

Evolution and Distribution of the Genus *Mya*, and Tertiary Migrations of Mollusca

GEOLOGICAL SURVEY PROFESSIONAL PAPER 483-G



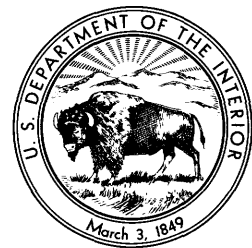
Evolution and Distribution of the Genus *Mya*, and Tertiary Migrations of Mollusca

By F. STEARNS MACNEIL

C O N T R I B U T I O N S T O P A L E O N T O L O G Y

G E O L O G I C A L S U R V E Y P R O F E S S I O N A L P A P E R 4 8 3 - G

*Known first in the early Tertiary of Japan, the genus *Mya* migrated to western North America, the Arctic Ocean, and to both the European and the American sides of the North Atlantic*



UNITED STATES DEPARTMENT OF THE INTERIOR
STEWART L. UDALL, *Secretary*
GEOLOGICAL SURVEY
Thomas B. Nolan, *Director*

The U.S. Geological Survey Library has cataloged this publication as follows :

MacNeil, Francis Stearns, 1909-

Evolution and distribution of the genus *Mya* and Tertiary migrations of Mollusca. Washington, U.S. Govt. Print. Off., 1964.

iv. 51 p. illus., map, diags. 30 cm. (U.S. Geological Survey. Professional Paper 483-G)

Contributions to paleontology.

Bibliography : p. 45-47.

1. Mollusks. 2. Paleontology—Tertiary. I. Title. (Series)

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CONTRIBUTIONS TO PALEONTOLOGY

EVOLUTION AND DISTRIBUTION OF THE GENUS *MYA*, AND TERTIARY
MIGRATIONS OF MOLLUSCA

By F. STEARNS MACNEIL

ABSTRACT

Two genera, *Mya*, a pelecypod, and *Neptunea*, a gastropod, were selected as vehicles for a study of late Tertiary to Recent faunal migrations from the Pacific to the Atlantic Ocean by way of the Arctic Ocean because they are mollusks of large size, and because they have unlike larval stages; *Mya* has small current-borne pelagic larvae, and *Neptunea* has large bottom-crawling benthonic larvae. This report considers chiefly the genus *Mya* but also includes a general discussion of Arctic faunal migrations and its bearing on Tertiary paleogeography of the Arctic. Available evidence suggests that during early Tertiary time the Arctic regions either had greatly reduced marine embayments, or they were entirely land. The earliest known marine Tertiary deposits in the high Arctic, found in northern Alaska and Spitzbergen, are of middle or late Miocene age. The first boreal species of Pacific origin to be found in Atlantic Ocean deposits is in the Yorktown Formation of Virginia. The Yorktown Formation is currently assigned to the Pontian (late Miocene) Stage.

All known species of the genus *Mya* are defined and delimited, and an attempt is made to resolve the synonymy of Japanese and American and Pacific and Atlantic species. American, Arctic, and European species are illustrated; Japanese species have been illustrated elsewhere.

The geographical distribution of *Mya* is treated from an evolutionary and migrational standpoint. The genus is restricted to the Northern Hemisphere. Its ancestry is unknown, but it may stem from temperate or subtropical early Eocene forms currently assigned to the genus *Sphenia*. The earliest known species of *Mya* occurs in late Eocene or early Oligocene beds of Japan. One indigenous Atlantic species is known. The remaining 16 recognizable taxa are indigenous to the North Pacific. Three, and possibly four, of the Pacific species migrated subsequently by way of the Arctic Ocean to northern Europe and the American Atlantic coast.

Nomenclatural and synonymic revisions in this paper include: suppression of the name *Mya grewingki nagaoi* Oyama and Mizuno as a synonym of *M. salmonensis* Clark; recognition of *M. kusiroensis* Nagao and Inoue, *M. grewingki* Makiyama, and *M. cuneiformis* (Böhm) in Alaska; acceptance of the name *M. japonica* Jay in preference to *M. oonogai* Makiyama for the species occurring in southern Japan; recognition of the name *M. elegans* (Eichwald) as the valid name for *M. crassa* Grewingk, *M. intermedia* Dall, and *M. profundior* Grant and Gale; recognition of the name *M. priapus* Tilesius as the valid name for the North Pacific and Bering Sea species identified by most modern Japanese authors as *M. japonica* Jay; recognition of *M. dickersoni* Clark as a close relative of *M. elegans*; and the recognition of *M. pullus* Sowerby as a valid species probably most closely related to *M. priapus*.

Two new species are described: *Mya fujiei* MacNeil, based on *M. japonica oonogai* Fujie (1957, pl. 2, figs. 1a-b) from the Takinoue Formation (early middle Miocene) of Hokkaido, and *M. arrosis* MacNeil, based on specimens in the collections of the University of California from the Cierbo Sandstone (middle late Miocene) of the San Pablo Group, Contra Costa County, Calif.

INTRODUCTION

The genus *Mya*, by virtue of both its morphological peculiarities and its heavy commercial harvest, should be one of the best understood mollusks. Instead, its comparatively few species, comparatively simple evolution, and comparatively restricted geographical occurrence involve subtleties that evade and confuse paleontologists and malacologists alike. Besides, there are still sizable gaps in our knowledge of phylogenetic lines.

Numerous attempts have been made to resolve the systematics of *Mya*. Until recently the most careful studies were by European and American workers whose main interest was in Atlantic and Arctic species, and who were dealing literally with the outermost fringes of the problem. In the last three decades, however, several important studies have been made by Japanese paleontologists. These studies show conclusively that the greater part of the genus evolved in East Asia, although its place of origin remains unknown. It remained for knowledge of the Japanese Tertiary species to be reasonably complete before any clear picture of the evolution of the genus as a whole could be had. Much of the basic study of the Japanese species was performed by Makiyama (1935), Nagao and Inoue (1941), and Minato, Matsui, and Uozumi (1950).

Fujie (1957 and 1962) further segregated some of the fossil forms, brought together the age, formational occurrence, and geographical distribution of the different species, pointed out the morphological details by which they can be distinguished, and he showed by differences in their chondrophores that they constitute two species groups. Unfortunately, Fujie had access to very little extra Japanese material, and most of his treatment of foreign species is based on literature that too often does

not describe or illustrate clearly the details he sought. Nevertheless, Fujie's work on the Japanese species contains the information necessary to a clear understanding of the origin and relationships of most myarian species, and it is unlikely that the present study could have been made without it.

If a genus so small, so clearly delimited, and so obviously isolated biologically from its closest relatives can pose such baffling problems, it can serve only to point up the complexity of organic evolution. It serves to show also how multiplied the problems can be in large multilinear groups in which separate lines of descent are morphologically parallel, less clearly marked, and complicated, moreover, by crisscrossing routes of migration. At least in the genus *Mya* the picture is not complicated by uncertainties in generic or subgeneric assignment, or by homeomorphy in lineages that have been distinct phylogenetically since Eocene time.

The present study has been carried on concurrently with a similar study of the gastropod genus *Neptunea*, a much more complex group. Comparable studies of *Neptunea* and *Mya*, with emphasis on migration, provide a comparison of the distribution pattern of a genus having small pelagic larvae with a genus having large benthonic larvae.

All photographs used in this paper were taken by Mr. Kenji Sakamoto, of the U.S. Geological Survey, Menlo Park, Calif. Mr. Sakamoto also translated the paper by Minato, Matsui, and Uozumi, as well as numerous other short passages from Japanese.

I am indebted to Dr. A. Andersson of the Naturhistoriska Riksmuseet, Stockholm, for permission to figure a specimen from the Nordenskiöld Yenisey Expedition collections, and to Dr. G. Spaink of the Netherlands Geological Survey for the loan of specimens from Pleistocene deposits of the Netherlands. Drs. G. A. Cooper and H. A. Rehder of the U.S. National Museum both loaned specimens for figuring. Considerable use was made of the collections of the University of California, Berkeley, The California Academy of Sciences, San Francisco, and Stanford University, Palo Alto, and I gratefully acknowledge the assistance of Dr. J. Wyatt Durham, Dr. Leo. G. Hertlein, and Dr. A. Myra Keen of these institutions, respectively, for permission to publish on specimens in their collections, and for critical reading of the manuscript.

MIGRATIONS OF PACIFIC AND ATLANTIC OCEAN MOLLUSKS

Next to *Neptunea*, *Mya* is the most conspicuous of those modern North Atlantic mollusks that clearly are immigrants from the Pacific. Because they are also

transArctic migrants, an understanding of Arctic migrations is a most important part of an understanding of myarian distribution.

Few genera have been the subject of worldwide monographic treatment, and even fewer of those monographed have been treated from the standpoint of evolution and migration. Such studies are not only the most reliable means of dealing with their taxonomy, but they have bearing on practically every phase of their geologic history. Many genera probably will be found to have nearly identical distribution patterns.

Migration studies would also aid materially in the solution of many stratigraphic and climatologic problems. Inasmuch as the temperature preference of many species is confined to fairly narrow limits, the species participating in Arctic migrations would reveal much concerning both the actual climate of each migration period and the relative amelioration of the polar climate for different periods. Two-way migrations give the greatest promise for accurate correlation of beds of departure with beds of arrival inasmuch as they can be checked both ways. A more detailed knowledge of paleogeography and of the time of opening of waterways would result.

BIOLOGICAL AND TEMPORAL ASPECTS OF MIGRATION

MIGRATION AND DISPERSAL

Migration can be defined as either an extension of the living area of an organism, or the complete abandonment of an area in favor of another. Dispersal can best be defined as the enlargement of the geographical distribution of an organism during any stage of its life, or death, by whatever means. Thus, migration can be accomplished by the dispersal of pelagic larvae by currents, but the most widespread dispersal of larvae cannot be construed as migration if the larvae are unable to establish themselves in new areas. The wide current dispersal of nautiloids, and probably ammonites, as gas-filled moribund individuals or floating dead shells is not migration.

MIGRATION AND ECOLOGY

It is impossible to lay down strictly geographical rules for the migration of species. Some elements of a fauna may migrate to a new area while other elements remain behind; still other elements may migrate to entirely different areas. Often it is difficult to see why a species does not occupy an area that seems open to it.

Viewed in the aggregate, migrations seem fortuitous. More probably, very careful selections of bottom, salinity, temperature, and other conditions are made.

In some molluscan migrations depth seems unimportant. In *Mya* it may be a limiting factor inasmuch as the genus is most prolific in very shallow water. Living specimens of both *M. arenaria* and *M. truncata* have been obtained as deep as 40 fathoms, but they are of small size and may not propagate at that depth.

The burrowing habit of *Mya arenaria* virtually restricts it to muddy and sandy bottoms. Its restriction to these substrata, however, does not necessarily restrict its migration because its larvae are pelagic. The stretch of unsuitable bottom the larvae could bypass would be limited, of course, to the duration of the larval period. According to Turner (1948), the length of the larval period of *M. arenaria* varies with temperature. Thorson (1950) stated that more than 70 percent of the Recent marine invertebrates have pelagic larvae, and that the larval period ranges from 2 to 4 weeks for those breeding in summer, and from 1 to 3 months for those breeding in winter. He also stated that up to 85 percent of the tropical species and up to 65 percent of the boreal species have pelagic larvae, but that such larvae are rare in the Arctic. Considering the number of species that have made successful transarctic migrations in the past, there must have been considerably warmer temperatures in the Arctic than the present temperature.

Cahn (1951, p. 86) quoted Yoshida (1938) as saying that bottom fixation takes place in *Mya japonica* before metamorphosis is completed, generally when the swimming larvae are from 0.24 to 0.30 mm long. At the end of metamorphosis the larger individuals may be as much as 3.2 mm long. Turner (1949) said that *M. arenaria* attaches to sand grains following metamorphosis by means of a byssus, and that until the tiny clams are about 25 mm long they remain exposed. After that they burrow into the substratum.

Mya arenaria is most common in bays and estuaries, and it may form dense colonies in the inner parts of estuaries where the salinity is reduced. Minato, Matsui, and Uozumi (1950, p. 1) qualified this by saying that *Mya* can live in brackish water provided there is sufficient salt in the substratum. Newcombe and Kessler (1936) showed that *M. arenaria* develops a heavier shell in water of high salinity. Merrill (1959) described specimens of *M. arenaria* attached to a buoy in the open sea that grew in 1½ years to the size reached by specimens in the normal bottom habitat in 2½ years.

Spawning temperatures probably are a more important factor in Arctic migrations than adult survival temperatures. *Mya arenaria* certainly can survive in bottom sands in areas where sea water freezes in winter, and Gunter (1957, p. 163) gives its lethal maximum

temperature as 40.6°C. This range might enable it to survive almost anywhere. According to Merrill (1959, p. 40), spawning begins before May in Wickford Harbor, R.I., but not until August at Malpeque, Prince Edward Island.

A detailed comparison of the migration patterns of *Mya* and *Neptunea* is deferred until the study of *Neptunea* is completed. Several seemingly important differences, however, have been determined thus far in the study that lead to the following generalizations.

Temperature is by far the most important factor in determining the global distribution of a species. Other factors, such as salinity and bottom conditions, are of local importance only; they may make areas within the preferred temperature range uninhabitable. Bathymetric preference is subsidiary to temperature preference. The spawning temperature is more critical than maturation or adult survival temperature. The isothermal boundaries of the spawning area, therefore, largely determine the geographical distribution of species. Pelagic larvae might mature outside the spawning area, and free-crawling adults may invade marginal areas, or areas well outside the spawning area.

The shape of a spawning area is determined by latitudinal isotherms and currents. Currents indent and extend the marginal configuration of the spawning area. A boreal breeding ground begins where incoming warm currents become sufficiently cool, and it ends where outgoing currents become too cold. The converse is true of cold currents. A species may or may not inhabit all of a possible spawning area, but migration is possible only within the thermogeographic limits of spawning.

The path and the direction of migration of species having pelagic larvae are controlled exclusively by currents. Benthonic organisms, on the other hand, can migrate with or against currents. They are confined to currents only if adjacent water is outside their temperature tolerance.

A cooling trend that makes the Arctic region too cold for spawning will, conversely, cause a shift in the spawning area to more southerly latitudes. The role currents play in determining the spawning area of species is fully as important as their role in transporting larvae. A species that spawns normally in boreal regions will follow warm currents into Arctic regions, and it will follow cold currents into temperate or subtropical regions.

Several apparently cool periods are indicated by the presence of cold-water species in beds of late Tertiary and Quaternary age in southern California. Un-

doubtedly these reflect cooling in Arctic regions. The occurrence, however, of mollusks now restricted to boreal regions at the latitude of Los Angeles, or farther south, does not indicate, necessarily, that boreal conditions existed at the time in southern California. They may indicate merely that a cool current flowed farther south than usual.

Arctic temperature changes seem to have caused greater advances and retreats of molluscan species on the American side of the Pacific than on the Asiatic side. Current distribution appears to minimize a cooling trend on the Asiatic side and exaggerate it on the American side.

Mya truncata, for instance, lives now as far south as southern Hokkaido and Puget Sound. It is a known fossil in beds of middle Miocene to Pleistocene age in Japan, but it is not known south of northern Honshu in beds of any age. It is found, however, in deposits of early Pliocene and early Pleistocene age as far south as Los Angeles on the American coast, a latitude more than a thousand miles south of its present southern limit.

Probably the boundary between warmer and colder water is more permanently located in East Asia where it marks the point of departure from the coast of the warm Kuro Shio current. The Kuro Shio feeds the Japan Current that flows eastward across the northern Pacific. The Japan Current divides near the American shore into northward and southward flowing branches. Throughout its transit across the northern Pacific the Japan Current is cooled by intermingling with the counterclockwise flowing Subarctic Current to the north. The Japan Current remains sufficiently warm for its northward flowing branch to have a moderating effect on the Gulf of Alaska, but it is cooled sufficiently for its southward flowing branch, the California Current, to have a cooling effect on the California coast. The degree to which the Japan Current is cooled by the Subarctic Current depends, in turn, on Arctic temperatures, and it has a major effect on the temperature of the California Current and its molluscan faunas from Canada to Mexico. The temperature of the California Current in its southern reaches, however, could be out of all proportion to adjacent land temperatures, and the mollusks it brings with it could at times be much colder types than those of adjacent estuarine faunas.

The Asiatic coast might be little affected by the same cooling trend that greatly reduces the temperature of California coastal waters, probably because of the less variable departure point of the Kuro Shio. Reduced Arctic temperatures might have a profound effect on the area from Hokkaido northward where water tem-

peratures are controlled by the Oya Shio, the southward flowing cold current of East Asia. The Japan Sea and the western side of Japan might also be cooled by a lowering of the temperature of the Oya Shio. It probably would not, however, displace the course of the Kuro Shio appreciably, nor would it cause an appreciable shift in the boundary between warm water and cold water faunas along eastern Japan.

MIGRATION AND SPECIFIC VARIABILITY

A factor that seems important to both ecology and the distribution of organisms is the nature of, and the reason for, specific variability. In particular, how do we determine whether local differences within greater populations are due to (1) differences in the substratum, salinity, light, available oxygen, temperature or current intensity, or (2) to genetics, or (3) to differences in the distribution of older populations? How can we tell an adaptation from a genetic innovation or a relict?

The thinking of marine biologists in general, whether in connection with studies of adjacent habitats of unlike nature, or of experimental transplants of organisms from one environment or another, seems to be that (1) a given variant results from an organism having entered, or having been left stranded in a given environment, (2) that the variant is specific to that environment, and (3) that the morphological response to the new environment is both immediate and reversible.

From the standpoint of both taxonomy and geologic history, it is important to know, for instance, whether a *Neptunea* living in a chilled fiord is merely a temperature variant of a species living in a warmer current flowing by its mouth (Golikov, 1960), or whether it is a relict of a stock that had a wider distribution in Pleistocene time. It is important to know whether the supposed intergradation with the species outside is a complete morphological gradation, or whether it is merely a progressive shift in the relative percentages of two discrete forms. Even in the former instance it would not be clear whether the morphological gradation was a response to temperature or other conditions, or whether it was an example of interbreeding between a species following the warm current and a relict stock in the fiord.

Soot-Ryen (1951, p. 2) discussed the relict character of faunas in Norwegian fiords. He pointed out that the warm Norwegian Current, which flows along the western side of Norway and rounds North Cape to flow thence along the Murman coast, virtually isolates the very cold water species in the fiords; there are sufficiently high thresholds to prevent warm water from

entering. He described Porsanger Fiord, near North Cape, as being the only real Arctic fiord in Norway, and only the innermost part, called Østerbotten, contains a completely Arctic fauna. Several species now widespread in the Arctic, but confined to fiords in Norway, ranged as far south as England during the Pleistocene. This would suggest that generally lower temperatures and a different terminal distribution of Atlantic currents existed during at least some stages of the Pleistocene.

The final answer to this problem could not be forthcoming without a knowledge of the Pleistocene species and subspecies and at least the major aspects of their distribution and migrations. If, for instance, the variants in fiords, the White Sea, or within the influence of the Labrador Current are a response to low temperature, it is a most important ecologic fact. If they are not, the assumption that they are cancels out one of the most important clues to past climate, evolution, migration routes, and Pleistocene history that we could ever hope to have. Furthermore, if they are attributed incorrectly to temperature, we are led to some entirely erroneous taxonomy. If any conclusion involving biology is based on a presumed knowledge of taxonomy, it is doubly important that the taxonomy be correct.

There certainly are some well-documented examples of physical change in organisms under different conditions of turbulence. The same coral species can be branching in quiet water and encrusting in turbulent water, and oysters tend to be more elongate in running water than in still water. There is danger of oversimplification, however, if all variants are regarded as the result of environment. If supposed environmental changes are used to interpret either geologic or Recent events, some entirely false conclusions can result. The great difficulty lies in being able to sort out the differences due to environment from those due to genetics, mutation, and hybridization. In all probability organisms respond morphologically to turbulence, but they select their temperature. If forced into an unfavorable temperature environment, they either adjust to it or perish. There is no incontrovertible evidence, however, that temperature alone can cause a mollusk to change morphologically.

MIGRATION AND EVOLUTION

Mya, as far as is known, reached the Atlantic coast of America and Europe well before *Neptunea*, and, moreover, the Atlantic representatives of *Mya* are less changed from their parent Pacific stock than are the first of the *Neptunea* found in Europe. This could well

be a function of both the means and the rapidity of their migration. *Mya*, which has pelagic larvae, probably is able to migrate rather rapidly, and because its larvae are current borne, probably all or most of its phenotypic forms go together. This would tend to maintain a uniformity in the varietal range of the migrating stock. *Neptunea*, on the other hand, has large benthonic larvae, and it has literally to crawl every inch of the way. There is a much greater chance for some variants to go astray and, in this sense, for the stock to evolve enroute. Time favors the possibility of mutational change as well.

In general, organisms that are pelagic during some stage of their life history are most apt to be distributed widely and with the least change. Wholly benthonic organisms change the most during migration; they take longer to migrate, and they are less indicative of temporal equivalence.

I am convinced that minor changes in genetic composition take place in migrating stocks along the entire route of migration. I am convinced, also, that a succession of intergrading variants can be taken as the trace of a migration route. The more distant representatives of a species may show significant and consistent differences. Possibly a genetic change due to the chance elimination of some of the variant types enroute is responsible. Only personal opinion, or the sentimentality inherent in nomenclature, can determine whether a species leaving the Pacific is the same species on arrival in Europe. Generally, however, there is no difficulty in identifying the Pacific stock from which it came; and if the distribution of the variants in the Pacific is well-enough known, there is no doubt as to which part of the Pacific it came.

MIGRATION AND CORRELATION

Ever since Huxley (1862; see Smith, 1904, p. 232) questioned the simultaneous occurrence of similar faunas in widely separated regions, there have been arguments as to whether such faunas were prima-facie evidence of temporal equivalence, or prima-facie evidence of an age difference owing to migrational lag. In all probability there is no universal rule. The answer would depend on the individual traits of each species or genus. The life history of each organism would have to be known before any positive statement could be made about the effect of migration on its evolution, or about the relative age of the beds in which it occurs.

It is hardly necessary to point out that the Recent fauna is not homogeneous throughout the world. There are important differences in the faunas of the

Caribbean, the Mediterranean, South Africa, Australia, Japan, and the west coast of the Americas. The faunas are not alike now, and there is no reason to suppose they were the same at any period in the past. Correlation of far-flung fossil faunas is tenuous and is based, usually, on intermediate correlations and on stratigraphic succession within units of epoch magnitude rather than on the identity of species.

Some genera are decidedly provincial and they appear not to have left the area in which they originated. Others, particularly in the Tethyan sea, have migrated to the opposite side of the world. It would be a mistake, however, to assume the occurrence of the same species to be synchronous everywhere.

TERTIARY PALEOGEOGRAPHY OF THE ARCTIC AND THE BOREAL REGIONS

Marine Paleocene deposits are known as far north as the Nugassuaq Peninsula in western Greenland at lat $70\frac{1}{4}^{\circ}$ N. The Midway sea of the American gulf coast extended as far north as North Dakota where there is a disconnected remnant of it known as the Cannonball Member of the Fort Union Formation. If there was a more northward extension of the Cannonball Member, or any kind of a connection between it and the Paleocene of Greenland by a Canadian passage, no geologic evidence for such a passage has been found to date. Identification of Paleocene beds in Alaska is still tentative, but even those that might be of this age are non-marine. In Europe the northernmost marine Paleocene beds known are in Denmark and southern Sweden.

Marine middle Eocene and Oligocene deposits are known from the northern Gulf of Alaska region at just past 60° north, and middle and late Eocene and Oligocene deposits are known in the Alaskan Peninsula below 56° north. There are marine Eocene and Oligocene beds in Kamchatka on the Asiatic side of the North Pacific. Marine Eocene deposits are known on the Atlantic coast of North America as far north as New Jersey, although they may be present below sea level farther north. In Europe the northernmost Marine Eocene and Oligocene deposits are found in southern England and Denmark.

In at least four areas in the high Arctic, northeastern Alaska (MacNeil and others, 1961, p. 1807, 17c), St. Lawrence Island in northern Bering Sea (ibid., 15), the Canadian Archipelago (Fortier, 1957, p. 437), and Spitzbergen (Schloemer-Jäger, 1958), early Tertiary beds are landlaid and, in part, coalbearing. Probably this area includes all or most of the present Bering Sea. The evidence available suggests, therefore, that more of the polar region was land than at present.

The probability that a continuous shoreline extended from eastern Asia to western North America close to the present southern margin of Bering Sea during the Oligocene is indicated both by the fact that the Oligocene fauna of the Alaskan Peninsula is predominantly Asiatic, most of the species having been described from Hokkaido, Sakhalin, and Kamchatka, and by the presence in the Oligocene strata of beds containing such large-sized Asiatic fresh-water mollusks as *Cipangopaludina* sp. and *Lanceolaria pisciformis* (Yokoyama). It would not be too surprising to find Asiatic marine mollusks in the Alaskan Peninsula inasmuch as their distribution might be controlled by currents, but the Asiatic fresh-water mollusks would be difficult to explain except by a continuous landmass. The large fresh-water pelecypod *Batissa*, which is found in the Puget Group (Eocene and Oligocene?) of Washington, and which is otherwise unknown except in eastern and southeastern Asia and in nearby Pacific islands within the sial line, probably reached America by the same land route.

A more nearly continuous shoreline also seems to have existed between Europe and North America throughout Eocene, Oligocene, and into Miocene time. Stage for stage throughout the Eocene and Oligocene there are both closely related and identical shallow-water species in Europe and the southeastern United States. Some nearly identical forms go under different names, largely because they were described in different continents rather than because of significant morphological differences. Some stocks that seem to have been peculiar to one continent or the other for several stages suddenly become very abundant and appear in the other continent. Such occurrences could be interpreted as a single coastal proliferation, because the mollusks are types that hardly could be expected to bridge an abyssal gap like the existing North Atlantic.

The Nuwok Formation of Dall (1919, p. 26A) in the vicinity of Camden Bay, northern Alaska, is the oldest known marine Tertiary in the American Arctic. The oldest fossiliferous part of the formation appears to be of Miocene age, either middle or late, and it contains several genera of Atlantic origin (*Arctica* and *Palliolium*) that, as far as is known, have never been in the Pacific. One of the genera present (*Submarginula*) is found subsequently in the Pacific.

The Nuwok Formation may represent much more than an invasion of the Arctic Ocean by an Atlantic fauna. It may well represent the first marine invasion of the high Arctic in Tertiary time; the beginning of the Arctic Ocean. The oldest fossiliferous marine Tertiary beds in Spitzbergen are of about the same age

(Hagg, 1927). Ravn (1922) regarded these beds as being of Paleocene age. The oldest fossiliferous beds contain species of *Arctica* and *Cyrtodaria* that strongly resemble species of these genera in the Nuwok Formation. Younger beds have yielded *Thyasira bisecta* Conrad, a species known from Oligocene to Recent in the Pacific and otherwise known only in the Pacific Ocean area. In my opinion the oldest fossiliferous marine Tertiary beds of Spitzbergen are not older than middle Miocene, and the *Thyasira bisecta*-bearing beds are younger; it hardly seems possible that they could antedate the first escape of Pacific species into the Arctic Ocean. (See p. G8.) Other lines of research that suggest a youthful age for the Arctic Ocean were reviewed by Pushcharovskiy (1960, p. 19).

The complete lack of marine Tertiary or Quaternary beds, except of very late glacial or postglacial age, in the Canadian Archipelago makes it unlikely that the Nuwok invasion was through that area. The presence of similar species of similar age in Spitzbergen, however, suggests that the invasion came from the region of the extreme North Atlantic Ocean and Barents Sea. The first faunal migrations probably were counterclockwise as in the existing Arctic Ocean. (See p. G9.)

The assumption that there was no Arctic Ocean, or at least a greatly reduced one in the form of epicontinental seas in areas such as the Laurentian and Angara basins, during the early and middle Tertiary could be of importance to supposed migrations of land mammals. No Tertiary land mammals of any kind have been found in Alaska, in spite of the insistence of vertebrate paleontologists that American-Asiatic and American-European migrations were commonplace. Even though Tertiary land mammals may be found eventually in Alaska, there probably were many alternate migration routes if much of the Arctic was land.

ARCTIC CLIMATE AND ITS EFFECT ON ORGANISMS

The northernmost Paleocene and Eocene faunas indicate a tropical or subtropical climate by modern standards. Certainly the most outstanding climatic event in the northern region from Oligocene to Recent time, however, has been a progressive deterioration of the polar climate. Northern mollusks had to adapt to a cold environment, and this resulted in a progressive differentiation of the mollusks into typically warm-water and typically cold-water forms. The change from south to north is gradational.

If, as seems to be indicated, there was no polar connection between the Atlantic and Pacific Oceans during

the early and middle Tertiary, even to the extent that the Arctic Ocean did not exist at that time, the net result seems to have been that mollusks characteristic of cold water were trapped in the northern parts of the two oceans. Once having become adjusted to cold water, they were incapable of migrating southward except by following cold water to ever-increasing depths, and those that may have ranged to the subtropics at depth were not able to gain access to the shallow waterways between the Pacific and the Caribbean.

With the gradual cooling of the polar regions during the Tertiary, some genera became characteristic of temperate and cold water and such genera are more apt to be restricted to the North Atlantic and North Pacific regions. Genera that are known as early as Eocene are more apt to have separate and indigenous Atlantic and Pacific species, but genera that did not become well defined until the middle Tertiary are apt to be restricted to one ocean or the other. Some of the cold-water genera peculiar to the North Pacific seem to be most closely related to warm-water stocks in the Indo-Pacific region, and they appear either to have invaded cold water successfully, or they were able to adapt to it after having been left stranded in it.

The apparent geographic differentiation of mollusks into warm- and cold-water species may, however, be subject to other interpretations. Probably there was a thermobathymetric gradation during Eocene time when surface layers seem to have been so universally warm. The cooling of polar waters may have caused normally cool, deepwater forms to invade shallow water in the Arctic regions, whereas the normally warm, shallow-water forms withdrew to shallow waters of the tropics. This interpretation would explain the apparent derivation of some Arctic genera from early Tertiary genera in tropical latitudes.

The presence of palms, *Exflabellaria groenlandica* (Heer) (LaMotte, 1952, p. 159), in the high Arctic during the Paleocene seems to indicate that the progressive cooling of the northern oceans during the Tertiary was due to more than the probable birth of the Arctic Ocean as a source of cold currents. Arctic land at that time was definitely warm. It was able to hold the insolation it received.

In general, shallow seas during the Eocene were more uniformly warm; tropical and subtropical genera are found as far north as Eocene deposits are known. Families and genera that were more universal during the Eocene are more apt to be restricted to subtropical regions at present, and they may be distributed in all warm seas.

PERIODS AND ROUTES OF MIGRATION

It has been recognized for a long while that the Tertiary to Recent distribution of molluscan genera indicates intermittent exchange of mollusks between Atlantic and Pacific waters in the near equatorial latitudes throughout most of Tertiary time. At far northern latitudes, however, there seems to have been exchange only in very late Tertiary to Recent time.

Probably the largest exchanges took place across northern South America in the early Tertiary, although there were lesser exchanges during the Miocene both there and possibly across Central America.

All these southern areas lie within the tropical and subtropical zones, a fact in keeping with the similarity of many Caribbean and tropical west American species. The existence of some nearly identical mollusks and echinoids in the Tamiami Formation (late Miocene and possibly including Pliocene) and in the Caloosahatchee Formation (regarded by most past authors as Pliocene but now known to contain *Equus*, a genus supposedly restricted to the Pleistocene) of Florida and in the Imperial Formation (late Miocene or early Pliocene) of southern California attests some kind of exchange not earlier than middle Miocene time and possibly later.

In the far north, there seems to have been no early or even middle Tertiary exchange of genera between the Atlantic and Pacific Oceans. By contrast, the late Miocene, Pliocene, and Pleistocene seem to have been periods of frequent exchanges of fauna. Many genera that underwent most of their evolution in the North Pacific, and that have a long Tertiary history there, appear suddenly on the Atlantic coast of North America and in northern Europe. At the same time, a few typically North Atlantic genera and species appear for the first time in the Pacific. In all probability the climate was warmer when the north passage was first opened than it was during the interglacial stages, or even at the present time.

The far greater number of Pacific migrants to the Atlantic than Atlantic migrants to the Pacific probably can be explained as due to the fact that most of the flow of water through Bering Strait is northward and to the fact that the passage between the Arctic and Atlantic Oceans is very large. Any Atlantic forms that entered the Pacific had first to find the comparatively narrow entrance through Bering Strait and then had to advance against outward flowing currents, or to find smaller counter currents, to enter the Pacific. In other words, Pacific species entering the Arctic Ocean found it easy to gain access to the Atlantic, but only

a few of the Atlantic species entering the Arctic ever found the entrance to the Pacific.

The earliest clear recorded occurrence of a Pacific boreal stock in the Tertiary sequence of the Atlantic coast is in the Yorktown Formation (late Miocene) of Virginia. Here *Mya arenaria*, a member of a species group that extends back to the late Eocene or early Oligocene of Japan, makes its first appearance in Atlantic waters. *Placopecten clintonius* (Say) may also have come from the Pacific. The earliest known occurrence of *M. arenaria* in Europe is in the Red Crag (early Pleistocene) of England. Another Pacific migrant, *M. truncata*, was reported by Wood from the Coralline Crag (late Pliocene) of England, but a specimen from the Coralline Crag in the Ipswich Museum is, in my opinion, *M. pseudoarenaria*, another Pacific derivative. At any rate, *M. truncata* occurs with certainty in the Norwich Stage of the Icenian Crag (late early Pleistocene) to which the specimen figured by Wood (1857, pl. 29, fig. 1) was reassigned by Chatwin (1961, fig. 24, no. 13).

Only one pre-Yorktown *Mya M. producta* Conrad, is known from the Atlantic. It occurs in the Chop-tank Formation (early middle Miocene) of Maryland and in equivalent beds in New Jersey. This species is unrelated to *M. arenaria*, or to any known Pacific species, and, presumably, it belongs to an indigenous Atlantic stock.

The first appearance of species of Atlantic origin in the Pacific Tertiary is in the Yakataga Formation (Miocene and Pliocene) along the northern coast of the Gulf of Alaska. About 8,000 feet above the base of the formation, and at a horizon believed to be either very late Miocene or very early Pliocene, there are found for the first time, *Astarte alaskensis* Dall (= *elliptica* Brown) and *Hiatella arctica* (Linné).

From Yorktown and mid-Yakataga time to the present time, migrations from one ocean to another are common. *Siliqua* appears in the Pacific, and a large number of Pacific genera and species appear in the Atlantic, among them *Acila*, *Neptunea*, *Thais*, *Boreoscala*, *Panomaya*, and *Macoma calcarea* (Gmelin).

Different stocks appear to have migrated to the Atlantic at different times and along different routes. Some, such as the stock of *Spisula voyi* (Gabb) (= *alaskana* Dall) are found only in postglacial deposits and living along the North American coast of the Atlantic where there is a species known as *Spisula polynyma* Stimpson. Others seem to have migrated to northern Europe directly by way of the western edge of the Canadian Archipelago, but they did not reach the American Atlantic coast.

Boreal and north-temperate mollusks also passed freely from the Pacific to the Atlantic during the Pleistocene, but the more southern forms apparently made the trip only during interglaciations that were even warmer than the present period. Although Arctic species now extend into boreal regions, there are boreal species common to both the North Atlantic and the North Pacific that do not live in the Arctic now.

A few boreal or cool-temperate species, having a Pacific origin and even more southerly habits, are now common to both oceans. Perhaps the most conspicuous of these is *Neptunea decemcostata* (Say). This species was described from the North Atlantic coast of the United States, where it lives from Grand Banks southward to Massachusetts. It is indistinguishable, except for a whiter shell and a more purplish coloring of the spiral ribs, from a form living around Kodiak Island. *Neptunea decemcostata* is a comparatively young species in the Gulf of Alaska, and its evolution there during the Pliocene and Pleistocene is well shown by specimens in the Geological Survey collections. This species appears to have been on the Atlantic coast only in Recent and sub-Recent time.

Many of the molluscan genera represented in both oceans have species groups that are typically Atlantic and typically Pacific. Probably they owe these differences to the fact that they were mutually isolated for a part of Tertiary time. Because of the late Tertiary and Quaternary migrations by way of the Arctic, however, the distribution pattern in Recent seas has been most confusing. Many of the independently derived pairs, or groups of species, are now circumarctic, with derivatives of both oceans inhabiting virtually the same areas. Because the species are congeneric, there have been suggestions that they are merely varieties of the same species.

Two such species are *Hiatella arctica* and *H. pholadis*. *H. arctica* has a long history in the Atlantic and clearly traces its origin to a form in the Oligocene of the Netherlands. The *H. pholadis* group, on the other hand, is known in the Pacific at least as far back as the *Echinophoria apta* zone of the Oligocene and Miocene on Sitkinak Island just south of Kodiak in the western Gulf of Alaska and in the Poul Creek Formation of the Yakataga district. This may be *H. sakhalinensis* (Takeda), a species described from the Maoka Group (Oligocene and Miocene) of Sakhalin. Because of the fact that adults of *H. arctica* often lose their bicarinate posterior ridge and become rounded, it is difficult to tell them from *H. pholadis*, particularly when they occur together.

Another peculiarity of Arctic distribution is the occurrence of Pacific species along the Arctic coast of western Siberia but not along the Arctic coast of eastern Siberia. In other instances the variants found west of the Taymir Peninsula are more like the variants found along the Arctic coast of Alaska than they are like the variants found along the coast of intervening eastern Siberia. Both pelecypods, which are current borne, and some species of *Neptunea*, which are wholly benthonic, are so distributed. On the other hand, both *Neptunea beringiana* and *N. ventricosa* have migrated westward along the Arctic coast at least as far as Wrangel Island. This suggests that even though some benthonic species may have migrated westward from Bering Strait, others migrated eastward and reached western Siberia by way of Spitzbergen, from whence they migrated eastward along the Siberian Arctic coast. For such species the East Siberian Sea is a province remote from the Bering Sea, inasmuch as they reached there by a counterclockwise migration all the way around the Arctic Ocean. Long shore currents along both the Siberian and Alaskan Arctic coasts flow eastward, a factor contributing to a counterclockwise migration pattern. The distribution of Arctic brachiopods leads to a similar conclusion (Elliot, 1956, p. 280).

This circumstance may also be a factor in the predominance of Pacific to Atlantic migrants over Atlantic to Pacific migrants. Those leaving the Pacific met currents that carried them along the Alaskan Arctic coast, the west side of the Canadian Archipelago, and thence around northern Greenland to the Atlantic entrance. *Thyasira bisecta* Conrad, which occurs in late Tertiary beds of Spitzbergen, probably represents one of the earliest of such migrations. Atlantic species entering the Arctic, however, were carried eastward along the much longer Norwegian and Russian coasts. As shown by Lavrova and Troitskey (1960, fig. 1), different Atlantic mollusks migrating eastward during the Pleistocene Boreal transgression (post-Riss; Sangamon) penetrated the Arctic coast unequal distances. Lines can be drawn showing where, first, *Cardium edule*, then *Pholas crispatus*, and finally *Arctica islandica* dropped out. Thus some Atlantic species not only did not enter Bering Strait; they did not reach Bering Strait.

Although such genera as *Arctica* and *Pallioium* reached northern Alaska in Nuwok time (middle or late Miocene and Pliocene), subsequent migrations did not extend that far. In the Pleistocene, *Arctica* got only as far as the Yenisey-Duduypta valley region in the Pechora Basin. Both Soot-Ryen (1932, p. 20) and MacNeil (1957, p. 104) discussed the occurrence of

Palliolium groenlandicum in the Recent fauna as far east as the East Siberian Sea; it does not live now in either the Chukchi or Beaufort Seas.

Migrations within the Pacific Ocean area seem to have been predominantly from west to east. Of the many species common to American and Asiatic waters, almost all have a known older history on the Asiatic side. There probably are genera with benthonic larvae that originated along the American coast and migrated westward along the northern fringes of the Pacific. *Fusitriton*, for instance, is known in middle Miocene beds in Alaska, but I can find no recorded occurrence of it in Japan before Pliocene time. Its range extends along the west coast of South America to Cape Horn and thence northward along the Atlantic coast to Brazil. It has not been found in the Caribbean, possibly because it is confined to deep water in tropical latitudes—water deeper than the isthmian straits.

Many eastern Asiatic species, on the other hand, have moved eastward along the Asiatic coast, some to enter Chukchi Sea and thence eastward along the Alaskan Arctic coast and others to migrate southward along the American coast as far as California and Baja California. Some of the best American index fossils, such as *Acila shumardi* and *Acila gettysburgensis*, are Asiatic species that made abrupt and temporary appearances in western North America. They belong to longer ranging Asiatic stocks. These species are not as critical for dating in East Asia where there are closely related earlier and later species. Species entering the Pacific from the Arctic seem to have favored the American side. A few, however, such as *Hiatella arctica* and *Astarte elliptica*, appear to have migrated westward to Japan.

Figure 1 shows what is probably the main path of migration for species having pelagic larvae during late Tertiary and Quaternary time. Owing to the fact that the main course and terminal distribution of currents may have varied from time to time with both climate and basinal configuration and as they are complicated, moreover, by countercurrents and eddies, the paths so indicated are not presumed to indicate the exact location of currents. They are presumed to indicate merely the origin, direction, and termination of species migrations.

The general pattern of Arctic faunal migrations is beginning to emerge more clearly, and the history of the study makes it obvious why they were recognized sooner by the workers in some areas than in others. Scandinavians have long recognized that many elements of their modern fauna are of northern Pacific origin. British workers of the last century stressed

the fact that many species "came down from the north." Western American workers (see Smith, 1904; Keen, 1940) have long been cognizant of the influx of Asiatic species to western America, but the idea of two way transarctic migrations has not been strongly put forth. Species or closely related species in the North Atlantic and North Pacific Oceans were regarded primarily as Arctic species that extended into the boreal parts of both oceans; periodic abandonments of the Arctic and reinvasions of the Arctic were believed to coincide with climatic changes.

Japanese workers have been preoccupied, and justifiably so, with the tremendously rich warm-water element of their modern fauna. New additions to the warm-water fauna came largely from the Tethys. They seem to have been the least aware, therefore, that the northern fauna, including that of the Kuril Islands, the Sea of Okhotsk, and Kamchatka, was the source of many elements of the western American and northern Atlantic faunas. Many Alaskan Tertiary fossils are now identified as Asiatic species. Further critical comparisons of American and Asiatic species may show much less endemism in East Asia than the current nomenclature suggests.

Although the main pattern of Pacific-Atlantic migrations is becoming clearer, many details remain to be worked out. Different species appear to have migrated during different preglacial periods in the late Tertiary and during different interglacial periods. Accurate determination of these species and of the time each species migrated would do much towards more accurate stage assignment of Arctic and boreal marine Pleistocene deposits, particularly those bordering the North Pacific which are farther removed from Europe and where more information is needed. A situation so complex and which at first glance might seem so completely hopeless, could, if completely understood, prove to be an extremely delicate tool in solving many of the temporal and climatic problems of the Pleistocene.

PHYLOGENY AND DISTRIBUTION OF SPECIES

IDENTITY OF *MYA JAPONICA* JAY

It would be extremely cumbersome to discuss or compare the various Pacific species of *Mya* without first clarifying the identity of *M. japonica*. Previous authors have interpreted this species differently, so that comparisons with "*Mya japonica*" by name are most confusing.

There are three Recent species of *Mya* in Japan. One is *M. truncata*. Another species lives from Hokkaido southward; a third species lives from Hokkaido northward. The southern species is closely re-

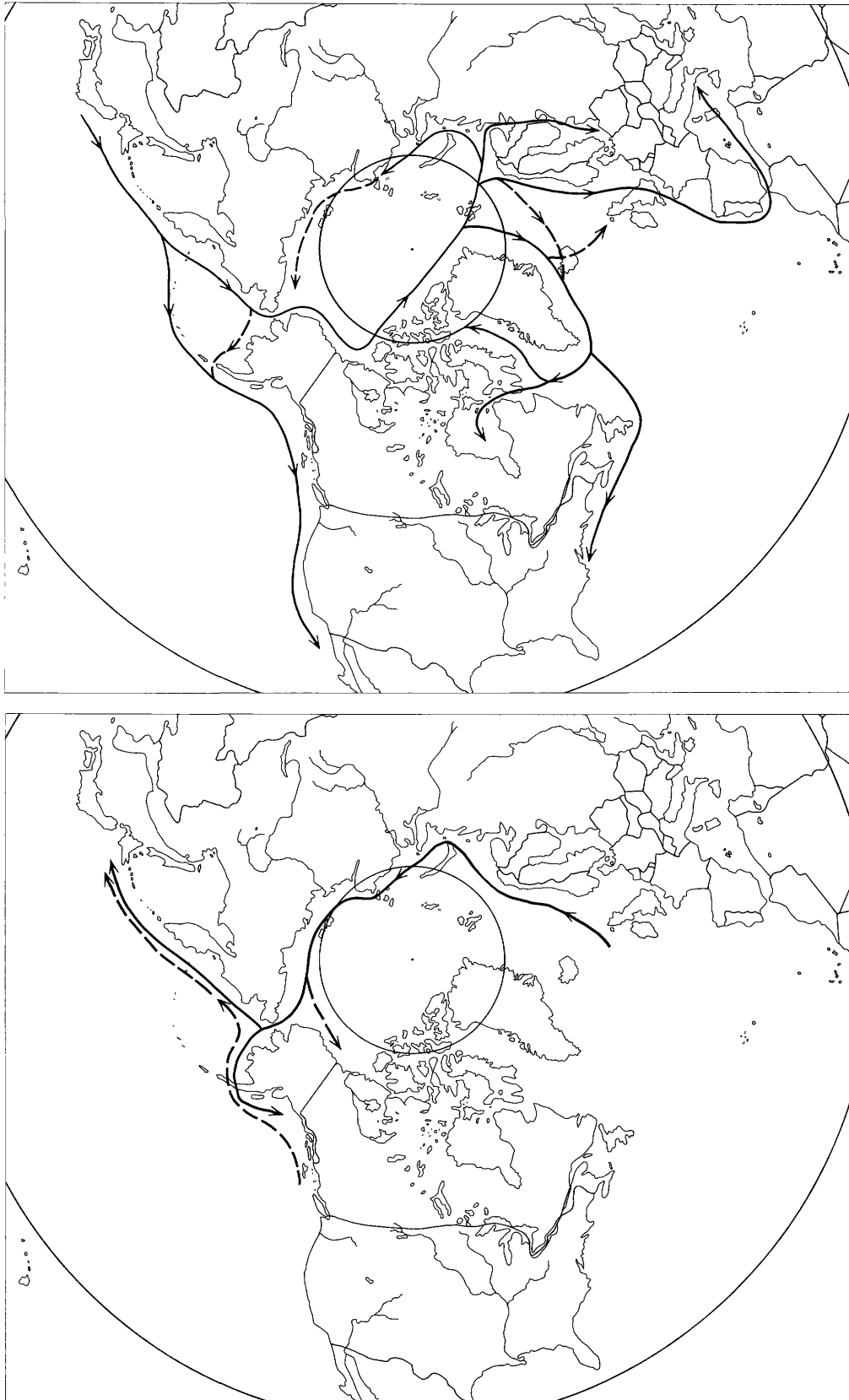


FIGURE 1.—Most probable late Tertiary and Quaternary migration routes between eastern Asia and western North America, and between the North Pacific Ocean and North Atlantic Ocean.

lated to *M. arenaria*. The northern species belongs to the *M. truncata* group.

Prior to 1931 most authors seem to have associated *Mya japonica* with *M. arenaria*. It was regarded, therefore, as being the southern species. Grant and Gale (1931, p. 412), on the other hand, used the name for the northern species. Makiyama (1934, 1935) and, as far as I can see, most subsequent Japanese authors also have applied the name *japonica* to the northern species. Makiyama (1935) proposed the name *M. oonogai* for the southern species. Whether Makiyama's action reflects Grant and Gale's opinion, or whether it is because the northern species is the common *Mya* in Uchiura-wan, Hokkaido (the "Volcano Bay, Yeddo" of Jay) is not clear. According to Fujie (1962, p. 400), however, *M. oonogai* also inhabits Uchiura-wan.

Grant and Gale's concept of *M. japonica* may very well have been based on Dall's identification of some very well preserved specimens from postglacial beds on Cottonwood Creek, Kachemak Bay, Alaska (Dall, in Martin and others, 1915, p. 92). Some of these specimens are figured in this report (pl. 11, figs. 1-3, 10, 13, 14).

Jay did not figure the spoon of his species, and his remarks are not sufficient to identify it beyond all question. His figures (Jay, 1856, pl. 1, fig. 7, 10; also Slodkewitsch, 1938, pl. 102, fig. 2), however, show it has the outline of *Mya oonogai*, and, more important, its pallial sinus is completely detached from the pallial line except at the posterior juncture. In the northern species, the lower leg of the pallial sinus coincides with the pallial line. The character alone indicates that *M. japonica* could only be the form Makiyama named *M. oonogai* and the form Fujie treated as *M. japonica oonogai* Makiyama.

Fujie recognized the possibility that *M. oonogai* and *M. arenaria* might be the same species, but his conviction was not strong enough to make him adopt Linné's name. Instead, he accepted it as a subspecies of the northern Japanese species to which it is only distantly related.

The name *Mya japonica* would not have priority for the northern Japanese species in any event. The species ranges from Hokkaido to northern Bering Sea and eastward to Cook Inlet, Alaska. There is no doubt in my mind that it is the species for which Steller prepared a description in 1743 from a live specimen from southern Kamchatka. The description and an illustration prepared under Steller's direction was salvaged and published by Tilesius in 1822 as *M. priapus*.

MYA CRASSA GREWINGK, MYA ELEGANS (EICHWALD), AND MYA INTERMEDIA DALL

I have been informed by Dr. O. A. Scarlato (written comm., Aug. 31, 1960) of the Zoological Institute, Academy of Science, Leningrad, that Grewingk's collection cannot be found; at least at this date none of the specimens he handled can be identified. This being so, we can judge his species only by his remarks and figures and by an attempt to reidentify his species.

Grewingk listed three species of *Mya*: *M. crassa* Grewingk, *M. arenaria* Linné, and *M. arenaria* var. The last is stated to have cardinal teeth and an external ligament and probably is a *Macoma*.

Mya crassa Grewingk and the form he identified as *M. arenaria* are fossils. The worst snarl in myarian taxonomy has developed from the fact that he thought these were different species, and both Dall, and Grant and Gale, although they expressed doubts, accepted them as such. Neither Dall, nor Grant and Gale, knew Grewingk's species except from his figures. In 1960, however, a large suite of *Mya* was collected from a locality in the Alaskan Peninsula northwest of Chignik Bay by the Gulf Oil Co. These fossils, which are now in the collections of the U.S. Geological Survey, compare perfectly with Grewingk's figures and they show, moreover, that both of Grewingk's forms are the same species. The range of variation within this suite, due both to individual variation and differential deformation, is even greater than indicated by Grewingk's figures. Furthermore, I can see no way in which the fossils can be differentiated from the large thick-shelled species now living in southeastern Bering Sea and on the south side of the Alaskan Peninsula.

Mya crassa is twice a homonym (Vallot, 1801; Wood, 1815). Grant and Gale (1931, p. 414) proposed *M. profundior* as a substitute name for *M. crassa*, and, in a footnote inserted in page proof, they called attention to *Anatina elegans* Eichwald as a possible earlier name. *Anatina elegans* Eichwald was proposed for Grewingk's second species, his *M. arenaria* Linné. The fact that both Grewingk's species are one makes the acceptance of this name unavoidable, but it is with the utmost reluctance that I accept a name so incorrect as to generic assignment and presumed age; Eichwald thought all Grewingk's fossils were of Turonian (Cretaceous) age!

Dall (1898, p. 857) suggested that Grewingk's *M. arenaria* might be called *M. intermedia*. At the same time, he said the shell grows to a very large size in the Alaskan Peninsula, indicating that he regarded it as the large Recent species. He also said, "*Mya crassa*, from the Miocene of Alaska, appears from the figures to be

distinct from *Mya intermedia*." Dall (1904, p. 117) expressed the opinion, however, that the two might be mutations of the same species.

Grewingk mentioned *Mya intermedia* Sowerby (a *Panope*) in connection with *M. crassa*. It seems improbable that Dall, who was entirely familiar with Grewingk's work, could have overlooked the earlier *M. intermedia* Sowerby. Possibly his original intention was that one of Grewingk's species might be assigned to *M. intermedia* Sowerby. Later, and possibly forgetfully, Dall (1921, p. 52, pl. 4) used the name "*Mya intermedia* Dall" for the large Alaskan Peninsula species, and according to MacGinitie (1959, p. 187, pl. 19, fig. 6), he purified the species by selecting a "lectotype" from Chignik Bay, Alaska. The selection of a lectotype must be in the form of a label in the U.S. National Museum.

Grant and Gale recognized *Mya profundior* (*M. crassa*) only as a fossil. The large Recent species (as *M. intermedia* Dall, a homonym) they placed in the synonymy of the northern species that they wrongly interpreted as *M. japonica* Jay (here interpreted as *M. priapus*). In their discussion of *M. profundior*, however, they said, "This may be but an unusual variation of the form for which Dall used the preoccupied name *intermedia*; and if it is decided to separate the latter from *japonica* [meaning *priapus*] and *dickersoni*, it may be possible to use this name for it." Thus they conditionally suggested the use of the name *profundior* for the large Recent species that Dall had called *M. intermedia*.

MacGinitie (1959), like Grant and Gale, realized that *Mya intermedia* was a homonym, and she said, "Since the name *intermedia* is unavailable, the figured shell [pl. 19, fig. 6] can undoubtedly be assigned to *M. japonica* Jay." Her *M. japonica*, however, was the southern Japanese species, the true *M. japonica*, rather than the northern species (= *M. priapus*) to which Grant and Gale applied the name.

MacGinitie (1959, p. 188) further pointed out that Dall (1924, p. 31, 32) identified specimens from two localities on the Arctic coast of Canada as *Mya intermedia*, and that these really belong to *M. pseudoarenaria* Schlessch. It is not clear what Fujie had in mind when he said, *M. japonica* (meaning *priapus*), *M. intermedia* (meaning *elegans*?, or perhaps Dall's Canadian Arctic species), and *M. pseudoarenaria* were all one species; at least he seems to have regarded *priapus* and *pseudoarenaria* as one species.

Any further discussion of the subtleties involved, however, are immaterial to the nomenclature at this date, because *M. crassa*, *M. profundior*, *M. arenaria* of

Grewingk, and *M. intermedia* of Dall are the same species, and *M. elegans* (Eichwald) is the earliest valid name for it. I do not believe the Recent representatives of this species are sufficiently distinct to justify even a subspecific name.

ANCESTRY OF *MYA*

The predecessor of *Mya* is at present unknown. Either the ancestor of *Mya* is an East Asian form as yet undiscovered, or it is some earlier non-Asian genus as yet unidentified. Both *Bicorbula* from the Eocene of Java and *Raetomya* from the Eocene of Egypt and Nigeria have been mentioned as possible antecedents, but, if so, there is a wide morphological gap between them.

In all probability the ancestor of *Mya* had a ligament that was more symmetrical dorsoventrally, and its ligament was almost certainly partly internal. One possible ancestor is *Sphenia? minor* Forbes (Wood, 1877, p. 23, pl. B, figs. 16a, b) from the British early Eocene.

INDIGENOUS ATLANTIC SPECIES—*MYA PRODUCTA* CONRAD

Of the known species of *Mya*, all but one can be interpreted on the basis of morphology and distribution as belonging to a group that underwent the greater part of its evolution in the North Pacific. The exception is *Mya producta* from the Choptank Formation of Maryland and the Kirkwood Formation of New Jersey, both middle Miocene.

This species is not only dissimilar in shape to other myarian species, but it is not related with certainty to any known Pacific species. As far as is known, *Mya producta* enjoyed only a brief existence in the western Atlantic, and it is clearly unrelated to *M. arenaria*, a species found on the Atlantic seaboard for the first time in the Yorktown Formation (late Miocene) of Virginia.

Mya producta is undoubtedly a true *Mya*, but its peculiarities suggest only that it probably had a common origin with the earliest of the Pacific species. If true, where or when the stock existed previously is not known.¹

EARLY PACIFIC SPECIES

The earliest known species of *Mya* is *M. ezoensis* Nagao and Inoue from the Wakkanabe Formation

¹ Since this paper was written, Mr. Druid Wilson, of the U.S. Geological Survey, has called my attention to an unidentified small *Mya* from beds of probable early Miocene age in North Carolina. The species has a pallial sinus like that of *M. producta*, but its shell is small, has crude concentric undulations, and some specimens are much distorted. Shells were found in holes in the upper surface of a bed of limestone, suggesting that it is a borer or, possibly, a nestler. The species is not related to any known Pacific species.

(late Eocene or early Oligocene) of the lower part of the Ishikari Group of Hokkaido, Japan.

Mya ezoensis probably gave rise directly to *M. kusiroensis* Nagao and Inoue, a species found in the Shitakara Formation (middle Oligocene) of the Urohoru Group of Hokkaido. The Urohoru Group is correlated with the upper part of the Ishikari Group. The earliest known *Mya* in America is found in the upper part of the *Acila shumardi* zone (middle Oligocene) of Popof Island in the Shumagin Islands, located south of the Alaskan Peninsula. This same species occurs in the basal part of the Poul Creek Formation in the Yakataga district along the northern side of the Gulf of Alaska; the lowermost part of the Poul Creek Formation as currently defined may also fall within the upper part of the *Acila shumardi* zone. The Alaskan species matches perfectly the available figures of *M. kusiroensis*, and it occurs in beds of about the same age.

The common *Mya* in the middle and upper part of the Poul Creek Formation (late Oligocene and early Miocene) is *M. salmonensis* Clark. *M. salmonensis* appears to be identical with *M. grewingki elongata* Nagao and Inoue (not Brocchi, 1814; renamed *M. nagaoi* Oyama and Mizuno) from the Poronai Series² (Oligocene and Miocene; generally considered to be equivalent to the Poul Creek Formation and the Blakely Formation of Washington) of Hokkaido.

Occurring with *Mya salmonensis* in the Poronai series of Hokkaido and in equivalent beds of Sakhalin is another species, *M. grewingki* Makiyama. One specimen from the Poul Creek Formation of Alaska is identified tentatively as this species. I do not regard either *salmonensis* or *grewingki* as being a subspecies of the other, but both probably are derived from *M. kusiroensis*. On the basis of its spoon, *M. salmonensis* is ancestral to *M. cuneiformis* and in turn to other members of the *M. truncata* group. *M. grewingki*, on the other hand, is related to *M. elegans* and *M. arenaria*.

Fujie stated that *M. grewingki* persisted until middle Miocene time in Hokkaido where it occurs in both the Horoshin and Chikubetsu Formations. I am not

entirely convinced that *M. grewingki* survived the early Miocene in Japan. Fujie (1957, p. 392, pl. 5, figs. 1-4) described a supposed "variety" from the Chikubetsu Formation as *M. grewingki* var. *haboroensis*. As discussed later, this form is very closely related to *M. dickersoni* Clark from the late Miocene of California, and it could be regarded as a subspecies of *M. dickersoni*. I am following Fujie, however, in regarding it as a subspecies of *grewingki*. *M. dickersoni* belongs to the *M. elegans* group. The specimen from the Horoshin Formation figured by Fujie (1957, pl. 5, fig. 7) also seems to be more like *M. elegans*. Except for *M. grewingki haboroensis*, I can find no recorded occurrence of *M. grewingki* in postearly Miocene beds of Japan or Alaska.

MYA ARENARIA GROUP

The different types of spoons in the two coexisting species, *M. grewingki* and *M. salmonensis*, suggests that the primary differentiation of the spoon into more rounded and more triangular types took place in an ancestor of both species, either in *M. kusiroensis* or in *M. ezoensis-kusiroensis* intermediates. The more archaic type of spoon in *M. ezoensis* is broader anteriorly and has a moderately strong indentation or concavity along its ventral margin opposite the boundary between the laminum attachment and the fibrum receptacle. This ventral marginal concavity persists in *Mya (Mya)*, but in *Mya (Arenomya)* the ventral margin of the spoon is convex; in *M. elegans* the greatest marginal convexity is located at about the same position as the concavity in *M. ezoensis*.

The early history of *M. arenaria* and its precise origin has been anything but clear. Fujie (1962, p. 401) thought *M. arenaria* and *M. japonica* (as *M. japonica oonogai*) might be conspecific, but he had no specimens of *M. arenaria* for comparison and he hesitated to combine them. He thought *M. japonica oonogai* could be traced back to the Takinoue Formation (early middle Miocene) (1957, pl. 2, figs. 1a-b, 2 of Hokkaido; however, he said there is no record of the species from younger Miocene deposits of Japan. He recorded four occurrences of *M. japonica oonogai* from Pliocene beds of Honshu (Fujie, 1962, p. 405). In my opinion the form in the Takinoue Formation is a new species, and it may be identical with the oldest of the forms that have been included in *M. dickersoni* in California. I am naming this species *M. fujiei*.

Mya dickersoni has been identified in the past from the Briones, Cierbo, and Neroly Formations of the San Pablo Group (late Miocene) of California. The spoon of *M. dickersoni* has never been figured, and

² Japanese stratigraphic names used in this paper are cited as in the source references, and no attempt is made to make them conform to the American Stratigraphic Code. Hatai and Nislyama (1952, p. 5) said, "Until comparatively recently in Japan little attention was paid to the use of uniform stratigraphic terms, and different authors changed the names of formations at will. Little or no distinction was made between terms used for lithologic units, time-rock terms, and divisions of geologic time."

Japanese stratigraphers do not regard the geographic component of a name as preempted by usage in a higher category. Thus, there may be the Takikawa Formation of the Takikawa Stage of the Takikawa Series. Series and group may be used interchangeably, although in recent years group has replaced series. Stage appears to be used most widely as a biostratigraphic zone.

neither the illustrations of the exterior nor the published remarks give much clue to its actual relationships. A study of the spoon and other characters, both in topotypes and in other specimens contained in the collections of the University of California, suggests that four possible taxa have been included in *M. dickersoni*. These are: *M. dickersoni* (closely related to *M. grewingki haboroensis*), *M. arrosi* n. sp., *M. cf. M. fujiei* n. sp. (as the paratype of *M. dickersoni*), and *M. arenaria*. The first belongs to the *M. elegans* group; the second may be ancestral to *M. japonica*; the last two belong to the *M. arenaria* group.

Clark figured two distinct species under *Mya dickersoni*. The holotype (Clark, 1915, pl. 63, fig. 3) came from the Neroly Formation (late late Miocene), the youngest formational unit of the San Pablo Group of central California. The paratype (Clark, 1915, pl. 63, fig. 4) came from J. C. Merriam's locality 197 from "near the base of the Contra Costa Miocene" on the west limb of the Pacheco syncline. A late notation in an unknown hand in the University of California locality catalog says, "Sobrante." However, I can find no other record of a *Mya* from the Sobrante Sandstone, the oldest formational unit referred to the Monterey Group (Miocene) in Contra Costa County, Calif. Weaver (1953, p. 68) listed *M. dickersoni* from the Briones Sandstone at a locality close to or identical with Merriam's locality 197 but none from the Sobrante Sandstone in the same area.

In all probability the paratype of *Mya dickersoni* is from the Briones Sandstone. Fujie (1957, p. 410) expressed the opinion that the holotype and paratype of *M. dickersoni* were different species, but he could not possibly have been aware of an age difference. He suggested the holotype might be related to *M. cuneiformis*. As discussed on page G17, typical *M. dickersoni* belongs to the *M. elegans* group. The paratype appears to be closely related to *M. fujiei* from the middle Miocene of Japan, and it may connect that species with *M. arenaria*, a species first recognized in the Cierbo Sandstone; the spoon of the paratype is unknown.

The Briones Sandstone (early late Miocene) appears, therefore, to be the earliest known occurrence of *Mya* in western North America, south of Alaska.

The University of California collections contain another species from the San Pablo Group of central California that is here described as *Mya arrosi*. This species has appeared in past check lists as *M. dickersoni*. A large specimen of *M. arrosi* from the Briones Sandstone is here figured (pl. 2, fig. 9; pl. 3, fig. 3). The holotype of *M. arrosi* comes from the Cierbo Sandstone. The species is present also in the Neroly Formation

where it occurs with *M. dickersoni* at the type locality of the latter.

Mya arrosi is a very variable species. It ranges from heavier individuals that are much more tumid anteriorly and very acuminate posteriorly, such specimens strongly resembling *M. cuneiformis* in shape, to less carinate, more elongate, thinner shelled individuals that are surprisingly like *M. japonica*.

I do not agree with Fujie that the form he figured from the Takinoue Formation (early middle Miocene) of Hokkaido as *Mya japonica oonogai* (Fujie, 1957, pl. 2, figs. 1a-b) is conspecific with *M. japonica* Jay. I am renaming this form *M. fujiei*, and I believe it is the immediate ancestor of *M. arenaria*. I regard *M. japonica* as descended also from *M. fujiei* but through the intermediate species, *M. arrosi*. It must be admitted, however, that the fossil record at this stage of evolution is scanty and a much better knowledge of it will be necessary before the matter can be settled to everyone's satisfaction. *M. japonica* could be interpreted as a relatively recent offshoot from typical *M. arenaria*. *M. japonica* is known for certain only in late Pleistocene beds and Recent. The more crudely sculptured *M. arenaria* appears to be the older of the two forms.

Mya japonica is more attenuated posteriorly and more inflated anteriorly than *M. arenaria*. Its shell is thinner and less crudely sculptured. The spoon of *M. japonica* is tilted downwards anteriorly, whereas in *M. arenaria* it is more horizontal. *M. japonica* has a longer posterior ridge and a more elongate posterior furrow, making the posterior side of the spoon more alate. Nevertheless, the two species have a striking morphological similarity. Most workers in the past have regarded *M. japonica* either a synonym or a subspecies of *M. arenaria*. In spite of the subtle differences, I do not believe there is any difficulty in telling them apart, and in my opinion they are distinct species.

Mya japonica is known from late Pleistocene beds near Lake Abashiri, Kitami province, in northern Hokkaido (Fujie, 1957, pl. 2, figs. 6a-c). The species made an invasion of the American coast during the late Pleistocene. It is found in lagoon deposits near Nome on Norton Sound, Alaska, and in terrace deposits near Cape Krusenstern, north of Bering Strait. Both these occurrences are, in my opinion, of middle Wisconsin age. Apparently the species still lives in the area. A large left valve and several live juveniles were collected from the present beach at Safety Spit near Nome. Several unworn shells were discovered in 1962 on the beach behind Sheshalik Spit in northern Kotzebue Sound. Another juvenile was found at Deering.

The species also made a deep southward penetration of the American coast during the Pleistocene. It is found in Pleistocene beds near Vancouver, British Columbia (Lamplugh, 1886; Wagner, 1959, pl. 1, figs. 19a-b; as *Mya arenaria*). Oldroyd (1924, p. 198), in a statement that has been challenged, said *M. arenaria* is found in Indian mounds on Vancouver Island. This may refer to *M. japonica* in the Pleistocene deposits.

The late Pleistocene migration that brought *Mya japonica* to the vicinity of Bering Strait, as well as to the Vancouver area, is the only undoubted establishment of the species, to my knowledge, on the American coast. It is of interest to note that *Protothaca adamsi* (Reeve), another Asiatic species, accompanied it to both areas. It has been found with *M. japonica* at both Cape Krusenstern and Nome, and it probably is the species reported by Frizzell (1931, p. 321) from Pleistocene beds at Port Blakely, Wash. A Recent form was described by Frizzell (1930, p. 120) as *Paphia restorationensis* and later (1931, p. 321) reassigned to *Venerupis (Protothaca) restorationensis*.

Mya japonica is the more southerly of the modern Japanese species. It ranges southward to Amakusa Island south of Nagasaki in western Kyushu and to the Gulf of Chihli near Tientsin on the China coast. It has been assumed by most Japanese authors that the species does not live north of southern Hokkaido. As already stated, however, the species may be living in Kotzebue Sound and Norton Sound, Alaska. Middendorff (1849, pl. 20, figs. 1-3) figured a malformed specimen (as *M. arenaria*) that is very similar to a malformed specimen from late Pleistocene beds near Nome, Alaska. No locality is given by Middendorff for his specimen, but of the localities he listed for the species, the most likely seems to be the Okhotsk Sea; the Arctic Ocean localities probably are of *M. pseudoarenaria*. Kotaka (1962, pl. 35, figs. 22-25) figured two very young specimens from the Okhotsk Sea as *M. arenaria*.

Some other poorly preserved internal molds from the Briones Sandstone (early late Miocene) have been identified as *Mya dickersoni*, but they may be more closely related to *M. arenaria*. A somewhat less tumid form is known from the Cierbo Sandstone (middle late Miocene) of central California. This form is referable to *M. arenaria*, and it is the earliest occurrence of the species I can find in the Pacific Ocean area. The Cierbo form may be derived directly from *M. fujiei*. If *M. arenaria* originated on the American side of the Pacific during the Miocene, it is an exception to the general rule that transpacific migrations, particularly of species having pelagic larvae, were from the Asiatic to the American side. I suspect it will be found eventually

that *M. arenaria* originated in Japan in middle Miocene time.

Four possible Pliocene occurrences of *Mya arenaria* (as *M. japonica oonogai*) in Honshu were recorded by Fujie. I believe the species in the Toshima Sand (Pleistocene) of the Atsumi Peninsula, east-central Honshu (Hayasaka, 1961, p. 64, pl. 8, figs. 10a, b; as *M. japonica oonogai*) is also *M. arenaria*.

The Etchegoin Formation (Pliocene) and the San Joaquin Formation (late Pliocene) of the central valley of California and the upper part of the Merced Formation (late Pliocene and early Pleistocene?) near San Francisco (Glen, 1959, p. 176, pl. 16, fig. 2) contain a form that must certainly be referred to typical *Mya arenaria*. Most authors in the past have identified the Etchegoin and San Joaquin species as *M. japonica*, but it was reidentified by Woodring and Stewart (in Woodring and others, 1940, p. 95) as *M. cf. M. dickersoni* Clark. Apparently Woodring and Stewart accepted Grant and Gale's interpretation of *M. japonica* (as being the *M. priapus* as here delimited). The Etchegoin and San Joaquin form undoubtedly is descended from the early variant of *M. arenaria* in the Cierbo sandstone, which at the time of Woodring and Stewart's writing was included in *M. dickersoni*; probably specimens of this form were the basis for their identification. The holotype of *M. dickersoni* is believed to be more closely related to *M. elegans*.

The Etchegoin and San Joaquin specimens have a more deeply incised pallial line and pallial sinus than is common for *Mya arenaria*. However, a nearly identical heavy-shelled Recent specimen from Long Island Sound is in the collection of Stanford University. This specimen was mentioned by Grant and Gale (1931, p. 411).

Most authors, with the exception of those who follow Grant and Gale's synonymy, seem to have taken for granted that *Mya japonica* is a synonym of *M. arenaria*, or at best a subspecies of it. Both of these species belong to the phylogenetic segment of *Mya* that have a large spatulate ligamental callus and a detached pallial sinus. However, in my opinion, their lineages have been distinct since Miocene time.

As I trace the history of *Mya arenaria* in the Pacific, therefore, it is descended from *M. fujiei* which is known from the Takinoue Formation (early middle Miocene) of Japan and possibly from the Briones Sandstone (early late Miocene) of California. An early form of *M. arenaria*, possibly a subspecies, occurs in the Cierbo Sandstone (middle late Miocene) of California. A later form of the species occurs in the Etchegoin Formation (Pliocene) of California and pos-

sibly in the Pliocene of Japan. The last undoubted occurrences are in the San Joaquin Formation (late Pliocene), in the upper part of the Merced Formation (late Pliocene or early Pleistocene) of California, and possibly the Toshima Sand (Pleistocene) of Japan.

The question of whether *Mya arenaria* survived until Recent time in the Pacific has been much discussed. No specimens from post-San Joaquin or post-Merced beds of western North America are referable to *M. arenaria*, and the species has not been seen from beds of any age in Alaska.

The known evidence suggests that *Mya arenaria* became extinct in the Pacific during early Pleistocene time and that Recent representatives of the species on the Pacific coast are derived from transplants brought from the Atlantic coast to San Francisco Bay about 1865. The species now lives from Monterey, Calif., to southeastern Alaska. Recent representatives of this species at Vancouver are not to be confused with *M. japonica* in late Pleistocene deposits in the Vancouver area (see p. G33), and around Willapa Bay in western Washington.

The migration that brought *Mya arenaria* to the Atlantic seems without doubt to have taken place in late Miocene time. Of all the known variants of *Mya arenaria* in the Pacific, the form in the Cierbo Sandstone of California is most like the form found in the Yorktown Formation of Virginia. *M. arenaria* is not known in the Alaskan Tertiary, either in the Alaskan Peninsula-Gulf of Alaska region or in the Nuwok Formation of Dall (1919) on the Arctic coast. It is difficult to see how it could have reached Virginia except by way of the Arctic; no *Mya* of any kind or any age is known from the West Indian-Gulf of Mexico region. I am inclined to believe that there was an Asiatic representative of the species corresponding to the Cierbo form, but to date it is not known. The first migration to the Arctic in late Miocene time probably was confined to the Asiatic coast of the Pacific.

Mya arenaria probably has persisted in the western Atlantic since Yorktown time. It is found at least as far south as Wilmington, N.C., in beds that are of late Miocene or Pliocene age.

No *Mya* is known from the Caloosahatchee Formation of Florida, nor has the genus been found in equivalent beds near Myrtle Beach, S.C. (Mansfield and MacNeil, 1937, p. 7, bed 1). No fossiliferous marine early or middle Pleistocene is known farther north, unless the Croatan Sand along the Neuse River, N.C., is of that age. Even so, this formation has not yielded *Mya*.

Mya arenaria is common in the Pamlico Formation (late Pleistocene; Sangamon or middle Wisconsin) of Maryland, and in the equivalent Jacob Sand of Long Island. It occurs from Hudson Bay and Labrador to Younges Island, S.C., in beds of late Pleistocene or post-Pleistocene age.

In Europe, *Mya arenaria* first appears in the Newbournian Stage of the Red Crag (early Pleistocene) of England and in possibly equivalent Merxemian beds of Belgium. It may have persisted until postglacial time in northern Europe where it is a common fossil in the sub-Recent "*Mya banks*" around Oslo Fiord.

In Europe, as in the Pacific, however, it has been believed by some workers that *Mya arenaria* became extinct in early glacial time, long before the "*Mya banks*" were deposited. Hessland (1946) believed it was reintroduced accidentally in the 16th or 17th century by sailing vessels and since that time has become distributed widely. Thus, it seems probable that the *M. arenaria* in both Europe and the west coast of North America were introduced by man from the last natural stand in the western Atlantic.

MYA ELEGANS GROUP

Mya elegans (Eichwald), which species must include both *M. crassa* and "*M. arenaria*" of Grewingk, is fairly closely related to *M. arenaria*. It might, however, with *M. dickersoni*, be made to constitute a group intermediate between the *M. arenaria* and *M. truncata* groups.

Mya elegans appears to stem from *M. grewingki* by way of the late Miocene species *M. dickersoni*. Typical specimens of *M. dickersoni* occur in the Neroly Formation (late late Miocene) of California, but there are no known earlier American occurrences. An earlier and presumably ancestral form, *M. grewingki haboroensis*, occurs in the Chikubetsu Formation (middle Miocene) of Hokkaido. This subspecies, which I regard as the earliest member of the *M. elegans* group, probably diverged from typical *M. grewingki* in early Miocene time, and probably the divergence took place in Japanese waters.

There is no recorded occurrence of this group in late Miocene deposits in East Asia, but in my opinion the *Mya cuneiformis* forma α of Fujie (1957, pl. 3, figs. 5a, b) from the Honbetsu Formation (Pliocene) of Hokkaido belongs to it; I refer this form to *M. elegans*, tentatively.

Grewingk's *Mya crassa* (not Vallot, 1801) appears to have been a fossil. He stated that it came from near Pavlof, a now-abandoned village near Settlement Point on the east side of Pavlof Bay in the Alaskan Peninsula.

I know of no beds in that immediate area from which it might have come; beds in that area are of Eocene age. It does occur, however, along with *Glycymeris aleuticus* Grewingk in beds of late Miocene or Pliocene age east of Yellow Bluff Creek, northwest of Chignik Bay. These beds were referred erroneously to the Meshik Formation by MacNeil, Wolf, Miller, and Hopkins (1961, p. 1802, 3a of fig. 1.). M. C. Lachenbruch (written communication, Mar. 25, 1963) told me that his field assignment of these beds to the Meshik Formation appears to have been incorrect; the type Meshik Formation is therefore still regarded as of Oligocene or Miocene age. I am now inclined to regard the *Mya*-bearing beds as being of Pliocene age.

Aside from its occurrence in late Tertiary beds in the Alaskan Peninsula, *M. elegans* is known from Pleistocene beds on St. Paul Island in the Pribiloffs. I can see no way to distinguish any of the fossils from the large species still living in the area. As such it still lives in the Pribiloffs, in Kuskokwim Bay, at several places around Bristol Bay, and it lives for certain in Chignik Bay on the south side of the Alaskan Peninsula. *M. elegans* may occur elsewhere along the Alaskan Peninsula.

In spite of the poor understanding various workers have had of this species owing to its relative geographic obscurity, *M. elegans* is one of the really distinctive species of *Mya*. It grows to a larger size than any other species of the genus.

MYA TRUNCATA GROUP

Like the *Mya arenaria* group, the *M. truncata* group also appears to stem from *M. kusiroensis*, a species found in the Oligocene of Alaska and Japan. The earliest clearly differentiated member of the *M. truncata* group is *M. cuneiformis* (Böhm), a species first known in the (middle?) Miocene of Japan. Fujie recognized that in Miocene time the geographical range of *M. cuneiformis* probably extended beyond the northern limit of occurrences known to him. This is borne out by the fact that it is a common fossil in the lower part of the Yakataga Formation (Miocene and Pliocene) of the northern part of the Gulf of Alaska. The Poul Creek Formation (late Oligocene and early Miocene) of the Yakataga district contains a different species, *M. salmonensis* Clark, that appears to be identical with the form in the Poronai Group, *E. grewingki elongata* Nagao and Inoue. *M. cuneiformis* occurs in beds of middle Miocene age on Kodiak Island in association with *Mytilus middendorffi* Grewingk.

It is not clear just how, or in what order, the subsequent species of the *Mya truncata* group arose. These

are *M. truncata* Linné, *M. pseudoarenaria* Schlessch, *M. priapus* Tilesius, and ?*M. pullus* Sowerby.

The earliest occurrence of *Mya truncata* in Japan is in the Takinoue Formation of the Kawabata Series (Fujie, 1957, p. 412; Uozumi, 1962, table 2). Japanese geologists assign this stage to the early Miocene; however, it is post-Poronai (the Poronai Series is correlated with the Poul Creek Formation of Alaska and the Blakeley Formation of Washington), and according to American standards it would be late early Miocene or early middle Miocene. The oldest specimens of *M. truncata* from Alaska in the Geological Survey collections are from about 700 feet above the base of the Yakataga Formation, which formation overlies conformably the Poul Creek Formation. The first appearance of *M. truncata* appears, therefore, to be nearly synchronous in Japan and Alaska, and probably it originated along a continuous coast connecting the two areas.

Mya truncata has lived continuously from middle Miocene to Recent time in the northern Pacific. Its southern limit in Japan has been at about the latitude of northern Honshu and southern Hokkaido at all times. *M. truncata* made at least one advance southward along the American coast in the early Pliocene as evidenced by its occurrence in the Coos Conglomerate at Coos Bay, Oreg., and in the Towsley Formation (late Miocene and early Pliocene) at Elsmere Canyon in the Ventura Basin, Los Angeles County, Calif. I am inclined to believe Reagan (1909) was correct in identifying a specimen from his Quillayute Formation (Pliocene) of Washington as this species, although Dall (1922, p. 312) reidentified it as *M. intermedia* Dall (= *elegans* (Eichwald)), and both Grant and Gale (1931, p. 412) and Weaver (1942, p. 254) reidentified it as *M. arenaria japonica* (in which they included both *elegans* and *priapus*).

In the early Pleistocene, *Mya truncata* again extended its range to southern California where it is found in both the "Upper Pico" (Waterfall, 1929, table, p. 78) of Ventura County and in the Timms Point Silt Member of the San Pedro Formation of the Palos Verdes Hills, Los Angeles (Woodring and others, 1946, p. 85).

Mya truncata is now one of the most widespread Arctic and boreal species. According to Soot-Ryen (1932, p. 21), it does not occur in the East Siberian Sea so that it is not truly circumarctic, but it extends from the Arctic Ocean to Hokkaido and Puget Sound in the Pacific and to Cape Cod and the Bay of Biscay in the Atlantic.

A puzzling fact regarding the distribution of *Mya truncata* and *M. arenaria*, if existing records are anywhere near complete, is that although *M. truncata* is

the more northern of the two species, it was preceded in the Atlantic by *M. arenaria*. *M. arenaria* is known in the Yorktown Formation (late Miocene) of Virginia, whereas the earliest recorded occurrence of *M. truncata* from the Atlantic is either in the Coralline Crag (late Pliocene) or in the Norwich Stage of the Icenian Crag (early Pleistocene), depending on the identity of the species in the Coralline Crag. It occurs unquestionably in the Norwich Stage. In my opinion, the species in the Coralline Crag, and possibly the one in the equivalent Sables de Kattendijk and Luchtbal of Belgium, is *M. pseudoarenaria*.

Mya truncata migrated as far south as Italy during the early Pleistocene where it occurs in upper beds of the Calabrian Stage in Sicily, Calabria, and Tuscany. Specimens have been reported from early Pleistocene beds of Iceland, but a specimen from there figured by Schlesch (1924, pl. 6, fig. 1), was identified as *M. truncata ovata* Jensen (= *M. pseudoarenaria* Schlesch).

In all probability, *Mya truncata* lived in northern European waters throughout the glacial Pleistocene. I can find no reference to its having invaded the Arctic coast of Siberia until the middle glacial Pleistocene. If current identifications and age assignments are correct, it occurs in Taymyr in beds beneath the drift of the "Maximum glaciation" (Riss); these beds are assigned to the Q₂ stage of Russian usage.

The fossil distribution of *Mya truncata* in eastern North America is similar to its Recent distribution. It has not been on the Atlantic coast very long, all its occurrences being postglacial, or mid-Wisconsin at the oldest. It is known as a fossil from near Thule, Greenland, and Hudson and James Bays to Massachusetts.

How *Mya truncata* reached eastern North America is not definitely known, but it certainly was in Europe previously. Soot-Ryen (1932, p. 29) discussed the much-debated occurrence of this and many other shallow-water forms strewn over the sea floor of the North Atlantic between Greenland, Iceland, and Jan Mayen at a depth of 1,300 fathoms. The maximum natural depth for any of the species found is about 600-700 meters, and they are rare at that depth. He quoted Jensen (1899) as saying that these shells were not transported by ice rafting. It is possible that shallower water existed between Greenland and the Barents Sea in late Pleistocene time and that *M. truncata* reached eastern North America by that route.

The range of *Mya priapus* (*M. japonica* of Fujie) is much less extensive than that of *M. truncata*. Fujie (1962, p. 400) combined *M. priapus* (his *japonica*) and *M. pseudoarenaria*. The geographic range Fujie gave

for *M. priapus* (the range he gave for *M. japonica*) is much greater, therefore, than it would be if these were regarded as distinct forms. Likewise, MacGinitie (1959, p. 188), who recognized *M. pseudoarenaria* as distinct, hesitated to give its exact geographic range "until collections are reexamined with a view to separating *M. japonica* and *M. pseudoarenaria*." MacGinitie used *M. japonica* in the sense I use it, and apparently the distinction was not being drawn between two members of the *M. truncata* group but between two species resembling *M. arenaria*.

Possibly both *Mya priapus* and *M. pseudoarenaria* are derived from *M. cuneiformis*, but, if so, I am inclined to believe they are coderivatives. If anything, the spoon of *M. pseudoarenaria* is more like that of *M. salmonensis*. At present, however, *M. priapus* is confined mainly to the North Pacific and Bering Sea, extending possibly to Wainwright, Alaska, whereas *M. pseudoarenaria* is mainly if not exclusively Arctic.

According to Fujie (1957, p. 412), *M. priapus* (as *japonica*) is known in the Togeshita Formation (late Miocene) of Hokkaido. It is known again in the Setana Formation (late Pliocene or early Pleistocene) of Hokkaido, and apparently it existed continuously in that area until the present day.

The species appears to be present in beds referred to the Pliocene about 4½ miles south of the entrance to Lituya Bay along the east side of the Gulf of Alaska. In my opinion, this is the most southern recorded occurrence of any age for the species from America.

During the Pleistocene, *Mya priapus* ranged at least as far north as the Chukotsk Peninsula where it occurs in post-Riss beds (Merklin and others, 1962, pl. 9, fig. 7; as *M. arenaria*) and to the area between the Kukpowruk and Kuk Rivers, Alaska. Specimens from Wingham Island, Controller Bay, Alaska, probably are this species (Dall, in Martin, 1908, p. 46; as "*Mya* near *arenaria*"). One of these specimens is figured in this report (pl. 11, fig. 8). The species occurs in very late Pleistocene beds at the mouth of Cottonwood Creek on the north shore of Kachemak Bay (Dall, in Martin and others, 1915, p. 92; as *Mya japonica*).

Mya priapus now lives from Hokkaido to northern Bering Sea, Chuckchi Sea at Point Lay, and east to Cook Inlet. It is the most abundant species in a large collection of Recent shells from St. Lawrence Island in the collections of the Geological Survey. Fujie (1962, p. 412) stated that the species (his *japonica*) ranges southward to Bellingham, Wash., but I have not seen a Recent specimen of *M. priapus* from east of Cook Inlet nor a fossil from south of the Lituya Bay district. Probably the occurrence to which Fujie referred comes

from MacGinitie's (1959, p. 188) statement regarding *M. japonica* (presumably typical) and *M. pseudoarenaria*. I am inclined to believe, however, that the species actually involved in both statements is *M. arenaria*. Neither *M. priapus* nor *M. pseudoarenaria* is present in the very fossiliferous postglacial deposits near Juneau, Alaska. *M. truncata*, which is very abundant, is the only *Mya* present.

Shells from north of Point Lay that appear most like *Mya priapus* are thinner, more attenuated posteriorly, and their spoon has a narrower more elongate posterior furrow than *M. priapus*. The outline of the shell is more like that of *M. arenaria*. The beaks are more twisted and the greatest inflation is along the anterior truncation; *M. arenaria* has less twisted beaks and the shell is more evenly inflated. As recognized by Soot-Ryen (1951, p. 3) and MacGinitie (1959, p. 186), this is *M. pseudoarenaria* Schlesch (new name for *M. truncata forma ovata* Jensen (not Donovan, 1802)). A fossil? specimen from West Greenland figured by Jensen (1899, p. 139, fig. 3) is the type.

Specimens from Point Barrow have a spoon much more like that of specimens of *Mya cuneiformis* from the Yakataga Formation than like that of *M. priapus* from northern Bering Sea; they resemble *M. salmonensis* even more closely. Probably, therefore, *M. pseudoarenaria* is a distinct species. It is related to *M. priapus* but probably not derived from it and it may have lived in the Pacific as a species distinct from *M. cuneiformis* at one time. I have seen no Recent specimens from either the Bering Sea or the Pacific Ocean, however, that can be considered to be *M. pseudoarenaria*. The species is now widespread throughout the Arctic. In my opinion, the species in the Coralline Crag (late Pliocene) of England is *M. pseudoarenaria*. It probably is present both in the Red Crag (early Pleistocene) of England and in the *Cardium groenlandicum* zone of the Icelandic Crag (early Pleistocene) of Iceland. Schlesch (1931, p. 136) had a "subfossil" specimen from Húnaflói Bay, northern Iceland that presumably came from some part of the Icelandic Crag.

Mya pseudoarenaria occurs in Pleistocene beds in Spitzbergen and in beds of the Boreal Transgression (post-Riss; Sangamon) at Gostinoj on the Yenisey River in the Pechora Basin, northern Russia. It probably occurs in late glacial or postglacial deposits of western Greenland, and possibly some recorded occurrences of *Mya truncata* in very young beds elsewhere in eastern North America are this species.

Mya pseudoarenaria is known to be living in northern Norway, Iceland, Greenland, Spitzbergen, northern Canada, and Point Barrow, Alaska. According to

Laursen (1944, p. 63), the species lives only on the western side of Greenland.

MORPHOLOGIC CHARACTERS

SHELL THICKNESS

The shell of *Mya* ranges from almost paper thin to very thick. The thickness of the shell in a given species may range within certain limits, depending on the physicochemical environment, particularly in open water as opposed to bays and in Arctic waters as opposed to warm boreal waters. The intraspecific differences are not as great, generally, as those found between normally thick shelled and normally thin shelled species.

SHELL SHAPE

The shell ranges from oval to elongate and from moderately sharp posteriorly, on the one hand, to very short and nearly straight posteriorly, on the other hand. The beaks are nearly central in the oval species. In the posteriorly pointed species the beaks are relatively more anterior, whereas in the posteriorly truncated species the beaks are more posterior. The shell may be either evenly inflated or more inflated anteriorly. Shells that are very inflated anteriorly generally are truncated along a line extending from the beak to the anteroventral margin. This anterior truncation is often accentuated by lateral crushing in fossils. The greatest height is generally either central or just anterior of center. *Mya producta* Conrad from the Miocene of Maryland is unique in having a broad median sulcus, making both its anterior and posterior areas higher and more inflated than the central area.

VARIABILITY OF FORM

It is difficult to make definite statements regarding the variability of a burrowing mollusk inasmuch as it may be influenced by the texture of the substratum. Some species such as *M. japonica* Jay seem to be much more uniform in shape than the closely related *M. arenaria* Linné, or the more distantly related *M. truncata* Linné. Whether this is an inherent character, or due to the fact that one lives mostly in a uniform substratum, whereas the other lives in a less sorted substratum is not known.

SCULPTURE

The sculpture of *Mya* consists of concentric growth lines. Random wrinkles are common on some species, notably *M. truncata*, and they probably reflect in the shell the coarse fleshy wrinkles of the tough siphonal sheath. The concentric sculpture is finer and more regular on some species than on others.

PALLIAL LINE AND PALLIAL SINUS

The pallial line ranges from very broad to thin; it may be continuous, or it may consist of disconnected segments; and it may be either deeply incised, or so nearly flush with adjoining areas as to make it indistinguishable except as a slightly smoother area.

The pallial sinus, both in its location, size, and shape and in the way it connects with the pallial line, is one of the most important species characters. It ranges in different species from (1) very short and high with its posterior side descending almost vertically to the pallial line (*Mya truncata*); to (2) more elongate with a sloping posterior margin and having a broad common boundary with the pallial line that generally is wider than the pallial line beyond the sinus (*M. priapus*); to (3) very long and subparallel with the pallial line but narrowly disconnected from it for nearly its entire length (*M. elegans*); to (4) moderately long and bluntly pointed and lying well above the pallial line, the space between the pallial line and the sinus being nearly as broad as the sinus itself (*M. arenaria*).

MUSCLE SCARS

The posterior adductor scar of *Mya* is the smaller and is located just under the dorsal shelving. In the shorter posteriorly truncated shells (*M. truncata* var. *uddevalensis*) the posterior scar lies in the posterodorsal corner, but in posteriorly attenuated shells (*M. producta*) it lies at more nearly the midpoint of the posterior dorsal margin.

The anterior adductor scar is narrower and more elongate, often tear shaped. The anterior adductor scar may be as dorsal as the posterior scar, and rarely it is more dorsal (*M. elegans*). More commonly at least part of the anterior adductor scar is more ventral than the posterior scar, and in *M. truncata*, in which it is narrowest and most elongate, the anterior scar extends well below the middle of the shell.

LIGAMENT

The myarian ligament is one of the most peculiar adaptations among the many completely dissimilar structural and mechanical devices developed in the pelecypods. The ligament is completely internal and asymmetrical anteroposteriorly. It is sharply inclined dorsoventrally so that it lies wholly within the right valve. The chondrophore of the right valve lines the umbonal cavity, whereas the chondrophore of the left valve (the spoon) projects into the umbonal cavity of the right valve.

The ligament of *Mya* retains all three of the primary layers, the outer noncalcareous, the inner noncalcar-

eous, and the calcareous (fibrous or spicular) layers. These are here named, the elasticum, laminum, and fibrum, respectively. The outer noncalcareous layer (elasticum), which often is detached from the other two layers and may be partly concealed by an overlapping fold of shell (*Solemya*, *Thracia*, *Periploma*), is vestigial in *Mya* and is present in the spoon only in very young shells. It attached to a groove along the posterior side of the main chondrophore in the right valve and to the posterior side of the posterior ridge of the spoon of the left valve. In adults the elasticum appears to withdraw from the spoon to reinforce the underside of the intervalve periostracum connection centrally. The thick central part of the intervalve connections consists of two layers, a thin amber-colored outer layer (periostracum) and a thick black inner layer (elasticum?). The inner black layer thins and disappears both anteriorly and posteriorly; the terminal parts of the intervalve connection consist only of the outer amber layer—the true periostracum.

In adults, the spoon retains only the inner noncalcareous and calcareous layers. The inner noncalcareous layer (laminum) serves as an intervalve connection, and the calcareous layer (fibrum), as always, is the shell-opening mechanism, which, by resisting compression, operates in opposition to the adductor muscles.

The posterior ridge, which probably arose as the attachment or concealing fold for the outer noncalcareous layer (elasticum), continues to grow after the abortion of the outer noncalcareous layer and becomes a stabilizing mechanism. It is in contact with and articulates with a crude buttress along the posterior side of the chondrophore in the right valve; probably it is the articulation point for a twisting of the valves along a dorsoventral axis, allowing either end to gap more or to be drawn more tightly together (Trueman, 1954, p. 291).

The noncalcareous layers can be observed only on Recent specimens, but the calcareous spicules of the fibrous layer are preserved in many fossils. No specific differences are accompanied in *Mya* by modifications in the position of the ligament layers, but there are differences in the concavity or convexity of their attachment surfaces. An understanding of the location of the ligament layers is essential to an understanding of the significance and terminology of parts of the chondrophore.

SPOON

The most detailed terminology proposed thus far for the parts of the spoon (the chondrophore of the left valve) is that of Fujie (1957, p. 391). Fujie does not

distinguish between the ligamental and nonligamental parts of the spoon, nor does he identify any of the named segments within the ligamental area with particular layers of the ligament. Fujie's diagram is reproduced in figure 2.

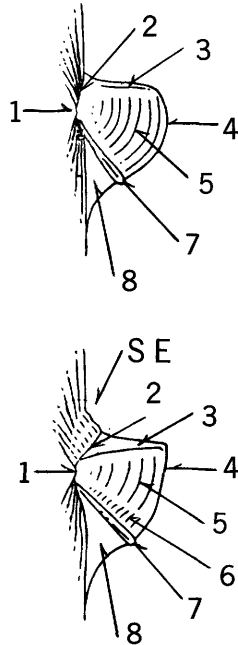


FIGURE 2.—Diagram showing terminology of parts of spoon. Upper figure is *Mya (Arenomya)*, and the lower figure is *Mya (Mya)*. From Fujie (1957).

<i>This report</i>	<i>Fujie</i>
1. Beak or umbo.....	Beak.
2. Anterior leg.....	Leg.
3. Anterior ridge.....	Anterior ridge.
4. Ventral margin.....	Outer margin.
5. Fibrum receptacle.....	Sculpture.
6. Laminum attachment.....	Undulated part.
7. Posterior ridge.....	Posterior ridge.
8. Posterior furrow.....	Furrow.
SE. Anterior subumbonal groove.....	Subumbonal excavation.

The terminology adopted here for the parts of the spoon is given as follows with Fujie's terms in parentheses.

The extraligamental parts of the spoon are:

2. The anterior leg (the leg)—a line or ridge, often undercut, marking the edge of the live mantle. The periostracum-elasticum connection between the two valves attaches to it.
3. The anterior ridge (the anterior ridge)—the anterior confining wall of the ligament receptacle. It may be narrow and overturned, or broad and flat. The dorsal part ranges from narrow to very wide.
7. The posterior ridge (the posterior ridge)—the posterior confining wall of the ligament. In adults its point of contact with a buttress in the right

valve forms an articulation or rocking point for the valves along a dorsoventral axis. In juveniles it is the attachment or concealing fold for the outermost of the two noncalcareous or conchiolin elements of the ligament (elasticum).

8. The posterior furrow (the furrow)—an excavated area occupied by mantle. The outermost border marks the edge of the live mantle; the innermost border is the posterior ridge.

SE. The anterior subumbonal groove (the subumbonal excavation)—a grooved area radiating from the beak and marking the outer edge of the inter-valve periostracum-elasticum connection and thus properly a part of the exterior of the shell; this is found only in the *Mya truncata* group.

The ligamental parts of the spoon are as follows:

6. The laminum attachment (the undulated part)—the attachment or insertion of the laminated and innermost of the two noncalcareous or conchiolin elements of the ligament (laminum).
5. The fibrum receptacle (the sculpture)—the receptacle or attachment of the calcareous (fibrous or spicular) element of the ligament (fibrum).

LIGAMENTAL CALLUS

Another very important feature of the myrian chondrophore has gone almost unnoticed by authors. It is here named the ligamental callus. Wood (1856, p. 280) was almost certainly referring to this structure in *Mya arenaria* from the Red Crag in his statement, "It was furnished with a large and strong ligament, or rather cartilage, the greater part of which is preserved in most fossil specimens." Woodring and Stewart (in Woodring and others, 1940, p. 95) observed it on specimens of *M. arenaria* (as *Mya* cf. *dickersoni* Clark) from the San Joaquin Formation (late Pliocene) of the Kettleman Hills, Calif. They commented that the San Joaquin species had "a more prominent deposit of callus on the middle of the chondrophore than that on Recent specimens" (of *M. priapus*; as *M. japonica*). The ligamental callus is shown very well on a specimen of *M. japonica* (as *M. oonogai*) from alluvial deposits around Lake Abashiri, Hokkaido, figured by Fujie (1957, pl. 2, fig. 6c), but he does not mention it.

The ligamental callus is best developed in *Mya arenaria* and *M. japonica* in which it is long and spatulate. *M. priapus* often has a callus, but in this species it is short and often has a comblike lower edge. A callus is much less frequent in *M. truncata*, and when present, it is very small and restricted to the upper anterior side of the ligament pit.

A diagram (fig. 3) shows the supposed phylogeny of myarian species and the distribution of the ligamental callus in the different species groups.

The ligamental callus does not appear to have been deposited during normal ligament growth. Its lowest extremity is well back from the edge of the chondrophore where ligament growth takes place. The callus seems, however, to be continuous with the last increment of shell deposited on the surface of the anterior ridge. A lobe of the mantle seems to have extended from the dorsal part of the anterior ridge into the ligament pit and downwards under the fibrous ligament, which at that stage was detached from the surface of the spoon. Apparently the ligament of *Mya* is so constructed that it cannot remain functional throughout its length for the life of the individual, a condition that is true particularly for the species having a high overturned anterior ridge such as *M. arenaria*. Stresses cause the oldest part of the fibrous ligament to be torn away from its attachment, and, inasmuch as the intervalve periostracum—elasticum connection is above the

spoon, a lobe of the mantle is free to invade the cavity and deposit a callus. It is not uncommon in pelecypods with a cardinal gape for the fibrum to be severed continuously with growth, but *Mya* is the only pelecypod known to me in which fibrum severance takes place in a wholly internal ligament. The ligamental callus is peculiar to the left valve.

The ligamental callus in *Mya arenaria* generally covers about two-thirds to three-quarters of the dorsal part of the fibrum receptacle. It does not cover any of the laminum attachment; this shows that the laminum does not become detached as does the fibrum. There is no ligamental callus in the right-valve chondrophore, showing that the fibrum becomes detached only from the spoon of the left valve.

Specimens of *Mya arenaria* from the Red Crag, a formation taking its name from the color imparted by large amounts of iron oxide, indicate that the ligamental callus is crystallographically different from other parts of the shell. In most specimens the ligamental callus is very dark brown, whereas the re-

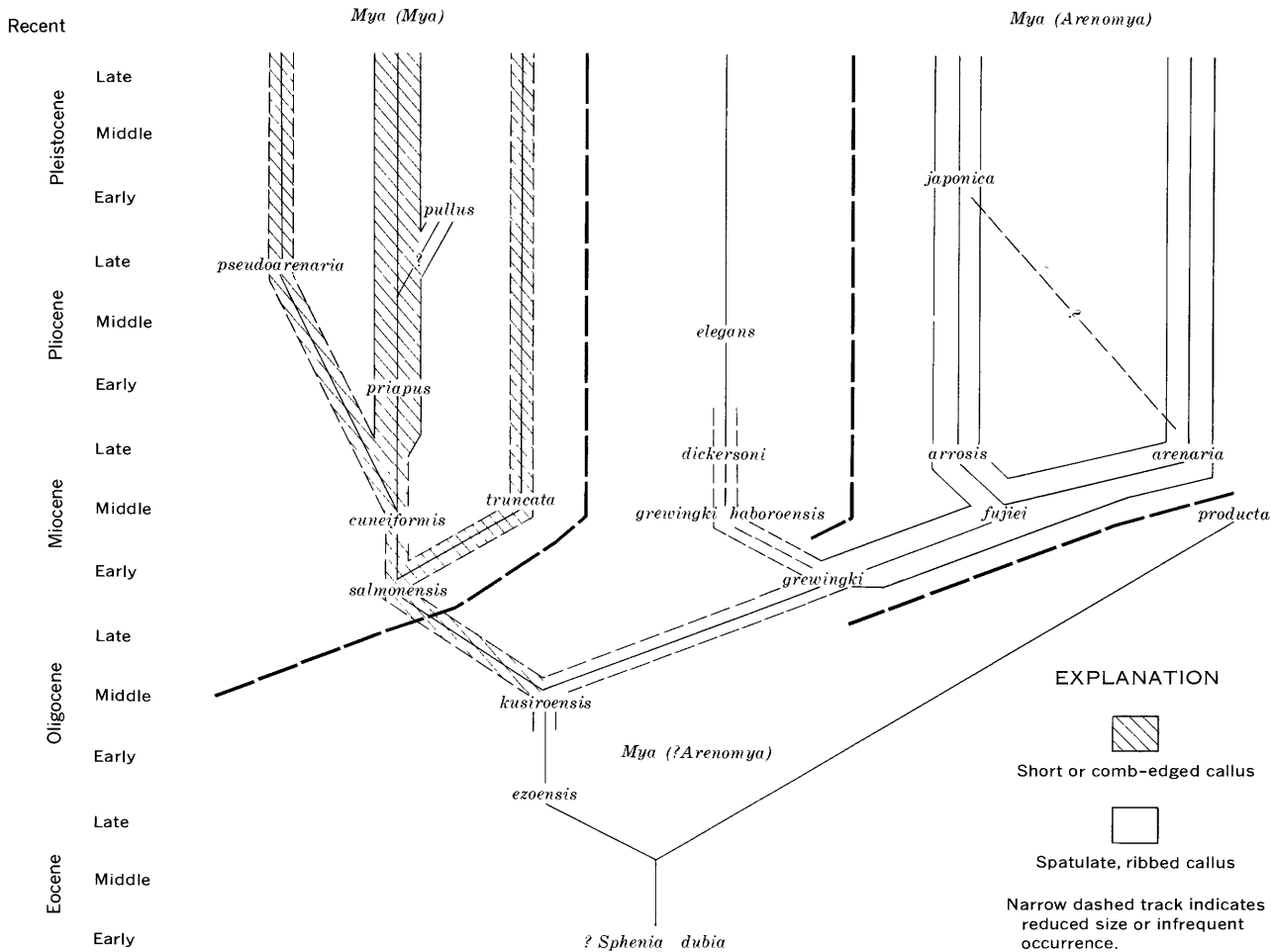


FIGURE 3.—Phylogeny of myarian subgenera and species, showing distribution of the two types of ligamental callus.

mainder of the spoon and shell are a pale yellowish brown. Some specimens show the impregnation of iron oxide to begin as rosettes with dark centers fading toward the edge; these enlarge and coalesce until the whole callus is stained dark brown.

SUBUMBONAL SOLUTION

Mya arenaria almost always shows a considerable amount of solution under the umbo of the left valve. It is less frequent in the right valve and, when present, is restricted to a narrow area along the margin immediately behind the umbo. This condition is found also in *M. japonica*, *M. elegans*, *M. grewingki*, and to a lesser extent in *M. producta*, but it is unknown in the *M. truncata* group. It thus seems to be characteristic of *Mya* (*Arenomya*) but not of *Mya* (*Mya*). Recent shells of *M. arenaria* show both that the solution cavity is lined with secondary conchiolin, probably elasticum, and that solution progresses in the shell behind the secondary seal.

Very young shells (18–25 mm) of *Mya japonica* from Nome, Alaska, have a thin but well-formed ligamental callus. At this stage there is no subumbonal solution. In shells 30 mm in length, however, there is a small solution cavity under the umbo of the left valve. The cavity clearly begins along the margin of the valve where the intervalve periostracum-elasticum connection attaches and not at the umbo where it might be expected if it started at a point of abrasion between the two valves.

Some species (*M. arenaria* and *M. japonica*) have both a ligamental callus and a large amount of subumbonal solution. Some species (*M. producta* and *M. elegans*) have subumbonal solution and no callus, whereas other species (*M. priapus* and *M. truncata*) may have a small callus but no solution in the left valve; some specimens of *M. priapus* may have a small solution pit at the top of the chondrophore of the right valve (pl. 11, fig. 15).

Structural weakness seems to be the only factor relating solution and callus. In all species, there seems to be a tendency for the fibrum to be pulled away from the dorsal part of the spoon. The mantle tends to heal the void with a deposit of callus. The same stresses that tear the fibrum from the spoon also cause a rupture of the intervalve periostracum-elasticum connection, and most commonly the rupture takes place where the intervalve connection attaches to the left valve above the spoon.

According to Trueman (1954, p. 291), *Mya arenaria* not only opens and closes its valves along the hinge axis, but it twists its valves on a dorsoventral axis, allowing

either end to gape more or to be drawn more tightly together. This motion could also be a factor in the rupture of both the fibrum and the intervalve connection.

The narrow slit of shell exposed by the periostracum-elasticum rupture is open to attack by sea water. The mantle, which becomes exposed, is able to seal itself off with a secondary deposit of elasticum. The secondary elasticum is fixed to the shell along the lower edge of the area of active solution, confining the solution, in effect, to the exterior of the shell. However, it is not able to permanently arrest solution. As the solution cavity enlarges, the secondary seal retreats to new positions. Its line of connection thus keeps enlarging in circumference, and the elasticum seal becomes a balloonlike sac filling most of the solution cavity.

A further relation between subumbonal solution and the ligamental callus can be seen in a few specimens of *Mya arenaria*. The dorsal end of the callus is enlarged or bulbous on some specimens and expands into the solution cavity where it is deposited on the surface already pitted by solution. In such specimens it may partly refill the solution cavity with a secondary deposit. If solution continues, however, it may in turn attack the callus. Several specimens examined showed a young solution pit cutting callus and original shell alike. Post-callus solution always seems to have taken place from the posterior dorsal side of the callus.

Either slight differences in the shape of the shell in *Mya* (*Mya*) and *Mya* (*Arenomya*) provide for different mechanical stresses in these two groups, or the intervalve periostracum-elasticum connection in *Mya* (*Mya*) is much stronger. Specimens of *M. priapus* in which the intervalve connection is preserved show that it forms a thick bundle below and anterior to the beaks. The subumbonal groove appears to mark the outer edge of the periostracum-elasticum bundle. In addition, the right valve of *Mya* (*Mya*) has a broad projecting spur along the anterior border of the chondrophore (pl. 8, figs. 2, 3). The outer edge of the spur inserts along the posterior side of the anterior ridge of the left valve. The dorsal surface of the spur serves as the attachment for the intervalve periostracum-elasticum connection at the apex of the chondrophore. This relatively broad attachment area makes possible the thick periostracum-elasticum bundle that in *Mya* (*Mya*) prevents subumbonal solution.

There is no broad projecting spur in the right valve of *Mya* (*Arenomya*); rather, there is a sharp narrow point (pl. 6, fig. 16) aligned with the dorsal margin of the shell. A relatively narrow intervalve connection of

periostracum and elasticum attaches to its thin dorsal edge.

The protruding spoon of *Mya* is the chondrophore of the left valve. The corresponding chondrophore of the right valve lines the umbonal cavity beneath the umbo. Differences corresponding to those in the left valve can be seen in the right valve, but owing to the prominence of the spoon, the left valve is the more definitive valve. Because of its more protected position, the spoon is more apt to be preserved in fossils that have paired valves. In fossils, the spoon is certainly easier to prepare. I have never seen any indication of a ligamental callus in a right-valve chondrophore. This fact seems to indicate that the fibrous ligament remains attached to the right valve when it tears away from the spoon. Consequently, only left valves and spoons are figured in this paper, and all discussions of relationship are in terms of the left valve.

SYSTEMATIC PALEONTOLOGY

Genus *MYA* Linné, 1758

Mya Linné, *Systema naturae*, ed. 10, p. 670, 1758.

Type.—(by subsequent designation, Children, 1822): *Mya truncata* Linné. Recent, North Atlantic, Pacific, and Arctic Oceans. Linné's specimen is from Europe.

Mya was added to the Official List of Generic Names in Opinion 94 of the International Commission on Zoological Nomenclature.

Hiatula Modeer, 1793, and *Myarius* Froriep, 1806, have the same type species.

Winckworth (1930, p. 15) attempted to restrict the genus by proposing the genus *Arenomya* (type, by monotypy, *Mya arenaria* Linné). His only justification was in the statement, "The marked conchological differences between adult *Arenomya* and *Mya* (type *truncata* L.) seem sufficient reason for giving this name." *Arenomya* has been accepted as a subgenus by several modern Japanese authors (Habe, 1952), and it is so regarded here. Most authors, however, have regarded *Arenomya* as superfluous; no one to my knowledge has followed Winckworth in recognizing it as a genus.

Mya (Mya) has an anterior subumbonal groove, and the ventral leg of its pallial sinus is confluent with the pallial line. The ligamental callus, when present, is small and lacks a radial ridge. There is no subumbonal solution in the left valve, although *M. priapus* often has a solution pit at the top of the chondrophore of the right valve.

Mya (Arenomya) has no anterior subumbonal groove, and the pallial sinus is detached. The ligamental callus is spatulate and generally has a radial

ridge posterior of its center. The left valve always has a subumbonal solution pit.

In addition, there are species ancestral to, and coexistent with, these subgenera that either are peculiar in some way, or they combine characters of both of the above subgenera. In general they seem to be more closely related to *M. (Arenomya)*; this residue of species is here treated as *M. (?Arenomya)*.

These species have no anterior subumbonal groove, and they all have a subumbonal solution cavity in the left valve. They may or may not have a ligamental callus, but when present it is like that of *M. arenaria*. The pallial sinus ranges from detached to confluent ventrally with the pallial line.

The exact time of origin of the ligamental callus is not known. There is reason to believe that it is not a genetic character. Rather, it seems to be a repair of a structural weakness, and in this sense it is analogous to subumbonal solution and to the balloonlike sac of elasticum that forms in the solution pit. I can find no indication of a callus in *Mya producta*. A thin callus may be present in a specimen from Alaska here referred to *M. kusiroensis*. *M. grewingki* appears from the available illustrations to have a callus. The only known spoon of *M. salmonensis* had a moderately large callus but it crumbled, along with part of the surface of the fibrum receptacle, in preparation.

Some species of both *Mya (Mya)* and *Mya (Arenomya)* have a callus, whereas other species have it only occasionally; in other species it appears to have become obsolete. Where found, the calluses of *Mya (Mya)* and *Mya (Arenomya)* have a different shape. In *Mya (Mya)* the callus is short, conforms more to the contour of the ligament pit, and in some specimens it has teeth or spurs along its ventral margin. In *Mya (Arenomya)* the callus is long and spatulate, and generally it has a rib or ridge near its posterior border.

The callus is largest in the *Mya arenaria* group, but it does not occur in *M. elegans*. *M. dickersoni* has variants with a small callus or no callus; *M. elegans* may have descended from the variant of *M. dickersoni* with no callus.

The callus is less common in the *Mya truncata* group. It is largest in *M. priapus*, and this seems to be the only species of the group in which it is always present. It is less frequent and smaller in *M. truncata*. Only a few specimens of *M. pseudoarenaria* have a callus, and when present it is restricted to the extreme dorsal end of the fibrum receptacle.

The emphasis in the following systematic treatment is on species outside Japan. An attempt is made to point out the apparent synonymy of American and

Japanese species. *Mya* has been a common mollusk in Japanese waters since Eocene time. Both *Mya* (*Mya*) and *Mya* (*Arenomya*) are represented in the Japanese Tertiary. Numerous species, subspecies, and varieties belonging to both subgenera have been described. Unfortunately, much of the fossil material is poorly preserved. Consequently, there are named forms that cannot be recognized with certainty, and it has been difficult for Japanese workers to obtain and prepare specimens of all recognizable species for adequate illustration. My concept of the Japanese species is mainly that of Fujie, and the synonymy expressed is modified from Fujie's work and the work of other recent Japanese authors. Without access to specimens, it would be impossible to form an opinion on the more dubious forms described from Japan.

Japanese workers seem to have accepted Grant and Gale's interpretation of *Mya japonica*, an interpretation that is in complete disagreement with that of most previous and subsequent American authors. In my opinion, Grant and Gale's interpretation is incorrect. The nomenclature used for the Recent Japanese species in this paper is not in accord, therefore, with recent Japanese usage.

Subgenus *ARENOMYA* Winckworth, 1930

Arenomya Winckworth, Malacological Soc. London Proc., v. 19, p. 15, 1930.

Type.—(by monotypy): *Mya arenaria* Linné. Recent, North Atlantic coast of North America, northern Europe, and the west coast of the United States from Monterey to southeastern Alaska. Both the European and the western American representatives are said to be introduced; Linné's specimen came from the North Sea.

Mya (?*Arenomya*) *producta* Conrad

Plate 1, figures 1-4, 7

Mya producta Conrad, Fossils of the medial Tertiary, p. 1, pl. 1, fig. 1, 1838.

Dall, Wagner Free Inst. Sci. Trans., v. 3, pt. 4, p. 858, 1898.

Glenn, Maryland Geol. Survey, Miocene, p. 283, pl. 68, figs. 1a, b, 2, 1904.

Richards and Harbison, Acad. Nat. Sci. Philadelphia Proc., v. 94, p. 202, pl. 16, figs. 11, 12, 1942.

Mya producta is one of the most peculiar species of *Mya*. It has no anterior subumbonal groove. The anterior ridge of the spoon is very short and weakly overturned. There is a very pronounced dorsal broadening, but it is produced anteriorly along the hinge axis rather than ventrally towards the end of the ridge; the ventral part of the anterior ridge is, in fact, quite narrow. The posterior ridge is nearly twice as long as the anterior

ridge. The spoon is broad and has a strongly rounded outer margin. The fibrum receptacle is rather deep and concave, and the angle it forms probably is the largest for any species of the genus. There is a flattening or even a slight convexity along the laminum attachment.

The shell is lower and longer than in any other *Mya*, and in this respect it resembles a *Panope*. The beak is slightly anterior of center, which makes the shell slightly longer posteriorly. There is a weak broad medial sulcus that becomes stronger in large shells and which tends to make the ventral margin nearly straight.

The pallial sinus of this species is very deep and broad, and its lower leg is confluent with the pallial line except for a slight recurving at the anterior end. This type of sinus is characteristic of the *Mya truncata* group.

Large specimens of *Mya producta* show a moderate amount of subumbonal solution in the left valve, a condition characteristic of the *M. arenaria* group and unknown in the *M. truncata* group. The anterior leg is more like that of *M. arenaria*, whereas the posterior part of the spoon is more like that of *M. pseudoarenaria* of the *M. truncata* group. It would seem, therefore, that among three distinct myarian groups—*M. producta* and the groups of *M. arenaria* and *M. truncata*—different single characters are peculiar to different combinations of two groups but not the odd group. This would be difficult to explain except as a differential survival of primitive characters in different phylogenetic lines.

If the pallial sinus of *Mya ezoensis* is found to be confluent with the pallial line, it would be a further indication that this type of sinus is the more primitive, and it would strengthen my contention that *M. producta* and the large Pacific complex of species are related through some Eocene species as yet unknown.

The holotype (according to Moore, 1962, p. 89) may be in the collection of the Wagner Free Institute of Science. The specimen figured by Glenn (1904) measures 123 mm in length, about 50 mm in height; convexity is 14 mm. The specimen figured here is numbered USNM 146004.

Occurrence: Maryland, Choptank Formation (middle Miocene), USGS 2451; New Jersey, Kirkwood Formation (middle Miocene).

Mya (?*Arenomya*) *ezoensis* Nagao and Inoue

Mya ezoensis Nagao and Inoue, Hokkaido Imp. Univ. Fac. Sci. Jour., v. 6, no. 273, p. 145, pl. 34, figs. 2, 7-9, 1941.

Minato, Matsui, and Uozumi, Shinseidai-no-Kenkyu (Studies of the Cenozoic), no. 7, p. 111, pl. 10, figs. 75, 78, 79, 81, 1950 (in Japanese).

Mya ezoensis var. *sagittaria* Minato and Uozumi, Shinseidai-no-Kenkyu, no. 7, p. 107, pl. 10, figs. 76, 77, 80, 83, 1950.

Mya ezoensis Fujie, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 9, no. 4, p. 383, pl. 8, figs. 1-10, 1957.

Oyama, Mizuno, and Sakamoto, Illustrated handbook of Japanese Paleogene molluscs; Japan Geol. Survey, p. 209, pl. 64, figs. 1a-b, 2a-f, 1960.

Fujie, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 11, no. 3, p. 403, 1962.

The known specimens of this species are poorly preserved. Fujie (1957, pl. 8, fig. 5) gave one photograph of its spoon, and he also included a drawing of it in his diagram of spoon types (1957, p. 391, fig. 2, A). It has no anterior subumbonal groove. Fujie's photograph shows the anterior ridge to be narrow ventrally and short. This character places it closer morphologically to *Arenomya* than to typical *Mya*. Judging from Fujie's photograph, there is a moderately strong convexity along the ventral margin of the spoon opposite the anterior margin of the laminum attachment, a character more typical of *Mya (Mya)*.

Apparently the pallial impressions are obscure on known specimens of the species and no one, unfortunately, has observed them. Nagao and Inoue describe the dorsal margin as nearly horizontal (straight?), a condition more typical of *Mya producta* than any known Pacific species.

This is the oldest known species of *Mya*. No *Mya* resembling this species, or of this age, is known from the American side of the Pacific.

Lectotype: Univ. Hokkaido Reg. 8997; selected by Hatai and Nisiyama, 1952. Measures 42 mm in length, 20.5 mm in height; convexity is 13 mm. The maximum length given for the species is 56.8 mm.

Occurrence: Wakkanabe Formation of the Ishikari Group, Hokkaido. Fujie gave the age as "probably Eocene." Oyama, Mizuno, and Sakamoto assign the Wakkanabe Formation to the early Oligocene.

***Mya* (?*Arenomya*) *kusiroensis* Nagao and Inoue**

Plate 1, figures 5, 6, 8-10

Mya grewinkii var. *kusiroensis* Nagao and Inoue, Hokkaido Imp. Univ. Fac. Sci. Jour., ser. 4, v. 6, no. 2, p. 150, pl. 32, figs. 2-6, 1941.

Minato, Matsui, and Uozumi, Shinseidai-no-Kenkyu [Studies of the Cenozoic], no. 7, p. 3, pl. 10, figs. 84-86, 1950.

Mya grewinkii var. *elongata* Fujie, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 9, no. 4, p. 389, pl. 7, figs. 3, 4, 8, 9, 1957 [in part].

Mya grewinkii kusiroensis Oyama, Mizuno, and Sakamoto, Illustrated handbook of Japanese Paleogene molluscs; Japan Geol. Survey, p. 211, pl. 65, figs. 1a-e, 1960.

The spoon of this species has not been illustrated previously. The rubber cast figured here (pl. 1, fig. 5), taken from the internal mold of a specimen from the basal part of the Poul Creek Formation of Alaska, shows that the spoon is rounded anteriorly and has a

moderately strong slightly overturned anterior ridge. The laminum attachment and the fibrum receptacle together form a surface that is weakly and evenly convex. The spoon appears to have a thin ligamental callus, although it is difficult to recognize a callus with certainty from a rubber cast; the cast shows only the surface contour and not the callus layer. The spoon of this species is closer to that of *Mya (Arenomya)*. At the same time, the species is closely related to *M. salmonensis*, the probable prototype of *Mya (Mya)*.

The shell of this species is moderately attenuated posteriorly. The anterior part is strongly inflated and evenly rounded, but the posterior part is very weakly inflated. The left valve has somewhat the shape and proportions of a right valve of *Macoma nasuta* Conrad.

This is the earliest known *Mya* in America. Its earliest occurrence is in the upper part of the *Acila shumardi* zone (probably equivalent to the type Lincoln Formation of Weaver, 1912, p. 10-22). This zone is of approximately the same age as the Shitakara Formation of the Urohoru Group of Hokkaido, the only known occurrence for *M. kusiroensis* in Japan.

Lectotype: Univ. Hokkaido Reg. 8268; selected by Hatai and Nisiyama, 1952: Measures 31 mm in length, 19 mm in height. Figured specimen USNM 644267 measures 60 mm in length and 38 mm in height; double convexity of internal mold is 20 mm.

Occurrence: Shitakara Formation, Urohoru Group (late middle Oligocene), Hokkaido, Japan. In Alaska it occurs in the upper part of the *Acila shumardi* zone (late middle Oligocene) on the north side of Popof Island, USGS M-1164, M-1655, in beds of middle Oligocene age (basal part of the Poul Creek Formation or the underlying Kulthieth Formation) near Hanna Lake in the Yakataga district, USGS 16864, 16891, and possibly in the middle part of the Poul Creek Formation (1,800 ft above the base of the formation) on the Kulthieth River, Yakataga district, USGS 16899.

***Mya* (?*Arenomya*) *grewinkii* Makiyama**

Plate 1, figure 11

Mya crassa Jimbo, Geol. Soc. Tokyo Jour., v. 5, no. 54, p. 227, pl. 1, fig. 3, 1887.

Makiyama, Geol. Soc. Tokyo Jour., v. 28, no. 334, p. 301, 1921.

Yokoyama, Tokyo Imp. Univ. Coll. Sci. Jour., v. 45, art. 3, p. 12, pl. 1, figs. 11-16, 1924.

Mya (Arenomya) grewinkii Makiyama, Kyoto Imp. Univ. Coll. Sci. Jour., ser. B, v. 10, no. 2, p. 156, pl. 7, figs. 50-52, 1934.

Mya grewinkii Nagao and Inoue, Hokkaido Imp. Univ. Fac. Sci. Jour., ser. 4, v. 6, no. 2, p. 147, pl. 32, figs. 1, 7-10, pl. 33, figs. 7, 8, 1941.

Minato, Matsui, and Uozumi, Shinseidai-no-Kenkyu, no. 7, pl. 10, fig. 83, 1950.

Watanabe, Arai, and Hayashi, Chichibu Mus. Hist. Bull., no. 1, pl. 4, fig. 11, 1950 [no discussion].

Mya (Arenomya) grewinkii Hirayama, Sci. Rept. Tokyo Kyōiku Daigaku, sec. c, v. 4, no. 29, p. 109, pl. 3, figs. 21-24, 1955.

- Mya grewingki* Fujie, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 9, no. 4, p. 386, pl. 5, figs. 6, 7, pl. 6, figs. 2, 4a-b, 1957.
 Oyama, Mizuno, and Sakamoto, Illustrated handbook of Japanese Paleogene molluscs; Japan Geol. Survey, p. 210, pl. 64, figs. 4a-c, 1960.
- Mya* (*Arenomya*) *grewingki* Kanno, Japan Soc. for the promotion of Science, Ueno, p. 317, pl. 45, figs. 4-7, 1960.
- Mya* cf. *M. truncata* MacNeil in Drewes and others, U.S. Geol. Survey Bull., 1028-S, p. 606, 1961.
- Mya grewingki* Fujie, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 11, no. 3, p. 404, 1962.
- Mya* (*Arenomya*) *grewingki* Kamada, Palaeont. Soc. Japan, Special Papers, no. 8, p. 140, pl. 17, figs. 1a-b, 1962.

As shown by Fujie (1957, p. 391), *Mya grewingki* has an *arenaria*-like spoon. Judging from his figures (Fujie, 1957, pl. 5), the spoon is more robust than that of *M. arenaria*, and it stands about midway, in this respect, between *M. arenaria* and *M. elegans*.

The pallial sinus of this species is very large. It is not clear from Fujie's heavy retouching whether the sinus is detached to the extent he shows, or whether it is partly confluent with the pallial line. I suspect that Fujie has traced the outer edge of the pallial line and the inner edge of the pallial sinus attachment, so that it appears to be narrowly detached throughout. *Mya arenaria* has the sinus wholly detached except for the posterior juncture, and *M. elegans* has the sinus narrowly detached either throughout or in part. In size the sinus of *M. grewingki* is most like that of *M. elegans*.

The shell of *Mya grewingki* is subtrigonal to suboval, and it is more inflated anteriorly. Its general proportions are more like those of *M. priapus*, *M. truncata*, and *M. elegans* than they are like *M. arenaria* or *M. japonica*.

I do not regard *Mya grewingki* as being conspecific with either *M. salmonensis* Clark (= *M. grewingki elongata* Nagao and Inoue; renamed *M. grewingki nagaoi* Oyama and Mizuno), or *M. kusiroensis* Nagao and Inoue (*M. grewingki kusiroensis* Nagao and Inoue). *Mya* is known from several localities in Alaska in beds of Oligocene or Miocene age, but only one specimen is doubtfully referred to *M. grewingki*; the others are referred to *M. salmonensis* and *M. kusiroensis*.

The similarity of *M. grewingki* to *M. elegans* (= *M. crassa*) was recognized by early Japanese authors.

Holotype: Kyoto Univ. No. JC-100010. Measures 64 mm in length, 47 mm in height.

Occurrence: This species occurs in Japan and Sakhalin in beds of late Oligocene to early Miocene age that locally are designated the Asagai, Poronai, and Maoka Stages. Its southernmost occurrence is in the Nenokami Sandstone in the Chichibu basin, Saitama Prefecture, Honshu. The holotype is from the Asagai Formation in the Joban coal field, Fukushima Prefecture, Honshu. It occurs also in the Poronai Formation of Hokkaido, in the Nishisakutan (= Nissakutan) Formation of

southern Sakhalin, and in the Marie Formation at Matchgar in northern Sakhalin.

Doubtful Alaskan occurrence: Poul Creek Formation, about 1,900 ft below the top of the formation, north flank of Yakataga Ridge, Yakataga district, Alaska, USGS 15433. This specimen measures 95 mm in length, 56 mm in height; double convexity is 48 mm.

In 1954, I identified some poorly preserved specimens, found in association with teeth of *Cornwallius* sp. in a green volcanic graywacke on Unalaska Island in the Aleutians, USGS M-1679, as *Mya* cf. *M. truncata* (Drewes and others, 1961, p. 606). Further preparation of these specimens, and a better knowledge of the species than I had then, indicates that this form is not *M. truncata*. These specimens are distorted internal molds and no spoons are visible. At the present time I am inclined to believe they are more likely to be either *M. grewingki* or *M. kusiroensis*.

***Mya* (?*Arenomya*) *grewingki haboroensis* Fujie**

Mya grewingki var. *haboroensis* Fujie, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 9, no. 4, p. 392, pl. 5, figs. 1-4, 1957.

This form was described from the Chikubetsu Formation of Hokkaido. As pointed out by Fujie, it has no anterior subumbonal groove and its spoon is more like that of *Mya grewingki*. The anterior ridge of the spoon is not as broadly shelved as in *M. elegans*, but, judging from the specimen shown in Fujie's plate 5, figure 2, neither is it as slender as shown in his diagram (Fujie, 1957, p. 391, fig. 2C). In my opinion, this subspecies is the prototype of the *M. elegans* group; it gave rise to typical *M. dickersoni* from which *M. elegans* is descended. No late Miocene representatives of this group are known from Japan.

Holotype: Univ. Hokkaido Reg. 11340. Measures 51 mm in length, 35 mm in height; convexity is 21.3 mm. A paratype bears the same register number.

Occurrence: Chikubetsu Formation (middle Miocene), Takinoue Stage, Kawabata Series, Hokkaido, Japan.

According to Uozumi (1962, p. 522), the Chikubetsu Formation is the cold-water equivalent of the warm-water Takinoue Formation.

***Mya* (?*Arenomya*) *dickersoni* Clark**

Plate 2, figures 1, 2, 5, 10, 11

Mya dickersoni Clark, California Univ. Pubs. in Geology, v. 8, no. 22, p. 478, pl. 63, fig. 3 [not fig. 4], 1915.

Fujie, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 9, p. 410, 1957.

The holotype of *M. dickersoni* comes from the Neroly Formation (late late Miocene) of the San Pablo Group, Contra Costa County, Calif. Clark figured another specimen (his fig. 4) that is believed to be from the Briones(?) Sandstone (early late Miocene) of the San Pablo Group, Contra Costa County, Calif. The latter specimen was listed as a "paratype" by Keen and Bentson (1944, p. 70), and they gave its occurrence as "Upper

San Pablo." I have been unable to find any other published reference to the stratigraphic occurrence of the "paratype."

Mya dickersoni is very similar to *M. truncata* externally. Fujie suggested that it might be related to *M. cuneiformis*.

Several spoons of *Mya dickersoni* were prepared from topotype material. They were found to range from ventrally elongate and deeply concave, with a broad dorsal shelving of the anterior ridge, a broad posterior furrow, and no ligamental callus to more triangular and shallower, with a narrower anterior ridge, a narrow posterior furrow, and a small thin callus having about the same location and shape as the rib in the callus of *M. arenaria*. The former type is like the spoon of *M. elegans*. The spoon with the small callus represents the morphological intermediate between the spoon of *M. arrosis* that has a large spatulate callus and the uncallused spoon of *M. elegans*. *M. elegans* is believed, therefore, to be derived from a form having a large spatulate callus.

The spoon of the holotype is not exposed, nor can it be prepared without destroying the figured valve. It is not known, therefore, which type of spoon it possesses. A specimen (pl. 2, figs. 10, 11) obtained from the same piece of matrix containing the holotype has a small narrow callus.

Holotype: Actually a lectotype, UC 11554, selected by Keen and Bentson (1944, p. 70). Measures 57 mm in length, 37 mm in height. Figured topotypes, UC 15001, 15002.

Occurrence: Neroly Formation (late late Miocene), San Pablo Group, Contra Costa County, Calif., UC 1617.

Doubtful identifications: A larger specimen from the Cierbo Sandstone (middle late Miocene), San Pablo Group, Contra Costa County, Calif., UC 1225, may be intermediate between typical *Mya dickersoni* and *M. grewingki haboroensis*. It is very tumid centrally. The posterior part of the shell is much less inflated, narrower, and subtruncate. It measures 67 mm in length, 47 mm in height; double convexity is 26.5 mm at the center and only 7.5 mm at the posterior end. Its spoon is not known. This specimen is not figured.

***Mya* (?*Arenomya*) *elegans* (Eichwald)**

Plate 2, figures 3, 4, 6-8, 12; plate 3, figures 1, 4

Mya crassa Grewingk, Russisch-Kaiserliche Mineralogische Gesellschaft zu St. Petersburg, Verhandlungen 1848-49, p. 355, pl. 6, figs. 2a-d, 1850.

Mya arenaria Grewingk, Russisch-Kaiserliche Mineralogische Gesellschaft zu St. Petersburg, Verhandlungen 1848-49, p. 356, pl. 6, figs. 3a-c, 1850.

Anatina elegans Eichwald, Geognostisch-palaeontologische Bemerkungen uber die Halbinsel Mangischalk und die Aleutischen Inseln, p. 119, 1871 (new name for *M. arenaria* Grewingk).

Mya crassa Eichwald, Geognostisch-palaeontologische Bemerkungen uber die Halbinsel Mangischalk und die Aleutischen Inseln, p. 124, 1871.

Mya intermedia Dall, Wagner Free Inst. Sci. Trans., v. 3, pt. 4, p. 857, 1898.

Mya crassa Dall, Wagner Free Inst. Sci. Trans., v. 3, pt. 4, p. 858, 1898.

Dall, Harriman Alaska Expedition, v. 4 (Geology), p. 117, 1904.

Mya arenaria Dall, Harriman Alaska Expedition, v. 4 (Geology), p. 117, 1904 [reissued by Smithsonian Inst., 1910].

Mya intermedia Dall, Washington Acad. Sci. Jour., v. 9, no. 1, p. 2, 1919.

Dall, U.S. Natl. Mus. Bull. 112, p. 52, pl. 4, 1921.

Mya (*Mya*) *arenaria* var. *japonica* Grand and Gale, San Diego Soc. Nat. History Mem., v. 1, p. 412, 1931 [in part].

Mya (*Mya*) *arenaria* var. *profundior* Grant and Gale, San Diego Soc. Nat. History Mem., v. 1, p. 414, 1931 [new name for *M. crassa* Grewingk].

Mya crassa Fujie, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 9, no. 4, p. 411, 1957.

Mya arenaria var. *profundior* Fujie, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 9, no. 4, p. 411, 1957.

Mya japonica MacGinitie, U.S. Natl. Mus. Proc., v. 109, no. 3412, p. 187, pl. 19, fig. 6, 1959 [in part; reassignment of "lectotype" of *M. intermedia* Dall].

This is the largest species of *Mya*, a fact that is reflected in three of the names given it; *crassa*, *profundior*, and *elegans*. Newly collected fossils indicate that there is no apparent way to separate the late Miocene and (or) Pliocene form from the Recent species (*M. intermedia* Dall).

Mya elegans has a very heavy spoon. The broad dorsal shelving of the anterior ridge and the posterior furrow are subequal in size. The angle formed by the posterior ridge and the posterior dorsal margin varies in size; in specimens in which the angle is wider, the posterior furrow is broader and more deeply concave. The most concave part of the ligament area lies along the anterior part of the fibrum receptacle adjacent to the anterior ridge. The posterior part of the ligament area—that part consisting of the posterior part of the fibrum receptacle and the laminum attachment—is more flattened or weakly convex. The ventral margin of the spoon is strongly convex; the most projecting part of the spoon is just posterior of its center. There is no anterior subumbonal groove. I have not seen a specimen of this species that has a ligamental callus. This species has the deepest pallial sinus of any *Mya*. The sinus is relatively narrow, however, and it lies close to the pallial line. The entire pallial sinus is narrowly detached from the pallial line in some specimens; in others only about the anterior half is separated. Morphologically, *M. elegans* lies between *M. arenaria* and *M. ja-*

ponica, species in which the pallial sinus is widely separated from the pallial line and *M. truncata* and *M. priapus*, species in which the sinus and pallial line are confluent throughout.

The posterior and anterior adductor muscle scars are subequal in size; the anterior scar may be slightly thinner and more elongate than the posterior scar. Both scars are located above the midline of the shell. This species has the smallest anterior muscle scar of any living *Mya*; it is less elongate than in other species, and it is the only species in which the anterior scar may be located in a more dorsal position than the posterior scar.

The shell ranges in shape from short oval to moderately elongate and has a narrower posterior end; in some specimens the posterior end is more squared than in others. The anterior part of the shell is the more inflated, and there may be a weak angulation extending from the beak to the anterior ventral margin; this may be greatly exaggerated in laterally compressed fossils. Dall (1921, pl. 4) showed the outline of 28 specimens from Chignik Bay.

This species is descended from *Mya grewingki* through *M. grewingki haboroensis* and typical *M. dickersoni*. One doubtful occurrence of *M. grewingki* is here recorded from the Poul Creek Formation (late Oligocene and early Miocene) of the Yakataga district, Alaska. Fujie (1957, p. 411) did not believe any known Japanese species was related to *M. elegans* (as *M. profundior*). In my opinion, however, his *M. cuneiformis* forma *a* (1957, pl. 3, figs. 5a-b) belongs to *M. elegans*.

Holotype: Lost (Scarlato, Zoological Institute, Leningrad, written commun., Aug. 31, 1960). I am designating as neotype of *Mya elegans* a specimen collected in 1960 from the Alaskan Peninsula. The specimen, from a large suite, is closest to the one figured by Grewingk as *M. arenaria* Linné and for which the name *M. elegans* was proposed. The locality from which this specimen was obtained may be close to the source of Grewingk's fossils; Pavlof, the locality given by Grewingk, probably was merely a base of operation. The neotype, an internal mold, USNM 644272 measures about 112 mm in length, 68 mm in height; double convexity is 40.5 mm.

A specimen from the same lot is designated as the neotype of *Mya crassa* Grewingk; the specimen, USNM 644271, measures 89 mm in length, 63 mm in height; double convexity is 41 mm.

Occurrence: Unnamed Pliocene formation (see p. G18), about 5.3 miles east of the lake north of Black Peak, northwest of Chignik Bay, Alaskan Peninsula, USGS M-807 (neotype locality); middle Pleistocene beds on St. Paul Island, Pribiloff Islands, Alaska, USGS M-1526; Recent, Pribiloff Islands, USGS M-1622, Kuskokwim Bay north of Cape Newenham, USGS M-363, Bristol Bay, Chignik Bay on the south side of the Alaskan Peninsula (lectotype locality of *Mya intermedia* Dall) and Kukak Bay on the west side of Shelikof Strait (Stanford University).

Other reported occurrences: Grewingk gives the southeast coast of Alaska near the settlement of Pavlof, Morzhovai Bay, Port Moller (?), Kodiak, Unga, and Atka; Eichwald added Unalaska. Some of these may represent other species.

***Mya (Arenomya) fujiei* MacNeil, n. sp.**

Plate 5, figure ?1

?*Mya dickersoni* Clark, California Univ. Pubs. in Geology, v. 8, no. 22, p. 478 [in part], pl. 63, fig. 4, 1915.

Mya japonica oonogai Fujie, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 9, no. 4, p. 403 [in part], pl. 2, figs. 1a,b, 2, 1957.
Fujie, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 11, no. 3, p. 404, 1962.

This species is based on the form occurring in the Takinoue Formation (middle Miocene) of Ishikari Prefecture, Hokkaido (Fujie, 1957, pl. 2, figs. 1a,b, 2). The paratype of *Mya dickersoni* from the Briones Sandstone (late Miocene) of California may be the same species.

The spoon, judging from Fujie's figure, is very similar to that of *Mya arenaria*. The posterior ridge is longer than in *M. arenaria*, which makes the posterior margin of the spoon less concave. The pallial sinus is large and deep and has a well-rounded anterior extremity.

The shell is less inflated anteriorly than *Mya japonica*, and the beaks are less opisthogyrate. The posterior extremity of the shell is less pointed than in *M. japonica*.

At present this species is known from only a few rather poorly preserved specimens.

Some workers might prefer to regard this form as a subspecies of either *Mya japonica* or *M. arenaria*, or to regard all three as one species. The present arrangement shows what I believe to be the true phylogenetic relationships of the three forms. If *M. fujiei* were combined with either or both of the other species, it probably would be the oldest recorded occurrence for a living species. Otherwise, only *M. truncata* is believed to have been in existence since middle Miocene time.

Holotype: Univ. Hokkaido Reg. no. 11334a. Measures 87.5 mm in length, 52 mm in height; convexity is 26 mm.

Occurrence: Takinoue Formation (early middle Miocene), Takinoue, Sorachi district, Ishikari Prefecture, Hokkaido. Uozumi (1962, p. 522) stated that the Takinoue Formation is the warm-water equivalent of the Chikubetsu Formation which carries a cold-water fauna. He mentioned *Mya* in the Chikubetsu but not in the Takinoue. The point raised in this apparent contradiction is not clear; according to Fujie's assignment *M. fujiei* would be a warm-water form.

Doubtful identifications: The paratype of *Mya dickersoni* from the Briones Sandstone (late Miocene) of California, UC 197, may be referable to *M. fujiei*, or it may be intermediate between it and *M. arenaria*.

Mya (*Arenomya*) *arrosis* MacNeil, n. sp.

Plate 2, figure 9; plate 3, figures 2, 3, 5, 6, 9

Mya dickersoni Clark, California Univ. Pubs. in Geology, v. 8, no. 22, 478 [in part], table opposite p. 416, UC 1227, 1915.

This species is based on specimens in the collections of the University of California.

The shell is very thin. It ranges in shape from moderately elongate anteriorly and only moderately inflated—such specimens more nearly resemble *Mya japonica*—to shorter, higher, and more inflated anteriorly, tapering sharply posteriorly (the latter variant has more the shape of *M. cuneiformis*).

The spoon is moderately large and inclined downwards anteriorly. The surface of the ligament area is flattened, the deepest part being immediately adjacent to the anterior ridge. The dorsal part of the anterior ridge is very broad, but it narrows ventrally. The posterior ridge is long, and the posterior furrow is moderately narrow with very little posterior alation.

The ligamental callus is large and spatulate, and its posterior edge stands up as a prominent ridge. There is no anterior subumbonal groove. A moderately large solution cavity lies immediately below the umbo.

The pallial sinus is not clearly defined on the internal mold, but it appears to be of much the same shape as in *Mya japonica*.

This form was included in *Mya dickersoni* in several early checklists, probably because it occurs in beds of the same general age as *M. dickersoni*, and because the spoon of *M. dickersoni* was not known at the time. It almost certainly is the form that led Woodring and Stewart (in Woodring and others, 1940, p. 95) to identify the species in the Etchegoin and San Joaquin Formations as *Mya* cf. *M. dickersoni*. The spoon of typical *M. dickersoni* is more like the spoon of *M. elegans*.

Mya japonica probably descended from a form of *M. arrosis* rather than from *M. arenaria*. No *Mya* of this group is known to date from late Miocene beds of Japan, but I suspect one will be found, eventually. In all probability *M. japonica* originated in East Asia.

Holotype: UC 15006 measures 78 mm in length, (incomplete, probably about 85 mm), 57 mm in height; double convexity is about 28 mm.

Occurrence: The holotype is from the Cierbo Sandstone (middle late Miocene), San Pablo Group, at a locality north of Grizzley Creek, and about half a mile west of south from Tice Valley, Contra Costa County, Calif., UC 1227.

A similar spoon was found among specimens from the type locality of *Mya dickersoni* in the Neroly Formation (late late Miocene), San Pablo Group. The shell is a fragment, and its shape cannot be determined.

The spoon, however, is much more strongly callused than in specimens that are regarded as topotypes of *M. dickersoni*.

Mya (*Arenomya*) *japonica* Jay

Plate 3, figures 7, 8, 10; plate 4, figures 1–11; plate 6, figure 16

Mya arenaria Middendorff, Malacozoologia Rossica; Acad. Sci. St. Petersburg Mem., ser. 6, v. 6, p. 586, pl. 20, figs. 1–3, 1849.

?*Mya arenaria* Middendorff, Reise in dem Aussersten Norden und Osten Sibiriens; K. Akad. Wiss., v. 2, pt. 1 (Mollusken), St. Petersburg, p. 269, no. 3, 1851.

Mya japonica Jay, in Narrative of the expedition of an American Squadron to the China Sea and Japan, 1852–54, under the command of Commodore M. C. Perry, v. 2, p. 292, pl. 1, figs. 7, 10, 1856.

Mya arenaria Crosse and Debeaux, Jour. conchyliologie, v. 11, p. 253, 1863.

Lischke, Japanische Meeres-conchylien, v. 1, p. 138, 1869.

Mya acuta Grabau and King, Shells of Peitaiho, p. 192, 1928.

Mya arenaria japonica Makiyama, Kyoto Imp. Univ. Coll. Sci. Mem., ser. B, v. 10, no. 2, art. 6, p. 159, 1934.

Mya oonogai Makiyama, Warera-no-Kobutsu, v. 4, no. 3, p. 137, text fig. 0, 1935.

Mya arenaria Foster, Johnsonia, v. 2, no. 20, p. 32, 1946 [in part].

Mya japonica Cahn, Clam culture in Japan; Supreme Commander Allied Powers Nat. Res. Sec. Rept., no. 146, p. 85, fig. 10 (unlettered), fig. 36, A–G, 1951.

(Hirase) Taki, Handbook of illustrated shells, pl. 52, fig. 7, 1951.

Mya (*Arenomya*) *japonica* Habe, Genera of Japanese Shells; Pelecypoda, v. 3, p. 237, fig. 612, 1952.

Mya (*Arenomya*) *japonica oonogai* Habe, Akkeshi Marine Biol. Sta. Pub., no. 4, p. 22, pl. 6, fig. 3, 1955.

Mya (*Arenomya*) *japonica* Kira, Coloured illustrations of the shells of Japan, pl. 61, fig. 22, 1955.

Mya japonica oonogai Fujie, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 9, no. 4, p. 403, pl. 2, figs. 3–6, 1957.

Mya (*Arenomya*) *japonica oonogai* Yamamoto and Habe, Marine Biol. Sta. Asamushi Bull.; Tôhoku Univ., v. 9, no. 3, p. 113, pl. 12, fig. 18, 1959.

Mya arenaria Wagner, Canada Geol. Survey Bull. 52, p. 8, pl. 1, figs. 19 a, b, 1959.

Mya japonica MacGinitie, U.S. Natl. Mus. Proc., v. 109, no. 3412, p. 187, pl. 19, fig. 8, 1959.

Mya oonogai Hopkins, MacNeil, and Leopold, 21st Internat. Geol. Cong. Rept., pt. 4, p. 52, 1960.

Mya (*Arenomya*) *japonica* Kira, Coloured illustrations of the shells of Japan, pl. 61, fig. 22, 1961 [revised and enlarged].

Mya japonica oonogai Fujie, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 11, no. 3, p. 400, 1962.

Mya (*Arenomya*) *arenaria* Kotaka, Tôhoku Univ. Sci. Repts., ser. 2, spec. v., no. 5, p. 154, pl. 35, figs. 22–25, 1962.

The characters that distinguish this species from *Mya arenaria* are discussed under the latter species.

Kira (1955 and 1961) appears to be the only Japanese author since 1955 to continue to use the name *Mya japonica* for the southern Japanese species. He figured only the exterior of a shell, but its attenuated posterior

end and his use of the Japanese vernacular name, Oñogai, a name used for the southern species, leaves little doubt as to which species he meant. Yamamoto and Habe (1959, p. 113), several years after Habe had accepted the transfer of the name *M. japonica* to the northern species (*M. priapus*), proposed a new vernacular name for the northern species, "Kitano-ono-gai."

Cahn (1951, p. 85), who must have had contact with Japanese workers at about the time the transfer of name became generally accepted, also used *M. japonica* for the southern species. Cahn gave a good account of the habits and distribution of the species in Japan, and he discussed the possibility of commercial culture. He gave some good illustrations of the veliger and successive juvenile stages. The successful culture of other edible clams has delayed any large scale culture of *M. japonica*, although experiments in harvesting the natural population have been carried out in Okayama Prefecture.

The transfer of the name *Mya japonica* to another species by Grant and Gale and the apparent acceptance of their interpretation by most modern Japanese authors was unfortunate. As reluctant as I am to reverse this action at this date, I can see no alternative to it. The pallial sinus on Jay's specimen indicates that it cannot be anything but the southern species that most modern Japanese authors call *M. oonogai*. Woodring and Stewart (in Woodring and others, 1940, p. 95) probably were also following Grant and Gale in their reference to *M. japonica* as a "living Alaskan and Japanese" species; the occurrence of *M. japonica* as here interpreted in Alaska has been known only since 1960. All other American and European authors, as well as the early Japanese authors, seem to have regarded *M. japonica* as being the southern Japanese species. Fixation of the name *M. japonica* on the northern species, in view of the pallial sinus shown in Jay's figure, could only be accomplished by the International Commission on Zoological Nomenclature, and I doubt if it could ever receive favorable action. Besides, the name *M. priapus* has priority for the northern species.

As further proof of my identification of *Mya japonica*, it might be pointed out that Jay's figure shows a large multiple solution cavity under the umbo of the left valve, and it appears to show a ligamental callus. As already discussed (p. G24), subumbonal solution is an almost universal condition in left valves of *M. arenaria* and *M. japonica*, but it has not been observed in left valves of *M. priapus*. Right valves of *M. priapus* occasionally have a single small solution pit

that indents the margin of the shell at the top of the chondrophore in the right valve.

Grabau and King (1929, p. 192) recorded *Mya acuta* Say from Peitaiho (near Tientsin in the Gulf of Chihli), China. Their statement that it is more pointed posteriorly than *M. arenaria* identifies it as *M. japonica*. Their use of the name *M. acuta*, however, makes one wonder what they had in mind. *Mya acuta* was described from the "southern coast of the United States," and it has long been placed in the synonymy of *M. arenaria*.

The most likely reason for their use of the name *Mya acuta* is that they followed Sowerby (1875-78, pl. 3, fig. 12b). Sowerby used the name for *M. japonica*, and he also recognized both *M. acuta* and *M. arenaria* on the Atlantic coast. However, inasmuch as *M. japonica* is the most southern of the Asiatic species, Grabau and King might have suspected the migration of a southern Asiatic species to the Atlantic and a retreat of the species to a southern geographic position in the Atlantic, or vice versa. The recent discovery of *M. japonica* north of Bering Strait makes such a circumstance possible, but whether it is true, and whether Grabau and King thought so, is difficult to say.

It remains to be determined also whether *Mya japonica* still lives north of Bering Strait. Specimens picked up on the beach behind Sheshalik Spit in 1962 are completely unworn, and they have pieces of all three ligament layers and the periostracum preserved. Another small specimen was found on the beach at Deering. In my opinion these are Recent shells, and in all probability a colony of the species lives in Kotzebue Sound.

Holotype: Location?; Dr. J. P. E. Morrison (written commun., Feb. 11, 1963) informed me that the type is not in the U.S. National Museum; he suspects it may have been added to the Jay collection, or remained in Perry's or other private hands. Until it is determined definitely whether or not Jay's specimen is in existence, nothing can be done about selecting a neotype. The rules are not specific regarding the necessity of designating a neotype if the original figure is recognizable, and in my opinion it is. If a neotype is required, it must be a specimen having a detached pallial sinus from Uchiura-wan, Hokkaido. The designation of a specimen having an attached pallial sinus, that is *M. priapus*, would be contested almost certainly.

Occurrence: I am dubious of the Miocene forms referred to this species. Fujie (1957, p. 412, table 3) gave some supposed Miocene occurrences (middle Miocene and older) but none from the late Miocene or Pliocene. The Miocene forms, in my opinion, are more like *Mya arenaria*. I have named this form *M. fujiei*.

Chinzei (1961, p. 126, pl. 3, fig. 13) figured an internal mold from the Togawa Formation of the Sannohe Group of north-eastern Honshu as *Mya japonica oonogai*. The Togawa Formation is assigned to the late Pliocene.

Although I am inclined to believe *Mya japonica* became differentiated during the Pliocene, the known occurrences of the species all seem to be in very young beds. The only unequivocal fossil specimen from Japan that I can find illustrated is from alluvial deposits around Lake Abashiri, northern Hokkaido (Fujie, 1957, pl. 2, figs. 6a-c). In 1962, Fujie (p. 419) gave the age of these deposits as Holocene (postglacial).

The species occurs at Nome, Alaska, USGS M-1440, M-1445, and at Cape Krusenstern, Alaska, USGS M-1577, in beds that I regard as of possible middle-Wisconsin age. It also occurs in beds in the vicinity of Vancouver, British Columbia, that are dated (Wagner, 1959, p. 1) as "25,000 or more years" old and of Pleistocene age or younger. The oldest occurrences in the Vancouver area would also be, according to this date, of middle-Wisconsin age. The same form occurs in recently discovered beds, probably Pleistocene, along the north side of Willapa Bay, Wash., USGS M-1681, M-1682, the southernmost American occurrence for the species.

Mya japonica lives today from southern Hokkaido to Amakusa Island off west-central Kyushu, Japan, and it lives also in the Gulf of Chihli, China. It may also live in the Okhotsk Sea. Specimens collected from Sheshalik Spit, northern Kotzebue Sound, USGS M-1665 and at Deering, southern Kotzebue Sound, Alaska, USGS M-1425, appear to be Recent, although none of them were found alive. A Recent left valve and several live juveniles were found near Nome, Alaska, USGS M-364.

Foster (1946, p. 35) reported *Mya arenaria*, presumably Recent, from Akutan Island in the eastern Aleutians. This could be an otherwise unreported occurrence of *M. japonica*, or it could be some other species. It might also be based on Grewingk's "*M. arenaria*" (= *M. elegans*), which occurs in the area. I can find no other record of either *M. japonica* or *M. arenaria* from the Aleutians.

Mya (Arenomya) arenaria Linné

Plate 5, figures 2-12; plate 6, figures 1-15, 17, 18

- Mya arenaria* Linné, Systema naturae, ed. 10, p. 670, 1758.
Mya communis Megerlé von Mühlfeld, Mag. Gesellsch. Naturforscher Freunde Berlin, v. 5, p. 46, 1811 [based on Chemnitz, Conchylien Cabinet, v. 6, pl. 1, figs. 3, 4, 1782].
Mya lata Sowerby, Mineral conchology Great Britain, v. 1, p. 185, pl. 81, 1815 [fossil from the Red Crag of England].
 Smith, Strata identified by organized fossils, London, pl. 2, fig. 9, 1816.
Mya acuta Say, Philadelphia Acad. Nat. Sci. Jour., v. 2, p. 313, 1822.
Mya mercenaria Say, Philadelphia Acad. Nat. Sci. Jour., v. 2, p. 313, 1822.
Mya arenaria Conrad, American marine conchology, p. 42, pl. 9, fig. 1, 1831-34.
Mya subovata Woodward, Geology of Norfolk, p. 43, pl. 2, fig. 5, 1833.
Mya subtruncata Woodward, Geology of Norfolk, p. 43, pl. 2, fig. 6, 1833.
Mya alba Agassiz, Soc. Sci. Nat. Neuchatel Mem., v. 2, p. 1, 1840.
Mya corpulenta Conrad, Fossils of the medial Tertiary, p. 68, pl. 39, fig. 1, 1845 [fossil from Petersburg, Va.].

- Mya arenaria* Wood, Palaeontographical Soc. London Mon., v. 9, p. 279, pl. 28, figs. 2a-f, 1857.
 Holmes, Post-Pleistocene fossils of South Carolina, p. 55, pl. 8, fig. 15, 1860.
 Verrill, Report upon the invertebrate animals of Vineyard Sound . . . ; U.S. Commissioner Fish and Fisheries Rept., p. 672, pl. 26, fig. 179, 1873.
 Wood, Palaeontographical Soc. London Mon., v. 27, p. 162, 1874.
Mya hemphilli Newcomb, Acad. Nat. Sci. Philadelphia Proc., v. 5, p. 415, 1874 [based on transplants in San Francisco Bay].
Mya arenaria Sars, Mollusca Regionis Arcticae Norvegiae; Universitets-program, Christiania, p. 91, 1878.
Mya elongata Locard, Prodrome de Malac. Francaise, p. 383, 586, 1886.
Mya arenaria Dall, U.S. Natl. Mus. Bull. n. 37, p. 70, pl. 49, fig. 9, pl. 55, fig. 2; pl. 61, fig. 2, 1889.
 Dall, Wagner Free Inst. Sci. Trans., v. 3, pt. 4, p. 857, 1898.
 Brøgger, Norges geol. undersøgelse Skrifter, no. 31, p. 605, fig. 64, 1901.
 Clark, Pliocene and Pleistocene; Maryland Geol. Survey, p. 194, pl. 53, figs. 5, 6; pl. 54, figs. 1-4, 1906.
Mya (Arenomya) arenaria Winckworth, Malacological Soc. London Proc., v. 19, p. 15, 1930.
Mya cf. *M. dickersoni* Woodring and Stewart, U.S. Geol. Survey Prof. Paper 195, p. 95, pl. 9, figs. 4-9, 1940.
Mya arenaria Gardner, U.S. Geol. Survey Prof. Paper 199-A, p. 138, pl. 22, fig. 8, 1943.
 Foster, Johnsonia, v. 2, no. 20, p. 32, pl. 20, figs. 1-4; pl. 21, fig. 1, 2, 1946.
 Hessland, Arkiv for Zoologi, Stockholm, v. 37, pt. 2, no. 8, p. 1-51, pl. 1, 1946.
 Dodge, Am. Mus. Nat. History Bull., v. 100, art. 1, p. 28, 1952.
 Richards, Am. Philos. Soc. Trans., new ser., v. 52, pt. 3, p. 70, pl. 12, fig. 15, 1962.

A complete synonymy for this species would run into many pages. The one given here probably includes all the synonyms and most of the works generally cited by authors.

Mya japonica is excluded from this species, although this procedure may not have the approval of some authors. Several authors have regarded *M. japonica* as a synonym of *M. arenaria*. Others might contend that if they are not identical, they are no more than local subspecies. In my opinion these species are members of parallel lineages. *M. japonica* does not live in the same area as *M. arenaria*, and I know of no accidental introductions of either species to an area inhabited by the other.

Mya arenaria has a heavier shell than *M. japonica*. The posterior end is less attenuated, the beaks are less twisted, which makes the anterior and posterior parts more evenly inflated, and the exterior of the shell is more irregular. The spoon of *M. arenaria* tends to be larger for a shell of the same size, and it is slightly more hori-

zontal; in some specimens of *M. japonica* the spoon is inclined downwards rather steeply towards the anterior. The posterior ridge is relatively longer in *M. japonica*, making the posterior margin of the spoon less indented.

The spoon of *Mya arenaria* is elongate and the ventral margin is strongly rounded; the ventral edge of the spoon extends well below the ventral end of the anterior ridge; the posterior margin of the spoon extends nearly vertically to the end of the posterior ridge. The posterior furrow is moderately deep, and it merges with the dorsal margin of the shell at a point well back from the end of the posterior ridge. The anterior ridge is narrow and generally curves over the anterior part of the fibrum receptacle rather strongly. In large shells the ventral part of the anterior ridge may be swollen and strongly hooked, whereas the dorsal part appears to have been resorbed, apparently by the mantle during its invasion of the dorsal part of the fibrum receptacle to deposit the ligamental callus. The anterior ridge does not broaden dorsally, and it forms a moderately sharp angle with the dorsal margin; generally the angle is recessed or indented.

Mya arenaria has a thick ligamental callus, it has no anterior subumbonal groove, and there is always a large amount of subumbonal solution.

The pallial sinus of *Mya arenaria* is moderately long, and it is completely detached from the pallial line; the space between the sinus and the pallial line is nearly as wide as the sinus itself. The sinus joins the pallial line only at its posterior terminus. The lower limb of the pallial sinus is not parallel with the pallial line but, rather, it is directed upwards from it. The innermost end of the sinus may be pointed, blunt, or squared. The pallial sinus and pallial line range from weakly impressed to very strongly impressed; that is, they may be flush with the shell or deeply indented.

The posterior muscle scar has about the shape of a three-quarter moon. The anterior scar is elongate tear shaped and moderately broad ventrally. It extends lower than the posterior scar; its ventral end is about opposite the inner end of the pallial sinus.

Mya arenaria and *M. japonica* are morphologically similar and probably closely related, but these two species are not very closely related to any other living *Mya*.

Holotype: According to Dodge (1952, p. 29), Linné's specimen, properly marked, is in the collection of the Linnean Society of London.

Occurrence: The occurrence of this species in Japan depends on how the delimitation of *Mya arenaria* and *M. japonica* is made. In my opinion, *M. arenaria* is the older species, and the form in the Takinoue Formation (middle Miocene) of Japan that Fujie (1957, pl. 2, figs. 1 a, b, 2) referred to *M. japonica oonogai* is ancestral to it. This species was reported

from the Kawabata Formation of Hokkaido as *M. arenaria* (Minato and others, 1950, p. 4). It is here named *M. fujiei*. The species in the Toshima Sand (Pleistocene) that Hayasaka (1961, p. 64, pl. 8, figs. 10a, b) identified as *M. (Arenomya) japonica oonogai*, I identify as *M. arenaria*, but, if this identification is correct, it is the last form from Japan that I would refer to this species. Kotaka (1962, p. 154, pl. 35, figs. 22-25) identified two young Recent specimens from Okhotsk Sea as *M. arenaria*. It is not clear from his figures what they are, but they may be juveniles of *M. japonica*.

In western North America, *Mya arenaria* is known in the following: the Cierbo Sandstone (middle late Miocene) of the Mount Diablo region, Alameda County, central California, U.C. 1224; the upper part of the Etchegoin Formation (Pliocene), Kettleman Hills district, western San Joaquin Valley, Fresno and Kings Counties, Calif. U.C. A-1686; San Joaquin Formation (late Pliocene), Kettleman Hills district, U.C. A-3167 (for further records see Woodring and others, 1940), Merced Formation (late Pliocene and early Pleistocene?), San Mateo County, Calif., U.C. B-4807; Recent from Monterey, Calif., to Southeastern Alaska. The Recent representatives all come, probably, from an introduction of the species in San Francisco Bay about 1865.

A species occurring in Pleistocene beds around Vancouver in southwestern British Columbia has been identified as *Mya arenaria*. Judging from Wagner's (1959, pl. 1, figs. 19a-b) figures, it has a thin shell and the spoon is tilted. It thus resembles more closely the late Pleistocene fossils from Nome and Kotzebue Sound, Alaska, here referred to *M. japonica*.

In eastern North America, *Mya arenaria* is known in the following: Yorktown Formation (late Miocene), Virginia, Yorktown, USGS 2247b, Petersburg, USGS 3122; Waccamaw Formation (Pliocene), North Carolina, Lake Waccamaw, Columbus County (fide Gardner, 1943, p. 139), Neill's Eddy Landing, Columbus County (fide Gardner, 1943, p. 139), Wilmington, USGS 2295; Richards (1962, p. 70) records the species from 45 Pleistocene localities (probably ranging in age from Sangamon to postglacial), Labrador (1), Hudson Bay (1), Newfoundland (6), Quebec (4), New Brunswick (4), Maine (10), Massachusetts (2), Vermont (3), New York (2), New Jersey (5), Delaware (1), Maryland (3), North Carolina (1), South Carolina (2); the species is known from the Recent of Labrador to North Carolina, but it is common only between the Gulf of St. Lawrence and Long Island Sound. The species from Greenland so identified probably is *M. pseudoarenaria*, USGS D-385.

In Europe, *Mya arenaria* was abundant in the Newbournian and Butleyan Stages of the Red Crag and in the Norwich Stage of the Icenian Crag (all early Pleistocene) of England. It does not occur, however, in the Waltonian (the earliest stage of the Red Crag), or in the underlying Coralline Crag (late Pliocene). Wood (1856, p. 279) gave "Bridlington" as a locality for this species, which may refer to the Bridlington Crag (early glacial Pleistocene) and thus place the species in post-Cromer Forest beds. In Belgium it occurs in the Sables du Kruisschans (the lower part of the Merxemien or Poederlien Stage; early Pleistocene), the probable correlative of the Newbournian Stage.

Most European workers seem to be of the opinion that *Mya arenaria* became extinct in Europe during the early part of the glacial Pleistocene. Some authors have thought that *M. arenaria* reinvaded Europe during the iron age, but according to Hessland (1946), it was first noticed as a prominent species

in the littoral fauna during the 17th century. The last emergent peripheral sediments of the Baltic Sea, the so-called *Mya* Sea, date from about this time. Hessland believed the species was brought to the coast of Europe during the 16th century by sailing vessels. At present the species is established from northern Norway to the southern part of the Bay of Biscay, southern France.

Subgenus *MYA* Linné 1758

***Mya (Mya) salmonensis* Clark**

Plate 7, figures 1, 4

- Mya salmonensis* Clark, Geol. Soc. America Bull., v. 43, p. 822, pl. 17, figs. 3, 4, 8, 1932.
- Mya grewingki* var. *elongata* Nagao and Inoue, Hokkaido Imp. Univ. Fac. Sci. Jour., ser. 4, v. 6, no. 2, p. 150, pl. 33, figs. 1-4, 1941.
- Minato, Matsui, and Uozumi, Shinseidai-no-Kenkyu (Studies of the Cenozoic), no. 7, p. 2, pl. 10, fig. 89, 1950.
- Fujie, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 9, no. 4, p. 389, pl. 7, figs. 1, 2, ?6, ?7, ?10, ?11, ?12, 1957 [in part].
- Mya grewingki nagaoi* Oyama and Mizuno, Japan Geol. Survey Bull., v. 9, no. 9, p. 603, 1958.
- Oyama, Mizuno, and Sakamoto, Illustrated handbook of Japanese Paleogene molluscs; Japan Geol. Survey, p. 211, pl. 64, figs. 3a-d, 1960.
- Mya (Arenomya) grewingki* var. *elongata* Kanno, Japan Soc. for the Promotion of Science, Ueno, p. 318, pl. 45, figs. 2, 3, 1960.

The spoon of *Mya salmonensis* has not been figured previously. Their similar shape, and the fact that this species and *M. grewingki elongata* from Japan are of the same approximate age, leaves little doubt in my mind that they are the same species. Fujie's illustrations of the spoon of the latter show it to be like that of *M. salmonensis*. The spoon is rounded anteriorly as in *M. arenaria*, but the anterior ridge is very broad dorsally as in *M. truncata*. The spoon has a simple but moderately large callus. *M. salmonensis* also has a well-defined anterior subumbonal groove. *M. salmonensis* appears in all respects to be the prototype of the *M. truncata* group.

Curiously, Fujie placed *Mya grewingki elongata* and *M. salmonensis* in different groups. The former he regarded as related to *M. japonica* (as *M. japonica oonogai*), whereas he suggested (1957, p. 411) that *M. salmonensis* resembled *M. cuneiformis*.

Unfortunately, the holotype of *Mya salmonensis* is a float specimen. According to the late D. J. Miller, who attempted to locate Taliaferro's localities, Salmon Creek must be a field name and its whereabouts is unknown; he thought from the lithology of the specimen, however, that it could only have come from the Poul Creek Formation.

Holotype of *Mya salmonensis*, UC 30397, measures about 56 mm in length, 32 mm in height; double convexity is 32 mm.

Lectotype of *M. grewingki elongata*, Univ. of Hokkaido Reg. 8987 and selected by Fujie, 1957, measures 63 mm in length, 35 mm in height; convexity is 18 mm.

Occurrence: This species occurs in the Poronai Stage of southern Sakhalin (type locality) and Hokkaido. In Alaska it is found in the Poul Creek Formation, UC 3851 (?loc.) and at two localities near Priest River, USGS 17783 (2,400 ft below the top of the formation), and USGS 17787 (1,100 ft below top of the formation).

***Mya (Mya) cuneiformis* (Böhm)**

Plate 7, figures 2, 3, 5-8, 12, 15

- Pleuromya cuneiformis* Böhm, Preuss. geol. Landesanstalt Jahrb., v. 26, p. 557, pl. 29, figs. la-c, text figs. 1, 2, 1915.
- Mya crassa* Yokoyama, Tokyo Imp. Univ. Fac. Sci. Jour., ser. 2, v. 1, p. 232, pl. 29, figs. 6-8, 1926.
- Mya arenaria* Yokoyama, Tokyo Imp. Univ. Fac. Sci. Jour., ser. 2, v. 1, p. 241, pl. 30, fig. 1, 1926.
- ?*Mya japonica* Matsumoto, Tōhoku Imp. Univ. Sci. Repts., ser. 2, v. 13, p. 98, pl. 39, fig. 11, 1930.
- Mya peternalis* Matsumoto, Tōhoku Imp. Univ. Sci. Repts., ser. 2, v. 13, p. 98, pl. 39, figs. 5-10, 1930.
- ?*Mya japonica* Kuroda [in Homma], Fossil Mollusca [in Geology of Central Shinano], p. 64, pl. 8, fig. 55, pl. 9, figs. 57, 58, 1931.
- Mya donaciformis* Kuroda [in Homma], Fossil Mollusca [in Geology of Central Shinano], p. 63, text fig. 7, 1931.
- Mya urusikuboana* Nomura, Saito Ho-on Kai Mus. Res. Bull., no. 5, p. 119, pl. 5, figs. 6, 7, 1934.
- Mya cuneiformis* Makiyama, Kyoto Imp. Univ. Coll. Sci. Mem., ser. B, v. 10, no. 2, art. 6, p. 157, 1934.
- Makiyama, Kyoto Imp. Univ. Coll. Sci. Mem., ser. B, v. 11, no. 4, art. 8, p. 216, 1936.
- Nagao and Inoue, Hokkaido Imp. Univ. Fac. Sci. Jour. ser. 4, v. 6, no. 273, p. 151, pl. 34, figs. 1-6, 1941.
- Minato, Matsui, and Uozumi, Shinseidai-no-Kenkyu [Cenozoic Research], no. 7, p. 3, pl. 10, figs. 90, 91, 1950.
- Fujie, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 9, no. 4, p. 395, pl. 3, fig. 5, pl. 4, figs. 1-6, 1957.
- Fujie, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 11, no. 3, p. 406, 1962 [?in part].
- Kamada, Palaeontological Soc. Japan, Special Papers, no. 8, p. 141, pl. 16, figs. 14-16, 1962.

Fujie (1962, p. 406) said this species occurs in Alaska. This may be based on his former (1957, p. 411) statement that *Mya salmonensis* Clark resembles *M. cuneiformis*. *M. cuneiformis* probably is descended directly from *M. salmonensis* and the boundary between them is not sharp. *M. salmonensis*, however, appears to have come from the Poul Creek Formation (late Oligocene and early Miocene), whereas the specimen I refer to *M. cuneiformis* are from the lower part of the Yakataga Formation and probably they are of middle Miocene age. As far as I am aware, the Yakataga occurrences of *M. cuneiformis* are recorded here for the first time.

The spoon of *Mya cuneiformis* is definitely triangular. The ventral margin is weakly concave, the concavity centering at about the boundary between the

laminum attachment and the fibrum receptacle. There is a well-defined subumbonal groove. The area bounded by the subumbonal groove and the anterior leg is triangular; the leg is nearly vertical and forms a right angle with the anterior margin of the shell. The configuration of the margin so formed is more like that of *Arenomya*, but *Arenomya* has no subumbonal groove. There is no indication of any subumbonal solution in *M. cuneiformis*. (See p. G24.)

The anterior ridge is of moderate width and has no marked dorsal broadening; the growth lines of the fibrum receptacle rise up the side of the anterior ridge and partly cover its crest. The ventral part of the anterior ridge is more projecting and weakly hooked over the fibrum receptacle, another character recalling *Arenomya*.

The fibrum receptacle is concave, the deepest part being immediately adjacent to the anterior ridge. The posterior part of the fibrum receptacle and the laminum attachment together form a moderately strong convexity. The posterior part of the laminum attachment, however, forms another narrow concave area. The posterior ridge is moderately strong. The most projecting part of the posterior part of the spoon is opposite the posterior ridge and the narrow concavity immediately anterior to it. The posterior furrow is moderately narrow to narrow; its dorsal posterior extremity forms a long narrow wing.

The pallial sinus is moderately broad and moderately deep; its ventral leg is confluent with the pallial line throughout. The posterior muscle scar is subrounded; the anterior scar is elongate and narrow.

The shell of *Mya cuneiformis*, as its name implies, is wedge shaped. The anterior is broad and rounded, but the shell narrows to a sharply rounded posterior extremity. The dorsal margin between the beak and the posterior end is nearly straight. The anterior part of the shell is more inflated than the posterior part, and the beak is set rather high. There is a weak angulation extending from the beak to the anteroventral margin, which, in laterally compressed specimens, may be quite sharp.

Some features of the spoon of this species, such as the backward curving of the anterior ridge over the fibrum receptacle and the nearly vertical strike of the anterior leg, are more resemblant of *Mya arenaria*. As one of the more primitive species of *Mya* (*Mya*) it is not strange that it has some features close to *Mya* (*Arenomya*). Its spoon, however, is heavier and more triangular than in any *Mya* (*Arenomya*) of comparable size, and it has a well-defined anterior subumbonal groove, a character typical of *Mya* (*Mya*). There is no

evidence of subumbonal solution in the left valves of *M. cuneiformis*, a circumstance that seems always to be linked with a subumbonal groove. (See p. G24.)

It is not clear at the present time whether *Mya cuneiformis* gave rise directly to *M. pseudoarenaria*, or whether both species are coderivatives from *M. salmonensis*. *M. cuneiformis takigawensis* Fujie (1957, p. 397, pl. 4, figs. 1a-c) from the Takigawa Formation (early Pliocene) of Hokkaido may connect these two species; judging from the figures it is closer morphologically to *M. pseudoarenaria*. At present, *M. cuneiformis* is extinct, and *M. pseudoarenaria* lives only in the Arctic Ocean and in the northern boreal Atlantic Ocean. *M. cuneiformis* probably gave rise directly to *M. priapus*, probably in late Miocene time.

Like Eichwald, who thought *Mya crassa* and *M. elegans* were of Turonian age, Böhm thought *M. cuneiformis* was of Cretaceous age.

Holotype: The holotype, if preserved, is in the Naturhistorischen Museum (Geologisches Staatsinstitut), Hamburg, Germany.

Occurrence: Böhm's specimens, including the type, are stated to be from Kap Jonquière (Due), west-central Sakhalin; they probably are from beds of middle Miocene age. Fujie (1957, p. 396) recorded this species from several formations in Hokkaido ranging in age from middle Miocene to early Pliocene: the Chikubetsu and Kawabata Formations (middle Miocene), the Togeshita and Wakkanai Formations (late Miocene), and the Honbetsu and Takigawa Formations (early Pliocene).

Kamada (1962, p. 142) recorded the species from three formations of middle Miocene age in the Joban coal field of Fukushima and Ibaraki Prefectures, Honshu. These are the Nakayama Formation of the Shirado Group and the Numanouchi and Kokozura Formations of the Taga Group.

The species is known for certain only in the lower 4,000 feet of the Yakataga Formation of Alaska. This part of the formation is assigned to the middle Miocene. The species is represented in the Geological Survey collections from: an unnamed creek north of and parallel to Yakataga Ridge, USGS 15437 (near base of formation), Oil Creek, USGS 17850 (in lower 100 ft of formation), the north end of Duktoth Mountain, USGS 17782 (in lower 200 ft of formation), Sunshine Point near mouth of Kulthieth River, USGS 17827 (about 1,000 ft above base of formation), the south flank of Kulthieth Mountain, USGS 17835 (about 3,000 ft above base of formation), and the west end of Yakataga Ridge, USGS 15431 (about 3,200 ft above base of formation).

The species is known from beds on Kodiak Island where it is associated with *Mytilus middendorffi* Grewingk, USGS 13372; these beds are also referred to the middle Miocene. Specimens from the lower part of an unnamed formation (370 ft above the base) on Cenotaph Island, Lituya Bay, USGS D169 (T) also appear to be this species; their spoon is unknown. The lower part of the unnamed formation is referred to the middle Miocene.

The identity of specimens in the late Miocene and Pliocene beds of Alaska is more problematical. No spoons have been seen on any specimens within this stratigraphic and biologic sequence,

but judging from the exterior of the known specimens, most of which are crushed or distorted, there seems to be an even gradation between *Mya cuneiformis* and *M. priapus*. These are assigned tentatively to *M. priapus*.

***Mya (Mya) pseudoarenaria* Schlesch**

Plate 7, figures 9–11, 13, 14; plate 9, figure ?4

- ?*Mya arenaria* Möller, Naturhist. Tidsskrift, ser. 1, v. 4, no. 1, p. 21, 1842.
 Middendorff, Malacozoologia Rossica; Acad. Sci. St. Petersburg Mem., ser. 6, v. 6, p. 586, 1849 [in part].
- ?*Mya truncata* Loven [in Heer], Kongl. Svenska Vetenskapsakad. Handl., v. 8, no. 7, p. 92, 1870.
- Mya arenaria* Leche, Kongl. Svenska Vetenskapsakad. Handl., v. 16, no. 2, p. 4, 1878.
- ?*Mya intermedia* Dall, Wagner Free Inst. Sci. Trans., v. 3, pt. 4, p. 857, 1898 [in part].
- Mya truncata* forma ovata Jensen, Videnskabelige Meddelelser naturhist. Forening, Copenhagen, p. 139, figs. 3, 4, p. 140, fig. 4, p. 141, fig. 6, p. 142, 1900 [not Donovan, 1802].
- Mya truncata ovata* Schlesch, Archiv f. Molluskenkunde Abh., v. 1, no. 3, p. 323, pl. 6, fig. 1, 1924.
- Mya intermedia* Dall [in O'Neill], Rept. Canadian Arctic Expedition 1913–18, v. 11, pt. A, p. 31, 32, 1924.
- Mya pseudoarenaria* Schlesch, Archiv f. Molluskenkunde, v. 63, p. 136, pl. 13, figs. 10–12, 1931.
- Mya truncata* forma ovata Laursen, Meddelelser om Grønland, v. 135, no. 8, p. 62, 1944.
- Mya pseudoarenaria* Foster, Johnsonia, v. 2, no. 20, p. 34, 1946.
- Mya truncata* forma ovata Madsen, Marine bivalvia; Zool. Iceland, v. 4, pt. 63, p. 76, 1949.
- Mya pseudoarenaria* Feyling-Hanssen and Jorstad, Norsk Polar-institutt Skrifter, no. 94, p. 74, 1950.
 Soot-Ryen, Astarte; Trømso Mus., no. 1, p. 3, 1951.
- Mya* cf. *M. arenaria* MacNeil, U.S. Geol. Survey Prof. Paper 294-C, p. 118, pl. 17, fig. 6, 1957.
- Mya pseudoarenaria* MacGinitie, U.S. Natl. Mus. Proc., v. 109, no. 3412, p. 186, pl. 19, fig. 7, pl. 25, fig. 4, 1959.
- Mya japonica* Fujie, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 11, no. 3, p. 401, 1962 [in part].
- Mya truncata ovata* Merklin, Petrov, and Amitrov, Atlas-Guide of mollusks of Quaternary deposits of the Chukotsk Peninsula; Commission for Study of the Quaternary Period, Acad. of Sci., U.S.S.R., p. 48, pl. 10, figs. 5–8, 1962.

Unless Dall had some suspicion of it in 1898, Jensen seems to have been the first to realize the existence of an Arctic species distinct from both *Mya truncata* and *M. arenaria*. Jensen's delimitation of the species was accurate by modern standards, and except for the addition of new records no revision is necessary.

The spoon of this species is subtriangular. The ventral margin of the spoon between the anterior and posterior ridges is weakly convex anteriorly and weakly concave posteriorly. In this respect it is more like *Mya cuneiformis* and *M. truncata*; the ventral margin of the spoon in *M. priapus* is more convex. The deepest part of the ligament area is along the anterior part of the fibrum receptacle adjacent to the anterior ridge. The

laminum attachment is convex. The anterior ridge is moderately thick ventrally and may be turned back rather strongly over the fibrum receptacle as in *M. arenaria*. The dorsal part of the anterior ridge is broad. The posterior ridge forms the most projecting part of the ventral margin of the spoon. The posterior furrow is moderately broad and it is extended posteriorly as a long wing. The wing may be nearly twice as long as the remainder of the spoon; in such shells it projects from the dorsal margin like a long lateral tooth.

The shell has a well-defined anterior subumbonal groove. None of the specimens I have examined show any evidence of subumbonal solution. Some specimens appear also to have a small very thin ligamental callus at the dorsal end of the ligament pit. The anterior leg parallels the subumbonal groove.

The pallial sinus is moderately large. Its anterior end is rounded and curves backwards slightly to the point where it joins the pallial line; the lower limb of the sinus and the pallial line are confluent. The pallial line is thicker where it adjoins the sinus. The anterior extension of the pallial line is often very wavy.

The anterior muscle scar is moderately narrow and elongate, its ventral end lying about opposite the mid-point of the sinus. The anterior part of the shell is high and inflated, and it narrows posteriorly; the posterior end is moderately acuminate. The exterior of the shell at the posterior extremity is often very wrinkled. The beaks are strongly opisthogyrate.

Mya pseudoarenaria is closely related to *M. cuneiformis* from which it probably is descended directly. Its spoon resembles the spoon of *M. truncata*. In my opinion, *M. cuneiformis* and *M. truncata* are coderivatives from *M. salmonensis*.

The most conspicuous difference in the spoon of *Mya cuneiformis* and *M. pseudoarenaria* is in the strike of the anterior leg and subumbonal groove. In *M. cuneiformis* the area bounded by the leg and the groove is triangular, and the leg is vertical; the posterior edge of the leg actually overhangs the dorsal extremity of the fibrum receptacle. In *M. pseudoarenaria* the leg and groove are more nearly parallel, and they are more inclined towards the anterior.

Holotype: Inasmuch as *Mya pseudoarenaria* is a substitute name for *M. truncata* var. *ovata* Jensen, one of Jensen's specimens must be recognized as the lectotype of the species. The specimen figured by Jensen (1899, p. 139, fig. 3) appears, from its dimensions, to be one of the Pleistocene fossils listed from western Greenland on his page 142. Presumably all of Jensen's specimens are in the Universitetets Zoologiske Museum, Copenhagen, Denmark. Of these, specimen *d* is closest in size to his figure, which he says is not enlarged. It measures 66 mm in length, 45

mm in height; convexity is 27 mm. His largest specimen has a length of 78 mm.

Occurrence: I know of no unequivocal record of this species in late Tertiary beds of the Pacific Ocean area, although I have no doubt of its descent from *Mya cuneiformis* of the middle Miocene. The earliest specimen known to me that could possibly belong to this species is one from the Coralline Crag (late Pliocene) of England; this specimen is on exhibit in the Ipswich Museum.

I believe also that a specimen I collected from the Chillesford Beds of the Icenian Crag (early Pleistocene) of England, USGS M-1671, belongs to this species. *Mya pullus* Sowerby from the Butleyan Stage of the Red Crag may also prove to be a diminutive form of *M. pseudoarenaria*, but, on the basis of two specimens I collected, I am inclined to doubt it. The species is known in Iceland in beds that may be of early Pleistocene age. It is known in beds of probable late Pleistocene age in the Chukotsk Peninsula, eastern Siberia, Point Barrow, Alaska, USGS 15937, and at Gostinoj on the Yenisey River in northern Russia. It also occurs in Pleistocene beds in Spitzbergen and western Greenland.

The species is known from the Recent of Point Barrow, Alaska, CAS 35052, the Arctic Coast of Canada as far east as Dolphin and Union Strait, western Greenland (but not eastern Greenland), USGS D-385, Iceland, Spitzbergen, northern Norway as far south as 67°8' N. and probably along the Arctic Coast as far east as the Taymir Peninsula. I can find no record of this species in present Bering Sea or elsewhere in the Pacific Ocean area; reports to the contrary are incorrect as nearly as I can determine.

Mya (Mya) truncata Linné

Plate 8, figures 1-12; plate 9, figures 1-3, 5-20

- Mya truncata* Linné, *Systema naturae*, ed. 10, p. 670, 1758.
Lamarck, *Système des animaux sans vertèbres*, p. 127, 1801.
- Mya ovalis* Turton, *Shells of the British Islands*, p. 33, pl. 3, figs. 1, 2, 1822.
- Sphenia swainsoni* Turton, *Shells of the British Islands*, p. 37, pl. 19, fig. 2, 1822.
- Mya truncata* Lyell, *Geol. Soc. London Trans.*, ser. 2, v. 6, art. 8, p. 137, pl. 17, figs. 5, 6, 1842 [Pleistocene of Quebec].
- Mya truncata* var. *uddevalensis* Forbes, *Geol. Survey Great Britain Mem.*, v. 1, p. 407, 1846.
- Mya truncata* Middendorff, *Malacozoologia Rossica*; *Acad. Sci. St. Petersburg Mem.*, ser. 6, v. 6, p. 585, pl. 19, figs. 13-15, 1849.
- Mya praecisa* Gould, *Boston Soc. Nat. History Proc.*, v. 3, p. 215, 1850.
- Mya truncata* Middendorff, *Reise in dem Ausersten Norden und Osten Sibiriens*; *K. Akad. Wiss.*, v. 2, pt. 1 (Mollusken), St. Petersburg, p. 266, pl. 25, figs. 11-14, 1851.
Wood, *Palaeontographical Soc. London Mon.*, v. 9, p. 277, pl. 28, figs. 1a-c, 1857.
- Mya truncata* var. *abbreviata* Jeffreys, *British Conchology*, v. 3, p. 67, 1865.
- Mya truncata* Wood, *Palaeontographical Soc. London Mon.*, v. 27, p. 163, 1874.
Sars, *Mollusca Regionis Arcticae Norvegiae*; *Universitetsprogram*, Christiania, p. 92, 1878.
Dall, *Wagner Free Inst. Sci. Trans.*, v. 3, pt. 4, p. 857, 1898.

- Jensen, *Videnskabelige Meddeleser naturhist. Forening*, Copenhagen, p. 147, 1900 [with extended synonymy].
- Brøgger, *Norges geol. Undersøkelse Skrifter*, no. 31, pl. 7, figs. 9a-b, 10, 12, 1901.
- Arnold, *U.S. Natl. Mus. Proc.*, v. 32, no. 1545, pl. 50, fig. 1, 1907.
- Dall, *U.S. Geol. Survey Prof. Paper* 59, p. 132, 1909.
- Oldroyd, *Stanford Univ. Pubs. Geol. Sci.*, v. 1, no. 1, p. 197, pl. 10, fig. 4, 1924.
- Grant and Gale, *San Diego Soc. Nat. History Mem.*, v. 1, p. 414, 1931 [with extended synonymy].
- Nagao and Inoue, *Hokkaido Imp. Univ. Fac. Sci. Jour.*, v. 6, no. 273, p. 155, pl. 33, figs. 5, 9, 10, 1941.
- Mya* sp. indet., MacNeil, *Jour. Paleontology*, v. 17, no. 1, p. 93, pl. 16, fig. 3, 1943.
- Mya truncata* Foster, *Johnsonia*, v. 2, no. 20, p. 30, pls. 17-19, 1946.
- Fujie, *Hokkaido Univ. Fac. Sci. Jour.*, ser. 4, v. 9, no. 4, p. 399, pl. 3, figs. 1-4, 1957.
- MacGinitie, *U.S. Natl. Mus. Proc.*, v. 109, no. 3412, p. 184, pl. 25, figs. 1-3, 1959.
- Fujie, *Hokkaido Univ. Fac. Sci. Jour.*, ser. 4, v. 11, no. 3, p. 410, 1962.
- Mya truncata truncata* Merklin, Petrov, and Amitrov, *Atlas-Guide of mollusks of Quaternary deposits of the Chukotsk Peninsula*; *Commission for Study of the Quaternary Period*, *Acad. of Sci., U.S.S.R.*, p. 47, pl. 10, fig. 3, 1962.
- Mya truncata uddevalensis* Merklin, Petrov, and Amitrov, *ibid.*, fig. 4.
- Mya truncata* is the most widespread living species of *Mya*. It is also the most variable species. It ranges in shape from specimens that have a moderately elongate tapering but truncated posterior end (pl. 8, fig. 11), to elongate and subrectangular, to very short and high with the posterior end less than a quarter the total length of the shell and the posterior margin long and nearly vertical, often concave. The latter variant was named *M. truncata* var. *uddevalensis* by Forbes. None of the variant types can be considered a geographical subspecies. Both the elongate varieties and the *uddevalensis* variety occur together in all areas where the species now lives, from the North Sea to the Gulf of Alaska. The same apparent varieties are found in the Yakataga Formation (Miocene and Pliocene) of Alaska, in very late Pleistocene (probably postglacial) beds near Juneau, Alaska, along the Gulf of St. Lawrence, eastern Canada, and at Uddevalla, Sweden, the locality from which the variety takes its name.
- The shell of *Mya truncata* is rugose and very often it is malformed, apparently by objects in the substratum. Even the spoon takes on forms that might better be described as abnormalities rather than variations.
- The spoon is more symmetrical than in *Mya pseudoarenaria*; the dorsal part of the anterior ridge is broader and the posterior furrow is not as alate. The ventral margin of the spoon is not as rounded as in *M. priapus*. The anterior subumbonal groove and the anterior leg

form a lower angle with the dorsal margin than in *M. pseudoarenaria*; that is, they are more nearly parallel with the dorsal margin. *M. pseudoarenaria* stands about midway between *M. cuneiformis* and *M. truncata* in this respect; in *M. cuneiformis* the anterior leg is nearly perpendicular to the dorsal margin. The boundary between the laminum attachment and the fibrum receptacle often stands up as a thin ridge in *M. truncata*, whereas in *M. pseudoarenaria* there is a broader convex area that includes the laminum attachment and the posterior part of the fibrum receptacle.

Mya truncata has the shortest pallial sinus of any *Mya*. It extends from the posterior muscle scar to the pallial line. The inner margin is nonlobate, the point of maximum depth being the juncture with the pallial line. In the more elongate variants the dorsal leg is moderately curved, but in the short *uddevalensis* variety it may be a much straighter line, inclined only a few degrees from vertical.

The anterior subumbonal groove in *Mya salmonensis* has a strike intermediate between that of the other two species; in *M. cuneiformis* it is more vertical, in *M. truncata* it is more horizontal.

M. truncata appears for the first time in Alaska in beds only a few hundred feet above the earliest occurrence of *M. cuneiformis* and yet is clearly distinct from the latter. It seems probable, therefore, that these two species are coterminous from *M. salmonensis*. Its abrupt appearance in Alaska suggests that it originated in East Asia, probably from the representative there of *M. salmonensis* that has been known as *M. grewingki* var. *elongata* Nagao and Inoue (= *M. grewingki nagaoi* Oyama and Mizuno).

Holotype: According to Dodge (1952, p. 28), there is a specimen in a properly marked box in the collection of the Linnaean Society of London.

Occurrence: The earliest recorded occurrences of this species are in beds of early middle Miocene age in the Pacific Ocean area. Inasmuch as its probable ancestor is the Oligocene to Miocene species *Mya salmonensis*, it is not likely that this range will be extended downwards. It occurs in the Takinoue (Chikubetsu?) Formation of the Kawabata Series of Hokkaido and in the lower part of the Yakataga Formation (about 700 ft above the base), Alaska.

Mya truncata is known from so many localities and stratigraphic levels in the northern Pacific that it would be pointless to list them; it is sufficient to say that it has existed continuously in the far northern Pacific from early middle Miocene to Recent time.

Its southernmost records are of interest, however, inasmuch as it is a cold-water species. (See p. G4.) It occurs in the Coos Conglomerate (early Pliocene) at Coos Bay, Oreg., and in the Towsley Formation (late Miocene and early Pliocene) at Elsmere Canyon in the Ventura Basin, Los Angeles County, Calif. It occurs also in the Timms Point Silt Member of the San Pedro

Formation (early Pleistocene) of the Palos Verde Hills, Los Angeles, and in the upper part of the Pico Formation, Ventura County, Calif. The upper part of the Pico Formation may be of early Pleistocene age.

The species now ranges southward to southern Hokkaido and Puget Sound. Known recorded occurrences in Japan indicate that it did not extend its range southward nearly as much on the Asiatic side of the Pacific as it did on the American side. Fujie gave one Miocene and two Pliocene occurrences in northern Honshu. There are no known Pleistocene occurrences south of Hokkaido.

Mya truncata is known as a fossil in eastern North America from Hudson Bay and Labrador south to Nantucket Island, Mass. According to Richards (1962, p. 12), all recorded occurrences north of Nantucket are in beds deposited by the sea that invaded areas vacated by melting Wisconsin ice, preceding post-glacial emergence. They are, thus, of post-Wisconsin age. The beds at Sankaty Head, Nantucket, he regarded as being of Sangamon age. Hyypä (1955) concluded, on the other hand, that the Sankaty beds are of middle-Wisconsin age. At any rate, *M. truncata* is known on the Atlantic Coast only in very young beds.

The species is known as a fossil in both Greenland and Iceland in beds that may also be very young. Probably the species in beds of early Pleistocene age in Iceland is *Mya pseudoarenaria*. *M. truncata* certainly was in Europe prior to its first appearance in North America and probably it reached America from the region of extreme northern Europe or Spitzbergen. Shells of the species are strewn over the floor of the North Atlantic Ocean between Greenland, Iceland, and Jan Mayen (Soot-Ryen, 1932, p. 29) at a depth of 1,300 fathoms, far deeper than its living depth. Possibly there was an isostatic rise in the North Atlantic Ocean in response to the depression of continental areas by Wisconsin ice, which, together with eustatic lowering of sea level, made the North Atlantic sufficiently shallow to allow *M. truncata* to migrate westward in Wisconsin time.

I have been unable to verify the occurrence of this species in the Coralline Crag (late Pliocene) of England. A specimen figured by Wood (1856, pl. 29, fig. 1) from supposed Coralline Crag beds at Ramsholt was refigured by Chatwin (1961, fig. 24, no. 13) as a Norwich Stage (late early Pleistocene) fossil. The Ipswich Museum has a specimen on display that I thought, when I examined it in 1960, was more probably *Mya pseudoarenaria*. Wood (1856, p. 278) stated that specimens from the Coralline Crag "are all of the longer variety." No very recent lists of fossils from the Coralline Crag have included *M. truncata*. Probably this point can be clarified by British workers.

If *Mya pullus* Sowerby from the Butleyan Stage of the Red Crag (early Pleistocene) is a diminutive form of this species, it may be its earliest occurrence in Europe. *M. pullus* may be conspecific, however, with *M. pseudoarenaria*, or it may be closer to *M. priapus*. I am equally uncertain of the identity of a juvenile specimen I collected at Chillesford; *M. truncata* has been reported from there as well.

Mya truncata is found unquestionably in the Norwich Stage of the Icenian Crag, and this may be its earliest European occurrence. The Norwich Stage is believed currently to be of late Calabrian age, corresponding approximately to the only known occurrence of *M. truncata* in the Mediterranean region; it is found in the upper part of the Calabrian Stage in Sicily, Calabria, and Tuscany.

Mya truncata probably lived in northern European waters throughout Pleistocene time. It has been reported from beds of middle Pleistocene age in the Taymir Peninsula, although I am not certain that the distinction between *M. truncata* and *M. pseudoarenaria* was clear at the time the identification was made.

The species is nearly circumarctic at the present time. Soot-Ryen (1932, p. 21) did not believe that it occurs in the East Siberian Sea. This would suggest, if true, that the species has not made a full counterclockwise migration of the Arctic Ocean. It ranges southward to Hokkaido and Puget Sound in the Pacific and to Cape Cod and the Bay of Biscay in the Atlantic.

***Mya (Mya) priapus* Tilesius**

Plate 10, figures 1-7; plate 11, figures 1-8, 10, 13-15

- Mya priapus* (Steller MSS) Tilesius, Acad. Sci. St. Petersburg Mem., v. 8, p. 295, pl. 9, fig. 1, 1822.
- Mya arenaria* Middendorff, Reise in dem Aussersten Norden und Osten Sibiriens; K. Akad. Wiss., v. 2, pt. 1 (Mollusken), St. Petersburg, p. 269, no. 2, pl. 24, fig. 12, 1851.
- ?*Mya* near *arenaria* Dall in Mertie, U.S. Geol. Survey Bull. 335, p. 46, 1908.
- Mya (Mya) arenaria* variety *japonica* Jay, Grant and Gale, San Diego Soc. Nat. History Mem., v. 1, p. 412, 1931 [in part].
- Mya japonica* Makiyama, Kyoto Imp. Univ. Coll. Sci. Mem., ser. B, v. 10, no. 2, art. 6, p. 159, 1934.
- Mya arenaria japonica* Kinoshita and Isahaya, Report of Aquatic Products; Hokkaido Fish Exp. Sta., no. 33, rept. 1, pl. 14, fig. 103, 1934.
- Mya japonica* Makiyama, Warera-no-Kobutsu, v. 4, no. 3, p. 37, text fig. j, 1935.
- Mya truncata* Stejneger, Georg Wilhelm Steller; Harvard Univ. Press, p. 397, pl. 24, fig. 1, 1936 [reproduction of Tilesius' plate labelled "*Mya priapus*"].
- Mya uzenensis* Nomura and Zinbo, Saito Ho-on Kai Mus. Res. Bull., v. 13, p. 167, pl. 22, fig. 17, 1937.
- Mya arenaria* var. *truncata* Slodkewitsch, Pal. U.S.S.R. (Tertiary Pelecypoda from the Far East), Acad. of Sci., U.S.S.R., v. 10, pt. 3, fasc. 19, pl. 103, fig. 4, 1938.
- Mya arenaria* Nagao and Inoue, Hokkaido Imp. Univ. Fac. Sci. Jour., v. 6, no. 273, p. 145, pl. 32, figs. 14, 14a, 1941. (On p. 147 name changes recommended by Makiyama are discussed.)
- Minato, Matsui, and Uozumi, Shinseidai-no-Kenkyu, no. 7, p. 3, pl. 10, fig. 82, 1950.
- Mya (Arenomya) japonica*, Habe, Akkeshi Marine Biol. Sta. Publ., no. 4, p. 22, pl. 7, fig. 12, 1955.
- Mya japonica* Fujie, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 9, no. 4, p. 406, pl. 1, figs. 1-5, 1957.
- Mya (Arenomya) japonica* Yamamoto and Habe, Marine Biol. Sta. Asamushi Bull.; Tohoku Univ., v. 9, no. 3, p. 113, pl. 12, fig. 24, 1959.
- Mya japonica* Fujie, Hokkaido Univ. Fac. Sci. Jour., ser. 4, v. 11, no. 3, p. 401, 1962.
- Mya arenaria* Merklin, Petrov, and Amitrov, Atlas-Guide of mollusks of Quaternary deposits of the Chukotsk Peninsula; Commission for Study of the Quaternary Period, Acad. Sci., U.S.S.R., p. 46, pl. 9, figs. 1-9, 1962.

In 1743, after Steller had returned to Kamchatka with the survivors of Bering's second and fateful voy-

age, he visited the northern Kuril Islands, and on the trip he spent some time at Bolsheretsk in southwestern Kamchatka. There he found a giant and wholly unfamiliar clam washed up on the beach at the mouth of the Bolshaya River. Among the things that Steller managed to have forwarded to St. Petersburg were some notes and a sketch of the animal and the shell made by an artist named Berkhan who accompanied him. The way in which this species eventually became published and named is given by Stejneger (1936, p. 396):

There was little interest in St. Petersburg at the time in the fauna of the sea. The new school of zoologists headed by Pallas were primarily interested in the land vertebrates. Pallas, however, intended his *Zoographica Rosso-Asiatica* to include the invertebrates, and when he left Russia in 1810 for Berlin he took with him Steller's notes and the illustrations which Berkhan had made of the specimens described. One of these was rescued and published by Tilesius under the name *Mya priapus*. The accompanying illustration is the only one attributed directly to Berkhan by name (whom Tilesius calls a "dexterimus pictor") and as it is so little known that it has been missed even by the authoritative Sherborn in his *Index Animalium*, it is here reproduced. Steller, who picked it up on the beach at the mouth of the Bolshaya, was so impressed by the startling appearance of this giant soft clam, of which the shell alone measured 4 inches, that he at once wrote a detailed description of it in latin which covers two and one-half quarto printed pages. Middendorff has since identified it with Linnaeus' *Mya truncata*, a name given to the European clam fifteen years after Steller found the species in the Okhotsk Sea.

Middendorff cited the species as "*Mya priapus vel Mentula marina Stelleri*," a nonbinomial expression, and possibly this treatment discouraged an investigation of the name by subsequent authors. However, Tilesius' plate is labeled simply "*Mya priapus*" which, for that date, constitutes a valid proposal.

The shell as depicted by Steller's artist, Berkhan, appears to be so crudely drawn that it could not possibly be identified. In my opinion, however, this is the common *Mya* of northern and western Bering Sea. Many individuals of the species are equally crude and misshapen. A large suite from St. Lawrence Island in northern Bering Sea in the collections of the Geological Survey contains several specimens that could well be the one drawn by Berkhan. Even granting that Berkhan's drawing of the shell cannot be identified with certainty, the large fleshy animal should be recognizable. I have little doubt that future attempts to identify it will show *M. priapus* to be the species here determined. The tough wrinkled siphonal tube is more like that of *M. truncata*, but it is shorter and thicker than in that species. The shell characters also indicate a close relationship to *M. truncata*.

Middendorff did not associate the name *Mya priapus* with this species. In 1849 (p. 585) he placed the species by name in the synonymy of *M. truncata*, but subsequently (1851, pl. 24, fig. 12) he figured a shell of the species as *M. arenaria*. Grant and Gale, and recent Japanese authors who follow them, interpreted this northern species as the *M. japonica* of Jay; the species ranges southward to Hokkaido.

Most Russian authors combine *Mya priapus*, *M. pseudoarenaria*, and probably *M. japonica* under "*M. arenaria*," apparently in the sense that Middendorff used the latter. Merklin, Petrov, and Amitrov (1962, pl. 9, figs. 1-9) illustrated several specimens from Pleistocene beds of the Chukotsk Peninsula as *M. arenaria*. The three spoons they figured are triangular, there is a well-defined anterior subumbonal groove, and there is no indication of subumbonal solution. None of these spoons could belong to a specimen of *M. arenaria*. Without illustrations of the spoon and pallial sinus of the rest of their specimens, it would be difficult to reidentify them with confidence. However, the specimens figured probably are all *M. priapus*. Their figure 7 is the youngest specimen figured. The specimen shown in their figure 1 is from beds they regard as pre-Riss, and it is the oldest specimen figured. The specimen shown in their figure 8 is very similar to a specimen from the Matsuzawa Formation (Miocene or Pliocene) of Honshu described by Nomura and Zinbo (1937, p. 167, pl. 22, fig. 17) as *M. ezenensis*. In my opinion both of these belong to *M. priapus*. The spoon of *M. ezenensis* is unknown.

The spoon of *Mya priapus* from different geographical areas shows some variation in shape. Northern Japanese specimens (Fujie, 1957, pl. 1, fig. 5b) have a spoon with a much straighter ventral margin than specimens from Bering Sea or Alaska. If the spoon of *M. ezenensis* is found to be similarly truncated, this name might be available as a subspecific name for the modern Japanese form.

Specimens from Bering Sea have a spoon with a well-rounded ventral margin. The entire ligamental area is deeply concave, although in some specimens there is a slight shallowing along the laminum attachment. The anterior ridge is thick, and it is very broad dorsally. The posterior furrow is broad, shallow, and produced posteriorly to form a winglike shelf. There is a well-defined anterior subumbonal groove set at a very low angle with respect to the dorsal margin.

Mya priapus has a moderately large ligamental callus. The callus is restricted to about the dorsal third of the fibrum receptacle, and generally it occupies only the anterior dorsal part. In some specimens the ventral

margin of the callus is toothed or comblike. The callus layer continues across the dorsal part of the anterior ridge and merges with the last deposited layer of the interior of the shell. The ligamental callus is almost always present in this species, and it is generally larger and thicker than the callus of *M. truncata*. The callus is not present in all specimens of *M. truncata*. A few specimens of *M. pseudoarenaria* have a very small callus at the dorsal end of the ligament pit. The callus of *M. priapus* is of moderate length, and it ranges from thin and smooth to thick and rough; the callus of *M. arenaria* is long and spatulate, often reaching nearly to the ventral margin of the spoon, and it generally has a pronounced radial ridge or swelling near its posterior margin.

The pallial sinus of *M. priapus* is of moderate depth. The dorsal leg descends to the pallial line in a gradually steepening curve; at the juncture the two are nearly perpendicular. The ventral leg is confluent with the pallial line. The anterior part of the pallial line may be wavy.

The anterior adductor scar is elongate and wider ventrally; it is less elongate and wider than in *M. truncata*.

The shell of *M. priapus* is quite variable in shape. It ranges from suboval to more attenuated posteriorly, and the part of the shell posterior to the beaks may be either longer or shorter than the anterior part. The exterior surface is often deeply pitted and irregular, probably indicating that it can live in an unsorted gravelly substratum.

Without any question, *Mya truncata* is the closest living relative of *M. priapus*. *M. truncata*, however, is known from older beds, and I am inclined to believe that *M. priapus* actually is descended from *M. cuneiformis*. The spoon of *M. cuneiformis* has a very pronounced shallowing or convexity of the posterior part of the ligament area, and in this respect it is more like *M. pseudoarenaria*; the ligament area of the spoon of *M. priapus* is more uniformly deep and concave. If *M. cuneiformis* and *M. priapus* are in linear succession, the modification in the spoon must have taken place during late Miocene time, and in forms whose spoon is unknown.

Mya priapus is unique in having a single sometimes moderately large solution pit at the top of the chondrophore of the right valve. There is no solution of the left valve as is common in the *M. arenaria* group. This species has its anterior subumbonal groove set at a lower angle than in other members of the *M. truncata* group, a condition that may weaken the strong intervalve periostracum-elasticum connection found ordinarily in

this group. The species also has a very deep ligament pit. Probably the fibrum element of the ligament is more apt to be torn away from a deep receptacle and in turn to be reinforced from behind by a deposit of ligamental callus. At any rate, a combination of greater fibrum severance and a weaker periostracum-elasticum connection probably contribute to a periostracum-elasticum rupture. This exposes a small area of the shell along the hinge to solution by sea water. Although the structural weaknesses responsible for a periostracum-elasticum rupture are similar in this species and in *M. arenaria*, the morphological differences provide for a slightly different vector of strain, causing the periostracum-elasticum rupture to take place along the margin of the right valve rather than the left valve.

Holotype: The historical evidence as given by Stejneger indicates that the specimen Steller found was not sent to St. Petersburg. Tilesius based the species on Steller's notes and on a drawing made under his direction. Although Tilesius' plate is the original indication of the species, it is not an identifiable illustration of the shell. The species, however, should be identifiable from the soft parts without difficulty. Until recently the only good illustration of the shell of this species was one given by Middendorff (1851, pl. 24, fig. 12) as *M. arenaria*.

Occurrence: Fujie (1962, p. 404) reported this species (as *M. japonica*) from the Tōgēsita Formation (late Miocene) of Hokkaido, the Kamiiso and Ikeda Formations (Pliocene) of Hokkaido, and the Matsuzawa and Tatsunokuchi Formations (Pliocene) of northern Honshu. He gave only one Pleistocene occurrence; an unnamed formation in southern Sakhalin.

The species probably occurs in late Miocene beds of eastern Russia, but available figures are difficult to determine. It certainly occurs in the Kavran Series (Pliocene?) of western Kamchatka (Slodkewitsch, 1938, pl. 103, fig. 2) where it has been identified as *Mya arenaria* var. *japonica*.

Merklin, Petrov, and Amitrov (1962, pl. 9, figs. 1-9) figured the species from middle and late Pleistocene beds of the Chokotsk Peninsula. The species was collected in 1963 from beds of the same approximate age span between the Kukpowruk and Kuk Rivers, Alaska.

The upper part of an unnamed formation in the Lituya district, Alaska, contains a form that appears to be intermediate between *Mya cuneiformis* and typical *M. priapus*. The part of the formation containing them is believed to be of very late Miocene or early Pliocene age. Specimens from the following localities are referred tentatively to *M. priapus*: cliff at east margin of Fairweather Glacier, USGS D-264, D-389, southwest shore of Cenotaph Island, USGS D-174, seacliff about 0.55 mile north of mouth of Topsy Creek, USGS D-180. The last locality is the southeasternmost record of any age for the species known to me.

The species occurs in a marine clay till of probable Pleistocene age at the southeast point of Wingham Island, Controller Bay, Alaska, USGS 4309 (Dall, in Martin, 1908, p. 46; as *Mya* near *arenaria*).

Mya priapus is living from southern Hokkaido to northern Bering Sea; it is one of the most abundant species in a large

collection of Recent shells from St. Lawrence Island, USGS M-1661, M-1663. It occurs in Alaska from near Port Clarence, USGS M-1430, southward to Unalaska, USGS D-53, and eastward to Kachemak Bay, USGS M-1625, an arm of Cook Inlet; I have not seen the species east of Homer Spit. The species occurs in postglacial beds, possibly a midden, at the mouth of Cottonwood Creek on the north side of Kachemak Bay, Alaska, USGS 5871.

***Mya (Mya) pullus* Sowerby**

Plate 11, figures 9, 11, 12

Mya pullus Sowerby, Mineral Conchology Great Britain, v. 6, p. 58, pl. 531, figs. 6-8 (2), 1826.

Mya arenaria Forbes and Hanley, History of British Mollusca, v. 1, p. 172, 1848 [in part].

Mya truncata Wood, Palaeontographical Soc. London Mon., v. 9, p. 278, pl. 28, figs. 1d, e, ?1f, 1857 [in part].

Wood, Palaeontographical Soc. London Mon., v. 27, p. 163, 1874 [in part].

?*Mya arenaria* Schlessch, Archiv f. Molluskenkunde, v. 63, p. 139, 1931 [in part].

Mya truncata Foster, Johnsonia, v. 2, no. 20, p. 30, 1946 [in part].

This small *Mya* is abundant in the Butleyan Stage of the Red Crag. It has been known to collectors for years, but most authors have regarded it either as the young of another species or an abnormality.

It has been suggested by some workers that *Mya pullus* is a cold-water dwarf and by others that it is a brackish-water dwarf. As such it has been placed in the synonymy of both *M. arenaria* and *M. truncata*. Its spoon and pallial sinus show that it definitely is not *M. arenaria*. If it is a dwarf, it is a dwarf of some member of the *M. truncata* group. It is difficult, however, to see how it could be a cold-water dwarf of a species that lives normally in very cold water.

I collected two valves of this form in 1960 when I visited East Anglia. I am not convinced that it is a diminutive form of *M. truncata*, but for the time being I would prefer to leave the question open. It is entirely possible that this is a diminutive form of *M. priapus*. It resembles juveniles of that species very closely, particularly the variant found in northern Japan. (See Fujie, 1957, pl. 1, fig. 2.) The right valve I collected has a tiny solution pit at the top of the chondrophore, a very common condition in *M. priapus* and one that, as far as I know, is peculiar to it. The form from the Butleyan Stage also has some resemblance to juveniles of *M. pseudoarenaria*.

Whatever the synonymy of *Mya pullus*, it is of significance in one way or another. If it is *M. truncata*, it is the earliest European recorded occurrence for the species, unless, of course, the species really occurs in the Coralline Crag. If it is *M. priapus*, it is the only

known occurrence of the species outside the Pacific Ocean-Chukchi Sea area. If it is *M. pseudoarenaria*, it takes priority in name. Pending a thorough study of this form, it would be unwise, therefore, to make any decision concerning it.

Holotype: In the British Museum?

Occurrence: Butleyan Stage of the Red Crag (early Pleistocene), England.

LOCALITIES

U.S. National Museum catalog numbers :

USNM 210970. Recent Kodiak Island, Alaska.

USNM 221269. Recent, Chignik Bay, south side of Alaskan Peninsula.

California Academy of Sciences locality :

CAS 35052. Recent marine shells from Deadman Island, Point Barrow, Alaska. G. D. Hanna, collector.

University of California (Berkeley) localities :

UC 197. On same horizon and about one-quarter of a mile to the northwest of loc. 189 (UC 189 very close to base of Miocene [locally] on south side of Muir Station syncline, about 1½ miles and 70° to southwest of town of Pacheco), Contra Costa County, Calif. Briones Sandstone (early late Miocene). J. C. Merriam, collector.

UC 1224. Near south edge of NE¼NE¼ sec. 2, T. 2 S., R. 2 W., about half a mile south of bend in Alameda-Contra Costa County line, Alameda County, Calif. Cierbo Sandstone (middle late Miocene). B. L. Clark, collector.

UC 1227. On top of knob about one-quarter of a mile southeast of Burton's (ranch) above loc. 1221 in altitude and stratigraphically (UC 1221 about 1½ miles north of Los Tramos Creek and about ½ mile a little to the west of south from Tice Valley on the side of Grizzly Creek), Contra Costa County, Calif. Cierbo Sandstone (middle late Miocene). B. L. Clark, collector.

UC 1617. About one-quarter of a mile east of town of Rodeo (as seen on Napa topographic sheet, 1902 edition, it is due west of the top of the letter R of Rodeo), about 150 ft below base of Pinole Tuff, Contra Costa County, Calif. Neroly Formation (late late Miocene). B. L. Clark, collector.

UC 1687. To north of road leading to Tice Valley, just west of Franklin fault and about 1.7 miles west of south from Walnut Creek (as seen on Concord quadrangle (areal geology), U.S. Geol. Survey Geol. Atlas Folio 193). Briones Sandstone (early late Miocene). R. E. Dickerson, collector.

UC 3851. Float, probably Poul Greek Formation. Not plotted on field map; location of Salmon Creek not known (fide D. J. Miller). Yakataga district, Alaska. N. L. Taliaferro, collector.

UC A-1686. 50-60 ft stratigraphically below A-1685 (UC A-1685 1 mile south of P. G. and E. compressor plant), Kettleman hills, Kings County, Calif. Etchegoin Formation (Pliocene). A. R. Hall, collector.

UC A-3167. "*Mya japonica*" zone, about 200 ft below base of Tulare Formation, NE¼ sec. 35, T. 21 S., R. 17 E., Kings County, Calif. San Joaquin Formation (late Pliocene). B. L. Clark field class, collectors.

UC B-4807. On beach, 7,000 ft north of Merced-Franciscan Formation contact at Mussel Rock; 850 ft due west of triangulation point just west of Edgemar Road; in cliff face at beach level, in massive grayish-blue medium- to fine-grained sandstone. William Glen, collector.

U.S. Geological Survey Tertiary localities (Washington catalog) :

USGS 2247b. "Fragmentary series," extending from one-quarter of a mile above Temple Place to half a mile above Yorktown, right bank of York River, York County, Va. Yorktown Formation (late Miocene). G. D. Harris, collector.

USGS 2295. Sewer excavation at corner of Nut and Mulberry Streets, Wilmington, New Hanover County N. C. Duplin (?) Formation (late Miocene). T. W. Stanton, 1891, collector.

USGS 2451. Jones Wharf at Drum Cliff, Patuxent River, St. Marys County, Md. Choptank Formation (middle Miocene). Frank Burns, collector.

USGS 3122. On the headwaters of a little creek about 2½ or 3 miles southwest of Petersburg, above the city waterworks reservoir, Dinwiddie County, Va. Yorktown Formation (late Miocene). Frank Burns, collector.

USGS 4309. Wingham Island, 5.58 miles W. 100° S. from northwestern point of Kayak Island, Controller Bay, Alaska. Pleistocene. A. G. Maddren, collector.

USGS 5871. Mouth of Cottonwood Creek, north side of Kachemak Bay, an arm of Cook Inlet, Alaska. Postglacial or Recent; this deposit may be a midden. G. C. Martin, collector.

USGS 6694. Mouth of large gulch on south slope of White River valley at foot of glacier; from talus but nearly in place (Bering Glacier A-4 quadrangle, 2.4 miles N. 14° E. of mouth of Fulton Creek), Yakataga district, Alaska. Yakataga Formation, about 1,500 ft above base (middle Miocene). A. G. Maddren, collector.

USGS 6697. Talus material (recent slide) from south face of Island Mountain, north side of main lobe of White River Glacier (Bering Glacier A-3 quadrangle, between 1 mile and 2.5 miles above the foot of the White River Glacier). Yakataga Formation, 3,000-5,000 ft above base (middle or late Miocene). A. G. Maddren, collector.

USGS 12480. North Dome, Kettleman Hills, sec. 35, T. 21 S., R. 17 E., 630 ft south of north section line, 1,630 ft west of east section line, Kings County, Calif. San Joaquin Formation (Pliocene). W. P. Woodring, collector.

USGS 13372. South side of Narrow Cape, at north side of entrance to Ugak Bay, eastern Kodiak Island, Alaska. *Mytilus middendorffi*-bearing beds (middle Miocene). S. R. Capps, collector.

USGS 15431. West end of Yakataga Ridge, 2.3 miles S. 88° W. of peak 2430 near west end of Yakataga Ridge (shown on Bering Glacier A-4 quad), Yakataga district, Alaska. Yakataga Formation, about 3,200 ft above base (middle Miocene). E. M. Spieker, collector.

USGS 15433. North flank of Yakataga Ridge at margin of Yakataga Glacier, 0.68 mile N. 34° W. of peak 2430 near west end of Yakataga Ridge (shown on Bering Glacier A-4 quad). Poul Creek Formation, about 1,900 ft below top (late Oligocene or early Miocene). E. M. Spieker, collector.

USGS 15437. Unnamed creek on north flank and parallel to Yakataga Ridge, 0.30 mile N. 16° E. of peak 2430 near west end of Yakataga Ridge (shown on Bering Glacier A-4 quad). Yakataga Formation near base (early middle Miocene). E. M. Spieker, collector.

USGS 15937. From a gravel terrace at Point Barrow, Alaska. Late Pleistocene. L. C. Barksdale, collector.

USGS 16864. West flank of Donald Ridge, 1.4 miles S. 61° E. of north end of Hanna Lake, Bering Glacier quad.,

- Yakataga district, Alaska. Poul Creek Formation, about 300 ft above base (the lower part of the Poul Creek Formation falls within the *Acila shumardi* zone; late middle Oligocene). D. J. Miller, collector.
- USGS 16891. West shore of Hanna Lake, 0.3 mile S. 50° W. of north end of lake, Bering Glacier quad, Yakataga district, Alaska. Float, from near base of Poul Creek Formation (the lower part of the Poul Creek Formation falls within the *Acila shumardi* zone; late middle Oligocene). D. J. Miller, collector.
- USGS 16899. East side of spur extending north into Bering Glacier, 14.6 miles N. 64° E. of north end of Hanna Lake, Bering Glacier quad, Yakataga district, Alaska. Poul Creek Formation, about 1,800 ft above base (probably late Oligocene). D. J. Miller, collector.
- USGS 17782. Cliff at north end of Duktotoh Mountain, 2.2 miles N. 06° W. of peak 4014 on Duktotoh Mountain (shown on Bering Glacier A-4 quad), Yakataga district, Alaska. Yakataga Formation, lower 200 ft (early middle Miocene). D. J. Miller, collector.
- USGS 17783. Crystal Creek, 1.58 miles N. 18° E. of junction with Priest River, Icy Bay D-2 and D-3 quad, Yakataga district, Alaska. Poul Creek Formation, about 2,400 ft below top (probably late Oligocene). D. J. Miller, collector.
- USGS 17787. Priest River, at mouth of bedrock canyon, 3.63 miles N. 85° W. of mouth of Carson Creek, Icy Bay D-2 and D-3 quad, Yakataga district, Alaska (late Oligocene or early Miocene). D. J. Miller, collector.
- USGS 17827. Gulch on south face of ridge at Sunshine Point, 1.9 miles S., 56° E. of mouth of Kulthieth River, Bering Glacier quad., Yakataga district, Alaska. Yakataga Formation, lower part (middle Miocene). R. B. Johnson, collector.
- USGS 17835. Gulch on south flank of Kulthieth Mountain, 0.94 mile S., 02° E. of peak 3447 (shown on Bering Glacier quad.), Yakataga district, Alaska. Yakataga Formation, about 3,000 ft above base (middle Miocene). D. J. Miller, collector.
- USGS 17850. Oil Creek, 3.1 miles S., 82° E. of Watson Peak, Bering Glacier A-4 quad., Yakataga district, Alaska. Yakataga Formation, lower 100 ft (early middle Miocene). D. J. Miller, collector.
- U.S. Geological Survey Tertiary localities (Denver catalog; specimens transferred to Menlo Park):
- USGS D-53. Recent, tidal flat of Usuf Bay, Unalaska Island, Aleutian Islands, Alaska. E. H. Meitzner and R. P. Platt, collectors.
- USGS D-169. Calcareous siltstone in sandstone unit, about 380 ft below top. Measured section, southeast shore of Cenotaph Island, 2,600 ft S. 29° W. of easternmost cape of island, Lituya Bay, Alaska. Unnamed formation, lower part (middle Miocene). D. J. Miller, collector.
- USGS D-174. Southwest shore of Cenotaph Island, 0.67 mile S. 70° W. of easternmost cape of island, Mount Fairweather quad., Lituya Bay, Alaska. Unnamed formation, about 1,170 ft above base; upper mudstone unit (probably Pliocene). D. J. Miller, collector.
- USGS D-180. Ocean beach reef, 0.55 mile N. 50° W. of mouth of Topsy Creek, Mount Fairweather quad., Lituya district, Alaska. Unnamed formation, about 3,100-3,200 ft above base; upper mudstone unit (probably Pliocene). D. J. Miller, collector.
- USGS D-264. Cliff at east margin of Fairweather Glacier, about 3.8 miles N. 80° W. of Mount Escures, Mount Fairweather quad., Lituya district, Alaska. Unnamed formation, probably in lower sandstone-siltstone unit (late Miocene or early Pliocene). D. J. Miller, collector.
- USGS D-385. Recent, strandline at Narssarsuk, 12 miles southwest of Thule, northwestern Greenland. W. E. Davies and G. Gold, collectors.
- USGS D-386. Raised beach, 10-35 ft above sea level, at Narssarsuk, 12 miles southwest of Thule, northwestern Greenland. Probably postglacial. W. E. Davies, collector.
- USGS D-389. Probably same locality as D-264. J. B. Fernstrom, collector.
- U.S. Geological Survey Tertiary localities (Menlo Park catalog):
- USGS M-214. Recent marine glacial deposits. Road north of bridge, south of Fish Creek, Douglas Island, Juneau area, Alaska. D. J. Miller, collector.
- USGS M-225. Recent, dead shells dredged from depth of 75 ft, east arm of Excursion Inlet, north side of Icy Strait, southeastern Alaska. D. J. Miller, collector.
- USGS M-237. Dead beach shells from several localities on Beardslee Island and shore of Glacier Bay, southeastern Alaska. D. J. Miller, collector.
- USGS M-363. Recent, on beach at mouth of Salmon River, about 25 miles north of Cape Newenham, southern Kuskokwim Bay, Alaska. D. M. Hopkins, collector.
- USGS M-364. Recent, lagoon behind Safety Spit, Nome, Alaska. D. M. Hopkins, collector.
- USGS M-807. East of Yellow Bluff Creek, about 5.3 miles east of lake north of Black Peak and 16.4 miles N. 55° W. of west end of Anguvik Island in Chignik Bay, altitude about 1,600 ft Unnamed formation (Yellow Bluff Zone of Western Gulf Oil Co. usage) (probably Pliocene). M. C. Lachenbruch, Western Gulf Oil Co., collector.
- USGS M-807a. Same locality as M-807, later collection.
- USGS M-1164. North shore of Popof Island, Shumagin Islands, Alaska; lat 55°20.6' N., long 160°26' W. Upper part of *Acila shumardi* zone (late middle Oligocene). C. A. Burk, Richfield Oil Co., collector.
- USGS M-1256. Dredge tailings near oil tanks in FAA Warehouse area on west side of Snake River, lat 64°30' N., long 165°25'30" W., Nome, Alaska. Submarine Beach (early Pleistocene). D. M. Hopkins, collector.
- USGS M-1425. Recent, beach at Deering, southern Kotzebue Sound, Alaska. D. M. Hopkins and D. S. McCulloch, collectors.
- USGS M-430. Recent, Lost River, lat 65°23'10" N., long 167°09'05" W., west of Port Clearance, Alaska. D. M. Hopkins, collector.
- USGS M-1440. Estuarine deposits at Nome, Alaska. "Second Beach" or younger. Pleistocene. D. M. Hopkins, collector.
- USGS M-1445. Estuarine deposits at Nome, Alaska, north wall of dredge pit no. 6. "Second Beach" or younger. Pleistocene. D. M. Hopkins, collector.
- USGS M-1493. 140 ft above base of glacial-marine sequence approximately 3,500 ft thick, at about midpoint of south end of Tugidak Island, Trinity Islands, Alaska. Late(?) Pliocene. G. W. Moore, collector.
- USGS M-1526. Upper fossiliferous bed at Tolstoi Point, east side of English Bay, St. Paul Island, Pribiloff Islands,

- Alaska. Pleistocene, probably middle. D. M. Hopkins, collector.
- USGS M-1577. Northeast end of lagoon behind Cape Kruzenstern, lat 67°11.75' N., long 163°32' W., Alaska. Late Pleistocene. D. S. McCulloch, collector.
- USGS M-1622. Recent, beach along Lukanin Bay near Tonki Point, St. Paul Island, Pribiloff Islands, Alaska. D. M. Hopkins, collector.
- USGS M-1625. Recent, Homer Spit at entrance to Kachemak Bay, an arm of Cook Inlet, Alaska. J. Wolfe, collector.
- USGS M-1634. Beach at Ferry Landing, Nanaimo, Vancouver Island, British Columbia. Recent. F. S. MacNeil, collector.
- USGS M-1655. North side of Popof Island, Shumagin Islands, Alaska; lat 50°20.35' N., long 160°25.6' W. Upper part of *Acila shumardi* zone (late middle Oligocene). A. Grantz, collector.
- USGS M-1662. Recent, about 9 miles east of southwest cape, St. Lawrence Island, northern Bering Sea. H. B. Allen, collector.
- USGS M-1663. Recent, beach about 3 miles west of Invute Mountain, St. Lawrence Island, northern Bering Sea. H. B. Allen, collector.
- USGS M-1664. Fur Sund at Branden Ferry, Jutland, Denmark. Postglacial or Recent. F. S. MacNeil, collector.
- USGS M-1665. Recent, east side of tip of Sheshalik Spit, northern Kotzebue Sound, Alaska. D. S. McCulloch, collector.
- USGS M-1668. Stratton Hall on River Orwell, Suffolk, England. Newbournian Stage, Red Crag (early Pleistocene). D. F. W. Baden-Powell, F. S. MacNeil, and D. M. Hopkins, collectors.
- USGS M-1669. Neutral farm, near Butley, Suffolk, England. Butleyan Stage, Red Crag (early Pleistocene). D. F. W. Baden-Powell, F. S. MacNeil, and D. M. Hopkins, collectors.
- USGS M-1670. Virtue farm, north of Alderton, Suffolk, England. Butleyan Stage, Red Crag (early Pleistocene). D. F. W. Baden-Powell, F. S. MacNeil, and D. M. Hopkins, collectors.
- USGS M-1671. Six feet below top of section, highest shelly layer below clay, Stackyard pit, Chillesford, Suffolk, England. Chillesford Beds, Icenian Crag (early Pleistocene). D. F. W. Baden-Powell, F. S. MacNeil, and D. M. Hopkins, collectors.
- USGS M-1672. Aldeburg, Suffolk, England. Norwich Stage, Icenian Crag (early Pleistocene). D. F. W. Baden-Powell, D. M. Hopkins, and H. E. P. Spencer, collectors.
- USGS M-1679. Road and building cuts on northeast side of Unalaska Lake near head of Illiuliuk Bay, Unalaska Island, Aleutian Islands, Alaska. From greenish volcanic gray-wacke containing *Cornwallius* teeth. H. F. Barnett, Jr., collector.
- USGS M-1681. Roadcut on Tokeland Road along north shore of Willapa Bay, approximately 45 ft above high-water mark, 1,700 ft south of NE. cor. sec. 6, T. 14 N., R. 10 W., Pacific County, Wash. Unnamed formation, probably Pleistocene. W. O. Addicott, collector.
- USGS M-1682. Roadcut on Tokeland Road along north shore of Willapa Bay, approximately 37 ft above high-water mark, 3,400 ft south and 2,200 ft east of NW. cor. sec. 5, T. 14 N., R. 10 E., Pacific County, Wash. Unnamed formation, probably Pleistocene. W. O. Addicott, collector.

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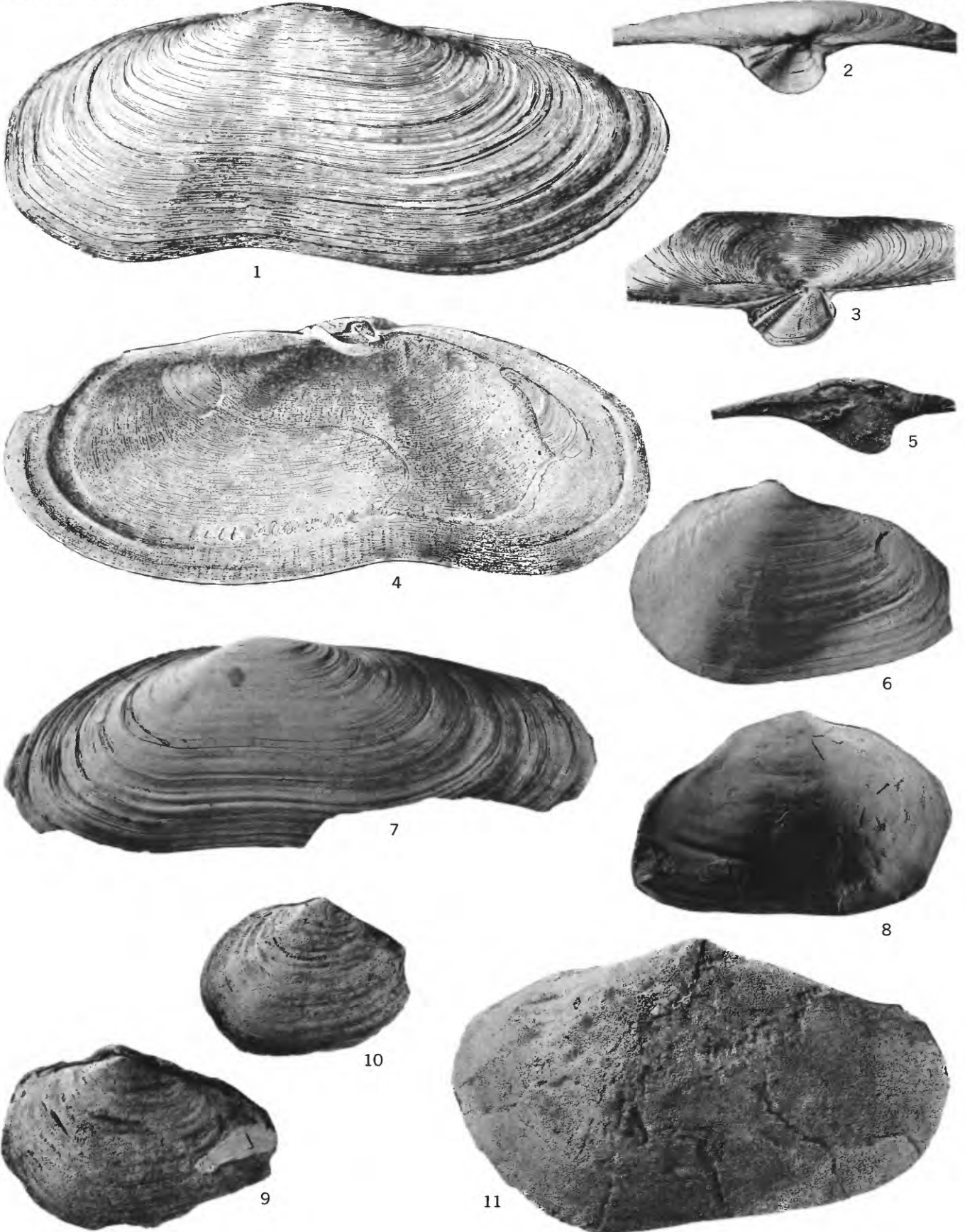
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PLATES 1-11

PLATE 1

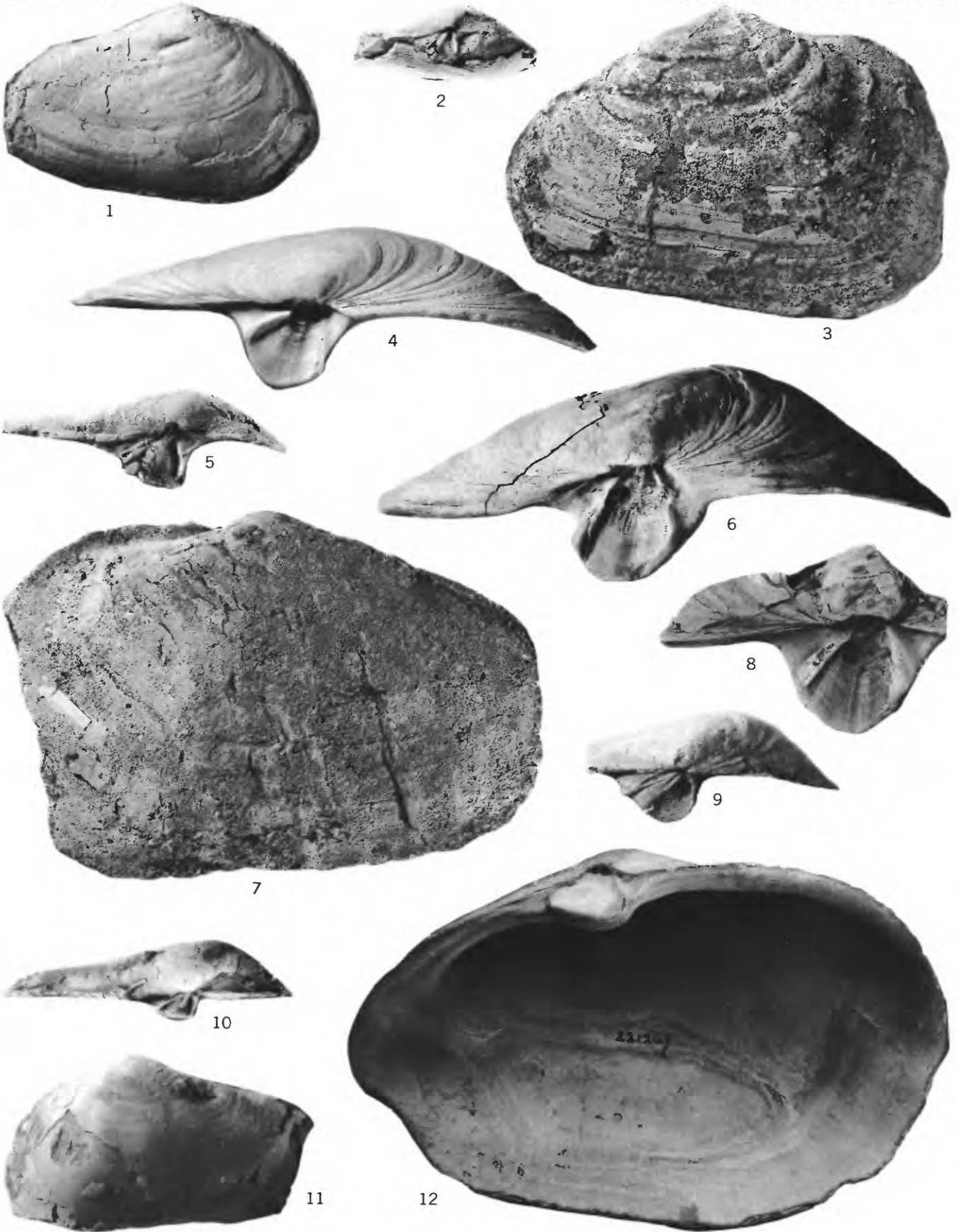
- FIGURES 1, 3, 4. *Mya producta* Conrad (p. G26).
Figured specimen ($\times 1$), after Glenn, 1904, pl. 68, figs. 1a, 1b, 2. Choptank Formation, Jones Wharf, Patuxent River, Md.
1. Left valve, exterior.
 3. Spoon.
 4. Interior showing pallial line and pallial sinus.
- 2, 7. *Mya producta* Conrad (p. G26).
Figured specimen, topotype ($\times 1$), USNM 146004. Choptank Formation, Jones Wharf, Patuxent River, Md., USGS 2451.
2. Spoon.
 7. Left valve, exterior. Length 113 mm, height (incomplete) 39 mm, convexity (not including spoon) 12 mm.
- 5, 6, 8. *Mya kusiroensis* Nagao and Inoue (p. G27).
Figured specimen ($\times 1$), USNM 644267. Base of Poul Creek Formation, west shore of Hanna Lake, Yakataga District, Alaska, USGS 16891.
5. Spoon, rubber cast.
 6. Left valve, exterior, rubber cast. Length 60 mm, height 38 mm.
 8. Right valve, internal mold, showing pallial line and pallial sinus. Double convexity 20 mm.
- 9, 10. *Mya kusiroensis* Nagao and Inoue (p. G27).
Figured specimens ($\times 1$). Upper part of *Acila shumardi* zone, north shore of Popof Island, Shumagin Islands, Alaska, USGS M-1164.
9. Left valve, internal mold, USNM 644268.
Length 52 mm, height 38.5 mm, double convexity 21.3 mm.
 10. Left valve, internal mold, USNM 644269.
Length 38.7 mm, height 29 mm, double convexity 16 mm.
11. *Mya cf. M. grewingki* Makiyama (p. G27).
Figured specimen ($\times 1$), USNM 644270. Poul Creek Formation, about 1,900 ft below top, Yakataga District, Alaska, USGS 15433. Length 93 mm, height 56 mm, double convexity 47 mm.



MYA FROM THE CHOPTANK FORMATION (MARYLAND), THE POUL CREEK FORMATION (ALASKA), AND THE ACILA SHUMARDI ZONE, POPOF ISLAND (ALASKA)

PLATE 2

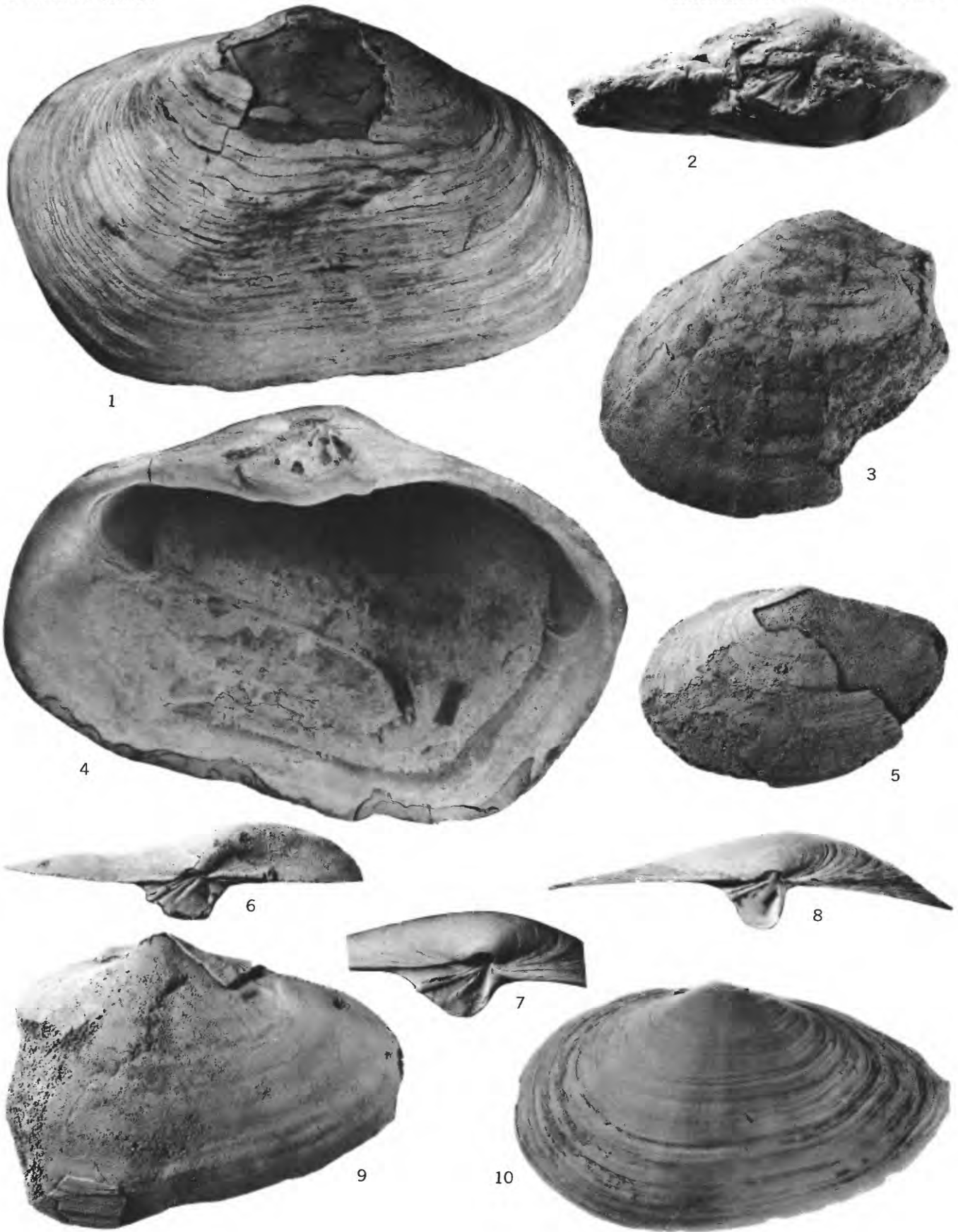
- FIGURE 1. *Mya dickersoni* Clark (p. G28).
Holotype ($\times 1$), UC 11554. Neroly Formation, San Pablo Group, Contra Costa County, Calif., UC 1617.
Right valve, exterior. Length 57 mm, height 37 mm.
- 2, 5. *Mya dickersoni* Clark (p. G28).
Figured specimen, topotype, UC 15001. Neroly Formation, San Pablo Group, Contra Costa County, Calif., UC 1617.
2. Spoon ($\times 1$). Length 35 mm, height 26.5 mm.
5. Same ($\times 2$), different illumination.
3. *Mya elegans* (Eichwald) (p. G30).
Figured specimen ($\times 1$), USNM 644271. This specimen is here designated the neotype of *Mya crassa* Grewingk. Beds of Pliocene age, east side of Yellow Bluff Creek near headwaters, northwest of Chignik Bay, Alaskan Peninsula, USGS M-807a. Right valve, exterior, partly testaceous. Length 89 mm, height 63 mm, double convexity 41 mm.
- 4, 12. *Mya elegans* (Eichwald) (p. G29).
Figured specimen ($\times 1$), USNM 221269. Recent, Chignik Bay, Alaskan Peninsula.
4. Spoon.
12. Left valve, interior, showing pallial line and pallial sinus. Length 113 mm, height 72 mm, convexity (not including spoon) 23 mm.
6. *Mya elegans* (Eichwald) (p. G29).
Figured specimen ($\times 1$), USNM 635283. Recent, southern part of Kuskokwim Bay, between Goodnews Bay and Cape Newenham, Alaska, USGS M-363. Spoon. Same specimen as pl. 3, figs. 1, 4.
7. *Mya elegans* (Eichwald) (p. G30).
Neotype ($\times 1$), USNM 644272. This specimen is here designated the neotype of *Mya arenaria* Linné Grewingk for which the name *Anatina elegans* Eichwald was proposed. Beds of Pliocene age, east side of Yellow Bluff Creek near headwaters, northeast of Chignik Bay, Alaskan Peninsula, USGS M-807. Left valve, internal mold. Length (incomplete) 108 mm, height 68 mm, double convexity 40.5 mm.
8. *Mya elegans* (Eichwald) (p. G29).
Figured specimen ($\times 1$), USNM 644273. Middle Pleistocene, upper bed at Tolstoi Point, St. Paul Island, Pribiloff Islands, USGS M-1526. Spoon.
9. *Mya arrosis* MacNeil, n. sp. (p. G31).
Figured specimen ($\times 1$), UC 15003. Briones Sandstone, San Pablo Group, Contra Costa County, Calif., UC 1687. Spoon. Same specimen as pl. 3, fig. 3.
- 10, 11. *Mya dickersoni* Clark (p. G28).
Figured specimen, topotype ($\times 1$), UC 15002. Specimen obtained from matrix enclosing holotype. Neroly Formation, San Pablo Group, Contra Costa County, Calif., UC 1617.
10. Spoon, showing small ligamental callus.
11. Left valve, exterior, decorticated. Length 59 mm, height 35 mm, convexity (not including spoon) 12 mm.



MYA FROM THE BRIONES AND NEROLY FORMATIONS (CALIFORNIA), PLIOCENE BEDS, CHIGNIK BAY (ALASKA), PLEISTOCENE BEDS, ST. PAUL ISLAND (ALASKA), AND RECENT (ALASKA)

PLATE 3

- FIGURES 1, 4. *Mya elegans* (Eichwald) (p. G29).
Figured specimen ($\times 1$), USNM 635283. Recent, southern part of Kuskokwim Bay, between Goodnews Bay and Cape Newenham, Alaska, USGS M-363.
1. Left valve, exterior. Length 115 mm, height 75 mm, convexity (not including spoon) 31 mm.
 4. Same, interior, showing pallial line and pallial sinus. Spoon on pl. 2, fig. 6.
2. *Mya arrosis* MacNeil, n. sp. (p. G31).
Figured specimen ($\times 1\frac{1}{2}$), UC 15004. Neroly Formation, San Pablo Group, Contra Costa County, Calif., UC 1617. Spoon.
3. *Mya arrosis* MacNeil, n. sp. (p. G31).
Figured specimen ($\times 1$), UC 15003. Briones Sandstone, San Pablo Group, Contra Costa County, Calif., UC 1687. Left valve, exterior, partly testaceous. Height 61 mm. Spoon on pl. 2, fig. 9.
5. *Mya arrosis* MacNeil, n. sp. (p. G31).
Figured specimen, topotype ($\times 1$), UC 15005. Cierbo Sandstone, San Pablo Group, Contra Costa County, Calif., UC 1227. Left valve, exterior, partly testaceous. Height 38.5 mm.
- 6, 9. *Mya arrosis* MacNeil, n. sp. (p. G31).
Holotype ($\times 1$), UC 15006. Cierbo Sandstone, San Pablo Group, Contra Costa County, Calif., UC 1227.
6. Spoon.
 9. Left valve, exterior, partly testaceous. Length (incomplete) 78 mm, height 57 mm, convexity (not including spoon) 15 mm.
7. *Mya japonica* Jay (p. G31).
Figured specimen ($\times 2$), USNM 644274. Late Pleistocene terrace deposit at Cape Kruzenstern, Alaska, USGS M-1577. Spoon.
- 8, 10. *Mya japonica* Jay (p. G31).
Figured specimen ($\times 1$), USNM 635284. Recent, Sheshalik Spit, northern Kotzebue Sound, Alaska, USGS M-1665.
8. Spoon.
 10. Left valve, exterior. Length 82.5 mm, height 47.5 mm, convexity (not including spoon) 15 mm. Same specimen as pl. 4, fig. 11.



MYA FROM THE BRIONES, CIERBO, AND NEROLY FORMATIONS (CALIFORNIA), PLEISTOCENE BEDS, CAPE KRUZENSTERN (ALASKA), AND RECENT (ALASKA)

PLATE 4

[All figures natural size]

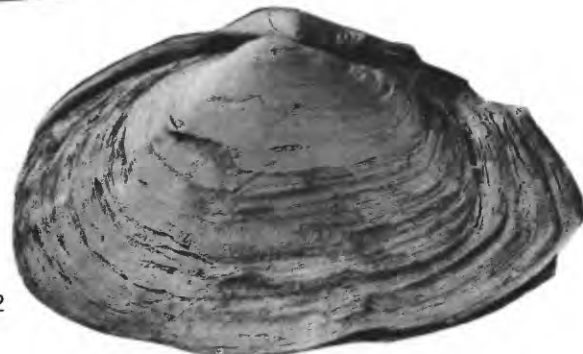
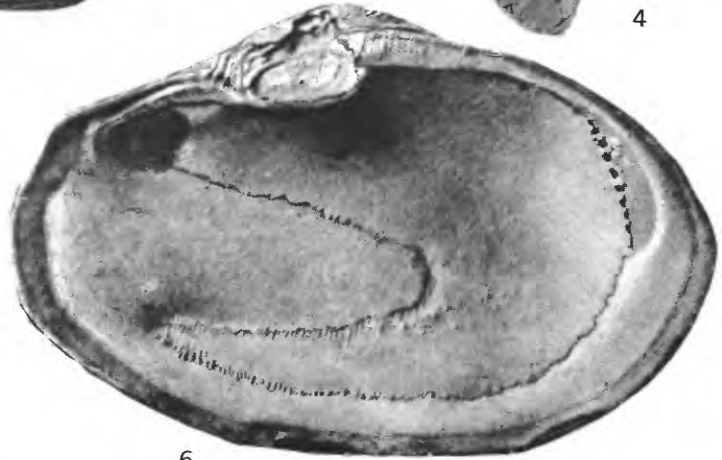
- FIGURES 1, 5, 8. *Mya japonica* Jay (p. G31).
Figured specimen, CAS 12534. Recent, Tokyo Bay, CAS 34859.
1. Left valve, exterior. Length (incomplete) 105 mm, height 66 mm, convexity (not including spoon) 22 mm.
5. Same, interior, showing pallial line and pallial sinus.
8. Same, spoon.
2. *Mya japonica* Jay (p. G31).
Figured specimen, USNM 644275. Late Pleistocene lagoon deposit, Nome, Alaska, USGS M-1445. "Second Beach" or younger. Spoon of a distorted specimen; for comparison with Middendorff, 1849, pl. 20, figs. 1-3.
- 3, 4. *Mya japonica* Jay (p. G31).
Figured specimen, USNM 644276. Late Pleistocene lagoon deposit, Nome, Alaska, USGS M-1440.
"Second Beach" or younger.
3. Spoon.
4. Left valve, interior, showing pallial line and pallial sinus. Length 69 mm, height 41 mm, convexity (not including spoon) 13 mm.
6. *Mya japonica* Jay (p. G31).
Figured specimen, USNM 635285. Recent, Safety Spit, near Nome, Alaska, USGS M-364.
- 7, 9, 10. *Mya japonica* Jay (p. G31).
Figured specimen, USNM 644277. Late Pleistocene lagoon deposit, Nome, Alaska, USGS M-1440.
"Second Beach" or younger.
7. Spoon.
9. Left valve, exterior. Length 70 mm, height 43 mm, convexity (not including spoon) 14 mm.
10. Left valve, interior, showing pallial line and pallial sinus.
11. *Mya japonica* Jay (p. G31).
Figured specimen, USNM 635284. Recent, Sheshalik Spit, northern Kotzebue Sound, Alaska, USGS M-1665. Left valve, interior, showing pallial line and pallial sinus. Same specimen as pl. 3, figs. 8, 10.



MYA FROM PLEISTOCENE BEDS, NOME (ALASKA), AND RECENT (JAPAN AND ALASKA)

PLATE 5

- FIGURE 1. *Mya* cf. *M. fujiei* MacNeil, n. sp. (p. G30).
"Paratype" of *Mya dickersoni* (Clark (\times 1), UC 11533. Briones Sandstone, San Pablo Group, Contra Costa County, Calif., UC. 197. Left valve, exterior partly decorticated.
- 2, 3. *Mya arenaria* Linné (p. G33).
Figured specimen (\times 1), USNM 644278. Yorktown Formation, Yorktown, York County, Va., USGS 2247b.
2. Left valve, exterior. Height 40.5 mm.
3. Spoon.
4. *Mya arenaria* Linné (p. G33).
Figured specimen (\times 2), USNM 644279. Yorktown Formation, 2½-3 miles southwest of Petersburg, Dinwiddie County, Va., USGS 3122. Spoon.
5. *Mya arenaria* Linné (p. G33).
Figured specimen (\times 1), UC 15007. Cierbo Sandstone, San Pablo Group, Alameda County, Calif., UC 1224. Left valve, exterior. Length 63 mm, height 36.8 mm, double convexity 22 mm.
6. *Mya arenaria* Linné (p. G33).
Figured specimen (\times 1), USNM 495304, after Woodring and others, 1940, pl. 9, fig. 7. San Joaquin Formation, North Dome, Kettleman Hills, Kings County, Calif., USGS 12480. Left valve, interior, showing pallial line and pallial sinus.
- 7, 8, 11. *Mya arenaria* Linné (p. G33).
Figured specimen (\times 1), UC 34840. Etchegoin Formation, Kettleman Hills, Kings County, Calif., UC A-1686.
7. Left valve, exterior. Length 92 mm, height 62 mm.
8. Spoon.
11. Left valve, interior, showing pallial line and pallial sinus.
- 9, 10. *Mya arenaria* Linné (p. G33).
Figured specimen (\times 1), UC 30802. San Joaquin Formation, Kettleman Hills, Kings County, Calif., UC A-3167.
9. Spoon.
10. Left valve, exterior. Height 39 mm.
12. *Mya arenaria* Linné (p. G33).
Figured specimen (\times 1), UC 30801. San Joaquin Formation, Kettleman Hills, Kings County, Calif., UC A-3167. Left valve, exterior.



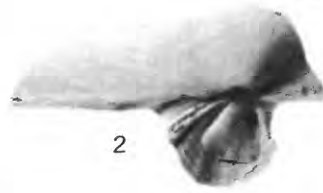
MYA FROM THE BRIONES, CIERBO, ETCHEGOIN, AND SAN JOAQUIN FORMATIONS (CALIFORNIA), AND THE YORKTOWN FORMATION (VIRGINIA)

PLATE 6

- FIGURES 1, 6, 9. *Mya arenaria* Linné (p. G33).
Figured specimen ($\times 1$), USNM 635286. Recent, Nanaimo, Vancouver Island, British Columbia, USGS M-1634.
1. Left valve, exterior. Length 82 mm, height 49 mm, convexity (not including spoon) 11 mm.
6. Left valve, interior, showing pallial line and pallial sinus.
9. Spoon.
- 2, 3, 4. *Mya arenaria* Linné (p. G33).
Figured specimens ($\times 1$). Newbournian Stage, Red Crag, Stratton Hall, Suffolk, England, USGS M-1668.
2. Spoon, USNM 644280.
3. Spoon, USNM 644281.
4. Spoon, USNM 644282.
5. *Mya arenaria* Linné (p. G33).
Figured specimen ($\times 1$), USNM 644283. Butleyan Stage, Red Crag, Neutral farm, Suffolk, England, USGS M-1669. Spoon.
- 7, 8, 10, 11, 12, 15. *Mya arenaria* Linné (p. G33).
Figured specimens ($\times 1$). Butleyan Stage, Red Crag, Virtue farm, Suffolk, England, USGS M-1760.
7. Spoon, USNM 644284.
8. Spoon, USNM 644285.
10. Spoon, USNM 644286.
11. Spoon, USNM 644287.
12. Spoon, USNM 644288.
15. Spoon, USNM 644289.
13. *Mya arenaria* Linné (p. G33).
Figured specimen ($\times 1$), USNM 644290. Norwich Stage, Icenian Crag, Aldeburg, Suffolk, England, USGS M-1672. Spoon.
14. *Mya arenaria* Linné (p. G33).
Figured specimen ($\times 1$), USNM 644291. Sub-Recent deposits, Brandon Ferry Landing, Fur Sund, Jutland, Denmark, USGS M-1664. Dorsal view showing spoon.
16. *Mya japonica* Jay (p. G24).
Figured specimen ($\times 2$), USNM 644292. Late Pleistocene lagoon deposit, Nome, Alaska, USGS M-1440. "Second Beach" or younger. Right-valve chondrophore showing pointed marginal projection at dorsal anterior edge; compare with broad spur at this position in *M. truncata*, pl. 8, figs. 2, 3.
- 17, 18. *Mya arenaria* Linné (p. G33).
Figured specimen ($\times 1$), after Wood, 1957, pl. 28, figs. 2a, b. Newbournian Stage, Red Crag, Sutton, Suffolk, England.
17. Left valve, exterior.
18. Left valve, interior, showing pallial line and pallial sinus.



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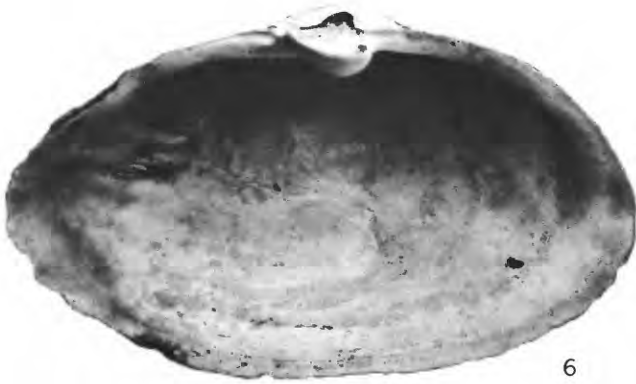
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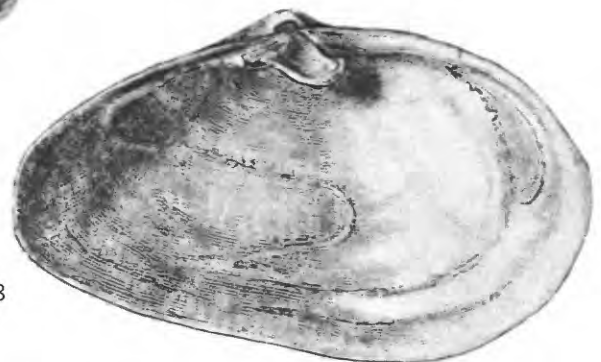
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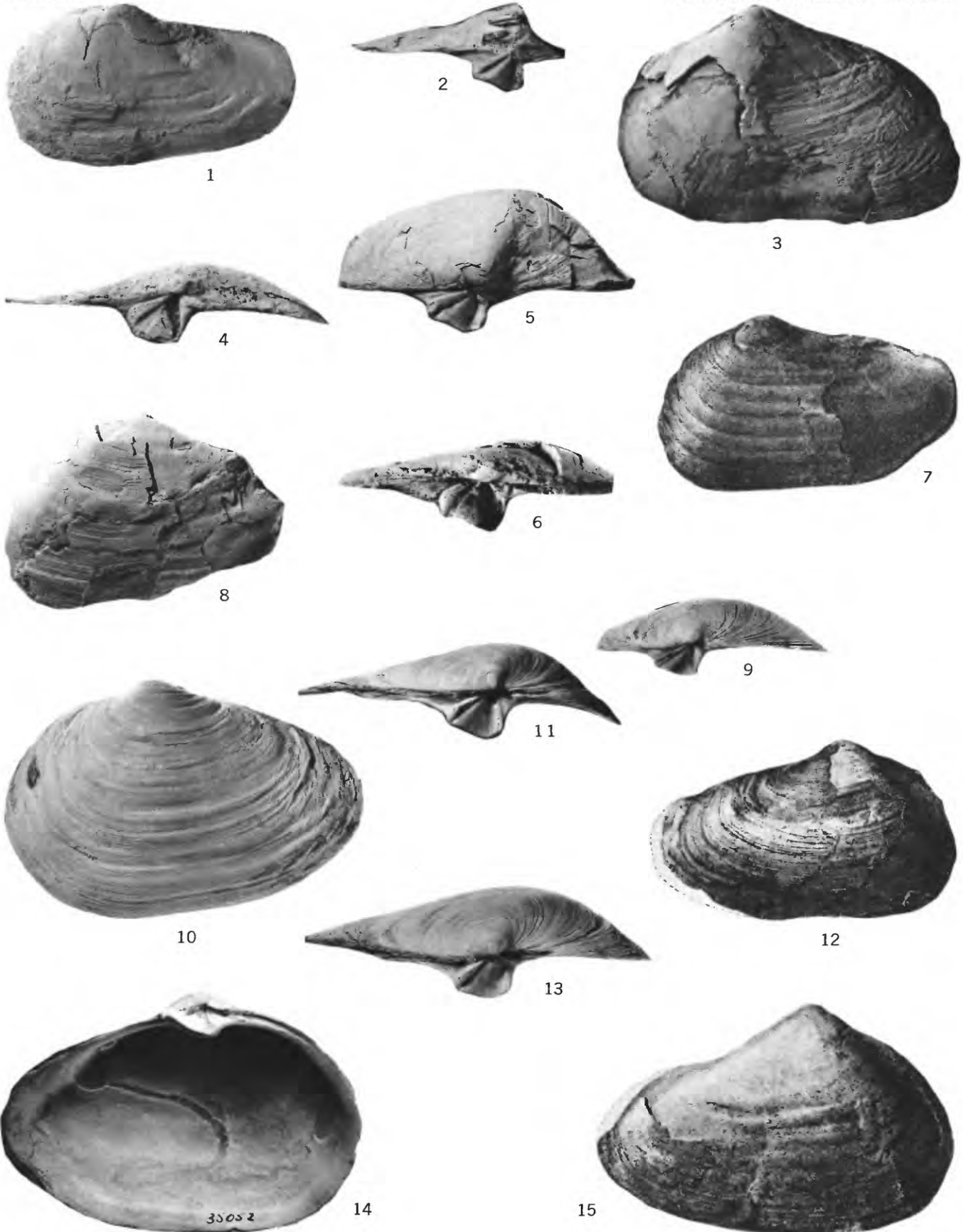


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MYA FROM THE RED CRAG AND ICENIAN CRAG (ENGLAND), PLEISTOCENE BEDS, NOME (ALASKA), AND RECENT (DENMARK AND BRITISH COLUMBIA)

PLATE 7

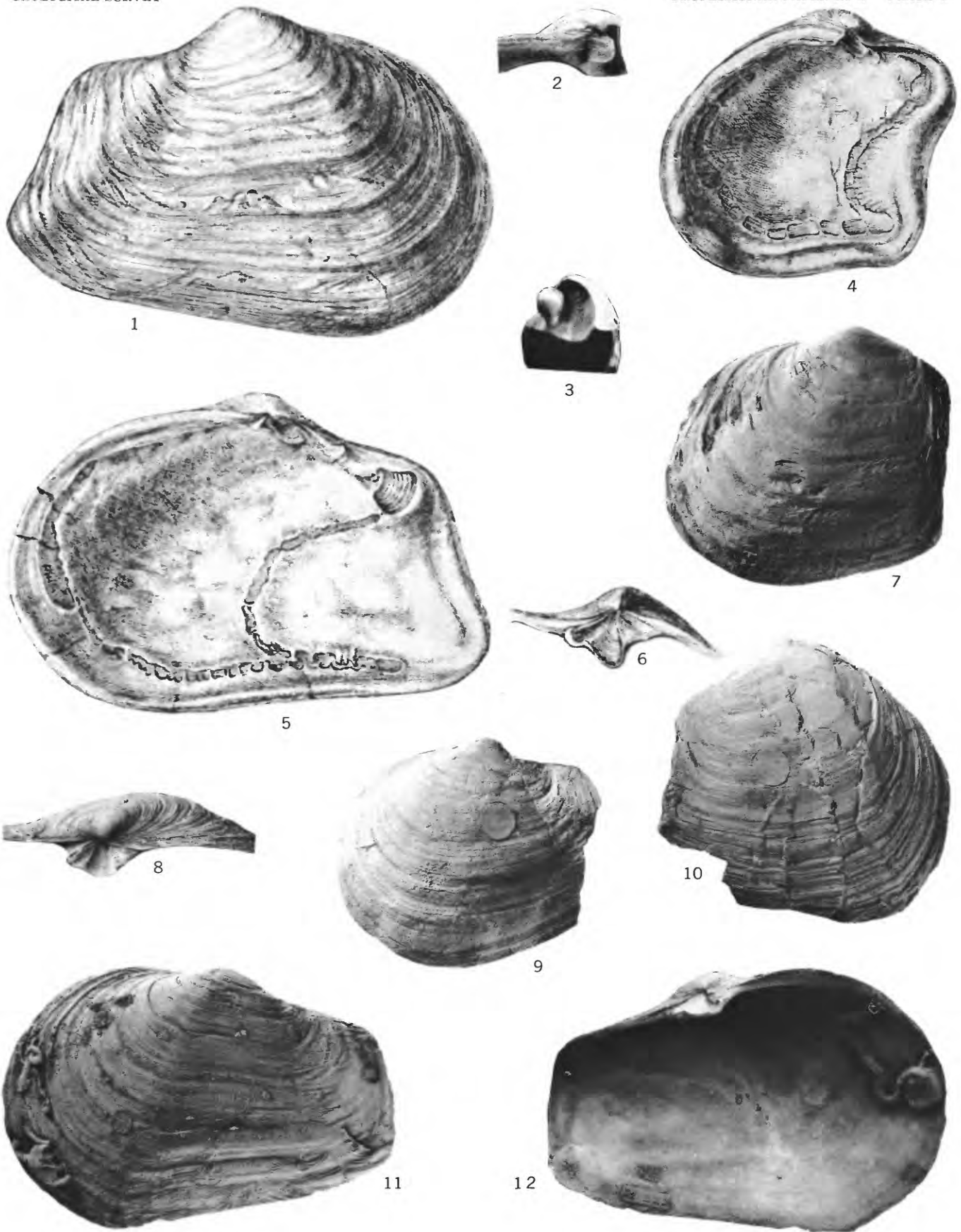
- FIGURES 1, 4. *Mya salmonensis* Clark (p. G35).
Figured specimen, USNM 644293. Poul Creek Formation, 2,400 ft below top, Yakataga District, Alaska, USGS 17783.
1. Left valve, exterior, partly testaceous ($\times 1$).
4. Spoon ($\times 1\frac{1}{2}$)
2. *Mya cuneiformis* (Böhm) (p. G35).
Figured specimen ($\times 1$), USNM 644294. Basal part of Yakataga Formation, Yakataga District, Alaska, USGS 15437. Spoon.
3. *Mya cueniformis* (Böhm) (p. G35).
Figured specimen ($\times 1$), USNM 644295. Basal part of Yakataga Formation, Yakataga District, Alaska, USGS 15437. Left valve, exterior, partly decorticated. Length 65 mm, height 42 mm, double convexity 29 mm.
5. *Mya cuneiformis* (Böhm) (p. G35).
Figured specimen ($\times 1$), USNM 644296. Basal part of the Yakataga Formation, Yakataga District, Alaska, USGS 15437. Spoon.
- 6, 8. *Mya cuneiformis* (Böhm) (p. G35).
Figured specimen ($\times 1$), USNM 644297. *Mytilus middendorffi*-bearing beds, mouth of Ugak Bay, Kodiak Island, Alaska, USGS 13372.
6. Left valve, exterior, incomplete.
8. Spoon.
- 7, 12, 15. *Pleuromya cuneiformis* Böhm (p. G35).
Figured specimens, topotypes ($\times 1$), after Böhm, 1915, pl. 29, figs. 1a, b, 2. The specimen shown in Böhm's text figure (right), p. 557, is here designated the lectotype. Middle Miocene beds at Kap Jonquièrre (?Cape Due), northern Sakhalin.
9. *Mya pseudoarenaria* Schlesch (p. G37).
Figured specimen ($\times 1$) (Riksmuseet, Stockholm). Middle Pleistocene beds at Gostinoj, Yenisey River, Russia, Nordenskiöld Yenisey Expedition, 1876, no. 1876b. Spoon.
- 10, 11, 13, 14. *Mya pseudoarenaria* Schlesch (p. G37).
Figured specimen ($\times 1$), CAS 12535. Recent, Point Barrow, Alaska, CAS 35052.
10. Left valve, exterior. Length 68 mm, height 45.5 mm, convexity (not including spoon) 14 mm.
11, 13. Spoon, different views and illumination.
14. Left valve, interior, showing pallial line and pallial sinus.



MYA FROM THE POUL CREEK AND YAKATAGA FORMATIONS (ALASKA), MIDDLE MIOCENE BEDS (SAKHALIN AND KODIAK ISLAND), PLEISTOCENE BEDS, YENISEY RIVER (RUSSIA), AND RECENT (ALASKA)

PLATE 8

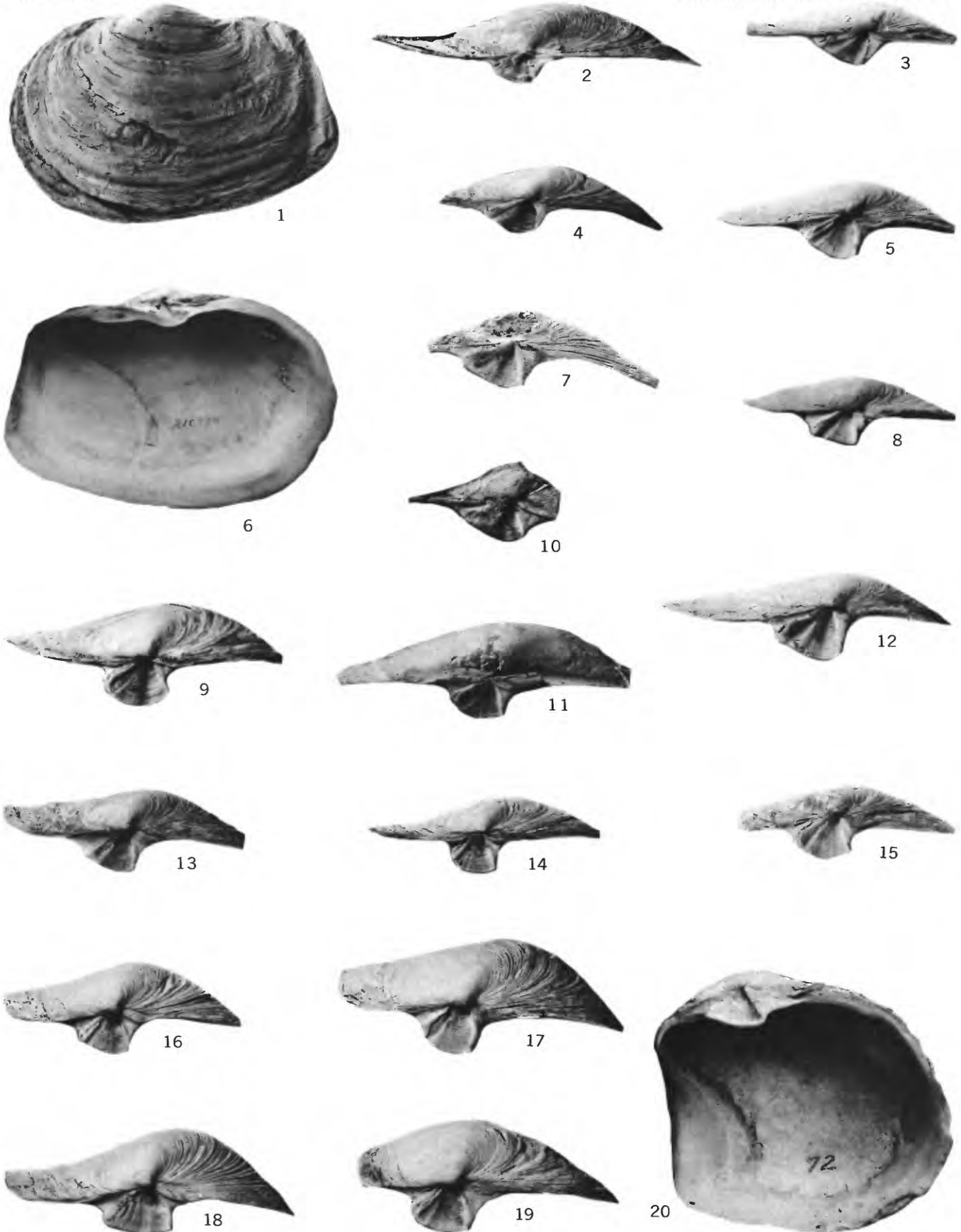
- FIGURES 1, 5, 6. *Mya truncata* Linné (p. G38).
Figured specimens ($\times 1$), after Wood, 1857, pl. 28, figs. 1a, 1b, 1f (assigned to Coralline Crag). Norwich(?) Stage, Icenian Crag, Ramsholt, Suffolk, England.
1. Right valve, exterior. This figure reproduced by Chatwin, 1961, fig. 24, no. 13 and reassigned to Norwich Stage of the Icenian Crag.
 5. Right valve, interior, showing pallial line and pallial sinus.
 6. Left valve, spoon.
- 2, 3. *Mya truncata* Linné (p. G24).
Figured specimen ($\times 2$) USNM 644298. Early Pleistocene, "Submarine Beach," Nome, Alaska, USGS M-1256.
2. Broad spur bordering right valve chondrophore, view from anterior side. Edge of spur inserts along posterior edge of anterior ridge of left valve.
 3. Same, viewed from posterior side.
4. *Mya truncata* var. *uddevalensis* Forbes (p. G38).
Figured specimen ($\times 1$), after Wood, 1857, pl. 28, fig. 1c. Late(?) Pleistocene, Clyde Beds, Scotland. Right valve, interior, showing pallial line and pallial sinus.
7. *Mya truncata* var. *uddevalensis* Forbes (p. G38).
Figured specimen ($\times 1$), USNM 635287. Recent, St. Lawrence Island, northern Bering Sea, USGS M-1663. Left valve, exterior. Length 54 mm, height 48 mm, convexity (not including spoon) 16 mm. Same specimen as pl. 9, figs. 19, 20.
- 8, 11, 12. *Mya truncata* Linné (p. G38).
Figured specimen ($\times 1$), USNM 635288. Recent, Excursion Inlet, north side of Icy Strait, Southeastern Alaska, USGS M-225.
8. Spoon.
 11. Left valve, exterior. Length 74 mm, height 50 mm, convexity (not including spoon) 17 mm.
 12. Left valve, interior.
9. *Mya truncata* Linné (p. G38).
Figured specimen ($\times 1$), USNM 644299. Yakataga Formation, 1,500 ft. above base, Yakataga district, Alaska, USGS 6694. Left valve, exterior. Length 53 mm, height 43 mm, double convexity 26 mm.
10. *Mya truncata* var. *uddevalensis* Forbes (p. G38).
Figured specimen ($\times 1$), USNM 644300. Yakataga Formation, float from 3,000 to 5,000 ft above base, Yakataga district, Alaska, USGS 6697. Right valve, exterior. Length 56 mm, height 65 mm, double convexity 27 mm.



MYA FROM THE YAKATAGA FORMATION (ALASKA), THE ICENIAN CRAG (ENGLAND), THE CLYDE BEDS (SCOTLAND), PLEISTOCENE BEDS, NOME (ALASKA), AND RECENT (ALASKA)

PLATE 9

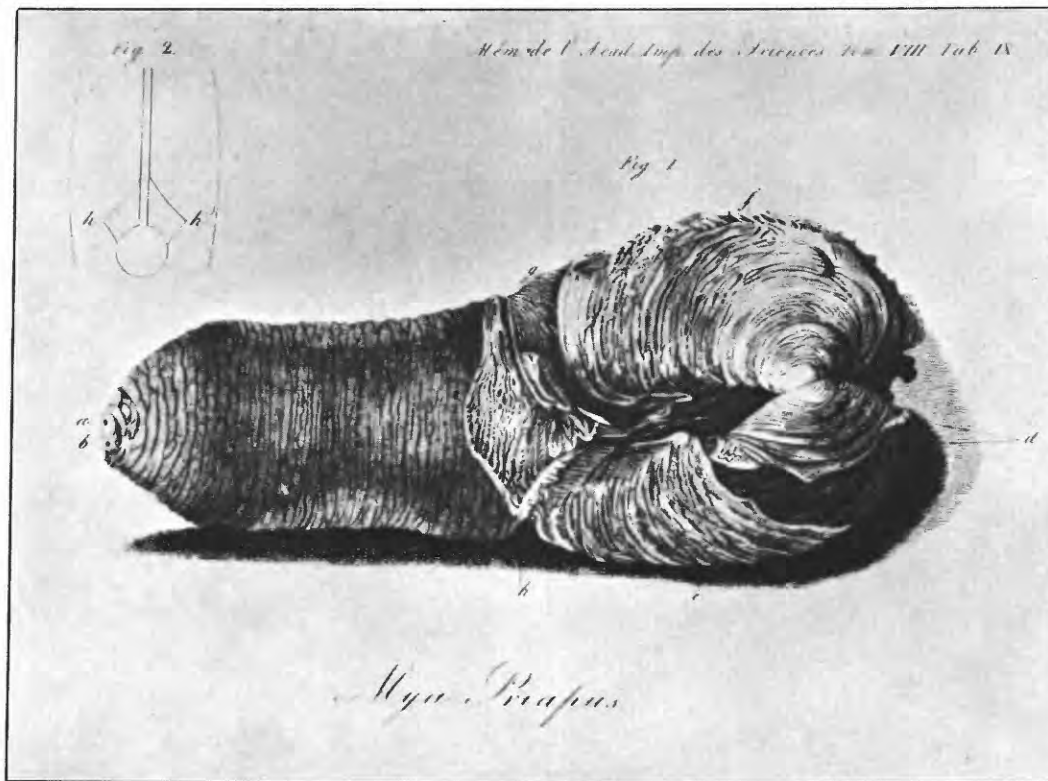
- FIGURES 1, 6, 9. *Mya truncata* Linné (p. G38).
Figured specimen ($\times 1$), (USNM 210970). Recent, Kodiak Island, Alaska.
1. Left valve, exterior. Length 61 mm, height 41.8 mm, convexity (not including spoon) 15 mm.
6. Left valve, interior, showing pallial line and pallial sinus.
9. Spoon.
2. *Mya truncata* Linné (p. G38).
Figured specimen ($\times 1\frac{1}{2}$), USNM 644301. Norwich Stage, Icenian Crag, Aldeburg, Suffolk, England, USGS M-1672. Spoon.
- 3, 5, 8, 12, 15. *Mya truncata* Linné (p. G38).
Figured specimens. Recent(?), 12 miles southwest of Thule, northwestern Greenland, USGS D-386.
3. Spoon ($\times 1\frac{1}{2}$) USNM 635289.
5. Spoon ($\times 1\frac{1}{2}$), USNM 635289.
8. Spoon ($\times 1$), USNM 635289.
12. Spoon ($\times 1\frac{1}{2}$), USNM 635289.
15. Spoon ($\times 1\frac{1}{2}$), USNM 635289.
4. *Mya* cf. *M. pseudoarenaria* Schlessch (p. G37).
Figured specimen ($\times 1\frac{1}{2}$), USNM 644302. Chillesford Beds, Icenian Crag, Chillesford, Suffolk, England, USGS M-1671. Spoon.
- 7, 10, 11. *Mya truncata* Linné (p. G38).
Figured specimens ($\times 1\frac{1}{2}$). Late(?) Pliocene, near base of section, Tugidak Island, south of Kodiak Island, Alaska, USGS M-1493.
7. Spoon, USNM 644303.
10. Spoon, USNM 644304.
11. Spoon, USNM 644305.
- 13, 16, 17, 18. *Mya truncata* Linné (p. G38).
Figured specimens ($\times 1$). Postglacial beds near Juneau, Alaska, USGS M-214.
13. Spoon, USNM 644306.
16. Spoon, USNM 644307.
17. Spoon, USNM 644308.
18. Spoon, USNM 644309.
14. *Mya truncata* Linné (p. G38).
Figured specimen ($\times 1$), USNM 635290. Recent, Beardslee Island, Glacier Bay, southeastern Alaska, USGS M-237. Spoon.
- 19, 20. *Mya truncata* var. *uddevalensis* Forbes (p. G38).
Figured specimen ($\times 1$), USNM 635287. Recent, St. Lawrence Island, northern Bering Sea, USGS M-1663. Same specimen as pl. 8, fig. 7.
19. Spoon.
20. Left valve, interior, showing pallial line and pallial sinus.



MYA FROM THE ICENIAN CRAG (ENGLAND), PLIOCENE BEDS, TUGIDAK ISLAND (ALASKA), POST-GLACIAL BEDS, JUNEAU (ALASKA), AND RECENT (GREENLAND AND ALASKA)

PLATE 10

- FIGURE 1. *Mya priapus* Tilesius (p. G40).
Engraving by Maslovsky from the original drawing by Berkhan, prepared under the direction of Georg Wilhelm Steller, Acad. Sci. St. Petersburg Mem., v. 8, pl. 9, 1822. Recent, mouth of Bolshaya River, southwestern Kamchatka.
- 2, 5, 6. *Mya priapus* Tilesius (p. G40).
Figured specimen ($\times 1$), USNM 635291. Recent, St. Lawrence Island, northern Bering Sea, USGS M-1662.
2. Left valve, exterior. Length 70 mm, height 48 mm, convexity (not including spoon) 17 mm.
5. Spoon.
6. Left valve, interior, showing pallial line and pallial sinus.
3. *Mya priapus* Tilesius (p. G40).
Figured specimen ($\times 1$), USNM 635292. Recent, St. Lawrence Island, northern Bering Sea, USGS M-1662.
Left valve, exterior, a specimen similar to the one in Berkhan's drawing, fig. 1.
4. *Mya priapus* Tilesius (p. G40).
Figured specimen ($\times 1$), USNM 635293. Recent, St. Lawrence Island, northern Bering Sea, USGS M-1662.
Spoon.
7. *Mya priapus* Tilesius (p. G40).
Figured specimen ($\times 1$), USNM 635294. Recent, St. Lawrence Island, northern Bering Sea, USGS M-1662.
Left valve, exterior. Same specimen as pl. 11, figs. 5, 6.



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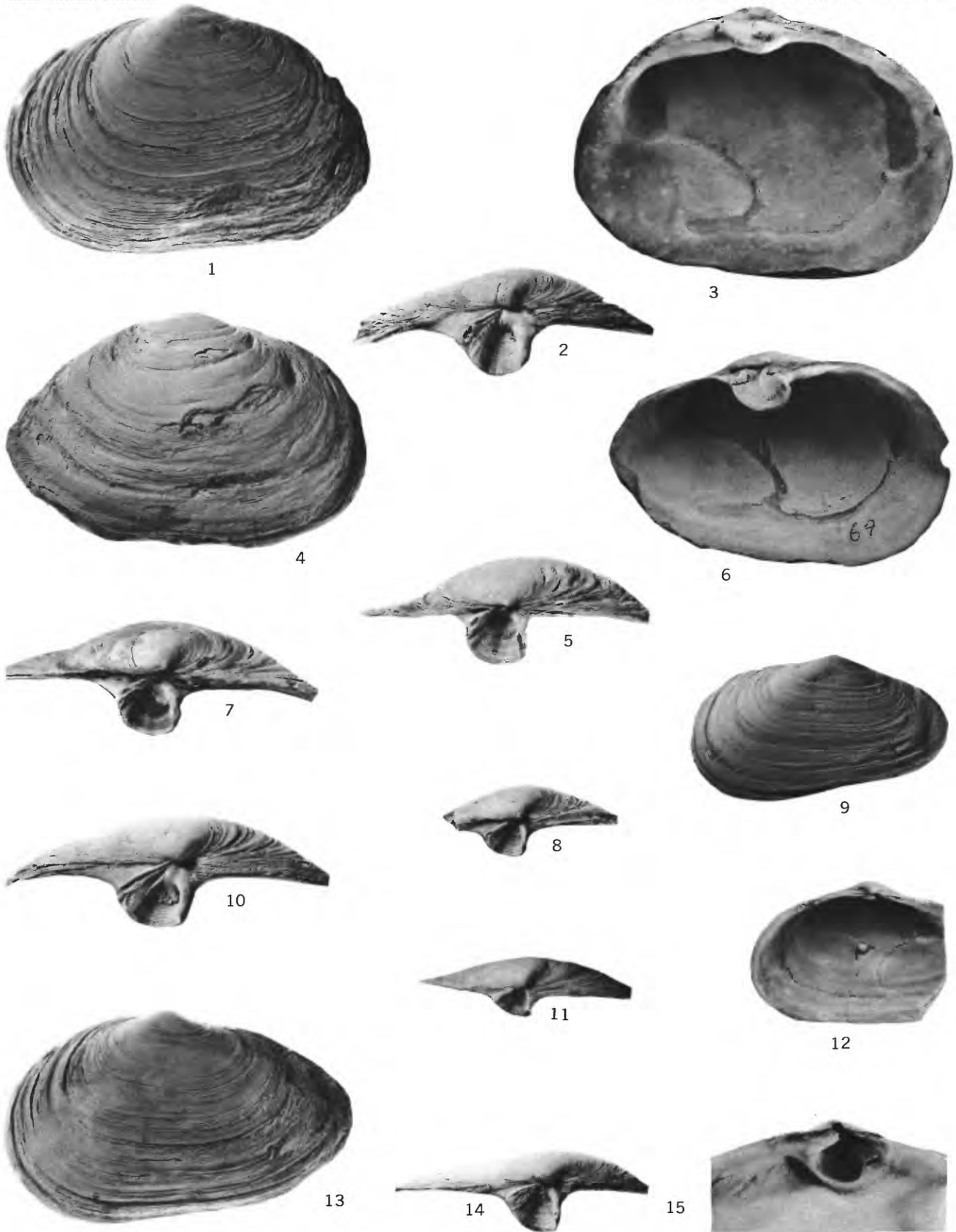
MYA FROM RECENT (KAMCHATKA AND ALASKA)

PLATE 11

FIGURES 1, 2, 3. *Mya priapus* Tilesius (p. G12).

Figured specimen ($\times 1$), USNM 644310. Postglacial(?) beds, mouth of Cottonwood Creek, north shore of Kachemak Bay, Cook Inlet, Alaska, USGS 5871. (*Mya japonica*, Dall, in Martin and others, 1915, p. 92; probably the source of Grant and Gale's, 1931, concept of *M. japonica*, followed by most modern Japanese authors).

1. Left valve, exterior. Length 69 mm, height 50 mm, convexity (not including spoon) 16 mm.
2. Spoon.
3. Left valve, interior, showing pallial line and pallial sinus.
4. *Mya priapus* Tilesius (p. G40).
Figured specimen ($\times 1$), USNM 635295. Recent, St. Lawrence Island, northern Bering Sea, USGS M-1662.
- 5, 6. *Mya priapus* Tilesius (p. G40).
Figured specimen ($\times 1$), USNM 635294. Recent, St. Lawrence Island, northern Bering Sea, USGS M-1662.
Same specimen as pl. 10, fig. 7.
5. Spoon; note comb-shaped ventral edge of ligamental callus.
6. Left valve, interior, showing pallial line and pallial sinus.
7. *Mya priapus* Tilesius (p. G40).
Figured specimen ($\times 1$), USNM 644311. Postglacial(?) beds, mouth of Cottonwood Creek, north shore of Kachemak Bay, Cook Inlet, Alaska, USGS 5871. Spoon.
8. *Mya* cf. *M. priapus* Tilesius (p. G42).
Figured specimen ($\times 1$), USNM 644312. Pleistocene, Wingham Island, Controller Bay, Alaska, USGS 4309. (*Mya* near *arenaria*, Dall, in Martin, 1908, p. 46). Spoon.
- 9, 11. *Mya pullus* Sowerby (p. G42).
Figured specimen ($\times 2\frac{1}{2}$), USNM 644313. Butleyan Stage, Red Crag, Neutral farm, Suffolk, England, USGS M-1669.
9. Left valve, exterior. Length 24 mm, height 14 mm, convexity (not including spoon) 4 mm.
11. Spoon.
12. *Mya pullus* Sowerby (p. G42).
Figured specimen ($\times 2\frac{1}{2}$), USNM 644314. Butleyan Stage, Red Crag, Neutral farm, Suffolk, England, USGS M-1669. Right valve, interior, incomplete, showing pallial line and pallial sinus.
10. *Mya priapus* Tilesius (p. G40).
Figured specimen ($\times 1$), USNM 644315. Postglacial(?) beds, mouth of Cottonwood Creek, north shore of Kachemak Bay, Cook Inlet, Alaska, USGS 5871. Spoon, showing comblike ventral margin of ligamental callus.
- 13, 14. *Mya priapus* Tilesius (p. G40).
Figured specimen ($\times 1$), USNM 644316. Postglacial(?) beds, mouth of Cottonwood Creek, north shore of Kachemak Bay, Cook Inlet, Alaska, USGS 5871.
13. Left valve, exterior. Length 65.5 mm, height 41 mm, convexity (not including spoon) 12 mm.
14. Spoon.
15. *Mya priapus* Tilesius (p. G24).
Figured specimen ($\times 2$), USNM 635296. Recent, St. Lawrence Island, northern Bering Sea, USGS M-1662. Right-valve chondrophore, showing round solution pit at dorsal end of chondrophore.



MYA FROM THE RED CRAG (ENGLAND), PLEISTOCENE BEDS, WINGHAM ISLAND (ALASKA), POST-GLACIAL BEDS, KACHEMAK BAY (ALASKA), AND RECENT (ALASKA)