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Herbivory in Antarctic fossil forests: evolutionary and palaeoclimatic significance

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Summary Many collections of Eocene Fossil leaves from Antarctica contain a rich store of insect trace fossils, indicating that insects were an important component of the unique forests that grew in polar regions. However, insect body fossils themselves are rare and so insect traces provide an excellent opportunity to examine both the palaeoentomology and the palaeoclimate of Antarctica. The fossils studied include Eocene leaves from both Seymour Island and King George Island on the Antarctic Peninsula. A database of all insect traces on the Antarctic fossil leaves was compiled and analysed in terms of the diversity of palaeoherbivory. The fossil leaves are diverse with several different plant species present such as *Nothofagaceae* and *Cunoniaceae*. The range of traces found includes leaf mines, galls and general leaf chewing, of which both marginal and non-marginal examples are present. The preliminary results of the comparison with modern day environments in South America will be shown, providing a greater indication of the types of insects that may have created such traces in Antarctica in the past.

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Introduction

Today, most of continental Antarctica is permanently covered by snow or ice, with only a small proportion of ice-free terrestrial habitats. The majority of terrestrial habitats are covered in snow for most of the year with widely variable, unpredictable conditions, both short term and seasonally (Convey, 1997). Therefore, it is not surprising that there are only two insects known to be living in Antarctica, both flightless midges (Diptera: Chironomidae) (Ashworth & Kuschel, 2003). They occur along the northwest coast of the Antarctic Peninsula where the conditions are warmer and wetter than elsewhere.

However, millions of years ago Antarctica was completely different, with areas covered in diverse vegetation similar to the forests of New Zealand and southern South America. Such ecosystems support a large number of insect species, therefore, the same might have been true for Antarctica, but few insect body fossils have been found due to difficulty in preservation, with only small fragments recovered in most studies. Presently, only limited information on the insect fauna has been published, such as a single leg segment of a weevil (Ashworth et al., 1997). Two species of fossil listroderine weevils (Coleoptera: Curculionidae: Rhytirhinini, Listroderina) were found in the Transantarctic Mountains. It is thought they were the descendants of Gondwanan species that lived in Antarctica continuously from the Late Cretaceous until they became extinct in the Neogene (Ashworth & Kushcel, 2003). This is also supported by the discovery of a fossil of a higher fly (Diptera: Cyclorrapha) from the same formation (Ashworth & Thompson, 2003).

Due to the rarity of insect body fossils from Antarctica it is possible to gain a better understanding of the insect fauna by examining indirect evidence of the insects' presence. For example, the evidence of an insect's behaviour preserved as fossils, known as trace fossils. There are three main categories of trace fossils that are shown on leaves: general chewing marks both marginal and non-marginal, leaf mines and galls. There is a large diversity of plants in the terrestrial fossil record and, as insects are the major group of herbivores, the trace fossils provide a unique and direct record of the plant-insect interactions in the past (Grimaldi & Engel, 2005). The trace fossils can indicate the type of insect that made the trace, at least to order, if not to family level, by the shape, size and position of the damage. This allows insect damage to be distinguished from other causes of damage such as mechanical damage or from other large herbivores.

There are several documentations of the vegetation of Antarctica for the past, especially during Cretaceous and Tertiary (Hunt and Poole, 2003)., but few mention the presence of insect traces However, if temperate rainforests were once present in Antarctica, then the palaeoecological reconstruction would not be complete without considering the insect fauna that could have been present. Therefore, the main aim of the project is to identify the presences of insects in Antarctica in the past by examining fossil leaf collections from different localities from the Eocene. The trace fossils found will then be compared with modern ecosystems to identify the causal insects and the palaeoclimate they lived in.

Localities

The fossil leaves examined were collected from deposits on two islands off the Antarctic Penninsula, both Eocene in age. King George Island in the South Shetland Islands is situated at a latitude of 62°S, similar to that in the early Tertiary (Lawver *et al.,* 1992). The island lies on the western, fore-arc margin of the former magmatic arc. Fossil leaves from several locations on King George Island were studied, such as Fossil Hill, Point Hennequin and Vaureal Peak.

Collections from Seymour Island were also examined. Seymour Island sits within the James Ross Island Basin, a back arc basin (Elliot, 1988). The sedimentary sequence exposed on Seymour Island is more than 2 km thick and represents the uppermost part of the infill of the James Ross Basin. The youngest beds, which outcrop on the northern part of the island, were grouped into the upper Palaeocene Cross Valley Formation and the Eocene, La Meseta formation and are placed together as the Seymour Island Group (Marenssi *et al*., 1998). All leaves belong to collections of the British Antarctic Survey.

Summary of Results

Fossil Leaf Data

The fossil leaves from both localities are impression and compression fossils which vary in preservation quality. The majority of leaves studied were angiosperms but several conifer species were also present. For the King George Island flora, the leaves are preserved either as carbonised compressions lacking cuticle, as pure impressions or as mineralised impressions. Leaf remains are preserved as dispersed organs or as leaf mats and range from entire to large fragments of the leaves. The leaves from Seymour Island are present mostly as fragmentary impressions; some fragments are large, being up to 75% of the leaf, but complete leaves are rare. Leaf margins and venation for both fossil floras are variably preserved which affects the visibility of traces, specifically leaf mines.

The leaves were previously described and organized into morphotypes by Hunt and Poole (2003) for the King George Island and Tosolini et al. (personal communication) for the Seymour Island flora using the terminology described by the Leaf Architecture Working Group (1999). This was also used in this study to describe specimens not identified previously, but poor preservation of higher order venation and high fragmentation made identification difficult for the Seymour Island collection.

A total of 1241 specimens were examined from King George Island and 1027 from Seymour Island to assess insect traces. From both localities samples had to be discounted from further analysis due to high fragmentation (6 samples from King George Island and 297 samples from Seymour Island). From King George Island, 156 leaves could be identified to a specific morphotype that was previously assigned (Hunt and Poole 2003) with a total of 40 different leaf morphotypes identified. Similarly, for Seymour Island, 273 leaves could be identified to a specific morphotype with also a total of 40 different morphotypes. The most abundant morphotypes were in the Family *Nothofagaceae* and the Family *Cunoniaceae* although *Lauraceae* and *Dictyllophylum* species were also present in large numbers.

Insect Trace Fossil Data

The main categories used to catalogue the insect trace fossils were general leaf chewing (both marginal and non-marginal),, mines and galls. The last category "other" was created for trace fossils which could not be grouped into the above herbivory types. The traces were organized into distinct trace types called morphotraces which were described and separated depending on plant morphotype, as well as features such as size, shape and position on the leaf surface

The trace fossil that provides the most common palaeontological evidence of plant-insect interaction is the presence of general leaf chewing marks (Scott & Paterson, 1984). General leaf chewing refers to feeding on the leaf which can be marginal, both continuous and discontinous, as well as non-marginal bullet holes within the leaf laminae. For both localities, the non-marginal general leaf chewing category had a total of 37 different morphotraces. These varied with size of trace and number of marks. The shape of the mark was also noted as circular, elliptical and oblong. Marginal general leaf chewing had 15 different morphotraces. All were continuous and varied with the size of area damaged (Figure 1a).

Leaf mines are a highly specialised form of feeding behaviour that also gives the insect protection from both predators and dehydration. A leafminer is the collective name given to an insect whose larvae feed inside the parenchyma or epidermis tissue of the plant, creating distinctive channels. The adult insects lay their eggs inside the tissue where the emerging larvae can feed and continue to develop (Hering, 1951). Leaf miners are insects in the extant orders Lepidoptera, Diptera, Coleoptera or Hymenoptera whose larvae feed inside the leaf, between the two laminae. This produces a characteristic mine with a distinctive shape and form, allowing the insect to be identified in the juvenile stage. The larvae may leave behind faecal material within the mines, which can also help with identification of the insect. A total of 5 morphotraces were identified as leaf mines, both blotch and linear mines. For example, morphotrace 4.2 had only one specimen that was a small linear mine which runs vertically along several areas starting and ending near the primary vein on a *Cunoneaceae* leaf (Figure 1b). Morphotrace 4.1 was a large to medium sized blotch which was between two secondary veins on a *Nothofagaceae* leaf fragment (Figure 1d).

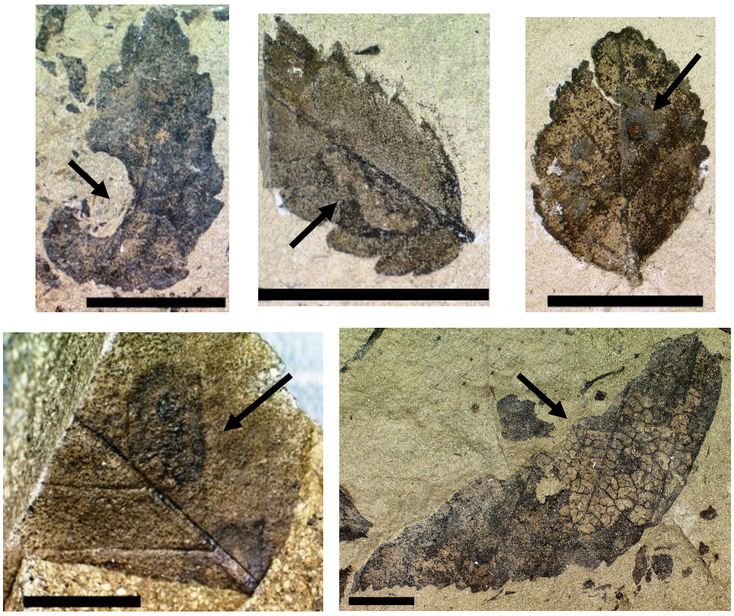

Figure 1. a) General leaf chewing on *Cunoniaceae* leaf. b) Linear leaf mine on *Cunoniaceae* leaf. c) Single gall on *Nothofagaceae* leaf. d) Blotch mine on leaf. e) Skeleton Feeding example. Scale bar 1cm.

Fossil galls are also visible on the fossil leaves. These are, caused by the extensive growth of the plant tissue due to a feeding insect or an ovipositing (egg-laying) female. This physiological reaction is caused by the production of abnormal tissue, either by abnormal cellular increase, by cellular growth and division or by cell differentiation (Stephenson & Scott, 1992). The gall that is produced provides both protection and food for the developing larvae. Insect galls are both highly tissue- and host-specific and so comparisons with extant forms can give a broad identification of the insect that caused them.

Sixteen different gall fossils were found. The galls that were found on fossil leaves were either raised from the surface of the leaf or compressed flat on the leaf. One distinct gall type, morphotrace 3.2, was only found on one specimen and had multiple small doughnut-shaped galls that were concentrated around the apical region of the upper epidermis. In contrast, morphotrace 3.1 was a single small circular gall situated next to the primary vein between two secondary veins and only on *Nothofagaceae* leaves (Figure 1c).

Only traces with a distinctive plant wound reaction were included in the database. Many plants have developed defensive reactions to protect them from invading insects, from physical defences to production of noxious chemicals at the site of wounding (Coley & Barone, 1996). The plant tissue forms a darkened ridge that hardens and deters the insects from feeding further. This ridge can be seen in some specimens, making it possible to determine that the damage occurred when the leaf was still alive. Generally, the wound reaction is best preserved on impression fossils where it can be identified by this distinctive darker colour or indentation around the damaged area. Absence of wound reaction may have been the result of mechanical damage to the leaf or damage when the leaf was abscised and thus not a record of insect activity.

Skeleton feeding of the leaf occurs when an insect scrapes out the leaf tissue, leaving the vein network intact. It is difficult to distinguish between skeleton feeding and natural decomposition, especially for fossil leaves, however, other studies have assumed that if the rest of the leaf is still intact and only one area is missing then it is an insect trace fossil (Scott 1992). Morphotrace 5.1 is an example of skeleton feeding on a *Nothofagaceae* leaf. The surrounding tissue is undamaged and there is a darkened ridge around the edge of the missing tissue, indicating the leaf was still alive when damaged.

Discussion

Examination of fossil leaves from King George Island and Seymour Island has highlighted a range of insect trace fossils, providing evidence that several insect species were present in Antarctica in the Eocene. In modern ecosystems, general leaf chewers can be found within many insect orders, such as the larvae of Lepidoptera and Hymenoptera (Suborder Symphyta), as well as adult Coleoptera, Orthoptera and Phasmida (Strong *et al*., 1984). Wratten (1981) observed that some taxa have specific modes of feeding, such as the Orthoptera that bite holes in the edges of the leaves, and the Curculionidae (Coleoptera) that are known to scoop out the edges of leaves at intervals.

Extant leaf mines are produced by the developing larvae of insects in the orders Lepidoptera, Hymenoptera, Diptera and Coleoptera. The majority of galls are produced by gall mites (Acari: Eriophyiade), gall gnats (Diptera: Cecidomyiidae), Hemiptera (Homoptera) and gall wasps (Hymenoptera: Cynipidae). Skeleton feeding occurs in extant species in the Curculonidae (Coleoptera: Curculionoidea) which are known to chew the surface of the leaves, sparing only the network of veins (Strong *et al*., 1984).

However, all the insect orders mentioned contain many families and species that all have different ecological requirements and life histories. Species vary not only geographically, but also with the plant species upon which they may be dependent. Therefore, to identify more specifically the insect that made the traces preserved in the fossil leaves, it is necessary to make comparisons with living insects. The vegetation in Antarctica during the Eocene may have been very similar to that of the Valdivian rainforests of southern Chile (Poole *et al*., 2003). Torres *et al.* (1994) described a total of 6 taxa of fossil woods having affinities with extant trees growing in cold temperate rainforest of southern South America, specifically the Valdivian and Magellanic forests. If the vegetation is similar, the phytophagous insect fauna may also likewise be comparable. Therefore, by investigating the insect faunas of modern day rainforests in Chile, a greater understanding of the insects of Antarctica may be obtained. As morphotraces on fossil leaves of the genus *Nothofagus* were most abundant, the insect fauna of present day *Nothofagus* is now being studied in several sites in southern Chile. Results of an investigation into the herbivorous insect fauna on *Nothofagus antarctica* and *Nothofagus pumilio* are currently under analysis.

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