



Microconchid encrusters colonizing land plants: the earliest North American record from the Early Devonian of Wyoming, USA

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Plant fossils in the Early Devonian Beartooth Butte Formation (Wyoming, USA) are colonized by microconchid encrusters which are found on several plant taxa, at two fossil localities in the formation, and whose tube coil diameters range from 230 to 1170 μm . Colonization is densest on broad *Drepanophycus devonicus* stems where microconchid individuals encompassing broad size ranges co-occur in close vicinity. This indicates exposure to microconchid colonization and, therefore, submergence of the plant material for relatively extended periods of time prior to burial. For *in situ* preserved *Drepanophycus*, this suggests that the plants grew partially submerged and their submerged parts were colonized by microconchids while still alive. In turn, this indicates that by the Early Devonian microconchids were colonizing freshwater environments. The Beartooth Butte Formation provides the first record of plant colonization by microconchids in North America and, along with only one other Early Devonian record from Germany, the oldest evidence for microconchids colonizing plant substrates. □ *Devonian, encrusters, microconchid, vascular plants, Wyoming.*

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Small, coiled, calcareous tubes produced by worms of the genus *Spirorbis* (Linnaeus 1758) are common on a variety of substrates in modern seas and oceans worldwide. *Spirorbis* is a polychaete annelid classified in the order Sabellida Dales 1962. Fossils reminiscent of *Spirorbis* tubes and referred to as spirorbiform fossils are known from the upper Ordovician onwards. They consist of minute tubes forming flat coils that range between less than 1 mm to slightly more than 3 mm in total diameter, coiling either dextrally or sinistrally (Taylor & Vinn 2006). Throughout their stratigraphic range spirorbiform tubes are found attached to a variety of firm or hard abiogenic and biogenic substrates, including hardgrounds (Vinn & Wilson 2010), oncoliths (Zatoń & Taylor 2009), stromatoporoids (Nield 1986), brachiopods (Fagerstrom 1996), bryozoans (Taylor 1984), bivalve molluscs (Trueman 1942; Van Der Heide 1956), trilobites (Šnajdr 1983), and marine (Jux 1964) and terrestrial plants (Schweitzer 1983; Kelber 1986; Falcon-Lang 2005).

Although apparently representing a single group of organisms characterized by the same size range, external morphology and ecology, spirorbiform tubes have been shown to fall into two categories produced by two groups of organisms (Taylor & Vinn 2006). The two categories differ in the structure and development

of the tube walls and do not overlap stratigraphically. Fossils assignable to the genus *Spirorbis* exhibit tubes with open proximal ends and wall structures consisting of chevron-shaped growth lamellae. These can be traced back with certainty only into the Middle Cretaceous and are found exclusively in marine deposits (Taylor & Vinn 2006). By contrast, the walls of pre-middle Jurassic spirorbiform tubes (which range down into the Late Ordovician) display lamellar microstructure, a closed bulb-like tube origin, and septa sealing off older portions (Weedon 1991; Taylor & Vinn 2006). These fossils, characteristic of a broader range of aquatic environments including salt-, brackish, and freshwater, are assigned to the genus *Microconchus* Murchison 1839 and other subsequently erected 'microconchid' genera (Taylor & Vinn 2006; Vinn 2006; Vinn & Taylor 2007; Zatoń & Krawczyński 2011; Wilson *et al.* in press). Microconchids (Order Microconchida, Weedon 1991; Class Tentaculita, Bouček 1964) are thought to be an extinct group of lophophorates based on characters shared with the brachiopods (microstructure and epithelial origin of calcified shells/tube walls) and bryozoans (bulb-like tube origin, tube wall microstructure). In terms of their vermiform morphology, microconchids are similar to the phoronid lophophorates (Taylor & Vinn

2006; Vinn & Mutvei 2009; Taylor *et al.* 2010; Vinn 2010; Zatoń & Vinn 2011).

Herein we describe microconchids on early terrestrial plants from the Lower Devonian Beartooth Butte Formation of Wyoming. Except for this formation (containing plant fossils at two localities – Dorf 1933; Blackstone & McGrew 1954), and for the Martin Formation of Arizona (Teichert & Schopf 1958), none of which has seen extensive publication, Western North America has been a blank spot on Early Devonian vegetation maps. Thus, floral assemblages of the Beartooth Butte Formation offer a crucial perspective into Early Devonian plant diversity and biogeography. The oldest known occurrences of microconchids attached to land plants are Early Devonian and were previously known only from Germany (Schweitzer 1983). The Beartooth Butte Formation fossils represent the second report of microconchids on land plant material in the Early Devonian worldwide, and the first such occurrence in North America.

Materials and methods

Early terrestrial plant fossils bearing microconchid tubes were recovered from the Beartooth Butte Formation at both of its exposures in northern Wyoming: Cottonwood Canyon (Big Horn Co., 44°52' N, 108°02' W) and Beartooth Butte (Park Co., 44°57' N, 109°37' W). Palynological analyses by D.C. McGregor (reported by Tanner 1983), suggest a Late Lochkovian to Early Pragian age at Cottonwood Canyon, and a Middle to Late Emsian age at Beartooth Butte. At both localities the Beartooth Butte Formation forms geometries reminiscent of channel fill deposits – long, narrow bodies of sediment with lenticular cross-sections – underlain by the Ordovician Bighorn Dolomite and overlain by the Upper Devonian Jefferson Limestone (Blackstone & McGrew 1954; Sandberg 1961). The formation consists mostly of clastic deposits formed in a carbonate-rich (calcareous, dolomitic) context (Dorf 1934; Blackstone & McGrew 1954). The fossiliferous layers are predominantly siltstone and shale with dolomitized sandstone interbeds, at Cottonwood Canyon, and massive dolomitized limestones at Beartooth Butte. The fossil content of the Beartooth Butte Formation includes fish, eurypterid and terrestrial plant fragments. Based on its fossil content and on geometry, the unit has been interpreted as brackish and freshwater deposits of estuarine to fluvial environments (Dorf 1934; Sandberg 1961; Fiorillo 2000).

Specimens used in this study come from the collections of the National Museum of Natural History – Smithsonian Institution (one specimen originally collected at Beartooth Butte by E. Dorf), the Denver

Museum of Nature and Science (specimen DMNS L.313/KJ9332/29588 collected by K.R. Johnson at Cottonwood Canyon), as well as from collections located at Humboldt State University (specimens HPH10, 13, 14, 157, collected by us at Cottonwood Canyon). The direction of tube coiling was observed on specimens from *Drepanophycus devonicus* (Weiland & Berendt) Schweitzer 1980 samples for which vertical orientation was recorded in the field. The material was imaged using Wild M5 and Leica MZ8 dissecting microscopes, and a Nikon Eclipse E400 compound microscope, with a Nikon Coolpix E8800 digital camera.

Results

The small, coiled fossils associated with the Beartooth Butte Formation floras conform in their morphology, size, ecology and age with microconchids. Coiling varies from tightly packed in most specimens (Fig. 1A, B) to specimens exhibiting a loosely separated outermost gyre (Fig. 1B, C). Faint transverse marks are visible on some of the specimens (Fig. 1A, C, I). The direction of coiling is predominantly dextral, but individuals coiled sinistrally are also present. Measured diameters of individuals vary between 230 and 1170 µm, well within the known size range of microconchid fossils (Taylor & Vinn 2006). Sub-optimal preservation prevents genus-level identification of the specimens, which appear most comparable to the genera *Microconchus* and *Palaeoconchus* Vinn 2006 (O. Vinn and M. Zatoń, personal communication, February 2011). Attempts to document the ultrastructure of the tube wall and the bulb-like origin of tubes in petrographic thin sections and in scanning electron microscopy of HCl-etched sections have been frustrated by pervasive diagenetic recrystallization and dolomitization.

At Cottonwood Canyon microconchids are abundant on plant material that was transported for short distances or even flooded and buried in growth position, as reflected by the large sizes of the plant fossils and the frequency of plant axes bearing attached roots or preserved in vertical position. Such is the case of beds consisting of dense agglomerations of large *Drepanophycus devonicus* stems, all of which host numerous microconchids (Fig. 1D–F), or of a large tuft of axes assignable to Tanner's (1983) 'morphotype III' and which radiate from a common point of attachment (Figs. 1F, G). In these cases of dense microconchid colonization of the plant material (sometimes in excess of 10 individuals/cm²), there appears to be no discernable pattern of microconchid distribution. The great majority of plant fossils exhibit wide ranges of variation in size of their microconchid populations (Fig. 1C, E). On the other hand, microconchids are

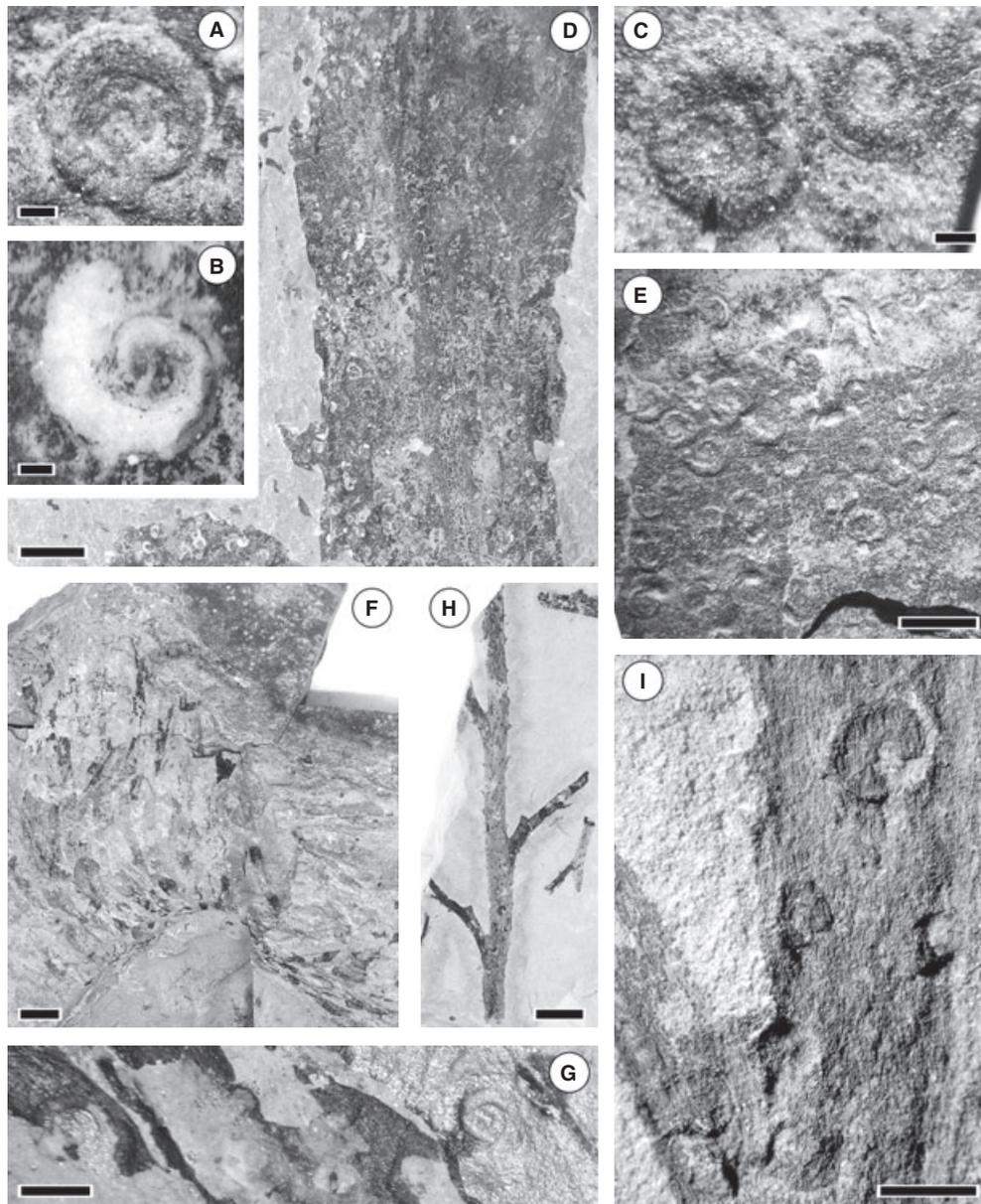


Fig. 1. Microconchid tubes on plant fossils from the Beartooth Butte Formation, Early Devonian, Wyoming, USA. A, tightly coiled specimen on *Drepanophycus devonicus* (Weiland & Berendt) Schweitzer 1980 stem; transverse marks on terminal part of the outermost gyre; HPH10, scale bar 200 μm . B, specimen with loosely separated outermost gyre on *D. devonicus* stem; HPH13, scale bar 200 μm . C, larger, tightly coiled specimen (left) next to a smaller specimen with loosely separated outermost gyre, on *D. devonicus* stem; a pattern of transverse marks is visible on the larger specimen; HPH14, scale bar 200 μm . D, *D. devonicus* stem colonized by numerous microconchids; HPH157, scale bar 5 mm. E, dense agglomeration of microconchid tubes of different sizes on *Drepanophycus* stem; HPH13, scale bar 2 mm. F, radiating tuft of axes of Tanner's (1983) 'morphotype III' plants and *D. devonicus* stem (upper right corner), both colonized by numerous microconchids; DMNS L.313/KJ9332/29588, scale bar 10 mm. G, two microconchid tubes (one at far left and one at far right) on 'morphotype III' axes, detail of lower right corner of Fig. 1F; scale bar 1 mm. H, *Psilophyton wyomingense* Dorf 1933 axes colonized by microconchids; Smithsonian Institution specimen (no number), scale bar 5 mm. I, detail of the lower branching zone in Fig. 1H, with several microconchids; the topmost specimen exhibits a pattern of transverse marks; scale bar 1 mm; A–G, Cottonwood Canyon locality (Big Horn Co.); H, I, Beartooth Butte locality (Park Co.).

absent from all plant fossils representing belowground plant parts likely preserved *in situ* – rhizomes, sometimes preserved in vertical position and roots. In horizons where the plant material is highly fragmented, reflecting transport over longer distances or under highly abrasive conditions, microconchids are rare;

they can nevertheless be recognized occasionally on fragments assignable to *Drepanophycus* Goepfert 1852.

In contrast to Cottonwood Canyon, where the plant material consists predominantly of carbonaceous compressions, with rare occurrences of oxidized

plant fossils, at Beartooth Butte the plant material is preserved almost exclusively as highly oxidized fossils – compressions in which the carbonaceous plant matter has been completely replaced by iron oxides and hydroxides. This renders the microconchid fossils significantly less conspicuous, so the extent of their presence, and their frequencies and distributional patterns are hard to characterize. In many cases, sterile axes assignable to *Hostimella* Stur 1882 display circular depressions or bumps that are reminiscent, in terms of size and distributional patterns, of the microconchid agglomerations seen on well preserved material. However, the lack of preservation of any detail precludes unequivocal identification of those structures as microconchid fossils. An exception at Beartooth Butte is represented by a *Psilophyton wyomingense* Dorf 1933 compression fossil characterized by a lesser degree of oxidation, and which preserves unequivocal microconchids (Fig. 1H, I). Taken together, our observations of the Beartooth Butte material suggest that microconchids may have been as frequent there as they are at Cottonwood Canyon. If such is the case, then oxidative preservation, as well as the longer distance of transport and dispersal of the Beartooth Butte plant material (suggested by the fact that fossils are widely spaced in the layers and were never found forming rich assemblage horizons) would explain the apparent scarcity of microconchids.

Discussion and conclusions

In the Beartooth Butte material a wide variability can be seen in the individual sizes of microconchids sharing any given area of a plant axis, with the largest at least three times the size of the smallest. Such wide variations in size suggest that once a suitable plant substrate became available (i.e. submerged), multiple generations would colonize it. Kelber (1986) has proposed rates of colonization of plant material, including Devonian plant fossils, by spirorbiform encrusters based on the ecology of modern *Spirorbis* polychaetes. However, since we now know that the pre-Cretaceous spirorbiforms belonged to an entirely different group of encrusting organisms (Taylor & Vinn 2006), Kelber's conclusions do not apply to such pre-Cretaceous fossils for which the rates of substrate colonization are unknown. Based on the co-occurrence of individuals that encompass broad size ranges on the Beartooth Butte Formation plants, we can nevertheless hypothesize that the plant material experienced relatively prolonged submergence times, possibly exceeding 1 month, coupled with slow rates of decay prior to burial.

The abundant agglomerations of *Drepanophycus* stems, some bearing small tufts of adventitious roots,

observed in some of the layers suggest that the plants are preserved *in situ* as a result of rapid burial by sediment. Colonization of these plants by microconchid populations that include wide size ranges, coupled with the obligate aquatic environment of microconchids, indicate that the plants grew at least partially submerged and were colonized while still alive. This fossil association therefore represents a rare glimpse into the environments and processes acting upon the Early Devonian Beartooth Butte Formation plant communities, and microconchid colonization of the *Drepanophycus* stems is a useful indicator of the life history of the plants. Conversely, the fact that they occur on *Drepanophycus* preserved *in situ* in these sediments that are interpreted as fluvial in origin (Fiorillo 2000) indicates that microconchids were present in freshwater environments. On the other hand, it is unlikely that all the plant taxa colonized by microconchids in the Beartooth Butte Formation floras were growing partially submerged. At least for some of these taxa microconchids must have settled on uprooted, transported plant fragments. Whether microconchid colonization in the latter case occurred during transport or after the plant fragments had settled on the bottom cannot be determined, as the original vertical orientation of samples was not available for specimens other than *Drepanophycus devonicus*.

The microconchid occurrence in the Beartooth Butte Formation is the first reported on plant substrates in North America. The Late Lochkovian – Early Pragian age of the Cottonwood Canyon material places it at par with the only other plant-associated Early Devonian microconchid occurrence, recorded by Schweitzer (1983) in the Rhenish Schiefergebirge (Germany), making the two the oldest microconchid occurrences associated with plants known to date.

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