Adaptive function and phylogenetic significance of novel skeletal features of a new Devonian microconchid tubeworm (Tentaculita) from Wyoming, USA

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Abstract.—A new genus and species of microconchid tubeworm, *Aculeiconchus sandbergi* n. gen. n. sp., is described from the Givetian (Devonian) Maywood Formation of Cottonwood Canyon, Wyoming, USA. It possesses unique hollow spines of various lengths on the tube underside, a position previously undocumented for these fossils. Like some cyclostome bryozoans possessing basal tubular extensions, the basal spines of *Aculeiconchus* n. gen. were presumably also used for fixation to flexible substrata, e.g., algal thalli, which is a previously undocumented adaptive strategy in microconchids. Together with other skeletal features, such basal spines could suggest that 'lophophorate' microconchids, unlike the other tentaculitoids, might be phylogenetically not as distant from bryozoans as previously thought. The Maywood Formation, which contains a few-millimeters thick, monospecific shell accumulation of the microconchids described herein, records deposition in an estuarine brackish setting within narrow channels that were cut into underlying strata. The microconchids were opportunistic taxa that repeatedly colonized these salinity-stressed estuarine channels, leading to a series of adaptive innovations, including colonization of plant stems during the Early Devonian (Beartooth Butte Formation) and possibly flexible, soft-algal substrata during the Middle Devonian (Maywood Formation, this study). Tectonic quiescence during the Early and Middle Devonian indicates that erosion and subsequent deposition of the Maywood and the underlying Beartooth Butte Formation channels were responses to major eustatic events. Over a span of nearly 30 Myr, channels were cut successively during lowstand conditions and a distinctive faunal assemblage with microconchids tracked marine transgressions into the channels.

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Introduction

Microconchids are an extinct group of generally small (cf. Zatoń and Mundy, 2020) tubeworms, which appeared during the Late Ordovician and disappeared from the fossil record at the end of the Middle Jurassic (e.g., Taylor and Vinn, 2006; Vinn and Taylor, 2007; Zatoń and Vinn, 2011). Based on superficial resemblance to Recent serpulid polychaete tubes, microconchids were often misidentified as *Spirorbis* Daudin, 1800 or *Serpula* Linnaeus, 1758 (e.g., Howell, 1964; Beus, 1980), or as 'vermiform' gastropods (Burchette and Riding, 1977; Bełka and Skompski, 1982). However, due to their completely different tube characteristics (i.e., bulbous larval shell, microlamellar and punctate tube), Weedon (1990, 1991, 1994) assigned the tubeworms to the tentaculitoids, and included them in a separate order Microconchida.

Microconchids first appeared in fully marine environments but colonized brackish habitats as early as the early Silurian

(Brower, 1975), and freshwater environments during the Early Devonian (Schweitzer, 1983; Caruso and Tomescu, 2012; see also Taylor and Vinn, 2006; Zatoń et al., 2012a). They were also a common constituent of microbial buildups (Peryt, 1974; Burchette and Riding, 1977; Toomey and Cys, 1977; Dreesen and Jux, 1995; He et al., 2012) and metazoan buildups (Pruss et al., 2007; Brayard et al., 2011), and in some cases formed their own bioherms (Beus, 1980; Wilson et al., 2011; Zatoń et al., 2018). Microconchids are the dominant, or even sole, encrusters in the aftermaths of some of the mass extinctions, and thus they are widely considered as an opportunistic, 'disaster' taxon (Fraiser, 2011; Zatoń and Krawczyński, 2011a; He et al., 2012; Yang et al., 2015, 2021; Zatoń et al., 2016a; Shcherbakov et al., 2021).

As encrusting organisms, microconchids colonized mainly firm and hard substrata, e.g., shells, cobbles, and hardgrounds in marine settings (Vinn and Wilson, 2010; Zatoń and Borszcz, 2013; Zatoń et al., 2014a). They also colonized plant remains in brackish to freshwater environments (Caruso and Tomescu, 2012; Zatoń et al., 2014b; Shcherbakov et al., 2021) utilizing different strategies (Vinn, 2010). On such substrates, the

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majority of microconchids cemented their tubes (e.g., Vinn and Taylor, 2007), with only their terminal parts elevated above the substratum (e.g., Zatoń and Krawczyński, 2011a, b). In some species, especially in those forming organic buildups, the larval shell (the planispirally coiled initial part of the tube) was cemented and the rest of the tube was helically uncoiled and oriented upward (Burchette and Riding, 1977; Beus, 1980; Wilson et al., 2011). Permian *Helicoconchus* Wilson, Vinn, and Yancey, 2011 from Texas, unlike any other species described, was able to bud new tubes from the parent tube (Wilson et al., 2011). Commonly, microconchid tubes are loosely scattered in sedimentary layers, a pattern that indicates that in many cases the tubes were transported from their original habitats (e.g., Suttner and Lukeneder, 2004). In other cases, the tubes were detached from degraded organic substrata, e.g., algae, or dissolved aragonitic shells that they encrusted (e.g., Zatoń and Peck, 2013).

Herein, we document Devonian microconchids that are abundantly preserved as isolated specimens in mixed siliciclastic and carbonate deposits, but that possess skeletal features of certain ecological adaptations not previously noted in these taxa. The novel structures have implications for the paleobiology, phylogenetic relationships, and evolutionary paleoecology of this still enigmatic group of tentaculitoids. We discuss their evolution, linked to the repeated development of eustatically driven, brackish water estuarine settings—episodes that were unique to the ancient Rocky Mountain region of Laurentia in the Devonian. A palynologic analysis provides an age constraint for the fossils and supports our interpretation of a brackish estuarine paleoenvironment.

Location, geologic and depositional setting

Samples for this study were collected at Cottonwood Canyon, Wyoming, USA (Fig. 1), on the western side of the northern Bighorn Mountains, ~28 km to the east of Lovell, Wyoming.

The study area is ~0.7 km into the canyon on the northern wall. At this site, a thick (33.6 m), narrow channel-fill of the Lower Devonian Beartooth Butte Formation rests on the Upper Ordovician Bighorn Formation. This is overlain by a laterally extensive, 10.2 m thick covered interval. Sandberg (1961) interpreted a covered interval at the same stratigraphic level in his section < 1 km to the southeast as the fine-grained upper Beartooth Butte Formation. We measured a section through the Maywood Formation (44°52′14.0″N, 108°03′26.5″W) that rests directly on the Bighorn Formation outside of the Beartooth Butte Formation channels (i.e., on an interfluve). The Maywood Formation is 5.24 m, including a 2.2 m thick covered interval near the base (Fig. 2). The Maywood is overlain by the Jefferson Formation along a rapidly gradational contact interval (Fig. 3).

The Beartooth Butte and Maywood formations are interpreted to represent infills of incised valleys that eroded into underlying rocks, primarily the Bighorn Dolomite, with deposition at different times during the Devonian (Dorf, 1934; Sandberg, 1961; Sandberg and McMannis, 1964): the Beartooth Butte Formation in the Lower Devonian (upper Lochkovian to Emsian, see Tanner, 1984; Elliot and Johnson, 1997) and the Maywood during the Givetian. At our Cottonwood Canyon section, the Beartooth Butte channel rests on the Bighorn and includes a narrow, deeply incised part at the base. The basal part consists of red, very coarse, conglomeratic debris-flow deposits, and the upper part that filled a broader valley consists of fine-grained facies. Sandberg (1961) established a late Lochkovian to Pragian age for this fine-grained interval in his section at Cottonwood Canyon.

The unconformably overlying Maywood Formation channels were cut into both the Bighorn Dolomite and the upper Beartooth Butte Formation. The overlying Jefferson Formation is assigned to the Frasnian (Sandberg, 1965) and consists of dolostone, dolomitic siltstone, and argillaceous dolomite. It is in turn overlain by the Mississippian Madison Limestone.
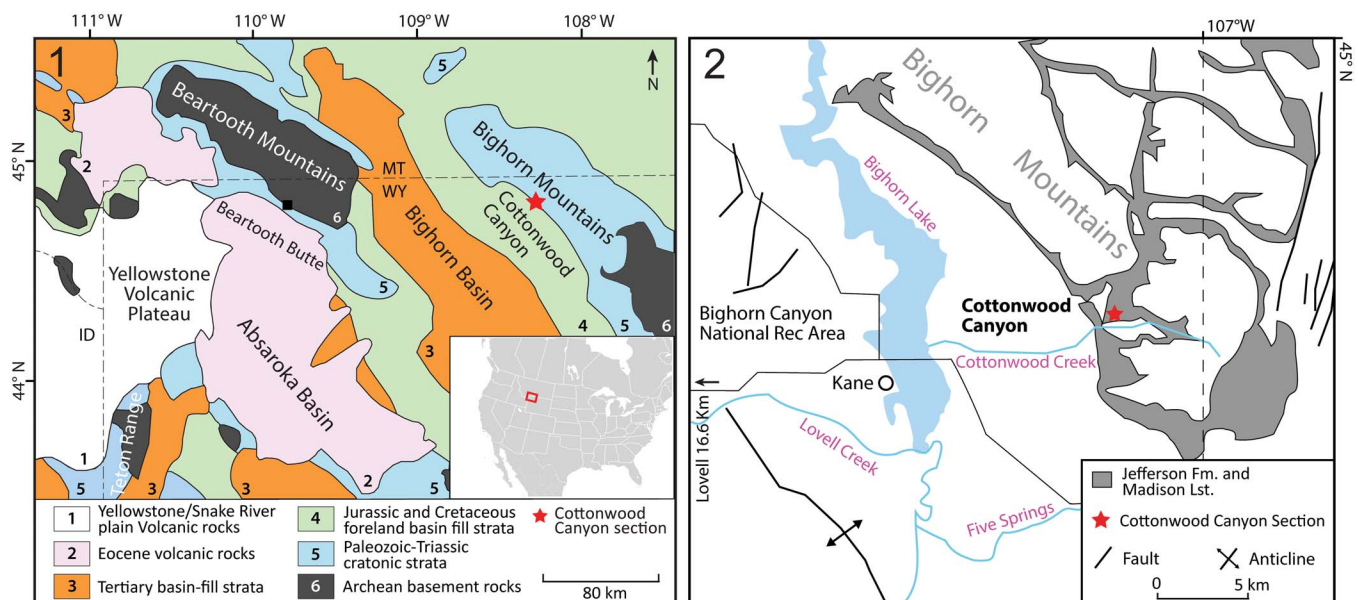
Figure 1. Location of the sampled site: (**1**) generalized geologic map of northern and northeastern Wyoming, showing the study site at Cottonwood Canyon, Wyoming (adapted from Malone et al., 2017); (**2**) generalized geologic map of Cottonwood Canyon area, Wyoming (adapted from Pierce and Nelson, 1971).
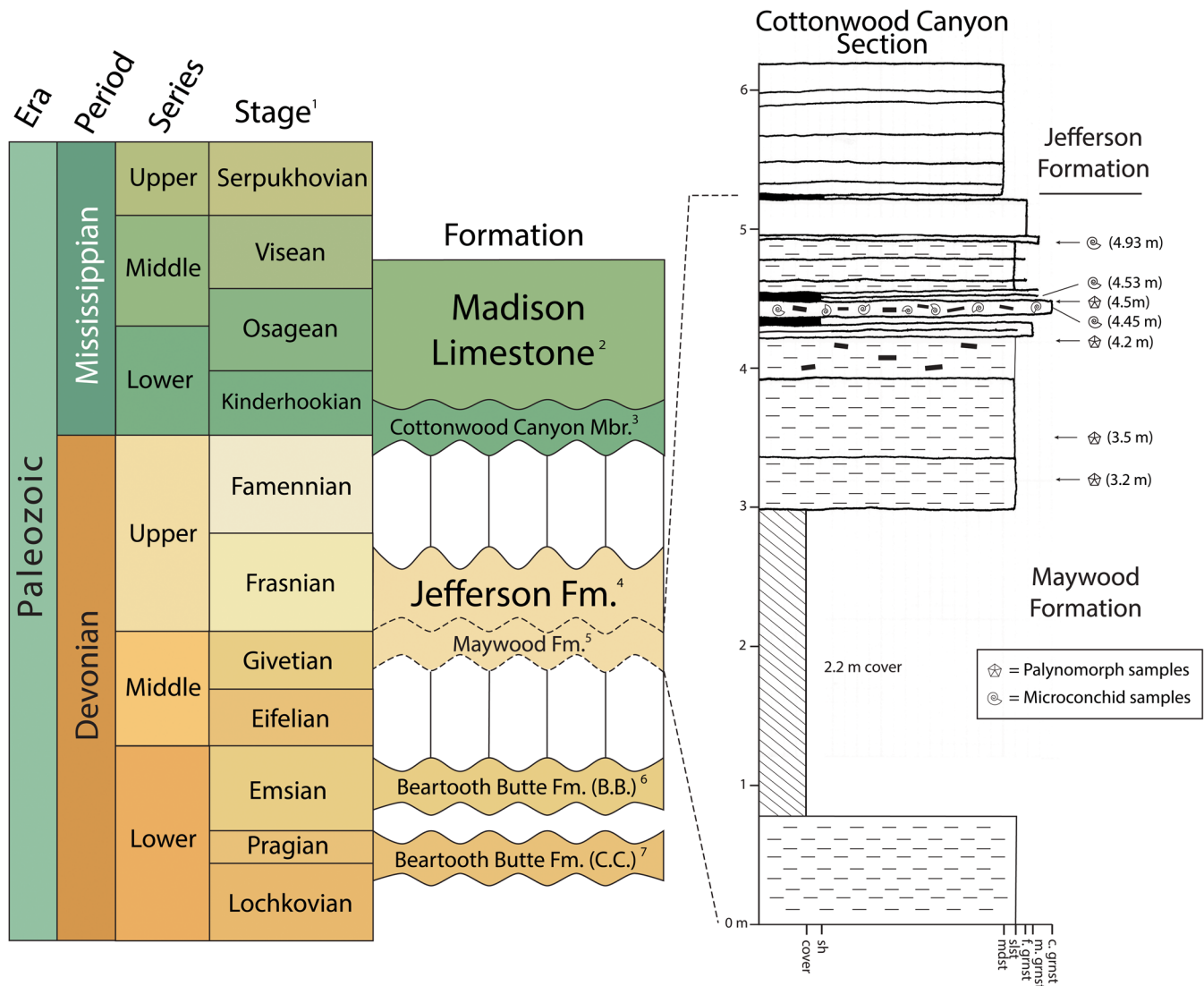
Figure 2. Devonian and Mississippian chronostratigraphic framework and stratigraphic units (left) and generalized stratigraphic column of Maywood Formation at Cottonwood Canyon, Wyoming (right). Chronostratigraphy of Devonian and Mississippian from Cohen et al. (2020). Vertical lines represent depositional hiatus between formations; dashed, wavy lines at base and top of Maywood Formation indicate uncertain ages of the unit. The vertical axis next to the stratigraphic column represents stratigraphic height (in meters). The numbers on the right indicate stratigraphic heights where microconchid and palynomorph samples were taken. Superscripts: 1 = North American stages (Kinderhookian and Osagean) are used for Lower Mississippian stages instead of Tournaisian; 2 = Peterson, 1981; 3 = Sandberg, 1967; 4 = Sandberg, 1963; 5 = Sandberg, 1963; 6 = Beartooth Butte (B.B.), Wyoming; 7 = Cottonwood Canyon (C.C.), Wyoming. Vertebrate fossils by Elliot and Johnson (1997) and spore fossils by Tanner (1984) and Noetinger et al. (in press) indicate different ages of two exposures of the Beartooth Butte Formation: Late Lochkovian–Pragian at Cottonwood Canyon, middle–late Emsian at Beartooth Butte. Strata: black = plant debris and coal fragments; fine dashes = minor clay component; thick dashes = plant material; crosshatch = cover. c. grnst = coarse grainstone; f. grnst = fine grainstone; m. grnst = medium grainstone; mdst = carbonate mudstone; sh = shale; slst = calcisiltite

The Maywood Formation is considered an equivalent of the Souris River Formation in Montana (Kauffman and Earll, 1963). Sandberg (1963) described the Maywood Formation at Cottonwood Canyon and noted the abundance of microconchids (attributed to *Spirorbis*) throughout his ~4.9 m (16 ft) section, located farther east within Cottonwood Canyon than the section we describe here. In our study site, the base of the formation consists of 80 cm of tan-weathering dolosiltite (Fig. 2). It is succeeded by a 2.2 m covered interval. The lower 1.22 m above the covered interval consists entirely of calcisiltite and dolosiltite. The rest of the formation (4.22–5.24 m) is better exposed and consists mostly of calcisiltite/dolosiltite facies, with a few shale and microconchid grainstone beds. The latter

contains both complete and broken microconchid specimens, some of which are coated by pyrite. Some microconchid grainstone beds are also rich in fish remains, rounded coal pebbles, macroscopic plant impressions, macerated plant stems, and megaspores. A lower Upper Devonian age was assigned to the formation based on these spores and vertebrate fossils (Sandberg, 1963).

The biota of the Maywood Formation in Cottonwood Canyon indicates a marginal marine environment, but whether the deposition was in brackish or fresh water remains uncertain based on microflora and fish fauna (Sandberg, 1963). The strata at Cottonwood Canyon were interpreted to be deposited in the upper reaches of a long, narrow estuary that extended into a
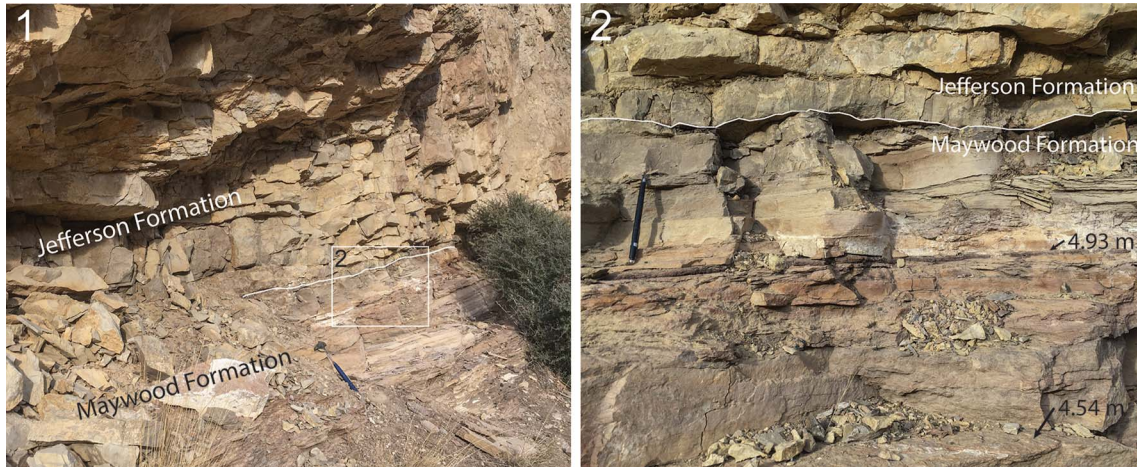
Figure 3. Maywood and Jefferson formations at Cottonwood Canyon, Wyoming: (**1**) red, fine-grained strata of the upper Maywood Formation and contact with the thin to medium bedded dolomudstone of the basal Jefferson Formation; (**2**) close-up of contact interval showing brown to gray calcisiltite and dolosiltite beds of the uppermost Maywood. Two mm thick layers of microconchids are indicated by black arrows. Scale = hammer ~33 cm (**1**); pencil ~14 cm (**2**).

retreating shoreline whereas the Maywood Sea transgressed southward and westward from the Williston Basin, Montana (Sandberg, 1963; Sandberg and McMannis, 1964). Many Maywood and associated Middle–Upper Devonian channel-fill deposits share similarities with the Lower Devonian Beartooth Butte Formation in channel geometry, lithology, and fossil assemblages. The Maywood Formation was noted to directly overlie the Beartooth Butte Formation in several stratigraphic sections, and deposition of both units took place within individual channels, which controlled and localized the Late Devonian transgression (Sandberg and McMannis, 1964).

Materials and methods

Our microconchid samples were collected from the middle and upper part of the Maywood Formation. The samples consist of fine to coarse grainstone collected from three stratigraphic horizons (samples 4.45, 4.53, and 4.93) of 3–4 mm thick grainstone beds.

The samples were first inspected with a Nikon SMZ 1000 binocular microscope, and subsequently sample fragments with selected specimens were imaged using a Philips XL30 environmental scanning electron microscope (ESEM) at the Institute of Earth Sciences, University of Silesia, Sosnowiec, Poland. The specimens were examined uncoated under low-vacuum conditions using back-scattered (BSE) imaging. Selected specimens were also documented using a Leica Wild M10 binocular microscope equipped with a Nikon NikCam Pro1 camera.

To better determine the age of the microconchid-bearing deposits and to decipher their paleoenvironments, four samples of organic-rich shale, calcareous shale, and calcisiltite (collected at 3.2 m, 3.5 m, 4.2 m, and 4.5 m; see Fig. 2) were subjected to palynological investigation. Standard palynologic maceration was followed using HCl (10%), HF (70%), and several washes of distilled water, allowing the neutralization of the residues, which were sieved using 5-μm meshes. Four slide mounts were made using a drop of residue mixed with one drop of polyvinyl alcohol. After drying, one drop of clear casting resin was

added, and the cover slip turned and sealed. The residues were oxidized with 3 ml of Schultz solution in a hot bath for a short time, and after washing and centrifuging until neutralization, a 10% solution of NH_4OH was added. The residues were then placed in a hot-water bath for two minutes and washed three or four times. Two sets of slides were created: one set with oxidized residues (3.5 m and 4.2 m) and another set with oxidized residues (3.2 m and 4.5 m) stained with a drop of Bismarck Brown Y. Microscopic analysis of the microfossils was performed using Nikon E200 and Leica DM500 light microscopes (bearing a fluorescence device), and images were taken with a Amuscope 14 Mp video camera.

Repositories and institutional abbreviations.—The specimens studied are housed at the Institute of Earth Sciences, University of Silesia, Sosnowiec, Poland (GIUS 4-3732). Palynological residues, slides, and extra rock samples are housed at Centro de Investigaciones Científicas y Tecnológicas de Transferencia a la Producción (CICYTIP-Pl; CICYTTP-CONICET-ER-UADER, of di Pasquo and Silvestri, 2014).

## Systematic paleontology

<p align="center">Class Tentaculita Bouček, 1964
Order Microconchida Weedon, 1991
Family Palaeoconchidae Zatoń in Zatoń & Olempska, 2017
Genus Aculeiconchus new genus</p>

Type species.—*Aculeiconchus sandbergi* n. gen. n. sp.

Diagnosis.—Microconchid tubeworm having microlamellar tube structure, possessing hollow spines on its underside (base).

Etymology.—*Aculei* (Latin) = spines; *concha* (Latin) = shell.

Occurrence.—Maywood Formation, Middle Devonian (Givetian), Cottonwood Canyon, Wyoming, USA (44°52′14.0″N, 108° 03′26.5″W).
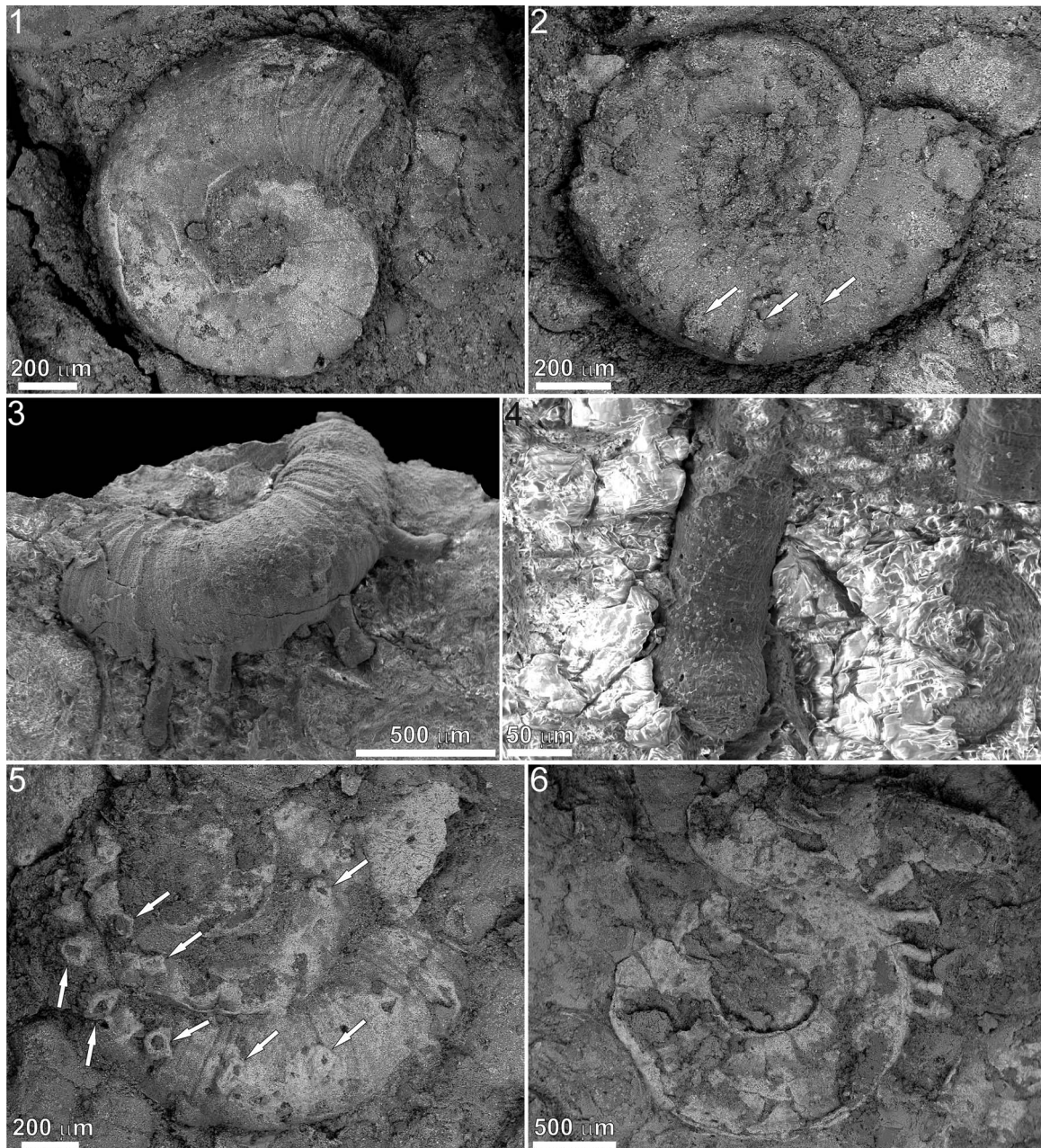
Figure 4. ESEM photomicrographs of *Aculeiconchus sandbergi* n. gen. n. sp. from the Devonian Maywood Formation, Wyoming: (**1**) dorsal side of planispirally coiled tube devoid of any spines, paratype, GIUS 4-3732/1; (**2**) tube underside with basal spines (arrows), paratype, GIUS 4-3732/2; (**3**) lateral view of holotype showing distinct basal spines, GIUS 4-3732/3; (**4**) detail of enlarged spine shown in (**3**); (**5**) tube underside with numerous hollow spines (arrows), paratype, GIUS 4-3732/4; (**6**) crushed tube with distinct basal spines in displaced, lateral positions, paratype, GIUS 4-3732/5.

Remarks.—*Aculeiconchus* n. gen. differs from other described microconchids by the presence of spines on the tube base.
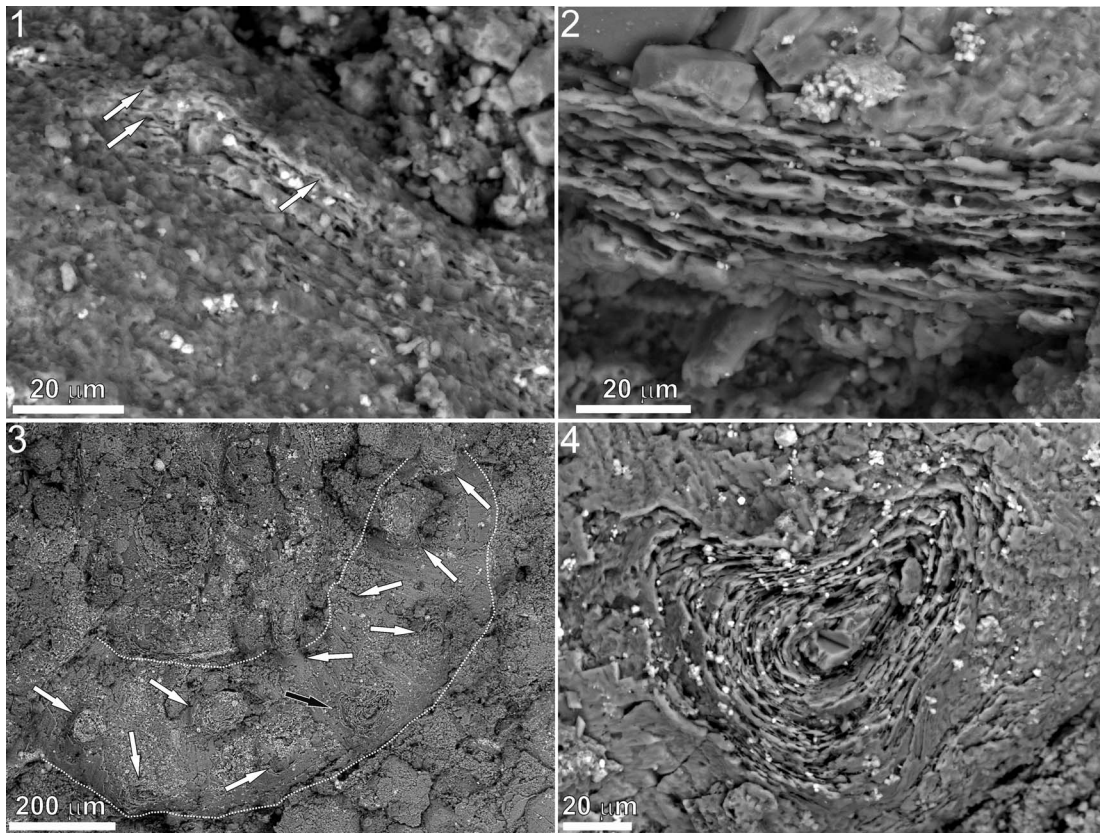
Aculeiconchus sandbergi new species
Figures 4–6

Type specimens.—Holotype (GIUS 4-3732/3) and paratypes (GIUS 4-3732/1, 2, 4–9) from Cottonwood Canyon, Wyoming, USA (44°52′14.0″N, 108°03′26.5″W), Maywood Formation, Middle Devonian (Givetian). Apart from the holotype and paratypes, other material comprises many variably preserved specimens embedded in the host rock of the Maywood Formation.

Diagnosis.—Planispirally coiled tube with a tendency to helically uncoil; dorsal and lateral sides of tube covered by fine, transverse riblets; tube base with hollow spines of differing lengths.

Occurrence.—Maywood Formation, Middle Devonian (Givetian), Cottonwood Canyon, Wyoming, USA (44°52′14.0″N, 108°03′26.5″W).

Figure 5. ESEM photomicrographs of *Aculeiconchus sandbergi* n. gen. n. sp., paratypes, from the Devonian Maywood Formation, Wyoming: (**1, 2**) lamellar tube microstructure, GIUS 4-3732/6 (**1**) and 4-3732/9 (**2**); (**3**) tube underside with numerous, variously arranged but broken basal spines (arrows), GIUS 4-3732/7; (**4**) close-up of hollow basal spine preserved on the tube in (**3**, black arrow), showing its microlamellar structure.
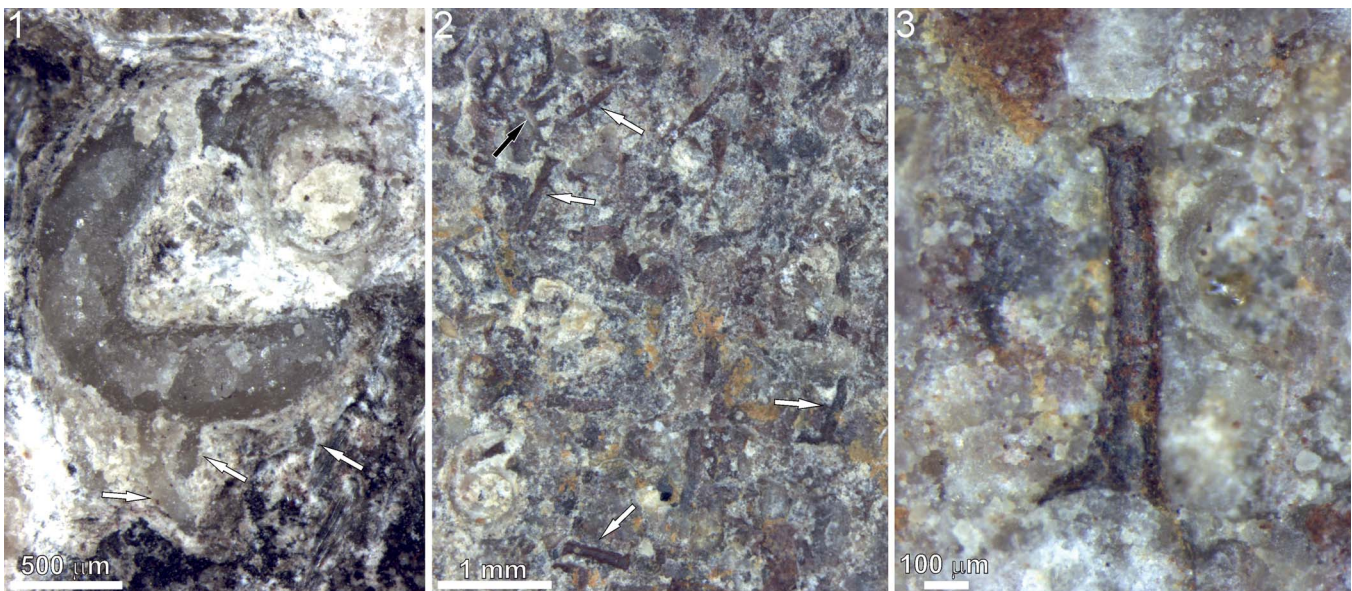
Figure 6. Stereomicroscopic photographs of *Aculeiconchus sandbergi* n. gen. n. sp., paratypes, and its spines, Maywood Formation, Wyoming: (**1**) planispirally coiled tube with its uncoiled terminal part and basal spines of varying lengths (arrows), GIUS 4-3732/8; (**2**) basal spines dispersed loosely on the sediment (white arrows) and attached to the tube fragment (black arrow); (**3**) magnified long basal spine showing slight widening at its distal end.

Description.—Tube dextrally (clockwise) coiling planispirally (Fig. 4), to 1.97 mm diameter, in some cases distally helically uncoiled into upright direction (Fig. 6.1). Umbilicus open with rounded margin; aperture rounded, to 0.4 mm in diameter. The tube exterior shows dense, fine transverse riblets running from umbilical margin to tube base (Fig. 4.1, 4.3). Tube microstructure lamellar (Fig. 5.1, 5.2, 5.4); distinct deflections of the laminae seen in tube cross sections, indicating presence of pseudo- or punctuation, not detected. Only locally, some laminae show some deflection (Fig. 5.1), which potentially could point to presence of poorly developed (or poorly preserved) pseudopunctuation.

Base of planispirally coiled tube rounded, with hollow spines of various lengths (Figs. 4.2–4.5, 5.3, 5.4). Spines projecting perpendicularly, or slightly obliquely, from tube base (Figs. 4.2, 4.3, 4.5, 6.1); arranged in single row or in irregular patterns with two spines on opposite sides of tube base (Figs. 4.5, 5.3); of varying length, with some as long as 0.7 mm (Fig. 6.3), circular to oval in cross section, but diameter can differ in single specimens (0.036–0.060 mm; in such cases, spine diameter increasing distally, forming flat base at top; Figs. 4.3, 6.3); ornamented with fine, transverse growth lines (Fig. 4.4); some with slight bending (Fig. 6.1); hollow inside; microlamellar structure not differing from that of tubes (Fig. 5.4); no spines observed on upper sides of tubes (Fig. 4.1).

*Etymology.*—Named in honor of Charles A. Sandberg, an eminent Devonian expert who explored the area studied.

Remarks.—The presence of lamellar tube structure lacking evident punctuation or pseudopunctuation could indicate that *Aculeiconchus sandbergi* n. gen. n. sp. was either entirely devoid of such microstructural features or that these were poorly developed. Thus, for the moment, the species *Aculeiconchus sandbergi* n. gen. n. sp. is best included in the family Palaeoconchidae, to which the spine-bearing microconchids of *Spinuliconchus* Zatoń and Olempska, 2017 have also been assigned (see Zatoń and Olempska, 2017). With respect to external tube morphology and ornamentation, the new species described here could be like other microconchid species, e.g., *Microconchus vinni* Zatoń

and Krawczyński, 2011b from the upper Givetian of the Holy Cross Mountains, Poland. However, *Aculeiconchus sandbergi* n. gen. n. sp. differs from all other described microconchid genera and species by its hollow spines located solely on the tube base. Two species of Devonian microconchids from the USA and Poland—*Spinuliconchus angulatus* (Hall, 1861) (see Zatoń et al., 2012b) and *Spinuliconchus biernatae* Zatoń and Olempska, 2017, respectively—possess short, hollow spines, but these are located exclusively on the dorsal and lateral sides of their tubes (Fig. 7). The latter species also comes from deposits of fully marine paleoenvironments, whereas the new species described here comes from estuarine, fresh to brackish water deposits. Because the basal spines present in the Maywood microconchids could have played a specific function different from those of *Spinuliconchus* spp. (see below), the erection of the new genus and species on the basis of these spines is fully justified.

For the moment, *Aculeiconchus sandbergi* n. gen. n. sp. is only known from the Devonian Maywood Formation of Wyoming and thus can be tentatively regarded as an endemic species. However, because microconchid tubeworms, and especially those from nonmarine deposits, are still poorly recognized, this genus and species could be found in other units in the future.

Microconchids, palynofacies and age of the Maywood Formation

The microconchid tubes are loose specimens in the host rock. Although the deposits also contain plant fragments, there is no clear evidence that microconchids encrusted them, as is the case of other assemblages associated with plants (e.g., Caruso and Tomescu, 2012; Zatoń et al., 2014b). In the Maywood Formation collections, only one microconchid was found adpressed to a plant fragment, whereas in the older Beartooth Butte Formation, tens of planispirally-coiled microconchids encrusted the plant remains of *Drepanophycus* Goeppert, 1852 (see Caruso and Tomescu, 2012). In our samples, the tubes are both isolated from each other and densely packed. Depending on the sample, ~15–50 tubes are present within 1 cm^2. The deposits are, in some cases, so rich in microconchid tubes that they form
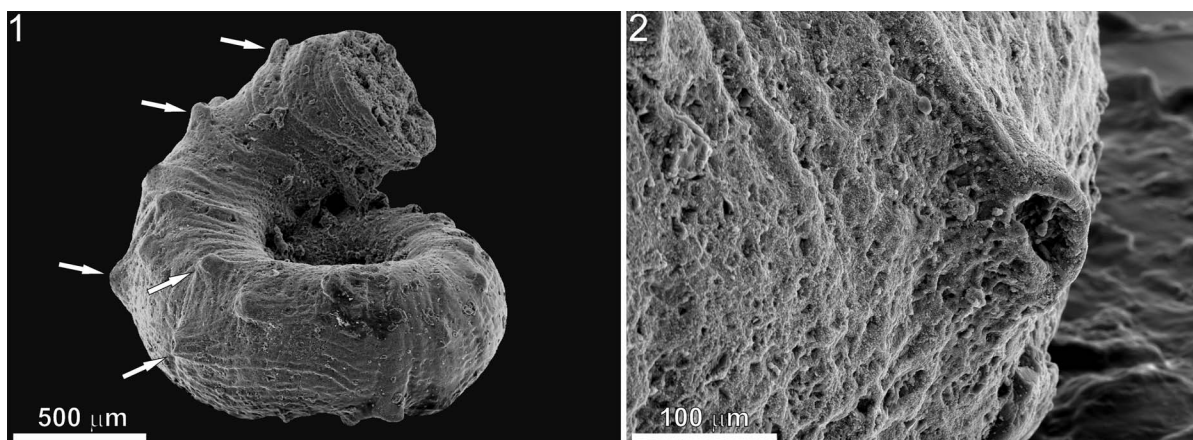
Figure 7. SEM photomicrographs of *Spinuliconchus biernatae* Zatoń and Olempska, 2017 from the Lower Devonian of the Holy Cross Mountains, Poland: (**1**) tube in lateral view showing short hollow spines on its dorsal and lateral sides (arrows); (**2**) magnified hollow lateral spine.

a 'microconchid grainstone.' The specimens are generally oriented parallel or oblique to bedding, and are commonly overturned. In some cases, the apertures of the helically uncoiled, distal parts of the tubes protrude from the layers and their openings are visible. In general, the specimens are relatively complete but can be flattened, and those tubes that are incomplete were probably broken during splitting of the rock samples. Some specimens are coated by iron oxides, most probably after pyrite weathering. The fossils could represent a mix of autochthonous and parautochthonous assemblages. Apart from microconchids and plant fragments, the deposits are also rich in phosphatic fish scales and teeth, some of which represent groups such as acanthodians, symmoriid chondrichthyans, and sarcopterygians (personal communication, M. Coates, 2021).

The four samples analyzed (Fig. 2) are dominated by amorphous organic matter (60–80%), but also contain a low-diversity assemblage of well-preserved trilete spores (15–30%), and low abundances of phytoclasts (tracheids) and indeterminate organic particles (5%). Pyrite (mostly euhedral) is present in low abundance in the exine of the spores, and embedded into algogenic organic matter (AOM) (fibrous, granular, and lumpy) that shows orange fluorescence (Fig. 8).

The samples are dominated by spores of *Geminospora lemurata* Balme, 1962 emend. Playford, 1983, along with some fragments of megaspores (*Biharisporites parviornatus* Richardson, 1965), and many tetrads (most frequently of *G. lemurata*). There are also some algal specimens in the 3.2 m sample that are identified as *Dictyotidium* sp. indet., *Leiosphaeridia* sp. indet., and *Quadrisporites* sp. indet.; some indeterminate forms are present in all four samples (Fig. 8).

The presence of the early–middle Givetian *Geminospora lemurata* (see Richardson and McGregor, 1986; Streel et al., 1987; Avkhimovitch et al., 1993; Melo and Loboziak, 2003; Breuer and Steemans, 2013) and scarce specimens of the middle–late Givetian *Samarisporites triangulatus* Allen, 1965 (e.g., Richardson and McGregor, 1986; di Pasquo et al., 2009; Noetinger and di Pasquo, 2011; Breuer and Steemans, 2013; Turnau, 2014; Noetinger et al., 2018), documented in samples from 3.5 m (Fig. 2), indicates a middle Givetian age for the Maywood Formation.

Discussion

Spines in microconchids and their possible function.—As mentioned above, in microconchid tubeworms, spines have been noted only in two formally described species that inhabited marine paleoenvironments: the Lower Devonian *Spinuliconchus biernatae* from Poland (Zatoń and Olempska, 2017) and *Spinuliconchus angulatus* from the Middle Devonian (Givetian) of the USA (Zatoń et al., 2012b; Zatoń and Olempska, 2017). Spines are also visible in the hand drawing of the Middle Devonian microconchid '*Spirorbis*' *spinulifera* 'Hall,' illustrated by Nicholson (1876), which could represent the genus *Spinuliconchus*. However, details of these spines are lacking.

In both *Spinuliconchus* species, the spines are short, located on the dorsal and lateral sides of the tube, and bent toward the aperture. They are more or less regularly spaced in a single row (*Spinuliconchus angulatus*) or several rows (*Spinuliconchus*

biernatae) on the tube. In *Spinuliconchus biernatae*, the spines are present on both the planispirally coiled and uncoiled parts of the tube (Fig. 7). In both species, the spines are crescent-shaped or circular in cross section, and hollow. Spines located in these positions on encrusting microconchids could have functioned as antipredatory structures against small perpetrators (tiny fish or arthropods), or as antifouling devices impeding overgrowth by other encrusters. However, the optimal place for spines functioning as antipredatory structures would be in close proximity to the aperture from which the lophophore extruded. Spines located in such a position are present in, e.g., bryozoans, where they are sharp and pointed (Taylor and Lewis, 2003; Taylor, 2020), in contrast to the rounded forms of the microconchids. Thus, in the case of the *Spinuliconchus* microconchids, the locations and arrangement of the spines better suggest an antiovergrowth function. In this respect, the spines could have served as natural obstacles hampering other epibionts from competitively overgrowing the microconchids. Similar hollow spines on some Late Ordovician and Silurian cornulitids (Vinn and Mutvei, 2005; Vinn and Eyzenga, 2021), a group from which the microconchids are thought to be derived on the basis of similar skeletal features (Vinn and Mutvei, 2005, 2009; Taylor et al., 2010), could have played a similar function.

Formation, function, and phylogenetic significance of the basal spines of microconchids from Wyoming.—The basal spines noted on the Devonian Maywood Formation *Aculeiconchus* n. gen. microconchids from Wyoming are very similar in shape and structure to spines located on the dorsal and lateral sides of tubes of *Spinuliconchus* microconchids, as discussed above. The basal spines of the Maywood specimens, however, in some cases are longer (to 700 μm versus 140 μm in *Spinuliconchus biernatae*), of greater diameter (∼90 μm versus ∼63 μm in *Spinuliconchus biernatae*), and distally wider. Also, unlike the dorsal and lateral spines of *Spinuliconchus*, the basal spines are oriented perpendicular to the tube base or are directed slightly obliquely, forward or backward of the aperture. Their lengths can differ in single individual fossils.

The overall similarity of the basal spines of the specimens of *Aculeiconchus* n. gen. to the dorsal and lateral spines of *Spinuliconchus* species, and the fact that the microlamellar structures of all of these spines and tubes are similar, clearly indicate that the formation mechanism of the dorsal/lateral spines in *Spinuliconchus* and the basal spines in *Aculeiconchus* n. gen. was the same. Moreover, as noted earlier by Zatoń et al. (2012b), the hollow spines of *Spinuliconchus angulatus* can be referred to as 'tubular hollow' spines, which are characteristic of siphonotretid and productide brachiopods (see Alvarez and Brunton, 2001), but also exist in some lingulate brachiopods, e.g., *Acathambonia portranensis* Wright, 1963 (see Wright and Nõlvak, 1997). Such spines in these brachiopods, as in *Spinuliconchus* microconchids, formed external ornamentation. According to Alvarez and Brunton (2001, p.109), tubular hollow spines grew from a separated bud of generative epithelium at the valve margin, which grew rapidly away from the valve surface, producing a complete tube of shell. Therefore, the spines in *Spinuliconchus* and the basal spines in the Maywood specimens of *Aculeiconchus* n. gen. formed in a similar manner (Fig. 9).
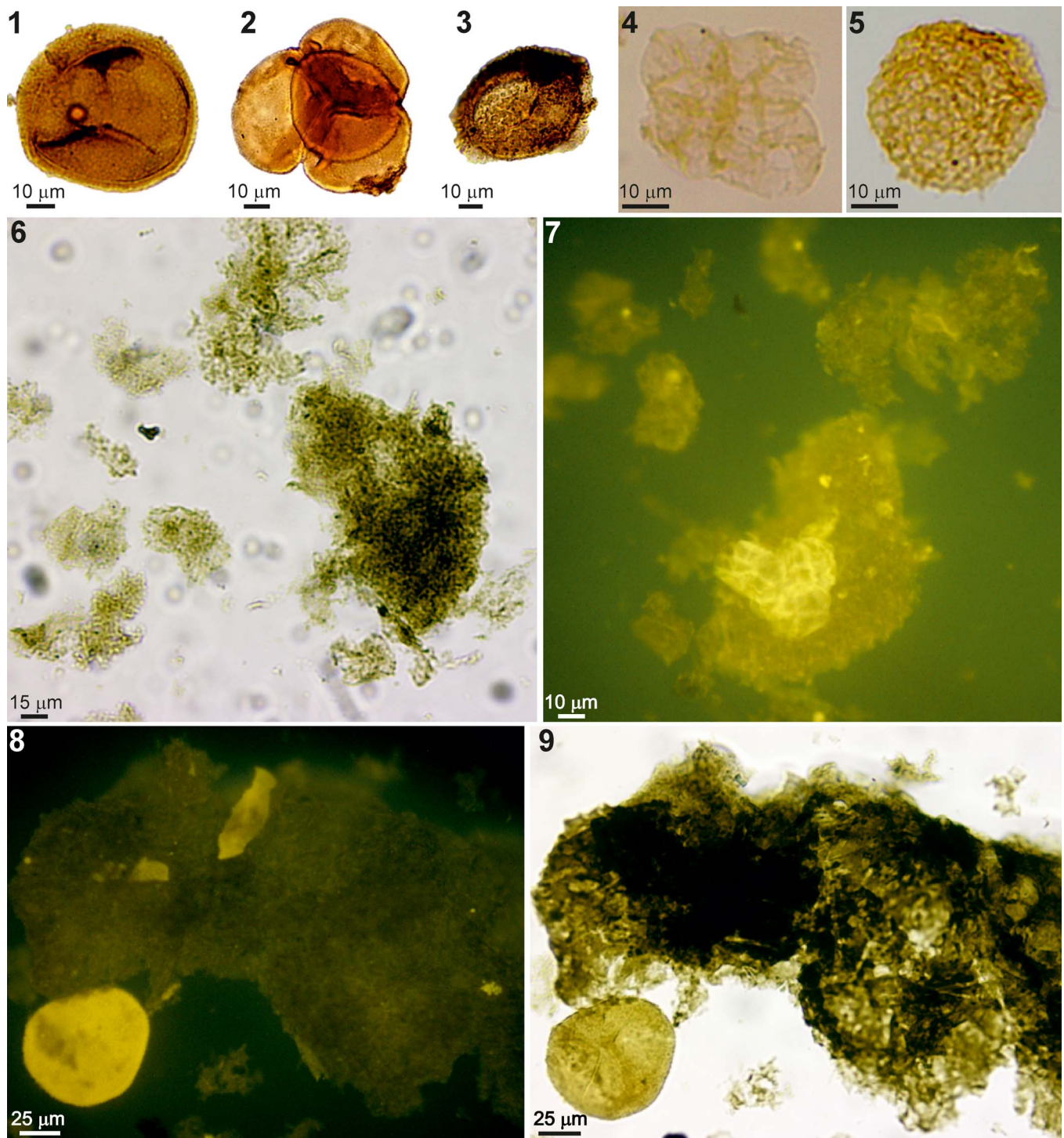
Figure 8. Some biostratigraphically important and characteristic palynomorphs from the Maywood samples: (**1**) *Geminospora lemurata* Balme, 1962 emend. Playford, 1983, CICYTTP-Pl 2606-R-3823-2A-ox England Finder coordinates (EF) H16/4; (**2**) *Geminospora lemurata* Balme, 1962 emend. Playford, 1983, CICYTTP-Pl 2605-R-3823-1A EF M24/1 (tetrad); (**3**) *Samarisporites triangulatus* Allen, 1965, CICYTTP-Pl 2606-R3823-2B EF P29/3; (**4**) *Quadrisporites* sp. indet., CICYTTP-Pl 2608-R3823-4A-ox EF M30/1; (**5**) *Dictyotidium* sp. indet., CICYTTP-Pl 2605-R3823-1C-ox EF O29; (**6**) amorphous organic matter under white light, CICYTTP-Pl 2607-R3823-3A EF O29; (**7**) algal colony revealed under flourescence not seen in (**6**), CICYTTP-Pl 2607-R3823-3A EF O29; (**8, 9**) *G. lemurata* and AOM lump under white light (**8**) and fluorescence (**9**), CICYTTP-Pl 2605-R3823-1A EF O29.

Interestingly, similarly hollow tubular projections also occur in some cyclostome bryozoans, e.g., *Tubulipora andersonni* Borg, 1926. In these bryozoans, the tubes are in fact extensions of their exterior colony walls, and the spaces within the tubes are confluent with body cavities of the living chambers of feeding zooids (Boardman, 1983). Thus, tubular extensions in these bryozoans also formed in a similar way as the microconchid hollow spines. Taking the close phylogenetic
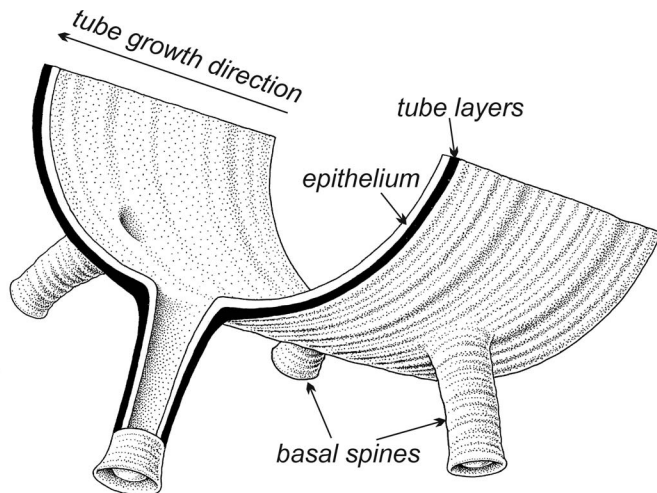
Figure 9. Schematic section through the tube and basal spine of *Aculeiconchus sandbergi* n. gen. n. sp., showing that these hollow spines probably grew from a separated bud of epithelium at a tube margin, as in some brachiopods.

relationships of microconchids and 'lophophorates' (a clade including phoronids, brachiopods, and bryozoans; see Taylor et al., 2010; Taylor, 2020) into account, the acceptance of a similar formation mechanism for hollow spines in these groups is justified. Below, the position and interpreted function of the basal spines in *Aculeiconchus* n. gen. microconchids is compared with its spine-bearing brachiopod and bryozoan relatives. It is well known that tubular hollow spines in productide brachiopods—e.g., *Horridonia horrida* (Sowerby, 1823) (see

e.g., Kaźmierczak, 1967) and *Levitusia humerosa* (Sowerby, 1822) (see Brunton, 1982) —served to stabilize shells on the soft sea bottom. The spines of chonetidine brachiopods served the same purpose, allowing them to survive in higher energy paleoenvironments (Mills and Leighton, 2008). The productide brachiopod *Heteralosia slocomi* King, 1938 used its prominent hollow spines for attachment, i.e., for clasping and cementing to other objects (Pérez-Huerta, 2013). The basal spines of the *Aculeiconchus* n. gen. microconchids could have been potentially used for anchoring the microconchid tube, providing additional stabilization in unconsolidated sediment, as in some productide brachiopods. The different lengths of the basal spines, noted in the *Aculeiconchus* n. gen. tubes and as broken specimens scattered loosely in the strata (Fig. 6.2, 6.3), indicate that they could have been elongated during the organism's life. The variable lengths, and the spines' flat and widened terminations, could have enhanced stabilization on the substratum (Fig. 10.1). As with some brachiopods, spine lengthening could have been possible due to the presence of epithelium within the spines, and proliferation of generative zones that secreted the tube material at the distal end of the spines (Brunton, 1976; Alvarez and Brunton, 2001; Pérez-Huerta, 2013). However, such a mode of life is unusual in microconchids, because the great majority of species are known to have cemented to hard, firm substrata along planispirally coiled tubes, and no species described to date possess basal spines. Of course, not all previously described microconchids had a fully encrusting mode of life, e.g., *Spathioconchus weedoni* Zatoń et al., 2016a from the Lower Triassic of Greenland, which coped well with soft bottom sediment. However, this species had a unique, nearly straight
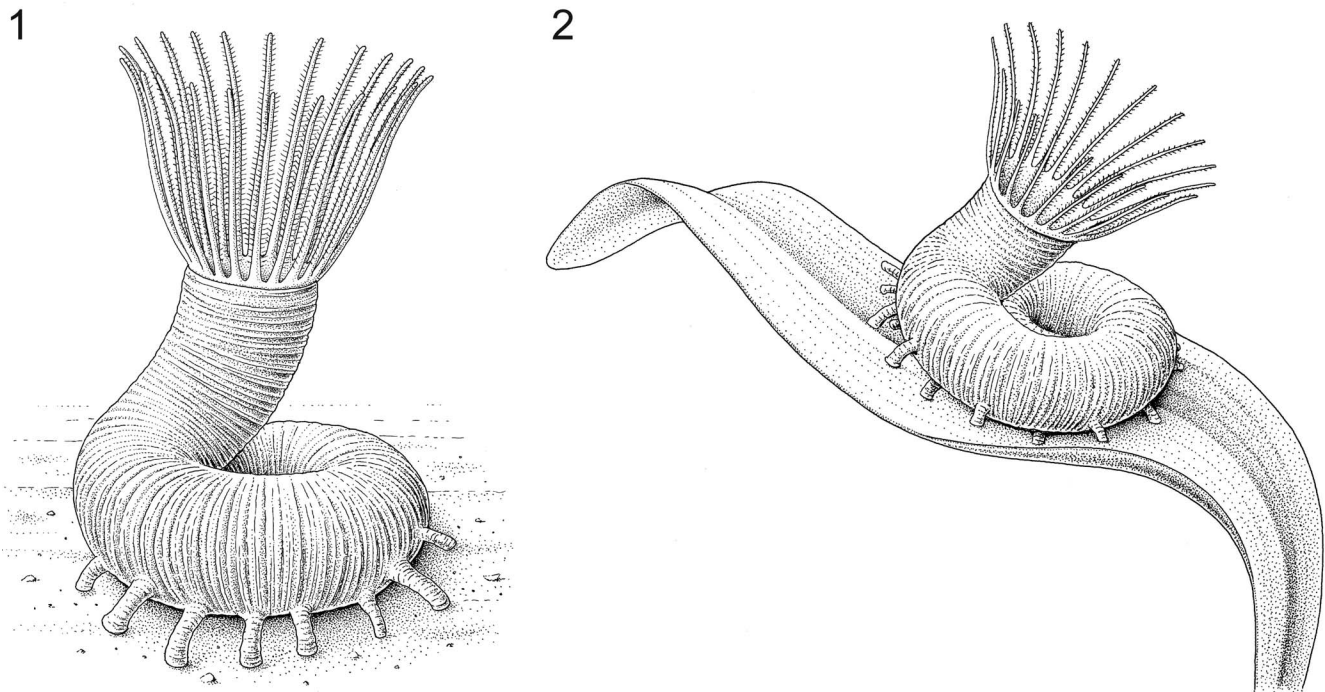
Figure 10. Reconstruction of *Aculeiconchus sandbergi* n. gen. n. sp.: (**1**) a productide brachiopod mode of life, in which the microconchid rests on unconsolidated substratum with basal spines serving as anchoring, stabilizing devices (less likely); (**2**) a cyclostome bryozoan mode of life, in which the microconchid colonizes an algal thallus with its basal spines serving as attachment extensions that were adapted for fixation to flexible substrata (preferred). The ciliated lophophore crown is hypothetical.

tube which, following larval attachment to any small, hard particle, was able to grow horizontally on the substratum, kept pace with aggregating sediment by accommodation of its tube growth, and formed small buildups (Zatoń et al., 2018). Thus, the small size and planispiral morphology of *Aculeiconchus* n. gen. seem to be rather unlikely features for stable residence on a soft bottom, even with the aid of thin, basal spines, which are present in some much larger brachiopods. It is very likely that such tiny organisms would have been easily displaced, covered by sediment, and smothered by any strong sedimentary event or the burrowing activities of benthic animals.

A much better analogy is provided by some Recent and fossil bryozoans. As mentioned above, examples of both modern cyclostome tubuliporines, e.g., *Tubulipora andersonni* and some fossil examples (see Voigt, 1992), possess calcified tubular extensions growing on the underside of the colonies, which enabled the bryozoans to efficiently fix to soft, flexible substrata, e.g., algae (Boardman, 1983; Voigt, 1992). Similar, but chitinous, basal extensions also occur in the order Cheilostomata (Voigt, 1992; Vieira and Stampar, 2014). Such basal tubular extensions, serving as restricted points of attachment, could prevent the bryozoan colonies from cracking during bending of flexible substrata, e.g., algal thalli. A similar role could have been played by the basal spines of *Aculeiconchus* n. gen. (Fig. 10.2), especially because some microconchids colonized algal substrata (e.g., Peryt, 1974; Zatoń and Peck, 2013; Shcherbakov et al., 2021). The terminations of some basal spines of microconchids are flat (Fig. 4.3, 4.6) like those of bryozoans (cf. Boardman, 1983, fig. 61.1; Voigt, 1992), suggesting a firm, wide attachment area. The variable length of basal spines in these microconchids, on other hand, is strong evidence that the encrusted substratum was flexible and uneven at the point of tube attachment, in part because by basal spine lengthening, the animal could adjust its tube growth on a flexible substratum. In many cases, microconchids are found as loosely scattered specimens, possibly indicating detachment following degradation of such unmineralized substrata. In the deposits of the Maywood Formation, specimens of *Aculeiconchus* n. gen. are also loosely scattered in the host deposit, being commonly preserved obliquely and as overturned individuals. This kind of preservation might have resulted from substratum degradation, followed by the scattering of specimens on the bottom. The lack of algal fossils preserved in the Maywood deposits certainly results from purely taphonomic processes. It is well known that noncalcified algae have very low fossilization potential, and if they are preserved, they are usually confined to dark, fine-grained Konservat-Lagerstätte deposits (e.g., LoDuca et al., 2011; Filipiak and Zatoń, 2016). Even carbonate thalli of charophyte algae usually disintegrate after algal death and source the fine-grained fraction of the bottom sediment (e.g., Apolinarska et al., 2011). Only their calcified female fructifications (gyrogonites) are usually fossilized and provide evidence for the presence of the charophyte. Such microconchid–gyrogonite associations are known from the fossil record (Racki and Racka, 1981; Ilyes, 1995; Zatoń and Peck, 2013; Shcherbakov et al., 2021), indicating that at least some microconchids might have colonized these algae. Assuming that *Aculeiconchus* n. gen. microconchids lived similarly to some bryozoans, their basal spines could be the sole evidence of the former presence of algae to which they attached.

As mentioned above, some specimens also have helically uncoiled tubes in an upright position. Such vertical growth mode could have resulted from several factors, including escape from other encrusting organisms, or in the case of inhabiting strictly benthic microhabitat (e.g., shells, stones), an attempt to keep pace with sediment aggradation (Burchette and Riding, 1977; Vinn, 2010). Given the absence of other associated epibionts in the Maywood deposits, and the assumption that microconchids colonized algal thalli well above the bottom sediment, the crowding of associated microconchids on a given substratum is a more likely explanation for helical tube growth in some of the specimens.

A bryozoan-like attachment mode, found for the first time in *Aculeiconchus* n. gen. microconchids, not only provides a completely novel attachment strategy in this group of tentaculitoid tubeworms, but also suggests that microconchids were even more phylogenetically close to their 'lophophorate' relatives (Taylor et al., 2010; Vinn and Zatoń, 2012). Analysis of characters (see Vinn and Zatoń, 2012) placed the entire tentaculitoid group close to the Brachiozoa (Brachiopoda + Phoronida). However, in addition to the calcareous skeleton, bulb-like tube origin, lamellar and punctate (with punctae pointed in a direction of skeletal accretion) tube microstructure, the presence of budding in some of the species (*Helicoconchus*, see Wilson et al., 2011), and encrusting mode of life characteristic for all microconchids in general (e.g., Taylor and Vinn, 2006; Taylor et al., 2010), the presence of hollow basal spines serving as devices for attachment to flexible substrata in *Aculeiconchus* n. gen. suggests that microconchids, unlike other tentaculitoids (see Vinn and Zatoń, 2012), might not have been as phylogenetically distant from bryozoans as previously thought.

Paleoecological implications.—The Maywood Formation is widely distributed in Montana and northern Wyoming (Sandberg, 1961; Kauffman and Earll, 1963; Sandberg and McMannis, 1964). As mentioned earlier, based on its faunal composition (fish and spores), the Maywood was deposited in brackish or fresh water (Sandberg and McMannis, 1964) within shallow, potentially long, narrow estuaries that extended from epicontinental seas during transgression of the Middle Devonian. Further transgression eventually led to widespread nonchannelized deposition of the marine Jefferson Formation in the early Late Devonian.

The paleosalinity range for microconchids is highly debated (Gierlowski-Kordesch and Cassle, 2015; Zatoń et al., 2016b). Taylor and Vinn (2006) and Zatoń et al. (2012a) showed that microconchid tubeworms as a group were tolerant of different paleosalinity regimes and habitats, and were able to thrive in various fully marine, brackish, or even freshwater paleoenvironments. Gierlowski-Kordesch and Cassle (2015), however, argued that osmoregulation from fully marine to fully freshwater conditions by the microconchids is highly unlikely, and that they would have only occupied marine- and brackish-water settings. They hypothesized that the existence of microconchids in association with freshwater fauna was due to transport of marine or brackish water microconchids by marine processes (e.g., storm surges). On the basis of numerous examples, Zatoń et al. (2016b) rejected this hypothesis and supported the idea that microconchids originated in the Late Ordovician in shallow

shelf environments and later colonized marginal marine environments, and eventually freshwater habitats by the Early Devonian through the evolution of osmoregulation (Zatoń et al., 2012a), as did ostracodes during their invasion of freshwater habitats (Bennett, 2008). Indeed, the colonization of freshwater habitats by microconchids is supported by firm paleontological evidence, e.g., their coexistence with such terrestrial or freshwater components as vascular plant remains (Sandberg, 1963; Brower, 1975; Mastalerz, 1996; Zatoń and Mazurek, 2011; Caruso and Tomescu, 2012; Florjan et al., 2012; Zatoń and Peck, 2013; Shcherbakov et al., 2021), charophytes (Ilyes, 1995; Zatoń and Peck, 2013; Shcherbakov et al., 2021), spinicaudatans, and freshwater ostracodes and bivalves (Trueman, 1942; Zatoń and Peck, 2013; Shcherbakov et al., 2021).

The *Aculeiconchus* n. gen. microconchids of the Maywood Formation are found in association with plant remains, but they also exist in carbonate facies that grade into the overlying, fully marine Jefferson Formation. These suggest a likely brackish water origin, although temporary fully freshwater conditions cannot be ruled out. This is supported by the organic microfossil data presented in this study. Indeed, the terrestrial spores recovered from the Maywood samples belong to progymnosperm, lycopsid, and primitive fern groups (see Supplemental Data 1), which were major components of swamp plant communities (Streel and Scheckler, 1990), suggesting very close proximity of freshwater sources to the depositional paleoenvironment of the Maywood Formation. The highly abundant progymnosperm *Geminospora* spp. indet., in particular, specifically suggests deposition in, or adjacent to, fluviolacustrine, lower floodplain, or paralic environments (Streel and Scheckler, 1990). Fine granular and fibrous AOM with orange fluorescence has been linked with various terrestrial and algal aquatic sources. In addition, well-preserved terrestrial spores, and the presence of megaspores, tetrads, and pyrite, all support a brackish, shallow-water depositional setting. This agrees with other fossiliferous and lithologic evidence provided in this and previous studies (e.g., Sandberg, 1963).

The large aggregations of monospecific microconchids likely reflect colonization of stressed environments (Zatoń et al., 2012a), specifically in waters of variable salinities, which we envision for the Maywood estuaries. The abundance of microconchids in these settings is due in part to environmental exclusion of predators and competitors, and an abundance of nutrients delivered directly from fluvial sources (Zatoń et al., 2012a; Shcherbakov et al., 2021).

A nearly identical suite of fossils, including microconchids, plant debris, spores, and fish fragments, are present in the underlying Beartooth Butte Formation at both Cottonwood Canyon and Beartooth Butte (Sandberg, 1961, 1963; Elliot and Johnson, 1997; Caruso and Tomescu, 2012). Those estuarine channel-fill deposits are Lockhovian/Pragian and Emsian in age, respectively, and thus the older strata at Cottonwood Canyon are nearly 30 Myr older than the Maywood strata (Elliot and Ilyes, 1996; Elliot and Johnson, 1997; Noetinger et al., in press). The reappearance of nearly identical lithofacies and suites of vertebrate, invertebrate, and flora is a remarkable paleogeographic and paleoecological pattern. Paleogeographically, channels cut during lowstands were repeatedly inundated by transgressing oceans, establishing estuarine valleys that were filled by fine-grained mixed siliciclastic–carbonate strata. This paleoecologic pattern was repeated over a

30 Myr interval and includes the colonization of dynamic, migrating, brackish to freshwater environments by opportunistic, monospecific microconchids and associated nektonic vertebrate and cartilaginous fauna. In the Cottonwood Canyon section, the Maywood channels were in the upper reaches of the estuarine system and were <5 m deep (Sandberg, 1963). This narrow, marginal marine realm, with its component fauna and flora, would have tracked the Givetian transgressing ocean, producing a characteristic lithofacial and biofacial assemblage that replicated those established earlier in the Lower Devonian during deposition of the Beartooth Butte Formation. However, the specific nature of microconchids changed from those encrusting *Drepanophycus* plants, as known from the Beartooth Butte Formation, to a completely new species that could have evolved basal spines adapted for fixation to flexible algal substrata.

The repeated incision of the Beartooth Butte and Maywood channels into bedrock preceded the Antler Orogeny and associated foreland basin (Speed et al., 1988; Dorobek et al., 1991), which largely affected areas far to the west (i.e., Nevada region) and was initiated after deposition of these units. The Antler Orogeny is generally attributed to mid-Frasnian at the earliest and generally Late Devonian to Early Mississippian (Silberling and Roberts, 1962; Smith and Ketner, 1968; Johnson and Pendergast, 1981; Macke, 1993; Ketner, 2012).

The Wyoming shelf was thus tectonically quiescent during most of the Devonian, which indicates that channel incision during lowstands was almost certainly driven by eustasy (Dehler, 1995; Grader and Dehler, 1999). The Beartooth Butte Formation, with channel-fills of Lockhovian/Pragian boundary (Cottonwood Canyon) and mid-Emsian (Beartooth Butte, Wyoming) ages, correspond to well-known regressive to transgressive episodes, specifically the bases of Johnson et al.'s (1985) Ia and Ic events, respectively (see also Johnson and Sandberg, 1988). The Maywood channels were filled during the Givetian, corresponding to the base of the IIb event (Johnson et al., 1985; Johnson and Sandberg, 1989). These eustatic events created narrow, stressed ecological niches that microconchids were well adapted to exploit, and they did so repeatedly over a long stretch of geologic time by tracking transgressive pulses within valleys cut during previous episodes of lowstand erosion.

Conclusions

Herein, we describe a new genus and species of microconchid, *Aculeiconchus sandbergi* n. gen. n. sp., from samples collected from the Devonian Maywood Formation of Wyoming, which has basal spines on the undersides of their tubes. In this regard, they are unusual relative to all previously described microconchid species, which either lack spines or have dorsal and lateral spines only. The spines are identical with respect to microstructure, and thus in formation mechanism, to spines of all other species of microconchids. All microconchid spines, including those of *Aculeiconchus* n. gen., are comparable to the tubular hollow spines known in some brachiopod groups, especially siphonotretids and productides. They are also like basal tubular extensions in some modern and fossil cyclostome bryozoans. The basal spines of *Aculeiconchus* n. gen. certainly had an adaptive function different from the dorsal and lateral spines in other microconchid species. Unlike some productide

brachiopods, which used the hollow spines for anchoring and stabilizing the shell on unconsolidated soft sediment, we propose that the basal spines of the *Aculeiconchus* n. gen. microconchids had a similar function to the tubular basal extensions of some cyclostome bryozoans, which use them for fixation to flexible algal thalli. Such an ecological adaptation is novel relative to all microconchids described to date, thus expanding their disparity and the range of known strategies for colonization of variable substratum types and paleoecological habitats, for this poorly recognized clade of opportunistic tentaculitoids. Moreover, the bryozoan-like basal spines found in *Aculeiconchus* n. gen. suggests that microconchids, although phylogenetically linked with 'lophophorates,' might not have been so distant from bryozoans.

The Maywood microconchids are both dispersed and make up very thin (a few mm) monospecific (*Aculeiconchus sandbergi* n. gen. n. sp.) shell accumulations. A wide variety of phosphatic cartilaginous and bony fish remains, and abundant plant fossils are found in association with these tubeworms. As with the underlying Lockhovian/Pragian Beartooth Butte Formation, which contains a nearly identical suite of fossils and was similarly deposited within channels, we interpret the Maywood as an estuarine, brackish water channel fill. The fauna and flora in both formations suggest that brackish water produced stressed environments that opportunistic microconchids repeatedly colonized over an ~30 Myr interval. These narrow, shallow-water environments tracked marine incursions through channels that were successively cut during repeated lowstands. Tectonic quiescence of the central to northern US Rocky Mountain region during most of the Devonian indicates that erosion and subsequent deposition were driven by major eustatic events.

These Devonian deposits record a remarkable paleogeographic and paleoecological pattern that is recorded by channel erosion, transgression, and colonization of a particular suite of flora and fauna, including microconchids. The specific salinity-stressed paleoenvironments led to a series of adaptive innovations in microconchids, specifically those that allowed colonization of a diverse suite of substrata from plant roots, to hard substrata, and to flexible soft algal thalli.

Acknowledgments

Data availability statement

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.wwpzgmsk7.

Supplemental Data 1. Botanical affinity of the taxa encountered in the Maywood Formation.

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