Attributes of the wood-boring trace fossil *Asthenopodichnium* in the Late Cretaceous Wahweap Formation, Utah, USA

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**Abstract**

A common, macroscopic, wood-boring trace fossil occurs in the Upper Cretaceous braided- and meandering-stream deposits of the upper and capping sandstone members of the Wahweap Formation in Grand Staircase-Escalante National Monument, Utah. Upon detailed examination, this trace warrants assignment to *Asthenopodichnium* (Thenius, 1979). *Asthenopodichnium* is a scooped-shaped pouch-like trace that is preserved as iron hydroxide rind casts of wood fragments and logs. The long axes of the scoops are typically aligned parallel or sub-parallel to the long axis of the preserved wood. In the upper and capping sandstone members, *Asthenopodichnium* characteristically occur in dense clusters in which pouches overlie one another, although they are found as isolated, individual traces and tight clusters of multiple individuals as well. The *Asthenopodichnium* trace maker has been purported to be the possible product of mayfly nymphs developed in moving fresh water. As a fresh water trace *Asthenopodichnium* may be used in conjunction with *Teredolites*, a marine or brackish indicator, to delimit the brackish-fresh water limit in estuarine deposits.

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1. Introduction

The oldest reported wood-borings are from the Carboniferous Period (Cichan and Taylor, 1982; Hasiotis and Brown, 1992; Scott, 1992; Scott et al., 1992). Complex insect-plant ecological interrelationships developed by the Early Permian and are often recognized through trace fossil associations with plants (Wooton, 1988; Hasiotis, 2002; Poiner and Poinar, 2008). Cretaceous amber deposits preserve a spectacularly diverse insect record matching the number of modern insect families (Poiner and Poinar, 2008). The diversification of insects suggests that insect-generated trace fossils should be more abundant in the rock record than currently documented; their under-recognition and possible under-representation need to be addressed. Grand Staircase-Escalante National Monument (GSENM) and the surrounding area in southern Utah have generated important new Cretaceous trace fossil discoveries involving invertebrates (Roberts and Tampnila, 2006; Roberts et al., 2007) and vertebrates (Simpson et al., 2010).

This paper reports on a prolific, previously unreported, macroscopic trace fossil, *Asthenopodichnium*, generated by insects on allochthonous wood from the Upper Cretaceous upper and capping sandstone members of the Wahweap Formation. *Asthenopodichnium* was probably constructed by mayfly nymphs (Thenius, 1979; 1988; Uchman et al., 2007). This paper describes these wood-related trace fossils and attributes them to the ichnogenus *Asthenopodichnium* (Thenius, 1979), discusses the palaeoenvironmental setting, and highlights the relationship between *Asthenopodichnium* and the widely recognized *Teredolites* ichnofacies.

2. Geological setting

In GSENM, Utah, the Upper Cretaceous Wahweap Formation conformably overlies the Straight Cliffs Formation, and is overlain by the Kaiparowits Formation (Fig. 1). The Wahweap Formation is informally divided, from oldest to youngest, into the lower, middle, upper, and capping sandstone members (Eaton, 1991). Fluvial units of the upper member are derived from the Mogollon highlands to the south, whereas those of the capping sandstone are sourced from the Sevier highlands to the west (Peterson, 1969; Eaton and Nations, 1991; Lawton et al., 2003). A Late Cretaceous Campanian age is constrained for the Wahweap Formation by Ar40/Ar39 radiometric ages from the lower member (Jinnah et al., 2009), the Kaiparowits Formation (Roberts et al., 2005), and microvertebrate biostratigraphy (Eaton, 1991, 2002).
Sandy, channel-dominated, meandering rivers, reflected by the dominance of trough cross-beds, characterize the depositional setting of the upper member (Lawton et al., 2003; Jinnah and Roberts, 2009). Wizevich et al. (2008) recognize the presence of alternating braided- and meander-dominated stream systems associated with the localized syndepositional, seismically active normal faults (Tindall et al., 2010). The capping sandstone member preserves a series of amalgamated braided-stream channels with few overbank deposits (Pollock, 1999; Lawton et al., 2003). Within the capping sandstone member, the low-sinuosity braided-stream deposits are associated with small eolian dune deposits as well as wind-ripple strata capping some fluvial bars (Simpson et al., 2008). The upper and capping sandstone members also contain extensive soft-sediment deformation zones attributed to local and regional seismic activity (Hilbert-Wolf et al., 2009).

### 3. Asthenopodichnium

The ichnogenus Asthenopodichnium (Thenius, 1979) consists of three ichnospecies: 1) A. xylobiotum (Thenius, 1979), 2) A. ossibiontum (Thenius, 1988), and 3) A. lithuanicum (Uchman et al., 2007). A. xylobiotum is applied to traces excavated in woody substrates (Fig. 3; Thenius, 1979). In contrast, A. ossibiontum (Thenius, 1988) is comprised of a shallower furrow, restricted to bone substrates, although both ichnospecies have a similar pouch-like morphology (Uchman et al., 2007). The third species, A. lithuanicum, is also a pouch-shaped trace with one end of the pouch "J"-shaped (Uchman et al., 2007). A. lithuanicum is reported from organic-rich silt deposits (Uchman et al., 2007).

The emended diagnosis of Asthenopodichnium is, “small, U-shaped spreiten or pouch-like structures in wooden, organic-rich or bone substrates” (Uchman et al., 2007). Thenius (1979) reports that Asthenopodichnium xylobiotum has dimensions equal to 1.5–3.0 mm in diameter and a maximum of 20.0 mm in depth. In addition, the long axis of A. xylobiotum is reported to be parallel or sub-parallel to the wood grain (Uchman et al., 2007). In contrast, Thenius (1979) states that the trace is independent of wood grain. A. lithuanicum consists of oval-like depressions that vary in length from 4.0–7.5 mm, have a width of 1.5–4.0 mm, and are at a maximum 7.5 mm deep. Form A of Uchman et al. (2007) ranges in length from 8.5–11.0 mm, width from 1.8 to 2.0 mm, and is at a maximum 2.0 mm deep (Uchman et al., 2007).

### 4. Description of Asthenopodichnium in the Wahweap Formation

Asthenopodichnium are preserved as iron hydroxide rind casts encasing the original external morphology of logs and wood fragments in the upper and capping sandstone members throughout GSENM (Fig. 2). The iron hydroxide casts are most commonly precipitated as cement in the surrounding lithic to quartz sandstone. The lower and middle members of the Wahweap Formation were not surveyed in this study.
The specimens display a range of sizes and orientations with respect to the long axis of the wood grain (Figs. 2C, 3–7). The average length, width, and depth of previously described *Asthenopodichnium* are 17.7 mm, 5.0 mm, and 3.1 mm, respectively; maximum dimensions are 40.5 mm, 11.4 mm, and 9.0 mm. The Wahweap *Asthenopodichnium* range of widths and lengths is greater than that reported for other *Asthenopodichnium*, but is still consistent in relative proportion of length versus width from reported measurements of *Asthenopodichnium* specimens described by Thenius (1979, 1988; Fig. 6).

Variable scoop orientations are present on some specimens (Figs. 3C, and 4B). Some samples contain multiple, superimposed borings (Fig. 5C and D). Typically the original boring is larger than the superimposed borings.

Minute features, such as scratches and pits, are weakly developed (Fig. 7). Discontinuous lineations, sub-millimeter width and millimeter or greater lengths, have been observed to parallel the long axis of the trace (Fig. 7A and B). Subtle small pits superimposed on wood grain are present (Fig. 7C and D). Fine wood grain is often preserved and in some cases it appears as a xenoglyph highlighting the trace.

### 5. Interpretation—*Asthenopodichnium*

The generation of iron hydroxide casts was probably initiated by the microbial decay of the wood submerged at the base of the channel or bars or possibly beneath the ground water table (Spicer, 1989). The buried microbial-induced wood degeneration controlled the local chemistry, enhancing the precipitation of iron hydroxides from the meteoric water surrounding the log (Figs. 3 and 4; for example, Spicer, 1989; Wengel et al., 2006; Miyata et al., 2007). Upon tree or tree limb death, the vascular cambium and secondary phloem decay, creating a layer of high hydraulic conductivity (Hickey, 2003). The mineral or iron-laden water flowing through this interface could either react with the surrounding wood or deposit minerals, infilling the borings generating a layer of precipitate (rind) on which the boring would be expressed as positive relief.

*Asthenopodichnium* described from the upper and capping sandstone members in GSENM are best attributed to the boring behavior of mayfly nymphs (Thenius, 1979, 1988). Amphilods, isopods, and weevils have not been ruled out (see Thenius, 1979, 1988; Uchman et al., 2007). The upper Miocene to Lower Pliocene termite trace fossil *Coatomichnus globus* superficially resembles the upper and capping sandstone member trace fossil, but differs in many aspects, such as: 1) ovoid structure, 2) tiered chambers, 3) small passageways, 4) inclined ramps, 5) chambers that are more elongate and 6) constructed feature not a boring (see Duringer et al., 2007).

There are no modern homologues that correspond to both the morphology and density of the Wahweap trace fossils. Mayflies exhibit behaviors that create borings in similar densities (Thenius, 1979), but the morphology of shallow larval chambers created by the Family Polyphaga match the location in the tree cross section (in shallow xylem) (Gillott, 1995).

Mayflies are recognized in the fossil record from the Pennsylvanian to Holocene (Sinitshenkova, 1991). Weevils underwent rapid diversification in the Middle Cretaceous (112 to 94.5 Ma) that was linked to angiosperm evolution (McKenna et al., 2009). Some mayfly nymphs use sclerotised mandibular tusks to bore into substrate-like silt, wood or bone (Hartland-Rowe, 1958; Bae and McCafferty, 1995), excavating borings that are wider, longer, and often deeper than the nymphs themselves (Hartland-Rowe, 1958). The number of destructive nymph stages varies depending on the species. During the process of degrading the wood, the action of the sclerotised mandibular tusks is preserved as small scratches and pits on the surface of the trace (Fig. 7). Vejablyhongse (1937) reports modern mayfly nymph-related borings in wood to be nearly parallel to the wood grain, and the rapid destruction of the wood took place over a five-year period. The larva of the family Polymiracididae...
which includes possible modern analogues *Asthenopus* sp., *Povilla* sp., and *Tortopus* sp., do not consume wood as their primary form of nutrition. Alternatively, they are algae filter feeders and can exploit woody substrates for gestation rather than nutritional purposes (Needham et al., 1935; Hartland-Rowe, 1958; Corbet et al., 1974; Thenius, 1979). This allows mayflies to utilize pieces of drift wood in the densities which are observed, because their larvae need nothing more than the space and protection available. Organisms whose developing larvae do use wood as food deposit their eggs more strategically so that their larvae do not have to compete with one another for nutritional resources. Mayfly nymphs may also bore into muddy substrates generating the trace *Asthenopodichnium lithuanicum* (Charbonneau and Hare, 1998; Uchman et al., 2007). The oral opening becomes vestigial in the adult stage of the mayfly (Needham et al., 1935), therefore all substrate excavations are restricted to the nymph stage.

Mayfly nymphs segregate spatially based on hydrodynamic and substrate conditions in modern fluvial systems with the body axis parallel to the flow direction, hence the resulting boring long axis is parallel to the flow direction (Berner and Pescador, 1988). Different types of Ephemeropteran nymphs prefer particular shear velocities; nymph body size increases with increased shear velocity (Sagnes et al., 2008). Change in orientation of the scoops within an individual autochthonous wood specimen may reflect multiple temporally separated infestations and/or a shift in wood orientation followed by colonization of nymphs to a different hydrodynamically efficient orientation. The orientation is modified by variations in wood density as is observed in boring around knots.

6. Discussion

*Asthenopodichnium* is reported only from freshwater settings, typically within isolated autochthonous logs (Thenius, 1979; Uchman et al., 2007). Additional types of wood borings and trace fossils in demonstrable fresh water settings have been described, but they are under-reported in the literature (Brues, 1936; Cichan and Taylor, 1982; Fisk and Fritz, 1984; Hasiotis, 2002; Lucas et al., 2010). *Asthenopodichnium* superficially resembles *Teredolites*, the key index to the *Teredolites* ichnofacies (Bromley et al., 1984). *Teredolites* possess key differences that allow separation from *Asthenopodichnium* and include (Fig. 8): 1) unbranched, clavate-shaped boring perpendicular to the wood (Leymerie, 1842; Bradshaw, 1980; Bromley et al., 1984; Kelly and Bromley, 1984; Kelly, 1998), 2) preserved aperture is smaller in diameter than the maximum diameter of the trace, and 3) roughly circular cross-sectional shape with rounded distal termination (Bradshaw, 1980; Sayrda, 1991).

The *Teredolites* trace and the larger-scale *Teredolites* ichnofacies are considered to be brackish to marine environmental indicators (Bromley et al., 1984; Aria, 1991; MacEachern et al., 2007). Plint and Pickerill (1985) reported *Teredolites* from non-marine settings in the Eocene of southern England and the Upper Cretaceous Dunvegan Formation, but MacEachern et al. (2007) argue that these units have a demonstrable brackish-water influence calling into question the non-marine interpretation of *Teredolites*. Brackish to marine conditions are often superimposed on the exposed xylic substrate (MacEachern et al., 2007).

Fig. 3. Photos of lower density *Asthenopodichnium* float samples collected from Grand Staircase-Escalante National Monument (5.0 cm ruler for scale). A–E) Top view of slabs containing *Asthenopodichnium*. Figs A–E scale is in cm. Note preserved knot in wood in C and the preferred orientation of the traces with the long axes of the specimens and the deflection around the knot in C.
The Teredolites ichnofacies is commonly linked to a base level rise in a marginal marine environment (MacEachern et al., 2007). As a consequence, Teredolites is used to delineate important sequence stratigraphic surfaces, such as maximum flooding and transgressive systems tracts typically in channelized fluvial/estuarine deposits (Shanley et al., 1992) but Asthenopodichnium currently is not used.
as a facies or stratigraphic marker. In fact, the recognition of the Asthenopodichnium trace fossil in the upper and capping sandstone members of the Wahweap Formation indicates that brackish tidal processes did not influence these fluvial systems in the central and western Kaiparowits basin. In addition, the easy distinction between Asthenopodichnium and Tereodolites may prove to be a mappable indicator to delineate the extent of the brackish water influence in an ancient estuarine system.

7. Summary

Asthenopodichnium is found throughout the Cretaceous upper and capping sandstone members of the Wahweap Formation. Asthenopodichnium is a wood boring trace probably made by mayfly nymphs but other types of insects have not been ruled out. Asthenopodichnium’s long axis parallels the wood grain of the fragment, is a scoop-like cast in appearance, and is semi-circular in cross-section. Asthenopodichnium is reported solely from fresh-water continental settings. The presence of Asthenopodichnium indicates that the upper and capping sandstone members of the Wahweap Formation in the western and central Kaiparowits basin are fresh-water fluvial systems, not tidally influenced, and may be used as a proxy for the extent of brackish influence in an estuary.

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References


Fig. 7. Small-scale markings on Asthenopodichnium from float specimens. A–B) Asthenopodichnium slab. Note short longitudinal marks in B. C) Wood grain with small superimposed pits. Small ticks on scale in mm. D) Rounded pits. Small ticks on scale in mm.


