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Quaternary Fossil Beetle Assemblages from South America

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s0005 Background

p0005 Studies of fossil beetle assemblages in South America have been directed at coming to a better understanding of how beetles respond to climate change and to the use of that information for interpreting paleoclimate. One of the primary challenges of the research has been to demonstrate that the results would be sufficiently robust for other researchers in archeology, plant paleoecology, glacial geology, and paleoclimatology to use with confidence in their studies. Of particular interest has been the question of whether a climatic reversal occurred in southern South America that was of similar magnitude and timing to the Younger Dryas interval defined from the North Atlantic region. The sites from which Pleistocene fossil assemblages have been studied in South America are located primarily in the Chilean lake region and the Chilean channels, between 40 and 50°S (Figure 1). A single fossil assemblage of early to mid-Holocene age has also been examined from the Falkland islands in the Atlantic Ocean between 51 and 52°S (Buckland and Hammond, 1997).

s0010 The Landscape of Southern Chile

p0010 In the Región de Los Lagos (lake region), the terrain is mountainous with the Cordillera de la Costa (coastal ranges) separated from the stratovolcanoes of the Cordillera de los Andes (Andes) by a wide north-south trending lowland, the Valle Longitudinal (central valley). Dense forests once cloaked the entire landscape of the lower elevations but have mostly been cleared for agriculture. Today, extensive tracts of native Valdivian rain forest and North Patagonian rain forests survive only at higher elevations in the lake region (Figure 2A). Above tree line, the forests are replaced by an Andean tundra (Figure 2B) that extends to the fell fields, and permanent snow and ice capping the higher volcanic peaks. Further south in the Chilean channels, the landscape is more fragmented. Island archipelagoes, criss-crossed by deep glacially excavated fjords, extend to the tip of the continent. The permanent snow line is lower, and outlet glaciers of the North and South Patagonian ice fields calve icebergs into the fjords

(Figure 3A). The lowland vegetation is a dense cold-temperate rainforest (Figure 3B) which, at higher elevations, is replaced by the saturated soils and blanket bogs of the Magellanic moorland (Figure 3C). The climate in southern South America, from the mid- to the high latitudes, is dominated by a westerly circulation stronger in the south than in the north. Whitlock *et al.* (2000) discuss the relationship between climate, vegetation, and the insect fauna.

The Existing Beetle Fauna

The beetle fauna of the forests, moorlands, and steppes of southern South America is unusually rich in endemic taxa. Endemism implies ancient evolutionary relationships and Patagonia is the home of many surviving lineages of ancient clades. The Migadopini, for example, are an exclusively Southern Hemisphere tribe of Carabidae (ground beetles) that have a typically Gondwanan distribution. They occur throughout southern South America, including the Falkland islands, Tasmania and southeastern Australia, and New Zealand and the Auckland islands. Similar restricted geographic distributions occur within several families of beetles in the southern South American fauna, notably the Protocujidae, Chalcodryidae, Nemonychidae, and Belidae. These groups are either monotypic or represented by a small number of genera that are associated with *Nothofagus* forest. The taxa in many of these families evolved during the late Cretaceous when southern South America was still connected to Antarctica. The connection was severed by seafloor spreading to form the Drake Passage between 34 and 30 Ma. The recent discovery of fossils of listroderine weevils in Neogene deposits, 500 km from the South Pole, confirms the evolutionary ties that South America had with Antarctica (Ashworth and Kuschel, 2003). Listroderine weevils are presently widely distributed in the forests, steppes, and moorlands of southern South America.

Joseph Banks, naturalist on the HMS Endeavour, Captain James Cook's first voyage of exploration, collected beetles from southern South America in 1769. One of those specimens, the ground beetle *Ceroglossus suturalis*, was described by Johann Fabricius in 1775. In the nineteenth century, Charles Darwin and other naturalists, who followed, sent their specimens back to Europe to be described by specialists in the natural history museums in London and Paris. Darwin was responsible for collecting one of the most distinctive beetles of

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2 Quaternary Fossil Beetle Assemblages from South America

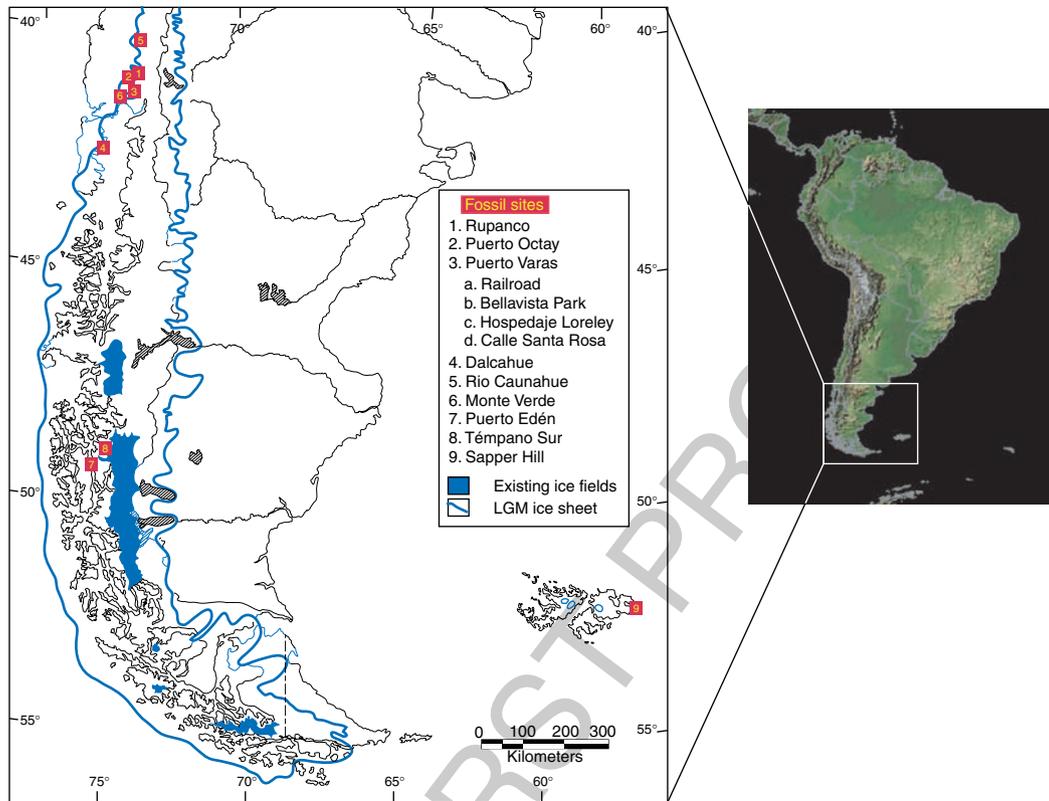


Figure 1 Location of fossil beetle assemblages from southern South America. The representation of the Patagonian ice sheet during the last glaciation is from Hollin and Schilling (1981).

the Chilean rain forest, the lucanid *Chiasognathus grantii* Stephens. The male is characterized by mandibles that are almost twice as long as its body (Figure 4A) giving rise to its common name in southern Chile of “ciervo volante” or “flying deer.” In *The Descent of Man*, Darwin wrote “But the mandibles were not strong enough so as to cause actual pain.” The specimens are preserved in the Natural History Museum, London, where the male is known as “the beetle that bit Darwin.” The nineteenth century naturalist who made the greatest contribution to the knowledge of the Chilean fauna was Claudio Gay. He made extensive collections of the fauna during travels between 1828 and 1842, and those specimens are described and illustrated in color in his 1849 and 1851 volumes of *La Historia Física y Política de Chile* (Figure 4A). More recently, Elizabeth Arias (2000) has described the most distinctive species of the fauna in *Coleópteros de Chile*.

There are numerous excellent taxonomic treatments of the existing beetle fauna which are invaluable as aids in the identification of Pleistocene fossils. There are few faunistic and ecological studies, however, on which to base paleoenvironmental and paleoclimatic interpretations. Ashworth and Hoganson (1987) made extensive collections in the

Parque Nacional Puyehue and other undisturbed habitats in the Chilean lake region (Figure 4B). They described a diverse fauna of 462 species from habitats collected systematically along an elevational transect from sea level to 1200 m. Their ordination analysis showed changes in beetle communities along the transect which generally correlated with changes in vegetation.

Fossil Studies

Chilean Lake Region

In the Chilean lake region, fossil assemblages ranging in age from 24 to 4.525 kyr BP have been examined. Assemblages from sites at Puerto Octay, Puerto Varas (Park and Railroad), Rio Caunahue, and Monte Verde have been described and their significance discussed in a series of papers (Hoganson *et al.*, 1989; Hoganson and Ashworth, 1992; Ashworth and Hoganson, 1993). Additionally, unpublished fossil assemblages have been studied by Ashworth from sites at Rupanco, Dalcahue, and Puerto Varas (Loreley and Calle Santa Rosa) (Figure 1). All of the sites, with the exception of Monte Verde, are from locations in the lowlands of the central valley that

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f0010 **Figure 2** Habitats in the Chilean lake region: A, The lower Valdivian rain forest in the lake region near Aguas Calientes, Parque Nacional Puyehue; B, the Andean tundra and krummholz at tree line west of Antillanca, Parque Nacional Puyehue. Volcán Casablanca is in the background. Photographs by A. C. Ashworth.

were glaciated during the Last Glacial Maximum. The Monte Verde site is located west of the terminal moraines of the last glaciation and is associated with a drainage that developed on glacial outwash.

p0035 The oldest fossil beetle assemblages to have been examined are from peat deposits near the west end of Lago Rupanco (Figure 1). Fossils were extracted from an *in situ* peat that is overlain by gravel, till, and volcanic deposits (Mercer, 1976; Denton *et al.*, 1999). The assemblages range in age from 19.5 to 24 kyr BP and are representative of the beetle fauna of the lake region immediately prior to the Last Glacial Maximum. The assemblages are the least diverse of any examined from the lake region consisting of only 9–10 species. Exceptionally well-preserved skeletal parts of the listroderine weevil *Germainiellus dentipennis* (Germain) (Figure 5), including heads, pronota, elytra, sternites, leg segments, and genitalia, make up 90% of the fossils.

p0040 Similar assemblages dominated by *G. dentipennis* occur within the lake region until about 14 to

f0015 **Figure 3** Habitats in the Chilean channels: A, The Glaciar Pio XI in the Chilean channels; B, dense rainforest of *Nothofagus betuloides* in the Fiordo Bernardo. C, Magellanic moorland in the coastal mountains west of Puerto Edén. Photographs by A. C. Ashworth.

14.5 kyr BP. The youngest of these assemblages, dated at 14.34 kyr BP, is from near Dalcahue on La Isla Grande de Chiloé (Chiloé). The peaty deposits are overlain by outwash gravels and till of the final major glacial advance in the mid-latitudes of South America (Figure 6). Included in the 22 taxa from this assemblage is the weevil *Paulsenius carnicollis* (Blanchard) and the ground beetle *Cascellius*

4 Quaternary Fossil Beetle Assemblages from South America



Figure 4 Modern beetle fauna: A, Enlargement of one of the plates from Gay's nineteenth century *Historia Física y Política de Chile*. The beetle with the large mandibles is the distinctive Valdivian rain forest lucanid *Chiasognathus grantii*; B, studies of the modern beetle fauna were essential to establishing the base for paleoclimatic interpretation. Photograph by A. C. Ashworth.

septentrionalis Roig-Juñent that today both inhabit higher elevations in the Andes. Villagrán (1990) made the observation that Magellanic moorland plants, which currently inhabit relict patches at 700 m elevation in the coastal ranges of Chiloé,

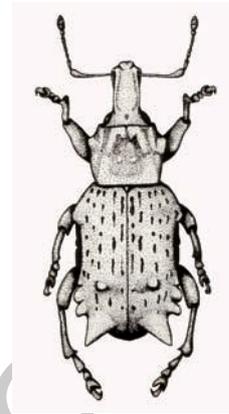


Figure 5 The weevil *Germainiellus dentipennis* (Morrone, 1993) whose exoskeletal remains are the most abundant in fossil assemblages dating from 24 to 14 kyr BP. Reproduced from Morrone JJ (1993) Revisión sistemática de un nuevo género de Rhytirrhini (Coleoptera, Curculionid), con un análisis biogeográfico del dominio subantártico. Boletín de la sociedad de Biología de Concepción, Chile, 64: 121–145.

grew near sea level during the last glaciation. Using an adiabatic lapse rate of 0.65 C/100 m, Ashworth and Hoganson (1993) estimated that mean summer temperature during the glacial interval was 4–5 C lower than today based on the species composition of fossil beetle assemblages. Denton *et al.* (1999) estimated that snow and tree line were lowered by 1000 m between 29.4 and 14.4 kyr BP representing mean summer temperatures 6–8 C lower than today.

Fossil assemblages postdating 14 kyr BP are fundamentally different in their composition. Not only are they considerably more diverse but also they contain higher percentages of taxa that are obligate forest inhabitants. Most of the assemblages that have been examined are from exposed cut bank sections on the Rio Caunahue, a large river that originates in the Andes and enters Lago Ranco on the east side. Rhythmically laminated deposits containing abundant organics and volcanic ashes were deposited in a narrow arm of the lake immediately following deglaciation (Figure 7A). The basal sediments are inorganic clays representing the deposition of rock flour. The 7-m sequence, with a basal age of 13.9 kyr BP (Ashworth and Hoganson, 1993), contains exceptionally well-preserved fossils (Figure 7B). The species compositions of 30 intervals pre-dating 10 kyr BP were reported in Hoganson and Ashworth (1992); the number of taxa identified was 154, of which 41–48% consisted of obligate forest taxa. All of the taxa currently inhabit the forests of the lake region, mostly the Valdivian rain forest.

The only other fossil beetle assemblage post-dating 14 kyr BP that has been examined from the lake region is from the archeological site at Monte



f0030 **Figure 6** A, At Dalcahue, Isla Grande de Chiloé, organic sediments (brown) contain the youngest fossil beetle assemblages representing the glacial beetle fauna. Fossil wood at the top of the section has an age of 14.34 kyr BP; B, organic sediments accumulated in a small depression on the surface of a weathered till. The surface was buried by outwash gravel (top of the section) during the last glacial advance in the lake region. Scale = cm divisions. Photographs by A. C. Ashworth.

Verde, near Puerto Montt (Figure 8). At Monte Verde, humans are believed to have constructed primitive shelters and hunted mastodon. Fossil beetles were retrieved from horizons considered to be contemporaneous with the human habitation (MV-6) dated between 13.565 and 11.79 kyr BP, and also from a peat bed (MV-5) that sealed the cultural horizon and is dated between 11.81 and 10.86 kyr BP (Dillehay, 1989). Statistical comparison of the 95 taxa occurring in MV-6 and MV-5 demonstrated that the assemblages were similar to one another (Hoganson *et al.*, 1989).

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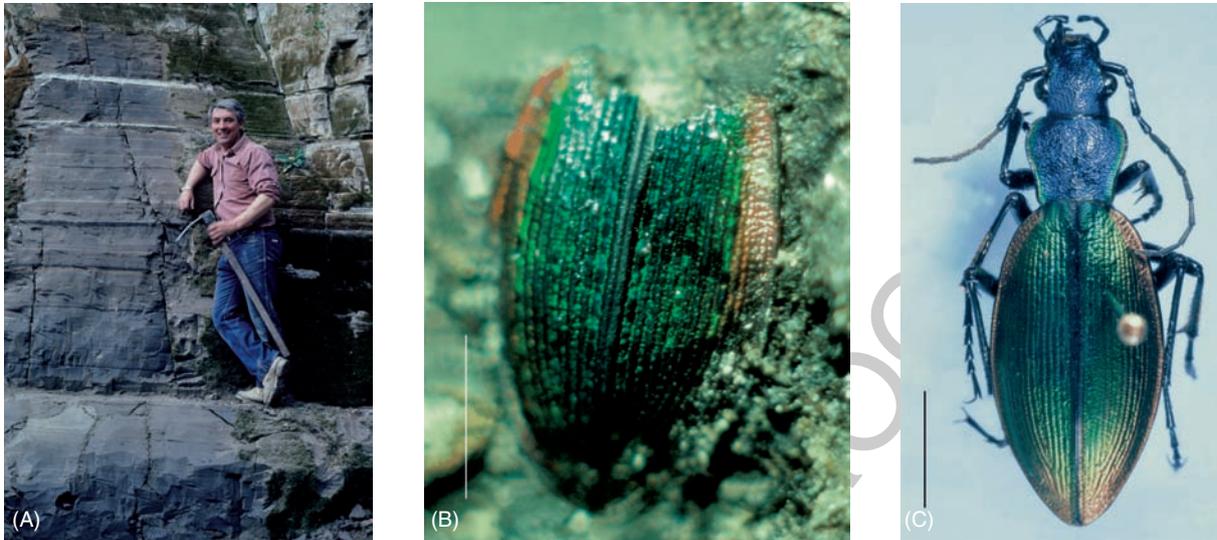
p0055 Using cluster analysis, the species compositions of the fossil assemblages were compared to modern communities from 41 locations within the Chilean lake region. The Monte Verde assemblage was most similar to the communities from slightly disturbed coastal forests and from the Valdivian Rain Forest at about 500 m elevation (Hoganson *et al.*, 1989).

The interpretation that the paleoclimate at Monte Verde was essentially similar to that of today during the human occupation is consistent with interpretations from similar-aged fossil beetle assemblages at the Rio Caunahue site.

One of the intriguing puzzles of the Monte Verde beetle assemblage is that no synanthropic beetles were identified. In Europe, fossil beetle assemblages from archeological sites ranging in age from Mesolithic to historical times show evidence of modification, especially those associated with agricultural. Why there would be no synanthropic insects at Monte Verde is unknown, but it is possible that hunter-gatherer groups did not disturb the natural environment to such an extent that it caused an ecological response in the beetle fauna. A similar observation was made for early Postglacial beetle faunas associated with human occupation in North America (Elias, 1994).

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6 Quaternary Fossil Beetle Assemblages from South America



f0035 **Figure 7** A, The Rio Caunahue assemblages are from laminated silts interbedded with volcanic ashes. The bench on which the person is standing has an age of 12.81 kyr BP and the prominent white volcanic ash above his head has an age of about 10.8 kyr BP. B, The fused fossil elytra (wing cases) of a specimen of the ground beetle *Ceroglossus*, that is from the horizon dated at 10 kyr BP. C, A modern specimen of *Ceroglossus* from the Valdivian rain forest. Scale bars = 5 mm. Photographs by A. C. Ashworth.

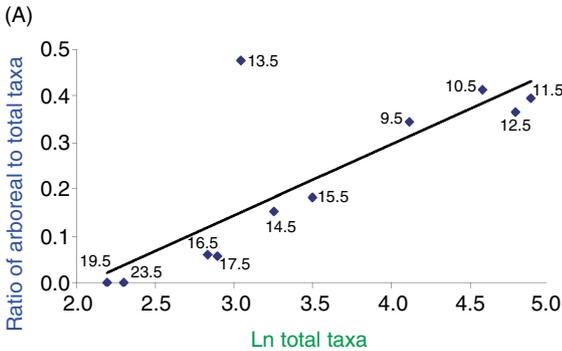
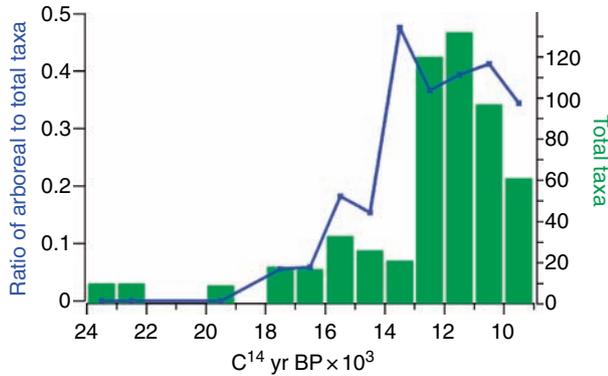


f0040 **Figure 8** The Monte Verde archeological excavation. An excavated hearth-like structure is visible in the foreground. The peat MV-5 which contains abundant fossil beetles and is dated between 11.81 and 10.86 kyr BP is visible at the base of the cut on the far wall of the excavation. Photograph by A. C. Ashworth.

To examine longer-term trends represented by the fossil beetle assemblages, the total taxa and the ratio of taxa dependent on trees are examined for 1 kyr intervals between 24 and 9 kyr BP (Figure 9A). The beetle fauna from 24 kyr BP to the time of the last glacial advance about 14 kyr BP was composed of species of wet moorland habitats. The assemblages are characterized by low diversity and low numbers of taxa dependent on shrubs and trees. Between 14 and 13 kyr BP the diversity is low but the percentage of arboreal taxa is higher. Between 13 and 12 kyr BP, the assemblages are at least 5 times as diverse as those of the glacial interval. The changes indicate that by 13 kyr BP, moorland habitats, which had existed in the central valley for more than 10 kyr, had been replaced by forested habitats similar to those that exist in the region today.

The numerical data are also used to test two null hypotheses (Figure 9B). The first is that no relationship exists between total taxa and ratio of arboreal taxa. This hypothesis was tested using linear regression ($\alpha = 0.05$). The null hypothesis was shown not to be true, and the relationship between total taxa and ratio of arboreal taxa was found to be highly significant ($P = 0.001$, $r^2 = 0.62$). The interval from 14 to 13 kyr BP has a studentized residual value of 11.5 making it very different from all other samples. The difference is explained because the sample represents most of the change in the transition between moorland and forested biomes.

The second null hypothesis is that no significant difference exists between the ratios of arboreal taxa



(B)

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Figure 9 Longer-term trends for the interval 24–9 kyr BP represented by a compilation of data from all of the fossil assemblages: A, plots of the total number of taxa (bar graph) and the ratio of obligate arboreal taxa (line graph); B, the relationship between total and ratio of arboreal taxa. The x-axis is natural log transformed. The labels shown are mid-ranges for samples, each of which represents a 1 kyr interval of time. The line represents a significant linear regression. The data point at 13.5 (14–13 kyr BP) is a significant outlier representing the time of major change between moorland and forest assemblages.

for two subsets of samples between 24–15 kyr BP and 13–9 kyr BP. The sample representing the 13–14 kyr BP interval was not included in the test because it is a statistical outlier. The null hypothesis was tested using a two-sample T-test ($\alpha = 0.05$). The result was that the null hypothesis was shown not to be true. The ratios of arboreal taxa to total taxa for the glacial interval 24–15 kyr BP are significantly different than for the postglacial interval between 13 and 9 kyr BP ($t = 9.842$, $df = 8.5$, $P < 0.001$).

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s0030 Chilean Channels

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Fossil beetle assemblages have been examined from two locations in the Chilean channels. The Puerto Edén site on the Canal Messier is from an excavation in a bog (Figure 10), and the Témpano Sur site is from an outcrop in the wall of an abandoned meltwater channel about 1 km from the margin of the Glaciar Témpano, an outlet glacier of the South



Figure 10 The bog at Puerto Edén is located between morainic arcs deposited by a glacier that retreated into the coastal ranges. Glacial ice also filled the Paso del Indio, the marine channel that leads northward to the Messier Canal. Photograph by A.C. Ashworth.

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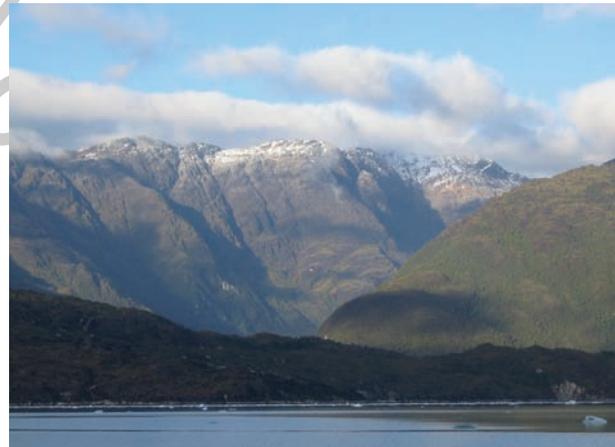


Figure 11 The fossil site at Témpano Sur is located behind the bedrock ridge in the foreground. It is located in an abandoned meltwater channel that has an outlet to the fjord at the extreme right of the photograph. The floating ice is from melting of the Glaciar Témpano about 1 km to the left of the image. Photograph by A. C. Ashworth.

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Patagonian ice field (Figure 11). At both sites, pollen and fossil beetles were examined from the same samples (Ashworth and Markgraf, 1989; Ashworth *et al.*, 1991). As the glacier at Puerto Edén receded westward to the coastal mountains, peat began to accumulate at about 13 kyr BP in a shallow depression between morainic ridges. Throughout the peat profile there is excellent agreement between the interpretations based on fossil beetles and those based on pollen (Ashworth *et al.*, 1991). Immediately following deglaciation, the colonizing plants and beetles were those of open ground communities, similar to those inhabiting active glacial outwash plains about 45 km east of the site. From 13 to about 9.5 kyr BP

8 Quaternary Fossil Beetle Assemblages from South America

the biota was that of a *Nothofagus* woodland which persisted until 5.5 kyr BP, when it was replaced by a rainforest-moorland mosaic similar to that existing in the region today. Sometime between 5.5 and 3 kyr BP, the biota changed dramatically on the moraines surrounding the bog, and the bog itself dried up. After 3 kyr BP, a biota similar to that which had existed between 9.5 and 5.5 kyr BP returned. Puerto Edén has a precipitation of about 3000 mm yr⁻¹. For the bog to completely dry up requires a very significant climatic change. Markgraf *et al.* (2003) reported changes in the sedimentology, paleontology, and geomorphology of Lago Cardiel (49° S) on the Patagonian steppe, east of Puerto Edén indicating severe droughts between 6 and 5000 kyr BP. They point out that widespread mid-Holocene aridity has been reported in records from the Patagonian steppe to the North American plains, but for which, as yet, there is no compelling climatological explanation.

p0085 At the head of the Témpano fjord, interbedded sands and peats infilled a bedrock-floored channel that was later eroded by meltwater. The basal peat is dated between 11.18 and 10.13 kyr BP. Fossil beetle and pollen assemblages from the peat indicate a fauna and flora very similar to that inhabiting stable substrates within the area today. The implication is that the South Patagonian ice field during the Younger Dryas interval was no larger than it is today and could even have been smaller (Ashworth and Markgraf, 1989).

s0035 Biogeographic Considerations

p0090 In the montane and island-fragmented landscape of southern Chile, the onset of the last phase of the glaciation is dated at 29.4 kyr BP (Denton, *et al.*, 1999). Nothing is known of the beetle fauna that existed before the final phase of glaciation; however, it is reasonable to assume that it was a forest fauna based on available pollen analyses. Further, it is reasonable to speculate that as the climate cooled, species became regionally extinct. It is assumed that these species survived in more northerly locations and were available for recolonization when the climate warmed between 14 and 13 kyr BP. The fauna that survived glaciation in the moorland habitat of the lake region has no modern analog. It consisted of: (1) species that had dispersed downslope from habitats high in the coastal ranges and the Andes and (2) species that were “climatic generalists” that could survive the lower temperatures. There is no evidence that cold-adapted species from more southerly latitudes migrated to the lake region.

p0095 The absence of evidence for latitudinal movement of beetle taxa in response to climate change during

the last glaciation makes southern South America very different than either Europe or North America where species were displaced more than 1000 km from their existing distributions (Ashworth, 2001). The prevailing hypothesis is that the biota south of Chiloé was completely extirpated during the last glaciation and consequently would not have been available to colonize more northerly regions. The hypothesis has serious flaws (see below), but even if pockets of biota did survive to the south, northward dispersal would have been blocked by barriers imposed by marine inlets and large glaciers.

Reconstructions of ice cover for southern South America during the Last Glacial Maximum portray an ice sheet that was continuous from latitude 43° S in the lake region to 56° S in Tierra del Fuego (Hollin and Schilling, 1981) (Figure 1). At the northern end, parts of Chiloé, the coastal ranges, and the central valley were ice free. South of Chiloé, however, ice is shown as covering the coastal mountains and extending to the Pacific Ocean. An equilibrium line altitude lowering of 900 m was used by Hubbard *et al.* (2005) to model the central regions of the Patagonian ice sheet between 45° and 48° S. Their model shows that by 21 kyr BP ice covered the Taitaó Peninsula extending to the coastal shelf, comparable to the Hollin and Schilling (1981) reconstruction. Using climatic forcing modified from the Vostok ice core, their model shows an ice sheet that slowly retreated until 14.5 kyr BP, after which it collapsed rapidly reaching its present-day configuration by 11 kyr BP after briefly stabilizing during the Antarctic Cold Reversal.

The effect of glaciation is considered to have been devastating to the flora and fauna, resulting in the total extirpation of species south of Chiloé. Two pieces of evidence, however, suggest that the extent of glaciation and extirpation of the biota may have been overestimated. The first is that there are several species of large- to moderate-sized flightless beetles in the basal layer of the bog at Puerto Edén with an age of about 13 kyr BP. The fossils include the ground beetles *Ceroglossus suturalis* F., *Creobius eydouxi* Guérin, *Cascellius gravesii* Curtis, and *C. septentrionalis* Roig-Juñent, and the weevils, *Aegorhinus kuscheli* Elgueta and *Germainiellus rugipennis* (Blanchard). For flightless species to be among the earliest colonizers of the bog implies that they had to have survived glaciation locally, either in the coastal mountains or more probably along the coast. The second piece of evidence supporting survival in local refugia is the high genetic diversity measured in isolated populations of the tree species *Pilgerodendron uvifera* (D. Don) Florin (Premoli *et al.*, 2003). If these populations were Holocene immigrants derived by long-distance dispersal from northern refugia, then

it would be expected that the severity of the genetic bottleneck they have been through would have resulted in the populations having much lower genetic diversity.

s0040 **The Younger Dryas Conundrum**

p0110 One of the enduring problems associated with paleoclimatic interpretation in the Chilean lake region is whether the pattern of climatic changes at the end of the last glaciation was identical to that of the North Atlantic region. In particular, the problems focused on the existence of a Younger Dryas equivalent between 11 and 10 kyr BP. Currently, the question involves whether there is a climatic cooling, the Huelmo-Mascardi cold reversal (Hajdas *et al.*, 2003), between 12.4 and 10 kyr BP. The initial disagreement centered on several interpretations based on pollen studies for a climatic reversal of 5–10 °C precisely correlated with the Younger Dryas (Heusser, 1974). The studies were considered to be strong evidence for the Younger Dryas being a global event. Ashworth and Hoganson (1993), however, argued that there was no evidence for any significant amount of cooling indicated by fossil beetle assemblages after 14 kyr BP precipitating a disagreement that continues today.

p0115 In southern South America, outside of the Chilean lake region, the evidence for climatic cooling coeval with the Younger Dryas is equally problematical. Ariztegui *et al.* (1997) reported indirect evidence for a Younger Dryas glacial advance on Monte Tronador, based on studies of sediments, diatoms, and pollen from Lago Mascardi. Redating of that event has demonstrated that the proposed cooling includes the Younger Dryas but pre-dates it by 550 yr (Hajdas *et al.*, 2003). Earlier, pollen studies in the region showed that there had been no response of vegetation to climate change between 11 and 10 kyr BP (Markgraf, 1984). In pollen records from the Chonos (44° S) and Taitao peninsulas (46°), the vegetation shows a unidirectional shift from heath to forest, with essentially the modern forest developed by 12.400 kyr BP (Bennett *et al.*, 2000; Haberle and Bennett, 2004). No evidence was found for cooling during either the Younger Dryas or the earlier Antarctic Cold Reversal. However, one of the possible explanations for changes in chironomid (midge) fossil assemblages from a lake studied by Bennett *et al.* (2000) was for climatic cooling during the Younger Dryas (Massaferro and Brooks, 2002). Further south in the Chilean Channels (49° S) combined analyses of fossil beetle assemblages and pollen also showed no evidence of a Younger Dryas climatic cooling (Ashworth *et al.*, 1991). At the Témpano

glacier, Ashworth and Markgraf (1989) reported that the North Patagonian ice field was within its present boundaries during the Younger Dryas. In Tierra del Fuego, Heusser and Rabassa (1987) reported a glacial and vegetational response consistent with cooling during the Younger Dryas. From the same region, Markgraf (1993) reported the occurrence of charcoal during the Lateglacial and preferred to interpret the pollen in terms of local environmental instability rather than climatic cooling.

Moreno *et al.*, (1999) reported a climatic cooling p0120 of 2–3° between 12.2 and 9.8 kyr BP in the Chilean lake region based mostly on the occurrence of the pollen of *Podocarpus nubigena* Lindl., a conifer which occurs in the North Patagonian and Valdivian rain forests. They discussed how the proposed cooling produced only minor changes in forest structure but still considered climate change to be the probable cause rather than disturbance from a non-climatic cause. Ashworth and Hoganson (1987) were unable to discriminate statistically between the modern beetle communities of the North Patagonian and upper Valdivian rain forest which, in terms of paleoclimatic interpretation, would translate to ±1 C. The difference between interpretations based on pollen and those on fossil beetle assemblages is now within ±1 C or what many paleoecologists would consider noise within the records and irresolvable between climatic and nonclimatic causes.

The situation now is very different than when p0125 disagreements between interpretations were initially stated. Then, the pollen evidence was unequivocally for a climatic cooling of similar magnitude and timing to the Younger Dryas in the North Atlantic. Currently, even proponents for climate change argue that it is subtle and that it begins 500–1200 yr before the Younger Dryas. Moreno (1997), Moreno *et al.* (1999), and Hajdas *et al.* (2003) still consider the cooling to be part of a globally synchronous event but Ashworth and Hoganson (1993), Markgraf (1993), and Bennett *et al.* (2000) find no evidence to support climatic reversals at the time of the Younger Dryas (11–10 kyr BP) or during the Antarctic Cold Reversal (14.5–12.9 kyr BP).

References

- Arias, E. T. (2000). *Coleópteros de Chile*. Fototeknika, Santiago de Chile. b0005
- Ariztegui, D., Bianchi, M. M., Massaferro, J., Lafargue, E., and Niessan, F. (1997). Interhemispheric synchrony of late-glacial climatic instability as recorded in proglacial Lake Mascardi, Argentina. *Journal of Quaternary Science* 12, 133–138. b0010

10 Quaternary Fossil Beetle Assemblages from South America

- b0015** Ashworth, A. C. (2001). Perspectives on Quaternary Beetles and Climate Change. In *American Association of Petroleum Geologists Studies in Geology, Geological Perspectives of Global Climate Change*, (L. Gerhard, W. Harrison and B. Hanson, Eds.) Vol. 47, pp. 153–168.
- AU7**
- b0020** Ashworth, A. C., and Hoganson, J. W. (1987). Coleoptera bioassemblages along an elevational gradient in the lake region of southern Chile and comments on the postglacial development of the fauna. *Annals of the Entomological Society of America* **80**, 865–895.
- b0025** Ashworth, A. C., and Hoganson, J. W. (1993). Magnitude and rapidity of the climate change marking the end of the Pleistocene in the mid-latitudes of South America. *Palaeogeography, Palaeoclimatology, Palaeoecology* **101**, 263–270.
- b0030** Ashworth, A. C., and Kuschel, G. (2003). Fossil weevils (Coleoptera:Curculionidae) from latitude 85° S Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **191**, 191–202.
- b0035** Ashworth, A. C., and Markgraf, V. (1989). Climate of the Chilean channels between 11,000 and 10,000 yr BP based on fossil beetle and pollen analyses. *Revista Chilena de Historia Natural* **62**, 61–74.
- b0040** Ashworth, A. C., Markgraf, V., and Villagrán, C. (1991). Late Quaternary climatic history of the Chilean channels based on fossil pollen and beetle analysis, with an analysis of the modern vegetation and pollen rain. *Journal of Quaternary Science* **6**, 279–291.
- b0045** Bennett, K. D., Haberle, S. G., and Lumley, S. H. (2000). The last Glacial–Holocene transition in southern Chile. *Science* **290**, 325–328.
- b0050** Buckland, P. C., and Hammond, P. M. (1997). The origins of the biota of the Falkland Islands and South Georgia. In *Quaternary Proceedings 5: Studies in Quaternary Entomology—An Inordinate Fondness for Insects* (A. C. Ashworth, P. C. Buckland and J. P. Sadler, Eds.), pp. 59–66. Wiley, Chichester.
- b0055** Denton, G. H., Lowell, T. V., Heusser, C. J., et al. (1999). Geomorphology, stratigraphy, and radiocarbon chronology of Llanquihue drift in the area of the southern Lake District, Seno Reloncavi, and Isla Grandé de Chilo., Chile. *Geografiska Annaler* **A81**, 167–229.
- b0060** Dillehay, T. D., and Pino, M. (1989). Stratigraphy and chronology. In *Monte Verde – A Late Pleistocene Settlement in Chile* (T. D. Dillehay, Ed.), pp. 133–145. Smithsonian Institution Press, Washington.
- b0065** Elias, S. A. (1994). *Quaternary insects and their environments*. Smithsonian Institution Press, Washington.
- b0070** Haberle, S. G., and Bennett, K. D. (2004). Postglacial formation and dynamics of North Patagonian rainforest in the Chonos Archipelago, southern Chile. *Quaternary Science Reviews* **23**, 2433–2452.
- b0075** Hajdas, I., Bonani, G., Moreno, P. I., and Ariztegui, D. (2003). Precise radiocarbon dating of late-glacial cooling in mid-latitude South America. *Quaternary Research* **59**, 70–78.
- b0080** Heusser, C. J. (1974). Vegetation and climate of the southern Chilean lake district during and since the last interglaciation. *Quaternary Research* **4**, 290–315.
- b0085** Heusser, C. J., and Rabassa, J. (1987). Cold climatic episode of Younger Dryas in South America. *Nature* **328**, 609–611.
- Hoganson, J., Gunderson, M., and Ashworth, A. (1989). Fossil-beetle analysis. In *Monte Verde – A late Pleistocene settlement in Chile* (T. D. Dillehay, Ed.), pp. 211–226. Smithsonian Institution Press, Washington.
- b0090**
- Hoganson, J. W., and Ashworth, A. C. (1992). Fossil beetle evidence for climatic change 18,000–10,000 years BP in South-Central Chile. *Quaternary Research* **37**, 101–116.
- b0095**
- Hollin, J. T., and Schilling, D. H. (1981). Late-Wisconsin–Weichselian mountain glaciers and small ice caps. In *The Last Great Ice Sheets* (G. H. Denton and T. J. Hughes, Eds.), pp. 179–206. Wiley, New York.
- b0100**
- Hubbard, A., Hein, A. S., Kaplan, M. R., Hulton, N. R. J., and Glasser, N. (2005). A modelling reconstruction of the late glacial maximum ice sheet and its deglaciation in the vicinity of the Northern Patagonian Icefield, South America. *Geografiska Annaler* **A87**, 375–391.
- b0105**
- Markgraf, V. (1984). Late Pleistocene and Holocene vegetation history of temperate Argentina: Lago Morenito, Bariloche. *Dissertationes Botanicae* **72**, 235–254.
- b0110**
- Markgraf, V. (1993). Younger Dryas in southernmost South America – An update. *Quaternary Science Reviews* **12**, 351–355.
- b0115**
- Markgraf, V., Bradbury, J. P., Schwab, A., et al. (2003). Holocene palaeoclimates of southern Patagonia: Limnological and environmental history of Lago Cardiel, Argentina. *The Holocene* **13**, 597–607.
- b0120**
- Massaferro, J., and Brooks, S. J. (2002). Response of chironomids to late Quaternary environmental change in the Taitao peninsula, southern Chile. *Journal of Quaternary Science* **17**, 101–111.
- b0125**
- Mercer, J. H. (1976). Glacial history of southernmost South America. *Quaternary Research* **6**, 125–166.
- b0130**
- Moreno, P. I. (1997). Vegetation and climate near Lago Llanquihue in the Chilean Lake district between 20,200 and 9500 14C yr BP. *Journal of Quaternary Science* **12**, 485–500.
- b0135**
- Moreno, P. I., Lowell, T. V., Jacobson, G. L., jr, and Denton, G. H. (1999). Abrupt vegetation and climate changes during the last glacial maximum and last termination in the Chilean Lake District: A case study from Canal de la Puntilla (41° S). *Geografiska Annaler* **A81**, 285–311.
- b0140**
- Morrone, J. J. (1993). Revisión sistemática de un nuevo género de Rhytirrhini (Coleoptera, Curculionidae), con un análisis biogeográfico del dominio Subantártico. *Boletín de la Sociedad de Biología de Concepción, Chile* **64**, 121–145.
- b0145**
- Premoli, A. C., Souto, C. P., Rovere, A. E., Allnut, T. R., and Newton, A. (2002). Patterns of isozyme variation as indicators of biogeographic history in *Pilgerodendron wuiferum* (D. Don) Florin. *Diversity and Distributions* **8**, 57–66.
- b0150**
- Villagrán, C. (1990). Glacial climates and their effects on the history of the vegetation of Chile: A synthesis based on palynological evidence from Isla de Chiloé. *Review of Palaeobotany and Palynology* **65**, 17–24.
- b0155**
- Whitlock, C., Bartlein, P. J., Markgraf, V., and Ashworth, A. C. (2001). The midlatitudes of North and South America during the last glacial maximum and early Holocene: Similar paleoclimatic sequences despite differing large-scale controls. In *Interhemispheric Climate Linkages* (V. Markgraf, Ed.), pp. 391–416. Cambridge University Press, Cambridge.
- b0160**