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RESURRECTING *SPHONDYLOPHYTON* AS A RHODOPHYTE ALGA FROM THE EARLY DEVONIAN

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Premise of research. Although largely neglected by the paleobotanical literature, the Early Devonian genus *Sphondylophyton* Schultes and Dorf is on record as the oldest sphenophyte. Given current understanding of the fossil record, a revised interpretation of the depositional environment at the fossil locality, and the discovery of new specimens, reconsideration of the taxonomic affinities of *Sphondylophyton* is necessary.

Methodology. All known *Sphondylophyton* specimens were examined for morphological comparison with plant and algal lineages exhibiting a similar whorled architecture.

Pivotal results. *Sphondylophyton* is characterized by sparsely branched, flexuous axes bearing whorled, simple, terete appendages with dimorphic apical morphology. Sphenophyte affinities are ruled out, as whorled taxis does not appear in vascular plants until the Late Devonian. Evidence for marine influences in the depositional environment of *Sphondylophyton* warrants consideration of algal affinities. Although dasycladalean and charophycean green algae share superficial morphological similarities with *Sphondylophyton*, they can be excluded upon detailed comparison (e.g., branching, lateral appendage dimensions and complexity). The combination of characters of *Sphondylophyton* falls within the morphospace of the Rhodophyta. Among these, *Sphondylophyton* is most similar to rhodomelacean taxa in overall habit, appendage morphology, and thallus durability. Generic and specific emended amplified diagnoses are provided.

Conclusions. *Sphondylophyton* is not a sphenophyte as previously suggested; dasycladalean and charophycean affinities are not supported. We demonstrate that *Sphondylophyton* is a red alga most comparable to Rhodomelaceae, although no taxonomic placement below the phylum rank is proposed; as such, it contributes to the limited fossil record of the Rhodophyta.

Keywords: algae, Devonian, fossil, Rhodophyta, Sphenophyta, Wyoming.

Introduction

The monotypic genus *Sphondylophyton* was erected by Schultes and Dorf (1938) for a small number of compression fossils from the Early Devonian Beartooth Butte Formation at Beartooth Butte, Wyoming, described as *Sphondylophyton hyenioides* Schultes and Dorf. Discussing the whorled arrangement of appendages, these authors considered both algal and sphenophyte affinities for *Sphondylophyton*. They concluded that *Sphondylophyton* was an early sphenophyte and proposed that it could represent a link between the algae and the early sphenophytes.

Since its original description, *S. hyenioides* remains unknown outside of the type locality. The taxon has seen only a few citations in the literature (Høeg 1942; Arnold 1947; Boureau 1964), and these are limited to passing commentary. The lack of recognition has continued in modern paleobotany, despite the provocative implication of Schultes and Dorf's interpretation, namely, that *Sphondylophyton* is the earliest rep-

resentative of the sphenophyte lineage and hence an important early vascular plant.

Forty years later, in a doctoral dissertation surveying the Early Devonian flora of the Beartooth Butte Formation of Wyoming, Tanner (1983) provided a revised treatment of *Sphondylophyton* based on four additional slabs bearing more than a dozen new specimens. Tanner's additional fossils were largely consistent with Schultes and Dorf's (1938) original description and provided evidence for variation in size and habit. Based on the morphology of the fossils and drawing on a revised interpretation of the depositional environment as largely continental but including some marine influences (Denison 1956), Tanner concluded that the sphenophyte affinities of *Sphondylophyton* were doubtful and that the fossils were more likely affiliated with an algal group such as the Characeae. However, except for the description of a new species of *Gosslingia* Heard (Tanner 1982), all the specimens and discussions in Tanner's dissertation remain unpublished.

To the best of our knowledge, there is no mention of *Sphondylophyton* in the primary literature following Tanner's work, and the genus is not discussed in the latest paleobotany textbooks that provide extensive taxonomic surveys (Stewart and Rothwell 1993; Taylor et al. 2009). Here, 75 years after Schul-

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tes and Dorf's initial description, we reconsider *Sphondylophyton* in light of (1) previously undescribed, well-preserved specimens, (2) a new interpretation of the depositional environment of the Beartooth Butte Formation, and (3) an improved understanding of the Paleozoic fossil record of sphenophytes and algae. This study is aimed at better characterizing *Sphondylophyton*, updating the diagnosis of the genus, and reassessing its taxonomic affinities. The improved characterization of the genus is achieved by examination of all known *Sphondylophyton* specimens. Taxonomic affinities are addressed by defining the morphospaces occupied by individual plant and algal lineages that exhibit the level of organization and whorled architecture of *Sphondylophyton* (this is done using the morphology of their living and extinct representatives) and then determining whether the combination of characters that defines *Sphondylophyton* is included in the different lineage morphospaces.

Age and Depositional Environment of the Beartooth Butte Formation

The Beartooth Butte Formation is a Lower Devonian unit underlain by the Ordovician Bighorn Dolomite and overlain by the Upper Devonian Jefferson Limestone (Blackstone and McGrew 1954; Sandberg 1961). The unit is plant fossiliferous at two localities in Wyoming: Beartooth Butte and Cottonwood Canyon (Dorf 1933; Blackstone and McGrew 1954; Tanner 1982, 1983). Palynological analyses by D. C. McGregor (reported in Tanner 1983) suggest a late Lochkovian-early Pragian age at Cottonwood Canyon and a middle-late Emsian age at Beartooth Butte, both confirmed by fish biostratigraphy (Elliot and Johnson 1997). Throughout northern Wyoming and southern Montana, the Beartooth Butte Formation has geometries reminiscent of channel-fill deposits (Schultes and Dorf 1938; Blackstone and McGrew 1954; Sandberg 1961). Fish and eurypterids are present in the unit along with the plant fossils (Denison 1956; Tetlie 2007). The unit has been interpreted, in broad terms, as fresh- and brackish-water deposits of estuarine to fluvial environments, based on its fossil content and on geometry (Dorf 1934; Denison 1956; Sandberg 1961).

The plant assemblages bring detail to this interpretation. At Cottonwood Canyon, plant fossils often occur in dense autochthonous and parautochthonous assemblages that include frequent instances of in situ preservation. Additionally, the lithology of plant-fossiliferous layers consists mostly of dolomitic sandstone, dolomitic siltstone, silty dolomite, and shale, with dolomitic limestone interbeds (Blackstone and McGrew 1954; Sandberg 1961), and reflects locally variable depositional environments within small lateral (meter-scale) and vertical (10–50-cm) distances. Together, these are consistent with preservation of plant fossils at Cottonwood Canyon in fluvial or estuarine sediments formed at the water-land interface, in areas with variable, rapidly changing environments of deposition (Tomescu et al. 2010).

In contrast, at Beartooth Butte, the unit consists of a dolomitized sequence including a basal limestone conglomerate overlain by limestone and limestone conglomerate interbedded with calcareous shale (Dorf 1934; Blackstone and McGrew 1954; Sandberg 1961). Plant fossils are rare, fragmentary, and

found dispersed as isolated specimens in limestone beds. The rarity and high degree of dispersion of plant fossils, along with lithology, indicate incidental preservation as a result of long-distance transport and deposition away from their living environments in a lower-energy, deeper environment. Within the overall picture of the Beartooth Butte Formation as fresh- and brackish-water deposits of estuarine to fluvial environments (Denison 1956; Sandberg 1961), these suggest for the plant-fossiliferous layers at Beartooth Butte a deeper depositional environment (e.g., estuary mouth) with marine influences. This interpretation is consistent with stable oxygen and carbon isotope data that indicate stronger marine influences at Beartooth Butte than at Cottonwood Canyon (Fiorillo 2000).

Material and Methods

Sphondylophyton is preserved as compressions in brick-red limy shales interbedded in a thick layer of massive limestone of the Beartooth Butte Formation (Dorf 1934; Schultes and Dorf 1938). All known specimens were collected at the Beartooth Butte locality (northern Wyoming, Park County, lat. 44°57'N, long. 109°37'W). We reexamined all previously described *Sphondylophyton* specimens, curated in the paleobotanical collections at the Field Museum of Natural History (Chicago); those on the single rock slab used in the original description by Schultes and Dorf (1938)—PP49107—and those collected and described by Tanner (1983)—PP49109, PP49113, PP49115, and PP49118.

A previously undescribed rock slab containing several *Sphondylophyton* fossils (YPM44602) was recently discovered in the paleobotanical collections at the Yale Peabody Museum of Natural History (New Haven, CT) by Shusheng Hu. Museum records lack a collection date and indicate only that the slab was collected by Erling Dorf at Beartooth Butte. The lithology of the slab, as well as its *Sphondylophyton* content, indicates that it belongs to the Beartooth Butte Formation. The quality of the fossils surpasses that of all other known specimens, suggesting that the new slab was collected after the 1938 publication. That this is a later collection of additional Beartooth Butte specimens is likely because Dorf continued his studies in the nearby Yellowstone region long after the initial Beartooth Butte discoveries. It is unclear how and when this slab was acquired by the Peabody Museum and why it was not considered by Tanner (1983).

The *Sphondylophyton* fossils are compressions. Much of the thickness of the Beartooth Butte Formation is oxidized, as reflected in the strong orange-red coloration of outcrops. Plant fossils in some layers of the unit exhibit oxidation colors (orange to red and brown), which suggest different degrees of diagenetic replacement of the carbonaceous material with iron oxides and hydroxides. *Sphondylophyton* compressions are purple-red to brown, and their thickness indicates robust tissues. The exact numbers of *Sphondylophyton* individuals on the different rock slabs are difficult to assess, as many specimens represent fragments, though we estimate that the combined collections of the Field Museum and the Peabody Museum include a minimum of 23 distinct shoots. Given the systematic implications of this study, we use algal terminology to describe the morphology of *Sphondylophyton*.

Neorhodomela larix specimens were collected from the in-

tertidal zone of northern Humboldt County, California. The material was studied using a Wild M5 dissecting microscope and a Nikon Eclipse E400 compound microscope equipped with a Nikon Coolpix E8800 digital camera. Some images were taken with the specimens immersed in 100% isopropanol for enhanced contrast (figs. 2A, 3G, 4B [bottom row, left]). Measurements were obtained using ImageJ (National Institutes of Health, Bethesda, MD). Images were processed with Pixelmator 1.67 (Pixelmator Team, London) and Adobe Photoshop 7.0 (Adobe Systems, New York).

Systematic Description

Phylum—Rhodophyta Wettstein

Genus—Sphondylophyton Schultes and Dorf

Generic emended diagnosis. Thalli of flexuous habit composed of axes bearing whorls of determinate branches at nodes. Nodes widely spaced, except near the tips, where the whorls are crowded. Indeterminate branches arising at nodes. Thallus base with rounded holdfast.

Type Species—Sphondylophyton hyenioides Schultes and Dorf

Specific emended diagnosis. Mature thalli at least 45 mm long. Thallus axis up to 2 mm wide, bearing whorls of four terete determinate branches at nodes. Determinate branches up to 2 mm wide, 14 mm long, slightly incurved and broadening toward apex. Nodes near axis apex bear determinate branches with papillate tips; proximal nodes bear determinate branches with rounded tips. Internodes ~5 mm and up to 20 mm long, becoming shorter toward axis apex. Indeterminate branches rare, arising at nodes. Holdfast round, ~2 mm across.

Holotype. PP49107, Field Museum of Natural History, Chicago (formerly Princeton University Paleobotanical Collections no. 24101; Schultes and Dorf 1938; fig. 1B).

Paratypes. Specimens from rock slabs YPM44602 (Yale Peabody Museum of Natural History, New Haven, CT; fig. 1A) and PP49109 (Field Museum of Natural History, Chicago; fig. 2A).

Stratigraphic position and age. Beartooth Butte Formation, middle to late Emsian (Early Devonian).

Locality. Beartooth Butte, Park County, Wyoming; lat. 44°57'N, long. 109°37' W.

Description

Sphondylophyton hyenioides consists of thalli of flexuous habit composed of a main axis with nodes and internodes. The nodes bear regular whorls of determinate branches (figs. 2A, 3C–3E) and rare indeterminate branches (fig. 2A). No complete thalli are known, though three thalli exhibit rounded structures (~2 mm in width; fig. 3B) at the base, interpreted as holdfasts; two thalli with complete apical regions are documented. No cellular-level detail or reproductive structures are preserved.

The largest (incomplete) specimens measure up to 45 mm in length and have main axes up to 2 mm across. The determinate branches are arranged in whorls composed of four

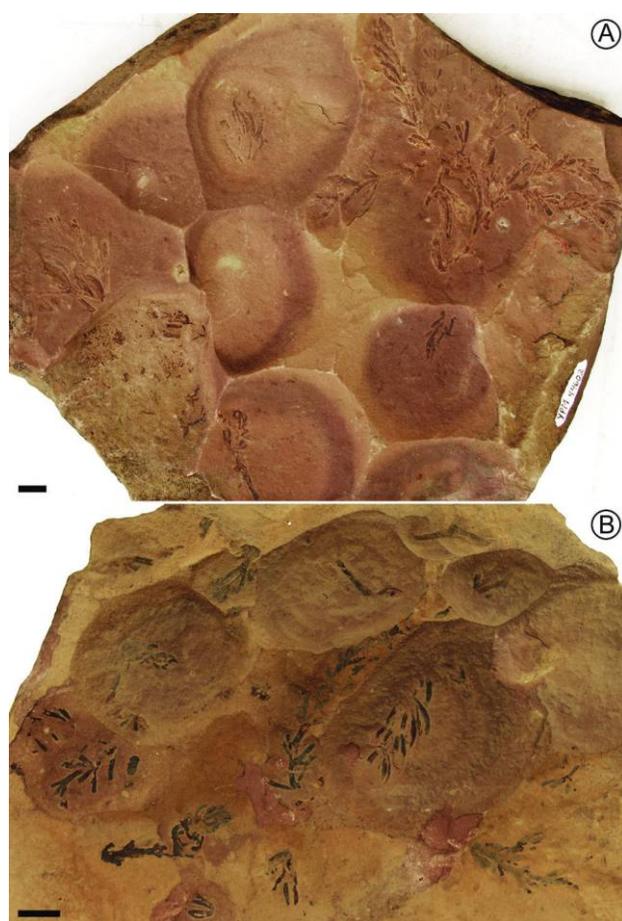


Fig. 1 *Sphondylophyton hyenioides* Schultes and Dorf, Early Devonian, Beartooth Butte, Wyoming. A, Paratype, discovered at Yale Peabody Museum of Natural History in 2009; YPM44602. B, Holotype, discovered by Erling Dorf in 1934; PP49107. Scale bars = 10 mm.

branches borne at an ~80° vertical angle from the axis. The largest specimen has six nodes (fig. 3C). Internodes are typically 4–6 mm long but can be up to 20 mm long in the basal portions of the largest specimens and as short as 1 mm in the apical portions of the thalli (fig. 3C, 3E).

Determinate branches are up to 14 mm long and 0.8–2 mm wide, incurved, and often broader distally (fig. 3D, 3F); these dimensions and proportions do not change depending on the plane of compression, indicating that the branches are terete. Determinate branches are characterized by variable apical morphology: papillate, round, and truncate (fig. 4E–4G). Papillate branches are restricted to the apical region of axes, tend to be curved apically toward the axis, and measure 6.2–11.0 mm in length. Round and truncate branches are restricted to lower positions on the axes and measure 4.5–14 and 3–7.8 mm in length, respectively.

The only unequivocal indeterminate branch (branch axis) occurs at a node and bears a single terminal whorl of determinate branches (fig. 2A). Because that node is incompletely preserved, with only one determinate branch present, it is not

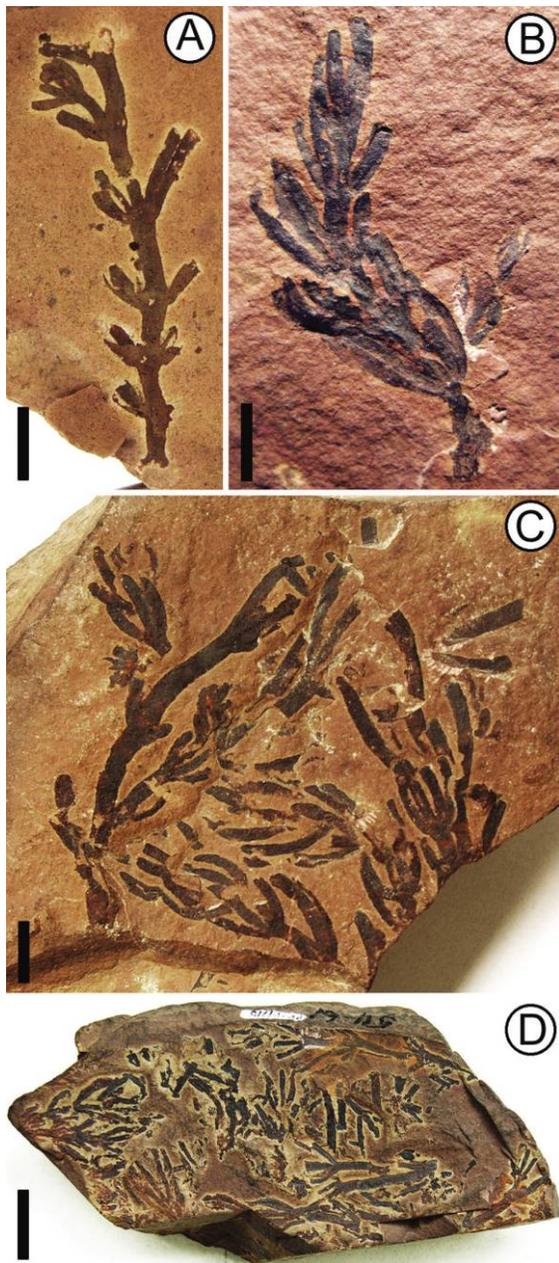


Fig. 2 *Sphondylophyton byenioides* Schultes and Dorf, Early Devonian, Beartooth Butte, Wyoming; specimens collected by William Tanner. A, PP49109; paratype with indeterminate branch at fifth node from base. B, PP49113; note flexuous habit and well-preserved determinate branches. Photograph by Ian Glasspool, Field Museum of Natural History. C, D, PP49118 and PP49115, respectively; fragmented specimens. Scale bars = 5 mm (A–C) and 10 mm (D).

possible to determine whether the indeterminate branch is replacing one of the four determinate branches of the node.

Discussion

Emended Diagnoses for Sphondylophyton

Careful microscopic examination of the entire collection of fossils produced no evidence to support the assertion of past

authors (Schultes and Dorf 1938; Tanner 1983) that *Sphondylophyton* had bifurcate determinate lateral appendages. The superimposition of determinate branch bases at nodes during preservation, combined with compression, could suggest a more complicated morphology and could explain past interpretations. Examination of specimens did not confirm the seven instances of main axis branching described by Tanner, with one exception (fig. 2A). This discrepancy is explained by coincidental orientation and overlap of many of the axes during fossilization, which lends the superficial appearance of frequently ramified axes. Adding to past descriptions of *Sphondylophyton*, determinate branches are shown to exhibit two distinct apical morphologies: rounded and papillate. Truncate appendages are interpreted as the result of mechanical damage to the organisms during life (see also “Rhodophytes and *Sphondylophyton*”). The new fossils contribute a previously unknown feature to the morphology of *Sphondylophyton*: a swollen and rounded basal structure that is interpreted as a holdfast.

A Need for Reassessment of Taxonomic Affinities

The standing interpretation of the taxonomic affinities of *Sphondylophyton* as a sphenophyte (Schultes and Dorf 1938) needs to be reconsidered for several reasons. Since Schultes and Dorf’s initial description and Tanner’s subsequent treatment, the interpretation of the Early Devonian depositional environment at Beartooth Butte has changed and new, well-preserved compression fossils have been discovered. The reinterpretation of the depositional environment as marine influenced renders less tenable Schultes and Dorf’s assertions that (1) the fossils were primarily associated with a terrestrial flora and that (2) the depositional environment was strictly non-marine. Their third assertion, that the remains were too well preserved to have been of algal origin, has also since been shown to be poorly supported, as examples of well-preserved fossil algae have been described (Fry 1983; LoDuca 1990, 1997; Anderson 2009). Furthermore, knowledge of the plant fossil record has grown considerably richer since Schultes and Dorf’s (1938) publication. These developments require a critical reassessment of the taxonomic affinities of *Sphondylophyton*.

Resolving the Taxonomic Affinities of Sphondylophyton

The fossil record presents the paleobotanist with numerous challenges, one of which is resolving the taxonomic affinities of fossils. This task is made difficult by the ease with which the modular body of many plants is fragmented by taphonomic processes, suboptimal presentation, or the very nature of the organisms studied (e.g., morphology and life cycle). All of these factors can contribute to the unavailability of key diagnostic features and limit the degree of certainty of taxonomic placements. Such is the case of many fossils preserved as carbonaceous compressions and placed among the algae, in which the lack of recognizable reproductive structures precludes phylum-level placement (Fry 1983).

The situation of *Sphondylophyton* is similar to that described above: the lack of reproductive features allows for a breadth of possible taxonomic placements ranging from vascular plants (Schultes and Dorf 1938) to several algal groups

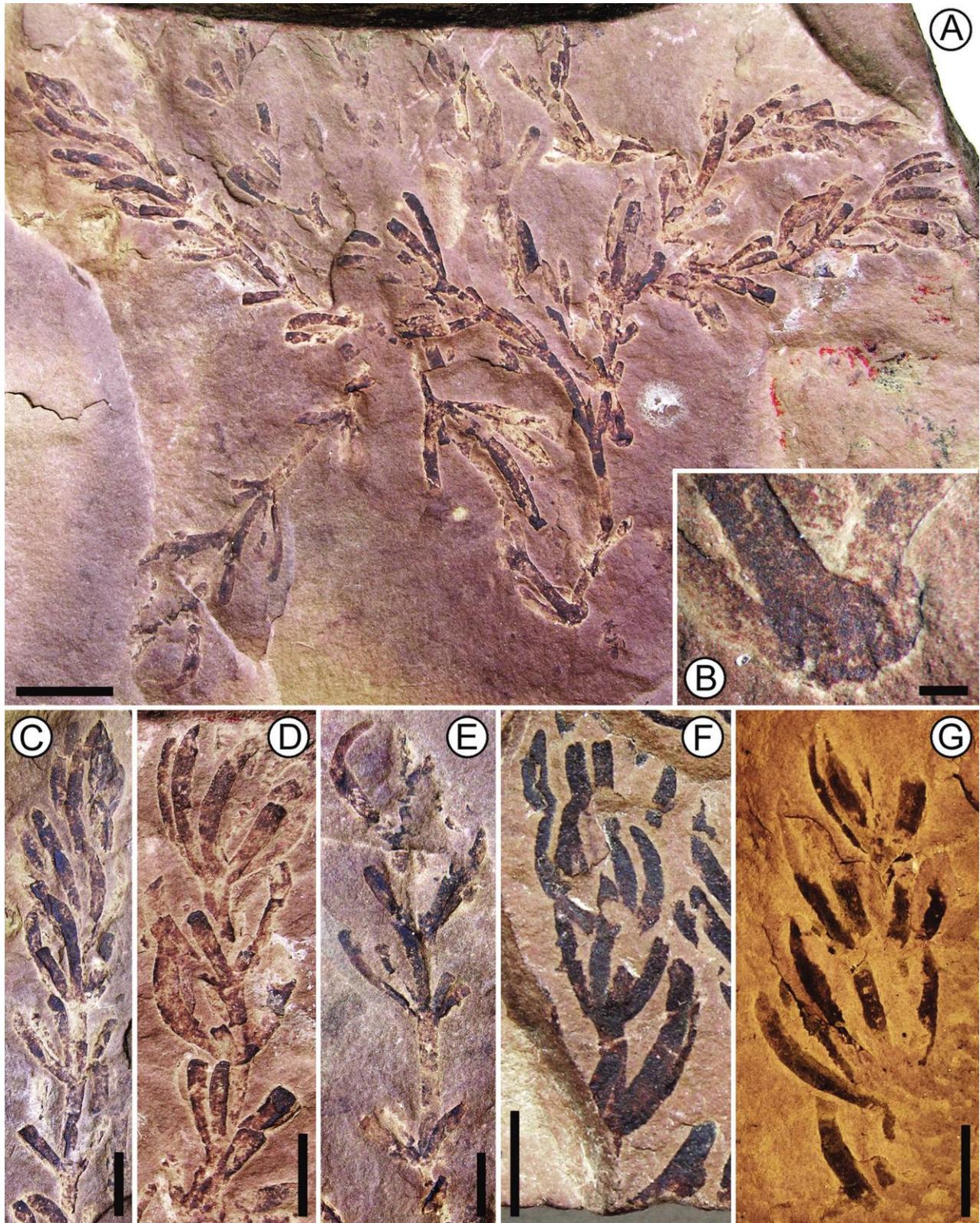


Fig. 3 *Sphondylophyton hyenioides* Schultes and Dorf, Early Devonian, Beartooth Butte, Wyoming. Details of fig. 1A: A, highest-quality specimens; B, bases of two axes with overlapping holdfasts; C, axis with preserved apical area—note appendage tip morphology at base and apex; D, E, note whorled architecture, conspicuous internodes, and variable appendage tip morphology. F, Detail of fig. 2C; note incurved determinate branches. G, Detail of fig. 1B. Scale bars = 10 mm (A), 1 mm (B), and 5 mm (C–G).

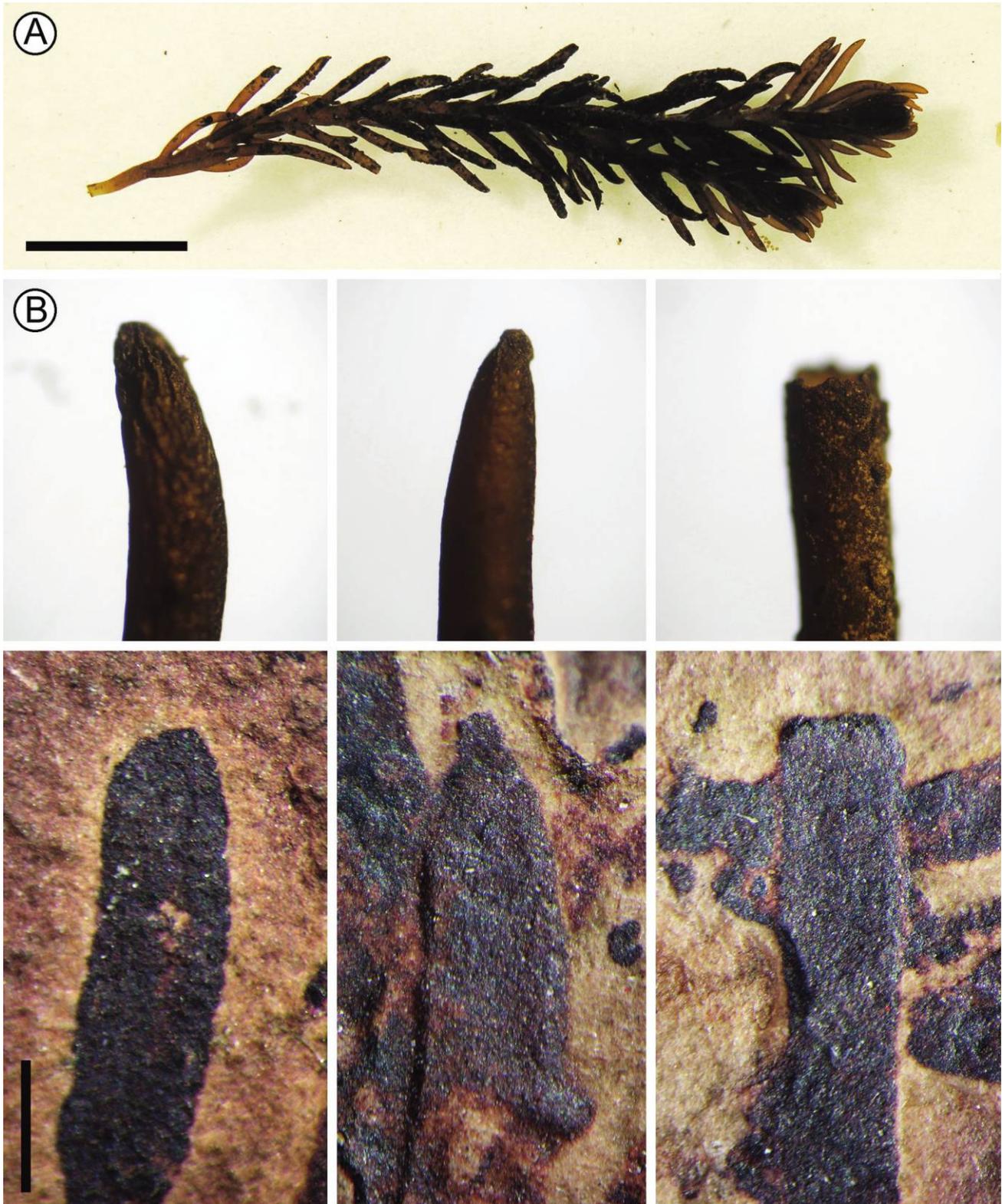


Fig. 4 A, Extant *Neorhodomela larix* (Turner) Masuda axis with one indeterminate branch (*bottom right*). B, Comparison of determinate branch morphologies in extant *Neorhodomela larix* (*upper row*) and *Sphondylophyton hyenioides* (*bottom row*): rounded (*left*), papillate (*center*), and truncate (*right*). Scale bars = 10 mm (A) and 1 mm (B).

(as discussed below). However, *Sphondylophyton* exhibits a specific combination of morphological characters: whorled, simple (i.e., unbranched and nonarticulated), terete appendages with dimorphic apical morphology. While not directly diagnostic, this combination of characters defines a level of organization that provides an effective means of constraining discussions of taxonomic affinities, especially when presented with data on the fossil record and morphological diversity within different lineages.

The approach taken here to resolve the taxonomic affinities of *Sphondylophyton* involves comparisons with lineages characterized by a comparable level of organization. Whorled organization places a first constraint, limiting the comparisons to lineages known to include representatives with whorled appendages (fossil or extant): sphenophytes, dasyclad and charophycean green algae, and red algae. The combination of characters seen in *Sphondylophyton* is compared with the realized morphospace of each of these lineages. The comparisons result in retention or rejection of lineages as possible taxonomic placements for *Sphondylophyton*. Such an approach is not uncommon in resolving the placement of taxonomically recalcitrant fossils, including algal taxa (LoDuca et al. 2003, p. 1153). While not free of potential error (e.g., the sum of morphological diversity of all known representatives of a lineage, living and extinct, provides only a minimum measure of the realized morphospace of that lineage), this approach is effective under existing constraints and provides a logical taxonomic placement for this study.

Sphondylophyton and the Sphenophytes

Sphenophytes are terrestrial vascular plants characterized by jointed stems with long internodes that bear whorls of leaves and branches at the nodes. The earliest unequivocal sphenophytes, recognizable by whorled appendages and their distinct node-internode morphology, appear in the fossil record in the Late Devonian: *Prosseria* Read (1953; Frasnian), *Eviostachya hoegii* Leclercq (1957; Famennian), *Hamatophyton verticillatum* Li, Cai, and Wang (Wang et al. 2006; Famennian), *Rotafolia songziensis* Wang, Hao, and Wang (Wang et al. 2006b; Famennian), *Pseudobornia ursina* Nathorst (Schweitzer 1967; late Famennian). All of these vascular plants have complex sporophytes differentiated into specialized organs (stem-leaf-root organography), and, therefore, their stems bear two distinct types of appendages: branches and leaves.

These unequivocal sphenophytes appear in the fossil record 20 million years after *Sphondylophyton* and feature morphologically complex leaves (simple undissected leaves are thought to have arisen in the sphenophytes later, by reduction of complex leaves; Stewart and Rothwell 1993). All polysporangiophytes and tracheophytes coeval with *Sphondylophyton* lack whorled architecture. They include taxa with characteristic lycopsid morphology (*Baragwanathia* Lang and Cookson, *Drepanophycus* Göppert) and plants composed of undifferentiated branching axes, grouped in the rhyniophyte, zosterophyll, and trimerophyte grades. The only early vascular plants approaching a whorled architecture are those exhibiting appendages arranged in tight helices (pseudowhorls), such as *Estinmophyton* Fairon-Demaret (Hao et al. 2004; Pragian), *Pertica* Kasper and Andrews (1972; Emsian), and *Ibyka* Skog and

Banks (1973; Givetian). However, aside from the fact that these plants did not produce true whorls, their lateral appendages are either complex, indeterminate branching systems (*Pertica*, *Ibyka*) or true leaves with dissected morphology (*Estinmophyton*).

In this context, if *Sphondylophyton* were an early sphenophyte, its whorled architecture would predate the oldest unequivocal sphenophytes by ~20 million years. While this is not impossible, it requires an explanation for the complete lack of plants with whorled architecture in the fossil record throughout the Middle Devonian. Within the Early Devonian vascular plant fossil record, the whorled architecture of *Sphondylophyton* is unique. This key difference in morphology, coupled with the temporal incongruity, outweighs any superficial similarities and warrants the exclusion of *Sphondylophyton* from the Sphenophyta specifically and from the vascular plants in general.

Sphondylophyton and the Algae

Past authors examining *Sphondylophyton* (Schultes and Dorf 1938; Tanner 1983) noted its morphological similarities to algal groups and considered algal affinities in their discussions. Schultes and Dorf dismissed the possibility of such an affinity primarily due to their interpretation of the depositional environment and the lack of co-occurring algae in the fossil assemblage. Tanner, informed by a revised interpretation of the depositional environment that included possible marine influences (Denison 1956), suggested that sphenophyte affinities were questionable and called for reconsideration of potential algal affinities. Such reconsideration is justified by morphology in the context of age (i.e., the morphology of *Sphondylophyton* is inconsistent with the morphology of coeval vascular plants) and by the marine-influenced depositional environment.

The level of organization seen in *Sphondylophyton* is recognized in all three major macroalgal lineages: Phaeophyta, Rhodophyta, and Chlorophyta (including Charophyta). Within these, convergent evolution of distinct morphological features is common across widely divergent groups. For example, simple (unbranched, nonarticulated) terete lateral appendages are present in brown (e.g., *Acrocarpia* Areschoug), red (Rhodomelaceae), and green (Caulerpaceae, Dasycladales) algae. However, a true whorled organization is known in living or extinct representatives of only three groups: the Dasycladales, the Charales, and the Rhodophyta.

Dasyclads and Sphondylophyton

Dasycladalean algae are shallow-marine green algae occurring in sheltered areas (Graham and Wilcox 2000). Extant dasyclads generally consist of unbranched or rarely dichotomously branching erect axes (Berger and Kaeffer 1992). The main axes bear lateral appendages that occur irregularly or in organized whorls and can be ramified multiple times (Wray 1977). Anatomically, they are characterized by a siphonous, nonseptate body plan (LoDuca 1997; Graham and Wilcox 2000), a feature that cannot be assessed in compression fossils. Most species exhibit a calcium carbonate sheath that, aside from its structural functions, facilitates fossilization and accounts for the dominance of calcified taxa in the dasyclad fossil

record (LoDuca et al. 2003). Dasyclads have the richest fossil record among algal macrophytes, although noncalcified dasyclad fossils preserved as carbonaceous compressions are comparatively rare.

Due to the frequency of whorled organization in the group, dasyclads constitute an interesting potential taxonomic placement for *Sphondylophyton*. Furthermore, noncalcified dasyclads are present in Lower Paleozoic rocks (LoDuca et al. 2003). However, a closer look reveals important morphological discrepancies between *Sphondylophyton* and dasyclads. These are summarized in table 1, which includes fossil and extant noncalcified dasyclads most similar in growth habit to *Sphondylophyton*. First, dasyclads are typically more gracile than *Sphondylophyton*: the widths of their main axes rarely approach 1 mm. Two notable exceptions are the extinct genera *Medusaegraptus* Ruedemann (Silurian) and *Chaetocladus* Whitfield (Ordovician-Silurian), which include species with axes up to 3–3.5 mm wide (Ruedemann 1925), comparable to *Sphondylophyton* (axes 2 mm wide). Second, the majority of noncalcified dasyclads have branched appendages, often with five or more orders of branching; *Medusaegraptus* and *Chaetocladus* are rare examples of dasyclads with unbranched appendages (Ruedemann 1925; LoDuca 1990). Third, whether branched or unbranched, dasyclad lateral appendages are thinner than those of *Sphondylophyton*. Although appendage lengths are similar to those of *Sphondylophyton* in a few taxa, dasyclad appendages are typically 0.15–0.2 mm wide—and often 0.1 mm or less—and do not exceed 1 mm in width even in the more robust taxa (*Medusaegraptus*; LoDuca 1990).

In summary, noncalcified dasyclads typically have branched lateral appendages and a more gracile habit than *Sphondylophyton*. All dasyclads have filiform lateral appendages, notably thinner than those of *Sphondylophyton*. Swollen appendages or appendage parts can be present in dasyclads, usually associated with reproductive structures (LoDuca et al. 2003), but nothing approaching the dimorphic tips of other-

wise morphologically similar lateral appendages of *Sphondylophyton* has been documented. Additionally, dasyclad axes are unbranched or rarely dichotomously branched (Berger and Kaefer 1992). Thus, when considered in all its dimensions, the realized morphospace of dasyclads does not include the combination of characters that defines *Sphondylophyton*. This justifies exclusion of dasycladalean algae as a taxonomic placement for *Sphondylophyton*.

Charophytes and Sphondylophyton

Charophycean algae are fresh- and brackish-water green algae with an extensive fossil record, consisting mostly of their calcified reproductive structures (oogonia), that extends to the Upper Silurian (Wood and Imahori 1965; Feist et al. 2005). Charophytes have axes defined by long internodes and nodes bearing whorls of determinate lateral appendages (branchlets); branch axes arise from the bases of branchlets (Bold and Wynne 1985). The thalli bear several types of morphological detail (ornamentation; e.g., cortication, spine cells, dactyls, stipulodes, bract cells) and distinctive reproductive structures (Fritsch 1935; Bold and Wynne 1985; Feist et al. 2005). Due to the paucity of vegetative thalli in the fossil record, little is known about the thalli of Paleozoic charophytes. Martin-Closas (2003), nevertheless, notes that Paleozoic charophytes have smooth axes, not unlike *Sphondylophyton*.

Like dasyclads, charophytes share broad morphological similarity with *Sphondylophyton* yet exhibit a number of key differences. For example, *Paleonitella cranii* (Kidston and Lang) Pia (Pragian) has branchlets that produce secondary and tertiary branchlets and is much smaller (axes are no more than 100 μ m across) than *Sphondylophyton* (axes 1–2 mm in width; Kelman et al. 2004). *Octochara* Gess and Hiller and *Hexachara* Gess and Hiller (1995; Frasnian-Famennian) are closer in size to *Sphondylophyton* but exhibit complex branchlet morphology with furcate appendages (e.g., quadrifurcate in *Oc-*

Table 1

Comparison with Fossil and Extant Noncalcified Dasyclads Most Similar Morphologically to *Sphondylophyton*

Taxa	Appendages per whorl	Appendage branching	Appendage width (mm)	Overall appendage length (mm)	Internode length (mm)	Axis width (mm)	References
<i>Medusaegraptus</i> Ruedemann	Not whorled	Unbranched	.2–1	6–10,666	n/a	.6–3	Ruedemann 1925; LoDuca 1990
<i>Chaetocladus</i> Whitfield	10–40	Unbranched	.07–.4	3–50	.5–2	.7–3.5	LoDuca 1997; LoDuca et al. 2011
<i>Callithamnopsis</i> Whitfield	2–4+	≥ 3 orders	.1–.33	<12	1.2–5	.3–.5	Whitfield 1894; Ruedemann 1925
<i>Uncatoella</i> Li and Cai	6	≤ 7 orders	.1–.3	<8	5.2–7.3	.4–1	Kenrick and Li 1998
<i>Heterocladus</i> LoDuca et al.	4–6	≤ 5 orders	.1–.25	5–13	3	.5	LoDuca et al. 2003
<i>Primicorallina</i> Whitfield	4–5	2 orders	.1–.2	2	.8	.4	Whitfield 1894
<i>Eocladus</i> LoDuca et al.	4	5 orders	<.12	10	.6	.25–.35	LoDuca et al. 2011
<i>Inopinatella</i> Elliott	4	2–3 orders	.08–.16	1.4	.4	.2–.3	Elliott 1971
<i>Batophora</i> ^a J. Agardh	8–16	4–7 orders	.17–.24	2–7	.3–2.5	.3–.6	Berger and Kaefer 1992; Gomez-Poot et al. 2002
<i>Acetabularia</i> ^a J. V. Lamouroux	6–12	≥ 3 orders	.07–.16	1.25–4.4	2.1–6.6	.25–.65	Berger and Kaefer 1992
<i>Sphondylophyton</i> Schultes and Dorf	4	Unbranched	.8–2	14	4–20	2	This study

Note. n/a = not applicable.

^a Extant taxa.

tochara gracilis Gess and Hiller). Compared to extant charophytes, *Sphondylophyton* is similar in size to *Nitella flexilis* (L.) C. Agardh, for example, and to *Lamprothamnium* J. Groves, among others, in its probable brackish environment. Many species of *Tolypella* (A. Braun) A. Braun and *Nitella* C. Agardh are comparable to *Sphondylophyton* in the lack of thallus ornamentation (Wood and Imahori 1965).

Despite similarities in size and general architecture, the determinate branches of *Sphondylophyton* distinguish it from all known charophytes. In *Sphondylophyton*, the determinate branches are simple, whereas the branchlets of charophytes are segmented (consist of cell filaments), usually bear distinguishable ornamentation, and can be branched (bearing secondary branchlets), dissected (bi- to quadrifurcate), or subtended by smaller appendages (e.g., stipulodes). Further distinguishing *Sphondylophyton* from charophytes are its macroscopic dimorphic branchlet apices; although species of *Nitella* and *Tolypella* exhibit polymorphic dactyl apices, these occur on second- to third-order bifurcations and are minuscule in comparison (Wood and Imahori 1965).

Sphondylophyton is also different from all charophyte fossils in being preserved as carbonaceous compressions. Known charophyte fossils are preserved as mineral replacement compressions or by lime encrustation or permineralization (Martin-Closas 2003). These modes of fossilization require specific environmental conditions that allow for the preservation of delicate organic material, such as charophyte thalli. To produce carbonaceous compressions like those of *Sphondylophyton*, the fossilized organism must have had a fleshy, robust thallus unlike any known charophyte.

In summary, several features discount charophyte affinities for *Sphondylophyton*: (1) differences in the organization of determinate appendages, (2) the morphological simplicity of *Sphondylophyton* as compared to the diversity of vegetative structures in typical charophytes, and (3) the robustness of the thallus of *Sphondylophyton*, as suggested by its mode of fossilization, which is incompatible with delicate charophyte thalli.

Rhodophytes and Sphondylophyton

The Rhodophyta are an extant group of largely marine algae that are common inhabitants of tropical and temperate near-shore waters. The complexity of the rhodophytes varies greatly, ranging from morphologically simple taxa (e.g., unicellular or filamentous) to comparatively more complex forms with terete to foliose thalli, with crustose to erect forms, all exhibiting complex life histories (Graham and Wilcox 2000). The red algal fossil record reaches as far back as the Precambrian (Butterfield et al. 1990; Xiao et al. 2004), though it is dominated by Mesozoic and Cenozoic calcified (coralline) taxa. The Paleozoic fossil record of noncalcified red algae is sparse and largely characterized by thalloid-foliose forms (Taylor et al. 2009).

Sphondylophyton compares well with the extant rhodophyte family Rhodomelaceae (Womersley et al. 2003) and, to a lesser extent, with the Ceramiaceae (e.g., *Sphondylothamnion* Nägeli). The Batrachospermaceae, although possessing whorled architecture, have axes with short internodes and whorls comprising high numbers of lateral appendages that

are uniseriate filamentous (Nechhi and Entwisle 1990). Additionally, they are much too delicate to be candidates for the mode of preservation exhibited by *Sphondylophyton*.

Within the Rhodomelaceae, *Neorhodomela* Masuda and *Coeloclonium* J. Agardh both exhibit morphologies similar to that of *Sphondylophyton* (Womersley et al. 2003). Although these genera have helically arranged determinate branches, one species, *Coeloclonium verticillatum* (Harvey) J. Agardh, exhibits whorled determinate branches and discrete node/internode organization. The overall dimensions of *C. verticillatum* (thalli 50–150 mm long, axes 1–2 mm wide, and internodes 5–15 mm long; Womersley et al. 2003) are similar to those of *Sphondylophyton*. Further, the consistent preservation of branch curvature in *Sphondylophyton*, along with the thickness of the fossil compressions, indicates that *Sphondylophyton* had a robust texture, comparable to the durable, cartilaginous texture characteristic of many red algae (including *Neorhodomela* and *Coeloclonium*).

The variable apical morphology of determinate branches, as well as their distribution along the axes of *Sphondylophyton*, are similar to those of *Neorhodomela* (fig. 4). In both these genera, papillate branches are grouped near the distal end of the axes, while appendages with rounded and truncate apices are restricted to the proximal portions of the axes. The truncate appendages in *Neorhodomela* are the result of mechanical abrasion due to the dynamic nature of its intertidal habitat. This causes older, less flexible appendages to break usually midlength and not at the point of attachment. Similar environmental conditions or transport prior to fossilization can account for the truncated appendages of *Sphondylophyton*.

These comparisons are useful in providing analogs for the morphology of the lateral appendages of *Sphondylophyton* and show that the combination of characters that define the genus falls well within the realized morphospace of the Rhodophyta. However, these comparisons cannot be used to assign *Sphondylophyton* to a specific lineage within the phylum. This is largely due to the convergent evolution of morphologies by different algal lineages; even among extant red algae, ordinal attribution based on vegetative morphology alone is difficult.

In summary, the Rhodophyta best accommodates the morphology of *Sphondylophyton* among all the algae, with the strongest comparisons drawn from genera within the Rhodomelaceae. This conclusion is based on the following characters: (1) a flexuous habit and cartilaginous, durable thallus; (2) thallus morphology and dimensions comparable to *Sphondylophyton*; (3) whorled appendages; and (4) distribution and apical morphology of determinate branches similar to *Sphondylophyton*. Additionally, the often inconspicuous reproductive structures of the red algae could have easily escaped fossil preservation, which could account for the absence of fertile structures on *Sphondylophyton*.

Conclusions

Reexamination of previously described specimens of *Sphondylophyton hyenioides* Schultes and Dorf and study of new, well-preserved specimens led to resurrection of a largely neglected taxon, resulting in emended diagnoses for the genus and species. The changes to the diagnoses include (1) whorls of four undissected determinate branches, (2) two types of

determinate branch apical morphology, (3) rare indeterminate branching, and (4) rounded holdfast. Paratypes are designated, and all known specimens of *Sphondylophyton* are illustrated.

Reconsideration of the taxonomic affinities of *Sphondylophyton* in the context of our current knowledge of extant and fossil algae and sphenophytes indicates that despite the characteristic whorled architecture of *Sphondylophyton*, sphenophyte, dasycladalean, and charophycean affinities are not supported. Rather, the habit and morphology of *Sphondylophyton* are consistent with rhodophyte affinities. Although features of *Sphondylophyton* are known in extant Rhodomelaceae, the high incidence of convergent morphologies among algae precludes taxonomic placement below the phylum rank in the absence of reproductive structures. Current understanding of the depositional environments of *Sphondylophyton* fossils at the Beartooth Butte locality includes probable marine influences that are consistent with placement among the algae. The inclusion of *Sphondylophyton* in the Rhodophyta adds to the long and morphologically diverse, yet limited, fossil record of the group. *Sphondylophyton* contributes an additional type—

axial, with terete whorled appendages—to the range of morphologies of noncalcified fossil red algae, dominated by foliose and strap-shaped thalloid forms.

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