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A Comparison of the Late Wisconsinan Molluscan Fauna of the Missouri Coteau District (North Dakota) with a Modern Alaskan Analogue

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A COMPARISON OF THE LATE WISCONSINAN MOLLUSCAN FAUNA
OF THE MISSOURI COTEAU DISTRICT (NORTH DAKOTA)
WITH A MODERN ALASKAN ANALOGUE

by

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Geol.

This dissertation submitted by Samuel J. Tuthill in partial fulfillment of the requirements for the Degree of Doctor of Philosophy from the University of North Dakota is hereby approved by the Faculty Advisory Committee under whom the work has been done.

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Samuel J. Dutlied

May 29, 1969

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ABSTRACT

Study of forty fossiliferous sites in late Wisconsinan sediments from the Missouri Coteau district in central North Dakota has defined the molluscan fauna of the period of geologic time between 12,000 and 9,000 C¹⁴ years before the present. The fauna includes twenty-eight taxa of nonmarine gastropods and bivalves and is dominated by branchiates. The modern molluscan fauna of the Missouri Coteau district in North Dakota lacks four species which were resident in the late Wisconsinan and contains no unionids, one additional aquatic species, and is strongly dominated by pulmonate gastropods.

The geology of the Missouri Coteau has been interpreted as being the sedimentary result of the stagnation of the marginal fifty to one hundred miles of the Wisconsinan ice sheet.

The interpretation of the paleoecology of the late Wisconsinan molluscan fauna derives from geologic, paleoautecologic, and paleo-synecologic data. It is hypothesized that at the time the late Wisconsinan continental ice sheet stagnated in central North Dakota,

the climate was less extreme and more humid than at present. Ponds and streams existed on the ice-cored topography of the Missouri Coteau. They were connected by a drainage system tributary to the Missouri River and populated by an abundant, branchiate-dominated molluscan fauna.

Fishes, probably of the families Percidae and Centrarchidae, lived in the ponds and rivers and unionid bivalves successfully populated many of the water bodies. Calcareous algae (Chara) and undoubtedly other species of aquatic vegetation colonized the clear, warm water of the drainage system. The ice-basined, drift-insulated lake was the most common lithotope in which fossil mollusks were preserved. The entire drainage system was supplied by greater rainfall and snowmelt than now occurs on the Missouri Coteau (probably in the order of 20 to 30 inches per year) and the precipitation - evapotranspiration ratio was positive. The humid climate changed toward the more arid climate of today before the ice core of the Coteau melted. Comparison with modern molluscan assemblages characteristic of defined habitats in Minnesota indicates that the mollusks which lived on the ice-cored Missouri Coteau, could have occupied small streams, medium-hardwater lakes, and/or hardwater prairie lakes. In consideration of the population dominance by branchiates, I believe that hardwater prairie lakes are not likely to have occurred on the late Wisconsinan Missouri Coteau.

In order to evaluate this hypothesis the terminus of the Martin River Glacier in south-central Alaska was studied. A molluscan fauna of ten fresh-water and thirteen terrestrial taxa was discovered on and in front of the stagnant terminus of the glacier. Twenty-three potential habitats for mollusks were studied and defined. Twelve of these were found to contain mollusks. The aquatic mollusks were found to occupy cool water (as low as 5°C) and warm water (above 10°C) and to be able to withstand very low concentrations of dissolved solids and high turbidity. Branchiate gastropods and bivalves were found to favor turbid environments next to the glacier and to populate successfully ice-basined, clear, warm lakes on the glacier. Terrestrial snails and slugs were found as much as a kilometer out on the drift-covered stagnant glacial terminus separated from the glacier ice by only 11 inches of alder-leaf-litter. Terrestrial snails were found in spruce forests only once. They were not found under willow bushes, young alder shrubs (less than 7 years in age), or on outwash gravel surfaces. Acid peat growths, and ponds developed in them, were also barren of mollusks. Edaphic conditions are assumed to account for their absence in these potential habitats.

The Alaskan studies lend credence to the hypothesis erected to explain the paleoecology of the late Wisconsinan molluscan fauna of the Missouri Coteau in that they prove that mollusks are vigorous pioneers near and on stagnating glaciers, that less than a foot of super-

glacial drift is sufficient to insulate terrestrial molluscan habitats, and that six feet of superglacial drift is sufficient to insulate ice-basined, clear, warm lakes from their containing ice walls. The studies further emphasize that terminal glacial features such as end moraines, outwash fans, dead-ice moraines, kettles, and superglacial lakes are the result of a non-glacial climate and the inference of glacial climate from such features is a fundamental error. The employment of fossil nonmarine mollusks as indicators of past water quality was brought under serious question by the studies reported here. The fact that aquatic mollusks live successfully in Alaskan waters which contain less than 1 ppm dissolved solids brings into question the practice of employing mollusks as paleolimnologic indicators of chemical aspects of their environments. I believe the use of mollusks as indicators of past water quality of their habitats must be discontinued.

INTRODUCTION

The studies reported here were the result of work begun in south-central North Dakota in 1960 and concluded in south-central Alaska in 1968. My paleontological and paleoecologic studies in North Dakota were a small part of the interpretation of the mode of deposition of the Pleistocene sediments of the Missouri Coteau district. The late Wisconsinan molluscan ecology, hypothesized by me, demanded a basis of evaluation in the form of a modern analogue before much confidence could be given it.

Study of the Pleistocene nonmarine molluscan fauna of the Missouri Coteau began in 1959 when surface geologic mapping of Stutsman County, North Dakota, was commenced jointly by the North Dakota Geological Survey and the United States Geological Survey. Dr. Harold A. Winters was the party chief of the work in 1959 and 1960. The mapping of the glacial geology of Logan County and northern McIntosh County, North Dakota, was accomplished in 1960 by Lee Clayton and John Bonneville (Bonneville, 1961 and Clayton, 1961b).

Clayton discovered and evaluated four collections of late Wisconsinan nonmarine mollusks in Logan County and summarized these studies in a report (Clayton, 1961a). His employment of the

fossils was as supportive evidence of his sedimentological conclusions. Winters (1963) mentioned the occurrence of fossil mollusks in Stutsman County, but no detailed paleoecologic work was done. Dr. Mark Rich of the Department of Geology, University of North Dakota, and temporarily in the field party studying in Stutsman County under Winters' direction in 1960, called my attention to the fossiliferous sediments located near Cleveland, North Dakota. My studies of this site culminated in a report (Tuthill, 1961) which employed the fossils as presumptive evidence for past climates.

In the summer of 1961 Clayton, assisted by G. G. Thompson, mapped McIntosh County, North Dakota, and in the latter part of the summer I joined them to investigate a number of fossil localities in that county and in Logan County. These studies culminated in several papers. Thompson (1962) reported the sedimentology of the deposits from a slough on the Coteau, the basin of which had its origin in a depression left by melted stagnant ice. Mollusks were contained in these sediments. Clayton (1962) recognized the fundamental importance of the fossils found in topographically high, flat-lying and collapsed stratified sediments which were surrounded by topographically lower till deposits, as irrefutable evidence of their freshwater lake mode of deposition. This proof of lithotope was critical to the general interpretation of the glacial geology of the entire Missouri Coteau. Clayton and Winters both concluded that the late Wisconsin glacier had stag-

nated over a broad band and that the topography was the result of the slow melting of ice buried beneath great thickness of superglacial drift. The development of freshwater habitats for mollusks on this surface required the presence of superglacial drift as an insulator upon the ice which formed the basins of the lakes and ponds.

The paleoecologic results of my studies, taken in the light of Clayton's and Winters' work, were summarized in Tuthill (1963b) and Tuthill, Clayton, and Holland (1963). I prepared a checklist of North Dakota nonmarine mollusks (Tuthill, 1962, 1963c) as a starting point for Quaternary molluscan studies in the State.

As the mapping program of the North Dakota Geological Survey expanded, other portions of the Missouri Coteau District were investigated. By 1963 I had had the opportunity to study the fossil nonmarine mollusks collected by geologists working for the North Dakota Geological Survey in Burleigh, Divide, and Sheridan Counties. These faunules were discussed in Sherrod (1963), Tuthill (1963b and 1965), and summarized in Tuthill (1967a).

Limnological studies conducted by Clayton and me under the direction of Dr. Wilson M. Laird, Professor of Geology and State Geologist, University of North Dakota, in Long Lake, Minnesota, resulted in a comparison of the fossil fauna of the Missouri Coteau with a living molluscan fauna of Minnesota (Tuthill, Clayton, and Laird, 1964). The reaction of the referees to this manuscript fortified our

conclusion that the modern ecologic literature about North American nonmarine mollusks was inadequate. The editorial critics doubted the paleoecologic reconstruction out of hand and flatly asserted that such a mesotrophic population of aquatic mollusks could not live in such close proximity to glacier ice.

Dr. Wilson M. Laird prepared a grant proposal to the National Science Foundation to study a stagnating glacier. My portion of the research was designed to investigate the nature, distribution and the habitats of any mollusks which might be found on or near the Martin River Glacier, Alaska.

The National Science Foundation granted the Department of Geology sufficient funds to conduct two summers of research in south-central Alaska. The 1962 and 1963 studies were partially reported in Reid (1963a and 1963b), Reid and Clayton (1963), Reid and Laird (1963), Clayton (1964), Callender (1964a and 1964b), Reid and Callender (1965), Tuthill (1963d), Tuthill and Laird (1963), and Laird and Tuthill (1964).

Further Alaskan research was conducted with the support of the National Science Foundation in 1964 with Laird as principal investigator. This research was directed toward an understanding of the geomorphic effects of the March 28, 1964 Alaskan earthquake and resulted in two papers (Tuthill, Laird, and Freers, 1964, and Tuthill and Laird, 1966).

I continued post-earthquake studies in 1965 at Sherman and Sheridan Glaciers, Alaska, with the support of the National Science Foundation. A large portion of my work concerned the description of the flora and molluscan fauna of the Sherman Valley, which is located about 30 miles west of the Martin River Glacier. This work was summarized in Tuthill, Field, and Clayton (1968). I summarized the paleoecologic implications of my work on Alaskan mollusks in a special longer paper before the Geological Society of America which is abstracted in considerable detail in Tuthill (1966).

In 1967, with National Science Foundation support, I studied problems related to tectonism and glaciation in the Katalla Valley, Alaska, which lies about 12 miles south of, and contiguous with, the region studied in 1962, 1963, and 1964 (Plate 4). The modern molluscan fauna was partially evaluated by me and three of my students. The results of these studies were reported in Tuthill and Johnson (in press). In 1967, Bickley collected the mollusks of the lower Tasnuna Valley (Bickley, in press).

In all, an area of about 3,500 square miles of Alaska has been investigated for its nonmarine molluscan fauna on at least a reconnaissance level of rigor and an attempt to define the available habitats in the region has been made.

The discussion which follows takes the form of: (1)

Descriptive information supportive to, and a statement of, the hypothesis erected to explain the late Wisconsinan molluscan ecology of the Missouri Coteau, (2) Description of the potential molluscan habitats of south-central Alaska, and (3) An evaluation of the hypothesis for the Missouri Coteau by comparison with the modern Alaskan analogue.

Ecology and Paleoecology

According to Odum and Odum (1959, p. 3) the word ecology was coined by Ernst Haeckel in 1869 and as a recognized subdiscipline of biology it dates from about 1900. The word derives from oikos, which means house or living place and the Odums stated that "literally, ecology is the study of organisms 'at home'." A more modern definition they give is that ecology is, "the study of the structure and function of nature (it being understood that mankind is a part of nature)."

Ecologic studies are of two types: (1) autecology, the study of the environments of individuals or small taxonomic groups; and (2) synecology, the study of living communities and the nature of their relationships to their physical and chemical environment and the manner in which the individuals and separate taxa interrelate. Fenton (1935, p. 67) stated:

Fossil organisms, like their modern descendants, formed interrelated societies. These societies, even more than the organisms themselves, are the concern of paleoecology paleoecology reaches the plane of general sociology--the sociology of all organisms.

As a theoretical statement Fenton's discussion was and still is excellent. Thirty-three years have elapsed since Fenton wrote, and during this period of time the paleontologic subdiscipline has followed trends which in general adhere to Fenton's injunction, but deviate very considerably in the practical mechanics of investigation.

The nature of the deviations are largely a function of the desire upon the part of the paleoecologist to render the most precise reconstruction of fossil biotopes possible and the failure to distinguish between the types of information inferrable from autecologic and synecologic studies. There is also the matter of taxonomic and chronologic separation impressed upon a paleoecologist which is not a necessary consideration of the ecologist.

Scott (1963) raised objections to the practice of modern paleoecologists of relying on the theory of uniformitarianism as the fundamental rationalization of their activity while actually viewing nature as a uniform system. Scott's argument was well documented with examples of paleoecologic work founded on poor judgment. This line of debate is valid only when directed towards condemning poor practice. It does not address the fundamentals of the theory. Scott pointed out what he regarded as the anomalous practice of accepting Darwin's theory of organic speciation in response to changing ecologic conditions and at the same time accepting a theory of a uniform nature. The main defects of his argument are (1) Darwin recognized that species level morphologic

change resulted from changing ecologic conditions, and (2) despite laudable attempts on the part of paleontologists to adopt the modern neontologic concept of the species, paleontologic taxonomy is required to make its divisions primarily on the basis of skeletal differences.

Johnson (1960), like Scott, raised the question of assuming that species have been incapable of shifting their ecologic preferences through time without specific morphologic shifts. A valid objection to paleoecologic reconstructions can be made on this line of reasoning only when the paleoecologic reconstruction is based on paleautecologic information or when taxonomic and chronologic separation is great. Paleoecologic reconstructions based on interpretations of entire communities of fossil organisms, with due consideration of lithotopic evidence, so thoroughly reduces the likelihood of error that Scott's and Johnson's arguments are rendered less than germane. If chronologic separation is small, parallel evolution of all the taxa of a community from one ecologic preference to another is not an acceptable theoretical objection in the absence of evidence. Paleoecologists have a right to expect their readership to understand that confidence in their reconstructions of biotope diminishes with the increase in both taxonomic and chronologic separation.

The questioning of current paleoecologic practice is still appropriate. The state of ecologic knowledge has imposed critical limitations on paleoecologists, even those working with assemblages of

organisms which contain no extinct taxa. The vast burden of ecologic information about nonmarine mollusks, for instance, is autecologic. Thus the paleoecologist must reconstruct the biotope of his fossil assemblage from a composite of autecologic data and zoogeographic information. The quality and completeness of information related to the various species of mollusks represented in his fossil assemblage varies widely. The ecology of certain gastropods which are of medical interest because of their host function for schistosomes has sometimes generated ecologic studies designed to facilitate their extermination. For these species we have some notion of their ecologic limits. Unfortunately, the limits investigated are usually induced chemical environments rather than natural ecologic conditions.

The distribution of certain freshwater pelecypods, which were formerly of commercial interest to the button industry is often well known at least for a restricted geographic area. An impression that synecologic information exists is created by a use of these distributional data. All of the autecologic information for the various species in the fossil faunule, when combined give the impression of being the paleosynecology of the faunule, but in fact they are not. Multiple paleoautecologic analyses do not sum to a paleosynecologic evaluation. They merely give that impression. It is this impression of precision which has justly given rise to criticism of paleoecologic practice, not the fundamental theoretical basis of paleoecology itself.

The impact of defective ecologic information, the details of which are discussed below, forces upon the paleoecologist a conservatism and a need to guard against excessive precision. It can be asked, "What is the use of doing paleoecologic work until our knowledge of modern ecology is complete?" It is the nature of any scientific investigation to remain forever incomplete. Termination of intellectual inquiry is motivated only by the economics of available energy as balanced against curiosity. Investigation stops when no one cares about the subject, not because everything about the subject is known. Thus it behooves the paleoecologist who still possesses curiosity to attempt to circumvent the defects of the body of ecologic knowledge extant in his time.

At present it appears, to me at least, the wisest course for paleoecologists to follow is to employ synecologic data of a low order of precision as the basis for the paleoecologic reconstructions. Where ecologic studies exist, they must be appropriately employed. Where no modern ecologic work exists, the paleoecologist must seek out the modern analogue for his fossil population.

One of the fundamental uses of autecologic information which has wide application in paleoecology is the use of morphologic structure for ecologic inference. Ager (1963, pp. 57-58) has discussed the type of deductions which can be made from morphologic structures. As an example of deduction in the absence of a modern homologue he cited

Romer (1945). Romer suggested the function of the large dorsal fin found in the extinct reptile Dimetrodon to have been a variable surface to facilitate exothermal control of blood temperature. Romer was denied the application of uniformitarianism because living reptiles do not possess such an organ. The validity of his deduction depends on the uniformity of the physiological phenomena (exothermicity) among the individual taxa of the group being considered (i.e., all reptiles are exothermal) and the lithotopic analysis which showed that Dimetrodon lived in a desert climate where temperature control would be a critical factor.

As an example of "bad paleoecological reasoning" Ager (1963, p. 62) cited Buckman (1919). Ager quoted Buckman's explanation of the function of secondary skeletal deposits on the septal necks of orthocone nautiloid cephalopods as follows:

The early Orthocones utilising the gas effusion which resulted from temporary indigestion under the nervous apprehension of danger, found that a cone thus made more buoyant was a help in rapid retreat from foes.

In its best paleoecologic usage, autecologic information provides an excellent basis for conclusions about past biotopes of fossil organisms. An example of the correct use of autecologic information is that of phenotypic shell morphologic accommodations to ecologic conditions in the organism's microhabitat, for instance, the manner in which unionids deposit the calcium carbonate elements of their shell.

The deposition of shell material is directly related to metabolic activity according to Gutsell (1931, p. 616-620). In brackish water he found that even temporary changes in salinity from the normal bay concentrations of about 3800 ppm to less than that value caused massive mortality in beds of bay scallops (Pecten irradians). Depression of water temperature from 9°C to 5°C did not greatly reduce gill activity, which he employed as a parameter of metabolic activity. Depression of temperature below 5°C to 0°C cause the halt of all gill activity and the clam remained in a dormant stage. One of the physiological processes which leaves a record of such dormant stages is the shell deposition. Clark (1968) has demonstrated that calcium carbonate shell material is deposited in daily increments along the line of commissure of both valves. Crowding of the daily increments before and after a dormant stage is seen on the shell as a slightly raised ridge. In middle and northern latitudes such "growth-interruption ridges" are regularly caused by the winter season. Thus growth-interruption ridges have been widely used as criteria for the age of individuals. An abnormally rough shell with irregularly spaced ridges may be interpreted as evidence for unfavorable ecologic conditions during the life of the clam.

Various species have different capacities to deposit shell and growth rates change during ontogeny, thus comparisons must be made within close taxonomic limits. When ecologic conditions fluctuate, irregular growth-interruption ridges result. A rugose shell on a single

or a few clams in a population may thus be inferred to mean that the individuals experienced poor health which made them more susceptible to slightly fluctuating ecologic conditions or that parts of the biotope were more rigorous than others. Abnormally rugose shells on nearly all of the fossils in an assemblage can be inferred to mean that ecologic conditions fluctuated widely or that nonfatal epidemic disease occurred in the population.

It will be noted that a synecologic approach to differentiate between essentially internal autecologic and external autecologic phenomena was used in the above discussion. This is not the same thing as attempting to convert a composite paleoautecology into a paleosynecology. Although the entire population was considered, it was done in order to sort out two types of paleoautecology so that a paleoautecologic conclusion could be reached.

The precision of the paleoautecologic reconstruction is a matter apart from its validity and depends upon the precision of autecologic information available at the time. The validity of the paleoecologic reconstruction is destroyed when it exceeds the precision of current ecologic information.

In some instances, modern symbiotic and parasitic relationships exist with a sufficient degree of regularity that they provide a basis for paleoecologic interpretation. The degree to which parasites infest a single host species is an excellent example of this type of

paleoautecologic information. Mites frequently infest the mantle flaps of modern Anodonta grandis. When the mites deposit eggs between the mantle and the inner shell surface, the infested clam frequently deposits pathologic growths of aragonite over the eggs, thus sealing them in pearl "blisters." These blisters are often visible on the shells of fossils and provide presumptive evidence of the past existence of, at least, similar infesting organisms, if not the exact species of associated mite.

In the sense of providing more precise information, autecologic studies are certainly the more valuable. Unfortunately, the amount of information of this type now available for nonmarine mollusks is small. Further, the great burden of information now available is not the product of strictly ecologic investigation. It is most often merely a form of notes taken by taxonomists or naturalists concurrent with the collection of specimens. An example from the most commonly employed source of North American nonmarine molluscan autecologic information, F. C. Baker (1928, p. 395-397) follows:

Ferrissia parallela (Haldeman)

ECOLOGY: Ferrissia parallela is usually found in quiet water, on plants, the water in such places ranging from .3 to 2 m. in depth. The animal is usually found near the surface but may occur on the lower part of such plants as Scirpus, near the bottom. Parallela appears to be a pond or lake species, at least in Wisconsin. The following specific habitats have been noted: Red Cliff Creek, 100 m. from mouth at Lake Superior, on Vallisneria and Potamogeton leaves; Lake Butte des Morts on Scirpus and Nymphaea; De Pere, Fox River, on wild rice; Sturgeon Bay. . . .

An equally commonly used source is that of Morrison (1932, p. 375) who said:

Ferrissia parallela (Haldeman)

pH = 6.05 - 8.37; fixed carbon dioxide = 2.75 - 25.75 ppm
Lake Superior Drainage: Ontonagon River, Michigan, 3 m. north of Tenderfoot Lake; Palmer Lake.

Flambeau Drainage: Boulder L.; Fishtrays L.; High L.; Mary L.; Mud L.; Outlet of Mann L.; Turtle River, below Lake of the Falls. Tomahawk Drainage: Tomahawk Lake, and kettle hole ponds in the vicinity (Baker); Stream, 10 m. southwest of Hazelhurst. Wisconsin Drainage: Deerskin River, 6 m. south of Phelps; Plum L.; Razorback Lake.

When converted into a paleoecologic reconstruction these statements frequently take on a connotative impression of precision in excess of their appropriateness. Neither Baker's or Morrison's statements constitute more than notations of conditions under which the specimens of Ferrissia parallela were found in specific localities in Wisconsin. Yet they have been employed as presumptive evidence for fossil faunas elsewhere. An example is Clark (1961, p. 28), who wrote as follows about the paleoecology of fossils from Erie County, Ohio:

Ferrissia parallela (Haldeman)

This species is found in enclosed bays, open swamps or small ponds, and swampy pools or swales. It is almost strictly a pond or small lake species, found in quiet waters whose depth varies from 1 to 6 feet and rarely occurs in sluggish streams. This species usually lives near the surface of the water but may be found on the lower part of such plants as Scirpus, near the bottom. It also lives on the under side of lily leaves (which gives a broad flat look to the shell) and on sticks in boggy swales (here the shell is higher and more compressed). F. parallela lives in waters whose pH ranges from 6.05 to 8.37 and whose fixed carbon dioxide varies from 2.75 to 25.75 p.p.m. The bottom may be sand

or mud covered with vegetation. The limiting factors for the distribution of this species are wave action (since it is found only in quiet water) and the presence of vegetation.

And in a reconstruction of the paleoecology he said:

Hydrogen ion concentration and carbon dioxide content

The water in which the faunas lived had pH limits of 6.0 to 8.5 but the normal value was probably nearer 7.5. The carbon dioxide content may have varied from 2.85 to 30.56 p.p.m. throughout the history of the deposit but a mean value of 14.0 p.p.m. is more probable.

As sources for his ecologic information on aquatic mollusks he has cited 24 papers by 14 authors. When these papers are examined only two, Morrison (1932) and Dennis (1928) cited quantitative water quality data for the entire fauna treated. Morrison concluded that the conditions of the water in which he found the mollusks in northeastern Wisconsin adequately characterized the ecology of the taxa for that region. I certainly do not question Morrison's conclusion, but that the Wisconsin studies characterize the ecologic limits of the taxa throughout their entire distribution is not supportable. There are no saline prairie ponds in northeastern Wisconsin; therefore, Morrison's work could not assess their tolerance of this habitat.

Dennis (1928, p. 33) actually concluded from his studies that ". . . the temperature, transparency, and pH of the water at Bass Island, Ohio apparently had little or no effect on the distribution of snails."

An example of just how erroneous the type of paleoecologic usage practiced by Clark and many others can be, we need only consider the works of Morrison, Clark, and Tuthill and Laird (1963) on Lymnaea humilis.

Morrison (1932, p. 371) states the following about this taxon which he called Fossaria obrussa (Say):

Fossaria obrussa (Say)

pH = 5.86 - 8.37; fixed carbon dioxide = 1.26 - 25.76 p.p.m.

Fossaria obrussa decampi (Streng)

pH = 7.42 - 7.7; fixed carbon dioxide = 10.65 - 18.87 p.p.m.

Clark (1961, p. 36) stated that Fossaria obrussa decampi (Streng) is the "second most abundant taxon in the deposit . . ." he studied. Thus we can assume he relied on it heavily in his paleoecologic reconstruction.

He cited (p. 28) the statement of reconstructed hydrogen ion concentration and carbon dioxide quoted above in the discussion of his use of Ferrissia.

In 1963 Tuthill and Laird (1963, p. 82-83) reported Lymnaea humilis = Fossaria obrussa from ponds in the Missouri Coteau which had a pH of 7.70 to 8.20 and total carbon dioxide of 150 to 870 ppm. Total dissolved solids for one of the ponds in which the taxon was found was 15,800 ppm. Clark thus did not have the final word on the water quality which the taxa represented in his fossil assemblage could withstand, yet he implied by the precision of his reconstruction that such ecologic information was available.

In some nonmarine molluscan groups, valuable autecologic information has been established. The currently most useful group is the family Unionidae, the freshwater mussels. Until the invention of methods of mass producing high quality plastic buttons, the freshwater mussels were of commercial interest to the button industry. The U.S. Bureau of Fisheries conducted several important studies designed to understand the life history of various commercially valuable species of mussels for the purpose of conservation. The studies, conducted at Fairport, Iowa, and reported by Coker and others (1919-1920), and regional surveys such as that of northern Minnesota reported by Wilson and Danglade (1914), because they do not pretend to be more than natural history, are among the most useful works now available.

Boycott (1934, 1936), Sparks (1961), Lozek (1964), Harris (1964), Cvancara and Harrison (1965), and Cvancara (1966), are the types of ecologic studies which are beginning to provide information which will eventually permit the kind of paleoecologic reconstruction Clark attempted. Harris' work in Iraq, Boycott's and Sparks' in the British Isles and Lozek's in Czechoslovakia, are not of particular help to the North American paleoecologist. Taylor (1965, p. 599), has stated the condition of modern North American molluscan ecologic knowledge as follows: ". . . present knowledge of the living fauna is imprecise . . . at least some recent and widely accepted work is seriously erroneous."

Taylor (1965, p. 611) went on to show that the long-accepted taxonomic work relative to the species Lymnaea palustris was founded on three different biologic entities. Thus the extant autecologic data related to L. palustris is useless to the paleoecologist. Taylor further stated:

In the long run strictly zoological studies will advance Pleistocene conchology more by adding to the foundations for interpretation of the fossils.

Distributions of living mollusks in North America are still too imperfectly known and correlations of distributive phenomena with ecologically significant conditions, too rare to yet warrant reliance upon sympatric analyses.

Synecology of a type similar to that employed by some paly-nologists is a technique which appears capable of producing significant paleoecologic reconstructions based on fossil North American nonmarine Mollusca. The comparison of fossil faunules with modern analogues and the contrasting of fossil faunules with the modern fauna living in the region, provide a valid basis for hypotheses of the conditions endured by past populations.

Distributions of species of mollusks in the north-central United States and south-central Canada are the most common data available on the subject. Several authors, most notably Dawley (1947), have indicated the species of aquatic mollusks which are frequently found together in a habitat. The main danger in this type of attempted

test of an hypothesis is the circularity of reasoning involved. The fossil assemblage, if found to be a necrocoenosis, is interpreted by comparing it with a modern assemblage of species found to live together and the description of the ecology of the analogue is apt to become the paleoecologic reconstruction. The hypothetical fossil biotope has not been proved in this instance and is rendered acceptable only because of the existence of a similar modern assemblage. This lends credence to the hypothesis but does not prove it valid. A major defect which can arise is the lack of a studied analogue comparable to the fossil group. At this juncture the paleoecologist must question either the validity of his conclusion that he is dealing with a fossil necrocoenosis or the thoroughness of modern ecologic studies.

The reasons I believe that synecologic studies of modern faunas having comparable habitat characteristics avoids the dangers of paleoautecology are as follows:

1. Paleoautecology is susceptible to the criticisms of the type of Scott (1963) and Johnson (1960). We simply do not know what changes in ecologic preference or requirement of a species have occurred during geologic time.
2. Furthermore, we do not know the rate at which changes in ecologic preferences or requirement occur. That acclimatization does occur we know from observation of organisms which can adjust to new and often radically

different conditions within a single lifetime.

3. Finally, I believe that the use of a population--both its species composition and its relative number of individuals--obviates the need to be too much concerned with the two problems discussed above. That entire faunas can change in their individual ecologic requirements without changing the frequency of occurrence of individuals seems highly unlikely. If a fossil population is compared with a living population the resulting paleoecologic reconstruction offers more hope of being accurate than if the faulty autecologic information known about the individual taxa is lumped together to form a sort of autecologic sum. Synecologic comparisons also permit the reduction of precision necessary for accuracy. For example, we can identify types of habitats occupied by modern animals and by comparison of taxonomic equals suggest that it was possible for animals of the past to occupy similar habitats. Thus the reconstruction of the ecologic conditions endured by fossils during their lives can be viewed as a part of an hypothetical ecosystem. Accumulated autecologic inferences work the paleoecologic reconstruction in the opposite direction--towards greater and greater precision and resultant inaccuracy.

PALEOECOLOGY OF THE MISSOURI COTEAU

Geographic and Geologic Description of the Missouri Coteau

The history of the usage of the term "Missouri Coteau" in North Dakota has been reviewed by Winters (1967). It is that portion of the state bounded on the west by the Coteau Slope district as defined by Clayton (1962, p. 14). On the east it is bounded by the Western Lakes section of Fenneman (1946). The Missouri Coteau district is characterized by a myriad of ponds and sloughs in closed depressions and almost totally non-integrated drainage. Figures 1 and 2 show the location and geographic extent of the Missouri Coteau in North Dakota.

Clayton (1967, p. 25-46) has summarized the hypothetical late Pleistocene history of the Missouri Coteau. He has stated:

About 13,000 B.P. the late Wisconsin glacier advanced to the present western edge of the Missouri Coteau, forming the Burnstad end moraine in south-central North Dakota. Stagnant ice accumulated behind the Burnstad moraine, and about 12,000 or 12,500 B.P. active ice formed the Streeter end moraine about 15 miles east of the Burnstad. The Streeter moraine was formed against Burnstad ice.

The active ice rapidly thinned during the general deglaciation near the close of the ice age. Where the thin ice flowed over the Missouri Escarpment onto the Coteau, it experienced compressive flow and intensive marginal thrusting, which dragged great quantities of subglacial drift up onto the ice.

Figure 1.--Map of North America showing the two regions in which research was conducted.

A. The Missouri Coteau district in North Dakota shown in solid black at A.

B. The Martin-Copper-Bering Rivers region, Alaska shown in black at B.

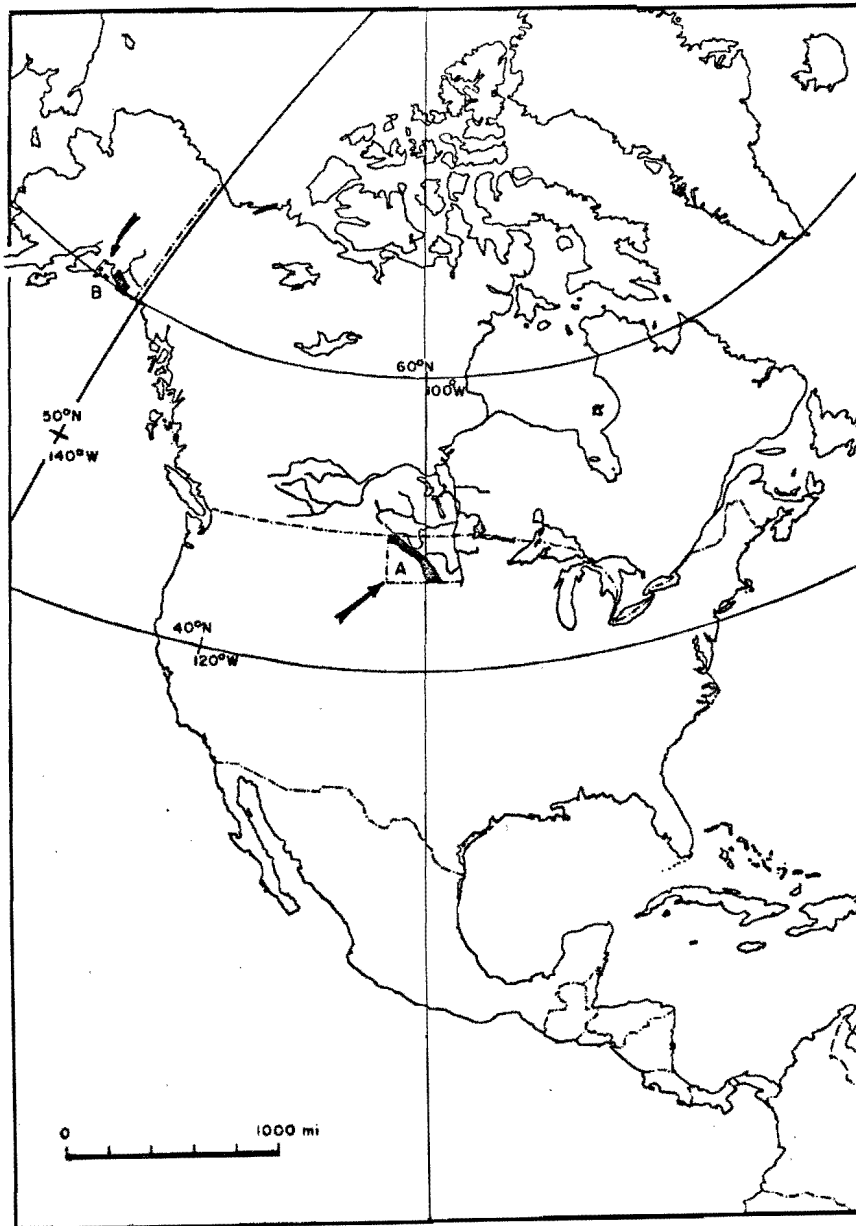
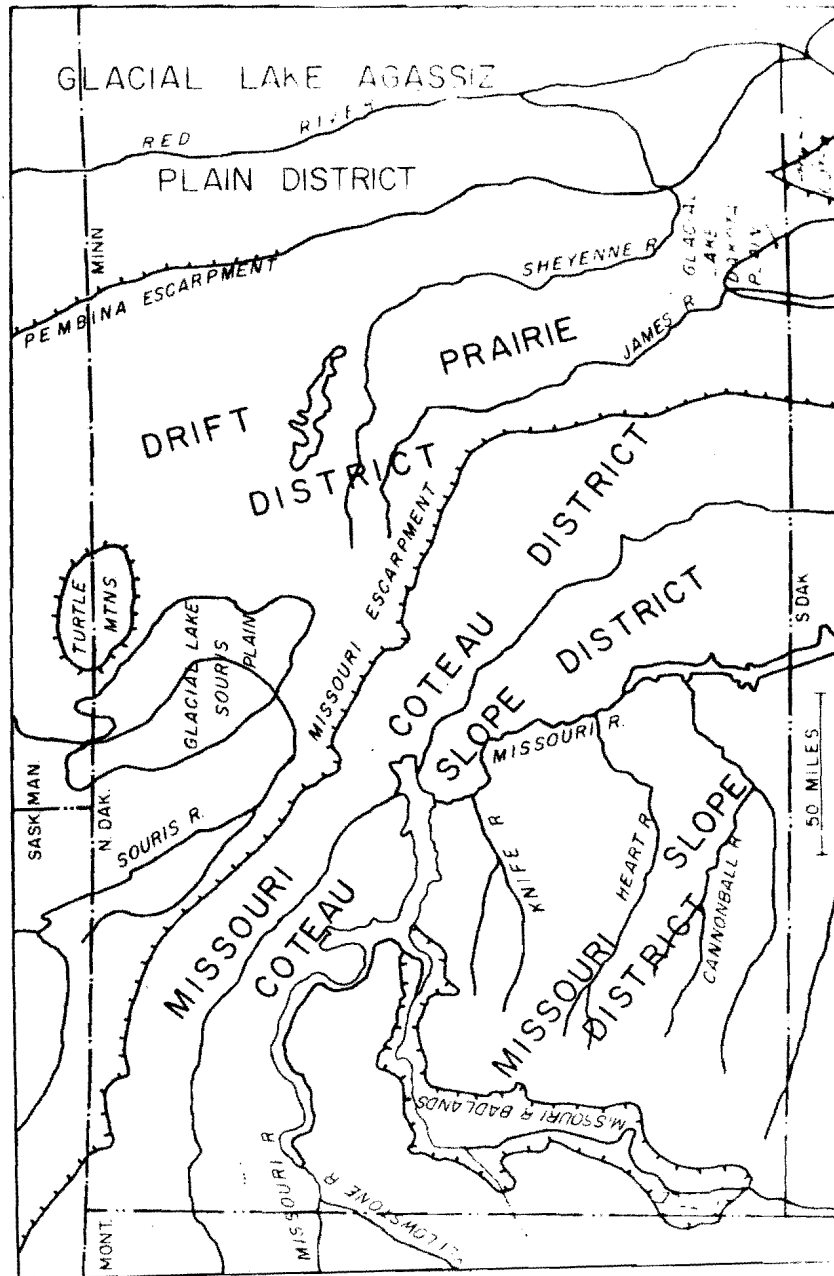


Figure 2.--Map of North Dakota showing the physiographic divisions.



As the ice melted, the till was concentrated on its surface, forming a nearly continuous blanket of superglacial till several tens of feet thick over most of the Coteau. This drift blanket insulated the ice, causing it to melt very slowly. A nearly continuous sheet of stagnant ice, initially a few hundred feet thick, covered almost the entire Coteau. Much of this ice persisted for at least 3,000 years, until 9,000 B.P.

The superglacial drift blanket was irregularly distributed, and, as a result, the ice melted irregularly, and the topography on the stagnant ice became hilly and pitted with irregular depressions. The superglacial till was water-saturated and was highly plastic or fluid; it slid or flowed down the ice slopes and accumulated in depressions. Mudflows were common. The thick drift in the depressions caused the underlying ice to melt more slowly, and the newly exposed ice melted more rapidly, resulting in continual inversions of the superglacial topography.

Locally, in lower areas, there had been extending flow, with no marginal thrusting, and no accumulation of superglacial till. The ice in these areas melted faster, forming large depressions that held lakes or superglacial valleys occupied by streams. The streams deposited much superglacial alluvium.

This environment was at first very active, with rapid melting of the ice, much mass movement of the superglacial drift, and continual alterations of the superglacial topography. As the ice continued to melt, the superglacial drift cover became thicker, causing the ice to melt more slowly. The environment gradually became more stable, and the water in the superglacial and ice-walled lakes and streams became more temperate; most of the water was runoff from local precipitation, rather than glacial meltwater. Fish were able to migrate up the superglacial streams from the Missouri tributaries. They carried the parasitic glochidia (larval stage) of at least three of the four species of mussels now found in the Missouri drainage. Birds probably brought aquatic snails and ostracods in mud on their feet into the lakes and streams in the stagnant glaciers. The algae Chara sp. (stonewort) and other aquatic plants also became established. Surrounding the lakes and streams, the superglacial drift was covered with spruce, tamarack, birch, poplar, aquatic mosses, and associated vegetation. The

mean annual precipitation was probably several inches higher, and the mean annual temperature was a few degrees cooler than at the present time.

Eventually, all of the ice melted, and all of the superglacial drift was let down, forming the hilly collapse topography that is characteristic of the Coteau today. The plains of the ice-walled lakes were left perched above the surrounding collapsed drift.

The drainage was then non-integrated; there were few if any streams, and the lakes had no outlets. The aquatic environments then slowly began to deteriorate as salts accumulated. In contrast to the period 9,000 to 12,000 years ago, mussels do not now occur, and gill-breathing snails are now a minor element of the fauna.

The stagnant-ice environment on the Coteau was in many ways comparable to the stagnant, drift-covered parts of the Bering, Malaspina, and Martin River Glaciers of south-central Alaska today.

Clayton's comments relative to the climatic environment and the terrestrial and aquatic habitats which existed while the Coteau was ice-cored are reconstructed from paleontological evidence. Twenty-eight taxa of aquatic and terrestrial mollusks have been recovered from forty fossiliferous sites. The mollusks are listed below and their associations at various sites on Table 1. The geographic locations of the 40 studied fossiliferous sites are given on Table 3.

Descriptive Paleontology of the Missouri Coteau

The autecologic information available and the apparent fossil associations are included in a discussion of each taxon. Also included are the synonymies I have employed for each taxonomic

entity. Plates 1 and 2 show photographs of the fossil fauna as a validation of my taxonomic assignments. In a separate section below, the various assemblages observed to have occurred in the Missouri Coteau are discussed as presumptive evidence of environments which now contain similar assemblages in the upper Midwest.

List of Fossil Mollusks:

Bivalves

- Anodonta grandis (Say) 1829
- Anodontoides ferussacianus (Lea) 1834
- Lampsilis luteolus (Lamarck) 1819
- Sphaerium simile (Say) 1817
- Sphaerium sp.
- Pisidium sp.

Gastropods

- Amiger crista (Linne) 1758
- Ferrissia sp.
- Gyraulus parvus (Say) 1817
- Gyraulus sp. (possibly other than G. parvus)
- Helisoma anceps (Menke) 1830
- H. campanulatum (Say) 1821
- H. trivolvis (Say) 1817
- Helisoma sp. (unassignable juveniles or fragments)
- Lymnaea humilis (Say) 1822, sensu Huberdick, 1951.

L. palustris (Muller) 1774, sensu Hubendick, 1951

L. stagnalis (Linne) 1758

Lymnaea sp. (unassignable juveniles or fragments)

Physa sp.

Promenetus exacuus (Say) 1821

? Gastrocopta sp. (fragmentary)

? Succinea avara (Say) 1824

Amnicola limosa (Say) 1817 (includes A. leightoni
Baker, 1920)

Amnicola sp. (unassignable juveniles and fragments)

V. lewisi Currier, 1868

V. tricarinata (Say) 1817

Valvata sp. (unassignable juveniles or fragments)

General Discussion of Fossil Mollusks:

In the following discussion several words are used in a precise sense. It is important that these words which are commonly used by paleontologists, but may be esoteric to scientists of other disciplines, be clearly understood. The word fauna is used to mean the species which inhabit a region during a period of geologic time (e.g., the late Wisconsinan fauna of the Missouri Coteau signifies the species listed above). The word faunule is used to mean the species represented in a collection from a site (e.g., the Nue Farm site faunule signifies the species found in collections taken from this site). The word population is used to mean the individuals in a defined geographic

Plate 1.--Late Wisconsinan Bivalvia from ice-contact sediments of the Missouri Coteau district in North Dakota.

Fig. 1. Anodonta grandis, UND-3007-1. Fractured right valve. Rough interior surface is caused by deposition of lamellar aragonite presumably induced by infestation by parasitic mite egg deposition.

Fig. 2. Sphaerium sp., UND-3521-1, X 5. Exterior of right valve.

Fig. 3. Sphaerium sp., UND-3301, X 4. Exterior of left valve.

Fig. 4. Pisidium sp., UND-3107, X 4. Interior of right valve.

Fig. 5. Baroque pearl, UND-3336, X 0.75. Fossil pearl from hinge region of a unionid clam.

Fig. 6. Lampsilis luteolus, UND-3241, slightly less than X 1. Right valve of a female L. luteolus. Note low relief of growth interruption lines on this valve and on those of fig. 8.

Fig. 7. Sphaerium sp., UND-3521, X 3 1/2. Interior of left valve.

Fig. 8. Lampsilis luteolus, UND-3279, X 0.75. Articulated valves of a male L. luteolus. Note remnants of ligament.

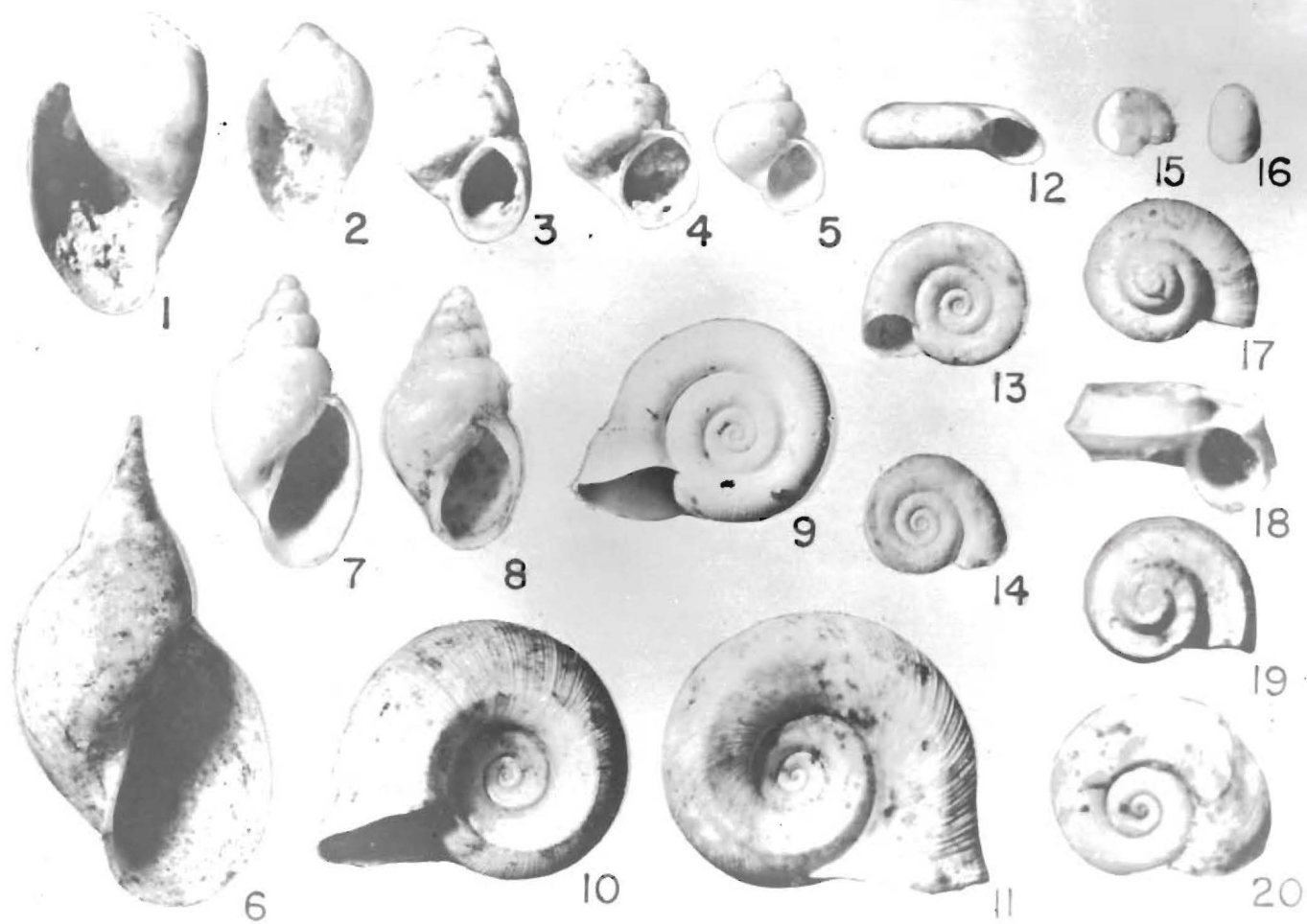


Plate 2.--Late Wisconsinan gastropoda from ice-contact sediments of the Missouri Coteau district in North Dakota.

- Fig. 1. Physa sp., UND-1764-1, 7 X; apertural view.
- Fig. 2. Physa sp., UND-3420-3, 7 X; apertural view.
- Fig. 3. Amnicola sp., UND-3385-2, 6 X; apertural view.
- Fig. 4. Amnicola limosa, UND-3569-1, 5 X; apertural view.
- Fig. 5. A. limosa, UND-3569-4, 5 X; apertural view.
- Fig. 6. Lymnaea stagnalis, UND-3209-3, 1 1/2 X; apertural view.
- Fig. 7. L. humilis, UND-3567-1, 5 X; apertural view.
- Fig. 8. L. humilis, UND-3567-1; apertural view.
- Fig. 9. Helisoma campanulatum, UND-3002, 5 X; apical view.
- Fig. 10. H. anceps, UND-3401, 5 1/2 X; apical view.
- Fig. 11. H. anceps, UND-3401, 5 1/2 X; abapical view.
- Fig. 12. Gyraulus parvus, UND-3574-3, 8 X; apertural view.
- Fig. 13. G. parvus, UND-3574-3; 8 X; abapical view.
- Fig. 14. G. parvus, UND-3574-3, 8 X; apical view.
- Fig. 15. Armiger crista, UND-3318, 11 X; apical view.
- Fig. 16. Ferrissia sp., UND-3256, 6 1/2 X; apical view.
- Fig. 17. Valvata lewisi, UND-3385-2, 5 X; apical view.
- Fig. 18. V. tricarinata, UND-3570-3; 8 1/2 X; apertural view.
- Fig. 19. V. tricarinata, UND-3284-5, 5 1/2 X; apical view.
- Fig. 20. Promenetus exacuus, UND-1794-1; apical view.



1930 1931 1932 1933 1934 1935 1936 1937 1938 1939 1940 1941 1942 1943 1944 1945 1946 1947 1948 1949 1950 1951 1952 1953 1954 1955 1956 1957 1958 1959 1960 1961 1962 1963 1964 1965 1966 1967 1968 1969 1970 1971 1972 1973 1974 1975 1976 1977 1978 1979 1980 1981 1982 1983 1984 1985 1986 1987 1988 1989 1990 1991 1992 1993 1994 1995 1996 1997 1998 1999 2000

locality at a specific time. The term implies that frequency of individuals of the various species which comprise the faunule is known and is a part of the definition of the population (e.g., the molluscan populations of the ice-basined, drift-insulated lakes of the late Wisconsin Missouri Coteau were dominated by branchiate species such as Valvata tricarinata and Amnicola limosa; this statement indicates that the number of individuals in any faunule was dominated by branchiates regardless of the number of branchiate or pulmonate species present). The word assemblage is used to indicate a group of species which typify some specific habitat (e.g., Dawley, 1947, lists the species she considered to be typical of nine aquatic habitats in Minnesota; these groups of species listed are called assemblages by me).

Statistical reductions have been used to identify species which are thought to favor specific habitats. A commonly used manipulation is known as Jaccard's coefficient and is described in Lipps and others (1968, p. 303). Jaccard invented the relationship as a means of reducing the effect of differences in a number of species in two faunas being compared and still obtaining a meaningful numerical expression of the degree to which the two faunas are similar. The fundamental assumption is that if two faunas have a large number of species in common their habitats must then have been similar. The formula applied to this type of data when Jaccard's coefficient is employed is:

$$C_{jac} = 100 n_c / n_1 + n_2 - n_c$$

When C_{jac} is Jaccard's coefficient, n_c is the number of species which occur in both faunas, n_1 is the number of species in one fauna and n_2 is the number of species in the other fauna being compared. It will be noted that the application of Jaccard's coefficient is to faunas.

I have redefined C_{jac} for use in comparing faunules from the late Wisconsinan Missouri Coteau with Dawley's habitat assemblages (C_{je}). Thus n_c is defined as the number of species common to both the faunule and the assemblage, n_1 the number of species in the faunule and n_2 is the number of species in the assemblage.

I have also employed C_{jac} to evaluate the associations of the various species in the molluscan faunas (C_{ja}). For this application n_c is the number of times the two taxa occur in the same faunule, n_1 is the number of times one taxon being compared occurs in the 40 faunules recovered from the Coteau and n_2 is the number of times the other taxon occurs in the 40 faunules.

So as to avoid confusion over the precise application of Jaccard's statistical method, I will refer to its use in the original sense as Jaccard coefficient of faunal similarity (C_{jac}), when modified to evaluate similarity of faunule with assemblages typical of modern habitats as Jaccard's coefficient of ecologic similarity (C_{je}), and when modified to evaluate degree of association between taxa of the faunas as Jaccard's coefficient of association (C_{ja}).

A means to judge intuitively the meaning of a Jaccard coefficient of faunal similarity exists in a discussion by Lipps and others (1968, p. 103). They stated:

To give some idea of the degree of fauna similarity these Jaccard coefficients may indicate, coefficients of pairs of collections of similar diversities from markedly different upper Pleistocene facies. exposed rocky shore and shallow lagoon commonly range from 5 to 15, but coefficients for volumetrically identical samples of a diverse assemblage that were collected side by side from the same lens may range as high as the upper 60's . . .

Associations and Pioneer Communities:

The apparent associations of each taxon are discussed as a part of the detailed description of each fossil taxon below. Table 1 is an association matrix designed to demonstrate the degree to which the various taxa occur in common in the late Wisconsin faunules of the Missouri Coteau. Four factors must be kept in mind when interpreting this table:

1. It is assumed that Jaccard's "coefficient de communaute" (C_{jac} as stated in Lipps and others (1968, p. 303)) is at least as powerful a method of reducing differences of n when used with faunules and assemblages (C_{je} and C_{ja}) as when it is used in comparisons of faunas.
2. The lithotope as indicated by sedimentologic studies must be considered as a complicating factor.
3. Zonation within a biotope must be assumed to be non-existent.

4. While assuming the efficacy of C_{jac} and C_{je} in reducing the impact of differences of \underline{n} in intrafaunal comparisons, gross number of occurrences is recognized as a limiting factor in association analysis (C_{ja}).

This modification is justified by the fact that the original C_{jac} was an arbitrary statistical manipulation and was not based on natural or mathematical models which would limit its applicability beyond that of parallellicity of purpose. Further the bias of increasing values of the various refinements of Jaccard's coefficient with decreasing \underline{n} is obvious. An example is the value $C_{ja} = 40$ for Helisoma trivolvis and Lymnea stagnalis on Table 1. H. trivolvis occurs at 5 sites and L. stagnalis at 2 and they occur in common twice. This is a large number of times, the absolute limit, for L. stagnalis. However, when compared with the value $C_{ja} = 22$ for L. stagnalis and Physa sp. (\underline{n} for Physa = 9) there is a C_{ja} value difference of almost two times despite the fact that L. stagnalis also occurs twice with Physa. This superficially indicates that the order of the association between L. stagnalis and Physa is only half as strong as that which exists between L. stagnalis and H. trivolvis. This is obviously false in respect to degree. The association is essentially identical for L. stagnalis and thus the evaluation is indicative only of ecologic fit of Physa and H. trivolvis. An examination of the two taxa with respect to their classification in the fauna as dominant, allied, adjunct, or

ancillary species is all that is necessary to correct any misimpressions arising from the fundamental statistical weakness. Dominant taxa are those which occur in 69 or more percent of the 40 faunules from the Missouri Coteau late Wisconsinan sediments, allied species are those taxa which occur in 39-68 percent of the faunules, adjunct species are those taxa which occur in 10-38 percent of the faunules and ancillary taxa are those which occur in less than 10 percent of the 40 faunules. On Table 1 the first 4 taxa are dominant ones, taxa numbered 5-7 are allied species, taxa numbered 8-18 are adjunct species, and 19-22 are ancillary species. Associations between ancillary and adjunct classes of the fauna are assumed to be less significant than those between the allied and dominant classes. The apparent strong associations are compared in the light of modern ecologic information where ecologic knowledge seems sufficient to warrant such speculation.

The degrees of association between the various taxa of the late Wisconsinan molluscan fauna of the Missouri Coteau have been referred to four groupings. Taxa which have C_{ja} of 50 or above are said to be first-order associates, those with C_{ja} of 49 to 30 are said to be second-order associates, and those with C_{ja} of 29 to 10 are said to be third-order associates. Those taxa which have C_{ja} of less than 10 are considered to be not associated.

Difference of lithotope, especially between stream and lake environments, are significant to interpretation. Obviously a faunule

recovered from stream-laid sediments is more capable of containing a mixed fauna than is a faunule recovered from lacustrine sediments. The Nue Farm site (pronounced "nīgh") in McIntosh County (see Table 3 for location) contains the largest number of species. It is a deposit of cross-bedded sand and gravel interbedded with finer grained sediments which contain thin marl zones. Taken as a whole, the Nue Farm faunule is a thanatocoenosis representing the entire spectrum of shallow aquatic molluscan environments. Thus, association of mollusks which lived at different times and in quite different environments, results. Regrettable as this may be, the manner of studying most of the 40 sites in the Missouri Coteau permits only the segregation of a few sites having multiple lithotopic evidence. Table 2a is an association matrix for the taxa found in lacustrine sediments only and Table 2b is an association matrix for the taxa found in fluvial and therefore mixed sediments. This treatment is merely an accommodation to the defects of collecting and studying the molluscan fauna of the Missouri Coteau. A genuine solution to the problem of biotope will be found only in detailed studies of a large number of sites. Only six sites in the Missouri Coteau were studied with a proper attention to minutely detailed stratigraphic and faunal changes in the vertical sequence. They are discussed below as a basis for insights into molluscan associations. Three are deposits of stream sediments interpreted to be the result of sedimentation in deltaic environments and three are interpreted to have

resulted from deposition in shallow lakes. The basis for these interpretations is treated in Tuthill (1963b) and will not be elaborated upon here.

It must be kept in mind that the associations suggested for the late Wisconsinan molluscan fauna of the Missouri Coteau are entirely paleontologic interpretations and do not rely upon modern synecologic information nor do they constitute modern synecologic information. They are merely the basis for comparing the fossil assemblage with modern assemblages.

Determination of pioneer species among fossil faunules may be approached from three sets of criteria, that is, by employing three different definitions of a pioneer fossil fauna and/or faunule. The concept of a pioneer community (Clements, 1916) is well established in ecology. It is a useful concept in paleoecology because it is, in its most direct analogy, the starting point of any paleosynecologic reconstruction. In ecologic studies, the biotic community which characterized the first seral stage, is determined by identifying the species of organisms which colonize a new surface.

To determine the pioneer community in a fossil site several conditions must be satisfied. First we must clearly understand whether we are defining "pioneer community" as the first assemblage to occupy a site or whether our definition is going to represent the first seral stage of the sere of communities of the entire depositional environment. If

we define "pioneer community" to be the first or lowest collection in an outcrop we will be allowed to apply our definition only to those sites where a proper attention to stratigraphic sequence has been paid. Unfortunately, collections made by field geologists, whose primary responsibility does not lie in gathering paleoecologic information, frequently take the form of channel samples which mix both the sediments and the faunules from the different horizons and lithologic units in the section. Even where a careful stratigraphic sequence is determined it is not always possible to be sure that the site where fossils were (1) preserved, and (2) found, was a typical sequence of habitats which typified the entire body of water. Thus the employment of a statistical approach which relies on the assumption that the most catholic or ubiquitous species will be members of the pioneer community is reasonable. A variant of this concept is that species which most frequently occur in small faunules can be assumed to be the pioneers. The rationale for this definition is that the conditions which exclude the more diverse communities are more rigorous; therefore, the species occupying the more rigorous habitats are pioneers. In the absence of human pollution this is an acceptable rationale, but the fact that it assumes a trend of more and more favorable conditions should be recognized.

Three definitions are thus available for suggesting the species composition of the late Wisconsinan pioneer molluscan community of the Missouri Coteau:

1. The most frequently occurring species are regarded as pioneers (i.e., those species found in the largest number of sites).
2. The species which occur in the lowest stratigraphic unit of a site are regarded as pioneers.
3. The species which most frequently occur in faunules having few taxa are regarded as pioneers.

Because each definition yields different results and is biased by a different set of assumptions, I have evaluated the late Wisconsinan molluscan fauna of the Missouri Coteau with respect to each definition. These are discussed below.

A pioneer community in a fossil fauna may be determined by establishing frequency of occurrence of taxa in the faunules studied. Table 1 shows not only the Jaccard's coefficients of association (C_{ja}) between the taxa of the late Wisconsinan Missouri Coteau molluscan fauna, but also the percent frequency of occurrence at the 40 sites which were studied (i.e., 100 times the number of sites where the taxon was found divided by the number of sites). The taxa which I have called dominant and allied species occur in a majority of the faunules. Ranked from the most frequent (84%) these are: Valvata tricarinata (84%), Gyraulus parvus (74%), Gyraulus sp. (69%), Pisidium sp. (69%), Amnicola limosa (64%), Lymnaea humilis (56%), and Promenetus exacuouus (54%). This evaluation of percent frequency

ignores the type of sediments which comprise the deposits at a site and thus obvious thanatocoenoses are mixed with necrocoenoses. If the refinement of eliminating from consideration all thanatocoenoses is made, the ambiguities implicit in frequency distribution analyses of mixed faunules is removed. When the frequency distribution of taxa with respect to faunules from sites having only lacustrine sediments is evaluated, the most frequently occurring taxa are the same as above, and their order is the same except for a reversal in rank of Gyraulus sp. with G. parvus. This is explained, I believe, by the fact that many of the specimens I have placed in Gyraulus sp. are in fact juveniles of G. parvus. In fluviatile sediments these juvenile specimens tend to be carried farther than the larger shells of adult G. parvus and are not deposited with them. In lacustrine sediments the mortality configuration of a population is reflected by the fossils because post-mortem transportation is not a factor which biases the frequency distribution.

The pioneer community may be composed of species which occur in the lowest stratigraphic unit of a site. It is assumed first that a complete record of entire successional sere is present and the sequence of sediments at a site is typical of the entire water body (evaluation and elimination of these assumptions can sometimes be accomplished). Of the six sites in the Missouri Coteau which were studied with a sufficient attention to detail to warrant this kind of evaluation of pioneer community, four of the sites were deposits of lacustrine sediments and two

were fluviatile sediments.

Taken together the species which first occur in the six sites and the number of sites in which they occur given within parentheses following the taxon are: Amnicola limosa (5), Valvata tricarinata (3), Gyraulus sp. (3), Anodonta grandis (2), unionids (2), Pisidium sp. (2), Armiger crista (2), Lymnaea humilis (2), Helisoma anceps (2), Gyraulus parvus (1), Ferrissia sp. (1), Lampsilis luteolus (1), and Sphaerium sp. (1). If we eliminate the faunules from fluviatile sediments from consideration the pioneer community under this definition would be: Amnicola limosa (3), Armiger crista (2), Valvata tricarinata (1), Gyraulus sp. (1), Pisidium sp. (1), Sphaerium sp. (1), Lymnaea humilis (1), Lampsilis luteolus (1), and Helisoma anceps (1). This refinement eliminates only Gyraulus parvus and Ferrissia sp. A further refinement is desirable, but at present impossible. The restriction of analysis to sites where clear evidence of a sedimentary sequence which included the first trophic stage in the succession of an aquatic habitat is highly desirable. Sedimentological evidence provides independent criteria for determining the paleolimnology of lacustrine sediments. The rarity of sites having clear evidence of a complete sequence may be more apparent than real. One of the six closely studied sites in the Missouri Coteau (Mummy Cat Slough site near Lehr, North Dakota) contains a complete sequence of sediments in which outwash, gravels, silts and clays, marls, marly clays, and sands occur in stratigraphic

sequence. Had more of the 40 sites been studied in close detail it is possible that this, the most philosophically valid, method of identifying pioneer communities would have a statistically valid base. At the Mummy Cat Slough site the following species constitute the pioneer community: Lampsilis sp. (probably L. luteolus), Amnicola limosa, and Armiger crista. Figure 4 shows the lithologic section and distribution of mollusks in the sedimentary sequence at this site.

The third definition by which fossil pioneer communities can be determined is the identification of the species which most frequently occur in the small faunules without reference to their occurrence in more diverse faunules. Three sites having lacustrine lithotopes which had faunules of three or fewer species were found in the Missouri Coteau. The taxa which occur in them and the number of sites at which each taxon was found (given in parentheses) are: Amnicola limosa (2), Anodonta grandis (1), unionids which could not be identified to genus (1), Lampsilis luteolus (1), and Helisoma anceps(1).

All of these definitions are complicated by the problem of assessing necrocoenoses vs. thanatocoenoses. This problem is implicit in all paleoecologic studies and creates a bias which favors the identification of lacustrine pioneer organisms over fluvial organisms. Beyond recognition of this fact there seems little the paleoecologist can do to remedy the situation.

The only species which is a pioneer under all three definitions is Amnicola limosa. I believe that the second definition restricted to faunules from lacustrine sediments is the one most analagous to the ecologic concept of a pioneer community. Despite the uneasy feeling I have about the assumptions underlying the use of paleontologic data, I feel that the species identified above under the restricted second definition are most likely to be elements of the late Wisconsinan Missouri Coteau molluscan fauna pioneer molluscan community.

Systematics:

In the following section the higher relationships between taxa and information pertinent to each taxon is discussed. I have followed the classification by Vokes (1967) for the Bivalvia and that of Taylor and Sohl (1962) for the Gastropoda. The synonymies are partial and are intended only as insights into the concepts of the species which I have employed. Measurements of the fossil shells are not included here because they are recorded in my master's thesis (Tuthill, 1963b). The hypotypes of the late Wisconsinan fossils figured on Plates 1 and 2 are curated in the paleontological cabinets of the Department of Geology, University of North Dakota, Grand Forks, North Dakota, and are curated under the accession numbers indicated in the caption to the plate.

Phylum Mollusca

Class Bivalvia

Subclass Palaeoheterodonta

Order Unionoidea

Superfamily Unionacea

Family Unionidae

Subfamily Anodontinae

Genus Anodonta Lamarck, 1799

Anodonta grandis Say, 1829

Plate 1, Figure 1.

Anodonta grandis Say, Baker (1928b, p. 152-155, Pl. 62, fig. 5).

A. grandis Say, Van der Schalie (1938, p. 33, fig. f, p. 50-52).

Anodonta grandis valves, found in the sediments of the Missouri Coteau, have all been smooth on the exterior and exhibit regularly spaced low growth-interruption lines. The interiors of many of the valves have pearl blisters which suggests that the clams were infested by parasitic mites when they lived.

Hibbard and Taylor (1960, p. 73-74) stated that A. grandis is found in relatively quiet, shallow, perennial bodies of water such as creeks, ponds, lakes, and marginal areas of large streams. According to Cvancara (personal communication March 1969), in the Missouri River drainage in North Dakota it occurs only in the tributary streams. Dawley (1947, p. 682-688) listed A. grandis as an element to be expected in the assemblages which typify (2) small rivers, (3) medium-

sized rivers, (4) large rivers, (6) soft-water lakes, (7) medium-hard-water lakes, and (8) hard-water prairie lakes. Van der Schalie (1938, p. 50-51) said that A. grandis is found in any lake in southeastern Michigan which harbors unionids. The only part of the Huron River system in which it was not found was in some of the small tributary creeks where Anodontoides ferussacianus takes its place in the unionid assemblage. He further stated that it was the species which is most common on a relatively soft bottom in quiet water and can exist on muck where few other species survive.

In the late Wisconsinan fauna from the Missouri Coteau A. grandis has a second order association with Sphaerium sp. ($C_{ja} = 20$) and Lymnaea stagnalis ($C_{ja} = 40$). Table 2b shows that there is first order association with Sphaerium, third order association with Valvata tricarinata, V. lewisi, Gyraulus sp., Promenetus exacuus, Armiger crista, and Helisoma campanulatum, and second order association with the other twelve taxa. Table 2a shows that in lacustrine sediment A. grandis is not associated with Valvata tricarinata, A. crista, Lymnaea palustris, L. stagnalis, or Helisoma anceps. It has a third order association with all other taxa of this assemblage. In fluvial sediments A. grandis has a first order association with unidentified unionid fragments and Sphaerium sp. It has a second order association with Gyraulus parvus, Gyraulus sp., Amnicola limosa, Lymnaea humilis, Helisoma anceps, Amnicola sp., Physa sp., Lampsilis luteolus,

Helisoma trivolvis, Lymnaea stagnalis, Ferrissia sp., and Anodontoides ferussacianus.

Modern workers are agreed that Anodonta grandis is among the most widespread mussels in North America today. It is likely that it is a pioneer among unionids today in the Midwest. Under the second and third definitions of paleoecologic pioneers discussed above, it is considered a pioneer of the Missouri Coteau during late Wisconsinan time.

Anodonta grandis, like most other unionids, requires a fish, probably of the families Centrarchidae or Percidae, as a host for its glochidial stage. The fossil A. grandis were collected in beds which represented necrocoenoses at the Cleveland, Nue Farm and the three Rosenthal sites. At the Nue Farm site beds of mussels were uncovered indicating a successful self-perpetuating colony which had been buried and killed in situ. The presence of A. grandis and other unionids is presumptive evidence for the presence of fishes of which no fossil evidence has been found in sediments of unquestionable late Wisconsinan age.

A. grandis is a filter feeder and thus aquatic; probably terrestrial vegetation had become established on the ice-cored Coteau before the mussels were successful in their colonization.

Permanent water conditions are indicated by the mere presence of mussels and the smooth condition of the Anodonta shell exteriors suggests that their habitat was not subject to temporary drying up during the lives of the fossil unionids.

Genus Anodontoides Simpson, 1898

Anodontoides ferussacianus (Lea) 1834

Not figured.

Anodontoides ferussacianus (Lea), Baker (1928b, p. 175-180, Pl. 67, figs. 3-7, Pl. 68, fig. 5, and Pl. 75, figs. 3-5).

Baker (1928b, p. 175) segregated a shell form of A. ferussacianus into a subspecies (A. ferussacianus subcylindraceus). Baker (1923, p. 123) also described a new species, A. birgei, from the mid-continent.

I have made no attempt to evaluate the possibility that the material from the Cleveland site might be assigned to the subspecies or to A. birgei. The fossil material from the Coteau was broken, and I felt assignment to the more widely distributed species A. ferussacianus could be justified on the criterion of umbonal prosopon, but the marginal shapes could not be reconstructed with sufficient accuracy to warrant subspecific differentiation, and the characteristic for more closely spread umbonal bars in A. birgei could not be demonstrated. The umbones of the fossil shells from the Coteau satisfy Van der Schalie's (1938, p. 34-35) key and figure and compare most favorably to Baker (1928b, Pl. 67, fig. 3).

In the Huron River drainage, Van der Schalie (1938, p. 25-26, 56-57) found A. ferussacianus in small and very small creeks of about 10 feet width and 1 to 3 feet depth of constant clear water flowing over sand or gravel bottoms where it occurred with three other unionids not included in the late Wisconsinan unionid fauna of the Coteau. He also found it in large creeks which differ from small creeks only in that they have mud or till bottoms as well as sand and gravel bottoms. In large creeks A. ferussacianus occurred with five other naiad taxa none of which are included in the late Wisconsin fauna of the Coteau. He found the species in small rivers which are 20 to 50 feet wide and 0.5 to 5 feet deep in which water flows at about four or five miles an hour over a solid bottom of sand and gravel or mud and sand. He stated that A. ferussacianus inhabits more or less quiet pools with sand or gravel bottoms, but does occur in mud. Baker (1928b, p. 177) stated that this species is found in small, quiet creeks where it lives on a sandy bottom in shallow water. He also cited a stream delta in a lake as a locality where it was found living in Wisconsin. I have found A. ferussacianus living among boulders in very swift water in the Turtle and Forest Rivers of eastern North Dakota. Cvancara (Associate Professor of Geology, University of North Dakota, personal communication October 1968) stated that A. ferussacianus occurs commonly in the upper reaches of tributary rivers in the Missouri River drainage system in North Dakota.

Since A. ferussacianus occurred at only one site, it is not possible to make a valid assessment of the associates of this species in the Missouri Coteau drainages of late Wisconsinan time. It is interesting to note that Van der Schalie did not find A. ferussacianus commonly associated with Anodonta grandis as was the case at the Cleveland site. Dawley (1947, p. 683, 687) noted the common occurrence of A. ferussacianus and Anodonta grandis in small rivers and medium-hard-water lakes only. Cvancara and Harrison (1965, p. 139) found these two species to be the only mussels in the headwaters of the Turtle River.

The only significance to the very minor presence of A. ferussacianus is to support the reconstruction suggested by the more common unionids Anodonta grandis and Lampsilis luteolus. Modern autecologic and synecologic information suggests that A. ferussacianus requires a more specific set of ecologic requirements. If this is true, and Dawley's placement of A. ferussacianus in a lake assemblage raises doubts as to the completeness of our knowledge of the ecologic preferences of this taxon, we could expect the species to be a more useful paleoecologic indicator than the more catholic species. Why A. ferussacianus has appeared in only one faunule is a problem. Perhaps the sediments from small creeks and rivers have been poorly preserved on the Coteau. More likely, I believe, the connecting drainages must have been more unstable than the ponds and perhaps the number of

niches available to A. ferussacianus for the period of time necessary to establish populations was small. Thus it may have been widely present in the form of glochidia in transit, but failed to become established for the want of suitable habitats. Certainly medium-hard-water lakes were common judging from both the fossil evidence and the sedimentological evidence.

Subfamily Lampsilinae

Genus Lampsilis Rafinesque, 1820

Lampsilis luteolus (Lamarck) 1819

Plate 1, Figures 6 and 8.

Lampsilis siligoidea (Barnes), Baker (1928b, p. 270-275, Pl. 89, figs. 5-8 and Pl. 90, fig. 1).

L. radiata siligoidea (Barnes), Van der Schalie (1938, p. 67-69).

L. radiata siligoidea (Barnes), Tuthill (1963b, p. 78-80).

Wheeler (1963) has discussed the reasons for placing Lampsilis siligoidea (Barnes, 1823) in subjective synonymy with L. luteolus. I accept her arguments and employ Lamarck's name despite the fact that most North American workers employ Barnes'.

I believe that I can assign whole valves and/or major fragments which contain the beaks and hinge teeth to this taxon without reservation.

Like other mussels L. luteolus infests certain species of fish during a glochidia stage. Baker (1928b, p. 273) listed bluegill (Lepomis pallidus), yellow perch (Perca favescens) and wall-eyed pike

(Stizostedion vitreum) as natural hosts of L. luteolus in Wisconsin. He also stated that artificial infection of the bass (Micropterus dolomieu and M. salmoides), the crappies (Pomoxis annularis and P. sparoides), and the sauger (Stizostedion canadense) has been successful. Baker found that in Wisconsin modern L. luteolus is indiscriminate in its selection of habitat, but is generally an inhabitant of shallow water.

As a part of the general fauna of the late Wisconsinan Missouri Coteau L. luteolus has only third order associations with the other taxa, except with Lymnaea palustris, Anodontoides ferussacianus, and Helisoma campanulatum with which there is no association indicated. In lacustrine sediments L. luteolus has a third order association with all other than Helisoma anceps, H. campanulatum, Physa sp., Valvata lewisi, Lymnaea palustris, and L. stagnalis with which no association exists. In fluviatile sediments a first order association with Sphaerium sp., Physa sp., Helisoma trivolvis, Lymnaea stagnalis, and Ferrissia sp.; a second order association with Armiger crista, H. campanulatum, Anodonta grandis and Valvata lewisi; a third order association with Gyraulus parvus, Pisidium sp., Amnicola limosa, Gyraulus sp., Lymnaea humilis, Promenetus exacuous, unionid fragments, and Amnicola sp. and no association with Valvata tricarinata, Helisoma anceps and Anodontoides ferussacianus.

It ranks as a pioneer in the general molluscan fauna under the second, (including all definitional restrictions) and third definitions of a paleopioneer community. L. luteolus was found in six of the 40 sites studied.

The presence of L. luteolus in large populations is presumptive evidence for the presence of freshwater fishes, probably members of the genera Lepomis, Perca, and Stizostedion. The modern mode of life of the mussels as filter feeders upon water-borne organic detritus suggests the presence of an extensive aquatic and probably terrestrial flora. The regularity of the shell exteriors of fossil L. luteolus is suggestive of stable ecologic conditions and good health among the individuals of the populations during their lives. This environmental stability does not necessarily apply to the entire Coteau at any one time. The conditions in any one stream or lake system may have differed sharply with those in nearby systems. The shells of the mussels merely tell us that while the clams were living the ecologic conditions were stable where they were living. Permanent water existed through at least 10 years at several sites if growth-interruption ridges are a valid index of age in years (assuming one interruption ridge per year).

Order Veneroida

Suborder Venerina

Superfamily Corbiculacea

Family Pisidiidae

Genus Sphaerium Scopoli, 1777

Plate 1, Figures 2, 3, and 7

Herrington (1962) has revised the taxonomy of the family Pisidiidae. His keys make it possible to assign shells to species on strictly shell-morphologic characters. I have not attempted assignment of fossil material below the genus for two reasons. First, I did not have comparative collections available by which I could develop experience in identifying this group. Secondly, I do not believe that Herrington's revision of the North American pisidiids clears up the matter of previous taxonomic confusion and ecologic preferences assigned the various species. If the ecology assigned to the various revised species derives from the work of malacologists who preceded Herrington, their confusion over the identity of various pisidiids certainly invalidates the composite ecology. Herrington grouped parts of various species in different revised species, and the ecologic preferences of these new species has yet to be determined.

As discussed above, the reports of the ecology of species of the genus are confusing because of taxonomic instability.

In the general late Wisconsinan fauna of the Missouri Coteau Sphaerium has third order associations with all other taxa except Anodonta grandis with which it has second order association.

The presence of Sphaerium assures that permanent water was present. It, no doubt, has much more significance, but at present I regard it to be better judgment to employ this genus in a very conservative manner in paleoecologic evaluations.

Genus Pisidium Pfeiffer, 1821
Plate 1, Figure 4

The discussion of Sphaerium taxonomy is equally applicable to Pisidium. I believe that the fossil material from the late Wisconsinan sediments of the Missouri Coteau contains several shell forms of perhaps specific rank. Where found, Pisidium is very abundant.

Class Gastropoda

Subclass Streptoneura

Order Mesogastropoda

Superfamily Valvatacea

Family Valvatidae

Genus Valvata Muller, 1774

Valvata tricarinata (Say) 1817

Plate 2, Figures 18 and 19

Valvata tricarinata (Say) Baker; (1928a, p. 11-20, Pl. 1, figs. 1-3).

Subspecies and mutations to which formal names have been given by Baker have not been recognized. LaRocque (1956) has discussed variations in carinae in this species. Bicarinate forms were rarely encountered in the fossil material. In Tuthill (1961) I misidentified these bicarinate variants as V. bicarinata. No ecarinate variants were found.

In his discussion of Valvata ecology in Wisconsin Baker (1928, p. 15) stated:

Valvata tricarinata, in one form or another, is perhaps the most abundant mollusk in many lakes and rivers. . . .

A recent study of a large collection of Valvata from Waukesha and Jefferson Counties Wisconsin indicates that the strongly tricarinate form is characteristic of rivers while the variations (simplex, perconfusa, etc.) are confined chiefly to lakes. . . .

These variations are to be regarded as mutations . . . they are not strictly ecological, for many of the variations may be found in any lot from one locality or habitat.

Cvancara (oral communication, September, 1968) has found V. tricarinata in North Dakota, living in small pools in a stream bed, between which there was no apparent flow of water. According to Dawley (1947) V. tricarinata is typical of almost half of the assemblages she has erected for Minnesota molluscan habitats. It was not found in small rivers, medium rivers, large rivers, and ponds in Minnesota.

Valvata tricarinata is, without doubt, the taxon most commonly found in late Wisconsinan Missouri Coteau faunules (84% of the sites studied). It has first order association with Gyraulus parvus,

Gyraulus sp., Pisidium sp., Amnicola limosa, Lymnaea humilis, and Promenetus exacuus; second order association with Helisoma anceps, unionid fragments and H. campanulatum; non-association with Lymnaea stagnalis, L. palustris, Ferrissia sp., and Anodontoides ferussacianus, and third order association with the balance of the fauna. In the analysis of associations among species taken from fluviatile sediments alone, the first order associations are the same except that Lymnaea humilis and Promenetus exacuus have second order association and Helisoma anceps has first order association. Where it occurs V. tricarinata numerically dominates the fossil population.

V. tricarinata is a branchiate and must therefore have had permanent water in which to live. It must have had vegetable detritus in adequate supply for food because its population was certainly successful. Thus, it is also good presumptive evidence for an aquatic flora. The species is a minor element in the ponds of the Coteau today which have high dissolved solids contents. Thus, its abundance in the fossil faunas is assumed to mean that dissolved solids did not accumulate to any great degree in the late Wisconsinan ponds of the Coteau.

Valvata lewisi (Currier) 1868

Plate 2, Figure 17.

Valvata lewisi (Currier), Baker (1928a, p. 26-30).

Dawley (1947, p. 687) indicated that V. lewisi is typical only of medium-hard-water lakes in Minnesota. Baker (1928, p. 28-29) stated that V. lewisi is largely a lake form.

V. lewisi has no first order associations in the late Wisconsinan Missouri Coteau fauna. It has second order association with Gyraulus parvus, Pisidium sp., Lymnaea humilis, Armiger crista, and Physa sp.

Other than the presence of permanent water, the inclusion of V. lewisi in the late Wisconsinan Missouri Coteau fauna has little significance. Despite the apparent agreement between Baker and Dawley that this species is a lake form, it was found in only 30% of the lacustrine deposits studied. I believe that the sedimentology is far more conclusive than the supposed ecologic preferences of the modern species.

Superfamily Rissoacea

Family Hydrobiidae

Genus Amnicola Gould and Haldeman, 1841

Amnicola limosa (Say) 1817

Plate 2, Figures 3, 4, and 5.

A. limosa superiorensis Baker, Baker (1928a, p. 101-102, Pl. 6, figs. 9-11 and Pl. 7, figs. 22-23).

A. limosa porata (Say), Baker (1928a, 98-101, Pl. 6, figs. 7-8, 18 and Pl. 8, figs. 1-3).

A. limosa parva Lea, Baker (1928a, p. 102-103, Pl. 6, figs. 12-14).

A. leightoni Baker, Baker (1928a, p. 120-121, Pl. 6, figs. 34-39).

A. limosa (Say), Berry (1943, p. 23-26).

Fundamental biometrics in Tuthill (1963c) show that A. leightoni, which is regarded by many as an index fossil of the pre-Recent Pleistocene, is in actuality a suite of large specimens of A. limosa. I measured several series of Baker's paratypic material for

A. leightoni (these were made available to me by the Illinois Geological Survey). I also measured modern shells identified by Baker of A. limosa, A. limosa porata, and A. limosa parva. A strong correlation existed between the specimens Baker called A. leightoni and individuals with a large number of whorls, but no significant difference existed between other parameters of the large specimens and those of smaller specimens measured. Thus, I have placed A. leightoni in subjective synonymy with A. limosa.

Baker (1928, p. 97) stated that A. limosa, ". . . is a species of rivers, streams and quiet bodies of water." Dawley (1947) listed this species for all of her Minnesota habitats except large rivers and ponds.

Amnicola limosa is found in 64% of the sites on the Missouri Coteau. It has first order association with V. tricarinata, Gyraulus parvus, Gyraulus sp., Pisidium sp., Lymnaea humilis, and Promenetus exacuous; second order association with Helisoma anceps, unionid fragments, and H. campanulatum; non-association with L. stagnalis, L. palustris, Helisoma trivalvis, Ferrissia sp., and Anodontoides ferussacianus, and third order association with the balance of the fauna. In faunules from lacustrine sediments alone A. limosa is one of the dominant species and occurs in 67% of the sites. It has first order association with the same species as it does in the general fauna discussed above.

Like the other branchiates A. limosa requires permanent water and like all the mollusks must have organic detritus as food. Thus, aquatic vegetation was well established in the habitats occupied by these snails.

Amnicola sp.

Small shells, presumably juveniles, and fragments of Amnicola limosa, were recovered from many of the sites. Because I did not believe that confident assignment of these specimens to species was possible, I have employed Amnicola sp. to designate their presence.

Subclass Euthyneura

Order Basommatophora

Superfamily Lymnaeacea

Family Lymnaeidae

Genus Lymnaea Lamarck, 1799

Lymnaea palustris (Muller) 1774

Not figured.

Lymnaea palustris (Muller), Hubendick (1951, p. 84, 85, 119-122, figs. 190, 191, 195-203, and 303, b, m, and v only).

Taylor, (1965, p. 597-611) has recommended discontinuation of the use of this name. He cites Jackiewicz (1959) who has established that L. palustris in Poland is actually three biologic entities. Taylor's logic is unassailable, but implementation is difficult, if not impossible

at present, because two of the three groups defined by Jackiewicz are indistinguishable on shell characters. At present it appears best to continue using the name while recognizing the problems of the taxonomy. The shell form represented by Baker (1928, p. 220, Pl. 13, figs. 23-26, 3-7, and 9-13) under the names Stagnicola umbrosa jolietensis (Baker) and S. palustris elodes (Say) appear to be similar to the shells of the form I have found in the sediments of the Missouri Coteau.

Baker (1928, p. 219) quoted Say as reporting that Stagnicola umbrosa, "inhabits the ponds and tranquil waters of the upper Missouri." In Wisconsin Baker found it in ponds and sloughs which became more or less dry in summer. He also found it in small creeks, ditches and along the shores of rivers. Of S. palustris elodes Baker (1928, p. 216) said, "the more distinctly malleated forms inhabit stagnant pools where the bottom is muddy . . ." The species is omnivorous. In North Dakota I have observed this snail in practically every slough east of the Missouri River which I have examined for mollusks. In the Missouri Coteau it clearly demonstrates a capacity to withstand protracted and extreme periods of dessiccation.

L. palustris has first order association with Ferrissia; third order association with only A. crista, Physa sp., Sphaerium sp., A. grandis and H. trivolvis; and is not associated with any of the other elements of the general late Wisconsinan fauna of the Missouri Coteau. The associations within the faunules from lacustrine sediments alone

indicate a first order association with Helisoma trivolvis and L. stagnalis and third order association with Physa sp. It was not found in fluviatile sediments.

The infrequent occurrence of L. palustris in the late Wisconsin Missouri Coteau sites is significant in that it demonstrates the the marked difference in the nature of the pre-Recent molluscan fauna with the Recent molluscan fauna of the region. It is an ancillary species in late Wisconsinan time and is limited to the type of environment from which it is most frequently reported in modern faunas. Thus it can be inferred that its ecologic preferences have not changed and that the number of receptive habitats in late Wisconsinan time was small. Where it was encountered in the fossil faunules it was not a major element in terms of frequency.

Lymnaea stagnalis (Linne) 1758

Plate 2, Figure 6.

Lymnaea stagnalis jugularis (Say), Baker (1928a, p. 198-204, Pl. 11, figs. 6, 9, 10, 12, 13, and Pl. 12, fig. 4).

L. stagnalis (Linne), Hubendick (1951, p. 118-119, fig. 300, e and f only).

Baker (1928a, p. 202) generalized that L. stagnalis ". . . is usually found in more or less stagnant parts of ponds or lakes and rivers about vegetation." L. stagnalis is omnivorous and has been observed attacking living fish. Dawley (1947, p. 682-688) indicated that this taxon is typically found in all the habitats she has defined except small streams and ponds.

L. stagnalis is an ancillary species in the general late Wisconsinan Missouri Coteau fauna. It has first order association with Ferrissia sp.; second order association with A. grandis and H. trivolvis; third order association with Physa sp., Sphaerium sp., L. luteolus, Armiger crista, and Amnicola sp.; and is not associated with the rest of the fauna. In faunules from only fluviatile sediments it has first order association with Sphaerium sp., Physa sp., L. luteolus, H. trivolvis, and Ferrissia sp.; second order association with V. lewisi, H. campanulatum, A. grandis, and A. crista. In faunules from only lacustrine sediments it has first order association with H. trivolvis and L. palustris; third order association with Gyraulus parvus and Physa sp.; and it is not associated with the remaining taxa.

The significance of L. stagnalis in the fossil fauna lies in its minor position in the populations where it is found and its rarity on the Coteau during Wisconsinan time. It and L. palustris dominate modern slough populations. Their ancillary position in the late Wisconsin fauna suggest the rarity or absence of such environments.

Lymnaea humilis Say, 1822

Plate 2, Figures 7 and 8.

Fossaria parva (Lea), Baker (1928a, p. 285-288, Pl. 16, fig. 7, Pl. 17, figs. 1-5).

F. dalli (Baker), Baker (1928a, p. 288-289, Pl. 16, fig. 11).

Lymnaea humilis Say, Hubendick (1951, p. 126-128, figs. 308, g and h only).

For a discussion of the taxonomy of L. humilis see the section on Alaskan nonmarine mollusks which follows.

Baker (1925, p. 287) stated that F. parva "inhabits wet, marshy places, generally out of the water, on sticks, stones, or muddy flats. The animal is more prone to leave the water than any other species of the family" and that F. dalli has an ecology "similar to" F. parva. Hibbard and Taylor (1960, p. 93-94) confirmed this habitat for F. dalli, which they observed out of the water on wet mud in Meade County State Park, Kansas.

L. humilis has first order association with V. tricarinata, G. parvus, Gyraulus sp., Pisidium sp., A. limosa and P. exacuus; second order association with H. anceps, A. crista, V. lewisi, and H. campanulatum; third order association with Physa sp., unionid fragments, Sphaerium sp., L. luteolus, A. grandis, and H. trivolvis; and is not associated with the other five species of the late Wisconsinan fauna. In faunules from fluvial sediments it has first order association with only A. limosa. In lacustrine faunules it has the same first order associations as in the general fauna.

Superfamily Ancylozoa

Family Ancylozoidae

Genus Ferrissia Walker, 1903 Plate 2, Figure 16.

The specimens assigned to this genus have not been identified at the species level because they were fragmentary. That they belong

to this genus is unquestionable, but I do not feel competent to make a more refined assignment.

Baker (1928, p. 393) stated that Ferrissia "occurs in running streams, quiet ponds, rivers, and lakes." In North Dakota I have found members of this genus only in streams (e.g., Forest River and Turtle River).

In the general late Wisconsinan fauna Ferrissia has first order association with only Lymnaea palustris and L. stagnalis; third order association with Sphaerium sp., L. luteolus, H. trivolvis, and L. stagnalis; second order association with V. lewisi, H. campanulatum, A. grandis, and A. crista; non-association with H. anceps and V. tricarinata; and third order association with the other eight species of the fluviatile fauna.

The major significance of Ferrissia in the fossil fauna is the manner in which it demonstrates the degree to which the molluscan fauna had developed in species composition on the ice-cored Missouri Coteau.

Family Planorbidae

Genus Gyraulus J. de Charpentier, 1837

Gyraulus parvus (Say) 1817

Plate 2, Figures 4 and 6.

Gyraulus parvus (Say), Dall (1905, p. 95).

G. parvus (Say), Baker (1928a, p. 374-378, Pl. 23, figs. 27-31, 39).

G. parvus (Say), Taylor (1960, p. 58, Pl. 4, figs. 1-13, 17, 18).
G. parvus (Say), Hibbard and Taylor (1960, p. 100-101, Pl. 6,
 figs. 2-3, 5-6, 8-9, 11-12, 15).

In sorting the small planorbid shells I have assigned to this name only those Gyraulus shells which were mature enough to show the apertural deflection and the expanded last whorl typical of G. parvus. There is no doubt that many of the shells, of less than three whorls, are juvenile G. parvus, but I have placed them in Gyraulus sp.

Gyraulus parvus is probably the most widely distributed taxon of North American freshwater snails. Baker (1928, p. 377) stated that this species is more often found on vegetation than in any other situation. Dawley (1947, p. 682-688) listed G. parvus as a characteristic element of small river and pond assemblages. She lists other species of Gyraulus (i.e., G. deflectus obliquus and G. hirsutus) from all but her small river, medium-sized river, large river, and pond assemblages. Because of my reservations about my ability to distinguish the small species of Gyraulus the possibility that G. deflectus and G. hirsutus are present and included here in Gyraulus sp. must be entertained.

In the general late Wisconsinan Missouri Coteau fauna G. parvus is the second most commonly encountered species and appears in 74% of the faunules. It has first order association with V. tricarinata, Gyraulus sp., Pisidium sp., A. limosa, L. humilis, and P. exacuus; second order association with H. anceps, A. crista, unionid fragments, V. lewisi, H. campanulatum and Physa sp.; third order association

with Sphaerium sp., L. luteolus, A. grandis, H. trivolvis, and Amnicola sp.; and is not associated with the other four species of the fauna. In fluviatile sediments its relationship with Gyraulus sp. and L. humilis drops to second order. I believe this is a function of the problem of identifying other than adult specimens and of settling velocity fractionation of the fossil shells. The smaller Gyraulus sp. and L. humilis do not settle out at the same spot as the mature Gyraulus which were the only candidates for assignment to G. parvus. In fluviatile environments G. parvus has at least third order association with all the other taxa.

The presence of G. parvus is significant primarily in the diversity which it lends to the general fauna. Certainly the conditions which favor its success were common on the Coteau during late Wisconsin time. If thick vegetation is necessary to this species as implied by Baker, then thick vegetation was no doubt present.

Gyraulus sp.

As mentioned above, all questionable specimens assignable to Gyraulus have been assigned to Gyraulus sp. I saw no material which could be confidently assigned to small species of Gyraulus other than G. parvus. The most common shell form assigned to Gyraulus sp. was a one and a half to two whorl shell which was perfectly planispiral (as opposed to the pseudoplanispiral form of G. parvus). The whorls are slightly involute and the aperture is not deflected. I believe that this

shell form represents juveniles or a variation of G. parvus also because the number of individuals is so great that adults would be expected to appear in the collections were they the offspring of other species.

In the general late Wisconsinan Missouri Coteau fauna Gyraulus sp. has association patterns which are significantly different from G. parvus only in its second order associates. The differences are reflected in a larger number of third order associations and a smaller number of second order associations with essentially the same first order and non-associations. G. parvus has second order association with six taxa and Gyraulus sp. with only two (i.e., Helisoma anceps and Lymnaea humilis). In fluviatile sediments Gyraulus sp. is less common (54% of the sites studied) than G. parvus (82%). This is interpreted as a function of sedimentological phenomena rather than differences in population structure. Gyraulus sp. being smaller and therefore capable of being transported by slower moving water was probably carried out of the streams and deposited in standing water bodies. The larger specimens of G. parvus were no doubt left behind by moving water and thus are more frequently encountered in fluviatile sediments.

Because of the taxonomic uncertainties no ecologic data can be confidently assigned to Gyraulus sp. and the paleoecologic significance must be limited to that of G. parvus.

Genus Promenetus Baker, 1935Promenetus exacuus (Say) 1821

Plate 2, Figure 20.

Promenetus exacuus (Say), Dall (1905, p. 91).Menetus exacuus (Say), Baker (1928, p. 361, Pl. 23, figs. 1-5; 1945, p. 182).P. exacuus (Say), Taylor (1960, p. 59).P. exacuus (Say), Hibbard and Taylor (1960, p. 107-110).

Taylor (1960, p. 59) stated that, "P. exacuus is found in shallow perennial or subpermanent, quiet water bodies, such as ponds, ox-bow lakes, marshes, and sloughs or backwaters along streams. It is usually on the submerged vegetation in such habitats. The isolated occurrence in Meade County, Kansas, can be explained by the summer-cool habitat furnished by artesian water in which this snail lives. In northern Nebraska it was found in permanent or nearly permanent quiet water." He also states that this species has a North American distribution north of about 39° N. lat. and southward in mountainous regions and the Atlantic Coastal Plain to North Carolina. In North Dakota we have found it living in saline (total dissolved solids 2280-5210 ppm) ponds (Tuthill and Laird, 1963, Table 4). P. exacuus is capable of withstanding widely variable ecologic conditions.

P. exacuus is a commonly occurring taxon in the late Wisconsinan molluscan fauna of the Missouri Coteau. It was found in 54% of the sites. It has first order association in the general fauna with V. tricarinata, G. parvus, Gyraulus sp., Pisidium sp., A. limosa, L. humilis, and Physa sp.; second order association with only H. anceps,

Armiger crista, and H. campanulatum; is not associated with Amnicola sp., L. stagnalis, L. palustris, Ferrissia sp., and Anodontoides ferussacianus; and has third order association with the five remaining species of the fauna.

Its associations in lacustrine sediments follows the pattern seen in the general fauna, but in fluviatile sediments it has only three first order associates (G. parvus, A. limosa, and Gyraulus sp.). In late Wisconsinan times P. exacuouus was quite clearly more common in lakes (59% of the sites in lacustrine sediments) than in streams (45%).

The presence of P. exacuouus is good evidence for the existence of quiet-water habitats which did not attain high temperatures in summer.

Genus Armiger Hartman, 1840

Armiger crista (Linne) 1758

Plate 2, Figure 15.

Armiger crista (Linne), Dall (1905, p. 96).

A. crista (Linne), Baker (1928a, p. 385-387, fig. 164; 1945, p. 78, Pl. 76, fig. 6).

A. crista (Linne), Taylor (1960, p. 58).

A. crista (Linne), Hibbard and Taylor (1960, p. 101-103, Pl. 6, figs. 1-2).

Hibbard and Taylor (1960, p. 103) quoted Gerjer as stating that in Germany A. crista occurs ". . . in ponds and marshes, even in those thickly overgrown. . . ." Kenk (1949, p. 53) stated that this species

. . . was taken . . . from March to June. Numerous individuals appear also in the culture of a soil sample from the bottom of the pond, prepared in October. No specimens

were collected from December to February. The animals obviously estivated buried in the dry mud and, after the pond had filled, remained inactive in the soil until the latter part of winter.

Baker (1928, p. 386) did not find A. crista alive in Wisconsin.

I have found it both as drift and living individuals in some of the thirteen ponds in the Missouri Coteau which were studied by Tuthill and Laird (1963). It successfully occupied saline lakes which had 1350-4730 ppm dissolved solids. We found it only where about 10 (range 7 to 13, mean 9.5) aquatic species of mollusks were found. It is thus a form which becomes established late in any seral stage of succession on the modern Missouri Coteau.

In the general late Wisconsinan Missouri Coteau fauna A. crista has a first order association with only Physa sp.; second order association with G. parvus, Pisidium sp., L. humilis, P. exacuous, H. anceps, and Valvata lewisi; third order associations with V. tricarinata, Gyraulus sp., Amnicola limosa, unionid fragments, Heliosoma companulatum, Sphaerium sp., Lampsilis luteolus, H. trivolvis, Lymnaea stagnalis, and L. palustris; and is not associated with the remaining four species of the fauna. The associations in lacustrine sediments are similar, but in fluviatile sediments A. crista has no first order associations. It is assumed that its inclusion in fluviatile sediments is an accident of transportation.

The presence of A. crista in one-third of the sites studied indicates the widespread occurrence of shallow-water habitats which contained a well developed molluscan fauna. Vegetation was no doubt present in these habitats.

Genus Helisoma Swainson, 1840

Helisoma trivolvis (Say) 1817

Not figured.

Helisoma trivolvis (Say), Dall (1905, p. 80, figs. 68-69).

H. trivolvis (Say), Baker (1928a, p. 330, Pl. 20, figs. 1-13, 23, 33).

H. trivolvis (Say), Frye and Leonard (1952, Pl. 16, fig. v).

H. trivolvis (Say), Taylor (1960, p. 59).

H. trivolvis (Say), Hibbard and Taylor (1960, p. 104, Pl. 10, figs. 10, 14, 17).

H. trivolvis can be identified even in fragmentary and immature specimens which contain the nuclear whorl.

Baker (1928, p. 332) stated, "typical H. trivolvis is always an inhabitant of quiet, more or less stagnant water. Many of the Wisconsin habitats have been formed behind beach barriers. . . ." We have found H. trivolvis in Long Lake, Minnesota (Tuthill, Clayton, and Laird, 1964, p. 354) and in 6 of the 13 sloughs studied on the Coteau (Tuthill and Laird, 1963, p. 54-55, 82-89).

In the general late Wisconsinan molluscan fauna H. trivolvis has no first order associations; second order association with only L. stagnalis; and it is not associated with A. limosa, H. anceps, unionid fragments, H. campanulatum and A. ferussacianus. It has third order association with the other 15 species of the fauna. H. trivolvis occurs

in only 10% of the sites and is an adjunct species. It is interesting to note its non-association with the other species of Helisoma. It is an ancillary species in fluviatile sediments.

Today H. trivolvis is a common species in the temporary ponds of the Coteau. Dawley (1947) indicated that it is a common element of all Minnesota habitats except soft-water lakes. Thus, it seems reasonable to conclude that few of the ponds on the Coteau during late Wisconsinan time were relatively rich in dissolved solids and that H. trivolvis is one of the taxa favored by conditions too rigorous for other pulmonates.

Helisoma campanulatum (Say) 1821

Plate 2, Figure 9

Helisoma campanulatum (Say), Dall (1905, p. 90, fig. 70).

H. campanulatum (Say), Baker (1928a, p. 345-353, Pl. 21, figs. 1-2, 4-5, 8-9, 13-14; and 1945, Pl. 108, figs. 1-12, 14-34, Pl. 109, figs. 1-6 only).

Fragments which include the nuclear whorl are confidently assigned to this taxon because of their size and the absence of a sub-rounded carina which is strongly developed in H. anceps and moderately developed in H. trivolvis.

Baker (1928, p. 347-348) stated that H. campanulatum " . . . is a species of lakes." He cites specific occurrences in Wisconsin in 6 lakes, 1 river and 1 small stream. In his section on distributions in the state he relates the occurrence of species to six major drainage systems "and streams flowing into Lake Michigan and Green Bay."

Thus it is difficult to justify employing H. campanulatum as presumptive evidence of lake environments. Further, Baker has recognized three subspecies on criteria which I feel are inappropriate. One of these H. campanulata ferrissi was found in Wisconsin only as a fossil. Baker states of this form, "the fossil record indicates a river habitat."

As of the summer of 1964, no live specimen of H. campanulatum had been reported from the state despite its abundance in northwestern Minnesota (e.g., Bemidji Lake, and Long Lake, Beltrami County, Minnesota). Dawley (1947, p. 672-688) found this species a typical element of the assemblages typical of all her modern Minnesota habitats except medium-sized rivers (3), large rivers (4), and ponds (5).

In the general late Wisconsinan molluscan fauna of the Missouri Coteau H. campanulatum is an adjunct species. It occurs in 26% of the faunules. It has no first order associates; second order association with V. tricarinata, G. parvus, A. limosa, L. humilis, and P. exacuus; it is not associated with L. luteolus, H. trivolvis, L. stagnalis, L. palustris, Ferrissia sp., and A. ferussacianus; and third order association with the 10 remaining taxa. In lacustrine sediments it has first order association with only Physa sp., and in fluviatile sediments it has first order association with only Sphaerium sp.

Dawley's characterization of the taxon as a small creek and small river or lake (excluding ponds) form is a modification of Baker's assertion that H. campanulatum is a snail typically found only in lakes.

This modification permits the interpretation of the occurrence of this species in about one-fourth of sites as indicative of the presence of quiet water which probably was low in dissolved solids. The absence of H. campanulatum from the North Dakota fauna supports the idea that the types of molluscan habitats present on the Missouri Coteau have changed radically since the late Wisconsinan despite the similarity of the late Wisconsinan molluscan fauna to the modern fauna when judged by species present in both faunas.

Helisoma anceps (Menke) 1830

Plate 2, Figures 10 and 11.

Planorbis bicarinata Say, Dall (1905, p. 87, fig. 64).

Helisoma antrosa (Conrad), Baker (1928a, p. 317-321, Pl. 19, figs. 8-15).

H. antrosa (Conrad), Frye and Leonard (1952, Pl. 15, fig. y).

H. anceps (Menke), Taylor (1960, p. 58-59).

H. anceps (Menke), Hibbard and Taylor (1960, p. 103-104, Pl. 10, figs. 1, 6, 7).

Baker (1928, p. 319) stated that H. anceps ". . . is primarily a river and creek species not living in the large lakes." We (Tuthill and Laird, 1963) found H. anceps in one of the 13 lakes we studied on the Missouri Coteau in 1963. It occurred in Beaver Lake at the western edge of the Missouri Coteau. The total dissolved solids in this body of water were 4,730 ppm in mid-October of 1962. We also (Tuthill, Clayton, and Laird, 1964, p. 354) found it in Long Lake, Minnesota. This occurrence in the modern Missouri Coteau fauna is in agreement with Dawley's (1947) designation of H. anceps as a species typical of hard-water prairie lakes (8). Furthermore, Dawley states

that the species is typical of small rivers (2), medium-sized rivers (3), soft-water lakes (6), and medium-hard-water lakes (7). She does not include it in the faunules typical of small streams (1), large rivers (4), and ponds (5) in Minnesota. Thus, it seems that the distribution of H. anceps in Wisconsin is not characteristic of the species. Of course, this was not a claim made by Baker. Emphasis of the point is made here because Taylor (1960, p. 58) and Hibbard and Taylor (1960, p. 104) employed only Baker's ecologic conclusions which I feel are invalid in the light of the above discussion.

In the general late Wisconsinan molluscan fauna of the Missouri Coteau, H. anceps is the most frequently occurring adjunct species (38% of the sites). It has first order association with none of the other taxa; second order association with V. tricarinata, G. parvus, Gyraulus sp., Pisidium sp., A. limosa, L. humilis, P. exacuus, A. crista, Sphaerium sp., and unionid fragments; third order association with V. lewisi, H. campanulatum, Physa sp., L. luteolus, and A. grandis; and it is not associated with the six remaining species. In lacustrine sediments it has first order association with only G. parvus and Physa sp., but it is not associated with only 5 taxa; L. stagnalis, L. palustris, A. grandis, H. trivolvis, and L. luteolus. It is interesting that it is not associated with H. trivolvis in any of the lithotopes.

The presence of H. anceps in the modern fauna and in the late Wisconsinan Missouri Coteau fauna is misleading. In Beaver Lake the

species is a very minor element of the modern faunule. But, in the late Wisconsinan faunules it is the most commonly occurring species of the genus, and in the faunules where it is present it is very abundant. Baker's conclusion that H. anceps is a river form is disregarded for interpretation of the Missouri Coteau fauna.

Family Physidae

Genus Physa Draparnaud, 1801
Plate 2, Figures 1 and 2.

I have, because of the confused state of the taxonomy of this genus, been reluctant to assign the specimens referable to this genus to species. As was the case with Pisidium, fundamental confusion over the taxonomy renders untrustworthy the ecology attributed to the species of the genus. The shell type found in late Wisconsinan sediments of the Missouri Coteau is described and figured in Tuthill (1963b, p. 86, 87, Pl. 1, figs. 12, 13).

Order Stylommatophora

Suborder Orthurethra

Superfamily Pupillacea

Family Pupillidae

Genus Gastrocopta Wollaston, 1878
Not figured.

Three specimens from the Shauer Farm site in Stutsman County, which has been radiocarbon dated at 9870 ± 290 y.b.p. (W-954), are the first Pleistocene record of the land snails east of the Missouri River. I am confident that these specimens were not in situ, but were recent contaminants. The lack of terrestrial mollusks in the late Wisconsinan sediments of the Coteau is a problem of the first order.

Because of the uncertainty of the stratigraphic position of these specimens, I do not employ them as a basis for the paleoecologic reconstruction of the late Wisconsinan Missouri Coteau nor regard them as a certain part of the late Wisconsinan molluscan fauna.

Suborder Heterurethra

Superfamily Succineacea

Family Succineidae

Genus Succinea Draparnaud, 1801

Succinea avara (Say) 1824

Not figured.

The specimens representing this species were collected by Clayton and reported by him (1961, p. 15). He informs me (personal communication, October, 1968) that the specimens were picked from the surface of a fresh roadcut and that the chance of contamination by Recent terrestrial snails was likely. I, therefore, reject this as a late Wisconsinan element in the fauna.

Paleoecologic Interpretation

In 1963 I attempted to compare the late Wisconsinan molluscan fauna of the Missouri Coteau district with the faunule from Long Lake, Beltrami County, Minnesota, (Tuthill, Clayton, and Laird, 1964). The Jaccard coefficient of faunal similarity for this comparison is 83. The Minnesota aquatic nonmarine molluscan fauna as summarized by Dawley (1947) can be compared with the late Wisconsinan molluscan fauna of the Missouri Coteau. The Jaccard coefficient of faunal similarity is 21. The restriction of the comparison to aquatic gastropods is justified because of reasons based on the following four facts:

1. The late Wisconsinan Missouri Coteau drained toward the Missouri River whereas Minnesota is drained by the Mississippi River.
2. The modern unionid fauna of the Missouri River drainage in North Dakota contains only five species of mussels (Cvancara, oral communication, November, 1968). Only two of these are different from the late Wisconsinan unionid fauna of the Missouri drainage system in North Dakota.
3. The modern Mississippi River unionid fauna has 45 species represented in Minnesota according to Dawley (1947, p. 690-692).

4. During a part of late Wisconsinan time, Glacial Lake Agassiz of eastern North Dakota was a part of the Mississippi drainage system. Glacial Lake Agassiz sediments have been found to contain only two species of unionids (possibly as many as 6 if the species mentioned by Dawley (1947, p. 680) were indeed from Glacial Lake Agassiz sediments).

From these facts it can be reasoned that during the nine thousand or so years available to the two unionid faunas (i.e., that of the upper Missouri River and that of the upper Mississippi River) the eastern drainage has far outstripped that of the west in diversity of species. I interpret this as a result of differences in the late Wisconsinan proglacial communities which were available as a colonizing stock in the two drainages. I believe this interpretation is supported by the fact that during the life of Glacial Lake Agassiz, its connection with the Mississippi was interrupted when an outlet to the east established drainage through the St. Lawrence drainage system. Connection between the Hudson Bay and Mississippi drainage systems does occasionally occur in modern times during exceptionally severe spring flooding of swamps which then connect the Mississippi and Rainy Rivers' headwaters (James Underhill, University of Minnesota, Department of Zoology, oral communication, December, 1961). The modern unionid fauna of the Hudson Bay drainage in North Dakota (Red River of the

North) could possibly have received new species since the time when Glacial Lake Agassiz ceased to be a part of the Mississippi drainage. But the great number of accidents necessary to import each new species suggests to me that most of the modern Red River unionid fauna was well established before the break in drainage between the lake and the Minnesota-Mississippi drainage system. Thirteen taxa comprise the present Red River unionid fauna (Cvancara, 1967, p. 187-196). As many as twenty-six taxa have been cited by various authors (Tuthill, 1967, Table 25) as having been a part of the modern unionid fauna of the Red River of the North, but Cvancara's thorough studies have produced only 13 species in recent years.

Thus, marked differences in available colonizing stocks clearly existed for Minnesota and for central North Dakota through late Pleistocene time and, therefore, comparisons of the two modern molluscan faunas, including the unionids, is not justified. It is also reasonable to exclude consideration of sphaeriid clams, because I have not attempted to identify them to species and Dawley did not evaluate them at all.

Differences in available stocks of gastropods are less significant for two reasons. First, gastropods can be carried as eggs or adults by waterfowl; and, secondly, during the time that ice occupied the northern part of the continent during late Wisconsinan time, nesting of waterfowl would have been peripheral to the ice front and flight

patterns would have either radiated from the central flyway or actually been parallel to the ice front over both North Dakota and Minnesota.

The Jaccard coefficient of faunal similarity for the aquatic non-marine gastropod fauna of Minnesota is 43. The Jaccard coefficient of faunal similarity for the aquatic nonmarine gastropod fauna of the modern Missouri Coteau and the modern aquatic nonmarine gastropod fauna of Minnesota is 38. Comparisons (C_{jac}) of Dawley's assemblages with the various faunal elements of North Dakota are shown on Table 4.

A greater precision of comparison between the late Wisconsinan molluscan fauna of the Missouri Coteau and modern mid-continent molluscan analogue can be accomplished by comparison of fossil faunules from the Missouri Coteau with assemblages of mollusks which Dawley asserted were typical of specific types of molluscan habitats in Minnesota.

The faunal similarity matrix (C_{je}) comparing Dawley's habitat assemblages (exclusive of the unionids and pisidiids) with the individual faunules of the late Wisconsinan Missouri Coteau fauna (Table 5) shows a strong dominance of habitat type 8, hardwater prairie lakes. Because of the occurrence of identical or very similar values (e.g., Brenneise site) in the two most comparable habitat comparisons, the last four lines on Table 5 were generated. Line 1 shows the fundamental validity of habitat 8 as the most comparable habitat. By increasing the number of comparisons considered to the two most comparable habitats in line 2

and the three most comparable habitats in line 3, a clear delineation between three habitats and the other five is seen. The conclusions available from this analysis are that three habitats dominated the ecology of the late Wisconsinan Missouri Coteau: hard-water prairie ponds, small streams, and medium-hard-water lakes. Most striking is the lack or paucity of high Jaccard coefficients of ecologic similarity in the comparison of late Wisconsinan Missouri Coteau faunules with Dawley's small rivers, medium-sized rivers, large rivers, ponds, and soft-water lake faunas.

The modern mid-continent analogues for the three faunal assemblages represented in the late Wisconsinan Missouri Coteau molluscan fauna can be constructed from Dawley (1947, 682-688).

Hard-Water Prairie Ponds:-- These are small to large shallow lakes in which total alkalinity varies from 150 to 300 ppm and the water contains " . . . other salts in addition to calcium salts," presumably sodium sulfate. The mollusks which characterize this habitat are Anodonta grandis, Lampsilis luteolus, Amnicola limosa, Gyraulus deflectus, Helisoma anceps, H. campanulatum, H. trivolvis, Lymnaea emarginata, L. stagnalis, Physa gyrina, and Valvata tricarinata. Population dominance by A. limosa, V. tricarinata, the three species of Helisoma and L. stagnalis is exhibited. One aspect of the assemblage as described by Dawley which does not parallel the late Wisconsinan Missouri Coteau molluscan fauna is the abundance of Lymnaeidae. She

states that they were strikingly abundant and each lake had its own "form" of L. emarginata. This suggests that the lack of interconnecting waterways favors the development of unique gene pools harboring similar mutants or at least genetically controlled ranges of variability. Over a protracted period of time distinct populations could thus develop. Lithologic as well as faunal evidence exists to show that small interconnecting streams did exist on the Coteau during late Wisconsinan time.

Dawley (1947, p. 688) mentions a fact which suggests that the ponds in southwestern Minnesota were undergoing a change toward a state more like their counterparts in the modern Missouri Coteau. "The lakes were very low that summer [1940] due to a series of dry years, and in many lakes there was a wide stretch of exposed beach covered with mussel shells." The expiration of the mussels and growing dominance of pulmonates suggests that the present hard-water prairie lakes are more comparable to the modern Missouri Coteau prairie potholes than they are to the late Wisconsinan Missouri Coteau ponds. Two considerations explain the strong similarity exhibited in the quantitative analysis shown on Table 5:

1. The assemblages typical of the Minnesota habitat, rather than the populations, are compared with the late Wisconsinan Missouri Coteau faunules. The Minnesota fauna includes forms which had become exterminated in

Minnesota by 1940. No information exists to indicate that a reversal of the trend reported by Dawley has occurred.

2. The faunules of southwestern Minnesota have had approximately 9,000 years in which to develop, whereas those of the late Wisconsinan Missouri Coteau had, at the most, 3,000 years in which to become colonized and develop before the final melting of the ice-core of the topography triggered cataclysmic destruction of the habitats of the molluscan fauna.

Small Streams:--Eight of the 40 faunules from late Wisconsinan deposits in the Missouri Coteau occur in sand or gravel. Thus, no question can exist that running water occurred on the Missouri Coteau during late Wisconsinan time. Nine of the faunules have Jaccard coefficients of ecologic similarity which show the greatest community with the assemblage which Dawley stated is characteristic of small streams in Minnesota. Only two of the comparable faunules exist in sand or gravel. One faunule comparable to Dawley's medium-sized river assemblage occurs in sand and gravel. Thus, only three faunules which are characteristic of running water are found in fluviatile sediments. One or more of five possible explanations may account for this:

1. The seven typically fluviatile faunules found in silts and marls are thanatocoenoses (i.e., transported after

death to the place where they were fossilized).

2. At inlets, running water environments intermingle with standing water environments and in cases where deltas form, the lacustrine lithotope actually includes a running water biotope.
3. Fossiliferous lacustrine sediments have been easier to find than small sinuous bodies of fossiliferous sand and gravel in regions of collapsed dead ice moraine.
4. Preservation in fluviatile sediments is typically poorer than in lacustrine sediments.
5. The faunal differences between Dawley's habitats are not very great, and, therefore, provide an inadequate basis for defining ecologic assemblages.

An indication of (5) is the fact that the Jaccard's coefficient of ecologic similarity for the comparison of the small stream assemblage and those from the medium-hard-water lakes assemblage (exclusive of unionids) is 50.

As a model for the sites on the late Wisconsinan Missouri Coteau which have faunules similar to the assemblage typical of small streams, the following applies. They are less than ten feet wide, shallow, with variable chemical conditions, they have swift current, gravel bottoms, and have abundant vegetation in quiet stretches. Characteristic taxa are Amnicola limosa, Ferrissia tarda, Gyraulus

deflectus, G. parvus, Helisoma trivolvis, H. campanulatum, H. anceps, Lymnaea humilis, L. palustris, L. stagnalis, Physa gyrina, P. integra, P. michiganensis, Planorbula armigera, and Valvata tricarinata. Dawley stated that among the gastropods, Physa integra dominates the populations. It is to be noted, and Dawley has pointed out (1947, p. 682), that all of the forms can live in other habitats.

Medium-Hard-Water Lakes:-- The assemblage typical of this habitat is not significantly comparable to the late Wisconsinan faunules of the Missouri Coteau when the analysis summarized on line 1 of Table 5 is considered. This line shows the totals of highest Jaccard coefficients of ecologic similarity for each faunule of Dawley's assemblages. Twenty of the late Wisconsinan faunules have second highest Jaccard coefficients that are within five points of their highest values. Differences between faunas characteristic of Dawley's habitats, as discussed above, are frequently less than observed in the comparison of late Wisconsinan Missouri Coteau faunules with the various modern habitat assemblages. The analyst is thus left in a position of having to make an intuitive choice. This does not negate the value of the Jaccard coefficient of ecologic similarity because the assignments of probability in a more formal statistical context are purely intuitive. Simpson and others (1939, p. 173) stated, "what the zoologist must be first concerned with is the biological significance of a demonstrated difference in samples being compared and for this kind of significance there is

no test but that of intuition, experience and intelligence."

In light of the demonstrable similarity of Dawley's assemblages it seems to me that differences in C_{je} of five or less are not significant. Thus line 2 on Table 5 summarizes the frequency of occurrence of highest and next highest Jaccard values for each of Dawley's assemblages when compared to the individual faunules from the late Wisconsinan Missouri Coteau. Extending the same logic to the highest three values line 3 was generated. Dawley's medium-hard-water lakes habitat type emerges as a significantly comparable habitat with this treatment. The mean deviation between highest and the third highest Jaccard value in the 37 comparisons in which three values exist is 12.2. The standard deviation of this range of variation is 5.65.

If inclusion in analysis is limited to those highest, second highest, or third highest values which have coefficients of 34 or more and to comparisons which have a range of variation between first and third highest of less than 16, the summary shown on line 4 of Table 5 is generated. The logic for establishing 34 as the lower limit derives from the practice of other workers employing Jaccard's method (see Lipps and others, 1968). The logic of excluding third or second highest values which vary by as much as 15 from the highest value is that of arbitrary choice of significance levels. Even with the above restrictions, small streams, medium-hard-water lakes, and hard-water-prairie lakes

are indicated by Jaccard's method as suitable analogues for the late Wisconsinan Missouri Coteau.

Other data affect the paleoecologic reconstruction. Moir (1958, p. 110) reported wood from a rooted white spruce stump at a depth of 15 to 18 feet near Tappan in Kidder County. He suggests that coniferous forest clumps had become established on the Missouri Coteau by $11,480 \pm 300$ y.b.p. (W-542). Examination of growth rings indicated conditions favorable to rapid growth of the spruce trees. This condition would require greater precipitation and cooler summer temperatures than now endure in central North Dakota.

McAndrew and others (1967, p. 101-113) have evaluated the fossil pollen and mollusks from bottom sediments taken from a modern slough (Woodworth Pond) in Stutsman County. The molluscan fauna, described in vertical section, shows a dominance of the population by Gyraulus parvus, Pisidium casertanum, and Valvata lewisi at a depth of 15-155 cm. These three taxa decline in number upward. Gyraulus parvus and Pisidium casertanum remain as elements of the fauna, but in very reduced proportions to the entire fauna throughout the time of deposition. Valvata lewisi, the only branchiate gastropod reported, is absent from the population above the 110-120 cm depth. A single fragment of landsnail shell was reported at 175-180 cm depth. The next higher appearance of any landsnail fossils was at 110-120 cm depth above which they remain a minor element of the molluscan population. Aquatic

pulmonate gastropods strongly dominate the entire fauna. At depth 13-140 cm the authors indicate a significant shift in pollen spectrum from grass and spruce domination to pine and sedge dominance. They postulate a fluctuation of climate from cool (205-210 cm depth), to warmer (175-205 cm depth), to temporary drought (165-125 cm) to increasing aridity (165-175 cm) to arid (60-125 cm) to decreasing aridity (15-60), and as present (0-15 cm). Because the basins of the modern prairie pot holes of the Missouri Coteau (kettles) were formerly occupied by blocks of ice during the time that the Coteau was an ice-cored body of glacial sediments, their sequence can be taken as the link between the late Wisconsinan molluscan fauna and the modern molluscan fauna. Unfortunately, McAndrew's work is not controlled by radiocarbon dates.

Thompson (1962, p. 16-21) has investigated a similar deposit in McIntosh County. He interpreted the presence of coniferous plant fragments and cones in the base of the deposit as probably contemporary with Moir's dated zone (i.e., 11,500 y.b.p.). Land and aquatic snails occur in a marl to a depth of 1.3 meters (4.3 feet) which lies over the unit containing wood material.

Clayton (1966, p. 11, and 1967, p. 34) stated that the ice core of the late Wisconsinan Missouri Coteau required about 3,000 years to melt. His estimate of time is based on radiocarbon dates obtained from unionid shells. It is Clayton's opinion that no extant radiocarbon date from the Coteau is related to any deposit formed by active

glacier ice (Clayton, oral communication, November, 1968). The dates obtained from mollusk shells from ice-contact deposits range from 11,650 y.b.p. (W-974) to 9,000 y.b.p. (W-1019). Clayton (1967, p. 40) further stated that the precipitation during the period 9,000 to 12,000-12,500 y.b.p. was higher than at present and that "temperatures were a few degrees lower." He has calculated that the increase in groundwater effected by melting of the ice would have amounted to about 1 inch per year (Clayton, 1967, p. 38). The number of extensive drainage systems developed during late Wisconsinan time on the surface of the ice-cored Coteau suggests a higher average precipitation than now occurs.

Summary

From strictly geologic evidence it can be hypothesized that:

1. A 100 by 300 mile band of the terminus of the late Wisconsinan continental glacier stagnated in south-central, central and northwestern North Dakota previous to 12,500 y.b.p. The deposits are assigned to the Burnstad and Streeter Drifts of Clayton (1962). This stagnant terminus was thickly covered by drift.
2. Before the ice became extensively eroded a complex of stream-connected lakes developed in ice-basins on the ice-cored Missouri Coteau.

3. Concurrent with the development of these lakes and streams the region became extensively colonized by plants and animals. The establishment of coniferous vegetation was accomplished before 11,480 y.b.p. and snails, clams, ostracods and calcareous algae became established before 11,650 y.b.p.
4. The climate was wetter than at present.
5. No significant amount of dissection has occurred since the disappearance of the ice core in the sediments of the Coteau.

From strictly paleontologic evidence we can suggest the following:

1. The mollusks which colonized the aquatic environments on the ice-cored Missouri Coteau during late Wisconsinan time are all extant in the upper Midwest (i.e., Minnesota).
2. Only three aquatic species now occur in the Coteau which did not occur during late Wisconsinan time, and only four aquatic species which were extant on the Coteau during late Wisconsinan time have been eliminated from the modern fauna.
3. The population structure of the late Wisconsinan Missouri Coteau molluscan fauna differed from that of the modern molluscan fauna in that late Wisconsinan populations

limosa, Valvata tricarinata, Gyraulus parvus, and Helisoma anceps.

A sequence in the development of the lacustrine environment has been determined from two sites. The most complete lithotopic and biotopic evidence comes from Mummy Cat Slough site (Tuthill, 1963b, p. 42-44). Figure 3 shows the section and notes the horizons at which different faunules occur. The detailed studies at this site give an unusual basis for the detailed hypothesis of the paleolimnology which follows.

In the cyclic process of topographic inversion a depression completely surrounded by ice-cored superglacial drift formed near the present site of Lehr, North Dakota. Its bottom was on previously deposited sediments, presumably till. The ice-basin was approximately 40 mi² in area, and deposits which settled in it are attributed to sedimentation in Glacial Lake Lehr. The portion of the shore, north of the Mummy Cat Slough site, was ice-covered drift, and the upper layer of it was outwash gravel. During a period of either thin or incomplete drift-cover, the lake was filled with turbid meltwater and finely-bedded (about 1/8 to 1/16 inch thick beds), light and dark brown clay and olive colored, silt-sized sediments were deposited alternately to a depth of 26 feet. After drift cover increased, either in thickness (up to six feet) or completeness around the margin of Glacial Lake Lehr, two feet of calcareous, clayey silt was deposited. The presence of

Figure 3.--Stratigraphic section of the Mummy Cat Slough site
(NW sec. 14, T. 132 N., R. 69 W., McIntosh County, North Dakota).

DEPTH FROM - SECTION - LITHOLOGY - MOLLUSKS - KEY TO MOLLUSK SPECIES SURFACE

DEPTH FROM SURFACE (feet)	SECTION	LITHOLOGY	MOLLUSKS	KEY TO MOLLUSK SPECIES
0		BLACK SOIL	NONE	
1		BROWN SOIL	NONE	
2		BROWN SILT	2,3,4.	1. LAMPUSILIS SP 2. PISIDIUM SP 3. VALVATA TRICARINATA 4. AMNICOLA LIMOSA 5. PHYSA SP 6. HELISOMA ANCEPS 7. GYRAULUS PARVUS 8. GYRAULUS SP 9. PROMENETUS EXACUOUS 10. ARMIGER CRISTA
3		MARL	1,2,3,4,5,6,7,8,9	
4		SAND	NONE	
5		SILTY MARL	4, 10.	
6		SAND	NONE	
7		CALCAREOUS CLAYEY SILT	4, 10.	
8		THINLY BEDDED ALTERNATING LIGHT AND DARK BROWN CLAYEY SILT	NONE	
33		SANDY GRAVEL	NONE	
34				

UNCONFORMITY

oögonia of the calcareous alga Chara sp. indicates that the water was clear. Fossil shells of Lampsilis sp. (fragmented), Amnicola limosa, and Armiger crista indicate that during summer the water temperature rose to at least 12°C and probably even higher.

A two-inch bed of unfossiliferous sand suggests the nearby presence of an inlet which transported coarse grain-sized sediments into the lake. The drainage, of which this inlet was a part, was not receptive to the mollusks available for colonization, perhaps because of cold temperature or brevity of existence.

The lake at this location returned to a quiet water state and a little more than a foot of vaguely-bedded silty marl was deposited. This water was a receptive habitat for Amnicola limosa and Armiger crista. Chara was again present, attesting to clear water conditions. Once again a stream diversion or perhaps a single flood deposited two inches of unfossiliferous fine sand.

A relatively pure freshwater limestone or marl, approximately four inches thick, marks a quiet, clear-water phase in the life of the lake at this place. Pisidium sp., V. tricarinata, A. limosa, Physa sp., H. anceps, Gyraulus parvus, and P. exacuous colonized the site at this time, and the populations were the most successful in the biotic history of the environment. One and a half feet of sparsely fossiliferous silt marks a period when inflow of detritus increased. Calcareous algae disappeared from the fossil record suggesting that the water had

become turbid. Pisidium sp., V. tricarinata, and A. limosa were able to withstand the deterioration of the biotope, but their populations suffered until they expired toward the end of the depositional sequence. The increased inflow of sediments and probably turbidity were no doubt the result of dynamic changes in the drainage system caused by collapse of drift on the surrounding ice-core as melting progressed. Approximately a foot and a half more of silt was deposited after the demise of the mollusks. The containing ice basin failed and Lake Lehr drained. Melting of the adjacent ice core let the outwash sands and gravels down into what is now the bottom of Mummy Cat Slough. Thick growths of sedges and cat-tails (Typha) deposited about two feet of vegetable mat in the slough. Concurrently a black soil was formed in the upper half foot of the uppermost unit of lake sediment. Caliche nodules formed in the upper one and a half feet of the lake sediments and prairie became established on the surface.

This sequence was occurring at many places throughout the Coteau between 12,500 y.b.p. and the present. The initiation of water bodies which would leave a sedimentary record depended upon the formation of a sedimentary basin with a bottom not on ice. The occurrence of environments receptive to aquatic mollusks depended upon the development of a sufficient thickness of superglacial drift to stabilize the streams and lakes and isolate them from large amounts of cold, turbid meltwater. Some species of mollusks could clearly survive in turbid

water, but their populations were marginal ones, and it was not until clear, vegetated, warmer waters became established that large and diverse populations of mollusks could survive.

At some places on the Coteau, as early as about 11,500 y.b.p., kettles developed, and clumps of coniferous trees became established around them. White spruce and tamarack grew to maturity in these habitats. The vegetative cover of the rest of the Coteau is in doubt. Pollen spectra indicate the presence of a diverse flora on or marginal to the Coteau. Besides the taxa mentioned above, pine, cedar, poplar, black ash, birch, ironwood, elm, oak, fir, alder, willow, soapberry, buffalo-berry, hazel, grasses, the goosefoot and amaranth families, sage, ragweed, bracken fern, sedges, cat-tails, bur-reed, water-milfoil, pondweed, arrowhead, and bladderwort (McAndrew and others, 1967, fig. H-2) grew in the region in greater or lesser numbers during the latter stages of the late Wisconsinan.

The absence of land snails in the sediments deposited on the ice-cored Missouri Coteau is a profound anomaly. With the diversity of flora indicated above there is no apparent associative biologic reason for their absence. In the upper unit of Woodworth Pond (McAndrew and others, 1967) which is undated, they are present as a minor element of the molluscan fauna. They were well established in the Sheyenne River valley by post-hypsithermal time (2540 ± 300 y.b.p., W-1185; Tuthill, 1964, p. 145-155). The actual time at which land snails first

appear in late Wisconsinan and/or Recent sediments is not now precisely known. They occur in terrace sediments of possible Yarmouthian (no older than late Kansan) or younger age in the Cannonball River valley beyond the late Wisconsinan glacial limit in Grant County (Tuthill and others, 1964a). They also occur in sediments deposited in the upper Norcross Beach of Glacial Lake Agassiz (Tuthill, 1963f) in Red Lake County, Minnesota. The Herman Beach stage formed before 11,740 y.b.p. (Y-1328) according to Wright and Ruhe (1956, p. 39). Clayton (1966, p. 17) has interpreted the sequence of Lake Agassiz beaches and placed the beginning of formation of the upper Campbell Beach before about 11,000 y.b.p. The Norcross Beach formed after the Herman and before the Campbell. This establishes that in western Minnesota, land snails had colonized glaciated surfaces between 11,000 and 11,700 y.b.p. Thus, we have records of Pleistocene land snail occurrences on both sides of the Coteau during late Wisconsinan or earlier Recent time, but no unquestionable occurrences on the Coteau itself.

The climate during late Wisconsinan time was, as reasoned by Clayton and discussed above, no doubt more humid than today. Clayton (1967, p. 40) stated that it was probably cooler on the Coteau during late Wisconsinan time than at present. I do not concur. The annual mean temperature probably was not much different from that of today (mean Jan. - 13°C, mean July +21°C (data from U. S. Department of

Agriculture, 1941)). It is probable, however, that summers were cooler and winters more mild. Unionid shells from fossil assemblages recovered from the Coteau sediments are remarkably smooth. All of the water bodies were relatively shallow. If the extremes of winter and summer temperatures which now occur in central North Dakota had existed during the time unionids occupied the ice-basined lakes of the late Wisconsinan, freeze-out would have hampered the development of successful populations. Furthermore, the formation of marls, which are a characteristic sediment of the late Wisconsinan lakes, is favored by a cool, but not a cold climate. I believe that temperature ranges on the Coteau are more extreme today than they were during the late Wisconsinan.

This climate changed to the subhumid-semiarid climate of today, which is characterized by a negative evapo-transpiration : precipitation ratio, before the ice-core of the Coteau melted completely; otherwise an, at least partially, integrated drainage would now exist on the Coteau.

Figure 4.--Schematic diagram of the manner of deposition of ice-basined lake sediments of late Wisconsinan age in the Missouri Coteau district, North Dakota.

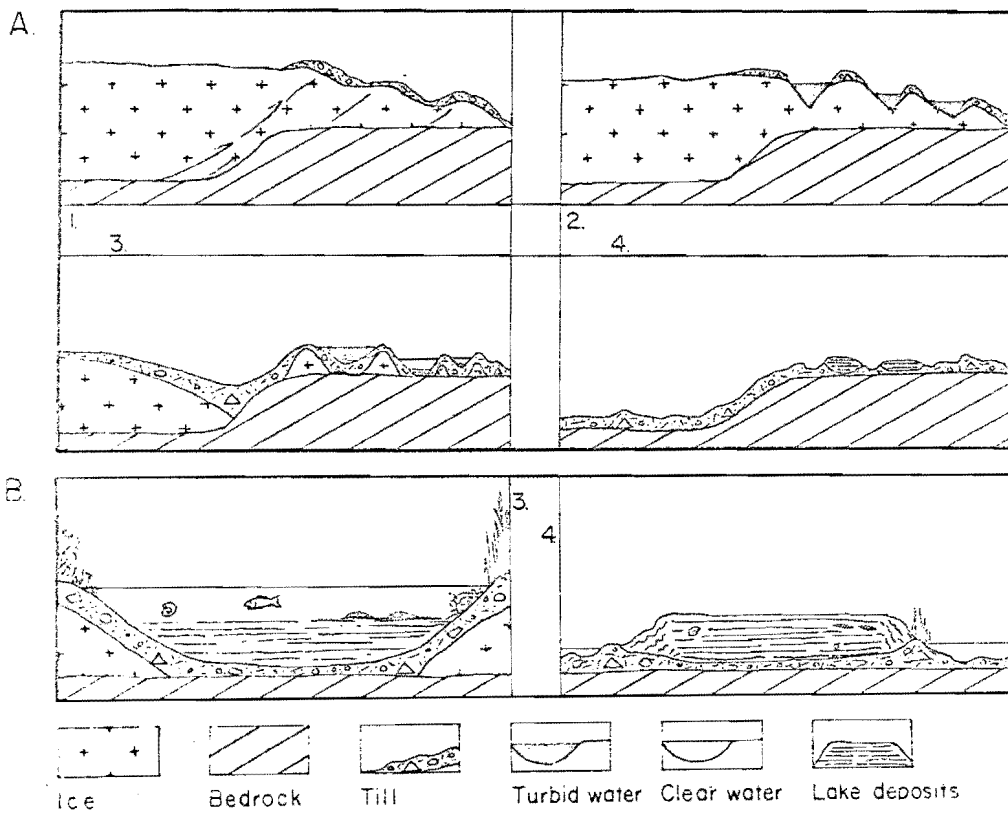
A. 1. Late Wisconsinan continental glacier over-rides the bedrock Missouri escarpment and thins as it extends across the Missouri Coteau district. Shearing brings large quantities of drift to surface of glacier.

A. 2. Glacier stagnates and ice-walled sinkhole lakes form in depressions on the stagnant terminus.

A. 3. Ice-basined lakes form as insulating drift stabilizes the debris on the wasting terminus. Some of the lakes catch deposits which accumulate to a greater thickness than that of the drift on and in the ice core which forms the lake basin.

A. 4. Lake sediments remain as topographically high bodies of sediments surrounded by collapsed outwash and till deposits.

B. 3. and B. 4. These two diagrams show details of panel A. 3. and A. 4. respectively.



MODERN ALASKAN STUDIES OF NONMARINE MOLLUSKS

History of Investigations

The hypothesis which I suggested to explain the fossils of the late Wisconsinan sediments on the Missouri Coteau (Tuthill, 1963b) was considered by some ecologists to be insupportable. Comparison with the modern mid-continent fauna such as we attempted in Tuthill, Clayton, and Laird (1964) was useful, but because the upper Midwest does not now have a continental glacier, strong confidence in the hypothesis was not generated. No proglacial or superglacial molluscan ecology could be found in a search of the literature. Thus, a genuine employment of the principle of uniformitarianism was not possible in 1962.

In late May of 1962 the Department of Geology, University of North Dakota Expedition to the Martin River Glacier, Alaska, established a base camp at the head of Lake Charlotte. Investigation of the proglacial and superglacial molluscan fauna of the region was my part of the expedition's scientific mission. During subsequent summer field seasons through 1964, this study was continued at "Miller" Lake, Martin Lake, Slide Glacier and Lake Tokun in the Martin River valley. The Muskingum College Expedition to Sherman and Sheridan Glaciers, Alaska, in 1965, the Muskingum College Expedition to Controller Bay,

Alaska, in 1967, and the Muskingum College Expedition to Tasnuna Valley in 1968 broadened the geographic base of the studies initiated in 1962. The areas most intensively studied for molluscan ecology were the Martin-Bering Rivers region and the Sherman-Sheridan Glaciers region.

The Martin-Bering Rivers region lies between lat. $60^{\circ} 15' N.$ and $60^{\circ} 45' N.$ and long. $144^{\circ} 00' W.$ and $144^{\circ} 45' W.$ United States Geological Survey topographic series quadrangles Cordova B-1 (1951), Plate 5; B-2 (1950), Plate 6; B-4 (1959), Plate 7; C-4 (1959), Plate 8, at a scale of 1:63360 show the region. Plate 3 shows the entire region at a smaller scale (i.e., 1:250,000).

The coastal portion of this region has been the site of intensive geologic investigation because of the presence of gas and oil in the Tertiary rocks of the foothills. The Kushtaka Lake region has been intensively studied because of the inclusion of high quality coking coal in the Tertiary rocks of that area. Martin (1904, 1905a, 1905b, 1906, 1907, 1908, and 1921), C. A. Fisher (1910), C. A. Fisher and Calvert (1914), W. L. Fisher (1912), Miller, Rossman and Hickcox (1945), Miller (1951), Barnes (1951), Kachadoorian (1955), Payne (1955), and Miller, Payne, and Gryce (1959) have reported on the stratigraphy, economic geology, engineering geology, and structural geology of the area. Coal explorations in the Kushtaka Lake area were recommenced by the Cortalla Coal Company of Cordova, Alaska, in 1968,

and recent petroleum exploration reached a peak of intensity along the coast of the Gulf of Alaska in 1967 with more than a dozen companies having field parties in the region that summer.

Geographic and Geologic Description of South-Central Alaska

Physiography:

There are several physiographic units and two geologic regions in this part of Alaska. Figure 5 shows Wahrhaftig's (1965) physiographic Provinces and Sections which are included in the region studied. Further division of the physiography of the region is not here necessary because good geographic maps exist and most topographic features are named.

The region to be discussed includes parts of the following physiographic units according to Wahrhaftig (1965, Plate 1).

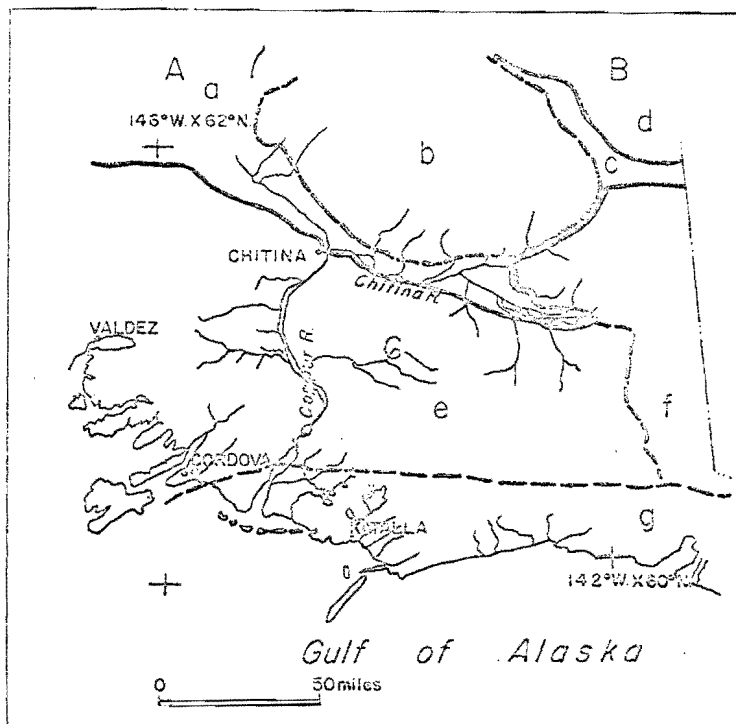
Pacific Mountain System Division:

This division lies south and west of the Kuskokwim-Yukon-Tanana Valleys and extends to the Pacific Coast.

Pacific Border Ranges Province:

This province includes Kodiak, Hinchbrook and Montague Islands; the mountainous and coastal regions east of Homer, Anchorage, and Palmer; the Chugach Mountains and coastal border south of the Glenn Highway and Chitna and southeast to Skagway and Juneau.

Figure 5.--Map of the physiographic divisions of south-central Alaska, modified from Wahrhaftig, 1965.



- PROVINCE BOUNDARY
- SECTION BOUNDARY
- POLITICAL BOUNDARY
- A COASTAL TROUGH PROVINCE
- B ALASKA-ALEUTIAN PROV.
- C PACIFIC BORDER RANGES PROV.
- a COPPER R. LOWLAN SECTION
- b WRANGELL MTS. SEC.
- c DUKE DEPRESSION SEC.
- d EASTERN ALASKA RANGE SEC.
- e KENAI-CHUGACH MTS. SEC.
- f ST. ELIAS MTS. SEC.
- g GULF OF ALASKA COASTAL SEC.

Kenai-Chugach Mountains Section:

Wahrhaftig (1965, p. 40-41) defines this section as follows:

General topography-- The Kenai-Chugach Mountains form a rugged barrier along the north coast of the Gulf of Alaska. High segments of the mountains are dominated by extremely rugged east-trending ridges 7,000-13,000 feet in altitude. Low segments consist of discrete massive mountains 5-10 miles across and 3,000-6,000 feet in altitude, separated by a reticulate system of through valleys and passes 1/2-1 mile wide that are eroded along joints and cleavage. . . . The entire range has been heavily glaciated, and the topography is characterized by horns, aretes, cirques, U-shaped valleys and passes, rock-basin lakes, and grooved and mammillated topography. The south coast is deeply indented by fiords and sounds, and ridges extend southward as chains of islands. . . . The north front is an abrupt mountain wall.

Drainage-- The drainage divide, generally an ice divide, is along the highest ridges, and is commonly only a few miles from the Pacific Ocean. Streams are short and swift; most head in glaciers. The Copper River crosses the eastern part of the Chugach Mountains in a canyon 6,000-7,000 feet deep.

Lakes-- Large lakes fill many ice-carved basins along the north margin of the Chugach Mountains and throughout the northern Kenai Mountains. Lake George is an ice-margin lake dammed by the Knik Glacier; it empties in an annual flood.

Glaciers and permafrost-- The firm line rises from an altitude of 2,500-3,500 feet on the south side of the mountains to 7,000-8,000 feet on the north side of the central Chugach Mountains. All higher parts of the range are buried in great icefields, from which valley and piedmont glaciers radiate. Many of the glaciers on the south side of the mountains end in tidewater. The extent of permafrost is unknown.

Geology-- The Kenai-Chugach Mountains are composed chiefly of dark-gray argillite and graywacke of Mesozoic age that are mildly metamorphosed and have a pronounced vertical cleavage that strikes parallel to the trend of the range. In the Prince William Sound area large bodies of greenstone are associated with the argillite and graywacke.

A belt of Paleozoic and Mesozoic schist, greenstone, chert, and limestone lies along the north edge of the Kenai and Chugach Mountains. All these rocks are cut by granitic intrusions.

The southern boundary of this section in the region discussed here is the head of the alluvial plain formed by Mountain Slough, Eyak River, Glacier River, Alaganik Slough, Pete Dahl Slough, Copper River, and Martin River, and the trace of the Chugach-St. Elias fault on the north side of the Martin River valley and the Martin River Glacier (see Pl. 1).

Gulf of Alaska Coastal Section:

Wahrhaftig (1965, p. 41-42) defines this section as follows:

General topography-- The Gulf of Alaska coastal section has a diversified topography carved in Tertiary rocks. A coastal plain marked by longitudinal beach and dune ridges, crossed in places by outwash plains and by belts of morainal topography, is backed by marine terraces as high as 800 feet in altitude and by rugged intricately gullied mountain ridges as high as 12,000 feet. The straight exposed coastline is broken at intervals of 50-100 miles by large fiords. . . .

Drainage-- Short melt-water streams of large volume cross the lowland. Bars built by coastal currents cause the river mouths to go through cycles of westward migration followed by breakthrough at their original sites during periods of high runoff.

Lakes--There are many ephemeral lakes along the margins of the piedmont glaciers. A few large lakes occupy ice-carved basins.

Glaciers and permafrost--The firn line is at an altitude of 2,000-4,000 feet. Icefields on higher mountains and valley glaciers in most of the valleys coming from the St. Elias and Chugach Mountains feed enormous piedmont glaciers, of which the Malaspina Glacier . . . is the largest. Glacier

advances within the last thousand years are greater than any advance recorded in the Pleistocene. Permafrost is absent.

Geology--The Cenozoic rocks are intensely deformed yet easily eroded claystone, sandstone, and conglomeratic sandy mudstone, all tightly folded and thrust to the south. Large thrust faults separate this section from mountains to the north and northeast. Marine terraces show that the area has been uplifted rapidly. The conglomeratic sandy mudstone interbedded in the Cenozoic section is interpreted to be marine tillite; it indicates recurrent tidewater glaciation on this coast as far back as Pliocene time or earlier.

Most of the studies reported here were conducted in the Gulf of Alaska Coastal Section. Wahrhaftig's (1965, p. 42) statement that, "glacial advances within the last thousand years are greater than any advance recorded in the Pleistocene" is in error. In 1967 we discovered a till at Cape Martin and Whale Island, the Cape Martin Till (Tuthill and Sirkin, in preparation), which is more than 40 feet thick. Stratigraphic relationships in the Cenozoic sediments in the Katalla Valley clearly establish that the glacier which deposited the Cape Martin Formation had entered and retreated from the region before $13,900 \pm 400$ y.b.p. (I-3796).

The existence of marine terraces in that part of the Gulf of Alaska Coastal Section between Cordova and Bering Glacier is questionable. Along the coast from Cape Martin westward to Martin Slough and on Whale Island no marine deposits are found on the surface which has been thought to be a marine terrace. The Cape Martin Formation (a till) lies directly on the steeply dipping bedrock. Sands occur above the

till on the southwest side of Whale Island, but no macro- or micro-fossils were found in them. It is more likely that these sands are outwash deposits laid down during the retreat of the icefront than that they are marine sediments.

Geology:-- The geology of the Controller Bay region is summarized in a report by Martin (1908). This study was confined to the Tertiary rocks east of Ragged Mountain, and south of the Martin River Glacier, and west of Bering Glacier. Miller (1951) restudied the area mapped by Martin and the Ragged Mountain region west to Martin Slough. He divides the region into three structural provinces. These are as follows:

Ragged Mountain:

Ragged Mountain is a late Mesozoic or early Tertiary thrust block having an eastward arcing north-south trend. It lies between the Copper River delta on the west and the Martin Lake and Katalla River valleys on the east. The fault can be observed along the southeast mile of the mountain at an elevation of about 1,000 feet. The rocks underlying Ragged Mountain are igneous, metamorphic and sedimentary. Diatoms taken by Miller from a site on the mountain indicate the likelihood of an early Tertiary age, but agreement on their stratigraphic significance is not general.

Martin Lake-Bering Lake Region:

Miller has stated that the structural axes in the area west of a line between Hamilton Mountain, down Dick Creek to the western shore of Bering Lake have a north-northwest to north orientation. This orientation is assumed to have been a result of the influence of the Ragged Mountain thrust fault.

Kushtaka Lake-Bering River Region:

East of the line mentioned above monoclinical structures and folds, having axes oriented in an east-northeast to northeast, predominate. Dr. William Fritz (oral communication, May 1964) informed me that studies of the structural geology of this region which he had conducted for Shell Oil Company in 1962-1963 inclined him to postulate glide tectonics as the mechanism by which the east-northeast and north-east trending structures had formed in the Tertiary rocks. A deep decollement, possibly a coal, at an inclination of about 7° below the horizontal was suspected in this region.

North of the Tertiary foothills and Ragged Mountain lies the Martin River valley. This valley coincides with the west-southwest trending Chugach-St. Elias fault. There are a pair of thrust faults which border the south flank of the Chugach Mountains east of the Copper River and which are visible at the surface. It is possible that the Chugach-St. Elias fault is a complex of fractures which underly the

entire Martin River valley. Plafker (1967) has summarized the geology of the Gulf of Alaska Tertiary Province.

Exploration and Land Use:-- Human traffic in the region has affected the dispersal of terrestrial snails. The Controller Bay-Copper River coast was the site of native villages at the now abandoned village of Katalla, the north end of Kayak Island and at Alaganik Slough. Fredrica de Laguna (1956) has treated the prehistoric and early historic events which occurred in Prince William sound. I have discussed the effect of native and non-native occupancy of the coastal regions and along the right of way of the Copper River and Northwestern Railroad upon the nonmarine molluscan fauna in an article which is scheduled to appear in the last half of 1969 (Tuthill and Johnson, in press). It appears to me that there is clear evidence to suggest that Vespericola columbiana, Haplotrema sportella, Succina cf., S. rusticana, Oxyloma cf., O. retusa, Vertigo ovata, V. modesta, and Lymnaea palustris have been introduced accidentally during the development of the above mentioned parts of the region.

Geographic Divisions of the Martin-Copper-Bering Rivers Region:

So that discussion of the geographic distribution of the various molluscan taxa to be discussed below can be facilitated, informal geographic districts and subdistricts have been defined below.

1. Katalla District

The valley drained by the Katalla River. The locality is bordered on the east by the Don Miller Hills, on the south by Katalla Bay of the Gulf of Alaska, on the west by Ragged Mountain and on the north by the drainage divides between the Katalla Valley and the Bering Lake and the Martin Lake drainages. Plates 4 and 6 are maps on which this district is shown.

a. East Katalla Beach. The region of beach, active dune sand, vegetated dunes and forested raised beach from the east bank of the Katalla estuary to Cave Point.

b. West Katalla Beach. The region of sand and shingle beach, vegetated dunes, and forest between the village site of Katalla and Palm Point.

c. Cape Martin. The region of beach, till, and bedrock cliffs, and the forest between the west end of Kahuntla Lake and the east end of Softuk Bar including Whale Island which, since the 1964 Alaskan Earthquake, is tied to the mainland by a tombolo.

d. Katalla Valley. The region of the central valley of the Katalla River below elevations of 100 feet (as shown on Plates 4 and 6) and above the tidal reach of the estuary.

2. Martin Lake District

The valley drained by the Martin Lake and Little Martin Lake outlets which connects with the Martin River. The locality is bordered on the east by Tokun Mountain (VABM 2462 Tok.), on the south by the drainage divide between the Katalla and Martin Lake valleys, on the west by Ragged Mountain and on the north by the Martin River. Plates 5 and 6 show this district.

a. Constance Lake. The lake at elevation 106 feet (see Pl. 6) east of Martin Lake and the valley which it drains. The region from its outlet west to Martin Lake is considered a part of the Martin Lake Valley subdistrict (2.c).

b. Little Martin Lake. The lake of this name (see Pl. 6) and the valley it drains.

c. Martin Lake Valley. The lake and the valley drained by the lake exclusive of the Constance Lake drainage (2.a). This includes the outlet of Martin Lake to its junction with the Martin River (see Pl. 6).

3. Martin River Valley

The valley drained by the Martin River from its origins in Slide and Martin River Glaciers. This district is bordered on the east by the Martin River Glacier, on the south by the northern spur of Tokun Ridge, Tokun Mountain (VABM 2462 Tok.), the Little Martin Lake and Martin Lake Valley subdistricts (2.b. and 2.c.) and Ragged Mountain, on the west by the Copper River valley and on the north by the Chugach

Mountains. It does not include the drainages of the McPhearson and Johnson Glaciers. Plates 5 and 6 show this district.

a. Slide Glacier. The terminal region of Slide Glacier and the valley of the part of the Martin River which originates in Slide Glacier to its junction with that part of the Martin River which originates in the Martin River Glacier (see Pl. 5). Slide Glacier has been called by the informal name of "Sioux" Glacier during the period 1962-1967.

b. Terminal Moraine. The terminal moraine of the Martin River Glacier between the Chugach Mountains, the Lake Tokun outlet region and the region south of Deadwood Lake (see Pl. 5 and 6).

c. Deadwood Lake. The region between subdistrict 3.b. and the stagnant terminus of the Martin River Glacier including one-half mile of the Deadwood Lake outlet and all of the valley drained by the Deadwood Lake outlet east (upstream) of this point (see Pl. 5).

d. Martin River Glacier. The terminal mile or so of the Martin River Glacier north and west of Charlotte Ridge (see Pl. 5).

e. Martin Valley. The main valley west of the terminal moraine of the Martin River Glacier (see Pl. 5 and 6).

f. Pistyll Lake. The portion of the northeast part of Charlotte Ridge which is drained by Pistyll Lake and Welsh River (see Pl. 5).

4. Tokun Lake

The valley drained by Tokun Lake and its outlet to the Martin River. Plate 5 shows this district.

5. Lake Charlotte

The valley drained by Lake Charlotte and the upper mile of Shepherd Creek. (see Pl. 5).

a. Bee and OH Lakes. The valley south of the Martin River Glacier and north of Lake Charlotte and the two small lakes it contains (see Pl. 5).

b. Lake Charlotte Valley. The Lake Charlotte valley and the upper mile of Shepherd Creek and the valley in which they lie (see Pl. 5). This subdistrict excludes the Bee Lake and OH Lake subdistrict.

6. Kushtaka Lake

The lake and the valley it drains plus the upper two miles of the Stillwater Creek and the inlet from the Kushtaka Glacier (a lobe of the Martin River Glacier). Plate 5 shows this district.

a. Shockum Lake. The moraine dammed lake in Sec. 30, T. 17S, R. 8E, the valley it drains and its outlet to Kushtaka Lake (see Pl. 5).

b. Stillwater Creek. The upper two miles of this river which is the outlet of Kushtaka Lake and the valley which it drains (see Pl. 5).

c. Kushtaka Outwash. The alluvial flats between Kushtaka Glacier and Kushtaka Lake (see Pl. 5).

7. Sherman-Sheridan Glaciers Region

The Sherman and Sheridan Glaciers region is bordered on the east by the ridge of which McKinley Peak is the seaward feature, is bordered on north by Sherman Glacier and Sheridan Glacier, on the south by the Copper River Highway, and on the west by the Scott Glacier valley (see Pl. 7 and 8).

a. Sherman Valley. The valley between Sherman and Sheridan Glaciers including the lateral moraines and bedrock valley sides north and south of Sherman Glacier two and one-half miles east northeast of the terminus on the north side and two and one-half miles east of the terminus on the south side of the glacier (see Pl. 8).

b. Falls Lake. The lake and the small valley it and its outlet drain southeast of the terminus of the Sheridan Glacier (see Pl. 8).

c. Sheridan Terminal Moraine. The terminal moraine complex south of Sheridan Glacier (see Pl. 8).

d. Sherman-Sheridan Outwash Plain. The alluvial flats between the Sheridan terminal moraine, the Copper River Highway, Scott Glacier valley and McKinley Peak (see Pl. 7).

8. Tasnuna Valley

The lower 3 miles of the valley of the Tasnuna River. This region is shown on U. S. Geological Survey Map, Valdez, Alaska, scale 1:250,000.

Nonmarine Molluscan Ecology
of the Martin-Copper-Bering Rivers Region, Alaska

List of Modern Nonmarine Mollusks:

Bivalves

Anodonta beringiana Middendorff, 1851

Sphaerium nitidum Jenyns, 1832

Pisidium compressum Prime, 1851

P. casertanum Poli, 1791

P. milium Held, 1836

Gastropods

Valvata mergella Westerlund, 1885

Lymnaea humilis (Say) 1822

L. palustris (Muller) 1774

Menetus callioglyptus (Vanatta) 1895

Gyraulus parvus (Say) 1817

Vertigo ovata Say, 1822

V. columbiana Sterki, 1892

V. modesta (Say) 1824

Succinea cf. S. rusticana var. Alaskana Dall, 1905

Oxyloma cf. O. retusa (Lea) 1834

Haplotrema sportella (Gould) 1846

Discus cronkhitei (Newcomb) 1865

Punctum cf. P. randolphi (Dall) 1895

Prophysaon cf. P. andersoni (J. G. Cooper) 1872

Vitrina alaskana Dall, 1905

Euconulus fulvus alaskensis Pilsbry, 1924

Deroceras laeve (Muller) 1774

Vespericola columbiana (Lea) 1838

Discussion of Modern Nonmarine Molluscan Fauna:

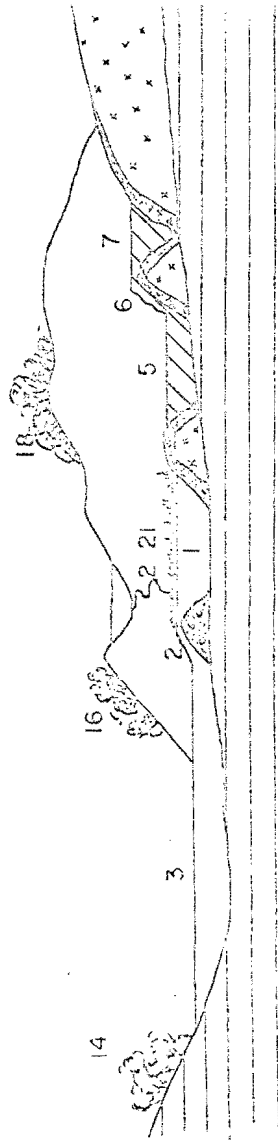
The nonmarine mollusks of the region are not abundant throughout the area I searched. In specific habitats they often occur in sufficient number to judge them to be successful populations. Twenty-three potential habitats were studied; eleven harbored mollusks. These habitats, both those occupied by mollusks and those in which mollusks never were found, are described next so that the discussion of each taxon which follows in a later section can refer to them. The potential habitats which harbored mollusks are shown in a schematic diagram on Figure 7.

Potential Molluscan Habitats:

Twenty-three potential molluscan habitats are defined and described below. These are environments which were searched for mollusks and in which I feel they might reasonably have been found

Figure 6.--Schematic diagram depicting the twelve potential habitats in which mollusks were found in south-central Alaska. Numbers correspond to the habitat.

1. Clear, warm, neutral, standing water.
2. Clear, warm, neutral, running water.
5. Turbid, warm, neutral, standing water.
6. Turbid, warm, neutral, running water.
7. Turbid, cool, neutral, standing water.
8. Turbid, cool, neutral, running water.
11. High, tidal pools.
14. Established alders on bedrock.
16. Established alders on till.
18. Established alders on superglacial drift.
21. Grassy lake borders.
23. Grass- and shrub-captured beach sands.



BEDROCK [diagonal lines] TILL [stippled] ICE [horizontal lines] CLEAR WATER [empty] TURBID WATER [dots]

or which had counterparts in the hypothetical ice-cored Missouri Coteau of late Wisconsinan time. Their definition was not begun until after the first field season and was not completed until this writing. Thus, the definitions did not constitute a bias to the collecting.

Potential Aquatic Habitats:-- The eleven potential aquatic habitats are described below. Seven of these contain mollusks. Beside their general characteristics, their water quality data and molluscan faunules are reported. Temperature was recorded by a custom-made remote sensing thermistor with a scale calibrated in tenths of degrees C. Dissolved solids and gasses were determined by a Helige model 950-A colorimeter. Values of pH were determined by a Beckman portable pH meter, except those determinations in geographic district 2 which were taken with pH papers and/or a Beckman pH meter. The pH meter was checked against the colorimeter four times during the 1962 field season and twice during 1963. Table 6 shows the water quality summaries for the various bodies of water which constitute the aquatic potential habitats.

A schematic diagram of the potential habitats and their more significant characteristics is shown on Figure 6.

1. Clear, warm, neutral, standing water. This habitat contains clear, standing water which attains mean surface high temperatures in the range of 8.5 to 14.5°C, mean summer pH in the range of 5.8 to 7.5, contains aquatic vegetation and is occupied or visited by water-

fowl and beaver. It is not the recipient of turbid meltwater from the glaciers. Lakes which comprise this type of habitat are: Constance Lake (geographic locality 2.a.), Martin Lake (2.c.), Black Lake (3.d.), Pistyll Lake and Dundaff Lake (3.f.), Lake Tokun (4), Shockum Lake (6.a.), Falls Lake (7.b.), and Sorehand Lake (8).

All of these lakes except Falls Lake contained mollusks. The distribution of species of mollusks in the lakes mentioned above is as follows:

	Constance Lk.	Martin Lk.	Black Lk.	Pistyll Lk.	Tokun Lk.	Shockum Lk.	Falls Lk.	Sorehand Lk.	Dundaff Lk.
<u>Anodonta beringiana</u>		X						X	
<u>Pisidium casternum</u>								X	
<u>Pisidium compressum</u>				X					X
<u>Pisidium milium</u>							No Mollusks	X	
<u>Valvata mergella</u>		X	X		X			X	
<u>Gyraulus parvus</u>		X	X		X	X		X	
<u>Menetus callioglyptus</u>		X	X		X		No Mollusks		
<u>Lymnaea humilis</u>	X	X	X	X	X	X	No Mollusks		X
<u>Lymnaea palustris</u>								X	

2. Clear, warm, neutral, running water. This habitat is rare in the Bering-Copper-Martin Rivers region. A stream near Miller Lake and the outlet of Black Lake (3.d.), Falls Lake outlet (7), Pistyll Lake and Dundaff Lake outlets (3.f.) and Sorehand Lake outlet (8) were the only such potential habitats evaluated. These habitats contained water which ranged between 12 and 15.5°C and in which pH ranged between 7.0 and 7.5. Algae (green) were the only observed aquatic vegetation. Only in the outlet of Sorehand Lake was detritus observed in transport.

The topography over which these streams flow is rugged ice-cored, deadice moraine in the case of the outlet of Black Lake; rugged marginal moraine in the case of Dundaff Lake and Pistyll Lake; flat outwash alluvium in the cases of the stream near Miller Lake and the outlet of Sorehand Lake and steep bedrock and talus in the case of Falls Lake.

The aquatic molluscan faunules found in the potential habitats of this type are as follows:

	stream near Miller Lake	Black Lake Stream	Falls Lake Stream	Sorehand Lake Stream
<u>Pisidium compressum</u>		X		
<u>Valvata mergellia</u>		X		
<u>Lymnaea humilis</u>	X			
<u>Lymnaea palustris</u>				X
<u>Gyraulus parvus</u>	X			
			No mollusks	

3. Clear, warm, acid, standing water. This potential habitat is the most common clearwater environment in the entire region. Ponds in muskeg typify this habitat. The area studied most intensively was on the west shore of Martin Lake. Geographic localities in which these habitats are found are as follows: All of the localities in district 1, muskeg areas in 2.c., muskeg on the lower slopes of the Chugach Mountains in 3.b., and muskeg areas in 7.d. Small acid ponds occur on Carbon Ridge and Charlotte Ridge and elsewhere in the Tertiary foothills above the recent moraines. Throughout the region, small wood ponds which are collections of snowmelt and rainwater become

acid as the summer season progresses, presumably by the addition of organic acids from decaying vegetation. The only localities where these were tested for pH and dissolved oxygen were on Charlotte Ridge in 1962. Oxygen content averaged 2 ppm in four trials from two ponds and ranged between extremes of 1.5 and 2.2 ppm. The pH averaged 5.0 and ranged between extremes of 4.5 and 6.0. Daytime surface water high temperatures ranged from 18.9 to 23.0°C. At Martin Lake (2.c.) 6 ponds were tested for pH and temperature. A limited variety of aquatic plants is found in this habitat. The most striking is the yellow pond lily which gives these ponds in the muskeg growths the appearance of being carefully tended ornamental pools. The temperature of these ponds averaged 22.0°C, pH averaged 5.0 and dissolved CO₂ averaged 3.8 ppm (see Table 6, Peat Ponds). No mollusks were ever found in this potential habitat.

4. Clear, warm, acid, running water. This potential habitat is the outlet complex of habitat type 3. Although untested for dissolved oxygen content, it can be assumed to differ in having higher O₂ values than standing water because of more thorough mixing of water in contact with the atmosphere as the water flows. The higher dissolved CO₂ content (3.8 ppm in the ponds, 6.2 in the outlet stream) appears to support this assumption. Water temperatures in the streams equal the surface temperature of the standing water bodies where the streams flow out; but the addition of water from the muskeg, which is a large surface

of evaporation, depresses the temperature of the running water to an average of 16.0°C in a region where surface pond water averaged 22.0°C . Low pH is general and was determined in the Martin Lake (2.c.) locality to average 4.9 and range between extremes of 4.8 and 5.5 in 18 trials. The slightly lower pH in the running water environment as compared to the standing water environment is probably because of greater saturation of the water by dissolved CO_2 for the same reason that O_2 solution is assumed to be higher.

No mollusks were ever found in this environment. The most obvious assumption here is that low pH excludes mollusks from this and habitat type 3. This may not be the case. Martin Lake contains an abundant and diverse molluscan fauna despite a low pH (mean 5.8). All of the environments of habitat types 3 and 4 are shallow and may freeze solid during the winter, thus excluding mollusks.

5. Turbid, warm, neutral, standing water. This potential habitat occurs anywhere that glacial meltwater flows from contact with ice into insulated basins (e.g., superglacial drift, till, outwash, or bedrock basins) and stands long enough to be warmed by the sun and the atmosphere. No significant amount of vegetation colonizes these habitats, but Equisetum was found in Deadwood Lake. Over a period of years it was observed that some of the ponds and lakes vary in amount of suspended detritus as inflow of glacial meltwater fluctuates. In early summer (May and June) they tend to be less turbid than in August

when glacial ablation is at its peak. This was not determined by testing the water colorimetrically but by observation during overflights.

The range of pH values was 5.0 to 7.6, surface water temperatures range from 9.5 to 15°C, and turbidity as high as 55 ppm. Lakes which are this type of potential habitat are: Little Martin Lake (2.b.), ponds in the terminal moraine of the Martin River Glacier (3.b.), Deadwood Lake (3.c.), James, John, and Susan Lakes in the stagnant terminus of the Martin River Glacier (3.d.), OH Lake (5.a.), sloughs in the outlet of Sherman Valley (7.c.), and sloughs in the Copper River and Tesanuna Valley (8).

Mollusks occupy some of these water bodies.

<u>Pisidium compressum</u>		Little Martin Lake	
<u>Sphaerium nitidum</u>		Ponds in the Martin River Terminal Moraine	
<u>Valvata mercetia</u>		James Lake	
<u>Lymnaea humilis</u>	X	John Lake	
<u>Menetus calliglyptus</u>		Nancy Lake	
<u>Gyraulus parvus</u>	X	OH Lake	X
	No Mollusks	Sherman-Valley Sloughs	No Mollusks
	X	Copper River Sloughs	No Mollusks
		Deadwood Lake	X X X X X

6. Turbid, warm, neutral, running water. This potential habitat differs from the preceding type only in having temperatures equal to the top foot or so of the water in ponds or lakes of which they are the outlet (above 9.5°C). Thus, they tend to have higher minimum and more uniform (not much colder at the bottom) temperatures. Perhaps dissolved oxygen and carbon dioxide is found in greater concentration than in standing water for the same reason as discussed above (habitat 4), but this was never determined. Values of pH were the same as those determined on the surface water of their sources and ranged between 7.0 and 7.2 at OH Lake outlets (5.a), 7.1 at Little Martin Lake outlet (2.b.), and 7.6 at Deadwood Lake outlet (3.c.).

The molluscan faunnes found in two of the habitats of this type are as follows:

			OH Lake Outlet	
			Little Martin Lake Outlet	
		X	Deadwood Lake Outlet	
		X	Deadwood Lake Inlet	
No Mollusks		X		
		X		
		X		
No Mollusks		X		

Valvata mercilla

Menetus calliclyptus

Lymnaea humilis

Gyraulus parvus

7. Turbid, cool, neutral, standing water. This potential

habitat is characterized by turbid glacial meltwater which issues either directly from an icefront or travels only a short distance across small outwash plains (less than 1 1/2 miles). The temperatures at the surface average 9.9°C (64 trials in Lake Charlotte and Bee Lake). The turbidity inhibits the warming of deeper water and thermal stratification is unstable when present, but more commonly it is completely absent. The pH ranged between 7.2 and 8.0 and averaged 7.1 (35 trials in Bee Lake and Lake Charlotte). Dissolved O₂ averaged 3.9 ppm (13 trials in Lake Charlotte), CO₂ averaged 2.5 ppm (24 trials in Lake Charlotte and 7 trials in Bee Lake), and turbidity ranged between 40 and 127 ppm and averaged 54.1 ppm (117 trials in Lake Charlotte and Bee Lake).

Mollusks found in this type of habitat were located only on the logs of beaver houses and in the case of I. humilis at Bee Lake out of the water on wet mud surfaces under grasses.

Lakes which constitute this type of habitat are: Bee Lake (5.a.), Lake Charlotte (5.b.), and Kushtraka Lake (5.d.).

The molluscan faunules collected from habitats of this type were:

	Bee Lake		
	Lake Charlotte		
	Kushtaka Lake		
<u>Lymnaea humilis</u>	X	X	X
<u>Manetus calliclavatus</u>	X	X	X

8. Turbid, cool, neutral, running water. This potential habitat consists of the outlets of potential habitat type 7 where water temperature is below 9.5°C . Martin River (3.e.), Bee Lake outlet to OH Lake (5.a.), Shepherd Creek (5.b.), and Stillwater Creek (6.b.) are habitats of this type. The temperature is relatively uniform with depth and has been observed to range between 6.2 and 8.5°C .

Mollusks were found in Stillwater Creek and at the head of Shepherd Creek, but they are rare even where they are found. Lymnaea humilis and Menetus callioglyptus were found in the Stillwater Creek, and M. callioglyptus was found in Shepherd Creek.

9. Turbid, cold, neutral, standing water. This potential habitat consists of glacial meltwater which is in contact with glacier ice in at least a part of its basin. The water temperature at the surface does not exceed 3°C except in isolated bays in which the lake basin is insulated by superglacial drift. In these bays on clear days, according to Callender (1964, figs. 23 and 27) surface temperatures were recorded above 4° but below 5°C . Wind quickly destroys the incipient thermal stratification in these bays and the highest mean surface temperature recorded in this potential habitat type was 4.5°C . The average temperature of surface water in seven lakes of this type was 2.3°C (161 trials).

Turbidity ranged between 362 and 910. Total dissolved solids for the ice-sinkhole lakes on the Lake Charlotte lobe of the Martin

River Glacier was 5.8 ppm. Callender obtained much higher values at Miller Lake than I did at the Lake Charlotte lobe lakes (see Table 6) but his analyses were made on unfiltered, turbid water.

The ice-sinkhole lakes on the Lake Charlotte lobe of the Martin River Glacier and "Miller Lake" in the terminus of the Martin River Glacier (3.d.) are potential habitats of this type.

No mollusk nor living vegetation was ever found in this potential habitat.

10. Turbid, cold, neutral, running water. This potential habitat consists of the outlets of potential habitat type 9 in the reaches where their temperatures have not warmed above 5°C. During early summer seasons of low flow and bright sunshine, pools in quiet portions of these streams sometimes attain temperatures as high as 7.4° (observed on one occasion). Because these conditions are temporary and not characteristic of the environment they do not constitute a cool water environment. The more constant low temperatures characterize the habitat and presumably mollusks are excluded by the cold.

The streams defined as this type of potential habitat never clear sufficiently to allow penetration of light and there are no growths of algae. The average temperature of the two streams flowing from the Lake Charlotte lobe of the Martin River Glacier into Lake Charlotte was 1.4°C and ranged between 7.4° and 0.9°C (482 trials) in 1962. No surface drainage was observed between the ice-sinkhole lakes, but

cataclysmic subglacial draining was observed twice in 1962 and has been described by Reid and Clayton, (1963). The outlet of Miller Lake and the turbid inlet of Lake Charlotte (S.d.) are potential habitats of this type.

No mollusks exist in this potential habitat.

11. High tidal pools. This type of potential habitat exists along the coast in the Katalla region (1.a., 1.b., and 1.c.). No ecologic data was obtained because of the destruction of the water sample in shipment. From tasting the water in the field it can be stated that it was strongly brackish. These pools which form behind the beach berm may receive water directly from the sea or from salt spray during violent spring storms, but groundwater probably leaches salt from the beach sands and accounts for the brackishness of the water in the pools. By July (1967) these pools had either evaporated or drained away due to lowering of the groundwater table, but in mid-August after a two-week period of heavy rain they had partially refilled.

Lymnaea palustris was found in large numbers in these pools. They were observed feeding on decaying grasses and other vegetative detritus and on the carcasses of dead marine fish.

Potential Terrestrial Habitats:--Twelve potential terrestrial habitats are defined and described below. Five were found to harbor mollusks. The reasons why mollusks are not found in seven of these potential habitats are not known, but my conjectural impressions based

only on field observations are stated. Attempts to measure some characteristics of the terrestrial environment failed for a variety of reasons. Inexperience and ignorance were no doubt the central reasons for failure in this attempt, but occurrences as bizarre as a brown bear chewing up a temposcribe and thus destroying both the temperature record and instrument can be cited. A lack of equipment also seriously hampered attempts at quantification of the terrestrial habitats.

12. Muskeg surfaces. This potential habitat abounds on the Tertiary foothills above and beyond the limits of recent glaciation. The area studied most thoroughly was in the region containing acid peat ponds (potential aquatic habitat type 3) west of Martin Lake (2.c.). Muskeg also exists in all of the localities of district 1, on the lower slopes of the Chugach Mountains (3.b.), and in locality 7.d. Search for mollusks in all of these localities failed. Two obvious aspects of the potential habitat, the low pH and the abundance of water at the surface suggest themselves as reasons for the absence of terrestrial mollusks.

13. Spruce growths. This potential habitat consists of the forest floor undergrowths of Sitka spruce (Picea sitchensis). These exist in all of the localities of the Martin-Copper-Bering Rivers region. The understory of the spruce forests is usually an assemblage of shade tolerant plants which includes ferns, devil's club, lichens, and mosses. In the five years in which field work was carried out only four specimens

of one species (Vertigo columbiana) of terrestrial snail was found in this potential habitat. The general absence of mollusks may be caused by the chemical nature of the leaf litter developed under spruce, the absence of plants with which the snails associate, or coolness due to the lack of direct sunlight.

14. Established alders on bedrock. This potential habitat consists of the leaf litter accumulated under alders (Alnus fruticosa) which had at least seven annular rings. Most of the alders growing on bedrock are of this age or older. Talus cones and avalanche scars usually support the younger alder growths.

This potential habitat is found wherever bedrock crops out in the Martin-Copper-Bering region. These are found in 1.b., 1.c., 1.d., 2.a., 2.b., 2.c., 3.a., 3.f., 4, 5.a., 5.b., 6.a., 7.a., 7.b., 7.d., and 8.

The molluscan faunule typical of this potential habitat is, in the order of frequency of the various taxa present, Vertigo columbiana, V. ovata, Euconulus fulvus alaskensis, Deroceras laeve, Punctum cf P. randolphi, and Discus cronkhitei.

15. Pioneer alder on bedrock. This potential habitat is in the leaf litter accumulated under alders having fewer than seven annular rings. No mollusks were collected in this habitat. Their absence may be because of missing bacterial or floral elements found under established alders, but this was never determined.

16. Established alders on till. This potential habitat is the leaf litter beneath alders which have seven or more annular rings and which are growing on till surfaces. Especially detailed distributional studies of the mollusks living in this habitat were made at Sheridan Glacier (7.c.) and reported in Tutthill, Clayton, and Field (1969). The mollusks found there were Vertigo columbiana and Euconulus fulvus alaskensis.

17. Pioneer alders on till. This potential habitat is the same as 16 except that the alders are younger (less than seven years of age). No mollusks were found in this potential habitat. As was the case in potential habitat type 15 the absence of mollusks is essentially inexplicable.

18. Established alders on superclacial drift. This potential habitat is the leaf litter accumulated under alders of seven years or more of age growing on the drift-insulated stagnant terminus of the Martin River Glacier. At one locality only 11 inches of accumulated leaf litter and humus separated the glacier ice from the atmosphere, yet the habitat was occupied by Vertigo columbiana and Euconulus fulvus alaskensis. This is the habitat type in which the largest populations of terrestrial snails lived. The populations were found as far as one-half mile onto the drift-insulated, stagnant terminus of the glacier. Very few plants other than alder were found in the habitat. Infrequently clumps of viviparus grasses and Nootka lupine (Lupinus noockatensis) occur under

the alders. This potential habitat occurs only in 3.d. In order of their frequency of occurrence and dominance of the faunales, the mollusks which are found in this habitat are: V. columbiana, Euconulus fulvus alaskensis, Deroceras laeve, Punotum cf. P. randolphi, Vitina alaskana, Discus cronkheti, and Prophysaon cf. P. andersoni.

19. Pioneer alders on superglacial drift. This potential habitat consists of the accumulated leaf litter under alders of less than seven years of age growing on the stagnant terminus of the Martin River Glacier. The rejection of this habitat by terrestrial mollusks was dramatically exhibited by the absence of snails from under the younger alders growing around a clump of older alders on the peninsula in Miller Lake where we made our 1963 camp. On the south side of the peninsula accumulations of leaf litter under younger alders were 20 to 27 inches deep, but no mollusks could be found. At the contact between young and older (up to 16 years, determined by annular ring counts) alders an abundant population of Vertigo columbiana and Euconulus fulvus alaskensis was found living in leaf litter which ranged in thickness between 4 and 16 inches. The greater thickness of leaf litter under the younger stands of alder is no doubt due to accumulation of wind blown leaves on the down wind side of the peninsula. It suggests that whatever it is that makes established alders a receptive habitat and pioneer alders an unreceptive habitat is not a difference in the leaves produced by alders of different age, because there is obviously mixing of leaves from one stand to

another in the fall. No mollusks were found in young alders growing on superglacial drift. The potential habitat is limited to geographic locality 3.d.

20. Willow growings. This potential habitat consists of the leaf litter accumulated beneath willow shrubs (Salix sp.). Willows are the first woody growths to appear on fine grain-sized sediments and generally tend to occupy wetter areas. At Martin Lake (2.c.) and at Sherman Valley (7.c.) mollusks were found living under established alders on bedrock and till respectively. Among the alders willow occurred as individual clumps. The leaf litter under these willows was without landsnails, and a marked contrast between mollusks living in alder leaf litter and not living in willow leaf litter was observed. Perhaps the willow produces a humus which is chemically unsuited for occupancy by mollusks.

21. Grassy lake borders. This potential habitat is the grassy lake borders of both clear and turbid lakes throughout the region except for lakes in muskeg. The most complete studies of this habitat were made at Lake Charlotte, Lake Tokun, Bee Lake, OH Lake, and parts of Martin Lake. The flora appears to be limited in its extent by the presence of woody shrubs such as alder and willow which when present crowd the grasses out. These shrubs are excluded from the shore zone through which fluctuations of lake level traverse. In the case of Lake Charlotte an eight foot fluctuation (rise) during a 24-hour period in 1956

was reported to us by Mr. James E. King (oral communication to W. M. Laird and Tuthill in Cordova, Alaska, June, 1962). At Lake Tokun in 1964 Laird and I witnessed a 6 1/2 foot rise in lake level during a five-day period. This zone through which the water level fluctuated is frequently occupied by grasses and flowering plants which harbor an abundant fauna of terrestrial snails. The mollusks which characteristically occupy this habitat in their order of frequency and population domination are: Vertigo columbiana, Euconulus fulvus alaskensis, Deroceras laeve, Discus cronkhitei, Punctum cf. P. randolphi, Vitrina alaskana, and Prophysaon cf. P. andersoni. At Bee Lake Lymnaea humilis was also found in this habitat.

22. Outwash surfaces. This potential habitat includes all of the medium to coarse grain-sized gravel deposits in the Martin-Copper-Bering Rivers region. These are alluvial deposits of the various streams and rivers. Regardless of the vegetative cover, be it grass, moss, alder of any age, willow or spruce, mollusks do not occupy outwash surfaces. Leaf litter was observed to dry out more rapidly on outwash during periods when rain was not actually falling than did the humus developed on till, bedrock, or superglacial drift. Perhaps this accounts for the absence of mollusks.

23. Grass-and shrub-captured beach sands. This potential habitat occurs in geographic localities 1.a., 1.b., and 1.c. Mosses grow in the wetter areas of stabilized dunes and eolian transport of

sand is minimal in these areas. Dead grasses and leaves (mostly alder) accumulate, and it is in this situation that terrestrial mollusks occur. The snails which were found living along the tops of sea cliffs at Cape Martin and Whale Island (1.c.) and in the grass-captured dunes behind Palm Point (1.b.) received spray from the surf during storms. The mollusks found in this habitat were: Haplotrema sportella, Vespericola columbiana, Deroceras laeve, Succinea cf. S. rusticana, Oxyloma cf. O. retusa, and Vertigo modesta.

The distribution of the molluscan taxa in the various potential habitats is summarized on Table 7.

Systematic Discussion of the Taxa:

Specimens of all the species collected in Alaska have been compared with the collections at the Academy of Natural Sciences, Philadelphia, and, as noted in the discussion of individual taxa, most have been determined by Allyn Smith, Associate Curator of Invertebrate Zoology, California Academy of Sciences. The hypotypes and representative collections are curated in the collections of the Department of Geology, University of North Dakota. Their accession numbers are given on Table 11 and Plate 9. As previously, I have employed the classificatory schemes of Vokes (1967) and Taylor and Sohl (1962).

The partial synonymies given are intended only to identify the concept of the species I have employed. As data by which my identification of the Alaskan specimens can be evaluated I have included measurements (Table 11) of selected specimens.

Plate 9.--Nonmarine mollusks of the Martin-Copper-Bering Rivers region, Alaska.

Fig. 1. Vespericola columbiana, UND-4008, X 1; apertural view.

Fig. 2. Succinea cf. S. rusticana var. alaskana, UND-4007, X 2.1; apertural view.

Fig. 3. Vitrina alaskana, UND-4005, X 4.6; apical view.

Fig. 4. Haplotrema sportella, UND-4009, X 1; apertural view.

Fig. 5. Euconulus fulvus alaskensis, UND-4003, X 7.0; apertural view.

Fig. 6. Vertigo columbiana, UND-4004, X 4.6; apertural view.

Fig. 7. Discus cronkhitei, UND-4010, X 1.9; apical view.

Fig. 8. Lymnaea humilis, UND-4006, X 1.8; apertural view.

Fig. 9. Gyraulus parvus, UND-4011, X 3.2; apical view.

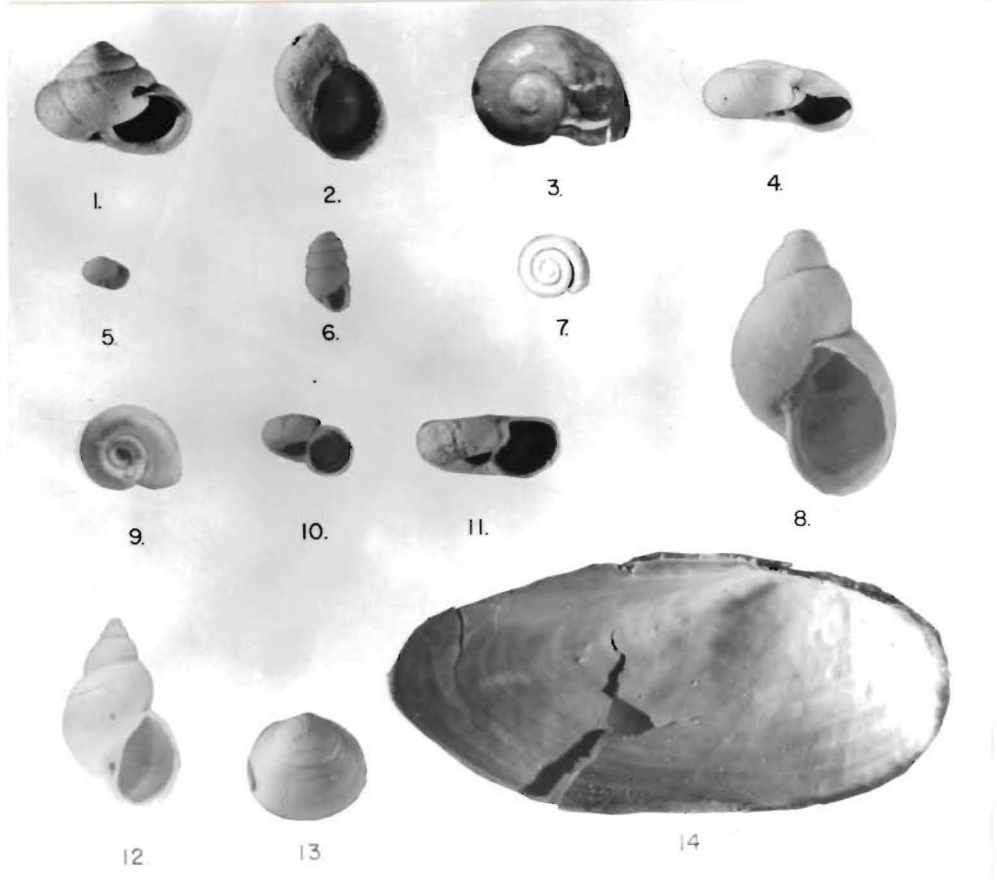
Fig. 10. Valvata mergella, UND-4000, X 4.0; apertural view.

Fig. 11. Menetus callioglyptus, UND-4013, X 3.4; apertural view.

Fig. 12. Lymnaea palustris, UND-4012, X 3.7; apertural view.

Fig. 13. Sphaerium nitidum, UND-4001, X 2.9; right valve.

Fig. 14. Anodonta beringiana, UND-4002, X 0.9; left valve.



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Phylum Mollusca

Class Bivalvia

Order Unionoidea

Superfamily Unionacea

Family Unionidae

Subfamily Anodontinae

Genus Anodonta Lamarck, 1799

Anodonta beringiana Middendorff, 1851

Plate 9, Figure 14.

Anodonta cellensis var. beringiana, Middendorff (1851, p. 273-308, 389-433).

A. youconensis, Lea (1867, p. 81).

A. youkanensis, Lea (1868, p. 287, Pl. 40, fig. 99).

A. beringiana, Tuthill (1964, p. 84-90).

The shell is very thin, comparable to the A. marginata of northern Minnesota, subquadrate, has a blue nacre and a dark brown periostracum which usually is absent from the beaks. Erosion of the beaks is very common and is presumably the result of chemical erosion affected by infestations of algae.

The animals are vigorous foragers judging by the tracks left from nightly travels. One trail was measured in sediments from which old trails had been obliterated by storm waves and was found to be 11.6 m long and followed an eccentric path (the commonest configuration observed). The foot is pale to bright orange. The animals inspected were usually heavily infested with encysting parasites.

The species was the only unionid encountered in this part of Alaska.

Besides Martin Lake (2.c.) and Sorehand Lake (8) the clam is known to exist in a pond east of McKinley Lake near Sheridan Glacier and in Eyak Lake at Cordova. Its distribution appears to be limited to clear, warm, shallow lakes with a soft muck bottom.

Dall (1905, p. 127-128) gives its range as follows:

Drainage into Bering Sea from Asia and America; also Cook Inlet drainage. Kenai Peninsula . . . , Kuskokwim River near Redoubt Kolmakof . . . , Yukon River below Anvik, in pools and quiet sloughs left by the receding freshets . . . , Avacha Bay, Kamchatka . . . , Amur River . . . , eastern Siberia and Mongolia.

This and my previous report (Tuthill, 1964) extend the range eastward and southward into the eastern Gulf of Alaska region.

Order Veneroida

Suborder Venerina

Superfamily Corbiculacea

Family Pisidiidae

Genus Sphaerium Scopoli, 1777

Herrington (1962) revised the taxonomy of the family Pisidiidae of North America. He employed conchological characteristics for the most part. His key to the species of the family is particularly useful to the paleontologist. The obviously confused state of the taxonomy of

this group and Herrington's own observations clearly indicate the wide range of variability of this taxon.

Herrington (1962, p. 11-12) stated that different ecologic conditions exhibit different ecotypic forms of the same species of this family. He cites an example in Pisidium ferrugineum which nearly always has tubercular beaks when it lives on sandy bottomed lakes, but has inflated beaks and less prominent striae when it lives on soft bottomed lakes. Baker (1928b, p. 306) cites an example of the extreme range of ecologic conditions in which Sphaerium is capable not only of surviving, but of maintaining a successful population.

It is thought that young in Musculium [equals Sphaerium according to Herrington (1962, p. 7-9)] may be carried in a marsupium for a year or more. In a pond under observation for a period of over a year, adults pisidiids are hermaphroditic were found in April to contain fully formed young. This pond was dry from July of the year preceding until it became filled by melting snow in March. It had no inlet or outlet and received no overflow floods from nearby ponds or streams.

I have observed specimens of both Sphaerium and Pisidium on the stalks of plants (e.g., Typha) growing under the edges of sloughs in North Dakota. The clams were seen to climb as high as 18 cm above water level on the plant stalks. They climbed by extending their foot, letting the moist surface of their foot adhere to the dry plant stalk, then retracted their foot, thus dragging their body upward. When disturbed they retreated within their shell completely and dropped into the water.

In Alaska I never observed pisidiids out of the water. No author of which I am aware has suggested, nor do I suggest, that the pisidiid terrestrial locomotion is a population radiation mechanism. I believe they are brought into drainages foreign to them or their previous generations by birds or possibly by fish. They do not have a free-living larval stage (Baker, 1928b, p. 303-306) and thus cannot immigrate as a larva. The adults are frequent items in the diet of fish, and as cited above the young are capable of remaining in the modified gill marsupium of the adult for protracted periods of time. It seems reasonable that even if adults could not stand the digestive processes of fish which ate them that there is a good chance that young might survive a trip through the digestive tract or at least transport to a new locality by a fish which died before the young clams were destroyed. Transport by water birds seems feasible. The adult clams are small and light and could easily be transported if accidentally included in mud which adhered to the bird's feet or feathers. Being hermaphroditic, a population could thus be established by a single such accident.

Sphaerium nitidum Jenyns, 1832

Plate 9, Figure 13.

Sphaerium nitidum Clessin, in Westerlund (1867, p. 102).

S. nitidum Clessin, Herrington (1962, p. 21, Pl. 1, fig. 6).

This species was collected in Deadwood Lake on 26 and 27 July, 1963 by picking it from small submerged logs which had been lifted from the bottom. Thirty specimens were recovered in this way.

A large population must occupy the lake, but because the lake water was turbid this conjecture could not be assessed. I did not have bottom sampling equipment with me at the time this lake was studied.

The taxonomic assignment of these specimens has not been confirmed by an expert in this group and relies for its accuracy upon my ability to interpret Herrington's key.

The presence of this species in turbid water (51 ppm, Table 7, Deadwood Lake) has paleoecologic significance. The success of this gill breathing bivalve in turbid water denies the paleoecologic use of the pisidiids as indicators of clear water. Their presence in only a turbid habitat is interpreted as merely an accident of colonization because the species is known to live in clear water environments over most of northern North America.

Genus Pisidium Pfeiffer, 1821

Pisidium compressum Prime, 1851

Not figured.

Pisidium compressum Prime (1851, p. 68).

P. compressum Prime, Herrington (1962, p. 35, Pl. 5, fig. 2, Pl. 7, fig. 14).

This small "pill" clam was found in Pistyll Lake (3.f.) and Black Lake (3.d.). It was collected in Black Lake from the submerged roots of sedges along the lake edge. In Pistyll Lake it was dredged from the bottom where it was attached to submerged aquatic vegetation.

P. compressum occurs in both turbid and clear water in the Martin River region. The significance of its occurrence in turbid water (OH Lake, 5.a.) is the same as that of Sphaerium nitidum as discussed above.

It is the second most common Pisidium in North America according to Herrington (1962, p. 35).

Pisidium casertanum (Poli, 1791)

Not figured.

Pisidium casertanum (Poli), Herrington (1962, p. 33-34, Pl. 4, fig. 1, Pl. 7, fig. 7).

Herrington has placed 41 species in synonymy with this taxon in his revision. The specimens collected from Sorehand Lake in the Tasnuna Valley (8) and reported by Bickley (in press) were identified by Herrington and are curated in his personal collections. This species was found only at Sorehand Lake.

According to Herrington (1962, p. 35) it is the most common Pisidium in North America.

Pisidium milium Held, 1836

Not figured.

Pisidium milium Held, Herrington (1962, p. 44-45, Pl. 4, fig. 3, Pl. 7, fig. 9).

Herrington identified the specimens collected and reported by Bickley. They came from Sorehand Lake in the lower Tasnuna Valley.

Class Gastropoda

Subclass Streptoneura

Order Mesogastropoda

Superfamily Valvatacea

Family Valvatidae

Genus Valvata Müller, 1774

Valvata mergella Westerlund 1885

Plate 9, Figure 10.

Valvata mergella Westerlund (1885, p. 209, Pl. 5, figs. 22, a-d).

V. siberica Middendorff, Tuthill (1963, p. 89).

V. mergella, Bickley (in press).

The assignment of the name V. mergella to the over 300 specimens taken from the Martin-Copper-Bering Rivers region is made upon the advice (letter of 14 April 1963) of Mr. Allyn G. Smith, Associate Curator, Department of Invertebrate Zoology, California Academy of Sciences. He wrote:

Valvata siberica Middendorff, 1851

The original description of this species (in Latin) is so loosely written that it might apply to almost any Valvata. The original material is stated to have come from rivers in Kamchatka. Dr. Hanna points out that many fresh-water mollusks species are circumboreal; consequently, it would not be surprising to find V. siberica in the Alaska area. However, we have no specimens of Valvata in our collection from Kamchatka so have no objective means for making a comparison with your material. We do have a small lot of Valvata labeled V. helicoidea Dall 1905, from "Ocean Pt., Colville River, Arctic Alaska" (CAS No. 34788) that are an exact match to your shells. Dall described V. lewisi var. helicoidea in 1905 (Harriman Alaska Expedition, p. 123-124, Pl. 11, figs. 1, 2) from the Yukon River area and also from the E. Kootenai district, British Columbia. He says: "This

form is very close to V. sibirica Middendorff, which however has a more depressed apex and uniform fine sharp sculpture." He goes on to say that his "var. helicoidea" differs somewhat from V. lewisi Currier, 1868, although it is found "with the type form, to some extent everywhere, but especially toward the Northwest." Considering the fact that fresh-water shells such as Valvata exhibit considerable individual variation within a given species I am inclined to discount the taxonomic value of V. helicoidea. Obviously, it cannot be said that it is a good geographic subspecies. Lacking authentic specimens of V. sibirica for comparison, there are two alternatives that can be followed: (1) Because of apparent close relationships of the northern species of Valvata, use the oldest available name in citation of the species, which is V. sibirica Middendorff, 1851; or (2) for lack of authentic material of V. sibirica, use the name that has been cited in the literature from the Arctic, the Canadian northwest and the Pacific northwest, which would be V. lewisi Currier, 1868 [new name for V. striata Lewis, 1856, preoccupied by V. striata Philippi, 1836]. Either course to be followed has arguments in favor of it. Whichever choice you make would be acceptable taxonomically, I am sure. You make the choice! [Incidentally, the only other reference to V. sibirica immediately available here is a mention of the species by W. J. Eyerdam (Nautilus, 52: 58, 1938), who says he collected it in 1932 in lakes on Unimak and Atka Ids. in the Aleutians but did not find it in Kamchatka. He gives its range as northern Sweden to N.E. Siberia.]

In 1967, Bickley (in press) found Valvata in Sorehand Lake in the lower Tasnuna Valley. He compared his specimens with those I had collected in 1962 and which Smith had verified and some 300 specimens I had collected in 1964. He concluded that the Valvata from the Tasnuna Valley were of the same species. After examining both suites of shells I concurred. He assigned the name V. sibirica tentatively

and asked Smith to evaluate the material. On 29 October, 1968, in a personal written communication to Bickley, Smith stated:

Taylor¹ puts Valvata lewisi helicoidea Dall, 1905, in the synonymy of V. mergella Westerlund, 1885, and I am inclined to agree with this assignment. The far northern Valvatas, like yours and several other lots in the CAS Collection, all seem to run rather large in size (well over 6 mm in major diameter) as adults. V. mergella calls for a shell 7 x 5 mm in diameter and height. Although we do not have any authentic specimens of V. mergella, Taylor has studied those in the USNM and those in the CAS and American list; and Junius Henderson seems to place the range of V. lewisi east of the Rocky Mts. Anyway, both V. mergella and V. helicoidea have somewhat less smooth sculpture than found on V. lewisi.

V. mergella is well established in Martin, Black, Tokun, and Deadwood Lakes and outlets. They are abundant in the clear water environment but were more abundant by ten times in the turbid environments. This is a crude measure, since it is based on counts of snails on 30 to 50 submerged objects as discussed above; but I believe the fact is clearly demonstrated that the turbid environment favors the taxon rather than inhibiting it. This is significant in that Valvata is a branchiate snail. In the paleoecologic reconstruction of the late Wisconsinan Missouri Coteau sediments it was assumed that branchiate mollusks could not survive turbid water conditions. It seemed reasonable that suspended detritus would foul the gill structures of a branchiate and cause its exclusion from such a habitat. The fact that Valvata mergella

¹The Taylor to whom he refers is Dr. Dwight Taylor, Department of Zoology, Arizona State University, Tempe, Arizona.

prefers turbid water is an important example of a gap in the completeness of the autecologic body of knowledge of North American branchiate nonmarine mollusks which pre-existed these studies. It is the type of information required by the paleoecologist and the gap in knowledge is the type which occasioned Taylor (1965, p. 597-612) to despair the practice of paleoecology based on Pleistocene nonmarine mollusks.

Subclass Euthyneura

Order Basommatophora

Superfamily Lymnalacea

Family Lymnaeidae

Genus Lymnaea Lamarck, 1799

Lymnaea humilis Say

Plate 9, Figure 8.

Galba humilis (Say), Baker (1911, p. 257-259; Pl. 29, figs. 26-30, Pl. 30, figs. 19-20).

G. Parva (Lea), Baker (1911, p. 243-248, Pl. 29, figs. 5-14, Pl. 30, figs. 9-12).

L. humilis Say, Hubendick (1951, p. 126-128, fig. 308).

In the face of the confusingly similar descriptions of the various Lymnaeidae, I have yielded to the temptation of Hubendick's (1951, p. 126-128, fig. 308) broad definition of the species L. humilis. Smith, after examining the specimens, wrote me on 19 April, 1963, as follows:

"Lymnaea humilis (Say, 1822) This name is as good as any for your

specimens. The taxonomy of the genus is in a state of flux at present."

This statement I viewed as a masterpiece of restraint!

After publication of my preliminary report of the molluscan fauna of the Martin River region (Tuthill, 1963) Dwight Taylor wrote to me on 29 October 1963 as follows:

After the October issue of The Veliger appeared I wrote to Allyn Smith about the identification of some snails from the Martin River area as Lymnaea humilis. I suspect he is mainly responsible for the unfortunate application of this name, but haven't heard from him as yet. Fossaria is a complicated group, and there has been no adequate revision. Nevertheless the occurrence together of forms with different shells that don't intergrade, the different geographic occurrence of slightly different shell types, the discovery by Burch of different chromosome numbers in forms with only slightly different shells, and the finding by Walter of consistent anatomical differences between species in the sense of Baker are all strong reasons for not following the sweeping synonymy of Hubendick, who lumped all American Fossaria as Lymnaea humilis. Especially in Alaska, where Baker thought the mainly Old World Fossaria truncatula might occur along with other forms. Critical attention to the habitat, internal morphology, and cytology will be necessary to establish the relationships of Fossaria and the other Lymnaeidae. I hope very much indeed you will not be persuaded by conchologists in the future to think that shells alone can provide an adequate systematic foundation in this group, or that Hubendick's superficial work is of value. Please understand that I'm not criticizing you personally or directly; most probably Smith or Hanna or some other source is responsible for giving poor advice or using a name that does not aid understanding of this complex group.

I do not disagree with Taylor's reasoning save in the matter of laying the blame on Smith and Hanna (Dr. G. Dallas Hanna, Curator of Geology and Paleontology, C.A.S.), but the fact remains that no conchological characteristics appear in the literature which permit a more precise assignment of the Alaskan material. I have continued to employ

the name L. humilis and have appended the phrase "sensu Hubendick, 1951" to signify the recognition that this is probably an inaccurate assignment, but the best that can be managed at present.

L. humilis, or whatever its true biologic identify may be, is the most widely distributed aquatic mollusk in the Martin River region with respect to types of habitat it will tolerate. Being a pulmonate it can be expected to have a greater capacity to survive temporary shifts in the conditions of its habitat and to be capable of short forays out of the water. It was found in all but two geographic districts in the Martin-Copper-Bering Rivers region (excluding the Katalla district (1) and the Sherman and Sheridan Glaciers district (7)), and it was found in every occupied habitat type except high tidal pools (11). It was the only aquatic mollusk besides Menetus callioglyptus to occupy a cool water (7) environment.

In turbid water habitats L. humilis had robust shells, but in clear, neutral water habitats the shells frequently lacked calcium carbonate reinforcement and were composed entirely of the soft leathery chitinous material of the periostracum. This condition was particularly noticeable in the Lake Tokun faunule.

Lymnaea palustris (Müller) 1774

Plate 9, Figure 12.

L. palustris (Muller), Hubendick (1951, p. 119-122, fig. 302).

The same general remarks about taxonomy as made with regard to L. humilis apply to L. palustris. As I have quoted in the introduction of this thesis, L. palustris in Europe is thought by Jackiewicz (1959) to be three distinct biological entities. According to Taylor (1965, p. 599) Jackiewicz's conclusion is based on the thorough anatomical study of 686 specimens from 75 localities in Poland. Unfortunately for the conchologist and the paleontologist, only one element of L. palustris as a complex taxon can be distinguished by shell features and for the paleoecologist, they have different, but overlapping ecologic and geographic distribution. Taylor also advises the discontinuation of the use of Müller's name as contrary to good practice. I agree in principle with Taylor, but am unable to do so in practice.

Superfamily Ancyloacea

Family Planorbidae

Genus Menetus H. and A. Adams, 1855

Menetus callioglyptus (Vanatta, 1895)

Plate 9, Figure 11.

Menetus callioglyptus cooperi (F. C. Baker) 1940.

This pulmonate gastropod is the most commonly encountered mollusk in habitat type 7 (turbid, cool, neutral, standing water) where it was found only on the logs of beaver houses and was sometimes accompanied by L. humilis. It was found in habitat types 1 (clear, warm, neutral, standing water), 5 (turbid, warm, neutral, standing

water), 6 (turbid, warm, neutral, running water), and 7 (turbid, cool, neutral, standing water). It was always a dominant element of any faunule of which it was a part. Despite the low amounts of dissolved solids and absence of colloidal-sized detritus in the clear water habitats occupied by M. callioglyptus it always had robust shells.

This observation has significance for the paleoecologist. Regardless of the reason for differences in ability to isolate the inorganic material necessary for shell reinforcement exhibited by various species of aquatic mollusks, the demonstrated ability of some species to build robust shells in waters of very low dissolved solids makes the employment of aquatic mollusks as paleoecologic indicators of water quality highly suspect. Perhaps when the physiology of the individual species becomes more fully known the practice can be justified within very narrow taxonomic limits, but at present it cannot be justified.

-Genus Gyraulus J. de Charpentier, 1837

Gyraulus parvus (Say, 1817)

Plate 9, Figure 9.

Planorbis parvus Say (1817, Pl. 1, fig. 5 and in unpaginated text).

Gyraulus parvus (Say), Baker (1928a, p. 374-378, Pl. 23, figs. 27-31, 39).

This species was found only in warm water and was tolerant of turbid water. Gigantism was common in the specimens from the Tasnuna Valley and from the Martin River region. One collected by Bickley measured 8.1 mm in diameter.

Order Stylommatophora

Suborder Orthurethra

Superfamily Pupillacea

Family Pupillidae

Genus Vertigo Müller, 1774

Vertigo ovata Say, 1822

Not figured.

Vertigo ovata Say, Pilsbry (1948, p. 953).

Bickley collected a dead shell of V. ovata from lake sediments taken from Sorehand Lake in the lower Tasnuna Valley (8). His identification was verified by Allyn Smith. Pilsbry (1948, p. 953) stated it is "the most widely distributed Vertigo." At the time of his writing, Pilsbry thought it had been reported from only three western states (Wyoming, Nebraska, and California). Dall cited its occurrence on Kodiak Island (Kodiak in modern usage) and in the Aleutian chain. Why it occurs only at Tasnuna Valley near the right of way of the Copper River and Northwestern Railroad is a mystery unless it too was introduced by white Americans in the late 19th and early 20th centuries.

Vertigo columbiana Sterki, 1892

Plate 9, Figure 6.

Vertigo columbiana Sterki, Dall (1910, p. 30).

V. columbiana Sterki, Pilsbry (1948, p. 959-960, fig. 533:12,13).

Dall cited the occurrence of this species on St. Paul Island, Bering Sea, Alaska, and Pilsbry also cited occurrence in coastal

Washington and Vancouver Island, British Columbia, Canada. The identification of the specimens collected near Lake Charlotte in 1962 were verified by Allyn Smith of the California Academy of Sciences.

This tiny landsnail is a vigorous pioneer. It was found on the glacier separated from ice by only 225 mm (9 in) of alder leaf litter. Where it occurs it is usually the dominant element of the molluscan populations. About 1300 specimens have been collected in this part of Alaska (the number collected by Bickley in Tasnuna Valley is not known at present, but 1,297 specimens are in my own collection). The average lot size of these collections is 27.6 specimens, the median is 6, and the range is between 1 and 321 (n specimens = 1,297). In the Tokun Lake district (4) for some reason V. columbiana was less dominant in terrestrial faunules. It was found at ten sites there and lots averaged 3.3 specimens per collection site, the median is 2, and observations range between 1 and 11 specimens per collection site.

Vertigo modesta (Say, 1824)
Not figured.

Vertigo modesta (Say), Dall (1911, p. 30).

V. modesta (Say), Pilsbry (1948, p. 982-985, figs. 527; 531: 1, 2; 528: 1-3).

Dall and Pilsbry both asserted that this is the most widely distributed Vertigo in arctic and subarctic North America. Johnson and I found the specimens from Katalla readily distinguishable from V. columbiana, but I have not found V. modesta elsewhere in the Martin-Copper-Bering Rivers region.

The many occurrences in the north cited by both Dall and Pilsbry (Dall's are included in Pilsbry) suggest it is a naturally distributed element of the northern terrestrial molluscan fauna. The fact that occurrences have been cited by white American geographic localities is a method forced upon authors by the fact that it was people of European stock or nationality that made the first maps. Thus, it cannot be determined from the literature whether populations of V. modesta are limited to late 19th and early 20th century settlements developed by Russian and American immigrants. Its unique occurrence at Katalla in the Martin-Copper-Bering Rivers region is puzzling if it is a taxon which is indeed a basic element of the fauna. Even at Katalla it was not a common snail. Only 12 specimens were found in two months' stay there.

Suborder Heterurethra

Superfamily Succineacea

Superfamily Succineidae

Genus Succinea Draparnaud, 1801

Succinea cf. S. rusticana var. alaskana Dall, 1905
Plate 9, Figure 2.

Succinea rusticana var. alaskana Dall, Pilsbry (1948, p. 824-825, fig. 446).

Succinea, Oxyloma, and Quickilla are defined at the species level on soft parts alone. Attempts to erect characters on shell morphology have thus far failed. The Succinea collected at Katalla (1.b.) were all empty shells with fresh periostracum covering them and are

thus unassignable to species with certainty. The configuration of the shells suggests that they are of the species S. rusticana var. alaskana. Succinea strigata Pfeiffer, S. rusticana var. alaskana Dall and Oxyloma retusa (Lea) are the only two Succinids listed in Pilsbry or Dall cited as occurring in Alaska, but S. avara Say and S. grosvenori Lea have northwest Canadian ranges which may better reflect the limit of search than it does the limit of the distribution of the species. If the specimens from Katalla represent typical adults of their species they are too small to be any of the species mentioned above. I have placed them tentatively in S. rusticana var. alaskana on the strength of Dall's statement (1911, p. 58) that his variety is more tumid than typical S. rusticana.

Genus Oxyloma Westerlund, 1885

Oxyloma cf. O. retusa (Lea) 1834
Not figured.

Oxyloma retusa (Lea), Pilsbry (1948, p. 785-788, fig. 421).

Three shells which I believe most closely resemble the shells of O. retusa were found at Katalla (l.a.) mingled with specimens of Succinea and Lymnaea palustris on the moist margins of the high tidal pools. No evaluation of soft parts was made, and, therefore, assignment to species is tentative. While scarce when I collected them, I had casually observed Succinids in relatively large numbers in this habitat. The decimation of their numbers between the time they were

first seen and when they were collected (about two weeks) was very likely the result of bird predation. The muddy margins were well marked by gull and tern tracks.

Suborder Sigmurethra

Infraorder Halopodopes

Superfamily Rhytidacea

Family Haplotrematidae

Genus Haplotrema Ancey, 1881

Haplotrema sportella (Gould) 1846

Plate 9, Figure 4.

Haplotrema sportella (Gould), Pilsbry (1940, p. 225-229, fig. 111).

This species occurs at Cordova, Alaska, where it was collected in 1963 by Mr. Rae Baxter. We found it at Palm Point (1.b.) in dune grass and at Whale Island (1.c.) at the tops of the sea cliffs. For the reasons discussed in Tuthill and Johnson (in press) and reiterated in the introduction of Alaskan studies in this paper and in the discussion of Vespericola below, I believe this snail was accidentally introduced by white Americans around the turn of the century.

The species has been reported from Unalaska Island and at Vancouver Island (Pilsbry, 1940, p. 226). I believe these specimens were also accidentally introduced by the ships which supplied the white settlements there. Their distribution would have been more general throughout the region if they had been transported into the area naturally.

Infraorder Aulacopoda

Superfamily Endodontacea

Family Edodontidae

Genus Discus Fitzinger, 1833

Discus cronkhitei (Newcomb) 1865

Plate 9, Figure 7.

Discus cronkhitei (Newcomb), Pilsbry (1948, p. 600-605, fig. 328, a-d).

This species is widely distributed in North America, and Pilsbry cited many coastal as well as inland occurrences in Alaska and Canada. It is a very minor element of the terrestrial molluscan fauna. Only 25 specimens were collected during the entire course of the study reported here. Most came from the Lake Charlotte district where the most thorough search was made. Thus, it seems reasonable that search over a protracted period elsewhere in the Martin-Copper-Bering Rivers region could be expected to turn up more D. cronkhitei in the habitats they favor.

D. cronkhitei was found under established alder on bedrock, till, and on superglacial drift and in grassy lake borders (habitats 14, 16, 18, and 21).

Genus Punctum Morse, 1864

Punctum cf. P. randolphi (Dall) 1895

Not figured.

Punctum randolphi (Dall), Pilsbry (1948, p. 646-647, fig. 353).

In 1962, Allyn Smith looked at a tiny snail which I thought was an immature Vallonia. He wrote me on 14 April 1963:

This is not a Vallonia but a Punctum. It looks very much like Punctum californicum Pilsbry, 1898, but if this is actually the species, it is a very great extension of range. P. californicum is common in the mountains of California and Arizona but has not been recorded from farther north than this. One would have to check with circumboreal species of the genus, which I can't do for lack of time at the moment. Suggest you cite this as "Punctum sp." and let it go at that, or else add a comment that it seems to be similar to P. californicum.

Twenty-two more specimens of Punctum were collected in 1963.

Close examination of these leads me to believe that they are more comparable to P. randolphi than to [P. californicum]. Pilsbry (1948, p. 648) points out that the two species may actually be one. He states, "This snail P. californicum is closely similar to P. randolphi, and with further study may possibly turn out to intergrade fully with that." The specimens from Alaska are smaller than indicated by measurements of P. californicum cited in Pilsbry (1948, p. 648) and are almost identical to those he cites for P. randolphi (p. 647). The striations are not as clearly defined on the Alaskan specimens as shown on the figure of the type specimen of P. californicum shown in Pilsbry (fig. 354) but are similar to that shown by Dall (1895, p. 128) in his figure of the type of P. randolphi. For these reasons I have chosen to compare the Martin River material with P. randolphi.

Family Arionidae

Genus Prophysaon Bland and Binney, 1873

Prophysaon cf. P. andersoni (J. G. Cooper) 1872

Not figured.

Prophysaon andersoni (J. G. Cooper), Pilsbry (1948, p. 682-688, figs. 372-374).

In 1962 Clayton collected a large slug from the surface of a rock on the superglacial drift about one-fourth mile from the terminus of the Martin River Glacier near ice-sinkhole lake "B" (see Plate V). The slug was preserved in alcohol without first being relaxed. I did not attempt to assign it to genus but sent it to Smith in late 1962. He wrote the following to me on 19 April 1963:

Larger slug

From the Martin Glacier. An interesting specimen. Not the genus Deroceras, which can be told at a glance because of the two narrow furrows longitudinally along the foot, giving it a tripartite aspect. I suspect your slug may belong in the genus Prophysaon but cannot be sure. The northern limit so far reported for Prophysaon is southern Alaska. It would be desirable to collect more of this if it can be found. . . .

Prophysaon has a habit of autotomizing its tail when disturbed. It does not have the foot grooves of Deroceras.

One additional specimen was collected at Lake Tokun on 10 July 1963. It was found on the underside of a driftwood alder log on the beach. Attempts to relax the slug before preservation were not wholly successful and no opportunity to dissect it presented itself in the field. It did not lose its tail during preservation, a behavior which Pilsbry (1948, p. 677) points out is a frequent but not an invariable occurrence.

Superfamily Zonitacea

Family Vitrinidae

Genus Vitrina Draparnaud, 1801Vitrina alaskana Dall, 1905

Plate 3, Figure 3.

Vitrina alaskana Dall (1911, p. 37-38).V. alaskana Dall, Pilsbry (1946, p. 503-504, fig. 276).

Three specimens of this species were collected. One specimen was seen by Smith, who concurred with my identification. Dall (1911, p. 38) stated that V. alaskana:

. . . is the most common land shell on most of the islands of Bering Sea and on the continent near the sea, where it usually occurs, but as we move southward we find it occurring at continually greater elevations and entirely absent from the warm dry plains and valleys. It attains from 7,500 to 10,800 feet elevation in the Sierra and Rocky Mountains.

The fact that two of the three specimens from the Martin River region came from under established alder growths on the glacier suggests that more thorough search of the alder on the mountain slopes on the north side of the Martin River valley might eventually have produced specimens. It was early in the season when I had the greatest opportunity to study this locality in 1964, and I was primarily occupied with other studies. Snow blanketed all but the most southern spurs of the Chugach mountains, and not much time was given to grubbing for mollusks.

The shells are extremely fragile, and measurements have not been obtained because apertural rims have been broken away during manipulation of the shells on the microscope stage. Preservation in alcohol seriously reduced the strength of the shells, and when dried they break from the force of thermal changes effected by evaporation of the alcohol.

Family Zonitidae

Genus Euconulus Reinhardt, 1883

Euconulus fulvus alaskensis (Pilsbry) 1899

Plate 3, Figure 5.

Euconulus fulvus alaskensis (Pilsbry), Pilsbry (1946, p. 238-239), fig. 118).

This is the second most common snail in the Martin-Copper-Bering Rivers region. Like Discus cronkhitei it occurs under established alders on bedrock, till, and superglacial drift and under grasses on the lake borders (habitat types 14, 16, 18, and 21). It was found in geographic districts 1 through 7, and I have little doubt that thorough late season search of appropriate habitats would disclose its occupancy of district 8 (Tasnuna Valley).

In 1962 I misidentified the specimens collected during the first field season as Retinella binneyana. Smith corrected my error in a letter dated 19 April 1963 as follows:

Retinella binneyana (Morse, 1894)

Pilsbry, in his monograph of the land shells of North America puts the genus Nosovitrea into the synonymy of Retinella, although subsequently H. B. Baker may have resurrected it. In any event, your shells are definitely not this genus or species but are Euconulus fulvus alaskensis Pilsbry, 1899, which is abundant all through the northwest. You have one lot of shells that have a lower spire than normal but I think even these are well within the limits of individual variation for the species (Subspecies).

I now completely agree with Smith's identification of my material.

Family Limacidae

Genus Deroceras Rafinesque, 1820Deroceras laeve (Müller) 1774

Not figured.

Deroceras laeve (Müller), Pilsbry (1948, p. 539-552, figs. 289-291).

This small dark grey slug is surprisingly ubiquitous in the Martin-Copper-Bering Rivers region. It was rarely encountered in groups. Of the 23 times it was encountered, only 12 times was it as more than a single specimen in the area collected. The average collection was 3 specimens, the median was 2 specimens, and the range was 1 to 12 specimens.

D. laeve is a common terrestrial mollusk of the north. Smith looked at some of my specimens and commented on 19 April 1963 in a letter to me as follows:

Deroceras cf. D. laeve (Müller, 1774)

These are the smaller blackish slugs, the northern records for which have been often cited in the literature as Deroceras hyperboreus (Westerlund, ? 1876). They are now generally considered to be D. laeve, a circumboreal species, which has many synonyms. Think you can omit the "cf." in this instance.

Infraorder Holopoda

Superfamily Polygyracea

Family Polygyracea

Genus Vespericola Pilsbry, 1939

Vespericola columbiana (Lea)

Plate 9, Figure 1.

Polygyra columbiana (Lea, Dall (1905, p. 24).

Vespericola columbiana (Lea), Pilsbry, 1940, p. 894-901, figs. 513-516.

As has been mentioned above and in Tuthill and Johnson (in press), I believe this species has been accidentally introduced into the Gulf of Alaska by ships serving the white American communities of this coast around the turn of the century. I have specimens of this species which were collected by Mr. Rae Baxter from the harbor region of the village of Cordova in 1963. These were found under discarded rotting lumber and other trash near the City Dock. Pilsbry (1940, p. 894-901) does list occurrences of Vespericola columbiana from Unalaska in the Aleutian chain. Mr. Baxter's collections constitute an extension of the range of this species of about one degree of latitude to the north. Strong association between the terrestrial taxa Haplotrema, Vespericola,

Succinea, and Vertigo modesta at Katalla and their absence elsewhere is interpreted as evidence of accidental introduction by white Americans. The occurrence of Vertigo ovata only at Tasnuna Valley may also be interpreted as accidental introduction during the building of the C.R. and N.W.R.R.

Population Density:

An attempt to determine population density was made. No completely satisfactory method of gathering data was developed. In 1962 elaborate quadrat systems were established on the lake-head delta of Lake Charlotte for determining the number of terrestrial gastropods per square meter in the various habitat type areas. The technique failed as a means of gathering data for valid statistical analysis because of the scarcity of snails, marked seasonal variation in the size of the land-snail population and the great concentration of snails in microhabitats within the general habitats they occupied. The Lake Charlotte region was the only locality where adequate time was available to carry out such investigations. The generally unsatisfactory results of these initial studies argued in favor of a program of intensive search in all possible microhabitats with mere discovery as the objective. This method provided data by which microhabitat preference and rejection could be determined and gave greater assurance that the true nature and distribution of the molluscan fauna would be learned. Also, I do not see the philosophic worth of rationalizing the usefulness of a

statistical value of the number of snails per square meter when all of

statistical value of the number of snails per square meter when all of the snails may have come from the underside of a two inch diameter stick, lying in the one clump of grass in a 100 square meter tract.

The determination of population density of aquatic forms was somewhat more successful in Tokun Lake and Martin Lake where the populations were the largest I observed during the five summers I worked in the region. The technique employed was to pick up an arbitrary number of objects (sticks and stones) which were submerged and collect the snails from them. Despite the unsophisticated nature of this technique, reproducible results were obtained if more than twenty objects were examined and if winds were moderate. When white caps appeared on the surface, I found that many of the aquatic snails detached themselves from the rocks and sticks on the surface of the lake basin and lodged between lower rocks without reattaching their feet to any surface.

Only two attempts were made to determine the degree to which negative phototropism biased quantitative collecting techniques. In 1963 at Martin Lake I placed 58 snails (*V. mergella* 16, *L. humilis* 21, *M. callioglyptus* 14, and *G. parvus* 7) in a one square meter enclosure of mosquito netting, the bottom of which was buried six inches below the gravel (shingle) and sand of the lake bottom. I collected the site seven days later in bright sunlight and employed the same method I used in my regular investigations. I recovered a total of 52 snails. One *V. mergella*, two *M. callioglyptus*, and three *L. humilis* were not

recovered by normally employed methods. A more intensive search in which a sieve was employed turned up the missing V. mergella and M. callioglyptus and one of the L. humilis (dead). Based on this one evaluation, the daylight collecting method proved to be capable of capturing about 90% of the population recoverable by a more elaborate technique, which consumed roughly five times the length of time required by the more cursory method. The quicker method was retained as adequate for the purposes of the investigation.

Another attempt to determine the effects of negative phototropism on collecting results was made at Tokun Lake later in 1963. In July it was dark during the period of about 2200 hours to 0300 hours. I searched the cobble and boulder shores on the north side of the lake with a flashlight to see if snails were browsing on the upper surfaces of these rocks. I did not move the rocks or collect the snails I observed. Thirty-nine snails were observed along 50 yards of this shore. During daylight the next day only eleven snails were seen. The day was overcast, not unusual for this region, so another search during bright sunlight was planned before the locality was collected. Unfortunately, it was necessary to leave the Tokun Lake area before a sunny day occurred. Collection of the area yielded an average of 15 snails per 30 submerged objects at three collecting localities. These values cannot be equated, but it is my impression that the majority of the snails avoid light and thus observation without disturbing the habitat would not produce meaningful results.

The problem of collecting deeper than arm length in any of the water bodies in south-central Alaska renders attempts to evaluate population density of aquatic mollusks essentially useless. The water is generally too cold and turbid to make even wet-suit aqualung investigations more rigorous than would be warranted by the amount of information which could reasonably be expected. In more than a thousand Echmann dredge samplings not one mollusk was captured alive or found as a dead shell.

Pioneer Communities:

As can be seen on Table 7 which summarizes the chemical limnology of aquatic habitats, water temperature appears to be the major limiting factor in interpreting patterns of distributions of aquatic mollusks. Thus, the taxa which can occupy the coldest water near the glacier are regarded to be the pioneers among the aquatic forms. These are Menetus callioglyptus and Lymnaea humilis. As can be expected, these species can and do also occupy less rigorous water bodies in the region.

The criteria for assigning terrestrial snails to pioneer status was that of proximity to the glaciers of the region and general frequency of occurrence. Euconulus fulvus alaskensis, Vertigo columbiana and the slug Deroceras laeve are the terrestrial pioneers.

I recognize that the origin of these studies of modern Alaskan nonmarine mollusks rests in the paleoecologic studies and provides a

fundamental bias for the establishment of criteria for pioneers. Several taxa, both aquatic and terrestrial are no doubt qualified as pioneers should other criteria be applied. The capability of L. palustris to occupy saline high tidal pools at Katalla no doubt shows a greater tolerance to rigorous ecologic conditions than does the occupancy of turbid glacier meltwater in drift-insulated ice-dammed lakes by L. humilis. My recognized bias is defended by the fact that it is the analogue of a superglacial fossil fauna that I was trying to understand.

Associations Among Alaskan Nonmarine Mollusks:

Tables 9a and 9b show the matrices of Jaccard coefficients of association (C_{ja}) for the aquatic and the terrestrial mollusks of the Martin-Copper-Bering Rivers region respectively. There is an exceptionally high degree of association between Gyraulus parvus and Valvata mergella ($C_{ja} = 80$). The notation of number of occurrences differs from that employed for evaluation of the late Wisconsinan molluscan fauna of the Missouri Coteau. In the evaluation of common occurrence of the Alaskan mollusks reference is made to the occurrence of a taxon in a habitat type, not in a specific locality. This refinement is possible in evaluating living populations, because the type of habitat the taxon occupies can be determined. This is not the case with fossil faunules.

Three species of aquatic snails and clams occur in five of the seven occupied habitats. These species are Gyraulus parvus, Menetus callioglyptus, and Lymnaea humilis. Associations among species which

occur in two or more habitats are generally high, except in the case of Lymnaea palustris and Pisidium. As I have discussed above, I believe L. palustris to have been accidentally introduced by white Americans, and, therefore, its low association with the balance of the aquatic mollusks would be expected.

Of the terrestrial mollusks Euconulus fulvus alaskensis, Vertigo columbiana, Deroceras laeve, and Discus cronkhitei occur in four of the five occupied habitats. The highest possible association ($C_{ja} = 100$) exists between Haplotrema sportella, Vespericola columbiana, Succinea rusticana, Vertigo modesta, and Oxyloma retusa. All of these species are restricted to the Katalla (1) district and are assumed to be introduced species.

Evolution of Lakes on the Stagnant Terminus of the Martin River Glacier:

During the course of the studies of the aquatic potential molluscan habitats, data were collected which made it possible to postulate an evolutionary system of lake development on the drift-insulated stagnant terminus of the Martin River Glacier. I suggest that the close dependence of the stages of this evolutionary system upon physical phenomena related to the stagnation of glaciers gives the system general applicability for all lakes on stagnant glaciers. Figure 7 shows, schematically, the evolution of lakes on stagnant glacier terminuses.

A glacier and the hydrologic cycle, regardless of the state of the glacier's mass budget, can be thought of as a natural conveyor belt.

Gravity motivates the cyclic system. Snow collects at the source area, compresses and metamorphoses to ice by its own weight, and when it has attained sufficient thickness (150 to 250 feet, depending on temperature and included material) it acts as a semi-plastic and flows down slope. The upper 150 to 250 feet (in section) remains rigid, and thus fractures under the impelling force of the mobile semi-plastic lower part of the glacier. Where the rigid "carapace" is in contact with the lithosphere it must fracture in a shear plane to permit the relief of the stress imparted by the down slope movement. Earth materials are carried along these shear planes to the upper portion of the glacier.

Ablation of the glacier is predominantly from the surface, and water is returned to the hydrologic cycle by runoff and evaporation of meltwater and by sublimation of the ice. The earth materials remain on the surface and collect in depressions as the result of mass wasting processes. This superglacial rock debris (drift) is an effective insulator and inhibits ablation of the ice it covers. Thus it becomes a major factor in the control of superglacial topography. Depressions form where superglacial drift is absent, or thin and raised areas of buried ice form where it is present and thickest. Mass wasting of superglacial drift is the dominant mechanism of transport in the process of inversion of superglacial topography and results from the effects of differential insulation. The thinly covered depressions become filled with slumped superglacial debris, and the former high areas which then become bared

by slumping of their drift cover and thus ablate faster and become depressions. This cycle continues until all the ice of the stagnant glacier has been melted. During the process, however, basins form in the ice which contain a sequence of five lake types.

The first is the ice-walled, cold, turbid lake. These are usually conic bodies of water which, because of the extensive ice-water interface, never attain temperatures above 2°C. They are closed systems receiving inflow of meltwater, but rarely having outflowing drainage system (Miller Lake is an exception). They are barren of all life of microscopic size save for a few insect larvae. The ice-sinkhole lakes on the Martin River Glacier are lakes of this type.

The second type of lake to form is the ice-basined, drift-insulated, turbid, cool (or warm) lake. The lake type occurs when down-melting of the terminal ice has advanced to the point where stability of the superglacial drift has been achieved. This does not frequently occur before the bottom of the depression in which the lake forms has achieved contact with the subglacial surface. The lake exists in a basin formed by stagnant glacier ice, but there is little or no contact between the ice and the water. John, James, and Susan Lakes are examples of this type of lake.

At this stage in the evolution of lakes on a stagnant glacial terminus one or two events may occur. If the buried ice becomes exposed sufficiently to completely melt a depression in the sediments which had

been superglacial drift (now known as ablation till) will form, and a kettle lake may form in the depression. If turbid meltwater flows into the depression, intermorainal, turbid, cool (or warm) lakes will form. Deadwood Lake is an example of this third type of lake.

When inflow of meltwater stops, the water of lake type three becomes clear and an intermorainal, warm, clear lake forms. Pistyll and Dundaff lakes are examples of this fourth lake type.

If inflow of meltwater is never present in the depressions formed in the stagnant glacial terminus, an ice-basined, drift-insulated, clear, warm lake is formed. Drift thicknesses of no more than six feet are all that is required to completely isolate the water of such a lake from its containing ice basin. Black Lake is a lake of this fifth type.

If a type five lake endures for a protracted period and collects a significant deposit of sediments, its sedimentary content may remain as a topographically high body of stratified sediments surrounded by ablation till deposits when the ice basin eventually melts.

Paleoecologic Significance of Modern Proglacial and Superglacial Molluscan Habitats in South-central Alaska

Several aspects of my studies constitute additions to the body of ecologic knowledge about nonmarine mollusks and thus provide a broader basis for paleoecologic use of nonmarine mollusks. Some of the autecologic data suggests that the employment of fossil mollusks now current in North American paleoecologic practice is unjustified and

should be discontinued. The regional setting of the molluscan habitats suggests the necessity of clearly revising the rationale of paleoecology with respect to the geologic and paleontologic evidence to be found in terminal glacial sediments.

It is clear from my studies that the thermal characteristics of water are more critical to the employment of the water as a favorable or useable habitat by aquatic mollusks than is turbidity. The turbidity effects the thermal characteristics of the water, but it is not the only controlling factor. For example, Bee Lake is a cool lake, partially because its turbidity decreases the effects of direct solar radiation and partially because it receives large amounts of cold glacier meltwater. The lowest temperature in OH Lake is warmer than the lowest temperature in Bee Lake by about $4\frac{1}{2}^{\circ}\text{C}$ because the sill of Bee Lake's outlet permits the delivery of only the warmer surface water to OH Lake. Thus, the consistency of the effect of turbidity on water temperature is faulty and cannot be inferred from sedimentary evidence.

Paleontological evidence could be expected to differentiate cool from warm or cold lakes. The population structure of molluscan faunules from cool lakes is characteristically few in number of species, limited to pulmonates, and few in number of individuals. If warm, the population of turbid lakes (e.g., Deadwood Lake) is not different from that of clear lakes of comparable temperature in either species composition or number of individuals. The absence of mollusks from lakes or

streams having an ice-water interface is significant. The presence of mollusks in englacial or proglacial sediments can, therefore, be taken to indicate the presence of a drift-insulation sufficient to permit water to warm above 5°C.

The fact that mollusks were distributed in the lakes and streams of the Martin River region without relationship to dissolved solids and with very minimal relationship to pH as low as 5.5 indicates that fossil mollusks cannot be regarded as trustworthy indicators of water quality. If both branchiate and pulmonate snails and bivalves can successfully occupy water with less than 1 ppm dissolved solids, they cannot reflect the quality of the water. The citation of dissolved solids determined concurrent with collection of mollusks in the lakes of Wisconsin (Morrison, 1932), or the lakes and ponds of Bass Island in Lake Erie (Dennis, 1938), or the ponds and sloughs of the Missouri Coteau (modern) in North Dakota (Tuthill and Laird, 1963) as a part of a paleoecologic analysis is also wrong. Even the mere implication that these water quality values are germane to the autecology of the species cited and, therefore, useful in a paleoautecologic evaluation is totally unjustified. As demonstrated in the introductory discussion on paleoecology, and as exemplified by the citation of Clark (1961) made earlier, this practice is current in paleoecologic reconstructions of Pleistocene fossil assemblages. It is my opinion that the work accomplished in Alaska requires the discontinuation of this practice.

The impression that close proximity to glacier ice inhibits colonization by animals, specifically mollusks, has been thoroughly disproven for both aquatic as well as terrestrial organisms. Aquatic snails occupy lakes in ice-dammed proglacial basins, albeit in small numbers and in faunules of few species, but they are nevertheless there. Terrestrial snails require no more than a foot of leaf litter between them and the underlying glacier ice to be able to establish large colonies as proven by the collections I made on the Lake Charlotte Lobe of the Martin River Glacier. As far as the mollusks of the Martin-Copper-Bering Rivers region are concerned, the substrata could as well be rock as ice. The extremely local edaphic controls on population distribution have been either identified or suggested in the absence of clear evidence.

It has been the hope of paleoecologists that fossil mollusks would give clues as to the paleoclimate of regions where they are found. The Alaskan studies reported here encourage this hope. The surficial geologic features which are in the process of deposition in the Martin River region are clearly glacially associated. The sediments in the ice-basined, drift-insulated, warm, clear lakes will contain fossils of the mollusks which now live and have lived in the lake. These shells unquestionably indicate the existence of conditions which favored the establishment and continuance of molluscan populations. These conditions are a result of the climate, which, at the terminus of the Martin

River Glacier, is temperate marine, not glacial. The Martin River Glacier exists in the region not because of the climatic conditions which the mollusks represent, but because of the close proximity of high glacierized mountains in a region of frequent incursions of moist warm air, heavy cloud cover and a short ablation season. Thus, the character of the streams and surficial topography suggest the presence of glaciers, but they do not assure the presence of glacial (cold) climate. In fact, the sediments and the topography suggest the presence of a warm, humid climate as much as the presence of mollusks do. It is a widespread and incorrect bias on the part of geologists that end and recessional moraines, ground moraine sheets, outwash plains, and other ice-contact features suggest conditions favorable to glaciers, when in fact they are irrefutable evidence of climatic conditions intolerable to glaciers. Were the climate arctic or even cold, the terminal ablation features would not have formed.

EVALUATION OF THE HYPOTHESIS ERECTED TO EXPLAIN
THE LATE WISCONSINAN MOLLUSCAN FAUNA
OF THE MISSOURI COTEAU (NORTH DAKOTA)

The paleontology and geology of the Missouri Coteau in North Dakota which has been discussed in an earlier section can be evaluated by means of the conditions which were studied near the Martin River Glacier with an unusual degree of scientific accuracy for paleoecologic studies. The absence from the literature of any proglacial or superglacial molluscan ecologic information enforced an unusual environment upon me and my colleagues while we were erecting the hypothesis. We could not have reasoned circularly if we had wanted to, and we were thus allowed to operate free from conscious or unconscious biases.

The assumptions which underlay the hypothetical reconstruction of the ecology of the late Wisconsinan Missouri Coteau were those normal in any paleoecologic work. We assumed that the small amount of nonmarine molluscan speciation which has occurred in the late Pleistocene justified the idea that ecologic requirements have changed little for the species of the late Wisconsinan fauna. We reduced the likelihood of error in this respect even further by inferring only the most general autecologic and synecologic conclusions available to us.

Instead of inferring water quality in the details of specific values of ionic concentration we suggested that evapo-transpiration : precipitation ratios were positive on the side of precipitation by a degree possibly no more striking than the modern differences between Beltrami County, Minnesota and McIntosh County, North Dakota (Tuthill, Clayton, and Laird, 1963). We inferred a more humid climate partly on the basis of fossil evidence and partly on sedimentological evidence. We postulated that thick drift cover permitted ice-basined lakes to warm and become clear, warm-water habitats receptive to mollusks despite the close proximity of stagnant glacial ice. The presence of unionid bivalves prompted us to postulate the presence of fishes which the clams require as hosts for their glochidial stage. The occurrence of oögonia of calcareous algae as well as the obvious need for an abundant food supply for the large molluscan populations which the fossils represented caused us to hypothesize the presence of abundant populations of both aquatic and terrestrial plants.

The fundamental question to be applied to these hypotheses is, "can such conditions really be expected on the ice-cored terminus of a stagnant glacier?" The fact that all of these conditions do exist on the Martin River Glacier is clear uniformitarian justification for the hypothesis. Details, such as the thickness of superglacial drift required to insulate the waters of the ice-basined lakes from the cooling effects of their ice basins were modified by the studies in Alaska.

We discovered that no more than six feet of superglacial drift need have been present to accomplish this, instead of the several hundreds of feet we had previously thought. The presence of abundant, highly successful branchiate populations in warm, turbid lakes was a surprise and occasioned the abandonment of the idea that mollusks could serve as indicators of turbidity or clarity of water. The seeming disregard for relatively low pH and extremely low dissolved solids by large populations of mollusks in Alaska invalidates the general practice of employing mollusks as indicators of water quality. The range of water temperature which affect the nature and size of molluscan populations was not clearly understood when we erected the hypothesis for the Missouri Coteau. That the water in the late Wisconsinan ponds in the Missouri Coteau was warm seemed obvious because of the great abundance of evidence of very successful molluscan populations, but natural population limits with respect to temperature were not fully considered by me. In light of the Alaskan studies, this is unquestionably the one aspect of ecology which the structure of a fossil nonmarine molluscan population can best illuminate for the paleoecologist.

Another aspect of the hypothesis which was not fully understood by me before the Alaskan studies was the effect upon a colonizing population of its source stock. In the mid-continent a diverse molluscan fauna of many species was available to colonize the newly deglaciated surfaces. In Alaska the number of species is small. Also, the mechanics

of transportation as a critical aspect of analysis of fossil faunas was sharply focused by the Alaskan work. The coastal region of Alaska is a great flyway for waterfowl, but is limited to the west coast of North America. The late Wisconsinan mollusks available for colonization of the ice-cored Missouri Coteau could have been distributed through the entire continent west of the Appalachian Mountains and east of the Rocky Mountains. This strongly bears on the practice of comparing fossil faunules with modern assemblages. Tables 10 and 11 are Jaccard matrices which compare the assemblages of the Martin River Glacier region with the faunules typical of habitat types postulated for the late Wisconsinan Missouri Coteau. Obviously, the level at which the comparison is made effects the result. Table 10 is a straightforward comparison of the species. Table 11 is a comparison of the two faunal groups with respect to the number of pulmonate and branchiate snail taxa, and number of unionid and pisidiid bivalve taxa. The question raised must be directed either at the method and practice of comparison or at the validity of the hypothesis. Much stronger coefficients of similarity are attained in the comparison of the late Wisconsinan molluscan fauna of the Missouri Coteau with modern Minnesota assemblages than its comparison with the Alaskan species. If the hypothesis depended solely on paleontological evidence we would surely be forced to reject the hypothesis if we accepted the Jaccard comparison as fundamentally valid. The hypothesis does not so depend on purely paleontological

evidence, but much more fully on geologic evidence and thus may be retained despite the low values on Table 12a. This retention of the hypothesis naturally requires an evaluation of the method of statistical evaluation. Jaccard coefficients are not designed to negate or diminish the effects of differences of ancestral stock. If a population is an extension of a pre-existing fauna it must then be limited to the species of that original stock and its evolutionary products. When we compare fossil faunules with modern faunas we must have some assurance, outside the method of statistical comparison, that the two groups being compared have the fundamental ability to be comparable, that of having the same ancestral stock. There are marked differences between the molluscan faunas of the various modern oceans, and, for that matter, the various parts of a single ocean. The modern west coast nonmarine molluscan fauna is strikingly different from that of the mid-continent, and in turn both are significantly different from that of the eastern continent. The terrestrial molluscan fauna of North Dakota has elements which are clearly related to the distinctive Rocky Mountain fauna (e.g., Zoogentetes harpa). Thus, I believe that the concept of retaining some faunal connection when employing statistical techniques for paleoecologic studies has applicability to all types of paleoecology, not just the problem being discussed here.

The absence of terrestrial snails from the fossil fauna of the Missouri Coteau and their abundance on the Martin River Glacier is a

mystery which remains unexplained to me. The environments in which the landsnails lived on the Alaskan glacier were not favorable ones for preservation, but the abundant populations in the grassy borders of the lake will surely be incorporated in marginal lake sediments and will appear in the fossil fauna of lakes like Bee Lake, Black Lake, Lake Charlotte, Little Martin Lake, Deadwood Lake, and Pistyll Lake. Land-snail fossils do occur in the slough deposits such as those studied by Thompson (1963) and McAndrews and others (1967). But these deposits are not clearly associated with the period during which ice existed in the sediments of the Missouri Coteau. They may represent the type of environment found at Pistyll Lake and may have coexisted with the ice-basined, drift-insulated, warm, clear lakes of the Coteau. The fossil landsnails do not appear in the lower sediments of the slough deposits, thus suggesting that colonization of the Missouri Coteau did not occur until Recent times. Further study of the modern terrestrial snail fauna of North Dakota and a more careful search for them in till deposits will be required before solution of the problem can be hoped for.

It can be said in summary that the Alaskan mollusk studies have provided an adequate basis for evaluating the hypothesis erected to explain the nonmarine molluscan fauna of the late Wisconsinan Missouri Coteau. That hypothesis has been modified in the matter of a few non-essential details, but the fundamental hypothesis can be accepted because a modern analogue exists.

APPENDIX

TABLE 1.--Association matrix for taxa of the late Wisconsinan molluscan fauna of the Missouri Coteau in North Dakota

	<i>Valvata tricarinata</i>	<i>Gyraulus parvus</i>	<i>Gyraulus sp.</i>	<i>Pisidium sp.</i>	<i>Amnicola limosa</i>	<i>Lymnaea humilis</i>	<i>Promenetus exacuus</i>	<i>Helisoma anceps</i>	<i>Armiger crista</i>	Unionids	<i>Valvata lewisi</i>	<i>Helisoma campanulatum</i>	<i>Physa sp.</i>	<i>Sphaerium sp.</i>	<i>Lampsilis luteolus</i>	<i>Anodonta grandis</i>	<i>Helisoma trivolvis</i>	<i>Amnicola sp.</i>	<i>Lymnaea stagnalis</i>	<i>Lymnaea palustris</i>	<i>Ferrissia sp.</i>	<i>Anodontoidea ferussacianus</i>
<i>Valvata tricarinata</i>	X	67	67	71	61	53	50	41	28	35	25	30	20	21	15	15	12	12	3	3	3	3
<i>Gyraulus parvus</i>		X	56	69	69	65	56	40	31	33	33	30	31	24	13	17	17	10	7	7	3	3
<i>Gyraulus sp.</i>			X	64	58	49	50	40	29	25	27	19	14	26	18	19	14	3	7	7	3	3
<i>Pisidium sp.</i>				X	64	58	50	35	38	25	31	20	24	26	14	19	14	11	4	4	4	4
<i>Amnicola limosa</i>					X	57	53	48	27	36	24	40	26	23	15	20	7	4	0	4	4	4
<i>Lymnaea humilis</i>						X	59	32	35	25	32	39	29	21	17	17	23	8	9	9	5	5
<i>Promenetus exacuus</i>							X	38	48	21	27	35	50	22	13	13	24	4	5	5	5	5
<i>Helisoma anceps</i>								X	33	33	29	25	26	30	11	11	5	6	0	6	0	7
<i>Armiger crista</i>									X	24	33	21	57	25	19	6	20	6	15	15	6	6
Unionids										X	26	28	15	25	27	44	6	31	7	0	8	8
<i>Valvata lewisi</i>											X	24	33	28	13	21	14	14	8	8	9	0
<i>Helisoma campanulatum</i>												X	27	21	7	14	7	17	9	0	10	0
<i>Physa sp.</i>													X	23	15	17	27	8	22	22	11	0
<i>Sphaerium sp.</i>														X	18	33	20	10	13	13	14	14

TABLE 1--Continued

		<i>Valvata tricarinata</i>
		<i>Gyraulus parvus</i>
		<i>Gyraulus</i> sp.
		<i>Pisidium</i> sp.
		<i>Amnicola limosa</i>
		<i>Lymnaea humilis</i>
		<i>Promenetus exacuus</i>
		<i>Helisoma anceps</i>
		<i>Armiger crista</i>
		Unionids
		<i>Valvata lewisi</i>
		<i>Helisoma campanulatum</i>
		<i>Physa</i> sp.
		<i>Sphaerium</i> sp.
		<i>Lampsilis luteolus</i>
		<i>Anodonta grandis</i>
		<i>Helisoma trivolvis</i>
		<i>Amnicola</i> sp.
		<i>Lymnaea stagnalis</i>
		<i>Lymnaea palustris</i>
		<i>Ferrissia</i> sp.
		<i>Anodontoides ferussacianus</i>
Dominance		
Dominant (68%)	X X X X	
Allied (38-68%)		X X X
Adjunct (9-38%)		X X X X X X X X X
Ancillary (10%)		X X X X X
Associations between taxa		
First-order associations	49 C _{1a}	
Second-order associations	49-30 C _{1a}	
		Third-order associations
		29-10 C _{1a}
		10 C _{1a}
		Not associated

TABLE 2a.--Association matrix for taxa of the late Wisconsinan molluscan fauna recovered from lacustrine sediments of the Missouri Coteau in North Dakota (C_{jac})

	<i>Valvata tricarinata</i>	<i>Gyraulus parvus</i>	<i>Gyraulus sp.</i>	<i>Pisidium sp.</i>	<i>Amnicola limosa</i>	<i>Lymnaea humilis</i>	<i>Promenetus exacuus</i>	<i>Helisoma anceps</i>	<i>Armiger crista</i>	Unionids	<i>Valvata lewisi</i>	<i>Helisoma campanulatum</i>	<i>Physa sp.</i>	<i>Sphaerium sp.</i>	<i>Lampsilis luteolus</i>	<i>Anodonta grandis</i>	<i>Helisoma trivolvis</i>	<i>Lymnaea stagnalis</i>	<i>Lymnaea palustris</i>
<i>Valvata tricarinata</i>	X	68	83	71	74	56	52	39	31	29	25	32	25	23	17	9	18	0	4
<i>Gyraulus parvus</i>		X	58	70	65	68	64	50	28	26	33	29	40	25	14	10	20	10	5
<i>Gyraulus sp.</i>			X	60	62	52	48	41	27	25	26	22	32	24	20	10	20	5	10
<i>Pisidium sp.</i>				X	54	64	52	32	41	17	29	19	29	26	14	11	15	0	5
<i>Amnicola limosa</i>					X	52	55	40	25	29	30	39	30	21	15	11	5	6	0
<i>Lymnaea humilis</i>						X	65	29	33	19	32	20	32	16	16	12	24	6	12
<i>Promenetus exacuus</i>							X	37	47	19	41	35	60	19	11	13	25	6	13
<i>Helisoma anceps</i>								X	38	36	29	31	64	44	7	0	8	0	9
<i>Armiger crista</i>									X	24	33	19	53	21	13	0	14	8	17
Unionids										X	21	23	13	17	40	10	0	0	0
<i>Valvata lewisi</i>											X	25	33	30	9	11	9	0	11
<i>Helisoma campanulatum</i>												X	50	20	0	13	0	0	0
<i>Physa sp.</i>													X	15	9	11	33	13	25
<i>Sphaerium sp.</i>														X	11	17	13	0	17
<i>Lampsilis luteolus</i>															X	17	13	0	0
<i>Anodonta grandis</i>																X	20	0	0

TABLE 2a--Continued

	Valvata tricarinata	Cyraulius parvus	Cyraulius sp.	Pisidium sp.	Amnicola limosa	Lymnaea humilis	Promenetus exacuus	Helisoma anceps	Armiger crista	Unionids	Valvata lewisi	Helisoma campanulatum	Physa sp.	Sphaerium sp.	Lampsilis luteolus	Anodonta grandis	Helisoma trivolvis	Lymnaea stagnalis	Lymnaea palustris	
Helisoma trivolvis																	X	67	67	
Lymnaea stagnalis																			X	100
Lymnaea palustris																				X
Percent Frequency	81	74	78	70	67	63	59	37	44	33	30	26	30	19	19	7	15	4	7	
Dominance																				
Dominant (68%)	X	X	X	X	X															
Allied (38-68%)						X	X													
Adjunct (9-38%)								X	X	X	X	X	X	X	X		X			
Ancillary (10%)																X		X	X	
Associations between taxa																				
First-order associations																			49	C _{ja}
Second-order associations																			49-30	C _{ja}
Third-order associations																			29-10	C _{ja}
Not associated																			10	C _{ja}

TABLE 2b.--Association matrix for taxa of the late Wisconsinan molluscan fauna recovered from fluvial sediments of the Missouri Coteau in North Dakota

	<i>Valvata tricarinata</i>	<i>Gyraulus parvus</i>	<i>Gyraulus sp.</i>	<i>Pisidium sp.</i>	<i>Amnicola limosa</i>	<i>Lymnaea humilis</i>	<i>Promenetus exacuus</i>	<i>Helisoma anceps</i>	<i>Armiger crista</i>	Unionids	<i>Valvata lewisi</i>	<i>Helisoma campanulatum</i>	<i>Physa sp.</i>	<i>Sphaerium sp.</i>	<i>Lampsilis luteolus</i>	<i>Anodonta grandis</i>	<i>Helisoma trivolvis</i>	<i>Amnicola sp.</i>	<i>Lymnaea stagnalis</i>	<i>Ferrissia sp.</i>	<i>Anodontoides ferussacianus</i>
<i>Valvata tricarinata</i>	X	67	55	73	50	45	45	50	18	45	27	27	9	18	9	27	9	16	9	9	9
<i>Gyraulus parvus</i>		X	36	70	78	40	56	63	22	40	33	33	11	22	11	33	11	30	11	11	11
<i>Gyraulus sp.</i>			X	56	44	37	57	37	33	22	13	13	17	33	17	29	17	11	17	17	17
<i>Pisidium sp.</i>				X	67	45	45	45	25	45	38	22	13	25	13	38	13	33	13	13	13
<i>Amnicola limosa</i>					X	71	50	71	29	50	43	43	14	29	14	43	14	37	14	14	14
<i>Lymnaea humilis</i>						X	43	25	17	43	13	33	20	40	20	33	20	29	20	20	20
<i>Promenetus exacuus</i>							X	43	40	11	33	33	20	40	20	14	20	13	20	20	0
<i>Helisoma anceps</i>								X	16	29	13	13	0	16	0	33	0	13	0	0	20
<i>Armiger crista</i>									X	17	33	25	33	33	33	25	33	20	33	33	0
Unionids										X	33	33	20	40	20	60	20	71	20	20	20
<i>Valvata lewisi</i>											X	20	33	25	33	25	33	40	33	33	0
<i>Helisoma campanulatum</i>												X	33	67	33	20	33	40	33	33	0
<i>Physa sp.</i>													X	50	100	33	100	25	100	100	0
<i>Sphaerium sp.</i>														X	50	67	50	20	50	50	50

TABLE 2b--Continued

Valvata tricarinata
 Gyraulus parvus
 Gyraulus sp.
 Pisidium sp.
 Amnicola limosa
 Lymnaea humilis
 Promenetus exacuus
 Helisoma anceps
 Armiger crista
 Unionids
 Valvata lewisi
 Helisoma campanulatum
 Physa sp.
 Sphaerium sp.
 Lampsilis luteolus
 Anodonta grandis
 Helisoma trivolvis
 Amnicola sp.
 Lymnaea stagnalis
 Ferrissia sp.
 Anodontoides ferussacianus

Dominance

Dominant (68%)	X	X	X																	
Allied (38-68%)		X		X																
Adjunct (9-38%)					X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Ancillary (10%)											X		X		X	X	X	X	X	X

Associations between taxa

First-order associations	49 C _{1a}
Second-order associations	49-30 C _{1a}
Third-order associations	29-10 C _{1a}
Not associated	10 C _{1a}

TABLE 3.--Location of studied Pleistocene molluscan fossil sites in the Missouri Coteau district, North Dakota

Site Name	$\frac{1}{4}$	$\frac{1}{4}$	Sec.	Twsp. N.	Range W.	County N.Dak.	C-14 Age y.b.p.	Ref. See Foot- note
1. Cleveland	SE	SW	17	139	67	Stutsman	11,070 \pm 300,W.956	1
2. Schauer	SE	SE	29	137	69	Stutsman	9,870 \pm 290,W.954	2,3
3. Biderman	SW	SW	9	136	69	Logan		2,4,5
4. Schlenker	NW	NW	28	135	68	Logan		2,4,5
5. Gutschmidt	NW	NW	20	135	67	Logan	9,000 \pm 300,W.1019	2,4,5
6. Brenneise	NW	NW	27	135	71	Logan		2,5
7. Kroeber	NW	NW	35	135	73	Logan		2
8. Huffnung- sthall	SW	NW	20	132	68	McIntosh	11,650 \pm 310,W.974	2,5
9. Lowenthall	SW	SE	16	132	69	McIntosh		2,5
10. Mummy Cat Slough	NW	NW	14	132	69	McIntosh		2,5
11. Clear Lake	SE	SE	21	132	70	McIntosh		2,5
12. Rosenthall No. 1	NW	NE	36	131	68	McIntosh		2
13. Rosenthall No. 2	N $\frac{1}{2}$		34	131	68	McIntosh		2,5
14. Rosenthall No. 3	NE	SE	25	131	68	McIntosh		2,5
15. Rosenthall No. 4	NW	NE	27	131	68	McIntosh		2,5

TABLE 3--Continued

Site Name	$\frac{1}{2}$ $\frac{1}{2}$	Sec.	Twsp. N.	Range W	County N. Dak.	C-14 Age y. b. p.	Ref. See Foot- note
16. Rosenthall No. 5	SE NE	6	131	68	McIntosh		2,5
17. Antelope No. 1	NW NW	30	131	67	McIntosh		2,5
18. Antelope No. 2	NE NW	16	131	67	McIntosh		2,5
19. Nue Farm	SE SE	36	130	68	McIntosh	9,620 \pm 350,W.1149	2,5
20. Iowa No. 1	SE SE	34	130	68	McIntosh		2,5
21. Iowa No. 2	SW SW	25	130	68	McIntosh		2,5
22. Podell	-- NW	14	135	66	LaMoure		2
23. Billingmeier	-- NW	12	144	75	Burleigh		2,6
24. Salt Lake	-- NE	12	144	76	Burleigh		6
25. Florence Lake	NW NW	17	144	76	Burleigh		2,6
26. Muller Ranch No. 1	NE NE	14	144	76	Burleigh		2,6
27. Muller Ranch No. 2	NW NW	14	144	76	Burleigh		2,6
28. Detlef Ranch	NE NW	22	144	76	Burleigh		2,6
29. Wheelock Ranch	NW SW	11	144	77	Burleigh		2,6
30. Painted Woods	NW NW	12	144	79	Burleigh	10,100 \pm 300,W.1434	2,6
31. Pelican Lake	NW SW	13	144	77	Burleigh		2,6
32. Boynton Ranch	SE NE	19	143	75	Burleigh	9,990 \pm 300,W.1436	2,6

TABLE 3--Continued

Site Name	$\frac{1}{2}$	$\frac{1}{2}$	Sec.	Twsp. N.	Range W	County N.Dak.	C-14 Age y.b.p.	Ref. See Foot- note
33. Toether	NE	NE	13	148	76	Sheridan		2,7
34. Neff	SE	SE	19	148	77	Sheridan		2,7
35. Prophets Mt.	NE	NE	29	147	78	Sheridan		2,7
36. Schroder	NE	SE	34	147	77	Sheridan		2,7
37. Silbermann	NE	SE	28	147	77	Sheridan		2,7
38. McCluskey	NE	NE	31	147	77	Sheridan		2,7
39. Stock	SW	NW	15	146	77	Sheridan		2,7
40. Rognle	SW	SW	34	160	96	Divide		2

References:

1. Tuthill, 1961
2. Tuthill, 1963
3. Winters, 1963
4. Clayton, 1961
5. Clayton, 1962
6. Tuthill, 1965
7. Sherrod, 1963

TABLE 4.--Association matrix for a comparison of the late Wisconsinan molluscan faunules of the Missouri Coteau in North Dakota, Dawley's modern Minnesota assemblages, and the modern Missouri Coteau molluscan fauna. (Cjac).

	Modern North Dakota	<u>Modern Minnesota Assemblages</u> ¹							
		Small streams	Small rivers	Medium-sized rivers	Large rivers	Ponds	Softwater lakes	Medium-hardwater lakes	Hardwater prairie lakes
Entire late Wisconsinan molluscan fauna from the Missouri Coteau	67	67	37	18	11	25	48	65	50
Late Wisconsinan molluscan fauna from lacustrine sediments only	75	57	30	19	10	27	46	57	52
Late Wisconsinan molluscan fauna from fluvial sediments only	61	62	33	19	13	21	50	69	45
Modern molluscan fauna of North Dakota in the Missouri Coteau	X	53	21	15	7	33	48	39	42

¹Dawley (1947).

TABLE 5.--Comparison of late Wisconsin Missouri Coteau faunules with the characteristic assemblages of eight of Dawley's (1947) Modern Molluscan Habitats in Minnesota. (Jaccard's coefficient of faunal similarity, C_{je} , is employed as the statistical method of comparison.)

Late Wisconsin faunules from the Missouri Coteau ¹	Dawley's Habitat Types ²								Types of sediments from which faunules were taken
	1	2	3	4	5	6	7	8	
A. Cleveland	46	25	23	11	13	31	34	45	Sand, gravel
B. Schauer	38	20	19	10	21	33	44	50	Clay, silt, marl
C. Riderman	44	23	21	5	7	30	40	38	Clay, silt
D. Schlenker	38	29	27	10	31	33	44	46	Silt, clay
E. Gutschmidt	24	9	8	6	0	20	21	30	Silt, clay
F. Brenneise	25	14	13	11	25	22	31	31	Marl
G. Kroeber	50	33	31	14	46	25	56	61	Marl
H. Huffnungsthal	46	27	33	16	13	24	34	26	Marl
I. Lowenthal	Unionids only - no comp. possible								
J. Mummy Cat Slough	47	28	27	10	31	40	44	58	Marl
K. Clear Lake	40	20	33	10	23	36	38	50	Marl
L. Rosenthal 1	36	17	23	11	8	17	34	23	Marl
M. Rosenthal 2	40	21	20	10	23	36	47	50	Marl
N. Rosenthal 3	50	31	28	16	45	36	47	63	Marl
O. Rosenthal 4	38	17	15	12	18	25	27	36	Marl
P. Rosenthal 5	15	10	18	14	0	6	14	9	Sand, gravel
Q. Antelope 1	40	31	28	5	33	36	47	63	Silt, clay
R. Antelope 2	13	8	7	5	18	16	19	36	Marl
S. Nue Farm	59	47	40	21	30	45	75	70	Sand, gravel, till balls, marl
T. Iowa 1	43	18	21	11	25	30	31	54	Clay, silt
U. Iowa 2	31	18	13	13	9	27	35	40	Silt
V. Podell	44	31	28	15	54	26	44	58	Peat
W. Billingmeier	8	0	0	0	0	0	0	0	Marl
X. Field	38	27	15	5	8	25	27	36	Silt
Y. Florence Lake	50	33	31	11	25	38	40	54	Gravel, sand
Z. Muller 1	36	15	14	11	27	31	34	45	Silt
AA. Muller 2	36	15	14	11	13	24	25	33	Gravel, sand
AB. Detlef	36	25	23	11	13	40	42	60	Gravel, sand
AC. Wheelock	50	31	28	10	13	43	47	63	Silt
AD. Painted Woods	57	28	27	5	14	40	44	72	Silt
AE. Pelican Lake	15	0	0	7	11	13	14	20	Marl
AF. Boynton	43	14	13	5	7	30	31	38	Silt
AG. Toether	15	0	0	7	11	13	14	20	Clay, silt
AI. Prophets	14	9	8	6	22	6	6	8	Clay
AJ. Schroeder	20	0	0	5	18	16	27	25	Silt
AK. Silbermann	8	0	0	7	0	7	7	10	Gravel, sand
AL. McCluskey	15	0	0	7	11	13	14	20	Clay

TABLE 5--Continued

Late Wisconsin faunules from the Missouri Coteau ¹	Dawley's Habitat Types ²								Types of sedi- ments from which faunules were taken
	1	2	3	4	5	6	7	8	
AM. Stock	31	8	8	6	9	19	20	40	Clay, silt Sand
AN. Rognle	26	15	15	19	44	16	35	36	
1. Number of highest value occurring in each column	9	0	1	0	2	0	3	24	
2. Number of highest two values occurring in each column	24	0	1	1	3	0	14	32	
3. Number of highest three values occurring in each column	35	2	3	2	5	2	35	34	
4. Number of highest three values occurring in each column excluding values below 34 and those more distant than 15 from highest	23	0	0	1	2	1	21	25	

¹Sites are described in Tuthill, 1963b.

- ²1. Small streams
 2. Small rivers
 3. Medium-sized rivers
 4. Large rivers
 5. Ponds
 6. Soft-water lakes
 7. Medium-hard-water lakes
 8. Hard-water prairie lakes

TABLE 6.--Water quality of selected water bodies in the Martin-Bering Rivers region, Alaska

Name	Water Quality																
	Turbidity ppm silica	Surface temp. °C.	pH	Diss. CO ₂ ppm	Diss. O ₂ ppm	Diss. Cl ₂ ppm	Diss. N ₂ ppm	Diss. SO ₃ ppm	Diss. SO ₄ ppm	Diss. NO ₂ ppm	Diss. NO ₃ ppm	Diss. Fe ppm	Total diss. Carb. ppm	Diss. Cu	Diss. SiO ₂ ppm	Phosphates ppm	
Constance Lake	0	<u>8.9</u> 4 2.8	<u>6.0</u> 4 0	<u>3.5</u> 4 0.1	(Top number is the mean value, middle number is the number of trials, and the bottom number is the difference between the highest and lowest observed value.)												
Martin Lake	0	<u>14.0</u>	<u>5.8</u> 21 5.9	<u>3.5</u> 12 3.1													
Peat Ponds	0	<u>22.0</u> 12 4.1	<u>5.0</u> 12 0.2	<u>3.8</u> 2 0.6													
Outlet of Peat Pond	0	<u>16.0</u> 18	<u>4.9</u> 18	<u>6.2</u> 2													
Deadwood Lake	<u>51</u> 16 11	<u>14.6</u> 30 2.1	<u>7.4</u> 16 0.4	<u>4.6</u> 3 0.3	<u>5.0</u> 3 2.1	0 3 0	<u>3.1</u> 3 4.8	<u>1.8</u> 3 4.0	<u>2.7</u> 3 2.1	<u>0.2</u> 3 0.7	<u>16.0</u> 3 12.0	0 3 0	<u>0.6</u> 3 1.2	<u>0.4</u> 3 0.2			
Black Lake	0 5 0	<u>13.9</u> 42 6.5	<u>6.8</u> 18 0.7	<u>7.5</u> 12 0.4	<u>11.5</u> 2 1.6	0 3 0	<u>1.5</u> 3 0.2	<u>6.0</u> 3 0	<u>3.8</u> 3 7.6	<u>0.3</u> 3 0.5	<u>7</u> 3 0	0 3 0	<u>0.2</u> 3 0	<u>0.9</u> 3 0.6			
Miller Lake	<u>621</u>	<u>2.7</u>	<u>8.9</u>	<u>2.0</u>					<u>11.7</u>	0	<u>0.3</u>	<u>30.0</u>	0	<u>14.8</u>	0		

(all data from Callender (1964), number of trials unknown)

TABLE 6--Continued

Name	Water Quality															
	Turbidity ppm silica	Surface temp. °C.	pH	Diss. CO ₂ ppm	Diss. O ₂ ppm	Diss. Cl ₂ ppm	Diss. N ₂ ppm	Diss. SO ₃ ppm	Diss. SO ₄ ppm	Diss. NO ₂ ppm	Diss. NO ₃ ppm	Diss. Fe ppm	Total diss. Carb. ppm	Diss. Cu	Diss. SiO ₂ ppm	Phosphates ppm
Ice Sink- hole Lakes	<u>362</u> 9 37	<u>1.8</u> 77 0.4	<u>7.4</u> 9 0.2		<u>6.3</u> 3 0.4			<u>0</u> 1	<u>0</u> 1	<u>0</u> 3 0	<u>0</u> 3 0	<u>1.7</u> 3 0.1	<u>2.6</u> 9 0.3	<u>0</u> 1	<u>1.6</u> 9 2.2	<u>0</u> 3 0
Martin River	535	<u>1.8</u> 77 0.4	7.4		6.3								46.3			
Pistyll Lake	<u>0</u>	<u>12.4</u> 14 0.6	<u>7.5</u> 2 0.5	<u>4.1</u> 2 0.3					<u>5.0</u> 2 4.0		<u>2.6</u> 2 0.2	<u>0.1</u> 2 0	<u>28.4</u> 2 3.6		<u>0</u> 2 0	
Lake Tokun	<u>0</u>	<u>14.3</u> 35 6.8	<u>7.2</u> 26 0.4	<u>2.8</u> 13 3.1		<u>0</u> 2 0	<u>0</u> 2 0	<u>3.0</u> 2 2.1	<u>2.5</u> 2 1.0	<u>0</u> 2 0	<u>3.7</u> 2 0	<u>0.9</u> 2 1.3	<u>28.0</u> 2 24.0	<u>0.3</u> 2 0.6	<u>1.9</u> 2 0	<u>0</u> 2 0
Bee Lake	<u>56</u> 7 23	<u>8.5</u> 13 3.0	<u>7.2</u> 7 0.2	<u>2.1</u> 7 2.1	<u>4.2</u> 1				<u>0.1</u> 2 0.2				<u>6.6</u> 3 8.6		<u>1.2</u> 1	
OH Lake	<u>68</u> 1	9.5	7.2	3.5	5.9				0.2				7.1		2.3	

TABLE 6--Continued

Name	Water Quality															
	turbidity ppm silica	Surface temp. °C.	pH	Diss. CO ₂ ppm	Diss. O ₂ ppm	Diss. Cl ₂ ppm	Diss. N ₂ ppm	Diss. SO ₃ ppm	Diss. SO ₄ ppm	Diss. NO ₂ ppm	Diss. NO ₃ ppm	Diss. Fe ppm	Total diss. Carb. ppm	Diss. Cu	Diss. SiO ₂ ppm	Phosphates ppm
L. Char-	<u>54</u>	<u>9.9</u>	<u>7.1</u>	<u>2.6</u>	<u>3.9</u>	<u>0</u>		<u>1.5</u>	<u>5.8</u>	<u>0</u>	<u>0</u>	<u>0.1</u>	<u>47.9</u>	<u>0</u>	<u>1.9</u>	<u>0</u>
lotte	<u>110</u>	<u>51</u>	<u>28</u>	<u>24</u>	<u>13</u>	<u>2</u>		<u>12</u>	<u>12</u>	<u>12</u>	<u>12</u>	<u>12</u>	<u>13</u>	<u>12</u>	<u>2</u>	<u>5</u>
	<u>87</u>	<u>14.8</u>	<u>0.6</u>	<u>4.7</u>	<u>4.4</u>	<u>0</u>		<u>3.8</u>	<u>10.6</u>	<u>0</u>	<u>0</u>	<u>0.5</u>	<u>27.0</u>	<u>0</u>	<u>0.6</u>	<u>0</u>
Glacier	<u>138</u>	<u>1.4</u>	<u>7.1</u>													
Stream at	<u>81</u>	<u>182</u>	<u>34</u>													
L. Char.	<u>279</u>	<u>6.5</u>	<u>0.4</u>													
Clear Str.	<u>0</u>	<u>16.2</u>	<u>8.1</u>		<u>6.0</u>			<u>7.2</u>	<u>9.0</u>			<u>0.1</u>	<u>6.0</u>		<u>6.7</u>	
at L.Char.		<u>27</u>	<u>12</u>		<u>1</u>			<u>2</u>	<u>2</u>			<u>2</u>	<u>2</u>		<u>2</u>	
from Char-		<u>7.1</u>	<u>0.8</u>					<u>3.4</u>	<u>1.0</u>			<u>0</u>	<u>0</u>		<u>14</u>	
lotte Ridge																
Clear Str.	<u>0</u>	<u>11.0</u>	<u>7.3</u>					<u>0</u>	<u>7.2</u>	<u>0</u>	<u>0</u>	<u>0.2</u>	<u>17.8</u>		<u>3.2</u>	
at L.Char.		<u>3</u>	<u>3</u>					<u>3</u>	<u>3</u>	<u>3</u>	<u>3</u>	<u>3</u>	<u>3</u>		<u>3</u>	
from Mt. on		<u>5.9</u>	<u>0.2</u>					<u>0</u>	<u>2</u>	<u>0</u>	<u>0</u>	<u>0.5</u>	<u>6.1</u>		<u>0.3</u>	
N.side of L.																

TABLE 7.--Distribution of the nonmarine molluscan taxa from the Martin-Bering Rivers region, Alaska, in the defined potential habitats

Taxa	Ecologic Characteristics of the Habitat Types (see note at bottom)																									
	Type of Water												Salt	Peat	Spruce	Alders						Willow	Grass	Outwash	Sand	Frequency
	S	R	S	R	S	R	S	R	S	R	S	R				E	P	E	P	E	P					
	7pH		7pH		Neutral				Cool		Cold		Rock	Till		Glac.		Ice								
	Warm	Clear	Warm	Clear	Turbid																					
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23				
Anodonta beringiana		X																						1		
Pisidium compressum	X	X			X																			3		
Pisidium casternum	X																							1		
Pisidium milium	X																							1		
Sphaerium nitidum					X																			1		
Valvata mergella	X	X			X	X																		4		
Lymnaea humilis	X	X			X	X	X	X												X				7		
Lymnaea palustris	X	X									X													3		
Menetus callio-glyptus	X				X	X	X	X																5		
Gyraulus parvus	X	X			X	X																		4		
Vespericola columbiana																							X	1		
Haplotrema sportella																							X	1		
Euconulus fulvus alaskensis													X		X		X			X				4		
Vitrina alaskana																	X			X				2		
Deroceras laeve													X				X			X		X		4		

TABLE 7--Continued

Taxa	Ecologic Characteristics of the Habitat Types (see note at bottom)																										
	Type of Water										Salt	Peat	Spruce	Alders						Willow	Grass	Outwash	Sand	Frequency			
	S	R	S	R	S	R	S	R	S	R				E	P	E	P	E	P								
	7pH		7pH		Neutral		Warm		Cool					Cold		Rock		Till							Glac.		
	Clear		Turbid															Ice									
1	2	3	4	5	6	7	8	9	10	14				15	16	17	18	19	20						21	22	23
<i>Discus cronkhitei</i>														X		X		X			X					4	
<i>Punctum</i> cf. <i>P.</i> <i>randolphi</i>														X				X			X					3	
<i>Prophysaon</i> cf. <i>P.</i> <i>andersoni</i>																		X			X					2	
<i>Succinea</i> cf. <i>S.</i> <i>rusticana</i>																										X	1
<i>Oxyloma</i> cf. <i>O.</i> <i>retusa</i>																										X	1
<i>Vertigo ovata</i>														X													1
<i>Vertigo modesta</i>																										X	1
<i>Vertigo columbiana</i>														X		X		X			X						4
Number of taxa in faunule	9	5	0	0	6	4	2	2	0	0	1	0	0	5	0	3	0	7	0	0	0	7	0	5			

Key to symbols at top of columns - S=standing water. R=running water. 7pH and Neutral=water that is at or near pH of 7. Warm=water above 10°C. Cool=water between 5 and 10°C. Cold=water between 0 and 5°C. Clear=0ppm turbidity. Turbid=20 or more ppm turbidity. Salt=brackish water in high tidal pools. Peat=vegetative detritus in muskegs. Spruce=understory and floor of Pacific Rain Forest, dominated by Sitka spruce. E=established growths of more than 6 years of age. P=pioneer growths of less than 7 years of age.

TABLE 7--Continued

Rock=bedrock. Till=surfaces underlain by till. Glac. Ice=drift-insulated stagnant glacier ice. Alders=leaf litter under alders. Willows=leaf litter under willows. Grass=grassy lake borders. Outwash=surfaces underlain by outwash gravels. Sand=vegetation captured sand dunes. Frequency=the number of habitat types in which a taxon occurs.

Numbers at the column heads indicate the potential habitat type as identified by these numbers in the text and on Figure 9.

TABLE 9.--Similarity matrix for the comparison of the late Wisconsinan molluscan fauna from the Missouri Coteau district in North Dakota and the modern nonmarine molluscan habitat assemblages of the Martin-Copper-Bering Rivers region, Alaska, with respect to the percentage of the total faunas included in four physiological groups

Habitat types	Comparison (C _{je}) of species	Comparison (C _{je}) of Genera
1. Clear, warm, neutral, standing water	24	40
2. Clear, warm, neutral, running water	20	27
5. Turbid, warm, neutral, standing water	18	31
6. Turbid, warm, neutral, running water	10	19
7. Turbid, cool, neutral, standing water	5	13
8. Turbid, cool, neutral, running water	5	13
11. High, tidal pools	5 C _{jac}	7 C _{jac}

TABLE 10.--Similarity matrix for the comparison of the late Wisconsinan molluscan fauna from the Missouri Coteau district in North Dakota and the modern aquatic nonmarine molluscan fauna of the Martin-Copper-Bering Rivers region, Alaska, with respect to the percentage of the total faunas included in four physiological groups

Percent of fauna	Unionids (Bivalves)	Pisidids (Bivalves)	Branchiates (Gastropods)	Pulmonates (Gastropods)
Late Wisconsinan North Dakota	20.0	13.3	15.8	58.0
Modern Alaskan	10.0	40.0	10.0	40.0

TABLE 11.--Biometrics of selected specimens of Alaskan nonmarine mollusks. Taxa appear in alphabetical order. All measurements are given in mm.

	Whorls	Height	Width	Aperture Height Interior	Aperture Height Exterior	Aperture Width Interior	Aperture Width Exterior	Number Measured (N)	Catalog Number (UND-)
1. <u>Anodonta beringiana.</u>									
Means (M)		41	87					9(H)	
Extremes (E)		38-46	76-93					11(W)	
standard deviations(s)		0.980	2.81						
Hypotype:	Left valve	40.5	78.6						4002
2. <u>Deroceras laeve.</u> Not measured, not figured.									
3. <u>Discus cronkhitei.</u>									
Hypotype:	4	2.6	5.2						4010
4. <u>Euconulus fulvus alaskensis.</u>									
M	3½	1.6	1.9					11	
E	2½-4 3/4	1.0-2.9	1.2-3.3						
s	-	0.611	0.871						
Hypotype:	4¼	1.3	2.8						4003
5. <u>Gyraulus parvus.</u>									
M	3½	1.4	4.1					10	
E	3½-4	1.2-2.0	3.7-4.6						
s	-	0.549	0.943						
Hypotype:	3 3/4	2.0	4.4						4011

TABLE 11--Continued

	Whorls	Height	Width	Aperture Height Interior	Aperture Height Exterior	Aperture Width Interior	Aperture Width Exterior	Number Measured (N)	Catalog Number (UND-)
6. <u>Haplotrema columbiana.</u>									
M	6	7.5	16.4		6.6	7.3	7.7	9	
E	5½-7	5.8-8.5	12.2-20.6		4.0-6.1	5.3-10.5	5.3-11.9		
s	-	0.892	1.230		0.000	0.283	1.042		
Hypotype:	5½	7.4	20.5		4.0	10.5	11.9		4009
7. <u>Lymnaea humilis.</u>									
M	4	9.2	5.6		5.2		3.5	14	
E	3½-4½	6.6-9.9	4.3-6.2		4.1-6.0		3.0-4.4		
s	-	1.290	0.549		2.000		1.987		
Hypotype:	4½	9.0	5.0		4.9		2.9		4006
8. <u>Lymnaea palustris.</u>									
M	5	17.8	9.4		9.3		6.3	420	
E	4-6½	14.0-22.5	7.0-12.0		7.0-13.0		5.0-8.5		
s	-	1.130	0.715		0.422		0.682		
Hypotype:	6	19.3	10.2		9.5		6.2		4012
9. <u>Menetus callioglyptus.</u>									
M	3 3/4	2.5	5.8		2.2		3.1	10	
E	3½-4	1.8-3.0	5.5-4.4		1.9-2.8		2.2-3.6		
s	-	0.844	0.472		0.521		0.396		
Hypotype:	3½	2.6	5.7		2.3		2.7		4013

TABLE 11--Continued

	Whorls	Height	Width	Aperture Height Interior	Aperture Height Exterior	Aperture Width Interior	Aperture Width Exterior	Number Measured (N)	Catalog Number (UND-)
10. <u>Oxyloma</u> cf. <u>O. retusa</u> .									
M	2 3/4	7.3	4.8		5.3		3.5	3	
E	2 1/4-3	6.1-9.6	3.6-6.9		4.6-6.6		2.9-4.5		
Not figured.									
11. <u>Pisidium casternum</u> , <u>P. milium</u> , and <u>P. compressum</u> not in my possession at time of this writing.									
12. <u>Prophysaon</u> cf. <u>P. andersoni</u> not measured and not figured.									
13. <u>Punctum</u> cf. <u>P. randolphi</u> not measured and not figured.									
14. <u>Sphaerium nitidum</u> .									
Hypotype:	Right valve	4.7	5.3						4001
15. <u>Succinea</u> cf. <u>S. rusticana</u> var. <u>alaskana</u> .									
M	2 3/4	8.4	4.8		6.0		3.4	4	
E	2 1/4-3	6.0-8.7	4.5-5.1		3.9-6.2		2.8-4.3		
Hypotype:	2 3/4	8.5	4.4		6.0		3.3		4007
16. <u>Valvata mergella</u> .									
M	3 1/2	2.6	4.3					18	
E	2 3/4-3 3/4	1.8-3.6	3.0-5.3						
s	-	0.548	0.783						
Hypotype:	2 3/4	1.8	3.1						4000

TABLE 11--Continued

	Whorls	Height	Width	Aperture Height Interior	Aperture Height Exterior	Aperture Width Interior	Aperture Width Exterior	Number Measured (N)	Catalog Number (UND-)
17. <u>Vespericola sportella.</u>									
M	6	11.2	15.6	6.5	9.1	5.1	6.2	14	
E	6-6½	9.1-12.3	14.0-16.6	4.3-5.6	5.5-6.7	6.0-7.0	8.8-10.3		
s	-	0.466	0.603	0.183	0.387	0.466	0.532		
Hypotype:	6½	12.3	16.6	4.9	6.5	6.7	10.3		4008
18. <u>Vertigo columbiana.</u>									
M	4½	2.0	1.4		0.7		0.8	37	
E	2 3/4-5½	0.9-2.8	1.1-1.6		0.4-1.1		0.5-1.0		
s	-	0.539	0.641		0.812		0.436		
Hypotype:	5½	2.4	1.4		0.8		0.8		4004
19. <u>Vertigo modesta.</u>									
M	5½	2.1	1.3					11	
E	4½-5½	1.9-2.4	1.3-1.4						
Not figured.									
20. <u>Vertigo ovata.</u> Specimens not in my possession (Bickley, in press).									
21. <u>Vitrina alaskana.</u>									
Hypotype:	2	2.8	4.4						4005

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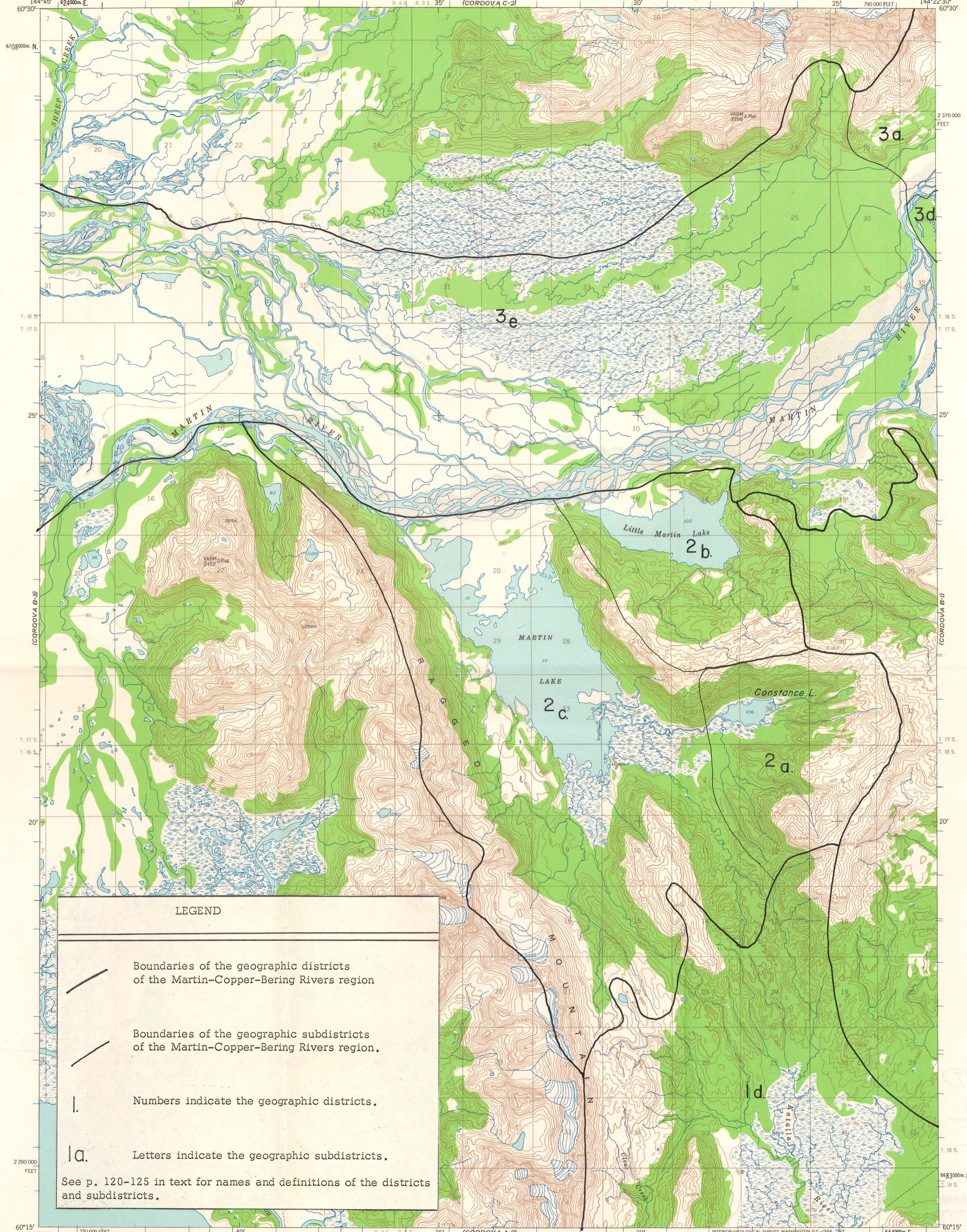
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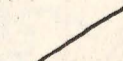


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(CORDOVA C-2)

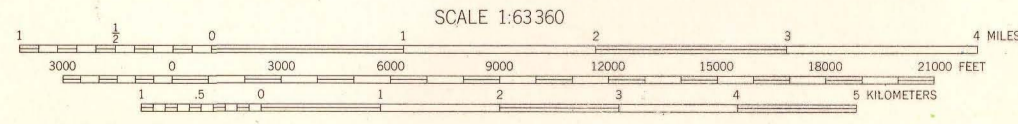
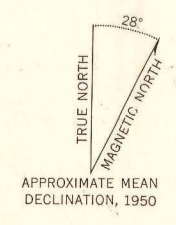
(CORDOVA C-1)



LEGEND

-  Boundaries of the geographic districts of the Martin-Copper-Bering Rivers region
 -  Boundaries of the geographic subdistricts of the Martin-Copper-Bering Rivers region.
 -  Numbers indicate the geographic districts.
 -  Letters indicate the geographic subdistricts.
- See p. 120-125 in text for names and definitions of the districts and subdistricts.

Mapped, edited, and published by the Geological Survey
Control by USGS and USC&GS
Topography by photogrammetric methods from aerial photographs taken 1950. Map not field checked
Universal Transverse Mercator projection, 1927 North American datum 10,000-foot grid based on Alaska coordinate system, zone 3 1000-meter Universal Transverse Mercator grid ticks, zone 6, shown in blue
Land lines represent unsurveyed and unmarked locations predetermined by the Bureau of Land Management Folios CR-6 and CR-10, Copper River Meridian
Swamps, as portrayed, indicate only the wetter areas, usually of low relief, as interpreted from aerial photographs
Entire land area is within the Chugach National Forest

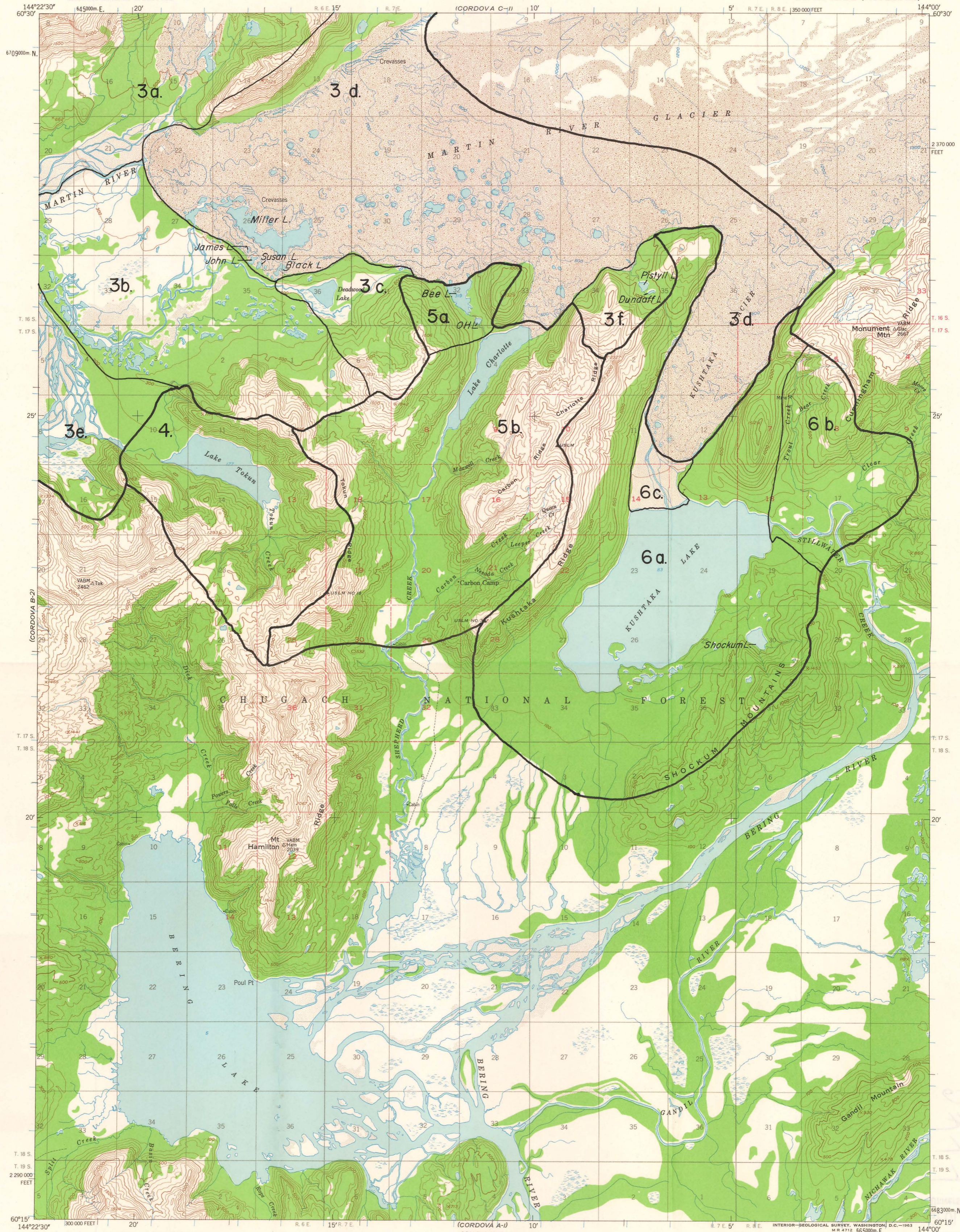


CONTOUR INTERVAL 100 FEET
DOTTED LINES REPRESENT 50-FOOT CONTOURS
DATUM IS MEAN SEA LEVEL
SHORELINE SHOWN REPRESENTS THE APPROXIMATE LINE OF MEAN HIGH WATER
THE AVERAGE RANGE OF TIDE IS APPROXIMATELY 8 FEET
FOR SALE BY U. S. GEOLOGICAL SURVEY
FAIRBANKS, ALASKA DENVER 25, COLORADO WASHINGTON 25, D. C.
A FOLDER DESCRIBING TOPOGRAPHIC MAPS AND SYMBOLS IS AVAILABLE ON REQUEST

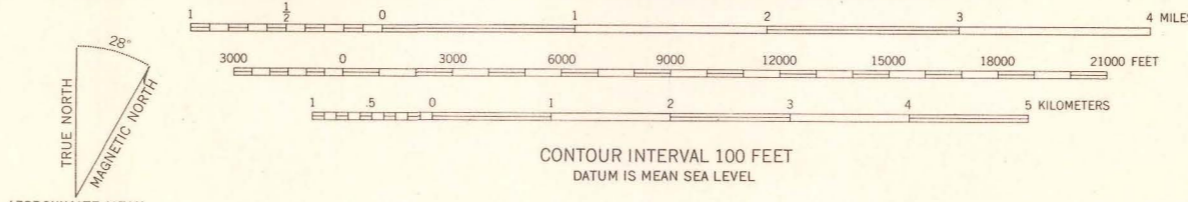


ROAD CLASSIFICATION
Trails
CORDOVA (B-2), ALASKA
N6015-W14422.5/15X22.5
1950
MINOR REVISIONS 1963

TUTHILL 1969



Mapped, edited, and published by the Geological Survey
Control by USGS and USC&GS
Topography by photogrammetric methods from aerial photographs
taken 1950, field annotated 1951. Map not field checked
Universal Transverse Mercator projection, 1927 North American datum
10,000-foot grid based on Alaska coordinate system, zone 3
1000-meter Universal Transverse Mercator grid ticks,
zone 6, shown in blue
Land lines printed in gray represent unsurveyed and
unmarked locations predetermined by the Bureau of
Land Management. Folios CR-6 and CR-10, Copper River Meridian
Dashed red land lines indicate approximate locations
of existing ground surveys
Swamps, as portrayed, indicate only the wetter areas,
usually of low relief, as interpreted from aerial photographs



CORDOVA (B-1), ALASKA
N6015-W14400/15X22.5
1951
MINOR REVISIONS 1962

FOR SALE BY U. S. GEOLOGICAL SURVEY
FAIRBANKS, ALASKA DENVER 25, COLORADO WASHINGTON 25, D. C.
A FOLDER DESCRIBING TOPOGRAPHIC MAPS AND SYMBOLS IS AVAILABLE ON REQUEST

ROAD CLASSIFICATION
Trails

TUTHILL 1969

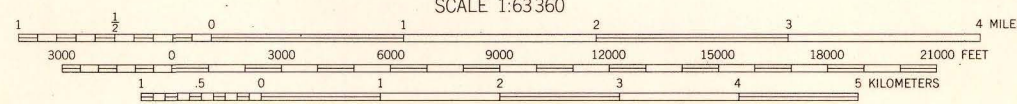
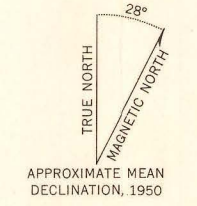
(CORDOVA B-3)
144°45'
60°15'

(CORDOVA B-2)

(CORDOVA B-1)
144°22'30"
60°15'



Mapped, edited, and published by the Geological Survey
Control by USGS and USC&GS
Topography by photogrammetric methods from aerial photographs taken 1950. Map not field checked
Selected hydrographic data compiled from USC&GS Chart 8513 (1960) (1:100,000 scale). This information is not intended for navigational purposes
Universal Transverse Mercator projection, 1927 North American datum 10,000-foot grid based on Alaska coordinate system, zone 3 1000-meter Universal Transverse Mercator grid ticks, zone 6, shown in blue
Land lines represent unsurveyed and unmarked locations predetermined by the Bureau of Land Management. Folio CR-10, Copper River Meridian
Swamps, as portrayed, indicate only the wetter areas, usually of low relief, as interpreted from aerial photographs
Entire land area is within the Chugach National Forest



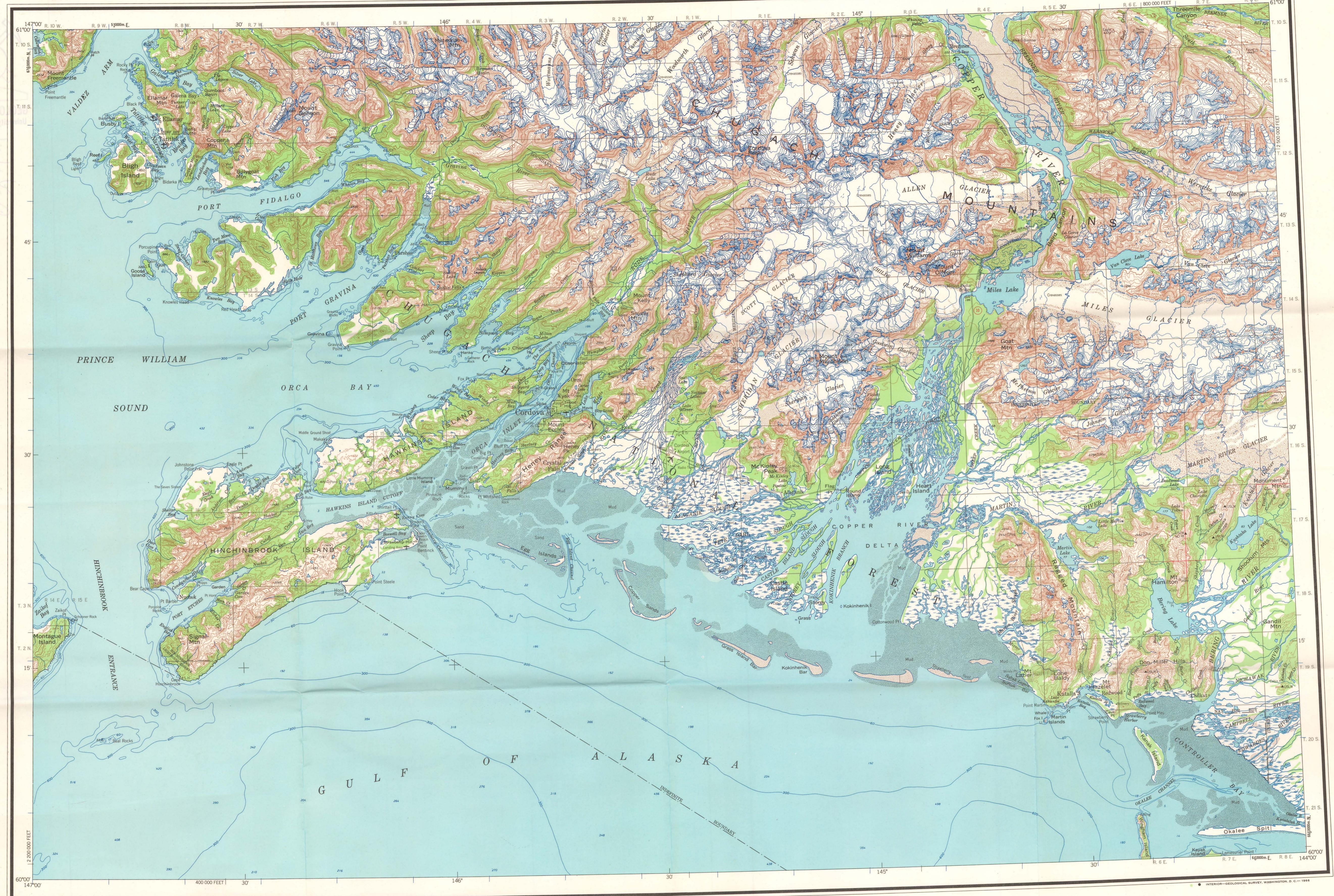
SCALE 1:63 360
CONTOUR INTERVAL 100 FEET
DATUM IS MEAN SEA LEVEL
DEPTH CURVES AND SOUNDINGS IN FEET-DATUM IS MEAN LOWER LOW WATER
SHORELINE SHOWN REPRESENTS THE APPROXIMATE LINE OF MEAN HIGH WATER
THE AVERAGE RANGE OF TIDE IS APPROXIMATELY 8 FEET
FOR SALE BY U. S. GEOLOGICAL SURVEY
FAIRBANKS, ALASKA DENVER 25, COLORADO WASHINGTON 25, D. C.
A FOLDER DESCRIBING TOPOGRAPHIC MAPS AND SYMBOLS IS AVAILABLE ON REQUEST



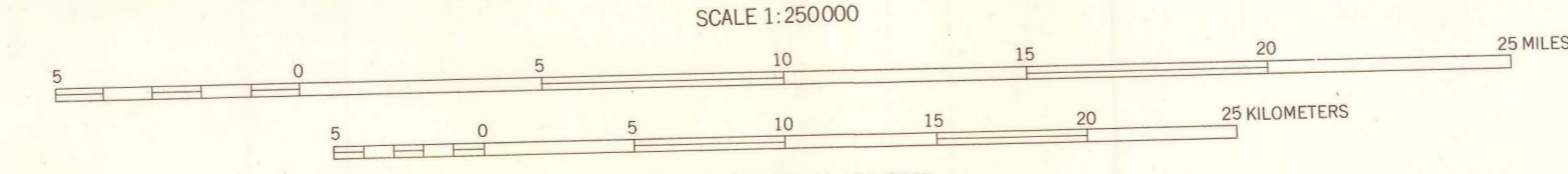
ROAD CLASSIFICATION
Trails

CORDOVA (A-2), ALASKA
N6000-W14422.5/15X22.5
1950
MINOR REVISIONS 1963

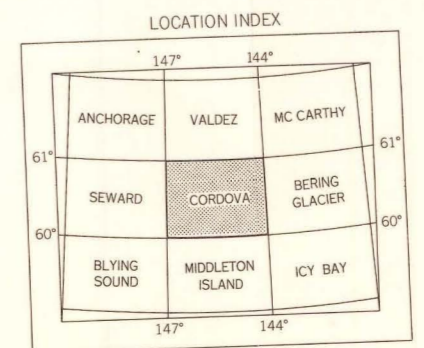
TUTHILL 1969



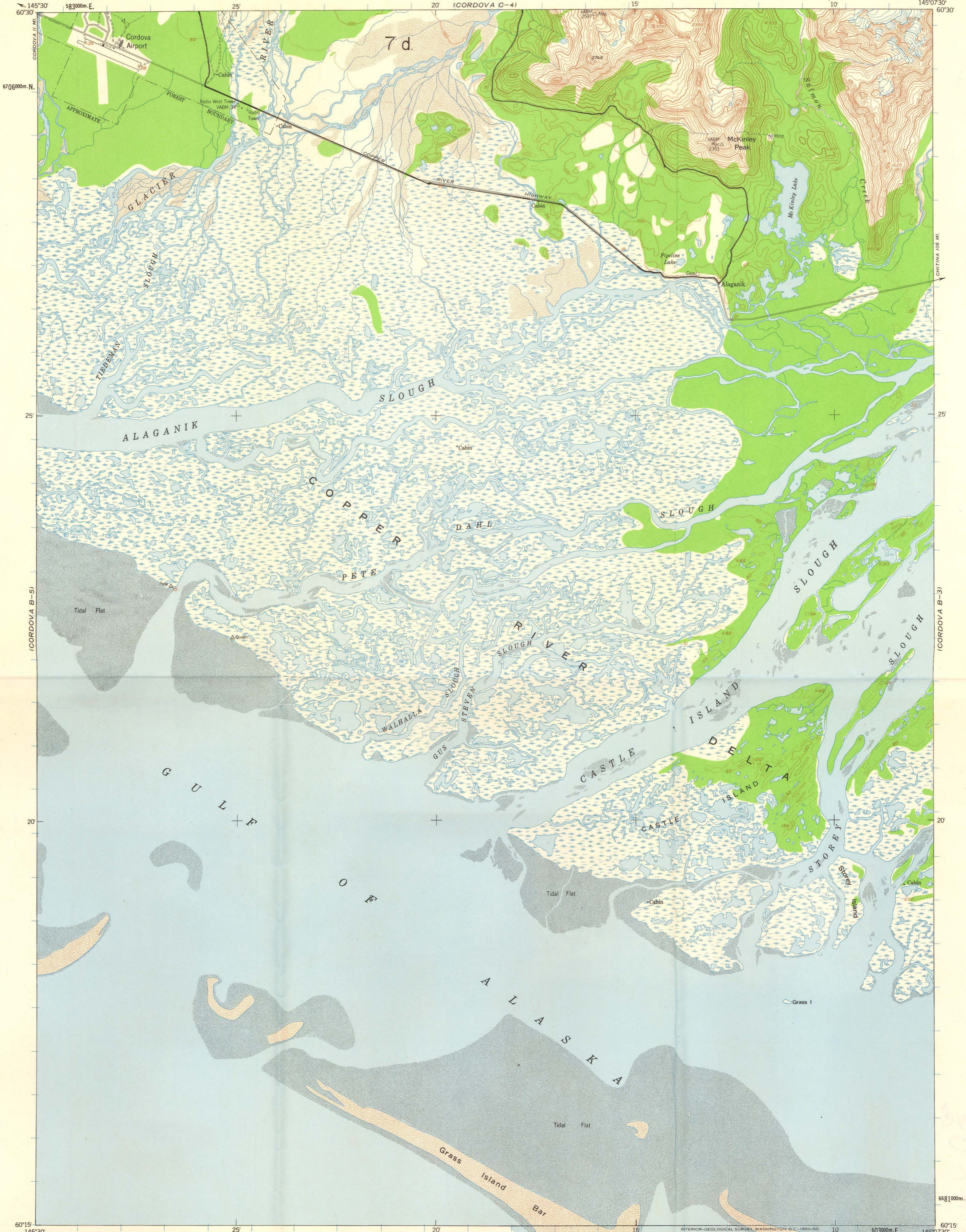
MAPPED, EDITED, AND PUBLISHED BY THE GEOLOGICAL SURVEY
CONTROL BY USGS, USC&GS, AND USCE
COMPILED IN 1964 FROM U.S. GEOLOGICAL SURVEY 1:63 360 SCALE MAPS,
SURVEYED 1950-1963, AND 1959 MAP NOT FIELD CHECKED
SELECTED HYDROGRAPHIC DATA COMPILED FROM USCGS CHARTS 8502 (1964),
8513 (1963), 8519 (1963), 8520 (1964), 8525 (1964), AND 8551 (1963)
THIS INFORMATION IS NOT INTENDED FOR NAVIGATIONAL PURPOSES
UNIVERSAL TRANSVERSE MERCATOR PROJECTION, 1927 NORTH AMERICAN DATUM
100,000 FOOT GRID BASED ON ALASKA COORDINATE SYSTEM, ZONE 3
10,000-METER UNIVERSAL TRANSVERSE MERCATOR GRID TICKS,
ZONE 6, SHOWN IN BLUE
GRAY LAND LINES REPRESENT UNSURVEYED AND UNMARKED LOCATIONS
PREDETERMINED BY THE BUREAU OF LAND MANAGEMENT
FOLIOS CR 5, CR 6, AND CR 10, COPPER RIVER MERIDIAN,
AND FOLIO S 14, SEWARD MERIDIAN
SWAMPS, AS PORTRAYED, INDICATE ONLY THE WETTER AREAS,
USUALLY OF LOW RELIEF, AS INTERPRETED FROM AERIAL PHOTOGRAPHS
LAKE ELEVATIONS ARE UNCHECKED



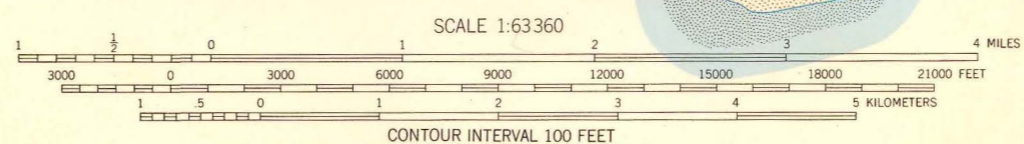
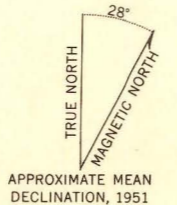
CONTOUR INTERVAL 200 FEET
DATUM IS MEAN SEA LEVEL
DEPTH CURVES AND SOUNDINGS IN FEET—DATUM IS MEAN LOWER LOW WATER
SHORELINE SHOWN REPRESENTS THE APPROXIMATE LINE OF MEAN HIGH WATER
1959 MAGNETIC DECLINATION AT SOUTH EDGE OF SHEET VARIES FROM 26°30' TO 27°30' EAST
THIS MAP IS AVAILABLE IN BOTH SHADED RELIEF AND CONTOUR EDITIONS
FOR SALE BY U.S. GEOLOGICAL SURVEY
FAIRBANKS, ALASKA, 99701, DENVER, COLORADO 80225, OR WASHINGTON, D.C. 20242
A FOLDER DESCRIBING TOPOGRAPHIC MAPS AND SYMBOLS IS AVAILABLE ON REQUEST



ROAD CLASSIFICATION
LIGHT-DUTY UNIMPROVED DIRT -----
STATE ROUTE ○
CORDOVA, ALASKA
N6000-W14400/60K180
1959



Mapped, edited, and published by the Geological Survey
Control by USGS and USC&GS
Topography from aerial photographs by photogrammetric
methods 1958. Aerial photographs taken 1950 and 1952,
field annotated 1951. Map not field checked
Hydrography compiled from USC&GS chart 8502
(1:969 761 scale, 1958) and from aerial photographs
Universal Transverse Mercator projection
1927 North American datum
1000-meter Universal Transverse Mercator grid ticks,
zone 6, shown in blue
Entire land area is within the Chugach National Forest except the
Cordova airport withdrawal area
Swamps, as portrayed, indicate only the wetter areas,
usually of low relief, as interpreted from aerial photographs
Unchecked elevations are shown in brown and blue



CONTOUR INTERVAL 100 FEET
DOTTED LINES REPRESENT 50 FOOT CONTOURS
DATUM IS MEAN SEA LEVEL
SHORELINE SHOWN REPRESENTS THE APPROXIMATE LINE OF MEAN HIGH WATER
THE MEAN RANGE OF TIDE IS APPROXIMATELY 8 FEET



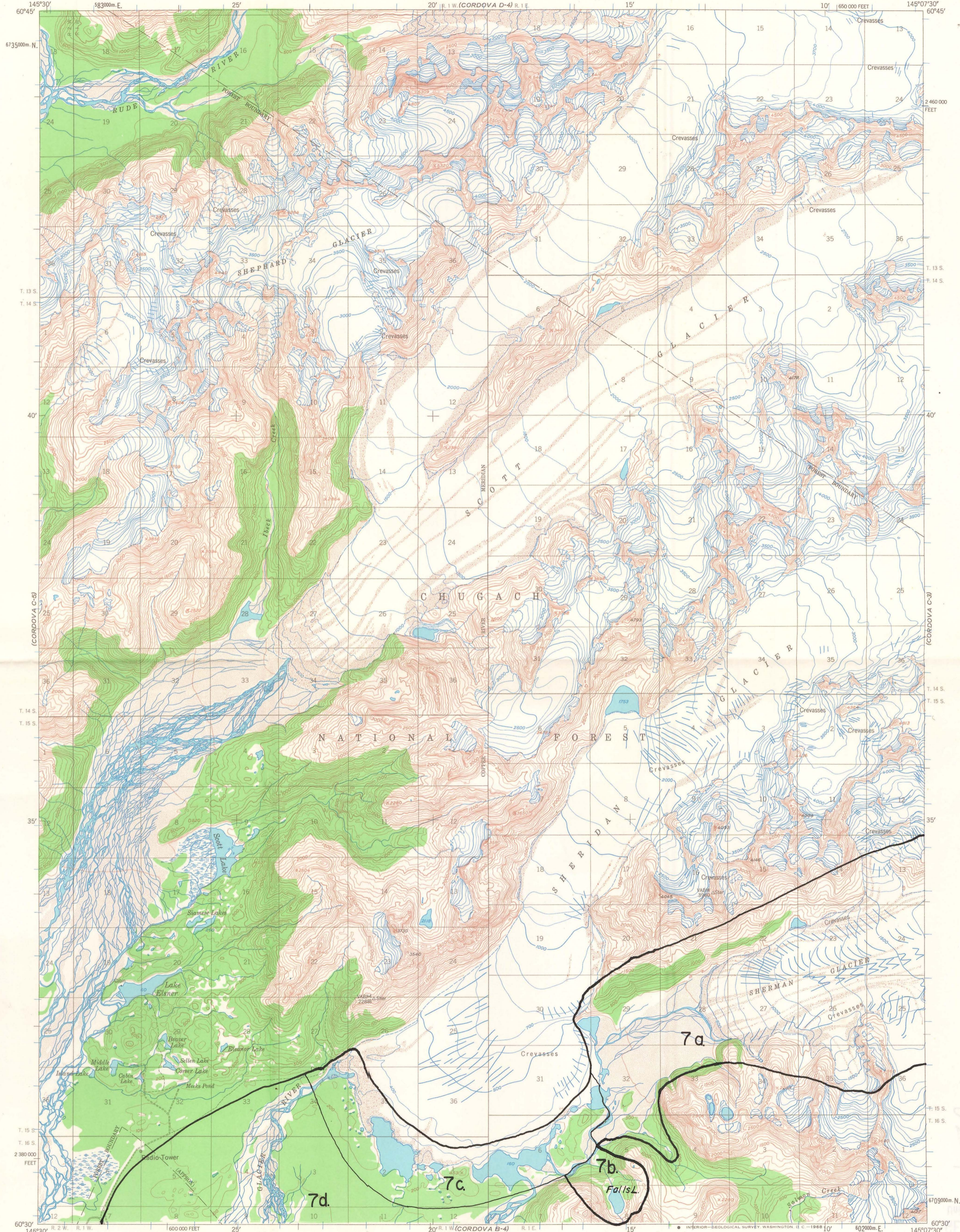
FOR SALE BY U.S. GEOLOGICAL SURVEY
FAIRBANKS, ALASKA DENVER 25, COLORADO WASHINGTON 25, D.C.
A FOLDER DESCRIBING TOPOGRAPHIC MAPS AND SYMBOLS IS AVAILABLE ON REQUEST

CORDOVA (B-4), ALASKA
N6015-W14507.5/15X22.5
1951

TUTHILL 1969

(CORDOVA D-3)

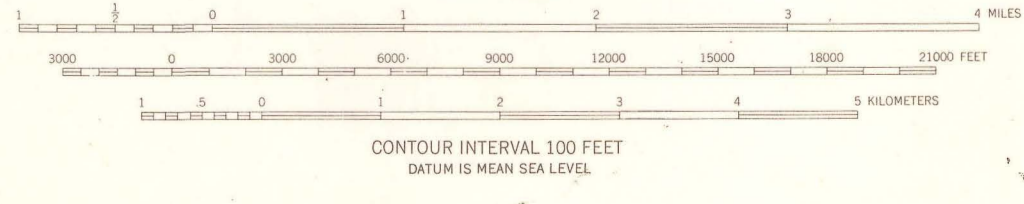
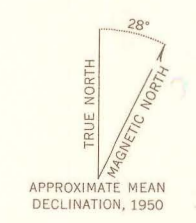
(CORDOVA D-3)



(CORDOVA B-3)

(CORDOVA B-3)

Mapped, edited, and published by the Geological Survey
Control by USGS and USC&GS
Topography by photogrammetric methods from aerial photographs
taken 1950, field annotated 1950. Map not field checked
Universal Transverse Mercator projection, 1927 North American datum
10,000-foot grid based on Alaska coordinate system, zone 3
1000-meter Universal Transverse Mercator grid ticks,
zone 6, shown in blue
Land lines represent unsurveyed and unmarked locations
predetermined by the Bureau of Land Management
Folios CR-5 and CR-6, Copper River Meridian



ROAD CLASSIFICATION
Light-duty ————— Unimproved dirt - - - - -

CORDOVA (C-4), ALASKA
N6030-W14507.5/15X22.5

1950
MAJOR REVISIONS 1964

FOR SALE BY U.S. GEOLOGICAL SURVEY
FAIRBANKS, ALASKA 99701, DENVER, COLORADO 80225, OR WASHINGTON, D. C. 20242
A FOLDER DESCRIBING TOPOGRAPHIC MAPS AND SYMBOLS IS AVAILABLE ON REQUEST

TUTHILL 1969