

PALEOENVIRONMENTAL INTERPRETATIONS OF HOLOCENE INSECT FOSSIL ASSEMBLAGES FROM THE LA POUDRE PASS SITE, NORTHERN COLORADO FRONT RANGE

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ABSTRACT

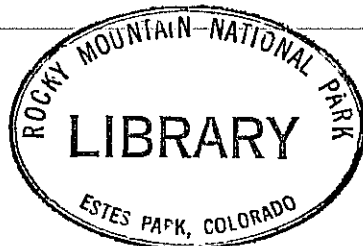
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A sequence of peats from the La Poudre Pass site, northern Front Range, Colorado Rockies, yielded abundant insect fossil assemblages. Studied intervals ranged in age from nearly 10 000 yr B.P. to about 5400 yr B.P. Seventy named insect taxa were extracted from the peat. Among these are a mixture of aquatic and terrestrial species. Several taxa from the lowest 10 cm are indicative of climatic conditions found today in montane forest regions, although conifers were probably not present at the site until several centuries after the initiation of peat deposition. Later insect assemblages contain a mixture of both tundra and forest faunal elements, suggesting the close proximity of altitudinal tree limit to the site from about 9500 yr B.P. through the uppermost level studied (5400 yr B.P.).

INTRODUCTION

La Poudre Pass is a col on the continental divide at the northern end of the Front Range in Colorado (Fig.1). The pass (altitude about 3103 m) separates the Colorado River on the southwest from La Poudre Pass Creek (also known as Long Draw Creek), which is a tributary of the Cache La Poudre River. During the Pinedale Glaciation, La Poudre Pass was ice filled, and this ice flowed into the Cache La Poudre and Colorado River valleys, feeding two of the largest glaciers in the Front Range region (Madole, 1980). Ice stagnated and downwasted during Pinedale deglaciation, developing kame and kettle topography. The Grand River ditch, constructed across La Poudre Pass, along with the channel of La Poudre Pass Creek, exposed peat overlying stratified drift (gravelly sand). Radiocarbon ages from La Poudre Pass peats have provided valuable evidence in the deglaciation chronology of the

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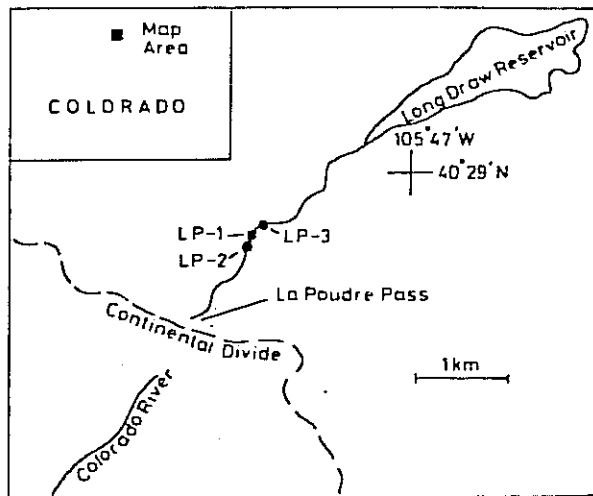


Fig.1. Map of the La Poudre Pass region, showing Madole's (1980) LP-1 and LP-2 sites, and the insect fossil site, LP-3.

northern Front Range, revealing that the culmination of the late stage of the Pinedale Glaciation in this region occurred more than 10 000 years ago (Madole, 1980). These radiocarbon dates, from the base of the La Poudre Pass peat, provide a minimum age of deglaciation. This investigation was undertaken to produce the first paleoenvironmental information on the site, based on fossil insects and peat stratigraphy.

Madole (1980) sampled basal peat overlying stratified drift from two sites along the Grand River ditch. These sites were designated LP-1 and LP-2 (Fig.1), and yielded radiocarbon ages of 9850 yr B.P. (base of LP-1), 9800 yr B.P. (just above the base of LP-1) and 8610 yr B.P. (base of LP-2). Madole (1980) noted that field relations between the two sites gave no cause to anticipate an age difference of 1000 years. A site a few meters away from LP-1 and LP-2 was sampled by the author for fossil insect study (LP-3). This site (Figs.1 and 2) was chosen for study not only because of the importance of the La Poudre Pass region in deglaciation chronology, but also because of the presumed sensitivity of the site to climatic change. The site lies in the forest-tundra ecotone. A major climatic change in the Rocky Mountain region during the interval of peat accumulation should be recorded in the flora and fauna of the site.

METHODS

A 1.54 m column of peat was sampled at the La Poudre Pass site, LP-3 (Fig.2). Blocks of peat, approximately ten cm deep, fifteen cm wide and fifteen cm long, were cut from the cleaned face of the peat bank, wrapped in plastic and aluminum foil, and transported to the Institute of Arctic and

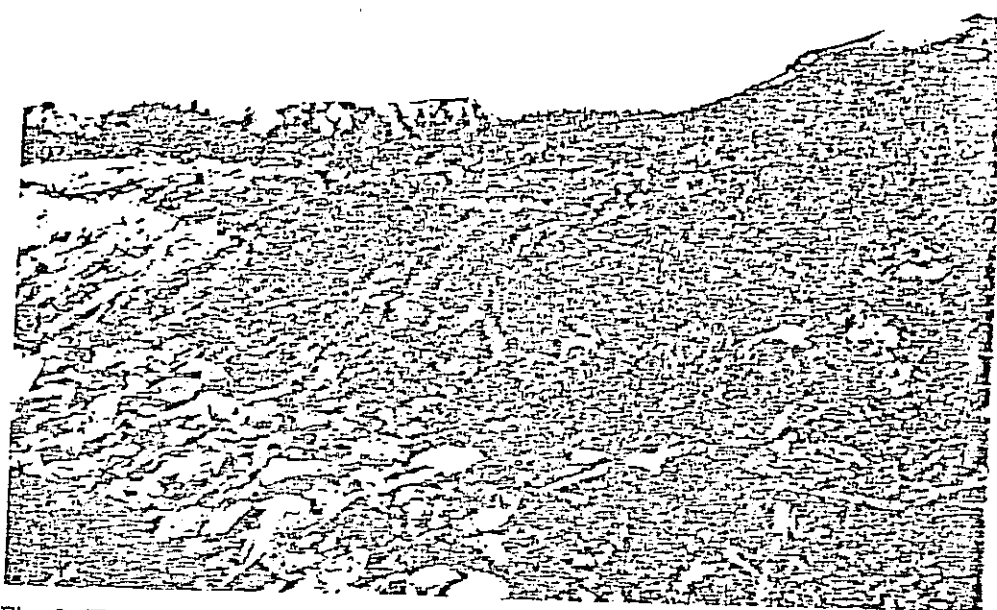


Fig. 2. The LP-3 site, looking northwest. Photograph taken just prior to sampling for insect fossils. Peat bank is approximately 1.6 m in height.

Alpine Research, University of Colorado, Boulder, for analysis. Peat blocks representing the levels 0.57–1.54 m were sampled at five or six cm intervals. The cut blocks of peat were soaked in 5% NaOH solution to aid disaggregation, then washed in a 300- μ m mesh sieve. The washed residue was then subjected to the kerosine flotation method (Coope, 1968) to concentrate and isolate the insect fossil fragments from the plant residue.

The fossils were sorted in alcohol under low power stereo binocular microscope. Identifiable insect fragments were either mounted with gum tragacanth on modified micropaleontology cards (more robust specimens), or stored in vials of alcohol. Caddis (Trichoptera) larval fragments were mounted on glass slides in Polyvinyl lactophenol medium. Fig. 3 is a summary of the stratigraphy of the LP-3 site peat monolith.

PEAT STRATIGRAPHY

The lowest fifteen cm of the peat (overlying sandy gravel) was well humified and contained upwards of twenty percent sand, silt and clay. *Picea* needles were found in all intervals from the 1.44 m level upwards. The levels 0.54–1.38 m were poorly humified peat. The principal plant macrofossil throughout the peat was *Carex* spp., and the seeds of aquatic vegetation were very common in all levels. A radiocarbon age of at least 9850 yr B.P. is correlated for the base of LP-3, based on the close proximity

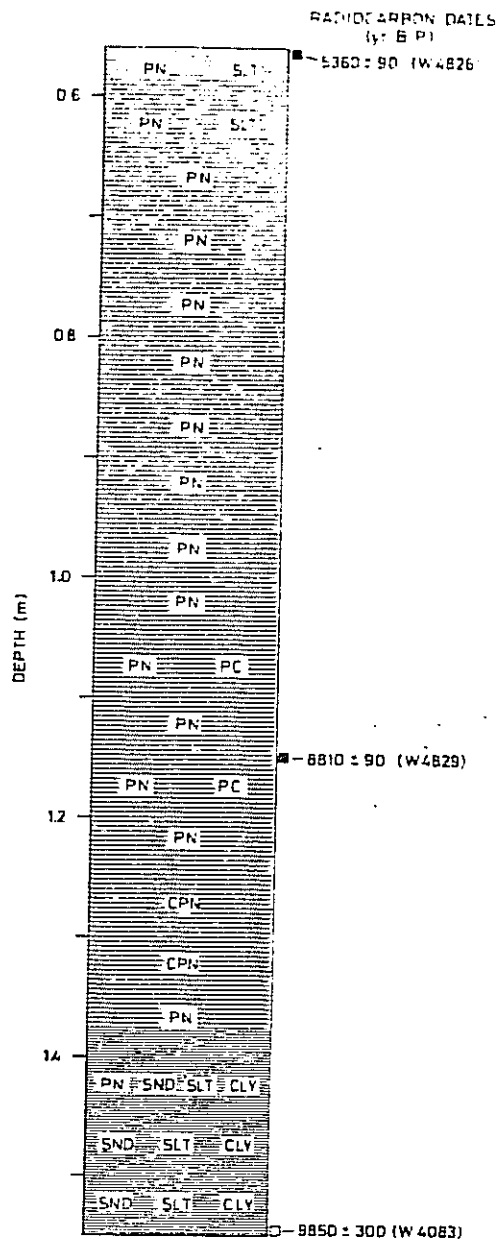


Fig.3. Peat stratigraphy, LP-3 site. Basal date is from LP-1 site. Other radiocarbon dates are from Madole, Elias and Rubin (unpublished data, 1982). CLY = clay; CPN = charred *Picea* needles; PC = *Picea* cones; PN = *Picea* needles; SLT = silt; SNT = sand. Density of lines indicate degree of peat humification.

of the LP-1 site. A radiocarbon age of 8810 yr B.P. has been established for the 1.15 m depth of LP-3 (Madole, Elias and Rubin, unpublished data). The uppermost level of LP-3 examined (0.54 m depth) yielded a radiocarbon age of 5360 yr B.P. (Madole, Elias and Rubin, unpublished data).

FOSSIL INSECT ASSEMBLAGES

Fossil insect fragments representing a minimum of 842 individuals were extracted from the site. Seventy insect taxa were identified, 31 species determinations were among these (Table I). Thirteen beetle (Coleoptera) families were found, as well as five families of insects from three other orders. The insect taxa represent a variety of terrestrial and aquatic habitats, and many of the identified species provide valuable paleoenvironmental data, based upon their modern ecological requirements and distribution patterns. At no time during the interval studied does there appear to be a dominance of either montane forest insects or alpine tundra insects, rather, a mixture of both elements was found in all levels.

Open ground fauna

Several of the insect species found in the La Poudre Pass peats occur today in the alpine tundra and/or forest-tundra ecotone regions of North America. The ground beetle *Patrobis septentrionis* (Fig.4A) inhabits the upper forest limits in North American mountains, and is found on grass and sedge vegetated banks of lakes, ponds and slow streams (Lindroth, 1961). Another ground beetle, *Bembidion grapsei*, is not at all riparian, but occurs only in the forest-tundra ecotone, and just above it, on dry, sandy gravels with sparse vegetation (usually moraines). *B. grapsei* is known from Canada, and south along the Rocky Mountains to Colorado, and the mountains of New England (Lindroth, 1963). *Pterostichus riparius* is a carabid beetle which is common in the montane forests of North America, but also ranges onto the tundra in the Rockies (Lindroth, 1966). Another carabid, *Trachypachus holmbergi* (Fig.4B, C), is commonly found on moraines, where the vegetation is sparse (Lindroth, 1961). The carabid species most indicative of alpine tundra environments among those found in the LP-3 materials is *Amara alpina*. Lindroth (1968) notes that this species occurs in the high north (true arctic tundra), and in the high Rockies, as well as in the White Mountains of New Hampshire (Fig.5D). While this species has been found below tree limit in a few localities, it appears to prefer open ground situations.

Predaceous water beetles (Dytiscidae) were abundant in many levels of LP-3 peat. Both of the identified species are found today at high altitudes. *Hydroporus occidentalis* (Fig.4D, E) is a western North American species, and is the most abundant *Hydroporus* in small, cold, silt-bottomed alpine pools (Larson, 1975). *Agabus inscriptus* is mostly found in *Spagnum* bogs, but also occurs in small alpine or subalpine pools, among sedges or mosses (Larson, 1975).

Taxonomic list of insect fossils from the LP-3 site, in minimum number of individuals per level

[illegible]

Gyrinidae										
<i>Gyrinus</i> sp.										
			4			2		3		1
Hydrophilidae										
<i>Helophorus</i> spp.										
		1			1					2
<i>Hydrobius fuscipes</i> L.										
	3	2		3						1
Staphylinidae										
<i>Oxytelus montanus</i> Csy.										
<i>Bledius</i> sp.										
							1			
<i>Arpedium</i> spp.										
	19	9	6	9	24	38	97	24	21	8
<i>Phlaeopterus</i> cf. <i>longipalpus</i> Csy.										
<i>Olophrum consimile</i> (Gyll.)										
	3	2	3	5	1		1		1	
<i>Olophrum rotundicollis</i> Sahlb.										
	2	1			7	3	2			
<i>Acidota quadrata</i> Zett.										
<i>Geodromicus</i> sp.										
	2	1				2	8	1	4	1
<i>Stenus</i> spp.										
	2	6		3	5	10	11	1	4	1
<i>Lathrobium</i> sp.										
			1		4					
<i>Philonthus</i> sp.										
	1		3	1	3	1	2	2		
<i>Heterothaps</i> sp.										
						1		3		
<i>Quedius</i> sp.										
		2				1		3		
<i>Tachyporus</i> sp.										
						1		3		
Tachyporinae indet.										
							1		1	
<i>Deinopis</i> sp.										
	1		1			2				
<i>Gymnus</i> sp.										
					3		1			
Leiodidae										
Genus indet.										
								2		

TABLE I (continued)

Taxon	Depth (m)									
	0.57- 0.67	0.67- 0.77	0.77- 0.87	0.87- 0.97	0.97- 1.07	1.07- 1.17	1.17- 1.28	1.28- 1.39	1.39- 1.49	1.49- 1.54
Scarabaeidae										
<i>Aegialia incustris</i> LeC.		1	1		2				5	
<i>Aphodius</i> sp.			1				2			
<i>Dialytes ulkei</i> Horn										
Genus indet.									2	2
Elaeteridae									2	2
Genus indet.					1		1	1		
Coccinellidae										
<i>Hyperaspis quadrivittata</i> Lec.										
Lathridiidae						1				
Genus indet.	1	1	1	2	1	3	1	1	3	1
Chrysomelidae										
<i>Chrysomela</i> sp.	1	1	1							
<i>Pyrrhalta</i> sp.			3	1						
<i>Donacia</i> spp.		2			1					
Curculionidae					1	4		1		
<i>Magdalis</i> sp.	1	1								
<i>Apion</i> sp.	1				1		1			1
Genus indet.				1	3	2	3		1	2

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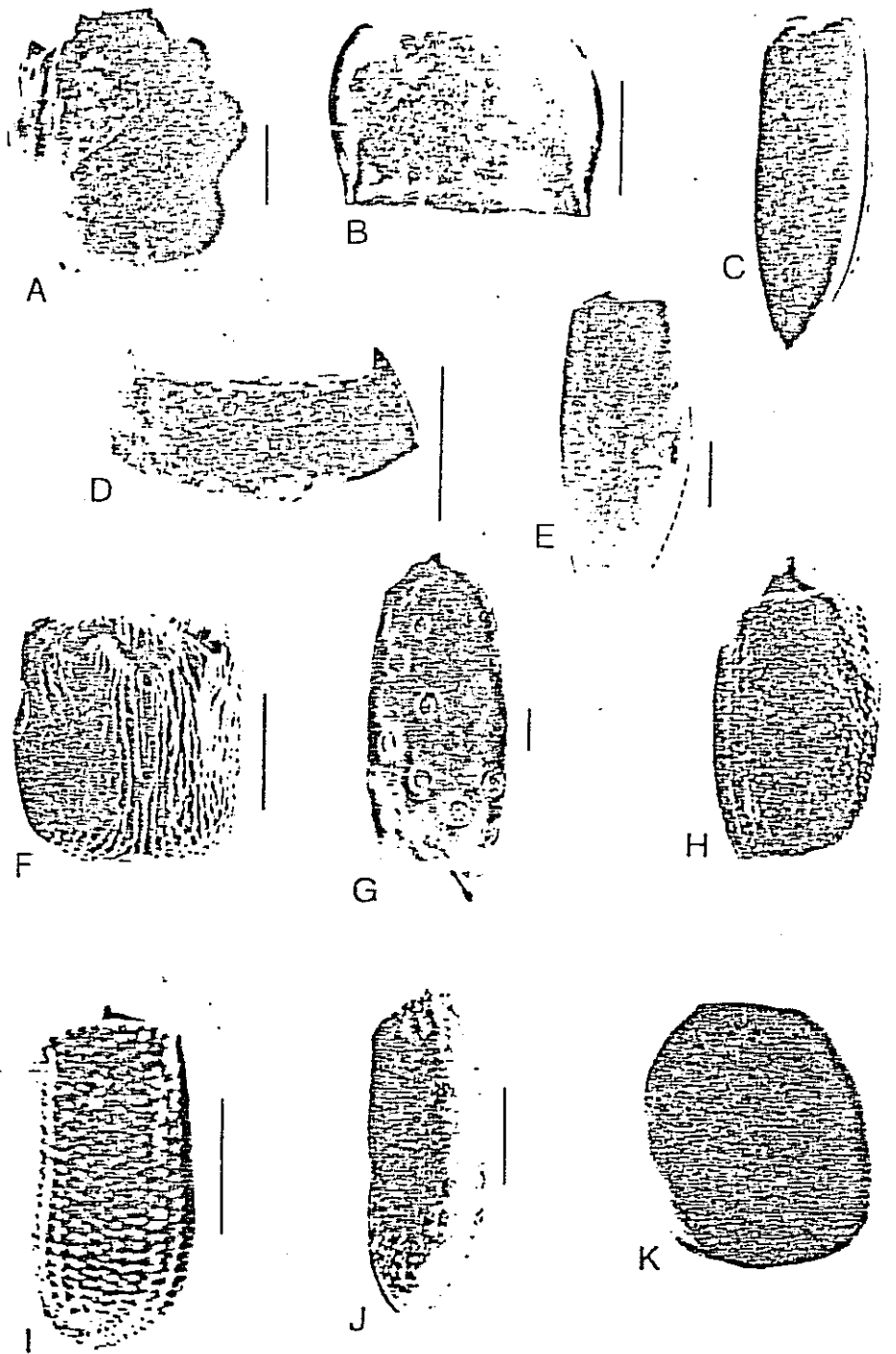


Fig. 4.

Two of the rove beetles (Staphylinidae) identified from LP-3 are common in the forest-tundra ecotone of the Rocky Mountains. *Acidota quadrata* lives in damp localities, especially in leaf litter by streams. *Phlaeopterus longipalpus* is frequently found in the alpine regions of the Rockies and Cascade Mountains (Hatch, 1957).

Of the scarabaeid beetles (Scarabaeidae) identified from LP-3, *Aegialia lacustris* is the only species occurring at high altitude. *A. lacustris* has a boreo-montane distribution, and has been collected both in the upper montane and alpine tundra zones of the Medicine Bow Mountains of Wyoming (Blake, 1945). The author has also taken this species above tree limit on Loveland Pass, Colorado.

The ant *Myrmica incompleta* (Fig.4F) is a western species, found mainly at higher elevations in colder zones (alpine and montane forest) as far south as Utah and Colorado (A. Francoeur, written comm., 1981).

Marsh or bog fauna

Several insect species indicative of a marsh or bog environment were found in LP-3 assemblages. Plant macrofossils from all of the peat levels are dominated by sedges, mosses and other aquatic or semi-aquatic plant taxa. The ground beetle *Elaphrus americanus* is today known from the border of standing or slowly moving water, where the ground is at least partly bare of vegetation. *Elaphrus clairvillei* (Fig.4G), in contrast, avoids exposed places and prefers shores shaded by vegetation, often in high, dense sedges (Lindroth, 1961). *Bembidion fortetrium* is a ground beetle occurring in *Carex* (sedge) swamps across Canada and south along the mountain chains of the United States (Lindroth, 1963). The carabid *Agonum affine* is found in nearly the same habitat as *B. fortetrium*.

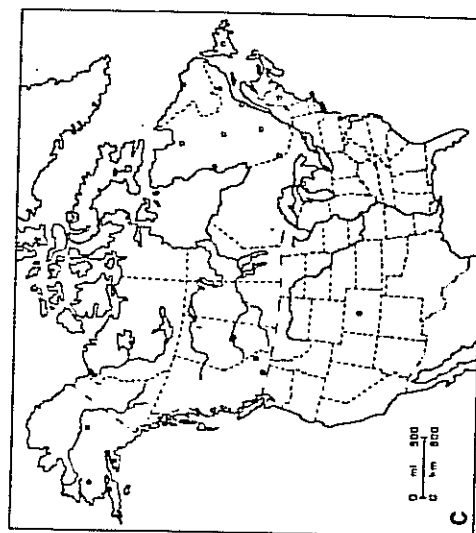
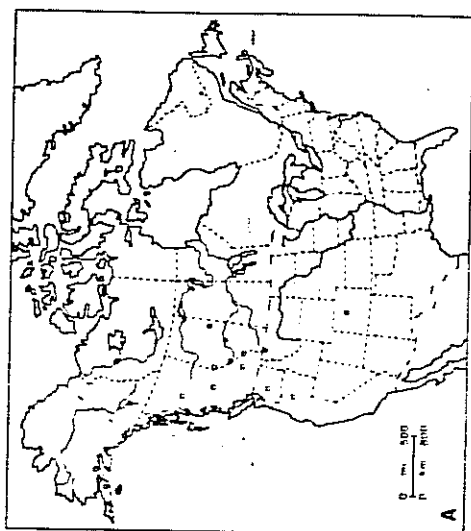
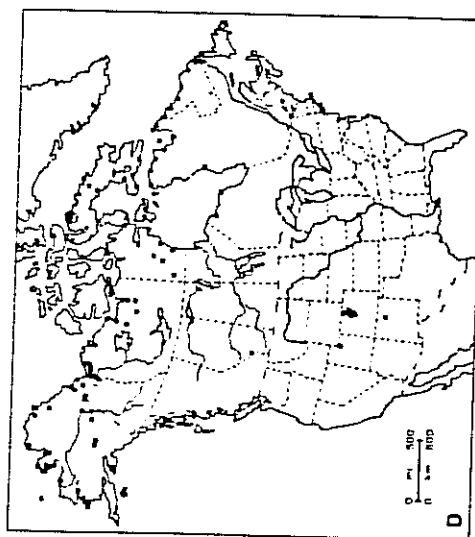
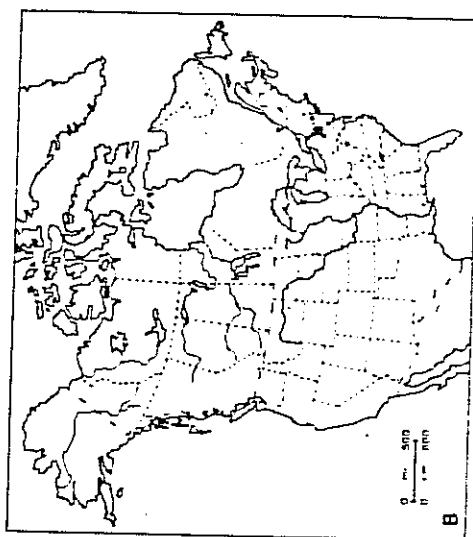
The staphylinid genus *Olophrum* contains several species commonly found in bogs and other areas of waterlogged vegetation.

O. rotundicolle, abundant in many LP-3 assemblages, is usually taken from submerged mosses, sedges or grasses at the edge of small pools. *O. consimile* is also associated with this type of habitat. Both species have a boreo-montane distribution across North America, and range onto the arctic and alpine tundra (Scheerpeltz, 1929).

Montane forest fauna

Bark beetles (family Scolytidae) were found in every level of LP-3 peat examined, including the lowest five cm, which may be as old as 10 000 years

Fig.4. Scanning-electron micrographs of LP-3 insect fossils. A. Head of *Patrobis septentrionis*; B. Pronotum of *Trachypachus holmbergi*; C. Right elytron of *T. holmbergi*; D. Pronotum of *Hydroporus* cf. *occidentalis*; E. Right elytron of *H. cf. occidentalis*; F. Head of *Myrmica incompleta*; G. Right elytron of *Elaphrus clairvillei*; H. Right elytron of *Scolytus piceae*; I. Left elytron of *Phloeotribus piceae*; J. Left elytron of *Polygraphus rufipennis*; K. Pronotum of *Pityophthorus tuberculatus*. Each scale bar equals 0.5 mm.



B.P. It must be acknowledged that at least some of the scolytids extracted from this site were probably not living at or near La Poudre Pass, but were carried up to high altitude by wind currents. This phenomenon and its paleoenvironmental significance have been discussed elsewhere (Elias, 1980). In general, the presence of bark beetles in high-altitude sites must not be interpreted as indicative of the close proximity of their host trees, unless macrofossils from the trees themselves (i.e. needles, cones and wood) are present in the same levels as the insect fossils. Spruce needles (and cones in some intervals) were found in all but the lowest ten cm of the LP-3 peat.

Among the scolytid species found in LP-3, several are known to attack spruces either primarily or exclusively. These beetle species are *Scolytus piceae* (Fig.4H), *Phloeotribus piceae* (Fig.4I), *Scierus annectans*, and *Dryocoetes affaber*. The species *Polygraphus rufipennis* and *Orthotomicus caelatus* attack all species of conifers in their ranges, whereas *Pityophthorus tuberculatus* (Fig.4J) is known to attack only pines (Bright, 1976). *P. tuberculatus* is found today in western coniferous forests of North America, but all of the other species mentioned above have transamerican distributions, in the boreal forest of Canada and south along mountain chains. The ants *Camponotus herculeanus* and *Formica rufa marcida* found in LP-3, are also common members of the boreo-montane insect fauna (Francoeur, 1973).

ZOOGEOGRAPHICAL IMPLICATIONS

Most of the insect taxa identified from the LP-3 assemblages probably occur in the northern Colorado Rockies today, although our knowledge of the distribution of most of these species is far from complete. Three of the beetle species from LP-3 occur only in the west of North America today. *Pterostichus riparius* has been collected today in western Canada, Alaska, and in the western mountain ranges of the United States (Fig.5A). *Phlaeopterus longipalpus* is recorded by Hatch (1957) from southern British Columbia, Washington, Oregon, Idaho and Utah. The ladybird beetle, *Hyperaspis quadrivittata*, is known from British Columbia, Washington, Oregon and Idaho. These last two species may also occur in Colorado today, but are not recorded from there, to the author's knowledge.

In contrast to the above, the dung beetle *Dialytes ulkei* is an eastern North American species, known from southern Quebec, south along the Appalachian Mountains to South Carolina (Fig.5B). *D. ulkei* was found in an LP-3 interval with an interpolated radiocarbon age of about 9600 yr B.P., but it is doubtful that this species lives west of the Mississippi River

Fig.5. Known modern North American distribution maps of: A. *Pterostichus riparius* (from Lindroth, 1966). B. *Dialytes ulkei* (from specimens at the Canadian National Insect Collection, Ottawa, and the United States National Museum of Natural History, Washington, D.C. C. *Patrobis septentrionis* (from Lindroth, 1961). D. *Amara alpina* (from Lindroth, 1968). Blackened circles represent specific collecting locality citations; open circles represent regional collecting locality citations.

today. *D. ulkei* was apparently much more widespread in early Postglacial times.

Several of the LP-3 insect species presently have a boreo-montane distribution in North America. These taxa occur widely across the Canadian boreal forest, and some of them also have disjunct populations to the south, along the mountain chains into the United States. The boreo-montane species from LP-3 include *Elaphrus americanus*, *Agonum affine*, *Patrobus septentrionis* (Fig.5C) and *Aegialia lacustris*. These and other species of insects which have isolated populations in the mountain chains south of the boreal forest represent a part of the "relict" fauna of these regions, stranded in the mountain forests after vegetation shifts occurred in the Holocene.

PALEOENVIRONMENTAL INTERPRETATIONS

The earliest ecosystem developing after deglaciation of the La Poudre Pass col appears to have been in wet, open ground. *Carex*-dominated vegetation probably formed the first stable plant community around the edges of ponds and pools (ca. 9800 B.P.), and this community type apparently continued until nearly recent times. During the first few centuries of peat accumulation, but before the first reliable evidence of spruce migration into the area, summer temperatures were probably quite similar to those found in the modern subalpine forest regions of Colorado. This is indicated by the presence in this interval of several beetle taxa which are today found in the boreal and montane forest regions, but are not directly tied to the trees themselves. These include the predatory beetles, *Elaphrus americanus*, *E. clairvillei*, and *Bembidion fortetrium*, and the dung beetle, *Dialytes ulkei*. This phenomenon of early postglacial or Lateglacial interstadial colonization by thermophilous insects into recently deglaciated areas, prior to the invasion of conifers, has been found in many sites, both in Europe (Coope, 1977) and in North America. Specifically, several of these sites from eastern North America have produced insect fossil assemblages apparently out of synchronization with the open ground plant communities inferred from the paleobotanical evidence (Morgan et al., 1981, 1982). Paleoenvironmental interpretations of these early postglacial intervals, based on the plant evidence, have often suggested that an arctic tundra climate coincided with the open ground flora, but the insect evidence from the same fossil assemblages tends to refute this conclusion.

The sedge-dominated marsh or bog at La Poudre Pass was apparently a very stable plant community for several thousand years in the Holocene. This infers an ample supply of water from snow and glacial meltwater in the col during this interval. Open water was present, at least in small pools, throughout the studied interval, as indicated by the continued presence of water beetles (Dytiscidae, Gyrinidae and Hydrophilidae). Again, the aquatic and semi-aquatic beetles from LP-3 assemblages are a mixture of boreo-montane and alpine-associated species. It would appear that nearly all of

the insect fossils from LP-3, with the exception of some of the bark beetles, were living at or near the site, and thus reflect local environmental conditions.

The combination of conifer-attacking bark beetles and spruce macrofossils in the LP-3 peats strongly suggests the presence of spruce trees at or very near the site by about 9500 yr B.P., and continuing through the uppermost level examined (5360 ± 90 yr B.P.). The mixture of alpine tundra and montane forest insects throughout the studied intervals, however, appears to indicate that the altitudinal tree limit was never far from the site during early to mid-Holocene times.

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