

EXPLORING ZOSTEROPHYLL RELATIONSHIPS WITHIN A MORE BROADLY
SAMPLED CHARACTER SPACE: A FOCUS ON ANATOMY

By

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ABSTRACT

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Important constituents of Siluro-Devonian floras, zosterophylls gave rise to the lycophytes. I explore the relationships of 18 zosterophyll species from 16 genera, maximizing sampling of anatomy. Using phylogenetic and phenetic methods, I (1) assess the influence of tree rooting, taxon sampling, and morphological vs anatomical characters on the stability of relationships; and (2) compare phylogenetic and phenetic methods in terms of relationships recovered. Phenetic analyses show sensitivity to taxon sampling and support placement of *Renalia* among zosterophylls, but do not provide results that are strongly congruent with those of phylogenetic analyses. Phylogenetic analyses demonstrate that taxon and character sampling significantly influence patterns of relationships. I consistently recovered two major clades: one, which lacks internal resolution and comprises the bulk of the zosterophyll taxa included in the analyses; the other clade includes the zosterophyll *Ventarura* and the lycopsid *Sengelia*, often accompanied by *Discalis* and *Trichopherophyton* (depending on taxon and character sampling). The placement of *Sengelia* in phylogenetic analyses supports earlier ideas that the zosterophyll ancestor of lycopsids had nonterminate fertile axes. Morphology- and anatomy-only analyses recover trees that differ from those obtained using

morphology+anatomy, highlighting the importance of broader sampling of the morphological character space. Breadth of character sampling and not the amount of phylogenetic resolution should be the primary criterion for selecting between alternative hypotheses of relationships.

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TABLE OF CONTENTS

ABSTRACT.....	ii
ACKNOWLEDGEMENTS	iv
LIST OF TABLES	vii
LIST OF FIGURES	viii
LIST OF APPENDICES.....	ix
INTRODUCTION	1
METHODS	7
Taxon Selection	7
Characters	8
Phylogenetic analyses	9
Phenetic analyses	10
Tables	12
Figures	15
RESULTS	19
Phylogeny	19
Taxon sampling.....	19
Character sampling	21
Phenetics	21
UPGMA	21
NMDS	22
DISCUSSION.....	23

Consistent patterns of relationships indicate presence of phylogenetic signal	23
Support for two major zosterophyll clades	24
Relationships within genera – <i>Zosterophyllum</i> and <i>Sawdonia</i>	26
Zosterophyll affinities of <i>Renalia</i>	28
The importance of “total” morphological evidence analyses	29
Phenetic approaches do not accurately reflect phylogenetic relationships among zosterophylls	32
CONCLUSIONS.....	34
REFERENCES	36
APPENDICES	40

LIST OF TABLES

Table 1. Taxon sampling, rooting, and character sampling in the different analyses performed.	12
Table 2. Results of analyses.	13
Table 3. Support values for analyses.	14

LIST OF FIGURES

Figure 1. Selected trees from phylogenetic analyses of zosterophylls.	16
Figure 2. Results of phenetic analyses using Jaccard's difference coefficient.	18

LIST OF APPENDICES

Appendix A. Taxa included in phylogenetic analyses (in alphabetical order) and literature used to score phylogenetic characters for each taxon.	40
Appendix B. Phylogenetic characters. A – characters used in the “anatomy-only” analysis; M – characters used in the “morphology-only” analysis.	44
Appendix C. Phylogenetic matrix.	47
Appendix D. Character scoring comments.	50
Appendix E. Phylogenetic matrix - NEXUS file.	55
Appendix F. Characters used in the phenetic analyses.	59
Appendix G. Phenetic matrix for UPGMA analyses; for the NMDS analyses, “?” is converted to “0”.	57

INTRODUCTION

Zosterophylls were a prominent component of Siluro-Devonian [Ludlow (Kotyk et al. 2002) to early Frasnian (Hueber & Banks 1979)] landscapes and gave rise to the once extensively diverse lycophyte clade. During this relatively brief stratigraphic presence, zosterophylls were a globally dispersed group of plants, which includes approximately thirty-seven accepted genera - a number that depends on the inclusion or exclusion of taxa which embody characteristics of zosterophylls as well as other groups (i.e., *Renalia* Gensel 1976), and of gametophyte fossils putatively attributed to zosterophylls (*Calyculiphyton*, *Kidstonophyton*, and *Sciadophyton* Remy et al. 1993).

Whereas zosterophylls are well known in comparison to the other early vascular plants (Banks 1975b), their taxonomy is still disputed. Banks published a proposed taxonomic classification in 1968, formally naming the Zosterophyllophytina. Generally speaking, zosterophylls are regarded as a basal grade in the lycophyte clade, with one of the zosterophyll groups thought to have given rise to the early lycopsids (Niklas and Banks 1990; Gensel 1992; Bateman 1996). Morphologically and anatomically speaking, zosterophylls are delineated as plants with vegetative organography consisting of simple undifferentiated axes, reniform bivalvate lateral sporangia, and exarch protosteles (Banks 1968, 1975). Even with these demarcations, there are taxa that combine zosterophyll features with those of other early vascular plant groups (i.e., *Renalia* Gensel 1976; *Huia* Geng 1985), making it difficult to circumscribe the group with certainty.

Banks (1968) initially divided Zosterophyllophytina into two families: the Zosterophyllaceae, which included taxa with naked axes and sporangia aggregated into spikes, and the Gosslingiaceae, which contained plants with ornamented axes and sporangia scattered along the axes. However, in his 1975 publication, Banks reversed this separation into two families. Although currently there is no consensus on taxonomy within the zosterophyll plexus, most studies (Banks 1968, Banks 1975, Hao and Xue 2013) recognize two large groups and place the origin of lycopsids among one of these. Differences between these studies primarily concern the membership of the two groups and the identity of taxa that are not included in either of the two. This situation is due, in part, to differences between the sets of taxa considered in the different studies.

In a pre-cladistic assessment of these discrepancies, Niklas and Banks (1990), discussing the patterns of symmetry and development of reproductive structures, distinguished two main zosterophyll groups: those with ‘terminate’ fertile axes (strobili) and those with ‘nonterminate’ reproductive morphology (fertile zones along indeterminate vegetative axes). They hypothesized that the immediate lycopsid ancestor had radial symmetry and ‘nonterminate’ growth in its fertile axes, like the zosterophyll *Discalis*, but unlike *Sawdonia* and *Crenaticaulis*, which possess bilateral fertile axes, or *Zosterophyllum*, which possesses terminate fertile axes.

With the advent of cladistics, the relationships of zosterophylls were addressed in a phylogenetic framework. Studies of the group have aimed to (1) assess the relationship of lycophytes and other basal vascular plants to zosterophylls (Gensel 1992, Kenrick and Crane 1997, Hao and Xue 2013); (2) provide classification schemes for the zosterophylls

(Kenrick and Crane 1997, Hao and Xue 2013); and (3) discern the relationships between zosterophyll groups (Kenrick and Crane 1997).

Gensel published the first phylogenetic analysis focused on zosterophylls and lycopsids in 1992, recovering all the zosterophylls and lycopsids included in the analysis in a clade with a large basal polytomy that also included *Renalia*. The lycopsids and zosterophylls each grouped into separate clades, except for *Zosterophyllum*, which was also a member of the basal polytomy of the zosterophyll+lycopsid clade.

The most in-depth study of zosterophyll phylogeny to date was undertaken by Kenrick and Crane (1997). This study set out to determine the relationship of zosterophylls to the lycopsids, like Gensel's (1992) study, but also addressed the relationships within the group. Kenrick and Crane recovered all the zosterophylls and other lycophytes (minus *Hicklingia*) as a large polytomy. Within this polytomy, a Zosterophyllopsida clade included *Zosterophyllum divaricatum* sister to a Sawdoniales clade, features unresolved relationships between two smaller clades (Sawdoniaceae and Barinophytaceae), *Thrinophyton*, *Hsua*, and a few genera circumscribed as Gosslingiaceae. A few traditional zosterophylls excluded from the Zosterophyllopsida (including several species of *Zosterophyllum*) were part of the basal polytomy of Lycophytina minus *Hicklingia*, while *Nothia* and *Zosterophyllum deciduum* were recovered more closely related to the lycopsids than to other traditional zosterophylls. More recently, focusing specifically on the plants of the Lochkovian Posongchong flora of Yunnan (China), Hao and Xue (2013) found zosterophylls forming a monophyletic group sister that is sister to a clade within which relationships between early lycopsids,

barinophytes, and euphyllophytes are not fully resolved. *Renalia* was recovered as the sister group of the large zosterophylls+lycopsids+barinophytes+euphyllophytes clade.

In all these taxonomic schemes, whether phylogenetically supported or not, a few trends arise. Most of the Zosterophyllopsida fall within two major groups – one that contains *Gosslingia* and other similar plants with bilateral symmetry of reproductive structures (Niklas and Banks 1990; Kenrick and Crane 1997), and another including plants with radially symmetrical reproductive structures, similar to *Zosterophyllum myretonianum* (Niklas and Banks 1990). However, the membership of these groups is not identical between the studies and there is no consensus on this potential classification scheme. For instance, whereas Hao and Xue (2013) recovered *Gosslingia* and *Sawdonia*, two zosterophylls from the bilaterally symmetrical group as a clade, the analysis of Kenrick and Crane (1997) placed bilaterally symmetrical zosterophylls in two separate families (*Gosslingia* in the Gosslingiaceae, and *Sawdonia* and *Serrulacaulis* in the Sawdoniaceae). Furthermore, the hypothesis of Niklas and Banks (1990), that lycopsids arose from zosterophylls with bilaterally symmetrical, non-terminate reproductive axes (i.e. with indeterminate growth) does not find support in these studies, some of which recover no resolution of the relationships between zosterophylls and lycopsids (Kenrick and Crane 1997; Gensel 1992). What these studies, taken together demonstrate, is that zosterophyll relationships are far from well understood.

Regardless of the questions posed in these studies, previous phylogenetic assessment has relied heavily on morphology, whereas anatomy was sampled very sparingly. Character matrices in these studies include 12-32 characters, of which only 3-7

characters code for anatomical features, despite a substantial body of existing data on zosterophyll anatomy (e.g., Banks and Davis 1969; Edwards 1969a,b; Zdebska 1982; Rayner 1983a; Kenrick and Edwards 1988; Lyon and Edwards 1991; Powell et. al. 2001). Far from being the fault of these studies' authors, the sparse sampling of anatomy rather reflected the broader taxonomic focus of the studies, wherein many of the crucial taxa were known exclusively from compressions that do not preserve anatomy. Nevertheless, anatomy is just as much an integral constituent of a species' identity as any of its other features, so it is important that it be included in characters toward achieving broader-evidence phylogenetic analyses. This is even more important in early tracheophytes with plesiomorphic organography, such as the zosterophylls, which exhibit relatively little in terms of complexity of external morphology for character construction. Additionally, a good number of zosterophyll species are preserved as permineralizations and have relatively well documented anatomy.

Here, I undertake the most character-rich assessment of zosterophyll phylogeny to date, using a matrix of 41 characters, of which 30 are applicable to permineralized specimens, and 12 of those 30 are strictly anatomical. I use parsimony-based phylogenetic analyses and phenetic methods to (1) explore phylogenetic relationships among zosterophylls with a more richly sampled dataset; (2) look at the influence of tree rooting and taxon sampling, and of morphological vs anatomical characters on the stability of relationships; and (3) examine how phylogenetic and phenetic methods compare in the taxonomic relationships recovered. My phylogenetic analyses find support for three major clades that do not align exactly with those recovered in previous

studies, and for the previously proposed origin of lycopsids for among a zosterophyll clade with ‘nonterminate’ reproductive morphology (Niklas and Banks 1990). Taxon sampling, tree rooting, and character sampling (morphology vs anatomy) impact significantly the resolution of the relationships recovered. Taxon sampling also impacts heavily the results of the clustering approach to phenetic analysis, and taxonomic groups supported by phenetic vs phylogenetic analyses show little overlap.

METHODS

Taxon Selection

I compiled a matrix of 18 zosterophyll species from 16 genera: *Crenaticaulis verruculosus* Banks and Davis (1969); *Deheubarthia splendens* Edwards et al. (1989); *Discalis longistipa* Hao (1989); *Euthursophyton hamperbachense* Mustafa (1978); *Gosslingia breconensis* Heard (1927), Edwards (1970), Kenrick and Edwards (1988a); *Huia gracilis* Geng (1985), Wang and Hao (2001); *Konioria andrychoviensis* Zdebska (1982); *Margophyton goldschmidtii* Zakharova (1981); *Nothia aphylla* Hoeg (1967), El-Saadawy and Lacey (1979), Kerp et al. (2001), Kerp (2017); *Sawdonia* (*Ensivalia*) *deblondii* Gerrienne (1996), Gensel and Berry (2016); *Sawdonia ornata* Hueber (1971), Rayner (1983a), Gensel and Berry (2016); *Serrulacaulis furcatus* Hueber and Banks (1979), Berry and Edwards (1994); *Stolbergia spiralis* Fairon (1967); *Thrinophyton formosum* Kenrick and Edwards (1988b); *Trichopherophyton teuchansii* Lyon and Edwards (1991); *Ventarura lyonii* Powell et al. (2001); *Zosterophyllum fertile* Leclercq (1942), Edwards (1969a); and *Zosterophyllum llanoveranum* Croft and Lang (1942), Edwards (1969b). *Zosterophyllum* and *Sawdonia* are each represented by two species (Appendix 1). These taxa were chosen to maximize the sampling of zosterophyll anatomy, in order to assess the influence of anatomy and morphology on phylogenetic resolution and patterns of relationships.

Tree searches were rooted with *Psilophyton dawsonii* (Banks et al. 1975) or *Renalia hueberi* (Gensel 1976). *Psilophyton dawsonii* is one of the best characterized of the trimerophytes, a group thought to form a grade from among which crown-group euphyllophytes evolved. As such, *P. dawsonii* is part of the clade sister to the lycophytes, which makes it one of the most closely related taxa that could be employed as an outgroup. *Renalia hueberi* is a vascular plant of uncertain taxonomic affinity (Gensel 1976, 1992; Kenrick and Crane 1997). Because *Renalia* combines zosterophyll and rhyniopsid features (Gensel 1992) and because rhyniopsids (or at least some of them) form a grade basal to the lycophyte-euphyllophyte divergence (Kenrick and Crane 1997), *Renalia* is another potential candidate for an outgroup.

A representative of crown-group lycopsids, *Sengelia radicans* (Matsunaga and Tomescu 2017), was included in analyses for methodological completeness, as at least some zosterophylls are generally regarded as paraphyletic with respect to a lycopsid clade (Kenrick and Crane 1997).

Characters

I constructed 40 characters (Appendix 2) that code for vegetative morphology and anatomy (26 characters), and sporangial morphology and arrangement (14 characters). Of the vegetative characters, 12 code for anatomical features. The characters were scored for each taxon based on the published literature and the data were recorded using Mesquite (Maddison and Maddison 2019) (Appendices 3-5).

In addition to tree searches using the full list of characters, I sub-sampled the list of characters in separate analyses to compare topological congruence and taxonomic implications between analyses using subsets of characters that can be scored only in compression fossils (“morphological” characters) and of those using characters that can be scored only in permineralizations (“anatomical” characters). The “morphology matrix” included 26 characters and the “anatomy matrix” 30 characters of the total of 40 (Appendix 2); the two subsets overlap partially as some of the characters can be scored in both permineralized and compression fossils.

Phylogenetic analyses

Phylogenetic searches were conducted in TNT 1.5 (Goloboff and Catalano 2016), using equally weighted parsimony as the optimality criterion, and 10,000 trees were held for comparison. The parsimony analyses were initiated using the command “ienum” to find all the most parsimonious (MP) trees. Once the tree search was complete and all MP trees were found, a consensus tree was calculated using the command “nelsen*”. Majority rule trees were calculated under a second tree search algorithm, using the commands “xmult = hits 20” and “bb;” to obtain the total number of most parsimonious trees. Once the tree search was complete, a majority rule 50 tree was calculated using the command “majority*”.

Tree searches were conducted under different taxon sampling regimes (for both ingroup and outgroup taxa) and character sampling regimes (Table 1). As part of the taxon sampling experiments, I excluded one or both of the two taxa with the highest

percentage of missing data (*Stolbergia*, 54% missing data; *Euthursophyton*, 44% missing data). From among all these analyses, all of which used the full set of characters, I selected the two taxon samplings that yielded the best-resolved topologies to perform the tree searches under different character sampling regimes: “morphological” characters vs “anatomical” characters. Trees were imaged in FigTree v1.4.4 (Rambaut 2018).

Phenetic analyses

Traditionally, numerical taxonomy studies have employed both clustering and ordination (Sneath and Sokal 1973), hence my choice of employing both of these methods of assessment. For the clustering analyses, I modified the 40 characters used in the phylogenetic analyses to render their scoring binary (Appendices 6, 7); some of the phylogenetic characters had to be split into two or more binary characters and this resulted in 57 characters. I used the unweighted pair group method with arithmetic mean (UPGMA; Sokal and Michener 1958), computed using PAST 3.24 (Hammer and Hammer 2019). UPGMA is a frequently used clustering method that, in this case, computes the average similarity of one included taxon to others when all are weighted equally (Sneath and Sokal 1973). In the UPGMA analyses, I used Jaccard’s difference coefficient because it takes into account only positive co-occurrences, which carry taxonomic signal, whereas absence of characters has no direct taxonomic implications (Sneath and Sokal 1973; Aldendorfer and Blashfield 1984). UPGMA clustering was performed only for two taxon samplings – ingroup taxa plus *Renalia*, either including or

excluding both *Stolbergia* and *Euthursophyton* – to test for the sensitivity of results to taxon sampling.

For the ordination analysis, I re-coded the binary characters used in the clustering analyses (Appendix 7) to replace all “?” with “0”. Using this matrix, I performed non-metric multidimensional scaling (NMDS) using PC-Ord (McCune and Grace 2002). Specifically, I used the “slow and thorough” procedure to select the optimum dimensionality for the ordination. This selection process included 250 runs with original data and 250 Monte Carlo randomized runs.

I excluded *Psilophyton* and *Sengelia* from both clustering and ordination analyses because I did not address their similarity to zosterophylls and because phenetic analyses do not require the character polarization that is necessary for phylogenetic analyses. I included *Renalia* in the phenetic analyses to test the hypothesis of its zosterophyll affinities in a non-phylogenetic framework.

Tables

Table 1. Taxon sampling, rooting, and character sampling in the different analyses performed.

Analysis	Taxon sampling – excluded taxa	Rooting	Character sampling
RPS	-	<i>Renalia</i>	All
PRS	-	<i>Psilophyton</i>	All
PS	<i>Renalia</i>	<i>Psilophyton</i>	All
RS	<i>Psilophyton</i>	<i>Renalia</i>	All
RS-S	<i>Psilophyton, Stolbergia</i>	<i>Renalia</i>	All
RPS-S	<i>Stolbergia</i>	<i>Renalia</i>	All
PS-S	<i>Renalia, Stolbergia</i>	<i>Psilophyton</i>	All
PRS-S	<i>Stolbergia</i>	<i>Psilophyton</i>	All
RS-SE	<i>Psilophyton, Stolbergia, Euthursophyton</i>	<i>Renalia</i>	All
RPS-SE	<i>Stolbergia, Euthursophyton</i>	<i>Renalia</i>	All
PS-SE	<i>Renalia, Stolbergia, Euthursophyton</i>	<i>Psilophyton</i>	All
PRS-SE	<i>Stolbergia, Euthursophyton</i>	<i>Psilophyton</i>	All
RS-SE Comp	<i>Psilophyton, Stolbergia, Euthursophyton</i>	<i>Renalia</i>	“Morphology” only
RS-SE Perm	<i>Psilophyton, Stolbergia, Euthursophyton</i>	<i>Renalia</i>	“Anatomy” only
PRS Comp	<i>Stolbergia, Euthursophyton</i>	<i>Psilophyton</i>	“Morphology” only
PRS-SE Comp	<i>Stolbergia, Euthursophyton</i>	<i>Psilophyton</i>	“Morphology” only
PRS-SE Perm	<i>Stolbergia, Euthursophyton</i>	<i>Psilophyton</i>	“Anatomy” only

Table 2. Results of analyses.

Analysis	Number of MP trees	Length of MP trees	Number of nodes resolved	Figured
RPS	722	90	1	-
PRS	722	90	1	-
PS	91	88	1	-
RS	672	83	1	-
RS-S	223	83	5	-
RPS-S	173	90	1	-
PS-S	40	88	3	-
PRS-S	173	90	1	-
RS-SE	40	81	7	Fig. 1C
RPS-SE	28	88	5	-
PS-SE	3	86	10	Fig. 1D
PRS-SE	28	88	5	Fig. 1B
RS-SE Comp	9	64	8	-
RS-SE Perm	44	58	6	-
PRS Comp	90	67	7	-
PRS-SE Comp	9	67	9	Fig. 1F
PRS-SE Perm	56	65	7	Fig. 1E

Table 3. Support values for analyses.

Tree	Consistency index	Retention index	Bootstrap average group support
RPS	0.522	0.574	7.4
PRS	0.522	0.574	6.8
PS	0.534	0.573	8.1
RS	0.542	0.578	7.4
RS-S	0.542	0.568	10.0
RPS-S	0.522	0.566	8.7
PS-S	0.534	0.564	10.7
PRS-S	0.522	0.566	9.0
RS-SE	0.556	0.576	10.5
RPS-SE	0.534	0.573	8.8
PS-SE	0.547	0.571	10.9
PRS-SE	0.534	0.573	9.4
RS-SE Comp	0.516	0.587	11.7
RS-SE Perm	0.603	0.614	14.9
PRS Comp	0.493	0.6	6.4
PRS-SE Comp	0.493	0.59	9.3
PRS-SE Perm	0.569	0.606	12.1

Figures

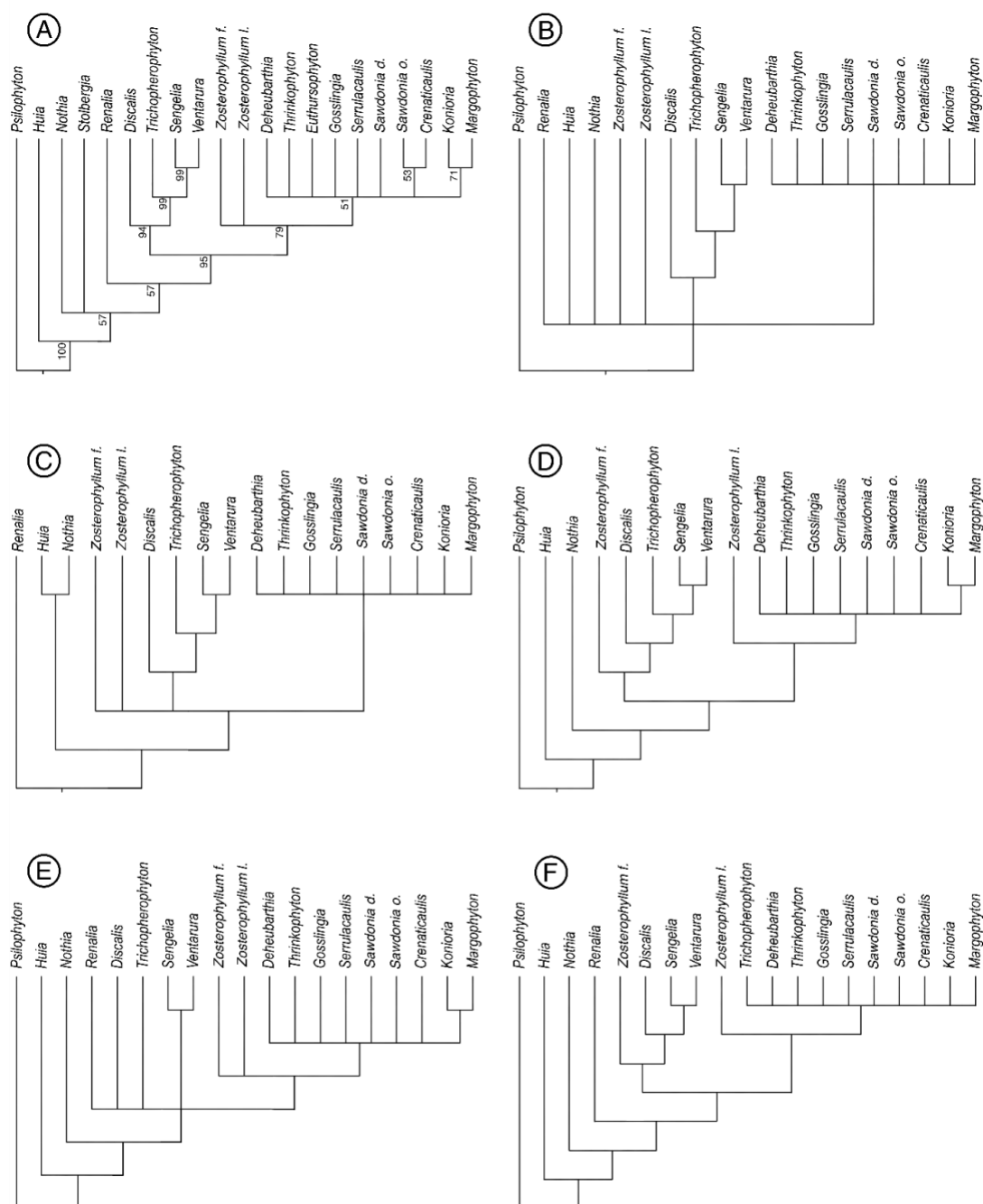


Figure 1. Selected trees from phylogenetic analyses of zosterophylls. A. 50% majority rule consensus of 720 most parsimonious (MP) trees generated by analysis including all ingroup taxa and rooted with *Psilophyton*. B. Strict consensus tree of 28 MP trees (length = 88) generated by analysis rooted with *Psilophyton* and excluding *Stolbergia* and *Euthursophyton*. C. Strict consensus tree of 40 MP trees (length = 81) generated by analysis rooted with *Renalia*, and excluding *Stolbergia* and *Euthursophyton*. D. Strict consensus of 3 MP trees (length = 86) generated by analysis rooted with *Psilophyton* and excluding *Stolbergia* and *Euthursophyton*. E. Strict consensus of 56 MP trees (length = 65) generated by analysis rooted with *Psilophyton*, excluding *Stolbergia* and *Euthursophyton*, and using only characters that can be scored in permineralized fossils (“anatomy-only” analysis). F. Strict consensus of 9 MP trees (length = 67) generated by analysis rooted with *Psilophyton*, excluding *Stolbergia* and *Euthursophyton*, and using only characters that can be scored in compression fossils (“morphology-only” analysis).

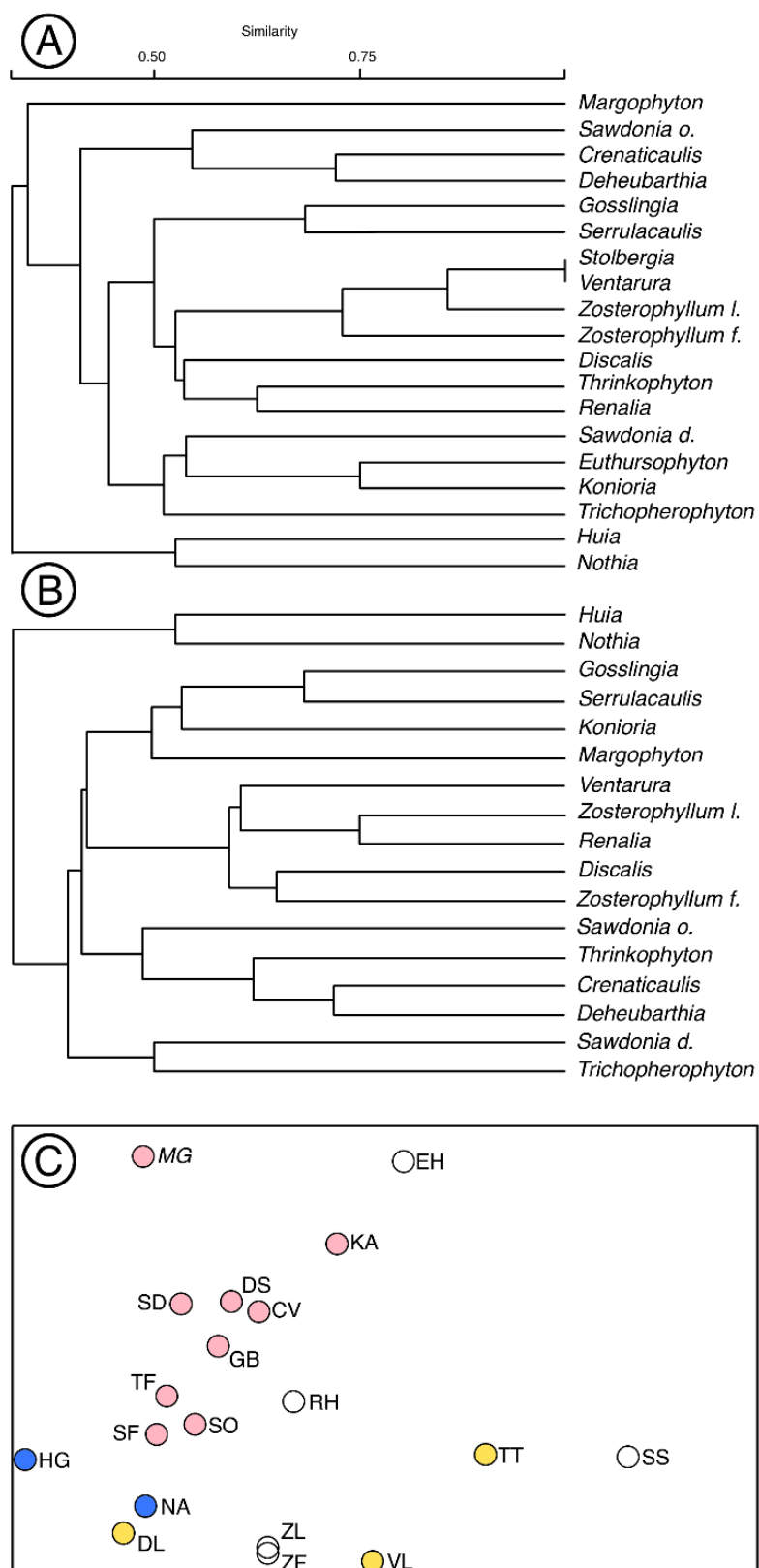


Figure 2. Results of phenetic analyses using Jaccard's difference coefficient. A. Dendrogram generated by UPGMA analysis that excluded *Psilophyton* and *Sengelia*. B. Dendrogram generated by UPGMA analysis that excluded *Psilophyton* and *Sengelia*, as well as *Stolbergia* and *Euthursophyton*. C. NMDS ordination plot of analysis that excluded *Psilophyton* and *Sengelia*; taxon acronyms consist of the genus name and specific epithet initials; blue circles – *Huia* (HG) and *Nothia* (NA); yellow circles – taxa of the clade that includes the lycopsid *Sengelia* (VL, TT, and DL); pink circles – “large zosterophyll clade” (MG, KA, DS, CV, SD, GB, TF, SF, and SO); white circles – taxa not recovered in consistent placements in the different phylogenetic analyses or excluded from some of the analyses (ZL, ZF, SS, EH). Abbreviation code as follows: MG – *Margophyton goldschmidtii*; EH – *Euthursophyton hamperbachense*; KA – *Konioria andrychoviensis*; DS - *Deheubarthia splendens*; CV – *Crenatacaulis verruculosus*; SD – *Sawdonia deblondii*; GB – *Gosslingia breconensis*; TF – *Thrinophyton formosum*; SO – *Sawdonia ornata*; SF – *Serrulacaulis furcatus*; RH – *Renalia heuberi*; HG - *Huia gracilis*; NA – *Nothia aphylla*; DL – *Discalis longistipa*; ZL – *Zosterophyllum llanoveranum*; ZF – *Zosterophyllum fertile*; VL – *Ventarura lyonia*; TT – *Trichopherophyton teuchansii*; SS – *Stolbergia spiralis*.

RESULTS

Phylogeny

Taxon sampling

The strict consensus trees of analyses that include all ingroup taxa show no resolution regardless of rooting (Table 2, Table 3). Nevertheless, two major clades are supported in the majority rule trees from the same analyses (e.g., fig. 1A). One of these clades includes *Sengelia*, *Ventarura*, *Discalis*, and *Trichopherophyton*, while the other contains the majority of the ingroup taxa (*Deheubarthia*, both species of *Sawdonia*, *Euthursophyton*, *Gosslingia*, *Serrulacaulis*, *Thrinophyton*, *Konioria*, and *Margophyton*).

The exclusion of taxa with highest percentages of missing data brings resolution to the strict consensus trees. Exclusion of *Stolbergia* (highest percentage of missing data – 54%), produces a strict consensus tree (Table 2, RS-S analysis; tree not shown) in which a clade consisting of *Huia* and *Nothia* is sister to a large polytomy that contains the rest of the ingroup taxa and within which the only clade resolved contains *Trichopherophyton*, *Ventarura*, and *Sengelia*. Subsequent exclusion of *Euthursophyton* (second highest amount of missing data – 44%) leads to a marked increase in strict consensus tree resolution compared to the previous analyses. Generally, the strict consensus trees (fig. 1B-D) include the same two major clades that were supported in the majority rule trees of the analyses that included all the ingroup taxa. The only exception is the addition of *Discalis* to the clade that includes the lycopsid *Sengelia*.

Resolution and the position of some specific taxa vary slightly depending on rooting and taxon sampling (compare Fig. 1B, 1C and 1D). Despite the fact that *Psilophyton* and *Renalia* only swap positions with each other in the PRS-SE (fig. 1B) and RPS-SE (tree not shown) analyses, without any other effect on consensus topology, exclusion of either *Psilophyton* (fig. 1C) or *Renalia* (fig. 1D) leads to increased resolution of the strict consensus trees. The two major clades supported in other analyses (Fig. 1A, B) are recovered consistently when either *Psilophyton* or *Renalia* is excluded. The *Huia*+*Nothia* clade supported in the RS-S analysis is resolved in the RS-SE analysis (fig. 1C), but in the other analyses these two taxa are either in a paraphyletic group basal to the rest of the ingroup, or part of a large polytomy. Additionally, the position of the two species of *Zosterophyllum* is unstable: they are either part of the basal polytomy of the clade that excludes *Huia* and *Nothia* (fig. 1B, C), or they are placed as sister to the clade that includes *Sengelia* (*Z. fertile*) and sister to the larger clade (*Z. llanoveranum*) (fig. 1D).

The consistently resolved clade that contains *Trichopherophyton*, *Venturura*, and *Sengelia* is supported in all analyses by character 34 (C34) – short sporangial stalk length. The position of *Discalis* as sister to this clade is supported by an epidermal layer internal cellular differentiation (C14) in the PRS-SE analysis (Fig. 1B), the presence of K-branching (C24) in the PS-SE analysis (Fig. 1D), and by both of the latter characters in the RS-SE analysis (Fig. 1C). However, of the four taxa, only *Discalis* and *Sengelia* can be scored for these characters, whereas the others have missing data. In the RS-SE

analysis (Fig. 1C), *Huia* and *Nothia* form a clade characterized by adaxially curved sporangia (C33).

Character sampling

The consensus trees of the PRS-SE sampling analyses that compared alternative character sampling regimes (Fig. 1E, F) exhibit higher resolution than those obtained using the full set of characters, but retain similar overall clade membership, with the exception of a few taxa. In the “anatomy” consensus tree (Fig. 1E), the clade that includes *Sengelia* collapses: *Trichopherophyton* and *Discalis* (along with *Renalia*) are part of the basal polytomy of the ingroup clade that excludes *Huia* and *Nothia*, and only *Ventarura* forms a clade with *Sengelia*. The two species of *Zosterophyllum* are recovered as part of a polytomy with the large clade that contains the remaining ingroup taxa. This clade is supported by the presence of a sclerified outer cortex (C9). In the “morphology” consensus tree (Fig. 1F), the *Discalis-Ventarura-Sengelia* clade is sister to *Zosterophyllum fertile* but *Trichopherophyton*, which is also associated with this clade in analyses that use the full set of characters, is recovered as a member of a different clade.

Phenetics

UPGMA

The clustering analyses show sensitivity to taxon sampling, i.e., the configurations of dendrograms differ dramatically between the analysis that included the taxa with the highest amount of missing data (*Stolbergia* and *Euthursophyton*) (Fig. 2A) and the analysis that excluded them (Fig. 2B). Furthermore, the major clades seen in the

phylogenetic analyses are not reflected in the similarity relationships conveyed by the dendrograms, apart from the grouping of *Huia* and *Nothia*, which has a high similarity score. Both analyses show high similarity scores between *Renalia* and the bulk of the zosterophyll taxa.

NMDS

Ordination did not reveal strong trends in the dataset. However, unlike the clustering analyses, ordination supports some of the taxonomic relationships implied by the results of the phylogenetic analyses. The bulk of the taxa present in the large clade that is recovered as a large polytomy in the phylogenetic analyses (except for *Konioria* and *Margophyton*) are closely associated in the NMDS ordination plot (Fig. 2C). Additionally, I found a close association of *Renalia* to this group.

DISCUSSION

Consistent patterns of relationships indicate presence of phylogenetic signal

The level of resolution and node support produced by my analyses is relatively low, even compared to those of other analyses addressing the deep phylogeny of early tracheophytes (Toledo et al. 2021; Durieux et al. 2021). Notably, the strict consensus trees of analyses including all the taxa lacked any resolution (Table 2). This was driven primarily by the high amount of missing data (especially in some of the taxa included in the analyses), as demonstrated by the improved resolution of analyses that excluded the taxa with highest amount of missing data (see discussion in Nixon 1996), but high levels of homoplasy due to the relatively simple morphology and anatomy of the plants probably also contributed to lowering resolution. Nevertheless, the consensus trees of all analyses that did produce better resolution (Fig. 1), recovered the same overall patterns of relationships and broadly consistent clades (with a few notable exceptions discussed below), irrespective of tree rooting choice, taxon exclusion, and even character subsampling. Together, these demonstrate the presence of a consistent (albeit weak) phylogenetic signal in the characters. It is not surprising, therefore, that the same signal is recovered in the majority rule consensus trees of the analyses that did not recover any resolution in the strict consensus. In turn, this confirms that in recalcitrant datasets, some phylogenetic signal can be gleaned from majority rule consensus trees. In the same vein, Kenrick and Crane's (1997) results demonstrate that exclusion of taxa to minimize the

amount of missing data in analyzes of relationships within lycophytes and zosterophylls recovered overall patterns of relationships similar to those obtained with more missing data, but with higher resolution.

Support for two major zosterophyll clades

In all the consensus trees, variations of two distinct clades are recovered as sister to one another (Fig. 1D, F), or as members of the same polytomy (Fig. 1B, C, E). The first clade, hereafter referred to as the “large zosterophyll clade”, is a polytomy that consists of the majority of the included taxa: *Deheubarthia*, *Thrinophyton*, *Gosslingia*, *Serrulacaulis*, both species of *Sawdonia*, *Crenaticaulis*, *Konioria*, and *Margophyton*. Despite some differences in taxon sampling, this clade is similar to the clade designated as the Sawdoniales by Kenrick and Crane (1997), and fits the bilaterally-patterned terminate fertile axis bauplan outlined by Niklas and Banks (1990). In my strict consensus trees, the large zosterophyll clade has little to no internal resolution. Some phylogenetic patterns nevertheless are apparent in majority rule consensus trees of five analyses (corresponding to the strict consensus trees shown in Fig. 1B-F). All these analyses recover within the large zosterophyll clade, in >50% of the strict consensus trees, a *Konioria*-*Margophyton* clade. In four of these analyses, >50% of the strict consensus trees recover a clade including *Crenaticaulis* and either both species of *Sawdonia* (forming a grade paraphyletic to *Crenaticaulis*), or just *Sawdonia ornata*. The “morphology-only” analysis excluding *Stolbergia* and *Euthursophyton* (strict consensus tree shown in Fig. 1F) recovers in >50% of the strict consensus trees a *Sawdonia* grade

paraphyletic to *Trichopherophyton*, with the clade formed by these three taxa sister to *Crenaticaulis*.

The other clade contains the lycopsid representative, *Sengelia*, as well as the zosterophyll *Venturura* in all trees, but *Discalis* and *Trichopherophyton* are also joined to this group in several analyses (Fig. 1B-D, F); in some analyses *Zosterophyllum fertile* is recovered as sister to the *Sengelia-Venturura-Trichopherophyton-Discalis* clade (Fig. 1D, F). Previous analyses have not recovered this clade, but *Discalis* is placed in a polytomy that includes the lycopsids in Kenrick and Crane's (1997) results, and the clade also aligns with Niklas and Banks' (1990) hypothesis for the phylogenetic place of origin of lycopsids among a group that may have included *Discalis*.

I also note a consistent association of *Nothia* and *Huia*, which form either a clade sister to the clade including all other zosterophylls, or a grade basal to that clade. *Nothia* and *Huia* differ notably, both anatomically and morphologically, from other zosterophyll taxa included in this study, as well as from one another. Both taxa have adaxially recurved sporangia, seen only in *Sawdonia ornata* among the other taxa. *Nothia* has axes with uneven surface relief (El-Saadawy and Lacey 1979), thought to be a natural feature of the plant and not a taphonomic artifact, which is not seen in other zosterophylls. *Huia* was originally described as having a centrarch pattern of xylem maturation, although that description states that protoxylem tracheids could not be isolated from the center of the vascular strand (Wang and Hao 2001). However, if the pattern of xylem maturation is indeed centrarch, it suggests *Huia* is combining characters of zosterophylls and rhyniophytes. Somewhat consistent with the placement of *Huia* and *Nothia* in my

analyses, both these taxa are placed outside the Zosterophyllopsida in Kenrick and Crane's (1997) study. There, *Nothia* is recovered as a member of the polytomic clade that also contains the lycopsids, whereas *Huia* is part of a polytomy which includes that clade.

Neither clade recovered in my study is reflected in Gensel's (1992) results. It is important to note, however, that while my analyses emphasized the relationships within zosterophylls, Gensel's focus was on the relationships among zosterophylls and other groups and, as such, coded for characters relevant to that question and included a different taxon sampling than this study.

Banks (1968) outlined a proposal to classify zosterophylls (Zosterophyllales) in two major groups: the Zosterophyllaceae, which included *Zosterophyllum* and *Bucheria* [renamed *Rebuchia* by Hueber (1970)]; and the Gosslingiaceae, which included *Gosslingia*, *Serrulacaulis*, "*Psilophyton* non-Dawson" [currently, *Sawdonia ornata* Hueber (1971)], and what he termed 'new genus of Lyon' [in reference to Lyon (1964), currently known as *Nothia aphylla* (Kerp et al. 2001)]. Banks later rescinded the classification (Banks 1975) upon considering additional zosterophylls discovered subsequent to his 1968 classification (e.g., Edwards 1969a,b; Edwards 1970a). Like Banks' earlier treatment, my analyses also support two major groups among zosterophylls, but these show no overlap with Banks' groups.

Relationships within genera – *Zosterophyllum* and *Sawdonia*

Zosterophyllum was the first erected zosterophyll genus (Penhallow 1892) and is presently the most speciose. Although in my analyses I only included two

Zosterophyllum species (*Z. fertile* and *Z. llanoveranum*), they are found in two different patterns of placement. In one, they are both part of the same polytomy, whether that is the polytomy that also includes the two major clades formed by most of the other zosterophylls (Fig.1 B, C) or a polytomy with the “large zosterophyll clade” (Fig.1E). In the other, each of the two major clades recovered in my analysis is sister to one of the two *Zosterophyllum* species (Fig.1D, F). Both Kenrick and Crane (1997) and Hao and Xue (2013) included multiple species of *Zosterophyllum* that similarly were not resolved as a clade. In my character matrix, *Z. fertile* and *Z. llanoveranum* differ in only a few characters, which relate to sporangial distribution and shape, and also to histology, as *Z. llanoveranum* has a sclerified outer cortex that is absent in *Z. fertile*. The inconsistent and notably never monophyletic resolution of these two species of the same genus suggests that a re-evaluation of *Zosterophyllum* may be needed.

The other genus represented by two species in this study is *Sawdonia*, typified by *S. ornata*. The second species, initially described as *Ensivalia deblondii* Gerrienne (1996), was reassigned by Gensel and Berry (2016) to the genus *Sawdonia* based on overall similarity with *Sawdonia ornata* and demonstration of unequal sporangial valves in the latter, like those documented in *Ensivalia deblondii*. Unlike the two *Zosterophyllum* species, the placement of both *Sawdonia* species is stable: they are consistently recovered as members of the same clade – the “large zosterophyll clade”. However, their finer taxonomic relationships to the other taxa of this clade are unknown, as the clade lacks internal resolution (with a few exceptions – Fig. 1D, E). Interestingly, the majority of consensus trees of several analyses support a paraphyletic grade formed

by *S. ornata* and *S. deblondii*. The vegetative morphology of the two species is broadly similar, with the exception of the presence of trichomes (*S. deblondii* does not have them and *S. ornata* does) and subaxillary tubercles (seen in *S. deblondii* but not in *S. ornata*); I scored trichomes present in *S. ornata* as suggested by the presence in the epidermis of rosettes of cells (Rayner 1983a) reminiscent of those present at trichome bases in most plants. However, *S. ornata* and *S. deblondii* differ in aspects of sporangial morphology – sporangium shape (more flattened dorsiventrally in *S. deblondii*): sporangial stalk (longer relative to the size of the sporangium in *S. deblondii*) – as well as sporangial orientation (recurved in *S. ornata*) and number of sporangium files. Thus, my results provide only circumstantial support for close relationships between the two *Sawdonia* species, possibly because my character construction did not emphasize enough their shared features.

Zosterophyll affinities of *Renalia*

Renalia is an early vascular plant with an interesting combination of characters. On one hand it has reniform, bivalvate sporangia (Gensel 1976) that are zosterophyll-like, but unlike in zosterophylls, the sporangia of *Renalia* are borne terminally on axes, like those of rhyniopsids, and have a seemingly paired arrangement. Taxonomic placement of *Renalia* has been hindered at least in part by the lack of detailed anatomical information – preserved as compressions, *Renalia* has only yielded some cellular patterns observed in cleared specimens and short strands of tracheids (Gensel 1976). In the original description of *Renalia*, Gensel (1976) compared it to cooksonioid rhyniophytes and to zosterophylls, opting for placement in the former, but suggesting the possibility of an

“intermediate” position between rhyniophytes and zosterophylls, with which later Hueber (1992) suggested closer affinities. My study provides some support for zosterophyll affinities of *Renalia*. Some of my phylogenetic analyses (Fig. 1E, F) recovered it nested among the zosterophylls (as opposed to sister outside of the clade formed by all the zosterophylls), and both the UPGMA and NMDS analyses (Fig. 2) relatively high levels of similarity of *Renalia* to other zosterophylls.

The importance of “total” morphological evidence analyses

Under identical taxon sampling, neither the “morphology-only” (Fig. 1F) nor the “anatomy-only” (Fig. 1E) analyses returned topologies identical to the all-character tree, although general patterns of relationships were similar in both cases to those recovered by the all-character analyses. The “large zosterophyll clade” seen in the all-character trees was also recovered in both the “anatomy” and “morphology” trees, except that this clade also includes *Trichopherophyton* in the “morphology” tree (Fig. 1F). The other main clade I recovered in most of my all-character analyses is represented only by *Sengelia* and *Ventarura* in the “anatomy” tree (Fig. 1E), but the “morphology” tree recovers a clade more consistent with the all-character trees, including *Sengelia*, *Ventarura*, *Discalis*, and *Zosterophyllum fertile* (Fig. 1F).

I additionally see a marked difference in the amount of resolution of the “morphology” and “anatomy” trees. In the anatomy-only tree (Fig. 1E), much of the resolution between groups is lost, a situation not present in the morphology-only tree. This is somewhat to be expected – the anatomy seen in these plants is highly homoplastic

and on its own will not produce results that reflect the resolution of those seen from more comprehensive datasets (Fig. 1C, D); the resolution in the anatomy-only consensus tree is probably driven primarily by the inclusion of sporangium characters in the anatomy dataset. On the other hand, while the morphology-only tree has the highest resolution of any of the trees in this study (Fig. 1F), it recovers a topology that is not entirely consistent with the majority of the other trees I approximated. For one, the species of *Zosterophyllum* are recovered as sister to one of each of the major clades, respectively, a topology seen only in one of the other trees (Fig. 1D). Additionally, the morphology-only analysis is the only one that recovers *Trichopherophyton*, which is most often placed as sister to *Ventarura*+*Sengelia*, as a member of the “large zosterophyll clade”.

A similar situation was reported by Niklas and Crepet (2020). In comparing results obtained when using subsets of characters with those obtained under full-character sampling, those authors showed that utilizing vegetative morphological characters resulted in trees with the highest resolution, consistent with my findings (Table 2; Fig. 1F). Niklas and Crepet (2020) also concluded that reproductive and anatomical features of the early sporophytes were less useful than morphological features at resolving the phylogeny of ancient tracheophytes.

The relative rarity of permineralization fossils, which preserve anatomical features, compared to compression fossils, which preserve morphological features, has resulted in a slower accumulation of anatomical data on zosterophylls (and other plants). Additionally, it is uncommon for the same species to be found preserved both anatomically and morphologically. As a result, the small number of taxa which can be

scored for characters that encompass both anatomy and morphology further discourages the use of anatomical data from those species known only as permineralizations.

Zosterophylls are no exception to these gaps in the data, and many species are known either only from compressions or only from permineralizations. Alongside the relative scarcity of permineralized taxa, the homoplastic nature of anatomical features in zosterophylls has placed the focus of phylogenetic study on more robust datasets extracted from compression fossils, and thus, morphology

Independent of these considerations, anatomical characters stand to improve analyses by 1) creating more comprehensive and detailed representations of the plants in a phylogenetic matrix; and 2) increasing the number of characters that can be employed to investigate relationships. Therefore, even though the morphology-only consensus tree (Fig. 1F) has very similar resolution to one of the all-character trees (Fig. 1D), while the anatomy-only tree (Fig. 1E) shows significantly lower resolution than either of the two, biological considerations support usage of the most inclusive character list available, i.e., all characters that can be defined and scored. Conversely, the slight discrepancies between the morphology-only tree and the all-character tree indicate that even when well-resolved, trees produced by analyses that under-sample the character space may support inaccurate relationships.

Phenetic approaches do not accurately reflect phylogenetic relationships among
zosterophylls

In extant plants, phylogenetic methods occupy a central place in systematics. By contrast, in paleobotany, phylogenetic methods have been significantly underutilized as means of exploring the taxonomic affinities of fossils. This situation was discussed recently by Durieux et al (2021), who point out the prevalence of comparative taxonomy in many areas of paleobotany, provide some reasons for this situation, as well as justifications for the use of both approaches. Using measures of similarity to group taxa, phenetic methods can be regarded as quantitative approaches to comparative taxonomy and, thus less prone to the “specialist bias” that could plague the traditional evolutionary systematics approaches (*sensu* Mishler 2009). However, because they distill differences or similarities between taxa based on multiple characters, into pairwise distances, phenetic methods hide diagnostic characters, which are one of the main currencies in systematics underlying the definition of taxonomic groups. For this and other reasons (e.g., they depict statistical patterns of similarity and not patterns of relationship due to inherited changes in distinct characters) phenetic methods have been largely abandoned, in their pure form, in systematics, or have morphed into more nuanced approaches of limited utility (e.g., morphospace analyses). Nevertheless, the congruence of results between phenetic and phylogenetic approaches has rarely been tested for a given dataset and no such test was performed recently. For all these reasons, I decided to compare the results of these two types of approaches – phylogenetics and phenetics – in the

zosterophylls, a group proven to be phylogenetically recalcitrant by previous analyses (Gensel 1992; Kenrick and Crane 1997).

UPGMA clustering is very sensitive to taxon sampling (compare Fig. 2A and 2B), and neither the clustering analysis nor the ordination reflect the results seen in the phylogenetic studies. One possible exception is the tight grouping in the ordination plot of some of the taxa (*Crenaticaulis*, *Serrulacaulis*, *Sawdonia ornata*, *Sawdonia deblondii*, *Thrinakophyton*, and *Gosslingia*; Fig. 2C) that are part of the “large zosterophyll clade”. Furthermore, there was no marked consistency between the results of clustering and ordination analyses.

These results confirm the lack of congruence between phenetic and phylogenetic methods, indicating that only the latter should be used in reconstructing evolutionary history. It is interesting, nevertheless, that despite not accounting for homology, both clustering and ordination analyses are congruent with the results of phylogenetic analyses in providing some support for zosterophyll affinities of *Renalia*: the latter is nested among zosterophylls at high levels of similarity in the UPGMA dendrograms, independent of taxon sampling, and plots closest to members of the large zosterophylls clade (as opposed to away from all the zosterophylls) in the NMDS ordination.

CONCLUSIONS

I explored the relationships of zosterophylls using a phylogenetic matrix that consists of 21 species selected primarily for preserved anatomy, scored for 40 characters that include the most extensive sampling of anatomical character space for the group, to date. To characterize the strength of phylogenetic signals in the dataset, I performed alternative rooting, taxon inclusion-exclusion, and character subsampling experiments, under parsimony constraints. The analyses recover relatively low resolution but find consistent support for two clades. One of these clades consistently includes *Ventarura* and the lycopsid *Sengelia*, typically accompanied by *Trichopherophyton* and *Discalis*. The consistent association of *Sengelia* with these zosterophylls suggests that the zosterophyll ancestor of lycopsids had bilaterally symmetrical, nonterminate fertile axes as suggested by Niklas and Banks (1990). The other main clade includes *Gosslingia*, *Crenaticaulis*, *Sawdonia*, *Deheubarthia*, *Serrulacaulis*, *Thrinophyton*, *Konioria*, and *Margophyton*, with majority rule consensus trees suggesting close relationships between *Margophyton* and *Konioria*, and between *Sawdonia (ornata)* and *Crenaticaulis*. The two species of *Zosterophyllum* included in analyses are not recovered as a clade under any rooting, taxon, or character sampling regime, which suggests that genus (the most speciose among zosterophylls) requires taxonomic re-evaluation. Subsampling of the matrix for characters that can be scored only in compression fossils or only in permineralized fossils yields differences in patterns of relationships, which indicate that anatomical and morphological characters carry slightly divergent phylogenetic signals,

and confirms that incomplete sampling of character space may recover spurious patterns of relationships. Phenetic analyses (ordination and clustering) performed on the same dataset produced patterns of similarity largely incongruent with the patterns of phylogenetic relationships, suggesting that numerical taxonomy approaches fail to discern patterns generated by evolutionary history.

In addressing zosterophyll relationships, future phylogenetic studies could explore the placement of additional zosterophyll species, less completely characterized and not included in this study, by adding them to this matrix one-by-one. This would minimize their wildcard effects (e.g., Nixon 1996) while also showing levels of support for several alternative placements (if applicable). Aside from clarifying the relationships of additional zosterophylls, such analyses could contribute to reevaluations of the phyletic status of speciose genera, especially *Zosterophyllum*, which this study has flagged as probably non-monophyletic. Broadening of outgroup sampling by inclusion of rhyniopsid and euphyllophyte taxa may improve resolution, by further polarizing characters and would allow for additional tree rooting experiments. These additions, along with inclusion of other lycopsids may bring better resolution to the position of zosterophylls among tracheophytes. Finally, discoveries of additional fossils, ideally with preserved anatomy, and definition of additional characters that may be revealed by these discoveries of by the development of new investigative methods, will further illuminate the relationships and evolutionary history of zosterophylls.

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APPENDICES

Appendix A. Taxa included in phylogenetic analyses (in alphabetical order) and literature used to score phylogenetic characters for each taxon.

Crenaticaulis verruculosus Banks & Davis 1969

Age: mid- to late Emsian

Rock unit: Battery Point Formation, Québec (Canada)

Preservation: Permineralizations, compressions

Source: Banks and Davis 1969

Deheubarthia splendens Edwards et al. 1989

Age: upper Lochkovian

Rock unit: Lower Old Red Sandstone, South Wales (UK)

Preservation: Permineralizations, compressions

Source: Edwards et al. 1989

Discalis longistipa Hao 1989

Age: Pragian

Rock unit: Posongchong Formation, Yunnan (China)

Preservation: Compressions

Source: Hao 1989

Euthursophyton hamperbachense Mustafa 1978

Age: late Eifelian

Rock unit: Brandenburg-Schichten, Germany

Preservation: Compressions, permineralizations

Source: Mustafa 1978

Gosslingia breconensis Heard 1927

Age: Siegenian-Emsian

Rock unit: Lower Old Red Sandstone, South Wales (UK)

Preservation: Permineralizations, compressions

Source: Kenrick and Edwards 1988a, Edwards 1970

Huia gracilis Wang and Hao 2001

Age: Pragian - early Emsian

Rock unit: Xujiachong Formation, Yunnan (China)

Preservation: Compressions

Source: Wang and Hao 2001

Konioria andrychoviensis Zdebska 1982

Age: Emsian

Rock unit: borehole samples from unnamed unit, Poland

Preservation: Permineralizations, compressions

Source: Zdebska 1982

Margophyton goldschmidtii Zakharova 1981

Age: Pragian - Emsian

Rock unit: Pridorozhnaya strata and others, Russia

Preservation: Permineralizations, compressions

Source: Zakharova 1981

Nothia aphylla Kerp et al. 2001

Age: Pragian

Rock unit: Rhynie Chert, Scotland

Preservation: Permineralizations

Source: El-Saadawy and Lacey 1979, Kerp et al. 2001

Psilophyton dawsonii Banks et al. 1975

Age: Mid- to late Emsian

Rock unit: Battery Point Formation, Québec (Canada)

Preservation: Permineralizations, compressions

Source: Banks et al. 1975

Renalia heuberi Gensel 1976

Age: Mid- to late Emsian

Rock unit: Battery Point Formation, Québec (Canada)

Preservation: Compressions

Source: Gensel 1976

Sawdonia (Ensivalia) deblondii Gensel and Berry 2016

Age: Pragian

Rock unit: Formation d'Acoz, Belgium

Preservation: Compressions, permineralizations

Source: Gerrienne 1996, Gensel and Berry 2016

Sawdonia ornata Hueber 1971

Age: Pragian - Emsian

Rock unit: Lower Old Red Sandstone, South Wales (UK); Battery Point Formation, Québec (Canada)

Preservation: Permineralizations, compressions

Source: Rayner 1983a, Gensel and Berry 2016

Sengelia radicans Matsunaga and Tomescu 2017

Age: late Lochkovian - Pragian
 Rock unit: Beartooth Butte Formation, Wyoming (USA)
 Preservation: Compressions
 Source: Matsunaga and Tomescu 2017

Serrulacaulis furcatus Hueber and Banks 1979
 Age: late Givetian - early Frasnian (late Givetian age based on Berry and Gensel 2019 for the Campo Chico Formation)
 Rock unit: Onenota Shale (Genesee Group) equivalent, New York (USA); Campo Chico Formation, Venezuela
 Preservation: Compressions
 Source: Hueber and Banks 1979, Berry and Edwards 1994

Stolbergia spiralis Fairon 1967
 Age: Eifelian - Givetian
 Rock unit: Vicht or Pepinster Formation, Belgium
 Preservation: Permineralizations
 Source: Fairon 1967

Thrinophyton formosum Kenrick and Edwards 1988b
 Age: Pragian - Emsian
 Rock unit: Lower Old Red Sandstone, South Wales (UK)
 Preservation: Permineralizations, compressions
 Source: Kenrick and Edwards 1988b

Trichopherophyton teuchansii Lyon and Edwards 1991
 Age: Pragian
 Rock unit: Rhynie Chert, Scotland
 Preservation: Permineralizations
 Source: Lyon and Edwards 1991

Ventarura lyonii Powell et al. 2000
 Age: Pragian
 Rock unit: Rhynie Chert, Scotland
 Preservation: Permineralizations
 Source: Powell et al. 2000

Zosterophyllum fertile Leclercq 1942 [includes information from Edwards' (1969a)
Zosterophyllum cf. fertile]
 Age: Pragian - Emsian
 Rock unit: Lower Old Red Sandstone, South Wales (UK)
 Preservation: Permineralizations, compressions
 Source: Edwards 1969a

Zosterophyllum llanoveranum Croft and Lang 1942

Age: Pragian - Emsian

Rock unit: Lower Old Red Sandstone, South Wales (UK)

Preservation: Permineralizations, compressions

Source: Edwards 1969b

Appendix B. Phylogenetic characters. A – characters used in the “anatomy-only” analysis; M – characters used in the “morphology-only” analysis.

Vegetative anatomy

1. Stele type: 0 = haplostele; 1 = actinostele [A]
2. Pattern of primary xylem maturation: 0: exarch; 1: centrarch [A]
3. Distribution of protoxylem: 0: diffuse; 1: discrete bundles [A]
4. Scleriform patterning of secondary wall thickenings (metaxylem): 0 = absent; 1 = present [A]
5. Degradation-resistant layer in secondary wall thickenings: 0 = lining the thickenings; 1 = pervasive degradation resistance [A]
6. Inter-scleriform thickening tracheid wall patterning: 0 = *Gosslingia*-type tracheids; 1 = lycopsid-type tracheids (Williamson’s striations); 2 = *Psilophyton*-type tracheids [A]
7. Stele shape: 0 = terete; 1 = elliptical; 2 = strap-shaped; 3 = lobed [A]
8. Cortex histology: 0 = homogeneous; 1 = stratified [A]
9. Sclerified outer cortex: 0 = absent; 1 = present [A]
10. Sclerified outer cortex thickness: 0 = ‘thin’ proportional to axis thickness; 1 = ‘thick’ proportional to axis thickness. This character is inapplicable for taxa in which C9 = 0 [A]
11. Histologically distinct mid-cortical layer: 0 = absent; 1 = present [A]
12. Mid-cortical layer thickness: 0 = single cell layer; 1 = multiple cell layers. This character is inapplicable for taxa in which C11 = 0 [A]
13. Epidermal cell size: 0 = cells of regular size (approximately the same size as adjacent cortical cells); 1 = large cells (larger than adjacent cortical cells); 2 = small cells (smaller than adjacent cortical cells) [A]
14. Cellular differentiation in the epidermis (other than stomata or trichomes): 0 = absent; 1 = present. This characters refers to cases in which some epidermal cells differ in size (or shape) from the majority of epidermal cells [A] [M]

15. Trichomes (hair-like extensions): 0 = absent; 1 = present [A] [M]

Vegetative morphology

16. Stout multicellular protrusions (more substantial than trichomes): 0 = absent; 1 = conical (spine-like); 2 = prismatic [A] [M]

17. Morphology of protrusions: 0 = monomorphic; 1 = dimorphic. This character is inapplicable for taxa in which C16 = 0 [M]

18. Tip of protrusions: 0 = sharp-tipped (spines); 1 = rounded tips; 2 = flat-tipped. This character is inapplicable for taxa in which C16 = 0 [M]

19. Wrinkled axis surface: 0 = absent; 1 = present [A] [M]

20. Leaves (i.e., vascularized appendages with regular taxis and adaxial-abaxial polarity): 0 = absent; 1 = present [A] [M]

21. Branching pattern of proximal plant axes: 0 = isotomous; 1 = pseudomonopodial [M]

22. Branching pattern of distal plant axes: 0 = isotomous; 1 = pseudomonopodial [M]

23. Branch laterals run parallel to main axis: 0 = absent; 1 = present [M]

24. K-branching (also known as H-branching): 0 = absent; 1 = present [M]

25. Subaxillary tubercles: 0 = absent; 1 = present [M]

26. Circinate tips: 0 = absent; 1 = present [A] [M]

Sporangial arrangement and morphology

27. Sporangial distribution: 0 = single; 1 = grouped (in discrete fertile zones); 2 = paired [A] [M]

28. Position of lateral sporangia: 0 = on more than one side of axis; 1 = only on one side of axis [A] [M]

29. Grouped sporangia: 0 = potentially intercalary fertile zone; 1 = terminal fertile zone. This character is inapplicable for taxa in which C27 = 0 or 2 [M]

30. Terminal fertile zone: 0 = lax terminal fertile zone (sporangia spaced out); 1 = compact terminal fertile zone (strobilus). This character is inapplicable for taxa in which C27 = 0 or 2 and C29 = 0 [M]
31. Sporangiotaxis: 0 = alternate; 1 = subopposite; 2 = opposite. This character is inapplicable for taxa in which C28 = 1 [M]
32. Ranks of sporangium files: 0 = one vertical rank; 1 = two vertical ranks; 2 = no ranks (may be helical) [A] [M]
33. Sporangium orientation: 0 = laterally oriented (dehiscence pointing away from the axis); 1 = apically oriented (oriented parallel with the axis and dehiscence pointing toward its tip) ; 2 = adaxially recurved (pointing toward the axis) [A] [M]
34. Sporangial stalk: 0 = absent (sessile sporangium); 1 = short (stalk $L:W \leq 1$); 2 = long (stalk $L:W > 1$) [A] [M]
35. Sporangium shape – proximo-distal: 0 = long ($L:W > 1$); 1 = short ($L:W \leq 1$) [A] [M]
36. Sporangium shape – dorsi-ventral: 0 = thick (dorsi-ventral flattening absent); 1 = flat (sporangia dorsi-ventrally flattened) [A] [M]
37. Relative size of porangium valves: 0 = isovalvate; 1 = abaxial valve larger/deeper; 2 = adaxial valve larger/deeper [A] [M]
38. Sporangium dehiscence: 0 = distal line; 1 = lateral line ('*Huia*-type') [A] [M]
39. Dehiscence rim thickening: 0: absent; 1: present [A] [M]
40. Protrusions on sporangia: 0 = absent; 1 = single-celled; 2 = multicellular [A] [M]

Appendix C. Phylogenetic matrix.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Psilophyton dawsonii</i>	0	1	-	1	0	2	0	1	1	1	0	-	2	0	0	0	-	-	0	0
<i>Renalia heuberi</i>	0	?	?	1	?	?	0/1	?	0	-	?	?	?	?	0	0	-	-	0	0
<i>Sengelia radicans</i>	1	0	1	1	?	?	3	?	0	-	?	?	?	0	0	0	-	-	0	1
<i>Crenaticaulis verruculosus</i>	0	0	1	1	?	?	1	1	1	1	0	-	0	1	0	1	0	1	0	0
<i>Deheubarthia splendens</i>	0	0	?	1	0	0	1/2	1	1	0	0	-	0	1	0	1	0	0	0	0
<i>Discalis longistipa</i>	?	?	?	1	?	0	?	?	?	?	?	?	?	0	0	1	0	1/2	0	0
<i>Euthursophyton hamperbachense</i>	0	0	0	1	1	?	0/1	1	1	1	0	-	?	?	0	1	0	0	0	0
<i>Gosslingia breconensis</i>	0	0	?	1	0	0	1	1	1	0	0	-	0	1	0	0	-	-	0	0
<i>Huia gracilis</i>	0	?	?	1	0	0	1	?	?	?	?	?	?	1	0	0	-	-	0	0
<i>Konioria andrychoviensis</i>	0	0	0	1	?	?	0/1	1	1	0	0	-	?	?	0	1	1	0	0	0
<i>Margophyton goldschmidtii</i>	0	0	?	1	0	?	1	?	?	?	?	?	?	?	0	1	0	0	0	0
<i>Nothia aphylla</i>	0	?	?	0	?	-	0	0	0	-	0	-	0/1	1	0	0	-	-	1	0
<i>Sawdonia deblondii</i>	0	0	?	1	0	0	1	?	?	?	?	?	?	?	0	1	0	0	0	0
<i>Sawdonia ornata</i>	0	0	?	1	?	?	2	1	1	?	0	-	0	1	1	1	0	1	0	0
<i>Serrulacaulis furcatus</i>	?	?	?	1	0	0	?	?	?	?	?	?	?	1	0	2	0	0	0	0
<i>Stolbergia spiralis</i>	0	0	0	1	0	0	0	1	?	?	0	-	0	?	0	0	-	-	0	0
<i>Thrinkophyton formosum</i>	0	0	?	1	1	0	1	?	?	?	?	?	?	?	1	0	-	-	0	0
<i>Trichopherophyton teuchansii</i>	0	0	0	1	?	0	0	1	0	-	0	-	2	?	1	0	-	-	0	0
<i>Ventarura lyonii</i>	0	0	?	1	0	0	0	1	0	-	1	1	?	?	0	0	-	-	0	0
<i>Zosterophyllum fertile</i>	0	0	?	1	?	0	0	1	1	0	?	?	?	?	0	0	-	-	0	0
<i>Zosterophyllum llanoveranum</i>	0	0	?	1	?	?	0	1	1	1	0	-	?	?	0	0	-	-	0	0

Character	21	22	23	24	25	26	27	29	29	30	31	32	33	34	35	36	37	39	39	40
<i>Psilophyton dawsonii</i>	0/1	0/1	0	0	0	0	2	-	-	-	-	-	1	2	0	0	-	1	0	0
<i>Renalia heuberi</i>	1	0	0	0	0	0	2	-	-	-	-	-	1	2	1	1	0	0	1	0
<i>Sengelia radicans</i>	-	-	-	1	0	0	1	0	0	-	0	2	1	0	1	?	0	0	?	0
<i>Crenatacaulis verruculosus</i>	0/1	?	0	0	1	1	1	0	0	-	1/2	1	1	1	1	0	1	0	?	0
<i>Deheubarthia splendens</i>	1	0	0	0	1	1	1	0	0	-	1/2	1	1	1	1	?	0	0	0	0
<i>Discalis longistipa</i>	?	?	?	1	0	1	1	0	1	0	0	2	1	2	1	1	0	0	1	2
<i>Euthursophyton hamperbachense</i>	1	0	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Gosslingia breconensis</i>	1	0/1	0	0	1	1	1	0/1	0	-	-	0	0	1	1	1	0	0	1	0
<i>Huia gracilis</i>	?	0	1	1	1	0	1	0	1	0	0	2	2	2	0	0	0	1	0	0
<i>Konioria andrychoviensis</i>	?	0/1	0	0	0	1	0	1	-	-	-	-	?	1	1	1	0	0	0	1
<i>Margophyton goldschmidtii</i>	1	0	1	0	1	0	0	1	-	-	-	-	0	1	?	?	0	?	?	0
<i>Nothia aphylla</i>	1	0	0	0	0	0	1	0	1	0	0	-	2	2	1	0	0	0	0	0
<i>Sawdonia deblondii</i>	1	?	0	1	1	1	1	1	0	-	-	0	1	2	1	1	1	0	0	2
<i>Sawdonia ornata</i>	1	?	1	1	0	1	1	0	0	-	2	1	2	1	1	0	1	0	0	2
<i>Serrulacaulis furcatus</i>	?	1	0	?	0	1	1	1	0	-	0	1	0	1	1	1	0	0	1	0
<i>Stolbergia spiralis</i>	?	?	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Thrinakophyton formosum</i>	1	0	0	0	1	1	1	0	0	-	2	1	1	1	1	1	0	0	1	0
<i>Trichopherophyton teuchansii</i>	?	?	?	?	0	1	?	?	?	?	?	?	1	0	1	1	1	0	0	1

Character	21	22	23	24	25	26	27	29	29	30	31	32	33	34	35	36	37	39	39	40
<i>Ventarura lyonii</i>	0	0	?	?	0	0	1	?	1	1	?	?	0	0	1	1	0	0	1	0
<i>Zosterophyllum fertile</i>	0	0	0	0	0	1	1	0	1	1	0	1/2	1	2	0	1	?	0	1	0
<i>Zosterophyllum llanoveranum</i>	?	?	?	?	?	?	1	0/1	1	1	-	0/1	1	2	1	1	0	0	1	0

Appendix D. Character scoring comments.

Crenaticaulis verruculosus – Banks and Davis 1969

C3: In their description, Banks & Davis (1969) suspect that the protoxylem forms multiple discrete strands at the periphery of the primary xylem, although they recognize that the exact organization of the protoxylem cannot be ascertained unequivocally.

C3, 4: p. 444

C6: possibly similar to Williamson's striations (p. 444)

C9, 10: p. 442, fig 26 and p. 444

C13: p. 443

C14, 15: p. 440, fig 13; p. 443

C21, 22: p. 444 only proximal portions available, scoring is polymorphic

C25, 28-30, 31, 32: p. 443

C31-32: p. 440, fig 6

C35, 36: p. 443

C37: p. 444

Deheubarthia splendens – Edwards et al. 1989

C3: p. 315

C5: p. 306, fig 35

C4, 6: p. 316

C9, 10: p. 305-306 (hypodermis), fig 30-32 (2 cells thick)

C13: p. 306, fig 30-32; p. 301

C14, 15, 17: p. 298 fig 2, p. 302 fig 12, p. 304 fig 27; diagnosis 299

C21, 22: p. 299; p. 298, fig. 1

C26, 27: p. 298

C29: Table, p. 297

C30: Table, p. 296

C31: p. 307 (for 'present'), short assumed from picture (p. 298), reconstruction (p. 300)

C32, 33: p. 307 (also figs 1, 3, 7, 28)

C34: Table, p. 297

C35, 36: p. 304, fig 28

Discalis longistipa – Hao 1989

C6: p. 165 Plate IV, Fig. 11 and 12

C15, 16: p. 158

C17: p. 160

C21-24: p. 159, 160

C27, 28, 29: p. 166

C30: p. 161 plate 1; p. 166 fig 6

C31, 34: p. 159

C32, 33: p. 161 fig 4

C36, 37: p. 159

Gosslingia breconensis – Heard 1927; Croft and Lang 1942; Kenrick and Edwards 1988a; Edwards 1970

C1, 2: p. 98, 99 (Kenrick Edwards 1988a)

C4, 5: p. 100 (Kenrick Edwards 1988a)

C9: ‘peripheral tissues’ p.103; p. 99 fig 1 (Kenrick Edwards 1988a)

C13: p. 233 fig 26 (Edwards 1970)

C14, 15: p. 230 (Edwards 1970); Heard (1927) describes protuberances bearing trichomes, but Edwards (1970) does not find any trichomes associated with the protuberances. Variable size and shape noted, irregular surface discussed as being present in number of zosterophylls but good specific detail is lacking.

C28: sporangia seen in both 2 ranks and single ranked p.229 (Edwards 1970)

C30, 31: p. 230 fig 21, p. 231 fig 54 (Edwards 1970)

C27-40: p.229-230 (Edwards 1970)

C38: p. 235, fig. 48 notes significant darkening of distal margin (Edwards 1970).

C41: thin cuticle on sporangia shows epidermal ‘bumps’. Heard (1927) attributes as trichome bases, Edwards (1970) finds no trichomes. Scored “0” (absent) because no conspicuous (i.e., large protrusions) are present on the sporangia.

Huia gracilis – Wang and Hao 2001

C1: p. 166, fig 1; p. 161

C2: although authors claim centrarch maturation pattern, figure (p. 166 fig 1) is unconvincing. Left unscored.

C4: p. 166, plate 4

C5: p. 166, fig 5

C6: p. 158

C7: p. 161

C9-12: p. 166, fig 1

C14-19: p. 159

C21, 22: p. 159

C23: p. 158

C24, 25: p. 159

C26, 28: p. 158

C30: p. 160 fig 2, 5; p. 161

C31: p. 158

C32, 33: p. 160, plate 1

C34, 35: p. 164 fig 6

C37: p. 160, plate 1

Konioria andrychoviensis – Zdebska 1982

C3: p. 253, fig 3

C4: p. 253, fig 7. Zdebska (1982) mentions and illustrates axis segments that yielded tracheids with alternate bordered pits; I did not score them as representing *Konioria*, as

no other zosterophyll is known to possess bordered pits, so those specimens represent most likely a different taxon.

C10: p. 253, fig 3

C15, 17: p. 251, fig 1-3

C21, 22: p. 249, fig 1, 4; p. 252, text fig. 1; diagnosis p. 256

C22: p. 249, fig 4

C31-34, 37: p. 254

***Margophyton goldschmidtii* – Zakharova 1981**

C15-17: p. 115

C21, 22: appears pseudomonopodial throughout in reconstruction, diagnosis says ‘monopodially and dichotomously’; seems to have lateral appendages with isotomous branching (Plate XI, fig. 3 and 7)

C24: p. 115

C30: plate XI fig. 1

C31: reconstruction, plate 11

C34: plate XI fig. 1

***Nothia aphylla* – El-Saadawy and Lacey 1979; Kerp et al. 2001**

C1-3: Kerp et al. 2001, Figure 4.5 A-H; El-Saadawy and Lacey 1979, p. 132

C4-6: El-Saadawy and Lacey 1979, p. 132

C9: El-Saadawy and Lacey 1979, p. 132

C13: El-Saadawy and Lacey 1979, plate I, fig 3

C14: El-Saadawy and Lacey 1979, plate I, fig. 1

C21, 22: Kerp et al. 2001 fig 4.3, 4.4

C25: El-Saadawy and Lacey 1979, p. 123

C26, 29: El-Saadawy and Lacey 1979, fig 2; p. 128/9

C30: El-Saadawy and Lacey 1979, fig 2

C31: El-Saadawy and Lacey 1979, fig 2

C32, 33: El-Saadawy and Lacey 1979, fig 2; Plate 4

C34: El-Saadawy and Lacey 1979, Plate 4 fig. 1, 2, 11; fig 4

C35: El-Saadawy and Lacey 1979, Plate 4 fig. 1, 2, 11

C36: El-Saadawy and Lacey 1979, Plate 4 fig. 1-3

***Psilophyton dawsonii* – Banks et al. 1975**

C5: plate 19, figs 27 and 28

C13: p. 85

C14: p. 105

C21, 22: p. 87, 89

***Sawdonia deblondii* – Gerrienne 1996**

C21, 22: isotomous and anisotomous (polymorphic); unclear if any differentiation present between proximal and distal axis segments.

Sawdonia ornata – Rayner 1983a, Gensel et al. 1975

C4, 6: Rayner 1983a, p. 85, fig. 4

C9, 10: Rayner 1983a, p. 85

C13: unknown anatomically but because they are monomorphic, assume ‘average’

C14: Rayner 1983a, fig 3 - trichomes scored present based on the presence of “rosettes” of cells in the epidermis, arranged around a central cell with different type of cuticle. In most plants such cell rosettes in the epidermis are associated with trichome bases. Some cells isodiametric, some elongated.

C21, 22: Rayner 1983a, p. 79-81

C16: Rayner 1983a, fig 1d

C32-37: Rayner 1983a, p. 90, fig 7

Serrulacaulis furcatus – Berry and Edwards 1994, Hueber and Banks 1979

C4-6: Berry and Edwards 1994, Plate 2 p.148

C14: Berry and Edwards 1994, p.149

C15-17: Berry and Edwards 1994, Plate I, fig 1

C21, 22: p.145 Berry & Edwards 1994

C29: Hueber and Banks 1979 p.175

C30: Hueber and Banks 1979 plate III fig 6, text fig 1

C34: Hueber and Banks 1979 plate 3 fig 6, p. 169

C32, 33: Hueber and Banks 1979 plate III fig 6, text fig 1

C34-36: Hueber and Banks 1979 p.175

Stolbergia spiralis – Fairon 1967

C12: histology of mid-cortical layer not described and difficult to assess due to preservation.

C21, 22: based on a single specimen, which may have had pseudomonopodial branching, if the appendage based don’t represent sporangial attachment points

Thrinophyton formosum – Kenrick and Edwards 1988b

C14: p.100

C32, 33: figs 1-5 p.101

Trichopherophyton teuchansii – Lyon and Edwards 1991

C4, 6: p.326 fig I

C9, 13: p.326 fig F

C21, 22: p.101, fig 1

C26, 28: Powell et al 2000 p.341

C30-34: p.325

C35: p.326 fig B, G

C36: p.326 fig B, G

C37: p.326 fig B

Venturura lyonii – Powell et al 2000

C1, 2: p.335 fig A

C6: p.339

C12: p.337

C14-17: p.332

C21, 22: p.332 - only short fragments available, branching is +/- equal isotomous and infrequent

C26, 28: p.339 – only isolated sporangia found, but author believes most likely in strobili

C30: p.339

C31, 33, 35, 37: p.339

C29, 32, 36: p.341

Zosterophyllum fertile – Leclercq 1942; Edwards 1969a

C4: Edwards 1969a p.926

C29: Edwards 1969a p.294

C9, 10: Edwards 1969a p.925

C21, 22: Edwards 1969a p.924

C23: K-branching known in other species of *Zosterophyllum*, not observed in *Z.fertile*

C29: Edwards 1969a p.924

C31-34: Edwards 1969a p.928 fig 1a, b, c

C36: Edwards 1969a p.926

Zosterophyllum llanoveranum – Croft and Lang 1942; Edwards 1969b

C2: Edwards 1969b p.202

C3: Edwards 1969b p.202

C4: Edwards 1969b p. 205

C9, 10: Edwards 1969b fig 13-15

C13: Edwards 1969b p.201

C14-18: Edwards 1969b fig 4, 24

C21, 22: Edwards 1969b p.201

C26, 28-37: p.202 fig 4, 20-26

C37: Edwards 1969b p.204

Appendix E. Phylogenetic matrix - NEXUS file.

```
#NEXUS

BEGIN TAXA;
  TITLE Taxa;
  DIMENSIONS NTAX=21;
  TAXLABELS
    Psilophyton_dawsonii Renalia_heuberi Sengelia_radicans
  Crenatacaulis_verruculosus Deheubarthia_splendens Discalis_longistipa
  Ensivalia_deblondii Euthursophyton_hamperbachense Gosslingia_breconensis
  Huia_gracilis Konioria_andrychoviensis Margophyton_goldschmidtii Nothia_aphylla
  Sawdonia_ornata Serrulacaulis_furcatus Stolbergia_spiralis
  Thrinophyton_formosum Trichopherophyton_teuchansii Ventarura_lyonii
  Zosterophyllum_fertile Zosterophyllum_llanoveranum
  ;

END;

BEGIN CHARACTERS;
  TITLE Character_Matrix;
  DIMENSIONS NCHAR=40;
  FORMAT DATATYPE = STANDARD RESPECTCASE GAP = - MISSING = ? SYMBOLS = " 0
1 2 3";
  CHARSTATELABELS
    1 Stele_type,
    2 Pattern_of_primary_xylem_maturation,
    3 Distribution_of_protoxylem,
    4 Scalariform_pattern_of_secondary_thickenings,
    5 'Degradation-resistant layer in secondary wall thickenings',
    6 'Inter-scalariform thickening tracheid wall patterning',
    7 Stele_shape,
    8 Cortex_histology,
    9 Sclerified_outer_cortex,
    10 Sclerified_outer_cortex_thickness,
    11 'Distinct mid-cortical layer',
    12 'Mid-cortical layer thickness',
    13 Epidermis_cell_size,
    14 'Cellular differentiation in the epidermis (other than stomata
or trichomes)',
    15 Trichomes,
    16 Multicellular_protrusions,
    17 Morphology_of_multicellular_protrusions,
    18 Tip_of_multicellular_protrusions,
    19 Wrinkled_axis_surface,
    20 Leaves,
    21 Proximal_branching_pattern,
    22 Distal_branching_pattern,
    23 Branch_laterals_run_parallel_to_main_axis,
    24 'K-branching',
    25 Subaxillary_tubercles,
    26 Circinate_tips,
    27 Sporangial_distribution,
    28 Position_of_lateral_sporangia,
    29 Grouped_sporangia,
    30 Terminal_fertile_zone,
    31 Sporangiotaxis,
```



```

32 Ranks_of_sporangium_files,
33 Sporangium_orientation,
34 Sporangial_stalk,
35 'Proximo-distal sporangium shape',
36 'Dorsi-ventral sporangium shape',
37 Sporangium_valves,
38 Sporangium_dehiscence,
39 Dehiscence_rim_thickening,
40 Protrusions_on_sporangia ;

MATRIX
  Psilophyton_dawsonii      01-10201110-2000--00{0 1}{0 1}00002-----
1200-100
  Renalia_heuberi          0??1??{0 1}?0-????00--001000002-----
12110010
  Sengelia_radicans        1011??3?0-???000--01---100100-02101?00?0
  Crenatacaulis_verruculosus 0011??11110-01010100{0 1}?0011100-{1
2}1111010?0
  Deheubarthia_splendens   00?100{1 2}1100-01010000100011100-{1
2}1111?0000
  Discalis_longistipa      ???1?0???????0010{1
2}00???10110100212110012
  Sawdonia_deblondii       00?1001???????0100001?0111110--012111002
  Euthursophyton_hamperbachense 00011?{0 1}1110-
??010000100001????????
  Gosslingia_breconensis   00?10011100-0100--001{0 1}00111{0 1}0--
001110010
  Huia_gracilis           0??1001???????100--00?0111010100222000100
  Konioria_andrychoviensis 0001??{0 1}1100-??011000?{0 1}000101----
?1110001
  Margophyton_goldschmidtii 00?10?1???????01000010101001---01??0??0
  Nothia_aphylla          0??0?-000-0-{0 1}100--1010000010100-
22100000
  Sawdonia_ornata         00?1??211?0-011101001?1101100-2121101002
  Serrulacaulis_furcatus   ???100???????1020000?10?01110-0101110010
  Stolbergia_spiralis      00010001??0-0?00--00?0000????????????
  Thrinkophyton_formosum   00?1101???????10--00100011100-2111110010
  Trichopherophyton_teuchansii 0001?0010-0-2?10--00????01???????10111001
  Ventarura_lyonii        00?100010-11??00--0000??001?11??00110010
  Zosterophyllum_fertile   00?1?00110????00--0000000110110{1
2}1201?010
  Zosterophyllum_llanoveranum 00?1??01110-??00--00?????1{0 1}11-{0
1}12110010

;

END;
BEGIN ASSUMPTIONS;
  TYPESET * UNTITLED = unord: 1- 40;

END;

BEGIN MESQUITECHARMODELS;
  ProbModelSet * UNTITLED = 'Mk1 (est.)': 1- 40;
END;

BEGIN NOTES;

  TEXT CHARACTER = 1 STATE = 0 TEXT = haplostele;
  TEXT CHARACTER = 1 STATE = 1 TEXT = actinosteale;

```

```

TEXT    CHARACTER = 1 STATE = 2 TEXT = plectostele;
TEXT    CHARACTER = 2 STATE = 0 TEXT = exarch;
TEXT    CHARACTER = 2 STATE = 1 TEXT = centrarch;
TEXT    CHARACTER = 2 STATE = 2 TEXT = other;
TEXT    CHARACTER = 3 STATE = 0 TEXT = diffuse;
TEXT    CHARACTER = 3 STATE = 1 TEXT = discrete;
TEXT    CHARACTER = 4 STATE = 0 TEXT = absent;
TEXT    CHARACTER = 4 STATE = 1 TEXT = present;
TEXT    CHARACTER = 5 STATE = 0 TEXT = lining_the_thickenings;
TEXT    CHARACTER = 5 STATE = 1 TEXT = pervasive_degredatin_resistance;
TEXT    CHARACTER = 6 STATE = 0 TEXT = '(G-type)';
TEXT    CHARACTER = 6 STATE = 1 TEXT = '(Lycopsid-type)';
TEXT    CHARACTER = 7 STATE = 0 TEXT = terete;
TEXT    CHARACTER = 7 STATE = 1 TEXT = elliptical;
TEXT    CHARACTER = 7 STATE = 2 TEXT = 'strap-shaped';
TEXT    CHARACTER = 7 STATE = 3 TEXT = lobed;
TEXT    CHARACTER = 8 STATE = 0 TEXT = homogenous;
TEXT    CHARACTER = 8 STATE = 1 TEXT = stratified;
TEXT    CHARACTER = 9 STATE = 0 TEXT = absent;
TEXT    CHARACTER = 9 STATE = 1 TEXT = present;
TEXT    CHARACTER = 10 STATE = 0 TEXT = thin_proportional_to_axis;
TEXT    CHARACTER = 10 STATE = 1 TEXT = thick_proportional_to_axis;
TEXT    CHARACTER = 11 STATE = 0 TEXT = absent;
TEXT    CHARACTER = 11 STATE = 1 TEXT = present;
TEXT    CHARACTER = 12 STATE = 0 TEXT = single_cell_layer;
TEXT    CHARACTER = 12 STATE = 1 TEXT = multiple_cell_layers;
TEXT    CHARACTER = 13 STATE = 0 TEXT = ''regular'' cells, i.e., about as
large as adjacent cortical cells (in transverse section)';
TEXT    CHARACTER = 13 STATE = 1 TEXT = 'large cells, i.e., significantly
larger than adjacent cortical cells (in transverse section)';
TEXT    CHARACTER = 13 STATE = 2 TEXT = 'small cells i.e. smaller than
adjacent cortical cells (in transverse section)';
TEXT    CHARACTER = 14 STATE = 0 TEXT = absent;
TEXT    CHARACTER = 14 STATE = 1 TEXT = present;
TEXT    CHARACTER = 15 STATE = 0 TEXT = absent;
TEXT    CHARACTER = 15 STATE = 1 TEXT = present;
TEXT    CHARACTER = 16 STATE = 0 TEXT = absent;
TEXT    CHARACTER = 16 STATE = 1 TEXT = conical;
TEXT    CHARACTER = 16 STATE = 2 TEXT = prismatic;
TEXT    CHARACTER = 17 STATE = 0 TEXT = monomorphic;
TEXT    CHARACTER = 17 STATE = 1 TEXT = dimorphic;
TEXT    CHARACTER = 18 STATE = 0 TEXT = 'sharp-tipped';
TEXT    CHARACTER = 18 STATE = 1 TEXT = 'round-tipped';
TEXT    CHARACTER = 18 STATE = 2 TEXT = 'flat-tipped';
TEXT    CHARACTER = 19 STATE = 0 TEXT = absent;
TEXT    CHARACTER = 19 STATE = 1 TEXT = present;
TEXT    CHARACTER = 20 STATE = 0 TEXT = absent;
TEXT    CHARACTER = 20 STATE = 1 TEXT = present;
TEXT    CHARACTER = 21 STATE = 0 TEXT = isotomous;
TEXT    CHARACTER = 21 STATE = 1 TEXT = pseudomonopodial;
TEXT    CHARACTER = 22 STATE = 0 TEXT = isotomous;
TEXT    CHARACTER = 22 STATE = 1 TEXT = pseudomonopodial;
TEXT    CHARACTER = 23 STATE = 0 TEXT = absent;
TEXT    CHARACTER = 23 STATE = 1 TEXT = present;
TEXT    CHARACTER = 24 STATE = 0 TEXT = absent;
TEXT    CHARACTER = 24 STATE = 1 TEXT = present;
TEXT    CHARACTER = 25 STATE = 0 TEXT = absent;
TEXT    CHARACTER = 25 STATE = 1 TEXT = present;
TEXT    CHARACTER = 26 STATE = 0 TEXT = absent;

```

```

TEXT    CHARACTER = 26 STATE = 1 TEXT = present;
TEXT    CHARACTER = 27 STATE = 0 TEXT = single;
TEXT    CHARACTER = 27 STATE = 1 TEXT = grouped;
TEXT    CHARACTER = 27 STATE = 2 TEXT = paired;
TEXT    CHARACTER = 28 STATE = 0 TEXT = on_all_sides_of_axis;
TEXT    CHARACTER = 28 STATE = 1 TEXT = only_on_one_side_of_axis;
TEXT    CHARACTER = 29 STATE = 0 TEXT =
potentially_intercalary_fertile_zone;
TEXT    CHARACTER = 29 STATE = 1 TEXT = terminal_fertile_zone;
TEXT    CHARACTER = 30 STATE = 0 TEXT = lax_terminal_fertile_zone;
TEXT    CHARACTER = 30 STATE = 1 TEXT = 'compact terminal fertile zone
(strobilus)';
TEXT    CHARACTER = 31 STATE = 0 TEXT = 'opposite/subopposite';
TEXT    CHARACTER = 31 STATE = 1 TEXT = alternate;
TEXT    CHARACTER = 32 STATE = 0 TEXT = one_vertical_rank;
TEXT    CHARACTER = 32 STATE = 1 TEXT = two_vertical_ranks;
TEXT    CHARACTER = 32 STATE = 2 TEXT = 'no vertical ranks (can be
helical)';
TEXT    CHARACTER = 33 STATE = 0 TEXT = 'laterally-oriented';
TEXT    CHARACTER = 33 STATE = 1 TEXT = 'apically-oriented';
TEXT    CHARACTER = 33 STATE = 2 TEXT = adaxially_curved;
TEXT    CHARACTER = 34 STATE = 0 TEXT = absent;
TEXT    CHARACTER = 34 STATE = 1 TEXT = 'short (L:W<= 1)';
TEXT    CHARACTER = 34 STATE = 2 TEXT = 'long (L:W > 1)';
TEXT    CHARACTER = 35 STATE = 0 TEXT = 'long (L:W > 1)';
TEXT    CHARACTER = 35 STATE = 1 TEXT = 'short (L:W <= 1)';
TEXT    CHARACTER = 36 STATE = 0 TEXT = ''fat'' (dorsi-ventral flattening
absent)';
TEXT    CHARACTER = 36 STATE = 1 TEXT = ''flat'' (dorsi-ventral
flattening present)';
TEXT    CHARACTER = 37 STATE = 0 TEXT = isovalvate;
TEXT    CHARACTER = 37 STATE = 1 TEXT = abaxial_valve_larger;
TEXT    CHARACTER = 37 STATE = 2 TEXT = adaxial_valve_larger;
TEXT    CHARACTER = 38 STATE = 0 TEXT = distal;
TEXT    CHARACTER = 38 STATE = 1 TEXT = 'lateral ('Huia-type')';
TEXT    CHARACTER = 39 STATE = 0 TEXT = absent;
TEXT    CHARACTER = 39 STATE = 1 TEXT = present;
TEXT    CHARACTER = 40 STATE = 0 TEXT = absent;
TEXT    CHARACTER = 40 STATE = 1 TEXT = 'single-celled';
TEXT    CHARACTER = 40 STATE = 2 TEXT = multicellular;

```

Appendix F. Characters used in the phenetic analyses.

1. **Distribution of protoxylem:** 0 = diffuse; 1 = discrete
2. **Scalariform patterning of secondary wall thickenings:** 0 = absent; 1 = present
3. **Degradation resistant layer in secondary wall thickenings:** 0 = lining; 1 = pervasive
4. ***Gosslingia*-type tracheids:** 0 = absent; 1 = present
5. **Stele terete:** 0 = absent; 1 = present
6. **Stele elliptical:** 0 = absent; 1 = present
7. **Stele strap-shaped:** 0 = absent; 1 = present
8. **Cortex:** 0 = homogenous; 1 = stratified
9. **Sclerified outer cortex thickness:** 0 = 'thin' proportional to axis; 1 = 'thick' proportional to axis
10. **Distinct mid-cortical layer:** 0 = absent; 1 = present
11. **Epidermal cells approximately the same as adjacent cortical cells:** 0 = absent; 1 = present
12. **Epidermal cells larger than adjacent cortical cells:** 0 = absent; 1 = present
13. **Epidermal cells smaller than adjacent cortical cells:** 0 = absent; 1 = present
14. **Cellular differentiation in 'normal' epidermal cells:** 0 = absent; 1 = present
15. **Trichomes:** 0 = absent; 1 = present
16. **Conical multicellular protrusions:** 0 = absent; 1 = present
17. **Prismatic multicellular protrusions:** 0 = absent; 1 = present
18. **Morphology of protrusions:** 0 = monomorphic; 1 = dimorphic
19. **Sharp multicellular protrusion tips:** 0 = absent; 1 = present
20. **Rounded multicellular protrusion tips:** 0 = absent; 1 = present
21. **Flat multicellular protrusion tips:** 0 = absent; 1 = present
22. **Wrinkled axis surface:** 0 = absent; 1 = present
23. **Isotomous branching of proximal plant parts:** 0 = absent; 1 = present
24. **Pseudomonopodial branching of proximal plant parts:** 0 = absent; 1 = present
25. **Isotomous branching of distal plant parts:** 0 = absent; 1 = present
26. **Pseudomonopodial branching of distal plant parts:** 0 = absent; 1 = present
27. **Branch laterals run parallel to main axis:** 0 = absent; 1 = present
28. **K-branching:** 0 = absent; 1 = present
29. **Subaxillary tubercles:** 0 = absent; 1 = present
30. **Circinate tips:** 0 = absent; 1 = present
31. **Sporangia borne singly:** 0 = absent; 1 = present
32. **Sporangia grouped:** 0 = absent; 1 = present
33. **Sporangia paired:** 0 = absent; 1 = present
34. **Sporangia on more than one side of axis:** 0 = absent; 1 = present
35. **Sporangia on one side of axis:** 0 = absent; 1 = present
36. **Grouped sporangia:** 0 = potentially intercalary fertile zone; 1 = terminal fertile zone
37. **Terminal fertile zone (TFZ):** 0 = 'lax' TFZ; 1 = compact TFZ (strobilus)

- 38. **Sporangiotaxis alternate:** 0 = absent; 1 = present
- 39. **Sporangiotaxis subopposite:** 0 = absent; 1 = present
- 40. **Sporangiotaxis opposite:** 0 = absent; 1 = present
- 41. **Sporangia in one vertical rank:** 0 = absent; 1 = present
- 42. **Sporangia in two vertical ranks:** 0 = absent; 1 = present
- 43. **Sporangia in not in vertical ranks (may be helical):** 0 = absent; 1 = present
- 44. **Sporangia laterally oriented:** 0 = absent; 1 = present
- 45. **Sporangia apically oriented:** 0 = absent; 1 = present
- 46. **Sporangia adaxially recurved:** 0 = absent; 1 = present
- 47. **Sporangial stalk:** 0 = absent; 1 = present
- 48. **Sporangial stalk length:** 0 = short; 1 = long
- 49. **Sporangium shape – proximo-distal:** 0 = long; 1 = short
- 50. **Sporangium shape – dorsi-ventral:** 0 = fat; 1 = flat
- 51. **Sporangia isovalvate:** 0 = absent; 1 = present
- 52. **Sporangia with larger abaxial valve:** 0 = absent; 1 = present
- 53. **Sporangium dehiscence:** 0 = distal line; 1 = lateral line
- 54. **Dehiscence rim thickening:** 0 = absent; 1 = present
- 55. **Protrusions on sporangia absent:** 0 = no; 1 = yes
- 56. **Protrusions on sporangia single-celled:** 0 = absent; 1 = present
- 57. **Protrusions on sporangia multicellular:** 0 = absent; 1 = present

Appendix G. Phenetic matrix for UPGMA analyses; for the NMDS analyses, “?” is converted to “0”.

Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
<i>Renalia hueberi</i>	?	1	?	?	1	1	0	?	0	?	?	?	?	?	?	0	0	0	?	?	?	?	0	0	1	1
<i>Crenaticaulis verruculosus</i>	1	1	?	?	0	1	0	1	1	1	?	1	0	0	1	0	1	0	0	0	1	0	0	1	1	?
<i>Deheubarthia splendens</i>	?	1	0	1	0	1	1	1	1	0	?	1	0	0	1	0	1	0	0	1	0	0	0	0	1	1
<i>Discalis longistipa</i>	?	1	?	1	?	?	?	?	?	?	?	?	?	?	0	0	1	0	0	0	1	1	0	?	?	?
<i>Sawdonia deblondii</i>	?	1	0	1	0	1	0	?	?	?	?	?	?	?	?	0	1	0	0	1	0	0	0	0	1	?
<i>Euthursophyton hamperbachense</i>	0	1	1	?	1	1	0	1	1	1	?	?	?	?	?	0	1	0	0	1	0	0	0	0	1	1
<i>Gosslingia breconensis</i>	?	1	0	1	0	1	0	1	1	0	?	1	0	0	1	0	0	0	?	?	?	?	0	0	1	1
<i>Huia gracilis</i>	?	1	0	1	0	1	0	?	?	?	?	?	?	?	1	0	0	0	?	?	?	?	0	?	?	1
<i>Konioria andrychovienensis</i>	0	1	?	?	1	1	0	1	1	0	?	?	?	?	?	0	1	0	1	1	0	0	0	?	?	1
<i>Margophyton goldschmidtii</i>	?	1	0	?	0	1	0	?	?	?	?	?	?	?	?	0	1	0	0	1	0	0	0	0	1	1
<i>Nothia aphylla</i>	?	0	?	?	1	0	0	0	0	?	?	1	1	0	1	0	0	0	?	?	?	?	1	0	1	1
<i>Sawdonia ornata</i>	?	1	?	?	0	0	1	1	1	?	?	1	0	0	1	1	1	0	0	0	1	0	0	0	1	?
<i>Serrulacaulis furcatus</i>	?	1	0	1	?	?	?	?	?	?	?	?	?	?	1	0	0	1	0	1	0	0	0	?	?	0
<i>Stolbergia spiralis</i>	0	1	0	1	1	0	0	1	?	?	?	1	0	0	?	0	0	0	?	?	?	?	0	?	?	?
<i>Thrinakophyton formosum</i>	?	1	1	1	0	1	0	?	?	?	?	?	?	?	?	1	0	0	?	?	?	?	0	0	1	1
<i>Trichophyton teuchansii</i>	0	1	?	1	1	0	0	1	0	?	?	0	0	1	?	1	0	0	?	?	?	?	0	?	?	?

Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
										0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6
<i>Ventarura lyonii</i>	?	1	0	1	1	0	0	1	0	?	1	?	?	?	?	0	0	0	?	?	?	?	0	1	0	1
<i>Zosterophyllum fertile</i>	?	1	?	1	1	0	0	1	1	0	?	?	?	?	?	0	0	0	?	?	?	?	0	1	0	1
<i>Zosterophyllum llanoveranum</i>	?	1	?	?	1	0	0	1	1	1	?	?	?	?	?	0	0	0	?	?	?	?	0	?	?	?

	2	2	2	3	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	5
Characters	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
<i>Renalia hueberi</i>	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	0	1	0	1	1	1	1
<i>Crenaticaulis verruculosus</i>	?	0	0	1	1	0	1	1	0	0	?	0	1	1	0	1	0	0	1	0	1	0	1	0
<i>Deheubarthia splendens</i>	0	0	0	1	1	0	1	1	0	0	?	0	1	1	0	1	0	0	1	0	1	0	1	?
<i>Discalis longistipa</i>	?	?	1	0	1	0	1	1	0	1	0	1	0	0	0	0	1	0	1	0	1	1	1	1
<i>Sawdonia deblondii</i>	?	0	1	1	1	0	1	0	1	0	?	?	?	?	1	0	0	0	1	0	1	1	1	1
<i>Euthursophyton hamperbachense</i>	0	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Gosslingia breconensis</i>	1	0	0	1	1	0	1	1	1	0	?	?	?	?	1	0	0	1	0	0	1	0	1	1
<i>Huia gracilis</i>	0	1	1	1	0	0	1	1	0	1	0	1	0	0	0	0	1	0	0	1	1	1	0	0
<i>Konioria andrychovien sis</i>	1	0	0	0	1	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1
<i>Margophyton goldschmidtii</i>	0	1	0	1	0	1	0	0	1	?	?	?	?	?	?	?	?	1	0	0	1	0	?	?
<i>Nothia aphylla</i>	0	0	0	0	0	0	1	1	0	1	0	1	0	0	?	?	?	0	0	1	1	1	1	0
<i>Sawdonia ornata</i>	?	1	1	0	1	0	1	1	0	1	1	0	0	1	0	1	0	0	0	1	1	0	1	0
<i>Serrulacaulis furcatus</i>	1	0	?	0	1	0	1	0	1	0	?	1	0	0	0	1	0	1	0	0	1	0	1	1

	2	2	2	3	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	5
Characters	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	
<i>Stolbergia</i>																									
<i>spiralis</i>	?	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Thrinckophyton</i>																									
<i>formosum</i>	0	0	0	1	1	0	1	1	0	0	?	0	0	0	0	1	0	0	1	0	1	0	1	1	
<i>Trichopherophyton</i>																									
<i>teuchansii</i>	?	?	?	0	1	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	0	?	1	1	
<i>Ventarura</i>																									
<i>lyonii</i>	0	?	?	0	0	0	1	?	?	1	1	?	?	?	?	?	?	1	0	0	0	?	1	1	
<i>Zosterophyllum</i>																									
<i>fertile</i>	0	0	0	0	1	0	1	1	0	1	1	1	0	0	0	1	1	0	1	0	1	1	0	1	
<i>Zosterophyllum</i>																									
<i>m</i>																									
<i>llanoveranum</i>	?	?	?	?	?	0	1	1	1	1	1	?	?	?	1	1	0	0	1	0	1	1	1	1	

Characters	51	52	53	54	55	56	57
<i>Renalia hueberi</i>	1	0	0	1	0	0	0
<i>Crenatacaulis verruculosus</i>	0	1	0	?	0	0	0
<i>Deheubarthia splendens</i>	1	0	0	0	0	0	0
<i>Discalis longistipa</i>	1	0	0	1	1	0	1
<i>Sawdonia deblondii</i>	0	1	0	0	1	0	1
<i>Euthursophyton hamperbachense</i>	?	?	?	?	?	?	?
<i>Gosslingia breconensis</i>	1	0	0	1	0	0	0
<i>Huia gracilis</i>	1	0	1	0	0	0	0
<i>Konioria andrychoviensis</i>	1	0	0	0	1	1	0
<i>Margophyton goldschmidtii</i>	1	0	?	?	0	0	0
<i>Nothia aphylla</i>	1	0	0	0	0	0	0
<i>Sawdonia ornata</i>	0	1	0	0	0	0	1
<i>Serrulacaulis furcatus</i>	1	0	0	1	0	0	0
<i>Stolbergia spiralis</i>	?	?	?	?	?	?	?
<i>Thrinckophyton formosum</i>	1	0	0	1	0	0	0
<i>Trichopherophyton teuchansii</i>	0	1	0	0	1	1	0
<i>Ventarura lyonii</i>	1	0	0	1	0	0	0
<i>Zosterophyllum fertile</i>	?	?	0	1	0	0	0
<i>Zosterophyllum llanoveranum</i>	1	0	0	1	0	0	0