

# B

## BEETLE RECORDS

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### Overview

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The study of fossil beetles (Coleoptera) from Quaternary deposits began in earnest in the 1950s in Britain and has since spread to many areas of the world, most recently to Australia, New Zealand, and Japan. Fossil beetle research has led to many exciting breakthroughs in our understanding of the pace and intensity of climate change in terrestrial landscapes. In many ways, beetles are the ideal proxy for tracking terrestrial environmental change.

### The Perfect Proxy?

If one were to design the ideal source of biological proxy for the reconstruction of Quaternary terrestrial environments, certain aspects of the nature of this ideal organism would have to conform to the following guidelines:

1. It must be sensitive to environmental change. Organisms that are able to withstand decades or centuries of adverse climate *in situ* before eventually dying out would be of far less use than organisms that simply could not survive such adversity.

2. There should be great species diversity within the group of organisms to be studied. Greater diversity yields more precise and diverse information on paleoenvironments. Taxonomic groups with only a few dozen species necessarily offer less precise information about past environments than groups with many thousands of species. Each species has its own ecological niche, so by studying the fossil record of a group that represents thousands of ecological niches, one is able to piece together a broad spectrum of information about past environments (climate, soils, water quality, and vegetation).

3. It should be highly mobile and thereby able to respond rapidly to environmental change by rapidly shifting its distribution into new areas where the environment is suitable. This quality ensures little or no problem with 'migration lag', wherein an organism requires decades, centuries, or even millennia to become established in regions with potentially suitable environments.

4. It should have an abundant, well-preserved fossil record. This allows regional reconstructions to be built up for given time intervals based on multiple study sites containing assemblages of the fossil type in question. If the fossil remains of an organism are too scarce or too poorly preserved to be identified, then their fossil record will contribute little to regional paleoenvironmental reconstructions.

5. It should be readily identifiable to the species level. Even if a group of organisms satisfy the first four criteria, their fossil record will be of limited value if their remains cannot be specifically identified. There is often a great deal of ecological variation among the species in a given genus, so a generic identification provides little that is useful to paleoenvironmental reconstruction.

6. It should have many species with narrow ecological or climatic tolerances. Again, this harkens back to the issue of specificity. The more specific the environmental requirements of the organism, the more specific the reconstruction that can be made, based on its presence in the fossil record. This criterion works together with criterion No. 2. If taxonomic groups with a great deal of species diversity also contain many species with very narrow ecological or climatic tolerances, then a complex mosaic image of the paleoenvironment can be constructed.

7. None of the previous criteria are of much use unless the taxonomic group has remained extant throughout the study period one is interested in. If the group of organisms has gone extinct, no matter how diverse, abundant, or well preserved, then we are left making educated guesses about the ecological or climatic requirements of the ancestral forms. The modern ecological and climatic data available for the surviving species in such a group of organisms can never be fully applied to extinct species.

8. Finally, it is a great help to the paleoecologist if the proxy group of organisms is well-known to science. In other words, if a group of organisms has been well studied in recent times, then we have at our disposal a great body of data, built up through many generations of scientific study, concerning the modern ranges and ecological requirements of the species.

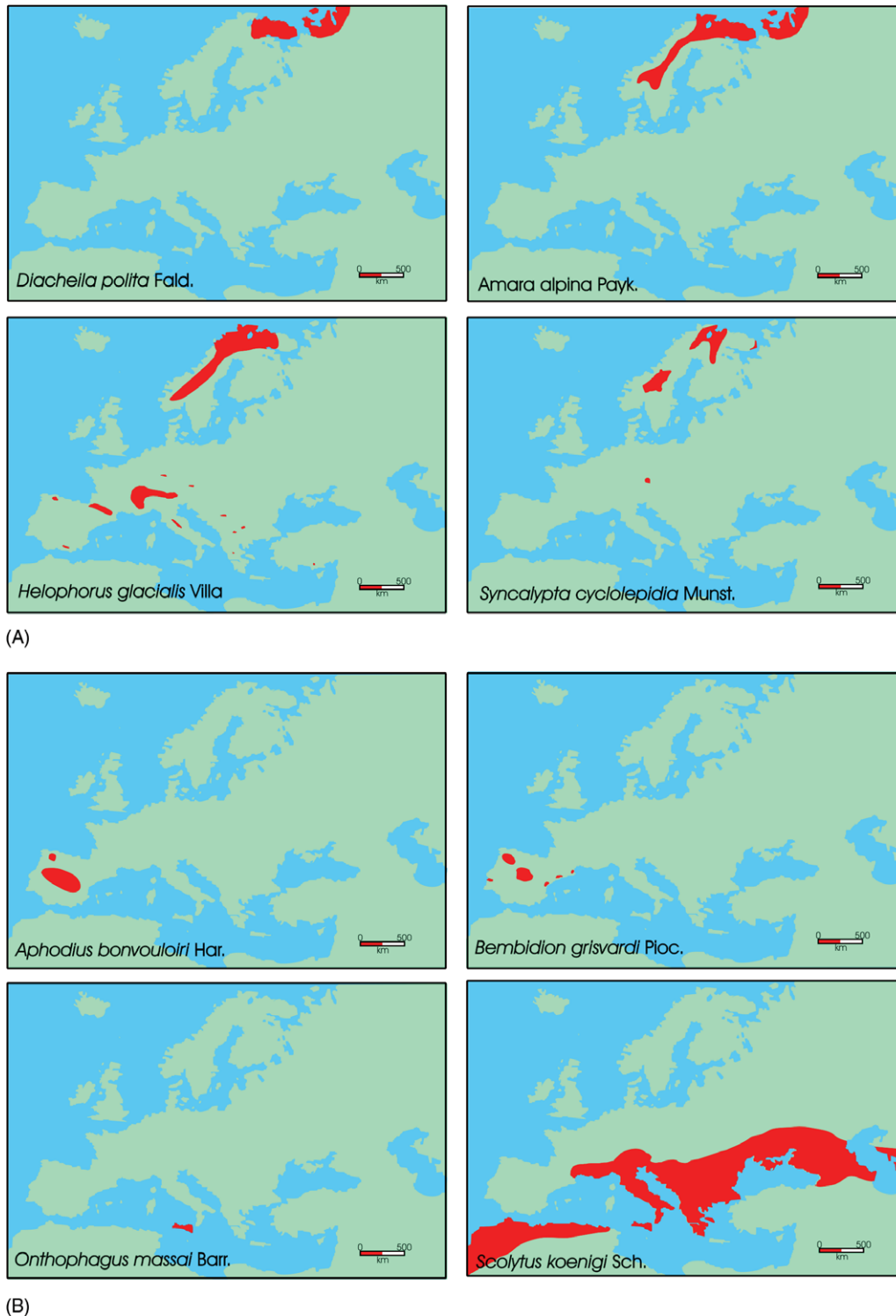
The reason why beetles (Coleoptera) are so useful as proxy indicators of past terrestrial environments is that they fulfill all these requirements. Beetles are the most diverse group of organisms on Earth, with more than 1 million species known to science. A large proportion of beetle species are known to be quite sensitive to environmental change and to shift their distributions across continents in order to become established in regions of suitable environment (Elias, 1994). Beetles have a well-preserved, abundant fossil record in many regions of the world. Beetle exoskeletons are reinforced with chitin, a highly durable compound that resists decay in water-logged and other anaerobic sedimentary environments. That chitinous exoskeleton is covered with taxonomically useful characters on the main body parts, including the head capsule, thoracic shield (pronotum), and wing covers (elytra). In many study regions, paleoentomologists are able to specifically identify up to 50% of these

fossil beetle sclerites; in some well-studied regions, this percentage is closer to 75%. Quaternary beetle faunal assemblages frequently contain hundreds of identified species, more than any other group of organisms preserved in Quaternary deposits.

Many beetle species are stenothermic, adapted to a narrow range of temperatures (Fig. 1). Predatory and scavenging families of beetles comprise less than half the total number of families, but their species' numbers are often proportionally high in fossil assemblages. These are the two groups that receive the most attention in paleoclimatic reconstructions. The rationale behind this decision is that predators and scavengers are not tied to particular species of host plants and thus are able to become established most rapidly in new regions in response to changing climates. For instance, the Pleistocene fossil record indicates that these groups have colonized newly deglaciated landscapes within a few years of ice-margin retreat (Coope, 1977). Perhaps because of beetle mobility in the face of changing environments, the fossil evidence strongly indicates that nearly all species found in Quaternary assemblages remain extant today. It appears likely that beetle populations never remained genetically isolated for sufficient lengths of time in the past 2.6 million years to develop new species. The constant mixing of gene pools through shifting distributions, in response to 50+ glacial/interglacial cycles, prevented this from happening (Coope, 1978). Finally, beetles are some of the best studied groups of insects, with modern ecological requirements and ranges well understood for many species living in the temperate and high-latitude regions (where the vast majority of fossil investigations have taken place).

### Where Fossil Beetles Are Found

Fossil beetle assemblages have been recovered from a wide variety of sedimentary environments, especially anoxic water-lain sediments that concentrate the remains in layers of organic detritus. Lacustrine (lake and pond) sediments have yielded abundant, diverse assemblages of fossil beetles, especially in deposits from the littoral zone and where a stream enters a lake or pond (Fig. 2). Such deltaic deposits can yield astonishing numbers of fossil beetle specimens. Fluvial sediments also yield fossil beetles. The most productive type of fluvial deposit is an accumulation of organic detritus, laid down in secondary channel bends, backflows, and pools between riffles (Fig. 3). Bogs, fens, and mires can also yield good accumulations of fossil beetles, especially in locations representing the edge of such bodies, where there is increased input from the upland beetle fauna (Fig. 4).



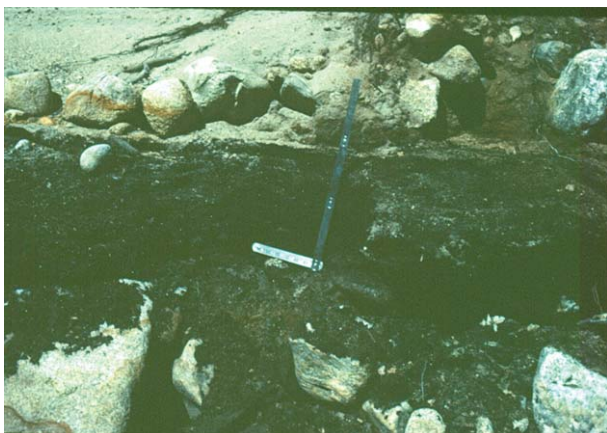
**Figure 1** Modern European distributions of stenothermic beetle species found in British Pleistocene deposits. (A) Cold-adapted species; (B) warm-adapted species.

One of the more unusual types of deposit-yielding beetle remains are the middens of certain rodents, including packrats or woodrats (*Neotoma*), the native group of North American rats. Their middens

(Fig. 5), intermittently wet and sticky from rat urine and feces, serve as traps for beetles entering the shallow caves and rock shelters of desert and semiarid regions where these rats thrive (Elias, 1990). Unlike



**Figure 2** Deltaic deposit exposed at Lake Isabelle, Colorado. The layers of organic detritus yielded thousands of fossil beetle specimens. Photo by S. A. Elias.



**Figure 3** Lense of organic detritus exposed after a flood on the Roaring River, Rocky Mountain National Park, Colorado. This late Holocene deposit contained a rich, diverse beetle fauna.

the waterlogged sediments of lakes, rivers, and bogs, packrat middens preserve beetle (and other arthropod) exoskeletons in extremely dry conditions, sometimes mummifying their soft tissues.



**Figure 4** Holocene peat from a high mountain bog at La Poudre Pass, Colorado, exposed along an irrigation canal.



**Figure 5** Packrat (*Neotoma*) midden sample from a rock shelter at Emery Falls, Grand Canyon, Arizona. Photo by Thomas Van Devender.

### Methods of Sampling and Extraction

When sampling the kinds of sediments discussed previously, the aim is to obtain a sufficient quantity of material to yield at least a liter of organic detritus. The details of sampling and extraction procedures are discussed in [Elias \(1994\)](#). In lacustrine sediments that are only 3–5% organic detritus by volume, this requires the extraction of many kilograms of sediment, followed by wet screening to isolate the organic fraction.

Generally, the quantity of sediment obtainable by piston coring of lake and pond sediments is insufficient to yield adequate amounts of detritus. Although some success has been achieved by taking multiple, large-diameter cores, this is not often practical. The best results are obtained by sampling exposures of sediments, either natural or man-made. Natural exposures include cutbanks of streams and ocean and lake bluffs. Man-made exposures include gravel and clay pits, irrigation ditches, trenches, and building sites.

The sequence of steps in extraction and mounting of insect fossils is summarized in [Figure 6](#). Fossil insect extraction is relatively safe, cheap, and easy. The only lengthy process that may be involved is the pretreatment of samples to disaggregate the organic detritus from inorganic matrix (i.e., calcareous sediments and clays) or to soften and then disperse felted peats or lignite. Processing procedures are largely a matter of personal preference and availability of equipment, and some workers use a slightly different procedure than the one discussed later. For instance, Russian workers sometimes prefer to skip the kerosene flotation step discussed later and sort through entire samples of washed organic detritus in order to maximize the recovery of such heavy-bodied groups as weevils (*Curculionidae*) that sometimes do not rise to the top during flotation. Japanese workers studying peat deposits prefer to split the individual layers of peat and examine each layer under a microscope.

Once disaggregated organic detritus is obtained, the next step is to wet screen the sample in a 300  $\mu\text{m}$  sieve. This process removes fine particles, such as silt, that may fill the concavities of rounded insect sclerites. Once the detritus has been screened, the residual material is placed, still damp, in a large bowl with a spout, or a rectangular dishpan, and processed by kerosene flotation to isolate and concentrate insect fossils. Kerosene or other lightweight oil is added to cover the sample and gently worked into the sample by hand for several minutes. The oil adheres to the insect sclerites but not to plant detritus. The remaining kerosene is decanted from the bowl and cold water is vigorously added to the oily detritus. In most samples, nearly all of the insect sclerites will rise to the top and float at the oil-water interface. Within 15–60 minutes, most plant residue sinks to the bottom of the bowl, and the now-concentrated insects may be decanted onto a screen to be washed gently in detergent and dehydrated in 95% ethanol before microscopic sorting. Small samples should be sorted completely rather than processed with kerosene. Also, samples that may need to be submitted for radiocarbon dating should not be exposed to kerosene.

Specimen sorting is done under low-power (10 $\times$ ) binocular microscope in alcohol or water. Specimens may be stored in vials of ethanol, or more robust specimens may be mounted with gum tragacanth (a water-soluble glue) onto micropaleontological slides. Identification of fossil specimens is usually done through comparison with modern identified specimens (often from museum collections). This is another potentially lengthy process.

### **Exoskeletal Parts Preserved in Quaternary Deposits**

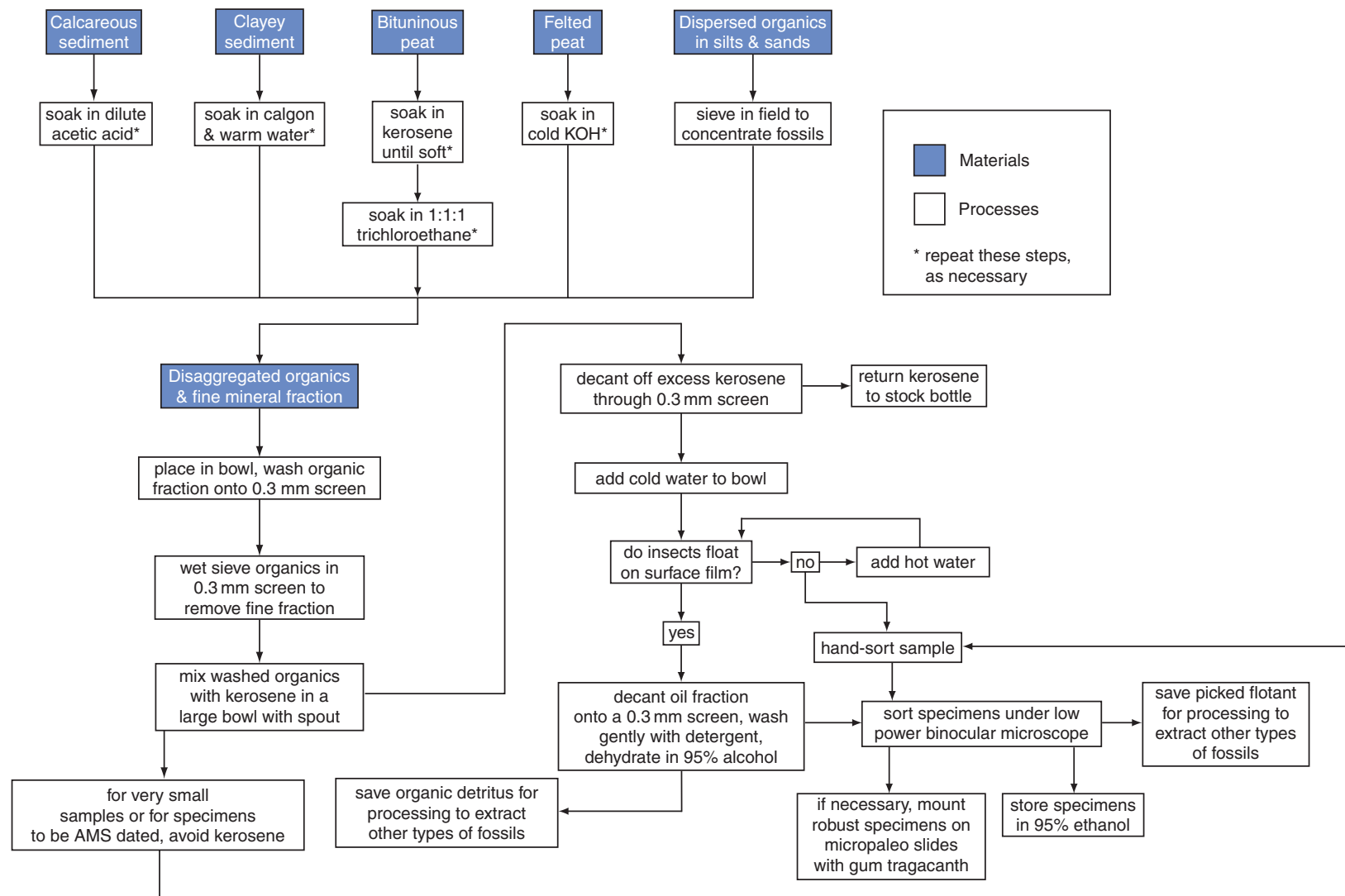
The chitinous remains of beetles often preserve extremely well in Quaternary sediments and can be matched exactly with modern specimens. The principal sclerites that are used in the identification of Quaternary beetles are the head, pronotum, and elytra ([Fig. 7](#)). The male genitalia (aedeagi) are likewise reinforced with chitin and are sometimes recovered from compressed groups of abdominal segments found in fossil assemblages. The aedeagus is often the most diagnostic sclerite in the identification of species, especially in genera that contain dozens or hundreds of species.

### **Useful Characters**

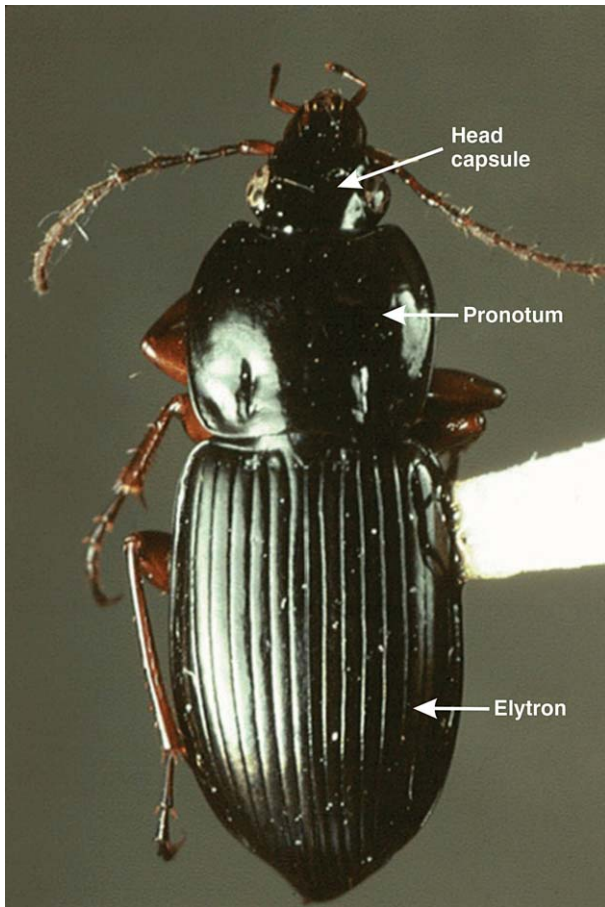
The process of identification begins with the shape and size of the main exoskeletal parts. Often, colors derived from pigments are preserved, and color patterns can be quite useful in the identification of groups that have spots, stripes, and other noticeable color variations on the elytra or pronota. Metallic coloration preserves extremely well because it is based on surface microsculpture rather than pigments. The depth, shape, and distribution of such surface features as striations, punctures, and microsculpture are all potentially diagnostic characters, as are the presence and placement of scales and setae in some groups. As discussed previously, the size and shape of the aedeagus are two of the most diagnostic characters for beetles, although these are not as commonly found as heads, pronota, and elytra.

### **Basic Assumptions for Use in Paleocology**

There are several basic assumptions made in the reconstruction of paleoenvironments based on fossil beetle assemblages. These assumptions fall within the framework of uniformitarianism in the sense that we assume that ancient beetle populations had the same environmental tolerances and behavior patterns as their modern counterparts.



**Figure 6** Flow chart of fossil beetle sample processing for kerosene flotation. Adapted from Elias (1994).



**Figure 7** The ground beetle, *Pterostichus leconteianus*, with principal body parts found in fossil assemblages identified.

### Species Constancy throughout the Quaternary

There are three lines of evidence that support the assumption that the beetle species found in Quaternary deposits are the same species that live today. The first is that the morphology of their exoskeletons has remained constant. In other words, we can find no differences between the fossil specimens and their modern counterparts that fall outside of the boundaries of known variation within the modern species. The youngest beetle fossils that exhibit morphological variations outside the bounds of modern species come from fossil assemblages that date to the Pliocene/Pleistocene boundary, approximately 2.6 million years ago. However, there are many reliably identified beetle species from Pliocene assemblages that exactly match modern species. The second line of evidence for Quaternary species constancy comes from the stability of shape and size of fossil aedeagae, as discussed previously.

The third line of evidence deals with the issue of constancy of physiology, as expressed in environmental tolerances. This issue can only be dealt with indirectly

because the exoskeletal evidence does not speak to it. However, what has been repeatedly observed in fossil beetle assemblages from sites throughout the world and ranging in age from early to late Quaternary times is that the species found together in fossil assemblages remain ecologically compatible today, even if they no longer live in the same geographic regions. For instance, a fossil assemblage associated with Pleistocene periglacial environments may contain a mixture of species found today in arctic and alpine habitats in various areas of the Northern Hemisphere. Conversely, an interglacial fauna may be found to contain large numbers of warm-adapted beetle species that today are found in a variety of temperate or subtropical habitats in various regions. In order for this persistence of ecological compatibility to occur, one of two scenarios must be invoked. Either whole suites of species have evolved unidirectionally during the Quaternary so that their past environmental tolerances have changed together, or their environmental tolerances have not changed at all. The latter scenario seems by far the likeliest because evolutionary theory indicates that each species evolves separately from others in response to its own unique set of selective pressures (Elias, 1994).

### Usefulness of Beetles as Paleoclimate Proxies

Insect ecologists support the idea that insect abundance and diversity may be controlled by biotic factors (e.g., predators and competition) in the central part of a species' range, but that climatic factors probably limit populations toward the edges of these ranges. Oxygen isotope records from deep-sea sediments and polar ice cores have shown that large-scale, climatic change was practically a constant feature of Pleistocene environments; it would appear that the shifting of insect distributions in response to these changes would have placed a large proportion of populations in this 'abiotic factor' zone of their respective ranges during much of the Pleistocene.

### Thermal Tolerances of Beetles

The modern distribution patterns of many beetle species in the temperate and high latitudes have been shown to coincide closely with climatic zones. The distribution of individual species reflects temperature regime, especially summer warmth and degree of seasonality (i.e., annual temperature range). Stenothermic species with limited thermal tolerances are found in most fossil assemblages (Fig. 1). The physiology of stenothermic species is closely tied to their thermal requirements. Experiments on metabolic rates of

ground beetles (Carabidae) (Thiele, 1977) showed that beetles' optimal metabolisms correspond with their thermal tolerance zones. This phenomenon is strengthened during the process of cold hardening, which takes place in late summer or fall. In preparation for winter cold, ground beetles in northern regions become progressively cold adapted (able to function at cold temperatures). Under these conditions, the beetles' metabolic rates peak at low temperatures, and they may become paralyzed or die if exposed to the temperatures they experience in mid-summer.

### Mutual Climatic Range Analysis of Fossil Assemblages

The mutual climatic range (MCR) method of paleoclimate reconstruction is based on the concept that the proxy organisms (in this case, beetles) live within the bounds of a set of climatic parameters, as defined by the climatic conditions within their geographic range. Thus, beetles live in a quantifiable piece of climate space. In the MCR method, the first step is to develop a climate envelope for the species of predators and scavengers that are found in the fossil assemblage (Fig. 8). The complete method is described by Atkinson *et al.* (1986) for European studies and by Elias *et al.* (1996) for North American studies. These envelopes are typically defined on the basis of the mean July and mean January temperatures of the locations where the species are known to occur today. The climatic parameters of each of these localities are plotted on diagrams of mean July temperature ( $T_{\max}$ ) vs the difference between the mean July and mean January temperature ( $T_{\text{range}}$ ). Once the individual species' climate envelopes are created, the envelopes for the species found together in a fossil assemblage are put together to find the area of overlap in climate space. This area is the mutual climatic range of the faunal assemblage. In the example shown in Figure 9, the climate envelopes of four cold-adapted species are combined to produce the MCR, shown in bright yellow.

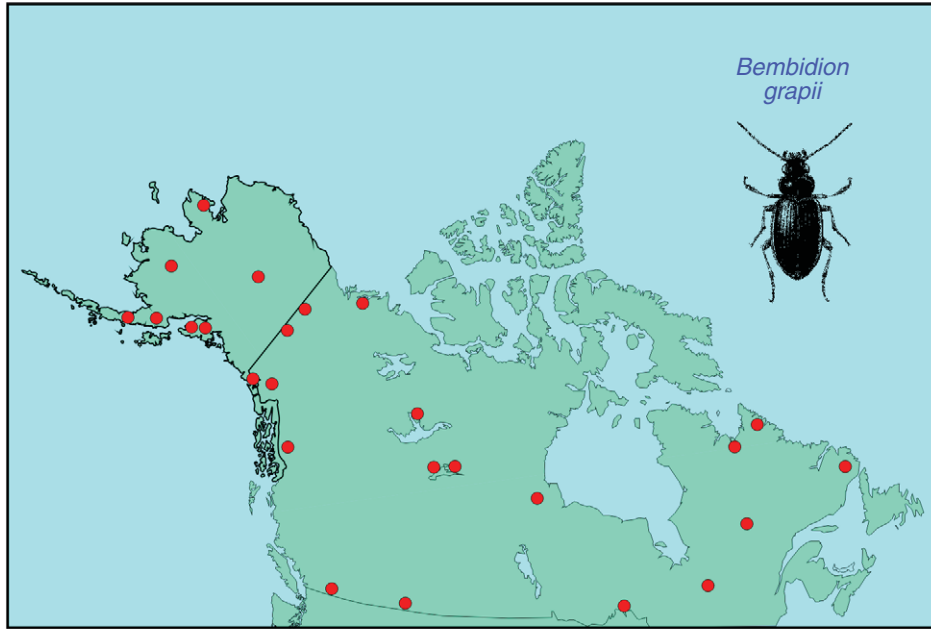
European and North American MCR studies have focused on species that are predators or scavengers. Plant-feeding species have been avoided because of the possibility that the migration rate of the host plants of these beetles may lag behind climatic change. For instance, in recently deglaciated landscapes, the process of ecological succession from bare mineral soil to mature forest stands may take many centuries to achieve. Predators and scavengers are able to exploit such landscapes as part of the earliest pioneering biological communities, as soon as the climate is suitable (Elias, 1994).

Modern tests of the reliability of the MCR method have been performed for the European and North American beetle faunas. These tests compared predicted with observed temperatures for a broad spectrum of sites using the MCR of species found today at localities to predict modern temperatures of those localities and comparing these predictions with modern climatological data for the same sites. For 35 sites in North America, a linear regression of actual vs predicted  $T_{\max}$  values yielded an  $r^2$  value of 0.94. A regression of observed vs predicted  $T_{\min}$  values yielded an  $r^2$  value of 0.82. The standard deviation for  $T_{\max}$  was 0.7° C and for  $T_{\min}$  was 10° C. Similarly for Europe, a linear regression of actual vs predicted  $T_{\max}$  values yielded an  $r^2$  value of 0.88, and a regression of observed vs predicted  $T_{\min}$  values yielded an  $r^2$  value of 0.88. The standard deviation for  $T_{\max}$  was 0.83° C, and for  $T_{\min}$  it was 2.42° C. Beetles living in regions with cold winters are poor indicators of winter air temperatures because they seek shelter from exposure to winter air through various means (e.g., burrowing in mud, leaf litter, or under bark or stones).

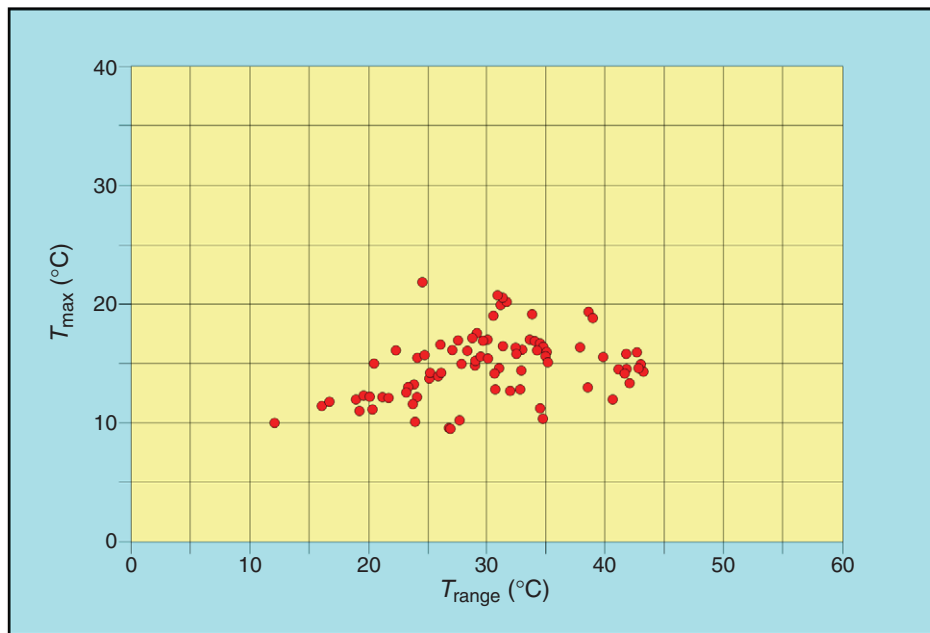
The MCR method has allowed paleoentomologists to produce quantified paleotemperature estimates for both summer and winter seasons for hundreds of fossil assemblages ranging in age from late Tertiary (Elias and Matthews, 2002) to the late Holocene (Lavoie and Arseneault, 2001). Regional summaries of MCR reconstructions have been prepared for northwest Europe (Coope, 1987; Coope *et al.*, 1998), eastern and central North America (Elias *et al.*, 1996), the Rocky Mountain region (Elias, 1996), and Alaska and the Yukon Territory of Canada (Elias, 2001). The principal findings in both Europe and North America are that late Pleistocene climatic changes were rapid and often of large scale. Interglacial climates were at least 3° C warmer than today in some regions, but during the Last Glacial Maximum (LGM),  $T_{\max}$  was depressed by 8–10° C in most temperate regions. The LGM summer temperatures of the Arctic regions were only depressed by 3–5° C in Beringia.  $T_{\min}$  was depressed by as much as 25° C in some mid-latitude regions, but  $T_{\min}$  was within 1 or 2° C of modern levels in most regions of eastern Beringia.

In New Zealand, collections of the modern beetle fauna are not sufficiently complete to allow species' climate envelopes to be constructed. Marra and colleagues have developed an alternative method, called the maximum likelihood envelope, that has allowed them to successfully reconstruct late Pleistocene climates. Another regional variation on the MCR method has been developed by Russian scientists working on northeastern Siberian fossil





(A)



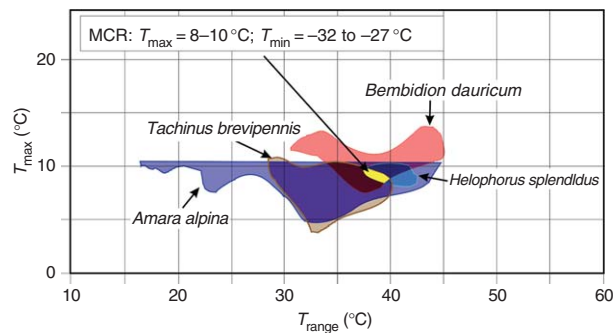
(B)

**Figure 8** (A) Modern North American distribution of the ground beetle, *Bembidion grapii*. (B) Species climate envelope for *B. grapii*, based on climatic parameters ( $T_{\max}$  and  $T_{\text{range}}$ ) of collecting localities shown in A.

beetle assemblages. They argue that certain plant-feeding beetle species should be included in MCR reconstructions because they feed on plants such as sedges and mosses that remained ubiquitous in Siberia throughout the Pleistocene. Hence, there should be no problem with plant migration lag in these circumstances.

### Multifaceted Paleoenvironmental Reconstructions

The order Coleoptera is the most diverse group of organisms on Earth, with a known modern fauna exceeding 1 million species. This number is roughly four times that of all the flowering plant species



**Figure 9** An example of the application of the MCR method showing the overlap of the climate envelopes of four species of cold-adapted beetles. In nearly all cases, far more species are involved in MCR reconstructions. The number is limited here for the sake of visual clarity.

(angiosperms) and more than 200 times the number of all mammal species. This incredible diversity carries through to Quaternary beetle faunal assemblages, which often contain between 100 and 200 species from dozens of families. Although predators and scavengers provide reliable information on past climates, plant-feeding species serve as proxies for the reconstruction of past plant communities and can provide such information as the relative maturity and health of forest stands and the presence of downed, rotting trees and associated fungi. In some cases, fossil beetle evidence may provide ‘smoking gun’ evidence for an environmental change. Such was the case when fossil remains of the elm bark beetle, *Scolytus scolytus*, were found in British sediments that date to the time of the Elm Decline in the mid-Holocene. The decline may have been due to Dutch elm disease, which is transmitted by the beetle (Girling, 1988).

Lacustrine aquatic beetles provide useful information on the temperature, trophic status, substrates, and size of lakes and ponds. Stream-dwelling beetles provide information on the size and velocity of streams, as well as temperature, trophic status, substrates, and degree of water clarity.

As in other macrofossil studies, the ‘story’ obtained from fossil beetle assemblages is a local one and needs substantiating with numerous regional replicates to produce a valid paleoenvironmental synthesis. However, because of the ubiquity of fossil beetle preservation in water-lain deposits, such regional syntheses are relatively easy (if time-consuming) to perform.

### Other Types of Studies

In addition to straightforward paleoenvironmental reconstructions, Quaternary beetle assemblages

have also been used to shed light on various aspects of biological and environmental history. Beetle species longevity, combined with our ability to identify the species of many fossil specimens, allows us greater understanding of how these animals have dealt with the vicissitudes of Pleistocene environmental change.

### Zoogeography

One application of fossil beetle data has been for zoogeographical studies. By plotting the shifts of beetle distributions through time and space, researchers have been able to reconstruct at least partial zoogeographic histories of various species. These studies have reinforced the theory that beetles have shifted their ranges repeatedly, and sometimes on very large spatial scales, in order to find regions of suitable climate. Such was the case for the tiny rove beetle, *Micropeplus hoogendorni*. This species was initially thought to have become extinct in the Pliocene or early Pleistocene because it was only known from a 5.7 million-year-old deposit in Alaska. However, Coope found mid-Pleistocene specimens of this beetle in Britain, and it has been found to be synonymous with a Siberian species, *M. dokuchaevi* (Elias, 1994).

The history of comings and goings of various groups of beetles across the Bering Land Bridge have been discussed by Elias *et al.* (2000), and the late Pleistocene and Holocene zoogeographic history of Chihuahuan Desert beetles was analyzed by Elias (1992). The fossil evidence used to develop these histories frequently disproves zoogeographic theories based solely on modern distributions (Elias, 1994). Fossil beetle evidence documents the importance of glacial refugia in maintaining high-latitude faunas through glacial periods. Beringia was the most important refugium of the cold-adapted fauna in the Arctic. At the other end of the world, the beetle evidence suggests that ice-free regions of the Chilean coast formed a refuge for the cold-adapted fauna of South America.

### Environmental Archeology

There are two types of fossil beetle studies done in aid of environmental archeology. The first is the reconstruction of natural environments associated with archeological sites. This kind of work has mainly been done in North America, where prehistoric human populations were mainly hunter-gatherers who had relatively light impacts on the landscape. With a few notable exceptions, these peoples built no permanent buildings, so they did not create any anthropogenic environments that attract

warmth-loving insects incapable of surviving winter climate outdoors. This kind of research has also been applied to Paleolithic sites in Britain, where fossil beetle assemblages have shed light on mid- and late Pleistocene environments that were experienced by *Homo erectus* and *Homo neanderthalensis*.

The other type of environmental archeological studies done with beetle (and other arthropod) remains concerns the reconstruction of anthropogenic environments—the houses, barns, and other man-made buildings where warmth-loving insects live as uninvited guests. This type of research is most common in Europe, where large-scale human disturbance of landscapes began by at least the beginning of the Bronze Age. In fact, one of the difficulties of mid- and late Holocene beetle studies in Europe is the inability to tease apart natural environmental change from anthropogenic change.

*See also:* **Beetle Records:** Late Tertiary and Early Quaternary; Middle Pleistocene of Europe; Late Pleistocene of Japan; Late Pleistocene of South America; Late Pleistocene of Northern Asia.

## References

- Atkinson, T. C., Briffa, K. R., Coope, G. R., Joachim, M., and Perry, D. (1986). Climatic calibration of coleopteran data. In *Handbook of Holocene Palaeoecology and Palaeohydrology* (B. E. Berglund, Ed.) Wiley, New York.
- Coope, G. R. (1977). Fossil Coleopteran assemblages as sensitive indicators of climatic changes during the Devensian (Last) cold stage. *Philosophical Transactions of the Royal Society of London, Series B* 280, 313–340.
- Coope, G. R. (1978). Constancy of insect species versus inconstancy of Quaternary environments. In *Diversity of Insect Faunas Symposium No. 9* (L. A. Mound and N. Waloff, Eds.), pp. 176–187. Royal Entomological Society of London, London.
- Coope, G. R. (1987). Fossil beetle assemblages as evidence for sudden and intense climatic change in the British Isles during the last 45,000 years. In *Abrupt Climate Change* (W. H. Berger and L. D. Labeyrie, Eds.), pp. 147–150. Reidel, Dordrecht, The Netherlands.
- Coope, G. R., Lemdahl, G., Lowe, J. J., and Walkling, A. (1998). Temperature gradients in northern Europe during the last glacial–Holocene transition (14–9 <sup>14</sup>C kyr BP) interpreted from coleopteran assemblages. *Journal of Quaternary Science* 13, 419–433.
- Elias, S. A. (1990). Observations on the taphonomy of late Quaternary insect fossil remains in packrat middens of the Chihuahuan Desert. *Palaïos* 5, 356–363.
- Elias, S. A. (1992). Late Quaternary zoogeography of the Chihuahuan Desert insect fauna, based on fossil records from packrat middens. *Journal of Biogeography* 19, 285–297.
- Elias, S. A. (1994). *Quaternary Insects and Their Environments*. Smithsonian Institution Press, Washington, DC.
- Elias, S. A. (1996). Late Pinedale and Holocene seasonal temperatures reconstructed from fossil beetle assemblages in the Rocky Mountains. *Quaternary Research* 46, 311–318.
- Elias, S. A. (2001). Mutual climatic range reconstructions of seasonal temperatures based on late Pleistocene fossil beetle assemblages in eastern Beringia. *Quaternary Science Reviews* 20, 77–91.
- Elias, S. A., and Matthews, J. V., Jr. (2002). Arctic North American seasonal temperatures in the Pliocene and early Pleistocene, based on mutual climatic range analysis of fossil beetle assemblages. *Canadian Journal of Earth Sciences* 39, 911–920.
- Elias, S. A., Anderson, K. H., and Andrews, J. T. (1996). Late Wisconsin climate in northeastern USA and southeastern Canada, reconstructed from fossil beetle assemblages. *Journal of Quaternary Science* 11, 417–421.
- Elias, S. A., Berman, D., and Alfimov, A. (2000). Late Pleistocene beetle faunas of Beringia: Where east met west. *Journal of Biogeography* 27, 1349–1363.
- Girling, M. A. (1988). The bark beetle *Scolytus scolytus* (Fabricius) and the possible role of elm disease in the early Neolithic. In *Archaeology and the Flora of the British Isles*, (M. Jones, Ed.) Oxford University Committee for Archaeology Monograph Vol. 14, pp. 34–38. Oxford University Press, Oxford.
- 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.
- Thiele, H. U. (1977). *Carabid Beetles in Their Environments*. Springer-Verlag, New York.

## Late Tertiary and Early Quaternary

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During the past 30 years, Quaternary insect paleontologists working in the northern high latitudes have had the opportunity to study extremely rare deposits of fossil insects that date back millions of years. In some cases, these fossil assemblages represent late Tertiary environments that preceded the earliest glaciations of the Quaternary. Other assemblages represent early Quaternary environments, when glacial–interglacial cycles were beginning. These fossil assemblages afford us rare glimpses into the history of the Arctic and sub-Arctic regions during periods when regional environments were startlingly different from today. In many cases, there are no modern analogs for the fossil assemblages. The challenge for insect paleontologists has been to make ecological sense of these fossil assemblages to reconstruct the environments in which they lived. It has been difficult, painstaking work that in some cases required decades of research to bring to completion.

These fossil insect faunas bridge a paleontological gap between the actual exoskeletal remains preserved in the unconsolidated sediments of the Pleistocene and the mineral replacements and trace fossils