National Library
of Canada

Canadian Theses Service

Ottawa, Canada
K1A 0N4

Bibliothèque nationale
du Canada

Services des thèses canadiennes

CANADIAN THESES

THÈSES CANADIENNES

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30. Please read the authorization forms which accompany this thesis.

THIS DISSERTATION
HAS BEEN MICROFILMED
EXACTLY AS RECEIVED

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30. Veuillez prendre connaissance des formules d'autorisation qui accompagnent cette thèse.

LA THÈSE A ÉTÉ
MICROFILMÉE TELLE QUE
NOUS L'AVONS REÇUE

NL 339 (r. 86/01)

Canada

National Library
of Canada

Canadian Theses Division

Ottawa, Canada
K1A 0N4

Bibliothèque nationale
du Canada

Division des thèses canadiennes

0-315-24829-7

PERMISSION TO MICROFILM — AUTORISATION DE MICROFILMER

- Please print or type — Écrire en lettres moulées ou dactylographier

Full Name of Author — Nom complet de l'auteur

LOW SUSSANNE D

Date of Birth — Date de naissance

08 - 08 - 57

Country of Birth — Lieu de naissance

U.S.A.

Permanent Address — Résidence fixe

7813 CAYUGA AVE BETHESDA MD USA 20034

Title of Thesis — Titre de la thèse

EVALUATING CAVE DEPOSITS AS [illegible]
PALYNOLOGICAL [illegible] STUDY SITE PERIMENTAL EVALUATION
PRYOR MOUNTAINS, MONTANA

University — Université

UNIVERSITY OF ALBERTA

Degree for which thesis was presented — Grade pour lequel cette thèse fut présentée

M.A.

Year this degree conferred — Année d'obtention de ce grade

1984

Name of Supervisor — Nom du directeur de thèse

DR CHARLES SCHWEGER

Permission is hereby granted to the NATIONAL LIBRARY OF CANADA to microfilm this thesis and to lend or sell copies of the film.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

L'autorisation est, par la présente, accordée à la BIBLIOTHÈQUE NATIONALE DU CANADA de microfilmer cette thèse et de prêter ou de vendre des exemplaires du film.

L'auteur se réserve les autres droits de publication; ni la thèse ni de longs extraits de celle-ci ne doivent être imprimés ou autrement reproduits sans l'autorisation écrite de l'auteur.

Date

12 OCTOBER 1984

Signature

Sussanne Low

NL-91 (4/77)

THE UNIVERSITY OF ALBERTA

Evaluating Cave Deposits as Palynological Study Sites: An Experimental Evaluation, Pryor Mountains, Montana

by

© Russanne Dorothy Low

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF Master of Arts

Anthropology

EDMONTON, ALBERTA
Fall 1984

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR Russanne Dorothy Low

TITLE OF THESIS Evaluating Cave Deposits as Palynological Study Sites: An Experimental Evaluation, Pryor Mountains, Montana

DEGREE FOR WHICH THESIS WAS PRESENTED Master of Arts

YEAR THIS DEGREE GRANTED Fall, 1984

Permission is hereby granted to THE UNIVERSITY OF ALBERTA LIBRARY to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

(SIGNED) Russanne L.

PERMANENT ADDRESS:

7313 [illegible] AVE
BETHESDA MD 20034
USA

DATED Oct. 12 1984

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Evaluating Cave Deposits as Palynological Study Sites: An Experimental Evaluation, Pryor Mountains, Montana submitted by Russanne Dorothy Low in partial fulfilment of the requirements for the degree of Master of Arts.

Charles Schweger

Supervisor

....

....

Date Oct. 12, 1984

Abstract

Pollen analysis of archaeological cave and rockshelter deposits is widely implemented as a technique to provide knowledge about prehistoric human adaptation and past vegetational environments. It is generally accepted that caves and rockshelters are characterized by little naturally occurring botanical material and are protected from pollen deposition by wind, but the dominant means of pollen transportation and the subsequent meaning of the resulting pollen assemblage is inadequately understood.

This study explores the dynamics of pollen deposition in caves and rockshelters located in the Pryor Mountains of south-central Montana. Pollen traps were placed in twelve cave and rockshelter sites situated along an altitudinal gradient for the 1981 pollination season. The resulting assemblages were compared to surface sample assemblages and ecological survey data. Analysis of these data demonstrate that wind is an important vector by which pollen enters caves and rockshelters, that the wind dominated pollen assemblage demonstrates the variability characteristic of local pollen rain, and the lack of intersite and intrasite comparability between contemporaneous pollen samples derived from cave and rockshelter samples strongly suggests a reappraisal of the utility of these deposits when attempting paleoenvironmental reconstructions in a fossil context.

Acknowledgements

The author is indebted to Dr. Charles Schweger for his guidance and support throughout the study, and to the members of her committee, Dr. David Lowell and Dr. Ruth Stockey, for useful suggestions on the manuscript.

Special thanks are due Dr. Thelma Habgood, who provided training in the art of pollen recognition, and assisted throughout the course of the project with difficult identifications.

Logistical support was provided by the Pryor Mountain International Field School and Research project, under the Direction of Robson Bonnichsen, University of Maine, Orono; and Dr. David Young, University of Alberta. Mr. George Schaller of the National Forest Service, Custer National forest, Beartooth Range District greatly facilitated the field work by providing maps, and reports on road and weather conditions, and lodging in the ranger station during inclement weather.

Rebecca Cole-Will and Richard Will are gratefully acknowledged for providing field assistance.

Thanks are due to Hans Reider, University of Tubingen for providing sediment samples from Hohlen Stein Cave, Schambach Valley, West Germany for pollen analysis.

Mr. Ingolf S. Askevold, University of Manitoba, provided identification of the insects found in the pollen traps.

Douglas Schnurrenberger is gratefully acknowledged for providing field assistance, editorial comments, and his technical help in formating this text.

Laboratory work and computer analysis were conducted with financial assistance provided by the Department of Anthropology, University of Alberta.

This project was made possible by research grants from the Society of Sigma Xi, the National Speleological Society, and the Anakeesta Foundation.

TABLE OF CONTENTS

INTRODUCTION 1

PREVIOUS RESEARCH 6

RESEARCH DESIGN 8

DESCRIPTION OF STUDY AREA 11

Climate 12

FIELD METHODOLOGY 13

LABORATORY METHODOLOGY 15

CLUSTER ANALYSIS 24

REGIONAL VEGETATION 26

Subalpine Forest and Meadow 29

Douglas Fir Zone 40

Utah Juniper-Blacksage 42

Vegetation Zones Adjacent to Study Sites 43

Rock Outcrop-Forest 43

Mountain Grassland 45

Streamside Hardwood 45

Sagebrush Grassland Zone 45

Red Desert Salt Shrub Zone 45

MODERN POLLEN RAIN 45

Englemann Spruce-Alpine Fir Forest and Meadow 49

Douglas Fir Forest 50

Utah Juniper-Blacksage Desert 57

ANALYSIS 60

Relationship Between Pollen Rain and Local Vegetation..60

Patterning in the Cave Samples........................69

Agencies of Pollen Influx into Caves................72

Biological Agencies.................................78

Human Agencies......................................88

CONCLUSION..90

BIBLIOGRAPHY...101

APPENDIX I...109

APPENDIX II..110

List of Figures

Figure Page

1. Cave and Rockshelter Study Sites, Pryor Mountains, Montana..5

2. Relative Percent Surface Sample Pollen Diagram for Cave and Rockshelter Sites, Pryor Mountains Montana ....In Pocket

3. Pryor Mountain Vegetation Zones and Study Sites.......28

4. Abbreviated Relative Percent Surface Sample Pollen Diagram for Cave and Rockshelter Sites, Pryor Mountains, Montana.................................48

5. Location of Sediment Samples, Cave Trap, and Vegetation Within Skylight Cave......................56

6. Similarity Demonstrated Between Contemporaneous Pollen Assemblages from Cave and Rockshelter Sites Located in Three Vegetation Zones, Pryor Mountains, Montana...62

7. Relationship Between Pollen Rain and Local Tree Composition...66

8. Schematic Model of Pollen Transport into Caves........74

9. Comparison of Pollen Composition of Cave Bear Coprolite, Hyaena Coprolite, and Unenriched Sediment Samples from Hohlen Stein, Schambach Valley, West Germany..87

10. Taphonomic Model for the Interpretation of Pollen Assemblages Derived from Cave and Rockshelter Deposits...93

List of Tables

Table Page

1. Description of Sites....................................10
2. Pryor Mountains Climate Data............................13
3. Density and Dominance of Vegetation Taxa by Site......30
4. Arboreal Survey Data....................................37
5. Absolute Influx by Cave or Rockshelter Site...........77
6. Composition of Multiple-species Agglomerates..........83

List of Plates

Plate Page

1. Comparison of Polypodiaceae Type and *Pseudotsuga* Grains....19
2. Comparison of Polypodiaceae Type and *Pseudotsuga* Grains....21
3. *Pinus* Grains....23
4. Multiple Species Pollen Agglomerates....81

INTRODUCTION

Pollen analysis has been widely applied to archaeological cave deposits in human paleoecological investigations. In Europe, fossil pollen records provide the biological basis for reconstructions of climatic change in Paleolithic cave and rockshelter sites (Leroi-Gourhan, 1965). Pollen analysis of cave fills has also figured prominently in archaeological research in the Americas (cf. Schoenwetter, 1970; Shreve-Brinkman, 1978), and, in Africa (Van Zinderen Bakker, 1982).

Despite numerous applications, it is widely recognized that cave deposits pose pollen analytical problems to the researcher (Van Zinderen Bakker, 1982). Pollen assemblages from cave deposits are notoriously sparse (Leroi-Gourhan, 1965), frequently poorly preserved (Donner, 1975), and are suspect to contamination resulting from the activities of human and nonhuman inhabitants (Couteaux, 1977). However, selection of cave deposits over other types of polliniferous deposits is often based on the poor preservational properties of surrounding open air sites (cf. Van Zinderen Bakker, 1982), or the lack of lakes or bogs providing a depositional history of the time period in question (Leroi-Gourhan, 1965), than on the intrinsic properties of the cave alone. For archaeological purposes, selection of cave deposits for analysis is encouraged by the *in situ* association of human artifacts within a pollen bearing deposit (Anderson, 1955).

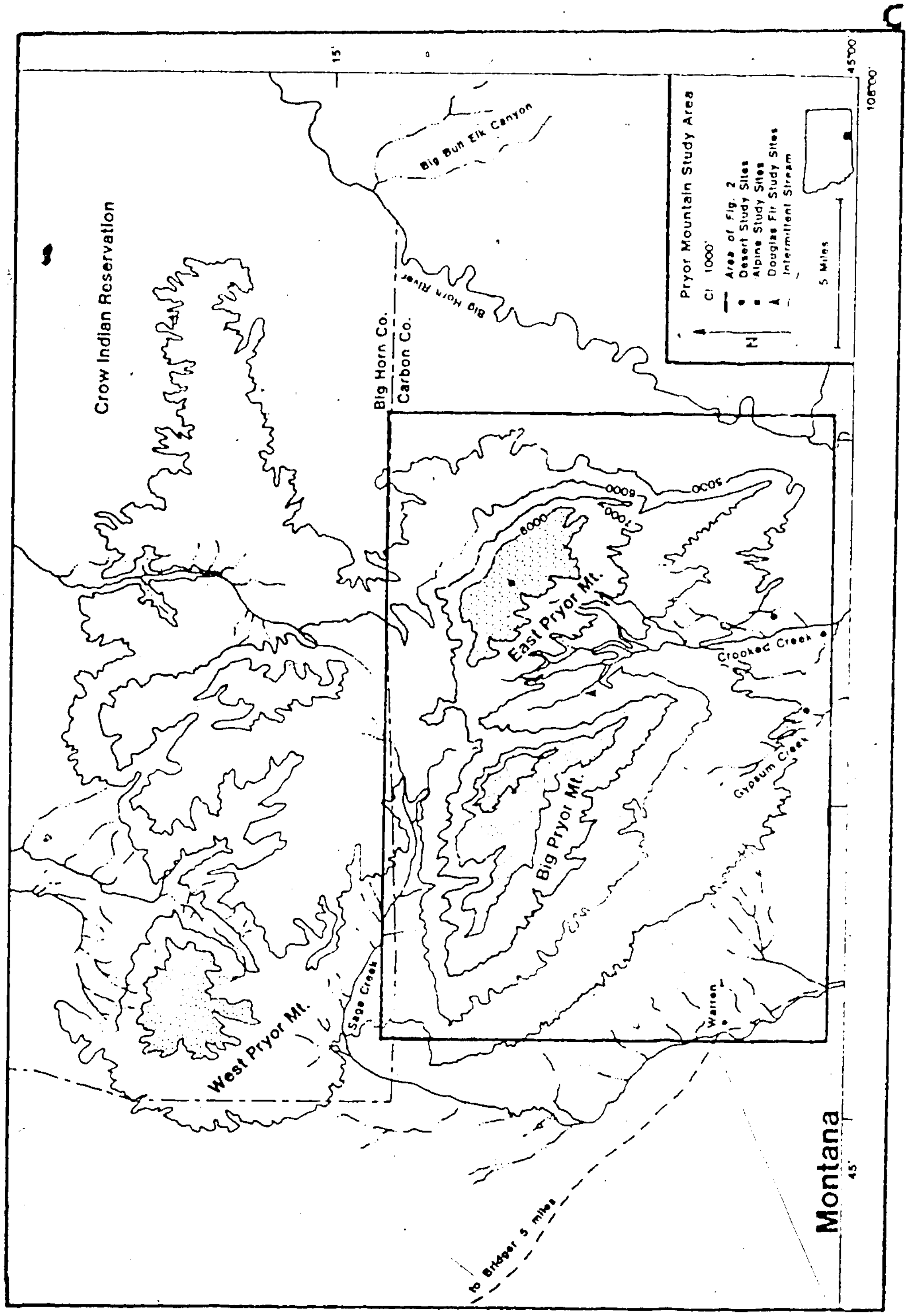
Site selection is, however, a critical part of a paleoenvironmental research design (Jacobsen and Bradshaw, 1981). For palynologically-based reconstructions to be statistically significant and comparable from site to site, it is necessary to establish that the sampling site records regional pollen rain (Janssen, 1973). This tenet holds true whether paleoenvironmental reconstructions are developed through the community analogue approach, as advocated in North America (Wright, 1967), or on the basis of AP/NAP (arboreal pollen/ nonarboreal pollen) ratios, as favored in European archaeological pollen analysis (Leroi-Gourhan, 1965).

Experimental studies of modern pollen production, dispersal, and deposition have established guidelines for selecting suitable lake, bog and open air sites (Jacobsen and Bradshaw, 1981). However, the relationship between pollen assemblages recovered from cave and rockshelter deposits, pollen rain, and surrounding vegetation have not been adequately explored. The implications for this are very serious: until the dynamic process of pollen transport into caves is fully established, much of our understanding of climatic history and human paleoecology as derived from fossil pollen records from caves must be viewed with great caution.

Thus, it is imperative that experimental studies of modern pollen transport into caves and rockshelters be initiated so that an understanding of the relationship between cave derived pollen assemblages, pollen rain, and vegetation may be established. Such data will provide more accurate interpretative models, guide site selection, and permit the reevaluation of current paleoenvironmental and human paleoecological reconstructions based on fossil pollen from cave and rockshelter deposits.

This study explores the dynamics of pollen deposition in caves and rockshelters located in the Pryor Mountains of south-central Montana (Fig. 1). A series of 12 cave and rockshelter sites situated along an altitudinal gradiant were fitted with pollen traps for the 1981 pollination season. Pollen traps, surface samples, and ecological measurements of the vegetation surrounding the caves, form a comparative data base to explore the suitability of cave and rockshelters as study sites for paleoenvironmental reconstructions based on fossil pollen data.

Figure 1. Cave and Rockshelter Study Sites, Pryor Mountains, Montana


Pryor Mountain Study Area
CI 1000'
Area of Fig. 2
Desert Study Sites
Alpine Study Sites
Douglas Fir Study Sites
Intermittent Stream
N
5 Miles
Crow Indian Reservation
Big Bull Elk Canyon
Big Horn River
Big Horn Co.
Carbon Co.
East Pryor Mt.
Big Pryor Mt.
West Pryor Mt.
Sage Creek
Crooked Creek
Gypsum Creek
Warren
to Bridger 5 miles
Montana
5000
6000
7000
8000
15'
45'
45°00'
108°00'
C
D

PREVIOUS RESEARCH

Little research has been directed toward understanding the mechanics of pollen transport into caves. Most models employed in the interpretation of fossil pollen spectra from caves were originally conceived by French palynologists and are based on empirical observations of fossil material. For instance, French cave deposits have repeatedly produced pollen assemblages characterized by high NAP frequencies, consisting predominantly of Poaceae and Asteraceae, for which an analogue has not been found in modern landscapes (Leroi-Gourhan and Leroi-Gourhan, 1965). Assemblages of similar composition have not been discovered in fossil assemblages from other types of sites, suggesting that this bias may be inherent to pollen deposition in caves (Couteaux, 1977; Leroi-Gourhan, 1965).

Leroi-Gourhan and Renault-Miskovsky (1977) suggest that this apparent bias toward low-lying herbs reflects the role played by animals in transporting pollen to caves. They characterize the feet and hair of animals, including humans, as mobile pollen traps, that sample the external vegetation, and transport pollen to the cave interior. Support for this hypothesis is sought by comparing samples at Renne Cave, Arcy-sur-Cure, France, where polliniferous samples are located in a cave opening of sufficient size to accomodate large animals (Leroi-Gourhan and Renault-Miskovsky, (1977).

The problems associated with interpreting high NAP frequencies has led to the development of an interpretative methodology based on AP and NAP ratios (Leroi-Gourhan, 1965). This method assumes that greater AP proportions indicate climatically controlled tree growth, and that pollen production has remained at Holocene rates throughout the Pleistocene (Brande and Bleich, 1975).

Both the technique used for paleoenvironmental reconstructions and the characterizations of pollen transport into caves demonstrate that many palynological reconstructions from European Paleolithic cave sites have little basis in the principles of plant ecology. This reflects the emphasis placed on archaeological palynology as a chronostratigraphic tool, which until recently, in this context, has been considered palynology's major contribution to archaeological research (cf. Laville, et al., 1980).

Contemporary pollen trapping experiments by Bui-Thi-Mai (1974) at Abri Vaufrey (France) were designed to determine the reliability of caves as sampling sites for paleoenvironmental analysis. They demonstrated that wind transport is a significant vector by which pollen enters caves. Nine contemporaneous pollen samples from in and around Abri Vaufrey were compared to determine whether they would demonstrate variation significant enough to yield differing climatic interpretations if observed in a fossil context.

Bui-Thi-Mai (1974) observed a general decrease of both total grains and arboreal grains in a transect across the cave floor from the entrance to the rear of the cave. Pollen samples from the rear of the cave reflected a bias toward lightweight, highly aerodynamic grains. The pollen traps centrally located in the chamber provided a pollen assemblage that best represented the vegetation at large; least representative were sampling sites where turbulence and localized air currents figured prominently, such as near the wall and opening of the cave.

However, this study at Abri Vaufrey also demonstrates that cave sites inject their own unique sampling biases which affect the taxonomic composition of the pollen assemblage. The potential for sample bias must be considered in any paleoenvironmental reconstruction derived from cave deposits. At Abri Vaufrey, Bui-Thi-Mai (1974) concluded that the statistical dissimilarities observed between her samples would not produce differing climatic reconstructions given the limits of interpretation of fossil data.

In summary, Bui-Thi-Mai concludes that a cave acts, "As an integrator of its pollen environment, similar to lake or bog localities, " (1976:9). However, because quantitative data on the surrounding vegetation was not collected, it is not possible to assess from the Abri Vaufrey study whether caves do in fact sample regional pollen rain: the characteristic that makes medium sized lakes and bogs highly suitable study sites for paleoenvironmental reconstructions.

RESEARCH DESIGN

The objective of this study was to provide a comparative data base with which to explore the factors which contribute to variation in cave and rockshelter pollen assemblages. The sampling design followed a nesting strategy, focusing on the three levels of resolution defined in Janssen's model of pollen transport (Janssen 1973). Jacobsen and Bradshaw's (1981) definitions of local (plants 20m or less), extralocal (20m to several hundred m) and regional (greater distances) pollen source areas are adopted in this paper.

At the regional level, 3 major vegetation types were sampled for comparison. These included Cave Ann and Cowboy Bob Rockshelter in the Subalpine zone; Caves 1, 2, and 3 West, Caves 1 and 2 East, Bobcat Rockshelter, and Skylight Cave in the mid-elevation Douglas Fir Zone; and Crooked Creek Rockshelter, Burnt Timber Rockshelter and Gyp Springs Rockshelter in the xeric lower elevation Utah Juniper-Blacksage Zone (Table 1). To investigate extralocal variation, 7 cave and rockshelter sites were located in the Douglas Fir zone. The influence of local variation was monitered by several samples clustered in Skylight Cave.

To provide a control and to compare the cave derived pollen assemblages to the vegetation, open air Tauber traps were positioned 10m from each cave or rockshelter site. Surface samples were collected from each site to determine whether cave floor material differs significantly from the pollen rain. Open air surface samples were again collected as a control. Through this hierarchical scheme it should be

Table 1

Description of Sites

Site	Elevation (m.a.s.l.)	Formation	Vegetation	Aspect (Azimuth)	Interior Dimensions	Comments
Cowboy Bob R.	2600	Madison Limestone	Alpine Fir/Englemann Spruce Forest Stands interspersed with Sub-Alpine Meadow	50°	6m x 6.5m	large lip mound, floor dips 45 toward back of cave
Cave Ann	2600	Madison Limestone	"	50°	5m x 10m	faces small hollow, protected on 2 sides by stone cliffs floor dips 5 towards entrance
Cave 1 East	1900	Madison Limestone	Douglas Fir Forest	270°	8m x 3.5m	talus slope 35-40 at mouth
Cave 2 East	1900	Madison Limestone	"	270°	5m x 4m	
Cave 1 West	1900	Madison Limestone	"	60°	11.5m x 7m	located on precipice 10m above talus slope
Cave 2 West	1900	Madison Limestone	"	10°	10m x 3.5m	5 lip mound, 20 talus slope
Cave 3 West	1900	Madison Limestone	"	10°	11m x 7m	
Skylight Cave	1900	Madison Limestone	"	180° 240°	22m x 9m	2 openings, constricted at center to opening of 2.5m x 1.5m
Bobcat R.	1800	Madison Limestone	"	340°	15m x 7m	shelter in small hollow, faced on two sides by stone cliffs
Crooked Creek R.	1500	Chugwater	Utah Juniper Blacksage Desert	200°	4.5m x 2m	floor dips 30 toward interior
Burnt Timber R.	1400	Chugwater	"	330°	3m x 2m	
Gyp Springs R.	1300	Chugwater	"	80°	9m x 2m	located on rimrock 30m above the flat

possible to evaluate whether the pollen derived from cave floor deposits are representative of the windborne pollen rain of caves and open air sites, and ultimately whether the pollen assemblage is representative of the local or regional vegetation.

DESCRIPTION OF STUDY AREA

The Pryor Mountains of south-central Montana are a series of fault blocks separated from the Bighorn Mountains by the deeply incised Bighorn River (Blackstone, 1975), (Fig. 1). The capping Paleozoic limestones dip steeply to the west. Stream valleys parallel the faults and separate the individual mountain blocks. Several deep canyons cross cut sedimentary strata and lead out of the mountains to the south towards the Big Horn Basin, and to a lesser extent, toward the west and north. Transition from the mountains to the basin is achieved in several areas by pediments dipping to the south.

The canyon forming rock in all parts of the Pryor Mountains is the Mississippian Madison Limestone Formation (Blackstone, 1975). The upper member of this formation, the Mission Canyon Member, forms the rim rock in several canyons. This strata contains numerous solution caverns, many of which were once filled with breccia and are presently in the process of reexcavation.

Climate

Because the Pryor-Big Horn Mountain chain is one of the most easterly of the Rocky Mountains, the orographic effect depletes air masses arriving from the west of their moisture content. Air masses from the south are blocked by the Owl Creek and Wind River Mountains. On the eastern flank, precipitation is generated by storm tracks which produce northeasterly winds (Lowry, 1960). The bulk of precipitation falls between April and September, 40-45% of the annual rainfall falling between May and June. Temperature and precipitation vary more with elevation than geographic location (Baker, 1944). Lack of weather monitoring stations within the Pryors limits a discussion of local climate around the study sites.

Ruffner (1978) provides an estimate of 15-20cm annual precipitation at Sage Creek Station, with the January average temperature ranging 1-11°C, and July average temperature ranging 13-32°C. South (1974) provides estimates of precipitation based on degree of soil development, which demonstrates at least a strong trend of climatic variation between the zones (Table 2).

Table 2

Vegetation Type	Annual Precipitation (cm)	Mean Soil Temp. °C	Days Frost Free
Subalpine Zone	38-51	3-6	40-50
Douglas Fir Zone	38-48	4-7	50-90
Utah Juniper Blacksage	15-25	6-7	70-85

(Adapted from South 1974)

Snowfall averages fall between 64-381 cm per year in the mountains, with accumulation directly proportional to elevation (Baker, 1944).

Field Methodology

In April, 1981, Tauber trap pollen samplers were placed in the selected low and mid elevation rock shelters. Tauber traps are static recepticles designed to collect the sedimentation of pollen from the air. A Tauber trap consists of a plastic jar fitted with a 15cm diameter lid with a 5cm diameter central aperature. The lid is aerodynamically designed to minimize air turbulence so that the vertical cross-section tapers from the central aperature to the edges.

Traps were placed in the higher elevation sites of Cowboy Bob and Cave Ann in June, 1981, by which time the snow drifts had melted back sufficiently for trap emplacement. At least 2 traps were located within each cave and rockshelter, one at the lip, another outside the dripline, and one or more deeper in the interior. A trap was placed 10m outside the mouth of the cave, away from the direct influence of vegetation surrounding the cave mouth to ensure comparability of the inner traps to the local vegetation (Wright, 1967).

Tauber traps were attached to plastic jars, and mounted on a one meter rebar rod driven approximately 30cm into the ground. Because of roof fall, some traps were placed on the floor of the cave, and wedged into a stable upright position with rocks. All traps were filled with a preservative solution composed of glycerine, acetic acid, and distilled water. Surface samples of sediment, moss or leaf litter were collected from both inside the cave or rockshelter, and near the open air traps.

Archeological test investigations were initiated in Cave Ann while pollen traps were in place. For approximately 3 weeks between 1 and 3 individuals were excavating with hand trowels in a 1x2 m excavation unit. As a result, it is necessary to consider that human activity may have played a significant role in forming the pollen assemblage at this site.

The vegetation surrounding each cave and rockshelter study site was sampled, using a point centered-quarter and a transect-intersect method (Grieg-Smith, 1962). Trees occurring at distances greater than 10m were recorded as absent, and clumps of grass were recorded as a single unit. Due to the lack of resolution of grass pollen morphology, no attempt was made to differentiate between species of grass in this study.

In October, 1981 all traps were drained into labeled screwtop jars, and rinsed 3 times with acetone. Several traps bore signs of animal activity, and those punctured or otherwise drained of their contents prematurely were removed and placed in plastic bags for rinsing in the laboratory.

LABORATORY METHODOLOGY

The trap contents were screened in order to remove large plant fragments, lithic debris, and insects. The insects were given to I. Askevold, U. of Manitoba, for identification (Appendix 1).

The trap contents were diluted 1:3 with distilled water, then passed through a 5.5 or 7cm millipore glass fibre filter by means of a vacuum apparatus. The pollen trapped on the filter was placed in a nalgene test tube. A Stockmar eucalyptus tablet (batch no. 106720) was added to the sample which was then treated with 10% HCL, centrifuged, rinsed with concentrated HCL, treated with 48% HF for one

›ur in a boiling water bath, and then let stand overnight. Processing then continued according to Faegri and Iversen's (1975) standard procedure. Processed samples were then placed into vials with a few drops of glycerine, and transferred to slides by means of a disposable pipet.

Sediment samples were treated by swirling and suspending the fine fraction of a 50g sample in distilled water, screening out the large vegetal material, and letting the sample stand in 10% HCL overnight. The sample was subsequently rinsed in concentrated HCL and suspended in a zinc bromide solution (sp. gravity 1.8). After centrifuging, the supernatant was passed through a 7 cm glass fiber filter. Processing of the glass filter and trapped pollen then proceded as described above.

Moss polster samples were measured volumetrically. Fifteen ml samples were processed according to the procedure for peat samples as described in Faegri and Iversen (1975). Because pollen accumulation rates cannot be calculated for sediment samples, moss polsters, or damaged pollen traps, eucalyptus spikes were not added to these samples.

An attempt was made to count a minimum of 500 grains, excluding spores, indeterminates, multiple species pollen agglomerates, and the eucalyptus spike. Wherever possible, if a single herbaceous taxon dominated the assemblage, the 500 grain count was made in addition to that taxon. Samples were counted with a Leitz SM-Lux binocular microscope, using 400x magnification. Traverses were spaced across the slide at regular intervals to avoid bias due to non-random distribution of pollen across the slide (Maher, 1977; Brookes and Thomas, 1967). Identifications were aided by the pollen reference collection at the University of Alberta, and keys supplied by Faegri and Iversen (1975), McAndrews *et al* (1973), and Moore and Webb (1978).

The identification of *Pseudotsuga* was complicated by the presence of a spore (Polypodiaceae type), which bears a resemblance to *Pseudotsuga* grains (Plates 1 and 2). These spores ranged from inapeturate, or weakly trilete, to trilete, demonstrated weak exine ornamentation, and were the same size as *Pseudotsuga*. The inapeturate to weakly trilete varieties of this spore, when found in a torn or folded condition, were mistakable for poorly preserved *Pseudotsuga* grains. As a result, it was necessary to impose strict criteria on *Pseudotsuga* determinations. In this study, *Pseudotsuga* totals are based on entire grains in fresh condition.

To better understand local and regional contribution of *Pinus*, it would have been useful to differentiate the Haploxylon (*Pinus flexilis*) from the Diploxylon (*Pinus contorta*) grains originating from upper elevations. Unfortunately, an attempt to carry out this distinction was discouraged by the poor condition of *Pinus* grains from the desert assemblages (Plate 3), and the surface samples from the Subalpine and Desert floor sites.

Plate 1. Comparison of Polypodiaceae Type and *Pseudotsuga* Grains

A. Polypodiaceae type, Skylight Cave, cave floor surface sample A

B. *Pseudotsuga menziesii*

Plate 2. Comparison of Polypodiaceae Type and *Pseudotsuga* Grains

A. Polypodiaceae type, Skylight Cave, cave floor surface sample A

B. *Pseudotsuga menziesii*

Plate 3. *Pinus* Grains

A. Broken, abraded *Pinus* grains, open air trap, Burnt Timber Rockshelter

B. *Pinus* grain, poorly preserved, cave trap, Cave Ann

All raw counts were converted to relative frequencies for analysis, and absolute influx was calculated where applicable. Pollen preservation, and other observations for each sample pertinent to analysis are described in Appendix 2.

Plant identifications were aided by the keys provided by Dorn (1977) and Hitchcock, *et al.*, (1977). Identified plants were verified using the collections from the herbarium at the University of Alberta. Relative frequency, density and dominance values were calculated for the arboreal data. An expression of relative frequency was not applicable to the transect sampling strategy employed for the local herbs, but density and dominance were calculated for these species.

Cluster Analysis

Visual inspection of the pollen diagrams shows that the variables influencing pollen introduction into cave sites are complex. To facilitate understanding of the patterns in the data, cluster analysis, a non-probabilistic statistical method was employed. Cluster analysis has been applied to a number of pollen analytical and phytoecological studies with reasonable success (Birks, *et al.*, 1975; McCord 1982; Gordon and Birks, 1972; see also Lambert and Dale 1964).

In this study, Ward's (1963) method, a minimum variance agglomerative method was employed, using the CLUSTAN 1C computer program developed by Wishart (1978). The advantages of the application of minimum variance cluster analysis to palynological data over other hierarchical methods is pointed out by Birks, *et al.*, (1975). Clusters are formed by obtaining groups through the calculation of a distance coefficient for each pollen sample, and grouping together those samples or clusters whose fusion yields the least increase in the error sum of squares (Ward, 1963; see also Orloci, 1967). In this way, distance (or similarity) relationships are specified between each group and the entire population, and the clusters are ranked in importance.

To facilitate computer analysis, the data were simplified from 128 taxa into 20 non-inclusive categories (see Fig. 2 in pocket). These categories reflect standard pollen analytical procedures: all major (greater than 1%) arboreal constituants received their own categories, all major nonarboreal taxa were represented, and Asteraceae was reduced to High and Low spine *Tubuliflorae* and *Liguliflorae*. Remaining herbaceous taxa were simplified into categories by family, using an ecological rationale following Fall, *et al.*, (1981). Because the miscellaneous unrepresented taxa would have no ecological meaning, they were excluded from analysis. In most cases, the balance of unrepresented taxa totalled under 2% of the total count.

To alleviate the problem of more variable species dominating the analysis, data were standardized to zero mean and unit variance (Wishart, 1978). Lambert and Dale (1964) point out that this procedure reduces bias in favor of numerically variable taxa, and slightly favors the commoner and rarer species, simulating pollen analytical procedures.

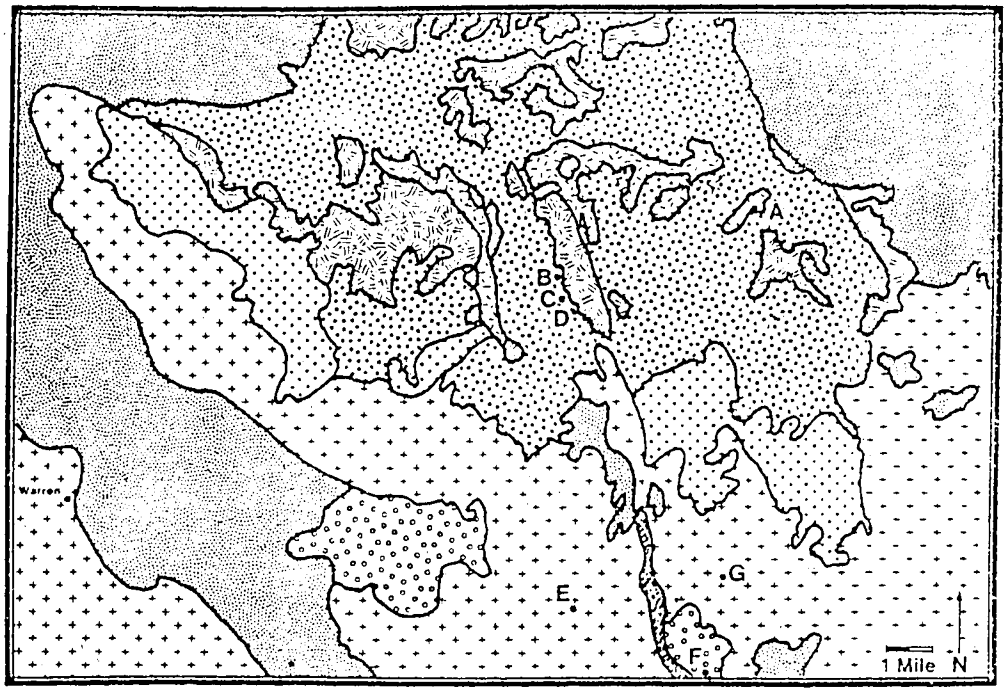
REGIONAL VEGETATION

The distribution of vegetation in the Pryor Mountains reflects a pattern of vegetation found throughout the Bighorn range. Communities of low growing forbs, and *Abies lasiocarpa-Picea engelmannii* forests are found at the upper elevations; *Pseudotsuga* forests are found at mid elevations; and a suite of xeric communities, including those South (1974) calls Sagebrush grasslands, Utah Juniper-Black Sage, and Red desert-Salt Shrub, are found at lower elevations. Birkhart (1976) and Despain (1973) observed the same plant associations in the Bighorn range, with the addition of *Pinus ponderosa* forests at elevations lower than are found in the Pryors.

On the basis of aerial reconaissance, ground vegetations surveys and landforms, South (1974) compiled a regional picture of the distribution of vegetation in the Pryors region (Fig. 3). While this study adopts South's terminology, the vegetation descriptions that follow are derived from surveys of flora adjacent to the cave and rockshelter study sites and may differ somewhat from South's more generalized descriptions in some particulars.

Figure 3. Pryor Mountains Vegetation Zones and Study Sites (adapted from South, 1974)

Pryor Mountain Vegetation Zones



Cave and Rockshelter Study Sites

- A Cowboy Bob Rockshelter & Cave Ann
- B Caves 1 & 2 East
  Caves 1, 2, & 3 West
- C Bobcat Rockshelter
- D Skylight Cave
- E Crooked Creek Rockshelter
- F Gyp Springs Rockshelter
- G Burnt Timber Rockshelter

Vegetation Zones

- ▨ Subalpine Plateau
- ☐ Subalpine Forest and Meadow
- ▨ Douglas Fir Forest
- ▨ Rock Outcrop-Forest
- ▨ Montana Grassland
- ▨ Streamside Hardwood
- + Utah Juniper-Blacksage
- ▨ Sagebrush Grassland
- ▨ Red Desert Salt Shrub

Subalpine Forest and Meadow

Cave Ann and Cowboy Bob rockshelter face east and west respecitively across a dry valley into a Subalpine Forest and Meadow, composed of scattered *Abies lasiocarpa* and *Picea engelmannii* stands, interspersed with subalpine meadow dominated by cool moist adapted forbs. *Picea glauca* and *Pinus contorta* are associated arboreal species. The valley recesses below the caves contain species of *Artemisia*, *Juniperus communis*, and isolated occurences of *Pinus contorta*. Above the rimrock, the vegetation moves into the Subalpine Plateau zone, consisting of forbs, sedges and grasses which form a dense matlike turf. Common plants include species of *Arenaria*, *Phlox*, *Castilleja*, *Anemone*, and *Lomatium* (Table 3).

Transect data from Cowboy Bob Rockshelter shows *Picea engelmannii* the dominant arboreal species, the density, frequency, dominance, and importance values being (50, 61, 46 52), respectively (Table 4). (For simplicity, in the suing discussion these values will be expressed in this manner). *Abies lasiocarpa* also figures prominantly (20, 19, 39, 26). *Pinus contorta* (30, 19, 15, 22) is the only other arboreal species. The most important herbaceous species overall include *Lupinus sericeus* (7, 6--density, dominance), *Vicia cracca* (*, 5), *Phlox hoodi* (5, 4), *Dodecatheon* (2, 4), and *Geum triflorum* (4, 4). Plants found in transects about the lip of the cave and across the mouth include *Draba*

Table 3. Density and Dominance of Vegetation Taxa by Site

		Inside Cave	Mouth Transect		Local Vegetation	
			Density	Dominance	Density	Dominance
Burnt Timber Rockshelter						
Asteraceae	*Antennaria rosea* Greene				11	1
	Chrysothamnus nauseosis (Pall. ex Pursh), Britt.				22	8
Pinaceae	*Pinus flexilis* James	x			22	6
Poaceae		x			44	32
Cactaceae	*Opuntia* Mill					
Cuppresaceae	*Juniperus osteosperma* Torr. (Little)					
Liliaceae	*Yucca glauca* Nutt.					
Rosaceae	*Cercocarpos ledifolius* Nutt.					
Crooked Creek Road						
Asteraceae	*Antennaria pulcherrima* (Hook.) Greene				8	8
	Artemesia tridentata Nutt.				8	7
	Chrysothamnus nauseosis				25	14
Cupressaceae	*Juniperus osteosperma*				17	63
Chenipodiaceae	*Atriplex confertifolia* (Torr. and Fren.) Wats.				17	9
Fabaceae	*Oxytropis sericea* Nutt.				30	8
Gyp Springs Site						
Asteraceae	*Artemesia tridentata*				20	21
	Chrysothamnus viscidiflorus (Hook.) Nutt.		66	71	31	18
	Cirsium Mill.					
Anacardiaceae	*Rhus trilobata* Nutt.	x	14	8		
Boraginaceae	*Cryptantha sobolifera*		14	2		
Capparidaceae	*Cleome lutea* Hook.	x				
Chenipodiaceae	*Atriplex confertifolia*					
	Sarcobatus vermiculatus (Hook.) Torr. in Emory					
Cupressaceae	*Juniperus communis* L.				7	27
Fabaceae	*Astragalus vexilliflexus* Sheld.	x	14	6	9	10
Nyctaginaceae	*Abronia fragrans* Nutt. ex Hook.					

Table 3 continued

Bobcat Rockshelter

Aceraceae	Acer glabrum Torr.	x	•		4	5
Asteraceae	Achillea millefolium L.					
	Antennaria pulcherrima					
	Antennaria racemosa Hook.		7	1		
	Antennaria rosea					
	Taraxicum officinale Weber in Wiggers					
Berberidaceae	Mahonia repens (Lindl.) G. Don					
Brassicaceae	Erysimum asperum (Nutt.) DC.					
Caprifoliaceae	Symphoricarpos oreophilus Gray					
Chenopodiaceae	Chenopodium L.		4	•	1	•
Cornaceae	Cornus stolonifera Michx.					
Eleagnaceae	Shepherida canadensis (L.) Nutt.					
Gentianaceae	Frasera speciosa Dougl. ex Griseb.					
Geraniaceae	Geranium viscossimum Fisch. and Mey. ex Mey.					
Grossulariaceae	Ribes montegenum McClatchie	x	25	14	12	14
Lamiaceae	Scutellaria L.		•	•		
Liliaceae	Smilacina racemose (L.) Desf					
	Streptopus amplexifolius (L.) DC. in Lam. and DC.					
Linaceae	Linum lewisii Pursh		•	•		
Pinaceae	Picea glauca (Moench) Voss		•			
	Pseudostuga menziesii (Mirb.) Franca		•			
Poaceae					14	10
Polygonaceae	Eriogonum umbellatum Torr.					
Ranunculaceae	Clematis columbiana var. dissecta (Nutt.) T. and G.					
	Delphinium bicolor Nutt.					
Rosaceae	Fragaria virginiana Duchesne					
	Geum triflorum Pursh					
	Physocarpus malvaeus (Greene) Kuntze	x			6	2
	Potentilla gracilis Dougl. ex Hook.		•	•		
	Potentilla norvegica L.					
	Prunus virginiana L.					
	Rubus ideaus L.				2	2
	Rubus parviflorus Nutt.					
	Rubus ursinus					
	Spirea betulifolia Pall.	x	32	9		
Saxifragaceae	Mitella nuda L.				7	2
Scropulariaceae	Cynoglossum officinale		11	3		
Urticaceae	Urtica dioica L.					
Valerianaceae	Valeriana dioica (?) L.		7	1		
Violaceae	Viola canadensis L.					
	Viola nuttallii Pursh		•	•		

Table 3 continued

Skylight Cave

Aceraceae	Acer glabrum					
Asteraceae	Achillea millefolium					
	Antennaria					
	Artemesia tridentata					
	Balsamorhiza saggitata (Pursh) Nutt.				8	20
	Taraxicum officinale					
	Tragopogon dubius Scop.					
	Unknown, Tubuliflorae series					
Brassicaceae	Draba incerta Payson		2			
	Erysimum asperum (Nutt.) DC.					
Boraginaceae	Mertensia (?) Roth					
Caprifoliaceae	Symphoricarpos oreophilus Gray					
Caryophillaceae	Cerastrium arvense L.					
Chenopodiaceae	Chenipodium L.		77	10		
Cupressaceae	Juniperus communis					
	Juniperus scrophulorum Sarg.				2	4
Cyperaceae	Carex brunnesens (Pers.) Poir.		5	13		
Fabaceae	Astragalus vexilliflexus				11	4
	Vicia cracca L. (Cracca)					
Pinaceae	Pseudostuga menziesii					
Poaceae					33	46
Polemoniaceae	Polemonium pulcherrimum Hook.				10	11
Rosaceae	Physocarpus malvaceus (Greene) Kuntze		5	31		
	Spirea betulifolia Pall.					
Rubiaceae	Galium boreale L.				12	5
Scrophularaceae	Pedicularis groenlandica Retz.					
	Penstemon cyaneus Pennell					
Unknown 1			2			
Unknown 2			2	12		
Unknown 3			2	2		

Cave 1 East

Berberidaceae	Mahonia repens (Lindl.) G. Don		18	23	18	16
Caprifoliaceae	Symphoricarpos oreophilus Gray					
Chenopodiaceae	Chenopodium freemontii Wats.	x	77	55		
Grossulariaceae	Ribes cereum Dougl.	x				
Liliaceae	Smilacina stellata (L.) Desf.		3	1	13	20
Poaceae			3	21		
Pinaceae	Pseudostuga menziesii				8	11
Rosaceae	Physocarpus malvaceus					
	Spriea betulifolia				30	24
Ranunculaceae	Actaea rubra (Ait.) Willd.					
	Clematis columbiana var. dissecta				18	20
Violaceae	Viola canadensis L.					

Table 3 continued

Cave 2 East						
Aceraceae	Acer glabrum	x	8	9	2	2
Asteraceae	Achillea millefolium		5	4		
	Antennaria pulcherrima		3	7		
	Arnica cordifolia Hook.		5	9		
Berberidaceae	Mahonia repens				20	16
Caprifoliaceae	Symphoricarpos albus L.		5	10		
	Symphoricarpos oreophilus		8	11	14	34
Liliaceae	Smilacina racemosa				11	4
Pinaceae	Pseudostuga menziesii		54	44	3	3
Poaceae					2	3
Rosaceae	Physocarpus malvaceus		11	7		
	Rubus idaeus	x				
	Spirea betulifolia				35	34
Saxifragaceae	Mitella nuda	x				
Cave 1 West						
Aceraceae	Acer glabrum				8	9
Asteraceae	Arnica cordifolia				11	10
Berberidaceae	Mahonia repens				17	14
Caprifoliaceae	Lonicera utahensis Wats.				6	11
Caprifoliaceae	Symphoricarpos albus					
	Symphoricarpos oreophilus					
Chenopodiaceae	Chenopodium freemontii Wats.		13	5		
Cupressaceae	Juniperus communis					
Grossulariaceae	Ribes montegenum	x	25	18		
Liliaceae	Smilacina racemosa				13	9
Pinaceae	Picea glauca (Moench) Voss					
	Pseudostuga menziesii				11	14
Poaceae						
Polypodiaceae					2	9
Ranunculaceae	Actaea rubra					
	Clematis columbiana var. dissecta					
Rosaceae	Physocarpus malvaceus		38	55		
	Rubus parviflorus				13	11
	Rubus ursinus	x				
	Spirea betulifolia					
	Rosa woodsii Lindl.					
Saxifragaceae	Mitella nuda	x			9	2

Table 3 continued

Cave 2 West

Aceraceae	*Acer glabrum*					8	10
Asteraceae	*Arnica cordifolia*						
Berberidaceae	*Mahonia repens*		×				
Brassicaceae	(immature)	×					
Caprifoliaceae	*Symphoricarpos oreophilus*					7	8
Cupressaceae	*Juniperus communis*					2	22
Grossularaceae	*Ribes cereum*	×					
Liliaceae	*Smilacina stellata*		×				
Pinaceae	*Picea glauca*						
Poaceae			×				
Ranunculaceae	*Clematis columbiana* var. *dissecta*						
Rosaceae	*Physocarpus malvaceus*						
	Rosa woodsii						
	Spirea betulifolia					26	24
Saxifragaceae	*Mitella nuda*						

Cave 3 West

Apiaceae	*Lomatium cous* Wats						
Asteraceae	*Arnica cordifola*						
	Achillea millefolium			3	1		
	Antennaria pulcherrima			3	4		
Berberidaceae	*Mahonia repens*			25	16		
Boraginaceae	*Mertensia oblongifolia* Nutt.						
	Mertensia (?)						
Caprifoliaceae	*Symphoricarpos oreophilus*			14	13	20	28
Cupressaceae	*Juniperus scrophulorum*			3	2	1	6
Fabaceae	*Oxytropis sericea* Nutt. in T. and G.						
Liliaceae	*Smilacina stellata*						
	Smilacina racemosa	×		25	9	17	9
Pinaceae	*Pseudostuga menziesii*			2	7		
Poaceae							
Rosaceae	*Fragaria virginiana*						
	Physocarpus malvaceus	×		3	30		
	Prunus virginiana			6	5	12	14
	Rosa woodsii						
	Spirea betulifolia			3	4	20	23
Ranunculaceae	*Delphinium bicolor*						
Violaceae	*Viola canadensis*			3	1		

Table 3 continued

Cave Ann

Asteraceae	Antennaria alpina L.				
	Arnica alpina L.				
	Arnica cordifolia				
	Cirsium (genus)				
	Erigeron caespitosus Nutt.				
	Erigeron (genus)	4	1		
	Haplopappus acaulis Nutt.				
	Senecio cymbalaroides Buek				
	Solidago (genus) L.	2	1		
	Taraxicum ceratophorum (Ledeb.) DC.	2	1		
Brassicaceae	Draba incerta Payson	4	2		
Caryophillaceae	Arenaria obtusiloba (Rydb.) Fern.	2	2		
	Cerastrum arvense L.	10	10		
Cupressaceae	Juniperus communis L.			4	14
Crassulaceae	Sedum stenopetalum Pursh	14	4		
Geranaceae	Geranium viscossimum	20	8		
Grossularaceae	Ribes cereum				
Hydrophyllaceae	Phacelia (genus) Juss.	2			
Liliaceae	Allium (genus) L.				
	Zygadenus racemosa			10	5
Pinaceae	Abies lasiocarpa (Hook.) Nutt.	2	11		
	Picea engelmarinii Parry ex Engelm.			2	6
Poaceae		12	8	29	16
Polemoniaceae	Phlox hoodii Richards. in Frankl.	2	1		
Polygonaceae	Polygonum bistortoides Pursh				
Ranunculaceae	Delphinium bicolor				
Rosaceae	Potentilla gracilis	4	33		
	Potentilla ovina Macoun	6	5		
Rubiaceae	Galium boreale L.				
Scrophularaceae	Castelleja sulphurea Rydb.				
	Pedicularis groenlandica Retz.			6	11
Unknown 1	(immature)	4	8		
Unknown 2	(immature)	4	5		
Unknown 3	(Bryophyte)	4	1		

Table 3 continued

Cowboy Bob

Apiaceae	Lomatium cous				
Asteraceae	Antennaria alpina				
	Antennaria pulcherrima				
	Artemesia norvegica Fries				
	Artemesia tridentata				
	Cirsium polyphyllum				
	Senecio cymbalaroides Buek				
	Taraxicum ceratophorum				
	Unknown, Chichoridae Tribe (Liguliflorae)				
Boraginiaceae	Myosotis alpenstris Schmidt				
Brassicaceae	Arabis drummondii Gray				
	Draba incerta	13	3		
Caryophyllaceae	Cerastrum arvense				
Crassulaceae	Sedum stenopetalum	4	1		
Fabaceae	Lupinus sericeus Pursh				
	Vicia cracca			7	6
Liliaceae	Zigadenus elegans			•	5
Pinaceae	Abies lasiocarpa	4	16		
	Picea engelmannii	4	14	1	9
	Pinus contorta Dougl. ex Loud.			1	5
Poaceae				•	4
Polemoniaceae	Phlox caespitosa Nutt.				
	Phlox hoodii	8	5	5	4
Polygonaceae	Eriogonum subalpinum Greene				
	Polygonum bistorta				
Portulacaceae	Claytonia lanceolata Pursh				
Primulaceae	Dodecatheon pauciflorum (Durand) Greene			12	4
Ranunculaceae	Anemone drummondii				
	Anemone patens L				
	Delphinium bicolor	4	1		
Rosaceae	Geum triflorum	4	2	4	4
	Potentilla ovina	30	18	•	•
Rubiaceae	Galium boreale				
Saxifragaceae	Saxifraga arguta D. Don	20	12		
Violaceae	Viola (genus)				
Unknown	(immature)	4	7		

Legend

x = presence inside cave lip noted
• = under 1%

TABLE 4
Arboreal Survey Data

Species	Points of Occurence	Trees	Total Basal Area(cm)	Distance (m)	%Frequency	%Density	%Dominance
SUBALPINE LOCALITIES							
Cowboy Bob Rockshelter							
Abies lasiocarpa	4	6	3822.48	19.1	20.0	19.4	38.5
Picea engelmannii	10	19	4578.98	73.4	50.0	61.2	46.0
Pinus contorta	6	6	1503.29	27.5	30.0	19.4	15.2
quadrats = 16	20	31	9904.75	120.0			
Cave Ann							
Abies lasiocarpa	17	41	8706.63	130.1	46.0	51.2	31.7
Picea engelmannii	11	24	13649.47	68.4	29.8	30.0	49.8
Pinus contorta	9	15	5076.12	63.8	24.3	18.8	18.5
Quadrats = 128	37	80	27432.12	262.3			
Average, Subalpine localities							
Abies lasiocarpa	21	47	12529.11	149.2	36.8	42.3	13.8
Picea engelmannii	21	43	18228.35	140.8	36.8	38.7	48.7
Pinus flexilis	15	15	6579.41	91.3	26.3	13.5	17.6
Quadrats = 144	57	111	37365.60	381.3			
WYOMING CREEK LOCALITIES							
Cave 1 East							
Acer glabrum	4	5	12.06	9.0	25.0	16.7	.1
Cornus stolonifera	1	1	2.00	2.0	6.3	3.3	.02
Juniperus scrophulorum	1	1	127.30	5.0	6.3	3.3	1.3
Pseudostuga menziesii	10	23	9319.23	62.5	76.6	98.5	79.2
total quadrats = 10	16	30	9460.55	78.5			
Cave 2 East							
Acer glabrum	17	27	91.13	74.0	34.0	29.3	.2
Juniperus scrophulorum	2	2	8.66	9.0	4.0	2.2	.02
Picea glauca	5	8	3548.08	28.5	10.0	8.7	8.9
Pseudostuga menziesii	26	55	36102.16	147.0	52.0	59.8	90.8
total quadrats = 28	50	92	39750.03	258.5			

Table 4 continued

Cave 1 West							
Acer glabrum	15	27	59.66	48.1	45.5	45.0	.3
Pseudostuga menziesii	16	31	17392.01	66.1	48.5	51.6	99.6
Prunus virginiana	2	2	10.80	1.5	6.1	3.3	.1
total quadrats = 16	33	60	17,462.50	115.6			
Cave 2 West							
Acer glabrum	12	20	56.10	33.0	30.7	29.9	.4
Cornus stolonifera	1	1	1.20	1.0	2.5	1.4	.01
Picea glauca	9	14	4236.60	40.5	23.1	20.9	27.4
Pinus flexilis	1	1	.07	1.0	2.5	1.4	.01
Pseudostuga menziesii	13	28	1137.50	66.0	33.3	41.8	72.0
Prunus virginiana	3	3	31.80	5.5	7.6	4.5	.2
total quadrats = 18	39	67	15463.44	147.0			
Bobcat Rockshelter							
Acer glabrum	17	23	141.90	50.8	13.7	11.1	.2
Juniperus scrophulorum	45	93	4314.60	312.8	36.0	44.9	6.6
Pinus flexilis	5	5	811.80	17.0	4.0	2.4	1.2
Pseudostuga menziesii	57	87	60385.60	280.6	46.0	42.0	92.0
total quadrats = 74	124	207	65654.10	661.2			
Skylight Rockshelter							
Acer glabrum	10	11	904.30	29.0	10.0	5.9	1.7
Cornus stolonifera	1	1	71.50	.5	1.0	5	13
Juniperus scrophulorum	49	115	13741.75	404.5	49.0	62.5	26.0
Picea glauca	3	4	2394.60	11.0	3.0	2.2	4.5
Pinus flexilis	2	2	509.90	2.0	1.1	1.0	
Pseudostuga menziesii	30	45	35226.60	145.0	30.0	24.5	66.6
Prunus virginiana	5	6	6.90	10.5	5.0	3.3	.01
total quadrats = 58	100	184	52856.00	608.5			
Average, Wyoming Creek Localities							
Acer glabrum	75	113	1265.30	21.0	17.7	6	
Cornus stolonifera	3	3	74.70	.8	.5	.04	
Juniperus scrophulorum	97	211	18192.30	27.2	33.1	9.0	
Picea glauca	11	22	10179.30	3.0	3.5	5.1	
Pinus flexilis	8	8	1321.80	2.2	1.3	7	
Pseudostuga menziesii	152	269	169563.10	127.9	42.7	42.2	84.5
Prunus virginiana	10	11	49.60	5.8	2.8	1.7	.02
total quadrats = 204	356	637	200646.22	187.9			

Table 4 continued

DESERT LOCALITIES							
Crooked Creek Site							
Juniperus osteosperma	56	130	6274.30	475.0	98.0	100.0	100.0
total quadrats = 57							
Burnt Timber Ridge							
Juniperus scrophulorum	36	54	1279.20	155.6	64.0	63.5	40.0
Pinus flexilis	25	31	1910.90	123.1	44.6	37.0	59.8
total quadrats = 56	61	85	3190.20	278.7			
Gyp Springs Site							
Juniperus scrophulorum	3	3	71.60	17.5	9.0	100.0	100.0
total quadrats = 33							
Desert Sites Average							
Juniperus	93	187	7683.30	648.1			
Pinus flexilis	25	31	1910.90	123.1	17.0	14.2	19.9
total quadrats = 146	108	218	9594.20	771.2			

incerta, *Sedum stenopetalum*, *Delphinium bicolor*, *Potentilla ovina*, and *Saxafraga arguta*. Across the valley from Cowboy Bob Rockshelter, Cave Ann is situated directly above a *Picea Englemanni-Abies lasiocarpa* stand. *Abies* is better represented around Cave Ann (46, 51, 32, 43) than it is around Cowboy Bob Rockshelter. *Picea* values are lower (30, 30, 50, 37) than across the valley, but *Pinus* is equally well represented (24, 19, 19, 21). Due to the southerly exposure, Cave Ann's herbacous cover is significantly different from that surrounding Cowboy Bob Rockshelter. Poaceae figures most prominently (29, 16), followed by *Zigadenus racemosa* (10, 5), *Pedicularis groenlandica* (6, 11) and *Juniperus communis* (4, 14). A wide variety of herbs are found around the mouth of the cave the most important include *Potentilla gracilis*, *Geranium viscossimum*, Poaceae, and *Cerastrium arvense*.

Douglas Fir Zone

Caves 1, 2, and 3 West, Caves 1 and 2 East, Skylight Cave and Bobcat Rockshelter are located within the Douglas Fir zone. At lower elevations, The Douglas Fir zone is confined to north facing slopes, and shaded areas, and is replaced by Limber Pine on the southern exposures. At higher elevations, Douglas Fir is found on sunny, dry exposures, and at the highest elevations, it is replaced on northern exposures and moist-shady localities by *Abies lasiocarpa*. *Picea glauca* and

Picea engelmannii occupy moist draws.

As shown on Table 4, it is apparent that the degree of dominance *Pseudotsuga* plays in the local vegetation composition varies among the sites. At Cave 1 West, *Pseudotsuga* is most strongly represented (49, 52, 99, 67), whereas at Skylight Cave, a more xeric site due to southerly exposure *Pseudotsuga* frequencies are lower (30, 25, 67, 40).

In the moister heavily wooded localities, Caves 1, 2, and 3 West and Caves 1 and 2 East, *Picea glauca*, and *Acer glabrum*, are present, with isolated occurences of *Prunus virginiana* and *Cornus stolonifera*. At Skylight Cave and Bobcat Rockshelter, which face onto xeric slopes, *Juniperus schropulorum* and *Pinus flexilis* are added to the species list.

The mean values for arboreal taxa in this zone are as follows: *Pseudotsuga* menziesii (43, 42, 85, 57); *Picea glauca* (3, 4, 5, 4); *Acer glabrum* (21, 18, 1, 13); *Juniperus scrophulorum* (27, 33, 9, 23); *Pinus flexilis* (2, 1, 1, 4); *Prunus virginiana* (3, 2, *, 2); and *Cornus stolonifera* (1, 1, *, 1).

Associated shrubs located at moist localities include *Symphoricarpos oreophillous*, *Spirea betulifolia*, *Lonicera utahensis*, and *Juniperus communis*. Species of *Rubus*, *Arnica*, *Smilacina* and Poaceae as well as *Mahonia repens*, and *Mitella nuda* dominate the understory. The more xeric localities have similar species composition, but grasses provide a greater portion of the cover area, and *Balsamhorizza saggitata*, *Astragalus vexilliflexus, and Lupinus sericeus* are important species on sunny slopes.

Utah Juniper-Blacksage

Gyp Springs, Burnt Timber and Crooked Creek rockshelters are all located at the lower elevations of the transect and represent variants of the Utah Juniper-Blacksage vegetation zone. Overall, the vegetation is sparse, dominated by *Juniperus osteosperma*, and several varieties of *Artemisia*. *Pinus flexilis* is associated at some localities, including the Burnt Timber Rockshelter study site. Characteristic drought-adapted vegetation includes *Chrysothamnus viscidiflorus*, *Atriplex confertifolia*, *Sarcobatus vermiculatus*, and *Cercocarpus ledifolius*. The understory is sparse, composed of lowgrowing species and cushion plants.

Despite species similarity, there was great variety in the vegetation composition among the 3 study sites in this zone. Burnt Timber Rockshelter site was 88% open, with grasses composing the majority of the understory vegetation (44, 32). *Chrysothamnus* constituted (22, 6) of the vegetation, with *Antennaria rosea* providing (11, 1). *Pinus flexilis* provided (45, 37, 60, 46) of the arboreal vegetation, *Juniperus osteosperma* figuring (64, 64, 40, 54).

The vegetation surrounding Crooked Creek Rockshelter site was surrounded by a vegetation 85% open. *Juniperus osteosperma* dominated the vegetation (17, 33) with associated *Chrysothamnus nauseosis (25, 14)*; *Atriplex confertifolia* (17, 9) and *Artemisia* (8, 7). *Oxytropis sericea* (30, 8) and *Antennaria pulcherrima* (8, 8) were the major herbs.

Vegetation around Gyp Springs Rockshelter site was 81% open, dominated by *Juniperus communis* (7, 27), *Artemisia tridentata* (20, 21), and *Chrysothamnus viscidiflorus* (31, 8). *Sarcobatus vermiculatus* (4, 7), *Atriplex confertifolia* (6, 2), *Rhus trilobata* (9, 4), and *Astragalus vexilliflexus* (9, 10) are associated species. Gyp Springs Rockshelter demonstrated more species diversity than the other study sites in this zone.

Vegetation Zones adjacent to Study Sites

All the study sites are situated in the vegetation zones described above. A discussion of the other vegetation zones shown in Fig. 3 is pertinent to the understanding of the other vegetative influences characterizing the regional pollen rain component. The following description summarize the findings of South (1974).

Rock Outcrop-Forest

Vegetation in this zone is sparse. *Pseudotsuga* menziesii and *Pinus flexilis* are characteristic tree species, associated with *Juniperus scrophulorum*. The understory is similar in composition to that found in the xeric variants of the Douglas Fir zone: *Rhus trilobata*, *Chrysothamnus nauseosis*, and *Eriogonum chrysops* are common, along with species of mustard and grass.

Mountain Grassland

Grasses are dominant in this zone, typically consisting of bluegrasses, wheatgrasses, Idaho fescue, and needlegrass. Forbs and shrubs are present according to available moisture, exposure, and soil type. The common forbs include lupine, balsamroot, geranium, and yarrow. Shrubs include *Artemesia tridentata* and *Potentilla fruticosa*.

Streamside Hardwood

The Streamside Hardwoods zone is rich and contains a variety of species variably distributed with elevation. The dominant species along the streams include several species of *Populus*, *Salix exigua*, *Betula occidentalis*, *Acer glabrum*, *Alnus incana*, *Prunus virginiana*, *Cornus stolonifera*, *Crataegus douglasii*, and *Rosa Woodsii*.

Sagebrush Grassland Zone

The vegetation in the Sagebrush Grassland zone is divided into two variants, reflecting species tolerances to soil fertility and moisture. The moist variant is a complex community dominated by grasses and forbs. *Artemisia* and *Chrysothamnus* are associated shrubs. The xeric variant consists of *Artemisia*-Poaceae associations, with species of *Atriplex* common in some localities.

Red Desert Salt Shrub Zone

Vegetation in the Red Desert-Salt Shrub zone is sparse, comprised of a scattered low ground cover. Several species of *Atriplex* dominate the landscape, along with *Artemisia spinescens*. Grasses, Chenopods, and *Opuntia* are associated with this vegetation.

MODERN POLLEN RAIN

The vegetation surveys conducted in the Pryors show that *Pinus* and *Artemisia*, two notorious overproducers of pollen, are present locally in each vegetation zone containing cave and rockshelter study sites. Thus it is not surprising that most pollen assemblages collected in the Tauber traps and from the surface samples are dominated by either *Pinus* or *Artemisia*. There are exceptions, however, which will be discussed in the text.

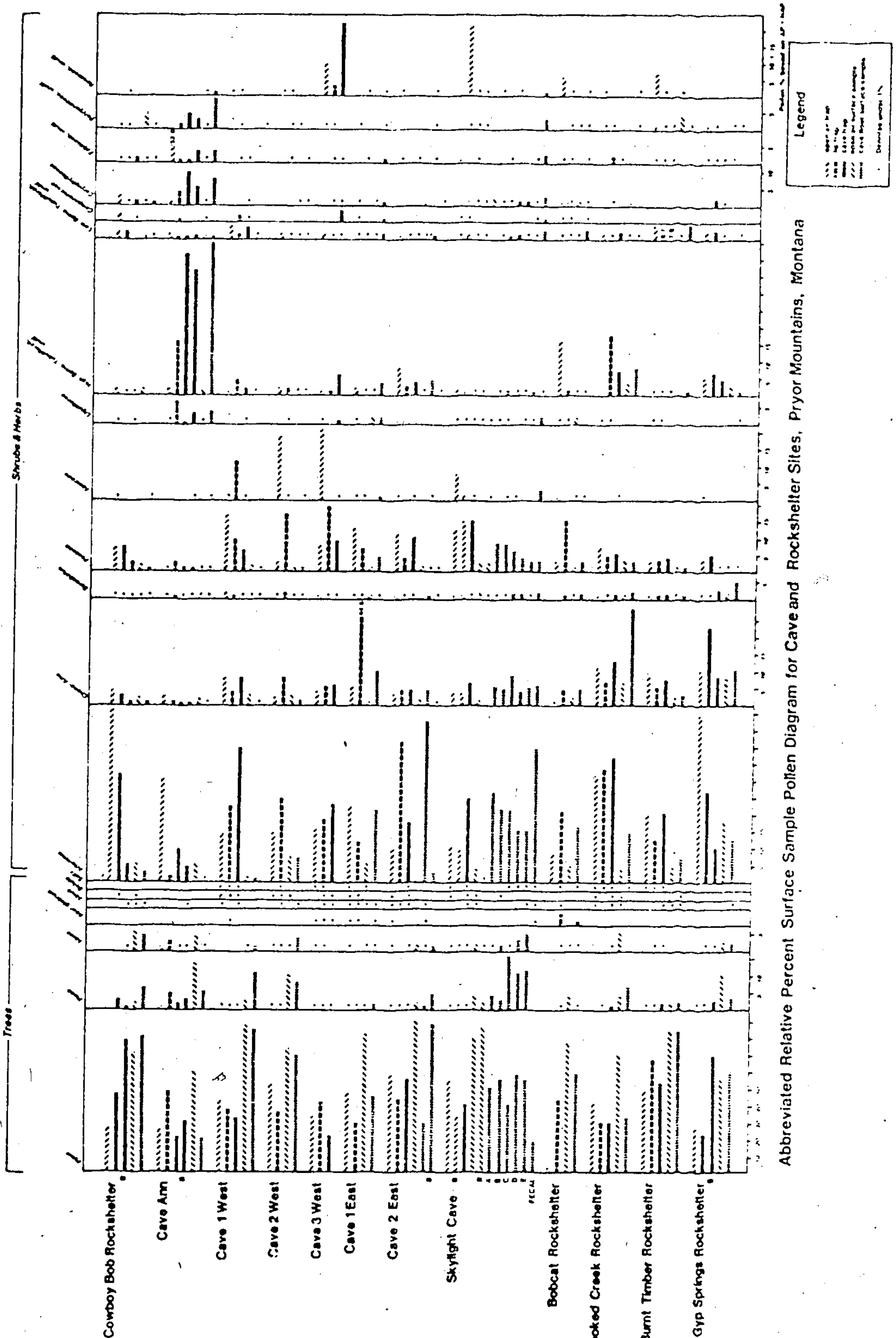
On occasion, the rarer, normally entomophillous pollen types were found in significant quantities in the pollen sample. Where possible, the insects found in the Tauber traps were identified to see if thy suggested contamination of the airborne pollen assemblage by insect borne pollen. Contamination would be suggested in cases where pollen of a plant type utilized by an insect was found in association with that insect. In no case did the correlation occur. Although the presence of insects in some of the traps indicate insect borne pollen contamination may have occurred, from the data available it is impossible to evaluate the extent and type of bias exhibited by the sample. Appendix I shows that the majority of identifiable insects are not sighted on flowers, and thus do not immediately suggest pollen importation.

The following discussion refers to Fig. 2 (in pocket), and Fig. 4 (a simplified version of Fig. 2). In the text, pollen frequencies are rounded to the nearest whole number, and expressed using the convention below:

(A, B, C, D, E) where: A=Open Air Trap
B=Lip Trap
C=Cave Trap
D=Open Air Surface Sample
E=Cave Floor Surface Sample

A slash denotes that there are 2 samples which fill that category (e.g., B/B; C/C etc.). For cave traps, the frequency following the slash always denotes the trap placed nearest the back wall of the cave (In the discussion, cave trap A describes the Tauber trap in the cave closest to the mouth, and cave trap B describes the Tauber trap nearest the

Figure 4. Abbreviated Relative Percent Surface Sample Pollen Diagram for Cave and Rockshelter Sites, Pryor Mountains, Montana



Abbreviated Relative Percent Surface Sample Pollen Diagram for Cave and Rockshelter Sites, Pryor Mountains, Montana back wall). An asterisk (*) indicates pollen frequencies of less than 1%. Missing values are noted with a placeholder (-).

Englemann Spruce-Alpine Fir Forest and Meadow

Of the five pollen assemblages from Cowboy Bob Rockshelter, three show similar compositions; Cave Trap B, open air surface sample, and cave floor surface sample (Fig. 4). The open air trap and the cave trap (A), on the other hand, provide very different pollen assemblages. Whereas *Pinus* dominates the cave trap (B), open air surface sample, and cave floor surface sample (27, -, 48/81, 72, 81), *Artemisia* contributes a greater share of the pollen in cave trap (A) and the open air trap (53, -, 34/6, 6, 4). Poaceae follows a similar pattern of distribution (7, -, 8/3, 2, 1). *Picea* (*, -, 2/1, 3, 7) and *Abies* (-, -, -/*, 5, 4), which are the dominant trees in the local vegetation, are underrepresented in all samples, although they appear to be slightly better represented in surface samples within and outside the cave.

Due to the overrepresentation of *Pinus* and *Artemisia*, other taxa do not demonstrate significant variation between samples. Observed differences in the AP/NAP ratios in the suite of samples from Cowboy Bob largely reflects the ratio of *Pinus* to *Artemisia*.

The pollen spectra derived from samples from Cave Ann are unlike those from Cowboy Bob Rockshelter. Overall, they are marked by lower frequencies of *Pinus*, and higher frequencies of herbaceous taxa. *Pinus* values do not exceed 61% in any sample (26, 49, 23/31, 61, 29).

Unlike Cowboy Bob Rockshelter, high *Artemisia* frequencies (31, 2, 10/5, 11, 1) do not account for the lower *Pinus* frequencies. Instead, samples from inside Cave Ann are characterized by strong representation of Asteraceae pollen; frequencies ranging between 24-50% of the total. The majority of Asteraceae pollen were high spine grains of the Tribe *Tubuliflorae* (2, 16, 42/37, 4, 45). Cave pollen samples also demonstrate relatively high values of Caryophyllaceae (1, 4, 10/6, *, 8) and Polygonaceae (*, 2, 5/3, 1, 9). Taxa within the Fabaceae family were strongly represented in the open air trap (32, 2, 1/4, *, 4), *Oxytropis* contributing 21% of the total in that sample. All samples from this site, demonstrate frequencies under 3% for both Poaceae (*, 3, 2/1, 1, 1) and Cheno-Ams (pollen of either Chenopodiaceae or Amaranthaceae) (3, 1, 1/1, 2, *).

In Cave Ann, *Picea* (1, 5, 2/3, 13, 1) and *Abies* (1, 3, */1, 4*) frequencies are low, an exception being the open air surface sample. Strong *Picea* representation in this sample likely reflects its proximity to a *Picea engelmannii* stand.

Douglas Fir Forest

At Cave 1 West, the surface samples are both characterized by *Pinus* frequencies of greater than 80% (44, 38, 33, 88, 85). However, percentages differ significantly between the surface samples for *Picea* (1, *, *, 3, 11). *Abies* is observed only in the surface samples (0, 0, 0, *, 1) but it represents a long distance component. The open air trap, lip trap and cave trap are all characterized by higher values than the surface samples; *Artemisia* (14, 23, 41, 2, 1); Poaceae (17, 10, 7, 2, 1) and Cheno-Ams (8, 5, 8, 4, 1). Frequencies of minor herbaceous taxa are greater for the trapped samples than the surface samples, and have slightly higher percentages for the lip and cave traps than for the open air trap. The lip trap has a higher percentage of Campanulaceae (0, 2, *, 0, 0) Apiaceae (*, 12, *, 0, 0). Trapped samples provide higher percentages of both high spine (1, 5, 2, *, 0), and low spine Tubulifloreae (4, 2, 4, *, 0) than the surface samples.

Like Cave 1 West, the surface samples at Cave 2 West provide pollen assemblages that closely resemble each other. Both samples have *Pinus* frequencies exceeding 70% (54, 36, *, 75, 70). *Picea* is well represented in both surface samples (0, 1, -, 10, 8). The cave floor surface sample contains 4% *Abies* (1, 0, -, *, 4). While shrubs and herbs are equally well represented in the surface samples, significant variation is expressed between the trapped samples. *Artemisia* (17, 25, -, 8, 8); Poaceae (3, 17, -, 1, 2); and Cheno-Ams (3, 8, -, 4, 2) have greater frequencies for the lip trap, while Apiaceae (mostly *Bupleurum* type) contributes 20% of the pollen in the open air trap (20, 1, -, 0, *).

The pollen spectra at Cave 3 West is distinguished from other sites by relatively low percentages of *Pinus* (34, 42, 22, -, -), moderate percentages of *Artemisia* (16, 19, 24, -, -), Poaceae (8, 19, 10, -, -) and Cheno-Ams (5, 6, 7, -, -); and high percentages of taxa within the Rosacea family (9, 3, 22, -, -). In the cave trap, the Rosaceae family is largely represented by *Sanguisorba* and *Spirea* types. The pollen assemblage from the open air trap has a high percentage of Apiaceae (21, 0, 1, -, -) pollen. Campanulaceae (0, 0, 4, -, -) is found in the cave trap, contributing 4% of the total pollen in this sample. Asteraceae contributes 8% of the pollen in the cave trap, primarily high spine varieties of the Tribe *Tubuliflorae* (1, 1, 6, -, -).

The samples from Cave 1 East provide a series of very different pollen records. *Pinus* frequencies vary from 30-82% (47, 30, -, 82, 45). *Picea* remains low, totalling 3% of the open air surface sample (1, *, -, 3, 2). The greatest variation observed among the shrub and herb pollen was in the Cheno-Ams, which ranges from 1-45% (5, 45, -, 1, 11). Variability is often great among the major NAP components; *Artemisia* (24, 13, -, 6, 12), and Poaceae (13, 8, -, 1, 5). The cave floor surface sample is characterized by a strong representation of minor herbaceous components: frequencies of one percent or greater were recovered for Campanulaceae, *Liguliflorae*, *Iva xanthiflora* type, Fabaceae, Polygonaceae, and Apiaceae. In addition, a variety of other herbs were found in trace quantities (Fig. 4).

Samples from Cave 2 East also provide a variable pollen record. The cave floor surface sample (b), and the open air surface sample provide very high frequencies of *Pinus* (58, 44, 56, 90, 28/88), and concomitantly low frequencies of *Artemisia* (10, 42, 19, 1, 48/3). The lip trap and cave floor surface sample (a), which have values for *Artemisia* in excess of 40%, also have similar values for Poaceae (12, 4, 10, 2, 7/1) and Cheno-Ams (4, 5, 5, 2, 5/1). *Picea* (1, *, 1, 2, 1/5) and *Abies* (*, 0, *, 3, */1) are best represented in the surface samples; and locally abundant *Acer glabrum* is relatively well represented in the cave floor surface sample (b) (*, 0, *, 2, 1/5). The open air trap contained 10% Asteraceae grains; predominantly High Spine varieties of the Tribe *Tubuliflorae* (8, 3, 4, *, 4/*) .

The open air pollen trap at Bobcat Rockshelter was contaminated by many insects, including wasps, which accounts for the high NAP frequencies derived from this sample. The pollen assemblage was dominated by *Symphoricarpos* (43%), a locally abundant shrub. As a result, *Pinus* freqeuncies for Bobcat Rockshelter ranged from 3-77% (3, 45, -, 77, 64). The lip trap differed from the surface samples in higher values of *Artemisia* (9, 22, -, 5, 17) and Poaceae (3, 15, -, 1, 3). Insect contamination is apparent in the high values of Rosaceae (6, *, -, 0, 1), High Spine

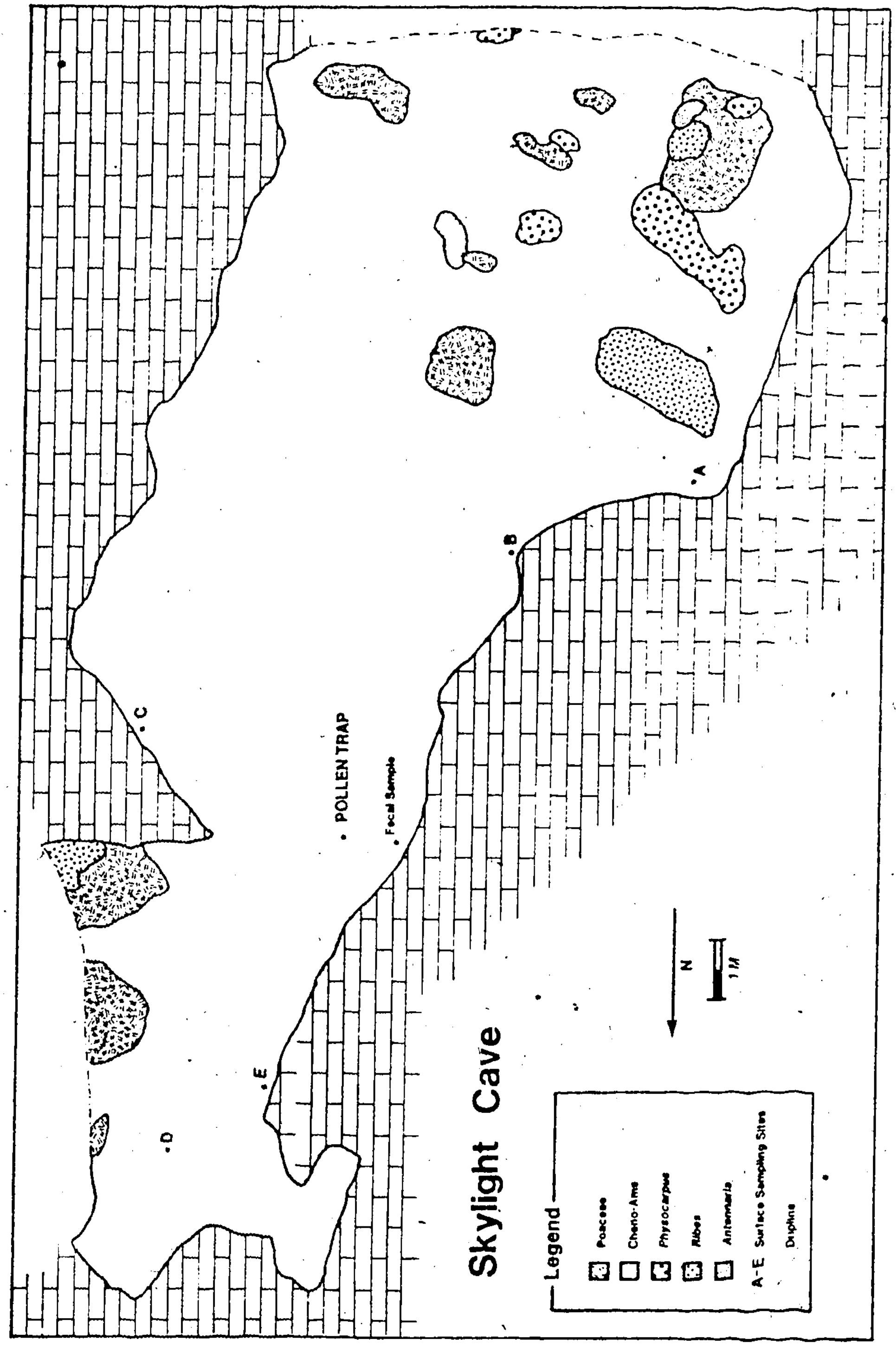
Tubuliflorae (16, 1, -, 1, 1) and *Allium* (15, 0, -, 0, 0), found in the open air trap.

Skylight Cave has two entrances, so open air traps and surface samples were positioned 10m in front of the cave mouth for both the south and east openings (Fig. 5). These open air surface samples have similar *Pinus* frequencies and are higher than the other samples, exceeding 80% (57/34, -, 42, 81/87, -); note: cave floor surface samples will be discussed separately in this section). The constraint posed by high *Pinus* in these open air surface samples causes the other major taxa to covary within 3% of each other (Fig. 4).

The cave traps have greater frequencies of *Artemisia* (12/10, -, 25, 4/1, -) and Cheno-Ams (4/4, -, 7, 2/1, -) than the open air traps. Poaceae frequencies are similar between the trap samples (13/15, -, 15, 2/3), but the open air traps have conspicuously high values of minor herb taxa. The open air trap (b) has Rosaceae pollen (*Sanguisorba* type) dominating the NAP component (0/21, -, 1, */0). Open air trap (a) has 8% Apiaceae pollen (8/1, -, *, 0/1).

Among the cave floor surface samples (Fig. 4) *Pinus* frequencies vary within the range established by the open air samples from 39-57% (51/55/39/57/55/17 -- samples A, B, C, D, E, Fecal, respectively). The long distance component, *Abies*, reaches 5% in sample E (1/2/*/3/5/0). The fecal [illegible]. which has a low frequency of *Pinus*, has [illegible]ondingly high *Artemisia* values (27/22/22/15/16/40). [illegible]e (9/8/6/4/3/6) and Cheno-Am (6/5/9/4/6/6) frequencies

Figure 5. Location of Sediment Samples, Cave Trap, and Vegetation Within Skylight Cave (Plan View)


Skylight Cave
Legend
Poaceae
Cheno-Ams
Physocarpus
Ribes
Antennaria
A-E Surface Sampling Sites
Dripline
N
1 M
A
B
C
D
E
POLLEN TRAP
Fecal Sample

show little variation between samples; Caryophyllaceae (1/2/2/2/*/3) Sarcobatus (*/1/2/2/*/3). A wide variety of minor herbs are well represented overall among the cave floor surface samples, but frequencies are generally greater by 1-3% in the fecal sample (Fig. 2).

Utah Juniper-Blacksage Desert

Despite the open nature of the vegetation from the Utah-Juniper Blacksage sites, *Pinus* is a major component of the pollen rain in all samples.

At the Crooked Creek Rockshelter, remarkable similarity is expressed between all samples, except the open air surface sample. This last sample has a conspicuously high frequency of *Pinus* (42, 30, 30, 70, 32). The brown color and abraded condition of *Pinus* grains in this sample suggest that this peak reflects a taphonomic factor rather than a sampling bias. It is hypothesized that pollen from years past become reairborne when the wind disturbs the loose sandy substrate and these sand-abraded grains enrich the surface samples.

The cave floor surface sample distinguishes itself from the other samples in its low percentage of *Artemisia* (32, 34, 37, 4, 15) and Poaceae (7, 4, 5, 2, 2) and high percentage of Cheno-Ams (14, 7, 13, 7, 29). Samples from inside the rockshelter overall demonstrate better representation of nonarboreal taxa, the bulk of the difference resulting from the high percentage of high spine *Tubuliflorae* in this sample (0, 18, 7, 3, 8).

At Burnt Timber Rockshelter, the two most similar samples are the surface samples. The highly abraded exine of the *Pinus* specimens once again suggests that the high frequencies of *Pinus* are due to redeposition of the past season's *Pinus* grains by wind. *Pinus* frequencies vary from 48-84% (48, 68, 53, 84, 82). For the other taxa observed among the surface samples, percentages come within 1% of each other, excepting low spine *Tubuliflorae* (4, 7, 8, 1, 4) and Polygonaceae (1, 1, *, 4, *), which vary 3-4%.

The lip trap is less similar to the open air and cave trap than they are to each other. The high value of *Pinus* in the lip sample constrains the percentage of *Artemisia* (20, 13, 21, 5, 6). For most of the other major taxa, frequencies come within a few percent of each other. Cheno-Ams (9, 8, 6, 2, 3) and Poaceae (3, 3, 4, 1, *) are the other major pollen types in these assemblages.

The Gyp Springs Rockshelter provides a more variable pollen spectra. *Pinus* frequencies range from 22-69% (27, -, 22/69, 55, 60). Low frequencies for *Pinus* in the open air trap is accounted for by a high percentage of *Artemisia* (49, -, 27/[illegible], 18, 12), and in the cave trap (a) by a high percentage of Cheno-Am pollen (10, -, 23/9, 8, 11). Poaceae (3, -, 5/1, 1, 4), Caryophyllaceae (0, -, 2/*, 0, 0), Asteraceae (7, -, 9/5, 3, 2), and *Sarcobatus* (*, -, 8/3, 2, 5) are slightly better represented in the cave trap (a) as well. Long distance components *Picea* (0, -, 0/0, 10, 3) and *Abies* (0, -, 0/0, 2, 2) were observed only in the surface samples.

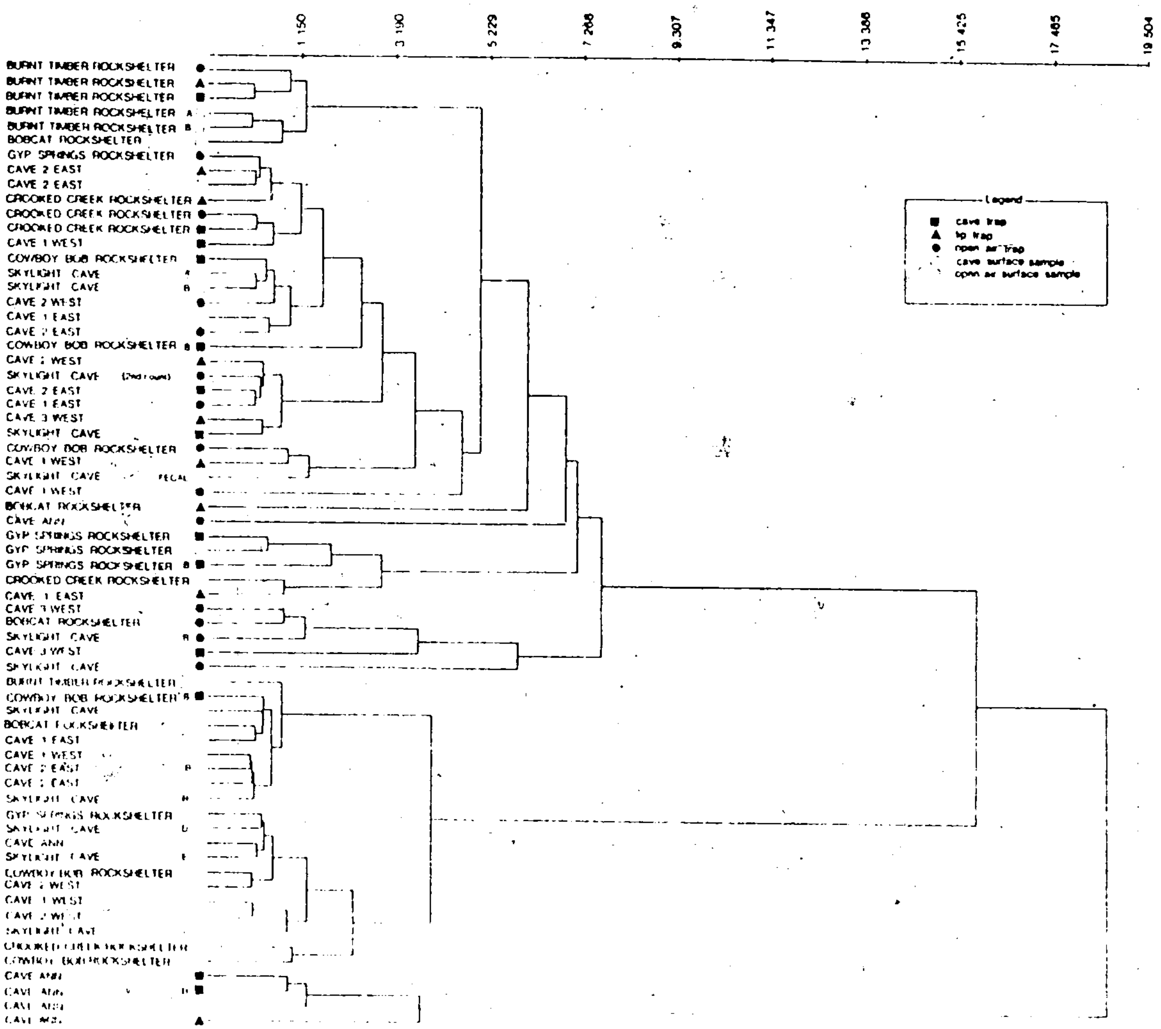
ANALYSIS

Relationship Between Pollen Rain and Local Vegetation

The dendrogram (Fig. 6) presents the results of the cluster analysis, and the degree of similarity exhibited between samples from each site and vegetative zone. Cluster analyses applied to surface sample data have recognized gross vegetation zones in other studies (e.g., Birks, 1973), however, in this study, sorting by vegetation zone was not evident. The samples from the Sub-Alpine plateau, Douglas Fir forest and the Utah Juniper-Blacksage zones seem randomly distributed throughout the dendrogram.

On the other hand, the clusters recognize the samples derived from Tauber traps and surface sediments as discrete groups. This reflects the fact that Tauber traps and sediment samples are not strictly comparable. Whereas the Tauber traps in this experiment sampled a single season's wind transported pollen, the pollen assemblages from sediment samples represented several seasons's pollen rain (net averaging effect) derived from a variety of transport components (Tauber, 1967) and subjected to oxidative and mechanical exine degradation processes. In the Pryor Mountains, the net effect of these variables caused the sediment samples to contain higher percentages of pine pollen, and lower percentages of *Artemisia*, Poaceae, Cheno-Ams and other NAP. The surface samples which clustered among the

Figure 6. Results of Cluster, Analysis (Wards, 1963) Between Contemporaneous Pollen Assemblages from Cave and Rockshelter Sites Located in Three Vegetation Zones, Pryor Mountains, Montana



Similarity demonstrated between contemporaneous pollen assemblages from cave and rockshelter sites located in three vegetation zones, Pryor Mts., Montana.

Tauber trap samples all contained less *Pinus* pollen and greater frequencies of NAP.

Two study sites provided pollen samples that clustered as a discrete group. Of these, Cave Ann is statistically the most unique. This is a function of the high percentage of herb pollen, especially Asteraceae pollen, found in the Cave traps.

The most internally consistent locality is Burnt Timber Rockshelter, where all samples except the open air surface sample cluster together. The open air surface sample was distinguished by low values of Asteraceae pollen, and higher Polygonaceae percentages than the other samples from this site.

The dendrogram indicates that the pollen assemblages recovered from the three ecological zones in this study are not sufficiently dissimilar to reflect the distinct vegetation zones observed on the landscape. This lack of resolution can be attributed to (1) the predominance in each zone of arboreal species that are notoriously unrepresented in the pollen rain (*Picea*, *Abies*, *Juniperus*, and *Pseudotsuga*), and, (2) the local presence of overproducers (*Pinus* and *Artemisia*).

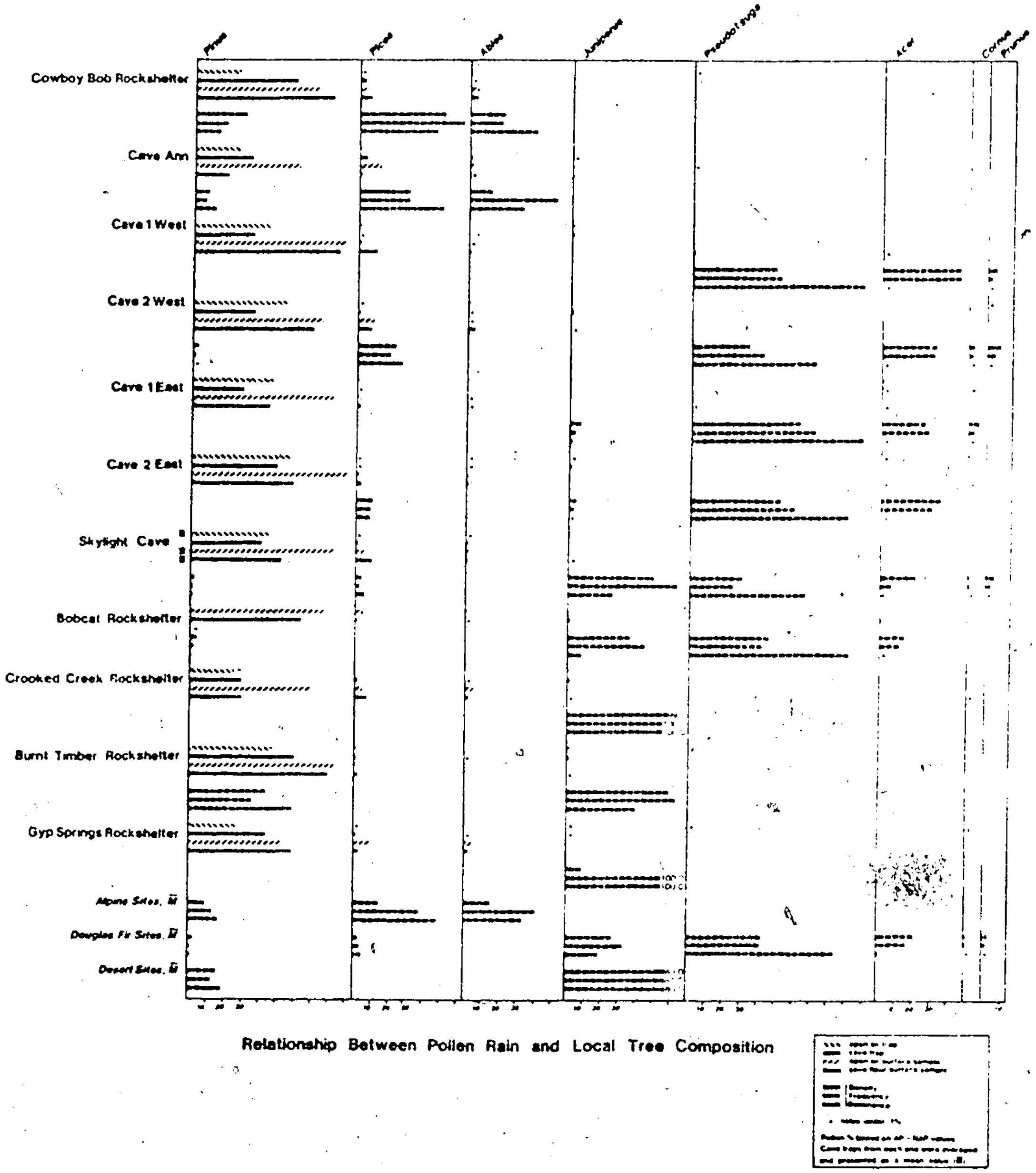
Although *Pinus* dominates the vegetation landscape at only one locality (Burnt Timber Rockshelter), and *Artemisia* figures as a minor vegetation component (less than 2% dominance) at all sites except the Crooked Creek Rockshelter and Gyp Springs Rockshelter, *Pinus* and *Artemesia* species were at least minimally present in each zone. In the Douglas Fir forest, species of *Artemisia* (predominantly *A. tridentata*) were observed on southern exposures and sunny slopes, accompanied by isolated occurences of *Pinus flexilis* and *Juniperus scrophulorum*. *Artemisia* was an important consitituant of the Subalpine Plateau and Forest-Meadow, in the valley recesses and on slopes. With few exceptions, (cave samples, Cave Ann; lip trap, Cave 1 East; cave floor surface sample, Crooked Creek Rockshelter) these two taxa dominate the pollen spectra from each site.

Fig. 7 presents schematically the relationship between the pollen rain and the density, dominance and frequency values observed in the vegetation surrounding the cave study sites. Cave traps from Cave Ann were the only samples where *Pinus* frequencies approximate the density or dominance of *Pinus* in the field, however, these depressed Pine values reflect the high incidence of Asteraceae pollen in these samples.

Pollen frequencies for *Juniperus* are quite low at all sites. While other studies have shown Cupressaceae pollen to have good areal influx and dispersal (McLennon, 1981; Ebell and Schmidt, 1964), *Juniperus* frequencies from all samples in this study are low, (under 5%). Pollen surface samples from the Bighorn Mountains, to the southeast, reported by Birkhart (1976), are as low as those reported here.

One possible explanation for the low frequencies of Cupressaceae pollen in pollen traps may be that large

Figure 7. Relationship Between Pollen Rain and Local Tree Composition



Relationship Between Pollen Rain and Local Tree Composition amounts of the past season's pollen may have been reintroduced into the air by wind blowing the loose substrate. This suggestion was also advanced to explain the degraded condition of *Pinus* grains from the desert sites. It is suspected that, due to its aerodynamic structure, *Pinus* is selectively resuspended by wind, due to the fresher appearance of grains of other taxa. If this is the case, reintroduced *Pinus* would depress the frequencies of other pollen types, particularly those such as *Juniperus*, which are highly susceptible to degradation, and less likely to sustain a season's weathering.

Picea and *Abies* frequencies are as high in some samples from the desert localities as they are in the *Picea engelmannii-Abies lasiocarpa* forest. *Picea* and *Abies* frequencies reported here from subalpine localities correspond to frequencies for *Picea* (2-4%) and *Abies* (0-4%) encountered by Birkhart (1976) in subalpine localities in the Bighorns.

At sites within the Douglas Fir Forest, *Picea* pollen is underrepresented in all pollen traps, although *Picea* pollen from sediment samples tend to be representative of the zonal average in the vegetation (Fig. 7). Picea frequencies in this study are similar to those reported Birkhart (1976) for Douglas Fir forest samples in the Bighorns.

The frequencies of *Pseudotsuga* reported here are lower than those found by Birkhart (1976). Birkhart's samples were also collected in *Pseudotsuga* stands, and yielded high percentages of *Pseudotsuga* pollen (12-23%). Wright (1967) found that *Pseudotsuga* pollen deposition falls to insignificant levels within 20m of the source. Low pollen production as well as great susceptibility to corrosion (Baker, 1976) contribute to its low incidence in the pollen record. While trace quantities of *Pseudotsuga* pollen have been reported from *Pseudotsuga* sites (Baker, 1976; McLennon, 1981; McAndrews and Wright, 1960), it is likely the low frequencies reported here are augmented by the stringent criteria imposed upon *Pseudotsuga* identifications in this study (see methodology section). Baker (1976) noted that the majority of *Pseudotsuga* grains in his study were found folded and broken, whereas here only *Pseudotsuga* grains in a fresh condition were counted.

From Fig. 7, it is clear that the vegetational composition of the plant communities observed in the Pryor Mountains are not reflected by the pollen assemblages. Although other studies of plant communities situated on an altitudinal gradient have produced pollen records that are sufficiently dissimilar to enable their recognition on the basis of their pollen assemblage (cf. Maher, 1963), the species dominating the various vegetation zones in the Pryor Mountains are poorly represented in the pollen rain.

In the absence of vegetation data the community analogue, or comparative approach (Wright, 1967) to interpreting pollen assemblages would not provide an accurate picture of the vegetation in the Pryors. However, an autecological, or, indicator-species approach (Birks and Birks, 1980) to the data would provide some insight to past vegetation composition. Some general trends are observed in the pollen record from the three vegetation zones.

Both Cowboy Bob Rockshelter and Cave Ann, located in the subalpine meadow with interspersed stands of *Abies lasiocarpa-Picea engelmannii*, are characterized by higher values of Caryophyllaceae, Polygonaceae (including *Polygonum bistorta*, *P. bistortoides*, and *Eriogonum*), and lower percentages of Cheno-Ams than those samples derived from the Douglas Fir Forest or the Utah Juniper-Blacksage zone. Samples from the Douglas Fir zone are the only samples which contain pollen of *Acer glabrum*, *Cornus stolonifera*, *Symphoricarpos*, *Spirea*, *Ribes*, *Shepherdia*, *Smilacina*, *Rubus*, and other woodland taxa all of which were located growing locally in the ecological survey (Table 3). Interestingly, pollen from *Arceuthobium*, a parasitic plant occuring in spruce forests, was found at Crooked Creek Rockshelter in the Utah Juniper-Blacksage Zone, where no *Picea* are to be found.

At the desert localities, *Sarcobatus* percentages were higher than found at most other localities. *Opuntia* pollen occurred in samples from the Utah-Juniper Blacksage zone more frequently than at other sites: it was observed only in cave floor surface samples at Skylight Rockshelter.

Patterning in the Cave Samples

One goal of this study was to determine whether the samples from the Pryor Mountains would reveal consistant biases unique to pollen assemblages derived from caves. Pollen records from Paleolithic cave sites often demonstrate high NAP percentages, for which no suitable analogue has been found among modern pollen studies of contemporary landscapes. This has led to the development of the hypothesis held by some researchers (cf.Leroi-Gourhan, 1965; Couteaux, 1977), that cave derived pollen assemblages consistently overrepresent nonarboreal pollen.

The samples from the Pryor Mountain caves and rockshelters do not show any consistent bias toward NAP. As discussed in the previous section, some cave samples demonstrate high NAP percentages (such as Cave Ann, Crooked Creek Rockshelter), but other cave traps produced the highest AP percentages of their suite of samples (cave trap (b), Gyp Springs Rockshelter; cave traps (a) and (b), Cowboy Bob Rockshelter).

Bui-Thi-Mai (1974) discovered that at Abri Vaufrey, light, aerodynamic pollen grains are better represented in samples at the rear of the cave. Comparisons of *Pinus* frequencies between cave traps (a) and (b) at Cowboy Bob Rockshelter, Cave Ann, and Gyp Springs Rockshelter also demonstrate this pattern. However, the lip traps which are located inside the cave but within 50cm of the mouth do not reflect this trend. Among the cave floor and surface samples no trend is apparent in the AP/NAP composition of assemblages.

At Cowboy Bob Rockshelter, Cave 1 West, Cave 2 East, and Burnt Timber Rockshelter, the cave floor surface sample exhibits the greatest arboreal representation observed among the suite of samples from each of these sites. Cave floor surface samples from Cave 2 East (a) and Cave Ann had the lowest arboreal representation of the suite of samples from these localities.

Sediment samples within caves represent the type of sample used in archeological pollen analysis, and comparison of the samples from Skylight Cave (Fig. 5) elucidates the problems facing paleoenvironmental interpretation of pollen samples from cave sediments. While the sediment samples recovered from the cave fall within the range of values established by the outside traps for the taxa *Pinus* and *Artemisia*; Poaceae frequencies range from 3-9%, for cave floor surface samples, whereas the frequencies from pollen traps cluster between 13-15%. Among the surface samples derived from inside the cave, *Picea* values range widely, from under 3%-16%. The occurence of *Abies*, too, ranges from 1-4%.

Overall, *Pinus* frequencies from surface samples are higher than those from pollen traps. This probably reflects the cumulative overrepresentation of pine, and its subsequent restraint on the appearance of other taxa, particularly those suseptible to oxidation. This process would produce a net averaging effect on the samples.

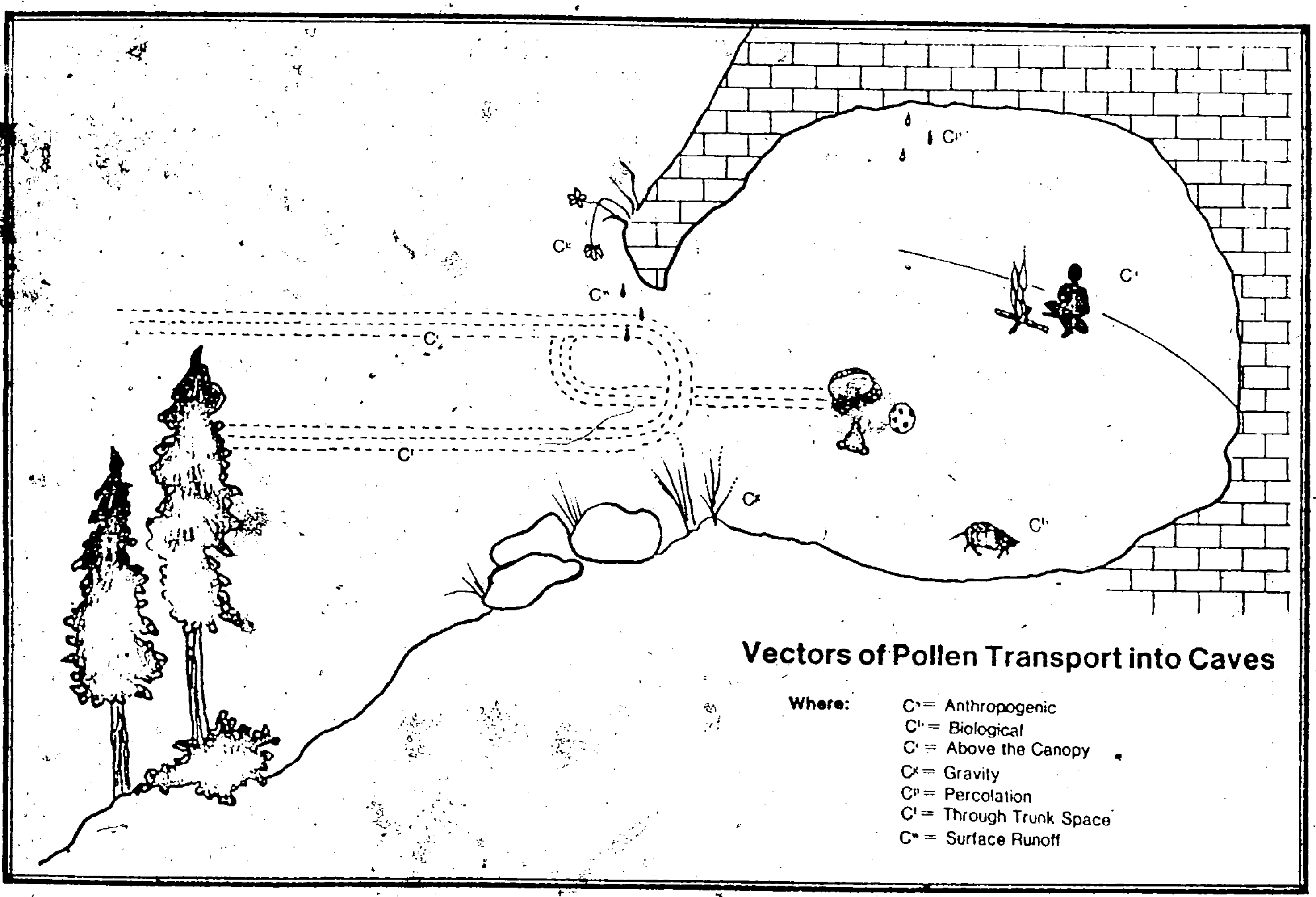
Agencies of Pollen Influx into Caves

Janssen (1966) and Tauber (1965, 1967) are primarily responsible for developing a model of pollen transport and representation. Jacobson and Bradshaw (1981) synthesize these ideas to produce a model of pollen transport to lake sites adding the additional component of gravity-controlled, vertical dry deposition of pollen and pollen bearing plant remains onto the sampling site. Using Janssen's (1966) and Tauber's (1965) original terminology, they define regional pollen rain as that derived from grains transported by rainfall(Cr) and above the canopy (Cc), extralocal pollen rain as transported through trunkspace (Ct), surface runoff (Cw), and above the canopy (Cc); and local pollen rain as transported by gravity (Cg), surface runoff (Cw), and trunk space (Ct).

All pollen sampling sites reflect these portions of the pollen rain to some degree. However, the dominant influence of one or more of these components results from the combined effects of environmental factors including size of site, topographic position, prevailing winds, type of vegetation surrounding the site, presence of inflowing streams or other sources of long distance pollen, and so on.

Cave deposits are subject to a different suite of pollen transport components than lakes, bogs and open air sites (Fig. 8). Because cave deposits are protected, rainfall (Cr) plays an insignificant role in transporting

Figure 8. Schematic Model of Pollen Transport into Caves



Vectors of Pollen Transport into Caves

Where:
C^a = Anthropogenic
C^b = Biological
C^c = Above the Canopy
C^g = Gravity
C^p = Percolation
C^t = Through Trunk Space
C^s = Surface Runoff

pollen, except near the cave mouth. Secondly, restricted wind access to these deposits constrains the deposition of the airborne pollen travelling through the trunkspace (Ct) or above the canopy (Cc). Windborne pollen must be carried into the cave entrance by air-currents, and subjected to turbulence and eddies which can cause differential pollen deposition across the cave surface (Bui-Thi-Mai, 1974).

The presence of snow drifts in or near the cave entrance will also cause differential pollen deposition. Pollen and other positively charged airborne organic particles tend to be deposited on wet rock surfaces or mineral soil which are either uncharged, or demonstrate a net negative charge (Benninghoff and Benninghoff, 1982). Melting snow in contact with the soil or bedrock through its meltwater would thus attract pollen through its net negative charge, whereas cold dry snow and ice stand a poor chance of collecting pollen as they represent a poor electrical ground. In cases where snowdrifts block the cave entrance for all or part of the pollenation season, the net electrical charge of the snowdrift as determined by its wet or dry condition can figure significantly in the ultimate collection of pollen in the cave sediment. This characteristic generates the hypothesis that periodic freezing and thawing of snowdrifts could bias the pollen assemblage derived from snowdrift meltwater toward those genera pollenating during warmer temperatures when the snowdrift was melting and exhibiting a net negative charge.

Influx data collected from cave and rockshelter sites in the Pryors confirm that the mechanisms by which anemophillous pollen enters caves is substantially different than those which operate on open air sites. For each locality where pollen influx data were available, pollen influx was lower for traps located inside the cave, than those in the open air sites (Table 5). This corroborates Bui Thi-Mai's (1974) suggestion that, at Abri Vaufrey, pollen deposition decreases with cave depth.

As indicated in Fig. 8, deposits located near the cave mouth are subjected to a wide variety of transport components, including gravity (Cg) and surface runoff (Cw). In most cases, it would be expected that air turbulence would be greatest at the opening of the cave, which would also contribute to uneven pollen deposition. Pollen influx rates from the lip traps vary dramatically, and demonstrate the complexity of pollen deposition around cave openings (Table 5). At Cave 3 West, the lip trap contained more pollen (4350 grains/cm²/yr) than either the open air trap (4268 grains/cm²/yr) or the cave trap (2528 grains/cm²/yr). The lip trap from Cave 2 East, on the other hand, contained less pollen (901 grains/cm²/yr) than the other 2 traps (cave: 1238 grains/cm²/yr; open air: 12,862 grains/cm²/yr). At the Crooked Creek Rockshelter, and Cave 1 West, pollen influx into the lip trap (2896 and 1400 grains/cm²/yr respectively) was less than the open air trap (4199 and 3753 grains/cm²/yr), but more than the cave trap (1456 and 855

Table 5

Absolute Influx by Cave or Rockshelter Site, grains/cm/yr

site	cave trap	lip trap	open air trap
Gyp Springs Shelter	11861		
	4965		
Crooked Creek Rockshelter	1456	2896	4199
Cowboy Bob Rockshelter	319		48586
Cave 1 East		6043	7392
Cave 2 East	1238	901	12862
Cave 1 West	855	1400	3753
Cave 2 West		318	3111
Cave 3 West	2528	4350	4268
Bobcat Rockshelter		3371	28016
Skylight Rockshelter	2720		6297
			5770

grains/cm²/yr).

Two additional vectors of pollen transport play potentially significant roles in forming the fossil pollen assemblage. These are biological activity (Cb) and anthropogenic activity (Ca). The role played by a third transport component, water percolation (Cp), has not been established empirically. While pollen have been found in suspension in ground water (Horowitz, 1980), its contribution to the pollen assemblage in caves is probably minor.

In terms of pollen analysis, the vegetation surrounding caves poses problems more similar to the case for open air sites, than the case for lakes and bogs. At lakes and bogs, the local vegetation belongs to a restricted environmental tolerance range, and is thus both readily defined and easily excluded from the pollen sum. Exclusion of "local" pollen elements from open air samples is a complicated process [illegible] modern samples (cf. Janssen, 1981), and impossible in fossil assemblages. The same is true for cave sites. Cave entrances characteristically support a concentration of the herbaceous elements present in the regional vegetation (Cubbon, 1976). In this study, surveys of the vegetation immediately proximate to the cave mouth, and inside the drip line produced plants which were relatively abundant in the transect surveys (see Table 4).

Biological Agencies

Animals have the potential to import pollen on their feet and fur, as well as through their feces. Pollen found in feces represent both intentional and unintentional intake of plant substances (Aikens, 1970). In recognizing the potential importance of pollen derived from animal waste to fossil assemblages, several researchers have conducted analyses of coprolites to determine their potential contribution to fossil pollen assemblages (cf. Draxler, 1972; Van Zinden Bakker, 1982).

In the Pryors, analysis of *Neotoma* droppings from Skylight Cave produced equivocal results (see Fig. 2). Pollen was no more abundant in the *Neotoma* droppings than in an equal volume of sediment. Arboreal pollen was quite low, under 20%, and *Artemisia* was high, exceeding 40%. The representation of minor nonarboreal taxa was only slightly higher (1-3%) than the other cave floor surface samples from this site.

A case can be made that degradation of feces may play a role in contributing to the pollen assemblage. Multiple-taxa pollen agglomerates have been observed Both in the fecal samples and in sediment samples (Plate 4). Becaue these pollen agglomerates were abundant in the fecal sample, somewhat abundant in some sediment samples and never observed in assemblages from pollen traps (see Appendix 2), it appears that the agglomerates are originally derived from feces.

Plate 4. Multiple Species Pollen Agglomerates. Note *Artemesia*, *Sarcobatus*, and *Pinus*. Cave floor sediment sample, Burnt Timber Rockshelter

Table 6 produces an analysis of the taxa composition of pollen agglomerates from the Burnt Timber Rockshelter sediment sample. Overall, these agglomerates demonstrate a herbaceous bias, however it is difficult to evaluate the contribution of pollen grains originally from agglomerates to the total pollen assemblage.

The potential importance of coprolite remains to fossil pollen assemblages seems less equivocal. Analysis of Pleistocene sediments from Hohlen Stein Cave, Schambach Valley, West Germany was undertaken by the author as part of this project. Out of 72 samples processed and counted, only 3 samples yielded greater than 50 grains. In two of the three polliniferous samples contained fecal material. One enriched with coprolites of *Ursus spelaeus*, was characterized with high values of Poaceae, *Tubuliflorae*, *Liguliflorae*, and Apiaceae (Fig. 9). Samples containing *Ursus spelaeus* coprolites, analyzed by Draxler (1973), had high frequencies of Dipsicaceae and Caryophyllaceae, in addition to these taxa. The sample enriched with Hyena coprolites, and the sample containing no evidence of enrichment, yielded high frequencies of *Betula*.

As a comparison, the sporadic pollen found in the remaining 69 samples were identified and are graphed alongside the three pollinferous samples. The lack of pollen in the other samples clearly demonstrates that pollen brought in by animals can, in certain cases, contribute very significant portion of the cave derived pollen

TABLE 6: Composition of Multiple-species Pollen Agglomerates, Burnt Timber Rockshelter Cave Floor Sediment Sample (110801)

Agglomerate no.	Artemesia	Cheno-Ams	Sarcobatus	Low Spine Asteraceae	High Spine Asteraceae	Poaceae	Gaura	Pinus	Bladders
1		2							1
2	1			2					
3	1			2					
4			1					1	
5	1	1							
6	1	1							1
7				1				2	
8				2				2	
9		3		1			1	2	
10	9							1	
11			1					1	
12		3						2	
13					1				
14	2	3	3						
15		1					1		1
16	6				2			1	
17	4			1					
18			1					1	
19			1					1	
20	2		1			1		3	
21	1	6							
22	5	3							
23	6							1	
24		1						3	
25	6	1		4					
26		1						3	
27	1	1							
28			8	1					
29		1		1				1	
30	12	1						1	
31					3			1	
32						1		1	
33	3	2			1			1	
34		2						1	
35		1							
36		5		1					
37	1	1							
38			1						
39	20			2					
40			1					1	

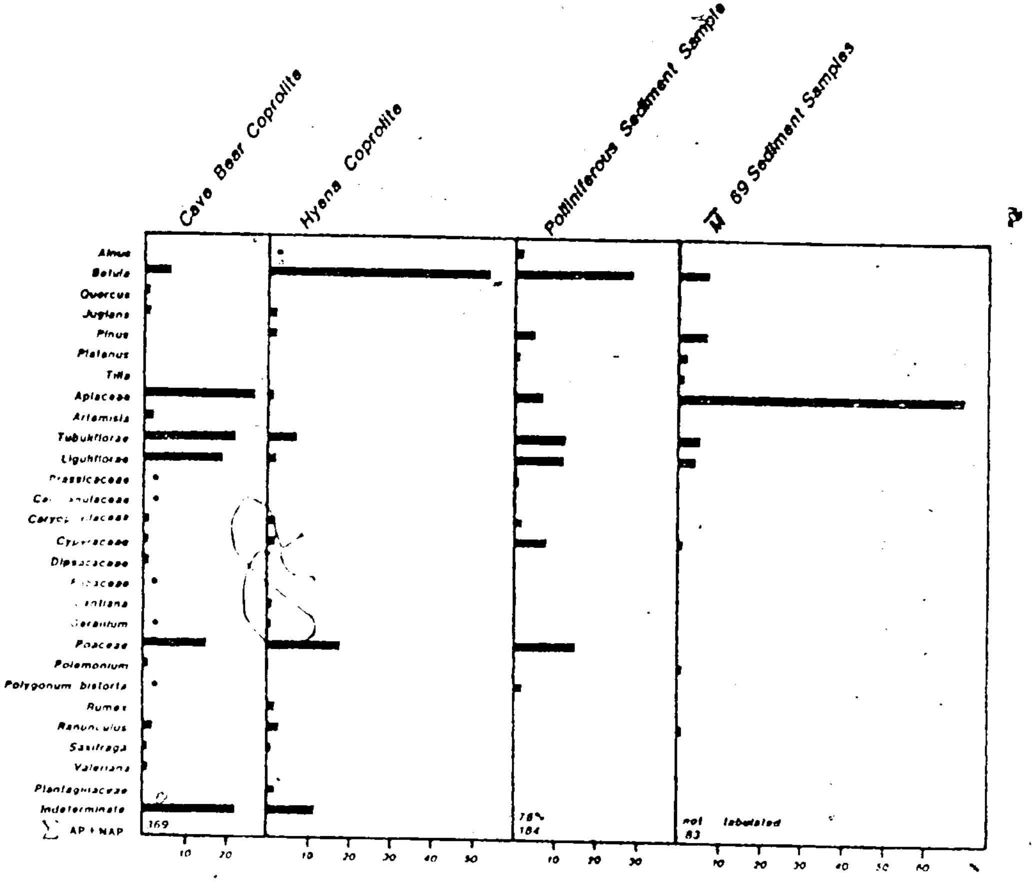
Table 6 continued

41	14							1
42	17			2				
43	6			5				
44		1						1
45	1			1				
46		1		1		10		
47	4							1
48	1		1					
49	1	4						
50	1							1
51	1							2
52	11	4		10				
53		6	1					1
54			1					1
55	3	1						1
56	1			1				5
57					1			1
58	10			7				
59					2			1
60	8			14				
61								1
62	1				1			1
63	9			1				
64		1						1
65		1				10		
66	4			1				1
67	1	4						1
68	1							1
69	1							1
70	11	4		10				
71		6	1					1
72	3	1						1
73				1				5
74	6				1			1
75							1	
76				10	2			
77	10							
78	8			7				
79				14				1
80	1			1	1			1

Table 6 continued

81	9			1				
82		11						1
83	1			2				
84	1			2	1			
85	1	1						
86	1	1						1
87				1			2	
88				2			2	
89		3		1		1	2	
90	9						1	
91							1	
92		3	1				2	
93				1				
94		1		1	1			
95		1						1
96	6							1
97		1			2		1	
98	3	2					1	
99	20			2	1		1	
100			1				1	

Figure 9. Comparison of Pollen Composition of Cave Bear Coprolite, Hyaena Coprolite, and Unenriched Sediment Samples from Hohlen Stein, Schambach Valley, West Germany



Comparison of Pollen Composition of Cave Bear Coprolite, Hyena Coprolite, and unenriched sediment samples from Hohlen Stein Cave, Schambach Valley, West Germany

preservation precluded differentiation between high and low spine Tubuliflorae

• values less than 1%

M̄-Calculated mean value

assemblage.

It is possible that biological vectors of pollen importation into caves are relatively more important to the formation of fossil assemblages than to modern ones. There have been no experimental studies on pollen preservation in caves, although pollen is notoriously sparse in cave deposits, and frequently poorly preserved. If the cave is formed in carbonate rock, the poor preservation of pollen in alkaline environments due to oxidation and fungal attack (Havinga, 1968), and extensive exposure to weathering due to slow rates of sedimentation could contribute to this phenomena. If these processes destroy all but the most resistant pollen, and coprolites constitute a more favorable environment to pollen preservation, the biological vector could play a very significant role in the formation of the thanatacoenosis.

In a sample of modern hyaena feces, Kruuk (1976) found that calcium constituted between 12-25% of the total weight. The crust of calcium salt responsible for the characteristic white color of hyaena scats may act as a deterent to fungal growth.

Human Agencies

Pollen analysis can yield vegetational reconstructions because it is assumed that the representation and relative proportions of taxa in an assemblage have ecological meaning. Particular caution must be applied to the analysis of archaeological sediments however, due to intensive vegetation disturbance normally incurred around a site (Baker, 1974; Kelso, 1970; Mehringer, 1967); the mixing of pollen assemblages by postdepositional disturbance (Butzer, 1982; Minnis, 1981); and palynological residues of cultural and subsistence activities.

Palynological assemblages from archaeological sites have been used to interpret prehistoric diet, and subsistence patterns (Fall *et al.*, 1981; Aikens, 1970; Kelso, 1970), season of site occupation (Bryant, 1969; in Bryant and Halloway, 1983), ritual (Hill and Hevly 1968; Leroi-Gourhan, 1975), and artifact usage, to define activity areas (Hill and Hevly, 1968), and utilization of native or cultivated plants (Kelso, in Aikens 1970). While providing great insight into man's past subsistence and cultural activities, the selective importation of pollen which characterizes some archaeological sites can also bias any forthcoming palynological reconstructions of past vegetation. For instance, at Hogup Cave, human agencies were the dominant mode of deposition within the cave, and the pollen residues of human activity obscured any evidence of the vegetation landscape existing at the time (Kelso, in Aikens, 1970).

Unintentional importation of pollen and mixing of fossil pollen on the cave floor by humans may have played a major role in forming the pollen spectra derived from Cave

Ann. While Tauber traps were in place, archaeological test excavations were conducted at Cave Ann. No insects or other biological sources of contamination were observed in the recovered Tauber traps, so it is possible that human activity could have been responsible for the anomalous *Tubuliflorae* values recorded from traps inside the cave. The high *Tubuliflorae* values may reflect selective importation of these grains by excavators. Further, the overall poor condition of the grains is reminiscent of those derived from desert sites (Plate 3), and suggests that the archeological activities disturbed the sediment on the cave floor, and reactivated the anemophilous grains into the air. A counter hypothesis may be that the cave's relatively sheltered position away from direct winds may figure significantly in low *Pinus* values, causing the concomitant rise in herb values. However, *Artemisia* dominates the open air trap assemblage, so it would be expected that the inside traps would, in this case, record high percentages of this taxon as well. Due to the protected position of the cave, it appears that human activity did figure significantly in the mixing of several seasons' pollen rain by raising dust.

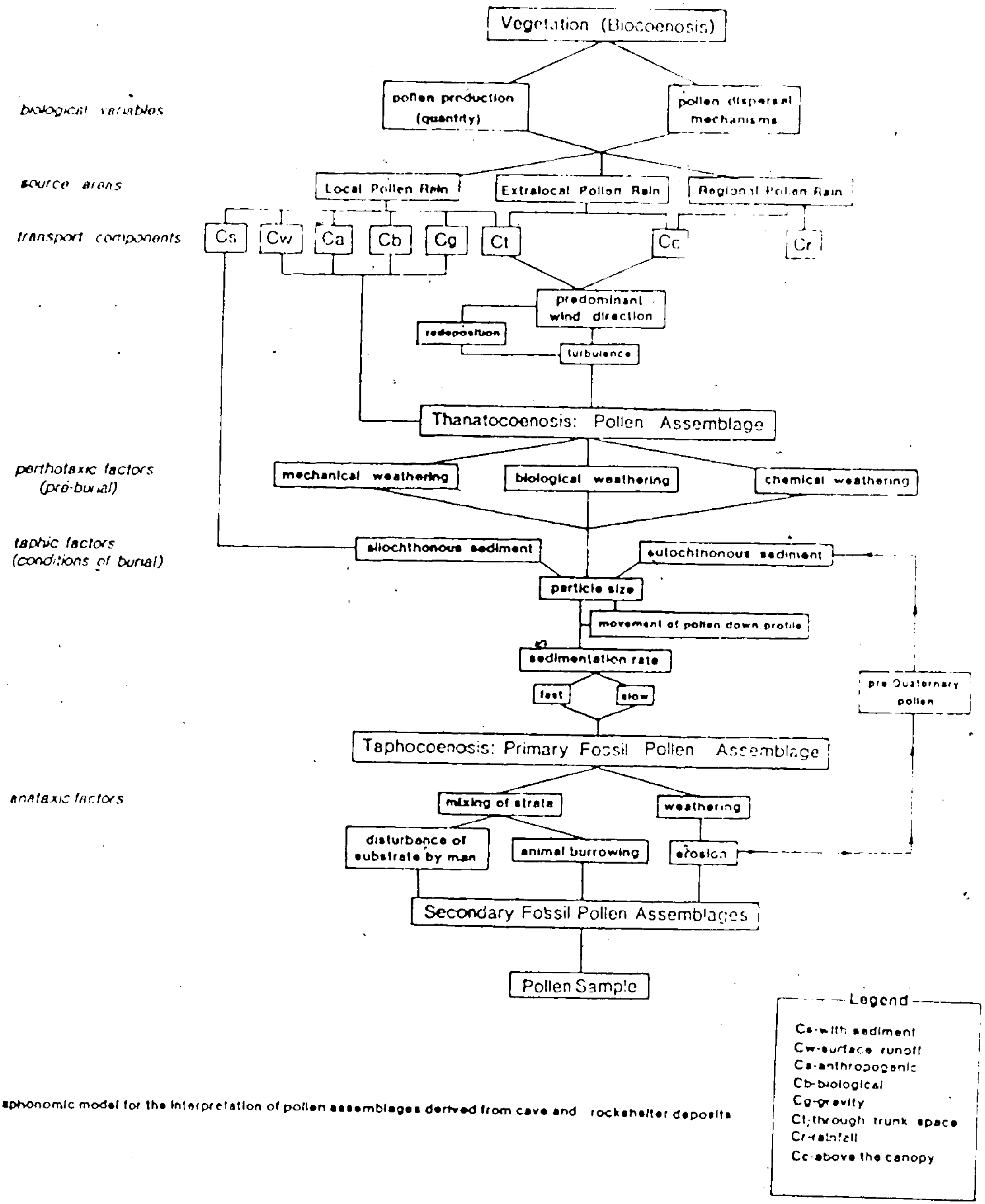
CONCLUSION

The dominance in the vegetation of species which are notoriously poorly represented in the pollen assemblage, clouds the interpretation of pollen transport into caves in the Pryor Mountains, and makes extrapolation of results from this study to other caves sites highly problematic. However, on the basis on the comparative data collected in this study, it is possible to challenge and confirm some currently held hypotheses about pollen transport to caves, and to discuss the potential of pollen analysis for cave deposits.

The critical issue in this study was to determine which source areas (e.g., local, regional, long distance) and which transport components (see Fig. 10) of the vegetation dominate the pollen assemblage derived from cave deposits; and ultimately, to determine whether the pollen assemblage (thanatocoenosis) lends itself to quantitative pollen analysis. Previous experimental research (Bui-Thi-Mai, 1974; Bui-Thi-Mai and Johnson, 1976), suggests that comtemporaneous pollen samples derived from caves do not demonstrate variation significant enough to produce differing climatic interpretations. Consistencies have also been observed between the climatic interpretation of clastic cave sediments and pollen analysis of contemporaneous samples (Laville *et al.*, 1980).

In sharp contrast to these experimental and empirical findings, comparisons between samples from cave and rockshelter sites in the Pryor Mountains demonstrate dramatic variability. For example, at Skylight Cave, *Picea* frequencies in the cave floor surface samples vary dramatically from under 3% to over 16%. In a *Pinus* dominated

Figure 10. Taphonomic Model for the Interpretation of Pollen Assemblages Derived from Cave and Rockshelter Deposits



Taphonomic model for the interpretation of pollen assemblages derived from cave and rockshelter deposits pollen spectrum, an increase of 13% *Picea* would be interpreted as an ecological or climatological. change if encountered in a time-transgressive pollen diagram. Similarly, the dramatic replacement of over 40% *Pinus* for *Artemisia* and Cheno-Ams, as observed between cave trap samples at Gyp Springs Rockshelter, would also be indicative of an environmental change. For at least these caves and rockshelters in the Pryor Mountains, ecological interpretation of the pollen spectra would be highly problematic.

Regarding intersite variation, the cave trap and cave floor surface samples from Cowboy Bob Rockshelter and Cave Ann give no indication that they are located in the same vegetation zone, even though the open air AP/NAP ratios between these sites are nearly identical. All samples from inside Cave Ann have high frequencies of Asteraceae pollen, and depressed *Pinus* frequencies, compared to Cowboy Bob Rockshelter. However, in this case, a 50% decrease in *Pinus* does not indicate climatic cooling or more xeric conditions; it likely reflects either the differences in position with respect to dominant wind directions, or the importation of Asteraceae pollen by biological agencies.

It was expected that the open air sites would demonstrate a wide range of variability between samples. Studies of pollen production and dispersal, have demonstrated that open air sites sample primarily the allochthonous elements of the vegetation which often obscures recognition of the important elements of the regional vegetation. Local pollen rain is distributed unevenly over the landscape and is thus less suitable for constructing paleoenvironmental reconstructions or for chronostratigraphic purposes, than samples recording regional pollen rain (Janssen, 1981).

For this reason, a comparison between the cave samples and open air samples analyzed in this study is provocative. It seems that cave samples demonstrate the same great variability shown in open air samples. Therefore, it appears that caves and rockshelters are not sampling regional pollen rain and therefore not, "acting as an integrator of the pollen environment, similar to lake and bog localities, "(Bui-Thi-Mai and Johnson, 1976:9), but are sampling local pollen rain, and are subjected to the uneven pollen deposition characterizing open air sites. If the dynamics of pollen transport into caves and rockshelters in the Pryor Mountains is representative of cave and rockshelter sites in general, it seems that these deposits do not fulfill a major requirement of the palynological method. Therefore the accuracy and resolution of regional paleoenvironmental reconstructions based on cave or rockshelter deposits are open to serious question.

. While this work has been concerned primarily with clarifying the relationship of the vegetation (biocoenosis) to the pollen assemblage found in a cave before burial (thanatocoenosis), it is recognized that both perthotaxic (post death, preburial) and anataxic (weathering, erosion, redeposition) factors contribute to the ultimate composition of the fossil assemblage (Fig. 10) (Morlan, 1980).

In this study, the wind transported pollen components demonstrated a bias toward the local vegetation. Numerous studies of pollen from archaeological sites have shown that an assemblage can be biased toward economic plant types, or toward low-lying herbaceous types by unintentional importation. Coprolites of man and other animals are capable of importing macro- and microscopic botanical materials into a cave.

The pollen record from Hohlen Stein and its preservational bias toward samples enriched with fecal material suggests that the nonrandom pollen sampling of animals may become even more important through time as pollen in the more alkaline deposits are destroyed by oxidative fungal attack, increasing the relative representation of pollen transported by the biological vector. While all sites of fossil accumulation are characterized by perthotaxic factors, this effect in alkaline cave and rockshelter sites may be more pronounced in comparison, due to the severity of the poor preservational environment.

However, other agencies contribute to the formation of the taphocoenosis. In general, caves are known to be among the most complex of depositional environments, composed of both externally derived material and internally produced sediments, which may be deposited unevenly across the cave landscape. The externally derived deposits, which include soil wash, stream beds, aeolian dust and sand, and cultural residues (Butzer, 1982) may contribute allocthonous pollen to the fossil assemblage. Internally generated deposits, which include roof and wall rubble, and in limestone bedrock, travertine and dripstone deposits (ibid.), provide an uneven surface upon which pollen and finer sediments are deposited. This characteristic makes correlation of contemporaneous pollen assemblages difficult across the cave floor and increases the potential of mixing time-transgressive pollen assemblages. Besides the size and type of sedimentary particles, the sedimentation rate will affect the resolution of the initial pollen assemblage (taphocoenosis). Subsequent weathering, erosion and redeposition, as well as disturbance by animal activity have the potential to rework older sediment into a younger matrix (cf. Butzer 1982). Over time these combined processes will produce a secondary fossil assemblage, potentially with a very different composition of taxa than either the thanatocoenosis or taphocoenosis. Thus, an understanding of the depositional history of the cave site, as well as the site's sampling and preservational biases, are fundimental to the formulation of accurate paleoenvironmental interpretations.

This study suggests that the pollen assemblages from cave and rockshelter sites are not characterized by sufficient ecological resolution to provide meaningful reconstructions when analyzed through the standard numerical technique of pollen analysis, as outlined by Faegri and Iversen (1975). Comparisons of the fossil assemblages from Hohlen Stein suggest that differential preservation may figure importantly in determining the taxa composition of the fossil assemblage, and such bias should be considered in any deposit of high pH (Cushing, 1967). At archaeological sites, cultural and subsistence activities have been shown to dominate the palynological assemblage so completely as to obscure all but the barest vestiges of the past vegetational environment (Kelso, in Aikens, 1970). Further, recent studies suggest that cave deposits, particularly those associated with archaeological sites, have a complex depositional history (Butzer, 1982). Without evidence to the contrary, it is impossible to assume that cave and rockshelter deposits commonly contain essentially undeteriorated pollen in a simple stratigraphic sequence without mixing or disturbance, a prerequisite of sites for paleoenvironmental reconstructions (Jacobsen and Bradshaw, 1981).

On the basis of these observations it appears that cave deposits provide a poor pollen record of the environment, making correlations between pollen assemblages from different cave sites both difficult and highly speculative. However, it is provocative that regional correlations between pollen records from caves are deemed so successful that Laville *et al.*, (1980) suggested that pollen would provide a solid basis for developing regional schemes of climatic change if it was found consistently cave deposits.

Before it can be determined whether these observed statistical similarities between pollen records reflect ecological similarity, it is necesssary to evaluate the assumptions and implications built into the interpretative model. It is not immediately apparent what constitutes analogous climatic oscillations when different vegetation types are being compared. Nor can it be assumed that changes observed in pollen diagrams reflect climatic events (Iversen, 1973), or that the changes reflect climatic oscillations that were regional in scope (Laville, *et al.*, 1980). Further study will determine whether observed correlations reflect similar environmental conditions, or simply the limitations of the ecological assumptions used in interpretation.

Assuming that the post depositional processes operating within the cave deposit leave the pollen assemblage representative of the thanatocoenosis, meaningful interpretations may be possible through techniques of analysis that do not ascribe ecological meaning to the proportional pollen composition of the fossil assemblage. Autecological methods, such as the indicator species approach (Webb, 1973; Birks and Birks, 1980) or analogies based on presence/absence of taxa, may be more applicable to the biased pollen representation of cave deposits than the numerical techniques developed for samples from bogs and lakes. Autecological methods have been applied to the fossil remains in packrat middens, including pollen, greatly contributing to our understanding of ecological successions in the American Southwest (Van Devender, 1978; Mead, 1981).

Further research is necessary to clarify some of the problems that have been discussed in this paper. An empirical understanding of preservational biases can be developed if discussions of pollen preservation and the sediment sample size required for analysis are included in each study. Pollen analyses of cave deposits should report on the sampling strategies employed, and analysis of pollen stratigraphy should be conducted within a model of the depositional and post depositional history of cave deposits, e.g. through a contextual approach (Butzer, 1980). Finally, further additional experimental research with modern cave floor surface samples needs to be conducted in areas not plagued with vegetation "blind spots" (sensu Davis, 1963), to test whether the results of this study are specific to the Pryor Mountain context, or are shared by cave and rockshelter sites in general. Further research in this area will clarify the limitations and ecological resolution of palynological analysis of cave and rockshelter sediments, and allow for the development of techniques that maximize use of the palynological resource stored in cave sediments.

BIBLIOGRAPHY

Aikens, C.M. (1970) Hogup Cave. *University of Utah Anthropological Papers* 93, 251-262.

Anderson, R. (1955). Pollen analysis: a research tool for the study of cave deposits. *American Antiquity* 21, 84-85.

Andersen, S. (1970). The relative pollen productivity and pollen representation of N. European trees, and correction factors for tree pollen spectra. *Danm. Geol. Unders., series II*, 96, 1-99.

Baker, F. (1944). Mountain climates of the western United States. *Ecological Monographs* 14, 223-254.

Baker, R.G. (1976). Late Quaternary History of the Yellowstone Lake Basin, Wyoming. *United States Geological Survey Professional Paper* 729 [illegible] 48p.

Benninghoff, W.S. & Benninghoff, A.S. 1982 . Airborne biological particles and electric fields. *Radio Science* 17, 135-155.

Bent, A. M., & Wright, H. E. Jr. (1963). Pollen analyses of surface materials and lake sediments from the Chuska Mts., New Mexico. *Bull. Geo. Soc. Am.* 74, 491-500.

Birkhart, M. R. (1976). *Pollen biostratigraphy and Late Quaternary vegetation history of the Bighorn Mountains, Wyoming.* Unpublished Ph.d. Dissertation, University of Iowa, 100p.

Birks, H. J. B. (1973). *Quaternary Plant Ecology.* Oxford: Blackwell Scientific Publications. 326p.

Birks, H. J. B., & Birks, H. H. (1980). *Quaternary Paleoecology*. Maryland: University Park Press.

Birks, H. J. B., Webb III, T., & Berti, A. A. (1975). Numerical analysis of pollen samples from central Canada: a comparison. *Review Palaeobotany Palynology*, 20, 133-169. Routledge and Kegan Paul.

Blackstone, D.L. (1975). Geology of the East Pryor Mountain Quadrangle, Carbon County, Montana. *State of Montana Bureau of Mines and Geology, Special Publication* 69.

Brande, G., and Bleich, K. E. (1975). Vegetationsgeschichtliche und pollen stratigraphische Undersuchungen zum Palaolithikum von Mauern un

Meilenhofen (Frankische Alb). *Quatar*, 26, 73-107.

Brookes, D., & Thomas, K. W. (1967). the distribution of pollen grains on microscope slides, part 1: the non randomness of distribution. *Pollen et Spores*, 9, 621-629.

Bryant, V.M. Jr., & Holloway, R. (1983). The role of palynology in archaeology. In (M.B. Schiffer, Ed.) *Advances in Archaeological Method and Theory* 6. New York: Academic Press, pp. 191-224.

Bui-Thi-Mai, M. (1979). Contribution a l'étude du transport et de la sedimentation des pluies polleniques dans un abri sous-roche l'Abris Vaufrey (Dordogne). Unpublished Ph.D. Dissertation, L'Universite de Bordeaux.

Bui-Thi-Mai, M. & Johnson, I. (1976). The computer used as a tool in Palynology. Annual Conference at the Computer Center, University of Birmingham, *Proceedings*, 5-12.

Butzer, K. W. (1982). *Archaeology as Human Ecology*. Cambridge: Cambridge University Press.

Couteaux, M. (1977). A propos de l'interpretation des analyses polleniques de sediments mineraux, principalement archeologiques. In, (H. Laville and J. Renault-Miskovsky, Eds) *Approche ecologique de l'homme fossile*. Paris: A.F.E.Q. *Bulletin*, supp. 47, 259-276.

Cubbon, B. D. (1976). Cave flora. In, (T. D. Ford and C. H. D. Cullingford, Eds) *Science of Speleology*, New York: Academic Press, pp. 423-452.

Curtis, J. T., & Cottam, G. (1962). *Plant Ecology Workbook*. Minneapolis: Burgess Publishing.

Cushing, E. J. (1967). Evidence for differential pollen preservation in late Quaternary sediments in Minnesota. *Review Palaeobotany Palynology* 4, 87-101.

Cwynar, L. C. (1979). *A Late Quaternary Vegetation History from Hanging Lake, N. Yukon*. Unpublished Ph.D. dissertation, University of Toronto.

Davis, M. B. (1963). On the theory of pollen analysis. *American Journal of Science* 261, 897-912.

Davis, M. B. (1967). Late glacial climate in Northern United States: a comparison of New England and the Great La Region. In, (E. J. Cushing and H. E. Wright, *Quaternary Ecology*. New Haven: Yale University Pres pp. 11-43.

De Wet, J. M. J. & Harlan, J. R. (1975). Weeds and domesticates: evolution in the man-made habitats. *Economic Botany* 29, 99-107.

Despain, D. (1973). Vegetation of the Big Horn Mountains, Wyoming, in relation to substrate. *Ecological Monographs* 43, 329-355.

Dimbleby, G. W. & Evans, J. G. (1974). Pollen and land snail analysis of calcareous soils. *Journal of Archaeological Science* 1, 117-133.

Donner, J. J. (1975) Pollen composition of the Abri Pataud Sediments. In (H. L. Movius, Jr., Ed.) Excavation of the Abri Pataud. *Bulletin, American School of Prehistoric Research* 30, 160-173.

Dorn, R.D. (1977). *Manual of the Vascular Plants of Wyoming.* New York: Garland Publishing Inc. 1498p.

Draxler, I. (1973). Pollenkörner als Nahrungsreste der Höhlenbären in Sedimenten Ostalpiner Bährenhöhlen. *Sixth International Congress of Speleology, Proceedings,* 281-286.

Ebell, L.F. & Schmidt, R.C. (1964). Meterological factors affecting conifer pollen dispersal on Vancouver Island. *Canadian Forestries Research Branch, Department of Forestries Publication No.* 1036.

Edwards, K. J. (1979). Palynological and temporal inference in the context of prehistory, with special reference to the evidence from lake and peat deposits. *Journal of Archaeological Science* 6, 255-270

Faegri, K. & Iversen, J. (1975). *Textbook of Pollen Analysis,* 3rd edition. Oxford: Blackwell Scientific. 295p.

Fall, P.L., Kelso, G. & Markgraf, V. (1981). Paleoenvironmental reconstruction at Canyon del Muerto, Arizona, U.S.A., based on principal component analysis. *Journal of Archaeological Science* 8, 297-308.

Gauch, H. G., & Whittaker, R. H. (1972). Comparison of ordination techniques. *Ecology* 53, 868-875.

Gordon, A. D., & Birks, H. J. B. (1972). Numerical methods in quaternary paleoecology, I. Zonations of pollen diagrams. *New Phytologist* 71, 961-979.

Greig-Smith, P. (1964). *Quantitative Plant Ecology.* London: Buttersworth and Co. Ltd.

Havinga, H. J. (1971). an experimental investigation into the decay of pollen and spores in various soil types. In (J. Brooks, P. R. Grant, M. D. Muir, P. van Gijzel and G. Shaw, Eds.) *Sporopollenin* London: Academic Press, pp. 446-479.

Heusser, C. J. (1969). Modern pollen spectra from the Olympic Penninsula, Washington. *Bull. Torrey Bot. Club* 96, 407-417.

Hill, J.N. & Hevly, R.H. (1963). Pollen at Broken K Pueblo: some new interpretations. *American Antiquity* 33: 200-210.

Hitchcock, C. L., Conquist, A. Ownby, M., & Thompson, J. W. (1955-1969). *Vascular Plants of the Pacific Northwest*. 5 Volumes. Seattle: University of Washington Press.

Horowitz, A. (1979). *The Quaternary of Israel*. New York: Academic Press.

Iversen, J. (1973). The development of Denmark's nature since the last glacial. *Danmarks Geol. Under*.5, 7-c.

Jacobson, G. L. Jr., & Bradshaw, R. H. W. (1981). The selection of sites for paleovegetational studies. *Quaternary Research* 16, 80-96.

Janssen, C. R. (1966). Recent pollen spectra from the deciduous and coniferous-deciduous forests of northwestern Minnesota: a study in pollen dispersal. *Ecology* 47, 804-825.

Janssen, C. R. (1970). Problems in the recognition of plant communities in pollen diagrams. *Vegetatio* 20, 187-198.

Janssen, C. R. (1973). Local and regional pollen depostion. In (H. J. B. Birks and R. G. West, Eds.) *Quaternary Plant Ecology*. London: Blackwell Scientific Publications, pp.31-42.

Janssen, C. R. (1981). Contemporary pollen assemblages from the Vosges (France). *Review Palaeobotany Palynology* 33, 183-213.

Kelso, G. (1970). Hogup Cave, Utah: comparative pollen analysis of human coprolites and cave fill. In (C. M. Aikens, Ed.) Hogup Cave. *University of Utah Anthropological Papers* 93, 251-262.

Kruuk, H. (1976). Feeding and social behavior of the striped hyaena (*Hyaena vulgaris* Desmarest). *East African Wildlife Journal* 14, 91-111.

Kurten, B. (1969). Cave Bears. *Studies in Speleology* 2, 13-24.

Lambert, J. M., & Dale, M. B. (1964). The use of statistics in phytosociology. *Advances in Ecological Research* 2, 59-98.

Laville, H. Rigaud J. P. & Sackett, J. (1980). *Rockshelters of the Perigord*. New York: Academic Press.

Leroi-Gourhan, A. (1965). Les analyses polleniques sur les sediments des Grottes. *A. F. E. Q. Bulletin*, 45-52.

Leroi-Gourhan, A. (1965). Chronologie des Grottes d'Arcy-sur-Cure. *Gallia Prehistoire* 7, 1-64.

Leroi-Gourhan, A. (1975). The flowers found with Shanidar IV, a Neanderthal burial in Iraq. *Science* 190, 542-564.

Leroi-Gourhan, A., & Renault-Miskovski, J. (1977). La palynologie applique a l'archeologie. In (H. Laville and J. Renault-Miskovsky, Eds.) Approche Ecologique de l'homme fossile. *A. F. E. Q. Bulletin*, supp. 47, 35-49.

Leroi-Gourhan, A. (1977). L'homme et le milieu vegetale. In (H. Laville and J. Renault-Miskovsky, Eds.) Approche ecologique de l'homme fossile. *A. F. E. Q. Bulletin*, supp. 47, 139-144.

Lichti-Federovich, S. & Richie, J. C. (1965). Contemporary pollen spectra in central Canada II. The forest grassland transition in Manitoba. *Pollen et Spores* 7, 63-87.

Lichti-Federovich, S., & Richie, J. C. (1968). Recent pollen assemblages from the Western interior of Canada. *Review Palaeobotany Palynology* 7, 297-344.

Loendorf, L.L. (1973). Prehistoric Settlement in the Pryor Mountains, Montana. Ph.D. dissertation, University of Missouri, Columbus.

Lowry, A.R. (1960). Climates of the States, Wyoming: Climatography of the United States no. 6048. *United States Department of Commerce, Weather Bureau*, 16p.

Mayer, L. J. Jr. (1963). Pollen analysis of surface materials from the southern San Juan Mountains, Colorado. *Bull. Geol. Soc. Am.* 74, 1485-1504.

McAndrews, J. H., and Wright, H. E. (1969). Modern pollen rain across the Wyoming Basin and northern Great Plains (USA). *Review of Paleobotany and Palynology* 9, 17-43.

McAndrews, J. H., Berti, A. A., & Norris, G. (1973). *Key to the Quaternary Pollen and Spores of the Great Lakes Region*. Ontario: Royal Ontario Museum.

McCourt, G. H. (1982). *Quaternary Palynology of the Bluefish Basin, Northern Yukon Territory*. Unpublished Msc., University of Alberta.

McLennon, D. S. (1981). *Pollen Transport and Representation in the Coast Mountains of British Columbia*. Unpublished Msc. thesis, Simon Fraser University.

Mead, J. (1981). The last 30,000 years of faunal history within the Grand Canyon, Arizona. *Quaternary Research* 15:311-326.

Mehringer, P. J. Jr. (1967). Pollen analysis of the Tule Springs area, Nevada. In (H. M. Wormington and D. Ellis, Eds.) Pleistocene Studies on South Nevada. *Nevada State Museum Anthropological Papers* 13, pt. 3, 129-200.

Minnis, P. E. (1981). Seeds in archaeological sites: sources and some interpretive problems. *American Antiquity* 46, 143-152.

Morlan, R. (1980). Taphonomy as an aid to archaeological reconnaissance and interpretation: an example from Yukon Territory. Abstracts, *American Quaternary Association*, 6th biennial meeting, Orono, Maine, 18-20.

Moore, P. D., & Webb, J. A. (1978). *An Illustrated Guide to Pollen Analysis*. London: Hodder and Stoughton.

Mott, R. J. (1969). Palynological studies in central Saskachewan. Contemporary spectra from surface samples. *Geological Survey of Canada Papers*, 69-32.

Nelson, N. C. (1943). Contributions to Montana archaeology. *American Antiquity* 9, 162-169.

Oldfield, F. (1970). Some aspects of scale and complexity in pollen-analytically based palaeoecology. *Pollen et Spores* 12, 163-171.

Orloci, R. (1967). An agglomerative method for classification of plant communities. *Journal of Ecology* 55, 193-206.

Paquereau, M. M. (1973). Palynological analysis. In (A. Montet-White, Ed.) Malpas Rockshelter. *University of Kansas Publications in Anthropology* 4, 32-35.

Petersen, G. M. (1976). Pollen analysis and the origin of cave sediments in the Central Kentucky karst. *National*

Speleological Society Bulletin 38, 53-58.

Ruffner, J. A. (1978). *Climates of the United States.* Detroit: Gale Research Co.

Rybnickova, E., & Rybníček, K. (1971). The determination and elimination of local elements in pollen spectra from different sediments. *Review Palaeobotany Palynology* 11, 165-176.

Schoenwetter, J. (1970). Archeological pollen studies of the Colorado Plateau. *American Antiquity* 35, 35-48.

Schreve-Brinkman, E. J. (1978). A palynological study of the Upper Quaternary sequence in the El Abra corridor and rock shelters (Columbia). *Paleogeography, Paleoclimatology, and Paleoecology* 25, 1-109.

South, R. (1974). *Pryor Mountain Ecosystems.* Paper prepared for the Department of Agriculture, Custer National Forest.

Tamboer Van den Heuvel, G., & Janssen, C. R. (1976). Recent pollen assemblages from the crest region of Vosges mountains (France). *Review Palaeobotany Palynology* 21, 219-240.

Tauber, H. (1965). Differential pollen dispersion and the interpretation of pollen diagrams. *Danm. Geol. Unders.*, ser. II, 89.

Tauber, H. (1967). Investigation of the mode of pollen transfer in forested areas. *Review Palaeobotany Palynology* 3, 277-286.

Van Zindern Bakker, E. M. (1982). Studies of the Wonderwerk Cave, South Africa. *Pollen et Spores* 24, 235-250.

Ward, J. H. (1963). Hierarchical grouping to optomize an objective function. *Journal of the American Statistical Association* 58, 236-244.

Webb, L. J., Tracey, J. G., Williams, W. T., & Lance, G. N. (1967). Studies in the numerical analyses of complex rainforest communities, I. A Comparison of methods applicable to site/species data. *Journal of Ecology* 55, 171-191.

Webb III, T. (1973). Corresponding patterns of pollen and vegetation in lower Michigan: a comparison of quantitative data. *Ecology* 55, 17-28.

White, R. K. (1980). *The Upper Paleolithic Occupation of the Perigord: a Topographic Approach to Subsistence and*

Settlement. Unpublished Ph.d. thesis, University of Toronto.

Wishart, D. (1978). *Clustan-User Manual* (3rd ed.). Inter-University Research Council Series: Report no. 47. Program Library Unit, Edinburgh University.

Wright, H. E. (1967). The use of surface samples in Quaternary pollen analysis. *Review Palaeobotany Palynology* 2, 321-330.

APPENDIX I. Identified Insects From Tauber Traps

Sample	Identification	Occurence on Plants
90301	1-Staphylinidae	NOF
	1-Coccinellidae	NOF
	1-*Scolytus* sp. (Scolytidae)	NOF
		1-Unknown
		sighted on *Taraxicum*
90101	1-Scarabaeidae	probably NOF
	1-Carabidae *Domius piceus*	arboricolous
	3-Alticinae	NOF
	1-Hydrophilidae	Aquatic
100101	1-Staphylinidae	NOF
80501	1-Ptinidae	NOF
80101	1-Coccinella sp.	NOF
	1-Elateridae *Ctenicera propol*	sighted on Mallow, Ninebark and Yarrow
	2-Staphylinidae	NOF
40501	1-Ptinidae	NOF
40301	2-Curculionidae	probably NOF
40101	1-Staphylinidae	NOF
60501	2-Staphylinidae	NOF
	38-Ptinidae	NOF
	1-Curculionidae *Brachyrhinus Ovatus*	common name "Strawberry Root Weevil"
60301	1-Elateridae prob. *Ctenicer*	sighted in grasses
601010	1-Melyridae	common name "softwinged Flower Beetle"
30101	1-Carabidae *Bembidion* sp.	usually riparian
	2-Hydrophilidae	aquatic
	4-Mordellidae	common name "softwinged Flower Beetle"
	1-Alticinae	NOF
	3-Throscidae *Drapetes* sp.	on flowers, chiefly milkweed, dogwood, and mayapple
120201	1-Coccinela sp.	NOF
	1-Alticinae (Chrysomelidae)	NOF
	1-Melyridae	common name "softwinged flower beetle"
120101	2-Scarabaeidae	NOF
	1-Ptinidae	NOF

* NOF=not found on flowers

Identifications provided by Ingolf S. Askevold, University of Alberta

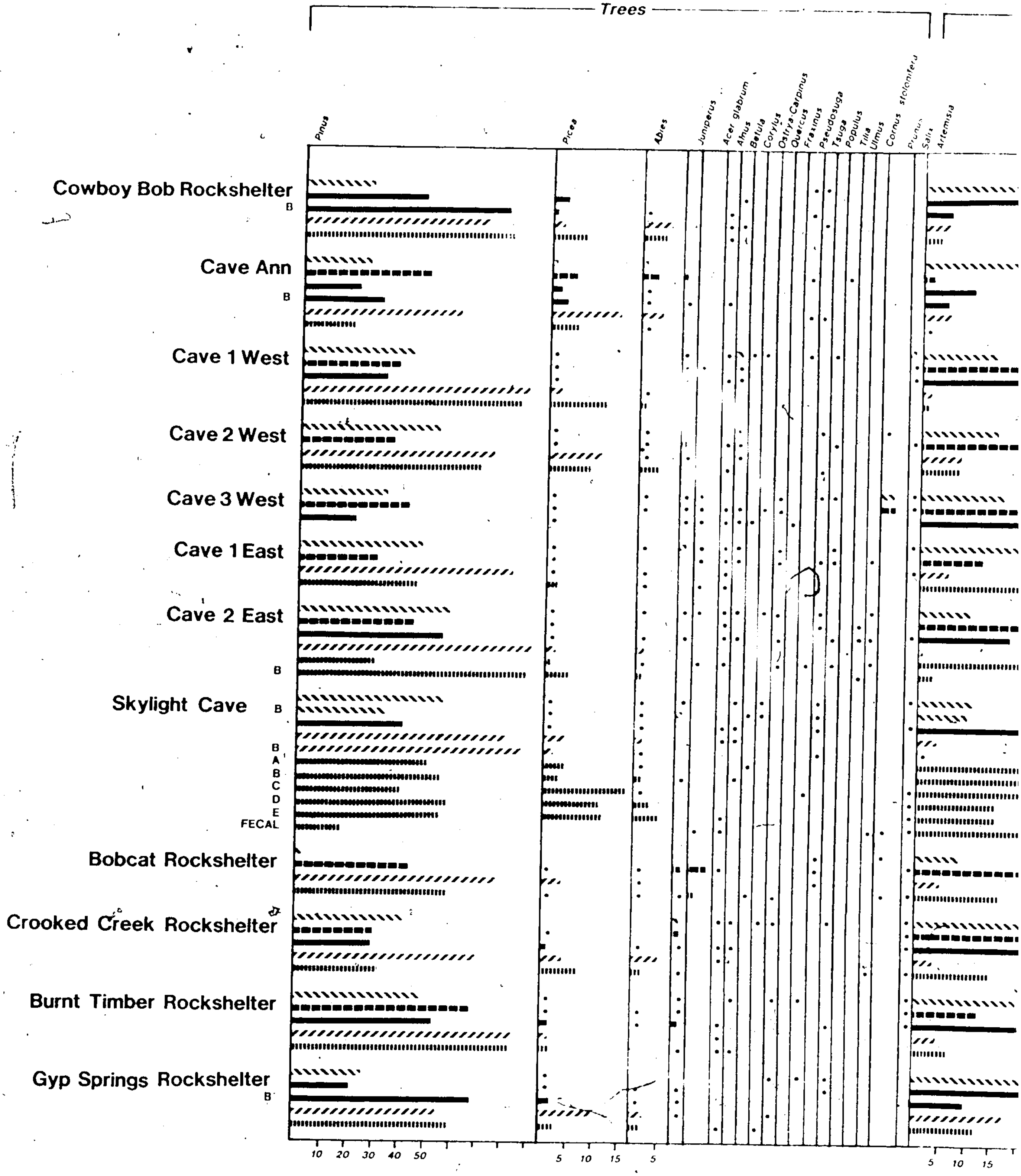
APPENDIX II. Description of Samples

No.	Sample	Locality	Kind of Sample	Notes
1	110101	Burnt Timber Ridge	open air trap	
2	110301	Burnt Timber Ridge	lip trap	
3	110501	Burnt Timber Ridge	cave trap	
4	110801	Burnt Timber Ridge	cave floor sediment	many pine, poor preservation, abraded
5	110802	Burnt Timber Ridge	cave floor sediment	2nd. count: for minor constituants. Many agglomerates.
6	110701	Burnt Timber Ridge	open air sediment	
7	040501	Cave 1 West	cave trap	
8	040301	Cave 1 West	lip trap	
9	040101	Cave 1 West	open air trap	
10	010501	Cowboy Bob Rockshelter	cave trap	
11	010502	Cowboy Bob Rockshelter	cave trap	2nd count: due to overabundance of eucalyptus
12	010101	Cowboy Bob Rockshelter	open air trap	grains fresh, but torn and broken bladders or bisaccate Tauber trap disc removed from recepticle by by animal activity
13	010601	Cowboy Bob Rockshelter	cave trap, deepest	
14	020101	Cave Ann	open air trap	
15	020501	Cave Ann	cave trap, shallow	v. poorly preserved; pine crumpled, broken high spine many recognized on one colpus only, est. low Caryophyllaceae crumpled and deformed, nearly all *Artemisia* and Polygonaceae torn
16	020601	Cave Ann	cave trap, deepest	2 packrat droppings in sampler discarded. v. poorly preserved, as above.
17	020301	Cave Ann	lip trap	poor, especially pine.
18	020701	Cave Ann	open air sediment	
19	020801	Cave Ann	moss from inside cave	
20	010801	Cowboy Bob Rockshelter	moss from inside cave	note: Bryophytes excluded from count
21	010701	Cowboy Bob Rockshelter	open air sediment	
22	040701	Cave 1 West	open air leaf litter	
23	040801	Cave 1 West	moss from inside cave	many multiple-species agglomerates accts. for high ind.
24	050701	Cave 2 West	open air sediment	
25	050801	Cave 2 West	cave floor sediment	
26	120501	Skylight Cave	interior trap	located center of blowway
27	120101	Skylight Cave	open air trap, west	contained one lepidoptera(unidentifiable). Accts. for high Apiaceae
28	120102	Skylight Cave	open air trap, west	2nd count: excluding Apiaceae
29	120202	Skylight Cave	open air trap, south	
30	060501	Cave 3 West	cave trap	
31	060301	Cave 3 West	lip trap	

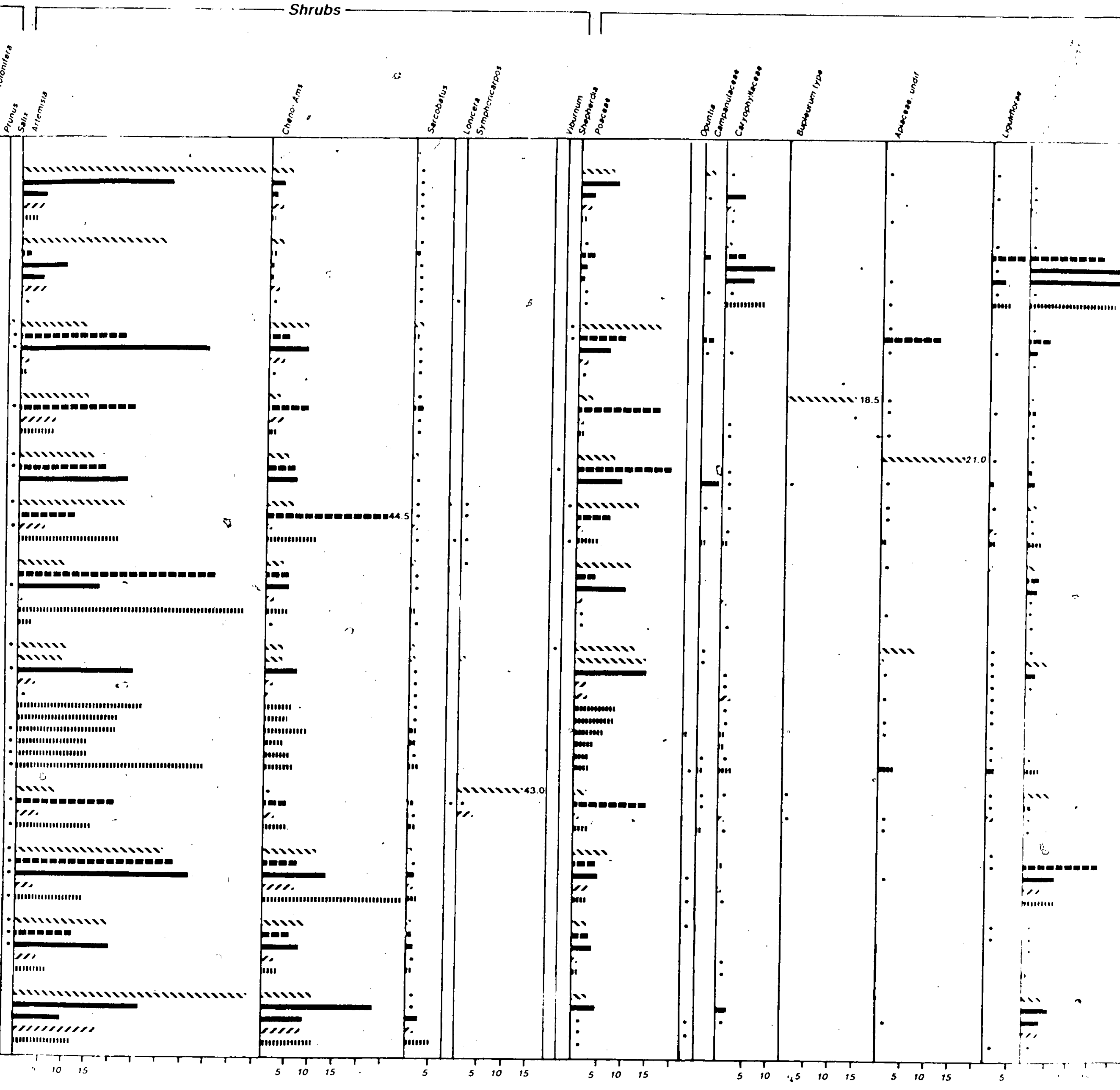
32	060101	Cave 3 West	open air trap	
33	050301	Cave 2 West	lip trap	
34	050101	Cave 2 West	open air trap	
35	120701	Skylight Cave	open air sediment, west	pine v. poor preservation. Criteria for i.d.: bladders show reticulae. Ind. bisaccate is largely pine
36	120901	Skylight Cave	open air sediment, south	same as above.
37	120801	Skylight Cave	cave floor moss	v. poor bisaccate, as above. Many multi-species agglomerates, accounts for high indeterminate count.
38	030701	Bobcat Rockshelter	open air sediment	
39	030801	Bobcat Rockshelter	cave floor moss	
40	070701	Cave 1 East	open air sediment	
41	070801	Cave 1 East	cave floor sediment	v. poor preservation, esp. bisaccate types
42	030301	Bobcat Rockshelter	lip trap	
43	030101	Bobcat Rockshelter	open air trap	trap contaminated by many insects, incl. wasps
44	080101	Cave 2 East	open air trap	
45	080301	Cave 2 East	lip trap	
46	080501	Cave 2 East	interior trap	
47	070101	Cave 1 East	open air trap	
48	070301	Cave 1 East	lip trap	
49	080801	Cave 2 East	cave floor sediment	v. poor preservation, many multi-species agglomerates many broken grains, crumpled bisaccates
50	081001	Cave 2 East	cave floor moss	
51	080701	Cave 2 East	open air sediment	
52	100101	Gyp Springs Shelter	open air trap	
53	100501	Gyp Springs Shelter	cave trap	
54	100601	Gyp Springs Shelter	cave trap,b	
55	100701	Gyp Springs Shelter	open air sediment	restricted overhang
56	100801	Gyp Springs Shelter	cave floor sediment	multi-species agglomerates, esp. *Artemisia*/Cheno-Ams prevalent
57	090101	Crooked Creek Road Site	open air trap	
~~58~~	~~090301~~	Crooked Creek Road Site	lip trap	
59	090501	Crooked Creek Road Site	interior trap	
60	090701	Crooked Creek Road Site	open air sediment	50g sample completely processed. infrequent grains, abraded pres.
61	090801	Crooked Creek Road Site	cave floor sediment	multi-species agglomerates accounts for high indeterminate count
62	120811	Skylight Cave	*Neotoma* feces	many multi-species agglomerates present.
63	120812	Skylight Cave	cave floor sediment	Good preservation.
64	120813	Skylight Cave	cave floor sediment	many multi-species agglomerates present.
65	120814	Skylight Cave	cave floor sediment	few agglomerates present (5-6)
66	120815	Skylight Cave	cave floor sediment	many multi-species agglomerates.

note: Polypodiaceae type spores dominate sediment samples and are not included in counts for samples 63-66.

1 of

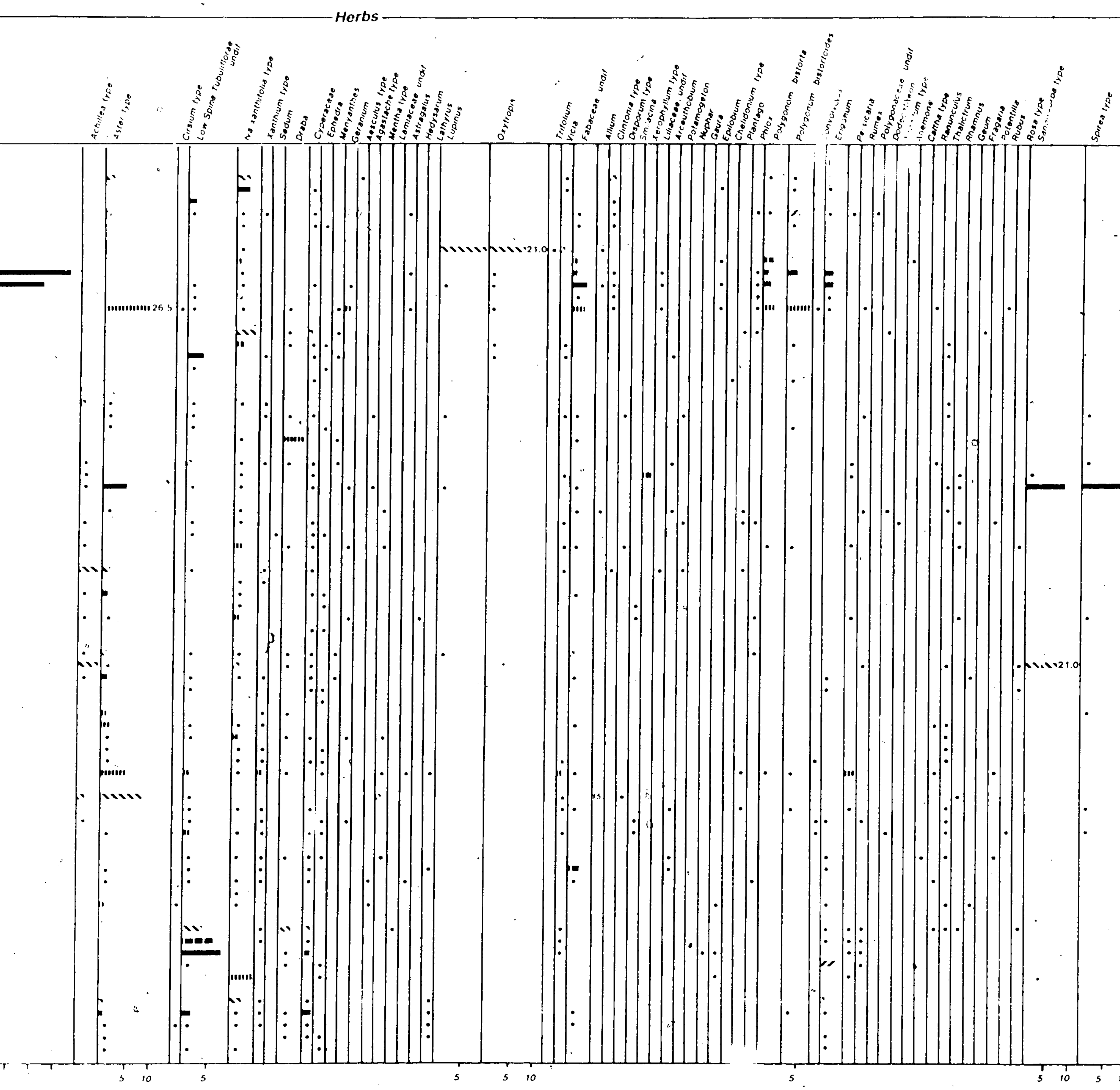

Trees
Pinus
Picea
Abies
Juniperus
Acer glabrum
Alnus
Betula
Corylus
Ostrya-Carpinus
Quercus
Fraxinus
Pseudosuga
Tsuga
Populus
Tilia
Ulmus
Cornus stolonifera
Prunus
Salix
Artemisia
Cowboy Bob Rockshelter
B
Cave Ann
B
Cave 1 West
Cave 2 West
Cave 3 West
Cave 1 East
Cave 2 East
B
Skylight Cave
B
B
A
B
C
D
E
FECAL
Bobcat Rockshelter
Crooked Creek Rockshelter
Burnt Timber Rockshelter
Gyp Springs Rockshelter
B
10
20
30
40
50
5
10
15
5
5
10
15

2of

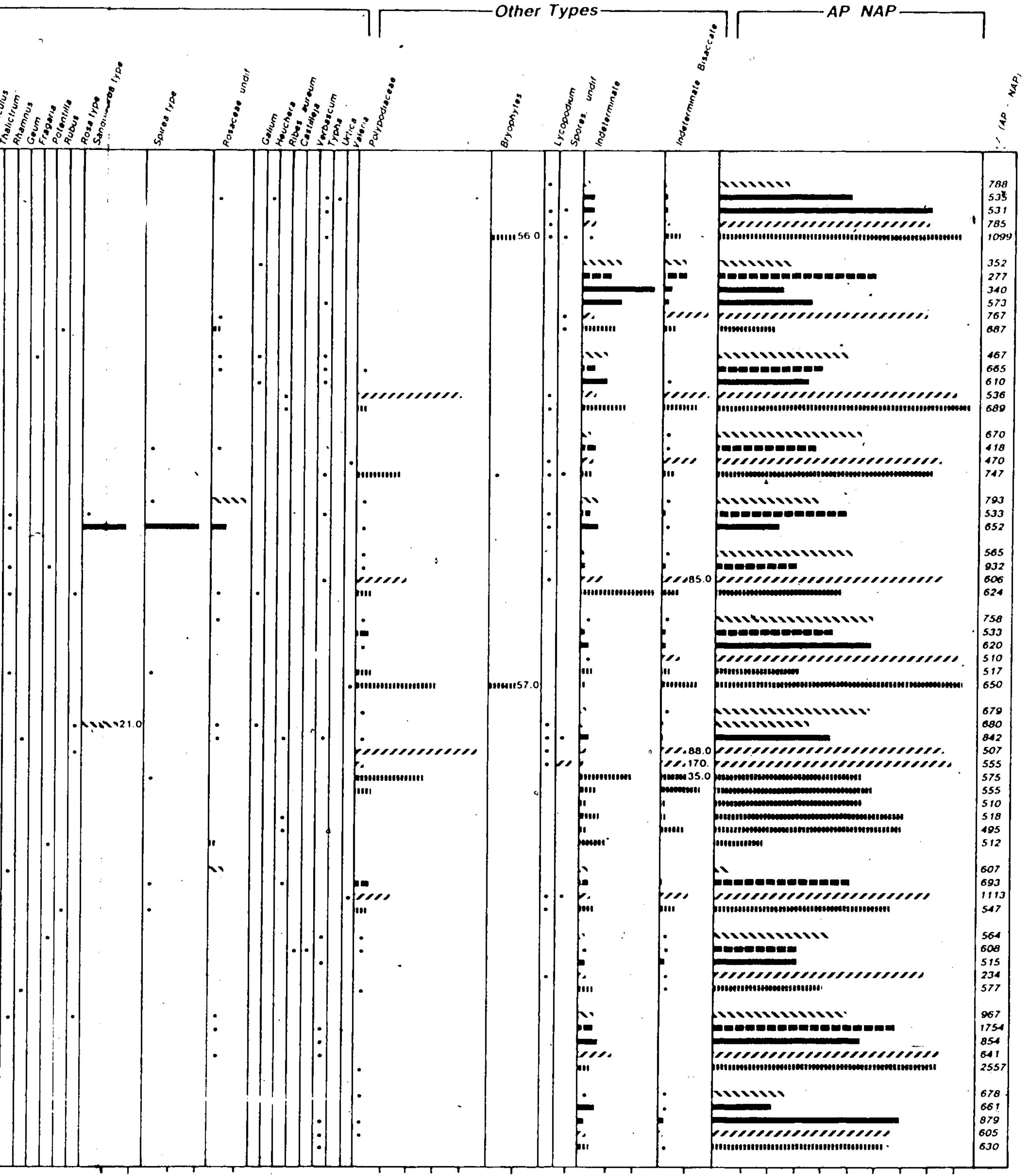


Relative Percent Surface Sample Pollen Diagram

3a/



or Cave and Rockshelter Sites, Pryor Mountains, Montan



s, Montana

4/4

Legend

- \\\\\\ open air trap
- ▬ ▬ ▬ lip trap
- ▬▬▬ cave trap
- //// open air surface sample
- IIIIII cave floor surface sample
- • Denotes under 1%