Marine and terrestrial invertebrate borings and fungal damage in Paleogene fossil woods from Seymour Island, Antarctica

Stephen McLoughlin

To cite this article: Stephen McLoughlin (2020) Marine and terrestrial invertebrate borings and fungal damage in Paleogene fossil woods from Seymour Island, Antarctica, GFF, 142:3, 223-236, DOI: 10.1080/11035897.2020.1781245

To link to this article: https://doi.org/10.1080/11035897.2020.1781245
**Marine and terrestrial invertebrate borings and fungal damage in Paleogene fossil woods from Seymour Island, Antarctica**

Stephen McLoughlin

Department of Palaeobiology, Swedish Museum of Natural History, Stockholm, Sweden

**ABSTRACT**

An assemblage of permineralized conifer and angiosperm woods collected from Paleogene marine strata on Seymour Island during the Swedish Antarctic expedition of 1901–1903 includes many specimens with internal damage caused by an array of xylophagous organisms. Short, broad, clavate borings referable to *Gastrocoenolites clavatus* are attributed to pholadid bivalves. Elongate borings with carbonate linings referable to *Apectoichnus longissimus* were produced by teredinid bivalves. Slender, cylindrical tunnels cross-cutting growth rings and backfilled in meniscoid fashion by frass composed of angular tracheid fragments were probably produced by a terrestrial beetle borer. They are most similar to tunnels generated by modern cerambycid and ptinid coleopterans. Less regular, spindle-shaped cavities and degraded zones flanking growth rings are similar to fungi-generated modern white pocket rot. Larger chambers in the heartwood referable to the ichnotaxon *Astenopodichnium lignorum* were produced by an alternative mode of fungal degradation. The biological interactions evident in the fossil woods illustrate additional terrestrial trophic levels enhancing the known complexity of ecosystems on and around the Antarctic Peninsula shortly before the initial pulse of mid-Cenozoic glaciation in Antarctica that caused extirpation of the majority of plants and animals in that region.

**Introduction**

For much of its history following the Late Palaeozoic Ice Age, Antarctica remained relatively ice free and hosted extensive forests (Plumstead 1962; Doktor et al. 1996; Rees & Cleal 2004; Francis et al. 2008; Escapa et al. 2011; Bomfleur et al. 2011; Cantrill et al. 2011; Cantrill & Poole 2012; Tosolini et al. 2013; Slater et al. 2015). Both dispersed palynomorphs and plant macrofossils reveal a complex terrestrial vegetation that responded through time to major environmental perturbations, but which retained a distinctly Gondwanan aspect (Cantrill & Poole 2012). Much less common is fossil evidence of the continental invertebrate fauna that interacted with this vegetation. In particular, insects and other terrestrial arthropods have a very meagre body fossil record in Antarctica, and most examples are known from pre-Cenozoic strata (Plumstead 1962; Tasch & Riek 1969; Carpenter 1970; Gressitt 1971; McLoughlin et al. 1997; Slater et al. 2015). The youngest Cenozoic examples are from Miocene–Pliocene strata of the Transantarctic Mountains (Ashworth & Kuschel 2003; Ashworth & Erwin 2016).

Trace fossils offer an alternative source of data on the activities of insects in Antarctica through time (McDonald et al. 2007). A few exceptional permineralized peat lenses of Permian and Triassic age have yielded prolific evidence of ancient plant-arthropod and plant-fungal interactions (Stubblefield & Taylor 1986; Weaver et al. 1997; Kellogg & Taylor 2004; Slater et al. 2012, 2015; Harper et al. 2013), but traces of herbivory, saprotrophy, parasitism or other interactions are otherwise scarce in the continental Antarctic fossil record.

Sporadic records of transported wood and *in situ* stumps fossilized in coastal and neritic settings, some with extensive molluscan borings, have provided exceptional insights into the interaction between ancient marine and terrestrial ecosystems through time (Gingras et al. 2004; McLoughlin et al. 2018; Hunter et al. in press). Additionally, McLoughlin et al. (1995) documented podocarpacean axes containing both marine bivalve borings and hyphal filaments within pocket rot chambers from Lower Cretaceous marine strata of Western Australia that highlighted the potential for preservation of even delicate terrestrial fungi in palaeo-driftwood. Further, Kustatscher et al. (2013) documented a sample of araucaria-conifer secondary wood from the Lower Cretaceous of Italy that preserved both terrestrial oribatid mite borings (cylindrical chambers ~ 225 μm in diameter oriented longitudinally in the secondary xylem) and teredinid excavations (clavate–cylindrical or slightly sinuous chambers of 10–12 mm diameter). These discoveries suggest that combinations of terrestrial and marine trace fossils may be locally common in permineralized driftwood. Such remains offer opportunities to sample the combined diversity of neritic molluscan borers and woody plants from adjacent continental settings, together with their arthropod herbivores and fungal saprotophs, in the same fossil assemblage.

A historically significant fossil wood collection recovered from Seymour Island during the Swedish Antarctic Expedition...
of 1901–1903 and curated in the Swedish Museum of Natural History (SMNH) includes some of the earliest fossils recovered from Antarctica. These remains provided some of the earliest evidence that Antarctica had once been forested. The fossil woods have subsequently provided information on the floristic diversity and palaeoclimate of Antarctica shortly before the Cenozoic glaciation of that continent (Gothan 1908; Oh et al. 2020). Fossil woods from correlative strata in the region also contain borings of marine molluscs that elucidate the ecology and palaeotemperatures of shallow marine waters around the Antarctic Peninsula before its separation from South America (Wiedman & Feldmann 1988; Pirrie et al. 1998).

Thin-sections of the predominantly silicified conifer and angiosperm woods in the SMNH collection have now revealed additional levels of complexity in the Eocene continental ecosystems through the discovery of slender borings of xylophilous terrestrial arthropods within podocarp secondary wood, together with fungal and bacterial degradation of several wood types. This study describes and evaluates the probable trace makers of the borings and decay pockets in the Paleogene wood from Seymour Island.

Geological setting

Stratigraphy

The precise provenance of the studied fossil wood specimens remains ambiguous, since the stratigraphic succession on Seymour Island was not resolved at the time the fossils were collected, and accompanying notes do not provide a precise geographic source. Notes on the museum specimen labels indicate that the woods were collected from Seymour Island on the Swedish Antarctic Expedition of 1901–1903 derive from an area west of Penguin Bight (or Bay; Fig. 1A–C). Mirabelli et al. (2017) suggested that the material derives from the Sobral Formation (Paleocene) based on the extensive exposures of that unit along the southern part of Penguin Bight and abundant representation of fossil wood in that unit. Many of the Sobral Formation woods contain marine bivalve borings (Tilley 2016; Mirabelli et al. 2017). However, two younger units, the Cross Valley Formation (Paleocene) and La Meseta Formation (Eocene) are also exposed to the west of the centre and northern sector of Penguin Bight (Fig. 1C). These units also contain abundant fossil plants including permineralized wood (Pujana et al. 2014). Sadler (1988) introduced the term “Telm” (an abbreviation of “Tertiary Eocene La Meseta”) for eight informal lithostratigraphic subdivisions of the La Meseta Formation. Marine bivalve borings are well represented in fossil woods from Telm 5 and Telm 7 within this formation (Wiedman & Feldmann 1988)—equating, respectively, to the Cucullanea I–II (uppermost Ypresian to lower Lutetian) and upper Submeseta (uppermost Lutetian to Priabonian) allo members of Marenssi et al. (1998). The latter allomember was raised in status to the Submeseta Formation by Montes et al. (2013).

Depositional environment

The Sobral, Cross Valley and La Meseta formations were all deposited in the James Ross Sub-basin, a component of the back-arc Larson Basin that developed in the lee of the Antarctic Peninsula volcanic arc through the Cenozoic (Hathway 2000). Each of these formations was deposited in shallow marine to estuarine settings with siliciclastic sedimentary components sourced primarily from the adjacent arc to the west (Sadler 1988; Cantrill et al. 2011; Mirabelli et al. 2017).

Paleocene to Eocene strata of Seymour Island host predominantly marine fossil assemblages. The fragmentary remains of terrestrial organisms washed into marine settings and preserved within the Paleogene strata provide a modest indication

Figure 1. Location details for the fossil woods. A. Map of Antarctica showing the position of the northern Antarctic Peninsula region (arrowed). B. Map of the northern Antarctic Peninsula showing the position of Seymour Island (arrowed). C. Geological map of Seymour Island showing the probable source area (red box) of fossil woods collected during the Swedish Antarctic Expedition of 1901–1903. Maps adapted from McLoughlin et al. (2016, fig. 2).
Figure 2. Details of *Podocarpoxylon aparenchymatosum* Gothan (1908), secondary wood anatomy (A–F) and contained terrestrial insect borings (G–M). A. Transverse section of wood showing well-defined growth rings of variable width; NRMS004109-01. B. Tangential longitudinal section of wood showing long tracheids interspersed with uniseriate rays of variable height; NRMS004109-02. C. Tracheids in radial longitudinal section showing biseriate bordered pitting; NRMS004109-04. D. Tracheids in radial longitudinal section showing uniseriate bordered pits; NRMS004109-04. E. Radial longitudinal section of wood showing tall rays with up to 20 cells; NRMS004109-03. F. Radial longitudinal section of wood showing mostly paired cross-field pits with oblique apertures; NRMS004109-04. G. Portion of insect boring infilled with irregular woody frass particles; NRMS004109-04. H. Proximal portion of insect boring showing the sharp transection of secondary wood tracheids along the margin; NRMS004109-03. I. Details of frass composed of coarse blocks of irregularly shaped secondary wood fragments containing well-preserved tracheids; NRMS004109-03. J. Longitudinal section of a frass-filled boring; NRMS004109-04. K. Longitudinal section of a frass-filled boring; NRMS004109-03. L. Longitudinal section of a boring showing meniscate backfilling of frass; NRMS004109-03. M. Weathered surface of wood cross-section showing a pale frass-filled insect boring transecting growth rings; NRMS004109. Scale bars = 1 mm for J, K, M; 500 μm for A, L; 200 μm for G, H; 100 μm for B; 50 μm for C, E, I; 20 μm for D, F.
of the biota living in the adjacent continental environments at that time. Key mammalian groups among the fossils of terrestrial organisms include marsupials (Goin et al. 1999; Reguero et al. 2002), gondwanotheres (Goin et al. 2006), ungulates (Marenssi et al. 1994; Gelfo et al. 2015) and xenarthrans (Davis et al. 2020). Apart from penguins, the fossil avifauna includes falconids, flamingos and other charadriiforms, albatrosses and other procellarids, ducks, gruiforms and pelagornithids (Marenssi et al. 1994; Tambussi & Acosta Hospitaleche 2007; Davis et al. 2020; Acosta Hospitaleche & Reguero 2020). Other fossil remains of likely terrestrial or freshwater origin are frogs (Mörs et al. 2020) and ciliate annelid cocoons (McLoughlin et al. 2016) that, based on spermatozoan morphology (Bomfleur et al. 2015), might be affiliated with brachiobdellids (so-called “crayfish worms”).

Terrestrial plant remains in these Paleocene–Eocene strata include woods and leaves of diverse angiosperms (Dusén 1908; Poole et al. 2000; Tosolini et al. 2013; Friis et al. 2017; Cantrill & Poole 2005), podocarp and araucarian conifers (Gohan 1908; Torres 1990; Francis 1986, 1991; Torres et al. 1994a, 1994b; Poole & Gottwald 2001; Poole et al. 2003, 2005; Francis & Poole 2002; Pujana et al. 2014; Mirabelli et al. 2017) and various ferns (Doktor et al. 1996; Cantrill et al. 2011). In addition, dispersed spore-pollen assemblages have revealed diverse terrestrial floras in the vicinity of Seymour Island during the Paleogene (Askin 1988, 1990, 1997; Zamaloa et al. 1987).

Material and methods

The Swedish Antarctic Expedition (1901–1903) collection contains about 57 specimens of fossil wood from Seymour Island situated at 64°17’S in the Weddell Sea, to the east of the northern tip of the Antarctic Peninsula (Fig. 1A–C). Material was studied in hand specimen and by light microscopy of 93 (transverse, radial longitudinal, and tangential longitudinal) thin sections cut from a selection of 29 blocks of silicified wood. All material is housed in the collections of the Palaeobiology Department, Swedish Museum of Natural History; specimens are prefixed NRMS. Specimens were photographed with an Olympus BX-51 compound transmitted light microscope and an Olympus SZX10 stereomicroscope, each equipped with an Olympus DP-71 digital camera. Microscopic features were measured using cellSens® Dimension version 1.6 (Olympus Soft Imaging Systems; Münster, Germany). For improved clarity of anatomical features, stacking of images from multiple focal planes was undertaken using Adobe Photoshop CC 2019 software.

Results

Fossil wood

Description and remarks. Fossil woods in the collections of the Swedish Antarctic Expedition of 1901–1903 were assigned to various taxa by Gohan (1908): Phyllocladoxylon antarcticum, Podocarpoxylon aparenchymatosum, Dadoxylon pseudoparenchymatosum, Laurinnoxylon uniseriatum, Laurinnoxylon? sp., Notofagoxylon scalariforme and several unidentified forms. One species, Dadoxylon pseudoparenchymatosum, was reassigned to Agathoxylon by Pujana et al. (2014) based on the recent proposal that the latter genus be used for all Araucariaceae-like fossil woods (Rößler et al. 2014). Wood of podocarpacean affinity dominates the assemblage—a characteristic also recognized by subsequent fossil wood collections from the La Meseta Formation (Pujana et al. 2014).

Since the fossil woods have been thoroughly described and illustrated by Gohan (1908) and Oh et al. (2020), and because the molluscan borers and fungal saprotrophs appear not to have favoured any particular wood taxon for occupation, here I provide only the essential anatomical characters of the single wood specimen hosting insect borings. That specimen was the single sample assigned to Podocarpoxylon aparenchymatosum by Gohan (1908) and its palaeoclimatic significance was outlined by Oh et al. (2020). Few additional anatomical details of this species can be added to those outlined by Gohan (1908).

In general features, the arthropod-bored wood is characterized by well-defined growth rings of variable width (11–29 cells wide or 610–1220 μm wide; Fig. 2A). False rings are absent. Rays are uniseriate and are 2–20 cells high (Fig. 2B). Radial walls of tracheids bear uniseriate (Fig. 2D) to biseriate (Fig. 2C) bordered pits. Cross-field pits are usually paired with oblique apertures (Fig. 2E,F).

Insect borings

Description. A single specimen (NRMS004109) of Podocarpoxylon aparenchymatosum Gohan (1908) contains terrestrial insect borings. The borings are cylindrical, straight or gently curved and located within the secondary xylem (Fig. 2M). The borings are orientated variably parallel or oblique to the growth rings. Lateral margins of the borings are parallel and defined by sharply transected cell walls (Fig. 2J–L). Borings are ~ 2 mm wide and >11 mm long. Tunnels are filled entirely by frass consisting of angular fragments of secondary xylem (tracheids) up to 100 × 150 μm (Fig. 2G–I). Frass particles are arranged into poorly ordered and weakly defined meniscate backfill bands (Fig. 2L). The apparently rounded terminus of one boring (Fig. 2J,H) is at the proximal end of the trace and probably represents simply the deviation of the boring direction into the plane of section. Cells surrounding the boring show no signs of fungal decay, but silica-filled fractures are concentrated along portions of the trace margin (Fig. 2J) and locally transect the tunnels (Fig. 2M). Borings do not intersect and there is minimal change in width along the length (Fig. 2J,K) to indicate size increase of the trace maker.

Remarks. These tunnels are markedly smaller than marine bivalve borings, lack wall linings and are characterized by meniscate backfillings of dense frass that are typical of arthropod borings. Boring by arthropods in terrestrial plants and macrofungi has a history extending back to at least the Early Devonian (Labandeira 2002, 2013). Globally, the majority of borings in terrestrial wood through time have been carried out by termites, the larvae of holometabolous insects (especially beetles) and oribatid mites (Labandeira 2002). Borings are particularly well known in Permian and Triassic woods of Antarctica owing to intensive studies of permineralized peats from that region (Weaver et al. 1997; Kellogg & Taylor 2004; Slater et al. 2012, 2015). Such damage occurs in both stem and root wood (Weaver et al. 1997; Slater et al. 2012), includes
pelletized frass, and has been attributed primarily to oribatid mites.

Oribatid mites excavate chambers of variable shape, location and orientation within primary or secondary wood (either following or transecting xylem growth rings) and various other plant tissues (Labandeira et al. 1997; Weaver et al. 1997; Strullu-Derrien et al. 2012; Fletcher & Salisbury 2014). This group dominated much of the early record of wood boring and both ancient and modern forms typically produce small pelletized coprolites that are loosely aggregated within, or locally fill, excavations (Labandeira et al. 1997). Since the Late Triassic, insects (especially Coleoptera and Isopota) have been the dominant borers of terrestrial wood (Labandeira 2006) and it is among these groups that the borer producing damage to the Antarctic Podocarpoxylon wood is likely to belong.

Termites (Isoptera) typically produce complex gallery systems and pelletized frass (polygonal in cross-section) that are not represented in the Antarctic wood. Various other insect groups (e.g. dipters, lepidopterans and hymenopterans) include specialist borers of primary tissues, secondary wood or cambial and bark tissues (Labandeira 2002), but most can be eliminated as the potential producers of the damage to Podocarpoxylon wood based on the architecture and location of the borings, together with the arrangement of frass. The subtle backfill structures in tunnels within the Seymour Island Podocarpoxylon wood are more reminiscent of the patterns produced by boring coleopterans (beetles) than oribatid mites or other insect groups. Xylophagous coleopterans have a fossil record extending back to at least the late Permian (Feng et al. 2017, 2019) and they progressively gained dominance over oribatid mites as the chief wood-feeding terrestrial arthropods around the end of the Triassic (Labandeira 2006).

As there is no reaction tissue developed in response to the wood boring and there is no obvious targeting of cambial tissues, it is unclear whether the tunnels were produced before or after death of the tree. Species of many insect families that live in dead wood feed almost exclusively, preferentially or opportunistically on fungi (Birkemoe et al. 2018)—an association that extends back to the late Palaeozoic (Feng et al. 2017). Obligate or facultative fungivorous insects commonly transfer fungal spores between plants to provide a food source for the offspring. The lack of fungal damage around the immediate area of the borings in Podocarpoxylon wood and the absence of fungal remains in the frass suggests that the borer was primarily xylophagous rather than fungivorous, and that boring took place during the life of the host tree rather than at some post-mortem stage when extensive saprotrophic damage could be expected.

Studies of wood-boring damage from austral landmasses indicate that southern temperate podocarps are vulnerable to xylophagy by several insect groups, especially platypodid and cerambycid beetles (Roughly & Welch 1923; Morgan 1960; Milligan 2009). Elsewhere, the wood and bark of extant podocarps are susceptible to attack by the podocarp bark borer Hirticlytus comossus (Coleoptera: Cerambycidae) (Sato 2005) and black twig borer Xylursosus compactus (Coleoptera: Cercurilionidae) (Tenbrink & Hara 2007). Dead wood of podocarps is known to be attacked by termites and various beetles of the families Ptinidae, Bostrichidae, Curculionidae (notably including Subfamily Platypodinae) and Cerambycidae (Louppe et al. 2008; Paap et al. 2018).

The damage traces produced by the various groups of modern insect borers are not always diagnostic to species, genus or family; however, some general patterns are discernible. Cerambycid (longhorn) beetle larvae commonly produce long, simple chambers that can be either empty or filled with frass (Monné et al. 2017; Haack 2017; Baker 2019). Ptinid (furniture) beetle larvae that tend to produce frass-filled tunnels semi-randomly through wood, excavating a small chamber immediately beneath the wood surface at the time of pupation (Leary 2002; Noldt & Noldt 2013). Bostrichid (auger or powderpost) beetles commonly produce tunnels that wind for several centimetres and are filled with very fine grained, tightly packed frass (Kollmann & Côté 1968; Woodruff & Basulo 2015; Western Australian Department of Primary Industries and Development, Agriculture and Food 2018). Platypodinid (pinhole) beetle borers tend to produce very narrow excavations that are empty and are lined with ambrosia fungi (on which the larvae feed), with frass removed to the exterior of the tunnel (Tilbury 2010; Hadlinton 2001). Curculionid (Scolytinae) bark beetle borers commonly produce complex parallel, radiating or meandering borings, especially in phloem and cambial tissues. Frass from these tunnels is typically removed to the exterior except where it may be used to block entrances (Kirkendall et al. 2015). Larvae of buprestid (jewel or metallic wood-boring) beetles are also known to attack a range of conifers, especially damaging weakened, injured or dead trees (Drooz 1985). Larvae of this group typically produce meandering tunnels, oval in cross-section and packed with dense frass, in the bark, cambium or secondary wood. The tunnels generally terminate in elongate pupal chambers connected to the surface by short exit holes.

No remains of the arthropod excavator are present in the borings within P. aparenchymatous wood. Nevertheless, the lack of pellet-like coprolites or production of distinctive brood chambers argues against production by oribatid mites (Labandeira et al. 1997; Feng et al. 2015), termites (Rozefelds & De Baar 1991) or ancient (Palaeozoic) beetle groups (Feng et al. 2019). The simplicity of the tunnels, absence of fungal remains or degradation along the tunnel walls, and backfilling of the excavations with tracheidal debris does not favour production by platypodinid, curculionid or bostrichid beetles. The roughly circular cross-sections and relatively straight course do not favor excavation by buprestid beetle larvae. Cerambycid or ptinid coleopterans are the strongest candidates to have produced these tunnels. Each group has a fossil record extending back to at least the Early Cretaceous (Zahradník & Háva 2014; Wang et al. 2014) and both are known to attack modern podocarps.

**Fungal and bacterial damage**

**Description**

Various forms of partial tissue degradation are evident in several fossil conifer and angiosperm wood specimens from Seymour Island. Some woods host densely spaced, longitudinally aligned spindle-shaped pockets (cavities) of decay within
the secondary xylem (Fig. 3A). The pockets are 0.5–14 mm long and 0.2–4 mm wide.

Other woods have irregular zones of degradation restricted to the heartwood (Fig. 3B). In these cases, degraded zones are left as hollows in the wood, but scattered ellipsoidal patches of non-degraded tissue may be retained within this zone.

At least one conifer wood contains elliptical (in cross-section) zones of strongly darkened and partially degraded secondary xylem tracheids (Fig. 3D). These zones span one or more growth rings and are not restricted to a consistent position within the wood. Cell walls in these zones appear to be strongly coated by, or embedded with, iron oxides and wall structure is poorly preserved.

The single wood specimen hosting insect borings also contains discrete zones of degraded wood that are restricted to the latewood of successive growth rings (Fig. 3E). These zones consist of semicircular to irregular pockets up to 2.5 mm thick and 7 mm wide containing void space and degraded remnants of secondary xylem (Fig. 3E). The pockets terminate sharply against the earlywood of the succeeding growth ring. A few cells

Figure 3. Fungal damage in fossil wood. A. Longitudinal view of spindle-shaped pocket rot in unidentified conifer wood; NRMS004111. B. Longitudinal view of rot with remnant ellipsoid segments in the heartwood of an unidentified conifer; NRMS004116. C. Nothofagoxylon scalariforme Gothan (1908), wood with opaque spherules reminiscent of bacterial clots clustered in vessels and fibres; NRMS004067-01. D. Transverse section of Agathoxylon pseudoparenchymatum (Gothan) Pujana et al. (2014), showing darkened elliptical zone of fungal or bacterial degradation; NRMS004052-02. E. Transverse section of Podocarpoxylon aparenchymatum (Gothan) (1908), wood showing zones of pocket rot along consecutive growth rings; NRMS004109. F. Transverse section of tracheids in secondary wood of P. aparenchymatum showing spherical bodies possibly representing fungal reproductive bodies; NRMS004109-05. Scale bars = 10 mm in A, B; 1 mm in E; 500 µm in D; 50 µm in C; 20 µm in F.
in the normal xylem tissue neighbouring these degraded pockets contain smooth-walled spherical bodies up to 25 μm in diameter attached to the inner surface of the cell wall (Fig. 3F).

Several woods of various species in the collection contain distinctive patches of minute spheroidal or otherwise granular opaque material. These are commonly concentrated in larger (earlywood) tracheids and vessel elements (Fig. 3C), but a few also occur in small-diameter fibres and parenchyma cells. These granules do not form recognizable filaments or other structures, but are typically coalesced into dense aggregations.

Remarks. Spindle-shaped partially or fully degraded zones in the Seymour Island woods (Fig. 3A, D, E) are reminiscent of stages in the development of white pocket rot – a common damage type in woods from the late Palaeozoic to present (Taylor et al. 2015; Tanner & Lucas 2013) and produced by various arboricormycete (Basidiomycota) fungal taxa (Stokland 2012). White rots occur widely in both conifer and angiosperm woods in modern forests (Taylor et al. 2015). Similar decay features reminiscent of white pocket rot have been reported previously from Eocene strata of both Seymour Island (Francis 1986, pl. 51, Figs. 2, 5; Torres et al. 1994a, fig. 4.1) and Patagonia (Pujana et al. 2009, fig. 4)—regions that was probably contiguous during the Paleogene. Neogene podocarpacean wood from northern Argentina also contains pocket-like and more irregular zones of fungal degradation arranged along growth-ring boundaries (Franco & Brea 2015, fig. 2A, C). Similar cavities attributed to white pocket rot, some retaining internal fungal hyphae, also have been reported from Lower Cretaceous marine strata elsewhere in the Southern Hemisphere (McLoughlin et al. 1995; McLoughlin & McNamara 2001), suggesting that even delicate terrestrial fungi can survive transport into marine settings and become fossilized if the permineralization process is sufficiently rapid.

The hollow spherical bodies in xylem cells adjacent to zones of degradation (Fig. 3F) might represent fungal reproductive bodies. Nishida et al. (1989) noted similar features in mid-Cenozoic angiosperm woods from southern Chile. Relatively featureless ~ 10–25 μm spherical bodies in the form of spores, oogonia and other reproductive structures are produced by a broad range of fungi and fungi-like organisms including Chitridiomyctota, Zygomycota, Glomeromyctota, Ascomycota, Basidiomycota and Peronosporomycetes (compare with Dennis 1970, figs 1–10; Krings et al. 2010, figs 1–5; McLoughlin & Strullu-Derrien 2016, fig. 6; Taylor et al. 2015, figs 4.37, 4.41, 6.12, 7.20). Alternatively, these structures might constitute tyloses, which are commonly produced in response to a range of environmental stimuli including water stress and defence against pathogens (Aist 1976; Weaver et al. 1997; Harper et al. 2012; Feng et al. 2013). Significantly, xylem cell walls around these putative fungal bodies are strongly darkened and this condition might represent a response to pathogens via thickening of the wall lignin. Indistinct linear features <2 μm in diameter in cell lumina associated with the spherical bodies (Fig. 3F) appear to be too small to constitute fungal hyphae (compare with branched septate hyphae secondary xylem cells in araucarian wood from the Paleocene Cross Valley Formation: Pujana et al. 2015, pl. 1, fig. 3) and may represent partial wall delamination features.

Heartwood decay (Fig. 3B) is a common feature of mature trees and can be produced by various fungi and bacteria, commonly in combination (Johnston et al. 2016; Singh et al. 2016), but it is especially a feature of deuteromycyte stem-canker fungi or basidiomycete white-rot fungi (Genise et al. 2012). Delicate primary tissues in the centre of the stem are initially attacked. Decay then expands into the surrounding secondary wood in an irregular fashion commonly leaving behind bulbous ellipsoidal or blocky patches of relatively unaffected wood. In ancient woods, such damage is typically assigned to the trace fossil Astenopodichium lignorum (Genise 2004; Genise et al. 2012; Mathur et al. 2018).

The densely clustered opaque granules in secondary xylem cell lumina (Fig. 3C) are similar to bacterial clots recorded in some extant plants (Mollenhauer & Hopkins 1974). It is possible that the opaque granules are simply aggregated mineral precipitates forming biomimetic structures (see, e.g. Klymiuk et al. 2013), but some form of bacterial degradation would be expected in most dead woods.

Molluscan borings

Bivalve borings represented by sediment-filled excavations in wood are abundant in the studied assemblage. About half the specimens of wood in the collection lack any indication of marine borers (online supporting data Table 1), but these are mostly small fragments that potentially are derived from larger woods that contained borings. Although the borings vary greatly in size and shape, two morphotypes are broadly discernible on the basis of dimensions, termination form and linings. One is typically short and club shaped, whereas the other is long, sinuous and commonly has a calcareous lining. Traditionally, such borings in wood have been ascribed to Teredolites clavatus Leymerie (1842) and Teredolites longissimus Kelly and Bromley (1984), respectively. However, Donovan (2018) and Donovan & Ewin (2018) have argued that substrate is a poor ichnotaxon, pointing out that essentially identical traces are produced (by several bivalve taxa) in wood, rock and shelly materials. Moreover, Donovan (2018) argued that the two ichnospecies are markedly dissimilar in form. On this basis, Donovan (2018) established a new ichnospecies, Apectoichnus, with “T.” longissimus as the type, for elongate, smooth-sided, sinuous to contorted and intertwined borings, commonly circular in section, either possessing or lacking a calcareous lining. Donovan & Ewin (2018) transferred the type species of Teredolites, T. clavatus, to Gastrochaenolites Leymerie (1842), which had been used previously for clavate borings in rocky or shelly substrates. The merit of segregating borings in wood versus in rock or shelly material into separate ichnotaxa is likely to be a topic of continuing debate. Foremost among considerations is that a distinctive trace fossil association (the “Teredolites ichnofacies”) is recognized on the basis of borings in submerged woody substrates (Bromley et al. 1984), and that some wood-boring organisms actively consume the plant tissues for nutrition (the traces representing a type of fodenichnia) rather than using the excavations solely as dwelling structures (domichnia).

Borings traditionally attributed to Teredolites (now Gastrochaenolites and Apectoichnus) have been reported
Figure 4. Marine bivalve borings in Eocene woods from Seymour Island. A–D. Gastrochaenolites clavatus (Leymerie 1842); E–J. Apectoichnus longissimus (Kelly & Bromley 1984). A. Large-diameter, sand-filled excavation in Agathoxylon pseudoparenchymatosum (Gothan) Pujana et al. (2014), wood; NRMS004107. B. Large-diameter borings in A. pseudoparenchymatosum wood; NRMS004113. C. Large, clavate, sand-filled borings, one (lower right) with growth increment impressions from interior of original pholadid bivalve shell, in A. pseudoparenchymatosum wood; NRMS004107. D. Densely clustered, unlined, sand-filled borings in an unidentified angiosperm wood; NRMS004110. E. Borings both cross-cutting and following the orientation of the secondary xylem tracheids in an unidentified conifer wood; NRMS004097. F. A single clavate mud-filled boring extracted from fossil wood; NRMS004088. G. Clavate, carbonate-lined boring cross-cutting the grain of Nothofagoxylon scalariforme Gothan (1908), wood; NRMS004053. H. Fractured valves of a teredinid bivalve preserved in a Apectoichnus longissimus boring that transects the grain of N. scalariforme wood; NRMS004053. I. Cross-section of a portion of a sand- and mud-filled Apectoichnus longissimus boring with a carbonate lining that transects the primary and secondary wood of A. parenchymatosum; NRMS004112-01. J. A mass of Apectoichnus longissimus borings in cross-section, some containing teredinid bivalve shells, preserved in N. scalariforme wood; NRMS004067. Scale bars = 10 mm for A–G, 1 mm for H, J, 500 µm for I.
widely from Cretaceous and Cenozoic strata of the Antarctic Peninsula region (Kelly 1988; Wiedman & Feldmann 1988; Pirrie et al. 1998; Césari et al. 2001; Ivany et al. 2008; Mirabelli et al. 2017), and in correlative strata across the Southern Hemisphere (e.g. Bradshaw 1980; Lindqvist 1986; Urreta 1987; McLoughlin et al. 1995; McLoughlin 1996; Kumar et al. 2011; Wild & Stilwell 2016; Cooper 2018). Borings in wood definitively recovered from the Sobral, Cross Valley and La Meseta formations by other workers have also been assigned to G. clavatus and A. longissimus, and their structure is relatively well understood (Kelly & Bromley 1984; Bromley et al. 1984; Kelly 1988). Consequently, the molluscan borings in the studied woods are only described briefly to supplement previous treatments of these ichnotaxa from the region.

Gastrochaenolites clavatus (Leymerie 1842)

Description. Large-diameter, but relatively short clavate borings in wood (Fig. 4A–D). They are circular to elliptical in cross-section (Fig. 4B,D) with maximum diameters in the range of 10–58 mm, and lengths generally <82 mm (Fig. 4A,C). The borings are filled by fine quartzose and glauconitic sand with a clay matrix. No calcareous lining was discernible around the borings. The margins of borings sharply truncate the wood texture. Borings may be either perpendicular (most common) or parallel to the wood grain. One specimen bears a sand-filled body cast of the bivalve tracemaker exposed on the eroded surface of the wood (Fig. 4C—lowermost right). The cast is roughly spindle shaped, with its long axis in the direction of the wood grain, and concentric growth increment traces of the shell are evident on the cast surface.

Remarks. These borings are attributable to Gastrochaenolites clavatus based on their large size, proportionately short clavate shape and lack of a distinct wall lining (Kelly 1988). The large bivalve body cast retained in one boring appears to be consistent in shape with pholadid bivalves (especially Martesia species) reported as body fossils from Cretaceous and Cenozoic strata elsewhere in the Antarctic Peninsula region (Kelly & Bromley 1984). Wood-boring pholadid bivalves, such as Martesia and Xylophaga, commonly have lacriform or flabellate shell forms in contrast to strongly sculptured, triangular and markedly curved valves of teredinid bivalves. The latter also produce a calcarous lining to the tunnel and two calcarous plates (pallets) that protect the elongate siphons (Turner 1966).

Apectoichnus longissimus (Kelly & Bromley 1984)

Description. Borings that vary greatly in shape depending on their size and position within the host wood (Fig. 4E–J). Many follow the wood grain and some are tightly contorted (Fig. 4E). All are ~1 mm in diameter at the exterior end of the boring and reach up to 10 mm in diameter near the position of the contained shell (interior terminus). Borings are circular, or less commonly elliptical to ovate, in cross-section (Fig. 4J). Borings are rimmed by a ~100 µm thick carbonate lining (Fig. 4G,I,J), probably representing remnants of the siphonoplax. Borings gently enlarge away from the entrance and have a rounded terminus (Fig. 4F,G). The chamber is filled by fine quartzose and glauconitic sand, with a clay matrix and a cement of silica and opaque iron oxides (Fig. 4I). Many of the borings contain shells of the tracemaker. These are commonly seen as cardioform cross-sections of articulated valves (Fig. 4I). Large borings commonly bear parallel-sided transverse striae (xyloglyphs) near the inner terminus. In a few cases, fracture surfaces through the wood expose surface details of the enclosed shells. These shells have a longitudinally plicate ornamentation (Fig. 4H) and fill the entire width of the boring. The shells enclose a globose body chamber now filled with sediment or sparry calcite (Fig. 4I).

Remarks. Apectoichnus longissimus traces are more slender (L.W ratio generally >5) than G. clavatus (L.W ratio <5) (Kelly & Bromley 1984), although there is some dimensional overlap between these ichnotaxa as recognized in previous studies (Kelly 1988; McLoughlin et al. 1995). Nevertheless, segregation of the ichnotaxa is useful since short, broad borings are commonly produced by filter feeders, whereas long borings are commonly produced by wood-digesting molluscan taxa.

Apectoichnus longissimus borings are much larger than the insect-generated traces in the same wood assemblage. The former also have more regular shapes and sharper boundaries than fungal decay pockets. Apectoichnus longissimus occurs in several wood types attributable to both conifers and angiosperms (Online supporting data Table 1). These borings are produced by various bivalves, although those studied here appear to have been excavated by teredinids based on the short, triangular, plicate-ornamented and markedly curved shells forming a globose body chamber (Kelly 1988). The apparent siphonoplax forming a carbonate lining to the boring also denotes a teredinid tracemaker.

Those marine bivalves targeting plants can develop borings in both driftwood and fixed submarine woody substrates. Such borings are particularly common where driftwood or submerged woody substrates are concentrated, especially in the condensed sections of transgressive systems tracts (Savrda et al. 2005). During rising sea levels, influxes of wood into marine settings result from the drowning of coastal plain vegetation and erosional exposure of existing woody substrates (e.g. peat deposits). Moreover, starvation of clastic sediment supply to the outer shelf during rising sea levels means that submerged driftwood accumulates in greater relative concentrations in neritic sediments than at other times. Consequently dense accumulations of contiguous xylic substrates and isolated driftwood (both typically hosting marine invertebrate borings) are named “wood-grounds” and “log-grounds”, respectively (Bromley et al. 1984; Savrda 1991). Paleogene beds on Seymour Island that are especially rich in fossils of terrestrial organisms, including wood, likely represent intervals of starved sediment supply during transgressive or highstand marine episodes.

Discussion

The Paleogene forests of the northern Antarctic Peninsula grew under a strongly seasonal climate at ~68°S palaeolatitude (Carter et al. 2017). Nevertheless, they incorporated a moderately diverse range of plants dominated by podocarp and araucarian conifers, and nothofagacean, lauracean and cunoniacean angiosperms (Gandolfo et al. 1998a, 1998b; McDonald et al. 2007). Such forests have been likened to the
modern Valdivian rainforests and Magellanic subpolar forests of southern South America (Torres et al. 1994a, b; Poole et al. 2003). Only a few studies have been undertaken on xylophagy in these South American temperate forests to facilitate meaningful comparisons with the borings in Podocarpoxylon wood from Antarctica but Cerambycidae are by far the dominant group (in terms of diversity) of wood- and root-feeding insects on the dominant Nothofagus species in these forests (Veblen et al. 1996). Globally, few studies have specifically surveyed extant podocarps for herbivory patterns. Nevertheless, several incidental reports have noted a range of insects feeding on modern podocarps. These include foliar herbivory by aphids (Miller & Halbert 2014), scale insects (Miller & Davidson 2005), sawflies and lepidopteran larvae (Forestry Department, Food and Agriculture Organization of the United Nations 2007; Graziosi et al. 2019), together with damage by bacterial and fungal blight (Erwinia amylovora and Pestalotiopsis podocarpi: Department of Agriculture, State of Hawai‘i 2019). Although modern podocarp axes are attacked by borers of the families Ptinidae, Bostrichidae, Platypodinae, Curculionidae and Cerambycidae (Louppe et al. 2008; Paap et al. 2018), the traces left by cerambycids and ptinids most closely match the borings preserved in the Seymour Island woods.

The wood-borings in this study add to the known diversity of continental invertebrates that inhabited the high-palaolatitude Paleogene forests of the Antarctic Peninsula. Since terrestrial insect body fossils are scarce, trace fossils provide some of the best evidence of this group in the geological record of this region (McDonald et al. 2007). Indeed, modes of exceptional preservation, such as entombment in leech cocoon walls (Bomfleur et al. 2015; McLoughlin et al. 2016), permineralizations (Poole et al. 2003; Pujana et al. 2014, 2015; Harper et al. 2016; Mirabelli et al. 2017) and trace fossils (McDonald et al. 2007) appear to provide the only evidence of terrestrial invertebrates and fungi from the Paleogene of the Antarctic Peninsula.

A survey of over 2000 Eocene leaves from the Antarctic Peninsula region by McDonald et al. (2007) revealed about 3.3% of specimens with insect-foliation interactions including margin feeding, hole feeding, skeletonization, leaf mining and galling. To this dataset, xylophagy can now be added, along with fungal saprotrophism. Together with fossils of several land mammals and amphibians, these collective results reveal that Antarctic terrestrial environments hosted complex trophic systems similar to, although possibly of lower diversity than, coeval forest communities represented in high temperate latitudes on adjacent landmasses, such as South America (Wilf et al. 2005) and Australia (Rozefelds 1988; Carpenter et al. 1994). The separation of Antarctica from Australia and South America, the establishment of the south circumpolar current, and intensification of polar glaciation around the end of the Eocene, undoubtedly contributed to a collapse of terrestrial ecosystems, a significant regional extinction of plants and their dependant animals, and a sundering of biotic interchange among the southern continents.

Acknowledgments

Financial support from the Swedish Research Council (VR) grant 2018-04527 to the author is gratefully acknowledged. Stephen Donovan and Conrad Labandeira are thanked for their constructive reviews of the manuscript.

Disclosure statement

No potential conflict of interest was reported by the author.

Funding

This work was supported by the Vetenskapssrådet [2018-04527].

ORCID

Stephen McLoughlin http://orcid.org/0000-0001-6723-239X

References


Cantrell, D.J., Tosolini, A.-M.P. & Francis, J.E., 2011: Paleocene flora from Seymour Island, Antarctica: revision of Dusén’s (1908) pteridophyte


