

Partial reconstruction and palaeoecology of *Sphenophyllum costae* (Middle Pennsylvanian, Nova Scotia, Canada)

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Recovery of a large, articulate portion of *Sphenophyllum costae* Sterzel from lower Cantabrian strata of the Sydney Coalfield, Nova Scotia, Canada, demonstrates that it is the largest sphenophyll yet known to inhabit clastic substrates of Euramerica. The specimen shows four orders of branching, with each axis characterized by whorls of leaves having distinct morphologies. Foliage clearly displays a tendency to become less divided on axes of ascending order. Furthermore, each branch order can be distinguished based on its internodal lengths and widths, which indicates that the species has a marked hierarchy of ramification similar to that found in the calamitalean sphenopsids. Axes of all orders apparently show epidogenetic followed by apoxogenetic growth patterns, which contributes to the high degree of heterophylly in the taxon. Comparison of axes and foliage of *S. costae* with other members of the genus reveals that sphenophylls from clastic substrates followed a fundamental ontogenetic pattern of growth and architecture, although subtle variations existed between taxa. Climber hooks are documented for the first time in the species, and the presence of these modified leaves supports the interpretation that *S. costae* formed dense, multi-branched thickets up to 2 m high comprising mutually supportive axes that rested upon, clung to, or entwined with adjacent axes. Palaeoecological and taphonomic evidence suggests that the plant formed as ground cover beneath arborescent medullosalean pteridosperms, and probably occupied well-drained (but moist) clastic habitats such as elevated channel margins or topographically raised hummocks on floodplains. • Key words: *Sphenophyllum*, heterophylly, architecture, reconstruction, palaeoecology, Pennsylvanian, Nova Scotia.

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Sphenophyllum Brongniart has a cosmopolitan palaeogeographic distribution in the palaeoequatorial tropical belt, including Gondwana, and is found in rocks ranging in age from Late Devonian to late Permian. The genus is characterized by delicate whorls of leaves arising from nodes on thin, woody axes of various orders, and was a scrambling plant that formed a ground cover of dense, multi-branching thickets on both clastic and peat-forming substrates (Batenburg 1977, 1981, 1982). The majority of sphenophyll species are heterophyllous, where morphology of the leaves depends on the order of the branch to which they were originally attached. For this reason, accurate taxonomic assignment is challenging when dealing with only fragmentary material. Although sphenophyll twigs of ultimate order are plentiful in Carboniferous strata, articulate remains with numerous orders of ramification preserved, or axes

with attached strobili, are rare. Accordingly, the discovery of large, articulate specimens with several orders of branching can yield important information for future taxonomic comparisons, particularly when the range of morphological variability of the foliage existing on different axes is documented.

Whole-plant reconstructions do not yet exist for *Sphenophyllum*, in part because rooting organs are rarely found in connection with aerial parts of the plant. Articulate specimens with both foliage and attached strobili are equally rare (exceptions include Storch 1966, Zodrow & Gao 1991, Cúneo *et al.* 1993). Regardless, several partial reconstructions focusing on foliated aerial axes have been proposed. For example, fertile models have been given for *Sphenophyllum angustifolium* (Germar) Göppert by Grand'Eury (1877, unknown dimensions), *Sphenophyllum*

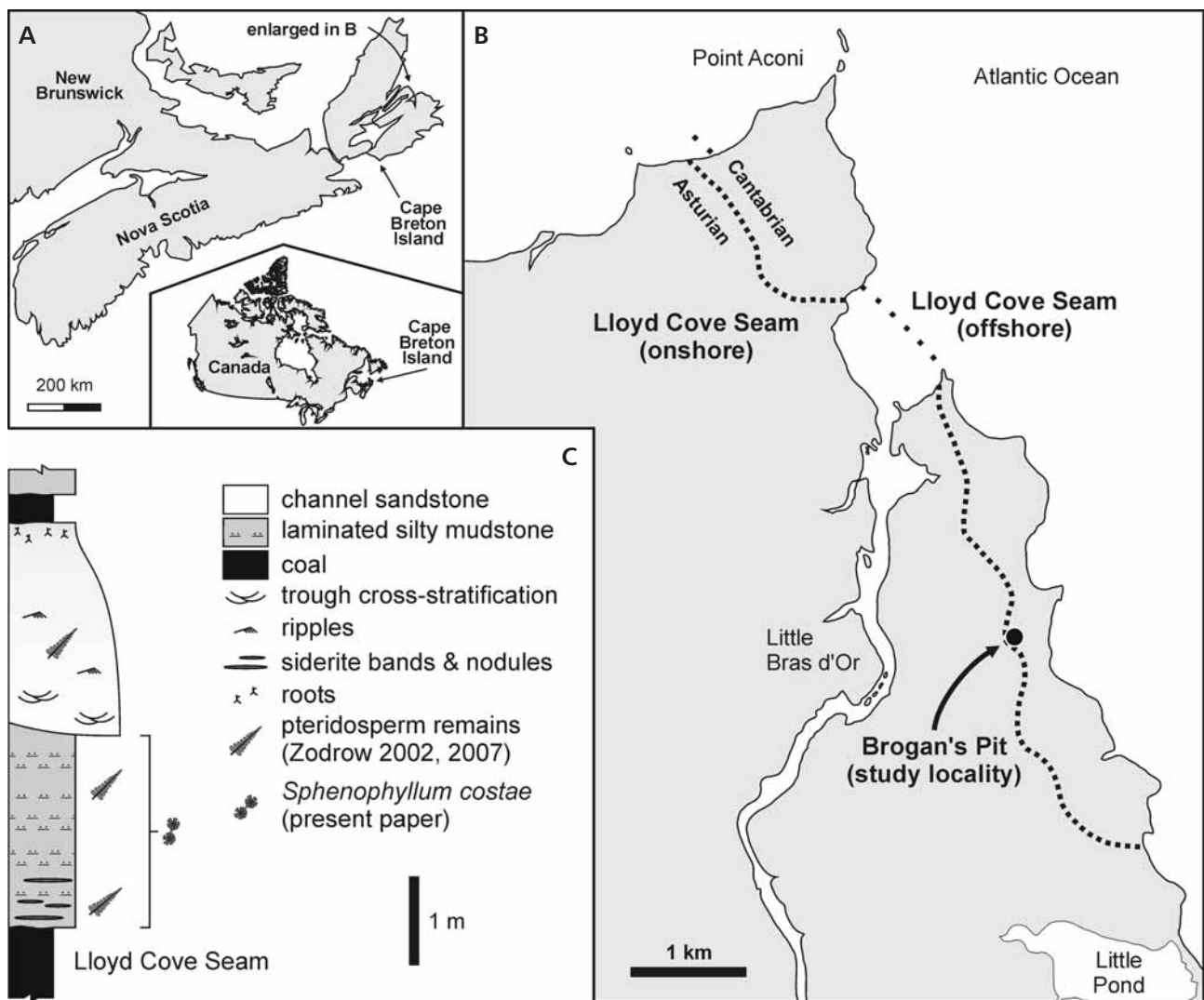


Figure 1. A – general location map showing Cape Breton Island, Nova Scotia, Canada. • B – lithostratigraphically highest part of Sydney Coalfield on Cape Breton Island, showing the onshore and offshore extent of the Lloyd Cove Seam (Asturian-Cantabrian boundary) and position of Brogan’s Pit, from which the study specimen was recovered. Entire area underlain by the Sydney Mines Formation (Morien Group). • C – representative stratigraphic section measured from the wall of Brogan’s Pit.

cuneifolium (Sternberg) Zeiller by Hirmer in Wettstein (1935, ca 60 cm long), and for *Leeites oblongifolis* Zodrow & Gao by Zodrow & Gao (1991, ca 24 cm long). Models of sterile, vegetative branches have been presented for *Sphenophyllum emarginatum* (Brongniart) Brongniart by Batenburg (1977, ca 30 cm long) and *Sphenophyllum costae* Sterzel by Zodrow (1989, ca 22 cm long). In a paper describing *Sphenophyllum oblongifolium* (Germar & Kaulfuss) Unger, Galtier & Daviero (1999) illustrated the longest articulate sphenophyll specimen known to date (ca 80 cm long), but did not provide a reconstruction of the species.

The present communication concerns the recent discovery of the largest known articulate, vegetative remains of *Sphenophyllum costae* from the Sydney Basin of Nova

Scotia, Canada. The specimen consists of four orders of branching, and demonstrates that the range of morphological variation in leaves of this species is far greater than previously assumed. The find contributes not only to a fuller understanding of the habit and palaeoecological preferences of sphenophyll species that occupied clastic substrates in palaeoequatorial Euramerica, but allows us to present a lifelike reconstruction of the aerial, vegetative portions of this plant.

Material and methods

The large, articulate specimen of *Sphenophyllum costae* came from the ca 2 m thick roof shale of the Lloyd Cove

Seam exposed in Brogan's Pit in the Sydney Coalfield, Cape Breton Island, Nova Scotia, Canada (Fig. 1A, B), which was an open pit coal mine that closed in 2003. This stratigraphic interval is in the upper part of the Sydney Mines Formation (Morien Group), and is earliest Cantabrian in age based on the fact that the top of the Lloyd Cove Seam represents the Asturian-Cantabrian boundary in the Sydney Coalfield (Zodrow 1982, Zodrow & Cleal 1985, Cleal *et al.* 2003). Unfortunately, the slab was not *in situ*, but rather represents loose waste rock broken up during mining of the Lloyd Cove Seam. However, the provenance of the slab can be confidently traced back to the roof shale based on sedimentological and lithological similarities (Fig. 1C).

The slab containing the study specimen is a gray, poorly laminated, silty mudstone with dimensions of 280 × 300 mm, and both the part and counterpart were recovered. Axes are preserved as adpressions (*sensu* Shute & Cleal 1987; *i.e.* by compression-impression), whereas the foliage is by incomplete natural maceration (*i.e.* it is cuticle-like). Careful degaging along the margins of the fossil with fine steel needles exposed hidden axial and foliar features, and permitted measurements of morphological features with a Wild/Heerbrugg binocular zoom microscope. Following Galtier & Daviero's (1999) nomenclature, the axes are labeled in ascending order as a1, a2, a3, and a4, with a1 being the thickest and most proximal aerial branch and a4 representing the thinnest axis of last order (*i.e.* an ultimate twig). The size and shape of the following characters were measured or observed: internodes, nodes, leaves, and teeth, sinuses, and clefts on distal margins. Internodal widths were taken at the middle of the internode where the diameter was unaffected by nodal swelling. The specimen was traced through a *camera lucida* setup attached to the microscope, and was photographed using a Carl Zeiss 35 mm camera equipped with an S-Planar 1:2.8 macro lens. All figures were created using CorelDRAW v.10 for Macintosh.

The study specimen is stored at Cape Breton University under the accession numbers UCCB 03-04/26a, b, and is curated by the second author. For the sake of understanding the full range of morphological variation within *Sphenophyllum costae*, observations and a few measurements were taken from material previously published by Zodrow (1986, 1989).

Previously known characteristics of *Sphenophyllum costae*

Sphenophyllum costae, erected by Sterzel (1903), is one of several sphenophyll species known from Carboniferous strata of Euramerica that has whorls of comparatively large leaves. Many informative examples of the taxon have been recovered over the past three decades from the Sydney Coalfield, principally from the roof shale of the Lloyd Cove and

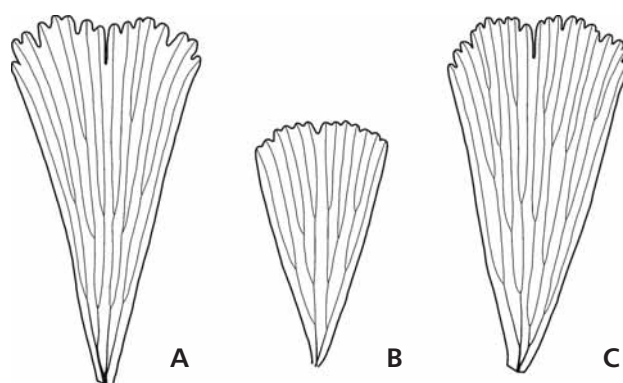


Figure 2. *Sphenophyllum costae*. Previously known range of morphological variation in leaves of ultimate twigs. • A – large, symmetrical leaf from neotype with pronounced mid and secondary clefts, Point Aconi Seam, Nova Scotia, Canada, UCCB 985GF-270. • B – small, symmetrical leaf with shallow mid cleft, Clinton, Missouri, USA, USNM 5679. • C – large, asymmetrical leaf with pronounced mid cleft, Cannelton, Pennsylvania, USA, USNM 18468. All line drawings x2. UCCB = Cape Breton University, USNM = National Museum of Natural History, Smithsonian Institution. Modified from Zodrow (1989, fig. 3).

Table 1. *Sphenophyllum costae*. Measurements of leaves from Sydney Coalfield, Nova Scotia. Based on data from Zodrow (1989, tables 1, 2).

Distal margin	allantoidal teeth (n = 11)	acuminate teeth (n = 3)
Leaf length, range (mean) (mm)	10.0–25.3 (17.9)	20.0–20.2 (20.0)
Leaf width, range (mean) (mm)	5.7–4.7 (11.7)	13.0–14.3 (13.5)
Number of teeth	11–22	14–15
Depth mid cleft (mm)	0.7–3.2	4.0–5.2

overlying Point Aconi seams (Fig. 1B, C). Although the remains, including the neotype, are almost exclusively axes and foliage of the last order (*i.e.* ultimate twigs), detailed examinations by Zodrow (1986, 1989) permitted emendation of the specific diagnosis and illustration of previously unknown characters for *S. costae*. The reader is referred to those papers for detailed systematic, descriptive and biostratigraphic information for *S. costae*, but a brief overview of previously known morphological traits is provided here.

Sphenophyllum costae is a markedly heterophyllous species, and variability in the morphology of leaves from ultimate twigs (based in part on synonymy) is given in Figs 2 and 3. The species is characterized by slightly trizygoid whorls comprising six leaves that attain lengths up to 25 mm (Table 1). Leaves generally have straight or slightly convex lateral margins, and distal margins with allantoidal (sausage-shaped) teeth separated by obtusely rounded sinuses (Figs 2, 3A). Leaves with acuminate teeth and acute sinuses are rare (Fig. 3C). Shallow clefts tend to exist in most leaves, and in the largest forms the distal margin can be bilobate, with asymmetrical placement of the main cleft resulting in two lobes of unequal width (Fig. 2C). An exceptional feature

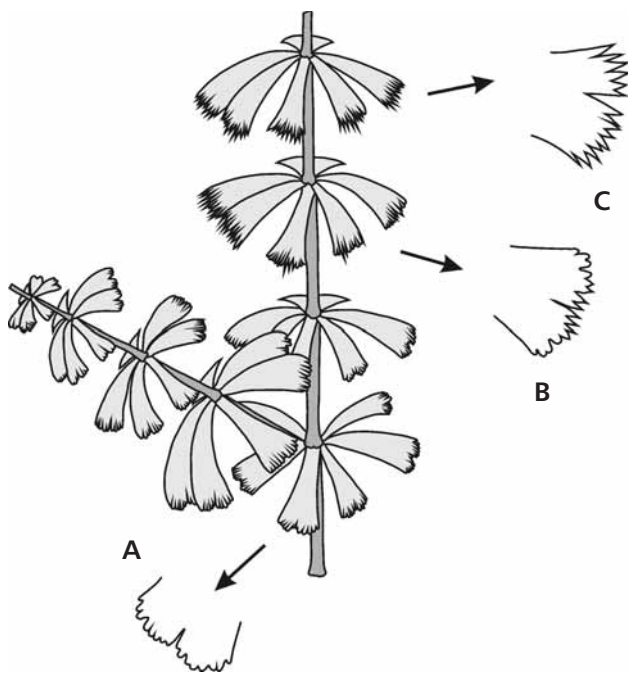


Figure 3. *Sphenophyllum costae*. Previous reconstruction of a vegetative portion of the plant, illustrating presumed acropetal transition in leaf morphologies. • A – typical form with allantoidal teeth. • B – heterodentate form with both allantoidal and acuminate teeth. • C – form with acuminate teeth. Reconstruction approximately 1/3 natural size. Details of dentition natural size. Modified from Zодrow (1989, fig. 4).

for this species is the existence of heterodentate leaves – the only known example within *Sphenophyllum* – with both allantoidal and acuminate teeth present on the distal margin of the same leaf (Fig. 3B; Zодrow 1989, pl. II). An early attempt at reconstructing a vegetative portion of *S. costae* is reproduced in Fig. 3, and shows the rapid apical decrease in leaf lengths typical of the taxon.

Description

Disposition in the slab

The specimen is not preserved along a single plane of lamination, but rather in vertically successive planes (Fig. 4). For example, the a1 and a2 axes are separated by 5 to 7 mm of rock, and the vertical distance between the a1 and a4 axes is between 42 and 45 mm. As a result, whorls are also entombed across several sedimentary laminae. Lacinate leaves tend to be represented as traces, as does much of the foliage preserved on the smaller branches. These factors combine to make degaging work a trying activity, particularly when attempting to expose delicate features that are not preserved flat along a single plane. However, this type of preservation is common in the Sydney Coalfield and in other Carboniferous basins, and imparts a certain three di-

mensionality to the fossil that has important taphonomic implications (see Taphonomy section below).

Leaves and axes

The entire specimen is approximately 200 mm long and axes are spread out over a width of 130 mm. It is composed of a single first order axis (a1), a single second order branch (a2), two third order branches (a3 proximal and a3 distal), and a short portion of a fourth order branch (a4) bearing leaves typical of *Sphenophyllum costae*. Magnified photographs of foliage from various branch orders are given in Fig. 5, and a tracing of the entire specimen is provided in Fig. 6. Lengths and widths of individual internodes from each axis are given in Table 2, and a scatterplot of these variables (Fig. 7) demonstrates that each type of branch can be more or less characterized by the lengths and widths of its internodes. Hairs or spines were not observed on any leaves or axes, which instead appear smooth or bear faint longitudinal striations. Tiny circular features interspersed on the first, second and third order branches (Fig. 5B) look superficially like the bases of hairs or spines, but they are actually 60 to 200 μm discs of sulfite adhering to the axes due to fossilization in a low Eh-pH geochemical environment. All axes comprise three longitudinal ribs, which is a common feature of the genus that presumably reflects the anatomical construction of the woody aerial axes (Galtier & Daviero 1999).

First order (a1) axes and leaves. – Only three complete and two incomplete internodes are preserved over a length of 198 mm. Internodes range in length from 38.0 to 46.0 mm, and in width from 4.4 to 4.8 mm, with the longest internodes in a distal position (Table 2, Fig. 8). The lengths and widths of a1 internodes are greater than and clearly distinct from those on branches of other orders (Fig. 7). Nodes are markedly swollen, and there is a single branch arising from a node. Information on the size and shape of a1 foliage is vague, although traces in the rock matrix indicate that leaves reach a length of at least 16.0 mm long. It is assumed that the leaves have a deeply divided, lacinate morphology, but the exact number of lobes and how each lobe terminates is unknown.

Second order (a2) axes and leaves. – A single branch ca 200 mm long is preserved with internodes ranging in length from 8.3 to 16.0 mm, and in width from 1.3 to 3.3 mm. A general acropetal increase in internodal length is discernible (Fig. 8). The internodal widths are variable throughout the entire axis, but there is a slight decrease in thickness distally (Table 2). The widest and shortest internode is at the point of attachment to the parent a1 axis (Fig. 6). On the whole, internodes of a2 axes are notably wider but only slightly longer than those belonging to a3 axes (Fig. 7),



Figure 4. *Sphenophyllum costae*. Entire specimen from Lloyd Cove Seam, Brogan's Pit shown, with several planes of lamination exposed in central part through which axes are disposed. UCCB 03-04/26a.

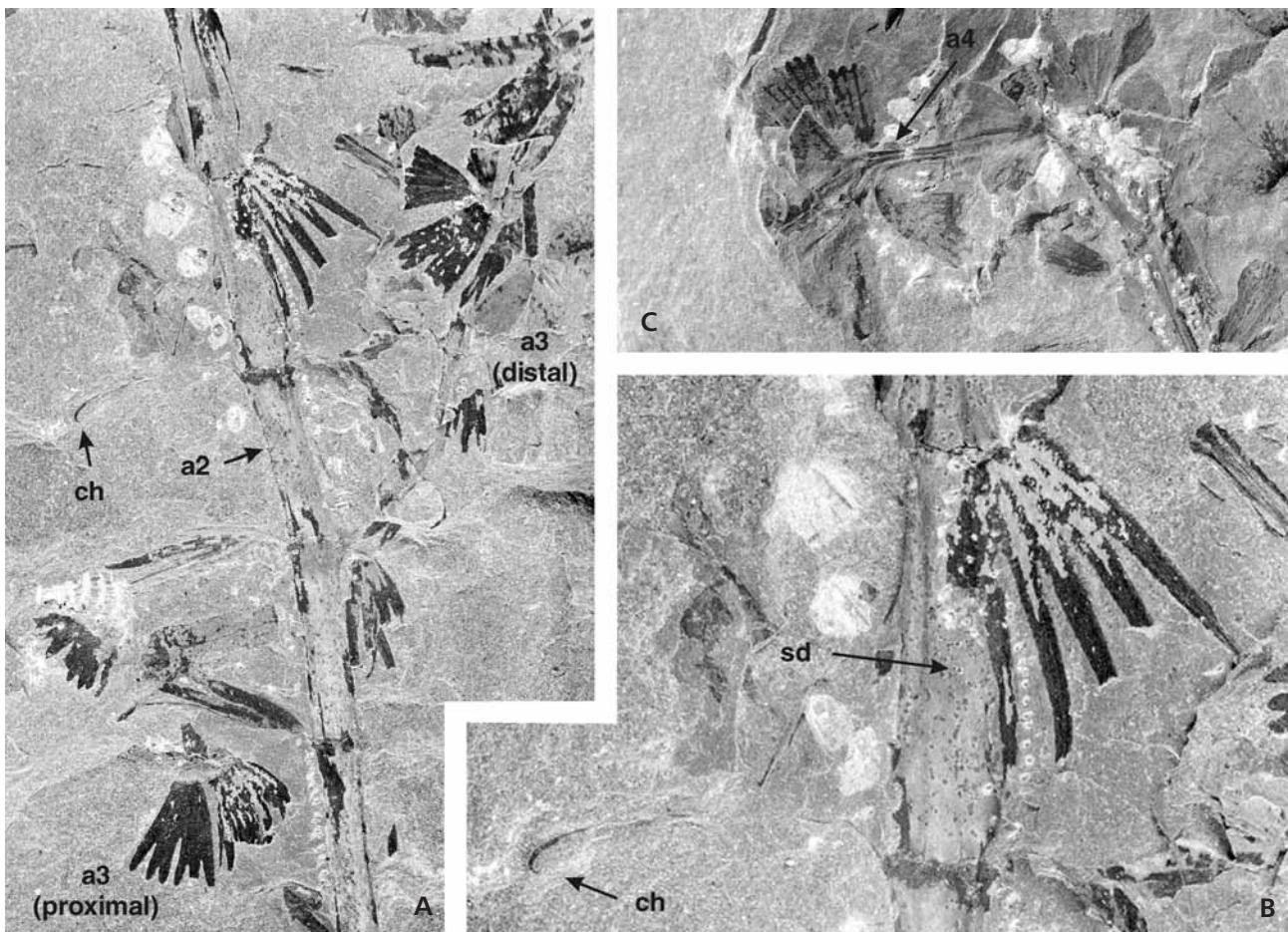


Figure 5. *Sphenophyllum costae*. Foliage from various orders of branching. • A – a2 axis from which shorter a3 (proximal) and longer a3 (distal) branches arise. Foliage of a2 branch deeply divided into four (possibly 5) lobes that terminate in climber hooks (ch). Foliage of a3 branches with moderately incised mid and secondary clefts and allantoidal teeth (see also inset in Fig. 6). UCCB 03-04/26b, X2. • B – magnification of a2 branch showing foliage with climber hooks (ch). Note tiny circular sulfite discs (sd) adhering to axis surface. UCCB 03-04/26b, X4. • C – ultimate twig (a4 axis) arising from a3 branch, with partially preserved whorl bearing cuneiform leaves with allantoidal teeth. UCCB 03-04/26a, X2.

although more overlap of these variables presumably existed in distal (unpreserved) parts of a2. Nodal swelling occurs but is not pronounced, and a single a3 branch arises from a node. One basic leaf morphology is preserved on this axis (Fig. 5A, B), comprising leaves that are 10.0 to 12.5 mm long and 3.0 to 6.5 mm wide, with leaves in medial positions possibly longer. Distal margins are deeply divided, although with a variable degree of incision, into four (or five?) elongate lobes that superficially appear to end in acuminate tips. Nonetheless, a leaf preserved in longitudinal section unequivocally indicates that a2 foliage terminates in recurved climber hooks (Fig. 5A, B), similar to those described in detail by Batenburg (1977).

Third order (a3) axes and leaves. – Two third order branches are preserved (Figs 5A, 6), the longest of which (a3 distal) reaches *ca* 78 mm. Internodes range in length from 7.5 to 11.1 mm, and in width from 1.0 to 1.8 mm. There is a clear but gradual acropetal increase in internodal

lengths to a short distance above the point of attachment to the parent a2 branch (Fig. 8). Internodal widths are variable, even over the short lengths preserved, but there is a general acropetal decrease in diameter (Table 2). The widest and shortest internodes are at the point of attachment to the parent a2 axis (Fig. 6). In general, internodes of a3 axes are somewhat thinner but only slightly shorter than those belonging to a2 axes, although some overlap in lengths exists between the longest a3 and shortest a2 internodes (Fig. 7). Nodal swelling is quite marked, and a single a4 branch is given off at a node. Leaves range from 7.5 to 8.5 mm long and 5.0 to 5.7 mm wide, and approach the morphology more typical of foliage borne on ultimate twigs of *Sphenophyllum costae* (see Fig. 2A). On the proximal a3 branch, a fragmentary whorl is preserved with a more or less intact leaf showing features of the distal margin (Figs 5A, 6). Mid and secondary clefts are moderately incised, and six or seven(?) obtusely rounded or allantoidal teeth are separated by obtusely to narrowly rounded sinu-

Table 2. *Sphenophyllum costae*. Measurements of axes and internodes from various branch orders of study specimen (UCCB 03-04/26a, b). Note that two third order (a3) branches exist – a3 distal and a3 proximal. Data arranged with proximal internode values at bottom of table, distal at top, na = data unavailable.

Branch order	First order (a1)	Second order (a2)	Third order (a3)	Fourth order (a4)
Total branch length (mm)	198	200	78 (distal)	21
Internode length, width (mm)	na, 4.4	13.4, 1.3	9.5, 1.3	12.5, 1.0
	46.0, 4.6	16.0, 2.1	11.1, 1.1	
	46.0, 4.8	15.6, 2.5	11.0, 1.2	
	38.0, 4.8	14.5, 1.9	9.4, 1.0	
		14.1, 3.2	8.1, 1.6	
		12.1, 2.8	7.5, 1.8	
		14.0, 2.9		
		15.8, 2.7	15 (proximal)	
		13.0, 2.6	8.2, 1.8	
		13.2, na		
		11.0, 2.6		
	12.3, 3.1			
	11.0, 2.3			
	8.3, 3.3			
Mean values (mm)	43.3, 4.6	13.2, 2.5	9.2, 1.4	12.5, 1.0

ses. It is possible that the teeth are actually terminated by climber hooks that are folded down into the rock matrix, but it is not possible to be certain without cuticular analysis.

Fourth order (a4) axes and leaves. – Only the most proximal internode and foliage-bearing node of an a4 axis (*i.e.* ultimate twig) are preserved (Fig. 5C), with a combined length of *ca* 21 mm. The internode has a length of 12.5 mm and width of 1.0 mm. It is of the same length as but thinner than a2 internodes, and compares closely with the longest and narrowest a3 internodes preserved in the study specimen (Fig. 7). However, when previously published measurements of internodes from two ultimate twigs (including the neotype) are added to the scatterplot, it becomes clear that a4 internodes generally are much longer than (up to 31.7 mm), and can clearly be differentiated from, both a2 and a3 internodes. According to the photograph of Zodrow (1986, pl. VI, fig. 1), internodal lengths decrease dramatically near the apex of ultimate twigs (Figs 3, 8). Swelling is minimal at nodes, and no hairs or spines are present in the study specimen. The fragmentary whorl on the a4 branch has leaves 6.0 to 8.8 mm long and 5.0 mm wide, and the distal margins have shallow mid and secondary clefts, narrowly blunt sinuses, and at least six allantoidal teeth (Fig. 5C). No leaves with acuminate teeth (*e.g.*, Fig. 3C) are found in the present material.

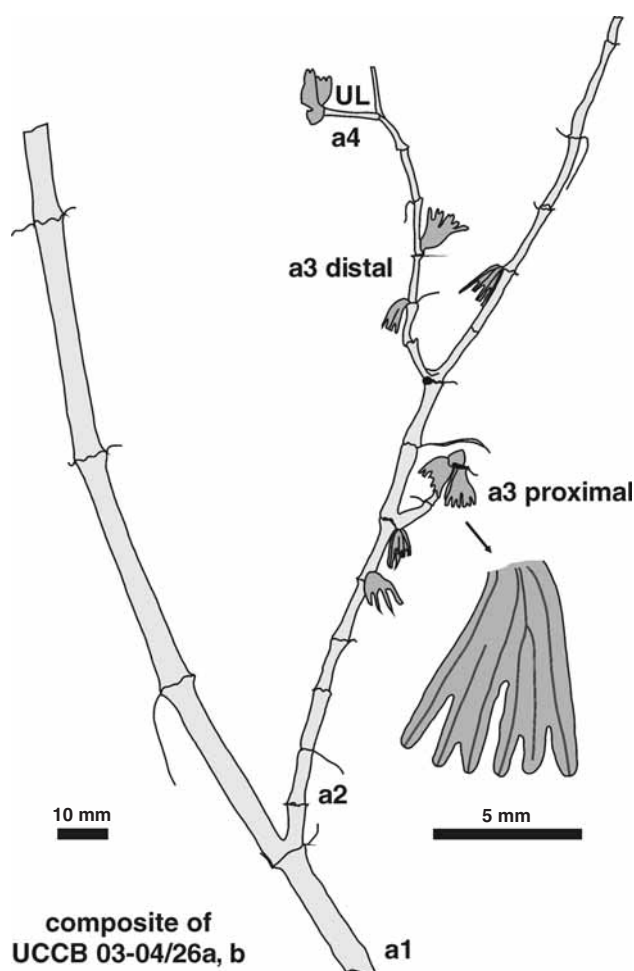


Figure 6. *Sphenophyllum costae*. Composite camera lucida drawing combining features observed on both part and counterpart of study specimen, demonstrating vegetative branching from proximal (a1) axis to distal (a4) ultimate twig (UL). Inset represents magnification of a3 leaf (see also Fig. 5A).

Confirmation of assignment to *Sphenophyllum costae*

As noted by Storch (1966), the most reliable basis for determining sphenophyll species is by comparison of foliage from ultimate twigs, as such leaves presumably are morphologically stable in any given taxon. Although the a4 whorls in the study specimen are not particularly well preserved (Fig. 5C), features observable on the distal margin of the leaves provide evidence for the identity of the specimen as *Sphenophyllum costae*. The leaves are smaller than is typical for this species, and not enough of them remain to exhibit the trizygoid shape of the whorls, but the shallow clefts, narrowly blunt sinuses, and allantoidal teeth compare closely with small leaves from basal or uppermost portions of ultimate twigs (compare with Fig. 2B; Zodrow 1986, pl. VI, figs 1, 2). It is presumed that if more apical portions of the ultimate twig were preserved in the study

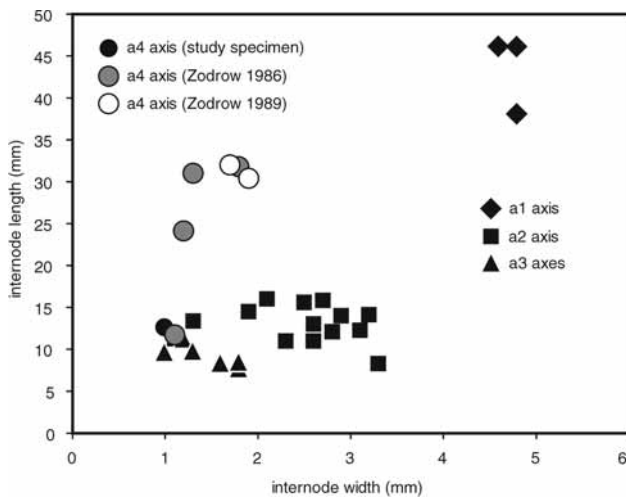


Figure 7. *Sphenophyllum costae*. Scatterplot comparing internodal widths versus lengths, demonstrating that branches of various orders segregate into separate fields. Additional measurements from ultimate twigs (a4) illustrated in Zodrow (1986, pl. VI, fig. 1) and Zodrow (1989, pl. II).

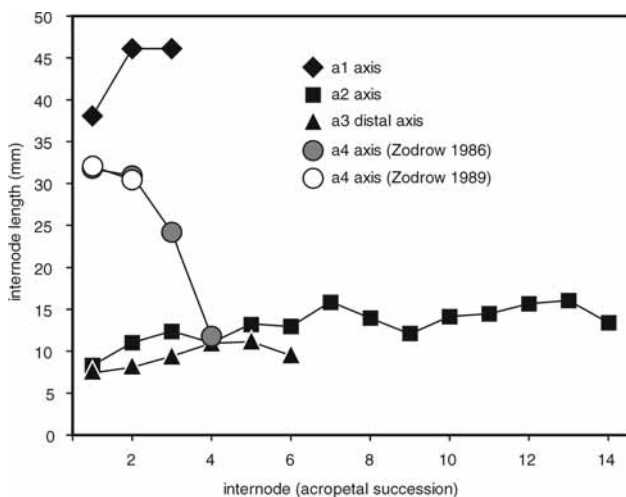


Figure 8. *Sphenophyllum costae*. Plot showing acropetal variation in internodal lengths on different branch orders. Additional measurements from ultimate twigs (a4) illustrated in Zodrow (1986, pl. VI, fig. 1) and Zodrow (1989, pl. II).

specimen, leaves would have rapidly attained the characteristic morphology of larger *S. costae* foliage (Fig. 2A, C).

The small leaf forms from a4 axes of *Sphenophyllum costae* resemble fully developed foliage from the ultimate twigs of *Sphenophyllum emarginatum*. In fact, they would be difficult to differentiate if found as isolated whorls. However, we can be confident that our specimen does not belong to the latter species, as the basal leaves of ultimate twigs in *S. emarginatum* are much narrower and have only one or two teeth along their distal margin (e.g., Batenburg 1977, pl. II, fig. 3, pl. III, fig. 3, pl. IV, fig. 4; Bashforth 2005, pl. 4, fig. 5). Leaves from the a3 branches in the study specimen (Figs 5A, 6) have moderately incised mid clefts

and allantoidal teeth, and thus resemble incised foliage on ultimate twigs of *Sphenophyllum majus* (Bronn) Bronn (e.g., Remy 1962, pl. 1; Zodrow 1989, fig. 9, pl. I, fig. 5). However, these species can be distinguished because the apparently similar leaves were borne on branches of different order (i.e. a3 axes in *S. costae*, a4 axes in *S. majus*).

Of the reconstructed species mentioned in the Introduction, the models proposed for *Leeites oblongifolis* and *Sphenophyllum oblongifolium* compare most closely with the aerial axes of *Sphenophyllum costae*. All show a definite tendency towards having less lacinate leaves on axes of ascending order (i.e. with increasing order of axes in the direction of ultimate twigs – compare Fig. 9, Zodrow & Gao 1991, fig. 1 and Galtier & Daviero 1999, fig. 4). However, the longer internodes, in combination with leaf morphology, sets *S. costae* apart from these two species.

Reconstruction

Although four orders of branching have been preserved in the study specimen, it undoubtedly represents only a smaller fragment of the original *Sphenophyllum costae* plant. Fig. 9 demonstrates our interpretation of the range of foliar morphologies in *S. costae*, and a lifelike vegetative reconstruction of the plant is given in Fig. 10. Crucial organs are not present in our material, such as the terminal parts of aerial branches, attached strobili, rooting structures, and the main cauline or proximal axis to which a1 axes were attached. In the absence of these features, we prefer to consider our model a partial, vegetative reconstruction that is open to modification with future discoveries. Furthermore, only a limited number of fragmentary whorls exhibiting complete leaves are preserved, which makes it difficult to understand the morphological differences between foliage on different branch orders, and the pattern of morphological change occurring in leaves along a single axis. For these reasons, our partial reconstruction depends in part on previously published information, particularly other specimens of *S. costae* documented by Zodrow (1986, 1989) from the Sydney Coalfield (*locus neotypicus*). As we discuss below, *S. costae* and *Sphenophyllum oblongifolium* show considerable similarities in their overall construction and range of variation in both axes and foliage (e.g., five orders of branching, trizygoid whorls), which enables us to rely on information provided for the latter by Zodrow (1989) from the Sydney Basin, and by Galtier & Daviero (1999) from the Graissessac Basin of France. We also consider the models proposed by Batenburg (1977) and Zodrow (1989) for *Sphenophyllum emarginatum* as a useful source of information, as it is evident that sphenophylls from clastic substrates generally followed a fundamental ontogenetic pattern of growth and architecture that varied to some extent between different species.

Branching and growth pattern

Internodes of the first order axis in our specimen are the longest (≤ 46 mm) known for any species of *Sphenophyllum* [e.g., ≤ 32 mm in *S. emarginatum* (Batenburg 1977); ≤ 36 mm in *S. oblongifolium* (Galtier & Daviero 1999)]. We envision a plant that attained heights well over 2 m and widths of at least 1 m, and was comparable to, but probably larger than, either *S. oblongifolium* or *S. emarginatum*. Information on the main cauline structure of *Sphenophyllum costae*, from which a1 axes arose, is lacking from the study locality, but it presumably was thicker than the 8 to 11 mm wide proximal axes described by Galtier & Daviero (1999) for *S. oblongifolium*. We have omitted the cauline axis from our reconstruction due to lack of evidence (Fig. 10).

At least four orders of branching existed in *Sphenophyllum costae*, and assuming that a proximal cauline stem existed, the plant likely had five orders. This is entirely consistent with *Sphenophyllum oblongifolium* (Galtier & Daviero 1999), but differs from *Sphenophyllum emarginatum*, which apparently had only three or perhaps four orders (Batenburg 1977, fig. 5). In *S. costae*, the angle between a branch and its parent stem ranges between 40° and 80° , and the angle progressively increases in ramifications between higher and higher orders – whether or not this is a real architectural feature or simply a taphonomic artifact is unknown. Branches probably were spirally arranged, as has been demonstrated for *S. emarginatum* (Batenburg 1977) and *S. oblongifolium* (Galtier & Daviero 1999), and our vegetative model (Fig. 10) has been speculatively drawn with branches arising dextrorsely following the conclusions of Batenburg (1977, p. 90). Although limited evidence is available in our specimen, it appears that only a single branch arose from a node in both *S. costae* and *S. oblongifolium*. This tendency is also shown by *S. emarginatum*, although the presence of two branches from one node has been documented several times for this species (e.g., Batenburg 1977, pl. V, fig. 2; Zodrow 1989, pl. VI and fig. 13; Bashforth 2005, pl. 4, fig. 9). The spacing between successive ramifications varies between two and six internodes (but may have been more), and the length of the gaps between branches likely was irregular. Galtier & Daviero (1999) considered the lack of a pattern in *S. oblongifolium* indicative of non-rhythmic growth with intermittent or diffuse branching, and we suggest the same for *S. costae*.

The a1 branch in the study specimen shows an acropetal increase in internodal lengths (Fig. 8), although only a short segment is preserved without enough data points to show a reliable trend. According to Galtier & Daviero (1999, fig. 8), however, internodal lengths of first order branches of *Sphenophyllum oblongifolium* gradually increased acropetally in their proximal parts (see their specimens 2060 and 2061), may have reached a maximum near

the middle of the branch, and then slowly decreased towards the top before rapidly diminishing near the very apex (see specimen 2082). A prompt length reduction was also noted for apical internodes on main axes of *Sphenophyllum emarginatum* (Batenburg 1977, p. 90). The a2 and longer a3 branches of *Sphenophyllum costae* show a clear but gradual acropetal increase in internodal lengths throughout most of their extent (Fig. 8), and the lowermost internodes of each are the shortest (and widest) at their attachment to the parent axis. This character, which is undoubtedly ontogenetic, also occurs in a2 branches of *S. oblongifolium* (Galtier & Daviero 1999, fig. 9). Not enough of the a4 branch is preserved in our specimen to be sure if it had the same acropetal increase in internodal lengths, but based on the fact that ultimate twigs of *S. costae* with fully developed whorls have internodes upwards of 32 mm long (Fig. 8; Zodrow 1986, pl. VI, fig. 1; Zodrow 1989, pl. II), we created our reconstruction with that supposition in mind. A slight acropetal decrease in internodal lengths occurs near the top of the a3 branch (Fig. 8), whereas the ultimate twig (a4) illustrated by Zodrow (1986, pl. VI, fig. 1) shows a dramatic shortening of internodes just before the apex. Ultimate twigs of *S. emarginatum* show the same feature (Batenburg 1977, p. 90). Eggert (1962) documented in the arborescent sphenopsids a similar transition from a phase of epidogenesis near stem bases to a phase of apoxogenesis near stem apices, and concluded that such axes had determinate and continuous growth. Based on this combination of evidence, we have assumed that all branch orders had an epidogenetic followed by apoxogenetic growth pattern for our reconstruction of *S. costae*.

Fig. 7 clearly indicates that axes of various orders can be differentiated based on their internodal lengths and widths, with only minimal overlap of these variables in the a2, a3 and shortest a4 branches. This is at variance with the findings of Galtier & Daviero (1999), who stated that it was difficult to distinguish between unattached axes of successive orders in *Sphenophyllum oblongifolium* because the lengths and widths of internodes in a given branch often reached values approximating those of its parent axis. In contrast, our data suggests that ramification in *Sphenophyllum costae* followed a more systematic pattern that resulted in a stronger hierarchy of branching, such as has been demonstrated for the calamitaleean sphenopsids (Eggert 1962). Despite this apparent segregation, we recognize that our data set is limited to a few specimens, and that measurements of more material could result in further merging of the parameters.

We agree with the hypothesis of Galtier & Daviero (1999) that branches with longer internodes (first and fourth order in *Sphenophyllum costae*) may have functioned as exploring axes. We speculate that the purpose of a1 branches may have been to reach for suitable stems with which to entwine or that could provide mechanical support

to the plant as it grew vertically and laterally, whereas longer a4 branches with abundant foliage served to search out areas with more available sunlight to increase photosynthetic efficiency. Second and third order branches with relatively shorter internodes may have provided structural rigidity to the plant. The presence of climber hooks on a2 axes indicates that these branches also functioned to grasp or cling to other parts of the plant. The overwhelming abundance of ultimate twigs versus branches of lower order in the plant fossil assemblage at the study locality suggests that these axes may have easily abscised.

Spines or hairs have not been observed on any axis in the study specimen, but they have previously been recorded from the axes of ultimate twigs in *Sphenophyllum costae* (Zodrow 1989, fig. 1a, pl. I, fig. 1) – see Fig. 9. However, they have been omitted from a4 axes of our reconstruction (Fig. 10) because they would not be visible at the illustration scale. Similar structures have been recorded in *Sphenophyllum emarginatum* and *Sphenophyllum zwickaviense* Storch (Batenburg 1977, 1981), *Leeites oblongifolis* (Zodrow & Gao 1991), and *Sphenophyllum spinulosum* Yabe & Oishi (Boureau 1964). In contrast, Galtier & Daviero (1999) found no evidence of hairs in *Sphenophyllum oblongifolium* despite having observed over 60 specimens.

Heterophylly

Fig. 9 provides our interpretation of the different morphological varieties of leaves in *Sphenophyllum costae* depending on their placement on branches of various orders, a concept termed the “dissection series” by Zodrow & Gao (1991, p. 64). Given that each branch order in *S. costae* shows evidence of having had a particular role in the functioning of the whole plant, it is hardly surprising that a distinct type of foliage characterizes each axis. Furthermore, the stems apparently had an epidogenetic followed by apoxogenetic phase during their development, which likely resulted in transitions between leaf morphologies throughout the length of each axis. “As a general rule, the extent of incision along the distal margin of leaves decreases, and the number of teeth increases, as the branch order increases.” In our reconstruction of *S. costae*, we have made the presumption that the basic whorl architecture was hexamerous (six leaves per whorl) regardless of the leaf shape.

Leaves of the first order axis are poorly preserved in our specimen, but they were almost certainly deeply divided and lacinate. Previous illustrations of whorls from a1 branches of other species show leaves that are undivided or divided nearly to their base into two linear lobes [e.g., *Sphenophyllum emarginatum* (Batenburg 1977, pl. V, figs 2, 4; Bashforth 2005, pl. 3, fig. 2); *Sphenophyllum zwickaviense* (Zodrow 1989, fig. 11a); *Leeites oblongifolis* (Zodrow & Gao 1991, fig. 1e)]. The number

of linear lobes in each leaf probably increased to three or four (or more?) in the middle parts of first order axes (Figs 9, 10), and the leaves may have been slightly less incised [e.g., *L. oblongifolis* (Zodrow & Gao 1991, fig. 1d); *Sphenophyllum oblongifolium* (Galtier & Daviero 1999, figs 3.8, 3.11, 3.12, 4a–d)]. We do not know what *S. costae* leaves looked like near the apices of first order branches, but they may have reverted to two-lobed forms as shown by Batenburg (1977, fig. 5c) for *S. emarginatum*. It is important to note that these linear lobes generally narrow into stiffened, recurved hooks at their ends in *S. emarginatum* (Batenburg 1977, pl. VI, fig. 3; Batenburg 1981, pl. IX, figs 1, 2, 5, 6; Bashforth 2005, pl. 4, fig. 1), *S. oblongifolium* (Barthel 1997, pl. IV, figs 8, 9; Galtier & Daviero 1999, figs 3.11, 5.17), *Sphenophyllum cuneifolium* (Barthel 1997, pl. I, fig. 4), and *S. zwickaviense* (Zodrow 1989, fig. 11a). These climber hooks may also have existed on first order branches in *S. costae*, but the a1 foliage is not well enough preserved in the study specimen to clarify this point.

Typical leaves on second order branches of *Sphenophyllum costae* are somewhat similar to those on first order axes, but differed in being less incised and in having four or five lobes that unequivocally terminate in climber hooks (Figs 5B, 9). Comparable morphologies have been shown on a2 branches of *Sphenophyllum oblongifolium* by Galtier & Daviero (1999, figs 3.10 at arrow, 4e, g, h) and *Leeites oblongifolis* by Zodrow & Gao (1991, fig. 1c), with the differences being that lobes had acuminate tips and lacked climber hooks in these species. The basal part of a2 axes may have had short linear leaves like those displayed by *S. oblongifolium* (Galtier & Daviero 1999, figs 2.3 at arrow, 4i). Similarly, we have no evidence for the type of leaves present in apical positions on a2 branches, but they may have been identical to those near the base.

Leaves on third order branches of *Sphenophyllum costae* are very similar to those of the ultimate twigs (Figs 5A, 6), differing only in the extent of incision along the distal margin. It is evident from the study specimen that the foliage of a3 axes attained their characteristic shape at or near the base of the branch. Nonetheless, it is probable that the leaves became increasingly less incised and may have had more teeth (i.e. approximating a4 foliage) in the middle parts of third order branches (Fig. 9). We do not know the leaf morphology in apical parts of a3 branches, but they may have been identical to those near the base. Equivalent a3 whorls were illustrated by Galtier & Daviero (1999, figs 4j, 5.14 on right hand side, 5.16) for *Sphenophyllum oblongifolium* and by Zodrow & Gao (1991, fig. 1b) for *Leeites oblongifolis*, albeit with acuminate teeth.

Ultimate twigs of *Sphenophyllum costae* have an array of leaf morphologies (Figs 2, 9). Only the lowermost leaf is preserved in the study specimen, and although it is relatively small, it is typical of the species. Galtier & Daviero

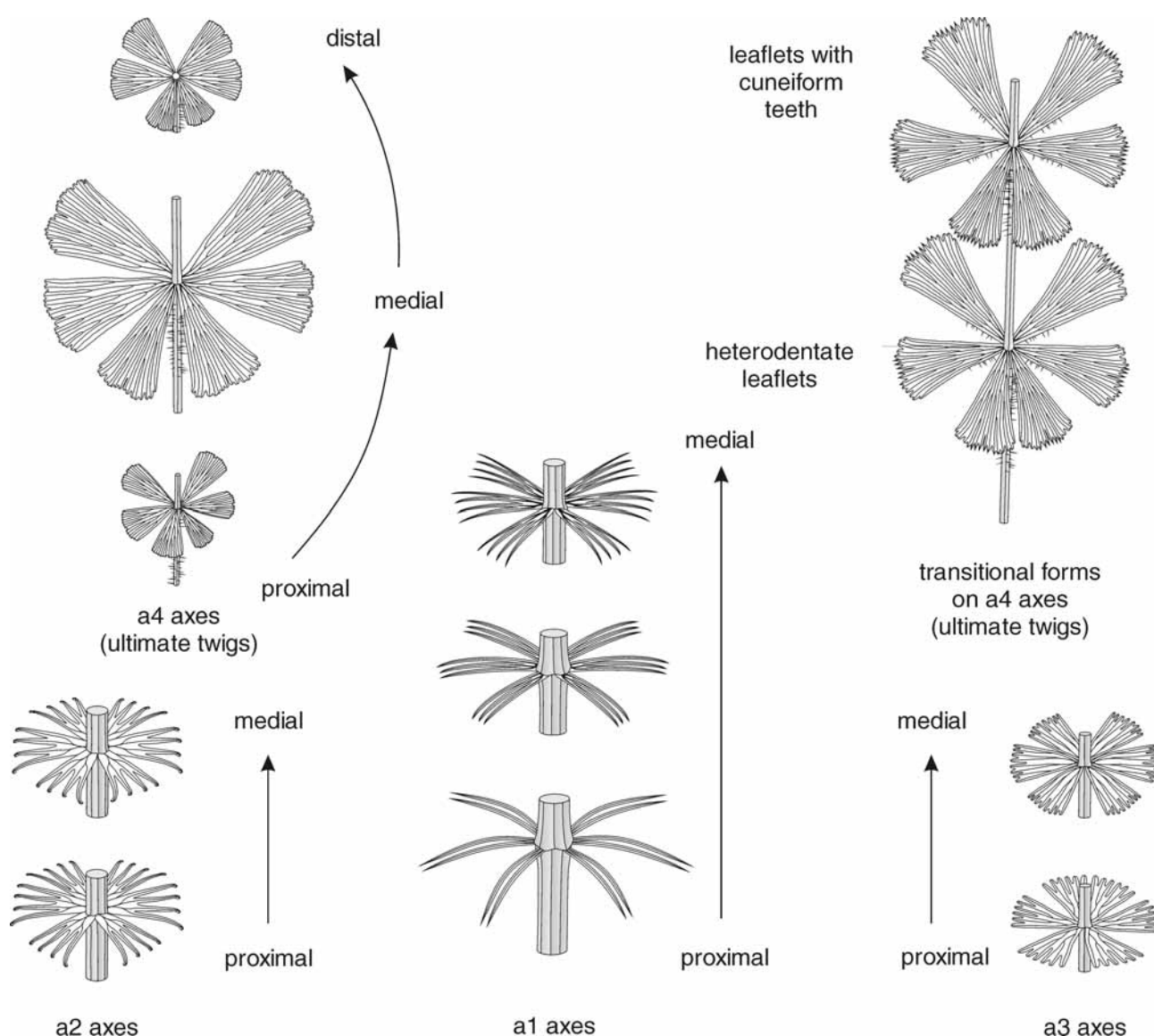


Figure 9. *Sphenophyllum costae*. Interpreted foliar “dissection series” showing the range of morphological variation in leaves depending on axes and point of insertion. First order (a1) axes with linear, lacinate leaves with an increasing number of acuminate lobes apically. Second order (a2) axes with partially lacinate leaves with lobes ending in climber hooks and sinuses decreasing in depth apically. Third order (a3) axes with prominent mid and secondary clefts on leaves with obtusely rounded lobes that increase in number apically. Ultimate twigs (a4) with slightly trizygioid leaves with obtusely rounded or allantoidal teeth and increasingly prominent, obtusely rounded mid and secondary clefts typical of *S. costae* (left), and transitional forms (right). Note the presence of hairs or short spines on axes and underside of transitional leaves. Reconstruction of foliage on a4 axes based on illustrations in Zodrow (1986, 1989). All foliage natural size.

(1999, fig. 5.14 on left side of photograph) have shown that a4 branches in *Sphenophyllum oblongifolium* had smaller whorls of leaves in basal positions, with successive whorls quickly increasing to their maximum size approximately 1/4 to 1/3 of the way up the branch. We believe that foliage of the ultimate twigs of *S. costae* showed the same pattern of development. The smallest leaves have no or very shallow clefts, short allantoidal teeth, and are slightly trizygioid (Figs 2B, 9; Zodrow 1986, pl. VI, fig. 2). As the leaves increased in size a short distance above the base,

there was an increase in the number and length of the allantoidal teeth, sinuses became slightly deeper to form secondary clefts on either side of a prominent mid cleft, and the trizygioid habit became more evident but remained subtler than in *S. oblongifolium* (Fig. 9). Some of these features are illustrated here (Figs 2A, C, 9), whereas further illustrations are provided by Zodrow (1986, pl. VI, figs 1, 3, fig. 9a) and Zodrow (1989, pl. I, fig. 1, pl. II, figs 2a–d, 5a, b). In the largest leaves, the distal margins are divided into two lobes of unequal width due to an asymmetrically

placed main cleft (Fig. 2C; Zodrow 1986, pl. VI, fig. 1). At the very apex of a4 branches, leaves of *S. costae* rapidly diminish in size, which presumably is a function of the equally prompt shortening of the internodes – retention of large whorls would have caused them to overlap, decreasing photosynthetic efficiency.

Sphenophyllum costae also has rare whorls of cuneiform leaves characterized by acuminate teeth (Figs 3C, 9; Zodrow 1989, pl. I, fig. 3, fig. 1b). Furthermore, some of the largest leaves are actually heterodentate and possess both allantoidal and acuminate teeth on the same distal margin (Figs 3B, 9; Zodrow 1989, pl. II – neotype); acuminate teeth are in a medial position and allantoidal teeth on the flanks. Based on the size and attachment of these rare morphological variants to long and thin branches, there is no doubt that they arose from ultimate twigs. However, we are uncertain of the placement of such leaf types on an individual a4 axis, or where those branches were located on the plant as a whole. A previous reconstruction of *S. costae* (Fig. 3) by Zodrow (1989) inferred that whorls of leaves with acuminate teeth succeeded those with allantoidal teeth, with the transitional heterodentate forms in between. [It is crucial to note that Zodrow's (1989) model inadvertently yet incorrectly placed the heterodentate whorls on a3 axes, a conclusion that we no longer endorse based on evidence from the current study.] It is quite plausible that the whorls of acuminate and heterodentate leaves served both photosynthetic and structural functions. Foliage with acuminate teeth surely would have more frictional resistance or clinging ability than leaves with obtusely rounded teeth. Hence, it is conceivable that acuminate leaves developed on an "as needed" basis, particularly when an ultimate twig was already resting on another branch or extending upwards in search of a prop to lean on. This interpretation is strengthened by the observation that short hairs occur along the proximal part of lateral margins of leaves with acuminate teeth (Fig. 9; Zodrow 1989, fig. 1b), although comparable structures are also seen on leaves with allantoidal teeth. We recognize that although a combination of hairs and leaves with acuminate teeth would have enhanced the plants ability to adhere, such features would not have had near as strong a grasp as the climber hooks present on second order branches of *S. costae*.

Of course, we acknowledge the possibility that the rare form of leaves with acuminate teeth, or combination of acuminate and allantoidal teeth on a single leaf, may simply result from taphonomic influences. Sides of the allantoidal teeth may have folded down into the matrix,

thus superficially appearing acuminate. However, without an analysis of cuticles from the distal margins of leaves from ultimate twigs of *Sphenophyllum costae*, it is not possible to be certain if acuminate teeth existed in this species.

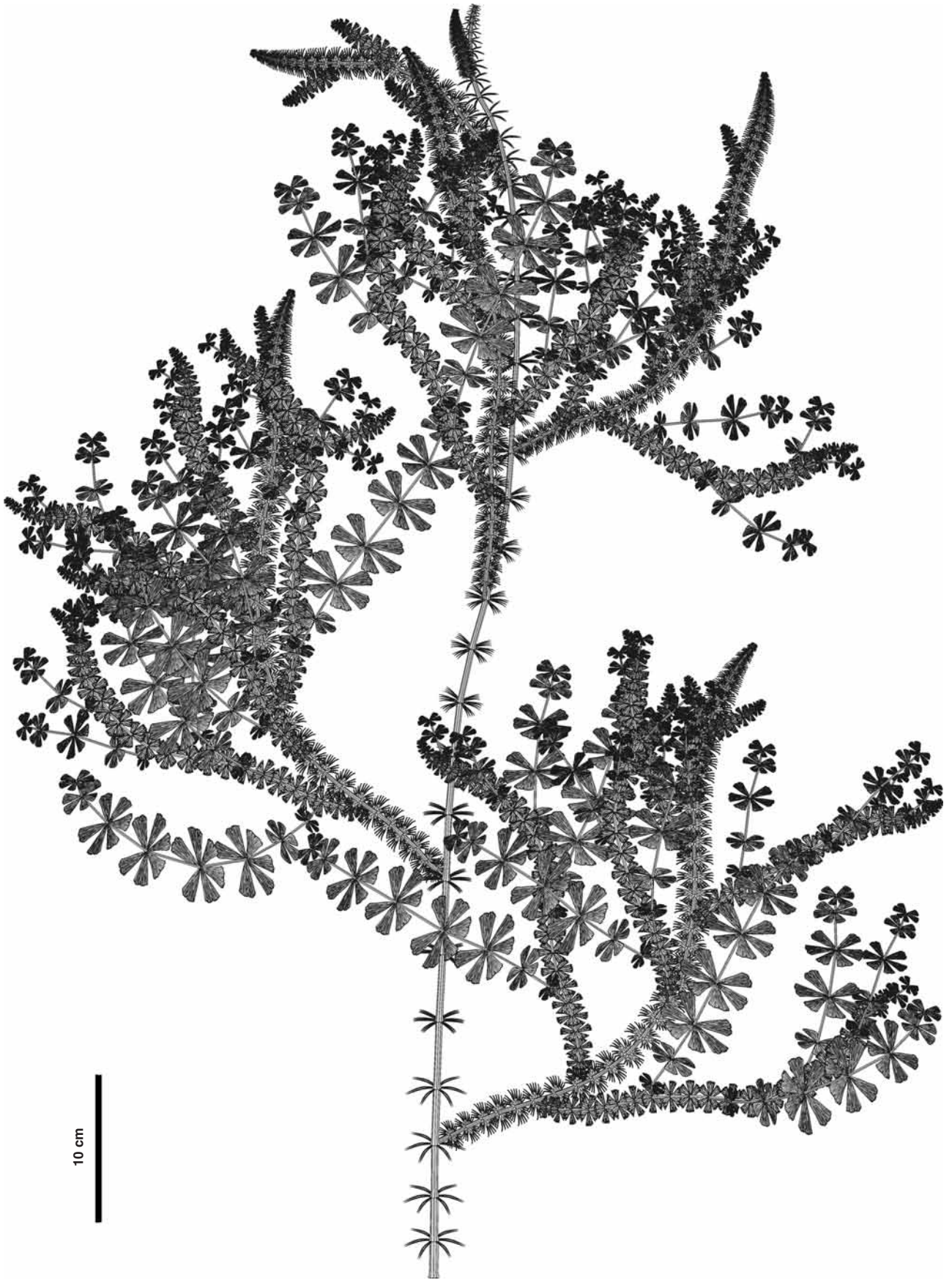
Ambiguous leaf types

In the course of reconstructing *Sphenophyllum costae*, we acknowledge that some previously illustrated leaf forms have been difficult to add to our proposed model. In particular, the leaf figured by Zodrow (1989, pl. I, fig. 2) has nearly parallel lateral margins and a distal margin that is only moderately incised to form five lobes with acuminate tips. In some respects, this morphology resembles foliage that we speculate might have existed in the middle parts of first order axes or on second order axes. Even more perplexing is the leaf illustrated by Zodrow (1986, fig. 9b), which also has parallel lateral margins but a distal margin terminated by three allantoidal teeth. This type of foliage has been documented in *Sphenophyllum emarginatum* by Batenburg (1977, fig. 5f) from the proximal part of shorter ultimate twigs attached near the apex of a2 branches. If the same inference could be made for *S. costae*, it would be logical to conclude that relatively shorter ultimate twigs were attached directly to the distal parts of first and second order branches.

Habit

Sphenophyllum costae was a multi-branched, woody shrub that formed dense thickets over 2 m high and up to 1 m wide. Without information on the proximal cauline portion of the plant it is difficult to be certain of its habit, but this axis may have crept laterally above or below ground level and intermittently gave rise to ascending branches of first order (a1 axes). In looking at our reconstruction, it is immediately obvious that this plant was unable to stand erect without the support of its own branching system. Axes of all orders were simply too long and too thin to withstand the considerable weight of their branches, foliage and fructifications. Instead, we suggest that ramifications of every order entwined with, clung to, and rested upon each other for support to remain upright and to grow both vertically and laterally. First (a1) and fourth (a4) order branches may have been comparatively longer exploratory axes, whereas second (a2) and third (a3) order branches may have provi-

Figure 10. *Sphenophyllum costae*. Partial vegetative reconstruction according to salient features discussed in the text. Neither the proximal cauline axis (to which a1 axes were attached), nor ultimate twigs with heterodentate or acuminate-toothed leaves, are represented. The vegetation shown in this reconstruction presumably did not stand alone, but instead rested upon and entwined with adjacent elements to remain erect.



ded more structural support. Climber hooks on a2 axes would have bolstered the ability of these branches to adhere or cling to adjacent props, and small, stiff spines or hairs on the axes and leaves of ultimate twigs may have served a similar function. Ultimate twigs bearing leaves with acuminate teeth may have developed on an “as needed” basis for the same purpose. Our reconstruction compares closely with the clinging or ascending habit previously proposed for *Sphenophyllum emarginatum* (Batenburg 1977) and *Sphenophyllum oblongifolium* (Galtier & Daviero 1999), thus providing evidence that several sphenophyll species occupying clastic substrates had similar ontogenetic growth patterns and architecture.

Taphonomy and palaeoecology

Despite the fact that the large, articulate specimen of *Sphenophyllum costae* was not found *in situ*, it can confidently be traced back to the roof shale of the Lloyd Cove Seam (Fig. 1C) by similarity of lithology. Accordingly, some useful palaeoecological inferences can be made based on observations of associated plant remains and equivalent strata in the open-pit mine. Rocks overlying the Lloyd Cove Seam are exceptionally fossiliferous (Zodrow 2002), and yielded abundant medullosalean foliage in association with large cauline axes, branches, and fertile organs that served the basis for reconstructing the arborescent plants bearing *Alethopteris zeilleri* Ragot (Zodrow 2007) and *Linopteris obliqua* (Bunbury) Zeiller foliage (Zodrow *et al.* 2007). Other plant fossil groups, such as lycophytes, calamitaleans, pecopteroids, cordaitaleans, and neuropteroids (*sensu lato*), are practically absent in the roof rocks.

Taphonomy

In previous studies at the locality (Zodrow 2002, 2007, Zodrow *et al.* 2007), the pteridosperm-dominated remains above the Lloyd Cove Seam were interpreted as a parautochthonous assemblage (*sensu* Gastaldo *et al.* 1995) that resulted from a single or multiple flood event(s). Several lines of evidence indicate that this claim should be largely maintained. The thickness of the *ca* 2.0 m fossiliferous unit above the Lloyd Cove Seam suggests that accumulation occurred in several pulses, with deposition resulting from successive flooding episodes. The fact that the *Sphenophyllum costae* specimen is preserved with 4 orders of branching indicates limited transport, as the relatively delicate axes presumably would have become disarticulated if transported far from the site of growth. Furthermore, associated plant remains are almost exclusively foliage, axes and fructifications of arborescent medullosalean plants

(see Zodrow 2002, table 2), with many axes of large size and still bearing branches. The preservation of an assemblage with maximal dominance and minimal evenness (Hammer & Harper 2006) implies that the medullosalean forest was entombed near its original habitat, as an increase in transport distance would have amplified the mixing of vegetative remains from a variety of plant communities. The large size of the sphenophyllous and pteridospermous debris suggests that it was removed from the same palaeoecological setting and transported together, although this hypothesis is speculative. Despite the fact that a detached root mantle and isolated roots of probable pteridosperm affinity were found in direct association with the sphenophyllous and seed-fern remains (Zodrow 2002), the absence of *in situ* rooting structures further supports the interpretation that this is a parautochthonous assemblage. It should be noted that Zodrow (2007) documented four stumps with a prominent basal flare in life position above the Lloyd Cove Seam on the quarry wall (*i.e.* at a laterally equivalent stratigraphic level), and interpreted them to be a stand of alethopterid trees with adventitious roots systems.

Taphonomic evidence suggests that the articulate specimen of *Sphenophyllum costae* was transported and buried during a storm event. It is significant that the sphenophyll is not preserved along a single plane of lamination, but instead is obliquely disposed through several of them over a vertical interval of *ca* 45 mm, thus imparting a three-dimensionality to the fossil. This type of preservation is indicative of rapid burial, such as by sediment-laden floodwaters, as opposed to slow settling of the plant from suspension in standing water, which typically results in debris coming to rest parallel to the sediment-water interface. In addition, branches on associated pteridosperm axes show signs of having been broken, bent or twisted (Zodrow 2002, figs 3–5, 8) and are invariably devoid of attached foliage. It is postulated that the branches were damaged and stripped of their vegetation by strong winds or heavy rains during a series of violent storm events, with aerial plant debris falling into and carried a short distance by concomitant floodwaters passing over the site of growth. Additional structural damage undoubtedly happened during transport and burial. These same floodwaters probably uprooted some pteridosperms and ground cover plants growing close to the forest floor (*i.e.* including *S. costae*), and ultimately deposited them together in parautochthonous assemblages in proximity to their original habitat.

Palaeoecology

According to the work of Gibling & Bird (1994), the Sydney Mines Formation of the Sydney Coalfield represents a succession of cyclothems, with strata deposited on broad coastal and alluvial plains that developed in response to

glacio-eustatic sea level fluctuations. The fossil-bearing unit of the Lloyd Cove Seam (Fig. 1C) conforms to what Gibling & Bird (1994, p. 111) termed “gray bay-fill and flood-plain deposits”, based on the coloration, lithologies, and presence of abundant plant fossils and siderite. These facies record predominantly fluvial deposition on a coastal plain that may have experienced periodic incursions of brackish waters. However, the presence of small nodules and thin bands of authigenic siderite, along with pyrite, in the basal 40–60 cm of the unit indicates formation under moderately to strongly reducing conditions in a non-marine environment (Krumbein & Garrels 1952). Taken together, the evidence suggests that *Sphenophyllum costae* and associated floras, at least in the Sydney Coalfield, inhabited fluvial-dominated settings in those portions of the coastal plain that were not affected by marine or brackish influences.

Sphenophyllum costae may have occupied a range of palaeoenvironments in the Sydney Coalfield, including peat-forming swamps, floodplains, or riparian habitats adjacent to the channels. Unfortunately, due to the transported nature of the specimen and associated pteridosperm debris, and fragmentation of the fossiliferous silty mudstone horizon by mining operations, it is challenging to be certain of the preferred habitat of this plant and its community. Zодrow (2002, p. 186) previously suggested that plant fossils found in the unit overlying the Lloyd Cove Seam could have been swamp-dwelling plants that were entrained in floodwaters passing over and effectively terminating peat formation. Although this remains a plausible interpretation, we acknowledge that plant remains in a roof shale often have no genetic relationship to the underlying coal seam (see discussion by Gastaldo *et al.* 1995).

Sphenophylls are known to have lived on both clastic and peat substrates. Peat-forming species apparently had abundant adventitious roots and aerial branch systems, that were often leafless, arising from prostrate, rooting main axes (Batenburg 1982). In contrast, species occupying clastic habitats had very rare adventitious roots and comprised ascending or climbing, self-supporting axes that formed dense, multi-branched thickets (Batenburg 1977, 1981, 1982). It has been suggested that the plants grew on unsubmerged, well-drained soils of floodplains and channel margins (Scott 1979, DiMichele *et al.* 1992). Although rooting organs have not been found in our material, the aerial vegetative components and presence of climber hooks clearly conform to the generalized growth strategy of the group of sphenophylls that preferred clastic substrates.

Additional pertinent information can be gained from previous palaeoecological interpretations of the associated arborescent pteridosperms. Zодrow (2002, 2007) and Zодrow & Mastalerz (2007) noted that *Alethopteris zeilleri* from this locality had thick, coriaceous pinnules with inrolled margins and highly cutinized cuticles with abun-

dant trichomes, characters that have been cited as indicators of growth under xeric or mesic conditions (Doubringer & Grauvogel-Stamm 1970, Šimůnek 1989, Kerp & Barthel 1993). Although morphological adaptations to physiological drought may result from living in truly edaphically drier settings, they may also be adapted by plants growing in nitrogen-deficient habitats (*e.g.*, in acidic, peat-forming environments), under harsh sunlight (Shields 1950, Mickle & Rothwell 1982), or in open canopies exposed to frequent winds (Cleal & Zодrow 1989). However, based on the observation of pteridosperm trunks rooted in clastic substrates above the Lloyd Coal Seam (Zодrow 2007), we believe that the *A. zeilleri* trees occupied non-peat-forming habitats in proximity to the swamps, where they may have been exposed to intense sunlight or wind. This habitat is consistent with recent findings from the Late Pennsylvanian of Texas (DiMichele *et al.* 2006, p. 100), who stated that *A. zeilleri* was a mesophyte that preferred growth in nutrient-rich, moist soils on the margin of areas of organic accumulation. Such a habitat could imply elevated hummocks on a floodplain, or poorly developed channel-flanking levees. We propose a similar habitat for *Sphenophyllum costae* based on its close association with the remains of *A. zeilleri*.

Discussion

Foliage on the aerial, vegetative portions of most sphenophylls exhibits a striking range of morphological variability. Zimmerman (1959) and Storch (1966) invoked the theory of recapitulation to explain the presence of linear or lacinate leaves on proximal branch orders and cuneiform leaves on distal branch orders of the stratigraphically higher (*i.e.* younger) members of *Sphenophyllum*. Accordingly, they implied that a type of neoteny was responsible for the retention of more “primitive” foliage on lower axes of the plant, rather than an expression of adaptation to a particular habitat niche (Storch 1966). While accepting that such an explanation had some merit, Batenburg (1977, 1981) contested that the primary reason for heterophylly amongst the sphenophylls was palaeoecological adaptation to a climbing or ascending growth habit. In particular, it was suggested that the stiffened, recurved lobe endings in linear or deeply divided leaves of many sphenophylls actually represent climber hooks that facilitated attachment to adjacent vegetation, and that spines or hairs on internodes and leaf margins presumably served a similar function (Batenburg 1977, 1981). Furthermore, Batenburg (1982) demonstrated that “petrification species” and “compression species” of *Sphenophyllum* had contrasting growth habits reflecting evolutionary modifications resulting from living in different environments – he intimated peat-forming substrates for the former group, and clastic substrates for

the latter. According to Batenburg (1982), climber hooks and spines or hairs were widespread in those sphenophylls occupying clastic substrates (*i.e.* his “compression species”), whereas such features were essentially absent in peat-forming sphenophylls (*i.e.* his “petrification species”). As a result, he concluded that sphenophylls from clastic habitats were multi-branched thickets comprising climbing or ascending, mutually supportive axes. The segregation of sphenophyll architectures based on their preferred habitat is of course a generalization, as some species with adaptations to grasping or clinging undoubtedly lived both in and adjacent to mires. For example, specimens of *Sphenophyllum oblongifolium* with climber hooks are also known to have grown in peat-forming swamps (Barthel 1997).

Based on our morphological and taphonomic observations of *Sphenophyllum costae*, we propose that the taxon can be added to a growing list of species from clastic substrates that evolved specialized modifications for a climbing habit. Comparison with similar species (*e.g.*, *Sphenophyllum emarginatum*, *Sphenophyllum oblongifolium*, *Sphenophyllum zwickaviense*) suggests that sphenophylls with a preference for clastic habitats share a number of similarities. This corroborates the previous conclusions of Batenburg (1982), and provides further insight into the growth strategy of clastic substrate sphenophylls. In members of this group, branches of all orders had epidogenetic succeeded by apoxogenetic growth, which resulted in considerable variability in leaf morphology depending on where on each axis whorls were borne. Similarly, each branch order was characterized by foliage of a particular type, and leaves showed a definite tendency to become increasingly less divided on axes of ascending order. The spacing between successive ramifications apparently was irregular, which implies non-rhythmic growth with diffuse or intermittent branching. Perhaps most importantly, structural adaptations to a clinging, climbing or scrambling habit, such as climber hooks and hairs or spines on axes or leaves, evolved in the majority of species from clastic habitats.

Despite the general architectural similarities between clastic substrate sphenophyll species, subtle variations in these basic architectural plans existed amongst most taxa. In particular, some species probably had (including the proximal cauline axis) five orders of branching (*e.g.*, *Sphenophyllum costae*, *Sphenophyllum oblongifolium*), whereas others had only three or four (*e.g.*, *Sphenophyllum emarginatum*) – such differences presumably influenced the overall size of the plant. Branches tended to arise singly from a given node, although in *S. emarginatum* two axes from a node was not uncommon (Batenburg 1977, Bashforth 2005). In *S. costae*, each branch order can be distinguished based on the lengths and widths of its internodes, resulting in a marked hierarchy between successive axes, similar to that documented for the calamitalean

sphenopsids (Eggert 1962). In contrast, internodal lengths and widths in any given branch of *S. oblongifolium* often attain sizes comparable to those of its parent axis (Galtier & Daviero 1999). Finally, the branch order upon which climber hooks were borne differs between species. In *S. costae*, these modified leaves were present on second order axes, whereas they existed primarily on first order axes in *S. emarginatum*, *S. oblongifolium*, and *Sphenophyllum zwickaviense*.

Conclusions

The results of our analysis of the largest known specimen of *Sphenophyllum costae* reveal that sphenophylls from clastic substrates followed a fundamental ontogenetic pattern of growth and architecture. Axes of various orders in *S. costae* can be differentiated based on their internodal lengths and widths, which indicates that a strong hierarchy of ramification existed in this taxon despite its apparent absence in other sphenophylls. Leaves modified to form climber hooks have been documented for the first time in the species. This type of foliage existed on second order branches in *S. costae*, despite the fact that such adaptations to a grasping or climbing habit generally are found on first order axes in other clastic substrate sphenophylls. The combination of these morphological attributes is a useful tool to facilitate the accurate identification and separation of *S. costae* from sphenophylls of the same age.

We propose that *Sphenophyllum costae* was a markedly heterophyllous species with each branch order bearing morphologically distinct whorls of leaves. The plant formed dense thickets of mutually supportive axes that climbed and ascended with the aid of climber hooks. It has the longest internodes known for any clastic substrate sphenophyll species, which suggests that it could have attained a height of up to 2 m by having branches that rested upon, clung to, or entwined with adjacent axes. In the Sydney Coalfield, *Sphenophyllum costae* grew as ground cover beneath canopies of the arborescent medullosalean pteridosperms *Alethopteris zeilleri* and *Linopteris obliqua*. This plant community probably inhabited well-drained (but moist) clastic substrates in a fluvial-dominated regime on coastal plains, such as on elevated channel margins (levees) or topographically raised parts of floodplains.

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