EVIDENCE OF ORIBATID MITE DETRITIVORY IN ANTARCTICA DURING THE LATE PALEOZOIC AND MESOZOIC

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ABSTRACT—Despite their importance in breaking down lignified tissue today, much is still unknown about the role of mites in the fossil record, especially with reference to the Paleozoic–Mesozoic transition. This study examines permineralized peat from three localities in the central Transantarctic Mountains, ranging in age from Permian to Jurassic, for evidence of diversity and abundance of wood-boring mites. Evidence of mites, in the form of coprolites and tunnels in wood and other tissues, was found at all three localities; the Triassic site included more than 10 times as many wood borings as the Permian site. Our results supplement prior evidence of wood-boring mites during the Mesozoic and thereby fill in the known geologic range of this plant/animal interaction.

INTRODUCTION

PLANT-ARTHROPOD INTERACTIONS play a pivotal role in the major functions of today's terrestrial ecosystems, including nutrient cycling, crucial food web links, and mutualistic relationships. These interactions range from presumably positive ones, such as pollination behaviors, to negative and so-called neutral interactions, such as herbivory and detritivory. Data suggest that such interactions have been going on for nearly as long as life has been on land (e.g., Shear, 1991; Shear and Selden, 2001). Shear (1991) notes that detritivory appeared first in terrestrial ecosystems and was followed later by herbivory and more complex types of interactions. Evidence for probable wounding of plants has been described from the Devonian (e.g., Kevan et al., 1975; Banks and Colthart, 1993) and coprolites with recognizable plant contents are known from the Late Silurian on (Edwards et al., 1995), both of which are consistent with herbivory (Labandeira, 1998). By the Mississippian, both coprolites and instances of wounding are fairly common (Scott and Taylor, 1983).

Wood boring is another type of plant-arthropod interaction that is relatively common in the fossil record. This feeding behavior involves burrowing through the xylem of woody plants and generally has a better fossil record than some other interactions because wood tends to be preserved in greater quantity and with higher quality than many other plant tissues. Wood boring pushes the limits of the definition of plant/animal interactions, due to the question of whether or not the plants were alive during the process. Since the majority of the cells in woody tissue (i.e., secondary xylem) are dead at maturity, wood-boring activity in the fossil record can rarely be conclusively designated as detritivory or herbivory. In addition to the difficulty of defining wood-boring activity is the question of determining which organisms are responsible for the borings. Most wood-boring species of arthropods today are insects, including bees, ants, moths, termites, beetles, and flies. Oribatid mites also bore through wood, but are often less well-known in the extant fauna due to their small size and the fact that they rarely bore into wood of living plants (Wallwork, 1967).

Almost all of the wood borings described prior to the Early Permian, when the first wood-boring insects are thought to have evolved, have been attributed to oribatid mites (e.g., Cichan and Taylor, 1982; Rex and Galtier, 1986; Chaloner et al., 1991; Goth and Wilde, 1992; Labandeira et al., 1997; Tomescu et al., 2001). There are many reports of wood boring attributed to oribatid mites in the Mississippian and Pennsylvanian, but the record both before and after this time period is comparatively sparse (Labandeira et al., 1997). Mite body fossils have been reported from the Early Devonian Rhynie chert (Hirst, 1923; Krivolutsky and Druk, 1986; Shear and Selden, 2001), the Middle Devonian of Gilboa, New York (Norton et al., 1988), and possibly from the Ordovician (Bagnoli et al., 2000). By the Late Triassic, insect wood borings increase in abundance and insects continue to be prevalent agents of this syndrome to the present (Jurasky, 1932; Brues, 1936; Walker, 1938; Linck, 1949; Jarzembowski, 1990). From the Early Permian to the Late Triassic, however, there are only a few reports of mite wood borers (Goth and Wilde, 1992).

We describe here evidence of wood boring, most likely produced by oribatid mites, that supplements our current knowledge of these interactions during this period of time. Late Permian, Middle Triassic, and Middle Jurassic permineralized peats from the central Transantarctic Mountains, Antarctica, have yielded anatomically preserved stems, petioles, and roots containing tunnels and coprolites within them. Using data from the Permian and Triassic, we also examine the frequency of wood borings through time.

MATERIALS AND METHODS

All fossils occur within permineralized peat deposits in the Beardmore Glacier area, Queen Alexandra Range, central Transantarctic Mountains (Taylor et al., 1989). The Late Permian peat is from Skaar Ridge (84°49′15.8″S, 163°20′18.9″E, Buckley Island Quadrangle; Barrett and Elliot, 1973). This site occurs within the upper part of the Buckley Formation of the Beacon Supergroup (Barrett et al., 1986) and has been dated Late Permian on the basis of palynomorphs within the peat (Farabee et al., 1991).

The Middle Triassic peat was collected from a saddle on the north side of Fremouw Peak (84°17′24.1″S, 164°21′24.2″E)

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FIGURE 1—Permian and Triassic coprolites. *1*, Cross section through Triassic wood showing tunnel and coprolites within (10808, E bot #3, 126×); *2*, Permian wood with typical coprolite for this site (CB476, B bot #1, 312×); *3*, two coprolites (lower in longitudinal section, upper in cross section) in Triassic wood, showing general shape and composition of fecal pellets (10808 G_1 top #1, 375×); *4*, transverse section of Triassic fern *Antarctipteris* petiole with coprolites replacing most of the inner cortex. Note V-shaped vascular strand with two pairs of traces at either end (arrows). Small root at lower left probably grew through the plant organ (10808 D top #2, 31×); *5*, parenchyma tissue showing two size classes of coprolites (Triassic) (arrows) (10808 I #1, 31×); *6*, higher magnification of coprolite showing partial pattern of reticulation (10808 F_1 bot #2, 625×).
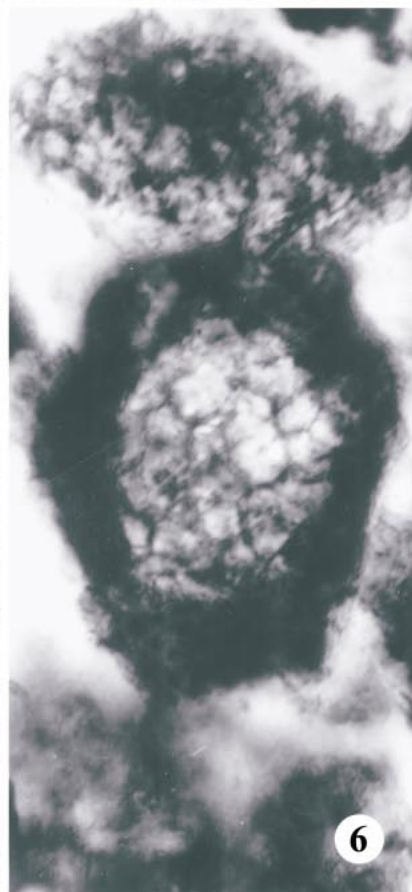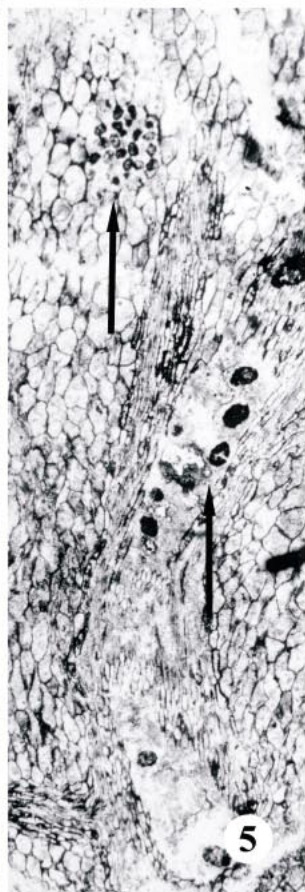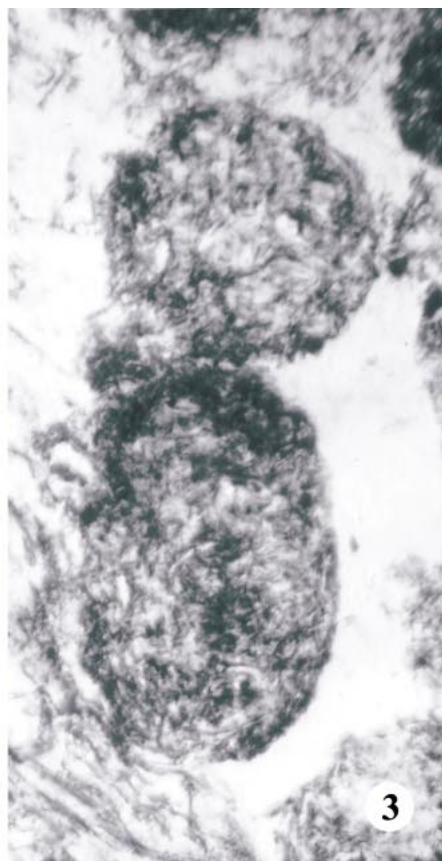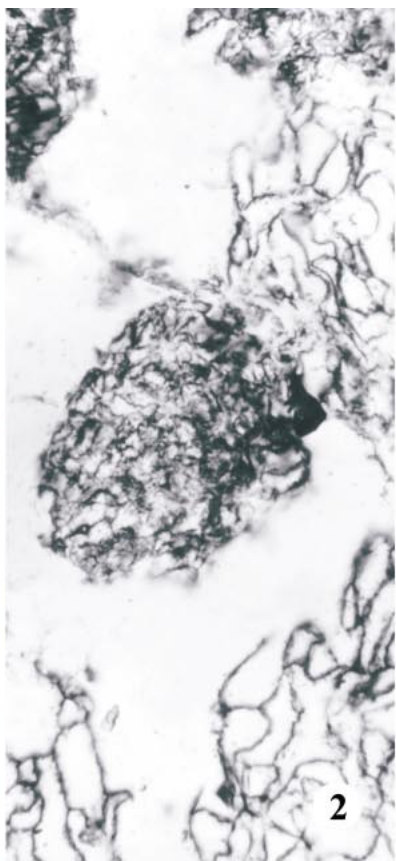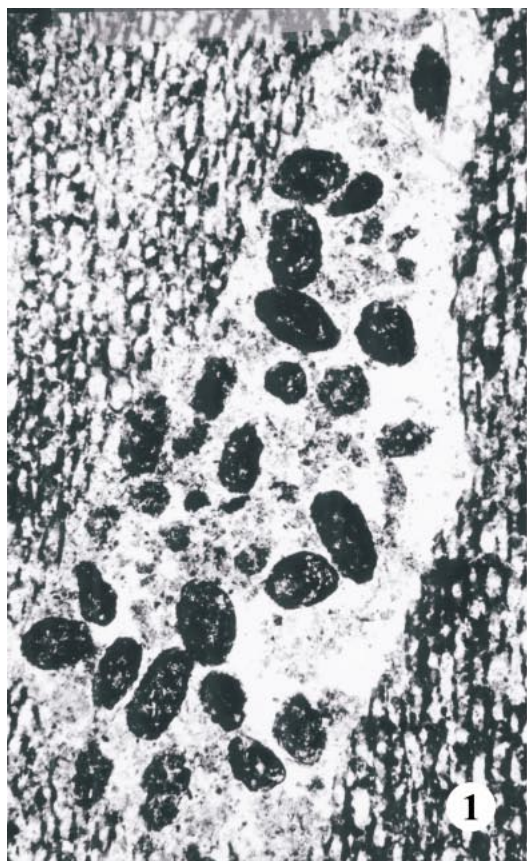
(Buckley Island Quadrangle; Barrett and Elliot, 1973). The locality occurs in the upper part of the Fremouw Formation; this portion of the formation has been dated as early Middle Triassic (Anisian) on the basis of vertebrate fossils (Hammer, 1987) and pollen recovered from the peat (Farabee et al., 1990).

The Middle Jurassic fossils were collected above a 500–600 ft-thick basalt outcrop (Kirkpatrick Basalt) on the west side of Storm Peak (84°35′S, 164°03′E, Buckley Island Quadrangle) (Barrett and Elliot, 1973). The material was obtained from a cherty layer of sedimentary interbeds and is included in the Kirkpatrick Formation (Barrett et al., 1986). Radiometric age determinations of the lavas place the age of the volcanics at this locality in the early Middle Jurassic (Elliot et al., 1985).

The plant material and coprolites are preserved in silica and were studied by means of the acetate peel technique after etching in concentrated hydrofluoric acid (Galtier and Phillips, 1999). Peels were examined for any traces of boring activity in the plant tissues. Once a tunnel was found, the plant organ, plant tissue type and size, shape, and texture of the coprolites within were noted.

To study the frequency of the borings, peels were examined under a dissecting microscope for any traces of boring activity in the plant tissues. From the Skaar Ridge locality, 950 peels were examined from 100 specimens and 760 peels from 100 specimens at the Fremouw Peak locality. Since the preservation in the Permian peat was more sporadic, it was necessary to examine more peels from that site. The Jurassic site was not included in this part of the study due to an insufficient quantity and quality of material. The presence of borings and the plant organ in which they occurred were recorded in material from all three localities.

The structure and organization of the coprolites in selected specimens were studied by mounting peels on microscope slides for examination in transmitted light. These specimens include acquisition numbers CB476, 6120, 10156, 10217, and 10808 and slide numbers 14508, 20008–20019, 21601–21625, and 26059–26068. All materials are housed in the Paleobotanical Collections of the University of Kansas Natural History Museum and Biodiversity Research Center.

RESULTS

Wood borings were found in plant material from all three localities (Fig. 1.1). The important morphological features of the coprolites within these wood borings are summarized in Table 1. The borings from each site differed from each other in the size of coprolites and the type of plant organ that was bored. For the Permian specimens, only xylem tissue in highly degraded stems was attacked. The coprolites within the tunnels of these specimens were circular to ovoid with a fairly regular outline (Fig. 1.2). While some coprolites were only lightly compacted with bits of tracheids recognizable, most were very dense with no recognizable elements. The size of the coprolites from the Permian peat ranged from 60 to 115 μm in length.

The coprolites in the Triassic peat were similar in shape (Fig. 1.3), but were found in a much more diverse range of plant organs than those in the Permian. Whereas the Permian borings were only found in stems, the Triassic ones occurred in stems, petioles, and roots. Several of the petioles which had been bored belonged to the fern genus *Antarctipteris* (Gleicheniaceae?) (Millay and

Taylor, 1990) and were nearly identical in the pattern of infestation: the entire inner cortex was eaten away with the exception of the vascular tissue, which consisted of a V-shaped vascular trace with two pairs of bundles at either end (Fig. 1.4). In place of the cortical parenchyma was a dense mass of coprolites. The Triassic borings extended through both parenchyma and xylem tissue. The coprolites within these tunnels had a highly regular outline and were roughly ovoid in shape. They were fairly densely textured with few to no recognizable components. There were also two distinct size classes of coprolites at this locality (Fig. 1.5). One size class (Triassic Group 1 in Table 1) ranged from 50 to 75 μm in length, while the other (Triassic Group 2 in Table 1) ranged from 95 to 110 μm in length. Coprolites in both size classes were fairly similar in content. A large number of the Triassic coprolites exhibited a reticulation pattern on their surface, which was not observed in the coprolites from the Permian peat. These reticulations appeared to represent several different levels of development. Some of the coprolites were composed of finely meshed plant material, probably tracheids, and were completely free of reticulations (Fig. 1.3). Other coprolites contained recognizable plant debris with variable amounts of reticulation on the surface of the coprolite (Fig. 1.6). Finally, some coprolites were covered completely by this reticulation pattern and contained no recognizable pieces of plant material (Fig. 2.1).

The tunnels from the Jurassic peat occurred in woody stems, fern rhizomes, and petioles. As was the case in the Triassic, both parenchyma and xylem were consumed. The coprolites found were circular to ovoid in shape and had few to no recognizable elements (Fig. 2.2). The two size classes ranged from 60 to 85 μm (Jurassic Group 1 in Table 1) and 170 to 250 μm (Jurassic Group 2 in Table 1) in length. The coprolites from this locality also possessed a reticulation pattern similar to that of the Triassic specimens. However, no coprolites from the Jurassic were found with recognizable plant tissue fragments, nor were there any with only partial reticulations, which correlates with the relatively poor preservation of the plants from this site.

The size of the tunnels at all three sites was highly variable, with some only 0.35 mm in width and others well over a millimeter. While the smaller classes of coprolites were often in smaller tunnels, there was a large degree of overlap in tunnel diameter among the various size classes. For instance, tunnels containing Triassic Group 2 coprolites (95–110 μm) were often as large as the tunnels containing Jurassic Group 2 coprolites (170–250 μm). There were two types of coprolite arrangement within the tunnels: clustered on one side (Fig. 2.3) or evenly distributed throughout the cross-sectional area (Fig. 2.4). This suggests that either the arthropod excavating the tissue was capable of hollowing out an area larger than itself, or that there were multiple arthropods in one tunnel at some point in time.

Of the 220 borings found in Triassic plants, 125 instances were found in roots, 16 in stems, 59 in petioles, and 20 in unidentifiable plant organs. In the material from the Permian, seven of the 16 borings were found in stems, six in roots, and three in unidentifiable plant organs.

DISCUSSION

Although the coprolites range from 50 to 250 μm, they fall into five distinct size classes (Table 1). With the exclusion of the

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FIGURE 2—Triassic and Jurassic coprolites. *1*, Cross section through a Triassic root showing tunnel with coprolites with full reticulations (10156 B bot #3ß, 126×); *2*, poorly preserved coprolites within Jurassic fern petiole. Note the density of the contents and lack of identifiable plant parts within the coprolites (6120 D top #18α, 120×); *3*, transverse section through a Triassic fern petiole showing tunnel with coprolites distributed only along one side (10217 E$_2$ bot #1α, 110×); *4*, oblique section of Triassic wood showing coprolites evenly distributed throughout the tunnel diameter (10217 D$_2$ top #1, 110×).
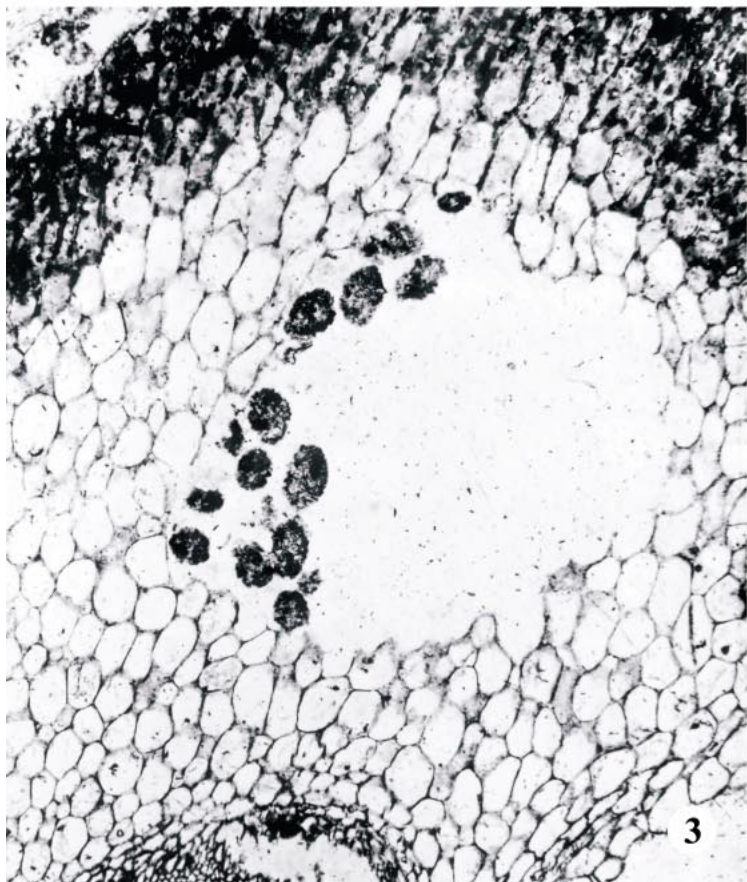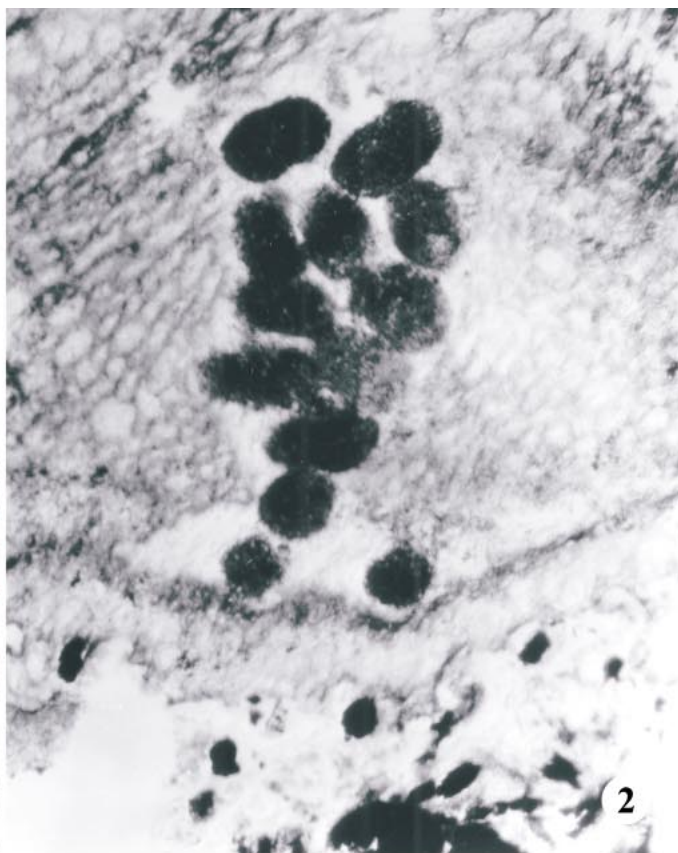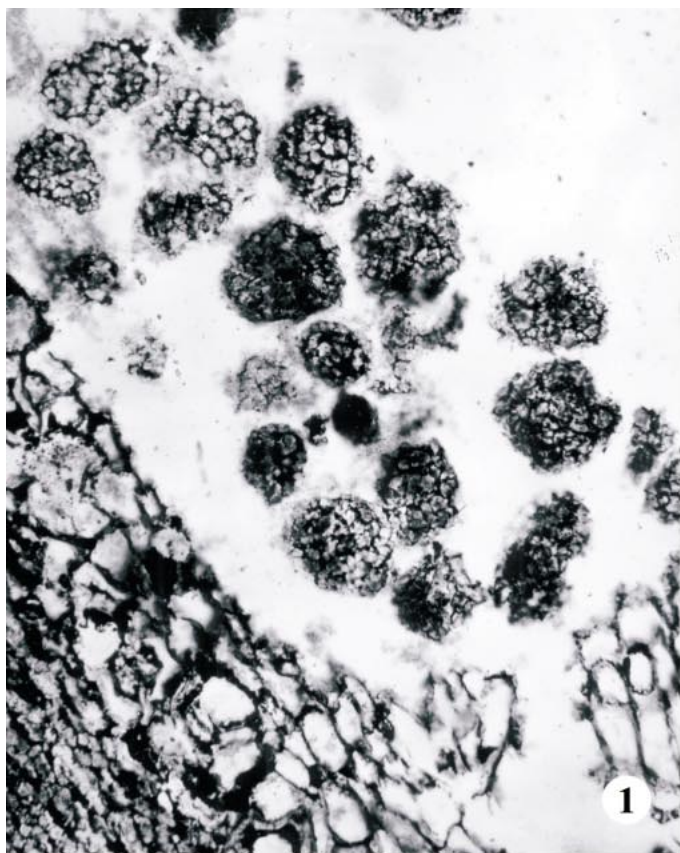
TABLE *1*—Morphological characteristics of coprolites from the Permian, Triassic, and Jurassic of Antarctica.

	Size	Shape	Texture
Permian	60–115 µm	Circular to ovoid	Slightly compacted, composed of tracheids
Triassic Group 1	50–75 µm	Circular to ovoid	Densely compacted, no recognizable elements
Triassic Group 2	95–110 µm	Circular to ovoid	Densely compacted, some with bits of tracheids
Jurassic Group 1	60–85 µm	Circular to ovoid	Densely compacted, no recognizable elements
Jurassic Group 2	170–250 µm	Circular to ovoid	Densely compacted, no recognizable elements

larger size class of coprolites from the Jurassic (Group 2–170 to 250 µm), all are within the size range produced by oribatid mites. The designation of a mite origin for the fecal pellets within this Antarctic wood is based on a list of features for determining the probable origin of fossil coprolites outlined by Labandeira et al. (1997). We have summarized these features and shown their distribution across various arthropod groups in Table 2. Features include size, shape, surface texture, contents, and presence in the extant fauna of organisms with a similar habit and feeding strategy, in this case, wood boring. The Antarctic material includes examples of borings in both wood and parenchyma tissue. Labandeira et al. (1997) found similar evidence of wood- and parenchyma-boring in Pennsylvanian coal ball plants and attributed this activity to oribatid mites. They found that most groups of arthropods could be eliminated from consideration by the size of their fecal pellets; this is true of the Antarctic borings as well. Today, only collembolans produce fecal pellets of comparable size to the oribatids (Table 2). These microarthropods live in the litter alongside oribatid mites, but produce fecal pellets with a rough, irregular surface, very different from the smooth, oval fecal pellets of oribatid mites (Labandeira et al., 1997) (Table 2). In addition, although collembolans eat many different plant and animal tissues, they do not specialize in xylophagy, as do some oribatid mites. Taking into account their ecology, as well as the fecal pellet structural features in Table 2, we attribute the borings from all three time periods to oribatid mites.

Coprolite distribution occurred in two basic patterns within the tunnels: along one side only or filling the tunnel diameter. Modern oribatid mites digest only a small amount of wood at a time, so that tunnels made exclusively by oribatids should generally be more or less filled with coprolites. In the asymmetrically distributed coprolites (Fig. 2.3), it is possible that the plant material was heavily degraded by bacteria or fungi prior to occupation by the arthropods. In this case the arthropod may have been consuming the fungi and/or bacteria in addition to, or in place of, the plant material. A portion of the wood from both the Permian and Triassic appears degraded and some of this has been attributed directly to fungi (Stubblefield and Taylor, 1986). It is also possible that these sections in the tunnel might have been kept empty for habitation purposes. Some extant wood-boring oribatid mites develop completely inside the tunnels (Wallwork, 1976).

The reticulation pattern found in the Triassic and Jurassic coprolites could be attributed to either remnants or impressions of fungal hyphae or the result of microbial activity. The increasing coverage of the reticulation pattern would then signify the increasing degradation of the coprolites. The lack of finely comminuted plant tissues in the coprolites of the Jurassic locality could be due to several different factors, the most important one being the spotty and somewhat poor preservation of the plant material from this locality. The lack of a reticulation pattern on any of the coprolites from Skaar Ridge (Permian) is interesting and may have resulted from taphonomic or preservational factors. Until we know more about the formation of these patterns, it is not possible to understand their distribution fully.

Records of mite wood borings are relatively widespread in the Paleozoic (Cichan and Taylor, 1982; Rex and Galtier, 1986; Chaloner et al., 1991; Goth and Wilde, 1992; Labandeira et al., 1997) and in the Quaternary (Haarløv, 1967; Krivolutsky and Ryabinin, 1976). A number of examples of borings attributable to oribatid mites are known from the Mesozoic, but these are primarily found in parenchyma tissue (e.g., Seward, 1924; Tidwell and Rozefelds, 1991; Yao et al., 1991; Saiki and Yoshida, 1999; Ash, 2000). Sharma and Harsh (1989) described fecal pellets in Jurassic araucarian wood, but did not attribute them to a particular group of arthropods. Although within the size range of mites, the coprolites are described as possessing a rough surface. Although no definitive mite wood borings have been reported from the Mesozoic, there is evidence of detritivorous oribatid mites in the form of body fossils from the Upper Cretaceous (Bulanova-Zachvatkina, 1974). Zhou and Zhang (1989) describe apparent insect wood borings in conifer wood from the Middle Jurassic of Henan, China. The coprolites they found fall into two size ranges: 100 to 165 µm × 70 to 105 µm and 50 to 55 µm × 20 to 40 µm, while the tunnels are uniformly large, measuring 200 to 500 µm in diameter. Utilizing Labandeira et al.'s (1997) criteria for distinguishing mite coprolites and Bal's (1970) size ranges, we believe that both of the size classes described by Zhou and Zhang as insect wood borings were probably produced by oribatid mites.

Of greater interest is the apparent absence of wood boring insect damage from all three of the Antarctic localities. While this absence could be explained in the Jurassic peat by the limited number of well-preserved specimens from this locality, the large amount of material sampled from the Permian and Triassic localities (950 and 760 peels examined, respectively) is much harder to dismiss. Additionally, wood borings that have been attributed to insects have been documented in wood from Permian localities in Prince Charles Mountains, East Antarctica (Weaver et al., 1997). Thus, it seems highly implausible that the absence of insect

TABLE *2*—Characteristics of mites and their coprolites, compared to those produced by other arthropods (data adapted from Labandeira et al., 1997).

	Possible coprolite producers					
Defining criteria:	Oribatid mites	Insects (adults)	Insects (larvae)	Collembolans	Diplopods	Enchytraeid worms
Size: 50–260 µm	X		X	X		X
Shape: Spherical to ovoid	X					
Surface texture: Smooth	X	X	X			
Contents: Fairly densely compacted; few recognizable elements	X	X	X			
Known wood borer	X	X	X		X	

wood borings can be explained by the age and/or paleolatitude of the Skaar Ridge and Fremouw Peak localities.

Based on paleogeographical information and floral diversity, the Triassic locality at approximately 70°–72°S is hypothesized to have been located at a paleolatitude approximately 10 degrees north of the Permian locality (Powell and Li, 1994; Grunow, 1999; Taylor et al., 2000). Based on the presence of tree rings and the depauperate flora found throughout Gondwana, the Late Permian climate is thought to have been cool-temperate and humid (Collinson, 1997). The more diverse flora and extensive fauna in the Middle Triassic suggest a warm temperate climate (Collinson, 1997). Thus, the hypothesized paleoclimate of the two fossil localities fits well within the range in which both insect and mite wood borers are found today.

Another possibility is that the lack of insect wood borers in the Antarctic peats is due to the environment of deposition and/or preservation type. Mite wood borings in the Paleozoic are primarily known from coal ball permineralizations and silicified peat which was deposited in swampy environments (e.g., Cichan and Taylor, 1982; Labandeira et al., 1997). However, Mesozoic examples of insect wood boring occur in petrifactions, many of which were deposited in drier, more riparian habitats (Walker, 1938; Linck, 1949; Tidwell and Ash, 1990). The logical extension of this hypothesis would be that insects are more prolific wood borers in dry environments and oribatid mites are dominant in swampy environments. The record of the Permian, Triassic, and Jurassic coprolites from Antarctica provides some support for this hypothesis. All three localities yield permineralized peat, which initially formed in a swampy environment. The environment of deposition of the Antarctic peats differs from that of northern hemisphere coal balls, however, since there is no coal directly associated with the Antarctic peats and they were deposited in fluvial sequences (Taylor et al., 1989). Unfortunately, there is not enough information available about the modern xylophagous mite fauna to determine whether these ecological relationships hold true today.

Considering their important position as decomposers in today's ecosystems, the discrepancy between the frequency of mite borings in the Late Permian and Middle Triassic has implications for the decomposition rates at the two localities. Since oribatid mites are often the most abundant part of the xylophagous fauna, a decrease in their abundance would have drastic implications for the decomposition rates of wood in an ecosystem. Some oribatid mites are known to play at least five pivotal roles in the decomposition process. They manually break apart plant tissues and hollow out cavities which increases the surface area for colonization by fungi and other microbes (Kevan, 1962; MacFayden, 1964). Their fecal pellets stimulate the growth of microbial spores. Microbes appear to be limited in their ability to disperse on their own; thus when the available energy in a certain area has been expended, the microbial biomass shuts down until new resources become available. The intestines of the mites provide sufficient nutrients to activate ingested microbial spores (Shereef, 1971; Luxton, 1972; Ponge, 1984; Lavelle et al., 1994; Lavelle, 1997). In some cases, fecal pellets are preferentially colonized by microbes over undigested plant material. The microbial activity of fecal pellets, combined with the wood-boring activity of the oribatid mites, serves to introduce microbes into the inner tissues of plant organs faster than fungi or bacteria would be able to do on their own. The presence of microbes increases the nutritive content of the fecal pellets which are often then reingested by other arthropods, breaking the plant material down even further and functioning somewhat like an "external rumen" (Mason and Odum, 1969; Crossley, 1970). Finally, oribatid mites and other microarthropods help to move organic material deeper into the soil (Saichuae et al., 1972). Thus, a low level of mite boring

activity as seen in the Permian locality could translate to a decrease in overall decomposition.

The abundance of mite activity in modern ecosystems can also reflect the amount of disturbance at the site. Oribatid mites are very poor dispersers as a whole; once they have been eliminated from a particular area, their small size and limited modes of dispersal make recolonization a slow process (Norton, 1980; Siepel, 1994). As Behan-Pelletier and Bissett (1994) observed in Canadian peat bogs, mite abundance is directly related to water levels. Therefore, if periodic submersion occurred at this Permian site, a reduced abundance of tissue-boring mites could reflect a lack of time for recolonization.

Additionally, latitude might have played a role in the decreased abundance of mite endophagy in the Permian since the proposed paleolatitude of this flora is about 10 degrees south of the Triassic locality. However, the effect of latitude on mite abundance or diversity is unclear. While some genera of extant oribatid mites (*Phthiracarus* Perty, 1839, *Steganacarus* Ewing, 1917, and *Atropacarus* Ewing, 1917) have lower levels of diversity at very high latitudes and in the tropics, there are a few genera for which this is not the case (*Plonaphacarus* Niedbala, 1986 and *Hoplophorella* Berlese, 1923) (Niedbala, 1991). Moreover, the harsh climate and lack of suitable habitat in the polar regions of today is drastically different from that of the paleoecosystems. Even when the cool-temperate and warm-temperate climates of the Permian and Triassic are taken into account, there are still insufficient data to compare diversity levels between these two climate regimes today. Differences in mite abundance across modern latitudinal gradients are equally unclear. Stanton (1979) found that mite abundance at sites in Wyoming and Costa Rica was dependent more upon the environment, especially the microenvironment, than upon latitude. Applying these results to the fossil record suggests that differences in mite abundance between the Permian and Triassic localities may have been controlled by moisture availability, type of flora, and litter quality more than by latitude.

The lower abundance of oribatid mites in the Permian peat may also suggest that the Glossopteridales, the dominant plant group in Gondwana during the Permian, possessed a toxicity that discouraged mite detritivory. This is unlikely, however, because there would be sedimentological evidence of decreased decomposition in the form of a scarcity of coals and an abundance of poorly decayed peats. In addition, there are known examples of glossopterid herbivory, although not by oribatid mites (Plumstead, 1963; Zavada and Mentis, 1992; McLoughlin, 1994a, 1994b). However, even if the glossopterids did not possess toxic secondary metabolites that discouraged detritivores, their dominance still may have played a role in the abundance of detritivorous oribatid mites. Hansen (2000) found decreased mite abundance in experimental forest plots with monotypic litter regimes. He attributes this to lower levels of habitat complexity within the litter in a monotypic regime. The overwhelming dominance of *Glossopteris* Brongniart, 1828 in the forest canopy and the general lack of evidence of understory plants (Taylor et al., 2000) would contribute to substrate homogeneity. Finally, if the Permian plant material were submerged too quickly to allow terrestrial oribatid mites to attack the wood, this could account for the presence of lower levels of wood boring. However, fungal attack of this wood appears identical to that formed in terrestrial environments (Stubblefield and Taylor, 1986), so this scenario seems unlikely.

CONCLUSION

The data presented here have several implications for mite ecology in both modern and fossil ecosystems. The first is that endophagous mites are present in all three localities and, as far as can be determined, they are the most prevalent component of the xylophagous fauna for each of these three localities. This in turn

brings into question the reason for the apparent absence of wood-boring insects from these localities during the Permian, Triassic, and Jurassic. Although we have presented several plausible hypotheses to explain this absence, it is clear that further Mesozoic fossil evidence is needed to clarify some of the early events in the evolution of xylophagous insects.

Additionally, there appears to be a large discrepancy in oribatid mite abundance between the Permian and the Triassic, at least at these high paleolatitudes. Since both deposits represent peat-forming environments, the change in abundance may reflect differences in plant hosts, habitat heterogeneity due to floral diversity, or some other as yet unknown factor. Unfortunately, while there are some data available on the distribution and life histories of oribatid mites in modern environments (e.g., Crossley and Bohnsack, 1960; Badejo, 1990) there are no broad syntheses, either by latitude or environment, and the data are insufficient for comparison with the fossil material. Thus, while the amount of information these fossils can yield is significant, a full understanding of their place in the paleoecosystem is constrained by the limitations of our knowledge of modern mite diversity and abundance.

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