

Article

"Pollen, Plant Macrofossils, and Insects from Fossil Woodrat (*Neotoma Cinerea*) Middens in British Columbia"

Richard J. Hebda, Barry G. Warner et Robert A. Cannings *Géographie physique et Quaternaire*, vol. 44, n° 2, 1990, p. 227-234.

Pour citer cet article, utiliser l'information suivante :

URI: http://id.erudit.org/iderudit/032820ar

DOI: 10.7202/032820ar

Note : les règles d'écriture des références bibliographiques peuvent varier selon les différents domaines du savoir.

Ce document est protégé par la loi sur le droit d'auteur. L'utilisation des services d'Érudit (y compris la reproduction) est assujettie à sa politique d'utilisation que vous pouvez consulter à l'URI https://apropos.erudit.org/fr/usagers/politique-dutilisation/

Érudit est un consortium interuniversitaire sans but lucratif composé de l'Université de Montréal, l'Université Laval et l'Université du Québec à Montréal. Il a pour mission la promotion et la valorisation de la recherche. Érudit offre des services d'édition numérique de documents scientifiques depuis 1998.

Pour communiquer avec les responsables d'Érudit : info@erudit.org

POLLEN, PLANT MACROFOSSILS, AND INSECTS FROM FOSSIL WOODRAT (NEOTOMA CINEREA) MIDDENS IN BRITISH COLUMBIA

Richard J. HEBDA, Barry G. WARNER and Robert A. CANNINGS; first author Botany Unit, Royal British Columbia Museum, Victoria, British Columbia V8V 1X4 and Biology Department, University of Victoria, P.O. Box 1700, Victoria, British Columbia V8W 2Y2; second and third authors: Department of Earth Sciences and Quaternary Sciences Institute, University of Waterloo, Waterloo, Ontario N2L 3G1; Invertebrate Unit, Royal British Columbia Museum, Victoria, British Columbia V8V 1X4.

ABSTRACT Bushy-tailed woodrats (Neotoma cinerea) occur commonly in cliffs, rock talus, and caves in the open Pseudotsuga menziesii and Pinus ponderosa forests throughout interior British Columbia. Fossil N. cinerea middens from two sites in central British Columbia were radiocarbon dated and examined for pollen, plant macrofossils and insect remains. The Oregon Jack Creek site contains a midden that is dated 1150 \pm 80 (WAT-1764) radiocarbon years ago. Pollen analyses reveal an abundance of Cupressaceae (Juniperus) and Pinus. Shrub and herb pollen types include Artemisia, Fabaceae, Poaceae, and Asteraceae. Juniperus scopulorum leaves, Pseudotsuga menziesii needles, Chenopodiaceae seeds, Rosa thorns and Artemisia leaflets are the main plant macrofossils. The remains of three beetle genera, Cryptophagus, Lathridius, and Enicmus represent insects that probably lived in the midden, eating decaying organic matter or moulds. Click beetle (Limonius) remains were probably brought into the midden from nearby soil or plant material. The Bull Canyon site contains a midden that dates to 700 \pm 80 (WAT-1765) years BP. Pollen and plant macrofossil assemblages are similar to those at the Oregon Jack Creek site. Woodrat middens offer a new dimension in reconstructing Holocene paleoenvironments in the arid interior of British Columbia, in much the same way as they do in the southwest United States.

RÉSUMÉ Le pollen, les macrofossiles de végétaux et les insectes recueillis dans les matières fécales de rats (Neotoma cinerea), en Colombie-Britannique. Les rats à queue touffue s'observent souvent dans les escarpements, les talus rocheux et les cavernes dans les forêts ouvertes de Pseudotsuga menziesii et de Pinus ponderosa de l'intérieur de la Colombie-Britannique. Des amoncellements de matières fécales fossilisés de N. cinerea recueillis dans deux sites du centre de la Colombie-Britannique ont été datés au radiocarbone et analysés pour leur contenu en pollen, en macrofossiles de végétaux et en restes d'insectes. Le site d'Oregon Jack Creek renferme un amoncellement daté à 1150 ± 80 BP (WAT-1764). Les analyses polliniques ont révélé qu'il y avait abondance de Cupressaceae (Juniperus) et de Pinus. Les grains de pollen d'arbustes et d'herbacées comprennent Artemisia, Fabaceae, Poaceae et Asteraceae. Les principaux macrofossiles de végétaux étaient des feuilles de Juniperis scopulorum, des aiguilles de Pseudotsuga menziesii, des graines de Chenopodiaceae, des épines de Rosa et des folioles d'Artemisia. Les restes de trois genres de coléoptères (Cryptophagus, Lathridius et Enicmus) représentent les insectes qui vivaient probablement dans les amoncellements, se nourrissant de la matière organique en décomposition ou des moisissures. Les restes de Limonius proviennent probablement du sol environnant ou des végétaux. Le site de Bull Canyon renferme un amoncellement qui date de 700 \pm 80 BP (WAT-1765). Les assemblages de pollen et de végétaux ressemblent à ceux du site d'Oregon Jack Creek. Les matières fécales du rat à queue touffue offrent de nouvelles possibilités de reconstitution des paléoenvironnements de l'Holocène de la région intérieure aride de la Colombie-Britannique, un peu comme c'est déjà le cas dans le sud des États-Unis.

ZUSAMMENFASSUNG Pollen, Pflanzen-Makrofossile und insekten von fossilen Waldrattenfäkalien in British Columbia. Ratten mit buschigem Schwanz (Neotoma cinerea) findet man oft in den Klippen, Schutthalden und Höhlen in den offenen Pseudotsuga menziesii und Pinus ponderosa Wäldern im ganzen Innern von British Columbia. Fosile N. cinerea Fäkalien von zwei Plätzen in Zentral British Columbia wurden mit Radiokarbon datiert und auf Pollen, pflanzliche Makrofossile und Insektenspuren untersucht. Der Platz Jack Creek in Oregon enthält einen Fäkalienfund, der auf 1150 ± 80 (WAT-1764) Radiokarbonjahre v.u.Z. datiert wird. Die Pollenanalysen enthüllen eine Fülle von Cupressaceae (Juniperus) und Pinus. Buschund Graspollenarten schliessen Artemisia, Fabaceae, Poaceae und Asteraceae ein. Blätter von Juniperus scopulorum, Nadeln von Pseudotsuga menziesii, Samen von Chenopodiaceae, Dornen von Rosa und Blättchen von Artemisia sind die hauptsächlichen Pflanzenmakrofossile. Die Reste von drei Käferarten, Cryptophagus, Lathridius und Enicmus repräsentieren Insekten, die möglicherweise in den Fäkalien lebten und verwesendes organisches Material oder Schimmel assen. Limonius-Reste wurden wahrscheinlich in die Fäkalien von nahegelegenem Erdreich oder Pflanzenmaterial gebracht. Der Platz Bull Canyon enthält Fäkalien, die auf 700 ± 80 (WAT-1765) Jahre v.u.Z. datiert werden. Pollen- und makrofossile Pflanzenansammlungen sind denen des Jack Creek-Platzes von Oregon ähnlich. Fäkalien von Waldratten liefern eine neue Dimension bei der Rekonstruktion der Paläoumwelt im Holozän im trockenen Innern von British Columbia, ganz in derselben Weise, wie sie das schon im Südwesten der Vereinigten Staaten tun.

INTRODUCTION

Studies of biotic remains in fossil middens of Bushy-tailed woodrats, *Neotoma cinerea* Say and Ord., from the southwest United States have revealed much about the vegetation and environmental history of that area (e.g. Spaulding *et al.*, 1983; Davis and Anderson, 1987; Van Devender *et al.*, 1987). The geographic range of this mammal, however, extends far beyond the southwest United States (Escherich, 1981). The climate of much of this range is too moist to preserve amberat (dehydrated and crystalized woodrat urine) in the middens. However, the climate of the dry interior of southern British Columbia is conducive to midden preservation. We report the first results of studies on pollen, plant macrofossils and insect remains in *neotoma cinerea* middens from two widely separated sites in British Columbia and discuss their potential for paleoenvironmental reconstructions in western Canada.

REGIONAL SETTING AND STUDY SITES

South central British Columbia (Fig. 1) has a hot and dry climate at low elevations, comparable to that of the intermontane Great Basin areas of the United States. Mean annual precipitation is less than 30 cm and mean daily July temperatures are greater than 20°C throughout much of the area (Research Branch, Ministry of Forests, 1988). Vegetation at lower elevations falls into three Biogeoclimatic Zones (Research Branch, Ministry of Forests, 1988):

- 1. Bunchgrass Zone This zone is dominated by bunchgrasses, especially bluebunch wheatgrass (*Agropyron spicatum*) in undisturbed sites, and big sagebrush (*Artemisia tridentata*) in very dry sites. Douglas-fir (*Pseudotsuga menziesii*) and Ponderosa pine (*Pinus ponderosa*) occur in draws.
- 2. Ponderosa Pine Zone Included here are open forests of ponderosa pine with Douglas-fir on cooler moist sites. There is an understory of bluebunch wheatgrass, rough fescue (Festuca scabrella) and herbs.
- 3. Interior Douglas-fir Zone Douglas-fir predominates and lodgepole pine (*Pinus contorta*) grows in burned areas. The understory consists of soopolallie (*Shepherdia canadensis*), kinnikinnick (*Arctostaphylos uva-ursi*), pine grass (*Calamagrostis rubescens*) and feather moss (*Hylocomium splendens*).

Numerous cliffs and rock faces provide suitable habitats for *N. cinerea*. Notable are the many crevices, rock overhangs and caves developed in the Upper Paleozoic limestones of the Marble Range and the Tertiary basalts of the Interior Plateau (Holland, 1976). Well-developed talus deposits are associated with the rock faces. Cliff faces and upper parts of the talus deposits often bear a distinctive open vegetation characterized by *Juniperus scopulorum*, grasses and herbs, and are often occupied by *N. cinerea*. Both study sites, Oregon Jack Creek and Bull Canyon (Figs. 2,3), occur at the base of such cliffs immediately above talus slopes. During historic times *N. cinerea* has moved into outbuildings and abandoned buildings.

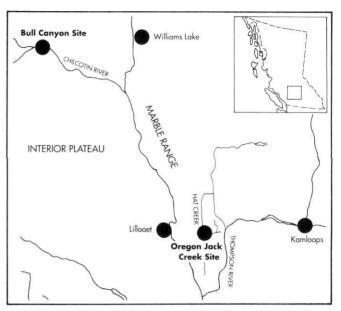


FIGURE 1. Location of the study site. Localisation de la région à l'étude.

OREGON JACK CREEK SITE

This study site is located in a small east-west trending, midelevation valley in the northeast corner of the Thompson Plateau physiographic unit of British Columbia (Holland, 1976). The valley cuts through Paleozoic limestone rocks and joins the main Thompson River Valley and the upper end of Hat Creek Valley (Fig. 1).

Near the study site, the Oregon Jack Creek Valley is narrow, with a relatively flat floor bounded by steep limestone cliffs and slopes. The rolling terrain of the valley floor is underlain by glacial deposits and covered by small lakes and ponds. Talus covers lower slopes, giving way to precipitous vertical and nearly vertical faces with relief nearly 400 m.

The vegetation is complex because of the variable topography and exposure. The site area fits predominantly into the Douglas-fir Biogeoclimatic zone, with open Pseudotsuga forests. Steep slopes support open plant communities having affinities with the Ponderosa Pine Biogeoclimatic Zone. Grasslands of the Bunchgrass Biogeoclimatic Zone occur within one kilometre of the study site and predominate in the nearby Hat Creek Valley. The sample site occurs at 1200 m a.s.l., and occupies a small rock shelter at the juncture of limestone bluffs and a short talus slope (Fig. 2). The lower part of the talus slope bears an open Pseudotsuga forest with sparse herbs and shrubs. On the upper part of the talus slope there are scattered Pseudotsuga trees and many individuals of Juniperus scopulorum. The predominant plant assemblage on the upper slope consists of thickets of Prunus virginiana with smaller shrubs such as Symphoricarpos and Rosa. The herbaceous stratum includes Galium sp., Chenopodium sp., Descurainia and grasses. Stunted trees, shrubs and herbs grow on cliffs. Plants growing on the cliffs near the midden include: Artemisia frigida, Potentilla sp., Phacelia hastata, Penstemon fruiticosus and Rosa woodsii.

^{1.} Plant nomenclature follows Taylor and MacBryde (1977).

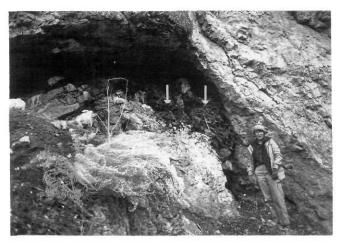


FIGURE 2. Oregon Jack Creek study site showing stick nest and amberat cemented midden (arrows).

Le site d'Oregon Jack Creek où l'on observe un nid fait de bouts de bois et un amoncellement de matières fécales consolidé avec de l'urine séchée (flèches).



FIGURE 3. Bull Canyon study site in cave at base of cliffs and adjacent grassland vegetation.

Le site de Bull Canyon dans une caverne sise au pied des escarpements et près de la prairie.

BULL CANYON SITE

The Bull Canyon site is located 80 km west of Williams Lake on the north face of an east-west trending valley. Here, the Chilcotin River has cut a steep-sided, deep and narrow canyon into Tertiary basalts of the Fraser Plateau (Holland, 1976). The canyon bottom is at 700 m a.s.l. and relatively flat. In most parts of the canyon, small hills of glacial sediments form the transition from valley bottom to slopes. Talus deposits underlie much of the lower slopes and grade into vertical basalt cliffs or steep bedrock slopes. The top of the plateau in this area is at about 940 m.

The vegetation in and around Bull Canyon is classified within the Interior Douglas-fir Biogeoclimatic zone (Research Branch, Ministry of Forests, 1988). However, numerous fires have encouraged successional *Pinus contorta* stands to cover much of the area, especially on the plateau. South-facing slopes and knolls in the valley are covered by patches of grassland with floristic affinities to the Bunchgrass Biogeoclimatic zone. The northwestern limit of this zone is about 30 km eastward of the study site in the valley of the Chilcotin River.

The midden sample was collected about 800 m a.s.l. from a small cave at the base of basalt cliffs, and at the top of the talus slope (Fig. 3). Below the cave a long, steep talus slope extends toward the valley bottom. Vertical cliffs rise nearly 150 m above the top of the talus.

The talus slope adjacent to the sample site consists of a grass-sagebrush community dominated by *Agropyron spicatum* and *Artemisia frigida*. Annual species, mainly members of the Chenopodiaceae, occur among the grass clumps. *Pseudotsuga* woodland begins about 50 m downslope from the cliff base. *Juniperus scopulorum* grows abundantly as a stunted tree or shrub in the transition between woodland and grass vegetation. Scattered *Rosa* and *Rubus* shrubs hug the base of the cliff. *Urtica dioica* patches occasionally occupy moist shaded spots. The vertical cliffs above the sample site are mostly unvegetated.

METHODS

FIELD PROCEDURES

Samples were collected by chipping away chunks of consolidated plant debris, faecal pellets and amberat from the main midden masses. The samples included the full thickness of the deposit at both sites, usually ranging from 5 to 10 cm.

LABORATORY PROCEDURES

Fresh midden samples were divided into four subsamples for pollen and macrofossil analysis, and for radiocarbon dating. Two subsamples of fresh midden material intended for pollen analysis were first soaked in hot water overnight, teased apart with a stirring rod, then passed through a 2 mm screen to remove large fragments. The residue was washed several times in water by decantation, and then treated according to the standard acetolysis method (Faegri and Iversen, 1975). The pollen concentrate was mounted in a glycerin jelly on glass slides and examined through a Nikon Biophot microscope. Pollen grains were counted and identified with the aid of a reference collection at the Royal British Columbia Museum and standard keys (e.g. McAndrews et al., 1973).

A bulk sample of midden material from each site was submitted to the University of Waterloo Radiocarbon Laboratory for dating. The dates are corrected for isotopic fractionation and are given to one sigma error.

For macrofossil analysis, a sub-sample of intact midden material was weighed, then soaked in water for several days to disaggregate plant material. Each sample was washed clean of rehydrated urine and fine detritus on a 250 μ m sieve with a gentle jet of tap water. All identifiable plant and insect fragments were picked out under a binocular microscope. Plant identifications were made with the aid of local floras and collections in the herbaria of the University of Waterloo and the Royal British Columbia Museum.

RESULTS AND INTERPRETATION

AGE OF THE MIDDENS

Radiocarbon dates were: $1150 \pm 80 \ (WAT-1764)$ on the Oregon Jack Creek material and $700 \pm 80 \ (WAT-1765)$ on the Bull Canyon material. These are the first radiocarbon dates on woodrat middens in Canada and confirm the fossil status of the deposits. Midden deposits in British Columbia rarely occur as thick and regular deposits. We assume that each midden sample under study must be dated.

POLLEN

Pollen assemblages from both middens are dominated by arboreal types (Table I). Two subsamples from the Oregon Jack Creek midden contained abundant *Juniperus* (Cupressaceae) and *Pinus* pollen whereas Bull Canyon samples contained about 50% *Juniperus* pollen and little *Pinus* pollen. *Pseudotsuga* pollen occurs in significant quantities in Oregon Jack Creek samples, but does not occur in Bull Canyon samples.

Non-arboreal pollen types are abundant in material from both localities. *Artemisia* pollen occurs in relatively high percentages especially in one sample from Bull Canyon (34.7%). Fabaceae pollen is exceptionally abundant. Notable also is the relatively high percentage of Rosaceae pollen in Bull Canyon

middens, and the occurrence of *Linum perenne* pollen at Bull Canyon.

Pollen assemblages only partly reflect the species present at study sites today. The abundance of Cupressaceae pollen at both sites is notable because it confirms observations, made far to the south, of the overrepresentation of this pollen type in middens (Thompson, 1985). *Juniperus scopulorum* is an abundant species at both sites. Although pine pollen is well represented at Oregon Jack Creek, it is poorly represented at Bull Canyon. *Pinus contorta* grows abundantly near both middens, but especially so on the plateau surface above Bull Canyon. Low relative percentages can be expected based on poor representation of regional types, especially pine, as observed in the southwest United States (Thompson, 1985). Still, the exceptionally low values at Bull Canyon raise the question whether the vegetation was significantly different from that of today.

Pseudotsuga values pose another interesting question. At Oregon Jack Creek, Pseudotsuga trees grow tens of metres distant and their pollen is well represented in samples. At Bull Canyon Pseudotsuga trees grow a little farther away from the site than at Oregon Jack Creek, but a large tree grows only 20 m distant at the base of the cliff. Surprisingly, no pollen is recorded in the midden samples although needles are abundant (Table II). We have observed chewed Pseudotsuga

TABLE I

Pollen and spore percentages of two Bushy-tailed Woodrat middens from Oregon Jack Creek and Bull Canyon study sites, British Columbia

	Oregon Jack Creek	Oregon Jack Creek	Bull Canyon	Bull Canyo
Sample #	# 1	# 2	# 1	# 2
Pollen or Spore type				
Pinus	15.0	33.0	4.5	2.3
Picea	0.3	2.3	_	
Abies	1.0	2.3	_	_
Tsuga heterophylla	-	0.7	-	_
Pseudotsuga	2.3	6.3	-	-
Cupressaceae	38.6	22.0	47.9	54.7
Alnus		2.7	-	0.3
Betula	_	0.3	-	_
Salix	1.3	_	0.3	,
Ericaceae	-	-	0.9	0.3
Rosaceae	0.7	_	4.5	4.3
Poaceae	3.0	3.0	1.2	1.3
Asteraceae Tubuliflorae	2.0	3.3	1.8	_
Artemisia	8.6	17.0	14.8	34.7
Chenopodiaceae-Amaranthaceae	0.7	1.3	_	1.3
cf. Brassicaceae	-0	_	1.5	_
Fabaceae -1	22.0	1.3	12.0	_
Fabaceae -2	-	_	0.9	_
Apiaceae	-	0.7	0.3	_
Galium type	0.7	_	_	_
Linum perenne	-	-	1.2	-
Monolete Fern spores	0.7	0.7	2.4	_
Equisetum	_	_	0.6	-
Unknown	3.0	3.0	5.1	0.7
Total Pollen and Spores	300	300	332	300

TABLE II

Plant macrofossils of two Bushy-tailed Woodrat midens from Oregon
Jack Creek and Bull Canyon study sites, British Columbia

	Oregon Jack Creek ²	Bull Canyon ³
TREES		
Pinaceae seed wings	1	_
cf. Pseudotsuga	4	_
Pseudotsuga microphyll	1	1-1
P. menziesii needles	15	29
Pseudotsuga cone bracts	1	1
Pseudotsuga cone and branch	1	_
Pseudotsuga immature cones	1	_
Betula papyrifera-type	1	-
SHRUBS ¹		
Juniperus scopulorum strobili	-	2
J. scopulorum staminate cone	_	1
J. scopulorum leaf fragments	14	26
J. scopulorum	1	1
Taxus brevifolia	_	1
Arctostaphylos uva-ursi	1	1
Cornus sericea	2	_
Rubus parviflorus-type	1	-
Rosa thorns	9	_
Artemisia leaflets	15	12
HERBS ¹		
Poaceae florets/seeds	3	7
Rumex/Polygonum	1	_
Chenopodiaceae	17	11
Chamaesyce serpyllifolia	-	1
Lappula redowskii-type	-	1
Ranunculaceae inflorescence	-	1
Potentilla diversifolia-type	=	1
Unidentifiable inflorescences	=	2

¹ Seeds unless otherwise specified

branchlets in woodrat nests. The absence of the pollen may relate to foraging habits of *Neotoma*; in that only the lower non-pollen bearing branchlets are dragged in. Similar underrepresentation of *Pseudotsuga* pollen was noted in a Late Pleistocene midden from Canyon de Chelly in northeastern Arizona (Betancourt and Davis, 1984). Further field observations are needed to test this hypothesis.

The non-arboreal component is diverse and includes high percentages of pollen types rarely encountered in lake or wetland sediments. *Artemisia frigida* grows very near both sites and parts of the plant are collected by *Neotoma*. The percentages are consistent with local abundance of *Artemisia*. In the southwest United States *Artemisia* is often well represented in middens (Thompson, 1985). At both sites Fabaceae pollen is very abundant in only one of two midden samples. The pollen may belong to an *Astragalus* species, possibly *Astragalus miser*, which is a common plant on dry talus slopes. The differential occurrence of such a pollen type in the same midden

or from one midden to another of the same age can be expected (Thompson, 1985: Davis and Anderson, 1987).

The near absence, in comparison to relative abundance, of Rosaceae pollen from Oregon Jack Creek and Bull Canyon sites respectively is noteworthy. This observation is particularly interesting since *Rosa* thorns are abundant in the Oregon Jack Creek midden (Table II). Today Rosaceae are abundant near both sites; *Prunus virginiana* at Oregon Jack Creek and *Rubus* sp. at Bull Canyon. *Prunus virginiana* forms thickets only 10-20 m away from the midden site at Oregon Jack Creek. This shrub may not have been present nearly 1000 years ago since *Prunus* pits often occur in southwest United States middens (e.g. Phillips, 1977).

The recovery of the distinct pollen of *Linum perenne* reveals that this herb grew near the Bull Canyon midden site (Fig. 4). Today, the plant is abundant several hundred metres away on the valley floor but was not noted on the slope adjacent to the site. Its occurrence is surprising since the plant produces little pollen and is insect pollinated. Presumably woodrats collected stems and brought them into middens.

MACROSCOPIC PLANT REMAINS

A total of 14 taxa of vascular plants were identified from the two sites, with tree and shrub taxa being the most common. Most of the plant taxa found in the middens represent plants growing within a fifty metre radius of midden deposits. The abundance of fossil remains of Pseudotsuga menziesii, Juniperus scopulorum (Fig. 5a), Rosa (Fig. 5b), and Artemisia reflect the abundance of these plants in close proximity to the cave, and the availability of this material for nest-building. It is possible that seeds of plants such as P. menziesii, J. scopulorum, Arctostaphylos uva-ursi (Fig. 5c), Poaceae (Fig. 5d), Rumex/Polygonum, Chenopodiaceae (Fig. 5c), Lappula redowskii-type (Fig. 5f), and Potentilla diversifolia-type could represent nearby food sources. The single seed of Taxus brevifolia is interesting because the species does not grow near the site today. This shrub is more characteristic at higher elevations and could represent long-distant transport by birds. Further work on foraging habits and nest-building habits of the woodrats in this region is needed to make more detailed paleoenvironmental interpretation of plant macrofossils in middens.

INSECTS

Oregon Jack Creek midden material contained the remains of beetles in at least four genera in three families: Cryptophagus varus Woodruff and Coombs in the Cryptophagidae (Silken Fungus Beetles), Lathridius sp. and Enicmus mimus Fall in the Lathridiidae (Minute Brown Scavenger Beetles) and Limonius sp. in the Elateridae (Click Beetles).

Cryptophagus is a large genus, with at least 40 species recognized in North America (Woodroffe and Coombs, 1961). They apparently feed on fungi and are found in macro-fungi as well as in places where moulds grow, such as in decomposing organic matter, bird and mammal nests, stored food products, and under tree bark (Woodroffe and Coombs, 1961). C. varus is recorded from southern British Columbia south to

² Number per 41.5 gm dry, unprocessed midden

³ Number per 78.5 gm dry, unprocessed midden

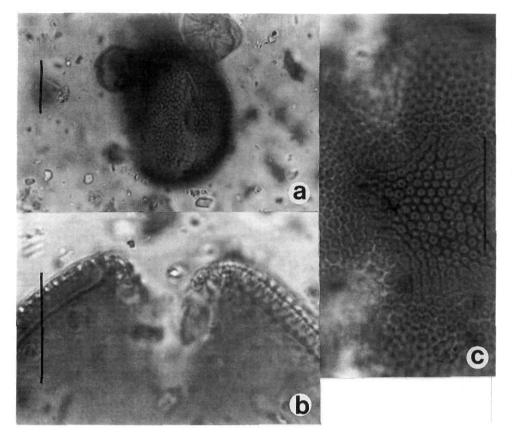


FIGURE 4. Light micrographs of Linum perenne pollen recovered from woodrat midden. a) Equatorial view of entire grain; b) optical section of pore; c) polar surface. Scale bar represents 20 µm.

Micrographes du pollen de Linum perenne recueilli dans les matières fécales du rat à queue touffue. a) vue équatoriale du grain; b) coupe optique d'un pore; c) surface des pores. Échelle verticale = 20 μm.

Utah, east to southern Manitoba and Michigan. Woodroffe and Coombs (1961) detail the records, including several from grain elevators, one from a pocket gopher (*Thomomys talpoides fuscus*) burrow near Ukiah, Oregon, and one from a "pack rat nest" in Logan Cave, Logan Canyon, Utah (type locality).

Members of the Lathridiidae also feed on moulds, and some adults have been found in conjunction with mycetozoan fruiting bodies. They are found on coniferous trees, in adjacent herbage, in plant debris, mammal nests, and in various stored plant products (Hatch, 1961). Although they are sometimes considered pests of such stored products, their presence is usually an indication of improper storage resulting in the growth of mould (Walkley, 1952). Enicmus mimus Fall has been raised from Pinus contorta and P. ponderosa. It ranges from southern British Columbia to Idaho and eastern Oregon. At least five species of Lathridius occur in British Columbia, two of which are probably introduced. One of the latter, the cosmopolitan L. minutus L., is widespread in the province, and has been reared from a wide variety of native trees such as Abies lasiocarpa, Picea engelmanni, Pinus contorta, P. monticola and P. ponderosa (Hatch, 1961). The unidentified specimen in the midden sample is probably either the common L. crenatus LeC., which ranges from southern British Columbia to Idaho and Oregon. or L. protensicollis Mann., which is widespread from Alaska south to California and Utah. Both have been collected in woodrat nests in Oregon (Hatch, 1961).

The Elateridae might not be expected to occur in woodrat middens; the larvae (wireworms) live mainly in soil and feed on plant roots and stems. Adults are common on foliage of all sorts, however, and may be found in rotting wood. *Limonius*

is a large genus containing many agricultural pests. The specimen collected is too decomposed for specific identification.

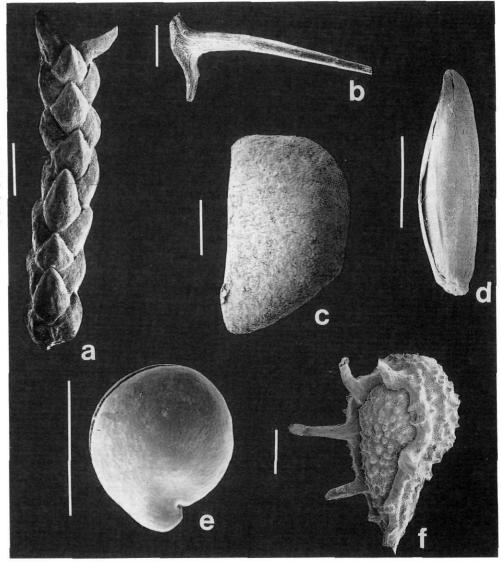
DISCUSSION AND CONCLUSIONS

Our results clearly reveal the potential of N. cinerea middens from interior British Columbia as a rich source of fossil material for the reconstruction of past environments. As in studies from the southwest United States, pollen and macrofossil remains within the middens reflect plant species growing today in the vicinity of the midden sites. There are, however, inconsistencies between the abundance of some species, notably Pinus and Pseudotsuga, and the amount of their pollen in the midden samples. Since we know little about N. cinerea behavior in British Columbia, particularly its plant collecting habits, it is premature to try to make much of the results in terms of environmental reconstruction. Nonetheless, one observation is that dry habitat taxa are much better represented than in traditional lake-core sites. For example, Oregon Jack Creek middens contain proportionately much more Artemisia and Juniperus pollen than do samples of the same age from Finney Lake in nearby Hat Creek Valley (Hebda, 1983). Consequently, the study of middens provides a method of completing environmental reconstructions of that part of the landscape not accessible by traditional lake-core studies.

Our analysis of insect remains is an innovation as far as paleoenvironmental studies in southern interior British Columbia are concerned. Insect remains may provide added information for understanding and reconstructing paleoenvironments of arid habitats. Various insects and related arthropods

FIGURE 5. Scanning electron micrographs of selected plant macrofossils recovered from the middens. a) *Juniperus scopulorum* branch; b) *Rosa* thorn; c) *Arctostaphylos uva-ursi* seed; d) Poaceae seed; e) Chenopodiaceae seed; f) *Lappula redowskii*-type seed. Scale bar represents 1 μm.

Micrographes de quelques macrofossiles de végétaux recueillis dans les matières fécales: a) branche de Juniperus scopulorum; b) épine de Rosa; c) graine d' Arctostaphylos uva-ursi; d) graine de Poacea; e) graine de Chenopodiaceae; f) graine du type Lappula redowskii. Échelle verticale = 1 μm.



(e.g. mites and ticks) can be expected in association with woodrat nests and middens, especially those forms living on decaying vegetable matter, fungi, animal carcasses, or on the living animals themselves. Fleas (Siphonaptera) and lice (Phthiraptera) are seldom collected away from the host species, but dead specimens or parts of these insects could be preserved in fossilized middens. Most material, however, would be expected from the Orders Lepidoptera (some moth larvae), Diptera (various families of true flies feeding on decaying organic material), and Coleoptera (beetles). Beetles would predominate because of the large number of taxa potentially inhabiting such substrates, and because their rugged exoskeletons preserve well.

In brief, we make the following conclusions from our preliminary study of woodrat middens:

- 1. Pollen grains and macrofossils are well-preserved, and represent diverse assemblages in British Columbia *N. cinerea* middens.
- 2. *N. cinerea* pollen assemblages record species that grow near the midden sites today but there are significant inconsistencies between past and modern communities.

- 3. The relative representation of some pollen types such as Cupressaceae, *Pinus* and *Artemisia* conforms to observations on pollen dispersal and representation in middens from the southwest United States.
- 4. There are several types of pollen such as *Pinus* and *Pseudotsuga* whose abundance varies significantly from the expected, based on local modern vegetation. These differences may be the result of changes in vegetation, or of different foraging preferences of *N. cinerea* over the past 1000 years or so.
- 5. Fossil woodrat middens in British Columbia contain a wellpreserved and diverse collection of macroscopic plant remains representative of nearby vegetation.
- Fossil insects are present also in the middens of British Columbia; they reveal an associated scavenger insect fauna often characteristic of woodrat middens.
- 7. Much more research needs to be undertaken on modern *N. cinerea* foraging ecology and nest-building habits in British Columbia in order to better interpret biotic remains found in fossil middens. Future research on woodrats and middens should

add much to the understanding of the environmental history of arid habitats in south-central British Columbia.

ACKNOWLEDGEMENTS

We thank Bob Powell, Ministry of Municipal Affairs, Culture and Recreation, and Colin McKean, Ministry of Environment, Province of British Columbia for help in the field. T. C. Brayshaw and Leon Pavlick assisted with plant identifications. Dr. 1. Bousquet (Cryptophagidae, Lathridiidae) and E. Becker (Elateridae) of the Biosystematics Research Centre, Agriculture Canada, Ottawa, identified insect specimens. Ramon Aravena of the University of Waterloo provided radiocarbon dates. David Nagorsen, Royal British Columbia Museum kindly reviewed an early draft of the manuscript and provided the photograph of the Oregon Jack Creek site.

Radiocarbon dating and plant macrofossil analyses were supported by an Operating Grant from the Natural Sciences and Engineering Research Council of Canada to B. G. Warner, for which we are grateful. Finally, we thank Dr. O. K. Davis and an anonymous reviewer for their useful comments.

REFERENCES

- Betancourt, J. L. and Davis, O. K., 1984. Packrat middens from Canyon de Chelly Northeastern Arizona: Paleoecological and Archaeological implications. Quaternary Research, 21: 56-64.
- Davis, O. K. and Anderson, R. S., 1987. Pollen in packrat (*Neotoma*) middens: pollen transport and the relationship of pollen to vegetation. Palynology, 11: 185-198.
- Escherich, P. C., 1981. Social biology of the Bushy-tailed woodrat, Neotoma cinerea. Museum of Vertebrate Zoology, University of California, Publications in Zoology, 110: 1-132.
- Faegri, K. and Iversen, J., 1975. Textbook of Pollen Analysis. 2nd edition. Hafner, New York, 295 p.
- Fulton, R. J., Warner, B. G., Kubiw, H. J. and Achard, R. A., 1989. Geology and paleoecology of Early Holocene lacustrine deposits in the Columbia River Valley near Fauquier, southern British Columbia. Canadian Journal of Earth Sciences, 26: 257-265.

- Hatch, M. H., 1961. The Beetles of the Pacific Northwest. Part III: Pselaphidae and Diversicornia I. University of Washington Press, Seattle, 503 p.
- Hebda, R. J., 1983. Postglacial history of grasslands of southern British Columbia and Adjacent Regions, p. 157-191. In A. C. Nicholson, A. McLean and T. E. Baker, ed., Grassland Ecology and Classification Symposium Proceedings. Ministry of Forests, Victoria.
- Holland, S. S., 1976. Landforms of British Columbia. British Columbia Department of Mines Bulletin 48, 1-138.
- McAndrews, J. H., Berti, A. A. and Norris, G., 1973. Key to Quaternary Pollen and Spores of the Great Lakes Region. Royal Ontario Museum, Life Sciences Miscellaneous Publication, 61 p.
- Phillips, A. M., 1977. Packrats, Plants and the Pleistocene in the Lower Grand Canyon. Ph.D. Thesis, University of Arizona, Tucson, 123 p.
- Research Branch, Ministry of Forests, 1988. Biogeoclimatic Zones of British Columbia 1988. Map, Research Branch, Ministry of Forests, Victoria.
- Spaulding, W. G., Leopold, E. B. and Van Devender, T. R., 1983. Late Wisconsin paleoecology of the American Southwest, p. 259-293. In S. C. Porter, ed., Late Quaternary environments of the United. States, the Late Pleistocene. University of Minnesota Press, Minneapolis, 407 p.
- Taylor, R. L. and MacBryde, B., 1977. Vascular plants of British Columbia: A descriptive resource inventory. University of British Columbia Press, Vancouver, 754 p.
- Thompson, R. S., 1985. Palynology and Neotoma middens. American Association of Palynologists, Contributions Series, 16: 89-112.
- Van Devender, T. R., Thompson, R. S. and Betancourt, J. L., 1987.
 Vegetation history of the deserts of southwestern North America;
 The nature and timing of the Late Wisconsin-Holocene transition,
 p. 323-352. In W. F. Ruddiman and H. E. Wright, eds., The geology of North America, North America and the adjacent oceans during the last deglaciation. Geological Society of America, Boulder, Colorado, 501 p.
- Walkley, L. M., 1952. Revision of the Lathridiini of the State of Washington. Proceedings Entomological Society of Washington, 54: 217-235.
- Woodroofe, G. E. and Coombs, C. W., 1961. A revision of the North American *Cryptophagus* Herbst (Coleoptera: Cryptophagidae). Miscellaneous Publications, Entomological Society of America, 2: 177-211.

APPENDIX

NOTES ON MACROFOSSIL IDENTIFICATIONS

- Betula papyrifera-type. Samara with wings at least as wide as nutlet and persistent stigmas. May include B. occidentalis, B. papyrifera, and B. neoalaskana.
- Juniperus scopulorum leaf and branch fragments. Leaves are linear, obtuse or acute, appressed or slightly ascending, arranged in twos, with entire margins.
- Taxus brevifolia. Seeds are elliptic-round in shape with a flattened, truncated base and a pointed apex, at least 4 mm long, smooth-slightly roughened surface.
- Rubus parviflorus-type. See Fulton et al. (1989).

- Chenopodiaceae. Seeds are round, black, shiny, and smooth.
- Chamaesyce serpyllifolia. Seeds obovate, triangular in cross-section, smooth or wrinkled.
- Lappula redowskii-type. Nutlets with well-developed ventral keel and armed with prickles arranged on dorsoventral margin.
- Potentilla diversifolia-type. Achenes not prominently ridged but may have some indistinct ridges, scar of style base at or above middle, subterminal. May include P. diversifolia, P. glandulosa, P. hyparctica, and P. rivalis.