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Cenozoic History of the Bering Land Bridge

The seaway between the Pacific and Arctic basins has often been a land route between Siberia and Alaska.

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Many facts of paleontology and biogeography (*1, 2*) indicate that the Old and New Worlds have sometimes been connected by a continuous land route that extended from Alaska across the present shallow floors of the Bering and Chukchi seas (Fig. 1) to Siberia. Recent geologic studies in western Alaska permit a more detailed consideration of the times at which the land bridge existed during the last 50 million years of Tertiary and Quaternary time. Some well-founded inferences can also be drawn concerning the climate and vegetation that prevailed on the land bridge during the last (Wisconsin) glacial interval, the most recent period during which the land bridge existed (*3*).

Character of the Sea Floor

The floor of the northeastern Bering Sea, Bering Strait, and Chukchi Sea is a wide platform extending from the Alaskan to the Siberian coast, covered by 100 to 500 feet of water (Fig. 2). The platform is separated from the much deeper floor of the western Bering Sea by a submarine escarpment more than 5000 feet high. A less abrupt escarpment descends from the northern edge of the Chukchi platform to the depths of the Arctic Ocean.

The Bering-Chukchi platform is monotonously flat. St. Lawrence Island, St. Matthew Island, the Pribilof and Diomede islands, and several smaller islands near the coast of Seward Peninsula are the only prominent topographic highs in the Bering Sea and Bering Strait. Herald Shoal, 42 feet deep, lies in the central Chukchi Sea. Aside from these, the surface of the platform is devoid of sharply defined topographic features. Bottom gradients are so small that they are difficult to measure (*4*, pp. 2–4). No features are recognized that can be interpreted as submerged valleys or submerged strand lines (*5*).

The nearly featureless topography of the surface evidently results from intense marine sedimentation during the last few thousand years (*6*). Very gentle slopes underlain by fine sand radiate from the mouths of the Yukon and Kuskokwim rivers, and a gently sloping ramplike surface underlain by fine sandy mud descends from the mouths of the Kobuk and Noatak rivers, through Kotzebue Sound, to the deeper part of the Chukchi Sea. The flat surface beneath the northwestern Bering Sea and the central Chukchi Sea is underlain by silt and clay containing numerous ice-rafted pebbles. Hydrogen sulfide is reported in many bottom samples from Chukchi Sea; its presence suggests rapid deposition in a reducing environment. Bering Strait has a sandy and rocky bottom that lies slightly below the general level of the adjoining parts of the Bering-Chukchi platform. The overdeepening and the coarser bottom sediments probably result from the strong, north-setting currents that pass through the strait.

Though the Bering-Chukchi platform happens to be a marine basin at present, the crustal structure below the veneer of young marine sediments resembles the structure of continental areas rather than the structure of typical ocean basins (*7*). Most of the present islands in the Bering Sea and Bering Strait are composed of typical continental rocks similar to those in parts of Siberia and Alaska.

Striking evidence for the structural continuity of the western Alaska and eastern Siberia land masses is provided by a comparison of the bedrock stratigraphy and structure of Wrangell Island on the continental shelf north of Siberia with the stratigraphy and structure of Lisburne Peninsula in northwestern Alaska (Fig. 3). Both areas are underlain by ancient sedimentary rocks of similar age, sequence, and character [compare geologic maps of Alaska and eastern Siberia (*8, 9*).] East-trending folds and faults that record the thrusting of older rocks northward over younger rocks on Wrangell Island correspond to south-southeast-trending folds and faults that record the thrusting of older rocks eastward over younger rocks on Lisburne Peninsula. The two areas evidently represent segments of a single mountain arc which once straddled the continents and is now partly submerged, extending from Wrangell Island eastward through Herald Island (in the Chukchi Sea), southeastward through Herald Shoal, and south-southeastward across Lisburne Peninsula.

The geological evidence indicates quite clearly that Siberia and Alaska represent segments of a single continental mass, separated by a segment only temporarily submerged, the Bering-Chukchi platform. Paleontological evidence indicates, however, that the land connection has been interrupted by tem-

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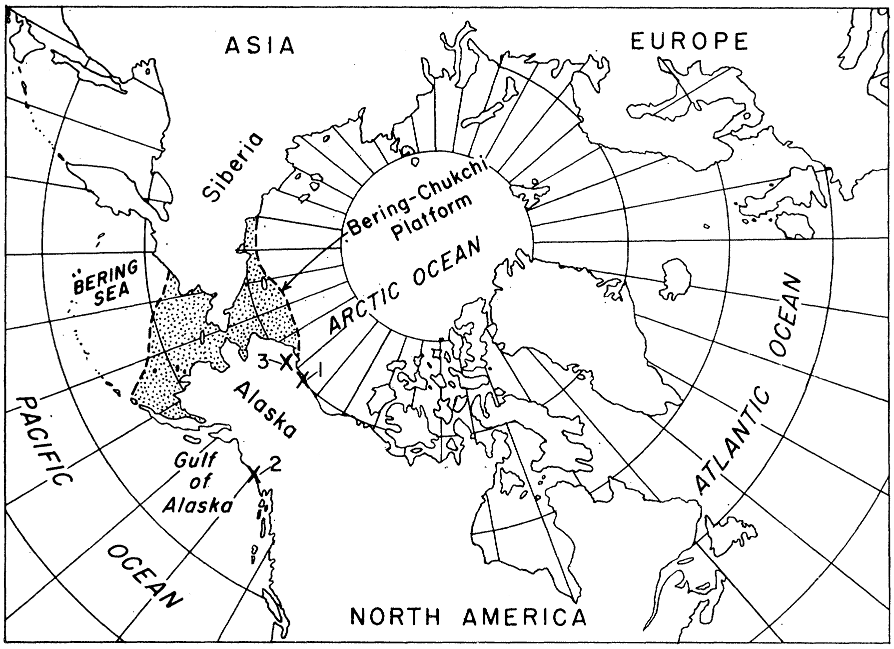


Fig. 1. The Bering land bridge as a barrier to marine organisms. Late Tertiary molluscan fauna at Camden Bay (1) on the Arctic coast of Alaska resembles contemporary faunas from the North Atlantic Ocean and differs sharply from contemporary faunas from the Gulf of Alaska (2); the Bering-Chukchi platform must have been a land barrier separating the Arctic Ocean from the Pacific Ocean when the Camden Bay fauna was living. The first opening of a marine connection between the Pacific Ocean and the Arctic Ocean is recorded by the *Neptunea* complex from the Gubik formation along the lower Colville River (3).

porary submergence in this area several times during the last 50 or 60 million years.

Land Bridge

Nonmarine sediments of Eocene age (containing *Sequoia* and other plant remains) are found on St. Lawrence Island (*10*), and marine sediments tentatively assigned a Pliocene age are found in several localities on Seward Peninsula (*11*) and on the Pribilof Islands (*12*). Aside from these isolated occurrences, no Tertiary sediments (1 to 60 million years old) have yet been surely identified in western Alaska north of the Aleutian chain. Consequently we must continue to rely, for a while, upon indirect evidence—evidence for and against intercontinental and interoceanic faunal migrations—in attempting to piece together the Tertiary history of the land bridge.

Simpson shows that major faunal interchanges took place between the continents and thus that a land connection existed in early Eocene, late Eocene, early Oligocene, late Miocene, and middle-to-late Pliocene time (*1, 13*). An almost complete lack of interchange during middle Eocene time seems to indicate the temporary existence of a water barrier on the Bering-Chukchi platform; reduced interchange during later Tertiary time may merely reflect the existence of unfavorable conditions for faunal migrations through the area of the land bridge (*1*, pp. 654–656).

A land bridge for vertebrates is, of course, a land barrier to marine organisms. The existence of such a barrier in the Bering-Chukchi region throughout most of Tertiary time is indicated by molluscan faunas that show no relationship to contemporaneous Atlantic faunas in sediments of early, middle, and late Tertiary age along the coast of the Gulf of Alaska (*14*) and by a molluscan fauna closely related to faunas of middle Tertiary age from the North Atlantic in beds of Miocene or Pliocene age at Camden Bay on the arctic coast of Alaska (*15*) (Fig. 1). Evidently molluscan populations dwelling in the North Atlantic could migrate freely across the northern edge of North America to the arctic coast of Alaska but were denied access to the North Pacific by a land barrier in the area of the Bering-Chukchi platform.

We may conclude that the area of the Bering and Chukchi seas lay above sea level throughout most of the last 50 or 60 million years. Water barriers between the continents existed only briefly, if at all, from middle Eocene until middle Pliocene time, and they resulted from crustal warping. The present basins of the Bering and Chukchi seas could not have come into existence until after the major exchange of land vertebrates that took place during middle-to-late Pliocene time, a few million years ago.

Initiation of Seaway

At some remote time near the beginning of the Pleistocene epoch, approximately a million years ago, the Bering-Chukchi platform was depressed, the Bering and Chukchi coasts of Alaska assumed approximately their present forms, and the water barrier between the continents came into existence. The outline of the original marine basin is recorded today by an abandoned wave-cut cliff that is traceable, with minor interruptions, from the Arctic Coastal Plain of Alaska southward to the Yukon River; a similar feature can be traced around the perimeter of isolated bedrock highlands on St. Lawrence Island (Fig. 3) (*16, 17*). The ancient wave-cut cliff is separated from the present strand by coastal lowlands ranging in width from a few hundred feet to a few miles; all marine sediments of Pliocene or Pleistocene age known in western Alaska lie seaward of the cliff.

In most areas in northwestern Alaska the cliff marks the abrupt coastward termination of a rolling upland that evidently represents an ancient erosion surface, now deeply dissected by valleys graded to present sea level (*18*). A similar rolling surface forms the summit of the isolated bedrock highlands of St. Lawrence Island and the cliffed islands off the coast of Seward Peninsula.

The old wave-cut cliff has not been positively identified and may be absent along the Alaskan coast south of the Yukon River; it is probable, nevertheless, that the southern part of the Bering-Chukchi platform was submerged at about the same time, for the earliest recognized molluscan faunas lying seaward of the cliff in the north are closely related to faunas of the same age from the Pribilof Islands and the Pacific Ocean.

The time at which the Bering-Chukchi platform was depressed to form a seaway connecting the Pacific Ocean with the Arctic Ocean is established with fair precision by stratigraphic evidence contained in the famous gold-bearing marine sediments at Nome and by recent studies of the history of the genus *Neptunea*, a large marine snail that was confined to the Pacific basin during most of Tertiary time and that first appears in the Atlantic basin in beds of earliest Pleistocene age.

The coastal plain at Nome is underlain by marine sediments that record three distinct intervals during which sea level stood as high as, or higher than, it does at present and during which water temperatures were warmer than they are at present (*11, 19, 20*). The two younger sets of marine sediments probably accumulated during the last (Sangamon) and the next-to-last (Yarmouth) Pleistocene interglacial intervals. The oldest may have accumulated during the first (Aftonian) interglacial interval, or it may have accumulated at about the beginning of Pleistocene time, prior to the lowering of sea level that accompanied the first (Nebraskan) glacial interval. The earlier age is suggested by the fact that these oldest marine deposits at Nome have yielded a mollusk, *Pecten hallae,* belonging to a subgenus (*Fortipecten*) that was previously known only from sediments of Pliocene age in Japan and Sakhalin (*11*), and a foraminifer, *Pseudopolymorphina ishikawaensis,* known previously only from sediments of Miocene or Pliocene age in Japan (*21*). The second known North American occurrence of *Fortipecten* was discovered in 1957, far north of Bering Strait, at the inner edge of the coastal plain at Kivalina, Alaska (*22*) (Fig. 3).

Marine sedimentation at Nome began, then, during or before the first Pleistocene interglacial age. The presence of *Fortipecten* and *Pseudopolymorphina ishikawaensis* in the oldest marine sediments at Nome and of *Fortipecten* at Kivalina indicates that by late Pliocene or early Pleistocene time a new seaway extended across the Bering-Chukchi platform, affording a migration route northward for marine organisms that had previously been confined to the North Pacific Ocean.

Evidence bearing on the age of the late Cenozoic submergence of the Bering-Chukchi platform is also provided by an unpublished recent study of the genus *Neptunea* by F. S. MacNeil: "The genus *Neptunea* apparently originated in the Pacific Ocean during early Tertiary time. Its earliest occurrences in the Atlantic province are in the basal Pleistocene deposits of England, Belgium, and

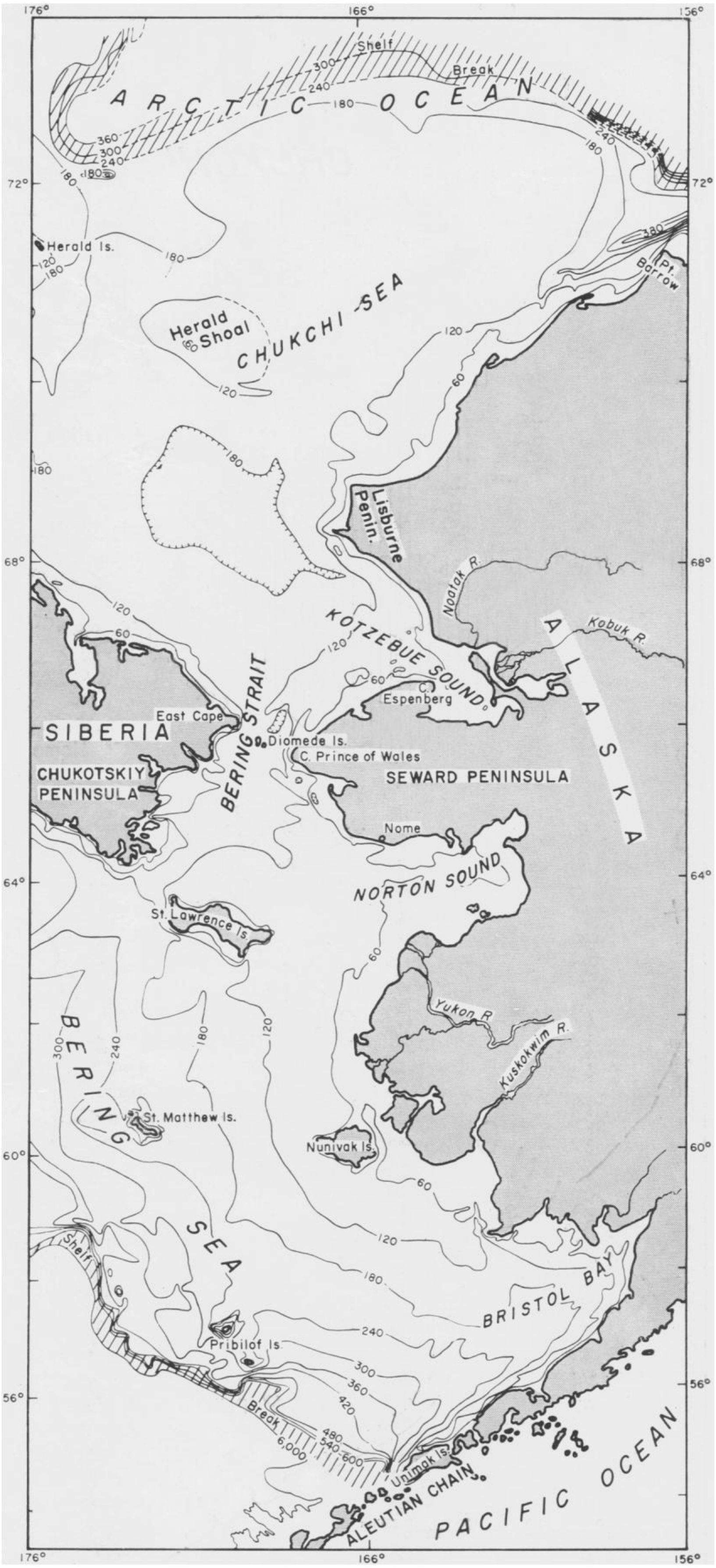
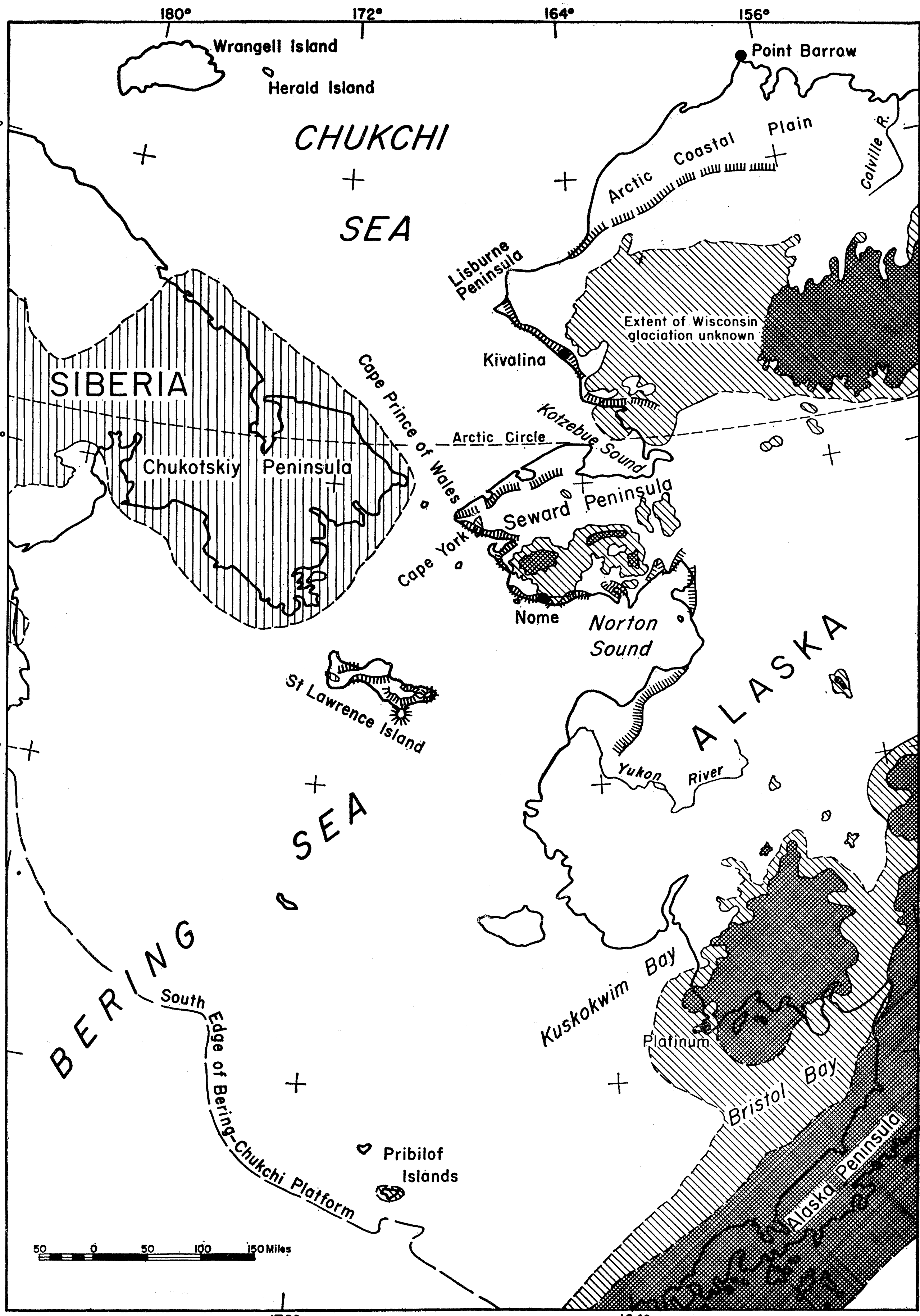


Fig. 2. Topography of the Bering-Chukchi platform (Mercator projection). Depth contours in feet. [Modified from U.S. Coast and Geodetic Survey charts Nos. 9032 and 9400]



180°
172°
164°
156°
Wrangell Island
Herald Island
Point Barrow
70°
CHUKCHI
SEA
Arctic Coastal Plain
Colville R.
Lisburne Peninsula
Extent of Wisconsin glaciation unknown
Kivalina
SIBERIA
Cape Prince of Wales
Kotzebue Sound
Arctic Circle
66°
Chukotskiy Peninsula
Seward Peninsula
Cape York
Nome
Norton Sound
ALASKA
St Lawrence Island
62°
Yukon River
BERING SEA
South Edge of Bering-Chukchi Platform
Kuskokwim Bay
Platinum
58°
Bristol Bay
Alaska Peninsula
Pribilof Islands
50 0 50 100 150 Miles
172°
164°

the Netherlands, where there is a variable population that contains varieties foreshadowing both of the living Atlantic species, the more northern *N. despecta,* and the more southern *N. antiqua.* An even larger and more variable intergrading population of *Neptunea* is found in the lower part of the Gubik formation along the Colville River in the Arctic coastal plain of Alaska [Fig. 1, location 3]. The collections from the lower Gubik formation include varieties similar to those originally found in Europe, as well as varieties that approach the typically North Pacific and Siberian living species, *N. ventricosa*" (*23*).

The sudden appearance of *Neptunea* at the beginning of Pleistocene time in Europe suggests that the genus had found a migration route from the Pacific to the Arctic basin a short time earlier, and the presence of possibly ancestral forms on the Arctic coastal plain of Alaska suggests that the lower part of the Gubik formation may be of late Pliocene or earliest Pleistocene age.

The available lines of evidence seem to agree in pointing to a submergence of the Bering-Chukchi platform near the end of the Pliocene epoch, approximately a million years ago. (i) The evidence of strong faunal interchange of land mammals between Eurasia and North America during middle and late Pliocene time indicates that the water barrier could not have come into existence until shortly before the beginning of Pleistocene time. (ii) The stratigraphic record at Nome indicates that the first marine deposits there were laid down during or before the first Pleistocene interglacial interval. (iii) The distribution in time and space of fossil *Neptunea* indicates that at, or shortly before, the beginning of the Pleistocene epoch a marine migration route opened, permitting molluscan populations from the North Pacific Ocean to invade arctic waters, and then spread along the northern margin of the continents into Atlantic waters; and (iv) the ancient wave-cut cliff lying at the inner edge of coastal plain areas throughout much of western Alaska marks the former shore of this early waterway.

Fig. 3 (at left). Pleistocene geology of western Alaska and eastern Siberia [Lambert conformal conic projection (*48*)]. The limits of glaciation are shown by a solid line (or by a dashed line where there is uncertainty).

Areas covered by ice during Wisconsin glacial stage.

Areas covered by ice during Illinoian glacial stage.

Areas in Siberia and Saint Lawrence Island covered by glacial ice of unknown age.

Old wave-cut scarp.

Sedimentation and Crustal Warping

One cannot assume, of course, that the surface topography of the Bering-Chukchi platform has remained unchanged throughout the lengthy period since it first submerged, near the beginning of the Pleistocene epoch. In the course of the long emergence during Tertiary time, a stream-sculptured topography must have developed that would now lie buried beneath the marine sediments that form the present monotonously flat sea floor. I believe that the rolling upland surface extending inland from the old wave-cut cliff throughout much of northwestern Alaska and the similar rolling surface that forms the summit area of the islands in Bering Sea represent remnants of this pre-Pleistocene stream-sculptured landscape persisting in areas that either formed highlands on the Tertiary land bridge or that were not involved in the general submergence that brought the Bering and Chukchi seas into existence. Herald Island and Herald Shoal appear to be submerged remnants of a low mountain range that once extended from Lisburne Peninsula, Alaska, to Wrangell Island, Siberia.

It is likely, then, that a stream-sculptured bedrock topography, having a relief of several hundred feet, lies buried beneath the Pleistocene and Recent marine sediments that mantle the Bering-Chukchi platform; it is also likely that the floors of the Bering and Chukchi seas have become progressively shallower, due to the deposition of marine sediments, during each succeeding interglacial interval of high sea level.

Crustal warping during Pleistocene time has affected the depth and extent of parts of the Bering and Chukchi seas; however, only along the south coast of western Seward Peninsula has the crustal disturbance been of a magnitude likely to affect the duration of temporary land connections between Siberia and Alaska during Pleistocene time. Even here, the effect of crustal warping has probably been to make Bering Strait shallower during successively more recent interglacial intervals.

The spectacular local deformation in western Seward Peninsula apparently results from repeated movement along an inferred fault that lies just offshore at Cape York and that may extend westward to or beyond Cape Prince of Wales, the eastern portal of Bering Strait (Fig. 3). In the Cape York–Cape Prince of Wales area, the ancient wave-cut cliff lies at the inner edge of a marine terrace as much as 3 miles wide that has been unevenly warped 300 to 750 feet above sea level (*17, 24*). The terrace is dissected by valleys graded approximately to present sea level, and the valleys contain glacial deposits of probable Illinoian (third glacial) age; thus, most of the crustal warping that resulted in uplift of the terraces took place prior to Illinoian time.

Elsewhere, the Alaskan coast south of the Yukon River appears to have been submerged by more than 100 feet during late Pleistocene time, probably as a result of isostatic adjustment to the heavy sediment load that has been delivered to the eastern Bering Sea by the Yukon and Kuskokwim rivers and to the weight of the large glaciers that invaded Kuskokwim Bay and Bristol Bay during Illinoian(?) and Wisconsin time (Fig. 3). The deeply indented fjord coast of southern and eastern Chukotskiy Peninsula may also have subsided in late Pleistocene time in response to a heavy load of glacial ice. Kotzebue Sound has been enlarged by slight tectonic subsidence of its southern shore east of Cape Espenberg (Fig. 2) since Illinoian(?) time (*25*).

Other parts of the Bering and Chukchi sea coasts appear to have remained relatively stable throughout Pleistocene time. Marine sediments containing faunas ranging in age from late Pliocene or early Pleistocene (*12*) to late Pleistocene (*26*) are found near present sea level on the Pribilof Islands, and old beach ridges recognizable on topographic maps are abundant below altitudes of 125 feet, and lacking at higher altitudes, on St. Lawrence Island, on the shores of Norton Sound, and along most of the Alaskan coast of Chukchi Sea.

The effects of sedimentation and crustal warping upon the depth and width of the Bering-Chukchi platform may be summarized as follows.

1) The deposition of marine sediments has tended to fill the marine basin and to lead to progressively shallower water during each succeeding interglacial interval.

2) Submergence due to isostatic loading of the Alaskan coast south of Norton Sound and of the south and east coasts of Chukotskiy Peninsula tended to widen and deepen the eastern and northwestern parts of the Bering Sea during late Pleistocene time. The submergence seems to have been localized in areas within a few tens of miles of the present coast, for St. Lawrence Island and the Pribilof Islands do not appear to have been affected.

3) Western Seward Peninsula is a tectonically active area. Deformation of the magnitude recognized between Cape York and Cape Prince of Wales would have resulted in appreciable changes in the depth of Bering Strait if the inferred coastal fault extends west of Cape Prince of Wales. Bering Strait may have been considerably deeper during early Pleistocene time than during late Pleistocene time.

One must conclude that a seaway at least as deep as the present one separated Siberia from Alaska during each Pleistocene interglacial interval and that the land bridge was open only when the surface of the sea lay considerably below its present level.

Fluctuating Sea Level

The repeated growth and disappearance of large glaciers during the Pleistocene epoch was accompanied by repeated changes in the position of sea level. The surface of the sea lay at least 100 feet higher than it does at present during the warmest interglacial intervals, when glacial ice disappeared almost completely throughout the world, and sea level was lowered by more than 300 feet during the most intense glacial intervals (*27*).

The application of radiocarbon dating to oceanographic and stratigraphic studies of late Pleistocene marine sediments has begun to yield a more detailed knowledge of the positions of sea level during the last 10,000 years and at least a sparse knowledge of positions of sea level during the preceding 30,000 years (Fig. 4). Curves showing the late Wisconsin and post-Wisconsin rise in sea level from – 180 feet to its present position are given with substantial agreement in at least three recent publications (*28*). Submerged shore-line features at depths of from – 150 to – 180 feet and from – 60 to – 80 feet in the Gulf of Mexico off the coasts of Texas (*29*) and Florida and Alabama (*30*) apparently record brief interruptions that occurred about 11,000 to 8000 years ago (*31*) in the otherwise steady and rapid late Wisconsin rise in sea level.

Most authors (*32*) have considered it probable that during earlier Wisconsin time sea level rose slowly but steadily from its lowest position (deeper than – 300 feet), held more than 35,000 years ago, to the position of – 180 feet, held 11,000 years ago; however, recently published radiocarbon dates from the Mississippi delta (*33*) seem to indicate that an initial rise from a depth of more than – 300 feet to a depth of less than – 150 feet (and possibly less than – 100 feet) was accomplished more than 35,000 years ago. The few radiocarbon-dated specimens having ages between 35,000 and 11,000 years, then, seem to record a renewed but lesser lowering of sea level to about – 200 feet during the interval from 25,000 to 13,000 years ago (*34*).

This modest reduction in sea level following an interval of relatively high sea level during middle Wisconsin time seems to be represented in a submarine drill core from Atchefalaya Bay, Louisiana, in which marine sediments 11,950 years old overlie the subaerially weathered surface of older marine sediments 27,700 years old at a depth of about – 110 feet (*35*). The evidence for relatively high sea level during the interval from 35,000 to 25,000 years ago, and for renewed lowering of sea level during the interval from 25,000 to 13,000 years ago, also accords closely with the radiocarbon-dated history of the final advance of the continental ice sheet from the vicinity of the Great Lakes to the Ohio River after middle Wisconsin time (*36*).

My interpretation of the history of sea level during Wisconsin time may be summarized as follows (see Fig. 4). Sea level was reduced more than 300 feet at the glacial maximum during early Wisconsin (Iowan ?) time, more than 35,000 years ago. Sea level then rose, apparently during an interval of relatively mild climates within the Wisconsin glacial interval, and seems to have been higher than – 150 feet during the interval from 35,000 to 25,000 years ago; the edge of the continental ice in North America at that time lay somewhere north of the Great Lakes (*37*).

The glacial advances of late Wisconsin time, reaching the latitude of the Ohio River, were reflected by a renewed lowering of the sea to a level of about – 200 feet. During the oscillating retreat represented by moraines of Tazewell, Cary, and Mankato age in the central United States, sea level rose again to a position between – 150 and – 180 feet. Submerged shore-line features at – 150 to – 180 feet in the Gulf of Mexico record a stable position of sea level about 11,000 or 12,000 years ago that may coincide with or may immediately precede the Valders of Thwaites (*38*) and Mankato readvances in the Great Lakes region.

A sharp warming of air and sea temperatures throughout the world from 11,000 to 9000 years ago was accompanied by an almost catastrophic retreat of the continental glaciers. Sea level rose to a new stable position, marked by submerged shore-line features at depths of – 60 to – 80 feet in the Gulf of Mexico; this position was occupied about 8000 years ago and may have coincided with or immediately preceded the readvance of the North American ice sheet to the vicinity of Cochrane, Ontario. The rapid rise in sea level began again about 7000 years ago, and sea level has lain within 10 feet of its present position throughout the last 5000 years.

Sea Level and the Land Bridge

The present-day surface of the Bering-Chukchi platform slopes so gently that changes in sea level of the magnitude recorded during the last 40,000 years would result in great modifications in the distribution of land and sea. A reduction in sea level amounting to 60 to 80 feet—the level at which sea level stood about 8000 years ago—would drain shallow indentations such as Norton Sound and Kotzebue Sound, and the west coast of Alaska would be considerably less deeply embayed (Fig. 5, A). If sea level were lowered 150 to 180 feet—the position recorded by submerged beaches 11,000 years old in the Gulf of Mexico—Bering Strait would be drained, and an intercontinental land connection would extend from St. Lawrence Island northward to the Diomede Islands (Fig. 5, C). If sea level lay only 120 feet below its present position—its approximate position 25,000 to 35,000 years ago—the continents would again be separated by a shallow channel locally only 20 miles wide (Fig. 5, B). A reduction in sea level of 300 feet—to the level recorded during early Wisconsin time more than 35,000 years ago—would result in the exposure of nearly all of the Bering-Chukchi platform, and Alaska and Siberia would be joined by an almost featureless plain extending nearly 1000 miles from the north shore of a shrunken Bering Sea to the south shore of the Arctic Ocean (Fig. 5, D).

Sedimentation on the Bering-Chukchi platform has been intense and rapid since the latest inundation by the rising sea, and the surface that was exposed during the last period of low sea level evidently lies buried beneath a cover of Recent marine sediments at least several tens of feet thick. Thus the intercontinental land connection may have been inundated still earlier in the course of the late glacial rise in sea level than is suggested by the present topography of the sea bottom.

Comparison of the sea floor topography with recorded fluctuations in sea level, then, suggests that (i) a land bridge more than 1000 miles in north-south width connected Siberia and Alaska during the most intensely glacial phase of early Wisconsin time, over 35,000 years ago; (ii) the land connection was greatly narrowed and probably severed when sea level rose to within less than 150 feet of its present position during a cool but prolonged middle Wisconsin interglacial interval, 25,000 to 35,000 years ago; (iii) the land connection resumed or widened again when sea level fell to about − 200 feet during the late Wisconsin glacial advances, from 25,000 to 12,000 years ago; (iv) the land bridge was closed by the rising sea for the last time between 10,000 and 11,000 years ago.

The land bridge ceased to exist at a time when world climates still were far

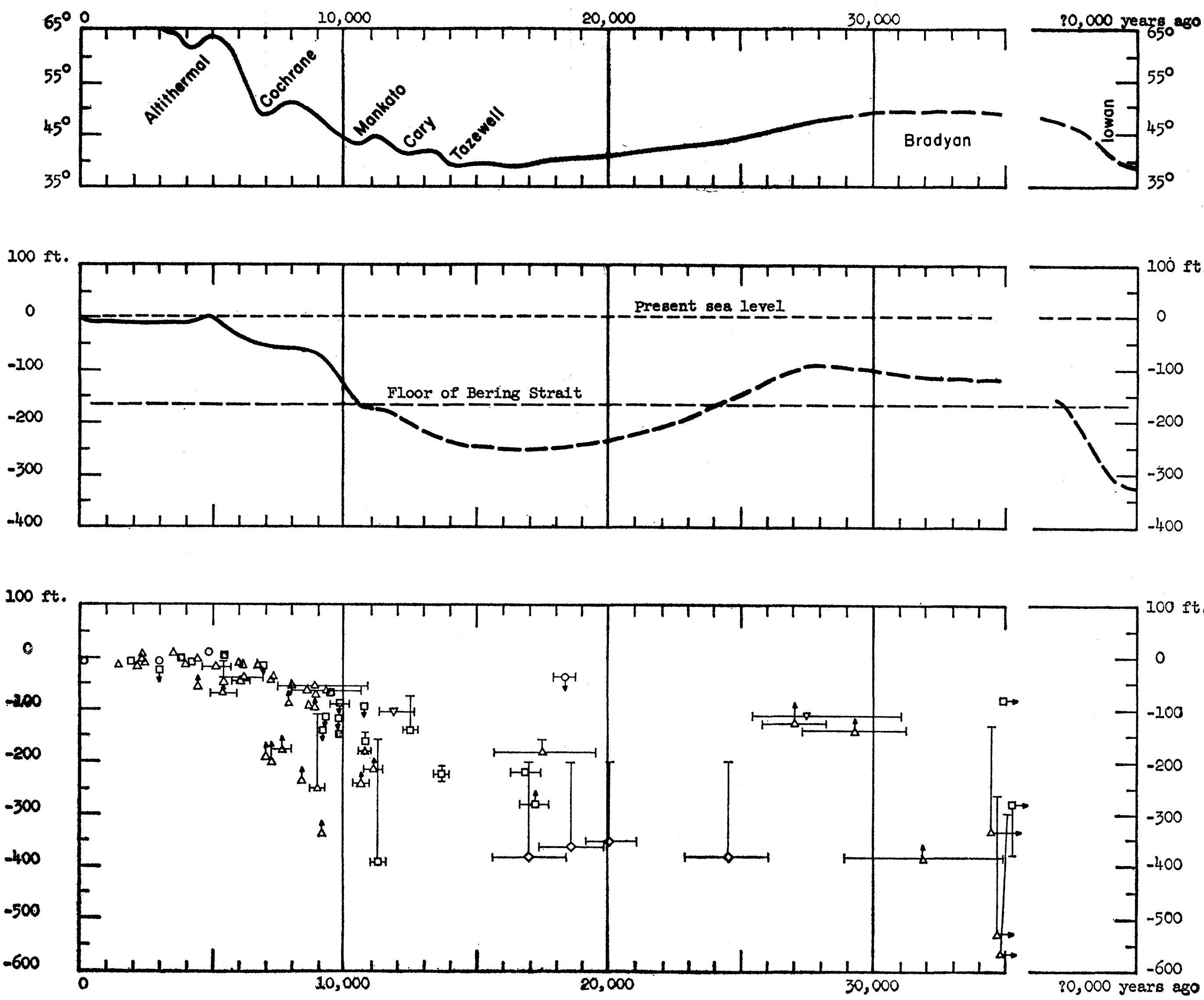


Fig. 4. Changes in sea level compared with fluctuations in the position of the margin of the continental ice sheet during and since the last glacial interval (*49*). (Top) The heavy line represents the position (latitude) of the southern limit of the continental ice sheet in North America. (Middle) The heavy line represents the position of sea level at various points in time. (Bottom) Past positions of sea level are indicated by radiocarbon dating of various specimens. The type of specimen is indicated as follows: (triangle, vertex up) shell; (square) wood; (circle) peat; (triangle, vertex down) organic residue in marine mud; (diamond) calcareous algae. The specimens are plotted at the depths at which they were collected. The vertical arrows indicate that the sea level was either lower or higher than the specimen. The vertical bars indicate the probable position of the sea level when the specimen was deposited. The horizontal bars indicate probable limits of dating error. The specimens without bars have a probable error too small to plot. A horizontal arrow indicates that the specimen is older than 35,000 years.

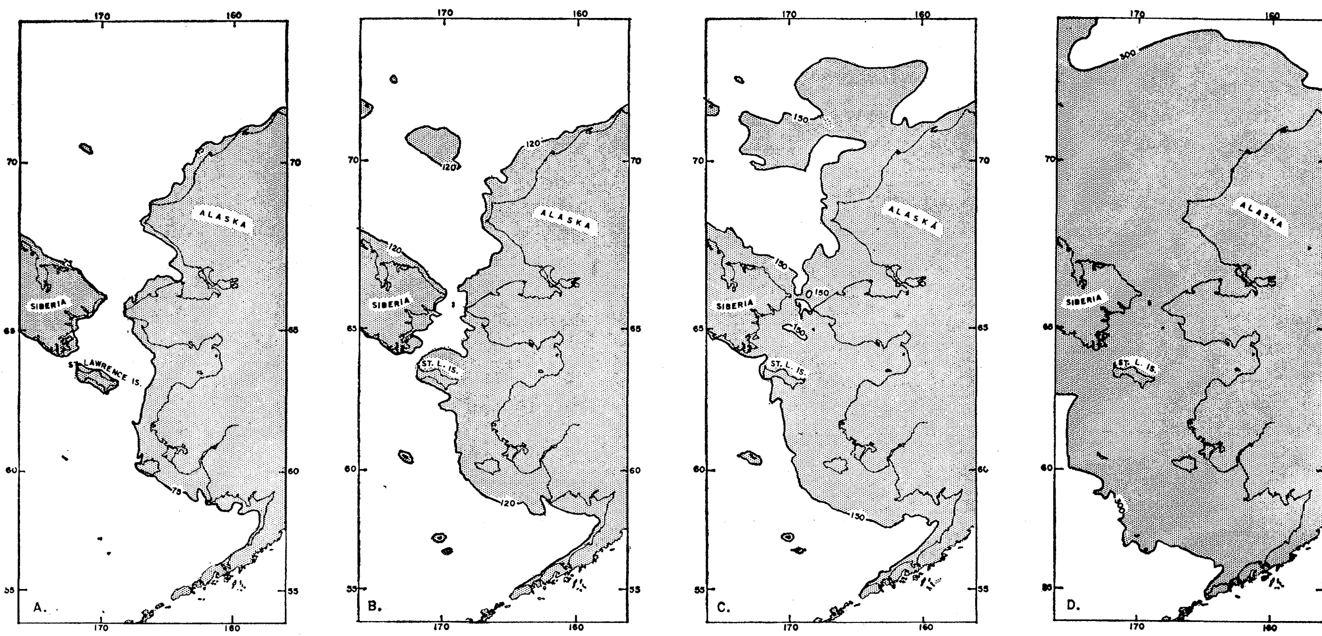


Fig. 5. The probable outlines of the Alaskan and Siberian coasts when the sea level was (A) 75 feet, (B) 120 feet, (C) 150 feet, and (D) 300 feet below the present level. Shading indicates areas above sea level.

more rigorous than they are at present and when the southern margin of the continental ice in east-central North America still stood near the United States–Canada border. The thickness of marine sediments on the Bering-Chukchi platform was less during earlier glacial ages, and consequently, smaller areas of the platform lay high enough to be exposed at any given position of sea level. It is probable that the land bridge was closed even earlier in the waning phases of the pre-Wisconsin glacial intervals, and it seems unlikely that the Bering land bridge was ever open during the Pleistocene epoch at a time when world climates were less severe than those of late Wisconsin time.

Glaciated and Ice-Free Areas on the Land Bridge

Most parts of the Bering land bridge have always been free of glacial ice, but glaciers did invade several areas near the present shores of Alaska and Siberia during the Illinoian and Wisconsin glacial intervals (Fig. 3) and probably during earlier glacial intervals. Small, local glaciers have existed in the past on St. Lawrence Island and possibly on the Pribilof Islands (*26*). However, even when the more extensive Illinoian glaciation was at its height, a broad ice-free corridor extended from central Alaska across the land bridge to eastern Siberia. Glaciers may have barred access to the central parts of North America and Asia, but they have never constituted a barrier to migration between eastern Siberia and central Alaska.

Forest or Tundra of the Land Bridge?

Recent paleobotanical studies in western Alaska establish clearly that the land bridge supported only treeless tundra during its most recent period of existence in late Wisconsin time. Moreover, a comparison of the vegetation of Alaska and Siberia suggests that the land bridge never supported forests during Pleistocene time.

The present-day continental limit of spruce forest in Alaska extends from the base of the Alaska Peninsula northward, parallel to the present coast but inland a few miles, to Kotzebue Sound and thence eastward, parallel to and a bit north of the Arctic Circle (*39*). During the Wisconsin glacial interval the western limit of spruce forest in Alaska lay even farther eastward. Pollen studies in the Cook Inlet area (on the south coast of Alaska east of the Alaska Peninsula) indicate, for example, that the first vegetation to take root on glacial drift of Wisconsin age consisted of treeless tundra and that the first trees did not appear until several thousand years after the area was deglaciated and after the Bering land bridge was drowned by the rising sea (*40*). Griggs has shown, moreover, that the spruce forest has been extending rapidly westward into tundra areas on the Alaska Peninsula during recent decades; the edge of the forest in southwestern Alaska now lies farther westward than it has lain for many thousands of years (*41*). Fossil pollen contained in pond sediments overlying drift of Wisconsin age near Platinum, several tens of miles west of the present limit of spruce in the Kuskokwim Bay area, records only tundra vegetation (*42*).

Paleobotanical studies in several parts of Seward Peninsula that lie west of the present continental limit of spruce, indicate that there, too, the vegetation consisted of tundra during the Wisconsin glacial interval. The continental timber line advanced temporarily several tens of miles beyond its present limits during a brief interval 8000 to 10,000 years ago, when summers were warmer than they are at present (*20, 43*), but this warm interval began at almost the moment that the rising sea closed the Bering land bridge. It is clear that forests never extended onto the land bridge beyond the present shores of the Bering and Chukchi seas during the Wisconsin glacial interval.

Little direct evidence is available concerning the character of the vegetation on the land bridge during its earlier periods of existence in Pleistocene time. However, comparisons of the living vegetation of Alaska and eastern Siberia and of the fossil floras of Pleistocene age known from both regions suggest that the tundra vegetations of the two continents have merged repeatedly and recently but that the forest vegetations have not been in contact with one another for a long time, probably not since the beginning of Pleistocene time. The tundra vegetation is made up largely of circumboreal species ranging widely on both continents (*44*), but no tree species is recognized as occurring in both Siberia and Alaska (*45*). In even the oldest of the Siberian Pleistocene floras the forest elements are Asiatic (*46*). The evidence of plant geography seems to indicate that the Bering land bridge has supported only tundra vegetation and that no continuous belt of forest ever extended across the land bridge from Siberia to Alaska during the Pleistocene epoch.

Pleistocene Climates on the Land Bridge

Several lines of evidence point to the conclusion that a severe arctic climate prevailed on the Bering land bridge during the Wisconsin glacial interval and presumably during the earlier periods of its existence within the Pleistocene epoch. The conclusion that the land bridge existed only during major glacial intervals leads to the inference that the climate there was at least as severe as the present climate around the shores of Bering and Chukchi seas. The paleobotanical evidence that the land bridge supported only tundra vegetation is most easily explained if one assumes that summers were too short and too cold to support forest vegetation (*47*). Finally, studies of fossil frost features on Seward Peninsula indicate that during the Wisconsin glacial interval summers were shorter and colder than they are at present, that winters were as severe as at present, and that snowfall in lowland areas was thin and patchy (*20*).

Conclusions

The interpretation of the Cenozoic history of the Bering land bridge offered in this article, resting as it does upon a synthesis of fragmentary data from many areas and several disciplines, must be regarded as tentative and rather speculative. Each new collection of Cenozoic mollusks from western Alaska, each new stratigraphic study of another coastal-plain area along the Bering or Chukchi coast, each new radiocarbon date relating to a position of sea level, can force some modification of the history as I have interpreted it. Much could be learned from submarine cores on the Bering-Chukchi platform deep enough to penetrate through the Recent marine sediments into older deposits. The most serious gap in present knowledge, however, is the lack of data on the stratigraphy and structure of the sediments in the deformed marine terraces of western Seward Peninsula adjoining Bering Strait; future studies in this area may result in profound modifications of the history that I have proposed here.

Though uncertainties persist, to be resolved by future work, these generalizations accord with the information now available. (i) The data of vertebrate paleontology suggest strongly that a seaway existed across the Bering-Chukchi platform during middle Eocene time, but physical evidence of its existence has not yet been found in Alaska or on the islands of the Bering Sea. (ii) The Bering-Chukchi platform was a land area during most of the remainder of the Tertiary period. (iii) A seaway across the Bering-Chukchi platform came into existence after middle Pliocene time and earlier than the beginning of the Pleistocene epoch. (iv) The continents were separated by a seaway on the Bering-Chukchi platform during each interglacial interval of the Pleistocene, and they were connected by a land bridge during each glacial interval. (v) Rising sea level eliminated the land bridge for the last time between 10,000 and 11,000 years ago. (vi) During Wisconsin time the land bridge had an arctic climate characterized by cold summers and severe winters; it supported treeless tundra vegetation; and animals migrating between the continents had to adapt to life in a tundra environment. The same conclusion is applied, with less conviction, to intercontinental land connections on the Bering-Chukchi platform during earlier glacial intervals.

References and Notes

G. G. Simpson, *Bull. Geol. Soc. Am.* 58, 613 (1947).
2. P. J. Darlington, *Zoogeography* (Wiley, New York, 1957); E. Hultén, *Outline of the History of Arctic and Boreal Biota during the Quaternary Period* (Stockholm, Sweden, 1937).
3. The geologic and paleoclimatic discussion is based chiefly upon field investigations which I made on Seward Peninsula, from 1946 to 1950, and in various parts of western Alaska, from 1955 to 1958. Publication is authorized by the director of the U.S. Geological Survey, Washington, D.C.
4. E. C. Buffington, A. J. Carsola, R. S. Dietz, *U.S. Navy Electronics Lab. Rept. No. 204* (1950), pt. 1.
5. R. S. Dietz, *U.S. Navy Electronics Lab. Rept. No. 148* (1949), pt. 9, pp. 1–2 (confidential).
6. The discussion of bottom sediments is summarized from E. C. Buffington *et al.* (*4*), pp. 4–15, and from A. P. Lisitsin, *Proc. Acad. Sci. U.S.S.R., Sect. Geol. Sci.* 118, 373 (1958) (Consultants Bureau translation, p. 45).
7. Seismic evidence confirming the continental character of the Bering-Chukchi platform is given by J. Oliver, M. Ewing, F. Press [*Bull. Geol. Soc. Am.* 66, 1063 (1955)].
8. J. T. Dutro and T. G. Payne, "Geologic map of Alaska, 1:2,500,000," *U.S. Geol. Survey Publ.* (1957).
9. D. V. Nalivkin, Ed., "Geologic map of the U.S.S.R., 1:2,500,000," *Ministry Geol. (U.S.S.R.) Publ.* (1956), sheet 6.
10. R. W. Chaney, *Science* 72, 653 (1930).
F. S. MacNeil, J. B. Mertie, H. A. Pilsbry, *J. Paleontol.* 17, 69 (1943).
12. W. H. Dall, *J. Wash. Acad. Sci.* 9, 1 (1919); G. D. Hanna, *Am. J. Sci.* 48, 216 (1919).
13. Simpson also discusses the evidence for faunal interchanges during Pleistocene time (*1*).
14. D. J. Miller, *U.S. Geol. Survey Map No. OM-187* (1957); F. S. MacNeil, U.S. Geological Survey paleontologist, oral communication, 1958.
15. F. S. MacNeil, *U.S. Geol. Survey Profess. Paper No. 294-C* (1957).
16. The description of the coastal topography is based chiefly upon reconnaissance field observations and study of air photographs and recent topographic maps. The ancient wave-cut cliff has not been described previously as a single continuous feature, though it has been recognized locally by several geologists, notably A. J. Collier (*17*).
17. A. J. Collier, *U.S. Geol. Survey Profess. Paper No. 2* (1902), p. 42.
18. The widespread ancient erosion surfaces of northwestern Alaska were also recognized and described by A. H. Brooks [*U.S. Geol. Survey Profess. Paper No. 45* (1906), p. 276]; by A. J. Collier [(*17*) and *U.S. Geol. Survey Bull. No. 278* (1906), p. 13]; and by F. S. MacNeil *et al.* (*11*, p. 70).
19. F. S. MacNeil *et al.* (*11*). The stratigraphic evidence has been summarized in more detail by D. M. Hopkins (*20*).
20. D. M. Hopkins, "Pleistocene climates and the Bering Sea land bridge," *Proc. Intern. Geol. Congr., 21st Congr.*, in press.
21. J. A. Cushman, *Contrib. Cushman Foundation for Foraminiferal Research No. 17* (1941), p. 33.
22. The *Fortipecten* from Kivalina was collected in 1957 by Martin Swan (a local hunter), was ultimately transmitted to G. D. Hanna, and was deposited in the Museum of the California Academy of Sciences.
23. F. S. MacNeil, written communication, 1958. The conclusions given here differ somewhat from those reached by MacNeil (*15*) and result from the study of additional material collected by G. D. Hanna on the Arctic Coastal Plain during 1956 and 1957.
24. E. Steidtmann and S. H. Cathcart, *U.S. Geol. Survey Bull. No. 733* (1922).
25. D. M. Hopkins, thesis, Harvard University (1955).
26. T. F. W. Barth, *U.S. Geol. Survey Bull. No. 1028-F* (1956).
27. R. F. Flint, *Glacial and Pleistocene Geology* (Wiley, New York, 1957), p. 270.
28. H. de Vries and G. W. Barendsen, *Nature* 174, 1138 (1954); F. P. Shepard and H. E. Suess, *Science* 123, 1082 (1956); H. Godwin, R. P. Suggate, E. H. Willis, *Nature* 181, 1518 (1958).
29. R. H. Parker and J. R. Curray, *Bull. Am. Assoc. Petrol. Geologists* 40, 2428 (1956).
30. J. C. Ludwick and W. R. Walton, *ibid.* 41, 2054 (1957).
31. F. P. Shepard, *Am. Petrol. Inst. 4th Quart. Rept. Proj. 51. No. 25* (1957), p. 5.
32. Among those who have expressed this opinion are H. N. Fisk and E. MacFarlan [*Geol. Soc. Am. Spec. Paper No. 62* (1955), p. 279].
H. R. Brannon, Jr., L. H. Simmons, D. Perry, A. C. Daughtry, E. McFarlan, Jr., *Science* 125, 919 (1957).
34. Specimens O-5A, O-126A, and O-105 [H. R. Brannon *et al.* (*33*)]; specimens L-291C, L-291D, L-291K, and L-291U [W. S. Broecker and J. L. Kulp, *Science* 126, 1324 (1957)]; dated specimens described by K. O. Emery [*Bull. Geol. Soc. Am.* 69, 39 (1958)].
35. E. E. Bray and H. F. Nelson, *Bull. Am. Assoc. Petrol. Geologists* 40, 173 (1956).
36. R. F. Flint and M. Rubin, *Science* 121, 649 (1955).
A. Dreimanis, *ibid.* 126, 166 (1957).
38. F. T. Thwaites, *Bull. Geol. Soc. Am.* 54, 87 (1943).

39. R. S. Sigafoos, *U.S. Geol. Survey Bull. No. 1061-E* (1959).
40. W. S. Benninghoff, University of Michigan paleobotanist, oral communication, 1959.
41. R. F. Griggs, *Ecology* 15, 81 (1934).
42. E. B. Leopold, U. S. Geological Survey paleobotanist, written communciation, 1958.
43. D. M. Hopkins and J. L. Giddings, *Smithsonian Inst. Publ. No. 4110* (1953), p. 25; D. M. Hopkins, *Bull. Geol. Soc. Am.*, in press; specimens W-461, W-463, and W-485 [M. Rubin and C. Alexander, *Science* 127, 1480 (1958)].
44. E. Hultén, "Flora of Alaska and Yukon," *Lunds Univ. Arsskr., Avd. 2* (1941–1950), vols. 37–46.
45. I. Hustich, *Arctic* 6, 149 (1953).
46. W. S. Benninghoff, *Cong. intern. botan., 8e Congr., Paris* (1954), vol. 6, p. 246.
47. D. M. Hopkins, unpublished.
48. The former distribution of glaciers shown in Fig. 3 is based upon "Geologic map of the U.S.S.R." (*9*) and upon maps, mostly unpublished, by the following geologists of the U.S. Geological Survey: R. E. Detterman (northern Alaska); D. M. Hopkins (Seward Peninsula, Kotzebue Sound, Platinum, and St. Lawrence Island); J. M. Hoare, W. L. Coonrad, E. H. Muller, James Platt (Kuskokwim Bay–Bristol Bay area); and T. F. W. Barth (Pribilof Islands). The trace of the old wave-cut cliff is based upon study of air photographs and *Alaska Topographic Series 1:250,000* maps.
49. The graphs in Fig. 4 are based upon descriptions and ages of relevant specimens given in radiocarbon-dating lists published in *Science* 113 to 127 (1951 to 1958); in F. P. Shepard, *J. Geol.* 64, 56 (1956); in L. M. J. U. van Straaten, *Geol. en Mijnbouw*, 16, 247 (1954); and in other sources (*28–37*).

Biochemical Theories of Schizophrenia

Part I of a two-part critical review of current theories and of the evidence used to support them.

Seymour S. Kety

The concept of a chemical etiology in schizophrenia is not new. The Hippocratic school attributed certain mental aberrations to changes in the composition of the blood and disturbances in the humors of the brain, but it was Thudichum (*1*), the founder of modern neurochemistry, who in 1884 expressed the concept most cogently: "Many forms of insanity are unquestionably the external manifestations of the effects upon the brain substance of poisons fermented within the body, just as mental aberrations accompanying chronic alcoholic intoxication are the accumulated effects of a relatively simple poison fermented out of the body. These poisons we shall, I have no doubt, be able to isolate after we know the normal chemistry to its uttermost detail. And then will come in their turn the crowning discoveries to which our efforts must ultimately be directed, namely, the discoveries of the antidotes to the poisons and to the fermenting causes and processes which produce them." In these few words were anticipated and encompassed most of the current chemical formulations regarding schizophrenia.

It may be of value to pause in the midst of the present era of psychochemical activity to ask how far we have advanced along the course plotted by Thudichum. Have we merely substituted "enzymes" for "ferments" and the names of specific agents for "poisons" without altering the completely theoretical nature of the concept? Or, on the other hand, are there some well-substantiated findings to support the prevalent belief that this old and stubborn disorder which has resisted all previous attempts to expose its etiology is about to yield its secrets to the biochemist?

An examination of the experience of another and older discipline may be of help in the design, interpretation, and evaluation of biochemical studies. The concepts of the pathology of schizophrenia have been well reviewed recently (*2*). As a result of findings of definite histological changes in the cerebral cortex of patients with schizophrenia which were described by Alzheimer at the beginning of the present century and confirmed by a number of others, an uncritical enthusiasm for the theory of a pathological lesion in this disease developed, and this enthusiasm penetrated the thinking of Kraepelin and Bleuler and persisted for 25 years. This was followed by a period of questioning which led to the design and execution of more critically controlled studies and, eventually, to the present consensus that a pathological lesion characteristic of schizophrenia or any of its subgroups remains to be demonstrated.

Earlier biochemical theories and findings related to schizophrenia have been reviewed by a number of authors, of whom McFarland and Goldstein (*3*), Keup (*4*), and Richter (*5*) may be mentioned (*6*). Horwitt and others (*7–9*) have pointed out some of the difficulties of crucial research in this area. It is the purpose of this review to describe the biochemical trends in schizophrenia research of the past few years, to discuss current theories, and to examine the evidence which has been used to support them.

Sources of Error

Because of the chronicity of the disease, the prolonged periods of institutionalization associated with its management, and the comparatively few objective criteria available for its diagnosis and the evaluation of its progress, schizophrenia presents to the investigator a large number of variables and sources of error which he must recognize and attempt to control before he may attribute to any of his findings a primary or characteristic significance.

Despite the phenomenological similarities which permitted the concept of schizophrenia as a fairly well defined symptom complex to emerge, there is little evidence that all of its forms have a common etiology or pathogenesis. The likelihood that one is dealing with a number of different disorders with a common symptomatology must be recognized and included in one's experimental design (*8, 10, 11*). Errors involved in sampling from heterogeneous populations may help to explain the high frequency with which findings of one group fail to be confirmed by those

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