A new marine woodground ichnotaxon from the Lower Cretaceous Mannville Group, Saskatchewan, Canada

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Abstract.—A new wood-boring ichnospecies is described from transgressive (lagoonal) deposits of the Lower Cretaceous Sparky Formation (Mannville Group) in west-central Saskatchewan, Canada. *Apectoichnus lignummasticans* new ichnospecies is a trace fossil that occurs in a thin coal bed and that was emplaced in an in situ xylic substratum (woodground). The ichnofossil is thin, elongate, unbranched, and straight to gently curved with a circular cross section and uniform diameter. *Apectoichnus lignummasticans* n. isp. is similar in many respects to modern borings in wood that are produced by marine isopods, e.g., *Limnoria lignorum* Rathke, 1799, for feeding and refugia. The recognition of *Apectoichnus lignummasticans* n. isp. in the rock record aligns with the modern observation that fossilized wood-boring assemblages should display higher ichnofossil diversities than commonly reported. Additionally, the stratigraphic occurrence of *Apectoichnus lignummasticans* n. isp. in association with other evidence of marine deposition reaffirms that certain wood boring morphologies (i.e., ichnotaxa) are useful as indicators of marine transgressions.

UUID: http://zoobank.org/880e722f-8944-42d7-bc38-423cc5a46413

Introduction

Woodground ichnofossils show a range of morphologies that reflect a variety of living strategies. The diversity of these strategies is more apparent in modern than in fossil ichnocoenoses. Fossil suites from marginal marine environments are exemplified by clasts and surfaces that exhibit putative bivalve borings (e.g., Kelly and Bromley, 1984; Plint and Pickerill, 1985; Savrda and King, 1993; Savrda et al., 1993; Mikuláš et al., 1995; Pirrie et al., 1998; Pickerill et al., 2003). Modern intertidal settings can show additional borings into the xylic substrata, including those of shrimp, isopods, barnacles, and even sponges (Gingras et al., 2004). The bivalve borings, referable to *Apectoichnus longissimus* (Kelly and Bromley, 1984) and *Teredolites clavatus* Leymerie, 1842, are almost exclusively associated with woody substrata and marginal to shallow marine environments (Bromley et al., 1984; Kiteley and Field, 1984; Savrda, 1991; Savrda et al., 1993; Pirrie et al., 1998; Pickerill et al., 2003; Mayoral et al., 2020; among others). However, Shipway et al. (2019) described a new freshwater species of teredinid bivalve that bores into carbonate substrata. *Apectoichnus* Donovan, 2018 and *Teredolites* Leymerie, 1842 are each characterized as elongate tunnels with approximately circular cross sections, but *Teredolites* differs from *Apectoichnus* in its overall turbinate morphology (Leymerie, 1842; Kelly and Bromley, 1984; Pickerill et al., 2003; Donovan, 2018).

Geologic setting

*Apectoichnus lignummasticans* new ichnospecies occurs within the Lower Cretaceous (early Albian stage) Sparky Formation of the Mannville Group in the Western Canadian Sedimentary Basin. The Mannville Group was deposited during an overall transgression of the Boreal Sea. The Sparky Formation has bounding discontinuities that correspond to marine flooding surfaces, which separate it from the underlying General Petroleum and overlying Waseca formations (Morshedian et al., 2012; Fig. 1). The trace fossils were present in a wood clast in a coal bed within a cored well bore from west-central Saskatchewan. The coal bed in which *Apectoichnus lignummasticans* n. isp. was found was truncated during a marine incursion and is demarcated by a transgressive surface of erosion. Locally bioturbated, shallow-marine sandstone and mudstone units overlie the bored surface (Fig. 1).

Materials and methods

Specimens.—The specimens were observed in a core from a wellbore near Bushy Lake, west-central Saskatchewan, Canada (Fig. 1). Two samples, UAI 0179 (Fig. 2.1, 2.3) and 0180 (Figs. 2.2, 3), comprise a single piece of gregariously bored wood that is 98 x 67 x 15 mm at its maximum. The trace fossils occurred within the Lower Cretaceous Mannville Group (Sparky Formation) in association with a transgressive surface of marine erosion.

Computed tomography scan analysis.—Computed Tomography (CT) is a nondestructive method whereby X-rays are directed through a rotating sample. X-ray attenuation that occurs at each angle is recorded and used for tomographic reconstruction (see Wildenschild and Sheppard, 2013 for detailed discussion). Previous studies have used similar techniques quite effectively.
in analyzing various bioerosion features (e.g., Beuck et al., 2007, 2008; Schönberg and Shields, 2008; Tapanila, 2008). CT scanning is particularly suitable for substrata with empty borings due to the low attenuation of the tunnels relative to the substratum. This results in images with burrows that are easy to visualize and can be analyzed spatially across multiple dimensions. Although the specimens cannot be viewed directly in full relief, Micro-CT imaging allows observation of additional detail, trace morphology, and overall trace length.

Repositories and institutional abbreviations.—Specimens examined in this study are housed in the Ichnology Research Group Trace Fossil Collection in the Department of Earth and Atmospheric Sciences, University of Alberta (UAI), Alberta, Canada. BM(NH) = The Natural History Museum, London.

Systematic ichnology

Borehole excavation in different substrata requires different behaviors and abilities (e.g., Dorgan, 2015). Thus, although ichnotaxa differ markedly from biological taxa, no paleontological, paleoecological, or taphonomic goal is achieved by lumping together traces excavated in lithic, osteic, and xylic substrata. This view was contested by Donovan and Ewin (2018), who considered *Teredolites clavatus* (xylic substratum) and *Gastrochaenolites turbinatus* Kelly and Bromley, 1984 (lithic substratum) to be synonyms because they are morphologically comparable. For the reasons discussed above, we consider substratum to be useful in taxonomic differentiation and advocate retaining both ichnotaxa (see also Zonneveld et al., 2015; Wisshak et al., 2019).

Ichnogenus *Apectoichnus* Donovan, 2018

Type ichnospecies.—*Teredolites longissimus* Kelly and Bromley, 1984.

Emended diagnosis.—Elongate borings in xylic substrata and associated resins, nearly circular in cross section, with an approximately constant diameter. Borings are straight to sinuous or contorted and intertwined and predominantly occur parallel to the fibers of xylic substrata (modified from Donovan, 2018; Mayoral et al., 2020).

Remarks.—Kelly and Bromley (1984) proposed *Teredolites longissimus* as a new ichnospecies commonly associated with boring bivalves. This combination was recently challenged by Donovan (2018) who proposed the ichnogenus *Apectoichnus* to describe wood borings that lack the clavate morphology of *Teredolites clavatus*. Donovan (2018) retained the species-level taxonomy of *Apectoichnus longissimus* and thus, prior to the present work, *Apectoichnus* has been a monospecific ichnogenus. Subsequent contributions have validated the ichnotaxon *Apectoichnus* (e.g., Donovan and Ewin, 2018; Donovan and Portell, 2019; Wisshak et al., 2019). Mayoral et al. (2020) revised the diagnosis of *Apectoichnus* to include amber and other solid resins as possible host substrata. We further emend the genus-level diagnosis to recognize that the trace fossils are generally aligned wood fiber-parallel, which was previously considered diagnostic at the ichnospecies level (Mayoral et al., 2020).
Apectoichnus longissimus (Kelly and Bromley, 1984)

**Holotype.**—BM(NH) Bensted Collection 38019, Kentish Rag, Lower Cretaceous (Aptian stage), Hythe, Kent, England, UK (Kelly and Bromley, 1984, figs. 9B, 11A, B).

**Emended Diagnosis.**—Apectoichnus with large (> 2 mm) diameter and relatively small length-to-width ratio.

**Remarks.**—Previous ichnospecific ichnotaxobases include length-to-width ratios > 5 and a tendency for the borings to

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Figure 2. *Apectoichnus lignummasticans* n. isp. assemblage in fossil wood: (1) sample UAI 079 (arrow indicates holotype); (2) Sample UAI 080; (3) close-up of UAI 079 showing the holotype and surrounding forms. Scale bars show 1 mm divisions.
align parallel to the wood fibers (see Mayoral et al., 2020). These characteristics are observed in the nonmolluscan borings examined herein and are therefore considered diagnostic at the ichnogenus level.

*Apectoichnus lignummasticans* new ichnospecies

*Holotype.*—UAI 0179 (Fig. 2.1, 2.3).

*Diagnosis.*—Straight to gently curved *Apectoichnus* with small (< 2 mm) diameter and relatively large (usually > 10) length-to-width ratio.

*Occurrence.*—Lower Cretaceous (early Albian stage) Mannville Group (Sparky Formation), near Bushy Lake, west-central Saskatchewan, Canada (Dominion Land Survey 16-15-44-20W3M; 52°47′45.0″N, 108°48′55.6″W [NAD83]; 630.0 m depth).

*Description.*—The holotype and associated borings comprise an assemblage of *Apectoichnus lignummasticans* n. isp. emplaced in fossil wood. The gently curved holotype is displayed in the elevation view of sample UAI 0179 (Fig. 2.1, 2.3). It has a preserved length of 22.8 mm, which is the longest of the assemblage, and a diameter of 0.9 mm (length-to-width ratio ∼25). An additional 20 borings were measured. Although the specimens cannot be viewed directly in full relief, Micro-CT imaging allows observation of additional detail, trace morphology, and overall trace length (Fig. 3). The preserved lengths vary considerably, averaging ∼12 mm. The
assemblage displays a range in diameter from 0.4–1.2 mm (mean = 0.9 mm, N = 21). The length-to-width ratio ranges from 7–38 (mean = 15, N = 21); 17 of the ratios are between 10 and 25.

*Etymology.*—The species name is derived from the Latin *lignum masticando* (‘wood chew’).

*Remarks.*—Although size alone is not normally an ichnotaxonomic character, the small diameters of *Apectoichnus lignummasticans* n. isp., paired with large length to width ratios, make it readily discernible from *Apectoichnus longissimus*. The small diameters and the large length-to-width ratios of *Apectoichnus lignummasticans* n. isp. are not ascribable to the teredinid bivalves that made *Apectoichnus longissimus*. The absence of radial bioglyphs that are sometimes associated with teredinid borings, and the lack of space available for calcareous boring linings or anterior caps further suggest a nonbivalve trace maker. The morphology of the structure is more consistent with mobile wood-boring marine arthropods (e.g., isopods, discussed below).

**Discussion**

Above we ascribe the occurrence of *Apectoichnus lignummasticans* n. isp. to marine and marginal-marine animals, owing to its similarity to borings made by the extant limnoid isopod genus.

*Figure 4.* Extant *Limnoria lignorum* borings: (1, 2) teredinid-bored wood with *Limnoria lignorum* borings on the exterior (note that the borings generally follow the grain of the wood); (3) example of branching *Limnoria lignorum* borings. Scale bars = 1 cm.
limiting salinity for boring activity varies inversely with water temperature and ceases altogether in salinities < 10 ppt (Eltringham, 1961); the optimal salinity at 20°C ranges from 30–34 ppt (Borges et al., 2009). The amount of boring activity could also be directly related to dissolved oxygen content and is significantly reduced at levels < 3.0 ppm (Anderson and Reish, 1967).

The presence of bored woodgrounds in the rock record is associated with transgressive coastal settings (Panos and Skacel, 1966; Bromley et al., 1984; Savrda, 1991; Shanley et al., 1992; Savrda et al., 1993; Gingras et al., 2004). Indeed, the colonization of in situ woodgrounds by marginal marine and marine organisms requires a rise in relative sea level (e.g., Gingras et al., 2004). Importantly, Limnoria can survive for only ~24 hours without water and thus commonly inhabits the intertidal zone (Menzies, 1957); populations are generally highest at low-tide levels where log-ground and woodground substrata are readily available.

### Table 1. Summary of formally recognized ichnospecies associated with wood substrata. *Type ichnospecies.*

| Ichnospecies                      | Inferred tracemaker | Diagnosis/description                                                                 |
|-----------------------------------|---------------------|---------------------------------------------------------------------------------------|
| **Continental woodground ichnospecies** |                     |                                                                                       |
| Asthenopodia (L. lignorum)        | Family Pinidae      | 1–1.5 mm wide; smooth cylindrical tunnels with circular cross sections               |
| Asthenopodia (L. tripunctata)     | Family Gammeridea (scud) | U-shaped sprints or pouch-like tunnels of 1.5–3 mm diameter; aligned perpendicular to substratum and penetrating wood to 20 mm |
| Asthenopodia (L. quadripunctata)  | Kingdom Fungi       | Shallow, elongate, lensoid to almond-shaped scoops; oriented parallel to wood grain; commonly occurring in clusters |
| Asthenopodia (L. lignorum)        | Family Kalotermitidae (drywood termite) | Boxwork of anastomosed longitudinal borings; interconnected by short tangential tunnels; lacking outer layer but filled with hexagonal fecal pellets |
| Glochidion (L. lignorum)          | Class Insecta       | 2–4 mm wide, smooth, unbranched, slightly kink-bent, cylindrical borings with circular cross sections and hemispherical terminations; aligned perpendicular to wood grain; fill massive |
| Paleobuprestis (L. lignorum)      | Family Buprestidae (jewel beetle) | 10 mm wide channels occurring just under bark and aligned perpendicular to wood grain; cuttings visible; borings filled with castings |
| Paleobuprestis (L. tripunctata)   | Family Buprestidae (jewel beetle) | 2 mm wide channels aligned perpendicular to wood grain; variably filled with castings |
| Paleobuprestis (L. quadripunctata) | Family Buprestidae (jewel beetle) | Straight to gently curved, shallow, narrow, randomly oriented channels of 2–4 mm diameter; unfilled |
| Paleoiodius (L. lignorum)         | Subfamily Scolytinae (bark beetle) | 5 mm wide tunnels with square to rectangular outlines and oval cross sections, each with one flat side; penetrating deep into wood; unfilled |
| Paleoiodius (L. tripunctata)      | Subfamily Scolytinae (bark beetle) | 2–3 mm wide tunnels with oval cross sections; filled with castings |
| Paleoiodius (L. quadripunctata)   | Subfamily Scolytinae (bark beetle) | 5 mm wide channels occurring just under bark, lacking preferred orientation; lacking cuttings and castings |
| Pecinolites (L. lignorum)         | None                | Large, straight to gently curved, tubular borings with reasonably constant diameters, finger-like terminations, and rare branching at 60–90°; unfilled |
| Scolytolarvarium (L. lignorum)    | Subfamily Scolytinae (bark beetle) | 1.5 mm wide borings diverging from central chamber; apparently filled with cuttings and castings |
| Scolytolarvarium (L. tripunctata) | Subfamily Scolytinae (bark beetle) | Subround plate with longitudinal-cylindrical mater tunnel with foveae on both sides and radiating larval tunnels |
| Scolytolarvarium (L. quadripunctata) | Subfamily Scolytinae (bark beetle) | Strongly entangled galleries, at least 13 mm wide, branching from parent gallery; unfilled |
| Stipitichnus (L. lignorum)        | Rhinostomus barbriostris | Unbranched longitudinal borings with circular cross sections; lacking outer layer; unfilled |
| Xylotrechus (L. lignorum)         | Fabricius, 1775 (bearded weevil) | Kidney-shaped borings with apertures oriented perpendicular to wood surface |
| Xylocreus (L. lignorum)           | Suborder Archostomatata |           |
| Xylonichus (L. lignorum)          | Family Buprestidae (jewel beetle) | Longitudinal borings with rectangular cross sections and rounded corners (height: width = 1:4); interconnected by tangential tunnels; with outer layer and filled with frass, or with meniscus structure |
| Xylonichus (L. tripunctata)       | Family Cerambycidae (longhorn beetle) | Longitudinal borings with oval cross sections (height:width = 1:3); interconnected by tangential tunnels, with radial tunnels of different sizes connecting to exterior; containing frass that is sometimes packed in backfill meniscae |
| Iptes (L. lignorum)               | Genus Iptes De Geer, 1775 (bark beetle; engraver beetle) | Regularly branched borings with larger central tunnel and smaller radiating tunnels; aligned parallel to substratum |
| **Marine woodground ichnospecies** |                     |                                                                                       |
| Apectoichnus (L. lignummaticans)  | Family Teredinidae (shipworm) | Elongate, curved to contorted borings with circular cross sections and relatively constant diameter |
| Apectoichnus (L. lignummaticans)  | Family Limnoriidae (grille) | Small, straight to gently curved borings with circular cross sections and uniform diameter |
| Teredoites (L. lignummaticans)    | Family Pholadidae (piddock) | Clavate borings with more or less circular cross sections, evenly tapered from aperture to base |

**Limnoria Rathke, 1799** (Fig. 4). Nevertheless, it is worth emphasizing that *Apectoichnus lignummaticans* n. isp. is morphologically different from terrestrial wood-boring ichnofossils (Table 1). The most common wood-boring species of *Limnoria* are *L. lignum* Rathke, 1799, *L. tripunctata* Menzies, 1951, and *L. quadripunctata* Holthuis, 1949 (e.g., Menzies and Turner, 1957; Jones, 1963; Borges et al., 2014). *Limnoria lignum* has a particularly widespread distribution due to its broad environmental tolerance (Borges et al., 2014). Environmental factors, e.g., temperature, salinity, and oxygen content, are directly related to the survival, distribution, and boring activity (i.e., egestion rate) of *Limnoria*; however, the most important constraint is the presence of an adequate food supply (i.e., wood) (Menzies, 1957). Mortality rates of *Limnoria* increase rapidly from 10–20°C, but boring activity is optimized in warmer water temperatures (20°C) and is significantly reduced below 10°C (Menzies, 1957; Eltringham, 1965). The limiting salinity for boring activity varies inversely with water temperature and ceases altogether in salinities < 10 ppt (Eltringham, 1961); the optimal salinity at 20°C ranges from 30–34 ppt (Borges et al., 2009). The amount of boring activity could also be directly related to dissolved oxygen content and is significantly reduced at levels < 3.0 ppm (Anderson and Reish, 1967).
Acknowledgments

The authors thank the Natural Science and Engineering Research Council of Canada (NSERC) for Discovery Grants awarded to MKG and JPZ that helped fund this research. Shell Canada generously donated the core that was used in this study. The manuscript has benefited greatly from the thoughtful comments of S. Donovan and two anonymous reviewers.

Accessibility of Supplemental Data

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.g1tvhmmn6.

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Accepted: 4 July 2020