1985

Late Quaternary environmental and climatic history of the southern Chilean Lake Region interpreted from coleopteran (beetle) assemblages

John W. Hoganson
University of North Dakota

Recommended Citation

Hoganson, John W., "Late Quaternary environmental and climatic history of the southern Chilean Lake Region interpreted from coleopteran (beetle) assemblages" (1985). *Theses and Dissertations*. 141.
https://commons.und.edu/theses/141

LATE QUATERNARY ENVIRONMENTAL AND CLIMATIC HISTORY OF THE SOUTHERN CHILEAN LAKE REGION INTERPRETED FROM COLEOPTERAN (BEETLE) ASSEMBLAGES

by
John W. Hoganson

Bachelor of Arts
North Dakota State University, 1970

Master of Science
University of Florida, 1972

A Dissertation

Submitted to the Graduate Faculty

of the

University of North Dakota

in partial fulfillment of the requirements

for the degree of

Doctor of Philosophy

Grand Forks, North Dakota

December
1985

This dissertation submitted by John W. Hoganson in partial fulfillment of the requirements for the Degree of Doctor of Philosophy from the University of North Dakota is hereby approved by the Faculty Advisory Committee under whom the work has been done.

F. D. Holland Jr.
(Chairperson)

Allan Ashworth

J. R. Reid

Richard D. LeFever

Francis A. Jacobs

This dissertation meets the standards for appearance and conforms to the style and format requirements of the Graduate School of the University of North Dakota, and is hereby approved.

Dean of the Graduate School

Permission

Title Late Quaternary Environmental and Climatic History of the Southern Chilean Lake Region Interpreted from Coleopteran (Beetle) Assemblages

Department Department of Geology

Degree Doctor of Philosophy

In presenting this dissertation in partial fulfillment of the requirements for a graduate degree from the University of North Dakota, I agree that the Library of this University shall make it freely available for inspection. I further agree that permission for extensive copying for scholarly purposes may be granted by the professor who supervised my dissertation work or, in his absence, by the Chairman of the Department or the Dean of the Graduate School. It is understood that any copying or publication or other use of this dissertation or part thereof for financial gain shall not be allowed without my written permission. It is also understood that due recognition shall be given to me and to the University of North Dakota in any scholarly use which may be made of any material in my dissertation.

Signature John W Hoganson

Date 12/5/85

TABLE OF CONTENTS

LIST OF PLATES

Plate

LIST OF FIGURES

Figure

Figure

LIST OF TABLES

Table

Table

Table

ACKNOWLEDGMENTS

It is difficult to express in words my gratitude to all the people that I have had the pleasure to work with and have contributed to the completion of this dissertation. I am particularly thankful to the Geology Departments of the University of North Dakota and North Dakota State University for supporting this cooperative project between the two institutions and for providing the facilities necessary to carry out the research. I also thank the North Dakota Geological Survey, my employer for the past four years, for recognizing the importance of the research problem and sustaining me through its completion.

The knowledge gained from the coleopterists with the Systematic Entomology Laboratory (USDA) and Department of Entomology at the National Museum of Natural History (Smithsonian Institution) and Biosystematic Research Institute, Agriculture Canada Research Branch, Ottawa was essential for completion of the project. I express my appreciation to those scientists and the numerous other coleopterists (listed in Appendix C) for examining specimens and providing insights into the ecological requirements of the beetles. I am particularly obliged to Robert Gordon, Systematic Entomology Laboratory (USDA), for helping with identifications, providing lodging during my visits to the Smithsonian, and assistance in the field in 1979. Guillermo Kuschel, Entomology Division of the Department of Science and Industrial Research at the Mount Albert Research Center, Auckland, New Zealand deserves special thanks for the enthusiasm that he expressed for the project and examining weevil specimens. I also thank Charles O'Brien, Florida A. & M. University, for graciously accepting me into his home and assistance during examination of his remarkable weevil collection. I am grateful to Volker Puthz, Schlitz/Hessen, West Germany for examining staphylinids and for naming Stenus hogansoni after me.

I am indebted to John Mercer, Polar Institute, Ohio State University, for having the vision that beetles could be used to decipher the paleoclimatic history of southern Chile and initially proposing the project. John guided Allan Ashworth and me to the fossil sites, helped excavate them and even collected a few modern beetles. A person can always single out one individual that provided the inspiration to undertake a major research project. In my case, that person was Allan Ashworth, North Dakota State University, a long-time friend and research adviser for this project. Allan has truly been an hombre simpático in this endeavor. To him, I express my sincere thanks. I am indebted to Howard Mooers, currently a doctoral student at the University of Minnesota, for providing assistance in the field during the first expedition to southern Chile. Nano, Maria, and Tito of the Aguilar Gomez family of Puerto Varas where instrumental in helping us overcome the many logistical problems, and provided warm hospitality, while we were in Chile. I wish them well.

Students often do not realize the amount of effort that is required by their advisory committee to complete the dissertation. I express special gratitude to my committee members, F.D. Holland, Jr., Richard LeFever, John Reid, Francis Jacobs, and Allan Ashworth for critically reviewing the dissertation and providing advise for its improvement. Bud Holland, chairman of the committee, through his energy, provided the impetus to complete the dissertation in the allotted time.

No project of this magnitude can be completed without the support of a few very special people. My mother and father always emphasized the importance of education and provided the necessary moral and financial support to pursue my academic training. To them I am particularly grateful and wish that my father had been able to see the completion of this degree. There is only one person who is ultimately responsible for completion of this dissertation, my wife Shelly. Shelly instilled in me, through her love and understanding, the necessary drive to complete the dissertation. I'm eternally indebted to her for standing by me during these stressful times. The people who have had to sacrifice so much, and yet have provided so much comfort to me over the years, have been my children, Kelly, Shawn, Josh, and Brian. I hope that someday they will understand why I was not able to spend the amount of time I should have with them.

The project was funded by the Geology Departments at the University of North Dakota and North Dakota State University, UND Graduate Student Research Grant 5021-1914-0169, and National Science Foundation Grants ATM 77-14683 to Ohio State University and ATM 78-20372 to North Dakota State University.

ABSTRACT

Geological and palynological studies have produced conflicting interpretations of the late-glacial climatic history of the southern Chilean Lake Region. Pollen studies indicate a sharp climatic deterioration between about 11,000 and 10,000 yr B.P., interpreted to be coeval with the European Younger *Dryas* Stade. No geological evidence has been found for glacier advance during this postulated cold and wet interval. Fossil beetle assemblages from four sites (18,000 to 4,500 yr B.P.) were analyzed to address this problem and to decipher the late Quaternary environmental and climatic history of the Lake Region.

Between 18,000 and 15,700 yr B.P. lakes and ponds in the Central Valley (Puerto Octay and Puerto Varas Park Sites) existed in an open-ground, treeless setting. Beetle faunas probably lived in a stressed, cold environment. This was, however, a period of contracted glaciers. Climate ameliorated sufficiently after the last glacial maximum (19,500 yr B.P.) to permit glacier withdrawal and invasion of beetles into the lowlands but was still severe enough to support only eurythermic species. Climatic amelioration continued between 15,000 and 14,000 yr B.P. and trees and tree-dwelling beetles (Puerto Varas Railroad Site) migrated into the Central Valley. Parkland habitats developed in the lowlands. These 15,000 to 14,000-year-old transitional beetle assemblages mark the pivotal shift toward interglacial conditions in the Lake Region. This interpretation is consistent with the record of

glacial activity in the area. The timing of the transition is generally synchronous with similar events recorded in other areas of the world.

Lacustrine deposition began at the Rio Caunahue Site before 13,900 yr B.P. after glacial retreat from the Lago Ranco basin. Colonization of the lake and its margin began about 13,900 yr B.P. By 12,800 yr B.P. rain-forest biota inhabited the area. The climatic amelioration that began 15,000 yr B.P. was uninterrupted through the late glacial interval. By 12,800 yr B.P. climatic conditions, similar to those in the Lake Region today, were established and remained relatively stable until at least 4,500 yr B.P. No Younger Dryas-equivalent climatic deterioration was detected. These interpretations corroborate results of glacial geological studies in the Lake Region.

INTRODUCTION

A disproportionately high percentage of the paleontological investigations carried out to reconstruct late Quaternary environments and climates have been from areas in the Northern Hemisphere. Consequently, the late Quaternary climatic history of Europe has often been taken to represent the normal sequence of global events. However, Mercer (1969) in an early, controversial article proposed that the North Atlantic was atypical during the last glacial maximum because it was bounded to the east and west by large ice sheets and presumably to the north by extensive ice shelves. He suggested that this cryospheric configuration would have had a unique influence on the climate of areas around the North Atlantic during deglaciation because decaying ice sheets and disintegrating ice shelves would have retarded post-glacial warming trends and could possibly have caused temporary reversals in the warming trends. Ruddiman and McIntyre (1981) presented oceanographic evidence supporting Mercer's proposal. In contrast, temperate South America was not bounded by large ice masses and the amount of land ice has not decreased significantly since the last glacial maximum (about 19,500 yr B.P.--^{14}C years Before Present). The major consequence of post-maximum climatic amelioration has been a decrease in the area covered by ice shelves. For this reason, Mercer (1976) believed that areas such as southern South America responded more rapidly during the last glacial-interglacial transition to forcing factors controlling climatic change; it therefore provides more representative evidence for such changes than the North Atlantic areas.

As with other areas of the Southern Hemisphere, paleoclimatic studies in southern South America have lagged behind those in the Northern Hemisphere even though many of the hypotheses relating to the causes of climate change are predicated on either in-phase or out-of-phase relationships between the polar hemispheres. Because the late Quaternary glacial record of the southern Chilean Lake Region (39° to 42° S. lat.) is one of the most extensive and detailed in the Southern Hemisphere, paleoclimatic investigations in the area can offset the bias of data from the Northern Hemisphere. Easily accessible, widespread, well exposed, and radiometrically datable late Quaternary deposits are present in the Lake Region. Numerous glacial geological (Mercer, 1972a, 1976, 1982, 1983, 1984a, 1984b; Laugenie and Mercer, 1973; Heusser and Flint, 1977; Porter, 1981) and palynological (Heusser, 1966a, 1966b, 1974, 1981, 1984a, 1984b; Heusser and Streeter, 1980; Heusser and others, 1981) studies have been conducted there. The investigations, however, have produced conflicting hypotheses concerning the late Quaternary climatic history of southern Chile.

The late glacial (Late Llanquihue) maximum in the Lake Region occurred (Mercer, 1976) about 19,500 years ago (herein years ago or years old means ^{14}C years). This culmination falls within the same time range, 20,000 to 18,000 yr B.P., as the last glacial (Late Wisconsinan-Late Weichselian) maxima in temperate latitudes of the Northern Hemisphere. According to Mercer (1972a), rapid glacial recession followed the 19,500 yr B.P. maximum and by 16,300 yr B.P. the glaciers were reduced to about one-half their maximum size. The warming trend that caused the recession was also noted by Heusser (1974) in pollen profiles from the Lake Region. One (Mercer, 1976, 1984b) or perhaps two (Porter, 1981) readvances interrupted the general trend of post-maximum deglaciation. The most unequivocal evidence suggests that only one readvance occurred, culminating about 14,500 yr B.P. (Mercer, 1984b). Rapid withdrawal followed the readvance. Glaciers had retreated into the mountains by about 12,500 yr B.P. and had contracted to their present position by 11,000 yr B.P., remaining smaller than today until Neoglacial time (Mercer, 1976). Mercer's geomorphological studies implied that interglacial climatic conditions were established in southern Chile by at least 11,000 yr B.P. and remained relatively stable until the Neoglacial.

Important differences exist betwen Mercer's scenario and that determined by palynological investigations from the Lake Region. Vegetational changes implied by pollen studies were interpreted by Heusser (1974) and Heusser and Streeter (1980) to represent gradual warming from about 13,000 yr B.P., culminating in temperatures warmer than today by 11,300 years ago. Their findings were in agreement with the geomorphic evidence indicating that glaciers retreated rapidly during that time and were within their present margins by 11,000 yr B.P. But they interpreted their paleobotanical evidence to indicate a marked reversal in this warming trend from 11,300 yr B.P. until about 9,500 years ago. Summer temperatures were estimated to have been about 6°C colder and precipitation much greater than today during that short but sharp period of climatic deterioration. A climatic setback of such magnitude should have caused glacier resurgence, an inference that is not corroborated by Mercer's geomorphological studies. Significantly, this postulated cold and wet phase is approximately coeval with the clearly defined Younger *Dryas* Stade of northwestern Europe, which resulted in glacier readvance there. The climatic history of southern Chile for the interval between 11,000 and 10,000 years ago, implied by palynological studies is, consequently, notably different than that inferred from glacial geomorphological studies.

Because the Younger *Dryas* was such an emphatic event in northwestern Europe, many Quaternary researchers consider it to have been a worldwide climatic reversal even though there is little, unequivocal evidence of climatic deterioration during that time in North America or, for that matter, anywhere outside of northwestern Europe. Interpretations of paleobotanical evidence from the Lake Region support the concept of a global deterioration of climate during the Younger *Dryas* whereas geological evidence from southern Chile does not. The importance of determining whether the Younger *Dryas* was a global phenomenon or geographically restricted has far-reaching implications because, for example, the global occurrence of the Younger *Dryas* Stade was assumed in setting the epoch boundary between the Pleistocene and Holocene at 10,000 yr B.P. (Mercer, 1972b).

Through analysis of fossil beetle assemblages, it is the intent of this study to:

(1) determine the environmental and climatic history of the southern Chilean Lake Region during the 18,000 to 4,500

yr B.P. time period;

(2) attempt to resolve the problem presented by the conflicting paleobotanical and geological interpretations concerning the timing and duration of climatic events in the Lake Region, especially during the time of the European Younger *Dryas* Stade;

(3) determine the time of the last glacial readvance in the Lake Region and the rapidity of warming and recession following the advance;

(4) compare the findings with other Southern and Northern Hemisphere records.

Although fossil beetles have been used extensively in the Northern Hemisphere, especially in western Europe and North America, to determine Quaternary environments and climates, no studies of this kind have previously been attempted in the Southern Hemisphere.

For the method to be successfully applied, well-dated sequences of fossil assemblages must be available and knowledge of the autecology of the taxonomic groups must be adequate. Four low-elevation sites (Puerto Octay, Puerto Varas Park, Puerto Varas Railroad, Rio Caunahue) in the southern Chilean Lake Region (Figures 1 and 4), previously discovered during glacial geological investigations, were chosen for this study because collectively they span the time interval of the last 18,000 years and, after cursory observation, were determined to contain beetle fossil. Identification of fossils and paleoecological interpretations based on them are dependent on systematic, ecological, and distributional knowledge of the existing fauna. Although the southern Chile beetle fauna is considered depauperate by entomologists, little is known of the community structure and population dynamics of the group. Consequently, it was necessary to gather a comparative collection of existing beetle species from the Lake Region to aid in identification of the fossils and to establish an elevational zonation of the Coleoptera fauna to attach climatic significance to the fossil assemblages. Results of the study of the existing coleopteran fauna are presented in Appendix A. The fossil sites and modern fauna were collected during two field seasons, each two months in duration, during the austral summers of 1977 and 1979.

PREVIOUS WORK

Quaternary Paleoclimatic Studies in Southern South America

Prior to this investigation, paleobotany and glacial geology were the only methods used to decipher the Quaternary climatic history of southern South America. According to Markgraf (1980a), the earliest pollen analyses were by von Post, the "father of pollen analysis," who described pollen profiles from peat sections collected by the Swedish glacial geologist, Caldenius, in Argentine Tierra del Fuego. Markgraf (1980a) presumed that his intent was to show the global applicability of the newly-developed science of palynology. It was during that period that palynological studies were initiated in Chile by the Finnish palynologist, Auer, resulting from collections obtained during the Finnish Expedition to Tierra del Fuego in 1928-1929. After the early exploratory expedition, Auer revisited the area he called Fuego-Patagonia on numerous occasions and collected samples for palynological analysis from over 120 sites, most of them were in Argentina but some were in the Magallanes area of Chile (Heusser, 1964). Auer established a comprehensive late Quaternary chronology for southern Patagonia based on tephrochronology and on sea-level comparisons with Scandinavia and followed the European system of three late-glacial and five post-glacial pollen zones (Markgraf, 1980a). Subsequent radiocarbon dating has demonstrated, however, that most of Auer's sections were Holocene in age (Auer, 1974; Markgraf, 1980a).

The modern era of paleoclimatic investigations in southern Chile, based on sequences of pollen assemblages, began with the 1959 American Geographical Society's expedition to Laguna de San Rafael in the Province of Aisen (46°40'S). The only prior palynological studies in Chile had been by Auer in the Province of Magallanes, and by Salmi (1955), who described the pollen recovered from giant ground sloth, Mylodon, droppings found in the cave at Ultima Esperanza also in the Province of Magallanes. The objectives of the American Geographical Society's expedition were to gain knowledge of Quaternary environmental changes in southern Chile and to determine if glacial events in both the Northern and Southern Hemispheres were in phase. Interpretations of pollen profiles from peat deposits collected at Laguna de San Rafael were reported by Heusser (1960, 1964, 1966a) in a series of articles. In these writings, Heusser attempted to correlate the San Rafael post-glacial pollen sequences with Auer's farther to the south and with those from Europe, North America, Colombia, and other areas in the Southern Hemisphere. He concluded that the San Rafael sequences were generally correlative with others in the Northern and Southern Hemispheres and suggested that the findings reinforced the view that climatic events were in-phase between the polar hemispheres during post-glacial time. He later extended the concept of synchrony of hemispheric climatic events to include the late-glacial (Heusser, 1966b) and reiterated this opinion in many later papers.

Heusser's palynological studies (Heusser, 1960, 1964, 1966a, 1966b, 1972a, 1972b, 1976, 1981, 1982, 1983, 1984a, 1984b; Heusser and Flint, 1977; Heusser and Streeter, 1980; Heusser and others, 1981) in southern Chile, spanning more than two decades, have included data from the provinces of Magallanes, Aisen, Chiloe, Llanquihue, Osorno, Valdivia, and O'Higgins from about 34° to 49°S latitudes. As a result of his work, a continuous pollen stratigraphy of the Lake Region has been established back to 43,000 yr B.P. Most of Heusser's interpretations were based on pollen frequency diagrams but Heusser and Streeter (1980) and Heusser and others (1981) used multivariate statistics in data analysis. Heusser and Streeter (1980) constructed regression equations relating present-day pollen taxa from surface samples to precipitation and temperatures in southern Chile and applied these equations to a 16,000 year-long, radiocarbon-dated, pollen sequence from a lake core recovered at Alerce near Puerto Montt. The record was extended back to about 43,000 yr B.P. by applying the same methods (Heusser and others, 1981) to a pollen sequence from a lake core at Taiquemó, Isla Chiloe. Results of their quantified approach indicated that about 43,000 years ago summer temperatures were about 2°C less and annual precipitation was about 1,500 mm more than at Taiquemó today. Between about 31,200 and 14,200 yr B.P. summer temperatures were relatively stable (about 4°C cooler than today) and precipitation, although it fluctuated, was on the average about 1,500 mm annual less than today. The trend to warmer and wetter conditions began about 16,000 yr B.P. (Alerce record) or 14,000 yr B.P. (Taiquemó record) and peaked at about 11,300 yr B.P. with summer temperatures 7°C warmer than at Alerce today. A cooling trend, between 11,300 and 9,500 yr B.P., followed and a temperature minima, 6°C colder than Alerce's average summer temperature, was reached by about 10,300 yr B.P. Between about 9,410 and 8,600 yr B.P. summer temperatures were about 5°C warmer than today's average. After this warming trend cooling set in and successive minima were reached between 4,950 and 3,160 yr B.P., between 3,160 and 800 yr B.P. and during recent centuries. This cooling was interrupted twice by temperatures higher than today at about 3,000 and 350 yr B.P. Precipitation maxima, much higher than today, were determined to coincide generally with temperature minima, peaking at 10,520 yr B.P., between 4,950 and 3,160 yr B.P., after 3,160 and before 890 yr B.P., and between about 350 yr B.P. and the present. Heusser and Streeter (1980) concluded that variations in temperature and precipitation recorded at Alerce closely paralleled glacial fluctuations in southern Chile over the past 10,000 years, and Heusser and others (1981) commented that the temperature and precipitation trends reflected by the Alerce and Taiquemó pollen records are generally representative of Quaternary climates in middle-latitude areas of the Southern Hemisphere. However, as was discussed earlier, these interpretations are not, at times, consistent with those formulated from geological studies and, as will be shown later, with those inferred from analyses of beetle assemblages.

For completeness, and because of some of the studies will be referred to later, the following noteworthy paleobotanical investigations in southern South America are included in this historical review. Other than Heusser's, the only palynological study from Isla Chiloe was by Godley and Moar (1973) who analyzed pollen from two post-glacial bog sections. The vegetational history of Vincente Perez

Rosales National Park, Chile was described by Villagran (1980). Aside from the early work of Auer, the palynological studies by Markgraf (1980a, 1980b, 1983, 1984) have contributed insight into the Quaternary paleoclimatic history of southern Argentina. Markgraf and Bradbury (1982) reviewed the Holocene climatic history of South America.

Because glaciers east of the Andes in southern South America terminated on semiarid plains, no chronology based on radiocarbon dating is obtainable. Despite this, the first systematic investigation of glacier activity in southern South America was by Caldenius in the 1930s who mapped four end moraine belts in the lake district of Argentina (Mercer, 1976). He traced the morainal systems from lat. 42°S to lat. 53°S. Based on varve chronology and preservation of the moraines, Caldenius concluded that the three inner moraines were correlatives of the Daniglacial, Gotiglacial, and Finiglacial end moraines in Scandinavia (Mercer, 1976, 1982, 1983). The Scandinavia moraines are now known to have been formed during the last 20,000 years (Mercer, 1984b), and of these, the Finiglacial moraine system is generally equated with the Younger _Dryas_ Stade (Clapperton, 1983). Caldenius speculated that only the oldest, outermost moraine was pre-Late Weichsel in age (Mercer, 1976). Farther north in Argentina, between lat. 39°S and lat. 43°S (east of the Chilean Lake Region), Flint and Fidalgo (1964, 1969) recognized three drift sheets based on weathering criteria. In their 1969 paper, they correlated the three drift sheets with Caldenius' three inner moraines but concluded that his outermost moraine was not present in the territory they mapped. They concurred with Caldenius that the Finiglacial moraine was Late Wisconsinan in age but believed that the Gotiglacial and Daniglacial moraines dated from the pre-Late Wisconsinan. Mercer (1982) determined that the Daniglacial moraine (second oldest of Caldenius' moraines) was covered by 177,000-year-old lava and concluded that Caldenius underestimated the age of all of his moraine belts. The chronology of the Argentine moraines and their relation to those on the west side of the Andes has yet to be established.

West of the Andes, south of 43°S, the glaciers advanced into the Pacific Ocean during glacial maxima and no chronology of glacial activity is obtainable. However, north of 43°S glaciers terminated on humid, vegetated lowlands and the timing of glacial events has been determined based on well-dated sequences of moraines on Isla Chiloe and in the Chilean Lake Region. Mercer (1976) summarized the results of Brüggen, Weischet, Olivares, Lauer, and Laugenie's early glacial geological investigations in the Lake Region, but these studies were completed without radiocarbon chronologic control.

Laugenie and Mercer (1973) and Mercer (1972a, 1976) mapped and named four end moraine systems in the southern part of the Lake Region (Figure 1); from oldest to youngest the morainal belts are: Rio Frio, Colegual, Casma, and Llanquihue. The oldest three are beyond the range of radiocarbon dating and are believed to have been deposited by either two or three glacial advances. Outwash gravels underlying and cropping out west of the Rio Frio end moraine are thought (Mercer, 1976) to represent one or more pre-Rio Frio glacial advances. Mercer (1976) speculated that the Rio Frio Drift may be of the same age, between 1.2 and 1.0 MY old, as drifts in Argentine Patagonia and that the underlying

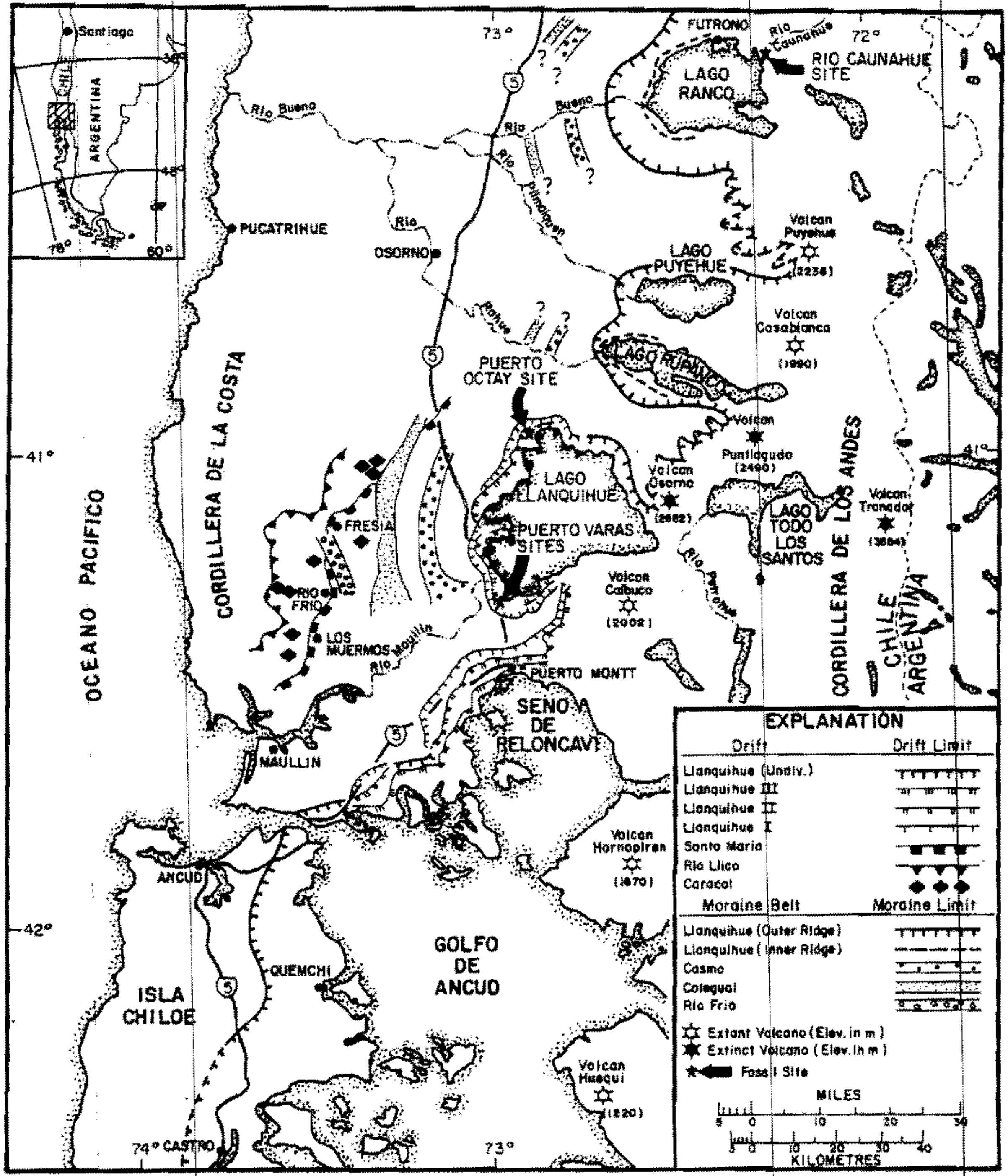


Figure 1. Map of the southern portion of the Chilean Lake Region showing drift sheets, moraine belts, volcanoes, and location of fossil sites. Compiled from Mercer (1976), Heusser and Flint (1977), and Porter (1981).

gravels may be similar in age to the mid-Pliocene to mid-Pleistocene Patagonian Gravel. He did not speculate on the age of the Colegual or Casma Drifts other than that they are younger than the Rio Frio, but he believed both may have been deposited during the same glacial stage. The Llanquihue moraine-complex, which dates from the last glaciation (Mercer, 1976), will be treated more fully below.

Porter (1981) identified four glacial drift sheets in the Lago Llanquihue area naming them, in order of decreasing age, Caracol, Rio Llico, Santa Maria, and Llanquihue (Figure 1). The three oldest are beyond the range of radiocarbon dating techniques. The Caracol Drift crops out locally in the Central Valley along the eastern slope of the coastal mountains and is usually overlain by Rio Llico till or outwash. The drift was deposited during a major glacial advance that extended, in certain areas, to the Coast Range. No end moraines have been identified associated with the Caracol Drift. The most widespread drift recognized by Porter, called Rio Llico, was laid down during an extensive advance that probably filled the Lago Llanquihue basin and perhaps reached the Pacific Ocean near Maullin. Again, no end moraines were found in conjunction with this drift. Most of the surficial sediments in the lowland west of Lago Llanquihue and Seno de Reloncavi are Santa Maria Drift. The glaciation resulting in deposition of this drift was not as extensive as those indicated by the Caracol or Rio Llico Drifts because its western limit is 7 to 14 km east of the maximum extent of the Rio Llico advance. According to Porter (1981), deposition resulted from a coalescing piedmont ice lobe complex from Lago Llanquihue, Seno de Reloncavi and Golfo de Ancud source areas. The three older moraine belts described by Mercer (1976) are within the Santa Maria Drift, indicating multiple ice advances into the valley. Radiocarbon dating indicates a minimum age of 57,800 years for the drift.

Heusser and Flint (1977) mapped two drift sheets on Isla Chiloe and interpreted them to indicate at least two glacial advances onto the island prior to 57,000 yr B.P. Their relationship to drifts on the mainland has not been studied.

Sediments deposited during the last glaciation were named the Llanquihue Drift by Mercer (1976), following the designation by Heusser (1974) of the last major glaciation in the Lake Region as the Llanquihue Glaciation. Heusser suggested that the glaciation was roughly equivalent to the Wisconsinan Glaciation of North America. Mercer (1976) identified two end moraine complexes formed by the glaciation (Figure 1). The westernmost (outer) ridge, most massive and associated with the greatest volume of outwash, was formed more than 40,000 years ago, probably more than 56,000 years ago. The eastern (inner) moraine belt, bordering the western margin of the lakes, was built by a less extensive advance that culminated about 19,500 years ago. Mercer interpreted the end moraines to reflect two major advances into the Region during the last glaciation. A third and perhaps fourth advance, discussed below, was proposed by Mercer (1976, 1984b) and Porter (1981).

Porter (1981) separated, on morphostratigraphic and sedimentologic criteria, the drifts deposited during Llanquihue time into three complexes of stadial rank. He informally called them Llanquihue I, II, and III and inferred that they document three or possibly four advances or readvances into the Region (Figure 1). Llanquihue I drift generally forms the outermost morainal arc about 5 km west of Lago Llanquihue and is locally characterized by kettle and kame topography with small lakes and bogs. It includes Mercer's (1976) westernmost Llanquihue Glaciation moraine. Although the drift has not been accurately dated, Porter stated that it may be substantially older than 57,800 years. He tentatively correlated moraines in the Seno de Reloncavi area with Llanquihue I moraines west of Lago Llanquihue. Mercer's easternmost moraine belt corresponds to Porter's Llanquihue II drift. It is most well developed south of Puerto Octay on the western margin of Lago Llanquihue and has been tentatively correlated by Porter with moraines southwest of Puerto Montt. The advance depositing the Llanquihue II drift and associated moraines is well dated, culminating between 20,000 and 19,000 years ago. This is the most reliable date for the last glacial maximum in the Southern Hemisphere (Mercer, 1984a). During this maximum the glacier complex was estimated to have been about 165 km wide in the latitude of Lago Llanquihue and as much as 800 to 1000 m thick in the Lago Llanquihue basin (Porter, 1981). Porter (1981) calculated that the snowline must have been about 1,000 m below its present elevation of 1,900 to 2,250 m.

By about 18,900 yr B.P. the ice had receded from the lake marginal end moraines (Mercer, 1984b) and by 16,270 yr B.P. had retreated from the Lago Llanquihue basin (Mercer, 1976). The inferred interval of shrunken glaciers was called the Varas Interstade (Mercer, 1972a, 1976). Porter (1981) proposed that a readvance occurred shortly after 14,200 yr B.P., culminating about 13,000 years ago, represented by a third morainal system, Llanquihue III, discovered in the Seno de Reloncavi area. However, the time of till deposition has not been accurately dated and no end moraines resulting from that advance have been found along the western margin of Lago Llanquihue. Mercer (1976) and Porter (1981) stated that sequences of lacustrine sediments interbedded with peats, exposed along the southwestern margin of Lago Llanquihue in the Puerto Varas embayment, provide evidence for the advance. Repeated lake level changes were inferred by them to have resulted from glacial fluctuations. Peats were deposited presumably during times of lowered lake level when the glacier receded far enough to the east of the lake to permit the lake to drain via its eastern outlet, the Rio Petrohue. That outlet has since been abandoned and is now partially filled with volcanic mudflow deposits from the volcanoes Osorno and Calbuco. The peats are overlain by lacustrine sediments. This submergence, terminating peat formation, was interpreted to have been caused by glacial advance blocking drainage through the eastern outlet thereby raising lake level. Mercer (1972a) believed the advance culminated about 14,800 years ago but later (Mercer, 1976) revised the date to about 13,000 yr B.P. Porter (1981), however, postulated that two advances are recorded by the drowned peats: the first began about 15,700 yr B.P. and culminated about 15,000 to 14,000 years ago and a second began about 14,000 yr B.P. and culminated approximately 13,100 years ago. Porter discussed the assumptions and problems associated with his postulated sequence of glacial events but stated that Heusser and Streeter's (1980) palynological record from the area appeared to be consistent with his geological interpretations. Later, Mercer (1984b) reflected that both glacial variations and volcanic activity may have affected the lake level and concluded, from more direct evidence found on Isla Chiloe, that the final full-glacial readvance occurred between about 15,000 and 14,500 yr B.P.

Glacial geological evidence from both southern Chile and southern Argentina indicates rapid deglaciation following the final late-glacial readvance in southern South America (Mercer, 1984a, 1984b). By 12,300 yr B.P. the glaciers were confined to the mountains and by 11,000 yr B.P. had retreated to their present positions and remained there until Neoglacial times (Mercer, 1976). No geomorphic evidence suggesting Neoglacial advances has been documented from the Lake Region but farther south in both Argentina and Chile glaciers readvanced during three periods and reached their Neoglacial maxima between about 4,600 and 4,200 yr B.P., between about 2,700 and 2,000 yr B.P., and during recent centuries (Mercer, 1982).

Beetles as Indicators of Quaternary Environments and Climates

For a group of organisms to be useful for reconstruction of Quaternary environments and climates it must be ecologically diverse and well represented in the fossil record. The fossils must be easily recoverable and reasonably easy to identify. In addition, to draw paleoclimatic inferences, the group must possess a demonstrated response to climate change. Moreover, before any paleoenvironmental interpretations can be postulated, it must be reasonably certain that the physiological requirements of species within the group have remained stable over the time of interest. Coope, in a number of reviews (Coope, 1967, 1970, 1975, 1977, 1978, 1979), discussed the attributes of beetles making them excellent indicators of Quaternary environments and climates and reviewed the tacit assumptions recognized relative to their use. Those attributes and assumptions are summarized below.

To occur in abundance in the fossil record a group must be diverse in species composition, species must generally generate high numbers of individuals, and the organisms must be preservable. Arnett (1971) estimated that there are well over 350,000 described beetle species and at least one out of every four named species of animals is a beetle. The Coleoptera are more diverse in species than any other group. They occur in all but the most northern and southern latitudes and have colonized almost all terrestrial and freshwater habitats and have even invaded the marine intertidal zone. Many species are remarkably restricted and precisely adapted to a particular environmental niche and have representatives in all trophic levels of the community food web. In addition to high species diversities, population density is often high in many Coleoptera species. Examples from study of the Chilean Lake Region fauna (Appendix A) include the discovery of over forty individuals of one species of Bembidion under a single boulder in an alpine tundra habitat and the recovery of thirty individuals of the dung beetle, Dichotomius torulosus, in one baited pitfall trap in the Valdivian Rain Forest. Such findings are particularly common in aquatic environments where beetles are most well preserved.

Preservation of Quaternary beetles is usually exquisite if the sediments have not been oxidized. The fossils are not replaced by secondary minerals but are preserved through the robustness of their original skeleton chitin. Chitin is known to be resistant to both chemical and biological disintegration for millions of years. However, complete beetle fossils are rarely recovered and, most frequently, beetle fossils are found as disarticulated skeletal elements consisting of heads, elytra and pronota. The less-chitinized anatomical parts, for example antennae, are often lost to decomposition. Nevertheless, the larger more durable fragments are generally the parts most useful for identification. Deterioration is usually minimal; and scales (e.g., Plate 2, Figure 4), setae (e.g., Plate 6, Figures 2 and 4), pubescence, structural color, and intricate patterns of microsculpture (e.g., Plate 5, Figure 4; Plate 6, Figure 2) are often preserved.

Present-day coleopteran species are differentiated by the morphology of the exoskeleton. The paleocoleopterist's concept of species is exactly the same as that of the neontologist and the same criteria are used to identify fossils as are used by entomologists to identify living forms. Even though preservation is sufficient to permit precise identification of the fossils, caution must be employed. Taphonomically induced aberrations, such as shape distortion, development of peculiar surficial rugosity, punctures or dimples and alteration or complete loss of color frequently occur in fossils. Postmortem changes can occur and must not influence taxonomic decisions. In addition, it must be kept in mind, when making paleoenvironmental interpretations based on assemblages of fossil beetles, that only a portion of the once-living community is represented. The success of paleoecological reconstructions depends on the researcher's ability to strip away taphonomic overprints (Lawrence, 1971).

Because of preservability, species diversity, and individual frequencies, beetles are often found in extraordinary abundances in Quaternary non-marine sequences. Beetle remains are often the most common component of the terrestrial fossil faunal assemblage. Although they have been found in organic silts and loess, beetle fossils occur most conspicuously in peats. However, extraction of fossils from peat is often difficult and so organic silts are generally the media of preservation most preferred because of relative ease in recovery. A simple and efficient extraction technique is described later. As a general rule, any sediments containing plant macrofossils will also yield beetle remains. Coope (1970, 1975) noted that fossils incorporated into sediments deposited in shallow pools, bogs or marshes on flood plains of rivers or into sediments deposited in lake marginal environments are the most informative in paleoenvironmental studies. Fossil assemblages deposited in these settings are not only representative of the aquatic environment but also the immediate terrestrial environment. A wide spectrum of ecologically varied beetle types will be incorporated into the fossil assemblages, reflecting the mosaic of microhabitats present in the vicinity of the actual site of deposition. Deep-water lacustrine sediments produce relatively depauperate beetle assemblages because most aquatic species live in shallow water and terrestrial forms are less likely to be carried into the deeper water.

Paleoclimatic interpretations are predicated on the assumptions that the distributions of species are controlled by climatic factors, principally temperature and moisture, and that the present-day geographic or elevational ranges of the species reflect the full climatic range that the species can occupy. Both assumptions are overgeneralizations. The first of these assumptions is often construed as being valid because beetles are poikilotherms and because many species are known to be restricted to fairly narrow climatic zones (Coope, 1977). However, the relationship of the distribution of beetles to climatic variables is complex and mostly not understood. Beetles live in microenvironments, but it is believed that the distribution of these microenvironments is largely governed by macroclimate (Coope and others, 1971). Other non-climatic factors, such as food availability, competition and disease, are known to regulate the distribution of some taxa, but Coope (1977) argued that these factors are density-dependent and are most important when climatic conditions are optimal for existence of the taxa. He also reflected that these controlling factors diminish at the periphery of the range and, in these cases, the distributional limit of the taxa are controlled by climate. Some species occupy habitats (e.g., leaf-litter, soil burrows) partially insulated from short-term climatic changes and the distributions of others, particularly those that are host specific on plants, animal dung or carrion, may be controlled by factors other than climate. It appears, however, that even in these situations climate is probably the most important secondary factor controlling distribution. Even though Coope (1967, 1977) described a number of ways in which climate can control species distributions, the roles that temperature and precipitation play in regulated distribution is unknown except for a few, well-studied species. Because this information is mostly lacking, the range of climatic variables within which a species exists is inferred from its geographic or elevational range. Whether a species' geographic or elevational range reflects the full climatic range in which the species can exist is seldom known. For these reasons, the geographic or elevational ranges of all species within a fossil assemblage are considered, not just a few selected indicator species, before interpretations of past climatic conditions are attempted.

Also, before past environmental and climatic conditions can be inferred from the fossils, it must be assumed that the species' physiological requirements were the same in the past as they are today. It has been demonstrated that beetles have maintained their specific integrity for at least the last half of the Quaternary Period (Coope, 1978). It is clear no large-scale morphological evolution has occurred in the group during that time interval. Of course, fossil evidence does not preclude the possibility of speciation within the Coleoptera, but the fact remains that there is no indication of evolutionary change in any of the late Quaternary European (Coope, 1975, 1978) or North American (Ashworth, 1979) species studied to date. Some idea as to how far back in geologic time constancy of beetle species extends is gained through Matthew's (1970, 1974a, 1974b, 1976a, 1976b, 1977) studies in Alaska and the Canadian Arctic Archipelago. He analyzed fossil assemblages from 400,000- to 800,000-year-old sediments recovered at Cape Deceit, Alaska, probably the oldest Quaternary fossil beetle-bearing deposits in North America. Many species from the site were found to be extant and still living in Alaska today. Assemblages from the Beaufort Formation, exposed on Meighen Island, arctic Canada, and estimated to be Miocene or Pliocene in age, contained beetle fossils falling within the range of variability of modern-day species. Other species from the same assemblages were found to be similar to, but not conspecific with, living forms. Furthermore, sediments overlain by lava radiometrically dated at 5.7 MY, exposed at Lava Camp in western Alaska, yielded assemblages that contained a mix of both extant, and apparently extinct, species. In view of these findings, Coope (1977) concluded that speciation in the Coleoptera, at least in temperate and northern latitudes, occurred mostly during the late Tertiary except, perhaps, in isolated geographic areas such as caves or islands.

The demonstration that late Quaternary beetles are morphologically identical to extant species does not necessarily mean that their ecological and environmental requirements have also been unchanging. Because there is no evidence of morphological evolution, it cannot be inferred that there has been no nonmorphologically-expressed physiological evolution. Although there is no way to test empirically the assumption that physiological stability in beetles has paralleled morphological constancy, there is substantial and growing circumstantial evidence from the fossil record that the assumption is valid. In species composition, late Quaternary fossil assemblages strongly resemble living beetle communities. There is no decrease or distortion of these species associations with time; this implies ecological and environmental consistency, as would be expected if no physiological changes had occurred. Ecological homogeneity of fossil assemblages is evident as far back in geologic time as the first signs of morphological stability; this apparently indicates that physiological evolution has proceeded at the same slow pace as morphological evolution. This conclusion draws corroboration from collateral information such as association of beetle fossils with other ecologically and environmentally compatible members of the biota. One example is the finding of host-specific phytophagous beetle fossils in the same stratigraphic horizon as remains of the appropriate plants. Geological evidence has also reinforced the assumption. For example, sediments believed to be deposited in cold climatic conditions because they contain fossils of tundra beetles may show physical evidence, such as cryoturbation features, of a severe climate.

Perhaps the most detrimental belief hindering the recognition that fossil beetles could be used to reconstruct Quaternary environments and climates was the concept that the fossils were remains of extinct animals and that the modern-day beetle fauna evolved rapidly during the latter part of the Quaternary. The belief was based on the premise that rapid extinction and evolutionary rates should be expected during times of intense and numerous climatic changes wherein populations become fragmented and isolated. After all, it was believed that more conspicuous members of the biota, for example mammals (Kurten, 1968), showed rapid evolution and extinction rates during the late Cenozoic, largely in response to fluctuating climates. Coope (1977) argued, however, that this climatic instability caused morphological and physiological constancy in the Coleoptera. He reasoned that the expansion and contraction of the range and continual movement of beetle populations as a result of climatic changes during the Quaternary would produce short periods of isolation but these episodes of population fragmentation would be followed by times of convergence. He envisaged that this type of mixing would maintain a homogenous gene pool thereby insuring species constancy. Whatever the mechanism was to maintain species integrity in the Coleoptera, the observation that fossils are the same species that live today permits a reasonably straight-forward approach in assessing past environmental and climatic conditions.

Coope (1979) emphasized that a beetle species has three options when environmental change makes an area uninhabitable for its existence. The species can either become adapted to the newly established environmental conditions, become locally extinct, or migrate to an area where conditions are still acceptable. Because most beetles are highly active in their adult stages and can readily run or fly considerable distances, they generally respond to environmental change by migration. It has been established through fossil studies that even relatively sedentary, apterous, ground beetle and weevil species have shifted their geographic ranges dramatically in response to Quaternary environmental changes (Coope, 1970). During the period of the last glaciation alone, certain species altered the limits of their geographic range in Europe by several thousand kilometres (Ullrich and Coope, 1974; Coope, 1975). Similar large-scale geographic shifts of beetle faunas in response to environmental change have also been documented in North America (Morgan and others, 1983). There is growing evidence that migration of beetle communities occurs <u>en masse</u> in response to fluctuating environmental conditions (Coope, 1978).

Beetles are excellent indicators of climatic change because they usually respond rapidly to climatic events. The extreme rapidity with which the specific composition of a beetle fauna can change from one ecological style to another is illustrated by the replacement within three or four hundred years, of arctic faunas by temperate faunas in Great Britain about 10,000 years ago (Ashworth, 1972). Coope (1977, 1981) reviewed other studies showing the rapidity with which beetles respond to environmental flux. A recurring theme in Coope's writings has been to promote beetles by arguing that they show a greater alacrity in response to changing environmental conditions than other members of the biota, especially trees (Coope, 1970, 1977; Coope and Brophy, 1972). For example, Coope and Brophy (1972) noted that some fossil sites in the British Isles contained assemblages of temperate beetles, but pollen spectra from the same sites implied tundra conditions because the spectra were devoid of tree pollen. They interpreted these paleontological discrepancies to indicate that the more mobile components of the biota, beetles, responded more rapidly to environmental changes than the more sedentary, arboreal members of the biotic community. Their conclusion was probably correct, but inferring that beetles always respond more rapidly than trees to environmental change is an unjustified generalization. The difference in arrival time of organisms depends on the species' ecology, dispersal ability, and distance the species have to travel. Apterous beetles will generally arrive later than beetles that can fly. It is conceivable that certain trees can arrive in a newly-opened habitat before such beetles that may be habitat specialists and are incapable of dispersing rapidly. In this respect, an ideal paleoenvironmental investigation should be interdisciplinary and employ beetles, pollen and macroplants, such as the one carried out by Ashworth and others (1981) at Norwood, Minnesota.

In consideration of the assumptions discussed above, reconstruction of past climates and environments based on beetles is a complicated process but has been demonstrated to work in Euorpe (Coope, 1977) and in North America (Morgan and others, 1983). Studies in the palearctic and nearctic regions have been successful primarily because professional and amateurs have been describing, documenting ranges and recording habitat preferences of existing beetles from those regions for many decades. Although the taxonomy of the Chilean beetle fauna is fairly well known compared to other areas of South America, the ecology and biogeography of most species has not previously been well documented and data have been insufficient for paleoenvironmental and paleoclimatic reconstructions. Consequently, the study of the modern-day fauna, summarized in Appendix A, is an integral part of this investigation because the knowledge gained provided base-line data on which paleontological comparisons and interpretations were based.

STUDY AREA

Physiography, Tectonic History, and Pre-Quaternary Geology

Chile is divided into five latitudinal zones. The Region de los Lagos (Lake Region), extending from about 39° to 42°S latitude, is in part included in the Sur Chico or Little South Zone (Koster, 1975). The portion of the Lake Region south of 41°S is in the area called Western Patagonia or Patagonia Occidental. The Region is divisible into three structural and physiographic longitudinal provinces (Figure 2): the Cordillera de la Costa (Coast Range), Valle Longitudinal (Central Valley), and Cordillera de los Andes (Andes).

Subduction of the Nazca Plate beneath the South American Plate began in the middle Cretaceous in conjunction with the beginning of seafloor spreading in the South Atlantic (Lowrie and Hey, 1981). This resulted in an episode of intense folding, batholith emplacements and uplift of the Andes--the initiation of the Andean Orogeny. Most of the Lake Region has been emergent since that mid-Cretaceous orogenic episode, but the continental margin of the Region remains a seismically active, tectonic boundary between the converging plates. Consumption of the Nazca Plate at the Peru-Chile trench results in volcanism on land, seismic activity along the Benioff zone and uplifted continental crust. Bending of the Nazca Plate at the trench causes extensional stresses producing tensional rather than compressional tectonics in the Lake

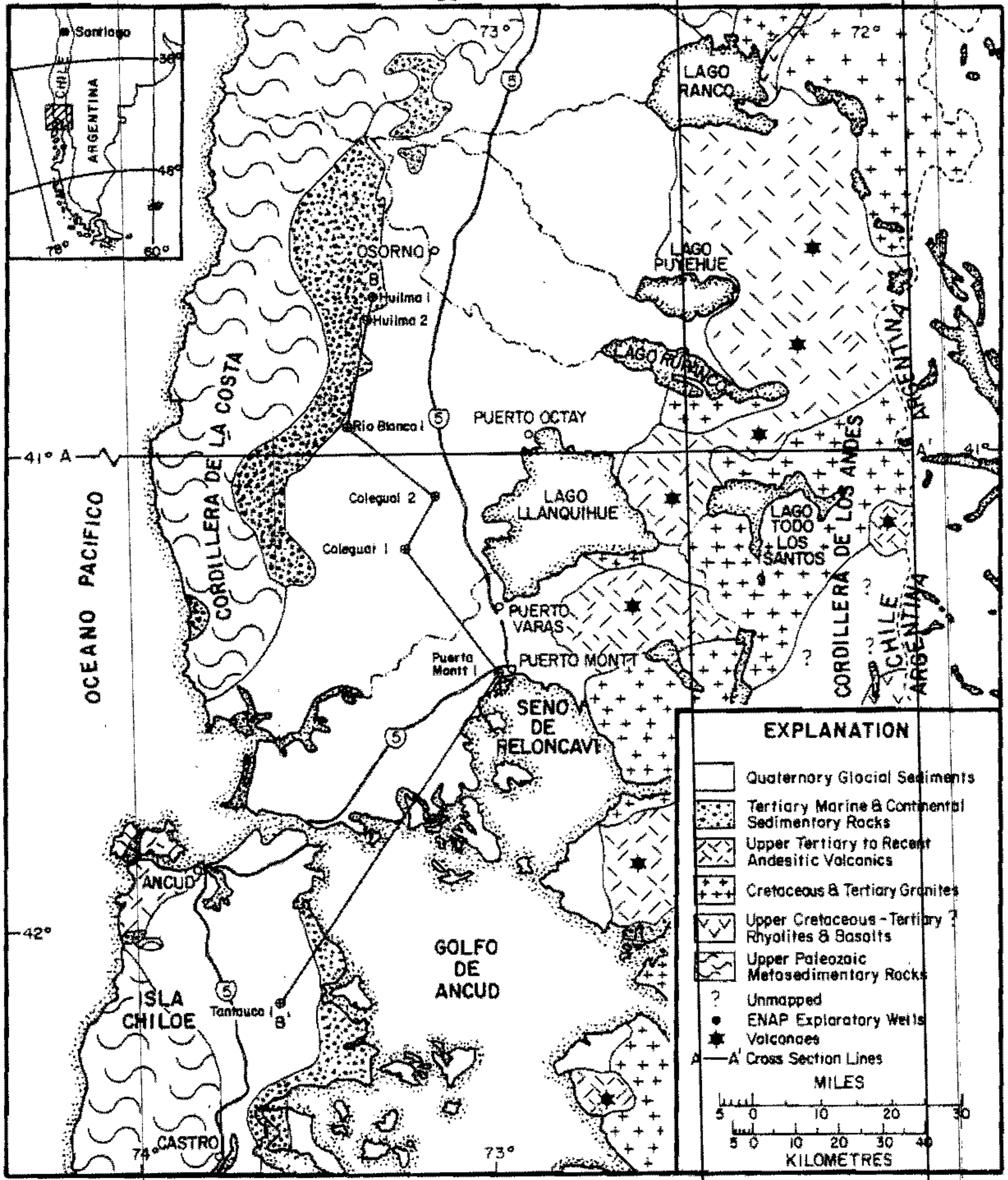


Figure 2. Generalized geologic (Chile only) map of the southern portion of the Chilean Lake Region. Compiled from Zeil (1964), Katz (1970, 1971), Koster (1975), Goudarzi (1977), and Diaz (1968).

Region (Katz, 1970, 1971; Gansser, 1973; Schweller and others, 1981). As a result, the late Cenozoic deformation pattern has been one of block-faulting and localized drag folds. Although the morphotectonic physiographic provinces, Coast Range, Central Valley, and Andes, generally trend north-south, that is, parallel to the coast, the strikes of faults, fractures and lineaments are transverse to the provinces and are characteristically oriented in west-northwest and northeast directions. These structural alignments, derived from pre-Andean tectonism, have been reactivated in the late Cenozoic producing the present block-tectonic framework. Portions of the Coast Range, Central Valley, and Andes bounded and transected by lineaments, have experienced repeated vertical tectonic displacements throughout the late Cenozoic with various blocks being displaced independently and, at times, in opposite directions.

The unglaciated, tectonically active Coast Range borders the Pacific Ocean and is about 30 km wide in the Lake Region. Elevations are low compared to the Andes and do not exceed 950 m except in the Rio Bueno area where summits reach heights of about 1500 m. Isla Chiloe is the southern extension of the Coast Range. Low-grade metasedimentary rocks, consisting principally of schist, quartzite, phyllite and gneiss and localized plutonics constitute (Plafker and Savage, 1970; Gonzalez-Bonorino and Aguirre, 1970; Gansser, 1973; Koster, 1975) the main body of the Coast Range (Figures 2 and 3). Radiometric dating indicates a late Paleozoic, perhaps Carboniferous, age for the metasedimentary basement complex (Munizaga and others, 1973). Volcanic episodes occurred on the present site of the Coast Range during the Permian

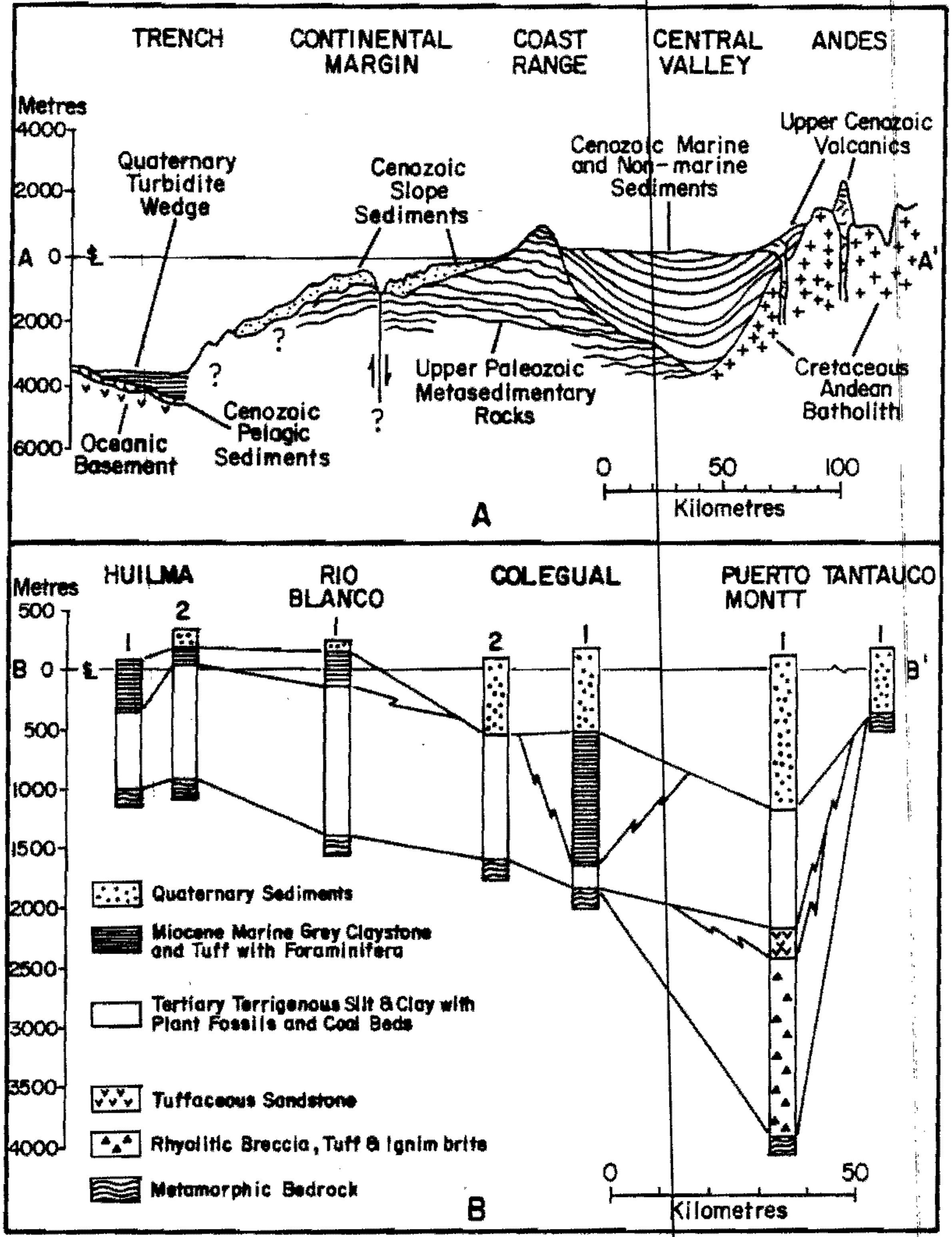


Figure 3. (A) Generalized cross-section along the 41st parallel from the Peru-Chile Trench to the Andes. Slightly modified from Scholl and others (1970, 1977). (B) North-south cross-section through the southern portion of the Lake Region drawn from ENAP exploratory well data. Modified from Katz (1970). See Figure 2 for location of cross-sections.

(Gonzalez-Bonorino and Aguirre, 1970) and in the Jurassic, early Cretaceous, late Cretaceous and early Cenozoic (Scholl and others, 1970). The rocks exposed in the truncated Coast Range are steeply folded and faulted and were, according to Zeil (1964), involved in at least two major orogenies and several deformations of less intensity. Strong pre-Mesozoic compressive tectonism is indicated by the early deformation but block faulting has dominated since the Mesozoic, was accentuated in the Pliocene, and continues today.

The Central Valley is an actively subsiding basin about 90 km wide at its maximum in the Lake Region (Figure 2). A series of piedmont lakes punctuates the valley, and this gives the name to the Region. The lakes occupy glacially scoured depressions and are dammed on their western margins by arcuate moraines. Lago Llanquihue, the largest, encompasses an area of about 850 km^2, has a surface elevation of 51 m, and attains depths of at least 350 m. The valley is submerged south of about 41°30'S latitude. Bays and sounds, for example Reloncavi and Ancud, were formerly glacial lakes such as those to the north but have been drowned by the sea through recent subsidence. The low-lying, graben-like Central Valley is filled with poorly consolidated terrestrial, marine and volcanic sedimentary rocks (Figures 2 and 3). Exploratory wells drilled by ENAP, the Chilean oil company, penetrated in excess of 4,000 m of Eocene and younger strata of which 1,340 m are of Quaternary age (Galli-Oliver, 1969; Scholl and others, 1970). These strata are underlain by crystalline basement rocks. Major normal faults bound and transect the basin indicating that, as with the coastal mountains, block tectonics has been the major structural control in the province during the late Cenozoic (Katz, 1970; Plafker and Savage, 1970; Gansser, 1973). Although the formations are generally flat-lying, Plafker (1972) noted subtle structural trends in the basin, such as monoclinal flextures and broad warps. As in the Coast Range, vertical tectonic displacement dates mainly from the Pliocene but continues today as reflected by the great thickness of Quaternary sediments.

The Andes is a highly glaciated mountain range complex about 130 km in breadth in the latitude of the Chilean Lake Region; however, most of its extent is in Argentina. Crestal elevations average about 2,000 m; but Tronador, a dormant volcano straddling the Chile-Argentina border and the highest peak in the area, has an elevation of 3,554 m. West of the main axis of the Andes is an alignment of stratified volcanoes reaching elevations of about 1,500 to 2,000 m. The most picturesque stratovolcano, Osorno, is 2,652 m high. Lakes do occur in the high Cordillera but are generally restricted to abandoned cirque basins. Although the Andean batholith complex dominates the Andes (Figures 2 and 3), it is a geologically complex province in which, according to Plafker and Savage (1970) and Hervé and others (1974), deformed Paleozoic metamorphic and Cretaceous through Tertiary sedimentary rocks are cut by granitic plutons of Cretaceous and Tertiary age. The older formations are unconformably overlain by relatively undeformed late Cenozoic andesitic volcanic sequences and are locally veneered by glacial drift. Halpern and Fuenzalida (1978) determined, from studies of plutonic rocks exposed in Argentina at the same latitude as the Chilean Lake Region, that magmatic activity began at least 150 MY ago. The main Andean

Orogeny appears, therefore, to have taken place during the Cretaceous with emplacement of the Andean batholith belt. Vergara and Gonzalez-Ferran (1972) recognized two phases of neovolcanism in the Lake Region. Fissural-type volcanism dominated during the Miocene to late Pliocene, forming volcanic plateaus in the Andes. Central-type volcanism began in the Plio-Pleistocene and continues today. They suggested that the transition period between the two volcanic styles was marked by block tectonism resulting in additional uplift of the Andes.

Quaternary Geology

The major modifying geologic processes active in the Lake Region during the late Quaternary are (1) tectonism, (2) volcanism, (3) glaciation, and (4) erosion.

Tectonic activity continued from the Tertiary into the Quaternary and continues today as evidenced by frequent and violent earthquakes. The opposing motions of the converging Nazca and South American Plates produce major shallow-focus earthquakes. As a result, Chile is one of the most highly seismic countries in the circumpacific region. The Lake Region has historically been the focal point of much of the major earthquake activity in the country. Recent tectonic activity has thus had a major affect on modifying the area's surficial geology. Valdivia, located in the northern part of the Lake Region has been severely damaged by earthquakes at least five times (Lomnitz, 1970). One of these disasters, the earthquake of February 20, 1835, resulted in uplift of coastal areas near Conception as much as 2.7 m (Darwin, 1839). The earthquake of 1960 was one of the major seismic events ever recorded on earth (M_s approx. 8.5). The cities of Valdivia and Ancud subsided more than 2 m during the event (Plafker and Savage, 1970). Interestingly, according to Plafker and Savage (1970), the earthquake occurred in essentially the same place as the 1835 tremor. Lomnitz (1970) estimated that seismic events of magnitude 8+ occur about once every ten years in the Lake Region. Recent tectonic activity is also indicated by the great thickness of Quaternary fill in the Central Valley.

Since the end of the Pliocene continuous central-type volcanism has been restricted to the Andes (Figures 1, 2, and 3). Thirty-three volcanoes have been active in historic times in Chile (Casertano, 1963; Segerstrom, 1964), many of which are situated in the Lake Region. The most elegant appearing volcano in the Lake Region, Osorno, was observed in eruption by Darwin (1839) on January 19, 1835, and was active as late as 1850. Volcan Calbuco, 30 km south of Volcan Osorno, was active in 1929 and 1960 (associated with the earthquake of that year). This latter event produced destructive massive mudflows followed by extrusion of andesitic lava (Casertano, 1963). The possibility of fault control of volcanic activity was suggested by Plafker and Savage (1970) because of the linear arrangement of volcanic centers and hot springs. The extrusives consist mostly of basaltic andesite, and andesite lava flows, and pyroclastics. Volcanic clasts and beds of tephra are often found incorporated into, interbedded with, and overlying glacial drifts in the Lake Region. Repeatedly occurring volcanic mudflows have at times, disrupted major drainage patterns (Mercer, 1976). Paleontological records have occasionally been interrupted by ash falls. Volcanic eruptions have undoubtedly affected the past and present plant communities of the Lake Region (Veblen and others, 1977).

During the Quaternary the Lake Region was, on numerous occasions, invaded by piedmont glacial lobes discharging from extensive ice fields capping the Andes (Figure 1). Glacial tongues flowing westward formed multiple end moraines west of the basins now occupied by lakes dammed by morainic ramparts. The glacial lobes are named for the lake basins that they scoured (e.g., Llanquihue Lobe). Glacial sediments are widespread and comprise most of the surficial deposits in the Central Valley. Locally, in the eastern part, recent lahars cover glacial sediments, as in the Volcan Calbuco area. At maximum extent, glaciers reached as far west as the eastern slopes of the Coast Range and perhaps as far as the Pacific Ocean near Maullin. Numerous drift sheets and terminal moraines have been recognized by comparison of composition, extent, morphological characteristics, depth of overlying pyroclastics, dissection of landforms, thickness of weathering rinds on volcanic clasts, extent of MnO_2 deposition on clasts and matrix, and by stratigraphic relationships (Mercer, 1976; Heusser and Flint, 1977; Porter, 1981). Outwash and till are the principal components of the drift sheets, but drift is commonly interbedded with non-glacial sediments (e.g., sand, loess, organics, tephra, and buried soils). Although numerous drift sheets have been identified (reviewed in an earlier section), their number, extent and lateral relationships have not been fully defined throughout the Lake Region. The drifts, particularly from the late glacial interval, are often intercalated with peats and highly organic sediments. The present climate is conducive to preservation of the organic material in the sediments. These organic-rich sediments have provided a basis for a reasonably good radiocarbon chronology for the drift sheets and palynological and insect material for paleoenvironmental studies.

Erosion has had a marked influence on landscape development, on continental and ocean margin sedimentation, and on the preservation of the Quaternary geologic record in the Lake Region. A combination of factors, tectonic activity, topographic relief, glaciations, and high annual rainfall, have caused incredible denundation rates. Landscape modification, for example, is illustrated by the entrenching of deep gorges by rivers draining the larger lakes. These major drainage ways, the Rios Bueno, Pilmaiquen, Rahue, and Maullin, carry discharge from Lagos Ranco, Puyehue, Rupanco, and Llanquihue, respectively, to the Pacific Ocean. These rivers, presumably following the ancient structural grain of the Region, flow slightly north of west across glacial sediments and transect the present structural provinces. Rapid erosion is also indicated by the great thickness, approximately 1340 m, of Quaternary sediments in the Central Valley. In addition, the substantial volume of sediment, mostly turbidites, literally filling the Peru-Chile trench in the latitude of the Lake Region, is believed (Schweller and others, 1981) to have been deposited within the last 1 MY (Figure 3). This wedge-shape deposit is up to 2 km thick and 75 km wide. Scholl and others (1970) estimated that 54 x 10^3 km^3 of sediment were deposited in the trench adjacent to the Region during the Quaternary, mostly during periods of glacial sea-level lowering, and that denudation rates have averaged 50 cm/10^3 yr. Although erosive processes have exposed Quaternary deposits for examination, the amount of information removed by the process is not known, but is probably substantial.

Present Climate

Because Chile spans almost 40° of latitude, it exhibits a great contrast in climate. The Atacama Desert, north of the 23rd parallel, receiving less than 5 cm of precipitation annually, is one of the driest regions on earth. In contrast, south of 43°S latitude, precipitation is as high as 750 cm per year. Most of Chile, however, enjoys a mild Mediterranean-type climate with cool, moist winters and dry, warm summers. Chile's climate is influenced principally by Antarctica and its ice masses. It is cooled by outbreaks of polar air and the transport of polar water toward the equator by the Peru Current.

The Lake Region lies in the latitude of prevailing west winds known colloquially as the "roaring forties." Because of its position proximal to the polar front, the boundary between subantarctic and subtropical air masses, it receives the brunt of cyclonic storms. The storms originate over the mid-Pacific Ocean where air masses of the subpolar westerlies and the subtropical Pacific anticyclone meet. These cyclonic storms, associated with frontal systems of the westerlies, repeatedly encounter the Region's coast and are manifest by strong winds and heavy precipitation (Miller, 1976). Storms occur most frequently in the winter because during the summer months the polar front shifts southward. Consequently, precipitation, which is almost entirely in the form of rain, occurs mostly in the fall and winter. Two-thirds of

Puerto Montt's 196 cm average annual rainfall (Table 1) is received during that time exemplifying the phenomenon of winter rainfall maxima. Throughout the Lake Region, precipitation amounts received during autumn and winter are characteristically twice those received in the spring and summer months. Average annual precipitation in the Region is about 150 to 200 cm per year, but the orographic influence of the Coast Range results in high, 400 cm, precipitation on the windward slopes of the range. The lee side of the coastal mountains and the Central Valley are in the rain shadow and receive relatively less rainfall. However, as the storms pass eastward, precipitation increases again resulting from the orographic influence of the Andes; average annual rainfall is commonly over 500 cm in the high Cordillera (Heusser, 1981). The climatological data presented in Table 1 illustrate the orographic influence of the mountain ranges on precipitation patterns in the Lake Region.

Air temperatures are controlled primarily by surface temperature of the south Pacific Peru Current and by the prevailing westerly winds (Heusser, 1974). The Peru Current, a branch of the West Wind Drift, originates in antarctic waters and travels northward along the Chilean coast producing cool temperatures in the Lake Region. At the Parque Nacional de Puyehue (40°S, 72°W) mean January (summer) temperatures are 14°C at the elevation of Lago Puyehue (Figure 1), and 11°C at tree-line (Muñoz S., 1980). Average temperature ranges in the Lake Region (Heusser, 1981) are 7-8°C in the winter (July) and 14-16°C in the summer (January).

Table 1. Temperature and precipitation records from selected stations in the Chilean Lake Region. Compiled by Heusser (1974) from Almeyda and Saez's (1958) data.

Station	Location	Elev. (m)	Average Temperature (°C)		Average Precipitation (mm)				Total
			Jan	July	Autumn	Winter	Spring	Summer	
Central Valley									
La Union	40°15'S, 73°02'W	29	--	--	360	560	216	125	1250
Rio Bueno	40°29'S, 72°55'W	58	--	--	363	469	217	132	1214
Osorno	40°35'S, 73°09'W	24	17.6	8.3	368	530	232	149	1330
Puerto Octay	40°59'S, 72°52'W	51	--	--	434	602	300	214	1600
Puerto Varas	41°20'S, 72°57'W	51	15.7	9.0	549	624	355	278	1823
Alerce	41°23'S, 72°54'W	107	--	--	513	689	396	277	1933
Puerto Montt	41°28'S, 72°56'W	5	15.3	7.6	540	685	415	320	1960
Andean Foothills									
Lago Ranco	40°14'S, 72°20'W	70	--	--	524	665	339	239	1809
Rupanco	40°50'S, 72°25'W	141	--	--	536	703	374	234	1894
Ensenada	41°12'S, 72°32'W	51	--	--	599	675	384	300	1993
Andean Cordillera									
Punirre	40°16'S, 72°12'W	120	--	--	990	1365	680	325	3400
Peulla	41°05'S, 72°02'W	190	--	--	930	1260	670	470	3468
Puntiagudo	41°05'S, 72°17'W	190	15.0	6.4	860	1065	590	500	3080
Petrohue	41°07'S, 72°23'W	190	--	--	970	1200	840	425	4000

The relationship of the beetle fauna to temperature and precipitation patterns in the Lake Region is discussed in Appendix A. It is inferred that migration of the polar front, presumably as a result of changes in atmospheric circulation in the southern polar latitudes, caused climatic changes in the Lake Region during the Quaternary (Heusser, 1981).

Regional Vegetation

In southern Chile, from about the latitude of the city of Osorno to the Province of Magallanes, the major vegetational type is temperate rain forest in which evergreen and deciduous species of the southern beech, *Nothofagus*, occur together and are the dominant trees in the forest community. Optimal growth of the rain forest is seen in the Lake Region, there called the Valdivian Rain Forest. The general characteristics of this complex rain forest community are described by Heusser (1966a, p. 274) as follows:

> The Valdivian rain forest is dense, dark and evergreen, consisting of a profusion of shrubs, lianas, epiphytes, ferns, mosses, hepatics and lichens, among trees whose strongly deliquescent trunks and branches at maturity can reach heights of 40 m or more. There is a multiplicity of species, many of which are monotypic and endemic. Because of an equable climate, the season for growth is lengthy, and near sea level, cessation of growth probably does not take place in most species. Flowering and fruiting occur throughout the year, some plants bearing flowers even in mid-winter (June and July). The forest floor is littered with slowly decaying fallen leaves and boles, overlying thick, damp, peaty soils. Lakes, bogs, swamps and rivers with their distinctive plant communities interrupt the forest continuity. . . .

Between 41°S latitude and the southern end of Isla Chiloe (43° 30'S), the Valdivian Rain Forest is the dominant vegetational unit from sea level to at least 650 m. Scattered remnants of a more northerly occurring forest called the Lowland Deciduous Forest (Heusser, 1981) range from the northern part of the Lake Region to about 41°S latitude, the northern limit of the Valdivian Rain Forest. Specifics of the floristic composition of the Valdivian Rain Forest and other vegetational communities occurring at higher elevations in the Lake Region are presented by Heusser (1966a, 1974, 1981) and Veblen and others (1977, 1979) and are summarized in Appendix A (Figure A2).

Prior to European colonization of the Lake Region in the 19th century, the Central Valley was completely forested (Heusser, 1974). The forest was cleared for agriculture, construction materials, and fuel. Today, only scattered remnants of the Valdivian Rain Forest, in a savanna-like setting of grasses and forbs, remain in the valley (Heusser, 1974; Veblen and others, 1977). Although the natural vegetation within the Central Valley has been significantly altered by the presence of man, fewer anthropogenic effects are seen in the cordilleran forest communities. Undisturbed stands of natural rain forest vegetation begin at an elevation of about 500 m in the Region's Andean foothills. However, instability of forest communities in the mountains is maintained by natural catastrophes such as earthquakes triggering mass movements, volcanism and forest fires (Veblen and Ashton, 1978; Veblen and others, 1979, 1980).

It is believed that rain-forest communities were much more extensive and continuous at various times during the Pleistocene (Heusser, 1972b). Remnants of rain-forest vegetation occur as disjunct plant communities in scattered areas of the coastal mountains and elsewhere in Chile, for example in the national parks of Fray Jorge and

Talinay (30° 30'S). In that area of the Coquimbo Province, rain-forest plant communities form enclaves in the semi-arid, shrub-succulent zone (Heusser, 1972b). Quaternary climatic fluctuations and associated glaciations appear to have been the fundamental causes of major vegetation pattern alterations. Temporal biotic changes in the Lake Region, resulting from Quaternary climatic flux, will be discussed in detail later.

METHODS

Field Methods

Surface exposures at the Puerto Varas Park and Rio Caunahue Sites were sampled after the vegetation had been cleared and the sections cut back, measured, and described (Figures 8 and 15).

The Puerto Varas Park Site was sampled in November 1977. The 10 cm-thick peat horizon was collected in two 5-cm intervals; each sample weighed about 14 kg (Figures 9 and 10).

The northeast portion of the Rio Caunahue exposure was sampled during the 1977 and 1979 field seasons (Figure 15). In 1977, samples were taken at 10-cm intervals from the base of the terrace gravels to a depth of 4.3 m (Figures 16 and 17). The lower 50 cm were collected from below water-level. A bulk sample (BS), from a stratigraphically higher horizon, was also taken from an exposure 500 m upstream from the main section. An additional 160 cm of the main section was exposed when the site was revisited in 1979 because of lowered river-level during the drought conditions that year. Seven samples of distinct organic horizons (PDO-PD6), ranging in depth from 30 cm above the prominant volcanic ash horizon to river level, were collected from the main section. In addition, three more samples (A1-A3) were taken from the upstream exposure and three samples (B1-B3), above the prominent volcanic ash marker horizon, were taken from an exposure about 100 m downstream from the main section. Each sample from the Rio Caunahue Site weighed about 3 kg. The total weight of sediment collected from the Rio Caunahue Site during the two field seasons was about 150 kg.

The Puerto Octay Site, a bog, was sampled with a piston corer in November 1977 (Figure 7). Nine complete cores, averaging 2.5 m in length and 5 cm in diameter, were obtained from an area 4 m in diameter in the center of the abandoned meltwater channel about 50 m west of highway U-55-V (Figures 5 and 6). Coring was terminated at a resistant volcanic ash horizon. Detailed lithologic descriptions of each of the cores were recorded and the cores were correlated by lithologic comparison. Each core was sampled at 10 cm intervals. A total of about 34 kg of sediment was collected from the Puerto Octay Site; individual samples on the average weighed 180 g.

The November 1977 excavation of the Puerto Varas Railroad Site was hindered by the emplacement of a concrete retaining wall constructed since Heusser's (1974) study of the site (Figure 12). A trench was dug behind the retaining wall to a depth of 160 cm before water seepage problems prevented further digging (Figure 13). Samples were collected at 10 cm intervals from the top of the excavation to a depth of 80 cm (Figure 14). Because of the water problems, samples were taken at 20 cm increments from a depth of 80 cm to the bottom of the excavation. A total of about 47 kg of sediment, each sample weighing about 4 kg, were collected from the Puerto Varas Railroad Site.

Individual samples from the four sites were secured in plastic bags with a label indicating collecting site and stratigraphic position.

They were air-freighted to the North Dakota State University (NDSU) Fossil Beetle Laboratory for processing.

Laboratory Procedures

Sample processing techniques for isolating insect fossils from Quaternary sediments have evolved from simply inspecting bedding planes to a wet-sieving and kerosene-flotation procedure. The flotation method was developed at the University of Birmingham, England, to expedite fossil recovery (Coope and Osborne, 1967; Coope, 1968). However, the process is still time consuming. Ashworth (1979) briefly described the procedure but a detailed outline of the method is provided in Appendix B.

All samples recovered from the Puerto Octay, Puerto Varas Park, Puerto Varas Railroad, and Rio Caunahue sites were processed according to this procedure except that the Calgon solution dispersion was seldom used because most samples disaggregated easily during wet sieving. A sample preparation report sheet was maintained for each processed sample recording weight, lithology, observed fossils and processing procedures used. Catalogs containing the report sheets for each fossil site studied are housed at the NDSU Fossil Beetle Laboratory. All subsamples retained for additional radiocarbon dating, pollen and macroplant analysis, and all washed residues are curated at NDSU.

Following the extraction procedure, the insect fossils were transferred from the storage vials into petri dishes containing ethanol. Beetle fossils were sorted, under the binocular microscope, into groups of similar skeletal elements (e.g., heads, pronota, etc.). In addition, they were segregated into taxonomic categories when possible. Fossils were removed from the petri dish with a dissecting forceps and mounted on micropaleontological slides with water-soluble, gum tragacanth glue. Other insects and arachnids were mounted on separate slides. The fossils on each slide were numbered. Information including fossil site, sample number, slide number and number of slides per sample was written on the edge of the slide. Data sheets, recording the types of skeletal elements and names of the fossils when obtained, were kept for each slide. In addition, summary data sheets were maintained for each sample indicating the species found, kind and number of skeletal elements on which the determinations were made, and minimum number of individuals per species. All slides and catalogs containing the data sheets are deposited in the NDSU Fossil Beetle Laboratory.

Identification to genus and species was attempted only with the fossil Coleoptera. Other insects and arachnids were identified to order or to family. Most fossils were identified by comparing them with species recovered during a modern faunal survey (Appendix A). Other specimens were named by careful comparison with identified specimens in the insect collections of the United States National Museum (USNM), Canadian National Collection (CNC) in Ottawa, and private collections (e.g., Dr. Charles O'Brien's weevil collection in Tallahassee, Florida). Fossil specimens not identified by these methods were sent to systematists in the United States and other countries for determinations. Many specimens were examined by these experts for confirmation of identifications.

All identifiable fossils were counted to determine relative abundances and diversities. In each sample, one left elytron, or one right elytron, or one head, or one pronotum from a beetle taxon, or a combination of single specimens of any or all of these skeletal elements was considered one individual. In many instances, numerous left elytra, right elytra, heads, and pronota of one taxon were recovered from each sample. The skeletal element that was present in highest numbers was considered an estimate of the number of individuals of that taxon in that sample.

Information concerning the ecological requirements and present geographical distribution of southern Chilean beetle species is rarely encountered in the literature because studies have concentrated on taxonomy. The paleoenvironmental and paleoclimatic interpretations presented herein are based largely on an integration of the ecological and distributional data derived from information obtained through study of the existing Lake Region fauna (Appendix A) and are governed by the fundamental assumptions summarized earlier. Supplemental information was gained by visits to major museums and private collections and from the sparse literature available. However, a great deal of pertinent ecological and distributional data were acquired through correspondence with numerous taxonomic experts. This knowledge was invaluable in defining the past environments in which the fossil communities lived; and because these coleopterists will be cited as personal communicants frequently, a list of their names and affiliations is presented in Appendix C.

To facilitate discussion and interpretation of the fossil assemblages from the four sites, the sequences were divided into intervals based on sedimentological breaks or changes in the fossil insect assemblages. The Puerto Octay sequence was divided into four intervals, the Rio Caunahue sequence into three and each of the Puerto Varas sequences into one. The intervals are not formally named and are not considered as zones to avoid the implication of biostratigraphic utility. The intervals are numbered according to the sample numbers they include (e.g., Puerto Octay interval 25 through 24). A paleoenvironmental analysis of each interval will be presented later based on the species associations within the interval.

Abundant datable material was available from the four sites studied. Twenty, either wood or peat, samples (fifteen from Rio Caunahue, three from Puerto Octay, one from each of the Puerto Varas sites) were submitted for radiocarbon dating (Appendix D).

Standard Scanning Electron Microscope techniques were used to produce the photomicrographs illustrated in Plates 2 through 8 of some of the representative and well preserved beetle fossils recovered during this study.

Mathematical Treatment

Cluster analysis, a technique for analysis of multivariate data sets, has been extensively developed in recent years (Sokal and Sneath, 1963; Sneath and Sokal, 1973; Krumbein and Graybill, 1965; Harbaugh and Merriam, 1968; Davis, 1973). These methods were initially devised for numerical taxonomy; subsequently, they have become of interest to researchers involved in bioassociational studies such as biostratigraphy, paleoecology, ecology, and biogeography because they provide consistent ways of searching for bioassociational patterns in large data sets. The methods are simple, repeatable, and objective, but they are not statistical because they have no theoretical statistical basis and no tests of significance have yet been devised.

In this study, the purpose of cluster analysis was to define collecting localities that have similar beetle faunas, so as to establish an elevational zonation of the fauna in the study area (see Appendix A). Further, the method was used to establish the similarity of fossil beetle assemblages, from various time intervals, to communities existing today at distinct localities and restricted elevations. This polythetic ecological and paleoecological approach was accomplished through utilization of digital computers to generate binary similarity coefficients and, ultimately, the clustering results. The approach is free of *a priori* or circular reasoning because the technique establishes that distinctive groups (bioassociations) are present before various taxa for the recognition of the bioassociations are determined.

Cluster analysis involves two computational procedures:

(1) the calculation of similarity coefficients, numerical measures of the similarities between all the objects to be clustered;

(2) and the grouping of samples on the basis of these similarity coefficients.

The type of similarity coefficient analysis employed is called Q-mode where the various samples are compared to one another on the basis of the taxa they contain. In this study, these coefficients are merely quantitative descriptive numbers based on the presence or absence of taxa. A number of binary (presence - absence) similarity coefficients have been used in bioassociational studies. The properties of those that have been most consistently used were compared by Cheetham and Hazel (1969). Every type of similarity coefficient has some bias which can introduce distortion into an analysis. It is, therefore, left up to researchers to choose the coefficient that best fits their concept of what they want the similarity measure to portray. That decision is governed by experience and through experimentation with a variety of coefficients.

The Jaccard coefficient omits consideration of negative matches (absence of a species from both samples being compared) and consequently, emphasizes differences. By contrast, although it is monotonic with the Jaccard, the Dice coefficient gives twice as much weight to matches as to mismatches, thereby emphasizing similarity. The Dice coefficient was developed by Dice (1945), advocated by Hall (1969) and is used in this study because it emphasizes similarity. Other coefficients (Jaccard, Fager, Otsuka, and Phi) were compared with the Dice but the latter yielded groupings that seemed more natural. The Dice coefficient is expressed by the formula:

$$C_D = \frac{2C}{N_1 + N_2} \times 100$$

where,

C_D = Dice coefficient

C = Number of taxa common to both samples

N_1 = Number of taxa present in the first sample

N_2 = Number of taxa present in the second sample

The program to calculate the Dice coefficients in this study was developed by Dr. Richard D. LeFever (unpublished, Geology Department, University of North Dakota).

A matrix of similarity coefficients is produced when coefficients are calculated between all pairs of samples. The data matrix is square and symmetrical about its principal diagonal. The diagonal contains no information and, because the matrix is symmetrical, only the upper or lower triangular portion of the matrix is needed to describe the relationships. Convention is to publish only the lower left triangular part of the matrix. In the matrices presented here, the coefficients have been replaced by symbols representing 10-point classes and are called shaded trellis diagrams (Figure 11 and Figure A7). The trellis diagram is read in the same manner as a road mileage chart. The pattern in the square at the intersection of the column of one sample and the row of another sample indicates the degree of similarity in faunal composition between the two samples. For example, the measure of similarity between samples 21 and 39 falls within the 31-40 percent similarlity level. Dark patterns proximal to the diagonal, as from localities 11 to 8, indicate groups of localities with many taxa in common.

Input for cluster analysis is the matrix of similarity coefficients. The clustering procedure is used to define interrelationships within the similarity coefficient matrix. Similar samples are grouped (clustered) and clusters are displayed in a two-dimensional tree-like hierarchical dendrogram. Although there are numerous clustering techniques, the most widely used are the weighted (WPGMA) and the unweighted pair-group averaging (UPGMA) methods developed by Sokal and Michener (1958) and discussed in detail by Sokal and Sneath (1963) and Sneath and Sokal (1973). Which method is generally best has been a subject of debate. Hazel (1970, 1972, 1977) and Sneath and Sokal (1973) recommend the use of the UPGMA because the generated dendrograms, when compared to the original similarlity matrices, show less distortion than those produced by WPGMA. However, Davis (1973) favors the WPGMA on empirical grounds. Nevertheless, the above authors agree that there are occasions when the WPGMA is preferable, especially when there is a disparity in the size of samples being compared. Such is the situation in this study and, consequently, the WPGMA technique was used. The computer program for the procedure is given by Davis (1973).

In the pair-group method all samples are compared to each other by using similarity coefficients. After the similarity coefficient matrix has been generated, the first step in WPGMA is to scan the matrix for the highest similarity value. The highest similarity coefficient indicated in Figure A7, is 52 percent between samples 2 and 5. These two samples are, therefore, considered to represent a group or cluster. The degree of similarity between the two samples is indicated on the dendrogram by closing the branch between the samples with a line drawn at the 52 percent similarity level. The similarity matrix is then recomputed treating the clustered samples, 2 and 5, as a single sample. Similarities between cluster 2,5 and other samples is calculated as the average between each sample in the cluster and each new sample. In the example (Figure A7) the similarity between cluster 2,5 and sample 12 would be calculated in the following way. The original similarity coefficient between samples 2 and 12 is 45 percent and the original similarity coefficient between samples 5 and 12 is 47 percent. The similarity between cluster 2,5 and sample 12 is simply the average of these two values: (45 percent + 47 percent)/2 = 46 percent. The degree of similarity between cluster 2,5 and sample 12 is entered onto the dendrogram by adding a branch to represent sample 12 and connecting it to cluster 2,5 with a line drawn at the 46 percent similarity level (Figure A7). The process is repeated until all samples or clusters of samples are joined together.

The resulting dendrogram, in summarizing the original matrix of similarity coefficients through the process of averaging together members of a cluster and treating them as a single new object, distorts the original relationships between the samples being compared. At times, the degree of similarity between two samples is masked. Valentine (1966), Valentine and Peddicord (1967) and Hazel (1970, 1972) counteracted this problem by using shaded trellis diagrams in conjunction with dendrograms because comparisons of samples between the major groupings can be determined in the trellis diagram, thereby compensating for the inherent distortion in the dendrogram. For example, as seen in Figure A7, some localities in bioassociation II and III have a number of taxa in common as indicated by dark patterns within the matrix. For that reason, combined trellis diagrams and dendrograms were used in this study.

Major clusters are distinguished on the completed dendrogram by tight groupings of samples joined at high similarity levels. The major clusters or bioassociations, I-V (Figure A7) and I-V, F_1 and F_2 (Figure 11) are indicated to the left of the trellis diagrams and are separated by patterns on the dendrograms.

It would have been ideal to subject all fossil assemblages to the clustering procedure, but this proved to be impossible because many samples did not exhibit enough diversity in species composition to make the analysis meaningful and because of limits imposed by the computer program. Therefore, the assemblages recovered from nine samples were chosen for the analysis because collectively they span the time interval from about 4,500 to about 15,700 yr B.P., although most are late glacial in age. In addition, all but one of the samples were radiocarbon dated. Eight of the samples were from the Rio Caunahue Site and the other was from Puerto Varas Park. No assemblages were used from the Puerto Varas Railroad or Puerto Octay sites because of inadequate species diversities. Hazel (1970) cautioned against using samples containing less than ten species in the cluster method. His recommendation was followed except for the Puerto Varas Park assemblage which contained only seven species. It was included in the analysis because it was older and appeared to be distinctive and markedly different than the Rio Caunahue assemblages. The samples used, their age and the number of species in each sample are presented in Table 2. The stratigraphic position of the samples and species used for the analysis are indicated on Plate 1.

Table 2. Fossil samples chosen for cluster analysis. The table also gives the ages of the samples and the number of species in each sample.

Site/Sample	Age ^{14}C yr B.P.	Number of Species
Rio Caunahue BS-A3	4,525 ± 145	65
Rio Caunahue 21	10,000 ± 280	11
Rio Caunahue 27	10,200 (estimate)	20
Rio Caunahue PD0	10,440 ± 240	26
Rio Caunahue PD1	11,290 ± 250	16
Rio Caunahue 42	11,680 ± 280	52
Rio Caunahue PD4	12,385 ± 340	20
Rio Caunahue PD6	12,810 ± 190	26
Puerto Varas Park PV1	15,715 ± 440	7

PUERTO OCTAY SITE

Location, Site Description, and Radiocarbon Chronology

The Puerto Octay Site (Figures 1, 4, 5, 6 and 7), in a former, eastwest trending, meltwater channel of Lago Llanquihue, is about 3 km north of Puerto Octay (lat. 40°56'40"S., long. 73°52'30"W.). The abandoned spillway's best geomorphic expression is about 150 m north of the intersection of routes U-55-V and U-925 where U-55-V crosses it. The channel, now a fen, has an elevation of 150 m or 100 m above present lake level and is located in an area of deforested pastureland. Coring at the site revealed a sequence of silty peat, silty clay, gyttja and volcanic ash to a depth of 2.5 m in the channel (Plate 1 and Table 3). Samples of the 2.5 m section were taken at 10-cm increments.

The channel drained a proglacial lake that occupied the area of the Lago Llanquihue basin northeast of Puerto Octay during the late glacial maximum when the glacier abutted against the western shore of Lago Llanquihue. Mercer (1976) suggested that the ice-marginal lake was not an ephemeral feature formed during ice recession; it occupied the basin for a considerable length of time but only when the glacier was in contact with the western shore. Porter (1981) argued, however, that the spillway drained the lake during early recession of the glacier from the Llanquihue II moraine because the channel truncates Llanquihue II outwash. Deposition of organic-rich sediments began in the channel

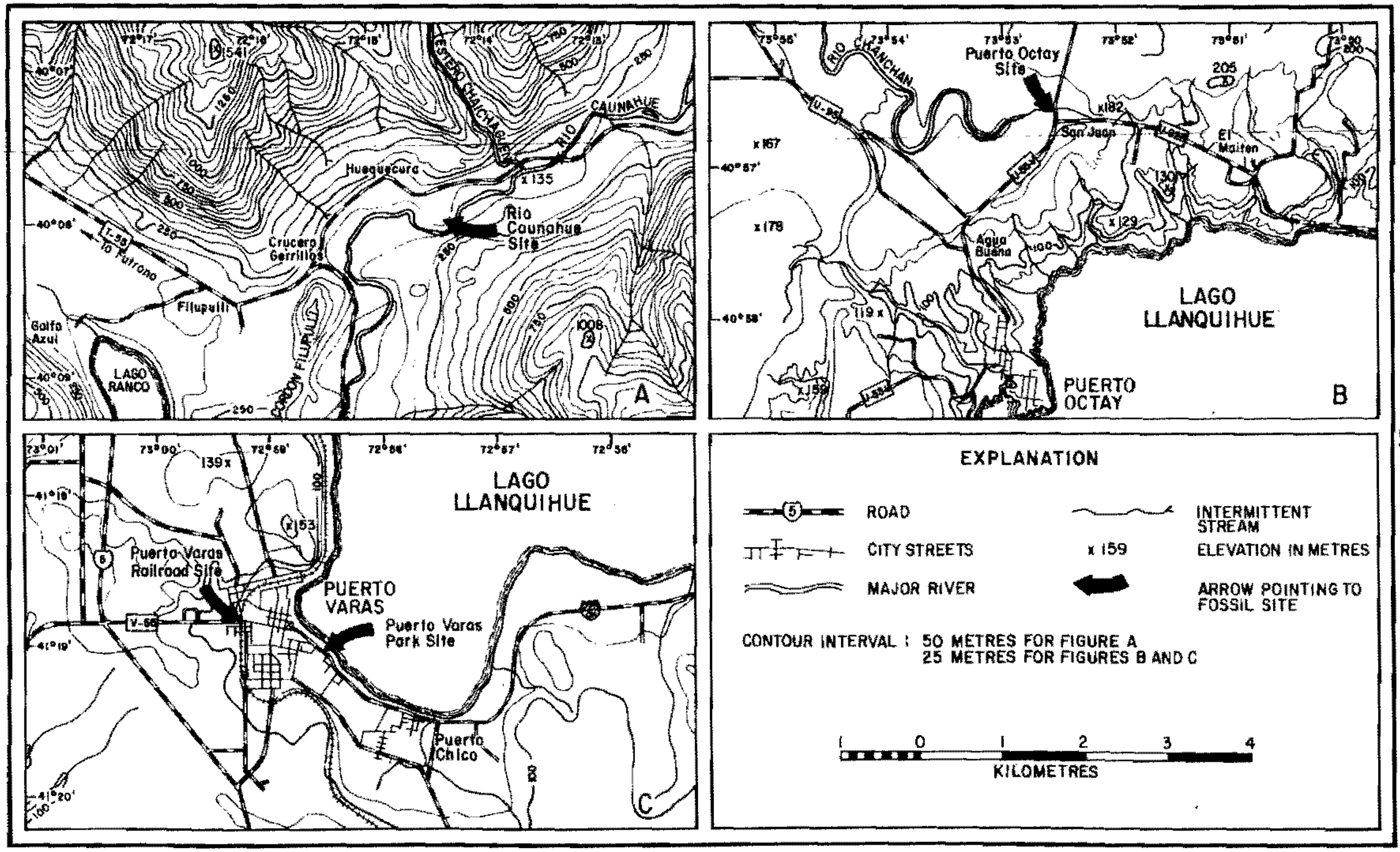


Figure 4. Topographic maps of the areas of fossil sites. (A) Rio Caunahue Site. (B) Puerto Octay Site. (C) Puerto Varas Sites. Redrawn from Instituto Geografico Militar de Chile, 1973, topographic map series, scale 1:50,000, Santiago.

Figure 5. View of the abandoned Puerto Octay spillway west from route U-55-V. Note terraces in background. Howard Mooers is with coring apparatus in the middle of the channel.

Figure 6. Photograph of the piston corer and some of the cores recovered from the Puerto Octay Site. The top of the cores is to the left. The dark layers are organic rich and the light contain volcanic ash. John Mercer is on the right and the writer on the left.

Figure 7. Photograph of coring at the Puerto Octay Site. John Mercer is on the left and Howard Mooers on the right. The abandoned spillway terrace is evident in the background. Note retrieved core in foreground.

Table 3. Lithologic description of the Puerto Octay Section. The composite section is based on nine cores.

Location. Abandoned meltwater channel 3 km morth of Puerto Octay (lat. 40°56'40"S., long. 73°52'30"W.). Cores taken 50 m west of highway U-555-V about 150 m north of the junction of U-55-V and U-925 (Figure 4).

Sample Numbers	Description	Thickness (cm)
Not sampled	Removed because of bioturbation by grazing cattle.	10
1-3	Black (5YR 2.5/1) silty peat. Penetrated by modern plant roots. Abrupt contact with unit below. Sample 3 (20-30 cm below top) dated at 1,190±135 ^{14}C yr B.P. (GX-5505).	30
4-9	Brown (10YR 4/3) slightly silty clay. Somewhat darker in upper 10 cm. Contains disseminatd volcanic ash. Gradational contact with unit below. Sample 9 (80-90 cm below top) dated at 16,000±540 ^{14}C yr B.P. (GX-5506).	60
10-23	Dark, reddish brown (5YR 2.5/2 to black (5YR 2.5/1) organic rich clay (gyttja). Becomes increasingly darker down hole. Thin volcanic ash laminae in sample 12 (120 cm below top) and in sample 19 (190 cm below top). Abrupt contact with unit below. Organics from the base of sample 23 (238 cm below top) dated at 18,170±650 ^{14}C yr B.P. (GX-5274).	140
24-25	Grayish brown (2.5YR 5/2) slightly sandy clayey silt. Probably water-lain volcanic ash.	13

Base of cored section

after the spillway was abandoned when the proglacial lake level was lowered during glacier recession. The date for these sediments has been taken as the age for retreat of the glacier from the western shore of Lago Llanquihue following the late glacial maximum (Mercer, 1976) or a minimum age for the late glacial maximum, Llanquihue II, advance (Porter 1981). The date of 18,170±650 ^{14}C yr B.P. (GX-5274) obtained during this study from the basal organic-rich sediments is slightly older than the date of 17,370±670 ^{14}C yr B.P. (RL-120) reported by Mercer (1972a, 1976) from the same stratigraphic level.

Two additional dates, 1,190±135 ^{14}C yr B.P. (GX-5505) from sample 3 (20-30 cm below the top of the section) and 16,000±540 ^{14}C yr B.P. (GX-5506) from sample 9 (80-90 cm below the top of the section), were obtained from the Puerto Octay Site (Plate 1, Table 3, and Appendix D). These dates indicate that either the upper 90 cm of the section is highly compressed or that a hiatus exists somewhere in the upper part of the sequence. The basal 1.5 m of section, however, contains beetle assemblages spanning the 18,000 to 16,000-year interval.

Analysis of the Fossil Assemblages

Representatives (Plate 1) of six orders of insects and two orders of arachnids were identified from the twenty-five samples collected at the Puerto Octay Site. Plate 1 also shows the minimum number of beetle individuals per identified taxon, the number of unidentified but potentially identifiable beetle fragments, and the number of additional insect and arachnid fragments recovered from each sample. The occurrence of charophyte oogonia, diatoms, quillwort macrospores and unidentified macroplant remains is indicated on the stratigraphic column (Plate 1). No mollusks or ostracods were found in any of the Puerto Octay samples.

Of the 516 identifiable beetle fossils recovered from the Puerto Octay Site (Tables 4 and 5), 498 (97 percent) were identified to family, 334 (65 percent) to genus and 179 (35 percent) to species. At least 42 species representing 14 beetle families, both aquatic and terrestrial, were recognized. Ninety-three percent of the taxa were identified by direct comparison to specimens collected during the modern faunal survey. The assemblage was dominated by five beetle families (Table 6). Twenty-three percent of the species were staphylinids, 14 percent hydrophilids, 11 percent curculionids, 14 percent carabids and 9 percent pselaphids.

The beetle fossils were not evenly distributed throughout the 2.5 m section. Interval 3 through 1, the upper peat horizon, contained a relatively diverse assemblage but interval 9 through 4, silty clay containing volcanic ash, was devoid of beetle fossils except for pselaphids (Table 5). A relatively diverse beetle assemblage, dominated by water beetles, mostly hydrophilids, and significant species of carabids and curculionids, was recovered from interval 23 through 10. Only a single aleocharine was found in the basal unit of presumed volcanic ash.

Representatives of five orders of insects (Table 7), in addition to the Coleoptera, were present. Hemiptera (bugs) including Saldidae (shorebugs), Homoptera, specifically Cicadellidae (leafhoppers),

Table 4. Taxonomic list of fossil Coleoptera recovered from the Rio Caunahue, Puerto Varas Park, Puerto Varas Railroad and Puerto Octay Sites indicating their present elevational ranges, skeletal elements from which they were identified and plates on which they are illustrated.

FOSSIL COLEOPTERA TAXA	ELEVATIONAL RANGE	RIO CAUNAHUE					PUERTO VARAS RAILROAD					PUERTO VARAS PARK					PUERTO OCTAY					PLATE NUMBER
		HEAD	PRONOTUM	LEFT ELYTRON	RIGHT ELYTRON	OTHER	HEAD	PRONOTUM	LEFT ELYTRON	RIGHT ELYTRON	OTHER	HEAD	PRONOTUM	LEFT ELYTRON	RIGHT ELYTRON	OTHER	HEAD	PRONOTUM	LEFT ELYTRON	RIGHT ELYTRON	OTHER	
TRACHYPACHIDAE																						
Systolosoma brevis Sol., 1849	6				X																	
CARABIDAE																						
Ceroglossus valdiviae (Hope, 1838)	4			X	X																	
Ceroglossus sp.	4			X																		
Creobius eydouxi Guer., 1839	4	X	X	X	X									?	?							
Creobius sp.	4								X	X												
Bembidion cf. *dubei* Sol., 1849	3																			X		
Bembidion marginatus Sol., 1849	4													X								
Bembidion cf. *posticalis* Gmn., 1906	2			X																		
Bembidion setiventre Neg., 1973	2			X	X																	
Bembidion sp. 5	2	X	X	X	X																	
Bembidion sp. 7	2				X																	
Bembidion sp. 8	2		X	X																		

Table 4. (Continued)

FOSSIL COLEOPTERA TAXA	RANGE	R. CAUNAHUE					P. VARAS RAILROAD					P. VARAS PARK					PUERTO OCTAY					PLATE
			P	L	R			P	L	R			P	L	R			P	L	R		
		H	T	E	E	O	H	T	E	E	O	H	T	E	E	O	H	T	E	E	O	
CARABIDAE (CONT.)																						
Bembidion spp.	6		X	X	X										X					X		
Aemalodera centromaculata Sol., 1849	3			X	X																	
Aemalodera dentimaculata Sol., 1849	2			X	X																	
Aemalodera spp.	4	X	X	X	X					X												
Trechisibus nigripennis Group Sol., 1849	6	X	X	X	X																	
Trechisibus sp.	6				X																	
Gipsyella patagonica Schw., 1958	2	X	X																			Pl.8, Fig. 2
Trechinotus striatulus Mateu & Neg., 1972	2	X	X	X	X																	Pl.8, Fig. 1
Trechini gen. indet.	6	X		X	X																	
Trirammatus (Feroniomorpha) sp. 1	2		X																			
Trirammatus sp.	2	X																				
Parhypates (sensu stricto) sp.	4		X	X	X																	
Metius sp. 1	3				X																	
Metius spp.	3				X																	
Abropus carnifex Fabr., 1775	6	X	X	X	X																	Pl.4, Fig. 1
Agonum sp. 1	1		X																			
Agonum sp. 2	4						?						X					X				Pl.5, Fig. 2
Agonum sp. 4	2		X	X																		
Agonum spp.	4	X			X			X				X			X				X			
Pterostichini gen. indet.	4	X			X																	
Pelmatellus (sensu lato) sp. 1	4	X		X																		
Pelmatellus (sensu lato) sp.	4								X	X												
Bradycellus (Goniocellus) sp.	4				X														X	X		

Table 4. (Continued)

FOSSIL COLEOPTERA TAXA	RANGE	R. CAUNAHUE					P. VARAS RAILROAD					P. VARAS PARK					PUERTO OCTAY					PLATE
			P	L	R			P	L	R			P	L	R			P	L	R		
		H	T	E	E	O	H	T	E	E	O	H	T	E	E	O	H	T	E	E	O	
CARABIDAE (CONT.)																						
Bradycellus (Liocellus) sp.	4									X												
Bradycellus (Stenocellus) sp.	2	X			X												X					
cf. Bradycellus (Stenocellus) sp.	4		X	X	X																	
Bradycellus spp.	4	?		X																		
Plagiotelum irinum Sol., 1849	6			X																		
Carabidae gen. indet.	6	X	X	X	X		X			X		X										
DYTISCIDAE																						
Lancetes sp.	3				X																	
Rhantus validus Sharp, 1882	2				X																	
Liodessus delfini (Rgmb., 1899)	6			X	X												?	X	X	X		
HYDRAENIDAE																						
Gymnochthebius spp.	3													X	X				X	X		
HYDROPHILIDAE																						
Hydrochus stolpi Gmn., 1901	1	X											X	X	X		X	X	X	X		Pl.4, Fig. 2
Tropisternus setiger (Germ., 1824)	2																X	X	X	X		
Enochrus fulvipes Sol., 1849	2																	X				
Enochrus vicinus Sol., 1849	4		X										X		X		X	X	X	X		

Table 4. (Continued)

FOSSIL COLEOPTERA TAXA	RANGE	R. CAUNAHUE					P. VARAS RAILROAD					P. VARAS PARK					PUERTO OCTAY					PLATE
		H	PT	LE	RE	O	H	PT	LE	RE	O	H	PT	LE	RE	O	H	PT	LE	RE	O	
HYDROPHILIDAE (CONT.)																						
Enochrus spp.	4	X											X	X			X	X	X	X		
Hydrophilidae gen. indet.	6																			X		
PTILIIDAE																						
Ptiliidae gen. indet.	4			X	X															?		
LEIODIDAE																						
Dasypelates sp. 1	3	X	X	X	X																	
Dasypelates spp.	3			X	?																	
Eunemadus chilensis Ptvn., 1914	4			X	X															?		Pl.7, Fig. 1
cf. Eunemadus sp.	4			X	X																	
Colon sp.	2			X	?																	
cf. Hydnobiotus sp.	3				X																	
cf. Neohydnobius sp.	4				X																	
Leiodidae gen. indet.	4		X	X	X														X			
SCYDMAENIDAE																						
Euconnus spp.	2			X	X																	
Scydmaenidae gen. indet.	2			X									X									

Table 4. (Continued)

FOSSIL COLEOPTERA TAXA	RANGE	K. CAUNAHUE					P. VARAS RAILROAD					P. VARAS PARK					PUERTO OCTAY					PLATE
			P	L	R			P	L	R			P	L	R			P	L	R		
		H	T	E	E	O	H	T	E	E	O	H	T	E	E	O	H	T	E	E	O	
STAPHYLINIDAE																						
Pseudopsis cf. adustipennis F.& G., 1861	+			X	X																	
cf. Pseudopsis spp.	+			X	X																	
Glypholoma pustuliferum Jean., 1962	2		X	X																		Pl.6, Fig. 3
Glypholoma sp.	4				X																	
Omaliopsis spp.	4			X	X																	
Neophonus bruchi Fauv., 1905	+	X		X	X																	Pl.7, Fig. 3
Omaliinae gen. indet.	4	X	X	X	X																	
Carpelimus spp.	+	X		X	X																	
Thinodromus sp. 1	2			X																		
Thinodromus sp. 2	1				X																	
Thinodromus sp. 3	2		?	X	X																	
cf. Thinodromus sp. 4	1			X	X																	
cf. Thinodromus sp. 6	2		X																			
cf. Thinodromus spp.	2		X	X	X																	
Anotylus chilensis C. & S., 1968	2							X	X	X												Pl.7, Fig. 6
Bledius cf. chilensis C. & S., 1968	2		X																			
cf. Oxytelinae gen. indet.	+			X	X																	
Stenus chilensis Ben., 1926	+	X			X												X	X	X			
Stenus spp.	4		X	X	X	M					M	X	X	X	X	M	X		X	X	M	
Baryopsis araucanus C. & S., 1968	2	X	X	X	X		?			?												Pl.4, Fig. 4
Baryopsis sp.	2																X					
Philonthus (Edeius) punctipennis (Sol., 1849)	6																	X				

Table 4. (Continued)

FOSSIL COLEOPTERA TAXA	RANGE	R. CAUNAHUE					P. VARAS RAILROAD					P. VARAS PARK					PUERTO OCTAY					PLATE
		H	PT	LE	RE	O	H	PT	LE	RE	O	H	PT	LE	RE	O	H	PT	LE	RE	O	
STAPHYLINIDAE (CONT.)																						
Cheilocolpus cf. sp. 2	5			X	X																	
Cheilocolpus sp. 3	4	X																				
Cheilocolpus sp. 4	2																X	?				
Cheilocolpus spp.	6	X	X	X	X													X				
Loncovilius (*Lienturius*) sp.	2		X	X	X																	
Loncovilius sp.	4		X																			
Quediinae gen. indet.	4		X																			
cf. *Bolitobius asperipennis* C.& S.,1968	+				X																	
Leucotachinus luteonitens (F.& G., 1861)	1	X	X	X	X																	Pl.7, Fig. 4
Nomimoceras marginicollis (Sol., 1849)	3	X	X	X	X													X				Pl.5, Fig. 4
Aleocharinae sp. 3	1			X	X																	
Aleocharinae sp. 8	2	X	X																			
Aleocharinae sp. 9	2		X	X	X																	
Aleocharinae sp. 10	4				X																	
Aleocharinae sp. 12	4			X																		
Aleocharinae Group 1	6	X	X															X	X	X		
Aleocharinae Group 2	2			X	X																	
Aleocharinae gen. indet.	6	X	X	X	X				X	X				X	X		X	X	X	X		
Homalotrichus cf. *impressicollis* Sol., 1849	+				X																	
Staphylinidae gen. indet.	6	X	X	X	X												X	X	X	X		

Table 4. (Continued)

FOSSIL COLEOPTERA TAXA	RANGE	R. CAUNAHUE					P. VARAS RAILROAD					P. VARAS PARK					PUERTO OCTAY					PLATE
			P	L	R			P	L	R			P	L	R			P	L	R		
		H	T	E	E	O	H	T	E	E	O	H	T	E	E	O	H	T	E	E	O	
PSELAPHIDAE																						
Dalminiomus araucanus Jean., 1962	2			X																		
Dalminiomus spp.	2		X	X	X									X	X		X		X	X		
Achillia spp.	6	X	X	X	X								X	X	X			X	X	X		
Tryopsis spp.	3	X	X	X	X									?	X				X	X		
Pselaphidae gen. indet.	6	X		X	X							X					X		X			
LUCANIDAE																						
Chiasognathus granti Steph., 1831						L																
Sclerognathus bacchus Hope, 1845				X		L																
Sclerognathus caelatus Blanch., 1837				X																		
cf. *Sclerognathus femoralis* Guer., 1839					X																	
Sclerognathus sp.						P																
SCARABAEIDAE																						
Sericoides chlorosticta Blanch., 1851	3			X	X																	
Sericoides viridis Sol., 1851	2	X	X	X	X																	
Sericoides sp. 2	2				X																	
Sericoides sp. 4	4		X	X	X																	
Sericoides sp. 5	2			X																		
Sericoides sp. 10	2		X																			
Sericoides sp. 11	2			X	X																	

Table 4. (Continued)

FOSSIL COLEOPTERA TAXA	RANGE	R. CAUNAHUE					P. VARAS RAILROAD					P. VARAS PARK					PUERTO OCTAY					PLATE
		PH	LT	RE	E	O	PH	LT	RE	E	O	PH	LT	RE	E	O	PH	LT	RE	E	O	
SCARABAEIDAE (CONT.)																						
Sericoides spp.	6	X	X	X	X			X		X							X					
Scarabaeidae gen. indet.	6	X	X		X			X										X				
HELODIDAE																						
cf. *Microcara* sp.	6	X	X	X	X																	
cf. *Cyphon* sp.	4		X																			
Prionocyphon sp.	4		X																			
Helodidae sp. 7	4																	X				
Helodidae gen. indet.	6	X	X	X	X													X				
CLAMBIDAE																						
Clambidae gen. indet.	3			X	X																	
BYRRHIDAE																						
cf. Byrrhidae gen. indet.	+			X																		
ELMIDAE																						
Austrolimnius chiloensis (Champ., 1918)	1	X			X																	Pl.6, Fig. 6
Austrolimnius sp.	1			X	X																	

Table 4. (Continued)

FOSSIL COLEOPTERA TAXA	RANGE	R. CAUNAHUE					P. VARAS RAILROAD					P. VARAS PARK					PUERTO OCTAY					PLATE
			P	L	R			P	L	R			P	L	R			P	L	R		
		H	T	E	E	O	H	T	E	E	O	H	T	E	E	O	H	T	E	E	O	
ELMIDAE (CONT.)																						
Neoelmis n. sp.	1		X	X	X																	Pl.8, Fig. 3
Neoelmis sp.	+				X																	
Stethelmis sp.	3		X	X	X																	
Hydora annectens S. & B., 1981	1			X	X																	Pl.5, Fig. 3
ELATERIDAE																						
Semiotus luteipennis Guer., 1838	4				X																	
Deromecus sp. 1	2				X																	
Deromecus spp.	6		?	X	?																	
cf. Medonia sp.	2				X																	
Negastrius sp.	2			X	X																	
Elateridae gen. indet.	6		X	X	X																	
LAMPYRIDAE																						
Pyractonema nigripennis Group Sol., 1849	6		X																			
CANTHARIDAE																						
Dysmorphocerus dilaticornis Guer., 1838	2																X					
Oontelus sp.	4		X	X	X																	
Hyponotum cf. krausei (Phil., 1861)	2	X																				

Table 4. (Continued)

FOSSIL COLEOPTERA TAXA	RANGE	R. CAUNAHUE					P. VARAS RAILROAD					P. VARAS PARK					PUERTO OCTAY					PLATE
			P	L	R			P	L	R			P	L	R			P	L	R		
		H	T	E	E	O	H	T	E	E	O	H	T	E	E	O	H	T	E	E	O	
CANTHARIDAE (CONT.)																						
Hyponotum cf. *violaceipenne* (Pic, 1928)	5	X																				
Hyponotum spp.	4	X	X																			
Micronotum nodicorne (Sol., 1849)	4	X	X																			
Plectocephalon testaceum (Pic, 1928)	6	X	X																			Pl.6, Fig. 7
cf. Cantharidae gen. indet.	6				X																	
DERODONTIDAE																						
Nothoderodontus dentatus Lawr., 1979	+	X	X	X	X																	Pl.3, Fig. 1
ANOBIIDAE																						
Byrrhodes nigricolor (Pic, 1912)	2				X																	
Byrrhodes sp.	2			X																		
Caenocara spp.	1	X	X	X	X																	Pl.3, Fig. 3
Stichtoptyohus cf. *brevicollis* (Sol., 1849)	2				X																	
Stichtoptyohus spp.	2			X	X																	
BOSTRIDHIDAE																						
Bostrichidae gen. indet.	+				X																	

Table 4. (Continued)

FOSSIL COLEOPTERA TAXA	RANGE	R. CAUNAHUE					P. VARAS RAILROAD					P. VARAS PARK					PUERTO OCTAY					PLATE
		H	PT	LE	RE	O	H	PT	LE	RE	O	H	PT	LE	RE	O	H	PT	LE	RE	O	
TROGOSITIDAE																						
cf. *Diontolobus* sp. 1	3	X	X	X	X																	
cf. *Diontolobus* sp. 2	3	X	X	X	X																	Pl.4, Fig. 3
cf. *Diontolobus* sp.	3				X																	
PELTIDAE																						
Acalanthis sp.	+				X																	
MELYRIDAE																						
Dasytes haemorrhoidalis Sol., 1849	3	X		X	X																	
Melyridae gen. indet.	3			X	X																	
NITIDULIDAE																						
Brachypterus n. sp.	2			X	X																	Pl.6, Fig. 2
Perilopsis flava Rttr., 1873	2	X	X	X	X																	Pl.3, Fig. 4
Cryptarcha sp. 1	1	X																				
Cybocephalus sp.	+	X		X																		
Nitidulidae gen. indet.	4			X	X																	
RHIZOPHAGIDAE																						
cf. Rhizophagidae gen. indet.	+			X	X																	

Table 4. (Continued)

FOSSIL COLEOPTERA TAXA	RANGE	R. CAUNAHUE					P. VARAS RAILROAD					P. VARAS PARK					PUERTO OCTAY					PLATE
			P	L	R			P	L	R			P	L	R			P	L	R		
		H	T	E	E	O	H	T	E	E	O	H	T	E	E	O	H	T	E	E	O	
CRYPTOPHAGIDAE																						
Pseudochrodes suturalis Rttr., 1876	1		X																			
Cryptophagidae gen. indet.	4			X	X																	
cf. Cryptophagidae sp. 3	+			X	X																	
COCCINELLIDAE																						
Rhizobius chilianus Mader, 1957	1				X																	
Orynipus spp.	4			X	X																	
Adalia kuscheli Mader, 1957	1			X																		
Adalia spp.	2		X	X																		
Sarapidus cf. *australis* Gord., 1977	2			X	X																	
Strictospilus darwini Brths., 1924	3	X	X	X	X																	Pl.3, Fig. 2
Coccinellidae gen. indet.	6			X										X	X							
LATHRIDIIDAE																						
Aridius heteronotus (Belon, 1891)	4				X																	
Lathridiidae cf. sp. 2	1				X																	
Lathridiidae gen. indet.	4			X	X														X			
COLYDIIDAE																						
cf. Colydiidae gen. indet.	+			X	X																	

Table 4. (Continued)

FOSSIL COLEOPTERA TAXA	RANGE	R. CAUNAHUE					P. VARAS RAILROAD					P. VARAS PARK					PUERTO OCTAY					PLATE
		H	PT	LE	RE	O	H	PT	LE	RE	O	H	PT	LE	RE	O	H	PT	LE	RE	O	
TENEBRIONIDAE																						
cf. *Adelium* sp.	2			X	X																	
SALPINGIDAE																						
Cycloderus rubricollis Sol., 1851	2				X																	
Vincenzellus sp.	+	X			X																	
Salpingidae gen. indet.	6				X																	
OEDOMERIDAE																						
Platylytra vitticollis F. & G., 1863	2			X																		
MELANDRYIDAE																						
Orchesia sp. 1	4	X	X	X	X									?	?							
Orchesia sp. 2	1			X	X																	
MORDELLIDAE																						
Mordellidae cf. sp. 3	2			X	X																	
Mordellidae gen. indet.	2			X	X																	

Table 4. (Continued)

FOSSIL COLEOPTERA TAXA	RANGE	R. CAUNAHUE					P. VARAS RAILROAD					P. VARAS PARK					PUERTO OCTAY					PLATE
		H	PT	LE	RE	O	H	PT	LE	RE	O	H	PT	LE	RE	O	H	PT	LE	RE	O	
ANTHICIDAE																						
Anthicidae gen. indet.	2	X		X																		
CERAMBYCIDAE																						
<u>Hoplonotus</u> <u>spinifer</u> Blanch., 1851	2		X																			
CHRYSOMELIDAE																						
<u>Pachybrachis</u> sp.	2	X																				
<u>Strichosa</u> <u>eburata</u> Blanch., 1851	3				X																	
cf. <u>Gavirga</u> sp.	5			X																		
<u>Altica</u> sp. 1	4			X	X																	
<u>Altica</u> sp. 2	5			X																		
Alticinae sp. 1	4	X	X	X	X																	
Alticinae gen. indet.	4	X	X	X	X																	
cf. <u>Crepidodera</u> sp. 1	2			X	X														X			
cf. <u>Crepidodera</u> sp.	2		X	X	X																	
<u>Chaetocnema</u> sp.	2																	X				
Chrysomelidae gen. indet.	4	X		X	X																	
NEMONYCHIDAE																						
<u>Rhynchitomacer</u> <u>flavus</u> Voss, 1937	+	X																				Pl.6, Fig. 5
<u>Rhynchitomacer</u> <u>fuscus</u> (Kusch., 1954)	+	X																				

Table 4. (Continued)

FOSSIL COLEOPTERA TAXA	RANGE	R. CAUNAHUE					P. VARAS RAILROAD					P. VARAS PARK					PUERTO OCTAY					PLATE
			P	L	R			P	L	R			P	L	R			P	L	R		
		H	T	E	E	O	H	T	E	E	O	H	T	E	E	O	H	T	E	E	O	
ANTHRIBIDAE																						
Ormiscus parvulus (Blanch., 1851)	1			X																		
Choraginae gen. indet.	+	X																				
Anthribidae gen. indet.	4		X	X	X																	
SCOLYTIDAE																						
Pityophthorus sp.	+			X																		
Monarthrum sp.	+			X	X																	Pl. 5, Fig. 1
Amphicranus sp.	+				X																	
cf. *Corthylus* sp.	+			X																		
cf. *Araptus* sp.	+			X																		
Gnathotrupes cf. *sextuberculatus* Schl., 1951	+		X	X	X																	
Gnathotrupes spp.	2		X	X	X																	
Phloeotribus cf. *spinipennis* Eggrs., 1930	+			X	X																	Pl. 6, Fig. 1
Scolytidae gen. indet.	2			X	X																	
ATTELABIDAE																						
Eugnamptoplesius violaceipennis (F. & G., 1860)	2			X	X																	
Minurus testaceous Wtrh., 1845	2	X		X	X																	Pl. 8, Fig. 6

Table 4. (Continued)

FOSSIL COLEOPTERA TAXA	RANGE	R. CAUNAHUE					P. VARAS RAILROAD					P. VARAS PARK					PUERTO OCTAY					PLATE
			P	L	R			P	L	R			P	L	R			P	L	R		
		H	T	E	E	O	H	T	E	E	O	H	T	E	E	O	H	T	E	E	O	
BELIDAE																						
Trichophthalmus miltomerus (Blanch., 1851)	3				X																	
CURCULIONIDAE																						
Nototactus angustirostris Kusch., 1952	3	X		X	X																	
Polydrusus nothofagi Kusch., 1950	2	X	X	X																		
Dasydema hirtella Blanch., 1851	4	X	X	X	X		X	X	X	X		X			X				X		M	Pl.2, Fig.4
Paulsenius carinicollis (Blanch., 1851)	6						X	X														
Listroderes dentipennis Gmn., 1895	6		X	X			X	X				X	X	X	X	A		X	X		A	Pl.2, Fig.1
Listroderes sp.	6											X	X		X							
Listronotus bonariensis (Kusch., 1955)	+											X										
cf. *Listronotus* sp.	+			X	X																	
Hylobiinae n. sp.	+				X																	
Tartarisus signatipennis (Blanch., 1851)	3					L																Pl.6, Fig.4
Nothofagobius brevirostris Kusch., 1952	4	X																				
Nothofaginoides andinus Kusch., 1952	5			X	X																	
Nothofaginus lineaticollis Kusch., 1952	+	X																				
Neopsilorhinus collaris (Blanch., 1851)	2	X																				
Neopsilorhinus sp.	1	X																				
Rhopalomerus tenuirostris Blanch., 1851	3			X	X																	Pl.7, Fig.2
Omoides sp.	3			X	?																	
Epaetius carinulatus Kusch., 1952	2	X		X	X																	Pl.7, Fig.5
Notiodes sp.	+			X	X																	

Table 4. (Continued)

FOSSIL COLEOPTERA TAXA	RANGE	R. CAUNAHUE					P. VARAS RAILROAD					P. VARAS PARK					PUERTO OCTAY					PLATE
			P	L	R			P	L	R			P	L	R			P	L	R		
		H	T	E	E	O	H	T	E	E	O	H	T	E	E	O	H	T	E	E	O	
CURCULIONIDAE (CONT.)																						
Aoratolcus estriatus Kusch., 1952	+			X	X																	
Wittmerius longirostris Kusch., 1952	+	X	X	X	X																	Pl.2, Fig.3
Erirrhinoides unicolor Blanch., 1851	+									X												
Erirrhininae n. sp. 1	5	X	X		X																	
Erirrhininae n. sp. 2	3	X	X	X	X																	
Erirrhininae gen. indet.	6		X	X	X																	
Aegorhinus vitulus bulbifer Kusch., 1951	4										L											
Aegorhinus sp.	6						X															
Apion spp.	4	X	X	?	?																	
Allomagdalis cryptonyx Kusch., 1950	+	X																				
Berberidicola crenulatus (Blanch., 1851)	3			?	X																	
Berberidicola exaratus (Blanch., 1851)	3			X	X				X													
Berberidicola sp.	3		X																			
Psepholax dentipes (Blanch., 1851)	2				X																	
Acalles tristis Blanch., 1851	5						X	X	X		M											
Acalles cf. sp. 4	2				X																	
Lophocephala fasciolata Blanch., 1851	+			X	X														X	X		Pl.8, Fig.4
Rhyephenes sp.	4					L																
Cryptorhynchinae n. sp. 1	+											X	X	X	X		X	X				
Cryptorhynchinae n. sp. 2	+			X																		
Cryptorhynchinae gen. indet.	4	X	X	X	X			?				X	X	X	X							Pl.8, Fig. 5
Dryophthorus canus (Phil., 1864)	+			X																		
Pentarthrum castaneum (Blanch., 1851)	+	X	X	X	X																	Pl.2, Fig. 2

Table 4. (Continued)

FOSSIL COLEOPTERA TAXA	RANGE	R. CAUNAHUE					P. VARAS RAILROAD					P. VARAS PARK					PUERTO OCTAY					PLATE
		P	L	R			P	L	R			P	L	R			P	L	R			
		H	T	E	E	O	H	T	E	E	O	H	T	E	E	O	H	T	E	E	O	
CURCULIONIDAE (CONT.)																						
Curculionidae gen. indet.	6	X	X	X	X				X				X		X		X		X			

Additional identifiable anatomical parts: M = Metasternum, P = Prosternum, A = Aedeagus, L = Leg.

The elevational range of existing species in the Parque Nacional de Puyehue area is indicated by:

1 = taxa ranging up to 150 m, 2 = taxa ranging up to 650 m, 3 = taxa ranging up to 1000 m,
4 = taxa ranging up to 1200 m, 5 = taxa occurring only between 1000-1200 m, 6 = taxa ranging above 1200 m,
+ = taxa not collected in the modern survey.

Familial order followed by the U.S. Department of Agriculture and U.S. National Museum.
Systematic order of infrafamilial taxa after Blackwelder (1944-1947).

Numbered species correspond to distinct but undescribed species collected during the modern faunal survey. See species list in Appendix A.

Table 5. Table indicating the number of identifiable beetle fossils recovered by sample from the Puerto Octay Site and the number and percent of the fossils identified to family, genus, and species. The table also shows the minimum number of identified taxa and the number and percent of taxa identified to genus and species in each sample. See Plate 1 for stratigraphic position of each sample.

Sample Number	Total Number of Identifiable Beetle Fossils	Total Number(%) Identified to Family	Total Number(%) Identified to Genus	Total Number(%) Identified to Species	Minimum Number of Identified taxa	Number (%) of Taxa Identified to Genus	Number (%) of Taxa Identified to Species
1	25	24 (96)	16 (64)	12 (48)	13	10 (77)	7 (54)
2	2	2 (100)	2 (100)	1 (50)	2	2 (100)	1 (50)
3	2	1 (50)	1 (50)	0 (0)	1	1 (100)	0 (0)
4	1	1 (100)	1 (100)	0 (0)	1	1 (100)	0 (0)
5	1	0 (0)	0 (0)	0 (0)	0	0 (0)	0 (0)
6	1	1 (100)	1 (100)	0 (0)	1	1 (100)	0 (0)
7	1	1 (100)	0 (0)	0 (0)	1	0 (0)	0 (0)
8	0	0 (0)	0 (0)	0 (0)	0	0 (0)	0 (0)
9	3	0 (0)	0 (0)	0 (0)	0	0 (0)	0 (0)
10	3	3 (100)	2 (67)	0 (0)	3	2 (67)	0 (0)
11	10	10 (100)	5 (50)	2 (20)	7	4 (57)	2 (29)
12	42	42 (100)	29 (69)	11 (26)	12	6 (50)	3 (25)
13	51	50 (98)	36 (71)	20 (39)	12	8 (67)	7 (58)
14	50	5 (100)	29 (58)	13 (26)	12	8 (67)	5 (42)
15	62	60 (97)	40 (65)	22 (35)	15	10 (67)	7 (47)
16	51	50 (98)	37 (73)	28 (55)	14	9 (64)	6 (43)
17	51	50 (98)	38 (75)	20 (39)	18	14 (78)	7 (39)
18	28	27 (96)	22 (79)	10 (36)	13	10 (77)	5 (38)
19	37	36 (97)	19 (51)	10 (27)	13	9 (69)	5 (38)
20	52	51 (98)	28 (54)	15 (29)	16	12 (75)	6 (38)

Table 5. (Continued)

Sample Number	Total Number of Identifiable Beetle Fossils	Total Number(%) Identified to Family	Total Number(%) Identified to Genus	Total Number(%) Identified to Species	Minimum Number of Identified taxa	Number (%) of Taxa Identified to Genus	Number (%) of Taxa Identified to Species
21	28	26 (93)	21 (75)	14 (50)	11	7 (64)	4 (36)
22	5	3 (60)	1 (20)	0 (0)	2	1 (50)	0 (0)
23	9	9 (100)	7 (78)	2 (22)	5	3 (60)	1 (20)
24	1	1 (100)	0 (0)	0 (0)	1	0 (0)	0 (0)
25	0	0 (0)	0 (0)	0 (0)	0	0 (0)	0 (0)
TOTAL	516	498 (97)	334 (65)	179 (35)			

Table 6. Families and number of species per family recovered from each site and the percent of each site's assemblage that these species represent.

	FAMILY	PUERTO OCTAY	PUERTO VARAS PARK	PUERTO VARAS RAILROAD	RIO CAUNAHUE
1.	Trachypachidae	0(0)	0(0)	0(0)	1(1)
2.	Carabidae	6(14)	6(22)	7(32)	34(14)
3.	Dytiscidae	1(2)	0(0)	0(0)	3(1)
4.	Hydraenidae	1(2)	1(4)	0(0)	0(0)
5.	Hydrophilidae	6(14)	3(11)	0(0)	3(1)
6.	Ptiliidae	1(2)	0(0)	0(0)	1(1)
7.	Leiodidae	2(5)	0(0)	0(0)	8(3)
8.	Scydmaenidae	0(0)	1(4)	0(0)	2(1)
9.	Staphylinidae	10(23)	2(7)	3(14)	38(16)
10.	Pselaphidae	4(9)	4(15)	0(0)	5(2)
11.	Lucanidae	0(0)	0(0)	0(0)	5(2)
12.	Scarabaeidae	2(5)	1(4)	2(9)	9(4)
13.	Helodidae	2(5)	0(0)	0(0)	4(2)
14.	Clambidae	0(0)	0(0)	0(0)	1(1)
15.	Byrrhidae	0(0)	0(0)	0(0)	1(1)
16.	Elmidae	0(0)	0(0)	0(0)	6(2)
17.	Elateridae	0(0)	0(0)	0(0)	6(2)
18.	Lampyridae	0(0)	0(0)	0(0)	1(1)
19.	Cantharidae	1(2)	0(0)	0(0)	7(3)
20.	Derodontidae	0(0)	0(0)	0(0)	1(1)
21.	Anobiidae	0(0)	0(0)	0(0)	5(2)
22.	Bostrichidae	0(0)	0(0)	0(0)	1(1)
23.	Trogositidae	0(0)	0(0)	0(0)	3(1)
24.	Peltidae	0(0)	0(0)	0(0)	1(1)
25.	Melyridae	0(0)	0(0)	0(0)	2(1)
26.	Nitidulidae	0(0)	0(0)	0(0)	5(2)
27.	Rhizophagidae	0(0)	0(0)	0(0)	1(1)
28.	Cryptophagidae	0(0)	0(0)	0(0)	3(1)
29.	Coccinellidae	0(0)	1(4)	0(0)	7(3)
30.	Lathridiidae	1(2)	0(0)	0(0)	3(1)
31.	Colydiidae	0(0)	0(0)	0(0)	1(1)
32.	Tenebrionidae	0(0)	0(0)	0(0)	1(1)
33.	Salpingidae	0(0)	0(0)	0(0)	3(1)
34.	Oedomeridae	0(0)	0(0)	0(0)	1(1)
35.	Melandryidae	0(0)	1(4)	0(0)	2(1)
36.	Mordellidae	0(0)	0(0)	0(0)	2(1)
37.	Anthicidae	0(0)	0(0)	0(0)	1(1)
38.	Cerambycidae	0(0)	0(0)	0(0)	1(1)
39.	Chrysomelidae	2(5)	0(0)	0(0)	10(4)
40.	Nemonychidae	0(0)	0(0)	0(0)	2(1)
41.	Anthribidae	0(0)	0(0)	0(0)	3(1)

Table 6. (Continued)

FAMILY	PUERTO OCTAY	PUERTO VARAS PARK	PUERTO VARAS RAILROAD	RIO CAUNAHUE
42. Scolytidae	0(0)	0(0)	0(0)	9(4)
43. Attelabidae	0(0)	0(0)	0(0)	2(1)
44. Belidae	0(0)	0(0)	0(0)	1(1)
45. Curculionidae	5(11)	7(26)	10(45)	35(15)
TOTAL	44	27	22	241

Table 7. Additional Insecta and Arachnida recovered from each fossil site.

FOSSIL	PUERTO OCTAY	PUERTO VARAS PARK	PUERTO VARAS RAILROAD	RIO CAUNAHUE
INSECTA				
Plecoptera (stonefly)				X
Hemiptera (bug)				
Saldidae (shorebug)	X			X
Other	X			X
Homoptera				
Cicadellidae (leafhopper)	X			X
Neuroptera				
Corydalidae (dobson fly)				X
Other				X
Trichoptera (caddisfly)	X	X		X
Diptera (fly)				
Chironomidae (midge)	X			X
Other	X			X
Hymenoptera				
Formicidae (ant)	X	X		X
Other	X	X		X
ARACHNIDA				
Chelonethida(pseudoscorpion)				X
Acari (mite)	X	X	X	X
Araneida (spider)	X			X

Trichoptera (caddisflies), Diptera (flies), including Chironomidae (midges), and Hymenoptera, including Formicidae (ants). Two arachnid orders were identified; the Acari (mites) and Araneida (spiders). Most of the insect fossils, other than Coleoptera, and the arachnids were identified by head capsules. The occurrence of these fossils closely followed the uneven distribution of the Coleoptera (Plate 1). Only mites and caddisflies were found in interval 9 through 4 and only mites in interval 25 through 24.

Diatoms of the genera Melosira and Anomoeoneis were observed throughout the section below sample 3 and were exceedingly abundant in samples 24 and 25. Charophyte oogonia were found in interval 3 through 1 and again in interval 23 through 10. Macrospores of the quillwort, Isoetes savatieri Franchet, occurred fairly consistently throughout the section below the upper peat and were extremely abundant in interval 25 through 24.

Paleoenvironmental and Paleoclimatic Interpretations

Interval 25 through 24 (slightly older than 18,000 yr B.P.)

Only one aleocharine (Staphylinidae) fragment was recovered from the water-lain volcanic ash horizon; it carries no environmental significance. No other insects were found, but the abundant diatoms, Melosira and Anomoeoneis, indicate (Bradbury, 1980) that the former spillway contained freshwater of low alkalinity at the time of deposition. Additional information on water quality was provided by abundant macrospores of the quillwort Isoetes savatieri. The plant favors shallow, oligotrophic aquatic habitats (Heusser, 1980).

Unfavorable substrate, water chemistry, oligotrophic conditions, low water temperature, or lack of open water could all explain the absence of an aquatic insect community. However, the almost complete absence of any insect fossils, including terrestrial forms, may suggest that severe climatic conditions were, at least in part, responsible for the sparsity of insects inhabiting the Puerto Octay area when glaciers were beginning to recede from the Central Valley about 18,000 years ago.

Interval 23 through 10 (18,000 to 16,000 yr B.P.)

A marked sedimentological change took place in the abandoned Puerto Octay channel about 18,000 years ago, indicated by an abrupt change from deposition of nearly abiotic volcanic ash to organic-rich sediment containing insect and macroplant fossils. The relatively diverse water beetle assemblage, including the hydrophilids, *Tropisternus setiger*, *Enochrus fulvipes* and *E. vicinus*, suggest that the depositional environment was an areally restricted, quiet, shallow pond. Rich aquatic plant growth is suggested by the dytiscid, *Liodessus delfini* which, according to Doyen and Ulrich (1978), spends at least part of its life cycle within mats of filamentous algae, the hydrophilids, whose larvae are herbaceous on living and decaying aquatic vegetation (Pennak, 1978), and chironomid larvae that are mostly herbaceous on algae and higher aquatic plants (Pennak, 1978). Shallow, well oxygenated water conditions are also reflected by the presence of high numbers of fossil caddisfly frontoclypeal apotomes and chironomid larval heads. The decrease in abundance of *Isoetes savatieri*, increase in unidentifiable vegetable matter, and presence of charophyte oogonia, as compared to the previous interval, indicate that eutrophic conditions were established in the pond.

The pond was probably partially fringed by vegetation, indicated by the occurrence of the cantharid Dysmorphocerus dilaticornis, the curculionid Dasydema hirtella (Plate 2, Figure 4), helodids, and leafhoppers. However, other areas of the shoreline were perhaps muddy and open, reflected by the water-marginal taxa, Agonum sp. 2 (carabid, Plate 5, Figure 2) Gymnochthebius (hydraenid), Hydrochus stolpi (hydrophilid, Plate 4, Figure 2), shorebugs (Saldidae), and the staphylinids, Stenus and Cheilocolpus. Marshy areas were probably present as inferred by the occurrence of the weevil, Lophocephala fasciolata (Plate 8, Figure 4), a phytophagous species host specific on the shrub, Pseudopanax laetivirens (Kuschel, 1981). The shrub is found today in marshy areas in southern Chile (Muñoz S., 1980).

In comparison to the relatively diverse aquatic beetle assemblages recovered from the interval, terrestrial species were exceedingly sparse. The only ground-dwelling taxa were the pselaphids, Dalminiomus, Achillia, and Tyropsis; the staphylinid, Baryopsis, and the weevil, Listroderes dentipennis (Plate 1, Figure 1). Only the latter provides an insight into the paleoenvironment of the region and is particularly significant for reconstructions of conditions during the 18,000 to 16,000-year time period. Kuschel (1981a, 1982) commented that Listroderes is generally found in open, dryish country feeding on cushion mat and rosette plants of all kinds of dicots, especially Umbelliferae, Cruciferae and Compositae. He further noted, however, that L. dentipennis may be one of the very few species in the genus that has become somewhat adapted to forest margins, but that it is unlikely the species could exist in a normal forest with a dense canopy. As Kuschel stated, although L. dentipennis lives today principally on the composite Senecio in forest margins from Valdivia to Isla Wellington (approx. 50° S. lat.), in the latitude of the Lake Region, it is confined to alpine and subalpine areas, broad riverbed lowlands and in open coastal areas. Kuschel's observations were confirmed by ecological information obtained in this study (Appendix A) because L. dentipennis was found only in tundra habitats (Bioassociation V) and in open forest areas inhabited by beetles of Bioassociation III. Its occurrence in this interval suggests that the pond was in an open-ground setting, and explains the absence of arboreal species in the site area between 18,000 and 16,000 years ago.

It is tempting to speculate that a tundra environment existed in the Puerto Octay area between 18,000 and 16,000 years ago because of the lack of arboreal taxa, occurrence of open-ground forms, low species diversities, temporal position of the interval and geographic location of the site. However, no modern analog for the beetle assemblages was observed during the survey of the existing Lake Region faunas. If the sparsity of terrestrial taxa and lack of arboreal elements, coupled with the presence of the open-ground species, Listroderes dentipennis, signifies tundra conditions, the assemblages are significantly different than the alpine tundra beetle faunas, Bioassociation V, identified in Appendix A. The terrestrial element of the fossil assemblages is much more depauperate than the terrestrial beetle faunas living in alpine tundra habitats in the Lake Region today, although L. dentipennis is a major faunal component in, but not restricted to Bioassociation V.

Most of the species recovered from the interval are eurythermic and cosmopolitan existing today in broad geographic and elevational ranges in southern South America. For example, many of the water beetles range from far to the north of the Lake Region to the Magallanes (Moroni, 1973) and also span numerous elevational zones (Appendix A). Listroderes dentipennis, Dasydema hirtella and Agonum sp. 2 also inhabit broad elevational ranges. The observation that most species can exit in cool climates perhaps strengthens the possibility that cold conditions existed in the area 18,000 to 16,000 years ago. However, data in Tables 4, 8, and 9 show that some taxa range only up to 150 m in the Lake Region today, indicating that open-ground conditions, not necessarily cold temperatures, was the main controlling factor. The fossil beetle assemblages may, therefore, represent an early seral stage of biotic succession into the region after temperatures had increased sufficiently to cause glacial retreat from the Central Valley, thereby opening new habitats for colonization. Without a modern analog, it cannot be certain whether climatic regime or habitat availability was ultimately responsible for the composition of the beetle faunas living in the Puerto Octay area during the time interval of 18,000 to 16,000 years ago.

Interval 9 through 4 (Age not precisely known but less than 16,000 yr B.P.

Although the contact is gradational, a significant sedimentological and biological change occurs between interval 9 through 4 and

Table 8. Table indicating the number and percent of Puerto Octay beetle taxa, in each sample, that occur today at restricted elevational ranges in the Lake Region determined through study of the modern fauna (Appendix A). See Plate 1 for stratigraphic position of each sample.

Sample Number	Minimum Number of Taxa	Number (%) Taxa Not Collected in Modern Survey	Number (%) Taxa Ranging up to 150 m	Number (%) Taxa Ranging up to 650 m	Number (%) Taxa Ranging up to 1000 m	Number (%) Taxa Ranging up to 1200 m	Number (%) Taxa Occurring Only Between 1000-1200 m	Number (%) Taxa Ranging Above 1200 m	Total Number (%) Taxa Occurring Only Below 650 m	Total Number (%) Taxa Occurring Only Below 1000 m	Total Number (%) Taxa Occurring Only Below 1200 m
PUERTO OCTAY											
1	13	1 (8)	0 (0)	3 (23)	2 (15)	4 (31)	0 (0)	3 (23)	3 (23)	5 (38)	9 (69)
2	2	1 (50)	0 (0)	1 (50)	0 (0)	0 (0)	0 (0)	0 (0)	1 (50)	1 (50)	1 (50)
3	1	0 (0)	0 (0)	0 (0)	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	1 (100)
4	1	0 (0)	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	1 (100)	1 (100)	1 (100)
5	0	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
6	1	0 (0)	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	1 (100)	1 (100)	1 (100)
7	1	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)
B	0	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
9	0	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
10	3	0 (0)	0 (0)	1 (33)	0 (0)	1 (33)	0 (0)	1 (33)	1 (33)	1 (33)	2 (67)
11	7	0 (0)	1 (14)	0 (0)	0 (0)	3 (43)	0 (0)	3 (43)	1 (14)	1 (14)	4 (57)
12	12	0 (0)	1 (8)	1 (8)	1 (8)	2 (17)	0 (0)	4 (33)	2 (17)	3 (25)	5 (42)
13	12	1 (8)	1 (8)	2 (17)	0 (0)	2 (17)	0 (0)	6 (50)	3 (25)	3 (25)	5 (42)
14	12	1 (8)	1 (8)	1 (8)	1 (8)	3 (25)	0 (0)	5 (42)	2 (17)	3 (25)	6 (50)
15	15	2 (13)	1 (7)	2 (13)	0 (0)	3 (20)	0 (0)	5 (23)	3 (20)	3 (20)	6 (40)
16	14	2 (14)	0 (0)	1 (7)	0 (0)	4 (29)	0 (0)	7 (50)	1 (7)	1 (7)	5 (36)
17	18	2 (11)	1 (6)	1 (6)	3 (17)	4 (22)	0 (0)	7 (39)	2 (11)	5 (28)	9 (50)
18	13	1 (8)	1 (8)	2 (15)	0 (0)	4 (31)	0 (0)	5 (38)	3 (23)	3 (23)	7 (54)
19	13	1 (8)	1 (8)	4 (31)	0 (0)	3 (23)	0 (0)	3 (23)	5 (38)	5 (38)	8 (62)
20	16	2 (13)	0 (0)	2 (13)	1 (6)	5 (31)	0 (0)	5 (31)	2 (13)	3 (19)	8 (50)
21	11	1 (9)	1 (9)	0 (0)	2 (18)	3 (27)	0 (0)	3 (27)	1 (9)	3 (27)	6 (55)
22	2	0 (0)	0 (0)	0 (0)	0 (0)	1 (50)	0 (0)	1 (50)	0 (0)	0 (0)	1 (50)
23	5	0 (0)	0 (0)	0 (0)	1 (20)	2 (40)	0 (0)	2 (40)	0 (0)	1 (20)	3 (60)
24	1	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)
25	0	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)

Table 9. Table indicating the number and percent of Puerto Octay beetle species, in each sample, that occur today at restricted elevational ranges in the Lake Region determined through study of the modern fauna (Appendix A). See Plate 1 for stratigraphic position of each sample.

Sample Number	Number (%) Taxa Identified to Species	Number (%) Species not Collected in Modern Survey	Number (%) Species Ranging up to 150 m	Number (%) Species Ranging up to 650 m	Number (%) Species Ranging up to 1000 m	Number (%) Species Ranging up to 1200 m	Number (%) Species Occurring Only Between 1000-1200 m	Number (%) Species Ranging Above 1200 m	Total Number (%) Species Occurring Only Below 650 m	Total Number (%) Species Occurring Only Below 1000 m	Total Number (%) Species Occurring Only Below 1200 m
PUERTO OCTAY											
1	7 (54)	1 (14)	0 (0)	3 (43)	1 (14)	1 (14)	0 (0)	1 (14)	3 (43)	4 (57)	5 (71)
2	1 (50)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
3	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
4	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
5	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
6	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
7	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
8	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
9	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
10	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
11	2 (29)	0 (0)	1 (50)	0 (0)	0 (0)	1 (50)	0 (0)	0 (0)	1 (50)	1 (50)	2 (100)
12	3 (25)	0 (0)	1 (33)	1 (33)	0 (0)	1 (33)	0 (0)	0 (0)	2 (67)	2 (67)	3 (100)
13	7 (58)	1 (14)	1 (14)	2 (29)	0 (0)	1 (14)	0 (0)	2 (29)	3 (43)	3 (43)	4 (57)
14	5 (42)	1 (20)	1 (20)	1 (20)	0 (0)	1 (20)	0 (0)	1 (20)	2 (40)	2 (40)	3 (60)
15	7 (47)	2 (29)	1 (14)	2 (29)	0 (0)	1 (14)	0 (0)	1 (14)	3 (43)	3 (43)	4 (57)
16	6 (43)	2 (33)	0 (0)	1 (17)	0 (0)	2 (33)	0 (0)	1 (17)	1 (17)	1 (17)	3 (50)
17	7 (39)	2 (29)	1 (14)	1 (14)	0 (0)	2 (29)	0 (0)	1 (14)	2 (29)	2 (29)	4 (57)
18	5 (38)	1 (20)	1 (20)	1 (20)	0 (0)	2 (40)	0 (0)	0 (0)	2 (40)	2 (40)	4 (80)
19	5 (38)	1 (20)	1 (20)	2 (40)	0 (0)	1 (20)	0 (0)	0 (0)	3 (60)	3 (60)	4 (80)
20	6 (38)	2 (33)	0 (0)	1 (17)	0 (0)	2 (33)	0 (0)	1 (17)	1 (17)	1 (17)	3 (50)
21	4 (36)	1 (25)	1 (25)	0 (0)	0 (0)	1 (25)	0 (0)	1 (25)	1 (25)	1 (25)	2 (50)
22	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
23	1 (20)	0 (0)	0 (0)	0 (0)	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	1 (100)
24	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
25	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)

interval 23 through 10. The high organic content of the sediment observed in interval 23 through 10 decreased upward, associated with increased amounts of volcanic ash in interval 9 through 4. The only insect fossils recovered from interval 9 through 4 were Trichoptera and pselaphids (e.g., Dalminiomus), neither of which provides much paleoenvironmental information, although the former suggests that the site was hygric. The high numbers of Isoetes savatieri and absence of charophyte oogonia imply that oligotrophic conditions returned to the Puerto Octay pond.

The dates bracketing this interval are extremely important because they indicate either that a hiatus exists somewhere in the interval or that the interval is highly compressed. In either case, this part of the sequence is of no value for paleoenvironmental and paleoclimatic reconstructions because of poor age control, potential long time span involved and scarcity of fossils. As will be shown later, however, the recognition of depositional anomalies in the upper part of the Puerto Octay section has direct bearing on the inferred paleoclimatic history of the Lake Region proposed by earlier workers.

Interval 3 through 1 (1,200 yr B.P. to Present)

The presence of Enochrus (hydrophilid), organic-rich sediment (peat), and charophyte oogonia and the absence of quillwort macrospores, suggest the rejuvenation of eutrophic conditions at the Puerto Octay Site by at least 1,200 years ago. The occurrence of Enochrus suggests that water depths were probably extremely shallow and, perhaps, only an ephemeral marsh existed at the site throughout this time, similar to today's setting. The ground-dwelling fauna inhabiting the shorelines consisted of staphylinids, including *Stenus* spp., *Philonthus* (*Edeius*) *punctipennis* and *Nomimoceras marginicollis* (Plate 5, Figure 4); *Gymnochthebius* (hydraenid); *Dalminiomus* (pselaphid) and the carabids, *Bradycellus* (*Goniocellus*) sp. and *Bradycellus* (*Stenocellus*) sp. A fairly diverse floral community probably existed in the area, suggested by the occurrence of the chrysomelids, cf. *Crepidodera* sp. 1, which was found only on *Fuchsia magellanica* during the survey of the existing fauna, and *Chaetocnema*, which was commonly found on *Amomyrtus luma* during the survey. Lathridiids, existing today in the Lake Region on a number of plants including *Nothofagus dombeyi*, cicadellid homopterans and Hemiptera also indicate a relatively well-established plant community in proximity to the site.

Aquatic conditions, similar to those observed today, were apparently established at the Puerto Octay Site by at least 1,200 years ago. However, at the present time, the site is surrounded largely by open pasture and farmland, not bearing a relatively diverse plant community as is inferred from beetle species present in the interval. As stated earlier, historical accounts have shown that the Lake Region was densely forested prior to European settlement in the early 19th century. The fossil record seems to confirm that the last deforestation of the Central Valley occurred in relatively recent time.

Most of the beetle taxa recovered from the interval do not range above 1000 m in the Lake Region today and a high percentage of the species occur only below 650 m (Tables 4, 8 and 9). It seems likely, therefore, that climatic conditions similar to today were established in the Central Valley by at least and, as will be shown later, probably much earlier than 1,200 years ago.

Discussion

Although Mercer (1976) and Porter (1981) expressed conflicting opinions regarding exactly when and for how long the Puerto Octay channel was an active spillway of proglacial Lago Llanquihue, both agreed that deposition of lacustrine sediments began in the depression after the spillway was abandoned when lake level fell during glacial recession. The date of the basal organic-rich sediment in the channel was taken as the age of the initial retreat of the glacier from the western shore of Lago Llanquihue after the late glacial maximum (Mercer, 1976; Porter, 1981). Both authors apparently inferred that the channel is floored by peat or gyttja probably because of Heusser's (1974) initial description of the site in which he reported gravel beneath gyttja in the bottom of his core. Gravel was not encountered at the base of any of the cores taken for this study from the abandoned spillway. All cores bottomed in a siliceous silt believed to be volcanic ash deposited in an oligotrophic lacustrine environment of low alkalinity, implied by the occurrence, in great abundance, of the freshwater diatoms, *Melosira* and *Anomoeones*, and *Isoetes* macrospores. The pond initially occupying the channel was essentially devoid of insects and was probably in a treeless setting inhabited by few terrestrial organisms. Climatic conditions may have been severe during that time. The thickness of the basal silt is not known and the type of sediments below the silt has not been determined. The age of the organic-rich sediment above the silt does not, therefore, provide a date for the onset of recession of the glacier from the western shore of Lago Llanquihue but indicates only that retreat had begun prior to 18,170 yr B.P. The date (about 19,500 yr B.P.) of the late glacial maximum is well established (Mercer, 1976; Porter, 1981), so recession of the glacier had to have begun sometime between 19,500 and 18,170 years ago.

Between 18,000 and 16,000 years ago, the abandoned spillway, at least in the sampled area, was occupied by a shallow, eutrophic, probably areally restricted pond containing abundant aquatic vascular plants and filamentous algae supporting a relatively diverse aquatic insect fauna. Hygrophilous vegetation was present in some of the pond marginal areas, although open, muddy shores were also common. Marshy areas were probably present adjacent to the pond, but essentially treeless, open-ground habitats characterized the regional setting in the Puerto Octay area.

Insufficient information is available regarding the meaning of the species associations and ecological requirements of the beetle species recovered from interval 23 through 10 to make an unequivocal statement about the climatic conditions during that time. The absence of arboreal beetle taxa, occurrence of open-ground forms and low beetle diversity may indicate that treeless conditions in a tundra environment existed in the site area between 18,000 and 16,000 years ago. It is equally plausible, however, that the beetle assemblage may represent an early seral stage of biotic succession into the area. Heusser's (1974) pollen diagram from the Puerto Octay section provides additional paleoenvironmental information. It is difficult to ascertain from the diagram why he divided the 18,000 to 16,000 yr B.P. interval into two, L-5 (lower) and L-4 (upper), pollen zones. The nonarboreal component of the spectra is consistently high (80 to 90 percent) throughout the entire interval and no major shifts in the percentages of other taxa are noted in the diagram. He interpreted the pollen spectra of zone L-4 to indicate a climatic amelioration and advance of beech forest around Puerto Octay even through the values for Nothofagus were extremely low and only traces of other tree pollen were present. In contrast, he interpreted the low values of Nothofagus in zone L-5 (even through the values were slightly greater than in zone L-4) to indicate a return of climate to glacial conditions. There is no indication from the beetles that climatic amelioration occurred or that trees invaded the Puerto Octay area during deposition of zone L-4. It is suggested here that there is little evidence of this in the pollen record either, and it is proposed that the pollen diagram indicates, similar to the beetles, that essentially treeless, perhaps tundra, conditions prevailed throughout the 18,000 to 16,000 year period.

It should be pointed out that Heusser had only one date, 17,370 yr B.P., from the base of the Puerto Octay section on which to base his interpretations. He believed that the upper boundary of zone L-5 dated from 12,000 yr B.P. because he correlated, by pollen stratigraphy, the Puerto Octay section with more well-dated sequences at Alerce located about 10 km northeast of Puerto Montt (Heusser, 1966a). The correlation proved to be inaccurate because the assumed date of 12,000 yr B.P. for the top of zone L-5 is much younger than the radiocarbon date of 16,000 yr B.P. obtained during this study from about the same stratigraphic position. Furthermore, Heusser (1974) correlated the Puerto Octay L-4 and L-5 zones with pollen zones L-4 and L-5 at the Puerto Varas Railroad Site; correlation of the pollen spectra from the two sites is difficult to accept because zone L-4 at the Puerto Varas Railroad Site contains about 68 percent Nothofagus pollen, whereas zone L-4 at the Puerto Octay Site contains only about 19 percent. Arboreal percentages are also much greater in the Puerto Varas Railroad L-5 zone than in zone L-5 at Puerto Octay. If the 16,000 yr B.P. date is accurate for the top of zone L-5 at Puerto Octay, both pollen zones L-5 and L-4 at Puerto Octay are older than the basal sediments at the Puerto Varas Railroad Site and correlation is not possible.

The 60-cm thick section within interval 9 through 4 is bracketed by the dates of 16,000 yr B.P. and 1,190 yr B.P. This modest amount of sediment deposited over a considerable length of time implies that a hiatus exists somewhere within the interval or that the section is compressed, probably as a result of very slow sedimentation rates, or both. About 16,000 years ago the eastern outlet (Rio Petrohue) of Lago Llanquihue opened (Mercer, 1976), resulting in a fall of lake level. Perhaps the Puerto Octay pond also drained at that time leaving very little water in the channel. A depositional hiatus may have resulted and sedimentation rates would have declined. The meager fossil evidence suggests that the site was, at least at times, hygric but apparently did not support an aquatic insect fauna or provide a depositional environment for terrestrial beetles. Consequently, no paleoclimatic information is available from the Puerto Octay Site from the 16,000 to 1,190 yr B.P. time period. Heusser (1974) divided the portion of the

Puerto Octay section equivalent to interval 9 through 4 into two pollen zones, L-6 and L-7. He inferred, as a result of the previously mentioned miscorrelation to the Alerce sequences, the base of zone L-6 (top of the zone L-5) to be 12,000 years old. In addition, he interpreted the top of zone L-6 to be 11,000 years old and the top of zone L-7 to date from 10,000 yr B.P. The radiocarbon date of 1,190 yr B.P. obtained during this study was from about the same stratigraphic level as Heusser's inferred 10,000 yr B.P. date. Pollen zone L-7, inferred by Heusser to span the 11,000 to 10,000 yr B.P. time interval, is particularly important because he interpreted the spectra from the zone to indicate a major climatic deterioration during that time. A discussion of the importance of the incompatibility of Heusser's pollen stratigraphy correlations and radiocarbon chronology for this critical time period will be deferred until later.

Heusser (1974) named the upper 30 cm (interval 3 through 1) of the Puerto Octay sequence pollen zone P-1. Beetle assemblages from the interval reflect deposition in a marshy environment surrounded by a fairly diverse floral community. Climatic conditions were probably similar to those of today. Heusser's pollen diagram of the interval, dominated by arboreal and aquatic plants, is consistent with the interpretation. However, Heusser thought, again because of pollen zone correlation with sections at Alerce, that the interval was deposited between 10,000 and 9,000 yr B.P., and he believed the record to indicate early postglacial invasion of tree taxa into the Central Valley. In actuality, the sediments were deposited after 1,190 years ago.

PUERTO VARAS PARK SITE

Location, Site Description, and Radiocarbon Chronology

The record of post-late glacial maximum ice-marginal fluctuations in the Lake Region is documented along the southwest margin of Lago Llanquihue (Figures 1 and 4). In and near the city of Puerto Varas, peat is overlain by lake sediment. Five such sequences have been identified, of which two were sampled for this study. The peats represent times of low lake level when organic sediments accumulated at elevations as low as 60 m (10 m above present lake level) around the borders of the Puerto Varas embayment. Advancing ice blocked the eastern outlet of Lago Llanquihue, the Rio Petrohue, resulting in lake level rise and cessation of peat accumulation. Mercer (1976) proposed that the sedimentary sequences are evidence of one advance culminating about 13,000 years ago. He later revised the date of the culmination to about 14,500 yr B.P. (Mercer, 1984a). Porter (1981), however, in consideration of elevational and age differences of the peats, suggested that a more complex history of ice-marginal fluctuations is indicated by the drowned peats and postulated two episodes of advance, one culminating about 15,000 to 14,500 years ago and the about 13,000 years ago. The Puerto Varas sites are significant because it is important to determine the time of the last glacial advance or advances into the Region. Determining the timing of the last glacial advance would provide a datum point for interpreting the rapidity of deglaciation and presumably the rate of climatic amelioration in the Region.

The Puerto Varas Park Site (Figures 1, 4, 8, 9 and 10), a north-facing roadcut, is exposed in Bella Vista Park. The site is located on route CH225 about 200 m east of the Bella Vista Hotel between Puerto Varas and the village of Puerto Chico (lat. 41°19'10"S., long. 72°58'30"W.). Approximately 10 m of sand, interpreted to be a lahar deposit by Porter (1981), overlies at least 25 cm of laminated lacustrine silt in the upper part of the section (Plate 1 and Table 10). The lahar is in turn overlain by about 2 m of tephra and loess. Beneath the lacustrine silts, at an elevation of 60.1 m or 9.1 m above present lake level, is a peat horizon 10 cm thick (Porter, 1981). In excess of 2 m of lacustrine silts and clays occur beneath the peat. The lacustrine silts were barren of fossil beetles and only the peat-horizon was sampled. A radiocarbon date (Plate 1, Table 10 and Appendix D) of 15,715±440 ^{14}C yr B.P. (GX-5275) was obtained for the upper 5 cm of peat.

Analysis of the Fossil Assemblages

Representatives (Plate 1) of three orders of insects and one order of arachnids were identified from the two (PV1 and PV2) samples collected at the Puerto Varas Park Site. No mollusks or ostracods were found in either of the samples.

Figure 8. Photograph of the Puerto Varas Park section exposed in Bella Vista Park taken from the north across route CH225. Allan Ashworth (kneeling) is examining the 15,700-year-old peat horizon. Most of the overgrown sediment above the peat is lahar and beneath it lacustrine clays. Left to right are: Allan Ashworth, Howard Mooers, Judy Mercer, Jane Soons and John Mercer.

Figure 9. Photograph of Allan Ashworth sampling the Puerto Varas Park peat horizon. Route CH225 and Lago Llanquihue are in the background. Howard Mooers is assisting Ashworth.

Figure 10. Photograph of part of the section at the Puerto Varas Park Site showing the upper peat horizon (dark) and underlying lacustrine clays. Tape is 65 cm long.

Table 10. Lithologic description of the Puerto Varas Park Section.

Location. North-facing roadcut on highway CH225 about 200 m east of the Bella Vista Hotel, Puerto Varas (lat. 41°19'10"S., long. 72°58'30"W.). Excavation made at Bella Vista Park (Figure 4).

Sample Numbers	Description	Thickness (cm)
Not sampled	Covered interval consisting mostly of medium sand containing angular grains of various lithologies.	approx. 1000
Not sampled	Dark gray (7.5Y 3/2), rhythmically bedded silt.	25
1-2	Very dark grayish brown (2.5Y 3/2), peaty silt. Under 5 cm (sample 1) dated at 15,715±440 ^{14}C yr B.P. (GX-5275).	10
Not sampled	Dark grayish brown (2.5Y 4/2), slightly sandy silt.	80
Not sampled	Gray, finely laminated, rhythmically bedded silt.	90
Not sampled	Covered to road level	approx. 250
Base of excavation		

Of the 302 identifiable beetle fossils recovered from the Puerto Varas Park Site (Table 4 and 11), 302 (100 percent) were identified to family, 255 (84 percent) to genus and 171 (57 percent) to species. At least 27 species representing 10 beetle families, both aquatic and terrestrial, were recognized. Ninety-three percent of the taxa were identified by direct comparison to specimens collected during the modern faunal survey. The assemblages were dominated by five beetle families (Table 6). Twenty-six percent of the species were curculionoids, 22 percent carabids, 15 percent pselaphids, 11 percent hydrophilids and 7 percent staphylinids.

The two samples collected at this site possessed similar assemblages of beetles but the upper sample was slightly more diverse. The assemblages were characterized by low species and family diversities but high numbers of individuals, particularly, the carabid Agonum sp. 2, the hydrophilid Hydrochus stolpi, and the curculionid Listroderes dentipennis (Plate 1). Other significant beetle taxa particularly weevils, were also found in the samples.

Representatives (Table 7) of two orders of insects, Trichoptera and Hymenoptera, including Formicidae, were recovered from the Puerto Varas Park Site in addition to the Coleoptera. Of the arachnids, only mites were found. As with the beetles, the upper sample exhibited a greater diversity of other insect groups than the lower sample. No arachnids and only Trichoptera were recovered from the lower sample (Plate 1). Macroplant fossils were observed in the samples but no attempt was made to identify them.

Table 11. Table indicating the number of identifiable beetle fossils recovered by sample from the Puerto Varas Park Site and the number and percent of the fossils identified to family, genus, and species. The table also shows the minimum number of identified taxa and the number and percent of taxa identified to genus and species in each sample. See Plate 1 for stratigraphic position of each sample.

Sample Number	Total Number of Identifiable Beetle Fossils	Total Number(%) Identified to Family	Total Number(%) Identified to Genus	Total Number(%) Identified to Species	Minimum Number of Identified taxa	Number (%) of Taxa Identified to Genus	Number (%) of Taxa Identified to Species
1	204	204 (100)	166 (81)	97 (48)	25	16 (64)	9 (36)
2	98	98 (100)	89 ((91)	74 (76)	15	10 (67)	4 (27)
TOTAL	302	302 (100)	255 (84)	171 (57)			

The beetle assemblage from sample PV1 was subjected to cluster analysis to determine its similarity to fossil assemblages from different ages and other localities and to beetle faunas living today (Appendix A) in the Lake Region. Assemblage PV1 (15,700 yr B.P.) grouped with the basal Rio Caunahue beetle assemblage from sample PD6 (12,800 yr B.P.) to form subcluster F_1 (Figure 11). This association is somewhat misleading, however, because the PD6 assemblage is actually more similar to the beetle assemblages from Rio Caunahue samples BS-A3, 42 and PDO as seen on the trellis diagram. This illustrates the usefulness of the trellis diagram in comparing samples between clusters. The assemblages in subcluster F_1 show similarities to beetle faunas in Bioassociation II. The PD6 assemblages is, however, about equally similar to beetle faunas in Bioassociations II and III and shows little resemblance to beetle faunas in Bioassociations IV and V, whereas, the PV1 assemblages is most similar to beetle faunas in Bioassociation II and shows little resemblance to beetle faunas in Bioassociation III, IV and V.

Paleoenvironmental and Paleoclimatic Interpretations

The 15,700-year-old Puerto Varas Park assemblages are less diverse than, especially in aquatic insects, but similar to the assemblages recovered from Puerto Octay interval 23 through 10 (18,000 to 16,000 yrs B.P.). The peaty nature of the sediment and presence of caddisflies and Enochrus, including E. vicinus, indicate that either an areally restricted, quiet, shallow pond or marsh existed at the Puerto Varas Park Site 15,700 years ago. Emergent vegetation, reflected by the

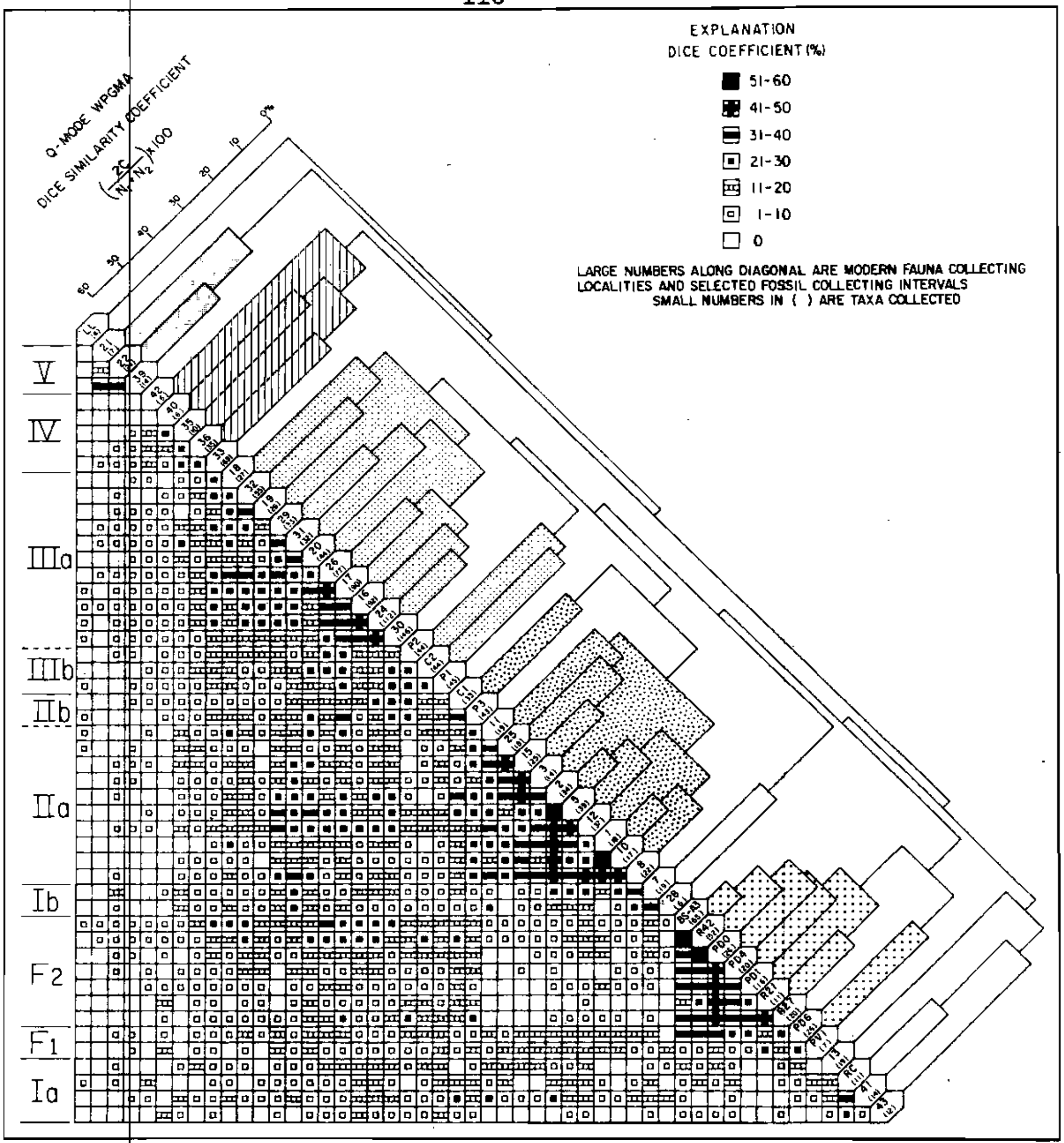


Figure 11. Similarity matrix (trellis diagram) and binary tree (dendrogram) showing patterns of similarity among 41 present-day, beetle-fauna, collecting localities and 9 fossil assemblages. See Appendix A for locations of modern fauna collecting localities and Plate 1 for stratigraphic position of the fossil assemblages. Similarity is measured by Dice's Coefficient. Large numbers along diagonal are collecting localities or fossil sample numbers, small numbers in parentheses are taxa collected. The pattern of each square in the matrix indicates the degree of similarity, as depicted in the explanation. The dendrogram shows the order of clustering by WPGMA. The major groups (clusters), I-V (modern fauna) and F_1 and F_2 (fossil assemblages), are indicated to the left of the matrix and are separated by patterns on the dendrogram. See text and Appendix A for further explanation and interpretations.

scydmaenids, scarabaeids and abundant coccinellids, grew in the marshy site area. Water-marginal areas, inhabited by the carabids, *Bembidion*, including *B. marginatus* and *Agonum*, including *A.* sp. 2; *Gymnochthebius* (hydraenid); *Hydrochus stolpi* (dytiscid) and *Stenus* (staphylinid), were probably, at least in part, muddy, open and bare. No strictly arboreal species were found but sparse, shrubby vegetation, possibly including *Nothofagus antarctica* may have existed near the site supporting *Dasydema hirtella* (curculionid) and the melandryid, *Orchesia* sp. 1. The ground-dwelling fauna was depauperate, consisting of the pselaphids, *Dalminiomus*, *Achillia*, and *Tyropsis*; *Listroderes* (curculionid), including *L. dentipennis* and cf. *Creobius eydouxi* (carabid). More than one species of *Listroderes* occurred in this interval, but *L. dentipennis*, found in comparatively high numbers, was, by far, the dominant species in the assemblages. As stated earlier, the occurrence of *L. dentipennis* in abundance, as well as the presence of other *Listroderes*, suggests that open-ground, probably treeless, conditions existed in the site area. A similar setting is suggested by *Listronotus bonariensis* (curculionid) because today the species lives in open, damp places where its larvae mine grass stems (Kuschel, 1982).

Because the Puerto Varas Park and Puerto Octay interval 23 through 10 assemblages are similar, it is inferred that similar environmental and climatic conditions existed at the two sites during their respective times of deposition. The climate and environment of the Central Valley, reflected by the 18,000- to 16,000-year-old Puerto Octay assemblages, appear to have been stable until at least 15,700 yr B.P., as indicated by the Puerto Varas Park fossils. No information was gained from the

Puerto Varas Park assemblages to either strengthen or preclude the speculation that tundra conditions existed in the Central Valley between 18,000 and 15,700 years ago. As with the Puerto Octay assemblages, most taxa recovered from Puerto Varas Park either occur below 150 m in the Lake Region or range to or extend above timberline (Tables 4, 12, and 13). Again the only conclusion that can be drawn from the data is that open-ground habitats dominated the regional setting in the Puerto Varas Park area 15,700 years ago.

To test the interpretation, the Puerto Varas Park assemblage from sample PV1 was subjected to the clustering procedure outlined previously. As shown in the trellis diagram (Figure 11), the assemblage is most similar to the beetle faunas of Bioassocation II, those living in disturbed lowland forest habitats, and exhibits very little similarity in species composition to faunas in Bioassociation III, IV, and V. This corroborates the inference that open-ground conditions were necessary for existence of the beetle fauna living the Puerto Varas Park area 15,700 years ago. Because open-ground conditions exist today in the Central Valley as a result of recent anthropogenic disturbance of natural forest habitats, it seems logical to suppose that climatic conditions were too severe to support a well developed floral and associated beetle fauna 18,000 to at least 15,700 years ago. However, the Puerto Varas Park assemblages and, as shown earlier, the Puerto Octay assemblages, are significantly different than the alpine tundra beetle faunas living in the Region today. This is confirmed by cluster analysis because the PV1 assemblage is only slightly similar in species

Table 12. Table indicating the number and percent of Puerto Varas Park and Puerto Varas Railroad beetle taxa, in each sample, that occur today at restricted elevational ranges in the Lake Region determined through study of the modern fauna (Appendix A). See Plate 1 for stratigraphic position of each sample.

Sample Number	Minimum Number of Taxa	Number (%) Taxa Not Collected in Modern Survey	Number (%) Taxa Ranging up to 150 m	Number (%) Taxa Ranging up to 650 m	Number (%) Taxa Ranging up to 1000 m	Number (%) Taxa Ranging up to 1200 m	Number (%) Taxa Occurring Only Between 1000-1200 m	Number (%) Taxa Ranging Above 1200 m	Total Number (%) Taxa Occurring Only Below 650 m	Total Number (%) Taxa Occurring Only Below 1000 m	Total Number (%) Taxa Occurring Only Below 1200 m
PUERTO VARAS RAILROAD											
1	9	0 (0)	0 (0)	1 (11)	0 (0)	3 (33)	1 (11)	4 (44)	1 (11)	1 (11)	5 (56)
2	5	0 (0)	0 (0)	0 (0)	0 (0)	2 (40)	1 (20)	2 (40)	0 (0)	0 (0)	3 (60)
3	5	0 (0)	0 (0)	0 (0)	0 (0)	2 (40)	1 (20)	1 (20)	0 (0)	0 (0)	3 (60)
4	3	0 (0)	0 (0)	0 (0)	0 (0)	1 (33)	0 (0)	1 (33)	0 (0)	0 (0)	1 (33)
5	1	0 (0)	0 (0)	0 (0)	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	1 (100)
6	4	0 (0)	0 (0)	0 (0)	1 (25)	2 (50)	0 (0)	1 (25)	0 (0)	1 (25)	3 (75)
7	0	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
8	1	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
9	3	0 (0)	0 (0)	0 (0)	0 (0)	1 (33)	1 (33)	1 (33)	0 (0)	0 (0)	2 (67)
10	5	1 (20)	0 (0)	0 (0)	0 (0)	1 (20)	1 (20)	0 (0)	0 (0)	0 (0)	2 (40)
11	3	0 (0)	0 (0)	0 (0)	0 (0)	1 (33)	0 (0)	2 (67)	0 (0)	0 (0)	1 (33)
12	5	0 (0)	0 (0)	0 (0)	0 (0)	3 (60)	0 (0)	2 (40)	0 (0)	0 (0)	3 (60)
PUERTO VARAS PARK											
1	25	2 (8)	1 (4)	2 (8)	1 (4)	9 (36)	0 (0)	9 (36)	3 (12)	4 (16)	13 (52)
2	15	1 (7)	1 (7)	1 (7)	1 (7)	5 (33)	0 (0)	4 (27)	2 (13)	3 (20)	8 (53)

Table 13. Table indicating the number and percent of Puerto Varas Park and Puerto Varas Railroad beetle species, in each sample, that occur today at restricted elevational ranges in the Lake Region determined through study of the modern fauna (Appendix A). See Plate 1 for stratigraphic position of each sample.

Sample Number	Number (%) Taxa Identified to Species	Number (%) Species not Collected in Modern Survey	Number (%) Species Ranging up to 150 m	Number (%) Species Ranging up to 650 m	Number (%) Species Ranging up to 1000 m	Number (%) Species Ranging up to 1200 m	Number (%) Species Occurring Only Between 1000-1200 m	Number (%) Species Ranging Above 1200 m	Total Number (%) Species Occurring Only Below 650 m	Total Number (%) Species Occurring Only Below 1000 m	Total Number (%) Species Occurring Only Below 1200 m
PUERTO VARAS RAILROAD											
1	3 (33)	0 (0)	0 (0)	1 (33)	0 (0)	1 (33)	1 (33)	0 (0)	1 (33)	1 (33)	3 (100)
2	3 (60)	0 (0)	0 (0)	0 (0)	0 (0)	1 (33)	1 (33)	1 (33)	0 (0)	0 (0)	2 (67)
3	2 (40)	0 (0)	0 (0)	0 (0)	0 (0)	1 (50)	1 (50)	0 (0)	0 (0)	0 (0)	2 (100)
4	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
5	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	1 (100)
6	3 (75)	0 (0)	0 (0)	0 (0)	1 (33)	1 (33)	0 (0)	1 (33)	0 (0)	1 (33)	2 (67)
7	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
8	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
9	2 (67)	0 (0)	0 (0)	0 (0)	0 (0)	1 (50)	1 (50)	0 (0)	0 (0)	0 (0)	2 (100)
10	3 (60)	1 (33)	0 (0)	0 (0)	0 (0)	1 (33)	1 (33)	0 (0)	0 (0)	0 (0)	2 (67)
11	2 (67)	0 (0)	0 (0)	0 (0)	0 (0)	1 (50)	0 (0)	1 (50)	0 (0)	0 (0)	1 (50)
12	2 (40)	0 (0)	0 (0)	0 (0)	0 (0)	2 (100)	0 (0)	0 (0)	0 (0)	0 (0)	2 (100)
PUERTO VARAS PARK											
1	9 (36)	2 (22)	1 (11)	0 (0)	0 (0)	5 (56)	0 (0)	1 (11)	1 (11)	1 (11)	6 (67)
2	4 (27)	1 (25)	1 (25)	0 (0)	0 (0)	1 (25)	0 (0)	1 (25)	1 (25)	1 (25)	2 (50)

composition to faunas of Bioassociation V. As with the assemblages from the 18,000 to 16,000 yr B.P. Puerto Octay interval, the Puerto Varas Park assemblages could indicate either severe climatic conditions or represent an early seral stage of biotic succession.

Discussion

The 15,700-year-old Puerto Varas Park beetle assemblages are similar to the 18,000 to 16,000 yr B.P. Puerto Octay assemblages. Open-ground, treeless, perhaps tundra habitats appear to have existed in the Central Valley from at least 18,000 to 15,700 years ago. But, as with the Puerto Octay assemblages, the Puerto Varas Park fossils may be indicative of an early seral stage of biotic succession into low elevation areas in the Lake Region and not severe climatic conditions. No pollen diagrams have been published from the Puerto Varas Park Site. Interpretation of the depositional history of the Puerto Varas Park Site will be included with discussion of the Puerto Varas Railroad record.

PUERTO VARAS RAILROAD SITE

Location, Site Description, and Radiocarbon Chronology

The Puerto Varas Railroad Site (Figures 1, 4, 12, 13 and 14) is a north-facing roadcut on route V-55 (Calle San Jose) on the western outskirts of Puerto Varas beneath the railway bridge (lat. 41°18'50"S., long. 72°59'20"W.). Approximately 440 cm of poorly consolidated sand and silt (Plate 1 and Table 14) overlie a 10 cm thick peat horizon at the site. The peat is at an elevation of 66.2 m or 15.2 m above present lake level (Porter, 1981). Heusser (1974) described the stratigraphy and pollen sequence of the site, interpreting the sands and silts to be volcanic ash, lapilli, and tuff. They were later interpreted to be lahar deposits (Porter, 1981). Heusser (1974) encountered 240 cm of gyttja underlain by gravel beneath the peat horizon. Reexcavation during this study exposed 150 cm of gyttja beneath the peat before digging was terminated. The gyttja and peat were sampled for beetle fossils.

A date of 14,060±450 ^{14}C yr B.P. (GX-5507) was obtained from the peat (Plate 1, Table 14 and Appendix D). This date is consistent with others, 13,300±550 ^{14}C yr B.P. (GX-2947) (Mercer, 1976) and 14,250±400 ^{14}C yr B.P. (GX-2948) (Heusser, 1974) for the horizon. Adequate organic material was not available to obtain a radiocarbon date from the basal part of the sequence. However, in an earlier study, Mercer (1972a,

Figure 12. Photograph of the north-facing Puerto Varas Railroad Site roadcut exposure taken from across Calle San Jose. The photograph shows the railroad bridge abutment, concrete retaining wall and lahar deposits, vegetation covered, above the peat. Peat horizon is being examined by Allan Ashworth (left) and Howard Mooers (right).

Figure 13. Photograph of the writer excavating the Puerto Varas Railroad Site. Dark horizon at the top of the excavation is the 14,000-year-old peat.

Figure 14. Photograph of the excavated Puerto Varas Railroad Site section. Dark horizon at top is peat underlain by gyttja to the bottom of the section. The tape is 170 cm long from the top to the bottom of the photograph.

Table 14. Lithologic description of the Puerto Varas Railroad Section.

Location. North-facing roadcut on highway V-55 (Calle San Jose). West side of Puerto Varas (lat. 41°18'50"S., long. 72°59'20"W). Excavation made at intersection of V-55 and railway overpass (Figure 4).

Sample Numbers	Description	Thickness (cm)
Not sampled	Very poorly sorted, massively bedded, medium sand with angular to subangular grains. Rare pebble-size clasts. Grains and clasts of mixed lithologies. Partially indurated.	120
Not sampled	Buff to yellow silt with plant fragments.	30
Not sampled	Very poorly sorted, massively bedded, medium sand. Grains subangular and of mixed lithologies. Less consolidated than upper sand unit.	286
1	Peat with large wood fragments dated at 14,060±450 ^{14}C yr B.P. (GX-5507).	5-10
2-12	Dark brown (10YR 3/3) to dark grayish brown (10YR 4/2), organic-rich, silty clay (gyttja). Limonitic staining in upper part. Rhythmically bedded.	150
Base of excavation		

1976) reported an age of 16,270±360 ^{14}C yr B.P. (RL-113) for a piece of wood collected from a depth of about 80 cm below the bottom level in this study. The beetles recovered from the site provide a paleoenvironmental record from about 15,000 to 14,000 years ago.

Analysis of the Fossil Assemblages

Fossil recovery was poor from the Puerto Varas Railroad Site. Representatives (Plate 1) of only one order of insects, Coleoptera, and one order of arachnids, Acari, were recovered from the twelve samples. No mollusks or ostracods were found in any of the samples.

Of the 99 identifiable beetle fossils recovered from the Puerto Varas Railroad Site (Tables 4 and 15), 96 (97 percent) were identified to family, 78 (79 percent) to genus and 63 (64 percent) to species. At least 22 species representing 4 beetle families were recognized. Ninety-five percent of the taxa were identified by direct comparison to specimens collected during the modern faunal survey. All of the species found are considered to be terrestrial. Forty-five percent of the species were curculionids (Table 6), 32 percent carabids, 14 percent staphylinids and 9 percent scarabaeids.

Although the sparse assemblage was rather evenly scattered throughout the 1.6 m section, the upper peat sample had higher diversity and greater numbers of fossils than the lower samples. The only species that occurred consistently throughout the sequence was the weevil, _Dasydema hirtella_. Even though the assemblages were impoverished, numerous, significant species were present. Of these, four curculionid species, _Paulsenius carinicollis_, _Erirrhinoides unicolor_, _Aegorhinus_

Table 15. Table indicating the number of identifiable beetle fossils recovered by sample from the Puerto Varas Railroad Site and the number and percent of the fossils identified to family, genus, and species. The table also shows the minimum number of identified taxa and the number and percent of taxa identified to genus and species in each sample. See Plate 1 for stratigraphic position of each sample.

Sample Number	Total Number of Identifiable Beetle Fossils	Total Number(%) Identified to Family	Total Number(%) Identified to Genus	Total Number(%) Identified to Species	Minimum Number of Identified taxa	Number (%) of Taxa Identified to Genus	Number (%) of Taxa Identified to Species
1	25	24 (96)	21 (84)	18 (72)	9	6 (67)	3 (33)
2	6	6 (100)	5 (83)	4 (67)	5	4 (80)	3 (60)
3	6	5 (83)	4 (67)	2 (33)	5	4 (80)	2 (40)
4	4	4 (100)	3 (75)	0 (0)	3	2 (67)	0 (0)
5	1	1 (100)	1 (100)	1 (100)	1	1 (100)	1 (100)
6	5	5 (100)	5 (100)	4 (80)	4	4 (100)	3 (75)
7	0	0 (0)	0 (0)	0 (0)	0	0 (0)	0 (0)
8	2	2 (100)	0 (0)	0 (0)	1	0 (0)	0 (0)
9	9	9 (100)	4 (44)	4 (44)	3	2 (67)	2 (67)
10	25	24 (96)	21 (84)	19 (76)	5	4 (80)	3 (60)
11	8	8 (100)	7 (88)	7 (88)	3	2 (67)	2 (67)
12	8	8 (100)	7 (88)	4 (50)	5	4 (80)	2 (40)
TOTAL	99	96 (97)	78 (79)	63 (64)			

vitulus bulbifer and *Acalles tristis*, were not found in any of the other three sites studied.

The impoverished nature of the assemblages is exemplified not only by the low diversity and numbers of Coleoptera fossils but also by the lack of other insects in the sediments. Not even the generally ubiquitous caddisflies were found. In addition, mites, usually common in Quaternary lacustrine sediments, were found only in the upper peat horizon. Macroplant fossils were observed only in the peat but no attempt was made to identify them.

Paleoenvironmental and Paleoclimatic Interpretations

Although the 15,000- to 14,000-year-old beetle assemblages recovered from the Puerto Varas Railroad Site contain species also found in the Puerto Varas Park and Puerto Octay interval 23 through 10 assemblages, they are, in some respects, notably different than the older assemblages. For example, no aquatic insect fossils were found in the Puerto Varas Railroad sediments, even though the organic rich silts and overlying peat imply deposition in an aquatic environment. As discussed earlier, a number of possible situations could have inhibited development of an aquatic insect community. It is uncertain what the cause was at the Puerto Varas Railroad Site, nevertheless, very little information is available to speculate on conditions of the aquatic habitat. The site was, however, apparently marshy because of the occurrence of *Erirhinoides unicolor* (curculionid) which is, according to Kuschel (1982), found today in open-ground, more or less swampy areas. The carabids, *Agonum* and *Pelmatellus*, and the staphylinid, *Stenus*, also indicate hygric conditions at the site.

Terrestrial components of the assemblages do, however, give some indication of the regional paleoenvironment of the area. Ground-dwelling species found were the carabids, *Creobius* and *Bradycellus* (*Liocellus*) sp.; the staphylinids, *Anotylus chilensis* (Plate 7, Figure 6) and cf. *Baryopsis araucanus*; and the weevils, *Listroderes dentipennis*, *Paulsenius carinicollis* and cryptorhynchines, including *Acalles tristis*. Most of these taxa are eurythermic and cosmopolitan, but *L. dentipennis*, *A. tristis*, *P. carinicollis*, and as mentioned before *E. unicolor*, indicate that open-ground habitats were prevalent near the site. Unlike the Puerto Varas Park and 18,000- to 16,000-year-old Puerto Octay assemblages, arboreal taxa, the polyphagous carabid, *Aemalodera* and the more fastidious weevils, *Aegorhinus*, including *A. vitulus bulbifer*, occurred in the Puerto Varas Railroad assemblages. The latter species is almost always found on *Nothofagus* and, as noted by Kuschel (1951), prefers *N. dombeyi*. The shrubs, *Berberis* and *Ribes*, probably grew in the area because *Berberidicola exaratus* (weevil) thrives on *Berberis* (Kuschel, 1979), but was also found on the currant, *Ribes*, during the survey of the existing fauna. *Dasydema hirtella*, because it occurs on almost all kinds of plants, may also indicate forest foliage. Because of the co-occurrence of both open-ground and arboreal taxa, it seems likely that stands of trees and shrubs, in a parkland setting, existed in the marshy site area about 15,000 to 14,000 years ago.

Almost all of the taxa recovered from the Puerto Varas Railroad Site are eurythermic, extend to treeline in the Lake Region today

(Tables 4, 12 and 13), and have broad latitudinal ranges in southern South America. Only circumstantial paleoclimatic interpretations are, therefore, obtainable from the assemblages. The open-ground conditions that dominated the Central Valley between 18,000 to 15,700 yr B.P., continued through the 15,000 to 14,000 year time interval. It is suggested, however, by the occurrence of arboreal taxa in the Puerto Varas Railroad assemblages, that conditions were conducive for growth of trees and associated shrubs between about 15,000 and 14,000 years ago. If the older Puerto Octay and Puerto Varas Park assemblages reflect tundra habitats, it is proposed that between about 15,000 and 14,000 years ago climatic conditions had ameliorated sufficiently to permit invasion of tree-dwelling taxa into the Central Valley. However, the Puerto Varas Railroad assemblages of mixed open-ground and arboreal taxa could represent a more advanced seral stage in a biotic succession that may have began about 18,000 years ago in the Central Valley. Although species diversities, in each sample, were too low to use cluster analysis to determine similarities between the Puerto Varas Railroad assemblages and existing Lake Region beetle faunas, the species associations are similar to those observed in Bioassociation IV--beetles living today in the subalpine forest.

Discussion

The depositional environment at the Puerto Varas Railroad Site, between about 15,000 and 14,000 yr B.P., did not support an aquatic insect community and, consequently, little information is available regarding the lacustrine conditions at the site. The co-occurrence of open-ground and arboreal beetle species in the fossil assemblages indicates that the site was in an area of open-ground with stands of trees, mostly Nothofagus, and shrubs probably in a parkland setting. Either climatic conditions ameliorated sufficiently between about 15,000 and 14,000 yr B.P. to permit invasion of arboreal biota into the Lake Region or the assemblages of mixed ecological indicators reflect continuation of biotic succession that had begun prior to 18,000 yr B.P. in the Central Valley. Pollen spectra from the bottom portion of the section analyzed for beetles are dominated by Nothofagus (up to 68 percent) (Heusser, 1974). Nothofagus decreases to a low of 23 percent in the upper part of the sequence but the percentage of arboreal pollen throughout the entire Puerto Varas Railroad section is greater than in the 18,000 to 16,000 yr B.P. interval at the Puerto Octay Site. Heusser's pollen diagram appears consistent with the interpretation, based on beetle fossils, that between about 15,000 and 14,000 years ago the Puerto Varas Railroad Site was in a grassland containing patches of trees and shrubs.

The numerous, but laterally and vertically (only 5 to 15 cm thick) restricted, peat deposits (including those at the Puerto Varas Park and Puerto Varas Railroad sites) accumulated in depressions or channels on a lacustrine terrace around the Puerto Varas embayment during a low water phase of Lago Llanquihue when the eastern outlet to the Rio Petrohue was opened, presumably as a result of glacial recession (Porter, 1981). The Rio Petrohue flows into the tidewater Fiordo Reloncavi, Lago Llanquihue could not drain via the outlet until the Fiordo Reloncavi was nearly ice-free (Mercer, 1976). Deposition of lacustrine sediments over the peats has been taken as evidence for closure of the eastern outlet by advancing ice and subsequent termination of peat formation by rising lake level (Mercer, 1976; Porter, 1981). Mercer (1972a) initially believed that the eastern outlet was dammed by ice about 14,800 years ago because off the age (14,820±230 ^{14}C yr B.P.) of the peat horizon at Calle Santa Rosa and concluded that the shores of Lago Llanquihue were submerged at virtually the same time up to the level of the western (Rio Maullin) outlet (Mercer, 1976). A date of 13,300±550 ^{14}C yr B.P., obtained later from peat at the Puerto Varas Railroad Site (Heusser, 1974), prompted Mercer (1976) to revise his date for the damming of the eastern outlet and final major readvance into the Lake Region to about 13,000 yr B.P. As a result of fairly recent field work, especially on Isla Chiloe, Mercer (1983, 1984a) reconsidered the timing of the last glacial readvance and reverted to his earlier view (although for different reasons) that the final incursion of glaciers into the Central Valley occurred between 15,000 and 14,500 years ago.

Porter (1981) carefully resurveyed the peat horizons in the Puerto Varas embayment and determined that they occur at different altitudes although all are vertically within 6 m of one another. He plotted the ages, plus one standard deviation, of the peats as a function of altitude and postulated that the resulting sinuous curve indicates two episodes of advance culminating about 15,000 to 14,500 yr B.P. and shortly after 13,100 yr B.P., separated by a brief period of lake-level lowering, presumably caused by opening of the eastern outlet as a consequence of glacial recession. Porter stated, however, that his interpretation of two advances is predicated on the assumptions that both the altitudes and radiocarbon ages of the peats at the Bella Vista Bluff (13,965±225 ^{14}C yr B.P.), Calle Santa Rosa (14,820±230 ^{14}C yr B.P.) and Bella Vista Park (15,715±440 ^{14}C yr B.P.) sites are different. According to his survey, the three sites differ in elevation by less than 2 m. Although he defended the accuracy of his survey, he did not rule out the possibility of differential postglacial uplift resulting from isostatic recovery. In addition, and somewhat surprisingly, he did not consider the possibility of differential tectonic activity in that area with known tectonic instability. He further questioned his postulated recession between the two advances after the late-glacial maximum by pointing out that at two standard deviations the radiocarbon dates for successive pairs of sites are statistically identical and could be interpreted as a simple curve indicating a continuously rising lake level caused by a single blockage of the eastern outlet by advancing ice prior to 15,000 yrs B.P. This interpretation would be consistent with Mercer's (1983) later view and, as will be shown later, consistent with interpretations from this investigation.

The scenarios presented by Mercer (1976, 1983) and Porter (1981), for the depositional history of the sedimentary sequences exposed around the Puerto Varas embayment, are based on the assumption that changes in Lago Llanquihue water levels were caused by the opening and closing of the eastern outlet as a result of glacier fluctuations. Mercer (1976) dispelled Brüggen's early suggestion that volcanic mudflow deposits were the damming agent, not glacial ice, of the eastern outlet but also noted that no end moraines have been discovered in the Lago Llanquihue area to document the final readvance. He did, however, speculate that the glacier may have reached a band of undated moraine ridges about 25 km east of Puerto Varas and inferred that the readvance did not reach the western shore of Lago Llanquihue. Apparently, glacial lobes (Rupanco, Puyehue, and Ranco) located farther north in the Lake Region did extend to the western margins of their respective lake basins during that time (Mercer, 1976). Porter (1981), at variance with Mercer, believed that the final readvance of the Llanquihue Lobe reached the western margin of the basin and formed kame terraces rather than end moraines along the western and southern shores of the Puerto Varas embayment. Lake sediments above the peat layers in the terraces along the western and southern margins of the embayment are overlain by a series of lahars. Porter argued that the lahars, presumably originating from eruptions of Volcan Calbuco, were deposited when the glacier abutted against the western and southern margins of the Llanquihue basin because, if the basin had been ice-free, the lahars would have flowed directly into the lake adjacent to the volcano rather than along the top of the terrace. Porter (1981) presented additional evidence for glacier fluctuations, after the late-glacial maxiumum, in the vicinity of Punta Penas, just west of Puerto Montt along the northern margin of Golfo de Reloncavi. At that locality, organic sedimentation was terminated about 14,200 yr B.P. by rising lake waters, presumably as a result of the Reloncavi Lobe advance. Locally occurring dropstones in the lacustrine sediments, intercalated with the peat horizons near Puerto Varas, were also cited as evidence for damming of the eastern outlet of Lago Llanquihue by glacial ice (Mercer, 1976; Porter, 1981). Both authors interpreted the dropstones to indicate that a calving glacier terminus was located within the Llanquihue basin but probably well east of Puerto Varas. The most direct and compelling attestation for a final late-glacial advance in the Lake Region was presented by Mercer (1983, 1984a) from Isla Chiloe. At Dalcahue, on the east coast of Isla Chiloe, an end moraine of outwash sediments beneath till covers peat. Dates from the peat were intrepreted by Mercer to indicate an advance of the Reloncavi Lobe from the mainland onto Isla Chiloe about 15,000 to 14,000 years ago.

Interpretations of the glacial and climatic history of the Lake Region after the late glacial maximum rely heavily on the record of events from sedimentary sequences located around the Llanquihue basin. The arguments presented by Mercer (1976) and Porter (1981) for the opening and closing of the eastern outlet and resultant raising and lowering of lake level by glacial activity are persuasive but more field work and additional radiocarbon dates are needed to completely rule out other possible causes, such as outlet damming by volcanic debris or differential tectonic movements in and around the basin, for those lake level fluctuations. If glacial advance was the cause of lake level rise, the eastern outlet would have had to been closed about 15,700 yr B.P. to terminate peat accumulation at the Puerto Varas Park Site. The Puerto Varas Park beetle record may indicate tundra conditions at that time and would be consistent with the interpretation of glacial advance resulting from a deterioration of temperatures. However, the Puerto Varas Railroad beetle assemblages and pollen spectra indicate that conditions had ameliorated sufficiently by at least 15,000 yr B.P. to permit arboreal biota to invade the area, implying that the inferred climatic deterioration was an ephemeral event. There is no indication from the Puerto Varas Railroad beetle assemblages or, as will be discussed later from the Rio Caunahue record, that a second and later glacial readvance, as proposed by Porter (1981), occurred in the Lake Region. The drowning of the peats around the Puerto Varas embayment was probably caused by continuously rising lake level due to damming of the eastern outlet by one glacial event about 15,700 years ago. Additional comparison of the Puerto Varas beetle records and interpretations of the timing of glacial activity in the Lake Region will be presented later.

RIO CAUNAHUE SITE

Location, Site Description, and Radiocarbon Chronology

One of the most complete postglacial sections exposed in southern Chile is a southeast-facing cutbank (Figure 15) of the Rio Caunahue located in the Andean foothills (Figures 1 and 4) near the northeast corner of Lago Ranco (lat. 40°07'55"S., long. 72°14'20"W.). The exposure is situated about 3 km north of where route T-55 crosses the Rio Caunahue and about 1.5 km below the confluence of the Rio Caunahue and Estero Chaichaguen in an area of slightly disturbed Valdivian Rain Forest. Although the cutbank is several hundred metres long, most of it is either overgrown or covered by slump blocks (Figure 15). Sample collecting was concentrated in the area of greatest vertical exposure (main section), but outcrops 500 m upstream (section A) and 100 m downstream (section B) from the main section were also sampled. The ancillary sections were correlated to the main section by radiocarbon chronology and by comparing volcanic ash horizons. Approximately 13 m of gently dipping, laminated silts and clays intercalated with numerous organic laminae and tephra horizons (Plate 1 and Table 16) are exposed above river level and below a prominent terrace (Figures 15, 16, and 17). The terrace, lowest of three mapped in the valley, is 150 m in elevation or 85 m above lake level. It is capped by 2 m of fluvial gravels similar to those in and on the shores of the river below.

Figure 15. Photograph of the southeast-facing Rio Caunahue cutbank exposure taken from across the river. Arrow points to the area sampled for this study. Much of the sampled section had been slumped over the time this photo was taken by Allan Ashworth in February, 1983. Note the great thickness of lacustrine clays overlain by terrace gravels.

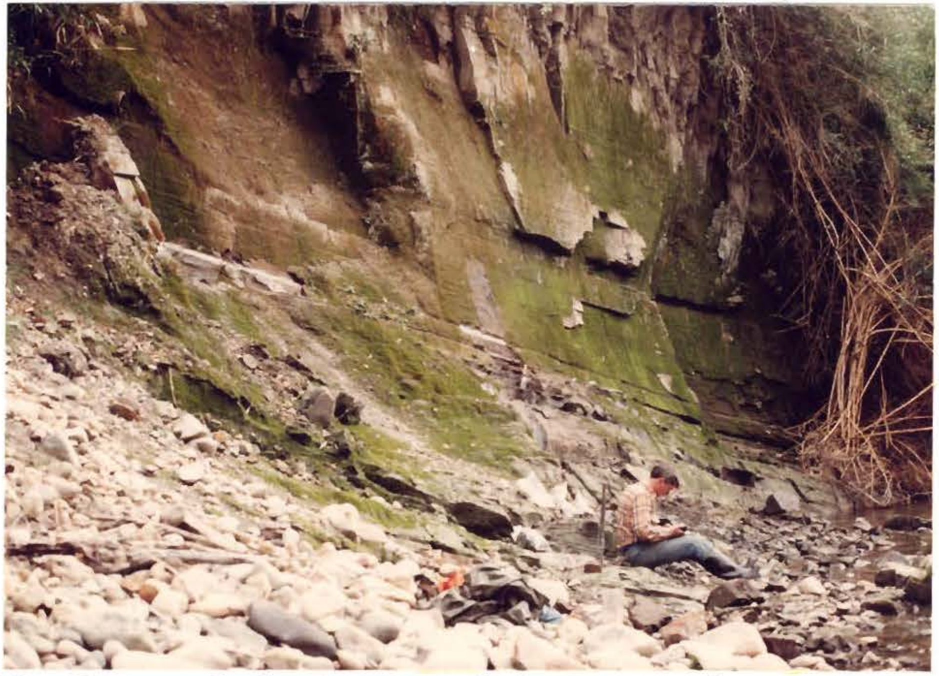


Figure 16. Photograph showing part of the Rio Caunahue section. This area of the exposure consists of lacustrine clays except for the light, volcanic ash horizon (center). The ash is about 10,500 years old and sediments at the base of the section were deposited about 12,800 yr B.P. Allan Ashworth is seen taking notes.

Figure 17. Photograph of part of the sampled sequence at the Rio Caunahue Site. The volcanic ash horizon being pointed out by Allan Ashworth is the same one seen in Figure 16. Note that some of the lacustrine clays, especially just above the ash, are rhythmically bedded.

Table 16. Lithologic description of the Rio Caunahue composite section.

Location. South-facing cutbank exposure along the Rio Caunahue about 5 km east of Lago Ranco (lat. 40°07'55"S., long. 72°14'20"W.). Excavation made about 1.5 km below the confluence with Estero Chaichaguen Figure 4).

Sample Numbers	Description	Thickness (cm)
Not sampled	Covered interval	approx. 200
Not sampled	Very coarse grained river terrace gravels. Hard pan limonitic surface at base (erosional surface).	200
BS&A3-A1	*Very dark grayish brown (10YR 3/2) rhythmically bedded silty clay. Occasional laminae of carbonized plant debris. Sample BS dated at 4,525±145 ^{14}C yr B.P. (GX-5510). Sample A1 dated at 5,220±240 ^{14}C yr B.P. (GX-6503).	approx. 200
Not sampled	Covered interval	unknown
1-8	Very dark grayish brown (10YR 3/2) rhythmically bedded silty clay. Occasional laminae of carbonized plant debris. Rare lapilli grains and wood fragments. Sample 3 (20-30 cm below terrace gravels) dated at 7,730±220 ^{14}C yr B.P. (GX-5502).	80
9	Similar to above with a 1 cm thick light yellow, silty sand lamina at base and a thin light gray lamina of volcanic ash 5 cm above base.	10
10-22	Very dark grayish brown (10YR 3/2) rhythmically bedded silty clay. Occasional laminae of carbonized plant debris. Wood fragments common. Scarce lapilli grains. Sample 21 (200-210 cm below terrace gravels) dated at 10,000±280 ^{14}C yr B.P. (GX-5503).	130

Table 16. (Continued)

Sample Numbers	Description	Thickness (cm)
23	Similar to above with two laminae of limonitic stained silty sand at base.	10
24-26	Very dark, grayish brown (10YR 3/2), rhythmically bedded, silty clay. Occasional laminae of carbonized plant debris. Wood fragments common. Sample PD0 (330 cm below terrace gravels) dated at 10,440±240 ^{14}C yr B.P. (GX-6508).	130
37	Prominent light gray volcanic ash horizon.	3.5
38-PD6	Very dark grayish brown (10YR 3/2), rhythmically bedded, silty clay. Occasional laminae of carbonized plant debris, volcanic ash laminae, and thin sand partings. Sample PD1 (395 cm below terrace gravels) dated at 11,290±250 ^{14}C yr B.P. (GX-6507). Sample 42 (420-430 cm below terrace gravels) dated at 11,680±280 ^{14}C yr B.P. (GX-5504). Sample PD3 (430 cm below terrace gravels) dated at 12,140±390 ^{14}C yr B.P. (GX-6506). Sample PD4 (445 cm below terrace gravels) dated at 12,385±340 ^{14}C yr B.P. (GX-6505). Sample PD6 (535 cm below terrace gravels) dated at 14,635±440 ^{14}C yr B.P. (GX-6504)**.	180

Base of excavation (1979 river level).

---

* Upper part of section, samples BS&A3-A1, collected about 500 m upstream from main section and correlated with main section by radiocarbon dating.

** A second date of 12,810±190 ^{14}C yr B.P. (I-12995) was obtained from the PD6 interval and is probably a more accurate age.

Approximately 2 m of soil occurs above the gravel. The basal 4 m of silt and clay are inorganic and are underlain by gravels consisting of angular to rounded boulders of mixed igneous lithologies. The laminated silts, organic laminae, and tephra horizons below the terrace gravels and above the inorganic silt and clay were sampled.

The lacustrine sediments and associated organic debris and tephra horizons were deposited in a narrow embayment of Lago Ranco that occupied the lower reaches of the Rio Caunahue valley after the glacier had receded from the lake basin into the mountains. Lake level, at that time, was apparently about 150 m higher (elevation of the highest terrace) than today. Partial, perhaps catastrophic, drainage of the lake in the late Holocene and subsequent fluvial erosion has exposed the sequence.

Fifteen radiocarbon dates, ranging from 4,525±145 ^{14}C yr B.P. (GX-5510) to 13,900±560 ^{14}C yr B.P. (GX-9979) were obtained from the site for this study (Plate 1, Table 16 and Appendix D). Sample PD6, the basal sample analyzed from the Rio Caunahue Site, produced a date of 14,635±440 ^{14}C yr B.P. (GX-6504). The date was considered suspect because it appeared too old relative to the well known chronology of the area and so a second sample from the same stratigraphic level was submitted for radiocarbon analysis. The 14,635 yr B.P. date was rejected in favor of the second date of 12,810±190 ^{14}C yr B.P. (I-12995) because the latter more accurately fit the chronology and, more specifically, because the PD6 sample is 76 cm stratigraphically above a wood sample dated at 13,900±560 ^{14}C yr B.P. (GX-9979).

Samples (B1-B3), from section B, produced anomalous dates. The dates were reversed, with the older coming from strata higher in the section than the younger. Because the section was not structurally aberrant, the problem probably resulted from laboratory error either in sample numbering or confusion at the dating facility. The three dates, all within one metre of section, centered around 10,500 yr B.P. and were statistically about the same at two standard deviations. It was decided, however, that the fossil assemblages from these samples, although they are almost identical to 11,000- to 10,000-year-old assemblages from the main section, would not be included, only briefly mentioned, in analysis of the Rio Caunahue record. The beetles from the particularly important Rio Caunahue Site provide a paleoenvironmental record from 12,800 to 4,500 years ago.

It should be noted that the Rio Caunahue Site had been completely altered between 1979 and 1983 as a result of slumping and continued fluvial erosion (Ashworth, 1983). Erosion had, by the latter time, exposed more lacustrine sediments and underlying gravels thereby providing additional data for interpretation of the depositional history of the site.

Heusser (1981) described the stratigraphy of the site and presented a pollen diagram for part of the section. His results will be discussed in a later section.

Analysis of the Fossil Assemblages

By far, the greatest number and highest diversity of insect fossils recovered during this study were from the Rio Caunahue Site.

Representatives of eight orders (Plate 1) of insects and three orders of arachnids were identified from the fifty-two samples. One ostracod and one immature gastropod, the only ones found during this investigation, occurred in sample PDO. No attempt was made to identify them.

Of the 4,586 identifiable beetle fossils recovered from the Rio Caunahue Site (Table 4 and 17), 4,129 (90 percent) were identified to family, 2,698 (59 percent) to genus and 1,783 (39 percent) to species. At least 241 species representing 44 beetle families, both aquatic and terrestrial, were recognized. Eighty-four percent of the taxa were identified by direct comparison to specimens collected during the modern faunal survey. Although diversity was high at the family level the assemblages were dominated by three beetle families (Table 6). Sixteen percent of the species were staphylinids, 15 percent curculionids and 14 percent carabids.

Although taxa diversity was greatest in interval A1 through BS-A3 and interval PD6 through 17, the relative balance of ecological types remained essentially consistent throughout the 5.5 m section (Plate 1). Diversity differences observed between specific stratigraphic intervals in the sequence will be discussed later. Beetles from numerous families associated today with rain forest habitats occurred consistently throughout the section and were represented by arboreal, understory shrub, forest floor, decaying wood and fungus taxa. Aquatic taxa were rare, scattered throughout the sequence and dominated by running-water species of the family Elmidae except in the top sample, BS-A3, and the basal sample, PD6, where standing-water forms were present. Shoreline taxa (e.g., certain carabids and staphylinids) and species occurring on

Table 17. Table indicating the number of identifiable beetle fossils recovered by sample from the Rio Caunahue Site and the number and percent of the fossils identified to family, genus, and species. The table also shows the minimum number of identified taxa and the number and percent of taxa identified to genus and species in each sample. See Plate 1 for stratigraphic position of each sample.

Sample Number	Total Number of Identifiable Beetle Fossils	Total Number(%) Identified to Family	Total Number(%) Identified to Genus	Total Number(%) Identified to Species	Minimum Number of Identified taxa	Number (%) of Taxa Identified to Genus	Number (%) of Taxa Identified to Species
BS-A3	615	530 (86)	376 (61)	294 (48)	119	87 (73)	68 (57)
A2	298	262 (88)	159 (53)	110 (37)	84	53 (63)	39 (46)
A1	288	251 (87)	184 (64)	130 (45)	80	59 (74)	44 (55)
1	13	13 (100)	6 (46)	4 (31)	6	4 (67)	3 (50)
2	6	5 (83)	3 (50)	1 (17)	4	2 (50)	1 (25)
3	23	21 (91)	12 (52)	9 (39)	10	7 (70)	4 (40)
4	21	17 (81)	8 (38)	4 (19)	11	6 (55)	4 (36)
5	12	10 (83)	5 (42)	2 (17)	10	5 (50)	2 (20)
6	10	9 (90)	2 (20)	1 (10)	5	2 (40)	1 (20)
7	10	8 (80)	3 (30)	2 (20)	6	3 (50)	2 (33)
8	13	12 (92)	4 (31)	2 (15)	7	4 (57)	2 (29)
9	15	14 (93)	6 (40)	3 (20)	9	6 (67)	3 (33)
10	10	7 (70)	3 (30)	2 (20)	5	3 (60)	2 (40)
11	11	9 (82)	3 (27)	2 (18)	7	3 (43)	2 (29)
12	22	19 (86)	6 (27)	2 (9)	10	5 (50)	2 (20)
13	12	12 (100)	6 (50)	2 (17)	6	3 (50)	1 (17)
14	12	12 (100)	6 (50)	3 (25)	9	5 (56)	3 (33)
15	5	5 (100)	4 (80)	2 (40)	5	4 (80)	2 (40)
16	18	17 (94)	9 (50)	6 (33)	9	5 (56)	4 (44)
17	69	65 (94)	27 (39)	15 (22)	33	14 (42)	12 (36)
18	29	27 (93)	12 (41)	8 (28)	13	9 (69)	5 (38)

Table 17. (Continued)

Sample Number	Total Number of Identifiable Beetle Fossils	Total Number(%) Identified to Family	Total Number(%) Identified to Genus	Total Number(%) Identified to Species	Minimum Number of Identified taxa	Number (%) of Taxa Identified to Genus	Number (%) of Taxa Identified to Species
19	40	37 (93)	20 (50)	10 (25)	16	10 (63)	6 (38)
20	28	25 (89)	15 (54)	9 (32)	14	10 (71)	6 (43)
21	54	50 (93)	32 (59)	16 (30)	26	20 (77)	13 (50)
22	15	14 (93)	8 (53)	5 (33)	11	7 (64)	5 (45)
23	5	5 (100)	3 (60)	0 (0)	4	3 (75)	0 (0)
24	15	15 (100)	7 (47)	3 (20)	10	6 (60)	3 (30)
25	18	17 (94)	6 (33)	5 (28)	13	6 (46)	5 (39)
26	14	14 (100)	4 (29)	1 (7)	5	3 (60)	1 (20)
27	95	87 (92)	51 (54)	38 (40)	49	27 (55)	23 (47)
28	25	25 (100)	9 (36)	5 (20)	17	9 (53)	5 (29)
29	31	28 (90)	16 (52)	14 (45)	12	9 (75)	7 (58)
30	54	47 (87)	24 (44)	15 (28)	24	15 (63)	10 (42)
31	38	35 (92)	16 (42)	10 (27)	18	13 (72)	10 (56)
32	27	27 (100)	19 (70)	6 (22)	13	9 (69)	5 (38)
33	31	30 (97)	15 (48)	12 (39)	14	10 (71)	7 (50)
PD0	246	225 (92)	153 (62)	88 (36)	60	47 (78)	28 (47)
34	26	23 (88)	15 (58)	9 (35)	16	10 (63)	6 (38)
35	26	24 (92)	11 (42)	8 (31)	11	6 (55)	4 (36)
36	35	30 (86)	17 (49)	14 (40)	16	12 (75)	9 (56)
37	0	0 (0)	0 (0)	0 (0)	0	0 (0)	0 (0)
38	48	45 (94)	23 (48)	18 (38)	17	10 (59)	7 (41)
39	35	21 (89)	15 (43)	9 (26)	13	8 (62)	5 (38)
PD1	199	176 (88)	121 (61)	72 (36)	55	35 (64)	23 (42)
40	19	19 (100)	11 (58)	8 (42)	11	8 (73)	5 (45)

Table 17. (Continued)

Sample Number	Total Number of Identifiable Beetle Fossils	Total Number(%) Identified to Family	Total Number(%) Identified to Genus	Total Number(%) Identified to Species	Minimum Number of Identified taxa	Number (%) of Taxa Identified to Genus	Number (%) of Taxa Identified to Species
PD2	191	175 (92)	125 (65)	65 (34)	57	43 (75)	23 (44)
41	125	116 (93)	72 (58)	53 (42)	39	25 (64)	16 (38)
42	929	834 (90)	615 (66)	429 (46)	108	84 (78)	54 (50)
PD3	296	271 (92)	185 (63)	105 (35)	68	48 (71)	29 (43)
PD4	169	156 (92)	103 (61)	65 (38)	47	34 (72)	22 (47)
PD5	68	67 (99)	51 (75)	37 (54)	30	22 (73)	12 (40)
PD6	172	156 (91)	92 (53)	50 (29)	61	44 (72)	30 (49)
TOTAL	4586	4129 (90)	2698 (59)	1783 (39)			

emergent vegetation (e.g., helodids and various coccinellids) were fairly common throughout the section.

Representatives of seven orders of insects (Table 7), in addition to Coleoptera, were identified. They are: Plecoptera (stoneflies), Hemiptera, including Saldidae, Homoptera, specifically Cicadellidae, Neuroptera, including Corydalidae (dobson flies), Trichoptera, Diptera, including Chironomidae, and Hymenoptera, including Formicidae. The three arachnid groups present were the Chelonethida (pseudoscorpions), Acari, and Araneida. These additional insect and arachnid fossils occurred consistently throughout the sequence but, like the beetles, were more abundant in interval A1 through BS-A3 and interval PD6 through 17 (Plate 1). Unidentified macroplant fossils and charophyte oogonia were common in the section but less abundant in interval 16 through 1. Isoetes savatieri was found only in the bottom two metres.

The beetle assemblages from eight Rio Caunahue samples (Table 2), ranging in age from 12,800 to 4,525 yr B.P., were subjected to cluster analysis to determine their similarity to fossil assemblages from different ages and other localities and to beetle faunas living today (Appendix A) in the Lake Region. Seven of the assemblages were from the critical 12,800 to 10,000 yr B.P. late-glacial time interval.

A number of factors are responsible for the disparity in species diversity observed between the fossil assemblages. The most obvious is merely a sampling artifact related to the amount of material available for processing. For example, the high numbers of species present in samples BS-A3 and 42 in attributable, at least in part, to having larger sediment samples than the other Rio Caunahue samples. This is not to imply, however, that the other samples were of inadequate size to yield representative assemblages. Even though most of the diversity differences are artifactual, the assemblages adequately reflect past environmental conditions in the site areas at their respective times of deposition. Some samples were, in addition, obviously richer in overall biotic content than others. This may be associated with changes, at various times, in diversity of microhabitats proximal to the basin of deposition or in the dynamics of the depositional system. In contrast, as shown earlier, the low diversity of the Puerto Varas Park assemblages is believed to reflect the depauperate nature of the beetle fauna living in the site area 15,700 years ago.

The relative faunal similarities between the 41 modern fauna collecting localities and the nine fossil assemblages is shown in the trellis diagram and dendrogram presented in Figure 11. It was assumed that introduction of fossil assemblages into the clustering program would alter the groupings obtained from analysis of the modern fauna (Figure A7) because of anticipated similarities of some of the fossil assemblages with contemporary faunas from specific collecting localities. This was not the case, and the exact bioassociational groupings of the modern fauna were maintained because the fossil assemblages, surprisingly, formed their own cluster (group F in Figure 11). These results indicate that the nine fossil assemblages are more similar in faunal composition to one another than to the contemporary faunas. Taphonomic intervention is probably at least partially responsible for this observed phenomenon.

Of particular interest, from a paleoenvironmental perspective, is that the assemblage of sample 42 (11,680 yr B.P.) is most similar to the assemblage of sample BS-A3 (4,525 yr B.P.) and that the assemblage of sample PDO (10,440 yr B.P.) is most similar to the assemblage of sample 42. In turn, the assemblage of sample PD4 (12,385 yr B.P.) is most similar to the assemblage of sample PDO.

The cluster of the fossil assemblages includes two subclusters, F_1 and F_2. Subcluster F_1 consists of the basal Rio Caunahue assemblage, PD6 (12,800 yr B.P.) and the Puerto Varas Park assemblage, PV1 (15,700 yr B.P.). The other seven Rio Caunahue assemblages, ranging in age from 4,525 to 12,385 yr B.P., comprise subcluster F_2.

The cluster of fossil assemblages, F_1-F_2, joins the major cluster consisting of Bioassociations II, III and Ib at about the 8 percent level, indicating that the fossil assemblages have a number of species in common with the faunas in those bioassociations. This broad similarity is rather meaningless for paleoenvironmental reconstructions. However, dark regions on the trellis diagram indicate that the fossil assemblages in subcluster F_2 are generally more similar to modern faunas in Bioassociation III and show little resemblance to those in Bioassociations IIa, IV and V. The F_2 assemblages are also similar to faunas in subcluster IIb, modern fauna collecting localities C1 and P3. The reason for this is that elmids, beetles living in running-water habitats and other stream-marginal species, found consistently in the F_2 assemblages were collected, almost exclusively, at localities C1 and P3. In contrast, the assemblages in subcluster F_1 are most similar to faunas in Bioassociation II. As explained earlier, the PD6 assemblage is about equally similar to faunas in Bioassociations II and III and shows little resemblance to faunas in Bioassociations IV and V, whereas, the PV1 assemblage is most similar to faunas in Bioassociation II and exhibits little similarity to faunas in Bioassociations III, IV and V. The importance of the trellis diagram in determining relative similarities between the fossil assemblages and modern faunas is evident. The interpretations of these clustering results will follow later.

Paleoenvironmental and Paleoclimatic Interpretations

Interval PD6 through 17 (12,800 to about 9,500 yr B.P.)

The beetle assemblages from interval PD6 through 17 and the other Rio Caunahue intervals discussed later are significantly different than those recovered from the Puerto Octay and Puerto Varas sites. The most apparent difference is the high numbers and diversity of obligate woodland taxa, illustrated by the assemblages from interval PD6 through 17, found in the Rio Caunahue deposits. However, shallow-water, aquatic beetles were scarce in the interval, represented by only one dytiscid, *Lancetes*, in sample PD1. Shallow-water beetle taxa (e.g., the hydrophilid *Enochrus*, including *E. vicinus*) were more common in the basal, 12,800 year old sample, PD6. The fact that the sediment is rhythmically bedded indicates deposition in relatively deep water in a reasonably large lake. Lacustrine beetles most frequently inhabit quiescent, shallow-water areas near the shore. Their remains are seldom carried to deeper depths, and this undoubtedly explains their scarcity in the sediments of the interval. Other apparently more easily transported shallow-water indicators (e.g., caddisflies, chironomoids and charophyte oogonis) were, however, consistently found in high numbers.

Laminae of organic debris, the numerous species of stream-dwelling elmids, *Austrolimnius* (e.g., *A.* *chiloensis*, Plate 6, Figure 6), *Stethelmis*, and cf. *Hydora* *annectens*, and abundant stoneflies and dobson flies in interval PD6 through 17 indicate that flood waters periodically discharged into the lake. The staphylinid, *Carpelimus*, may also indicate a similar setting because Puthz (1981) noted its preference today for riparian habitats. The noteworthy absence of elmids, stoneflies and dobson flies in sample PD6 will be discussed later. The influence of fluvial systems is, at least in part, responsible for the diversity of terrestrial beetles found in the interval from which a great deal of regional paleoenvironmental and paleoclimatic information was obtained for the 12,800 to 9,500 year period.

The numerous hygrophilous shoreline taxa, including the carabids, *Bembidion* (e.g., *B.* cf. *posticalis* and *B.* *setiventre*), *Trechisibus* *nigripennis* Group, *Trirammatus* (e.g., *T.* (*Ferionimorpha*) sp. 1), *Agonum*, *Bradycellus* (e.g., *B.* (*Stenocellus*) and *B.* (*Goniocellus*)), and *Pelmatellus* (*sensu* *lato*) sp. 1; the hydrophilid, *Hydrochus* *stolpi*; and the staphylinids, *Thinodromius*, *Stenus* (e.g., *S.* *chilensis*), *Loncovilius* (*Lienturius*), *Cheilicolpus* and *Nomimocerus* *marginicollus*, imply that an array of microhabitats, marshy to bare, open and muddy, fringed the lake. Emergent vegetation, growing near the margins, provided habitats for staphylinids, helodids (e.g., cf. *Microcara* and *Prionocyphon*), alticine chrysomelids, coccinellids, *Hyponotum* (cantharid), *Strichtoptyophus* cf. *brevicollis* (anobiid) and *Pseudochrodes* *suturalis* (cryptophagid). The weevil, *Notiodes*, living today on aquatic and semiaquatic vegetation (Kuschel, 1981a), also indicates that a relatively diverse aquatic flora was present.

The consistent occurrence of organic laminae containing macroplant fossils, including leaves, twigs, and seeds, and forest-dwelling beetle taxa, indicates that a dense forest existed near the lake and probably extended to its shoreline. The numerous polyphagous, forest-dwelling beetles recovered from the interval that occur today in the Valdivian Rain Forest on a variety of both trees and understory vegetation include: the carabid, cf. Aemalodera centromaculata; the staphylinid, Leucotachinus luteonitens (Plate 7, Figure 4); the scarabaeid, Sericoides (e.g., S. viridis); the elaterids, Deromecus and cf. Medonia; the lampyrid, Pyractonema nigripennis Group; the cantharid, Plectocephalon testaceum (Plate 6, Figure 7); the anobiid, Caenocara (Plate 3, Figure 3); the trogositids, cf. Diontolobus sp. 1 and cf. Diontolobus sp. 2 (Plate 4, Figure 3); the nitidulid, Perilopsis flava (Plate 3, Figure 4); the coccinellids, Orynipus and Sarapidus cf. australis; the salpingid, Cycloderus rubricollis; the melandryid, Orchesia sp. 1; the chrysomelid, Pachybrachis; and the weevils, Dasydema hirtella, Neopsilorhinus and Psepholax dentipes. The abundant leafhopper and Hemiptera fossils also indicate a well established forest proximal to the site of deposition.

An insight into the specific composition of the forest vegetation was gained by the many strongly host-specific beetle taxa in the assemblages. Evidently, the southern beech, Nothofagus, and quite probably more than one species, were the dominant trees in the forest similar to today's Valdivian Rain Forest. Beetle taxa recovered from the interval, that were found exclusively or most commonly on *Nothofagus* during the survey of the existing fauna, include: the carabid, *Abropus carnifex* (Plate 4, Figure 1); the elaterid, *Semiotus luteipennis*; the nitidulid, *Cryptarcha* sp. 1; the coccinellids, *Rhizobius chilianus* and *Strictospilus darwini* (Plate 3, Figure 2); the anthribid, *Ormiscus parvulus*; and the weevils, *Nototactus angustirostris*, *Polydrusus nothofagi*, *Nothofagobius brevirostris*, *Epaetius carinulatus* (Plate 7, Figure 5), Erirrhininae n. sp. 1 and Erirrhininae n. sp. 2. Of these weevils, *P. nothofagi*, *N. angustirostris*, Erirrhininae n. sp. 1 and Erirrhininae n. sp. 2 were also noted by Kuschel (1950, 1979) to prefer *Nothofagus*. *Nothofaginus lineaticollis* (weevil), although collected only by trampling water-marginal vegetation during the survey of the modern fauna is found on *Nothofagus pumilio* and *N. dombeyi* (Kuschel, 1952, 1981a). The weevils, *Wittmerius longirostris* (Plate 2, Figure 3) and *Allomagdalis cryptonx* and the nemonychids, *Rhychitomacer flavus* (Plate 6, Figure 5) and *R. fuscus* were not collected during the survey, but Kuschel (1981a) stated that they are host-specific on *Nothofagus*. Other trees in the forest surrounding the site probably included *Drimys winteri*, reflected by the occurrence in this interval of the nitidulid, *Brachpterus* n. sp. (Plate 6, Figure 2), and *Laurelia serrata* as indicated by the weevil, *Tartarisus signatus* (Plate 6, Figure 4). The latter, according to Kuschel (1952), is commonly abundant on that plant species. *Saxegothaea* may also have been present in the forest because *S. darwini* and *N. brevirostris*, although more frequently found on *Nothofagus*, was also collected on *Saxegothaea* during the modern faunal survey.

The understory flora were apparently equally as diverse as the arboreal component of the forest. The bamboo-like plant, *Chusquea*, was probably growing in the forest as reflected by the occurrence of *Micronotum nodicorne* (cantharid), *Dasytes haemorrhoialis* (melyrid), *Aridius heteronotus* (lathridiid) and *Vincenzellus* (salpingid). The cerambycid, *Hoplonotus spinifer*, perhaps indicates the presence of *Flotovia acanthoides*. The occurrence of *Pseudopanax laetevirens* is suggested by the weevil, *Lophocephala fasciolata*. The chrysomelid, cf. *Crepidodera* sp. I and the attelabids, *Eugnamptoplesius violaceipennis* and *Minurus testaceous* (Plate 8, Figure 6) were found almost exclusively on *Fuchsia* during the survey, implying the presence of that plant in the forest. Voss (1951), however, noted the preference of those attelabids for *Myrceuginella*, *Myrceugenia* and *Amomyrtus*. The coccinellid, *Adalia kuscheli*, the chrysomelid, *Strichosa eburata* and, according to Kuschel (1979), the weevils, *Berberidicola exaratus* and *B. crenulatus*, are found today almost exclusively on *Berberis*, suggesting its presence in the flora. Kuschel (1952) noted that the pollen-feeding weevil, *Rhopalomerus tenuirostris* (Plate 7, Figure 2) occurs on a great number of flowering plants including the shrubs, *Baccharis spaerocephala* and *Caldeluvia paniculata* and the tree, *Eucryphia cordifolia*, perhaps indicating that one or all of these plants grew in the forest.

A well developed forest, probably with a dense canopy, is also indicated by the forest-floor and other highly specialized forest-dwelling beetles. The following ground-dwelling taxa from the interval characteristically live in the Valdivian Rain Forest today: the trachypachid, *Systolosma brevis*; the carabids, *Ceroglossus*, *Creobius* eydouxi, Trechinotus striatulus (Plate 8, Figure 1), Parhypates and Metius; the leiodids, Dasypelates, Eunemadus chilensis (Plate 7, Figure 1), Colon and cf. Neohydrobius; the elaterid, Negastrius; the staphylinids, Gypholoma pustiliferum (Plate 6, Figure 3), Omaliopsis, Baryopsis araucanus (Plate 4, Figure 4), and Neophonus bruchii (Plate 7, Figure 3); the pselaphids, Dalminiomus, Achillia and Tyropsis; and cryptorhynchine (Plate 8, Figure 5) weevils. Thayer and Newton (1978) observed that G. pustiliferum occurs in Nothofagus forest-floor, leaf litter. The abundance of ant, pseudoscorpion, and spider fossils also indicate a diverse forest-floor fauna. Perhaps it should be noted here that the open-ground-dwelling weevil, Listroderes dentipennis, was found in the interval but only in the bottom sample, PD6. Its postulated significance will be discussed later. Of the highly specialized forest-dwelling species, Nothoderodontus dentatus (derodontid; Plate 3, Figure 1), although rarely collected today and not collected during the survey, is one of the most interesting. According to Lawrence and Havoc (1979) the species has been found living today only on Isla Chiloe. They suggested that it probably lives on molds growing on and under the bark of Nothofagus, similar to the New Zealand derodontid species. Other species that apparently prefer living under the bark of trees or in decaying wood are the lucanids, Sclerognathus bacchus and cf. Sclerognathus femoralis. In addition, Coiffait and Saiz (1968), found that Pseudopsis cf. adustipennis (staphylinid) prefers to live in rotten wood.

The forest was not only diverse in floral composition but must also have been well established. This is confirmed by the numerous wood-boring beetle taxa found in the interval, many of which apparently prefer large dying or dead, felled trees. These taxa include bostrichids and the scolytids, Pitycophthorus, Amphricranus, cf. Corthylus, Gnathotrupes (e.g., G. cf. sextuberculatus), and Phloeotribus cf. spinnipennis (Plate 6, Figure 1). In addition, O'Brien (1980) stated that the weevil, Pentarthrum castaneum (Plate 2, Figure 2) exhibits similar wood-boring habits as the bostricids and scolytids. The apparent significance of the lack of scolytids and bostricids in sample PD6 will be discussed later.

The occurrence of the above-mentioned beetle taxa leaves little doubt that a large lake with a forested margin existed at the Rio Caunahue Site from 12,800 to about 9,500 years ago. To test this conclusion, assemblages from samples 21 (10,000 yr B.P.), 27 (approximately 10,200 yr B.P.), PD0 (10,440 yr B.P.), PD1 (11,290 yr B.P.), 42 (11,680 yr B.P.), PD4 (12,300 yr B.P.) and PD6 (12,800 yr B.P.) were subjected to cluster analysis (Figure 11) to determine their similarity in species composition to beetle faunas living today at specific localities in the Lake Region. Samples 21, 27, PD0, PD1, 42, and PD4 formed a tight cluster, F_2, indicating that the beetle faunas living in the Rio Caunahue area were very similar throughout the 12,300 to 10,000 year time interval. This, in turn, implies that environmental and climatic conditions were reasonably stable during that time. Figure 11 also shows that these assemblages are remarkably similar to the 4,500 year old assemblage from sample BS-A3. The significance of this observation will be discussed later. In addition, patterns within the trellis diagram indicate that the assemblages comprising cluster F_2 are most similar to beetle faunas of Bioassociation III which inhabit the Valdivian Rain Forest. Therefore, cluster analysis not only confirms that environmental and climatic conditions remained reasonably stationary betwen 12,300 and 10,000 years ago, but also that the climate, during that time, must have been similar to those areas in the Lake Region today inhabited by Valdivian Rain Forest biota. Additional support for the interpretation, at least for the 11,000 to 10,000 year period, was provided by the beetle assemblages from the three samples collected at the Rio Caunahue B section. The assemblages were essentially identical to those from samples PD5 through 17. In addition, the data in Tables 18 and 19, show that a very high percentage of the taxa recovered from interval PD6 through 17 occur only between the elevations of 200 to 1000 m in the Lake Region today.

The beetle assemblage from the basal, 12,800-year old sample (PD6) requires a slightly different interpretation than the other assemblages from the interval. That assemblage differs from others in the interval in having: (1) fewer forest-dwelling taxa; (2) more shallow-water aquatic forms; (3) no stream-dwelling elmids; (4) no wood-boring bostrichids and scolytids; and (5) the open-ground weevil Listroderes dentipennis. The differences between these assemblages may reflect either a shift in environmental conditions or a change in the dynamics of the depositional system at the site between 12,800 and 12,300 years ago. The beetles provide evidence for both.

The higher diversity of shallow-water, aquatic, beetle taxa in sample PD6 compared to other assemblages in the interval implies that

Table 18. Table indicating the number and percent of Rio Caunahue beetle taxa, in each sample, that occur today at restricted elevational ranges in the Lake Region determined through study of the modern fauna (Appendix A). See Plate 1 for stratigraphic position of each sample.

Sample Number	Minimum Number of Taxa	Number (%) Taxa Not Collected in Modern Survey	Number (%) Taxa Ranging up to 150 m	Number (%) Taxa Ranging up to 650 m	Number (%) Taxa Ranging up to 1000 m	Number (%) Taxa Ranging up to 1200 m	Number (%) Taxa Occurring Only Between 1000-1200 m	Number (%) Taxa Ranging Above 1200 m	Total Number (%) Taxa Occurring Only Below 650 m	Total Number (%) Taxa Occurring Only Below 1000 m	Total Number (%) Taxa Occurring Only Below 1200 m
RIO CAUNAHUE											
BS-A3	119	19 (16)	4 (3)	25 (21)	16 (13)	28 (24)	4 (3)	20 (17)	29 (24)	45 (38)	77 (65)
A2	84	7 (8)	4 (5)	18 (21)	14 (17)	17 (20)	1 (1)	15 (18)	22 (26)	36 (43)	54 (64)
A1	80	7 (8)	7 (8)	18 (23)	9 (11)	15 (19)	3 (4)	17 (21)	25 (31)	34 (43)	52 (65)
1	6	0 (0)	0 (0)	2 (33)	1 (17)	2 (33)	0 (0)	1 (17)	2 (33)	3 (50)	5 (83)
2	4	0 (0)	0 (0)	1 (25)	0 (0)	1 (25)	0 (0)	1 (25)	1 (25)	1 (25)	2 (50)
3	10	1 (10)	0 (0)	4 (40)	2 (20)	1 (10)	0 (0)	2 (20)	4 (40)	6 (60)	7 (70)
4	11	0 (0)	1 (9)	2 (18)	1 (9)	2 (18)	0 (0)	3 (27)	3 (27)	4 (36)	6 (55)
5	10	2 (20)	0 (0)	3 (30)	0 (0)	1 (10)	0 (0)	1 (10)	3 (30)	3 (30)	5 (50)
6	5	2 (40)	0 (0)	0 (0)	0 (0)	1 (20)	0 (0)	2 (40)	0 (0)	0 (0)	1 (20)
7	6	0 (0)	0 (0)	2 (33)	0 (0)	1 (17)	0 (0)	3 (50)	2 (33)	2 (33)	3 (50)
8	7	0 (0)	0 (0)	1 (14)	2 (29)	1 (14)	0 (0)	2 (29)	1 (14)	3 (43)	4 (57)
9	9	0 (0)	1 (11)	2 (22)	1 (11)	1 (11)	0 (0)	3 (33)	3 (33)	4 (44)	5 (56)
10	5	1 (20)	0 (0)	1 (20)	1 (20)	0 (0)	0 (0)	1 (20)	1 (20)	2 (40)	2 (40)
11	7	0 (0)	0 (0)	2 (29)	1 (14)	1 (14)	0 (0)	1 (14)	2 (29)	3 (43)	4 (57)
12	10	1 (10)	0 (0)	1 (10)	1 (10)	2 (20)	0 (0)	3 (30)	1 (10)	2 (20)	4 (40)
13	6	0 (0)	0 (0)	1 (17)	1 (17)	1 (17)	0 (0)	2 (33)	1 (17)	2 (33)	3 (50)
14	9	1 (11)	0 (0)	2 (22)	1 (11)	0 (0)	0 (0)	4 (44)	2 (22)	3 (33)	3 (33)
15	5	0 (0)	1 (20)	2 (40)	0 (0)	1 (20)	0 (0)	0 (0)	3 (60)	3 (60)	4 (80)
16	9	0 (0)	1 (11)	2 (22)	2 (22)	2 (22)	0 (0)	1 (11)	3 (33)	5 (56)	7 (78)
17	33	3 (9)	1 (3)	5 (15)	3 (9)	6 (18)	0 (0)	6 (18)	6 (18)	9 (27)	15 (45)
18	13	2 (15)	0 (0)	3 (23)	2 (15)	1 (8)	0 (0)	2 (15)	3 (23)	5 (38)	6 (46)
19	16	3 (19)	1 (6)	3 (19)	3 (19)	2 (13)	0 (0)	2 (13)	4 (25)	7 (44)	9 (56)
20	14	1 (7)	0 (0)	4 (29)	2 (14)	3 (21)	0 (0)	3 (21)	4 (29)	6 (43)	9 (64)
21	26	4 (15)	3 (12)	6 (23)	4 (15)	4 (15)	0 (0)	3 (12)	9 (35)	13 (50)	17 (65)
22	11	0 (0)	1 (9)	3 (27)	1 (9)	1 (9)	0 (0)	5 (45)	4 (36)	5 (45)	6 (55)
23	4	0 (0)	0 (0)	1 (25)	0 (0)	1 (25)	0 (0)	1 (25)	1 (25)	1 (25)	2 (50)
24	10	0 (0)	0 (0)	3 (30)	1 (10)	1 (10)	0 (0)	4 (40)	3 (30)	4 (40)	5 (50)
25	13	0 (0)	0 (0)	3 (23)	4 (31)	1 (8)	0 (0)	1 (8)	3 (23)	7 (54)	8 (62)
26	5	0 (0)	0 (0)	1 (20)	1 (20)	0 (0)	0 (0)	3 (60)	1 (20)	2 (40)	2 (40)
27	49	8 (16)	4 (8)	11 (22)	6 (12)	7 (14)	0 (0)	8 (16)	15 (31)	21 (43)	28 (57)
28	17	4 (24)	1 (6)	3 (18)	1 (6)	3 (18)	0 (0)	4 (24)	4 (24)	5 (29)	8 (47)
29	12	1 (8)	1 (8)	4 (33)	2 (17)	2 (17)	0 (0)	2 (17)	5 (42)	7 (58)	9 (75)
30	24	1 (4)	1 (4)	5 (21)	7 (29)	4 (17)	0 (0)	5 (21)	6 (25)	13 (54)	17 (71)
31	18	3 (17)	2 (11)	6 (33)	2 (11)	2 (11)	0 (0)	2 (11)	8 (44)	10 (56)	12 (67)
32	13	2 (15)	0 (0)	3 (23)	3 (23)	2 (15)	0 (0)	3 (23)	3 (23)	6 (46)	8 (62)

Table 18. (Continued)

Sample Number	Minimum Number of Taxa	Number (%) Taxa Not Collected in Modern Survey	Number (%) Taxa Ranging up to 150 m	Number (%) Taxa Ranging up to 650 m	Number (%) Taxa Ranging up to 1000 m	Number (%) Taxa Ranging up to 1200 m	Number (%) Taxa Occurring Only Between 1000-1200 m	Number (%) Taxa Ranging Above 1200 m	Total Number (%) Taxa Occurring Only Below 650 m	Total Number (%) Taxa Occurring Only Below 1000 m	Total Number (%) Taxa Occurring Only Below 1200 m
RIO CAUNAHUE Continued											
33	14	3 (21)	0 (0)	3 (21)	2 (14)	2 (14)	1 (7)	3 (21)	3 (21)	5 (36)	8 (57)
PD0	60	11 (18)	5 (8)	10 (17)	6 (10)	13 (22)	1 (2)	10 (17)	15 (25)	21 (35)	35 (58)
34	16	1 (6)	0 (0)	5 (31)	3 (19)	2 (13)	1 (6)	3 (19)	5 (31)	8 (50)	11 (69)
35	11	2 (18)	0 (0)	2 (18)	0 (0)	3 (27)	0 (0)	4 (36)	2 (18)	2 (18)	5 (45)
36	16	1 (6)	0 (0)	4 (25)	3 (19)	3 (19)	0 (0)	4 (25)	4 (25)	7 (44)	10 (63)
37	0	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
38	17	2 (12)	0 (0)	4 (24)	1 (6)	3 (17)	0 (0)	5 (29)	4 (24)	5 (29)	8 (47)
39	13	1 (8)	0 (0)	3 (23)	4 (31)	2 (15)	0 (0)	3 (23)	3 (23)	7 (54)	9 (69)
PD1	55	12 (22)	3 (5)	8 (15)	7 (13)	10 (18)	1 (2)	10 (18)	11 (20)	18 (33)	29 (53)
40	11	0 (0)	0 (0)	1 (9)	4 (36)	2 (18)	0 (0)	2 (18)	1 (9)	5 (45)	7 (64)
PD2	57	6 (11)	5 (9)	13 (23)	3 (5)	14 (25)	1 (2)	13 (23)	18 (32)	21 (37)	36 (63)
41	39	5 (13)	5 (13)	6 (15)	6 (15)	4 (10)	0 (0)	9 (23)	11 (28)	17 (44)	21 (54)
42	108	15 (14)	9 (8)	23 (21)	15 (14)	26 (24)	2 (2)	17 (16)	32 (30)	47 (44)	75 (69)
PD3	68	8 (12)	6 (9)	16 (24)	8 (12)	9 (13)	1 (1)	13 (19)	22 (32)	30 (44)	40 (59)
PD4	47	6 (13)	2 (4)	14 (30)	5 (11)	8 (17)	1 (2)	8 (17)	16 (34)	21 (45)	30 (64)
PD5	30	4 (13)	2 (7)	7 (23)	3 (10)	6 (20)	0 (0)	6 (20)	9 (30)	12 (40)	18 (60)
PD6	61	8 (13)	4 (7)	8 (13)	6 (10)	21 (34)	0 (0)	10 (16)	12 (20)	18 (30)	39 (64)

Table 19. Table indicating the number and percent of Rio Caunahue beetle species, in each sample, that occur today at restricted elevational ranges in the Lake Region determined through study of the modern fauna (Appendix A). See Plate 1 for stratigraphic position of each sample.

Sample Number	Number (%) Taxa Identified to Species	Number (%) Species not Collected in Modern Survey	Number (%) Species Ranging up to 150 m	Number (%) Species Ranging up to 650 m	Number (%) Species Ranging up to 1000 m	Number (%) Species Ranging up to 1200 m	Number (%) Species Occurring Only Between 1000-1200 m	Number (%) Species Ranging Above 1200 m	Total Number (%) Species Occurring Only Below 650 m	Total Number (%) Species Occurring Only Below 1000 m	Total Number (%) Species Occurring Only Below 1200 m
RIO CAUNAHUE											
BS-A3	68 (57)	7 (10)	4 (6)	21 (31)	15 (22)	13 (19)	3 (4)	5 (7)	25 (37)	40 (59)	56 (82)
A2	39 (46)	2 (5)	3 (8)	12 (31)	11 (28)	7 (18)	1 (3)	3 (8)	15 (38)	26 (67)	34 (87)
A1	44 (55)	4 (9)	7 (16)	12 (27)	8 (18)	7 (16)	2 (5)	4 (9)	19 (43)	27 (61)	36 (82)
1	3 (50)	0 (0)	0 (0)	1 (33)	1 (33)	1 (33)	0 (0)	0 (0)	1 (33)	2 (67)	3 (100)
2	1 (25)	0 (0)	0 (0)	0 (0)	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	1 (100)
3	4 (40)	0 (0)	0 (0)	2 (50)	1 (25)	1 (25)	0 (0)	0 (0)	2 (50)	3 (75)	4 (100)
4	4 (36)	0 (0)	1 (25)	1 (25)	1 (25)	1 (25)	0 (0)	0 (0)	2 (50)	3 (75)	4 (100)
5	2 (20)	1 (50)	0 (0)	1 (50)	0 (0)	0 (0)	0 (0)	0 (0)	1 (50)	1 (50)	1 (50)
6	1 (20)	0 (0)	0 (0)	0 (0)	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	1 (100)
7	2 (33)	0 (0)	0 (0)	2 (100)	0 (0)	0 (0)	0 (0)	0 (0)	2 (100)	2 (100)	2 (100)
8	2 (29)	0 (0)	0 (0)	1 (50)	1 (50)	0 (0)	0 (0)	0 (0)	1 (50)	2 (100)	2 (100)
9	3 (33)	0 (0)	0 (0)	1 (33)	1 (33)	1 (33)	0 (0)	0 (0)	1 (33)	2 (67)	3 (100)
10	2 (40)	1 (50)	0 (0)	1 (50)	0 (0)	0 (0)	0 (0)	0 (0)	1 (50)	1 (50)	1 (50)
11	2 (29)	0 (0)	0 (0)	1 (50)	1 (50)	0 (0)	0 (0)	0 (0)	1 (50)	2 (100)	2 (100)
12	2 (20)	1 (50)	0 (0)	0 (0)	0 (0)	1 (50)	0 (0)	0 (0)	0 (0)	0 (0)	1 (50)
13	1 (17)	0 (0)	0 (0)	0 (0)	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	1 (100)
14	3 (33)	1 (33)	0 (0)	1 (33)	1 (33)	0 (0)	0 (0)	0 (0)	1 (33)	2 (67)	2 (67)
15	2 (40)	0 (0)	0 (0)	1 (50)	0 (0)	1 (50)	0 (0)	0 (0)	1 (50)	1 (50)	2 (100)
16	4 (44)	0 (0)	1 (25)	1 (25)	1 (25)	1 (25)	0 (0)	0 (0)	2 (50)	3 (75)	4 (100)
17	12 (36)	2 (17)	0 (0)	3 (25)	2 (17)	5 (42)	0 (0)	0 (0)	3 (25)	5 (42)	10 (83)
18	5 (38)	1 (20)	0 (0)	2 (40)	1 (20)	1 (20)	0 (0)	0 (0)	2 (40)	3 (60)	4 (80)
19	6 (38)	2 (40)	1 (17)	1 (17)	1 (17)	1 (17)	0 (0)	0 (0)	2 (33)	3 (50)	4 (67)
20	6 (43)	1 (17)	0 (0)	2 (33)	2 (33)	1 (17)	0 (0)	0 (0)	2 (33)	4 (67)	5 (83)
21	13 (50)	2 (15)	3 (23)	3 (23)	3 (23)	2 (15)	0 (0)	0 (0)	6 (46)	9 (69)	11 (85)
22	5 (45)	0 (0)	1 (20)	2 (40)	1 (20)	1 (20)	0 (0)	0 (0)	3 (60)	4 (80)	5 (100)
23	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
24	3 (30)	0 (0)	0 (0)	1 (33)	1 (33)	1 (33)	0 (0)	0 (0)	1 (33)	2 (67)	3 (100)
25	5 (38)	0 (0)	0 (0)	2 (40)	2 (40)	1 (20)	0 (0)	0 (0)	2 (40)	4 (80)	5 (100)
26	1 (20)	0 (0)	0 (0)	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	1 (100)	1 (100)
27	23 (47)	3 (13)	4 (17)	8 (35)	5 (22)	3 (13)	0 (0)	0 (0)	12 (52)	17 (74)	20 (87)
28	5 (29)	1 (20)	1 (20)	1 (20)	1 (20)	1 (20)	0 (0)	0 (0)	2 (40)	3 (60)	4 (80)
29	7 (58)	0 (0)	1 (14)	3 (43)	2 (29)	1 (14)	0 (0)	0 (0)	4 (57)	6 (86)	7 (100)
30	10 (42)	0 (0)	1 (10)	2 (20)	6 (60)	1 (10)	0 (0)	0 (0)	3 (30)	9 (90)	10 (100)

TABLE 19. (Continued)

Sample Number	Number (%) Taxa Identified to Species	Number (%) Species not Collected in Modern Survey	Number (%) Species Ranging up to 150 m	Number (%) Species Ranging up to 650 m	Number (%) Species Ranging up to 1000 m	Number (%) Species Ranging up to 1200 m	Number (%) Species Occurring Only Between 1000-1200 m	Number (%) Species Ranging Above 1200 m	Total Number (%) Species Occurring Only Below 650 m	Total Number (%) Species Occurring Only Below 1000 m	Total Number (%) Species Occurring Only Below 1200 m
RIO CAUNAHUE Continued											
31	10 (56)	2 (20)	2 (20)	4 (40)	2 (20)	0 (0)	0 (0)	0 (0)	6 (60)	8 (80)	8 (80)
32	5 (38)	1 (20)	0 (0)	1 (20)	2 (40)	1 (20)	0 (0)	0 (0)	1 (20)	3 (60)	4 (80)
33	7 (50)	1 (14)	0 (0)	2 (29)	2 (29)	0 (0)	1 (14)	1 (14)	2 (29)	4 (57)	5 (71)
PD0	28 (47)	5 (18)	4 (14)	6 (21)	5 (18)	7 (25)	0 (0)	1 (4)	10 (36)	15 (54)	22 (79)
34	6 (38)	0 (0)	0 (0)	2 (33)	2 (33)	1 (17)	1 (17)	0 (0)	2 (33)	4 (67)	6 (100)
35	4 (36)	1 (25)	0 (0)	1 (25)	0 (0)	2 (50)	0 (0)	0 (0)	1 (25)	1 (25)	4 (100)
36	9 (57)	1 (11)	0 (0)	3 (33)	3 (33)	2 (22)	0 (0)	0 (0)	3 (33)	6 (67)	8 (89)
37	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
38	7 (41)	2 (29)	0 (0)	3 (43)	1 (14)	1 (14)	0 (0)	0 (0)	3 (43)	4 (57)	5 (71)
39	5 (38)	1 (20)	0 (0)	1 (20)	3 (60)	0 (0)	0 (0)	0 (0)	1 (20)	4 (80)	4 (80)
PD1	23 (42)	6 (26)	2 (9)	6 (26)	5 (22)	3 (13)	1 (4)	0 (0)	8 (35)	13 (57)	17 (74)
40	5 (45)	0 (0)	0 (0)	1 (20)	2 (40)	2 (40)	0 (0)	0 (0)	1 (20)	3 (60)	5 (100)
PD2	23 (40)	3 (13)	4 (17)	7 (30)	2 (9)	5 (22)	1 (4)	1 (4)	11 (48)	13 (57)	19 (83)
41	16 (41)	2 (13)	4 (25)	2 (13)	5 (31)	3 (19)	0 (0)	0 (0)	6 (38)	11 (69)	14 (88)
42	54 (50)	6 (11)	8 (15)	14 (26)	12 (22)	9 (17)	2 (4)	3 (6)	22 (41)	34 (63)	45 (83)
PD3	29 (43)	4 (14)	5 (17)	9 (31)	6 (21)	1 (3)	1 (3)	3 (10)	14 (48)	20 (69)	22 (76)
PD4	22 (47)	3 (14)	2 (9)	9 (41)	4 (18)	2 (9)	1 (5)	1 (5)	11 (50)	15 (68)	18 (82)
PD5	12 (40)	2 (17)	2 (17)	5 (42)	2 (17)	1 (8)	0 (0)	0 (0)	7 (58)	9 (75)	10 (83)
PD6	30 (49)	5 (17)	4 (13)	6 (20)	5 (17)	9 (30)	0 (0)	1 (3)	10 (33)	15 (50)	24 (80)

the Rio Caunahue lake was probably shallower 12,800 years ago than between 12,300 and 10,000 yr B.P. In addition, sediments at the bottom of the section exhibit less distinct rhythmic bedding than those higher in the sequence, suggesting deposition in shallower water. The absence of elmids in sample PD6 and fewer laminae of organic debris in the basal portion of the sequence probably indicate that stream flood waters were not discharging into the lake as frequently during that time. The relatively few numbers and low diversity of forest-dwelling taxa in sample PD6 may have been caused merely by the absence of a mechanism (i.e., stream discharge) to transport terrestrial elements into the basin of deposition. Shallow-water lacustrine conditions and apparent decrease of fluvial activity 12,800 years ago may indicate drier climatic conditions during that time than betwen 12,300 and 10,000 yr B.P. If that was the situation, moisture deficiency would have retarded optimal development of forest and its associated beetle fauna. Less than optimal forest development 12,800 years ago may also be reflected by the absence of wood-boring scolytids and bostricids in the PD6 assemblage. This is not meant to imply, however, that terrestrial vegetation was sparse in the Rio Caunahue Site area 12,800 years ago. The PD6 assemblage is dominated by forest-associated beetle taxa, indicating the presence of both trees and understory shrubs but, apparently, the forest was not as dense during that time as between 12,300 and 10,000 years ago. Indeed, tracts of open ground must have existed in the forest 12,800 years ago as inferred by the occurrence of <u>Listroderes</u> <u>dentipennis</u> in sample PD6. This interpretation is supported by cluster analysis (Figure 11). When compared to beetle faunas living today in the Lake Region, the PD6 assemblage is about equally similar in species composition to faunas in Bioassociation III (Valdivian Rain Forest) and Bioassociation II (Lowland Disturbed Forest). The analysis confirms that forest habitats existed in the Rio Caunahue Site area 12,800 years ago but that open-ground areas were also prevalent.

Climatic conditions, although possibly somewhat drier, were apparently not significantly different 12,800 years ago than between 12,300 and 10,000 yr B.P. in the Rio Caunahue Site area. That is to say, the climate was temperate and humid and probably not much different than conditions existing in the Central Valley and lower slopes of the Andes today. If the interpretation of the Puerto Varas Railroad assemblages is correct, environmental conditions in the Lake Region were sufficient to permit patchy forest growth in the Central Valley between about 15,000 to 14,000 years ago. The 12,800-year-old PD6 assemblage may reflect continuing development of forest habitats in the Lake Region and perhaps marks a late phase in the continuum from mostly open-ground habitats reflected by the 18,000- to 16,000-year-old Puerto Octay and 15,700-year-old Puerto Varas Park assemblages to optimal forest development indicated by the 12,300- to 10,000-year-old Rio Caunahue assemblages. If this is correct, the PD6 assemblage illustrates that, although amenable climatic conditions had been established much earlier, the biota had not reached equilibrium with the climatic conditions.

Interval 16 through 1 (about 9,500 to about 7,500 yr B.P.)

A significant decrease in both the numbers of fossils and diversity of beetle taxa, from all ecological categories, was noted in this interval compared to the preceding, PD6 through 17 interval. This change, however, is gradational, and the boundary was chosen where the transition becomes most evident. The upper boundary of interval 16 through 1 is an erosional unconformity between sparsely fossiliferous lacustrine sediments below and unfossiliferous fluvial gravels above. The rhythmic bedding of the lacustrine sediment and absence of shallow-water beetle taxa suggest that the lake was deep and probably areally extensive. Algae and other emergent vegetation grew in the shallow-water, lake-marginal areas as reflected by the abundant caddiflies, chironomids and charophyte oogonia in the deposits. The shoreline contained both marshy and muddy areas as inferred by the occurrence of the carabid, Bradycellus (Stenocellus) and the staphylinids, Thinodromus, Nomimocerus marginicollis, and Bledius cf. chilensis. Bledius is a lake-marginal mud burrower (Herman, 1962) while the other taxa mostly scavenge marshy shorelines.

The scarcity of stream-derived organic-rich laminae in interval 16 through 1 is apparently responsible for the notable decrease in terrestrial taxa compared to interval PD6 through 17. The decrease of fluvial influence is also evidenced by the sparsity of stream-dwelling elmids (only one Austrolimnius was recovered from the basal portion of the interval) and dobson flies. A period of decreased precipitation may be inferred by this finding which, in turn, could suggest that fewer forest-dwelling taxa lived adjacent to the site of deposition. However, lowering of lake level would, presumably, also have accompanied a decrease in precipitation. As shown earlier, this was not the case.

Indeed the beetles, even though not as common or diverse as in interval PD6 through 17, indicate that a dense, well-established forest existed adjacent to the lake during that time. This implies that a change in the depositional system, in this case an increased sedimentation rate and less frequent flood water discharge, resulted in fewer terrestrial beetles deposited in the area of the lake that was subsequently sampled for this study.

The presence of a forest proximal to the site of deposition is indicated by the occurrence of the following beetle taxa that today live on a variety of plants in the Valdivian Rain Forest: *Caenocara* (anobiid), cf. *Diontolobus* sp. 1 (trogositid), *Perilopsis flava* (nitidulid), *Orchesia* sp. 1 (melandryid), cf. *Crepidodera* sp. 1 (chrysomelid) and *Dasydema hirtella* (curculionid). The commonly occurring leafhoppers and Hemiptera also indicate abundant vegetation near the site. *Nothofagus*, reflected by the coccinellid *Strictospilus darwini* and the weevils, *Polydrusus nothofagi*, *Wittmerious longirostris* and Erirrhininae n. sp. 2, must have been a commonly occurring tree in the forest. The existence of a well-established forest is confirmed by the wood-boring scolytids, including *Gnathotrupes* and *Phloeotribus* cf. *spinnipennis*. The forest floor was inhabited by the carabid, *Parhypates* (*sensu stricto*); the leiodid, *Dasypelates* sp. 1; the staphylinid, *Neophonus bruchi*; the elaterid, *Negastrius*; the pselaphids, *Dalminiomus* and *Tryopsis*; crytorhynchine weevils, and ants, pseudoscorpions and spiders.

The fossil evidence indicates that no major environmental or climatic changes occurred between about 9,500 and about 7,500 years ago in the Rio Caunahue area. It appears that climatic conditions similar to today, in the Rio Caunahue area, were established by at least 12,800 years ago, and remained essentially stable until at least 7,500 yr B.P. and, as will be shown below, probably much later. Although species diversities in each assemblage of this interval were too low to test this interpretation by cluster analysis, the data presented in Tables 18 and 19 show that most of the taxa recovered do not range above 1000 m in the Lake Region today implying similar climatic conditions to areas inhabited by the existing Valdivian Rain Forest biota.

Interval A1 through BS-A3 (5,200 to 4,500 yr B.P.)

Although no paleoecological record is preserved younger than about 7,500 yr B.P. at the Rio Caunahue main section, additional fossiliferous lacustrine sediment, dating from 5,200 to 4,500 yr B.P. and cropping out about 500 m upstream from the main section, escaped erosion and provided an extension of the record. Unfortunately, no information is available for the 7,500 to 5,200 yr B.P. interval. As at the main exposure, stream erosion has truncated the top of the upstream sequence terminating the Rio Caunahue record at 4,500 yr B.P. The beetle assemblages are remarkably similar to those recovered from interval PD6 through 17 and, consequently, reflect a similar paleoenvironmental and paleoclimatic setting. Cluster analysis confirms this similarity because the BS-A3 assemblage clusters with assemblages from selected samples in interval PD6 through 17 (Figure 11). The beetle assemblages from interval A1 through BS-A3 are, however, more diverse than those from interval PD6 through 17 and provide additional paleoecological information.

The aquatic environment at the Rio Caunahue Site may have been slightly different between 5,200 and 4,500 years ago than between 12,800 and about 7,500 yr B.P. The rhythmic bedding of the sediments of interval A1 through BS-A3 indicates deposition in deep water similar to interval 16 through 1 and, at least, the upper part of interval PD6 through 17. Unlike the lower intervals, however, the occurrences of the dytiscids, Rhantus validus and Liodessus delfini, in interval A1 through BS-A3, suggest that shallow water habitats with abundant aquatic plant growth were not far removed from the site of deposition, probably implying that the sample site was somewhat closer to shoreline than the main section. In contrast to interval 16 through 1, the numerous laminae of organic debris and presence of elmids, including Neoelmis n. sp. (Plate 8, Figure 3) and Hydora annectens (Plate 5, Figure 3), and stoneflies and dobson flies in interval A1 through BS-A3, indicate that periodic fluvial discharge into the lake was prevalent between 5,200 and 4,500 years ago. Both the beetle and nonbeetle taxa found in interval A1 through BS-A3, indicative of emergent flora in the shallow-water areas, are essentially the same as those in interval PD6 through 17. This is also true of the shoreline taxa, except for the addition of the carabids, Gipsyella patagonica (Plate 8, Figure 2) and Metius sp. 1, both of which prefer marshy areas. Collectively, the shoreline taxa suggest a variety of microhabitats around the margins of the lake.

The terrestrial beetle taxa recovered from interval A1 through BS-A3 are mostly the same as those from interval PD6 through 17 and indicate that a well-developed *Nothofagus* forest was present in the site area 5,200 to 4,500 years ago. Beetle taxa not found in interval PD6 through 17 but recovered from interval A1 through BS-A3, that live today on numerous plants in the Valdivian Rain Forest, strengthen the interpretation. These taxa are the carabids, *Aemalodera centromaculata*, *A. dentimaculata* and *Plagiotelum irinum*; lucanids, *Chiasognathus granti* and *Sclerognathus caelatus*; scarabaeids, *Sericoides* (e.g., *S. chlorosticta*); cantharids, *Oontelus* and *Hyponotum* cf. *krausei*; tenebrionid, cf. *Adelium*, and oedemerid, *Platylytra vitticollis*. Forest-floor dwelling beetle taxa where common in interval A1 through BS-A3 and were again the same as those collected from interval PD6 through 17 except for *Ceroglossus valdiviae* (carabid) and cf. *Hydnobiotus* (leiodid) which were found only in interval A1 through BS-A3. This is also true for the wood-boring beetles except for the scolytids, *Monarthrum* (Plate 5, Figure 1) and cf. *Araptus* and the weevil, *Dryopthorus canus* which were not present in interval PD6 through 17. The anobiids, *Byrrhodes* (e.g., *Byrrhodes nigricolor*), that live today in fungal growths on trees in the Valdivian Rain Forest, were recovered only from interval A1 through BS-A3. Although the forest was evidently well-established and dense 5,200 to 4,500 years ago in the Rio Caunahue area, the occurrence of *Listroderes dentipennis* implies that open patches existed in the forest.

The beetle assemblages from interval A1 through BS-A3 leave little doubt that the Rio Caunahue lake was situated in a rain-forest setting between 5,200 and 4,500 years ago. This interpretation is supported by the data presented in Tables 18 and 19 which show that most of the taxa do not range above 1000 m, that is above the Valdivian Rain Forest in the Lake Region today. Furthermore, cluster analysis shows that the beetle assemblage from sample BS-A3, in addition to being very similar to assemblages from interval PD6 through 17, is similar in species composition to faunas in Bioassociation III (Figure 11). It is inferred from these findings that climatic conditions, between 5,200 and 4,500 yr B.P., were not significantly different than areas in the Lake Region occupied by the Valdivian Rain Forest today. These conditions evidently remained reasonably stable from 12,800 to 4,500 yr B.P., excluding the 7,500 to 5,200 year period of no record.

Discussion

The Rio Caunahue section was exposed only to the 12,800 yr B.P. level (sample PD6) during the final (1979) visit to the site for this investigation. An additional 5 m of lacustrine sediments was exposed beneath sample PD6 when Ashworth revisited the site in 1983. Although most of the newly exposed section consisted of inorganic silts and clays, Ashworth located an organic horizon, the basal plant debris (13,900 ± 560 ^{14}C yr B.P.) horizon in the Rio Caunahue sequence, 76 cm below sample PD6. The discovery and radiocarbon dates of these older lake sediments have caused a reevaluation of the inferred glacial history of the Lago Ranco basin and consequently the entire Lake Region. Mercer and Laugenie (1973) mapped the end moraines west of Lago Ranco and estimated the inner (eastern), undated, moraine ridge to have been deposited 14,500 to 14,000 years ago, implying that the basin was ice-filled at that time. They also inferred that the glacier had retreated out of the basin by 12,000 yr B.P., the age of the oldest known organic horizon then exposed at the Rio Caunahue Site. That postulated sequence of events was compatible with Mercer's (1972a) opinion that final readvance of the Llanquihue Lobe occurred about 14,800 yr B.P. Later, Mercer (1976) advocated an extremely rapid deglaciation of the Lake Region and revised the date of the final readvance, and age of the easternmost end moraines on the western margin of Lago Ranco, to 13,000 yr B.P. Discovery of progressively older organic horizons, 12,800 and 13,900 yr B.P., at the site prompted Mercer (1983) to revert to his original view that the final readvance occurred about 14,500 years ago. There is no doubt that final deglaciation of the Lago Ranco basin must have occurred prior to deposition of the basal lacustrine sediments exposed at the Rio Caunahue Site.

The following interpretation of the depositional history of the Rio Caunahue Site is based on geomorphological, stratigraphical, sedimentological, and paleontological evidence. Glacial debris and possibly colluvial gravels floored the valley after retreat of the Ranco Lobe from the basin and prior to deposition of lacustrine sediment. Sedimentation began in a drowned arm of Lago Ranco in the lower reaches of the Rio Caunahue valley before 13,900 years ago. The initial sediments were mostly inorganic, suggesting little vegetation in and around the lake at that time. The lake was presumably at the level of the highest terrace, about 150 m above present lake level, and drained by a western outlet. The glacier terminus was probably still at low elevation in the drowned valley east of the site and, as reflected by dropstones incorporated into the lake sediments, icebergs were calving into the lake. Colonization of the lake margin began about 13,900 years ago, the age of the basal organic horizon in the sequence. Beetle assemblages indicate that by 12,800 yr B.P. the climate had ameliorated sufficiently to permit invasion of forest biota around the lake and by 12,300 yr B.P. a well-established forest had developed in the Rio Caunahue area.

Climatic conditions similar to those of lowland areas in the Lake Region today were established by at least 12,800 years ago and, assuming no change during the 7,500 to 5,200 yr B.P. interval of no record, remained relatively stable until at least 4,500 yr B.P. The pollen profile presented by Heusser (1981) for the late glacial portion of the Rio Caunahue sequence is consistent with these interpretations. Correlation using radiocarbon dates and tephra horizons indicates that his pollen profile spans the 13,000 to 10,000 yr B.P. interval. Heusser divided the sequence into three pollen zones. The lower zone (RC-3) was defined by the presence of *Podocarpus andinus* and slightly higher percentages of Graminae and the upper zone (RC-1) was differentiated by a slight increase of *Weinmannia* at the expense of the *Nothofagus dombeyi* type of pollen. Heusser, however, did not indicate why he divided the sequence into three zones and did not interpret the climatic conditions reflected by the spectrum. The remarkably consistent relative percentages of pollen types and dominance of *Nothofagus* imply forest conditions and a relatively constant climate.

Lake level remained higher than today until about 4,500 yr B.P. because the western outlet was not deeply entrenched through the morainal ridges. Throughout much of the time that the lake was in existence, periodic stream flood waters contributed organic detritus to the basin of deposition and, on occasion, volcanic ash was deposited in the lake. During the Late Holocene a morainic dam was breached by the western outlet and partial, perhaps catastrophic, drainage of the lake occurred. Downcutting of the Rio Caunahue through the lacustrine sediments commenced, exposing the sequence, and the exposed lake bottom was colonized by Valdivian Rain Forest biota. Today, the Rio Caunahue exposure is rapidly being altered by continuing fluvial erosion and mass wasting.

DISCUSSION OF THE LATE QUATERNARY CLIMATIC HISTORY OF THE LAKE REGION

Three distinct beetle fossil associations are present in full glacial to late Holocene sediments of low elevation sites in the Lake Region of southern Chile. Between 18,000 and 15,700 yrs B.P. beetle faunas living in the Central Valley consisted primarily of species adapted to open-ground, bog habitats. The open-ground forms were joined by arboreal species between about 15,000 to 14,000 years ago, forming transitional faunas of mixed habitat specialties. By 12,800 yr B.P. faunas were dominated by obligate woodland taxa, indicating that forest conditions were well established in the Central Valley by that time. Those conditions remained relatively stable until at least 4,500 yr B.P., the youngest assemblages evaluated for this study.

According to Mercer (1976, 1984a) and Porter (1981), the last glacial maximum (Llanquihue II) in the southern Lake Region culminated about 20,000 to 19,000 years ago and was generally synchronous with last glacial maxima in North America, Europe, Australia, New Zealand, and Antarctica. Geological investigations have shown that by about 18,900 yr B.P. the Llanquihue Lobe had receded from the position of its maximum extent (Porter, 1981; Mercer, 1984a) and by 16,000 yr B.P. had retreated far enough to open the eastern outlet of Lago Llanquihue (Mercer, 1976). This interval of contracted glaciers, lowered lake level, and presumably higher temperatures, was termed the Varas Interstade (Mercer, 1972a,

1976) and was suggested to be coeval with the Erie Interstade recognized by Mörner and Dreimanis (1973) in eastern North America (Mercer, 1976).

The low species diversity of the 18,000- to 15,700-year-old Puerto Octay and Puerto Varas Park beetle assemblages and dominance of open-ground taxa (e.g., *Listroderes dentipennis*) may suggest that the faunas existed in a stressed, possibly cold environment. No modern analog has been found for these assemblages but they are almost identical in species composition and diversity to assemblages from the Rupanco Site (24,000 yr B.P. and 28,490 yr B.P.) near Lago Rupanco in the Lake Region, and the Dalcahue Site (14,970 yr B.P.) on Isla Chiloe, which are believed to have accumulated during glacial conditions (Ashworth and Hoganson, unpublished). The interpretation that the 18,000- to 15,700-year-old beetle assemblages reflect cold climatic conditions is supported by Heusser's (1974) pollen diagram from the 18,000 to 16,000 yr B.P. interval at the Puerto Octay Site interpreted to indicate essentially treeless, probably tundra conditions and Heusser and others' (1981) palynological study of a core from Isla Chiloe.

In the absence of a modern analog, the paleoclimatic significance of the Puerto Octay and Puerto Varas Park beetle assemblages is equivocal but strongly suggests that glacial retreat during the Varas Interstade was not caused by a significant climatic warming. Perhaps the temperature fluctuation that caused the glacier recession was such a minor or ephemeral event that it did not affect the beetle fauna (or flora) existing in the Central Valley. There is also the possibility that the glacial retreat was not caused by thermal increase. Decreased precipitation, especially during times of generally depressed temperatures, may have caused glacier recession. In consideration of Heusser and others' (1981) estimate that mean annual precipitation was about 1000 mm less than today in the Lake Region during that time interval, the possibility of glacial withdrawal through starvation cannot be ruled out.

Cessation of peat accumulation at numerous sites along the southern edge of Lago Llanquihue by rising lake level has been taken as evidence for a glacial advance that blocked the eastern outlet of the lake (Mercer, 1972a, 1976; Porter, 1981). Because the evidence is indirect, a controversy has developed as to how many readvances took place and when they occurred. Mercer (1972a) proposed one advance about 14,800 yr B.P. but he later (1976) retracted that date in favor of a 13,000 yr B.P. culmination. Porter (1981), however, postulated two readvances (Llanquihue III) culminating about 15,000 and 13,000 yr B.P. The only direct evidence for a final glacial incursion into the Lake Region comes from the island of Chiloe where Mercer (1984a) obtained dates of 14,355, 14,970, and 15,600 yr B.P. on peats buried by till of an end moraine of the Reloncavi Lobe. From this evidence Mercer (1984a) inferred that there was only one late glacial advance that culminated between 15,000 and 14,500 years ago.

If the Llanquihue Lobe was acting in concert with the Reloncavi Lobe and the Llanquihue Lobe closed the eastern outlet of Lago Llanquihue, the advances must have begun shortly after 15,700 yr B.P., the age of the lowest peat horizon (Puerto Varas Park Site) drowned by the rising lake level. If so, the Llanquihue Lobe terminus must not have receded very far to the east of the outlet during the previous retreat. The regional extent of the event is unknown but presumably the end moraines that dam lakes Ranco, Rupanco and Puyehue were formed at that time. Deglaciation proceeded rapidly after this last major readvance into the Lake Region and by 12,500 yr B.P. the glaciers had withdrawn into the mountains (Mercer, 1976, 1982, 1984a).

The final period of expanded glaciers lasted only a few hundred years because by about 15,000 yr B.P. climate had ameliorated sufficiently to permit migration of forest-dwelling beetles into the Central Valley as documented at the Puerto Varas Railroad Site. These transitional beetle assemblages of mixed environmental indicators mark the pivotal shift toward interglacial conditions in the Lake Region between about 15,000 and 14,000 years ago. Initiation of post-glacial warming at about that time is also indicated by the temperature curve, based on palynological data presented by Heusser and others (1981). In addition, radiocarbon dates obtained at the Rio Caunahue Site suggest that lacustrine deposition began after final deglaciation of the Lago Ranco basin, prior to 13,900 yr B.P. The recognition of a full glacial readvance and subsequent rapid warming is important because this change from glacial to interglacial conditions is generally synchronous with similar events recorded in other areas of the world.

Glacial studies in New Zealand have shown that the last main Pleistocene glacial event, the Kumara-3 pulse of the Otira Glaciation, ended before 14,000 yr B.P. and was followed by rapid recession (Suggate and West, 1967; Zinderen Bakker, 1969; Suggate and Moar, 1970; Burrows and Gallatly, 1982; Chinn, 1982). Palynological studies indicated that warming, accompanied by postglacial spread of shrubland and forest, began about 14,000 yr B.P. (Moar, 1973; Moar and McGlone, 1977; Wilson, 1978), and by 12,000 yr B.P. a podocarp forest had expanded widely over much of New Zealand (McGlone and Topping, 1973). Stewart and Neall (1984) determined the accumulation rates of detrital quartz and biogenic carbonate and silica in a deep-sea core recovered east of southern North Island. The percentages of these sedimentary constituents, much higher during glacial than post-glacial times, showed a synchronous, rapid decline at about 14,700 yr B.P. A similar late glacial history is also documented in Australia and Tasmania. Glaciers had mostly disappeared by 14,500 yr B.P. from the Snowy Mountains in southeast Australia (Bowler and others, 1976). Glacial aridity, reflected by maximum eolian activity and lowered lake levels in Australia, ended about 14,500 yr B.P. (Bowler, 1978) and by 12,000 years ago the dunes were stabilized. The post-glacial warming trend in southern Tasmania began well before 11,500 yr B.P. (Macphail, 1979) and the glaciers had begun to retreat about 14,000 years ago (Burrows, 1979).

Marion Island south of Africa in the southwest Indian Ocean, ice-covered during the last glaciation, was mostly deglaciated by 14,000 yr B.P. as a result of abrupt warming (Zinderen Bakker, 1969, 1973).

A similar late-glacial sequence of climatic events has also been recognized in Europe. Although poorly dated, the last major readvance of the Scandinavian Ice Sheet to the position of the Pomeranian moraines in Germany occurred about 14,800 years ago (Mercer, 1972b, 1984a). Rapid recession of the Alps glaciers in Switzerland between 14,000 and 13,000 yr B.P. was documented by Anderson (1981).

The chronology of glacial activity during the late glacial in North America is better known than in Europe because of the availability of more radiocarbon datable sequences. The last major readvance (Cary) of the Laurentide Ice Sheet south of the Great Lakes region culminated about 14,700 to 14,300 years ago and was followed by rapid recession (Dreimanis, 1977; Mayewski and others, 1981; Mickelson and others, 1983). By 14,500 yr B.P. the ice had retreated into the basins of the Great Lakes (Mickelson and others, 1983). However, farther west, the Des Moines Lobe did not reach its late Wisconsinan maximum position in Iowa, Minnesota, and South Dakota until about 14,000 yr B.P. (Mayewski and others, 1981; Clayton and Moran, 1982; Mickelson and others, 1983). Soon after 14,000 yr B.P. the Laurentide ice front was in full retreat throughout its southern margin--the beginning of the Cary-Port Huron interstade (Mayewski and others, 1981). Mayewski and others (1981) inferred that the recessional event after the short-lived Cary advance was initiated by rapid climatic amelioration.

Paleontological records from areas south of the Laurentide ice front reflect the onset of the transition to interglacial conditions shortly after 15,000 yr B.P. As a result of his paleobotanical studies in Florida and Tennessee, Watts (1983) determined that the first response of trees to warming climate in the southeast United States occurred about 15,000 yr B.P. In the Midwest, tundra flora present between 20,500 and 14,700 yr B.P. at Wolfcreek, Minnesota, was replaced by Picea earlier than 13,600 years ago (Birks, 1976). As the Laurentide Ice Sheet was receding in the Midwest about 14,000 years ago, a mixed forest of mostly deciduous taxa replaced the Picea forest (Webb and others, 1983). Between 16,700 and 15,300 yr B.P. the arctic-subarctic beetle fauna living south of the Laurentide ice front was nearly totally exterminated as a result of climatic warming (Schwert and Ashworth, 1984).

Rapid deglaciation of moutainous and intermontane areas in western North America also occurred at about that time. Valley glaciers in the Colorado Front Range began to recede after the last Pinedale Glaciation advance between 14,600 and 13,000 years ago (Nelson and others, 1979; Madole, 1980). Deglaciation of many mountain valleys, according to Porter and others (1983), started well before 14,000 yr B.P. By about 15,000 yr B.P. one of the largest glaciers in the southern Rocky Mountains, the San Juan icefield in southwestern Colorado, had disintegrated (Carrara and Mode, 1979; Carrara and others, 1984); and by 13,680 years ago the South Park Range was largely ice-free (Carrara and others, 1984). Deglaciation of the Pinedale ice cap on the Yellowstone Plateau was mostly completed by about 14,000 yr B.P. (Pierce, 1979) and extensive deglaciation of west-central Montana occurred prior to 12,750 years ago (Lemke and others, 1975). Termination of the Angel Lake Glaciation occurred before 13,000 yr B.P. in Lamoille Canyon, Ruby Mountains, Nevada (Wayne, 1984).

The Fraser-Puget Lobe of the Cordilleran Ice Sheet attained its maximum late Pleistocene position between about 15,000 and 14,000 years ago in the Puget lowland of Washington during the Vashon Stade of the Fraser Glaciation (Mayewski and others, 1981; Hollin and Schilling, 1981; Barnosky, 1981) and withdrew quickly during rapid climate warming.

Tundra-parkland vegetation was replaced by a mixed woodland of subalpine and lowland conifers at Davis Lake in the southern Puget Lowland as a result of this climate amelioration (Barnosky, 1981). In the Cascade Range of Washington, valleys south of the Cordilleran Ice Sheet were mostly deglaciated between 14,000 and about 12,500 years ago (Porter and others, 1983; Beget, 1984). Elk Valley in British Columbia was also ice free before 13,400 yr B.P. (Ferguson and Osborn, 1981).

Rapid glacial retreat and ice disintegration, marking the shift to interglacial conditions, has been dated at about 13,500 yr B.P. in the north-central Alaskan Range (Ten Brink and Ritter, 1980) and at about 14,000 yr B.P. in the St. Elias Mountains on the Alaskan-Yukon border (Denton, 1970). The onset of interglacial climatic warming has also been documented by pollen records from many areas of Alaska. Ager (1983) found that a full glacial herbaceous tundra flora was replaced by dwarf Betula about 14,500 to 14,300 years ago in the Squirrel Lake area in northern Alaska. Climatic warming just before 14,000 yr B.P. is indicated by the pollen spectrum from Hidden Lake on the Kenai Peninsula (Ager, 1983). In addition, Rymer and Sims (1982) noted a sedimentological break in a core from Hidden Lake at the same level as the change in the pollen record and suggested that the break marks the time of recession of the glacier from the Hidden Lake drainage basin. The glacial to interglacial change from herbaceous tundra plants to dwarf Betula, at about 14,000 yr B.P., has also been recognized in numerous cores from southwest Alaska (Ager, 1983).

In the tropical areas of the world that have adequate radiocarbon dating control (northern South America, New Guinea and equatorial

Africa), glaciers reached their maximum late-glacial extent about 15,000 to 14,000 years ago (Mercer, 1983; Clapperton, 1983). Glacial retreat began earlier than 13,000 yr B.P. in Venezuela (Schubert, 1974) and was mostly completed by 12,700 yr B.P. (Hollin and Schilling, 1981). Glaciers in Colombia (Gonzalez and others, 1966; Herd and Naeser, 1974) and Peru (Mercer, 1982, 1983) also began to distintegrate about that time. Deglaciation in the mountain valleys of New Guinea started shortly after 15,000 yr B.P. (Walker, 1978; Bowler and others, 1976). A pollen record from the Mt. Carstensz area of New Guinea was interpreted by Burrows (1979) to indicate the beginning of post-glacial warming by about 14,000 years ago. The youngest moraines in the Ruwenzori Range of Uganda, just north of the equator in the Lake Victoria area, were abandoned shortly after 14,700 yr B.P. (Livingstone, 1962). Deglaciation of mountainous areas in Ethiopia was completed by 11,500 years ago (Hamilton, 1977; Gillespie and others, 1983). Pollen records from southern and eastern Africa reflect post-glacial warming beginning about 14,000 years ago (Coetzee, 1967; Zinderen Bakker and Coetzee, 1972). The tropical and subtropical areas of Africa, almost totally arid during the late glacial maximum, were inundated by monsoonal rains during the climatic amelioration about 14,000 yr B.P. (Fairbridge, 1983).

Additional evidence for the initiation of post-glacial warming about 15,000 years ago is provided by deep-sea and ice-cap cores. Based mainly on foraminiferid productivity, Ruddiman and McIntyre (1981) measured meltwater influx into the North Atlantic and determined that between 16,300 and 13,000 years ago the Northern Hemisphere ice sheets disintegrated rapidly. Slightly more than 50 percent of the ice disappeared during that time interval. Duplessy and others (1981) also estimated that the beginning of deglaciation in the North Atlantic occurred about 15,000 yr B.P., but Berger and others (1985) suggested that the event began about a millenium later. Hays (1978) reported that the relative abundance of the cold-indicating radiolarian, *Cycladophora davisiana*, in a core from the southern Indian Ocean, declined abruptly about 15,000 years ago and noted that many cores from the Subantarctic sector of the Indian Ocean showed similar trends. He also stated that a sharp reduction of sea-ice cover south of the oceanic Polar Front occurred about 14,000 yr B.P. The transition from low oxygen-isotope values, representing the last glacial maximum, to higher values, indicating change to post-glacial climatic conditions, occurred about 15,000 to 14,000 years ago in the Dome C (Lorius and others, 1979) and the Byrd and Vostok ice cores (Burrows, 1979). Microparticle accumulation in the Greenland and Antarctic ice cores, presumably resulting from the high eolian activity during the late glacial maximum in many parts of the Southern Hemisphere, also declined abruptly about 15,000 to 14,000 years ago (Bowler, 1978; Thompson and Mosley-Thompson, 1981; Fairbridge, 1983).

The concept that the last, major, globally synchronous, glacial-interglacial transition occurred between about 15,000 to 14,000 years ago has been strengthened during the last decade or so by investigations of deep-sea cores and the recognition that many areas of western North America were deglaciated much earlier than previously thought. The sparsity of information from the Southern Hemisphere, especially the temperate, glaciated areas of South America, has hindered recognition of the magnitude of the event. The final, unequivocal, major, climatically controlled excursion of glaciers into the Lake Region of Southern Chile about 15,000 yr B.P., documented by Mercer (1984a), and subsequent climatic amelioration implied by beetle fossils provide additional evidence to support the concept. It is interesting to note, however, that as early as 1972, Mercer (1972b) suggested that the last major world-wide warming occurred about that time and lobbied, to no avail, for placement of the Pleistocene-Holocene boundary at the onset of that warming trend rather than at 10,000 yr B.P. Recently, he reflected (Mercer, 1984a) that this last glacial-interglacial cycle is more suitable for comparison of the timing of climatic changes between the Northern and Southern Hemispheres because it was a much more sharply defined event, in both hemispheres, than the earlier late-glacial maximum when the Laurentide ice front oscillated over a rather long time interval between 21,000 to 14,000 years ago.

The climatic amelioration that began about 15,000 years ago was uninterrupted through the late glacial interval; and by 12,800 yr B.P. forest habitats, although probably somewhat open, were well established in the Lake Region, as indicated by beetle assemblages from the Rio Caunahue Site. Climatic conditions similar to those of the lowland areas today were reached by that time and remained relatively stable until at least 4,500 years ago. Beetle species associations, virtually the same as those observed in the undisturbed Valdivian Rain Forest today, were not, however, established until about 12,300 yr B.P.; this illustrates the role of succession in development of the Lake Region's beetle fauna. There is no indication of climatic deterioration that would have caused readvance of glaciers into the Central Valley about 13,000 yr B.P., as proposed by Porter (1981), or an emphatic cold period coeval with the European Younger *Dryas* Stade, as advocated by Heusser (1974, 1984a,b). Results of the present study are consistent, however, with the chronology of glacier activity in the Lake Region determined by Mercer (1982, 1983, 1984a, 1984b).

Perhaps the most controversial topic concerning the late-glacial climatic history of southern South America is whether or not a climatic deterioration equivalent to the European Younger *Dryas* Stade occurred in southern Chile. Heusser (1966a) initially proposed an event equivalent to the Younger *Dryas* in the Lake Region from the Alerce I pollen record recovered by coring a bog located northeast of Puerto Montt. The dominance of *Nothofagus dombeyi*-type pollen and presence of *Podocarpus nubigenus* and *Pseudopanax laetiverens* between 11,000 and 10,000 yr B.P. (Zone III) suggested to him that the post-glacial warming trend was interrupted by cooler and moister conditions during that time. He employed the European system of three late glacial and five post-glacial pollen zones and proposed that the European chronology was applicable in correlating the Chilean record with that of the northwestern United States, even though many of the Chilean zonal boundaries did not coincide with the temporal boundaries of the European zonation. He interpreted his data to lend support for harmonious climatic fluctuations between the Northern and Southern Hemispheres during late glacial time.

Heusser (1966b) again used European zonal terminology in presenting interpretations of additional pollen profiles from the Lago Llanquihue area and suggested that the spectra supported his argument for a Younger *Dryas*-equivalent event in the Lake Region. His interpretation was based on the occurrence, in the 11,000 to 10,000 yr B.P. interval, of the same plant taxa as those found in Zone III of the Alerce I core plus an influx of *Fitzroya*-type pollen. Based on that information he estimated that summer temperature was about 5°C lower than today and speculated that glaciers became stationary or even advanced during that time. He again proposed in-phase, hemispheric, climatic changes and stated that back to 16,000 yr B.P. temperature trends have been identical in equatorial latitudes as well as in higher latitudes of both hemispheres.

Heusser (1974) interpreted a similar pollen association, from what he assumed to be the 11,000 to 10,000 yr B.P. interval at the Puerto Octay Site, to reflect a period of deteriorated climate coeval with the Younger *Dryas*. His assumption was based however, as was discussed earlier in the section concerning the Puerto Octay Site, on faulty biostratigraphic correlation with pollen diagrams from Alerce. Heusser's interpretation was therefore founded on a circular argument and *a priori* reasoning and illustrates the caution that Watts (1980) expressed in using pollen zones for correlation even in localized areas. Heusser did note that a Younger *Dryas*-equivalent climatic deterioration was not supported by any geological evidence of an ice advance.

The high percentages of *Podocarpus andinus* pollen between 10,440 and 10,000 yr B.P. at the Rucañancu Site (39°33'S) was the evidence that prompted Heusser (1984a, 1984b) to infer that climate during that period was 5-8°C colder and about 2,000 mm annually wetter than present in the site area. He cited the occurrence of that plant as definitive evidence for a Younger *Dryas*-equivalent climate deterioration in the northern part of the Lake Region.

Thus, Heusser's argument for an event equivalent to the Younger *Dryas* in southern Chile is based on the dominance of *Nothofagus dombeyi*-type pollen and occurrence of *Podocarpus nubigenus*, *Pseudopanax laetiverens* and, at times, *Fitzroya* pollen, in samples from the 11,000 to 10,000 yr B.P. interval from the southern Lake Region and *Podocarpus andinus* in a spectrum from the northern Lake Region. Birks (1981) reviewed the assumptions involved and limitations of this floristic or indicator-species palynological approach. He pointed out that the major limitation of the method is that it must be assumed that the distribution of a particular indicator-species is controlled by one or a few climatic variables. The autecology of the species must be precisely known. Heusser's argument calls for distribution of his indicator-species to be controlled by temperature alone. It is suggested here that their distribution may be influenced more by edaphic, moisture and, in the case of *Fitzroya*, historical factors rather than temperature.

Although, on numerous occasions, Heusser cited the dominance of *Nothofagus dombeyi*-type pollen as indicative of cool and humid climatic conditions, seven of the ten species of Nothofagus found in the Chilean flora are grouped into that pollen category, and species cannot be differentiated on pollen alone (Heusser, 1966b, 1974). Species that generate N. dombeyi-type pollen range from sea-level to timberline in the Lake Region and occur as far south as the southern tip of South America. In addition, Heusser has not been consistent in evaluating the significance of N. dombeyi-type pollen in his profiles. For example, he (1972a) interpreted N. dombeyi-type pollen at the Puerto Eden Site (Isla Wellington) to reflect decreased precipitation and decreased storminess because, as he pointed out, cooling and greater storm frequency are restrictive to N. dombeyi-type pollen. At that site, he suggested that occurrence of this pollen indicated enhanced edaphic conditions for forest development.

The distributions of Podocarpus nubigenus, P. andinus and Pseudopanax laetiverens are probably also controlled more by edaphic and moisture conditions rather than temperature. Podocarpus nubigenus is characteristic of peaty paludified soils in moist climates (Heusser, 1972a). P. andinus is a low latitude species adapted to withstand summer drought conditions (Heusser, 1984b). According to (Munoz S., 1980), Pseudopanax laetiverens thrives in many low-elevation, marshy areas in southern Chile today. As with N. dombeyi-type pollen, Heusser has been inconsistent in interpretation of the climatic significance of P. nubigenus. In section 2 on Isla Chiloe, a site older than 57,000 yr B.P., he interpreted the peak of P. nubigenus, when herb percentages were lowest, to indicate an episode of maximum warmth (Heusser and Flint, 1977).

Of all the species Heusser used to imply thermal decline equivalent to the Younger Dryas, the most puzzling is the influx of Fitzroya pollen in some diagrams. It is true, as Heusser (1974, 1981) noted, that today Fitzroya inhabits upper montane areas in the Lake Region. However, prior to European colonization, Fitzroya forests were extensive in the Central Valley (Heusser, 1974, 1981). The plant's absence in areas of low elevation today has resulted from logging.

Heusser and Streeter (1980), using a multivariate approach, derived regression equations relating taxa from surface pollen samples to mean summer temperatures and annual precipitation based on estimates from meteorological records. They then applied the equations to the Alerce I fossil pollen spectrum and generated paleotemperature and paleoprecipitation curves back to 16,000 yr B.P. Their exercise showed a warming trend after about 16,000 yr B.P. Maximum summer temperatures, about 7°C warmer than at Alerce today, were reached about 11,300 yr B.P. A cold interval between 11,300 and 9,400 yr B.P. (peaking at about 10,250 yr B.P.), at which time they estimated summer temperature to have been about 6°C lower than today's, interrupted the warming trend. According to their paleoprecipitation curve, although they noted that their estimate was unrealistically high, annual precipitation was 3,000 mm more than today during the inferred cold interval. They concluded that the extremely wet and cold interval was equivalent to the Younger Dryas Stade. It should be noted that the 6°C thermal decline postulated during the interval is greater than Heusser and others' (1981) estimate, using the same multivariate technique on the pollen diagram from

Taiquemó (Isla Chiloe), for the late glacial maximum (about 19,500 yr B.P.) in the Lake Region. A thermal decline of such magnitude, especially accompanied by a marked increase in precipitation, would surely have triggered a pronounced glacier readvance into the Central Valley. As noted earlier, glaciers were generally quiescent during that period. It is difficult to reconcile how such slight changes in the Alerce I pollen profile (minor relative percentage changes in Nothofagus dombeyi-type pollen, Podocarpus nubigenus, Myrtaceae, Tepualia, and Weinmannia) during the inferred cold interval (Heusser, 1966a) could produce the major changes observed in the paleotemperature and paleoprecipitation curves.

As discussed by Birks (1981), the basic assumption of the multivariate or vegetational assemblage approach, that modern vegetation must be in equilibrium with climate and past vegetation must have been in equilibrium with past climate, has been invalidated by many paleobotanical studies. The paleoclimate curves presented by Heusser and Streeter (1980), considered suspect because of the amplitude of changes in the curves compared to subtle changes in the pollen record, are even more questionable in light of Birks (1981) appraisal of the multivariate method.

On numerous occasions Heusser has cited evidence from other areas in the Southern Hemisphere to support his argument for a Younger Dryas-equivalent climatic deterioration in southern Chile. Heusser (1974) and Heusser and Streeter (1980) noted that glaciers advanced on Mount

Carstensz, New Guinea at that time (Galloway and others, 1973; Bowler and others, 1976). However, Galloway and others (1973) concluded that the advances may have been confined to particular valleys and Bowler and others (1976) believed that they were caused by local snowfall events. Overall, Bowler and others (1976) determined that ice retreat in New Guinea began about 15,000 to 14,000 yr B.P. and proceeded rather steadily until about 10,000 yr B.P., at which time most mountains were ice-free. Galloway and others (1973) stated the fluctuations equivalent to the Younger Dryas are unknown in New Guinea; Bowler and others (1976) reflected that evidence for an Allerød oscillation in New Guinea is absent from the record.

Burrows (1975) and Burrows and Gellatly (1982) reported that glaciers were active in New Zealand during this critical time interval. Heusser and Streeter (1980) and Heusser (1984b) cited their results as corroborating evidence to support the argument for a Younger Dryas equivalent in the Southern Hemisphere. However, Burrow's (1975) estimate of the age of the Wildman moraines from Cameron Valley in the Arrowsmith Range, on which he made his interpretations, was based on extrapolation and not radiocarbon dates. Burrows and Gellatly's (1982) evidence for glacial advance between 14,000 and 9,000 yr B.P. was supported only by a minimum number of dates and on relative dating methods. Moreover, they suggested (1982) that more data are needed to establish a concise glacial chronology for that period. Suggate and West (1967) concluded that no correlative of the European Younger Dryas moraines has been recognized in New Zealand; glaciers are not known to have paused significantly in their recession after the last (about 14,000 yr B.P.) advance. According to Chinn (Salinger, 1981), climatic conditions similar to those in New Zealand today were established by about 13,500 years ago. Furthermore, no Allerød oscillation equivalent has been recognized in pollen diagrams from South Island (Moar, 1966, 1971).

A Younger Dryas-equivalent climatic deterioration is also absent from the southern Australian record (Bowler and others, 1976). In Tasmania, palynological studies have shown that a rapid rise in temperature, accompanied by forest development, occurred between about 11,500 and 9,500 years ago (Macphail, 1979; Colhoun and others, 1982).

Heusser and Streeter (1980) cited a study on South Georgia Island in the Subantarctic to support the Younger Dryas hypothesis. On that island, a stillstand or readvance of valley glaciers occurred earlier than 9,000 yr B.P. (Clapperton and others, 1978). But the dates for the event are minimal ages and are only permissive to support the argument. Pollen diagrams from other Subantarctic islands (Marion and Tristan da Cunha), according to Burrows (1979), show no changes attributable to climatic flux in the last 12,000 years. Zinderen Bakker (1973) has shown that climate has been similar to today's on Marion Island for the past 11,000 to 12,000 years.

Mercer and Palacios (1977) documented a late glacial readvance of the Quelccaya ice cap in Peru which Heusser and Streeter (1980) cited as additional evidence of a Younger Dryas event in South America. However, Mercer and Palacios (1977) emphasized that the minor advance of the ice cap occurred 500 to 800 years earlier than the Younger Dryas Stade in Europe. The only other reports supporting a climatic deterioration equivalent to the Younger Dryas in South America are from Colombia. Van der Hammen and others (1981) reported glacier advances equivalent in age to Younger Dryas advances in Europe. Clapperton (1983) observed, however, that no absolute radiocarbon dates support the events and that their interpretations were based on a combination of minimal dates, extrapolation, and palynological interpretations. Van der Hammen and Vogel (1966) suggested that late-glacial climatic changes in Colombia were identical to those in Europe. But Mercer (1969, 1972a) noted an unresolved discrepancy in their radiocarbon chronology and, furthermore, because the palynological sites on which they based the interpretations were at high elevation, suggested that the changes in the pollen record may be a result of precipitation rather than temperature changes. Watts (1970) commented that drawing a direct comparison between the Colombian and European pollen records was unjustified.

The Younger Dryas climatic deterioration, between 11,000 and 10,350 yr B.P., was first recognized at its type locality in Denmark in 1901. Subsequently, the event has been documented throughout western Europe south of the Fennoscandian moraines (see Anderson, 1981, for a review). Evidence for an abrupt, severe but short-lived cooling comes not only from geological studies (Mercer, 1984a) but also from paleobotanical (Watts, 1980) and fossil beetle (Ashworth, 1972, 1973; Coope and Joachim, 1980) investigations. There appears to be little doubt that this sharp cooling, that brought full-glacial conditions back to northern Europe, was climatically caused. It was such an emphatic event that many authors believed (a few still do) that it was an astronomically-caused, global phenomenon. There is no reliable evidence, however, that glaciers advanced during that time anywhere except in the northern North Atlantic area (Mercer, 1984a).

The Sumas Stade in the North American Pacific Northwest and the Valders advance of the Lake Michigan Lobe, initially thought to be coeval with the Younger *Dryas*, did not occur at the same time as the European event (Mercer, 1969, 1972b, 1976, 1984a). A stillstand of the portions of the Laurentide Ice Sheet (Algonquin Stade) in the Great Lakes region, also initially thought to be a Younger *Dryas* equivalent, may have been caused by ice dynamics rather than climatic reversal (Mayewski and others, 1981). There is no evidence for glacier advances equivalent to the Younger *Dryas* in the Rocky Mountains (Porter and others, 1983) and glaciers on the St. Elias Mountains of Alaska had shrunk to near their present margins by 11,300 yr B.P. (Denton, 1974). Pollen records from New England (Davis, 1983), southeastern United States (Watts, 1983), midwestern United States (Webb and others, 1983), Pacific Northwest (Barnosky, 1981), southwestern United States (Martin and Mehringer, 1965) and the northern Rocky Mountains of the United States (Waddington and Wright, 1974; Baker, 1976, 1983; Mehringer and others, 1977) show no record of cooling equivalent to the Younger *Dryas* Stade. In view of the paleobotanical records from the United States, Watts (1983) concluded that a search for a Younger *Dryas* equivalent in North America is futile because no comparable event occurred in North America.

The evidence indicating that the Younger *Dryas* climatic deterioration was restricted to northern Europe is pervasive. The localized influence of the event was illustrated by Watts (1980) who discovered that the cooling produced a marked change in the flora of northwestern Europe; but farther south in central Europe, it is weakly expressed in the paleobotanical record and was merely a delaying factor in a little-changed floral succession. There are few geological or paleobotanical data supporting a Younger *Dryas* equivalent in North America and reports of its occurrence in the Southern Hemisphere are equivocal. In southern Chile the fossil beetle record indicates relatively constant climatic conditions, similar to those of today, and there is no evidence for regional expansion of glaciers during that time (Mercer, 1976, 1983, 1984a, 1984b). In addition, no change in the interval has been noted in pollen diagrams from adjacent areas of Argentina (Markgraf and Bradbury, 1982; Markgraf, 1983, 1984). Furthermore, some of Heusser's pollen profiles from southern Chile, most notably those from Rio Caunahue (Heusser, 1981) and Tagua Tagua (Heusser, 1983) show very little or no change during the critical time period.

As early as 1969, Mercer suggested that the Younger *Dryas* event was not a global setback in the post-glacial warming trend but a local event confined primarily to northwest Europe. He hypothesized that the cooling was caused by eruption, into the North Atlantic Ocean, of large amounts of ice produced by the break-up of ice shelves in the Arctic Ocean and not by cosmic factors. It was not until 1981 that Mercer's hypothesis gained support from Ruddiman and McIntyre's (1981) paleo-oceanographic studies in the North Atlantic.

Perhaps it is appropriate to end this discussion on a defensive note. Heusser (1984a, 1984b), in defense of his argument for a Younger Dryas equivalent in southern Chile, questioned Hoganson and Ashworth's (1981, 1982a, 1982b) interpretation of the beetle record from the Rio Caunahue Site. He argued that the beetle assemblages would be difficult to interpret because they are virtually all allochthonous, having been transported to the site through fluvial activity. It is true that most of the fossils found in the Rio Caunahue sediments were washed into the basin by stream discharge, and it is conceivable that species from different climatic zones could be found in association in that type of situation. However, Ashworth and Hoganson (1984b) pointed out that if mixing occurred, then species adapted to higher elevation habitats would have been found together with those from low-elevation habitats. On the contrary, the Rio Caunahue assemblages were completely dominated by low-elevation taxa. Therefore the type of contamination proposed by Heusser can be ruled out. In addition, the late-glacial beetle assemblages from the Rio Caunahue Site are almost identical in species composition to a 13,000-year-old beetle assemblage from the Monte Verde paleoindian site near Puerto Montt that accumulated in a bog not influenced by periodic floodwater discharge (Ashworth and Hoganson, 1984a). In actuality, the configuration of the depositional system at the Rio Caunahue Site was ideal because a wide spectrum of habitats, not only those in the basin but also those around the basin of deposition, are represented by the fossil assemblages. The assemblages, therefore, seem to provide an intricate picture of the ecological and environmental conditions of the area.

Heusser (1984a, 1984b) concluded that the Rio Caunahue beetle data, indicating relatively stable climatic conditions over a relatively long time span from about 12,800 to 4,500 yr B.P., are equivocal because cooling during the early Neoglacial (occurring after 6,850 yr B.P. and culminating about 4,500-4,000 yr B.P.) is not documented by the beetles. Although it was a minor event, it was the most extensive of the three Neoglacial advances recorded in southern South America (Mercer, 1976). Evidence for the first Neoglacial is from only a small number of glaciers, all located south of 46°S latitude (Mercer, 1982). Glaciers were apparently not active during that time in the Lake Region. However, Heusser (1974) proposed that summer temperatures were 2°C cooler than today's in the Lake Region between 6,500 and 4,500 years ago because of the occurrence of Fitzroya and Podocarpus in zone P-3 at the Alerce Site. Heusser and Streeter's (1980) paleoclimatic curves, based on the Alerce record, show only a slight thermal decline during the interval but a major increase in precipitation (about 3,000 mm annually more than today's average). The upper portion of the Alerce section is poorly dated and Heusser and Streeter's evidence for a correlation between their paleoclimate curves and neoglaciations is weak.

Even if very minor neoglacial advances did occur in the Lake Region it is doubtful if the climate was sufficiently modified to be reflected by the Rio Caunahue beetle assemblages. Another possible explanation is that the minor glacier advances were caused more by increased precipitation than thermal decline. Beetle faunas are generally less sensitive to precipitation changes (especially when the change is from rain-forest conditions to even wetter rain-forest conditions) than temperature changes. Heusser and Streeter's (1980) paleoclimatic curves support this possible explanation for the suggested neoglaciations.

One of the most important topics of investigation, that has direct bearing on hypotheses concerning the mechanism and causes of climate change, is to differentiate between major climatic events that were definitely global phenomena and events of lower rank, that were emphatic but not world wide in extent. The European Younger Dryas Stade appears to be one of these lower-rank climatic events. Interpretations of geological and fossil beetle evidence from southern Chile support this contention but interpretations of palynological data do not. Additional studies in southern Chile, spanning the critical time interval, are therefore warranted perferably on sites that are conducive to both paleoentomolgoical and paleobotanical analyses.

CONCLUSIONS

(1) Cluster analysis was found to be a useful method to define collecting localities with similar beetle faunas and to establish an elevational zonation of the beetle fauna living today in the Lake Region of southern Chile. Four zones or bioassociations were defined by the method. The procedure also proved to be useful in comparing the similarity of fossil beetle assemblages to contemporary faunas. The Dice similarity coefficient was determined to be the best coefficient to use for these purposes.

(2) Deposition of lacustrine sediments began at the Puerto Octay Site sometime between 19,500 and 18,170 yr B.P. after the spillway was abandoned when lake level fell as a result of glacier recession. After it became inactive, the spillway initially contained an oligotrophic pond with freshwater of low-alkalinity. Very few insects lived in it or in the vicinity. Severe climatic conditions may have been responsible for the sparsity of insects inhabiting the Puerto Octay area at that time. Between about 18,000 and 16,000 yr B.P. the spillway was occupied by a shallow, well-oxygenated, eutrophic, probably areally restricted lake containing abundant aquatic vascular plants, filamentous algae, and a relatively diverse aquatic insect fauna. Hygrophilous vegetation was present in some of the pond-marginal areas although open, muddy shores were also common. Essentially treeless, open-ground probably bog

habitats characterized the regional setting in the Puerto Octay area during that interval. No information is available from the Puerto Octay Site from 16,000 yr B.P. to 1,190 yr B.P. From about 1,190 yr B.P. to the present, the Puerto Octay Site has been a marsh and, until recent centuries, was surrounded by a fairly diverse flora.

(3) Either an areally restricted, quiet, shallow pond or marsh existed at the Puerto Varas Park Site 15,700 years ago. Emergent vegetation grew in the marsh; and water-marginal areas were probably, at least in part, muddy, open and bare. Sparse, shrubby vegetation grew in the vicinity but mostly open-ground, probably treeless habitats existed around the site.

(4) The beetle faunas living in the Central Valley between 18,000 and 15,700 years ago, although no modern analog was observed to assist in the interpretation, probably existed in a stressed, cold environment. This was, however, a period of contracted glaciers (Varas Interstade). It is suggested that climate may have warmed sufficiently to permit invasion of beetles into the lowlands but was still severe enough to support only the most eurythermic species.

(5) The marsh that existed at the Puerto Varas Railroad Site, between about 15,000 to 14,000 yr B.P., was in an area of open-ground with stands of trees, mostly Nothofagus, and shrubs in a parkland setting.

(6) The final glacial advance into the Lake Region, that began about 15,700 yr B.P., lasted for only a few centuries; because, by about 15,000 yr B.P., climate had ameliorated sufficiently to permit migration

of forest-dwelling beetles into the Central Valley. These transitional beetle assemblages of mixed environmental indicators mark the pivotal shift toward interglacial conditions in the Lake Region. This change from glacial to interglacial conditions is generally synchronous with similar events recorded in other areas of the world and supports the concept that the last major, globally synchronous, glacial-interglacial transition occurred between about 15,000 and 14,000 years ago.

(7) Lacustrine deposition began at the Rio Caunahue Site before 13,900 yr B.P. after the Ranco Lobe retreated from the Lago Ranco basin. Initially, few organisms existed in and around the lake. The glacier terminus was still at low elevation in the drowned valley east of the site and icebergs were calving into the lake. Colonization of the lake and its margin began about 13,900 years ago, and by 12,800 yr B.P. rainforest biota inhabited the area around the lake. By 12,300 yr B.P. a well-established forest, similar to the modern Valdivian Rain Forest, had developed in the Rio Caunahue area. Throughout much of the time that the lake was in existence, periodic stream flood waters contributed organic detritus to the basin of deposition and, on occasion, volcanic ash was deposited in the lake. Lake level remained higher than today until about 4,500 yr B.P.; and during the late Holocene, partial, perhaps catastrophic, drainage of the lake occurred. Downcutting of the Rio Caunahue through the lacustrine sediments commenced, exposing the sequence, and the dry lake bottom was colonized by Valdivian Rain Forest biota.

(8) The climatic amelioration that began about 15,000 years ago continued uninterrupted through the late glacial interval. By 12,800 yr

B.P. climatic conditions similar to those in the Lake Region today were established. Those conditions remained relatively stable until at least 4,500 years ago.

(9) There is no indication from the fossil beetle assemblages of a climatic deterioration that would have caused readvance of glaciers into the Central Valley about 13,000 yr B.P. as proposed by Porter (1981).

(10) The determination that the climate of southern Chile from 11,000 yr B.P. to 10,000 yr B.P. was similar to that of today supports Mercer's interpretation, from geological evidence, that a Younger *Dryas*-equivalent climatic deterioration did not take place in southern Chile and does not support Heusser's view, based on palynological studies, that the late glacial climate of southern Chile followed the same pattern as that of Europe.

ILLUSTRATIONS OF REPRESENTATIVE BEETLE FOSSILS

It is beyond the scope of this study to include a systematic treatment of the fossil beetle taxa. The following illustrations (Plates 2 through 8) are included to show the variety of skeletal elements recovered, exquisite preservation of the specimens, and some of the representative taxa on which paleoenvironmental and paleoclimatic interpretations were based.

Plate 2

Scanning electron photomicrographs of representative fossil Coleoptera from the Puerto Varas Park and Rio Caunahue sites. Scale bars equal 1 mm except where indicated.

Figure 1. *Listroderes dentipennis* Gmn., Curculionidae.

1a. Head. Puerto Varas Park Site. Sample PV1.

1b. Thorax. Puerto Varas Park Site. Sample PV1.

1c. Articulated left and right elytra. Puerto Varas Park Site. Sample PV1.

1d. Penis. Puerto Varas Park Site. Sample PV1.

Figure 2. *Pentarthrum castaneum* (Blanch.), Curculionidae.

2a. Head. Rio Caunahue Site. Sample 42.

2b. Thorax. Rio Caunahue Site. Sample 42.

2c. Left elytron. Rio Caunahue Site. Sample 42.

2d. Right elytron. Rio Caunahue Site. Sample 42.

Figure 3. *Wittmerius longirostris* Kusch., Curculionidae.

3a. Head. Rio Caunahue Site. Sample 42.

3b. Thorax. Rio Caunahue Site. Sample 42.

3c. Left elytron. Rio Caunahue Site. Sample 42.

3d. Right elytron. Rio Caunahue Site. Sample 42.

Figure 4. *Dasydema hirtella* Blanch., Curculionidae.

4a. Head. Rio Caunahue Site. Sample BS-A3.

4b. Thorax. Rio Caunahue Site. Sample BS-A3.

4c. Magnified view of a portion of the thorax showing preservation of scales. Rio Caunahue Site. Sample BS-A3.

4d. Articulated left and right elytra. Rio Caunahue Site. Sample 35.

Plate 2

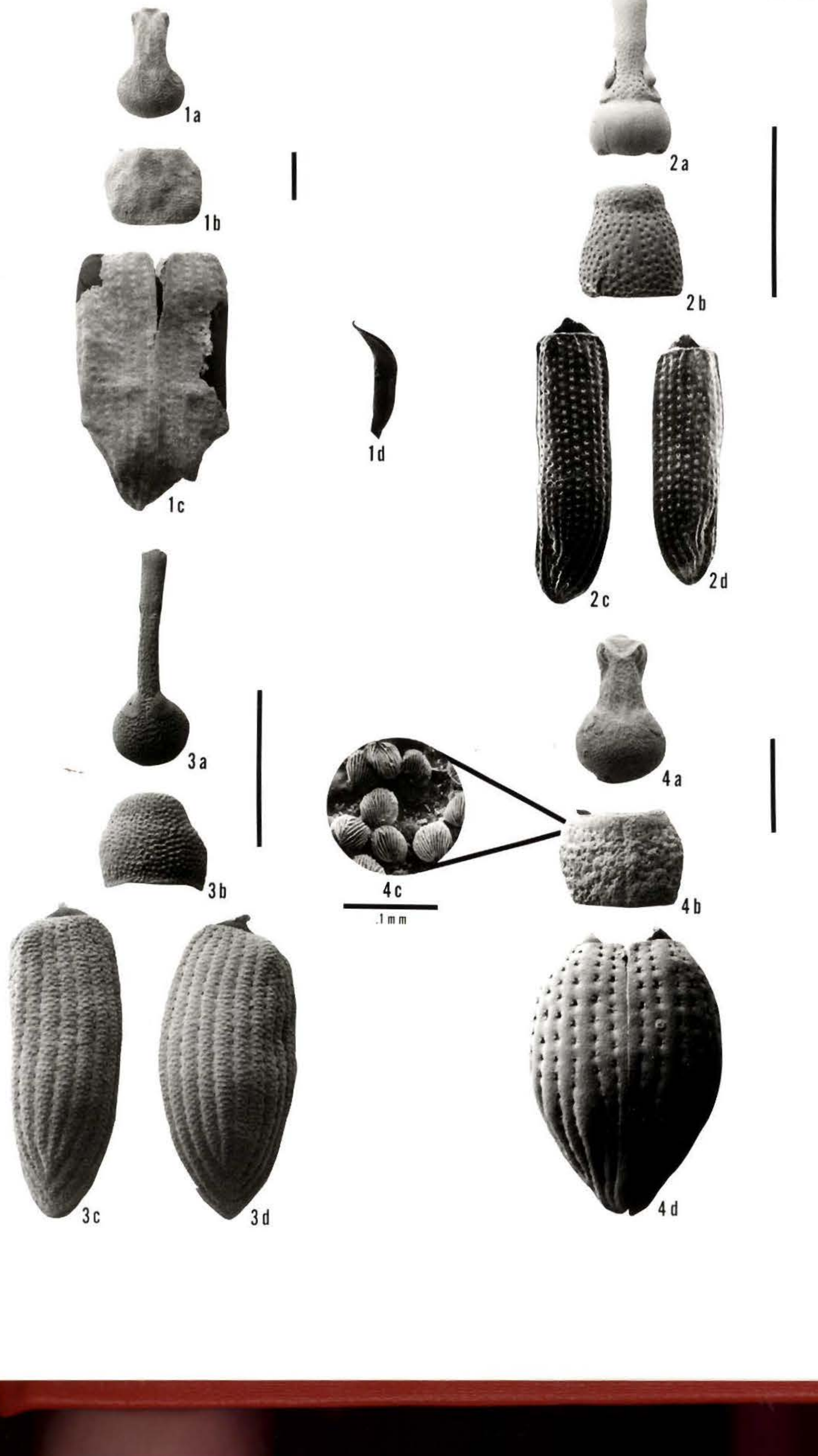


Plate 3

Scanning electron photomicrographs of representative fossil Coleoptera from the Rio Caunahue Site. Scale bars equal 1 mm.

Figure 1. Nothoderodontus dentatus Lawr., Derodontidae.

1a. Articulated head and thorax. Rio Caunahue Site. Sample PDO.

1b. Left elytron. Rio Caunahue Site. Sample 42.

1c. Right elytron. Rio Caunahue Site. Sample 42.

Figure 2. Strictospilus darwini Brths., Coccinellidae.

2a. Articulated head and thorax. Rio Caunahue Site. Sample PD1.

2b. Left elytron. Rio Caunahue Site. Sample 42.

2c. Right elytron. Rio Caunahue Site. Sample 42.

Figure 3. Caenocara sp., Anobiidae.

3a. Head. Rio Caunahue Site. Sample PDO.

3b. Thorax. Rio Caunahue Site. Sample 42.

3c. Left elytron. Rio Caunahue Site. Sample 42.

3d. Right elytron. Rio Caunahue Site. Sample 42.

Figure 4. Perilopsis flava Rttr., Nitidulidae.

4a. Head. Rio Caunahue Site. Sample PD1.

4b. Thorax. Rio Caunahue Site. Sample BS-A3.

4c. Left elytron. Rio Caunahue Site. Sample BS-A3.

4d. Right elytron. Rio Caunahue Site. Sample BS-A3.

Plate 3


1a


1b


1c


2a


2b


2c


3a


3b


3c


3d


4a


4b


4c


4d

Plate 4

Scanning electron photomicrographs of representative fossil Coleoptera from the Puerto Octay, Puerto Varas Park and Rio Caunahue sites. Scale bars equal 1 mm.

Figure 1. Abropus carnifex Fabr., Carabidae.

1a. Head. Rio Caunahue Site. Sample BS-A3.

1b. Thorax. Rio Caunahue Site. Sample BS-A3.

1c. Left elytron. Rio Caunahue Site. Sample BS-A3.

1d. Right elytron. Rio Caunahue Site. Sample BS-A3.

Figure 2. Hydrochus stolpi Gmn., Hydrophilidae.

2a. Head. Rio Caunahue Site. Sample PD6.

2b. Thorax. Puerto Octay Site. Sample 13.

2c. Left elytron. Puerto Varas Park Site. Sample PV1.

2d. Right elytron. Puerto Varas Park Site. Sample PV1.

Figure 3. cf. Diontolobus sp. 2, Trogositidae.

3a. Head. Rio Caunahue Site. Sample A1.

3b. Thorax. Rio Caunahue Site. Sample BS-A3.

3c. Left elytron. Rio Caunahue Site. Sample BS-A3.

3d. Right elytron. Rio Caunahue Site. Sample BS-A3.

Figure 4. Baryopsis araucanus C. and S., Staphylinidae.

4a. Head. Rio Caunahue Site. Sample PD6.

4b. Thorax. Rio Caunahue Site. Sample PD6.

4c. Left elytron. Rio Caunahue Site. Sample A1.

4d. Right elytron. Rio Caunahue Site. Sample BS-A3.

Plate 4

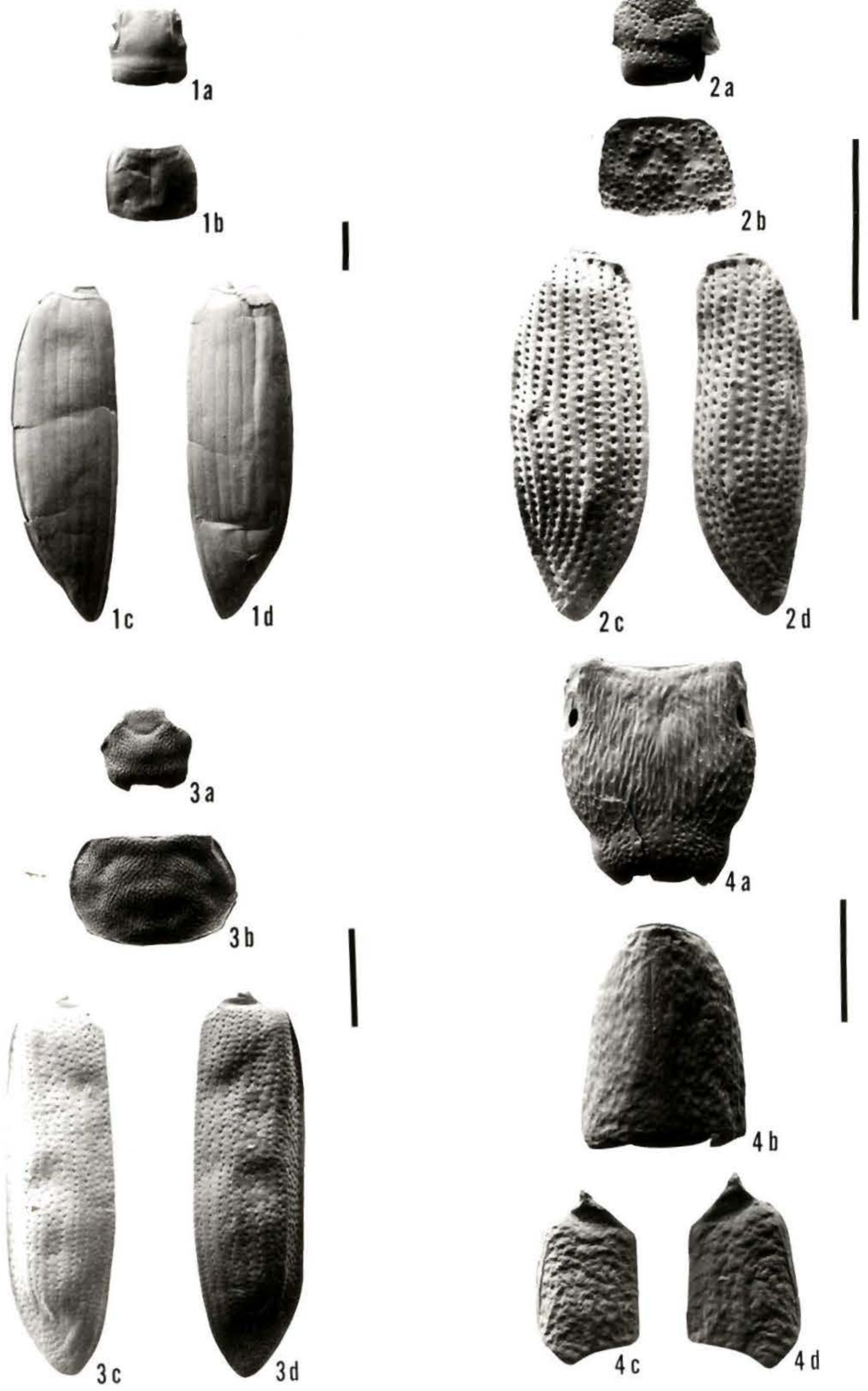


Plate 5

Scanning electron photomicrographs of representative fossil Coleoptera from the Puerto Varas Park and Rio Caunahue sites. Scale bars equal 1 mm except where indicated.

Figure 1. Monarthrum sp., Scolytidae. Left elytron. Rio Caunahue Site. Sample BS-A3.

Figure 2. Agonum sp. 2, Carabidae. Thorax. Puerto Varas Park Site. Sample PV1.

Figure 3. Hydora annectens S. and B., Elmidae. Right elytron. Rio Caunahue Site. Sample A2.

Figure 4. Nominocerus marginicollis (Sol.), Staphylinidae.

4a. Head. Rio Caunahue Site. Sample 36.

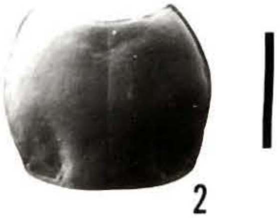
4b. Thorax. Rio Caunahue Site. Sample PD3.

4c. Left elytron. Rio Caunahue Site. Sample PD3.

4d. Magnified view of a portion of the left elytron showing microsculpture and setal puncture. Rio Caunahue Site. Sample PD3.

4e. Right elytron. Rio Caunahue Site. Sample 17.

Plate 5


2

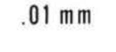

1


3


4a


4b


4c


4d

.01 mm


4e

Plate 6

Scanning electron photomicrographs of representative fossil Coleoptera from the Rio Caunahue Site. Scale bars equal 1 mm except where indicated.

Figure 1. *Phloeotribus* cf. *spinipennis* Eggrs., Scolytidae. Left elytron. Rio Caunahue Site. Sample 42.

Figure 2. *Brachypterus* n. sp., Nitidulidae.

2a. Magnified view of the right elytron hinge area showing microsculpture and setae. Rio Caunahue Site. Sample PD3.

2b. Right elytron. Rio Caunahue Site. Sample PD3.

Figure 3. *Glypholoma pustuliferum* Jean., Staphylinidae. Left elytron. Rio Caunahue Site. Sample BS-A3.

Figure 4. *Tartarisus signatipennis* (Blanch.), Curculionidae.

4a. Magnified view of the tibial distal end showing ornamentation and setae. Rio Caunahue Site. Sample BS-A3.

4b. Articulated femur and tibia. Rio Caunahue Site. Sample BS-A3.

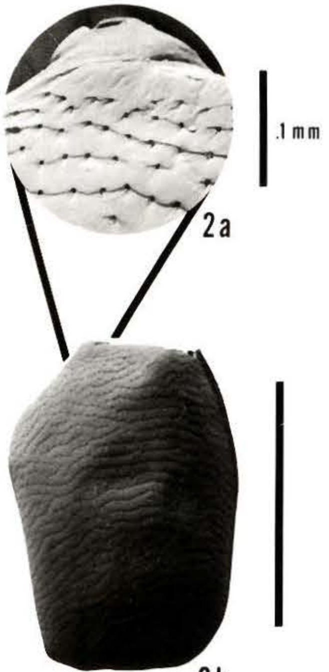
Figure 5. *Rhynchitomacer flavus* Voss, Nemonychidae. Head. Rio Caunahue Site. Sample 36.

Figure 6. *Austrolimnius chiloensis* (Champ.), Elmidae. Thorax. Rio Caunahue Site. Sample 41.

Figure 7. *Plectocephalon testaceum* (Pic), Cantharidae. Head. Rio Caunahue Site. Sample A2.

Plate 6

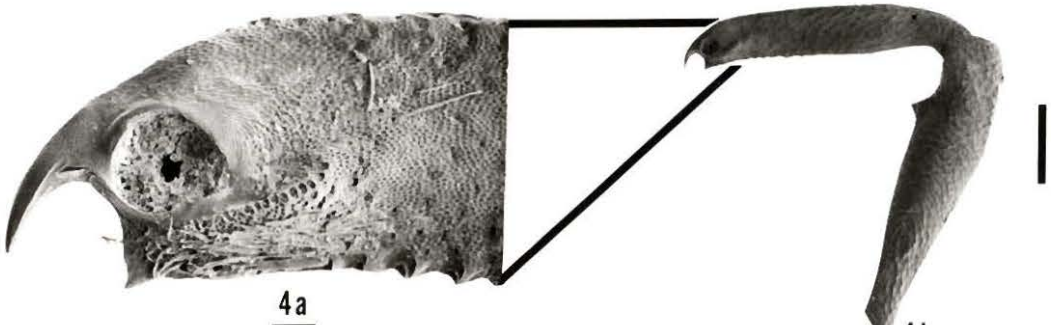
1



2a

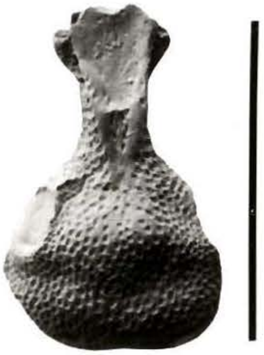
2b

3



4a

4b



5

6

7

Plate 7

Scanning electron photomicrographs of representative fossil Coleoptera from the Puerto Varas Railroad and Rio Caunahue sites. Scale bars equal 1 mm except where indicated.

Figure 1. *Eunemadus chilensis* Ptvn., Leiodidae.

1a. Right elytron. Rio Caunahue Site. Sample BS-A3.

1b. Magnified view of the right elytral humeral area showing ornamentation. Rio Caunahue Site. Sample BS-A3.

Figure 2. *Rhopalomerus tenuirostris* Blanch., Curculionidae. Left elytron. Rio Caunahue Site. Sample BS-A3.

Figure 3. *Neophonus bruchi* Fauv., Staphylinidae.

3a. Head. Rio Caunahue Site, B section. Sample B2.

3b. Right elytron. Rio Caunahue Site, B section. Sample B1.

Figure 4. *Leucotachinus luteonitens* (F. and G.), Staphylinidae.

4a. Thorax. Rio Caunahue Site. Sample 42.

4b. Right elytron. Rio Caunahue Site. Sample 42.

Figure 5. *Epaetius carinulatus* Kusch., Curculionidae.

5a. Head. Rio Caunahue Site. Sample BS-A3.

5b. Left elytron. Rio Caunahue Site, B section. Sample B1.

Figure 6. *Anotylus chilensis* C. and S., Staphylinidae.

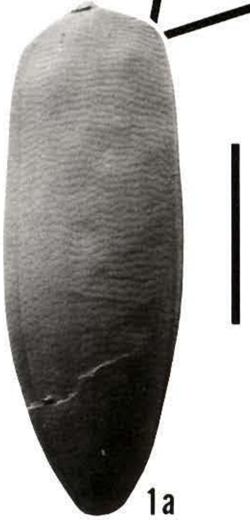
6a. Thorax. Puerto Varas Railroad Site. Sample 1.

6b. Right elytron. Puerto Varas Railroad Site. Sample 1.

Plate 7


1b


3a


1a


2


3b


4a


5a


6a


4b


5b


6b

Plate 8

Scanning electron photomicrographs of representative fossil Coleoptera from the Rio Caunahue Site. Scale bars equal 1 mm.

Figure 1. Trechinotus striatulus Mateu and Neg., Carabidae.

1a. Thorax. Rio Caunahue Site. Sample A1.

1b. Left elytron. Rio Caunahue Site. Sample BS-A3.

Figure 2. Gipsyella patagonica Schw., Carabidae.

2a. Head. Rio Caunahue Site. Sample 1.

2b. Thorax. Rio Caunahue Site. Sample 1.

Figure 3. Neoelmis n. sp., Elmidae.

3a. Thorax. Rio Caunahue Site. Sample BS-A3.

3b. Right elytron. Rio Caunahue Site. Sample A1.

Figure 4. Lophocephala fasciolata Blanch., Curculionidae. Left elytron. Rio Caunahue Site. Sample BS-A3.

Figure 5. Cryptorhynchinae gen. indet. Curculionidae. Articulated left and right elytra. Rio Caunahue Site. Sample BS-A3.

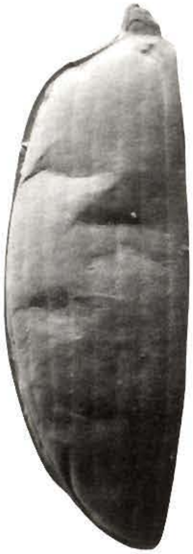
Figure 6. Minurus testaceous Wtrh., Attelabidae. Right elytron. Rio Caunahue Site. Sample A1.

Plate 8

1a

2a

3a



1b

2b

3b

4

5

6

APPENDICES

APPENDIX A

COLEOPTERA BIOASSOCIATIONS ALONG AN ELEVATIONAL GRADIENT IN THE LAKE REGION OF SOUTHERN CHILE AND COMMENTS ON THE POSTGLACIAL DEVELOPMENT OF THE FAUNA

COLEOPTERA BIOASSOCIATIONS ALONG AN ELEVATIONAL GRADIENT IN THE LAKE REGION OF SOUTHERN CHILE AND COMMENTS ON THE POSTGLACIAL DEVELOPMENT OF THE FAUNA

Allan C. Ashworth

Department of Geology, North Dakota State University,
Fargo, North Dakota 58105, U.S.A.

and

John W. Hoganson

North Dakota Geological Survey, University Station,
Grand Forks, North Dakota, 58202, U.S.A.

ABSTRACT

A diverse Coleoptera fauna of 462 species in 48 families was collected from 41 locations in the Parque Nacional de Puyehue and adjacent parts of the Lake Region of southern Chile. The sample locations ranged from rain forest habitats at sea-level to Andean tundra habitats at 1500 m msl. Cluster analysis of a Dice similarity coefficient matrix revealed a broad pattern of bioassociations within the large data base. Boundaries between the bioassociations correspond largely with those of the major vegetation zones implying that the distribution of the fauna is strongly influenced by the distribution of plants. Evidence from fossils indicates that the lowland beetle fauna during the interval 26,000 to 15,500 yr B.P. had a low diversity and was dominated by species of open-ground habitats. Forest species appeared in the lowlands between 15,000 and 14,000 yr B.P., at about the time of the last deglaciation. A fauna with similar characteristics to that of the Valdivian Rain Forest was not in place until about 13,000 yr B.P. No evidence was found to support claims made from palynological studies for a pronounced episode of colder and wetter climatic conditions in the interval from about 11,000 to 9,500 yr B.P. The patterns observed in the fauna began to develop about 13,000 yr B.P. and continued to do so until the present without any significant disruptions.

INTRODUCTION

The first beetles from southern Chile to arouse scientific curiosity were collected on voyages to the Pacific during the eighteenth and nineteenth centuries. Specimens were carried back to Europe and described by eminent systematists. Johann Fabricius, for example, described the Patagonian endemic carabid species Ceroglossus suturalis in 1775. Charles Darwin collected extensively from the forests on the Isla Chiloe and from the vicinity of Valdivia during 1833 and 1834. Although beetles were an early love of Darwin's, he did not describe any Chilean specimens preferring to leave the systematics to Waterhouse, Hope, and Babington. Many of the holotypes, such as that of the carabid Ceroglossus darwini described by Hope in 1838, are perfectly preserved in the British Museum.

The French naturalist Claudio Gay, collected numerous beetles during his travels in Chile from 1828 to 1842. The specimens were described by Solier, Blanchard and Spinola and the descriptions with color plates were included in the 1849 and 1851 volumes of Gay's monumental treatise "Historia fisica y politica de Chile". The descriptions and illustrations in these volumes are still useful, and after more than a hundred years, the work remains the most comprehensive treatment of the Chilean Coleoptera fauna. Essentially no other information, neither distributional nor ecological, was included in the descriptions, and consequently the work is principally of systematic interest.

Studies of the Lake Region biota increased dramatically following the German colonization in the middle part of the nineteenth century. Systematic study flowered under the direction of Rodolfo Philippi, a

German refugee, who followed Claudio Gay as the director of the Museo Nacional in Santiago. Coleoptera collected by Philippi and his assistant the French entomologist Filiberto Germain, were sent to Europe to be described by eminent systematists in France, Germany, and England. In recent years collections made by the Chilean entomologist, Luis Peña, have added enormously to the knowledge of the Coleoptera fauna. The number of revisionary studies has grown exponentially with the result that the systematics of some groups is well-known. At least 43 percent of the species that we identified in our study had been previously described. The fauna is especially interesting because of the importance of the region to the biogeography of the Southern Hemisphere (Darlington, 1965). Kuschel (1969) discussed the affinities and origins of the coleopterous fauna and provided (1960) an excellent survey of the biology of the major biomes.

Through the study of fossils we are analyzing the effects that glaciation had on the fauna. In order to interpret the significance of the fossil assemblages we needed to know more about the structure of the fauna along an elevational gradient and hence the reason for this study. The most intensive fieldwork was carried out in the Parque Nacional de Puyehue but samples were also collected from locations in the northern part of the Isla Chiloe, from the southern and western shores of Lago Llanquihue in the Valle Longitudinal, and from Pucatrihue in the Cordillera de la Costa (Figure A1).

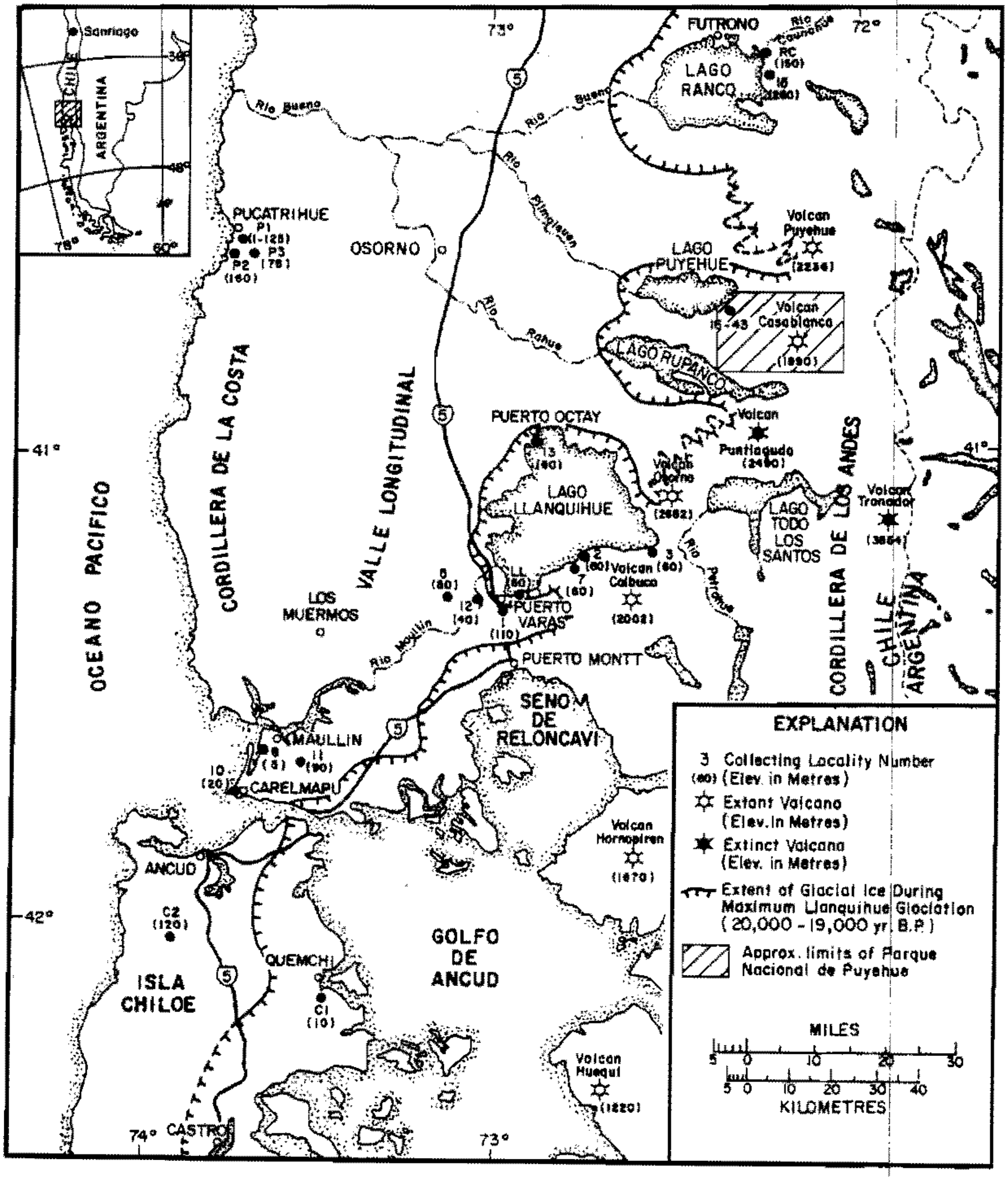


Figure A1. Map of the southern Chilean (see insert) Lake Region showing location and elevation of beetle fauna collecting sites, location of the Parque Nacional de Puyehue, extent of glacial ice during the last glacial maximum and location of extant and inactive volcanoes. Extent of glacial ice compiled from Mercer (1976), Heusser and Flint (1977), and Porter (1981). Information on volcanoes from Casertano (1963).

THE PARQUE NACIONAL DE PUYEHUE

Physiography and Geology

The Parque Nacional de Puyehue (the park), between latitudes 40°30'S and 41°10'S, and longitudes 71°50'W and 72°30'W, lies on the western flanks of the Cordillera de los Andes (the Andes). In the eastern and central parts of the Andes, deformed sedimentary and metamorphic rocks are intruded by granites of the Cretaceous and Tertiary-aged Andean batholith (Plafker and Savage, 1970; Hervé and others, 1974). Along the western margin extant strato-volcanoes are aligned on a south-north axis. Volcan Tronado (3554 m msl), an inactive volcano straddling the Chile-Argentina border, is the highest peak in the region. According to Vergara and Gonzalez-Ferran (1972), the existing central-type volcanism began in the Plio-Pleistocene, following an early phase of fissure eruptions. The park is bordered to the west by the Valle Longitudinal (Central Valley), a 90 km-wide rift valley (Galli-Oliver, 1969; Scholl and others, 1970). The lakes, such as Llanquihue, Rupanco, Puyehue, and Ranco, that give the region its name are located in the valley. They occupy glacially-scoured depressions, dammed on their western margins by a series of arcuate moraines. To the west, the relatively low (950 m msl), unglaciated Cordillera de la Costa (Coastal Mountains), rise between the Central Valley and the Pacific Ocean. The topography results from the region being at the margin of the converging South American and Nazca Plates. The Nazca Plate is being subducted at the Peru-Chile Trench, resulting in volcanism, seismicity, and uplift of continental crust.

The park is located on Volcan Casablanca, a strato-volcano with an elevation of 1990 m. There is no historical record of eruption but the unweathered tephra, and the youthful form of cinder cones, such as Cerro Haique, imply activity within the past few centuries. Volcan Calbuco, 30 km to the south, has erupted several times in this century; the last eruption was in 1961 (Casertano, 1963; Simkin and others, 1981). Darwin (1839) observed Volcan Osorno (Figure A6) erupting in 1834 and in 1835 while the HMS Beagle was at anchor off the Isla Chiloe; the last eruption on Vn. Osorno was in 1869 (Simkin and othrs, 1981). Earthquakes are also relatively common in the Lake Region; Lomnitz (1970) estimated that seismic events of M_s 8+ have a frequency of one per decade in the area. The 1960 earthquake (ca. M_s 8.5), was one of the greatest seismic events ever recorded (Plafker and Savage, 1970). Veblen and Ashton (1978) and Veblen and others (1980) discussed the importance of catastrophic events, mainly earthquake induced landslides and volcanic eruptions, to the maintenance of Nothofagus-dominated forests. The dynamic character and lack of long term stability in these forests must influence the distribution of all other components of the biota, including the Coleoptera.

Most of the collecting sites for our study were located in the broad gently sloping Antillanca Valley in which the Rio Chanleufu and other streams flow westward to Lago Puyehue, where they are constructing a delta with the Rio Golgol. At the last glacial maximum, ice existed as far west as Entre Lagos at the west end of Lago Puyehue. At that time glacial ice presumably covered the entire region of the park. The glacial form of the Antillanca Valley is still obvious even though it has been modified by volcanic activity.

Glaciations that resulted in ice periodically advancing from the Andes into the Valle Longitudinal and the climatic changes that produced them, have disrupted the biota on a larger scale than either tectonism or volcanism. A radiocarbon chronology of glacial events has been established during the last decade through the studies of Mercer (1972, 1976, 1982), Laugenie and Mercer (1973), Heusser and Flint (1977), and Porter (1981). The last glacial maximum, according to Mercer (1976), culminated about 19,200 yr B.P. (^{14}C years Before Present) and was approximately synchronous with the glacial maxima of the Northern Hemisphere. Porter (1981) estimated that the glacial complex at that time was about 165 km wide in the southern Lake Region, and the ice as much as 800 to 1000 m thick in the Lago Llanquihue basin. To account for the ice volume, he calculated that snowline would have been 1000 m below its present elevation of 1,900 to 2,250 m.

The deglaciation that followed was interrupted by one (Mercer, 1976) or perhaps two (Porter, 1981) significant readvances. The best evidence (Mercer, 1984) for the last glacial advance in the Lake Region is that it occurred between 15,000 and 14,500 yr B.P. Mercer (1976) believed that the glaciers had retreated to their present positions high in the Andes by 11,000 yr B.P. Neoglacial ice advances have not been documented for the Lake Region, but based on evidence from further south (Mercer, 1976, 1982), several minor advances may have occurred. Small glaciers, at most a few km in length, presently occur in cirques and high valleys at elevations of greater than 2000 m. Isolated peaks, such as the volcanoes Osorno and Calbuco, are ice-capped remnants of the once extensive glacial cover.

Climate

The climatic data available for the park are summarized from compilations by Muñoz S. (1980) and Veblen and others (1977). The range of mean temperatures for the warmest (January) and coldest (August) months at Central Pilmaiquen, near the western end of Lago Puyehue, is from 15°C to 6°C, and at Antillanca, near treeline on Volcan Casablanca, is from 11°C to 3°C. Over the same gradient precipitation increases from 1950 mm/yr to 5420 mm/yr. The number of frost days/yr is less than 10 at the elevation of Lago Puyehue and about 150 at treeline. The number of days with snow cover also increases with elevation, from a few at elevations below 250 m, to about 180 at elevations above treeline. In 1977 snow did not melt from the large crater above Antillanca at 1250 m until the middle of December.

The climate of the Lake Region is controlled by proximity to the polar front and position next to the cold Peru current. The region is in the "roaring forties" and as a result receives frequent cyclonic storms. Precipitation is heaviest in the fall and winter because of northward shifts in the position of the polar front (Miller, 1976). The ocean-facing slope of the Coastal Mountains receives about 4000 mm/yr precipitation whereas the lee side, and the Central Valley in the rain shadow receive about 2000 mm/yr (Almeyda and Saez, 1958). As the storms pass eastward, precipitation rises to over 5000 mm/yr due to the orographic influence of the Andes.

Vegetation

The vegetation of the Chilean Lake Region has been described by

Schmithüsen (1956, 1960) and Oberdorfer (1960). Summaries of their studies together with earlier floristic works were included in Heusser's (1966) description of the vegetation. The following comments on the vegetation in the park are based on our own observations, the descriptions of Heusser (1974, 1981, see Figure A2 for position of vegetational zones), the floristic studies of Muñoz S. (1980), and the ecological and community studies of Veblen and Ashton (1978) and Veblen and others (1977, 1979, 1980).

The native vegetation of the Central Valley and the foothills of the Andes up to elevations of 500 m has been disrupted by man. Prior to European colonization in the mid-nineteenth century, the Central Valley was probably extensively forested (Heusser, 1974). Presently only tiny remnants of the Valdivian Rain Forest survive at low elevations. In the vicinity of Lago Puyehue, relatively undisturbed forest occurs on the delta, and along the road east of Termas Puyehue. The vegetation of most of the Central Valley and of the low foothills consists of meadows and forest remnants (Figure A3). The flora is a mixture of native and introduced species. European imports such as buttercups (Ranunculus), plantains (Plantago), and dandelions (Taraxacum officinale), are evident in every meadow, and blackberries (Rubus ulmifolius), gorze (Ulex europeaeus), and foxgloves (Digitalis purpurea) are common in hedgerows and woodland margins.

The Valdivian Rain Forest (Figure A4) is present to about 850 m msl. In the park the forests above 500 m are relatively undisturbed except for selective logging of the largest trees along the road to Antillanca. The wet temperate climate and the thick volcanic soils support a lush rain

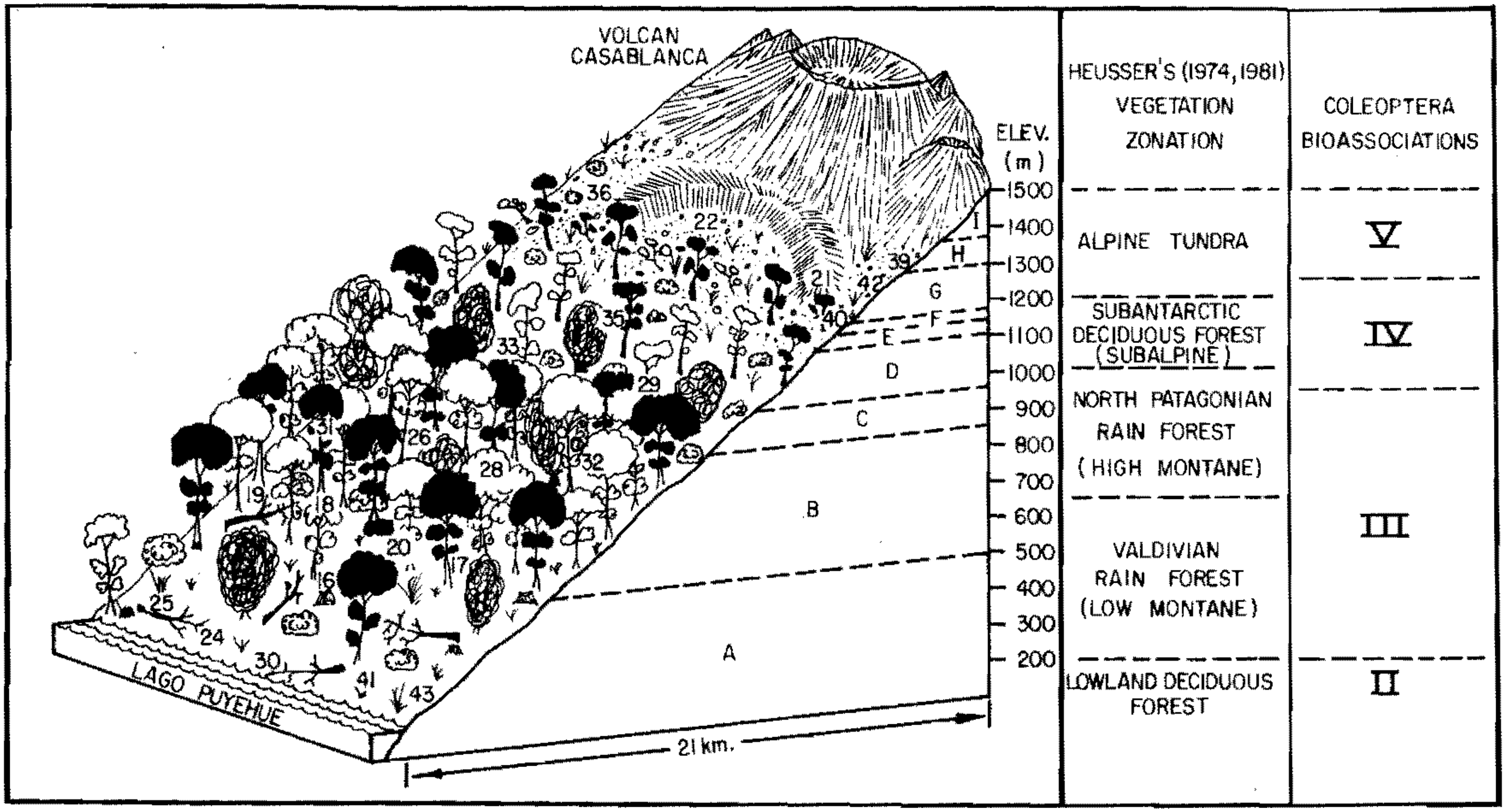


Figure A2. Schematic representation of vegetational and Coleoptera associations from an elevational transect in the Parque Nacional de Puyehue, Osorno Province, Chile. See Figure A1 for location. Vegetational zonation indicated by letters is adapted from Veblen and others (1977): (A) Disturbed forest, (B) Dombeyi-Eucryphietum forest (Coigue-Ulmo forest), (C) Laurelio-Weinmannietum forest (North Patagonia Teniu forest), (D) Mixed *Nothofagus betuloides-N. pumilio* forest, (E) *Nothofagus pumilio* forest, (F) *Nothofagus* krummholz, (G) Scrub-grassland, (H) Fellfield, (I) Bare scoria. Vegetation zonation indicated in column from Heusser (1974, 1981). Numbers on diagram are beetle fauna collecting localities. Coleoptera bioassociations II-V are from this study.

Figure A3. The delta at the west end of Lago Puyehue (elev. 205 m above msl), Parque Nacional de Puyehue. Disturbed lowland forest habitats occupied by Bioassociation II. Volcan Puyehue is in the background.

Figure A4. Laguna La Copa in the Parque Nacional de Puyehue (elev. 530 m above msl). Undisturbed Valdivian Rain Forest habitats occupied by Bioassociation III.

forest. The larger trees reach heights of 40 m and have trunk diameters of 1.5-3 m. Within the area of Aguas Calientes, near the park headquarters, the forests are composed of 13 species of trees, and 11 species of shrubs.

The dominant trees are the evergreen, broad-leafed species Laurelia philippiana, Nothofagus dombeyi, and Eucryphia cordifolia, and the confier Saxegothaea conspicua. The tree species Aetoxicum punctatum, Weinmannia trichosperma, Caldcluvia paniculata, Dasyphyllum diacanthoides, Drimys winteri, and Embothrium coccineum are also common. Trunks are covered in mosses, lichens, fungi, climbing plants with red flowers as Asteranthera, and Mitraria, and lianas of the genus Hydrangea.

The undergrowth consists of trees and shrubs of Fuchsia magellanica, Buddleya globosa, Amomyrtus luma, Myrceugenella apiculata, Myrceugenia planipes, Berberis darwini, and Ribes magellanicum. Ferns, including the magnificant Lophosoria quadripinnata with leaves 2 m in length, and the ubiquitous, almost impenetrable cane Chusquea quila also thrive in the undergrowth. The cane and the large-leaved Gunnera chilensis are especially common along rocky ravines and slopes where the vegetation has been disturbed. Sunlight rarely penetrates the forest floor, which consists of thick, wet accumulations of leaf litter and deadfall timber. Abundant invertebrates including numerous beetles, large 5-cm diameter snails, slugs, leeches, scorpions, large spiders, and earthworms are present in this habitat.

The numerous small lakes in the park, such as Lago Espejo, have a rich aquatic and emergent vegetation and species of sedges (Carex), reeds (Juncus), and shrubs of Escallonia occur in water-marginal environments.

Stunted trees of Nothofagus antarctica are present in some lake-marginal environements and in bogs that have formed from the infilling of lakes.

Forests with a high diversity of tree species and abundance of shrubs, lianas, epiphytes, ferns, mosses, hepatics and lichens extend up to about 960 m msl but between 650 m and 850 m, the composition changes. Heusser (1974, 1981) referred to the middle montane forest as the "high montane", or "North Patagonian Rain Forest" (Figure A2). The dominant trees remain the broad-leaved evergreens Nothofagus dombeyi and Laurelia philippiana, and the confier Saxegothaea conspicua, but the white-flowered Eucryphia cordifolia, so evident in flower in the lower forest in January, does not occur above 650 m. Nothofagus nitida appears at 690 m and Nothofagus betuloides and Nothofagus pumilio, the dominant trees of the upper montane forest, appear near 900 m. The understory is much less diverse, and not as dense as that of the forests on the lower slopes. An obvious visual difference is that the species of cane Chusquea couleu that replaces C. quila does not form such impenetrable thickets. The red-and-yellow flowers of the shrub Desfontainea spinosa, and the pink bell-shaped flowers of the vine Philesia magellanica are colorful additions to this forest.

The mixed Nothofagus forest above 960 m, referred to by Heusser (1974) as the "subalpine" or the "Subantarctic Deciduous Forest" (Figure A2), is very different from the middle montane forest. This forest, consisting of the deciduous Nothofagus pumilio, and the evergreen Nothofagus betuloides, is much less diverse and has a more uniform appearance than those lower down the slopes (Figure A5). Three are smaller with heights rarely exceeding 15 m, and trunk diameters rarely

Figure A5. Base of the rim of the large crater on Cerro Colorado above Antillanca (elev. 1200 m above msl), Parque Nacional de Puyehue. Subantarctic Deciduous Forest habitats occupied by Bioassociation IV.

Figure A6. View to the south from the rim of the large crater on Cerro Colorado (elev. 1350 m above msl), Parque Nacional de Puyehue. Andean tundra habitats occupied by Bioassociation V. The pointed peak to the left is Cerro Puntiagudo. The classical, snow-capped stratovolcano on the right is Volcan Osorno.

larger than 50 cm. The understory is also less dense and more diverse than that of the lower and middle montane forests. Common shrubs include Embothrium coccineum, Berberis buxifolia, Drimys winteri var. andina, Ovidia andina and the ubiquitous cane Chusquea tenuiflora. The cane is not present in the forests above 1000 m. In clearings, such as the military airfield near Refugio Antillanca, lycopods and the shrubs Pernettya, Empetrum, and Escallonia are well-represented. Gunnera occurs on rock slides and in rocky ravines. This forest extends to elevations ranging from 1040-1200 m on south- and north-facing slopes, respectively. Above 1050 m only stunted, snow damaged, and flagged trees of N. pumilio are present immediately downslope from the krummholz.

The narrowly-restricted krummholz on the steep slopes above Refugio Antillanca consists of a 20 m-wide zone of low shrubs of Nothofagus antarctica and Nothofagus pumilio. South and east of the crater, on gentler slopes, the krummholz is up to 500 m-wide. Lycopods are common in the ground cover, and the shrubs of the upper montane forests Empetrum, Pernettya, and Maytenus, are especially abundant together with clumps of the composite Senecio.

The high Andean grassland (Figure A6) or Andean tundra referred to as the "alpine tundra" by Heusser (1974), consists of lower association of grasses, low-lying shrubs, and abundant brightly colored flowering herbs. The shrubs include, Maytenus, Embothrium, and Empetrum and the ericaceous species Gaultheria and Pernettya. Fell fields with discontinuous patches of mosses, lichens, lycopods and individual plants of the herbs of Senecio, Nassauvia, and the legume Adesmia extend above the shrub grasslands to elevations of 1550 m.

METHODS

Beetles were sampled during two field seasons that, when combined, span an entire austral summer. Sites were revisited monthly so that adults emerging at different times would be included in the samples. The weather during the first field season, October-December, 1977, was unusually wet; during the second, January-March 1979, it was exceptionally dry, and forest fires (rare events in southern Chile) were widespread in the Central Valley.

Sampling stations within the park were established at approximately 150 m elevational increments (Figure A2). Collections were made from the delta on Lago Puyehue (el. 195 m msl) to the slopes above the large crater on Cerro Colorado (el. 1500 m msl). On the lower slopes collections were made from the valley of the Rio Chanleufu; and on the upper slopes from the valley of the Rio Pescadora, and the valley of the Rio Pileufu. All locations collected from outside of the park were below 200 m msl; most were less than 100 m (Figure A1).

Selection of specific collecitng locations was dictated by ease of accessibility and diversity of microhabitats available for sampling. Locations were sought that exhibited a mosaic of arboreal, aquatic and open-ground habitats. Success in locating sites varied between areas in the Lake Region. For example, undisturbed forest habitats were rare in the Central Valley because of deforestation; open-ground areas were scarce in the rain forests of the park, and aquatic conditions were seldom encountered on the Andean tundra.

All available microhabitats were sampled at each location using common collecting and trapping methods (e.g., aquatic netting, sweeping, sifting leaf litter, beating, bark peeling, log and rock turning, unbaited and human dung-baited, pitfall traps and fence traps). Light trapping was attempted on numerous occasions with little success, and the nocturnal fauna was mostly obtained by "headlamping". Animal droppings, carcasses, and burrows were inspected where available.

Determinations of pinned and labeled specimens were made by reference to keys and descriptions in the literature, and by direct comparison to previously collected and identified specimens in the collections of the Smithsonian Institution, the Canadian National Collection, and the British Museum. Specimens not located in the collections of these museums were sent to systematic experts for identification. Species which have either not been described, or for which names could not be found are represented in the collection by voucher specimens (e.g., *Agonum* sp. 1, *Agonum* sp. 2, etc.) (Table A1). The collection is maintained in the NDSU Fossil Beetle Laboratory.

All species, with the exception of those obviously foreign to a locality, were used in the quantitative analysis. For example, the aviate, phytophagous scarab, *Brachysternus spectabilis*, occurs on the snow banks on the tundra but is carried there on thermals from the upper montane forest. Localities vary in species numbers because of the diversity of microhabitats available for sampling, number of sampling techniques employed at each locality, and amount of time spent at each locality. The latter two variables were kept as constant as possible, therefore, disparity in faunal diversity between samples is largely a

Table A1: Taxonomic list of the Coleoptera from the Parque Nacional de Puyehue and other locations in the southern Chilean Lake Region; the vegetational zones, bioassociations, and habitats in which they occur, their abundance, and dates when collected.

COLEOPTERA TAXA	VEGETATIONAL ZONES PARQUE NACIONAL DE PUYEHUE					ADDITIONAL LOCALITIES				
	1	2	3	4	5	6	7	8		
BIOASSOCIATIONS	V	IV		III		II	II/III			
	ANDEAN TUNDRA (>1200 m)	TREELINE (1200 m)	SUBANTARCTIC DECIDUOUS FOREST (1000 - 1200 m)	NORTH PATAGONIAN RAIN FOREST (650 - 1000 m)	VALDIVIAN RAIN FOREST (150 - 650 m)	CENTRAL VALLEY (0 - 150 m)	ISLA CHILOE (10 - 120 m)	COASTAL (0 - 100 m)	DATES COLLECTED	HABITATS
TRACHYPACHIDAE										
Systolosoma brevis Sol., 1849	*			*	***	*		*	23/XI to 7/II	T1,T5,T8,T9,A12
Systolosoma lateritium Nèg., 1973	*		*	***	*				14/XII to 26/I	T1
CARABIDAE										
Tropopsis biguttata Sol., 1849					*				8/XII	T9
Ceroglossus chilensis (Esch., 1829)		***	**	***	**			*	5/XII to 9/II	T1,T4,T8,T9,V32
Ceroglossus darwini (Hope, 1838)				**	***	*		*	22/XI to 6/II	T1,T8,T9,V26
Ceroglossus speciosus Gerst., 1858								*	6/II to 7/II	T1
Ceroglossus suturalis (Fabr., 1775)				***	*				5/XII to 18/I	T1,T8,T9
Ceroglossus valdiviae (Hope, 1838)		*	***	***	***				5/XII to 1/II	T1,T4,T8,T9
Monolobus testaceus Sol., 1849					*				8/XII	V32
Tropopterus sp.		*							18/XII	T9
Cascellius sp.	*		**.	*					14/XII to 22/I	T1,T8,T9,A12
Creobius eydouxi Guér., 1839			***	**	***	*			10/XI to 23/II	T1,T4,T8,T9
Pericompsus circuliformis (Sol., 1849)					*				8/XII	T9
Bembidion dubei Sol., 1849				*	***	***	**	*	10/XI to 21/II	T4,T5,T10,V4,V32,A10,A12
Bembidion sp. 3					***				15/XII to 1/II	T5,A1,A10,A12
Bembidion cf. *posticalis* Gmn., 1906					*	**	*		18/XI to 13/II	T9,T10,A12
Bembidion setiventre Nèg., 1973					***	**	*		18/XI to 23/II	T5,T9
Bembidion sp. 5					**		*		8/XII to 23/II	T9,T10,A12
Bembidion sp. 7					***	*	***		18/XI to 21/II	T5,T7,T10,A1,A4,A10,A12
Bembidion sp. 8					***	*	*		18/XI to 13/II	T5,T7,T9,T10,A4,A10,A12

Table A1 (continued)

COLEOPTERA TAXA	1 AT	2 TL	3 SDF	4 NPRF	5 VRF	6 CV	7 IC	8 C	DATES	HABITATS
CARABIOAE (continued)	V	IV			III	II		II/III		
Bembidion sp. 9					*				1/II	A1
Bembidion marginatum Sol., 1849			*	*	***	***			18/XI to 21/II	T1,T5,T9,T10,V32,A8,A12
Bembidion sp. 11					*				15/XII	T1
Bembidion sp. 12					*				8/XII	A12
Bembidion sp. 13			*			***			10/XI to 19/I	V4,A12
Bembidion sp. 14	***								21/XII to 24/I	T8,T10
Aemalodera centromaculata Sol., 1849				*	*				9/XII to 18/I	V9,V23,V32
Aemalodera dentimaculata Sol., 1849					*			*	5/XII to 7/II	T1,V11,V32
Aemalodera limbata brunneipennis (Jean., 1962)			*	*	**		*		5/XII to 23/II	V6,V8,V10,V17,V26,V31,V32 A10
Aemalodera limbata fumosa Sol., 1849			*	*	*				7/XII to 22/I	T4,V11,V12,V23,V32
Aemalodera limbata limbata Sol., 1849			*	*	*			*	10/I to 7/II	V6,V11,V32
Aemalodera testacea (Jean., 1962)					*		*		8/XII to 14/II	V26,V29,V32
Trechisibus nigripennis Group Sol., 1849	***			*	*	*			20/XI to 21/II	T1,T10,A12
Gipsyella patagonica Schw., 1958					*	*	**		29/I to 21/II	T7,T10,A2
Trechinotus flavocinctus Jean., 1962			*						17/XII	ND
Trechinotus striatulus Mateu and Nèg., 1972					*				29/I	T8
Trechini sp. 1					*				5/XII to 14/I	T7,T8
Bothynoproctus sp.	*	*			**	*			20/XI to 24/I	T4,T5,T9,T10,A12
Trirammatus (Feroniomorpha) sp. 1					***	***	*		10/XI to 13/II	T1,T5,T9,T10,V3,A1,A10,A12
Trirammatus (Feroniomorpha) sp. 2					***	*	**		18/XI to 13/II	T1,T4,T5,T9,T10,V3,V32
Parhypates (Argutoridius) sp.					**	*			18/XI to 9/I	T4,T9,T10,V3
Parhypates (sensu stricto) sp.			***	**	***	*	*	*	19/XI to 7/II	T1,T4,T5,T8,T9,T10,V3,V32
Metius sp. 1				*	***	**		*	23/XI to 21/II	T4,T5,T9,A1,A10,A12
Metius sp. 2					**	*			23/XI to 10/I	T1,T4,T5,T9,V32,A12
Abropus carnifex Fabr., 1775	*		*	*	***				8/XII to 29/I	T4,T10,V23,V24,V32,A12
Agonum sp. 1						***			10/XI to 22/XII	V3,A12
Agonum sp. 2			***	***	***	***			19/XI to 18/I	T1,T4,T8,T9,T10,A12
Agonum cf. sp. 2			*			*			18/XI to 17/XII	T10,A12
Agonum sp. 3				*					16/XII	T1
Agonum sp. 4					**	**	*		18/XI to 13/II	T5,T10,A1,A10,A12
Allendia chilensis (Sol., 1849)					*	*			18/XI to 9/I	ND
Pelmatellus (sensu lato) sp. 1			*		***	*			10/XI to 1/II	T1,T4,T5,T9,A1,A10
Pelmatellus (sensu lato) sp. 2					**				5/XII to 1/II	T1,T8,T9
Pelmatellus (sensu lato) sp. 3					*				15/XII to 1/II	T9,A1,A10
Bradycellus (Goniocellus) sp.			*			**	*	*	20/XI to 14/II	T8,V8,A12
Bradycellus (Liocellus) sp. 1			*		*				13/XII to 9/I	T9

Table A1 (continued)

COLEOPTERA TAXA	1 AT	2 TL	3 SDF	4 NPRF	5 VRF	6 CV	7 IC	8 C	DATES	HABITATS
	V	IV			III	II	II/III			
CARABIDAE (continued)										
Bradycellus (Liocellus) sp. 2					*		*		15/XII to 13/II	T5,T10
Bradycellus (Stenocellus) sp.					***	***			10/XI to 1/II	T4,T5,T9,T10,A10,A12
cf. *Bradycellus (Stenocellus)* sp.			*		*				5/XII to 29/I	T1,T8,T9
Plagiotelum irinum Sol., 1849	*	*	**	*					16/XII to 26/I	T4,T10,V11,V12,V21,V25
Dromius cf. *sulcatulus* Sol., 1849					*				15/XII	T4
cf. *Dromius* sp.								*	7/II	V32
Mimodromius sp. 1					*				15/XII	T9
Mimodromius sp. 2					*				1/II to 23/II	V3,V11
DYTISCIDAE										
Laccophilus chilensis Sharp, 1882					*	*			22/XI to 16/I	A12
Laccornis copelatoides (Sharp, 1882)						*			10/XI to 19/XI	A12
Lancetes mixtus (Wtrh., 1881)				*					17/I	ND
Lancetes nigriceps Erich., 1832					***		**	*	29/I to 13/II	A3,A4,A5,A6,A11
Lancetes rotundicollis Bbgt., 1841					*				16/I	ND
Lancetes varius (Fabr., 1775)				**	*	**			18/XI to 1/II	A6,A12
Rhantus signatus (Fabr., 1775)	*				***	***	**	**	18/XI to 13/II	T4,A3,A4,A6,A10,A12
Rhantus validus Sharp, 1882					*	*	*	*	22/XI to 13/II	A3,A12
Rhantus sp.					*				5/XII	ND
Liodessus delfini (Rgmb., 1899)	**	*	***	***	***	***		**	18/XI to 9/II	T5,A3,A4,A5,A12
HYDRAENIDAE										
Gymnochthebius clandestinus Perk., 1980					*				31/I	A5
Gymnochthebius germaini (Zzv., 1908)				*	**	**		*	10/XI to 9/II	T4,A4,A12
Gymnochthebius topali (J. B-B., 1971)					*			*	5/XII to 9/II	A12
Gymnochthebius undifferentiated				**	***	***		***	18/XI to 9/II	A4,A5,A12
HYDROPHILIDAE										
Hydrochus stalpi Gmn., 1901						***		*	10/XI to 6/II	V3,A12
Hemiosus dejeani (Sol., 1849)					***				29/I	A4
Tropisternus setiger (Germ., 1824)					***	***	*	**	10/XI to 13/II	A6,A12
Paracymus corrinae Wldge., 1969					*				10/I to 16/I	A12
Paracymus graniformis Bruch., 1915						**			18/XI to 1/XII	A12
Enochrus fulvipes Sol., 1849					**	***		***	10/XI to 9/II	T5,V3,A8,A12
Enochrus vicinus Sol., 1849			*	*	***	***		**	10/XI to 9/II	A12,A3

Table A1 (continued)

COLEOPTERA TAXA	1 AT	2 TL	3 SDF	4 NPRF	5 VRF	6 CV	7 IC	8 C	DATES	HABITATS
HYDROPHILIDAE (continued)	V •	IV	•	III	• II •		II/III			
Enochrus sp.							*		13/II	A3
Cercyon sp.					*				22/XII	T4
Cercyon n. sp.	*								29/I	T1
Andotypus ashworthi Spang., 1979					*			*	7/XII to 7/II	T1
PTILIIDAE										
Ptiliidae sp. 1			**	**	***				5/XII to 1/II	T1,T2,T8
Ptiliidae sp. 2					*				7/XII	T1
Ptiliidae sp. 3					**				5/XII to 9/I	T1
LEIODIDAE										
Dasypelates sp. 1				*	*				7/XII to 16/XII	T1
Dasypelates sp. 2				*				*	16/XII to 7/II	T1
Eunemadus chilensis Ptvn., 1914			*	***	***	*		***	10/XI to 7/II	T1,T2,T8,T9,V32
Nemadiopsis sp.					*				8/XII	T1
Nemadiolus sp.			*	*	*				7/XII to 17/I	T1
Colon sp.					*				8/XII	T1
Hydnobiotus bicolor Jean., 1962					*				15/I	T1
cf. *Hydnobiotus* sp.				*					17/I	T8
Hydnodiaetus cf. *brunneus* Jean., 1962					*				15/I	T1
cf. *Neohydrobius* sp.		*			*			*	18/XII to 6/II	T1,T8
Hydnobiini n. gen.					*				29/I	T8
Leiodidae undifferentiated		*		*	*				7/XII to 15/I	T1
SCYDMAENIDAE										
Euconnus sp.					*				29/I	T8
cf. *Euconnus* sp.					*				5/XII	A8
SILPHIDAE										
Oxelytrum lineatocolle (Lpt., 1840)					*			*	1/II to 6/II	T1,T4

Table A1 (continued)

COLEOPTERA TAXA	1 AT	2 TL	3 SDF	4 NPRF	5 VRF	6 CV	7 IC	8 C	DATES	HABITATS
STAPHYLINIDAE	V •	IV		•	III	• II	•	II/III		
Glypholoma temporale T. & N., 1978		*							18/XII	T1
Glypholoma pustuliferum Jean., 1962					*				5/XII	T1
Omaliopsis sp.		**			*				18/XII to 21/XII	T1
cf. *Omaliopsis* sp.			*	**	*				15/I to 22/I	T1
Thinodromus sp. 1					*				8/XII to 17/I	T4,V14
Thinodromus sp. 2								*	6/II	V32
Thinodromus sp. 3					***	***	*		18/XI to 13/II	T1,T4,T5,T10,A9,A10,A12
cf. *Thinodromus* sp. 4								*	9/II	A9
Thinodromus sp. 5						*			20/XI	T10
cf. *Thinodromus* sp. 6					*				29/I	A10
Anotylus sulcicollis G. & H. 1868	*			*	*				17/I to 1/II	T1
Anotylus complanatus (Er., 1840)					*				22/XII to 1/II	T1
Bledius chilensis C. & S., 1968					*				8/XII	A12
Bledius claviventris F. & G., 1861					*				8/XII	A12
Stenus saizi Pz., 1972			**	**	***	***			10/XI to 19/I	A12
Stenus hogansoni Pz., 1983			*	**	***	***		*	10/XI to 9/II	V3,V32,A8,A12
Lithocharis ochraceus Grav., 1802						*			22/XII	A12
Stilicus chilensis Sol., 1836						*			22/XII	A12
Stilicus sp.				*	*				8/XII to 1/II	T3,T9,V32,A12
Baryopsis araucanus C. & S., 1968					*				21/XII	T1
Philonthus varians (Pykl., 1789)	**			*	*				9/I to 1/II	T1,T3,A10
Philonthus (Endeius) punctipennis (Sol., 1849)	*			**	***	**		*	18/XI to 6/II	T1,T5,T9,T10,A1,A4,A10,A12
Philonthus sp.					*				8/XII	T1
Cheilocolpus impressifrons (Sol., 1849)	*								7/XII	ND
Cheilocolpus sp. 1				*					16/XII	T1
Cheilocolpus sp. 2			*						22/I	V11,V21
Cheilocolpus sp. 3			*	*					16/XII to 22/I	T1
Cheilocolpus sp. 4					*	*			22/XII to 1/II	T8,A12
Valdiviodes ashworthi Smet., 1980		*	*		**				16/XII to 29/I	T1,T8
Loncovilius (Lienturius) cf. *heeri* (Bkw., 1944)				*	*	**		*	18/XI to 9/II	A12
Loncovilius (Lienturius) sp.					*	*			19/XI to 22/XII	T5,V3,A12
Loncovilius (Loncovilius) sp. 1		*							25/I	T1,V13
Loncovilius (Loncovilius) sp. 2		*	*						17/XII to 25/I	V13,V25
Leucotachinus luteonitens (F. & G., 1861)								*	6/II	V32

Table A1 (continued)

COLEOPTERA TAXA	1 AT	2 TL	3 SDF	4 NPRF	5 VRF	6 CV	7 IC	8 C	DATES	HABITATS
STAPHYLINIDAE (continued)	V •	IV	•	III		• II •	II/III			
Nomimocerus marginicollis (Sol., 1849)				*		*			22/XI to 22/XII	A12
Aleochara sp.					*	*			19/XI to 15/XII	T1,A12
Aleocharinae sp. 1					*				1/II	A1
Aleocharinae sp. 2	*		*						22/I to 29/I	T1
Aleocharinae sp. 3								*	7/II	T1
Aleocharinae sp. 4					*				8/XII	A8
Aleocharinae sp. 5				*					18/I	T8
Aleocharinae sp. 6					**				22/XII to 1/II	T1
Aleocharinae sp. 7					*				1/II	A1,A10
Aleocharinae sp. 8					*				1/II	T8
Aleocharinae sp. 9					*				29/I	T8
Aleocharinae sp. 10			*	***	**			*	6/XII to 7/II	T1
Aleocharinae sp. 11					*				8/XII	A8
Aleocharinae sp. 12		***	**	*					16/XII to 25/I	V13,V21,V28,V32,A8
Aleocharinae sp. 13			*	**				*	14/XII to 7/II	T1
Aleocharinae sp. 14					*				5/XII	T1
Aleocharinae Group 1	**		*	**	***	***		*	18/XI to 7/II	T1,T4,T10,V3,V12,A8,A12
Aleocharinae Group 2					*		*	**	5/XII to 13/II	V32,A8
Aleocharinae Group 3			*	*	***		*		5/XII to 14/II	V6,V32,A1,A7,A8,A12
Aleocharinae Group 4		***	***	*	*		*		8/XII to 23/II	T8,V6,V11,V13,V21,V23,V25, V28,V32,A8
PSELAPHIDAE										
Dalminiomus araucanus Jean., 1962					*				1/II	T1
Achillia sp. 1						*			22/XII	A12
Achillia sp. 2	*								24/I	T10
Tyropsis adumbrata Rttr., 1885				*					16/XII	T1
Tyropsis delamarei Jean., 1962								*	6/II	T8
Tyropsis sp.					*				8/XII	T9
LUCANIDAE										
Chiasognathus granti Steph., 1831					***	*			8/XII to 1/II	T9,V19,A10
Chiasognathus latreillei Sol., 1851	***		*						7/XII to 29/I	T9,T10,V3
Sclerognathus bacchus Hope, 1845					**	*		*	23/XI to 6/II	T1,T5,T7,V3,V32
Pycnosiphorus caelatus Blanch., 1837				*	***	*	*	**	22/XI to 14/II	T1,T4,T5,T7,T8,T9,V3,V12, V23,V32

Table A1 (continued)

COLEOPTERA TAXA	1 AT	2 TL	3 SDF	4 NPRF	5 VRF	6 CV	7 IC	8 C	DATES	HABITATS
LUCANIDAE (continued)	V	IV			III	II		II/III		
Pyonosiphorus femoralis Guér., 1839		*	*	*	*			*	5/XII to 7/II	T8,T9,V3,V21,V23,V32
Pyonosiphorus cf. *femoralis* Guér., 1839			*		*		*	*	9/I to 14/II	T1,T8,T9
Pyonosiphorus sp. 1								*	7/II	T9
Pyonosiphorus sp. 2			*						17/XII	V3
SCARABAEIDAE										
Dichotomius toruloeus (Esch., 1822)				**	***				5/XII to 29/I	T1
Aphodius fulviventris Frmr., 1860				**	*				8/XII to 16/XII	T1
Aphodius granarius (L., 1767)						*			18/XI	V3
Martinezostes asper (Phil., 1859)								*	6/II	T1,T8
Trox chilensis Hld., 1872				*	**				17/I to 29/I	T1
Trox longitarsis Hld., 1872				*	**				15/XII to 29/I	T1,T4
Frickius variolosus Gmn., 1897	*	*		*		*			1/XII to 29/I	T1,T8
Bolborhinum laesicolle (Frmr., 1856)					*				15/XII	T9
Astaenus sp.	**	*							18/XII to 25/I	T1,T10
Sericoides sp. 1		*							18/XII	T1,T9
Sericoides sp. 2					*				25/XII	V32
Sericoides sp. 3	***								7/XII to 29/I	T1,T8,T9,T10
Sericoides sp. 4			*		*				14/XII to 21/XII	T4,A12
Sericoides sp. 5					**				22/XII to 1/II	T4,V32
Sericoides sp. 6	**								18/XII to 24/I	T10
Sericoides sp. 7	*								19/XII to 21/XII	T1,T10
Sericoides chlorostictus Blanch, 1851				*	**				15/XII to 22/XII	T1,T4
Sericoides sp. 9					*				10/I	V6
Sericoides sp. 10					*				8/XII to 15/XII	T5,V32
Sericoides sp. 11					*				29/I	T8
Sericoides sp. 12					*				1/II	T9
Sericoides cf. *chlorostictus* Blanch., 1851				*					18/I	T1
Sericoides sp. 14		*							25/I	T1
Sericoides viridis Sol., 1851					***	**	*	*	24/XI to 21/II	T4,T9,V17,V26,V32,A12
Sericoides sp. 15					*				9/I to 1/II	T4
Orystomorphus bimaculatus Guér., 1830					**	*			8/XII to 21/II	T4,T9,V3,V32,A10
Brachysternus spectabilis Erich., 1847	***	*	**		**	*			20/XI to 1/II	T4,V21,V22,V25
Hylamorpha elegans Burm., 1844					*			*	2/XI to 23/II	T10,V11,V32,A1,A10,A11
Ligyrus villosus Burm., 1847								*	6/II	T7

Table A1 (continued)

	1	2	3	4	5	6	7	8		
COLEOPTERA TAXA	AT	TL	SDF	NPRF	VRF	CV	1C	C	DATES	HABITATS
	V	IV		III		II	II/III			
HELODIDAE										
cf. *Microcara* sp.	*		*	*	**	*			5/XII to 21/II	T4,T10,V6,V12,V17,V32 A12
Cyphon sp. 1					*				9/I	V32
Cyphon sp. 2					*				1/II	T4
Cyphon sp. 3		*							27/I	V21
Cyphon sp. 4				**	**				5/XII to 10/I	V6,V11,V12,V16,V23,V24,V32
Prionocyphon sp.			***	**	***	**	*	*	19/XI to 21/II	T4,V12,V17,V24,V32,A8,A12
Helodidae sp. 1			*	*	***		*	*	5/XII to 13/II	V6,V11,V17,V32,A8
Helodidae sp. 2					*				5/XII to 10/I	V6,V32
Helodidae sp. 3				*		*			24/XI to 9/XII	V32
Helodidae sp. 4			*		*				9/I to 22/I	V11,V17
Helodidae sp. 5					*				8/XII to 10/I	T4,V17,V23,A1
Helodidae sp. 6				*	*				5/XII to 14/XII	V8,V23,V32
Helodidae sp. 7			**	*	***	**	**	*	19/XI to 14/II	T4,V6,V11,V14,V18,V21,V23, V31,V32,A1,A8,A12
Helodidae sp. 8					*				8/XII	V23
CLAMBIDAE										
cf. Clambidae sp.				*					18/I	V31
PSEPHENIDAE										
Tychepsephenus cf. *felix* Wtrh., 1876						*			20/XI	A12
HETEROCERIDAE										
Heteroceridae sp.						**		*	22/XI to 9/II	A12
ELMIDAE										
Austrolimnius chiloensis (Champ., 1918)								**	9/II	A9
Austrolimnius sp.							**	***	9/II to 13/II	A9
Neoelmis n. sp.							*	*	9/II to 13/II	A9
Stethelmis sp.				*				*	18/I to 9/II	A9
Hydora annectens S. & B., 1981						*			20/XI	T10
Elmidae n. gen.				*			*	**	18/I to 13/II	A9

Tabla A1 (continued)

COLEOPTERA TAXA	1 AT	2 TL	3 SDF	4 NPRF	5 VRF	6 CV	7 IC	8 C	DATES	HABITATS
ELATERIDAE	V •	IV	•		III •	II •	II/III			
Campyloxenus pyrothorax Frmr., 1860					*				5/XII	T9
Anaspasis parallela (Sol., 1851)					*				10/I to 23/II	V11,V12
Semiotus luteipennis Guér., 1838			*	*					9/XII to 21/XII	V25
cf. *Cosmesus* sp. 1	*								21/XII	T1
cf. *Cosmesus* sp. 2	*								21/XII	T1
Agriotes australis Frmr., 1883			*						17/XII	T1,V3
Ischnodes reedi Cand., 1881					*				1/II	V32
cf. *Ctenicera* sp. 1				*					9/XII	V23
cf. *Ctenicera* sp. 2				*					9/XII	V23
cf. *Ctenicera* sp. 3				*					17/I	V32
Deromecus impressus (Sol., 1849)					*				22/XII	T4
Deromecus sp. 1					**		*	*	5/XII to 14/II	T4,T9,V8,V9,V12,V17,V26,V32
Deromecus sp. 2					*				17/I	V32
Deromecus sp. 3					*				8/XII to 17/I	V14,V23,V32
Deromecus sp. 4								*	6/II to 7/II	V32
Deromecus sp. 5					*				22/XII to 9/I	V16,V32
Deromecus sp. 6						*			23/XI	A12
Deromecus sp. 7					*				29/I	V32
Deromecus sp. 8				*	*				15/XII to 17/I	V32,A12
Deromecus sp. 9					*				15/XII	T4
Deromecus sp. 11					*	*			24/XI to 1/II	T4,V17,V32
Deromecus sp. 12	*		*	*					16/XII to 22/I	V11,V12
Deromecus sp. 13								*	7/II	V32
Deromecus sp. 14					*	*			23/XI to 9/I	T9
Deromecus sp. 15					*				7/XII	V23
cf. *Deromecus* sp. 1					*				5/XII	V18
cf. *Deromecus* sp. 2		*							25/I	V32
Gamnephorus candezei Fleut., 1907					*				6/XII	T9
Hypolithus magellanicus (Blanch., 1851)	***				*				7/XII to 29/I	T1,T8,T9,T10
Medonia sp. 1								*	6/II	V32
Medonia sp. 2					*		*		5/XII to 14/II	T5,V12
Negastrius atomus (Cand., 1878)	*								18/XII to 29/I	T1,T10
Negastrius sp.					**				15/XII to 22/XII	T5,T10
Pomachilius sp.			*		*				9/I to 22/I	V11,V17
LAMPYRIDAE										
Pyractonema albomarginata Sol., 1849					**				17/I	V14,V32

Table A1 (continued)

COLEOPTERA TAXA	1 AT	2 TL	3 SDF	4 NPRF	5 VRF	6 CV	7 IC	8 C	DATES	HABITATS
	V	IV			III	II		II/III		
LAMPYRIDAE (continued)										
Pyractonema angustata McD., 1960					*				29/I	V32
Pyractonema latior McD., 1960		*		*	**				5/XII to 20/XII	T1,V21,V23,V32
Pyractonema cf. *latior* McD., 1960		*	*						22/I to 25/I	V21,V32
Pyractonema nigripennis Group Sol., 1849	*	*	***	*	***	**	*	*	18/XI to 14/II	T1,T5,T9,T10,V3,V5,V9,V10, V11,V12,V13,V14,V18,V19,V20, V21,V23,V25,V29,V32,A8,A10
Pyractonema rhododera Sol., 1849			*		*				5/XII to 22/I	V11,A8
Pyractonema sp. 1					***				5/XII to 29/I	V10,V32,A10
Pyractonema sp. 2					*				1/II	A10
CANTHARIDAE										
Dysmorphocerus dilaticornis Guér., 1838					***	***			18/XI to 23/II	V6,V11,V12,V14,V17,V26,V32 A1,A8
Oontelus sp.			*			*			1/XII to 22/I	V11,V32
Chauliognathus variablis (Sol., 1849)		*	*	**	***	**	*	*	19/XI to 21/II	V8,V12,V14,V17,V19,V21,V23, V28,V29,V32,A1,A8,A12
Hyponotum albocinctum (Pic, 1926)				*	**			*	10/I to 9/II	V6,V12,V32
Hyponotum grandicolle (Pic, 1928)		*			**				9/I to 23/II	V11,V13,V16,V17,V26,V32,A1
Hyponotum krausei (Phil., 1861)					*				11/I	V32
Hyponotum violaceipenne (Pic, 1928)			**						17/XII	V25,A8
Hyponotum sp.				*					17/I	V32
Micronotum nodicorne (Sol., 1849)			***	*					14/XII to 22/I	V7,V11,V32
Plectocephalon testaceum (Pic, 1928)	*			*	*				7/XII to 21/XII	T4,V32
Cantharidae sp. 1					*				1/II	A1
ANOBIIDAE										
Xyletomerus sp.						*			24/XI	V32
cf. *Xyletomerus* sp.					*				22/XII	V32
Byrrhodes nigricolor (Pic, 1912)					*				8/XII	V1
Byrrhodes sp.					*				8/XII	V1
Caenocara discoidalis (Pic, 1923)								**	7/II to 23/II	V10,V26,V32
Caenocara nigra (Phil., 1864)								*	9/II to 23/II	V11,V32
cf. *Pachotelus* sp.					*				1/II	V23
Strichtoptychus cf. *brevicollis* (Sol., 1849)					*				1/II	A12

Table A1 (continued)

COLEOPTERA TAXA	1 AT	2 TL	3 SDF	4 NPRF	5 VRF	6 CV	7 IC	8 C	DATES	HABITATS
	V	IV		III		II	II/III			
TROGOSITIDAE										
Calitys sp.					*				22/XII	T4
CLERIDAE										
Natalia impressa (Spin., 1849)					*				I/II	V32
Isolemidia sp. 1								*	7/II to 23/II	V11,V32
Eurymetopum sp. 1			*						22/I to 23/II	V11,V21
Eurymetopum sp. 3			*						22/I	V11
Eurymetopum sp. 4			*						22/I to 23/II	V11
Eurymetopum sp. 5					*				9/I	V17
Eurymetopum sp. 6			*						22/I	V11
Eurymetopum sp. 7	*		*						22/I to 27/I	V11,V21
Eurymetopum sp. 9					*			*	16/I to 7/II	V17,V32
Eurymetopum sp. 10					*				8/XII	V18
Cleridae sp.			*					*	22/I to 7/II	V28,V32
MELYRIDAE										
cf. *Astylus* sp.					*				15/XII	ND
Dasytes haemorrhoidalis Sol., 1849				*	*			*	6/XII to 6/II	V11,V32
Dasytes marginipennis Sol., 1849						*			19/XI to 23/XI	V32,A12
NITIDULIDAE										
Brachypterus n. sp.					*				6/XII	V12
Perilopsis flava Rttr., 1873					*		*		10/I to 23/II	V6,V11,V26,V32
cf. *Cychramus* sp.					**				8/XII to 22/XII	T1,T4
Cryptarcha sp. 1							*		14/II	V26
Cryptarcha sp. 2			*		*			*	9/I to 9/II	V11,V32
PROTOCUCUJIDAE										
Eriamodes fuscitarsis Rttr., 1878				**	***				7/XII to 23/II	V6,V9,V11,V17,V23,V26
Eriamodes sylvaticus Phil., 1864				*	***	*	*	*	23/XI to 14/II	V6,V8,V9,V12,V16,V17,V26,V32
CUCUJIDAE										
Cryptamorpha redtenbacheri Rttr., 1876				**					9/XII to 18/I	V31,V32

Table A1 (continued)

	1	2	3	4	5	6	7	8		
COLEOPTERA TAXA	AT	TL	SDF	NPRF	VRF	CV	IC	C	DATES	HABITATS
CRYPTOPHAGIDAE	V •	IV	•		III •	II •		II/III		
Pseudochrodes suturalis Rttr., 1876						*		*	19/XI to 6/II	V32,A12
Cryptophagidae sp. 1					*				15/XII to 1/II	T4,V32,A1
Cryptophagidae sp. 2		*	*	*	*				5/XII to 17/I	T1,V12,V17,V32
cf. Cryptophagidae sp. 2			*		*				7/XII to 22/I	V21
PHALACRIDAE										
Phalacridae sp.						**			19/XI	A12
COCCINELLIDAE										
Rhizobius chilianus Mader, 1957							*		14/II to 23/II	V26
Scymnus (Pullus) sp.			*		*				10/I to 23/II	V11,V26
Cranoryssus chilensis (Crtch., 1874)					*				7/XII	V23
Cranoryssus germaini Crtch., 1874					*				8/XII	V12
Cranoryssus sp.							*		13/II	V32
Orynipus chilensis (Crtch., 1874)							*		14/II	V26
Orynipus darwini Brths., 1924				*					18/I	V31
cf. *Orynipus* n. sp. 1			*						22/I	V11
cf. *Orynipus* n. sp. 2					*			*	10/I to 9/II	V6,V32
Eriopis connexa chilensis Hfmn., 1972	*				***	***		**	9/II to 21/II	T9,T10,V14,V32,A1,A10
Adalia angulifera Muls., 1850						**			19/XI	A8
Adalia deficiens Muls., 1850					***	**			8/XII to 23/II	V3,V5,V6,V11,V14,V23,V32
Adalia kuscheli Mader, 1957							*		23/XI to 14/II	V8,V9,V32
Psyllobora picta (Gmn., 1854)					*	*			24/XI to 15/XII	V32
Sarapidus australis Gord., 1977					*			**	5/XII to 9/II	V18,V23,V32
Strictospilus darwini Brths., 1924				*	*		*	*	1/II to 18/II	V23,V31,V32,A12
Coccinellina n. sp.					*				15/XII to 23/II	V9,V32
LATHRIDIIDAE										
Aridius heteronotus (Belon, 1891)			*		*				8/XII to 22/I	V11,V17,V32,A1
Lathridiidae sp. 1					**	*	*	*	19/XI to 14/II	V6,V23,V32,A1,A8,A12
Lathridiidae sp. 2								*	7/II	V32

Table A1 (continued)

COLEOPTERA TAXA	1 AT	2 TL	3 SDF	4 NPRF	5 VRF	6 CV	7 IC	8 C	DATES	HABITATS
TENEBRIONIDAE	V ·	IV	·		III	· II	·	II/III		
Thinobatis rufipes penai Frde., 1960								***	6/II	T5
Nycterinus abdominalis Esch., 1829								***	6/II	T3,T5
Praocis costata Sol., 1840								***	6/II	T3,T5
Oligocara nitida Sol., 1851					*			*	15/XII to 6/II	T9,V32
cf. *Adelium* sp.					*				15/XII	V32
Heliofugus impressus Guér., 1830						*			16/XI to 23/II	T9,V3
Homocyrtus dromedarius (Guér., 1830)				*	*				5/XII to 17/I	V32
SALPINGIDAE										
Cycloderus rubricollis Sol., 1851					**	*			29/XI to 23/II	V11,V12,V32
Salpingidae sp.	*								18/XII	ND
OEDOMERIDAE										
Mecopselaphus maculicollis Sol., 1849				*	**	*	*	*	19/XI to 14/II	V5,V9,V12,V26,V32,A8
Platylytra vitticollis F. & G., 1863					*				9/I	V32
Sisenecantharis chilensis (Frmr., 1863)				*					14/XII to 16/XII	V7,V12
MELANDRYIDAE										
Orchesia sp. 1			**		*		*	**	10/I to 14/II	V6,V8,V11,V17,V21,V32
Orchesia sp. 2								*	7/II	T1
Melandryidae sp.							*		14/II	V26
SCRAPTIIDAE										
Scraptiidae sp.					*				15/XII to 22/XII	V5,V32
MORDELLIDAE										
Mordella alboguttata Sol., 1851								*	7/II	V32
Mordellidae sp. 1					*				29/I	V10
Mordellidae sp. 2					*				1/II	T4
Mordellidae sp. 3					**			*	15/XII to 9/II	V6,V12,V32

Table A1 (continued)

COLEOPTERA TAXA	1 AT	2 TL	3 SDF	4 NPRF	5 VRF	6 CV	7 IC	8 C	DATES	HABITATS
MELOIDAE	V	IV			III	II		II/III		
Epicauta sp.						*			14/I to 23/II	T6,V32
ANTHICIDAE										
Anthicidae sp.					***	*	*	*	18/XI to 14/II	V32,A1,A8,A12
PEDILIDAE										
Copobaenus cf. *nobilis* (F. & G., 1863)					*				15/XII	V5
Lagrioida obscurella F. & G., 1860								**	6/II	T7,V32
CERAMBYCIDAE										
Microplophorus magellanicus Blanch., 1851					*				15/XII	T4
Holopterus chilensis Blanch., 1851					*				15/XII	V29
Sibylla coemeterii Thomson, 1857			*						17/XII to 21/XII	T4,V25,V29
Chariergus testaceus (Blanch., 1851)					*	*			23/XI to 1/II	V23,V29,V32
Callideriphus laetus Blanch., 1851					*				15/XII to 1/II	T4,V29
Callideriphus sp.					*				15/XII	V29
Hoplonotus spinifer Blanch., 1851					*			*	10/I to 9/II	T8,V16,V32
Aconopterus cristatipennis Blanch., 1851								*	7/II	V32
Hebestola cf. *carcharias* Lamre., 1893						*			1/XII	V32
CHRYSOMELIDAE										
Pachybrachis sp. 1					*				1/II	V32
Pachybrachis sp. 2					*			*	1/II to 9/II	V32
cf. *Cryptocephalus* sp.		*	*			*			1/XII to 27/I	V21,V32
cf. *Habrophora* sp.					*	*		*	22/XI to 7/II	V32
Strichosa eburata Blanch., 1851				***	***	*	***		22/XI to 14/II	T5,V5,V8,V32
Phaedon semimarginatus argentinensis Bêch., 1950					**				17/I	V14
Phaedon semimarginatus cyanopterus Guér., 1844					***	***		*	18/XII to 6/II	T5,V14,V19,V32,A1,A8,A12
cf. *Gavirga* sp.		**							25/I	T1,T8
Aulonodera n. sp.					*				7/XII	T1

Table A1 (continued)

COLEOPTERA TAXA	1 AT	2 TL	3 SDF	4 NPRF	5 VRF	6 CV	7 IC	8 C	DATES	HABITATS
CHRYSOMELIDAE (continued)	V •	IV •			III •	II •		II/III		
Altica sp. 1			*	***	***	***			18/XI to 23/II	T9,V16,V18,V19,V32,A1,A3, A8,A12
Altica sp. 2			**						22/I	V21
Alticinae sp. 1			*		*				8/XII to 17/XII	V14,A8
Alticinae sp. 2					*				15/XII	T1,V23
Alticinae sp. 3					*				7/XII	V11
Alticinae sp. 4								*	6/II	V32
Alticinae sp. 5		*							25/I	T1
cf. *Crepidodera* sp. 1					*				7/XII	V17
cf. *Crepidodera* sp. 2								*	7/II	V32
Aulacochlamys sp.					*				5/XII to 10/I	V6,V17
Chaetocnema sp.					*		*	*	1/II to 14/II	V6,V32
Kuschelina decorata (Blanch., 1851)					*		*	*	29/I to 14/II	V32,A4
Oyarzuna sp.				*					18/I	T8
Psathyrocerus cf. *unicolor* (Blanch., 1851)					*				9/I	V17
cf. *Planagetes* sp.		***	***	***	**				7/XII to 18/I	T8,V11,V12,V18,V21,V22,V23. V24,V25,V28,V32
cf. *Varicoxa* sp.		***	***						22/I to 27/I	T1,V21,V32
ANTHRIBIDAE										
Ormiscus parvulus (Blanch., 1851)							*		14/II	V26
cf. *Plintheria* n. gen. sp. 1							*		14/II	V26
cf. *Plintheria* n. gen. sp. 2			*						22/I	V21
cf. *Plintheria* n. gen. sp. 3							*		14/II	V26
cf. *Plintheria* n. gen. sp. 4							*		14/II	V26
SCOLYTIDAE										
Gnathotrupes sp.					*				8/XII to 15/XII	T1
ATTELABIDAE										
Eugnamptoplesius violaceipennis (F. & G., 1860)					*				5/XII	V18
Minurus testaceus Wtrh., 1842					*			*	5/XII to 6/II	V18,V32

Table A1 (continued)

COLEOPTERA TAXA	1 AT	2 TL	3 SDF	4 NPRF	5 VRF	6 CV	7 IC	8 C	DATES	HABITATS
BELIDAE	V ·	IV	·		III ·	II ·	II/III			
Trichophthalmus miltomerus (Blanch., 1851)				*	*	*			19/XI to 17/I	V6,V15,V32
CURCULIONIDAE										
Nototactus angustirostris Kusch., 1952				**					9/XII to 14/XII	V23,V24,V32
Polydrusus nothofagi Kusch., 1950					**			**	15/XII to 9/II	V23,V32
Megalometis spinifera Boh., 1842				*	***		**		5/XII to 14/II	T1,V11,V12,V16,V26,V32
Hybreoleptops tuberculifer (Boh., 1842)				*		*	**	*	19/XI to 14/II	V11,V26,V32
Dasydema hirtella Blanch., 1851		*	***	**	***		***	***	5/XII to 14/II	T1,V2,V5,V6,V8,V9,V10,V11,V13,V14,V16,V17,V18,V21,V23,V25,V26,V28,V32
Philippius superbus (Reed, 1872)					*				15/I	T1
Paulsenius carinicollis (Blanch., 1851)	***				*				7/XII to 29/I	T1,T8,T10
Listroderes angusticeps Blanch., 1851						*			18/XI	A12
Listroderes attenuatus Gmn., 1895					*				21/XII to 11/I	T1
Listroderes dentipennis Gmn., 1895	*				**				5/XII to 31/I	T4,T9,T10,A10
Listroderes fulvicornis Gmn., 1895	*								18/XII to 29/I	T1,T10
Listroderes sp.			*		*				15/XII to 22/I	T4,T9,V2
Listronotus lineaticollis (Blanch., 1851)						*			22/XI	A12
Listronotus minutus (Blanch., 1851)					*	*			10/XI to 1/II	V32,A12
Parergus axillaris (F. & G., 1861)						*			20/XI to 23/II	T9,A12
Tartarisus signatipennis (Blanch., 1851)				*					18/I	T8
Nothofaginoides andinus Kusch., 1952		*							18/XII to 20/XII	V21
Nothofagobius brevirostris Kusch., 1952		*		*		*	**	*	1/XII to 14/II	V23,V25,V31,V32
Neopsilorhinus collaris (Blanch., 1851)					*				15/XII	V5
Neopsilorhinus variegatus (Blanch., 1851)					*				1/II	V32
Neopsilorhinus sp.								*	7/II to 14/II	V32
Rhopalomerus tenuirostris Blanch., 1851				*	***	*	*	*	23/XI to 14/II	V5,V6,V8,V12,V26,V32
Omoides validus Kusch., 1952				*					9/XII	V32
Omoides variabilis (Phil., 1864)					*				7/XII to 15/I	V11,V32
Epaetius carinulatus Kusch., 1952					*				14/XII	V24
cf. *Aoratolcus* n. sp.							*		14/II	V8
Erirrhininae n. gen. sp. 1		**	***						17/XII to 25/I	V21,V25
Erirrhininae n. gen. sp. 2				**	**				5/XII to 10/I	V23,V26,V32

Table A1 (continued)

	1	2	3	4	5	6	7	8		
COLEOPTERA TAXA	AT	TL	SOF	NPRF	VRF	CV	IC	C	DATES	HABITATS
CURCULIONIDAE (continued)	V	IV			III	II	II/III			
Erirrhininae gen. indet.	*								24/I	T9
Aegorhinus nodipennis (Hope, 1836)		*	**		***	*			24/XI to 23/II	V11,V14,V21,V23,V25,V26, V29,V32
Aegorhinus ochreolus Kusch., 1951				***	***		***		5/XII to 14/II	V12,V23,V32
Aegorhinus oculatus Kusch., 1951	***								7/XII to 24/I	T10
Aegorhinus opaculus (Desbr., 1910)					*		*		8/XII to 13/II	V19,V32
Aegorhinus servillei (Sol., 1839)				*	*	*		*	19/XI to 6/II	V5,V12,V32
Aegorhinus vitulus bulbifer Kusch., 1951		*	**	**	*	**	**		22/XI to 14/II	V23,V26,V32
Scirpicola chilensis (Blanch., 1851)						*			18/XI	A8,A12
Apion sp. 1					***				1/II	V32
Apion sp. 2					***	*			22/XI to 1/II	T4,V32,A1,A8
Apion sp. 3			***				*		22/I to 14/II	V11,V26
Apion sp. 4				*	**	*			22/XI to 23/II	V11,V23,V26,V32
Apion sp. 5					**		*		22/I to 14/II	V9,V11,V26
Apion sp. 6			*		*		*	*	17/XII to 23/II	V11,V22,V26,V32
Anthonomus ornatus Blanch., 1851		*			***		**		5/XII to 14/II	V8,V9,V12
Berberidicola crenulata (Blanch., 1851)				*	***	*	**		22/XI to 14/II	V5,V8,V9,V11,V17,V26,V29,V32
Berberidicola exarata (Blanch., 1851)				*					16/XII	V30
Polylophus elegans Blanch., 1851					*				9/I	V17
Psepholax dentipes (Blanch., 1851)					**	*			24/XI to 1/II	T8,V5,V20,V32
Acalles pictus Blanch., 1851								*	7/II	V32
Acalles tristis Blanch., 1851			*						22/I	T9.
Acalles cf. *variegatus* Blanch., 1851					*				15/XII	V23
Acalles sp. 1					*				15/XII	T4
Acalles sp. 2					*				5/XII	V32
Acalles sp. 3				*					18/I	V11
Acalles sp. 4					*				1/II	V32
Rhyephenes goureaui (G. & S., 1839)						*			1/XII	V32
Rhyephenes maillei (G. & S., 1839)		*		*	***	*	*		24/XI to 14/II	V3,V5,V21,V23,V26,V27,V29, V32
Chilebaris tenuis (Blanch., 1851)						*			1/XII	V32
Euoolus thoracicus (Phil., 1864)						***			18/XI to 24/XI	V32,A12
Torcus luteolus Hust., 1939					***	***			24/XI to 10/I	V32,A8,A12

Table A1 (continued)

1. Systematic order of coleoptera infrafamilial taxa after Blackwelder (1944-1947).

2. Familial order followed by U.S. Department of Agriculture and U.S. National Museum.

3. Number of individuals: * = 1-5, ** = 6-10, *** = >10.

4. Habitat types: T1 = dung-baited pitfall traps, T2 = dung-baited pitfall traps on open sand, T3 = in cattle dung, T4 = light trapping, T5 = on open sand, T6 = on rocks, T7 = open sandy area (wet), T8 = unbaited pitfall traps, T9 = under log, T10 = under rock, V1 = in fungus, V2 = in leaf litter, V3 = in rotten wood, V4 = in wet leaves, V5 = on *Aextoxicon punctatum*, V6 = on *Amomyrtus luma*, V7 = on *Azara* sp., V8 = on *Berberis darwini*, V9 = on *Berberis* sp., V10 = on *Chusquea quila*, V11 = on *Chusquea* sp., V12 = on *Drimys winteri*, V13 = on cf. Ericaceae, V14 = on *Escallonia virgata*, V15 = on fern, V16 = on *Flotovia acanthoides*, V17 = on *Fuchsia magellanica*, V18 = *Fuchsia* sp., V19 = on *Gunnera chilensis*, V20 = on *Myrceugenella* sp., V21 = on *Nothofagus antarctica*, V22 = on *Nothofagus betuloides*, V23 = on *Nothofagus dombeyi*, V24 = on *Nothofagus nitida*, V25 = on *Nothofagus pumilio*, V26 = on *Nothofagus* sp., V27 = on *Nothofagus* sp. (deadfall), V28 = on *Ovidia andina*, V29 = on *Persea lingue*, V30 = on *Ribes* sp., V31 = on *Saxegothaea* sp., V32 = on vegetation, A1 = in moist vegetation (pond marginal), A2 = in moss near waterfall, A3 = in shallow water, A4 = in shallow water (mud bottom), A5 = in shallow water (no vegetation), A6 = in shallow water (weedy), A7 = on aquatic flowers, A8 = on emergent vegetation, A9 = shallow running water, A10 = shoreline debris, A11 = small algal choked pools, A12 = trampling water marginal vegetation, ND = no habitat data.

function of the uneven distribution of microhabitats.

The objective of the mathematical analysis was to discover patterns within the large data set. This was achieved (Figure A7) by cluster analysis of coefficients generated to express the similarity in species content between pairs of collecting localities. A Q-mode type of analysis was employed in which the various samples were compared to one another on the basis of the taxa they contain. In this study, these coefficients are merely quantitative descriptive numbers based on the presence or absence of taxa. Although a number of binary (presence-absence) similarity coefficients have been used in bioassociational studies, the Dice coefficient, developed by Dice (1945) and advocated by Hall (1969), was used in this study because it emphasizes similarity.

The Dice coefficient is expressed by the formula:

$$C_D = \frac{2C \times 100}{N_1 + N_2}$$

where C_D = Dice coefficient, C = number of taxa common to both samples; N_1 = number of taxa present in the first sample, N_2 = number of taxa present in the second sample. Coefficients were computer generated using a program written by R. D. LeFever, Geology Department, University of North Dakota.

A computerized version (Davis, 1973) of the WPGMA clustering procedure was used to define relationships within the similarity coefficient matrix. This particular method of cluster analysis was chosen over others because of the disparity in the size of samples being compared. Similar samples were grouped (clustered) and clusters are displayed in a dendrogram (Figure A7). The dendrogram, in summarizing

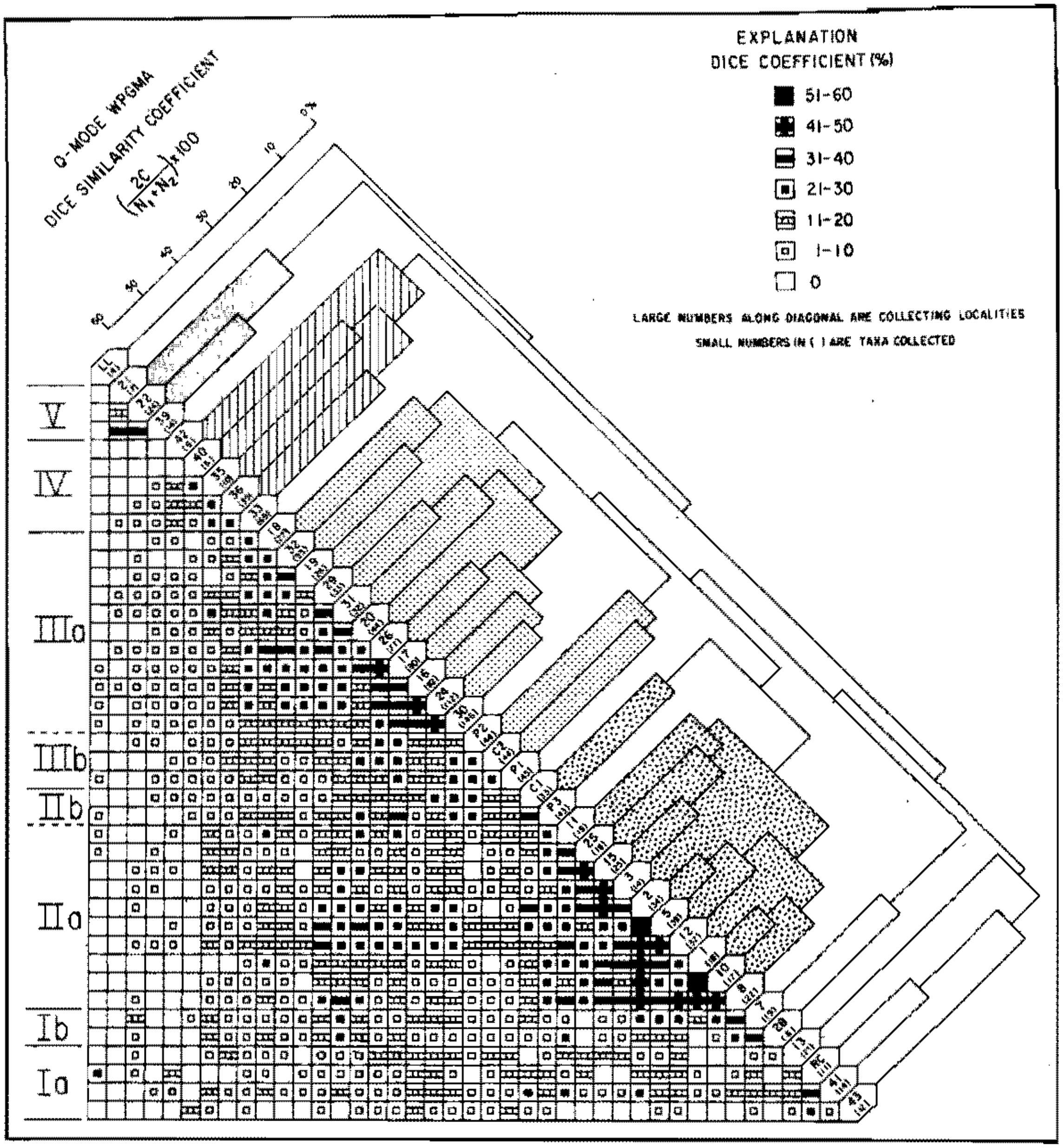


Figure A7. Similarity matrix (trellis diagram) and binary tree (dendrogram) showing patterns of similarity among 41 beetle fauna collecting sites. See Figure A1 and Figure A2 for location of sites. Similarity is measured by Dice's Coefficient. Large numbers along diagonal are collecting localities, small numbers in parentheses are taxa collected. The pattern of each square in the matrix indicates the degree of similarity, as depicted in the explanation. The dendrogram shows the order of clustering of the localities by WPGMA. Dark patterns proximal to the diagonal, as from localities 11 to 8, indicate groups of localities with many taxa in common. The major groups (clusters), II-V, are indicated to the left of the matrix and are separated by patterns on the dendrogram. Dark patterns within the matrix (for example between localities of group II and III) indicate that some localities within the groups have a number of taxa in common.

the original matrix of similarity coefficients through the process of averaging, distorts the original relationships between the samples being compared. At times, the degree of similarity between two samples is masked. That problem was counteracted by showing similarities within the original matrix of similarity coefficients as a shaded trellis diagram (Figure A7).

RESULTS

A total of 462 species representing 48 families were collected from 41 locations in the park and surrounding region. The vegetational zones and habitats from which the species were collected, their relative abundance, and the range of dates when collected are shown in Table A1. The number of taxa that occur in each zone and the percentage of taxa restricted to each zone are shown in Figure A8.

The results of the cluster analysis of the similarity coefficients are shown in Figure A7. Major clusters are distinguished on the completed dendrogram by tight groupings of samples joined at high similarity levels. Four principal clusters of localities, separated by faunal discontinuities, are evident in the dendrogram. The faunaly-related groups of samples are also indicated by darkened regions in the trellis diagram. Each major group is defined by an elevationally restricted, Coleoptera bioassociation.

Bioassociation II (BA II) consists of one major cluster, IIa, including the faunas from localities 11 through 8 and subcluster, IIb, including the faunas from localities C1 and P3 (Figures A2 and A7). All localities (Figure A1) in this group occur in lowland areas less than

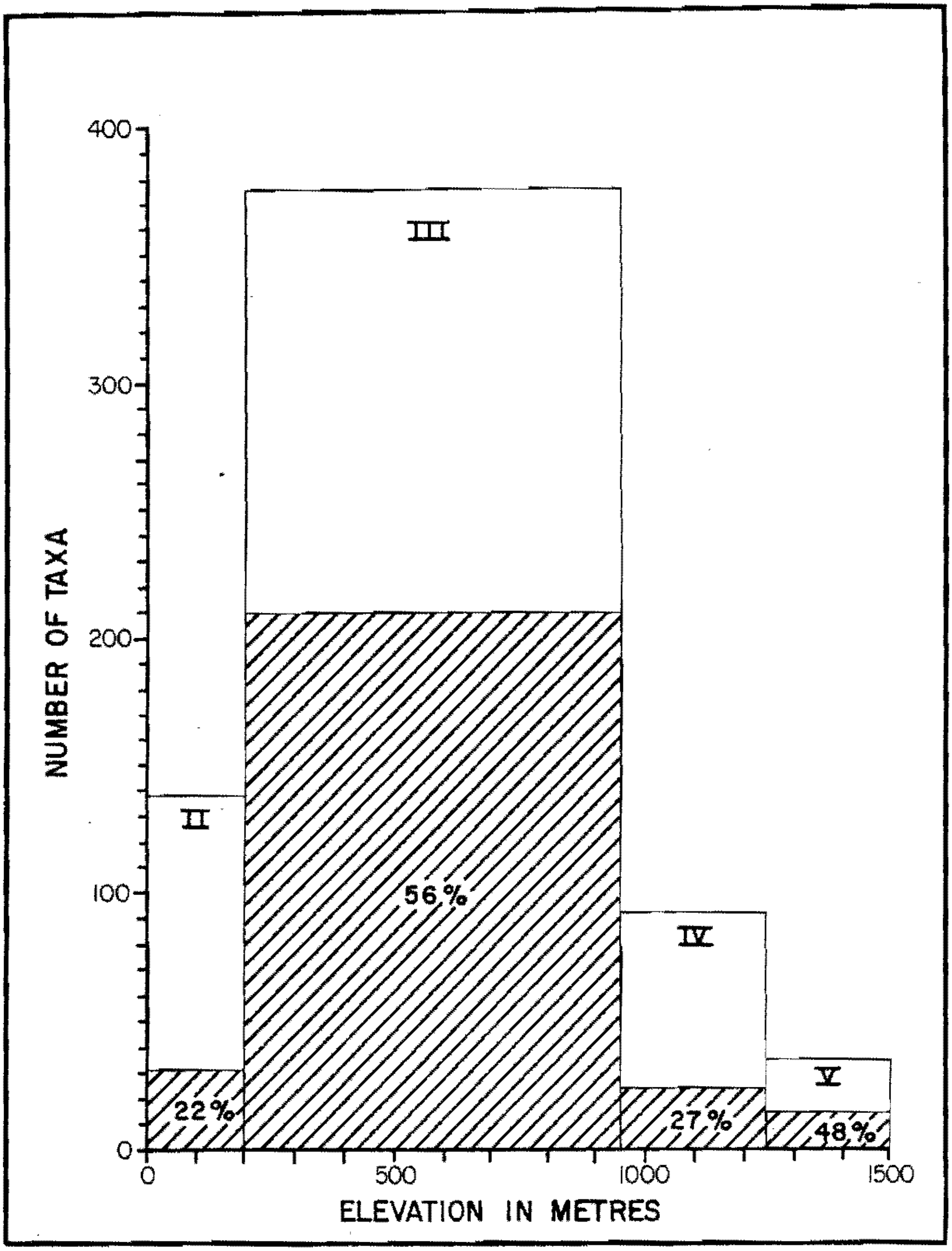


Figure A8. Diversity diagram showing the number of taxa occurring in each bioassociation (II–V) and the number and percent of taxa restricted to each bioassociation.

200 m msl in elevation where natural habitats have been disturbed. Localities C1 and P3 are in lowland areas on Isla Chiloe and near coastal Pucatrihue, respectively. Although C1 and P3 are in separate and distinct geographic areas in the Lake Region, they are similar in faunal composition to the other disturbed lowland sites in cluster IIa as indicated in the dendrogram and are therefore included in BA II.

Bioassociation III (BA III) consists of one major cluster, IIIa, including the faunas from localities 18 through 30 and a subcluster, IIIb, includign the faunas from localities P2, C2 and P1 (Figures A2 and A7). All localities in cluster IIIa occur in natural rain forest habitats ranging in elevation from about 200 m to about 950 m in the park (Figure A4). Localities P1 and P2 are in coastal mountain rain forest habitats near Pucatrihue and C2 is a rain forest locality on Isla Chiloe (Figure A1). The faunas of the localities in subcluster IIIb are included in BA III because they are similar to the faunas of localities in IIIa are indicated in the dendrogram even though they are from distinct geographic regions.

The affinity of the disturbed lowland fauna, BA II, with the rain forest fauna of BA III is well defined by the clustering technique. Darker regions in the trellis diagram also illustrate that the faunas of some of the localities in BA II are similar in species composition to some localities in BA III. As noted earlier, all of the Lake Region was densely forested prior to European colonization. Today, in the lowland area, only scattered remnants of the rain forest remain between cultivated fields and pastureland. BA II is therefore a mix of remnants of a once well established rain forest fauna and species that have invaded since the forest clearance. This includes native species adapted to open habitats and also species such as *Aphodius granarius* L., a dung beetle, introduced from Europe with cattle. The major effect of man's intervention, however, has been to cause a marked reduction in the diversity of the lowland fauna. This is illustrated by both the relatively low number of species in, and the low percentage of species restricted to BA II as compared to BA III (Figure A8).

BA III contains the greatest number and highest diversity of species of any of the bioassociations (Table A1, Figure A8); 52 percent of the 43 families and 64 percent of the 214 genera have the upper limit of their range within the zone, and 56 percent of the 375 species are restricted to the bioassociation. The faunal diversity reflects the diversity of the vegetation and habitats available within the Valdivian Rain Forest.

The fauna associated with vegetation in BA III is the most abundant. For example, beetles of 19 families were collected on *Nothofagus* spp., of which weevils were the most abundant. Some common distinctive beetles restricted to BA III but which also may occur in the undisturbed forest fauna of BA II are the carabids, *Ceroglossus darwini*, the dytiscids *Rhantus signatus*, and *Lancetes nigriceps*, the hydrophilid *Tropisternus setiger*, the lucanids *Chiasognathus granti*, *Sclerognathus baccus*, and *Pycnosiphorus caelatus*, the scarabs *Dichotomius torulosus* and *Sericoides viridis*, the cantharid *Dysmorphocerus dilaticornis*, the protocucujids *Ericmodes fuscitarsis*, and *E. sylvaticus*, the coccinellids *Eriopis connexa* and *Adalia deficiens*, the chrysomelids *Strichosa eburata*, and *Phaedon semimarginatus*, and the weevils *Megalometis* spinifer, Rhopalomerus tenuirostris, Aegorhinus ochreolus, and Berberidicola crenulatus.

Many common species of BA III are also abundant at higher elevations. These include the trachypachid Systolosoma brevis, the carabids Ceroglossus chilensis, C. valdiviae, Creobius eydouxi, and Abropus carnifax, the dyticid Liodessus delfini, the hydrophilid Enochrus vicinus, the leiodid Eunemadus chilensis, lampyrids Pyractonema nigripennis Group, the cantharid Chauliognathus variablis, the oedomerid Mecopselaphus maculicollis, and the weevils Dasydema hirtella, Nothofagobius brevirostris, Aegorhinus nodipennis, A. vitulus, and Rhyphenes maillei.

BA IV (Figures A2 and A7) includes the faunas from localities 42 through 33 in the Subantarctic Deciduous Forest and the krummholz from about 950 m to about 1250 m msl. (Figure A5). The fauna is relatively depauperate compared to that of BA III. Most of the 93 species (Table A1) that comprise BA IV also occur at lower elevations; only 27 percent (Figure A8) are restricted to this group. Beetles restricted to, or most abundant in Bioassociation IV are the carabids Cascellius sp., and Plagitelum irinum, the scarab Brachysternus spectabilis, and cantharids Hyponotum violaceipenne, and Micronotum nodicorne, and the chrysomelid cf. Varicoxa sp.

BA V (Figures A2 and A7) includes the faunas of localities 21 through 39, all in Andean tundra habitats (Figure A6) from about 1250 m to 1550 m msl. This bioassociation is characterized by low taxa diversity and a high percentage of species exclusive to the bioassociation (Table A1, Figure A8). Low taxa diversity is also indicated by the numbers of species to genera: 33 species in 31 genera. Occasionally individuals were especially abundant. For example 42 specimens of Bembidion sp. 14 were collected from beneath a rock with an area of about 1 m^2. Species restricted to BA V are the carabid Bembidion sp. 14, the pselaphid Achillia sp. 2, the scarabs Sericoides spp., the elaterids cf. Cosmesus spp. and Negastrius atomus, the staphylinid Cheilocopus impressifrons, an unidentified salpingid, and the weevils Listroderes fulvicornis, Aegorhinus oculatus, and an undetermined species of Erirrhininae. Species common on the tundra but which also occur occasionally at lower elevations include carabids of the Trechisibus nigripennis Group, the lucanid Chiasognathus latreillei, the scarab Astaenius sp., the elaterid Hypolithus magellanicus, and the weevils, Paulsenius carinicollis and Listroderes dentipennis. Some species collected on the tundra, particularly on snow banks, are believed to have been carried there on thermals. Among these are the carabids, Abropus carnifax, and Plagiotelum irinum, the dytiscid Rhantus signatus, the scarab Brachysternus spectabilis, the helodid cf. Microcara sp. the cantharid Plectocephalon testaceum, and the coccinellid Eriopis connexa.

The faunas of seven out of the total of 41 samples (sites in BA Ia, Ib and locality LL), did not cluster where expected. All but one (site 28), in BA Ia and Ib are from disturbed lowland habitats. Their faunal content, as shown in the dendrogram, is intermediate between BA II and III, reflecting partially disturbed rain forest. The fauna, only 5 species, of locality 28 at an elevation of 750 m msl in the park might have been expected to have clustered in Bioassociation III rather than with the fauna of locality 7, a lowland disturbed site. The best reason for the unexpected result is simply the small sample size. Hazel (1970) cautioned against using samples of less than 10 species in the cluster method because in comparing samples with few species to samples with many species low similarity values are generated. This also explains why the fauna of locality LL, a lowland site near Lago Llanquihue containing only four species, clusters at a very low level.

DISCUSSION

The pattern of bioassociations developed because species were determined to have restricted elevational ranges. Undoubtedly further sampling will extend the range of some species and may permit the subdivision of BA III. More extensive investigations of the faunas from the geographically distinct regions of the Coastal Mountains, including the Isla Chiloe, are needed to determine if those faunas are really as similar to the faunas of the Central Valley and the Andes as inferred from the cluster analysis.

The range of individual species is controlled by the complex interactions of large number of factors; such as competition for food and shelter, predation and disease, and microclimatic conditions that permit survival. How these factors act to limit the range of particular species is generally poorly understood, and especially so for the Lake Region Coleoptera. Undoubtedly the marked decrease in the diversity of Coleoptera that accompanies elevation (Figure A8) results directly from less favorable climatic conditions. The decrease in seasonal temperatures, the increase in number of days with snow cover and frost, and the increase in the effects of wind that accompany progressively higher elevations in the park act in concert to produce conditions less favorable for insects. The most distinctive components of the fauna are those of the Valdivian and North Patagonian Rain Forests, BA III, and the Andean tundra, BA V; the former has 56 percent, and the latter 48 percent of its species restricted to the zone (Figure A8). The fauna of the Subantarctic Deciduous Forest, BA IV, is much less distinct, representing an overlap between the lower forest fauna and the tundra. Congeneric species for the majority of the restricted tundra species occur in the forests, suggesting that the tundra fauna may have been derived by competitive exclusion from the forest faunas. An interesting example could involve the large lucanids of the genus Chiasognathus (Table A1). As might be expected for a large lucanid, the well-known, C. granti inhabits the dense forests of the Valdivian Rain Forest zone. By contrast, the similar-sized, C. latreillei, seems out of place on the tundra and in openings in the Subantarctic Deciduous Forest, where it apparently feeds on low ericaceous plants.

In view of the large number of unknowns and inherent complexity the faunal clusters might be perceived to be accidental coincidences of the system. However, with a single exception, there is a Coleoptera bioassociation for each vegetation zone. The exception is that the Valdivian Rain Forest and the North Patagonian Rain Forest are represented by a single bioassociation (Figure A2). Notably the vegetation of these two zones is very similar and differs mostly in the species content and density of the undergrowth. The striking correlation between the bioassociational boundaries and those between the principal vegetational zones (Figure A2) implies the existence of controlling factors and leads to the questions of why the zonation exists and when it developed.

Terbough (1971) tested three models in an attempt to explain the distribution limits of a large sample of birds in the Peruvian Andes. In his analysis, distribution limits could be determined by "factors in the physical or biological environment that vary continuously and in parallel with the gradient", or by "competitive exclusion", or by "habitat discontinuities (ecotones)". He concluded that all play a role but that the most important was an individualistic response to the changing character of the physical and biological factors along the gradient. The least important was the control exerted by the ecotone. In a general discussion of the distribution of plant species along gradients, Whittaker (1975) rejected the hypothesis that competing species exclude one another along sharp boundaries; and that evolution leads to the formation of distinct zones each with its own assemblage of species adapted to one another, and separated from others by sharp boundaries. He preferred the hypothesis that species act in an individualistic manner, and that competition does not produce sharp boundaries; and that evolution will not result in well-defined groups of species (zones). In a general way, our evidence supports the formation of groups, but that is not surprising considering that many of the beetles, especially the weevils, are host-plant specific (Table A1). To assume, however, that the distribution of beetles is simply controlled by the distribution of plants would be wrong. Beetles, as important pollinating agents, exert an equally strong influence on plant distribution, especially in Chilean rain forests. The coincidence of the boundaries between the Coleoptera bioassociations and the principal vegetational zones is perhaps better explained by reference to another of Whittaker's hypotheses (1975, p. 113) that while competition does not produce sharp boundaries, the evolution of species towards adaptation to one another will result in the appearance of groups of species with similar distributions.

More information is available to answer the question of when the fauna began to assume its present configuration. During the last glacial maximum glaciers extended well out into the Central Valley (Figure A1), and the park was entirely covered by ice. The zonation could only have developed subsequent to deglaciation. Mercer (1976) provided evidence from the moraines at the western end of Lago Rupanco that the last glacial maximum occurred about 19,200 yr B.P. The position of the ice-front may have fluctuated but it was not until about 14,000 yr B.P. (based on evidence from Lago Ranco), that deglaciation of the Andean valleys commenced (Mercer, 1984). Furthermore, according to Mercer (1976), glaciers had receded to their present diminuitive conditions by 11,000 yr B.P., and the western slopes of the Andes were open for colonization.

Our studies of fossil beetles from the Lake Region provide direct evidence of the history of development of the fauna. Very little is known about the Coleoptera that existed prior to the last glacial maximum. Scant fossil evidence from peats older than 40,000 yr B.P. exposed in the sea cliffs southeast of Puerto Montt indicate the occurrence of a forest biota in lowland areas prior to the last phase of glaciation. Based on fossil evidence from the western end of Lago Rupanco (Ashworth and Hoganson, unpub. ms.), the character of the lowland fauna at 26,000 yr B.P. was completely different than that of the earlier forest fauna. The fauna lacked forest species and, compared to both earlier and later faunas, was depauperate. We speculate that the reason for the depauperate fossil assemblages is that most forest species were unable to tolerate the colder climatic conditions associated with glaciation, and were regionally exterminated. Some support for this idea, other than the direct glacial evidence, comes from a palynologically-based interpretation by Heusser and others (1981), that mean summer temperatures were several degrees colder from about 40,000 to about 14,000 yr B.P. Depauperate faunas also existed at Puerto Octay from 18,000 to 16,000 yr B.P., and at Puerto Varas until about 15,500 yr B.P.(Hoganson, 1985). Further to the south, near Castro on the Isla Chiloe, faunas of this type existed until about 14,500 yr B.P.

Between 15,000 and 14,000 yr B.P. forest-dwelling beetles began to appear in lowland sites around Puerto Varas (Hoganson, 1985) following climatic amelioration and the initiation of deglaciation. By about 13,000 yr B.P., based on fossils from lacustrine sediments exposed along the Rio Caunahue east of Futrono (Figure A1), the fauna was much more diverse and dominated by species characteristic of BA III, the Valdivian Rain Forest fauna (Hoganson and Ashworth, 1981; Ashworth and Hoganson, 1984; Hoganson, 1985). Additional fossil assemblages from the Rio Caunahue sections indicate that Valdivian Rain Forest-type faunas existed in the Rio Caunahue Valley from about 13,000 to 4,500 yr B.P.

No fossil assemblages younger than 4,500 yrs old have been examined from the Lake Region but there is no reason to suspect that they would represent anything other than a Valdivian Rain Forest fauna.

From pollen studies, Heusser (1966, 1974, 1984) has proposed that a marked cooling between 11,000 and 9,500 yr B.P. ago interrupted the post-glacial climatic amelioration in the Lake Region. Heusser (1984) further interpreted this climatic reversal to be a South American equivalent of the emphatically cold Younger Dryas interlude of Europe. Heusser and Streeter (1980) used multivariate statistics to quantify the pollen data in order to produce paleoclimatic curves back to 16,000 yr B.P. The results of their analysis indicate that, during the reversal in the warming trend, mean January temperatures were as much as 6°C cooler than at present and that annual precipitation was more than twice the present amount of 2000 mm. Changes of this magnitude would have had a devastating effect on the beetle fauna.

No change was observed in our examination of the fossil beetle assemblages from the Rio Caunahue sections that would support an extermination of the fauna between 11,000 and 9,500 yr B.P. Based on this evidence we questioned the existence of a marked climatic reversal in the warming trend of the Lake Region (Hoganson and Ashworth, 1982; Ashworth and Hoganson, 1984; Hoganson, 1985). Heusser (1981) also observed no significant changes in the pollen profile that he presented for this interval at the Rio Caunahue site, but he has never, to our knowledge, discussed how the absence of change apparently contradicts his other paleoclimatic interpretations. In a recent palynological study from lacustrine sediments near Castro on the Isla de Chiloe, Villagran (1985) did not find any evidence for a climatic deterioration during the interval in question. She interpreted the climate from about 12,000 to 8,500 yr B.P. to be slightly warmer and wetter relative to that of the present. This supports our conclusion that after 13,000 yr B.P. no significant disruptions occurred in the development of the Coleoptera zonation which had begun to develop following deglaciation.

The glacial climate of the Lake Region was too severe for survival of most species of the Valdivian Rain Forest biota. However, the rapidity with which the Coleoptera fauna, including a compliment of flightless species, became established in the Rio Caunahue valley between 14,000 to 13,000 yr B.P. after deglaciation implies that refugia were not too distant. The most probable locations for refugia were to the north in the Central Valley but the possibility that pockets of Valdivian Rain Forest biota survived in sheltered valleys in the Cordillera de la Costa cannot be ruled out.

A final puzzle concerns the location of refugia for the Andean tundra beetle fauna, BA V. The 26,000 to 15,500 yr B.P. fossil assemblages representing the "glacial" fauna do not contain any species that are presently exclusive inhabitants of the Andean tundra. Furthermore, forest species and not tundra species, are in the oldest fossil-bearing sediments of the Rio Caunahue sections. This implies that the Andean tundra species did not simply disperse into the uplands from adjacent lowlands in which the fossil sites are located. Locations of full-glacial refugia for the tundra species are therefore unknown. One possibility is that these species never inhabited the lowlands but survived glaciation within the region in low-montane enclaves between glacial lobes. Another possibility is that they survied in lowland refugia to the north and with deglaciation dispersed southward and to higher elevations through the foothils, never inhabiting the lowlands adjacent to the southern part of their present range. Yet another possibility, less likely for flightless species such as the weevil _Aegorhinus_ _oculatus_, is that the tundra species survived in montane refugia to the north and have dispersed to their present position through the high montane areas above treeline.

REFERENCES

Almeyda, A. E., and Saez, S. F., [1958], Recopilacion de datos climaticos de Chile y mapas sinopticos respectivos: Santiago, Ministerio de Agricultura, 195 p.

Ashworth, A. C., and Hoganson, J. W., 1984, Testing the late Quaternary climatic record of southern Chile with evidence from fossil Coleoptera, in Vogel, J. C., ed., Late Cainozoic palaeoclimates of the Southern Hemisphere: Rotterdam, A. A. Balkema, p. 85-102.

Blackwelder, R. E., 1944-1947, Checklist of the coleopterous insects of Mexico, Central America, the West Indies and South America, Parts 1-5: Smithsonian Institution, United States National Museum Bulletin, v. 185, p. 1-925.

Casertano, L., 1963, General characteristics of active Andean volcanoes and a summary of the activities during recent centuries: Seismological Society of America Bulletin, v. 53, p. 1415-1433.

Darlington, P. J., Jr., [1965], Biogeography of the southern end of the world: Cambridge, Massachusetts, Harvard University Press, 236 p.

Darwin C., [1839], Journal of researches into the geology and natural history of the various countries visited by the H.M.S. Beagle: New York, Hafner, 615 p. (facsimile reprint of the first edition).

Davis, J. C., [1973], Statistics and data analysis in geology: New York, John Wiley and Sons, 550 p.

Dice, L. R., 1945, Measures of the amount of ecologic association between species: Ecology, v. 26, p. 297-302.

Galli-Oliver, C., 1969, Climate--A primary control of sedimentation in the Peru-Chile Trench: Geological Society of America Bulletin, v. 80, p. 1849-1852.

Hall, A. W., 1969, Avoiding informational distortion in automatic grouping programs: Systematic Zoology, v. 18, no. 3, p. 318-329.

Hazel, J. E., 1970, Binary coefficients and clustering in biostratigraphy: Geological Society of America Bulletin, v. 81, p. 3237-3252.

Hervé, A. F., Moreno, H. H., and Parada, R. M., 1974, Granitoids of the Andean range of Valdivia Province: Pacific Geology, v. 8, p. 39-45.

Heusser, C. J., 1966, Late-Pleistocene pollen diagrams from the province of Llanquihue, southern Chile: Proceedings of the American Philosophical Society, v. 110, no. 4, p. 269-305.

Heusser, C. J., 1974, Vegetation and climate of the southern Chilean Lake District during and since the last interglaciation: Quaternary Research, v. 4, no. 3, p. 290-315.

Heusser, C. J., 1981, Palynology of the last interglacial-glacial cycle in mid-latitudes of southern Chile: Quaternary Research, v. 16, no. 3, p. 293-321.

Heusser, C. J., 1984, Late-glacial-Holocene climate of the Lake District of Chile: Quaternary Research, v. 22, p. 77-90.

Heusser, C. J., and Flint, R. F., 1977, Quaternary glaciations and environments of northern Isla Chiloe: Geology, v. 5, p. 305-308.

Heusser, C. J., and Streeter, S. S., 1980, A temperature and precipitation record of the past 16,000 years in southern Chile: Science, v. 210, p. 1345-1347.

Heusser, C. J., Streeter, S. S., and Stuiver, M., 1981, Temperature and precipitation record in southern Chile extended to 43,000 yr ago: Nature, v. 294, p. 65-67.

Hoganson, J. W., [1985], Late Quaternary environmental and climatic history of the southern Chilean Lake Region interpreted from coleopteran (beetle) assemblages: Ph.D. dissertation, University of North Dakota, 303 p.

Hoganson, J. W., and Ashworth, A. C., 1982, The Late-glacial climate of the Chilean Lake Region implied by fossil beetles: North American Paleontological Convention, 3rd, Montreal, Canada, 1982, Proceedings, p. 251-256.

Kuschel, G., 1960, Terrestrial zoology in southern Chile: Proceedings of the Royal Society, B., v. 152, p. 540-550.

Kuschel, G., 1969, Biogeography and ecology of South American Coleoptera, in Fittkau, E. J., Illies, J., Klinge, H., Schwabe, G. H., and Sioli, H., eds., Biogeography and ecology in South America: The Hague, W. Junk, p. 709-722.

Laugenie, C. A., and Mercer, J. H., 1973, Southern Chile: A chronology of the last glaciation: IX INQUA Congress Abstracts, Christchurch, New Zealand, p. 202-203.

Lomnitz, C., 1970, Major earthquakes and tsunamis in Chile during the period 1535 to 1955: Geologische Rundschau, Band 59, Heft 3, p. 938-960.

Mercer, J. H., 1972, Chilean glacial chronology 20,000 to 11,000 Carbon-14 years ago: Some global comparisons: Science, v. 176, p. 1118-1120.

Mercer, J. H., 1976, Glacial history of southernmost South America: Quaternary Research, v. 6, p. 125-166.

Mercer, J. H., 1982, Holocene glacier variations in southern South America: Striae, v. 18, p. 35-40.

Mercer, J. H., 1984, Late Cainozoic glacial variations in South America south of the equator, in Vogel, J. C., ed., Late Cainozoic palaeoclimates of the Southern Hemisphere: Rotterdam, A. A. Balkema, p. 45-58.

Miller, A., 1976, The climate of Chile, in Schwerdtfeger, W., ed., World survey of climatology. Volume 12. Climates of Central and South America: Amsterdam, Elsevier, p. 113-145.

Muñoz, S., M., [1980], Flora del Parque Nacional Puyehue: Santiago, Chile, Editorial Universitaria, S. A., 557 p.

Oberdorfer, E., [1960], Pflanzensoziologische studien in Chile-ein vergleich mit Europa: Weinheim, J. Cramer, 208 p.

Plafker, G., and Savage, J. C., 1970, Mechanism of Chilean earthquakes of May 21 and 22, 1960: Geological Society of America Bulletin, v. 81, p. 1001-1030.

Porter, S. C., 1981, Pleistocene glaciation in the southern Lake District of Chile: Quaternary Research, v. 16, no. 3, p. 263-292.

Schmithüsen, J., 1956, Die räumliche Ordnung der chilenischen vegetation: Bonner Geographische Abhandlugen, v. 17, p. 1-86.

Schmithüsen, J., 1960, Die Nadelhölzer in den Waldgesellschaften der südlichen Anden: Vegetatio, v. 9, p. 313-327.

Scholl, D. W., Christinsen, M. N., von Huene, R., and Marlow, M. S., 1970, Peru-Chile Trench, sediments and sea-floor spreading: Geological Society of America Bulletin, v. 81, p. 1339-1360.

Simkin, T., Siebert, L., McClelland, L., Bridge, D., Newhall, C. and Latter, J. H., [1981], Volcanoes of the world: Stroudsburg, Pennsylvania, Hutchinson Ross, 232 p.

Terborgh, J., 1971, Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru: Ecology, v. 52, p. 23-40.

Veblen, T. T., and Ashton, D. H., 1978, Catastrophic influences on the vegetation of the Valdivian Andes, Chile: Vegetation, v. 36, p. 149-167.

Veblen, T. T., Ashton, D. H., Schlegel, F. M., and Veblen, A. T., 1977, Plant succession in a timberline depressed by vulcanism in south-central Chile: Journal of Biogeography, v. 4, p. 275-294.

Veblen, T. T., Schlegel, F. M., and Escobar, R. B., 1980, Structure and dynamics of old-growth *Nothofagus* forests in the Valdivian Andes, Chile: Journal of Ecology, v. 68, p. 1-31.

Veblen, T. T., Veblen, A. T., and Schlegel, F. M., 1979, Understory patterns in mixed evergreen-deciduous *Nothofagus* forests in Chile: Journal of Ecology, v. 67, p. 809-823.

Vergara, M., and Gonzales-Ferran, D., 1972, Structural and petrological characteristics of the late Cenozoic volcanism from Chilean Andean region and west Antarctica: Krystalinikum (Prague), v. 9, p. 157-182.

Villagran, C. M., 1985, Análisis palinológico de los cambios vegetacionales durante el Tardioglacial y Postglacial en Chiloe, Chile: Revista Chilena de Historia Natural, v. 58, p. 57-69.

Whittaker, R. H., [1975], Communities and ecosystems: New York, Macmillan, 385 p.

APPENDIX B

SAMPLE PROCESSING PROCEDURES FOR EXTRACTION OF INSECT FOSSILS

APPENDIX B

Sample Processing Procedures for Extraction of Insect Fossils

Equipment and Supplies

sample preparation report sheets
4 dram vials (patent lip)
Neoprene rubber vial stoppers (size 0)
card vial labels
pencil
magic marker (permanent ink)
masking tape
plastic tape
Munsell soil color chart
high capacity, general purpose balance
lamp with magnifier
binocular microscope
electric hot plate
2 wash bottles (500 ml)
sink with rubber hose
aluminum foil
plastic wash basins
2 50-mesh (297 u) sieves)
pizza pan
large aluminum pot
large wooden stirring stick
stainless steel spatula
teaspoon
dissecting forceps
Pyrex petri dishes (60 x 15 mm)
Pyrex beakers (500 ml, 750 ml)
hand towels
rubber gloves
detergent (dish soap)
Calgon solution
95 percent ethanol
kerosene
distilled water
Ziplock food bags
dissecting needles
illuminator

Procedure

1. Record the fossil site name and sample interval number on the sample preparation report sheet.

2. Label two 50-mesh sieves, plastic washing basins, petri dishes and 750-ml beakers with the sample number in pencil on masking tape.

3. Weigh the sample in its bag and record bulk weight on the report sheet.

4. Place the sample into one of the labeled plastic wash basins.

5. Describe the lithology of the sample and record it on the report sheet. Include notes on organic content (wood, peat, modern rootlets, insects, ostracods, mollusks, etc.), grain size and color (use the Munsell soil color chart).

6. Remove samples for radiocarbon dating, pollen analysis, etc. and wrap them in aluminum foil or place them in Ziplock bags. If aluminum foil is used, label the sample in pencil on masking tape. If bags are used label the bag with a permanent ink marker.

7. If the sample is compressed and peaty, split along bedding planes and inspect the surfaces under the lamp magnifier for visible or intact insect fossils. Remove fossils from the sediments with dissecting forceps or needles and place in a small petri dish containing ethanol.

8. If the sample is exceedingly compressed, break along bedding planes into small pieces and place them in the large aluminum cooking pot. Cover the sample with Calgon solution* and place on the electric hot plate. Boil gently to disaggregate the sample, stirring occasionally with the large wooden stirring stick to prevent the sample from sticking to the bottom of the pot.

   *Calgon solution formula: Place 38 g Calgon and 8 g sodium carbonate (Na_2CO_3) in a 1-litre beaker with water to make 1 litre of solution.

   Note: Organic fragments treated with the Calgon solution are contaminated and should not be radiocarbon dated.

9. Place the sample in a labeled, plastic wash basin and add water to cover the sample. Gently agitate and disaggregate the sample with your fingers. Abusive treatment will cause fossil breakage at this point, therefore, extreme caution must be employed. If the Calgon treatment was used additional washing is necessary to neutralize the solution. Pour the murky water and disaggregated sediment into a 50-mesh sieve. The finer sediment fraction will wash through with the coarser grain sediment, plant debris, mollusks, ostracods and insect fragments remaining in the sieve. Rinse the residue in the sieve with a gentle stream of water.

10. Allow the residue to drain in the sieve, weigh it while it is still in the sieve and subtract the weight of the sieve. Record the wet residue weight on the report sheet.

11. "Pizza-pan" the sample. Place a heaping teaspoon of washed residue into a pizza pan and add about ¼ to ½ inch of tap water. Inspect the pan for insect fragments using the lamp magnifier. Insect fragments can be distinguished from the remaining residue by colored and/or lustrous chitin surfaces and differential movements of the fragments. Carefully remove the fossils from the pan with a forceps and place them in an ethanol filled petri dish. Representative samples of the seeds, ostracods and mollusks can also be taken at this time and placed in a vial filled with ethanol. Wood fragments should also be removed and placed in a petri dish filled with distilled water. Caution: Wood fragments must be removed with a forceps as finger oil can contaminate the wood negating its value for radiocarbon dating. Repeat until all the residue is scanned. Record findings on the report sheet under fossil content before flotation.

12. Pour the residue remaining in the pizza pan back into the sieve and let drain for five minutes.

13. Pour kerosene into a labeled 750-ml beaker.

14. Transfer the drained residue from the sieve into a clean, dry, labeled plastic wash basin. If the sieve is more than 3/4 full, split the sample into two or more subsamples and place them in separate labeled plastic wash basins.

15. Add enough kerosene to the basin to just cover the residue.

16. For five minutes, using your fingers, very gently mix the kerosene with the residue. Note: Rubber gloves can be worn for skin protection. If properly mixed, the kerosene will adhere to the fossil insect chitin. Again, caution must be employed to minimize damage to the fossils.

17. Pour the excess kerosene back into the 750-ml beaker being careful not to allow residue to fall into it.

18. With the rubber hose, very slowly add tap water to the residue in the wash basin. Undercut the residue with a gentle stream of water initially, then allow the hose to rest under the water surface until the wash basin is filled to about two inches below the top. Turn the water off and carefully remove the hose from the basin. With a water-filled wash bottle, rinse the part of the hose that was in contact with the residue into a clean 50-mesh sieve.

19. Allow the basin to sit undisturbed for 15 minutes. The kerosene coated fossil chitin will float to the surface.

20. Carefully decant the floating fossil material into the clean sieve.

21. Repeat steps 18 through 20.

22. Place the sieve containing the fossil material into another plastic wash basin.

23. Pour the residue remaining in the wash basin into the original sieve and let drain.

24. Using the same kerosene, repeat steps 14 through 21. If fossils are exceptionally abundant steps 14 through 21 may be repeated a third time.

25. Carefully wash the floated fossil material in the sieve with a solution of 1/3 dish detergent and 2/3 water. The kerosene will be removed from the fossils by this procedure. Thoroughly rinse the material with a gentle stream of water to remove the soap.

26. Transfer the cleaned fossil material from the sieve to a clean, labeled 500-ml beaker using an ethanol-filled wash bottle. Fill the beaker with about 300 ml of ethanol.

27. Record the kerosening procedure used on the sample preparation report sheet (e.g., kerosened twice with two decants each).

28. Pour the remaining sample residue from the washing basin into a sieve and allow to drain. Place the sieve contents into a dry wash basin, spread it out and let it air dry. Put the dried residue back into the sample bag.

29. Make vial labels for insect fragments and seeds. Place them in separate 4 dram vials filled about 2/3 full with ethanol. Note: Additional vials may be prepared for mollusks, ostracods, etc. if desired.

30. Pour a small amount of the fossil material into a petri dish containing ethanol. Remove the insect fossils (seeds, mollusks, etc.) with a forceps by picking through the fossil material under a binocular microscope. Repeat until all desired fossils are removed and record a general description of the fossil content after flotation on the record sheet.

31. After fossil removal, pour the remaining material into a sieve and allow to drain. Remove the material from the sieve and wrap in aluminum foil. Label the packet with a pencil on masking tape. Place the packet inside the plastic sample bag containing the dried residue. Tape the bag closed with plastic tape and label the outside of the bag with a permanent ink magic marker. Store the sample for future reference.

32. Place Neoprene stoppers in the labeled vials containing the extracted fossils. Store the vials until ready for mounting.

<u>Note</u>: If only a small amount of residue remains after the initial wet sieving process, the kerosening procedure may be omitted. The drained residue may be placed directly in water and picked under the binocular microscope. All other steps remain the same.

APPENDIX C

LIST OF COLEOPTERISTS CONSULTED DURING THIS STUDY

Appendix C

List of coleopterists consulted during this study indicating their affiliation and taxonomic expertise and whether they examined fossil fragments or modern, pinned specimens.

	BEETLE FAMILY	SPECIMEN TYPE	
COLEOPTERIST		MODERN	FOSSIL
Dr. Donald M. Anderson Systematic Entomology Laboratory - USDA National Museum of Natural History Smithsonian Institution Washington, D.C. 20560	Scolytidae	X	
Dr. Ross H. Arnett, Jr. 1330 Dillon Heights Avenue Baltimore, Maryland 21228	Oedemeridae Salpingidae	X X	
Dr. Edward U. Balsbough, Jr. Department of Entomology North Dakota State University Fargo, North Dakota 58105	Chrysomelidae	X	
Dr. John R. Barron Hymenoptera and Arachnida Section Biosystematic Research Institute Agriculture Canada Research Branch Ottawa, Ontario K1A 0C6 Canada	Trogositidae	X	
Dr. Edward C. Becker Coleoptera Division Biosystematic Research Institute Agriculture Canada Research Branch Ottawa, Ontario K1A 0C6 Canada	Elateridae	X	
Dr. D. E. Bright Coleoptera Division Biosystematic Research Institute Agricultural Canada Research Branch Ottawa, Ontario K1A 0C6 Canada	Scolytidae	X	

COLEOPTERIST	FAMILY	MODERN	FOSSIL
Dr. J. M. Campbell Coleoptera Division Biosystematic Research Institute Agricultural Canada Research Branch Ottawa, Ontario K1A 0C6 Canada	Staphylinidae	X	X
Dr. W. A. Connell Department of Entomology and Applied Ecology 249 Agricultural Hall University of Delaware Newark, Delaware 19711	Nitidulidae	X	
Dr. Ginter Ekis Entomology Carnegie Museum of Natural History 440 Forbes Avenue Pittsburgh, Pennsylvania 15213	Cleridae	X	
Dr. Terry L. Erwin Department of Entomology National Museum of Natural History Smithsonian Institution Washington, D.C. 20560	Carabidae Trachypachidae	X X	X X
Dr. Robert D. Gordon Systematic Entomology Laboratory - USDA National Museum of Natural History Smithsonian Institution Washington, D.C. 20560	Scarabaeidae Coccinellidae	X X	X X
Dr. Henry F. Howden Department of Biology Carleton University Ottawa, Ontario K1S 5B6 Canada	Scarabaeidae	X	
Dr. John M. Kingsolver Systematic Entomology Laboratory - USDA National Museum of Natural History Smithsonian Institution Washington, D.C. 20560	Anthribidae Helodidae	 X	X

COLEOPTERIST	FAMILY	MODERN	FOSSIL
Dr. Guillermo Kuschel Department of Scientific and Industrial Research Entomology Division Mt. Albert Research Center Private Bag Auckland, New Zealand	Curculionidae	X	X
	Nemonychidae		X
	Colydiidae		X
	Belidae	X	
	Anthribidae	X	
	Attelabidae	X	
Dr. John F. Lawrence Commonwealth Scientific and Industrial Research Organization Division of Entomology P.O. Box 1700 Canberra City, A.C.T. 2601 Australia	Derodontidae	X	X
Dr. Alfred F. Newton, Jr. Department of Entomology Museum of Comparative Zoology Harvard University Cambridge, Massachusetts 02138	Staphylinidae	X	
Dr. Charles O'Brien Entomology and Structural Pest Control Florida A & M University Tallahassee, Florida 32307	Curculionidae	X	X
Dr. Stuart Peck Department of Entomology Carleton University Ottawa, Ontario KIS 5B6 Canada	Leiodidae	X	
	Silphidae	X	
Dr. Phillip Perkins Department of Entomology National Museum of Natural History Smithsonian Institution Washington, D.C. 20560	Hydraenidae	X	
Dr. Volker Puthz Vorderburg 1 D-6407 Schlitz/Hessen West Germany	Staphylinidae	X	

COLEOPTERIST	FAMILY	MODERN	FOSSIL
Dr. Paul J. Spangler Department of Entomology National Museum of Natural History Smithsonian Institution Washington, D.C. 20560	Elmidae Hydrophilidae Dytiscidae Psephenidae	X X X X	
Dr. Ales Smetana Coleoptera Division - Room 4058 Biosystematic Research Institute Agriculture Canada Research Branch Ottawa, Ontario K1A 0C6 Canada	Staphylinidae	X	X
Dr. Eric H. Smith Division of Insects Field Museum of Natural History Roosevelt Road at Lake Shore Drive Chicago, Illinois 60605	Chrysomelidae	X	
Dr. Ted Spilman Systematic Entomology Laboratory-USDA National Museum of Natural History Smithsonian Institution Washington, D.C. 20560	Tenebrionidae Cucujidae Cryptophagidae Salpingidae	X X X X	
Dr. Walter R. Suter Biology Department Carthage College Kenosha, Wisconsin 53141	Scydmaenidae	X	
Dr. Barry D. Valentine Department of Zoology Ohio State Univerity 1735 Neil Avenue Columbus, OH 43210	Anthribidae	X	X
Dr. John A. Wagner Biology Department Kendall College Evanston, Illinois 60204	Pselaphidae	X	
Dr. Richard E. White Systematic Entomology Laboratory-USDA National Museum of Natural History Smithsonian Institution Washington, D.C. 20560	Chrysomelidae Anobiidae	X X	

COLEOPTERIST	FAMILY	MODERN	FOSSIL
Dr. Donald R. Whitehead Systematic Entomology Laboratory - USDA National Museum of Natural History Smithsonian Institution Washington, D.C. 20560	Curculionidae Belidae	X X	
Dr. W. Wittmer Naturhistorisches Museum Basel CH-4051 Basel Augustinergasse 2 Basel, Switzerland	Cantharidae Melyridae	X X	
Dr. Stephen L. Wood Brigham Young University Monte L. Bean Life Science Museum 290 MLBM Provo, Utah 84602	Scolytidae Bostrichidae	X	X X
Dr. Daniel K. Young Department of Entomology Michigan State University East Lansing, Michigan 48824	Pedilidae	X	

APPENDIX D

RADIOCARBON DATES OBTAINED FOR THIS STUDY

APPENDIX D

Radiocarbon dates obtained for this study (GX dates from Geochron Laboratory, Cambridge, Masschusetts, and I date from Isotopes Laboratory, Westwood, New Jersey).

Laboratory Number	Age: ^{14}C years B.P.	Locality, sample number and stratigraphic position	Sample Material
GX-5510	4,525±145	Rio Caunahue Site. Sample number BS. Sample taken at river level about 525 m upstream from main section.	Twig fragments and leaves
GX-6503	5,220±240	Rio Caunahue Site. Sample number A1. Sample taken at river level about 500 m upstream from main section.	Peat
GX-5502	7,730±200	Rio Caunahue Site. Sample number 3. Sample taken from 20-30 cm below terrace gravels.	Wood
GX-5503	10,000±280	Rio Caunahue Site. Sample number 21. Sample taken from 200-210 cm below terrace gravels.	Wood
CX-6508	10,440±240	Rio Caunahue Site. Sample number PD0. Sample taken from 330 cm below terrace gravels and 30 cm above prominent volcanic ash horizon.	Peaty plant debris
GX-6507	11,290±250	Rio Caunahue Site. Sample number PD1. Sample taken from 395 cm below terrace gravels and 35 cm below prominent volcanic ash horizon.	Peaty plant debris
GX-5504	11,680±280	Rio Caunahue Site. Sample number 42. Sample taken from 420-430 cm below terrace gravels and 60-70 cm below prominent ash horizon.	Wood

Laboratory Number	^{14}C Age: years B.P.	Locality, sample number and stratigraphic position	Sample Material
GX-6506	12,140±390	Rio Caunahue Site. Sample number PD3. Sample taken from 430 cm below terrace gravels and 70 cm below prominent ash horizon.	Peaty plant debris
GX-6505	12,385±340	Rio Caunahue Site. Sample number PD4. Sample taken from 445 cm below terrace gravels and 85 cm below prominent ash horizon.	Peat
GX-6504	14,635±440	Rio Caunahue Site. Sample number PD6. Sample taken from 535 cm below terrace gravels and 175 cm below prominent ash horizon.	Wood
I-12995	12,810±190	Rio Caunahue Site. Additional date for the PD6 sample.	Wood
GX-9979	13,900±560	Rio Caunahue Site. Sample taken from 251 cm below prominent ash horizon.	Wood
GX-6500	10,050±230	Rio Caunahue Site. Sample number B3. Sample taken from 30 cm above prominent ash horizon about 100 m downstream from main section.	Peat
GX-6501	10,900±305	Rio Caunahue Site. Sample number B2. Sample taken from 91 cm above prominent ash horizon about 100 m downstream from main section.	Wood and Peat
GX-6502	11,145±260	Rio Caunahue Site. Sample number B1. Sample taken from 123 cm above prominent ash horizon about 100 m downstream from main section.	Wood

Laboratory Number	^{14}C Age: years B.P.	Locality, sample number and stratigraphic position	Sample Material
GX-5507	14,060±450	Puerto Varas Railroad Site. Sample number 1. Sample taken from a peat horizon in the Llanquihue III terrace beneath lacustrine sediments and lahars.	Wood
GX-5275	15,715±440	Puerto Varas Park Site. Sample number PV1. Sample taken from the upper 5 mm of a peat horizon in the Llanquihue III terrace beneath lacustrine sediments and lahars.	Peat
GX-5505	1,190±135	Puerto Octay Site. Sample number 3 - core 8. Sample taken from 20-30 cm below surface of a spillway channel cut in Llanquihue II outwash.	Peat
GX-5506	16,000±540	Puerto Octay Site. Sample number 9 - core 8. Sample taken from 80-90 cm below surface of a spillway channel cut in Llanquihue II outwash.	Peat
GX-5274	18,170±650	Puerto Octay Site. Sample number 23 - core 8. Sample taken from 230 to 240 cm below surface of a spillway channel cut in Llanquihue II outwash. Basal peat in channel.	Peat

REFERENCES

References Cited

Ager, T. A., 1983, Holocene vegetational history of Alaska, in Wright, H. E., Jr., and Porter, S. C., ed., Late-Quaterary environments of the United States, v. 2, The Holocene: Minneapolis, University of Minnesota Press, p. 128-141.

Almeyda, A. E., and Saez, S. F., [1958], Recopilación de datos climaticos de Chile y mapas sinopticos respectivos: Santiago, Ministerio de Agricultura, 195 p.

Anderson, B. G., 1981, Late Weichselian ice sheets in Eurasia and Greenland, in Denton, G. H., and Hughes, T. J., eds., The last great ice sheets: New York, John Wiley and Sons, p. 1-65.

Arnett, R. H., [1971], The beetles of the United States: Ann Arbor, Michigan, The American Entomological Institute, 1112 p.

Ashworth, A. C., 1972, A late-glacial insect fauna from Red Moss, Lancashire, England: Entomologica Scandinavica v. 3, p. 211-224.

Ashworth, A. C., 1973, the climatic significance of a late Quaternary insect fauna from Radbaston Hall, Staffordshire, England: Entomologica Scandinavica v. 4, p. 191-205.

Ashworth, A. C., 1979, Quaternary Coleoptera studies in North America: past and present, in Erwin, T. L., and others, eds., Carabid beetles their evolution, natural history, and classification: The Hague, Dr. W. Junk Publications, p. 395-406.

Ashworth, A. C., 1983, Oral communication to the writer, April 14, 1983.

Ashworth, A. C., and Hoganson, J. W., 1984a, Fossil beetles from Monte Verde in the context of a late Pleistocene paleoclimatological record from the southern Andes: Geological Society of America, Abstracts with Programs, v. 16, p. 433.

Ashworth, A. C., and Hoganson, J. W., 1984b, Testing the late Quaternary climatic record of southern Chile with evidence from fossil Coleoptera, in Vogel, J. C., ed., Late Cainozoic palaeoclimates of the Southern Hemisphere: Rotterdam, A. A. Balkema, p. 85-102.

Ashworth, A. C., Schwert, D. P., Watts, W. A., and Wright, H. E., Jr., 1981, Plant and insect fossils at Norwood in south-central Minnesota: a record of late-glacial succession: Quaternary Research, v. 16, p. 66-79.

Auer, Väinö, 1974, The isorhythmicity subsequent to the Fuego-Patagonian and Fennoscandian ocean level transgressions and regressions of the latest glaciation: Annales Academiae Scientiarum Fennicae A III, v. 115, p. 1-88.

Baker, R. G., 1976, Late Quaternary vegetation history of the Yellowstone Lake Basin, Wyoming: U.S. Geological Survey Professional Paper 729-E, 48 p.

Baker, R. G., 1983, Holocene vegetational history of the western United States, in Wright, H. E., Jr., and Porter, S. C., eds., Late-Quaternary environments of the United States, v. 2, The Holocene: Minneapolis, University of Minnesota Press, p. 109-127.

Barnosky, C. W., 1981, A record of late Quaternary vegetation from Davis Lake, southern Puget Lowland, Washington: Quaternary Research, v. 16, no. 2, p. 221-239.

Beget, J. E., 1984, Tephrochronology of late Wisconsin deglaciation and Holocene glacier fluctuations near Glacier Peak, North Cascade Range, Washington: Quaternary Research, v. 21, no. 3, p. 304-316.

Berger, W.H., Killingley, J. S., and Vincent, E., 1985, Timing of deglaciation from an oxygen isotope curve for Atlantic deep-sea sediments: Nature, v. 314, p. 156-158.

Birks, H. J. B., 1976, Late-Wisconsin vegetational history at Wolf Creek, central Minnesota: Ecological Monographs, v. 46, p. 395-429.

Birks, H. J. B., 1981, The use of pollen analysis in the reconstruction of past climates: a review, in Wigley, T. M. L., Ingram, M. J., and Farmer, G., Climate and History: Cambridge, Cambridge University Press, p. 111-138.

Blackwelder, R. E., 1944-1947, Checklist of the coleopterous insects of Mexico, Central America, the West Indies and South America, Parts 1-5: Smithsonian Institution, United States National Museum Bulletin, v. 185, p. 1-925.

Borror, D. J., and DeLong, D. M., [1964], An introduction to the study of insects (3rd ed.): New York, Holt, Rinehart and Winston, 812 p.

Bowler, J. M., 1978, Glacial age aeolian events at high and low latitudes: a Southern Hemisphere perspective, in Zinderen Bakker, E. M., van, ed., Antarctic glacial history and world palaeoenvironments: Rotterdam, A. A. Balkema, p. 149-172.

Bowler, J. M., Hope, G. S., Jennings, J. N., Singh, G., and Walker, D., 1976, Late Quaternary climates of Australia and New Guinea: Quaternary Research, v. 6, p. 359-394.

Bradbury, J. P., 1980, Written communication to Dr. A. C. Ashworth dated November 12, 1980.

Burrows, C. J., 1975, Late Pleistocene and Holocene moraines of the Cameron Valley, Arrowsmith Range, Canterbury, New Zealand: Arctic and Alpine Research, v. 7, no. 2, p. 125-140.

Burrows, C. J., 1979, A chronology for cool-climate episodes in the Southern Hemisphere 12,000-1,000 yr B.P.: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 27, p. 287-347.

Burrows, C. J., and Gellatly, A. F., 1982, Holocene glacier activity in New Zealand: Striae, v. 18, p. 41-47.

Carrara, P. E., and Mode, W. N., 1979, Extensive deglaciation in the San Juan Mountains, Colorado prior to 14,000 yr B.P.: Geological Society of America, Abstracts with Programs, v. 11, p. 399.

Carrara, P. E., Mode, W. N., Rubin, M., and Robinson, S. W., 1984, Deglaciation and postglacial timberline in the San Juan Mountains, Colorado: Quaternary Research, v. 21, no. 1, p. 42-55.

Casertano, L., 1963, General characteristics of active Andrean volcanoes and a summary of the activities during recent centuries: Seismological Society of America Bulletin, v. 53, p. 1415-1433.

Cheetham, A. H., and Hazel, J. E., 1969, Binary (presence-absence) similarity coefficients: Journal of Paleontology, v. 43, no. 5, p. 1130-1136.

Chinn, T. J. H., 1982, Possible causes of irregular glacial events in Southern Alps, New Zealand: INQUA-South American Regional Meeting Abstracts, Universidad Nacional del Comahue, Neuquén, Argentina, 1982, p. 61-63.

Clapperton, C. M., 1983, The glaciation of the Andes: Quaternary Science Reviews, v. 2, p. 83-155.

Clapperton, C. M., Sugden, D. E., Birnie, R. V., Hanson, J. D., and Thom G., 1978, Glacier fluctuations in South Georgia and comparison with other island groups in the Scotia Sea, in Zinderen Bakker, E. M., van, ed., Antarctic glacial history and world palaeoenvironments: Rotterdam, A. A. Balkema, p. 95-104.

Clayton, Lee, and Moran, S. R., 1982, Chronology of late Wisconsinan glaciations in middle North America: Quaternary Science Reviews, v. 1, no. 1, p. 55-82.

Coetzee, J. A., 1967, Pollen analytical studies in east and southern Africa, in Zinderen Bakker, E. M., van, ed., Palaeoceology of Africa, v. 3, 146 p.

Coiffait, H., and Saiz, F., 1968, Les Staphylinidae (sensu lato) du Chili: Biologie de L'Amérique Australe, v. 4, p. 339-468.

Colhoun, E. A., van de Geer, G., and Mook, W. G., 1982, Stratigraphy, pollen analysis, and paleoclimatic interpretation of Pulbena Swamp, northwestern Tasmania: Quaternary Research, v. 18, p. 108-126.

Coope, G. R., 1967, The value of Quaternary insect faunas in the interpretation of ancient ecology and climate, in Cushing, E. J., and Wright, H. E., Jr., eds., Quaternary paleoecology: New Haven and London, Yale University Press, p. 359-380.

Coope, G. R., 1968, An insect fauna from Mid-Weichselian deposits at Brandon, Warwickshire: Philosophical Transactions of the Royal Society London, Ser. B., v. 254, p. 425-456.

Coope, G. R., 1970, Interpretations of Quaternary insect fossils: Annual Review of Entomology, v. 15, p. 97-120.

Coope, G. R., 1975, Climatic fluctuations in northwest Europe since the last interglacial, indicated by fossil assemblages of Coleoptera, in Wright, A. E., and Moseley, F., eds., Ice ages: ancient and modern: Liverpool, Seel House Press, p. 153-168.

Coope, G. R., 1977, Quaternary Coleoptera as aids in the interpretation of environmental history, in Shotton, F. W., ed., British Quaternary studies: Oxford, Clarendon Press, p. 56-68.

Coope, G. R., 1978, Constancy of insect species versus inconstancy of Quaternary environments, in Mound, L. A., and Waloff, N., eds., Diversity of insect faunas: Oxford, Blackwell Scientific Publications, p. 176-187.

Coope, G. R., 1979, Late Cenozoic fossil Coleoptera: evolution, biogeography, and ecology: Annual Review of Ecology and Systematics, v. 10, p. 247-267.

Coope, G. R., 1981, Episodes of local extinction of insect species during the Quaternary as indicators of climatic changes, in Neale, John, and Flenley, John, eds., The Quaternary in Britain: Oxford and New York, Pergamon Press, p. 216-221.

Coope, G. R., and Brophy, J. A., 1972, Lateglacial environmental changes indicated by coleopteran succession from North Wales: Boreas, v. 1, no. 2, p. 97-142.

Coope, G. R., and Joachim, M. J., 1980, Lateglacial environmental changes interpreted from fossil Coleoptera from St. Bees, Cumbria, NW England, in Lowe, J. J., Gray, J. M., and Robinson, J. E., eds., The Lateglacial of North-West Europe: Oxford, Pergamon Press, p. 55-68.

Coope, G. R., and Osborne, P. J., 1967, Report on the coleopterous fauna of the Roman well at Barnsley Park, Gloucestershire: Transactions of the Bristol and Gloucestershire Archaeological Society, v. 86, p. 84-87.

Coope, G. R., Morgan, Anne, and Osborne, P. J., 1971, Fossil coleoptera as indicators of climatic fluctuations during the last glaciation in Britain: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 10, p. 87-101.

Darlington, P. J., Jr., [1965], Biogeography of the southern end of the world: Cambridge, Massachusetts, Harvard University Press, 236 p.

Darwin Charles, [1839], Journal of researches into the geology and natural history of the various countries visited by the H.M.S. Beagle: New York, Hafner, 615 p.

Davis, J. C., [1973], Statistics and data analysis in geology: New York, John Wiley and Sons, 550 p.

Davis, M. B., 1983, Holocene vegetational history of the eastern United States, in Wright, H. E., Jr., and Porter, S. C., eds., Late-Quaternary environments of the United States, v. 2, The Holocene: Minneapolis, University of Minnesota Press, p. 166-181.

Denton, G. H., 1970, Late Wisconsin glaciation in northwestern North America: ice recession and origin of Paleo-Indian Clovis complex: American Quaternary Association, First Meeting, Abstracts, Bozeman, Montana, August 28-September 1, 1970, p. 34-35.

Denton, G. H., 1974, Quaternary glaciations of White River valley, Alaska, with regional synthesis for the northern St. Elias Mountains, Alaska and Yukon Territory: Geological Society of American Bulletin, v. 85, p. 871-892.

Diaz, J. C., 1968, Mapa geologico de Chile: Instituto De Investigaciones Geologicas, Santiago, Chile.

Dice, L. R., 1945, Measures of the amount of ecologic association between species: Ecology, v. 26, p. 297-302.

Doyen, J. T., and Ulrich, G., 1978, Aquatic Coleoptera, in Merritt, R. W., and Cummins, K. W., eds., An introduction to the aquatic insects of North America: Dubuque, Iowa, Kendal/Hunt Publishing Company, p. 203-231.

Dreimanis, A, 1977, Late Wisconsin glacial retreat in the Great Lakes region, North America: New York Academy of Science Annals, v. 288, p. 70-89.

Duplessy, J. C., Delibrias, G., Turon, J. L., Pujol, C., and Duprat, J., 1981, Deglacial warming of the northeastern Atlantic Ocean: correlation with the paleoclimatic evolution of the European continent: Palaeogeography, Palaeoclimatology, v. 35, p. 121-144.

Ernst, W. G., 1975, Systematics of large-scale tectonics and age progressions in alpine and Circum-Pacific blueschist belts: Tectonophysics, v. 26, p. 229-246.

Fairbridge, R. W., 1983, The Pleistocene-Holocene boundary: Quaternary Science Reviews, v. 1, p. 215-244.

Ferguson, A. J., and Osborn, G., 1981, Minimum age of deglaciation of upper Elk Valley, British Columbia: Canadian Journal of Earth Sciences, v. 18, no. 10, p. 1635-1636.

Flint, R. F., and Fidalgo, F., 1964, Glacial geology of the east flank of the Argentine Andes between latitude 39° 10'S. and latitude 41° 20'S: Geological Society of American Bulletin, v. 75, p. 335-352.

Flint, R. F., and Fidalgo, F., 1969, Glacial drift in the eastern Argentine Andes between latitude 41° 10'S. and latitutde 43° 10'S: Geological Society of America Bulletin, v. 80, p. 1043-1052.

Galli-Oliver, C., 1969, Climate--A primary control of sedimentation in the Peru-Chile Trench: Geological Society of America Bulletin, v. 80, p. 1849-1852.

Galloway, R. W., Hope, G. S., Loffler, E., and Peterson, J. A., 1973, Late Quaternary glaciation and periglacial phenomena in Australia and New Guinea, in Zinderen Bakker, E. M., van, Sr., ed.., Palaeoecology of Africa: Cape Town, A. A. Balkema, v. 8, p. 125-138.

Gansser, A., 1973, Facts and theories on the Andes: Journal Geological Society of London, v. 129, no. 2, p. 93-131.

Gillespie, R., Street-Perrott, F. A., Switsur, R., 1983, Post-glacial arid episodes in Ethiopia have implications for climate prediction: Nature, v. 306, p. 680-683.

Godley, E., and Moar, N. T., 1973, Vegetation and pollen analysis of two bogs on Chiloe: New Zealand Journal of Botany, v. 11, p. 255-268.

Gonzalez, E., Van der Hammen, T., and Flint, R. F., 1966, Late Quaternary glacial and vegetational sequence in Valle de Lagunillas, Sierra Nevada del Cocuy, Colombia: Leidse Geologische Mededelingen, v. 32, p. 157-182.

Gonzalez-Bonorio, F., and Aguirre, L., 1970, Metamorphic facies series of the crystalline basement of Chile: Geologische Rundschau, Band 59, Heft 3, p. 979-994.

Goudarzi, G. H., 1977, Geologic map of South America: United States Geological Survey, scale 1:15,000,000.

Hall, A. V., 1969, Avoiding informational distortion in automatic grouping programs: Systematic Zoology, v. 18, no. 3, p. 318-329.

Halpern, M., and Fuenzalida, R., 1978, Rubidium-strontium geochronology of a transect of the Chilean Andes between latitudes 45° and 46°S: Earth and Planetary Science Letters, v. 41, p. 60-66.

Hamilton, A. C., 1977, An upper Pleistocene pollen diagram from highland Ethiopia: X INQUA Congress, Abstracts, Birmingham, England, p. 193.

Harbaugh, J. W., and Merriam, D. F., [1968], Computer applications in stratigraphic analysis: New York, John Wiley and Sons, 282 p.

Hays, J. D. 1978, A review of the late Quaternary climatic history of Antarctic seas, <u>in</u> Zinderen Bakker, E. M., van, ed., Antarctic glacial history and world palaeoenvironments: Rotterdam, A. A. Balkema, p. 57-71.

Hazel, J. E., [1970], Binary coefficients and clustering in biostratigraphy: Geological Society of America Bulletin, v. 81, p. 3237-3252.

Hazel, J. E., 1972, On the use of cluster analysis in biogeography: Systematic Zoology, v. 21, no. 2, p. 240-242.

Hazel, J. E., [1977], Use of certain multivariate and other techniques in assemblage zonal biostratigraphy: examples utilizing Cambrian, Cretaceous and Tertiary benthic invertebrates, <u>in</u> Kauffman, E., and Hazel, J., eds., Concepts and Methods of Biostratigraphy: Stroudsburg, Pennsylvania, Dowden, Hutchinson and Ross, p. 187-212.

Herd, D. G., and Naeser, C. W., 1974, Radiometric evidence for pre-Wisconsin glaciation in the northern Andes: Geology, v. 2, p. 603-604.

Herman, L. H., Jr., 1972, Revision of <u>Bledius</u> and related genera. I. The <u>aequatorialis</u>, <u>mandibularis</u>, and <u>semiferrugineus</u> groups and two new genera (Coleoptera, Staphylinidae, Oxytelinae): Bulletin American Museum of Natural History, v. 149, no. 2, p. 111-254.

Hervé, A. F., Moreno, H. H., and Parada, R. M., 1974, Granitoids of the Andean range of Valdivia Province: Pacific Geology, v. 8, p. 39-45.

Heusser, C. J., 1960, Late-Pleistocene environments of the Laguna de San Rafael area, Chile: The Geographical Review, v. 50, p. 555-577.

Heusser, C. J., 1964, Some pollen profiles from the Laguna de San Rafael area, Chile, in Cranwell, L. M., ed., Ancient Pacific floras, the pollen story: Honolulu, University of Hawaii Press, p. 95-114.

Heusser, C. J., 1966a, Late-Pleistocene pollen diagrams from the province of Llanquihue, southern Chile: Proceedings of the Amercan Philosophical Society, v. 110, no. 4, p. 269-305.

Heusser, C. J., 1966b, Polar hemispheric correlation: palynological evidence from Chile and the Pacific north-west of America, in Sawyer, J. S., ed., World climate from 8000 to 0 B.C.: London, Royal Meteorological Society Proceedings, p. 124-141.

Heusser, C. J., 1972a, An additional postglacial pollen diagram from Patagonia Occidental: Pollen et Spores, v. 14, no. 2, p. 157-167.

Heusser, C. J., 1972b, On the occurrence of Lycopodium fuegianum during late-Pleistocene interstades in the Province of Osorno, Chile: Torrey Botanical Club Bulletin, v. 99, no. 4, p. 178-194.

Heusser, C. J., 1974, Vegetation and climate of the southern Chilean Lake District during and since the last interglaciation: Quaternary Research, v. 4, no. 3, p. 290-315.

Heusser, C. J., 1976, Palynology and depositional environment of the Rio Ignao nonglacial deposit, Province of Valdivia, Chile: Quaternary Research, v. 6, p. 273-279.

Heusser, C. J., 1980, Written communication to the writer dated July 17, 1980.

Heusser, C. J., 1981, Palynology of the last interglacial-glacial cycle in mid-latitudes of southern Chile: Quaternary Research, v. 16, no. 3, p. 293-321.

Heusser, C. J., 1982, Palynology of cushion bogs of the Cordillera Pelada, Province of Valdivia, Chile: Quaternary Research, v. 17, no. 1, p. 71-92.

Heusser, C. J., 1983, Quaternary pollen record from Laguna de Tagua Tagua, Chile: Science, v. 219, p. 1429-1432.

Heusser, C. J., 1984a, Late-glacial-Holocene climate of the Lake District of Chile: Quaternary Research, v. 22, p. 77-90.

Heusser, C. J., 1984b, Late Quaternary climates of Chile, in Vogel, J. C., ed., Late Cainozoic palaeoclimates of the Southern Hemisphere: Rotterdam, A. A. Balkema, p. 59-83.

Heusser, C. J., and Flint, R. F., 1977, Quaternary glaciations and environments of northern Isla Chiloe: Geology, v. 5, p. 305-308.

Heusser, C. J., and Streeter, S. S., 1980, A temperature and precipitation record of the past 16,000 years in southern Chile: Science, v. 210, p. 1345-1347.

Heusser, C. J., Streeter, S. S., and Stuiver, M., 1981, Temperature and precipitation record in southern Chile extended to~43,000 yr ago: Nature, v. 294, p. 65-67.

Hoganson, J. W., and Ashworth, A. C., 1981, Late glacial climatic history of southern Chile interpreted from Coleopteran (beetle) assemblages: Geological Society of America, Abstracts with Programs, v. 13, p. 474.

Hoganson, J. W., and Ashworth, A. C., 1982a, The Late-glacial climate of the Chilean Lake Region implied by fossil beetles: North American Paleontological Convention, 3rd, Montreal, Canada, 1982, Proceedings, p. 251-256.

Hoganson, J. W., and Ashworth, A. C., 1982b, The Chilean lake region late-glacial climate: interpreted from beetle assemblages: Seventh Biennial Conference, American Quaternary Association Abstracts, University of Washington, Seattle, Washington, June 28-30, 1982, p. 106.

Hollin, J. T., and Schilling, D. H., 1981, Late Wisconsin-Weichselian mountain glaciers and small ice caps, <u>in</u> Denton, G. H., and Hughes, T. J., eds., The last great ice sheets: New York, John Wiley and Sons, p. 179-206.

Katz, H. R., 1970, Randpazifische Bruchtektonik am Beispiel Chile und Neuseelands: Geologische Rundschau, Band 59, Heft 3, p. 898-926.

Katz, H. R., 1971, Continental margin in Chile--is tectonic style compression or extensional?: American Association of Petroleum Geologists Bulletin, v. 55, no. 10, p. 1753-1758.

Koster, R., 1975, Chile, <u>in</u> Fairbridge, R. W., ed., Encyclopedia of world regional geology, Part I, Western Hemisphere (including Antarctica and Australia): Stroudsburg, Pennsylvania, Dowden, Hutchinson and Ross, Inc., p. 237-243.

Krumbein, W. C., and Graybill, F. A., [1965], An introduction to statistical models in geology: New York, McGraw-Hill Book Company, 475 p.

Kurten, B., [1968], Pleistocene mammals of Europe: London, Weiderfeld and Nicolson, 317 p.

Kuschel, Guillermo, 1950, Nuevos Brachyderinae y Magdalinae chilenos (Coleoptera Curculionidae): Arthropoda, v. 1, p. 181-195.

Kuschel, Guillermo, 1951, La subfamilia Aterpinae en America: Revista Chileno de Entomologia, v. 1, p. 205-245.

Kuschel, Guillermo, 1952, Los Curculionidae de la Cordillera Chileno-Argentina: Revista Chilena de Entomologica, v. 2, p. 229-279.

Kuschel, Guillermo, 1960, Terrestrial zoology in southern Chile: Proceedings of the Royal Society, B., v. 152, p. 540-550.

Kuschel, Guillermo, 1969, Biogeography and ecology of South American Coleoptera, in Fittkau, E. J., Illies, J., Klinge, H., Schwabe, G. H., and Sioli, H., eds., Biogeography and ecology in South America: The Hauge, W. Junk Publishers, p. 709-722.

Kuschel, Guillermo, 1979, Written communication to the writer dated November 21, 1979.

Kuschel, Guillermo, 1981a, Written communication to the writer dated March 2, 1981.

Kuschel, Guillermo, 1981b, Written communication to the writer dated April 2, 1981.

Kuschel, Guillermo, 1982, Written communication to the writer dated May 14, 1982.

Laugenie, C. A., and Mercer, J. H., 1973, Southern Chile: A chronology of the last glaciation: IX INQUA Congress Abstracts, Christchurch, New Zealand, p. 202-203.

Lawrence, D. R., 1971, The nature and structure of paleoecology: Journal of Paleontology, v. 45, no. 4, p. 593-607.

Lawrence, J. F., and Hlavoc, T. F., 1979, Review of the Derodontidae (Coleoptera: Polyphaga) with new species from North America and Chile: Coleopterists Bulletin, v. 33, no. 4, p. 369-414.

Lemke, R. W., Mudge, M. R., Wilcox, R. E., and Powers, H. A., 1975, Geological setting of the Glacier Peak and Mazama ash-bed markers in west-central Montana: U.S. Geological Survey Bulletin 1395-H, 31 p.

Livingstone, D. A., 1962, Age of deglaciation in the Ruwenzori Range, Uganda: Nature (London), v. 194, p. 859-860.

Lomnitz, C., 1970, Major earthquakes and tsunamis in Chile during the period 1535 to 1955: Geologische Rundschau, Band 59, Heft 3, p. 938-960.

Lorius C., Merlivat, L., Jouzel, J., and Pourchet, M., 1979, A 30,000-yr isotope climatic record from Antarctic ice: Nature (London), v. 280, p. 644-648.

Lowrie, Allen, and Hey, Richard, 1981, Geological and geophysical variations along the western margin of Chile near lat 33° to 36° S and their relation to Nazca plate subduction, in Kulm, L. D., and others, eds., Nazca Plate: Crustal formation and Andean convergence: Geological Society of America Memoir 154, p. 741-754.

Macphail, M. K., 1979, Vegetation and climates in southern Tasmania since the last glaciation: Quaternary Research, v. 11, p. 306-341.

Madole, R. F., 1980, Time of Pinedale deglaciation in north-central Colorado: further considerations: Geology, v. 8, p. 118-122.

Markgraf, Vera, 1980a, Paleoclimatic reconstruction of the last 15,000 years in subantarctic and temperate regions of Argentina: Proceedings IV Symposium of Palynology, 1979, Langue Franc, Paris, 14 p.

Markgraf, Vera, 1980b, New data on the late and postglacial vegetational history of "La Mision", Tierra del Fuego, Argentina: Proceedings IV International Palynological Conference, 1976-1977, Lucknow, India, v. 3, p. 68-74.

Markgraf, Vera, 1983, Late and postglacial vegetational and paleoclimatic changes in subantarctic, temperate, and arid environments in Argentina: Palynology, v. 7, p. 43-70.

Markgraf, Vera, 1984, Late Pleistocene and Holocene vegetation history of temperate Argentina: Lago Morenito, Bariloche: Dissertationes Botanicae, v. 72 (Festschrift Welten), p. 235-254.

Markgraf, Vera, and Bradbury, J. P., 1982, Holocene climatic history of South America: Striae, v. 16, p. 40-45.

Martin, P. S., and Mehringer, P. J., Jr., 1965, Pleistocene pollen analysis and biogeography of the southwest, in Wright, H. E., Jr., and Frey, D. G., eds., The Quaternary of the United States: Princeton, Princeton University Press, p. 433-451.

Matthews, J. V., Jr., 1970, Two new species of Micropeplus from the Pliocene of western Alaska with remarks on the evolution of Micropeplinae (Coleoptera: Staphylinidae): Canadian Journal of Zoology, v. 48, p. 779-788.

Matthews, J. V., Jr., 1974a, A preliminary list of insect fossils from the Beaufort Formation, Meighen Island, District of Franklin: Geological Survey of Canada Paper 74-1A, p. 203-206.

Matthews, J. V., Jr., 1974b, Quaternary environments at Cape Deceit (Seward peninsula, Alaska): evolution of a tundra ecosystem: Geological Society of America Bulletin, v. 84, p. 1353-1384.

Matthews, J. V., Jr., 1976a, Insect fossils from the Beaufort Formation: geological and biological significance: Geological Survey of Canada Paper 76-1B, p. 217-227.

Matthews, J. V., Jr., 1976b, Evolution of the subgenus Cyphelophorus (Genus Helophorus: Hydrophilidae, Coleoptera): description of two new fossil species and discussion of Helophorus tuberculatus Gyll.: Canadian Journal of Zoology, v. 54, p. 652-673.

Matthews, J. V., Jr., 1977, Coleoptera fossils: their potential value for dating and correlation of late Cenozoic sediments: Canadian Journal of Earth Science, v. 14, no. 10, p. 2339-2347.

Mayewski, P. A., Denton, G. H., and Hughes, T. J., 1981, Late Wisconsin ice sheets in North America, in Denton, G. H., and Hughes, T. J., eds., The last great ice sheet: New York, John Wiley and Sons, p. 67-178.

McGlone, M. S., and Topping, W. W., 1973, Late Otiran/early Aranuian vegetation in the Tongariro area, central North Island, New Zealand: New Zealand Journal of Botany, v. 11, p. 283-290.

Mehringer, P. J., Jr., Arno, S. F., and Petersen, K. L., 1977, Postglacial history of Lost Trail Pass Bog, Bitterroot Mountains, Montana: Arctic and Alpine Research, v. 9, p. 345-368.

Mercer, J. H., 1969, The Allerød Oscillation: a European climatic anomaly?: Arctic and Alpine Research, v. 1, p. 227-234.

Mercer, J. H., 1972a, Chilean glacial chronology 20,000 to 11,000 Carbon-14 years ago: Some global comparisons: Science, v. 176, p. 1118-1120.

Mercer, J. H., 1972b, The lower boundary of the Holocene: Quaternary Research, v. 2, p. 15-24.

Mercer, J. H., 1976, Glacial history of southernmost South America: Quaternary Research, v. 6, p. 125-166.

Mercer, J. H., 1982, Holocene glacier variations in southern South America: Striae, v. 18, p. 35-40.

Mercer, J. H., 1983, Cenozoic glaciation in the Southern Hemisphere: Annual Review of Earth and Planetary Science, v. 11, p. 99-131.

Mercer, J. H., 1984a, Stimultaneous climatic change in both hemispheres and similar bipolar interglacial warming: evidence and implications: Geophysical Monograph 29-Climate Porcesses and Climate Sensitivity-Maurice Ewing, v. 5, p. 307-313.

Mercer, J. H., 1984b, Late Cainozoic glacial variations in South America south of the equator, in Vogel, J. C., ed., Late Cainozoic palaeoclimates of the Southern Hemisphere: Rotterdam, A. A. Balkema, p. 45-58.

Mercer, J. H., and Palacios, O. M., 1977, Radiocarbon dating of the last glaciation in Peru: Geology, v. 5, p. 600-604.

Mickelson, D. M., Clayton, L., Fullerton, D. S., and Borns, H. W., Jr., 1983, The late Wisconsin glacial record of the Laurentide Ice Sheet in the United States, in Wright, H. E., Jr., and Porter, S. C., eds., Late-Quaternary environments of the United States, v. 1, The Late Pleistocene: Minneapolis, University of Minnesota Press, p. 3-37.

Miller, A., 1976, The climate of Chile, in Schwerdtfeger, W., ed., World survey of climatology. Volume 12, Climates of Central and South America: Amsterdam, Elsevier, p. 113-145.

Moar, N. T., 1966, Post-glacial vegetation and climate in New Zealand, in Sawyer, J. S., ed., World climate from 8,000 to 0 B.C.: London, Royal Meteorological Society, p. 155-156.

Moar, N. T., 1971, Contributions to the Quaternary history of the New Zealand flora 6. Aranuian pollen diagrams from Canterbury, Nelson, and north Westland, South Island: New Zealand Journal of Botany, v. 9, p. 80-145.

Moar, N. T., 1973, Late Pleistocene vegetation and environment in southern New Zealand, in Zinderen Bakker, E. M., van, Sr., ed., Palaeoecology of Africa: Cape Town, A. A. Balkema, v. 8, p. 179-198.

Moar, N. T., and McGlone, M. S., 1977, Otiran (last glaciation) vegetation and climate in New Zealand: X INQUA Congress Abstracts, Birmingham, p. 304.

Morgan, A. W., Morgan, A., Ashworth, A. C., and Matthews, J. V., Jr., 1983, Late Wisconsin fossil beetles in North America, in Wright, H. E., Jr., and Porter, S. C., eds., Late-Quaternary environments of the United States, v. 1, The Late Pleistocene: Minneapolis, University of Minnesota Press, p. 354-363.

Mörner, N.-A., and Dreimanis, A., 1973, the Erie Interstade, in Black, R. F., Goldthwait, R. P., and Willman, H. B., eds., The Wisconsinian Stage: Geological Society of America Memoir 136, p. 107-134.

Moroni, J., 1973, Elenco sistematico, sinonimico y distribucion de coleopteros acuaticos chilenos: Revista Chilena de Entomologia, v. 7, p. 193-106.

Munizaga, F., Aguirre, L., and Hervé, F., 1973, Rb/Sr ages of rocks from the Chilean metamorphic basement: Earth and Planetary Science Letters, v. 18, p. 87-92.

Muñoz, Schick, M. [1980], Flora del Parque Nacional Puyehue: Santiago, Chile, Editorial Universitaria, S. A., 557 p.

Nelson, A. R., Millington, A. C., Andrews, J. T., and Nichols, H., 1979, Radiocarbon-dated upper Pleistocene glacial sequence, Fraser Valley, Colorado Front Range: Geology, v. 7, no. 8, p. 410-414.

Oberdorfer, E., [1960], Pflanzensoziologische studien in Chile-ein vergleich mit Europa: Weinheim, J. Cramer, 208 p.

O'Brien, C. W., (1980), Oral communication to the writer, January 16, 1980.

Pennak, R. W., [1978], Fresh-water invertebrates of the United States (2d ed.): New York, John Wiley, 803 p.

Pierce, K. L., 1979, History and dynamics of glaciation in the northern Yellowstone National Park area. U.S. Geological Survey Professional Paper 729-F, 90 p.

Plafker, G., 1972, Alaskan earthquake of 1964 and Chilean earthquake of 1960: Implications for arc tectonics: Journal of Geophysical Research, v. 77, no. 5, p. 901-925.

Plafker, G., and Savage, J. C., 1970, Mechanisms of Chilean earthquakes of May 21 and 22, 1960: Geological Society of America Bulletin, v. 81, p. 1001-1030.

Porter, S. C., 1981, Pleistocene glaciation in the southern Lake District of Chile: Quaternary Research, v. 16, no. 3, p. 263-292.

Porter, S. C., Pierce, K. L., and Hamilton, T. D., 1983, Late Wisconsin mountain glaciation in the western United States, in Wright, H. E., Jr., and Porter, S. C., eds., Late-Quaternary environments of the United States, v. 1, The Late Pleistocene: Minneapolis, University of Minnesota Press, p. 71-111.

Puthz, Volker, 1981, Written communication to the writer dated January 9, 1981.

Ruddimann, W. F., and McIntyre, Andrew, 1981, The North Atlantic Ocean during the last deglaciation: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 35, p. 145-214.

Rymer, M. J., and Sims, J. D., 1982, Lake-sediment evidence for the date of deglaciation of the Hidden Lake area, Kenai Peninsula, Alaska: Geology, v. 10, p. 314-316.

Salinger, M. J., 1981, Palaeoclimates north and south: Nature, v. 291, p. 106-107.

Salmi, K., 1955, Additional information on the findings in the Mylodon cave at Ultima Esperanza: Acta Geographica, v. 14, p. 314-333.

Schmithüsen, J., 1956, Die räumliche Ordnung der chilenischen vegetation: Bonner Geographische Abhandlungen, v. 17, p. 1-86.

Schmithüsen, J., 1960, Die Nadelhölzer in den Waldgesellschaften der südlichen Anden: Vegetatio, v. 9, p. 313-327.

Scholl, D. W., Christinsen, M. N., von Huene, R., and Marlow, M. S., 1970, Peru-Chile Trench, sediments and sea-floor spreading: Geological Society of America Bulletin, v. 81, p. 1339-1360.

Scholl, D. W., Marlow, M. S., and Cooper, A. K., 1977, Sediment subduction and off scraping of Pacific margins, in Talwani, M., and Pitman III, W. C., eds., Maurice Ewing Series I - Island arcs, deep sea trenches and back-arc basins: American Geophysical Union, Washington, D. C., p. 199-210.

Schubert, C., 1974, Late Pleistocene Merida glaciation, Venezuelan Andes; Boreas, v. 3, p. 147-152.

Schweller, W. J., Kulm, L. D., and Prince, R. A., 1981, Tectonics, structure, and sedimentary framework of the Peru-Chile trench, in Kulm, L. D., and others, eds., Nazca Plate: Crustal formation and Andean convergence: Geological Society of America Memoir 154, p. 323-349.

Schwert, D. P., and Ashworth, A. C., 1985, Late Quaternary history of the northern beetle fauna of North America: a synthesis of fossil and distributional evidence (submitted for publication).

Segerstrom, K., 1964, Quaternary history of Chile: Brief outline: Geological Society of America Bulletin, v. 75, p. 157-170.

Simkin, T., Siebert, L., McClelland, L., Bridge, D., Newhall, C., and Latter, J.H., [1981], Volcanoes of the world: Stroudsburg, Pennsylvania, Hutchinson Ross, 232 p.

Sneath, P. H. A., and Sokal, R. R., [1973], Numerical taxonomy: San Francisco, W. H. Freeman and Company, 573 p.

Sokal, R. R., and Michener, C. D., 1958, A statistical method for evaluating systematic relationships: University of Kansas Science Bulletin, v. 38, p. 1409-1438.

Sokal, R. R., and Sneath, P. H. A., [1963], Principles of numerical taxonomy: San Francisco, W. H. Freeman and Company, 359 p.

Stewart, R. B., and Neall, V. E., 1984, Chronology of palaeoclimatic change at the end of the last glaciation: Nature, v. 311, p. 47-48.

Suggate, R. P., and Moar, N. T., 1970, Revision of the chronology of the Late Otira Glacial: New Zealand Journal of Geology and Geophysics, v. 13, p. 742-746.

Suggate, R. P., and West, R. G., 1967, The substitution of local stage names for Holocene and post-glacial: Quaternaria, v. 9, p. 245-246.

Ten Brink, N. W., and Ritter, D. F., 1980, Glacial chronology of the north-central Alaska Range and implications for discovery of early-man sites: Geological Society of America, Abstracts with Programs, v. 12, p. 534.

Terborgh, J., 1971, Distribution on environmental gradients; theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru: Ecology, v. 52, no. 1, p. 23-40.

Thayer, M. K., and Newton, A. F., Jr., 1978, Revision of the south temperate genus Glypholoma Jeannel, with four new species (Coleoptera: Staphylinidae: Omaliiae): Psyche, v. 85, no. 1, p. 25-63.

Thompson, L. G., and Mosley-Thompson, E., 1981, Microparticle concentration variations linked with climatic change: evidence from polar ice-cores: Science, v. 212, p. 812-815.

Ullrich, W. G., and Coope, G. R., 1974, Occurrence of the east palaeartic beetle Tachinus jacuticus Poppius (Col. Staphylinidae) in deposits of the last glacial period in England: Journal of Entomology, v. 42, no. 2, p. 207-212.

Valentine, J. W., 1966, Numerical analysis of marine molluscan ranges on the extratropical northeastern Pacific shelf: Limnology and Oceanography, v. 11, p. 198-211.

Valentine, J. W., and Peddicord, R. G., 1967, Evaluation of fossil assemblages by cluster analysis: Journal of Paleontology, v. 41, no. 2, p. 502-507.

Van der Hammen, T., and Vogel, J. C., 1966, The Susacá-interstadial and the subdivision of the late-glacial: Geologie en Mijnbouw, v. 45, p. 33-35.

Van der Hammen, T., Barelds, J., De Jong, H., and De Veer, A. A., 1981, Glacial sequence and environmental history in the Sierra Nevada del Cocuy (Columbia): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 32, p. 247-340.

Veblen, T. T., and Ashton, D. H., 1978, Catastrophic influences on the vegetation of the Valdivian Andes, Chiles: Vegetation, v. 36, p. 149-167.

Veblen, T. T., Ashton, D. R., Schlegel, F. M., and Veblen, A. T., 1977, Plant succession in a timberline depressed by vulcanism in south-central Chile: Journal of Biogeography, v. 4, p. 275-294.

Veblen, T. T., Schlegel, F. M., and Escobar, R. B., 1980, Structure and dynamics of old-growth Nothofagus forests in the Valdivian Andes, Chile: Journal of Ecology, v. 68, p. 1-13.

Veblen, T. T., Veblen, A. T., and Schlegel, F. M., 1979, Understory patterns in mixed evergreen-deciduous Nothofagus forests in Chile: Journal of Ecology, v. 67, p. 809-823.

Vergara, M., and Gonzalez-Ferran, D., 1972, Structural and petrological characteristics of the late Cenozoic volcanism from Chilean Andean region and west Antarctica: Krystalinikum (Prague), v. 9, p. 157-182.

Villagran, C. M., 1980, Vegetationsgeschichtliche und pflanzensoziologische Untersuchungen im Vicente Perez Rosales National Park (Chile): Dissertationes Botanicae, v. 54, p. 1-165.

Villagran, C. M., 1985, Análisis palinológico de los cambios vegetacionales durante el Tardiglacial y Postglacial en Chiloe, Chile: Revista Chilena de Historia Natural, v. 58, p. 57-69.

Voss, E., 1951, Ueber einige Rhynchitinen der chilenischen fauna: Revista Chilena de Entomologia, v. 1, p. 175-185.

Waddington, J. C. B., and Wright, H. E., Jr., 1974, Late Quaternary vegetational changes on the east side of Yellowstone Park, Wyoming: Quaternary Research, v. 4, p. 175-184.

Walker, D., 1978, Quaternary climates of the Australian region, in Pittock, A. B., Frakes, L. A., Jenssen, D., Peterson, J. A., and Zillman, J. W., eds., Climatic change and variability: a southern perspective: Cambridge, Cambridge University Press, p. 82-94.

Watts, W. A., 1970, Criteria for identification of late-glacial climatic oscillations with special reference to the Bølling Oscillation: First Meeting, American Quaternary Association Abstracts, Bozeman, Montana, August 28-September 1, 1970, p. 144-145.

Watts, W. A., 1980, Regional variation in the response of vegetation to late glacial climatic events in Europe, in Lowe, J. J., Gray, J. M., and Robinson, J. E., eds., The Lateglacial of North-West Europe: Oxford, Pergamon Press, p. 1-21.

Watts, W. A., 1983, Vegetational history of the eastern United States 25,000 to 10,000 years ago, in Wright, H. E., Jr., and Porter, S. C., eds., Late-Quaternary environments of the United States, v. 1, The Late Pleistocene: Minneapolis, University of Minnesota Press, p. 294-310.

Wayne, W. J., 1984, Glacial chronology of the Ruby Mountains-East Humboldt Range, Nevada: Quaternary Research, v. 21, no. 3, p. 286-303.

Webb, III, T., Cushing, E. J., and Wright, H. E., Jr., 1983, Holocene changes in the vegetation of the Midwest, in Wright, H. E., Jr., and Porter, S. C., eds., Late-Quaternary environments of the United States, v. 2, The Holocene: Minneapolis, University of Minnesota Press, p. 142-165.

Whittaker, R. H., [1975], Communities and ecosystems (2d ed.): New York: Macmillan, 385 p.

Wilson, A. T., 1978, Glacial history of New Zealand and the Ross Dependency, Antarctica, in Zinderen Bakker, E. M., van, ed., Antarctic glacial history and world palaeoenvironments: Rotterdam, A. A. Balkema, p. 15-23.

Zeil, W. [1964], Geologie von Chile: Berlin, Gebrüder Borntraeger, 233 p.

Zinderen Bakker, E. M., van, Sr., 1969, Quaternary pollen analytical studies in the Southern Hemisphere with special reference to the Sub-Antarctic, in Zinderen Bakker, E. M., van, Sr., ed., Palaeoecology of Africa: Cape Town, A. A. Balkema, v. 5, p. 175-212.

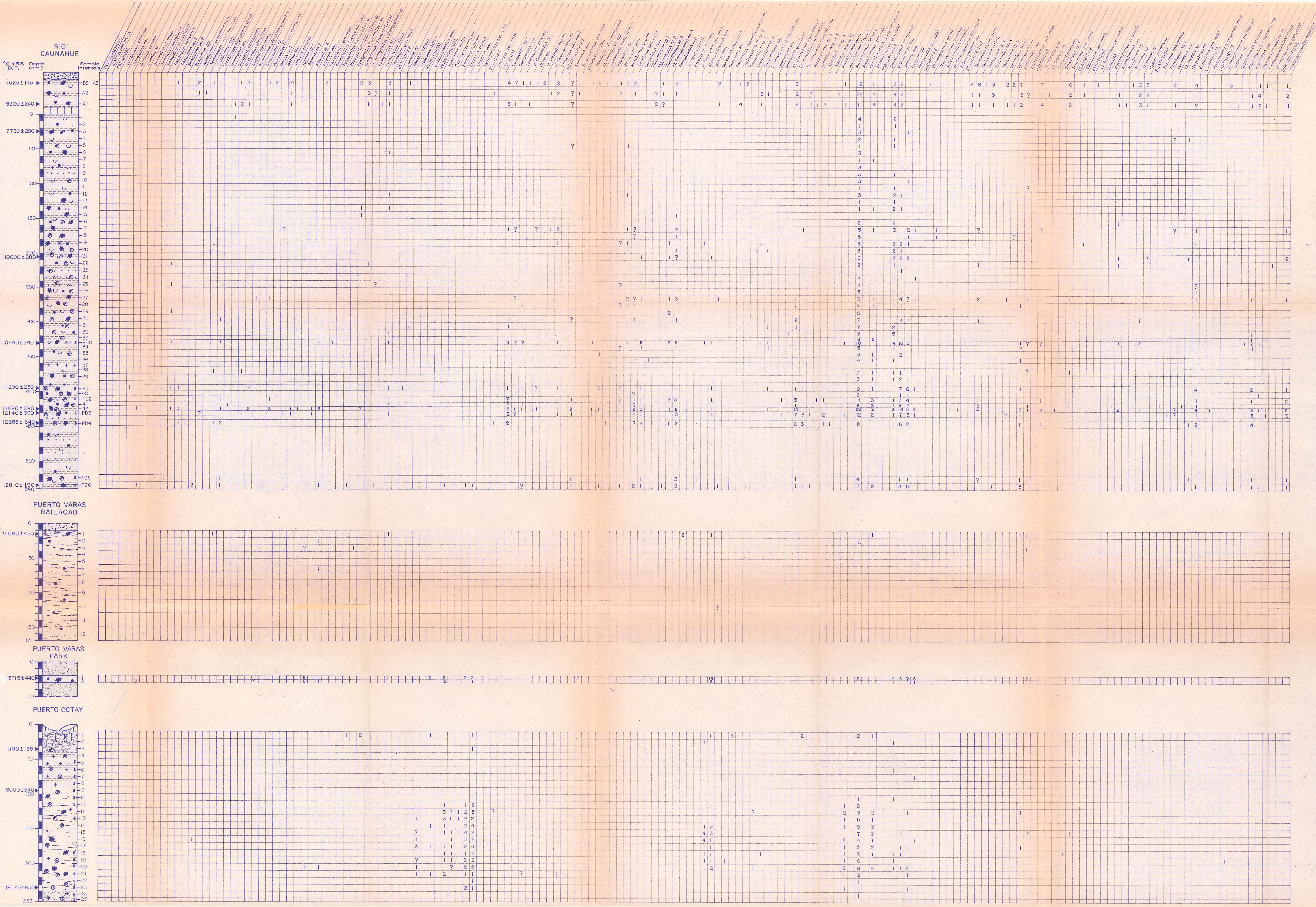
Zinderen Bakker, E. M., van, Sr., 1973, The glaciation(s) of Marion Island (Sub-Antarctic), in Zinderen Bakker, E. M., van, Sr., ed., Palaeoecology of Africa: Cape Town, A. A. Balkema, v. 8, p. 161-178.

Zinderen Bakker, E. M., van, Sr., and Coetzee, J. A., 1972, A re-appraisal of late-Quaternary climatic evidence from tropical Africa, in Zinderen Bakker, E. M., van, Sr., ed., Palaeoecology of Africa: Cape Town, A. A. Balkema, v. 7, p. 151-181.

HOGANSON (1985) PLATE IA

CHART SHOWING STRATIGRAPHIC SECTIONS OF THE FOSSIL SITES, SAMPLE INTERVALS, LEVELS OF RADIOCARBON DATES, TAXONOMIC LIST OF COLEOPTERA AND OTHER INSECTS AND ARACHNIDS AND FOSSIL ABUNDANCES (PART).

T1985
H678
Plate IA



EXPLANATION

- ▨ GRAVEL
- ▨ MEDIUM GRAINED SAND
- ▨ FINE-GRAINED SAND (IN SILTY CLAY)
- ▨ SANDY SILT
- ▨ SILT
- ▨ SILTY CLAY
- ▨ GYTTJA (ORGANIC RICH CLAY)
- ▨ PEAT
- ▨ SECTION CONCEALED
- ▨ SECTION REMOVED
- ▨ PUMICE
- + VOLCANIC ASH
- ◡ MICA
- ▨ PLANT REMAINS
- ● CARBONIZED PLANT FRAGMENTS
- ▨ MODERN PLANT ROOTS
- S MACROSPORES
- ▨ CHAROPHYTE OOGONIA
- ▨ DIATOMS
- ▨ GASTROPOD
- ▨ OSTRACOD

NUMBERS EQUAL MINIMUM NUMBER OF BEETLE INDIVIDUALS, EXCEPT FOR POTENTIALLY IDENTIFIABLE FRAGMENTS AND ADDITIONAL INSECTA AND ARACHNIDA WHICH EQUAL ACTUAL NUMBER OF FOSSIL FRAGMENTS

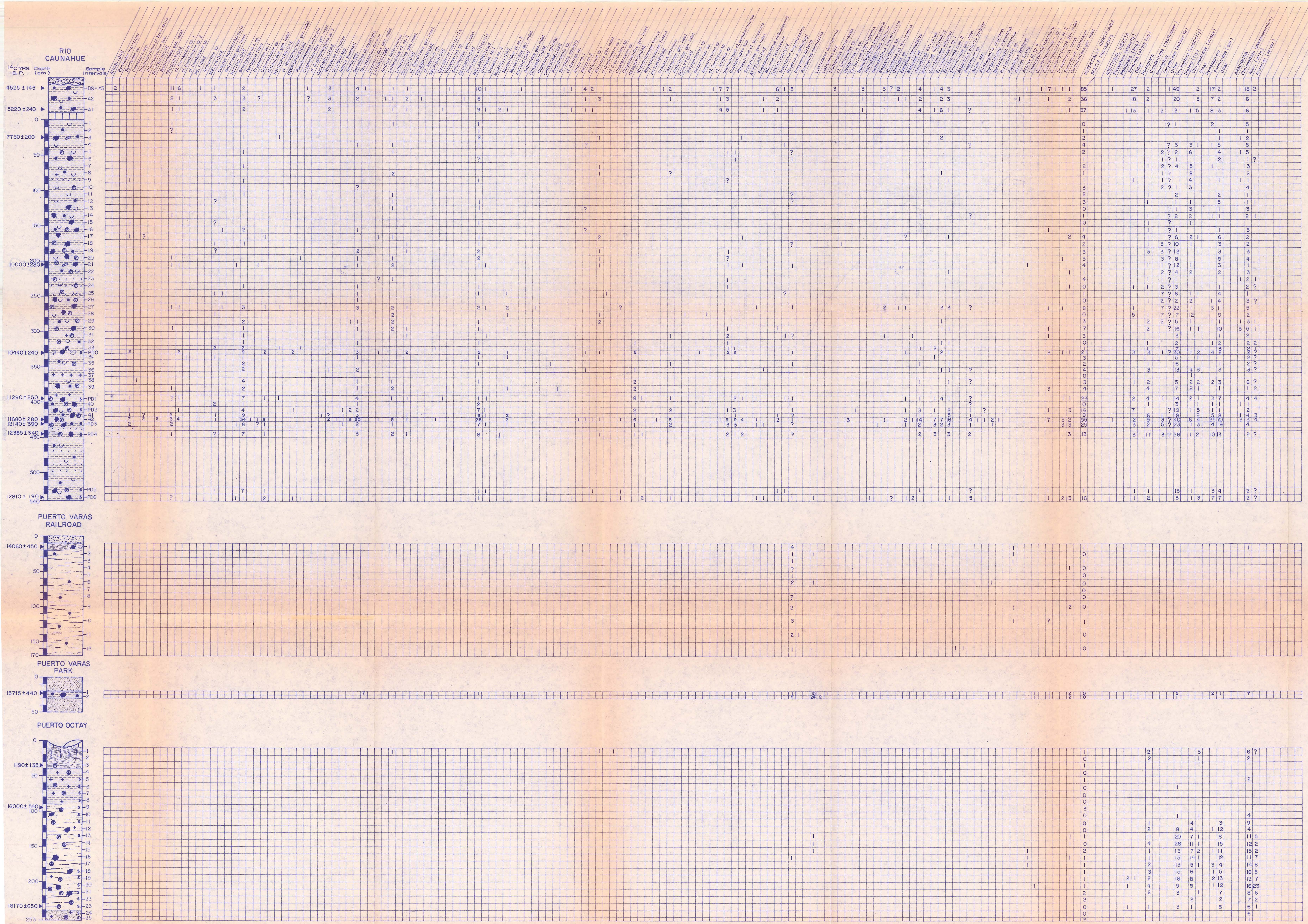
COLEOPTERA FAMILIAL ORDER FOLLOWED BY U.S. DEPARTMENT OF AGRICULTURE AND U.S. NATIONAL MUSEUM.

SYSTEMATIC ORDER OF INFRAFAMILIAL COLEOPTERA TAXA AFTER BLACKWELDER (1944-1947)

ORDER OF ADDITIONAL INSECTA GROUPS AND ARACHNIDA AFTER BORROR AND DELONG (1964)

HOGANSON (1985) PLATE IB

CHART SHOWING STRATIGRAPHIC SECTIONS OF THE FOSSIL SITES, SAMPLE INTERVALS, LEVELS OF RADIOCARBON DATES, TAXONOMIC LIST OF COLEOPTERA AND OTHER INSECTS AND ARACHNIDS AND FOSSIL ABUNDANCES (CONTINUED).



EXPLANATION

- ▨ GRAVEL
- ▨ MEDIUM GRAINED SAND
- ▨ FINE-GRAINED SAND (IN SILTY CLAY)
- ▨ SANDY SILT
- ▨ SILT
- ▨ SILTY CLAY
- ▨ GYTTJA (ORGANIC RICH CLAY)
- ▨ PEAT
- ▥ SECTION CONCEALED
- ▥ SECTION REMOVED
- ▨ PUMICE
- + VOLCANIC ASH
- ◡ MICA
- ▨ PLANT REMAINS
- ● CARBONIZED PLANT FRAGMENTS
- ⦚ MODERN PLANT ROOTS
- S MACROSPORES
- ⊘ CHAROPHYTA OOGONIA
- ⊗ DIATOMS
- ▨ GASTROPOD
- ▨ OSTRACOD

NUMBERS EQUAL MINIMUM NUMBER OF BEETLE INDIVIDUALS, EXCEPT FOR POTENTIALLY IDENTIFIABLE FRAGMENTS AND ADDITIONAL INSECTA AND ARACHNIDA WHICH EQUAL ACTUAL NUMBER OF FOSSIL FRAGMENTS

COLEOPTERA FAMILIAL ORDER FOLLOWED BY U.S. DEPARTMENT OF AGRICULTURE AND U.S. NATIONAL MUSEUM.

SYSTEMATIC ORDER OF INFRAFAMILIAL COLEOPTERA TAXA AFTER BLACKWELDER (1944-1947)

ORDER OF ADDITIONAL INSECTA GROUPS AND ARACHNIDA AFTER BORROR AND DELONG (1964)