or are of the next subspecies.

**Material seen:** 64 West American lots.

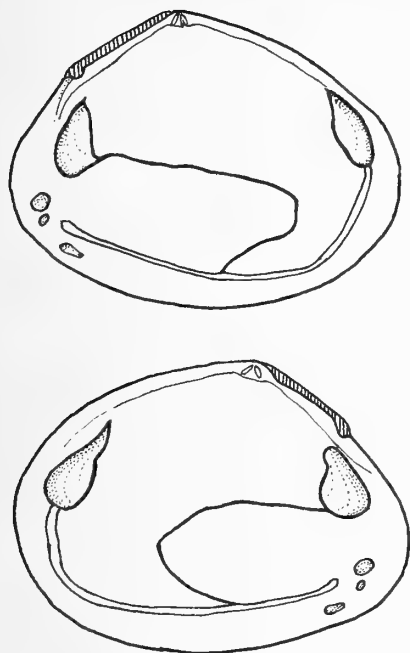


Figure 16

*Macoma moesta moesta*, internal view of valves  
USNM 606413, Point Barrow, Alaska; 25 mm

#### Geologic Distribution and Biogeography:

I know of no West American fossil records, nor of similar Asian species from south of Kamchatka.

#### *Macoma (Macoma) moesta alaskana* Dall, 1900

(Plate 7, Figure 38; Text figure 17)

#### *Macoma alaskana* Dall

- DALL, 1900a: 309, 323-324, 325; plate 3, figure 5  
 OLDROYD, 1924: 55, 208; plate 4, figure 5  
 I. OLDROYD, 1925: 177-178; plate 13, figure 14  
 BURCH & BURCH, 1943: 22, 25 (text figure - mislabeled  
 as *Macoma moesta*)  
 BURCH, 1945a: 3 (text figure), 15; 1945b: 17  
 T. BURCH, 1945: 30, 33; plate 2, figures 50, 51  
 DUNNILL & ELLIS, 1969: 6-8, 33; figures 2 (2), 9 (i)

#### Type Material:

USNM 108652, lectotype herein, pair, 14.4 mm; USNM 663878, paralectotypes, several juvenile specimens, some pairs. Plate 7, Figure 38.

#### Type Locality:

Lituya Bay, Alaska; W. H. Dall, 15 m, in sand.

#### Nomenclatural Commentary:

Specimens of this subspecies account for records of *Macoma moesta moesta* from east and south of the western end of Shelikoff Strait. Dall's type specimens were juveniles, and this may be the reason that he did not realize the similarity between his species and *M. moesta*.

There are moderately elongate, inflated specimens of this species-complex from the north end of the Bering Sea, and there are oval, flattened specimens of *M. moesta alaskana* from southern Alaska. The occurrence of specimens seems to be continuous, and the degree of inflation and elongation seems to be more or less gradational along this distribution. Such gradation and the fact that the name "*Macoma alaskana*" is well-known in British Columbia, have influenced my decision to reach a nomenclatural compromise. However, I do not consider this problem solved, never having had the opportunity to study all available material at one time. Most collections have only a few lots. I would recommend that further study be carried out, using statistical measurements of several characters.

#### Description:

Small (to 25 mm); elongate; moderately inflated; thin; much longer, rounded anteriorly; pointed, truncate posteriorly; periostracum thin, adherent, shiny; pallial sinuses partially detached from pallial line, that in left valve larger. Other internal details as in Text figure 17.

#### Geographic Distribution and Ecology:

Kodiak Island area, Alaska (USNM 208625, 40216), to Tofino, outer coast of Vancouver Island, British Colum-

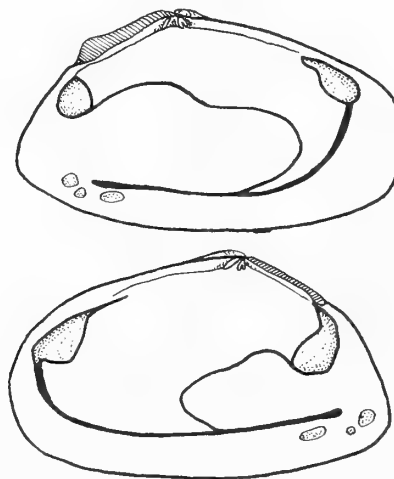


Figure 17

*Macoma moesta alaskana*, internal view of valves  
USNM 108652, lectotype (herein); 14.4 mm

bia (Cowan Collection), and Seattle, Washington (University of Washington Collection). The source of MACGINITIE'S (1959) record from Monterey, California, is unclear and presumably in error. It has been taken from 1 to 260 m, especially below 50 m, in several bottom types (DUNNILL, 1968; DUNNILL & ELLIS, 1969).

**Material seen:** 35 lots.

#### Geologic Distribution and Biogeography:

There is only one probable fossil record of this subspecies, SMITH (1919) in the late Pleistocene of Victoria, British Columbia, as "*Macoma krausei*." Its closest affinities are, of course, with the northern *M. moesta moesta*.

*Macoma (Macoma) crassula* (Deshayes, 1855)  
(Plate 7, Figures 39, 40; Plate 8, Figure 41; Text figure 18)

*Tellina crassula* Deshayes

DESHAYES, 1855: 354

SOWERBY, 1868: plate 54, figures 319a, 319b

*Macoma inflata* Dawson, ex Stimpson MS, but not the *Macoma inflata* Dawson of authors

DAWSON, 1872: 377-378; plate 5, figure 5

[Not preoccupied by *Tellina inflata* GMELIN, 1791, ex CHEMNITZ MS: 3230]

*Tellina (Macoma) torelli* Jensen, ex J. Steenstrup MS

JOHNSTRUP, 1882, ex J. STEENSTRUP MS: 8 [*nomen nudum*] [as a "*forma*" of *Tellina crassula*]

JENSEN, 1905a: 34-38, 52; plate 1, figures 3a-3i

JENSEN, 1905b: 149-151

JENSEN, 1905c: 343-345 (figures 3a-3h)

OCKELMANN, 1959: 134-135; plate 2, figure 12 [*Macoma*]

#### Type Material:

*Tellina crassula* - BM(NH), without registry number, holotype, pair, 16 mm. Plate 7, Figure 39.

*Macoma inflata* - Redpath Museum, McGill University, 6151, lectotype herein, figured by DAWSON (1872), right valve, about 13 mm; paralectotypes, 5 valves in same lot, 6 valves in 6152, and 10 valves in an unnumbered lot. The last includes 3 valves of *Macoma loveni* (Jensen). Plate 7, Figure 40.

*Tellina torelli* - Zoologiske Museum, University of Copenhagen, lectotype herein, pair, about 12.8 mm. This specimen is regarded as a lectotype because Jensen had material from many sources. Plate 8, Figure 41.

#### Type Localities:

*Tellina crassula* - "Northern Ocean"; Cuming collection. This specimen probably came from either the Canadian or Alaskan Arctic.

*Macoma inflata* - Rivière du Loup, Quebec, Canada; Pleistocene; J. W. Dawson.

*Tellina torelli* - West Greenland; Captain C. Holböll.

#### Nomenclatural Commentary:

This typically high-arctic species has usually been known as *Macoma torelli* (Jensen). *Tellina crassula*, described from an unknown locality in the "Northern Ocean," seems to be a senior synonym of this species. JENSEN (1905a) considered this possibility, because the first appearance of *M. torelli* (as a *nomen nudum*) was as a "form" of *T. crassula* by JOHNSTRUP (1882). After studying drawings of the holotype of *T. crassula* he concluded that Deshayes' specimen differed from his material in having shorter, nearly equal pallial sinuses. This conclusion is verified in my photographs of the type specimens of both species. These differences seem to be within the range of variation of the species. This requires further verification as there are few specimens available for study.

In any case, it may be wise to synonymize *Tellina torelli* with *T. crassula*, because this species would have to change names anyway. Many workers assumed that *Macoma inflata* Dawson was a *nomen nudum*, evidently missing Dawson's figure validating the name. Many also assumed that the name was preoccupied by GMELIN (1791), but the latter was proposed in *Tellina* and is a *Tellina* (*Tellina inflata* Sowerby, 1867, is a *Macoma*, but that combination cannot preoccupy Dawson's name, since Sowerby's name is preoccupied by Gmelin's). Having worked out this nomenclatural tangle, I suspected that Dawson's name would be the older one for the well-known Arctic *Macoma loveni* (Jensen), because authors had always listed *M. inflata* as a synonym of the former and Dawson's figure did appear to be of *M. loveni*. At last locating the type specimens of *M. inflata*, I was surprised to find that they were almost entirely *M. torelli*, rather than *M. loveni*, including the valve figured by Dawson.

Apparently the same species or a very similar one is found off northern Japan, where it has been reported as *Macoma nipponica* (Tokunaga, 1906) (HABE & ITO, 1965; GOLIKOV & SCARLATO, 1967). What is reported and illustrated by HABE & ITO (*op. cit.*) from the Bering Sea as *M. torelli* appears to be *M. balthica*.

Specimens I have studied (or seen illustrated) from the Pleistocene and Recent of the North Atlantic and from Point Barrow are more triangular, have more prominent beaks, and are thinner and more sharply truncate posteriorly than the one valve from Nunivak Island, Alaska, and the two lots from Japan in the USNM. It is possible that Atlantic-Arctic material may be separable from Bering Sea-Japanese material, either as a species or subspecies. As few specimens are available and members of the genus are variable, I do not feel justified in making a firm decision now.

**Description:**

Small (to 21 mm; Japanese specimens to 30 mm); ovate to ovate-elongate; inflated; proportionately heavy; longer, rounded anteriorly; abruptly truncate posteriorly; beaks often prominent; periostracum dark, thin; pallial sinuses partially detached from pallial line, that in left valve larger. Other internal details as in Text figure 18.

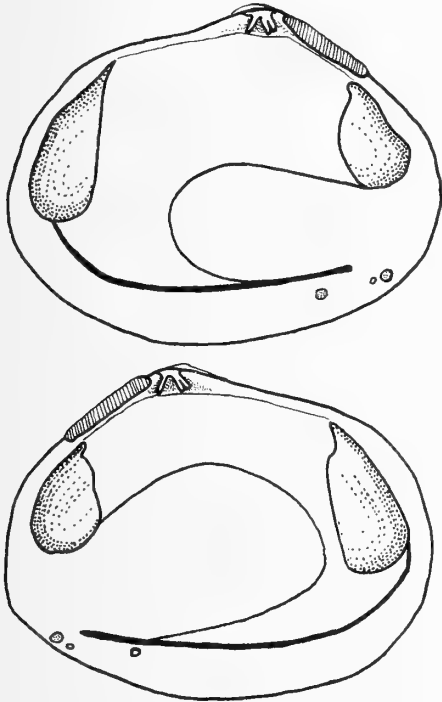


Figure 18

*Macoma crassula*, internal view of valves outline and details of left valve from CAS 34342, Point Barrow, Alaska; 17 mm. Details of right valve from JENSEN, 1905a.

**Geographic Distribution and Ecology:**

Evidently circum-arctic; in Alaska it has been taken only at Point Barrow (CAS 34242) and at the north end of Nunivak Island (USNM 664920). It is found from 16 to 161 m, in gravel (OCKELMANN, 1959; GOLIKOV & SCARLATO, 1967).

**Material seen:** 2 West American lots.

**Geologic Distribution and Biogeography:**

As a fossil, the species is known only from the Pleistocene of the North Atlantic. As is the case with other species of *Macoma*, it may have had its origin in the northern Pacific and may be a recent arrival in the Arctic-Atlantic.

*Macoma (Macoma) loveni* (Jensen, 1905)

(Plate 8, Figures 42, 43; Text figure 19)

*Tellina (Macoma) loveni* Jensen, ex J. Steenstrup MS

JOHNSTRUP, 1882, ex J. STEENSTRUP MS: 8 [*nomen nudum*] [as a "forma" of *Tellina moesta*]

JENSEN, 1905a: 45-52; plate 1, figures 5a-5h

JENSEN, 1905b: 151-152

JENSEN, 1905c: 348-350 (figures 5a-5e)

SOOT-RYEN, 1958: 24-25 [*Macoma*]

OCKELMANN, 1959: 132-134; plate 2, figure 11

HABE & ITO, 1965: 146; plate 50, figure 17

GOLIKOV & SCARLATO, 1967: 125-126 (figure 108)

**Type Material:**

Zoologiske Museum, University of Copenhagen, lectotype herein, smaller right valve, 12 mm. This valve seems to be one figured by JENSEN (1905a: plate 1, figure 5h) (the label with the lot also bears instructions in Jensen's writing for the preparation of a figure from the smaller of two specimens; his figure 5h is closest to the size of this valve); paralectotype, larger right valve. Plate 8, Figure 42.

**Type Locality:**

Asåby, east coast of Vendsyssel, northern Denmark; Pleistocene ["*Yoldia*-layer"].

**Nomenclatural Commentary:**

Some workers have regarded *Macoma inflata* Dawson, 1872, as a synonym of this species. However, the type specimens prove to be of the preceding species.

**Description:**

Small (to 17 mm); oval; very inflated; thin; longer, rounded, expanded anteriorly; rounded, very slightly truncate posteriorly; periostracum thin, brown; pallial sinuses partially detached from pallial line, that in left valve larger (Plate 8, Figure 43). Other internal details as in Text figure 19.

**Geographic Distribution and Ecology:**

Circum-arctic. In Alaska it has been taken only near Point Barrow (CAS 34341, 34342, 34343, 34344, 34597, 34598), but it has been reported in the Bering Sea (HABE & ITO, 1965) and at Possiet Bay, Siberia (GOLIKOV & SCARLATO, 1967), and there are USNM specimens from northern Japan. It may eventually be found along the eastern edge of the Bering Sea. It has been taken in from 4 to 816 m, in various bottom types, most common in coarse sediments (SOOT-RYEN, 1958; OCKELMANN, 1959; GOLIKOV & SCARLATO, 1967).

**Material seen:** 6 West American lots.

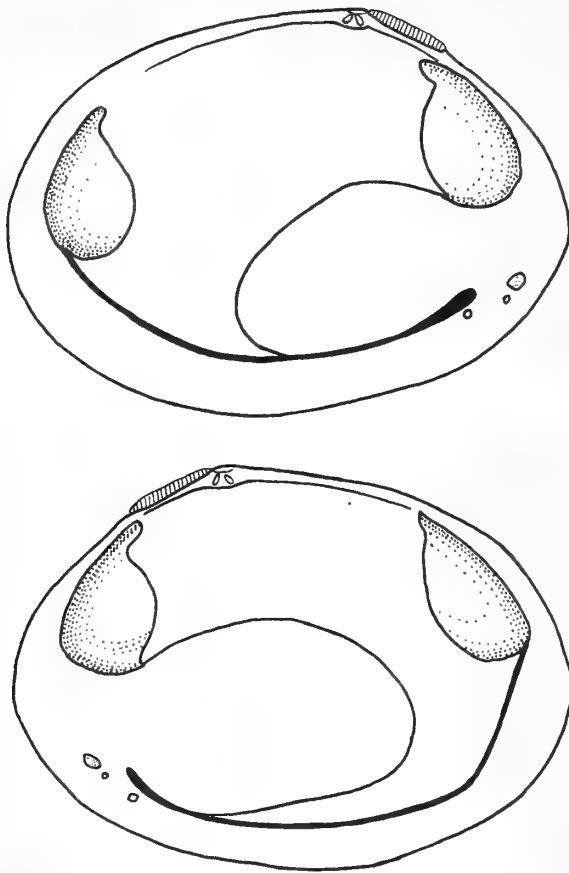


Figure 19

*Macoma loveni*, internal view of valves, CASGTC 13621  
CAS locality 34342, Point Barrow, Alaska; 15.2 mm

#### Geologic Distribution and Biogeography:

There are no fossil records in the northern Pacific, but the species is present in the Pleistocene of Canada and northern Europe.

#### *Macoma (Macoma) lama* (Bartsch, 1929) (Plate 8, Figures 44, 45; Text figure 20)

##### *Macoma lama* Bartsch

BARTSCH, 1929: 133; plate 2, figures 8-14

GOLIKOV & SCARLATO, 1967: 127 (figure 110)

##### *Macoma planiuscula* Grant & Gale

GRANT & GALE, 1931: 372, 908, 922; plate 14, figure 11, plate 20, figure 8

BURCH & BURCH, 1943: 21, 25 (text figure)

BURCH, 1945a: 3 (text figure), 14; 1945b: 17

MACGINITIE, 1959: 180

*Macoma carlottensis* Whiteaves, of authors, not of Whiteaves  
[not WHITEAVES, 1880: 196B-197B (text figure 1) - see same]

DALL, 1900a: 308

#### Type Material:

*Macoma lama* - USNM 369064, holotype, pair, 28.7 mm.  
Plate 8, Figure 44.

*Macoma planiuscula* - SUPTC 977, holotype, pair, 23.3 mm;  
SUPTC 8066, paratype, pair. Plate 8, Figure 45.

#### Type Localities:

*Macoma lama* - Uncertain; K. Derjugin. The description implies the west coast of Kamchatka, but the USNM labels and catalogue say "near Vladivostok, Manchuria," and are more likely correct.

*Macoma planiuscula* - Nunivak Island, Alaska; probably originally from USNM material.

#### Nomenclatural Commentary:

In addition to the complications indicated above, MACGINITIE (1959) first suggested that this Recent Pacific-Arctic species may be equivalent to *Macoma praetenuis* (Woodward, 1833), described from the Red Crag (Pleistocene) of England and known only from the Red Crag and equivalent deposits on the mainland of Europe. Some consistent morphological differences, however, can be found. *Macoma praetenuis* is larger, thinner, more rounded and less flexuous posteriorly, and it has a less prominent posterior diagonal ridge. To set aside Pleistocene material

#### Explanation of Plate 8

Figure 41: *Macoma crassula*. Lectotype (herein) of *Tellina torelli*. Zoologisk Museum, University of Copenhagen; 12.8 mm

Figure 42: *Macoma loveni*. Lectotype (herein) of *Tellina loveni*, Zoologisk Museum, University of Copenhagen; 12 mm

Figure 43: *Macoma loveni*, CASGTC 13621, CAS locality 34342, Point Barrow, Alaska; 15.2 mm

Figure 44: *Macoma lama*, holotype, USNM 369064; 28.7 mm

Figure 45: *Macoma lama*. Holotype of *Macoma planiuscula*, SUPTC 977; 23.3 mm

Figure 46: *Macoma yoldiformis*, lectotype (herein), USNM 4507; 11.7 mm



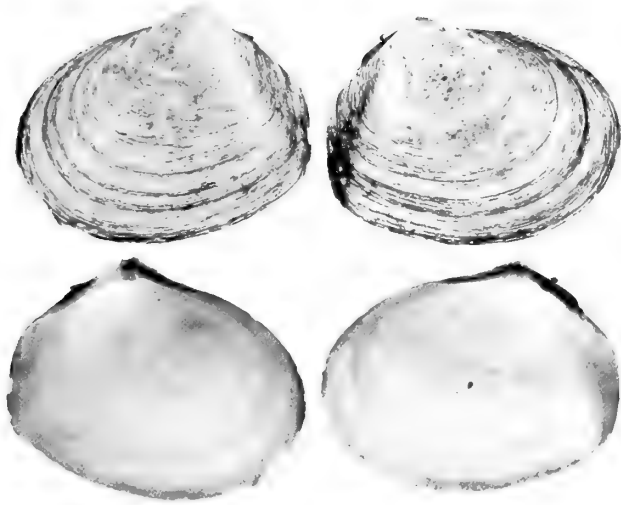


Figure 41



Figure 42

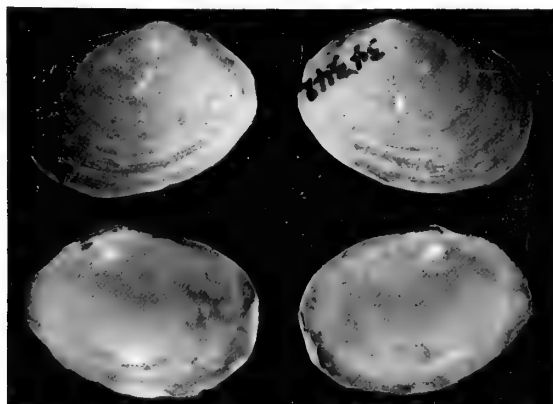


Figure 43

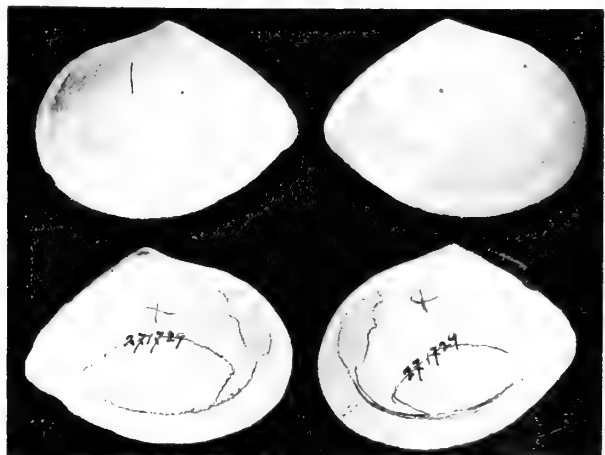


Figure 45

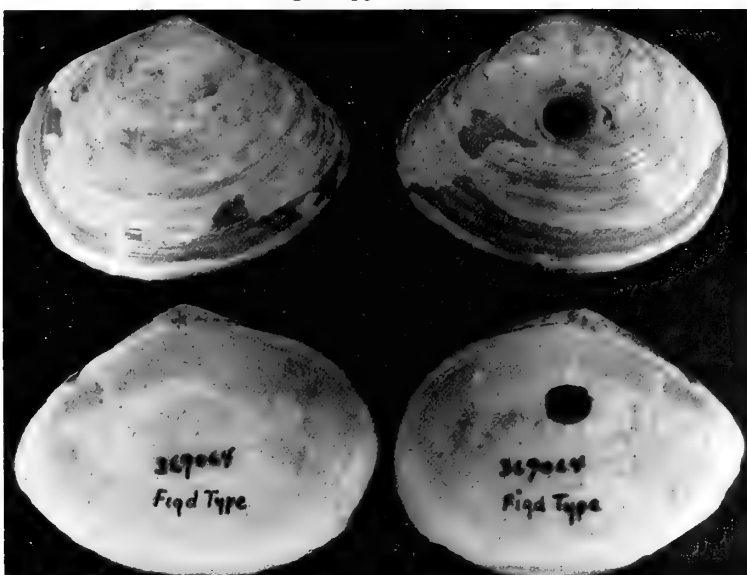


Figure 44

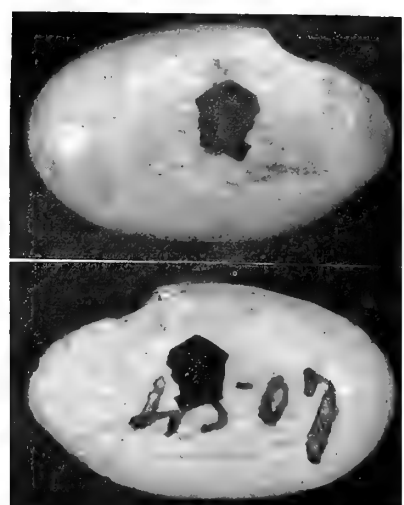


Figure 46



as species distinct from Recent ones is not a common practice. However, because this species is no longer living in the Atlantic sector of the Arctic and because there are consistent morphological differences, I defer to the expressed preference of European workers (Sealy, in correspondence).

#### Description:

Medium-sized (to 41 mm); oval; flattened; heavy; almost equilateral to somewhat longer posteriorly; rounded anteriorly; pointed, often slightly twisted to right posteriorly; periostracum heavy, shiny; pallial sinuses partially detached from pallial line, that in the left valve larger. Other internal details as in Text figure 20.

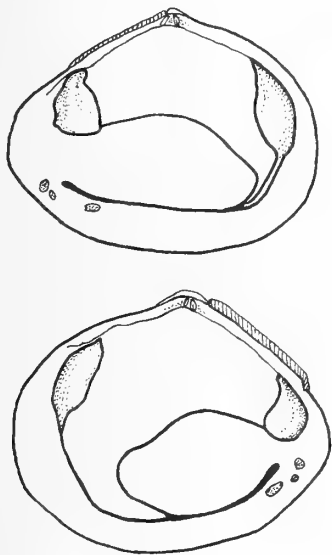


Figure 20

*Macoma lama*, internal view of valves

USNM 271729, Saint Paul Island, Pribilof Islands, Alaska  
36 mm

#### Geographic Distribution and Ecology:

Dease Inlet, Arctic Alaska (USNM 363166), along the Bering Sea coast of Alaska, throughout the Aleutian Islands, Kamchatka, and south to the Vladivostok area (GOLIKOV & SCARLATO, 1967), along the south coast of Alaska, to the northern end of the Queen Charlotte Islands, British Columbia (SU 8754). It occurs from the intertidal area to 183 m, probably on fairly exposed coasts, in sand (GOLIKOV & SCARLATO, *op. cit.*).

Material seen: 104 lots.

#### Geologic Distribution and Biogeography:

I know of no West American fossil records except as misidentifications of *Macoma elimata* Dunnill & Coan, 1968. The presence of an ancestor in the Pleistocene of Europe and not in the northern Pacific suggests that differentiation of this species may have been associated with the second period of submergence of Bering Strait, that in the early Pleistocene. Among Recent species, it seems most closely related to *Macoma moesta moesta*.

(*Psammacoma*) Dall, 1900a

[Type species: *Psammotaea candida* Lamarck, 1818, by original designation]

Small to large in size (20 to 70 mm); thin; inflated, especially anteriorly; approximately equivalve; rounded to elongate; generally longer and sharply rounded anteriorly; conspicuously pointed or truncate and very slightly twisted to right posteriorly; periostracum thin, dark to shiny; no escutcheon or lunule present; ligament sometimes slightly sunken; pallial sinuses comparatively short, approximately equal in size to somewhat longer in left valve, detached from pallial line along at least half of their length.

The last two species are only tentatively assigned to this subgenus.

*Macoma (Psammacoma) yoldiformis* Carpenter, 1864

(Plate 8, Figure 46; Text figure 21)

*Macoma yoldiformis* Carpenter

CARPENTER, 1864a: 602, 611, 639 [1872: 88, 97, 125]

CARPENTER, 1865c: 55

DALL, 1900a: 309

ARNOLD, 1903: 165, 394; plate 16, figure 6

PACKARD, 1918: 280; plate 25, figure 6

OLDROYD, 1924: 54-55, 214; plate 41, figure 6

I. OLDROYD, 1925: 177; plate 44, figure 6

GRANT & GALE, 1931: 373

BURCH & BURCH, 1943: 22, 24 (text figure)

BURCH, 1945a: 3 (text figure), 15; 1945b: 16; 1945c: 30

T. BURCH, 1945: 30, 33; plate 2, figures 48, 49

PALMER, 1958: 17, 22, 27, 34, 38, 48, 108-109, 339; plate 14, figures 2-4

DUNNILL & ELLIS, 1969: 7, 30-33; figures 2 (2), 9 (j)

#### Type Material:

USNM 4507, lectotype herein, left valve, 11.7 mm. PALMER (1958) suggested that this valve be made a neotype on the grounds that Swan was not among the originally listed collectors. However, Swan was mentioned in the original account (CARPENTER, 1864a), and the other lots have apparently been subsequently lost. Plate 8, Figure 46.

**Type Locality:**

Neah Bay, Washington; J. G. Swan.

**Nomenclatural Commentary:**

None necessary.

**Description:**

Small (to 25 mm); elongate; inflated; thin; longer, rounded anteriorly; pointed, rostrate posteriorly; postero-dorsal margin often somewhat produced into a flange; periostracum shiny, adherent; pallial sinuses partially detached from pallial line, approximately equal in size to slightly larger in left valve. Other internal details as in Text figure 21.

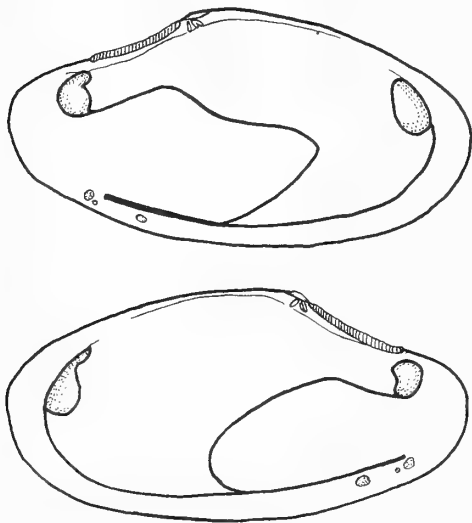


Figure 21

*Macoma yoldiformis*, internal view of valves outline from USNM 4507, lectotype (herein); 11.7 mm  
Internal details from USNM 73465, San Diego, California

**Geographic Distribution and Ecology:**

Dall Island, southern Alaska (UCLA 20511), with

many records along the coasts of British Columbia, Washington, Oregon, and California, and to Bahía San Bartolomé, Baja California Sur (USNM 266150, 554483, 554531). Depth records are from the intertidal area to 93 m, in bays and offshore, in silt to sand (BURCH, 1945a; DUNNILL, 1968; DUNNILL & ELLIS, 1969).

**Material seen:** 100 lots.

**Geologic Distribution and Biogeography:**

In the late Pleistocene this species has been reported from Goleta, California (OLDROYD & GRANT, 1931), to Laguna San Ignacio, Baja California Sur (JORDAN, 1924; HERTLEIN, 1934), with several intermediate records. In the early Pleistocene, it is known only from the San Pedro area, California (ARNOLD, 1903; CLARK, in NATLAND, 1957). It has also been reported from southern Californian formations transitional between the Pliocene and the Pleistocene, as well as in the Pliocene of central California. *Macoma wilcoxi* Hall & Ambrose, 1916, described from the Miocene of central California, may be related.

I know of no related Asian species. *Macoma yoldiformis* most closely resembles the next species, from which it differs in being thinner and more rostrate posteriorly. Of species in the Panamic province, it differs from *M. (Psammacoma) elytrum* Keen, 1958a, in being shorter anteriorly, more rostrate, and more shiny; it differs from *M. (P.) siliqua* (C. B. Adams, 1852a) in being larger, less inflated, less twisted and not so broadly truncate posteriorly, and more shiny. There are also Caribbean species that belong in this subgenus.

*Macoma (Psammacoma) acolasta* Dall, 1921

(Plate 9, Figures 47, 48; Text figure 22)

*Macoma acolasta* Dall

DALL, 1921b: 21-22

DALL, 1925: 19, 36; plate 8, figures 2, 3

GRANT & GALE, 1931: 371, 908, 922; plate 14, figure 7, plate 20, figures 4a, 4b, 10 [as a variety of *Macoma moesta* (Deshayes)]

*Macoma morroensis* T. Burch

T. BURCH, 1945: 30, 33; plate 2, figures 46, 47

**Explanation of Plate 9**

Figure 47: *Macoma acolasta*, lectotype (herein), USNM 333133; 22 mm

Figure 48: *Macoma acolasta*. Holotype of *Macoma morroensis*, USNM 434051; 20 mm

Figure 49: *Macoma carlottensis*, lectotype (herein), NMC 316; 13 mm

Figure 50: *Macoma carlottensis*. Holotype of *Macoma inflatula*, USNM 107643; 23.8 mm

Figure 51: *Macoma carlottensis*. Lectotype (herein) of *Macoma quadrana*, USNM 225421; 12.3 mm

Figure 52: *Macoma leptonoidea*, holotype, USNM 125532; 16.5 mm

Figure 53: *Macoma secta*. Holotype of *Tellina secta*, BM(NH) Nuttall collection 1861.5.21.161; 50 mm

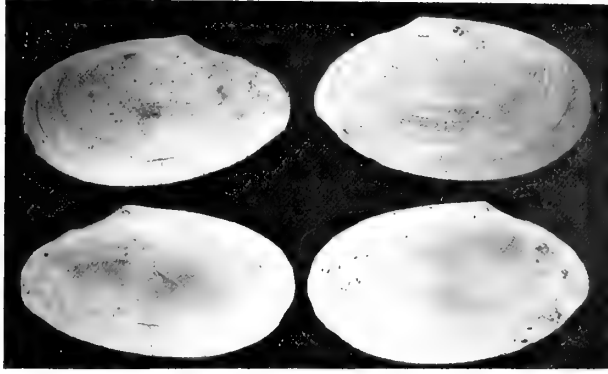


Figure 47

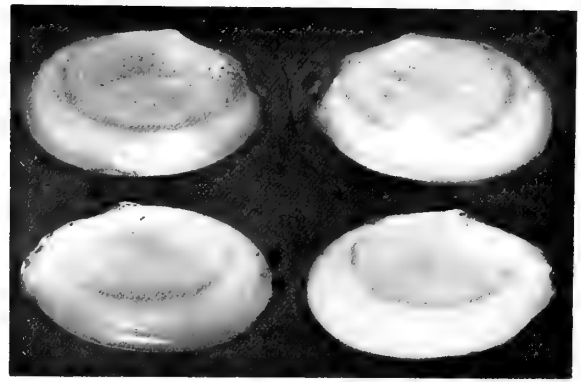


Figure 48

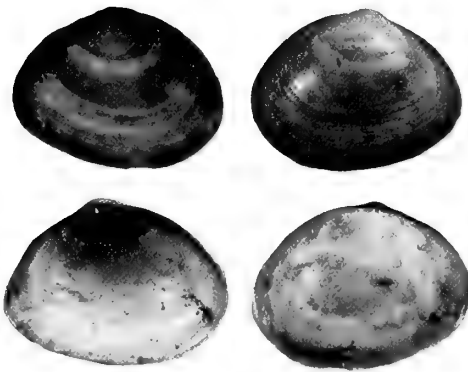


Figure 49

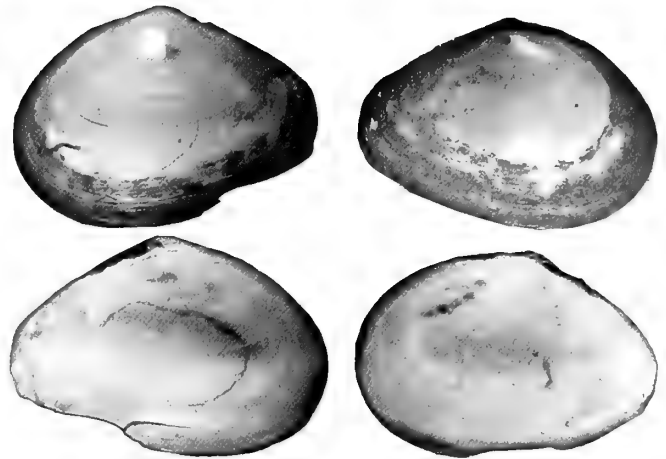


Figure 50

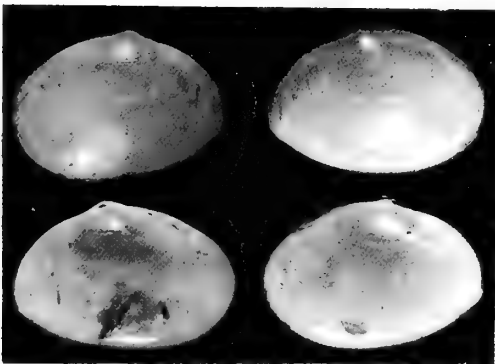


Figure 51

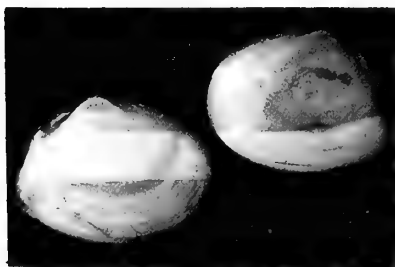


Figure 53

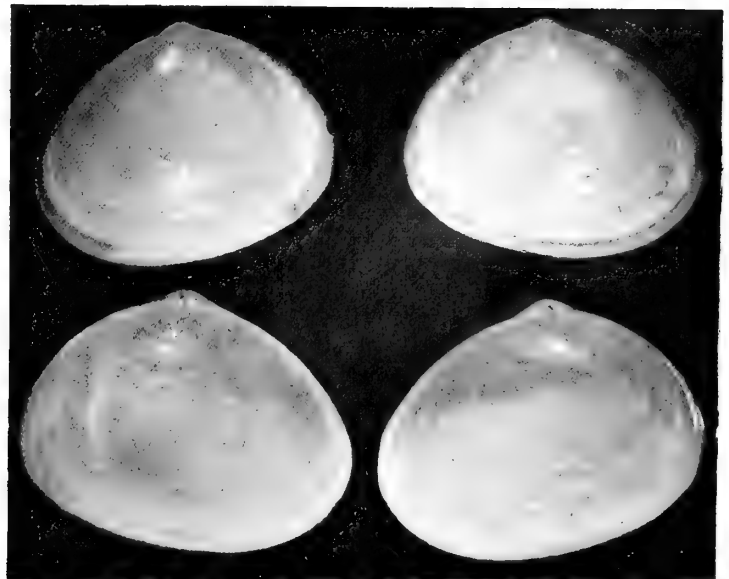


Figure 52



**Type Material:**

*Macoma acolasta* – USNM 333113, lectotype herein, right valve, 22 mm; USNM 645418, paralectotype, left valve, 21.5 mm. Plate 9, Figure 47.

*Macoma morroensis* – USNM 434051, holotype, pair, 20.0 mm; UCLA 20516, paratypes, 2 pairs. Plate 9, Figure 48.

**Type Localities:**

*Macoma acolasta* – Bahía San Quintín, Baja California Norte; late Pleistocene [as “late Pliocene or early Pleistocene”]; C. R. Orcutt.

*Macoma morroensis* – Morro Bay, California; M. Caruthers, intertidal area.

**Nomenclatural Commentary:**

It is unfortunate that Tom Burch overlooked Dall's Pleistocene name. His description of *Macoma morroensis* and comparisons were thorough and well stated.

This species was confused by GRANT & GALE (1931) with *Macoma moesta*. It differs from the latter in being longer and less angular posteriorly, in having a thinner and less adherent periostracum, and in having more equal pallial sinuses.

**Description:**

Small (to 30 mm); elongate; inflated; thin; longer, rounded anteriorly; pointed to truncate posteriorly; periostracum adherent, shiny; pallial sinuses partly detached from pallial line, approximately equal in size. Other internal details as in Text figure 22.

**Geographic Distribution and Ecology:**

Bodega Bay, California (Roth Collection), to San Diego, California (SDNHM L2388), with several intermediate records. It has been collected in the intertidal area to 73 m, in sand.

Material seen: 20 lots.

**Geologic Distribution and Biogeography:**

In the late Pleistocene, *Macoma acolasta* is known from Goleta, California (GRANT & GALE, 1931), to Bahía San Quintín, Baja California Norte (DALL, 1921b; JORDAN, 1926; MANGER, 1934; VALENTINE & MEADE, 1961), with three intermediate localities.

My comments for the preceding species with regard to relationships also apply to the present one.

***Macoma* (? *Psammacoma*) *carlottensis* Whiteaves, 1880**

(Plate 9, Figures 49 - 51; Text Figure 23)

***Macoma carlottensis* Whiteaves**

WHITEAVES, 1880: 196B-197B (text figure 1)

I. OLDROYD, 1925: 175-176

GRANT & GALE, 1931: 372, 922; plate 20, figures 1, 2

BURCH & BURCH, 1943: 21, 24, 25 (text figures)

BURCH, 1945a: 3, 4 (text figures), 13, 14; 1945b: 17; 1945c: 30

DUNNILL & ELLIS, 1969: 13-15, 21, 33; figures 6 (l), 9 (k)

***Macoma inflatula* Dall**

DALL, 1897: 11-12; plate 1, figures 19, 20

DALL, 1900a: 307

OLDROYD, 1924: 54, 208; plate 4, figure 6

I. OLDROYD, 1925: 174; plate 1, figures 2, 8, plate 13, figure 15

***Macoma quadrana* Dall**

DALL, 1916a: 37 [nomen nudum]

DALL, 1916b: 414

OLDROYD, 1924: 55

I. OLDROYD, 1925: 175; plate 3, figure 6

BURCH & BURCH, 1943: 20-21, 25 (text figure)

BURCH, 1945a: 3 (text figure), 14; 1945b: 17, 21

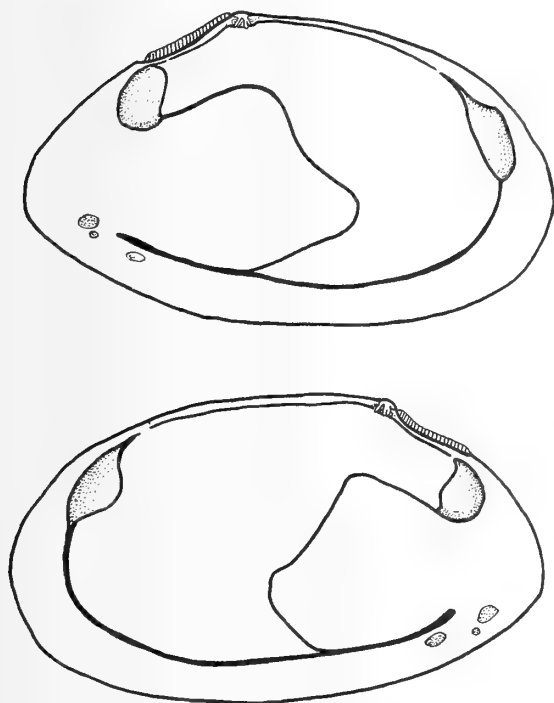


Figure 22

*Macoma acolasta*, internal view of valves  
USNM 194311, Santa Barbara, California; 21 mm

**Type Material:**

*Macoma carlottensis* – NMC 316, lectotype herein, largest pair, 13.0 mm; NMC 40577, paralectotypes, 6 pairs and 2 valves. Plate 9, Figure 49.

*Macoma inflatula* – USNM 107643, holotype, pair, 23.8 mm.  
Plate 9, Figure 50.

*Macoma quadrana* – USNM 225421, lectotype herein, pair, 12.3 mm; USNM 663891, paralectotypes, 6 pairs. Plate 9, Figure 51.

#### Type Localities:

*Macoma carlottensis* – Virago Sound, Graham Island, Queen Charlotte Islands, British Columbia; G. M. Dawson, 15 to 27 m.

*Macoma inflatula* – Dutch Harbor, Captain's Bay, Unalaska Island, Aleutian Islands, Alaska; W. H. Dall, 9 m.

*Macoma quadrana* – South and slightly west of Point Conception, California, about halfway to San Miguel Island; USFC 2892, 519 m, in yellow mud.

#### Nomenclatural Commentary:

GRANT & GALE (1931) were the first to discover what the true *Macoma carlottensis* was and to conclude that *M. inflatula* is a synonym of it. Whiteaves' specimens were juveniles and rather equilateral.

Populations of this species are found continuously along the entire West Coast, from Alaska to Baja California. In the northern portion of the range, large, inflated specimens are more common than they are in California, but one can find occasional southern Californian lots that con-

tain large individuals. Young specimens are often more quadrate than adults, and I cannot see sufficient grounds for recognizing *Macoma quadrana*.

#### Description:

Small (to 30 mm); ovate-elongate; inflated, most so anteriorly; thin; almost equilateral to longer anteriorly; rounded anteriorly; pointed to broadly truncate posteriorly; periostracum shiny, adherent, straw-colored; pallial sinuses detached from pallial line, that in left valve larger. Other internal details as in Text figure 23.

#### Geographic Distribution and Ecology:

Adak Island, Aleutian Islands, Alaska (USNM 108678), along the south coasts of Alaska, throughout British Columbia, Washington, Oregon, and California, and south to Islas Los Coronados, Baja California Norte (USNM 209263, 211233) and Isla Las Animas, Gulf of California (Berry Collection 35622, 35630). Dall's record from the Arctic Ocean proves to be based on specimens of *Macoma frigida* (Hanley). Other records from Baja California Sur are in error. It has been taken in from 5 to 1547 m, in silt to fine sand (DUNNILL, 1968; DUNNILL & ELLIS, 1969) and occurs in shallower water in the northern portion of its range.

Material seen: 162 lots.

#### Geologic Distribution and Biogeography:

Specimens of this species (or its synonyms) have been reported in the late Pleistocene of Capistrano, California (WILLET, 1938, as "cf."), from the early Pleistocene of the Santa Barbara area, California (KEEN & BENTSON, 1944; DIBBLEE, 1966, both as "cf."), and the San Pedro area, California (WILLET, 1937; BURCH, 1947).

I know of no close relatives in Asia nor in the Panamic province. Considering this lack of related species and its abundance in fine, offshore sediments, I would suggest that it be compared with *Macoma diabloensis* Clark, 1915, and *M. pabloensis* Clark, 1915, from the Miocene of central California.

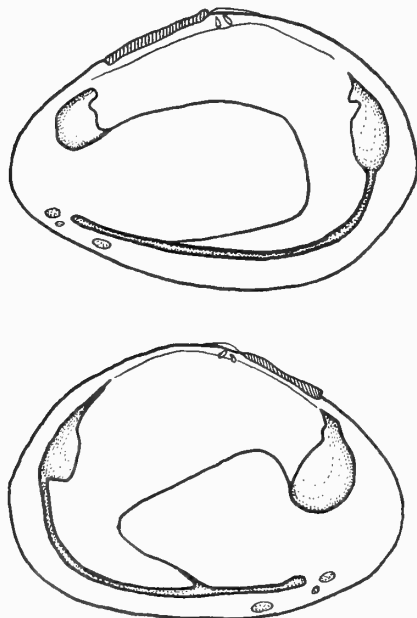


Figure 23

*Macoma carlottensis*, internal view of valves  
USNM 108690, Captain's Bay, Unalaska, Aleutian Islands, Alaska  
25 mm

*Macoma* (? *Psammacoma*) *leptonoidea* Dall, 1895  
(Plate 9, Figure 52; Text figure 24)

*Macoma leptonoidea* Dall

DALL, 1895: 33

DALL, 1900a: 308, 323, 325, 326; plate 4, figures 4, 9

I. OLDRYD, 1925: 175

BURCH & BURCH, 1943: 21

BURCH, 1945a: 13-14; 1945b: 17



**Type Material:**

USNM 125532, holotype, pair, about 16.5 mm. Plate 9, Figure 52.

**Type Locality:**

"Matagorda Bay, Texas," in error, probably from the larger of two USNM lots, USNM 108578, USFC 2903, north of the eastern end of Santa Rosa Island, about halfway between Santa Rosa Island and the mainland, Santa Barbara Channel, California, 589 m, in gravel and mud. How the locality confusion occurred is not clear.

**Nomenclatural Commentary:**

None necessary.

**Description:**

Small (to 20 mm); oval; inflated; very thin; slightly longer anteriorly; beaks and hinge minute; rounded anteriorly and posteriorly; periostracum very thin, adherent, shiny; pallial sinuses partially detached from pallial line, almost equal in size. Other internal details as in Text figure 24.

**Geographic Distribution and Ecology:**

This species has been taken only four times, and only off Santa Barbara, from about 483 to 594 m, in silt.

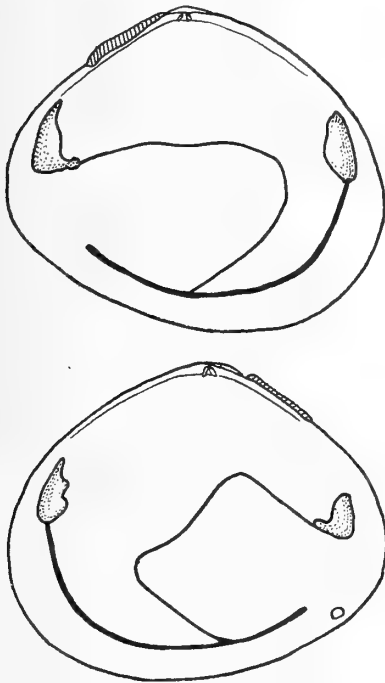


Figure 24

*Macoma leptonoidea*, internal view of valves  
USNM 108579, probable paratype, Santa Barbara Channel,  
California; 22 mm

Material seen: 6 lots.

**Geologic Distribution and Biogeography:**

Most closely related to *Macoma carlottensis*, this species differs in being thinner and more rounded. It should be compared to *M. congesta* (Conrad, 1855), from the Miocene of California.

*Rexithaerus* Tryon, 1869,  
ex Conrad MS

[Type species: *Tellina secta* Conrad, 1837, by subsequent designation of DALL, 1900a]

Medium to large in size (50 to 120 mm); thin to medium in thickness; inflated; equivalve or with right valve larger; equilateral to longer posteriorly or anteriorly; evenly to sharply rounded anteriorly; rounded, pointed, or broadly truncate posteriorly; often slightly flexed to right posteriorly; posterior slope often set off by a fold and postero-dorsal area often set off internally by a ridge forming a dorsal flange; periostracum thin, shiny; pallial sinuses high, usually wholly confluent with pallial line, but in some species partially detached for a quarter or more of their length, larger in left valve.

*Macoma (Rexithaerus) secta* (Conrad, 1837)  
(Plate 9, Figure 53; Plate 10, Figures 54, 55;  
Text figure 25)

***Tellina secta* Conrad**

CONRAD, 1837: 257  
HANLEY, 1846: 327-328; plate 65, figures 245, 248  
CARPENTER, 1857a: 213  
CARPENTER, 1857b: 195, 211, 212, 213, 232, 234, 284,  
302, 349, 351, 352  
CARPENTER, 1864a: 526, 528, 536, 540, 600, 639, 665  
[*Macoma*] [1872: 12, 14, 22, 26, 86, 125, 151]  
DALL, 1900a: 309 [*Macoma (Rexithaerus)*]  
DALL, 1900b: 1053  
ARNOLD, 1903: 164, 394; plate 16, figure 5  
PACKARD, 1918: 280; plate 25, figure 8  
OLDROYD, 1924: 55-56, 214; plate 41, figure 8  
I. OLDROYD, 1925: 178-179; plate 44, figure 8  
GRANT & GALE, 1931: 374, 922; plate 20, figures 6a, 6b  
BURCH & BURCH, 1943: 22-23, 25 (text figure)  
BURCH, 1945a: 3 (text figure), 16; 1945b: 17  
KEEN, 1966a: 170  
DUNNILL & ELLIS, 1969: 28-30, 33; figures 8 (2), 9 (c)

***Tellina ligamentina* Deshayes**

DESHAYES, 1843: plate 81  
JAY, 1850: 26 [as a synonym of *Tellina secta*]

***Macoma secta edulis* Carpenter, ex Nuttall MS**

CARPENTER, 1860: 2 [*nomen nudum*]  
CARPENTER, 1864a: 526, 600, 639 [1872: 12, 86, 125]

**Type Material:**

*Tellina secta* – BM(NH) Nuttall collection, 1861.5.21.161, holotype, smaller pair, 50 mm. The larger pair, according to the label, is from the Columbia River area. Plate 9, Figure 53.

*Tellina ligamentina* – Lost, according to Roger (in correspondence). The original figure, measuring 63 mm, is sufficient to identify the taxon. Plate 10, Figure 54.

*Macoma secta edulis* – USNM 3426, lectotype herein, pair, 91.5 mm; USNM 663896, paralectotypes, 3 pairs. Plate 10, Figure 55.

**Type Localities:**

*Tellina secta* – San Diego, California; T. Nuttall, in muddy marshes.

*Tellina ligamentina* – Unknown.

*Macoma secta edulis* – Puget Sound, Washington; C. B. R. Kennerly.

**Nomenclatural Commentary:**

PALMER (1958) overlooked Carpenter's name, *Macoma secta edulis*, which can hardly be considered a *nomen nudum*; he intended it to represent a northern variety. With a continuous distribution along the coast and only minor morphological differences between northern and southern specimens, I do not think the name is useful.

**Description:**

Large (to 120 mm); oval; right valve more inflated; moderate in thickness; longer, rounded anteriorly; broadly truncate posteriorly; postero-dorsal margin set off as a flange; periostracum thin, shiny; pallial sinuses meet pallial line at about a right angle, approximately equal in size. Other internal details as in Text figure 25.

**Geographic Distribution and Ecology:**

Marina Island, inner coast of Vancouver Island (NMC 40254), and Esperanza Inlet, outer coast of Vancouver Island (MCZ 235227), British Columbia, to Bahía Magdalena, Baja California Sur (SU 24063). Specimens in collections from Acapulco (UCLA 24180) and Oaxaca (MCZ 38394) probably represent labeling errors. It has been taken from the intertidal area in bays and offshore from 10 to 46 m on semi-protected coast, in sand (BURCH, 1945a; DUNNILL & ELLIS, 1969).

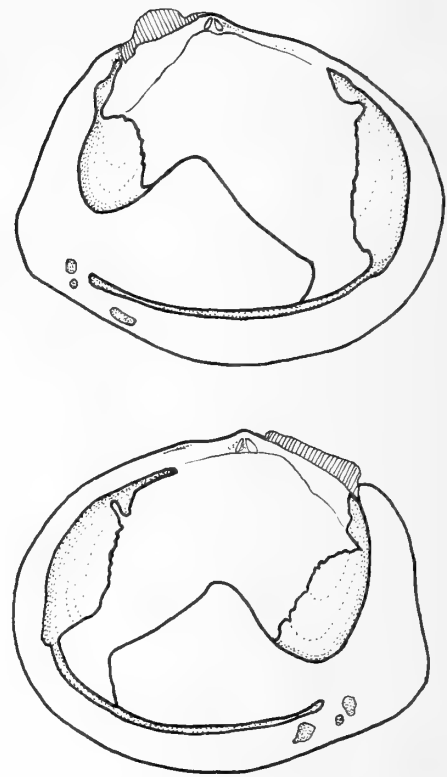


Figure 25

*Macoma secta*, internal view of valves  
MCZ 199403, Mugu, California; 69 mm

**Material seen:** 235 lots.

**Geologic Distribution and Biogeography:**

In the late Pleistocene, this species has been reported from southwestern British Columbia (DRAYCOT, 1951) to Bahía Magdalena, Baja California Sur (JORDAN, 1924, 1936), with many intermediate records. There are records in the early Pleistocene of the San Pedro area, California (CRICKMAY, 1929a; BURCH, 1947; VALENTINE & MEADE, 1961), and it has been reported from the Plio-

**Explanation of Plate 10**

Figure 54: *Macoma secta*. Original illustrations of *Tellina ligamentina*; 63 mm

Figure 55: *Macoma secta*. Lectotype (herein) of *Macoma secta edulis*, USNM 3426; 91.5 mm

Figure 56: *Macoma indentata*. Lectotype (herein) of *Macoma indentata* and holotype of *Macoma indentata tenuirostris*, USNM 15229; 54.2 mm

Figure 57: *Macoma indentata*, probable paralectotype, USNM "15630", Santa Barbara or San Pedro, California; 39.1 mm

Figure 58: *Macoma expansa*, lectotype (herein), USNM 663886; 38.7 mm

Figure 59: *Macoma expansa*. Lectotype (herein) of *Macoma liotricha*, USNM 107642; 44.8 mm



Figure 54

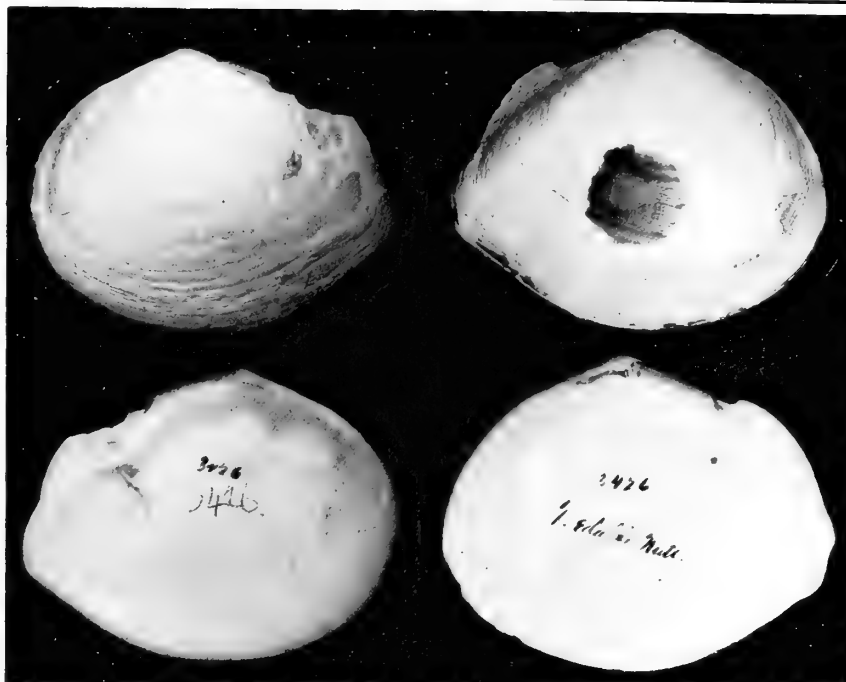


Figure 55

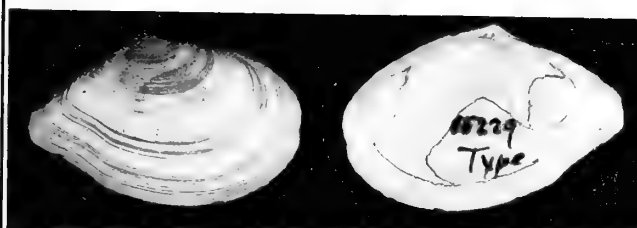


Figure 56

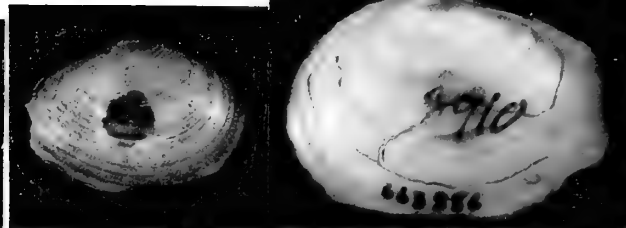


Figure 58

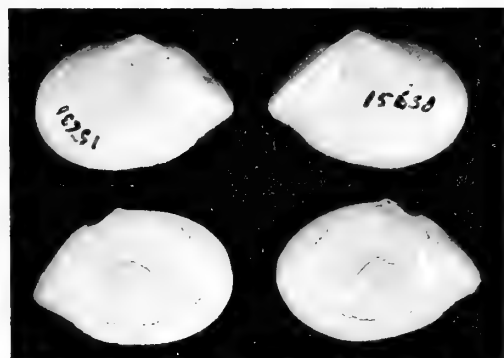


Figure 57

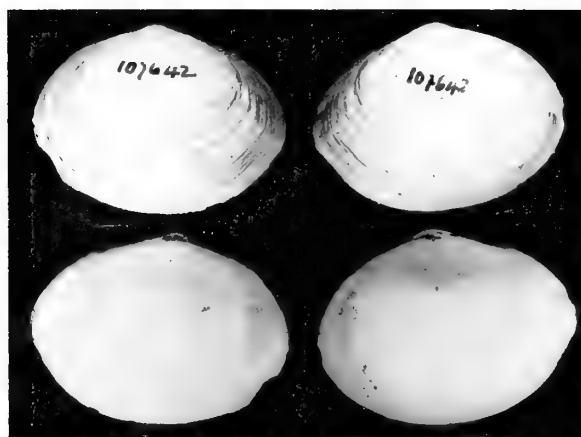


Figure 59



cene of California and the Miocene of Washington, Oregon, and California. *Macoma piercei* Arnold, 1910, from the Miocene of California may be a synonym.

There is an Asian homologue, *Macoma sector* Oyama, 1950, which differs in being smaller, more elongate, less inflated, and thinner. One suspects that the species was of Asian origin, being introduced in the Miocene and isolated by cooling in the Pliocene or Pleistocene.

*Macoma (Rexithaerus) indentata* Carpenter, 1864

(Plate 10, Figures 56, 57; Text figure 26)

*Macoma indentata* Carpenter

CARPENTER, 1864a: 611, 639 [1872: 97, 125]

CARPENTER, 1865a: 208

DALL, 1900a: 309 [*Macoma (Rexithaerus)*]

ARNOLD, 1903: 161-162, 394; plate 16, figure 1

PACKARD, 1918: 277-278; plate 25, figure 4

OLDROYD, 1924: 55, 214; plate 41, figure 4

I. OLDROYD, 1925: 178; plate 44, figure 4

GRANT & GALE, 1931: 374-375

BURCH & BURCH, 1943: 23, 25 (text figure)

BURCH, 1945a: 3 (text figure), 15; 1945b: 17; 1945c: 30

PALMER, 1958: 16, 22, 27, 34, 38, 48, 109-110, 341; plate 16, figures 1, 2

*Macoma (Rexithaerus) indentata tenuirostris* Dall

DALL, 1900a: 309, 324

I. OLDROYD, 1925: 178

BURCH & BURCH, 1943: 23

BURCH, 1945a: 16; 1945b: 17; 1945c: 30

*Macoma (Rexithaerus) rickettsi* Steinbeck & Ricketts, ex Rehder MS

STEINBECK & RICKETTS, 1941: 510 [*nomen nudum*; ICZN Article 13 (a) (i-ii)]

**Type Material:**

*Macoma indentata* - USNM 15229, lectotype herein, right valve, 54.2 mm, figured by PALMER (1958) as "holotype." It is the only remaining specimen in the USNM collection that is beyond question from Carpenter's original material. It also matches the measurements given by CARPENTER (1865a). Plate 10, Figure 56.

*Macoma indentata tenuirostris* - USNM 15229, holotype, the same specimen.

**Type Locality:**

*Macoma indentata* and *Macoma indentata tenuirostris* - San Pedro, California; J. G. Cooper. CARPENTER's (1864a: 639) citation of San Diego was presumably in error.

**Nomenclatural Commentary:**

DALL (1900a) intended to distinguish an elongate form from a broader one by means of a varietal name, and there do, indeed, seem to be two such morphological varieties of this species. They seem equally common in collections. Unfortunately, the type specimen he chose for the elon-

gate form was the only demonstrably original Carpenter specimen left in the USNM. There are also a number of intermediate specimens, and the two forms have been found throughout most of the range. I do not think that they can be regarded as distinct species, nor does the concept of a subspecies seem applicable. One can only speculate on the reasons for this dimorphism. The more elongate form seems to be more common offshore. The problem would be an interesting one for further study.

**Description:**

Medium-sized (to 63 mm); elongate, degree of elongation variable; moderately inflated; average in thickness; inequivalve, right valve more convex; almost equilateral to longer anteriorly; rounded anteriorly; elongate, pointed posteriorly; posterior slope set off by a distinct flexure; postero-dorsal are often set off as a wing; periostracum thin, adherent, shiny; pallial sinuses meeting pallial line at a right angle to partially detached, slightly longer in left valve (Plate 10, Figure 57). Other internal details as in Text figure 26.

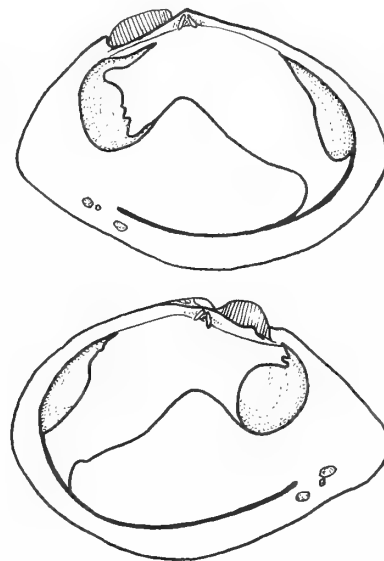


Figure 26

*Macoma indentata*, internal view of valves  
Roth collection 6705, Monterey, California; 39 mm

**Geographic Distribution and Ecology:**

Trinidad, California (Talmadge Collection), to and through the Gulf of California, as far south as Isla Cerralvo, Baja California Sur, and Guaymas, Sonora. Specimens from Alaska (MCZ, no number) probably represent a labeling error. The record from Puget Sound (DALL,

1921a) cannot be verified, and may be based on young specimens of *Macoma secta*. It is found from the intertidal area in bays to from 10 to 91 m offshore on semiprotected coast, in silt to sand (BURCH, 1945a).

**Material seen:** 172 lots, including Gulf of California specimens.

#### Geologic Distribution and Biogeography:

There are a number of records in the late Pleistocene, from the Santa Monica area, California (HOOTS, 1931; GRANT & GALE, 1931; VALENTINE, 1956), to Bahía San Quintín, Baja California Norte (ORCUTT, 1921b; JORDAN, 1926; MANGER, 1934). In the early Pleistocene, the species is known from the Santa Barbara area, California (UPSON, 1951), to the San Pedro area, California (T. OLDROYD, 1925; BURCH, 1947; CLARK, in NATLAND, 1957).

There are records in southern California formations transitional between the Pliocene and Pleistocene and many records in the Pliocene of California. The species is probably synonymous with *Macoma vanvolecki* Arnold, 1910, described from the Pliocene of California. There are records from the Miocene of California which should be reconfirmed. *Macoma indentata flagleri* Etherington, 1931, from the Miocene of Washington may be a matrid.

Panamic material differs from Californian material in being broader, although not as much so as in *Macoma secta*. I know of no Asian or Caribbean homologue.

#### *Macoma (Rexithaerus) expansa* Carpenter, 1864

(Plate 10, Figures 58, 59; Text figure 27)

##### *Macoma expansa* Carpenter

CARPENTER, 1864a: 602, 639 [1872: 88, 125]

CARPENTER, 1865c: 56

DALL, 1900a: 308

I. OLDROYD, 1925: 176

BURCH & BURCH, 1943: 21

BURCH, 1945a: 15; 1945b: 17

PALMER, 1958: 17, 22, 27, 38, 48, 108, 338; plate 13, figures 1-3

DUNNILL & ELLIS, 1969: 16-18, 33; figures 5 (1, 2), 9 (g)

##### *Macoma liotricha* Dall

DALL, 1897: 12; plate 1, figure 21

DALL, 1900a: 308

I. OLDROYD, 1925: 176; plate 22, figure 8

BURCH, 1945a: 15; 1945b: 17

#### Type Material:

*Macoma expansa* - USNM 663886, formerly "3910" (not a USNM number), lectotype herein, right valve, 38.7 mm; USNM 663885, paralectotype, left valve; USNM

663887, paralectotype, pair, a specimen of *Macoma carlottensis*. Plate 10, Figure 58.

*Macoma liotricha* - USNM 107642, lectotype herein, pair, 44.8 mm; USNM 663879, paralectotypes, 2 pairs and 1 valve. Plate 10, Figure 59.

#### Type Localities:

*Macoma expansa* - Puget Sound, Washington; C. B. R. Kennerly.

*Macoma liotricha* - North side of Korovin Bay, Atka Island, Aleutian Islands, Alaska; W. H. Dall.

#### Nomenclatural Commentary:

The distribution of material seems continuous along the coast, and although southern material is slightly more elongate posteriorly than northern, I do not think subspecific rank is warranted.

#### Description:

Medium-sized (to 50 mm); ovate-elongate; inflated; thin; almost equilateral to longer posteriorly; rounded anteriorly; produced but rounded posteriorly; periostracum thin, adherent, shiny; pallial sinuses perpendicular to pallial line, approximately equal in size. Other internal details as in Text figure 27.

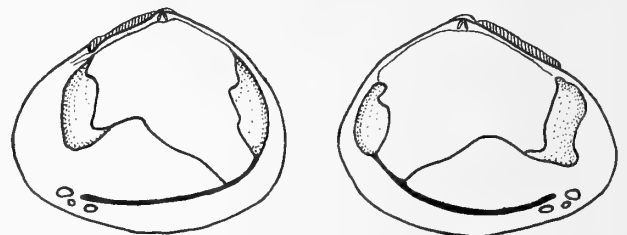


Figure 27

*Macoma expansa*, internal view of valves  
USNM 663879, Atka Island, Aleutian Islands, Alaska; 45.5 mm

#### Geographic Distribution and Ecology:

Attu Island, Aleutian Islands, Alaska (USNM 108698), through the Aleutian Islands, along the southern coasts of Alaska, throughout British Columbia, Washington, Oregon, and in California as far south as Oceano (SU 30878). It occurs in the intertidal area in protected localities and just below the surf-influenced zone to 27 m, even on exposed coast, in sand (DUNNILL, 1968; DUNNILL & ELLIS, 1969).

**Material seen:** 52 lots.

#### Geologic Distribution and Biogeography:

In the late Pleistocene, this species is known from

Puget Sound, Washington (HENDERSON, 1927, as "cf."), Point Año Nuevo, California (ADDICOTT, 1966), and Bahía San Quintín, Baja California Norte (ORCUTT, 1921a; VALENTINE & MEADE, 1961). I would question the last records. DALL's (1874) record from the Pliocene of San Diego is incorrect (HERTLEIN & GRANT, 1944).

I know of no Asian homologue.

### SUBGENERA UNCERTAIN

Into this category must be placed the following three unrelated species:

*Macoma nasuta* may be most closely related to the Indo-Pacific genera *Homalina* Stoliczka, 1870, and *Macomona* Finlay, 1927.

*Macoma inquinata* seems most closely related to *Austromacoma* Olsson, 1961, and less to *Gastrana* Schumacher, 1817, and *Heteromacoma* Habe, 1952. The last genus seems to be a senior synonym of *Sinomacoma* Yamamoto and Habe, 1959.

Finally, *Macoma balthica* is a mystery. It may be a brackish-water derivative of *Macoma* (*Macoma*), perhaps closest to *M. (M.) obliqua* and *M. (M.) middendorffi*.

#### *Macoma nasuta* (Conrad, 1837)

(Plate 11, Figures 60 - 62; Text figure 28)

#### *Tellina nasuta* Conrad

CONRAD, 1837: 258-259

MIDDENDORFF, 1849: 577-578

MIDDENDORFF, 1850: 256; plate 23, figures 8-11 (only) [in part]

CARPENTER, 1857a: 213

CARPENTER, 1857b: 192, 195, 211, 219, 221, 223, 232, 234, 283, 296, 302, 347, 351, 367

CARPENTER, 1864a: 534, 536, 540, 585, 600, 639 [1872: 20, 22, 26, 71, 86, 125] [*Macoma*]

DALL, 1900a: 307-308

ARNOLD, 1903: 163, 394; plate 16, figures 2, 3

PACKARD, 1918: 279-280, 378, 430; plate 23, figures 1a-1d, plate 49

OLDROYD, 1924: 53, 213; plate 32, figures 1a-1d

I. OLDROYD, 1925: 174; plate 45, figures 1a-1d

GRANT & GALE, 1931: 365-366, 922; plate 20, figures 11a, 11b

BURCH & BURCH, 1943: 17-18, 24-25 (text figures)

BURCH, 1945a: 3-4 (text figures), 11-12; 1945b: 17

KEEN, 1966a: 170

DUNNILL & ELLIS, 1969: 27-29, 33; figures 8 (1), 9 (h)

#### *Tellina tersa* Gould

GOULD, 1853: 398, 408 [reprint: 25, 35]; plate 16, figure 2

GOULD & CARPENTER, 1857: 199

CARPENTER, 1857b: 226, 229, 303

GOULD, 1862: 188

CARPENTER, 1864a: 532, 639 [1872: 20, 125] [as = *nasuta*]

JOHNSON, 1964: 158

#### *Macoma kelseyi* Dall

DALL, 1900b: 1052, 1622; plate 49, figure 7

ARNOLD, 1903: 164

OLDROYD, 1924: 53-54

I. OLDROYD, 1925: 171-172

GRANT & GALE, 1931: 366-367

BURCH, 1945a: 14; 1945b: 17

### Type Material:

*Tellina nasuta* - BM(NH) 1861.5.21.158, lectotype herein, pair, 76.5 mm. This is markedly larger than Conrad's stated measurement of 44.6 mm. The original lot must have consisted of several specimens. Plate 11, Figure 60.

*Tellina tersa* - Lost (JOHNSON, 1964). Dr. Keen (verbal communication) was unable to locate the specimen at the BM(NH), and I could not find it among the Gould material at the USNM. Gould's figure is 27.5 mm long. Plate 11, Figure 61.

*Macoma kelseyi* - USNM 147690, lectotype herein, left valve, figured by Dall, 92 mm; USNM 645417, paralectotype, a smaller, right valve. Plate 11, Figure 62.

### Type Localities:

*Tellina nasuta* - Near San Diego, California; T. Nuttall.

According to KEEN (1966a), the label bears a notation by Nuttall, "eaten by Chinooks at the estuary of the Oregon." This implies that he may also have collected specimens from the Columbia River estuary, so it is possible that material from two sources may have been mixed.

*Tellina tersa* - "Panama," presumably in error; E. Jewett.

*Macoma kelseyi* - City Park, San Diego, California; upper Pliocene (HERTLEIN & GRANT, 1944) [as "Pleistocene"]; R. E. C. Stearns.

### Nomenclatural Commentary:

The synonymy of *Macoma nasuta* with Gould's *Tellina tersa* must remain uncertain as the type specimen of the latter is lost. The original figure does not seem to be any of the common Panamic species of *Macoma* and does seem close to young of *M. nasuta*.

The name *Macoma kelseyi* has been used in the Recent fauna for northern specimens with an especially elongate and truncate posterior end, although Dall's type specimen was not so much elongate posteriorly as pointed. It is also heavy for the species, not unlike specimens living subtidally on open coasts.

### Description:

Large (to 110 mm); elongate-ovate; moderately inflated; average in thickness; equilateral to longer posteri-

orly; rounded anteriorly; pointed, truncate posteriorly; smooth or with sculpture of irregular, low concentric ribs; traces of brownish periostracum ventrally; pallial sinuses confluent with pallial line, larger in left valve, reaching anterior adductor muscle scar. Other internal details as in Text figure 28.

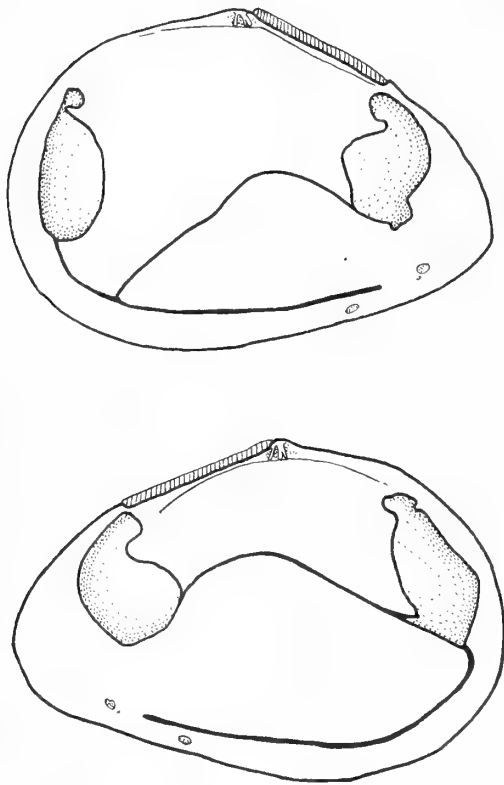


Figure 28

*Macoma nasuta*, internal view of valves  
SU 305, Brown Island, San Juan Islands, Washington; 80 mm

#### Geographic Distribution and Ecology:

Sitkalidak Island, southeastern coast of Kodiak Island

(USGS M2066), and Kodiak Island, Alaska (USNM 108718), throughout the entire West Coast to Cabo San Lucas, Baja California Sur (CAS 17663a), with many intermediate records. MIDDENDORFF (1849, 1851) reported it from the Bering Sea, but the record has never been confirmed. It is found in the intertidal area in bays and below wave line on more open coast to about 46 m, in sandy-silt (BURCH, 1945a; ADDICOTT, 1952; FILICE, 1958; JONES, 1964). The species spawns in spring or early summer in Oregon (EDMONDSON, 1920).

**Material seen:** 310 lots.

#### Geologic Distribution and Biogeography:

This species is very common in the late Pleistocene; it has been reported from the Queen Charlotte Islands, British Columbia (DAWSON, 1880), to Bahía Magdalena, Baja California Sur (JORDAN, 1924, 1936), with many intermediate records. It is known in the early Pleistocene from the Elk River area, Oregon (ARNOLD & HANNBAL, 1913), to San Pedro, California (ARNOLD, 1903; T. OLDROYD, 1925; CRICKMAY, 1929a; BURCH, 1947; CLARK, in NATLAND, 1957; VALENTINE & MEADE, 1961). There are several records in southern Californian formations transitional between the Pliocene and the Pleistocene and in the Pliocene of California. *Macoma jacalitosana* Arnold, 1910, described from the Pliocene of central California, is probably synonymous. There are also records in the Miocene and one questionable one in the Oligocene.

An analogous Asian species is *Macoma tokyoensis* Makiyama, 1927 [*Tellina dissimilis* von Martens, 1865, non Deshayes, 1855], which differs in having a beveled escutcheon, being more regular in outline, and having a pallial sinus in the left valve which does not reach the anterior adductor muscle scar. It seems thicker and heavier on an average than the Californian species.

*Macoma inquinata* (Deshayes, 1855)

(Plate 11, Figures 63, 64; Text figure 29)

*Tellina inquinata* Deshayes

DESHAYES, 1855: 357

CARPENTER, 1857b: 192, 302

#### Explanation of Plate 11

Figure 60: *Macoma nasuta*. Lectotype (herein) of *Tellina nasuta*, BM(NH) 1861.5.21.158; 76.5 mm

Figure 61: *Macoma nasuta*. Original illustrations of *Tellina tersa*; 27.5 mm

Figure 62: *Macoma nasuta*. Lectotype (herein) of *Macoma kelseyi*, USNM 147690; 92 mm

Figure 63: *Macoma inquinata*. Lectotype (herein) of *Tellina inquinata*, BM(NH) 1841.3.9.27; 45 mm

Figure 64: *Macoma inquinata*. Holotype of *Macoma inquinata arnheimi*, USNM 122537; 36.9 mm

Figure 65: *Macoma balthica*. Potential lectotype of *Tellina balthica*, Linnean Society of London; 15.5 mm



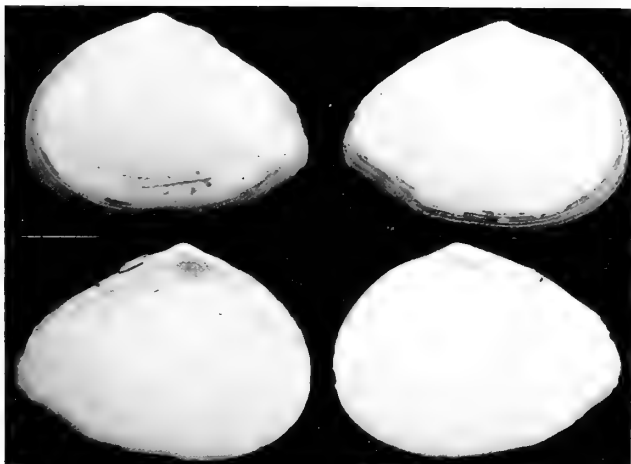


Figure 60

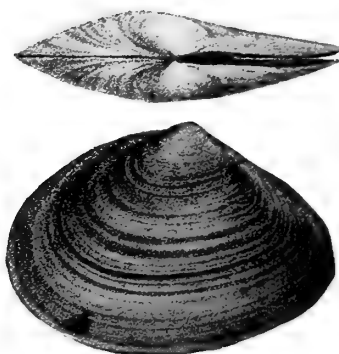


Figure 61

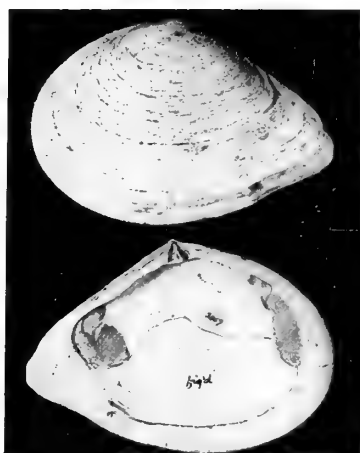


Figure 62

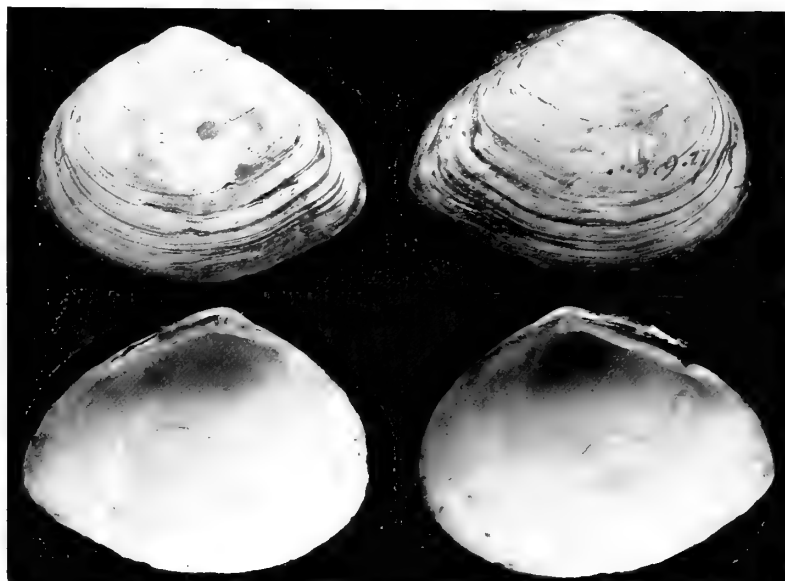


Figure 63



Figure 64

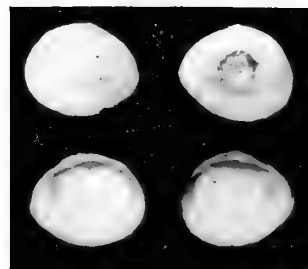


Figure 65



- CARPENTER, 1864a: 525, 594, 611, 627, 639, 682  
 [1872: 11, 80, 97, 113, 125, 168] [*Macoma*]  
 SOWERBY, 1867: plate 30, figure 164 [*Tellina*]  
 DALL, 1900a: 307 [*Macoma*]  
 ARNOLD, 1903: 162, 394; plate 16, figure 4  
 PACKARD, 1918: 278, 378, 380; plate 23, figures 2a, 2b,  
 3a, 3b, plate 24, figures 1a, 1b, plate 48  
 OLDROYD, 1924: 54, 213; plate 32, figures 2a, 2b, 3a, 3b  
 I. OLDROYD, 1925: 172; plate 45, figures 2a, 2b, 3a, 3b  
 GRANT & GALE, 1931: 367, 922; plate 20, figure 5  
 BURCH & BURCH, 1943: 18, 25 (text figure)  
 DUNNILL & ELLIS, 1969: 23-25, 33; figures 7 (1, 2), 9 (d)

*Tellina irus* Hanley, of authors, not of Hanley

- [not HANLEY, 1845: 166]  
 SALISBURY, 1934: 85; plate 12, figures 5-8  
 BURCH, 1945a: 3 (text figure), 12; 1945b: 17; 1945c: 30  
 KEEN, 1962: 161

*Macoma inquinata arnheimi* Dall

- DALL, 1916a: 36 [nomen nudum]  
 DALL, 1916b: 414  
 OLDROYD, 1924: 54, 209; plate 10, figure 3  
 I. OLDROYD, 1925: 172; plate 42, figure 9  
 GRANT & GALE, 1931: 367-368  
 BURCH & BURCH, 1943: 19 [as a synonym of *Macoma incongrua*]  
 BURCH, 1945a: 10 [as a synonym of *Macoma incongrua*]

#### Type Material:

*Tellina inquinata* - BM(NH) 1841.3.9.27, lectotype herein, pair, 45 mm. There are also two specimens in the BM (NH) from the Cuming collection from Puget Sound that were probably examined by Deshayes and are regarded as paralectotypes. Plate 11, Figure 63.

*Macoma inquinata arnheimi* - USNM 122537, holotype, pair, 36.9 mm. Plate 11, Figure 64.

#### Type Localities:

*Tellina inquinata* - "Columbia" [near mouth of Columbia River, Washington]; K. D. Wigram collection.

*Macoma inquinata arnheimi* - Kodiak Island, Alaska; J. S. Arnheim.

#### Nomenclatural Commentary:

Due to a superficial examination of type material in the BM(NH), SALISBURY (1934) concluded that *Tellina irus* Hanley was a senior synonym of *T. inquinata* Deshayes. Further study (KEEN, 1962) demonstrated that the two species belong in different genera and that *T. irus* is Japanese. *Heteromacoma* ?

Dall described a rather short specimen of this species as *Macoma inquinata arnheimi*. Some workers suggested that this specimen may have been *M. obliqua* (BURCH & BURCH, 1943; BURCH, 1945a), probably because I. OLDROYD (1924, 1925) illustrated a specimen of the latter as Dall's subspecies (SUPTC 6314). As short individuals occur throughout the range of the species, I do not feel that such specimens represent a subspecies.

#### Description:

Medium-sized (to 55 mm); rounded to rather elongate; moderately inflated; heavy; somewhat longer posteriorly; rounded anteriorly; pointed, only slightly truncate posteriorly; sculpture of conspicuous concentric undulations; periostracum in ventral patches only; pallial sinuses confluent with pallial line, that in left valve longer but not reaching anterior adductor muscle scar. Other internal details as in Text figure 29.

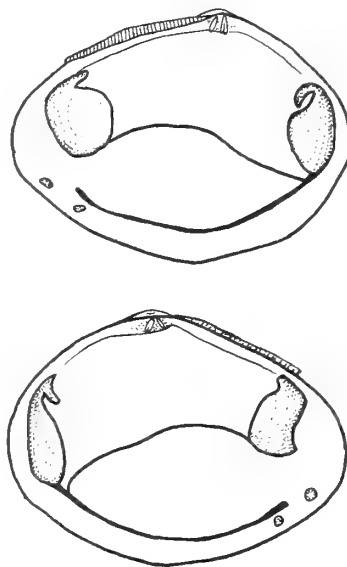


Figure 29

*Macoma inquinata*, internal view of valves  
 SU 299/6, Sitka, Alaska; 56 mm

#### Geographic Distribution and Ecology:

Siberia (USNM 108704, 223069), with no other records from the northern end of the Bering Sea; Atka Island, Aleutian Islands (ANSP 177975; MCZ 92210), and Hagenmeister Island, Alaska (USNM 219474), through the eastern Aleutian Islands, southern Alaska, British Columbia, Washington, Oregon, and in California as far south as San Pedro (SU 296/1; BURCH, 1945a). It is rare south of Santa Barbara, California, and there may not normally be a population established south of that point. It occurs in the intertidal area in bays and to 48 m offshore, below the surf line, in silt (BURCH, 1945a; ADDICOTT, 1952; FILICE, 1958; DUNNILL, 1968; DUNNILL & ELLIS, 1969).

**Material seen:** 280 lots.

### Geologic Distribution and Biogeography:

*Macoma inquinata* is known in the late Pleistocene from the southwestern portion of British Columbia (NEWCOMBE, 1914; CRICKMAY, 1925, 1929b; DRAYCOT, 1951; WAGNER, 1960) to Punta Baja, Baja California Norte (EMERSON & ADDICOTT, 1958; VALENTINE & MEADE, 1961). JORDAN's (1924) record from Laguna San Ignacio proved to be *M. nasuta* (HERTLEIN, 1934). In the early Pleistocene, there are records from Elk River, Oregon (ARNOLD & HANNIBAL, 1913), to the San Pedro area, California (ARNOLD, 1903; T. OLDROYD, 1925; CRICKMAY, 1929a; CLARK, 1931; DE LONG, 1941; BURCH, 1947; VALENTINE & MEADE, 1961). It has been reported in the Pliocene of California, although an ancestral Pliocene species is *Macoma affinis* Nomland, 1917, described from central California. It is not yet clear where *M. affinis plena* Stewart, in Woodring, Stewart, & Richards, 1941, fits into the picture.

Some workers have considered "*Mya*?" *subsinuata* Conrad, 1857a, from the Miocene (?) of Monterey County, California, a synonym of this species. As the type specimen is lost and the description and figure insufficient to identify Conrad's species, it must be regarded as a *nomen dubium*.

*Macoma moliniana* Dall, 1909, from the Oligocene of Oregon, may be ancestral to *M. affinis* and equivalent or related to: *Macoma sookensis* Clark & Arnold, 1923, and *Metis vancouverensis* Clark & Arnold, 1923, from the Oligocene of British Columbia; *Tellina gibsonensis* Palmer, 1918, and *Apolymetis twinensis* Durham, 1944, from the Oligocene of Washington; *Metis rostellata* Clark, 1918, from the Oligocene of California; *Macoma montesanoensis* Weaver, 1912, from the Miocene of Washington; *Macoma panzana* Wiedey, 1928; *Macoma sespeensis* Loel & Corey, 1932, and *Macoma menkeni* Hanna & Hertlein, 1938, all from the Miocene of California.

An Asian homologue is *Macoma contabulata* (Deshayes, 1855), which differs in being more rounded ventrally. It more closely resembles the extinct *M. affinis* than it does living *M. inquinata*. I would suggest that as this species-complex has had a long history in the northern Pacific, a study of its evolution might prove interesting and have stratigraphic utility.

### *Macoma balthica* (Linnaeus, 1758)

(Plate 11, Figure 65; Plate 12, Figures 66 to 69; Text figure 30)

- Tellina balthica* Linnaeus  
 LINNAEUS, 1758: 677  
 LINNAEUS, 1767: 1120  
 GMELIN, 1791: 3241  
 CARPENTER, 1857b: 221  
 CARPENTER, 1864a: 534 [*Macoma*] [1872: 20]  
 DALL, 1900a: 308-309  
 DALL, 1900b: 1051  
 PACKARD, 1918: 277, 382, 426; plate 25, figures 1, 2, 9, plate 47  
 OLDROYD, 1924: 54, 214; plate 41, figures 1, 2, 9  
 I. OLDROYD, 1925: 172; plate 44, figures 1, 2, 9  
 GRANT & GALE, 1931: 371-372, 908, 922; plate 14, figures 6a, 6b, plate 20, figures 7a, 7b  
 BURCH & BURCH, 1943: 20  
 DODGE, 1952: 51-52
- Tellina solidula* Pulteney [a European synonym; type not searched]  
 PULTENEY, 1799: 29  
 MIDDENDORFF, 1849: 577  
 MIDDENDORFF, 1851: 260-263; plate 22, figures 3-6
- Tellina solidula normalis* Middendorff  
 MIDDENDORFF, 1851: 262
- Tellina petalum* Valenciennes, in Humboldt & Bonpland  
 VALENCIENNES, in HUMBOLDT & BONPLAND, 1821: 222; plate 48, figures 2a, 2b  
 HANLEY, 1846: 317; plate 66, figure 263  
 CARPENTER, 1857b: 170, 302  
 KEEN, 1958b: 190 [as a synonym of *Heterodonax bimaculatus*]
- Tellina inconspicua* Broderip & Sowerby  
 BRODERIP & SOWERBY, 1829: 363  
 SOWERBY, in GRAY, 1839: 153; plate 41, figure 6  
 CARPENTER, 1857b: 175, 221, 347  
 CARPENTER, 1864a: 526, 532, 534, 576, 600, 639, 681 [*Macoma*] [1872: 12, 18, 20, 62, 86, 125, 167]  
 BURCH, 1945a: 13; 1945b: 17; 1945c: 30  
 DUNNILL & ELLIS, 1969: 20-23, 33; figures 6 (1), 9 (1)
- Sanguinolaria californiana* Conrad  
 CONRAD, 1837: 231; plate 17, figure 7  
 CARPENTER, 1857a: 212  
 CARPENTER, 1857b: 195, 221, 301  
 CARPENTER, 1864a: 526, 576, 600, 639 [as a synonym of *Macoma inconspicua*] [1872: 12, 62, 86, 125]  
 KEEN, 1966a: 171

### Explanation of Plate 12

Figure 66: *Macoma balthica*. Lectotype (herein) of *Tellina petalum*, Musée d'Histoire Naturelle de Paris; 16 mm

Figure 67: *Macoma balthica*. Original illustration of *Tellina inconspicua*; 23.3 mm

Figure 68: *Macoma balthica*. Original illustration of *Sanguinolaria californiana*; 28.6 mm

Figure 69: *Macoma balthica*. Holotype of *Tellina rotundata*, BM (NH) without registry number; 32.5 mm

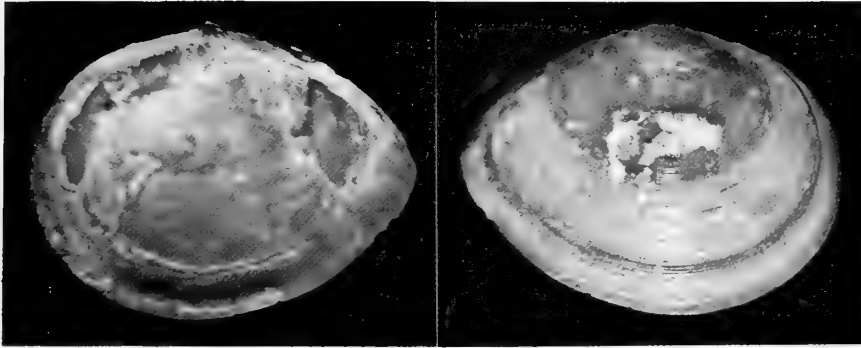


Figure 66

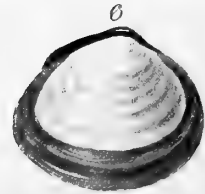


Figure 67

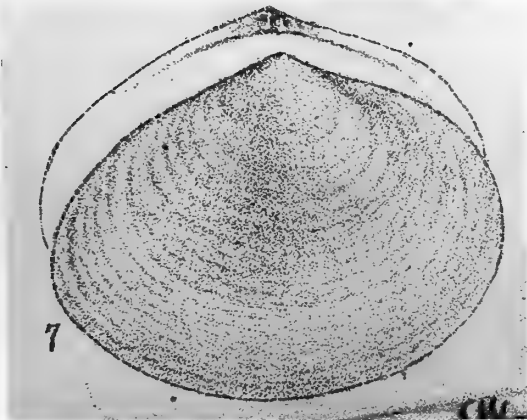


Figure 68

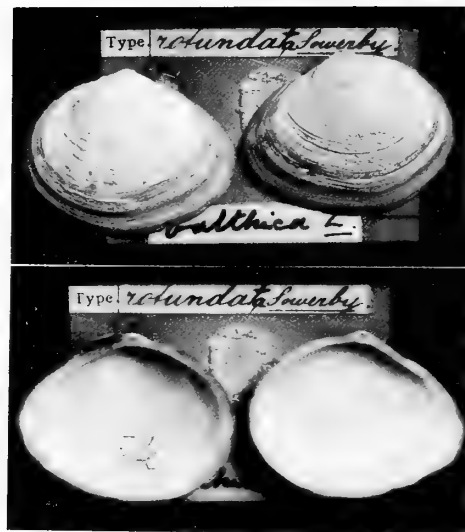


Figure 69



*Tellina californica* Carpenter, "ex Conrad MS" [misspelling for *Sanguinolaria californiana*]

CARPENTER, 1857b: 195, 211, 302 [*nomen nudum*]

CARPENTER, 1864a: 532 [as a synonym of *Macoma inconspicua*]

*Tellina rotundata* Sowerby, not Montagu

SOWERBY, 1867: plate 27, figure 146

[not MONTAGU, 1803: 71-72; plate 2, figure 3]

*Tellina rotunda* Salisbury, 1934, new name for *Tellina rotundata* Sowerby, not Montagu

SALISBURY, 1934: 87

#### Type Material:

*Tellina balthica* – Linnean Society of London, potential lectotype, largest pair, 15.5 mm; potential paralectotypes, 4 pairs. It is for European workers to study the history of these specimens and designate a lectotype. Plate 11, Figure 65.

*Tellina solidula normalis* – Presumably in the Zoologische Institut, Leningrad.

*Tellina petalum* – Musée d'Histoire Naturelle de Paris, lectotype herein, largest specimen, right valve, probably figured by Valenciennes, 16 mm. (Salvat, in correspondence); paralectotypes, 2 large valves (possibly a pair), 2 small pairs. Plate 12, Figure 66.

*Tellina inconspicua* – Lost; the original description and 23.3 mm-long figure (SOWERBY, in GRAY, 1839) are sufficient to identify the taxon. Plate 12, Figure 67.

*Sanguinolaria californiana* – Lost; Conrad's description and 28.6 mm-long figure are satisfactory. Plate 12, Figure 68.

*Tellina rotundata* – BM(NH) without registry number, holotype, pair, about 32.5 mm. Plate 12, Figure 69.

#### Type Localities:

*Tellina balthica* – Baltic Sea; probably by Linnaeus.

*Tellina solidula normalis* – Bering Sea.

*Tellina petalum* – "Acapulco"; F. H. A. von Humboldt & A. J. A. Bonpland. This locality is probably in error, as the species does not occur in the Panamic province. Considering the travels of this expedition, it is more likely that the specimens came from the east coast of North America.

*Tellina inconspicua* – Icy Cape, Arctic Alaska; voyage of the *Blossom*.

*Sanguinolaria californiana* – Columbia River estuary, Washington; T. Nuttall, "muddy marshes near the limits of salt water."

*Tellina rotundata* – None given in original account. The name is mentioned here because this species has been regarded, in error, as a synonym of *Macoma obliqua* (see same, above). SALISBURY (1934) cites the unlikely localities of India and Ceylon.

#### Nomenclatural Commentary:

A study of a great deal of material has convinced me that there is no easy way to separate Pacific from Atlantic specimens of this variable species. A world-wide statistical study might be of significance. Until a project of this

sort is attempted it is probably best to consider this as one circum-arctic species.

#### Description:

Small (to 30 mm, rarely to 45 mm); rotund; moderately inflated; usually heavy, but bay specimens occasionally thin; longer posteriorly; rounded anteriorly; rounded to somewhat pointed posteriorly; beaks usually worn; periostracum as ventral traces; often reddish; pallial sinuses approximately equal in size, confluent with pallial line, difficult to distinguish against internal gleam. Other internal details as in Text figure 30.

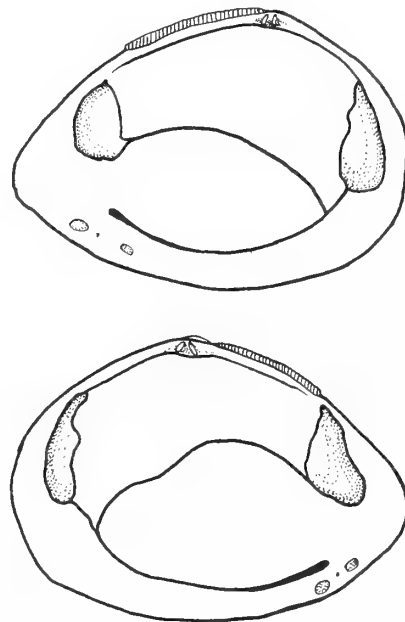


Figure 30

*Macoma balthica*, internal view of valves  
SU 47236, Unalakleet, Alaska; 30 mm

#### Geographic Distribution and Ecology:

Circum-arctic. In the eastern Pacific it is found throughout the Alaskan coast, British Columbia, Washington, Oregon, and commonly as far south as San Francisco Bay, California (many records). There are isolated records from Santa Cruz, Monterey, Pismo Beach, Santa Barbara, San Pedro, and San Diego. These may, in part, represent transport in crevices of ships. I was not successful in locating living or dead specimens in Elkhorn Slough, Monterey Bay, and there seem to be no living populations

south of San Francisco. It is found in the upper intertidal area in bays, especially brackish areas, to about 37 m in quiet offshore areas, in silt (BURCH, 1945a; FILICE, 1958; VASSALLO, 1969).

**Material seen:** 327 lots from area studied.

#### Geologic Distribution and Biogeography:

There are records from the Pleistocene of the Northwest Territories (DALL, 1919, 1924), southeastern Alaska (DALL, 1904; SMITH, 1919; BUDDINGTON & CHAPIN, 1929; TWENHOFEL, 1952), southwestern British Columbia (NEWCOMBE, 1914; ARMSTRONG & BROWN, 1954; WAGNER, 1960), and Puget Sound, Washington (HENDERSON, 1927). Records from the Goleta terrace (OLDROYD & GRANT, 1931; GRANT & GALE, 1931), prove to be based on a juvenile specimen of *Macoma inquinata*, and the same may be true of the record from the Ventura terrace (PUTNAM, 1942). The species is also known in the Pleistocene of the East Coast (RICHARDS, 1962) and of Europe (British Museum [Natural History], 1963).

Japanese workers have renamed the species *Macoma takahokoensis* Yamamoto & Habe, 1959.

#### OTHER SPECIES

A few other specific names were encountered during this study which have not yet been discussed.

- (1) *Tellina diegoana* CONRAD, 1855, described from either the Pleistocene or Pliocene of San Diego, is a *nomen dubium*. The type specimen is lost, and the description and illustration are insufficient to identify the taxon.
- (2) *Tellina pedroana* CONRAD, 1855, from the Pleistocene of San Pedro, is a *nomen dubium* for the same reasons.
- (3) *Tellina ulloana* HERTLEIN, 1968, was reported as *Tellina declivis* SOWERBY, 1868, by DALL (1916a) and others from Catalina Island, California, based on a single lot (USNM 198897). This lot was catalogued in 1907 with other material from the same station, but neither the name of the collector nor what were the other species in the material is given in the catalogue. It has not been taken in California since, and the most northerly documented material available is from Bahía Magdalena, Baja California Sur. Thus, the Californian record of this species is regarded with much question.
- (4) *Tellina miniata* GOULD, 1851, and *Tellina gemma* GOULD, 1853, were incorrectly attributed to California by JOHNSON (1964). Gould's San Juan locality is in Baja California Sur at about 27° N on the Gulf of California (C. B. ADAMS, 1852a, b).
- (5) *Tellina rubescens* HANLEY, 1844a, has been reported in the late Pleistocene of southern California but as it does not occur in the Recent fauna, it is more properly considered in the Panamic fauna. I have not seen Pleistocene material, and possibly these records are based on specimens of *Tellina simu-*

*lans* C. B. ADAMS, 1852a, because of the confusion between the two species.

- (6) *Tellina lamellata* CARPENTER, 1857c, was reported from California by CARPENTER (1864a). The type specimen of this species proved to be a juvenile specimen of *Semele* (KEEN, 1968), and the Californian specimen (USNM 15579) proves to be a juvenile *Cumingia*.
- (7) *Macoma truncaria* DALL, 1916b [1916a, *nomen nudum*], was based on a specimen of *Thracia* (COAN, 1969b).

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### ECOLOGIC

AND

### BIOGEOGRAPHIC CONCLUSIONS

#### ECOLOGY

Ecologic trends become apparent when the ecologic information about each species is presented in tabular form.

(Table, see next page)

The data available for most tellinid species are difficult to interpret because it is not easy to correlate the various pieces of ecologic information, both what has been published and what one finds on collection labels, especially as to bottom type and coastal exposure. Also, the depths and bottom types listed are ranges, not averages. What is necessary to compare the environment of one species with others is more specific information about the area in which each is most abundant.

One can, however, see certain trends and arrive at some generalizations. Within the family, only two species of *Tellina* can be termed characteristic of sandy substrates on open beaches, *T. lutea alternidentata* and *T. bodegensis*. They therefore are comparable to those of the *Tellina* communities described by THORSON (1961) for the northern Atlantic, the Mediterranean, and Australia.

Most of the species seem more characteristic of what might be termed protected or semi-protected conditions. They have been regarded as characteristic of bays, but also occur offshore below the area of wave action in the appropriate substrates. Paleontologists attempting to interpret fossil assemblages must take this into account. Those species more abundant offshore often have records of maximum depth greater than those more common in bays. The following tables list the species in these two categories:



Table 1

Species	Depth range, meters	Bottom type	Coastal exposure
<i>Tellina lutea alternidentata</i>	0 - 84	sand	exposed, beaches
<i>Tellina bodegensis</i>	0 - 96	sand	exposed, beaches
<i>Tellina idae</i>	0 - 91	sand	protected, bays and offshore
<i>Tellina nuculoides</i>	0 - 73	various	protected, bays and offshore
<i>Tellina meropsis</i>	0 - 48	sand	protected, bays and offshore
<i>Tellina carpenteri</i>	0 - 441	various	protected, bays and offshore
<i>Tellina modesta</i>	0 - 91	silty-sand to sand	protected, bays and offshore
<i>Leporimetis obesa</i>	0 - 46	sand	protected, bays and offshore
<i>Macoma calcarea</i>	2 - 320	silt	protected, offshore
<i>Macoma elimata</i>	15 - 435	silty-sand to sand	protected, offshore
<i>Macoma brota</i>	14 - 260	silt to sand	protected, offshore
<i>Macoma lipara</i>	26 - 259	silt to fine sand	protected, offshore
<i>Macoma middendorffi</i>	27 - 32	sand	protected? offshore
<i>Macoma obliqua</i>	0 - 183	sand to gravel	protected, offshore
<i>Macoma frigida</i>	unknown	unknown	unknown
<i>Macoma moesta moesta</i>	0 - 260	silt	protected, offshore
<i>Macoma moesta alaskana</i>	11 - 260	various	protected, offshore
<i>Macoma crassula</i>	16 - 161	gravel	protected, offshore
<i>Macoma loveni</i>	4 - 816	coarse	protected, offshore
<i>Macoma lama</i>	0 - 183	sand	exposed? offshore
<i>Macoma yoldiformis</i>	0 - 93	silt to sand	protected, bays and offshore
<i>Macoma acolasta</i>	0 - 73	sand	protected, bays and offshore
<i>Macoma carlottensis</i>	5 - 1547	silt to fine sand	protected, offshore
<i>Macoma leptonoidea</i>	483 - 594	silt	protected, offshore
<i>Macoma secta</i>	0 - 46	sand	semi-protected, bays and offshore
<i>Macoma indentata</i>	0 - 91	silt to sand	semi-protected, bays and offshore
<i>Macoma expansa</i>	0 - 27	sand	semi-protected, bays and offshore
<i>Macoma nasuta</i>	0 - 46	sandy-silt	protected, bays and offshore
<i>Macoma inquinata</i>	0 - 48	silt	protected, bays and offshore
<i>Macoma balthica</i>	0 - 37	silt	protected, bays, including brackish ones, and offshore

Table 2

Species more common in bays

Species	Depth range meters
<i>Tellina meropsis</i>	0 - 48
<i>Leporimetis obesa</i>	0 - 46
<i>Macoma secta</i>	0 - 46
<i>Macoma nasuta</i>	0 - 46
<i>Macoma inquinata</i>	0 - 48
<i>Macoma balthica</i>	0 - 37

Table 3

Species more common offshore

Species	Depth range meters
<i>Tellina idae</i>	0 - 91
<i>Tellina nuculoides</i>	0 - 73
<i>Tellina carpenteri</i>	0 - 441
<i>Tellina modesta</i>	0 - 91
<i>Macoma yoldiformis</i>	0 - 93
<i>Macoma acolasta</i>	0 - 73
<i>Macoma indentata</i>	0 - 91
<i>Macoma expansa</i>	0 - 27

Finally, a few species are characteristic of the offshore environment, rather than that of shallow beaches or bays. These are mainly members of *Macoma* (*Macoma*).

Table 4

Species	Depth range meters
<i>Macoma</i> ( <i>Macoma</i> ) <i>calcareo</i>	2 - 320
<i>Macoma</i> ( <i>Macoma</i> ) <i>elimata</i>	15 - 435
<i>Macoma</i> ( <i>Macoma</i> ) <i>brota</i>	14 - 260
<i>Macoma</i> ( <i>Macoma</i> ) <i>lipara</i>	26 - 259
<i>Macoma</i> ( <i>Macoma</i> ) <i>middendorffi</i>	27 - 32
<i>Macoma</i> ( <i>Macoma</i> ) <i>obliqua</i>	0 - 183
<i>Macoma</i> ( <i>Macoma</i> ) <i>moesta moesta</i>	0 - 260
<i>Macoma</i> ( <i>Macoma</i> ) <i>moesta alaskana</i>	11 - 260
<i>Macoma</i> ( <i>Macoma</i> ) <i>crassula</i>	16 - 161
<i>Macoma</i> ( <i>Macoma</i> ) <i>loveni</i>	4 - 816
<i>Macoma</i> ( <i>Macoma</i> ) <i>lama</i>	0 - 183
<i>Macoma</i> (? <i>Psammacoma</i> ) <i>carlottensis</i>	5 - 1547
<i>Macoma</i> (? <i>Psammacoma</i> ) <i>leptonoidea</i>	483 - 594

Within each ecologic group, one may expect species to differ from one another in geographic distribution, depth and sediment preference, and feeding method.

The abundance of species is reflected in their frequency in collections. The number of lots studied may well be a better indication of relative abundance than the total number of specimens, because the latter quantity varies in collections with the average size of individuals. Curators tend to retain in museums fewer specimens of larger species.

Table 5

	Number of lots seen
<i>Macoma balthica</i>	327
<i>Macoma nasuta</i>	310
<i>Macoma inquinata</i>	280
<i>Macoma secta</i>	235
<i>Macoma obliqua</i>	203
<i>Tellina lutea alternidentata</i>	193
<i>Macoma indentata</i>	172
<i>Macoma calcarea</i>	169
<i>Tellina bodegensis</i>	164
<i>Macoma carlottensis</i>	164
<i>Tellina modesta</i>	151
<i>Tellina carpenteri</i>	143
<i>Tellina nuculoides</i>	118
<i>Macoma lama</i>	104
<i>Macoma brota</i>	102

<i>Macoma yoldiformis</i>	100
<i>Tellina idae</i>	100
<i>Leporimetis obesa</i>	92
<i>Tellina meropsis</i>	82
<i>Macoma elimata</i>	65
<i>Macoma expansa</i>	52
<i>Macoma moesta alaskana</i>	35
<i>Macoma lipara</i>	32
<i>Macoma moesta moesta</i>	30
<i>Macoma middendorffi</i>	28
<i>Macoma acolasta</i>	20
<i>Macoma loveni</i>	6
<i>Macoma leptonoidea</i>	6
<i>Macoma crassula</i>	2
<i>Macoma frigida</i>	1

Members of the genus *Macoma* represent the five most common species, reflecting the success of this group in shallow, protected areas. The eleven least common species are also members of the genus *Macoma* and are mostly Arctic or deep-water forms.

## BIOGEOGRAPHY

The species of the Tellinidae may be grouped geographically in terms of the so-called molluscan provinces. There is some controversy as to how provinces should best be defined, whether by percent endemism or by degree of faunal change at their borders. There is no one paper that gives a balanced definition or final terminology with which I can agree. A recent review is provided by VALENTINE (1966). For present purposes, I will define the molluscan provinces mentioned here by the following geographic boundaries:

- Arctic** – Arctic Ocean and the Bering Sea to Bristol Bay, Alaska
- Aleutian** – Eastern Aleutian Islands to Cape Flattery, Washington
- Oregonian** – Cape Flattery, Washington, to Point Conception, California
- Californian** – Point Conception, California, to Punta Eugenio, Baja California Sur
- Panamic** – Punta Eugenio, Baja California Sur, to Punta Aguja, northern Peru.

The following table (Table 6) demonstrates the predominance of the genus *Macoma* in colder water. If a series of such tables were available for other molluscan groups, they could provide paleontologists with a readily usable means of comparing fossil assemblages with generalized information about Recent species.

Table 6

Arctic	Aleutian	Oregonian	Californian	Panamic
1. <i>M. middendorffi</i> <i>M. frigida</i> <i>M. crassula</i> <i>M. loveni</i>	4. <i>T. bodegensis</i> <i>T. carpenteri</i> <i>M. secta</i> <i>M. carlottensis</i>			
2. <i>T. lutea alternidentata</i> <i>M. calcarea</i> <i>M. brota</i> <i>M. obliqua</i> <i>M. moesta moesta</i> – <i>M. moesta alaskana</i> <i>M. lama</i>		3. <i>M. indentata</i>		
3. <i>M. balthica</i>			2. <i>T. meropsis</i> <i>L. obesa</i>	
2. <i>M. lipara</i> <i>M. expansa</i>		1. <i>T. idae</i> <i>M. leptonoidea</i>		
3. <i>T. nuculoides</i> <i>T. modesta</i> <i>M. elimata</i> <i>M. yoldiformis</i> <i>M. nasuta</i> <i>M. inquinata</i>				
		2. <i>M. acolasta</i>		

In this table, the following abbreviations are used:

1. Species occurring in one province only, that is, narrowly restricted
2. Species occurring in two provinces
3. Species occurring in three provinces
4. Species occurring in four provinces, that is, widely ranging

*T.* – *Tellina*  
*L.* – *Leporimetis*  
*M.* – *Macoma*

Distributions in the late Pleistocene are substantially the same as those in the Recent fauna. Most exceptions are probably due either to the lack of information about the Pleistocene north of California or about the Recent fauna on the Pacific coast of Baja California. An exception to this is the presence of *Leporimetis obesa* in the Pleistocene of Tomales Bay, which may be explained by the isolation there of populations during one of the warm interglacial periods.

Putting together our knowledge of the relationships of certain Recent West American species with their published fossil records can demonstrate some relationships, of which I would like to discuss here the most conspicuous.

As explained by GHISELIN (1969), the terms "homology" and "analogy" refer to correspondence between elements or features of some larger unit. They are not to be confused with "similarity," which refers to the overall property of larger units. Homology implies close correspondence of particular elements which are presumed to have a common ancestry. Analogy refers to a looser correspondence not based on a common ancestry.

Thus, the term which should be used for species pairs within given genera between biogeographic provinces, presumably as a result of common ancestry, is "homologues." Species which are presumed to be homologous are ones which are morphologically similar to one another in features of shell morphology. Analogous species, on the other hand, might either be similar species of unrelated taxa or species occupying the same ecological "niche" within different faunas, but belonging to different taxa.

The species having closest affinities with the Panamic or Caribbean provinces are:

*Tellina meropsis* – Panamic province with a Caribbean homologue; earliest fossil record in northwest America, Pleistocene.

*Tellina carpenteri* – Panamic province, with a possibly related Caribbean form; earliest fossil record in northwest America, Pleistocene.

*Leporimetis obesa* – closely related species in the Panamic and Caribbean provinces; earliest fossil record in northwest America, Miocene.

*Macoma yoldiformis* and *M. acolasta* – Related species in Panamic and Caribbean provinces; possibly related species in Miocene of northwest America.  
*Macoma indentata* – Panamic province; earliest fossil record in northwest America, Miocene.

Among Arctic species, a significant story is that of the *Macoma obliqua* group (COAN, 1969a), which is discussed in the text under that species and under *M. mid-dendorffi*.

*Macoma calcarea* is a trans-arctic species and seems to have relatives in the Oligocene of northwestern America. It probably reached the Atlantic and the Arctic from the Pacific. It does not occur in Asia but seems closely related to *M. orientalis*, which does.

*Macoma balthica* is a trans-arctic species and has West American and European fossil records only as far back as the Pleistocene. One suspects that it is recently evolved.

Finally, *Macoma moesta*, *M. crassula*, and *M. loveni* are trans-arctic but have no substantial fossil records, so that it is difficult to establish their origins. I suspect that *M. moesta* and *M. lama* may be related.

The following are non-trans-arctic species that are most closely related to Asian forms or that also occur in Asia:

These relationships suggest modes of isolation that may have provided so many tellinid species, especially of *Macoma*, on the west coast of North America.

First, there are closely related temperate species on the coasts of Asia and North America. These may be remnants of species once occurring all the way across the North Pacific along the Aleutian Islands that were subsequently isolated at some point during the Cenozoic by cooling. On the other hand, currents in the northern Pacific are assumed to have run mainly from the west to the east throughout the Cenozoic. It would not be surprising for products of Asian evolution to have been brought occasionally to western North America and become established.

Secondly, Bering Strait has been submerged during two main periods in the Cenozoic, as outlined by HOPKINS (1967) and COAN (1969a). This has provided an absolute isolating mechanism that may account for the large number of species of *Macoma*.

Thirdly, the closing of the long-open sea passage across Panama in the late Miocene isolated species in the Caribbean from closely related species in the Panamic province.

Table 7

Species	Asian homologue	Earliest northwest American record (or that of probable ancestral species)
<i>Tellina lutea</i> <i>alternidentata</i>	<i>T. lutea lutea</i>	Miocene
<i>T. nuculoides</i>	<i>T. lubrica</i>	early Pleistocene; ?Miocene
<i>Macoma lama</i>	also occurs in Asia	no record
<i>M. secta</i>	<i>M. sector</i>	Miocene
<i>M. nasuta</i>	<i>M. tokyoensis</i>	Miocene; ?Oligocene
<i>M. inquinata</i>	<i>M. contabulata</i>	Miocene

A few other species that are not predominantly arctic seem to have no close relatives in other provinces:

Table 8

Species	Earliest northwest American record (or that of probable ancestral species)
<i>Tellina bodegensis</i>	Oligocene
<i>T. idae</i>	Oligocene
<i>T. modesta</i>	Miocene
<i>Macoma elimata</i>	Miocene
<i>M. brota</i>	Miocene
<i>M. lipara</i>	Pliocene
<i>M. carlottensis</i>	Pleistocene; ?Miocene
<i>M. leptonoidea</i>	Recent; ?Miocene
<i>M. expansa</i>	Pleistocene

Finally, populations may have become established in bays substantially north of their normal occurrences. The protection of such embayments may cause water temperatures to reach the proper level for gonad ripening, spawning, and larval development and settling. For example, *Leporimetis* lived in Tomales Bay in the late Pleistocene, where it does not now occur. If such a situation continued for some time and gene flow with the main population were interrupted, speciation might have taken place.



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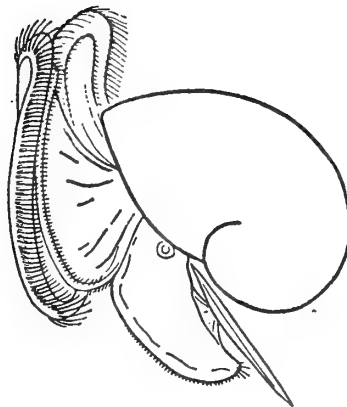
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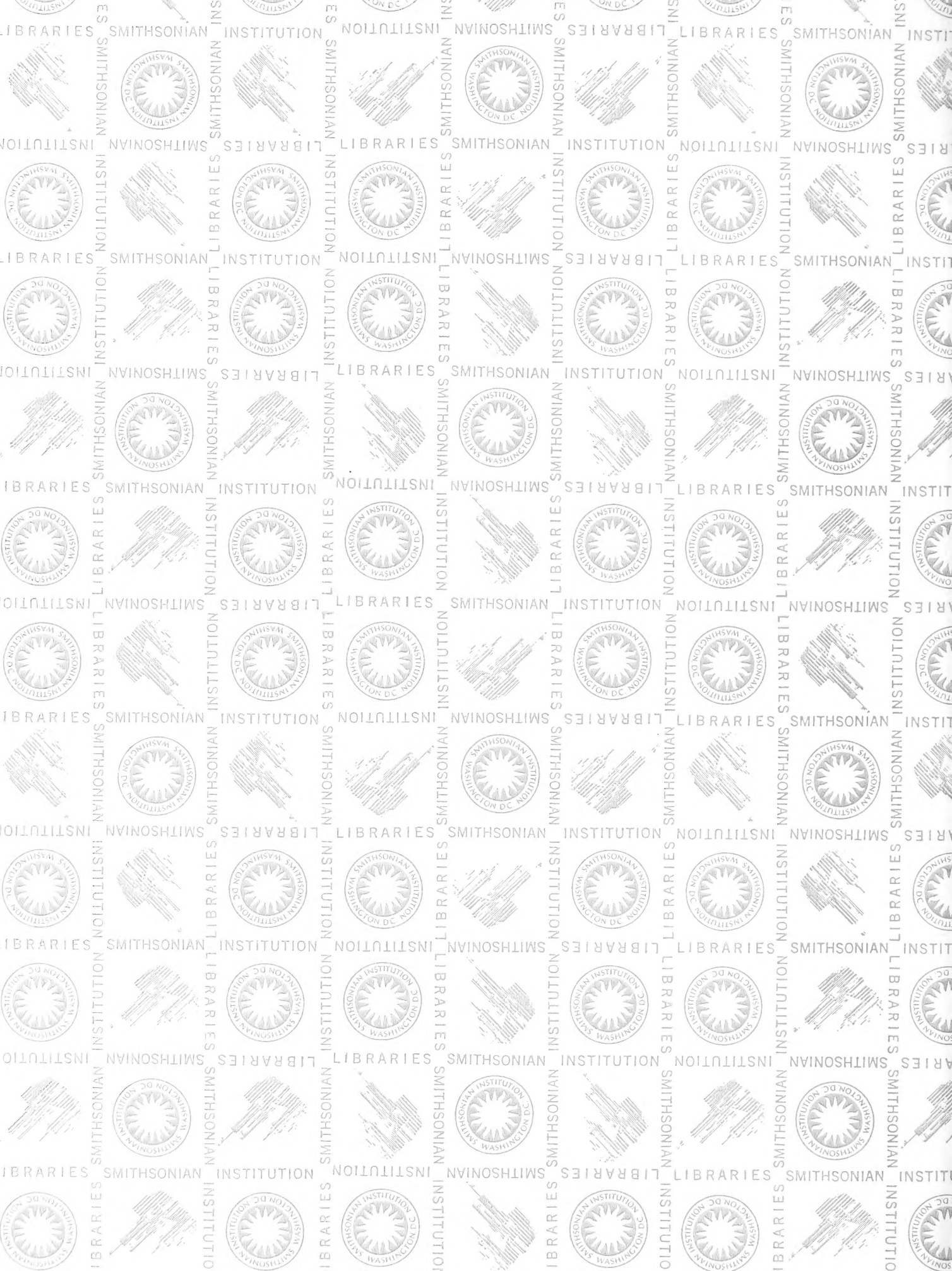
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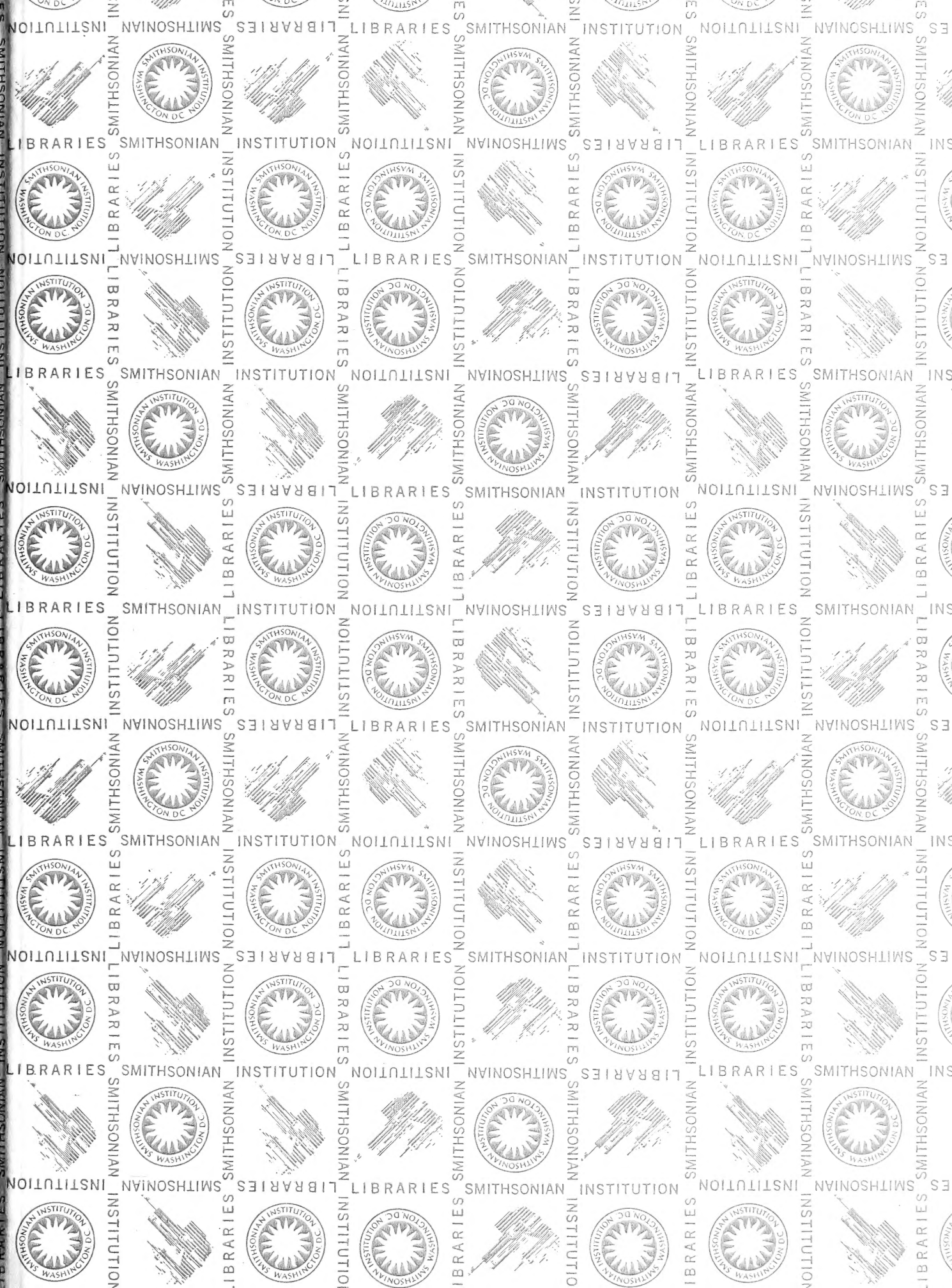












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