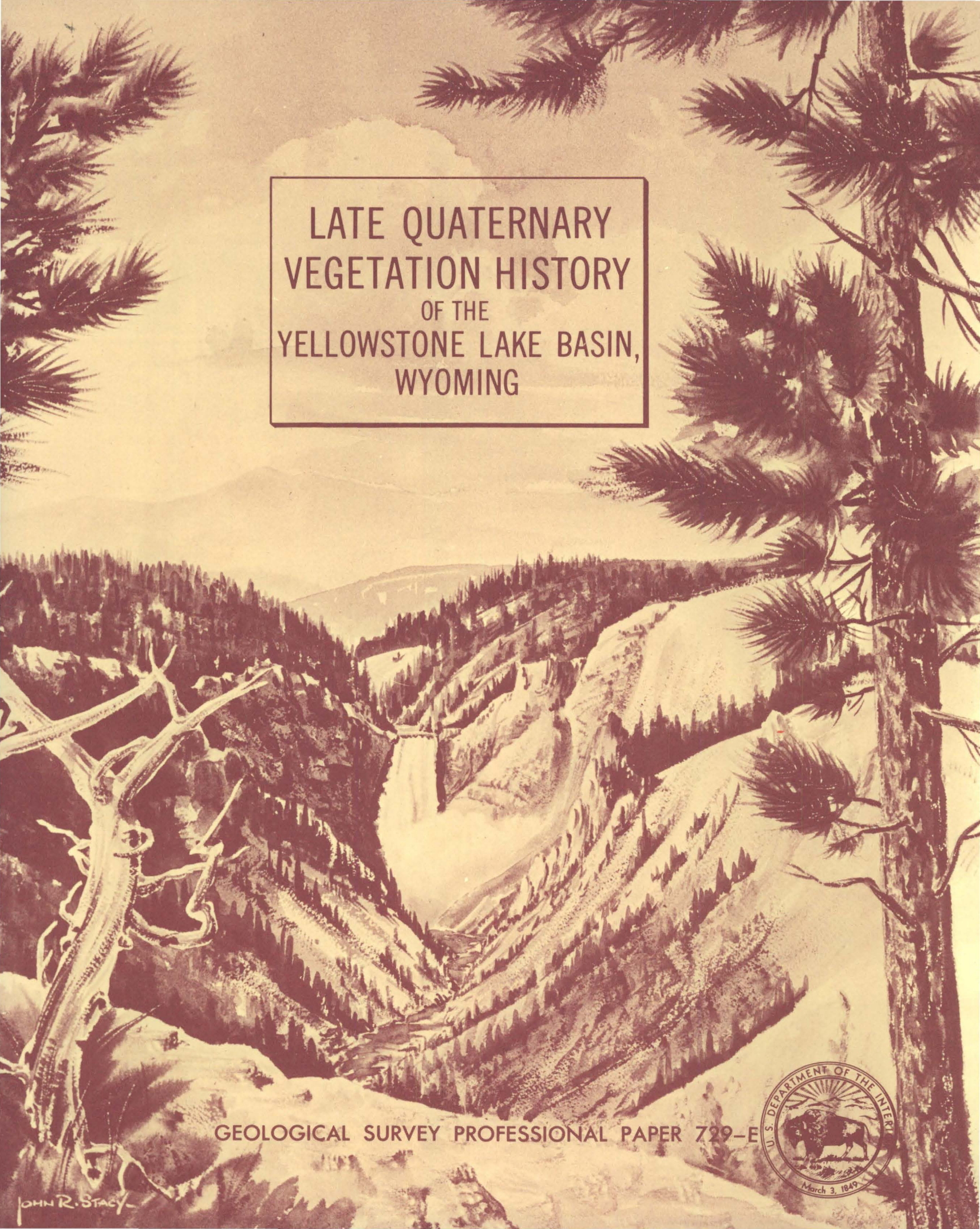
LATE QUATERNARY VEGETATION HISTORY OF THE YELLOWSTONE LAKE BASIN, WYOMING



GEOLOGICAL SURVEY PROFESSIONAL PAPER 729-E

Late Quaternary Vegetation History of the Yellowstone Lake Basin, Wyoming

By RICHARD G. BAKER

GEOLOGY OF YELLOWSTONE NATIONAL PARK

GEOLOGICAL SURVEY PROFESSIONAL PAPER 729–E

Analyses of pollen and plant macrofossils from sediment cores indicate complex changes in the vegetation succession from deglaciation about 13,000 years ago to the present

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Yellowstone National Park, the oldest of the areas set aside as part of the national park system, lies amidst the Rocky Mountains in northwestern Wyoming and adjacent parts of Montana and Idaho. Embracing large, diverse, and complex geologic features, the park is in an area that is critical to the interpretation of many significant regional geologic problems. In order to provide basic data bearing on these problems, the U.S. Geological Survey in 1965 initiated a broad program of comprehensive geologic and geophysical investigations within the park. This program was carried out with the cooperation of the National Park Service, and was also aided by the National Aeronautics and Space Administration, which supported the gathering of geologic information needed in testing and in interpreting results from various remote sensing devices. This professional paper chapter is one of a series of technical geologic reports resulting from these investigations.

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METRIC-ENGLISH EQUIVALENTS

Metric unit		English equivalent	
Length			
millimetre (mm)	=	0.03937	inch (in)
metre (m)	=	3.28	feet (ft)
kilometre (km)	=	.62	mile (mi)
Area			
square metre (m^2)	=	10.76	square feet (ft^2)
square kilometre (km^2)	=	.386	square mile (mi^2)
hectare (ha)	=	2.47	acres
Volume			
cubic centimetre (cm^3)	=	0.061	cubic inch (in^3)
litre (l)	=	61.03	cubic inches
cubic metre (m^3)	=	35.31	cubic feet (ft^3)
cubic metre	=	.00081	acre-foot (acre-ft)
cubic hectometre (hm^3)	=	810.7	acre-feet
litre	=	2.113	pints (pt)
litre	=	1.06	quarts (qt)
litre	=	.26	gallon (gal)
cubic metre	=	.00026	million gallons (Mgal or 10^6 gal)
cubic metre	=	6.290	barrels (bbl) (1 bbl=42 gal)
Weight			
gram (g)	=	0.035	ounce, avoirdupois (oz avdp)
gram	=	.0022	pound, avoirdupois (lb avdp)
tonne (t)	=	1.1	tons, short (2,000 lb)
tonne	=	.98	ton, long (2,240 lb)
Specific combinations			
kilogram per square centimetre (kg/cm^2)	=	0.96	atmosphere (atm)
kilogram per square centimetre	=	.98	bar (0.9869 atm)
cubic metre per second (m^3/s)	=	35.3	cubic feet per second (ft^3/s)
Specific combinations—Continued			
litre per second (l/s)	=	.0353	cubic foot per second
cubic metre per second per square kilometre [$(m^3/s)/km^2$]	=	91.47	cubic feet per second per square mile [$(ft^3/s)/mi^2$]
metre per day (m/d)	=	3.28	feet per day (hydraulic conductivity) (ft/d)
metre per kilometre (m/km)	=	5.28	feet per mile (ft/mi)
kilometre per hour (km/h)	=	.9113	foot per second (ft/s)
metre per second (m/s)	=	3.28	feet per second
metre squared per day (m^2/d)	=	10.764	feet squared per day (ft^2/d) (transmissivity)
cubic metre per second (m^3/s)	=	22.826	million gallons per day (Mgal/d)
cubic metre per minute (m^3/min)	=	264.2	gallons per minute (gal/min)
litre per second (l/s)	=	15.85	gallons per minute
litre per second per metre [(l/s)/m]	=	4.83	gallons per minute per foot [(gal/min)/ft]
kilometre per hour (km/h)	=	.62	mile per hour (mi/h)
metre per second (m/s)	=	2.237	miles per hour
gram per cubic centimetre (g/cm^3)	=	62.43	pounds per cubic foot (lb/ft^3)
gram per square centimetre (g/cm^2)	=	2.048	pounds per square foot (lb/ft^2)
gram per square centimetre	=	.0142	pound per square inch (lb/in^2)
Temperature			
degree Celsius (°C)	=	1.8	degrees Fahrenheit (°F)
degrees Celsius (temperature)	=	[(1.8×°C)+32]	degrees Fahrenheit

LATE QUATERNARY VEGETATION HISTORY OF THE YELLOWSTONE LAKE BASIN, WYOMING

By RICHARD G. BAKER

ABSTRACT

A large icecap flowed radially from the Yellowstone Lake basin during Pinedale (late Pleistocene) time. As it melted, kettles, ice-marginal lakes, and associated ice-contact deposits formed between the glacier and the basin sides. With further wasting, lake levels dropped, beaches formed at progressively lower elevations, and lagoons occupied the kettles. A core from Buckbean fen, an abandoned lagoon 15 feet above modern lake level, was analyzed for pollen and seeds. Macrofossils from the base of lagoon sediments in Lilypad pond 40 feet above the lake were also examined.

Surface pollen samples were collected to relate modern pollen rain to vegetation distribution and to aid in the interpretation of fossil pollen spectra. Steppe, *Pinus contorta* forests, and *Picea-Abies-Pinus albicaulis* forests can be recognized from their pollen rain. Pollen rain in alpine tundra is similar to that in subalpine parklands, but both are distinct from pollen rain in other vegetation associations. Few data are available from *Pseudotsuga* forests.

The Buckbean fen core has two pollen zones—a lower zone and an upper zone. The lower zone (960 – 770 cm) is characterized by more than 50 percent nonarboreal pollen with maxima of *Picea*, *Abies*, *Pinus albicaulis*, *Betula*, *Juniperus*, *Populus*, Graminceae, and Compositae. It has two subzones—the *Betula* and the *Populus*. The *Betula* subzone (960 – 875 cm) has a *Betula* pollen maximum, *Betula glandulosa* seeds, a few alpine macrofossils, and very rare arboreal macrofossils. This fossil assemblage suggests that the site was about at treeline for some time after the glacier melted and that treeline was about 2,000 feet lower than at present in this part of Yellowstone National Park. The assemblage suggests that the climate was cold and moist. The sediments of the subzone contain too little organic matter for radiocarbon dating, but the base of the subzone is estimated to be about 14,500 years old.

The *Populus* subzone (875 – 770 cm) contains a *Populus* maximum and common arboreal macrofossils. *Betula* pollen decreases, but other pollen types remain at nearly constant levels. This subzone marks the invasion of forest in the area and suggests a slightly warmer climate. The top of the *Picea-Abies-Pinus albicaulis* zone is radiocarbon dated at 11,630± 180 years B.P. (before present).

The upper pollen, or *Pinus contorta*, zone (770 – 0 cm) is characterized by *Pinus contorta* pollen and needles and by 60 – 85 percent total *Pinus* pollen. Three subzones are defined, as follows.

A *Pinus contorta-Pinus albicaulis* subzone (770 – 600 cm) is characterized by pollen and needles of both *Pinus albicaulis* and *Pinus contorta*. The two pines apparently grew together locally in the absence of *Picea* and *Abies*, which suggests a cool, dry climate. This subzone was deposited from about 11,630 to about 10,160 years B.P.

A *Pinus contorta* subzone (600 – 420 cm) contains high values of pine pollen, mainly lodgepole, and low values of *Pinus albicaulis*, *Picea*, and *Abies*. This subzone includes the Altithermal period, and represents a warmer, drier climate from about 10,160 to about 5,000 years B.P., but a hiatus representing as much as 4,000 years is probably present in this interval.

A *Picea-Abies-Pinus contorta* subzone (420 – 0 cm), representing about the last 5,000 years, shows a recurrence of *Picea* and *Abies* pollen and needles. This is the Neoglacial period, and the pollen suggest a climate that is cooler and moister than during deposition of the preceding subzone.

INTRODUCTION

The primary purpose of this study was to deduce the vegetation history during the last 13,000 years of the Yellowstone Lake region. Secondary purposes were (1) to infer general climatic changes during this period, and (2) to provide a standard sequence of dated climatic and vegetation changes for correlation with glacial fluctuations.

The fieldwork was carried out in 1966 and 1967 under the supervision of G. M. Richmond, as part of the glacial geology project, Yellowstone National Park study, conducted by the U.S. Geological Survey in cooperation with the National Aeronautics and Space Administration and the National Park Service.

LOCATION AND CLIMATE

Materials for this study were collected from Yellowstone National Park, northwest Wyoming. Much of the park is a plateau (referred to informally in this report as the Yellowstone plateau) that is 8,000 – 9,000 feet above sea level. The Absaroka Range on the eastern margin of the park exceeds 11,000 feet, and isolated peaks in the park exceed 10,000 feet. Fossil pollen samples were collected from depressions near the tip of the Southeast Arm of

Yellowstone Lake (figs. 1 and 12). The elevation of the coring area is about 7,800 feet, and local relief is as much as 1,500 feet.

The climate of Yellowstone National Park has been summarized by Fletcher (1927a and b) and Lowery ([undated] and 1960). Data from 30-year records for Mammoth (elev 6,241 ft) and Yellowstone Lake (Lake Ranger Station, elev 7,762 ft) are compared with predicted climatic curves (Baker, 1944) in figure 2. Shorter unpublished records from 10 ranger stations are also available from the National Park Service. No climatic recording stations are located in the southeast corner of the park near the coring sites, but generalized maps are available (Lowery, 1960).

Mean annual temperature at Mammoth is 38.9°F, and at Yellowstone Lake it is 32.8°F. In summer, the cold water of Yellowstone Lake depresses daytime temperatures along its shoreline (Lowery [undated]), and mean annual temperatures are lower by a few degrees near the lake than elsewhere (Fletcher, 1927a). Mean minimum temperatures for July and January are a few degrees cooler in the Southeast Arm of Yellowstone Lake than at the Lake Ranger Station (Lowery, 1960).

The average annual precipitation recorded in the park increases from less than 14 inches at Lamar Ranger Station in the northeast to 38 inches at Bechler River Ranger Station in the southwest (National Park Service, unpub. data). The coring area receives about 32 inches per year (Lowery, 1960). Unlike any other area in the Rocky Mountain region, Yellowstone National Park has precipitation rather evenly distributed throughout the year (Baker, 1944). At Mammoth and Yellowstone Lake, precipitation averages about 1 – 2 inches every month.

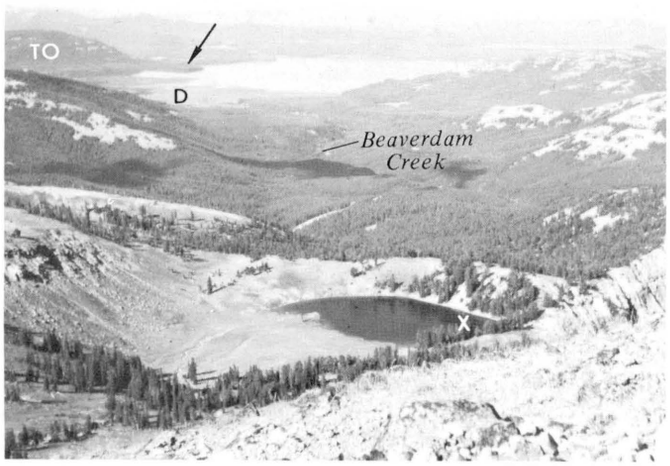


FIGURE 1.—Southeast Arm of Yellowstone Lake, viewed to the west from Absaroka Range showing coring area. D, Yellowstone River delta; TO, Two Ocean Plateau. Arrow indicates coring area; X, surface sample locality SS – 38. Lake in foreground is dammed by a moraine of late Pinedale age.

Snowfall ranges in amount from less than 100 inches at lower elevations to well over 200 inches (locally about 400 inches) at higher elevations (Lowery [undated]). Snowfall in the coring area is probably close to 200 inches per year (Fletcher, 1927a).

Summers in the park tend to be sunny, with 65 – 75 percent sunshine, and winters more cloudy, with an average of 40 percent sunshine (Lowery [undated]). Prevailing wind directions at Mammoth are southwesterly throughout the year (Fletcher, 1927a). No wind records are available from around the lake.

ACKNOWLEDGMENTS

John Good, former Chief Naturalist, Yellowstone National Park, granted permission to use an unpublished map of the vegetation of the park as source material for the map published herein. Robert Morey and W. F. White, National Park Service, extended many courtesies while I was in the field. William Hendrickson, Research Biologist, National Park Service, provided advice and information on the climate and vegetation of the park. W. A. Weber, University of Colorado, identified plants and cooperated in the assembly of the seed collection of the University of Colorado Herbarium. This paper is the outgrowth of a Ph. D. dissertation, and W.C. Bradley and P.W. Birkeland, University of Colorado, and Robert Tschudy, U.S. Geological Survey, offered many helpful suggestions during the preparation of the manuscript. Special thanks are extended to E.B. Leopold, for making available the facilities of the palynology laboratory of the U.S. Geological Survey, to Meyer Rubin, for radiocarbon dating a number of samples from critical levels in the cores, and to W.C. Bradley, who served as my dissertation advisor. The final year of support came from National Science Foundation grant B – 81590 to E. B. Leopold.

METHODS OF STUDY

For the purpose of this study, cores for pollen and plant-macrofossil analysis were taken from four abandoned lagoons of Yellowstone Lake. During and after the melting of the last Pleistocene icecap in the Yellowstone Lake basin, the successively lower lake levels left a series of shorelines between 220 feet and the present lake level (Richmond, 1969c) (figs. 3 and 4). Open lagoons associated with the old shorelines were abandoned as the lake fell and were left as isolated, shallow ponds. The ponds gradually filled with sediment and are now covered with semiaquatic vegetation. Cores were taken from lagoons at eleva-

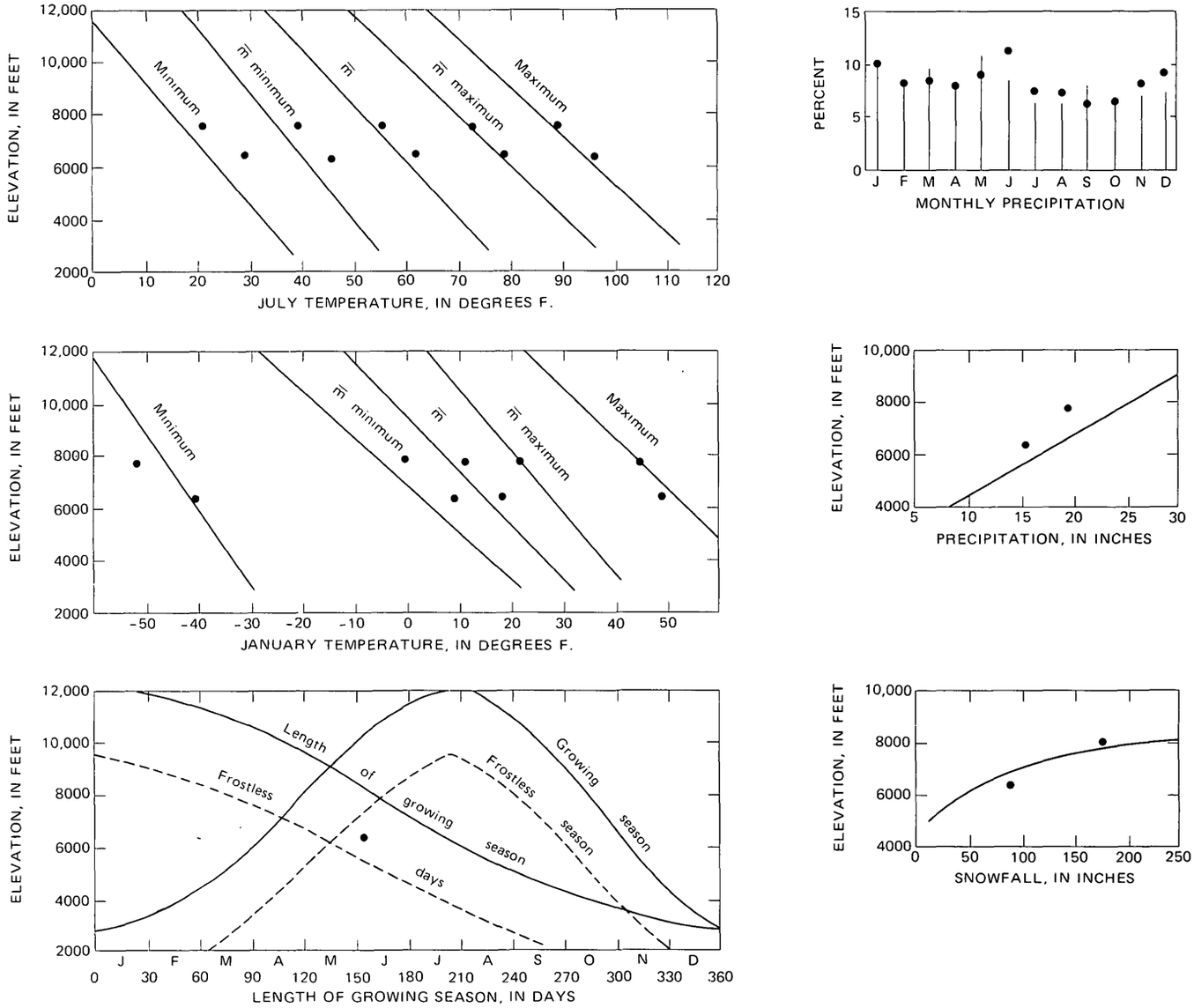


FIGURE 2.—Summary of climatic data (dots) for Yellowstone National Park compared with predicted climatic curves (lines). Dots at 6,241-foot elevation are data for Mammoth; dots at 7,762-foot elevation are data for Yellowstone Lake (Lake Ranger Station). (From F. S. Baker, 1944; data from Becker and Alyea, 1964a and b, Lowery, [undated] and 1960.)

tions of 90, 40, 25, and 15 feet above modern lake level. The core from the 15-foot lagoon (here informally called Buckbean fen) contained the most complete sequence and was selected for detailed pollen and seed analysis. Macrofossils from the basal 2 m of the 40-foot lagoon (here informally called Lilypad pond) are shown in a separate diagram and correlated with the bottom 2 m of the Buckbean fen core.

The pollen assemblages represent mainly upland plants whose pollen was produced in large quantities, was efficiently dispersed, and was well preserved. Analysis provided information on regional vegetation patterns down to the level of families or selected genera. Species and even some genera cannot be established from pollen alone. Some of the pollen types apparently blew in from considerable distances. Study of plant macrofossils (seeds, fruits, bracts, leaves, flowers, twigs, and cone scales) provided information on local vegetation, usually to the level of species. The pollen and macrofossil data that show changes in vegetation through time are plotted in figures 15 and 17. Radiocarbon dates on organic material from the core, which show the ages at four levels in the core, are also plotted in figures 15 and 17.

Studies of modern vegetation and pollen rain in Yellowstone National Park were important aids in interpreting past vegetation. Modern vegetation associations, with increasing elevation, are *Artemisia*

FIGURE 3.—Shorelines above Southeast Arm of Yellowstone Lake. Lower benches are 110, 90, 60, and 25 feet above the lake; higher benches are kame terraces or rock surfaces. View is to the northeast.

steppe, *Pseudotsuga* forest, *Pinus contorta* forest, *Picea-Abies-Pinus albicaulis* forest, and alpine tundra. A generalized vegetation map of the southeast corner of Yellowstone National Park (fig. 6) was made from field observations, topographic maps, and an unpublished vegetation map by the National Park Service. In addition, a reconnaissance map was made of local vegetation types around the coring sites (fig. 7).

The coring sites are located near the boundary between two vegetation types (fig. 7). *Pinus contorta* forests occupy lower, drier areas, and *Picea-Abies-Pinus albicaulis* forests extend up north-facing slopes to the Two Ocean Plateau (fig. 7). Past climatic fluctuations caused this boundary to migrate across the coring sites, and these migrations are recorded in the pollen macrofossil sequences.

Modern pollen was analyzed from surface sediments in ponds situated in the major vegetation associations and the data were plotted (fig. 13). Pollen rain from most associations is sufficiently distinctive to allow its recognition in fossil pollen assemblages. Some fossil assemblages do not match any modern samples, however, and these may represent ancient vegetation associations not now present in the Yellowstone National Park area.

Elevational limits of modern vegetation associations are controlled by climate, but precise relationships are still poorly known. Where the distributional limits of certain plant taxa are found to coincide with a specific mean temperature, past distributional limits of those taxa may suggest paleotemperatures (Wolfe and Leopold, 1967). This approach must be used with caution because the coincidence may not be simply a cause-and-effect relationship. In this study only broad climatic changes can be inferred from most of the past vegetation changes.

Glacial deposits and topographic features of late Quaternary age in Yellowstone National Park have been mapped by G. M. Richmond, K. L. Pierce, and H. A. Waldrop (U.S. Geological Survey, 1972). Radiocarbon dates suggest that the Pinedale Glaciation began after 27,000 ±800 years ago in nearby Jackson Hole, Wyo. (Levin and others, 1965). Pinedale glaciers had retreated extensively by about 13,000 years ago in Yellowstone National Park

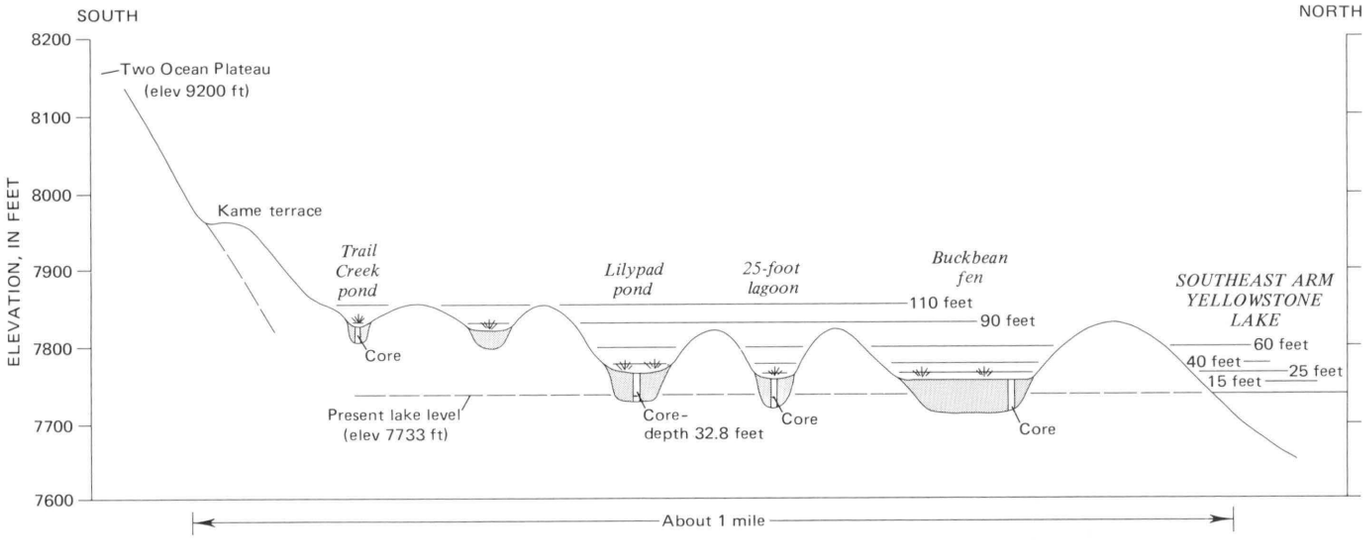


FIGURE 4.—Schematic cross section showing relationship between Two Ocean Plateau, the filled lagoons, the lake levels, and the coring sites. See figure 7 for location of ponds.

(Richmond, 1970b; Bender and others, 1971). Dates on glacial advances elsewhere in the western cordillera (Richmond, 1965, 1970b; Porter and Denton, 1967) correlate well with cool, moist periods inferred from my paleobotanical record and support geomorphic and soil-stratigraphic correlation of the Yellowstone glacial deposits with the standard Rocky Mountain glacial sequence (Richmond, 1965).

Our knowledge of late Quaternary regional climatic changes is still sketchy. This study provides new data in an area heretofore unstudied. More data of this sort will contribute answers to questions such as the following: How synchronous were regional climatic changes? Were climatic changes similar in nature from one region to another?

GLACIAL HISTORY

Yellowstone National Park was glaciated several times during early and mid-Quaternary time (Richmond, 1969c, 1970a). Glacial till underlies an ash-flow tuff about 600,000 years old near Tower Falls (U.S. Geological Survey, 1972) and mid-Quaternary sections containing glacial deposits are known from scattered sections elsewhere in the park.

The Bull Lake Glaciation is the oldest glaciation that has extensive till and constructional topographic features remaining. The Bull Lake icecap was somewhat larger than the succeeding Pinedale icecap, and large areas underlain by Bull Lake Till are found in the western part of the park (U.S. Geological Survey, 1972). Bull Lake Till underlies wood-bearing lake sediments dated at greater than 42,000 years B.P. (before present) and greater than 45,000 years B.P. in the Yellowstone Lake basin (Richmond, 1969c, 1970a).

Pinedale Glaciation is estimated to have begun about 25,000 years ago and stagnated about 14,500 – 13,000 years ago in the Yellowstone National Park region (Richmond, 1970a, b; Waddington and Wright, 1974). The Pinedale icecap centered along a north-south axis through Yellowstone Lake (Richmond and Pierce, 1968, 1972; Richmond, 1969c). Ice flowed radially from the lake area to the north, to the east through divides in the Absaroka Range, and to the south and southwest across the rugged plateaus and ridges. As the Pinedale icecap melted, local ice-marginal lakes and kame terraces formed in the northeastern part of the Yellowstone Lake basin and gradually extended southward (Richmond, 1969a; U.S. Geological Survey, 1972). Channels carried the melt water away from the basin at several points around the lake (Richmond, 1969a). In the coring area a kame terrace formed along the lower slopes at the northwest margin of the Two Ocean Plateau (fig. 5, phase 1). Later, large ice blocks calved off, became buried by outwash and lake sediments, and formed kettles approximately parallel to the ice margin (locations shown in fig. 5, phase 2).

After the Pinedale icecap had melted, cirque and valley glaciers readvanced in the Absaroka Range and on the Two Ocean Plateau (Richmond and Pierce, 1972). Some valley glaciers were 5 miles long, and their terminal moraines (fig. 1) reached elevations as low as 7,880 feet, but averaged 8,400 feet (Richmond, 1969b). Outwash terraces extended from these moraines down the valleys to a level about 60 feet above Yellowstone Lake. Lake sediments beneath a delta that graded to the 60-foot level at Grouse Creek on the South Arm of Yellowstone Lake were dated at 9,060 ± 300 years B.P. (Sullivan and others, 1970, sample W – 2041; Richmond, 1970a). The coring sites were not glaciated and apparently received no glacier-derived sediments at this time.

An interval of maximum warmth and dryness (the Altithermal interval) is recognized in the Rocky Mountain area following the retreat of late Pinedale ice (Richmond, 1965, p. 227). Antevs (1955) placed the Altithermal interval between 7,500 and 4,000 years B.P.; however, these boundaries have not been consistently used, and they may transgress time. Valley and cirque glaciers apparently retreated during this warm period.

Neoglaciation is the period of glacier expansion following the Altithermal period and extending to the present time. In the Rocky Mountain region it has been divided into the Temple Lake Stade, thought to have formed moraines about 2,800 years B.P. (Richmond, 1969b), and the Gannett Peak Stade, which began about 700 years ago and continues to the present (Porter and Denton, 1967, p. 201). Recently, however, Birkeland and Miller (1973), Miller and Birkeland (1974), and Currey (1974) showed that the type section of the Temple Lake in the Wind River Range is pre-Altithermal and may be late Pinedale in age. A new type section and name should be chosen for this 2,800-year-old glacial advance. Hence, the report will use the term "early neoglacial," rather than "Temple Lakes." In the Absaroka Range the average elevation is 9,460 feet for early neoglacial end moraines and 9,845 feet for Gannett Peak end moraines (Richmond, 1969b).

Recent evidence suggests that some areas experienced glacial expansion as early as 5,000 years ago (Porter and Denton, 1967, p. 198). No moraines of this age are recognized in Yellowstone National Park,

but radiocarbon dates are lacking. The pollen record suggests that post-Altithermal cooling began at about that time. Neoglaciation in the park could thus include all sediments younger than 5,000 years. This usage is consistent with a recent definition of Neoglaciation (Porter and Denton, 1967, p. 205): "We * * * define Neoglaciation as the climatic episode characterized by rebirth and/or growth of glaciers following maximum shrinkage during the Hypsithermal (Altithermal) interval." Neoglaciation is a geologic-climate unit. Boundaries of such units need not be isochronous (Am. Comm. Strat. Nomenclature, 1961, p. 660).

Nearly continuous shorelines that locally grade into kame deposits are found around the south shore of Yellowstone Lake at about 110 and 90 feet above modern lake level. The rarity at these levels of spits and bars, whose formation depends on a large fetch, suggests that the lake was not entirely open at this time (Richmond, 1969a). The 110-foot shoreline is not preserved in the coring area, but Trail Creek pond was a shallow lagoon that formed behind the 90-foot beach (fig. 5, phase 2, and fig. 7). Peat from this lagoon is 10,360 ± 350 years B.P. (sample W – 2289). The 90-foot lake level is probably older than this date because the peat sampled lies an undetermined distance above the basal organic sediments, and the break between sand of the lagoon floor and basal organic sediments may represent a diastem. This

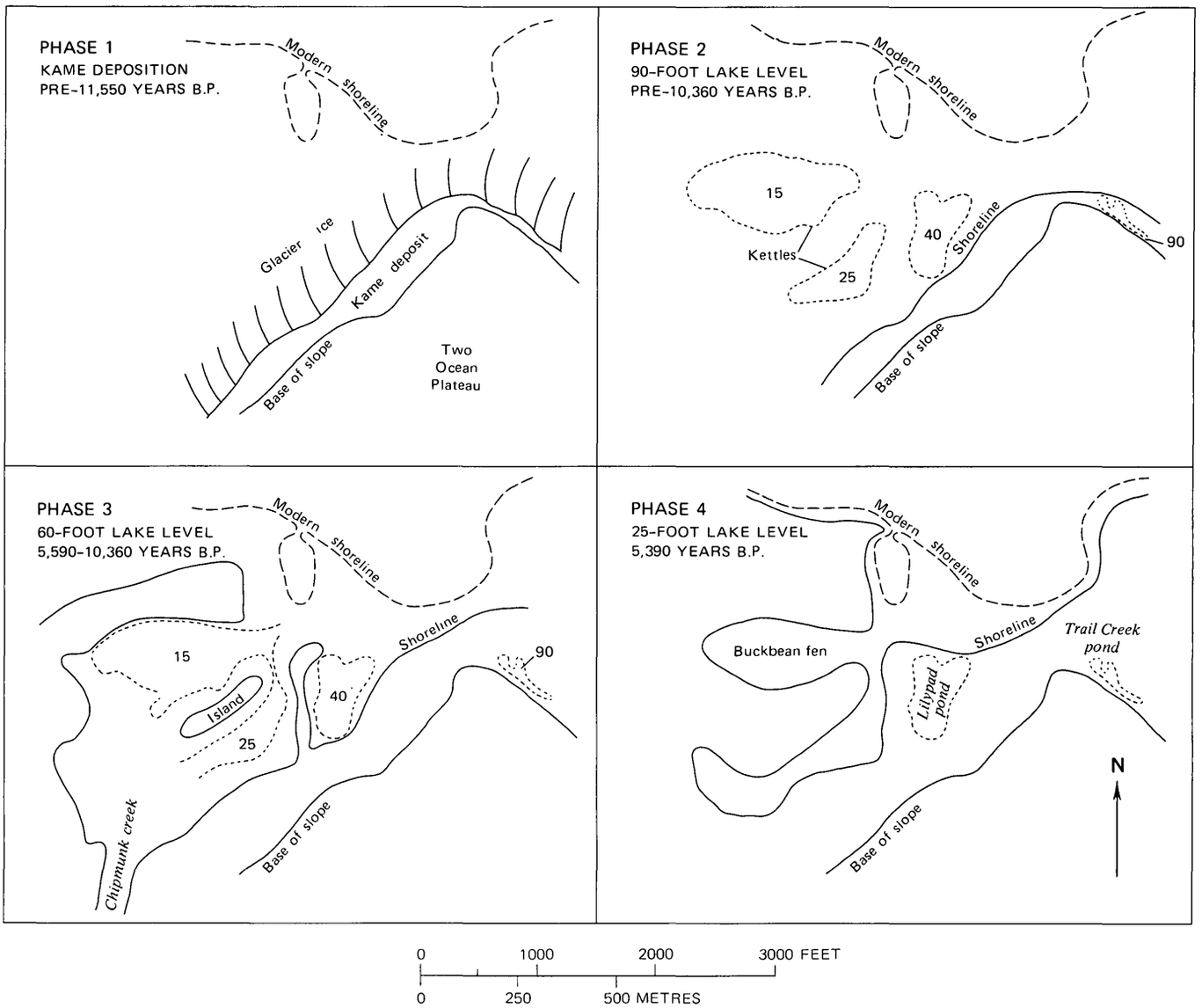


FIGURE 5.—Geomorphic development of coring area as glacier ice melted and lake level fell. Numbers in kettles indicate height of "baymouth bars," in feet above present lake level, that protected the lagoons and controlled their formation.

90-foot lagoon probably formed during retreat of middle Pinedale ice; the organic sediment may have formed in part during the late Pinedale advance.

Lower shorelines at 60, 40, 25, 15, 10, and 5 feet above modern lake level have associated large spits, bars, and lagoons similar in size to modern ones. Richmond (1969a) concluded that these lower beaches formed in an open, ice-free Yellowstone Lake after the icecap had entirely melted because the lower shorelines are cut into kame deposits and do not grade into them.

The 60-foot shoreline correlates with a glacial advance (late Pinedale of Richmond, 1970b; Birkeland and others, 1971) that ended about 9,000 years B.P. in Yellowstone National Park. When the lake was at the 60-foot level, rims of kettles must have projected above water to form isolated bays in the coring area (fig. 5, phase 3).

Subsequent lowering of lake level converted Lilypad pond, Buckbean fen, and other kettles to lagoons and finally to isolated ponds (fig. 5, phase 4). Radiocarbon dates of 5,590 ± 250 years B.P. (sample W – 2286) from Lilypad pond and 5,390 ± 250 years B. P. (sample W – 2281) from Buckbean fen indicate that lake level had fallen below these lagoons before about 5,500 years ago. The late Pinedale and younger levels were apparently controlled by erosion of glacial drift along the Yellowstone River (Richmond, 1969a).

VEGETATION OF YELLOWSTONE NATIONAL PARK AND SURROUNDING AREA

Yellowstone National Park has distinct elevational zonation of vegetation similar to that of other parts of the Rocky Mountain region (Daubenmire, 1943). Five broad vegetation zones, herein called vegetation associations, are briefly discussed. Scientific names of plants, and common names if available, are listed in table 1.

TABLE 1.—*Scientific names, and common names if available, of plant taxa mentioned in text, tables, and illustrations*

[(p), pollen or spores of the taxon were found; (m), macrofossils of the taxon were found]

Scientific name and author	*Common name, if available*
DIVISION CHOLOROPHYTA	
HYDRODICTYACEAE	
(m) *Pediastrum*	
DIVISION CHAROPHYTA	
CHARACEAE	
(m) *Chara*	
DIVISION BRYOPHYTA	Mosses

TABLE 1.—*Scientific names, and common names if available, of plant taxa mentioned in text, tables, and illustrations*—Continued

Scientific name and author	*Common name, if available*
DIVISION BRYOPHYTA—Continued	
AULACOMNIACEAE	
(m) *Aulacomnium palustre* (W. & M.) Schw.	
HYPNACEAE	
Climacium dendroides (Hedw.) W. & M.	
(m) *Drepanocladus*	
LESKEACEAE	
Helodium blandowii (W. & M.) Warnst.	
SPHAGNACEAE	
(m) *Sphagnum*	Sphagnum moss
(m?) *Sphagnum warnstorfianum* Dr.	
DIVISION PTERIDOPHYTES	
EQUISETACEAE	
(p) *Equisetum*	Horsetail
ISOËTACEAE	
Isoëtes	Quillwort
SELAGINELLACEAE	
(p) *Selaginella densa* Rydb.	Rock selaginella
Selaginella selaginoides (L.) Link	
POLYPODIACEAE	
(p)	Fern
DIVISION SPERMATOPHYTA	
CUPRESSACEAE	
(p) *Juniperus*	
(p)?(m) *Juniperus communis* L.	Common juniper
Juniperus virginiana L. var. *scopulorum* Lemmon	Redcedar, Rocky Mountain juniper
PINACEAE	
(p) (m) *Abies lasiocarpa* (Hook.) Nutt.	Subalpine fir
(p) (m) *Picea engelmannii* (Parry) Engelm.	Engelmann spruce
Picea pungens Engelm.	Colorado blue spruce
(p) (m) *Pinus albicaulis* Engelm.	Whitebark pine
(p) (m) *Pinus contorta* Dougl.	Lodgepole pine
(p)? *Pinus flexilis* James	Limber pine
(p)? *Pinus ponderosa* Laws.	Ponderosa pine
(p) (m) *Pseudotsuga menziesii* (Mirb.) Franco	Douglas-fir
(p) *Tsuga heterophylla* (Rafn.) Sarg.	Western hemlock
(p) *Tsuga mertensiana* (Bong.) Carr.	Mountain hemlock
EPHEDRACEAE	
(p) *Ephedra torreyana* S. Wats.	
(p) *Ephedra viridis* Coville	Green jointfir
ACERACEAE	
(p) *Acer*	Maple
(p) AMARANTHACEAE	
BETULACEAE	
(p) (m) *Alnus tenuifolia* Nutt.	Thinleaf alder

TABLE 1.—*Scientific names, and common names if available, of plant taxa mentioned in text, tables, and illustrations*—Continued

Scientific name and author	*Common name, if available*
DIVISION SPERMATOPHYTA—Continued	
BETULACEAE—Continued	
(p) *Betula*	Birch
(p) (m) *Betula glandulosa* Michx.	Bog birch
(p)? *Betula occidentalis* Hook.	River birch
BORAGINACEAE	
Mertensia	Bluebell, chiming bells
CALLITRICHACEAE	
Callitriche	Water-starwort
CAMPANULACEAE	
Campanula rotundifolia L.	Common harebell
CAPRIFOLIACEAE	
(p)	Honeysuckle family
(p) CARYOPHYLLACEAE	
CERATOPHYLLACEAE	
(m) *Ceratophyllum demersum* L.	Hornwort
(p) CHENOPODIACEAE	
(p)? *Atriplex* sp.	Saltbush
(p) *Sarcobatus vermiculatus* (Hook.) Torr.	Greasewood
(p) CHENOPODIACEAE-AMARANTHACEAE	Cheno-Ams
COMPOSITAE	
(p) Subfamily Tubuliflorae	
Achillea lanulosa Nutt.	Yarrow
(p) *Ambrosia*	Ragweed
Antennaria	Pussytoes
(p) *Artemisia*	Sagebrush
(p) *Artemisia tridentata* Nutt.	Big sagebrush
Aster	
Chrysothamnus	Rabbitbrush
(p)? *Franseria*	Sand bur
(p) Subfamily Liguliflorae	
CRASSULACEAE	
Sedum lanceolatum Torr.	Stonecrop
(m) *Sedum rhodanthum* Gray	Rosecrown
Sedum rosea (L.) Scop. ssp. *integrifolium* (Raf.) Hultén	Kings Crown
(p) CRUCIFERAE	
Arabis	Rockcress
Arabis glabra (L.) Bernh.	Tower mustard
(m) *Descurainia californica* (A. Gray) Schulz	Tansymustard
(m) *Rorippa islandica* (Oeder) Borbas	Marshcress
ELEAGNACEAE	
(p) *Shepherdia canadensis* (L.) Nutt.	Buffaloberry
ERICACEAE	
Arctostaphylos uva-ursi (L.) Spreng.	Kinnikinnik, bearberry

TABLE 1.—*Scientific names, and common names if available, of plant taxa mentioned in text, table, and illustrations*—Continued

Scientific name and author	*Common name, if available*
DIVISION SPERMATOPHYTA—Continued	
ERICACEAE—Continued	
Kalmia polifolia Wang.	Swamp laurel
Ledum glandulosum Nutt.	
Phyllodoce empetriformis (Smith) D. Don	Mountainheath
Vaccinium myrtillus L.	Myrtle blueberry
FAGACEAE	
(p) *Quercus*	Oak
GENTIANACEAE	
Gentianopsis thermalis (O. Kuntze) Iltis (=*Gentiana thermalis* Kuntze)	Rocky Mountain fringed gentian
HALORAGACEAE	
(m) *Myriophyllum*	
(m)? *Myriophyllum spicatum* L. ssp. *exalbescens* (Fern.) Hultén	Watermilfoil
(m)? *Myriophyllum verticillatum* L.	Greenmilfoil
HYDROPHYLLACEAE	
Phacelia	Scorpion-weed
JUGLANDACEAE	
(p) *Juglans*	Walnut
(p) LEGUMINOSAE	
Lupinus argenteus Pursh.	Silvery lupine
LENTIBULARIACEAE	
Utricularia minor L.	Small bladderwort
Utricularia vulgaris L.	Common bladderwort
LORANTHACEAE	
(p) *Arceuthobium*	
(p)? *Arceuthobium americanum* Nutt.	Lodgepole pine dwarf mistletoe
Arceuthobium campylopodum Engelm.	Western dwarf mistletoe
Arceuthobium douglasii Engelm.	Douglas-fir dwarf mistletoe
MENYANTHACEAE	
(p) (m) *Menyanthes trifoliata* L.	Buckbean
NYMPHAEACEAE	
(p) (m) *Nuphar luteum* Sibth. & Sm. ssp. *polysepalum* (Engelm.) Beal	Yellow pond lily
OLEACEAE	
(p) *Fraxinus*	Ash
(p) ONAGRACEAE	
(m)? *Epilobium adenocaulon* Hausskn.	
(m)? *Epilobium glandulosum* Lehm.	
(m) *Epilobium lactiflorum* Hausskn.	Pale willow-herb

TABLE 1.—*Scientific names, and common names if available, of plant taxa mentioned in text, tables, and illustrations*—Continued

Scientific name and author	*Common name, if available*
DIVISION SPERMATOPHYTA—Continued	
PLATAGINACEAE	
(p) Plantago	Plantain
POLEMONIACEAE	
Phlox multiflora A. Nels.	Common phlox
(p) *Polemonium*	Jacobs ladder
POLYGONACEAE	
(p) *Bistorta*	
(p) *Bistorta bistortoides* (Pursh.) Small (=*Polygonum bistortoides* Pursh)	Bistort
(p)? *Bistorta vivipara* (L.) S. Gray (=*Polygonum viviparum* L.)	Viviparous bistort
(p) *Eriogonum*	Umbrellaplant
(p) *Koenigia islandica* L.	
(p) *Oxyria*	Alpine sorrel
(p)? *Persicaria amphibia* (L.) S. Gray (=*Polygonum amphibium* L.)	Water smartweed
(p)? *Persicara maculata* (Raf.) S. Gray (=*Polygonum persicaria* L.)	Ladysthumb
(p)? *Polygonum ramosissimum* Michx.	Bushy knotweed
(p) *Rumex*	Dock
(p)?(m) *Rumex fueginus* Phil. (=*Rumex maritimus* L. var. *fueginus* (Phil.) Dusen)	Golden dock
Rumex paucifolius Nutt.	
(p)?(m) *Rumex salicifolius* Weinm. ssp. *triangulivalvis* Danser	Willow dock
RANUNCULACEAE	
Aconitum columbianum Nutt.	Monkshood
Anemone multifida Pair. var. *globosa* (Nutt.) T & G.	Globose anemone
(p) *Ranunculus*	
(m) *Ranunculus aquatilis* L.	Water crowfoot
(p) *Thalictrum*	Meadow rue
RHAMNACEAE	
(p)? *Ceanothus velutinus* Dougl.	Sticky-laurel
(p) ROSACEAE	
(p)? *Cercocarpus*	Mountainmahogany
Fragaria	Strawberry
Geum macrophyllum Willd.	Large-leaf avens
Pentaphylloides floribunda (Pursh) A. Love (=*Potentilla fruticosa* L.)	Shrubby cinquefoil
(m)? *Potentilla biennis* Greene	
(m)? *Potentilla gracilis* Dougl. *ex*. Hook.	Soft cinquefoil

TABLE 1.—*Scientific names, and common names if available, of plant taxa mentioned in text, tables, and illustrations*—Continued

Scientific name and author	*Common name, if available*
DIVISION SPERMATOPHYTA—Continued	
(p) ROSACEAE—Continued	
(m)? *Potentilla norvegica* L.	Norway cinquefoil
(p)?(m) *Potentilla palustris* (L.) Scop.	Marsh cinquefoil
(m) *Sibbaldia procumbens* L.	
RUBIACEAE	
Galium trifidum L.	Small bedstraw
SALICACEAE	
(p) *Populus*	
(p)?(m) *Populus balsamifera* L.	Balsam poplar
Populus tremuloides Michx.	Quaking aspen
Populus trichocarpa Torr. and Gray	Black cottonwood
(p) *Salix*	Willow
Salix arctica Pallas.	
Salix ligulifolia (Ball) Ball	
(m)? *Salix subcoerulea* Piper	Blue willow
SAXIFRAGACEAE	
(m) *Saxifraga caespitosa* L.	Matted saxifrage
(m) *Saxifraga rhomboidea* Greene	Diamondleaf saxifrage
(p)? SCROPHULARIACEAE	
(p)? *Pedicularis*	
Pedicularis groenlandica Retz	Elephantella
(p)? *Mimulus*	Monkey flower
(p) UMBELLIFERAE	
URTICACEAE	
(p) *Urtica*	Nettle
(p) CYPERACEAE	
(m) *Carex aquatilis* Wahlenb.	
(m) *Carex canescens* L.	
(m) *Carex diandra* Schrank	
Carex geyeri Boott	
Carex hoodii Boott	
(m) *Carex limosa* L.	
Carex phaeocephala Piper	
(m) *Carex utriculata* Boott (=*Carex rostrata* Stokes)	
(m) *Carex vesicaria* L.	
(m) *Eleocharis macrostachya* Britt.	Spikerush
Eriophorum	Cottongrass
Scirpus acutus Muhl.	Hardstem bulrush
(p) GRAMINEAE	
Agropyron	Wheatgrass
Bromus	Bromegrass
Bromus inermis Leyss.	Smooth brome
Calamagrostis canadensis (Michx.) Beauv.	Bluejointgrass
Calamagrostis inexpansa A. Gray	Northern reedgrass
Deschampsia caespitosa (L.) Beauv.	Tufted hairgrass
Elymus	Wild-rye
Glyceria borealis (Nash) Batchelder	Northern mannagrass

TABLE 1.—*Scientific names, and common names if available, of plant taxa mentioned in text, tables, and illustrations*—Continued

	Scientific name and author	*Common name, if available*
DIVISION SPERMATOPHYTA—Continued		
(p) GRAMINEAE—Continued		
(m)	*Glyceria maxima* (Hartm.) Holmb. ssp. *grandis* (Wats.) Hulten (=*Glyceria grandis* S. Wats.)	Large mannagrass
	Poa	Bluegrass
	Sitanion longifolium J. G. Smith (=*Sitanion hystrix* (Nutt.) J. G. Smith)	Squirrel-tail
	Stipa	Needlegrass
JUNCACEAE		
	Luzula parviflora (Ehrh.) Desv.	Woodrush
	Luzula spicata (L.) DC.	Spike woodrush
NAIADACEAE		
(m)	*Naias flexilis* (Willd.) Rostk. and Schmidt	Naiad
(m)	*Potamogeton alpinus* Balbis	Northern pondweed
(m)	*Potamogeton filiformis* Pers.	
(m)	*Potamogeton gramineus* L.	
(m)?	*Potamogeton illinoensis* Morong	
	Potamogeton pectinatus L.	Sago pondweed
	Potamogeton vaginatus Turcz.	
SPARGANIACEAE		
(p)?	*Sparganium*	
	Sparganium angustifolium Michx.	Burreed
	Sparganium minimum Fries	Arctic burreed
TYPHACEAE		
(p)?	*Typha angustifolia* L.	Narrowleafed cattail
(p)	*Typha latifolia* L.	Broadleaf cattail

REGIONAL VEGETATION

ARTEMISIA STEPPE ASSOCIATION

The lowest vegetation type in the park is *Artemisia* (sagebrush) steppe at the base of the north edge of the Yellowstone plateau (fig. 6). *Artemisia tridentata* is the dominant plant in this association, but *Sarcobatus vermiculatus* (greasewood) and *Atriplex* spp. (saltbush) are common on clayey or alkaline sites, and in many places *Chrysothamnus* spp. are scattered among the sagebrush. Grasses including *Elymus* spp. (wild-rye) and *Bromus* spp. (bromegrass) are locally common. This type occurs between Mammoth and Gardiner in the northern part of the park and is common around the margins of the park below about 6,000 feet. Large areas of *Artemisia* steppe on the Snake River Plain southwest of the park may be an important source of *Artemisia* pollen.

The lower limit of trees above the *Artemisia* steppe is highly variable because of local factors. Near Mammoth, it ranges from about 5,800 to 6,800 feet. East of the park in the rain shadow of the Absaroka Range it is 6,500–7,600 feet (H. E. Wright Jr., unpub. data, 1967). At Mammoth it is associated with a mean annual temperature of about 40°F, mean January temperature of 18°F, mean July temperature of 63°F, and mean annual precipitation of 15.5 inches.

Artemisia tridentata (big sagebrush) also dominates in forest openings up to several acres in size on the Yellowstone plateau, where it is more stunted than at lower elevations. In the southeast corner of the park, these *Artemisia* openings occur on dry south-facing slopes adjacent to the Southeast Arm of Yellowstone Lake (fig. 3). They occur locally on south-facing slopes of Buckbean fen and adjacent lagoons (fig. 7).

Plants associated with *Artemisia* in the southeast part of the park include *Eriogonum subalpinum* (umbrellaplant), *Lupinus argenteus* (silvery lupine), *Achillea lanulosa* (yarrow), *Antennaria* sp. (pussytoes), *Phacelia* sp. (scorpion-weed), *Arabis glabra* (rockcress), *Phlox multiflora* (common phlox), *Carex hoodii* (sedge), *Carex petasata* (sedge), *Agropyron* spp. (wheatgrass), *Stipa* spp. (needlegrass), *Bromus inermis* (bromegrass), *Campanula rotundifolia* (common harebell), *Sitanion hystrix* (squirrel-tail), and *Arctostaphylos uva-ursi* (kinnikinnick). *Artemisia tridentata* in this community may have been an important supplier of *Artemisia* pollen in the fossil record.

PSEUDOTSUGA ASSOCIATION

Pseudotsuga menziesii (Douglas-fir) is dominant in the next lowest vegetation association but is sporadic in occurrence in the Yellowstone region. Locally *Pinus flexilis* (limber pine) and *Populus tremuloides* (quaking aspen) are common in this association. *Pinus ponderosa* (ponderosa pine), which normally occurs in this elevational zone, is not present in northwestern Wyoming (Choate, 1963). *Juniperus virginiana* var. *scopulorum* (Rocky Mountain juniper) occurs at lower elevations along the forest-steppe boundary. *Pseudotsuga menziesii* is not common on the Yellowstone plateau, but it grows sparsely about 6 miles north of the coring sites and on the east slope of the Absaroka Range about 12 miles to the east.

The *Pseudotsuga* association grows as low as 6,000 feet in an open savanna, along stream valleys, and in closed forests as high as about 8,000 feet (H. E.

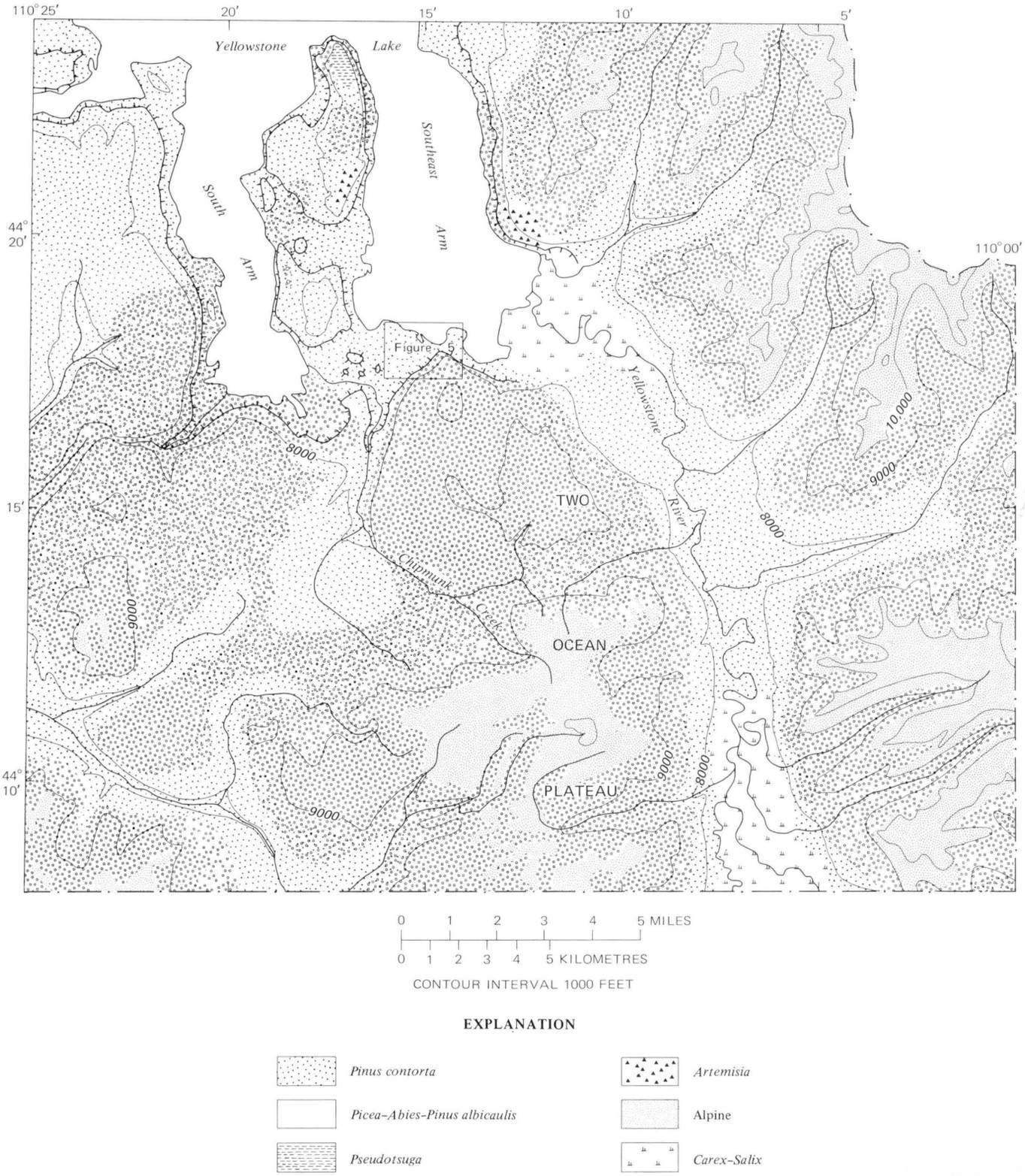


FIGURE 6.—Vegetation map of the southeast corner of Yellowstone National Park. The hachured line is 110 feet above Yellowstone Lake; it shows the highest lake level interpolated from the base maps. Contacts between vegetation units are approximate and are not marked by lines. In part from unpublished map of vegetation of Yellowstone National Park by National Park Service. Base from U.S. Geological Survey Eagle Peak, Frank Island, Mount Hancock, and Two Ocean Pass 1:62,500 topographic quadrangles, 1959.

Wright Jr., unpub. data, 1973). No climatological data were available for this association.

PINUS CONTORTA FOREST ASSOCIATION

The *Pinus contorta* (lodgepole pine) forest is by far the most common vegetation type in Yellowstone National Park. It covers about 80 percent of the total forested area (National Park Service, unpub. data). *Picea engelmannii* (Engelmann spruce) and *Abies lasiocarpa* (subalpine fir) grow in the upper part of this type. Most *Pinus contorta* forests are open and dry and contain little underbrush, and they commonly grow on porous grus soils. Near the coring sites the common understory plants are *Juniperus communis* (common juniper), *Shepherdia canadensis* (buffaloberry), *Vaccinium myrtillus* (myrtle blueberry), *Arctostaphylos uva-ursi*, *Eriogonum subalpinum*, *Arabis* spp., and various composites and grasses. *Pinus contorta* is more dominant on the flat plateau areas of the park than in the dissected southeast corner, but it still is the most common tree in the southeast corner (fig. 3).

Pinus contorta forests are usually found between 7,000 and 8,500 feet (McDougall and Baggley, 1956). They are best developed where annual precipitation exceeds 18 – 21 inches, growing season is short (60 – 100 days), and mean July temperature is 55° – 63°F (Tackle, 1961).

Pinus contorta spreads rapidly after fires (Porter, 1962; Tackle, 1961) and is commonly said to be a successional tree. Tackle believed that it is a climax species in some areas, and some of the forest in the park appear to be climax. Küchler (1964) mapped Yellowstone National Park as potentially a *Pseudotsuga* climax forest, but the scarcity of *Pseudotsuga* on the Yellowstone plateau and the relatively high precipitation and cool summers there argue for *Picea-Abies* as more probable potential climax species in the absence of fire. On the average, 32 fires, mostly small ones, occur in the park every year (National Park Service, unpub. data). In the northern part of the park, Houston (1973) estimated that 8 – 10 extensive fires have occurred in the last 300 – 400 years. Judged from the abundance of charcoal in cores and in some exposures, fires have been common throughout postglacial time. Large fires occurred in 1931 (a dry year) and 1940 in the southern part of the park.

PICEA-ABIES-PINUS ALBICAULIS FOREST ASSOCIATION

The *Picea-Abies-Pinus albicaulis* forest occurs throughout the park above the *Pinus contorta* forest. In the southeastern corner of the park, this association occurs on most of the Two Ocean Plateau (fig. 6) and in the high parts of the Absaroka Range. *Picea* and *Abies* also occur in some areas along the lake, probably because in summer the lake creates a cooling effect around its margin. This forest also grows along the north-facing slopes of the Two Ocean Plateau close to the coring sites (fig. 6).

Picea engelmannii (Engelmann spruce) and *Abies lasiocarpa* (subalpine fir) are the dominant trees of this type. In many places *Pinus albicaulis* (whitebark pine) is an associate, especially at higher elevations or in dry rocky or porous soils. *Pinus contorta* is commonly associated with *Picea* and *Abies* below 8,500 feet, and *Populus tremuloides* (quaking aspen) is occasionally present. The understory commonly includes *Carex geyeri* (sedge), *Luzula parviflora* (woodrush), *Juniperus communis*, *Vaccinium* spp., *Mertensia* spp. (bluebell), *Aconitum columbianum* (monkshood), and *Lupinus argenteus*.

Picea-Abies-Pinus albicaulis forests occur from about 8,500 feet to treeline in the park. Treeline is about 9,200 – 9,800 feet in the Absaroka Range and 9,400 – 10,000 feet on the Two Ocean Plateau. In the Yellowstone National Park region the *Picea-Abies-Pinus albicaulis* forest is probably best developed where mean annual temperatures are 30°F – 35°F, mean January temperatures are 5°F – 15°F, mean July temperatures are 45°F – 55°F, and mean annual precipitation is 25 – 35 inches.

ALPINE ASSOCIATION

Alpine vegetation is developed more extensively on the Beartooth Plateau, northeast of Yellowstone National Park (Porter, 1962; Johnson and Billings, 1962), but it also occurs on high areas in the park including the Absaroka Range and the Two Ocean Plateau (fig. 6).

Gramineae (Grass family), Cyperaceae (Sedge family), and Juncaceae (Rush family) are abundant in alpine areas of the park as are many other perennial herbs. In the southeast corner of the park, the most common perennial plants include *Bistorta vivipara* (viviparous bistort), *Bistorta bistortoides* (bistort), *Polemonium* spp. (Jacobs ladder), *Potentilla* spp. (cinquefoil), *Salix arctica* (arctic willow), *Saxifraga rhomboidea* (diamondleaf saxifrage), *Saxifraga caespitosa* (matted saxifrage), and *Selaginella densa* (small clubmoss).

Alpine vegetation is found from about 9,200 – 9,800 feet up to the highest peaks. No climatic data are available for the alpine association in Wyoming. At the University of Colorado's alpine climatic station in the Front Range at 12,300 feet, the mean annual, mean January, and mean July temperatures were, respectively, 26°, 7°, and 47°F, some 7° – 10°F

cooler than at the subalpine station at 10,000 feet for the years 1953 – 64 (Marr and others, 1968). Precipitation averaged about 26 inches annually at the subalpine and the alpine stations in Colorado for the years 1953 – 64.

LOCAL VEGETATION AROUND THE CORING SITES

A reconnaissance map of the local vegetation was made in early September, 1966 and 1967. Four mesic to xeric communities and five semiaquatic communities (herein called vegetation types) are recognized (fig. 7). Of the mesic to xeric communities, *Pinus contorta* forest surrounds the coring area, and *Picea-Abies-Pinus albicaulis* forest grows down to the base of the steep slope along the north edge of the Two Ocean Plateau (fig. 7). Grass-forb meadows grow on gentle slopes underlain by silty lake sediments, and *Artemisia* openings occur on south-facing steeper slopes underlain by gravel (fig. 7). The two forest types and the *Artemisia* openings are predominant in the regional vegetation and were discussed in the

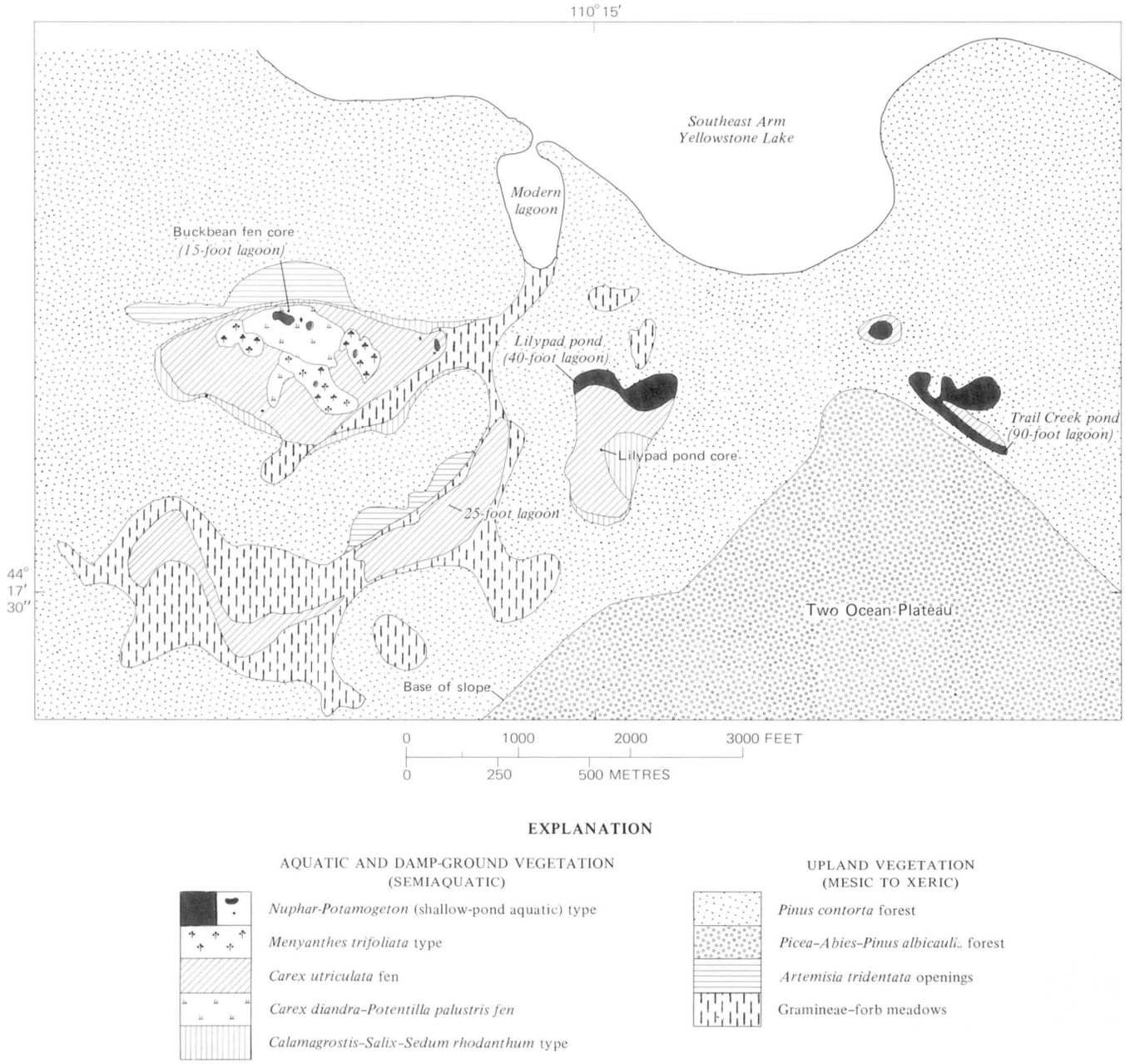


FIGURE 7.—Map of local vegetation around coring sites, showing surface sample and core localities at Buckbean fen and Lilypad pond.

preceding section. Grass-forb meadows are locally common where lake silts are present. The five semiaquatic types are discussed in the following paragraphs.

NUPHAR-POTAMOGETON TYPE

This type is the only true aquatic community. It is found in ponds on Buckbean fen and Lilypad pond (figs. 7, 8, and 9). The aquatic flora contains *Nuphar luteum* ssp. *polysepalum* (yellow pond lily), *Utricularia vulgaris* (common bladderwort), *U. minor* (small bladderwort), *Potamogeton alpinus* (northern pondweed), and *Potamogeton* sp. (pondweed). Only two or three of these species usually occur in any one pond.

MENYANTHES TRIFOLIATA TYPE

The *Menyanthes trifoliata* type occurs locally only in Buckbean fen (fig. 7) and perhaps should be included in the *Nuphar-Potamogeton* type. It contains mainly *Menyanthes trifoliata* (buckbean) with occasional *Carex utriculata* (sedge). The dominant moss is *Drepanocladus* sp. These species grow on organic mud which was covered with a few inches of water in the fall in 1966 and 1967. The mudflats may be filled-in remnants of small ponds.

CAREX UTRICULATA TYPE

The *Carex utriculata* type is the most widespread of the fen communities (figs. 7, 8, and 10). Its habitat ranges from standing water to fairly dry peaty turf.

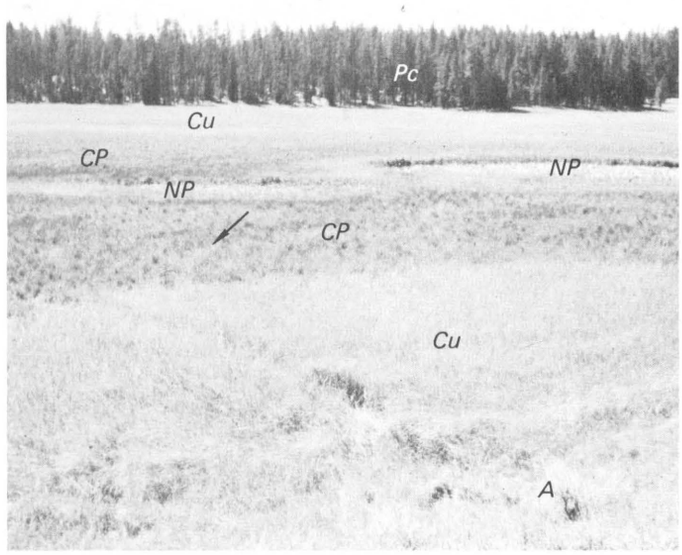


FIGURE 8.—Coring site (arrow) at Buckbean fen; viewed from the north. Vegetation types are *Pinus contorta* (*Pc*), *Carex diandra - Potentilla palustris* (*CP*), *Carex utriculata* (*Cu*), which is 3–4 feet high, *Nuphar - Potamogeton* (*NP*), and *Artemisia* (*A*).

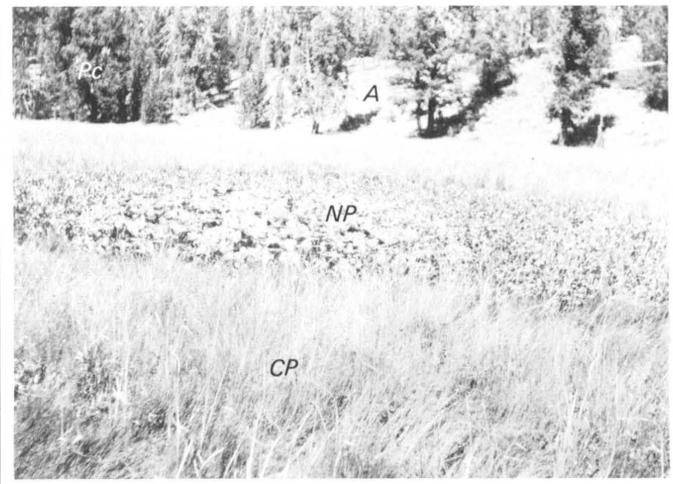


FIGURE 9.—Closeup of small pond shown on left in figure 8. Vegetation types are *Carex diandra – Potentilla palustris* (*CP*) *Nuphar - Potamogeton* (*NP*), *Artemisia* (*A*) opening in *Pinus contorta* (*Pc*) forest. Sedges in foreground are about 1 foot high. View to northwest.

Carex utriculata is by far the dominant plant, with occasional *Carex aquatilis*, and rare *Galium trifidum* (small bedstraw), *Salix ligulifolia*, *S. subcoerulea* (blue willow), and *Persicaria amphibia* (water smartweed). The dominant moss is *Drepanocladus* sp.

CAREX DIANDRA-POTENTILLA PALUSTRIS TYPE

This fen community is one of the most distinctive of the semiaquatic communities (fig. 11). It is limited to the Buckbean fen. The fen had no standing water on it in late summer, 1966 and 1967, but the roots of the plants were in water-saturated peat. The dominant plants are *Carex diandra*, *C. limosa*, *C. aquatilis*, *Potentilla palustris* (marsh cinquefoil), *Eriophorum*

FIGURE 10.—*Carex utriculata* type. Extensive poorly drained flats underlain by peat and covered by 3- to 4-foot-high sedges.

FIGURE 11.—*Carex diandra – Potentilla palustris* type. Poorly drained flats underlain by peat and covered by sedges and other forbs 0.5 – 2 feet high.

sp. (cottongrass), with occasional *Galium trifidum*, *Calamagrostis inexpansa* (northern reedgrass), *C. canadensis* (bluejoint grass), *Menyanthes trifoliata* and *Carex utriculata*. The dominant moss is *Drepanocladus* sp.

CALAMAGROSTIS-SALIX-SEDUM RHODANTHUM TYPE

The community grows mainly around the margins of the depressions, though an impoverished form of this community grows on a gently sloping surface on the south part of Lilypad pond (fig. 7). This community is the richest of the semiaquatic communities. Common plants are *Sedum rhodanthum* (rosecrown), *Pedicularis groenlandica* (elephantella), *Gentianopsis thermalis* (Rocky Mountain fringed gentian), *Anemone multifida* (globose anemone), *Salix subcoerulea*, *S. ligulifolia*, *Calamagrostis canadensis*, *C. inexpansa*, *Luzula parviflora*, *Carex canescens*, and *Aster* spp., with occasional *Pentaphylloides floribunda* (shrubby cinquefoil), *Bromus* sp., *Deschampsia caespitosa* (tufted hairgrass), *Luzula spicata* (spike woodrush), *Carex phaeocephala*, and *Geum macrophyllum* (large-leaf avens). The dominant mosses are *Climacium dendroides* and in wetter places *Aulacomnium palustre* and *Helodium blandowii*. *Drepanocladus* sp. is less common in this community.

OTHER PALEOBOTANICAL WORK IN THE AREA

Three cores from nearby localities were recently analyzed for pollen (H. E. Wright, Jr., written commun., 1967; Waddington and Wright, 1970, 1974). One of these was taken at Cub Creek pond 12 miles west of the East Entrance to Yellowstone National Park (SS – 26 in fig. 12), where modern vegetation is similar to that of Buckbean fen. The other cores were collected from two ponds in steppe vegetation near Cody, Wyo. Cub Creek pond pollen curves closely resemble those from Buckbean fen and suggest a similar paleoecological history. A C^{14} - date on pine, where it shows an abrupt increase at the boundary between the two major zones, is 11,630 ± 180 years B.P. (sample I – 2285). The record from the two ponds near Cody dates from after Altithermal time, and the sequences are difficult to correlate with that at Buckbean fen.

Other Wyoming pollen diagrams are of cores taken from lower elevations and are dominated by steppe elements. R. C. Bright (written commun., 1967) has two unpublished diagrams from sites near Pinedale just south of the Wind River Range (fig. 12); one pollen sequence dates from late Pinedale to present time, and the other from middle Pinedale(?) to present time. Hansen (1951) reported two postglacial diagrams from the Eden Valley archeological site (fig. 12).

Bright (1966) discussed vegetation history inferred from pollen and plant macrofossil diagrams of cores from Swan Lake,west of Red Rock Pass, southeastern Idaho (fig. 12). Red Rock Pass also has a steppe vegetation at present, and the diagrams are dominated by pollen from steppe plants during postglacial time. The Swan Lake record extends back to about 12,000 years B.P.

Elsewhere in the Rocky Mountains, pollen records have been published from Glacier National Park, Mont. (Hansen, 1948); from the Front Range, Colo., (Pennak, 1963; Maher, 1972); from the San Juan Mountains, Colo. (Maher, 1963); and from the Chuska Mountains, N. Mex.(Bent and Wright, 1963; Wright and others, 1973). Bent and Wright (1963) and Maher (1963) include pollen surface samples as well as fossil-pollen diagrams.

POLLEN SURFACE SAMPLES

Pollen released by plants may be preserved in certain depositional environments. The pollen rain on any surface bears some relationship to the vegetation associations from which it is derived (Davis, 1965). If pollen rain and modern vegetation are known quantitatively, a transform function can be derived that will convert pollen percentages to numbers of plants growing in the region (Davis, 1963). If only the broad vegetational associations are known, as in Yellowstone National Park, these associations may be recognizable from their pollen rain, even though quantitative terms cannot be used. If fossil and

modern pollen assemblages are similar, it is assumed that they were derived from similar vegetation associations. Yellowstone National Park is well suited for comparison of surface pollen assemblages with fossil pollen assemblages because of its undisturbed vegetation and simplicity of forest composition.

The relationship between the modern pollen rain and modern vegetation was examined for analogs for interpreting fossil pollen assemblages. Surface mud samples were collected for pollen analysis from ponds in the major vegetation associations of the park (fig. 12; table 2). Where pond sediments were not available moss polsters were collected. A description of the vegetation association around each surface-sample site (table 2) aids in comparing the pollen rain with the vegetation associations. The results of the surface-sample study are plotted in figure 13.

Pollen was prepared for analysis by taking about one cm^3 of sediment and adding successively KOH, HCl, HF, HCl, and acetolysis solution (9 parts acetic anhydride + 1 part H_2SO_4). The preparations were mounted in silicone oil (viscosity 12,000 centistokes) for preservation and counting. Pollen percentages are based on the sum of 300 or more grains (for most samples) of total terrestrial-plant pollen (fig. 13).

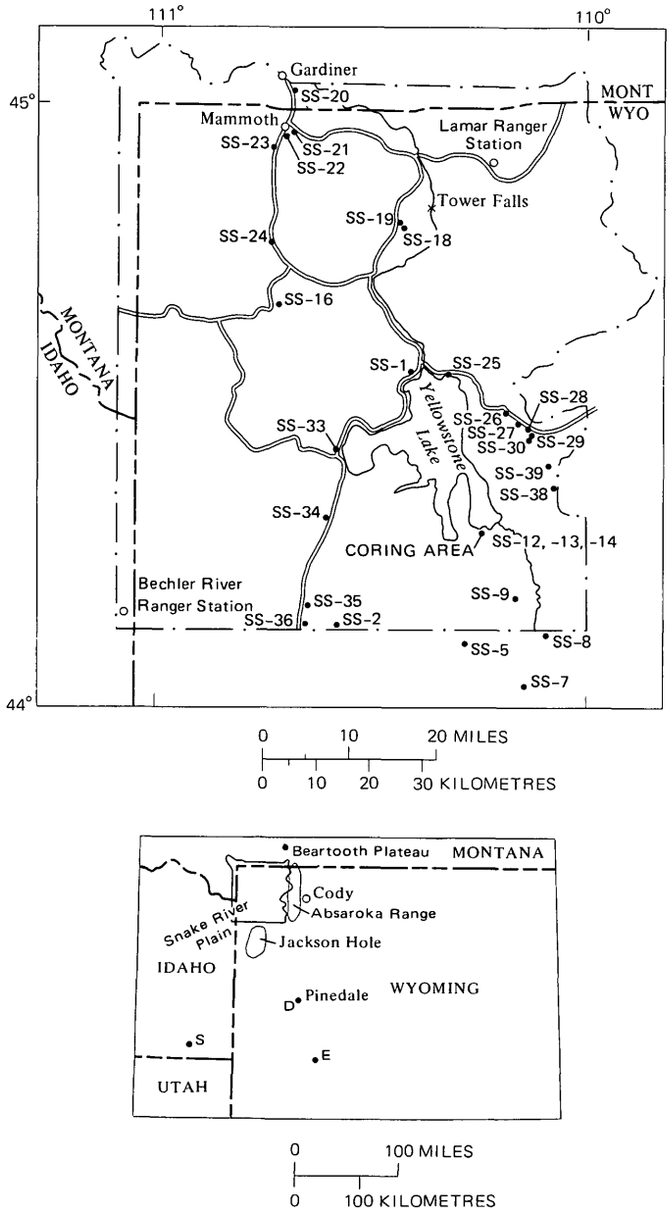


FIGURE 12.—Map of Yellowstone National Park, showing localities of surface samples and coring area. Surface sample SS – 26 is Cub Creek pond (Waddington and Wright, 1970). SS – 12, – 13, and – 14 are surface samples from the coring area. Lower map shows location of other fossil pollen work: E, Eden Valley archeological site (Hansen, 1951); S, Swan Lake (Bright, 1966); D, Dew Lake (R. C. Bright, unpub. data, 1967).

SURFACE SAMPLES FROM THE *ARTEMISIA* STEPPE

Pollen rain in the *Artemisia* steppe association near the north edge of the Yellowstone plateau is fairly distinctive (fig. 13). *Pinus* pollen percentages are lower (45 – 60 percent) than almost anywhere else in the park, and Chenopodiaceae-Amaranthaceae (hereafter called Cheno-Ams) are abundant. *Sarcobatus* (greasewood) is nearly 20 percent in sample SS – 20 and is absent in sample SS – 21 (figs. 12 and 13). *Artemisia* pollen percentages are suprisingly low (less than 10 percent) considering that *Artemisia tridentata* grows abundantly at sites SS – 20 and SS – 21.

Maher (1963) found low *Artemisia* percentages at low elevations near the San Juan Mountains, Colo., and H. E. Wright, Jr. (unpub. data, 1967) found similar results in the upper levels of cores near Cody, Wyo. Bright (1966). however, found 20 – 60 percent *Artemisia* and less than 10 percent *Pinus* in surface samples from a steppe region in southeastern Idaho. Bright's samples were from a largely unforested area of steppe, whereas the other samples were from steppe regions bordered by large forests.

Pinus and *Picea* pollen in the *Artemisia* steppe samples probably are the same species that occur at higher elevations in the park. The few grains of *Picea* pollen probably represent *Picea engelmannii*. *Picea pungens* (blue spruce), a spruce of lower elevations, is not abundant in the park, and McDougall and Baggley (1956) list only one record of it. The *Pinus* pollen represents mainly *Pinus contorta* type, though no attempt was made to differentiate *Pinus ponderosa*, which does not occur in northwest Wyoming and adjacent areas (Critchfield and Little, 1966). *Pinus contorta* type pollen is distinct from that of *Pinus*

TABLE 2.—*Locality and description of surface samples and collection stations, Yellowstone National Park and vicinity*

No. in fig. 12 (SS—)	Elevation (ft above sea level)	Locality	Description
1	7,840	North of Lake Lodge, north edge of Yellowstone Lake.	Surface muds of small artificial pond. Forb meadow opening in *Pinus contorta* forest.
2	9,140	Huckleberry Ridge 4.2 miles east of South Entrance.	Surface muds of small pond. *Carex*-Gramineae meadow in *Picea-Abies* parkland. *Pinus albicaulis* in nearby areas, but none at the site.
5	8,660	2.3 miles south of Fox Creek patrol cabin south of park boundary, at west edge of large burn area.	Surface muds of small pond; pond surrounded by mosses and some Cyperaceae species, forest was mixed *Pinus contorta-Picea-Abies*.
7	8,100	Two Ocean Pass, south of the park.	Moss polster from large sedge fen. Fen with *Carex utriculata*, *C.* spp., and *Salix* spp., *Pinus contorta* locally up to 8,300 ft, but *Picea-Abies-Pinus albicaulis* forest on surrounding slopes.
8	7,860	Near outlet at west end of Bridger Lake, in Yellowstone River valley 0.5 mile south of park boundary.	Surface muds; *Carex* fen surrounds outlet area; *Pinus contorta* dominates valley-bottom forest; *Picea* and *Abies* grow on higher valley slopes.
9	9,880	Lake on Two Ocean Plateau between Phlox and Lynx Creeks and 3 miles north of south boundary of park.	Moss polster from margin of lake; alpine vegetation with *Picea-Abies-Pinus albicaulis* parkland on nearby slopes.
12	7,750	South edge of Buckbean fen (fig. 5).	Surface muds from *Carex utriculata* community.
13	7,750	....do	Moss polster from *Calamagrostis-Salix-Sedum rhodanthum* community.
14	7,750	Near north side of Buckbean fen (fig. 5).	Surface muds from small pond. Surface peat from the core in the Buckbean fen; *Carex diandra-Potentilla palustris* fen.
16	7,940	1.1 miles east of Beryl Spring in Gibbon Canyon, southeast of Gibbon Geyser Basin.	Surface muds of pond. Aquatics *Nuphar*, *Potamogeton*, and *Callitriche* in pond; narrow ring of *Carex aquatilis* and *C. utriculata* around pond margin; forest is pure *Pinus contorta* with understory of *Juniperus communis*.
18	10,000	North side of Mount Washburn, along moist streambank just above treeline.	Moss polster; tundra vegetation with *Pinus albicaulis* parkland just below.
19	9,760	Northwest side of Mount Washburn; near generator.	Soil sample. *Pinus albicaulis-Picea* parkland, *Abies* rare.
20	5,360	About 1 mile south of North Entrance of park.	Surface muds from small (ephemeral?) pond; steppe with *Sarcobatus vermiculatus*, *Artemisia tridentata*, and abundant *Bromus*, *Elymus*, and other Gramineae.
21	5,960	About 1 mile southeast of Mammoth near Gardner River.	Surface muds from pond; pond surrounded by dense growth of *Scirpus* cf. *acutus* and other sedges, grasses, and rushes; upland steppe vegetation with *Artemisia tridentata*, *Sarcobatus*, *Chrysothamnus*, and numerous Gramineae.
22	6,800	Hoodoos landslide area about 1 mile south of Mammoth.	Surface muds from pond; open *Populus tremuloides-Pseudotsuga* forest; *Shepherdia canadensis*, *Ceanothus velutinus*, *Juniperus virginiana*, and *Artemisia tridentata* common in open areas.
23	7,240	Swan Lake Flat, Gardners Hole southwest of Mammoth.	Mud from between rocks in depression; large open meadow with *Carex*, Gramineae, *Pentaphylloides floribunda*; *Artemisia tridentata* on higher unforested slopes below *Pinus contorta* forest.
24	7,560	South Twin Lake, north from Norris Junction.	Surface muds from north end of lake; *Nuphar*, *Myriophyllum*, and *Sparganium* in lake; *Vaccinium*, *Kalmia polifolia*, *Carex*, and Gramineae along margin; *Picea* and *Abies* sparse near lake; *Pinus contorta* forest on upland.
25	7,750	Squaw Lake on north edge of Yellowstone Lake.	Moss polster from east side of lake; a few *Picea*, *Abies*, and *Pinus albicaulis* near lake; Gramineae-*Artemisia tridentata* steppe surrounding lake; mainly *Pinus contorta* forest on surrounding uplands.
26	8,200	Cub Creek pond about 1.6 miles east of Yellowstone Lake along East Entrance Road (also site of Waddington and Wright's (1970) core).	Surface muds from north edge of pond; large *Carex utriculata* fen surrounding lake; upland forest is *Pinus contorta-Picea-Abies*-with occasional *Pinus albicaulis*.
27	8,414	Southwest side Sylvan Lake, on East Entrance Road.	Surface muds from shallow bay; *Potamogeton alpinus* and *Sparganium* in bay; few pond margin *Carex*; *Picea-Abies-Pinus albicaulis-Pinus contorta* forest.
28	8,466	Southeast end of Eleanor Lake on East Entrance Road.	Silty surface sands. *Picea-Abies-Pinus albicaulis-Pinus contorta* forest.
29	9,000	First pond on stream south of Eleanor Lake.	Surface muds from northwest shore of pond; *Isoetes* in pond; *Picea-Abies-Pinus albicaulis* forest. *Juniperus communis* and *Ledum glandulosum* in understory.
30	9,080	Highest lake south of Eleanor Lake.	Surface muds from north end of lake; *Vaccinium*, *Carex*, and *Phyllodoce empetriformis* on shore; *Picea-Abies-Pinus albicaulis* forest.
33	7,790	Duck Lake near West Thumb.	Surface muds from southwest end of lake; *Sparganium angustifolium*, *Persicaria amphibia*, and *Isoetes* in lake; *Carex vesicaria* and several Gramineae spp. around lake border; *Picea-Abies* on south and east sides of lake, *Pinus contorta* elsewhere.
34	7,780	Lewis Lake.	Surface muds from fen on north side of lake; *Carex utriculata*, *Persicaria amphibia*, *Salix* sp., and *Vaccinium* sp. in fen; surrounded by *Pinus contorta* forest.
35	7,380	Small artificial(?) pond between road and Lewis Canyon about 3 miles north of South Entrance.	Surface muds from pond; *Pinus contorta* forest.
36	6,880	Pond between road and Snake River 0.2 mile north of South Entrance.	Surface muds from pond; pond aquatics are *Nuphar luteum*, *Sparganium angustifolium*, *Eleocharis macrostachya*, and *Carex* spp.; forest is *Pinus contorta* with reproduction of *Pinus flexilis*(?).
38	9,684	Pond 1 mile northwest of Mount Schurz, Absaroka Range.	Surface muds from pond; parkland near upper edge of *Picea-Abies-Pinus albicaulis* forest.
39	9,640	Pond at southeast end of saddle southeast of Mount Langford, Absaroka Range (pond not shown on Eagle Peak quadrangle).	Surface muds from pond; *Picea-Abies-Pinus albicaulis* parkland.

flexilis and *Pinus albicaulis*. (See "Pollen and Seed Identification," p. E24). The latter two species are haploxylon pines with verrucae on the distal face of the pollen grain; the former species is diploxylon and has no verrucae (Ting, 1966, p. 7). Pollen of *Pinus albicaulis* type includes pollen of *Pinus flexilis*. Ecological considerations suggest that, of these two, *Pinus flexilis* pollen should prevail in the *Artemisia* steppe

and *Pinus albicaulis* pollen should dominate in higher vegetation associations, although no distinction between pollen of these pines is made here.

SURFACE SAMPLE FROM *PSEUDOTSUGA* ASSOCIATION

Pollen rain from one sample in an open *Pseudotsuga* forest cannot be distinguished from that in other forest types. Less than 1 percent *Pseudotsuga* pollen was found (fig. 13). *Pseudotsuga* is apparently a very small pollen producer; in other surface sample studies less than 5 percent *Pseudotsuga* pollen is usually found, even in *Pseudotsuga* stands (Bent and Wright, 1963; Maher, 1963; Bright, 1966). Its pollen apparently ruptures easily; the grains found in this study were commonly broken. Small fragments cannot be identified; hence,counts of *Pseudotsuga* may be low partly because of poor preservation. No other pollen types diagnostic of this vegetation association were found.

SURFACE SAMPLES IN *PINUS CONTORTA* FORESTS

Pinus pollen makes up over 80 percent of the pollen rain in *Pinus contorta* forests, and nonarboreal pollen is low except in large meadows (fig. 13; table 2). *Pinus contorta*-type pollen is usually substantially more abundant than *Pinus albicaulis* type. *Abies* and *Picea* pollen range from 0 to 1 percent in pure *Pinus contorta* stands and from 1 to 4 percent where these species grow locally in mixed forests with *Pinus contorta.* Diversity of pollen types is least in this vegetation association.

SURFACE SAMPLES FROM *PICEA-ABIES-PINUS ALBICAULIS* FORESTS

Pinus pollen percentages are 80 and 85 percent, *Picea* is over 3.5 percent, and *Abies* is 1.5 percent in this forest association (fig. 13). *Pinus albicaulis* type pollen is several times as abundant as *Pinus contorta* type.

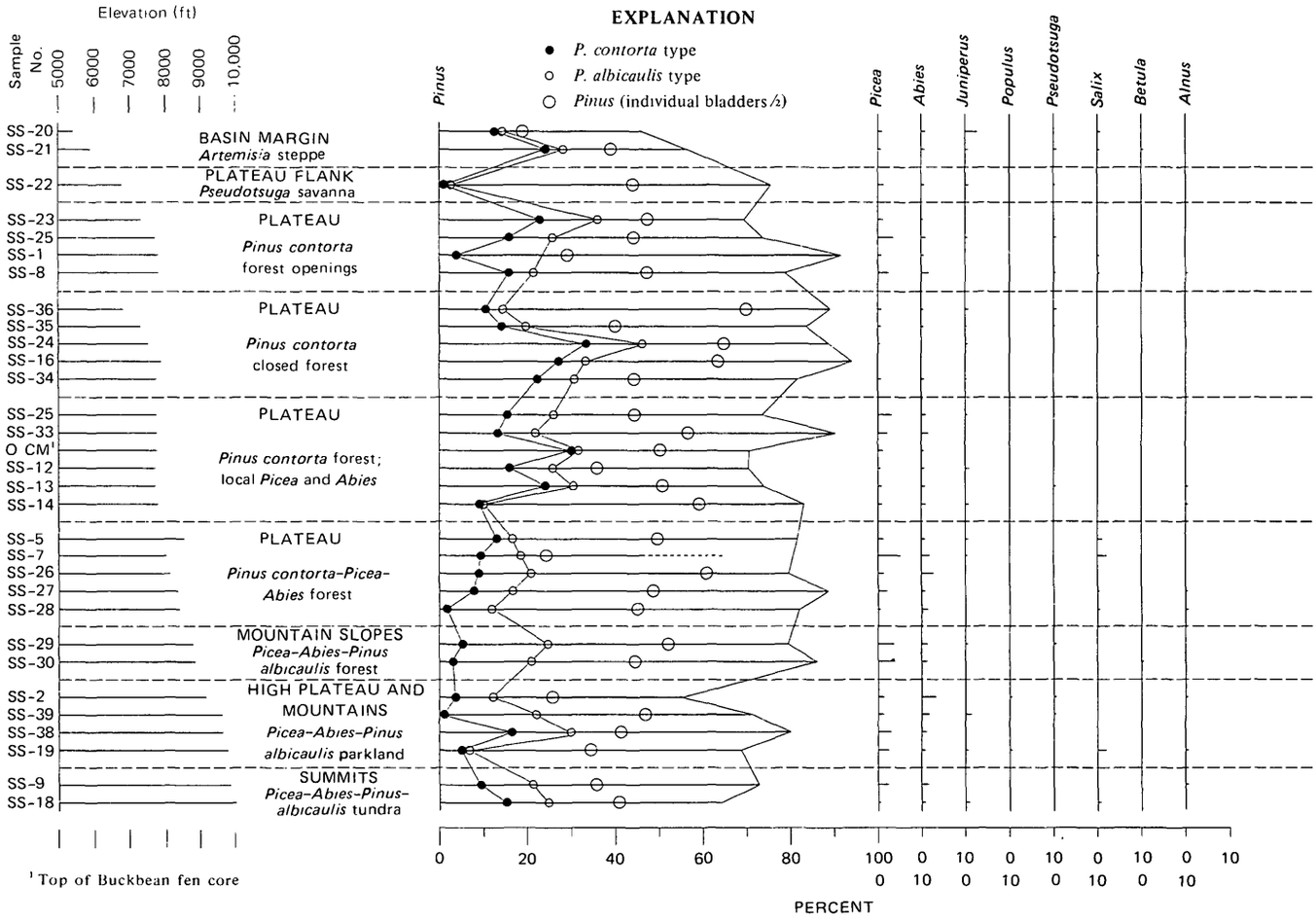


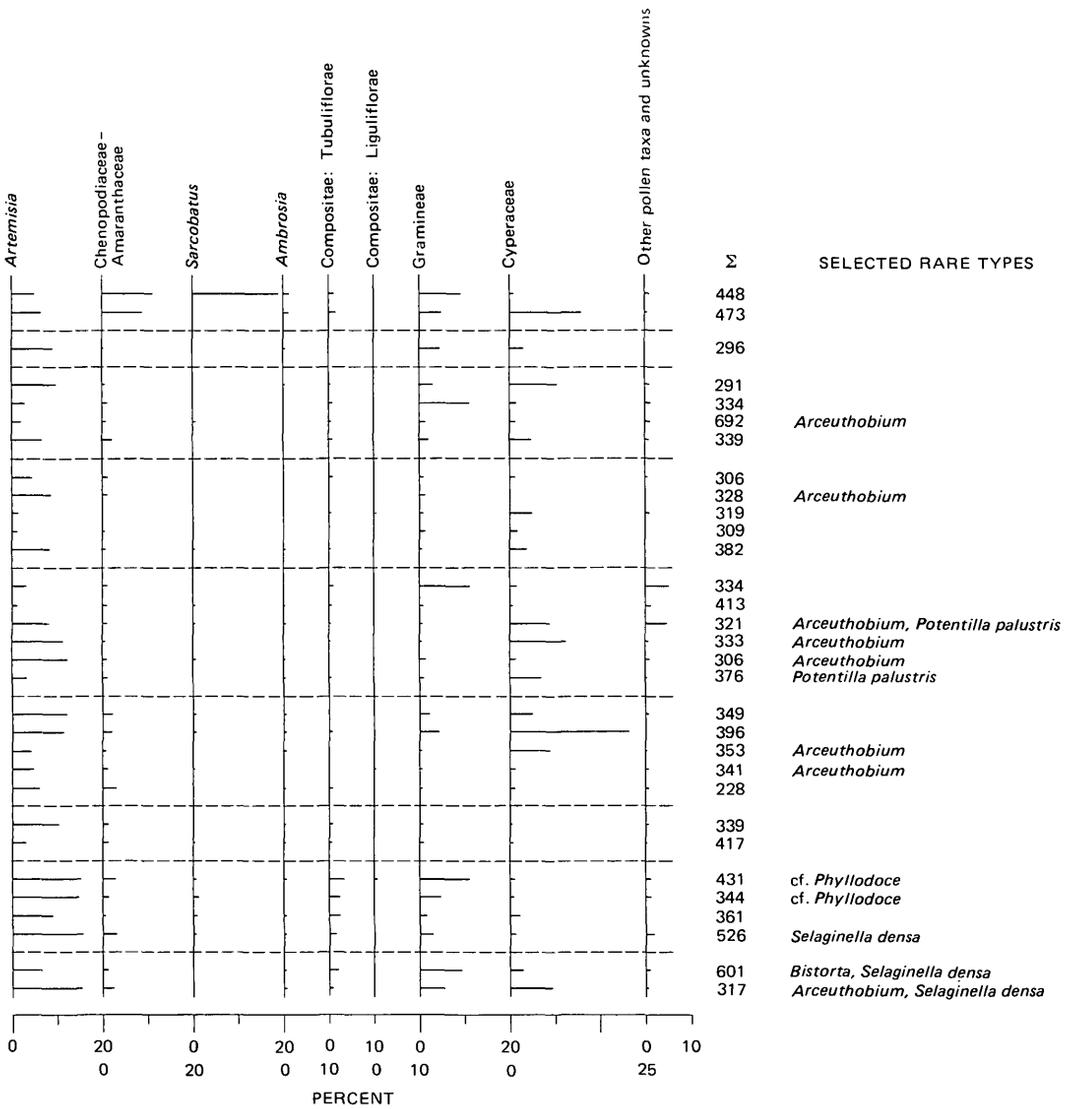
FIGURE 13.—Pollen from surface samples arranged by elevations and by vegetation types. Dashed line in sample SS – 7 shows

SURFACE SAMPLES FROM *PICEA-ABIES-PINUS ALBICAULIS* PARKLANDS AND TUNDRA

Insufficient data are available to distinguish high-level *Picea-Abies-Pinus albicaulis* parklands from tundra, but together they can be distinguished from other associations by their pollen rain (figs. 13, 14). Parklands and tundra receive an average of about 70 percent *Pinus* pollen in Yellowstone National Park. Samples from these associations differ from those in forests by having low but consistent values of Compositae (1 – 3 percent) and Gramineae (4 – 10 percent), and they do not have the high Cheno-Ams or *Sarcobatus* of steppe samples. Occasional grains of plants common in alpine associations, such as *Bistorta* and *Selaginella densa*, help to define alpine and subalpine parkland pollen rain.

Maher (1963) found that in the San Juan Mountains, Colo., the *Pinus* pollen values are higher in alpine tundra than in *Picea-Abies* forests. Such is not the case in Yellowstone National Park samples. However, *Pinus albicaulis* is a common tree in *Picea-Abies* forests just below treeline in Yellowstone National Park; no ecologically analogous species is present in the San Juan Mountains. Also, my alpine sites are all from slightly above timberline. Samples from far above timberline might have higher *Pinus* percentages.

Artemisia pollen percentages are also higher (up to 18 percent) in subalpine and tundra areas than at lower elevations where *A. tridentata* grows (up to 7



the *Pinus* curve with Cyperaceae excluded from the pollen sum. Pine curves are cumulative.

percent) both in Yellowstone National Park and in the San Juan Mountains. Maher (1963) suggested that cirque lakes contain high values of *Artemisia* because the lakes remain frozen during the early flowering season. Pollen that falls on the ice is washed out during the melt season, and only pollen from late-flowering plants, such as *Artemisia*, is incorporated into the lake sediments. This process may explain the abundance of *Artemisia* pollen in high-elevation lakes in Yellowstone National Park.

Whether the flowering season is important or not, the source of the *Artemisia* pollen in alpine surface samples is still a problem. Does the pollen come from local subalpine or alpine species or does it blow in from steppe vegetation surrounding the park? The alpine species are small and produce less pollen than the larger steppe species. Pollen of other steppe species apparently were blown 10 – 20 miles laterally and 4,000 – 5,000 feet upward before deposition.

The presence of *Sarcobatus* and Cheno-Ams pollen in small amounts at some alpine sites (fig. 13) provides evidence that pollen from the steppe association does blow up to the tundra; these taxa grow abundantly in steppe areas but are absent from alpine areas. Compositae and Gramineae pollen in alpine sites may likewise blow up from their abundant steppe representatives, but plants in these families grow at all elevations in the park. *Pinus* and *Picea* certainly blow up from just below treeline, and in tundra areas where pollen production is low, relatively small amounts of pollen blowing in from afar could yield high pollen percentages.

POLLEN RATIOS

Ratios between two pollen types often show trends that are masked by other curves on the aggregate pollen diagram (Maher, 1963). A number of ratios were tested in the surface sample and fossil pollen diagrams, and two proved useful. *Pinus albicaulis/ Pinus contorta* ratios delimit *Picea-Abies-Pinus albicaulis* forests from other forest types (fig. 14). The dominance of *Pinus contorta* over such large areas in the park makes this pollen ratio low (less than 1.3) except where *Pinus albicaulis* grows locally. At several sites preservation of pine pollen was not good enough to identify a large proportion of the grains as to species. Even with imperfect identification, however, most pine-pollen ratios were ecologically reasonable. The assumption that the two *Pinus* types are preserved equally well and are representative of the entire sample seems valid.

Gramineae/*Pinus* ratios distinguish forested from nonforested areas (fig. 14). These ratios are high (about 0.050 – 0.209) in the steppe and alpine vegetation associations and in large forests openings; they are low (less than 0.025) in forested areas (fig. 14; table 2).

Picea/Pinus ratios that were used successfully by Maher (1963) as an indication of subalpine vegetation show no meaningful trends in Yellowstone National Park surface samples, probably because of pollen production of *Pinus albicaulis* in the subalpine vegetation of the park. Lack of an ecologically analogous pine in the San Juan Mountains makes the *Picea/Pinus* ratio a more effective indicator of subalpine vegetation.

QUATERNARY PALYNOLOGY

MATERIALS AND PROCEDURES

The cores were taken with a modified 2-inch Livingstone piston sampler (Wright and others, 1965) in early October 1966 and early September 1967. Long cores were taken from Buckbean fen and Lilypad pond (fig. 7), and shorter cores were extracted from Trail Creek pond. When core length was less than penetration, it was arbitrarily assumed for labeling purposes that the basal segment of each drive was missing. The cores were wrapped in the field in saran and heavy-duty aluminum foil, sealed with masking tape, and stored in a refrigerator. Reported here are pollen and macrofossil analyses from the 10-m core taken in Buckbean fen and macrofossil analyses from the basal 2 m of the core taken in Lilypad pond. For Buckbean fen, pollen samples were taken at about 10-cm (centimetres) intervals in the basal 2 m and at about 20-cm intervals in the remainder of the core. These samples received the same chemical treatment as the surface samples.

Plant macrofossils were prepared by soaking a 50-ml (millilitre) sample of sediment for as long as 2 days in very weak (less than 5 percent) KOH. The sample was then washed through 32- and 140-mesh (0.5 and 1.0 mm) screens with a shower nozzle. Macrofossils were picked from the washed samples with a small brush and stored in glycerin.

The pollen was identified by comparison with the reference collection at the U.S. Geological Survey, Denver, Colo. The collection is large but is incomplete for Rocky Mountain species. Macrofossils were identified by comparison with the seed collection at the University of Colorado Herbarium. The collection is small and is fairly complete only for taxa encountered as fossils.

The certainty of identification of pollen and macrofossils is indicated by the use of "type" and "cf."

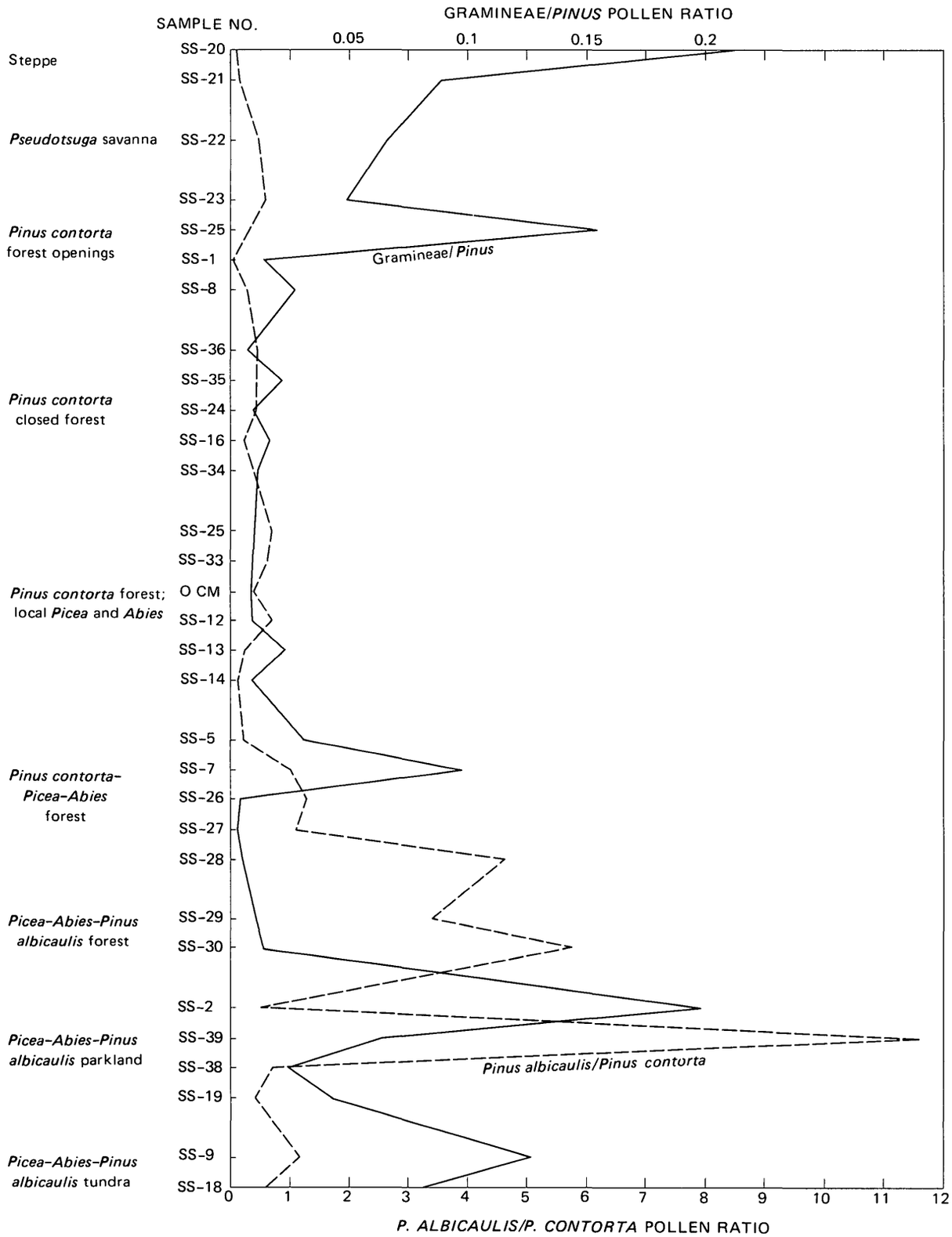


FIGURE 14.—Ratios for surface pollen samples.

If the name of a taxon is followed by "type," the specimen matches not only that taxon but also others, and the name is selected for ecological or geographical reasons. The use of "cf." (=confere) means that identification is uncertain because of poor preservation, inadequate reference materials, or ill-defined morphology (Watts and Winter, 1966).

Relative pollen frequencies were determined with few exceptions from counts of at least 300 grains/slide. The slides used in this study are stored in the University of Colorado Museum. Percentage curves in the pollen diagram (fig. 15) are based on a pollen sum of total pollen excluding spores and aquatic-plant pollen.

The *Pinus* pollen curve is a cumulative plot of four curves (fig. 15). *Pinus albicaulis* type is plotted at the base of the total pine curve. Above that curve is plotted *Pinus contorta* type. The next higher curve compresses individual bladders (treated as half grains) of *Pinus* pollen (times 1/2, that is, two half pines are counted as one pine); the top curve comprises whole *Pinus* grains that could not be differentiated as to

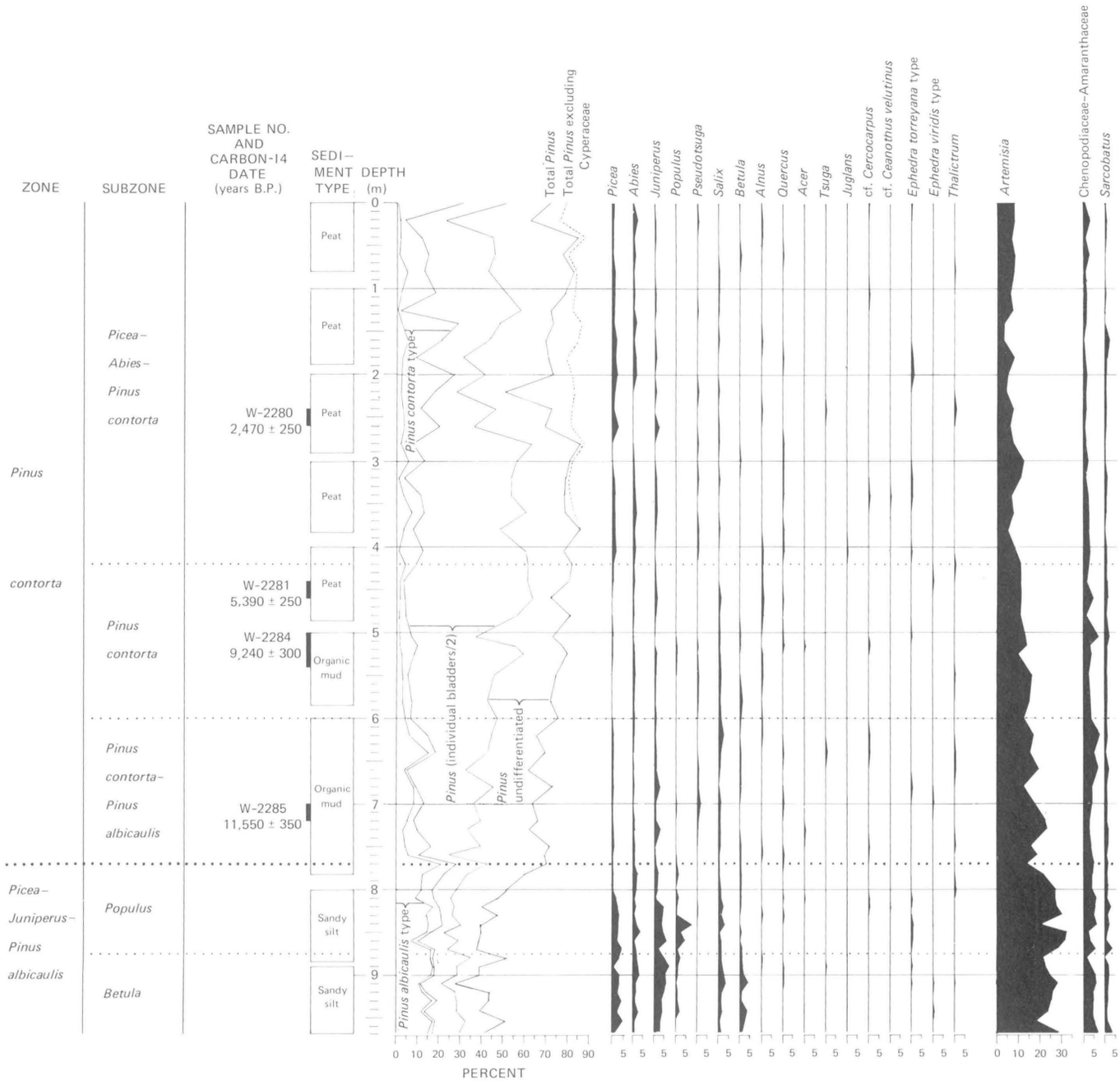
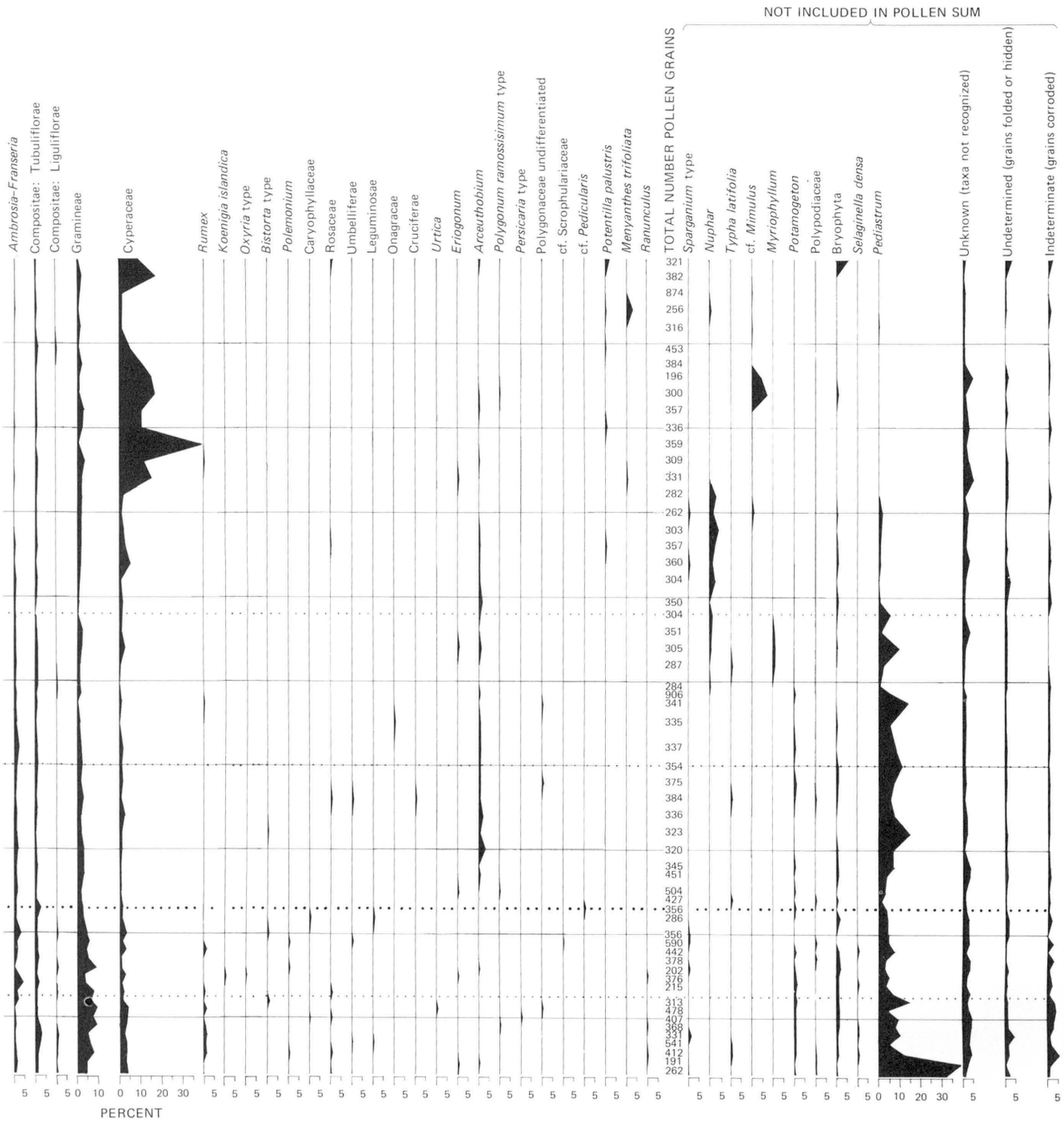


FIGURE 15.—

species. A separate total *Pinus* pollen curve is plotted for the upper 400 cm of the core. This curve excludes Cyperaceae pollen from the pollen sum because of its local origin.

The pollen diagram (fig. 15) is divided into two pollen assemblage zones (hereafter simply called zones). The zones are biostratigraphic units called assemblage zones as defined by the American Commission on Stratigraphic Nomenclature (1961). The zones are defined by their fossil content and position in the core. The name of each zone carries implications about the ecological conditions at the time of deposition. Similar zones appear in the core from Cub Creek pond (Waddington and Wright, 1970) and other cores (R. G. Baker, unpub. data). This regional similarity of zones implies that vegetation changes



Pollen from Buckbean fen core.

were similar throughout the region. The zonation of the diagram is summarized in table 3, and the pollen counts for Buckbean fen are listed in table 4.

The time and stratigraphic relationship between the assemblage zones, the C^{14} dates, and the glacial periods is shown in figure 16.

POLLEN AND SEED IDENTIFICATION

Pollen and spores were identified using the reference collection of the U.S. Geological Survey, Denver, Colo. Plant macrofossils were identified by comparison with a collection that I assembled from the University of Colorado Herbarium. On plates 5–10, the COLO numbers are the University of Colorado Herbarium numbers of voucher specimens for reference seeds, needles, and bracts. RGB numbers are my own collection. Some of the criteria for identification are discussed here so that the pollen and macrofossil taxa can be better evaluated.

SELAGINELLACEAE

Trilete spores in the lower part of the Buckbean fen core match *Selaginella densa* perfectly (pl. 1), and this is the only species reported in the modern park flora (McDougall and Baggley, 1956). It is most common above timberline. Two other species occur in eastern Wyoming (Porter, 1962). Another species, *S. selaginoides*, occurs at middle elevations in western Wyoming, but its spores can be distinguished from those of *S. densa* on morphologic grounds.

PINACEAE

A few grains were found that match *Pseudotsuga menziesii* (pl. 1). *Larix occidentalis* Nutt. and *Larix lyallii* Parl. have similar but smaller grains, and these trees now grow from central Idaho westward (Bright, 1966). *Pseudotsuga* grows locally in Yellowstone National Park. I have, therefore, identified the pollen as *Pseudotsuga*. One needle of *Pseudotsuga* was found (pl. 5).

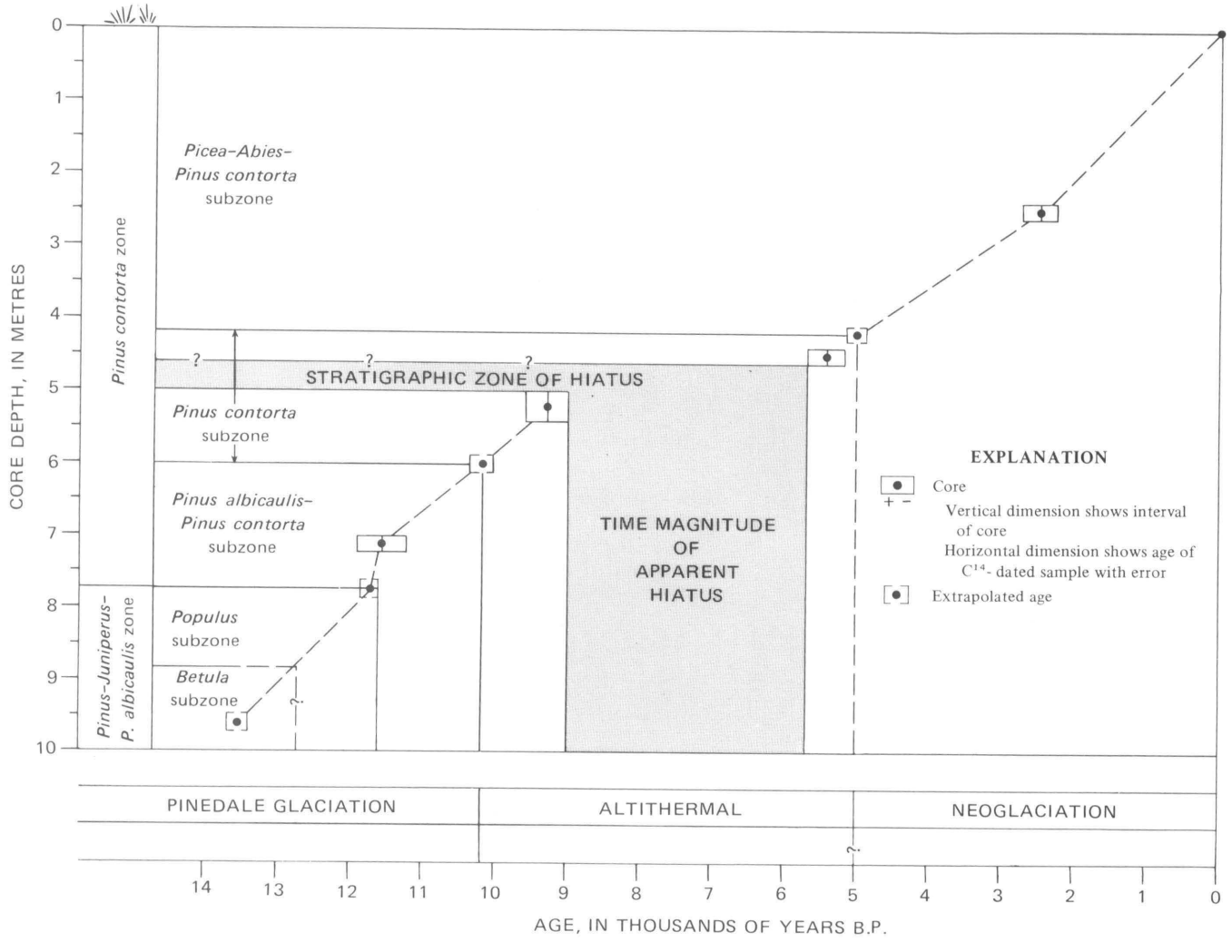


FIGURE 16.—Relationships between assemblage zones, carbon-14 and extrapolated ages, and time-stratigraphic boundaries.

TABLE 3.—*Summary of inferred changes in environment at Buckbean fen during the last 12,000+ years*

Pollen zone	Subzone	Core depth (cm)	C^{14} date (interpolated dates in brackets)	Terrestrial plant community	Aquatic and semiaquatic plant community	Inferred climate	Water depth at coring site (ft)	Lake level above present level	Glacial advance or glacial retreat
Pinus contorta	*Picea-Abies-Pinus contorta*	240, 260	2,470±250	Mixed *Picea engelmannii*, *Abies lasiocarpa*, *Pinus contorta* forest. Sparse *Pseudotsuga menziesii*.	Fen vegetation with *Carex diandra*, *C. utriculata*, *C. vesicaria*, *C. limosa*, *Potentilla palustris*, and *Menyanthes trifoliata*.	Slightly cooler and moister.	0	Present level	Gannett Peak Stade, Neoglaciation.
			[2,800]						
					Small, shallow pond with *Nuphar*; fen with *Carex diandra* and *C. utriculata*, encroaching into pond.		0	10 ft to present level.	Temple Lake Stade, Neoglaciation.
		420	[5,000]						
	Pinus contorta	440, 460	5,390±250	Closed-*Pinus contorta* forest	Shallow-water aquatic vegetation with *Nuphar luteum*, *Myriophyllum* sp., *Naias flexilis*, and *Potamogeton gramineus*.	Maximum warmth and dryness.	[1] 0–35	10-, 15-, 25-, and 40-ft levels.	Altithermal.
			UNCONFORMITY(?)						
		500, 540	9,240±300						
		600	[10,160]						
	Pinus contorta-Pinus albicaulis			Open *Pinus albicaulis-Pinus contorta* forest with *Picea*, *Abies* and *Pseudotsuga* rare.	Aquatic and shoreline macrofossils rare.	Warm ↑ dry cool, ↑ warm	45–65	60-ft level(?)	Late stade, Pinedale Glaciation.
		700, 724	11,550±350						
		770	[2] 11,630±180						
Picea-Juniperus-Pinus albicaulis	*Populus*			*Picea engelmannii-Abies lasiocarpa-Pinus albicaulis* parkland, with *Populus balsamifera* and *Juniperus communis*.	Aquatic and shoreline macrofossils rare.	Cool, moist.	70–100	90-ft level(?)	Middle stade, Pinedale Glaciation.
		875							
	Betula			Tundra(?) but with subalpine herbs, *Juniperus communis* and *Betula glandulosa*. Occasional *Picea* or *Pinus albicaulis* may be present nearby.	Pioneer aquatics *Potamogeton filiformis* and *Potamogeton alpinus*.	Cold, moist.		90-or 110-ft level	Middle stade, Pinedale Glaciation.
		960	[2] 14,360±400						

[1]The 15-ft lagoon, Buckbean fen, dried up during this time.
[2]Date by correlation with Cub Creek pond.

TABLE 4.—*Pollen counts for Buckbean fen,*

Depth in cm	Total *Pinus*	*Pinus* undifferentiated	*Pinus albicaulis* type	*Pinus contorta* type	*Picea*	*Abies*	*Pseudotsuga*	*Betula*	*Salix*	*Juniperus*	*Populus*	*Quercus*	*Alnus*	*Cercocarpus* type	*Ephedra torreyana* type	*Ephedra viridis* type	*Thalictrum*	*Artemisia*	Chenopodeaceae-Amaranthaceae	*Sarcobatus*	*Ambrosia* type	Compositae: Tubuliflorae	Compositae: Liguliflorae
0	230	129	4	97	5	1	0	0	0	0	0	1	0	2	2	0	0	28	3	1	1	1	0
20	241	223	8	10	3	8	3	0	0	1	0	0	1	0	0	0	0	31	13	3	2	1	0
40	748	644	19	85	5	6	0	0	0	4	0	0	1	0	0	0	0	62	10	6	0	4	0
60	200	161	4	35	2	4	0	3	0	0	0	2	0	0	0	0	0	22	7	0	1	2	0
80	262	221	16	25	6	1	0	0	2	0	0	0	0	0	0	0	1	26	5	0	1	1	0
105	357	275	10	72	8	5	0	0	1	1	0	0	1	1	0	0	0	30	9	1	0	8	1
125	278	272	2	4	6	2	1	0	1	1	0	0	0	0	0	0	0	30	7	1	0	4	0
140	143	86	5	52	2	3	0	0	0	0	0	0	0	0	0	0	0	7	3	0	0	1	0
160	211	147	17	47	7	2	0	0	1	1	0	0	1	0	0	0	0	11	2	6	1	2	0
180	253	223	10	20	7	6	0	0	0	2	0	1	0	0	2	0	0	29	4	2	0	3	0
200	246	155	8	83	8	6	0	0	0	0	0	0	0	0	0	4	0	17	5	2	1	4	0
220	181	118	8	55	5	0	2	0	1	2	0	0	0	0	0	0	0	16	4	1	1	2	0
240	223	187	10	26	2	0	0	0	0	0	0	0	1	0	0	0	1	24	3	1	0	5	0
260	228	152	12	64	10	0	0	0	1	7	0	0	0	0	0	0	0	21	2	1	1	3	0
280	241	219	6	16	1	0	0	0	1	0	0	2	0	0	0	0	0	22	3	0	0	1	0
300	211	176	15	20	0	1	0	1	0	0	0	1	0	0	0	0	0	33	6	0	0	2	0
320	238	227	3	8	3	2	2	0	1	2	0	1	0	0	1	0	0	33	3	3	0	2	0
340	280	243	10	27	6	4	0	0	0	4	0	2	0	1	0	1	0	23	9	1	2	4	0
360	231	195	20	16	4	5	0	0	0	3	0	0	0	0	0	0	0	22	7	2	0	1	0
380	260	237	10	13	5	2	2	0	1	1	0	1	0	0	0	0	0	15	8	0	2	2	0
405	272	229	3	40	7	3	2	0	0	0	0	2	2	0	0	1	0	30	11	2	1	2	0
420	249	221	12	16	2	2	0	0	0	1	0	0	1	0	0	0	1	33	7	2	2	0	0
440	282	271	5	6	2	3	1	0	0	1	0	0	1	0	1	0	0	38	6	2	1	2	0
460	220	209	4	7	0	1	0	0	3	4	0	1	3	0	0	0	0	34	14	4	1	3	0
480	235	224	2	9	0	1	0	0	1	1	0	0	1	0	0	0	0	31	4	3	2	3	0
505	208	188	3	17	1	0	0	1	2	0	0	0	0	0	0	1	0	37	21	5	1	4	0
515	697	610	13	74	1	2	1	1	2	0	1	3	0	2	0	0	0	126	29	7	8	5	1
525	271	244	8	19	1	2	0	0	2	3	1	0	1	0	0	0	0	34	12	3	2	2	0
550	248	231	9	8	0	2	2	0	3	2	0	0	1	0	0	0	1	54	9	4	3	1	0
580	241	217	9	15	0	1	1	4	2	1	0	0	0	0	0	0	0	50	11	4	8	2	0
600	265	243	14	8	0	2	0	1	3	4	0	0	1	0	0	0	0	43	10	3	5	5	0
620	243	188	26	29	3	1	0	0	8	2	0	0	1	2	0	0	0	63	27	4	5	4	0
640	266	195	58	13	2	0	0	1	4	4	0	1	0	1	0	0	1	59	19	1	3	2	0
660	207	192	12	3	2	1	1	1	2	3	0	0	0	0	0	0	1	65	22	6	3	3	0
680	236	208	25	3	3	1	1	2	0	10	0	0	0	0	1	0	0	39	12	3	3	1	0
700	203	163	27	13	1	0	5	1	3	2	1	1	0	0	0	0	0	56	13	4	6	2	0
720	227	200	17	10	0	2	2	0	3	4	0	0	0	0	0	0	0	76	10	3	3	5	0
730	277	234	13	30	3	2	1	0	5	12	0	0	0	0	0	0	0	105	14	8	5	4	0
750	361	282	20	59	6	4	0	2	4	2	0	0	1	1	0	0	1	78	17	6	6	1	0
760	294	250	24	20	1	3	0	2	2	2	2	2	1	0	0	0	0	80	17	2	4	3	0
770	249	150	76	23	1	3	0	0	0	2	2	2	0	0	0	0	0	48	17	5	0	8	0
782	172	107	34	31	1	6	0	1	1	6	5	0	0	0	0	0	0	61	12	3	2	4	0
801	182	121	42	19	3	5	0	0	4	6	0	0	0	0	0	0	3	97	15	6	10	3	1
810	279	172	58	49	13	5	0	4	7	1	10	3	2	0	0	1	0	161	35	6	8	9	0
820	175	86	75	14	12	7	2	2	9	19	5	0	0	0	0	0	1	122	26	11	8	4	0
830	179	99	53	27	14	3	1	0	6	0	1	3	2	0	0	0	0	113	18	6	4	7	0
842	79	34	30	15	7	4	0	0	6	7	16	0	0	0	0	1	0	41	13	4	0	2	1
850	149	89	53	7	11	14	0	2	2	16	8	0	1	0	0	0	0	121	9	4	7	5	0
860	83	61	14	8	6	1	0	0	3	13	9	0	1	0	0	1	0	67	7	1	9	4	0
870	136	71	59	6	17	6	0	5	6	7	3	0	0	0	0	0	0	102	20	13	5	4	1
880	167	113	51	3	11	6	0	3	5	15	4	0	2	0	0	0	0	69	5	0	7	3	0
890	186	101	82	3	5	11	0	6	9	33	5	1	1	0	1	0	0	106	18	9	1	6	0
900	157	86	65	6	16	12	0	6	10	20	4	1	0	0	0	0	0	97	23	8	2	5	0
910	101	60	38	3	14	4	0	14	13	21	1	0	2	0	1	1	1	103	21	7	4	9	0
920	144	98	39	7	10	5	0	3	5	15	3	0	1	0	0	0	0	85	16	5	1	10	2
930	233	129	87	17	24	5	0	3	9	19	4	0	3	0	0	0	0	135	24	7	2	14	2
943	160	108	47	5	11	10	0	15	7	16	9	0	0	0	0	1	0	97	18	3	4	6	2
953	98	64	32	2	10	2	0	4	1	6	0	0	0	0	0	0	0	36	9	2	3	3	0
958	109	67	38	4	5	3	0	2	3	7	0	1	0	0	0	0	0	75	18	9	3	4	1

Juniperus pollen is common at the bottom of the core (pl. 1). Species of *Juniperus* cannot be distinguished by their pollen, but needles and a twig of *Juniperus communis* are identified from two levels (pl. 5). *Juniperus communis* is the only juniper that grows from low elevations below the plateau up to and above timberline. *Juniperus virginiana* L. var. *scopulorum* Lemmon grows only at low elevations around Mammoth and in other areas. I believe most of the *Juniperus* pollen to be *Juniperus communis*.

Picea pollen (pl. 1) was not differentiated as to species, but *Picea engelmannii* is the only spruce that grows abundantly on the plateau. The only fir that grows in the park is *Abies lasiocarpa*. Needles of *Picea engelmanii* have been identified (pl. 5). Probably all the spruce and fir pollen belongs to these two species.

Pine pollen (pl. 1) was grouped into haploxylon (with distal verrucae) and diploxylon (without distal verrucae) (Ting, 1966). Two haploxylon pines, *Pinus flexilis* and *Pinus albicaulis*, occur in the park (McDougall and Baggley, 1956). *Pinus flexilis* grows only at low elevations around the margins of the plateau. *Pinus albicaulis* grows mostly up near timberline but also on rocky cliffs and ledges at lower

given in numbers of pollen or spores in tallies

Graminae	Cyperaceae	*Rumex*	*Bistorta* type	*Polemonium*	Caryophyllaceae	Rosaceae	*Ranunculus*	*Arceuthobium*	*Potentilla palustris*	*Nuphar*	*Typha latifolia*	*Myriophyllum*	*Potamogeton*	Polypodiaceae	Bryophyta	*Selaginella densa*	*Pediastrum*	Unknown	Undetermined	Indeterminate	Others
2	29	0	0	0	0	2	0	4	7	2	0	0	0	2	20	0	1	5	9	7	0
9	66	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	2	1	0
12	15	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	14	1	0	0
2	3	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	2	1	3	*Menyanthes* 7.
7	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	4	0	1	0
5	24	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	3	0	0	Caprifoliaceae 1, *Equisetum* 1.
8	45	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	4	1	1	0
2	30	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	18	2	1	0
3	50	0	0	0	0	0	0	1	0	0	0	0	0	0	4	0	0	25	0	0	*Polygonum ramosissimum* type 1.
10	37	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	7	1	0	0
8	34	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	9	2	5	0
2	142	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	1	0
10	36	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	7	3	0	*Tsuga* 1.
5	50	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	16	3	0	*Eriogonum* 1, *Menyanthes* 1.
5	5	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	1	2	3	0
4	3	0	0	0	0	0	0	0	0	4	0	0	0	0	1	0	4	7	0	0	0
5	6	0	0	0	0	0	0	1	0	12	0	0	0	0	0	0	3	5	0	0	0
6	9	0	0	0	0	0	0	2	2	8	0	0	0	0	1	0	3	5	3	2	cf. *Ceanothus velutinus* 1.
5	14	0	0	0	0	0	0	1	0	4	0	0	0	0	2	0	2	9	0	1	*Sparganium* 1.
3	1	0	0	0	0	0	0	1	0	7	0	0	0	0	0	0	0	4	6	0	0
2	6	0	0	0	0	0	0	6	0	0	0	0	0	0	2	0	2	2	5	2	*Juglans* 1.
0	3	0	0	0	0	0	0	1	0	3	0	0	0	0	1	0	16	2	0	0	0
8	3	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	3	11	1	0	0
6	7	0	0	0	0	0	0	3	0	1	0	2	0	0	1	0	30	2	2	0	*Eriogonum* 1.
3	2	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	6	3	1	0	0
3	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	2	4	0
14	3	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	54	15	0	3	0
0	4	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	50	3	0	1	0
3	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	18	4	0	1	Onagraceae 1.
5	5	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	29	3	1	3	0
7	4	0	0	0	0	0	0	1	0	0	0	1	0	0	3	0	39	3	0	0	0
4	7	0	0	0	0	0	0	2	0	0	0	0	3	0	3	0	26	5	1	1	*Polygonum* 1.
10	2	0	0	0	0	2	0	1	0	0	1	0	1	1	1	0	21	2	0	1	Cruciferae 1, Umbelliferae 1.
6	7	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	25	6	0	1	0
6	3	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	47	6	1	1	0
10	3	0	0	0	0	0	0	8	0	0	0	0	0	0	1	0	21	1	0	0	0
10	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	23	10	2	2	0
13	2	0	0	0	0	0	0	1	0	0	0	0	0	0	4	0	16	12	2	5	*Acer negundo* 1.
9	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	13	6	0	0	*Polygonum ramosissimum* 1 *Eriogonum* 1.
8	4	0	0	0	0	0	0	0	0	0	2	0	0	1	1	0	4	3	0	2	0
9	6	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	11	5	0	0	cf. *Pedicularis* 2.
8	3	0	0	0	1	0	0	0	0	0	0	0	0	0	4	0	11	7	3	3	Leguminosae 1, *Equisetum* 1.
11	8	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	15	7	3	0	*Sparganium* 1.
32	7	0	0	1	3	0	0	0	0	0	0	0	0	1	0	0	21	0	15	14	*Sparganium* 1, *Acer* 3, cf. Scrophulariaceae 1.
17	14	5	0	0	0	0	0	0	0	0	0	0	3	0	4	2	34	4	0	0	*Fraxinus* 1.
19	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	13	11	0	10	0
18	1	0	0	1	0	0	0	1	0	0	0	0	0	0	3	0	6	5	2	1	0
12	11	0	0	0	0	0	1	0	0	0	0	0	2	0	4	0	17	6	2	5	*Eriogonum* 1, *Oxyria* 1, *Koenigia* 1.
8	2	0	0	0	0	0	0	0	0	0	0	0	2	0	2	1	7	3	2	4	0
29	8	2	0	0	0	2	0	0	0	0	0	0	1	0	4	0	23	12	1	2	0
20	3	0	0	0	0	0	0	0	0	0	0	0	3	0	3	1	47	7	2	11	*Erigonum* 3.
45	19	7	0	0	0	0	0	0	0	0	0	0	1	0	8	0	21	13	3	18	*Urtica* 3, *Eriogonum* 3.
28	15	0	1	0	1	1	0	0	0	0	0	0	0	0	4	0	37	17	5	11	*Polygonum persicaria* 1.
34	12	2	0	0	0	0	1	0	0	0	0	0	1	0	5	1	29	14	6	9	*Polygonum ramosissimum* type 1, *Plantago* 1.
15	7	4	0	0	0	0	0	0	0	0	0	0	0	0	1	1	32	13	0	3	*Sparganium* 4.
31	19	5	0	0	0	0	0	0	0	0	1	0	1	0	1	2	29	15	9	10	Umbelliferae 1, Leguminosae 1.
31	12	6	0	1	0	2	1	0	0	0	1	0	1	2	3	3	51	17	6	21	0
9	6	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	75	5	0	3	*Eriogonum* 1.
11	10	0	0	0	0	1	0	0	0	0	0	0	1	1	2	0	85	4	5	2	0

elevations on the plateau. Haploxylon pine needles are fairly common in the cores (pl. 5), but no morphological criteria have been found to distinguish *Pinus flexilis* from *Pinus albicaulis* needles. In fact, the living trees are distinguished only by difference in cone length. Considering present distribution, the pollen and needles are referred to *Pinus albicaulis* type, and they almost certainly represent this species.

The only diploxylon pine that grows in or near the park is *Pinus contorta*. *Pinus ponderosa* is absent from northwest Wyoming. Needles are identified with certainty as *Pinus contorta* (pl. 5).

A few grains of *Tsuga* were found in the core (pl. 1). Both *T. mertensiana* and *T. heterophylla* are represented. A *Tsuga* grain also was found in the surface samples, and all grains are attributed to long-distance transport. Both species have mainly a west coast distribution, though both extend inland to northern Idaho.

BETULACEAE

Betula pollen grains are most abundant near the bottom of the *Picea-Abies-Pinus albicaulis* zone in Buckbean fen. They are even more abundant in this zone at Cub Creek pond (Waddington and Wright,

1974). No *Betula* macrofossils were found in Buckbean fen core, but in the equivalent zone of the Lilypad pond core *Betula glandulosa* seeds and catkin scales are common (pl. 6). *Betula occidentalis*, the only other birch that occurs in northwestern Wyoming, is found at lower elevations. The pollen of the birch peak, therefore, is attributed to *B. glandulosa*.

Alnus pollen, which occurs sparsely but continuously in the *Pinus contorta* subzone of the *Pinus contorta* zone, probably represents *Alnus tenuifolia*. It is the only species that occurs in Wyoming today, and one fruit of *Alnus tenuifolia* was found (pl. 6). The fruits are wingless and cannot be confused with other species of western alder or birch.

COMPOSITAE

A single Compositae seed was found in the Lilypad pond core. It may be identifiable to species, but the reference collection for the large family has not been completed. Compositae pollen was separated into *Ambrosia* type (pl. 2), *Artemisia*, subfamily Tubuliflorae, and subfamily Liguliflorae (pl. 2). *Ambrosia* type probably includes pollen of *Franseria*, a western plant of semiarid regions.

CRASSULACEAE

The *Sedum* seed is referred to *S. rhodanthum*. *S. rosea* has similar seeds, but a delicate epidermal reticulum and black tip seem to be absent on seeds of *S. rosea*. *S. rhodanthum* now grows on the margins of the fen surface.

CRUCIFERAE

Seeds of *Rorippa* occur in both Lilypad pond and Buckbean fen (pl. 10). They match *R. islandica* but cannot be distinguished on the basis of our reference material from other Rocky Mountain *Rorippa* species.

One seed of *Descurainia californica* was found in the Lilypad pond (pl. 8). This species has broader seeds with coarser surface reticulum than other species in this area. It is a montane to subalpine species in Colorado (Harrington, 1954).

HALORAGACEAE

Four-pored *Myriophyllum* pollen occurs at the same level as the single seed in Buckbean fen (pl. 2). The seed cannot be assigned to a species, but *Myriophyllum spicatum* ssp. *exalbescens* and *M. verticillatum* are the only two species that grow in the park today (McDougall and Baggley, 1956). Seeds of *Myriophyllum* occur abundantly in cores from nearby sites.

LORANTHACEAE

No attempt was made to identify *Arceuthobium* pollen to species because of insufficient reference material (pl. 2). Three species occur in northwest Wyoming: *A. douglasii* infects *Pseudotsuga* as its principal host, *A. campylopodum* is parasitic mainly on *Pinus ponderosa*, and *A. americanum* is parasitic on *Pinus contorta* (Hawksworth and Wiens, 1972). Because the fossil pollen occurs mainly in the *Pinus contorta* zone, the most likely species is *Arceuthobium americanum*.

MENYANTHACEAE

Menyanthes trifoliata pollen and seeds both can be confidently identified from the upper part of the Buckbean fen core (pls. 3 and 6). The plant now grows on the fen and elsewhere in the park.

NYMPHAEACEAE

Nuphar luteum ssp. *polysepalum* is distinct from eastern subspecies of the species because of its longer seeds (pl. 7). Pollen of this genus is also well represented and is easily identified by its monosulcate, echinate grains (pl. 2).

ONAGRACEAE

Epilobium seeds are found in several cores and in a surface sample. The *Epilobium lactiflorum* seed that occurs in Lilypad pond is small and has parallel rows of separate, long, narrow tubercles (pl. 8). The specimens in the *Pinus contorta* zone of Buckbean fen are more elongate, with rows of short projections; the rows are connected by low crossbars (pl. 8). They are referred to *Epilobium glandulosum* type which includes *E. adenocaulon*.

POLEMONIACEAE

Pollen of *Polemonium* (pl. 3) is distinct from other genera in the family, because of its striate or striate-reticulate sculpture and its periporate apertures (Stuchlik, 1967). Reference collections were insufficient to attempt a specific identification.

POLYGONACEAE

Pollen of *Polygonum* (including *Bistorta*) can be separated into three types. *Bistorta* type is tricolporate, tectate, prolate, and psilate, with prominent columellae; it has slitlike furrows and an equidimensional pore (pl. 3). *Polygonum persicaria* type is periporate with a coarse reticulum. *Polygonum ramosissimum* type is tricolporate, prolate, and psilate, but with transverse furrows. *Bistorta* type includes *Bistorta bistortoides* and *Bistorta vivipara*, both subalpine to alpine plants. Because of incomplete reference material, species included in the other two types are unknown.

Single pollen grains of *Koenigia* and *Oxyria* type were found at 850 cm in Buckbean fen. *Koenigia* pollen is periporate, echinate, and tectate, with about 12 small, elongate pores. The fossil is about 22 μm

(micrometres) in diameter, whereas the reference material is about 25 μm. *Oxyria*-type pollen is spheroidal, tricolporate, psilate, and tectate, with slit-shaped furrows and small pores. Both plants are restricted to arctic-alpine environments, and *Koenigia* is rare in the modern flora of the tundra in the Rocky Mountains (Weber, 1967).

The pollen of *Eriogonum* or *Rumex* could not be separated into morphological types. However, one fragmentary and one whole seed of *Rumex salicifolius* (pl. 6) suggest that *Rumex* pollen (pl. 4) belongs to that species in the *Picea-Juniperus-Pinus albicaulis* zone. The seeds also resemble the adventive *R. crispus* but are distinct in size and shape from other native species. *Rumex fueginus* seeds and perianths are present in the *Pinus contorta* zone of Buckbean fen and they are abundant in the upper zones of other cores in the area. The distinctive denticulate valves of *R. fueginus* (pl. 6) distinguish it from all other species. The separate seeds closely resemble those of *R. paucifolius*.

RANUNCULACEAE

Only two fruits of *Ranunculus aquatilis* were found (pl. 8). The distinctive ribbed achenes distinguish it from all other species of *Ranunculus*.

ROSACEAE

Potentilla seeds were difficult to identify as to species because of the large number of species in the Rocky Mountain area. The *Potentilla* cf. *gracilis* is smaller than all the reference material, but it comes closest in size and shape to *Potentilla gracilis* (pl. 8). *Potentilla biennis* type matches both the striated seeds of *P. biennis* and *P. norvegica* (pl. 8). For plant-geographical and autoecological reasons, the seeds are referred to as *P. biennis*. The large, broad seeds of *P. palustris* are distinct from all other species (pl. 8), and the striate pollen is also distinctive (pl. 4). *Sibbaldia procumbens*, a genus closely related to *Potentilla*, has larger and broader seeds distinct in shape from species of *Potentilla*. It is a subalpine and alpine plant.

SALICACEAE

The bracts referred to *Populus balsamifera* (pl. 6) also resemble *Populus trichocarpa*. The former is a boreal forest tree extending from Northeastern United States through western Canada with disjunctions south to the Yellowstone National Park area (Fowells, 1965). *Populus trichocarpa* is a west coast tree whose distribution extends inland to the Yellowstone National Park area (Fowells, 1965). Their present ranges overlap, and the acceptance of *Populus balsamifera* in Yellowstone National Park by McDougall and Baggley (1956) is in need of verification. Fossils of these two species are difficult to distinguish, but bracts of *P. balsamifera* are narrower than those of *P. trichocarpa* in our material. *Populus trichocarpa* grows along streambanks and flood plains at low elevations. *Populus balsamifera* is not strictly riparian, and it grows in the montane and subalpine zones up to 11,000 feet (Porter, 1967; Weber, 1967). Ecological and morphological considerations support the referral of the fossil bracts to *Populus balsamifera*, and the pollen probably is of this species also (pl. 4).

A fairly distinct morphologic type of *Salix* pollen (pl. 4) was found in some alpine surface samples. Inadequate reference material for this genus has made careful study unwarranted. Buds of *Salix* have not been identified to species, but a few leaf bases can tentatively be referred to *Salix subcoerulea*. Seed and leaf reference collections are also incomplete for this genus.

SAXIFRAGACEAE

A single seed of *Saxifraga caespitosa* was found in the Lilypad pond core (pl. 10). The seed is ovate-oblong and has a surface pattern of linear rows of tiny beadlike projections. Only *Saxifraga rivularis* has a similar beaded pattern, but in that species the beads form a reticulum. I have collected *Saxifraga caespitosa* from the Two Ocean Plateau and from the Beartooth Plateau, and it is an alpine species.

Another saxifrage seed is referred to *Saxifraga rhomboidea* (pl. 10). It also is ovate-oblong, and its surface is traversed by discontinuous, often indistinct ridges. This species ranges from the plains to the alpine tundra.

CYPERACEAE

Although the genus *Carex* is represented by many species in the Rocky Mountain region, collections from wet-ground species in Yellowstone National Park have allowed several species to be identified from their fruits. Usually the perigynium, an inflated sac covering the achene, must be present for identification.

Several fruits with perigynia of *Carex aquatilis* were found (pl. 9). Separate achenes, when preservation was excellent, were placed in this species, but others less well preserved or with different morphology were placed under *Carex* biconvex. *Carex aquatilis* is the commonest of the *Carex* species with biconvex achenes that grow in wet places in Yellowstone National Park.

Carex canescens fruits are biconvex and their small plump perigynia are strongly veined (pl. 9). *Carex diandra* fruits (pl. 9) have a corky-based perigynium that tightly encases the achene. The achenes are shaped somewhat like *Scirpus* fruits, but they are round rather than biconvex in cross section. Achene

and perigynium are usually found together but can be recognized separately. *Carex limosa* fruits were never found with perigynia. The achenes are weakly triangular to round in cross section, obovate, and usually indented in one side (pl. 7). They match reference material perfectly, and *Carex limosa* grows at present in the *Carex diandra-Potentilla palustris* community on the fen. *Carex vesicaria* and *C. utriculata* are two other species now common on the fen. Their perigynia are distinguished by shape; *C. vesicaria* perigynia taper gradually to a slender base, whereas those of *C. utriculata* are abruptly expanded to a broader base (pl. 7).

A single *Eleocharis macrostachya* fruit, corroded but identifiable, was found in the Buckbean fen core (pl. 9). These fruits are much more common in other cores from this area. These biconvex fruits with the small, broad-based tubercle connected only at the top of the fruit are easily separable from other species in the area.

GRAMINEAE

Seeds of this family generally have thin seed coats and only a few genera with thick seed coats fossilize. Spikelets of *Calamagrostis* are abundant in one macrofossil surface sample from Buckbean fen but are not found as fossils. *Calamagrostis canadensis* and *C. inexpansa* are common on the fen surface today, and they probably grew there throughout most of postglacial time.

Seeds of *Glyceria maxima* ssp. *grandis* are present at only one horizon of the Buckbean fen core but are abundant in other cores from the area (pl. 9). This species has seeds similar to *G. borealis*, but the seed tip is blunt in *G. maxima* and sharp in *G. borealis*. The reference specimens are somewhat larger than the fossil material. Other species are quite different in morphology and size.

NAIADACEAE

Seeds of *Naias flexilis* are easily distinguishable from other species in the genus by size and surface texture (pl. 9). This species is not reported from the present flora of Wyoming or Colorado, though it does occur in Utah (Porter, 1963; Matsumura and Harrington, 1955). I have found seeds of *Naias flexilis* in approximately the midpostglacial from four ponds in Yellowstone National Park. The plant probably grows in Wyoming and Colorado, but it is unreported because it is inconspicuous and because aquatic plants are not commonly collected.

Several species of *Potamogeton* have very distinctive fruit-stones, and many of the North American species are treated in keys (Jessen, 1955; Martin and Barkley, 1961). In *Potamogeton alpinus* the lid reaches the top of the fruit-stone and is remote from the style base. One specimen was found with its soft outer covering intact (pl. 7). *Potamogeton filiformis* fruit-stones also have the lid remote from the style base, but the lid does not reach the top of the fruit-stone (pl. 7). It is similar to but smaller than fruit-stones of *P. vaginatus* and *P. pectinatus*. *P. gramineus* fruit-stones are rather small with a low central depression and a low-keeled lid (pl. 7). One fruit-stone without a lid best matches *P. illinoensis*, but certain identification is not possible. It occurs with a fruit-stone of *P. alpinus*.

TYPHACEAE

Fruits of *Typha* cannot be identified to species (pl. 10). Pollen of *Typha latifolia* remains in tetrads, so this species is recognizable (pl. 2). *Typha angustifolia* pollen cannot be distinguished from pollen of *Sparganium* or broken tetrads of *Typha latifolia*, and the pollen is here called *Sparganium* type because fruits of *Sparganium angustifolium* and *S. minimum* have been found in other nearby cores.

OTHER TYPES OF FOSSILS

Other types of macrofossils were tallied on a scale from one (rare) to five (very abundant). No attempt was made to differentiate among bryophyte spores, although the one shown on plate 1 is the commonest type. Abundance of *Sphagnum* leaves was noted, because the two types of cells in the leaves make them easy to recognize.

ALGAE

Pediastrum colonies (pl. 4) were counted and plotted in the pollen diagram (fig. 15) because they indicate an aquatic environment. They are present in many surface samples, especially those from larger or deeper ponds.

Oogonia of charophytes were tallied in the macrofossil diagrams (figs. 17 and 18). They disappear above 820 cm in the Buckbean fen core, but they are present in younger horizons from other cores in the area.

One species of diatom (*Melosira*?) was large enough to be caught by the 140-mesh sieve; specimens were sent to R. C. Bright for identification. The species occurs below 800 cm in Buckbean fen and Lilypad pond cores.

Statoblasts of freshwater bryozoa and shells of rhizopods were not further identified. Both occur mainly in the small pond stage of the Buckbean fen core in the interval 275 – 475 cm.

DESCRIPTION OF POLLEN ZONES

PICEA-JUNIPERUS-PINUS ALBICAULIS ZONE (960—770 cm)

The basal zone is defined by relatively low (30 – 50 percent) *Pinus* pollen (dominantly *Pinus albicaulis*

type) and by maxima in *Picea, Abies, Juniperus, Salix, Artemisia,* Gramineae, Compositae (subfamilies Tubuliflorae and Liguliflorae), and *Rumex* (fig. 15). A mixture of subalpine and alpine macrofossils is present in this zone, and large diatoms (longer than 0.5 mm) and charophytes are nearly limited to this zone (figs. 17 and 18). The concentration of the alga *Pediastrum* reaches 40 percent of the pollen sum at the base, and bryophyte spores are consistently present.

This pollen zone occurs in the lower 190 cm of the core from Buckbean fen and the lower 200 cm of the Lilypad pond core (figs. 15, 17, and 18). The sediment in both sections overlies a basal gravel and consists of 100 – 200 cm of gray sandy silts (table 5). The sandy silts in this zone contain too little carbon for C^{14}-dating, but on the basis of two other dates on deglaciation (Sullivan and others, 1970; Bender and others, 1971) the sediments in this zone probably began to accumulate before 13,500 years ago. Also, an ash layer near the base of the Lilypad pond core (table 5) may represent the Glacier Peak ash dated at 12,000 years B.P. (Wilcox, 1965), but the ash was too thin and mixed with sediment to be identified. The age of the sediments at the top of the zone is unknown here, but the top of the correlative zone at Cub Creek pond is dated by C^{14} at 11,630±180 years B.P. (I – 2285, Waddington and Wright, 1974). The zone is divided into two subzones on the basis of pollen and plant macrofossils: a lower *Betula* subzone and an upper *Populus* subzone.

BETULA SUBZONE (960 – 875 cm)

The *Betula* subzone is defined primarily by low but persistent values (1 – 3.5 percent) of *Betula* pollen (fig. 15). *Rumex* (dock) pollen is consistently present, and Compositae pollen, especially subfamily Liguliflorae, is most common in this subzone. *Pinus albicaulis/ Pinus contorta* ratios are highest in this subzone, ranging from 5.5 to 27 (fig. 19).

The lower 100 cm of the Lilypad pond core (fig. 18) is tentatively referred to this subzone on the basis of (1) presence of mixed alpine- and subalpine-plant macrofossils, (2) distribution of *Betula glandulosa* (bog birch) fruits and catkin scales, and (3) rare presence of arboreal macrofossils. The Cub Creek pond sequence (Waddington and Wright, 1970) shows a similar *Betula* pollen peak at the base of the core.

Betula glandulosa and *Rumex salicifolius* (willow dock) were identified from macrofossils from the Lilypad pond core (fig. 18), and these are probably the species represented by pollen (fig. 15). The *Betula* pollen is small mostly less than 21 μm in diameter. *Betula glandulosa* is a common shrub of wet subalpine areas in the Rocky Mountains (Weber, 1967). *Rumex salicifolius* grows on dry sites at elevations from 3,500 to 9,500 feet in Wyoming (Porter, 1968).

Several local habitats are suggested by the pollen and macrofossils (figs. 15, 17, and 18). *Rumex salicifolius, Potentilla* cf. *gracilis,* and *Descurainia californica* are weedy species that probably grew in dry, disturbed areas or along the shores of the ancestral lake. *Juniperus* (probably *J. communis*) and various composites may have shared dry forest openings with these species. Pollen of steppe

TABLE 5.—*Lithologic description of Buckbean fen and basal section of Lilypad pond*

Penetration (cm)	Core length (cm)	Description
		Buckbean fen
0 – 100	0 – 81	Sedge peat, dark-brown fibrous; with intertwined rootlets. Rootlets of woody plants (*Salix* spp?) from 0 – 10 cm.
100 – 200	100 – 188	Sedge peat, dark-brown, somewhat decomposed; not so fibrous as 0 – 81 cm, coarse *Carex* leaves from 100 – 115 cm; abundant bryophytes from 130 – 188 cm.
200 – 300	200 – 290	Sedge peat, brown, somewhat decomposed, with bryophytes common.
300 – 400	300 – 383	Peat, brown, with sedge remains, wood fragments, and *Nuphar* seeds from 300 – 340 cm; mainly bryophyte peat from 340 – 383 cm.
400 – 500	400 – 487	Bryophyte peat, brown from 400 – 410 cm, grading to olive-colored gyttja at 425 cm. Fine-grained detrital peat from 430 – 487 cm, black from 430 – 442 cm, brown from 442 – 487 cm.
500 – 600	500 – 585	Gyttja (organic sediments of eutrophic lakes), brown, silty, fine-grained, inelastic, crumbly.
600 – 700	600 – 699	Gyttja, brown, silty, fine-grained, inelastic, crumbly from 600 – 620, solid from 620 – 640 cm.
700 – 800	700 – 783	Gyttja, brown, silty, clayey, inelastic; crumbly from 700 – 710 and 751 – 783 cm, firm elsewhere, dark band from 717 – 722.
800 – 890	800 – 884	Silt, organic, highly diatomaceous; finely laminated (varved?) from 810 – 856 cm, crumbly from 800 – 820 cm, very firm from 820 – 840 cm, sand layer at 805 cm, becoming gray silt mottled with dark spots from 856 – 884 cm. Sand lense at 873 cm.
890 – 975	890 – 960	Silt, gray, sandy, highly diatomaceous, with dark mottling from 890 – 928 cm, lenses of gray medium-grained sand at 910 and 951.5 – 954.5 cm, crumbly from 939—945 cm, firm elsewhere. Pebbles impacted into bottom of core.
		Lilypad pond
800 – 900	800 – 892	Silt, gray, sandy, highly diatomaceous below 825 cm, sand layer at 854 – 855 cm, streaks of black sand at 881 and 883.5 cm, gray clay from 887 – 890 cm, laminated brown and buff silt from 890 – 892 cm.
900–1,000	900–1,000	Clay, gray, sticky, from 907 – 910 cm; coarse gray sand from 900 – 907 and 910 – 917 cm. Silt from 917 – 1,000 cm: gray, sandy, dark layers at 950, 953.4, 996.5, and 997.5 cm; ash layer at 974.2 – 974.5 cm.

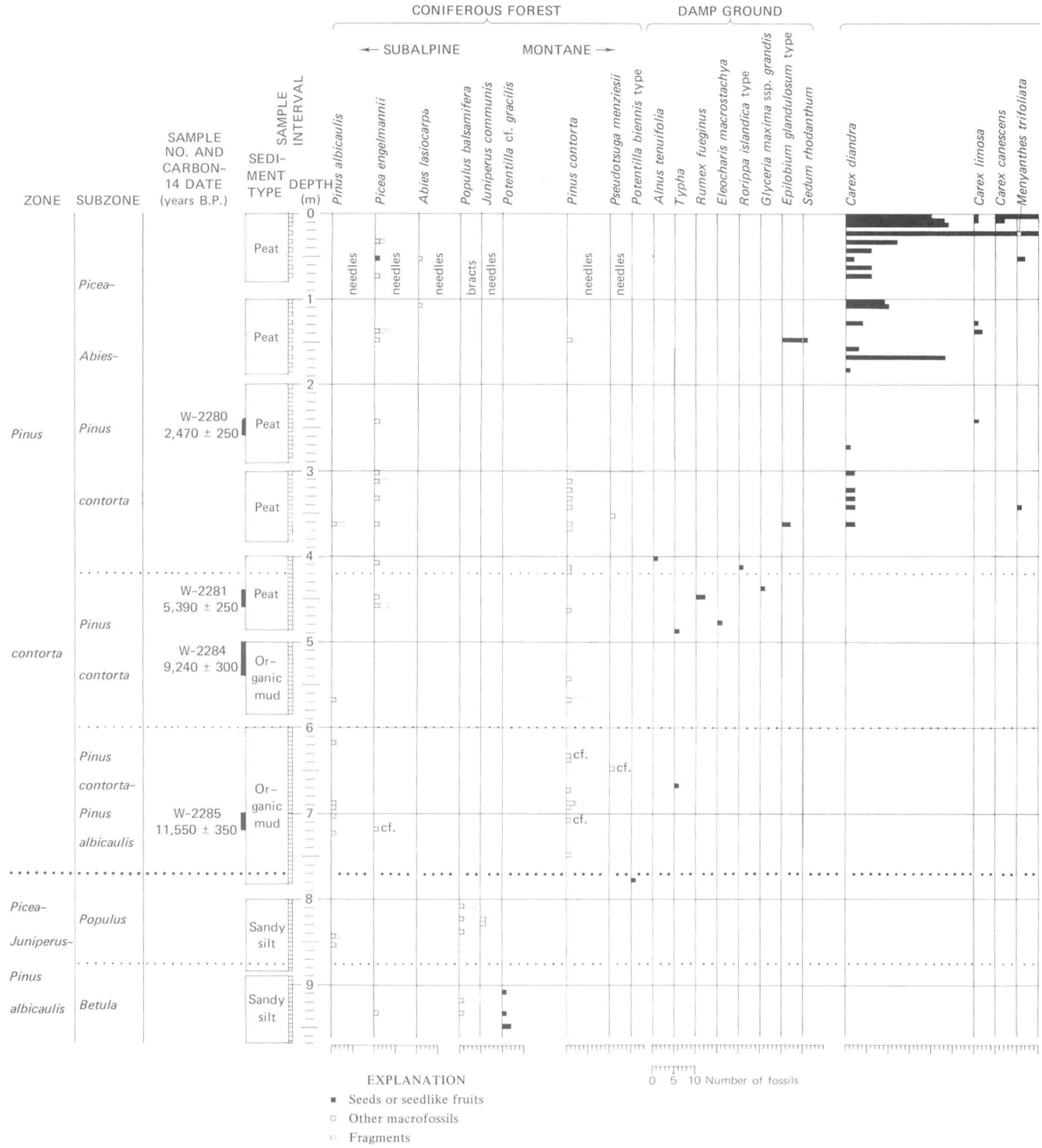
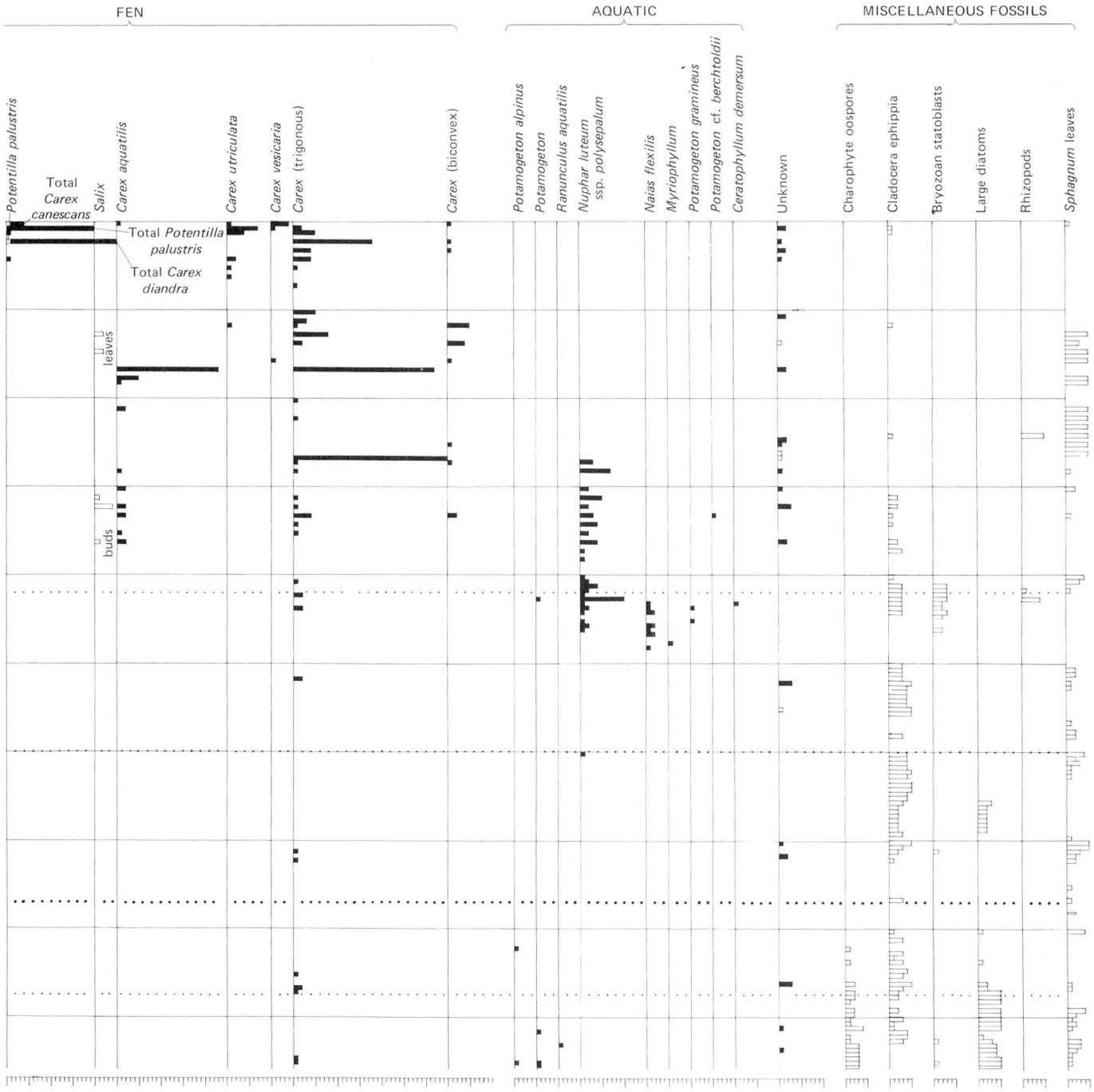


FIGURE 17 (above and right). —Plant macrofossils from Buckbean fen core.

elements, such as *Artemisia*, Cheno-Ams, and *Sarcobatus*, is common in this subzone, but it seems ecologically unreasonable that these plants grew near the coring sites. Woodland or tundra species of *Artemisia* may have contributed some pollen, but long-distance transport probably accounted for much of the pollen of steppe elements, as it apparently does at present in alpine sites.

Pollen of *Potamogeton*, fruit-stones of *Potamogeton alpinus* and *P. filiformis*, and fruits of *Ranunculus*



NO. OF UNITS	ABUNDANCE
1	Rare
2	Infrequent
3	Common
4	Abundant
5	Very abundant

aquatilis (water crowfoot) indicate that pioneer aquatics had colonized the shallow lake margins. A few pollen grains of *Typha latifolia* (broadleaf cattail) and *Sparganium* (burreed) type suggests that these plants may also have grown in shallow water or along the shore (figs. 15, 17, and 18).

Macrofossils of *Saxifraga caespitosa, S. rhomboidea, Potentilla* sp., *Sibbaldia procumbens,* and *Betula glandulosa,* and pollen of *Bistorta* and *Polemonium* suggest that subalpine or alpine meadows were present in the area (figs. 17 and 18). These plants at present are common in the alpine parts of the Two

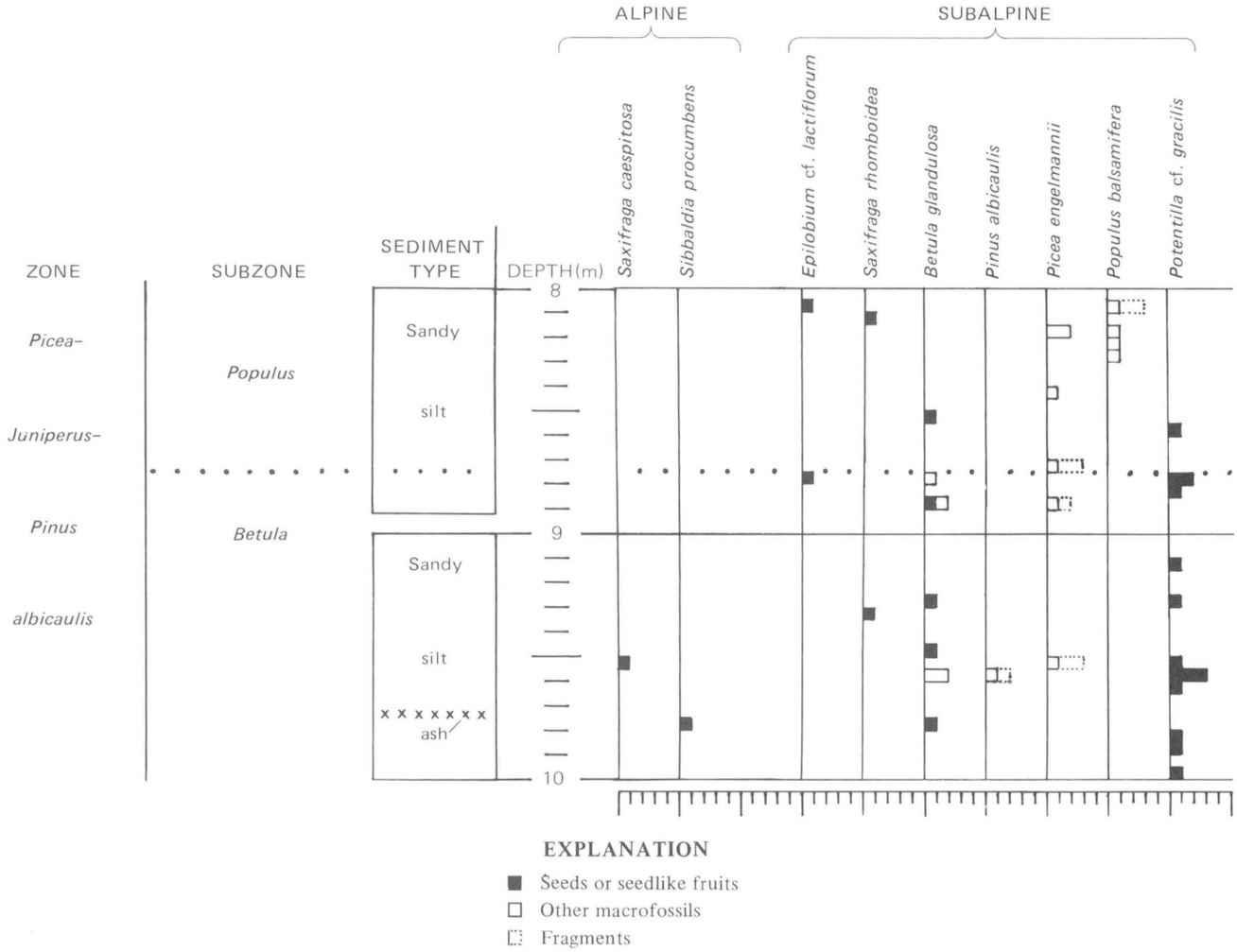


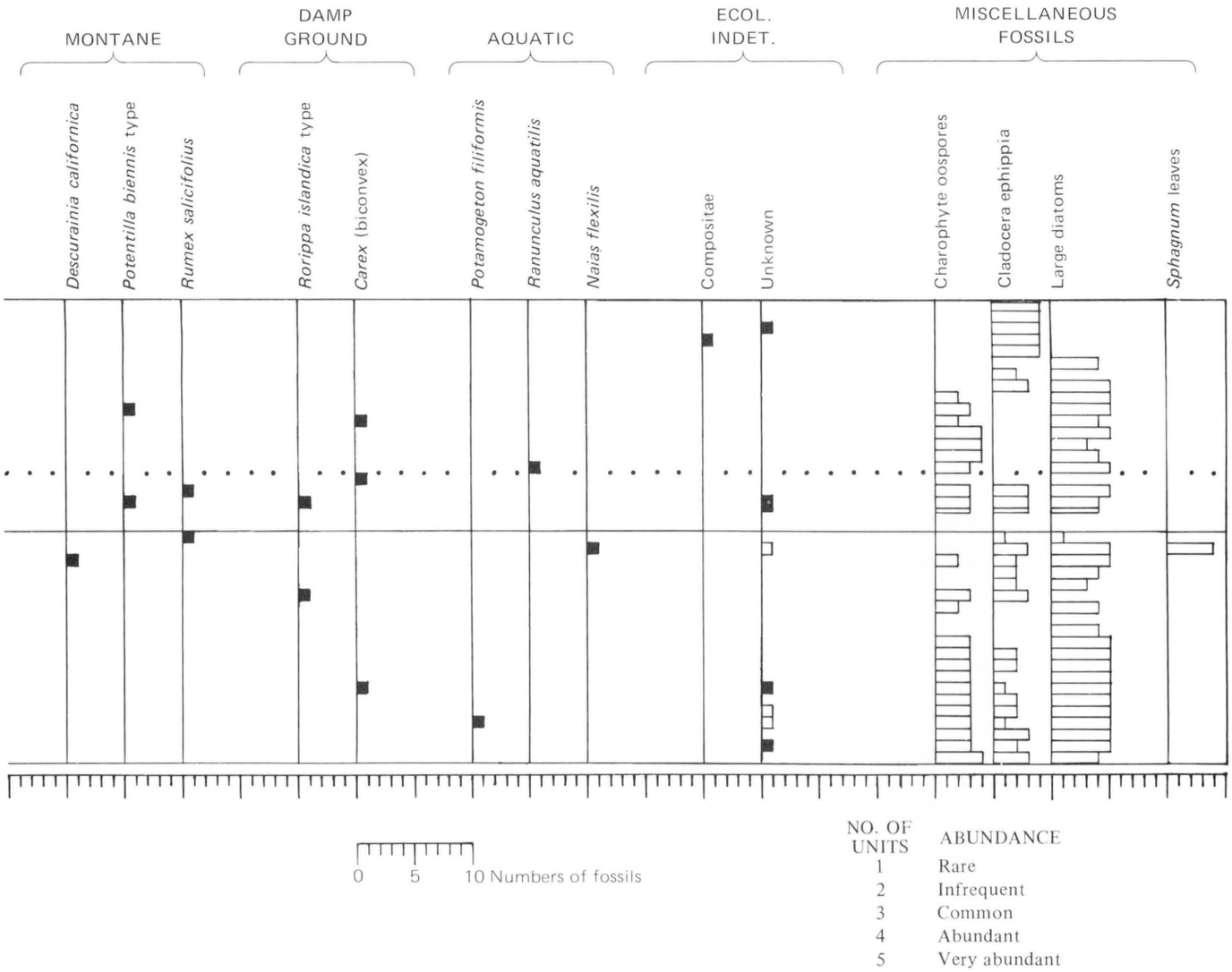
FIGURE 18 (above and right). —Plant macrofossils from lower 2 metres of Lilypad pond core.

Ocean Plateau, but only *Saxifraga caespitosa* is limited to the alpine tundra.

Rare *Picea* and *Pinus albicaulis* needles and a *Populus* bract suggest that only a few trees may have grown in favorable nearby habitats (figs. 17 and 18). Pollen percentages of *Picea, Abies,* and nonarboreal types compare best with modern surface samples from low alpine and parkland sites (figs. 13 and 15). *Pinus* pollen values are about 20 percent lower in the *Betula* subzone than in these surface samples. Low tree-pollen percentages might be expected at that time if the surface of the plateau was covered by tundra or mixed parkland and tundra instead of forest. Pollen ratios also support the conclusion that the site was near timberline during *Betula* subzone time. *Pinus albicaulis/Pinus contorta* and Gramineae/*Pinus* ratios are high (1 – 11 and 0.025 – 0.2) in modern surface samples collected at or above timberline (fig. 14). Both ratios are high (5.5 – 11 and 0.1 – 0.33) in the *Betula* subzone (fig. 19).

The proximity of trees to the coring site is difficult to determine. No nearby forested areas below this tundra or parkland were present, because the ancestral lake covered all lower ground in the vicinity. Conifer needles can blow for some miles when caught in the updraft of large forest fires. R. F. Bucknam and B. B. Kropf (written commun., 1969) reported conifer needles falling in Denver, Colo., during a forest fire on Mount Evans, which lies about 35 miles west and at least 6,000 feet higher. All the needles were carbonized, however, whereas most needles from the *Betula* subzone in the core studied were not.

Picea, Abies, Pinus albicaulis, and possibly *Populus balsamifera* (balsam poplar) were probably the only trees growing on the plateau parklands at this time. *Pinus contorta* type pollen percentages of less than 2



percent (fig. 15) suggest that this tree was not present on the Yellowstone plateau, although it probably grew in lowlands around the margins of the plateau.

Trees apparently did not require a long time to migrate onto the plateau after the melting of the icecap. The high ridges and plateaus in the southern and eastern parts of the park would have been above climatic treeline during this time and would have acted as barriers to migration. Migration probably took place along valleys, progressing gradually inward to the Southeast Arm of Yellowstone Lake as the valleys became free of ice. Scattered trees may have been present within a few miles of the coring area when it first became exposed.

An alternate hypothesis for forest migration would be that trees survived locally on nunataks and migrated a shorter distance down to the coring area. However, no nunataks are known nearby that would have been below the climatic treeline.

The pollen and macrofossils of this subzone suggest subalpine to alpine vegetation and a cold, wet climate. Present lack of climatic stations in the subalpine and alpine areas of Yellowstone National Park makes it difficult to quantify the late-glacial climate, but average July temperature below 50°F now characterizes the areas above treeline (Marr and others, 1968) or north of it (Wolfe and Leopold, 1967). If subalpine spruce-fir-whitebark pine parkland occurred near Yellowstone Lake, such conditions probably prevailed.

POPULUS SUBZONE (875–770 cm)

The *Populus* subzone of the *Picea-Abies-Pinus albicaulis* zone is defined by a peak in *Populus* pollen and by bracts of *Populus balsamifera* (figs. 15, 17, and

18). A peak in the curve for *Ambrosia* also occurs in this subzone (fig. 15). Alpine-plant macrofossils are no longer present, *Picea* and *Pinus albicaulis* needles are more common, and *Juniperus communis* needles appear (figs. 17 and 18). *Pinus albicaulis/Pinus contorta* and Gramineae/*Pinus* ratios decrease throughout this zone and range from 1.1 to 7.5 and from 0.047 to 0.228, respectively (fig. 19).

Several local habitats may be inferred from the fossils in this subzone. *Betula glandulosa, Potentilla* cf. *gracilis, Rorippa islandica* (marshcress) type, and *Epilobium* cf. *lactiflorum* (pale willow-herb) macrofossils (fig. 18) suggest a moist subalpine meadow nearby. A dry, open subalpine environment, such as might have been found near the shores of Yellowstone Lake, is inferred from macrofossils of *Rumex salicifolius* and *Potentilla biennis* type. The fossil aquatic flora includes *Ranunculus aquatilis, Potamogeton alpinus,* and *Naias flexilis* (naiad). *Naias flexilis* is not reported from the modern floras of Wyoming or Colorado. Single pollen grains of *Oxyria* (alpine sorrel) and *Koenigia islandica* at 850 cm suggest that alpine plants may have persisted for a while on exposed sites.

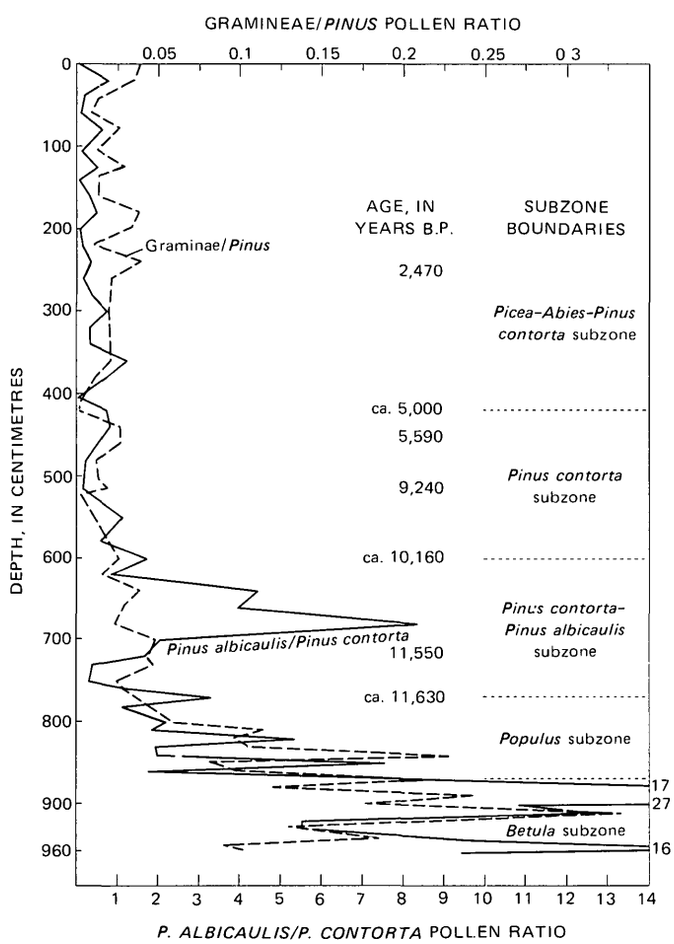


FIGURE 19.—Ratios for fossil pollen from Buckbean fen.

Picea engelmannii, Pinus albicaulis, Populus balsamifera, and probably *Abies lasiocarpa* were present locally in a subalpine parkland environment. This interpretation is suggested by analogy with surface samples and from the composition of the pollen and plant-macrofossil spectra. A closed *Picea-Abies-Pinus albicaulis* forest is ruled out by the high nonarboreal pollen curves and high Gramineae/*Pinus* ratios that typify surface samples from modern parkland or tundra (figs. 14, 15, and 19).

Populus balsamifera probably was a pioneer species along the shores of Yellowstone Lake, perhaps as early as during the previous subzone. *Populus trichocarpa* (black cottonwood), a closely related species, is an early migrant onto deglaciated surfaces in southeast Alaska (Lawrence, 1958). *Populus* pollen maxima indicate that it was an early migrant in northwest Minnesota after deglaciation (McAndrews, 1967), and macrofossils of three species, including *P. balsamifera,* were found in sediments of late glacial age in southern Manitoba (Ritchie and de Vries, 1964).

To summarize the environments of the *Picea-Abies-Pinus albicaulis* zone, the basal subzone represents an environment at or slightly above timberline with few, if any, trees present. During the time of the upper subzone, trees were present in a subalpine parkland-type vegetation. The climate for this zone was probably comparable to that of the high subalpine or low alpine associations today in Yellowstone Park. Treeline was approximately 2,000 feet lower than it is today.

PINUS CONTORTA ZONE (770 – 0 cm)

This zone is defined by high percentages (65 – 88 percent) of the total pine pollen and by *Pinus contorta* macrofossils (figs. 15 and 17). *Artemisia* declines from more than 20 to less than 10 percent in this zone, and values of *Juniperus, Picea, Abies, Betula,* and most nonarboreal pollen are low (fig. 15).

The sediments in this zone are silty gyttja in the interval 770 – 500 cm, transitional organic detritus in the interval 500 – 410 cm, and peat from 410 cm to the surface (table 5). No dates are available from sediments at the base of this zone, but a date at the zone boundary at Cub Creek pond is 11,630 ± 180 years B.P. (sample I – 2285; Waddington and Wright, 1970).

The zone is divided into the following three subzones: the *Pinus contorta-Pinus albicaulis* subzone (770 – 600 cm), the *Pinus contorta* subzone (600 – 420 cm), and the *Picea-Abies-Pinus contorta* subzone (420 – 0 cm) (fig. 15, table 3).

PINUS CONTORTA-PINUS ALBICAULIS SUBZONE (770—600 cm)

This subzone is defined by a resurgence of *Pinus albicaulis/Pinus contorta* ratios up to 8.3 (fig. 19), and the occurrence of needles of both pine species (fig. 17). *Pinus* pollen percentages average 65 – 70 percent, and *Artemisia* ranges from 15 to 20 percent (fig. 15). *Arceuthobium* (dwarf mistletoe) is persistently present, and a few grains of *Pseudotsuga* occur. Concentrations of *Picea, Abies, Juniperus, Populus, Betula, Salix, Ambrosia,* Compositae, and Gramineae, all significant in the lower subzones, are several times lower in this subzone (fig. 15).

A radiocarbon date near the base of this subzone gives an age of 11,550 ± 350 years B.P. The age of the top of this subzone is interpolated to be 10,160 years B.P. (figs. 15 and 16, table 3), using the rate of sedimentation calculated from adjacent radiocarbon dates.

The pollen spectra from this subzone compare approximately with modern surface samples from forest openings (fig. 13). Gramineae/*Pinus* ratios for this subzone are between 0.025 and 0.050; these ratios are lower than those of modern surface samples in forest openings and parklands but higher than ratios in closed forests (figs. 14 and 19). An open, mixed forest with *Pinus contorta, Pinus albicaulis,* and *Pseudotsuga menziesii* probably grew in the area during the interval represented by this subzone. (Pollen values of *Pseudotsuga* as low as 1 percent probably indicate its local presence, based on surface samples.) The most significant change in vegetation after deposition of the lower zone was the arrival of *Pinus contorta* and *Pseudotsuga* in the coring area (figs. 15 and 17).

It is difficult to infer other habitats that might have been present during this period because few macrofossils other than pine needles are present. A few *Carex* fruits and a *Typha* fruit (fig. 17) suggest a possible pond-shore habitat.

Persistence of *Arceuthobium* in the pollen profile, beginning at 730 cm (fig. 15), gives evidence for a tentative mean annual temperature during that time. Its pollen appears at about the same level that *Pinus contorta* needles first appear (fig. 17). I could not determine the species using pollen morphology, but it is probably *Arceuthobium americanum,* a parasite that occurs exclusively on *Pinus contorta* in this region. It is the only species of *Arceuthobium* reported from the park by McDougall and Baggley (1956), but Hawksworth and Wiens (1972) reported *A. douglasi,* a parasite on *Pseudotsuga,* from the park as well. At present the upper limits of *Arceuthobium americanum* coincide with the 30°F mean annual isotherm in Colorado and Wyoming (Gill, 1957), suggesting that the temperature when *Arceuthobium* first appeared was about the same as it is now.

The coexistence of *Pinus contorta, Pinus albicaulis,* and probably *Pseudotsuga menziesii,* and the low values of *Picea* and *Abies* suggest a climate drier than the climate of the preceding zone and also the present climate.

PINUS CONTORTA SUBZONE (600—420 cm)

This subzone is defined by 70 – 80 percent *Pinus* pollen, low ratios of *Pinus albicaulis/Pinus contorta* pollen, and needles of *Pinus contorta* (figs. 15, 17, and 19). *Pseudotsuga* pollen is less common than in the preceding subzone, and *Picea* and *Abies* are low throughout. *Artemisia* pollen ranges from 10 to 15 percent, and *Arceuthobium* and *Alnus* are present at low but persistent values (fig. 15).

A sediment sample from interval 500 – 541 cm in the Buckbean fen core gives a C^{14} date of 9,240±300 years B.P. (W – 2284). Another sample from interval 440 – 460 cm is dated at 5,390 ± 250 years B.P. (W – 2281). Interpolation between older and younger dates suggests that this subzone began about 10,160 years ago and ended about 5,000 years ago (fig. 15, table 3), but the 4,000-year span of the dates in the zone, over only a 70-cm interval, suggests a hiatus in the core. (See fig. 16.)

The fossil assemblage suggests that a virtually pure *Pinus contorta* forest was the dominat vegetation association around the coring site during this period. Fossils from local vegetation types are poorly represented, especially from interval 600 – 487 cm in this subzone.

From interval 487 – 420 cm, macrofossils of *Nuphar luteum* ssp. *polysepalum, Naias flexilis, Myriophyllum* sp. (water milfoil), *Potamogeton gramineus,* and *Ceratophyllum demersum* (hornwort) and pollen of *Nuphar* and *Myriophyllum* suggest a small, warm-water pond habitat (fig. 17). The presence of this habitat requires that Yellowstone Lake had fallen to a level within 15 feet of its present level by about 5,000 years ago.

One fragment of an *Alnus tenuifolia* (thinleaf alder) fruit at 405 cm (fig. 17) suggests that the *Alnus* pollen is also of that species. It is the only species of *Alnus* that now occurs in Wyoming (Porter, 1967), and it suggests that the habitat was the margin of a lake, pond, or fen.

Macrofossils of *Glyceria maxima* ssp. *grandis* (large mannagrass), *Rumex fueginus, Carex utriculata,* and

Typha sp. also provide evidence for a wet-ground vegetation around the margins of the pond (fig. 17).

PICEA-ABIES-PINUS CONTORTA SUBZONE (420 – 0 cm)

This subzone is defined by low but persistent values of *Picea* and *Abies* pollen, by their macrofossils, and by low pollen ratios of *Pinus albicaulis/Pinus contorta* (figs. 15 and 19). The *Artemisia* curve is at its lowest (4 – 10 percent) in the entire core. Cyperaceae pollen percentages are high but irregular in the subzone, but macrofossils indicate that the pollen comes from local fen species of *Carex* (figs. 15 and 17).

A sample from interval 240 – 260 cm gave a C^{14} date of 2,470±250 years B.P. (W – 2280). The subzone represents the period from about 5,000 years ago by interpolation to the present. An interpolated date of 2,800 years B.P. marks a rise in *Picea*, *Abies*, and Cyperaceae pollen percentages (figs. 15 and 16, table 3).

Pollen and macrofossils of *Pinus contorta*, *Picea*, and *Abies* indicate that these trees were dominant in the forest association when this subzone was deposited (figs. 15 and 17). Pollen and a needle of *Pseudotsuga menziesii* and a needle of *Pinus albicaulis* type suggest that these trees may have been present early during this period, but they played a decreasing role in the forest association.

Most *Picea* needles in this subzone are charcoal. Frequent fires nearby might explain the carbonization, though other conifer needles are not charcoal. No prominent charcoal layers were observed in this core, but charcoal is abundant in some horizons of other cores taken in the area. Fires would favor propagation of *Pinus contorta* (Tackle, 1961) and might tend to eliminate *Picea* and *Abies* from the forest. However, no injurious long-term effects of fire on *Picea* and *Abies* can be recognized in the pollen diagram (fig. 15).

Changes in the local environment are well documented in this subzone by plant macrofossils (fig. 17). From interval 420 – 375 cm, macrofossils of aquatic and pond-margin plants are still present, suggesting that little change in environment had occurred from the top of the previous subzone.

From interval 375 – 275 cm, fen plants, such as *Carex aquatilis*, *C. diandra*, a trigonous *Carex*—probably *C. utriculata*—*Salix* sp., *Menyanthes trifoliata*, and *Epilobium glandulosum* type, appear (fig. 17). *Nuphar luteum* ssp. *polysepalum* pollen and seeds, *Potamogeton* fruits, and *Pediastrum* still are present (figs. 15 and 17). These macrofossils suggest that a fen began to encroach into the pond. The pond was probably becoming very shallow and was surrounded by sedges, grasses, and other fen plants, perhaps growing on a floating mat. The aquatic macrofossils testify that a small pond was still present.

From 275 cm to the surface, macrofossils of truly aquatic plants, such as *Nuphar*, are absent (fig. 17). The Cyperaceae pollen curve is high except between 100 and 40 cm and represents chiefly fen species of *Carex*. The Cyperaceae curve ranges from 10 to 40 percent in the interval 260 – 175 cm (fig. 15). A small pollen peak at 260 cm is associated with many achenes of a trigonous *Carex*, probably *C. utriculata* or *C. vesicaria* (figs. 15 and 17). The abrupt disappearance of aquatic-plant macrofossils and the abundance of sedges imply that this interval represents the demise of the pond at this coring site.

In the interval 260 – 175 cm, few *Carex* macrofossils are found, even though the Cyperaceae pollen curve reaches its maximum at 220 cm (figs. 15 and 17). *Sphagnum* moss leaves are very abundant in this interval, and the local sedges may have been choked out by this bog moss. The high Cyperaceae pollen values suggest that *Carex* was still abundant in other parts of the bog, however. *Sphagnum warnstorfianum* seems to be the most common *Sphagnum* in the park today, and the fossil leaves are morphologically similar to leaves of this species. *Sphagnum* liberates acids in its metabolic processes (Parihar, 1965); hence, it creates a rather acidic environment. It apparently grew along the margin of the pond, at least sporadically, throughout the earlier history of this site, and it was able to colonize the bog surface when the lake became overgrown. The most abundant *Sphagnum* interval coincides with the inferred cooler, moister period about 2,800 to 1,000 years B.P. (see following paragraphs and table 3), but its sporadic occurrence in the core could be controlled by local plant succession.

From interval 175 – 100 cm, *Carex diandra*, *C. aquatilis*, and the trigonous *Carex* are very abundant, and definite *Carex utriculata* and *C. vesicaria* (with perigynia) and *C. limosa* are sparsely present (fig. 17). Cyperaceae pollen values range from 10 to 17 percent (fig. 15). *Sphagnum* leaves disappear above 125 cm, and *Salix* sp. leaves are present. These data suggest a change from an acid bog to a neutral or slightly alkaline fen. The community was similar if not identical to the *Carex limosa-Carex diandra-Potentilla palustris* community that now grows at the coring site.

In the interval 100 – 40 cm, Cyperaceae pollen curves drop to less than 2 percent, and only fruits of the sedge *Carex diandra* are abundant (figs. 15 and 17). Several causes of this locally important change are possible. Recurring fires on the fen surface might

have such an effect, but charcoal horizons that would record fire history are not present. The sedges apparently were not again choked by *Sphagnum* moss inasmuch as no leaves were found. A rising water level in the fen might explain all the changes. As the water level began to rise, *Carex* might have initially been favored over *Sphagnum*. As water levels continued to rise, the *Carex* too might die out locally and survive only on the margins of the basin. There is some support for this latter hypothesis. A few pollen grains (but no seeds) of the water lily *Nuphar* occur in this interval, whereas none occur in the adjacent sediments above or below (fig. 15). There also is a recurrence of the colonial alga *Pediastrum* at 80 cm (fig. 15). These plants are suggestive of higher water levels, but further evidence is needed to document this hydrologic change.

From a depth of 40 cm to the surface, Cyperaceae pollen percentages rise, and fruits of *Carex diandra*, the trigonous *Carex*, and *Potentilla palustris* are very abundant, at least in some horizons (figs. 15 and 17). Fruits of *Carex utriculata*, *C. vesicaria*, *C. limosa*, *C. aquatilis*, *C. canescens*, and *Menyanthes trifoliata* appear near the top. The present fen vegetation apparently became reestablished above the 40-cm level. Slight changes in climate in this subzone are apparently marked by subtle shifts in pollen percentages. The recurrence of small amounts of *Picea* and *Abies* pollen, substantiated by macrofossils, suggests a cooler, moister climate during the last 5,000 years than in the 11,600- to 5,000-year interval. Two cooling pulses may be indicated by the spruce pollen curve here and at Cub Creek pond (Waddington and Wright, 1974): a mild one that apparently began about 5,000 years ago, and a stronger one that began about 2,800 years ago. Pollen and macrofossils of *Pinus albicaulis*, *Pseudotsuga menziesii*, and *Pinus contorta* that occur in the interval from 5,000 to 2,800 years ago suggest that climate was not as moist during that period as it was from 2,800 to the present, when these species were absent.

The Cyperaceae pollen maximum in the *Picea-Abies-Pinus contorta* subzone is demonstrably local, and it would seem logical to regard it as a successional phenomenon without any climatic significance. However, the Cyperaceae curve at Cub Creek pond (Waddington and Wright, 1970) is very similar in its form and its relationship with the increase in *Picea* and *Abies*. The apparently identical timing of local lake to fen succession at these two sites may be coincidental. But this succession may also have been triggered at all potential sites by cooler, moister conditions at the end of the Altithermal. Further pollen and plant macrofossil work in progress at sites near the 15-foot lagoon should help clarify this problem.

DISCUSSION AND CONCLUSIONS

Sediments in Buckbean fen record a vegetational succession beginning with the *Betula* subzone (of the *Picea-Juniperus-Pinus albicaulis* zone) about 12,000 – 14,500 years ago (table 3). The initial vegetation following deglaciations was probably open and tundralike with few if any trees, but subalpine as well as alpine plants were present. The climate was cold and moist, but it was probably comparable to that of nearby modern high subalpine or low alpine areas. This cold period is correlated with the late stages of the Pinedale Glaciation. The base of this zone is dated at 13,500 ± 130 years B.P. in Swan Lake Flat (sample WIS – 432; Bender and others, 1971). A date of 13,140 ± 700 years B.P. (sample W – 2037; Sullivan and others, 1970) on plant material in silts about 7 miles northeast of Buckbean fen closely postdates retreat of middle Pinedale ice. Waddington and Wright (1974) recently obtained a date of 14,360 ± 500 years B.P. (sample W—2780) from the base of Cub Creek pond.

The *Populus* subzone marks the invasion of subalpine forest into the coring area. Treeline presumably migrated above the coring area up the slopes of the Two Ocean Plateau as the climate ameliorated. The forests were more open, but otherwise similar to the *Picea-Abies-Pinus albicaulis* forests in the park today. The climate was still cool and moist, probably much like that in the present subalpine vegetation association. This period probably postdates the last stages of melting of the middle Pinedale icecap.

The basal subzone of the *Pinus contorta* zone represents about the period 11,630 – 10,160 years B.P. The *Pinus contorta-Pinus albicaulis* forest inferred from this subzone was different from any modern vegetation association. The two species at present overlap in their elevational distribution, but they do not grow together in extensive mixed forests in the park. Their joint occurrence suggests a slight lowering of vegetation associations, and a climate slightly cooler than at present. Both trees occur on drier sites, suggesting less precipitation than at present. This inferred cool, dry period postdates retreat of middle Pinedale glaciers, but its relationship to late Pinedale glacial advance is still uncertain.

A *Pinus contorta* forest much like the modern one was present during deposition of the middle subzone of the *Pinus contorta* zone, extending from about

10,160 to 5,000 years ago. *Picea* and *Abies*, which now grow in suitable habitats at lake level, were apparently present only at higher elevations on the slopes of the Two Ocean Plateau at that time. Perhaps the gravelly soils near Buckbean fen accentuated the dry conditions and locally exterminated *Picea* and *Abies*. The climate was the warmest and driest of any inferred from the core, and this interval is correlated with the Altithermal period.

Radiocarbon dates of 9,240 and 5,390 years in the *Pinus contorta* subzone are separated by less than 1 metre of sediment (fig. 15), suggesting that a hiatus is present between 500 and 460 cm. The dates seem reliable, but no break in the pollen diagram occurs in this interval. Macrofossils and sediment lithology suggest a change from a large open-lake environment to a small pond environment between 500 and 460 cm, but this change could be explained without postulating a hiatus. A period of erosion or nondeposition probably occurred in this interval, but more evidence is needed to substantiate it. A smiliar hiatus occurred in the Chuska Mountains, N. Mex., during the Altithermal interval (Bent and Wright, 1963).

The distribution of *Picea* and *Abies* apparently expanded from the slopes of the Two Ocean Plateau down to lake level and they grew in mixed forests with *Pinus contorta* during the upper subzone of the *Pinus contorta* zone about 5,000 years ago. Proportions of *Picea* in these forests probably increased about 2,800 years ago during the climax of Neoglacial activity. Little change in the pollen spectra can be seen during the last 2,800 years. *Picea* does not now grow at the coring site (elev 7,750 ft), but it grows at the same elevation in many areas around the Southeast Arm of Yellowstone Lake (fig. 6). The pollen sequence supports Porter and Denton's (1967) suggestion that post-Altithermal cooling began about 5,000 years ago.

The pollen sequence at Cub Creek pond (Waddington and Wright, 1970, 1974) correlates well with that from Buckbean fen. The basal date of 14,360 B.P. at Cub Creek pond (H. E. Wright, written commun., 1973) is about 1,000 years older than other dates on deglaciation in Yellowstone National Park. No sedimentological evidence shows contamination with older carbon, and the date is tentatively correlated with the base of Buckbean fen. Pollen curves in the two diagrams are remarkably similar, and they suggest that climatic changes triggered nearly synchronous changes in vegetation over large areas on the Yellowstone Plateau. The primary zonation in the diagrams is identical and a date of 11,630 years B.P. on the boundary between the two zones at Cub Creek pond corresponds well with the Buckbean fen date of 11,550 years B.P. just above the boundary.

Zone 1 at Cub Creek pond contains relatively high percentages of *Picea*, *Juniperus*, *Abies*, *Betula*, Gramineae, and *Artemisia* pollen, and low values of *Pinus*. Most of the pine in this zone is *Pinus albicaulis* type. This assemblage suggests a pollen rain identical to that in my *Picea-Juniperus-Pinus albicaulis* zone. The *Betula* and *Populus* subzones cannot be recognized at Cub Creek pond (H. E. Wright, written commun., 1973).

Zone 2 at Cub Creek pond has very high *Pinus* (mainly *P. contorta*) pollen percentages, and low values of most other taxa as in my *Pinus contorta* zone. Other pollen diagrams from Yellowstone National Park which I have prepared (unpub. data) support the zonation of Buckbean fen.

Tentative correlation of pollen sequences of Buckbean fen with those from more distant areas is summarized in table 6. Different vegetation, both past and present, in the other areas complicates correlation of vegetation changes, although direction of shifts may be related. The chart does show that the general climatic trend in all areas is from cold to cool to warm and back to cool again.

Further work is needed to resolve several problems that arose during this study. I have proposed that sediments representing part of Altithermal time are missing in Buckbean fen. Pollen and plant macrofossil work in progress from nearby lagoons, and appropriate C^{14} dates, may clarify the validity and nature of this period of erosion or nondeposition. Cores should be taken from other areas in the park to evaluate the areal extent of this hiatus.

More precise dating of high stands of Yellowstone Lake may also be possible with further paleobotanical work and C^{14} dating of cores related to each lake level, if sediments deposited during these stands are preserved in abandoned lagoons along the lake. Lagoons at the different levels all became open for lacustrine sedimentation when the lake was 110 feet above its present level, but lagoon isolation progressed from highest to lowest elevations as lake level fell. The horizon of isolation might be recognized in core sediments from lagoons formed by the lake at each of its major levels by a change in macrofossils of aquatic plants from deep- to shallow-water forms. By such a study the horizons could be dated by radiocarbon and the sequence worked out.

Many plant species from arctic tundra grow on peaks in the Rocky Mountains far south of their continuous arctic distribution. Modern alpine tundra in the park appears to have fewer species and

TABLE 6.—*Tentative correlation of pollen sequences*

[Under "Inferred climate" columns, comparative climatic terms should be read from bottom upward. X = radiocarbon date; query (?) = interpretation not given in sources cited; solid lines (——) = separation of zones; dashed lines (— —) = subzones; wavy line (∿∿) = hiatus(?)]

Approx. age (C^{14} years B.P. $\times 10^3$)	Osgood Swamp, Sierra Nevada, Calif. (Adam, 1967)			Swan Lake, southeast Idaho (Bright, 1966)			Buckbean fen, Yellowstone National Park (this paper)			Kirchner Marsh, southern Minnesota (Wright and others, 1963; Watts and Winter, 1966)			Rogers Lake, southern New England[1] (adapted from Davis, 1967)		
	Zone	Inferred vegetation	Inferred climate	Zone	Inferred vegetation	Inferred climate	Zone	Inferred vegetation	Inferred climate	Zone	Inferred vegetation	Inferred climate	Zone	Inferred vegetation	Inferred climate
0	1	?	Cooler.	S-1	Sagebrush steppe.	Warmer.							C-3	Oak-chestnut.	?
1				X						X					
2				S-2	Sagebrush steppe (treeline lowered).	Cooler.	X(2)	Spruce-fir-lodgepole pine forest.	Cooler, moister.				C-2	Oak-hickory.	?
3															
4										C-c	Oak forest.	Cooler, moister.			
5							X			X			C-1	Oak-hemlock.	Warmest and driest(?)
6	2	?	Climatic optimum.	S-3	Sagebrush chenopod steppe.	Maximum warmth and dryness.									
7							∿∿	Lodgepole pine forest.	Maximum warmth.	C-b	Prairie.	Maximum warmth.			
										X					
8										C-a	Maple, basswood, oak, elm, forest.	Warmer, drier.	B	Pine-birch forest.	Warmer, drier.
9				S-4	Sagebrush steppe.	Increasing warmth and dryness.	X								
10	3 X	Mixed coniferous forest.	Cool.							B X	Conifer-hardwood forest.	Rapid warming trend.	A-4	Spruce forest.	Warming.
				X											
				S-5	Sagebrush steppe with Douglas-fir.	Warming.		Lodgepole pine-whitebark pine forest.	Cool, drier.	A-b	Spruce forest.	Cool.	A-1, 2, and 3	Open spruce woodland,	Cool.
11				S-6	Pine woodland.	Cool.									
							X								
12	4	Sagebrush with scattered pine-juniper(?).	Cold.	S-7	Spruce-pine woodland.	Cold, wet.		Spruce-fir-whitebark pine parkland.	Cool, moist.	X			T	Tundra.	Cold.
				X			(3)			A-a	Spruce forest.	Cool.			
13								Parkland-tundra transition.	Cold, moist.	X K	Spruce parkland.	Cold.			

[1] Rogers Lake has 47 radiocarbon dates, on entire sediment column. Individual dates not shown.
[2] *Pinus contorta.*
[3] *Picea-Juniperus-Pinus albicaulis.*

community types than tundra of the Beartooth Plateau, Mont., to the north or that of the Wind River Range, Wyo., and the Front Range, Colo., to the south. The few late-glacial fossils of arctic-alpine plants from Lilypad pond indicate that these plants grew about 2,000 feet lower than they grow today. These fossils support the theory that during glacial periods, when treelines were lower, areas like the park may have been routes of southward migration for arctic species. When treelines rose in postglacial time, alpine species became isolated on high peaks and were eliminated in areas of lower elevation. Additional detailed pollen and plant-macrofossil studies are needed to determine areal and elevational distribution and composition of late-glacial tundra vegetation.

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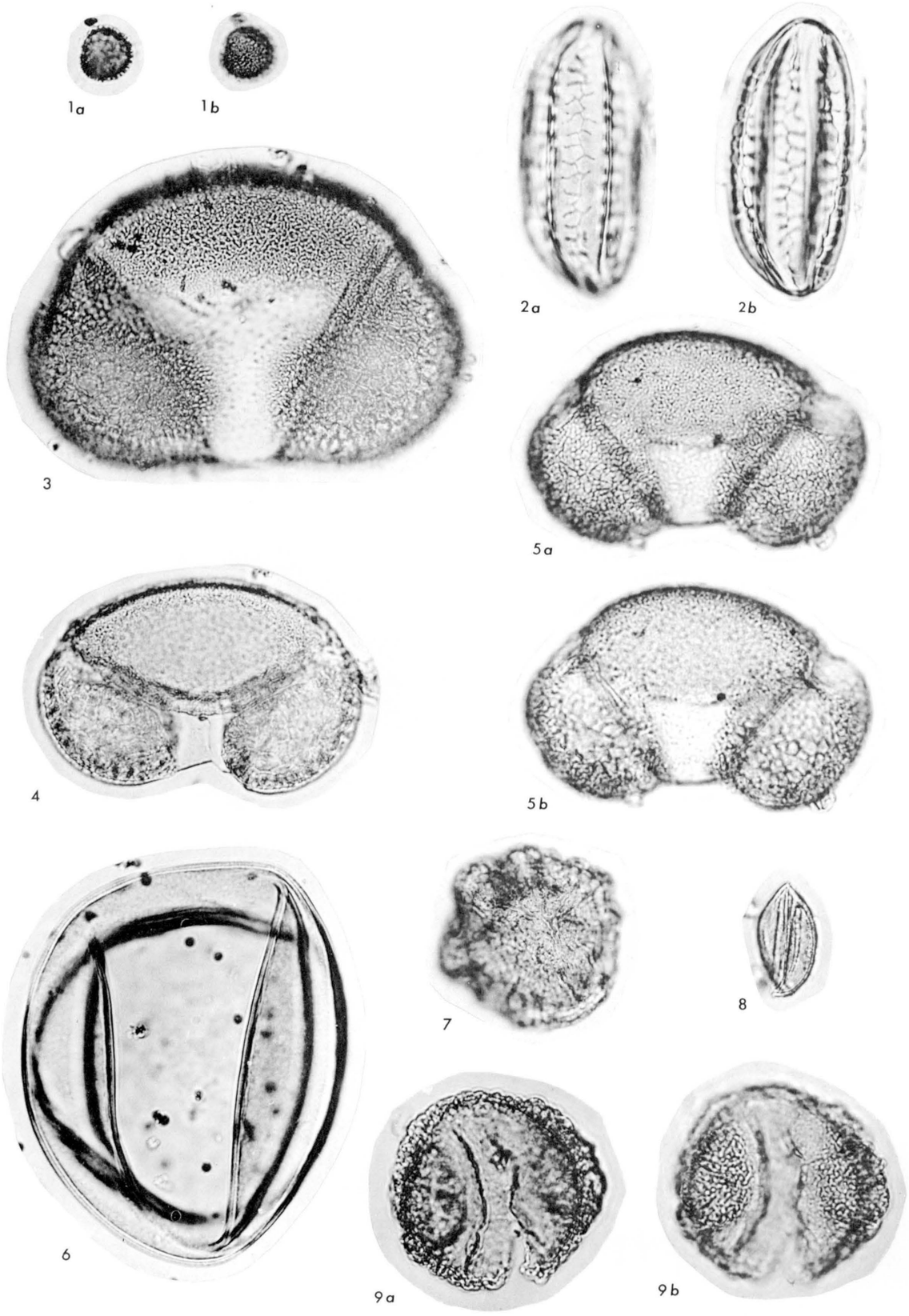
PLATES 1—10

Contact photographs of the plates in this report are available, at cost, from the U.S. Geological Survey Photographic Library, Box 25046 Federal Center, Denver, Colorado 80225.

PLATE 1

Fossil spores and pollen from Buckbean fen core. × 535.

FIGURE 1. Bryophyte spore; 890-cm depth.
  1*a*. Midfocus.
  1*b*. High focus.
2. *Ephedra viridis* type pollen; 340-cm depth.
  2*a*. High focus.
  2*b*. Midfocus.
3. *Picea* pollen; 850-cm depth.
4. *Pinus contorta* type pollen; 160-cm depth.
5. *Pinus albicaulis* type pollen; 920-cm depth.
  5*a*. High focus.
  5*b*. Slightly lower focus.
6. *Pseudotsuga* pollen; 700-cm depth.
7. *Selaginella densa* spore; 920-cm depth.
8. *Juniperus* pollen; 890-cm depth.
9. *Tsuga mertensiana*; 240-cm depth.
  9*a*. Midfocus.
  9*b* High focus.



BRYOPHYTE, *EPHEDRA, PICEA, PINUS, PSEUDOTSUGA, SELAGINELLA, JUNIPERUS,* AND *TSUGA*

PLATE 2

Fossil pollen from Buckbean fen core. × 1,054.

FIGURE 1. *Nuphar*; 340-cm depth.
2. *Typha latifolia* tetrad; 943-cm depth.
3. *Sarcobatus*; 700-cm depth.
   3*a*. High focus.
   3*b*. Slightly lower focus.
4. Compositae, subfamily Liguliflorae; 920-cm depth.
   4*a*. High focus.
   4*b*. Midfocus.
5. *Ambrosia*; 850-cm depth.
6. *Myriophyllum*; 440-cm depth.
   6*a*, High focus, to 6*c*, midfocus.
7. *Arceuthobium*; 700-cm depth.
   7*a*. High Focus.
   7*b*. Midfocus.
8. cf. *Mimulus*; 160-cm depth.
   8*a*. High focus.
   8*b*. Midfocus.

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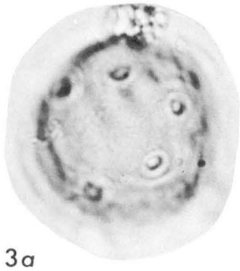
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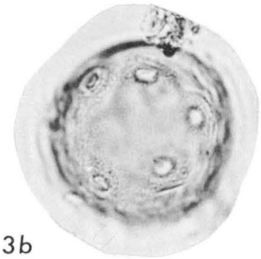
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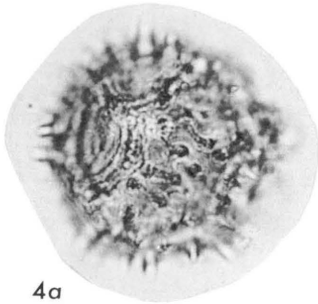
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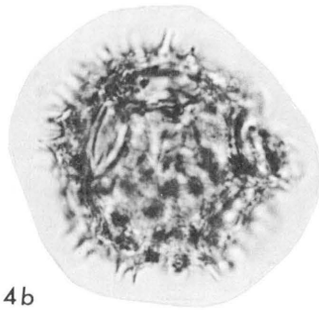
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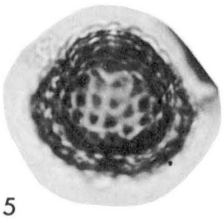
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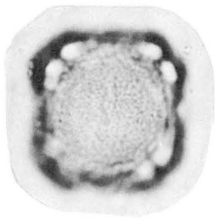
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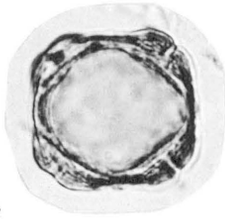
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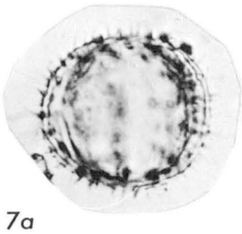
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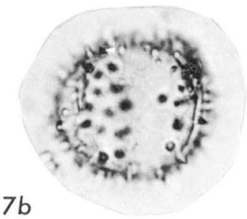
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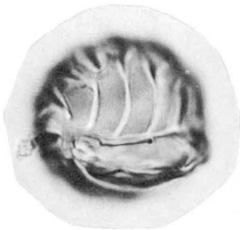
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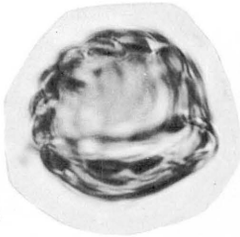
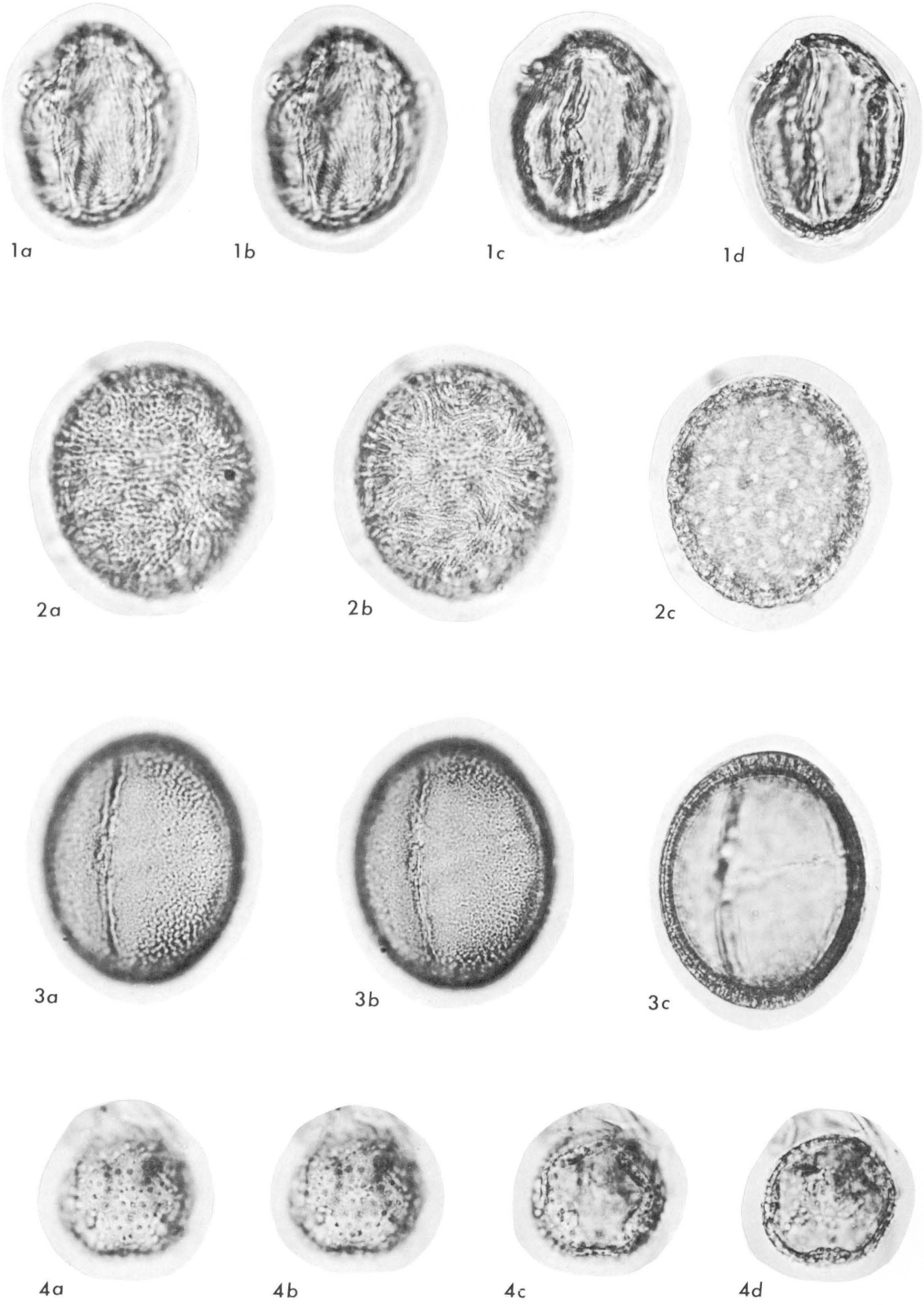

8b

NUPHAR, TYPHA, SARCOBATUS, COMPOSITAE, *AMBROSIA, MYRIOPHYLLUM, ARCEUTHOBIUM,* AND *MIMULUS*

PLATE 3

Fossil pollen from Buckbean fen core. × 1,054.

FIGURE 1. *Menyanthes*; 60-cm depth.
1*a*, High focus, to 1*d*, low focus.
2. *Polemonium*; 842-cm depth.
2*a*, High focus, to 2*c*, midfocus.
3. *Bistorta*; 900-cm depth.
3*a*, High focus, to 3*c*, midfocus.
4. *Koenigia islandica*; 850-cm depth.
4*a*, High focus, to 4*d*, midfocus.

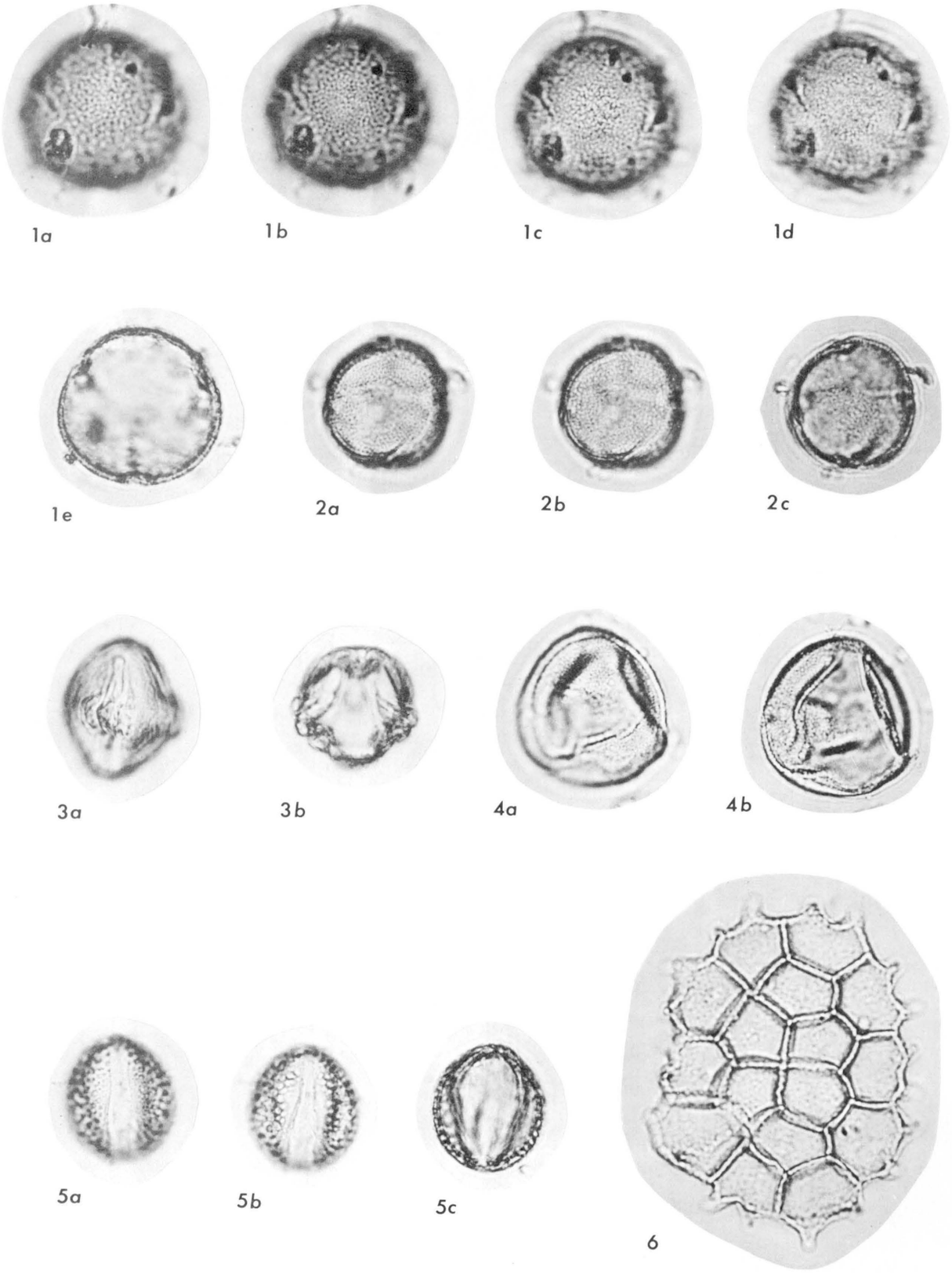


MENYANTHES, POLEMONIUM, BISTORTA, AND *KOENIGIA*

PLATE 4

Fossil pollen and alga from Buckbean fen core. × 1,054.

FIGURE 1. *Oxyria* type pollen; 850-cm depth.
1*a*. High focus, to 1*e*, midfocus.
2. *Rumex* pollen; 920-cm depth.
2*a*. High focus, to 2*c*, midfocus.
3. *Potentilla palustris* pollen; 0-cm depth.
3*a*. Equatorial view.
3*b*. Polar view.
4. *Populus* pollen; 842-cm depth.
4*a*. High focus.
4*b*. Slightly lower focus.
5. *Salix* pollen; 900-cm depth.
5*a*, High focus, to 5*c*, midfocus.
6. *Pediastrum*, a green alga; 920-cm depth.



OXYRIA, RUMEX, POTENTILLA, POPULUS, SALIX, AND *PEDIASTRUM*

PLATE 5

Fossil and modern conifer needles. × 11.

FIGURE 1–3. *Juniperus communis*.

1. Fossil needle tip; Buckbean fen core, 820- to 825-cm depth.
2. Fossil needle (near base); Buckbean fen core; 825- to 830-cm depth.
3. Modern needle; RGB–199.

4, 5. *Picea engelmannii*.

4*a*, Fossil needle, and 4*b*, cross section; Lilypad pond core, 930- to 935-cm depth.

5*a*, and 5*b*, Modern needle, and 5*c*, cross section; COLO 180762.

6, 7. *Pinus albicaulis*.

6*a*, Fossil needle, and 6*b*, cross section; Buckbean fen core, 360- to 365-cm depth.

7*a*, Modern needle, and 7*b*, cross section; R. G. Baker collection.

8, 9. *Pinus contorta*.

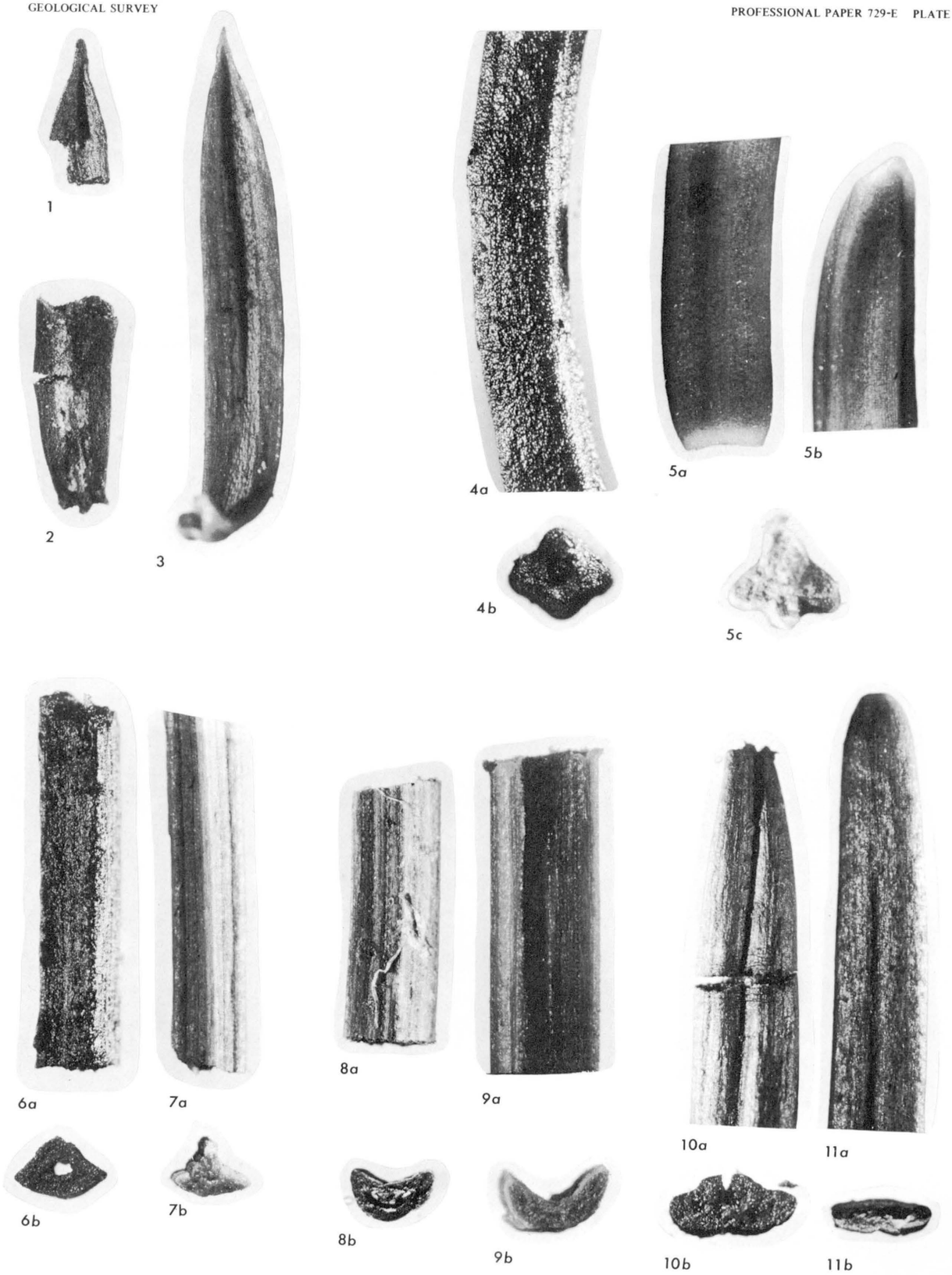
8*a*, Fossil needle, and 8*b*, cross section; Buckbean fen core, 360- to 365-cm depth.

9*a*, Modern needle, and 9*b*, cross section; R. G. Baker collection.

10, 11. *Pseudotsuga menziesii*.

10*a*, Fossil needle, and 10*b*, cross section; Buckbean fen core, 350- to 355-cm depth.

11*a*, Modern needle, and 11*b*, cross section; R. G. Baker collection.



JUNIPERUS, PICEA, PINUS, AND *PSEUDOTSUGA*

PLATE 6

Fossil and modern fruits, scales, seeds, perianth, and bracts. × 11.

FIGURE 1, 2. *Alnus tenuifolia* fruits.
1. Fossil fragment; Buckbean fen core, 400- to 405-cm depth.
2. Modern; COLO 2181.

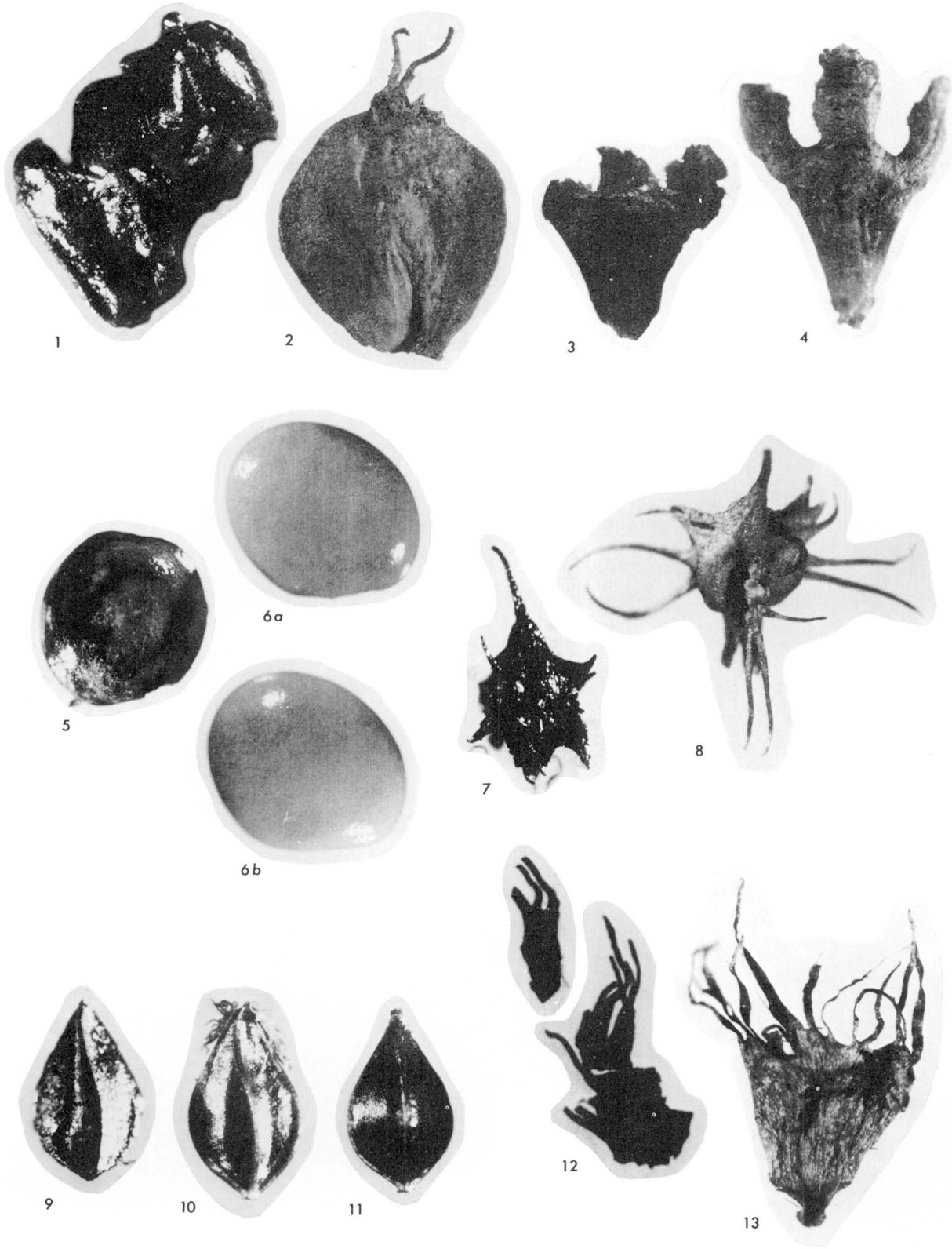
3, 4. *Betula glandulosa* catkin scales.
3. Fossil; Lilypad pond core, 885- to 890-cm depth.
4. Modern; COLO 2250.

5, 6. *Menyanthes trifoliata* seeds.
5. Fossil; Buckbean fen core, 55- to 60-cm depth.
6*a*, 6*b*. Modern; RGB–197.

7, 8. *Rumex fueginus* perianth.
7. Fossil; Buckbean fen core, 445- to 450-cm depth.
8. Modern; COLO 56854.

9–11. *Rumex salicifolius* fruits.
9. Fossil; Lilypad pond core, 880- to 885-cm depth.
10, 11. Modern; COLO 181168.

12, 13. *Populus balsamifera* bracts.
12. Fossil fragments; Buckbean fen core, 805- to 810-cm depth.
13. Modern; COLO 107394.



ALNUS, BETULA, MENYANTHES, RUMEX, AND *POPULUS*

PLATE 7

Fossil and modern fruits, perigynia, and fruit-stones. × 11.

FIGURE 1. *Nuphar luteum* ssp. *polysepalum*. Fossil fruit; Buckbean fen core, 360- to 365-cm depth.

2 – 4. *Carex limosa* fruits.
- 2. Fossil; Buckbean fen core, 0- to 5-cm depth.
- 3, 4. Modern; RGB – 152.

5 – 7. *Carex vesicaria* perigynia.
- 5. Fossil; Buckbean fen core, 0- to 5-cm depth.
- 6, 7. Modern; RGB – 87.

8 – 10. *Carex ultriculata* perigynia.
- 8. Fossil; Buckbean fen core, 5- to 10-cm depth.
- 9, 10. Modern; RGB – 277.

11, 12. *Potamogeton alpinus* fruit with covering.
- 11. Fossil; Buckbean fen core, 820- to 825-cm depth.
- 12. Modern; COLO 131646.

13, 14. *Potamogeton filiformis* fruit-stones.
- 13. Fossil; Lilypad pond core, 980- to 985-cm depth.
- 14. Modern; COLO 199776.

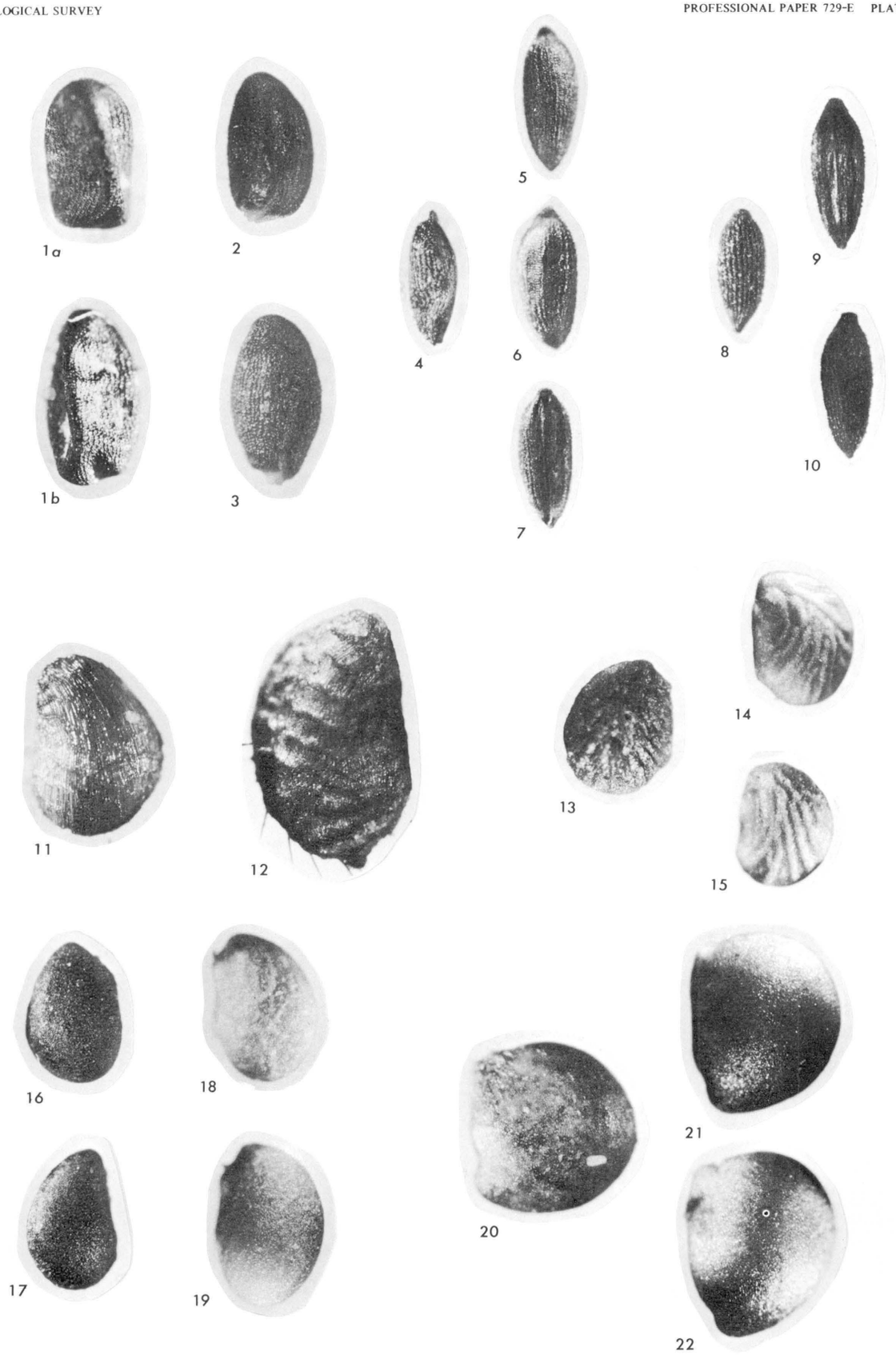
15 – 17. *Potamogeton gamineus* fruit-stones.
- 15. Fossil; Buckbean fen core, 450- to 455-cm depth.
- 16, 17. Modern; COLO 72388.

NUPHAR, CAREX, AND *POTAMOGETON*

PLATE 8

Fossil and modern seeds and fruits. × 17.

FIGURE 1–3. *Descurainia californica* seeds.
1*a*, 1*b*. Fossil; Lilypad pond core, 910- to 915-cm depth.
2, 3. Modern; COLO 13079.
4–7. *Epilobium glandulosum*-type seeds.
4. Fossil; Buckbean fen core, 145- to 150-cm depth.
5–7. Modern—*Epilobium adenocaulon* (included within this morphological type); COLO 181161.
8–10. *Epilobium lactiflorum* seeds.
8. Fossil; Lilypad pond core, 805- to 810-cm depth.
9, 10. Modern; COLO 134413.
11, 12. *Ranunculus aquatilis* fruits.
11. Fossil; Lilypad pond core, 870- to 875-cm depth.
12. Modern; RGB–151.
13–15. *Potentilla biennis* fruits.
13. Fossil; Lilypad pond core, 885- to 890-cm depth.
14, 15. Modern; COLO 209920.
16–19. *Potentilla gracilis* type fruits.
16, 17. Fossil; Lilypad pond core, 955- to 960-cm depth.
18, 19. Modern; RGB–124a.
20–22. *Potentilla palustris* fruits.
20. Fossil; Buckbean fen core, 5- to 10-cm depth.
21, 22. Modern; RGB–148.



DESCURAINIA, EPILOBIUM, RANUNCULUS, AND *POTENTILLA*

PLATE 9

Fossil perigynia, fruits, and seeds from Buckbean fen core and modern perigynia, fruits, and seeds. × 16.

FIGURE 1, 2. *Carex aquatilis* perigynia and fruits.
1. Fossil; 165- to 170-cm depth.
2. Modern; COLO 53127.

3–5. *Carex canescens* perigynia and fruits.
3. Fossil; 0- to 5-cm depth.
4, 5. Modern; R. G. Baker collection.

6–8. *Carex diandra* perigynia and fruits.
6. Fossil; 0- to 5-cm depth.
7, 8. Modern; RGB–147.

9–11. *Eleocharis macrostachya* fruits.
9. Fossil, corroded; 475- to 480-cm depth.
10, 11. Modern; COLO 95235.

12–14. *Glyceria maxima* ssp. *grandis* seeds.
12. Fossil; 435- to 440-cm depth.
13, 14. Modern; COLO 20242.

15, 16. *Naias flexilis* seeds.
15. Fossil; 475- to 480-cm depth.
16. Modern; COLO 106552.

CAREX, ELEOCHARIS, GLYCERIA, AND *NAIAS*

PLATE 10

Fossil and modern fruits and seeds. × ca. 27

FIGURE 1. cf. *Vaccinium*. Fossil seed; Lilypad pond core, 990- to 995-cm depth.

2–6. *Saxifraga rhomboidea* seeds.

2*a*, 2*b*. Fossil; Lilypad pond core, 930- to 935-cm depth.

3—6. Modern; COLO 38885.

7–11. *Saxifraga caespitosa* seeds.

7. Fossil; Lilypad pond core; 930- to 935-cm depth.

8—11. Modern; COLO 180253.

12–14. *Rorippa islandica*-type seeds.

12. Fossil; Buckbean fen core, 410- to 415-cm depth.

13, 14. Modern; COLO 197251.

15–17. *Typha* fruits.

15. Fossil; Buckbean fen core, 665- to 670-cm depth.

16. Modern fruit with covering membrane; COLO 41239.

17. Modern fruit with membrane removed; COLO 41239.

cf. *VACCINIUM, SAXIFRAGA, RORIPPA,* AND *TYPHA*

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