Geography Occasional, University of Birmingham, Birmingham, UK.

Buckland, P. C. (1981). The early dispersal of insect pests of stored products as indicated by archaeological records. *Journal of Stored Product Research* 17, 1–12.

Buckland, P. C., and Dinnin, M. J. (1993). Holocene woodlands: The fossil insect evidence. In *Dead Wood Matters: The Ecology and Conservation of Saproxylic Invertebrates in Britain* (K. Kirby and C. M. Drake, Eds.), English Nature Science No. 7, pp. 6–20. English Nature, Peterborough, UK.

Buckland, P. C., and Wagner, P. E. (2001). Is there an insect signal from the 'Little Ice Age'? *Climatic Change* 48, 137–149.

Coope, G. R. (1986). Coleoptera analysis. In *Handbook of Holocene Palaeoecology and Palaeohydrology* (B. E. Berglund, Ed.), pp. 703–713. Wiley, Chichester, UK.

Coope, G. R. (1994). The response of insect faunas to glacial–interglacial climatic fluctuations. *Philosophical Transactions of the Royal Society of London B* 344, 19–26.

Coope, G. R. (1998). Insects. In *Late Quaternary Environment Change in Northwest Europe: Excavations at Holywell Coombe, Southeast England* (R. C. Preece and D. R. Bridgland, Eds.), pp. 213–233. Chapman & Hall, London.

Coope, G. R., and Brophy, J. A. (1972). Late Glacial environmental changes indicated by a coleopteran succession from North Wales. *Boreas* 1, 97–142.

Girling, M. A. (1984). A Little Ice Age extinction of a water beetle from Britain. *Boreas* 13, 1–4.

Kelly, M., and Osborne, P. J. (1965). Two faunas and floras from the alluvium at Shustoke, Warwickshire. *Proceedings of the Linnean Society of London* 176, 37–65.

Kenward, H. (2004). Do insect remains from historic-period archaeological occupation sites track climate change in Northern England? *Environmental Archaeology* 9, 47–59.

Lemdahl, G. (1997). Late Weichselian and early Holocene colonisation of beetle faunas in S. Sweden. *Quaternary Proceedings* 5, 153–164.

Lemdahl, G. (2000). Lateglacial and early Holocene insect assemblages from sites at different altitudes in the Swiss Alps—Implications on climate and environment. *Palaeogeography, Palaeoclimatology, Palaeoecology* 159, 293–312.

Mayewski, P. A., Rohling, E. E., Stager, J. C., *et al.* (2004). Holocene climate variability. *Quaternary Research* 62, 243–255.

Osborne, P. J. (1969). An insect fauna of late Bronze Age date from Wilsford, Wiltshire. *Journal of Animal Ecology* 38, 555–566.

Osborne, P. J. (1974). An insect assemblage of Early Flandrian age from Lea Marston, Warwickshire and its bearing on the contemporary climate and ecology. *Quaternary Research* 4, 471–486.

Osborne, P. J. (1976). Evidence from the insects of climatic variations during the Flandrian period, a preliminary note. *World Archaeology* 8, 150–158.

Osborne, P. J. (1978). Insect evidence for the effect of man on the lowland landscape. In *The Effects of Man on the Landscape: The Lowland Zone* (S. Limbrey and J. G. Evans, Eds.), Research Report No. 21, pp. 32–34. Council for British Archaeology, London.

Osborne, P. J. (1979). Insect remains. In *Fisherwick: The Reconstruction of an Iron Age Landscape* (C. Smith, Ed.), No. 61, pp. 189–193, 85–87. British Archaeological Reports, Oxford.

Osborne, P. J. (1982). Some British later prehistoric insect faunas and their climatic implications. In *Climatic Change in Later Prehistory* (A. Harding, Ed.), pp. 68–74. Edinburgh University PressEdinburgh, UK.

Osborne, P. J. (1988). A Late Bronze Age insect fauna from the River Avon, Warwickshire, England: Its implications for the terrestrial and fluvial environment and for climate. *Journal of Archaeological Science* 15, 715–727.

Osborne, P. J. (1997). Insects, man and climate in the British Holocene. *Quaternary Proceedings* 5, 193–198.

Ponel, P. (1997). Late Pleistocene coleopteran fossil assemblages in high altitude sites: A case study from Prato Spilla (Northern Italy). *Quaternary Proceedings* 5, 207–218.

Ponel, P., and Coope, G. R. (1990). Lateglacial and Early Flandrian Coleoptera from La Taphanel, Massif Central, France: Climatic and ecological implications. *Journal of Quaternary Science* 5, 235–249.

Ponel, P., and Jeanne, C. (1997). Un carabique nouveau pour la faune française: *Syntomus fuscomaculatus* (Motschoulsky, 1844) dans les Bouches-du-Rhône [Coleoptera Lebiidae]. *Nouvelle Revue d'Entomologie* 14, 353–357.

Ponel, P., Andrieu-Ponel, V., Reille, M., and Guiter, F. (2004). A cross-comparison of insect and pollen data of the last 13 ka in the French Pyrénées, XI International Palynological Congress, Granada (Spain) pp. 4–9, July 2004. *Polen* 14, 234.

Smith, D. N. (2000). Disappearance of elmid 'riffles beetles' from lowland river systems—The impact of alluviation. In *People as an Agent of Environmental Change* (R. A. Nicholson and T. P. O'Connor, Eds.), pp. 75–80. Oxbow Books, Oxford.

Postglacial North America

S A Elias, Royal Holloway, University of London, Surrey, UK

Introduction

The exoskeletal remains of beetles (Coleoptera) preserve well in waterlogged sediments of Pleistocene and Holocene age. Although the transition from the last glaciation to postglacial environments was a time-transgressive phenomenon, in most regions of North America this climatic transition took place between 14,000 and 11,550 years ago (12,000–10,000 ^{14}C yr BP). Most of the North American fossil beetle assemblages greater than 11,500 years in age are discussed in the article entitled 'Late Pleistocene Beetle Records from North America.' In this article, I discuss the late glacial fossil beetle record of just the Maritime region of Canada, as well as Holocene records from across the continent.

In recent decades, studies of postglacial fossil beetle assemblages have been carried out in many regions of North America. Table 1 lists 24 postglacial faunal sites from eastern and central North America, and Table 2 lists 20 postglacial sites from western North America. This article reports on the major findings of these studies, in terms of paleoenvironmental reconstructions and shifting distribution patterns (biogeography) of the species found in the fossil assemblages, all of which remain extant today. Some of the fossil assemblages discussed here formed part

Table 1 Summary of fossil beetle assemblage data from sites in central and eastern North America

Site	Age (cal yr BP × 1000)	Holocene		Modern		Change in Temperature		References[1]
		TMAX (°C)	TMIN (°C)	TMAX (°C)	TMIN (°C)	July ΔT	January ΔT	
1) Benacadie, Nova Scotia	13.73	9–13	−31 to −14	18.1	−5.5	−9.1 to −5.1	−25.5 to −8.5	Miller and Elias, 2000
2) Collins Pond, Nova Scotia/Lower	13.73	10–12.5	−20.5 to −11	16.3	−3.9	−6.3 to −3.8	−16.6 to −7.1	Miller and Elias, 2000
3) Todd Mountain, New Brunswick	13.42	10–13	−30.5 to −18	19.1	−9.1	−9.1 to −6.1	−21.4 to −8.9	Miller and Elias, 2000
4) Campbell, Nova Scotia	13.16	11.5–14.5	−27.5 to −8	18.6	−8	−7.1 to −4.1	−19.5 to 0	Miller and Elias, 2000
2) Collins Pond, Nova Scotia/Upper	12.82	11–14	−21.5 to −7.5	16.3	−3.9	−5.3 to −2.3	−17.4 to −3.6	Miller and Elias, 2000
5) Amaguadees, Nova Scotia	12.73	14.5–15.5	−28 to −23.5	18.1	−5.5	−3.6 to −2.6	−22.5 to −18	Miller and Elias, 2000
6) West Mabou, Nova Scotia	12.53	11–14	−18 to −5	18.6	−8	−7.6 to −4.6	−10 to +3	Miller and Elias, 2000
7) Rainy River, Ontario/Site E-13	12.24–11.75	13–15	−27 to −22	18.8	−16.2	−5.8 to −3.8	−10.8 to −5.8	Bajc et al. 2000
8) Wales, Ontario	12.1	N/A	N/A	20.5	−8.1	N/A	N/A	Miller et al. 1987
9) Rainy River, Ontario/Site RR54	11.68	14.5–15.5	−27 to −23.5	18.8	−16.2	−4.3 to −3.3	−10.8 to −7.3	Bajc et al. 2000
10) Mosbeck, Minnesota/Unit E	11.50	15–20	−21 to −5	20.2	−16.9	−5.2 to −0.2	−4.1 to +11.9	Ashworth et al. 1972
11) Lockport Gulf, New York/L03	11.45	17–20.5	−15.5 to −3.5	21.5	−4.8	−4.5 to −1	−10.7 to +0.3	Miller and Morgan, 1982
12) Seibold, North Dakota	11.08	17–21.5	−16 to −5	20.5	−14.9	−3.5 to +1	−0.6 to +9.9	Ashworth and Brophy, 1972
10) Mosbeck, Minnesota Unit D	10.91	16.5–20	−18 to −6.5	20.2	−16.9	−3.7 to −0.2	−1.1 to +10.4	Ashworth et al. 1972
11) Lockport Gulk, New York/LO4	10.87	15–22	−22.5 to −1	21.5	−4.8	−6.5 to +0.5	−17.7 to +4.3	Miller and Morgan, 1982
11) Lockport Gulk, NY/LO5	10.36	18.5–22	−19.5 to −10.5	21.5	−4.8	−3 to +0.5	−14.2 to −5.2	Miller and Morgan, 1982
10) Mosbeck, Minnesota Unit C	9.44	15–21	−24 to −1.5	20.2	−16.9	−5.2 to +0.8	−7.1 to +15.4	Ashworth et al. 1972
13) Saint Flavien, Quebec Unit 1	7.83	16.75–20	−12.25 to −7	18.7	−13	−1.95 to+1.3	+0.75 to +6	Lavoie et al. 1997a
14) Ennadai Lake, NWT Unit D	7.2–6.86	10–14.5	−28.5 to −23	13	−32	−3 to +1.5	+3.5 to +9	Elias, 1982a
14) Ennadai Lake, NWT Unit C	6.86–2.92	12–15	−25 to −19	13	−32	−1 to +2	+7 to +13	Elias, 1982
15) Boniface River, Quebec	6.66–1.91	11.8–14.5	N/A	9.4	−24.8	+2.4 to +5.1	N/A	Lavoie et al. 1997
16) Radisson, Quebec	5.84–0	14.5–17.5	N/A	13.4	−3.4	+1.1 to +4.1	N//A	Lavoie, 2001
17) Charlevoix, Quebec	5.25–0	N/A	N/A	19.2	−12.8	N/A	N/A	Lavoie, 2001
18) Au Sable River, Michigan	4.66–4.55	17–18	−14 to −12	20	−5	−3 to −2	−9 to −7	Morgan et al. 1985
13) St Flavien, Quebec Unit 2	4.49–3.55	15–20	−14 to −5	18.7	−13	−3.7 to +1.3	−1 to +9	Lavoie et al. 1997
19) Bongards, Minnesota	3.55–0	N/A	N/A	23.1	−11.2	N/A	N/A	Schwert and Ashworth, 1985
20) Roberts Creek, Iowa	3.19–0	N/A	N/A	22.4	−8.9	N/A	N/A	Schwert, 1996
13) St Flavien, Quebec/Unit 4	3.19–0	16–20	−23.5 to −5	18.7	−13	−2.7 to +1.3	−10.5 to +8	Lavoie et al. 1997
21) Umiakoviarusek, Labrador	2.21–0.89	12–13.5	−23 to −12	10.7	−18.5	+1.3 to +2.8	−5.5 to +6.5	Elias, 1982
22) Cahokia, Illinois	AD 1050	N/A	N/A	26.6	−1.5	N/A	N/A	Pauketat et al. 2002
23) Boston, Massachusetts	17th century	N/A	N/A	23.1	−1.9	N/A	N/A	Bain, 1998
24) Quebec City, Quebec	19th century	N/A	N/A	19.2	−12.8	N/A	N/A	Bain, 2001

[1]References available from the 'QBib' web site: http://www.bugs2000.org/qbib.html

Table 2 Summary of fossil beetle assemblage data from sites in western North America

Site	Age (cal yr BP×1000)	Holocene		Modern		Change in Temperature		References[1]
		TMAX (°C)	TMIN (°C)	TMAX (°C)	TMIN (°C)	July ΔT	January ΔT	
1) False Cougar Cave, Montana	11.59	15.5–17.75	−4.5 to +0.25	13.5	−10.1	+2 to +4.25	+5.6 to +10.4	Elias, 1996
2) Huntington Canyon, Utah	11.46	15–17	−6 to 0	16	−9.1	−1 to +1	+3.1 to +9.1	Elias, 1996
3) La Poudre Pass, Colorado	11.39	15–18	−17.5 to −7	11.3	−7.7	+3.7 to +6.7	−9.8 to +0.7	Elias, 1996
4) Lake Isabelle Delta, Colorado	10.12	11.75–14.5	−31.25 to −15	10.8	−8.2	+1 to +3.7	−23 to −6.8	Elias, 1996
3) La Poudre Pass, Colorado	9.89	13.5–16.5	−19.5 to −9	11.3	−7.7	+2.2 to +5.2	−13.6 to −1.3	Elias, 1996
4) Lake Isabelle Delta, Colorado	9.48	10.5–13	−23.5 to −16	10.8	−8.2	−0.3 to +2.2	−15.3 to −7.8	Elias, 1996
4) Lake Isabelle Delta, Colorado	8.70	11–13	−14 to −9	10.8	−8.2	+0.2 to +2.2	−5.8 to −0.8	Elias, 1996
4) Lake Isabelle Fen, Colorado	7.90	10.25–13	−14.75 to −7.5	10.8	−8.2	−0.6 to +2.2	−6.6 to +0.7	Elias, 1996
3) La Poudre Pass, Colorado	6.14	12.5–13.5	−12.5 to −11.5	10.8	−8.2	+1.7 to +2.7	−4.3 to −3.3	Elias, 1996
3) La Poudre Pass, Colorado	3.79	11.75–15	−21.25 to −14.5	11.3	−7.7	+0.4 to +3.7	−11.8 to −6.8	Elias, 1996
4) Lake Isabelle Fen, Colorado	3.17	10.25–13	−14.5 to −7.5	10.8	−8.2	−0.6 to +2.2	−6.3 to +0.7	Elias, 1996
5) Longs Peak Inn, Colorado	3.14	12–15.5	−26.5 to −14	14.5	−5	−2.5 to +1	−21.5 to −9	Elias, 1996
5) Longs Peak Inn, Colorado	2.82	13.5–15.5	−24 to −15	14.5	−5	−1 to +1	−19 to −10	Elias, 1996
6) Roaring River, Colorado	2.49	14.25–14.75	−18.25 to −16.5	14.3	−5.5	0 to +0.5	−12.75 to −11	Elias, 1996
7) Rat's Nest Cave, Alberta	1.97–0	N/A	N/A	16.2	−8.9	N/A	N/A	Bain *et al.* 1997
8) Mount Ida Bog, Colorado	0.85	10.25–12	−14.75 to −9	9.3	−11.5	+1 to +2.7	−3.25 to +2.5	Elias, 1996
5) Longs Peak Inn, Colorado	0.43	13.5–15.5	−24.5 to −15	14.5	−5	−1 to +1	−19.5 to −10	Elias, 1996

(*Continued*)

Table 2 (*Continued*)

Site	Age (cal yr BP×1000)	Holocene		Modern		Change in Temperature		References[1]
		TMAX (°C)	TMIN (°C)	TMAX (°C)	TMIN (°C)	July ΔT	January ΔT	
Chihuahuan Desert Packrat Midden Faunas								
9) Sacramento Mountains, NM	11.91–0.44	Not available						Elias and Van Devender, 1992
10) Tunnel View, BBNP, Texas	11.39–10.05	Not available						Elias and Van Devender, 1992
11) Hueco Mountains, Texas	11.18–2.60	Not available						Elias and Van Devender, 1992
12) Sierra de la Misericordia, Coahuila	10.57–0.720	Not available						Elias *et al.* 1995
13) Puerto de Ventanillas, Coahuila	9.75–.59	Not available						Elias *et al.* 1995
14) Maravillas Canyon Cave, Texas	9.22–.09	Not available						Elias and Van Devender, 1990
15) Cañon de la Fragua, Coahuila	6.52–.51	Not available						Elias *et al.* 1995
Great Basin Packrat Middens								
16) Glen Canyon region, Utah	9.69–1.42	Not available						Elias *et al.* 1992
17) Canyonlands National Park, Utah	7.82–4.24	Not available						Elias *et al.* 1992
Sonoran Desert Packrat Mideens								
18) Puerto Blanco Mountains, Arizona	12.40–0	Not available						Hall *et al.* 1990
19) Ajo Mountains, Arizona	11.47–1.09	Not available						Hall *et al.* 1989
20) Cataviña, Baja California	1.1	Not available						Clark and Sankey, 1999

[1]References available from the 'QBib' web site: http://www.bugs2000.org/qbib.html

of purely paleontological research projects. Others formed part of archeological research, as noted in the text.

The paleotemperature estimates discussed are derived from the Mutual Climatic Range (MCR) method of paleoclimate analysis, as discussed in the Overview for this section. For sites in eastern and central North America, the MCR method was used to provide estimates of mean temperatures of the warmest (TMAX) and coldest (TMIN) months of the year. TMAX and TMIN estimates are discussed in terms of departures from the modern TMAX and TMIN of the study sites in question.

Research in Eastern North America

Fossil beetle assemblages of postglacial age have been studied in eastern Canada, New England, along the Mississippi drainage in the mid-western United States, and in the Canadian Northwest Territory of Keewatin (Fig. 1). Many of these assemblages represent early postglacial environments (Table 1, sites 1–14). Only a few mid-Holocene assemblages have been described from these regions (Table 1, sites 15–18). Late Holocene assemblages, including three from archeological sites, span the interval 3.5 to 0.1 kya (Table 1, sites 19–24).

Late Pleistocene-Holocene Transition

The fossil beetle record from many parts of North America indicates a relatively smooth transition from glacial to interglacial climates, beginning about 17 kya (calibrated years ago × 1,000) (Elias *et al.*, 1996). Throughout most of North America, paleotemperature reconstructions based on beetle assemblage data do not show a climatic reversal during the late glacial interval (17–11 kya). The one prominent exception to this comes from the Maritime region of Canada. Miller and Elias (2000) reconstructed mean July temperatures (TMAX) and mean January temperatures (TMIN) from radiocarbon-dated fossil beetle assemblages from a suite of late-glacial sites in this region. These assemblages date from 14.9 kya to 12.5 kya. In the Maritime region, multiple lines of evidence, including stratigraphy, palynology, chironomid fossils, and beetles, suggest a climatic deterioration during the Younger Dryas chronozone. MCR estimates suggest several 'events' in the regional fossil beetle record that appear similar to climate events recorded in the GRIP ice core record, including the Younger Dryas cooling event from GI-1a to GS-1, beginning ca. 12,650 GRIP yr BP. The results of MCR-based temperature reconstruction suggests a drop in TMAX of about 5°C between 13 kya (at Brookside, Nova Scotia) and 12.5 kya (at West
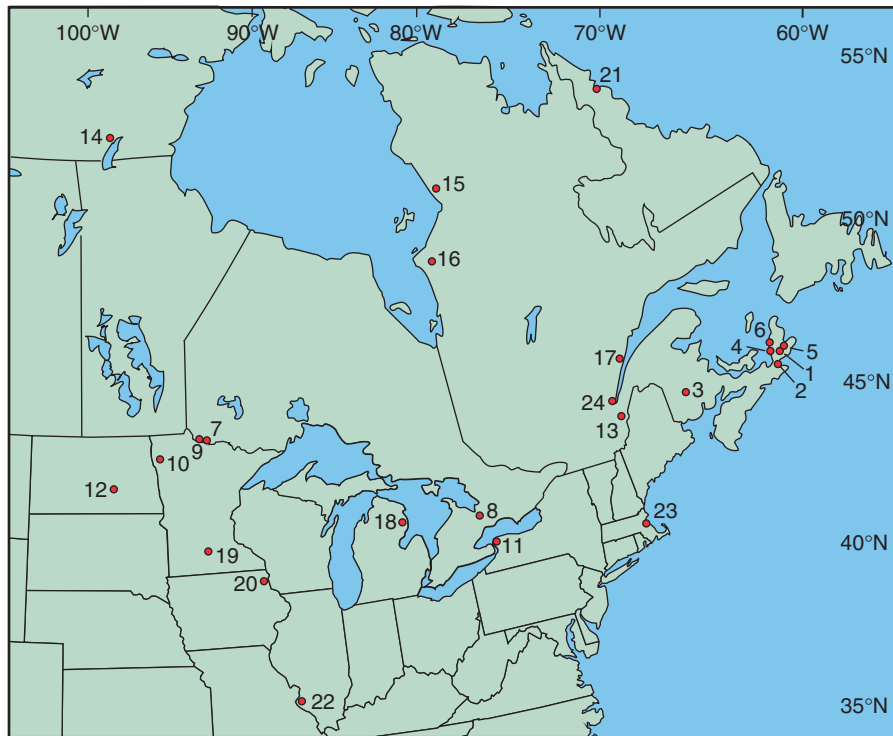
Figure 1 Map of eastern and central North America, showing location of fossil sites discussed in text. Site numbers match those in **Table 1**.

Mabou, Nova Scotia). These results compare well with the temperature reconstruction of summer surface waters based on chironomids (Levesque et al., 1997; Lotter et al., 1999). The fact that there is little fossil beetle evidence for a Younger Dryas cooling event elsewhere in North America lends support for the paleoceanographic model (Duplessy et al., 1996) that links this cooling event with changes in circulation patterns in the North Atlantic. The only other North American region from which beetle records indicate a Younger Dryas cooling is arctic Alaska (Elias, 2000). However, few continuous series of beetle assemblages have been studied from this time interval in most regions of North America.

Most early postglacial beetle faunas from eastern and central North America are indicative of climatic regimes close to modern parameters (Table 1). The exceptions to this include sites that were located in close proximity to large bodies of glacial meltwater, such as Lockport Gulf, New York. Here, at 11.45 kya, TMAX was 1–4.5° C colder than today (Elias et al., 1996). Climatic amelioration through the early Holocene is indicated by the mid-western beetle assemblages. Schwert and Ashworth (1988) discussed the discrepancy between early postglacial environments deduced from insect assemblages and paleobotanical reconstructions in the mid-western United States as follows. Pollen and plant macrofossils that accumulated in ice-marginal deposits just after deglaciation reflect tundra-like communities with sedges and Dryas, and are lacking trees and shrubs. However, the insect faunas are consistently different, being analogous to modern faunas from the middle of the boreal forest zone. At each study site, the discrepancy between the plant and insect evidence has been accounted for by invoking a substantial lag in the arrival and establishment of woody plants on deglaciated landscapes. As in central Europe, this lag may represent the time needed for ecological succession from open ground to herbaceous cover, shrub cover, and finally forest cover. The most recent paleobotanical reconstructions for the eastern and central United States (e.g., Grimm and Jacobson, 2004) suggest that such lags may have lasted for centuries, not for millennia. The paleoclimatic interpretations from the two disciplines (beetles and pollen) seem to be coming into closer agreement in recent years. For instance, a syntheses of palynological data (Grimm and Jacobson, 2004) concluded that "the climate of the Northeast was warmest and driest during the early Holocene··· from about 10,200–6,000 cal yr BP—a time of enhanced summer insolation." This conclusion agrees well with fossil beetle reconstructions.

Elias (1982), Lavoie et al. (1997), and Lavoie and Arsenault (2001) studied late Holocene beetle assemblages from sites near arctic tree line in northern Quebec and Labrador, Canada. Based on MCR analysis, Lavoie et al. (1997) found that summer temperatures in northern Quebec were 2.8–5.5° C higher than modern from 6.7–1.9 kya. Elias (1982) found evidence of climatic cooling in northeastern Labrador from 2.7–0.9 kya. However, Lavoie and Arsenault (2001) found no evidence of cooling in the James Bay region during the last 5.7 kya. This suggests either that climates varied in different parts of Quebec–Labrador during the late Holocene, or that the northern tree-line faunas were more sensitive to small-scale changes than faunas that lived nearer the center of the boreal forest.

Environmental Archeology Studies

One of the principal differences between European and North American postglacial environments has been the relatively strong human influence on the landscapes of Europe during at least the last 5,000 years, compared with the relatively weak human disturbance of many North American landscapes until at least late prehistoric times. The difficulties experienced by European researchers in disentangling the effects of human perturbation from the effects of climate change on postglacial beetle faunas (see Postglacial Europe) have not hindered North American workers to the same extent. The hunter-gatherer societies of the Americas did not clear forests and plant crops until the last few centuries.

Fossil beetle assemblages taken from archeological sites in eastern and central North America have documented physical environments and human living conditions at several sites. Fossil insects were studied from disposal pits at Cahokia, Illinois (Pauketat et al., 2002). One of the aims of this study was to determine the timing of the disposal events represented by deposition of refuse in barrow pits. All but one of the studied deposits contained sizable quantities of insects active during the warm months between April and October. The fossil assemblages were dominated by beetles (58%), fly pupae (28%), and ants (14%). Some assemblages were indicative of rich mounds of discarded plant and animal wastes that were exposed for sufficient time, several days to several weeks, to allow insect colonization.

Bain (1998) studied beetle remains from a colonial-era archeological site in Boston, Massachusetts. The fossil assemblages were extracted from sediments that accumulated in a latrine. Bain identified 42 beetle species, including 22 European taxa, and one that was possibly of Caribbean origin. Five beetle species in the fossil assemblage normally attack wood,

suggesting that woodworking took place nearby, such as a sawmill, a furniture shop, house building, or stacks of firewood. A large number of granary weevils (*Sitophilus granarius*) were found, indicating weevil infestation of stored grain or flour.

Bain's (2001) study of insects from the Îlot Hunt site in Quebec City, Canada indicates that the late nineteenth century was a time of great change in urban sanitary regulations and awareness of public health problems. Bain analyzed insect fossil samples from two latrines, a drain, and an abandoned well, representing both domestic and commercial establishments.

Research in Western North America

Postglacial sites in western North America include eight sites in the Rocky Mountain region (Table 2, sites 1–8) and twelve sites in the arid southwest (Table 2, sites 9–20). The Rocky Mountain sites represent organic deposits sampled from lake sediments, peat bogs, and one cave deposit (Rat's Nest Cave, Alberta). The southwestern sites are all woodrat middens.

Studies in the Rocky Mountains

In many ways, the Rocky Mountain region is ideally suited for Quaternary insect studies. The vertical relief of the mountain chain has provided regional biota with a wide variety of physical environments, expressed in the development of ecological communities ranging from grasslands in the eastern foothills zone through several types of montane and subalpine forest communities, to the alpine tundra at or near mountaintops. Furthermore, the ecotones, or boundaries, between these communities have undergone noticeable shifts in elevation in the late Quaternary, facilitating the study of environmental change, as a given site documents different biological communities through time.

Fossil insects from the Rocky Mountains have left us important records of past events and biotic responses. The atmospheric moisture caught by the Rockies makes this mountain chain wetter than the adjacent plains, and this in turn has led to the accumulation and preservation of organic deposits.

Rocky Mountain study sites (Fig. 2) span an elevational range from the foothills zone to the Alpine tundra. The general trend in regional faunas was that cold-adapted species lived at high elevations during the postglacial warm interval, but during the last glaciation, these beetles shifted their ranges downslope by 300–1,500 m (Short and Elias, 1987; Elias and Toolin, 1989).
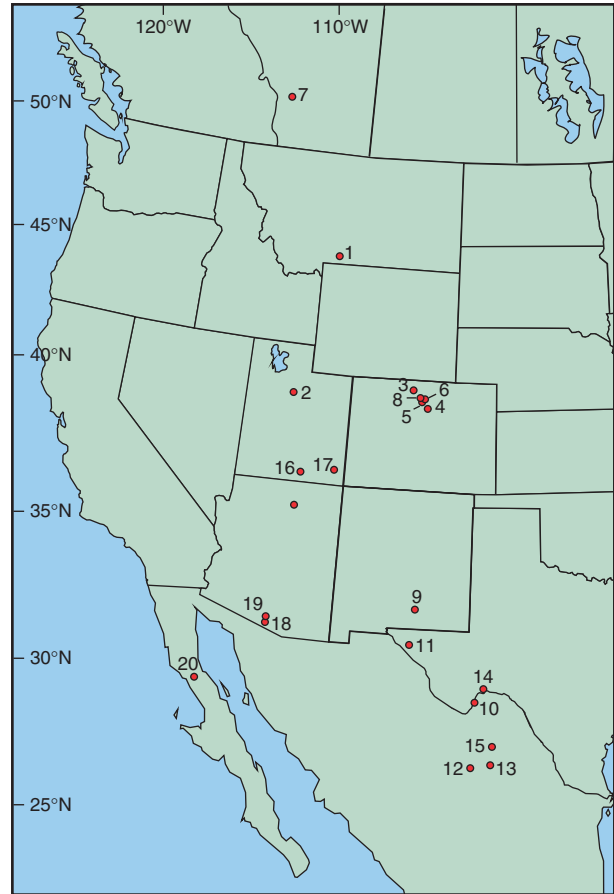
Figure 2 Map of western North America, showing location of fossil sites discussed in text. Site numbers match those in **Table 2**.

MCR analysis of fossil beetle assemblages from the Rockies indicates that following deglaciation, postglacial summer warming was rapid. This is indicated by an assemblage dating 16.2 kya, with TMAX only 2.1° C cooler than modern. By 11.6 kya, several assemblages indicate warmer than modern TMAX and TMIN values. Pollen evidence suggests that coniferous forests did not reach their modern elevations until about 10 kya, more than 1,000 years after climatic amelioration had reached modern levels, based on the beetle evidence. By that time, beetle MCR reconstructions indicate that both summer and winter temperatures were already beginning to decline from early postglacial maxima.

TMAX values remained above modern levels and TMIN values remained below modern levels until about 3.2 kya. These long-term trends were followed by a series of small-scale oscillations in the late Holocene. Pollen spectra from sites in the Colorado Front Range show substantial changes after 3.8 kya, interpreted as either a lowering of tree line, or a thinning of subalpine forests, or both (Short, 1985). Pine pollen also became less abundant in subalpine pollen

spectra at this time. These changes were inferred to be a response by the vegetation to climatic cooling.

The site of Rat's Nest Cave in Alberta yielded organic detritus that accumulated at the bottom of a deep natural shaft inside the mouth of a cave (Bain et al., 1997). The beetle faunas span the last 2,000 years, and their composition suggests environmental conditions similar to modern parameters at the site. This is in contrast to beetle assemblages from this interval from farther south, in the Central Rocky Mountains. The latter are indicative of a series of climatic oscillations during this time, with a relatively warm period about 1 kya, followed by a relatively cold period in the last 500 years.

Biogeography of the Rocky Mountain Beetle Fauna

Because of the persistently cold climates at high elevations, the Rockies have been a refuge for many cold-adapted species of both plants and animals, even during the warmest interglacial intervals. Species that shifted southward in front of glacial ice advances in the interior of North America had only two options for survival when the climate began warming and the ice receded at the end of the last glaciation. They had to migrate either northward or up the slopes of mountains, in search of suitably cold climate. Thus, cold-adapted beetles that lived on the plains south of Denver toward the end of the last glaciation have retreated to the Alpine tundra in the Colorado Front Range (Elias, 1986). In contrast to the Rocky Mountain fauna, cold-adapted species living in the central Great Plains region were not able to migrate north at the end of the last glaciation. At that time, climatic warming caused the extirpation (regional extinction) of much of the cold-adapted beetle fauna in this region, with small populations of Arctic and subArctic species surviving in Alpine habitats of the Cordillera and Appalachians, or in short-lived habitats associated with stagnant ice (Schwert and Ashworth, 1988).

There have been a number of regional extirpations from the Rocky Mountain beetle fauna during the last 17 kya, probably as a result of large-scale climatic change (Fig. 3). Six of the eight species extirpated before the Holocene have shifted their distributions to the north. These are all cold-adapted animals, either Arctic or boreo-Arctic species. The most extreme displacement of distribution is that of a rove beetle (Staphylinidae), *Holoboreaphilus nordenskioeldi*, which lives today in Arctic Canada, 3,000 km north of its late glacial locality at Marias Pass, Montana (Fig. 2). Two additional species made their last Rocky Mountain appearance in an assemblage from Marias Pass, dated at just over 13.3 kya. These are a ground beetle (Carabidae), *Bembidion sulcipenne hyperboroides*, and a carrion beetle (Silphidae), *Thanatophilus trituberculatus*. *B. sulcipenne hyperboroides* is a northwestern North American species, living today in northern British Columbia, the Yukon Territory, and Alaska. *T. trituberculatus* is a northern, cold-adapted carrion-feeder, which probably also feeds on other insects inhabiting carrion. Its modern range extends north to the Arctic in Canada and Alaska, but its southern limit does not reach the lower 48 states of the United States.

Two species make their last appearance in the Rocky Mountain fossil record at approximately 14.7 kya, from the Mary Jane site in Colorado. One of these is the water scavenger beetle
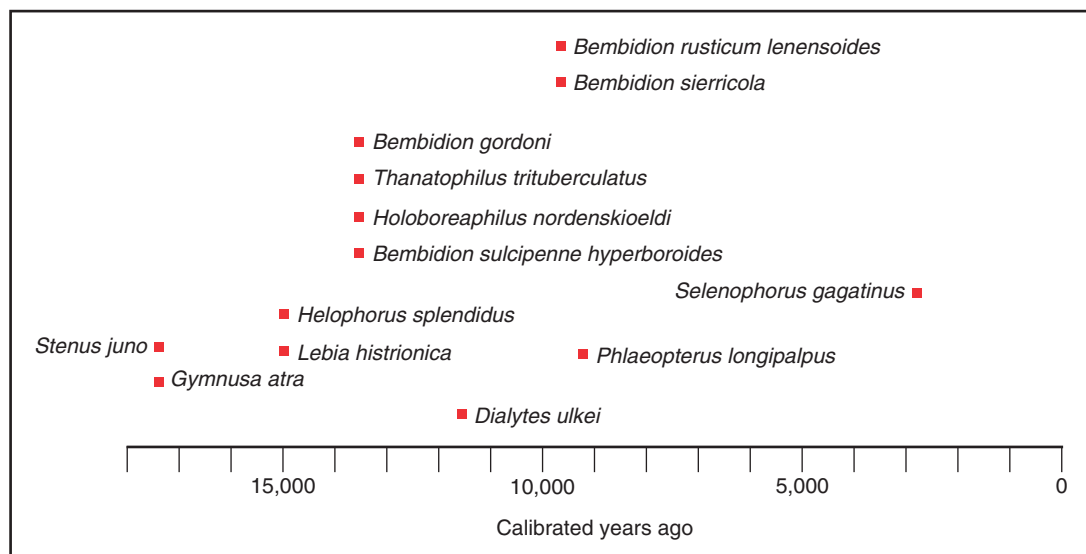
Figure 3 Last recorded fossil occurrence of various beetle species in Rocky Mountain region postglacial fossil assemblages. After Elias, 1981.

(Hydrophilidae), *Helophorus splendidus*. This beetle is found today in the northern Holarctic regions, including northeastern Siberia and the arctic coast of the Canadian Northwest Territories. It was found also in the 17.8 kya-assemblage from Lamb Spring, and is indicative of tundra conditions at this site.

The Huntington Canyon site, in the subAlpine zone of the Wasatch Mountains of Utah, yielded one species that has been regionally extirpated. The assemblage dates to 13.2 kya. *Bembidion gordoni* is a riparian ground beetle that lives on the banks of fast-running mountain streams. Today, however, its distribution is restricted to the mountains of the Pacific Northwest, from British Columbia to Oregon. Based solely on its modern distribution, a biogeographer might describe *B. gordoni* as endemic to the Pacific Northwest, but the Huntington fossil record demonstrates that it was more widespread in the recent past (i.e., 'recent' in terms of the longevity of the species).

Of the species extirpated during the Holocene, only one has shifted its distribution to the north. The riparian ground beetle, *Bembidion rusticum*, now lives only in British Columbia and northward, a distance of more than 2,600 km from Lake Emma, Colorado, where it was found as an early Holocene fossil. Lake Emma also yielded *Bembidion sierricola*, which is restricted today to the mountains of the Pacific Northwest, from California to southern British Columbia (Lindroth, 1963). The dung beetle (Scarabaeidae) *Dialytes ulkei*, was extirpated from the Rockies sometime after 9,600 yr BP. Its last occurrence in the regional fossil record was at La Poudre Pass, Colorado (Fig. 2). *D. ulkei* is an eastern North American species today, ranging from southern Quebec, southward in the Appalachian Mountain chain to South Carolina. Finally, the ground beetle, *Selenophorus gagatinus*, was last recorded from Colorado in a 2,400 yr BP assemblage from the Roaring River, in Rocky Mountain National Park (Fig. 2). Today *S. gagatinus* is an eastern North American species, ranging as far west as Indiana. In the late Quaternary interval, it was widespread in western North America, as it was also found in ancient packrat middens from the northern Chihuahuan Desert (Fig. 4), in assemblages ranging from 24 to 4.7 kya (Elias and Van Devender, 1990).

Based on the fossil evidence discussed above, it is clear that the current biological communities of the Rocky Mountain region developed only since the end of the last glaciation. They are the product of changing Quaternary environments. Changes in distribution have been large-scale and rapid. These changes demonstrate the great mobility of many beetle species, and their ability to move great distances in order to satisfy their ecological requirements in the face of changing climates. These changes also suggest that the current insect communities of the Rocky Mountain region are simply the latest reshuffling of species, and that species composition is probably in a more or less continuous state of flux (Elias, 1991).

Since the 1980s, insect fossils from packrat middens have received intensive study. Fossil insect research has been done in the Sonoran Desert and the Great Basin, but the most intensively studied region (191 midden insect fossil samples from 27 sites) is the Chihuahuan Desert (Elias and Van Devender, 1990, 1992; Elias *et al.*, 1995). The fossil insect assemblages from the southern Chihuahuan Desert in Mexico contain mixtures of desert- and temperate-zone species (Fig. 4) in almost every interval from the late glacial through to the late Holocene. Midden assemblages from locations farther north in the Chihuahuan Desert are generally separated into glacial-age faunas with temperate-zone affinities and postglacial faunas with desert-zone affinities. The 'no modern analog' faunal assemblages indicate that the late Quaternary environments in this region were unlike any that exist today. After 14 kya, most temperate-zone beetle species in the central and northern regions of the Chihuahuan Desert were replaced by either desert species or by more cosmopolitan taxa. The faunal change suggests a climatic shift from cool, moist conditions of Wisconsin glacial times to hotter, drier conditions in the early Holocene.

In the northern Chihuahuan Desert, woodland environments persisted until 13 kya, but the insect data suggest considerable open ground, with grasses at least locally important at the midden sites. The transition from the temperate (glacial) fauna to the more xeric postglacial fauna started by 14.7 kya. The timing of this faunal change was essentially synchronous throughout the northern Chihuahuan Desert. A major difference between the Big Bend and northern Chihuahuan Desert scenarios is the nature of this faunal change. In the Big Bend region, the transition was characterized by the disappearance of nearly all temperate species at about 14 kya. However, the xeric-adapted fauna did not appear in the Big Bend records until about 8.4 kya. In the northern Chihuahuan Desert assemblages, the xeric species first appeared at 14.7 kya, and several of the temperate grassland species that had lived there during the last glaciation persisted well into the Holocene. This mixture of xeric and temperate elements makes ecological sense, because these northern faunas were living close to the edge of the Chihuahuan Desert. The gradual shifting of northern desert boundaries in the
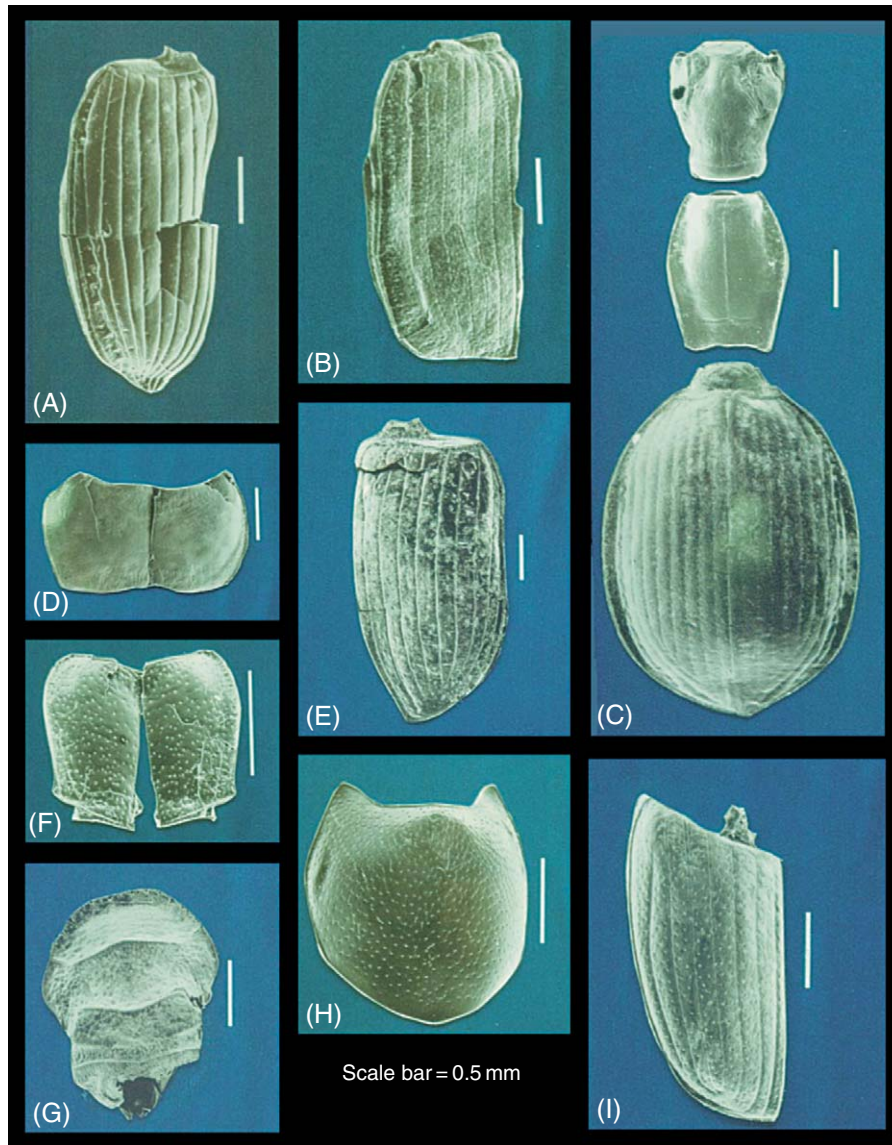
Figure 4 Scanning electron micrographs of fossil beetles from Chihuahuan Desert packrat midden assemblages. (A) left elytron of the ground beetle *Selenophorus gagatinus*; (B) left elytron of the ground beetle *Lebia lecontei*; (C) head, pronotum, and elytra of the ground beetle *Agonum (Rhadine) longicolle*; (D) pronotum of the ground beetle *Harpalus herbivagus*; (E) right elytron of the ground beetle *Piosoma setosum*; (F) pronotum of the ground beetle *Cymindis* cf. *borealis*; (G) head capsule of the dung beetle *Onthophagus brevifrons*; (H) pronotum of the dung beetle *Onthophagus cavernicollis*; (I) left elytron of the dung beetle *Onthophagus brevifrons*.

Holocene probably created many marginal habitats for temperate species. By about 8.4 kya, the dominance of xeric species indicates establishment of desert environments, including desert grasslands, throughout the Chihuahuan Desert region. After 2.6 kya, the last of the temperate species was replaced by species associated with desert-scrub communities.

Work on late Quaternary insect faunas from the Colorado Plateau region (Elias *et al*., 1992) suggests that late Wisconsin climatic conditions were cooler and moister than present, and that the plateau supported a mosaic of grassland and shrub communities without modern analog. The temporal and spatial coverage of midden sites is relatively poor for this enormous region, especially in comparison with the work done on middens from the Chihuahuan Desert. However, it is possible to say that the transition from glacial to postglacial climatic regimes took place after 17 kya. Paleobotanical data suggest that major regional warming was well underway by 13 kya (Cole, 1990). The fossil insect data indicate that the most arid conditions in the Great Basin region occurred within the last 1,500 years.

Insect faunas have also been studied from several sites in the Sonoran Desert (Hall *et al*., 1989, 1990; Clark and Sankey, 1999). Unlike the Chihuahuan

Desert insect fauna, the Sonoran Desert fauna indicates little change from the late Pleistocene through to modern times. All taxa found in the Sonoran middens probably live within a few kilometers of the midden sites today. The Sonoran arthropod fauna showed a marked increase in diversity during the late Holocene, as more subtropical plants and warmer climates became established about 4.5 kya. Many warm-adapted beetles probably dispersed into southern Arizona from Sonora, Mexico, during the last 4 kyr. The increase in diversity in fossil arthropod assemblages has been correlated with the frequency of winter freezes, and secondarily with the amount of summer precipitation. This late Holocene peak in species richness is in sharp contrast to the Chihuahuan Desert insect record, which showed the least number of species in late Holocene samples. If the Sonoran Desert insect fauna truly was stable through the late Quaternary, then this represents a significant difference between the Sonoran and Chihuahuan desert insect faunal histories.

On the whole, the results of North American postglacial beetle studies tend to agree well with reconstructions based on other proxy data, such as pollen and plant macrofossils. The only important discrepancies concern early postglacial environments. The fossil beetle records of all studied North American regions show unequivocally that at least summer temperatures reached modern levels very early in the postglacial period. Warm-adapted beetles were colonizing the recently deglaciated landscapes in the midwest and the Rockies, providing evidence of this warming, even though low herbaceous vegetation persisted in these regions for up to 1,000 years after deglaciation. Likewise, in the Chihuahuan Desert, the shift from cool-temperate to warm-xeric beetle faunas anticipated the major changes in regional vegetation (notably, the upslope shift in lower tree lines) by up to 1,000 years (Elias and Van Devender, 1992). The rapidity and magnitude of postglacial warming identified in the fossil beetle records from both North America and Europe has been verified by rapid changes seen in oxygen isotope ratios of Greenland ice cores (Dansgaard *et al.*, 1989).

See also: **Beetle Records**: Overview; Postglacial Europe.

References

Bain, A. L. (1998). A seventeenth century beetle fauna from colonial Boston. *Historical Archaeology* **32**, 38–48.

Bain, A. (2001). Archaeoentomological and Archaeoparasitological Reconstructions at Îlot Hunt (CeEt-110): New Perspectives in Historical Archaeology (1850–1900). *British Archaeological Reports* S973.

Bain, A. L., Morgan, A. V., Burns, J. A., and Morgan, A. (1997). The paleoentomology of Rat's Nest Cave, Grotto Mountain, Alberta, Canada. *Quaternary Proceeding* **5**, 23–34.

Clark, W. H., and Sankey, J. T. (1999). Late Holocene Sonoran Desert arthropod remains from a packrat midden, Cataviña, Baja California Norté, México. *Pan-Pacific Entomologist* **75**, 183–199.

Cole, K. L. (1990). Reconstruction of past desert vegetation along the Colorado River using packrat middens. *Palaeogeography, Palaeoclimatology, Palaeoecology* **76**, 349–366.

Dansgaard, W., White, J. W. C., and Johnson, S. J. (1989). The abrupt termination of the Younger Dryas climate event. *Nature* **339**, 532–534.

Duplessy, J. C., Labeyrie, L. D., and Paterne, M. (1996). North Atlantic sea surface conditions during the Younger Dryas cold event. In *Late Quaternary Palaeoceanography of the North Atlantic Margins* (J. T. Andrews, W. E. N. Austin, H. Bergsten, and A. E. Jennings, Eds.), *Geological Society Special Publication* **111**, 167–175.

Elias, S. A. (1982). Holocene insect fossil assemblages from northeastern Labrador. *Arctic Alpine Research* **14**, 311–319.

Elias, S. A. (1986). Fossil insect evidence for late Pleistocene paleoenvironments of the Lamb Spring site, Colorado. *Geoarchaeology* **1**, 381–386.

Elias, S. A. (1991). Insects and climate change: fossil evidence from the Rocky Mountains. *Bioscience* **41**, 552–559.

Elias, S. A. (2000). Late Pleistocene climates of Beringia, based on fossil beetle analysis. *Quaternary Research* **53**, 229–235.

Elias, S. A., Anderson, K., and Andrews, J. T. (1996). Late Wisconsin climate in the northeastern United States and southeastern Canada, reconstructed from fossil beetle assemblages. *Journal of Quaternary Science* **11**, 417–421.

Elias, S. A., Mead, J. I., and Agenbroad, L. D. (1992). Late Quaternary arthropods from the Colorado Plateau, Arizona and Utah. *Great Basin Naturalist* **52**, 59–67.

Elias, S. A., and Toolin, L. J. (1989). Accelerator dating of a mixed assemblage of late Pleistocene insect fossils from the Lamb Spring site, Colorado. *Quaternary Research* **33**, 122–126.

Elias, S. A., and Van Devender, T. R. (1990). Fossil insect evidence for Late Quaternary climatic change in the Big Bend region, Chihuahuan Desert, Texas. *Quaternary Research* **34**, 249–261.

Elias, S. A., and Van Devender, T. R. (1992). Insect fossil evidence of late Quaternary environments in the northern Chihuahuan Desert of Texas and New Mexico: comparisons with the paleobotanical record. *Southwest. Naturalist* **37**, 101–116.

Elias, S. A., Van Devender, T. R., and De Baca, R. (1995). Insect fossil evidence of Late Glacial and Holocene environments in the Bolson de Mapimi, Chihuahuan Desert, Mexico: comparisons with the paleobotanical record. *Palaios* **10**, 454–464.

Grimm, E. C., and Jacobson, G., Jr. (2004). Late-Quaternary vegetation history of the eastern United States. In *The Quaternary Period in the United States* (A. R. Gillespie, S. C. Porter and B. F. Atwater, Eds.), pp. 381–402. Elsevier, Amsterdam.

Hall, W. E., Olson, C. A., and Van Devender, T. R. (1989). Late Quaternary and modern arthropods from the Ajo Mountains of southwestern Arizona. *Pan-Pacific Entomologist* **65**, 322–347.

Hall, W. E., Olson, C. A., and Van Devender, T. R. (1990). Late Quaternary and modern arthropods from the Puerto Blanco Mountains, Organ Pipe Cactus National Monument, southwestern Arizona. In *Packrat Middens, the last 40,000 years of biotic change* (J. L. Betancourt, T. R. Van Devender, and P. S. Martin, Eds.), pp. 363–379. University of Arizona Press, Tucson.

Lavoie, C., Elias, S. A., and Payette, S. (1997). Holocene fossil beetles from a treeline peatland in subarctic Québec. *Canadian Journal of Zoolology* **75,** 227–236.

Lavoie, C., and Arseneault, D. (2001). Late Holocene climate of the James Bay area, Québec, Canada, reconstructed using fossil beetles. *Arctic, Antarctic, and Alpine Research* **33,** 13–18.

Levesque, A. J., Cwynar, L. C., and Walker, I. R. (1997). Exceptionally steep north-south gradients in lake temperatures during the last deglaciation. *Nature* **385,** 423–426.

Lotter, A. F., Walker, I. R., Brooks, S. J., and Hofmann, W. (1999). An intercontinental comparison of chironomid palaeo-temperature inference models: Europe vs North America. *Quaternary Science Reviews* **18,** 717–735.

Miller, R. F., and Elias, S. A. (2000). Late-glacial climate in Maritime Canada, reconstructed from Mutual Climatic Range analysis of fossil Coleoptera. *Boreas* **29,** 79–88.

Pauketat, T. R., Kelly, L. S., Fritz, G. J., Lopinot, N. H., Elias, S. A., and Hargrave, E. (2002). The residues of feasting and public ritual at early Cahokia. *American Antiquity* **67,** 52–65.

Schwert, D. P., and Ashworth, A. C. (1988). Late Quaternary history of the northern beetle fauna of North America: a synthesis of fossil distributional evidence. *Memoirs of the Entomological Society of Canada* **144,** 93–107.

Short, S. K. (1985). Palynology of Holocene sediments Colorado Front Range: vegetation and treeline changes in the subalpine forest. *American Association of Stratigraphic Palynologists Contribution Series* **16,** 7–30.

Short, S. K., and Elias, S. A. (1987). New pollen and beetle analysis at the Mary Jane site, Colorado: evidence for Late-Glacial tundra conditions. *Geological Society of American Bulletin* **98,** 540–548.

Beringia *see* **Archaeological Records**: Global Expansion 300,000-8000 years ago, Americas; **Beetle Records**: Late Pleistocene of North America; **Dune Fields**: High Latitudes; **Glaciations**: Late Pleistocene Events in Beringia; **Paleoceanography, Records**: Late Pleistocene North Pacific; **Plant Macrofossil Records**: Arctic North America; **Pollen Records, Late Pleistocene**: Northern North America; **Vertebrate Records**: Late Pleistocene of North America; Late Pleistocene of Northern Asia

---

Biogenic Carbonate Studies *see* **Carbonate Stable Isotopes**: Biogenic Studies

---

Bond Cycles *see* **Paleoclimate Reconstruction**: Sub-Milankovitch (DO/Heinrich) Events