

## Late Pleistocene of North America

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Beetles are the most diverse group of organisms on Earth, and their exoskeletal remains preserve well in water-logged sediments of Pleistocene age. Studies of late Pleistocene fossil beetle assemblages have been carried out throughout many regions of North America in recent decades. 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.

The paleotemperature estimates reported here are derived from the mutual climatic range (MCR) of paleoclimate analysis, as discussed in the overview article for this section. For the sites in eastern and central North America, the MCR method was used to provide estimates of mean temperatures of the warmest ( $T_{\max}$ ) and coldest ( $T_{\min}$ ) months of the year.  $T_{\max}$  and  $T_{\min}$

estimates are discussed in terms of departures from the modern  $T_{\max}$  and  $T_{\min}$  of the study sites in question.

### Research in Eastern North America

Pleistocene insect fossil studies began in earnest in the 1970s, with the most intensively studied region of North America being the central and eastern United States and southeastern Canada. Several fossil beetle assemblages in eastern North America are thought to represent Marine Isotope Stage (MIS) 5e, the last interglaciation. However, the ages of these fossil assemblages are tentative. One of the richest beetle faunas in this group is from Innerkip, Ontario (Fig. 1, No. 1). This fauna includes several warm-adapted species, and MCR analysis of the fauna (Table 1) yielded an estimate of  $T_{\max}$  that is essentially the same as modern parameters. The fossil assemblage from the Pointe-Fortune site on the southern Ontario–Quebec border (Fig. 1, No. 2) is also thought to derive from MIS 5 (Anderson *et al.*, 1990). This fauna contains boreal species that indicate colder than modern climate (Table 1), so perhaps it reflects a late MIS 5 environment. Likewise,



Figure 1 Map of eastern and central North America showing locations of fossil sites discussed in text. Site numbers match those in Table 1.

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

Site	Age (cal yr BP × 1000)	Late Pleistocene		Modern		Change in Temperature		References <sup>a</sup>
		T <sub>max</sub> (°C)	T <sub>min</sub> (°C)	T <sub>max</sub> (°C)	T <sub>min</sub> (°C)	July ΔT (°C)	January ΔT (°C)	
1. Innerkip, Ont.	MIS 5e	16–19	–16 to –8	20.4	–6.3	–4.4 to –1.4	–9.7 to –1.7	Pilny and Morgan (1987), Churcher <i>et al.</i> (1990)
2. Pointe Fortune, Que	MIS 5	14–17	–22.5 to –6	19.3	–9.8	–5.3 to –2.3	–12.7 to +3.8	Anderson <i>et al.</i> (1990)
3. Henday, Man.	MIS 5	8.5–10	–32.5 to –27.5	15.3	–25.8	–6.8 to –5.3	–6.7 to –1.7	Nielsen <i>et al.</i> (1986)
4. Owl Creek, Ont.	MIS 5	13–15	–24 to –19	17.4	–17.5	–4.4 to –2.4	–6.5 to –1.5	Mott and DiLabio (1990)
5. Chaudiere Valley, Que	>52	10–10.5	–30 to –28	18	–13	–8 to –7.5	–17 to –10	Matthews and Mott (1987), Elias (1999)
6. Titusville, PA #6	46.5	12.75–13.5	–19.3 to –17.5	20.3	–5.1	–7.4 to –6.8	–14.2 to –12.4	Cong <i>et al.</i> (1996), Elias (1999)
6. Titusville, PA #5	45.7	15–15.5	–24 to –23	20.3	–5.1	–5.3 to –4.8	–18.9 to –17.9	Cong <i>et al.</i> (1996), Elias (1999)
6. Titusville, PA #4	45	18.5–19.3	–10.5 to –8.25	20.3	–5.1	–1.8 to –1	–5.4 to –3.2	Cong <i>et al.</i> (1996), Elias (1999)
6. Titusville, PA #3	44.3	13.5–14.5	–30.5 to –27.5	20.3	–5.1	–6.8 to –5.8	–25.4 to –22.4	Cong <i>et al.</i> (1996), Elias (1999)
6. Titusville, PA #2	43.7	12–13	–31 to –28	20.3	–5.1	–8.3 to –7.3	–25.9 to –17.5	Cong <i>et al.</i> (1996), Elias (1999)
6. Titusville, PA #1	43.2	11.8–12.5	–31.3 to –22.5	20.3	–5.1	–8.5 to –7.8	–26.2 to –17.4	Cong <i>et al.</i> (1996), Elias (1999)
7. Clarksburg, Ont.	>40.6	10–12	–31 to –17	19.1	–8.9	–9.1 to –7.1	–22.1 to –8.1	Warner <i>et al.</i> (1988), Elias (1999)
8. St. Charles, IA	40.1	17–20.5	–16.5 to –6.5	23.8	–6.9	–6.8 to –3.3	–9.6 to +0.4	Baker <i>et al.</i> (1991), Elias (1999)
9. Athens, IL	29.9–26.7	13–15	–19.5 to –13	24.6	–4.1	–11.6 to –9.6	–15.4 to –8.9	Morgan (1987), Elias (1999)
10. Wedron, IL	25.8	12–12.5	–30 to –26.5	23.6	–5.9	–11.6 to –11.1	–24.1 to –20.6	Garry <i>et al.</i> (1990), Elias (1999)
11. Elkader, IA	24.5	13–15	–27 to –22	22.6	–9.2	–9.6 to –7.6	–17.8 to –12.8	Schwert (1992), Elias (1999)
12. Salt River, MO	23.3	14.5–16	–22.3 to –15.5	22	–4.4	–7.5 to –6	–17.9 to –11.1	Schwert <i>et al.</i> (1997), Elias (1999)
13. Salt Spring Hollow, IL	22.5	12.8–14.8	–27.3 to –19.3	24.6	–3.5	–11.8 to –9.8	–23.8 to –15.8	Schwert <i>et al.</i> (1997), Elias (1999)
14. Bonfils Quarry, MO	20.8	14–16.3	–26 to –17	26.6	–1.5	–12.6 to –10.3	–24.5 to –15.5	Schwert <i>et al.</i> (1997), Elias (1999)
15. Conklin Quarry, IA	20.7	11.5–12.5	–29 to –27	22.3	–9	–10.8 to –9.8	–20 to –18	Baker <i>et al.</i> (1986), Elias <i>et al.</i> (1996a)
16. Saylorville, IA	19.4	12–16	–30 to –10	22.7	–9.1	–10.7 to –6.7	–20.9 to –0.9	Schwert (1992), Elias <i>et al.</i> (1996a)
17. Ft. Dodge, IA/I	18	12–13	–26 to –20	23.1	–9.4	–11.9 to –10.9	–16.6 to –10.6	Schwert (1992), Elias <i>et al.</i> (1996a)
17. Ft. Dodge, IA/II	17.3	11.5–12.5	–28.5 to –19.5	23.1	–9.4	–11.4 to –12.4	–19.1 to –10.1	Schwert (1992), Elias <i>et al.</i> (1996a)
18. Weaver Drain, MI	17	12.5–16.5	–29.5 to –6.5	21.1	–6.2	–8.6 to –4.6	–23.3 to –0.3	Morgan <i>et al.</i> (1981), Elias <i>et al.</i> (1996a)
19. Winter Gulf, NY/W08	15.4	17.7–20.5	–10 to –4.5	20.4	–5.2	–2.9 to +0.1	–4.8 to +0.7	Schwert and Morgan (1980), Elias <i>et al.</i> (1996a)
20. Gage St., Ont./G8	15.0–14.5	11.5–13.5	–25.5 to –11.5	19.9	–7.5	–8.4 to –6.4	–18 to –4	Schwert <i>et al.</i> (1985), Elias <i>et al.</i> (1996a)

(Continued)

**Table 1** (Continued)

Site	Age (cal yr BP × 1000)	Late Pleistocene		Modern		Change in Temperature		References <sup>a</sup>
		$T_{\max}$ (°C)	$T_{\min}$ (°C)	$T_{\max}$ (°C)	$T_{\min}$ (°C)	July $\Delta T$ (°C)	January $\Delta T$ (°C)	
19. Winter Gulf, NY/W06	14.8	16.5–21	–11.5 to –4	20.4	–5.2	–3.9 to +0.6	–8.6 to +1.2	Schwert and Morgan (1980), Elias <i>et al.</i> (1996a)
21. Rostock, Ont.	14.7	12–15	–28 to –20	19.4	–7.8	–7 to –4.4	–20.2 to –12.2	Pilny and Morgan (1987), Elias <i>et al.</i> (1996a)
22. Newton, PA	14.6	10–15	–31 to –9	19.7	–5.6	–9.7 to –4.7	–25.4 to –3.4	Barnowsky <i>et al.</i> (1988), Elias <i>et al.</i> (1996a)
23. Norwood, MN/Peat	14.5	16.5–21.5	–17.5 to –3	22.1	–12.3	–5.6 to –0.6	–5.2 to +9.3	Ashworth <i>et al.</i> (1981), Elias <i>et al.</i> (1996a)
19. Winter Gulf, NY/W04	14.5	15–21.5	–14 to 0	20.4	–5.2	–5.4 to +1.1	–9.8 to +5.2	Schwert and Morgan (1980), Elias <i>et al.</i> (1996a)
20. Gage St., Ont./G7	14.5–12.8	20–21	–5.5 to –2.5	19.9	–7.5	0 to +1.1	+2 to +5	Schwert <i>et al.</i> (1985), Elias <i>et al.</i> (1996a)
23. Norwood, MN/M.S.	13.8	15–20	–25 to –12	22.1	–12.3	–7.1 to –2.1	–12.7 to –0.3	Ashworth <i>et al.</i> (1981), Elias <i>et al.</i> (1996a)
21. Rostock, Ont/65–75	13.6	15–20.5	–22.5 to –4.5	19.4	–7.8	–4 to +0.6	–14.7 to +3.3	Pilny and Morgan (1987), Elias <i>et al.</i> (1996a)
24. Two Creeks, WI	13.6	12.5–13.5	–16.5 to –11.5	21.1	–7.3	–8.8 to –7.8	–10.2 to –4.2	Morgan and Morgan (1979), Elias <i>et al.</i> (1996a)
25. Kewaunee, WI	13.5	12.5–17.5	–28 to –5	20.8	–7.8	–8.3 to –3.3	–20.2 to +2.8	Garry <i>et al.</i> (1990), Elias <i>et al.</i> (1996a)
23. Norwood, MN/U.S.	13.4	17–18	–11 to –7	22.1	–12.3	–5.1 to –4.1	+1.3 to +5.3	Ashworth <i>et al.</i> (1981), Elias <i>et al.</i> (1996a)
21. Rostock, Ont/55–65	13.3	17–21	–15.5 to –2.5	19.4	–7.8	–2.4 to +1.6	–7.7 to +5.3	Pilny and Morgan (1987), Elias <i>et al.</i> (1996a)
27. Brookside, NS	13	12.5–20	–31.5 to 5	18.4	–7.4	–5.9 to +1.6	–24.1 to +12.4	Mott <i>et al.</i> (1986)
28. St. Eugene, Que	12.9	10–12.5	–31 to –18.5	17.2	–13.1	–7.2 to –4.7	–17.9 to –5.4	Mott <i>et al.</i> (1981)
29. Lockport Gulf, NY L01	12.8	17.5–21.5	–14 to –3	21.5	–4.8	–4 to 0	–9.2 to +1.8	Miller and Morgan (1982)
30. Johns Lake, ND	12.7	13.5–15.5	–26.5 to –20	20	–17	–6.5 to –4.5	–6.5 to 0	Ashworth and Schwert (1992)
31. Eighteen Mile R., Ont.	12.4	14–15	–16.5 to –10	19.8	–5.8	–5.8 to –4.8	–10.7 to –4.2	Ashworth (1977)
29. Lockport Gulf, NY L02	12	12.5–17.5	–25 to –5	21.5	–4.8	–9 to –4	–20.2 to +0.2	Miller and Morgan (1982)
32. St. Hilaire, Que	11.7	16.5–17.5	–15 to –10	20.7	–10.2	–4.2 to –3.2	–4.8 to +0.2	Mott <i>et al.</i> (1981)
26. Nichols Brook, NY-C	11.5–10.1	14.5–18	–21 to –12.5	18.1	–10	–3.5 to –0.1	–11 to –2.5	Fritz <i>et al.</i> (1987)

<sup>a</sup>References available from the QBib Web site, [www.bugs2000.org/qbib.html](http://www.bugs2000.org/qbib.html)

faunal assemblages from the Henday site in northern Manitoba (Fig. 1, No. 3) and the Owl Creek site in northeastern Ontario (Fig. 1, No. 4) indicate climates that were colder than today (Table 1), based on the presence of Arctic ground beetles (Carabidae).

Assemblages from MIS 4 and 3 have been described from several localities in the Great Lakes region, as summarized by Elias (1994) and Ashworth (2004). MIS 4 assemblages from southeastern Canada contain tundra and tree-line beetle faunas. Faunal assemblages containing the same species also occur in regional MIS 2 assemblages, so it appears that tundra and tree-line species inhabited the margins of the Laurentide ice sheet continually during Wisconsinan time.

A series of insect faunas indicate changing conditions during the last (Wisconsin) glaciation. To date, late Pleistocene beetle assemblages have been published from 26 sites in this region (Table 1). These range in age from >52,000 calibrated years before present (>52 kya) to 11.5 kya. The mid-Wisconsin interstadial, MIS 3, is thought to have lasted from approximately 65–25 ka. Isotopic data from Greenland ice cores and North Atlantic oceanic cores show multiple, abrupt climate changes during marine isotope stage 3 (Groote et al., 1993). Events within the first half of this interval cannot be dated by the radiocarbon method, and organic deposits that are stratigraphically correlated to the mid-Wisconsin interval are poorly dated in many regions of North America. The analysis of fossil beetle assemblages has progressed sufficiently in North America to allow reconstructions of the timing and intensity of MIS 3 climatic change (Elias, 1999).

### Paleoenvironments of Central and Eastern North America during the Last Glaciation

The oldest MIS 3 beetle fauna considered here comes from the Chaudière valley, southeastern Quebec (Fig. 1, No. 5). The fauna is associated with a mid-Wisconsin cold interval. Radiocarbon ages of this formation include a date of >54 ka. The sediments that yielded the fossils were underlain by a glacial till and overlain by late Wisconsin till. The beetle fauna is indicative of arctic tundra environments and includes many cold-adapted species.  $T_{\max}$  was depressed by approximately 6°C, and  $T_{\min}$  was approximately 13°C colder than today (Table 1).

The clearest indication of the strength of interstadial warming in eastern North America comes from the series of beetle faunal assemblages from Titusville, Pennsylvania (Fig. 1, No. 6). The six fossil assemblages were deposited between approximately

46 and 43 kya. Within this interval, the Titusville faunas reflect climatic amelioration, followed by cooling. The oldest fauna (46.5 kya) indicates cooling of both  $T_{\max}$  and  $T_{\min}$  to approximately the same level as at the Chaudière valley site (Table 1). At the height of regional warming (ca. 45.7 kya),  $T_{\max}$  was only 2°C less than modern levels, and  $T_{\min}$  was approximately 6°C colder than modern. This warm interval occurred at approximately the same time as the Upper Warren Interstadial in Britain and the warm sea-surface temperature interval between Heinrich events 4 and 5 (Elias, 1999). By the end of the interstadial event (43.2 kya), regional climates had cooled to even lower levels than previously. Thus, in the space of approximately 3,000 years, regional climates oscillated from subarctic to boreal and back again.

A beetle assemblage dated 38.5 kya from St. Charles, Iowa (Fig. 1, No. 8), reflects prairie or savanna environments with patches of conifer-hardwood forest (Baker et al., 1991). The St. Charles beetle fauna was indicative of somewhat milder climate than during full glacial conditions but well below the levels of warming suggested by the interstadial fauna from Titusville. Later in the MIS 3 interval (32.9–28.9 kya), fossil assemblages from Illinois and Iowa indicate closed spruce forests. The sketchy picture that emerges for the early and mid-Wisconsinan is one of spatial and temporal heterogeneity in which populations of plants and insects were responding more dynamically than at any time during the Holocene (Ashworth, 2004).

By approximately 30 kya, the beetle evidence suggests that central North American climates had cooled to full-glacial levels (Table 1).  $T_{\max}$  was approximately 10°C colder than today at sites such as Athens and Wedron in Illinois (Fig. 1, Nos. 9 and 10). Regional faunas contained mixtures of boreal and arctic species, depending on latitude. Southerly sites, such as Salt Spring Hollow, Illinois (Fig. 1, No. 13), contained boreal beetle assemblages just before and during the Last Glacial Maximum (LGM). More northerly sites, such as Conklin Quarry, Iowa (Fig. 1, No. 15), contained beetles with Arctic and subArctic affinities.

In the mid-western region, Arctic beetles replaced the boreal forest fauna along the southern margin of the Laurentide ice sheet at approximately 25.8 kya. Colonization was probably from populations that dispersed southward in front of the growing ice sheet and from populations that dispersed westward and eastward from montane refugia in the Appalachian and Rocky Mountains, respectively (Schwert and Ashworth, 1988). From 25.8–17.7 kya, Arctic and subArctic species inhabited a

discontinuous tundra zone along the margin of the ice sheet. Fossil assemblages typical of this time have been reported from Iowa to New York (Ashworth, 2004). At the end of the glaciation, these cold-adapted faunas were forced to migrate in order to survive. Some species found refuge in high mountains, such as the Rocky Mountains in the west and the tops of the Appalachian Mountains in the east. Other species died out in the middle latitudes of the continent, and only their Beringian populations in ice-free regions of northwestern North America survived beyond the end of the Pleistocene.

The earliest sign of warming following the LGM comes from Weaver Drain, Michigan (Fig. 1, No. 18). This site was ice proximal at 17 kya, but MCR analysis (Table 1) shows that  $T_{\max}$  had started to rise above the levels reconstructed from a 17.3-ka assemblage at Fort Dodge, Iowa (Fig. 1, No. 17). Ice proximal sites showed the effects of local cooling until the ice margin retreated and pockets of stranded dead ice melted, after approximately 12.6 kya.

By approximately 15.4 kya, substantial warming had occurred at Winter Gulf, New York (Fig. 1, No. 19).  $T_{\max}$  values were less than 3° C cooler than modern, and  $T_{\min}$  values were less than 5° C cooler than modern. This degree of warming was not seen in the oldest assemblages from Gage St., Ontario (Fig. 1, No. 20). However, during the interval 14.5–12.8 kya,  $T_{\max}$  and  $T_{\min}$  at Gage St. rose above modern levels (Table 1). This was also the case at Nichols Brook, New York (Fig. 1, No. 26) and Rostock, Ontario (Fig. 1, No. 21) between 13.3 and 11.5 kya.

Between approximately 12.9 and 11.5 kya, a third set of sites (St. Eugene and St. Hilaire, Quebec, Eighteen Mile River, Ontario, and Lockport Gulf, New York) were situated near large bodies of glacial meltwater (proglacial lakes and the Champlain Sea). The large bodies of chilled water adjacent to these sites strongly affected local climates (Ashworth, 2004). After 11.5 kya the ice sheet margin had retreated well north of the study sites, and all the fossil assemblages reflect  $T_{\max}$  values near modern parameters (Table 1).

Beetle MCR reconstructions from northwest Europe show a sudden rise in seasonal temperatures by approximately 15.9 kya, followed by a general cooling through the late glacial interstadial, before dramatic cooling at 12.9 kya (the Younger Dryas chronozone), followed by a sudden rise in temperatures at approximately 11.5 kya (Coope and Lemdahl, 1995). The eastern North American results show almost a plateau of summer temperatures from 13–10 ka. The vegetation history, as reconstructed from fossil pollen assemblages, also suggests no climatic reversals during this interval (Grimm and

Jacobson, 2004). The lack of oscillations in the North American assemblages may be due to the effects of continental climate, whereas late glacial climates in northwest Europe were strongly affected by shifts in North Atlantic surface water (Coope and Lemdahl, 1995). The only insect evidence for cooling between 12.9 and 11.5 kya in North America comes from the maritime provinces of Canada (Walker, et al., 1991) and from Arctic Alaska.

## Research in Western North America

Late Pleistocene beetle assemblages have also been studied from a number of sites in western North America (Table 2). Insect fossils of this age from the Rocky Mountain region are discussed by Elias (1990, 1991). Full glacial age faunas, such as the assemblage dated 17.7 kya from Lamb Spring, Colorado (Fig. 2, No. 1), indicate that  $T_{\max}$  was 10–11° C colder than today. The earliest evidence for the start of postglacial warming is a 16.9-kya assemblage at the Mary Jane site in Colorado (Fig. 2, No. 2). Rapid warming occurred after 13.3 kya, with summer temperatures becoming warmer than present by 11.5 kya at False Cougar Cave, Montana (Fig. 2, No. 4). Many of the cold-adapted species in the Late Pleistocene Rocky Mountain fossil assemblages have since retreated upslope to the Alpine tundra, but not all species were able to do this. For instance, the cold-adapted rove beetle, *Holoboreaphilus nordenskiöldi*, was found in a late glacial age assemblage from Marias Pass, Montana (Fig. 2, No. 3). This species apparently died out in the midlatitudes at the end of the last glaciation. It is found today only in Arctic North America (Elias, 1991).

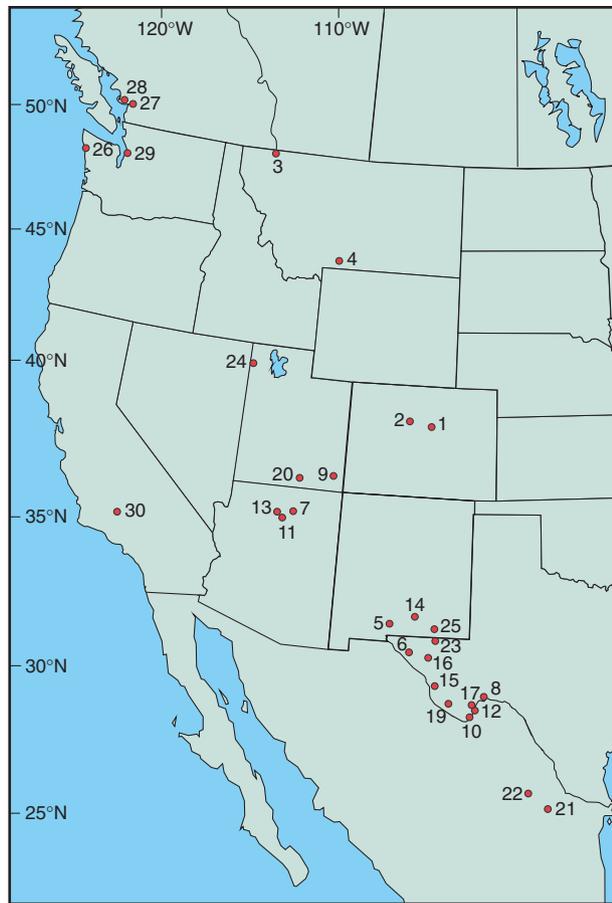
In the past 20 years, insect fossils from arid regions of the southwestern United States and northern Mexico have received intensive study. These studies are based on fossil remains extracted from packrat (*Neotoma*) middens. Packrat middens are caches of objects, including edible plants, cactus spines, insect and vertebrate remains, small pebbles and feces, brought to the rat's den site for a variety of reasons, including food, curiosity, and den protection; then they are cemented into black tarry masses by packrat urine. Late Pleistocene insect fossils have been studied from the Great Basin, but the most intensively studied region is the Chihuahuan Desert (Fig. 3). Most packrat midden beetle assemblages from the Sonoran Desert date to the Holocene.

Late Pleistocene faunas from the arid southwest were mixtures of temperate and desert species not seen in any one region today. Since the end of the Pleistocene, some of these species have become established in different desert regions (Elias, 1992). Others now live outside the desert zone, in temperate

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

Site	Age (cal yr BP × 1000)	Late Quaternary		Modern		Change in Temperature		References <sup>a</sup>
		T <sub>max</sub> (°C)	T <sub>min</sub> (°C)	T <sub>max</sub> (°C)	T <sub>min</sub> (°C)	July ΔT (°C)	January ΔT (°C)	
1. Lamb Spring, CO	17.7	10–11	–31 to –27	21.4	–1.3	–11.4 to –10.4	–29.7 to –25.7	Elias and Toolin, 1990; Elias, 1996
2. Mary Jane, CO	16.2	9.8–10.2	–29.3 to –27.6	13.4	–8.6	–3.6 to –3.2	–20.7 to –19	Short and Elias, 1987; Elias, 1996
2. Mary Jane, CO	15.4	10–10.2	–29.1 to –27.6	13.4	–8.6	–3.4 to –3.2	–20.5 to –19	Short and Elias, 1987; Elias, 1996
3. Marias Pass, MT	14.2	11–14	–30 to –16	13.9	–9	–2.9 to +0.1	–21 to –7	Elias, 1988, 1996
4. False Cougar Cave, MT	11.5	15.5–17.7	–4.5 to +0.25	13.5	–10.1	+2 to +4.25	+5.6 to +10.4	Elias, 1990, 1996
<i>Chihuahuan Desert and Great Basin packrat midden faunas</i>								
5. S. Organ Mountains, NM	>46.3–41.2	NA	NA	NA	NA	NA	NA	Elias and Van Devender (1992)
6. Hueco Mountains, TX	44.9–12.4	NA	NA	NA	NA	NA	NA	Elias and Van Devender (1992)
7. Kaetan Cave, AZ	35.8–17.5	NA	NA	NA	NA	NA	NA	Elias <i>et al.</i> (1992)
8. Maravillas Canyon, TX	32.7–13.8	NA	NA	NA	NA	NA	NA	Elias and Van Devender (1990)
9. Salt Creek Canyon, UT	32.4	NA	NA	NA	NA	NA	NA	Elias <i>et al.</i> (1992)
10. Baby Vulture Den, TX	31–17.5	NA	NA	NA	NA	NA	NA	Elias and Van Devender (1990)
11. Bida Cave, AZ	29.2–19.5	NA	NA	NA	NA	NA	NA	Elias <i>et al.</i> (1992)
12. Tunnel View, TX	28.9–12.3	NA	NA	NA	NA	NA	NA	Elias and Van Devender (1990)
13. Owl Roost, AZ	25.7	NA	NA	NA	NA	NA	NA	Elias <i>et al.</i> (1992)
14. Sacramento Mountains, NM	22.1–12.4	NA	NA	NA	NA	NA	NA	Elias and Van Devender (1992)
15. Bennett Ranch, TX	21.9–12.9	NA	NA	NA	NA	NA	NA	Elias and Van Devender (1992)
16. Streeruwitz Hills, TX	21.7–12.7	NA	NA	NA	NA	NA	NA	Elias and Van Devender (1992)
17. Ernst Tinaja, TX	20.6–13.3	NA	NA	NA	NA	NA	NA	Elias and Van Devender (1990)
18. Shafter, TX	19.2–13.3	NA	NA	NA	NA	NA	NA	Elias and Van Devender (1992)
19. Terlingua, TX	18.3	NA	NA	NA	NA	NA	NA	Elias and Van Devender (1990)
20. Bechan Cave, UT	16.2–13.4	NA	NA	NA	NA	NA	NA	Elias <i>et al.</i> (1992)
21. Puerto de Ventanillas, Coahuila, Mexico	16.2–15.2	NA	NA	NA	NA	NA	NA	Elias <i>et al.</i> (1993)
22. Cañon de la Fragua, Coahuila, Mexico	16.1–14.5	NA	NA	NA	NA	NA	NA	Elias <i>et al.</i> (1993)
23. Guadalupe Mountains, TX	15.9–13.8	NA	NA	NA	NA	NA	NA	Elias and Van Devender (1992)
24. Bonneville Estates, UT	13.6	17.5–19	NA	23.9	NA	–6.4 to –4.9	NA	Rhode (2000)
25. Guadalupe Mountains, NM	12.4–11.6	NA	NA	NA	NA	NA	NA	Elias and Van Devender (1992)
<i>Pacific regional sites</i>								
26. Kalaloch, WA	24.1–20.5	14–17	–19 to –11	18.9	5.2	–4.9 to –1.9	–24.2 to –16.2	Cong and Ashworth (1986)
27. Mary Hill, BC	22.6–22.5	11–18	–29 to –4	18.1	4.8	–7.1 to –0.1	–24.2 to –8.8	Miller <i>et al.</i> (1985)
28. Port Moody, BC	22.1	11–18	–29 to –4	18.1	4.8	–7.1 to –0.1	–24.2 to –8.8	Miller <i>et al.</i> (1985)
29. Discovery Park, WA	18	15–17	–16 to –10	18.1	4.8	–3.1 to –1.1	–24.8 to –14.8	Nelson and Coope (1982)
30. McKittrick, CA	14.3	NA	NA	NA	NA	NA	NA	Miller (1983)

<sup>a</sup>References available from the QBib Web site, [www.bugs2000.org/qbib.html](http://www.bugs2000.org/qbib.html)



**Figure 2** Map of western North America showing locations of fossil sites discussed in text. Site numbers match those in **Table 2**.

regions. The fossil insect record indicates that even sedentary, flightless beetles (e.g., the heavy-bodied weevils) have undergone marked distributional shifts in the American southwest within the space of a few centuries. Moreover, even highly specialized cave dwellers have somehow managed to move from one cave system to another in response to changes in late Wisconsin and Holocene environments.

Late Pleistocene beetle assemblages from the southern Chihuahuan Desert of Mexico (**Fig. 2**, Nos. 21 and 22) contain mixtures of desert and temperate zone species (Elias *et al.*, 1995). 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. Faunal assemblages with no modern analog are indicative of the late Quaternary environments unlike any that exist today. This conclusion is also borne out by the plant macrofossil record.

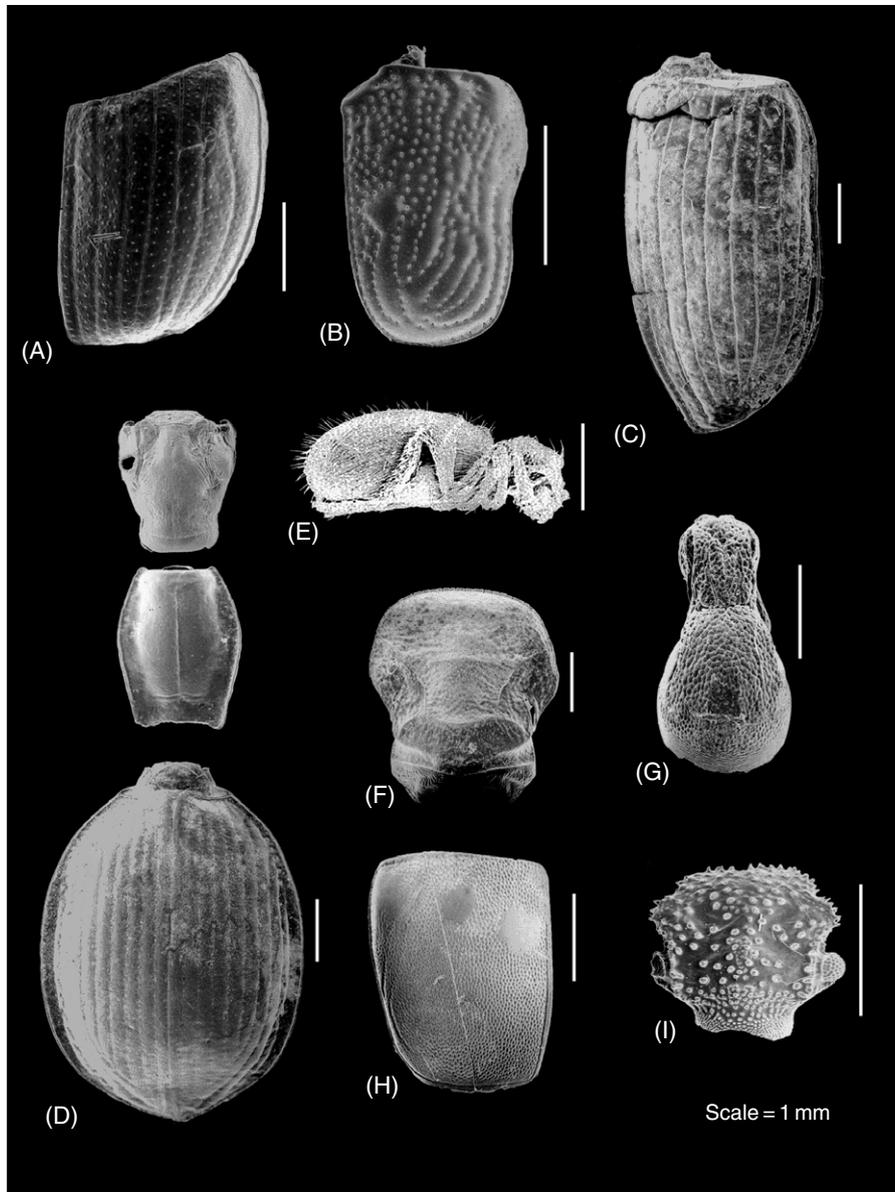
The insect faunas from the Big Bend region of southwest Texas (**Fig. 2**, Nos. 8, 10, 12, 17, and 19) suggest that there was greater effective moisture from

35–14 kya (Elias and Van Devender, 1990). During the late Wisconsin (MIS 2), many temperate grassland species lived in the Big Bend region. After 14 kya, most of these species were replaced by either desert species or more cosmopolitan taxa. The faunal change suggests a climatic shift from cool, moist conditions of full glacial times to hotter, drier conditions during the late glacial and early Holocene.

In the northern Chihuahuan Desert, full glacial (26.5–21.6 kya) faunal assemblages (**Fig. 2**, Nos. 5, 6, 14–16, 23, and 24) suggest widespread coniferous woodland at elevations as low as 1,200–1,400 m above sea level (Elias and Van Devender, 1992). These woodland environments persisted until 12.9 kya, but the insect data suggest considerable open ground, with grasses at least locally important at the midden sites. The grassland nature of the arthropod fauna was also suggested in the regional vertebrate record. The transition from the temperate Wisconsin fauna to the more xeric postglacial fauna started by 14.8 kya. The timing of this faunal change was essentially synchronous throughout the region. 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 from the record of all but one of the temperate insect species by approximately 14 kya. However, the xeric-adapted fauna did not appear in the Big Bend records until approximately 8.3 kya. In the northern Chihuahuan Desert assemblages, the xeric species first appeared at 14.8 kya, and several of the temperate grassland species from the Wisconsin interval 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 postglacial times probably created many marginal habitats for temperate species in ecotones between grassland and desert scrub.

Work on late Quaternary insect faunas from the Colorado Plateau region (**Fig. 2**, Nos. 7, 9, 11, 13, and 20) suggests that late Wisconsin climatic conditions there were cooler and moister than present, and that the plateau supported a mosaic of grassland and shrub communities without modern analog (Elias *et al.*, 1992).

MCR analysis of arid southwestern faunas (Elias, 1998) suggests that effective moisture exerts greater control on desert beetle distributions than does temperature. The author's MCR analysis of late Pleistocene beetle assemblages from the Mojave Desert (Elias, unpublished data) indicates that  $T_{\max}$  was 7–8° C cooler than it is today from 38–36 kya,



**Figure 3** Scanning electron micrographs of late Pleistocene fossil beetle specimens from the Chihuahuan Desert. (A) Elytron of *Onthophagus lecontei*; (B) elytron of *Pachybrachis mitis*; (C) elytron of *Piosoma setosum*; (D) head, pronotum, and elytra of *Rhadine longicollis*; (E) intact exoskeleton of *Ptinus*; (F) head of *Onthophagus cochisus*; (G) head of *Sapotes longipillis*; (H) elytron of *Hypocaccus estriatus*; (I) head of *Rhagoderma costata*.

and mean annual precipitation (MAP) was 3.5–4.4 times greater than it is today. In the eastern Great Basin, the Bonneville Estates site yielded a beetle fauna dated 13.6 kya. Several of the species in this fauna are found today in the Pacific Northwest region. MCR analysis of this fauna indicated that  $T_{\max}$  was 5–6°C cooler than today, and MAP was 525–675 mm, compared to modern MAP at the site of approximately 190–210 mm. These results agree well with paleoclimate reconstructions based on ancient pluvial lake levels (Benson, 2004) and regional paleobotany (Thompson *et al.*, 2004).

Miller (1983) discussed insect fossil assemblages from California asphalt deposits at McKittrick (Fig. 2, No. 29) and at Rancho La Brea in Los Angeles. The Rancho La Brea assemblages remain undated; the late Pleistocene McKittrick fauna dates to approximately 14.3 kya. Unlike the faunas of most other regions discussed here, the McKittrick and Rancho La Brea assemblages reflect conditions similar to those in southern California today.

Nelson and Coope (1982) described a diverse insect fauna dating from 18 kya from Seattle, Washington (Fig. 2, No. 28). Although the pollen

spectra associated with this assemblage suggest conditions substantially colder than present, the insects are characteristic of the modern Puget lowland. Nelson and Coope suggest that the discrepancy between the flora and insect fauna may be due to increased climatic continentality just before the last glacial advance. MCR analysis of this assemblage (Table 2) suggests that  $T_{\max}$  was 1–3° C colder than modern at the site, and that  $T_{\min}$  was considerably colder than modern.

Cong and Ashworth (1996) described a beetle fauna from the Kalaloch site in northwest Washington (Fig. 2, No. 25). This fauna dates from 24.1–20.5 kya, and MCR analysis indicates that summer temperatures were only slightly cooler than today (Table 2). Most of this fauna can be found today in the lowlands of the Pacific Northwest, but a few species are restricted today to the northern boreal forest regions (Ashworth, 2004).

In southern British Columbia, Miller *et al.* (1985) studied insect fossils from 22.6–22.1 kya at Mary Hill and Port Moody (Fig. 2, Nos. 26 and 27). These assemblages represent an open coniferous forest floor community, developed in cool, dry climatic conditions between two advances of the Cordilleran ice sheet.

Throughout western North America, both temperature and precipitation regimes changed dramatically throughout the late Pleistocene. These climatic changes brought about wholesale changes in regional ecosystems, as reflected in the fossil beetle record. Unlike eastern North America, the western regions are topographically diverse, with dozens of mountain ranges interspersed with valleys, canyons, and flatlands. Cold-adapted beetles dominated many late Pleistocene faunal assemblages, expanding their ranges downslope and southward in response to climatic cooling, then retreating upslope and northward in response to warming.

### Research in Eastern Beringia

During the late Pleistocene, eastern Beringia comprised the unglaciated regions of Alaska and the Yukon Territory. This region was an important refuge for arctic biota, including insects. Because of preservation in permafrost, the fossil beetle record of this region extends back into the late Tertiary. The nature of Pleistocene environments in eastern Beringia is a topic of considerable debate. Some patterns concerning Beringian paleoenvironments are beginning to emerge, but our reconstructions are far from complete. When I reported on the state of Pleistocene insect fossil research in this region in 1994, I noted that ‘an enormous amount of work is yet to be done.’ Although our knowledge has

increased in the past decade, the statement remains equally true today. The following discussion deals with published fossil data from 28 sites (Table 3, Fig. 4). The evidence has been reviewed most recently by Elias (2000, 2001) and Ashworth (2004).

Based on their stratigraphic position, a number of fossil beetle assemblages can be confidently placed in MIS 6 (Table 3), including assemblages from the Old Crow site (Fig. 4, No. 1), Chi’jee’s Bluff (Fig. 4, No. 2), and Kulukbuk Bluffs (Fig. 4, No. 3). These faunas reflect climates with depressed summer temperatures, but some sites yielded MCR estimates of  $T_{\min}$  that are near modern levels. Based on stratigraphic relationships with sediments containing the Old Crow tephra (dated 140 kya), several beetle assemblages from Alaska and the Yukon indicate that prior to the onset of full interglacial conditions in MIS 5e, temperatures were beginning to warm. This evidence comes from several sites on the Noatak River in northwestern Alaska (Fig. 4, Nos. 4–6) and the Nuyakuk site in southwestern Alaska (Fig. 4, No. 7). Full interglacial warming peaked at levels that varied from region to region. In southwestern Alaska, the height of MIS 5e amelioration was as much as 3.5° C warmer than modern at the Nuyakuk site. At the NK-37 site in northwestern Alaska,  $T_{\max}$  climbed to as much as 4.5° C above modern levels. Further east, summer temperatures were probably closer to modern levels. The best constrained estimate of average winter temperatures during MIS 5e comes from Chi’Jee’s Bluff. This estimate suggests that  $T_{\min}$  was approximately 4–7° C warmer than today, even though average summer temperatures at this site may have been slightly cooler than modern. Boreal insects and paleobotanical evidence combine to document the presence of coniferous forests in much of eastern Beringia during MIS 5e.

Beetle faunas associated with younger intervals of MIS 5 have yielded MCR estimates showing climatic cooling, with  $T_{\max}$  levels declining 2–3° C below modern parameters (Table 3). Two faunas thought to derive from MIS 4 indicate that summer temperatures continued to cool. The MIS 4 faunal assemblage from Hungry Creek, Yukon (Fig. 4, No. 9), yielded a  $T_{\max}$  estimate 6–9° C cooler than modern.

The long MIS 3 interstadial complex in eastern Beringia is represented by 25 faunal assemblages from 18 different sites. Warming intervals are indicated by faunas from the Titaluk River in northern Alaska (Fig. 4, No. 12) (46.4, 36, and 33.6 kya), from Cape Deceit on the Seward Peninsula (Fig. 4, No. 14) (42.2 kya), and from Kulukbuk Bluffs in southwestern Alaska (35 kya). The strongest indication of interstadial warming comes from the Titaluk River fauna dated 33.6 kya. This fauna yielded a  $T_{\max}$

**Table 3** Summary of fossil beetle assemblage data from sites in eastern Beringia

Site	Age (cal yr BP × 1000)	Late Quaternary		Modern		Change in Temperature		References <sup>a</sup>
		T <sub>max</sub> (°C)	T <sub>min</sub> (°C)	T <sub>max</sub> (°C)	T <sub>min</sub> (°C)	July ΔT (°C)	Jan ΔT (°C)	
1. Old Crow CRH15 78–91	MIS 6	8.75–10	–29 to –31.75	16	–29	–7.25 to –6	–2.75 to 0	Morlan and Matthews (1983)
2. Chi'jee's Bluff Stn 1A, 4	MIS 6	12.5–13.25	–20.5 to –18.5	16	–29	–3.5 to –2.75	+8.5 to +10.5	Matthews <i>et al.</i> (1990a)
3. Kulukbuk Bluff 25A	MIS 6	7.25–9.25	–32.75 to –28.75	14.8	–22.6	–7.55 to –5.55	–10.15 to –6.15	Elias (1992a)
4. Noatak NK-26 Unit 4	140	3.75–10.5	–17.5 to –36.25	11	–25.8	–7.25 to –0.5	–10.45 to +8.3	Elias <i>et al.</i> (1998a)
5. Noatak NK29a unit 3, lower	140	5–9	–29 to –21.5	11	–29	–6.0 to –2.0	0 to +7.5	Elias <i>et al.</i> (1998a)
2. Chi'jee's Bluff Stn 4, I&J	140	3.5–9.5	–36 to –21	16	–29	–12.5 to –5.5	–7.0 to +8.0	Matthews <i>et al.</i> (1990a)
2. Chi'jee's Bluff 87-2	MIS 6-5 transition	11.75–12.5	–28 to –27.5	16	–29	–4.25 to –3.5	+1.0 to +1.5	Matthews <i>et al.</i> (1990a)
5. Noatak 29A unit 3, upper	MIS 6-5 transition	12–12.5	–29 to –27	11	–25.8	+1.0 to +1.5	–3.2 to –1.2	Elias <i>et al.</i> (1998a)
6. Noatak 37 MEE 0.13–0.22	MIS 6-5 transition	9–11	–25.5 to –22	11	–25.8	–2.0 to 0	+0.3 to +3.8	Edwards <i>et al.</i> (2003)
7. Nuyakuk 13-1	MIS 6-5 transition	12.5–13	–29.25 to –28	12.7	–9.7*	–0.2 to +0.3	NA	Elias and Short (1992)
6. Noatak 37 MEE2 140–153	MIS 5e	12.5–15	–28.5 to –19	11	–25.8	+1.5 to +4	–2.7 to +6.8	Edwards <i>et al.</i> (2002)
6. Noatak 37 MEE2 0.97–1.06	MIS 5e	12–16	–27 to –16	11	–25.8	+1 to +5	–1.2 to +9.8	Edwards <i>et al.</i> (2002)
8. Eva Creek 3-1A	MIS 5e	12.5–13	–22.5 to –20	16.9	–23.4	–4.5 to –3.9	+0.9 to +3.4	Matthews (1968)
3. Kulukbuk Bluff 25Z	MIS 5e	11.75–12	–22.5 to –20.5	14.8	–22.6	–3.05 to –2.8	+0.1 to +2.1	Elias (1992a)
2. Chi'jee's Bluff Stn 4, N-A	MIS 5e	12–13.25	–23 to –20.25	16	–29	–4.0 to –2.75	+6.0 to +8.75	Matthews <i>et al.</i> (1990a)
2. Chi'jee's Bluff Stn 4, N-B	MIS 5e	14.5–15.5	–25.25 to –21.5	16	–29	–1.5 to –0.5	+3.75 to +7.5	Matthews <i>et al.</i> (1990a)
7. Nuyakuk 13-2	MIS 5e	13–16.25	–30 to –21.75	12.7	–9.7*	+0.3 to +3.55	NA	Elias and Short (1992)
7. Nuyakuk 13-4	Late MIS 5	12.5–12.75	–12 to –11.25	12.7	–9.7*	–0.2 to +0.05	NA	Elias and Short (1992)
7. Nuyakuk 13-7	Late MIS 5	10.5–12	–20 to –19.5	12.7	–9.7*	–2.2 to –0.7	NA	Elias and Short (1992)
6. Noatak 37 94-25	Late MIS 5	7.5–9	–26.5 to –22.5	11	–25.8	–3.5 to –2	–0.7 to +3.3	Elias (1997)
9. Hungry Creek 52&53	Early MIS 4	6.5–10.25	–34.5 to –24.75	16	–29	–9.5 to –5.75	–5.5 to +4.25	Hughes <i>et al.</i> (1981)
10. Igushik 9-M-2	Early MIS 4	9–10	–30 to –23	12.7	–9.7*	–3.7 to –2.7	NA	Lea <i>et al.</i> (1991)
7. Chi'jee's Bluff Sample A	52 K	8.25–10	–32.75 to –27.25	16	–29	–7.25 to –6	–3.75 to +1.75	Matthews and Telka (1997)
9. Hungry Creek 27	Early MIS 3	11.5–12.5	–30 to –28	16	–29	–4.5 to –3.5	–1.0 to +1.0	Hughes <i>et al.</i> (1981)
10. Igushik 1-4	Early MIS 3	8.5–10	–30.5 to –22	12.7	–9.7*	–4.2 to –2.7	NA	Lea <i>et al.</i> (1991)
10. Igushik 4-M-1	Early MIS 3	12.5–15.5	–28 to –19	12.7	–9.7*	–0.2 to +2.8	NA	Lea <i>et al.</i> (1991)
11. Kuskokwim KBR/24	Early MIS 3	11–12.75	–24.25 to –19.75	14.8	–22.6	–3.8 to –2.05	–1.65 to +2.85	Elias (1992a)
11. Kulukbuk Bluff Unit C, A	Early MIS 3	9.75–11.5	–31.25 to –26.5	14.8	–22.6	–5.05 to –3.3	–8.65 to –3.9	Elias (1992a)
9. Hungry Creek 35	Mid-MIS 3	10–12.5	–19.5 to –13	16	–29	–6 to –3.5	+9.5 to +16.0	Hughes <i>et al.</i> (1981)
1. Old Crow 77-51	MIS 3	14.5–15.5	–28.5 to –25	16	–29.0	–1.5 to –0.5	+0.5 to +4.0	Morlan and Matthews (1983)
12. Titaluk River 17A	46.4	9.5–10	–31 to –28	10.3	–25.2	–0.8 to –0.3	–5.8 to –2.8	Elias (1997)
13. Cutler River	46.3	8–9.5	–26 to –22	11	–25.8	–3.0 to –1.5	–0.2 to +3.8	Elias (1997)
14. Cape Deceit Peat 5	43.3	6–10.5	–35.5 to –18	12.1	–20.4	–6.1 to –1.6	–15.1 to +2.4	Matthews (1968)
15. Upper Porcupine River	42.2	9.5–10	–29 to –27.5	16	–29	–6.5 to –6.0	0 to +1.5	Matthews and Telka (1997)
14. Cape Deceit S-5	42.2	11–11.75	–20.25 to –19.75	12.1	–20.4	–1.1 to –0.35	+0.15 to +0.65	Matthews (1968)
16. Blue Babe Site	41.8	6–10.5	–32.5 to –18.5	16	–24.4	–10 to –5.5	–8.1 to +5.9	Guthrie (1990)
8. Eva Creek 3-1A	38.5	11–13.5	–24 to –17	16.9	–23.4	–5.9 to –3.4	–0.6 to +6.4	Matthews (1968)
7. Chi'jee's Bluff Stn 1, B	37.8	10–11	–27.5 to –23	16	–29	–6.0 to –5.0	+1.5 to +6.0	Matthews <i>et al.</i> (1990a)
17. Isabella Basin IS-69	36.6	12–14.25	–32 to –22.25	16.9	–23.4	–4.9 to –2.65	–8.6 to +1.15	Matthews (1974)
12. Titaluk River 7D15	36	8–9.5	–31.5 to –25.5	10.3	–25.2	–2.3 to –0.8	–6.3 to –0.3	Nelson and Carter (1987)

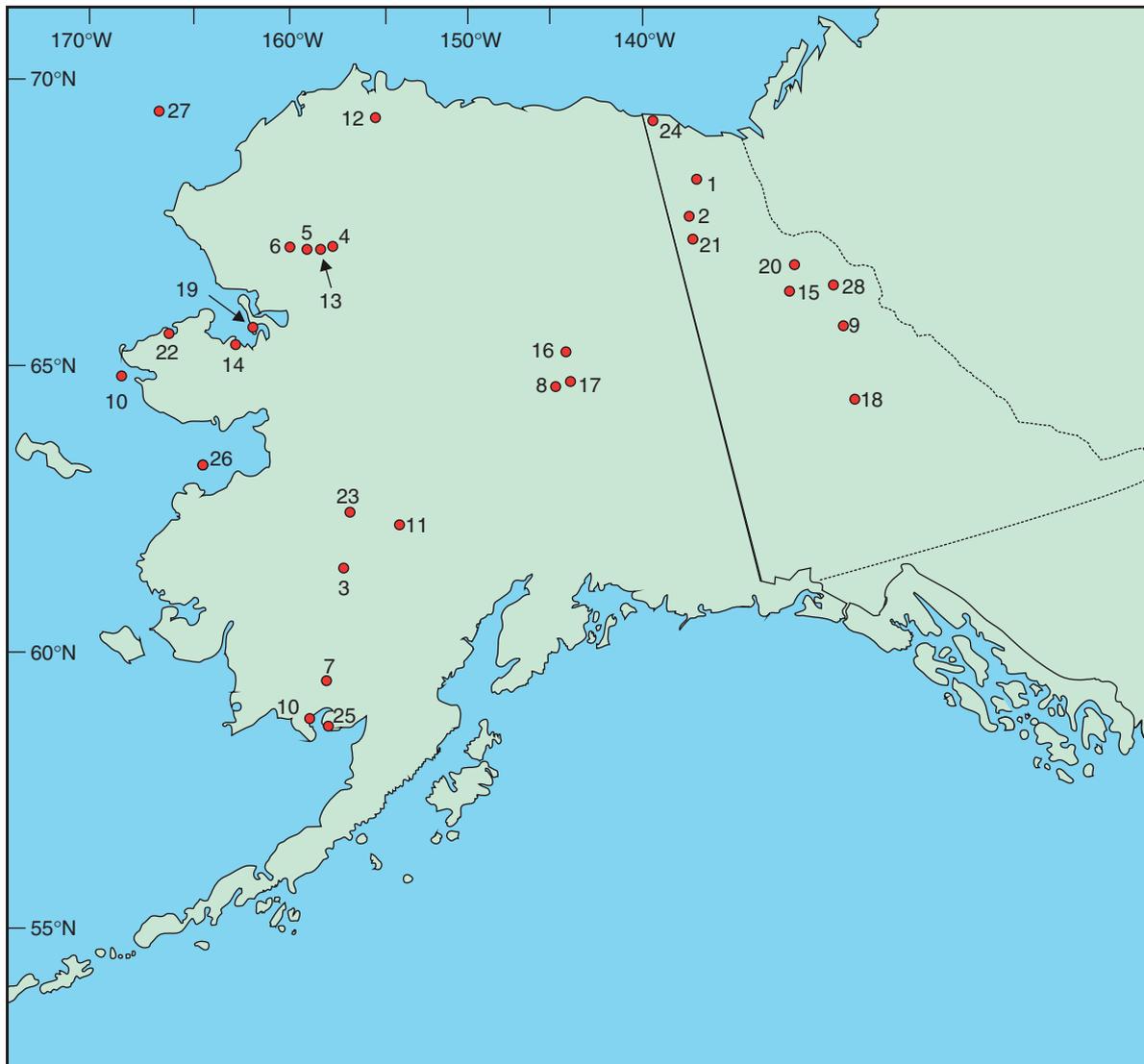
(Continued)

**Table 3 (Continued)**

Site	Age (cal yr BP × 1000)	Late Quaternary		Modern		Change in Temperature		References <sup>a</sup>
		$T_{\max}$ (°C)	$T_{\min}$ (°C)	$T_{\max}$ (°C)	$T_{\min}$ (°C)	July $\Delta T$ (°C)	Jan $\Delta T$ (°C)	
8. Eva Creek 3-3B	35.2	8.5–9.5	–31.5 to –26	16.9	–23.4	–8.4 to –7.4	–8.1 to –2.6	Matthews (1968)
11. Kulukbuk Bluffs Unit C, B	35	12.25–13	–30.75 to –28	14.8	–27.6	–2.55 to –1.8	–3.15 to –0.4	Elias (1992a)
12. Titaluk River 20A	33.6	10.75–12.25	–20 to –19.25	10.3	–25.2	+0.45 to +1.95	+5.2 to +5.95	Nelson and Carter (1987)
18. Mayo Village Unit 1	31.5	9–9.75	–29.75 to –28	15.2	–29	–6.2 to –5.45	–0.75 to +1.0	Matthews <i>et al.</i> (1990b)
19. Baldwin Peninsula	31.5	8.5–9.5	–31 to –28	12.1	–18.3*	–3.6 to –2.6	NA	Hopkins <i>et al.</i> (1976)
20. Rock River	30.1	9.5–10.5	–28 to –22.5	16	–29	–6.5 to –5.5	+1.0 to +6.5	Matthews and Telka (1997)
9. Hungry Creek 49	26.1	11–12.25	–29.5 to –25.5	16	–29	–5.0 to –3.75	–0.5 to +3.5	Hughes <i>et al.</i> (1981)
10. Bering Shelf 78-15	24.9	5.5–10.5	–34.5 to –18.75	10.8	–15.6*	–5.3 to –0.3	NA	Elias <i>et al.</i> (1996, 1998b)
21. Bluefish	24.1	8.5–9.5	–31.5 to –28	16	–27.8	–7.5 to –6.5	–3.7 to –0.2	Matthews and Telka (1997)
22. Bering Land Bridge Park	21.7	5.5–9.5	–34 to –21	8.4	–18.3*	–2.5 to +1.1	NA	Elias (1997)
14. Cape Deceit S-1	ca. 21.6	9.5–10.5	–25 to –22	16	–20.4*	–6.5 to –5.5	NA	Matthews (1968)
23. Colorado Creek	18.2	11.25–12.5	–21.25 to –18.25	14.8	–22.6	–3.55 to –2.3	+1.35 to +4.35	Elias (1992b)
24. Clarence Lagoon	15.3	9.25–15.25	–35.25 to –19.25	7.5	–26	+1.75 to +7.75	–9.25 to +6.75	Matthews (1975)
25. Flounder Flat 3-M-8	15	12.5–13	–30.5 to –28	12.7	–9.4*	–0.2 to +0.3	NA	Elias (1992b)
26. Bering Shelf 76–121	13.4	11.5–13	–28.5 to –23.5	10.8	–15.6*	+0.7 to +2.2	NA	Elias <i>et al.</i> (1996, 1998b)
6. Noatak NK35-95AHA-60	13.2	15–16	–26 to –20.5	11	–25.8	+4.0 to +5.0	–0.2 to +5.3	Elias (1997)
27. Chukchi Shelf 85-69	12.9	9.25–10.25	–32.25 to –27.25	4	–27.7*	+5.25 to +6.25	NA	Elias <i>et al.</i> (1996, 1998b)
6. Noatak NK35-94AHA-24	12.3	12.5–13.5	–22 to –18	11	–25.8	+1.5 to +2.5	+3.8 to +7.8	Elias (1997)
6. Noatak NK32A-94AHA-17	12.3	10–10.5	–30 to –28.5	11	–25.8	–1.0 to –0.5	–4.2 to –2.7	Elias (1997)
28. Eagle River	11.5	12–13.5	–31.25 to –27	14.9	–30.5	–2.9 to –1.4	–0.75 to +3.5	Matthews and Telka (1997)

<sup>a</sup>References available from the QBib Web site, [www.bugs2000.org/qbib.html](http://www.bugs2000.org/qbib.html)

\*Coastal sites with unreliable reconstructions of TMIN. See text for discussion.



**Figure 4** Map of northwestern North America showing locations of fossil sites discussed in text. Site numbers match those in **Table 3**.

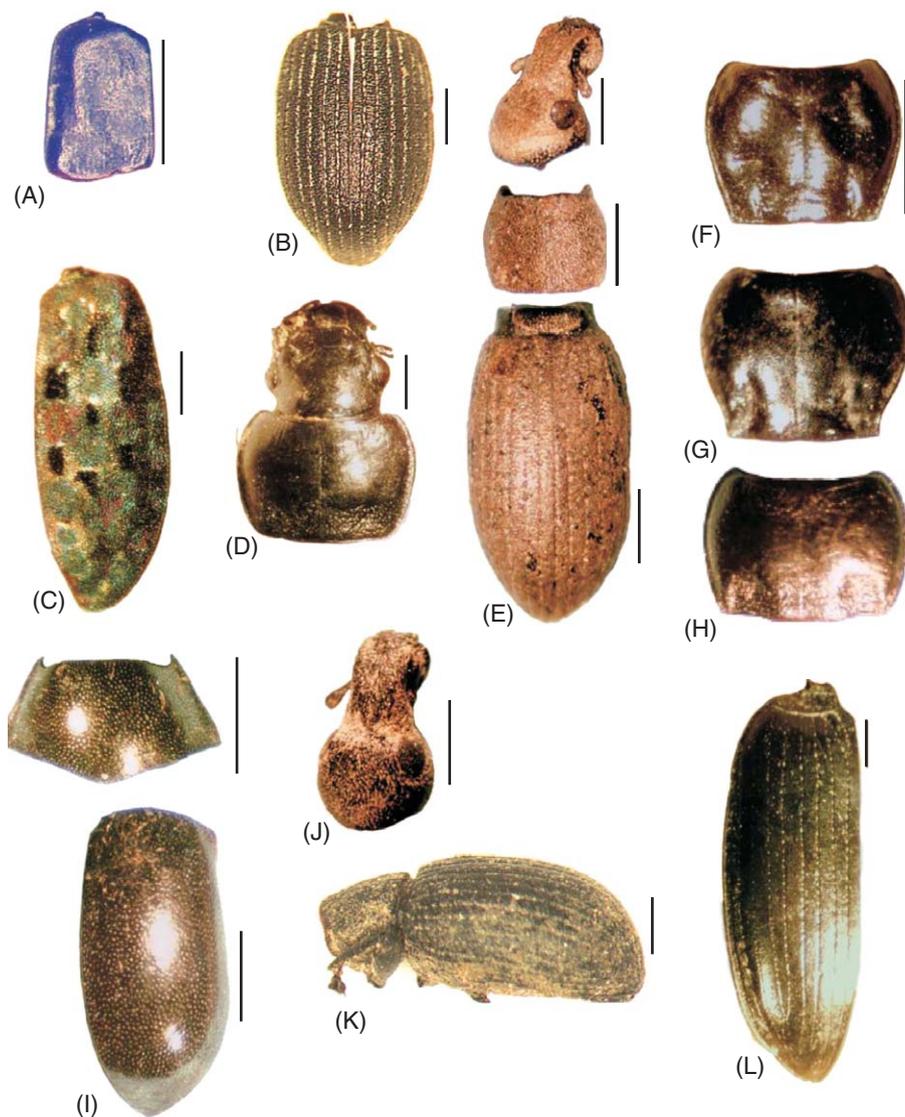
estimate  $0.5\text{--}2^{\circ}\text{C}$  warmer than modern. The other faunas discussed previously yielded  $T_{\text{max}}$  estimates that were  $0.5\text{--}2^{\circ}\text{C}$  cooler than modern. Interestingly, a fauna dated 31.5 kya from Mayo Village, Yukon (**Fig. 4**, No. 18), indicates that regional  $T_{\text{max}}$  had fallen to  $5\text{--}6^{\circ}\text{C}$  colder than modern levels. Likewise, a fauna dated 35.2 kya from Eva Creek, interior Alaska (**Fig. 4**, No. 8), indicated  $T_{\text{max}}$  levels  $7\text{--}8^{\circ}\text{C}$  colder than modern. Thus, within the space of 2,000 years, temperatures appear to have oscillated dramatically in eastern Beringia. The beetle faunas that yielded the indications of interstadial warming are composed of species found today in open-ground habitats within the boreal forest. They do not rely on the presence of trees. The paleobotanical evidence suggests that most if not all of eastern Beringia remained open-ground tundra or steppe-tundra throughout MIS 3.

During the LGM, the beetle evidence indicates that  $T_{\text{max}}$  was depressed in eastern Beringia, but that  $T_{\text{min}}$  was within  $1\text{--}2^{\circ}\text{C}$  of modern levels in most regions. *Elias et al. (1999)* discussed difficulties in reconstructing  $T_{\text{min}}$  from faunal assemblages sampled from coastal sites. First, the ancient coastline of Beringia was removed from its current position by more than 1,000 km in some regions. Therefore, the modern  $T_{\text{min}}$  of a coastal site, greatly influenced by maritime climate, bears little relation to the ancient climate of the same site when it was hundreds of kilometers inland because of lowered sea level. Also, even the modern  $T_{\text{min}}$  of coastal sites is a poor reflection of winter temperatures at these sites because of the incursion of Arctic air masses during the winter season. These periods of very low

temperature are sufficiently long, and sufficiently frequent, to virtually eliminate the less cold-resistant beetle fauna of coastal Alaska.

Following the LGM, beetle faunas from throughout eastern Beringia are indicative of climatic amelioration, beginning by at least 15.3 kya. This warming is especially noteworthy in the Arctic zone, where  $T_{\max}$  rose above modern levels during the late glacial interval. The warming indicated by faunas from the subArctic zone is less marked during this interval. There is also evidence, again from the Arctic assemblages, for a brief climatic oscillation during the Younger Dryas chronozone (Elias, 2000).

Two principal ecosystems appear to have dominated eastern Beringia during late Pleistocene glacial periods: steppe–tundra and mesic tundra. Steppe–tundra, or ‘mammoth steppe’ as Guthrie (1990) described it, was rich in grasses and sagebrush (*Artemisia*). It supported a diverse, abundant megafauna of grazers and their predators. In Alaska and the Yukon, this ecosystem also had a characteristic beetle fauna, dominated by the ground beetles *Amara alpina* (Fig. 5H) and several species of *Harpalus* (Fig. 5D) pill beetles (Byrrhidae) in the genus *Morychus* (Fig. 5I), dung beetles in the genus *Aphodius*, and the weevils *Lepidophorus lineaticollis* (Figs 5J and 5K) and *Connatichela artemisiae*



**Figure 5** Light microscope photographs of late Pleistocene fossil beetle specimens from eastern Beringia. (A) Left elytron of *Tachinus brevipennis*; (B) elytra of *Vitavitus thulius*; (C) right elytron of *Elaphrus parviceps*; (D) head and pronotum of *Harpalus amputatus*; (E) head, pronotum, and elytra of *Connatichela artemisiae*; (F) pronotum of *Pterostichus brevicornis*; (G) pronotum of *Pterostichus pinguedineus*; (H) pronotum of *Amara alpina*; (I) pronotum and right elytron of *Morychus* sp.; (J) head of *Lepidophorus linneaticollis*; (K) pronotum and elytron of *L. linneaticollis*; (L) left elytron of *Pterostichus nearcticus*. Scale bars = 1 mm.

(Fig. 5E). This steppe–tundra fauna, first recognized by Matthews (1983), is commonly found in fossil assemblages throughout the Yukon and interior Alaska. However, in other regions of Alaska, a different suite of beetle taxa dominate late Pleistocene assemblages. This group includes the *Cryobius* group of ground beetles in the genus *Pterostichus* (Figs 5F and 5G), several other ground beetles associated with mesic and moist habitats, rove beetles in the subfamily Omaliinae, and weevils that feed on dwarf birch and dwarf willow. This mesic tundra fauna has been found in fossil assemblages throughout southwestern and northwestern Alaska, as well as in samples taken from the ancient Bering Land Bridge that connected Alaska to Siberia during intervals of lowered sea level (Elias *et al.*, 2000). The land bridge may have served as a biological filter, keeping dry-adapted species, such as the woolly rhinoceros, from entering North America (Guthrie, 2001).

## Conclusions

Late Pleistocene beetle assemblages from sites throughout North America have documented large-scale, rapid climatic changes. During MIS 3, beetle assemblages have demonstrated oscillating interstadial warming and cooling events that coincide with climatic patterns inferred from oxygen isotope records in Greenland ice cores. The pace and severity of such changes have often gone undetected in paleoenvironmental reconstructions based on fossil pollen, although new analytical methods are making breakthroughs (Grimm and Jacobson, 2004). As has been noted in the history of the European beetle fauna (Coope, 1978), North American beetles appear to have responded to the vagaries of Pleistocene climates by shifting their distributions in order to stay within climatic conditions to which they are best adapted. Thus, the Pleistocene beetle fauna of North America remains extant today, albeit living in different regions. Each new climatic regime of the Pleistocene brought new associations of species together in a given region. Many of the species in given types of associations remained constant through long stretches of time, but different species were added or subtracted from the fauna of any specific region as ecosystems waxed and waned.

*See also:* **Beetle Records:** Overview; Late Tertiary and Early Quaternary; Late Pleistocene of Europe; Postglacial North America. **Ice Core Records:** Greenland Stable Isotopes. **Paleoceanography, Physical and Chemical Proxies:** Oxygen Isotope Stratigraphy of the Oceans. **Plant Macrofossil Methods and Studies:** Rodent Middens.

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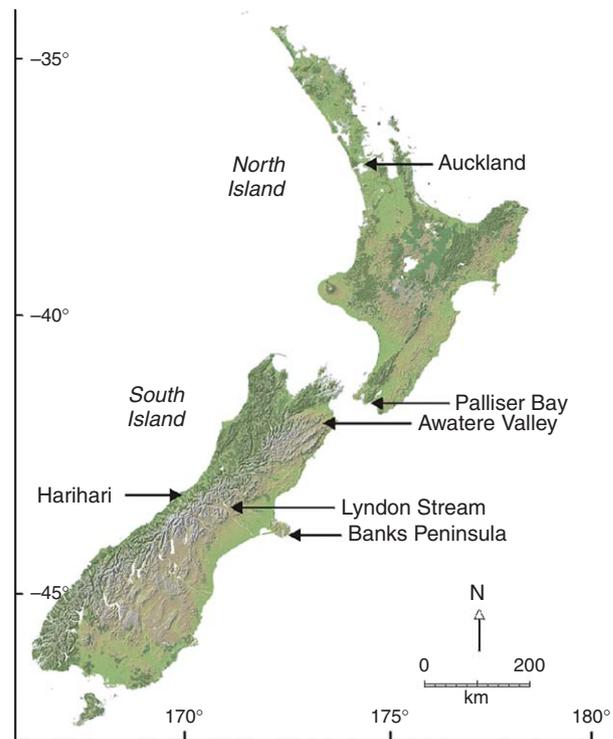
## Late Pleistocene of New Zealand

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### Introduction

Fossil beetle reconstructions are relatively new in New Zealand (NZ) with the first published work dating only to 2000. Before 2000, terrestrial paleoenvironmental reconstructions relied mainly on pollen



**Figure 1** Map of New Zealand showing location of research sites mentioned in the text. (map courtesy of Geographix)

records, which defined regional vegetation patterns for the late Quaternary and from which broad climate inferences were drawn. Quantitative estimates for past climate remained less well defined because there is no clear relationship between temperature and vegetation. Hence, there was a need for additional proxies and particularly for proxies capable of quantifiable paleoclimatic reconstruction.

To date, late Pleistocene beetle assemblages have been recorded from five NZ sites (Fig. 1) ranging in age from marine isotope stage (MIS) 7 to MIS 2. The late Pleistocene literature to date includes the development of a beetle-based climate estimation model and its application to two Last Glacial Maximum (LGM) sites. The paleoecology is described for each site, detailing ecosystems at a local scale and at community and species levels. The following is a review of this literature prefaced by a summary of present knowledge of the modern beetle fauna, and a brief description of the NZ physical environment, identifying factors that affect beetle distribution.

### Background

#### Modern Fauna

Knowledge of the modern fauna underpins both fossil identification and the ecological controls on distribution that are the basis for climate modeling. The NZ